Mesozooplankton community structure in the vicinity of the Prince Edward Islands (Southern Ocean) 37°50'E, 46°45'S

by

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Submitted in fulfillment of the requirements for the degree of Master of Science at Rhodes University

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February 2000

Dedicated to the memory of Keith Mann

Contents

List of Figures

Chapter 1 - Introduction

Chapter 2 – Material and Methods

Chapter 3 – MIOS 1 (1996)

Chapter 4 – MIOS 2 (1997)

Chapter 5 – MIOS 3 (1998)

List of Tables

Chapter 2 – Materials and Methods

Chapter 3 – MIOS 1 (1996)

Chapter 4 – MIOS 2 (1997)

Chapter 5 – MIOS 3 (1998)

Chapter 6 – MIOS 4 (1999)

Chapter 7 – Inter-annual comparison (1996-1999)

Appendix

List of figures

List of tables

Acknowledgements

First and foremost I would like to thank Evgeny Pakhomov. In this regard it is difficult to know where to begin. I began this project almost a sea-going novice and definitely a novice in the field of zooplankton ecology. Under Evgeny's guidance I have, I think gained my "sea legs" in both respects. Evgeny's role in the project began with ensuring that adequate data was collected on three of the four cruises to Marion, in 1996, 1997 and 1999. In the laboratory I will always be grateful for his patience and willingness to share his wealth of experience. Never was a request for help in identifying a new species turned down, a tribute to Evgeny's undying enthusiasm for the subject. Numerous discussions, and dissection of ideas, have hopefully made this a better thesis.

Two other people helped in the identification process. I am very grateful to Val Meaton for the identification of copepod species, and to Ofer Gon, for a day dedicated to teaching me the basics of larval fish identification.
I need to thank Christopher McQuaid for reading the final manuscript and providing a refreshingly new perspective at a very appropriate time.
And, as many students have done before, thanks to Martin Villett for sound advice in statistical procedure.

A number of different people were involved on each trip to the islands. Amongst these were William Froneman, the man responsible for my being lured into Southern Ocean biology, and chief scientist in 1998. Isabelle Ansorge, from the Department of Oceanography, UCT, who directed the collection of oceanographic data. Alistar Grinham, a good ship mate, and an enthusiastic bongo man. Marianne Balarin, honours students from both Rhodes and UCT, Sea Fisheries officers, and the crew of the "SA Aguhlas" all contributed to the data collection process and the smooth running of each trip.

Finally, Leigh Gurney, for help in data collection, listening to my ideas, reading a lengthy manuscript, and, last but not least, for being my companion and enduring a final few months of dedication to my thesis. Thank you very much.

Funding for this project was provided by the Department of Environmental Affairs and Tourism (DEAT) and the National Research Foundation (NRF).

Abstract

Mesozooplankton community structure in the vicinity of the Prince Edward Islands (PEIs) was investigated during six surveys conducted in late austral summer (April/May), 1996 to 1999. Each year zooplankton samples were collected with a bongo net (300 μm mesh) at stations upstream (west), between and downstream (east) of the islands. Chlorophyll *a* concentrations were determined fluorometrically, corresponding with each net tow. The positions of the Subantarctic Front (SAF) and the Antarctic Polar Front (APF), in relation to the islands in the upstream region, were determined by a line of CTD and/or XBT stations. Both the SAF and the APF were characterised by a high degree of meridional variation in position. Changes in position of the fronts were shown to occur very rapidly. In 1999 the APF moved southwards by ~40nm and the SAF northwards by ~60nm in a period of two weeks, while in 1996 the SAF appeared to move ~120nm northwards in a two week period. The positions of the SAF and APF appeared to have a significant impact on phytoplankton biomass in the vicinity of the PEIs, through the alteration of local flow dynamics. Water retention in 1996, associated with the location of the SAF and APF far to the north and south of the PEIs respectively, corresponded with high chlorophyll *a* concentrations in the inter-island region (reaching 1.54 $mg.m^{-3}$). When the fronts were close to the islands, in 1997 and 1999, and a flow through environment existed, chlorophyll *a* concentrations in the inter-island region were comparatively low. Although biomass enhancement was only observed at the SAF in 1996, phytoplankton size structure in 1999 indicated that, when close to the PEIs, frontal production may be transported to the island system. This is potentially an important source of allochthonous input into the island system.

Zooplankton assemblages were a mix of sub-Antarctic and Antarctic communities, with a weak presence of sub-tropical species. Cluster analysis showed that during each survey the region in the vicinity of the PEIs was divided into different, spatially separated zooplankton communities, associated with water masses of different origins. These communities were identified by variations in the abundance and biomass of species rather than variation in species composition and, in general, there was a relatively high degree of similarity both within and between surveys. Inter-annual community analysis revealed

that, in many cases, there was greater similarity between communities from different years than communities within years, indicating that short-term variability exceeded inter-annual variability. Multiple regression analysis showed that the major correlate with zooplankton community structure during all surveys was sea temperature, accounting for as much as 77% of the variation in community structure. Temperature was indicative of the relative contribution of sub-Antarctic and Antarctic communities, with low temperatures being characterised by an increased predominance of Antarctic communities and *vice versa*. The differentiation between sub-Antarctic and Antarctic waters, and their respective communities, was particularly pronounced when the SAF and APF were in close proximity to the islands. Surface salinity and sounding had limited effect on community structure. The affect of sounding was intrinsically related to zooplankton interaction with the island ecosystem. Predation by the islands' land based predators and benthic fish appears to decrease zooplankton biomass over the island shelf, particularly the macrozooplankton size fraction. However, this may only be an important factor under conditions of water retention when replenishment of zooplankton stocks is low. The low densities of many macrozooplankton species, and other deep migrators, on the island shelf may be due to their limited advection onto shallow topography. By contrast, there are indications that zooplankton species occurring at shallower depths may be concentrated in the inter-island region by mesoscale flow patterns.

Analysis of the population structure of the copepod *Calanus simillimus* showed that this species occurred at different stages in its life cycle during different years, even though sampling took place in the same calendar months, indicating that there was inter-annual variation in the timing of the biological season. Differences in the population structure of species, and consequently their contribution to abundance and biomass, may therefore have been an important contributor to inter-annual variation in community structure.

Evidence is provided for a long-term trend of southward movement of the SAF. This may have a significant affect on the PEI ecosystem, increasing the proportion of allochthonous input and altering the tropho-dynamics of the island ecosystem.

Chapter 1

Introduction

1.1. General background:

The Prince Edward Island (PEI) archipelago, comprising Marion Island and Prince Edward Island, is located in the Indian Ocean sector of the Southern Ocean at approximately 46°50'S and 37°50'E (Figure 1.1.) The islands lie directly in the path of the easterly flowing Antarctic Circumpolar Current (ACC) (Lutjeharms and Vallentine, 1984; Lutjeharms, 1985). More specifically they are located within the Polar Frontal Zone (PFZ), the region of transition between Antarctic and sub-Antarctic waters (Deacon, 1983; Lutjeharms, 1985). The PFZ is bounded by the Antarctic Polar Front (APF) in the south and the Sub-Antarctic Front (SAF) in the north (Lutjeharms and Vallentine, 1984). These two fronts are regions of steep meridional gradients of temperature, salinity and nutrients (Emery, 1977; Deacon, 1982; Lutjeharms, 1985; Nowlin and Klinck, 1986) and consequently represent important biogeographic boundaries separating distinct zooplankton communities (Backus, 1985; Boden *et al*., 1988; Pakhomov *et al*., 1994; Froneman *et al*., 1995; Tarling *et al*., 1995). However, steep physical gradients do not necessarily beget sharp changes in zooplankton community structure with, for example, fronts separating regions of different species composition (Fasham and Angel, 1975; Backus, 1985; Gibbons, 1997). On the contrary, the PFZ is characterised by numerous widespread eurytypic species that can be used to characterise biogeographic zones through varying levels of abundance and biomass (Vervoort, 1951; Foxton, 1966; Kane, 1966; Park, 1980; Deacon, 1982; Kirkwood, 1984).

A number of zooplankton surveys have been carried out in the vicinity of the PEIs. In 1976 a joint South African and French team studied the region, undertaking both

biological and oceanographic surveys (Frost *et al*., 1976; Grindley, 1978). Between 1980 and 1985 six exploratory surveys were conducted (Miller, 1982; Miller *et al*., 1984; Allanson *et al*., 1985; Boden and Parker, 1986; Perissinotto and Boden, 1989). These surveys showed, amongst other things, that the offshore and terrestrial environments are intrinsically linked. In order to address this more thoroughly the Marion Offshore Ecological Study (MOES) was designed to: (a) determine the existence, dynamics and factors responsible for an island mass effect; (b) study factors responsible for the enhanced primary production observed in the inter-island region; (c) examine the relationship between these trophic subsystems and the land-based predators (Perissinotto *et al*., 1990 b).

The above mentioned surveys showed that the zooplankton community in the vicinity of the PEIs is highly variable, containing a mix of Antarctic and sub-Antarctic species as well as a weak presence of subtropical species (Frost *et al*., 1976; Grindley, 1978; Grindley and Lane, 1979; El-Sayed *et al*., 1979; Lutjeharms and Vallentine, 1984; Allanson *et al.*, 1985; Miller, 1985; Boden and Parker 1986; Boden, 1988; Duncombe Rae, 1989 a,b; Pakhomov and Froneman, in press). Initial conclusions were that the strong Antarctic community was the result of upwelling of Antarctic deep water in the lee of the islands (Grindley, 1978; Grindley and Lane, 1979). However, this was contradicted by the low silica concentrations recorded in the same region, as Antarctic deep water is typically silica enriched (El-Sayed *et al*., 1979). Subsequently it was suggested that the mixed communities observed were the result of eddies, produced far afield, transporting plankton communities across the frontal boundaries into the PFZ (Miller *et al*., 1984; Allanson *et al*., 1985; Boden and Parker 1986; Froneman *et al.*, 1995; Pakhomov and McQuaid, 1996). Deacon (1983) described the PFZ in the vicinity of the PEIs as a region characterised by “more interchange and less clear gradation between Antarctic and sub-Antarctic waters”. Sections through the PFZ show it to be highly complex due to the meandering of its boundaries (the SAF and APF) and a high incidence of eddies of both Antarctic and sub-Antarctic characteristics (Emery, 1977; Sievers and Emery, 1978; Peterson and Whitworth, 1989). The physical environment within the PFZ therefore

appears conducive to cross-frontal mixing of Antarctic and sub-Antarctic communities and the communities recorded in the vicinity of the PEIs are a reflection of this.

Due to their geographic position within the ACC the PEIs surroundings can be divided into upstream, inter-island and downstream regions (Pakhomov and Froneman, 1999 b). High zooplankton biomass levels recorded in the inter-island region (Frost *et al*., 1976; Boden, 1988) indicate that certain flow conditions may effectively concentrate zooplankton in this region. Concentration of zooplankton in the shelf region has also been observed at South Georgia (Atkinson and Peck, 1990). However, elevated zooplankton biomass levels are not always observed in the inter-island region of the PEIs (Perissinotto and McQuaid, 1992). Levels are on occasion lower than those in the offshore regions (Pakhomov and Froneman, 1999 b). Highest zooplankton biomass has also been recorded in the downstream region (Grindley and David, 1985; Perissinotto, *et al*., in press). The factors responsible for these distribution patterns remain poorly understood. Of particular interest is the role of the prevailing oceanographic and corresponding current regimes.

Most past analyses of zooplankton community structure at the PEIs have been qualitative (Frost *et al*., 1976; Grindley, 1978; El-Sayed *et al*., 1979; Grindley and Lane, 1979; Miller, 1982; Lutjeharms and Vallentine, 1984; Allanson *et al.*, 1985; Boden and Parker 1986). Furthermore, they have focussed on higher taxonomic groups (Order to Class) (Allanson *et al*., 1985; Boden and Parker, 1986), considered only select taxa (Grindley and Lane, 1979; Miller, 1982) or focussed on specific size fractions of the community (Perissinotto, 1989). Only recently have detailed, species level, multivariate numerical analyses been undertaken using data from this region (Froneman and Pakhomov, 1998; Ansorge *et al*., 1999; Froneman *et al*., 1999). Multivariate analyses have been widely used in recent times and are extremely useful in defining zooplankton community structure, interpreting variability in community patterns, and identifying species associations (Dodge and Priddle, 1987; Boysen-Ennen and Piatkowski, 1988; Siegel and Piatkowski, 1990; Clarke, 1993; Hopkins *et al*., 1993; Hosie, 1994; Hosie and Cochran, 1994; Pakhomov *et al*., 1994; Pinca and Dallot, 1995; Tarling *et al*., 1995; Dower and Mackas, 1996; Gibbons, 1997; Barange *et al*., 1998; Umani *et al*., 1998; Brodeur *et al*.,

1999; Duro *et al*., 1999; Pakhomov *et al*., 1999 b). Coupled with environmental data they can give valuable insight into factors governing zooplankton distribution patterns (Hosie, 1994; Duro *et al*., 1999). However, these analyses have typically focussed on abundance data. Biomass analyses in the vicinity of the PEIs have been confined to the contribution of zooplankton size fractions, specific taxonomic groups and key species (Pakhomov *et al*., 1994; Froneman and Pakhomov, 1998). One of the primary objectives of this study was therefore to make detailed, species level, investigations of zooplankton community structure in terms of both abundance and biomass data.

The frequent occurrence of phytoplankton blooms over the PEI shelf has led to the suggestion that the islands generate an 'island mass effect' (El-Sayed, 1979; Miller, 1982; Parker, 1984; Allanson *et al*., 1985; Boden, 1988; Duncombe Rae, 1989 b). The PEIs support vast seasonal populations of mammals and seabirds, amounting to an estimated 4 to 6 million individuals (Williams *et al*., 1979; Condy, 1981). Burger *et al*. (1978) estimated guano production on the islands to be approximately 33 000 tons per annum. Furthermore, it has been estimated that approximately 428 694 kg dry weight of feathers is shed per annum on Marion Island alone (Williams and Berruti, 1978). An annual rainfall of ~2000 mm per annum (Smith, 1991) results in high nutrient run-off and elevated reduced nitrogen (e.g. ammonia and urea) and phosphate levels have been observed in the near shore waters on numerous occasions (Miller, 1982; Boden, 1988; Duncombe Rae, 1989 b; Ismail, 1990; Perissinotto *et al*., 1990 a,b; Pakhomov and Froneman, 1999 b). Perissinotto *et al.* (in press) observed a concentration gradient of ammonia and urea spreading outwards from the islands and extending ~80 km off-shore.

These high nutrient concentrations are believed to be partly responsible for the elevated phytoplankton biomass observed over the island shelf. However, using non-linear regression analysis, Perissinotto *et al*. (1990 c) showed that most of the variance in phytoplankton production is accounted for by water column stability and mixed layer depth. During May 1987 stability explained over 80% of the total variance in phytoplankton photosynthetic capacity. Duncombe Rae (1989 b) showed that if retained over the island shelf fresh water run-off could significantly decrease the density of the

mixed layer, consequently increasing water column stability. Perissinotto and Duncombe Rae's (1990) calculation that the development of a phytoplankton bloom requires a minimum of ~15 days further illustrates the necessity for water retention if the enhanced primary production potential over the island shelf is to be expressed. Analysis of data from six cruises in the 1980's showed that an anticyclonic eddy occurred over the island shelf on at least four occasions, the effect of which was demonstrated by the associated high chlorophyll *a* concentrations (Perissinotto and Duncombe Rae, 1990).

The occurrence of water retention appears to be determined by the interaction between the eastward flowing ACC and the PEIs shelf, and particularly the velocity of the current as it approaches the upstream region (Ansorge and Lutjeharms, submitted). It is predicted that during periods of low current velocity frictional forces prevail over advective forces resulting in water retention over the island shelf (Ansorge and Lutjeharms, submitted; Perissinotto *et al*., in press), as well as the shedding of cyclonic eddies in the downstream region (Duncombe Rae, 1989 b; Perissinotto and Duncombe Rae, 1990). Conversely, during periods of high current velocity advective forces prevail, resulting in a von Karman Street vortex wake in the downstream region, becoming a meandering Rosby Wave (Allanson *et al*., 1985; Ansorge and Lutjeharms, submitted; Perissinotto *et al*., in press). Recent oceanographic surveys at Cato Island in the Western Coral Sea lend support to this prediction (Coutis and Middleton, 1999). A wake zone was observed in the downstream region of Cato Island during periods of high current velocity. Conversely, when current velocities were low, flow disturbance in the downstream region was less pronounced and recirculation of water was observed in the lee of the island, accompanied by increased chlorophyll *a* concentrations.

Analysis of the drift trajectories of FGGE satellite tracked buoys clearly illustrated that the SAF and APF are regions of enhanced current flow (Hofmann, 1985). Approximately 75% of the ACC's baroclinic transport is associated with these two fronts, while the PFZ itself is characterised by comparatively reduced flow (Nowlin and Klinck, 1986). The proximity of the SAF and the APF to the islands may therefore significantly influence the prevailing oceanographic conditions (Perissinotto *et al*., in press). Both the SAF and the

APF show a high degree of positional variability in the vicinity of the PEIs (Lutjeharms and Vallentine, 1984; Lutjeharms and Foldvik, 1986; Nagata *et al.* 1988; Duncombe Rae, 1989 a,b; Lutjeharms, 1990). When the fronts are in close proximity to the islands advective forces may prevail and when far from the islands frictional forces may prevail, promoting water retention.

Alternation between these two modes has important implications for the PEI ecosystem. Bloom conditions, associated with water retention may be an important energy source for the island system. Sedimentation of bloom material may transport this autochthonous production to benthic suspensoid feeders (Perissinotto *et al*., 1990 a). Benthic suspensoid feeders form an important component of the diet of the caridean shrimp *Nauticaris marionis* (Kuun, 1998). In turn, *N. marionis* is a dominant component of the diet of inshore feeding land based predators, including the imperial cormorant and gentoo, rock-hopper and macaroni penguins (Brown and Klages, 1987; Perissinotto *et al*., 1990 a). The autochthonous production associated with phytoplankton blooms is therefore indirectly transferred to the terrestrial ecosystem. Conversely when a flow-through mode exists allochthonous input may be the principal energy source. In this scenario phytoplankton may be transported directly to the benthos due to the strong mixing of water over the island shelf (Perissinotto *et al*., 1990 a), or retained in the island system through grazing by *N. marionis* megalope larvae (Perissinotto and McQuaid, 1992). Of primary interest when a flow-through environment exists is whether the enhanced production often associated with the SAF and APF (Lutjeharms *et al*., 1985; Laubscher *et al*., 1993; Froneman *et al*., 1995; Froneman and Ansorge, 1998; Froneman *et al*., 1998) is channelled into the island system. The effect of alternation between these two modes on zooplankton community structure in the vicinity of the islands has yet to be investigated.

Meridional shifts in the position of the SAF and APF may have significant short-term influences on zooplankton communities in the vicinity of the PEIs, particularly through promoting interchange of Antarctic and sub-Antarctic waters via eddy generation and cross-frontal advection. Positional shifts may also create a dynamic environment over the PEI shelf, alternating between retentive and flow-through modes. The recent observation

that the average position of the SAF has moved southwards since the late 1950's (Pakhomov *et al*., unpublished), and a corresponding increase in sea surface temperature at the PEIs (Smith and Steenkamp, 1990), indicates that these short term changes may in fact be oscillations within a long term trend of ecological change.

1.2. Aims:

- To give a detailed, species level, numerical analysis of mesozooplankton community structure in the vicinity of the Prince Edward Islands from four consecutive years, using both abundance and biomass data.

- To identify the physical and biological parameters responsible for zooplankton distribution patterns and community structure, with particular emphasis on the effect of the oceanographic environment and meridional shifts in the position of the SAF and the APF.

- To use a four year data set to investigate inter-annual variation in the oceanographic environment and mesozooplankton community structure, and possibly gain insight into long term trends.

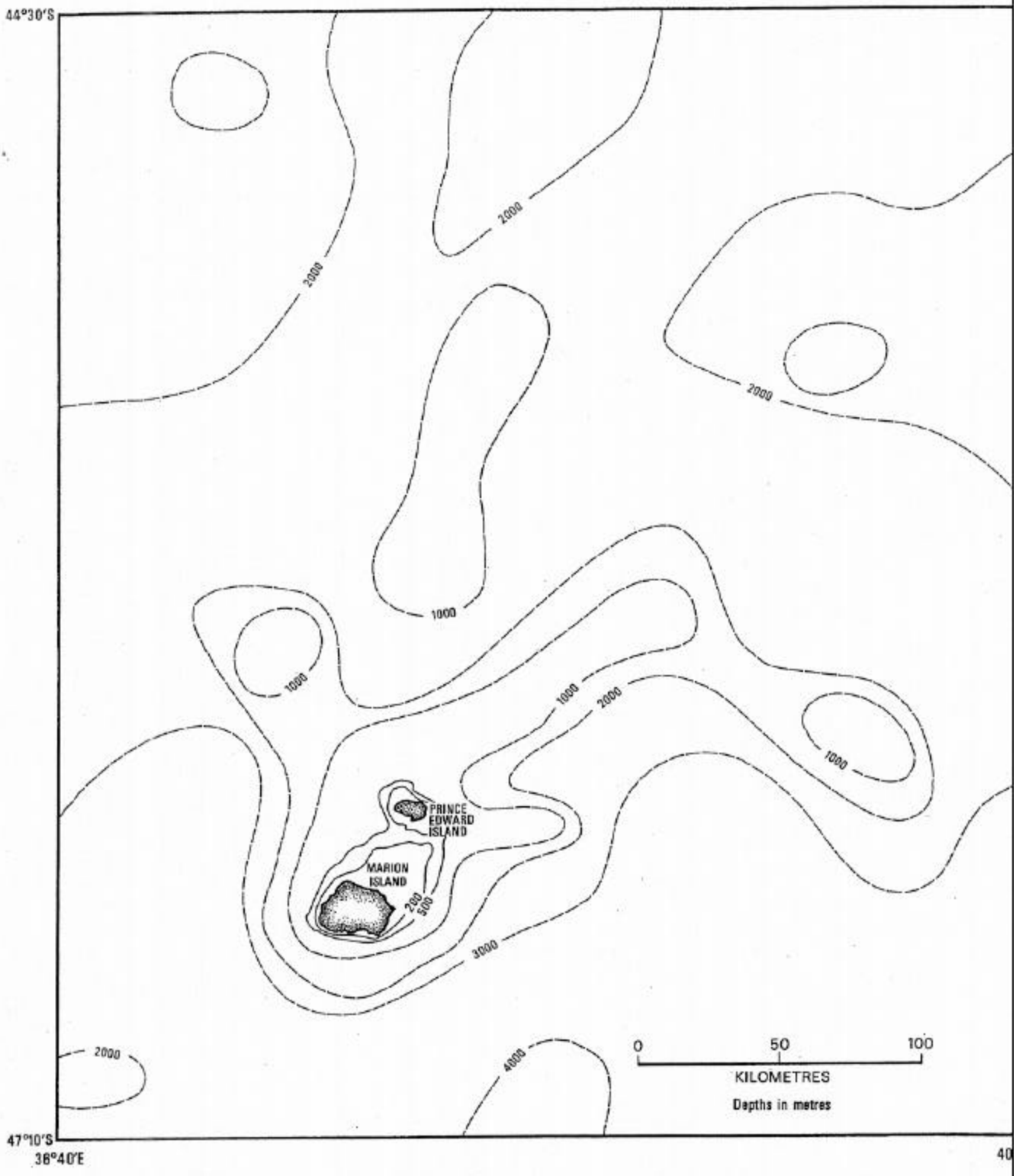


Figure 1.1. Map of the Prince Edward Island (PEI) archipelago. Isobars show depth in meters.

Chapter 2

Materials and Methods

2.1. Survey details:

The data used in this study were collected during four separate cruises to the PEIs, conducted annually between 1996 and 1999 in late austral summer (April/May). All data were collected as part of the Marion Island Oceanographic Survey (MIOS) program aboard the research and supply vessel MV "SA Aghulhas". The successive cruises conducted between 1996 and 1999 were named MIOS 1 to MIOS 4.

Four zooplankton surveys, one during each year of study (1996 to 1999), were repeats of the same survey grid. This included a line of stations in the region upstream of the islands, as well as two transects over the island shelf (Figure 2.1.). In addition to this repeated survey, supplementary second surveys were carried out in 1997, 1998 and 1999. The second survey in 1997 included eight north-south transects between 46^{o}S and 48^{o}S, and from 36^{o}10'E to 42^{o}E. Two transects were conducted upstream of the islands, one along the same longitude as the islands and five downstream of the islands. In 1998 the second survey comprised a set of ten inter-island stations (<300m). The second survey in 1999 included two transect lines, one north and one south of the islands, between 45^{o}S and 48^{o}S, and a large number of inter-island stations.
The detailed structure of all surveys conducted between 1996 and 1999 is presented in Appendix 1.

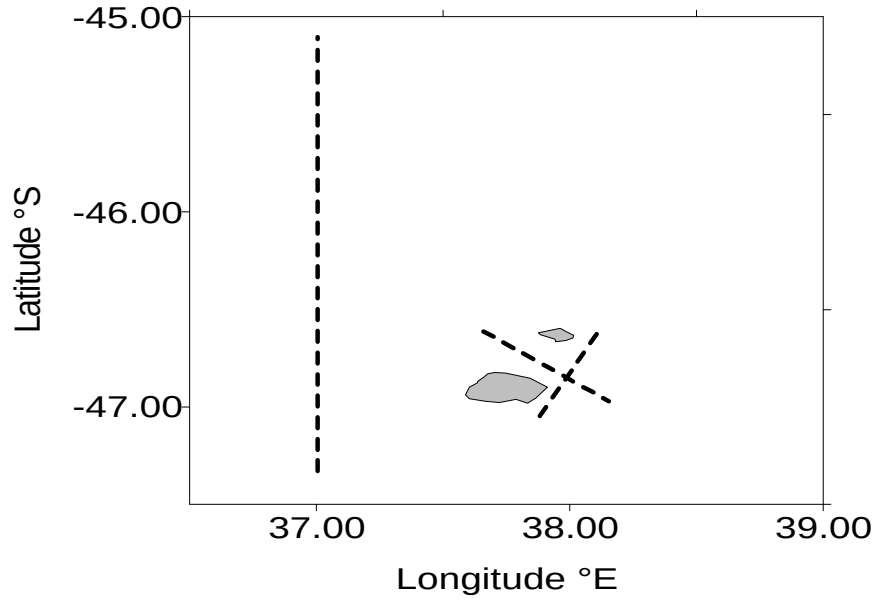


Figure 2.1. Structure of the survey repeated during each year of study (1996 to 1999). This included an upstream transect along 37°E and two inter-island transects sampling the island shelf and the downstream region.

2.2. Oceanography:

The thermal structure of the water column was investigated using a CTD (Conductivity-Temperature-Depth) probe fitted with a Neil Brown Instrument system Mark 3B underwater unit, or Sippican T7 XBT (Expendable Bathythermograph) probes, with a maximum depth range of 760m. Prior to deployment the XBT probes were calibrated against sea surface temperature.

The principal aim of the oceanographic surveys was to locate the position of the SAF and the APF, as well as to identify the position of anomalous water masses. For the purpose of this study the APF was defined by the position of the 2°C isotherm at 200m (Lutjeharms and Emery, 1984), and the SAF by the position of the 7°C isotherm at 100m (Nagata *et al.*, 1988).

Each zooplankton survey had a corresponding oceanographic survey, with CTD and/or XBT deployment generally corresponding with net tows (details presented in Appendix 1). In 1998 and 1999 additional transects were conducted to the north of the islands,

reaching 41°S in 1998 and 31°S in 1999. Details of these transects are presented in Froneman and Ansorge (1998) and Pakhomov *et al*., (1999 a).
During all transects between Cape Town and the PEIs XBT's were deployed at regular intervals (approximately every fifteen minutes latitude).

2.3. Phytoplankton:

Surface chlorophyll *a* concentrations were determined in conjunction with each net tow. For all surveys during MIOS 1, MIOS 2 and MIOS 3, water samples for pigment analysis were collected using a shipboard pump (Iwaki Magnet Pump), made from polyvinyllidene fluoride and ceramic materials, and operated at a flow rate of ~ 4 l/min (Allanson *et al.*, 1981). The pump inlet was 5 m below the sea surface and seawater was supplied to the laboratory through PVC piping. Previous studies have shown that using the shipboard pump does not significantly alter phytoplankton community structure (Allanson *et al.*, 1981). During MIOS 4, surface water was collected with either Niskin bottles or a bucket. A 250 ml water sample was filtered at ~500 mm Hg through a serial filtration unit and fractionated into the pico (<2.0 μm), nano (2.0 - 20.0 μm) and microphytoplankton (>20 μm) size fractions. Chlorophyll *a* concentrations were determined fluorometrically with a Turner Design fluorometer after extraction in 90 % acetone for 24 h (Holm-Hansen and Riemann, 1978), and subsequently expressed as $mg.m^{-3}$.
A Kruskal-Wallace test was used to investigate differences in chlorophyll *a* concentrations between the upstream, downstream and inter-island regions and a Mann-Whitney U test was used to define these differences. For the purpose of this study the inter-island region was determined by the 300 m isobath.

2.4. Zooplankton:

2.4.1. Sampling:

Mesozooplankton samples were collected using a bongo net with a mesh size of 300 μm. The net was fitted with a Universal Underwater Unit (U^3) which continuously monitored

temperature and depth during each tow. Towing speed varied between 1.5 - 2.5 knots and the net was towed obliquely between 300 m and the surface, or between the bottom and the surface. During MIOS 3, all night tows were made to a maximum depth of 200m, while day tows were made to a maximum depth of 300m. The volume of water filtered during each tow was calculated from data collected by an electronic flow meter. The flow metre did occasionally fail. In these instances the volume of water filtered was determined by multiplying mouth area by distance travelled (calculated from ship speed and duration of trawl). The effect of towing speed was also taken into account (Pakhomov and Froneman, 1999 a). A t-test comparing volume filtered determined using both techniques showed that there was no significant difference between them ($p>0.05$). Surface temperature and surface salinity were measured in conjunction with each net tow and the continuous temperature measurements recorded by the U^3 were integrated to obtain an average water temperature for the duration of each tow.

Samples were fixed in 4-6% buffered formalin. Zooplankton species were identified using the keys of Boltovskoy (1981), Vinogradov *et al*. (1982), Efremenko (1983), Kellermann and North (1989), Gon and Heemstra (1990), and Razouls (1994). The abundance of all mesozooplankton species was determined from sub-samples, obtained using a Folsom plankton splitter, ranging between 1/2 and 1/32 aliquots of the total, depending on sample size. All sub-samples contained 200 to 500 animals. Whole samples were analysed for large and rare species. Abundance was expressed as individuals.m^{-3} (Froneman and Pakhomov, 1998). All species from the sub-samples for abundance analysis were oven dried at 60^{o}C for 36h and weighed to the nearest 0.001 mg using a Sartorius Micro MC1 electronic microbalance. Large individuals from the whole sample were wet weighed and subsequently converted to dry weights using regressions derived from Mizdalski (1988). Biomass data were expressed as mg dry weight m^{-3}.

In the case of the copepod species *Calanus simillimus* individuals were identified down to copepodite stage 2. For the purpose of the community structure analysis copepodite stages were combined.

2.4.2. Numerical analysis:

A total of six surveys were used in the intra-annual analysis of community structure. This included the repeat survey grid conducted in each year of study as well as the second surveys conducted in 1997 and 1999 (Table 2.1.). For the purpose of the intra-annual analysis the two surveys conducted in 1997 and 1999 were combined. All of the net tows used in the numerical analysis of community structure were conducted at night (7pm to 7am), with the exception of stations MS1-2,3,7,8,11,13,14 and 33 of MIOS 1 which were conducted during the day.

Table 2.1. Dates of the six surveys conducted between 1996 and 1999 that were used in the numerical analysis (s1 = survey 1; s2 = survey 2).

	1996	**1997 s1**	**1997 s2**	**1998**	**1999 s1**	**1999 s2**
Survey date	1 May – 11 May	30 April – 4 May	8 May – 17 May	17-25 April	5-13 April	24-28 April
Survey	MIOS 1	MIOS 2	MIOS 2	MIOS 3	MIOS 4	MIOS 4

Station by species matrices were produced for each cruise using the zooplankton abundance data. The analysis of community structure was carried out on each of the four data sets using Plymouth Routines in Multivariate Ecological Research (Primer) (Clarke and Warwick, 1994). Prior to analysis all data were transformed using the function $\log_{10}(x+1)$ (Legendre and Legendre, 1983) to reduce the weighting of high abundance species and to increase the weighting of low abundance species. After transformation, cluster analysis (q-type) was used to group stations based on the Bray-Curtis similarity measure and complete linkage classification (Field *et al*., 1982). The choice of station clusters used for the community analysis was a compromise between the degree of similarity within clusters, the number of stations within a cluster, and the total number of clusters (Tarling *et al*., 1995). Similarity levels were adjusted to obviously meaningful groupings rather than forcing clusters to a fixed level (Siegel and Piatkowski, 1990). The level of similarity used as a cut off point for station cluster determination thus varied

between years. Significance levels between groupings were tested using ANOSIM, a multivariate analogue of a one-way ANOVA (Clarke and Warwick, 1994).

A number of descriptive community and environmental parameters were calculated for each station cluster. The community parameters included species number, species richness (Margalef), species diversity (Shannon-Wiener), and total zooplankton abundance. The environmental parameters included integrated temperature, surface temperature, surface salinity, sounding, and total surface chlorophyll *a*. A Kruskal-Wallace test was used to investigate differences between clusters and a Mann-Whitney U test was used to identify sources of difference between clusters.

Following the cluster analysis, the similarity matrix was ordinated using non-metric multidimensional scaling (NMDS). The goodness of fit between the original data and the ordination map is indicated by a stress value, ranging between 0 and 1, which is a measure of the distortion involved in compressing the community data into a small number of dimensions (Field *et al*., 1982). A low stress value (< 0.2) indicates that the community data are well represented by the ordination map (Clarke and Warwick, 1994). A 2-axis ordination was used for all years. The ordination scores, which summarised the zooplankton community in terms of the abundance data, were regressed against the measured environmental variables to determine sources of variation in the observed zooplankton community structure (Hosie, 1994). The environmental variables used were: integrated temperature for the duration of the tow; surface temperature; surface salinity; surface chlorophyll *a* concentration; sounding. For the regression analysis, environmental parameters were treated as the dependent variables and the ordination scores for each axis as the independent variables (Hosie, 1994). The output was a table of beta regression coefficients for the x and y axis of the 2-D ordination, R^2 and Adjusted R^2 values indicating the amount of variation in community structure accounted for by any particular variable, and significance levels (F and p values).

Cluster analysis provided a data summary, revealing large-scale community structure patterns, but masking the species differences responsible for these patterns. The

percentage contribution of species to within-group similarity and between-group dissimilarity, based on station abundance levels, was determined using the similarity program SIMPER (Clarke and Warwick, 1994). For the purpose of this study species responsible for eighty percent of the similarity and dissimilarity measured were used in the analysis as this was found to highlight the species making the greatest contribution to each measure. SIMPER analysis is well suited to mesoscale surveys, such as this, where differences in zooplankton abundance and biomass account for a greater percentage of variation in community structure than differences in species composition (Mackas, 1984).

Inverse analysis (r-type) was used to identify species associations. This involved grouping species according to their station abundance levels by means of cluster analysis. The cluster analysis grouped species based on the Bray-Curtis similarity measure and complete linkage classification, after standardisation of the species data as percentage of total abundance in all hauls (Field *et al*., 1982). Prior to analysis the data set was reduced to a subset of species to avoid the random association of rare, low abundance species (Field *et al*., 1982). For the purpose of this study the subset was defined as those species responsible for 80% of the similarity **within** groups and 80% of the dissimilarity **between** groups. This placed most species within the selection criteria set by Field *et al*. (1982) (species occurring at greater than 4 % abundance in any one net tow), and all species within the selection criteria used by Tarling *et al.* (1995) (species occurring in more than three net tows). Differences in the abundance of species between station groups, defined by q-type analysis, were investigated using a Kruskal-Wallace test. A Mann-Whitney U test was used to determine the station group to which each species showed the strongest association. In this way species assemblages specific to station groups were identified.

SIMPER analysis and inverse analysis identify species that are indicators by virtue of varying levels of abundance. An alternative type of indicator is one that defines a group by its presence or absence and frequency of occurrence in stations within a group. Frequency indicators were identified using Field's information statistic ($2\Delta I_I$) (Field *et al*., 1982) which assesses species differences between station clusters using the following formula:

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

where I_{ti} = total information content of both station clusters. $I_{ti} = N_t\log N_t - A_{ti}\log A_{ti} - (N_t\text{-}A_{ti})\log(N_t\text{-}A_{ti})$: N_t = combined sample number of both station clusters; A_{ti} = number of samples in which species i is present; $(N_t\text{-}A_{ti})$ = number of samples from which species i is absent. Similarly the information content I_{1i} and I_{2i} was obtained for clusters 1 and 2 respectively. The resulting $2\Delta I_I$ values were compared with $\chi 2$ values at 5% and 1% probability levels for 1 degree of freedom, based on the premise that $2\Delta I_I$ approximates a $\chi 2$ distribution (Field *et al*., 1982).

The relationships between abundance levels of zooplankton species and environmental variables were investigated using regression analysis. Only common species, defined as those responsible for 80% of the similarity within groups and 80% of the dissimilarity between groups, were used in the analysis, and only significant relationships are presented in the results.

Data in the literature indicate that small zooplankton species are most highly abundant, while species contributing most to total biomass show a large variation in size (Hopkins, 1985; Rodhouse *et al*., 1994). The biomass and abundance data sets from 1999 were used to plot average individual size of species (mg dry weight.m^{-3}) against total abundance (individuals.m^{-3}) and total biomass (mg dry weight.m^{-3}). All data were $\log_{10}$ (x+1) transformed prior to analysis (Rodhouse *et al*. 1994).

Using abundance data focuses the analysis on small (low biomass), high abundance, mesozooplankton species (Figure 2.2.a). Conversely large, low abundance, mesozooplankton species may make a large contribution to total biomass (Figure 2.2.b). Using biomass data consequently focuses the community structure analysis on a different species set to that highlighted by analysis of abundance. The methodology described above for the analysis of community structure based on abundance data was therefore repeated for each survey using species biomass data.

The data from the second survey, conducted over the shelf, in 1998 were added to the data from the repeat survey for the same year for an analysis of regional differences in the abundance and biomass of zooplankton groups. The day samples collected in 1998 were used in an analysis of the vertical migration patterns of dominant zooplankton species (see Chapter 5).

Finally, all six surveys in Table 2.1. were combined for an inter-annual analysis. For the purpose of this analysis only net tows conducted at night were used. Consequently the day net tows used in the analysis of the 1996, MIOS 1, survey were omitted. The stations in all other surveys remained the same as those used in the intra-annual analysis.

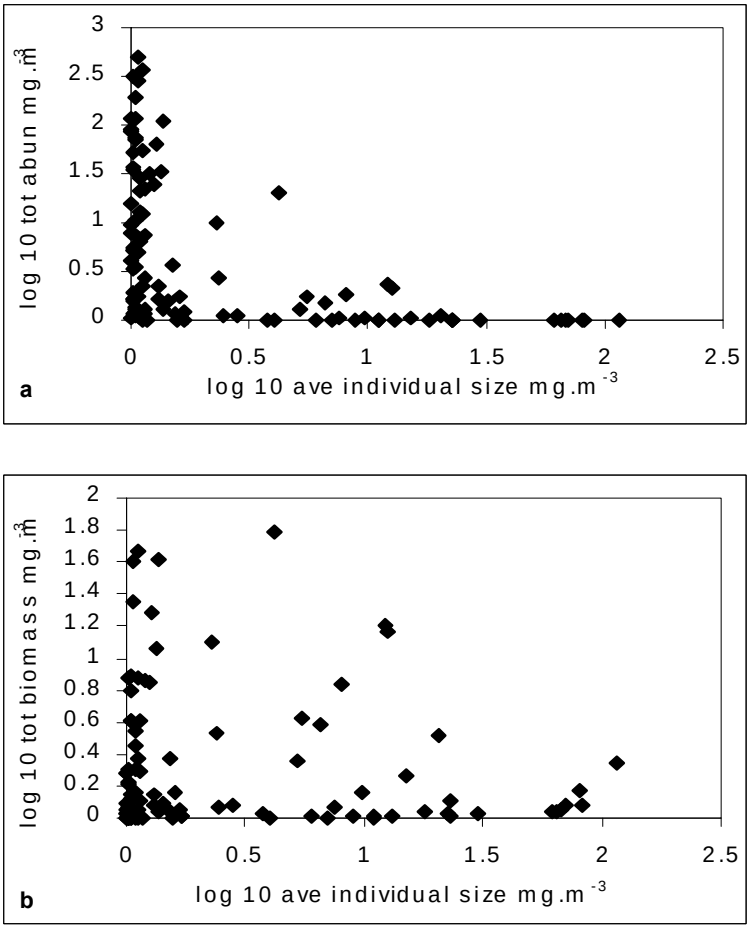


Figure 2.2. The relationship between average individual size and total abundance (a) and total biomass (b) for all species collected in 1999. All data were $\log_{10}(x+1)$ transformed prior to analysis.

Chapter 3

RESULTS: MIOS 1 (1996)

3.1. Oceanography:

Based on the position of the 7^{o}C isotherm at 100m (Nagata *et al*., 1988) the SAF was located between 46^{o}S and 45^{o}S in the region upstream of the islands during the MIOS 1 zooplankton survey (Figure 3.1.). The most vertically orientated isotherms between 3^{o}C and 5^{o}C have also been used to define the position of the SAF (Sievers and Emery, 1978). Based on this criterion, and considering the southern most position of the 7^{o}C isotherm at 100m, the position of the SAF was more accurately determined as being approximately 46^{o}S. Two weeks later, on the return voyage to Cape Town, the SAF was located further north at approximately 44^{o}S (Froneman *et al*., 1998). The front had therefore moved ~120 nautical miles northwards in a two week period.

3.2. Chlorophyll *a*:

A Kruskal-Wallace test showed that total chlorophyll *a* concentrations varied significantly ($p<0.05$) between the upstream, inter-island and downstream regions (Figure 3.2.). A Mann-Whitney U test showed that average chlorophyll *a* concentrations at the SAF (1.61 mg.m^{-3}) were significantly ($p<0.05$) higher than chlorophyll *a* levels recorded in the upstream and downstrean regions but not the inter-island region. High chlorophyll *a* concentrations were recorded at MS1-27 and MS1-30 in the inter-island region, and at MS1-29 and MS1-32 situated off the shelf in the downstream region. The average chlorophyll *a* concentration at these four stations was 1.36 mg.m^{-3}. Differences in chlorophyll *a* concentration were largely attributed to differences in micro and nanophytoplankton. High concentrations of these size classes were recorded at the SAF and at stations MS1-27, MS1-30, MS1-29 and MS1-32. A Mann-Whitney U test showed

that picophytoplankton occurred at significantly ($p<0.05$) higher concentrations at the SAF, but showed little variation between all other stations.

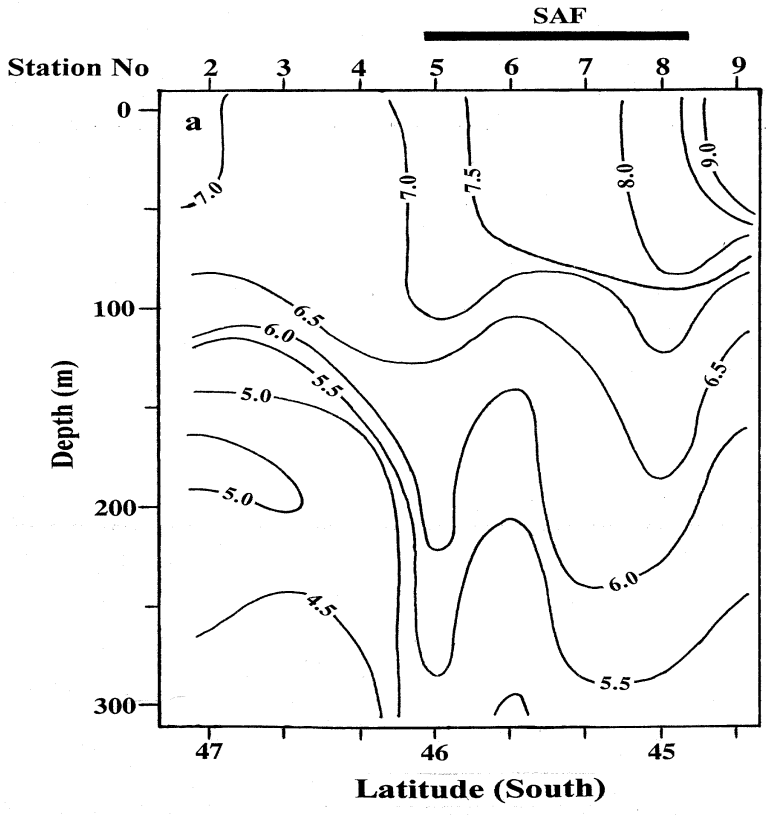


Figure 3.1. Temperature profile of the water column along 37°E at the time of the MIOS 1 zooplankton survey. Figure taken from Pakhomov and Froneman (1999 a).

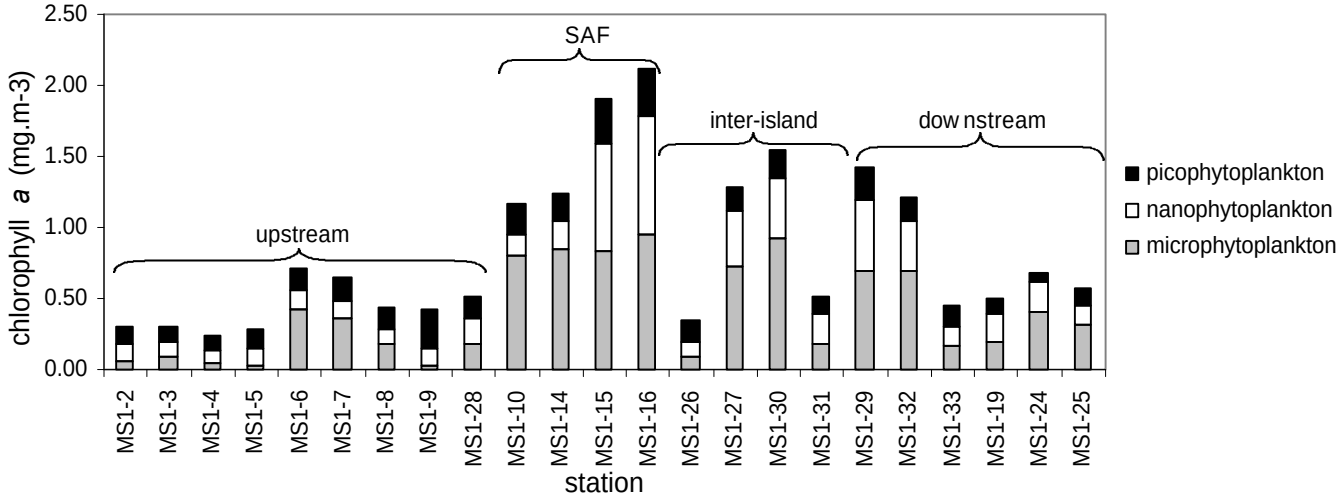


Figure 3.2. Size fractionated chlorophyll *a* concentrations corresponding with net tows during MIOS 1. Regions discussed in the analysis are bracketed.

3.3. Zooplankton:

3.3.1. Abundance:

The cluster analysis identified four zooplankton groupings at approximately the 52% level of similarity (Figure 3.3.). Group 1 contained one inter-island station and three stations on the downstream side of the island shelf. Group 2 contained one station upstream of the island shelf, one inter-island station and two downstream stations. Group 3 comprised eleven upstream stations, including three stations at the SAF, and two inter-island stations. Group 4 contained two upstream stations situated at the SAF, one inter-island station and one downstream station. ANOSIM showed that all station groups differed significantly from each other ($p<0.05$), with the exception of Group 3 and Group 4 ($p=0.08$). Due to the differences observed in community structure between groups 3 and 4 (Table 3.2.) they were kept separate for the purpose of the analysis.

Species richness and diversity differed significantly between station groups (Figure 3.4.b,c), the highest values being recorded within Group 3 and the lowest within Group 2. Significantly higher total zooplankton abundance was recorded within groups 2 and 4 than groups 1 and 3 (Figure 3.4.d). Surface salinity was significantly higher within Group 1 than any other group (Figure 3.4.e). There was no significant difference in species number, surface temperature, integrated temperature, sounding and total surface chlorophyll *a* between groups (Figures 3.4.a,f,g,h,i).

Surface temperature accounted for 42% of the variation in zooplankton community abundance data (Table 3.1.). Surface salinity accounted for 20% of the variation in abundance data but this was not a significant amount. Sounding accounted for a significant amount ($p<0.05$) of variation in the Y-axis of the ordination map, but not the abundance data as a whole. None of the other variables accounted for a significant amount of variation in the abundance data.

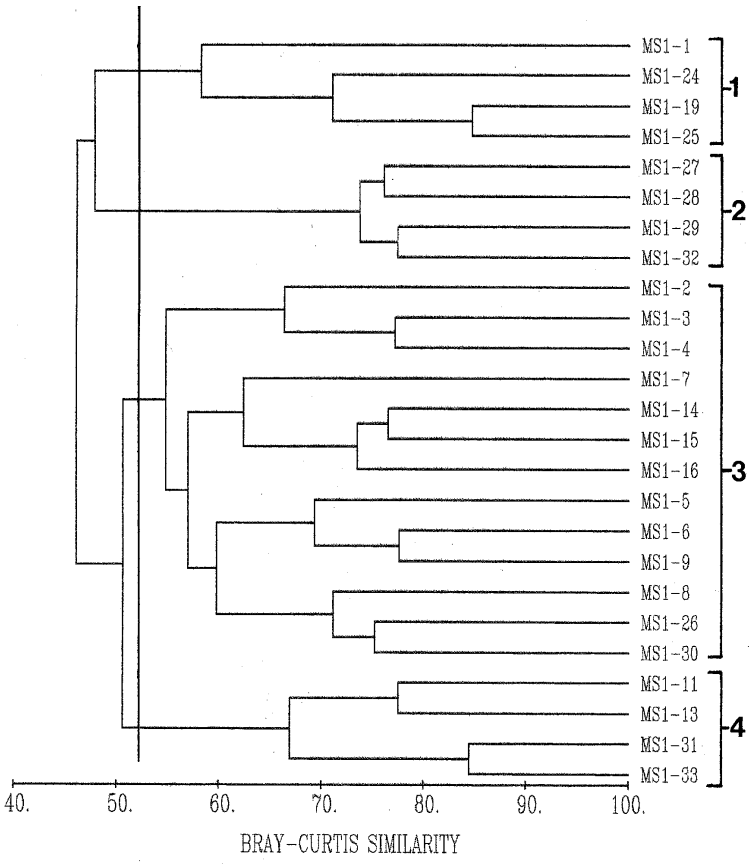
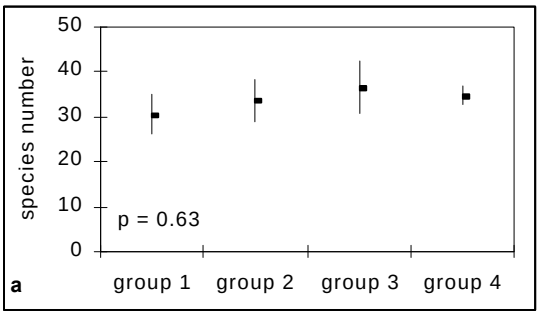
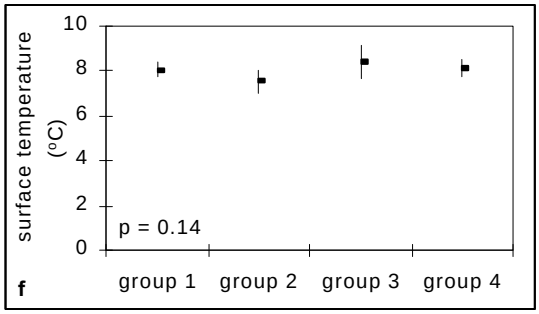


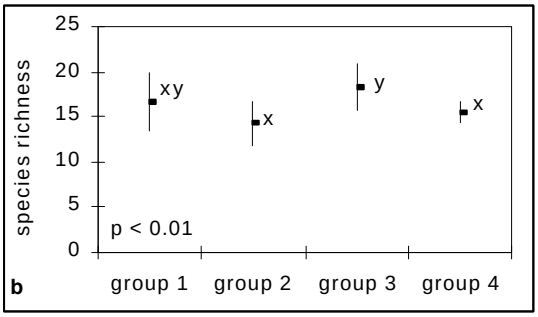
Figure 3.3. Dendrogram of the cluster analysis comparing zooplankton abundance data between stations conducted during MIOS 1. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species abundance data. Station groupings selected for the analysis are bracketed.

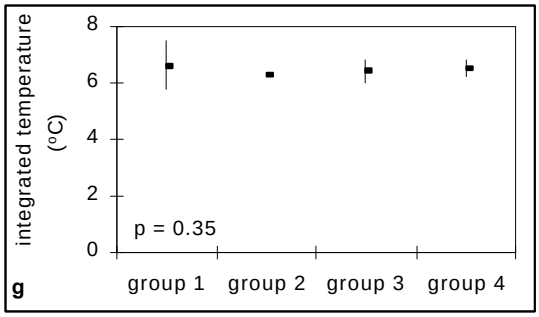
Overleaf:

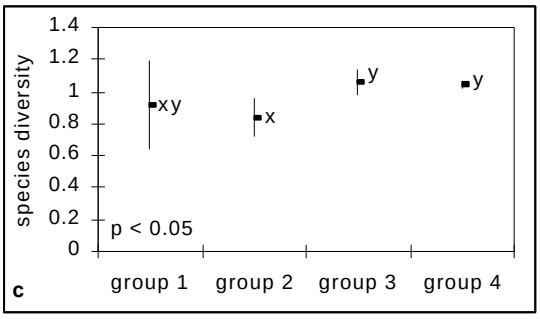
Figure 3.4. Average and standard deviations of variables, recorded for the station groups identified by cluster analysis of MIOS 1 abundance data. The significance level of between group variation, determined using a Kruskal-Wallace test, is indicated on each graph (p-value). Significant differences between station group pairs, determined using a Mann-Whitney U test, are indicated by different letters. Sharing of a letter indicates no significant difference.

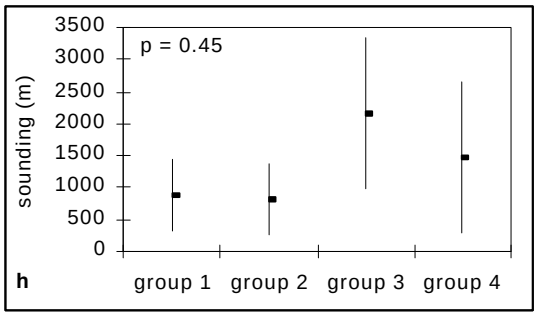

species number
50
40
30
20
10
0
p = 0.63
group 1
group 2
group 3
group 4
a

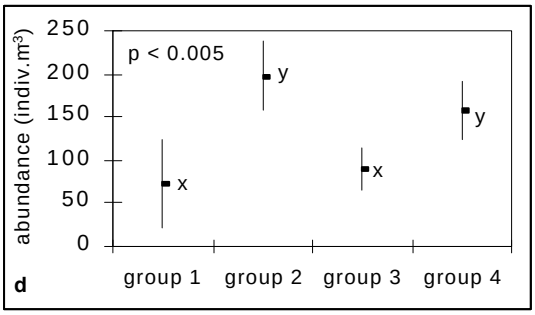

surface temperature (°C)
10
8
6
4
2
0
p = 0.14
group 1
group 2
group 3
group 4
f

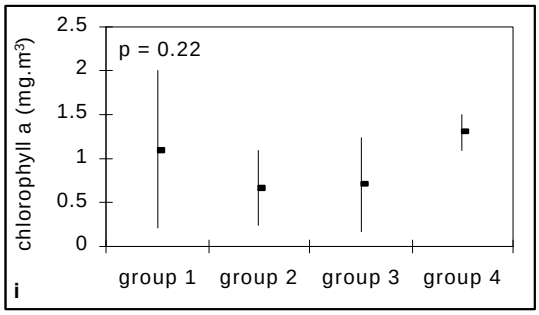

species richness
25
20
15
10
5
0
xy
x
y
x
p < 0.01
group 1
group 2
group 3
group 4
b


integrated temperature (°C)
8
6
4
2
0
p = 0.35
group 1
group 2
group 3
group 4
g


species diversity
1.4
1.2
1
0.8
0.6
0.4
0.2
0
xy
x
y
y
p < 0.05
group 1
group 2
group 3
group 4
c


sounding (m)
3500
3000
2500
2000
1500
1000
500
0
p = 0.45
group 1
group 2
group 3
group 4
h


abundance (indiv.m³)
250
200
150
100
50
0
p < 0.005
x
y
x
y
group 1
group 2
group 3
group 4
d


chlorophyll a (mg.m³)
2.5
2
1.5
1
0.5
0
p = 0.22
group 1
group 2
group 3
group 4
i

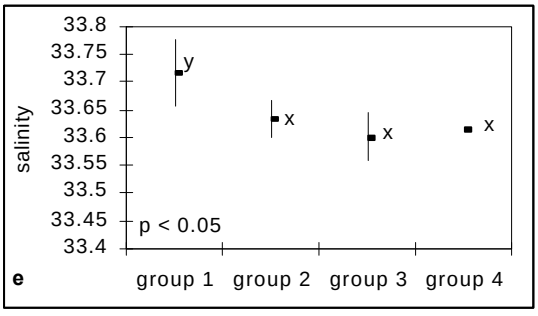

salinity
33.8
33.75
33.7
33.65
33.6
33.55
33.5
33.45
33.4
y
x
x
x
p < 0.05
group 1
group 2
group 3
group 4
e

Table 3.1. Results of the multiple regression of environmental variables against NMDS ordination scores for MIOS 1 abundance data (stress = 0.18). (degrees of freedom = 2.14)

	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	-0.36	0.12	0.12	-0.01	0.98	0.39
Surface temperature	0.45	0.67	0.49	0.42	6.81	< 0.01
Surface salinity	0.28	-0.41	0.30	0.20	3.03	0.08
Sounding	0.16	0.56	0.29	0.19	2.84	0.09
Chlorophyll *a*	0.31	-0.35	0.28	0.17	2.66	0.11

The lowest average similarity within station groupings was 65.9% within Group 3, followed by 67.5% within Group 1 (Table 3.2.). Similarity within groups 2 and 4 was greater than 70%. Together, the copepods *Clausocalanus brevipes, Metridia lucens* and *Oithona frigida*, the chaetognaths *Eukrohnia hamata and Sagitta gazellae,* the euphausiid *Thysanoessa vicina,* and Ostracods contributed to between 63.7% and 71.1% of the similarity within all groups. *Clausocalanus brevipes* was the most important contributor to within group similarity in all groups. *Clausocalanus brevipes* and *M. lucens*, occurred at highest abundance within Group 2, together contributing 32.9% to the similarity within this group. Group 4 had the highest abundance of *E. hamata*, the copepods *O. frigida* and *Rhincalanus gigas*, and the pteropod *Limacina helicina*.

Table 3.2. Species responsible for 80% of the similarity within the four station groups identified by cluster analysis of MIOS 1 abundance data. Within group similarity is in parenthesis under group number. Cells indicate average species abundance (individuals.m^{-3}) within a group and percentage contribution to within group similarity is in parenthesis.

Group 1 (67.47%)	**Group 2** (75.78%)	**Group 3** (65.92%)	**Group 4** (73.24%)
C. brevipes 36.37 (16.45%)	*C. brevipes* 78.63 (16.91%)	*C. brevipes* 21.34 (17.25%)	*C. brevipes* 35.81 (14.03%)
M. lucens 5.6 (13.26%)	*M. lucens* 45.33 (16.01%)	*E. hamata* 9.45 (11.08%)	*O. frigida* 23.4 (12.31%)
E. hamata 6.51 (11.79%)	*O. frigida* 7.91 (8.79%)	*M. lucens* 7.62 (9.88%)	*E. hamata* 19.34 (11.36%)
Ostracods 4.35 (10.96%)	Ostracods 8.07 (8.32%)	Ostracods 5.62 (8.54%)	*M. lucens* 13.19 (8.42%)
S. gazellae 2.6 (8.87%)	*S. gazellae* 4.02 (5.97%)	*S. gazellae* 3.63 (7.98%)	*L. retroversa* 8.34 (7.33%)
T. vicina 2.16 (7.92)%	*S. minor* 5.62 (5.93%)	*O. frigida* 4.17 (7.8%)	*S. gazellae* 5.25 (6.7%)
C. simillimus 1.16 (5.75%)	*T. vicina* 4.24 (5.56%)	*Pleuromamma* spp. 4.31 (5.65%)	Ostracods 8.62 (6.69%)
P. macropa 0.67 (3.11%)	*C. citer* 2.72 (5.06%)	*T. vicina* 2.25 (4.78%)	*R. gigas* 3.7 (5.47%)
	C. simillimus 2.32 (4.16%)	*L. retroversa* 4.99 (3.26%)	*T. vicina* 2.66 (3.95%)
		C. simillimus 1.44 (2.84%)	*L. helicina* 8.91 (3.48%)

The highest dissimilarity between groups was 41.7% between groups 4 and 1. The dissimilarity between all other groups was less than 40%. The species contributing to dissimilarity between groups were largely the same as those contributing to similarity within groups. The copepods *M. lucens, C. brevipes, O. frigida, Pleuromamma abdominalis, Ctenocalanus citer, Scolecithricella minor* and *Calanus simillimus,* the chaetognath *E. hamata*, the pteropod *Limacina retroversa,* and Ostracods together accounted for between 38% and 63% of the dissimilarity between groups. The Antarctic copepod *R. gigas* (Vervoort, 1951) was an important component of groups 3 and 4, contributing a relatively high percentage to the dissimilarity between these groups and groups 1 and 2 (Table 3.3). The copepods *Oncaea antarctica* and *Metridia gerlachei,*

both of which are predominantly Antarctic species (Razouls, 1994), were most abundant within Group 3 and contributed between 2.6% and 4.9% to the dissimilarity between this group and all other groups. The sub-Antarctic copepod *Pleuromamma gracilis* (De Decker, 1984) contributed >4.5% to dissimilarity between Group 4 and all other groups.

Table 3.3. Percentage contribution of *Rhincalanus gigas*, *Oncaea antarctica*, *Metridia gerlachei* and *Pleuromamma gracilis* to dissimilarity between station group pairs. The station group within which each species was most abundant is indicated in parenthesis (- indicates that a species was absent from one of the groups in a pair).

Group pair	*R. gigas*	*O. antarctica*	*M. gerlachei*	*P. gracilis*
3,2	3.04% (3)	2.72% (3)	4.90% (3)	-
3,2	2.83% (3)	2.61% (3)	3.03% (3)	-
3,4	4.62% (4)	2.68% (3)	3.20% (3)	4.97% (4)
1,2	2.75% (2)	2.53% (2)	2.50%(1)	-
1,4	5.40% (4)	-	3.20% (1)	4.87% (4)
2,4	5.38% (4)	2.38% (2)	-	4.78% (4)

The inverse analysis identified seven species clusters at the 50% level of similarity (Figure 3.5.). The first cluster contained *L. helicina,* which occurred at significantly higher abundance within station Group 4, and five species with no significant station group associations, although predominantly occurring at highest abundance within station Group 3 (Table 3.4.). The second, fourth and fifth clusters contained species occurring at highest abundance within station Group 4 while the third, sixth and seventh clusters were dominated by species occurring at highest abundance within station Group 2. The fifth and seventh clusters were dominated by Antarctic species (Vervoort, 1951; Timonin, 1968; Park, 1980; Boltovskoy, 1981; Razouls, 1994) while the sixth cluster was dominated by sub-Antarctic species (Vervoort, 1951; De Decker, 1984; Guglielmo and Ianora, 1995; Gibbons and Hutchings, 1996).

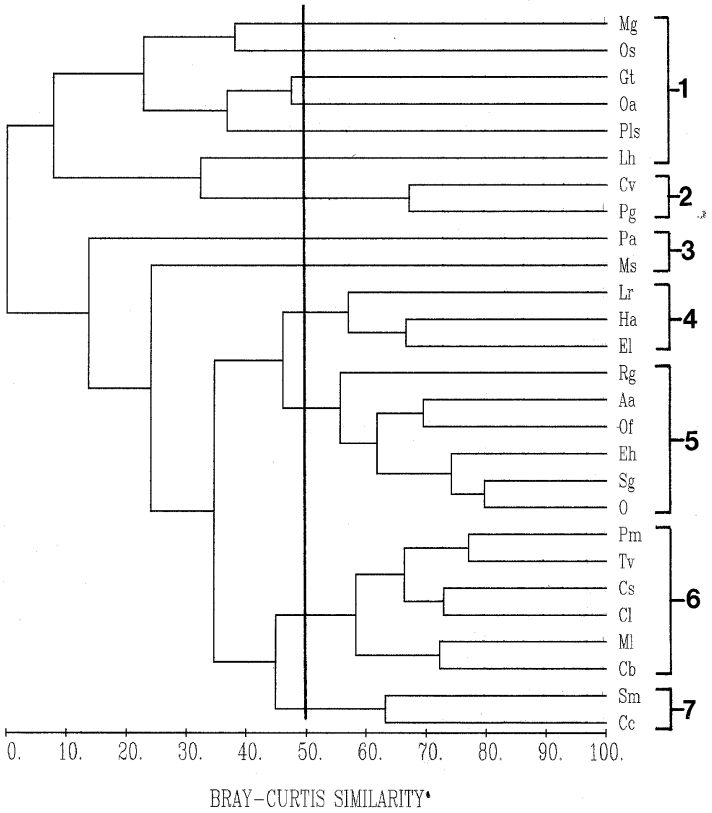


Figure 3.5. Dendrogram of the inverse cluster analysis comparing the dominant zooplankton species identified by SIMPER analysis of MIOS 1 abundance data. The Bray-Curtis similarity measure was used after standardisation of the data set. Abbreviations follow those in Table 3.4.

Table 3.4. Species, abbreviations and names, used in the inverse analysis and the station groups within which each species occurred at highest abundance. Station groups within which a species occurred at significantly higher abundance, determined by Mann-Whitney U tests, are in bold. Significant differences in the abundance of species between station groups, determined by Kruskal-Wallace tests, are indicated by p (- indicates no significant difference).

Species	**Group**	**p**
Mg – *Metridia gerlachei*	3	-
Os – *Oithona similis*	1	-
Gt – *Gaidius tenuispinus*	2	-
Oa – *Oncaea antarctica*	3	-
Pls – *Pleuromamma* spp.	3	-

Table 3.4. continued		
Species	**Group**	**p**
Lh – *Limacina helicina*	**4**	< 0.005
Cv – *Ctenocalanus vanus*	4	-
Pg – *Pleuromamma gracilis*	4	-
Pa – *Pleuromamma abdominalis*	2	-
Ms – *Microcalanus* spp.	2	-
Lr – *Limacina retroversa*	**4**	< 0.05
Ha – *Heterorhabdus austrinus*	4	-
El – *Eucalanus longiceps*	4	-
Rg – *Rhincalanus gigas*	4	-
Aa – *Aetideus armatus*	4	-
Of – *Oithona frigida*	**4**	< 0.005
Eh – *Eukrohnia hamata*	4	-
Sg – *Sagitta gazellae*	4	-
O – Ostracod	4	-
Pm – *Primno macropa*	4	-
Tv – *Thysanoessa vicina*	2	-
Cs – *Calanus simillimus*	**2**	< 0.05
Cl – *Clausocalanus laticeps*	2	-
Ml – *Metridia lucens*	**2**	< 0.05
Cb – *Clausocalanus brevipes*	**2**	< 0.05
Sm – *Scolecithricella minor*	2	-
Cc – *Ctenocalanus citer*	**2**	< 0.05

Chlorophyll *a* accounted for a significant amount of variation in the abundance of the chaetognaths *S. gazellae* and *E. hamata,* and the hyperiid amphipod *Primno macropa* (Table 3.5.). *Primno macropa* was also negatively correlated with sounding indicating that it occurred at highest abundance at the inter-island stations with high chlorophyll *a* concentrations. The copepods *Heterorhabdus austrinus* and *P. abdominalis* were positively correlated with surface salinity while surface temperature accounted for a significant amount of variation in the abundance of *Ctenocalanus vanus*. *Oncaea antarctica* was positively correlated with sounding.

A number of frequency indicators were identified by the information statistic (Table 3.6.). Group 3 was characterised by the presence of the subtropical species *P. sedentaria* (Vinogradov *et al*., 1982) and *Cymbulia* sp. (Boltovskoy, 1981), the typically sub-Antarctic species' *E. similis* (Baker, 1965) and *E. hyalinus* (Guglielmo and Ianora, 1995), and the Antarctic species' *C. maxima* (Siegel *et al*., 1992; Razouls, 1994), *S. vervoorti*

(Park, 1980) and *S. glacialis* (Vervoort, 1951). Groups 1 and 2 both contained Antarctic species including *S. vervoorti* and *S. antarcticus* (Hopkins, 1985). Group 1 also contained the sub-Antarctic copepod *G. minor* (Razouls, 1994). Within Group 4 the SAF station MS1-13 contained the sub-tropical fish species *E. cryomargarites* (Gon and Heemstra, 1990).

Table 3.5. Significant regressions of environmental variables against abundance for species contributing most to within group similarity and between group dissimilarity (degrees of freedom = 1.15).

Species	Variable	Beta	R^2	Adjusted R^2	F	p
S. gazellae	Chlorophyll *a*	0.66	0.44	0.40	11.65	< 0.005
E. hamata	Chlorophyll *a*	0.55	0.30	0.26	6.56	< 0.05
P. macropa	Sounding	-0.50	0.25	0.20	4.92	< 0.05
	Chlorophyll *a*	0.49	0.24	0.19	4.77	< 0.05
H. austrinus	Surface salinity	0.49	0.25	0.20	4.92	< 0.05
O. antarctica	Sounding	0.64	0.40	0.36	10.16	< 0.01
C. vanus	Surface temperature	-0.70	0.49	0.46	14.52	< 0.005
P. abdominalis	Surface salinity	0.53	0.28	0.23	5.74	< 0.05

Table 3.6. Frequency of occurrence of indicator species distinguishing cluster groups. Species above the blank line have 2)I > 6.63 (p=0.01), and those below the line have 2)I > 3.84 (p=0.05). The number of samples in a group is in parenthesis below group number.

Species	Group 1 (4)	Group 2 (4)	Group 3 (13)	Group 4 (4)
Phronima sedentaria	0	0	2	0
Euphausia similis	0	0	3	0
Paraeuchaeta biloba	0	0	3	0
Candacia maxima	0	0	2	0
Scaphocalanus antarcticus	0	2	0	0
Eucalanus hyalinus	0	0	2	0
Scaphocalanus vervoorti	1	0	1	0
Gaetanus minor	1	0	0	0
Echiodon cryomargarites	0	0	0	1
Ihlea megalhanica	0	1	0	0
Cymbulia sp.	0	0	1	0
Scolecithricella glacialis	0	0	1	0

3.3.2. Biomass:

Cluster analysis identified four station groupings at approximately the 35% level of similarity (Figure 3.6.). Group 1 contained two upstream stations and one inter-island station. Group 2 contained five upstream stations and three downstream stations. Group 3 contained four upstream stations, two inter-island stations and one downstream station. Finally, group 4 contained three upstream stations, one inter-island station and two downstream stations.

ANOSIM showed that all station groupings were significantly different from each other at the 1% level, with the exception of groups 4 and 1 which differed at the 5% level.

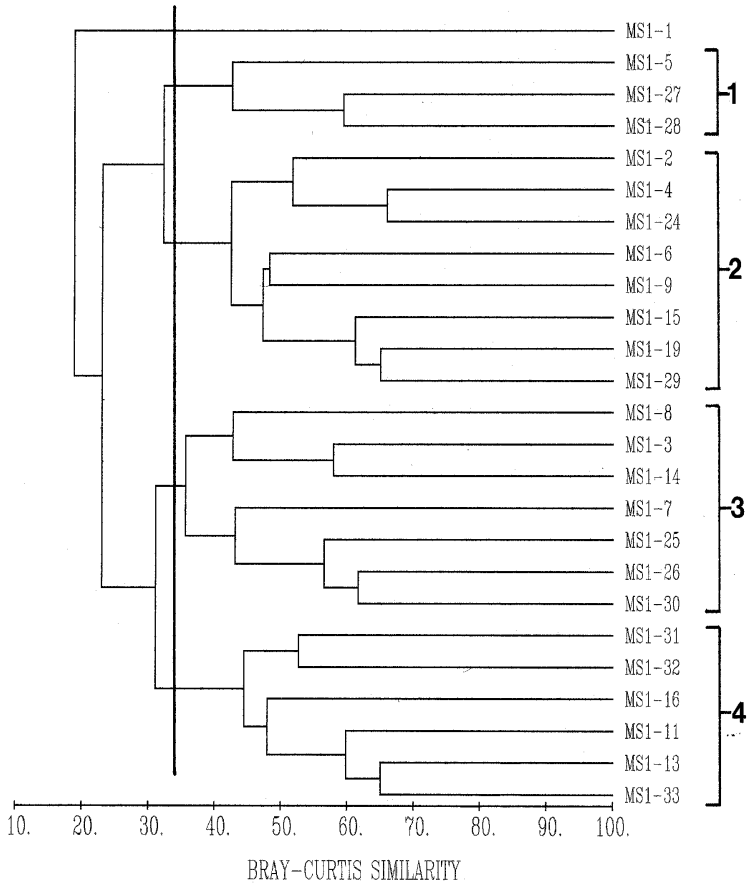


Figure 3.6. Dendrogram of the cluster analysis comparing zooplankton biomass data between stations conducted during MIOS 1. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species biomass data. Station groupings selected for the analysis are bracketed.

A Kruskal-Wallace test of biological and physical variables showed that there was a high degree of similarity between station groups (Figure 3.7.). The only variable that differed significantly between groups was species diversity. A Mann-Whitney U test showed that diversity was significantly higher within groups 2, 3 and 4 than within Group 1 (Figure 3.7.c).

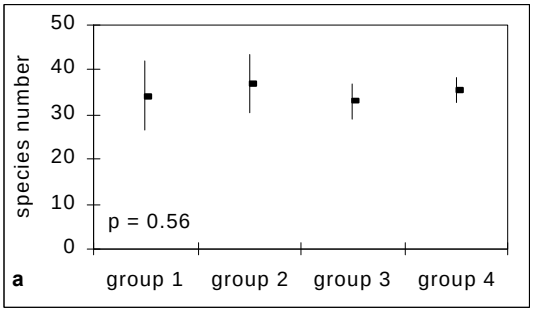
Sounding accounted for 22% of the variation in the biomass data, however, this relationship was not significant ($p>0.05$) (Table 3.7). Sounding did account for a significant amount of variation in the x-axis ($p<0.05$). No other variable was significantly correlated with the biomass data.

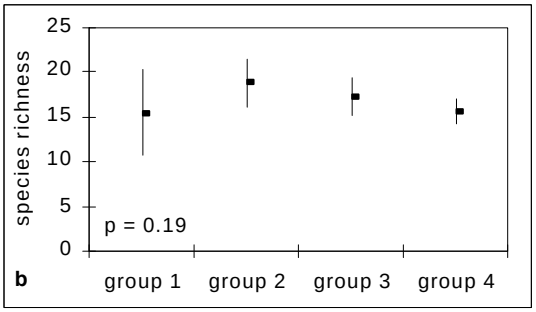
Table 3.7. Results of the multiple regression of environmental variables against NMDS ordination scores for MIOS 1 biomass data (stress = 0.20). (degrees of freedom = 2.14)

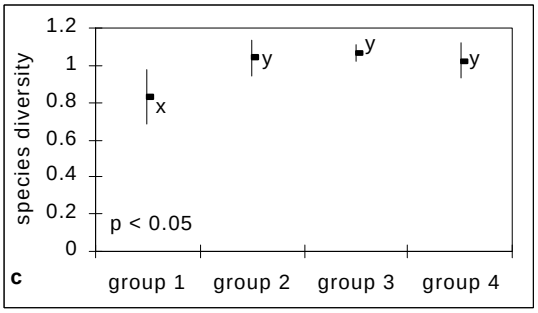
	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	0.21	0.18	0.06	-0.08	0.42	0.66
Surface temperature	-0.17	0.08	0.04	-0.09	0.31	0.73
Surface salinity	0.11	0.08	0.01	-0.13	0.09	0.90
Sounding	-0.56	0.01	0.31	0.22	3.20	0.07
Chlorophyll *a*	-0.12	-0.19	0.04	-0.09	0.29	0.75

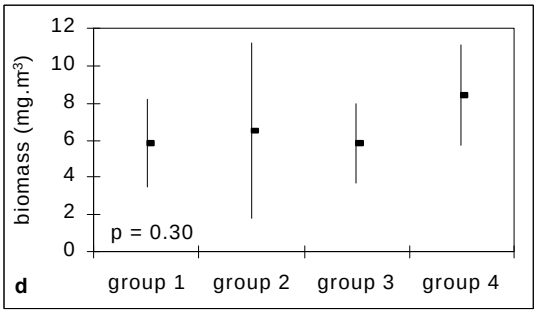
Overleaf:

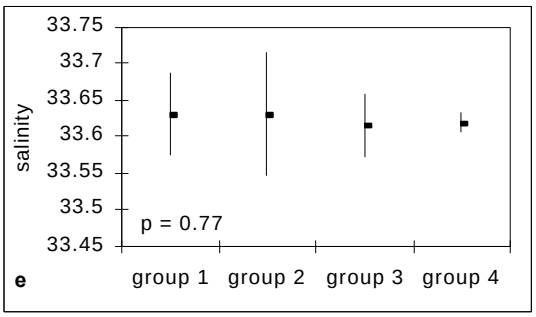
Figure 3.7. Average and standard deviations of variables, recorded for the station groups identified by cluster analysis of MIOS 1 biomass data. The significance level of between group variation, determined using a Kruskal-Wallace test, is indicated on each graph (p-value). Significant differences between station group pairs, determined using a Mann-Whitney U test, are indicated by different letters. Sharing of a letter indicates no significant difference.

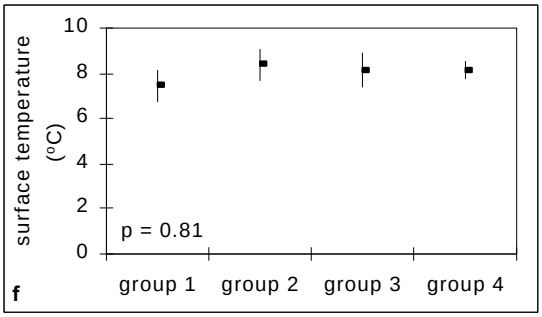

species number
50
40
30
20
10
0
p = 0.56
group 1
group 2
group 3
group 4
a

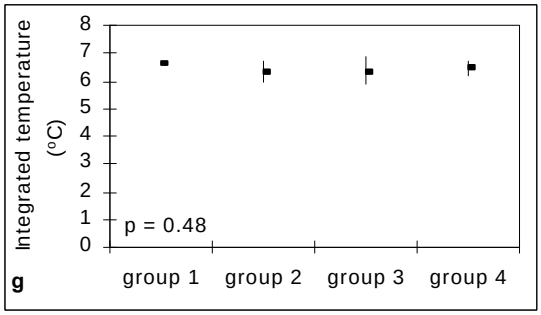

species richness
25
20
15
10
5
0
p = 0.19
group 1
group 2
group 3
group 4
b

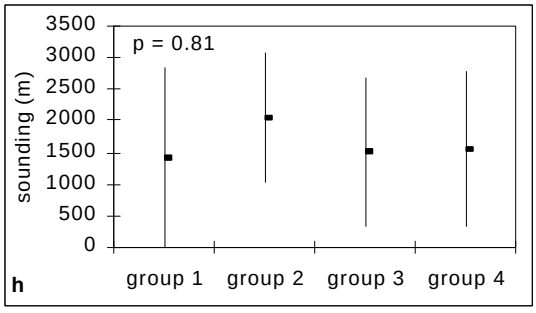

species diversity
1.2
1
0.8
0.6
0.4
0.2
0
x
y
y
y
p < 0.05
group 1
group 2
group 3
group 4
c

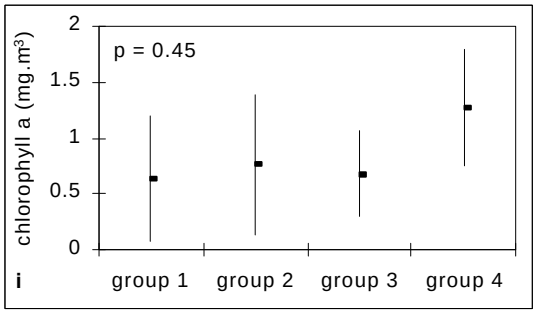

biomass (mg.m3)
12
10
8
6
4
2
0
p = 0.30
group 1
group 2
group 3
group 4
d


salinity
33.75
33.7
33.65
33.6
33.55
33.5
33.45
p = 0.77
group 1
group 2
group 3
group 4
e


surface temperature (oC)
10
8
6
4
2
0
p = 0.81
group 1
group 2
group 3
group 4
f


Integrated temperature (oC)
8
7
6
5
4
3
2
1
0
p = 0.48
group 1
group 2
group 3
group 4
g


sounding (m)
3500
3000
2500
2000
1500
1000
500
0
p = 0.81
group 1
group 2
group 3
group 4
h


chlorophyll a (mg.m3)
2
1.5
1
0.5
0
p = 0.45
group 1
group 2
group 3
group 4
i

The lowest within group similarity occurred within Group 3 (47.3%) (Table 3.8.). All other groups had a within group similarity of >50%. Group 1 was dominated by copepods with *C. brevipes*, *P. abdominalis* and *M. lucens* together contributing 49.8% to within group similarity. The euphausiid species *Euphausia longirostris*, *Thysanoessa vicina* and *E. vallentini* contributed 33.1% to the similarity within Group 2. *Eukrohnia hamata*, *S. gazellae*, *C. brevipes, M. lucens* and Ostracods together contributed 52.8% and 46.2% to similarity within groups 3 and 4 respectively. *Rhincalanus gigas* and the pteropod *Clio pyramidata* contributed a relatively high percentage to the similarity within Group 4.

Table 3.8. Species responsible for 80% of the similarity within the four station groups identified by cluster analysis of MIOS 1 biomass data. Within group similarity is in parenthesis under group number. Cells indicate average species biomass ($mg.m^{-3}$) within a group and percentage contribution to within group similarity is in parenthesis.

Group 1 (50.34%)	**Group 2** (51.74%)	**Group 3** (47.29%)	**Group 4** (53.72%)
C. brevipes 1.42 (21.42%)	*E. longirostris* 1.42 (20.75%)	*E. hamata* 0.87 (25.10%)	*E. hamata* 1.27 (18.65)
P. abdominalis 3.71 (16.05%)	*T. vicina* 0.52 (13.36%)	*C. brevipes* 0.33 (16.13%)	*C. brevipes* 0.89 (14.09%)
T. vicina 0.80 (13.31%)	*E. hamata* 0.59 (11.22%)	*S. gazellae* 0.49 (8.64%)	*R. gigas* 0.57 (8.12%)
M. lucens 0.80 (12.28%)	*E. vallentini* 0.82 (8.98%)	Ostracods 0.20 (8.30%)	*S. gazellae* 0.44 (7.71%)
S. gazellae 0.90 (9.70%)	*C. brevipes* 0.42 (8.40%)	*M. lucens* 0.12 (4.61%)	*T. vicina* 0.46 (7.06%)
	S. gazellae 0.40 (5.94%)	*H. austrinus* 0.14 (4.02%)	*M. lucens* 0.41 (5.74%)
	M. lucens 0.37 (4.48%)	*T. vicina* 0.27 (3.48%)	Ostracods 0.30 (4.98%)
	Ostracods 0.15 (3.84%)		*C. pyramidata* 0.21 (4.59%)
			M. melo 0.49 (4.32%)
			H. austrinus 0.22 (3.78%)

The dissimilarity between all groups was greater than 55%. The species *E. hamata, S. gazellae, P. abdominalis, C. brevipes, M. lucens, R. gigas, E. longirostris, E. vallentini, T. vicina.* and *L. helicina* together accounted for 42% to 64% of the dissimilarity between station groups. The fish *Gymnoscopelus* spp. and *Protomyctophum choriodon* together contributed to between 3.1% and 5.6% of the dissimilarity between Group 2 and all other groups.

The inverse analysis identified five species clusters at the 50% level of similarity (Figure 3.8.). The first cluster was dominated by species with no significant association with station groups (Table 3.9.). *Pleuromamma abdominalis* occurred at significantly higher biomass within Group 1 and *R. gigas* occurred at significantly higher biomass within groups 3 and 4. The second cluster contained the euphausiids *E. vallentini* and *E. longirostris,* which occurred at significantly higher biomass within station Group 2. The third cluster contained species occurring at highest biomass within station Group 4. The fourth cluster contained *M. lucens* and *C. brevipes,* which occurred at highest biomass within station Group 1. Finally, the fifth cluster contained a mix of species occurring at highest biomass within station groups 1, 3 and 4.

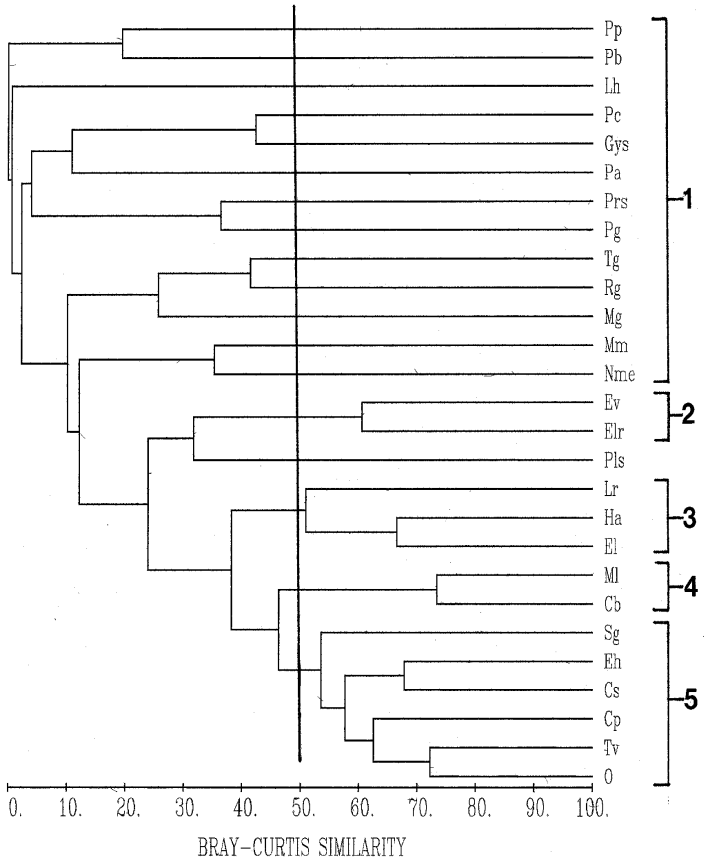


Figure 3.8. Dendrogram of the inverse cluster analysis comparing dominant zooplankton species, identified by SIMPER analysis of MIOS 1 biomass data. The Bray-Curtis similarity measure was used after standardisation of the data set. Abbreviations follow those in Table 3.9.

Table 3.9. Species, abbreviations and names, used in the inverse analysis and the station groups within which each species occurred at highest biomass. Station groups within which a species occurred at significantly higher biomass, determined by Mann-Whitney U tests, are in bold. Significant differences in the biomass of species between station groups, determined by Kruskal-Wallace tests, are indicated by p (- indicates no significant difference).

Species	**Groups**	**p**
Pp – *Periphyla periphyla*	1	-
Pb – *Paraeuchaeta biloba*	3	-
Lh – *Limacina helicina*	4	-

Table 3.9. continued		
Species	**Groups**	**p**
Pc – *Protomyctophum choriodon*	2	-
Gys – *Gymnoscopelus* spp.	2	-
Pa – *Pleuromamma abdominalis*	**1**	< 0.05
Prs – *Protomyctophum* spp.	4	-
Pg – *Pleuromamma gracilis*	4	-
Tg – *Thysanoessa gregaria*	4	-
Rg – *Rhincalanus gigas*	**4**	< 0.05
Mg – *Metridia gerlachei*	3	-
Mm – *Melophysa melo*	4	-
Nme – *Nematoscelis megalops*	4	-
Ev – *Euphausia vallentini*	**2**	< 0.05
Elr – *Euphausia longirostris*	**2**	< 0.005
Pls – *Pleuromamma* spp.	4	-
Lr – *Limacina retroversa*	4	-
Ha – *Heterorhabdus austrinus*	4	-
El – *Euchaeta longiceps*	4	-
Ml – *Metridia lucens*	1	-
Cb – *Clausocalanus brevipes*	**1**	< 0.05
Sg – *Sagitta gazellae*	1	-
Eh – *Eukrohnia hamata*	**4**	< 0.05
Cs – *Calanus simillimus*	3	-
Cp – *Clio pyramidata*	4	-
Tv – *Thysanoessa vicina*	1	-
O – Ostracods	1	-

Limacina retroversa biomass showed a significant positive correlation with surface temperature ($p<0.01$) (Table 3.10.). *Eukrohnia hamata*, *H. austrinus*, *C. vanus* and *P. abdominalis* biomass values had similar correlations with environmental variables to those identified by the abundance analysis. The copepod *P. biloba* had a significant negative correlation with integrated temperature ($p<0.03$).

Table 3.10. Significant regressions of environmental variables against biomass for species responsible for 80 % of the similarity within and dissimilarity between groups (degrees of freedom = 1.15).

Species	**Variable**	**Beta**	**R^2**	**Adjusted R^2**	**F**	**p**
L. retroversa	Surface temperature	0.64	0.40	0.36	10.19	< 0.01
E. hamata	Chlorophyll *a*	0.65	0.42	0.38	11.05	< 0.001
H. austrinus	Surface salinity	0.50	0.25	0.20	4.93	< 0.05

Table 3.10. continued						
Species	**Variable**	**Beta**	**R^2**	**Adjusted R^2**	**F**	**p**
P. biloba	Integrated temperature	-0.52	0.27	0.22	5.65	< 0.05
C. vanus	Surface temperature	-0.70	0.49	0.46	14.52	< 0.001
P. abdominalis	Surface salinity	0.53	0.28	0.23	5.74	< 0.05

Both Groups 1 and 2 were characterised by the presence of the sub-tropical hyperiid amphipod *P. sedentaria* (Vinogradov *et al*., 1982) (Table 3.11.). Group 2 also contained the Antarctic copepod *S. antarcticus*. Group 3 had a high incidence of the Antarctic copepod *C. maxima*, and also contained the Antarctic species *S. glacialis* and *S. vervoorti*, and the sub-Antarctic species *G. minor* (Razouls, 1994). Group 4 contained the Antarctic tunicate *I. magalhanica* (O'Sullivan, 1983) and the sub-tropical fish species *E. cryomargarites* (Gon and Heemstra, 1990).

Table 3.11. Frequency of occurrence of indicator species distinguishing cluster groups. Species above the blank line have $2)I > 6.63$ (p=0.01), and those below the line have $2)I > 3.84$ (p=0.05). The number of samples in a group is in parenthesis below group number.

Species	**Group 1 (3)**	**Group 2 (8)**	**Group 3 (7)**	**Group 4 (6)**
Candacia maxima	0	0	2	0
Phronima sedentaria	1	1	0	0
Scaphocalanus antarcticus	0	1	0	1
Ihlea magalhanica	0	0	0	1
Echiodon cryomargarites	0	0	0	1
Scolecithricella glacialis	0	0	1	0
Scaphocalanus vervoorti	0	0	1	0
Gaetanus minor	0	0	1	0

Chapter 4

RESULTS: MIOS 2 (1997)

4.1. Oceanography:

En route to the islands the SAF was located at 45°25'S and 36°26'E on 29 May (Figure 4.1.a). Survey 1 commenced on 30 May and the upstream transect identified the position of the SAF at 46°S along 37°E (Figure 4.1.b). The SAF therefore appeared to meander southwards as it approached the islands. A warm water feature, with characteristics of sub-Antarctic surface water (Ansorge *et al*., 1999; Lutjeharms and Vallentine, 1984), was encountered at 47°20'S, corresponding with station MS2-1, along 37°E (Figure 4.1.c).
During Survey 2 the SAF was located in line with the islands at 36°E but was deflected sharply northwards as it approached the island shelf (Figure 4.2.). The position of the SAF along 37°E was further north in Survey 2 than in Survey 1. Downstream of the islands the SAF appeared as a slightly meandering front along 46°S. Froneman *et al*. (1999) identified the position of the APF, based on the 100m isotherm ranging between 5.8°C and 4°C, to the south of the islands in the upstream region. For the purpose of this study the APF was defined by the position of the 2°C isotherm at 200m (see Chapter 2). Consequently this cold water in the vicinity of station MS2-48 was classified as Antarctic surface water (following Lutjeharms and Vallentine, 1984), although its presence, as well as the high temperature gradient in the upstream region ($0.05^{o}C.km^{-1}$), indicate the close proximity of the APF. The APF proper was located in the downstream region at 48°S and 42°E (Figure 4.1.d).
Two eddies were located during Survey 2 (Ansorge *et al*., 1999; Figure 4.2.). The first was a warm core eddy located south of the islands, along the same line of longitude as the islands, with sub-Antarctic surface water characteristics. The position and physical characteristics of this eddy indicated that it was the same oceanographic feature that was sampled during Survey 1 at station MS2-1. In the period between survey 1 and 2 the eddy had moved in a SE direction following the flow of the ACC around the island shelf.

The second was a cold core eddy located downstream of the islands with Antarctic surface water characteristics (Ansorge *et al*., 1999).

4.2. Chlorophyll *a*:

Total chlorophyll *a* concentrations averaged 0.50 $mg.m^{-3}$ during Survey 1 and 0.38$mg.m^{-3}$ during Survey 2, when station MS2-37 was excluded from the analysis (Figure 4.3.). The latter station had chlorophyll *a* levels at bloom concentrations. When MS2-37 was excluded from the analysis, average chlorophyll *a* concentrations recorded for the inter-island region (0.61 mg.m-3) were significantly higher ($p<0.05$) than levels in all other regions, with the exception of the downstream region from Survey 1. Differences in total chlorophyll *a* concentrations were largely attributed to pico and nanophytoplankton. A Mann-Whitney U test showed that these size fractions differed significantly in concentration between upstream, inter-island and downstream regions ($p<0.05$). Station MS2-37 was dominated by microphytoplankton.

Continued on page…42

Figure 4.1. Temperature profiles, determined by XBT (a,b,c) and CTD (d), illustrating (a) the crossing of the SAF at 45°25'S and 36°26'E on 29 May; (b) the crossing of the SAF during Survey 1 on 30 May at 46°S and 37°E; (c) the sub-Antarctic surface water located at 47°20'S and 37°E, corresponding with the station MS2-1; (d) the crossing of the APF at 48°S and 42°E. Figures taken from Ansorge *et al.* (1998).

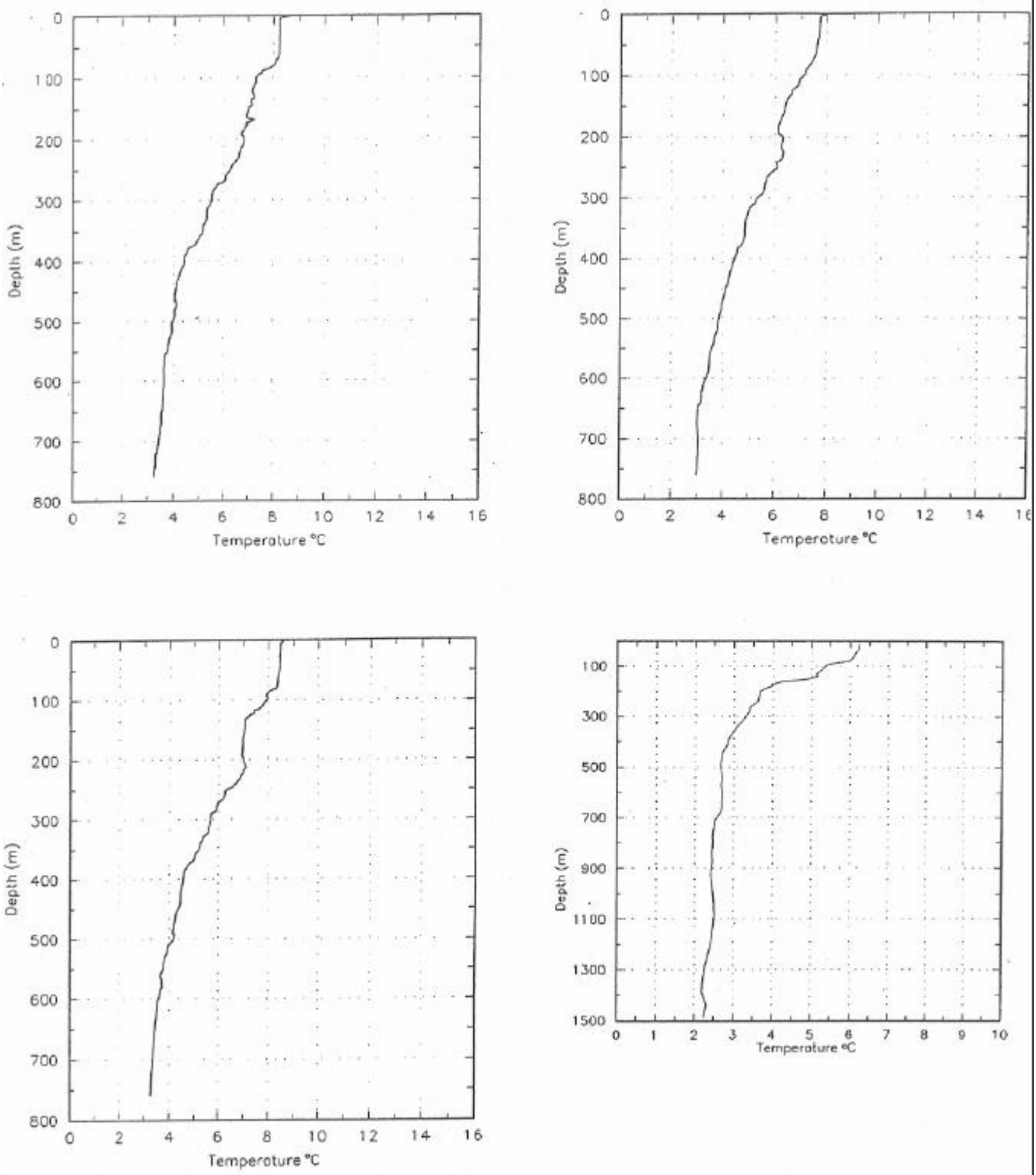


Figure 4.1. Temperature profiles, determined by XBT (a,b,c) and CTD (d), illustrating (a) the crossing of the SAF at 45°25'S and 36°26'E on 29 May; (b) the crossing of the SAF during Survey 1 on 30 May at 46°S and 37°E; (c) the sub-Antarctic surface water located at 47°20'S and 37°E, corresponding with the station MS2-1; (d) the crossing of the APF at 48°S and 42°E. Figures taken from Ansorge *et al.* (1998).

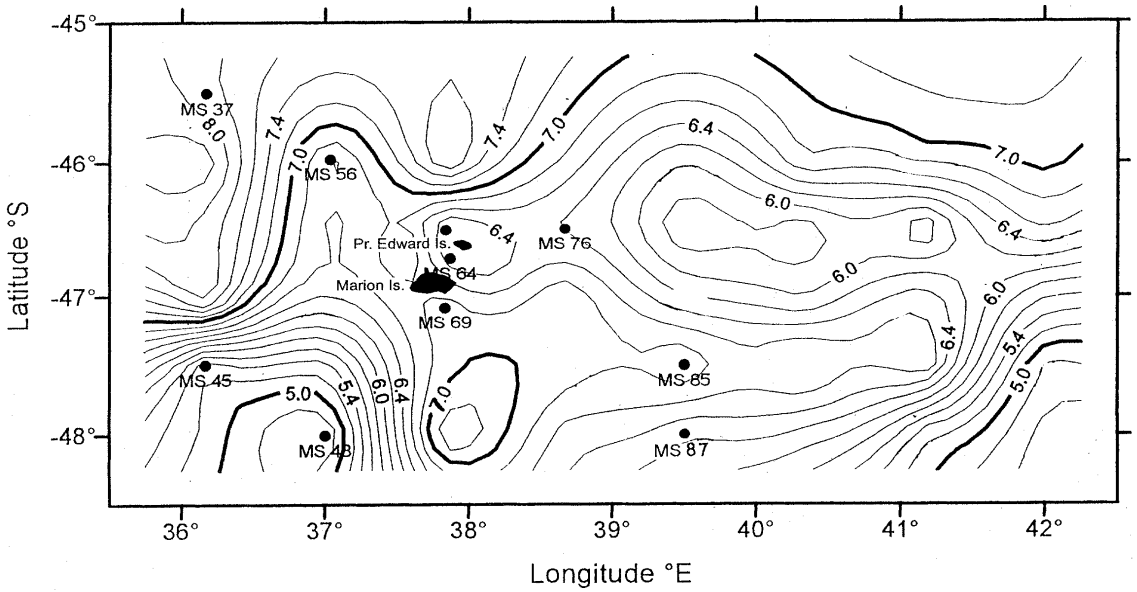


Figure 4.2. Temperature at 100m depth, and position of night bongo tows, during Survey 2 1997. Figure taken from Froneman *et al*. (1999).

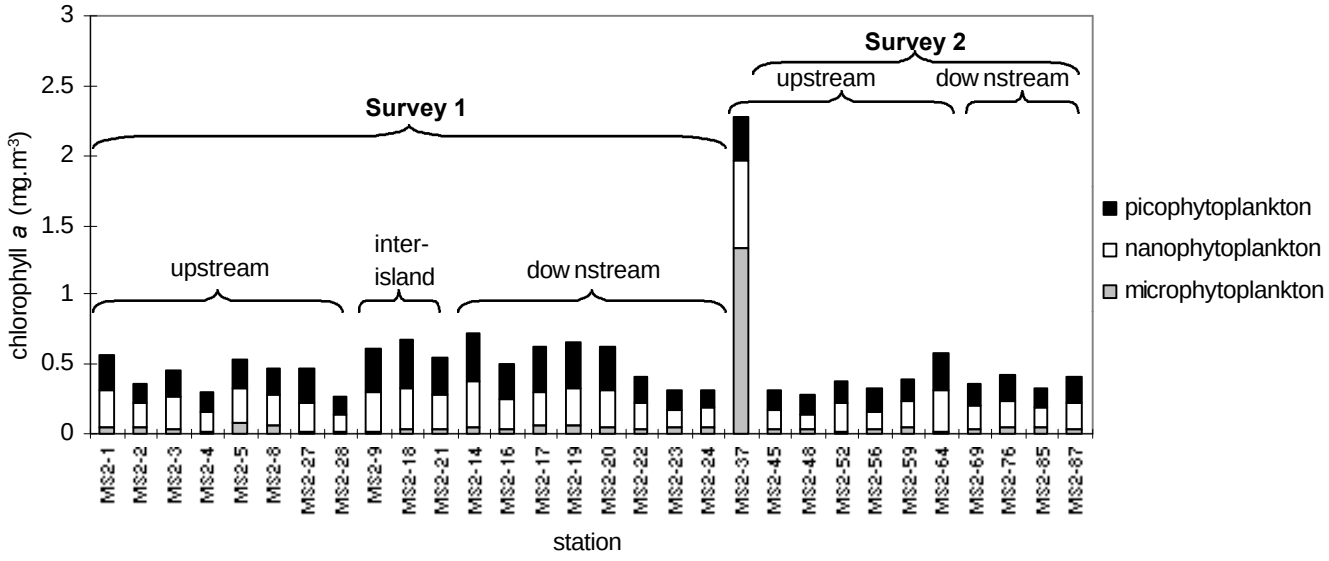


Figure 4.3. Size fractionated chlorophyll *a* concentrations corresponding with net tows during MIOS 2. Regions discussed in the analysis are bracketed.

4.3. Zooplankton:

4.3.1. Abundance:

Cluster analysis identified four station groups at approximately the 57% level of similarity (Figure 4.4). Group 1contained all of the upstream stations from Survey 1, with the exception of MS2-5, as well as an upstream station from Survey 2 which was in close proximity to the SAF. Group 2 contained four inter-island and four downstream stations from Survey 1. Group 3 contained three oceanic stations from Survey 2, including MS2-45 and MS2-48 located in the vicinity of the APF, and MS2-76 on the edge of the cold core eddy. Finally, Group 4 contained one upstream station, located in the vicinity of the SAF, and four downstream stations from Survey 1, as well as two upstream stations, including MS2-37 north of the SAF, and two downstream stations from Survey 2.
ANOSIM showed that all station groups were significantly different from each other ($p<0.01$).

Species richness and diversity differed significantly between the station groups identified by cluster analysis with the highest values being recorded within Group 1 and the lowest within Group 2 (Figure 4.5.b,c). Group 3 had significantly higher zooplankton abundance levels than all other groups, with the exception of Group 4, while the lowest abundance levels were recorded within Group 1 (Figure 4.5.d). Sounding reflected the location of stations. The lowest average values were recorded for Group 2, which had numerous inter-island stations, while the highest values were recorded for Group 1, which contained only upstream oceanic stations (Figure 4.5.h). Average chlorophyll *a* concentrations within Group 2 were significantly higher than within groups 1 and 3 (Figure 4.5.i). The high standard deviation recorded for Group 4 was largely due to this group containing the station MS2-37, where bloom level chlorophyll *a* concentrations were recorded (Figure 4.3.). There was no significant difference in surface and integrated temperature between groups, but the lowest average values were recorded within Group 3 (Figure 4.5.f,g). There were no significant differences in species number or salinity between groups (Figure 4.5.a.e).

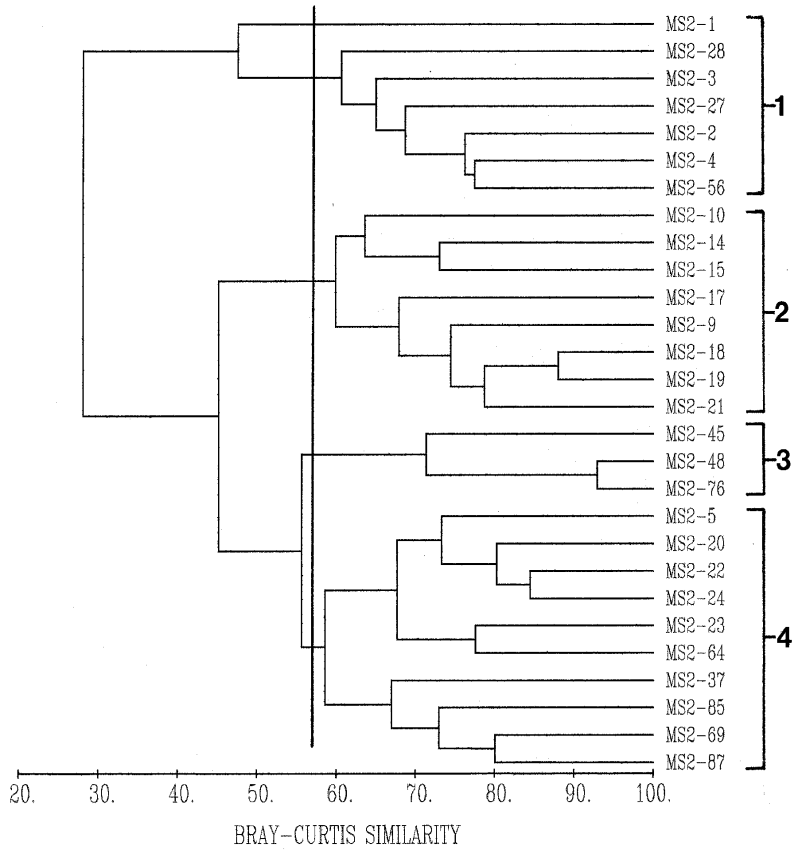
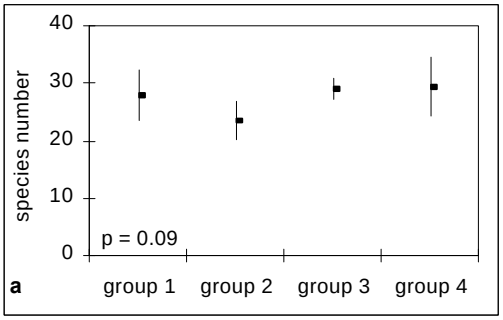
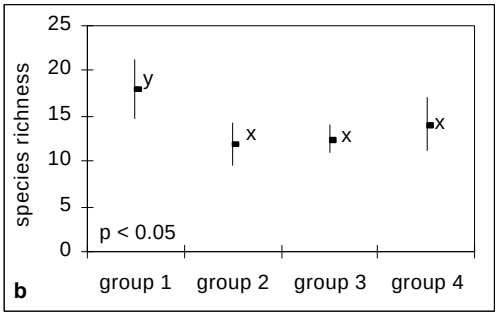


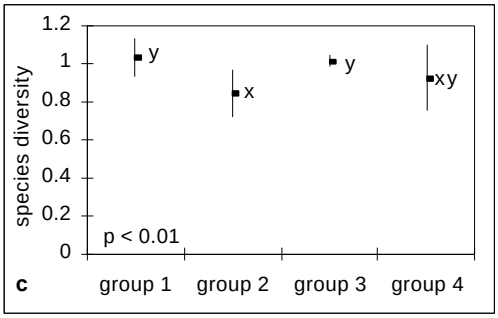
Figure 4.4. Dendrogram of the cluster analysis comparing zooplankton abundance data between stations conducted during MIOS 2. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species abundance data. Station groupings used in the analysis are in parenthesis.

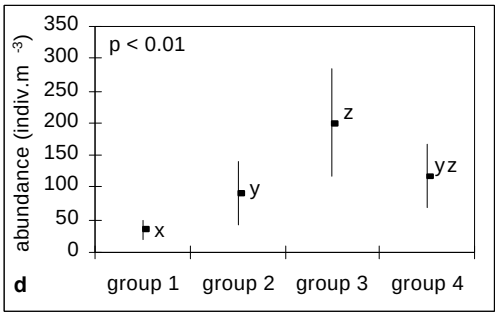
Overleaf:

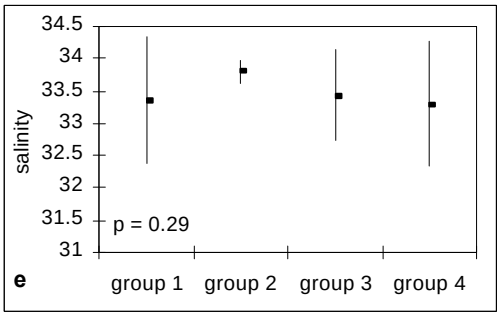
Figure 4.5. Average and standard deviations of variables, recorded for the station groups identified by cluster analysis of MIOS 2 abundance data. The significance level of between group variation, determined using a Kruskal-Wallace test, is indicated on each graph (p-value). Significant differences between station group pairs, determined using a Mann-Whitney U test, are indicated by different letters. Sharing of a letter indicates no significant difference.

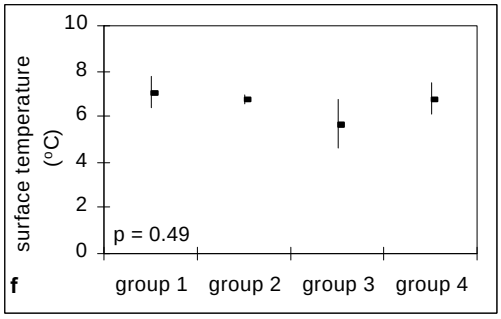

species number
40
30
20
10
0
p = 0.09
a
group 1
group 2
group 3
group 4

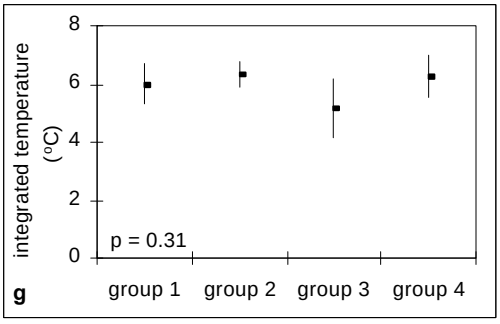

species richness
25
20
15
10
5
0
y
x
x
x
p < 0.05
b
group 1
group 2
group 3
group 4

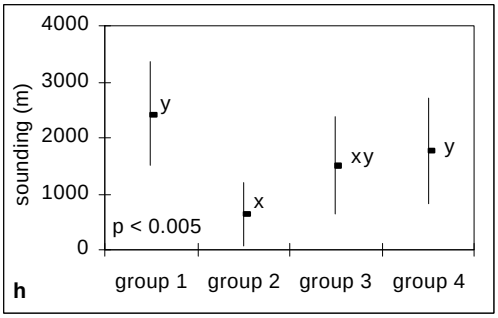

species diversity
1.2
1
0.8
0.6
0.4
0.2
0
y
x
y
xy
p < 0.01
c
group 1
group 2
group 3
group 4

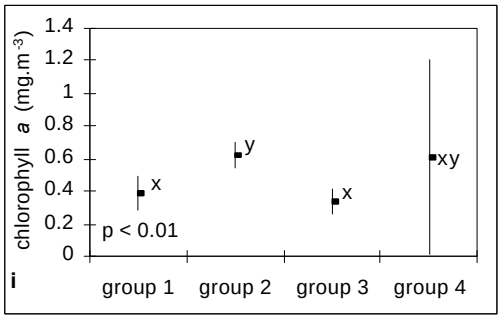

abundance (indiv.m -3)
350
300
250
200
150
100
50
0
p < 0.01
x
y
z
yz
d
group 1
group 2
group 3
group 4


salinity
34.5
34
33.5
33
32.5
32
31.5
31
p = 0.29
e
group 1
group 2
group 3
group 4


surface temperature (°C)
10
8
6
4
2
0
p = 0.49
f
group 1
group 2
group 3
group 4


integrated temperature (°C)
8
6
4
2
0
p = 0.31
g
group 1
group 2
group 3
group 4


sounding (m)
4000
3000
2000
1000
0
y
x
xy
y
p < 0.005
h
group 1
group 2
group 3
group 4


chlorophyll a (mg.m-3)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
x
y
x
xy
p < 0.01
i
group 1
group 2
group 3
group 4

Surface temperature accounted for 30% of the variation in zooplankton abundance data (Table 4.1.) and hence was an important variable in determining the observed station clustering. Sounding accounted for a significant (p=0.03) amount of variation in the x-axis of the ordination of abundance data, but not for the x and y axes combined. No other variable significantly affected the zooplankton community structure.

Table 4.1. Results of the multiple regression of environmental variables against NMDS ordination scores for MIOS 2 abundance data (stress = 0.13). (degrees of freedom = 2.2).

	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	-0.35	-0.20	0.14	0.06	1.85	0.18
Surface temperature	-0.61	-0.09	0.37	0.30	5.79	0.01
Surface salinity	-0.07	0.08	0.01	-0.09	0.13	0.88
Sounding	-0.48	-0.15	0.23	0.15	2.99	0.07
Chlorophyll *a*	-0.01	-0.25	0.06	-0.03	0.67	0.52

The lowest within group similarity was 64% within Group 1. Similarity within all other groups was >70%. Together, the copepods *Clausocalanus brevipes, Metridia lucens, Ctenocalanus vanus*, the chaetognath *Eukrohnia hamata* and Ostracods accounted for between 45% and 62.6% of the similarity within all groups. The euphausiid *Thysanoessa vicina* contributed a relatively high percentage to the similarity within groups 1 and 2, which were dominated by Survey 1 stations. Groups 3 and 4 were characterised by the high abundance of *M. lucens*. Group 3 also contained the highest abundance of the copepods *Calanus simillimus, Oithona frigida, Clausocalanus laticeps* and *Scolecithricella minor*.

Table 4.2. Species responsible for 80% of the similarity within the four station groups identified by cluster analysis of MIOS 2 abundance data. Within group similarity is in parenthesis under group number. Cells indicate average species abundance (individuals.m^{-3}) within a group and percentage contribution to within group similarity is in parenthesis.

Group 1 (64.00%)	**Group 2** (70.11%)	**Group 3** (78.98%)	**Group 4** (71.65%)
M. lucens 5.36 (13.40%)	*C. brevipes* 38.82 (20.57%)	*C. simillimus* 38.34 (12.65%)	*M. lucens* 40.83 (16.53%)
Ostracods 4.35 (11.76%)	*M. lucens* 10.85 (14.78%)	*M. lucens* 35.47 (12.00%)	*C. brevipes* 18.04 (13.21%)
Pleuromamma spp. 3.53 (11.66%)	*C. vanus* 14.18 (12.10%)	*O. frigida* 28.28 (10.26%)	*O. frigida* 10.15 (10.96%)
C. brevipes 4.39 (11.15%)	Ostracods 5.81 (11.21%)	*C. vanus* 17.37 (9.65%)	*Pleuromamma* spp. 8.73 (9.98%)
T. vicina 1.75 (8.71%)	*O. frigida* 5.55 (8.27%)	Ostracods 17.02 (8.59%)	*C. vanus* 11.62 (9.45%)
C. vanus 5.32 (8.24%)	*T. vicina* 3.38 (7.68%)	*C. brevipes* 10.08 (7.95%)	Ostracods 5.98 (7.65%)
E. hamata 2.13 (6.86%)	*E. hamata* 1.52 (3.91%)	*E. hamata* 7.35 (6.87%)	*E. hamata* 4.67 (6.90%)
P. abdominalis 1.20 (6.28%)		*C. laticeps* 6.75 (5.64%)	*P. abdominalis* 3.31 (5.27%)
		S. minor 5.23 (3.81%)	

The dissimilarity between groups 4 and 2, and groups 4 and 3, was 35% and 34% respectively. The dissimilarity between all other groups was greater than 40%. The species contributing to dissimilarity between groups were largely the same as those contributing to similarity within groups. *Clausocalanus brevipes, C. laticeps, M. lucens, O. frigida, Pleuromamma abdominalis, C. vanus, C. simillimus, E. hamata, T. vicina* and Ostracods together contributed to between 48.9% and 57.9% of the dissimilarity between groups. The Antarctic copepod *Rhincalanus gigas* (Vervoort, 1951) was an important component of Group 3 contributing to between 6.2% and 7.3% of the dissimilarity between this group and all other groups.

The inverse analysis identified five species clusters at the 35% level of similarity (Figure 4.6.). The first cluster contained species occurring at highest abundance within station Group 3 (Table 4.3.). The second cluster contained the euphausiids *Euphausia vallentini* and *T. vicina*, which occurred at significantly higher abundance within Group 2. The third cluster contained species with no significant group associations, but occurring at highest abundance within Group 4. Clusters 4 and 5 contained species generally occurring at highest abundance within Group 3 although some species were strongly associated with groups 2 and 4. The species within these two clusters were generally widely distributed between stations. Indeed the species *C. brevipes, M. lucens, C. vanus, E. hamata* and Ostracods, identified as contributing to between 45.1% and 62.6% of the similarity within all station groups, all resided within cluster 5.

A number of species' abundance levels had significant negative correlations with surface and integrated temperature (Table 4.4.), including the typically Antarctic copepods *R. gigas* and *O. frigida* (Vervoort, 1951), the copepod *S. minor* and the chaetognaths *S. gazellae* and *E. hamata* which occur at highest abundance in Antarctic waters (David, 1958; Timonin, 1968; Park, 1980). All of these species occurred at highest abundance within Group 3 which was comprised of the two stations conducted in the vicinity of the APF and the station occupied within the cold core eddy. *Ctenocalanus brevipes* abundance was negatively correlated with sounding. This species occurred at highest abundance within Group 2, which contained inter-island and downstream stations from Survey 1 and had a low average sounding (Figure 4.5.). The temperate species *M. lucens* (Gibbons and Hutchings, 1996) was positively correlated with temperature and it occurred at highest abundance within Group 4.

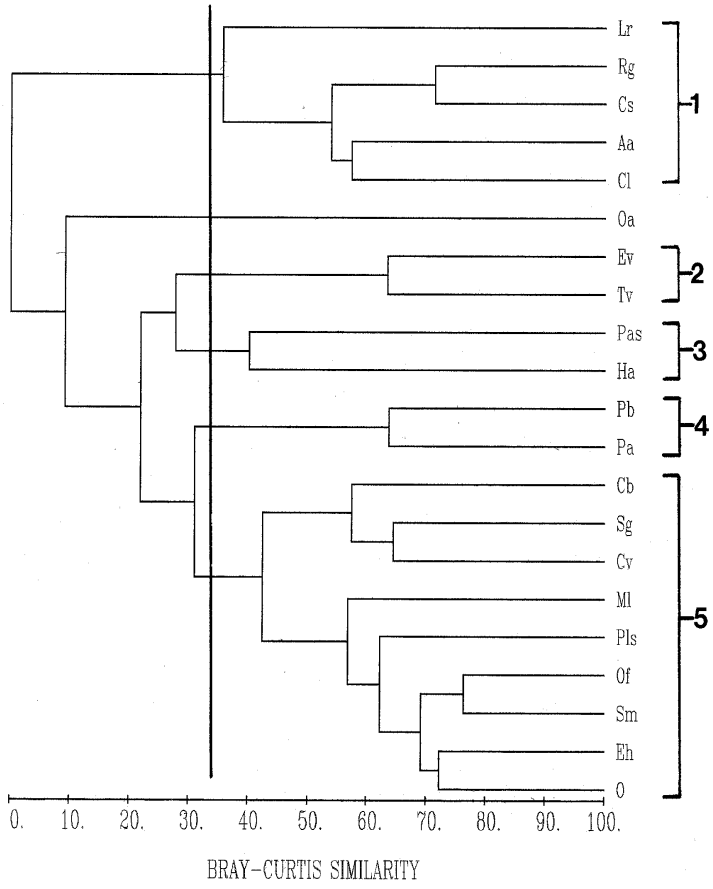


Figure 4.6. Dendrogram of the inverse cluster analysis comparing dominant zooplankton species, identified by SIMPER analysis of MIOS 2 abundance data. The Bray-Curtis similarity measure was used after standardisation of the data set. Abbreviations follow those in Table 4.3.

Table 4.3. Species, abbreviations and names, used in the inverse analysis and the station groups within which each species occurred at highest abundance. Station groups within which a species occurred at significantly higher abundance, determined by group pair comparison using Mann-Whitney U tests, are in bold. Significant differences in the abundance of species between station groups, determined by Kruskal-Wallace tests, are indicated by p (- indicates no significant difference).

Species	**Groups**	**p**
Lr – *Limacina retroversa*	3	-
Rg – *Rhincalanus gigas*	**3**	< 0.001
Cs – *Calanus simillimus*	3	-
Aa – *Aetideus armatus*	3	-
Cl – *Clausocalanus laticeps*	**3**	< 0.01
Oa – *Oncaea antarctica*	**4**	< 0.01
Ev – *Euphausia vallentini*	**2**	< 0.05
Tv – *Thysanoessa vicina*	**2**	< 0.01
Pas – *Paraeuchaeta* spp.	4	-
Ha – *Heterorhabdus austrinus*	4	-
Pb – *Paraeuchaeta biloba*	**3**	< 0.05
Pa – *Pleuromamma abdominalis*	**3**,**4**	< 0.001
Cb – *Clausocalanus brevipes*	**2**	< 0.001
Sg – *Sagitta gazellae*	3	-
Cv – *Ctenocalanus vanus*	3	-
Ml – *Metridia lucens*	**3**	< 0.005
Pls – *Pleuromamma* spp.	**3**	< 0.004
Of – *Oithona frigida*	**3**	< 0.01
Sm – *Scolecithricella minor*	3	-
Eh – *Eukrohnia hamata*	**3**	< 0.05
O – Ostracods	3	-

Table 4.4. Significant regressions of environmental variables against abundance for species contributing most to within group similarity and between group dissimilarity (degrees of freedom = 1.21).

Species	**Variable**	**Beta**	**R^2**	**Adjusted R^2**	**F**	**p**
S. gazellae	Surface temperature	-0.52	0.27	0.23	7.75	< 0.01
	Sounding	-0.49	0.24	0.20	6.49	< 0.05
E. hamata	Surface temperature	-0.69	0.48	0.45	19.36	< 0.005
	Integrated temperature	-0.66	0.43	0.40	15.86	< 0.005
L. retroversa	Surface temperature	-0.67	0.45	0.43	17.32	< 0.005
	Integrated temperature	-0.63	0.39	0.37	13.68	< 0.005
R. gigas	Surface temperature	-0.43	0.19	0.15	4.88	< 0.05
C. simillimus	Surface temperature	-0.49	0.24	0.21	6.67	< 0.05
	Integrated temperature	-0.44	0.20	0.16	5.11	< 0.05
M. lucens	Integrated temperature	0.52	0.27	0.23	7.70	< 0.01
	Chlorophyll *a*	0.81	0.66	0.64	40.88	< 0.005
P. biloba	Surface salinity	-0.60	0.36	0.33	12.04	< 0.005
O. frigida	Surface temperature	-0.47	0.22	0.18	5.92	< 0.01
C. laticeps	Surface temperature	-0.52	0.27	0.23	7.67	< 0.01
C. brevipes	Sounding	-0.48	0.23	0.20	6.39	< 0.05
P. abdominalis	Surface salinity	-0.59	0.35	0.31	11.08	< 0.005
S. minor	Surface temperature	-0.50	0.25	0.21	6.95	< 0.05
	Integrated temperature	-0.42	0.17	0.14	4.44	< 0.05
Ostracods	Surface temperature	-0.54	0.29	0.25	8.50	< 0.01
	Integrated temperature	-0.46	0.21	0.17	5.67	< 0.05

Group 1 was characterised by the high frequency of occurrence of the polychaete *Rhynchonerella* sp. and the copepod *C. falcifera*, as well as the presence of *S. thompsoni* (Table 4.5.). No indicator species were identified within groups 2 and 3. Group 4 was characterised by the high frequency of occurrence of the Antarctic copepod *O. antarctica* (Razouls, 1994), as well as the presence of sub-tropical indicator species including *Cymbulia* sp. (Boltovskoy, 1981), *P. sedentaria* (Vinogrodov *et al*., 1982), *Stemonosudis* sp. (Gon and Heemstra, 1990), *E. similis* var. *armata* (Baker, 1965) and *I. zonaria* (O' Sullivan, 1983).

Table 4.5. Frequency of occurrence of indicator species distinguishing cluster groups. Species above the blank line have $2)I > 6.63$ (p=0.01), and those below the line have $2)I > 3.84$ (p=0.05). Number of samples in a group is in parenthesis below the group number.

Species	**Group 1 (7)**	**Group 2 (8)**	**Group 3 (3)**	**Group 4 (10)**
Rhynchonerella sp.	3	0	0	0
Oncaea antarctica	0	0	0	5
Candacia falcifera	2	0	0	0
Cymbulia sp.	0	0	0	1
Phronima sedentaria	0	0	0	1
Stemonosudis sp.	0	0	0	1
Iasis zonaria	0	0	0	1
Euphausia similis var. *armata*	0	0	0	1
Salpa thompsoni	1	0	0	0

4.3.2. Biomass:

Cluster analysis identified five groups of stations at the 35% level of similarity based on the biomass data (Figure 4.7.). Group 1 contained one inter-island and two downstream stations from Survey 1. Group 2 contained three downstream stations, three inter-island stations and one upstream station from Survey 1, and one upstream station from Survey 2. Group 3 contained two upstream stations from Survey 1, including MS2-1 within the warm water feature south of the SAF, and the upstream station MS2-37 located to the north of the SAF. Group 4 contained three downstream stations and four upstream stations from Survey 1, including MS2-5 at the SAF, and two oceanic stations from Survey 2, including MS2-56 in the vicinity of the SAF. Finally Group 5 contained oceanic stations from Survey 2 including MS2-45 and MS2-48 in the vicinity of the APF, and MS2-76 on the edge of the cold core eddy.
ANOSIM showed that all groups were significantly different from each other ($p<0.05$), with the exception of groups 1 and 3 ($p = 0.1$). Due to the difference in community structure between these two groups (Table 4.7.) they were kept separate for the purpose of this analysis.

Species number, species richness, diversity and surface salinity did not differ significantly between the five station groups identified by cluster analysis (Figure 4.8.a,b,c,e). Group 1 recorded a significantly higher average zooplankton biomass than the other groups, and Group 5 recorded a significantly higher biomass than groups 2 and 3 (Figure 4.8.d). Average surface and integrated temperature did not differ significantly between groups. The highest values were recorded within Group 3 and the lowest within Group 5 (Figure 4.8.f,g). Group 3 had the highest average sounding while the lowest was recorded within groups 1 and 2 (Figure 4.8.h). Average chlorophyll *a* concentrations were significantly higher within groups 1 and 2 than within groups 4 and 5 (Figure 4.8.i).

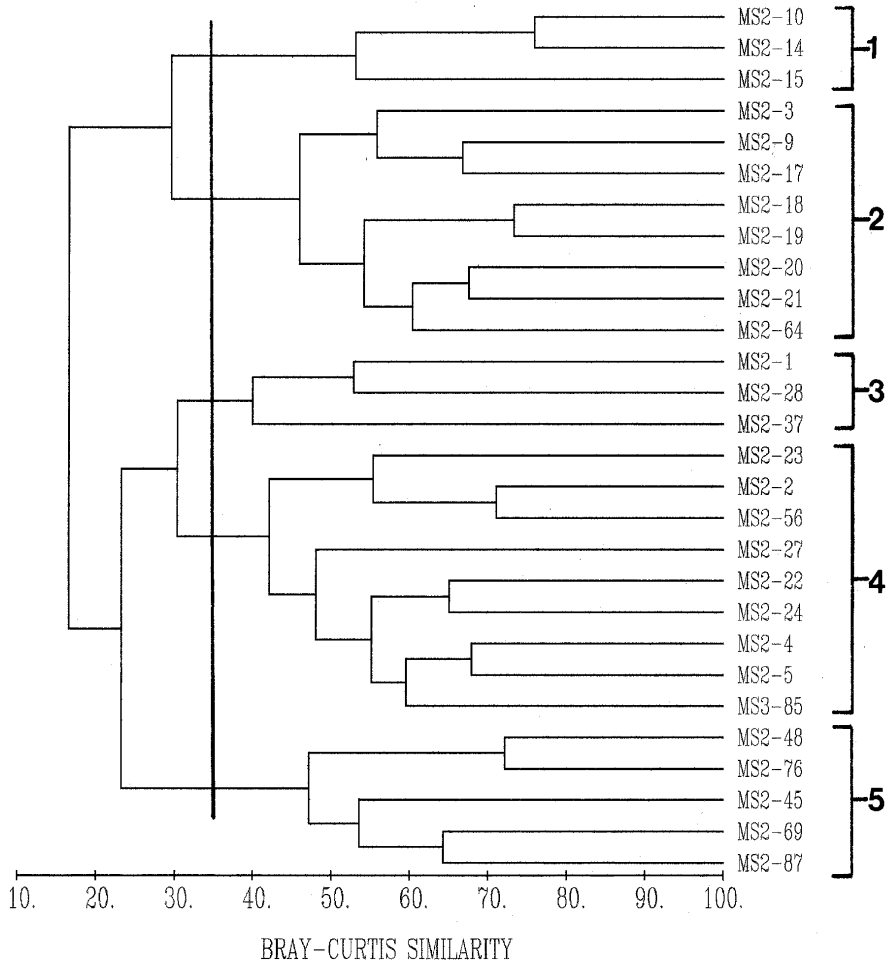
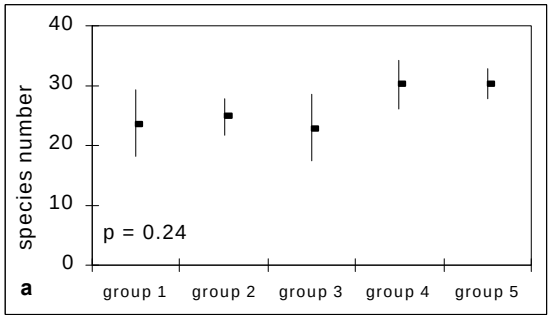
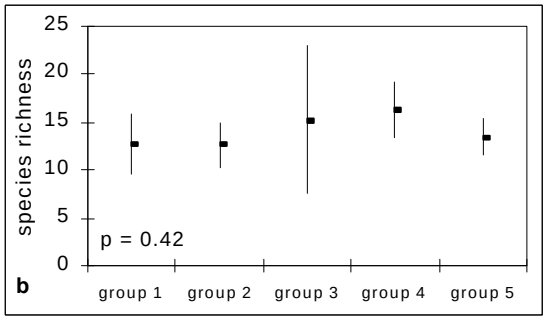


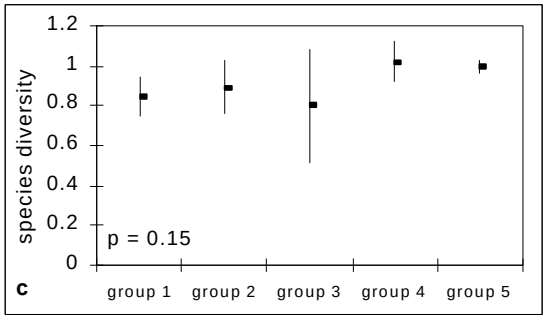
Figure 4.7. Dendrogram of the cluster analysis comparing zooplankton biomass data between stations conducted during MIOS 2. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species biomass data. Station groupings selected for the analysis are bracketed.

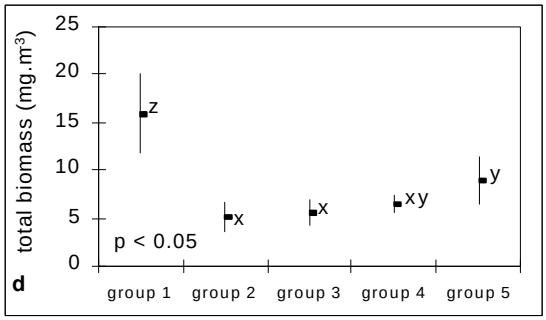
Overleaf:

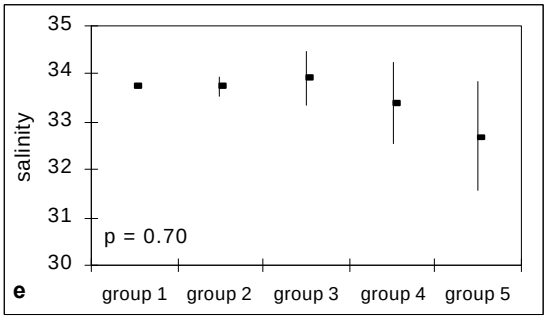
Figure 4.8. Average and standard deviations of variables, recorded for the station groups identified by cluster analysis of MIOS 2 biomass data. The significance level of between group variation, determined using a Kruskal-Wallace test, is indicated on each graph (p-value). Significant differences between station group pairs, determined using a Mann-Whitney U test, are indicated by different letters. Sharing of a letter indicates no significant difference.

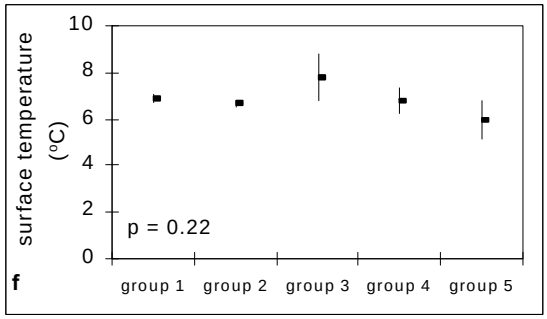

species number
40
30
20
10
0
p = 0.24
a
group 1
group 2
group 3
group 4
group 5

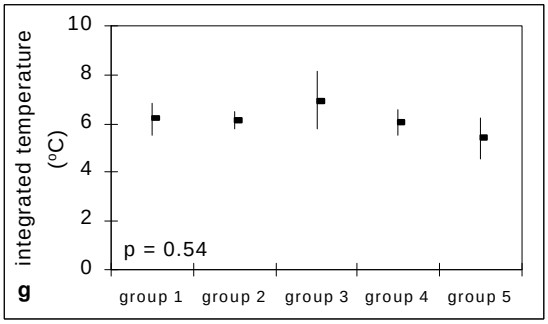

species richness
25
20
15
10
5
0
p = 0.42
b
group 1
group 2
group 3
group 4
group 5

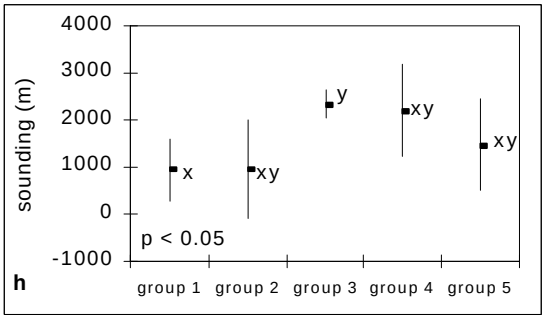

species diversity
1.2
1
0.8
0.6
0.4
0.2
0
p = 0.15
c
group 1
group 2
group 3
group 4
group 5

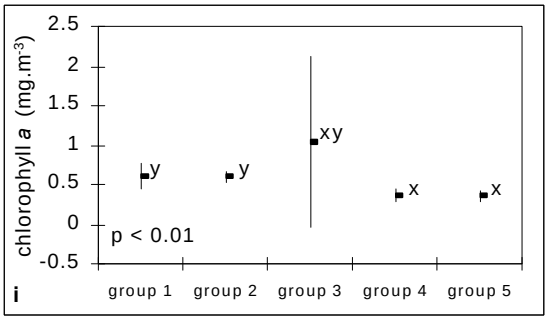

total biomass (mg.m3)
25
20
15
10
5
0
z
x
x
xy
y
p < 0.05
d
group 1
group 2
group 3
group 4
group 5


salinity
35
34
33
32
31
30
p = 0.70
e
group 1
group 2
group 3
group 4
group 5


surface temperature (oC)
10
8
6
4
2
0
p = 0.22
f
group 1
group 2
group 3
group 4
group 5


integrated temperature (oC)
10
8
6
4
2
0
p = 0.54
g
group 1
group 2
group 3
group 4
group 5


sounding (m)
4000
3000
2000
1000
0
-1000
x
xy
y
xy
xy
p < 0.05
h
group 1
group 2
group 3
group 4
group 5


chlorophyll a (mg.m-3)
2.5
2
1.5
1
0.5
0
-0.5
y
y
xy
x
x
p < 0.01
i
group 1
group 2
group 3
group 4
group 5

Integrated temperature accounted for 41% and surface temperature for 36% of the variation in zooplankton biomass data (Table 4.6). No other variables accounted for a significant amount of variation in the biomass data.

Table 4.6. Results of the multiple regression of environmental variables against NMDS ordination scores for MIOS 2 biomass data (stress = 0.17). (degrees of freedom = 2.2)

	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	0.49	0.58	0.45	0.41	8.36	< 0.005
Surface temperature	0.41	0.59	0.42	0.36	7.15	< 0.005
Surface salinity	0.39	0.35	0.22	0.15	2.88	0.08
Sounding	-0.31	0.26	0.19	0.12	2.45	0.11
Chlorophyll *a*	0.29	0.37	0.18	0.09	2.13	0.14

The similarity within Group 1 was dominated by the euphausiids *T. vicina* and *E. vallentini*, with the latter contributing 62.6% to within group similarity (Table 4.7.). *Euphausia vallentini* and *T. vicina* were also an important component of Group 2 contributing 55% to within group similarity. *Nematoscelis megalops* occurred at highest biomass within groups 3 and 4 and contributed substantially to similarity within these two groups. Copepods were an important component of Group 4 as was the euphausiid *E. longirostris*. Similarity within Group 5 was dominated by copepods.

The dissimilarity between all groups was greater than 50%. Euphausiids were important contributors to dissimilarity between groups. *Euphausia longirostris* only occurred within groups 4 and 5, *N. megalops* occurred at highest biomass within Group 3, and *E. vallentini* occurred at highest biomass at the stations over the island shelf (Table 4.8).

Table 4.7. Species responsible for 80% of the similarity within the five station groups identified by cluster analysis of MIOS 2 biomass data. Within group similarity is in parenthesis under group number. Cells indicate average species biomass ($mg.m^{-3}$) within a group and percentage contribution to within group similarity is in parenthesis.

Group 1 (62.08%)	**Group 2** (59.93%)	**Group 3** (47.67%)	**Group 4** (55.69%)	**Group 5** (54.85%)
E. vallentini 9.26 (62.61%)	*E. vallentini* 1.49 (30.69%)	*N. megalops* 0.90 (32.74%)	*N. megalops* 1.00 (16.51%)	*P. abdominalis* 1.20 (13.74%)
T. vicina 1.12 (13.46%)	*T. vicina* 1.10 (24.36%)	*P. biloba* 0.57 (16.67%)	*T. vicina* 0.70 (12.79%)	*P. biloba* 1.03 (12.67%)
	C. brevipes 0.69 (10.44%)	*T. vicina* 0.54 (14.14%)	*E. longirostris* 0.83 (11.38%)	*M. lucens* 0.46 (9.29%)
	C. vanus 0.35 (8.04%)	*E. vallentini* 0.30 (11.24%)	*P. abdominalis* 0.54 (10.66%)	*E. hamata* 0.49 (7.91%)
	Ostracods 0.19 (6.06%)		*Pleuromamma* spp. 0.29 (5.22%)	Ostracods 0.49 (7.67%)
			Ostracods 0.20 (4.93%)	*Pleuromamma* spp. 0.66 (6.75%)
			E. hamata 0.23 (4.34%)	*C. simillimus* 0.83 (5.84%)
			C. brevipes 0.20 (4.32%)	*T. vicina* 0.34 (4.81%)
			M. lucens 0.26 (4.02%)	*C. brevipes* 0.28 (4.58%)
			C. vanus 0.18 (3.68%)	*E. vallentini* 0.30 (4.09%)

Table 4.8. The distribution of *Euphausia longirostris*, *E. vallentini* and *Nematoscelis megalops* biomass ($mg.m^{-3}$) amongst stations identified by cluster analysis.

Group	***E. longirostris***	***E. vallentini***	***N. megalops***
1	0.00	9.26	0.33
2	0.00	1.49	0.05
3	0.00	0.30	0.90
4	0.83	0.31	0.33
5	0.37	0.30	0.35

The inverse analysis identified four species clusters at approximately the 35% level of similarity (Figure 4.9.). The first cluster contained *E. vallentini*, which occurred at

significantly higher biomass within station Group 5, and three copepod species occurring at highest biomass within station groups 1 and 2 (Table 4.9.). The second cluster contained *E. longirostris* and *H. austrinus*, both of which occurred at highest biomass within station Group 4. The third cluster was dominated by species occurring at highest biomass within station Group 5, although some species in this cluster occurred at high biomass levels within station groups 3 and 4, including the euphausiid *N. megalops*. The fourth cluster contained species most strongly associated with station Group 5.

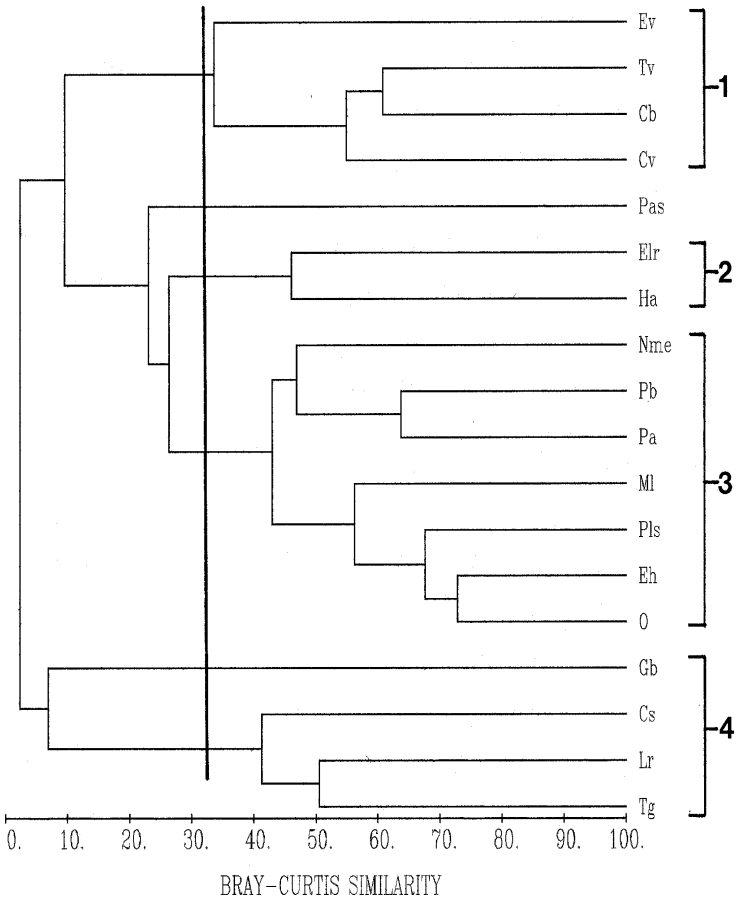


Figure 4.9. Dendrogram of the inverse cluster analysis comparing dominant zooplankton species, identified by SIMPER analysis of MIOS 2 biomass data. The Bray-Curtis similarity measure was used after standardisation of the data set. Abbreviations follow those in Table 4.9.

Table 4.9. Species, abbreviations and names, used in the inverse analysis and the station groups within which each species occurred at highest biomass. Station groups within which a species occurred at significantly higher biomass, determined by group pair comparison using Mann-Whitney U tests, are in bold. Significant differences in the biomass of species between station groups, determined by Kruskal-Wallace tests, are indicated by p (- indicates no significant difference).

Species	**Groups**	**p**
Ev – *Euphausia vallentini*	**5**	< 0.001
Tv – *Thysanoessa vicina*	1	-
Cb – *Clausocalanus brevipes*	1	-
Cv – *Ctenocalanus vanus*	2	-
Pas – *Paraeuchaeta* spp.	4	-
Elr – *Euphausia longirostris*	**4**	< 0.001
Ha – *Heterorhabdus austrinus*	4	-
Nme – *Nematoscelis megalops*	**3,4**	< 0.05
Pb – *Paraeuchaeta biloba*	**5**	< 0.005
Pa – *Pleuromamma abdominalis*	**5**	< 0.005
Ml – *Metridia lucens*	3	-
Pls – *Pleuromamma* spp.	5	-
Eh – *Eukrohnia hamata*	5	-
O – Ostracods	**5**	< 0.05
Gb – *Gymnoscopelus braueri*	5	-
Cs – *Calanus simillimus*	5	-
Lr – *Limacina retroversa*	5	-
Tg – *Themisto gaudichaudii*	5	-

The biomass data for the species *E. hamata, L. retroversa, N. megalops, C. simillimus, M. lucens, P. biloba, C. brevipes, P. abdominalis, S. minor* and Ostracods showed the same relationships with environmental variables as their abundance data (Table 4.10.). *Nematoscelis megalops* biomass had a significant positive correlation with surface temperature. This euphausiid is predominantly a temperate species (Gibbons, 1997) and occurred at highest biomass within Group 3 which also recorded the highest average surface temperature. The hyperiid amphipod *T. gaudichaudii* was negatively correlated with surface temperature and occurred at highest biomass within Group 5.

Table 4.10. Significant regressions of environmental variables against biomass for species contributing most to within group similarity and between group dissimilarity (degrees of freedom = 1.21).

Species	Variable	Beta	R^2	Adjusted R^2	F	P
E. hamata	Surface temperature	-0.70	0.49	0.47	20.20	< 0.001
	Integrated temperature	-0.61	0.37	0.34	15.09	< 0.001
L. retroversa	Surface temperature	-0.62	0.38	0.35	13.07	< 0.001
	Integrated temperature	-0.40	0.16	0.12	4.99	< 0.05
N. megalops	Surface temperature	0.45	0.20	0.16	5.31	< 0.05
C. simillimus	Surface temperature	-0.60	0.36	0.33	11.89	< 0.005
	Integrated temperature	-0.50	0.25	0.22	8.80	< 0.01
M. lucens	Surface temperature	0.55	0.30	0.27	9.12	< 0.01
	Integrated temperature	0.40	0.16	0.13	5.01	< 0.05
	Chlorophyll *a*	0.84	0.71	0.70	51.41	< 0.001
P. biloba	Surface salinity	-0.60	0.36	0.33	12.04	< 0.005
C. brevipes	Sounding	-0.48	0.23	0.20	6.40	< 0.05
P. abdominalis	Surface salinity	-0.59	0.35	0.31	11.08	< 0.005
S. minor	Surface temperature	-0.50	0.25	0.21	6.95	< 0.05
Ostracods	Surface temperature	-0.54	0.29	0.25	8.51	< 0.01
	Integrated temperature	-0.46	0.21	0.18	6.84	< 0.01
T. gaudichaudii	Surface temperature	-0.55	030	0.27	9.15	< 0.01
	Integrated temperature	-0.56	0.31	0.28	11.71	< 0.01

No frequency indicators were identified within groups 1, 2 or 3 (Table 4.11.). Group 4 was characterised by the presence of the tunicate *S. thompsoni*, the sub-tropical indicator species *Cymbulia* sp., *I. zonaria* and *Stemonosudis* sp., as well as a relatively high incidence of *P. choriodon, Scolecithricella* spp. and *C. falcifera*. Group 5 was characterised by the presence of the sub-tropical indicators *P. sedentaria* and *E. similis* var. *armata*.

Table 4.11. Frequency of occurrence of indicator species distinguishing cluster groups. Species above the blank line have $2)I > 6.63$ (p=0.01), and those below the line have $2)I > 3.84$ (p=0.05). Number of samples in a group is in parenthesis below the group number.

Species	**Group 1 (3)**	**Group 2 (8)**	**Group 3 (3)**	**Group 4 (9)**	**Group 5 (5)**
Protomyctophum choriodon	0	0	0	2	0
Scolecithricella spp.	0	0	0	2	0
Candacia falcifera	0	0	0	2	0
Cymbulia sp.	0	0	0	1	0
Phronima sedentaria	0	0	0	0	1
Salpa thompsoni	0	0	0	1	0
Iasis zonaria	0	0	0	1	0
Stemonosudis sp.	0	0	0	1	0
Euphausia similis var. *armata*	0	0	0	0	1

Chapter 5

RESULTS: MIOS 3 (1998)

5.1. Oceanography:

En route to the PEIs the SAF was encountered at approximately 45°45'S on 5 April (Figure 5.1.a). By the time of the northern transect on 15 April the SAF had moved 25 nautical miles further northwards to be located at approximately 45°20'S (Figure 5.1.b). On the return leg to Cape Town the SAF was located at 45°30'S, on 8 May (Figure 5.1.c), having moved ten nautical miles southwards.

5.2. Chlorophyll *a*:

For the analysis of chlorophyll *a* distribution samples collected in conjunction with both day and night net tows were used. During MIOS 3 total chlorophyll *a* concentrations in the upstream, downstream and inter-island regions averaged 0.20 $mg.m^{-3}$, 0.25 $mg.m^{-3}$ and 0.22 $mg.m^{-3}$ respectively (Figure 5.2.). A Kruskal-Wallace test showed that both microphytoplankton and total chlorophyll *a* concentrations differed significantly between regions ($p<0.001$). A Mann-Whitney U test showed that both occurred at significantly ($p<0.05$) higher concentrations within the inter-island region than the regions upstream or downstream of the islands.

Continued on page…64

Overleaf:

Figure 5.1. XBT Temperature sections along 37°E during MIOS 3. The position of the SAF was determined by the position of the 7°C isotherm at 100m. (a) Cape Town to PEI underway transect; (b) northern transect; (c) PEI to Cape Town underway transect. Figure taken from Pakhomov *et al*. (in press).

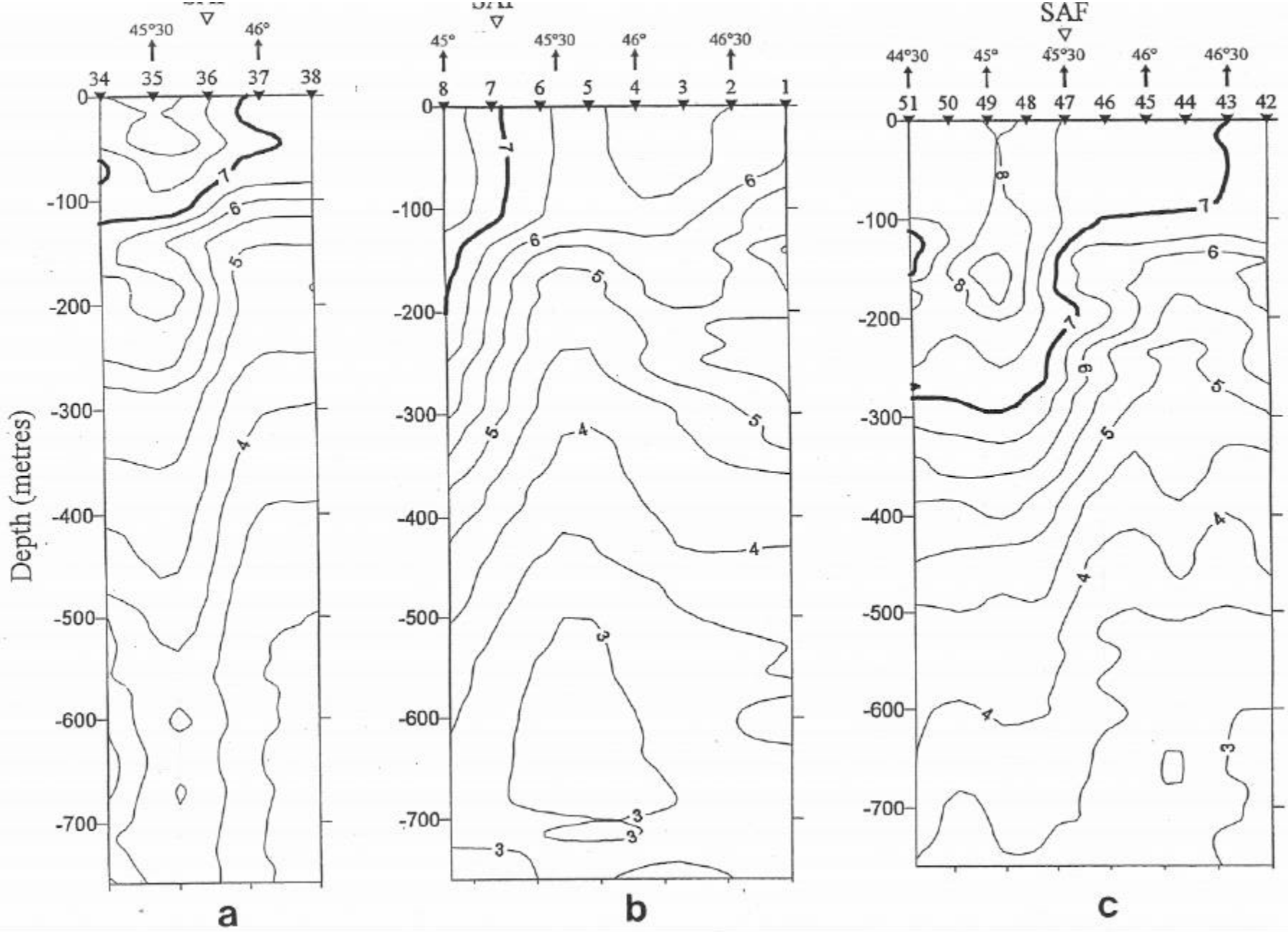

SAF
45°30
46°
34 35 36 37 38
45°
45°30
46°
46°30
8 7 6 5 4 3 2 1
44°30
45°
45°30
46°
46°30
51 50 49 48 47 46 45 44 43 42
Depth (metres)
0
-100
-200
-300
-400
-500
-600
-700
a
b
c

Figure 5.2. Size fractionated chlorophyll *a* concentrations corresponding with net tows during MIOS 3. Regions discussed in the analysis are bracketed

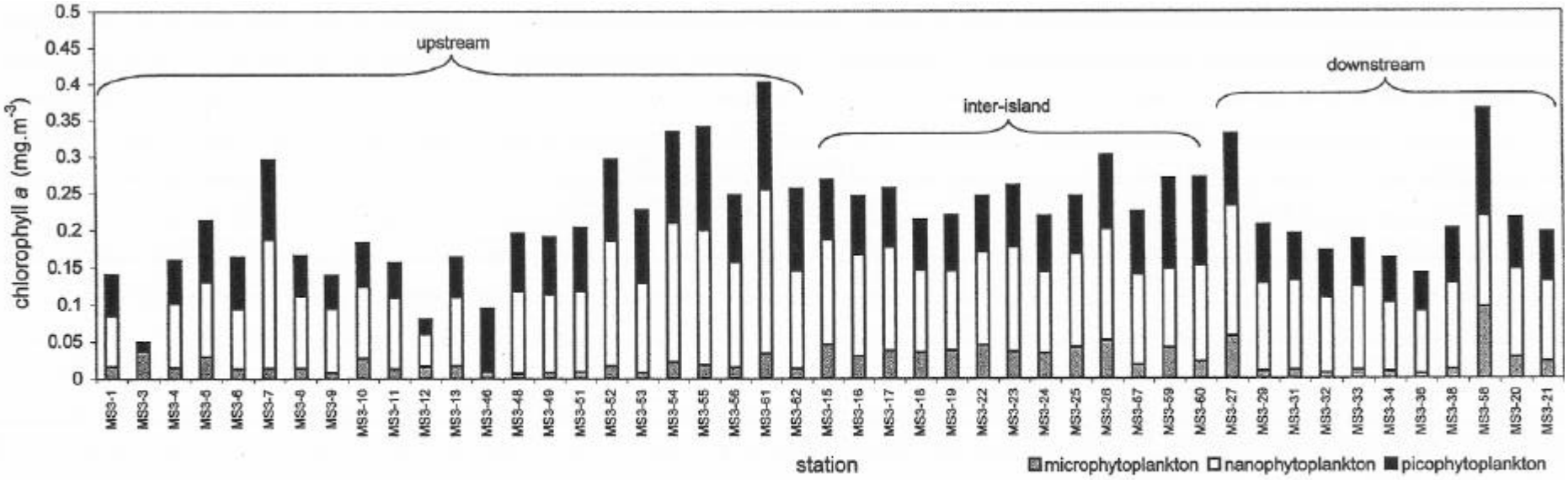


Figure 5.2. Size fractionated chlorophyll *a* concentrations corresponding with net tows conducted during MIOS 3. Regions discussed in the analysis are bracketed.

5.3. Zooplankton:

5.3.1. Abundance:

Four station clusters were identified at approximately the 50% level of similarity, with station MS3-23 being an outlier (Figure 5.3.). Initial analysis showed that there was no significant difference ($p>0.05$) in zooplankton abundance data between the stations MS3-23, MS3-18, MS3-4, MS3-5, MS3-58, MS3-6 and MS3-10. These stations were consequently merged as Group 1 for the remainder of the analysis, giving a total of three station groups. Group 1 contained the four most northerly upstream stations, one downstream station and two inter-island stations. Group 2 contained two upstream stations, two downstream stations and five inter-island stations. Finally, Group 3 contained six upstream stations, three downstream stations and three inter-island stations. ANOSIM showed that all station groupings were significantly different from one another ($P<0.001$).

There was no significant difference in the number of species recorded within the three station groups, although species richness was significantly lower within Group 2 than within groups 1 and 3 (Figure 5.4.a,b). Diversity was significantly lower within Group 1 than within groups 2 and 3 (Figure 5.4.c). Average total zooplankton abundance was highest within Group 2 (Figure 5.4.d). The large standard deviation recorded for Group 2 was due to the extremely high abundance levels at the downstream station MS3-34 (449.83 individuals.m^{-3}). There was no significant difference in surface salinity, surface temperature and integrated temperature between station groups, but the highest values were recorded within Group 1 (Figure 5.4.e,f,g). Sounding and chlorophyll *a* showed no significant difference between station groups (Figure 5.4.h,i).

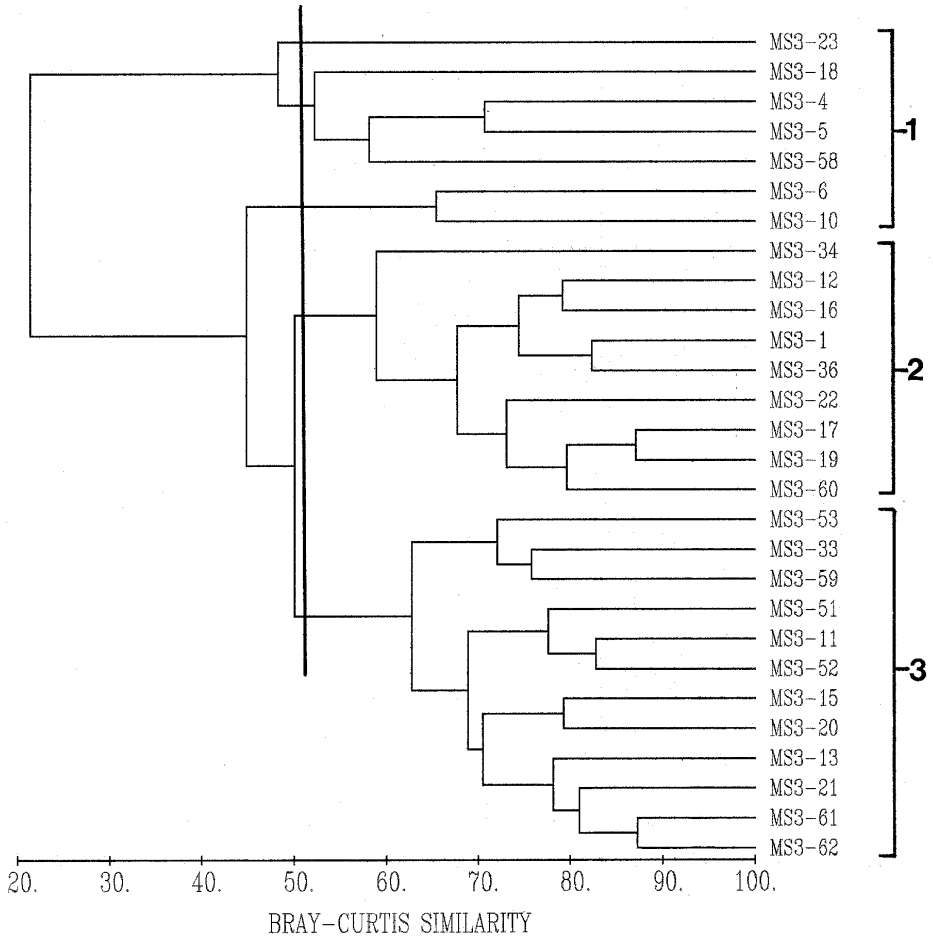
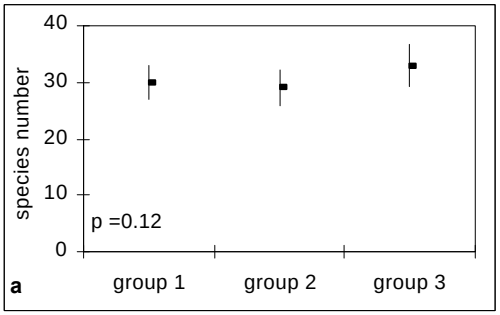
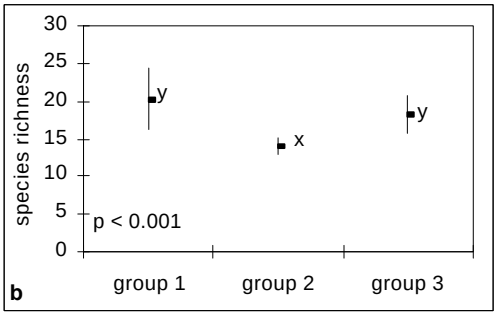


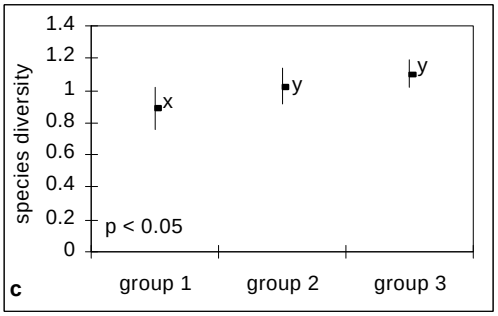
Figure 5.3. Dendrogram of the cluster analysis comparing zooplankton abundance data between stations conducted during MIOS 3. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species abundance data. Station groupings used in the analysis are bracketed.

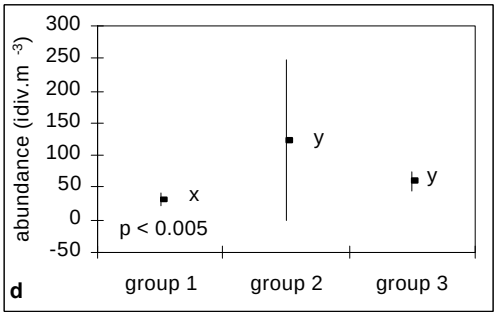
Overleaf:

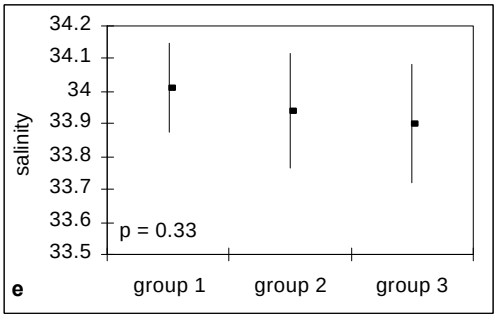
Figure 5.4. Average and standard deviations of variables, recorded for the station groups identified by cluster analysis of MIOS 3 abundance data. The significance level of between group variation, determined using a Kruskal-Wallace test, is indicated on each graph (p-value). Significant differences between station group pairs, determined using a Mann-Whitney U test, are indicated by different letters. Sharing of a letter indicates no significant difference.

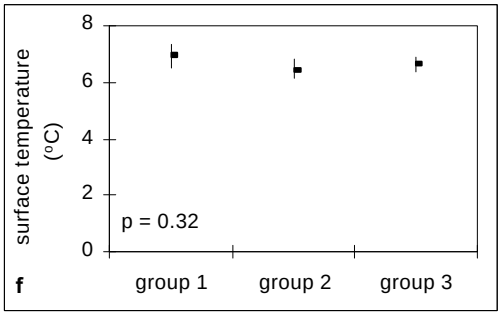

species number
40
30
20
10
0
p =0.12
a
group 1
group 2
group 3

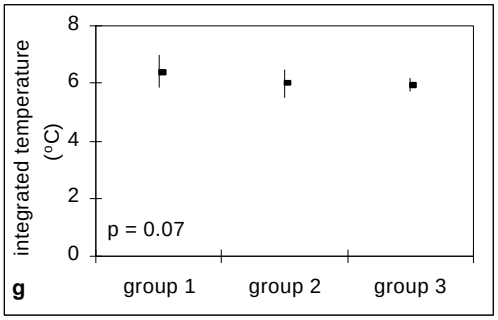

species richness
30
25
20
15
10
5
0
y
x
y
p < 0.001
b
group 1
group 2
group 3

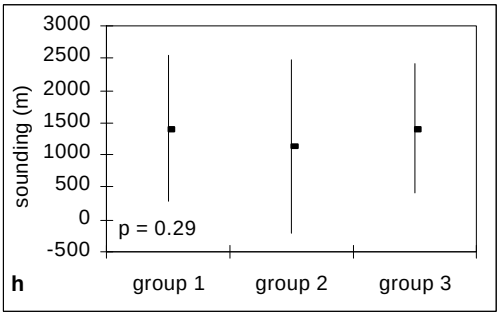

species diversity
1.4
1.2
1
0.8
0.6
0.4
0.2
0
x
y
y
p < 0.05
c
group 1
group 2
group 3

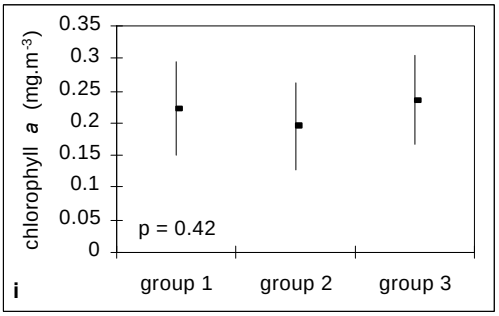

abundance (idiv.m -3)
300
250
200
150
100
50
0
-50
x
y
y
p < 0.005
d
group 1
group 2
group 3


salinity
34.2
34.1
34
33.9
33.8
33.7
33.6
33.5
p = 0.33
e
group 1
group 2
group 3


surface temperature (°C)
8
6
4
2
0
p = 0.32
f
group 1
group 2
group 3


integrated temperature (°C)
8
6
4
2
0
p = 0.07
g
group 1
group 2
group 3


sounding (m)
3000
2500
2000
1500
1000
500
0
-500
p = 0.29
h
group 1
group 2
group 3


chlorophyll a (mg.m-3)
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
p = 0.42
i
group 1
group 2
group 3

Surface temperature accounted for a 22% of the variation in the zooplankton abundance data, and sounding accounted for 27% (Table 5.1.). No other variables accounted for a significant amount of variation in zooplankton abundance data.

Table 5.1. Results of the multiple regression analysis of environmental variables against NMDS ordination scores for MIOS 3 abundance data (stress = 0.13). (degrees of freedom = 2.2)

	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	-0.21	-0.12	0.06	-0.02	0.76	0.48
Surface temperature	-0.53	0.05	0.28	0.22	4.30	< 0.05
Surface salinity	-0.01	-0.26	0.07	-0.01	0.83	0.45
Sounding	-0.46	0.41	0.33	0.27	5.34	< 0.01
Chlorophyll *a*	0.30	-0.15	0.10	0.02	1.24	0.31

Group 1 had a within group similarity of 52.6% while groups 2 and 3 had within group similarities of greater than 70% (Table 5.2.). The species *L. retroversa, C. brevipes, C. vanus, S. gazellae, E. hamata, T. vicina* and Ostracods accounted for greater than 60 % of the similarity within all groups. The pteropod *L. helicina* and euphausiid *E. vallentini* contributed 5.3% and 4.8% respectively to the similarity within Group 1. The copepods *O. frigida* and *M. lucens* contributed 6.7% and 6% to similarity within Group 2, while *M. lucens* and *S. minor* contributed 7.2% and 4.9% to similarity within Group 3

The percentage dissimilarity between groups 2 and 1 and groups 3 and 1 were 48.3% and 47.3% respectively. The average dissimilarity between groups 2 and 3 was relatively low at 30.4%, indicating a high degree of similarity between these two groups.

Greater than 70% of the dissimilarity between all three groups was accounted for by the same thirteen species indicating a high degree of homogeneity in the zooplankton community. These included the copepods *C. vanus, C. simillimus, C. brevipes, O. frigida, M. lucens, C. laticeps, S. minor, O. similis*, the chaetognath *E. hamata*, the euphausiid *T. vicina*, the pteropod *L. retroversa*, and Ostracods.

Table 5.2. Species responsible for 80% of the similarity within the three station groups identified by cluster analysis of MIOS 3 abundance data. Within group similarity is in parenthesis under group number. Cells indicate average species abundance (individuals.m^{-3}) within a group and percentage contribution to within group similarity is in parenthesis.

Group 1 (52.58%)	**Group 2** (72.9%)	**Group 3** (73.95%)
L. retroversa 8.24 (17.75%)	*C. vanus* 12.63 (11.98%)	*C. brevipes* 12.51 (13.94%)
T. vicina 2.77 (13.5%)	*L. retroversa* 16.76 (11.78%)	*C. vanus* 6.61 (10.20%)
Ostracods 2.65 (13.29%)	*C. brevipes* 14.10 (11.65%)	*E. hamata* 5.91 (9.91%)
C. brevipes 4.25 (10.25%)	Ostracods 7.93 (8.20%)	Ostracods 4.96 (9.57%)
C. vanus 1.5 (6.73%)	*T. vicina* 5.17 (7.25%)	*M. lucens* 4.16 (7.2%)
L. helicina 1.19 (5.26%)	*O. frigida* 3.46 (6.7%)	*C. simillimus* 2.37 (5.77%)
S. gazellae 0.65 (5.18%)	*C. simillimus* 33.88 (6.37%)	*T. vicina* 2.28 (5.46%)
E. vallentini 0.82 (4.79%)	*M. lucens* 4.96 (6%)	*L. retroversa* 3.27 (5.09%)
	E. hamata 6.40 (5.95%)	*S. minor* 2.40 (4.91%)
		S. gazellae 1.56 (4.74%)

The inverse analysis identified 5 species clusters at the 50% level of similarity (Figure 5.5.). Cluster 1 contained species with no specific group associations (Table 5.3.). Cluster 2 contained species occurring at highest abundance within station Group 3. Cluster 3 contained the pteropods *L. retroversa* and *L. helicina,* which occurred at significantly higher abundance within station Group 2. Clusters 4 and 5 contained species that occurred at highest abundance within station groups 2 and 3. This included the typically Antarctic species' *E. hamata, S. minor, O. frigida* and *S. gazellae* (Vervoort, 1951; David, 1958; Timonin, 1968; Park, 1980; Razouls, 1994), the sub-Antarctic species' *C. laticeps, C. brevipes, C. vanus* (Vervoort, 1951; De Decker, 1984; Guglielmo and Ianora, 1995), and the temperate species *M. lucens* (Gibbons and Hutchings, 1996). *Calanus*

simillimus was identified as an outlier, and occurred at highest abundance within station Group 2.

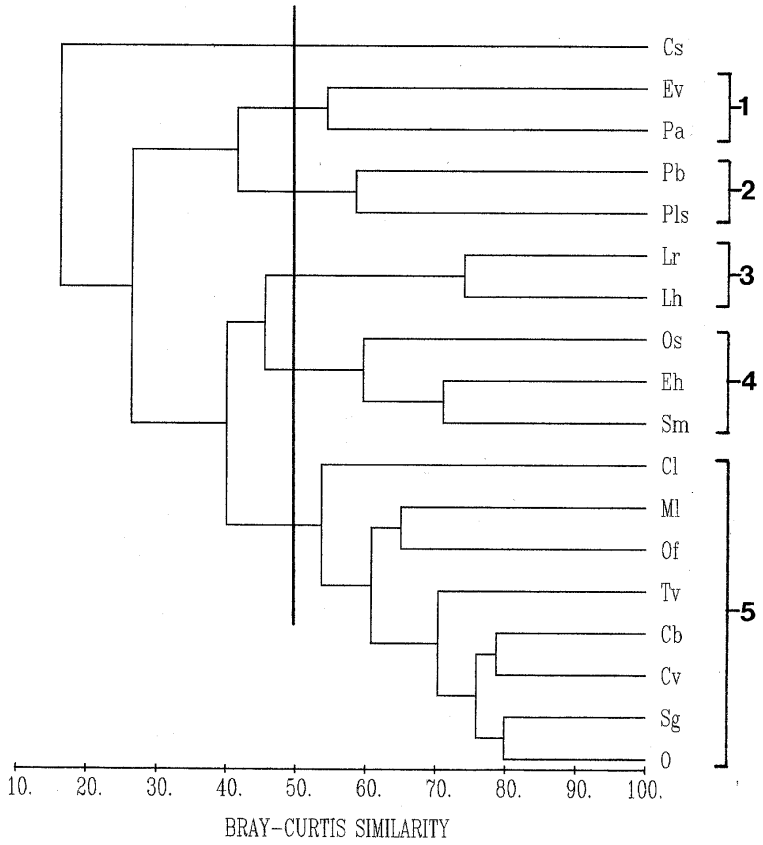


Figure 5.5. Dendrogram of the inverse cluster analysis comparing dominant zooplankton species, identified by SIMPER analysis of abundance data. The Bray-Curtis similarity measure was used after standardisation of the data set. Abbreviations follow those in Table 5.3.

Table 5.3. Species, abbreviations and names, used in the inverse analysis and the station groups within which each species occurred at highest abundance. Station groups within which a species occurred at significantly higher abundance, determined by group pair comparison using Mann-Whitney U tests, are in bold. Significant differences in the abundance of species between station groups, determined by Kruskal-Wallace tests, are indicated by p (- indicates no significant difference).

Species	**Group**	**p**
Cs – *Calanus simillimus*	**2**	< 0.01
Ev – *Euphausia vallentini*	1	-

Table 5.3. continued		
Species	**Group**	**p**
Pa – *Pleuromamma abdominalis*	3	-
Pb – *Paraeuchaeta biloba*	3	-
Pls – *Pleuromamma* spp.	3	-
Lr – *Limacina retroversa*	**2**	< 0.001
Lh – *Limacina helicina*	**2**	< 0.01
Os – *Oithona similis*	3	-
Eh – *Eukrohnia hamata*	3	-
Sm – *Scolecithricella minor*	**3**,**2**	< 0.05
Cl – *Clausocalanus laticeps*	3	-
Ml – *Metridia lucens*	2	-
Of – *Oithona frigida*	**3**	< 0.005
Tv – *Thysanoessa vicina*	2	-
Cb – *Clausocalanus brevipes*	2	-
Cv – *Ctenocalanus vanus*	**2**	< 0.001
Sg – *Sagitta gazellae*	2	-
O – Ostracods	2	-

Eukrohnia hamata abundance had a significant negative correlation with integrated temperature (Table 5.4.). This chaetognath occurred at highest abundance within groups 2 and 3, both of which had lower average integrated temperatures than Group 1 (Figure 5.4.). The predominantly Antarctic copepod *S. minor* (Park, 1980) was negatively correlated with integrated temperature and surface salinity and occurred at significantly higher abundance within groups 2 and 3 (Table 5.3.). *Euphausia vallentini* and *P. abdominalis* were both positively correlated with sounding while the copepod *C. brevipes* was positively correlated with chlorophyll *a*.

Table 5.4. Significant regressions of environmental variables against abundance for species contributing most to within group similarity and between group dissimilarity (degrees of freedom = 1.23).

Species	**Variable**	**Beta**	**R^2**	**Adjusted R^2**	**F**	**p**
E. hamata	Integrated temperature	-0.58	0.34	0.31	11.58	< 0.005
E. vallentini	Sounding	0.46	0.21	0.18	6.20	< 0.05
P. abdominalis	Sounding	0.51	0.26	0.22	7.86	< 0.01
C. brevipes	Chlorophyll *a*	0.43	0.19	0.15	5.23	< 0.05
S. minor	Integrated temperature	-0.50	0.25	0.22	7.83	< 0.01
	Surface salinity	-0.49	0.24	0.21	7.17	< 0.01

Group 1 was characterised by the complete absence of Antarctic indicator species and a high incidence of subtropical indicator species, including the hyperiids *P. sedentaria* and *C. magellanicus* (Vinogrodov *et al*., 1982), and the subtropical fish *Stemonosudis* sp. (Gon and Heemstra, 1990) (Table 5.5.). Groups 2 and 3 were characterised by the high frequency of occurrence of the siphonophore *D. arctica* and the presence of *S. thompsoni* and *T. mullerei*. Group 3 also recorded a high frequency of the sub-Antarctic and Antarctic copepod *O. cristatus* (Razouls, 1994) and the polychaete *T. lobifera*, as well as the presence of the sub-tropical hyperiid *P. sedentaria* and tunicate *I. zonaria* (O'Sullivan, 1983).

Table 5.5. Frequency of occurrence of indicator species distinguishing cluster groups. Species above the blank line have $2)I > 6.63$ (p=0.01), and those below the line have $2)I > 3.84$ (p=0.05). Number of samples in a group is in parenthesis below the group number.

Species	**Group 1 (7)**	**Group 2 (9)**	**Group 3 (12)**
Onchocalanus cristatus	0	0	3
Travisiopsis lobifera	0	0	2
Salpa thompsoni	0	1	3
Dimophyes arctica	1	7	11
Phronima sedentaria	2	0	1
Cyllopus magellanicus	1	0	0
Typhloscolex mullerei	0	2	1
Iasis zonaria	0	0	1
Stemonosudis sp.	1	0	0

5.3.2 Biomass:

Three station groupings were identified at approximately the 25% level of similarity (Figure 5.6.). Group 1 contained five upstream stations, including three of the four stations north of 46°30'S, as well as one inter-island station and two downstream stations. Group 2 contained three inter-island stations and one downstream station. Group 3 contained eight upstream stations, three downstream stations and five inter-island stations.

ANOSIM showed that all stations were significantly different from each other ($p<0.01$).

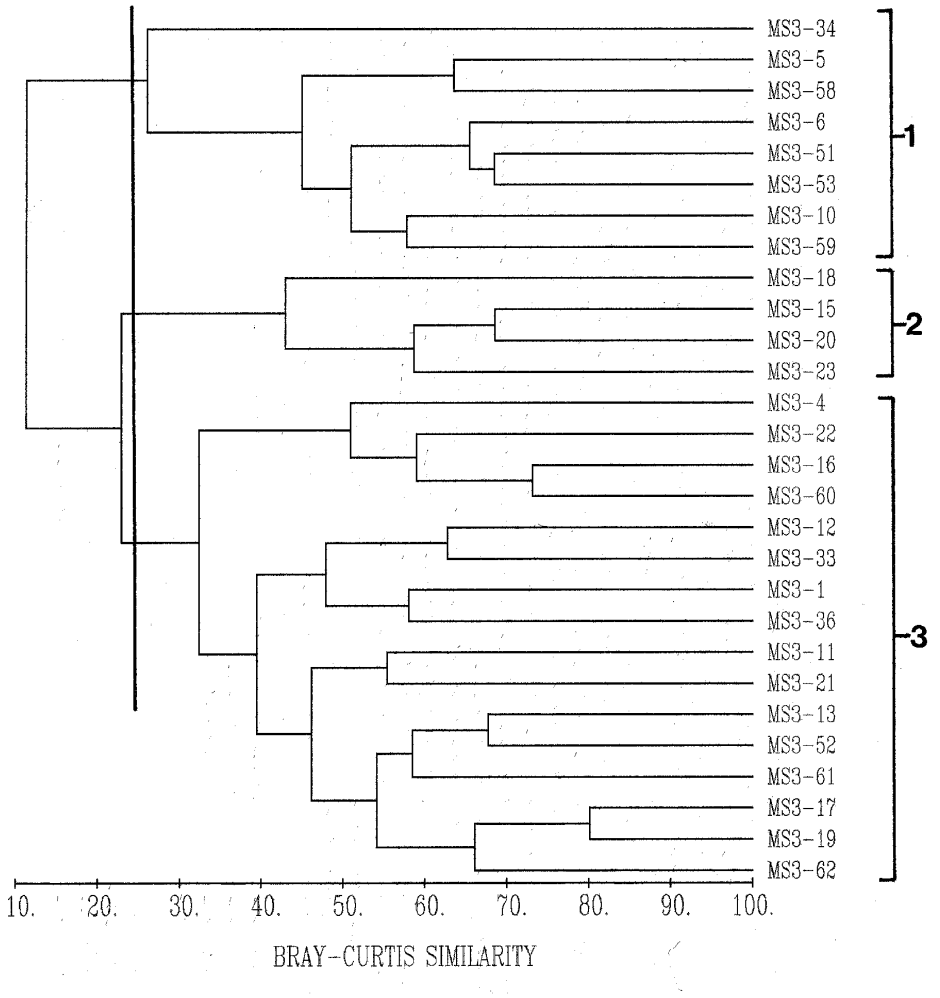


Figure 5.6. Dendrogram of the cluster analysis comparing zooplankton biomass data between stations conducted during MIOS 3. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species biomass data. Station groupings selected for the analysis are bracketed.

The highest number of species was recorded within Group 1 (Figure 5.7.a). Total zooplankton biomass recorded for Group 3 was significantly higher than within Group 2 (Figure 5.7.d). Sounding was significantly lower within Group 2 than within Group 1 (Figure 5.7.h). No other variables differed significantly between station groups.

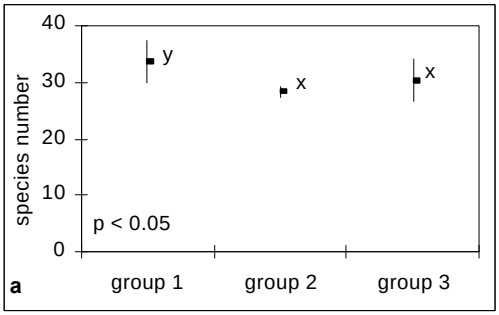
Sounding accounted for 19% of the variation in zooplankton biomass data (Table 5.6.). No other variable accounted for a significant amount of variation in zooplankton biomass data.

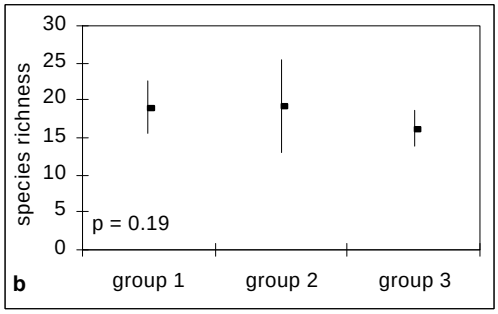
Table 5.6. Results of the multiple regression analysis of environmental variables against NMDS ordination scores for MIOS 3 biomass data (stress = 0.19). (degrees of freedom = 2.2).

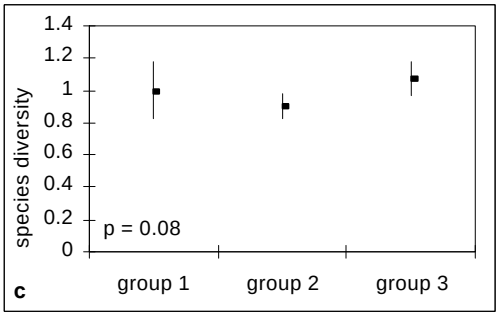
	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	0.18	-0.02	0.03	-0.06	0.36	0.70
Surface temperature	-0.17	-0.03	0.69	-0.06	0.37	0.69
Surface salinity	0.22	0.03	0.05	-0.04	0.59	0.56
Sounding	-0.52	0.11	0.26	0.19	3.78	< 0.05
Chlorophyll *a*	0.18	-0.14	0.04	-0.05	0.47	0.63

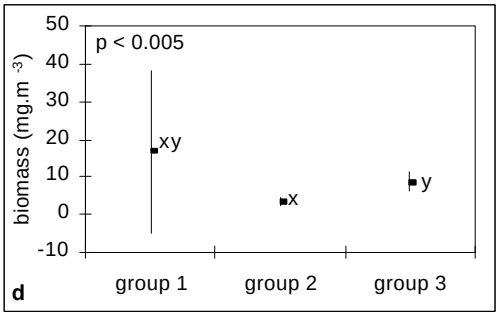
Overleaf:

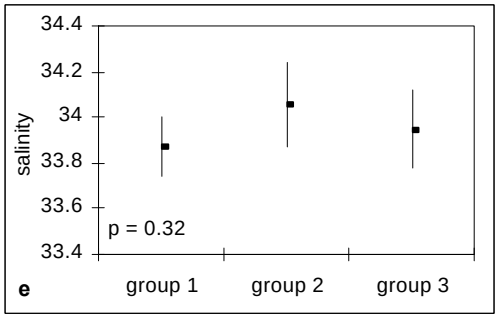
Figure 5.7. Average and standard deviations of variables, recorded for the station groups identified by cluster analysis of MIOS 3 biomass data. The significance level of between group variation, determined using a Kruskal-Wallace test, is indicated on each graph (p-value). Significant differences between station group pairs, determined using a Mann-Whitney U test, are indicated by different letters. Sharing of a letter indicates no significant difference.

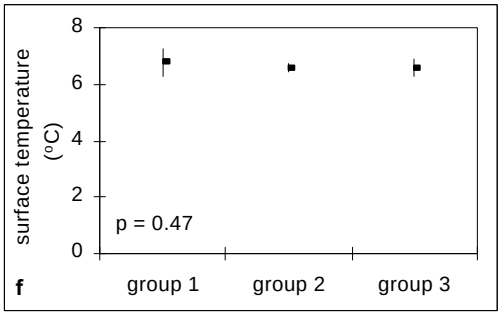

species number
40
30
20
10
0
y
x
x
p < 0.05
a
group 1
group 2
group 3

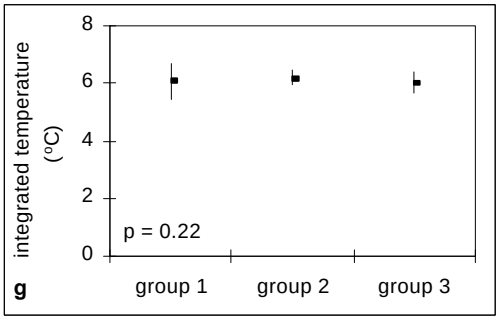

species richness
30
25
20
15
10
5
0
p = 0.19
b
group 1
group 2
group 3

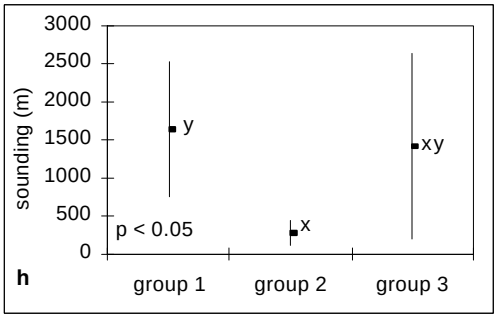

species diversity
1.4
1.2
1
0.8
0.6
0.4
0.2
0
p = 0.08
c
group 1
group 2
group 3

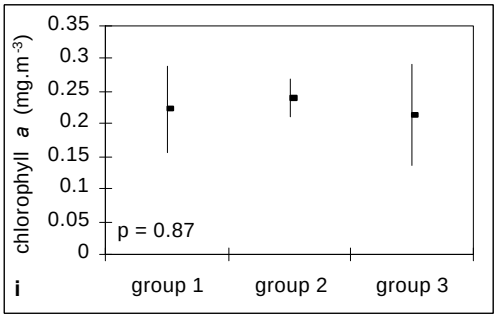

biomass (mg.m -3)
50
40
30
20
10
0
-10
p < 0.005
xy
x
y
d
group 1
group 2
group 3


salinity
34.4
34.2
34
33.8
33.6
33.4
p = 0.32
e
group 1
group 2
group 3


surface temperature (°C)
8
6
4
2
0
p = 0.47
f
group 1
group 2
group 3


integrated temperature (°C)
8
6
4
2
0
p = 0.22
g
group 1
group 2
group 3


sounding (m)
3000
2500
2000
1500
1000
500
0
y
xy
x
p < 0.05
h
group 1
group 2
group 3


chlorophyll a (mg.m-3)
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
p = 0.87
i
group 1
group 2
group 3

The average similarity within groups was 50.7%, 54.3% and 52.8% within groups 1, 2 and 3 respectively (Table 5.7.). Group 1, dominated by upstream oceanic stations, had a high biomass of *E. vallentini,* contributing 41.1% to the similarity within this group. The euphausiids *T. vicina, N. megalops* and *E. longirostris* contributed 11.1%, 7.2% and 3.5% respectively to within group similarity. Group 2 was dominated by relatively few species. Together *L. retroversa*, *P. macropa* and *T. vicina* contributed to over 60% of the similarity within this group. Euphausiids occurred at low densities within Group 2. Their total biomass amounted to 0.64 mg dry wt.m^{-3}. The highest contributors to similarity within Group 3 were, in order of importance, *T. vicina, P. macropa* and *L. retroversa.*

Table 5.7. Species responsible for 80% of the similarity within the three station groups identified by cluster analysis of MIOS 3 biomass data. Within group similarity is in parenthesis under group number. Cells indicate average species biomass (mg.m^{-3}) within a group and percentage contribution to within group similarity is in parenthesis.

Group 1 (50.70%)	**Group 2** (54.26%)	**Group 3** (52.81%)
E. vallentini 4.16 (41.06%)	*L. retroversa* 0.65 (29.62%)	*T. vicina* 1.34 (19.69%)
T. vicina 0.81 (11.08%)	*P. macropa* 0.58 (16.68%)	*P. macropa* 0.88 (15.66%)
N. megalops 0.57 (7.21%)	*T. vicina* 0.25 (16.67%)	*L. retroversa* 1.37 (13.6%)
P. abdominalis 0.41 (4.94%)	*C. brevipes* 0.25 (7.69%)	*E. vallentini* 0.93 (8.95%)
P. macropa 0.95 (4.89%)	*Protomyctophum* spp. 0.22 (5.79%)	*E. hamata* 0.43 (6.11%)
L. retroversa 1.26 (4.07%)		*C. simillimus* 0.55 (4.82%)
E. longirostris 0.42 (3.5%)		*C. brevipes* 0.23 (4.64%)
Ostracods 0.25 (2.98%)		*C. vanus* 0.18 (4.04%)

The average dissimilarity between groups 2 and 1 was 67.4%. The dissimilarity between groups 3 and 1 and groups 3 and 2 was greater than 55%. Euphausiids were an important component of the biomass analysis contributing to between 21% and 39.4% of the

dissimilarity between groups. Group 1 was characterised by a relatively high biomass of the sub-Antarctic species *Euphausia similis* (Baker, 1965), and the predominantly temperate species *N. megalops* (Gibbons, 1995).

The inverse analysis identified three species clusters at the 40% level of similarity (Figure 5.8.). The first and second clusters contained a mix of species with varying station group associations (Table 5.8.). The third cluster was dominated by euphausiids, containing *E. vallentini*, *E. longirostris* and *N. megalops*, all of which occurred at highest abundance within station Group 1. Also within cluster 3 were the copepod *P. abdominalis* and the decapod *N. marionis.* The latter occurred at highest biomass within station Group 3.

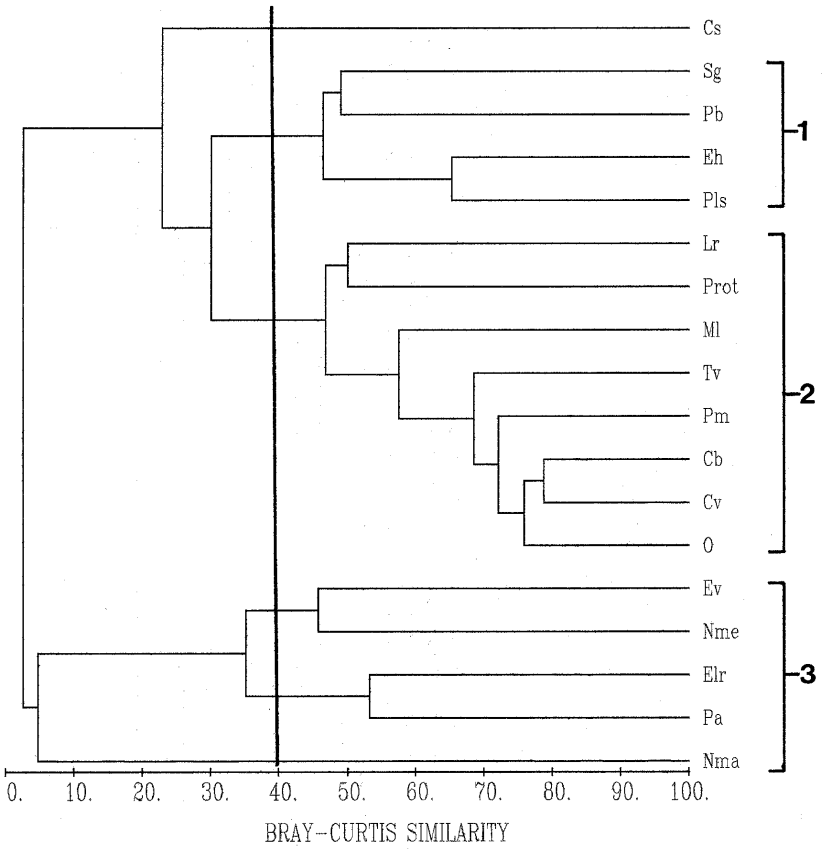


Figure 5.8. Dendrogram of the inverse cluster analysis comparing dominant zooplankton species, identified by SIMPER analysis of biomass data. The Bray-Curtis similarity measure was used after standardisation of the data set. Abbreviations follow those in Table 5.8.

Table 5.8. Species, abbreviations and names, used in the inverse analysis and the station groups within which each species occurred at highest biomass. Station groups within which a species occurred at significantly higher biomass, determined by group pair comparison using Mann-Whitney U tests, are in bold. Significant differences in the biomass of species between station groups, determined by Kruskal-Wallace tests, are indicated by p (- indicates no significant difference).

Species	**Group**	**p**
Cs – *Calanus simillimus*	1	-
Sg – *Sagitta gazellae*	3	-
Pb – *Paraeuchaeta biloba*	1	-
Eh – *Eukrohnia hamata*	1	-
Pls – *Pleuromamma sp.*	**1**	< 0.05
Lr – *Limacina retroversa*	3	-
Prot – *Protomyctophum sp.*	2	-
Ml – *Metridia lucens*	1	-
Tv – *Thysanoessa vicina*	**3**	< 0.001
Pm – *Primno macropa*	**1**	< 0.05
Cb – *Clausocalanus brevipes*	2	-
Cv – *Ctenocalanus vanus*	3	-
O – Ostracod	1	-
Ev – *Euphausia vallentini*	**1**	< 0.001
Nme – *Nematoscelis megalops*	**1**	< 0.01
Elr – *Euphausia longirostris*	1	-
Pa – *Pleuromamma abdominalis*	**1**	< 0.01
Nma – *Nauticaris marionis*	3	-

The biomass data for *E. hamata, P. abdominalis* and *C. brevipes* had similar relationships with environmental data to those identified by the abundance data (Table 5.9.). *Calanus simillimus* biomass was negatively correlated with sea surface temperature, and *Protomyctophum* spp. biomass had a significant negative correlation with surface salinity.

Table 5.9. Significant regressions of environmental variables against biomass for species contributing most to within group similarity and between group dissimilarity (degrees of freedom = 1.23).

Species	**Variable**	**Beta**	**R^2**	**Adjusted R^2**	**F**	**p**
E. hamata	Integrated temperature	-0.44	0.19	0.16	5.52	< 0.05
Protomyctophum spp.	Surface salinity	0.40	0.16	0.13	4.47	< 0.05
P. abdominalis	Sounding	0.51	0.25	0.22	7.86	< 0.01
C. brevipes	Chlorophyll *a*	0.43	0.19	0.15	5.23	< 0.05
C. simillimus	Surface temperature	-0.43	0.19	0.15	5.36	< 0.05

Group 1 was characterised by the high frequency of occurrence of the sub-tropical hyperiid *P. sedentaria*, as well as *G. braueri* and *Sergestes* spp. (Table 5.10.). The sub-tropical species *I. zonaria* and *Stemonosudis* sp. were also present within Group 1. Group 3 was characterised by the relatively high frequency of occurrence of *Rhynchonerella* sp. and *P. triloba*. Group 2 contained the sub-tropical hyperiid *C. magellanicus,* but stood out through the absence of a number of species that occurred at high frequency within groups 1 and 3.

Table 5.10. Frequency of occurrence of indicator species distinguishing cluster groups. Species above the blank line have 2)I > 6.63 (p=0.01), and those below the line have 2)I > 3.84 (p=0.05). Number of samples in a group is in parenthesis below the group number.

Species	**Group 1 (8)**	**Group 2 (4)**	**Group 3 (16)**
Phronima sedentaria	3	0	0
Gymnoscopelus braueri	3	0	0
Sergestes spp.	3	0	0
Rhynchonerella sp.	0	0	2
Pegantha triloba	0	0	2
Oncaea antarctica	4	0	6
Paraeuchaeta biloba	4	0	8
Pleuromamma abdominalis	7	0	8
Euphausia longirostris	5	0	6
Racovitzanus antarctica	3	0	4

Table 5.10.			
Species	**Group 1 (8)**	**Group 2 (4)**	**Group 3 (16)**
Iasis zonaria	1	0	0
Cyllopus magellanicus	0	1	0
Stemonosudis sp.	1	0	0

5.3.3. Regional Distribution of Abundance and Biomass, and Vertical Migration:

Total abundance of zooplankton groups differed significantly between regions and between day and night samples (Table 5.11.). The highest abundance levels were recorded in the downstream region at night and the lowest in the upstream region during the day. However, only pteropods and euphausiids showed significant differences in abundance levels. Pteropods occurred at highest abundance in the inter-island and downstream regions at night, while daytime abundance in the inter-island region was the lowest. Euphausiids were most abundant within the inter-island region. Euphausiid abundance in all regions was significantly higher at night than during the day, with the exception of the inter-island region where abundance levels remained relatively high during the day.

Total zooplankton biomass was significantly higher at night than during the day in all regions with the exception of the region downstream of the islands. (Table 5.12.). The highest biomass levels were recorded in the downstream region at night and the lowest in the inter-island region during the day. Copepod biomass differed significantly both regionally and between day/night samples. The highest copepod biomass levels were recorded in the downstream region at night, and the lowest in the upstream region during the day. The biomass of euphausiids was significantly higher at night than during the day in all regions. Fish biomass was significantly higher at night in the region downstream of the islands than all other regions, and all regions recorded higher fish biomass levels at night than during the day. No other zooplankton groups showed significant variation in biomass levels between regions or between day and night tows.

The average individual size of zooplankton in the six groups contributing most to biomass generally increased at night (Figure 5.9.). The exceptions were pteropods in the upstream and inter-island regions and copepods in the downstream region. Fish, euphausiids, decapods and copepods all recorded lowest average size in the inter-island region.

Differences between day and night biomass levels reflected diel vertical migration patterns. Vertical migration was most pronounced in fish, represented only by *Protomyctophum* spp. (prot), and Euphausiids, although most copepod species showed a similar pattern of decreased biomass during the day (Figure 5.10.). Chaetognath and pteropod biomass showed little difference between night and day indicating that they remain predominantly within the surface layers. A number of species occurred at highest biomass over the island shelf including *E. hamata* (Eh), *L. retroversa* (Lr), the copepods *C. brevipes* (Cb), *C. vanus* (Cv) and *Paraeuchaeta* spp. (Pas), and the Euphausiids *E. vallentini* (Ev) and *T. vicina* (Tv). *Euphausia longirostris* (Elr) and *P. abdominalis* (Pa) were virtually absent from day offshore tows indicating that they migrate below 300m. Both of these species were also virtually completely absent from the island shelf.

Table 5.11. Average abundance of dominant zooplankton groups recorded from the upstream, inter-island and downstream regions of the PEIs during MIOS 3. Significant differences in group abundance between regions and between day/night net tows were determined by two-way ANOVA of log transformed data (no significant difference indicated by -). The effect of the interaction between regional and day/night differences on group abundance was investigated using a Newman-Keuls multiple range test. Significant differences in the distribution of zooplankton groups are indicated by different letters, while sharing of a letter indicates no significant difference. All data were normally distributed.

	Night			**Day**			**Significance levels**	
Group	**Upstream**	**Inter-island**	**Downstream**	**Upstream**	**Inter-island**	**Downstream**	**Regions**	**Day/night**
Pteropoda	7.36 **xy**	12.40 **y**	16.99 **y**	5.44 **xy**	2.18 **x**	8.06 **xy**	-	P<0.05; F=6.35
Ostracoda	4.27	6.05	7.61	3.83	6.93	5.89	-	-
Copepoda	31.18	44.72	87.19	17.07	38.62	31.26	-	-
Euphausiacea	4.07 **yz**	5.61 **z**	3.59 **yz**	0.48 **x**	1.42 **xy**	0.77 **x**	-	p<0.001; F=41.40
Decapoda	0.02	0.02	0.00	0.0005	0.02	0.0004	-	-
Hyperiidea	0.15	0.22	0.29	0.20	0.15	0.09	-	-
Chaetognatha	5.09	12.39	11.85	6.33	6.71	11.69	-	-
Osteichthyes	0.14	0.17	0.17	0.09	0.11	0.14	-	-
Total abundance	52.62 **xy**	81.77 **xy**	128.41 **y**	33.73 **x**	56.53 **xy**	58.86 **xy**	p<0.05; F=3.64	p<0.05; F=5.79

Table 5.12. Average biomass of dominant zooplankton groups recorded from the upstream, inter-island and downstream regions of the PEIs during MIOS 3. Significant differences in group biomass between regions and between day/night net tows were determined by two-way ANOVA of log transformed data (no significant difference indicated by -). The effect of the interaction between regional and day/night differences on group biomass was investigated using a Newman-Keuls multiple range test. Significant differences in the distribution of zooplankton groups are indicated by different letters, while sharing of a letter indicates no significant difference. All data were normally distributed.

	Night			**Day**			**Significance levels**	
Group	**Upstream**	**Inter-island**	**Downstream**	**Upstream**	**Inter-island**	**Downstream**	**Regions**	**Day/night**
Pteropoda	0.87	1.48	2.18	0.71	0.2	0.84	-	-
Ostracoda	0.15	0.21	0.26	0.13	0.23	0.20	-	-
Copepoda	1.56 **xy**	1.95 **xy**	7.59 **y**	0.54 **x**	1.07 **xy**	2.17 **xy**	$p<0.05$; $F=3.35$	$p<0.05$; $F=4.30$
Euphausiacea	4.13 **y**	4.15 **y**	4.51 **y**	0.65 **x**	0.37 **x**	0.41 **x**	-	$p<0.001$; $F=30.99$
Decapoda	0.26	0.13	0	0.01	0.01	0.01	-	-
Hyperiidea	0.73	0.91	1.42	0.40	0.69	0.30	-	-
Chaetognatha	0.47	1.29	1.3	0.55	0.46	1.09	-	-
Osteichthes	0.2 **x**	0.31 **x**	0.88 **y**	0.03 **x**	0.03 **x**	0.05 **x**	$p<0.01$; $F=7.57$	$p<0.001$; $F=26.09$
Total biomass	8.42 **y**	10.32 **y**	18.27 **y**	3.13 **x**	3.10 **x**	5.47 **xy**	-	$p<0.01$; $F=22.49$

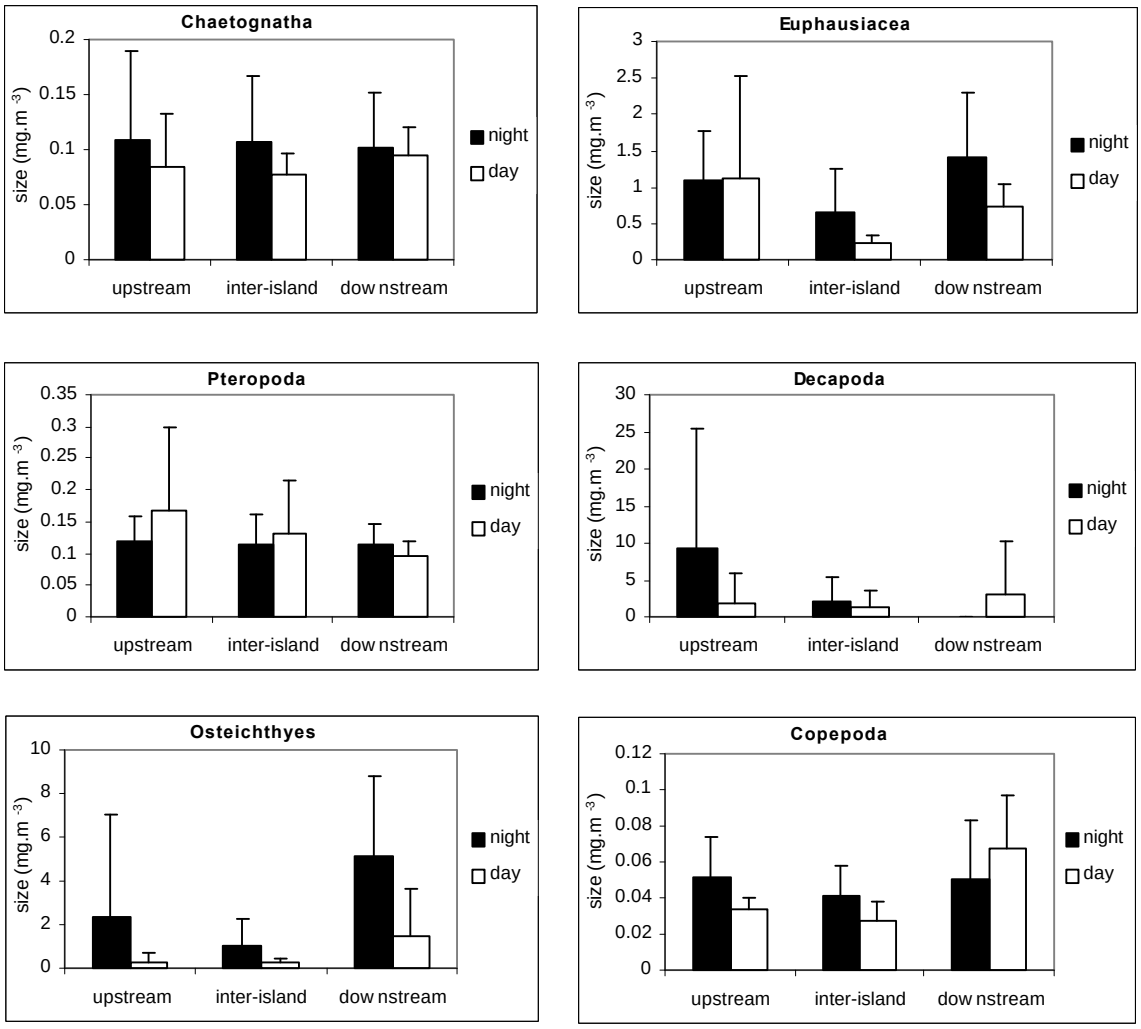


Figure 5.9. Regional differences in average individual zooplankton size ($mg.m^{-3}$) and standard deviations for the six groups contributing most to zooplankton biomass. Day and night biomass levels are indicated.

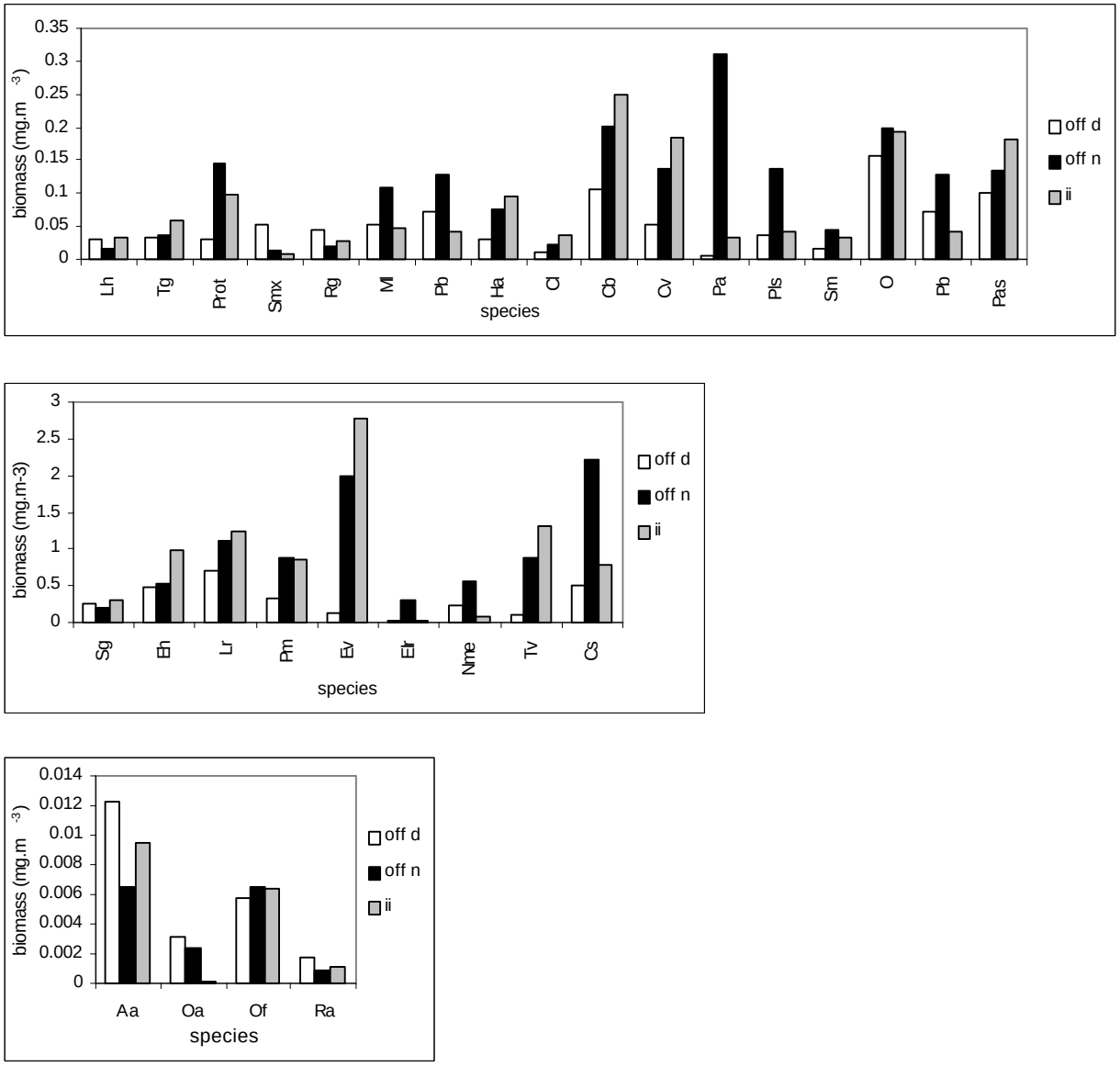


Figure 5.10. Average biomass ($mg.m^{-3}$) recorded for major zooplankton species during the day (d) and night (n) in the offshore region and during the night in the inter-island region (ii). Species abbreviations follow those in Table 5.3., Table 5.8. and Table 6.8.

Chapter 6

RESULTS: MIOS 4 (1999)

6.1. Oceanography:

During Survey 1 the SAF and APF were found in close proximity to one another in the region upstream of the PEIs. The APF was located at approximately 47°20'S (Figure 6.1.a) while the SAF was located at approximately 46°30'S (Figure 6.1.b) along the 37°E upstream transect. On the outward leg of the northern transect the SAF was located at approximately 45°30'S and 39°E in the region downstream of the PEIs, showing that it was deflected in a north easterly direction around the islands (Figure 6.2.a). Conversely the APF appeared to be deflected in a westerly direction, remaining to the south of the PEIs in the downstream region.

During the return leg of the northern transect, immediately prior to Survey 2, the SAF was crossed at approximately 45°00'S, 30 nautical miles further north than on the outward leg (Figure 6.2.b). On the return voyage to Cape Town, immediately after the completion of the second zooplankton survey, the SAF was crossed at approximately 45°30'S in the upstream region (Pakhomov *et al*., 1999 a), sixty nautical miles further north than in Survey 1. The APF lay to the south of the islands and was not crossed before the completion of the transect to 48°S. It had therefore moved at least 40 nautical miles southwards. The oceanographic environment had therefore changed quite dramatically in the two-week period between surveys. The northward movement of the SAF away from the islands resulted in a drop in average surface temperature from 8.1°C to 6.39°C, and average integrated temperature from 7.13°C to 5.79°C between Survey 1 and Survey 2.

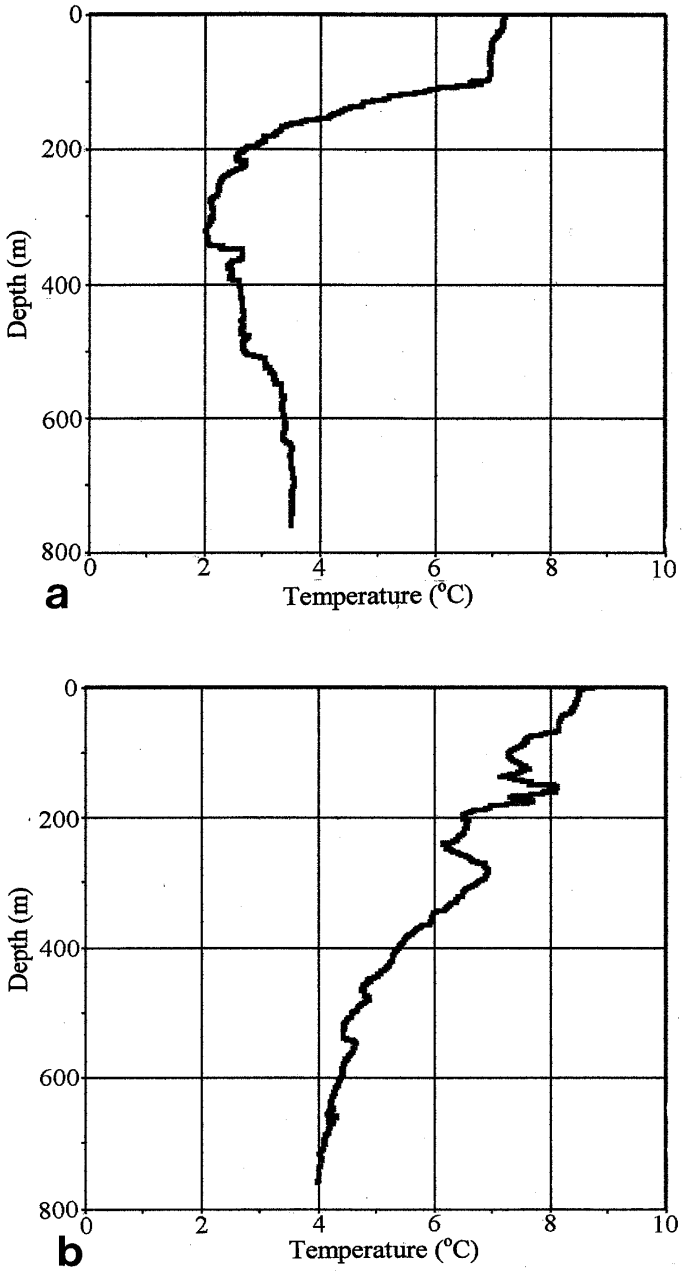


Figure 6.1. Temperature profile, measured by XBT, showing the position of (a) the APF at station MS4-5 and (b) the SAF at station MS4-2 (stations positions are presented in Appendix 1).

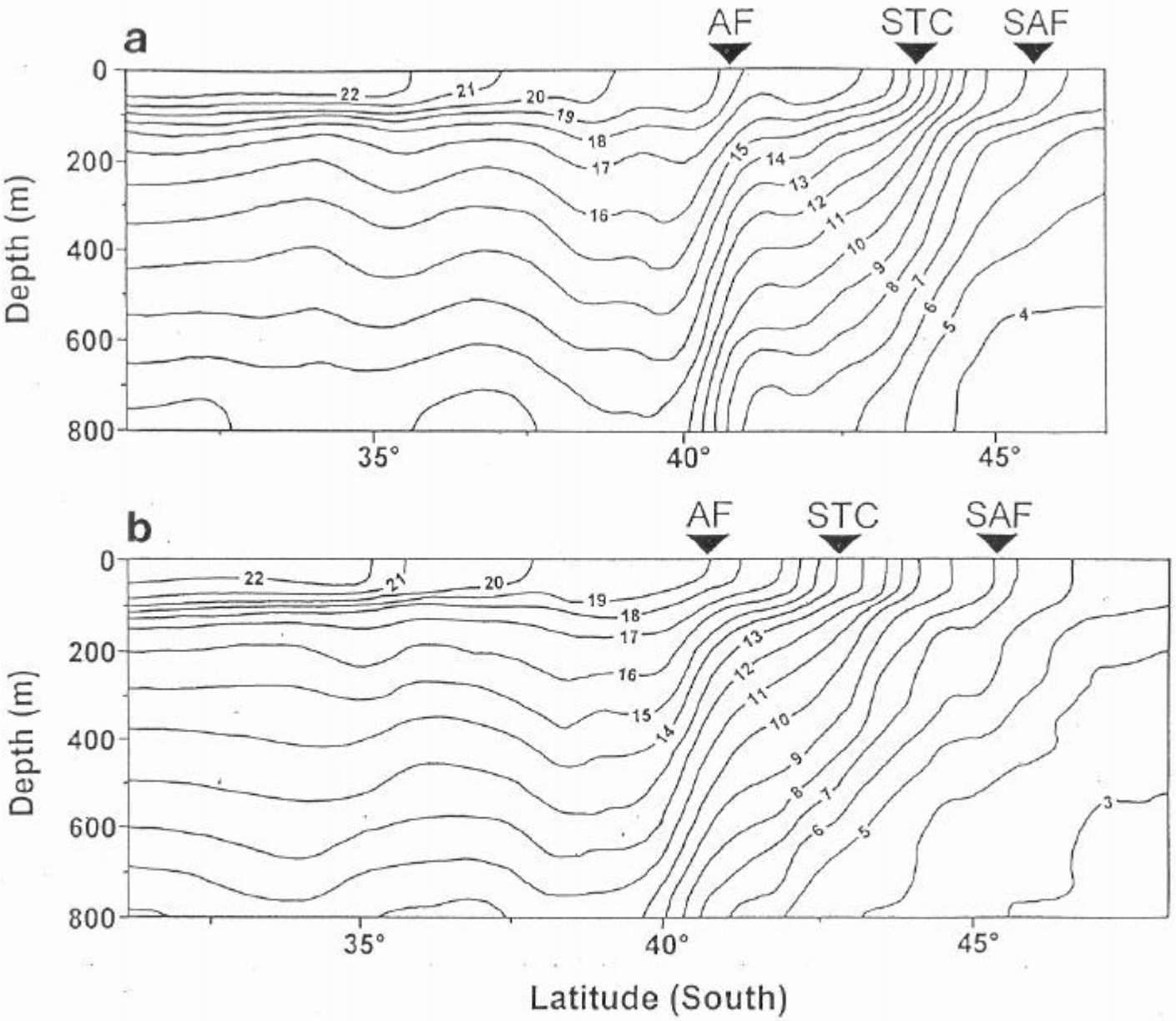


Figure 6.2. Temperature profile of the water column determined by XBT's during the (a) outward leg of the northern transect and (b) the return leg of the northern transect conducted during MIOS 4. Figure taken from Pakhomov *et al.* (1999 a).

6.2. Chlorophyll *a*:

During Survey 1 surface chlorophyll *a* concentrations varied between 0.16 $mg.m^{-3}$ and 2.39 $mg.m^{-3}$ (Figure 6.3.a). Generally chlorophyll *a* concentrations did not exceed 0.5 $mg.m^{-3}$. The three downstream stations, MS4-9, MS4-10 and MS4-14, had the highest chlorophyll *a* concentrations (1.32 - 2.39 $mg.m^{-3}$). These stations were dominated by high concentrations of microphytoplankton. In the upstream and inter-island stations from Survey 1 micro, nano and picophytoplankton contributed, on average, 30%, 31% and 38% respectively to total chlorophyll *a*.

During Survey 2 surface chlorophyll *a* concentrations varied between 0.11 $mg.m^{-3}$ and 0.62 $mg.m^{-3}$ (Figure 6.3.b). On average micro, nano and picophytoplankton contributed 21%, 28% and 51% respectively to total chlorophyll *a*.

A Mann-Whitney U test showed that the Survey 1 downstream stations had significantly higher ($p<0.01$) total chlorophyll *a* concentrations than any other region during both surveys. The upstream and inter-island stations from Survey 1 had significantly higher ($p<0.05$) total chlorophyll *a* concentrations than the upstream and downstream regions from Survey 2, but not the inter-island region.

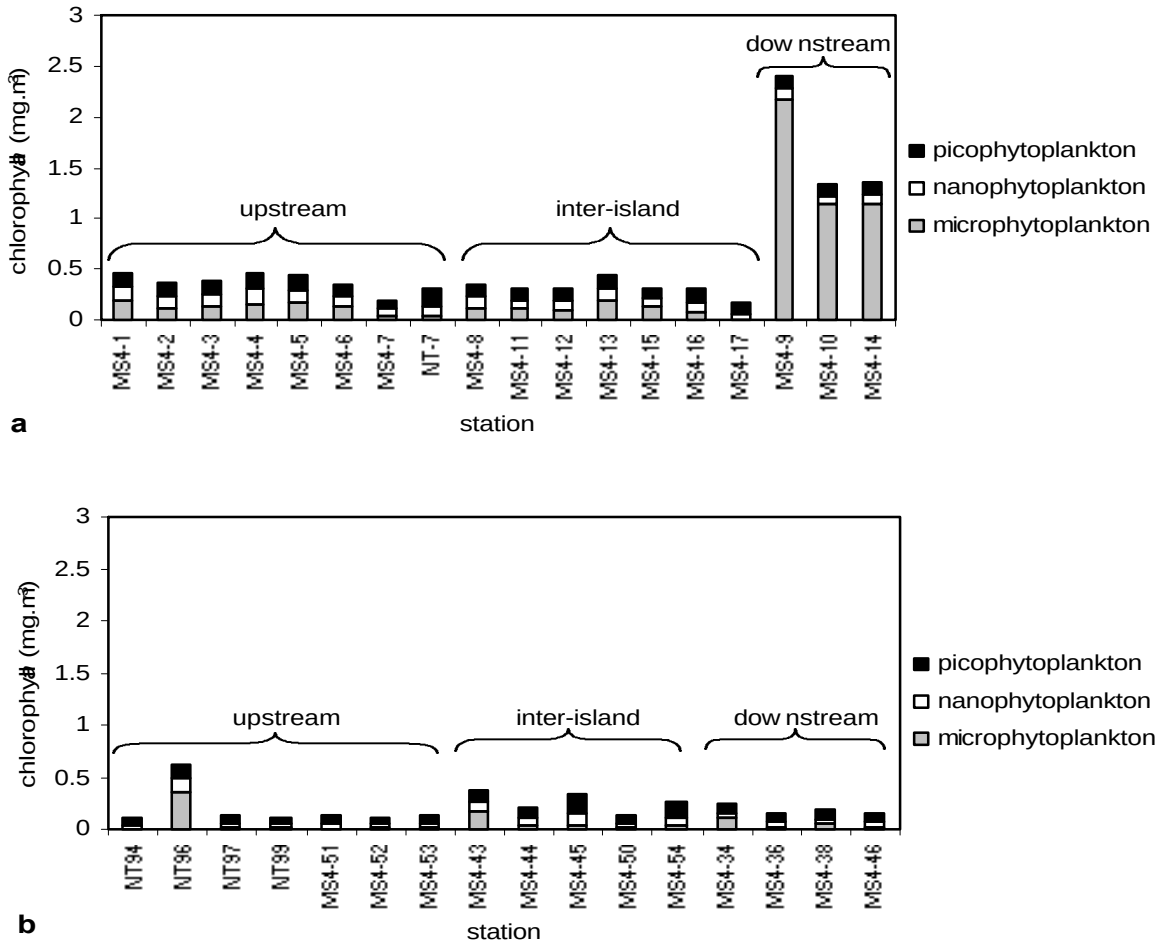


Figure 6.3. Size fractionated surface chlorophyll *a* concentrations ($mg.m^{-3}$) corresponding with net tows during (a) Survey 1 and (b) Survey 2. Regions discussed in the analysis are bracketed.

6.3. Zooplankton:

6.3.1. Abundance:

Six station clusters were identified at approximately the 55% level of similarity (Figure 6.4.). Initial analysis showed that there was no significant difference ($p>0.1$) between the two clusters containing the stations MS4-8, MS4-8A, MS4-11, and MS4-16 and MS4-17. These two clusters were subsequently joined as Group 1, giving a total of five station groups. Group 1 consisted entirely of inter-island stations from Survey 1. Group 2

contained of a mix of stations from surveys 1 and 2, both oceanic and inter-island. Group 3 contained stations from Survey 2, largely inter-island and including oceanic stations south of 46°30'S. Group 4 contained oceanic stations at and north of the SAF. Group 5 included station MS4-5 at the APF, and five inter-island stations.

A one-way ANOVA showed that all station groupings were significantly different from each other ($p<0.05$).

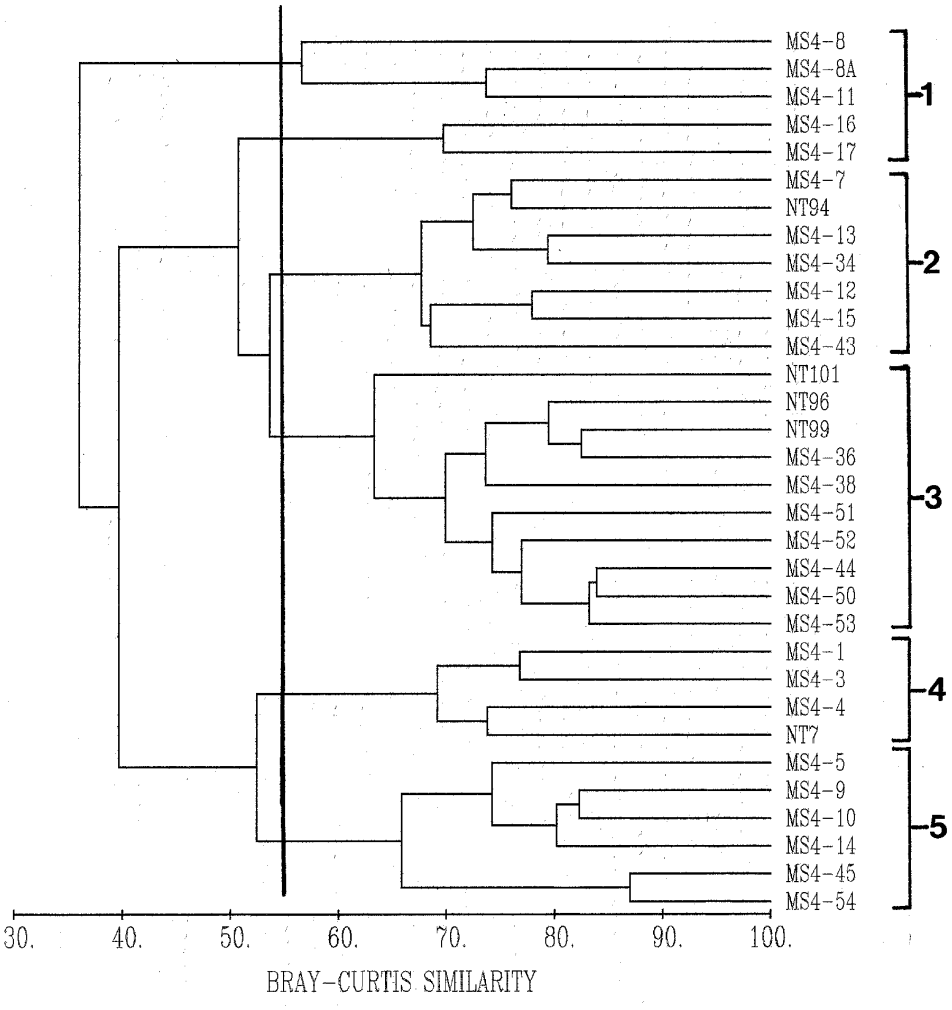
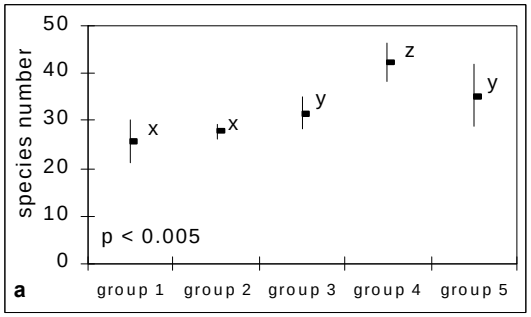


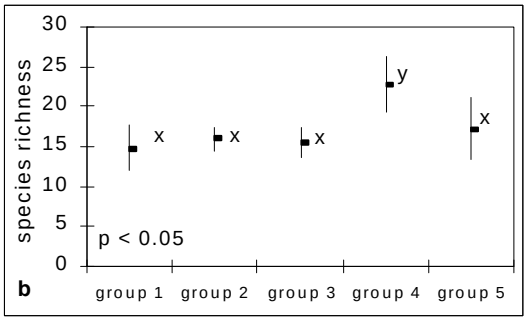
Figure 6.4. Dendrogram of cluster analysis comparing zooplankton abundance data between stations conducted during MIOS 4. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species abundance data. Station groupings selected for the analysis are bracketed.

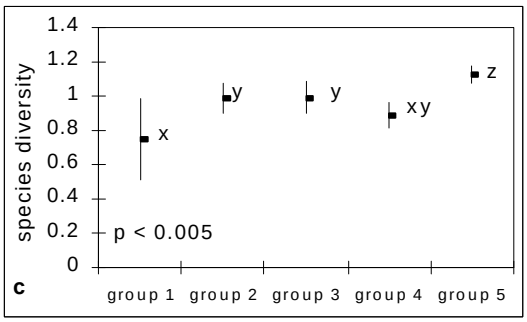
Group 4 had a significantly higher number of species and species richness than all other groups (Figure 6.5.a,b). Group 5 had a significantly higher diversity than all other groups (Figure 6.5.c). The lowest species number, species richness and diversity were all recorded within Group 1. The highest zooplankton abundance levels were recorded within groups 3 and 5, and the lowest within groups 1 and 2 (Figure 6.5.d). The highest average surface salinity and integrated temperature were recorded within groups 1 and 4 (Figure 6.5.e,g), while surface temperature was significantly higher within Group 4 than all other groups (Figure 6.5.f). Conversely, the lowest average temperature (surface and integrated) and salinity values were recorded within groups 3 and 5. Sounding was highest within Group 4, which contained only offshore stations, and lowest within Group 1, which contained only inter-island stations (Figure 6.5.h). Group 5 recorded significantly higher chlorophyll *a* concentrations than all other groups (Figure 6.5.i). This was attributed to the bloom conditions recorded at stations MS4-9, MS4-10 and MS4-14.

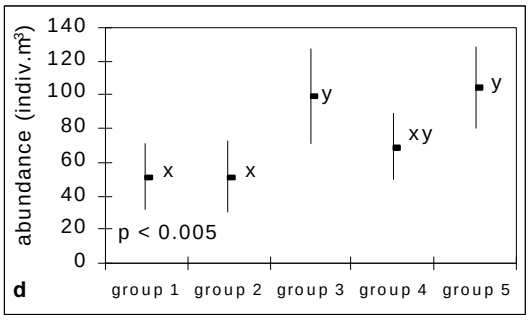
Overleaf:

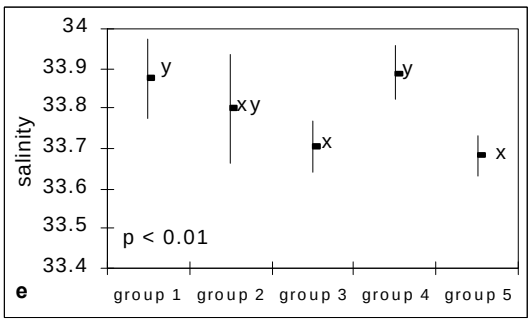
Figure 6.5. Average and standard deviations of variables, recorded for the station groups identified by cluster analysis of MIOS 4 abundance data. The significance level of between group variation, determined using a Kruskal-Wallace test, is indicated on each graph (p-value). Significant differences between station group pairs, determined using a Mann-Whitney U test, are indicated by different letters. Sharing of a letter indicates no significant difference.

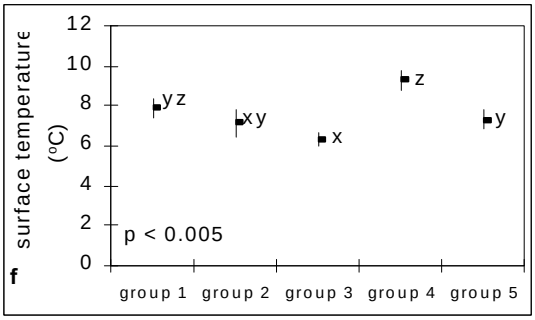

species number
50
40
30
20
10
0
x
x
y
z
y
p < 0.005
a
group 1 group 2 group 3 group 4 group 5

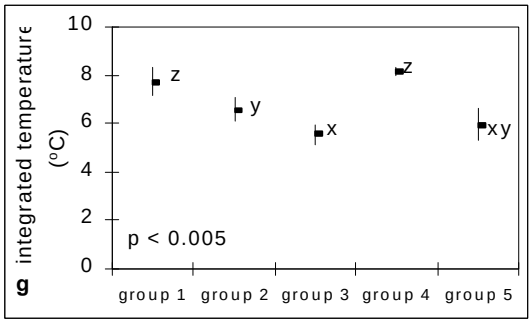

species richness
30
25
20
15
10
5
0
x
x
x
y
x
p < 0.05
b
group 1 group 2 group 3 group 4 group 5

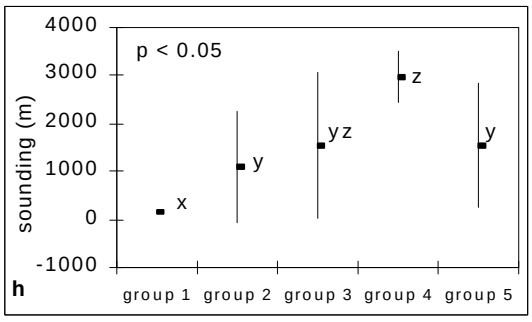

species diversity
1.4
1.2
1
0.8
0.6
0.4
0.2
0
x
y
y
xy
z
p < 0.005
c
group 1 group 2 group 3 group 4 group 5

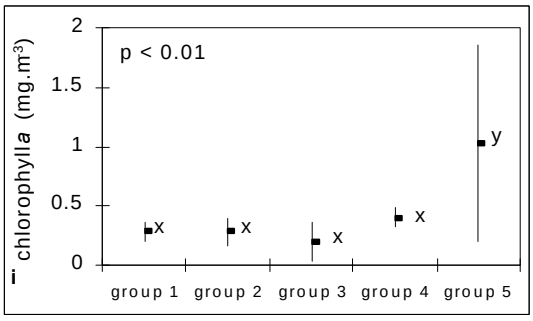

abundance (indiv.m³)
140
120
100
80
60
40
20
0
x
x
y
xy
y
p < 0.005
d
group 1 group 2 group 3 group 4 group 5


salinity
34
33.9
33.8
33.7
33.6
33.5
33.4
y
xy
x
y
x
p < 0.01
e
group 1 group 2 group 3 group 4 group 5


surface temperature (°C)
12
10
8
6
4
2
0
yz
xy
x
z
y
p < 0.005
f
group 1 group 2 group 3 group 4 group 5


integrated temperature (°C)
10
8
6
4
2
0
z
y
x
z
xy
p < 0.005
g
group 1 group 2 group 3 group 4 group 5


sounding (m)
4000
3000
2000
1000
0
-1000
p < 0.05
x
y
yz
z
y
h
group 1 group 2 group 3 group 4 group 5


chlorophylla (mg.m³)
2
1.5
1
0.5
0
p < 0.01
x
x
x
x
y
i
group 1 group 2 group 3 group 4 group 5

Integrated water temperature accounted for 69% of the variation in zooplankton abundance data (Table 6.1.). Surface temperature and surface salinity both accounted for greater than 50% of the variation. Neither chlorophyll *a* concentration nor sounding accounted for a significant amount of variation in zooplankton abundance data.

Table 6.1. Results of the multiple regression of environmental variables against NMDS ordination scores for MIOS 4 abundance data (stress = 0.15). (degrees of freedom = 2.27)

	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	0.05	-0.84	0.72	0.69	34.07	< 0.001
Surface temperature	-0.24	-0.78	0.59	0.56	19.10	< 0.001
Surface salinity	0.20	-0.67	0.54	0.50	15.74	< 0.001
Sounding	-0.44	-0.01	0.19	0.13	3.12	0.06
Chlorophyll *a*	-0.22	0.09	0.07	-0.01	0.97	0.39

Group 1 had a within group similarity of 60.5%, while groups 2 to 5 had within group similarities of greater than 70% (Table 6.2.). Together the copepods *C. brevipes, M. lucens, C. simillimus,* the chaetognaths *S. gazellae* and *E. hamata*, the pteropod *L. retroversa,* and Ostracods, accounted for greater than 66% of the similarity within all groups. Group 3 was dominated by the high abundance of *E. hamata*, *C. simillimus* and *L. retroversa*, and was also characterised by the relatively high abundance of the Antarctic copepod *O. frigida* (Vervoort, 1951). Group 4 was dominated by the high abundance of *M. lucens* and *C. brevipes*, and contained a relatively high abundance of *P. abdominalis*. Group 5 was characterised by the high abundance of *E. hamata* and Ostracods, and contained a relatively high abundance of the Antarctic species *R. gigas* and *S. minor* (Vervoort, 1951; Park, 1980).

Table 6.2. Species responsible for 80% of the similarity within the five zooplankton groups identified by cluster analysis of MIOS 4 abundance data. Within group similarity is in parenthesis under group number. Cells indicate average species abundance (individuals.m^{-3}) within a group and percentage contribution to within group similarity is in parenthesis.

Group 1 (60.46%)	**Group 2** (72.53%)	**Group 3** (74.66%)	**Group 4** (72.99%)	**Group 5** (74.65%)
C. brevipes 11.66 (20.07%)	*L. retroversa* 10.68 (15.47%)	*E. hamata* 20.23 (14.88%)	*M. lucens* 27.71 (21.05%)	*E. hamata* 20.85 (11.35%)
T. vicina 4.04 (13.52%)	*E. hamata* 9.5 (13.12%)	*C. simillimus* 24.67 (14.46%)	*C. brevipes* 17.54 (17.62%)	Ostracod 10.56 (9.77%)
E. hamata 2.37 (8.88%)	*C. simillimus* 7.81 (12.88%)	*L. retroversa* 13.41 (9.91%)	Ostracod 3.12 (8.68%)	*M. lucens* 10.48 (8.84%)
Ostracod 1.13 (8.21%)	*C. brevipes* 3.61 (10.89%)	*C. brevipes* 7.61 (8.29%)	*E. hamata* 2.57 (7.37%)	*C. simillimus* 7.12 (8.64%)
M. lucens 4.68 (7.99%)	Ostracod 5.72 (10.14%)	*M. lucens* 5.93 (7.6%)	*Ctenocalanus* sp. 2.53 (7.1%)	*L. retroversa* 6.33 (7.92%)
C. simillimus 7.77 (6.35%)	*T. vicina* 2.99 (8.67%)	Ostracod 5.8 (6.96%)	*S. gazellae* 1.53 (5.5%)	*C. brevipes* 9.06 (7.22%)
Ctenocalanus sp. 1.38 (5.49%)	*M. lucens* 2.61 (5.8%)	*T. vicina* 2.36 (4.56%)	*T. vicina* 1.43 (4.97%)	*S. gazellae* 3.78 (5.83%)
S. gazellae 0.81 (5.48%)		*O. frigida* 2.83 (4.35%)	*P. abdominalis* 1.1 (3.76%)	*R. gigas* 4.1 (5.83%)
		Pleuromamma spp. 3.06 (3.89%)	*Pleuromamma* spp. 1.15 (3.13%)	*T. vicina* 6.87 (5.43%)
		S. gazellae 1.57 (3.78%)		*S. minor* 1.83 (3.65%)
				C. laticeps 1.98 (3.62%)

The lowest level of dissimilarity was 29.7% between groups 5 and 3. The dissimilarity between groups 5 and 2 and groups 3 and 2 was 36.2% and 33.1% respectively. The dissimilarity between all other groups was > 40%. *Limacina retroversa, M. lucens, C. brevipes, C. simillimus, Pleuromamma* spp., *E. hamata, Ostracods* and *T. vicina* together contributed to between 41% and 64% of the dissimilarity between groups. The species

responsible for dissimilarity between groups were therefore largely the same as those responsible for similarity within groups. *Oithona frigida*, *S. minor* and *C. laticeps* contributed to a relatively high percentage of the dissimilarity between groups 3 and 5 and all other groups (2.1% - 6.3%), and were most abundant within groups 3 and 5. *Oncaea antarctica* and *R. gigas* were most abundant within Group 5 and contributed to a relatively high percentage of the dissimilarity between this group and all other groups (1.6% - 6.5%).

The inverse analysis identified five species clusters at approximately the 50% level of similarity (Figure 6.6.). Cluster 1 contained species occurring at highest abundance within station groups 4 and 5 (Table 6.3.). Cluster 2 contained species occurring at highest abundance within station Group 4. Cluster 3 was dominated by species that occurred at highest abundance within station Group 3. Clusters 4 and 5 were dominated by species occurring at highest abundance within station Group 5.

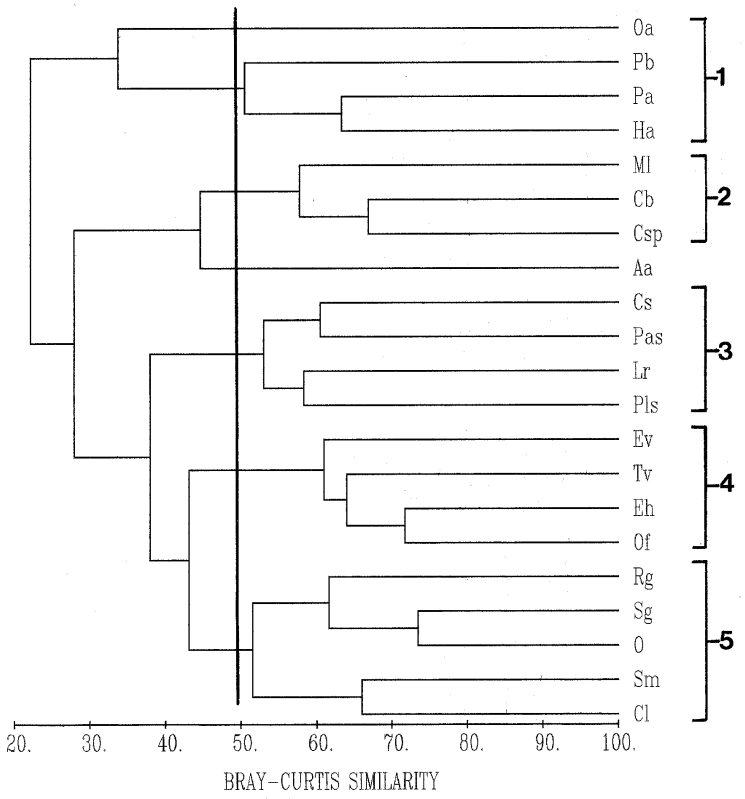


Figure 6.6. Dendrogram of the inverse cluster analysis comparing dominant zooplankton species, identified by SIMPER analysis of abundance data. The Bray-Curtis similarity measure was used after standardisation of the data set. Abbreviations follow those in Table 6.3.

Table 6.3. Species, abbreviations and names, used in the inverse analysis and the station groups within which each species occurred at highest abundance. Station groups within which a species occurred at significantly higher abundance, determined by group pair comparison using Mann-Whitney U tests, are in bold. Significant differences in the abundance of species between station groups, determined by Kruskal-Wallace tests, are indicated by p (- indicates no significant difference).

Species	**Groups**	**p**
Oa – *Oncaea antarctica*	5	-
Pb – *Paraeuchaeta biloba*	**4**	< 0.01
Pa – *Pleuromamma abdominalis*	**5**	< 0.05
Ha – *Heterorhabdus austrinus*	**4**	< 0.05
Ml – *Metridia lucens*	4	-
Cb – *Clausocalanus brevipes*	**4**	< 0.05
Csp – *Ctenocalanus* spp.	4	-
Aa – *Aetideus armatus*	4	-
Cs – *Calanus simillimus*	**3**	< 0.05
Pas – *Paraeuchaeta* spp.	**3**	< 0.005
Lr – *Limacina retroversa*	3	-
Pls – *Pleuromamma* spp.	5	-
Ev – *Euphausia vallentini*	5	-
Tv – *Thysanoessa vicina*	5	-
Eh – *Eukrohnia hamata*	**3**,**5**	< 0.001
Of – *Oithona frigida*	5	-
Rg – *Rhincalanus gigas*	**5**	< 0.005
Sg – *Sagitta gazellae*	**5**	< 0.05
O – Ostracods	**5**	< 0.005
Sm – *Scolecithricella minor*	5	-
Cl – *Clausocalanus laticeps*	5	-

Eukrohnia hamata had a strong negative correlation with surface temperature, integrated temperature and surface salinity, while *S. gazellae* was negatively correlated with surface salinity (Table 6.4.). Previous investigations have shown these two chaetognath species to occur at highest abundance at and south of the APF (David, 1958; Timonin, 1968). Both species occurred at highest abundance within groups 3 and 5 indicating that the stations within these groups had Antarctic affinities. Both groups 3 and 5 were characterised by relatively low average sea temperatures and salinity (Figure 6.5.).

Ostracods were negatively correlated with surface temperature and salinity, and occurred

at highest abundance within Group 5. *Calanus simillimus* had a strong negative correlation with integrated temperature, surface temperature and salinity. This species was most abundant within Group 3.

Clausocalanus brevipes was positively correlated with sea surface temperature. This species is typically sub-Antarctic (Guglielmo and Ianora, 1995) and occurred at highest abundance within Group 4, containing stations at and north of the SAF. Group 1, also characterised by a high abundance of *C. brevipes*, contained inter-island stations with integrated temperatures not significantly different from Group 4 (Figure 6.5.g) and surface temperatures characteristic of sub-Antarctic surface water (Lutjeharms and Vallentine, 1984). *Metridia lucens* had a significant positive correlation with sea surface temperature. This is a temperate species (Gibbons and Hutchings, 1996) and also occurred at highest abundance within Group 4.

Oithona frigida, S. minor, O. antarctica and *R. gigas* were all negatively correlated with integrated temperature. Furthermore *O. frigida* and *S. minor* were both negatively correlated with salinity. *Oithona frigida* is predominantly an Antarctic species (Vervoort, 1951), as are *R. gigas* (Vervoort, 1951), and *O. antarctica* (Razouls, 1994). *Scolecithricella mino*r occurs widely in the Antarctic and sub-Antarctic but is most abundant in the Antarctic (Park, 1980). All of these species were most abundant within Group 5. Group 3 had a high abundance of *O. frigida* and *S. minor* and both groups 2 and 3 had a relatively high abundance of *R. gigas*.

Table 6.4. Significant regressions of environmental variables and abundance for species contributing most to within group similarity and between group dissimilarity. Only significant ($p<0.05$) relationships are shown (degrees of freedom = 1.28).

Species	Variable	Beta	R^2	Adjusted R^2	F	p
E. hamata	Integrated temperature	-0.63	0.39	0.37	18.07	< 0.001
	Surface temperature	-0.68	0.45	0.43	23.49	< 0.001
	Surface salinity	-0.66	0.43	0.41	21.11	< 0.001
S. gazellae	Surface salinity	-0.39	0.15	0.12	5.05	< 0.05
Ostracod	Surface temperature	-0.50	0.25	0.22	9.34	< 0.01
C. simillimus	Integrated temperature	-0.58	0.33	0.31	14.03	< 0.005
	Surface temperature	-0.68	0.47	0.45	24.59	< 0.001
	Surface salinity	-0.44	0.19	0.16	6.55	< 0.05
C. brevipes	Surface temperature	0.39	0.15	0.12	4.91	< 0.05
M. lucens	Surface temperature	0.62	0.38	0.36	17.40	< 0.001
	Chlorophyll *a*	0.68	0.46	0.45	24.60	< 0.001
R. gigas	Integrated temperature	-0.45	0.21	0.18	7.23	< 0.01
O. frigida	Integrated temperature	-0.38	0.14	0.11	4.74	< 0.05
	Surface temperature	-0.41	0.17	0.14	5.75	< 0.05
	Surface salinity	-0.48	0.23	0.20	8.40	< 0.01
O. antarctica	Integrated temperature	-0.37	0.14	0.11	4.47	< 0.05
S. minor	Integrated temperature	-0.45	0.21	0.18	7.20	< 0.01
	Surface salinity	-0.40	0.16	0.13	5.24	< 0.05

A number of frequency indicators were identified by the Information statistic (Table 6.5.). Group 4 had a high incidence of the sub-tropical hyperid amphipods *P. sedentaria* and *C. magellanicus* (Vinogrodov *et al.*, 1982). Also within this group were the sub-tropical fish species *E. cryomargarites* and *Stemonosudis* sp. (Gon and Heemstra, 1990), and the sub-tropical/temperate euphausiid *E. similis* var. *armata* (Baker, 1965). Group 5 was characterised by a high frequency of the fish *P. choriodon*. Station MS4-5 stood out within Group 5 due to the presence of the typical APF species *E. triacantha* (Baker, 1965) and the Antarctic copepod *G. antarcticas* (Razouls, 1994). Group 3 was characterised by a relatively high frequency of *Beroe* sp. No frequency indicators were identified within groups 1 and 2.

Table 6.5. Frequency of occurrence of indicator species distinguishing cluster groups. Species above the blank line have $2)I > 6.63$ (p=0.01), and those below the line have $2)I > 3.84$ (p=0.05). Number of samples in a group is in parenthesis below the group number.

Species	**Group 1 (5)**	**Group 2 (7)**	**Group 3 (10)**	**Group 4 (4)**	**Group 5 (6)**
Phronima sedentaria	0	0	0	3	0
Cyllopus magellanicus	0	0	0	3	0
Protomyctophum choriodon	0	0	0	0	3
Beroe sp.	0	0	2	0	0
Melophysa melo	0	0	0	0	2
Sergestes sp.	0	0	0	1	0
Stemonosudis sp.	0	0	0	1	0
Echiodon cryomargarites	0	0	0	1	0
Euphausia similis var. *armata*	0	0	0	1	0
Gaetanus antarcticus	0	0	0	0	1
Euphausia triacantha	0	0	0	0	1

6.3.2. Biomass:

Six station clusters were identified at the 40% level of similarity based on average species biomass (Figure 6.7.). Initial analysis showed that there was no significant difference ($p=0.07$) between the clusters containing stations MS4-1, MS4-3, MS4-4, NT7, and MS4-8 and NT-94. These two clusters were subsequently merged as Group 2. Station MS4-8A was identified as an outlier and was ignored for the remainder of the analysis. Group 1 comprised inter-island stations from Survey 1. Group 2 contained the stations from Group 4 in the abundance analysis, as well as an inter-island station from Survey 1 and a northerly oceanic station from Survey 2. Group 3 comprised inter-island and oceanic stations from Survey 2. Group 4 contained one upstream station and one inter-island station from Survey 1, as well as one inter-island station from Survey 2. Group 5 contained three downstream stations from Survey 1 as well as station MS4-5 conducted at the APF, and three inter-island stations from Survey 2.
ANOSIM showed that all station groupings were significantly different from one another ($p<0.05$).

There was no significant difference in species number and species richness between station groups (Figure 6.8. a,b), although the highest values were observed within Group 2. Diversity was highest within groups 4 and 5 and lowest within Group 2 (Figure 6.8.c). Total zooplankton biomass was highest within Group 4, while the lowest levels were recorded within Group 1 (Figure 6.8.d). Groups 1 and 2 were characterised by higher salinity, surface temperature and integrated temperature than all other groups (Figure 6.8.e,f,g). Conversely, groups 3 and 5 were characterised by lower salinity, integrated temperature and surface temperature than all other groups. There was no significant difference in sounding and total chlorophyll *a* between groups (Figures 6.8.h,i).
The analysis of physical parameters associated with station groups indicated that groups 3 and 5 in the biomass analysis correspond with groups 3 and 5 in the abundance analysis. Similarly, groups 1 and 2 in the biomass analysis correspond with groups 1 and 4 in the abundance analysis.

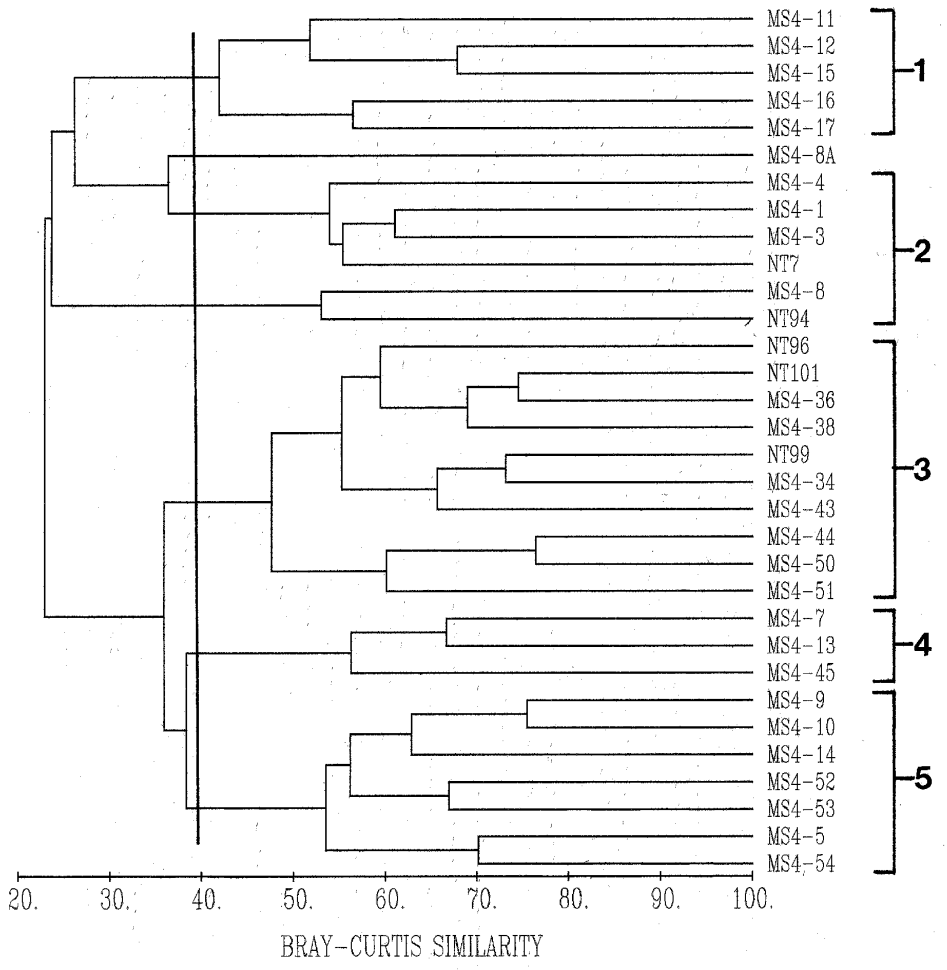
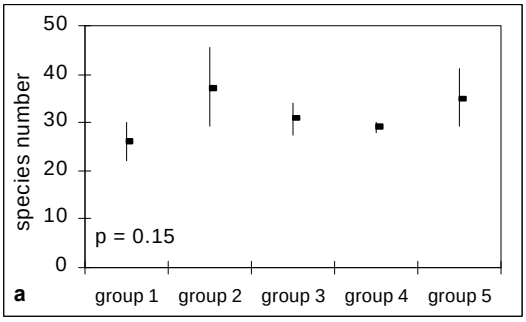
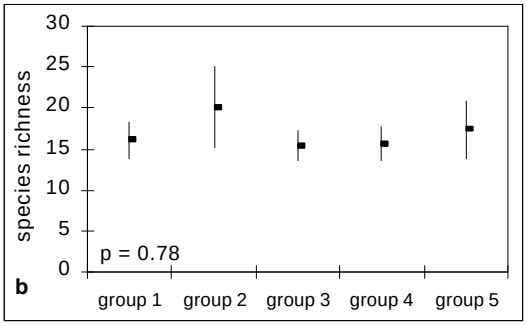


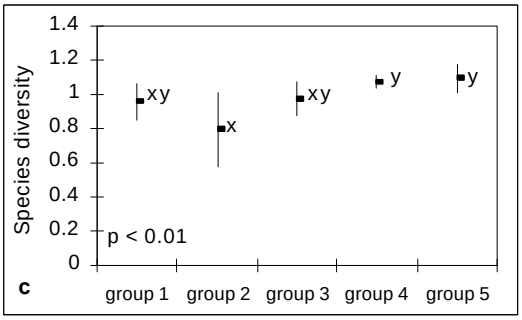
Figure 6.7. Dendrogram of cluster analysis comparing zoopankton biomass data between stations conducted during MIOS 4. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species biomass data. Station groupings selected for the analysis are bracketed.

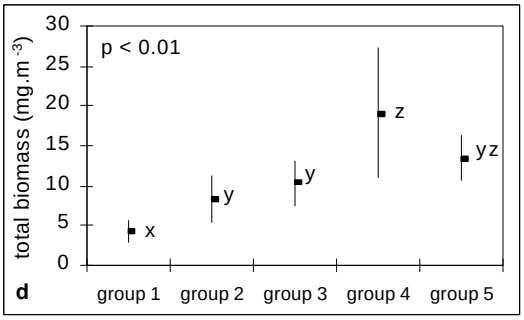
Overleaf:

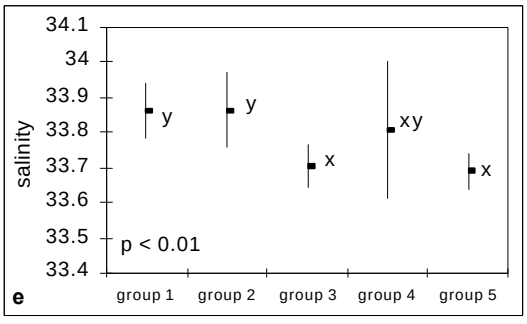
Figure 6.8. Average and standard deviations of variables, recorded for the station groups identified by cluster analysis of MIOS 4 biomass data. The significance level of between group variation, determined using a Kruskal-Wallace test, is indicated on each graph (p-value). Significant differences between station group pairs, determined using a Mann-Whitney U test, are indicated by different letters. Sharing of a letter indicates no significant difference.

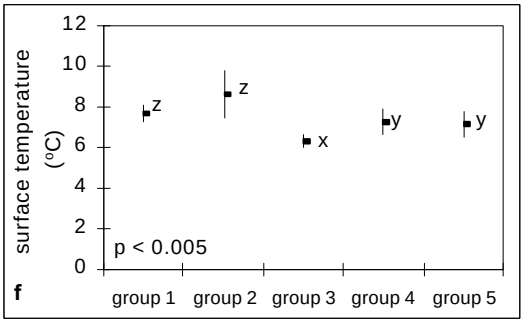

species number
50
40
30
20
10
0
p = 0.15
a
group 1
group 2
group 3
group 4
group 5

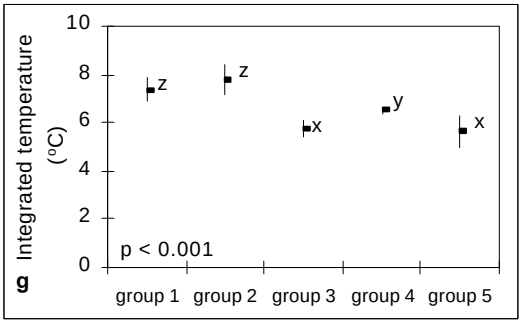

species richness
30
25
20
15
10
5
0
p = 0.78
b
group 1
group 2
group 3
group 4
group 5

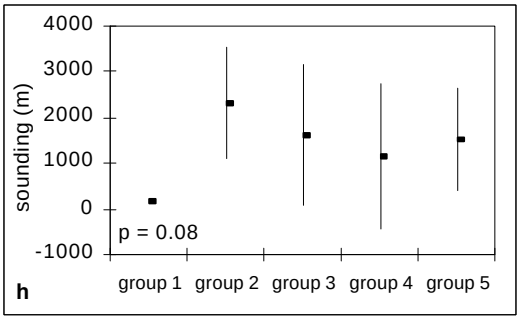

Species diversity
1.4
1.2
1
0.8
0.6
0.4
0.2
0
xy
x
xy
y
y
p < 0.01
c
group 1
group 2
group 3
group 4
group 5

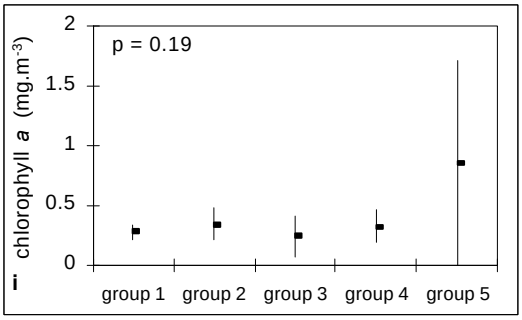

total biomass (mg.m-3)
30
25
20
15
10
5
0
p < 0.01
x
y
y
z
yz
d
group 1
group 2
group 3
group 4
group 5


salinity
34.1
34
33.9
33.8
33.7
33.6
33.5
33.4
y
y
x
xy
x
p < 0.01
e
group 1
group 2
group 3
group 4
group 5


surface temperature (°C)
12
10
8
6
4
2
0
z
z
x
y
y
p < 0.005
f
group 1
group 2
group 3
group 4
group 5


Integrated temperature (°C)
10
8
6
4
2
0
z
z
x
y
x
p < 0.001
g
group 1
group 2
group 3
group 4
group 5


sounding (m)
4000
3000
2000
1000
0
-1000
p = 0.08
h
group 1
group 2
group 3
group 4
group 5


chlorophyll a (mg.m-3)
2
1.5
1
0.5
0
p = 0.19
i
group 1
group 2
group 3
group 4
group 5

Integrated temperature accounted for 75 % of the variation in the zooplankton biomass data (Table 6.6.). Surface temperature and surface salinity accounted for 64% and 44 % of the variation respectively. Sounding and chlorophyll *a* were not significantly correlated with zooplankton biomass data.

Table 6.6. Results of the multiple regression of environmental variables against NMDS ordination scores for MIOS 4 biomass data (stress = 0.21). (degrees of freedom = 2.27).

	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	0.65	0.54	0.77	0.75	44.80	< 0.001
Surface temperature	0.46	0.64	0.66	0.64	27.02	< 0.001
Surface salinity	0.53	0.37	0.48	0.44	12.20	< 0.001
Sounding	0.04	0.09	0.01	0.06	0.12	0.87
Chlorophyll *a*	-0.17	0.26	0.09	0.02	1.34	0.28

The average similarity within groups 1 and 2 was 52.8% and 48.3% respectively (Table 6.7.). Groups 3, 4 and 5 had an average within group similarity of greater than 60%. The species *E. hamata, T. vicina, L. retroversa, C. simillimus, E. vallentini* and *S. gazellae* together accounted for >48% of the similarity within all station groups.

Important within Group 1, containing only inter-island stations, was the benthic decapod *Nauticaris marionis,* an indicator of island shelf stations (Branch *et al*., 1993). *Nematoscelis megalops*, a typically temperate euphausiid species (Gibbons, 1995), contributed 12.2% to the similarity within Group 2. This species was also an important component of Group 1. The Antarctic copepod *R. gigas* was also an important contributor to similarity within Group 5.

Table 6.7. Species responsible for 80% of the similarity within the five station groups identified by cluster analysis of MIOS 4 biomass data. Within group similarity is in parenthesis under group number. Cells indicate species biomass ($mg.m^{-3}$) and percentage contribution to within group similarity is in parenthesis.

Group 1 (52.82%)	**Group 2** (48.3%)	**Group 3** (62.32)	**Group 4** (60.5%)	**Group 5** (62.28%)
T. vicina 0.76 (30.6%)	*T. vicina* 0.81 (21.28%)	*E. hamata* 1.66 (21.41%)	*E. vallentini* 10.79 (40.54%)	*E. vallentini* 2.35 (17.38%)
C. simillimus 0.73 (12.3%)	*N. megalops* 1.12 (12.23%)	*L. retroversa* 1.95 (17.09%)	*L. retroversa* 0.99 (12.66%)	*T. vicina* 1.82 (12.87%)
S. gazellae 0.26 (8.9%)	*L. retroversa* 1.96 (8.51%)	*C. simillimus* 1.6 (14.83%)	*T. vicina* 2.45 (11.36%)	*E. hamata* 1.77 (12.63%)
E. vallentini 0.8 (8.7%)	*S. gazellae* 0.34 (7.35%)	*T. vicina* 1.09 (11.86%)	*E. hamata* 0.98 (7.25%)	*C. simillimus* 0.9 (8.5%)
E. hamata 0.23 (7.8%)	*T. gaudichaudii* 0.36 (5.77%)	*S. gazellae* 0.59 (5.8%)	*C. simillimus* 0.48 (5.9%)	*S. gazellae* 0.8 (6.99%)
N. megalops 0.32 (6.1%)	*E. vallentini* 0.41 (5.55%)	*Paraeuchaeta* spp. 0.43 (5.44%)		*L. retroversa* 0.64 (5.09%)
N. marionis 0.24 (5.3%)	*M. lucens* 0.29 (4.96%)			*P. abdominalis* 0.52 (4.94%)
	C. brevipes 0.26 (4.96%)			*R. gigas* 0.61 (4.58%)
	P. abdominalis 0.22 (4.15%)			*T. gaudichaudii* 0.95 (4.26%)

The percent dissimilarity between groups 5 and 3 and groups 5 and 4 was 44.9% and 45.35% respectively. The percent dissimilarity between all other groups was greater than 50%.

The species responsible for dissimilarity between groups were largely the same as those responsible for similarity within groups. *Eukrohnia hamata, L. retroversa, C. simillimus, N. megalops, E. vallentini, S. gazellae, Paraeuchaeta* spp*., T. vicina, E. longirostris* and *T. gaudichaudii* together accounted for >50% of the dissimilarity between all groups. The temperate species *M. lucens* contributed >4.3% to the dissimilarity between Group 2 and all other groups. *Euphausia longirostris* was almost entirely absent from groups containing only inter-island stations, and occurred at highest biomass within station Group 5. *Euphausia similis*, *S. thompsoni* and *T. gregaria* all occurred at highest biomass within Group 2.

The inverse analysis identified six species clusters at approximately the 55% level of similarity (Figure 6.9.). The first was not a cluster but rather a group of species occurring at highest abundance within station groups 2, 3 and 4 (Table 6.8.). The only species with a significant group association within this cluster was *E. vallentini*. The second and third species clusters were dominated by species occurring at highest biomass within station Group 5. The fourth and fifth clusters contained species with few significant group associations, occurring at highest abundance within station groups 2, 3 and 5. The final cluster contained species that occurred at highest biomass within station groups 1,3,4 and 5.

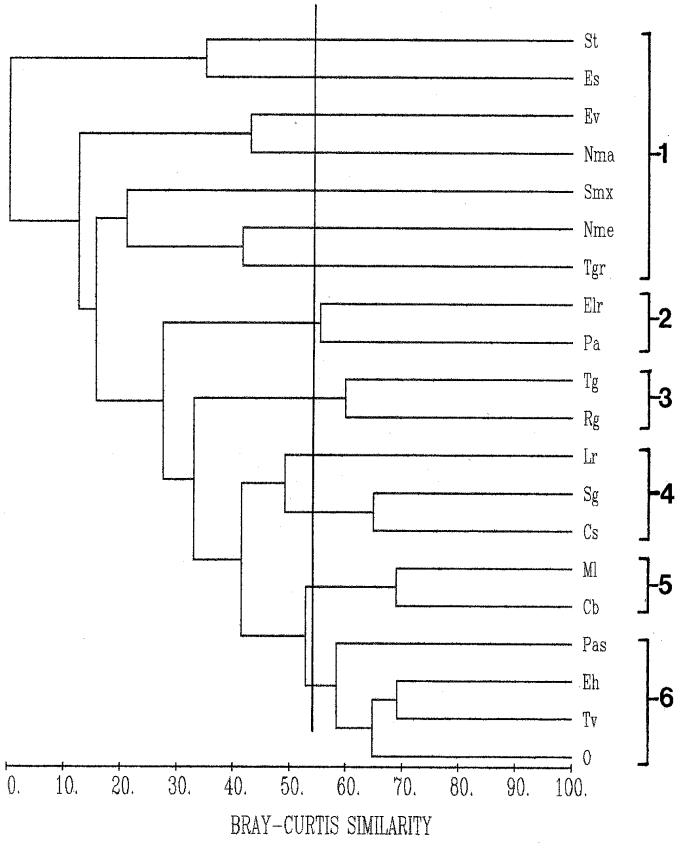


Figure 6.9. Dendrogram of the inverse cluster analysis, comparing zooplankton species dominating biomass, identified by SIMPER analysis of biomass data. The Bray-Curtis similarity measure was used after standardisation of the data set. Abbreviations follow those in Table 6.8.

Table 6.8. Species, abbreviations and names, used in the inverse analysis and the station groups within which each species occurred at highest biomass. Station groups within which a species occurred at significantly higher biomass, determined by group pair comparison using Mann-Whitney U tests, are in bold. Significant differences in the biomass of species between station groups, determined by Kruskal-Wallace tests, are indicated by p (- indicates no significant difference).

Species	**Group**	**P**
St – *Salpa thompsoni*	**2**	< 0.01
Es – *Euphausia similis*	2	-
Ev – *Euphausia vallentini*	**4**	< 0.005
Nma – *Nauticaris marionis*	4	-
Smx – *Stylocheiron maximum*	3	-
Nme – *Nematoscelis megalops*	2	-
Tgr – *Thysanoessa gregaria*	4	-
Elr – *Euphausia longirostris*	**5**	< 0.01
Pa – *Pleuromamma abdominalis*	**5**	< 0.01
Tg – *Themisto gaudichaudii*	**5**	< 0.05
Rg – *Rhincalanus gigas*	**5**	< 0.01
Lr – *Limacina retroversa*	3	-
Sg – *Sagitta gazellae*	**5**	< 0.05
Cs – *Calanus simillimus*	3	-
Ml – *Metridia lucens*	2	-
Cb – *Clausocalanus brevipes*	2	-
Pas – *Paraeuchaeta sp.*	1	-
Eh – *Eukrohnia hamata*	**3**	< 0.005
Tv – *Thysanoessa vicina*	4	-
O – Ostracods	**5**	0.05

The biomass data for *Eukrohnia hamata, S. gazellae, R. gigas, C. simillimus, M. lucens* and *C. brevipes* showed similar relationships with environmental variables to those identified by the abundance data (Table 6.9.). *Metridia lucens* and *C. brevipes* occurred at highest biomass within the warm water station Group 2 (Figure 6.8.; Table 6.8.). The other species all occurred at highest biomass within station groups 3 and 5, which were characterised by low temperature and salinity.

The tunicate *S. thompsoni* was positively correlated with surface temperature and was most abundant within the warm water Group 2. *Nauticaris marionis* was negatively correlated with sounding, which is indicative of this species inhabiting the island shelf,

and occurred at highest biomass within station Group 4 (Table 6.8.). *Pleuromamma abdominalis* was positively correlated with total chlorophyll *a*.

Table 6.9. Significant regressions of environmental variables and biomass for species contributing most to within group similarity and between group dissimilarity (degrees of freedom = 1.28).

Species	**Variable**	**Beta**	**R^2**	**Adjusted R^2**	**F**	**p**
E. hamata	Integrated temperature	-0.76	0.57	0.56	37.80	< 0.001
	Surface temperature	-0.68	0.47	0.45	24.50	< 0.001
	Surface salinity	-0.67	0.45	0.43	23.30	< 0.005
S. gazellae	Surface salinity	-0.42	0.17	0.14	5.85	< 0.05
S. thompsoni	Surface temperature	0.43	0.18	0.15	6.30	< 0.05
N. marionis	Sounding	-0.36	0.13	0.10	4.09	< 0.05
R. gigas	Integrated temperature	-0.44	0.19	0.16	6.50	< 0.05
C. simillimus	Integrated temperature	-0.58	0.34	0.31	14.30	< 0.01
	Surface temperature	-0.68	0.46	0.44	24.10	< 0.005
	Surface salinity	-0.46	0.21	0.18	7.30	< 0.01
M. lucens	Surface temperature	0.42	0.18	0.15	6.07	< 0.05
C. brevipes	Surface temperature	0.39	0.15	0.12	4.90	< 0.05
P. abdominalis	Chlorophyll *a*	0.65	0.47	0.45	24.60	< 0.005

The Information statistic showed that Group 2 was characterised by a high frequency of the sub-tropical species *P. sedentaria* and *C. magellanicus,* as well as the fish *E. carlsbergi* (Table 6.10.). Group 2 was further characterised by the presence of the sub-tropical species *E. similis* var. *armata, Stemonosudis* sp. and *E. cryomargarites*, as was station Group 4 in the abundance analysis. Group 5 was characterised by the presence of the Antarctic species *E. triacantha* and *G. antarcticus*.

Table 6.10. Frequency of occurrence of indicator species distinguishing cluster groups. Species above the blank line have $2)I > 6.63$ (p=0.01), and those below the line have $2)I > 3.84$ (p=0.05). Number of samples in a group is in parenthesis below the group number.

Species	**Group 1 (5)**	**Group 2 (6)**	**Group 3 (10)**	**Group 4 (3)**	**Group 5 (7)**
Phronima sedentaria	0	3	0	0	0
Cyllopus magellanicus	0	3	0	0	0
Electrona carlsbergi	0	3	0	0	0
Melophysa melo	0	0	0	0	2
Stemonosudis sp.	0	1	0	0	0
Echiodon cryomargarites	0	1	0	0	0
Euphausia similis var. *armata*	0	1	0	0	0
Gaetanus antarcticus	0	0	0	0	1
Euphausia triacantha	0	0	0	0	1

Chapter 7

RESULTS: Inter-annual comparison (1996 to 1999)

7.1. Oceanography:

The position of the SAF showed a high degree of variability between surveys (Figure 7.1.). During both the 1996 and 1998 zooplankton surveys it was situated to the north of its average position. In 1997 the SAF was located to the south of its average position during both surveys and moved slightly northwards from the first to the second survey. During Survey 1 in 1999 the SAF was relatively far to the south of its average position being in close proximity to the islands at 46°30'S. Two weeks later, upon completion of the second survey, the SAF was located at approximately its average position.
The APF was in close proximity to the islands in 1997 and 1999. During Survey 2 1997 the APF was crossed in the region downstream of the islands and was in close proximity to the islands themselves (Chapter 4). During Survey 1 1999 the APF was located at approximately 47°20'S along 37°E (Chapter 6).

A Kruskal-Wallace test showed that both surface and integrated temperature differed significantly between surveys ($p<0.005$). A Mann-Whitney U test showed that surface temperature was significantly higher during Survey 1 1999 than during all other surveys (Figure 7.2.a). Integrated temperature was highest during Survey 1 1999, but not significantly higher than during the 1996 survey (Figure 7.2.b). The lowest average temperature was recorded during Survey 2 of 1999. There was no significant difference in surface or integrated temperature between both surveys 1 and 2 of 1997, 1998 and Survey 2 1999.

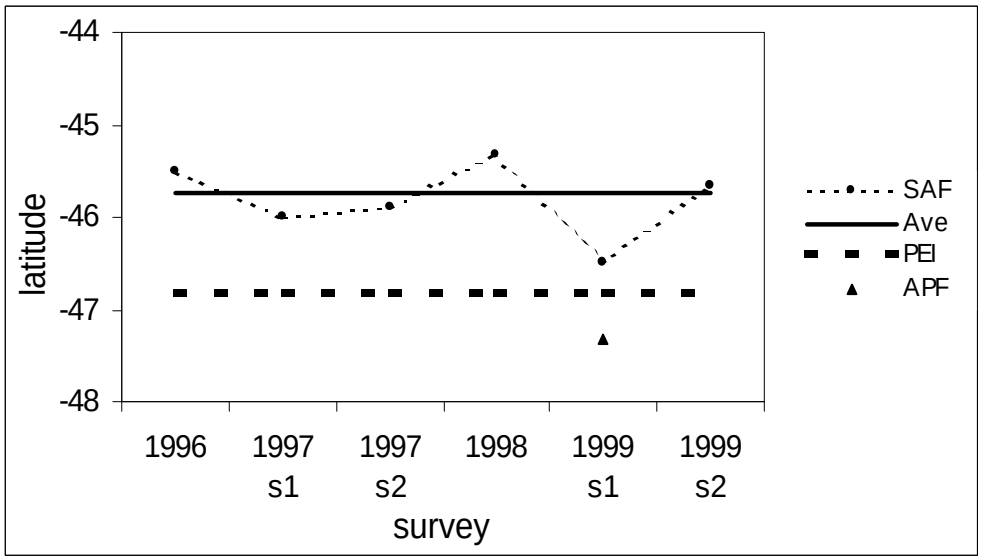


Figure 7.1. The position of the SAF along 37°E recorded during six surveys between 1996 and 1999 (s1 = survey 1; s2 = survey 2). The average position of the SAF (Ave) in the vicinity of the PEIs was determined from eleven crossings between 1987 and 1999. The latitude of the PEIs is indicated by the solid line. The location of the APF during Survey 1 1999 (along 37°E) is indicated by a triangle.

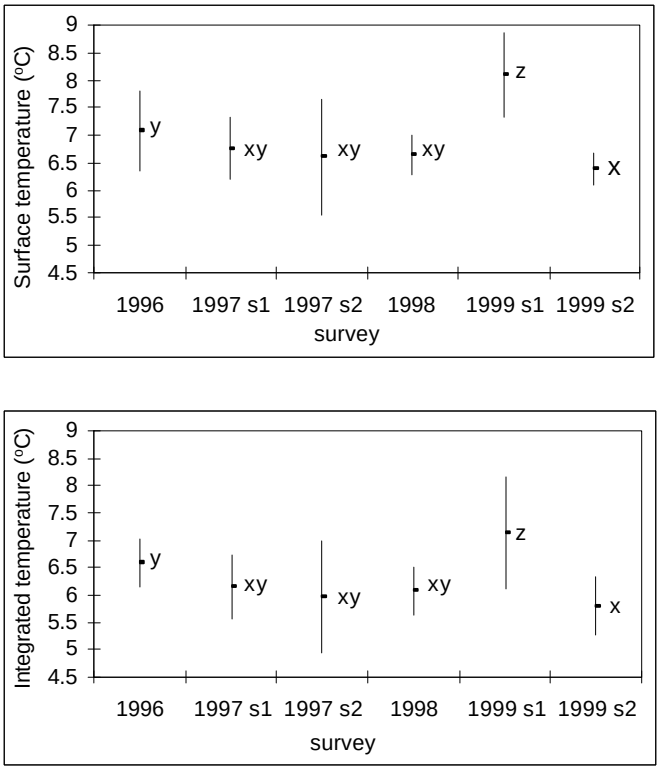


Figure 7.2. Average and standard deviation of surface (a) and integrated temperature (b) recorded for the six surveys conducted between 1996 and 1999. Significant differences ($p<0.05$) between surveys, determined by Mann-Whitney U tests of survey pairs, are indicated by different letters. Sharing of a letter indicates no significant difference.

7.2. Chlorophyll *a*:

A Kruskal-Wallace test showed that surface chlorophyll *a* concentrations differed significantly between surveys ($p<0.001$). Chlorophyll *a* concentrations were highest in 1996, although not significantly higher than levels recorded during surveys 1 and 2 of 1997 and Survey 1 1999 (Figure 7.3.). The lowest chlorophyll *a* concentrations were recorded during 1998 and Survey 2 1999. The 1996 survey, Survey 2 1997 and Survey 1 1999 were characterised by high standard deviations due to bloom level chlorophyll *a* concentrations being recorded at some stations.

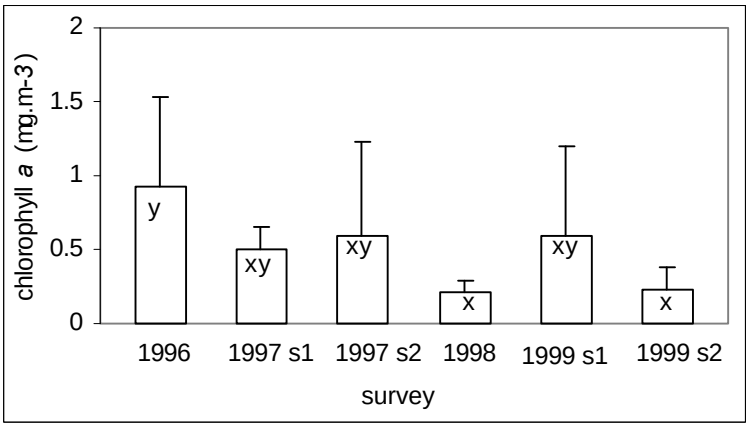


Figure 7.3. Average chlorophyll *a* concentrations ($mg.m^{-3}$) and standard deviations recorded for the six surveys conducted between 1996 and 1999. Significant differences ($p<0.05$) between surveys, determined by Mann-Whitney U tests of survey pairs, are indicated by different letters. Sharing of a letter indicates no significant difference.

7.3. Zooplankton:

7.3.1. Community structure:

SIMPER analysis identified a high degree of similarity **within** all surveys (> 60%) in terms of their respective zooplankton communities. The similarity **between** surveys was at least 50 % in all cases and exceeded 60% between surveys 1 and 2 of 1997, and surveys 1 and 2 of 1999. Community structure was therefore relatively similar between surveys.

In the cluster analyses of both abundance and biomass data (Figure 7.4.a,b) stations from the six surveys did not form completely separate, survey specific, clusters. Stations from the same survey did cluster out together, but in many instances these clusters were more similar to clusters of stations from different surveys. It therefore appeared that the different communities identified by the **intra-annual** analyses (chapters 3-6) retained their integrity in the **inter-annual** analysis, but that in most cases they were more similar

to communities from other surveys than to the different communities from their own survey. The biomass analysis (7.4.b) was characterised by greater mixing of stations from different surveys than the abundance analysis (Figure 7.4.a), indicating a higher degree of within survey heterogeneity in the biomass data.

The SIMPER analysis identified twenty-five species as responsible for 80% of the similarity within, and dissimilarity between, surveys in the abundance analysis. Inverse (r-type) analysis identified five species clusters within this species set (Table 7.1.a) at the 38% level of similarity. The first cluster was dominated by species occurring at highest abundance during 1998. The second, third and fourth clusters contained species showing no particular association with any one survey. The fifth cluster contained the copepods *M. gerlachei, E. longiceps* and *C. citer*, all of which occurred at significantly higher abundance during 1996.

Twenty-eight species contributed to 80% of the similarity within, and dissimilarity between, surveys in the biomass analysis. The inverse analysis identified six clusters, as well as five species with no significant inter-species relationships, at the 27% level of similarity (Table 7.1.b). The first cluster contained *P. pyramidata* and *M. melo,* both of which occurred at highest biomass during the 1996 survey. The remaining five clusters contained species with no specific survey associations.

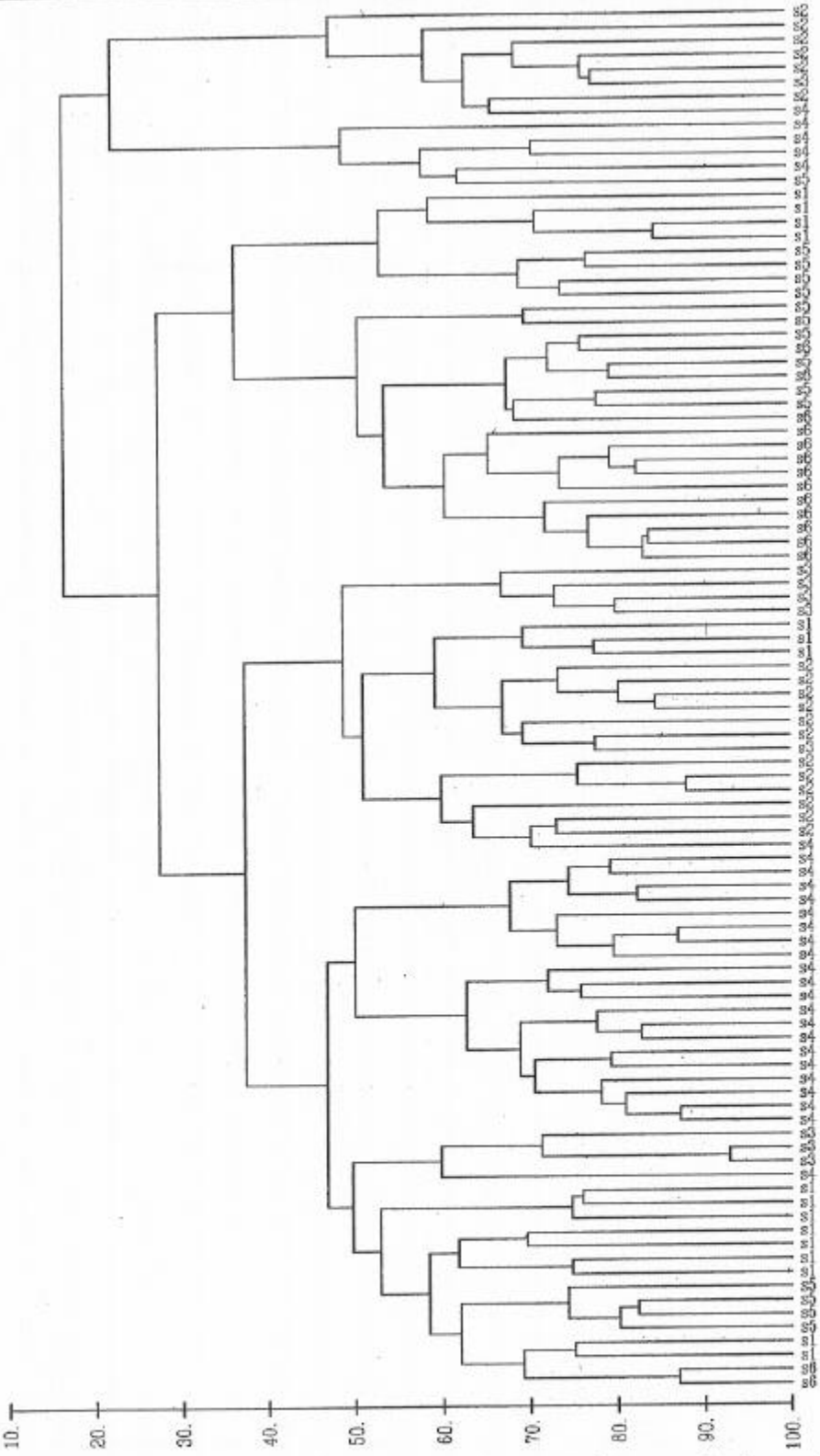


Figure 7.4.a. Dendogram of the cluster analysis comparing zooplankton abundance data between surveys. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species abundance data. [s1 = 1996; s2 = survey 1 1997; s3 = Survey 2 1997; s4 = 1998; s5 = Survey 1 1999; s6 = Survey 2 1999].

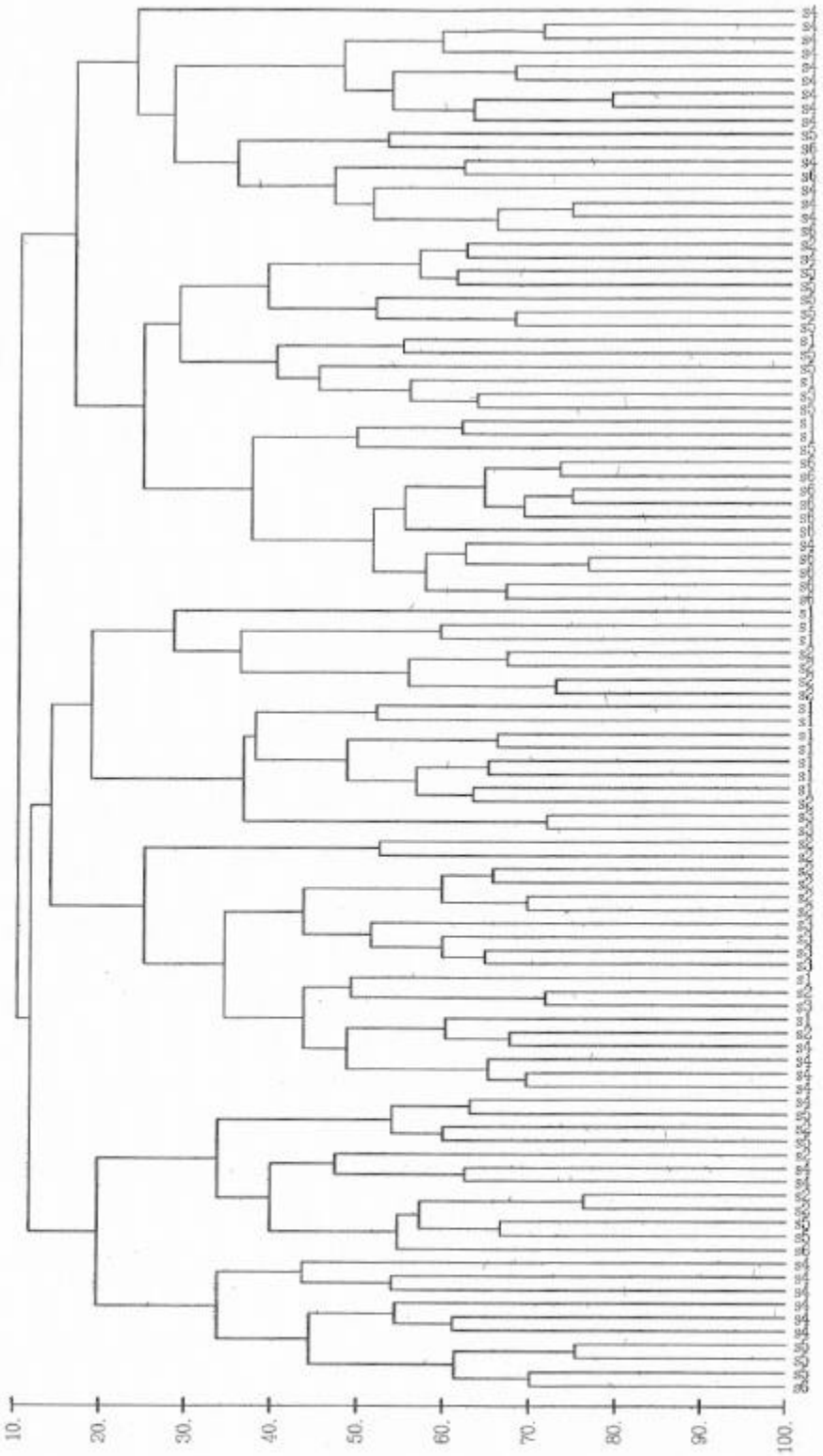


Figure 7.4.b. Dendrogram of the cluster analysis comparing zooplankton biomass data between surveys. The Bray-Curtis similarity index was used after $\log_{10}(x+1)$ transformation of species biomass data. [s1 = 1996; s2 = survey 1 1997; s3 = Survey 2 1997; s4 = 1998; s5 = Survey 1 1999; s6 = Survey 2 1999].

Table 7.1.a. Average abundance of species responsible for 80% of the similarity within, and dissimilarity between, surveys. Species clusters, identified by inverse analysis (r-type) at the 38% level of similarity, are indicated by shared numbers (• indicates a species not part of a cluster). One-way ANOVA was run on abundance values, normalized by $\log_{10}(x+1)$ transformation, in order to investigate differences in species biomass levels. Significance levels are indicated by p (- indicates no significant difference). Subsequently, Newman-Keuls multiple range tests were used to identify differences between the six surveys. Significantly higher abundance levels are in bold and underlined. Surveys with highlighted abundance levels for the same species are not significantly different from each other.

Cluster	Species	1996	1997 s1	1997 s2	1998	1999 s1	1999 s2	F	p
1	*L. helicina*	1.197	0.110	0.080	**1.539**	0.230	0.021	11.54	< 0.01
1	*O. similis*	0.321	0.116	0.000	**1.506**	0.012	0.120	10.98	< 0.01
1	*C. vanus*	0.089	**10.996**	**12.565**	**7.269**	0.009	0.000	48.97	< 0.001
2	*R. gigas*	**0.949**	0.051	**1.742**	0.108	**1.411**	**0.964**	5.60	< 0.01
2	*A. armatus*	**0.586**	0.117	**0.379**	0.196	0.156	**0.284**	3.26	< 0.01
3	*O. antarctica*	**0.885**	0.236	0.259	0.177	**0.566**	0.208	3.31	< 0.01
3	*H. austrinus*	0.437	0.484	0.315	0.213	0.306	0.325	-	-
3	*P. abdominalis*	**3.565**	1.256	**3.370**	0.875	0.982	0.427	3.09	< 0.01
•	*P. biloba*	0.060	0.376	**2.561**	0.282	0.433	0.730	15.19	< 0.005
4	*E. vallentini*	**0.191**	**0.579**	0.125	**0.592**	**0.432**	**0.676**	3.12	< 0.01
4	*L. retroversa*	4.060	0.379	0.906	**8.849**	7.833	**12.195**	14.05	< 0.01
4	*C simillimus*	1.862	0.516	13.888	12.046	5.445	**19.359**	13.47	< 0.01
4	*P. macropa*	**0.673**	0.430	0.419	0.024	**0.670**	**0.832**	22.13	< 0.005
4	*C. laticeps*	1.120	0.729	2.746	1.477	0.761	1.118	-	-
4	*S. minor*	1.883	1.221	2.871	1.860	0.776	1.334	-	-
4	*S. gazellae*	**3.858**	0.596	0.763	1.423	1.595	1.836	19.80	< 0.005
4	*E. hamata*	8.752	2.660	5.130	5.067	5.533	**21.016**	12.93	< 0.01
4	*T. vicina*	**2.949**	**2.616**	0.842	**3.335**	**3.166**	3.636	3.96	< 0.01
4	*O. frigida*	5.529	5.001	**16.213**	2.224	0.876	3.056	9.93	< 0.01
4	*M. lucens*	15.753	11.188	**47.463**	3.940	11.398	5.057	11.35	< 0.01
4	*C. brevipes*	**35.701**	**21.487**	**17.552**	10.952	9.743	7.554	5.76	< 0.01
4	*Ostracods*	6.989	5.364	9.734	5.336	4.995	6.133	-	-
5	*M. gerlachei*	**0.824**	0.000	0.000	0.002	0.000	0.000	7.16	< 0.01
5	*E. longiceps*	**0.556**	0.057	0.000	0.005	0.154	0.148	8.09	< 0.01
5	*C. citer*	**1.243**	0.000	0.000	0.000	0.000	0.000	26.43	< 0.001

Table 7.1.b. Average biomass of species responsible for 80% of the similarity within, and dissimilarity between, surveys. Species clusters, identified by inverse analysis (r-type) at the 27% level of similarity, are indicated by shared numbers (• indicates a species not part of a cluster). One-way ANOVA was run on biomass values, normalized by $\log_{10}(x+1)$ transformation, in order to investigate differences in species biomass levels. Significance levels are indicated by p (- indicates no significant difference). Subsequently, Newman-Keuls multiple range tests were used to identify differences between the six surveys. Significantly higher biomass levels are in bold and underlined. Surveys with highlighted biomass levels for the same species are not significantly different from each other.

Cluster	Species	1996	1997 s1	1997 s2	1998	1999 s1	1999 s2	F	p
•	***G. braueri***	0.002	0.140	0.035	0.024	0.000	0.008	-	-
•	***L. helicina***	0.539	0.005	0.001	0.018	0.007	0.002	-	-
1	***C. pyramidata***	**0.138**	0.000	0.000	0.027	0.020	0.001	12.99	< 0.005
1	***M. melo***	**0.145**	0.030	0.061	0.001	0.012	0.000	3.72	< 0.01
•	***N. marionis***	0.000	0.000	0.000	0.101	0.095	0.103	-	-
•	***T. gregaria***	0.048	0.043	0.060	0.086	0.154	0.190	-	-
2	***T. gaudichaudii***	0.046	0.067	**0.317**	0.033	**0.411**	**0.291**	4.72	< 0.01
2	***R. gigas***	**0.193**	0.004	**0.222**	0.015	**0.243**	**0.166**	4.57	< 0.01
3	***E. similis***	0.036	0.048	0.000	0.227	0.137	0.035	-	-
3	***C. simillimus***	0.207	0.033	0.585	**1.583**	0.415	**1.462**	5.56	< 0.01
•	***Gymnoscopelus* spp**	0.247	0.000	0.006	0.029	0.047	0.031	-	-
4	***L. retroversa***	0.103	0.059	0.084	**1.235**	**0.952**	**1.609**	11.61	< 0.005
4	***P. macropa***	0.060	0.028	0.024	**0.856**	0.036	0.110	20.42	< 0.001
4	***Protomyctophum* spp**	0.010	0.023	0.008	**0.151**	0.012	0.067	8.63	< 0.01
4	***C. vanus***	0.002	**0.213**	**0.251**	**0.141**	0.000	0.000	16.01	< 0.005
5	***E. longirostris***	0.681	0.231	0.674	0.221	0.171	0.281	-	-
5	***N. megalops***	0.026	**0.583**	**0.447**	**0.423**	**0.410**	0.445	2.53	< 0.05
5	***P. biloba***	0.019	0.120	**0.763**	0.090	0.090	0.094	18.75	< 0.001
6	***M. lucens***	0.387	0.227	**0.668**	0.093	0.223	0.163	11.62	< 0.005
6	***O. frigida***	0.017	0.015	**0.057**	0.007	0.003	0.010	11.00	< 0.005
6	***C. brevipes***	**0.712**	0.428	0.331	0.218	0.194	0.158	6.18	< 0.01
6	***H. austrinus***	0.104	0.115	0.065	0.051	0.037	0.041	-	-
6	***P. abdominalis***	0.884	0.311	0.879	0.217	0.243	0.113	2.80	< 0.05
6	***E. vallentini***	0.533	2.249	0.389	1.752	2.235	1.415	-	-
6	***S. gazellae***	0.443	0.092	0.118	0.207	0.319	**0.692**	7.95	< 0.01
6	***E. hamata***	0.775	0.170	0.371	0.553	0.457	**1.762**	14.20	< 0.005
6	***T. vicina***	0.535	**1.000**	0.295	**1.046**	**0.961**	**1.583**	6.32	< 0.01
6	***Ostracods***	0.241	0.185	0.427	0.184	0.172	0.217	-	-

7.3.2. Group composition:

Total abundance during all surveys was dominated by copepods (Figure 7.5.a), this group accounting for between 52% and 88% of the total zooplankton catch. Copepods were particularly dominant during 1997 contributing 82% and 88% to total abundance within surveys 1 and 2 respectively. A Newman-Keuls test showed that copepod abundance was significantly higher during Survey 2 1997 (average = 153.38 individuals.m^{-3}) than in any other survey (Table 7.2.a). There was no significant difference in copepod abundance between any other surveys, and the variation in percentage contribution of this of the group to total abundance therefore largely represents variation in the abundance of other groups.

Chaetognaths were an important component of the zooplankton community during Survey 2 1999, contributing 23% to total zooplankton abundance. The abundance of chaetognaths recorded during this survey was significantly higher than in any other survey. Chaetognaths contributed between 13% and 4% to total abundance within all other surveys.

Pteropods comprised between 13% and 15% of the total abundance recorded during 1998 and surveys 1 and 2 from 1999. The highest abundance for this group was recorded during 1998 and Survey 2 1999. Pteropod abundance was relatively low in 1996 and 1997, contributing between 1% and 5% to total abundance.

Euphausiids occurred at relatively low abundance during all surveys, but a Newman-Keuls test showed that they occurred at significantly lower levels during Survey 2 1997, contributing only 1% to total abundance. Ostracods showed no significant difference in abundance between years and contributed between 6% and 9% to total abundance. The highest abundance of hyperiids was recorded during the 1999 surveys, although they contributed only 1% to total abundance. Fish, hydromedusae, siphonophores, tunicates, decapods and ostracods contributed relatively little to total abundance and there was no significant difference in the abundance of these groups between surveys.

A comparison of total abundance between surveys indicated a high degree of similarity. The significantly higher abundance levels recorded during Survey 2 1997 were attributed to the high copepod abundance recorded during this survey.

Total zooplankton biomass was dominated by euphausiids and copepods during all surveys conducted between 1996 and 1999 (Figure 7.5.b). This was particularly evident in 1997 when these two groups together contributed 87% and 81% to the total biomass of surveys 1 and 2 respectively. During the 1996, 1998 and 1999 surveys euphausiids and copepods contributed between 62% and 67% to total biomass. The biomass of Euphausiids recorded during 1996 and Survey 2 1997 was significantly lower than in the other four surveys (Table 7.2.b). Both of these surveys were characterised by the dominance of copepod over euphausiid biomass, with Survey 2 1997 having significantly higher copepod biomass than all other surveys.

Hyperiid biomass was significantly higher during 1998 than all other surveys, despite the relatively low abundance of this group recorded during the same survey. Chaetognaths occurred at significantly higher biomass during Survey 2 1999, reflecting the high abundance levels recorded during this survey. Pteropods showed a similar correspondence between abundance and biomass and highest levels were recorded in 1998 and surveys 1 and 2 of 1999.

Fish, hydromedusae, siphonophores, tunicates, decapods and ostracods contributed relatively little to total biomass and there was no significant difference in the biomass of these groups between surveys. Of these groups fish and ostracods each contributed to between 1% and 4 % to total biomass.

There was no significant difference in total biomass between surveys although values recorded during 1998 and 1999 were higher than those recorded in 1996 and 1997.

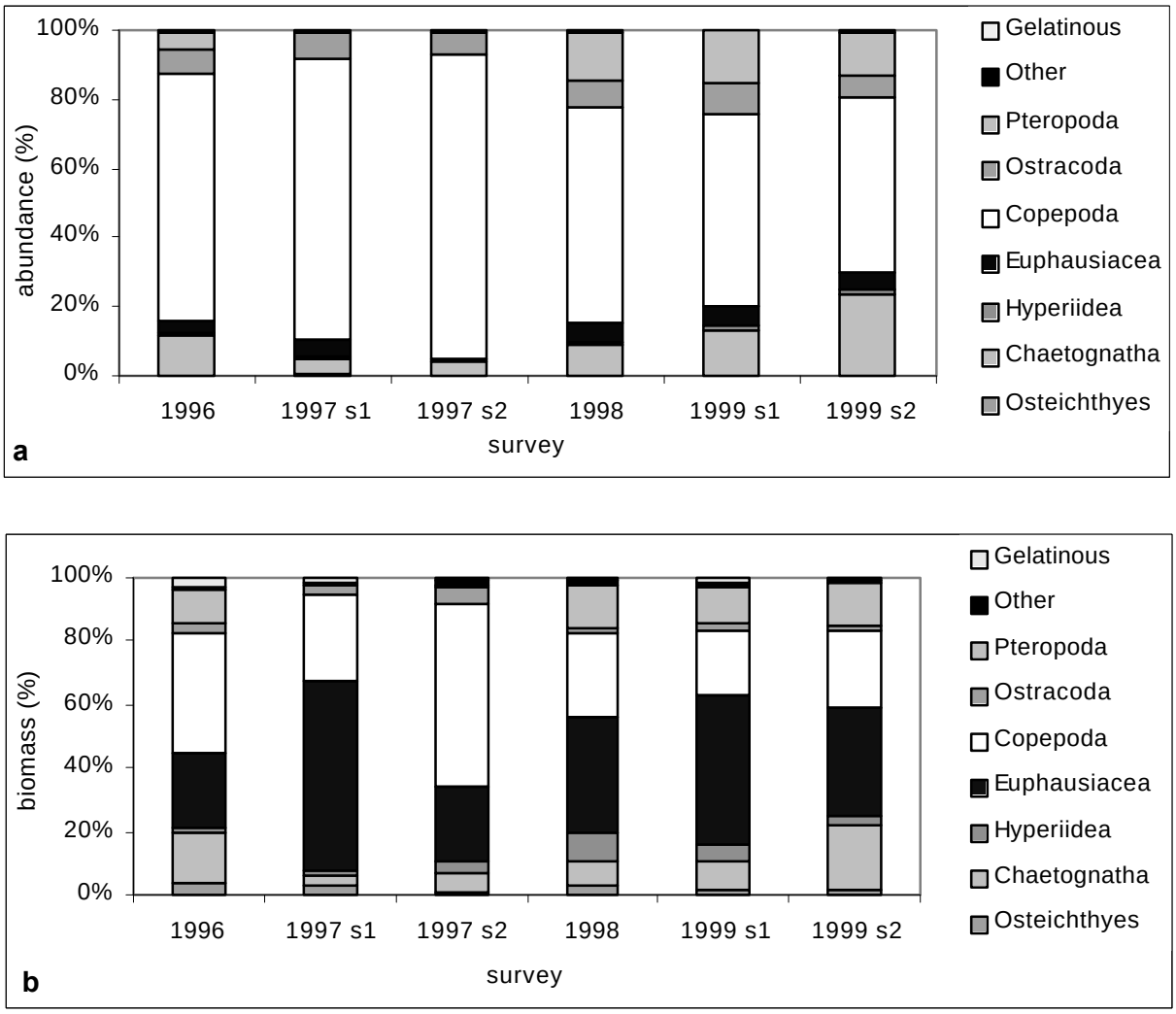


Figure 7.5. Percentage contribution of zooplankton groups to (a) total abundance and (b) total biomass recorded for the six surveys conducted between 1996 and 1999.

Table 7.2.a. Abundance (individuals.m^{-3}) and standard deviations (sd) of zooplankton groups for the six surveys between 1996 and 1999. One-way ANOVA was run on abundance data, normalized by $\log_{10}(x+1)$ transformation, to determine whether species abundance levels differed significantly between surveys. Significant differences are indicated by F and p. Subsequently Newman-Keuls Multiple Range tests were used to identify the surveys responsible for these differences. Significantly higher ($p<0.05$) abundance levels are in bold and underlined. Surveys with highlighted abundance levels for the same zooplankton group are not significantly different from each other.

Group	1996	sd	1997 S1	sd	1997 S2	sd	1998	sd	1999 S1	sd	1999 S2	sd	F	p
Hydromedusae	0.105	0.135	0.046	0.056	0.023	0.030	0.007	0.126	0.002	0.006	0.047	0.087	-	-
Siphonophora	0.192	0.169	0.109	0.085	0.164	0.142	0.185	0.257	0.085	0.150	0.271	0.257	-	-
Pteropoda	5.550	7.690	0.494	0.520	0.986	1.827	**10.506**	10.995	8.119	14.993	**12.793**	10.171	15.01	< 0.005
Other	0.148	0.032	0.059	0.014	0.097	0.023	0.105	0.028	0.057	0.015	0.102	0.023	-	-
Ostracoda	6.989	3.742	5.364	2.883	9.734	7.833	5.336	4.834	4.995	4.453	6.310	4.475	-	-
Copepoda	75.752	51.104	59.082	41.588	**134.791**	69.381	45.844	60.919	37.039	21.129	47.726	17.990	6.1	< 0.01
Decapoda	0.001	0.002	0.001	0.004	0.000	0.001	0.013	0.026	0.021	0.040	0.023	0.046	-	-
Euphausiacea	**3.420**	1.796	**3.352**	1.899	1.102	0.596	**4.065**	2.560	**3.774**	2.559	**4.733**	4.702	4.43	< 0.01
Hyperiidea	**0.820**	0.623	0.483	0.327	0.456	0.316	0.189	0.165	**0.927**	0.614	**1.091**	0.614	16.39	< 0.01
Chaetognatha	12.610	7.771	3.256	2.377	5.893	3.683	6.490	5.408	7.128	5.380	**23.360**	10.870	15.81	< 0.05
Tunicata	0.022	0.044	0.004	0.015	0.000	0.000	0.007	0.035	0.006	0.012	0.001	0.002	-	-
Osteichthyes	0.103	0.071	0.276	0.402	0.138	0.080	0.164	0.107	0.096	0.069	0.151	0.102	-	-
Total	105.713	51.284	72.526	43.313	**153.384**	72.127	72.950	72.587	65.250	25.399	96.609	30.929	4.27	< 0.01

Table 7.2.b. Biomass ($mg.m^{-3}$) and standard deviations (sd) of zooplankton groups for the six surveys between 1996 and 1999. One-way ANOVA was run on biomass data, normalized by $\log_{10}(x+1)$ transformation, to determine whether species biomass levels differed significantly between surveys. Significant differences are indicated by F and p. Subsequently Newman-Keuls Multiple Range tests were used to identify the surveys responsible for these differences. Significantly higher ($p<0.05$) biomass levels are in bold and underlined. Surveys with highlighted biomass levels for the same zooplankton group are not significantly different from each other.

Group	1996	sd	1997 S1	sd	1997 S2	sd	1998	sd	1999 S1	sd	1999 S2	sd	F	P
Hydromedusae	0.036	0.085	0.016	0.063	0.002	0.003	0.034	0.114	0.000	0.000	0.001	0.002	-	-
Siphonophora	0.163	0.296	0.063	0.107	0.090	0.105	0.039	0.104	0.044	0.078	0.013	0.012	-	-
Pteropoda	0.839	2.226	0.065	0.093	0.085	0.168	**1.418**	1.710	**1.005**	1.845	**0.623**	1.214	7.68	< 0.005
Other	0.044	0.023	0.003	0.001	0.004	0.001	0.025	0.012	0.006	0.003	0.007	0.003	-	-
Ostracoda	0.241	0.129	0.185	0.099	0.336	0.270	0.184	0.167	0.172	0.153	0.217	0.154	-	-
Copepoda	2.977	2.656	1.932	0.894	**4.694**	1.642	2.716	6.846	1.795	1.149	2.921	1.205	4.85	< 0.01
Decapoda	0.015	0.058	0.037	0.107	0.067	0.202	0.116	0.319	0.098	0.165	0.103	0.269	-	-
Euphausiacea	1.890	1.546	**4.172**	3.140	1.880	1.205	**3.768**	2.946	**4.097**	4.108	**4.094**	4.010	3.26	< 0.01
Hyperiidea	0.118	0.083	0.095	0.159	0.352	0.454	**0.906**	1.050	0.466	0.863	0.421	0.480	8.14	< 0.005
Chaetognatha	1.217	0.818	0.261	0.161	0.437	0.305	0.760	0.928	0.776	0.740	**2.455**	1.035	18.77	< 0.001
Tunicata	0.041	0.122	0.023	0.095	0.000	0.000	0.010	0.030	0.100	0.166	0.041	0.149	-	-
Osteichthyes	0.327	0.940	0.187	0.589	0.051	0.088	0.351	0.460	0.151	0.204	0.152	0.130	-	-
Total	7.907	4.254	7.522	4.288	7.998	2.357	10.326	11.745	8.712	5.531	12.049	4.550	0.92	0.47

7.3.3. Regional distribution of abundance, biomass and zooplankton size:

Abundance levels in all regions, and from all surveys, were dominated by copepods (Figure 7.6.a), reflecting the results of the intra-survey analysis of group composition (Figure 7.5.). The abundance levels of most zooplankton groups were masked due to their relatively low levels in comparison to copepods. Abundance and biomass levels of groups were generally positively correlated, although some exceptions were observed (7.6. a,b). In 1996 the inter-island region had the highest total abundance, yet total biomass was low, indicating that the average size of zooplankton in this region was small. This was supported by Figure 7.7. (see below). During Survey 1 1997 abundance levels were highest in the inter-island region but biomass levels were very similar to the downstream region, while during Survey 2 1997 abundance levels were very similar in the upstream and downstream regions but biomass levels were highest in the latter. Figure 7.7. showed that in both surveys, and particularly Survey 2, the average size of certain zooplankton groups was higher in the downstream region. Of more importance in Survey 1 was the high contribution of the group "Other", containing 99% decapods, to biomass levels in the downstream region (Figure 7.6.b).

Biomass levels recorded in all regions, and from all surveys, were dominated by copepods and euphausiids (Figure 7.6.b). In 1996 the highest zooplankton biomass was recorded in the upstream region and the lowest in the inter-island region. Copepods, pteropods and fish were important components of the upstream region, relative to the inter-island and downstream regions where the latter two groups were virtually absent. Euphausids occurred at highest biomass in the downstream region, while in the inter-island region they exhibited the lowest biomass levels recorded for any survey, or region, during the course of this study. The groups occurring at highest biomass in the inter-island region were copepods and chaetognaths.

During Survey 1 1997 similar copepod biomass was recorded in all three regions. Upstream euphausiid biomass was relatively low while fish biomass was high in comparison to the inter-island and downstream regions. Highest euphausiid biomass was

recorded in the inter-island region. As mentioned above the biomass of the group "Other" was relatively high in the downstream region.

During Survey 2 1997 biomass in both the upstream and downstream regions was dominated by copepods while euphausiid biomass was relatively low. Group biomass distribution was similar between regions, although copepod and total biomass were higher in the downstream region.

The upstream and inter-island regions were relatively similar in 1998 although the inter-island region had slightly lower euphausiid and copepod biomass. Total biomass in the downstream region was double that of the latter two regions. This was largely due to copepods, although the biomass recorded for fish, hyperiids, pteropods and chaetognaths were all higher than recorded in the upstream and inter-island regions.

During Survey 1 1999 biomass was lowest in the inter-island region and highest in the downstream region. Copepod, euphausiid, hyperiid and chaetognath biomass levels in the inter-island region were relatively low. Conversely, pteropod biomass was relatively high.

During Survey 2 1999 all regions had similar total biomass, although levels were slightly lower in the upstream region. Euphausiid biomass was highest in the inter-island region, while copepods and pteropods contributed more to biomass in the upstream and downstream regions.

It was difficult to identify clear regional trends in the average size of individuals in zooplankton groups (Figure 7.7.). The average size of fish recorded in the inter-island region was always lower than in the upstream region, and lower than in the downstream region in 1996, 1998 and Survey 1 1999. The largest average size was recorded in the upstream region during 1996, Survey 1 1997 and Survey 2 1999, and in the downstream region during 1998 and Survey 1 1999.

Euphausiids were of a smaller average size in the inter-island region during all surveys, with the exception of 1996 and Survey 2 1999. The largest average size recorded for this group varied between the upstream and downstream regions.

Hyperiids were of a smaller average size in the inter-island region during all surveys with the exception of Survey 2 1999, when they were smaller in the downstream region. During Survey 2 1997 they occurred at a larger average size in the downstream region.

Pteropods were of a smaller average size in the downstream region during all surveys with the exception of 1996 and Survey 2 1997. There was no consistent pattern to the distribution of average copepod and chaetognath size between regions.

In 1996 the zooplankton groups containing small species were characterised by smaller average individual size in the inter-island region than in the up and downstream regions. During Survey 2 1997 there was a general pattern of increased individual size in the downstream region. During Survey 2 1999 the zooplankton groups containing larger individuals showed a decrease in average size in the downstream region.

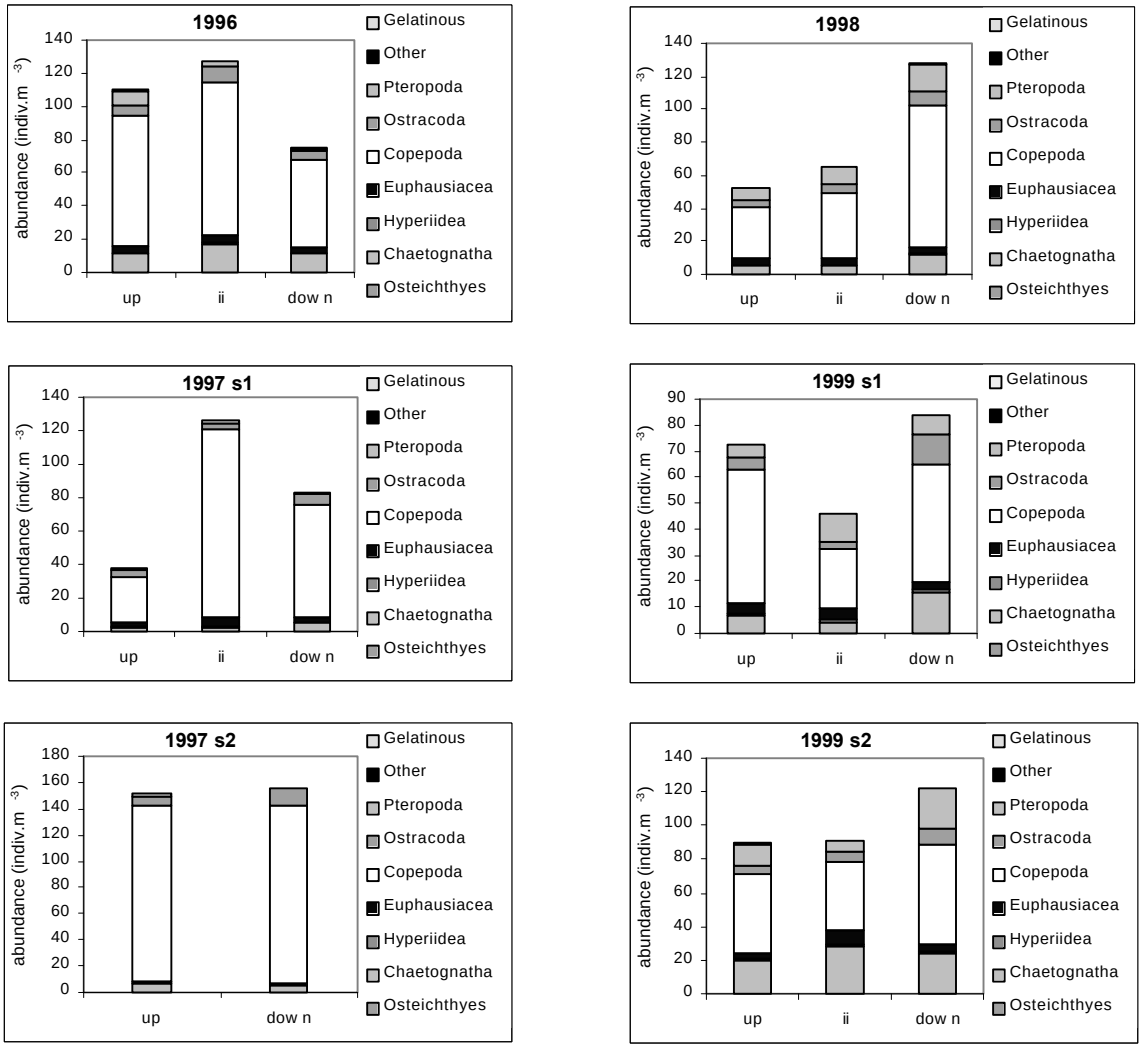


Figure 7.6.a. Average abundance of zooplankton groups recorded in the regions upstream (up), between (ii) and downstream (down) of the islands for the six surveys conducted between 1996 and 1999. No inter-island samples were collected during Survey 2 1997. The group "Other" contained polychaetes, gamariids, decapods and isopods while the group "Gelatinous" contained siphonophores, ctenophores, tunicates and hydromedusae.

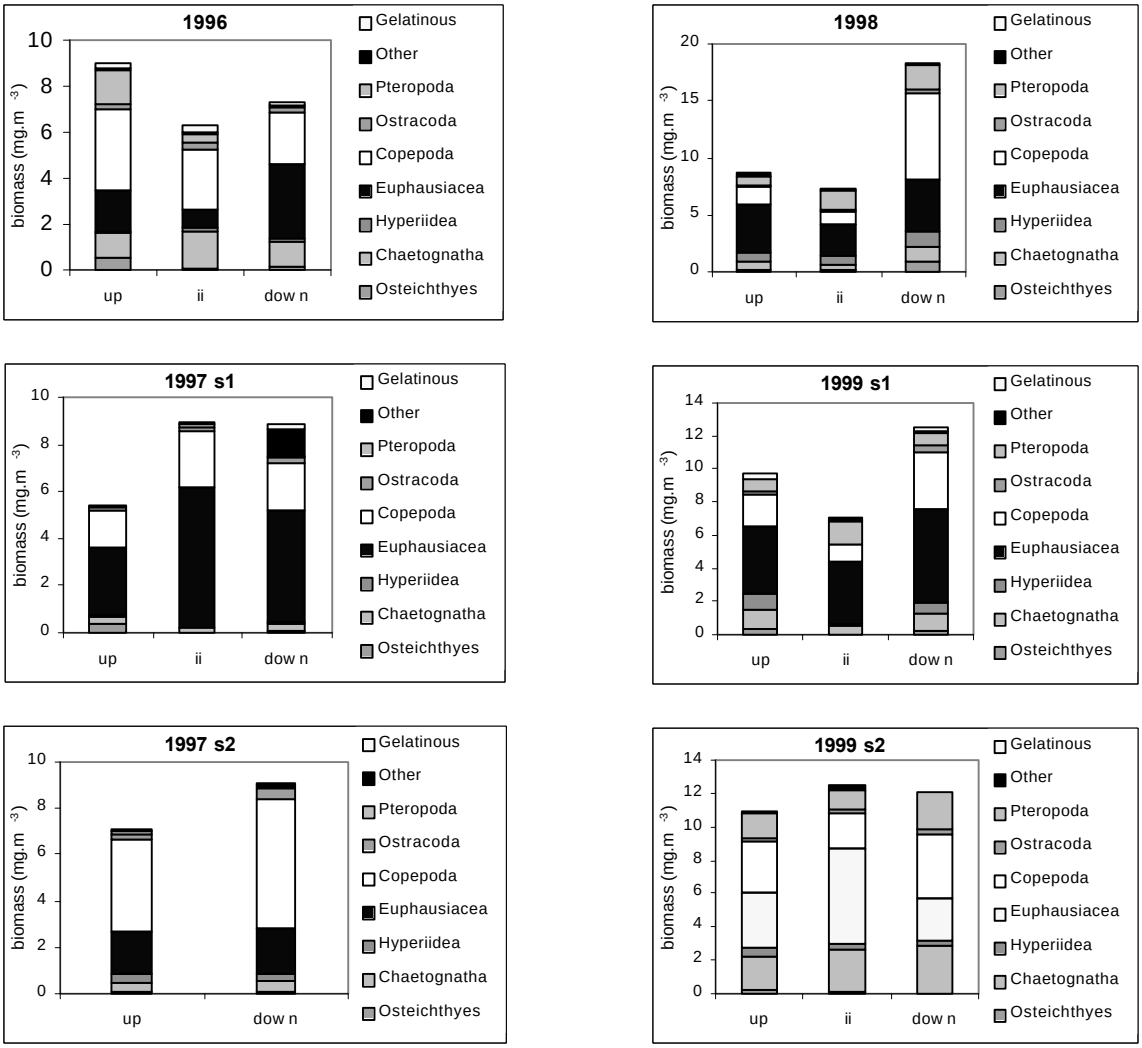


Figure 7.6.b. Average biomass of zooplankton groups recorded in the regions upstream (up), between (ii) and downstream (down) of the islands for the six surveys conducted between 1996 and 1999. No inter-island samples were collected during Survey 2 1997. The group "Other" contained polychaetes, gamariids, decapods and isopods while the group "Gelatinous" contained siphonophores, ctenophores, tunicates and hydromedusae.

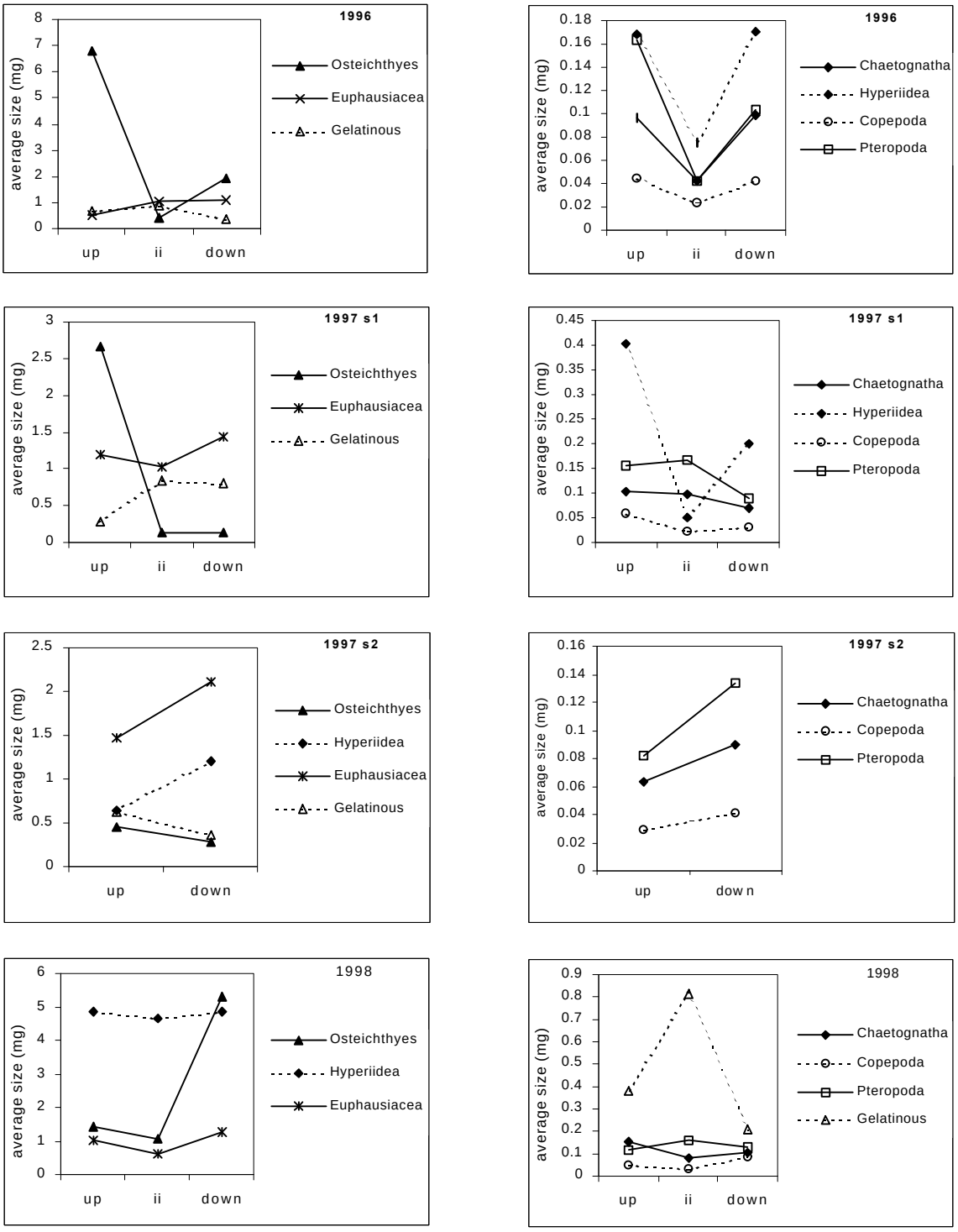


Figure 7.7. Average individual size (mg) recorded for the dominant zooplankton groups in the upstream (up), inter-island (ii) and downstream (down) regions of the PEIs for the six surveys conducted between 1996 and 1999. Due to the large differences in average size of zooplankton groups two y-axes with different scales have been used for each survey. *Figure 7.7. continued overleaf...*

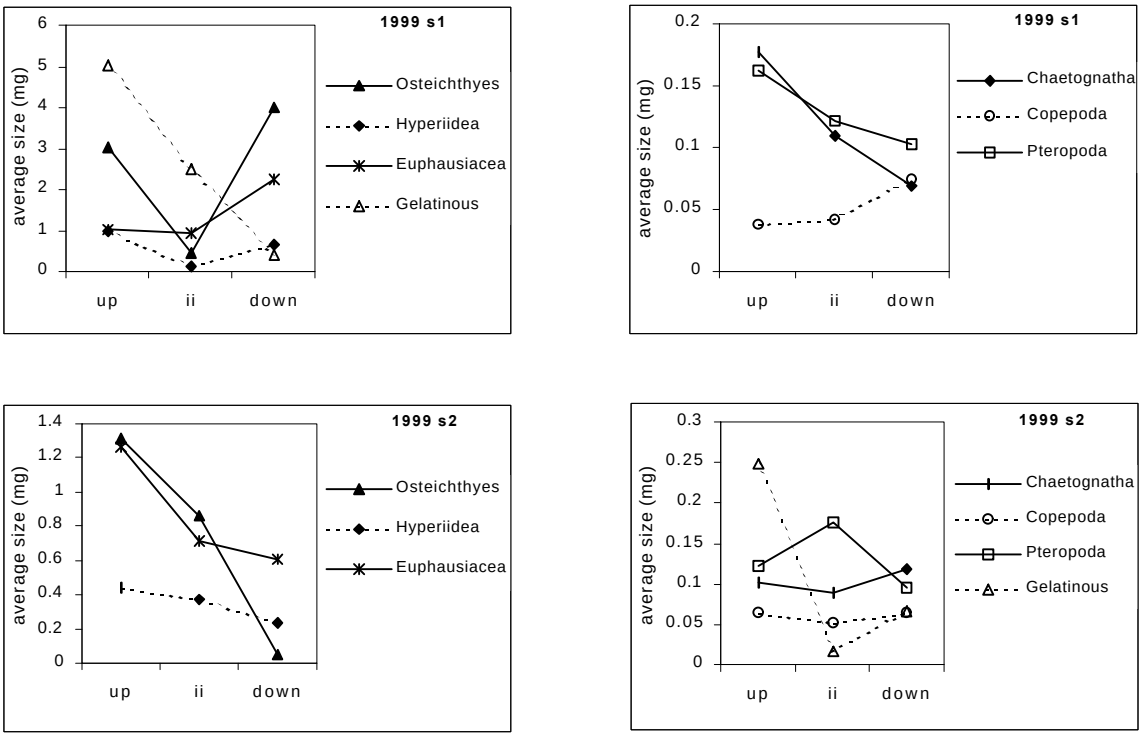


Figure 7.7. *continued*

7.3.4. Sources of variation in community structure:

Of the environmental variables recorded during each survey surface and integrated temperature, surface salinity and sounding accounted for a significant amount of variation in community structure (Table 7.3.). Surface temperature accounted for a significant amount of variation during all years. The correlation between temperature and zooplankton community structure was generally strong, while for sounding it was relatively weak. Surface salinity was only an important factor during 1999 when it accounted for approximately 50% of the variation in community structure, in terms of both abundance and biomass data.

Table 7.3. Significant R^2 values ($p<0.05$) for the multiple regression of environmental variables against NMDS ordination scores, for the abundance and biomass analyses from 1996 to 1999 (- indicates no significant difference).

	Surface temperature		**Integrated temperature**		**Surface Salinity**		**Sounding**		**Chlorophyll *a***	
	Abun	**Biom**	**Abun**	**Biom**	**Abun**	**Biom**	**Abun**	**Biom**	**Abun**	**Biom**
1996	0.49	-	-	-	-	-	-	-	-	-
1997	0.37	0.42	-	0.45	-	-	0.23	-	-	-
1998	0.28	0.69	-	-	-	-	0.33	0.26	-	-
1999	0.59	0.72	0.66	0.77	0.54	0.48	-	-	-	-

Neither surface nor integrated temperature accounted for a significant amount of variation in zooplankton community structure, represented by abundance data, when all surveys were combined (Table 7.4.). However, sounding, chlorophyll *a*, and surface salinity were important determinants of community structure.

Table 7.4. Results of the multiple regression of environmental variables against NMDS ordination scores for the combined, 1996 to 1999, abundance data (stress = 0.21). (degrees of freedom = 2.2).

	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	0.18	-0.07	0.04	0.01	1.51	0.23
Surface temperature	0.09	-0.12	0.02	-0.01	0.95	0.39
Surface salinity	0.09	0.25	0.08	0.05	3.34	< 0.05
Sounding	0.09	-0.31	0.10	0.08	4.56	< 0.01
Chlorophyll *a*	-0.21	-0.28	0.13	0.11	6.06	< 0.01

Surface salinity, sounding and chlorophyll *a* accounted for a significant amount of variation in zooplankton community structure as measured by biomass data (Table 7.5.).

Table 7.5. Results of the multiple regression of environmental variables against NMDS ordination scores for the combined, 1996 to 1999, biomass data (stress = 0.27). (degrees of freedom = 2.2).

	Regression coefficients					
Variable	**X**	**Y**	**R^2**	**Adjusted R^2**	**F**	**p**
Integrated temperature	-0.17	-0.14	0.04	0.01	1.5	0.22
Surface temperature	-0.07	-0.23	0.05	0.03	2.17	0.12
Surface salinity	-0.33	0.18	0.17	0.15	8.54	< 0.01
Sounding	0.29	-0.34	0.25	0.23	13.32	< 0.01
Chlorophyll *a*	0.35	-0.00	0.12	0.10	5.8	< 0.01

7.3.5. Population structure of *C. simillimus*:

The surveys conducted in 1996 and 1997 were characterised by the complete absence of the adult copepodite stage. The 1996 survey was dominated by stage 3 copepodites (C3) while the 1997 surveys were dominated by C2. Adult copepodites dominated in 1998 and the 1999 surveys were dominated by C4.

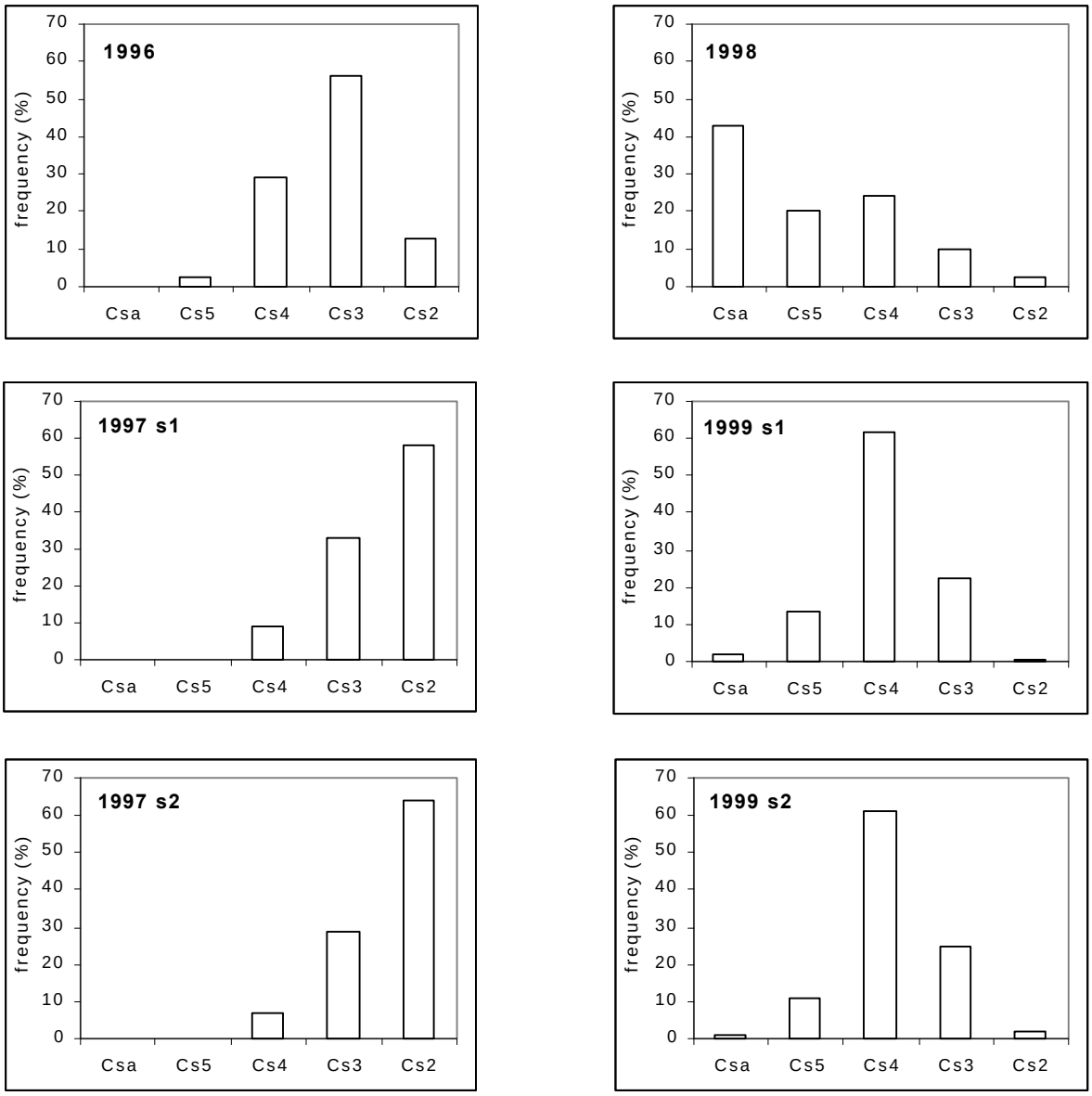


Figure 7.8. Percentage frequency of occurrence of developmental stages of *C. simillimus* for the six surveys (s1 = survey1; s2 = survey 2) conducted between 1996 and 1999. Cs2 to Cs5 = *C. simillimus* copepodite stages 2 to 5.; Csa = *C. simillimus* adult.

Chapter 8

Discussion:

8.1. Oceanographic environment:

The SAF and APF in the vicinity of the Prince Edward Islands are characterised by a high degree of latitudinal variation in position (Lutjeharms and Vallentine, 1984; Nagata *et al*., 1988; Duncombe Rae, 1989 a,b; Lutjeharms, 1990). In the six surveys conducted between 1996 and 1999 the position of the SAF fluctuated between 46°30'S and 45°20'S, although located even further north, at approximately 44°S, in 1996 by Froneman *et al*. (1998), while the APF was twice encountered in close proximity to the islands. A striking feature of this positional fluctuation was the high speed at which it occurred. Rapid variation in the width of the PFZ has previously been observed by Sievers and Emery (1978), while Nowlin and Klinck (1986) recorded frontal shifts of as much as 100km in 10 days within the ACC. The oceanographic environment in the vicinity of the PEIs is therefore a dynamic one. Not only do physical conditions show a high degree of variation but changes can occur over a short period of time. This was particularly well illustrated during the 1999 survey with average sea surface temperatures changing from 8.1°C to 6.39°C and average integrated temperature changing from 7.13°C to 5.79°C between surveys 1 and 2.

8.2. Chlorophyll a:

According to the physical parameters set out by Perissinotto and Duncombe Rae (1990) and Ansorge and Lutjeharms (submitted), the oceanographic environment during 1996, 1998 and Survey 2 of 1999 was conducive to water retention and consequently enhanced primary production levels over the island shelf (see Chapter 1). During the 1996 MIOS 1 survey bloom level chlorophyll *a* concentrations were observed in the inter-island region and on the downstream side of the island shelf. Furthermore, Pakhomov and Froneman

(1999 a) observed a four-fold increase in total chlorophyll *a* concentrations, from ~0.5 $mg.m^{-3}$ to 2.0 $mg.m^{-3}$, in the inter-island region during the course of the MIOS 1 survey, indicating the development of a phytoplankton bloom.

Conversely, during 1998 and Survey 2 of 1999, chlorophyll *a* concentrations were extremely low. In 1998 enhanced primary production levels were not observed over the island shelf (Balarin, 1999). Oceanographic data showed that a flow through environment existed in the trench between the islands (Pakhomov *et al*., in press), despite the SAF being positioned far to the north of the islands. However, significantly higher microphytoplankton concentrations were recorded in the inter-island region. Previous investigations have shown microphytoplankton to dominate phytoplankton blooms at the PEIs (Allanson *et al*., 1985; Boden, 1988; Perissinotto and Boden, 1989; Pakhomov and Froneman, 1999 a,b). Thus, the phytoplankton community composition indicated that some degree of production enhancement occurred over the island shelf, possibly due to limited water retention coupled with the island mass effect (Boden, 1988). However, the residence time of water over the island shelf may have been too short to result in a full scale phytoplankton bloom. It has previously been estimated that the minimum time period necessary for the generation of a bloom is ~15 days (Perissinotto and Duncombe Rae, 1990). Short residence time may also have been an important reason for the low chlorophyll *a* concentrations observed over the island-shelf during Survey 2 1999. The SAF had been located in close proximity to the islands two weeks previously, during Survey 1. It is therefore possible that even if water retention was occurring over the shelf a phytoplankton response was limited by time.

The fronts may have a more direct effect on chlorophyll *a* concentrations in the vicinity of the islands. Both the SAF and the APF are regions of enhanced primary production (Allanson *et al*., 1981; Lutjeharms *et al*., 1985; Laubscher *et al.,* 1993; Froneman *et al*., 1995; Froneman and Ansorge, 1998; Froneman *et al*., 1998). This was evident during the MIOS 1 survey when chlorophyll *a* concentrations averaged 1.61 $mg.m^{-3}$ at the SAF. It is possible that when the fronts are in close proximity to the islands their elevated production may be transported to the island system (Froneman and Pakhomov, 1998). However, this was not supported by this study. Although chlorophyll *a* concentrations in

1997 were relatively high in comparison to 1998 and Survey 2 of 1999, no enhancement was observed at the SAF and levels remained within the range typical for the PFZ (Laubscher *et al*., 1993; Fiala *et al*., 1998; Froneman and Ansorge, 1998; Froneman *et al*., 1998; Pakhomov *et al*., 1999 a). The high standard deviation recorded for Survey 2 1997 was due to one station situated to the north of the SAF with chlorophyll *a* concentrations of 2.27mg.m^{-3}, indicating isolated phytoplankton enhancement.

Relatively high average chlorophyll *a* concentrations were also observed during Survey 1 1999. However, as in 1997, no production enhancement was observed at stations in the vicinity of either the SAF or the APF (Figure 6.3.). The high chlorophyll *a* concentrations were largely due to three stations, MS4-9, MS4-10 and MS4-14, on the downstream side of the island shelf. These stations had chlorophyll *a* concentrations equivalent to bloom conditions (1.32 – 2.39 mg.m^{-3}). As demonstrated by this study the oceanographic environment in the vicinity of the PEIs can change rapidly. It is possible that conditions may have favoured water retention prior to Survey 1 and that these three stations represented the remnants of a phytoplankton bloom in the inter-island region, being swept downstream due to the close proximity of the SAF. Two weeks later during Survey 2 no elevated chlorophyll *a* concentrations were recorded in the inter-island or downstream regions.

When stations MS4-9, MS4-10 and MS4-14 were excluded from the analysis there was no significant difference ($p<0.05$) in chlorophyll *a* concentrations between surveys 1 and 2 of 1999, despite the proximity of the SAF during Survey 1. However, Survey 1 differed from Survey 2 in that microphytoplankton made a relatively large contribution to total chlorophyll *a*. High chlorophyll *a* concentrations at the SAF are often characterised by high microphytoplankton concentrations (Froneman *et al*., 1995; Froneman *et al*., 1998). The relatively large contribution of microphytoplankton to total chlorophyll *a* during Survey 1 may therefore have been due to the close proximity of the SAF to the islands and consequently advection of water from the vicinity of the front into the inter-island region. The difference in the contribution of phytoplankton size fractions certainly concurs with the change in oceanographic environment recorded between the two surveys.

Strong positive correlations were observed between some copepod species and chlorophyll *a* concentrations during all surveys. Enhanced mesozooplankton biomass associated with high phytoplankton biomass has previously been observed near South Georgia (Atkinson *et al*., 1996). The positive correlations between chlorophyll *a* and predatory chaetognaths and the hyperiid *Primno macropa* during MIOS 1 were most likely a direct result of the increased copepod densities. The high productivity associated with the SAF and the island shelf may therefore have a significant influence on zooplankton community structure. However, neither of these regions demonstrated consistently high phytoplankton biomass during this study. Previous studies have shown that a high degree of variation in chlorophyll *a* concentrations is typical of the SAF (Laubscher *et al*., 1993; Froneman *et al*., 1998).

8.3. Zooplankton:

8.3.1. Position of the fronts:

The rapid variation in the position of the fronts has a number of implications for zooplankton community structure at the PEIs. Oceanic frontal systems represent strong biogeographic boundaries, separating distinct zooplankton communities (Backus, 1985). Tarling *et al*. (1995) showed that although the regions to the north and south of the SAF have a number of species in common, these regions are clearly separated through varying species abundance levels. Fluctuations in the position of the SAF, as well as the APF, may therefore directly affect community structure at the PEIs by bringing different biogeographic realms into the region.

The positional variability of the SAF and APF is partly due to extensive meandering (Hofmann, 1985), a feature enhanced by bottom topography (Gordon *et al*., 1978; Nowlin and Klink, 1986; Belkin and Gordon, 1996; Trathan *et al*., in press). Meanders in both the SAF and APF were evident during MIOS 2 and MIOS 4 and have previously been observed by a number of authors (Sievers and Emery, 1978; Hoffman, 1985, Nowlin and

Klinck, 1986). Frontal meandering appears to be particularly strong in the region of the Southern Ocean south of Africa (Belkin and Gordon, 1996; Moore *et al*., 1999). The breakdown of frontal meanders is considered to be an important mechanism for the generation of eddies (Gouretski and Danilov, 1994; Froneman *et al*., 1999; Lutjeharms and Vallentine, 1988; Pakhomov and Froneman, in press). Indeed, the extensive meandering in this region corresponds with the high incidence of eddy generation observed by Daniault and Menard (1985). This was clearly illustrated by the 1997 surveys when two eddies, one warm-core and one cold-core, were located in the vicinity of the islands. Eddies may provide an important mechanism for cross frontal advection of water masses into the PFZ. The two eddies observed in 1997 extended to a depth of at least 1500m (Pakhomov and Froneman, in press). They were thus discrete water bodies with the potential to transport distinct communities into the PFZ. This was supported by the zooplankton analysis (see below). Subsequent breakdown of these eddies would facilitate the interchange of zooplankton communities with the surrounding waters (Angel and Fasham, 1983). The oceanographic conditions in the vicinity of the PEIs therefore appear highly conducive to the mixing of waters of both Antarctic and sub-Antarctic origins.

The SAF and APF have also been observed to be regions of high zooplankton densities in relation to inter-frontal zones (Pakhomov *et al*., 1994; Pakhomov and McQuaid, 1996). Zooplankton densities in the vicinity of the PEIs may therefore be elevated when the fronts are in close proximity. This was clearly not the case during the four years of this study. Zooplankton biomass showed no significant difference between surveys and highest levels were recorded during Survey 2 1999 when neither the SAF nor the APF were close to the islands.

8.3.2. Community structure:

Cluster analysis of zooplankton data, in terms of both abundance and biomass, separated stations into distinct groups within each year of study. All station groups **within** years differed significantly, with the exception of groups 3 and 4 of the abundance analysis in 1996 and groups 1 and 3 of the biomass analysis in 1997. Despite significant differences between station groups SIMPER and inverse analysis clearly showed that within all years there was a high degree of similarity in species composition. Differences between station groups were largely determined by variation in the relative abundance and biomass of species, rather than variation in species composition. This is typical of zooplankton communities over spatial scales of less than one thousand kilometers (Mackas and Sefton, 1982).

The major source of variation in community structure, within all years of study, was consistently sea surface and integrated temperature (Table 7.3.). The variation in average temperature recorded for the station groups identified by cluster analysis, particularly in 1999, indicated that these groups represented different zooplankton communities collected from different water masses. This was supported at the species level by the numerous significant correlations between zooplankton and water temperature. Particular species clearly showed strong temperature related associations with different water masses.

In 1996 the upstream zooplankton community appeared to be strongly separated from the inter-island and downstream regions. The upstream region included stations at and to the north of the SAF, consequently recording higher average temperatures, and was characterised by the presence of typically sub-tropical indicator species. The stations in the inter-island and downstream regions recorded a higher density of typically Antarctic species. It therefore appears that at least two different zooplankton communities were sampled.

The two 1997 surveys appeared to have been dominated by zooplankton communities of sub-Antarctic origins. The stations situated at and to the north of the SAF did not form a discrete cluster and showed a high degree of similarity to stations within the PFZ. Indeed station groups 1, 2 and 4 identified by the abundance analysis had sub-Antarctic surface water (SASW) characteristics (Lutjeharms and Vallentine, 1984; Ansorge *et al*., 1999). This was supported by the associated zooplankton. Of the species responsible for 80% of the similarity within station groups *M. lucens, C. laticeps, C. vanus, C, brevipes* and *P. abdominalis* are all more abundant in the sub-Antarctic than the Antarctic (Vervoort, 1951; Guglielmo and Ianora, 1995; Gibbons and Hutchings, 1996).

The station MS2-1 conducted at the warm core eddy during Survey 1 clustered out with stations having properties of SASW. The relatively high biomass of temperate and sub-tropical species recorded at this station provided biological evidence for the origin of the warm core eddy to the north of the SAF.

The group containing the stations conducted near the APF and in the cold-core eddy was characterised by a high abundance and biomass of Antarctic species. The high similarity of the zooplankton community recorded within these stations clearly indicated their relatedness and provided biological evidence for the origin of the cold core eddy to the south of the APF. Furthermore it supported the conclusion from the oceanographic data that the eddy was a discrete water mass.

In MIOS 3, as in MIOS 1, the physical environment was relatively homogenous, although cluster analysis identified one station group with a relatively high average temperature. This warm water group was characterised by a high incidence of occurrence of sub-tropical indicator species. The two other station groups identified by cluster analysis, which showed a high percentage similarity, recorded a relatively high density of typically Antarctic species. A combination of zooplankton and oceanographic data therefore indicated the presence of at least two separate zooplankton communities in the vicinity of the PEIs.

In 1999 two groups of stations from Survey 1 were identified with sub-Antarctic surface water (SASW) characteristics (Lutjeharms and Vallentine, 1984; Ansorge *et al*., 1999).

One grouping contained stations at and to the north of the SAF and the other contained stations in the inter-island region. They recorded a high abundance and biomass of typically sub-Antarctic and temperate species as well as the presence of numerous sub-tropical indicator species. The warm water, high salinity stations at and to the north of the SAF recorded the highest species richness. Increasing species richness with increasing temperature has previously been observed by Tarling *et al*. (1995). The majority of the warmer water groups identified during the 1996, 1997 and 1998 surveys showed a similar pattern of increased species richness.

Two station groupings were identified with physical characteristics of PFZ water (Lutjeharms and Vallentine, 1984; Ansorge *et al*., 1999). These groupings were characterised by a relatively high biomass and abundance of typically Antarctic species. The presence of the Antarctic indicator species *E. triacantha* at station MS4-5 confirmed that the APF was sampled during Survey 1. A final station grouping, intermediate in physical characteristics between the SASW and PFZ stations, contained a mix of species of Antarctic and sub-Antarctic origins.

In general the clusters identified by the biomass analysis reflected those of the abundance analysis. However, this was not always the case. The abundance analysis focussed on mesozooplankton while the biomass analysis gave greater importance to macrozooplankton. For example, in 1998, a group of inter-island stations clustered out together due to their extremely low euphausiid biomass. However, in the abundance analysis they showed a high degree of similarity to other stations due to the relatively small contribution that euphausiids made to the abundance data.

The 1996 biomass analysis was affected by the inclusion of samples collected during the day. The day and night upstream net tows differed substantially in the contribution of euphausiids, as well as fish, to total biomass, with lowest levels generally occurring during the day (Figure 8.1.b). Consequently, a number of day upstream stations clustered out with night inter-island stations, which were also characterised by low euphausiid biomass.

Conversely, in the abundance analysis the upstream daytime tows showed a higher degree of similarity to the night tows conducted in the same region (Figure 8.1.a). This

indicated that diel differences in mesozooplankton community structure were lower than those observed in the macrozooplankton community. Total abundance and biomass values support this with the difference between day and night average abundance levels (110.2 and 105.7 individuals.m^{-3}) being more similar than average biomass levels (5.6 and 7.9 mg.m^{-3}). The animals contributing to the increased night biomass contributed little to abundance indicating that they were of the macrozooplankton size fraction.

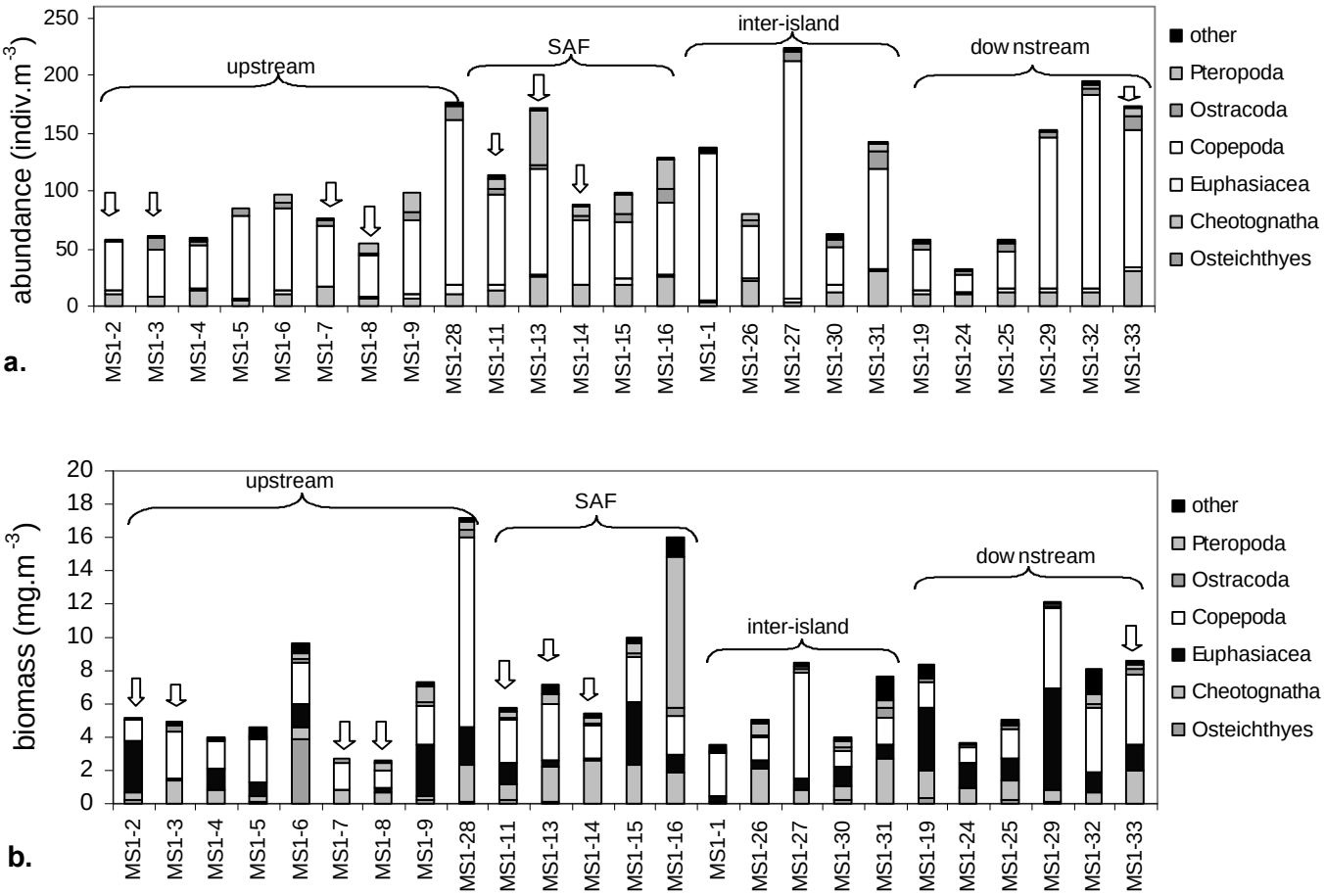


Figure 8.1. The contribution of zooplankton groups to total abundance (a) and biomass (b) in stations from the upstream, inter-island and downstream regions and the SAF. Stations conducted during the day are indicated by an arrow.

Groups identified by the biomass analysis were characterised by lower within group similarity levels than groups identified by the abundance analysis. This was highlighted by the higher NMDS ordination stress values recorded for the biomass analyses in

comparison to the abundance analyses, indicating that macrozooplankton had a more patchy distribution than mesozooplankton. However, Bongo nets are not considered appropriate gear for collecting macrozooplankton (Pakhomov and Froneman, in press) and the distribution patterns exhibited by this size fraction may therefore have been affected by biased sampling of the water column due to net avoidance. Another factor is that large, low abundance, species can make a significant contribution to total biomass thus increasing the between station heterogeneity.

The zooplankton community data showed that the PFZ in the vicinity of the PEIs comprised a mix of sub-Antarctic and Antarctic species. Numerous other studies have shown this to be typical of the region (Frost *et al*., 1976; Grindley, 1978; El-Sayed *et al*., 1979; Grindley and Lane, 1979; Lutjeharms and Vallentine, 1984; Allanson *et al.*, 1985; Miller, 1985; Boden and Parker, 1986; Boden, 1988; Duncombe Rae, 1989 a,b; Pakhomov and Froneman, in press). The zooplankton community structure is indicative of the PFZ being a region of mixing and transition between sub-Antarctic and Antarctic waters. However, mixing does not necessarily imply homogeneity. A combination of oceanographic and biological data clearly showed that the region was divided into discrete, spatially separated water masses during each survey. This was highlighted by the importance of temperature in determining community structure. The differentiation between Antarctic and sub-Antarctic waters, and their respective zooplankton communities, was particularly pronounced when the SAF and APF were in close proximity to the islands. A mesoscale analysis of community structure around South Georgia gave similar results to this study, identifying a number of different water masses with distinct communities strongly linked to water temperature (Atkinson *et al*., 1990).

8.3.3. Regional biomass differences:

During MIOS 1 the inter-island stations were characterised by low euphausiid biomass (Figure 8.1.b). The factors contributing to low euphausiid biomass may differ between regions. Vertical migration can result in large diel changes in euphausiid and fish (particularly Myctophidae) biomass in offshore waters (Pakhomov and Froneman, 1999

a; Figure 5.10.). That the inter-island stations were conducted at night appears to rule out this factor in explaining the reduced euphausiid biomass in this area. Low euphausiid biomass over the island shelf has previously been attributed to the predation impact of the large populations of land-based mammals and seabirds found on the PEIs (Perissinotto, 1989; Perissinotto and McQuaid, 1992; Pakhomov and Froneman, 1999 b). The islands also support relatively large populations of benthic fish (Gon and Klages, 1988). Genin *et al*. (1988) showed that fish can have a significant impact on zooplankton biomass over shallow topography. However, low euphausiid biomass is not always observed over the island shelf and may on occasion be higher than in the offshore regions (Table 4.8.; Figure 5.10.; Figure 7.6.). Accoustic surveys in 1997 identified a high incidence of backscatter over the island shelf (Pakhomov and Froneman, 1999 b) and net tows showed that euphausiids were an important component of this backscatter (Pakhomov and Froneman, in press).

During 1996 there was evidence for water retention over the island shelf. Increased residence time over the island shelf may have been responsible for the low euphausiid biomass, through making zooplankton more susceptible to predation. Conversely, when advective forces prevail, as in 1997 and 1998, zooplankton biomass may constantly be replenished (Perissinotto, 1989). Predation impact in 1996 was supported by the low average size of fish, chaetognaths, pteropods, copepods and hyperiids in the inter-island region, although no reduction in euphausiid size was observed, as one would expect the larger zooplankton to be consumed first. Further analysis showed that the pattern of reduced size in the inter-island region was by no means unique to 1996. Low average fish size was observed in this region during all surveys and low euphausiid size was recorded during survey 1 of both 1997 and 1999, when the SAF was in close proximity to the islands. Of particular interest was the almost complete absence of the euphausiid *E. longirostris* and the copepod *P. abdominalis* from the inter-island region during all surveys. Predation pressure may have been responsible for this absence but this is in contradiction to the high biomass of macrozooplankton species, including *N. megalops*, *T. gregaria* and *E. vallentini*, recorded in this region during some surveys. Furthermore, *E. longirostris* and *P. abdominalis* have never been recorded from the stomach contents

of top predators (Steele and Klages, 1986; Brown and Klages, 1987; Cooper and Brown, 1990), indicating that some factor other than predation must be responsible for their absence.

Atkinson and Peck (1990) observed that the biomass of mesopelagic zooplankton species, occurring predominantly below 250m, was depleted over the South Georgia shelf in relation to offshore waters. Both *P. abdominalis* and *E. longirostris* were virtually absent from day tows indicating that they occurred predominantly below a depth of 300m during the day, while at night they were found within the top 200m (Figure 5.10.). Acoustic data collected, during 1997, indicated that due to obstruction of current flow by the island shelf most macroplankton / micronekton flowed around the islands (Pakhomov and Froneman, 1999 a). This is consistent with the observations of Boehlert and Genin (1987) and Roden (1987). Genin *et al*. (1994) recorded reduced abundance levels of strongly migrating zooplankton, including *Euphausia pacifica* and *Pleuromamma* spp., in patches downstream of a seamount. Patches were formed by the daytime advection of these species around the shallow topography, creating a region of low abundance above it. The strong diel vertical migrations exhibited by *P. abdominalis* and *E. longirostris,* as well as many other macrozooplankton species, may therefore limit their advection onto the shallow island shelf. Weakly migrating taxa that occur predominantly in surface waters, including chaetognaths, pteropods and numerous copepod species, typically occurred at similar densities in the offshore and shelf environments during this study, a feature also observed by Genin *et al*. (1988).

Elevated *E. vallentini* and *T. vicina* biomass levels were recorded in the inter-island region in 1997, 1998 and 1999 while high biomass of the copepods *C. brevipes* and *C. vanus* was observed in 1998. The difference between regions may be attributed to the samples being taken from different water masses. Alternately they may be the result of interaction of zooplankton with the island shelf. Elevated zooplankton densities, with patchy spatial distributions, have previously been observed over the shelf regions of the PEIs (Pakhomov *et al*., in press) and South Georgia (Atkinson and Peck, 1990). It is suggested that these biomass distribution patterns may be the result of small-scale

concentration by localised flow patterns stimulated by shallow topography (Pakhomov *et al.*, in press).

8.4. Inter-annual comparison:

8.4.1. Zooplankton community structure:

Each of the six surveys conducted between 1996 and 1999 was characterised by the presence of a number of separate communities. Despite this the SIMPER analysis calculated a relatively high degree of similarity **within** surveys, exceeding the similarity **between** surveys. However, in the cluster analyses of abundance and biomass data the different surveys did not cluster out as completely separate groups. Conversely there was a high degree of inter-survey mixing. The distinct communities identified within surveys retained their integrity in the cluster analyses but in most instances appeared to be more similar to communities in other surveys than to communities within their own survey.

The strong relatedness of communities from different surveys points to a high degree of inter-annual similarity in the zooplankton community structure in the PFZ. This was highlighted by the SIMPER analysis. Twenty-five and twenty-eight species were responsible for 80% of the similarity and dissimilarity between zooplankton communities in terms of abundance and biomass data respectively. The majority of these species were commonly found in all surveys but differed significantly in both abundance and biomass. Surveys were therefore differentiated by variation in abundance and biomass of species rather than variation in species composition. This was typical of the intra-annual analysis and its occurrence between surveys is indicative of a high degree of constancy in the zooplankton communities in the vicinity of the PEIs. The similarity between surveys was further highlighted by the inverse analysis. Only three out of eleven species clusters identified had specific survey associations, and only one of the eight species within these three clusters was present in just one survey.

When each survey was analysed separately, surface and integrated temperature accounted for a high percentage of the variation in zooplankton community structure. However, in the combined survey analysis temperature was not an important factor. Within surveys temperature differences were an indicator of separate water masses and correspondingly separate communities. Across surveys it appeared that structurally different communities occurred at similar temperatures and *vice versa*. Physical conditions may place the ultimate limit on community composition but biological interactions, acting on the available species set may play an important role in determining community structure. For example, Colebrook (1986) indicated that summer zooplankton community structure is largely dependent on the survival of the over-wintering stock. This is intrinsically linked to successional processes involving the initial community (Margalef, 1967; Levin, 1977).

Total zooplankton biomass and abundance did not differ significantly between surveys, with the exception of the high abundance levels recorded during Survey 2 1997. Copepods dominated abundance in all surveys while copepods and euphausiids together dominated biomass. This is consistent with previous studies in the vicinity of the islands (Grindley and Lane, 1979; Boden and Parker 1986; Perissinotto, 1989), with the exception of a survey in May 1982 when chaetognaths dominated both abundance and biomass (Boden and Parker, 1986). The relative contribution of some groups therefore shifted slightly between surveys but in general zooplankton group composition was relatively constant.

8.4.2. Seasonality:

Copepods in the Southern Ocean exhibit strong seasonality in their life cycles (Atkinson, 1998). The stage structure of copepod populations is characterised by regional variation, due to difference in the timing of life cycles (Marin, 1987; Ward *et al*., 1997). However, although different water masses were sampled during the different surveys conducted in 1997 and 1999, there was negligible within year variation in percentage composition of *C. simillimus* copepodite stages. Ward *et al*. (1997) considered the area from the Scotia Sea to the SAF to be one region, while Marin (1987) made a comparison between the

Weddell Sea and the ACC. Differences in life cycle timing within years therefore appear to occur at the macroscale level and are not applicable to this study.

Analysis of the population structure of *C. simillimus* between years showed that this copepod was sampled at different stages in its seasonal cycle between 1996 and 1999. Atkinson (1991) proposed that the life cycle of *C. simillimus* contained two generations per year. This included a main spawning event in spring and a second in April/May by the adults of the spring generation. Despite the 1996 and 1997 surveys being conducted one to three weeks later in the year they were characterised by the almost complete absence of the stage 5 copepodites (C5) and adults (Figure 7.8.). This indicated that in both 1996 and 1997 sampling occurred relatively early in the life cycle of *C. simillimus,* with 1997, dominated by C2, being the earliest. The 1999 surveys were conducted later in the life cycle than 1996, containing some adults and being dominated by C4. The dominance of adults in 1998 indicated that this survey was conducted latest in the life cycle of *C. simillimus*.

Variation in the timing of the biological season between years, as shown by *C. simillimus* population structure, has important implications for the community structure analysis. The total abundance and biomass of copepods shows strong seasonal variation both in quantity and in vertical distribution in the water column (Schnack-Schiel *et al*., 1998). This variation is associated with the general seasonal pattern exhibited by copepods in the Southern Ocean, which includes strong seasonal vertical migrations between deep waters in winter and the surface waters from spring to autumn (Atkinson, 1989; Atkinson, 1991; Schnack-Schiel and Mizdalski, 1994; Atkinson, 1998). After spring reproduction total copepod biomass increases through to a high in autumn due to growth and development from C1 to C5. Schnack-Schiel *et al*. (1998) recorded an increase in total copepod biomass from 1.7 mg C m^{-3} in late winter / early spring to 3.7 mg C m^{-3} in autumn in the eastern Weddell Sea. Vidal and Smith (1986) recorded an increase in zooplankton biomass from < 1gC.m^{-2} to 10-14gC.m^{-2} in the Bering Sea between April and May 1980. Over 50% of this increase was attributed to the growth of *Neocalanus plumchrus* and *N.*

christatus from C4 to C5. The dry weight of *Neocalanus* copepodites has been shown to increase roughly 20 fold from stage C1 to C5 (Goldblatt *et al*., 1999).

The surveys conducted during 1998 and 1999 were characterised by a higher average individual zooplankton size as well as higher total zooplankton biomass than the 1996 and 1997 surveys (Figure 8.2.). Copepods represented an important component of the total zooplankton biomass during all surveys. The higher biomass in 1998 and 1999 may therefore be due, in part, to sampling occurring later in the biological season when larger copepod size classes dominate and total copepod biomass is higher (Voronina, 1984; Atkinson, 1991; Ward *et al*. 1995; Atkinson, 1998). Other mesozooplankton groups also show strong seasonal cycles (Knox, 1994). The difference in life cycle stage observed in *C. simillimus* may therefore apply to other components of the community.

Within the general seasonal pattern individual copepod species differ in mating depth, timing of reproduction, depth distribution and duration of their life cycles (Atkinson, 1991). The contribution of a species to total abundance and biomass may therefore vary dramatically with their life cycle stage at the time of sampling. Differences in the timing of the biological season between years may therefore have been an important contributor to the observed variation in community structure.

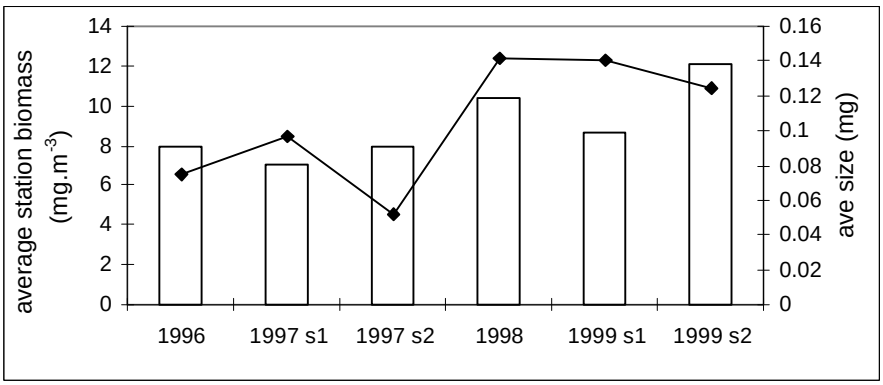


Figure 8.2. Average zooplankton biomass (columns) and average individual zooplankton size (line) recorded per net station for each of the six surveys conducted between 1996 and 1999 (s1 = survey1; s2 = survey 2).

8.4.3. Long term changes:

Data collected at Marion Island between 1951 and 1988 have revealed some long term trends in the local climate. Average air temperature has increased by 0.93^{o}C, at an average of 0.025^{o}C per year, and there has been a corresponding increase in average sea surface temperatures (Smith and Steenkamp, 1990). When the data collected during this study were combined with data collected from the previous zooplankton and oceanographic studies in the vicinity of the islands a similar trend of increased temperature was observed (Figure 8.3.a). Corresponding with this was a decrease in average chlorophyll *a* (Figure 8.3.b). Both of these trends suggest that the SAF has moved southward since the first oceanic survey in 1976. This would bring warmer water into the region as well as increase average current velocities consequently favouring a flow-through environment. The latter scenario prevents eddy trapping over the island shelf and associated phytoplankton blooms. Unfortunately the position of the SAF was accurately determined on only six of the PEI surveys. Nevertheless, a trend of southward movement of the SAF is evident (Figure 8.3.c). This trend is better illustrated by a data set of thirty crossings of the SAF collected between 1959 and 1999 in the region upstream of the islands. Regression analysis showed that the SAF moved significantly ($p<0.05$) southwards during this time period (Pakhomov *et al*., unpublished).

Although these data sets are characterised by a high degree of inter-annual variation it appears that this variation has long term trends. The apparent southward movement of the SAF may have a significant effect on trophic dynamics in the vicinity of the PEIs. The prevalence of a flow-through environment favours allochthonous input into the island ecosystem. It has been suggested that this is responsible, through favouring the offshore feeding mode, for the altered balance observed during the last two decades in offshore versus inshore feeding top predators (Pakhomov *et al*., unpublished). An intrinsic assumption in this is that food availability for inshore feeders is lower when a flow-through environment exists, and/or higher for offshore feeders.

Sedimentation of the high primary production associated with water retention is believed to be an important energy source for the benthic community (Perissinotto *et al*., 1990 b).

Considering that benthic suspensoid feeders are an important component in the diet of *N. marionis* (see Chapter 1), reduced autochthonous input, by reducing energy transport to the benthic community, may result in decreased *N. marionis* biomass and consequently reduce food availability for inshore feeders. However, benthic filter feeders may well benefit from the close proximity of the SAF through the episodic advection of the high phytoplankton biomass occasionally observed at this front into the inter-island region. The well-mixed water column, typical of the island shelf, enables the benthos to utilize this energy source, particularly in the shallow inshore regions (Perissinotto *et al.*, 1990 a). Zooplankton also form a component of the diet of *N. marionis* (Perissinotto and McQuaid, 1990), and the availability of zooplankton may be higher when a flow through environment exists. At this stage, it is therefore difficult to assess the affect that the different island modes will have on *N. marionis* biomass.

Fluctuation in *N. marionis* biomass is supported by the dietary analysis of inshore feeders. Pronounced inter-annual variation has been observed in the proportions of prey type consumed as well as in species consumed (Brown and Klages, 1987; Brown *et al*., 1990). Of particular relevance is the almost complete absence of *N. marionis* from their diet in some years, and a corresponding dominance of allochthonous zooplankton. Whether this dietary shift is due to decreased *N. marionis* biomass or increased availability of allochthonous biomass, favoured by a flow-through system, remains undetermined. The latter scenario is distinctly possible given that *N. marionis* biomass may well be maintained in a flow through environment. Another consideration is that the recruitment success of *N. marionis* may be affected by the degree of water retention over the island shelf (Kuun, 1998). Recruitment is possibly lower when water retention is limited, resulting in natural fluctuations in the biomass of *N. marionis*. However, low *N. marionis* biomass would appear to be compensated for by increased allochthonous zooplankton biomass.

Indications are that food availability for inshore feeders is not necessarily affected by the existing island mode. The altered balance of offshore versus inshore predators may therefore be solely due to increased food availability for the offshore component. However, the reasons for the observed patterns in predator population structure are

confounded by man made impacts from which predator populations may still be recovering (Cooper and Brown, 1990; Hofmeyr *et al*., 1997; Pakhomov *et al*., unpublished).

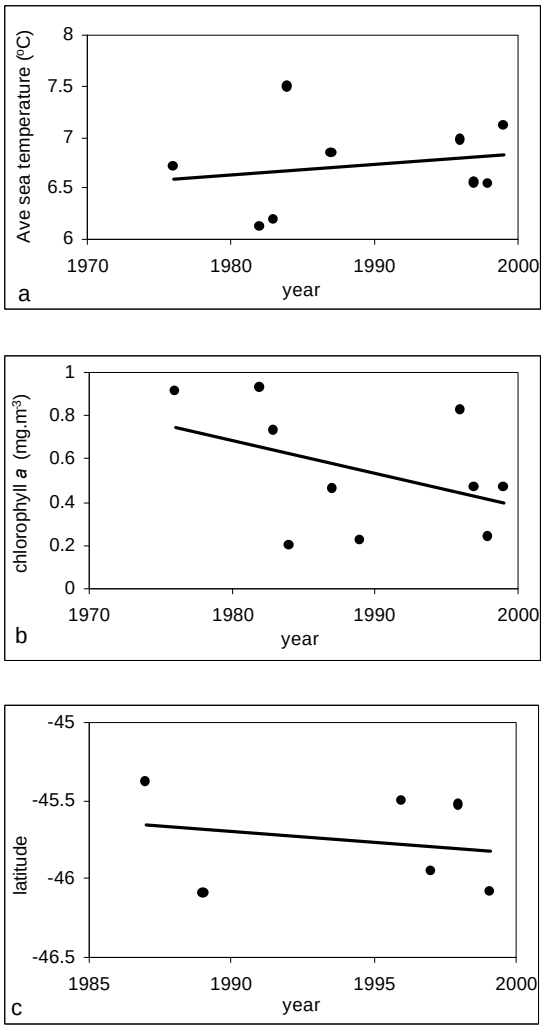


Figure 8.3. Average sea surface temperature (a), chlorophyll *a* concentration ($mg.m^{-3}$) (b), and position of the SAF (c) recorded during PEI surveys between 1976 and 1999. Data for these graphs were taken from several sources (El-Sayed, 1979; Allanson *et al*. 1985; Boden and Parker, 1986; Boden, 1988; Duncombe Rae, 1989 a,b; Ansorge *et al*., 1999; Pakhomov and Froneman, 1999 b).

Summary

1. Conclusions:

1.1. The SAF and the APF in the vicinity of the PEIs are characterised by a high degree of positional variation. This positional variation takes place over large spatial scales and can occur very rapidly.

1.2. The oceanographic environment, and the position of SAF and APF in particular, has a significant impact on the biological environment in the vicinity of the PEIs:

1.2.1. The proximity of the SAF and APF to the PEIs may indirectly influence chlorophyll *a* concentrations through alteration of local flow dynamics over the island shelf. When the SAF is far to the north of the islands frictional forces predominate over advective forces resulting in water retention over the island shelf. Under these physical conditions a phytoplankton bloom may occur, as was observed during MIOS 1. However, evidence from MIOS 3 suggests that water retention does not necessarily occur when the SAF lies to the north of the islands. Furthermore, the high frequency of positional fluctuation may limit the residence time of water over the shelf, preventing the build up of phytoplankton biomass.

1.2.2. When the SAF and/or the APF are in close proximity to the islands the high phytoplankton biomass associated with the fronts may be transported to the islands. There was little evidence for increased phytoplankton biomass in the vicinity of the fronts during this study. However, phytoplankton size structure during MIOS 4 indicated that the inter-island phytoplankton community was a reflection of the SAF community. Therefore when increased production occurs at the SAF it may be an important source of allochthonous phytoplankton input into the PEI ecosystem.

1.2.3. The zooplankton community in the vicinity of the PEIs reflected the oceanographic environment. The positional variability of the SAF and APF and cross frontal mixing, in part due to eddy shedding, result in the interchange of sub-Antarctic and Antarctic communities across the PFZ. In terms of species composition the zooplankton community in the vicinity of the islands was relatively homogenous. Varying abundance and biomass levels of common species, and the presence of indicator species, showed that during each survey the region contained different, spatially separated, zooplankton assemblages, associated with water masses identifiable through their physical characteristics. The major source of variation was in the relative contribution of Antarctic and sub-Antarctic communities. The differentiation between communities was particularly pronounced when the SAF and APF were in close proximity to the islands.

1.3. Interaction of zooplankton with the shallow topography may affect community structure in a number of ways:

1.3.1. It is possible that predation pressure is enhanced over the island shelf resulting in a decrease in zooplankton biomass, particularly the macrozooplankton fraction, in this region. However, this may only be an important factor under conditions of water retention and low replenishment of zooplankton stocks.

1.3.2. Zooplankton species characterised by deep vertical migration may be subject to limited advection onto the island shelf. This will predominantly affect the macrozooplankton size fraction.

1.3.3. There are indications that zooplankton may become concentrated over the island shelf, possibly due to mesoscale flow patterns stimulated by the interaction of the ACC with the shallow topography.

1.4. Inter-annual zooplankton community analysis showed that the PFZ in the vicinity of the PEIs is characterised by a high degree of inter-annual stability in species

composition and community structure. In a number of instances communities were more similar between surveys than within surveys, indicating that annual variability exceeded inter-annual variability. The occurrence of structurally different communities under similar physical conditions, and *vice versa,* suggests that biological interactions may play an important role in determining zooplankton community structure.

1.5. Although all of the surveys were conducted at a similar time of year, analysis of the population structure of *C. simillimus* showed that this species occurred at different stages in its life cycle during different surveys. This suggests that the timing of the biological season varied between years. Differences in the population structure of species, associated with life-cycle stage, may be an important contributor to inter-annual variability in community structure.

1.6. Numerous crossing of the SAF, coupled with increasing air and sea temperatures at the PEIs, point to a long-term trend of southward movement of this front. This may have a significant effect on the PEI ecosystem, decreasing autochtonous phytoplankton input and increasing allochthonous input. Decreased phytoplankton concentrations over the island shelf in recent decades provides some evidence for this. However, whether such a change will alter trophic dynamics at the PEIs is as yet undetermined.

2. Suggestions for future research:

2.1.Although the focus of much speculation, the flow dynamics in the immediate vicinity of the PEIs remains an enigma. This subject however is of primary importance to the understanding of zooplankton community structure in the island realm. Major unanswered questions include:

- How much of the flow of the ACC is directed over the island shelf and how much is deflected around the islands during periods when no water retention is observed? This may significantly affect the quantity of zooplankton advected onto the island shelf.

- Are flow patterns responsible for the high biomass of zooplankton occasionally observed over the island shelf? It is possible that even when a flow through environment exists some water entrapment may occur in the inshore regions. This may serve to concentrate zooplankton over shallow topography. The build up of biomass on the island shelf may be an important link between the oceanic and terrestrial environment through the feeding of land based predators.

- What is the structure of the water column when water retention occurs and how frequently and to what extent does it occur? Of particular importance is how the zooplankton community is affected by water trapping. Is it subject to biomass reduction due to increased predation? Does water retention occur for long enough for zooplankton to respond to increased phytoplankton biomass?

Positioning of current meters on the island shelf would give insight into the mesoscale flow dynamics in this region. Coupled with high resolution zooplankton surveys this could give insight into some of these questions.

2.2. It is believed that flow dynamics on the island shelf are intrinsically linked to the position of the SAF and APF. However, the exact nature of this relationship is as

yet undetermined. Flow meters on the island shelf, coupled with satellite monitoring of the position of the fronts in relation to the islands, may give greater insight into the relationship between the offshore and shelf environments.

2.3. Biological interactions may play an important role in determining zooplankton community structure. It is suggested that future studies should pay closer attention to the role of species associations and interactions. Of interest would be whether particular species associations, species abundance and dominance levels occur consistently, and further, whether patterns observed are linked to successional processes.

2.4. Increased attention needs to be paid to the benthic community with emphasis on the population dynamics of *Nauticaris marionis.* Of particular importance, regarding the role of *N. marionis* as a food source for inshore predators, is how long term changes in the position of the SAF may effect the available biomass of this species. Long term changes in *N. marionis* population structure may be investigated directly through net tows or indirectly through dietary analysis of land based top predators. Another important consideration is whether annual flow characteristics, and particularly the degree of water retention, affect recruitment success and consequently standing stocks.

2.5. Long-term data sets from the sub-Arctic Pacific have revealed long term-changes in zooplankton community structure and standing stocks, which are intrinsically linked to climate change (Mackas and Tsuda, 1999). Continued monitoring of the PEIs and its environs is required in order to determine whether similar long-term trends are effecting Southern Ocean biota. There is already some evidence for the southward movement of warmer sub-Antarctic waters, which may be linked to climate change.

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Appendix

1. MIOS 1

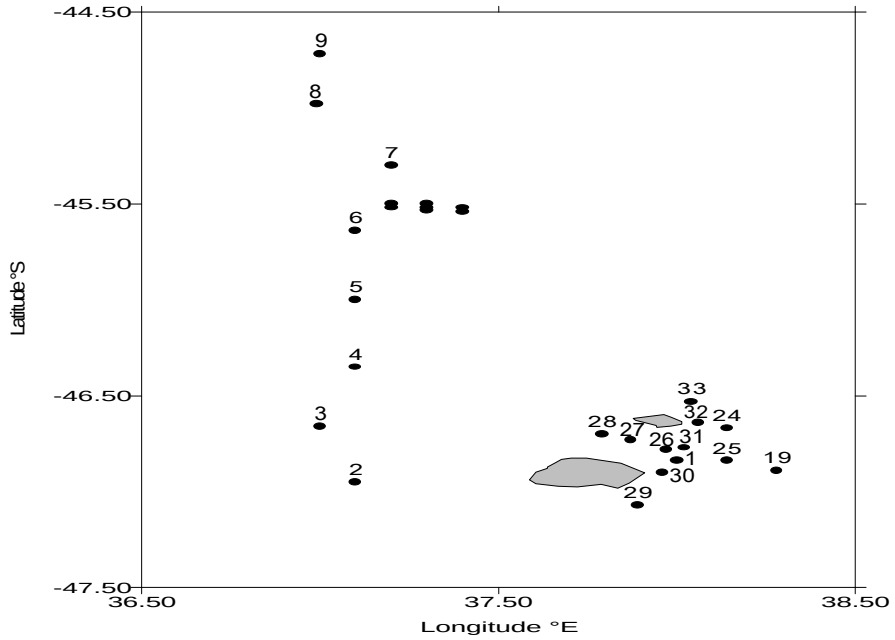

Figure 1A. Position of net tows conducted during MIOS 1. Numbers on the map correspond with station numbers in Table 1A. The encircled stations indicate the position of the 24-hour station conducted at the SAF (net tows MS1-11 to MS1-16).

Table 1A. Details of net tows conducted during MIOS 1 including station position, date, time, sounding, and the means of oceanographic data collection. CTD casts were conducted to 300m.

Station	Latitude	Longitude	Date	Local Time	Sounding (m)	Oceanography
MS1-1	46 50.29S	38 00.04E	01-May	20:57	139	CTD
MS1-2	46 57.18S	37 06.00E	04-May	04:47	999	CTD
MS1-3	46 40.07S	37 00.09E	04-May	13:37	3000	CTD
MS1-4	46 21.42S	37 00.70E	04-May	16:45	3000	CTD
MS1-5	46 00.23S	37 00.75E	04-May	23:14	3000	CTD
MS1-6	45 38.54S	37 00.78E	05-May	02:03	3000	CTD
MS1-7	45 18.47S	37 01.53E	05-May	08:05	1400	CTD
MS1-8	44 58.84S	36 59.89E	05-May	11:15	1400	CTD
MS1-9	44 43.34S	37 00.45E	05-May	19:03	3000	CTD
MS1-11	45 30.55S	37 01.92E	06-May	05:08	3000	CTD
MS1-13	45 31.20S	37 01.83E	06-May	09:04	1500	CTD
MS1-14	45 31.46S	37 01.38E	06-May	13:06	3000	CTD
MS1-15	45 31.87S	37 02.19E	06-May	16:57	3000	CTD
MS1-16	45 31.40S	37 02.43E	06-May	21:06	3000	CTD
MS1-19	46 53.46S	38 17.02E	07-May	17:09	1000	CTD

Table 1A. continued						
Station	**Latitude**	**Longitude**	**Date**	**Local Time**	**Sounding (m)**	**Oceanography**
MS1-24	46 40.73S	38 08.87E	09-May	15:32	900	CTD
MS1-25	46 50.52S	38 08.91E	09-May	19:05	1500	
MS1-26	46 46.94S	37 58.70E	09-May	19:29	145	
MS1-27	46 44.35S	37 52.73E	09-May	20:34	259	
MS1-28	46 42.37S	37 47.42E	09-May	21:47	1000	
MS1-29	47 04.49S	37 53.51E	10-May	20:14	1500	
MS1-30	46 54.32S	37 57.67E	10-May	23:54	140	
MS1-31	46 46.29S	39 00.34E	11-May	01:05	150	
MS1-32	46 38.49S	38 03.95E	11-May	02:56	460	
MS1-33	46 31.94S	38 05.24E	11-May	04:14	1200	

2. MIOS 2:

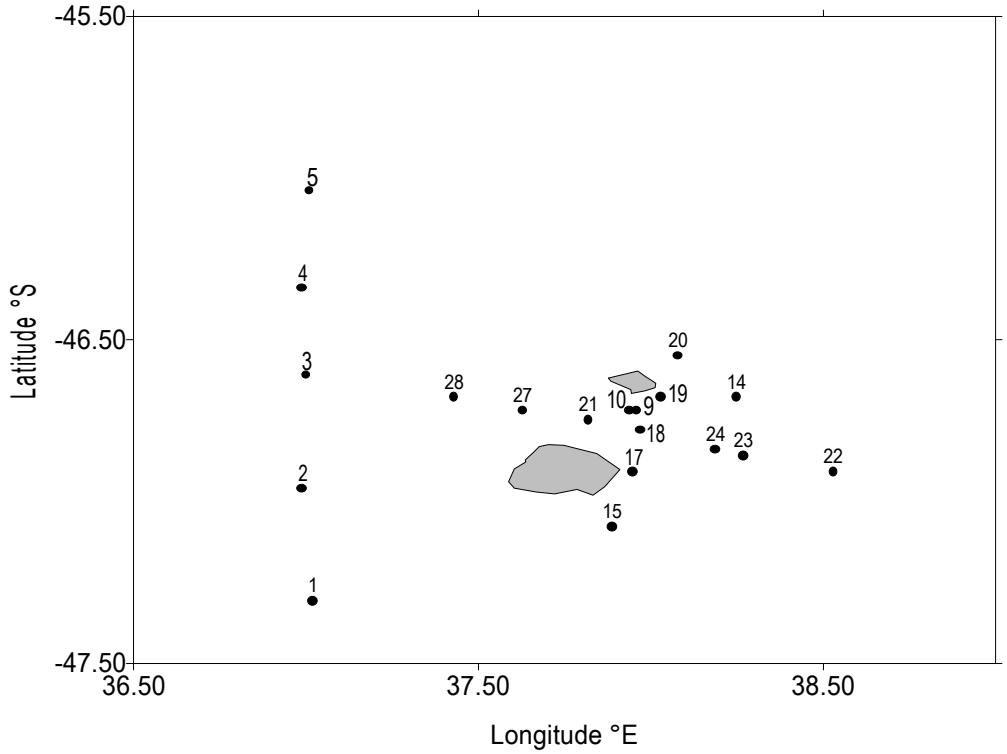

Figure 2A. Position of net tows conducted during Survey 1 of MIOS 2. Numbers on the map correspond with station numbers in Table 2A.

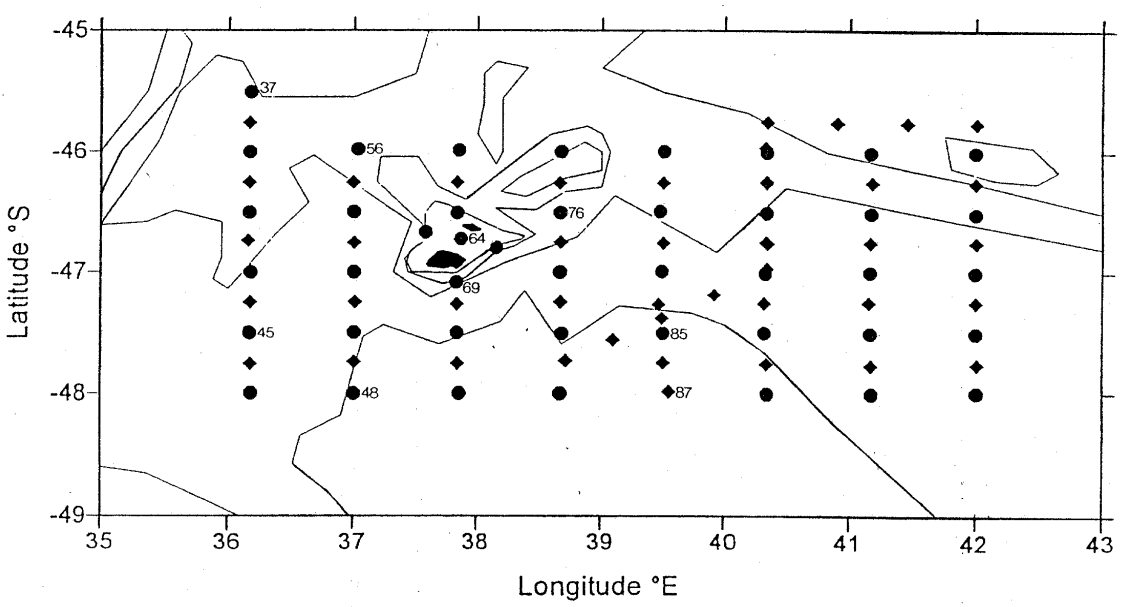

Figure 3A. Position of net tows conducted during Survey 2 of MIOS 2 are indicated by number. Numbers on the map correspond with station numbers in Table 2A. CTD casts are indicated by a square and XBT's are indicated by a circle. Figure taken from Ansorge and Lutjeharms (submitted).

Table 2A. Details of net tows conducted during MIOS 2 including station position, date, time, sounding, and the means of oceanographic data collection (All CTD's were conducted to 300m).

Station	Latitude	Longitude	Date	Local Time	Sounding (m)	Oceanography
MS2-1	47 18.89S	37 01.36E	30-Apr	21:20	2000	XBT
MS2-2	46 57.73S	36 59.68E	30-Apr	00:00	3634	XBT
MS2-3	46 37.17S	37 00.09E	30-Apr	02:24	2994	XBT
MS2-4	46 20.62S	36 59.96E	30-Apr	04:40	3020	XBT
MS2-5	46 02.41S	37 00.03E	30-Apr	06:56	2766	XBT
MS2-9	46 43.70S	37 57.87E	01-May	20:33	230	XBT
MS2-10	46 43.55S	37 56.71E	01-May	19:03	234	XBT
MS2-14	46 41.26S	38 15.35E	02-May	19:41	1500	XBT
MS2-15	47 05.36S	37 53.45E	03-May	20:34	1086	XBT
MS2-17	46 54.62S	37 57.29E	03-May	23:00	1322	XBT
MS2-18	46 46.94S	37 58.38E	03-May	00:21	150	XBT
MS2-19	46 41.35S	38 01.98E	03-May	03:10	346	XBT
MS2-20	46 33.32S	38 05.03E	03-May	04:40	2008	XBT
MS2-21	46 45.05S	37 49.88E	03-May	06:58	185	XBT
MS2-22	46 55.11S	38 32.14E	04-May	19:55		XBT
MS2-23	46 51.71S	38 16.79E	04-May	21:34	1000	XBT
MS2-24	46 50.79S	38 11.74E	04-May	00:10	1800	XBT
MS2-27	46 43.77S	37 38.00E	04-May	04:22	850	XBT
MS2-28	46 41.26S	37 25.94E	04-May	03:50	2500	XBT
MS2-37	45 30.64S	36 11.59E	08-May	04:20	2500	CTD
MS2-45	47 30.33S	36 10.14E	09-May	22:32	1000	CTD
MS2-48	47 59.57S	37 00.83E	09-May	07:00	2500	CTD

Table 2A. continued						
Station	**Latitude**	**Longitude**	**Date**	**Local Time**	**Sounding (m)**	**Oceanography**
MS2-56	45 59.58S	37 00.25E	10-May	00:15	2000	CTD
MS2-64	46 43.37S	37 51.81E	11-May	20:05	399	CTD
MS2-69	47 04.94S	37 50.31E	11-May	03:18	374	CTD
MS2-76	46 29.56S	38 39.73E	12-May	19:56	1000	CTD
MS2-85	47 31.09S	39 30.17E	13-May	21:18	2500	CTD
MS2-87	47 59.18S	39 29.90E	13-May	00:01	2500	XBT

3. MIOS 3:

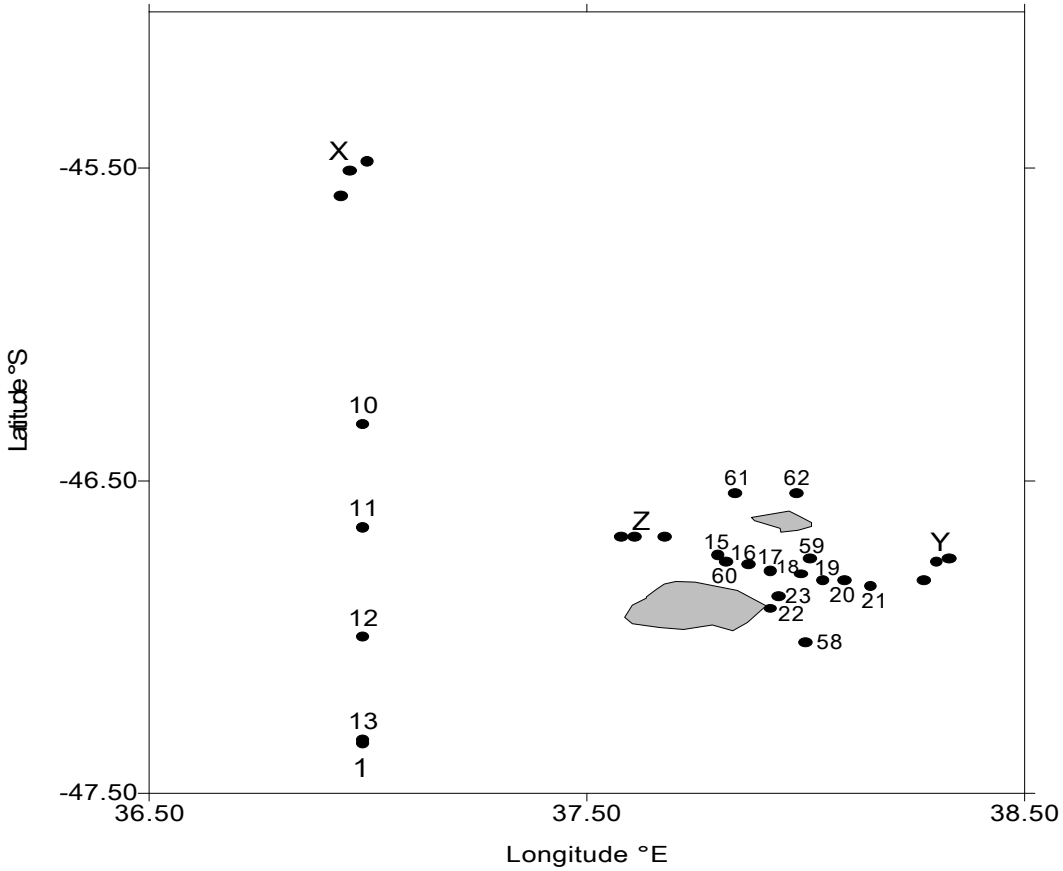

Figure 4A. Position of night net tows conducted during Survey 1 (repeat survey) of MIOS 3. Numbers on the map correspond with station numbers in Table 3A. The net tows constituting the 24-hour station conducted at the SAF are encircled. X = stations MS3-4,5,6; Y = stations MS3-33,34,36; Z = stations MS3-51,52,53.

Table 3A. Details of night net tows conducted during survey 1 (repeat survey) of MIOS 3 including station position, date, time, sounding, and the means of oceanographic data collection. CTD casts were conducted to a maximum depth of 300m, with the exception of MS3-1, which was lowered to 1500m.

Station	Latitude	Longitude	Date	Local Time	Sounding (m)	Oceanography
MS3-1	47 20. 56S	36 59.57E	10-Apr	21:36	3000	CTD
MS3-4	45 29. 20S	37 00.16E	17-Apr	19:48	1000	CTD
MS3-5	45 31.15S	36 57.90E	17-Apr	23:29	2181	
MS3-6	45 35.84S	36 56.86E	17-Apr	03:38	2547	
MS3-10	46 19.50S	36 59.95E	18-Apr	20:07	2902	CTD
MS3-11	46 39.30S	36 59.59E	18-Apr	23:27	2300	CTD
MS3-12	47 00.00S	36 59.53E	18-Apr	02:45	3655	CTD
MS3-13	47 20.10S	36 59.73E	19-Apr	05:47	3657	CTD
MS3-15	46 44.43S	37 48.45E	19-Apr	19:04	250	CTD
MS3-16	46 46.20S	37 52.26E	19-Apr	20:14	200	CTD
MS3-17	46 47.43S	37 55.47E	19-Apr	21:21	200	CTD
MS3-18	46 48.30S	37 59.40E	19-Apr	22:39	150	CTD
MS3-19	46 49.45S	38 02.56E	19-Apr	23:35	200	CTD
MS3-20	46 49.67S	38 05.86E	19-Apr	01:00	525	CTD
MS3-21	46 50.75S	38 09.47E	19-Apr	02:24	550	CTD
MS3-22	46 55.09S	37 55.25E	20-Apr	04:52	150	CTD
MS3-23	46 52.41S	37 56.80E	20-Apr	05:39	200	CTD
MS3-33	46 49.25S	38 16.70E	21-Apr	21:55	1400	CTD
MS3-34	46 45.05S	38 20.20E	21-Apr	01:59	1500	CTD
MS3-36	46 45.86S	38 18.21E	22-Apr	05:53	1092	
MS3-51	46 41.24S	37 36.96E	24-Apr	21:59	1500	
MS3-52	46 40.81S	37 35.16E	24-Apr	01:54	2214	CTD
MS3-53	46 41.19S	37 40.82E	25-Apr	05:58	1500	
MS3-58	47 01.62S	38 00.37E	25-Apr	19:17	862	CTD
MS3-59	46 45.51S	38 00.56E	25-Apr	21:39	180	CTD
MS3-60	46 45.90S	37 49.61E	25-Apr	23:30	250	CTD
MS3-61	46 32.65S	37 50.59E	25-Apr	02:00	1155	CTD
MS3-62	46 32.81S	37 59.33E	25-Apr	04:05	1633	CTD

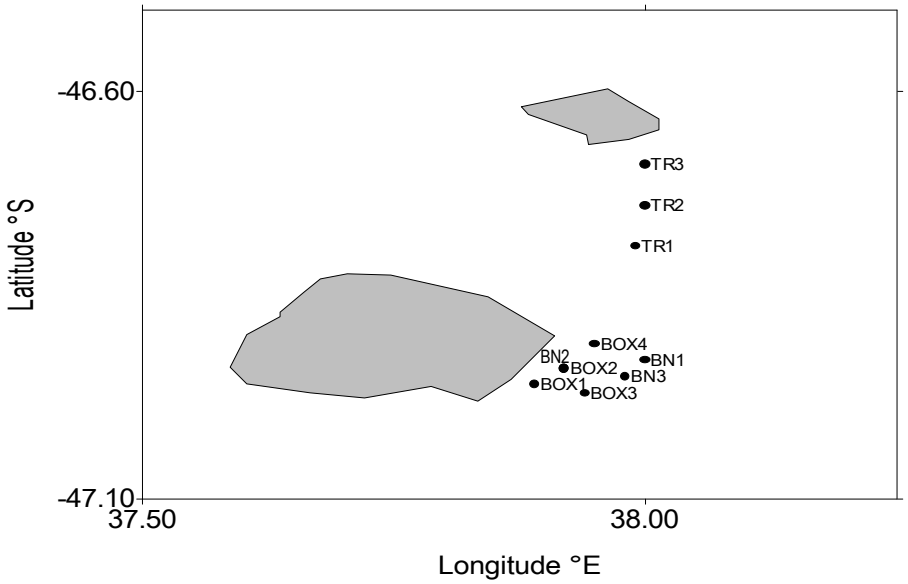

Figure 5A. Position of the ten night net tows conducted during the second survey, MIOS 3. Numbers on the map correspond with station numbers in Table 4A (BN = BON).

Table 4A. Details of the second survey, comprising ten night net tows, conducted during MIOS 3 including station position, date, time, sounding, and the means of oceanographic data collection. CTD casts were conducted to a maximum depth of 300m.

Station	Latitude	Longitude	Date	Local Time	Sounding (m)	Oceanography
TR1	46 47.46S	37 59.55E	08-Apr	19:16	150	CTD
TR2	46 44.75S	38 00.22E	08-Apr	21.05	250	CTD
TR3	46 41.51S	38 00.35E	08-Apr	22.24	200	
BOX1	46 58.09S	37 53.47E	12-Apr	20.1	150	
BOX2	46 56.67S	37 55.61E	12-Apr	20.55	150	
BOX3	46 58.76S	37 56.64E	12-Apr	21.52	200	
BOX4	46 54.97S	37 57.58E	12-Apr	22.51	150	
BON1	46 56.15S	38 00.49E	06-Apr	19:41	200	
BON2	46 56.69S	37 55.48E	06-Apr	21:06	150	
BON3	46 57.33S	37 59.33E	06-Apr	22:34	175	

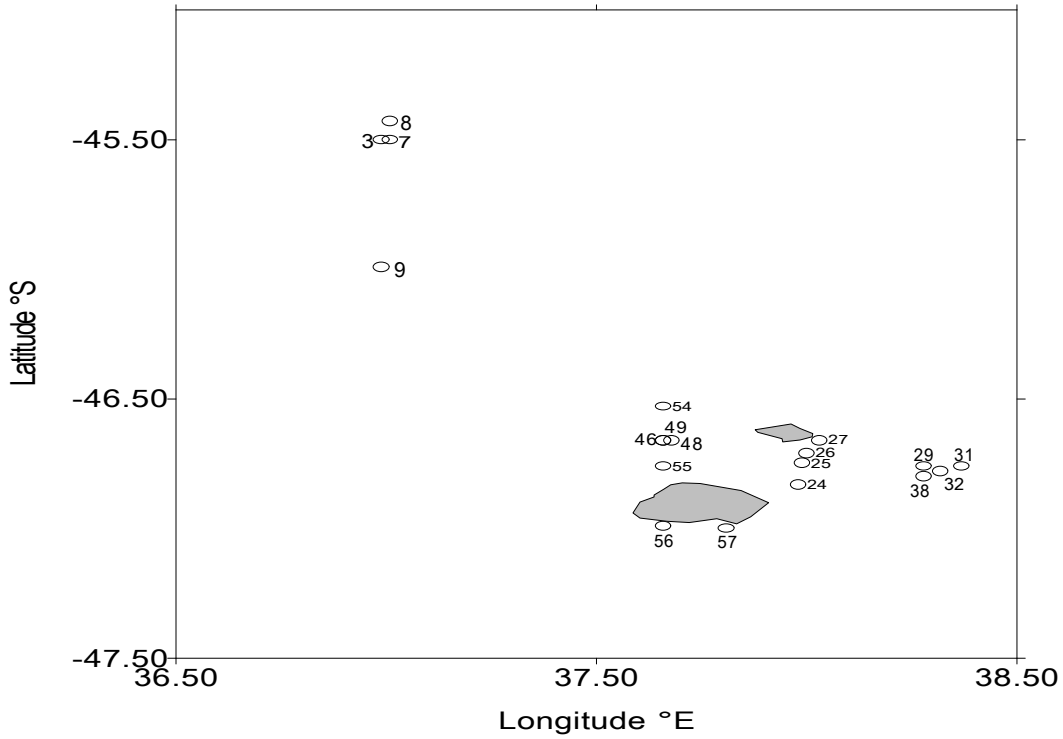

Figure 6A. Position of the day net tows collected during Survey 1 (repeat survey) of MIOS 3. Numbers on the map correspond with station numbers in Table 5A.

Table 5A. Details of the day net tows collected during survey 1 (repeat survey) of MIOS 3, including station position, date, time, sounding, and the means of oceanographic data collection. CTD casts were conducted to a maximum depth of 300m

Station	Latitude	Longitude	Date	Local time	Sounding (m)	Oceanography
MS3-3	45 29.91S	36 59.68E	17-Apr	15:52	1800	CTD
MS3-7	45 29.87S	37 01.07E	18-Apr	07:04	1000	CTD
MS3-8	45 26.48S	37 01.20E	18-Apr	11:16	1000	CTD
MS3-9	45 59.84S	36 59.57E	18-Apr	16:48	2934	CTD
MS3-24	46 50.17S	37 58.49E	20-Apr	06:45	200	CTD
MS3-25	46 45.55S	37 59.94E	20-Apr	07:49	200	CTD
MS3-26	46 43.34S	38 00.91E	20-Apr	10:00	300	CTD
MS3-27	46 40.75S	38 02.15E	20-Apr	11:22	400	CTD
MS3-29	46 46.54S	38 17.04E	21-Apr	09:42		CTD
MS3-31	46 46.07S	38 22.25E	21-Apr	13:57	1300	
MS3-32	46 47.22S	38 19.12E	21-Apr	17:54	1300	CTD
MS3-38	46 48.34S	38 17.94E	22-Apr	09:58	2000	CTD
MS3-46	46 40.18S	37 41.13E	24-Apr	09:38	1500	CTD
MS3-48	46 40.34S	37 40.46E	24-Apr	13:59	1297	CTD
MS3-49	46 40.12S	37 40.15E	24-Apr	17:26	1500	CTD
MS3-54	46 32.93S	37 39.88E	25-Apr	09:18	1200	CTD
MS3-55	46 46.06S	37 40.08E	25-Apr	12:42	623	CTD
MS3-56	46 59.61S	37 40.70E	25-Apr	16:13	506	CTD
MS3-57	47 00.09S	37 49.90E	25-Apr	17:38	200	CTD

4. MIOS 4:

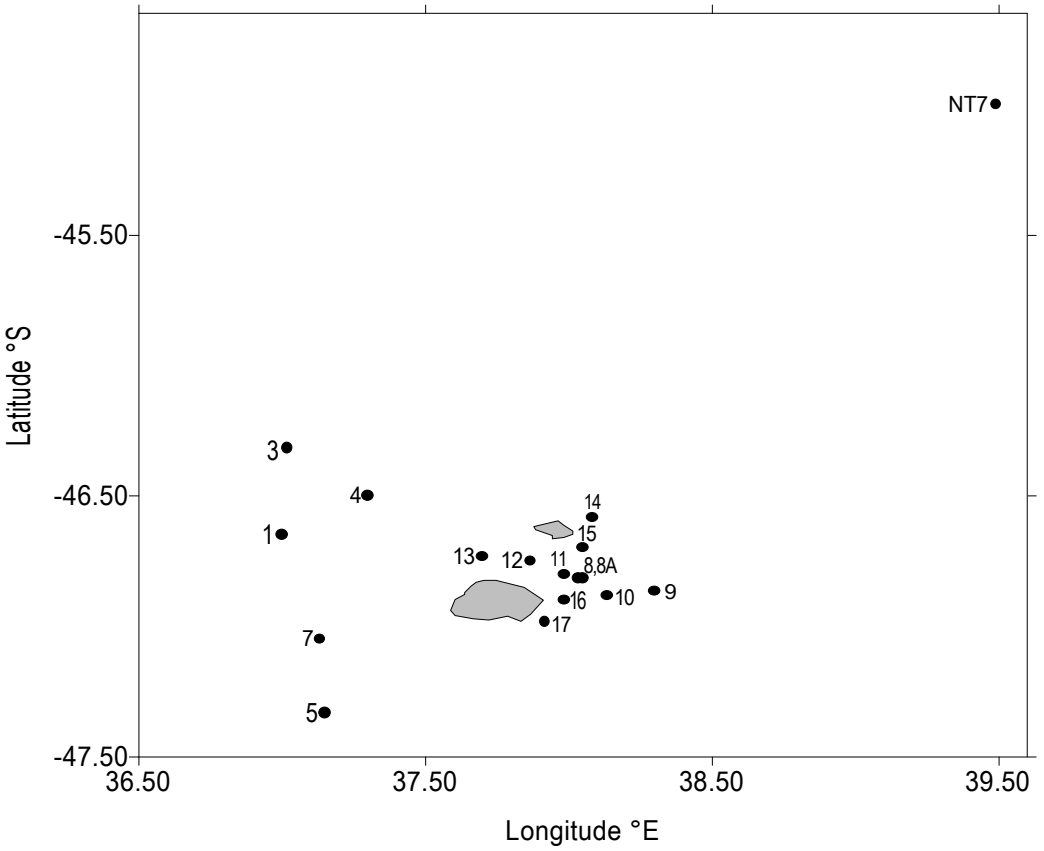

Figure 7A. Position of net tows conducted during Survey 1 of MIOS 4. Numbers on the map correspond with station numbers in Table 6A.

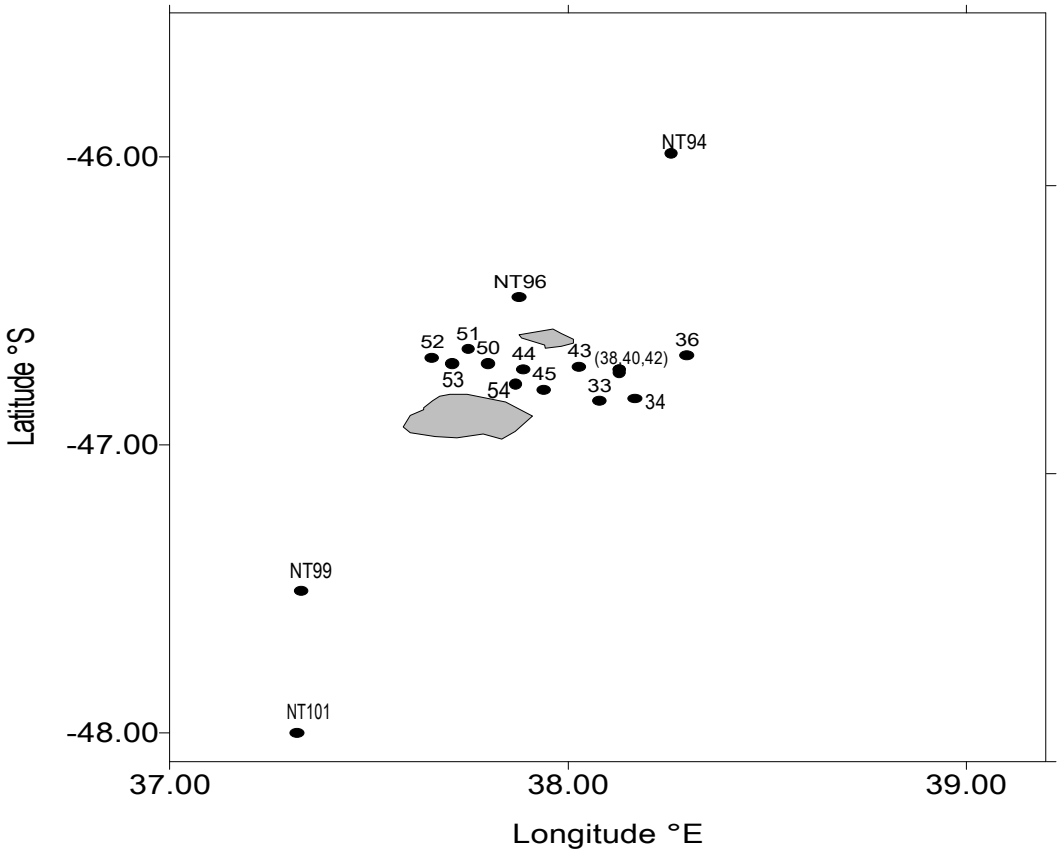

Figure 8A. Position of net tows conducted during Survey 2 of MIOS 4. Numbers on the map correspond with station numbers in Table 6A.

Table 6A. Details of net tows conducted surveys 1 and 2 of MIOS 4 including station position, date, time, sounding, and the means of oceanographic data collection.

Station	Latitude	Longitude	Date	Local time	Sounding (m)	Oceanography
MS4-1	46 39.20S	37 00.52E	5-Apr	21:12	3074	XBT
MS4-3	46 19.32S	37 01.10E	5-Apr	23:40	3400	XBT
MS4-4	46 30.24S	37 18.65E	5-Apr	02:06	3200	XBT
MS4-5	47 20.10S	37 09.63E	6-Apr	22:57	3000	XBT
MS4-7	47 03.55S	37 08.07E	7-Apr	02:00	3000	XBT
MS4-8	46 49.34S	38 03.94E	7-Apr	02:47	170	XBT
MS4-8A	46 49.60S	38 02.93E	7-Apr	02:52	160	XBT
MS4-9	46 52.36S	38 18.92E	8-Apr	20:24	3000	XBT
MS4-10	46 53.46S	38 08.70E	8-Apr	22:07	1700	XBT
MS4-11	46 48.92S	37 59.51E	8-Apr	23:40	130	XBT
MS4-12	46 45.77S	37 52.47E	8-Apr	00:39	174	XBT
MS4-13	46 44.82S	37 42.96E	8-Apr	01:47	300	XBT
MS4-14	46 35.20S	38 05.28E	9-Apr	04:18	1200	XBT
MS4-15	46 42.32S	38 03.01E	9-Apr	05:00	225	XBT
MS4-16	46 54.97S	37 59.45E	9-Apr	19:42	145	XBT
MS4-17	46 59.74S	37 55.26E	9-Apr	21:20	245	XBT

Table 6A. continued

Station	Latitude	Longitude	Date	Local time	Sounding (m)	Oceanography
NT7	45 00.13S	39 32.46E	13-Apr	01:00	2200	CTD
NT94	45 59.89S	38 16.17E	24-Apr	20:20	1900	CTD
NT96	46 29.89S	37 53.22E	24-Apr	00:40	1903	CTD
NT99	47 30.69S	37 20.08E	25-Apr	19:30	4082	CTD
NT101	48 00.33S	37 19.24E	25-Apr	23:00	4418	
MS4-33	46 51.39S	38 05.02E	26-Apr	17:24	1000	XBT
MS4-34	46 50.74S	38 10.62E	26-Apr	20:50	2000	XBT
MS4-36	46 41.55S	38 18.30E	26-Apr	00:10	1500	XBT
MS4-38	46 44.84S	38 07.93E	27-Apr	03:45	500	XBT
MS4-40	46 44.91S	38 07.86E	27-Apr	07:49	400	XBT
MS4-42	46 45.00S	38 07.95E	27-Apr	11:22	470	XBT
MS4-43	46 44.03S	38 01.85E	27-Apr	20:45	225	XBT
MS4-44	46 44.54S	37 53.73E	27-Apr	22:16	245	XBT
MS4-45	46 48.61S	37 56.60E	27-Apr	23:13	150	XBT
MS4-50	46 43.55S	37 48.56E	28-Apr	21:17	235	XBT
MS4-51	46 40.25S	37 45.51E	28-Apr	22:26	956	XBT
MS4-52	46 42.18S	37 40.03E	28-Apr	23:34	980	XBT
MS4-53	46 43.47S	37 42.68E	28-Apr	00:50	533	XBT
MS4-54	46 47.90S	37 52.25E	28-Apr	02:24	160	XBT

Table 7A. Species list for samples collected during all surveys (MIOS 1 to MIOS 4).

Taxa	
Hydromedusae	**Copepoda**
Hydromedusa gen. spp	*Aetideus armatus*
Pantachogon haeckeli	*Arietellus simplex*
Pegantha triloba	*Calanus* spp
	Calanus simillimus
Scyphomedusae	*Candacia spp*
Periphylla periphylla	*Candacia falcifera*
	Candacia maxima
Siphonophora	*Centrophages spp*
Dimophyes arctica	*Clausocalanus brevipes*
Lensia spp	*Clausocalanus laticeps*
Melophysa melo	*Ctenocalanus* spp
Siphonophore	*Ctenocalanus citer*
	Ctenocalanus vanus
Ctenophora	*Eucalanus hyalinus*
Beroe spp	*Eucalanus longiceps*
	Euchirella rostromagna
Polychaeta	*Gaetanus antarcticus*
benthic polychaete	*Gaetanus minor*
Phalacrophorus pictus	*Gaetanus tenuispinus*
Rhynconerella spp	*Heterorhabdus austrinus*
Tomopterus spp	*Metridia lucens*
Travisiopsis levinseni	*Metridia gerlachei*
Travisiopteus lobifera	*Microcalanus* spp
Typhloscolex mulleri	*Microcalanus pygmaeus*
Vanadis longissima	*Oithona similis*
	Oithona frigida
Mollusca	*Oncaea antarctica*
Clione limacina antarctica	*Onchocalanus cristatus*
Clio pyramidata	*Paraeuchaeta biloba*
Cymbulia spp.	*Paraeuchaeta* spp
Gonatus spp	*Paraeuchaeta exigua*
Limacina retroversa	*Pleuromamma* spp
Limacina helicina antarctica	*Pleuromamma abdominalis*
Limacina inflata	*Pleuromamma gracilis*
Spongiobranchia australis	*Pseudochirella mawsoni*
	Racovitzanus antarcticus
Isopoda	*Rhincalanus gigas*
isopod	*Scaphocalanus* spp
	Scaphocalanus antarctica
Ostracoda	*Scaphocalanus farrani*
Ostracods	*Scaphocalanus vervooti*
	Scolecithricella spp
	Scolecithricella glacialis
	Scolecithricella minor

Table 7A continued

Euphausiacea
Euphausia spp
Euphausia longirostris
Euphausia similis
Euphausia similis var. armata
Euphausia triacantha
Euphausia vallentini
Nematoscelis megalops
Stylocheiron maximum
Thysanoessa gregaria
Thysanoessa macrura
Thysanoessa spp *(vicina)*

Amphipoda
Archaeoscina spp
Cyllopus magellanicus
Cypocharis faurei
Gondogenia spinicoxa
Mimonectes sphaericus
Paraphronima gracilis
Phronima sedentaria
Primno macropa
Themisto gaudichaudii
Scina spp
Vibilia antarctica

Decapoda
Nauticaris marionis
Nematocarcinus spp
Nematocarcinus longirostris
Pasiphaea longispina
Sergestes spp

Chaetognatha
Eukrohnia hamata
Sagitta gazellae

Tunicata
Iasis zonaria
Ihlea magalhanica
Salpa thompsoni

Osteichthyes
Dissostichus eleginoides
Echiodon chryomargarites
Electrona carlsbergii
Gymnoscopelus spp
Gymnoscopelus braueri
Gymnoscopleus hintonoides
Gymnoscopelus opisthopterus
Gymnoscopelus bolini
Krefftichthys anderssoni
Notothenia larseni
Protomyctophum spp
Protomyctophum choriodon
Protomyctophum bolini
Protomyctophum tenisoni
Stemonosudis spp
Stomias boa boa