UNIVERSITY OF SOUTHAMPTON

Mesoscale zooplankton distribution patterns and euphausiid population ecology in the south-west Atlantic

Geraint Andrew Tarling B.A.$_{oxon}$

Doctor of Philosophy

Oceanography Department

Submitted August, 1995

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE
OCEANOGRAPHY

Doctor of Philosophy

Mesoscale zooplankton distribution patterns and euphausiid population ecology the south-west Atlantic Ocean

by Geraint Andrew Tarling

Two mesoscale net sampling surveys were conducted in the south-west Atlantic between 34° and 55°S. The first survey was in the austral spring of 1990 and used both an RMT8 net which was trawled obliquely down to 200 or 300 m and caught mainly macrozooplankton and a Bongo net which was deployed at the surface and sampled mesozooplankton. The second survey was in the austral spring of 1991 and used a Bongo net which was deployed obliquely down to 50 m and sampled mesozooplankton. This thesis considers the species composition and abundance of these samples and represents one of the first insights into the mesoscale biogeography of zooplankton communities in the south-west Atlantic.

155 species from 9 taxonomic groups were considered including euphausiids, hyperiid amphipods, chaetognaths, salps, siphonophores, and nektonic/planktonic fish. Multivariate analyses were used to highlight species assemblage distribution patterns and determine strongly correlated environmental variables. In the 1990 RMT8 samples, species assemblages showed a distribution pattern related to the location of water masses, which was reflected in a combination of water mass and latitude being the most strongly correlated environmental variables. In the 1990 Bongo samples, a combination of sea-surface temperature and latitude were most strongly correlated environmental variables and different species assemblages showed a pattern of being located in exclusive temperature ranges. The two sample sets did exhibit some common distribution patterns especially in the warm, sub-tropical waters to the north and the Falkland Shelf to the south. However, there were fundamental differences in the mid-latitudes regions, possibly reflecting the reduced ability of larvae to counteract expatriating forces when compared with adults. Further comparisons made between the 1990 and 1991 Bongo sample sets highlighted some of the causal factors behind distribution patterns. For instance, the precise definition of the boundary between sub-tropical and sub-Antarctic assemblages by the 17.3°C isotherm despite the multitude of expatriating phenomena suggested that many organisms were at the edge of their physiological limits in this region. In polar waters, distribution patterns were consistent but temperatures variable suggesting that advection rather than temperature tolerance was more influential. Further data from Montu (1977) and the Discovery Investigations was examined to add a seasonal dimension to the above patterns as well as providing an insight into the importance of population ecology on community distribution. Studies were concentrated on euphausiid species from which it was apparent that size structure and species dominance changed considerably with season. Estimates of the productivity of these species showed that weight-specific rates were comparable with more sub-tropical regions despite biomass levels being proportionally low.

The use of satellite thermal images for predicting faunal distribution patterns was assessed with respect to future biogeographic analysis of this region. Images were a good predictor at the sub-tropical boundary but a poor predictor in other regions highlighting the fact that in situ net sampling methods still appear to be the most effective and reliable investigative tools for biogeographic analysis.

Acknowledgements

I would firstly like to thank the officers and crew of the MV *Falkland Protector* for their assistance in the field and Paul Rodhouse (British Antarctic Survey) for the initial inception of this project. Thanks is also owed the following for their efforts in the on-shore logistics and for the deployment of gear and data collection at sea: Emma Hatfield, Douglas Bone, Elizabeth Marrow, Martin Collins, Conor Nolan, John Barton and Grant Monroe. Guidance with the identification of various taxa was given by N. Merrett, P. Pugh, F. Pages, A. C. Pierrot-Bults, J. -P. Casanova and P. Hargreaves. Invaluable input was also given by Demetrio Boltovskoy in obtaining scientific material, providing South American literature, advising with statistics and reading of manuscripts as well as Andrew Hirst for advice on production modelling. Satellite images were provided through collaboration with Professor D. Olson and Dr. P. Podesta from data collected by the Estacion HPRT of the Servicio Meteorlogico Nacional of Argentina as part of a cooperation agreement with the University of Miami. Assistance in obtaining *Discovery* samples was given by Ben Borman, the curator of the collections at the Institute of Oceanographic Sciences, U.K.. Statistical software was kindly granted by Martin Carr of Plymouth Marine Laboratories, U.K..

Thanks must additionally go to staff and colleagues at the Oceanography Department, especially John Gibbs for the construction of a user friendly Folsom Spitter, Jeremy Brooks and Dr. Steve Hutchinson for help with un-user friendly computer software, Lauretta Hall and Andy Geary for constantly tracking down lost equipment, Dr. Lawrence Hawkins for the loan of his equipment and Bob Stringer for solving logistical nightmares. My sanity is owed to all inhabitants of Room 12, especially Andrew Hirst and Sarah Bronsdon, as well as to Darren Williams, all of which helped keep me smiling on even the darkest of days. My supervisors, John Williams and Martin Sheader gave much help in planning and structuring this thesis as well as a great deal of constructive advice on various drafts. Finally, my greatest thanks goes to Peter Ward of the British Antarctic Survey whose intellectual and moral support throughout the course of this Ph.D. made its completion possible.

This thesis is dedicated to Anna for her love and to my parents for their immeasurable support.

THERE ARE ROUGHLY ZONES

We sit indoors and talk of the cold outside.
And every gust that gathers strength and heaves
Is a threat to the house. But the house has long been tried.
We think of the tree. If it never again has leaves,
We'll know, we say, that this was the night it died.
It is very far north, we admit, to have brought the peach.
What comes over a man, is it soul or mind -
That to no limits and bounds he can stay confined?
You would say his ambition was to extend the reach
Clear to the Arctic of every living kind.
Why is his nature forever so hard to teach
That though there is no fixed line between wrong and right,
There are roughly zones whose laws must be obeyed?
There is nothing much we can do for the beech tonight,
But we can't help feeling more than a little betrayed
That the northwest wind should rise to a height
Just when the cold went down by so many below.
The tree has no leaves and may never have them again.
We must wait till some months hence in the spring to know.
But if it is destined never again to grow,
It can blame the limitless trait in the hearts of men.

Robert Frost, 1936

List of contents

Chapter 1 Introduction 1

1.1 - Layout of the thesis 7

Chapter 2 Materials and Methods 9

2.1 - Field sampling methods 9
2.1.1 - 1990 RMT8 and Bongo survey 12

2.1.2 - 1991 Bongo survey 13

2.1.3 - Collection of oceanographic data 13

2.2 - Laboratory methods for zooplankton distribution studies 13
2.2.1 - Sorting of 1990 RMT8 and Bongo samples

2.2.2 - Identification 14

Chapter 3 Assumptions and errors of zooplankton sampling methods 17

3.1 - Net sampling errors 17

3.2 - Sub-sampling error 20
3.2.1 - Estimation of the degree of sub-sampling error ... 21

Chapter 4 Hydrography of the study area 25

4.1 - Introduction 25

4.2 - Description of currents and water masses 26

4.2.1 - Physical properties of water masses 27
4.2.2 - Hydrographic variability 29

4.3 - Position of fronts and water masses during 1990 and 1991 surveys derived from XBT profiles 33
4.3.1 - Description of 1990 frontal positions and surface temperatures 34
4.3.2 - Description of 1991 frontal positions and surface temperatures 37

4.4 - Comparison of SST satellite images and the position of water masses 39
4.4.1 - Mesoscale SST patterns in 1990 and 1991 surveys 41

Chapter 5 Biogeography of the study area 56

5.1 - Theoretical overview 56

5.2 - History of biogeographic research in the south-west Atlantic 67

5.3 - Contemporary biogeographic studies of the south-west Atlantic 68

Chapter 6 Distribution patterns of RMT8 and Bongo 1990 79

6.1 - Introduction 79

6.2 - General patterns of distribution 83
6.2.1 - Introduction 83
6.2.2 - Calculation methods of community parameters in 1990 RMT8 and 1990 Bongo samples 84
6.2.3 - Results and analysis 85
6.2.4 - Discussion 96

6.3 - Multivariate analysis - justification and description of multivariate techniques used 106
6.3.1 - Hierarchical classification 108
6.3.2 - Factor analysis 110
6.3.3 - Multivariate analysis of abiotic factors (BIOENV) 112

6.4 - Multivariate analysis of RMT8 1990 117
6.4.1 - Hierarchical classification of RMT8 1990 117
6.4.2 - Factor analysis of RMT8 1990 125
6.4.3 - Relationship of multivariate groups to abiotic factors 130
6.4.4 - Discussion 131

6.5 - Multivariate analysis of Bongo 1990 138
6.5.1 - Hierarchical classification of Bongo 1990 138
6.5.2 - Relationship to abiotic factors 140
6.5.3 - Discussion 145

6.6 - Discussion 154
6.6.1 - Comparison of RMT8 1990 to Bongo 1990 multivariate groups 154
6.6.2 - Comparison of present study to other contemporary studies 159

6.7 - Conclusions 168

Chapter 7 Interannual comparison of zooplankton patterns, water mass positions and satellite sea-surface temperatures 171

7.1 - Introduction 171

7.2 - Comparison of 1990 and 1991 survey areas and the position of water masses/SST resolved features 174

7.3 - Bongo 1991 sorting/analysis method 184
7.3.1 - Station groups distribution 184
7.3.2 - Species composition 187
7.3.3 - Relationship to environmental factors 191

7.4 - Discussion 202

7.5 - Conclusions 213

Chapter 8 Euphausiid life cycles and production 215

8.1 - Introduction 215
8.1.1 - The importance of euphausiids in the south-west Atlantic pelagic ecosystem 215
8.1.2 - Review of present knowledge of euphausiid life cycles 215

8.2 - Methods 226
8.2.1 - Temperature methods and analysis 226
8.2.2 - Methods used in the reinterpretation of larval and adult densities from Montu (1977) 228
8.2.3 - *Discovery*/*William Scoresby* sorting methods 229
8.2.4 - Length and weight measures of larvae and methods 233
8.2.5 - Analytical methods applied to larval and adult stage frequencies 236

8.3 - Results and Interpretation of euphausiid cycles 239
8.3.1 - Population cycle of *E.vallentini* 240
8.3.2 - Population cycle of *E.lucens* 258
8.3.3 - Population cycle of *T.gregaria* 278

8.4 - Discussion 295
8.4.1 - Reanalysis of *E.vallentini* 295
8.4.2 - Reanalysis of *E.lucens* 298
8.4.3 - Reanalysis of *T.gregaria* 302
8.4.4 - General Discussion 306

8.5 - Conclusions 313

Chapter 9 Production of euphausiids on the Patagonian shelf 315

9.1 - Introduction 315

9.2 - Rationale to the calculation of production 317

9.3 - Methods 326
9.3.1 - Treatment of densities from Montu (1977) 326
9.3.2 - Estimation of average weight of each size class 327
9.3.3 - Estimation of biomass 329
9.3.4 - Application of Ikeda-Motoda model 329

9.4 - Results and Interpretations 332
9.4.1 - Intra-specific comparison of biomass 332
9.4.2 - Inter-specific comparison of biomass 334
9.4.3 - Intra-specific comparison of production rates 335
9.4.4 - Inter-specific comparison of production rates 340
9.4.5 - Intra-specific comparison of P:B d^{-1} 340
9.4.6 - Inter-specific comparison of P:B d^{-1} 342
9.4.7 - IP and P/B yr^{-1} 344

9.5 - Discussion 346
9.5.1 - Seasonal and geographic patterns in biomass 346
9.5.2 - Seasonal and geographic patterns in PR and P:B d^{-1} 353
9.5.3 - IP and P/B yr^{-1} in relation to other studies 356

9.6 - Conclusion 365

9.7 - Overview of euphausiid life-cycles and production on the Patagonian shelf 367

Chapter 10 Conclusions 373

Chapter 11 Future work 380

Bibliography

Appendices

Chapter 1 Introduction

The south-west Atlantic is a dynamic oceanographic region containing two western boundary currents and an energetic convergence zone where warm-core and cold-core mesoscale eddies are numerous. The position of fronts are notoriously variable and there is a strong contrast in the physical attributes of water masses. The region is also characterised by an extensive continental shelf area which spans the whole of the eastern coastline of South America from 30° to 55°S and may reach up to 500km from land (fig 1a).

The south-west Atlantic has recently received renewed interest since the emergence of squid fisheries both off the Falkland Islands and on the Patagonian and Argentinean continental shelves. There are currently two exploited squid species, *Illex argentinus* and *Loligo gahi* (Csirke, 1987) but unexploited stocks of other species are likely to be fished commercially in the future (Rodhouse, 1990). Investigations carried out on the dispersal and recruitment of squid stocks (Patterson, 1988; Rodhouse and Hatfield, 1990; Rodhouse et al., 1992, Hatfield, 1992) as well as on squid diet (Ivanovic and Brunetti, 1994; Clarke et al., 1994) have highlighted that more information on trophic interactions in the region needs to be obtained. Such information can only be achieved through detailed understanding of the zooplankton ecology.

Unfortunately, there has been comparatively little study of zooplankton ecology of the south-west Atlantic compared to other oceanographic regions (Angel, 1979; Boltovskoy, 1986) despite the fact that there have been a number of past expeditions that have surveyed the area (eg. *Discovery*, Kemp & Bennet (1929), *Dana*, Jespersen (1923, 1935), *Meteor*, Hentshel (1938)) as well as more recent expeditions by the *Shankai Maru*

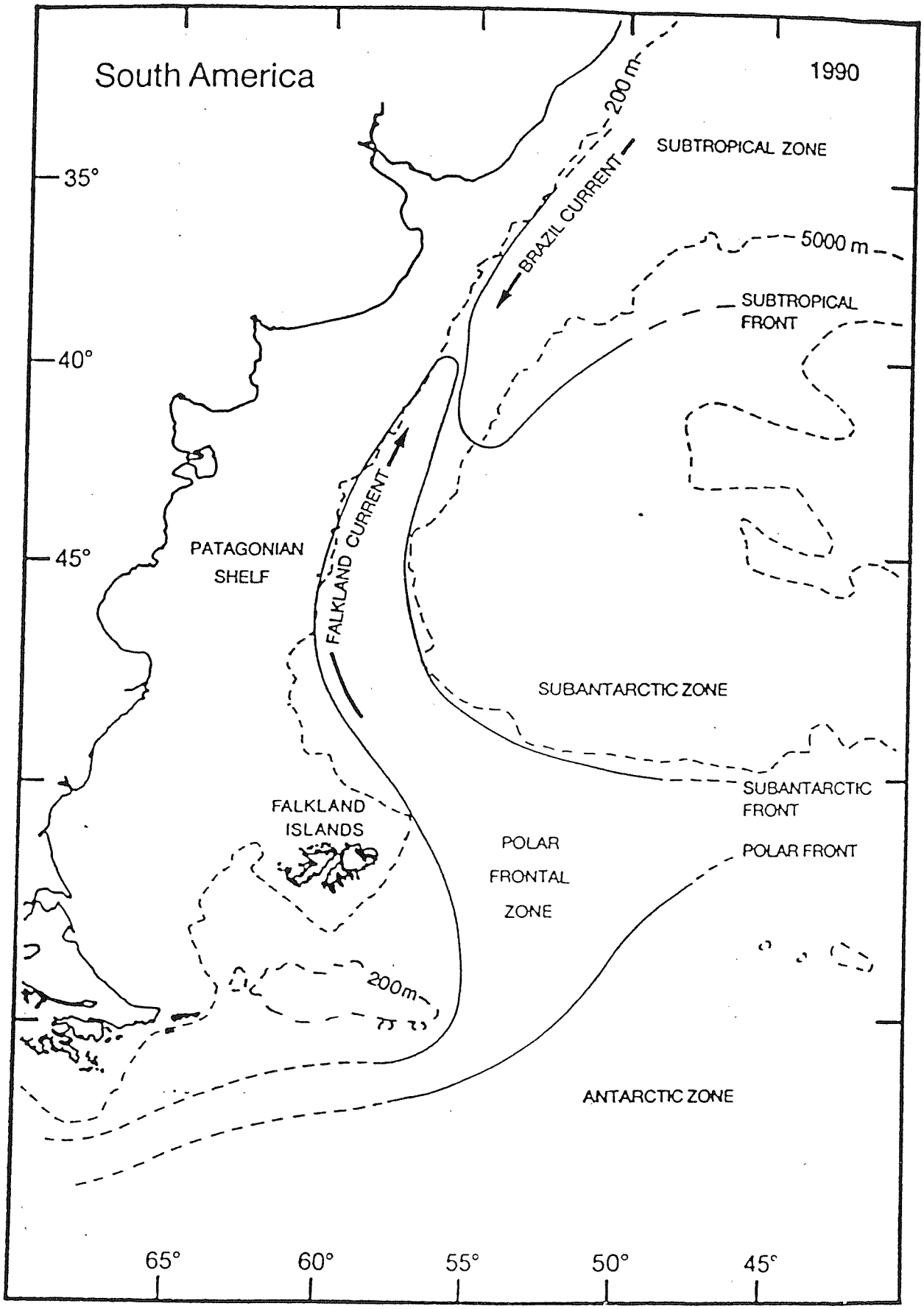


Fig. 1a: **Major geographic and hydrographic features of the south-west Atlantic**

and the *Walter Herwig* on the Patagonian shelf (Dadon, 1989, Mazzoni, 1990). The problem with most such investigations is that they concentrated on single taxonomic groups which can often be misleading when trying to define general patterns of zooplankton distribution as a first stage to understanding the ecology of a region (Boltovskoy, 1986). An exception was the study of Dadon and Boltovskoy (1982), in which distributional records of a number of taxonomic groups were analysed using multivariate techniques. Their proposed distribution patterns were derived from a large amount of biological information compiled from the literature. However, the sampling methods of the cited zooplankton surveys varied and their quantitative information was not comparable. The study was therefore restricted to a qualitative approach, analysing information based on the presence or absence of species in designated regions.

The present study concentrated on samples obtained by the Falkland Islands Government Fisheries Department vessel, the M/V *Falkland Protector*, which carried out a series of research cruises between 1990 and 1992 with the objective of examining the distribution of paralarval and juvenile cephalopods in the south-west Atlantic in relation to the major oceanographic features (Rodhouse et al., 1992). Two types of net were used, the first, an RMT8 net, had a mesh size of 4.5mm and as well as catching cephalopod juvenile and paralarval cephalopods, it retained macrozooplankton and nektonic species. The second, a Bongo net, had a mesh size of either 335μm or 500μm and retained mesozooplankton as well as the target paralarval squid. The surveys were temporally synoptic, carried out simultaneous hydrographic measurements and had a mesoscale[1] spatial resolution. Therefore, analysing the zooplankton bi-catch of these cruises gives an almost unique insight into

[1] Mesoscale is defined as having a spatial resolution of between 100 and 1000km (Haury et al., 1978)

distributional ecology of zooplankton assemblages in the south-west Atlantic.

The general approach adopted by this study was to consider the zooplankton ecology of the region from a principally biogeographic perspective and to this end, it attempted to fulfil the main objectives of biogeographic investigation first outlined by McGowan (1971) and recently by the 2nd Pelagic Biogeography conference held in Amsterdam (July, 1995). These are:

1, to describe what species are present

2, to describe, quantitatively, their patterns of abundance

3, to understand what maintains the patterns

4, to determine how and why the patterns developed

5, to describe and delineate the communities

6, to determine how these community-ecosystems are structured and how they function

Such objectives are quite extensive and within this study, only the first 3 were addressed adequately enough to draw any definitive conclusions. With respect to the first objective it was aimed to consider as many taxonomic groups as possible in order that a broad spectrum of species making up the zooplankton community was considered when establishing general patterns of distribution. Nine taxonomic groups were considered in total including crustaceans, coelenterates and chaetognaths. One problem with the second objective was that the amount of data collated was beyond the realm of straight forward description. Multivariate analytical techniques were therefore employed since they provided an objective means of picking out pronounced patterns both in terms of community composition and distribution. Given the dominance of the oceanographic regime on the ecology of the south-west Atlantic (Rodhouse et al., 1992), the third objective of understanding the maintenance of patterns was considered mostly in terms of concurrent

hydrographic information. Nevertheless, the population ecology of major species in the region was also considered, especially the timing of spawning and the effect of ontogenetic migration. The last 3 objectives were not directly addressed since their questions search far beyond the scope of the present investigation but many discussions touched on these subject areas. Furthermore, through addressing the first 3 objectives alone, it was possible to build up a fundamental picture of zooplankton ecology of the region which enhances current understanding of the south-west Atlantic ecosystem.

A wider role of biogeographic investigation is to provide information for large scale models designed to measure the extent and implications of global fluxes. One further aim of this study was therefore to establish what relationships exist between hydrographic variability and biological distribution patterns. This allows important factors influencing the pelagic biological system to be identified and assists in making pelagic biogeography models less complex and more accurate. To this end, the present investigation attempts to evaluate the use of satellite imagery in both improving the synoptic interpretation of zooplankton cruise data and in evaluating the potential of this tool for predicting zooplankton community distribution patterns.

Another aim was to understand the population ecology of major components of the zooplankton community since this enhances insights gained from biogeographic analyses as well as highlighting potential trophic interactions, beneficial in fisheries management. It was therefore considered important that analyses on life cycles and productivity of abundant and widespread species in the region were carried out. One difficulty however was that there was a large number of species that were both abundant and widespread, so it was necessary to concentrate on just one taxonomic group. The euphausiids were chosen for this purpose since they had the greatest displacement volumes in the RMT8 samples as well as one of the

highest numerical abundances. One fundamental problem however was that the surveys of the M/V *Falkland Protector* were not carried out in all seasons but were restricted to the Austral Spring and so another source of seasonal data had to be obtained. Fortunately, a number of additional resources were found, including the *Discovery* Investigations which sampled this area over a number of years during the earlier part of this century and whose collections are still retained at the Institute of Oceanographic Sciences, U.K. as well as raw data published by Montu (1977) from a series of seasonally spaced zooplankton research cruises on the Patagonian Shelf. Life history and secondary production analyses were therefore carried out using this information.

Overall, this study examines the mesoscale ecology and biogeography of zooplankton communities in the south-west Atlantic between 34° and 55°S including the Argentinean Basin, the Patagonian slope and shelf and the Falkland Shelf using samples collected by M/V *Falkland Protector* in 1990 and 1991. Other information was considered from the seasonal surveys by Montu (1977) and the *Discovery* Investigations including the analysis of *Discovery/William Scoresby* preserved plankton samples. Furthermore, hydrographic information, including concurrent satellite images, was used in the interpretation of spatial and temporal patterns with the aim of identifying the most pertinent factors influencing the zooplankton ecology of the region. Ultimately, this thesis attempts to provide information that adds to current understanding of the south-west Atlantic ecosystem, especially with respect to the management of fisheries as well as contributing to the wider body of knowledge on what influences biogeographic patterns in the pelagic system.

1.1 Layout of thesis

The following chapter describes the sampling programmes undertaken in the south-

west Atlantic by the M/V *Falkland Protector* during the Austral Springs of 1990 and 1991. Laboratory methods of subsampling and enumerating the catches are then described as well as details on the keys that were used to carry out the species identification on the 9 taxonomic groups that were considered. The procedures for analysing and interpreting the extracted information are critically dependent on the strengths and weaknesses of the sampling programme (Atkinson, 1990) and so Chapter 3 investigates the major sources of both net sampling and subsampling errors. Chapter 4 then describes the general hydrographic features that are normally encountered within the study region followed by a precise description of the prevailing conditions during the 1990 and 1991 survey periods.

Biogeography is a very wide ranging field with indistinct subject boundaries so it is essential that the aims of the present investigation are clearly defined. The description of such aims would nevertheless have very little context without firstly describing general biogeographic theory as well as the history of biogeographic study in the present study area so both these aspects are dealt with in Chapter 5. Chapter 6 applies the adopted biogeographic approach to the species abundance and distribution data extracted from the 1990 Bongo and RMT8 catches through firstly describing general distribution patterns in terms of community parameters such as displacement volume, diversity and frequency of species occurrence before applying multivariate techniques to pick out pertinent patterns in the distribution of species assemblages. Chapter 7 carries on from this approach by comparing the patterns observed in the 1990 Bongo data set to those in the 1991 Bongo data set, employing satellite images to assist in the interpretation.

Chapters 6 and 7 concern multispecies distributions but the last 2 chapters (8 and 9) are restricted to three major euphausiid species to investigate how patterns at the population level affect community level distribution. Chapter 8 examines the life cycles of the 3 species

from raw data extracted from Montu (1977) and specimens taken from the collections of the *Discovery* Investigations. Chapter 9 goes on to assess the importance of these species to the trophic ecology of the region through estimating seasonal biomass and production. Chapter 10 briefly summarises the conclusions of each of the preceding chapters and gives a broad overview of the importance of these findings to present knowledge of the south-west Atlantic ecosystem whilst the final Chapter outlines future work that would further benefit our understanding of this region.

Chapter 2 Materials and Methods

2.1 Field Sampling Methods

During October and November 1990 and 1991, net sampling surveys were carried out aboard the M/V *Falkland Protector*. A combination of Bongo nets with either 335μm or 500μm mesh and an RMT8 net with 5mm mesh were used. All station positions and sampling times are given in Appendix I.

2.1.1 1990 RMT8 and Bongo surveys

The 1990 survey consisted of a series of latitudinal transects and was split into a northern and southern phase (fig. 2a). The southern phase (Phase I) was carried out in the vicinity of the Falkland Islands between 50 and 53°S with transects covering shelf waters of 200m or less in depth. The northern phase (Phase II) surveyed an area between 34° and 48°S at 2° latitudinal intervals. The survey region fell outside the South American 200 mile exclusion zone but covered slope waters adjacent to the Patagonian shelf and the western sector of the Argentine basin.

In the northern phase, the RMT8 net was deployed obliquely from the surface to 300m and towed for 90 minutes whilst in the southern phase, the net was deployed obliquely from the surface to 200m or the bottom and towed for 60 minutes. The Bongo net, which had 335μm mesh, was deployed for 30 minute surface hauls in both the northern and the southern phases. All sampling was carried out at a nominal speed of 2 knots and net depths were monitored by an IOS acoustic monitor (RMT8) and a Benthos time-depth recorder (Bongo).

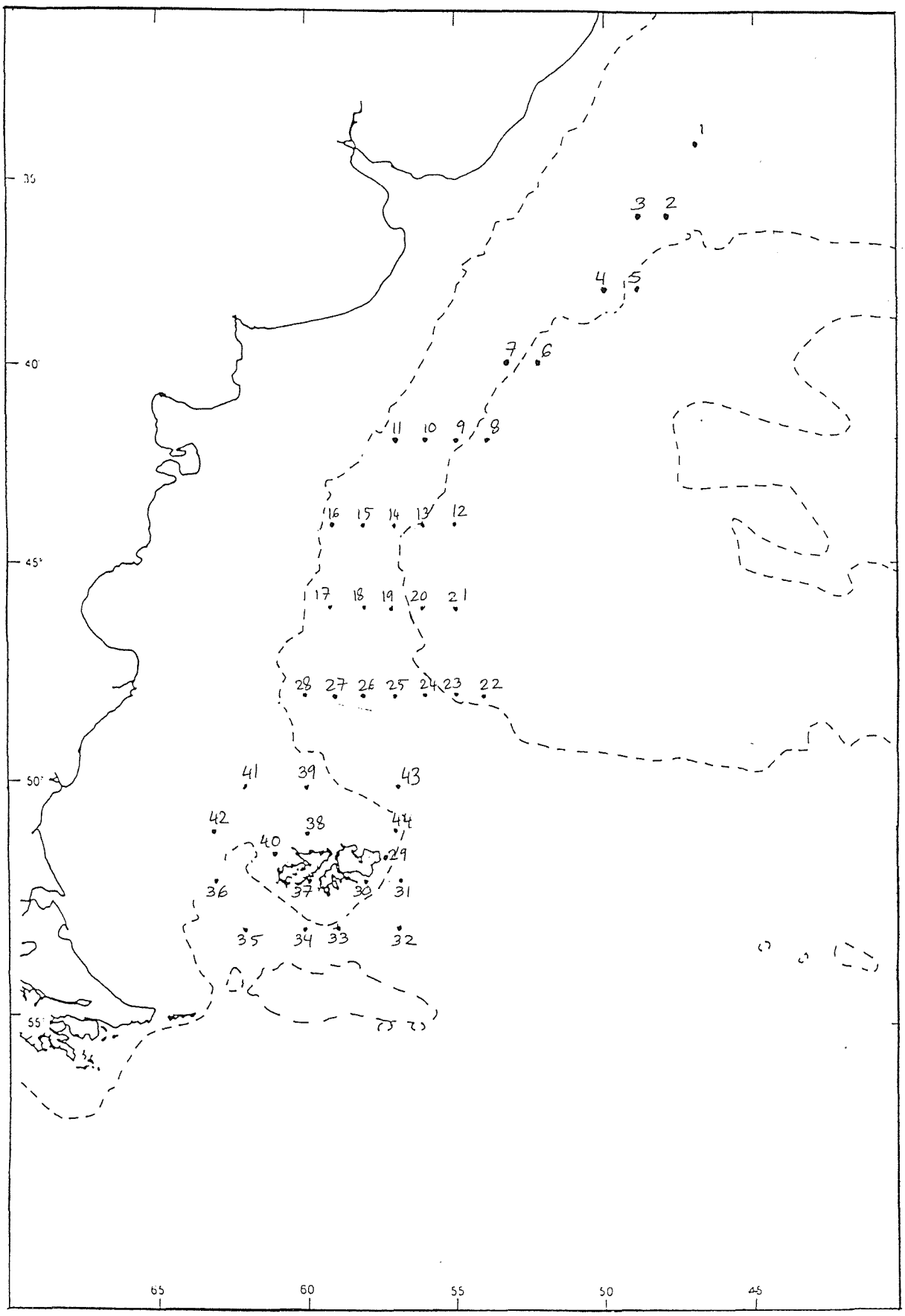


Figure 2a: 1990 RMT8 and Bongo stations

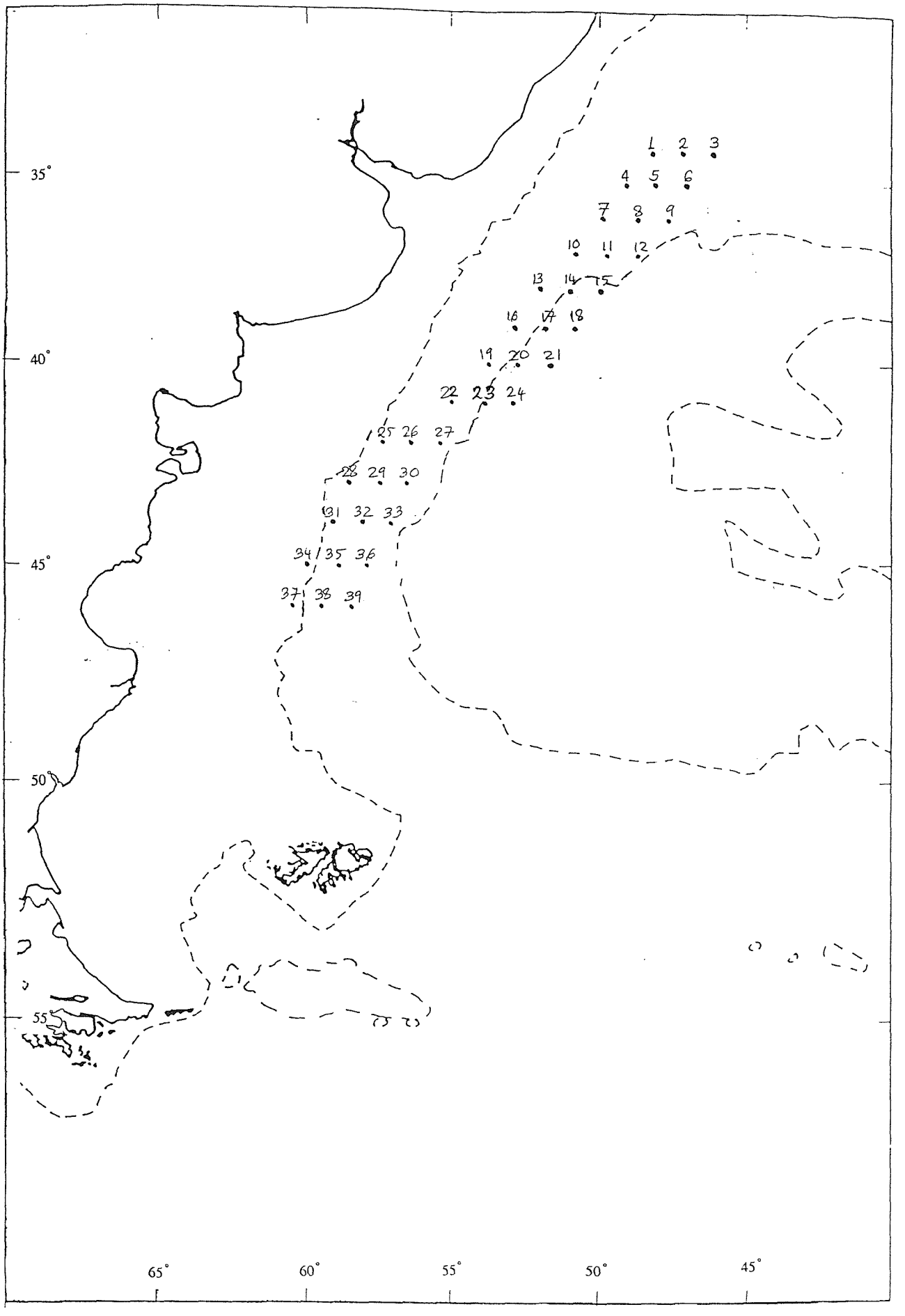


Figure 2b: 1991 Bongo stations

2.1.2 1991 Bongo survey

The 1991 surveys was also split into a series of latitudinal transects but at 1° rather than 2° intervals (fig 2b). It surveyed a region between 34°S and 46°S which again covered the Patagonian slope and Argentinean Basin but did not reach as far south as the Falkland Shelf. Only a Bongo net with a 500μm was trawled at each station and this was deployed obliquely from the surface to 50m for 30 minutes. Sampling was carried out at a nominal speed of 2.5 knots with the net depth being monitored by a Benthos time-depth recorder.

Flow meters were not deployed on either the Bongo or RMT8 nets but filtered volume can be estimated through multiplying the effective mouth area by the distance travelled. The Bongo nets had a rigid mouth frame, 0.6m in diameter making the effective mouth area 0.283m^2. In 1990, the nets were deployed at 2 knots (1.028 m/s) for 30 minutes (1800s), making the distance travelled 1850.400 m and giving a filtered volume of 523.664m^3. In 1991, the nets were deployed for 30 minutes at 2.5 knots (1.285 m/s) which gives a filtered volume of 654.58m^3. Estimating the filtered volume of the RMT8 net is not as straightforward since there are bridles controlling the height of the net and this alters the effective mouth area depending on the speed and angle of the tow. Nevertheless, this problem was considered by Pommeranz et al. (1982) who carried out sea trials on the stability of the net during oblique tows and derived equations that allowed reliable estimates of volume filtered. With a net width (W) of 2.83m, height (H_o) of 4.0m (Clarke, 1969) and velocity (V) of 2 knots, the effective mouth area was 9.830m^2. The distance travelled during the 90 min northern phase tows was 5556m which gave a filtered volume of 54 687m^3. The 60 min southern phase tows can be

assumed to filter 2/3 of this amount, which was 36 468m^3.

2.1.3 Collection of oceanographic data

During both 1990 and 1991, vertical temperature profiles were obtained to a maximum depth of 750m using T7 expendable bathythermographs (XBT's). During 1990, an XBT was deployed at each sample site in the northern phase, with additional deployments also made to the east of the survey area during the transit stage whilst, in the southern phase, deployments were carried out on 2 transects. During 1991, deployments were made at each sample site.

In all surveys, preliminary sorting for cephalopods was done at sea. The entire samples were subsequently fixed in 4% formalin and later transferred to Steedman's solution (Steedman, 1976) during further sorting in the laboratory.

2.2 Laboratory methods for zooplankton distribution studies

2.2.1 Sorting of 1990 RMT8 and Bongo samples

During laboratory analysis, the preserving solution was drained from the samples as thoroughly as possible. The displacement volume of the whole sample was then measured. A preliminary sort of the sample was carried out, during which most of the larger organisms such as fish, decapods and large salps were removed and counted.

Because many of the smaller animals were highly abundant it was necessary to sub-sample the remainder of the material. This was carried out by splitting the sample into fractions using a two chambered Folsom plankton splitter, which divides a sample by repeated halving.

The aim of splitting is to obtain an aliquot that is small enough to sort efficiently but is also representative of the whole sample. A decision must therefore be made as to what is a practical sorting method and what numbers of organisms should be counted. A number of theoretical works have been published considering ways of standardising the error incurred through using a Folsom splitter (Dahiya, 1980; Griffiths et al., 1984). Many of the methods described are time consuming and not practical to implement. Through consulting other works where a Folsom splitter was used (Atkinson, 1991; Thomas, 1992), it was decided that the best course was to separate approximately 100 to 150 individuals in a particular group. The taxonomic level of a group depended on the extent to which identifications could be made through unaided visual inspection. The level varied, since some taxa were more morphologically distinct than others. For example, it was possible to distinguish hyperiid genera by unaided inspection but not euphausiids, which were grouped as an order. Numbers in a particular group were estimated from scanning the complete sample. If the numbers were estimated to be less than 150, the group would be separated before splitting. If a lot more than 150 were estimated to be present, then the appropriate number of splits were made before the group was separated. A fuller evaluation of the errors incurred through sub-sampling is discussed in a further chapter.

2.2.2 Identification

Individuals were identified as far as possible with the aid of magnification. These taxa were counted to obtain their relative abundance and if there was sufficient quantity, their displacement volumes were measured.

Identifications were based on the following keys:

Euphausiids

Baker et al. (1990)	*Euphausiids of the world*
Gopalakrishnan (1975)	*Biology and taxonomy of the genus Nematoscelis*

Amphipods

Bowman et al. (1973)	*Families and genera of Hyperidea*
Bowman (1978)	*Revision of the pelagic amphipod genus Primno*
Vinogradov (1982)	*Hyperiid amphipods*
Barnard (1932)	*Amphipoda, Discovery report*

Siphonophores

Totton et al. (1965)	*A synopsis of the siphonophora*
Alvarino (1981)	*Siphonophores in "Atlas del zooplankton del Atlantico sudoccidental" ed. D. Boltovskoy*

Hydromedusa

Browne et al. (1939)	*Hydromedusa of the Falkland Islands, Discovery Report*
Kramp (1959)	*The hydromedusa of the Atlantic, Discovery report*

Decapods

Kensley (1972)	*Shrimps and prawns of South Africa*
Crosnier and Forest (1973)	*Les crevettes profondes de l'Atlantique oriental Tropical*

Fish

Smith and Heemstra (1986)	*Smith's sea fishes*

	Nafpaktitis (1977)	*Fishes of the N.W. Atlantic part VII*
Salps		
	Esnal (1981)	*Salpidae in "Atlas del Zooplankton del Atlantico sudoccidental" ed. D. Boltovskoy*

Chapter 3 Assumptions and errors of zooplankton sampling methods

It is important to consider in any sampling program that measured differences between stations reflect not only true biological variability but also the inaccuracy and imprecision in experimental technique (Atkinson, 1990). There are two main areas where errors may be incurred, during net sampling and during sub-sampling. This chapter discusses the nature of these errors and the degree to which they confound the results.

3.1 Net Sampling Error

The objective of a net system is to retain all target species in its path and enable the volume of water filtered to be determined. Error can occur in three main areas:

1, Organisms can escape through the mesh

2, Organisms can avoid the net

3, The amount of water filtered can be wrongly estimated.

None of the surveys used flow meters during net deployment so it is not possible to consider the variability in the amount of water filtered. The subsequent discussion shall therefore concentrate on the first two sources of error listed above.

Net sampling errors are now comparatively well documented through the use of underwater photography and test tanks (Unesco report, 1966; Pillar, 1984). The retention width of different zooplankton groups was examined by Bernhard et al. (1973) who used an assembly of six nets and demonstrated that the minimum total retention width of an animal is almost linearly related to the mesh size of the net and that, to ensure complete retention, the mesh diameter must be no more than 75% of the width of the organism. The main factors that act to confound such linear relationships are the

size, shape, plasticity of the organism as well as its ability to escape (Vanucci, 1966). If organisms are smooth and plastic they are more likely to escape through the mesh than spiny, rigid organisms of the same size. It has also been shown by Saville (1958) that the degree to which many zooplankton species can alter their shape is quite considerable.

Active escapement through mesh is a function of the size, shape and behaviour of the organism. Squeezing through mesh involves behavioural patterns that vary with the species and its developmental stage. It is probable that larger organisms deviate from the general retention ratio of Bernhard et al. (1973) since they are relatively stronger, more mobile and have a greater ability to escape.

The other main source of error in zooplankton sampling to be considered is net avoidance. Anecdotes of net avoidance are commonplace and comments are often made such as that of MacKintosh (1934) who wrote that "Euphausiaceans could clearly be seen to leap backwards out of the way of the approaching net". However, more empirical studies of net avoidance have produced conflicting results. Pillar (1984), for instance, found that there was no evidence of avoidance by either copepods or euphausiid larvae when comparing the performance of 4 different zooplankton samplers. Clutter and Anruku (1968) reviewed papers dealing with three variables that contribute to net avoidance; net size, towing velocity and light conditions. The conclusions of papers looking at net size were inconsistent probably because of the problems associated with patchiness and net mesh selection. Increasing towing speed was found by Tranter (1966) to increase the number of organisms caught.

Vision associated avoidance was demonstrated for mesopelagic fish by Pearcy and Laurs (1966). However, this is not true for all taxa. Investigations by the Institute of Oceanographic Sciences, U.K., found that smaller zooplankton species such as ostracods

(Angel and Fasham, 1975) and copepods (Roe, 1972) were caught in greater overall numbers by day. Euphausiids (James *in* Angel, 1977) and decapods (Foxton, 1972) were found to be more abundant in night catches.

Overall, larger, more mobile species and those with well developed sensory organs tend to show the greatest degree of net avoidance. However, there are certain other factors not associated with avoidance which may act to produce the same conclusion. For instance, the degree of vision associated avoidance cannot be separated from the effect of diurnal vertical migration of animals since the above studies mostly compare day and night time hauls at different depth strata. Thus, results showing that animals were caught in greater numbers at night could also be equally be explained by dispersive behaviour during the day and aggregating behaviour during the night (*see* Angel, 1977).

Any sampling program is a compromise between gaining the most accurate picture possible and doing what is logistically feasible and, as in any sampling programme, there are advantages and disadvantages to the approach taken by the present surveys. For the RMT8 nets, potential errors such as net avoidance and patchiness are minimised through the use of a large net, towed at a moderate speed for a relatively long time span. Such errors are more prevalent in the Bongo nets however since they have a smaller mouth area and were deployed for a much shorter duration. Other variables such as the effect of diurnal vertical migration or the depth distributions of populations remain unaccounted for in both net types since deployment was carried out on arrival at a station irrespective of the time of day. Nevertheless, oblique trawls are more likely to obtain samples that are more representative of the whole water column (Pugh, 1975) and so this source of error is likely to have been reduced in the RMT8 samples and the 1991

Bongo samples which were deployed obliquely to depths of 200/300m and 50m respectively. The 1990 Bongo samples stand to affected most by this error caused by vertical migration since they were taken from the surface layers only. Despite these problems, the distinct advantage of the present sampling programmes was that they sampled a large area at a mesoscale resolution over a relatively short time span. Such spatial resolution is unique in this region and the large absolute survey area allows comparisons to be made between waters with different physical attributes. Furthermore, the fact that the surveys were temporally synoptic means that seasonal shifts in zooplankton distribution are likely to be minimal and this is otherwise a large source of error in oceanic zooplankton sampling.

3.2 Sub-sampling error

Ideally, target taxa should be counted completely to estimate variability in sampled populations (Venrick, 1971). However, sub-sampling is a necessity when samples contain more organisms than is reasonable or affordable to count (Horwood and Driver, 1976). Sub-sampling has two purposes, firstly to obtain an aliquot of the sample which is truly representative and secondly to increase the efficiency of measurement. The sub-sampling device used in this study was the Folsom splitter. Its use was recommended by Van Guelpen et al.(1982) who evaluated the accuracy, precision and speed of several zooplankton sub-sampling techniques.

Generally, it has been assumed that the errors incurred by sub-sampling are small compared to the variation among samples. This has been recently disputed, most notably by Van Guelpen et al. (1982), Griffiths (1984) and Dahiya (1980). Van Guelpen et al.

(1982) recommended that the contribution of sub-sampling error to the total variance should be determined. There are several sources of error in sub-sampling. The main ones the result of, firstly, bias in the sub-sampler causing uneven divisions and, secondly, the effect of interference from the clumping or entangling of animals.

Bias in the particular Folsom splitter used in this study was accounted for by incorporating adjustable legs and a spirit level into the design. The spirit level was calibrated through a series of splits using known volumes of water. Adjustments were made until the volumes of water in each chamber were to within +/- 2ml. The position of the spirit level was marked and further water trials were carried out to verify that there was no bias in the splitter once appropriately adjusted.

It is more difficult to account for the non-homogenous nature of the sample. This is because one of the main assumptions made in a sub-sampling procedure is that the movement of any individual is independent of all others. The entanglement of animals causing clumps means that a particular aliquot is not representative of the sample as a whole. Griffiths (1984) described a method of detecting clumps in split samples which involved the sorting of several split fractions. Although this may improve the accuracy it is also particularly time consuming and therefore not an efficient means of measurement.

3.2.1 Estimation of the degree of sub-sampling error

Van Guelpen et al. (1982) found that variances in accuracy differed between taxa. To a certain degree this can be associated with the morphology of the animal. For instance it was found that chaetognaths had a particularly high variance. These animals, from personal observation, are particularly susceptible to entanglement due to their string like bodies and large hooks which ensnare the bodies of other chaetognaths. It was

therefore important that typical variances for each taxa should be determined.

To gain an estimate of the variances for the major taxa in this study, a representative sample was chosen that had a typical mixture of animals. The sample was divided into 1/8 aliquots through carrying out three levels of division. Seven taxa were then separated and counted in each of 8 aliquots. The variation in the numbers counted in each aliquot was estimated for each taxa through calculating the percentage coefficient of variation (CV) (Van Guelpen et al., 1982).

$$\% \text{ Coefficient of Variation(CV)} = \frac{\text{Standard deviation (S)}}{\text{Mean(X)}} \times 100$$

The mean number of individuals counted and their respective CV values are given below.

Taxa	Mean number counted	% Coefficient of variation (CV)
Chaetognaths	34.1	24.9
Euphausiids	90.9	8.3
Siphonophores	117.1	8.6
Amphipods	8.1	43.4
Salps	17.6	27.8
Decapods	10.0	28.8
Heteropods	0.5	151.2

Table 3.1: Taxon specific coefficients of variation from 1/8 aliquots

Data that Van Guelpen et al. (1982) obtained had CV values ranging between 4.8 to 19.4%. It can be seen from the above table that a number of the taxa exceed this value. It is to be noted however that those taxa that have high CV values also have a low mean count. The two taxa that have suitable mean counts (N~100), the siphonophores and the euphausiids, also have reasonable CV values. In practice, the taxa with the lower

mean counts would have been separated earlier. To show the affect this has on the CV value, aliquots were combined to obtain sub-sample counts for two levels of division - this gives 4 sub-samples instead of 8.

Taxa	Mean number counted	% Coefficient of variation (CV)
Chaetognaths	67.5	10.1
Euphausiids	181.5	4.4
Siphonophores	232.3	7.0
Amphipods	16.3	12.7
Salps	35.3	4.8
Decapods	20.0	10.8
Heteropods	1.0	14.1

Table 3.2: Taxon specific coefficients of variation from 1/4 aliquots

The observed decrease in the CV of most of the taxa could be due to two reasons. One possibility is the reduction of cumulative error through only carrying out 2 divisions instead of 3. The other possibility that increasing the size of the sub-sample decreases the variability. Horwood and Driver (1976) said that the variance after "k" splits with the Folsom splitter is the same as that generated by a device that divides the sample into 2^k sub-samples. Thus it can be assumed that cumulative error is not important.

What this simple experiment shows is that the CV and hence the sub-sampling error is affected by the sub-sample size. Through combining aliquots the CV values of the less abundant taxa were reduced. The CV values for abundant taxa, such as the euphausiids and especially the siphonophores, do not decrease as much in comparison.

Therefore, it may be assumed that counting approximately 100 individuals is sufficient, for beyond this the increase in accuracy is not enough to warrant the extra effort required.

Error resulting from sub-sampling this material is approximately the same between taxa and the fact that the average CV is around 8% illustrates that this source of error is not small. It is therefore important to consider this value of error in sub-sampled taxa when evaluating variability between samples. It can be further deduced from the above table that certain taxa, such as amphipods and heteropods have particularly low abundances. It follows that these organisms will have a high CV value and the accuracy of the abundance estimate will be low. Most taxa encountered in a limited volume of water are represented by only a few individuals but the sum of these uncommon taxa can be a numerically significant part of the community. Furthermore many of them occupy key positions in food webs, for instance, as carnivores which are rarer than their prey (Fager and McGowan, 1963; McGowan and Fraundorf, 1966) and so it is important that their distributions are analysed despite the fact that it must also be acknowledged that evaluation of their abundances are not very accurate.

Chapter 4 Hydrography of the study area

4.1 Introduction

One of the first general accounts of the hydrography of the South Atlantic was given by Deacon (1933). He divided the surface water masses of the region into four zones, Antarctic, Sub-Antarctic, Sub-Tropical and Tropical. The area has since received a considerable amount of study but his basic zonation is still valid with a few minor modifications. There has been a wide range of terminology used in naming the various fronts and water masses in this region and so, to avoid confusion, the nomenclature used by Peterson and Whitworth (1989) will be adopted in this review. The main oceanographic features found in the survey area have been summarised in Rodhouse et al. (1992), including a description of the major currents and the position of water masses for both 1990 and 1991 M/V *Falkland Protector* surveys. As well as conveying this information, the aim of this review is to consider the different physical properties of water masses and other hydrographic phenomena which may affect the distribution of zooplankton. Furthermore, a comparison will be made to satellite images of sea surface temperature (SST) so that the hydrographic features identified within the sampling grid can be considered in terms of larger scale oceanographic processes in the south-west Atlantic.

4.2 Description of currents and water masses

The main oceanographic features are illustrated in fig. 1a. The Brazil and Falkland Current are strongly flowing western boundary currents which are highly stratified and occur in the immediate offshore region of the South American continental

shelf. The Falkland Current is a northward extension of the Antarctic Circumpolar Current and carries Antarctic and Sub-Antarctic Water northwards. Analysis of satellite pictures carried out by Roden (1986) and Legeckis and Gordon (1982) showed that the Falkland Current was approximately 100km wide and followed the 200m isobath until reaching its northern limit around 40°S. The Brazil Current, contrary to the classical picture of a broad southward flow, was found to be a narrow and jet like with predominant wavelike perturbations along its flanks (Roden, 1986). The Brazil Current becomes a prominent feature around 8°S and it flows southwards along the shelf edge carrying Sub-Tropical Water into the confluence zone with the Falkland Current. The confluence is marked by the Sub-Tropical Front (STF), which has a variable position between 35° and 39°S. Following their confluence, both currents move offshore and, with the Brazil Current dominating, continue in a south-easterly direction to at least 40°S. At this point the currents separate and the Brazil Current turns northwards to form a quasi-stationary meander of South Atlantic Central Water.

Current speeds were measured by Gordon and Greengrove (1986) using surface drifters. They found values to be relatively high, the Falkland Current between 35 to 40 cm s^{-1} and its return being between 55 and 65 cm s^{-1}. The Brazil Current was measured at 68 cm s^{-1} with its return being variable with values ranging between 27 and 64 cm s^{-1}. The current speed was strongest in the confluence region, with values as high as 85 and 98 cm s^{-1}.

Associated with the boundary current are two fronts. The Sub-Tropical Front (STF) is found at the confluence zone and marks the boundary between the cold waters of the Falkland Current and the warmer Brazil Current waters. Garzoli and Bianchi (1987) used the 10°C isotherm to locate the Sub-Tropical Front, whereas Roden (1986)

and Ikeda et al. (1989) used this same isotherm at 300m as the identifier. Roden (1986) also traced the STF using the 34.8 isohaline. He stated that although temperature, density and salinity fields need not be present simultaneously, strong thermohaline fronts accompany both the STF and the Sub-Antarctic Front (SAF). The SAF is associated with the Falkland Current and is the northern limit of the cold Antarctic Water. Ikeda et al. (1989) used the 3-5°C surface isotherm as the principle identifier of the SAF. Peterson and Whitworth (1989) found that the SAF corresponded closely to the 4°C isotherm at 400m.

Both these fronts are significant features within the survey grid and they delimit a number of prominent water masses. The STF marks the southern limit of the Sub-Tropical Zone (STZ) and the northern Sub-Antarctic Zone (SAZ), whilst the SAF marks the southern limit of the SAZ and the northern limit of the Polar Frontal Zone (PFZ). Variation in the physical properties of these water masses is quite considerable and so their physical characteristics will be reviewed in the following section.

4.2.1 Physical properties of water masses

Sub-Tropical Zone (STZ)

Deacon (1933) stated that surface temperatures in the southern part of the STZ varied from about 11.5°C in Winter to 14.5°C in Summer, although the temperature may have been as much as 5°C higher when there was strong southward movement. The salinity of the STZ was estimated to be at least 34.9‰ and possibly as much as 35.5‰. The oxygen content was high, around 95% saturation and the nitrate and phosphate content at the surface relatively low. In another review, Semenov and Berman (1977) also noted the influence of warm fresh water from the La Plata river on the coastal water of the STZ.

Sub-Antarctic Zone (SAZ)

The surface temperatures of the SAZ vary considerably within their geographic range, with temperature and salinity generally decreasing from north to south. Deacon (1933) stated that, near to the STF (or Sub-Tropical Convergence as it was referred to), the temperature ranged between 11.5°C in Winter and 14.5°C in Summer with the salinity being approximately 34.4‰. Near to its southern limit at the SAF, the temperature can be as low as 3°C in Winter and 6°C in Summer, with the respective salinities 33.95‰ and 34.10‰ .

SAZ waters are therefore generally colder and fresher than STZ waters and as Roden (1986) indicated, the transition between the two is rather abrupt. Indeed Deacon (1933) stated that in crossing the STF there was a sudden change in surface temperature of at least 4°C and a change in salinity of 0.5‰. There were also marked differences in the nutrient content, with phosphate increasing from 10mg m^{-3} in the STZ to 60mg m^{-3} in the SAZ and similarly nitrate increased from 50 to 150mg/m^{-3}. There is little stratification and a great deal of mixing in sub-Antarctic waters because of the large influence of the West Wind Drift (Semenov and Berman, 1977) and this may play a part in producing the high nutrient values observed.

Polar Frontal Zone (PFZ)

The PFZ, to the south of the SAF, was first described by Gordon et al. (1977) who, on investigating the Polar Front, found that there was a complex region of mixing that was 2 to 4° latitude in width. The term Polar Front was modified to Polar Frontal Zone, with the SAF bounding it to the north and the Polar Front limiting it to the south.

Peterson and Whitworth (1989) estimated the change in temperature from SAZ to

PFZ waters to be around 3°C. This was combined with a drop in salinity and an increase in oxygen at the surface. Although the zone was not characterised in Deacon's monograph, he described waters around the region as between 3.5°C in the Winter and 5.5°C in the Summer. Oxygen values near the zonal front were 89.2% saturated and salinity values in the Falkland sector of the PFZ were between 33.87 and 34.15‰ (Deacon, 1933).

The physical characteristics of the PFZ were attributed by Peterson and Whitworth (1989) to the rise of Antarctic Intermediate Water (AAIW) in this region. AAIW is a sub-surface water mass that is present in all three of the southern hemisphere oceans and is characterised by a layer of low salinity below the thermocline. AAIW is traditionally believed to be formed from Antarctic surface and sub-surface water sinking below Sub-Antarctic surface water. However, more recent theories propose alternative sources of AAIW from small scale mixing across the Polar Front, divergence of geostrophic transport in the south-east Pacific and deep winter mixing in the Sub-Antarctic Zone of the south-east Pacific (Piola and Gordon, 1989).

4.2.2 Hydrographic variability

One aspect of the hydrography of this region that is of particular interest to this study is the variability seen in the position of currents and their associated fronts. This has been highlighted through the analyis of satellite sea surface temperature (SST) patterns by Legeckis and Gordon (1982) and Olson et al. (1988). The region is particularly suited to satellite SST analysis because there are strong surface thermal gradients between the warm waters associated with the Brazil Current and the cold waters associated with the Falkland Current which allows the position of these features

to be resolved through analysing variation in surface temperature. In February, for instance, the eastern and western boundaries of the cold surface water associated with the Falkland Current were located by the cross stream SST gradient of 1°C per 2km. Even more significant temperature changes were observed at the northern boundary of the cold surface water where the SST gradient was 5°C per 2km. However, thermal gradients in the surface waters are not significant identifiers of all features and certain surface water boundaries are not easily identifiable. An example is the eastern boundary of the warm surface water associated with the Brazil Current where warm surface waters are also found to the immediate east, making the resolution of the SST boundary difficult. Seasonal effects may also affect the resolution of SST boundaries in the surface waters. Legeckis and Gordon (1982), for instance, found that the SST boundaries of the cold surface waters associated with the Falkland Current were not always recognisable between May and October because convective overturning and wind mixing made mixed layer temperatures less distinct between regions. However, Olson et al. (1988) reported that temperature differences between the surface waters associated with the two currents remained fairly constant throughout the year.

Both the Falkland and Brazil Currents follow along the line of the 200m isobath but they separate from the shelf as they approach the confluence and move in an offshelf direction. Olson et al. (1988) used SST images to determine the point that the warm surface waters associated with the Brazil Current and the cold surface waters associated with the Falkland Current separated from the shelf. They found that the point of separation fromm the shelf varied with time and although the mean separation points of the Brazil and Falkland Currents were 35.8° and 38.8°S respectively, the total range of the former was 4.4° and of the latter was 4.8°. There was a certain degree of

consistency in the manner of variation with the separation points of both currents being further north in the Winter than in Summer. Such variations in points of separation are relatively large compared to other systems such as the Gulf Stream and Kuroshio region.

The two currents and their associated fronts lie fairly close together as they move offshore but then separate as they travel to the north-east. Olson et al. (1988) found there to be considerable variation in the modal positions of the offshore extensions of the SST boundaries through time. The SST boundary associated with the Brazil Current was found to be the most variable and it occupied its average position only 45 to 60% of the time. The SST boundary associated with the Falkland Current occupied its average position 60 to 75% of the time. The SST boundaries frequently made significant north-south excursions and, in many cases, were found to reverse on themselves.

Variability was also observed in the western SST boundary of surface waters associated with the Brazil Current, which were the result of time-dependent cross stream fluctuations (Legeckis and Gordon, 1982). Such fluctuations occur over a time scale of about a week and cause along stream displacements of up to 200km. A further source of variability are zonal oriented meanders which are extensions of the eastern SST thermal boundary associated with the equatorward return flow of the Brazil Current. Typical meanders have a zonal wavelength of 200 to 400km and longitudical amplitudes of 100 to 300km. Such meanders were most frequently observed by Legeckis and Gordon (1982) around 40°S and 50°W and they were also observed by Reid et al. (1977). However, they are not always easy to identify because of the warm waters found to the east of the eastern SST boundary, as explained above.

The meridional displacements of the warm water are accompanied by the intermittent formation of eddies, which fill the transitional area between the two thermal

boundaries (Olson et al., 1988). The eddies are usually south of the southern limit of the warm surface water but occasionally they are also found to the west and east. Between the period September 1975 and April 1976, Legeckis and Gordon (1982) recorded the formation of 20 different eddies south of 38°S and east of the cold surface water associated with the Falkland Current. They considered that warm core eddies were formed in three different ways:

1, The pinching off of wave-like meanders observed along the western SST boundary associated with the Brazil Current, similar to the method described by Saunders (1971) for the Gulf Stream.

2, The pinching off of the southern SST boundary associated with the Brazil Current resulting from the sheer instabilities in the area of current reversal.

3, The result of instability in a series of wave like meanders that appear along the western SST boundary associated with the Brazil Current.

The eddies are usually eliptical with a mean major axis of 180km and a mean minor axis of 120km although the major and minor dimensions may vary by a factor of 2. After formation, they move southwards at a rate between 4 to 35km d^{-1} and there some evidence suggests that the southward displacement slows down with time. Despite the fact that the eddies move southwards, most do not seem to be reabsorbed by the current as is the case in the North Atlantic where the warm core eddies re-enter the Gulf Stream. Gordon (1981) observed a series of thick and relatively warm, saline intrusions in the mid thermocline depths (300 to 600m) along 38°S. He interpreted these features as being derived from Winter cooled warm eddies. It is possible that after being cooled, the eddies lose their surface signature and eventually sink and spread northwards to re-enter the South Atlantic Sub-Tropical Gyre. The separation from the main body of the

Sub-Tropical Gyre is long enough to force the reabsorption to occur below the surface water layer.

Although cold core eddies are also formed in this region they are considerably rarer than warm core eddies and have subsequently received far less study. Cold core eddies may be formed as a result of changes in zonally oriented meander patterns, often observed near 40°S, 50°W, since they are mostly found north of such meanders. Legeckis and Gordon (1982) noted that a cold core eddy may have resulted from a meander pattern they observed in December 1975 which was in the process of enclosing relatively colder water at 39°S, 50°W. However, there have been no recorded observations of the full evolution and eventual fate of cold core eddies in this region.

To summarise, the region is hydrographically complex. It contains two significantly strong western boundary currents and their highly energetic confluence. Between the two currents there are a multitude of thermal phenomena in various stages of development and decay such as meandering fronts and warm and cold core eddies. Furthermore there is variation in both the position and the physical attributes of the water masses and their associated fronts.

4.3 Position of fronts and water masses during 1990 and 1991 surveys derived from XBT profiles

During the 1990 and 1991 surveys, vertical temperature profiles (XBT's) were obtained for the upper 750m in order to locate the major fronts and associated water masses. Although frontal positions are generally determined through using both

temperature and salinity, the use of temperature alone was sufficient in this instance because the water masses in this region have such strong thermal signals. The approach of Rodhouse et al. (1992) was adopted by this study in which the fronts and water masses were identified using the criteria outlined by Peterson and Whitworth (1989). These were:

STF: the 8°C isotherm >500m deep

SAZ: the 4°C isotherm >500m deep

SAF: the northern extent of the 4°C isotherm at 200m

PFZ: the 4°C isotherm <200m deep and deepening rapidly towards the SAF

PF: the northern extent of the 2°C isotherm near 200m

AAZ: a temperature minimum of <2°C which is <200m deep

The analysis of the XBT profiles was originally carried out by Dr. C. Symon, formerly of the British Antarctic Survey. The locations of the water masses and fronts in the 1990 and 1991 surveys are given in figs 4.3a and 4.3b, along with the bucket surface temperature readings taken at the time of net sampling and the approximate positions of currents.

4.3.1 Description of 1990 frontal positions and bucket surface temperatures

The 1990 survey grid encompassed both the STF and SAF and their associated zonal waters, the STZ, SAZ and PFZ. The STZ was located between 37°S and 38°S and bounded 4 STZ sampling stations to the north. The SAF appeared as a tongue like protrusion within the sampling grid and enclosed 7 PFZ stations which extended from 44°S to 48°S. The remaining 16 offshelf stations above 48°S were located within the SAZ. Most of the SAZ stations were found either to the north or to the west of the PFZ

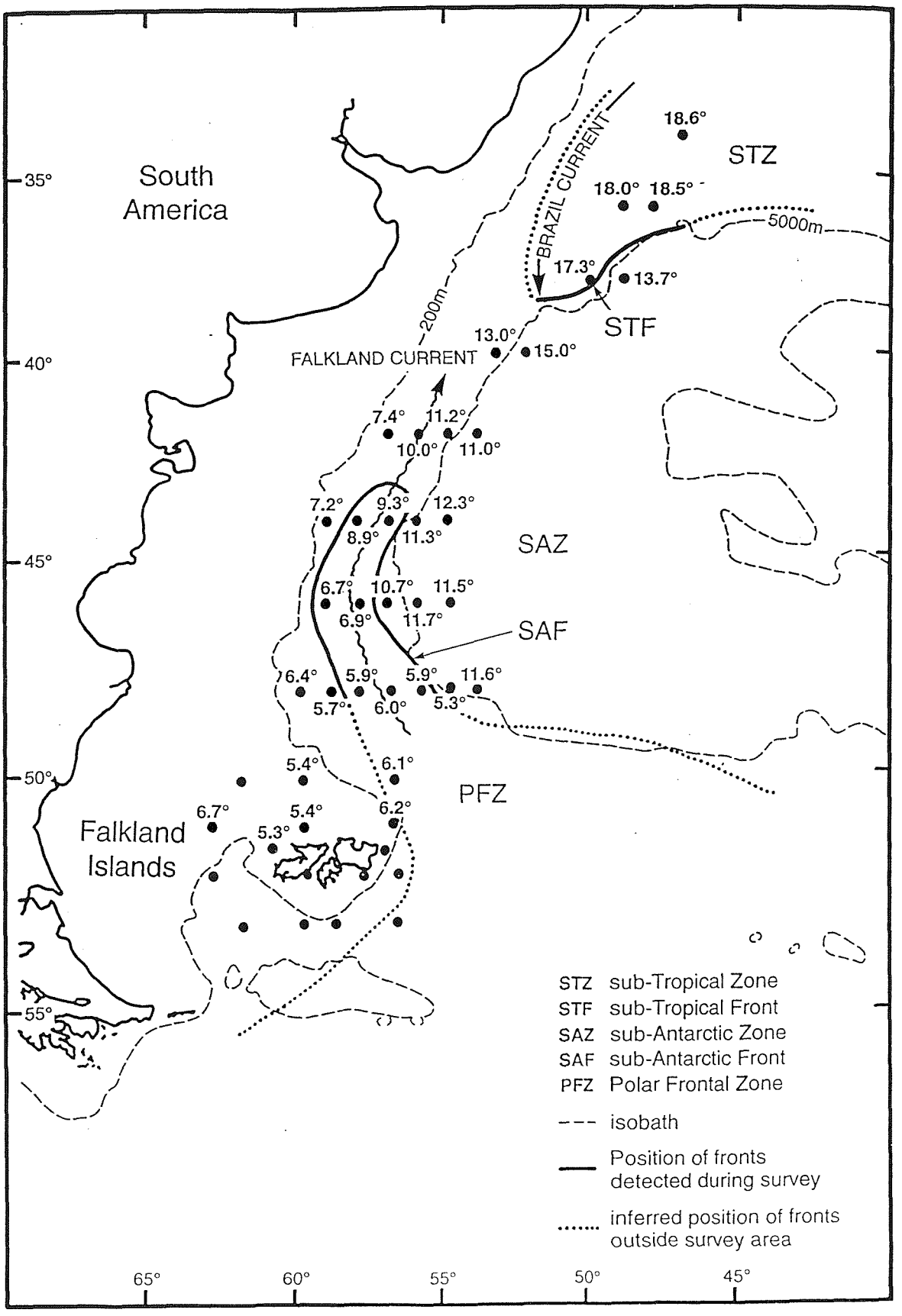


Figure 4.3a Bucket surface temperatures and frontal positions during 1990 Survey

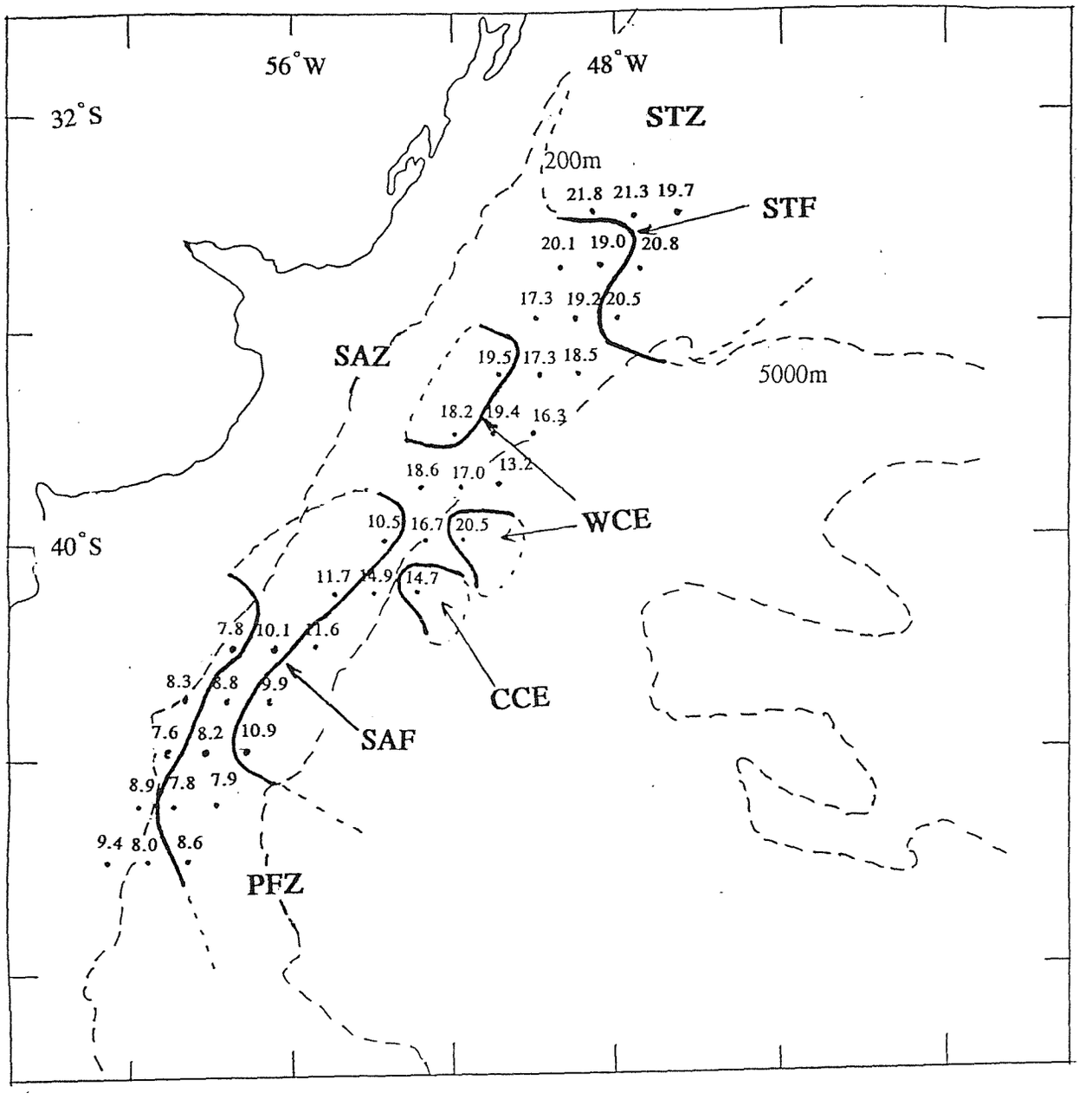


Figure 4.3b Bucket surface temperatures and frontal positions during 1991 Survey

protrusion. However, 3 SAZ stations were bound between the PFZ to the east and the 200m isobath to the west. All stations below 48°S were generally on-shelf tows and were therefore not comprehensively sampled with XBT's because neritic regions were not deep enough to relate to the temperature depth identifiers used to distinguish oceanic water masses. From the few XBT profiles that were taken it was apparent that the neritic waters in this region were generally well mixed during the sampling period and showed little temperature stratification.

In relation to the bucket surface temperature values, it was apparent that there was a striking difference between those stations lying to the north and south of the STF. Sub-tropical stations had characteristic temperatures of around 17-18°C whereas sub-Antarctic stations generally had temperatures between 11°C and 12°C, although northerly stations close to the STF had higher values between 13°C and 15°C. Southern SAZ stations lying to the west of the SAF appeared to have colder surface temperatures (5°C to 7.5°C) than those on the eastern side (10.7°C to 12°C). It is possible that stations on the western side were more affected by interaction with the northward flow of the Falkland Current and temperature was lowered through mixing with PFZ water across the SAZ. Temperature on the eastern side may have been warmed by the Falkland Current return which carries water that has been come into contact with the Brazil Current. Warm core eddies travelling south in this region may also increase the temperature of eastern station relative to those further west. The surface temperatures on the Falkland Shelf are generally the same as oceanic surface temperatures in the PFZ and SAZ further north.

4.3.2 Description of 1991 frontal positions and bucket surface temperatures

The 1991 sampling grid also encompassed the STF, SAF and their associated zonal waters, the STZ, SAZ and PFZ, as was found during the 1990 survey. However, unlike the 1990 survey, two warm core eddies and one cold core eddy were also present within the 1991 sampling grid.

The STF was bounded by 5 STZ stations to the north and was located between 34°S and 36°S, much further north than during the 1990 survey. This may be a result of the pinching off of the southern boundary of the warm waters associated with the Brazil Current, creating warm-core eddies and leaving a more northerly STF frontal position. The northernmost warm core eddy encompassed 2 sampling stations at 37°S, 51°W and 38°S, 52°W. The other warm core eddy, at 41°S, 55°W was quite significantly displaced from the STF and indeed was at the same latitude as the most northerly reaches of the SAF. The SAF appeared as a tongue like protrusion, as in 1990, enclosing 8 PFZ stations between 41°S and 46°S but, like the STF, was further north than in 1990. There was also a cold core eddy at 42°S, 56°30'S which contained a further station with the PFZ sub-surface thermal signature. The remaining stations were located within the SAZ which covered almost the entire latitudinal range of the sampling grid and bounded the PFZ protrusion and the warm and cold core eddies.

Unlike the 1990 sampling grid, there was no marked difference between surface bucket temperatures either side of the STF. This may be a reflection of greater warm core eddy activity during the 1991 survey carrying warm waters further south and raising SAZ surface temperatures through diffusive effects. However, when making temperature comparisons between surveys, the fact that the 1991 survey was carried out 3 weeks later than the 1990 survey and had a greater latitudinal resolution, must be taken into account since both these factors may act to raise the surface temperatures observed. Nevertheless,

there was a sharp contrast seen in surface temperatures with respect to the more southerly warm core eddy. The one station enclosed within the eddy had a temperature of 20.5°C, which is comparable to the highest STZ temperatures seen during the survey, whereas the stations surrounding the eddy had temperatures ranging between 17.0°C and 13.2°C, giving an average cross eddy difference of approximately 5°C. This difference is quite considerable and illustrates that the surface temperatures of a warm-core eddy can persist to quite southerly regions in this area.

A considerable temperature difference was also observed between the most northerly PFZ stations and the adjacent SAZ stations where the characteristic PFZ temperatures were 10.1°C to 11.7°C and the adjacent SAZ waters were 14.9°C to 18.6°C. However, more southerly SAZ stations found to the immediate west and east of the SAF had temperatures that were only slightly higher than those of the PFZ stations. Unlike, 1990, there was little temperature difference between SAZ stations lying to the west and SAZ stations to the east of the PFZ protrusion but this again could be possibly be a result of the 1991 survey being carried out relatively closer to the Summer.

4.4 Comparison of SST satellite images, bucket surface temperatures and the position of water masses

Determining the position of hydrographic features simply within the sampling grid gives only a limited picture of oceanographic process in the region and their potential influence on the south-west Atlantic ecosystem. In terms of features such as the STZ, gaining a view over a limited area makes it difficult to ascertain whether fronts or mesoscale eddies have been identified since the geographic range of the grid is not large

enough to adequately distinguish between them. The advent of satellite imaging allows instantaneous pictures to be taken of entire regions such as the south-west Atlantic and allows *in situ* observations be placed into a larger scale context. Improvements over the past decade in the signal to noise ratio and of the spatial resolution of infa-red scanners has allowed oceanographers to recognise SST patterns associated with major currents and fronts, and several studies have been carried out on the south-west Atlantic region (Legeckis and Gordon, 1982; Olson et al. 1988; Podesta et al. 1991). The confluence is particularly suited to study by remote sensing because satellite based sensors provide the synoptic monitoring capabilities required to adequately describe the complex mesoscale variability of the region. The processes of interest also have strong thermal signals at the ocean surface. Therefore, in order to gain a synoptic view of the oceanographic dynamics during 1990 and 1991 survey periods, satellite images were obtained through collaboration with D. B. Olson and G. P. Podesta at the University of Miami.

The satellite data was collected by the Estacion HRPT of the Servicio Meteorologico Nacional of Argentina as part of a cooperative agreement with the University of Miami. High resolution HPRT data, with a spatial resolution of approximately 1 km, was collected for the periods 21/10/94 to 15/11/90 and 1/11/91 to 20/11/91, covering the sampling periods of both the 1990 and 1991 M/V *Falkland Protector* cruises. The processing of the HPRT satellite data was carried out as described in Olson et al. (1988). Certain algorithms were initially applied to the data to accomodate the effects of water vapour and aerosol absorption on the accuracy of measurements. The SST imagery was then mapped on to a fixed geographic grid using a cylindrical equi-rectangular projection covering the area from approximately 30° to 50°S and 63° to 36°W. Each image was subsequently cloud filtered to overcome the

problem of cloudiness and then composited into a 5 day mosaic using a warmest pixel approach. The images are presented in figs. 4.4a to 4.4i, with the position of the M/V *Falkland Protector* sampling stations and location of the STF and SAF superimposed. Bucket surface temperatures were also included on images that corresponded with station sampling dates.

4.4.1 Mesoscale SST patterns in 1990 and 1991 surveys

Mesoscale SST patterns in 1990

In 1990 the survey region was dominated by the movement of a zonal oriented meander of warm surface water associated with the Brazil Current at approximately 40°S, 50°W. During the dates covered by figs. 4.4a and 4.4b, this meander appeared to separate from the front to form a mesoscale eddy. This type of eddy formation corresponds to the second type described by Legeckis and Gordon (1982) where the southern SST boundary is pinched as a result of shear instabilities in the area of current reversal. It is apparent in figs. 4.4c and 4.4d however, that this eddy does not progress southwards, as would be expected, but reconnects with the surface thermal boundary to reform a zonal oriented meander. In fig 4.4e, this meander again appeared to be in the process of pinching off. To the east of the meander there was a region of slightly colder water. This is probably SAZ water which has been warmed through interaction with the warm water front and its frequent eddy formation. The high temperatures found in this region east of the meander were also noted in previous SST observations of the region made by Legeckis and Gordon (1982).

None of the 1990 satellite SST images pick out the SAZ/PFZ transition as clearly as the SAZ/STZ transition. In the previous section, it was noted that the gradient in

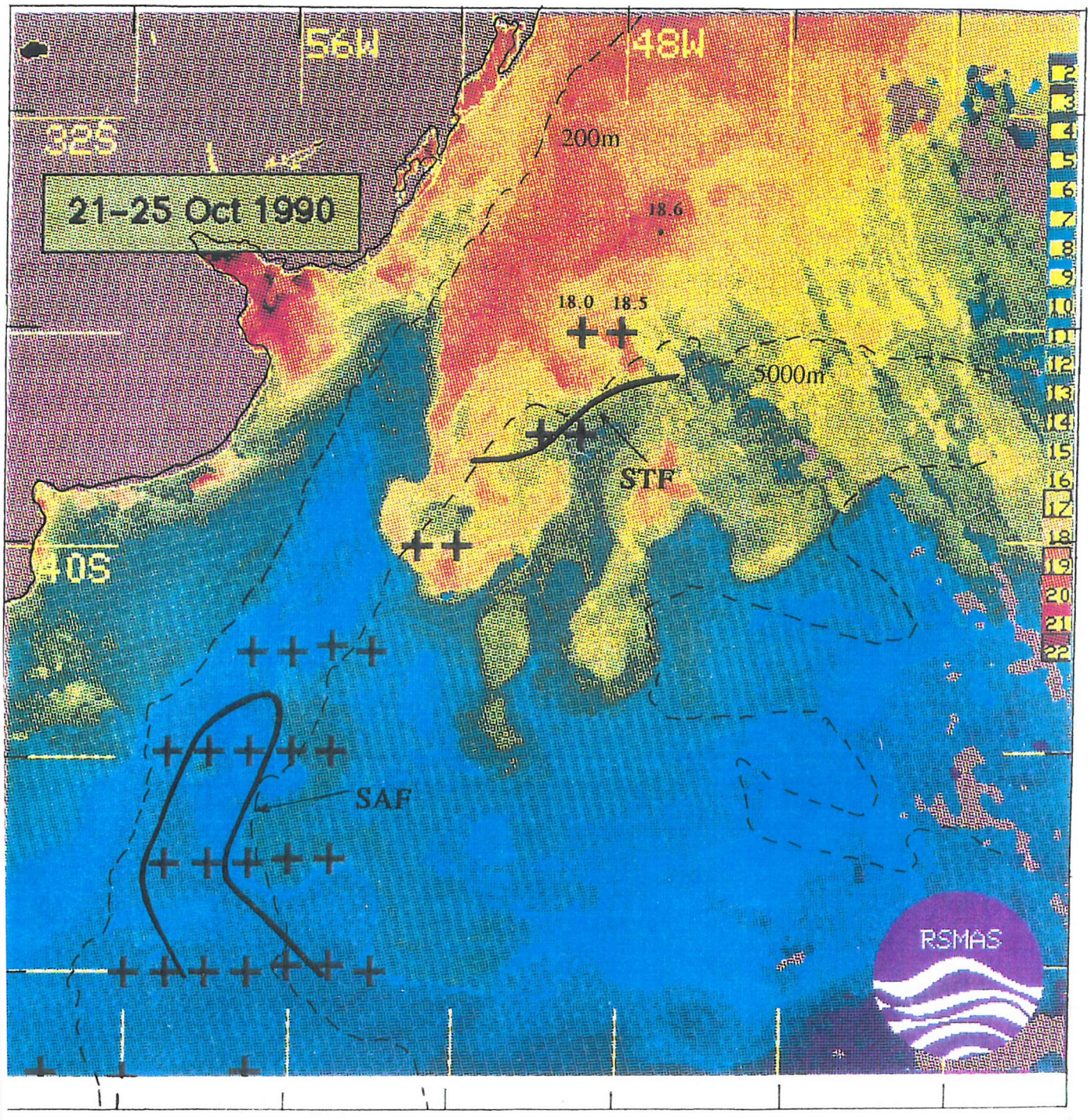

56W
48W
32S
200m
21-25 Oct 1990
18.6
18.0 18.5
5000m
STF
40S
SAF
RSMAS

Figure 4.4a

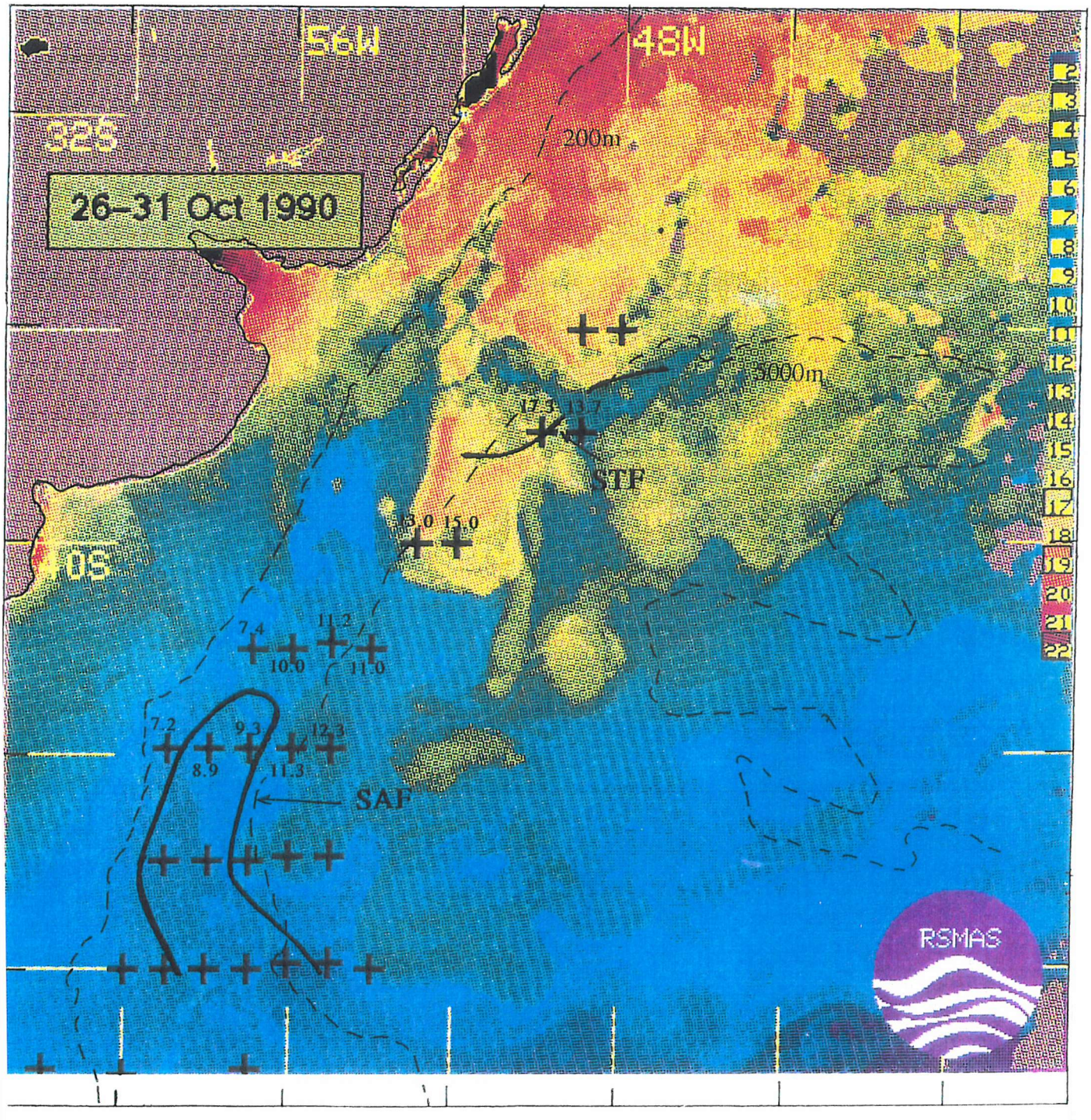

56W
48W
32S
26-31 Oct 1990
200m
3000m
STF
SAF
13.0
15.0
7.4
10.0
11.2
11.0
7.2
8.9
9.3
11.3
12.3
RSMAS

Figure 4.4b

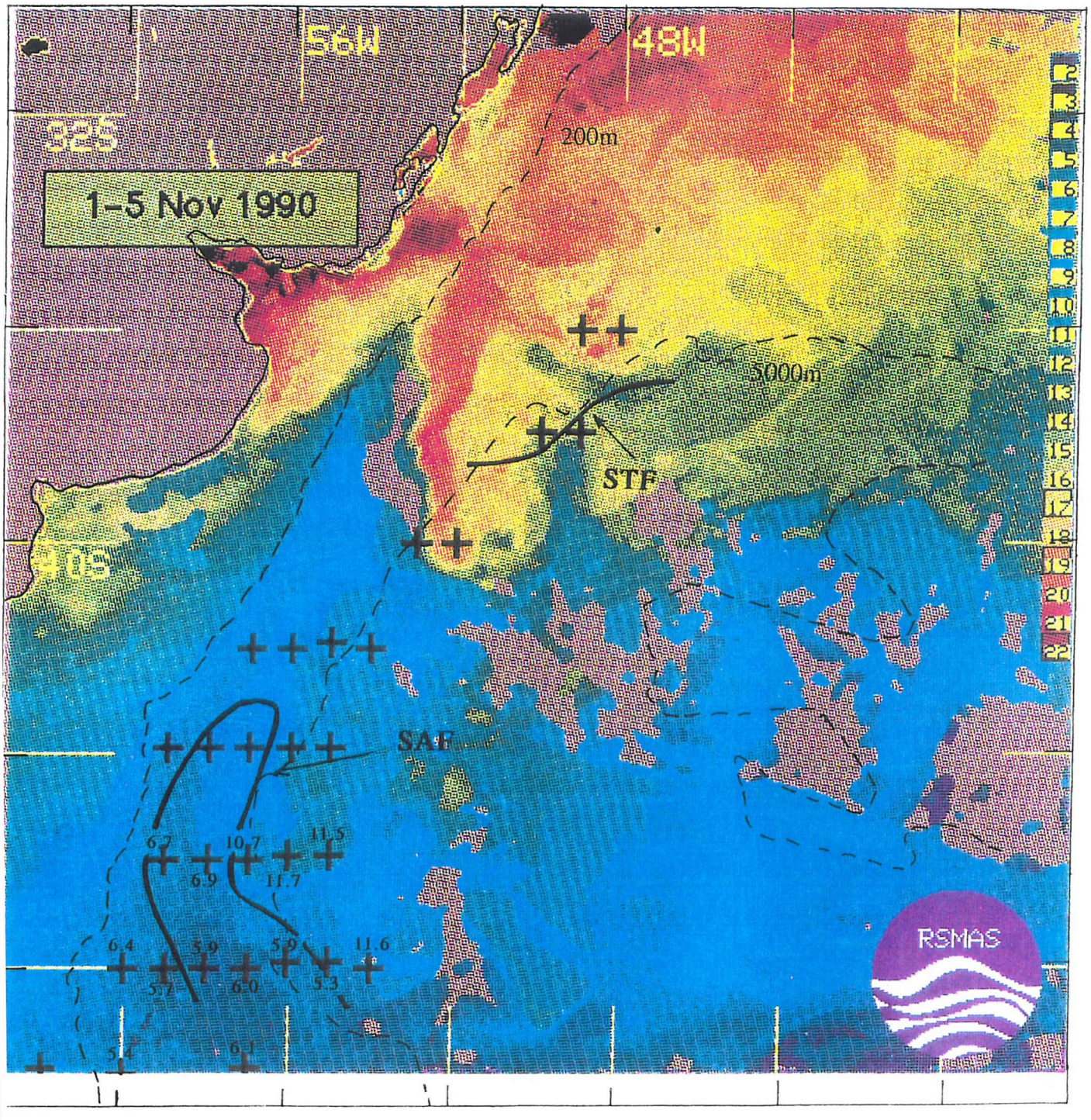


Figure 4.4c

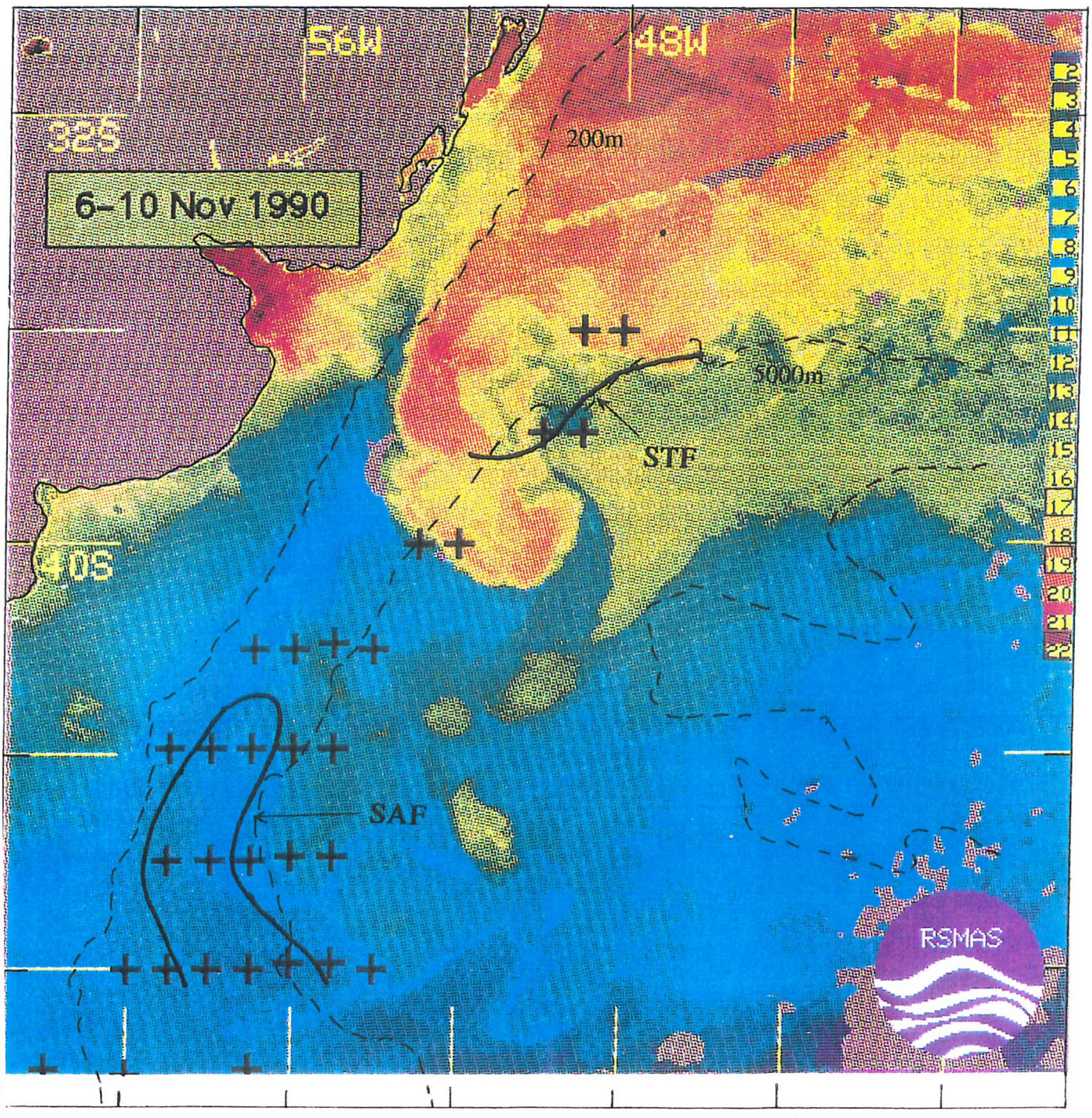


Figure 4.4d

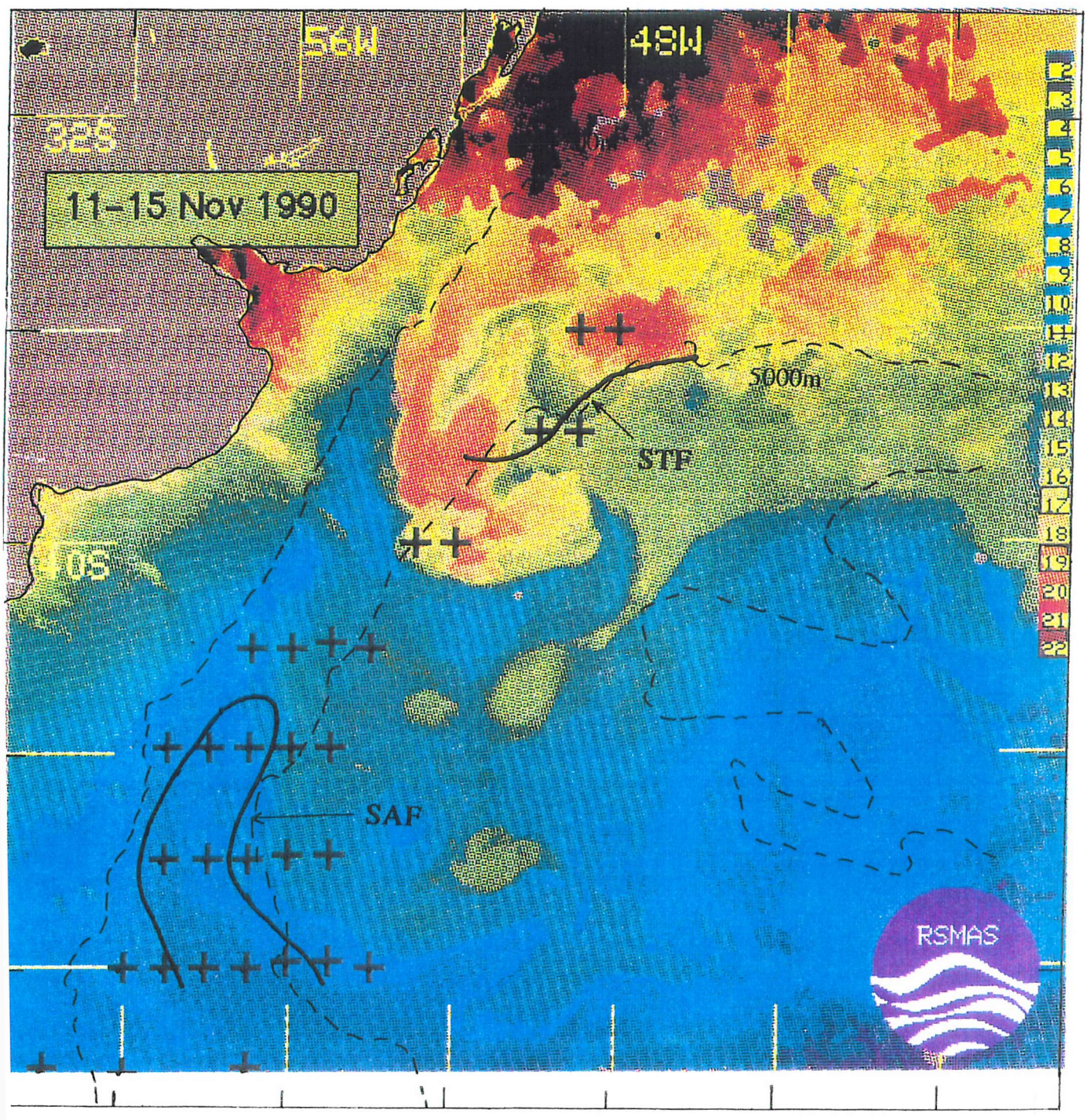


Figure 4.4e

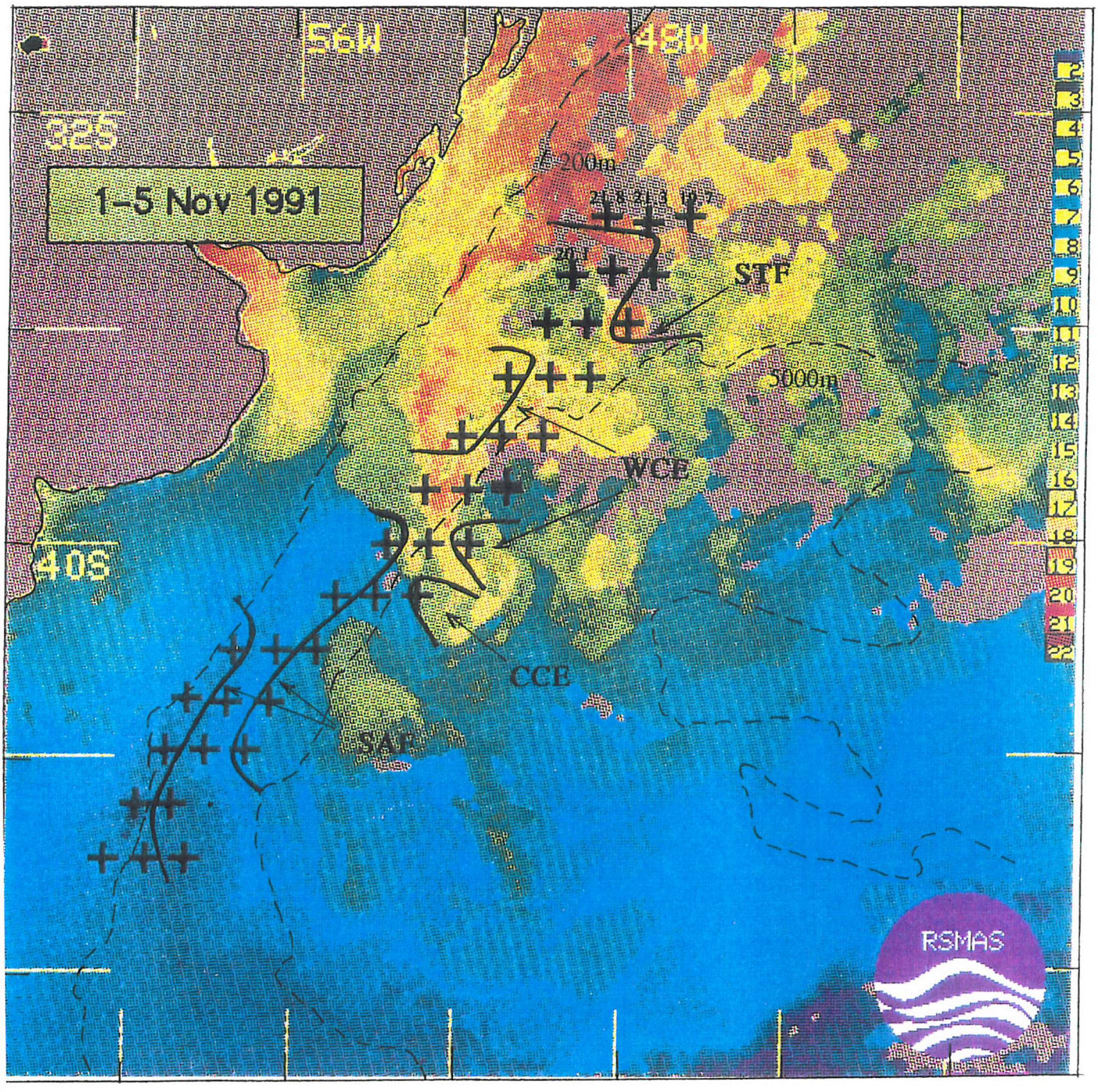


Figure 4.4f

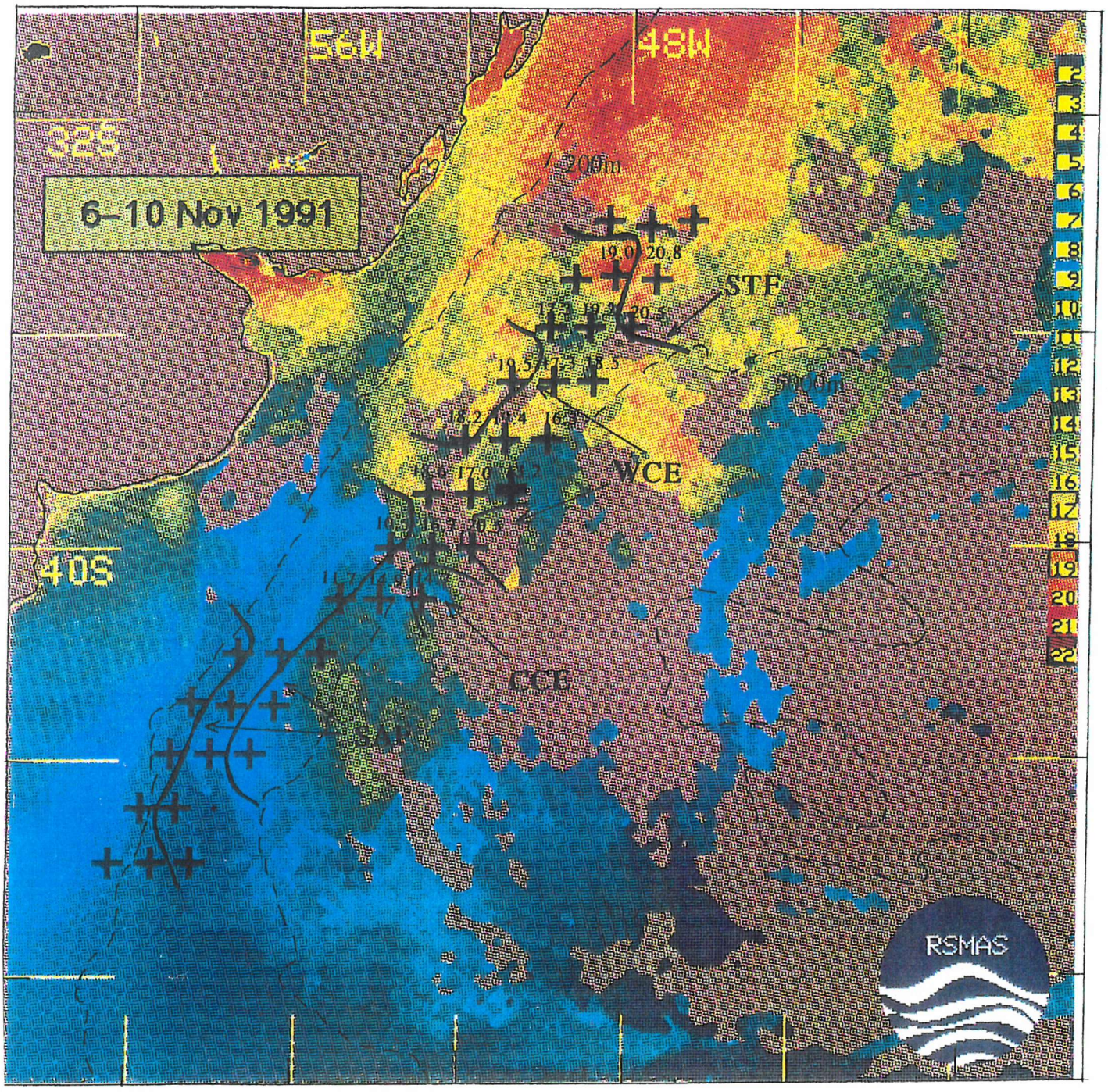


Figure 4.4g

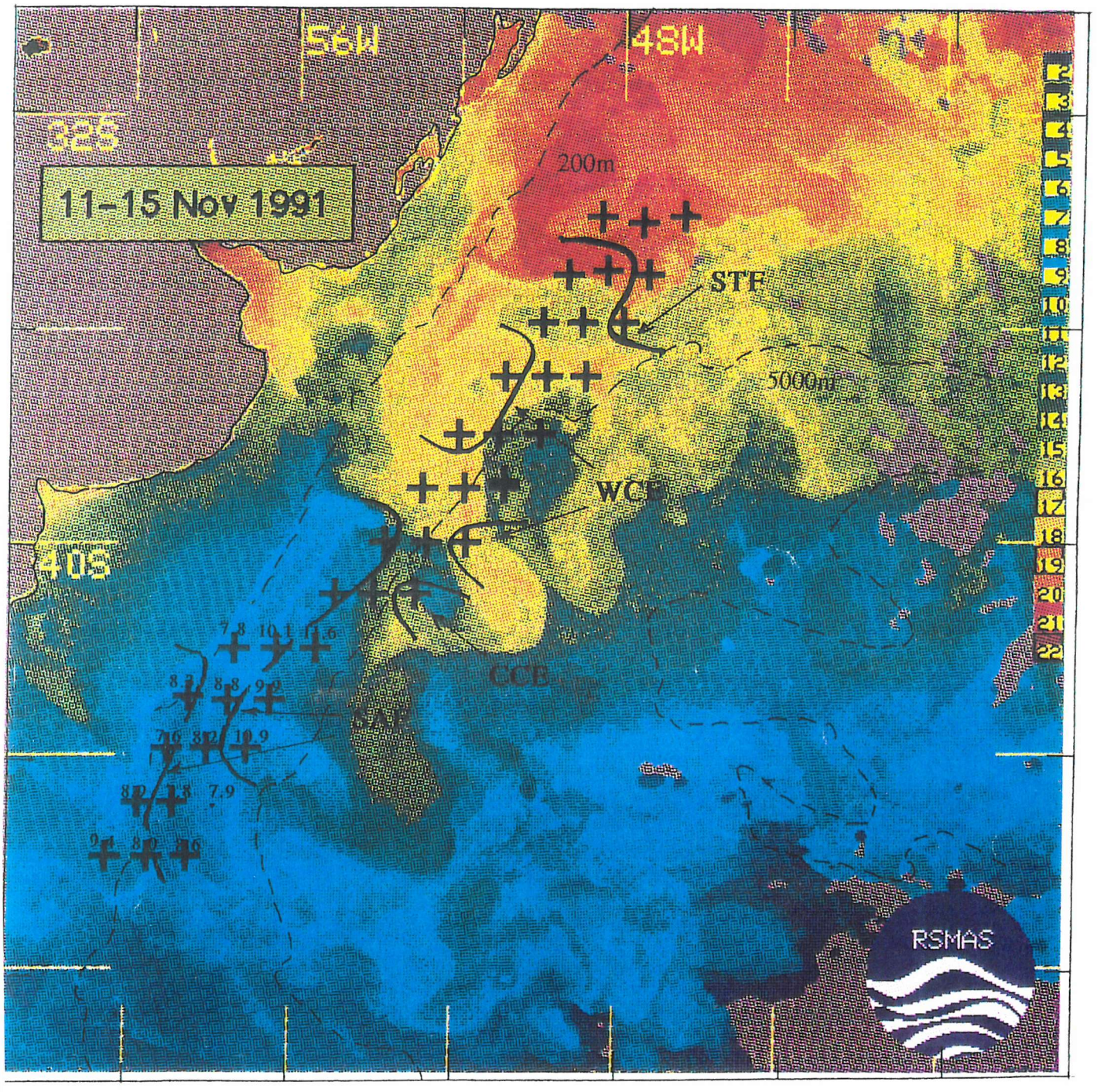


Figure 4.4h

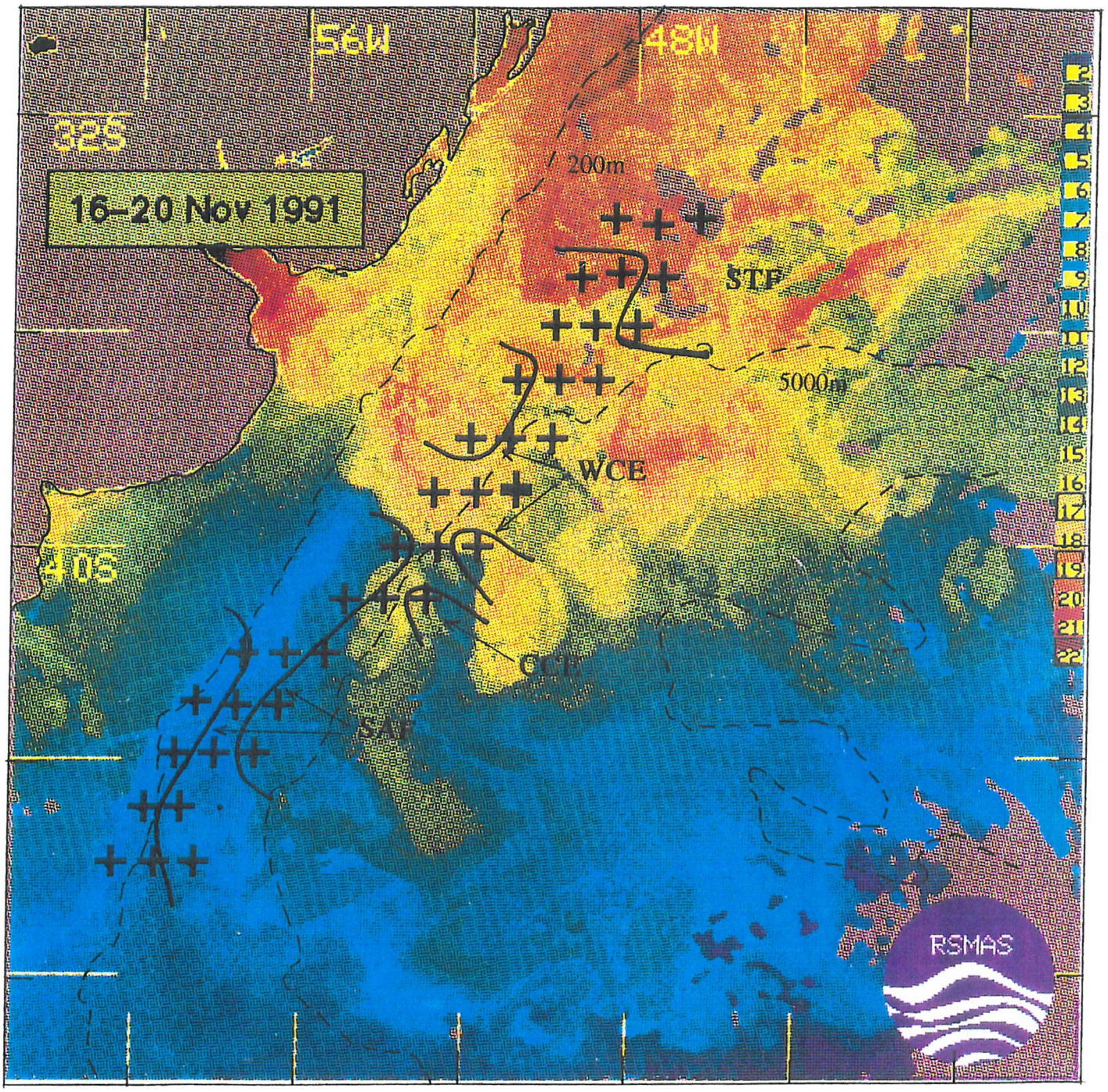


Figure 4.4i

The narrow extended zonal oriented meander cuts across the sampling grid between 38° and 40°S, and stations to the north-east of the meander can be seen to be within a region of blue surface water which appeared to be almost enclosed to the south in fig. 4.4h because of the near vicinity of the zonal oriented meander to warm waters extending from further east. This process of enclosure was also noted by Legeckis and Gordon (1982) and it was suggested to be the method by which cold core eddies were formed in this region. However, in the next satellite image in the temporal sequence, fig. 4.4i, this region of cold water loses its surface signature probably because of interaction with warmer waters and so it was not possible to determine whether a cold core eddy was formed.

As in 1990, it was hard to distinguish PFZ from SAZ waters because the gradient in surface temperatures was not sufficiently marked. The protrusion of very cold, dark blue surface water appeared to be much further north in 1991 compared to 1990, reaching almost 40°S in fig. 4.4g. The northern extension of light blue surface waters appeared to be similar to 1990 and again PFZ surface waters appeared to directly interact with the warm surface water thermal boundary along the shelf edge.

Relationship between SST temperatures and sampling station bucket surface temperatures

The relationship between the bucket surface temperatures and the satellite SST appears to be generally good, with the absolute temperatures of the SST images measured to the nearest °C appearing to be quite close to corresponding bucket surface temperatures values. The match is especially clear when considering dramatic changes in temperature over short distances. In the two stations sampled at 38°S in 1990, there was a marked difference in the bucket surface temperatures with the western station having a

temperature of 17.3°C and the eastern station of 13.7°C. In fig. 4.4b, which covers the sampling dates of these two stations, it is evident that the warmer station is found within a warm core eddy and the colder station within a small region of cold, blue surface water to the east of the eddy. Using the temperature scale of the satellite image, the eastern station was situated in 13°C water and the western station in 17°C water, which agrees well with the bucket surface temperatures values given above.

There are one or two anomalies where the absolute bucket surface temperatures do not correspond to the surface temperatures on the satellite images. This is especially seen in the eastern stations below 40°S (fig. 4.4c) where the bucket surface temperatures are considerably higher (11.6°C to 12.3°C) than estimated from the satellite images (10°C to 12°C). Such absolute differences of between 1° and 2°C are to be expected given the problems in calibrating for atmospheric effects in satellite readings, a factor also implicated by Legeckis and Gordon (1982) when considering similar degrees of variance in their comparison of satellite and bucket surface temperatures. Furthermore, bucket surface temperature readings may be affected by small scale temperature variance which cannot be resolved by satellite images which mainly consider temperature at the mesoscale level. Nevertheless, even in cases where there are discrepancies in absolute temperatures, satellite SST and bucket temperature patterns still broadly agree, as in the above example, where both means of measurement show that warmer surface temperatures are found in eastern stations below 40°S.

One further problem in relating bucket surface temperature readings to satellite images is cloud interference which prevents certain regions of satellite images from being resolved. This was especially a problem in 1991, where a large part of the images in fig. 4.4f and 4.4g were unresolved. A general picture of mesoscale temperature

differences can nevertheless be discerned from such images and in both the above images, the general patterns in satellite SST distributions approximated distribution patterns in bucket surface temperature.

Relationship between satellite mesoscale temperature patterns and the position of fronts within the 1990 and 1991 survey grids

The resolution of oceanographic features such as fronts through satellite measurements of sea surface temperature and through examinination of the sub-surface temperature structure was examined by Legeckis and Gordon (1982). They compared the results of 2 *in situ* hydrographic surveys to corresponding satellite images and found that satellite SST fronts directy related to the deep reaching sub-surface temperature structure. The mixed layer depth was further found to agree with the surface temperature patterns of the Brazil Current and 2 warm core eddies.

Such findings are in contrast to the present study where correspondence was found to be very approximate, especially with respect to the agreement between warm surface water thermal boundaries and the STF. In figs. 4.4a and 4.4b, when the STF stations were sampled in 1990, it can be seen that the position of the STF is considerably further north than the warm surface water boundary, found at approximately 40°S. Resolving the surface temperature boudary between PFZ and SAZ stations is more difficult because of the similar surface temperatures in the areas where the zones are adjacent. However, in fig. 4.4c, when the PFZ and SAZ stations were sampled, it is apparent that the protrusion of dark blue water representing the core of cold surface temperatures does not correspond to the position of the PFZ stations as would be expected.

It is more difficult to analyse the correspondence between the warm surface water boundary and the position of the STF in 1991 because of cloud interference during the time the northernmost stations were sampled. This problem does not even allow the position of features such as the cold core and warm core eddies determined from XBT analysis to be compared to satellite images. One feature that was discernable in the satellite images however was the PFZ/SAZ transition. Furthermore, in fig. 4.4g, it can be seen that there was a marked temperature change along the western stations at 40°S which corresponds to the northernmost position of the SAF determined from XBT analysis. As in 1990 however, the protrusion of dark blue water marking the coldest surface water does not correspond to the distribution of PFZ stations.

Overall, it was evident that the satellite measurements of surface temperature corresponded well with the bucket surface temperatures taken during the time stations were sampled. The synoptic view gained from the satellite images allows many of the anomalies in bucket surface temperature values to be explained in terms of the mesoscale oceanographic features apparent during the time of sampling. Contrary to previous findings however, (eg. Legeckis and Gordon, 1982) correspondence between surface temperature boundaries and the positions of fronts and eddies determined through XBT analysis were very approximate showing that the correspondence between surface and sub-surface thermal phenomena was not entirely direct.

Chapter 5 Biogeography of the study area

5.1 Theoretical overview

The science of pelagic biogeography concerns the study of large scale patterns in geographical distributions of pelagic organisms in the World's oceans, the factors which lead to the formation of these patterns in the geological past and the ecological interactions which are now maintaining them (Krause and Angel, 1994). The field has received comparatively little study compared with terrestrial biogeography despite the fact that the pelagic oceanic environment covers 71% of the Earth's surface, a bias that was termed as "terrestrial chauvinism" by Robert May in a Royal Society Conference in 1993 addressing generalisations across marine and terrestrial environments. The lack of study into pelagic biogeography is a reflection of the much greater difficulties involved in sampling the marine environment, leading to the amount and quality of data being considerably less than for terrestrial studies. The oceanic pelagic environment has nevertheless been sampled from as early as 1874, with the first *Challenger* expeditions and other extensive surveys such as the *Gazelle* expeditions (1974-1876), the *Southern Cross* (1899-1902) and the *Discovery* (1901-1903). Significant scientific contributions were made about two decades later from data collected from the *Meteor* (Hentschel, 1938), the *Dana* (Jespersen, 1923, 1935) and the *Discovery*, *Discovery II* and *William Scoresby* expeditions which were carried out between 1925 and the early 1950's. These studies provided the basis of the "grist of the zoogeographical mill" (Haedrich and Judkins, 1979) and allowed Ekman in 1935 to produce the "Zoogeography of the Sea" which was one of the first syntheses of the world-wide distribution patterns of pelagic fauna and recognised a number of biogeographic regions mostly reflecting warm and

cold water patterns. Beyond this, probably the most significant step made in pelagic biogeography studies resulted from the definition of water masses by Svedrup, Johnson and Fleming (1942) which were subsequently shown to be a dominant factor determining the distributional patterns described by pelagic biogeography (Beaufort, 1943). From these findings, Ekman (1953), in a revised version of the "Zoogeography of the Sea", laid the foundations on which biogeographical studies are now based.

Since then pelagic biogeography has proceeded in two major directions, the historical approach and the ecological approach (Cohen, 1973). The historical approach has phylogeny as a unifying theme and it seeks to understand a group through the study of systematics and the distribution of related species. Van der Spoel (1994a) split this approach into two further categories, the explanation of present day distribution patterns through "vicariance" (ie. the division of faunas through hydrotectonic factors) and through "dispersion" (ie. the movement of faunas from points of origin through forces such as currents). The ecological approach has habitat as the unifying theme and an effort is made to understand the physical environmental parameters that describe and bound the habitats of faunal assemblages and communities. Again, Van der Spoel (1994a) divided this approach into further categories, those that examine community composition and those that investigate food web relations and feeding behaviour. As discussed by Haedrich and Judkins (1979), the historical approach has been the dominant theme in oceanic zoogeography as is shown in the large volume of *Dana* reports and studies such as Brinton (1962), Fleminger and Hulsemann (1974), Pierrot-Bults (1974), Fleminger (1975) and more recently Van der Spoel et al. (1990). However, the assimilation of taxonomic knowledge allowing accurate and repeatable identifications to be made and the introduction of multivariate techniques combined with advances in

computer processing power have recently opened up the ecological field and allowed a great deal of progress to be made in this area of pelagic biogeography.

It was probably as a result of the limitations in taxonomy and analysis that the first pelagic ecological studies mainly concentrated on the distribution patterns of single taxa. Such studies proved to be of great value through the identification of "indicator species", as was used by Russell (1935) who defined the "Russell cycle" using chaetognath species found in the North Sea and North Atlantic, and by Fraser (1967) with siphonophores and Fleminger and Hulsemann (1977) with copepods. Indicator species may be used either as a tracer of water movement or as a sensor of oceanographic parameters (Boltovskoy, 1986). The difference between these two applications is subtle and sometimes overlapping, which often leads to confusion in their application. A good tracer is a species which should be fairly but not extremely sensitive to ecological parameters, sensitive enough not to inhabit more than one of the currents or water masses under study in a particular area but not as sensitive as to disappear from its habitat as soon as environmental conditions change slightly. The criterion for the goodness of a tracer is usually derived from hydrological patterns established on the basis of physical studies and an organism is considered a good tracer if its distributional range matches the known or suspected course of a current and that it still survives in its waters when these are no longer distinguishable by their physical parameters. A good sensor is a species that is snugly restricted to a single water mass such that it has a rather narrow environmental tolerance and a distribution that matches a more or less homogenous TS envelope. Tracer or sensor indicator species initially selected for their fidelity to currents or water masses often end up as being the main material for defining biogeographic areas and as stated by Boltovskoy (1986) "this happens so frequently and

to such an extent that it often is difficult to discern whether a particular report is dealing with water masses or with biogeographic areas". Because certain species are good sensors of water masses or tracers of currents it is implied that water mass boundaries define the limits of the larger pelagic community and that currents displace all species in the same way. This may be true for a number of species but, as pointed out by Ekman (1953), for such statements to be made empirically, the distribution of species must firstly be determined and then subsequently compared to physical boundaries if coincidence between abiotic and biotic distributional limits is to be discerned. Generalisations made about biotic distribution patterns from indicator species analyses must therefore be carefully defined to avoid tautologous arguments and mostly their use is best confined to highlighting complexity in hydrographic features.

Nevertheless, even when biogeographic zones are defined through determining the distribution patterns of species empirically, there are still a number of difficulties that arise through restricting the analysis to a single taxa. This was highlighted by Boltovskoy (1986) when comparing the major biogeographic zonations of the southwest Atlantic according to different authors using different single taxonomic groups. Although the biogeographic charts were all similar in that they distinguished warm-water from cold-water assemblages, it was apparent that there was little agreement over the number of distinct zones and the location of boundaries. Environmental parameters do not affect all species of planktonic plants and animals identically (Dadon and Boltovskoy, 1982, Backus, 1986) and so it is unsurprising that distributional boundaries for one taxonomic group differ from another even though the changes experienced in the physical environment are the same. Furthermore, the study of just a single taxonomic group gives a rather limited insight into biogeographic zonation because the morphological similarity

of species within the taxonomic group makes it more probable that member species would react in a relatively monotonous way to environmental gradients and so it is unwarranted to suppose that one group could be indicative of distribution patterns in the larger biological community. For these reasons, numerous studies consider biogeographic patterns at the community level through the utilization of several high-level taxa to ensure a more averaged insight into the significance of biogeographic patterns. Furthermore, in considering biogeographic distribution at the community level of organisation, the potential influence of the biological as well as the physical environment is being considered in the analysis.

The first problem of considering systems at the community level is defining the parameters of the system. There is a long and turbid history to the attempts made at defining communities (Fager, 1963; Mills, 1969). Some schools view communities as largely abstract and consisting of mosaics (Poore, 1955), others consider that communities are concrete quantifiable units (Whittaker, 1962). One of the main practical difficulties is to reduce the number of subjective decisions necessary to define a community. Fager (1963) considered that the decision as to what parameters should be set "ultimately rests on experience and intuition". However, as stated by McGowan (1971), "while the subjective impressions of a highly skilled naturalist as to what constitutes a community are often very useful, they are not very reproducible". Mills (1969) concluded that because of the different kinds of marine communities, a single rigorous definition was impossible. Communities should otherwise be considered as "working hypotheses" that allow the ecologist to be free to investigate biological relationships without unwarranted presuppositions.

The increasing trend towards more quantitative methods in community ecology

has necessitated the use of multivariate statistical methods which provides the investigator with a relatively objective summarization of data and facilitates the ecologists comprehension of the data as well as providing a means for effective communication of results (Gauch, 1982). The application of multivariate methods partially overcomes the problem of subjective interpretation and lack of consistency, as highlighted by McGowan (1971). However, as stated by Gauch (1982), although multivariate methods increase the objectivity of data analysis, their application in community ecology is still "a product of interaction between communities and ecologists through observations and analysis; like human knowledge in general, it is a joint product of the observer and the observed". Essentially, the approach that is taken is one of "successive refinement" ie. repeated cycles of knowledge, questions and observations which is necessary because crucial questions in community ecology may not be evident until some work has already been done. This approach differs somewhat from the Popperian scientific method of conjecture and refutation employed in most scientific investigations because it is impossible to test hypotheses through experimental manipulation within the time and space scales of community ecology (Mertz and McCauley, 1980).

One of the first plankton ecologists to apply multivariate methods was Williamson (1961) who used an ordination technique called Principal Component Analysis (PCA) to distinguish groups of species in the plankton and to examine whether these groups show similar fluctuations in abundance from year to year. PCA techniques are suitable for analysing sets of samples where all entities are almost always present. However, as Fager (1957, 1963) pointed out, most surveys find that the majority of species are rare or absent in most samples and such data would not be appropriate for PCA analysis

because the technique groups species according to variations in number. A natural framework to community structure where patterns are discontinuous is provided by an alternative multivariate technique called Classification. Involving environmental data within the analysis provides another later of complexity and more powerful multivariate procedures such as classical Canonical Correlation and Canonical Correspondence Analysis are often employed, a problem that has been partially overcome by the BIOENV procedure developed by Clarke and Ainsworth (1993).

Multivariate analysis of biotic data produces groups of faunal assemblages containing co-occurring species with geographic distributions varying in range and discreteness. Although these co-occurrence patterns are a product of relatively objective analytical procedures, there is a subsequent problem in determining whether co-occurring species are functionally related or simply statistical correlates since as stated by Boltovskoy (1986) "co-occurrence is a necessary but not sufficient requirement for the community concept". This problem was further addressed by Van der Spoel (1994b) who pointed out that if a community is nothing more than the specimens and species inhabiting a limited space, it seems logical to expect there to be dependent or related communities in the ocean. There will be strong interactions between members of related communities but still more so within a related community. For pelagic communities there is little or no information on the actual interactions between specimens and species and communities are mostly described on the presence or absence of species (McGowan, 1971; Dadon and Boltovskoy, 1982). Therefore, according to Van der Spoel (1994b) biogeographical data and not ecological data have been used to distinguish communities and for this reason the community concept is, operationally, not an ecological concept.

Using co-occurrence to define ecological communities also runs into danger when

considering how patterns vary with time and as pointed out by Roe (1974) and Haury (1976), the composition and relative abundances of species in assemblages of macrozooplankton are changing all the time. Species may co-occur at some times, but not at others and the particular assemblage that is encountered is as much a function of time of day, geography and the ontogenetic stage of the organisms involved as it is of anything else. It would seem therefore that opportunities for individual species' interactions are rare and although there are certain examples where coevolution has probably taken place such as obligate and often species specific association of hyperiid amphipods with salps, Medusae, ctenophores and siphonophores (Madin and Harbison, 1977; Harbison et al., 1977; Laval, 1980), cases of coevolution are generally infrequent within the pelagic community. Hence, as concluded by Haedrich and Judkins (1979) it may be more a matter of convenience than of reality to speak of "oceanic communities" and the "communities" referred to in most pelagic studies are probably best understood as working hypotheses subject to successive refinement rather than discrete biotic units with predictable composition and location.

Despite the difficulties with the definition of communities and species interactions, the analysis of distribution patterns reveals a great deal about certain biogeographic and ecological aspects of pelagic fauna. For instance, there are fundamental differences between inshore and off-shore faunas with pronounced changes being apparent in species abundance, composition and diversity at the shelf-edge (Grice and Hart, 1962; Haedrich and Judkins, 1979; Tremblay and Roff, 1983) as well as a strong correspondence between gradients in community composition and temperature. In oceanic studies, the emphasis has been more on the total hydrography rather than on single environmental variables (Haedrich and Judkins, 1979) and many studies have

sought to investigate the relationships between water masses and distributions (eg. Pickford, 1946; Fager and McGowan, 1963; Sheard, 1964, Fasham and Angel, 1975; Hargreaves, 1985). In a review of such studies, McGowan (1971, 1974) stated that there were rather few basic patterns that corresponded with the range of surface water masses and that certain faunas, such as those within the North Pacific Central Gyre were stable, diverse and regulated by *in situ* processes. However, such systems are by no means representative of all zooplankton communities, and as Ekman (1953) pointed out, there is a significant number of species (what he termed "cosmopolites") that are widespread throughout a number of water masses. This has been confirmed by studies such as Angel and Fasham (1975), Pugh (1977), Hargreaves (1985) and Boltovskoy (1989). Furthermore, other species have distributional bounds (Boltovskoy, E., 1981; Brinton, 1962) or at least abundance maxima (Fasham and Angel, 1975) well within water mass limits. Indeed, it is by no means agreed that water masses do have a strong influence on zooplankton distribution. Briggs (1974) concluded that "only a few nektonic or planktonic species are known to be restricted to a single water mass" and "on the whole, the case for the distinct fauna concept seems to be rather weak".

Observed differences in the distribution patterns and water mass fidelity of faunal assemblages probably results from the changing importance of different regulatory factors in various regions. For instance, in the large stable North Pacific central gyre, biotic factors, such as food and predation, were identified by Hayward and McGowan (1979) as being the main limiting factors, with competition by interference and frequency dependent predation being inferred as strong regulatory mechanisms. By contrast, environmental factors were found to be of greatest influence on the distribution and composition of the euphausiid community off the west coast of North America,

where year to year fluctuations in the direction and southerly penetration of the California Current were found to be correlated with changes observed in the abundance and even the presence of absence of euphausiid species (Brinton and Reid, 1986). The system studied by Hayward and McGowan (1979) has a semi-enclosed circulation system and it is assumed that these "ecosystems" have been in existence for millions of years and that over this period, climax communities have evolved within them. It between these core areas are zones of biological and physical mixing, such as the California Current, which create were termed by McGowan (1971) as "ecotones" within which community structure is likely to be affected by short term changes in advection. Identifying specific regulatory factors is often difficult since most regulatory mechanisms are subtle, indirect and inter-related.

Understanding factors affecting distribution patterns is made even more difficult through the fact that organisms may show different types of responses to changes in location and environmental conditions, with some exhibiting an absolute responses (ie. presence or absence) and others responding more flexibly through adaptations in behaviour or physiology (Van der Spoel, 1994b). Indeed, both types of response may be shown by the same species of organism depending on the conditions encountered. For instance, *Nematoscelis megalops* was found to submerge with time during the evolution of cold-core eddies in the Gulf Stream (Wiebe and Boyd, 1978; Boyd et al., 1978). It was believed that the species was acting to maintain its distribution within its preferred temperature range but its consequent submergence was detrimental to the condition of the animal as it became displaced from its preferred food source in the surface layers. In this case, the organism initially exhibited a flexible response, but the eventual result of expatriation was absolute as it became unable to physiologically tolerate the changes in

transformation from its current, outlying position amongst the oceanographic sciences. Nevertheless, theoretical limitations must be overcome and future resources must be secured if its potential is to be wholly fulfilled.

5.2 History of biogeographic research in the south-west Atlantic

There have been several extensive surveys carried out in the South Atlantic, mostly in the late 19th and early 20th century. The first of these to have significant scientific value was *H.M.S. Challenger* which sailed in 1874 where, unlike previous expeditions, care was taken in preserving specimens and detailed descriptions, most notably of a number of euphausiids and hyperiid amphipods, were made on the ship's return. The *Gazelle* expedition (1874-1876) also carried out valuable scientific work around this period but exploration became more intense around the turn of the century with expeditions such as the *Southern Cross*, 1899 to 1902 and 1902 to 1904, the *Gauss*, 1901 to 1903 and *Discovery* in 1901 to 1903. Of particular scientific value was the data collected by *Meteor* expedition (Hentschel, 1936), which covered the central and southern Atlantic on fourteen latitudinal profiles, during which 310 stations were worked. The *Dana* expeditions (Jespersen, 1923,1935) which surveyed mainly in the sub-tropic and tropical latitudes, covered quite an extensive geographical range.

The *Discovery* investigations began in 1925 with the original objective of understanding the distribution of whales in the South Atlantic whaling grounds (Kemp and Bennet, 1929). The *Discovery* carried out a sampling program every year between 1925 and 1939. In 1950/51 three ships, the *RRS Discovery*, the *William Scoresby* and *Discovery II* were used, with two of the ships frequently working simultaneously. The

Discovery investigations represent one of the largest and most extensive series of samples ever collected in the Southern Ocean.

5.3 Contemporary biogeographic studies of the south-west Atlantic

One of the first biogeographic charts that included the region was published by Mesenheimer (1905) and subsequent studies have been carried out by Steuer (1933), Hentschel (1938), Bogdanov (1961), McIntyre and Be(1967) and Nesis (1974) (fig. 5.3a, [taken from Boltovskoy (1986)[1]]). In 1981, Boltovskoy published "Atlas del zooplankton del Atlantico sudoccidental" which included investigations on the species distributions on a number of south-west Atlantic by numerous authors including Alvarino (siphonophores), Angel (Ostracoda), Bjornberg (Copepoda), Brinton and Antezana (euphausiids), Boschi (decapod larvae), Esnal (thaliaceans and appendicularians) and E. Boltovskoy (Foramanifera). Boltovskoy also made accounts of the distributions of the Radiolaria, Chaetognatha himself and of the Pterapoda in collaboration with Van der Spoel. The "Atlas" stands out as an invaluable foundation to studies into the taxonomic and ecological biogeography of plankton in the south-west Atlantic.

One feature that is apparent from comparing both the early biogeographic charts and the studies in Boltovskoy (1981a) is that, although all the biogeographic patterns are similar in that they distinguish warm-water from cold-water assemblages, the actual limits of these regions vary widely. Furthermore, the Transition is absent from over half of these schemes (fig 5.3b, [taken from Boltovskoy, 1986: fig 3]). In fact, the actual

[1] This figure was actually taken from Boltovskoy (1989) fig. 13, which was slightly revised from the original figure published in Boltovskoy (1986) fig. 2

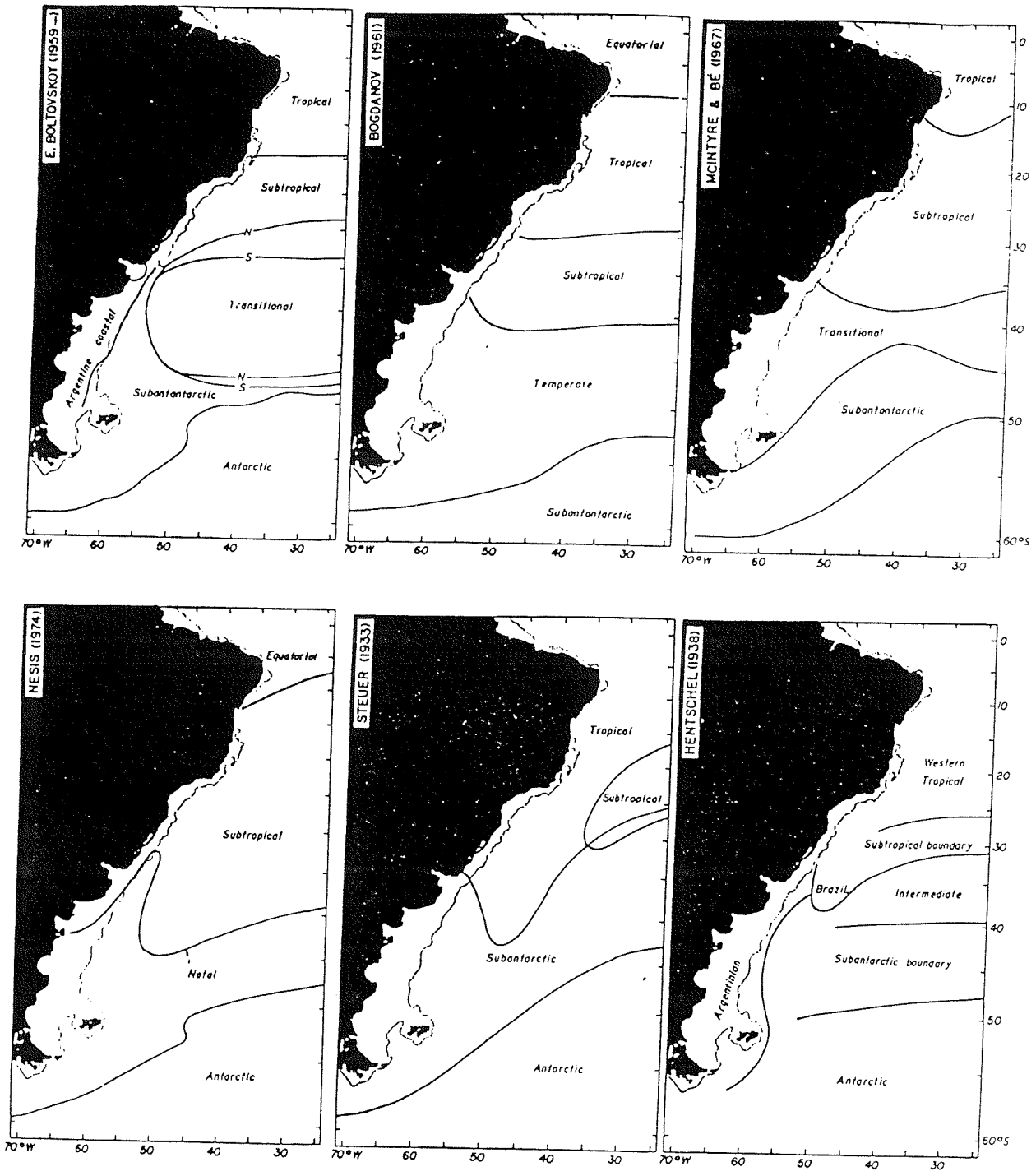
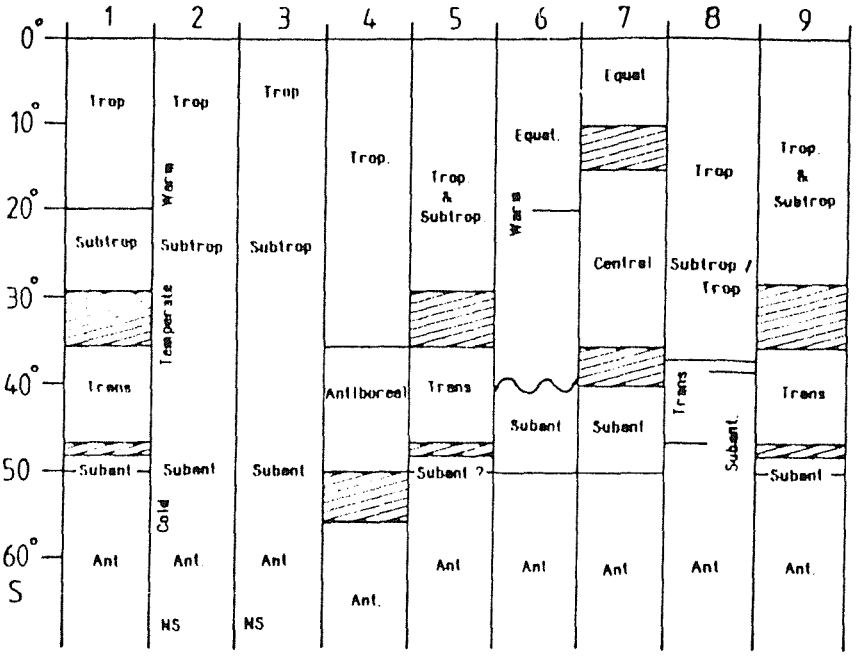


Fig. 5.3a: Early biogeographic charts of the south-west Atlantic (taken from Boltovskoy, 1986)



Approximate limits of distinctive faunal planktonic assemblages in the Southwestern Atlantic (pelagic waters). 1 : Foraminifera (E. Boltovskoy, 1970a;1981a,b); 2 : Tintinnina (Souto,1981); 3 : Siphonophorae (Alvariño, 1981); 4 : Hydromedusae (Ramírez & Zamponi, 1981; based on Kramp, 1957); 5 : Pteropoda (Van der Spoel & Boltovskoy, 1981); 6 : Ostracoda (Angel, 1981); 7 : Copepoda (Bjornberg, 1981); Euphausiacea (Antezana & Brinton, 1981). NS : limits between zones not specified.

Fig. 5.3b

detail of the biogeographic zonation patterns has not improved greatly since the chart published by Hentschel (1938) based on the results collected by the "Meteor". This chart shows a basic division between sub-tropical and sub-Antarctic waters but has also identifies an "intermediate" region between these two water masses and also a southward extension of western sub-tropical faunal boundary associated with the Brazil Current. There is also a division between the oceanic and neritic regions in the sub-Antarctic zone.

The lack of correspondence between studies may be the result of several factors. Firstly, most investigations are either temporally or spatially limited, if not both, and are therefore subject to the natural variability within samples, especially within dynamic regions such as the Transition regions. Secondly, most studies are limited to a single taxonomic group which, as discussed in Section 5.1, gives a rather limited insight in biogeographic zonation because the morphological similarity of species within the taxonomic group would make it more probable that member species would react in a relatively monotonous way to environmental gradients. Since environmental parameters do not affect all species of planktonic plants and animals identically (Dadon and Boltovskoy, 1982, Backus, 1986) it is unsurprising that distributional boundaries for one taxonomic group differ from another even though the changes experienced in the physical environment are the same. Thirdly, there is also the danger that many studies have inferred that water mass boundaries are also faunal distribution boundaries from making the observation that many species show a strong association to a single water masses. Although this may be true in a number of instances it has been shown by a number of other studies to not be universal (Brinton, 1962; Boltovskoy, E., 1981; Boltovskoy, 1986) and making such an inference without empirical observation is

unjustifiable and may be a further source of discrepancy between biogeographic studies.

The one biogeographic study carried out in the south-west Atlantic that is not subject to the above criticisms is that of Dadon and Boltovskoy (1982). Their study considered 3 taxonomic groups (chaetognaths, euphausiids and pteropods) for which they sought patterns of co-occurrence through applying multivariate methods. The biogeographic distribution patterns that were defined were consequently more objective than the studies mentioned previously since no assumptions were made with respect to the faunal limits and results were a more averaged insight into biogeographic zonation through not being restricted to a single taxonomic group. Nevertheless, an inevitable consequence of this increased objectivity is that the biogeographic patterns are more complex and less definite than zonations devised through more subjective means which partly tailor results for ease of comprehension. The results of Dadon and Boltovskoy's (1982) study was the identification of 8 zoogeographic zones which were partly associated with one region and wholly associated with others. The distribution of these 8 patterns are illustrated in figure 5.3c which is taken from Dadon and Boltovskoy (1982) [fig 22-29] and were defined as follows (Nb. brackets denote part associations):

(i) Antarctic oceanic

(ii) Sub-Antarctic oceanic

(iii) Sub-Antarctic (transitional) neritic

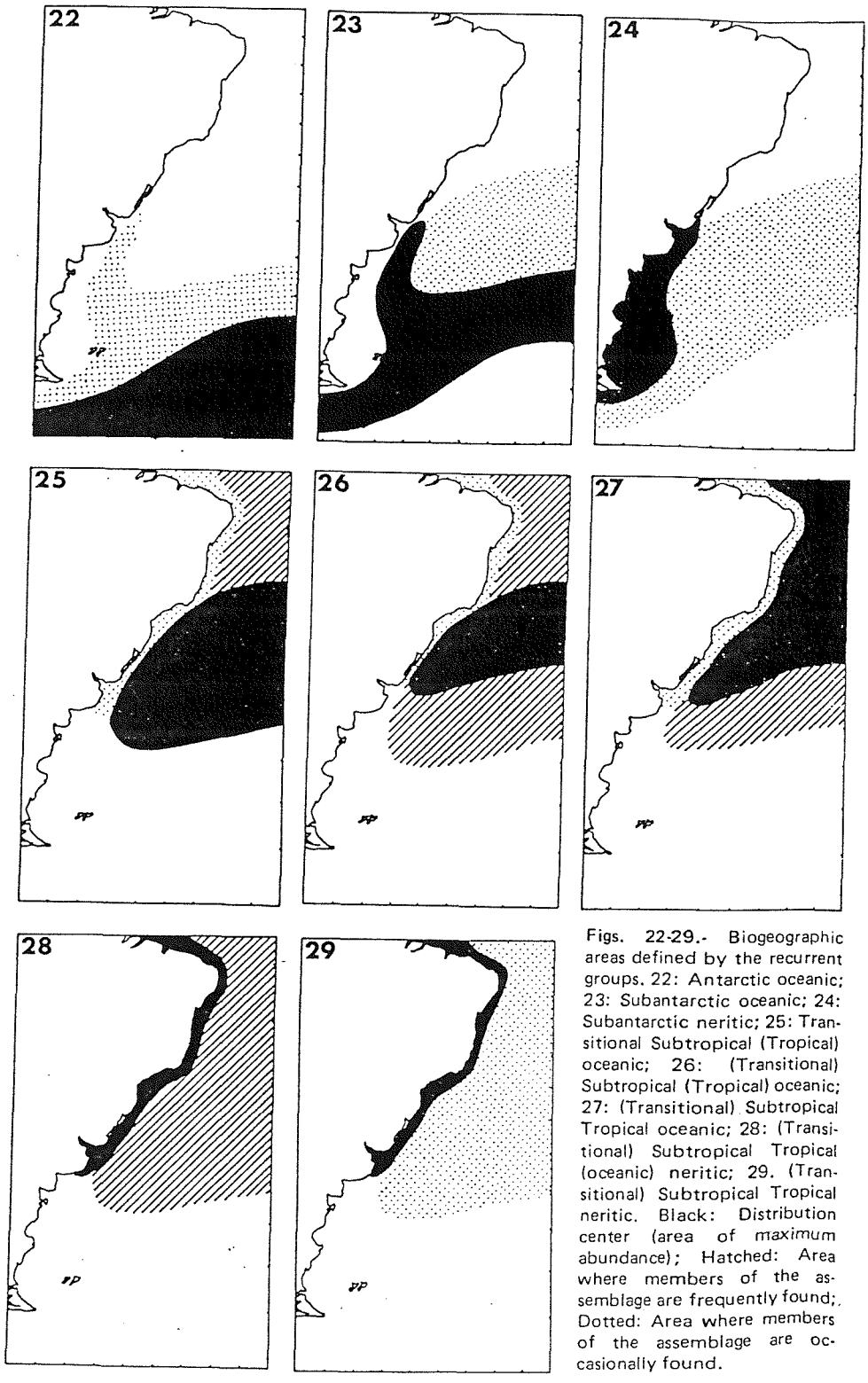
(iv) Transitional sub-tropical (tropical) oceanic

(v) (Transitional) sub-tropical (tropical) oceanic

(vi) (Transitional) sub-tropical tropical oceanic

(vii) (Transitional) sub-tropical tropical (oceanic) neritic

(viii) (Transitional) sub-tropical tropical neritic



Figs. 22-29.- Biogeographic areas defined by the recurrent groups. 22: Antarctic oceanic; 23: Subantarctic oceanic; 24: Subantarctic neritic; 25: Transitional Subtropical (Tropical) oceanic; 26: (Transitional) Subtropical (Tropical) oceanic; 27: (Transitional) Subtropical Tropical oceanic; 28: (Transitional) Subtropical Tropical (oceanic) neritic; 29. (Transitional) Subtropical Tropical neritic. Black: Distribution center (area of maximum abundance); Hatched: Area where members of the assemblage are frequently found; Dotted: Area where members of the assemblage are occasionally found.

Fig. 5.3c: Zones identified from the analysis of Dadon and Boltovskoy (1982)

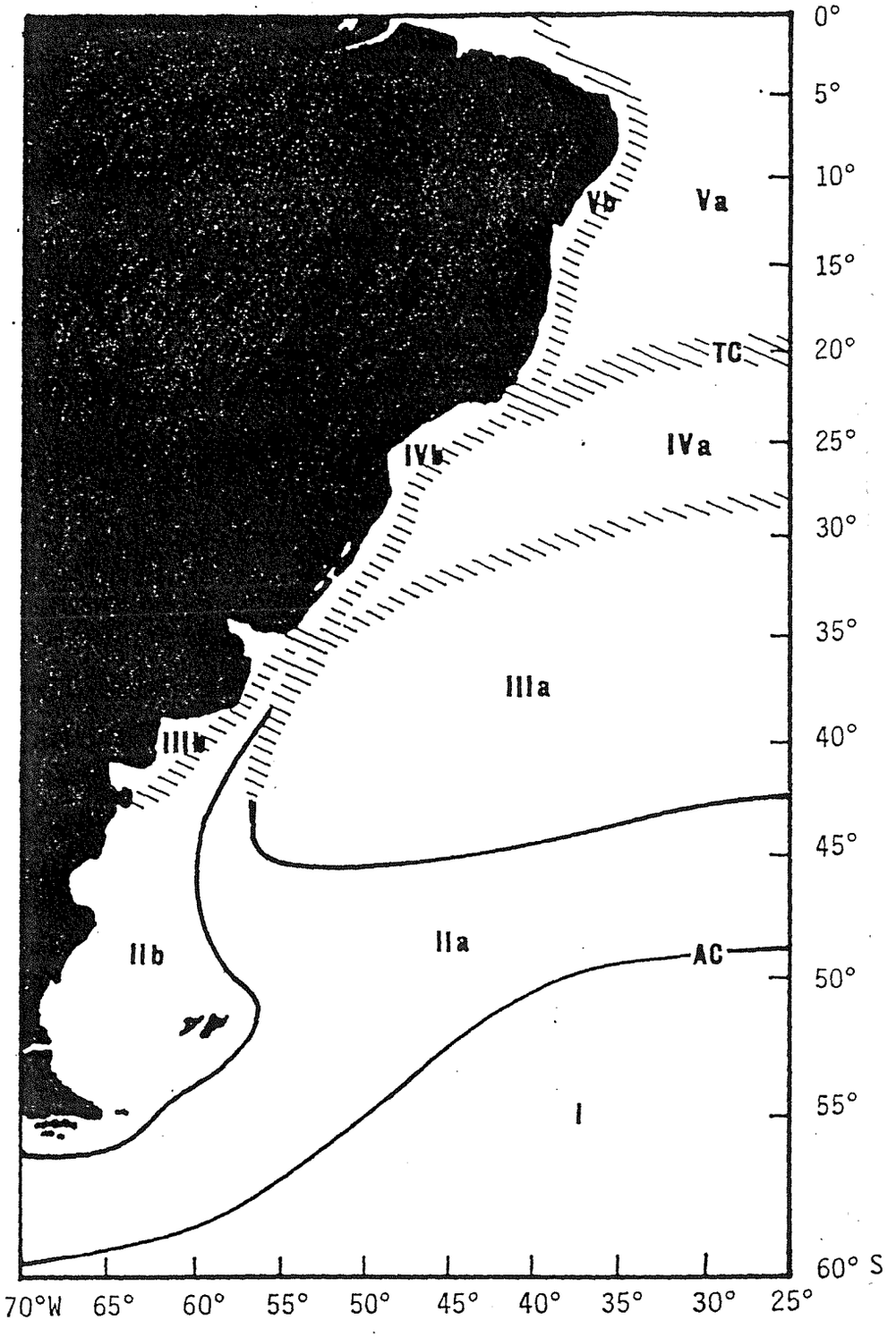


Fig. 5.3d: Biogeographic zones in the south-west Atlantic according to Dadon and Boltovsky (1982)

I: Antarctic oceanic; IIa: sub-Antarctic oceanic; IIb: sub-Antarctic neritic; IIIa: Transitional oceanic; IIIb: Transitional neritic; IVa:sub-tropical oceanic; IVb: sub-tropical neritic; Va: Tropical oceanic; Vb: Tropical neritic; AC - Antarctic convergence; TC Tropical convergence

It can be seen that none of the distribution patterns were restricted to a single water mass but most of them do have distribution centres (or abundance maxima) effectively limited by a single water-type. A further apparent feature was that southern cold and cold-transitional limits were much sharper than those separating warm water assemblages, an observation mainly attributed to the instability of the northern and north-western limits of the Transition zone. Also, it was apparent that all the sub-tropical and tropical oceanic types of distribution pattern invade the neritic domain and vice-versa although faunal differences between coastal and open ocean environments still do exist. From these considerations, Dadon and Boltovskoy (1982) put forward a biogeographical scheme (fig 5.3d) which, on the whole, appears to be quite similar to that put forward by Hentschel (1938) although the northern sub-Antarctic boundary is more defined and the sub-tropical/tropical boundary is more diffuse in the scheme of Dadon and Boltovskoy (1982).

The neritic domain within the south-west Atlantic has been subject to a far greater degree of research than the adjacent oceanic regions although unfortunately, the studies that have been carried out have been restricted to a single taxonomic group. Of particular interest is the work of Dadon (1989) on pteropods and Mazzoni (1990) on chaetognaths. Both studies identified three distinct biogeographic regions on the continental shelf of the south-west Atlantic between 35° and 55°S (fig 5.3e):

(i) Region Costera Templada

(ii) Region Magallanica

(iii) Region Malvinense

The "Region Costera Templada" represents a coastal region which has a southerly limit around 48°S and follows the 100m isobath northwards up to 35°S. Essentially, this

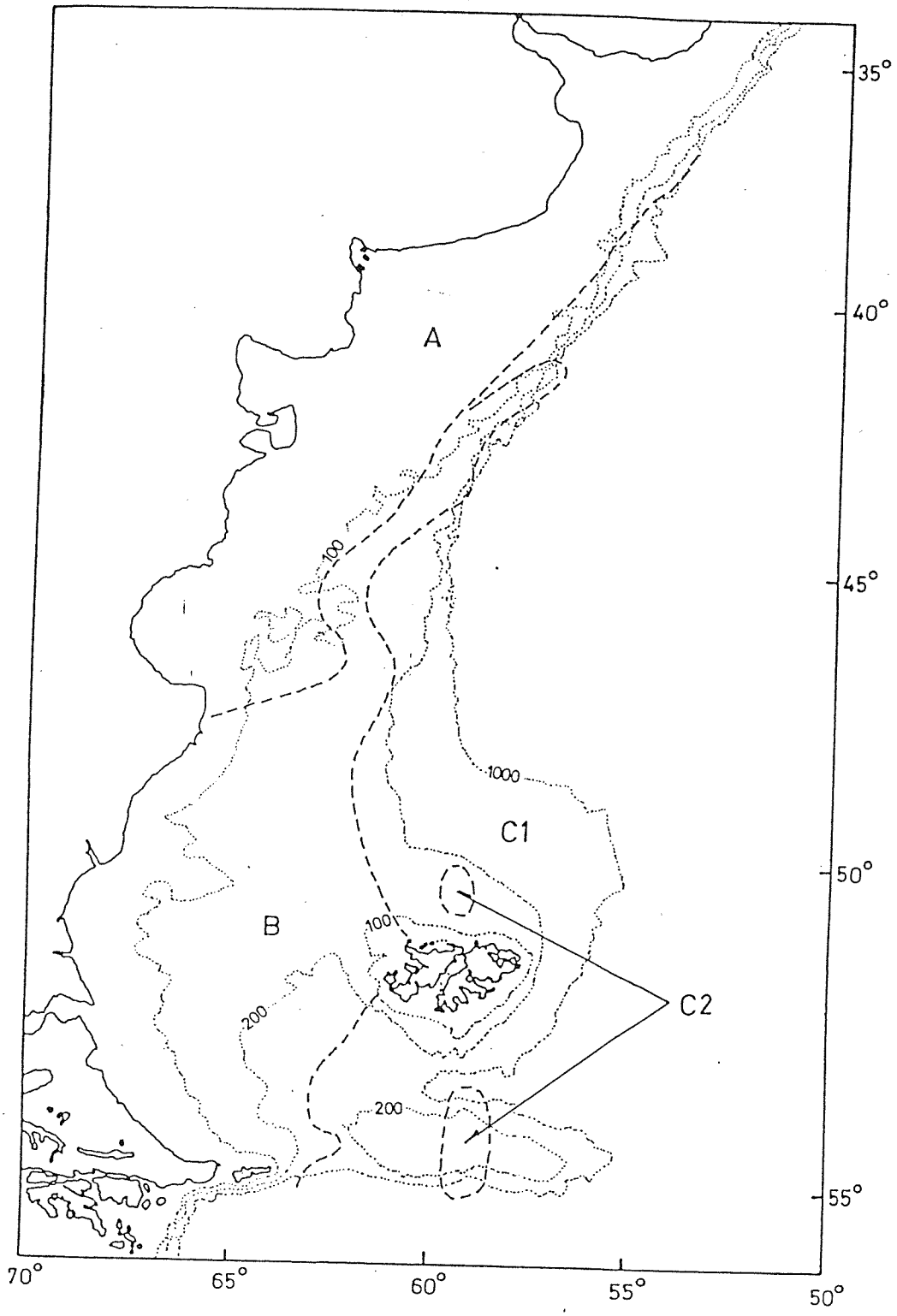


Fig. 5.3e: Biogeographic zonation of the South American continental shelf during Summer (taken from Mazzoni, 1990)

A: Region Costera Templada; B: Region Magallanica; C: Region Malvinense

zone is part of the continental platform most protected from the influence of the dominant currents which allows the development of a typical neritic fauna. This region was also recognised by Lopez (1964), Boschii et al. (1981) and Menni and Lopez (1984).

The "Region Magallanica" occupies the mid-region of the platform at the Golfo San Jorge and continues in a NNE direction between 38°S and 42°S. At the latitude of the Falkland Islands, there is another tongue with an easterly direction with a maximum extension between Winter and Spring reaching the surroundings of the archipelago. The zone is made up of waters of mixed origin. It receives a constant influence from the Falkland Current and also from South Pacific water which traverses the Magellan Straits and the Cape Horn Current. These characteristics make this region an area of transition between the "Region Costa Templada" and the Falkland Current but it is also characterised by faunistic elements from the Pacific. This region was also recognised by Menni and Lopez (1984) and Bastida et al. (1986).

The "Region Malvinense" is limited by the path of the Falkland Current and essentially occupies the whole of the continental slope. The Falkland Current is, undoubtedly, the principal environmental factor that affects the composition and distribution of zooplankton in this region carrying cold-water species to relatively low latitudes. Nevertheless, Mazzoni (1990) found that the western limit of the "Region Malvinense" did not have the same spatial regularity or temporal stability as the Falkland Current which illustrates the degree of mixing and faunal overlap in this region. In addition to its role as a faunistic carrier, the Falkland Current also acts as a barrier for it effectively limits the ingression of sub-tropical organisms into the shelf regions from the east. Its faunal composition is also seen to vary with season, as in the case of the

chaetognaths that characterise this region, *Eukrohnia hamata* and *Sagitta gazellae*, which alternate in their dominance of the chaetognath fauna in the region. The region has been recognised by a number of other studies such as Boschi et al. (1981), Menni and Lopez (1984) and Bastida et al. (1986) although not all identify the region through empirical observations on species distribution.

Chapter 6 Distribution patterns of 1990 RMT8 and Bongo samples

6.1 Introduction

The use of biogeographic methods is a fundamental step to building up a picture of the ecology of any region and given the comparatively limited number of biogeographic studies on the zooplankton of the south-west Atlantic, further studies are necessary to add to the rather small body of knowledge that has been obtained so far. Nevertheless, it is not the aim of this investigation to repeat studies that have already been carried out, but to gain a different perspective on certain biogeographic aspects. The most objective insight into the biogeography of the south-west Atlantic was obtained by Dadon and Boltovskoy (1982) whose methods have been discussed in the previous section. Their investigation was based on a large number of literature records which although broad ranging, was limited in terms of spatial resolution, which was macro-scale[1] at best, and unaccommodating towards seasonal and inter-annual variability. The present investigation has an almost synoptic temporal resolution and can identify mesoscale[2] features. This degree of temporal and spatial resolution in zooplankton patterns has been obtained very rarely in this region and allows an almost unique biogeographic perspective.

In section 5.1, it was stated that biogeographic investigations can be essentially divided into taxonomic and ecological disciplines. The taxonomic aspects of biogeography, although possibly referred to in certain discussions, will not be considered

[1] Macroscale features were defined by Haury et al. (1978) as having a range between 1000 to 3000km

[2] Mesoscale features were defined by Haury et al. (1978) as having a range between 100 and 1000km

within this investigation since the major aim is to use biogeographic information to assist in gaining a fuller understanding of the ecology of the region. Furthermore, through concentrating on the ecological aspects, greater emphasis will be placed on the more abundant and possibly more widespread species rather than the rare and distributionally restricted species, since it is the former that dominate major ecological attributes such as production and community interaction as well as probably providing the major food sources for commercially exploited fish and squid species. Despite this emphasis, this investigation will nevertheless analyse the species composition and abundance of 9 taxonomic groups which is a considerably broader taxonomic coverage than most other studies into zooplankton community composition patterns (eg. Fager and McGowan, 1963; Sheard, 1964; Fasham and Angel, 1979; Dadon and Boltovskoy, 1982). Consideration of a large number of groups is more suited to determining biotic zonation and the distribution patterns of hypothesised "functional" communities because it overcomes many of the problems associated with the consideration of just one or two taxonomic groups which may have unique responses to environmental parameters (see Section 5.3). The use of multivariate methods to analyse the large species/samples data matrices further provides greater objectivity in determining any apparent biotic zonation resulting from co-occuring distribution patterns.

The hydrographic regime in the south-west Atlantic is particularly complex (see Chapter 4) and an objective means of comparison needs to be employed to determine its influence on biotic patterns. Until recently, most studies related environmental variables to biotic patterns through graphical means one variable at a time, which relied more on the subjective interpretations of the investigator than on empirical relationships within the data. Multivariate methods have now been developed that allow all the potentially

influential environmental variables to be related to biotic patterns simultaneously so that the subset of these variables showing strongest biotic associations can be identified. Determining the most important factors influencing biotic patterns gives a great deal of insight into the nature of the community and its principal regulatory factors. Ultimately this approach may also have a predictive capacity in that if consistent relationships between biotic distributions and environmental variables are found, zooplankton community composition may be discerned through monitoring environmental fluctuations alone. These multivariate procedures are applied to south-west Atlantic zooplankton patterns for the first time in the following investigation and their insight into the principal regulatory factors affecting zooplankton in this region is unique.

Beyond searching for influential environmental variables and principal regulatory factors for predictive purposes, the analysis of biotic distribution patterns is conversely also very revealing in highlighting complex oceanographic features. The use of biological indicators has shown that easily measurable physical and chemical parameters often do not adequately reflect the complex pattern of oceanic dynamics (Dadon and Boltovskoy, 1982). The interpretation of the distribution of planktonic species allows one to evaluate factors usually ignored by physical and chemical studies such as the history of the water. This is particularly important in this region where there are a number of mesoscale features, such as eddies and currents, which have a profound influence of community distribution patterns but are not always discernable from their physical characteristics. Analysing biotic patterns is also revealing in examining the "biological quality" of the water (Raymont, 1983) such as food availability, conditions for breeding and growth and factors that affect behavioural or physiological responses. Such factors often reflect the close interaction between the physical environment and biotic factors

which lead to the distribution patterns that are observed. Often, it is hypothesised that discrete differences in these "qualities" between water masses leads to the frequent observation of species distributions being limited by water mass boundaries (McGowan, 1971, 1974). However, such correspondence does not always exist (Boltovskoy, 1986) which may highlight a number of important aspects about the physical environment and the nature of the biotic communities.

As discussed by Angel (1977), the potential resolution of a survey is a compromise between sampling precision and the need to achieve maximum geographic coverage. Despite certain problems in accounting for day/night effects and vertical stratification, the resolution obtained by this investigation was both unique and valuable. A total of 44 stations were sampled over a wide latitudinal and geographic area with a virtually synoptic temporal resolution. The spatial resolution of the survey allowed mesoscale community patterns to be resolved for virtually the first time in this region. Combined with extensive taxonomic coverage, the complexity of analysis and the incorporation of a number of environmental features into subsequent interpretations, this investigation represents one of the broadest and most detailed insights into the distribution patterns of zooplankton communities of this region yet obtained.

6.2 General patterns of distribution

6.2.1 Introduction

155 species were identified within the 9 taxonomic groups considered in the analysis of 1990 RMT8 samples (Appendix IIa) and 62 species were identified within 6 taxonomic groups considered in the 1990 Bongo samples (Appendix IIb). The analysis of such large scale data sets is unavoidably complex and as such, it is often valuable to consider some of the simple community parameters of zooplankton samples such as total biomass, total abundance, species richness and diversity as well as some general species distribution patterns such as the frequency of occurrence and the total and average abundance. The analysis of such parameters often reveals a great deal about community ecology of zooplankton in a particular region in addition to aiding in the choice of more complex further analysis. Recently, latitudinal trends in species richness have been given a great deal of study (Fisher, 1981; Boltovskoy, 1982; Rohde, 1986, 1992; Clarke, 1992; Rohde et al., 1993) and the considerable latitudinal range of the present survey (34° to 53°S), determining any latitudinal trends in species richness or any other community parameters in the present data set would be of considerable interest. As discussed in Chapter 4, the region is dominated by dynamic oceanographic features and so it is also valuable to consider whether any relationships exist between community parameters and physical features such as water masses, surface thermal fronts, bucket surface temperature values and topographic features such as the Patagonian shelf and slope.

Defining biogeographic zones is most empirical where the species have high abundances and restricted distributional ranges. However, such species distribution

patterns are not always apparent and, as was illustrated in Boltovskoy and Riedel (1987) for Polycystina Radiolaria, a pattern where the most abundant species are also the most widespread is common. In such cases, analyses which are able to separate distribution patterns according to differences in abundance rather than presence or absence would be most suitable. Establishing the nature of general patterns in species distributions is therefore an important initial consideration.

6.2.2 Calculation methods of community parameters in 1990 RMT8 and 1990 Bongo samples

Total station biomass was estimated by measuring the displacement volume of the whole sample as described in Chapter 3. In the RMT8 samples, the displacement volume of the whole sample was virtually equivalent to the sum of the individual displacement volumes of the 9 taxonomic groups considered. However, in many of the 1990 Bongo samples, a significant contribution to the total displacement volume was made up by copepods which were not considered in this analysis. Copepods were not present in significant proportions in the RMT8 samples because the mesh size was too coarse to retain them. Station abundance (N) was calculated as the sum of individuals within the 9 RMT8 and 6 Bongo taxonomic groups. Diversity was estimated through calculating the species richness (S) which is the sum of the number of species per sample within the 9 taxonomic groups considered and also the equitability (E) which represents the distribution of the numbers of individuals between species. There are a number of diversity indices that combine these two parameters to give a "diversity index value", such as the Simpson diversity index (D) (Simpson, 1949) and the Shannon-Wiener index (H) (Shannon and Weaver, 1963). In this study, where the main emphasis is on

comparative differences between stations, the difference between the indices is somewhat arbitrary and the Simpson diversity index was used.

$$\text{Simpson's index (D)} = \frac{1}{\sum_{i=1}^{S} P_i^2}$$

Where P_i is the proportion of the total number of individuals represented by the i^{th} species.

The equitability value (E) was also calculated so that the effect of the distribution of numbers between species on the value of D could be quantified.

$$E = \frac{1}{\sum_{i=1}^{S} P_i^2} \times \frac{1}{S}$$

The equation gives values between 0 and 1 with higher values being more equitable.

In terms of general patterns in the distribution of species, the main parameters considered in this analysis were the total number of individuals (N_i) and the frequency of occurrence (f). N_i is the total number of individuals of the i^{th} species in the entire sample set and f is the number of stations in which the i^{th} species was found. The average number of individuals per station was calculated as N_i/f.

6.2.3 Results and Analysis

Comparison between 1990 RMT8 and 1990 Bongo samples

The sampling methods of the RMT8 and the Bongo samples differed in the depth range and duration of the tows and in the mouth area and mesh diameter of the nets (see Chapt. 3). These differences have a profound effect on the nature of the zooplankton obtained and consequently there may not necessarily be any correspondence between geographic trends in the community parameters of the RMT8 and Bongo samples. It is therefore important, as a first step, to establish whether there is a relationship between

the RMT8 and Bongo samples in the community parameters considered in this analysis.

Plots of the distribution of displacement volumes of RMT8 and Bongo samples are given in figs. 6.2a and 6.2b and respective station abundance (N) distributions are given in 6.2c and 6.2d. A regression of RMT8 displacement volume on Bongo displacement volume found that there was a significant linear relationship ($P=0.035$, $r^2=0.104$) between the two sample sets. There was no significant linear relationship between station abundance in the RMT8 and Bongo samples. Within the two sample sets, there was a significant relationship between displacement volume and N in the RMT8 samples ($P=0.011$, $r^2=0.146$) but a non-significant relationship between the 2 parameters in the Bongo samples.

The distribution of species richness (S) amongst the RMT8 and Bongo stations is illustrated in fig. 6.2e and 6.2f respectively. A Mann-Whitney rank-sum test found that there was a significant difference ($P<0.001$) between the species richness of RMT8 and Bongo samples with the RMT8 having the largest number of species per station (RMT8(S) median=17.5; Bongo(S) median=8). A significant difference between the two sample sets was also seen with respect to the Simpson Diversity Index (D) (Mann-Whitney, $P=0.029$) with the RMT8 sample set having the highest D value (RMT8(D) median=2.820; Bongo(D) median=2.061). In terms of equitability (E), the Bongo samples had significantly higher values than the RMT8 samples (Mann-Whitney, $P=0.018$; B90(E) median=0.242; RMT8(E) median=0.168).

Latitudinal relationships

One of the major difficulties in analysing latitudinal trends in community parameters is that anomalous geographic features may obscure underlying patterns. In the present

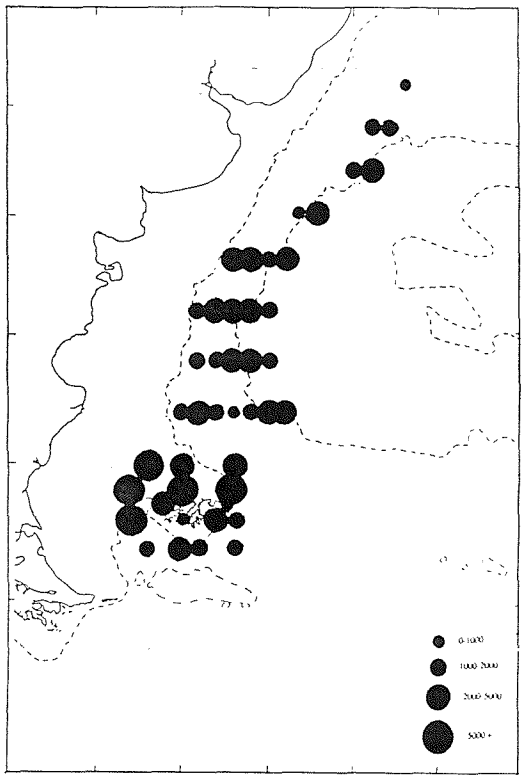


Figure 6.2a: Station abundance (N) of 1990 RMT8 samples

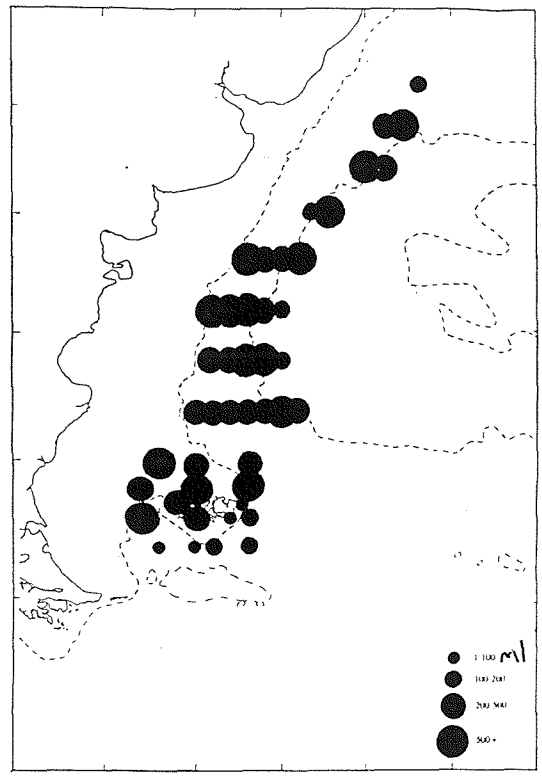


Figure 6.2c: Displacement volume of 1990 RMT8 samples

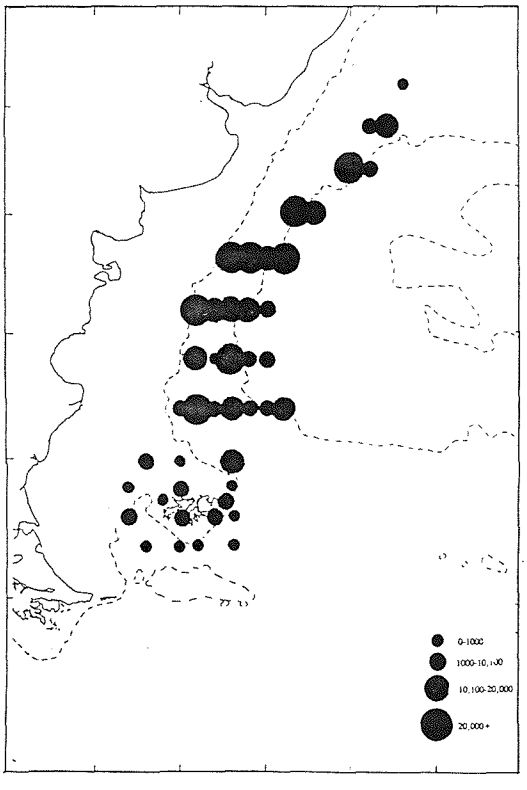


Figure 6.2b: Station abundance (N) of 1990 Bongo samples

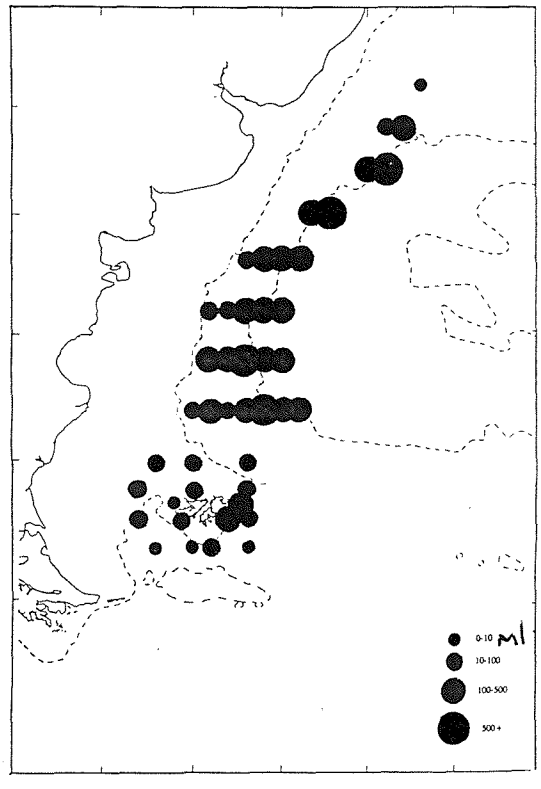


Figure 6.2d: Displacement volume of 1990 Bongo samples

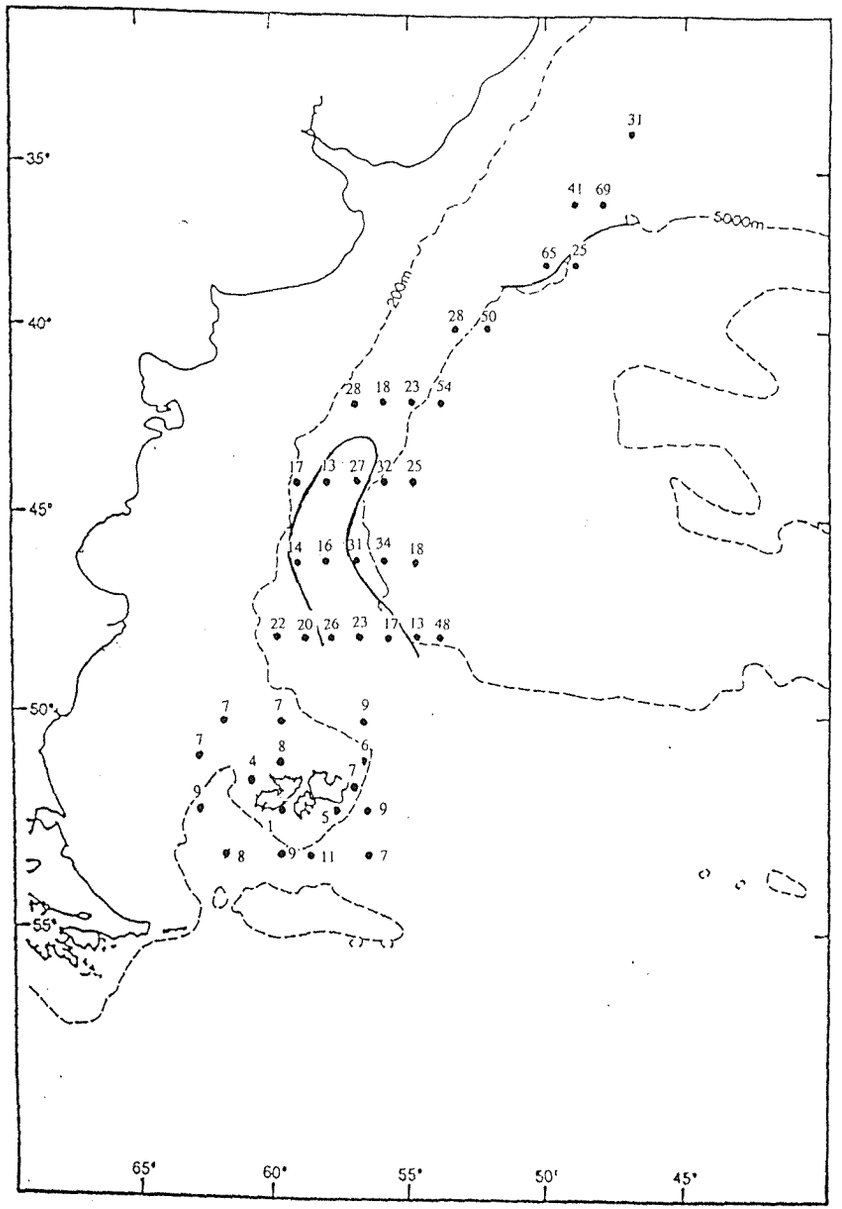


Figure 6.2e: Species richness (S) of 1990 RMT8 samples

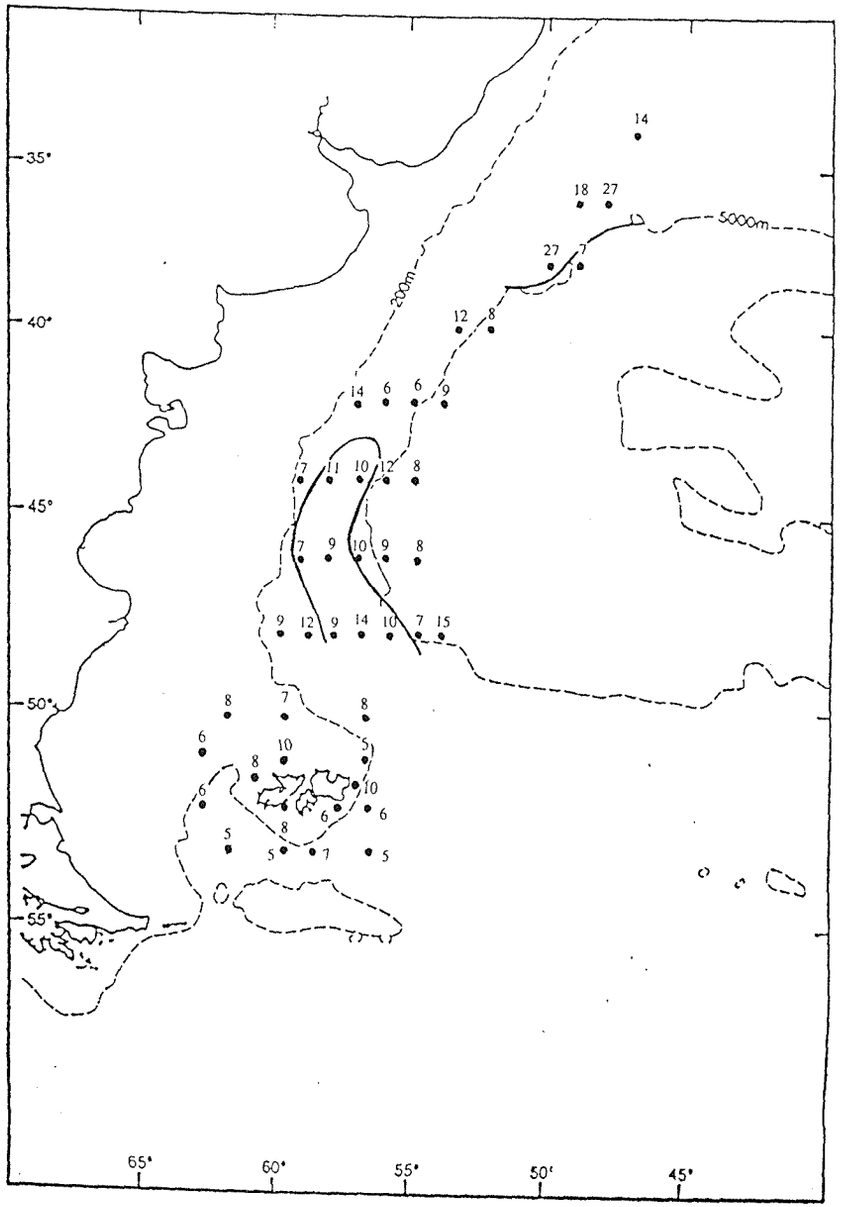


Fig. 6.2f: Species richness (S) of 1990 Bongo samples

sampling grid, the northerly stations were sampled off-shelf whilst the southerly stations were sampled on-shelf and so latitudinal trends over the entire sampling grid may be confounded by any on-shelf/off-shelf effect on community parameters. These difficulties were partly overcome by omitting the shelf stations from the analysis and simply examining latitudinal trends in offshelf stations between 34° and 48°S.

Latitude was regressed linearly against displacement volume, N, S, D and E. Only species richness (S) was significantly related to latitude both in the RMT8 and the Bongo sample sets (RMT8 $P=0.003$, $r^2=0.286$; Bongo $P=0.011$, $r^2=0.223$), decreasing linearly with increasing latitude. In the RMT8 samples, the highest S value was 69 species found at 36°S and the lowest, 13 species, at 48°S. In the Bongo samples, the highest S value was 27 species found at both 36°S and 38°S, whilst the lowest was 6 species at 42°S.

Water mass relationships

Three water masses were identified in the present study area (see Chapt. 4) and the influence of water mass location on community parameters was analysed by dividing the stations into water masses groups and testing for differences between them using either a Kruskall-Wallis test on non-normal data or 1-way Anova test on normal data. All stations ~~found~~ located on-shelf (ie. all those below 48°S) were omitted since, although they were mostly influenced by Sub-Antarctic Water, their community parameters may differ from other stations because of features associated uniquely with the shelf environment.

In both the RMT8 and the Bongo samples, no significant differences were found between water masses with respect to displacement volume, N, S, E and D.

Surface thermal front relationships

In Chapter 4, it was found that mesoscale patterns in the surface thermal values seen in satellite images differed from the position of water masses. Given that water masses did not have any significant effect on the values of the community parameters in either sample set, it was considered that the location of surface thermal fronts may be more influential. Rough visual analysis of the satellite images highlighted 2 lines where there were abrupt transitions in temperature, the first marked by the 13°C isotherm and the second by the 10°C isotherm. The Bongo and RMT8 data sets were consequently divided into three groups, the first being those stations found to the north of the 13°C isotherm (>13°C), the second, those stations between the 13°C and the 10°C isotherm (10°C<>13°C) and the third, those stations to the south of the 10°C isotherm (<10°C). Shelf stations were again omitted.

A combination of Kruskall-Wallis and 1-way Anova tests were used to test for differences between groups in each of the community parameters. In the Bongo samples there were no significant differences found between any of the groups with respect to displacement volume, N, S, D and E. In the RMT8 samples, there were no significant differences between groups with respect to displacement volume, N and D. However, S values were found to be significantly higher in the >13°C group compared to the <10°C group ($P<0.05$) and values for E were found to be significantly higher in the 10°C<>13°C group compared to the <10°C group ($P<0.05$). Differences between the other surface thermal groups with respect to S and E were not significant.

Bucket surface temperature relationships

Although the study region can be divided into regions marked by water mass

boundaries or dramatic transitions in surface temperature seen in satellite images, it is also true that surface temperature may vary, sometimes considerably, within these regions (see Chapt. 4). Therefore, it is possible that absolute temperature may show a relationship to community parameters despite the fact that hydrographic zone location was found to have no significant influence.

Bucket surface temperature values, obtained at the sampling stations of the 1990 survey, were regressed as the independent variable against each of the community parameters of both samples sets. In the Bongo data set there was a significant positive regression found between bucket surface temperature (x) and S (y) ($y=3.349+0.738x$, $P<0.001$, $r^2=0.362$). However no significant relationship was found between bucket surface temperature and displacement volume, N, D and E. In the RMT8 samples, bucket surface temperature showed a significant positive relationship with S ($y=-4.079+3.034x$, $P<0.001$, $r^2=0.601$) and with D ($y=1.796+0.182x$, $P=0.044$, $r^2=0.121$) and also a significant negative relationship with E ($y=0.318-0.014x$, $P=0.007$, $r^2=0.206$). There were no significant relationships between bucket surface temperature and displacement volume or N.

On-shelf vs off-shelf relationships

The 1990 survey covered both oceanic areas off the Patagonian shelf and Falkland shelf waters but the nature of the survey was such that on-shelf stations were at a significantly higher latitude that off-shelf stations. It was therefore important to exclude any latitudinal effects on community parameters prior to any analysis of on-shelf/off-shelf influences. In the above analyses on latitudinal relationships, it was shown that latitude was not significantly related to N, E, D and displacement volume. Therefore,

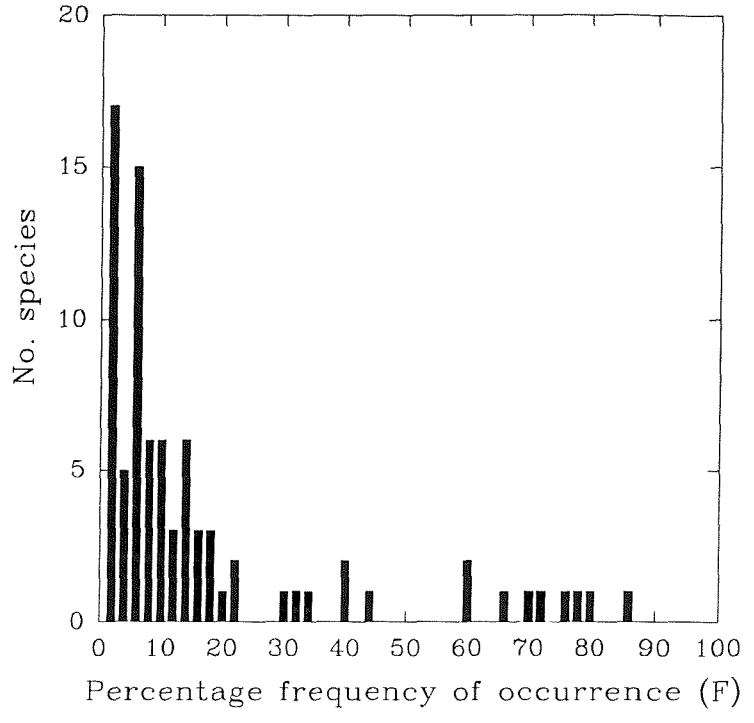
on-shelf/off-shelf differences can be determined simply through pairwise Mann-Whitney tests on on-shelf vs. off-shelf values. However, latitude was found to be significantly related to S and so, in this case, a more complex approach to determining on-shelf/off-shelf differences was necessary. The Bongo and RMT8 regression equations derived from relating S to latitude were applied to the latitudes of the Falkland shelf stations to predict S values at these latitudes, assuming that the regression extends linearly to higher latitudes. These predicted values were then tested against the observed values using a Wilcoxon signed-rank test for the non-normal Bongo data and a paired t-test for the normal RMT8 data.

In the Bongo samples, significant on-shelf/off-shelf differences were found with respect to N ($P<0.001$) and displacement volume ($P<0.001$), with both parameters being higher off-shelf. Values for D, E and predicted vs. observed S were found not to differ significantly between on-shelf and off-shelf stations. In the RMT8 samples, significant differences were found with respect to displacement volume ($P<0.001$), E ($P<0.001$) and predicted vs. observed S ($P<0.001$). E values were highest on-shelf, displacement volume values were highest off-shelf and the observed values of S were lower than expected.

General species distribution patterns

One of the principal factors that needs to be established in general species distribution patterns is how often species occur within the sample grid. This provides information on whether species are generally restricted to a small area or are widespread throughout the region. Histograms of the frequency of occurrence (f) against the number of species at that frequency in the RMT8 and Bongo samples sets are presented in fig 6.2g. It can be

Occurrence frequency of species fron 1990 RMT8 net samples



Occurrence frequency of species from 1990 Bongo net samples

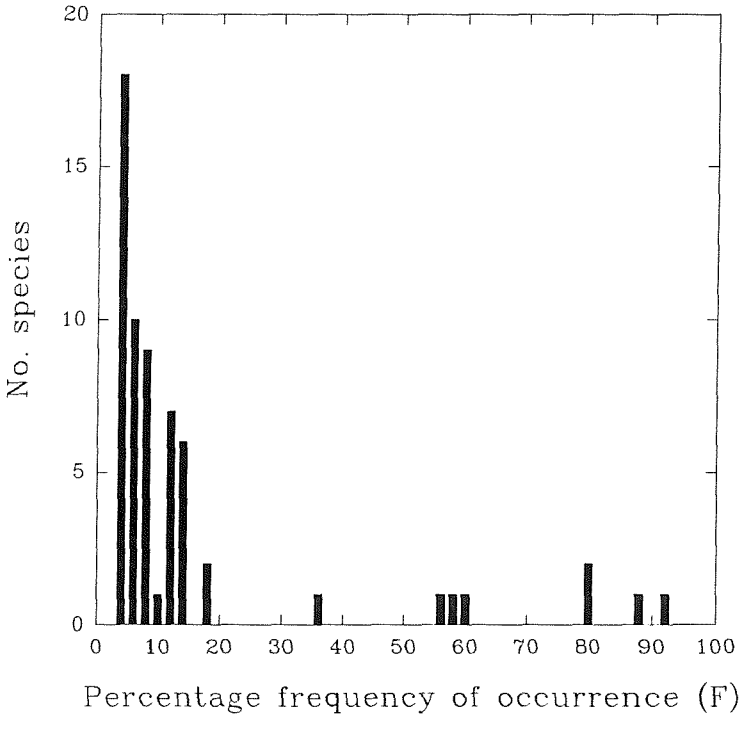


Figure 6.2g

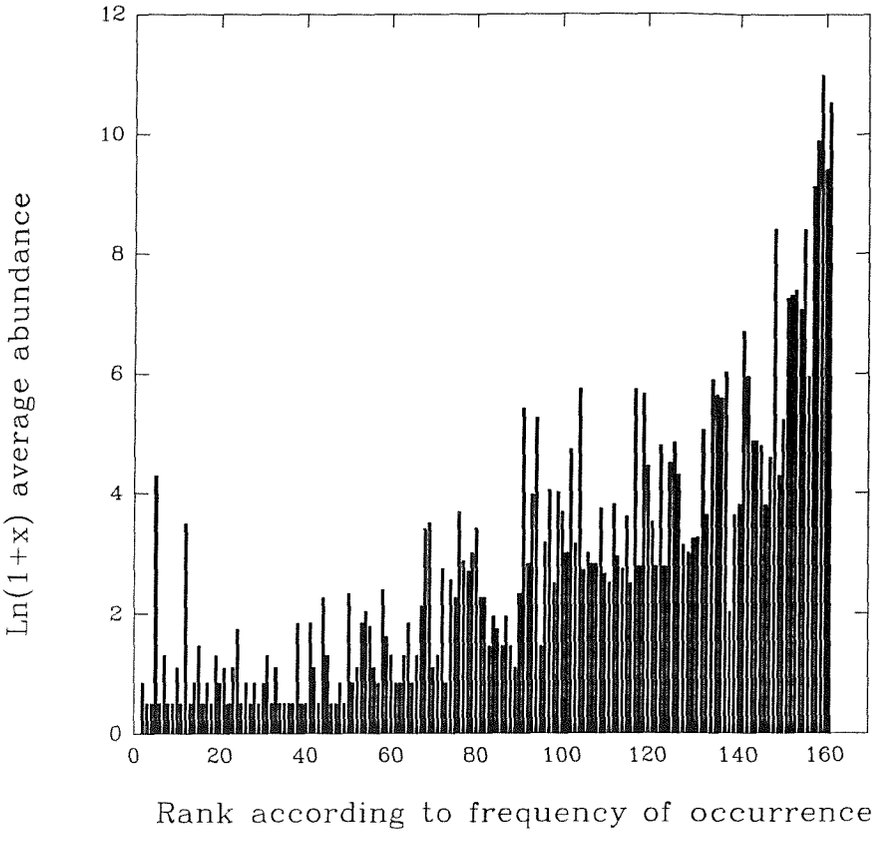
seen that most species generally have low frequencies of occurrence with only 10% of the species in the RMT8 samples and 4% of the species in the Bongo samples occurring at more than 70% of the stations.

One of the problems with this description however, is that it gives little idea as to the nature of occupation ie. whether the less widespread species are concentrated and are more highly abundant in the areas they occupy or whether the more cosmopolitan species are the most highly abundant. To consider this aspect, the logged frequency of occurrence of species was regressed against the log of their total abundance (N_i). It was found that there was a significant positive correlation between these two parameters in both the Bongo and RMT8 data sets (Bongo $P<0.001$, $r^2=0.643$, RMT8 $P<0.01$, $r^2=0.773$) showing that widespread species had the highest abundances. Indeed, the total abundance of widely found species was several orders of magnitudes higher than the species found less frequently.

Despite the fact that there is a significant positive correlation between N_i and f, this does not state conclusively that station abundance (N) is dominated by widespread species. The higher N_i of widespread species could be caused by the accumulation of moderate abundances over the large number of stations they occupy. To determine this aspect, the average abundance (N_i/f) of a species was calculated and plotted against its rank in terms of frequency of occurrence. The plots for the RMT8 and Bongo data set are presented in fig. 6.2h.

In both the RMT8 and the Bongo data sets it is apparent that, unlike total abundance (N_i), the average abundance (N_i/f) of more frequently found species is not several orders of magnitude greater than the species caught less often. In the RMT8 data set, there is nevertheless a positive relationship between average abundance and rank

The logged average abundance of species against rank determined from the frequency of occurrence in 1990 RMT8 net samples



The logged average abundance of species against rank determined from the frequency of occurrence in 1990 Bongo net samples

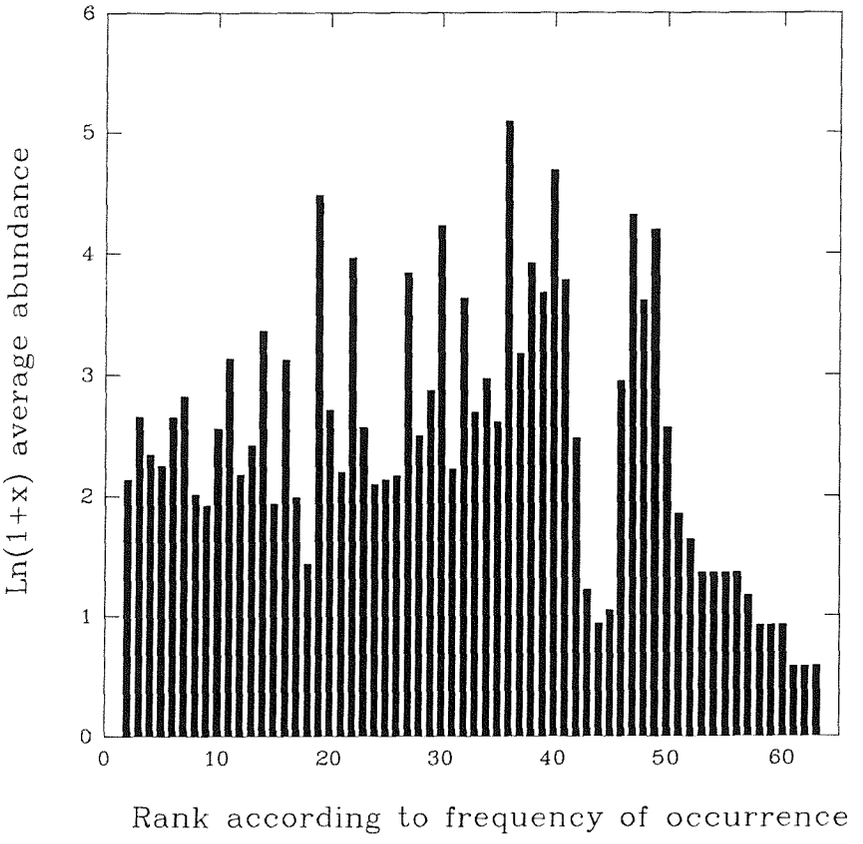


Figure 6.2h

according to frequency of occurrence, thus, at any one station, the majority of individuals are those that are generally most widespread. The same is not true for the Bongo samples however. In fig. 6.2h it is apparent that average abundance values generally oscillate with increasing frequency of occurrence. This would suggest that widespread species do not always dominate station abundance and that less widespread species may also make a significant contribution to the value of N at a particular station.

6.2.4 Discussion

Comparison between RMT8 and Bongo samples

One of the major differences found between the two sample sets was with respect to measurements of diversity (S, D and E), with the RMT8 sample set having the greatest species richness (S) whilst the distribution of individuals between species (E) was more even in the Bongo samples. The larger S value in the RMT8 samples may be a result of the occurrence a large number of species at low abundances. This is partly indicated by the lower E value of RMT8 samples compared with Bongo samples. However, in fig. 6.2g, it was apparent that occurrence frequency patterns were generally the same in the two sample sets which indicates that the significantly larger S values in the RMT8 samples were not the result of greater numbers of chance occurrences. This is further indicated by the fact that the D values, which combine the S and E parameters, were significantly higher in the RMT8 samples.

It is important to note that the significantly higher D and S values in the RMT8 samples do not necessarily mean that the diversity of zooplankton at the surface is reduced with respect to other pelagic layers within the study region. The RMT8 tows

were oblique and so samples represent a diversity value integrated over 200 or 300m. Furthermore the amount of water sampled by the RMT8 was larger since both the mouth area and the length of tow were much greater. This would mean that the probability of encountering less abundant species is greater and so the larger S and D values are to be expected in the RMT8 samples for purely methodological reasons. It is important that these aspects are taken into account when making further comparisons between these two sample sets.

The relationship of community parameters to biogeographic and hydrographic factors

Latitudinal variation in zooplankton species richness in the south-west Atlantic has been previously considered by Boltovskoy (1982) who pooled the results from investigations by a number of workers, originally presented in Boltovskoy (1981a). The south-west Atlantic was divided into 5° latitudinal bands from the equator to 70°S. The area between 0° and 20°S was considered to be the Tropical zone, 20°S to 40°S, the Sub-Tropical zone, 40°S to 55°S, the Sub-Antarctic zone and 55°S to 70°S, the Antarctic zone. Species richness values were given for each 5° interval for Foramanifera, Chaetognatha, Ostracoda, Pterapoda, Salipidae and Appendicularia with only those species that either totally or partially inhabited the epipelagial zone being considered. A figure from Boltovskoy (1982) showing the latitudinal distribution of S values is illustrated in fig. 6.2i. Values represent the percentage of the total number of species found in the south-west Atlantic that are present in each respective zone.

The highest percentages of species were within the Sub-Tropical zone (72 to 82%). Percentages then dropped towards the equator (68 to 71%) and towards the

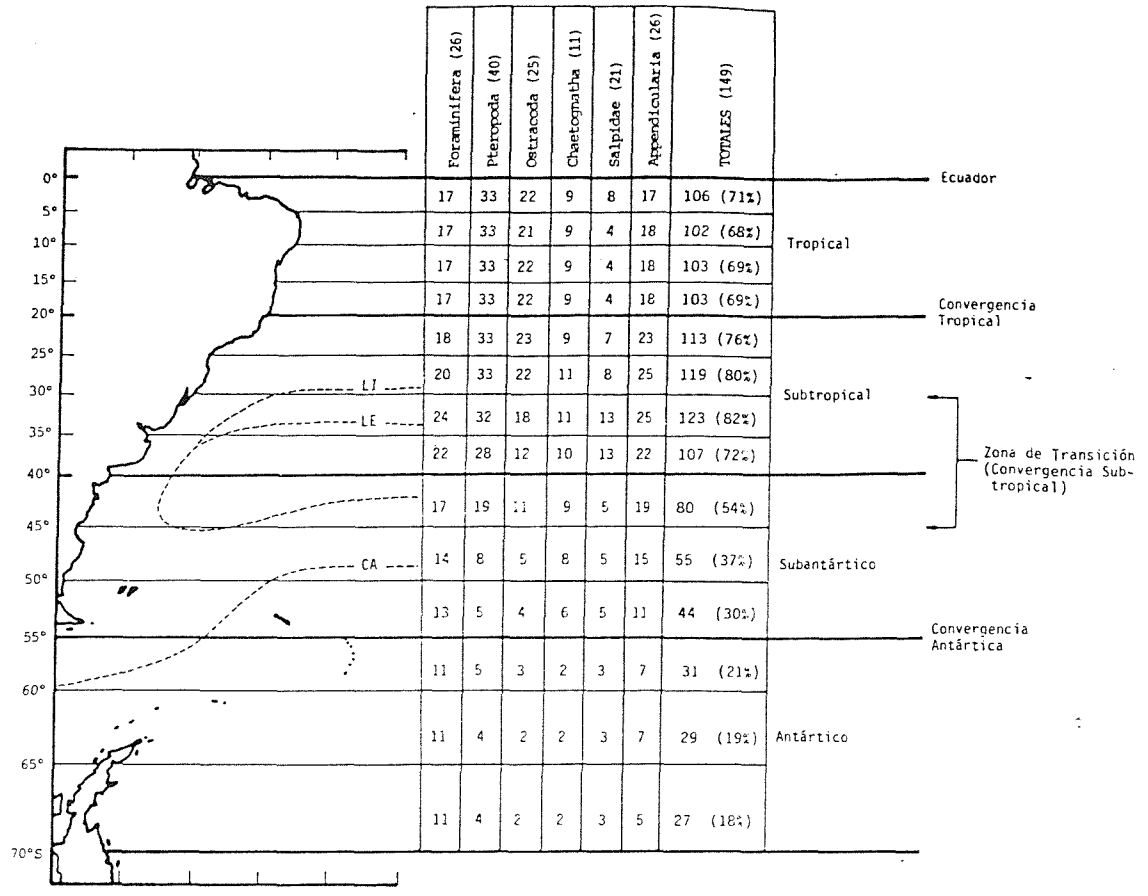


Figure 6.2i: Species richness of latitudinal bands in the south-west Atlantic (taken from Boltovskoy, 1982)

1: Basado sobre Bé y Tolderlund (1971), Océano Mundial; 2: Basado sobre McGowan (1971), Pacífico Norte; 3: De Angel (1979), Atlántico; 4: De D. Boltovskoy (1978), excluyendo las especies cosmopolitas, Atlántico Sudoccidental; 5: De Soest (1979), especies epipelágicas solamente, Océano Mundial; 6: Este trabajo.

	1	2	3	4	5	6
	Foraminifera	*Foraminifera* Radiolaria Polychaeta Copepoda *Euphausiacea* Pteropoda Heteropoda Chaetognatha	*Coccolithophorida* Foraminifera Myctophidae	*Foraminifera* Pteropoda Chaetognatha Salpidae *Appendicularia*	*Foraminifera* Medusae Siphonophorae Tomopteridae *Mysidacea* Euphausiacea Hyperiidae Phronimidae Copepoda Pteropoda Heteropoda Chaetognatha Thaliacea Appendicularia	Foraminifera Pteropoda Ostracoda Chaetognatha Salpidae Appendicularia
Polares	18%	---	1%	23%	10%	20%
Subpolares	30%	18%	12%	30%	60%	55%
Transición	67%	11%	40%	---	---	82%
Subtropicales	70%	48%	60%	88%	91%	82%
Tropicales	74%	51%	52%		84%	71%
Total de especies consideradas	27	104	109	178	586	149

Table 6.2(i): Pecentages of the total number of species found in respective global climatic zones (taken from Boltovskoy, 1982)

Antarctic, which contained the lowest percentages (18 to 21%). The sub-Antarctic values dropped incrementally from north to south, with the 40° to 45°S band having a value of 54%, 45° to 50°S, 37% and 50° to 55°S, 30%. The area between 30°S and 45°S, which spans the two southernmost latitudinal bands of the Sub-Tropical and the northernmost latitudinal band of the Sub-Antarctic zone, was defined as the Transition zone. It was in the northernmost band of the Transition zone that the highest percentage of total species considered (82%) was observed. Boltovskoy (1982) went on to determine the universality of such zonal differences in zooplankton species richness by using studies on other oceanic regions to calculate climatic zone species percentages on a global scale. Six studies were considered altogether and the results are presented in Table 6.2(i) which generally agree with those for the south-west Atlantic with highest percentages being in the sub-tropical region and values within the Transition zone being almost equivalent. Tropical region percentages were mostly lower than the sub-tropical values but in two cases they were higher. Percentage values in the sub-Antarctic region were, on the whole, considerably lower than values in the sub-tropical and tropical regions and the Antarctic percentage values were, in all cases, the lowest found in any climatic zone. Overall, Boltovskoy (1982) concluded that, within the world ocean, the species percentage values in the superficial waters of the global climatic zones oscillate around the following values: Polar - 20%, Sub-Polar - 30%, Transitional, 70-80%, Sub-Tropical, 70-80% and Tropical 75-75%.

Only 4 of the 14 latitudinal bands defined by Boltovskoy (1982) are covered by the present survey, but if the region between 35°S and 55°S in Boltovskoy's scheme is considered in isolation, there is a general agreement. In Boltovskoy (1982), percentage values drop in a consecutive fashion from north to south in the three bands that cover the

present survey area with the highest value in the north being 82%, and subsequent values being 72% and 54% respectively. The present study found that there was a significant linear relationship between S and latitude over the survey area which also agrees with Boltovskoy's findings.

Although the study of Boltovskoy (1982) covers a considerable area of the south-west Atlantic, it has the disadvantage of only being able to resolve patterns at a relatively coarse scale. This makes the study unable to consider the importance of certain finer scale physical factors that may influence diversity patterns. For instance, the fact that species percentages appear to be different between distinct biogeographic zones suggests the possibility that species richness is a trait associated with water masses because they have a profound influence on the distribution of biogeographic zones (Pickford, 1946). Consequently one may expect to see a marked change in S values across water mass boundaries. Averaging over 5° latitudinal intervals is too coarse a scale to examine the effect of water mass location on S since the difference between intervals could equally be caused by gradual change through each region rather than across water mass boundaries. The present survey, with a latitudinal resolution of 2°, as well as values for several discrete longitudes at each latitude, allows the potential influence of features such as water masses and fronts on values of S to be examined more closely.

In Section 6.2.3, it was found that neither the location of water masses nor surface thermal fronts had any significant influence on the value of S. The one factor that was found to have a significant influence was latitude. Therefore, it would appear that S changes gradually at the mesoscale level and, within water masses, higher values would be expected at low latitudes and lower values at higher latitudes. In this way, the

change in S could be seen to have fractal qualities since the change seen at the global scale is mirrored by the same pattern of change at the mesoscale level.

Within the RMT8 samples, another abiotic variable that was found to show significant relationships to community parameters was bucket surface temperature. Both Equitability (E) and Simpson's Diversity Index (D) showed significant relationships with E being negatively related to temperature such that sample stations at lower temperature had a more even distribution of abundances amongst species whereas D was positively related such that warmer stations had higher values. The significant rise in E with decreasing temperature could be the result of either (i) the number of species making significant contributions to total sample abundance being larger in absolute terms of or (ii) the absolute number of rare (ie. low abundance, occasional occurrence) species becoming less. From the analysis of general species distribution patterns, it was evident that the majority of species were rare. Furthermore, the significant relationship between S and temperature showed that numbers of species at lower temperatures was less. Therefore, compared to higher temperature stations, the drop in the number of species in lower temperature stations is probably through the number of rare rather than dominant species being less. Hence, the most likely cause of higher E values is an absolute decrease in the number of rare species rather than an absolute increase in the number of abundant species. D is essentially the product of species richness (S) and equitability (E), such that the larger the value of S and E, the larger the value of D. The fact that D increases with temperature could be the result of corresponding increases in both S and E. However, from the analyses discussed above, it is evident that whereas S increases with temperature, E decreases. The equation determining the value of D does not combine S and E in a linear fashion and so it cannot be stated that the influence of the

change in S is more important than that of the change in E on the resulting value of D. However, it can be said that with increasing temperature, the equitability does not drop to such an extent that it counteracts the effect of increasing species richness on the value of D.

Probably the most profound community parameter differences were observed between on-shelf and off-shelf environments. In the Bongo samples both displacement volume and station abundance (N) were found to be significantly higher off-shelf. In the RMT8 samples, displacement volume was found to be significantly higher off-shelf, E significantly higher on-shelf and S significantly lower than predicted on-shelf. With respect to displacement volume and N, the higher off-shelf values are in contrast to the findings of other studies that have considered on-shelf/off-shelf differences. Grice and Hart (1962) analysed samples from an on-shelf/off-shelf transect covering latitudes between 33°N and 41°N off the east coast of North America. In each of the 5 months that were covered, the largest displacement volumes and numerical abundances were found in on-shelf regions. The same was also true in waters around South Georgia (SW Atlantic, 55°S), where higher biomass values were present in the surface layers of the continental shelf during Winter (Atkinson, 1990). However, there was no significant difference found during the Summer months. Pillar (1986) found that euphausiid and copepod biomass in waters off South Africa (31°S to 56°S) was highest nearest the coast, although it was also noted that biomass was most variable in inshore areas. Most significantly, Boltovskoy (1979) considered that the Patagonian Shelf region had a higher relative biomass in the upper 100m (101-200 mg/m^3) than the adjacent "transgressive area" offshelf (51-100 mg/m^3).

For the RMT8 samples, this anomalous pattern could partly be the result of

mesopelagic species being excluded from the shelf areas, a phenomenon previously observed by Vidal and Smith (1986) in the Bering Sea and Hopkins et al. (1981) in waters off Florida. This is supported by the fact that S has a significantly lower than expected value and E a significantly higher value on-shelf. However, the same reasoning cannot be applied to Bongo samples which mostly contain strictly epipelagic zooplankton. Tremblay and Roff (1983) and Atkinson (1990) considered that one of the major factors influencing the composition of zooplankton communities on the shelf were aperiodic exchanges of water between the oceanic and shelf regions. In figs. 6.2b and 6.2d, it is apparent that displacement volume and N values are lowest to the west of the Falkland Islands. A branch of the Falkland Current flows through this region and it is possible that it may carry shelf populations northwards and off-shelf, on a seasonal basis. However, there is little hydrographic information on this region that can be used to test this hypothesis.

One way of gaining greater insight into factors behind anomalous patterns in community parameters, such as on-shelf/off-shelf differences, is through examining the species composition and distribution patterns of the zooplankton communities. With a knowledge of the general biogeographic distribution of species, the hydrographic influences on a particular region can be discerned even when other indicators such as temperature and salinity can no longer identify water origin because of the effects of diffusion (Boltovskoy, 1989). Furthermore, the analytical approach taken in this section, although useful in looking at the influences on communities at a general level, is somewhat restricted in investigating correlations with abiotic factors since it is mostly limited to examining linear relationships. Biotic relationships to environmental variables may be more far more complex and methods that allow relationships to be examined in

many dimensions are necessary to understand the structure and its major influences more fully. In the following sections, this approach to the examination of zooplankton community ecology is taken through applying certain multivariate analyses to the environmental and species data.

6.3 Multivariate Analysis - justification and description of multivariate techniques used

Walker et al.(1979) summarized 3 alternative approaches to the analysis of survey data:

1, A search for patterns amongst the biological variables with an attempt to interpret these in terms of environmental data.

2, A search for patterns of relationships between the biotic and environmental data simultaneously eg. canonical analysis (Cassie, 1972).

3, A search for patterns amongst the physical variables followed by a search for related patterns in the biotic data.

There are problems in taking any of these approaches. However, in an ecosystem where it is firstly not feasible to measure all physical variables and secondly not possible to determine which ones are of most importance, the latter two approaches appear to be least appropriate. Field et al. (1982) and Day et al. (1971) considered the first approach of "letting the species tell their story" the best general procedure to adopt. This avoids making unjustified assumptions about the relationship between biotic and environmental variables. In line with this recommendation, the present study will analyse the biotic data set to reveal emergent patterns and subsequently look for relationships with the available environmental data.

Multivariate analysis provides an objective way of summarising large sample/species matrices that can reveal any apparent structure and lead to the generation of hypotheses about the underlying causes. It is a descriptive method which represents a single stage in the stepwise analysis of communities (Atkinson, 1990) and it aims to reduce the amount of noise and redundancy in a data set whilst indicating relationships

among species and samples (Gauch, 1982). As described in Chapter 5, two of the most commonly used means of multivariate analysis are classification and ordination. Classification is a natural framework for conceptualising communities where community variation is discontinuous whilst ordination is more appropriate where community variation is continuous. It is apparent from considering the general patterns in this data set that both types of distribution patterns are exhibited by different species since many species are rare and have distribution patterns that are patchy and discontinuous, whilst other species are found to be common throughout the survey area. This presents certain problems with respect to analysing the whole data set but one possible approach is to split the data according to variation type and to carry out separate analyses. This approach was taken by Thomas (1992) who divided a data set of zooplankton distributions off the British Columbian coast into two parts, one biased towards the more ubiquitous species and one biased towards the spatially rarer and more patchy taxa. Thomas (1992) applied classification techniques to both data sets but in most situations, ordination techniques are more appropriate to data sets where species show continuous distributions.

Before multivariate analysis can be applied a number of decisions must be made as to how to divide the data set and what transformations to apply. There is the further problem of choosing between the many different kinds of algorithms involved in classification. In many cases, decisions are arbitrary but it is important that the results of the analyses are robust and not dependent on the exact transformation or algorithms used. Atkinson (1990) and Thomas (1992) experimented with different species lists, transformations and algorithms until it was decided that robust results were being obtained and this will also be the general approach taken by this study.

6.3.1 Hierarchical Classification

Hierarchical classification is a classification technique where similar samples are clustered and arranged into dendrograms to show their relationship. The first step in the procedure is to calculate the similarity coefficient between samples or species. There are a number of potential measures that can be used but it is important that the measure is robust and able to take account of joint absences. The measure used in the present analyses was the Bray-Curtis similarity coefficient (Bray and Curtis, 1957) because, as discussed by Field et al. (1982), the algorithm is particularly robust and suitable for applying to marine data. The measure has the net effect of giving more weight to abundant species (on comparing samples) than to rare ones.

The next step in the analysis is to cluster samples or species according to their similarity values. The clustering can be carried out through various techniques of which typical examples include: (1) complete linkage clustering - which joins two groups of samples/species at the greatest dissimilarity level within each group (2) single linkage clustering - which joins two groups at the minimum dissimilarity level within each group and (3) average linkage clustering - which joins two groups at the average dissimilarity level between all members of one group and all members of the other. The method applied in this analysis was average linkage clustering because it is a particularly effective at producing distinct, easily defined groupings (Clifford and Stevenson, 1975).

The samples/species are subsequently arranged into a dendrogram according to their similarity/dissimilarity values. A decision then has to be made about the similarity coefficient cut-off level that is used to define clusters. Strauss (1982) put forward a

method of determining values for separation that produced statistically significant clusters. However on applying the method to the present data it was found that, firstly, the methodological procedure was complex and very time consuming and, secondly, it resulted in large numbers of samples being left outside clusters. This second problem meant that the method was particularly unsuited to the aims of the present analysis which are to geographically define faunal zones encompassing as many stations as possible. Separation values were therefore determined through eye-fitting since this allowed greater flexibility in revealing associations between stations and between species. A number of different similarity coefficient separation levels were tested with the overall aim of finding a suitable compromise between the strength of group association and the number of clusters. In the case of the clustering of species, once a separation level had been decided upon, the significance of the resulting species cluster groups was tested for through determining whether the species within each cluster showed matching significant distributional differences between station cluster groups.

Having resolved species and station clusters, the final part of the analysis was to determine the relationship between the species clusters and the geographic regions defined by the station clusters ie. finding out where the strongest associations lie. There is no set routine that will determine this relationship and so a method was applied which calculated the Bray-Curtis similarity coefficient value of every species towards each of the defined station clusters. Theoretically, each of the species within a species cluster should show a strongest association to the same station cluster and so, in this way, the geographic affiliation of each species cluster can be defined.

6.3.2 Factor Analysis

Factor analysis is an ordination technique which is powerful in identifying groups and reducing the number of variables being studied (Johnson, 1977). It differs from another commonly used ordination technique, Principal Component Analysis (PCA) in the treatment of the variance when calculating correlations. PCA considers the variance as a whole whereas Factor Analysis splits the variance into two parts, the unique and the common variance. Only the common variance is referred to when determining the position of the factors.

Factor analysis rewrites the original data matrix into another form in which the new variables are:

i, Weighted representatives of the original set, and

ii, Uncorrelated with one another

The aim is to find mean variables that are as close as possible to the original variables. The method involves matrix algebra and the mean variable extracted is termed the principal eigenvector or factor. The relationship of each variable to the factor is called the factor loading and the squares of these loadings indicate the degree to which the factor subsumes the original variable. The success of each factor in summarising the variance in the original data matrix is measured by the eigenvalue which is the sum of the factor's squared factor loadings. Each subsequent factor has a smaller eigenvalue since there is a decreasing amount of variance to be explained. The degree to which the variance of a sample or species is represented by the analysis is measured by the communality. This is the sum of the variable's squared factor loadings. The communality is used to weight the importance of each variable in the analysis, so that the factors are pulled closer to the variables which show the strongest associations to each other. Certain factor analysis techniques make assumptions about the communality

in carrying out calculations. The technique employed in this study, Principal Component Factoring, does not make such assumptions and is more appropriate in the first stages of an investigation (Davies, 1982).

The analysis produced a number of factors towards which the original variables show different degrees of association. Variables are assigned to the factor they are most subsumed by and this is determined from their factor loadings. The loadings are between 0 and 1 and a variable is considered to be strongly associated to a factor if its loading is in excess of 0.7. Since each subsequent factor accounts for a diminishing amount of variance a cut off value must be assigned below which factors are considered insignificant. This can be done subjectively or by a mathematical method. Cattell's Scree test was employed in this analysis following the recommendation of Angel and Fasham (1975).

One of the problems of Factor analysis is that the factors frequently do not account for a high proportion of the total variance. As a result, an incomplete picture of species or sample associations is obtained. A method used to highlight associations is axis rotation. This process moves the data set as close as possible to a hypothetical, ideal factor structure. There are a number of rotation methods that can be applied. The method used in this analysis was Varimax rotation. It is to be noted that factors do not necessarily remain in order of importance as a result of rotation.

Before both classification and ordination analyses can be carried out, it is necessary to transform the data because the abundances of some species are often orders of magnitude greater than others and so swamp the analyses. There are a number of transformations that are commonly employed including $\ln(1+x)$ which was used by Angel and Fasham (1975) and $\sqrt{\sqrt{x}}$ used by Field et al. (1982). Both these

transformations were applied to the data sets used in this analysis to compare their effects and assess the robustness of factor analysis procedures. However, it was arbitrarily decided to use ln(1+x) for the final calculations.

Another important prior consideration is the degree to which the data set must be restricted so that it only includes "continuously" distributed species. If the data is not adequately continuous, the results would not be robust and repeatable. Although easily separable at their extremes, there is a continuum between species that show continuous and discontinuous distributions and it is difficult to separate the two types without imposing a subjective criteria. One effective way of testing whether the restriction is appropriate is to determine the robustness of a number of data sets ranging in their lower frequency of occurrence limits. Where the use of different transformations on the restricted data set has no effect on the results, the restriction can be assumed to be adequate for producing robust factor analysis patterns.

6.3.3 Relationship of multivariate groups to abiotic factors

Having discerned the biotic structure of the data set and let the species "tell their story", as advocated by Day et al (1971) and Field et al. (1982), the next stage is to try and interpret these patterns in terms of environmental data. The approach taken by Field et al. (1982) was to relate environmental variables to the derived biotic structure through graphical means, one variable at a time. Such an approach is somewhat restrictive and does not allow certain aspects to be explored such as (1) how well community structure is explained by the full set of environmental variables measured or (2) which variables are redundant in the sense of failing to strengthen the "explanation" of biotic patterns once certain other variables have been taken into account. Certain multivariate methods

such as Canonical Correlation (eg Mardia et al., 1979) or the variant known as Redundancy Analysis (Rao, 1964) try to relate multiple environmental variables to the biotic structure through assuming that sample dissimilarities are well represented by Euclidean distance for both environmental and species data and that the abundances are linearly related to environmental gradients. Another technique, Canonical Correspondence Analysis (Jongman et al., 1987), makes the assumption that the species abundances have unimodal responses across measured environmental gradients. Making such linear or monotonic assumptions is unjustified when relating biotic and abiotic variables because the types of relationships between species distributions and environmental factors may range considerably within a data set. For instance, whereas some species may be related linearly to an environmental gradient within a particular data set, other species may be related non-linearly but monotonically or even non-linearly and non-monotonically over the ranges of one or several abiotic variables.

In response to these problems, Clarke and Ainsworth (1993) put forward a multivariate technique that allowed multiple abiotic variables to be related to the biotic structure of a sample set without making any *a priori* assumptions about the nature of the relationship between them. The method essentially compares separate sample ordinations from biotic and abiotic variables and then chooses that subset of environmental variables which provides a good match between the two configurations. The analysis works on the premise that pairs of samples which are similar in terms of a suite of physico-chemical variables would be expected to have similar species composition provided the relevant variables determining community structure have been included in the analysis. An ordination of these abiotic variables, representing the mutual environmental similarities among samples, should closely resemble the ordination or

classification of samples based on the biota. Selecting different combinations of the full environmental variable set should then allow an optimal match of the separate biotic and abiotic ordinations to be determined. The omission of key determinants will degrade the match, as will the inclusion of environmental variables that differ markedly between samples but have no effect on community composition.

In determining among-sample similarities in the biotic and abiotic variables separately, different multivariate techniques can be applied to the biotic or abiotic data, so that the method most appropriate to each is used. As discussed earlier, biotic data sets normally contain a large number of 0's because many of the species have restricted distributions and so the most appropriate analytical technique applied to such data sets is classification involving similarity coefficients such as the Bray-Curtis measure. Environmental data, by contrast, is continuous and more normally distributed and so it is analysed most appropriately by ordination techniques. The ordination techniques applied by Clarke and Ainsworth (1993) measured among-sample similarities through Euclidean distance.

Once the among-sample similarities have been calculated, it is then necessary to determine the best method to link the two data sets without making any unjustifiable assumptions about the underlying nature of the relationship between the biotic and abiotic structure. Clarke and Ainsworth (1993) believed that the similarity matrices produced by the among-sample analyses were the fundamental constructs, representing all that is known about sample relationships. Constructing the biotic similarity matrix is necessary only once but, in order that all possible combinations of abiotic variables can be related to the biotic structure, the abiotic matrix must be constructed a number of times at every level of complexity (ie. variables taken singly, 2 at a time, 3 at a time

etc.)

After deriving the similarity matrices, linking the biotic to the abiotic data was considered to be best achieved by determining the rank correlations between all elements of the two matrices. One problem was that there were a large number of terms that involved distant pairs of samples[1], and so "weighted" coefficient was applied that down-weighted larger values so that the within-group coefficients were relatively more important. This weighted rank correlation formulation, algebraically derived by Clarke and Ainsworth (1993), was termed "harmonic rank correlation".

The end result of the analysis is to produce a list of the rank correlation coefficients of all combinations of environmental variables, so that the combinations with the highest values, ie. the greatest explanatory power, can be picked out. As emphasised by Clarke and Ainsworth (1993) the method should be thought of as exploratory and there is a great deal of further study that is necessary to determine what undetected underlying assumptions are being made and under what circumstances the results are misleading. From the practical point of view, it must be noted that although the technique does pick out the combinations of environmental variables with the greatest explanatory powers from those that have been measured, it does not preclude the possibility that better explanations could be obtained through including other environmental parameters which were not measured. Therefore, the best explanation is only a relative one and it is by no means definitive in finding the most important combination of abiotic variables that affect biotic structure. Nevertheless, in terms of

[1] This is because in, for instance, 15 samples that are strongly clustered into 5 groups of 3, there are only 15 within-group similarities but 90 between group similarities. Since the primary purpose of the analysis is to search for the abiotic variables which discriminate these same 5 clusters, the precise disposition of the groups in relation to each other is of less significance but they would tend to dominate the unweighted rank correlation coefficient

analysing a set amount of biotic and abiotic data, the analytical approach is probably the most objective and comprehensive yet devised and will be adopted by this investigation.

6.4 Multivariate analysis of RMT8 1990

Sampling was carried out on arrival at a sampling station and so the time of day each sample was taken varied throughout the sampling grid. Community composition may vary with the time of day for a number of reasons such as diel vertical migration patterns (Angel, 1986), different visual avoidance capabilities with the changing ambient light levels (Angel, 1977) and swarming (Mauchline, 1980). It is important therefore that such day/night factors are accomodated for prior to multivariate analyses so they do not confound any underlying geographic patterns. This was carried out through splitting day-time samples (06.00-19.00) and night-time samples (19.00-06.00) and then applying either a Mann-Whitney Rank Sum test for non-normal data or a *t*-test for normal data to determine whether there were significant differences between the two groups. It was found that 16 species had significantly greater abundances in night-time than in day-time catches (Table 6.4(i)), those of note being *Thysanoessa gregaria*, *Nematoscelis megalops*, most of the decapods and many myctophiid fish. These species were subsequently excluded from further analysis.

6.4.1 Hierarchical classification of RMT8 1990

a, Station clusters

Hierarchical classification techniques were applied to the day/night restricted RMT8 data set to highlight geographic patterns in the distributions of abundances of common species and discontinuities in occurrences of rarer species. The data set was transformed using $\ln(1+x)$ and clustered using the Bray-Curtis similarity

RMT 1990	Largest no.	Bongo 1990	Largest no.
Nematoscelis megalops	Night	*Euphausia lucens* (adult)	Night
Thysanoessa gregaria	Night	*E. vallentini* (adult)	Night
Sergestes henseni	Night	*Vibilia* spp.	Night
S. diapontis	Night	*Primno macropa*	Night
S. arcticus	Night	*Themisto gaudichaudii* (larvae)	Day
Gennadas gilchristi	Night		
G. tinayrei	Night		
Systellapsis debilis	Night		
Stegacephalidae	Night		
Lysianissadae	Night		
Gymnoscopelus braueri	Night		
Bathylagus spp.	Night		
Lepidophanes guentheri	Night		
Centroscopelus warmingii	Night		
Diaphus meadi	Night		
Protomyctophum tenisoni	Night		

Table 6.4(i): Species showing significant differences in abundance between day and night samples in 1990 RMT8 and 1990 Bongo data sets

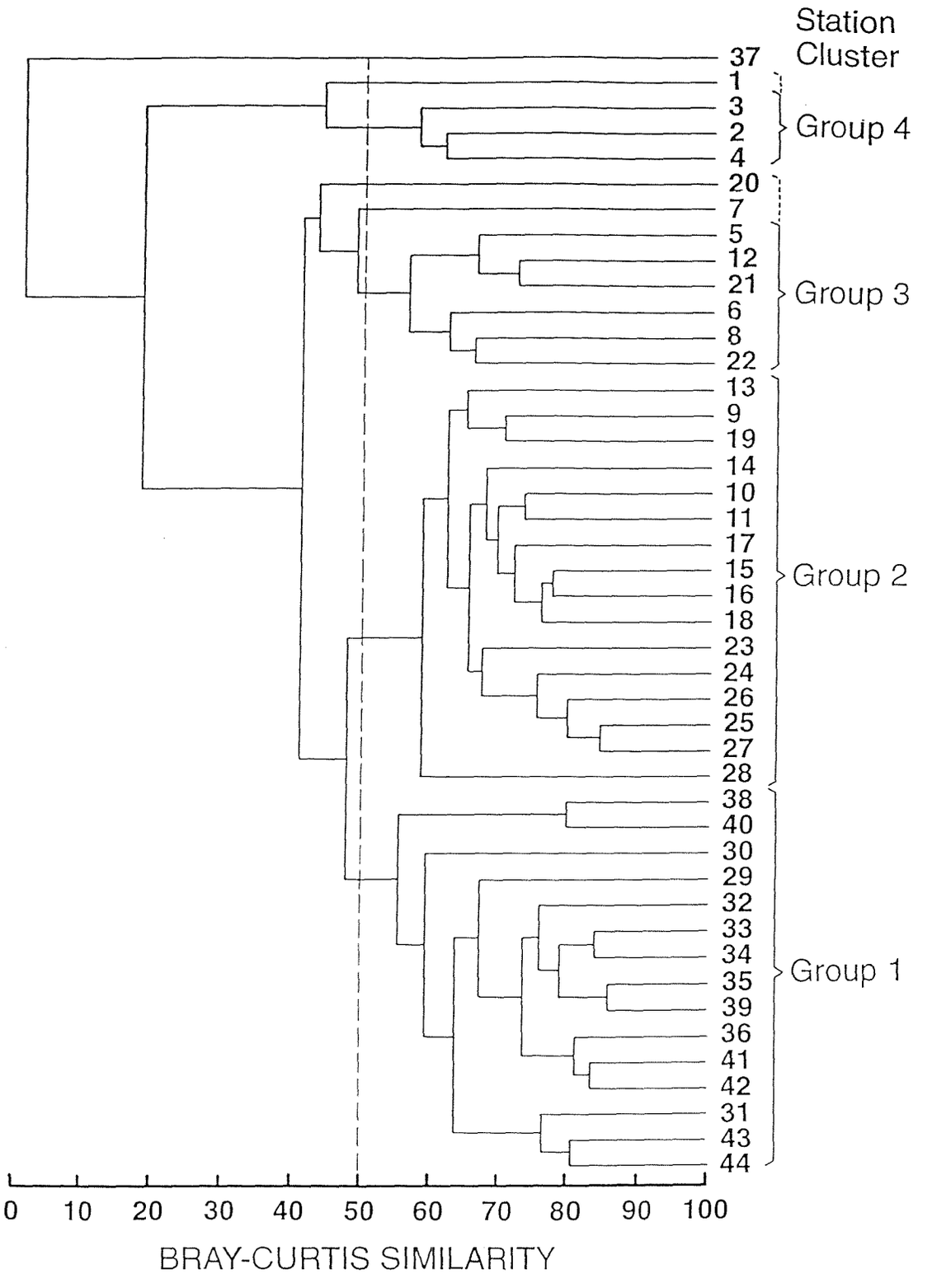


Figure 6.4a: Dendrogram showing 1990 RMT8 station groups

coefficient and average linkage (fig. 6.4a). Experimental separations of groups at a number of similarity levels were carried out with the aim of revealing associations between stations as fully as possible. Separation at the 50% level of similarity was eventually decided upon since it was a suitable compromise between the strength of group association and the number of clusters. The geographic distribution of the resulting groups is illustrated in fig. 6.4b, with the matrix of between-group dissimilarities presented in Table 6.4(ii).

b, Species clusters

A second classification, this time involving the clustering of species, was carried out in order to determine the relationship between species and station clusters. Unlike the data set used to determine the station groups, the data set used in the analysis was restricted to species that occurred at more than 3 stations. The purpose of this analysis was to define groups of species that co-occurred and this could not be sufficiently ascertained in species that were found at less than 3 stations. Values were subsequently transformed using $\ln(1+x)$ and clustered as above (fig. 6.4c). Separation at the 50% level of similarity was again decided upon and this gave 9 groups containing 2 or more species. The validity of each species cluster was then determined through testing each species for significant differences in abundance between station groups. Rare species with non-normal distributions were tested using a Kuskall-Wallis test, whilst a Dunn's test was applied to common, normally distributed species. A species cluster was accepted only if all of its species showed significant differences between 3 of the 4 station groups. Of the 9 species clusters, 8 passed this criterion. Finally, the strength of the association between the station groups and each of the species within the 8 species clusters was

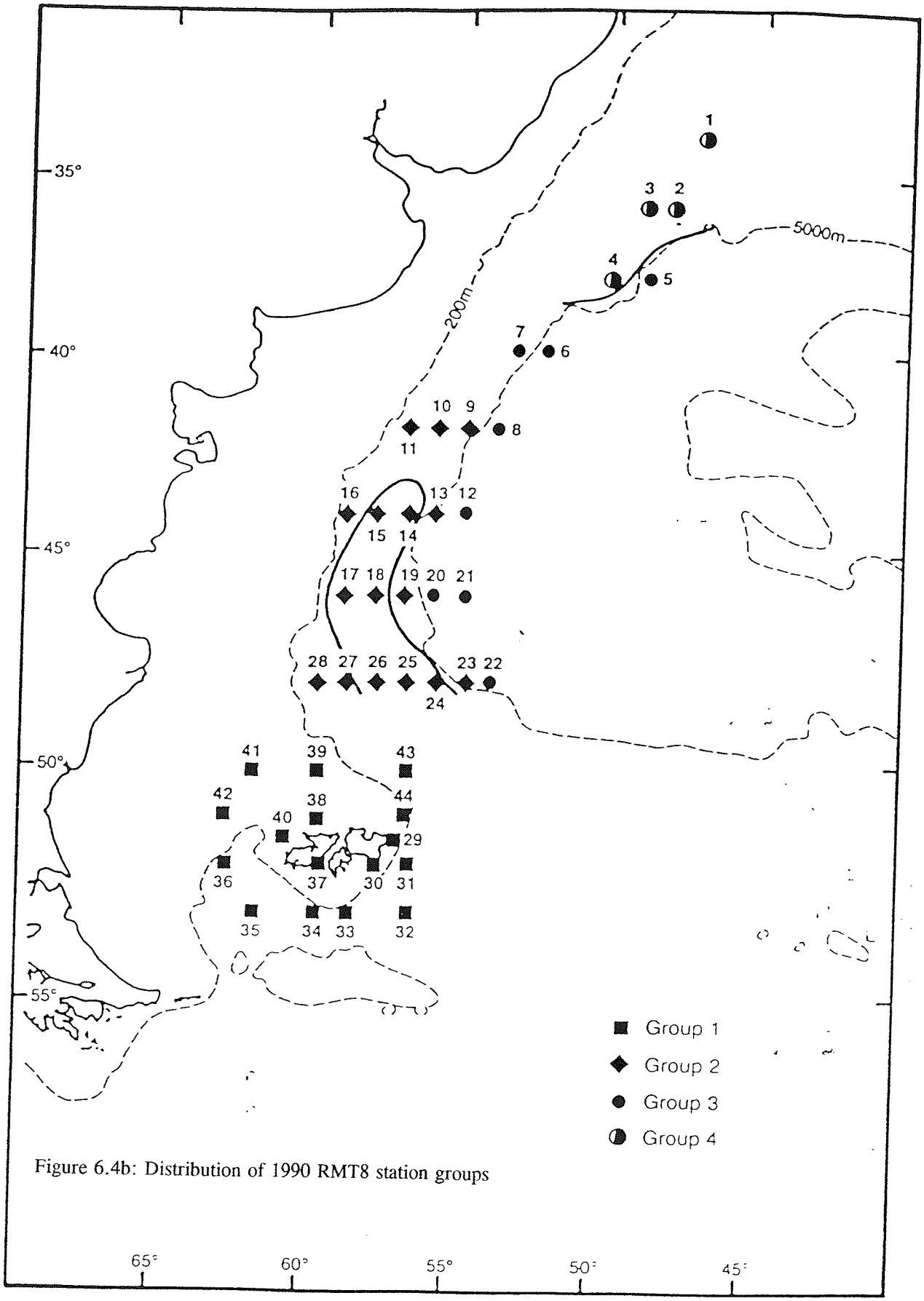


Figure 6.4b: Distribution of 1990 RMT8 station groups

	Group 1	Group 2	Group 3	Group 4
Group 1	0			
Group 2	52.23	0		
Group 3	64.90	54.04	0	
Group 4	93.35	90.17	79.07	0

Table 6.4(ii): Average coefficients of dissimilarity between all members of each station group for RMT8 data set using the Bray-Curtis similarity coefficient.

Spp. cluster 1	St. clust	Spp. cluster 2	St. clust
Protomyctophum bolini *Primno macropa* *Salpa thompsoni* (aggregate) *Salpa thompsoni* (solitary) *Stylocheiron maximum* *Euphausia similis* *E. triacantha*	2	*Sagitta gazellae* *Euphausia lucens* *E. vallentini* *Themisto gaudichaudii*	1
Spp. cluster 3		Spp. cluster 4	
Diaphus hudsoni *Argyropelecus hemigymnus* *Lampanyctus pulsillus*	3	*Vinciguerria powerie* *Scopelosaurus spp.* *Iasis zonaria* *Lampanyctus pulsillus* *Sio nordenskjoldii* *Scina spp.*	4
Spp. cluster 5		Spp. cluster 6	
Hemityphis tenuimanus *Brachyscelus crusculum* *Phrosina semilunata* *Platyscelus armatus* *Streetsia challengeri* *Phronima bucephalata* *Thysanopoda monocantha* *Argyropelecus aculeatus* *Valencienellus tripunctulatus*	4	*Nematobranchion flexipes* *Euphausia spinifera* *E. recurva* *Stylocheiron abbreviatum* *Phronima sedentaria*	4
Spp. cluster 7		Spp. cluster 8	
Sagitta planctonis *S. hexaptera* *Hippopodus hippopus* *Chelophyes appendiculata*	3/4	*Anguilliformes larvae* *Paraphronima gracilis*	4

Table 6.4(iii): Species found within each species cluster and the station cluster to which they show the strongest association

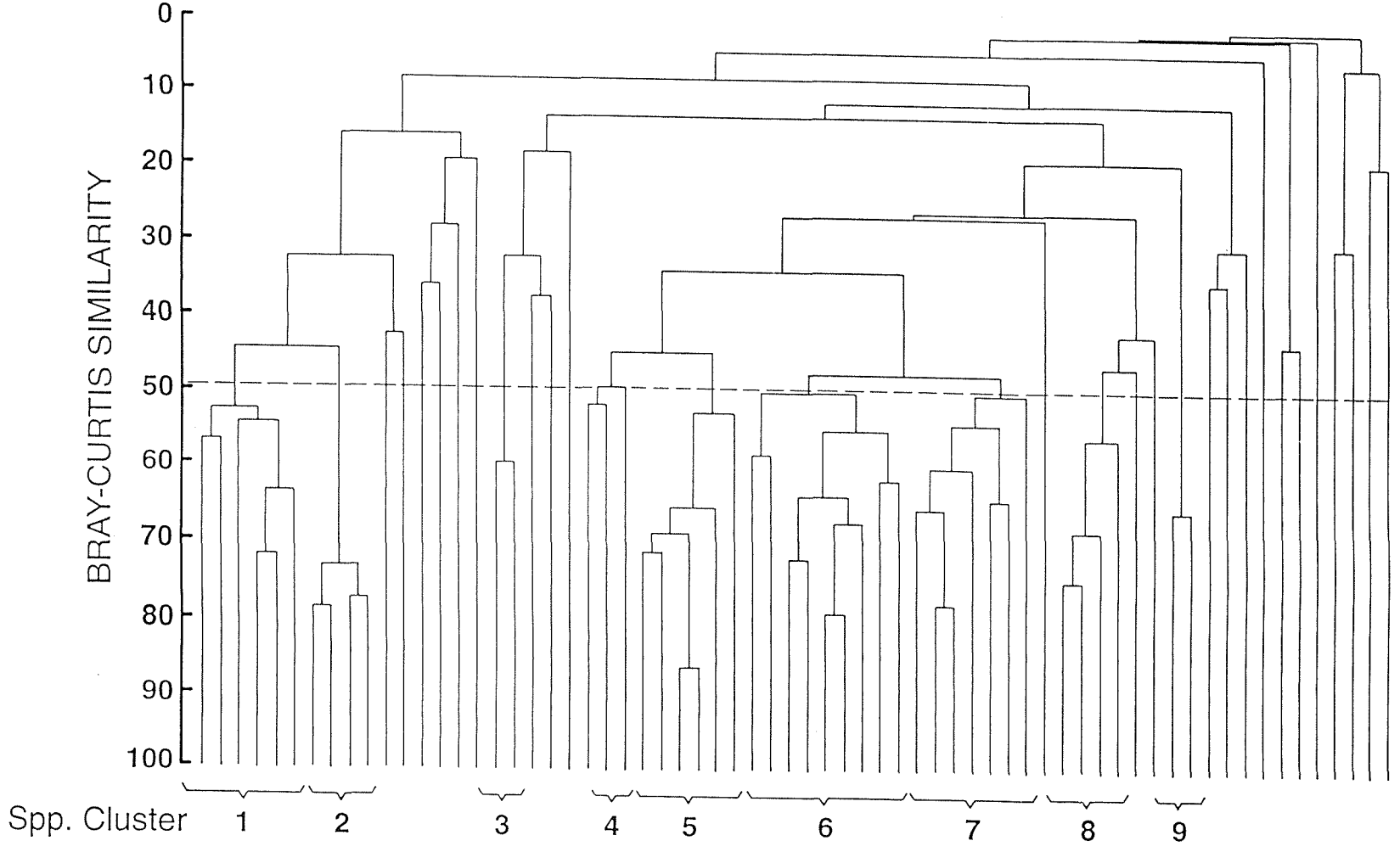


Figure 6.4c: Dendrogram showing 1990 RMT8 species clusters

	Total spp. present	No. spp. with strongest fidelity	Simpson Diversity Index (D)	Equitability Index (E)
Group 1	19	14	2.302	0.121
Group 2	67	24	8.983	0.134
Group 3	103	47	8.036	0.078
Group 4	104	82	4.060	0.039

Table 6.4(iv): Community collective attributes of the groups obtained from hierarchical clustering

calculated using the Bray-Curtis similarity coefficient. Table 6.4(iii) shows the species in each of the 8 species clusters and the station groups to which they show strongest association.

Diversity (D) and Equitability (E) was calculated using the Simpson Diversity Index described in Section 6.2. Species fidelity was determined from calculating the mean abundance of every species in each station group. A species was considered to have strongest fidelity to the station group where its mean abundance was greatest. The number of species that occurred at least once within a station group was also determined and presented along with D, E and strongest fidelity in Table 6.4(iv).

6.4.2 Factor analysis of RMT8 1990

Factor analysis was applied to a number of data sets, containing different numbers of species, and their *robustness* was tested for through applying two different types of transformations and checking for consistency in the two sets of results. Three different data sets were used containing 41, 21 and 20 taxa respectively and each was transformed using either $\ln(1+x)$ or $\sqrt{\sqrt{x}}$.

The analysis of the first data containing 41 species that occurred at at least 3 stations least, produced 12 factors using both the log and the double-root transformations. Species were considered to be associated with a factor if their factor loadings were greater than 0.7 and it was evident that there were considerable differences between the results of the log and double-root transformed data sets. It was concluded that the data set contained species that had distributions that were too discontinuous to be considered by Factor Analysis in a robust fahion.

The species ommitted from the second data set were those with frequencies of occurrence of less than 20%. The analysis produced 6 factors in both the log and the double-root transform data sets. The groupings in the two data sets showed that there was a considerable resemblance between them although there were minor differences in the size of the factor loadings in some of the taxa showing split groupings[1], and in the affiliation of one species, *Euphausia vallentini*, which was grouped with *Euphausia lucens* and *Thysanoessa gregaria* in the double-root transformation results, but with *Themisto gaudichaudii* in the log transformation results.

Analysis of the third data set containing 20 taxa was carried out to investigate whether the groupings were stable and not dependent on the exact species list. The species that was ommitted from the data set was abundant and widespread since these qualities have the greatest effect on factor loadings. The analysis found that the resulting groupings were exactly the same as the data set which included the species and only very small differences were observed in the factor loadings. It was therefore concluded that the data set which excluded any species with frequencies of occurrence of less than 20% was sufficiently continuous to be analysed by Principal Component Factoring.

Following the factor analysis, Cattell's Scree test was applied and this distinguished 6 factors that had eigenvalues greater than unity. Together, these factors accounted for 73.2% of the variance. The factor matrix was subsequently rotated using the Varimax rotation method in order to improve the interpretation of factors. Since the eigenvalues may be affected by rotation, it was necessary to

[1] Those species that had strong affiliations to more than one factor group

compare the factor matrices before and after rotation to check that the factors had not changed in order of importance. The lists of species associated with each factor were comparable and it was evident that the order of importance had remained the same after rotation. Table 6.4(v) lists the analysed species beneath the factor to which they had the highest loading.

The geographical integrity of these factor groups was determined from their Factor scores using the following equation from Harman (1967).

$$F_{qi} = \sum_{j=1}^{n} a_{jq} z_{ji} / \lambda_q$$

Where n is the number of taxa, a_{jq} is the factor loading of the jth species on the qth factor, λ_q is the eigenvalue for the qth factor and z_{ji} is the double-root transformation of the abundance of taxon j in haul i.

A high factor score means that the factor group is strongly associated with that station. Factor scores for the first four factors are shown in fig. 6.4d.

Factor 1	Factor 2	Factor 3
Hippopodus hippopus *Chelophyes appendiculata* *Eukrohnia hamata* *Sagitta hexaptera* *S. planctonis* *Argyropelecus hemigymnus*	*Primno macropa* *Euphausia triacantha* *Sagitta gazellae* *Protomyctophum bolini* *(Stylocheiron maximum)* *(Themisto gaudichaudii)*	*Euphausia longirostris* *E. similis* *Rosacea plicata* *(Stylocheiron maximum)*
Factor 4	Factor 5	Factor 6
Euphausia vallentini *E. lucens* *(Themisto gaudichaudii)*	*Salpa thompsoni* (aggregate) *S. thompsoni* (solitary) *Gymnoscopelus bolini*	*Gennadus valens*

Table 6.4(v): Species occurring at more than 20% of stations grouped under the most strongly associated factors (parenthesis indicate joint affiliation to two factors)

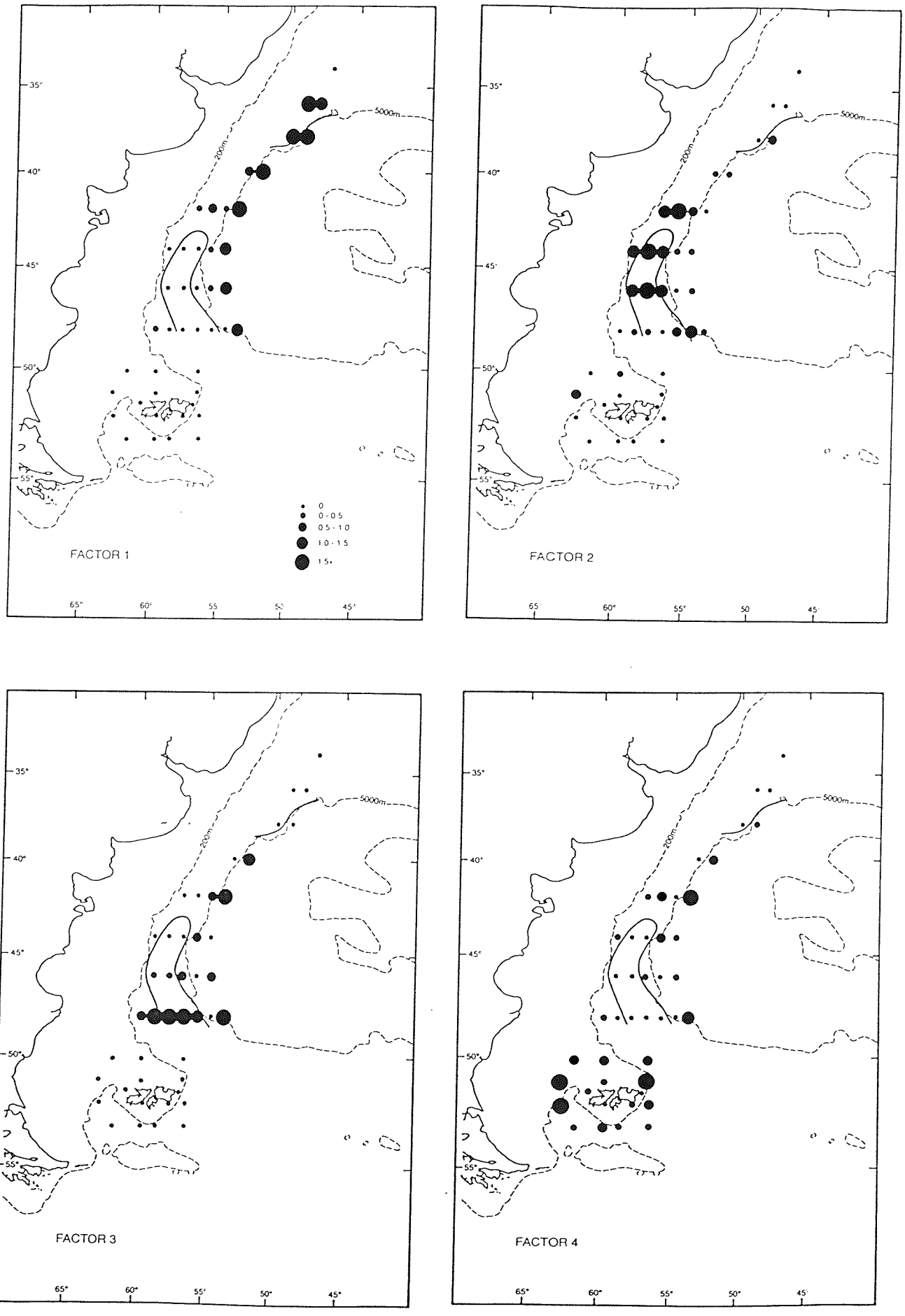


Figure 6.4d: Distribution of factor scores for the first four factors from the RMT8 analysis

6.4.3 Relationship of multivariate groups to abiotic factors

The method of relating abiotic to biotic variables developed by Clarke and Ainsworth (1993) initially requires similarity matrices for the biotic and abiotic data sets to be calculated. The biotic similarity matrix was determined using the Bray-Curtis similarity measure as part of the hierarchical classification procedure described in Section 6.4.1. In terms of the abiotic variables, a total of 7 were included in the analysis, which were:

(1) Depth of the water at each sampling station

(2) Spot surface temperature values (bucket surface temperature) at each station

(3) The latitude of each station

(4) The distance of each station from the nearest land

(5) The distance of each station from the 200m isobath, which essentially is a measure of the distance of each station from the shelf (on-shelf stations are given minus values measuring their distance within the 200m isobath).

(6) The water mass region in which each station was located. The water masses were coded such that those stations within the STZ were given values of 4, those within the SAZ, 3 and those within the PFZ, 2. One apparent problem with the system was that a significant number of species were located on the Falkland Shelf which could not strictly be considered to be a water mass. To include it as a separate water mass code (ie. 1) would possibly confound the analysis because, despite the fact that the physical structure of shelf waters is markedly different and comparable to differences observed between the water masses, any biotic differences may also be a result of shelf-effects, as discussed in Section 6.2. For

this reason, it was decided to exclude all Falkland shelf stations from the analysis.

(7) The surface thermal zone in which each station was located. As described in Section 6.6.3, the region could be divided into distinct zones according the surface temperature patterns revealed by satellite images and spot surface temperature values. There were 3 distinct zones delimited by sharp transitions in surface temperature, the first being north of the 13°C thermocline (coded as 4), the second between 10°C and 13°C (coded as 3) and the third below 10°C (coded as 2). Falkland stations were not included in the analysis for the reasons given in (6) and because satellite images did not cover the Falkland shelf region.

A Euclidean distance similarity measure was applied to all combinations of variables at every level of complexity and the resulting matrices were related individually to the biotic matrix and their rank correlation coefficients determined from the harmonic rank correlation algorithm derived by Clarke and Ainsworth (1993). The resulting list of correlation values showed that maximum correlation to the biotic similarity matrix was achieved by a combination of water mass and latitude ($r=0.561$). The other environmental variables degraded the match between abiotic factors and the biotic structure and so they can be assumed not to be key determinants of community composition of RMT8 samples. Furthermore, it must be noted that the optimal match of the biotic structure was with the combination of water mass and latitude and not with either of these variables taken independently.

6.4.4 Discussion of multivariate analysis of RMT8 1990 samples

When interpreting these results, one of the first considerations must be the

scale of resolution achieved by each multivariate analysis. Hierarchical classification divided stations into cluster groups according to degrees of association and imaging these patterns provided a resolution of around 1000 km. Under the definitions of scale given by Haury et al. (1978), such patterns would be termed macroscale and would show a moderate contrast in species composition as well as highs and lows in species abundance. This scale would be appropriate for considering the affinity of faunal groups to water masses. Imaging the patterns from Factor analysis gave a finer resolution (between 500 and 1000 km) because, in addition to simply categorising associated stations, the strength of a factor group's relationship to a station was resolved. The potential of resolution of this analysis was approximately mesoscale (Haury et al., 1978), and would be able to define populations of faunal groups associated to features such as eddies and boundary currents.

It can be seen that, the cluster groups produced by Hierarchical Classification in fig. 6.4d are geographically distinct and define four zones within the study area. Station group 1 occupies the shelf stations around the Falkland islands, group 2, stations from the edge of the Patagonian shelf to the outer slope, group 3, the most oceanic stations along the 5000 m isobath and group 4, the most northern stations. Environmental analyses showed that, with respect to the abiotic factors considered, community composition was most greatly influenced by a combination of water mass location and latitude. As can be seen in fig. 6.4b, there is a particularly clear relationship between geographic ranges of these faunal zones and the position of the water masses. Group 2 stations are centred around the PFZ, group 3 stations dominate the eastern SAZ stations and group 4 stations exclusively

occupy the STZ. It is important to note however that station group 2 is not limited to the PFZ but also occupies those stations immediately outside the bounds of the water mass. Surface temperatures of the SAZ are considerably lower in the region immediately adjacent to the PFZ than in the area further east and so it is probable that there is mixing across the Sub-Antarctic Front which affects the community composition of SAZ stations close to the PFZ.

The dissimilarity matrix (Table 6.4(ii)) shows that station group 1, found on the Falkland shelf, is most closely associated to station group 2, the PFZ cluster. The species most strongly associated to station group 1, although predominantly neritic, have widespread distributions throughout the survey area. Two of the species, the chaetognath, *Sagitta gazellae* and the hyperiid, *Themisto gaudichaudii* are considered to be most strongly associated with colder, polar waters (David, 1958; Bowman, 1960; Hurley, 1969). This would suggest that PFZ water has a strong influence on the fauna of the Falkland shelf.

Among the species showing strong affinities to station group 2 stations are the euphausiid species, *Euphausia triacantha*, *E.similis* and *Stylocheiron maximum*. The latter two species are not widely noted as being predominantly polar species, but are nevertheless considered to be widespread in the area. (Dilwyn-John, 1936, Antezana & Brinton, 1981, Mauchline 1980). *E. triacantha* and the other species found in this species cluster, *Primno macropa*, *Salpa thompsoni* and *Protomyctophum bolini* are all characteristic of polar regions (Baker, 1959; Barnard, 1932; Foxton, 1966; Smith & Heemstra, 1986) and are good indicator species of the PFZ.

There are two species clusters showing association to station group 3. The

first group contains 3 mesopelagic fish, *Diaphus hudsoni*, *Argyropelecus hemigymnus* and *Lampanyctus pulsillus*. The latter species are mainly sub-tropical species, whilst *D.hudsoni* is commonly found between the sub-tropical convergence and 50°S (Smith & Heemstra, 1986). The second species cluster, containing *Sagitta hexaptera*, *S.planctonis*, *Hippopodus hippopus* and *Chelophyes appendiculata* shows a joint affiliation to station group 4. This species group contains mostly sub-tropical species. Records of the chaetognath *S.hexaptera* are almost exclusively from the sub-tropical and tropical regions (Alvarino, 1969, Boltovskoy, 1981b) and although *S.planctonis* was reported as being Antarctic/sub-Antarctic zones by Boltovskoy, (1975), following the work of Alvarino (1969), this evaluation has since been considered to be the result of misidentification and the true origins are sub-tropical (Pierrot-Bults, pers. comm.). *Hippopodus hippopus* and *Chelophyes appendiculata* are oceanic siphonophora and have been noted by Alvarino (1981) to have distributions between the equator and 46°S, although there are records from as far south as 50°S. Surface temperatures in this station group are notably high for sub-Antarctic water which may be explained by the fact that the group occupies the path of the Falkland Current return. These waters have been mixed and warmed as a result of encountering the sub-Tropical waters of the Brazil Current which may increase the sub-tropical species' ability to tolerate latitudes that are further south than their normal range. It must also be noted that many of the species associated to this station group are mesopelagic and may occupy different water masses below the sub-Antarctic surface water.

Station group 4 is the most distant group from each of the other three station groups in the factor matrix, signifying that its fauna is distinctly different

from that occupying the rest of the survey area. Table 6.4(iv) shows that, although it has only one more species found within its zone compared to station group 3, it has almost double the number of species with strongest fidelity to the station group. Furthermore, 5 of the 8 species clusters show an association to this station group. Nevertheless, the values for D and E calculated from the Simpson Diversity Index were lower than respective values for station groups 2 and 3. This was probably the result of most species in this region being rare and station abundance being dominated by a small number of species, especially the chaetognath *Sagitta gazellae* which was highly abundant throughout most of the survey area and the siphonophore *Chelophyes appendiculata*, which exhibited an extremely high abundance within the Group 4 region only. The greatest contribution to the numbers of strongly associated species was made by hyperiid amphipod taxa, of which, from a total of 26 species found throughout the survey area, 22 are present and 9 are found exclusively within group 4 stations.

The high species richness and strong species fidelity of group 4 are characteristic features of central gyre communities (McGowan, 1971, 1974). Nevertheless, a study of wider scope which includes a more thorough consideration of the hydrography of the region would be necessary to verify that the gyre features of group 4 result from the influence of the South Atlantic Central Gyre. In station groups 2 and 3, although the actual numbers of species may be quite high, their fidelity to those regions is considerably lower than in station group 4. These station groups are best considered as Transition zones in which most of the species found together have their distribution centres elsewhere. Boltovskoy (1986) estimated that expatriate species make up 70-90% of the total inventory of the

Transition zone in the south-west Atlantic. Station group 1, the Falkland shelf cluster, contains by far the least number of species, which is in keeping with most other studies comparing oceanic and neritic communities (eg. Tremblay & Roff, 1983, Sabates, 1989, Atkinson & Peck, 1990). It is notable that most of the species associated with this station group were also relatively common at many off-shelf stations and it would therefore seem that the shelf community differs from the more oceanic groups only in the fact that many species have been excluded.

There is a considerable degree of overlap between the plots obtained from factor analysis and the results of the hierarchical classification analysis. Nevertheless, in being able to reveal the strength of a factor group's association to stations, factor analysis has given an extra degree of resolution and has revealed some interesting details. For instance, the species list and distribution of factor 1 strongly complies with that of station group 4 although it is interesting to note that the strongest associations are in the north and they weaken southwards. This would indeed fit with the hypothesis that this region is dominated by a sub-tropical fauna which is carried beyond its normal range by the warm Falkland Current return or mesoscale features such as warm core eddies. Factors 2 and 3 comply with station group 2, but show a further separation between species found to be prominent in the northern most projection of the PFZ and those predominantly limited to the 48°S transect. As yet there is insufficient information to provide any possible environmental reason for this pattern but it cannot be ruled out that it may be an anomaly caused by the day/night regime of the survey.

Of particular interest is the distribution of factor 4, which would otherwise comply with station group 1 but for a strong distribution in stations immediately

north of the PFZ. *Euphausia vallentini* and *Euphausia lucens* are neritic species common to the Falkland and Patagonian shelves and it is possible that their occurrence so far off-shelf is a result of being transported eastward by the Falkland Current as it encounters the Brazil Current. Curtolo et al. (1990) suggested that these species of euphausiids were transported along the shelf by the Falkland current, although whether they make up the same population as those found north of the PFZ needs to be determined.

6.5 Multivariate analysis of Bongo 1990

Hierarchical classification was carried out on the Bongo 1990 full data set in order that comparisons of the geographic distribution of station groups and the affiliation of species clusters could be made to those obtained from the RMT8 samples. Factor analysis was not applied to this data since it was considered that its results were particularly susceptible to confounding factors associated with different sampling methods and so would not be of value in a comparative context. The comparison between RMT8 and Bongo samples were considered to be best achieved through looking for distinct discontinuities between community composition and distribution for which only hierarchical classification techniques were appropriate.

6.5.1 Hierarchical classification of 1990 Bongo samples

The hierarchical classification analysis of the Bongo 1990 data set was the same as that applied to the RMT8 data set which was described in Section 6.4.1. As in the RMT8 analysis, it was also necessary to exclude those species that showed significant day/night differences in abundance before carrying out the multivariate procedures. Mann-Whitney and *t*-tests revealed that 5 species showed significant differences between day and night samples (Table 6.4(i)) and these were excluded from the data set which was subsequently transformed using ln(1+x). Stations were then clustered using the Bray-Curtis similarity measure and the resulting dendrogram is presented in fig. 6.5a. A number of separation values were experimented with and the 39% level of association was decided upon since separation at higher similarity levels produced too many groups comprising of just 1 or 2 stations. This separation level placed 90% of the stations into

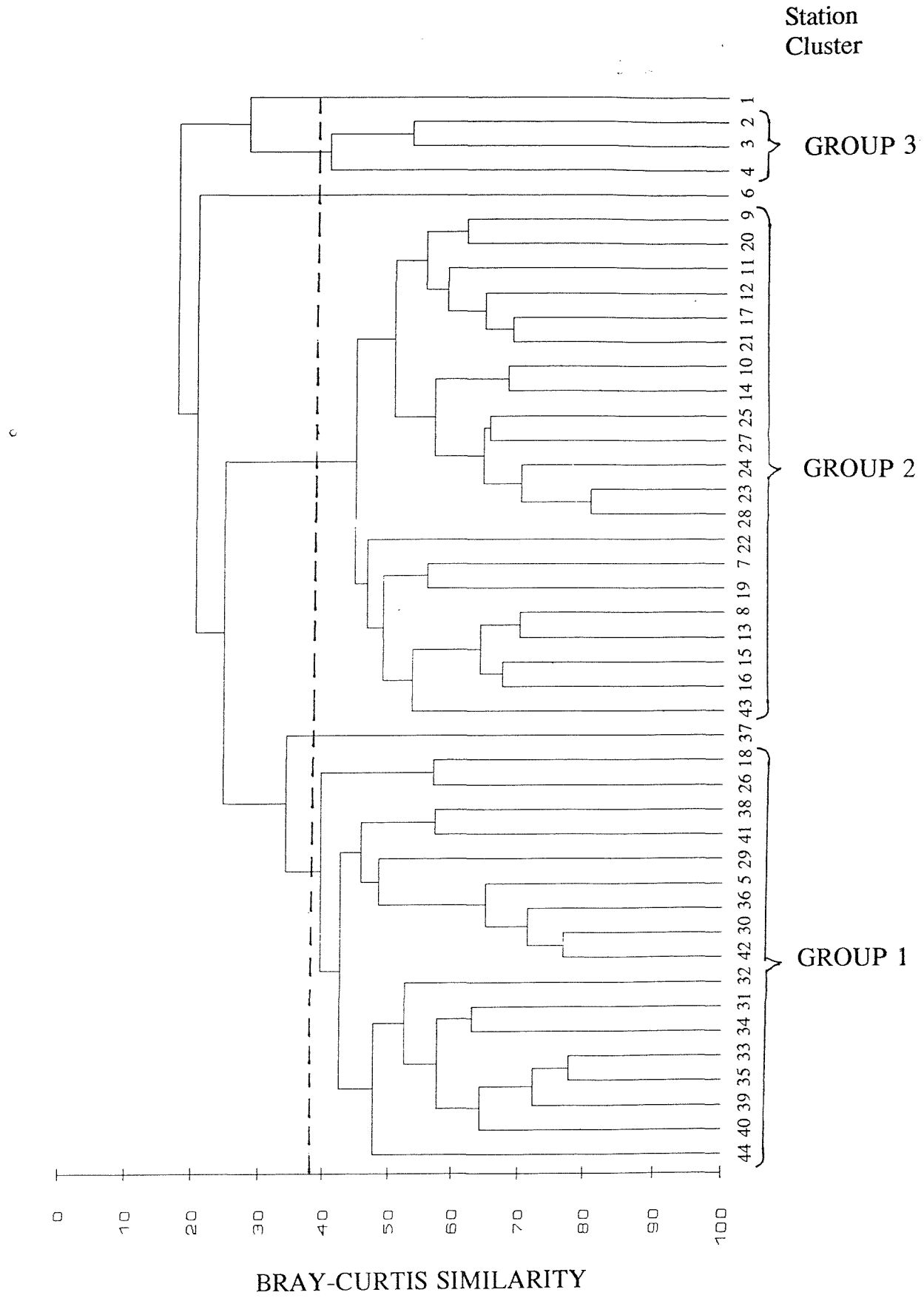


Figure 6.5a: Dendrogram showing 1990 Bongo stations groups (full data set)

clusters of 3 or more stations. The geographic distribution of the resulting station groups is illustrated in fig. 6.5b with the dissimilarity matrix showing distance between station groups presented in Table 6.5(i).

For the analysis to determine species clusters, the data set was restricted to those species that occurred at 3 or more stations for the reasons given in Section 6.4.1. Values were transformed using ln(1+x) and clustered using the Bray-Curtis similarity measure. The resulting dendrogram is presented in fig. 6.5c. After some experimentation, separation at the 50% level was carried out and this gave 9 species clusters with 2 or more species. Only 5 out of these 9 species clusters were found to be valid in terms of containing sufficient numbers of member species that had significantly different distributions between 2 out of the 3 station groups. The strength of association between these 5 species clusters and station groups was then calculated using the Bray-Curtis similarity coefficient. Table 6.5(ii) presents the species contained in the 5 valid species clusters and the station group(s) to which they show strongest association.

As in the case of the RMT8 analysis, D and E from the Simpson Diversity Index, the number of species occurrences and the species fidelity was determined for each station group and these values are presented in Table 6.5(iii).

6.5.2 Relationship of multivariate groups to abiotic factors

As in Section 6.4.3, the biotic similarity matrix was taken from the hierarchical classification analysis. The same 7 environmental variables (Section 6.4.3) were chosen to form the multiple abiotic similarity matrices and, as previously discussed, the Falkland stations were excluded from the analysis. The Euclidean distance measure was applied to all combinations of environmental variables at every level of complexity and

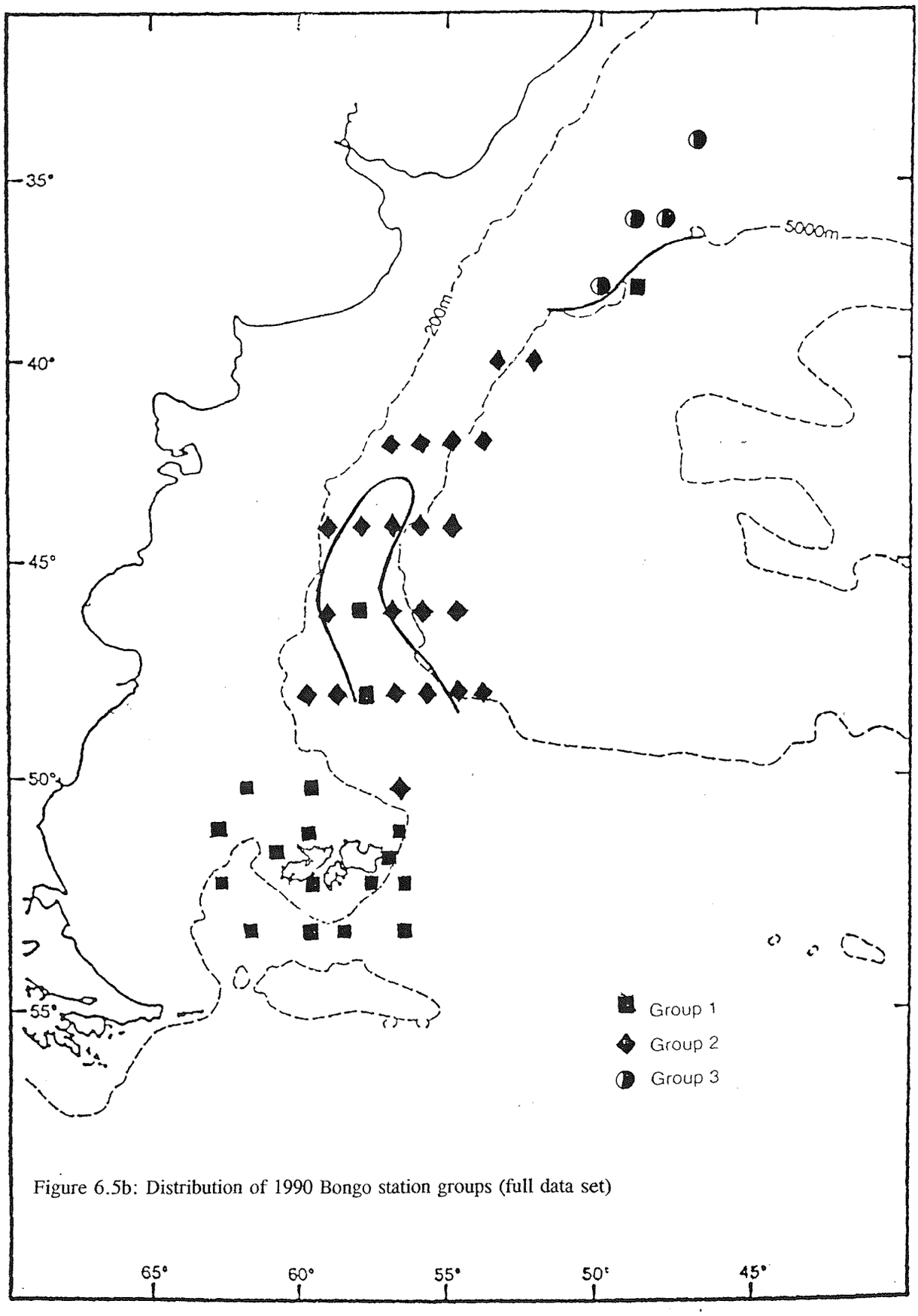


Figure 6.5b: Distribution of 1990 Bongo station groups (full data set)

	Group 1	Group 2	Group 3
Group 1	0		
Group 2	74.76	0	
Group 3	84.78	78.65	0

Table 6.5(i): Average coefficients of dissimilarity between all members of each station group for Bongo 1990 data set using the Bray-Curtis similarity coefficient

Species Cluster 1	Station cluster
Fish larvae *Thysanoessa gregaria*-furcilia (total) *T.gregaria*-furcilia I(i) *T.gregaria*-furcilia I(ii) *T.gregaria-furcilia II*	2
Species Cluster 2	
Sagitta tasmanica *S. gazellae* *Themisto gaudichaudii* *Thysanoessa gregaria*-adult	1 (minor association to 2)
Species Cluster 3	
Euphausia vallentini-furc. (total) *E.vallentini*-calytopes (total) *E.vallentini*-calytopsis II *E.vallentini*-calytopsis III	2 (minor association to 1)
Species Cluster 4	
Thysanoessa gregaria-post-larvae *T.gregaria*-furcilia III *Euphausia lucens*-post-larvae	2
Species Cluster 5	
Sagitta serrodentata *S.hexaptera* *Phrosina semilunata* *Phronima sedentaria* *Stylocheiron* spp. *Euphausia recurva*	3

Table 6.5(ii). Species found within each species cluster and the station group to which they show strongest association

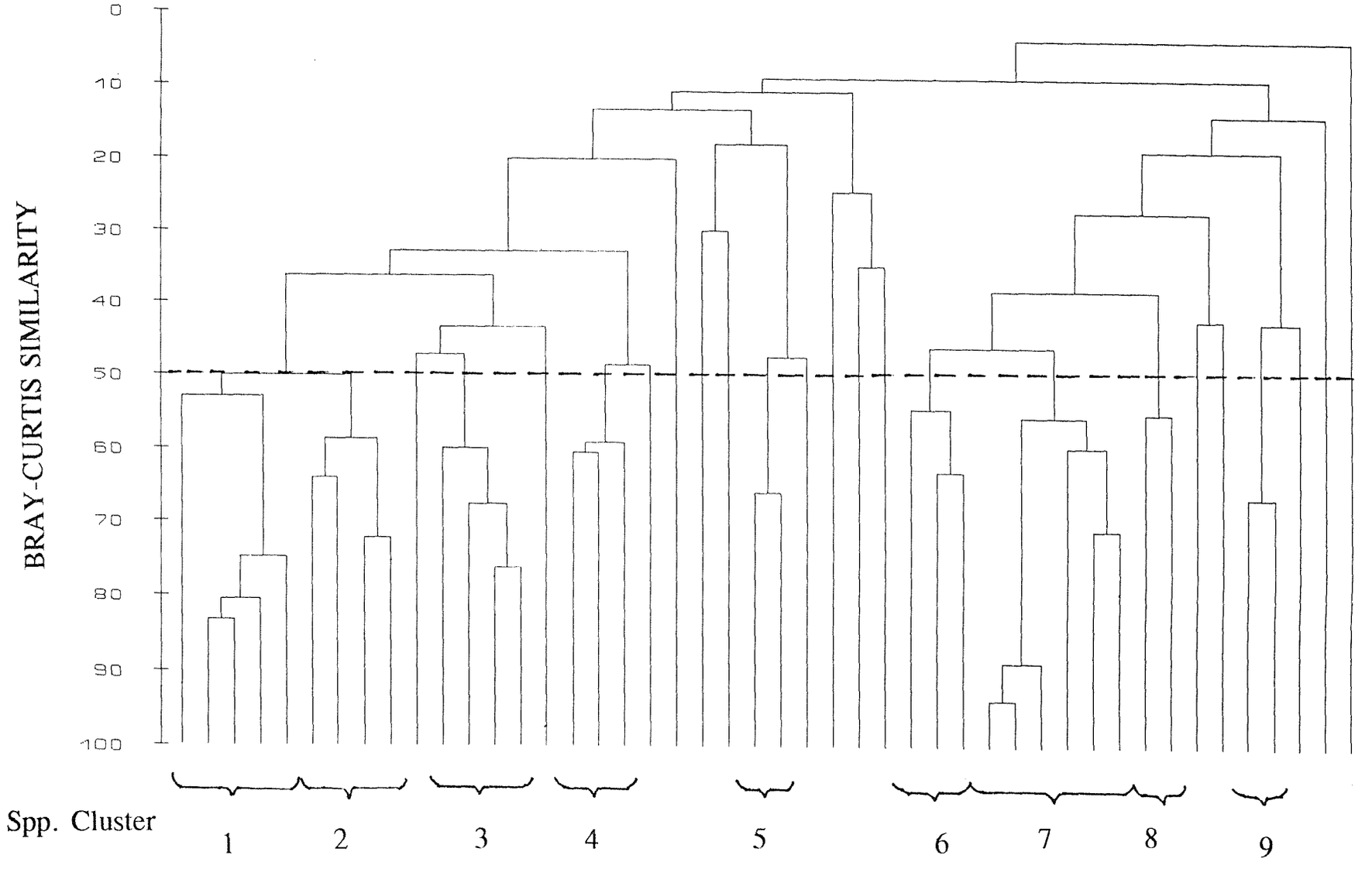


Figure 6.5c: Dendrogram showing 1990 Bongo species clusters (full data set)

	Total species present	No. of spp. with strongest fidelity	Simpson Diversity Index (D)	Equitability Index (E)
Group 1	19 (30)	3 (3)	5.080	0.267
Group 2	36 (89)	36 (55)	5.932	0.165
Group 3	48 (66)	48 (50)	5.460	0.111

Table 6.5(iii): Community collective attributes of the groups obtained from hierarchical clustering (brackets denote values obtained when all developmental stages are considered separately).

the resulting matrices were related individually to the biotic matrix using the Harmonic Rank (Weighted Spearman) correlation algorithm. The resulting list of correlation values showed that the maximum correlation to the biotic matrix was achieved by a combination of surface temperature and latitude (r=0.540). Other variables degraded the match between the abiotic and biotic variables and so can be considered not to be key determinants of community composition in the Bongo 1990 samples.

6.5.3 Discussion of the multivariate analysis of Bongo 1990 analysis

From fig. 6.5b, it can be seen that the distribution of station groups has distinct geographic integrity, with Group 3 covering the most northerly 4 stations, Group 2, stations between 40°S and 48°S and Group 1, the Falkland shelf stations and a few off-shelf stations to the immediate north of the shelf. The one anomaly was the presence of a Group 1 station at 38°S, adjacent to Group 3 stations. From the satellite images presented in Chapter 4, it can be seen that this station lies within a cold filament adjacent to a southward meander of warm water associated with the Brazil Current. The marked transition in the waters in this region is further reflected in the bucket surface temperature, which is 13.7°C for the anomalous station but between 15°C and 18.5°C for those stations immediately adjacent to it. The correspondence between such a localised difference in community composition and a marked transition in surface temperature is broadly in line with the findings of the abiotic variable analysis which revealed that surface temperature was an important influence on community composition. However, it must be acknowledged that latitude was also an important influence in combination with surface temperature and that the occurrence of the Group 1 station at a comparatively lower latitude is contrary to the general pattern.

Following on from the above point, it is evident that the distribution of station groups does generally agree with the findings of the environmental analysis in that they have distinctively different surface temperature and latitudinal ranges. Group 1 stations had surface temperatures between 5.3°C and 6.9°C and latitudes between 46°S and 53°S, with exception of the one anomalous station to the north which had a temperature of 13.7°C and a latitude of 38°S. Group 2 stations had temperatures between 5.7°C and 15.0°C and a latitudinal range of 40°S to 48°S and Group 3 stations had temperatures between 15.0°C and 18.6°C and a latitudinal range of 34°S to 40°S. The location of water masses appeared less influential on the distribution of station groups particularly with respect to the PFZ and SAZ which were both covered by Group 2 stations. Group 3 stations did show some adherence to the location of the STZ, although there was one station showing a joint adherence to station group 2 and 3 to the south of the STZ. The most striking pattern was the close correspondence between the Falkland shelf and the distribution of Group 1 stations. Even in this case however, there were some anomalies such as the northern Group 1 station mentioned earlier and two Group 1 stations to the immediate north of the Falkland shelf.

The number of species clusters that showed significant differences in abundance between station groups was much less than in the RMT8 analysis. This may indicate that, in general, species found in the Bongo analysis have more widespread or less geographically discrete distributions. This is also reflected in the fact that two of the species clusters, 2 and 3, showed a major association to one station group and a minor association to another. In the case of species cluster 2, the major association was towards station group 1 and the minor association towards station group 2 whereas for species cluster 3, the major association was towards station group 2 and the minor association

towards station group 1. Station group 3 had only one species cluster associated to it, species cluster 5 which showed no other associations to any other station group, suggesting that the fauna associated to this zone had a more discrete and restricted distributional range. This point is supported further by the between station group dissimilarity matrix. The average dissimilarity between station group 3 and both station group 1 and station group 2 was greater (78.65 and 84.78 respectively) than the dissimilarity between station groups 1 and 2 (74.76). This shows that the fauna associated with station group 3 overlaps with the other station groups much less than the apparent overlap between station groups 1 and 2.

A number of the species that were associated with station group 3 were also found in the RMT8 samples, where they were associated with the STZ station group. The one species that was not found in the RMT8 samples was *Sagitta serrodentata*. The distribution of this species was described by Pierrot-Bults (1974) as being tropical to sub-tropical with a southernmost limit in the South Atlantic of around 35°S. *Phrosina semilunata* was found by both the RMT8 and Bongo samples to be restricted to the STZ despite the fact that Barnard (1932) considered it to have a distribution stretching from 30°S to the Antarctic continent. The same is true of the distribution of *Phronima sedentaria*, which was considered by Shih (1969) to occur between 45°N and 50°S in the Atlantic, in contrast to Barnard's observation that it did not penetrate further south than 35°S. This study would seem to suggest that, in this region of the Atlantic at least, the main centres of abundance of these species are to the north of the sub-tropical zone and that those found in the sub-Antarctic represent chance occurrences.

Sagitta hexaptera was found by the RMT8 study to have a distribution that extended from sub-tropical waters to warmer sub-Antarctic waters located along the

5000m isobath whereas, in the Bongo analysis, this species was restricted to the STZ. One explanation for this pattern is the submergence of the species with increasing latitude. A pattern of submergence was noted by Angel (1979) for the chaetognath *Eukrohnia hamata* where the animal was found at epipelagic to shallow mesopelagic depths in high latitudes but at deep mesopelagic depths in low latitudes. Angel (1979) further observed that the pattern corresponded with the fact that the cold surface water of higher latitudes submerges below warmer surface water at lower latitudes such that the species maintains itself in virtually the same body of water but becomes vertically distributed at different depths. This scenario would not appear to apply to the movement of *S.hexaptera* in this instance because the species is mainly sub-tropical and the waters at greater depth beyond its normal surface layer range are colder rather than warmer. An alternative explanation may be provided by the movement of warm water eddies which are frequent along the 5000m isobath and deepen as they reach latitudes of 43° to 48°S (Olson et al., 1988). It is possible that *S.hexaptera* may be frequently trapped in such eddies and alter their vertical distribution to correspond with the deepening of the eddy as it moves south. Such changes in vertical distribution to correspond with the effects of decay in an eddy have been observed in euphausiids (Wiebe and Flierl, 1983) and it is possible that the same type of behaviour is exhibited by *S.hexaptera*. However, much more detailed analysis would be necessary to ascertain whether the species does frequently get entrapped in warm core eddies and has the ability to adjust its vertical distribution in response to environmental factors.

The species associated with station group 1, the Falkland Shelf group, are similar to those found in the RMT8 analysis, ie. *Sagitta gazellae* and *Themisto gaudichaudii*. In addition, the Bongo analysis found *Sagitta tasmanica* and *Thysanoessa gregraia* adults

were associated with the Falkland Shelf station group. *S.tasmanica* was considered by Pierrot-Bults (1974) and Boltovskoy (1981b) to have a sub-Antarctic distribution in the Atlantic from 35°S to 65°S but neither study found that main centres of distribution of the species were over shelf regions. *Thysanoessa gregaria* was omitted from the RMT8 analysis because it showed significant day/night differences in abundance. The neritic distribution of the adults of this species agrees with Montu (1977,1982) and Ramirez and Dato (1983) although a much wider distribution of the species in the northern hemisphere was implied by Mauchline and Fisher (1969) who stated that *T.gregaria* was a characteristic species of central and transition waters.

Despite their greater abundances over the Falkland Shelf, most Group 1 species are widespread and common throughout the survey region. This point is highlighted by the presence of a Group 1 station adjacent to the STF. In terms of species composition, this station is devoid of almost all species apart from *Themisto gaudichaudii*, *Thysanoessa gregaria*, *Sagitta tasmanica* and the STZ associated species, *Sagitta hexaptera*. It would therefore appear that the species associated with Station Group 1 are not discretely distributed and unique to the region but are instead widespread and presumably tolerant of conditions that would appear to exclude most other species.

Another feature of Group 1 is that it is characterised by the exclusion of many species with the number of species that occur within its distributional range (19) being considerably less than the numbers found in station group 2 (36) and station group 3 (48) (Table 6.5(iii)). This difference is emphasised by the number of species showing strongest fidelity to individual station groups, with station group 1 having just 3 species whilst station groups 2 and 3 had 22 and 37 species respectively. As discussed in the RMT8 analysis, the high species number and fidelity values of Group 3 stations may be

related to the fact that the region probably represents the southern extension of the South Atlantic Central Gyre, which is characterised by high species richness and strong species fidelity.

In station group 2, the value for the number of occurrences was proportionally higher than the value for the number of species showing strongest fidelity (75% and 60% of Group 3 value respectively). Group 2 covers the Transition region between sub-tropical and sub-polar waters and is dominated by species expatriated from their normal distributional ranges. The smaller proportion of species showing strongest fidelity to this region is therefore to be expected and what is most significant is how close species numbers in this region are to the sub-tropical values, despite the fact that the Transition region is much colder and not directly influenced by a high diversity gyre system as is probably the case for the Group 3 stations. One further point of particular note is that the number of occurrences and the numbers of species showing strongest fidelity is in fact higher in station group 2 compared to station group 3 when the developmental stages are included in the calculation. Most of these developmental stages are of sub-polar euphausiid species and the lack of sub-tropical euphausiid developmental stages in the Group 3 region may be a result of the time of year sampling was carried out. The fact that these species show strongest fidelity to the Transition region is nevertheless an indication that developmental stages appear to concentrate in the area despite the fact that they are probably expatriates.

One other notable aspect about the distribution of developmental stages is that different stages of the same euphausiid species belong to different species clusters and that, in certain cases, these clusters have different station group affiliations. In *Thysanoessa gregaria*, for instance, early furcilial stages (FI(i), FI(ii) and FII) were

found in species cluster 1 whereas the late furcilial stages and post-larvae were found in species cluster 4 and the adults in species cluster 2. Furthermore, whereas species clusters 1 and 4 were affiliated with stations group 2 (Transitional region), species cluster 2 was affiliated with station group 1 (Falkland Shelf). It was not possible to determine whether adult and larvae showed different station group affiliation in the other major euphausiid species, *E. vallentini* and *E. lucens*, because the adults were excluded from the Bongo analysis as a result of showing significant differences in abundance between day and night-time samples. From the RMT8 analyses however, it was apparent that both these species were members of a Falkland Shelf cluster which contrasts with the Transitional region (station group 2) affiliation of their larval stages in the Bongo analysis. Nevertheless, the clusters did show minor associations with the Falkland Shelf station group which indicates that the differences are principally the result of variations in abundance rather than the presence or absence of stages.

The differences in the clustering of larval stages and in their geographic affiliations may be related to differences in their vertical distribution patterns. Differences in the vertical layering and diurnal vertical migrations of euphausiid developmental stages have been noted by a number of studies (Angel and Fasham, 1973; Williams and Lindley, 1982; Hirota et al., 1984; Williams and Fragopoulu, 1985; Barange, 1990). Almost all found that younger stages tended to live at shallower depths and that their diurnal vertical migrations became more extensive with each progressive developmental stage. Studies carried out by Pillar (1984b) and Pillar et al. (1989) in waters off South Africa specifically examined these differences in the developmental stages of *Euphausia lucens*, a species also common to the south-west Atlantic. Both studies found that the eggs and nauplii were located within the surface layers and that the

calyptopes showed no evidence of movement to deeper layers. The first stages that showed vertical migratory behaviour were the furcilia although these were still generally restricted to the upper layers. At juvenile stage, the vertical migratory capabilities of the species matched that of the adult and the animals were capable of reaching the bottom layers.

The coastal environment, in which the adults of the major euphausiid species in the present investigation are centred, is generally characterised by stronger horizontal and vertical circulation systems and by more advective processes than the oceanic environment. Neritic species would have to interact with markedly different current systems in order to maintain themselves on the shelf. Because of the differences in vertical distribution and migratory capabilities of various developmental stages, the currents acting on early reproductive stages may be different to those acting on older larvae and adult stages. Pillar et al. (1989) found that early developmental stages of *E. lucens* that were restricted to the surface layers were advected offshore by Ekman transport. It is feasible that such processes are affecting the populations of *E. lucens* and the other neritic euphausiid species, *E. vallentini* and *Thysanoessa gregaria*, in the same way so that the larvae which are restricted to the surface layers are found off-shore whilst the adults are able to maintain an in-shore distribution through being able to migrate either to the more constant deeper environments or between counter-currents so that their average position is maintained.

Klinkenberg (1994) carried out coarse scale (1-1000km) spatial analyses on the horizontal and vertical distribution of the above 3 euphausiid species and found that significantly higher numbers were found at the surface at night even after controlling for day/night differences in avoidance levels. Although this may not establish that the adults

of these species avoid being transported off-shelf by currents through shifting their vertical positions, it does show that they are capable of vertically migrating in shelf waters and as a result only spend a limited amount of time in the surface advective layers. Unfortunately, the larvae of these species were not sampled and so it was impossible to find out whether their vertical distributions were mainly restricted to the surface layers. Nevertheless, considering that Pillar (1984b) and Pillar et al. (1989) both found the larvae of *E.lucens* restricted to the surface layers, it is very likely that the same type of behaviour in this and the other shelf species is exhibited in this shelf region also. The problem that is then apparent is how the shelf populations are able to maintain themselves assuming that a large proportion of the larvae are swept offshore with the surface currents into the Falkland Current.

6.6 Discussion

6.6.1 Comparison of RMT8 1990 and Bongo 1990

One feature that distinguishes the RMT8 species clusters from the Bongo species clusters is that a larger number of RMT8 clusters show significant differences between station groups. One possible explanation for this difference is that zooplankton in the surface layers have comparatively larger distributional ranges and do not show strong affiliations to any one station group as a result. However, from fig. 6.2g, it is apparent that the percentage of species with frequencies of occurrence above 70% is lower in the Bongo samples than in the RMT8 samples which refutes the wide, surface layer distribution hypothesis. The only other explanation therefore is that the geographic coherence of species cluster members in the Bongo samples is not as distinct as in the RMT8 samples which means that the absolute distributional ranges of co-occurring species are not as well matched in the Bongo samples as they are in the RMT8 samples. This may indicate that advective forces are more influential to species restricted to the surface layers, making community composition more heterogenous and less geographically distinct.

Despite the above differences, the geographic distributions of certain RMT8 and Bongo station groups appear to be the same. For instance, the analyses of both sample sets identified one group restricted to stations north of the STF and another group centred over the Falkland shelf. The characteristic features of the species clusters associated with these station groups also appeared to be the same. In the species clusters associated to the STZ, the two samples sets appeared to share a number of common species including *Phrosina semilunata*, *Phronima sedentaria*, *Euphausia recurva* and

Stylocheiron spp.. The species associated with these clusters were also similar in the fact that their distributions were mostly restricted to STZ stations and were virtually absent from the rest of the survey grid. This is further illustrated in Tables 6.4(iv) and 6.5(iii) where the STZ station groups in both sample sets (Group 4 for RMT8 and Group 3 for Bongo) had the highest numbers of species with strongest fidelities. It was also apparent that both station groups had the highest numbers of species occurrences, a feature possibly associated with the influence of the South Atlantic Central Gyre.

Species clusters associated with the Falkland Shelf station group in both samples sets were also found to contain common species. These included *Sagitta gazellae* and *Themisto gaudichaudii* and species such as *Euphausia lucens*, *E.vallentini* and *Thysanoessa gregaria* would probably have shown a common affiliation if they had not been excluded from the analyses because of significant day/night differences. The species associated with the Falkland Shelf station group in both sample sets were generally widespread and relatively abundant throughout the survey region but showed highest abundances over the shelf region. It was also apparent that the numbers of species occurrences within the station group region was low in both sample sets (Table 6.4(iv) for RMT8 and Table 6.5(iii) for Bongo) which appeared to show that many species were excluded from the shelf region.

There was less similarity between the net sample sets with respect to the region between the STF and the Falkland shelf. In the RMT8 analysis, 2 distinct station groups were found within the region whereas in the Bongo analysis, only 1 station group was apparent. The difference was associated with the fact that the SAF appeared to be a major influence on the RMT8 distribution patterns such that one station group was associated with the PFZ and the other with the sub-Antarctic, Transitional waters located

around the 5000m isobath. In the Bongo samples, the PFZ did not appear to have a discernable influence on community composition and the whole region was covered by a single station group.

The difference between the two sample sets was also reflected in the associated faunas. In the RMT8 sample set, the species cluster associated to the PFZ station group contained a mixture of euphausiids (*Euphausia similis*, *E.triacantha*), salps (*Salpa thompsoni*), hyperiids (*Primno macropa*) and myctophiids (*Protomyctophum bolini*). The species cluster associated with the Transition/5000m isobath station group were the myctophiid species *Diaphus hudsoni*, *Argyropelecus hemigymnus* and *Lampanyctus pulsillus*. The species clusters associated with the one Bongo station group in this region mostly contained the larvae of the euphausiids, *Euphausia vallentini*, *E.lucens* and *Thysanoessa gregaria*. The species in the respective RMT8 and Bongo species clusters also differed in their typical vertical distributions and migratory capabilities. All the species within the RMT8 PFZ and Transition species clusters exhibit distinct diurnal vertical migration behaviour (Dilwyn-John, 1934; Foxton, 1966; Thurston, 1976), which, in the case of the myctophiids, can be quite extensive (Badcock and Merrett, 1977). The euphausiid larvae, by contrast, have very limited vertical migratory ranges and are mostly restricted to the surface layers (see Section 6.5.3). Through being separated vertically, the dissimilar communities that were sampled by the RMT8 and Bongo nets were possibly subjected to markedly different abiotic and biotic factors which may have led to the contrasting distribution patterns observed.

Multivariate analysis on abiotic factors revealed that a combination of water mass location and latitude were the principal influences on the RMT8 biotic distribution patterns, whilst the main influences on the Bongo biotic patterns were a combination of

surface temperature and latitude. The surface temperatures at either side of the SAZ generally varied very little at the same latitude (approximately +/- 2°C) and so it is unsurprising that there is no discernable difference across the front in the community composition of the Bongo samples. The physical transition between the PFZ and the SAZ is seen more at depth, where the 4°C isotherm is seen to deepen rapidly towards the SAF approaching from the PFZ. Any physical influence on the distribution of communities is therefore more likely to be seen in deeper living organisms such as the ones associated with the PFZ and Transition station groups in the RMT8 analysis. Nevertheless, caution must be exercised before making any conclusions about physical limitations on deeper living organisms that exhibit strong vertical migrations because the range of tolerance may be considerable as highlighted by Williams and Frangopoulu (1985), who observed that the adults of *Nyctiphanes couchii* made nocturnal vertical migrations across a summer thermocline gradient greater than 7°C. As well as strong temperature and salinity gradients at their boundaries, water masses typically have characteristic chemical and nutrient levels which may affect primary production levels, feeding efficiencies and, ultimately, trophic structure. Although difficult to determine empirically, these biotic factors may have a more profound influence on the distributional ranges of macrozooplankton communities than temperature/salinity boundaries (Van der Spoel, 1994b). The ability of these plankton to vertically migrate potentially allows them to move out of strong current shears or to oscillate between currents with different directions and so maintain themselves within optimum biotic conditions.

The lack of an ability to vertically migrate may be one of the principal reasons why the distribution of euphausiid larvae is displaced relative to the distribution of the

adults. The same pattern is also observed in the distribution of *Sagitta gazellae* and *Themisto gaudichaudii*, where the larvae and small adults from the Bongo samples, with probably a limited vertical range, have an off-shelf centre of distribution in the Transition region whilst adults in the RMT8 samples are located on-shelf. One of the potential advective forces which may carry these organisms off-shelf is Ekman transport which is particularly significant in the surface layers and has been found to be a major influence on larval transport in other regions (Wickett et al., 1967; Pillar et al. 1991). Another potential advective force is the Falkland Current which splits around the Falkland Islands and may cause significant off-shelf transport from the western Falkland Shelf.

The fact that larvae are swept off the Falkland and Patagonian shelves towards the oceanic Transition region does present a problem in terms of how the shelf populations are maintained. As discussed by Olson (1986) and Boltovskoy (1989), the Transition zone in the south-west Atlantic has a unidirectional flow eastwards into the South Atlantic ocean and there is no known mechanism of repatriation for organisms swept into the zone. The shelf community is dominated by adults and relative abundances of larvae are reduced compared to their levels off-shelf. Considering that the shelf community contains such large abundances, it would appear somewhat unlikely that the large amount of larvae found in the Transition region represent an advective loss to the shelf population.

One possible retentive mechanism which may counteract the net oceanic advection of the Transition region was revealed by Olson (1986) who carried out research on satellite tracked ARGOS drifters deployed in the confluence and upstream of the Brazil Current and found that many drifters showed prolonged residence time in a

region where there was frequent eddy formation before eventually being swept east. The average residence time in this region was 3.8 months and 2 drifters remained in the region for over 6 months. Boltovskoy (1989), in considering these results, concluded that such retentive mechanisms were not sufficient to maintain meso and macrozooplankton although they may be sufficient to maintain local stable populations of several phytoplankton species with short generation times. However, if one assumes that adults are able to vertically migrate into less advective waters and move against the net unidirectional flow, then it is only necessary for the retention to be sufficiently long enough for the euphausiid larvae to mature into adults. As is shown in Chapter 8, the average amount of time for euphausiid larvae to mature into adults is approximately 3 to 4 months and considering that by the time they reach the Transition region from their on-shelf spawning sites, they would be approximately 2 to 3 weeks old, the necessary retention time could possibly be shorter. The feasibility of adults being able to move against a unidirectional current is not so remote considering that current speeds are variable on time scales of hours and that swimming speeds of older stage euphausiids may be sufficient to move downstream during slack periods (Nelson and Hutchings, 1987). Furthermore, net advective currents at the surface such as Ekman transport have counter currents at greater depths (ie. Ekman's spiral) which may be exploited by organisms, such as euphausiids and hyperiids, with strong vertical migratory capabilities.

6.6.2 Comparison of the present study to other contemporary studies

There have not been any zooplankton surveys in this region with the same scale and resolution as the present investigation. However, similar types of surveys were carried out on the Pataganion shelf by Dadon (1989) and Mazzoni (1990) who studied

the seasonal distributions of pterapods and chaetognaths respectively. Pterapods were not considered by this investigation but the chaetognath species which were identified by Mazzoni (1990) as being the principal inhabitants of the shelf, *Sagitta gazellae*, *S. tasmanica* and *Eukrohnia hamata* were also common to this study. The one species found by Mazzoni (1990) that was absent from this investigation was *Sagitta frederici*, a species that is mostly restricted to inshore regions. Both Dadon (1989) and Mazzoni (1990) defined similar biogeographic regions as described in Chapter 5 and in the case of the chaetognaths, *Sagitta frederici* was dominant inshore, *S.tasmanica* dominant mid-shelf and *Eukrohnia hamata* dominant in the outer-shelf with *S.gazellae* being limited to zones within the outer-shelf region.

The only area in which these studies overlap with the present investigation is in the Falkland shelf region which Mazzoni (1990) defined as being principally dominated by *Eukrohnia hamata* and also by *Sagitta gazellae* in regions further off-shelf. These findings agree with this investigation in the case of *Sagitta gazellae* which was most strongly associated to the Falkland shelf station groups in both the RMT8 and Bongo sample sets. However, in contrast to Mazzoni (1990), *Eukrohnia hamata* was found to have a much wider distribution and in the RMT8 factor analysis it was a member of factor group 1 which had a distribution centred in the STZ and along the 5000m isobath in the region of the survey that was furthest off-shelf (see fig. 6.4d). This would appear to indicate that this species has a cosmopolitan distribution and exhibits high abundances in oceanic regions as well as in outer-shelf regions.

The RMT8 and Bongo samples collected in 1990 were also analysed by Rodhouse et al. (1992), along with further material collected in 1991, to study the relationship between water masses and cephalopod larvae. It was found that the STZ had the greatest

number of species and individuals with 14 taxa and 42 specimens, the SAZ contained 9 taxa and 14 specimens and the PFZ, 3 taxa and 26 specimens. The species lists did overlap between water masses but there were some species found exclusively in either the SAZ or the STZ. It was concluded that there was a marked association between the distribution of cephalopod species and the water masses which agrees with the findings for the RMT8 samples in this investigation. However, the association between cephalopod larval distributions and surface temperature or latitude were not investigated and considering their importance to the near-surface zooplankton in this study, comparisons to further environmental and geographical variables may be illuminating.

The above studies are all based on the analysis of a single, higher level taxon and the only study to consider the collective distributional patterns in several higher level taxa in this region was that of Dadon and Boltovskoy (1982) which has previously been considered in Chapter 5. Dadon and Boltovskoy's (1982) study covers a much larger scale than this investigation, but there does appear to be a reasonable degree of agreement where the two study areas overlap. The species groupings are particularly consistent. For example, the recurrent group containing *Euphausia lucens* and *E.vallentini* in Dadon & Boltovskoy (1982) complies with factor 4 and species cluster 2 of this investigation. Two further recurrent groups, *Sagitta gazellae/Euphausia triacantha* and *E.longirostris/E.similis* are equivalent to factor group 2 and factor group 3 respectively. The distributions of these recurrent groups also match this study in two of the three cases. The *E.lucens/E.vallentini* recurrent group shows a mainly neritic distribution, similar to factor 4, whilst the *E.similis/E.longirostris* recurrent group shows an association with a region between 50°S and 55°S corresponding to factor 3. However, the *S.gazellae/E.triacantha* recurrent group is associated to a region much

further south than the area covered by this survey and does not appear to comply with the distribution plot of factor group 2. The results of this survey show that *S.gazellae/E.triacantha* have a strong and definite relationship with the PFZ at lower latitudes. In the case of *E.triacantha*, these findings agree with those of Baker (1959), who recorded the strong occurrence of the species at these lower latitudes.

The study of Dadon and Boltovskoy (1982) is subject to a number of limitations. The data was taken from literature records and consisted of samples taken with a wide range of net designs with different selectivities and so there is a series of unaccountable biases within the data set. Furthermore, the nature of the study makes it impossible to account for seasonal biological variance and variation in the position of influential hydrographic features. Such inadequacies limited Dadon and Boltovskoy (1982) to defining megascale (Haury et al., 1978) zoogeographic zones. However, investigating variations in abundance within these zones is an essential consideration at the community level since smaller, mesoscale patterns may highlight important influences on the larger scale distribution of a faunal group. For instance, the Falkland Current is a mesoscale feature that was shown by Factor analysis to be a major influence on zooplankton distribution in this region both in Factor 4, which showed strongest associations to stations along the northward flow of the current and Factor 1 which showed a pattern associated with the southward return of the Current.

One mesoscale level comparison that can be made is with a study carried out by Pakhomov et al. (1994) who presented results from a synoptic survey carried out in the vicinity of the Sub-Tropical and Antarctic Polar Front in waters directly south of South Africa (20°W) at latitudes between 40°S and 50°S. An RMT8 net was used to sample between 0 and 300m so direct comparisons to the present data set are possible without

making accommodations for methodological differences. Almost all the species found by Pakhomov et al. (1994) were also present in the present survey, illustrating that there is a definite coherence in sub-tropical/sub-Antarctic fauna throughout the South Atlantic, probably resulting from the circulation of the South Atlantic Central Gyre. Nevertheless, the hydrographic affinities of the species in the present survey do not agree with the findings of Pakhomov et al. (1994) in all cases. The cluster and factor analysis carried out on the RMT8 sample set from this investigation found that, as in waters south of South Africa, species such as *Phronima sedentaria*, *Euphausia spinifera*, *E.recurva* and *Euhkronia hamata* showed affinities to the sub-tropical region, close to the STF. However, other species, such as *Sagitta hexaptera*, *Chelophyes appendiculata* and *Hippopodus hippopus* showed distributions that extended from the sub-tropical region into sub-Antarctic waters, especially those waters along the 5000m isobath. In Section 6.4, the possible explanations put forward for this distribution pattern included the influence of the warm Falkland return current and the effect of warm core eddies, carrying organisms beyond their normal distributional range. The study of Pakhomov et al. (1994) was not extensive enough to investigate the extent to which organisms may be carried beyond their normal distributional ranges but they did note the dramatic effect of eddy shedding on the faunal composition of their region and noted the occurrence of the mainly sub-tropical species *Phronima sedentaria*, at the Antarctic Polar Front as an example.

A notable aspect of the present RMT8 analysis was that, although strongly associated to water mass location, the faunas that characterised the PFZ, SAZ and Falkland shelf were not restricted within the water mass boundaries. This feature has also been observed by Bary (1963), Briggs (1974) and Angel & Fasham (1975) amongst

others. It would appear therefore that fronts associated with water masses or physical regions in this study do not present insurmountable physical barriers that cannot be physiologically tolerated by organisms that cross them. Fronts also represent the limits to water masses and physical regions such as continental shelves which have distinct chemical and nutrient characteristics. An alternative hypothesis that may explain observed associations between distribution patterns and water masses may therefore be a selective pressure on organisms to remain within a discreet biotic environment with distinct chemical and nutrient levels and associated food types of certain qualities. Advective forces may act to expatriate organisms from their optimum environments which would necessitate behavioural responses, such as vertical migration, as counteracting measures. Those areas in which organisms are found at lower abundances possibly represent cases where counteractive behavioural responses were not able to maintain them within an optimum environment causing expatriation into another water mass or physical region where they are either unable to breed or suffer high mortality because of unfavourable biotic conditions.

The observation that physical features such as the shelf-edge or the sub-Antarctic front are not insurmountable physical barriers to distributions is also shown in the strong dispersal of neritic larvae in the oceanic Transition zone. The fact that these larvae do not possess some of the behavioural capacities of adults such as vertical migration and strong swimming abilities, makes them more vulnerable to advective forces such as Ekman transport in the surface layers, as was found by Wickett (1967) in the North Pacific. In this instance, the limits of their distribution are primarily determined by physical factors resulting in their distributional range being a function of the strength and direction of the physical forcing mechanism and their ability to tolerate the varying

conditions they encounter. If the environmental gradients at the front were beyond their physiological tolerance, then the observed distribution would be limited to a region inside the front as is probably the case reported by Pillar et al. (1991) where the distribution of both larvae and adult *E.lucens* were distinctly limited by a frontal system. The fact that larvae are found well beyond their presumed origin shows that intervening environmental gradients were within their tolerance limits. From the Bongo sample set it appears that the larvae of the neritic euphausiids, *Themisto gaudichaudii* and *Sagitta gazellae* were able to tolerate conditions throughout the Transition region and were principally limited by the STF. Whether it is the environmental gradients of the STF or the opposing advective forces of the Brazil Current that limit the further distribution of these larvae is a matter that needs further examination.

An important feature that was apparent from studies by Brinton (1962), Fasham and Angel (1975) and E.Boltovskoy (1981) was that some water masses may be subdivided into more than one faunal zone on the basis of distinct differences in abundance. The patterns produced from Factor analysis of the RMT8 sample set also showed that abundances of assemblages may differ considerably within a water mass. From the abiotic multivariate analysis, it was found that a combination of latitude and water mass location were the principal influences on biotic distribution patterns. Latitude is principally associated with factors such as day-length, seasonality and temperature. Indeed, for this latter parameter, a significant linear relationship was found between surface temperature and latitude over the survey area. Factors such as the amount of solar energy may act together with characteristic water mass parameters to determine the quantity of food available. The nutritional value of this food depends on further factors such as the temperature at which digestion takes place since the enzymatic reaction

regulating an organisms metabolism and processes such as assimilation and digestion are temperature dependent. Therefore, it may be important for an organism to be at a particular latitude as well as in a particular water mass and this may influence the zonation observed within water mass boundaries.

Another important factor that may contribute to the differences in abundance observed within water masses such as is found in the present study is the heterogeneity of the food source. For instance, Weber and El-Sayed (1985) found that the swarm biomass of Antarctic krill was correlated with the amount of chlorophyll-*a* and adenylates. The geographical variability in phytoplankton biomass and primary productivity in the south-west Atlantic was found to be considerable (El-Sayed and Weber, 1982) with some standing stock and productivity values being much higher than expected at open ocean stations and stations within the PFZ. Such localised enhancement or impoverishment of phytoplankton in this region is the result of a number of factors although, as yet, they are little understood (El-Sayed and Weber, 1982). Considering that a large number of the zooplankton species in the RMT8 faunal assemblages are herbivorous, such localised variability may be a significant influence on observed distribution patterns and may be influenced in the zonation of faunal assemblages within water masses.

Although the zonation of faunal assemblages was mainly distinguished through differences in abundance in the case of the SAZ, PFZ and Falkland Shelf station groups, the STZ was more characterised by the presence or absence of species. The STF exhibits some of the strongest temperature gradients in the South Atlantic (Pakhomov et al., 1994) so the possibility of the STF presenting a strong physical barrier is distinctly feasible. Nevertheless, it cannot be ruled out that STZ associated species may maintain

their position within the water mass through behavioural counter-measures against expatriating advective forces as was found by Boucher (1984) at the Ligurian marine front.

Overall, it would appear that the faunal zones defined by species distribution patterns do correspond with physical features such as water masses, surface temperature and geographic factors such as latitude. However, the nature by which the zones are derived signify that physical boundaries are not always distributional limits and their degree of influence varies. In some cases the fronts may present environmental gradients that cannot be tolerated by organisms encountering them, in others, they simply define the limits to chemical and nutrient levels which are influential in biotic processes and the resulting community structure. Indeed each of the fronts found in this survey region may play both roles with respect to different species. The zonal patterns nevertheless reflect the fact that the distribution of species assemblages is the result of a number of complex factors with the influence of physical and behavioural components being effectively inseparable.

6.7 Conclusions

1, A total of 155 zooplankton species were identified from 9 taxonomic groups in the 1990 RMT8 samples. 62 species were identified from 6 taxonomic groups in the 1990 Bongo samples.

2, The majority of the species were not found at more than 15% of the stations in the RMT8 sample set, with the few species that were widespread also being the most abundant at individual stations. Even fewer species were found frequently in the Bongo samples with the widespread species not always being the largest contributor to station abundance.

3, Classification analysis on the faunal composition of RMT8 stations produced four groupings which showed distinct geographic integrity. An abiotic multivariate analysis revealed that a combination of water mass location and latitude were most strongly related to these biotic classification groupings.

4, A second classification analysis considering the distribution of species in the RMT8 data set produced 8 groups, 5 showing an affiliation to the STZ station group, 1 to the PFZ group, 1 to Falkland shelf group and 2 to the SAZ group (although one of these was jointly affiliated to the STZ group). The dissimilarity matrix showed that the STZ group was very distant from each of the other three station groups, suggesting that its faunal composition was very different from that found in the rest of the survey area.

5, Factor analysis on the RMT8 data set gave further resolution to the station cluster patterns. Factor 1 supported the view that the SAZ group was influenced by the warm Falkland current return, Factors 2 and 3 showed a north/south separation in the species associated with the PFZ station group and Factor 4 suggested that the Falkland

current may significantly affect the distribution of shelf species, sweeping them into oceanic areas to the north.

6, Classification analysis on the Bongo data set produced 3 groupings which showed distinct geographic integrity. The abiotic analysis showed that a combination of bucket surface temperature and latitude were most strongly related to the biotic classification groupings.

7, Classification analysis on Bongo species distributions produced 9 clusters, of which 5 showed significant differences in abundance between station groups. One cluster showed strongest associations to the high temperature stations in the north, 3 clusters to the intermediate temperature stations at mid-latitudes and 1 cluster to the low temperature stations to the south.

8, Comparisons between the RMT8 and Bongo analyses showed that there were similarities in geographic distributions and faunal composition between the STZ RMT8 group and the high temperature, northern Bongo station group and also between the Falkland RMT8 group and the southern, low temperature Bongo group. Strong similarities between sample sets were not found in mid-latitude stations, with the RMT8 analysis producing 2 station groups and the Bongo analysis producing 1. The faunas associated with these mid-latitude groups also differed between sample sets, with vertically migrating species such as salps, euphausiids and myctophiids being associated with RMT8 groups whilst euphausiid larvae with limited vertical ranges were assoicated with the Bongo group.

9, The adults of the larvae associated to the mid-latitude Bongo group were principally found over the Falkland Shelf and this distributional difference may be a result of variation in the behaviour patterns of developmental stages and their interaction

with physical advection forces.

10, Evidence from the dissimilarity matrix, faunal group associations and the fidelity of individual species to station groups in both the RMT8 and the Bongo sample sets suggest that the boundary between the STZ and SAZ is one strongly characterised by differences in species composition whilst the boundaries between the SAZ, PFZ and Falkland shelf are revealed mostly by variations in species abundance.

Chapter 7 Interannual comparison of zooplankton patterns and their relationship to abiotic factors

7.1 Introduction

The 1990 surveys highlighted a number of potential biotic and abiotic environmental influences on the observed distributional patterns of faunal assemblages. However, restricting observations to one particular period limits the degree to which these findings can be more widely applied because it is not possible to establish whether these influences are permanent features or just transient correlations with the biotic patterns during the time of sampling. To determine the consistency of the relationship between environmental variables and biotic distribution patterns, repeat sampling within the region at time intervals ranging from months to years is necessary.

The hydrography of the south-west Atlantic is dynamic and the location of hydrographic features and the values of environmental variables are likely to vary quite considerably over time. The region is also greatly influenced by seasonality in the water column and it is likely that the relative influence of certain variables will alter through the year as a result. This makes it difficult to distinguish functional[1] relationships between environmental variables and biotic distribution patterns on a time scale of months. The effect of seasonality can be excluded through examining samples taken from the same time of year and although the effect of interannual variance must then be taken into account, observed similarities in the relationship between environmental variables and biotic distributions may highlight potentially functional relationships and

[1] "Functional" is taken as being a relationship resulting from the direct or indirect influence of abiotic or biotic factors as opposed to simple correlation which may also be an artifact of the sampling procedures or analytical techniques used.

distinguish them from those that are merely transient correlations.

One problem in making comparisons between years is that the synopticity of the surveys may be different and confound any similarities. For instance, one survey may have sampled a region moving north to south over a two week period whilst another survey, carried out at the same time in a subsequent year, may have sampled the region south to north in four weeks. Although the surveys are roughly similar in terms of resolution and time of year, the different time scales of sampling may result in short-term environmental changes affecting the results to different extents and this may adversely affect the comparisons that are made. Making concurrent abiotic measurement may overcome some of these problems because biotic patterns can be placed within the context of prevailing conditions before they are compared with results from other years. However, biotic distributions may also be influenced by prevailing conditions in the recent past which cannot be accommodated by making concurrent measurements. The only way these types of influences can be accounted for is through analysing a series of synoptic profiles of the hydrographic features in the region before and during the sampling period to determine the nature of recent environmental influences. To this purpose, a number of studies on plankton distribution have employed the use of sea-surface temperature satellite images (eg. Thomas and Emery, 1988; Thomas, 1992) for identifying mesoscale hydrographic features from their thermal signatures. Employing satellite images also gives a synoptic overview that can be used to judge what effect the temporal sequence in which samples were collected had on the results. Incorporating satellite images of sea surface temperature (SST) into the analysis of interannual differences between surveys would also appear to be particularly relevant in this instance in light of the findings of Chapter 6 where near-surface zooplankton distribution patterns

collected from the 1990 Bongo samples were principally correlated with a combination of surface temperature and latitude.

A further set of Bongo samples covering approximately the same geographic region and having a similar sampling resolution were obtained in 1991 at the same time of year as 1990 Bongo samples. The analysis of these samples was carried out so that comparisons could be made to the 1990 samples in order to assess the degree of variability in biotic distribution patterns between years and to determine the nature of the relationship between these patterns and abiotic variables. The overall aim was to distinguish between environmental factors that were transiently correlated with biotic distribution patterns and those that were functionally related to them initially through determining whether the same factors were principally correlated with the biotic patterns in different years. The main approach was to consider the absolute interannual differences in the values of the important environmental factors and to see how they related to the distributions of faunal groups. Greater interannual similarity in the range of values associated with analogous faunal groups would suggest that the absolute values of this factor were most important in limiting distributions and point to physiological tolerance and behaviour being major influences. If environmental variables associated with analogous faunal assemblages differed markedly between years, it would suggest that these organisms were able to physiologically tolerate a relatively wide range of conditions and that advective forces may limit their absolute ranges.

7.2 Methods

As described in Section 6.2, the sampling protocols differed between 1990 and 1991 surveys. In 1990, two types of net were deployed, an RMT8 net that was towed obliquely between 0 and 200-300m and a Bongo net (mesh size 335μm) and that was used to sample surface waters (0-5m). Only a Bongo net (mesh size 500μm) was used in 1991 and it was deployed obliquely between 0 and 50m. The distinct difference in the sampling depth, mouth diameter and mesh size of the RMT8 compared to the Bongo net would probably confound any observable inter-annual variance in faunal assemblage distributions and so inter-annual comparisons were restricted to the Bongo samples only. However, even for these nets there were differences between years in mesh size and deployment depth so certain accommodations were necessary to exclude any variance that was an artefact of methodological differences before analysis of the biotic variance could be undertaken.

It is likely that the 1991 samples have a much greater sample diversity than the 1990 samples because the fauna was integrated over a much wider depth interval. Therefore, to make a valid comparison between years, the data sets would need to be restricted to those species that are ubiquitous to both surveys. A number of possible methods of achieving this restriction were considered and the most feasible options were as follows[1]:

1, Restriction to night-time stations only - This would cancel out the absence of species from the day-time "shallow" samples as opposed to "deeper" samples through only

[1] To ease the discussion, the 1990 data set will be termed the "shallower" data set whilst the 1991 data set will be termed the "deeper" data set.

considering those samples taken at night, when many species have migrated to the surface layers. The disadvantage of this approach is that it would cut the data set by half.

2, Identification of indicator species assemblages from "deeper" data set - This would ensure that the 2 years are analysed using homologous data sets through employing assemblage groups revealed through the analysis of the "deeper" data set and taking these groups to be indicators of the position of station groups in the analysis of the "shallower" data set. However, this approach does make the fundamental assumption that co-occurrence patterns are the same in the two sample sets which is not entirely appropriate since one of the aims of this analysis is to determine whether the contribution of species to station group distribution remains constant between years.

3, Restriction to species found in the "shallower" data set - This approach is almost the reverse of the "indicator species" method above in that it bases the restriction of the data sets on the "shallower" samples. It is probable that the "shallower" data set is a subset of the " deeper" data set and so restricting the analysis to those species found in the "shallower" data set would ensure that all the species are ubiquitous. This approach does not make any assumptions about co-occurrence patterns between years nor does it involve excluding any stations. One problem however is that the different proportions of time spent by each of the surveys sampling the one common depth interval (0-5m) means that the relative proportions of species may exhibit variance that is an artefact of the different sampling methods.

On balance, the analytical approach of the third option was considered to be most harmonious with the overall aims of this investigation. It was considered that applying an $\ln(1+x)$ transformation to the data sets would reduce possible artefactual differences in

the relative proportions of species between sample sets.

The full data set of the 1990 Bongo survey (Appendix II) was analysed by hierarchical classification techniques in Chapter 6. The analysis distinguished 4 station groups and 5 species clusters that exhibited distinct distributional differences between station group regions. The species making up these clusters were considered to be good indicators of station group regions and so the subsequent analyses were restricted to these species, listed in Table 6.2(ii). Before carrying out the analyses however, certain further exclusions were necessary. Although the regions covered by the 1990 and 1991 surveys overlapped considerably, their absolute geographic ranges were different. The northerly limits in both surveys were approximately the same, around 33° to 34°S but the southerly limit of the 1991 survey was 48°S whilst that of the 1990 survey was 53.5°S as it covered the Falkland Shelf region. Analyses carried out in Chapter 6 showed that on-shelf/off-shelf factors were one of the principal influences on faunal assemblage patterns in this region and so the inclusion of Falkland Shelf stations in the 1990 survey may act to obscure any comparison between the sample sets. For this reason the Falkland Shelf stations were excluded from the 1990 data set.

Hierarchical classification clusters groups according to the species that are absent as much as the species that show variations in abundance and so excluding those species that do not show strong contributions to intra-group similarity as well as those stations found on the Falkland Shelf may have an effect on the distribution of station groups. For this reason, it was necessary to carry out another classification analysis on the restricted data (Appendix IIIa) set to verify that the station group distributions had not changed. The restricted 1990 data set was analysed following the same hierarchical classification procedures outlined for the classification analyses carried out in Chapter 6. Clustering of

station groups was carried out using the Bray-Curtis similarity coefficient and average linkage. Experimental separations at a number of similarity levels were applied to the resulting dendrogram and separation at the 45% association level was decided to be a suitable compromise between the strength of group association and the number of clusters. This produced 4 groups (fig. 7.2a). Species clusters were not determined since, compared to station group membership, species cluster membership was more sensitive to variance in the relative proportions of species and the possible influence of methodological differences on relative proportions made this analysis unsuitable. However, the contribution that each of the species made to the intra-station group similarity was calculated using a Bray-Curtis similarity coefficient and in Table 7.2(i) species are listed under the station group to which they made their greatest intra-group similarity contribution.

Analysis on the 1991 "deeper" Bongo samples was restricted to the same species used in 1990 "shallower" Bongo analysis for the reasons explained earlier (Appendix IIIb). Station group clustering was carried out as for the 1990 data set and separation at the 45% similarity level was chosen, producing 4 distinct station groups (fig. 7.2b). The relative contributions of species to intra-station group similarity was calculated using the Bray-Curtis similarity coefficient and in Table 7.2(ii) species are listed under the station group to which their strongest similarity contributions were made.

A further multivariate analysis involving abiotic variables was also carried out to establish whether the same abiotic factors were most strongly associated to the biotic distribution patterns in both years. As in Chapter 6, the biotic similarity matrix was taken from the Bongo 1990 and Bongo 1991 analyses and the same 7 environmental variables described in Section 6.4.3 were taken to form the multiple abiotic similarity

matrices. The Euclidean distance measure was applied to all combinations of environmental variables at every level of complexity and the resulting matrices were related individually to the biotic matrix using the Harmonic Rank correlation algorithm (Clarke and Ainsworth, 1993).

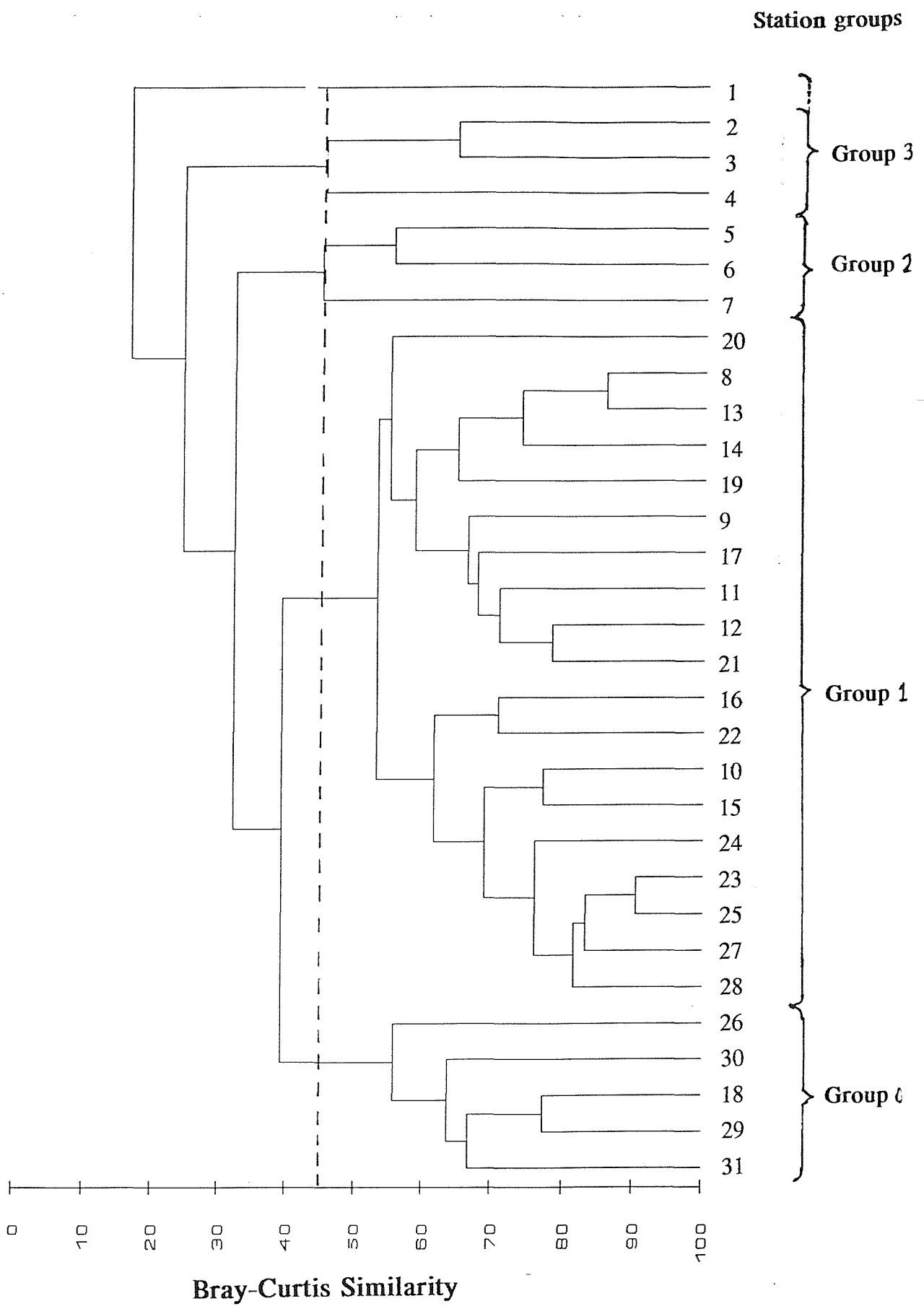


Fig 7.2a: Dendrogram showing station groups from Bongo 1990 (with species and stations restricted)

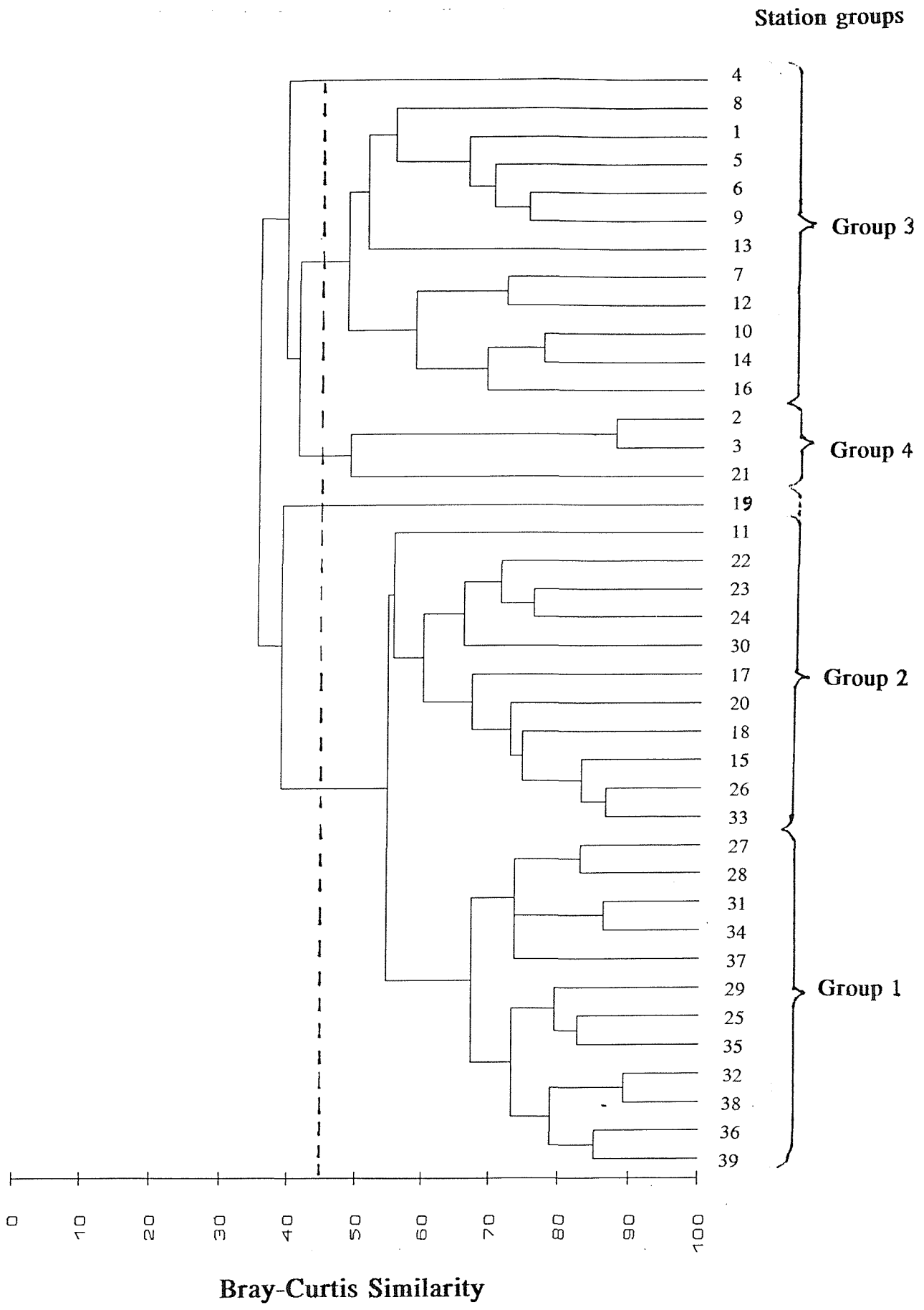


Fig. 7.2b: Dendrogram showing station groups from Bongo 1991 (with species restricted)

Station group 0	Station group 1	Station group 2	Station group 3
(*T.gregaria* Ad.)	*S.gazellae*	*T.gaudichaudii*	*T.gregaria* Ad.
(*S.gazellae*)	*T.gregaria* FI	*S.tasmanica*	*T.gregaria* PL
(*T.gaudichauddii*)	*T.gregaria* FIII	*E.lucens* PL	*E.recurva*
(*S.tasmanica*)	*T.gregaria* C	*S.hexaptera*	*S.serrodentata*
	E.vallentini C		*P.sedentaria*
	E.vallentini F		*P.semilunata*
			Stylocheiron spp.

Table 7.2(i): The station groups to which species show strongest intra-group similarity values in the Bongo 1990 samples. Brackets in Station Group 0 denote species that contributed to intra-group similarity but had stronger associations in other station groups. (F=furcilia, C=calyptopes, PL=post-larvae, Ad.=adult, I and III are respective developmental stages)

Station group 1	Station group 2	Station group 3	Station group 3a
T.gregaria FI	*T.gregaria* Ad.	*E.recurva* Ad.	*Stylocheiron* spp.
T.gregaria FIII	*T.gregaria* PL	*E.recurva* F+C	
E.vallentini C	*E.lucens* PL	*S.serrodentata*	
E.vallentini F		*S.tasmanica*	
S.gazellae		*S.hexaptera*	
T.gaudichaudii		*P.sedentaria*	
		P.semilunata	

Table 7.2(ii): The station groups to which species show strongest intra-group similarity values in the Bongo 1991 samples. (F=furcilia, C=calyptopes, PL=post-larvae, Ad.=adult, II and III are respective developmental stages)

Both the 1991 and the off-shelf restricted 1990 abiotic analyses found that a combination of latitude and bucket surface temperature showed the maximum correlation to the biotic similarity matrix (1991 r=0.461; 1990 r=0.540). It was therefore decided to compare the distribution of station groups to satellite images of sea-surface temperature (see Chapt. 4) so that any potentially influential thermal features could be identified. The satellite images each covered periods of 5 days and in order to maintain the synopticity of the comparison, these images were combined to produce a single image for 1990 and 1991, where the thermal pattern in each region corresponded to the time of sampling +/- 2 days. This was not possible in all cases because of cloud cover and in 1991 there was only one viable image available for the whole sampling period. This image was therefore assumed to be representative of other dates outside its own 5 day range. In figs. 7.2c and 7.2d, the distribution of the 1990 and 1991 station groups respectively were superimposed onto their associated integrated satellite thermal images.

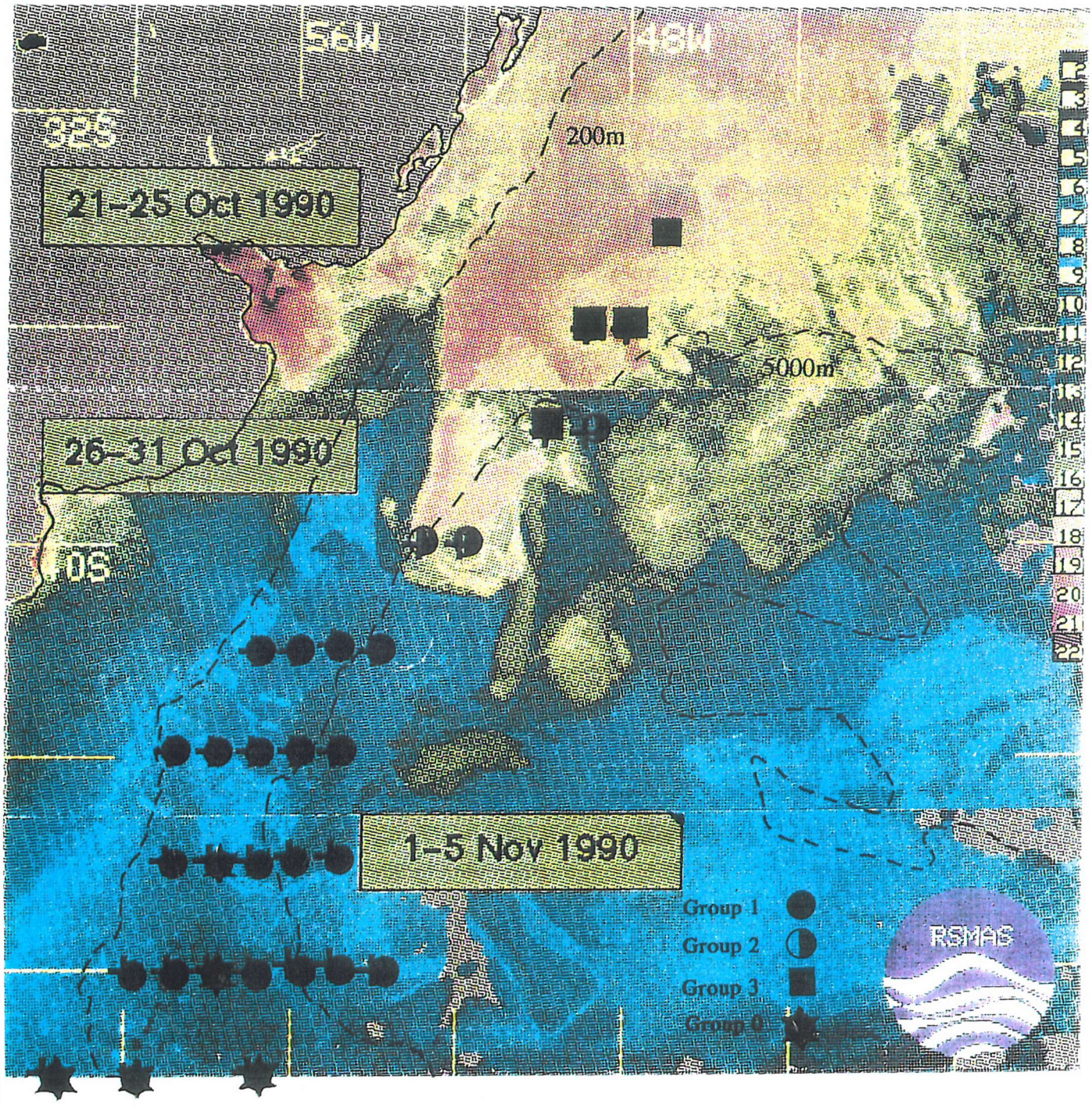


Fig. 7.2c: Integrated satellite images during 1990 survey period with 1990 Bongo station groups superimposed

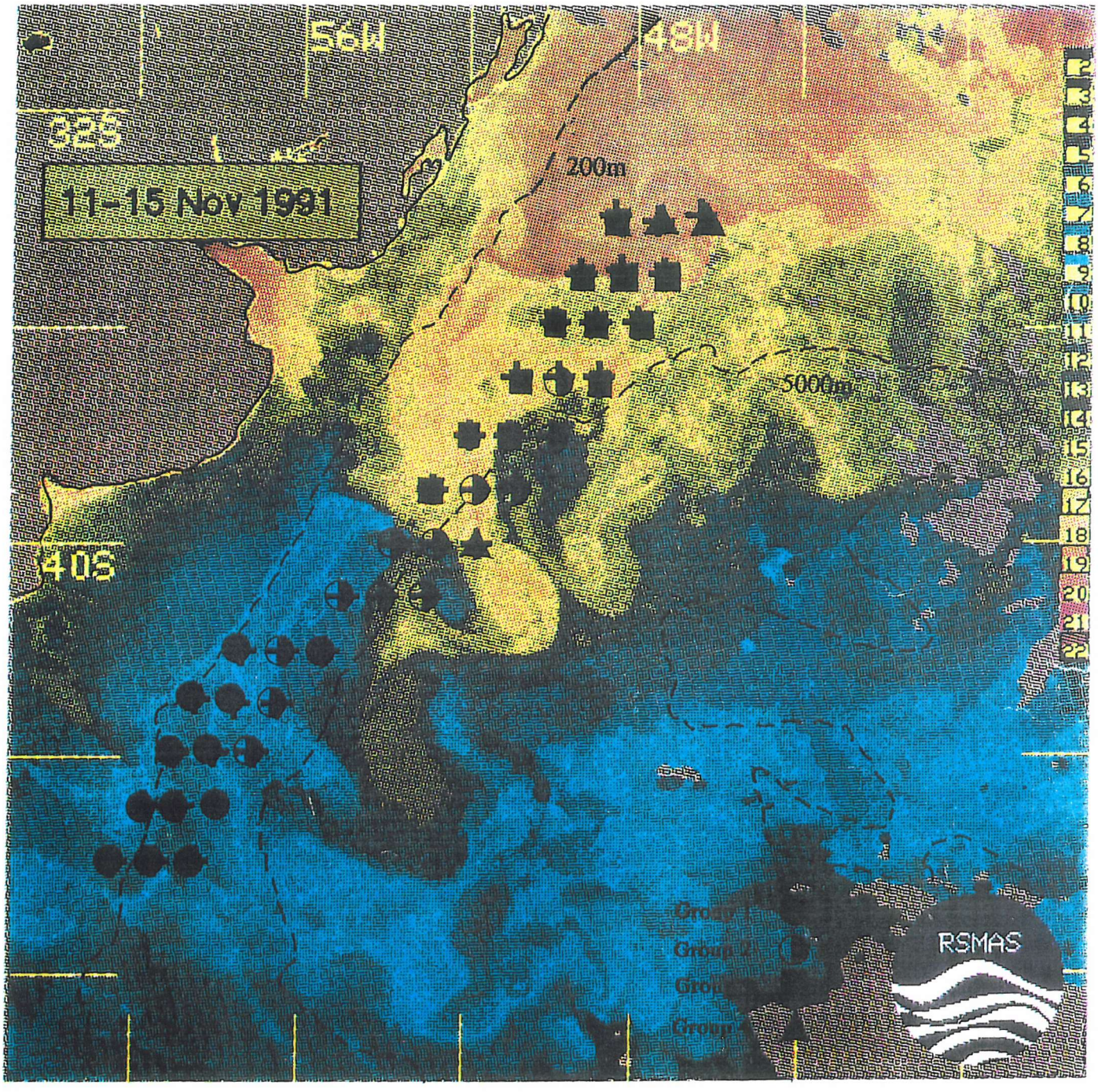


Fig. 7.2d: Satellite image during 1991 survey period with 1991 Bongo station groups superimposed

7.3 Results and Interpretation

7.3.1 Station group distribution

The geographic distributions of the station groups produced from the 1990 and 1991 classification analyses are presented in figs. 7.3a and 7.3b. It can be seen that the station groups had distinct geographic integrity in both analyses. Station groups that were approximately geographically equivalent in the 1990 and 1991 surveys have been given the same codes (ie 1, 2 or 3) to facilitate comparisons between the surveys. The geographic ranges of certain further groups are not directly comparable to groups in the other analysis as a result of the differing absolute coverage of surveys and these groups have been given unique codes. For example, in 1990 it can be seen that there is one group occupying stations to the extreme south which is a region outside the coverage of the 1991 survey. This group has been coded uniquely as Group 0, without an equivalent in the 1991 analysis. In the other instance where this was necessary, a group located in the extreme north of the 1991 survey, outside the coverage of the 1990 survey, was coded as Group 4 without an equivalent in the 1990 analysis.

Although 1990 and 1991 station groups with equivalent codes occupy approximately similar geographic regions, their absolute ranges varied considerably between the surveys and it is necessary compare the geographic distributions of these station groups as a first step in analysing inter-annual variation. Station group 1 in 1990 and 1991 (STGRP1'90 and STGRP1'91) have very similar latitudinal ranges but the longitudinal range of the 1990 group is a lot broader than that in 1991. In 1990, it can be seen that STGRP1'90 covers a number of station to the east of 56°W whilst STGRP1'91 is limited to stations to the west of this longitude despite the fact that there

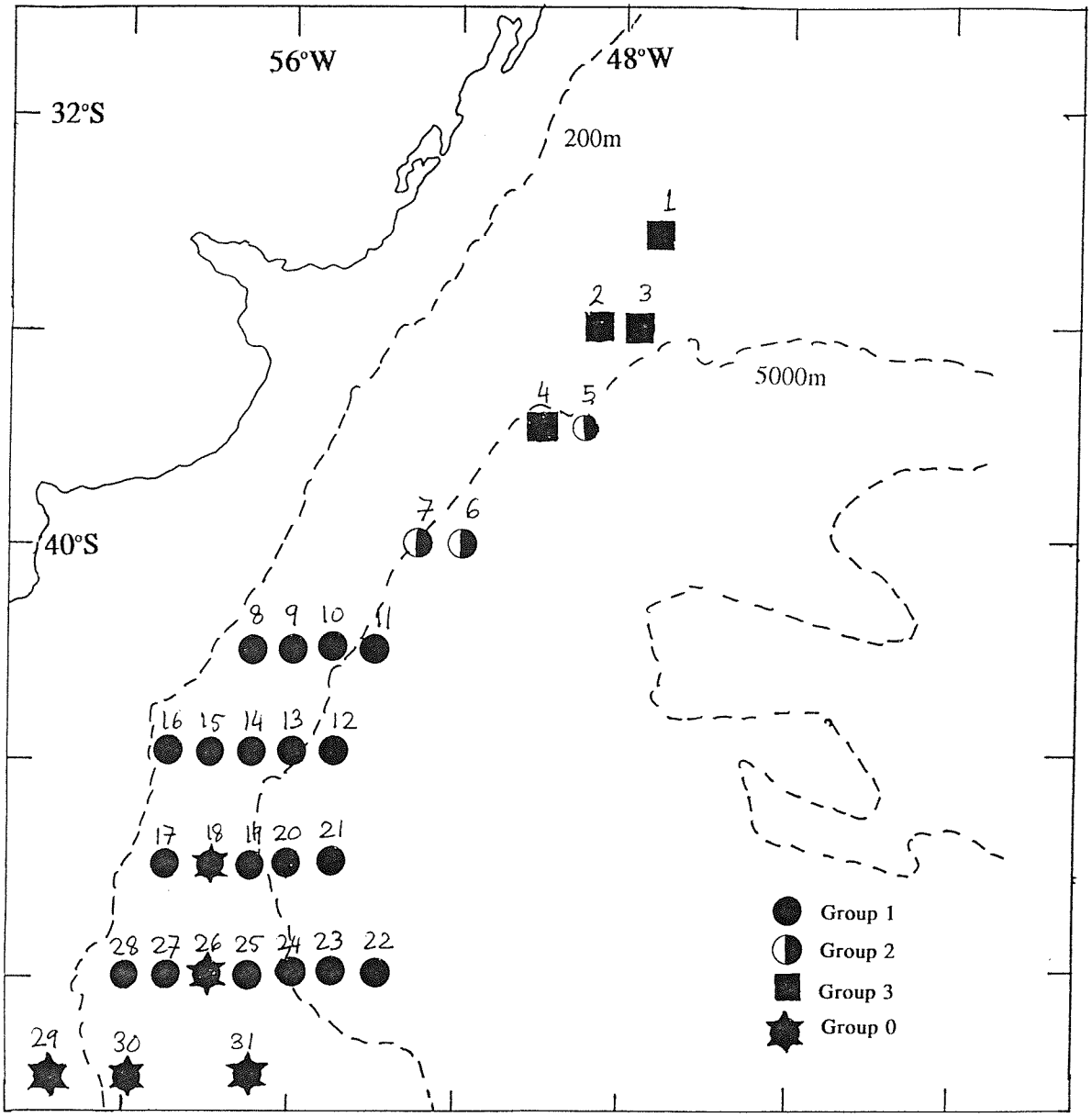


Fig. 7.3a: Distribution of 1990 Bongo station groups (with species and station groups restricted)

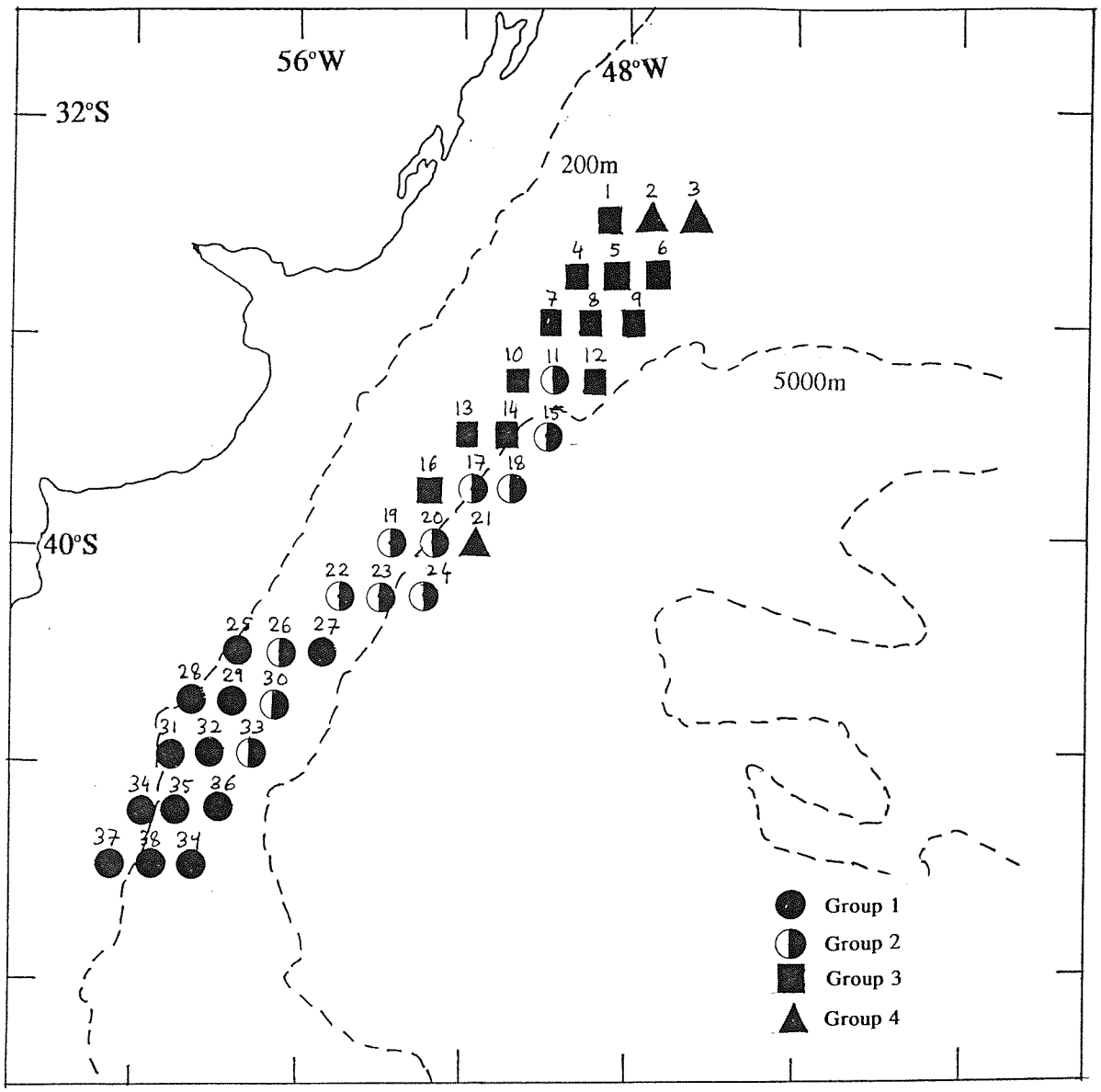


Fig. 7.3b: Distribution of 1991 Bongo station groups

were 5 more easterly stations within its latitudinal range. An even greater variation was observed in the geographic ranges of STGRP2'90 and STGRP2'91. In 1990, the group was limited to 3 stations between 38°S and 40°S, whilst in 1991, the group occupied an extensive geographic range between 36°S and 44°S encompassing 12 stations. The same pattern was evident when comparing STGRP3'90 and STGRP3'91, with the 1990 group occupying a much more limited geographic range than the 1991 group. The absolute southern limits of these groups were nevertheless very similar and the more extensive range of the 1991 group to the north was probably a result of latitudes below 40°S being sampled much more extensively in the 1991 survey.

In broad terms, the distribution patterns correspond with those seen in RMT8 analyses (ie. Falklands, PFZ, Transition and STZ groups) although at a finer scale, the position of station group boundaries and ranges differ considerably from those of the RMT8 groups.

7.3.2 Species composition

The comparison of species most strongly associated to station groups is a further important aspect to determining the equivalence of community distribution patterns between years. As outlined in the methods, the same species were used in the 1990 and 1991 classification analyses, so the difference between years is with respect to the variance in the station group affiliations of these species rather than any absolute differences in the species lists.

In Tables 7.2(i) and 7.2(ii), species are listed under the station group to which they made their greatest intra-group similarity contribution. In STGRP1'90 and STGRP1'91, the lists of associated species are almost identical, with both groups

containing *E.vallentini* calyptopes, *T.gregaria* furcilia and *Sagitta gazellae*. Nevertheless, two species were present in one year and absent in the other. *Themisto gaudichaudii* was present in STGRP1'91 but in 1990 it was most strongly associated to STGRP2'90. This species was widespread and abundant throughout a large part of the sampling areas of both surveys. The difference in its affiliations between years is therefore probably more a reflection of subtle changes in abundance rather than any major inter-annual shift in distribution. *T.gregaria* calyptopes were present in the STGRP1'90 but were absent in STGRP1'91 and indeed all other 1991 station groups. It was apparent from the raw data that this early developmental stage of *T.gregaria* was very rarely found in the 1991 survey. It is possible that this may be the result of these stages not being retained in the larger mesh size used in the 1991 survey. However, the presence of early stage furcilia of *T.gregaria* in the 1991 samples make this unlikely because they are almost the same size as the calyptopes and so would also not be retained. A more feasible explanation may lie in the fact that the 1991 survey was carried out slightly later in the season than the 1990 survey and such a temporal shift may have resulted in the 1991 survey sampling populations in a more advanced stage of development.

The only species that was common to both STGRP2'90 and STGRP2'91 was *Euphausia lucens* post-larvae. The other species associated to STGRP2'90 were *Themisto gaudichaudii*, *Sagitta tasmanica* and *S.hexaptera* whereas *T.gregaria* adults and post-larvae were the other members of STGRP2'91. *S.tasmanica*, like *T.gaudichaudii*, showed a cosmopolitan distribution and was found throughout a large part of the survey grid and its strongest association to this Transitional station group agrees with the findings Boltovskoy (1981). *S.hexaptera* is more of a sub-tropical species and, as discussed in Chapter 6, its occurrence south of the STF may be through associations

with warm-core eddies. The fact that *T.gregaria* adults and post-larvae were associated with a different station group to their larvae confirms the findings of the full 1990 Bongo data set analysis in Chapter 6. There, however, *T.gregaria* was associated with shelf stations and the fact that the shelf was not sampled in 1991 has probably resulted in the observed station group association of these stages being displaced to another region ie. STGRP2'91 located in the Transition region.

The fact that STGRP2'90 and STGRP2'91 do not have many common associated species does not mean that these station groups are not analogous. The similarity matrix from which these groups are derived is as dependent on patterns of presence or absence as it is on variance in abundance and the fact that the analyses carried out on both surveys identified a group between the PFZ and the STZ supports the validity of this station group as a consistent feature. The fact that the species associated with the group are not entirely the same is to be partly expected considering that Transitional regions are highly advective environments where immigration and emmigration take place on a grand scale (Boltovskoy, 1986).

There are a number of species common to both STGRP3'90 and STGRP3'91 including *Euphausia recurva*, *Sagitta serrodentata*, *Phronima sedentaria* and *Phrosina semilunata*. The strong association of these species to Group 3 is emphasised by the fact that none of them contribute to the intra-group similarities of any other station group. Nevertheless, there are a few species whose association to Group 3 stations is somewhat puzzling. *S.tasmanica* was found to be associated with STGRP3'91 despite the fact that in 1990, the species was associated with STGRP2'90. Other studies such as Boltovskoy (1981) have defined this species to be mainly associated with Transitional waters and their presence within the STZ would appear to be outside its preferred distributional

range. What is even more perplexing is the fact that animals would have to move upstream against the Brazil Current in order to move from the Transition region into the STZ. This suggests that either a large amount of mixing has occurred, from features such as cold water filaments for instance, producing a mixed sub-tropical and sub-Antarctic fauna in the STGRP3'91 region or that a viable population of *S.tasmanica* is present within the STZ region. The same problems are apparent in explaining the association of *T.gregaria* adults and post-larvae to the STGRP3'90 station group. In the 1991 analysis, these stages were found to be associated with STGRP2'91 and in the analysis of the 1990 Bongo full data set, they were associated with the shelf station group. Excluding the shelf stations from this analysis has resulted in the associations of these stages being displaced to another group but the fact that the next strongest association was towards STGRP3'90 rather than to the group neighbouring the Falkand Shelf, STGRP2'90, is somewhat perplexing. Their strong association to stations north of the STF could be the result of the cold-water filament mixing processes as inferred with *S.tasmanica* or they may be the result of advective forces carrying these stages off the northen regions of the Argentinean shelf.

STGRP0'90, which was the one group in the 1990 analysis that had no equivalent in the 1991 analysis, did not have any species showing strongest intra-group similarity contributions towards it. Those species that showed minor contributions towards this group were *T.gregaria* (adult), *Sagitta gazellae*, *Themisto gaudichaudii* and *S. tasmanica*. In the 1990 Bongo full data set analysis, these species were associated with the shelf station group and so the association towards these stations just to the north of the shelf is not surprising.

The one group in the 1991 analysis without a 1990 equivalent was STGRP4'91.

The only species to have a strongest intra-group similarity contribution towards this group was *Stylocheiron* spp. In 1990, this species was a member of STGRP3'90 and it is possible that this further station group would have also been distinguished in the 1990 analysis had the survey sampled more stations at lower latitudes. One interesting feature about the geographic distribution of this group is that, in addition to those stations restricted to the most northerly region of the grid, there is a further isolated station located around 40°S. As will be shown in the following section, this highlights the marked influence of the environment on the distribution patterns of near-surface zooplankton.

7.3.3 Relationship to environmental factors

The multivariate analyses relating the biotic matrices to abiotic variables showed that a combination of bucket surface temperature and latitude were most strongly correlated with the biotic distribution patterns of the Bongo samples in both 1990 and 1991. This contrasts with the findings of the 1990 RMT8 analysis (Chapt. 6) where a combination of water mass location and latitude were found to be most strongly correlated with the biotic similarity matrix. The fact that the same combination of abiotic variables was most strongly correlated with the biotic similarity matrices of the Bongo samples in both years adds to the significance of these findings and provides good grounds to hypothesise that factors relating to temperature variation at particular latitudes are major determinants of near-surface zooplankton community composition in this region.

In figs. 7.3c and 7.3d surface temperature values are superimposed onto the distribution of station groups in 1990 and 1991 respectively whilst Table 7.3(i) shows

	1990 (°C)	1991 (°C)
STGRP0	5.4 - 6.9	
STGRP1	5.7 - 12.3	7.6 - 9.4
STGRP2	13.0 - 13.7	9.9 - 17.3
STGRP3	17.3 - 18.6	17.3 - 21.8
STGRP4		19.7 - 21.3

Table 7.3(i): Bucket surface temperature ranges of station groups

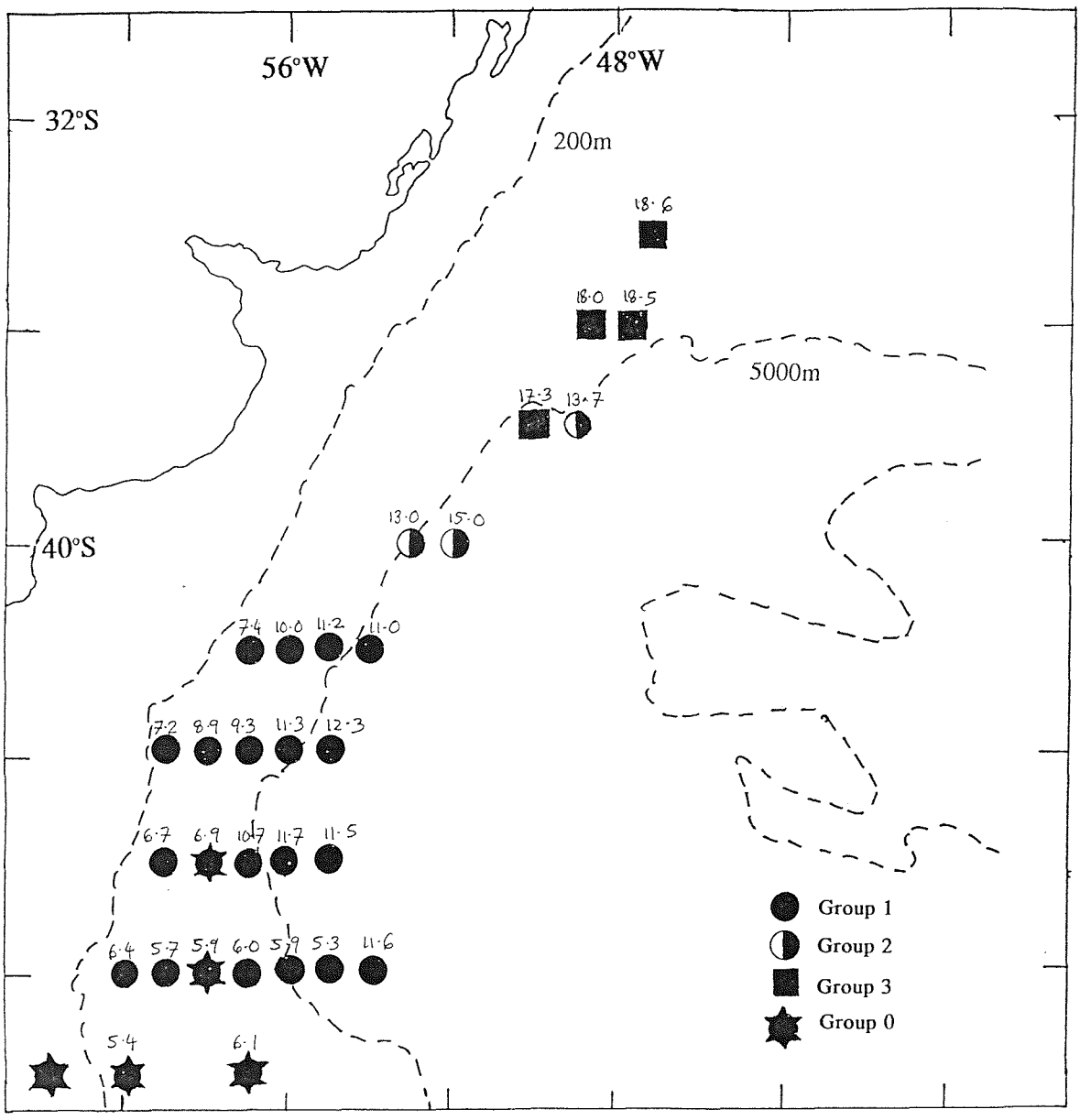


Fig. 7.3c: 1990 Bongo station groups with spot surface temperature superimposed

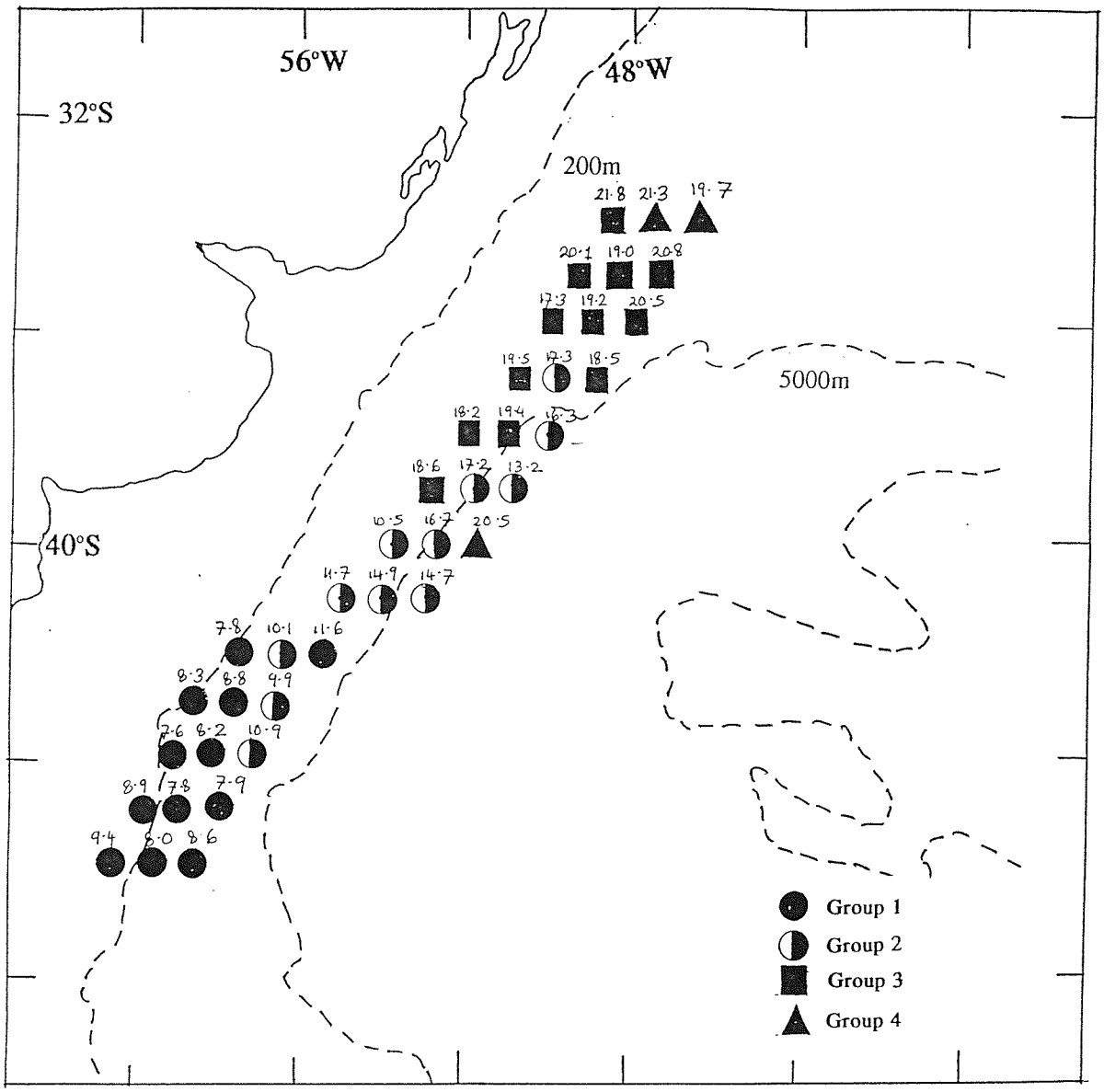


Fig. 7.3d: 1991 Bongo station groups with spot surface temperature superimposed

the temperature range of each station group in both years. From these figures, it is evident that values in corresponding geographic locations between years are more similar at mid to low latitudes than at higher latitudes. In the mid to low latitudes, the maximum temperature difference was +/- 1°C. At higher latitudes, especially in those stations towards the south-west, 1991 temperature values were higher in the 1991 survey by between 2° and 3°C. If factors relating to surface temperature variation are major determinants of community composition then this discrepancy in high latitude temperature values between surveys would be expected to result in greater variability in the distributions of faunal assemblages in this region. However, this is not strictly observed and the group that mainly occupies this region, STGRP1, exhibits quite consistent distributions between years, occupying a latitudinal range from 42°S to 48°S in both surveys despite the fact that the temperature range of STGRP1'90 (5.7-12.3°C) is quite different to STGRP1'91 (7.6-9.4°C). It would therefore seem that, although relative changes in surface temperature presumably affect the distribution of STGRP1 in both surveys, the nature of this influence varies such that the absolute relationship between surface temperature and the distribution of this station group differs between years. However, there does appear to be a strong absolute relationship between the distribution of this group and latitude and it is possible that latitudinally associated effects such as day-length and the strength of seasonality may be relatively more influential than surface temperature on community distribution patterns in this region. Species that made the most significant contributions to the intra-group similarity of STGRP1 were ones that generally exhibited quite widespread distributions and so it would be unlikely that these species were physiologically limited by temperature transitions in this region. In Chapter 6, these same species were found to be mainly

associated with the Falkland Shelf through showing elevated abundances in that region. It is possible that the occurrence of these species in regions outside the Falkland Shelf could be related to advective currents running in an off-shelf direction. This, in turn, may be observed as an indirect latitudinal effect since as the current runs northwards from the Falkland shelf, a corresponding significant decrease in the numbers of expatriated organisms with distance off-shelf would be expected.

The absolute relationship of STGRP2 to both latitude and surface temperature varies between years and it would seem that the nature in which the distribution of this station group is influenced by these two abiotic factors differs in each survey. This conclusion is not surprising considering that the species associated with STGRP2'90 differ markedly to those associated with STGRP2'91 for it is quite likely that these species have different responses to changes in abiotic variables. The biotic and abiotic nature of the Transition region is very much dependent on external influences and considering the profound hydrographic variability in this region, differences in the species composition and distributional limits of faunal assemblages are to be expected. Predicting community composition from measuring the most influential environmental variables is therefore not particularly viable in this region.

The distributional ranges of STGRP3'90 and STGRP3'91 are very similar in terms of both surface temperature and latitude. As well as illustrating that biotic patterns show a consistent absolute relationship to both of these parameters between years, this observation also illustrates that the abiotic parameters themselves are consistent inter-annual features ie. within this region, the same temperature is observed at approximately the same location in both 1990 and 1991. The consistency of the abiotic parameters may be a result of much less mixing within this region possibly through the presence of a

strong surface thermal boundary that separate the waters. A further feature that is apparent when comparing these groups is that the list of associated species are more similar than those of any of the other analogous groups, with many species not being found in any other part of the survey region. The fact that temperature and latitude are consistently co-related to such an extent in this region makes is difficult to discern whether one or both of these parameters is primarily influencing the patterns because it is not easy to distinguish inter-annual differences in their absolute relationships to the biotic patterns. However, closer analysis of the biotic patterns shows that the southern distributional limit of Group 3 is distinctly marked by the 17.3°C isotherm but not also by a discrete latitute. Therefore surface temperature would appear to be more influential than latitude in preventing the southward emmigration of species and the northward immigration of species into the Group 3 region. The mechanism by this may be achieved is nevertheless not clear for, in addition to possibly representing the limits to physiological tolerance to many organisms, it may also mark the position of a strong current or the boundary to a biotically homogenous region within which organisms may act to maintain their distributions.

The anomolous Group 4 station located a considerable distance to the south of the other Group 4 stations shows a particularly distinct relationship to surface temperature because its location correponds with an anomolously high surface temperature value. This value, 20.5°C, is between 3 and 5°C higher than the temperatures of the surrounding stations. Temperature depth profiles identified this station as being located within a warm core eddy and from the satellite images presented in Chapter 4 and the amalgamated images in figs. 7.2a and 7.2b, it can be seen that this eddy has a distinct surface temperature signature. The association of a displaced Group 4 station with a

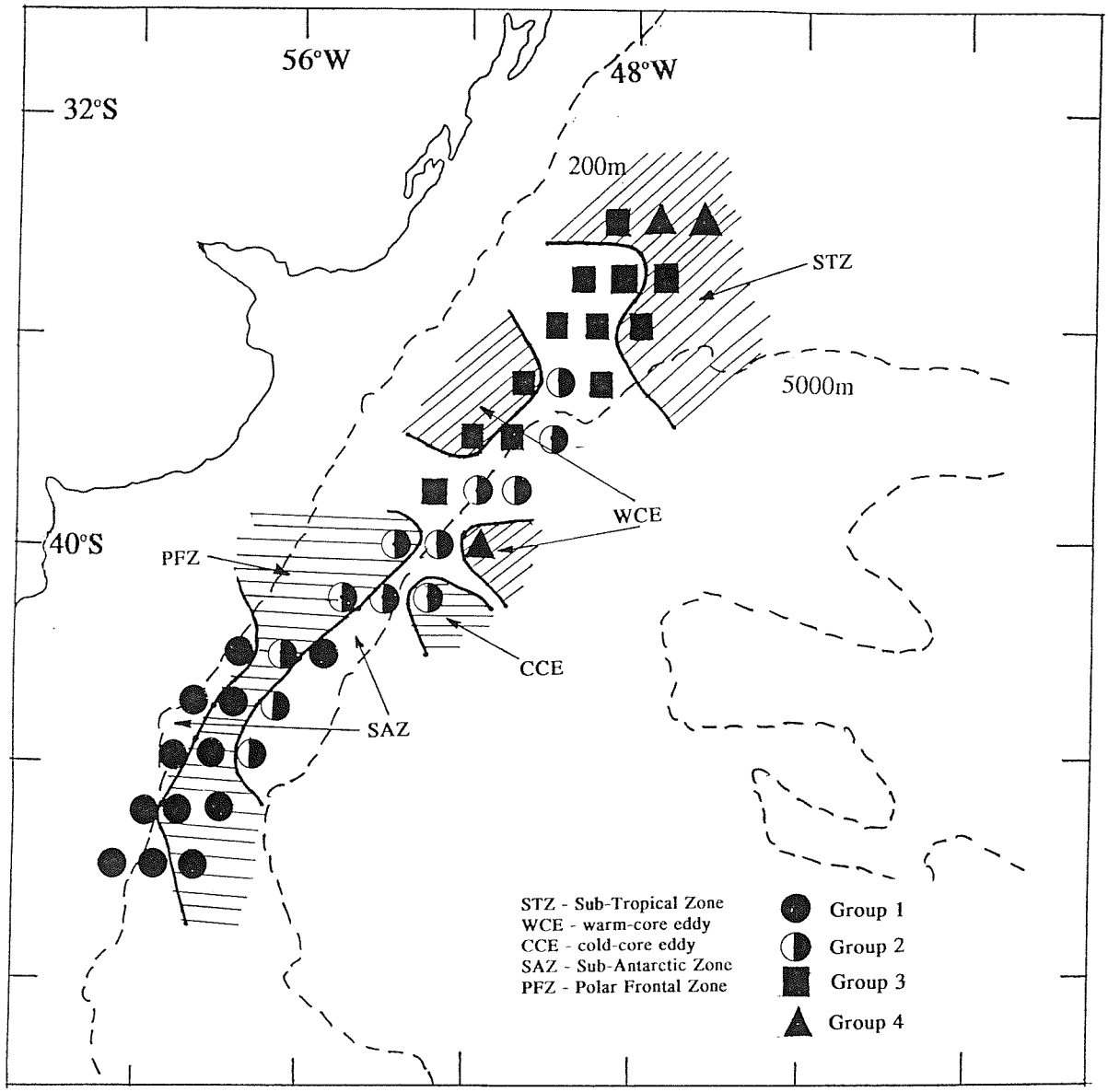


Fig. 7.3e: 1991 Bongo station groups with water mass and eddy boundaries superimposed

warm core eddy not only illustrates that eddies have a profound influence on the distribution of communities in this region but that the integrity of the faunal composition of eddies may be maintained for a considerable distance and time after separation. The temperature-depth profile analysis presented in Chapter 4 identified 2 further eddies within the 1991 survey grid (fig. 4.3b). However, superimposing water mass and eddy boundaries onto the distribution of station groups (fig. 7.3e) showed that neither of these eddies corresponded with any observed anomolous station group locations.

The dynamics of the surface thermal structures located by the satellite images in 1990 and 1991 was discussed in Chapter 4 and one of the main differences between the two surveys was that the warm water was displaced more to the south in 1991 compared to 1990. Furthermore, several warm core eddies appeared to have trajectories within the survey region during 1991. The eddies that were resolved by the images were those that had distinct surface thermal signatures and such signatures become less identifiable over time through interaction with the atmosphere despite the fact that the sub-surface features are still apparent. It is therefore possible that there were other eddies within the 1990 and 1991 survey regions that were not resolved or which had recently interacted with waters within the survey regions and had since dissipated. Given that the trajectories of warm core eddies in 1991 appeared to cross the survey region far more than in 1990, it is feasible that unresolved as well as resolved eddies influenced the faunal composition of 1991 stations far more than 1990 stations. Eddies act to expatriate organisms and often produce faunas with mixed distributional origins, which, in this investigation, is the main characteristic of the Group 2 "Transitional" stations. The wider distributional range of Group 2 stations in 1991 as opposed to 1990 may reflect greater eddy activity.

Although a combination of surface temperature and latitude were found to be

most correlated with the overall distribution of faunal assemblages, the absolute relationship of one or both of these parameters to biotic patterns appeared to change between years in certain regions. The absolute distributional limits of Group 1 appeared to have a similar latitudinal range but a very different temperature range. In Group 3, although temperature and latitude were a lot more co-related, the southern limits were much more precisely defined by the former rather than the latter. Beyond their similarity in terms of their strong correlation to surface temperature and latitude, the varying degrees of influence these parameters have towards different groups may imply that different mechanisms are operating to produce the observed distributions in the various regions. In Group 1 for instance, the stronger absolute adherence of distribution to latitude may possibly be the result of an advective current transporting organisms with decreasing effectiveness with distance off-shelf. In Group 3, the isotherm boundary may reflect the physiological tolerance limit of a number of species, a hydrographic boundary or the limits to a homogenous biotic zone. Many warm core eddies separate from the Group 3 region and so it would partly be expected that species common to Group 3 region would be commonly transported to the Transition region to the south. The fact that many Group 3 species are not found in other parts of the grid would appear to indicate that physiological or behavioural factors are more influential on their distribution pattern in this region than any hydrographic feature. This contrasts with the situation for Group 2 which is the region into which warm core eddies from the north and the cold frontal zone waters from the south penetrate. The distributional limits and the faunal composition of this group would appear to be directly influenced by variations in the hydrography of these surrounding regions. Therefore, the difference in both the distribution and the fauna of these groups between years is not surprising considering

that the group is essentially a melting pot for anything expatriated from regions which have dynamic and variable hydrographic features.

7.4 Discussion

The major finding of this investigation was that environmental factors were a major cause of the observed variation in distribution patterns between years. The dominating influence of abiotic factors on zooplankton distribution patterns is a common finding of many studies carried out in hydrographically dynamic environments such as this one (eg. Tranter et al., 1983; Tremblay and Roff, 1983; Roman et al. 1985; Allison and Wishner, 1986; Brinton and Reid, 1986; Boucher et al. 1987; Thomas and Emery, 1988; Thomas, 1992; Kane, 1993; Chiu and Hsyu, 1994; Pedersen et al. 1995). These types of environments have been termed as "pelagic ecotones" (McGowan, 1971, 1974) where species that have evolved under very different conditions are mixed together and community structure is determined primarily by advective mixing processes.

Logistical difficulties prevent most investigations from studying distribution patterns within a particular region for more than two to three years. The few areas where such investigations have been carried out stand out as case studies towards which many other temporally limited zooplankton investigations compare their results. In many instances, these long-term studies have illustrated that variance in environmental factors is strongly related to observed fluctuations in the abundance and distributional limits of species through time. One example is a study carried out by Colebrook (1978) on data collected by the Continuous Plankton Survey Recorder surveys between 1948 and 1975. Through applying Principal Component Analysis techniques it was found that the differentiation between taxa with respect to their annual fluctuations in abundance was strongly related to density independent, environmental factors which, in total, accounted for half of the observed variability in the annual means. This was mainly reflected in the

observation that there was a clear separation between species associated with warm/low salinity waters, those associated with warm/high salinity waters and those associated with cold waters. It was also found that species which showed similar annual fluctuations tended to have similar geographical distributions.

Long term studies also illustrated other influential features on the abundance and distribution of species, such as the duration of anomalous features and the history of the water, which are not aspects that can be resolved through straightforward comparisons of interannual variance in biotic distributions and abiotic variables over periods of 2 to 3 years. For example, Brinton and Reid (1986) analysed the distributions and biomass of species making up the euphausiid community off the west coast of North America, between 25° and 45°N over a number of years and compared fluctuations in distribution patterns to variance in values of abiotic parameters. It was found that one of the main environmental fluctuations was temperature and that this correlated with changes in dominance of species within the euphausiid community, with northern cold-water species, such as *Euphausia pacifica*, dominating the region during cold years and southern warm-water species, such as *E.eximia* and *Nyctiphanes simplex*, dominating the region during colder years. However, when further considering how the relative biomass of these species fluctuated, it was found that values for *E.pacifica* did not fluctuate between a "normal year" and a "warm year" despite the fact that the distributional range of the species had changed significantly. Nevertheless, there were significant differences between two separate warm years (1978 and 1984), and considering that temperature values were the same the only other feasible explanation for the difference was that higher than average temperatures were observed in the year previous to 1984 whereas normal temperatures were found in the year prior to 1978. Therefore, in this instance,

the duration and history of the feature was more important in influencing interannual biomass variations than the absolute value of the abiotic variables.

The history of water may not only influence biotic patterns inter-annually but also intra-annually as illustrated by studies such as Tremblay and Roff (1983) and Pedersen et al. (1995). Tremblay and Roff (1983) examined community gradients in Scotian Shelf zooplankton over a 3 year period and found that temperature, salinity and distance off-shore were correlated with community patterns. However, substantial differences were found between cruises which were attributed to aperiodic incursion of slope water onto the shelf. Similarly, an incursion of warm water between samples taken in 1989 and 1990 was attributed by Pedersen et al. (1995) to be responsible for distributional shifts seen in copepod species inhabiting the central Barents Sea.

In the above examples, although patterns can be recognised and related to environmental fluctuations such as incursions of different water types, it is difficult to make any insights into the underlying factors causing the observed variations in interannual distribution patterns because it is hard to determine where such incursions originated and what regions they travelled through before arriving at the survey area at the time of sampling. Employing satellite images has been widely shown to be effective in tracking the origin of hydrographic features and determining the main influential factors during the course of their development and subsequent movement (Ring Group, 1981; Legeckis and Gordon, 1982; Olson et al, 1988). Their use has been shown to be potentially very illuminating with respect to monitoring faunal assemblage patterns in areas where the dynamics of the hydrographic environment are dominant influences on the distribution of biotic communities. Two examples that illustrate how effective the use of satellite information may be in this context are the studies of Thomas and Emery

(1988) and Thomas (1992). Thomas and Emery (1988) considered the relationships between near surface phytoplankton and zooplankton concentrations and satellite measured SST's off the west coast of British Columbia. They found that not only were the relationships between plankton concentrations and surface hydrography maintained when compared with satellite measured SST's but that they also formed coherent and relatively unambiguous spatial patterns similar to those in the satellite imagery. Following on from this observation, they subsequently used data of phytoplankton and zooplankton concentrations to make statistical estimates on the ability of satellite images to represent plankton distributional patterns. They found that the "plankton images" of chlorophyll and log zooplankton reproduced the general patterns indicated from the sampling although they did fail to show smaller scale peaks in concentration associated with the hydrographic frontal zone.

The study of Thomas (1992) tested the hypothesis that patterns of surface temperature evident in SST satellite images reflected spatial patterns in zooplankton community composition within the same geographic region as Thomas and Emery (1988). Multivariate techniques applied to the species data produced patterns that had distinct geographic integrity. Furthermore, these groups showed distributions that were similar to patterns in the surface thermal gradients separating hydrographic regimes visible in both *in situ* hydrographic data and satellite images. It was concluded that, in regions where biological spatial patterns are strongly controlled by physical processes, SST satellite images contain valuable information about the spatial distribution of zooplankton communities.

The dominance of physical processes in the south-west Atlantic would also appear to be responsible for the correspondence between the distribution of certain faunal

assemblages and thermal features observed in SST satellite images in this investigation. Distributional limits such as the southern limit of Group 3 appeared to correspond with the transition between warm sub-tropical and cold sub-Antarctic waters in both 1990 and 1991 and the location of a southerly Group 4 stations coincided with the presence of a warm core eddy resolved in the 1991 images. However, the satellite images, did not correspond with the boundary separating Group 1 from Group 2 in either 1990 or 1991 despite the fact that this region is probably as dominated by advective forces as anywhere else in the study region. Furthermore, the *in situ* measurement of surface temperature revealed that absolute temperature in this region differed between 1990 and 1991 with seemingly only a moderate effect on the location of the faunal boundary. Nevertheless, information contained within the satellite images may be of use in this instance also since it may reveal the histories of waters entering this region and the probable effects on the faunal composition the may have.

Mesoscale eddies probably have a considerable influence on the fauna of this region, especially within the Transition zone between the sub-tropical and sub-Antarctic waters. The physical aspects of their formation and structure in the south-west Atlantic have been studied by Legeckis and Gordon (1982) but the inter-seasonal or inter-annual variability in these features is yet to be discerned within this region. Comparison with other dynamic regions where mesoscale eddies are produced may nevertheless be instructive in the temporal variability of these feature and the potential impact they have on the faunal composition of regions. Most of the eddies that occur within this region of the south-west Atlantic are warm core eddies formed either through the pinching off of wave like meanders or sheer instabilities in the warm Brazil Current water (see Chapt. 4). A similar process appears to result in the shedding of sequences of warm core eddies

from the Tasman Front in the East Australian Current and also in the Gulf Stream. Studies carried out on the zooplankton composition of eddies in these regions showed that there was a gradual transition in the associated fauna through time with slope water species invading and increasing in biomass (*East Australian Current*: Tranter et al., 1983; Young, 1989; *Gulf Stream*: Roman et al, 1985; Davis and Wiebe, 1985). The biomass of chlorophyll-a has also been observed to be higher than the surrounding waters in satellite images from several studies (Tranter et al., 1980; McCarthy and Nevins, 1986) which is somewhat surprising considering that the eddies originate in oligotrophic waters. Yentsch and Phinney (1985) illustrated that this productive capacity was the result of two mechanisms, isopycnal mixing bringing deep, nutrient rich water to the surface and convectional mixing followed by stabilisation. Therefore, the slope water species would appear to be invading a region of higher productive capacity and, considering the unique faunal composition of the eddies, their success may also be a result of the depleted effect of predation on their populations. One possible mechanism by which invasion can occur is through lateral mixing at the surface layers (Olson, 1986) or through a process termed as "seeding". In the study of Davis and Wiebe (1985) for instance, whisp-like streamers of slope water were resolved becoming entrained in the warm-core eddy and it was proposed that these injected the ring with "inocula" of slope water animals.

In relation to the south-west Atlantic, the above studies suggest that the frequent occurrence of warm-core eddies would increase the production of the region into which they are shed, most notably in the Transition, such that population abundances and biomass would be elevated. More importantly, with respect to community composition, eddy shedding would appear to expatriate considerable numbers of warm-water species

beyond their normal distributional range. In this investigation, the differences observed between years in the geographic range of the Transition region may be the direct result of the greater eddy shedding such that the mixed fauna Transition group covered a much larger part of the survey grid during 1991 compared to 1990. This was not particularly reflected in the satellite images with there being approximately the same number of eddies in 1990 as 1991. The main difference was that the trajectory of the eddies in 1991 were much closer to the survey grid than in 1990. The southernmost warm core eddy, which was located within the survey grid in 1991, was found to have a profound effect on the observed community composition as discussed earlier but this effect appeared to be comparatively localised and would not explain the greater prevalence of mixed fauna in 1991. Nevertheless, the fact that the general position of the warm surface water associated with the Brazil Current is more southerly in 1991 may be very important with respect to the trajectories of other eddies previous to those resolved in the 1991 images in that they may have crossed the survey region to a greater extent than in 1990.

From observations made on the depth distribution of organisms associated with cold core rings in the Gulf Stream, Wiebe and Flierl (1983) predicted that as an eddy moved through a region, associated species were left in its wake through a mechanism that would appear to equally apply to warm core eddies also. The general principal rests on the observation that there is a downward shift of organisms to maintain themselves within optimum conditions since core waters submerge as waters from the surrounding region start to invade the surface layers. As the organisms reach deeper layers the advective forces associated with the ring weaken and they organisms at these layers are eventually left behind. This then results in expatriates being left in regions over which the ring has passed ie. the wake region. With respect to the present investigation, the

trajectory of eddies in 1991 appear to cross the survey grid to a greater extent than in 1990. It may therefore be expected that more expatriated organisms would occupy the Transition region within the 1991 survey grid through being left in the wake of eddies.

The thermal boundary separating warm surface waters associated with the Brazil current from cold surface waters associated with the Falkland Current shows quite a marked transition in temperature values. A similar feature was observed at the northern boundary of the Gulf Stream where warm waters extending from the Sargasso Sea come into contact with cold Transition zone waters. Studies such as Grice and Hart (1962), Angel (1979) and Wishner and Allison (1986) showed that this Gulf Stream boundary was the northern distributional limit of many warm water species and the southern distributional limit of many cold water species. Although cross stream transport was likely within the southern limits of the Gulf Stream as it passes through the warm Sargasso Sea, Wishner and Allison (1986) stated that surface zooplankton were unlikely to be mixed across the northern front where the Transition waters were encountered. Nevertheless, some mixing was carried out through the formation and decay of mesoscale features and by smaller dynamical disturbances of the Gulf Stream meanders. The same physical processes are evident at the warm current/cold Transition water boundary in this survey region yet the organisms associated with the warm water appear to be distinctly limited by the same isotherm in both years illustrating that boundary is a distinct faunal barrier. Considering the scale and frequency of eddy shedding within this region it is unlikely that organisms are able to either directly or indirectly counteract the influence of physical mechanisms acting to expatriate them. It is therefore more probable that most of the Group 3 organisms associated with the warm waters are at their physiological limits where even subtle changes in their physical or biological

environment would be sufficient to cause mortality. The effect of expatriation has been illustrated in studies carried out by Wiebe and Boyd (1978) and Boyd et al. (1978) on *Nematoscelis megalops* in the north-west Atlantic where there was a cessation of growth, a drastic reduction in the number of males compared to females, reproductive incapacitation and ultimate extinction. More rapid effects of expatriation were also illustrated by Bushing and Fiegenbaum (1984) who found that warm water chaetognaths transported into cool shelf waters in a Gulf Stream intrusion near Chesapeake Bay were already dead or dying in the water column when sampled.

Unlike the Group 2/3 boundary, the Group 1/2 boundary is not distinctly defined by the same isotherm in both years. Indeed the surface temperatures associated with station groups differed by up to 2° to 3°C between years. This would suggest that physiological constraints were not of primary importance in limiting the distribution of species associated with these regions. The near vicinity of the Falkland Current, especially towards the south-west of the survey grids, would suggest that the region is a classic ecotone where advective processes are the primary determinant of distribution. As discussed in Chapter 6, some organisms, especially larvae which are restricted to the surface layers, simply act as tracers of the advective path of the current and may have distributions that extend to regions which are a considerable distance from their point of origin. Nevertheless, other taxa, especially adults that have a greater capacity to control at least their vertical distribution, may not act as simple tracers but interact with different currents such that the net effect is to broadly maintain a geographic position. Wishner and Allison (1986) found that there was a distinct differentiation in the dispersal of various species of copepods within the Gulf Stream that was principally attributed to different diel vertical migration patterns. According to the depths that were occupied,

different taxa had different probabilities of downstream and cross stream transport with downstream transport being more probable in the warm, high velocity core a few hundred metres at depth and at the surface near the northern edge whilst cross stream was most probable at the surface around the southern edge. Although the temperatures associated with Group 1 and its boundary limits differ between years, the actual species composition remained relatively constant. It is therefore possible that the interaction between the advective influence of the Falkland Current and the behaviour of these organisms remains relatively constant and that the main variable between years is differential entrainment of waters and fluctuating climatic influence on physical parameters.

One of the aims of this investigation was to try and define the relationship between the environment and faunal assemblage patterns such that the distribution of zooplankton communities in this region could be predicted from simple measurements such as *in situ* temperature and analysis of satellite image sequences. Thomas and Emery (1988) for instance, found that the statistical relationships between thermal patterns in satellite images and patterns in zooplankton and phytoplankton concentrations off the coast of British Columbia were sufficient to use the images in both an interpolatory and a predictive role. However, such an approach is only strictly valid where the biological component to plankton distributions (ie. nutrient uptake, grazing, diel vertical migration) is reduced in relation to or strongly correlated with the physical component (ie. mixing and advection). This was true in the case of Thomas and Emery (1988) but from the analyses carried out in this investigation, the biological component has been found to have, in some cases, profound implications in the resulting distribution patterns.

Nevertheless, it does seem that the 17.3°C isotherm was found by this

investigation to be a distinct and consistent faunal barrier and although it may be valid to use this isotherm for predicting the southern distributional limits of warm water fauna, many further observations would be necessary to verify this point. However the Group 1 and 2 boundary would be much harder to define using physical measurements alone because distributions in this region appear to be influenced by the interaction between advective forces and the behavioural characteristics of entrained organisms. The extent of the geographic distribution of Group 2 may be predicted to some degree through analysing the displacement of warm water meanders and the trajectories of warm core eddies but defining an empirical relationship may again be difficult.

Being unable to define absolute, empirical relationships between the distribution and abundance of faunal assemblages and physical parameters also makes it difficult to make any useful contribution to predictive models of interannual variability in zooplankton stock within the region. Nevertheless, being able to compare the relationship between distribution patterns and physical parameters between years has revealed a great deal about the factors regulating faunal assemblage patterns in this region and has highlighted that the most influential factors may not be the same in different regions. Studies such as these may lead to a much greater understanding of the functional links between the biota and the environment at the community level. Furthermore, they may assist in the design of models based more on functional details rather than simple correlation based information.

7.5 Conclusions

1, Multivariate analyses carried out on the 1990 and 1991 Bongo data sets produced station groupings that had distinct geographic integrity and which showed a certain degree of correspondence in their distributions between years. Both analyses identfied a group located in warm water to the north (Group 3), a group located in the cold water to the south (Group 1) and a Transition group between these two (Group 2). The absolute geographic ranges of these groups was nevertheless found to vary with the greatest difference observed in the Transition group which occupied a much more restricted area in 1990 than in 1991.

2, Comparison of the affiliations of species to the 1990 and 1991 station groups showed that similar lists of species were associated to Group 1 in the south and Group 3 to the north but the species associated to Group 2, in the Transition region varied between years.

3, Multivariate analyses relating the biotic matrices to abiotic variables found that the strongest correlation was shown towards a combination of bucket surface temperature and latitude in both 1990 and 1991.

4, For Group 3, the southern distributional limit was clearly defined by the 17.3°C thermocline in both 1990 and 1991. This consistent limit to warm water faunal distributions was believed to result from organisms not being able to tolerate environmental change across this boundary rather than through physical restriction since, despite the multitude of mesoscale phenomena within this region that act to expatriate warm water organisms, very few were present within the Transition region.

5, The distributional range of Group 1 appeared to be similar between 1990 and

1991 despite the fact that temperature in this region differed considerably between years. It was believed therefore that physiological restriction in terms of temperature tolerance was not the most profound influence in this region but that interaction between the behaviour of organisms and advective forces was more important.

6, The distributional range of Group 2 did not show any similarities between years with respect to temperature or latitudinal range. It was believed that the mixed fauna of this region had a larger geographic range in 1991 because of the greater past and present interaction with warm core eddies which appeared to have had more westerly trajectories in 1991.

7, Although a certain degree of coherence between the patterns in environmental variables and faunal assemblages was evident, it was concluded that it was not possible to accurately predict distribution patterns in near-surface zooplankton communities from using environmental variables and satellite images alone because there were discernable biological components to distribution patterns and the nature of these components appeared to differ between regions.

8, The comparison of biological distribution patterns to environmental variables between years appeared to be very illuminating with respect to revealing functional relationships between the biota and the environment and the incorporation of satellite information proved to be invaluable in discerning potential influences on distribution patterns that were not possible through *in situ* measurements alone.

Chapter 8 Euphausiid life cycles on the Patagonian Shelf

8.1 Introduction

8.1.1 The importance of euphausiids

The abundance and age structure of species at any one place reflects both the previous reproductive activity and the stage reached in the current reproductive cycle (Atkinson, 1990) as well as size related patterns of mortality and ontogenetic migration patterns. Therefore, to gain a greater understanding of the mesoscale and macroscale distribution patterns revealed in the previous chapters, information on the population ecology of the major zooplankton fauna needs to be obtained. Investigating the population ecology of all zooplankton groups was beyond the scope of this study. However, through concentrating on one zooplankton group that was both a significant part of the zooplankton community and an important link to higher trophic levels, a number of pertienet features about the ecology of zooplankton at the population level may be revealed. Euphausiids provided the most obvious choice of group since they were one of the most numerically abundant groups and also one of the most dominant with respect to displacement volume in the RMT8 samples. Furthermore, they showed regional differences in the composition of euphausiid developmental stages, illustrating that the population ecology of this group is very influential on the zooplankton community structure of the region.

Euphausiids have been found to be an important part of the zooplankton community by a number of studies. Mauchline and Fisher (1969), for instance, concluded that euphausiids represented a major fraction of total biomass of plankton. Ponomareva (1966) considered that euphausiids were of outstanding importance in

marine food chains and estimated a total world biomass of 28 M tons. One feature that makes euphausiids such an important resource in their marked swarming behaviour which results in them being present in huge numbers over large areas. Baker (1970) found surface swarms of *E.krohni* with an estimated density of 31 000 ind. m^{-3} and Forsyth and Jones (1966) found swarms of *Thysanoessa longicaudata* in the Shetland Islands approaching 60 000 ind. m^{-3}. The high biomass, concentrated distribution and relatively large size of euphausiids has made them attractive as a potential major fishery resource, especially *E.superba* in Antarctica where the standing stock biomass (150 M tons, cf. Ross and Quetin, 1988) and annual production (28.6 M to 96.7 M tons per year for Atlantic sector, Trathan et al., 1995) are particularly large. Indeed, at one point it was believed that exploiting the krill resources in Antarctica would double the annual yield of the world's fisheries and solve world hunger problems. However, within such estimates, consideration was not given to the consumption of krill by higher predators or the effect such exploitation would have on the Antarctic ecosystem. A krill fishery has been operating in Antarctica since 1961, but the degree of exploitation has been comparatively low because of the high unit cost of krill and krill products resulting from the remoteness of the resource from recognised markets and limited throughput (Everson, 1984). It is possible that fisheries in areas local to major human populations would be more amenable to exploitation.

Even if the euphausiid populations do not themselves represent a viable fishery resource, they are still important as a primary food source for many commercially exploited species. Two of the main exploited species within the south-west Atlantic are the cephalopods, *Illex argentinus* and *Loligo gahi*. Ivanovic and Brunetti (1994) found that euphausiids along with the hyperiid species, *Themisto gaudichaudii*, were the most

important dietary components of *I.argentinus*. Although dietary studies are yet to be carried out on *L.gahi*, another *Loligo* species native to Irish waters, *L.forbesi* (Collins et al., 1994), was found to have a diet largely consisting of crustacean prey. Therefore, improved knowledge on the ecology of local euphausiid populations would enhance present understanding of the population dynamics of commercially exploited species in the south-west Atlantic greatly.

8.1.2 Review of present knowledge of euphausiid life cycles

General synopsis of euphausiids and variation in life cycles

The euphausiids are grouped within the superorder Eucarida and are characterised by the possession of a carapace fused with all thoracic somites, stalked eyes, the absence of oostegites (ventral flaps which form a brood pouch) and a hepatopancreas. Mating involves the transfer of spermatophores by males to the thelycum of females using modified pleopods. The eggs are fertilised by the spermatophore as they pass out through the genital pore. The spermatophore is lost during moulting along with the chitinous exoskeleton (Nicol, 1989). Eggs are either shed freely into the water column or adhere for a brief period to the posterior thoracic limbs.

Development is non-direct, that is, there is a series of larval stages or instars leading to the adult. There has been debate for a number of decades on the actual number of stages that make up the larval sequence with proposed sequences varying enormously (Frost 1935; Fraser 1936; Dilwyn-John 1936; Boden 1950, 1951; McLaughlin 1965; Soulier, 1965) and although a standardised scheme for categorising the developmental sequence has been proposed by Soulier (1965) this has not been universally adopted. It is generally agreed however that the larvae pass through a series

of 5 major forms which, in turn, consist of a varied number of stages. In order of sequence these forms are the nauplius and metanauplius forms which constitute one stage each, the calytopes, three stages, the furcilia, six or seven stages and the cyrtopia six stages. For some genera, eg. *Euphausia*, the cyrtopia form is omitted. Variation in the larval sequence is common both inter-specifically through the dominance of different larval stages (Macdonald, 1927; Dilwyn-John, 1936) and intra-specifically within different regions and seasons (Einarsson, 1945; Mauchline, 1959, 1965; Sheard, 1953) possibly as the result of variation in environmental factors (Ross, 1981).

The life-cycles of euphausiids are also subject to inter-specific and intra-specific variation. A standard life cycle in temperate regions normally lasts for 1 year and consists of a single breeding episode but many temperate species deviate from this standard pattern. In *Meganyctiphanes norvegica* for instance, although breeding occurs after 1 year, the majority of the population survives to breed a second year (Mauchline, 1980). Other species, such as *Thysanoessa longicaudata* in the north Atlantic exhibit a discrete 2 cohort pattern where the Spring generation matures to breed by Autumn and the Autumn generation forms an over-wintering population that matures and breeds the following Spring (Lindley, 1978). Longer lived species, such as *Euphausia superba*, perform a number of annual spawning episodes and exhibit sexual regression after each one (Thomas and Ikeda, 1987). Ross and Quetin (1983) proposed that the species is capable of extended periods of continuous reproduction within one season. Tropical and certain temperate species, such as *Euphausia pacifica*, have comparatively shorter life-cycles but maintain a high fecundity level through continuous reproduction. Off the coast of California (Brinton, 1976) and Oregon (Smiles and Pearcy, 1971) populations of *E.pacifica* have a portion of breeding females present during all times of the year

although the intensity of breeding varies over time (Brinton, 1976).

Such is the variation in euphausiid life histories that the life cycle of a particular species cannot be generalised from the study of just one region or season. For the purposes this study, although certain features of the life cycle of Patagonian shelf euphausiids can be inferred from studies carried out on the same species elsewhere, it is imperative that seasonal data obtained from the region is examined in order to gain an accurate picture of euphausiid life histories.

Review of studies on euphausiid life-cycles on the Patagonian shelf between 35° and 55°S

The major euphausiid species that occur on the Patagonian shelf are *Euphausia vallentini*, *E.lucens* and *Thysanoessa gregaria*. *Nematoscelis megalops* occurs along the continental slope but is rare on the shelf. Studies on the life-cycles of these species in this region are limited. Three investigations have examined seasonal population patterns (Montu, 1977, 1982; Ramirez and Dato, 1983) with a fourth looking at the distribution of adults and larvae during the Spring spawning period (Curtolo et al. 1990). It is necessary to review these studies in detail to give appropriate background to this investigation. The methods, the geographic coverage and the temporal coverage of each will be described initially and the observations of these studies will then be drawn together in Table 8.1(i) with the conclusions being briefly compared in a subsequent section

Montu (1977, 1982) - These two studies were based on the same data set with the first concentrating on the general distribution of larval and adult euphausiids and the second examining the life history aspects in greater detail. The data was obtained from 4

identical surveys carried out at approximately 3 month intervals (1969-1970) between 45° and 53°S. Samples were obtained with a biconical net with a mesh diameter of 300μm which was deployed from 100m to the surface, water depth permitting. Each of the 4 surveys sampled 79 stations on average. The 1977 study identified the larval stages of *T.gregaria* using the key of Gurney (1947), *E.vallentini* using Dilwyn-John (1936) and *E.lucens* using Bary (1956). Adults were not staged according to state of maturity in the 1977 study, but females were separated into 1 of 4 stages based on the size of the ovary and the superficial appearance of the eggs (Roger, 1973). The attachment of spermatophores on females was also noted.

Ramirez & Dato (1983) studied euphausiids obtained from a combination of 2 surveys carried out from May 1978 to February 1979. The two surveys were not geographically coincident and the study was restricted to a common area between 49° and 53° S. Samples were obtained by a biconical (Bongo) net with a mesh diameter of 330μm deployed obliquely in the top 100m. A total of 26 stations were sampled with a temporal sequence covering 9 months. Furcilial stages were identified using the key of Soulier (1965) and stages earlier than this were not considered. Total length (rostrum tip to the end of the 6th abdominal segment) of each specimen was recorded and the maturity state of randomly removed females was discerned using the scale of Roger (1973) (modified to consist of 3 rather than 4 stages). Ovaries were also measured and the attachment of spermatophores on females was noted.

Curtolo, Dadon and Mazzoni (1990) considered euphausiids collected during one cruise between 20th October and 11th November, 1978. The survey area covered 46°S and 36°S. A biconical (Bongo) net with a mesh diameter of 505μm was deployed obliquely at 37 stations although the depth fished was not given. Larval identifications were based

on keys by Frost (1935), Dilwyn-John (1936), Bary (1956), Mauchline (1971) and Casanova (1974), although larval *E.vallentini* and *E.lucens* were not distinguished. No length measurements or assessments of adult maturity were made.

	Spring Aug/Sep/Oct	**Summer** Nov/Dec/Jan	**Autumn** Feb/Mar/Apr	**Winter** May/Jun/Jul
E.vallentini Montu (1982)	Main period of reproduction. Majority of adult population dies	Individuals reached furcilia and juveniles. Second peak in gravid females	Individuals reached furcilia and juveniles. Some become adult at end of Autumn	Individuals become adults. Majority of females gravid. Spawning at the end of Winter
E.vallentini Ramirez and Dato (1983)	Gravid females in late Spring	Onset of spawning (Nov). Furcilia and post-larvae evident by Jan/Feb	Population bimodal with large adults still persisting	Population normalised by May
E.lucens Montu (1982)	Adults dominant. Calytopes appear. Adults die after spawning	Furcilia stages dominant. High % of gravid females	Number of juveniles and adults increase in relation to younger stages	Juvenile and adult stages dominant
E.lucens Ramirez and Dato (1983)	Gravid females appear (Aug)	Spawning occurs (Nov/Dec). Few adults persist	2nd cohort (Jan/Feb) as shown by presence of larvae of 3 and 5mm. Most likely source from rapidly maturing adults from 1st cohort	Bimodal distribution (May), with smaller individuals being post-larvae
T.gregaria Montu (1982)	Intense reproduction. High proportion of gravid females	Furcilia I-III modal category. Low proportion of gravid females	Fucilia dominant. Low proportion of gravid females	Adults dominant. High propotion of gravid females. Intense reproduction late Winter
T.gregaria Ramirez and Dato (1983)	Highest numbers of gravid females apparent. Spermatohpores present on females	Gravid females apparent. Spermatophores present on females. Peak spawning Nov/Dec.	Gravid females apparent. Spermatophores present on females. Large numbers of furcilia and PL apparent Jan/Feb. Large numbers of mature females apparent, mean size lower than in Spring. 2nd cohort possible	
T.gregaria Curtolo et al. (1990)	Furcilia I and II prevalent late Spring/early Summer			Spawning late Winter/early Spring

Table 8.1(i): Major conclusions from studies on the life-cycle of Patagonian shelf euphausiid species

Comparing between the conclusions of these studies (Table 8.1(i)) it is apparent that there are a number of discrepancies in the life histories proposed for the 3 main Patagonian shelf euphausiid species. For *E.vallentini*, the results of Ramirez & Dato (1983) suggest that the timing of spawning was late Spring/early Summer whilst Montu (1982) proposed that spawning takes place in late Winter/early Spring. Furthermore, in Ramirez and Dato (1983), post-spawn adults appeared to persist in the population until late Summer/early Autumn (Jan/Feb) whilst in Montu (1982) all adults were considered to have died by Spring. Evidence for further spawning later in the season appears stronger in Montu's (1982) study with a Summer increase in gravid (final ovaric stage) females as well as the appearance of larvae in Autumn. Curtolo et al. (1990) does not add much information to the issue of whether spawning takes place in late Winter/early Spring or late Spring/Summer since larval *E.vallentini* and *E.lucens* were not separated during identification.

For *E.lucens* gravid females were found in Winter and Summer in Montu's (1982) study as opposed to only in Spring in Ramirez & Dato (1983). Montu (1982) concluded that spawning took place in Spring as opposed to Ramirez & Dato (1983), who considered it to take place in early to mid Summer. Data from both studies provide evidence supporting the production of a second cohort, although Montu (1982) made no comment on its existence.

Differences in the proposed timing of the principal spawning period were also evident for *T.gregaria*. Montu (1982) and Curtolo et al. (1990) suggested that spawning took place during late Winter/early Spring whereas Ramirez & Dato (1983) proposed that spawning occurred in early to mid Summer. Gravid females appeared to be prevalent far earlier in the season in Montu's (1982) study compared to that of Ramirez

& Dato (1983), as did the larvae. Evidence for a 2nd cohort appeared stronger in Ramirez & Dato's (1983) study where there were a considerable number of mature females in early Autumn. The proportion of mature females in Summer and Autumn was low in Montu (1982).

The discrepancies between the above studies may, in part, be caused by the different geographic ranges and temporal integrations of the surveys. The surveys analysed by Montu (1977, 1982) encompassed latitudes of 45°S to 53° S, and each took approximately 3 to 4 weeks to complete. Spatial and temporal averaging of the results produced a large scale view of euphausiid population dynamics on the shelf. The geographic ranges of Ramirez and Dato (1983) (49°S to 53°S) and Curtolo et al. (1990) (46°S to 36°S) were limited by comparison and involved a much smaller number of stations. Direct comparison of these studies is therefore misleading given that euphausiid species found elsewhere have been shown to exhibit different life cycles in different biogeographic regions (eg. *Euphausia pacifica*, Ponomareva, 1966; Smiles and Pearcy, 1971; Brinton, 1976) or even within the same biogeographic zone (Hulsizer, 1971). However, this does pose the problem as to which of the accounts is more accurate and how widely its findings can be applied.

It is quite possible that environmental conditions varied between the surveys which may, in turn, lead to differences in the developmental cycles. Reinterpreting these studies in respect to potential geographic differences in biotic and abiotic conditions may result in a more harmonious account of euphausiid life cycles in this region. Unfortunately, the effect of food availability cannot be investigated because there is little available data. However, Montu (1977) included detailed temperature/depth plots for

each station in the four surveys studied. The paper also included appendices of raw data on larval and adults densities and the exact dates of sampling have been subsequently obtained (D. Boltovskoy, pers.comm.).

To consider differences in the timing of larval pulses in the population, it was decided to reanalyse the data given in Montu (1977), taking into account the exact time and place of sampling and differences in temperature. However, the attainment of sexual maturity and the timing of spawning could not be considered through such reanalysis because the raw data was not available. Nevertheless, it was possible to examine this aspect through analysis of a different set of samples taken by the *Discovery/William Scoresby* expeditions, which surveyed the Patagonian shelf extensively during the 1920's and 1930's, although certain decisions had to be made about the maturity scale applied to adult specimens. Both Montu (1982) and Ramirez and Dato (1983) used Ruud (1932) scale (adapted by Roger, 1973) which considers the size and superficial appearance of the ovaric cells. This scale has been criticised by Cuzin-Roudy and Amsler (1991) who concluded that there was no correlation between germ cell size and development to maturity. Therefore, in order to gain a more accurate picture of maturity patterns, a different maturity scale derived by Makarov and Denys (1980) was used which considers the external secondary sexual characteristics of the animals as well as the size and state of the female ovaric chamber. The external sexual characteristics are an important indicator of the breeding state of the population because the period of spermatophore attachment to the female is relatively brief. As well as being a potential source of adults, the *Discovery/William Scoresby* samples also contained larvae so it was also possible to obtain stage lengths and weights for the determination of growth rates.

In summary, the following investigation will reanalyse the raw data from

previous work on euphausiid populations in this region, giving greater consideration to temporal and geographic differences and the effect of temperature. Seasonal adult maturity patterns will also be determined from *Discovery/William Scoresby* samples using the scale of Makarov and Denys (1980) and regressions of stage to length and weight for larvae and adults will also be carried out to obtain growth rates that will allow comparison to other studies and assessment of the validity of results. Overall it is believed that this approach will give the most detailed insight into the population cycles of euphausiid species on the Patagonian shelf yet obtained.

8.2 Methods

8.2.1 Temperature methods and analysis

Montu (1977) presented temperature data for each station by means of profiles superimposed onto the geographic distribution of stations. The actual data used was not included in an appendix and neither was in obtainable from the author or from the Argentinean Hydrographic Office and so it was decided to extrapolate the data directly from the plots as described in Appendix IVa. Principal component factoring was chosen to analyse the data set because its methods are more harmonious to a continuous data set of this sort (Gauch, 1982). After the initial analysis, a scree test identified 2 factors. The geographic distribution of the stations belonging to factor 1 and 2 are illustrated in figure 8.2a. Those stations that were excluded from the multivariate analysis because they had no equivalent station in Spring were inferred to belong to either factor 1 or 2 according to their position relative to the geographic distribution of the factor groups. In Appendix IVb the defining statistical characters of the 2 groups are considered in detail. In brief temperature factor 1 had a distribution to the north of the shelf although it did also protrude in a coastal region to the south where it may contain waters flowing from the Straits of Magellan. Temperature factor 2 covered the southern, offshore part of the shelf including waters around the Falklands. Factor 2 stations were, on average, colder than factor 1 stations with the mean factor 2 temperature being 1.393°C less than factor 1. Water temperature between 0 and 75m in both regions was highly seasonal and it ranged from low Winter (7.525°C, 0m) and Spring (6.915°C, 0m) temperatures to high Summer (13.138°C, 0m) and Autumn (12.420°C, 0m) temperatures in temperature factor 1 but remained cooler for most of the year in temperature factor 2 with Winter

being colder by approximately 1°C, Spring by 0.6°C and Autumn by almost 3°C. Both factors had strong thermoclines in the Summer with similar surface temperatures. Summer bottom temperatures were slightly higher in the factor 1 region which is probably instrumental in causing a significant difference in the strength of the Summer thermoclines. Generally though, bottom water temperatures changed little throughout the year, being virtually the same in both regions.

8.2.2 Methods used in the reinterpretation of larval and adult densities from Montu (1977)

Montu (1977, 1982) analysed samples taken from 4 surveys which were carried out between 1969 and 1970 by the *Servicio de Hidrografia Naval* in collaboration with the *Proyecto de Desarrollo Pesquero (FAO - Gobierno, Argentina)*. The sampling dates were as follows:

Pesquero XI (Autumn) - 20/3/69 to 17/4/69

Pesquero XII (Winter) - 26-27/6/69 to 15/7/69

Pesquero XIII (Spring) - 13/10/69 to 2/11/69

Pesquero XIV (Summer) - 12-13/1/70 to 30/1/70

Each survey sampled the grid in the same order, in a snake-like fashion starting in the north-west and finishing in the south-west (Figure 8.2a)

To overcome the problem in Montu (1977, 1982) of averaging over the 3 to 4 week cruise period, they were split into 3 to 4 day intervals. One difficulty was the occurrence of temporal breaks in the sampling schedules which varied in timing and duration between surveys. Another problem, as previously discussed, was the fact that the positions of sampling stations were not identical between surveys. Accordingly the

sampling grids of each survey were split up so that (i) temporally, sample groups did not contain the large breaks between samples and (ii) geographically, each of the four sample groups covered equivalent areas in each season (eg. sample group 1 covered the uppermost quarter of the sampling grid in each survey) (Fig. 8.2a). Sample groups, on average, contained 17 stations although this did vary between 11 and 22 stations. Sample group 1 lay within the temperature factor 1 region and sample group 3 within the temperature factor 2 region. Different ratios of temperature factor 1 stations to temperature factor 2 stations were apparent in sample groups 2 and 4 (2:1 in sample group 2 and 3:2 in sample group 4).

8.2.3 *Discovery/William Scoresby* sorting methods

The R.R.S. *Discovery* from 1925-1927 and the R.R.S. *William Scoresby* from 1931-1938 carried out an extended series of surveys of the Patagonian shelf region. A combination of nets were used, euphausiid larvae and adults being captured mainly by the Nansen 70 and Nansen 100 nets. The Nansen 70 had a 70cm mouth diameter and mesh size of approximately 340μm. The mouth diameter of the Nansen 100 was 100cm, with the mesh size being 1560μm before 1927 and 2270μm after 1927. The timing and coverage of the series of surveys varied but, taken as a whole, each season was covered at least once during the 9 year duration of the expeditions.

The major objective of analysing the *Discovery/William Scoresby* samples was to obtain specimens from the same area and the same season as the samples analysed by Montu (1977) so that complimentary studies firstly on the maturity state of adults and secondly on the stage-length and stage-weights of larvae could be carried out. It was therefore assumed that seasonal temperature patterns in the region had remained constant

through time so that the temperature factor regions could be superimposed onto the *Discovery/William Scoresby* sampling grids. Samples from each season were subsequently divided into groups belonging to either temperature factor 1 or 2. Although the process improved the quality of the data set for comparison, it did also result in certain temperature factor regions (eg. Winter temperature factor 1) not containing samples.

All the *Discovery/William Scoresby* samples were preserved in formalin so they were drained and transferred to Steedman's sorting solution (Steedman, 1976) before being processed. During sorting it was necessary to process individuals as randomly as possible so that the size ranges of larval stages and the maturity frequencies of adults were representative. The requisite numbers for each sort category were therefore obtained through an encounter based method. A random sub-sample was placed in a petri dish and individuals were identified, removed and placed into a container for the appropriate category. The procedure was carried out moving from the top right to the bottom left of the dish. Individuals were no longer removed if the required number for that category had been obtained. Sorting continued until either the requisite number for all categories had been obtained or there were no further euphausiids in the sample. More specific details on the sorting methods of adults are further explained in Appendix IVc.

After the individuals were separated from the sample, maturity state was designated based on the scale given by Makarov and Denys (1980). The key was simplified by slight modifications to the labels and the exclusion of further sub-divisions of sub-adults males and females. Such sub-divisions were considered to be irrelevant with respect to resolving maturity patterns in adult populations. Other details were kept

Classification	Description
Female sub-adult	Developing thelycum visible, its colour ranging from white to pale red
Female A	Thelycum bears no spermatophores
Female B	Spermatophores attached to thelycum. Empty space between ovary and body wall.
Female C	Spermatophores attached. Ovary fills thoracic space.
Female D	Spermatophores attached. Carapace noticeably swollen by enlarged ovary
Female E	Carapace swollen in contour, but with large hollow space owing to the recent spawning of eggs. The stress of capture frequently causes the carapace of E-type females to collapse.
Male sub-adult	Developing petasma visible. Ampullae small and pale
Male with spermatophores	Spermatophores extruding from pore on ampullae.
Male without spermatophores	Spermatophores not present in ampullae.
Immature	External sexual features not present
Parasitised	With *Thalassomyces fagei* apparent on the carapace

Table 8.2(i): Classification of adult sexual maturity (modified from Makarov and Denys, 1980)

the same. The key is summarised in Table 8.2(i). The length of every individual was measured from rostrum tip to telson tip with SIGMASCAN electronic digitising apparatus fitted to a Wild 308700 microscope with a measuring accuracy of +/- 0.05mm. The dry weights of all specimens were then obtained through drying samples in a fan assisted oven at 70°C for 36 hours and then weighing on a Mettler MT5 electronic balance.

Larval specimens were identified following the same keys used by Montu (1977), which were Gurney (1947) for *T.gregaria*, Dilwyn-John (1936) for *E.vallentini* and Bary (1956) for *E.lucens* in order that measurements were as directly comparable as possible. Larvae were mostly restricted to N70 samples and they were not as abundant as adults. Although it was preferable to try and obtain individuals from every season and each temperature factor region, the rarity of larvae in most samples restricted the analyses to a limited number of seasons. In fact, for *T.gregaria* and *E.vallentini*, statistically significant numbers of individuals of each stage (ie. 30) were obtained from only a single factor region in one season. In *E.lucens*, adequate numbers were obtained from the factor 1 region in Summer and Autumn.

Each specimen was measured from rostrum tip to telson tip using the SIGMASCAN digitising apparatus. After measurement, the specimen was rinsed in distilled water and placed in a pre-weighed aluminium capsule. A total of up to 10 specimens of known length were placed inside an individual capsule before it was carefully squeezed at the rim to prevent the loss of specimen material during handling. The capsules were placed inside a fan assisted oven at 70°C for 36 hours before being reweighed using a Mettler MT5 electronic balance.

8.2.4 Length and weight measures of larvae and adults

Several problems were encountered in obtaining length and weight values for larval and adult stages which made a number of assumptions necessary. It is important that these assumptions are made apparent before interpretations on population cycles of the 3 euphausiid species are presented.

The most important consideration in the estimation of stage weight is calibrating for dry weight loss caused by chemical preservation. Without direct measurements on fresh specimens, the only other means of accounting for this loss is through literature estimates. Giguere et al. (1989) found there to be between 37% and 43% dry weight loss, dependent on factors such as the length of time preserved and the body length of the specimen. An equation was derived to estimate dry weight loss after 66 weeks (at which time it was assumed that weight losses had stabilised):

$$\ln(\text{dry weight loss}) = 4.1499 - 0.576.\text{Length}^{0.333}$$

The equation was unable to explain 42% of the variance in dry weight loss. Furthermore, no study has considered the potential weight loss after 60 years, during which time long term structural changes may have taken place. Nevertheless, without suitable alternatives, the above equation was applied to estimate true dry weights from the measured dry weights of *Discovery/William Scoresby* specimens.

The dry weights of stages may differ between seasons and regions (Huntley and Brinton, 1991; *Euphausia superba*). Adult specimens were present in sufficient numbers in the *Discovery/William Scoresby* samples to obtain season/region specific weight estimates. The larvae were not so abundant and the only inter-season comparison that

was possible was between Summer and Autumn for *E.lucens* in the temperature factor 1 region. T-tests comparing stage weights between seasons found there to be no significant difference. Considering the lack of seasonal coverage, there is little alternative but to assume that there is no stage weight difference between these and other seasons for *E.lucens*. Furthermore, the same assumption had to be made for the 2 other species, *E.vallentini* and *T.gregaria*, for which statistically significant numbers were obtained in one season only.

Euphausiid larval development is variable and within a species "larvae of the same form can vary in body length at different times" (Mauchline and Fisher, 1969). This causes difficulties in estimating the mean body length of any one stage (Mauchline, 1980). Comparing the Summer and Autumn *E.lucens* larval specimens, significant length differences were found between 5 of the 6 furcilia stages (Table 8.2(ii)). It was therefore preferable that larval stage to length conversions were carried out on a season specific basis. Fortunately, *E.lucens* larvae were rare in Winter and Spring in the data of Montu (1977) and there was no need to obtain stage length values for these seasons. *E.vallentini* larvae from the *Discovery/William Scoresby* samples were only available for the Spring, but again, this was adequate for the larval stage to length conversion of the results of Montu (1977). The major problem was in the stage to length conversion of *T.gregaria*. The larvae of this species are apparent in Montu (1977) in every season but specimens from the *Discovery/William Scoresby* were only available for the Autumn. The Autumn stage lengths were taken to be representative in this case but it is necessary that caution is applied when making any growth comparisons, in terms of length, for this species.

Stage	Signficant difference	Probability	Mean difference	Longest length
Furcilia I	Yes	P=0.044	0.132mm	Summer
Furcilia II	Yes	P=0.001	0.349mm	Summer
Furcilia III	Yes	P=0.001	0.652mm	Summer
Furcilia IV	Yes	P=0.001	0.708mm	Summer
Furcilia V	Yes	P=0.001	0.730mm	Summer
Furcilia VI	No	P=0.125	0.228mm	Summer

Table 8.2(ii): Table of the length differences in *E.lucens* larval stages between Summer and Autumn

8.2.5 Analytical methods applied to larval stage frequencies and adult length frequencies

Larval stage frequency analysis

Only a limited number of larval stages were present in the majority of seasons and stage frequency distributions consequently appeared discontinuous and modal. The modes generally consisted of consecutive larval stages and it was assumed that they were the result of discrete pulses in reproduction. Modal progression analytical methods were therefore applied in order that the fate of cohorts could be traced through time and that larval growth rates could be estimated.

In the case of *E.vallentini*, although more than one cohort was produced per year, there was only a single larval mode in any one season and the mean modal category could be determined directly. In the stage frequency distributions of *E.lucens* and *T.gregaria* however, it was apparent that there was potentially more than one modal group in certain seasons and it was necessary to find a method of discriminating between them. A number of techniques are available to determine whether different modes are statistically distinguishable within stage frequency distributions. The mathematical optimisation model (Macdonald and Pitcher, 1979) is one of the more objective methods but it is not applicable to this data set where only densities and not the sample size is known. Other methods, such as the probability paper method described by Harding (1949) and Cassie (1950, 1954) can be applied to such data. However, the method is quite laborious and involves a degree of subjectivity in the determination of inflexion points. In the few trial cases where the probability paper method was applied, the results did not appear to be any more accurate than through separation by eye. The latter method was therefore considered adequate to separate modal groups. Stages were

converted to lengths and the mean length and standard deviation was determined for each modal group. Modal groups were considered to be valid if their mean lengths were separated by three standard deviations, as advocated by Grant et al. (1987) and Grant (1989). All of the "eye-fitted" modal groups were found to adhere to this criterion.

A modal peak category was determined for each modal group. The modal peak category was defined as being the stage with the highest density within the modal group. The category was most probably produced during the time of peak spawning activity and it was considered to be a good tracer of the progression of the cohort through time. Growth rates were determined by comparing the mean length of the modal peak categories in different seasons and dividing by the number of intervening days.

Adult length frequency analysis

Euphausiid adults, with the exception of certain species such as *E.superba*, exhibit indeterminate growth, ie. they continue to grow during adulthood, so length frequency analysis of adults has the potential of separating cohorts if more than one is present within the adult population. Most adult length frequency distributions appeared to be unimodal and normally distributed but in some cases, length frequency was bimodal or skewed, suggesting that more than one cohort was present. Since adult growth rates are slower than those of larvae, their sizes converge and the criteria applied to separating larval modal groups would be too severe in determining whether more than one modal group was present. It was therefore decided to determine whether there was any significant deviation from the expected normal distribution using the Kolmogorov-Smirnov test. None of the distributions were found to be significantly different from that expected from a normal curve. However, this does not mean that the adult population is

only ever made up of individuals from a single cohort for it is possible that the slowing of growth rates makes the separation of adult generations hard to discern.

8.3 Results and interpretation of euphausiid life cycles

The results for the reanalysis of Montu (1977) are presented in figures 8.3.1(a-d), 8.3.2(a-d) and 8.3.3(a-d). The temperature factor origin of contributing stations is superimposed, through shading, onto the stage-frequency bars. Graphs are given in both linear and log axes (ln(1+100x). The linear axes give a better representation of the absolute differences in density between sample groups and seasons, whereas the log axes give better resolution on relative density changes with and between seasons. Graphs are ordered sample group 1 to 4 in each season and the dates given represent the survey period covered by that particular graph. It is to be noted that sample groups represent analogous geographic areas in all species and in every season (fig. 8.2.2a). In certain log axes graphs, modal groups are drawn in by hand for greater clarity.

The results for the analysis of adults from the *Discovery/William Scoresby* are presented in figures 8.3.1(e-g), 8.3.2(e-h) and 8.3.3(e,f). It was decided to divide the sample population into 1mm size classes. This was considered adequate to resolve any major patterns in size frequency distributions. Different maturity stages were superimposed onto size frequency bars through different shadings. Samples were rarer in the temperature factor 1 region and analyses were not possible on adults from this region in certain seasons.

In the following account, the results from the Montu (1977) reanalysis and the *Discovery/William Scoresby* adult maturity stage analysis are dealt with for each species in turn. Each species section is followed by a consideration of calculated growth rates in relation to estimates from other studies.

8.3.1 Population cycle of *E.vallentini*

Montu (1977) reanalysis

Winter (fig. 8.3.1d) - Adults and post-larvae appeared to be dominant in this season with the only larvae present being a small number of calytopes III in sample group 1. There was a disproportionately low number of post-larvae and adults from temperature factor 1 stations in sample group 4 but the significance of this is not certain.

Spring (fig. 8.3.1a) - Larvae were far more abundant with the absolute and relative densities of adults and post-larvae much reduced from the Winter levels. The absolute density of larvae appeared to increase from sample group 1 to 4, the peak density being 0.3 ind.M^{-3} in sample group 2 and 1.55 ind.M^{-3} in sample group 4.

There was no bi-modality in the stage-frequency distributions of any of the sample groups suggesting the larvae were produced from the same spawning episode. There was a decrease in the number of individuals from the calyptopes stages to late furcilia and the modal peak category appeared to shift to later stages from sample group 1 to 4 (ie. the modal peak category was calytopes III in sample group II, but in sample group IV it was furcilia I).

There have been no studies on the developmental times of *E.vallentini* but laboratory studies have been undertaken by Ross (1981) on *E.pacifica*. The latitudinal range of *E.pacifica* in the north Pacific mirrors that of *E.vallentini* in the south Atlantic and both species have has a similar maximum body lengths so the development of *E.vallentini* is therefore probably very similar to that of *E.pacifica*. Ross (1981) gave median developmental times for individuals at 8° and 12°C. Spring temperatures were approximately 7°C and so the time of peak spawning[1] can be roughly estimated by

[1] Spawning refers to the release of eggs into the water column

extrapolating back from the survey dates using the 8°C development times of Ross (1981). Peak spawning would have occurred between 1/10-3/10 for sample group 2 and between 7/10-11/10 for sample group 3 and 4. Peak spawning time for sample group 1 cannot be calculated because numbers were still rising at cI, making it impossible to determine whether the modal peak category was present. All that can be noted is that the cI stage is achieved in *E.pacifica* at 8°C after 8 days and if the cI level was the modal peak, the peak spawning time in this region would take place at approximately the same time as that in sample group 2.

Extrapolating further from Ross (1981) and assuming that some of the post-larvae originate from this spawning episode, the earliest spawning would have taken place from mid to late August in all sample group regions. It would therefore seem that there was a prolonged spawning effort over the whole Spring period, starting in August and still ongoing in late October/early November.

Summer (fig. 8.3.1b) - Absolute density of individuals had fallen dramatically from Spring to Summer. This was most pronounced in the sample group 4 region which had the greatest larval densities in Spring but hardly any larval stages in Summer and only a moderate increase in the number of adults. Small densities of larval stages were found in sample group 1 and 3 with increased numbers of older stages. This suggests that only the larvae from the tail end of the Spring cohort were still apparent in the water column by mid Summer (Jan). Nevertheless, the fact that there was not a dramatic increase in the number of post-larval and adult stages points either to a large degree of mortality or, alternatively, emigration to another region or to waters below the maximum sampling depth of 100m.

Autumn (fig 8.3.1c) - The low absolute level of larval density was further apparent in

Autumn. The log density graphs do nevertheless reveal the presence of calyptopes and early stage furcilia in sample group 1 and 2, and late stage furcilia in sample group 4. Since larvae are all but absent from the Summer population, it is justifiable to consider these larvae as members a second cohort. This second cohort does not appear to be temperature factor specific because sample group 2 is dominated by temperature factor 2 individuals whereas sample group 1 consists of stations situated entirely within temperature factor 1. There does appear to be a greater density of second cohort larvae in the northerly sample groups (1 and 2) as opposed to the southerly sample groups (3 and 4).

Mean Autumn temperature was 11°C in the temperature factor 1 region and 8.5°C in the temperature factor 2 region. Development times from Ross (1981) for 12°C were applied to temperature factor 1 individuals and for 8°C for temperature factor 2 individuals. For sample group 1, first spawning was estimated to take place around early February and peaked during early March. For sample group 2, first spawning was early February and the peak was around late February. For sample group 4, first spawning was mid February and peak spawning was in late February.

The absolute adult densities were further reduced in relation to Summer levels in all sample groups. The adult population in sample groups 2 and 4 appeared to be dominated by specimens from the temperature factor 2 region, as they were in Winter and Spring.

In summary, there was one major spring cohort (cohort A) which derived from a prolonged spawning period between early August and early to mid November. The peak spawning period was approximately a week earlier in the northerly regions. The greater

relative density of larvae from the temperature factor 2 stations suggests that conditions here were more suitable for spawning and larval development during Spring. A weak second cohort was apparent in the northerly stations during Autumn with a peak spawning period from late February to late March.

Adult absolute densities do not rise in Summer and Autumn as would be predicted via the influx of individuals from the Spring cohort. However, adult absolute densities increased dramatically in Winter where adults and post-larvae were the only stages present. This suggests that the true population was not sampled in the Summer and Autumn and that adults had either emigrated to a region outside the sampling grid or had moved to below the 100m maximum sampling depth. Examples of Summer diapause in temperate euphausiid species have not been widely reported but this may be the result of insufficient sampling since it has been reported to occur in the temperate copepod species, *Calanus finmarchicus* (McClaren and Corkett, 1986; Davis, 1987).

Stage frequencies of *E.vallentini* during Winter

(renanlysed from Montu, 1977)

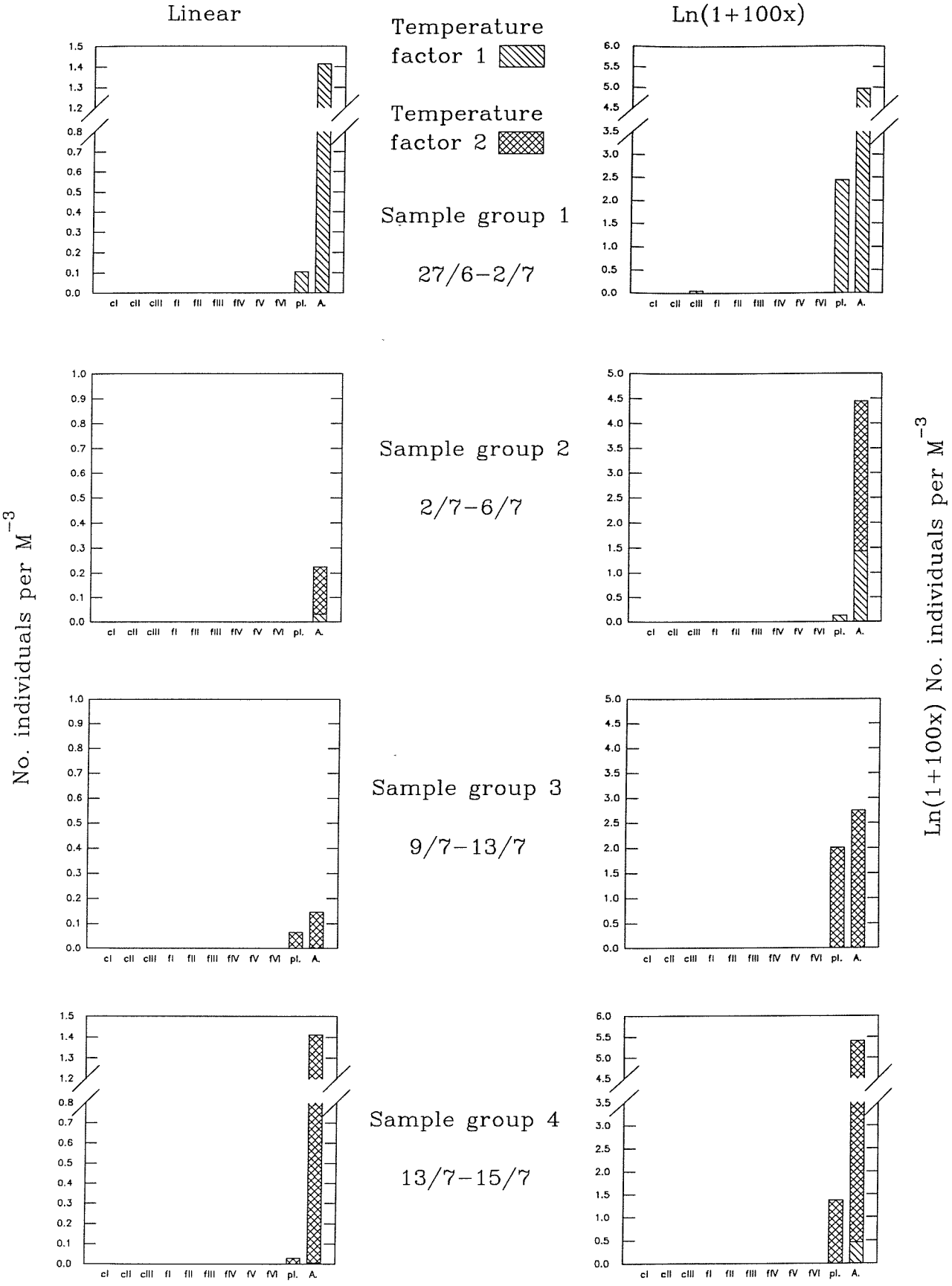


Figure 8.3.1d

Stage frequencies of *E.vallentini* during Spring

(renanlysed from Montu, 1977)

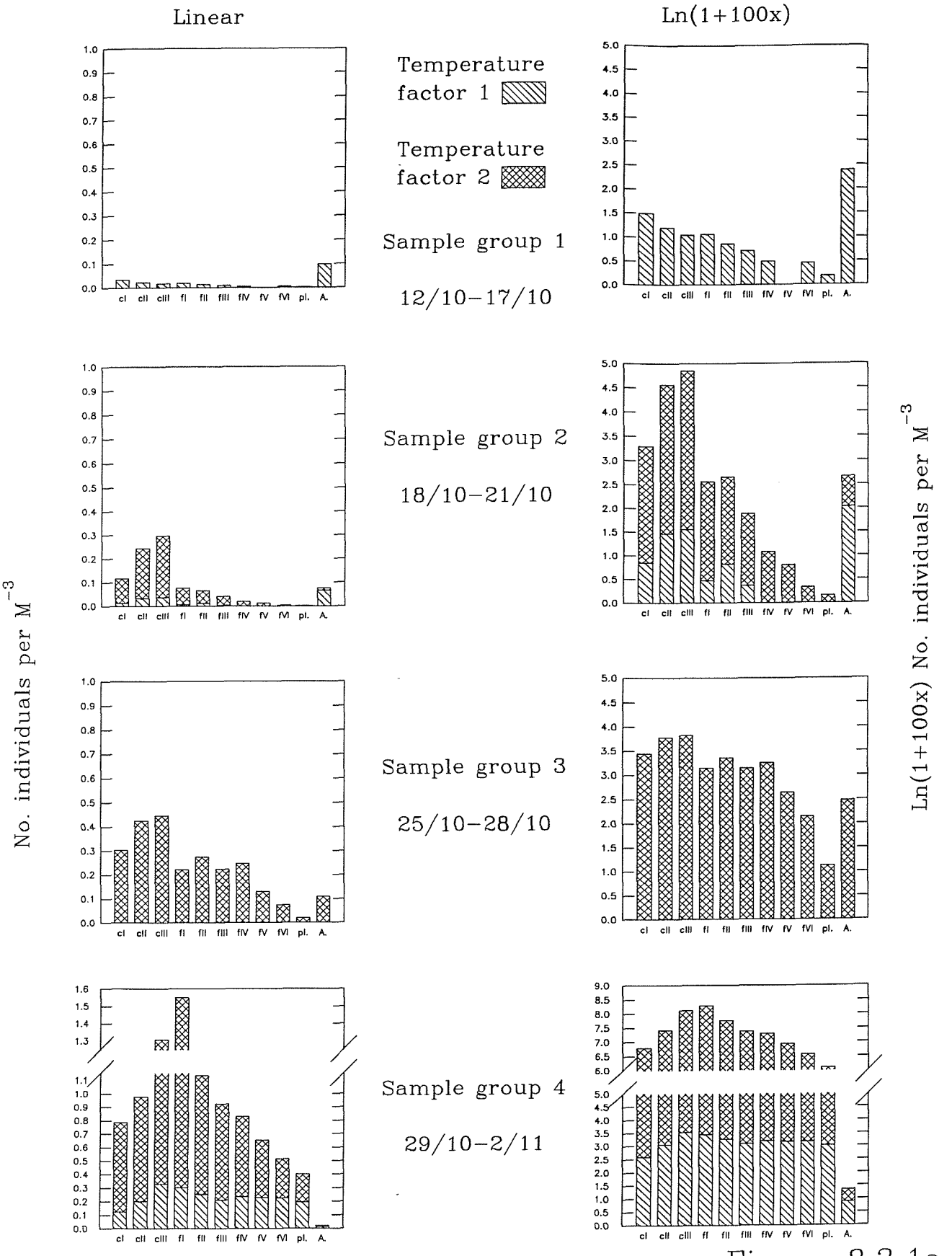


Figure 8.3.1a

Stage frequencies of *E.vallentini* during Summer

(renanlysed from Montu, 1977)

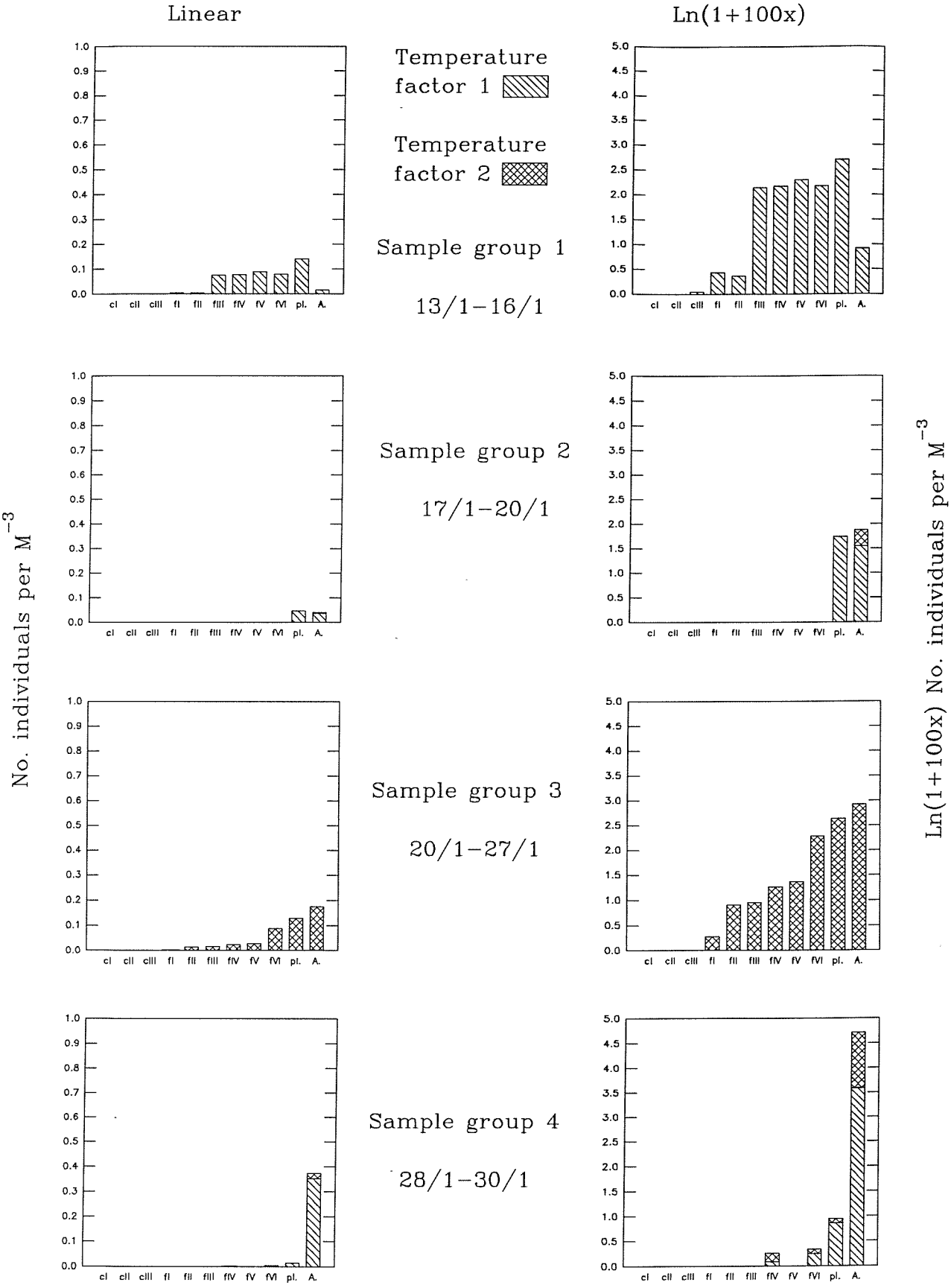


Figure 8.3.1b

Stage frequencies of *E.vallentini* during Autumn

(renanlysed from Montu, 1977)

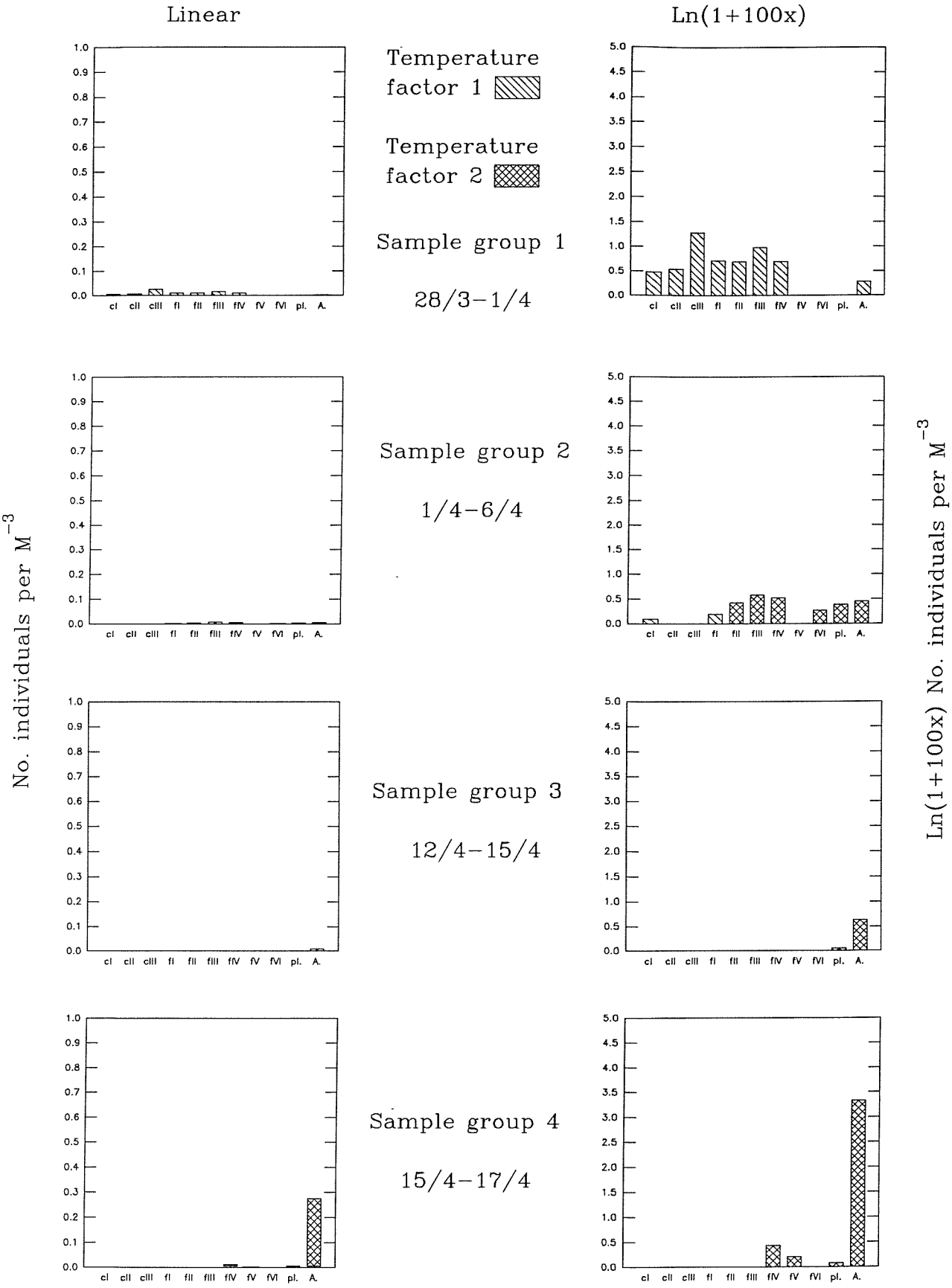


Figure 8.3.1c

Adult maturity

Most data used to analyse adult maturity was derived from the temperature factor 2 region since there were insufficient samples to analyse adult maturity or post-larvae size structure in the temperature factor 1 region during Summer, Autumn and Winter.

Temperature factor 1 (8.3.1e)

Spring - A large number of mature males and females appeared to be in an advanced breeding condition with Female B and D stages being dominant. The size frequency distribution appeared unimodal ranging between 16 and 23mm with the modal peak category at 19mm. Males with spermatophores were dominant in smaller size classes and post-mate females made up greater relative proportions of the larger size classes.

Temperature factor 2 (fig. 8.3.1f,g)

Spring - The length frequency distribution of the adult population appeared to be skewed towards the smaller size. There was a large proportion of mature males across all size classes and despite there being a number of Female D in the larger size classes, most females were Female A. Although Montu (1977) found there to be post-larvae during Spring in the temperature factor 2 region, samples were inadequate to determine their size structure in this season.

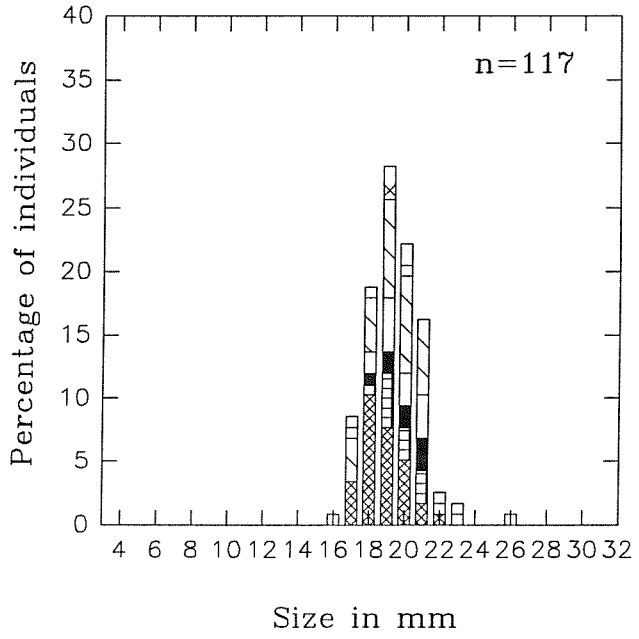
Summer - Compared with the Spring population, the number of larger size classes had reduced in relative proportion. There is a suggestion of bimodality with a primary peak at 14mm and secondary peak at 17mm although a Kolmogorov-Smirnov test did not find the distribution to deviate significantly from normality (K-S distance=0.196, $P>0.200$). The majority of the population was sexually immature, with the remainder being sub-

adult females. The post-larvae consisted of individuals between 8 and 12mm, with the largest numbers being in the 11 and 12mm classes.

Autumn - Although not significantly deviating from normality (K-S distance=0.154, $P>0.200$) the frequency distribution appeared to be bimodal with a primary modal peak at 14mm and a secondary peak at 17mm. The population was made up primarily of immature and sub-adult females. Sub-adult females were dominant in the smaller size classes and there were proportionally more immature individuals in the larger size classes. There was a small number of Female A at 10, 12 16 and 17mm and sub-adult males in the 13 and 14mm size classes. Post-larvae ranged between 9 and 12mm with 12mm containing the greatest proportion of individuals.

Winter - The size frequency distribution appeared unimodal with the majority of the population being sexually immature. Other minor components were sub-adult males and females and Female A. Post-larvae were between 10 and 12mm with 12mm containing the greatest proportion of individuals.

Size classes of *E.vallentini* adults from the *Discovery/William Scoresby* collections in the Factor 1 region



Spring

(19/10/31–21/10/31)

Figure 8.3.1e

Immature

sub–Male

Male with spermatophores

Male without spermatophores

sub–Female

Female A

Female B

Female C

Female D

Female E

Parasitised

Size classes of *E.vallentini* adults from the Discovery collections in the Factor 2 region

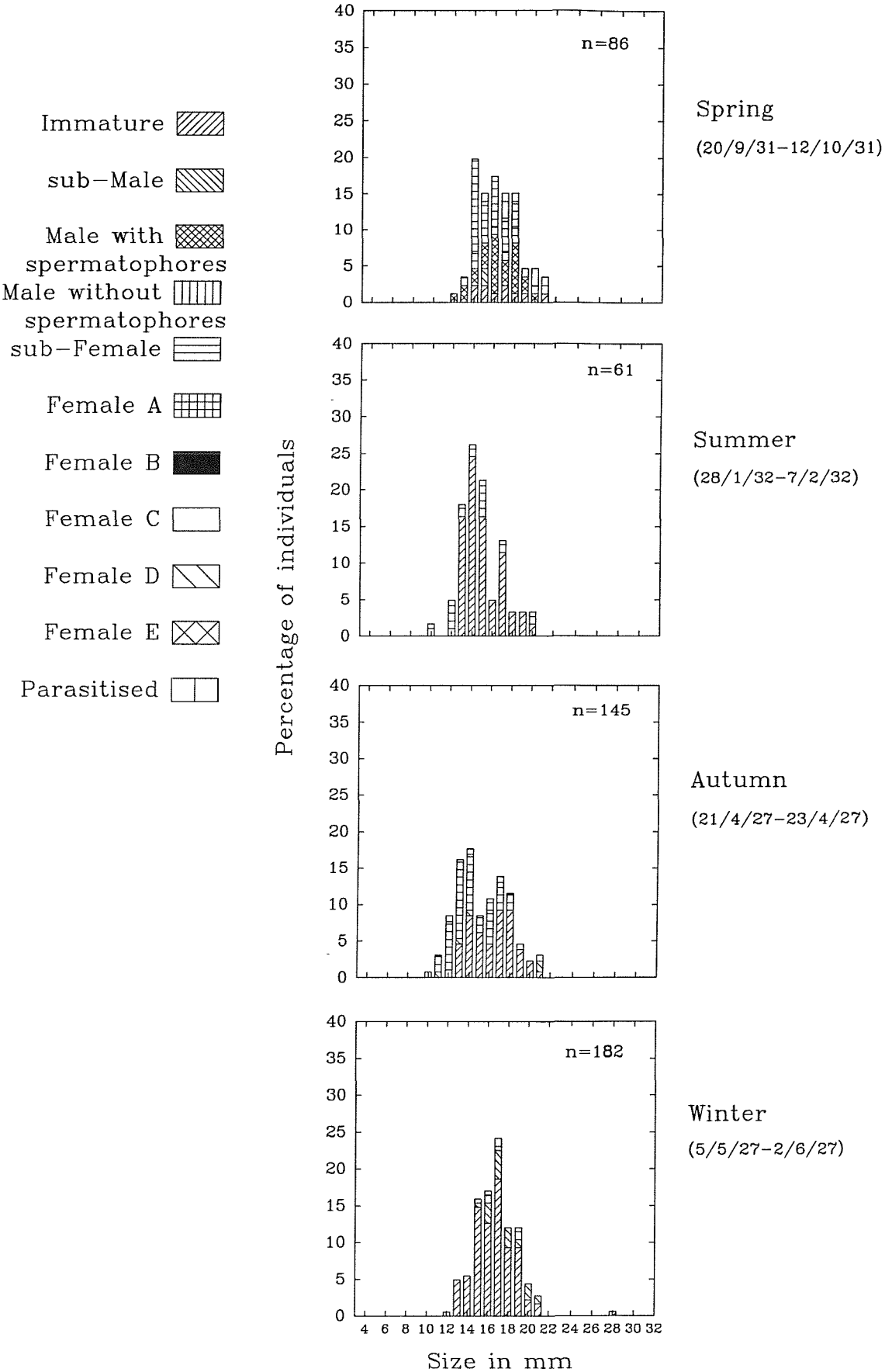


Figure 8.3.1f

Size classes of *E.vallentini* post-larvae from the Discovery collections in the Factor 2 region

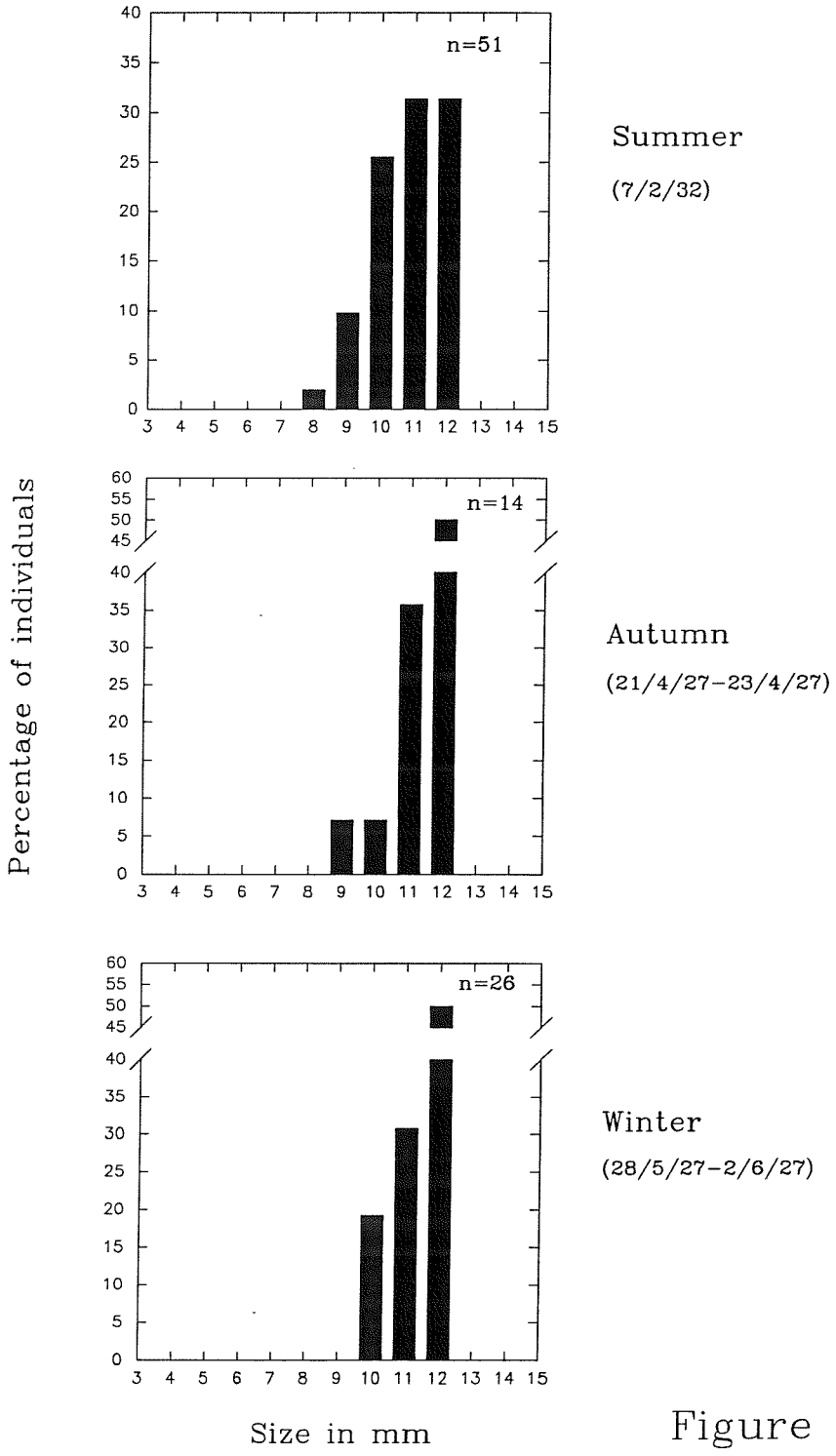


Figure 8.3.1g

The most important prior consideration to interpreting the above patterns is that, from analysing the absolute adult density results of Montu (1977), it is likely that a large part of the adult population migrates to waters below 100m in Summer and Autumn. It is therefore difficult to determine whether the results obtained for Summer and Autumn are representative of size frequency and maturity patterns in these seasons. In terms of maturity patterns, it is probable that if ripe adults were present that they would be within the sampling depths of 0 to 100m since spawning appears to take place within these depths in other seasons. However, it is more difficult to decide on the validity of the size frequency structure since downward migration may take place on a size specific basis.

Taking these reservations into account, a number of things can be determined from these results. The Spring spawning episode seen in the larval analysis is reflected in the maturity state of the adults. Mature males were proportionally more abundant and the majority of females in temperature factor 2 were pre-mated whilst those in temperature factor 1 were post-mated. Summer and Autumn size frequencies show a large proportion of small sized immature adults and, even taking the above reservations into account, their presence does indicate an influx of new adults during these periods. The lack of mature adults in Summer is not surprising since the second, Summer cohort was very much weaker in the southerly, temperature factor 2 region where these adults were sampled. The larger average size structure of the population in Winter, combined with the findings from Montu (1977) of increased adult absolute density suggests immigration into the sampled water column during this period possibly in readiness to spawn. The majority of the population is still nevertheless, mostly immature at this stage of the season.

Life cycle and growth

From the above evidence, the following life-cycle for *E. vallentini* on the Patagonian shelf is proposed:

1, Spawning starts in August and peaks during early October.

2, This is followed by a reduction in the proportion of large individuals in the adult population, accompanied by a significant decrease in absolute and relative densities of adults. The majority of this loss could be attributed to post-mate mortality in males and post-spawn mortality in females. It is also possible that a part of the adult population migrates down to unsampled depths or to areas outside the survey grid.

3, Rapid development of the larvae occurs between Spring and Summer and by late Summer (Jan) only small numbers of larvae, representing the tail end of the Spring cohort, are present.

4, There is an increase in the proportion of small stage adults in Summer, although their absolute densities are low in comparison to the pre-spawn adult population in Winter. It is probable that, on reaching adult size, individuals migrate to depths below 100m.

5, A small second spawning episode occurs in the northerly regions during Autumn. This second cohort either suffers 100% mortality or reaches post-larvae and adult stages by Winter.

6, Through Summer, Autumn and Winter, the majority of larger individuals are either immature or sub-adult. There is a significant shift from sub-adult female domination in Autumn to immature adult domination in the Winter. This is either caused by sexual regression or immigration of immature individuals into the sampled water column during Winter.

7, The normal unimodal size-frequency distribution of the adult population during

Winter signifies that either the pre-spawn population is made up entirely of individuals spawned the previous Spring (0 year class) or of a mixture of 0 and 1 year classes, with the 1 year old class showing no growth since spawning in the previous Spring.

Following the above conclusions about this species life cycle, certain growth estimates can be made:

(i) Spring-Summer larval development - The modal peak categories occurred at cIII for sample group 2 and 3 and at fI for sample group 4. It was not possible to ascertain a modal peak for sample group 1 and it was not included in the following analysis. Spring spawned larvae had mostly reached post-larvae and adult stages by Summer. Relative densities of post-larvae and adult vary between sample groups. In sample group 2 and 3 adult densities were slightly higher than larvae. The modal peak category of post-larvae was at 12mm and for 0 year adults at 14mm. Therefore, on average, the modal peak of the 0 year population is at 13mm (representing lengths between 13.00-13.99mm, giving a mean of 13.5mm). In sample group 4, adult to post-larvae relative densities were approximately 6:1. In this case, it can be assumed that the adult modal peak category alone is a good approximation of the mean modal peak of the 0 year cohort, giving a mean population length of 14.5mm.

Lengths and weights of cIII and fI larvae were measured directly from *Discovery/William Scoresby* samples. Weights for adults were estimated from a length weight regression of adult specimens from the same *Discovery/William Scoresby* samples (fig. 8.3.1h). All "preserved" dry-weights were subsequently converted to "true" dry-weights using the length dependent equation given by Giguere et al. (1989). Growth in terms of length $[(D_i - D_{i-1})/t]$ and weight $[(W_i - W_{i-1})/t]$ are given in Table 8.3.1(i),(ii)

(p. 293-294).

(ii) Summer-Winter adult development - Between Summer and Winter, it is hypothesised that the developing 0 year adult population migrated out of the sampled water column and reappeared during the immediate pre-spawning period in Winter. The average length of the 0 year Summer population, as previously discussed, was 13.5mm. The modal peak in Winter was 17mm (17.5mm average length). Lengths/weight relationships were calculated as above and the results are presented in table 8.3.1(ii) (p. 293-294).

Logged length–weight relationship of male, female and immature *E.vallentini* adults

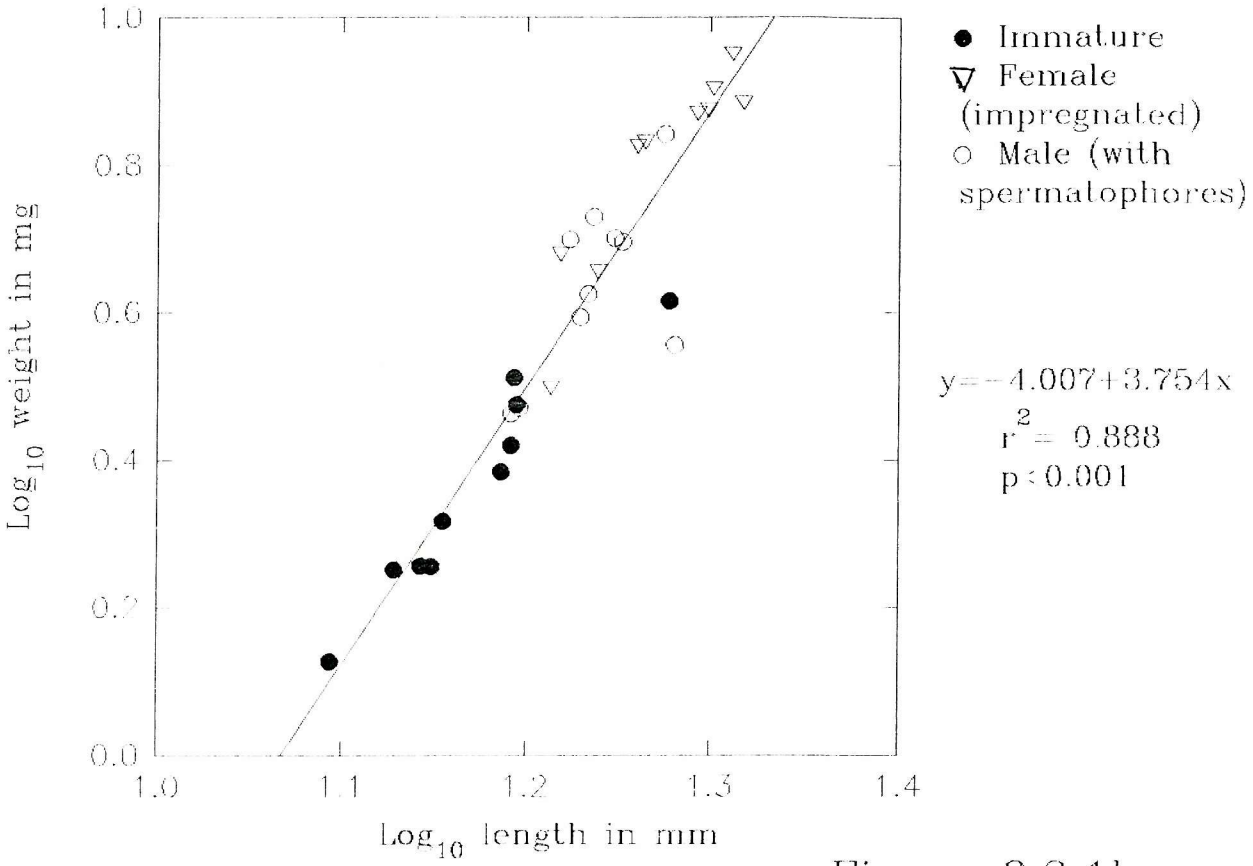


Figure 8.3.1h

8.3.2 Population cycle of *Euphausia lucens*

Montu (1977) reanalysis

Spring (fig. 8.3.2a) - The absolute and relative density of this species was very small in the northerly sample groups (1 and 2) during Spring. The species was completely absent in the southerly groups. Adults were present in the greatest density and those larvae that were present were either calyptopes or early stage furcilia.

Summer (fig 8.3.2b) - The absolute density of larvae and adults was much greater in the northerly sample groups (1 and 2) compared to the southerly sample groups. Sample group 1 had a normal distribution with a modal peak at furcilia IV. The stages with the greatest relative densities in sample group 2 were the post-larvae and adults, with densities decreasing towards the earlier furcilial stages. Calyptopes were absent. The absolute density of sample group 3 was very small, although all the furcilia stages, post-larvae and adults were represented. Sample group 4 had a moderate absolute density of adults with post-larvae, furcilia II and furcilia V also being present.

The modes in each sample group were considered to represent the same cohort (cohort A). Spawning times for sample groups 1, 3 and 4 can be estimated using the developmental times obtained by Pillar (1984b) for South African *E.lucens* specimens held in laboratory conditions with excess food at 13°C. Sample group 2 was not included in the analysis because it comprised mostly of post-larvae and adult stages[2].

For sample group 1, taking the modal peak to be fIV, peak spawning would have occurred in mid December. The earliest spawning time is hard to discern because most developed individuals are at the post-larval stage. Nevertheless, a conservative estimate

[2] Pillar (1984b) only investigated intermoult times of cIII to fVI. Thus, back-calculation of post-larval and adult stages is beyond the scope of this data

would be late November/early December. For sample group 3, taking the modal peak to be fII, peak spawning would have taken place in early January. Earliest spawning probably occurred in mid-December. The stage frequency distribution in sample group 4 is discontinuous and fII is, at best, a rough estimate of the modal peak category. This would put peak spawning at early January with earliest spawning in late December.

Autumn (fig. 8.3.2c) - The absolute densities of adults were greater in the southerly sample groups (3 and 4) compared to the northerly sample groups. Larvae were present in the northerly groups (1 and 2) but were absent from the southerly groups. The stage frequency distributions had modal peaks at furcilia I in sample group 1 and furcilia 2 in sample group 2. The relative density of adults had increased from Summer levels and was greater than that of post-larvae. The furcilia and calyptopes present in the northerly groups were probably the result of a second spawning event (cohort B). Cohorts A and B have been marked in for clarity in fig 8.3.2c.

Taking the modal peak of sample group 1 to be fI, peak spawning of cohort B would have taken place during mid March, with earliest spawning around late February. For sample group 2, taking the modal peak to be fII, peak spawning would have also occurred around mid March with earliest spawning around early March.

Winter (fig. 8.3.2d) - Adults were the dominant stage in all sample groups apart from sample group 1 where post-larvae have approximately the same absolute density. There were a small number of furcilia in all sample groups. These could either be late spawned individuals from cohort B or members of a relatively minor additional cohort. In most cases, the stage frequency distribution was discontinuous between these larvae and the post-larvae/adults that were also present. Therefore, these individuals were considered as a further relatively minor cohort (cohort C).

In summary, evidence from the reanalysis of Montu (1977) indicates that several spawning episodes appeared to take place during the year. The first major cohort (cohort A) derived from a peak spawning period in mid December whilst the second major cohort (cohort B) was derived from a peak spawning period in mid March. Cohort B was mainly detected in the sample group 1 and 2 regions and was dominated by individuals from temperature factor 1 stations. Another minor cohort (cohort C), with low absolute densities, was detected in Winter. Low densities of larvae were also found in Spring but the numbers were too small to conclude that they were representative of a spawning episode.

There did appear to be regional differences in the strength of cohorts. In the northerly sample groups (1 and 2), cohorts A and B were strong and only cohort C appeared minor. In the southerly sample groups, only cohorts A and B were apparent and both were present in comparatively minor densities. However, the absolute density of adults increased in the southerly sample groups during Autumn whilst absolute density of adults in the northerly sample groups remained at a comparatively low level. This suggests that, compared to larvae, adults have a potentially wider geographic range and can move to other regions.

Stage frequencies of *E.lucens* during Spring

(reanalysed from Montu, 1977)

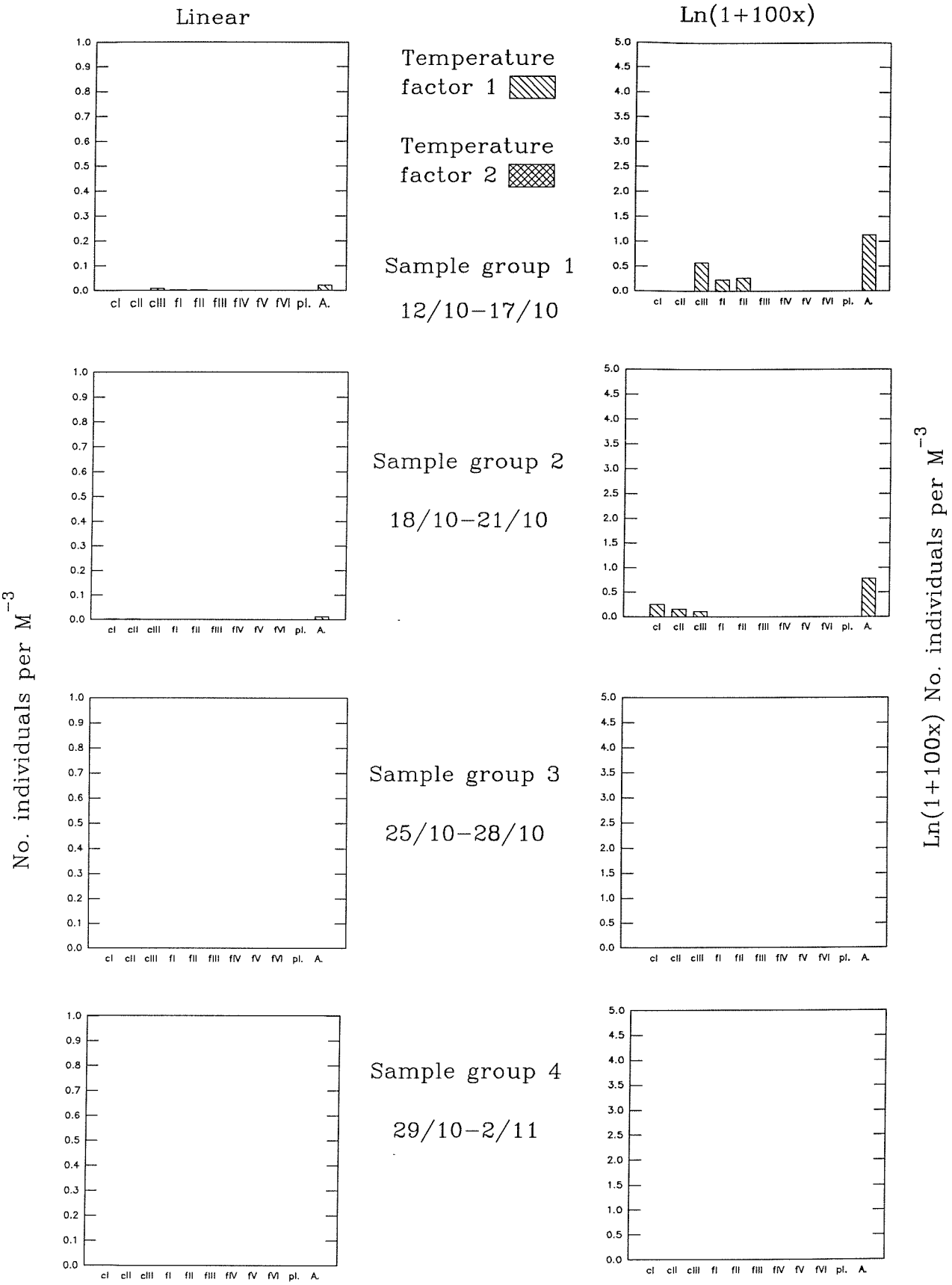


Figure 8.3.2a

Size frequencies of *E.lucens* during Summer

(reanalysed from Montu, 1977)

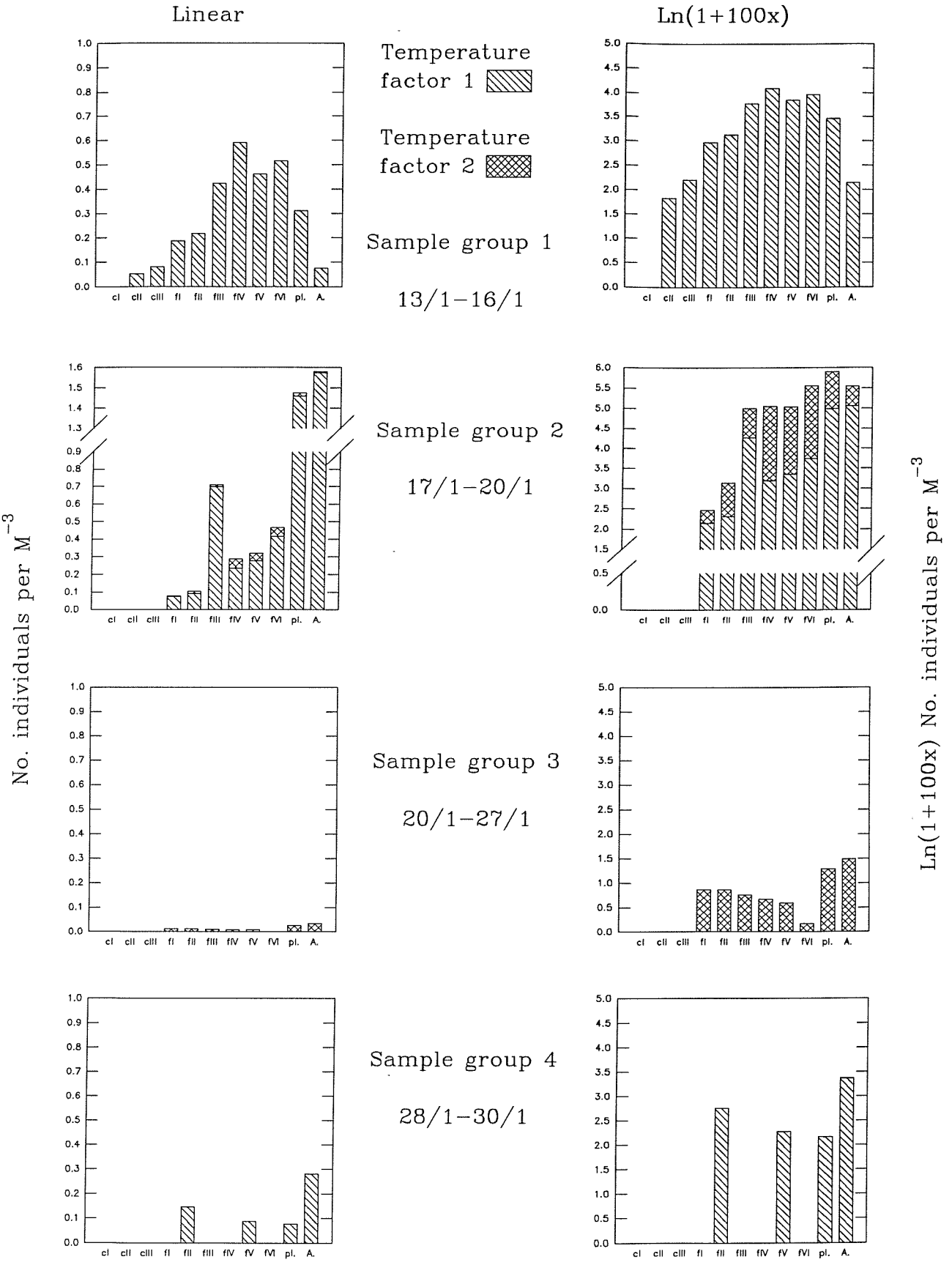


Figure 8.3.2b

Stage frequencies of *E.lucens* during Autumn

(reanalysed from Montu, 1977)

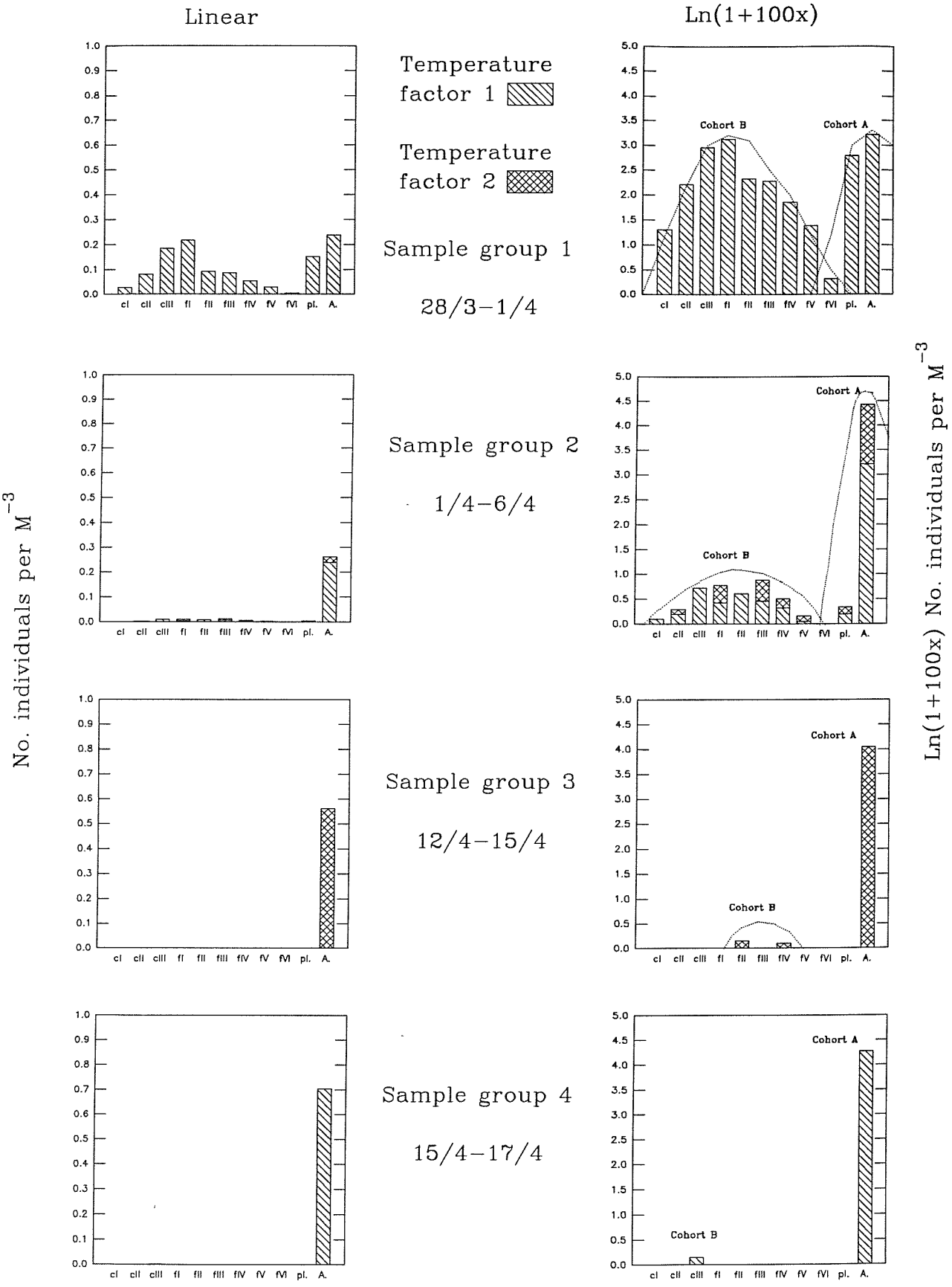


Figure 8.3.2c

Stage frequencies of *E.lucens* during Winter

(reanalysed from Montu, 1977)

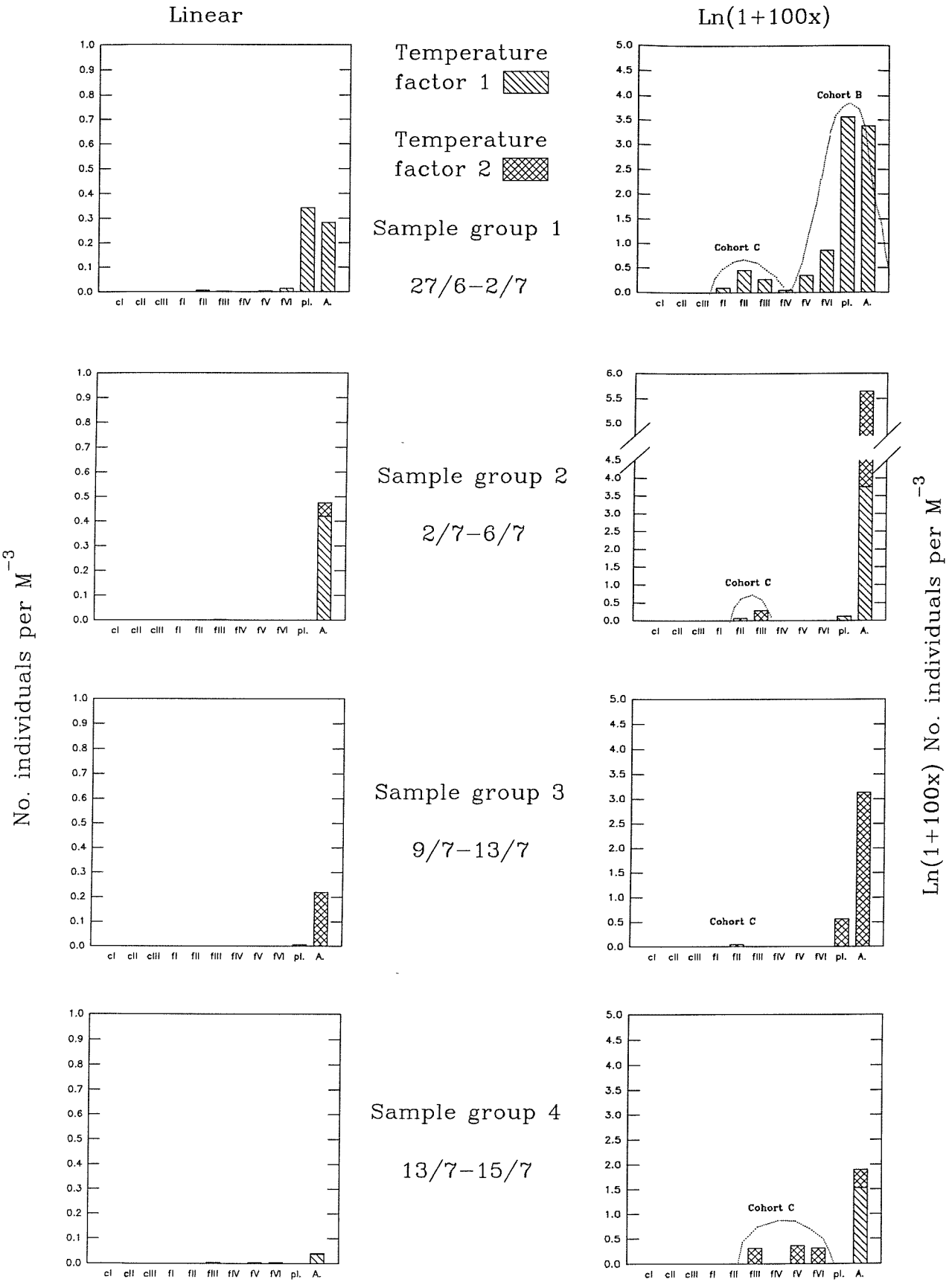


Figure 8.3.2d

Adult maturity

Temperature factor 1 (fig. 8.3.2e,g)

[3] Late Spring - The majority of the population was made up of sexually mature individuals. Males with spermatophores dominated the smaller size classes and Female B, C and D were dominant in the larger size classes. The population was unimodal with a modal peak at 14mm. Although no post-larvae were recorded by Montu (1977) they were present in these samples. They ranged between 7 and 9mm, with the 9mm class being present in the greatest proportion.

Early Summer - The early Summer population had virtually the same maturity and size structure as the late Spring population. Smaller size classes were dominated by males with spermatophores whilst the larger size classes were mainly Female B, C and D. The modal peak category was 14mm. There were a larger proportion of Female A in the mid size ranges compared to late Spring. The post-larvae ranged between 5 and 7mm with the 6mm size class containing the greatest proportion of individuals.

Autumn - The population was made up of mostly of individuals that were either sub-adult or immature. The average size of the population was smaller with the modal peak being at 13mm. The size frequency distribution was unimodal. Although the presence of post-larvae was indicated in the data of Montu (1977), none were found in the limited number of samples available.

Winter - No samples were available in the *Discovery/William Scoresby* collections to analyse the adult/post-larvae population structure of this season within the temperature factor 1 region.

---

[3] Spring and Summer were qualified as being late and early respectively. Their sampling dates were separated by only 2 weeks because samples more suitably spaced in time were not available

Size classes of *E.lucens* adults from the Discovery collections in the Factor 1 region

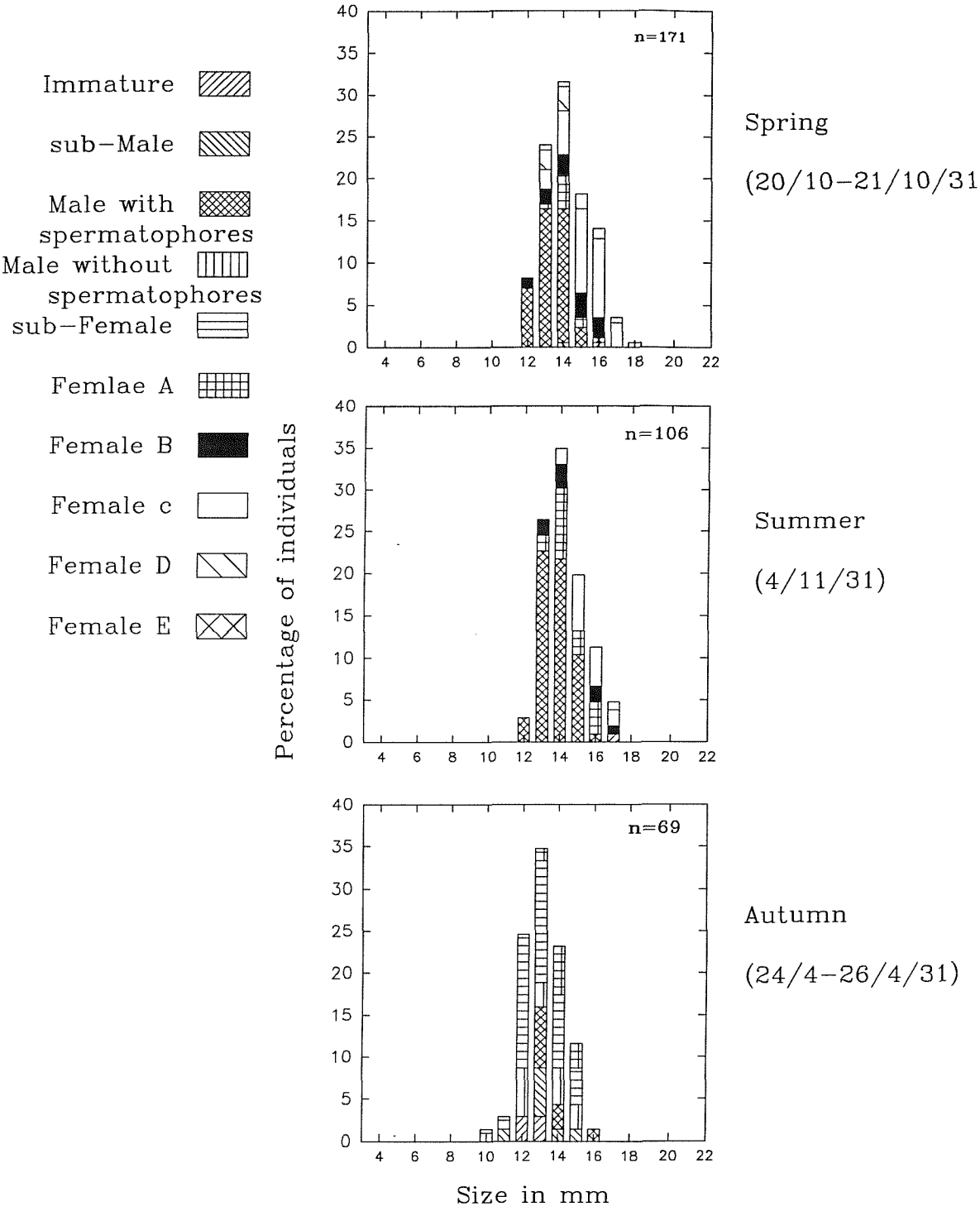
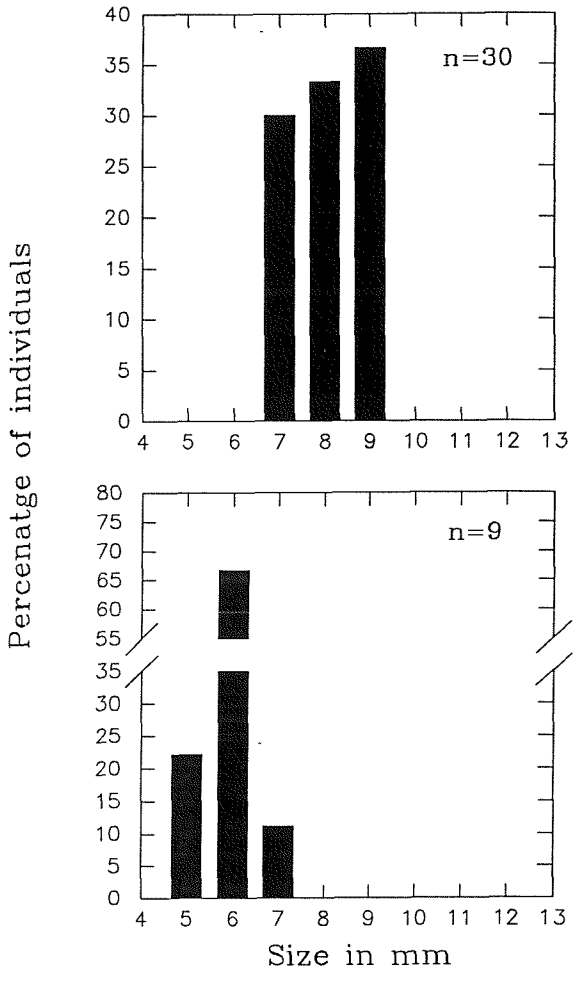


Figure 8.3.2e

Size classes of *E.lucens* post-larvae from the Discovery collections in the Factor 1 region



Spring

(30/10-31/10/90)

Summer

(4/11/31)

Figure 8.3.2g

Temperature factor 2 (fig. 8.3.2f,h)

Spring - The average size of the population was smaller in the temperature factor 1 region with the modal peak category being 12mm. Males with spermatophores were proportionally abundant especially in the 11 and 12mm size classes. Females were less mature compared to temperature factor 1, with the majority being Female A. Other stages present were Female B and D, with Female D being more abundant in the larger size classes (13 and 14mm). The size frequency distribution was unimodal. Although no post-larvae were recorded in the data of Montu (1977), they were present in these samples. The size classes ranged between 6 and 9mm, with the 9mm size class being present in the greatest relative abundance.

Summer - The average size of the population was reduced from the Spring, with the median size class being 10mm. The size frequency distribution was bimodal with peaks at 9 and 11mm, although the size structure did not deviate from normality (K-S distance=0.194, $P>0.200$). Males with spermatophores and Female A were the most common maturity states with the other major classes being sub-adult male and female and immature. The size classes of the post-larvae ranged from 6 to 9mm with the greatest proportion of individuals being contained in the 9mm size class.

Autumn - The average size of the population increased from the Summer and was comparable to the sizes observed in Spring. The modal peak category was 12mm. The population was made up of equal proportions of immature, sub-adult male and female, Female A and males without spermatophores. The size frequency distribution was unimodal. Post-larval specimens were absent from the examined samples which is to be expected since they were present in very small numbers and restricted to the most northerly stations in Montu (1977).

Winter - The mean size of the population was the largest observed within the temperature factor 2 region with the modal peak category being 14mm. Most of the population was either immature or sub-adult male and female, with a few Female A being present at 15 and 16mm. The size frequency distribution was unimodal. The size classes of post-larval specimens ranged between 7 and 9mm, with the 8 and 9mm size classes being present in highest proportions.

Size classes of *E.lucens* adults from the Discovery collections in the Factor 2 region

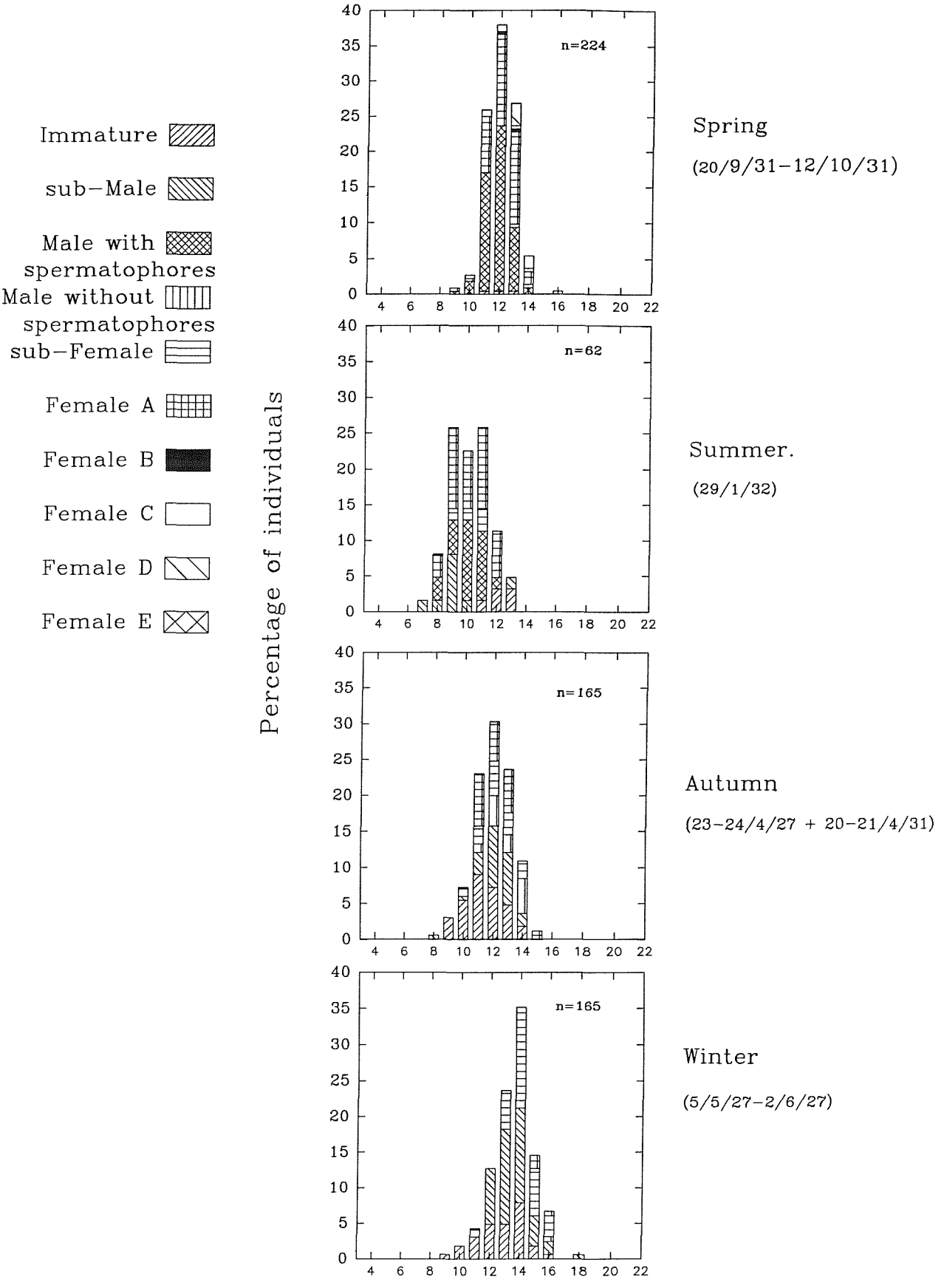
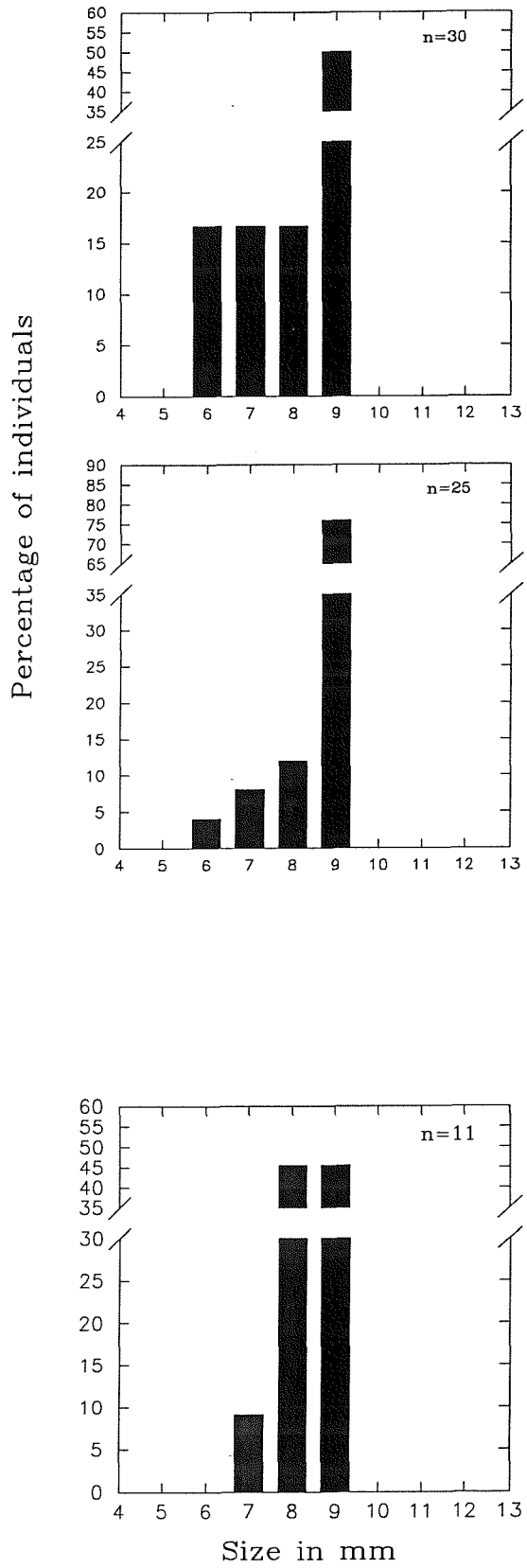


Figure 8.3.2f

Size classes of *E.lucens* post-larvae from the Discovery collections in the Factor 2 region



Spring

(1/11/90-2/11/90)

Summer

(29/1/32-7/2/32)

Winter

(28/5/27)

Figure 8.3.2h

Overall, the adult population appeared to reach peak maturity during Spring and Summer in both temperature factor regions. Temperature factor 1 contained a greater proportion of post-mate females in both seasons and adults average size was larger. The proportion of males with spermatophores was approximately the same in both regions. Average size of the adult population was seen to change far more dramatically between seasons in temperature factor 2. This may be explained, in part, by the quantity of samples being less in temperature factor 1 which led to compromises in the interseasonal temporal spacing of samples.

The reanalysis of the larval data indicated that the adult maturity patterns generally support the conclusion that a multi-cohort population cycle exists. However, adults appear far earlier in the season than the cohort analysis predicts. The peak spawning period of cohort A was around mid-December and earliest spawning in late November/early December. Although, post-mated, gravid females were present in early November, the same stages of advanced maturity were also found in late October. It is therefore possible that there was a spawning event prior to cohort A. A small number of larvae were seen in October in the northerly sample groups, but their densities were insufficient to be representative of a major spawning episode. However, these larvae may have been the start of a spawning event that was undetected because it occurred in a brief pulse just after the Spring survey period. Theoretically, the resulting larvae should have become post-larvae before the Summer survey in January. Small post-larvae were found in early November in the *Discovery/William Scoresby* temperature factor 1 samples, which agrees with this hypothesis. *E.lucens* furcilia were also common in surveys carried out by the *M/V Falkland Protector* during October and November, 1990 and 1991 (see Chapters 6 and 7), although they were mainly found in off-shelf samples.

Only the analysis of samples from further Spring surveys can confirm the existence of a Spring cohort (cohort X) on the shelf.

Despite the presence of males with spermatophores, very few females in an advanced state of maturity were found between the spawning of cohorts B and C, in April. For cohort B, turnover of the adult population or sexual regression would be likely after a spawning episode. However, some adults would be expected to be approaching sexual maturity in order to spawn cohort C. It must be noted however, that cohort C is a relatively minor cohort and only a small proportion of the adult population would be expected to contribute to its production.

As evidence of recruitment of cohorts into the adult stages, major shifts in the adult size structure were seen in the temperature factor 2 region more than in the temperature factor 1 region, although it must be noted that there were few samples in the latter region. The main shift seen in the temperature factor 1 region was from Summer to Autumn where the median size class was seen to reduce from 14mm to 13mm. This reduction of mean size may have been influenced by recruitment of cohort A individuals into the adult stage during this period. In the temperature factor 2 region, there was a dramatic decrease in adult size from Spring to Summer, with a shift from a unimodal distribution with a peak modal category at 12mm, to a bimodal distribution with peaks at 9 and 11mm, although it must be noted that the bimodal peaks do not differ significantly ($P > 0.200$). The 9mm peak may be produced by cohort A or cohort X individuals and the 11mm peak, from overwintering individuals which are yet to spawn. In Autumn and Winter, there was an increase in the mean adult size with the modal groups being 12 and 14mm respectively. This corresponds with the lack of subsequent cohorts in this region after Summer and so there was no recruitment into the adult population during this

period. Autumn/Winter recruitment of cohort B individuals into the adult population would be expected in the temperature factor 1 region, but unfortunately this cannot be verified because of the unavailability of samples.

Life cycles and growth

The population dynamics of *E.lucens* appear to show differences between temperature factor 1 and 2. Different life cycles for each region are therefore proposed from the available evidence.

Temperature factor 1

1, Although not confirmed by larval data, a cohort (cohort X) may be produced in October which reaches the post larval stage by January at the latest. This was spawned by overwintering adults.

2, Cohort A is spawned during Summer from as early as late November/early December with spawning peaking in mid December. The cohort may have been spawned from the same adults that produced the unconfirmed Spring cohort (cohort X) or from individuals that overwintered as post-larvae.

3, Cohort B is spawned in Autumn from as early as late February although spawning peaks in mid March. The cohort was probably spawned by individuals that overwintered as post-larvae or possibly from individuals spawned in Spring. It is further possible that the adults that spawned in Spring or Summer may also contribute to this cohort.

4, Cohort A individuals begin to be recruited into the adult population during late Summer/Autumn and probably make up the major part of the adult population going into Winter.

5, Cohort B individuals probably overwinter as post-larvae or small adults.

Temperature factor 2

1, As with temperature factor 1, there is the possibility of a Spring spawning episode since there are post-mate gravid females in the population. If so, the spawning of cohort X would have taken place at the end of October by individuals that overwintered as adults. Individuals from cohort X would have reached post-larval stages by January.

2, Cohort A is spawned as early as mid December although spawning peaks in early January. The cohort is produced from over-wintered adults which possibly also contribute to the unconfirmed Spring cohort.

3, Cohort A individuals develop rapidly and may start contributing to the adult population as early as late January. By April all individuals are adult.

4, No further cohorts are produced and the mean size of the adult population increases through Autumn and reaches a peak during Winter.

Based on the above conclusions, certain growth estimates can be made. Unfortunately growth estimates cannot be obtained for temperature factor 1 because *Discovery/William Scoresby* samples are too limited in this region. Growth estimates can nevertheless be made for the temperature factor 2 region where adequate *Discovery/William Scoresby* samples are available. However, these estimates must be limited to cohort A, since this was the only cohort discernable in more than one season.

(i) Summer-Autumn larval development - Estimates were only made for sample group 3, since densities were too low in the other sample groups to gain an acceptable estimate of the peak modal category. The modal peak in sample group 3 was furcilia II. The length and weight of fII specimens was measured directly from specimens found in the *Discovery/William Scoresby* Summer collections (the mean length was 4.09mm and the

mean weight 0.0384mg). By Autumn, cohort A individuals had reached adulthood. The adult population had a unimodal distribution with a modal peak at 12mm (12.50mm) average length. The weight of these individuals was estimated from the length-weight regression carried out on *E.lucens* adults from the *Discovery/William Scoresby* collections (fig. 8.3.2i). All weights were converted from "preserved" to "true" weights using the equation derived by Giguere et al. (1989). Results are presented in Table 8.3.2(i) (p.293-294).

(ii) Autumn-Winter adult development - The adult Winter size frequency distribution was unimodal with a modal peak at 14mm (14.50mm average length). Taking the above reservations about the contribution of cohorts to the adult population into account, it was assumed that the length increase in the modal peaks of the Autumn and Winter populations represented adult growth between these seasons. The mean length of the Winter population was assumed to be 14.5mm and the mean weight calculated using the length weight regression mentioned above. All "preserved" weights were converted to "true" weights as before. The results are presented in Table 8.3.2(ii) (p.293-294).

Logged length weight relationship of male, female and immature *E.lucens* adults

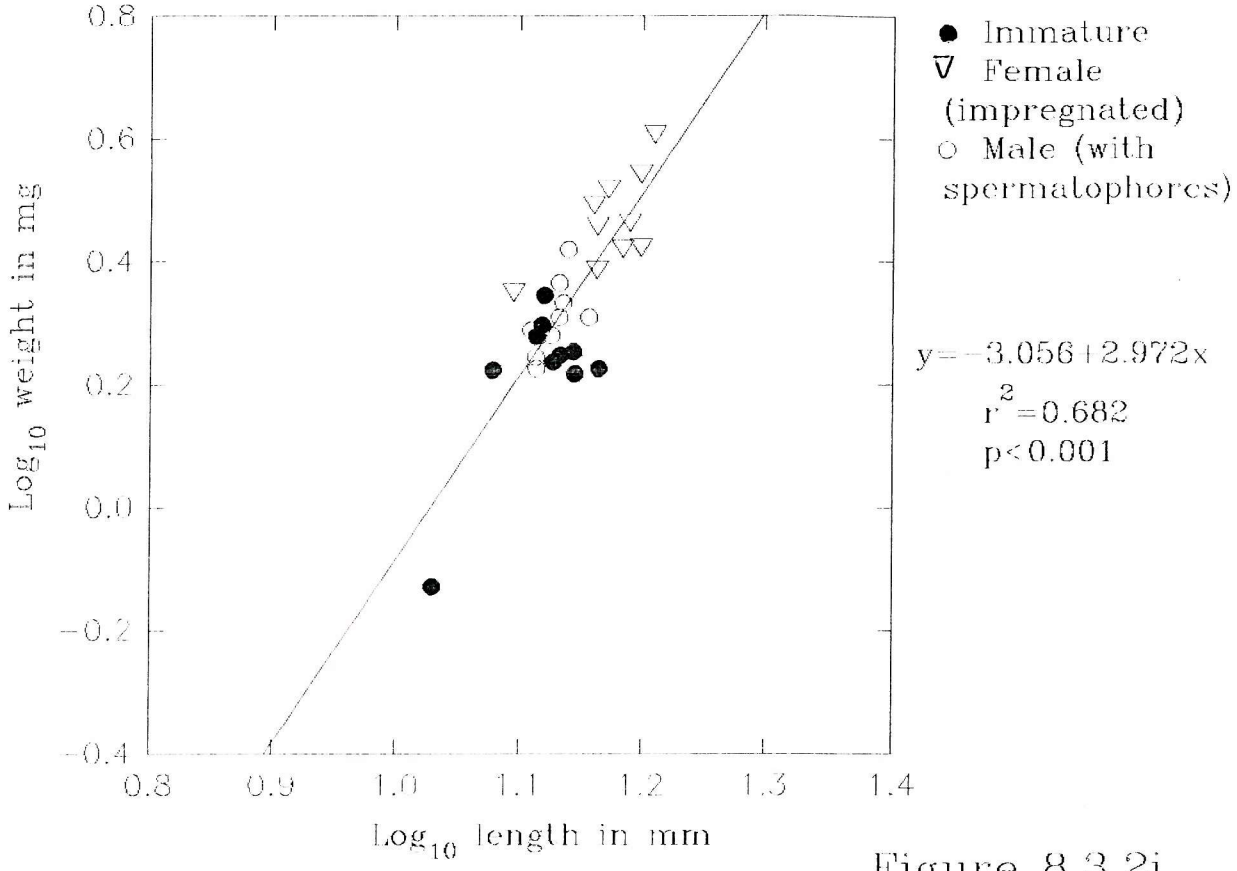


Figure 8.3.2i

8.3.3 Population cycle of *Thysanoessa gregaria*

Montu (1977) reanalysis

Spring (fig. 8.3.3a) - Moderate absolute densities of adult, calyptopes and early stage furcilia were apparent. Modal groups were identified in all sample groups and these were considered to represent the same cohort (cohort A). The modal peak category of sample group 3 was calyptopes III and for sample group IV, furcilia I. Although modal groups were also identifiable in sample groups 1 and 2, the calyptopes I class contained the highest densities. It was therefore not possible to ascertain whether peak densities were present at the time of the survey and the modal peak category could not be identified.

There is no recorded study of the intermoult period of *T.gregaria* in the literature. Laboratory studies have been carried out on other *Thysanoessa* species in different regions. Species of similar size to *T.gregaria* and subject to temperature regimes similar to that of the Patagonian shelf include *T.spinifera*, *T.raschii*, *T.longipes* and *T.longicaudata*. Jerde and Lasker (1966) found that *T.spinifera* kept at temperatures ranging between 8.3°C and 12.2°C had an intermoult period of 5 to 6 days. Paranjape (1967) found *T.spinifera*, *T.raschii* and *T.longipes* had intermoult periods of 4 to 6 days at temperatures ranging between 11 and 15°C. Both studies found that moulting frequency was independent of body size. Back calculation to an estimated time of spawning was made using an intermoult period of 5 days, since this figure is an approximate average of the above studies. It was assumed that there was one moult per larval stage. Using these approximations, peak spawning in sample groups 3 and 4 occurred during early October and earliest spawning in early September. Earliest spawning in sample group 1 and 2 was late and early September respectively.

It is evident in sample groups 2, 3 and 4 that there were moderate relative

densities of late stage cyrtopia. These individuals have either overwintered as larvae from a cohort spawned in Autumn or they were spawned in mid to late Winter.

Summer (fig. 8.3.3b) - There were bimodal stage frequency distributions in all sample groups. Splitting the distribution into later and earlier stage modes, the later stage modal peak ranges between cyrtopia III and V and the earlier stage modal peak between furcilia III and V. It is probable that the cyrtopia observed in Spring had since developed into adults. Therefore, the later stage mode was probably cohort A. The early stage modal group represents a subsequent cohort (cohort B), as marked in fig 8.3.3b. Peak spawning of cohort B would have occurred between early and mid December, with earliest spawning just slightly before those dates.

Adults were again present in moderate densities in all sample groups and are only a minor component of the population.

Autumn (fig. 8.3.3c) - The stage frequency distribution of all sample groups were again bimodal. The later stage mode had modal peaks at either cyIV or cyV. The modal peak of the earlier stage mode ranges between fII and fIV. Applying the same reasoning as before, it is probable that the cyrtopia in the previous season (cohort A) had developed into adults and that the present cyrtopia represented cohort B. The earlier stage mode represents another cohort (cohort C). Peak spawning of cohort C would have taken place between late February and early March and earliest spawning between mid to late February.

Adult densities were greater in the southerly sample groups (3 and 4) compared to the northerly sample groups. The absolute density of adults was moderate throughout the sample groups but they were the dominant stage with respect to the rest of the population.

Winter (fig. 8.3.3d) - Adults were present in moderate absolute densities in all sample groups although they had the greatest relative density within the population. Larvae were present in low absolute densities and were mostly late stage cyrtopia. These cyrtopia were taken to represent cohort C. In sample groups 1 and 2, small numbers of early stage furcilia were present. These may represent the spawning of a late Autumn/Winter cohort in the more northerly regions which would correspond with the cyrtopia found in the following Spring mainly in the northerly regions.

Stage frequencies of *T.gregaria* during Spring

(renanlysed from Montu, 1977)

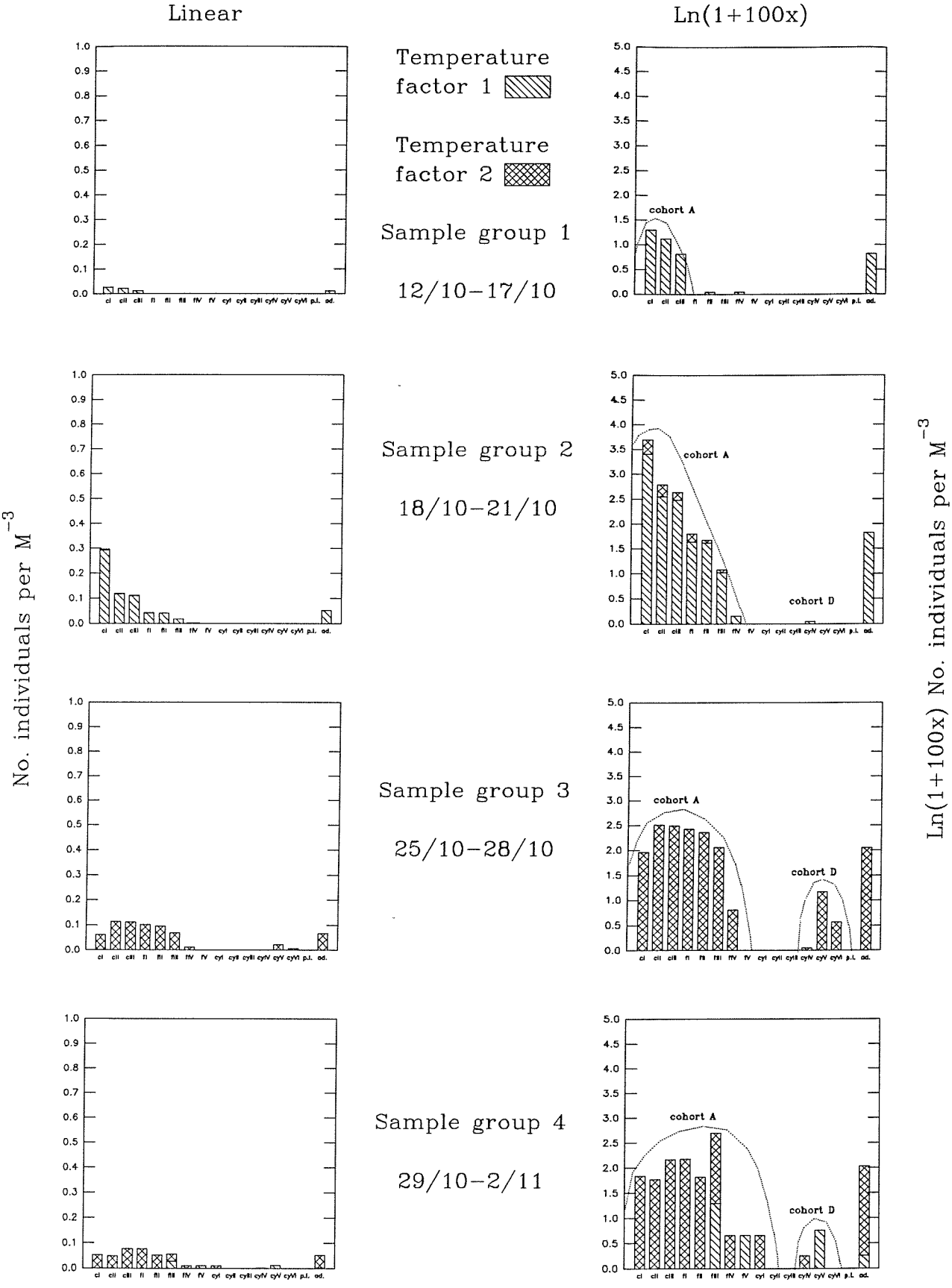


Figure 8.3.3a

Stage frequencies of *T.gregaria* during Summer

(renanlysed from Montu, 1977)

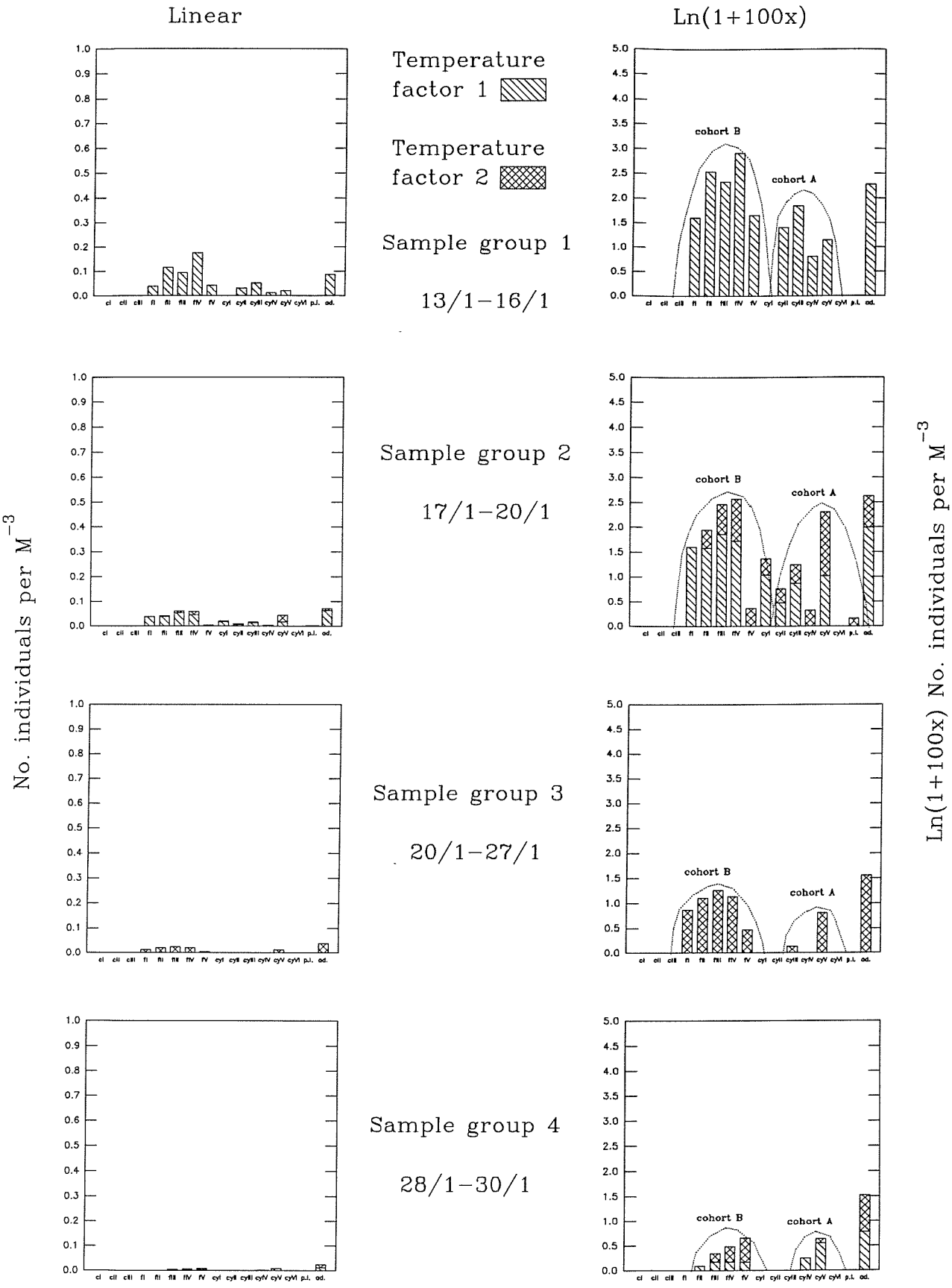


Figure 8.3.3b

Stage frequencies of *T.gregaria* during Autumn

(renanlysed from Montu, 1977)

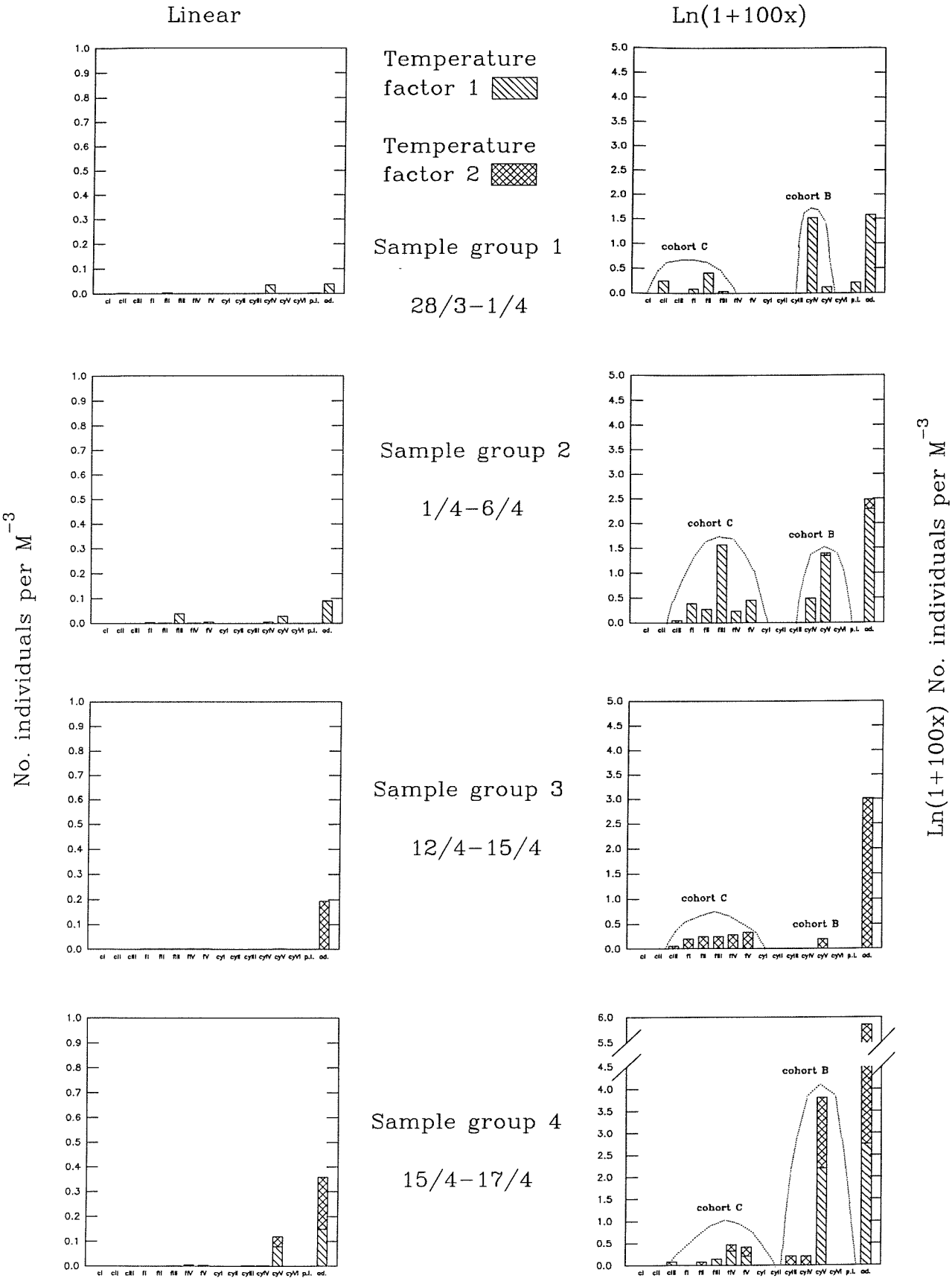


Figure 8.3.3c

Stage frequencies of *T.gregaria* during Winter

(renanlysed from Montu, 1977)

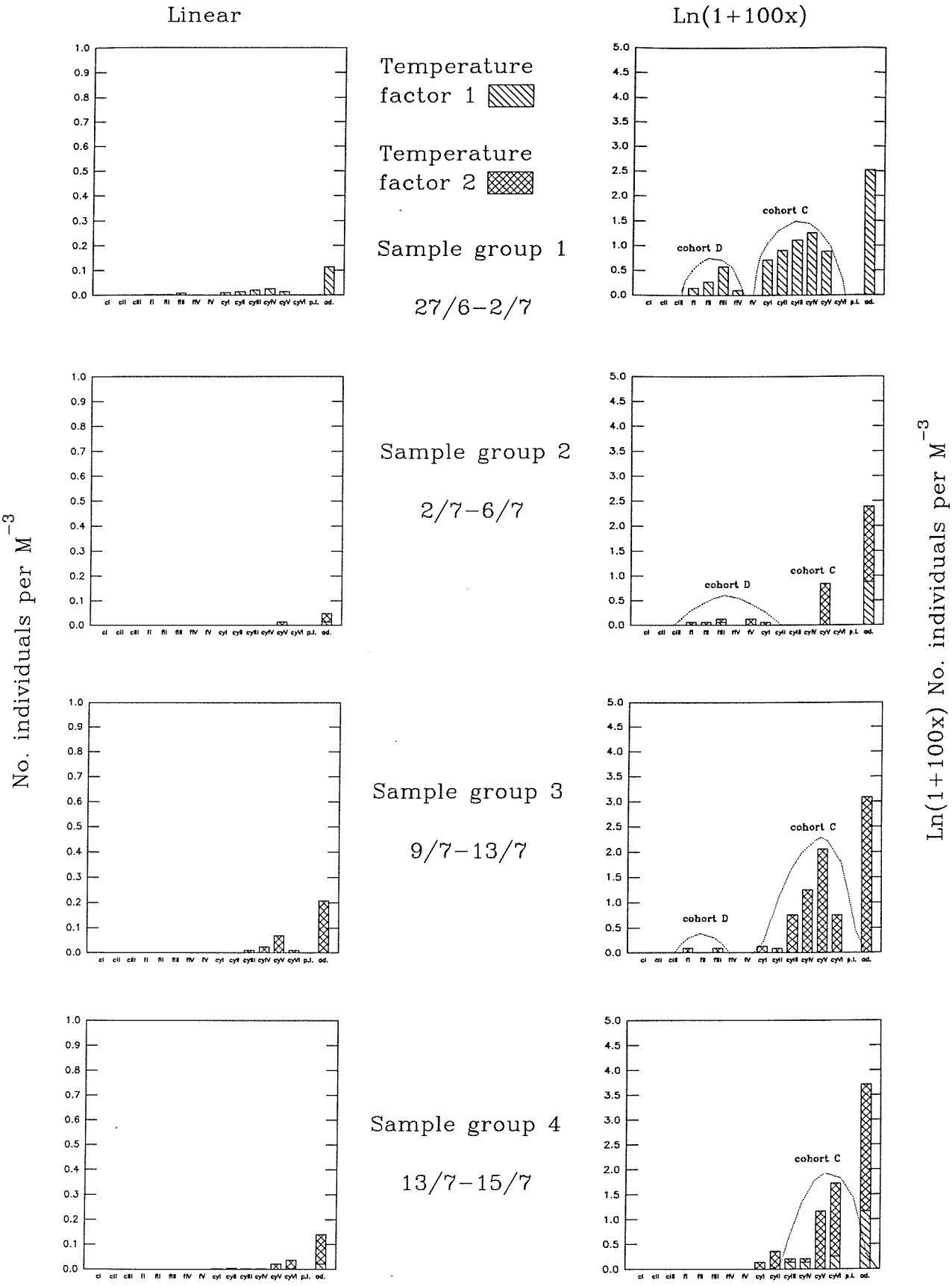


Figure 8.3.3d

Adult maturity

Temperature factor 1 (fig 8.3.3e)

Spring - The size frequency distribution was approximately unimodal although the upper range was extended somewhat by the presence of small proportions of individuals in the consecutive size classes between 17 and 20mm. Nevertheless, the distribution did not deviate from normality (K-S distance=0.231, P=0.100). The modal peak category was 14mm. There was a large proportion of males with spermatophores in the 10mm to 17mm size classes. The rest of the population was dominated by post-mate female stages.

Temperature factor 2 (fig. 8.3.3f)

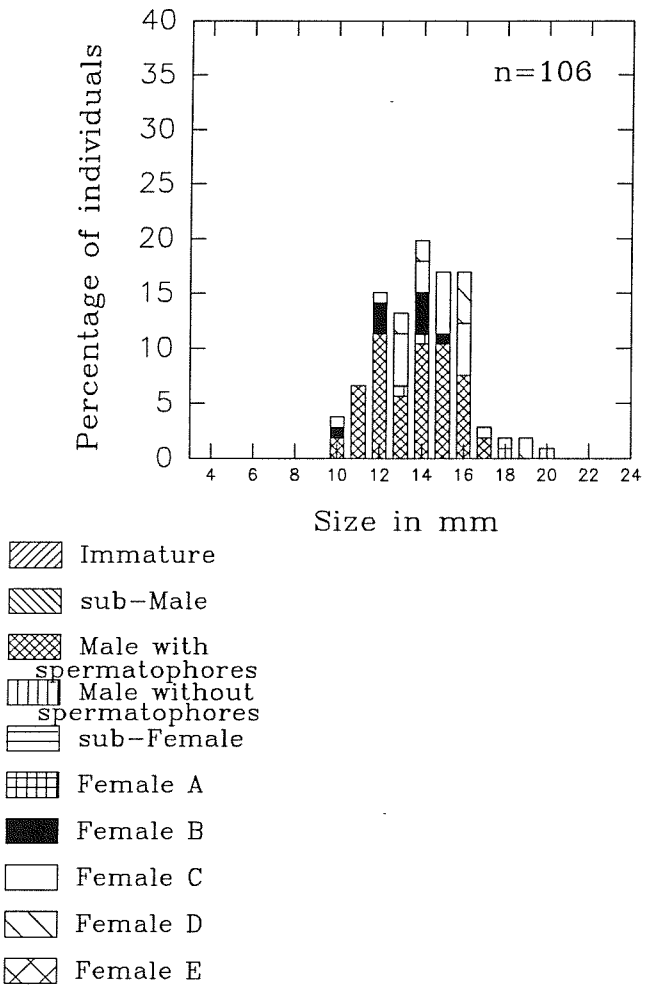
Spring - The size frequency distribution was unimodal with an extended upper range and the modal peak was at 10mm. This was considerably smaller than during Spring in temperature factor 1, although the sampling dates in this region were approximately one month earlier. The earlier sampling dates may also explain the comparatively less advanced state of adult maturity in this region. Nevertheless, males with spermatophores were a dominant part of the population in all size classes. The other major components were pre-mate females, which were mostly Female A, with small numbers of Female B and C being present in the larger size classes (ie. 12mm to 16mm classes).

Summer - The size frequency distribution was bimodal with modal peaks at 9mm and 12mm. However, adult size did not deviate from normality (K-S distance=0.189, P>0.200). The smaller size class mode was dominated by immature specimens with small numbers of sub-adult males and males with spermatophores. There were greater proportions of sub-adult females and Female A in the longer length mode. Female C were also present.

Autumn - The size frequency distribution was unimodal with a modal peak at 13mm. The smaller size classes were dominated by immature, sub-adult male and Female A. Males with spermatophores were the dominant group in the 12 to 15mm size classes. Female A were the other major component of these size classes. Sub-adult females and Female B were also found in the larger size classes.

Winter - Although the 10mm and 12mm size classes contained slightly greater proportions than the 11mm size class, the size frequency distribution was approximately unimodal with a modal peak at 11mm. The majority of the population in all size classes was dominated by immature and sub-adult male stages. Other components were males with spermatophores, males without spermatophores and sub-adult females. There were also Female A and C stages in the 15 to 17mm size classes which made up an extended upper range in the size frequency distribution, although this did not deviate from a normal distribution (K-S distance=0.222, P=0.131).

Size classes of *T.gregaria* adults from the Discovery collections in the Factor 1 region



Spring

(19/10/31)

Figure 8.3.3e

Size classes of *T.gregaria* adults from the Discovery collections in the Factor 2 region

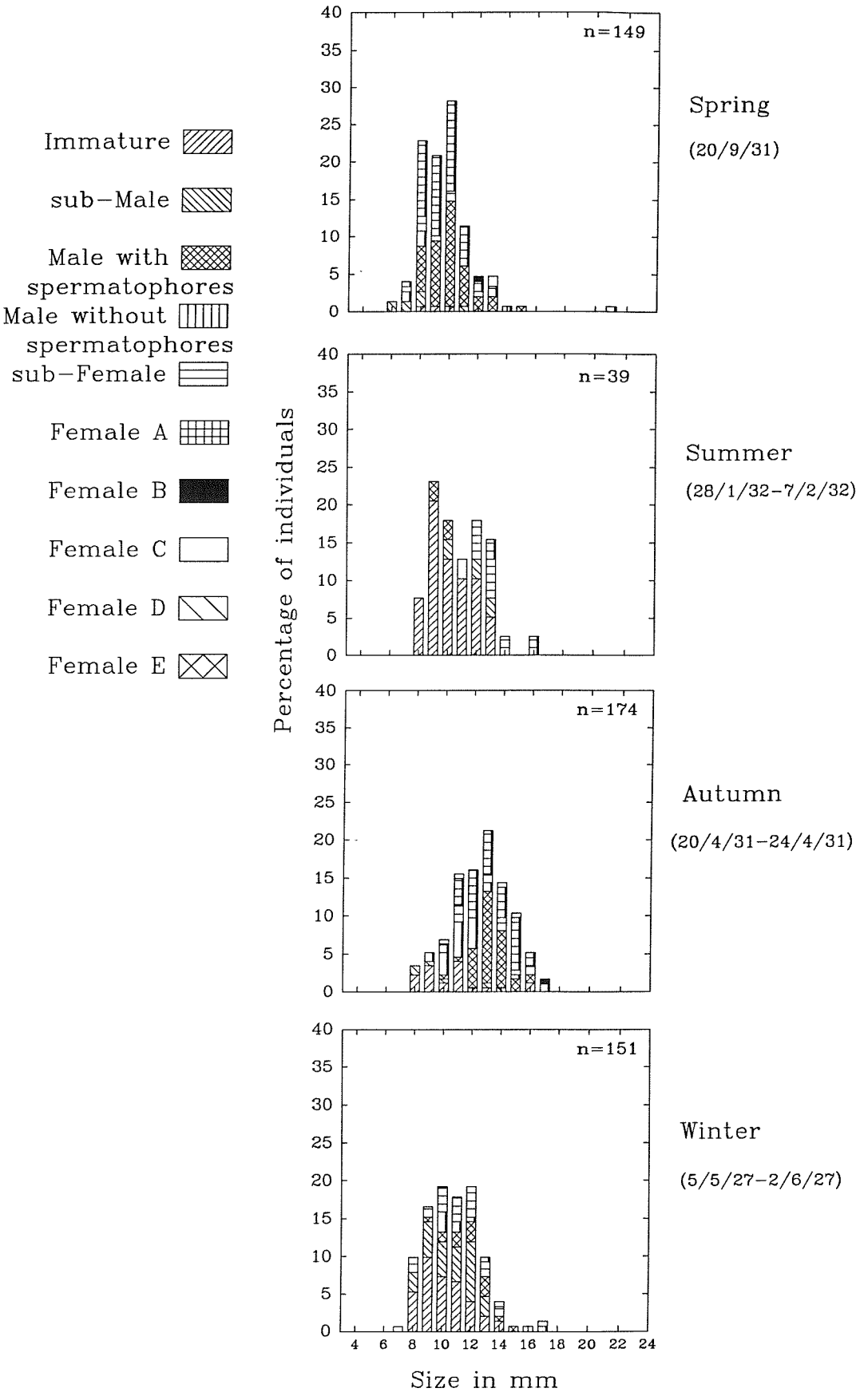


Figure 8.3.3f

The reanalysis of Montu (1977) highlighted the fact that cohorts were produced throughout the year and that the adult population always remained at a moderate density. This would suggest there was a continuous turnover of adults and that there were always individuals at or near reproductive maturity. This was seen to a certain extent in the analysis of adult maturity from the *Discovery/William Scoresby* samples. Although the proportion of males with spermatophores was greatest in Spring and Autumn, they were also present in Summer and Winter. Female A and sub-adult females always made up significant proportions of the adult population in every season. Therefore reproduction was feasible throughout the year.

It is difficult to determine anything specific in terms of mortality from the size frequency structure of the population. This is because the continual influx of cohorts into the adult stages would influence the average size structure to an unknown extent. Difficulties also arise because the temporal match between the Montu (1977) surveys and the *Discovery/William Scoresby* samples is not exact, making it difficult to determine exactly when maturity is achieved. Nevertheless, in order to gain a rough idea of the average age attained, an approximation has been made using larval and adult growth rates of *Euphausia lucens* gained from this present reanalysis. *E.lucens* are roughly the same size and weight as *T.gregaria* at most developmental stages so the growth rates of *E.lucens* are probably a reasonable approximation of those of *T.gregaria*. Following cohort A, cyrtopia stages IV and V (5.5mm average length) are reached by January. If it is assumed that specimens exhibit the growth rate of an *E.lucens* larvae/post-larvae (0.1051 $mm.d^{-1}$) until they reach adulthood at 8 mm and then adopt the growth rate of *E.lucens* adults (0.0227 $mm.d^{-1}$), the cohort would have reached 9.2mm by Autumn. At this point, cohort A would only be part of the smallest adult fraction. Applying the same

adult growth rate until Winter, the cohort would have reached 11.2mm where it would comprise the modal peak category. By Spring, the majority of the adult population was below 11mm, so even assuming that there was no growth over Winter, the major part of cohort A had died within 12 months of spawning. It must be emphasised that the above estimate is a rough approximation only. However, if such a lifespan were typical, then it is possible that *T.gregaria* adults are involved in two or three spawning events since the smallest adult size classes are capable of reaching reproductive maturity.

Large adults in excess of 16mm were also present in the population. If the above growth rates are approximately correct, then such individuals would be 2 years old. However, these were only a minority of the adult population. Thus, even though a lifespan beyond 12 months is possible, it is not common in this region.

Life cycle and growth

From the above evidence, the following conclusions can be made on the population cycle of *T.gregaria* on the Patagonian shelf:

1, At least 3 to 4 discrete cohorts may be produced in one year with those that were identified being spaced evenly between seasons

2, Larvae typically reach adulthood within 4 months

3, Reproductive maturity may be attained as soon as adulthood is reached

4, On average, a cohort remains part of the adult population for 8 months during which time it may contribute to the production of two or three cohorts. However, it is not known whether *T.gregaria* is capable of multiple spawning

5, The adult population remains at approximately the same moderate density throughout the year, which suggests that recruitment and mortality of adults remains approximately

balanced at all times.

6, On average, the lifespan of an individual is 12 months. Large individuals which were probably two years old were observed but these were only a minority of the adult population.

Because it was not possible to identify cohorts within the adult population, growth estimates could only be obtained for larvae. The sample groups appeared to have analogous cohorts (ie. cohort A for instance was apparent in all sample groups with modal peaks in similar larval stages). It was therefore possible to estimate growth rates of cohorts in all sample groups and subsequently obtain a mean growth rate for a cohort across sample groups. Lengths were obtained from direct measurements of larvae in the *Discovery/William Scoresby* collections. Weights were obtained from a length-weight relationship (fig. 8.3.3g) as for the previous species. Mean growth rates for each cohort in terms of length and weight are presented in Table 8.3.3(i).

Logged length weight relationship of male, female and immature *T.gregaria* adults

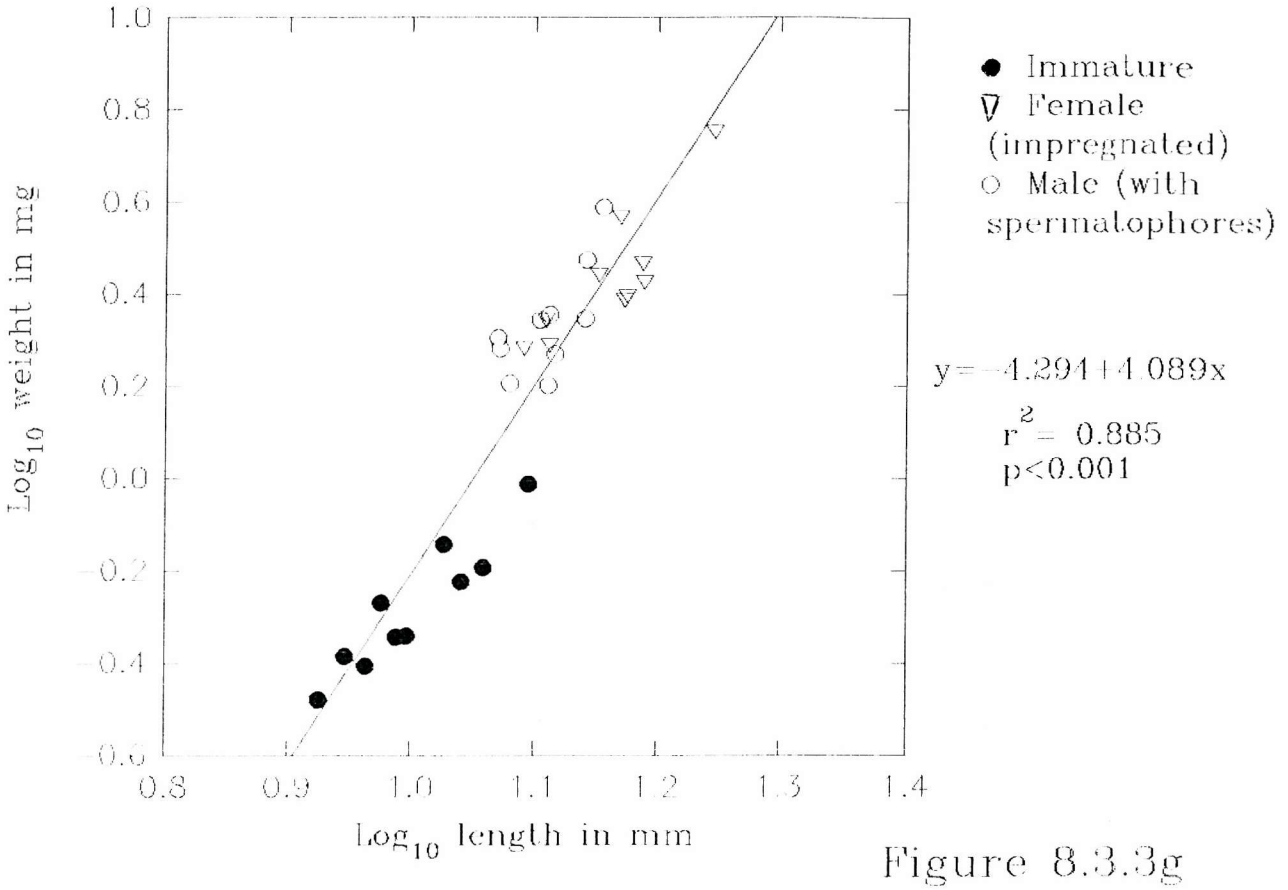


Figure 8.3.3g

Sample group	Summer-Winter interval	Growth in mm	Growth in mg
1	167 days	0.0240 $mm.d^{-1}$	0.0172 $mg.d^{-1}$
2	167 days	0.0240 $mm.d^{-1}$	0.0172 $mg.d^{-1}$
3	168 days	0.0238 $mm.d^{-1}$	0.0171 $mg.d^{-1}$
4	166 days	0.0241 $mm.d^{-1}$	0.0173 $mg.d^{-1}$

Table 8.3.1(ii): Growth in 0 year *E.vallentini* adults between Summer and Winter

Sample group	Autumn-Winter interval	Growth in mm	Growth in mg
3	88	0.0227 $mm.d^{-1}$	0.01026 $mg.d^{-1}$

Table 8.3.2(ii): Growth in *E.lucens* adults between Autumn and Winter

Sample-Group/Cohort	Interval between measurements	Growth in mm	Growth in mg
2 (A)	91 days	0.1159 $mm.d^{-1}$	0.0191 $mg.d^{-1}$
3 (A)	89 days	0.1185 $mm.d^{-1}$	0.0196 $mg.d^{-1}$
4 (A)	90 days	0.1175 $mm.d^{-1}$	0.0249 $mg.d^{-1}$

Table 8.3.1(i): Larval growth in *E.vallentini* between Spring and Summer

Sample-Group/Cohort	Interval between measurements	Growth in mm	Growth in mg
3 (A)	80 days	0.1051 $mm.d^{-1}$	0.0199 $mg.d^{-1}$

Table 8.3.2(i): Larval growth in *E.lucens* between Summer and Autumn

Sample-group/Cohort	Interval between measurements	Growth in mm	Growth in mg
1-4 (A)	90 days	0.0411 $mm.d^{-1}$	0.001818 $mg.d^{-1}$
1,2,4 (B)	77 days	0.0358 $mm.d^{-1}$	0.001633 $mg.d^{-1}$
1-4 (C)	90 days	0.0276 $mm.d^{-1}$	0.001205 $mg.d^{-1}$
2,3 (D)	107 days	0.0303 $mm.d^{-1}$	0.001278 $mg.d^{-1}$

Table 8.3.3(i): Larval growth in *T.gregaria* between Summer and Autumn

8.4 Discussion of euphausiid life cycles

8.4.1 Reanalysis of *E.vallentini*

Comparison to Montu (1977, 1982)

There were certain similarities and some distinct differences between the conclusions drawn by Montu (1982) and the results of this reanalysis. Both studies agree that spawning of the principal cohort occurred in Spring but whereas Montu (1982) states that the furcilia and juvenile stages were reached during the Summer and Autumn, the present study suggests that larval development took place mainly between Spring and Summer. Montu (1982) further proposed that adult stages were reached at the end of Autumn/start of Winter whereas the present study found that adult stages were reached as early as Summer by individuals spawned at the start of Spring and that all individuals were at adult stages by mid-Autumn. The main reason the present analysis draws this conclusion is the absence of calyptopes and early stage furcilia in Summer combined with a large decrease in the adult size distribution, although the probable downward migration of the population during Summer and Autumn makes it difficult to be certain as to when adulthood was attained.

Both this reanalysis and Montu (1982) agree that the majority of the adult population dies after spawning. The Summer and Autumn adult histograms show bimodality in proportional size structure which, although not statistically significant, can be taken as evidence that some post-spawn adults survive to these seasons at least. The size structure in Winter is unimodal which suggests that post-spawn adults die rather than over-winter. A further observation made by Montu (1982) was increased levels of stage IV females later in the season. This agrees with results from the present reanalysis which

show a small, second cohort mainly in the northerly sample groups.

Comparison to Ramirez and Dato (1983)

Conclusions on the timing of spawning made by this study disagree fundamentally with the findings of this reanalysis. Ramirez and Dato (1983) suggested that female maturity and spermatophore attachment were not achieved until the end of Spring/start of Summer. Consequently, peak spawning was estimated to occur at the start of Summer. These estimates are more than two months later than those of this reanalysis despite the fact that their survey area is geographically coincident with the temperature factor 2 region.

What is further surprising is that the above discrepancy is apparent despite the observations on the population structure made by both studies being quite similar. Ramirez and Dato (1983) found the size structure of the adult population was unimodal in Winter (May) with a peak at 10mm and bimodal in Summer (Jan/Feb) with peaks at 7 and 16mm[1] with furcilia and post-larvae also being apparent in Summer which is almost identical to that found in the present reanalysis. Furthermore, if spawning time was predicted from the size-frequency data of Ramirez and Dato (1983) using the same methods applied in the present reanalysis, spawning times would be very similar in both studies. Therefore, it appears that the methods employed by Ramirez and Dato (1983) appear to be unreliable and their predictions on the timing of spawning are much later than even their own size frequency distribution data would suggest.

Comparison to other regions

The only other notable study on the life cycle and population dynamics of *E.vallentini* was carried out by Ridoux (1988). The study area was around Crozet Islands in the

[1] These figures are from January (Ramirez and Dato, 1983)

Indian Ocean and samples were obtained from the gut contents of penguins. Total length was estimated from carapace measurements and mature adults appeared to attain much greater lengths than those found on the Patagonian shelf (eg. modal peak categories were found at 24mm around Crozet Islands as opposed to 17-18mm on the Patagonian shelf). Peak mating peak was estimated to occur during October/November (using the Makarov and Denys (1980) scale), and recruitment of post-larval individuals took place from December to January onwards. There was fast growth until May and then no Winter growth between June and mid-August. Minimum total length at maturity was estimated at 16mm, but it was stated that individuals were unlikely to mate in significant numbers at this stage and that most spawning individuals were 2 years old.

Without exact knowledge of the foraging behaviour of marine predators, it is difficult to ascertain whether gut content samples are representative of the population. Selectivity towards more nutritious, larger individuals in foraging behaviour would seriously affect any size frequency study such as that of Ridoux (1988). Nevertheless, the significant proportion of individuals in excess of 20mm within the gut content samples does suggest a 2 year life cycle. Whether individuals spawn for one or both of these years is more difficult to discern. Results from the Patagonian shelf show that, on average, lengths of 17mm are achieved within 1 year. Most individuals between 10 and 20mm in the Crozet Island region were juvenile suggesting that maturity is not attained in 1 year old individuals in this region. Temperature around the Crozet islands appear to be considerably lower than on the Patagonian shelf. The highest sea surface temperature attained around the islands was 7°C, compared to an average of 12-13°C in the surface layers on the shelf. Different growth rates and generation times are therefore to be expected.

Johnson and Brinton (1963) considered *E.vallentini* to be a sub-Antarctic relative of *E.pacifica* and their life cycles and growth rates appear to be very similar. For instance, growth rates of approximately 0.12 $mm.d^{-1}$ during the Spring-Summer interval when larval development was at its peak and 0.024 $mm.d^{-1}$ between Summer and Winter when the population was mostly represented by late juvenile and adult stages (Table 8.3.1(i),(ii)). compares quite favourably with the findings of Bollens et al. (1992) for *E.pacifica* where larvae produced in the Spring and early Summer tended to have a high growth rate (0.08 $mm.d^{-1}$ to 0.12 $mm.d^{-1}$), whilst juveniles had rates between 0.04 $mm.d^{-1}$ and 0.08 $mm.d^{-1}$ during the Summer and typically towards the end of this range during Autumn. The growth rates of adult *E.pacifica* were more variable but mostly ranged between 0.036 $mm.d^{-1}$ to 0.083 $mm.d^{-1}$, with lower rates (eg. 0.003 $mm.d^{-1}$) interspersed between more rapid periods of growth. Such growth rates are typical of a number of other studies on *E.pacifica* (Fulton and LeBrasseur, 1984; Heath, 1977; Smiles and Pearcy, 1971).

8.4.2 Reanalysis of *E.lucens*

Comparison to Montu (1977, 1982)

The finding of the present study and that of Montu (1977, 1982) agree with respect to the high proportion of gravid females in Spring. However, whereas Montu (1982) concludes that the calyptopes which appear in this season reach furcilia stages by Summer, the present analysis hypothesised that the calyptopes reached the post-larval stage by the Summer (Cohort X). Montu (1982) also considered that the juvenile and adult stages of the Spring spawned cohort were not reached until Winter. Such growth rates are unfeasibly slow when compared to other studies on euphausiid growth (Pillar,

1984b; Bollens et al., 1992) and it is much more likely that adulthood is reached within 6 months as is hypothesised by the present study rather that 9-12 months as advocated by Montu (1982).

One further conclusion made by Montu (1982) was that the post-spawn adult population died during Spring and the start of Summer. This point is not clear in the present reanalysis because adult densities appear so variable between sample groups and seasons. This variability may be the result of a combination of sampling error and the various pulses of recruitment into adult stages from the numerous cohorts produced through the year. The timing of peak adult death is also not clear from the size frequency distribution of adults in the *Discovery/William Scoresby* samples. Average adult size does drop between Spring and Summer and the Summer population appears bimodal, although not significantly so. Although overwintered adults probably still make up a significant part of the upper peak it is impossible to ascertain the degree of mortality that has led to the decrease in average size. Difficulties also arise because (i) it is not possible to ascertain the amount of the adult population that has contributed to the spawning effort and (ii) it is difficult to determine whether individuals die after spawning or are capable of more than one spawning episode. Montu (1982) did note the high percentage of stage IV females in the Summer population. However, there was no mention of the possibility of several spawning events occurring within a year.

Comparison to Ramirez and Dato (1983)

The findings of Ramirez and Dato (1983) are more in line with those of the present reanalysis. Ramirez and Dato (1983) noted that gravid females were present in early Spring. Peak spawning was estimated to occur some time after this, in November and December, with furcilia not apparent in the water column until December and January.

Cohort X, from the present reanalysis, was hypothesised to occur mainly on the grounds that the adult population was in an advanced state of maturity long before cohort A was spawned. It was not possible to obtain direct evidence of larvae being present in the water column during October and November because the surveys in Montu (1977) did not cover this time period. Ramirez and Dato (1983) carried out surveys in both October and November and did not find furcilia or post-larvae in either month. Post-larvae of 6mm in length were found by January, but these could, quite feasibly, have been spawned in November, which would give a growth rate of approximately 0.075 $mm.d^{-1}$. Evidence from Ramirez and Dato (1983) would therefore suggest that cohort X was relatively minor.

Ramirez and Dato (1983) found that there was a large decrease in the average size of the population between November and January, indicating significant adult mortality in the intervening period. Mature females and furcilia of 3 and 5mm were present in late Summer/early Autumn and furcilia of 3 to 5mm in the water column and the production of a second cohort from individuals spawned in November/December was proposed. It was not possible in the present analysis to determine whether cohort B was spawned by overwintered adults or rapidly matured Spring spawned individuals. Evidence from Ramirez and Dato (1983) would suggest the latter alternative is more probable.

Comparison to other regions

E. lucens is the dominant euphausiid species in the southern Benguela upwelling region around southern Africa (Nepgen, 1957). Laboratory studies on individuals from this region carried out by Stuart (1992) found that females maintained in the laboratory were capable of continuously spawning for a period of 2.5 months and producing between 33

and 40 broods. It was further estimated that, in the field, females may be reproductively active for up to 9 months during which time they may release 135 broods and a total of 6345 eggs.

From the available evidence on the Patagonian shelf, it is unlikely that prolonged periods of reproduction take place. The stage frequency distributions of the larvae appear normal and signify that reproduction was carried out in discrete pulses. The different reproductive biology of the species in the Benguela region may be caused by greater feeding potential in the more productive upwelling waters. Temperature is also considerably higher in the Benguela region. The average surface temperature over the year is approximately 16°C and the range is between 12°C and 20°C. This compares to an average surface temperature of 10°C on the Patagonian shelf and a range between 7°C and 13°C. Environmental conditions may therefore be more suitable for prolonged breeding efforts in the Benguela region. Nevertheless, the fact that *E.lucens* is capable of multiple broods does make interpretations of the fate of post-spawn adults difficult. The present reanalysis indicated that overwintered adults were still present in the Autumn adult population. It is therefore also possible that these adults had multiple broods and contributed to the production of both cohort A and B. Further studies on the reproductive strategy of *E.lucens* in this region are therefore recommended.

Studies on the growth rates of *E.lucens* in the Benguela region were carried out by Pillar (1984b) and Pillar and Stuart (1988). Pillar (1984b) carried out laboratory experiments measuring growth rates of larvae between 2.5 and 6.5mm. Pillar and Stuart (1988) carried out further laboratory experiments on juveniles between 6.5 and 12mm, as well as modal progression analyses on the size frequency distributions of adults sampled between January and May. Pillar (1984b) found the larvae to have a mean

growth rate of 0.132 $mm.d^{-1}$. Pillar and Stuart (1988) found the mean growth rate in juveniles to be 0.047 $mm.d^{-1}$ and in adults to be 0.026 $mm.d^{-1}$ approximately. This compares quite favourably with the results of the present reanalysis. For larvae and post-larvae between 4mm and 12.5mm the mean growth rate was 0.1051 $mm.d^{-1}$ and for adults between 12.5mm and 14.5mm, the growth rate was 0.023 $mm.d^{-1}$. Therefore, despite profound differences in the reproductive biology, the growth rates of *E.lucens* in the Benguela region and the Patagonian shelf are relatively similar.

8.4.3 Reanalysis of *T.gregaria*

Comparison to Montu (1977, 1982)

There are a number of differences between the conclusions of Montu (1982) and those drawn from the present reanalysis of *T.gregaria* population cycles. Montu (1982) stated that reproduction was most intense during Winter and Spring. Although, in the present reanalysis, it is clear that reproduction does take place in both Winter and Spring, there is evidence that spawning was equally intense during Summer and further indications from the state of adult maturity that another spawning event took place in Autumn.

Montu (1982) also stated that Spring calyptopes reached furcilial stages by Autumn. As was discussed for *E.lucens*, such a developmental rate would require intermoult periods of 20 to 30 days, which is a lot longer than the 4 to 6 day intermoult periods estimated for other *Thysanoessa* species. The present reanalysis estimated that cyrtopia and post-larval stages were reached within 10 to 12 weeks of being spawned. A Spring cohort (cohort A) therefore reached cyrtopia stages by Summer and early adult stages by Autumn.

Finally, Montu (1982) concluded that Spring spawned individuals reached adulthood by Winter, spawned at the end of Winter and died. The present reanalysis suggests that Spring born individuals (cohort A) could mature and spawn as early as Autumn. Nevertheless, cohort A probably comprises the majority of the adult population at the end of Winter and is therefore the major contributor to the Spring cohort. It is also likely, from growth estimates, that the majority of cohort A adults die during Spring because a major part of the adult population after then are smaller than the predicted size of cohort A individuals. Therefore this reanalysis agrees with the conclusions of Montu (1982) that the average life cycle lasts for typically 12 months.

A fundamental difference between the findings of Montu (1982) and this reanalysis is that Montu (1982) makes no mention of the possibility that several cohorts may be produced through the year despite the fact that high percentages of stage IV females and furcilia I to III modal categories were found in 2 out of the 4 seasons.

Comparison to Ramirez and Dato (1983)

The findings of Ramirez and Dato (1983) and this reanalysis are very similar. Ramirez and Dato (1983) observed that gravid females were present all year round and attachment of spermatophores was evident throughout Spring, Summer and early Autumn. This agrees with the present reanalysis with the further possibility that spawning may also occur during late Autumn/Winter.

Ramirez and Dato (1983) did not mention the possibility of an early Spring cohort despite the presence of mature adults in this period. The primary spawning peak was considered to be in early to mid-Summer (Nov/Dec). The present reanalysis found both Spring and Summer cohorts (cohorts A and B respectively) which both occurred at comparatively moderate densities.

Ramirez and Dato (1983) also suggested that furcilia and post-larvae found in late Summer/early Autumn (Jan/Feb) were derived from a mid Summer spawning episode (ie. a 6 to 8 week intervening period) which is slightly more rapid than the growth rate estimated from the present reanalysis. Ramirez & Dato (1983) further noted that there was a peak in the maturity of adult specimens in Autumn, although their mean size was a lot lower than in Spring. It was proposed that these adults resulted from a fast growing Summer population. This pattern would indeed match the early life history of cohort A which was spawned in the Spring. It is also possible that fast developing individuals from cohort B reached adulthood and reproductive maturity by Autumn although it was estimated that the majority of this cohort were at late cyrtopia stages in this season.

Overall, the findings of Ramirez and Dato (1983) support the view gained from the present reanalysis that reproduction in *T.gregaria* is ongoing through the year and that the population remains stable through continuous recruitment and mortality.

Comparison to Curtolo et al. (1990)

This study only covered the Spring period and found there to be larvae in the water column. This is in agreement with this study and confirms that a Spring cohort is a regular feature in this region despite the fact that it was not found by Ramirez and Dato (1983).

Comparison to other species and regions

Despite having a distribution in the north as well as the south Atlantic, there has been very little study of the reproduction and life history of *T.gregaria* beyond those cited above. Nevertheless, comparisons can be made within the *Thysanoessa* genus, especially with those species common to temperate or sub-polar regions.

The extended breeding season found in *T.gregaria* is also common to *T.inermis*.

The species has a spawning period of 3 months in the Bay of Fundy (Kulka and Corey, 1978) and in the Gulf of St. Lawrence (Berkes, 1973). Populations from distinct areas were found to have a number of overlapping size modes indicating that there may be several spawning pulses within the breeding season (Kulka and Corey, 1978; Ponomareva, 1966). Unlike *T.gregaria* however, *T.inermis* has a 2 to 3 year life cycle and only reaches maturity in its second year at sizes in excess of 20 mm.

T.longicaudata is a similar sized species to *T.gregaria* and exhibits a 12 month life cycle. Einarsson (1945) carried out an extensive analysis of the population dynamics and growth of this species within the Gulf Stream. The sampling region had Summer surface temperatures of 6.5 to 8.5 °C, which are roughly the same as those found around the Patagonian shelf and so the study is worthy of comparison to the findings of the present analysis.

The surveys analysed by Einarsson (1945) covered May to September. Only one spawning event occurred within this period and the development of this cohort was traced at weekly intervals from the end of May, as larvae, to late August, by which time they had reached adulthood (10mm total length). By Autumn, these individuals had begun developing external sexual characteristics. The adults did not to grow beyond 10mm for the remaining 6 to 8 months and the absence of the 10mm size class in late Summer was taken as an indication that the adult population had died after spawning in May.

Through making rough calculations from graphs presented by Einarsson (1945), the predicted larval growth in *T.longicaudata* was 0.1 $mm.d^{-1}$. This is comparable to predictions made by the present reanalysis for the larval growth rate of *E.lucens* and *E.vallentini* but is 2 to 3 times greater than the *T.gregaria* estimated growth rate. This

suggests that growth rates may have potentially been underestimated in the reanalysis of *T.gregaria* data. The distinct modal distributions of the larvae indicate that reproduction was pulsed throughout the year. However, it is possible that certain cohorts passed through the entire larval sequence within the intervening periods between surveys. Therefore, the reproduction pulses may well have been more frequent than was resolved and growth rates somewhat higher.

The study of Einarsson (1945) also poses a further problem in that it assumes there is no further somatic growth once adulthood is reached. If this is true, then it would be impossible to determine the lifespan of *T.gregaria* on the Patagonian shelf by modal analysis because it has continuous recruitment throughout the year and the modal category remains approximately constant. Einarsson (1945) based the assumption of no adult somatic growth on the fact that the adult population had a modal peak at 10mm both in September and in the following May. Considering that a proportion of the individuals spawned in May were sexually mature by August, it is possible that there was an Autumn cohort that was undetected because it was outside the sampling period of the survey. Recruitment from this cohort would potentially balance selective mortality of larger individuals and keep the modal category at a constant length. Such an explanation is likely because, although there may be zero growth over Winter, it is unusual for there to be no somatic growth in adult euphausiids in other seasons (Bollens et al., 1992). The modal progression methods used in the present reanalysis therefore probably provide a reasonable estimate of the lifespan of *T.gregaria* on the Patagonian shelf.

8.4.4 General Discussion

"Understanding the population biology of an oceanic species depends in large part

upon the extent to which a representative part of the population can be representatively sampled" (Brinton, 1976). Determining the degree to which results are representative is quite difficult. One of the fundamental problems that has yet to be overcome by population studies is determining whether the same population is being continuously sampled (Mauchline and Fisher, 1969). Beyond this there is a great deal of variability in the collection and analysis of population data that is hard to account for. Therefore it is necessary to consider factors that contribute to this variability in order put the above interpretations into context.

Sampling errors

The selectivity of the net is one of the fundamental areas where large errors could be incurred. If all life stages included in the analysis are not representatively sampled relatively if not absolutely, then stage or length frequencies will be biased and modal progression analyses grossly inaccurate. The surveys analysed by Montu (1977) used a net with a 300μm mesh. Ramirez and Dato (1983) used a similarly sized mesh (330μm). However, whereas Montu (1977, 1982) assumed the mesh selectivity to not significantly affect the relative and absolute densities of life stages, Ramirez and Dato (1983) considered that stages earlier than furcilia were not representatively sampled. Pillar and Stuart (1988) carried out a comparative net study and found that all larval stages of *E.lucens* were representatively retained by a 300um mesh net. The reservations of Ramirez and Dato (1983) therefore appear to be unfounded.

The avoidance of nets by plankton has already been considered extensively in Chapter 3. With respect to euphausiids it is to be expected that adults are more capable of avoiding nets than larvae because of their greater sensory capabilities and motility

(Angel, 1977). Pillar (1984b) found there to be no evidence of zooplankton sampler avoidance by euphausiid larvae. It is to be expected therefore that this factor would lead to adult densities being underestimated with respect to larvae.

Length/stage frequency analysis

Jones (1981) stated "size frequency analysis by graphical means is extremely difficult to apply satisfactorily when the data are few". Macdonald and Pitcher (1979) recommended a minimum sample size of at least 50 individuals per age class. France et al. (1991) found that sample sizes between 200 and 500 were sufficient to discriminate between age classes. Although it was aimed to obtain 200 adults from each season and temperature factor region in the *Discovery/William Scoresby* samples, the limited number of available samples made it impossible to reach this target number in some cases. Where target numbers were not reached, distinguishable modal groups may have been missed. The data in Montu (1977) was presented only as densities and it was not possible to determine the numbers of animals considered. However, taking into account the typical numbers of individuals per sample from the *Discovery/William Scoresby* collections and the total number samples analysed by Montu (1977), it is believed that each histogram in the Montu (1977) reanalysis represents numbers far in excess of 200.

A further criticism of length frequency analyses made by Brinton (1976) was that even when there was steady, uniform recruitment, peaks and troughs would appear in length frequency distributions because of differing growth rates and survivorship among life phases. It was found that there was "piling-up" of juveniles and adults later in the growing season which made interpretation difficult. Bollens et al. (1992) commented that selective mortality on smaller size classes may lead to the overestimation of modal

progression and inflated growth rates. The nature of the data set makes it impossible to estimate mortality at different life phases, so the influence of this factor cannot be accounted for in the present reanalysis.

Ovaric maturity

Early studies on euphausiid reproduction assumed that individuals produced single broods and that the spawning period was very brief (Mauchline and Fisher, 1969). However, there is now mounting evidence that the production of multiple broods is common among euphausiid species (*Meganyctiphanes norvegica*: Cuzin-Roudy, 1993; *Euphausia pacifica*: Ross, 1981; *E.superba*: Ross and Quetin, 1983; Cuzin-Roudy, 1993; *E.lucens*: Stuart, 1992). It was evident from the present reanalysis that several cohorts were produced per year in *T.gregaria* and *E.lucens* populations. Although all adult size ranges appeared to contribute to the spawning effort in both species it was difficult to discern whether adults contributed each of the several cohorts or whether they matured only once and died after spawning.

Histological squashes of ovarian cells from *Euphausia superba* have shown that there are a number of different types of germ cells (Kikuno and Kawamura, 1983; Cuzin-Roudy, 1987; Saprykina and Mukhina, 1987). Constant gametogenic activity may provide the mechanism for new production of oocytes and thus for multiple spawnings. Ovarian development and female maturity is therefore not a simple stepwise process and the key of Makarov and Denys (1980) is inadequate at detecting the subtle differences between a primary spawn and a subsequent spawn mature females[2]. Methods are

[2] "Primary spawn" refers to females who are releasing eggs for the first time, "subsequent spawn" refers to females who have released eggs already.

becoming available by which such physiological differences may be detected in females (Cuzin-Roudy and Amsler, 1991). As yet however, they are too complex to be rapidly applied to the large sample sizes necessary in population analysis.

Effect of environmental variables

Even when a population cycle has been determined it is difficult to ascertain whether it is representative because breeding and growth patterns have been found to vary considerably between years and regions.

Mauchline (1960) found there to be a 35% difference between years in the proportion of 1 year old breeding *Meganyctiphanes norvegica* adults. Growth rates were also found to have a great deal of interannual variance. Brinton (1976) found that the intensity of spawning and recruitment of *E.pacifica* varied considerably over a 4 year study period with single cohorts being produced in 2 of the years but 3 cohorts being produced in another. Nepgen (1957) reported interannual differences in the spawning period of *E.lucens* with egg production in one year being between October and March but in the following year being between August and November.

The time of spawning shows a great deal of variability in species with large geographic ranges. *Thysanoessa inermis* for instance was found to start breeding as early as March in certain areas (Plymouth: Lebour, 1924; Norway: Ruud 1927, 1928; Gulf Stream: Einarsson, 1945; Skagerrack: Wiborg, 1967, 1971) but as late as May or June in other regions (West Greenland: Einarsson, 1945; Bay of Chaleur: Lacroix, 1968; Gulf of St Lawrence: Berkes, 1973). Such variation is also evident in the spawning periods of *E.pacifica* (Smiles and Pearcy, 1971; Ponomareva, 1966; Brinton; 1976). The spawning season of *E.lucens* in the Benguela system was found to have different times and

durations even within the same geographic area (Pillar and Stuart, 1988). Similar local variation has also been observed in growth rates. Measurements made by Hulsizer (1971) on 1st year *E.pacifica* in Carr Inlet found the growth rate to be 0.095 $mm.d^{-1}$, a figure which agrees with Heath (1977) and Smiles and Pearcy (1971) for the same developmental period. In Port Susan however, Hulsizer (1971) found first year individuals to have growth rates of 0.066 $mm.d^{-1}$.

Temperature has an important influence on population cycles. Significant effects on development times were found by Ross (1981) in *Euphausia pacifica* where individuals took 45 days to pass from egg to juvenile 1 at 12°C but 68 days at 8°C. Similarly, Sameoto (1976) estimated the intermoult period in *Thysanoessa inermis* to be 6 days at 15°C but 15 to 16 days at 0°C. Temperature differences were considered by Sheard (1953) and Makarov (1974) to be influential in altering developmental pathways. The time and duration of spawning has also been reported to be influenced by temperature. Einarsson (1945) compared 5 areas in the NE Atlantic and found that spawning of *Thysanoessa* species occurred earlier in the warmer areas. Ponomareva (1966) noted that breeding of *Thysanoessa inermis* and *T. raschii* in the NE Pacific commenced when temperatures reached 1°C and that breeding was delayed in cold years. Breeding was completed when temperatures reached 8° to 9°C. Berkes (1973) found a similar pattern in the Gulf of St. Lawrence where surface temperatures of 10°C marked the end of breeding. However, the influence of temperature on the timing of breeding has been ruled out in a number of other studies (Brinton , 1976; Ross et al., 1982; Pillar and Stuart, 1988).

Mid-latitude oceanographic conditions are irregular both seasonally and interannually. Maintaining flexibility in the reproductive cycle increases the likelihood

that the reproductive effort during the year has at least some degree of success (Cole, 1954; Brinton, 1976; Pillar and Stuart, 1988). Therefore, variation in the population cycles with respect to multiple spawning, additional cohorts and larval mortality are to be expected through time and between regions. One feature that was prominent in all species was that reproduction appeared to take place in sequential pulses. The causal factors behind this pattern are still very much unknown and may stem from periodic food availability, predation or abiotic influences which may act as cues to promote reproductive activity or affect the survivorship of newly spawned larvae. What has been established however is a detailed pattern of the population ecology of euphausiids on the Patagonian shelf which is a basis on which further aspects of trophic ecology and community distribution in this region can be examined.

8.5 Conclusions on euphausiid life cycles

1, Spawning by *Euphausia vallentini*, *E.lucens* and *Thysanoessa gregaria* on the Patagonian shelf occurred as discrete pulses forming cohorts that were distinguishable within the sample population. The cohorts appeared as modes in length frequency distributions and could be traced through seasons.

2, *E.vallentini* produced one major cohort during Spring. The majority of the post spawn adult population subsequently died. A second minor cohort was produced in Autumn mainly in the northern part of the shelf. This was spawned either by surviving 1 year old adults or fast growing individuals spawned in the Spring.

3, Spring spawned *E.vallentini* reached post larvae and adult stages by Summer. Larval growth rate was approximately 0.12 $mm.d^{-1}$/0.02 $mg.d^{-1}$. On reaching adulthood, it is believed the population migrated out of the sampled water column until Winter. Adult growth rate between Summer and Winter was approximately 0.02 $mm.d^{-1}$ or 0.02 $mg.d^{-1}$.

4, *E.lucens* produced 2 (possibly 3) cohorts in the warmer temperature factor 1 region compared to 1 (possibly 2) cohorts in the colder temperature factor 2 region. A Spring cohort may have been produced in both regions but supporting evidence for this was only indirect. The major cohort in both temperature factors 1 and 2 was produced in Summer. A further cohort was spawned Autumn in temperature factor 1.

5, *E.lucens* took between 2 and 3 months to pass from egg to adult. Larval growth rates were approximately 0.11 $mm.d^{-1}$ or 0.02 $mg.d^{-1}$. Individuals remain as adults for 9 months during which time several cohorts may have been produced. It is not certain whether all or a fraction of the adult population contributes to each of these

spawning efforts although sexual maturity was evident in all size classes. Approximate adult growth rate was 0.02 $mm.d^{-1}$ or 0.01 $mg.d^{-1}$.

6, *T.gregaria* produced at least 4 discrete cohorts during the year with little regional differentiation in the frequency or size of spawning pulses. The cohorts were evenly spaced between seasons although the Winter cohort was weaker than the other three. It is possible that further cohorts were produced in the intervening survey periods and were subsequently missed.

7, *T.gregaria* typically took 4 months to pass from egg to adult. Larval growth rates were estimated at between 0.03 $mm.d^{-1}$/0.01 $mg.d^{-1}$ and 0.04 $mm.d^{-1}$/0.02 $mg.d^{-1}$.The adult population density remained at the same moderate level throughout the year. This was probably the result of steady recruitment and mortality during all seasons. Assuming the same adult growth rates as *E.lucens*, adult life span was approximately 8 months.

8, Comparing between species, *E.vallentini* adults and larvae dominate the water column during Spring especially in the southerly regions. *E.lucens* adults and larvae are most apparent during Summer and have reach greatest densities in the northerly regions. They are also dominant in greater adult densities during Autumn although larval densities are reduced from Summer levels. In Winter, *E.lucens* and *E.vallentini* adults are equally dominant. *T.gregaria* adults and larvae make up minor proportion of the euphausiid population in each season.

Chapter 9 Production of euphausiids on the Patagonian shelf

9.1 Introduction

Determining the life history of the euphausiid species on the Patagonian shelf is necessary when considering the potential of the euphausiid population as a resource but there are further parameters which also need consideration. The timing of reproduction and the number of broods per year indicate how frequently individuals are recruited into a population, but not how large this recruitment is. To gain an idea of the level of resource which can be safely exploited, the rate and total amount of biomass being produced must be determined, as well as how quickly this biomass is being turned over. Biomass, production and the P/B ratio are complimentary parameters which must be considered when assessing the potential of any population as a resource.

The quantitative seasonal data for euphausiid populations on the Patagonian Shelf collected by Montu (1977, 1982) provides a basis from which values for these parameters can be obtained. The measurement of such parameters has a great deal of value in a relative sense, especially in comparing seasonal fluctuations in parameter values to life history patterns and fluctuations in the commercial squid stocks. Furthermore, comparison to production and P/B values obtained for euphausiid populations in other regions allows the relative importance of euphausiids in this region to be assessed. Nevertheless, as was highlighted by the analysis in Chapter 8, the data set provided by Montu (1977, 1982) is far from comprehensive and a number of assumptions are necessary in order to estimate certain parameter values. It is also imperative that these measurements are placed in their proper context because the

absolute values in themselves are of limited usefulness both in relation to estimating the levels of euphausiid stock which can be safely exploited and estimating the quantity available to the commercial squid population. For such estimates to be made it is neccessary to have a detailed knowledge of the food web and predatory consumption levels of which neither have been considered in any detail for this region. Nevertheless, the following chapter represents one of the first attempts to estimate secondary production and P/B in this region and their measurement makes a considerable contribution to the understanding of the dynamics of the Patagonian shelf ecosystem.

9.2 Rationale to the calculation of production

The term "secondary production" has been used to mean various things in different studies such as an instantaneous rate (Rigler and Downing, 1984, p. 38), a rate averaged over a time interval (Clarke et al. 1946) or a quantity integrated over a time interval. This study has adopted the approach defined by Kimmerer (1987) who defined three separate parameters within the term "secondary production" with the aim of clarifying concepts and making calculation methods more intelligible. The first parameter is the "production rate" (PR), which represents the instantaneous rate of production of biomass by a population:

$$PR_i = g_i + e_i + r_i \qquad \text{(i)}$$

$$PR = \sum PR_i \,.\, (B_i \text{ or } D_i) \qquad \text{(ii)}$$

Where i represents subpopulations/ life stages which have different growth rates, g is growth rate due to increase in body size, e is moulting rate, r is reproduction rate, B is biomass and D is density. B or D are used depending on the units of g.

PR at discrete times can be determined by measuring biomass or density and estimating growth rates from cohort progression analyses or by physiological methods. It is an instantaneous measure of a continuously varying property and is useful in examining the status of a population at a particular time.

The second parameter is the "weight specific production rate" or "P:B"

$$P{:}B = PR/\sum B_i \qquad \text{(iii)}$$

This is the mean daily growth rate of the population, weighted by the biomass in each life stage or sub-population having a different growth rate. This term may be otherwise known as the "specific growth rate", the "instantaneous rate" or "weight-specific

production rate" and has units of inverse days. It is to be noted that this term is different to P/B which is the annual mean production to mean biomass. P:B cannot simply be related to P/B because P/B is integrated over a time interval during which the P:B may vary. In the present analysis, P:B will be followed by the suffix d^{-1} and P/B by the suffix yr^{-1} so that these two parameters are easily distinguishable.

The third parameter is the "integrated production" (IP)

$$IP = \int_{t1}^{t2} PR \, dt \qquad \text{(iv)}$$

IP is the production rate integrated over any suitable time interval and has units of biomass per unit area.

There is no single method that provides the best estimate of production and methods vary considerably in terms of the kind of data collected and their analyses (Omori and Ikeda, 1984). Methods can basically be divided into two approaches (i) the population dynamic method and (ii) the laboratory based physiological budget method. The population dynamic method relies either on the identification of cohorts in a population or, in situations where recruitment through the year is continuous, the accurate determination of the size frequency distribution of the population through the year. Population dynamic methods consider simultaneous changes in the number of standing stock biomass and mean individual weight between sampling intervals in estimating IP. In instances where cohorts can be distinguished, analytical methods such as increment summation, removal summation, instantaneous growth and Allen curves can be applied. In cases where recruitment is continuous, methods involving development times, such as those derived by Winberg (1971) and subsequently applied to euphausiids by Ritz and Hosie (1982) may be employed. Laboratory budget physiological budget

methods involve the maintenance of animals in cultures where growth rates or physiological rates can be measured. This allows the determination of growth rates which can be applied to field data on density or biomass through time to gain PR's assuming that differences between laboratory and field conditions do not make physiological rates significantly different.

There is an advantage to estimating production using field measurements as many experimental artifacts are avoided (Redfield, 1958). For this very reason however, the precision and accuracy of the field sampling are crucial. It is evident from analyses in this study (Chapt. 8) that euphausiid populations on the Patagonian shelf produce distinguishable size cohorts which can be traced between seasons. However, Montu (1977, 1982) only sampled between 0 and 100m which presents certain problems when trying to apply cohort methods for estimating production. Cohort methods rely on there being no size dependent movement or mortality in the sampled water column. In Chapter 8, it was hypothesised that there was size dependent movement to waters below 100m by larger members of the *E. vallentini* population during Summer and Autumn making cohort methods inappropriate. A more suitable method must be able to assume that the productive proportion of the population is within the sampled water column and that the part of the population lying outside sampling depths is not important.

One possible approach is to apply the growth rates estimated from the cohort analyses in Chapter 8. However, these estimates were calculated assuming a linear growth rate over sampling intervals. Although such an estimate is valid for comparison between euphausiid growth rates calculated in the same way, the fact that growth rates are allometric over most of a euphausiids' lifespan makes such estimates inadequate for use in production calculations. Furthermore, the sole use of growth rate due to increase

in body size for estimating PR_i ignores the contribution of moulting and reproduction to the rate of production.

Laboratory based physiological budget methods allow production to be estimated without making assumptions about the population lying outside the sampled water column through applying PR_i measured from physiological rates to animals densities in the sampled water column. Physiological budget based estimates of PR_i can be gained either directly or indirectly. Direct measurement involves the estimation of growth due to increase in body size, moulting and reproduction in the laboratory. Laboratory rearing experiments were not possible in this instance and gaining information on these parameters from the literature was also unfeasible because of the lack of suitable studies that have been carried out. Indirect measurement consists of measuring metabolic physiological rates in laboratory maintained animals and calculating PR_i through assuming certain relationships between physiological rates and rates of production. This approach is commonly termed the "Carbon balance" approach and it attempts to account for the input (ingestion or assimilation) and the output (defecation, respiration, excretion) of carbon or a related unit and thus estimating production rate by determining the difference between the two. This approach has been widely covered in the literature and there are a number of studies from which to suitable information can be extracted (Ikeda, 1974; Sameoto, 1976; Ikeda and Motoda, 1978; Ross, 1982b; Huntley and Boyd, 1984; Ikeda, 1984; Hirche, 1984; George, 1985).

The biggest problem in estimating PR_i through indirect measurement is testing the validity of the assumptions made by models relating physiological rates to production rates. One of the only studies to consider this problem in euphausiids was carried out by Ross (1982b). Laboratory measurements of weight-specific production (P:B d^{-1}) in terms

of both Carbon and Nitrogen during the lifespan of *Euphausia pacifica* were made both directly (as the sum of growth, moulting and reproduction) and indirectly (as assimilation minus metabolism and leakage) at two different temperatures (8°C and 12°C). Considerable differences were noted between the P:B d^{-1} measured directly (from growth) and indirectly (from the model) (fig 9.2a) suggesting that the physiological measurements made or the model used to estimate weight-specific production were inappropriate, if not both. Nevertheless, an alternative model may well produce values more compatible with those derived from direct measurements.

One problem in deriving an appropriate model is taking account of various influential abiotic and biotic influences on production rates, the most important of which are temperature and body weight. Evidence of the effect of temperature on production rates has been illustrated by Huntley and Boyd (1984) who pooled the results of a large number of zooplankton growth studies and found an exponential relationship between maximum weight-specific growth rate and temperature. Considering euphausiids, Ross (1982b) found that the weight-specific growth rate in *Euphausia pacifica* differed between 8° and 12°C with a Q_{10} for carbon growth of 3.65. Body size is not as universally accepted as temperature as being an influence on production rates and in zooplankton production models such as Huntley and Lopez (1992), it was assumed that the weight specific growth rate was body size independent. However, by contrast Mauchline (1977) reviewed a number of euphausiid growth studies and illustrated that the percentage of growth at each moult (defined as the growth factor) decreased with size despite the intermoult periods being approximately the same in duration, so weight-specific growth rate was shown to decrease with increasing body weight. Therefore, it was considered advisable to adopt a method that enabled both temperature and body size

to be taken into account when calculating PR through indirect physiological budget methods.

There are a number of proposed models relating physiological rates to production rates. Most models incorporate temperature as an important factor affecting PR_i (Ikeda and Motoda, 1978; Huntley and Boyd, 1984; Huntley and Lopez, 1992) but not all incorporate body size as a further important factor and in some P:B d^{-1} is assumed to be size independent (Huntley and Lopez, 1992). One of the most important physiological rates used in production rate models is respiration and many studies on euphausiids found that weight specific respiration rate remained constant with increasing body size (*E.pacifica*: Lasker, 1966; Small et al., 1966; Paranjape, 1967; Small and Hebard, 1967; Pearcy and Small, 1968; *E.lucens*: Staurt, 1986) which agrees with the weight independent assumptions of the Huntley-Boyd (1984) and Huntley-Lopez (1992) models. However, such findings on respiration rate do not agree with Pearcy et al. (1969) and Ross (1982b) who determined the respiration rate of *Euphausia pacifica* to be a power function of body weight. Indeed, Ross (1982b) argued that the weight range considered by most of the reported studies on euphausiids was not sufficient to obtain the variation in respiration rates that were evident throughout an animal's lifespan.

Accepting that euphausiid respiration rate is probably body size dependent and that the P:B d^{-1} from direct measurements decreases with increasing body size adds support to the argument that body size as well as temperature dependence must be a necessary part of any model that is likely to produce values more compatible to the direct measurements of Ross (1982b). One such model was developed by Ikeda and Motoda (1978) from laboratory data on weight and temperature specific respiration rates

collected by Ikeda (1974). The model was later adapted by Uye et al. (1987). Respiration is estimated using a stepwise regression of the form:

$$\log_{10}R_i = \log_{10}a + b \log_{10}W_i \qquad (v)$$

Where R_i is respiration rate of stage i (ul O_2/animal per h), W is body weight of stage i (mg/animal) and constants a and b are both functions of habitat temperature:

$$\log_{10}a = 0.02538T - 0.1259 \qquad (vi)$$

$$b = -0.01089T + 0.8918 \qquad (vii)$$

Where T is habitat temperature in °C.

A respiratory quotient of 0.8 was adopted to convert oxygen to respired carbon so daily respiration rate of stage i (Rc, μgC animal^{-1} d^{-1}) is given by:

$$Rc_i = 0.8 \,.\, (12/24) \,.\, 24 \,.\, aW_ib \qquad (viii)$$

PR_i was estimated from respiration using balanced equations proposed for fishes by Winberg (1956):

$$0.8F_i = PR_i + Rc_i \qquad (ix)$$

$$K_{1i} = PR_i/F_i * 100 \qquad (x)$$

$$K_{2i} = PR_i/0.8F_i * 100 \qquad (xi)$$

Where F is feeding rate, K_1 is gross growth efficiency, K_2 is net growth efficiency and 0.8 is digestion efficiency in fish.

PR_i was derived so that:

$$PR_i = K_{1i}Rc_i/(80-K_{1i}) \qquad (xii)$$

and values of 70% for digestion efficiency and 30% for K_{1i} were chosen as realistic values of zooplankton in the field. This gave the equation:

$$PR_i = 30Rc_i/(70-30) = 0.75Rc_i \qquad (xiii)$$

The validity of the Ikeda and Motoda (1978) model with respect to euphausiids was tested by comparing P:B d^{-1} values predicted by the model (using equations (xiii), (ii) and (iii)) against directly measured values presented in table by Ross (1982b) for given weights at 8°C and 12°C (fig 9.2a). The Ikeda-Motoda model fits the directly measured rates much better than the Ross model at both temperatures, particularly in the fact that both the direct measurements and the Ikeda-Motoda model show decreasing P:B d^{-1} values with increasing weight.

The fact that the difference between the P:B d^{-1} values of the Ikeda-Motoda model and the directly measured values is almost 50% towards the lower end of the weight range still leaves cause for concern in using the model to ultimately estimate IP for the present data set. Nevertheless, these errors must be put into context with respect to the eventual calculation of PR which also requires the determination of density. Density in aggregations can reach 100 or 1000 times the average density of the population (Omori and Hamner, 1982) and such patchiness is difficult to account for unless a large number of replicate samples are taken at each site over a prolonged period. Such sample replication was not carried out in obtaining the present data set and although density values are assumed to be representative, it is possible that some may be incorrect by orders of magnitude. Adopting the Ikeda-Motoda model as opposed to making direct laboratory estimates of production means that PR would vary, at most, by a factor of 2 and probably a lot less considering that the model approximates directly measured P:B d^{-1} very closely over a large part of the euphausiid body weight range. The Ikeda-Motoda model was therefore applied to the population densities and corresponding temperatures given by Montu (1977) to estimate of season specific PR and P:B and ultimately annual IP and P/B.

Carbon production for *E.pacifica* measured directy and with models using data from Ross, 1982

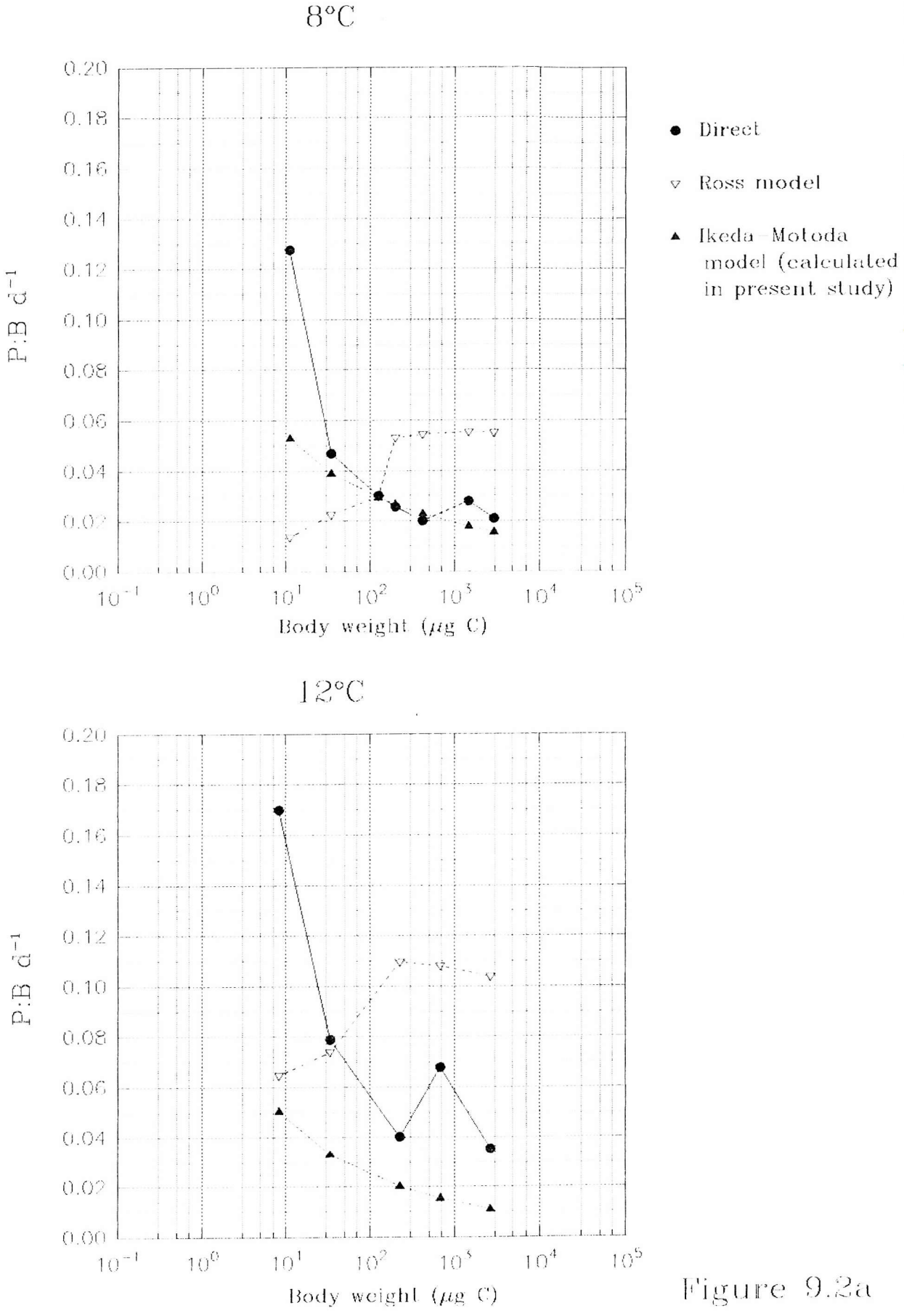


Figure 9.2a

9.3 Methods

The calculation of biomass from the data and PR, P:B d^{-1} IP and P/B yr^{-1} via the Ikeda-Motoda model involved a number of steps which are outlined below.

9.3.1 Treatment of densities from Montu (1977)

Densities of larvae were directly calculated from the data given in Montu (1977). Total density for a season was initially subdivided into sample groups and then further split according to temperature factor region (ie. sample groups 2 and 4 consist of stations found in both temperature factors 1 and 2; see Chapt. 8 for further details). Because of the large body size range within the post-larvae and adult categories it was decided to split the post-larvae and adult densities according to the proportions of each size category identified in the analysis of *Discovery/William Scoresby* collections (see Chapt. 8). In seasons where such proportions were not available for both temperature factor regions, the proportions available from the one temperature factor region were taken to be representative of the other. In seasons where there were no samples analysed for either temperature factor region, the post-larvae and adult densities derived from Montu (1977) were sub-divided equally between all the size categories (eg. for *E. vallentini* post-larvae in Spring, where inadequate specimens were available to determine the post-larval size frequency distribution, the Spring post-larval densities for each sample group in each temperature factor region were split so that each size category contained 20% of the total. So for sample group 1 in temperature factor 1, the total post-larval density of 2.105×10^{-3} ind.m^{-3} was divided equally between the 8 to 13mm categories so that in each size category contained a density of 0.412×10^{-3} ind.m^{-3}).

9.3.2 Estimation of average weight of each size classes

Larvae

Average weight per stage was calculated for larvae using dry weight values (DW) obtained from the *Discovery/William Scoresby* samples. Where there were inadequate specimens to estimate the weight of a particular stage, weights were taken from species specific larval length-weight regressions (fig 9.3a and b). Typical lengths for the missing stages were taken from the literature (*Euphausia vallentini* - Dilwyn-John, 1936; *E.lucens* - Bary, 1956; *Thysanoessa gregaria* - Gurney, 1947). In the case of *T.gregaria*, typical lengths of calyptopes stages were not available from the literature so weights were determined by using furcilia to calytopes weight proportions observed in *E.lucens* (the weight ratio of furcilia I to calytopes I, II and III were determined for *E.lucens* and these ratios were applied to the weight of furcilia I in *T.gregaria* to estimate weight in calytopes I, II and III). A further problem was that Montu (1977) identified a cyrtopia VI stage despite the fact that the stage is not contained in the key (Gurney, 1947) that Montu (1977) reportedly used. This stage was included within the present analysis to maintain compatibility with the data of Montu (1977) and its average weight was estimated through averaging the weight of the stages either side of cyrtopia VI (ie. cyrtopia V and post-larvae).

Post-larvae and adults

Average adult weight per size category was calculated from length-weight regressions presented in Chapter 8 (*E.vallentini* - 8.3.1h; *E.lucens* - 8.3.2i; *T.gregaria* - 8.3.3g). The same regressions were used to calculate the weights of post-larval size categories.

Logged length–weight relationship of calytopes and early furcilia stages of *E.vallentini*

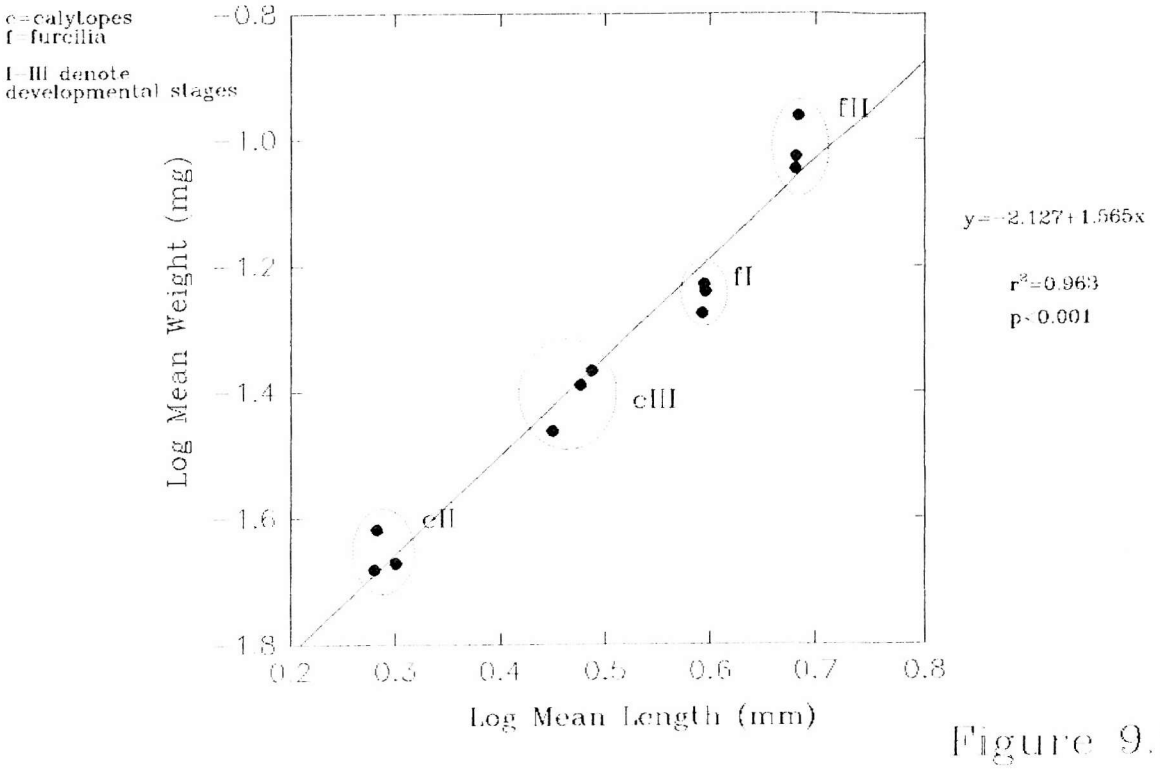


Figure 9.3a

Logged length–weight relationship of *E.lucens* furcilia

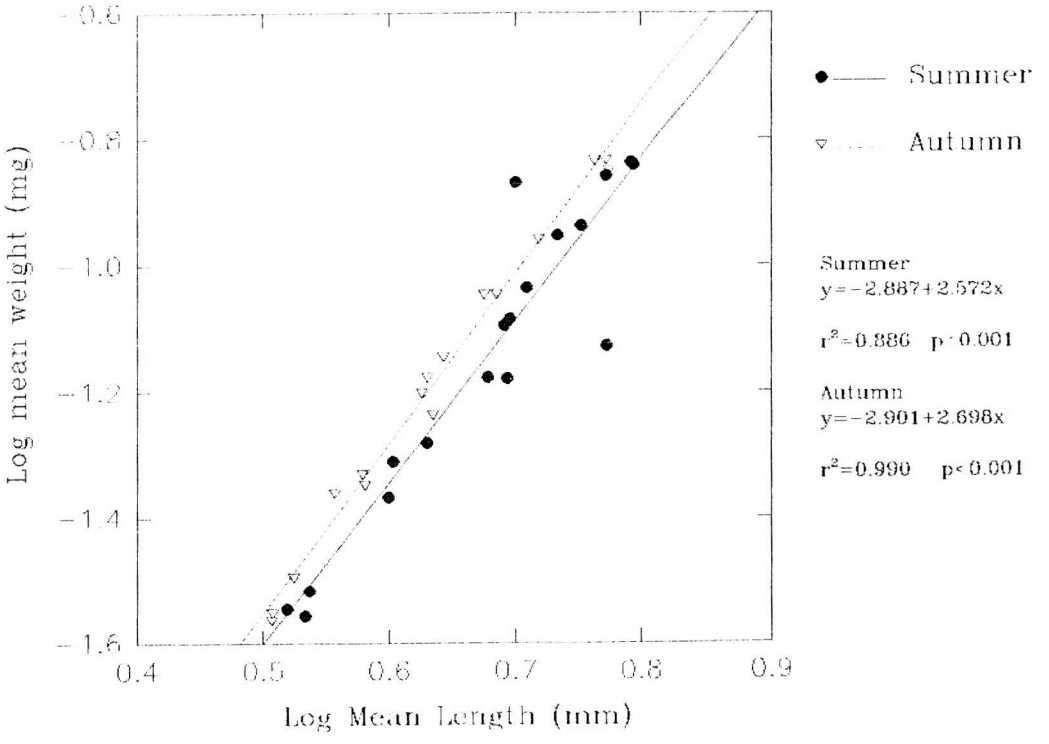


Figure 9.3b

9.3.3 Estimation of biomass

Biomass was calculated by multiplying the dry weight values by the densities described in section 9.3.1. As described in 8.2.3, weight loss caused by preservation was estimated from the equation derived by Giguere et al. (1989) and suitable corrections were made to the preserved DW measures. Where sample groups were subdivided into temperature factors 1 and 2, these were summed so that biomass for each stage was sample group specific. The biomass of each stage was then summed to obtain the biomass for a sample group.

9.3.4 Application of the Ikeda-Motoda model

Temperature

As previously described, the Ikeda-Motoda model estimates respiration rate as a function of both weight and temperature according to equations (v), (vi) and (vii) which are:

$$\log_{10}R_i = \log_{10}a + b \log_{10}W_i \qquad (v)$$

Where R_i is respiration rate of stage i (ul O_2/animal per h), W is body weight of stage i (mg/animal) and constants a and b are both functions of habitat temperature:

$$\log_{10}a = 0.02538T - 0.1259 \qquad (vi)$$

$$b = -0.01089T + 0.8918 \qquad (vii)$$

Where T is habitat temperature in °C.

$Log_{10}a$ and b were calculated for both temperature factors in each season using average temperatures derived from Montu (1977) given in Appendix IVb.

Respiration/PR_i

R_i was subsequently calculated for each stage/size category for both temperature factor regions in each season using equation (v) and employing the average weights given in Section 9.3.1. R_i, which represents an hourly rate in terms of oxygen, was converted into carbon units per day (Rc_i) using an equation from Uye et al. (1987):

$$Rc_i = 10.286 \, . \, R_i \qquad \text{(xiv)}$$

Where Rc_i is the daily respiration rate of stage i in terms of carbon (μg C animal^{-1} d^{-1}).

PR_i was calculated from Rc_i using equation (xiii):

$$PR_i = 0.75 \, Rc_i \qquad \text{(xiii)}$$

Where PR_i is the production rate of stage i (μgC animal^{-1} day^{-1}).

Production rate (PR)

In calculating PR for a complete sample group region in a particular season, it was necessary to confirm that the correct PR_i was used for the different temperature factor regions (see fig 8.2a) (for example, sample group 2 contains some stations positioned in temperature factor 1 and others in temperature factor 2 so within the same sample group it was necessary to apply different PR_i). The appropriate PR_i was subsequently multiplied by the density of the respective stage in each sample group. PR_i's were then summed to calculate the PR for each sample group region according to equation (ii).

$$PR = \sum PR_i \, . \, D_i \qquad \text{(ii)}$$

Where PR is the production rate of the sub-population (sample group) (ug C animal^{-1} d^{-1}) and D_i is the density of stage i (animals m^{-3}).

In cases where the sample group was subdivided because it contained stations from both temperature factor regions, these subdivisions were summed. In order to obtain PR values in mg dry weight (DW), the values were divided by the C/DW ratio of

0.42 for *Euphausia pacifica* (Lasker, 1966).

P:B d^{-1}

P:B d^{-1} were obtained by dividing sample group biomass values (see Section 9.3.3) into the respective PR values according to equation (iii).

$$P:B = PR/\sum B_i \qquad \text{(iii)}$$

Where B_i is the biomass of stage i.

Annual integrated production (IP yr^{-1}) and P/B yr^{-1}

There were two main problems encountered in obtaining values for integrated production over the year. Firstly, the number of PR values through the year in a sample group were limited to 4 ie. 1 per season. Secondly, the trajectory between the PR values was unknown. Kimmerer (1987) considered that a linear trajectory between points was best and so this type of integration was adopted.

P/B yr^{-1} was calculated firstly by estimating the average biomass through the year for each sample group by adding together the biomass values for each season and dividing by 4 and then dividing this value into the respective IP value.

9.4 Results and Interpretations

9.4.1 Intra-specific comparison of biomass (fig. 9.4a)

Euphausia vallentini

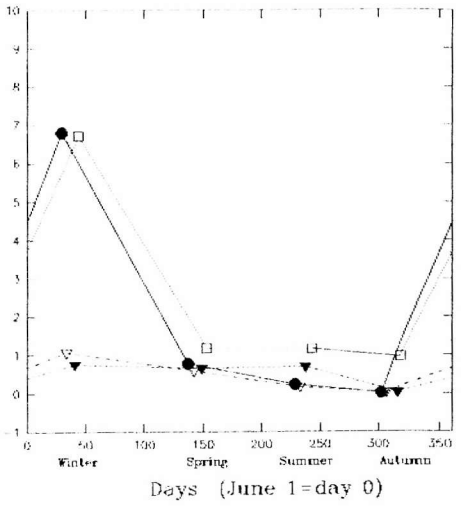
Biomass between Spring and Autumn appeared to be relatively constant in all sample groups, ranging between 0.01 to 1.18 mg DW m^{-3} Sample group 4 had the highest biomass values in these seasons, followed by sample group 3, 1 and 2 respectively. During Winter, biomass values remained approximately the same in sample groups 2 and 3, but were elevated seven fold in samples group 1 and 4, reaching approximately 7 mg DW m^{-3}. Overall biomass was highest in the Winter but dropped through the rest of the season.

Euphausia lucens

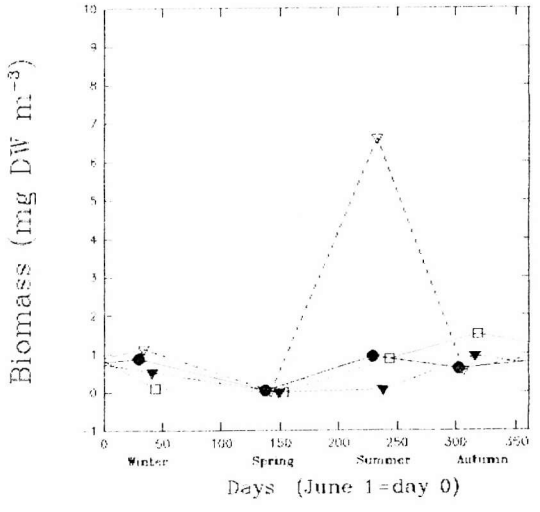
The biomass of all sample groups was lowest during Spring, with values between 0 and 0.05 mg DW m^{-3}. In all cases, biomass was higher in Summer and peaked in sample groups 1 and 2, particularly in sample group 2 with a value of 6.6 mg DW m^{-3}. Sample groups 3 and 4 reached peak biomass in Autumn, attaining values of 0.55 and 0.94 mg DW m^{-3} respectively. Sample group 1 fell slightly from its Summer peak of 0.92 mg DW m^{-3} to 0.61 mg DW m^{-3} in Autumn. A dramatic decrease was seen in the biomass of sample group 2 which reached an Autumn level of 0.55 mg DW m^{-3}. Sample groups 1 and 2 rose by a relatively small amount between Autumn and Winter with sample group 3 dropping by a comparable amount. A clear biomass decrease occurred between Autumn and Winter in sample group 4, dropping from 1.5 mg DW m^{-3} to 0.09 mg DW m^{-3}. Overall, biomass was typically lowest in Spring while peak biomass was attained in Summer in the more northerly groups and Autumn in the southerly groups.

Biomass through the year
in sample groups 1 to 4

E.vallentini



E lucens



T.gregaria

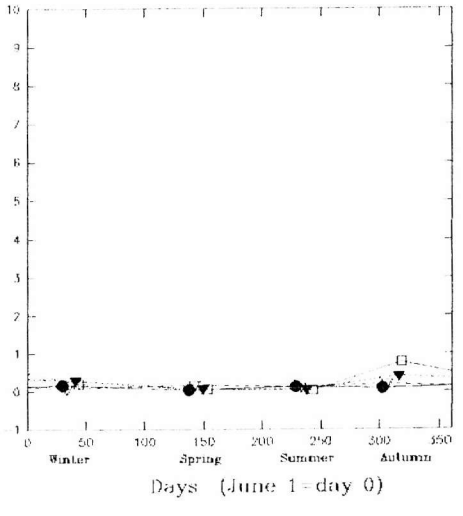


Figure 9.4a

Thysanoessa gregaria

Spring and Summer biomass levels were relatively low in all sample groups, ranging between 0.03 and 0.17 mg DW m^{-3}. In sample groups 2, 3 and 4 biomass peaks were attained in Autumn, and were 0.20, 0.41 and 0.78 mg DW m^{-3} respectively. In sample group 1, the Autumn biomass value remained low at 0.09 mg DW m^{-3} but peaked during Winter with a value of 0.15 mg DW m^{-3}. Generally seasonal biomass remained low throughout the early to mid part of the year and rose slightly in the latter part of the year.

9.4.2 Inter-specific comparison of biomass

Comparing between species, it is evident that the biomass of *T.gregaria* through the year is considerably smaller than that of *E.lucens* and *E.vallentini*. The average biomass peak in *T.gregaria* was 0.385 mg DW m^{-3} as opposed to 2.49 mg DW m^{-3} in *E.lucens* and 3.835 mg DW m^{-3} in *E.vallentini*. In terms of general trends in biomass through the year it appears that *E.valletini* shows a pattern that is contrary to that found in *T.gregaria* and *E.lucens*. Whereas biomass levels in *E.vallentini* are at their between Autumn and Spring, biomass levels in *T.gregaria* and *E.lucens* are mostly at their lowest levels during this period. Peak biomass levels in *E.lucens* and *T.gregaria* are mostly apparent from Spring to Autumn when *E.vallentini* biomass levels are at their lowest.

There do not appear to be any inter-specific trends in sample group values. Whereas, the major peaks in *E.vallentini* were produced in sample groups 1 and 4, in *E.lucens*, the major peak was apparent in sample group 3. Similarly, while the highest overall biomass in *E.vallentini* was found in sample group 4, in *E.lucens* it was found in sample group 2. In *T.gregaria*, there was no major difference in peak magnitude or

overall biomass between sample groups.

9.4.3 Intra-specific comparison of production rates

Daily production rates through the year for each of the three species are presented in fig 9.4b. These data are also compared to respective biomass values for each sample group in figures 9.4c, 9.4d and 9.4e. It is apparent in each of the PR to biomass comparisons that seasonal trends in PR match those of biomass very closely.

E.vallentini

The highest production rates were found in Winter, especially in sample groups 1 and 4 where values reached as high as 0.12 and 0.11 mg DW d^{-1} respectively. Production rates declined through Spring, Summer and Autumn in all sample groups with the exception of sample group 3 where there was a slight increase in Spring and Summer. In every season after Winter however, all PR values were below 0.020 mg m^{-3} DW d^{-1} apart from Spring in sample group 4 where PR was 0.033 mg m^{-3} DW d^{-1}.

E.lucens

PR for all samples was typically below 0.02 mg DW m^{-3} d^{-1} but with specific peaks in either Summer or Autumn. In Summer in sample group 2, PR reached 0.097 mg DW m^{-3} d^{-1} and in Autumn, sample group 4 PR was 0.031 mg m^{-3} DW d^{-1}.

T.gregaria

All values were below 0.020 mg m^{-3} DW d^{-1} and the vast majority were below 0.010 mg DW d^{-1}. Highest PR values were found in Autumn in sample groups 3 to 4 and in Summer in sample group 1. Winter PR values were relatively higher than Spring and Summer values in sample groups 3 and 4. In sample group 2, Winter PR was the lowest annual value and PR increased through Spring and Summer to peak in Autumn. In

Daily Production Rate (PR) through the year
in sample groups 1 to 4

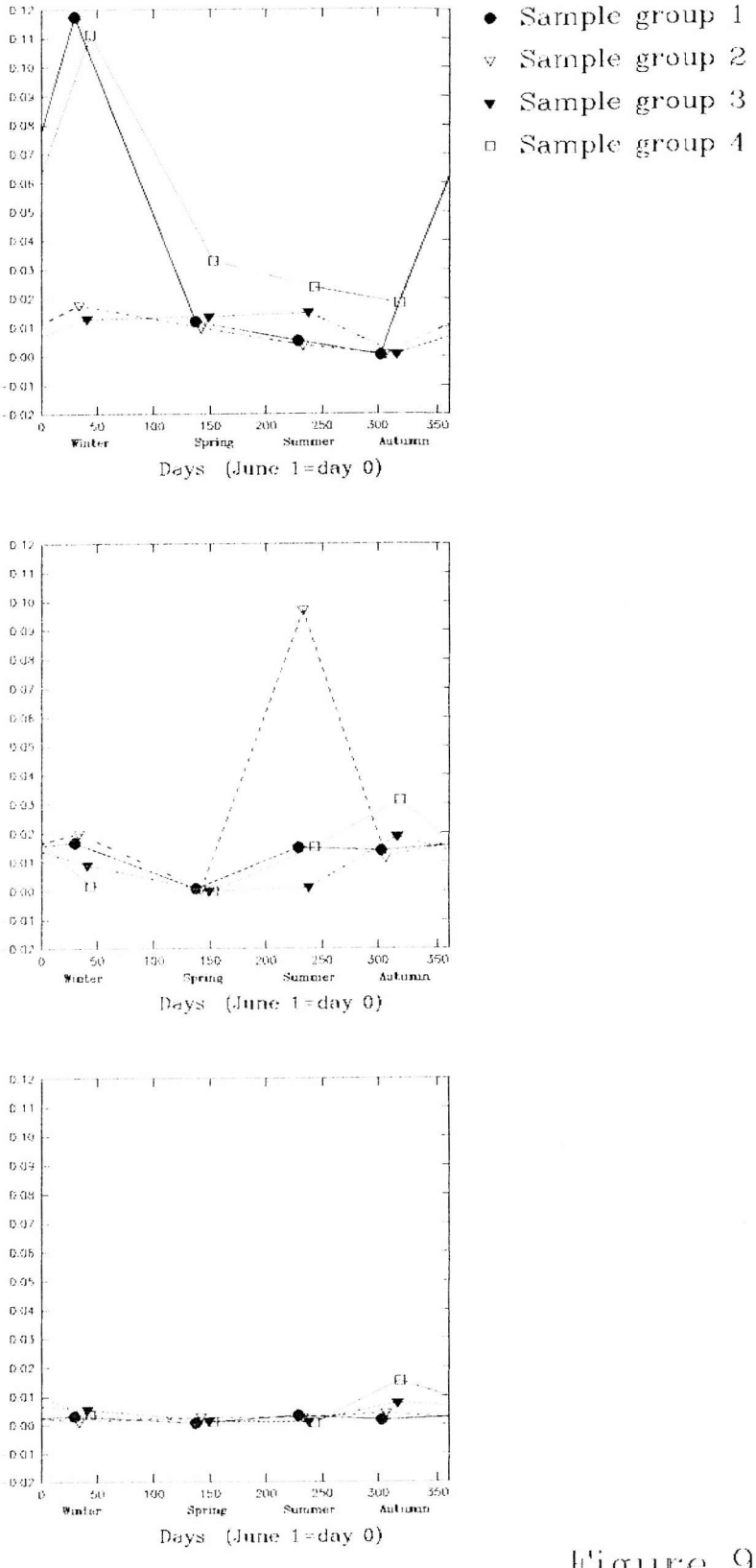


Figure 9.4b

Biomass vs daily production rate (PR) through the year for *E.vallentini*

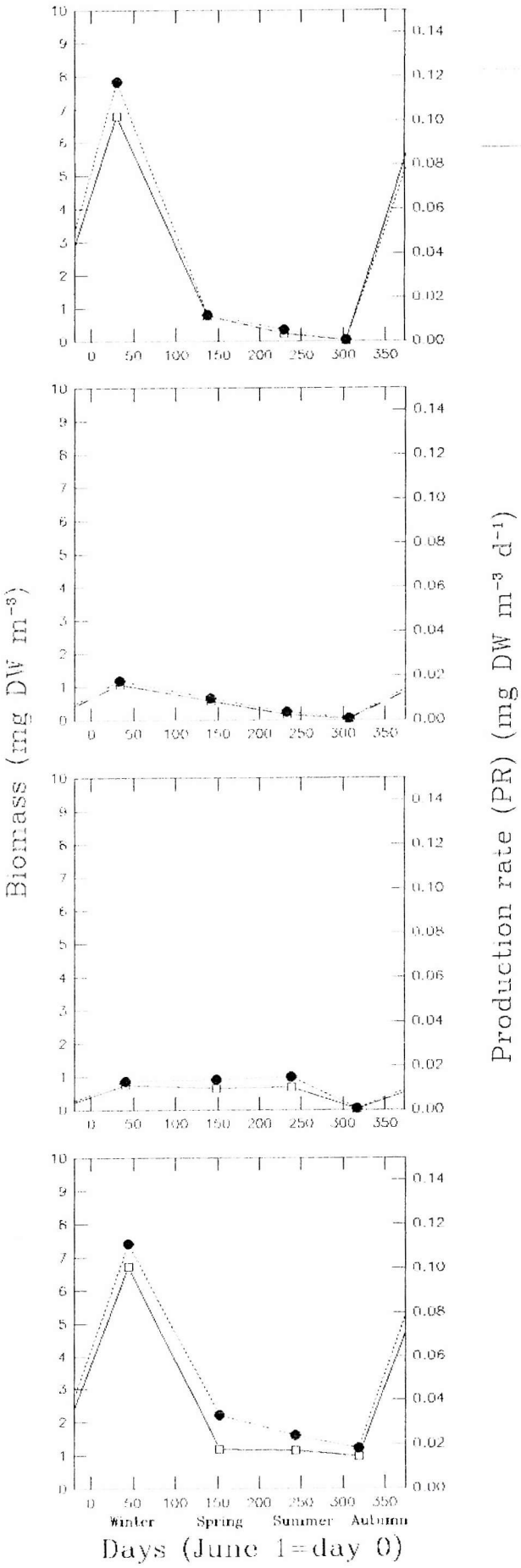


Figure 9.4c

Biomass vs daily production rate (PR) through the year for *E.lucens*

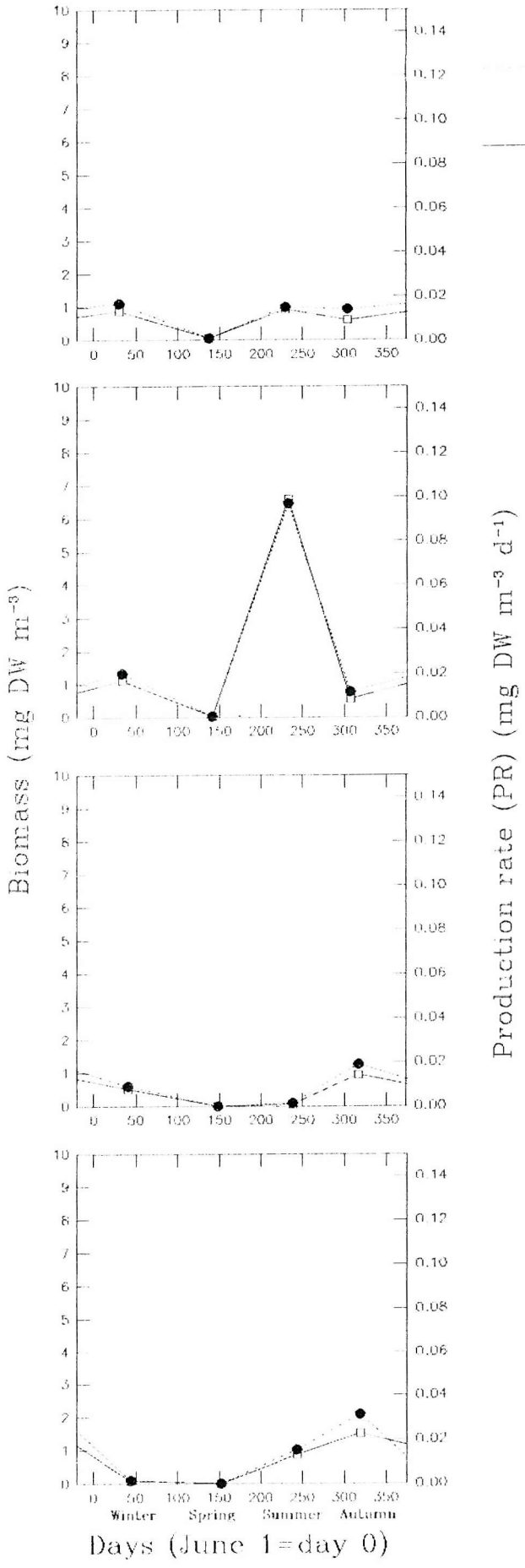


Figure 9.4d

Biomass vs daily production rate (PR) through the year for *T.gregaria*

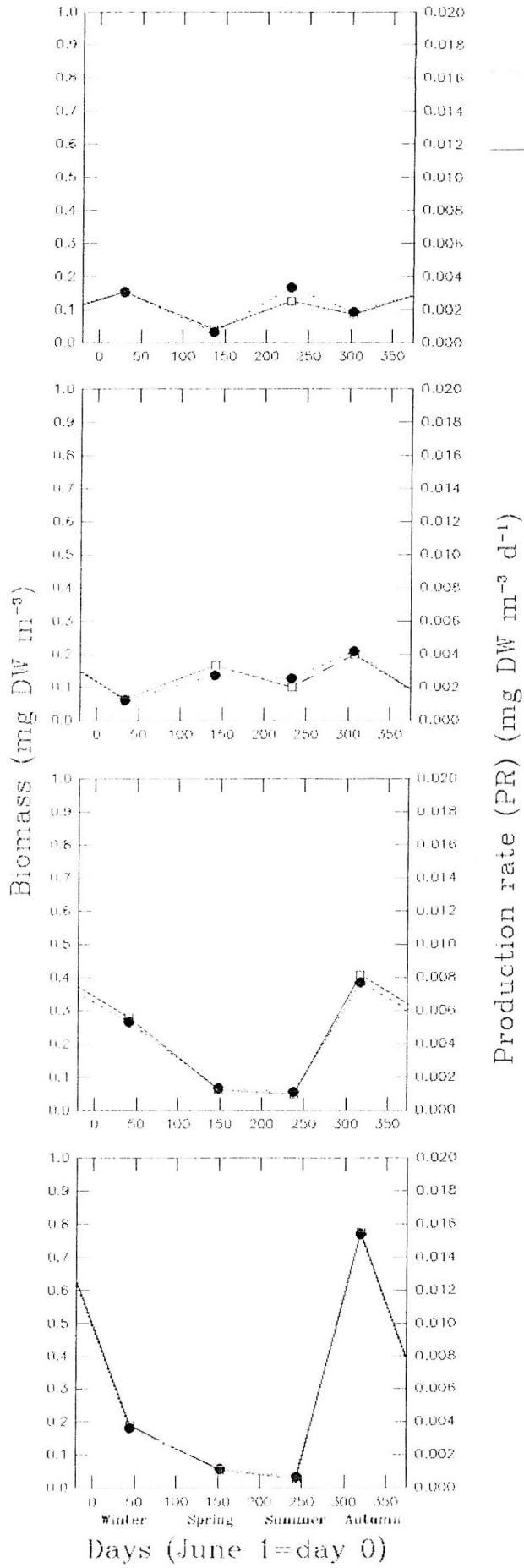


Figure 9.4e

sample group 4, PR values oscillated between highs in Autumn and Winter and lows in Spring and Summer.

Overall, PR in *E.vallentini* was highest during Winter and decreased through the rest of the year whereas in *E.lucens* and *T.gregaria*, highest PR values were found in Summer or Autumn. Common seasonal trends in PR values between sample groups appeared to be minimal.

9.4.4 Inter-specific comparison of production rates

Because of the similarities between biomass and PR seasonal patterns, observations on inter-specific differences in PR through the year are much the same as those made for biomass in section 9.4.2. PR values for *T.gregaria* are smaller than those of *E.vallentini* and *E.lucens* with typical values for the latter species generally being between 0.01 and 0.03 mg DW m^{-3} d^{-1}, whereas typical values for the former were below 0.01 mg DW m^{-3} d^{-1}. There was an asynchrony in the timing of peak PR between species, with *E.vallentini* peaking in Winter and *E.lucens* and *T.gregaria* peaking in Summer or Autumn. Finally, there were no sample group specific trends between species in terms of relative levels of PR between sample groups.

9.4.5 Intra-specific comparison of P:B d^{-1} (Fig. 9.4f)

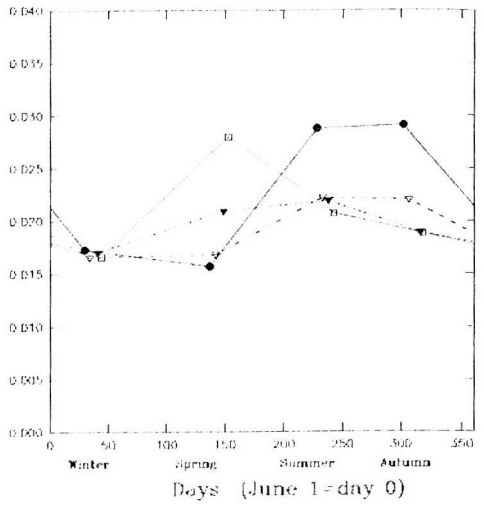
E.vallentini

P:B d^{-1} was generally higher in Summer and Autumn than Spring and Winter, with the exception of sample group 4 where there was a

peak of 0.028 d^{-1} in Spring. The highest P:B d^{-1} was found in sample group 1 during Summer and Autumn, where values of 0.029 d^{-1} were reached. Sample group 1 also

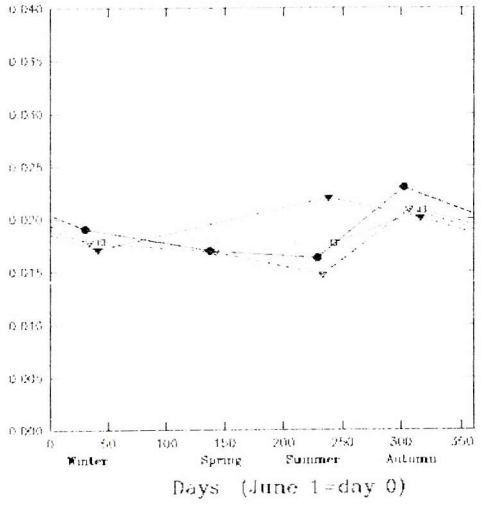
Daily P:B ratio through the year in sample groups 1 to 4

E.vallentini



- Sample group 1
- Sample group 2
- Sample group 3
- Sample group 4

E lucens



T.gregaria

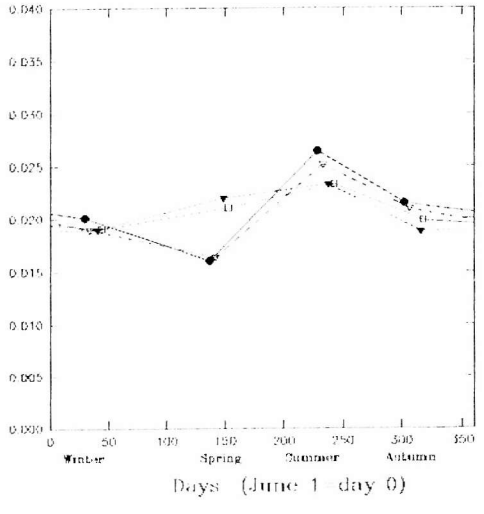


Figure 9.4f

contained the lowest P:B d^{-1} value of 0.0157 d^{-1} in Spring. In all but sample group 1, the lowest P:B d^{-1} were found in Winter.

E.lucens

Highest P:B d^{-1} values were found in Autumn, with the exception of sample group 3 which peaked in Summer. The highest P:B d^{-1} was found in sample group 1 in Autumn which had a value of 0.023 mg DW d^{-1}. Apart from sample group 3, the second highest P:B d^{-1} values for every sample group were found in Winter and values in Spring and Summer were relatively lower. The lowest P:B d^{-1} was found in sample group 2 in Summer where the value was 0.0147 d^{-1}.

T.gregaria

Highest values were present in Summer, where the highest P:B d^{-1} of 0.027 d^{-1} was found in sample group 1. Sample group 1 further contained the lowest value of 0.016 d^{-1} which was found in Spring, when sample group 2 also dropped to its lowest value. The lowest values in sample groups 3 and 4 were found both in Autumn and Winter with almost the same value of approximately 0.019 d^{-1} for each group in both seasons.

9.4.6 Inter-specific comparison of P:B d^{-1}

In terms of seasonality, highest P:B d^{-1} was either found in Summer or Autumn in all sample groups. However, it must be noted that although every sample group had its highest values in one of these two seasons, some also had their lowest values in the other. Therefore it cannot be stated that high P:B d^{-1} values are distinctly associated with Summer or Autumn but it can be stated more empirically that high values are not associated with Winter of Spring. Every season contained a lowest sample group value for in at least one species. In *E.vallentini* lowest values were most common in Winter, in

E.lucens, Summer and in *T.gregaria*, all seasons apart from Summer. Lowest P:B d^{-1} values in all species were approximately the same, at around 0.015 d^{-1}. However, highest P:B d^{-1} values were greater in *E.vallentini*, with a peak value of 0.029 d^{-1}, than in *E.lucens*, where the highest P:B d^{-1} was 0.025 d^{-1}. The highest P:B d^{-1} value in *T.gregaria* was intermediate between *E.vallentini* and *E.lucens* at 0.027 d^{-1}. One further interesting seasonal feature was that the spread of P:B d^{-1} values was less in Winter than in any other season for all species, although the significance of this is not fully understood.

In terms of sample group trends between species, it was evident that the highest P:B d^{-1} values were found in sample group 1 in all 3 species. In *E.vallentini* and *T.gregaria*, sample group 1 also contained the lowest P:B d^{-1}, with sample group 2 having the lowest value in *E.lucens*. It was also evident that there was a close similarity between sample groups 1 and 2 seasonal values in all species. The one exception was in Summer and Autumn in *E.vallentini*, where sample group 2 values were approximately 5% below sample group 1. Nevertheless, the overall trends in groups 1 and 2 were similar with the Summer and Autumn having approximately the same values which were, in turn, higher than Winter and Spring values. In the same manner, there was a close match between sample group 3 and 4 seasonal values in *T.gregaria* although this match did not also apply to *E.vallentini* and *E.lucens*. In all cases, sample groups 3 and 4 did not match the seasonal trends seen in sample groups 1 and 2.

Overall, P:B d^{-1} values were approximately within the same range in all species, although *E.vallentini* did have greater peak value than *E.lucens*. Seasonal oscillations were greatest in sample group 1 and the match between sample group 1 and 2 values appeared to be marked in all species.

9.4.7 IP and P/B yr^{-1}

The IP and P/B yr^{-1} values for each species and each sample group are presented in Table 9.4(i) with the annual mean biomass also being presented for comparative purposes. IP was greatest in sample group 4 in both *E.vallentini* and *T.gregaria*. In *E.lucens*, greatest IP was found in sample group 2. There were no apparent common trends in sample group IP values between species. There was a general increase between sample groups 1 and 4 in *T.gregaria* but an oscillating sequence of peaks and troughs between sample groups 1 and 4 in *E.vallentini* and *E.lucens*.

In terms of absolute IP between species, it was apparent that IP was substantially lower in *T.gregaria* than the other two species, with its largest IP value, 1.64 mg m^{-3}, being below the smallest values seen in *E.vallentini* and *E.lucens*. Values in *E.vallentini* and *E.lucens* were generally comparable, with the largest values of 12.77 and 10.20 mg m^{-3} being an order of magnitude larger than typical IP values in *T.gregaria*.

Trends in the IP values were reflected in the annual mean biomass, with an especially close match when looking at trends between sample groups. For instance, there were high Group 1 and 4 values of both IP and biomass in *E.vallentini* and high Group 2 values in both IP and biomass in *E.lucens*. There was also considerable interspecific correspondence between trends in IP and annual mean biomass with, for example, *T.gregaria*, which was found to have IP values that were much smaller than the other species, having corresponding smaller biomass values.

P/B yr^{-1} were comparable in all species, ranging between 4.1 and 6.3 yr^{-1} in *E.vallentini*, 4.9 and 6.4 yr^{-1} in *E.lucens* and 5.8 and 6.7 yr^{-1} in *T.gregaria*. Averaging over sample groups, values were highest in *T.gregaria* (6.35 yr^{-1}) and lowest in *E.vallentini* (5.13 yr^{-1}), with *E.lucens* having a value between these two (5.65 yr^{-1}).

Species/Sample group	Annual Mean Biomass (mg DW m^{-3} yr^{-1})	Integrated Production (IP) (mg DW m^{-3} yr^{-1})	P/B yr^{-1}
E. vallentini Sample group 1	1.955	8.078	4.131
Sample group 2	0.463	2.306	4.980
Sample group 3	0.533	3.368	6.318
Sample group 4	2.502	12.772	5.104
E. lucens Sample group 1	0.614	3.405	5.539
Sample group 2	2.078	10.195	4.907
Sample group 3	0.381	2.182	5.728
Sample group 4	0.616	3.971	6.443
T. gregaria Sample group 1	0.102	0.663	6.532
Sample group 2	0.133	0.900	6.782
Sample group 3	0.200	1.162	5.825
Sample group 4	0.262	1.642	6.277

Table 9.4(i): Calculated values for annual mean biomass, IP and P/B yr^{-1} for each sample group

9.5 Discussion

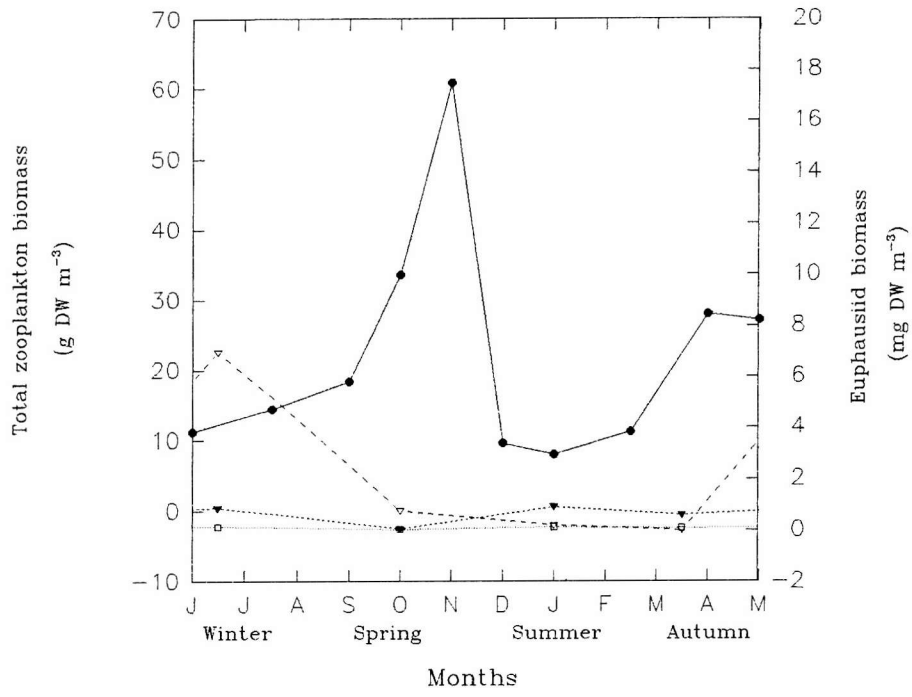
9.5.1 Seasonal and geographic patterns in biomass

The seasonal patterns observed in euphausiid biomass are best considered when placed into the context of seasonal biomass patterns of other zooplankton studies in this region. The following section therefore will therefore aim to compare what seasonal biomass information there is available for zooplankton in the south-west Atlantic to the results of the present investigation. Unfortunately, there have not been any other investigations into seasonal euphausiid biomass fluctuation in this region and any comparisons are limited to a small number of seasonal studies on other zooplankton species (*copepods* - Ramirez, 1966, 1981; *chaetognaths* - Mazzoni, 1990; *Pteropods* - Dadon, 1989) and one on seasonal biomass patterns in the zooplankton community as a whole (Ciechomski and Sanchez, 1983).

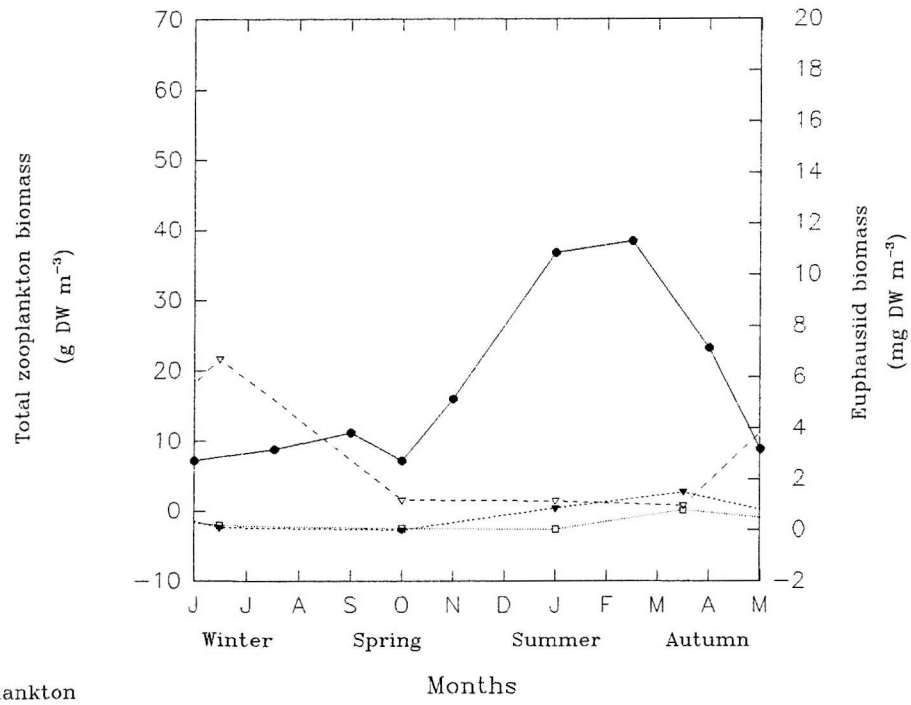
Ciechomski and Sanchez (1983) analysed the annual cycle in zooplankton and ichthyoplankton abundances in two areas of the Patagonian shelf, 42°S to 44°S and 51°S to 53°S which correspond approximately with the geographic areas covered by sample groups 1 and 4 respectively. Dadon (1989) and Mazzoni (1990) both considered the seasonal samples taken over one year which covered the entire Patagonian shelf between 35°S and 55°S. Ramirez (1966, 1981) covered an area between 45° and 50°S although unlike the other studies, abundances were considered in terms of subjective qualitative scale rather than a quantitative one.

All studies showed strong seasonality in biomass levels through the year. The total zooplankton biomass patterns considered by Ciechomski and Sanchez (1983) showed seasonal patterns which varied at different parts of the shelf (fig. 9.5a). In the

Total zooplankton biomass through the year from Ciechomski and Sanchez (1984) between 42°S and 44°S and euphausiid biomass through the year from sample group



Total zooplankton biomass through the year from Ciechomski and Sanchez (1984) between 51°S and 53°S and euphausiid biomass through the year from sample group



Total zooplankton

E.vallentini

E.lucens

T.gregaria

Figure 9.5a

northerly region, there were two major peaks in the seasonal cycle, the largest occurring in the Spring around November and the smaller peak occurring in Autumn around August. In the southerly region, there was only one major peak in the Summer which covered a period between December and March. Peak biomass levels were greater in the northerly region although the one peak in the southerly region was sustained over a much longer period. This generally agrees with the classical annual production cycle in temperate regions (cf. Cushing, 1975) with the variability in the number and timing of biomass peaks corresponding with observations made by Colebrook (1982, 1984) on North Sea and north Atlantic zooplankton.

The qualitative seasonal patterns of copepods described by Ramirez (1966, 1981) generally agree with the total zooplankton patterns of Ciechomski and Sanchez (1983) with there being a biomass peak in mid Spring dominated by immature cold water *Calanus* spp. and lower biomass levels in the Autumn, when smaller warm water species were dominant such as *Paracalanus parvus* and *Centropages brachiatus*. Chaetognath patterns determined by Mazzoni (1990) did not show such agreement towards total zooplankton seasonal pattern in any of the three species considered. In northern regions for instance, there were biomass peaks in the Winter in *Eukhronia hamata*, *Sagitta tasmanica* and *S.gazellae*. In southern regions there was further asynchrony in relation to total zooplankton biomass patterns, with all species showing an Autumn peak and *Sagitta gazellae* and *S.tasmanica* also showing a Spring peak. All species had a low biomass level during Summer, when there was a peak in total zooplankton biomass.

The pteropod, *Limacina retroversa* studied by Dadon (1989) also exhibited a seasonal biomass pattern that did not match the total zooplankton biomass pattern. There were biomass peaks in both the northerly and the southerly part of the shelf during

Winter. Biomass levels subsequently dropped during Spring in the north but then peaked again during Summer. In the south, apart from a slight drop in July, the Winter biomass peak persisted until Spring and then dropped to a low level for the rest of the year.

One important consideration when examining seasonal biomass levels of individual species is that their biogeography is taken into account. In the case of the chaetognath species, for instance, their general distribution is primarily associated with waters that are colder than those found on the shelf through most of the year (see Chapt. 5 and 6). Therefore their Winter biomass peak may well be a reflection of the suitability of shelf temperatures allowing greater infiltration from the slope and oceanic regions. Considering total zooplankton biomass on the shelf partly overcomes the need to consider the biogeography of each individual species since it averages out seasonal biogeographic anomalies, allowing fairer comparisons to be made.

In figure 9.5a, a comparison is made between the annual pattern in total zooplankton biomass and euphausiid biomass. To maintain geographic coherence, the data provided by Ciechomski and Sanchez (1983) for 42°S to 44°S was plotted against values obtained for sample group 1 and for 51°S to 53°S against values for sample group 4. Ciechmonski and Sanchez (1983) obtained biomass values through displacement volume in units of mm^{-3} m^{-3} so this was converted to dry weight using a conversion factors of 1ml to 160mg DW from Cushing et al. (1958). From the comparison it was evident that there was not a great deal of agreement between the annual biomass peaks of euphausiid species and total zooplankton especially in the northerly region. Whereas the northerly total zooplankton biomass peaked in Spring and Autumn, the biomass peak of *E.vallentini* was in Winter and *E.lucens* in Summer. There was better agreement between the biomass cycles of *E.lucens* and *T.gregaria* and total zooplankton biomass in the

southerly group. However, *E.vallentini* was again asynchronous with a biomass peak in Winter.

A major consideration in analysing euphausiid annual biomass in this study is the low temporal resolution of sampling points through the year. It is possible that between sampling points there may be increases or decreases in biomass that may correspond to the higher temporal resolution study of Ciechomski and Sanchez (1983). In the Winter to Spring sampling interval for instance, the present study may miss a continued rise in biomass in *E.vallentini* which may match the general rise in zooplankton biomass during the phytoplankton bloom seen in most other zooplankton species in temperate regions. The data are therefore insufficient to be conclusive about the asynchronous nature of the observed annual biomass cycles of certain euphausiids and total zooplankton in this region.

Despite the above reservations, a certain feature that is evident when comparing euphausiids species is that *E.vallentini* and *E.lucens* biomass peaks do not coincide in either the northerly or southerly regions and whereas *E.vallentini* is dominant in the early part of the year, *E.lucens*, combined with the small biomass of *T.gregaria* are dominant during the latter part of the year. *E.vallentini* is bigger and is common to much colder areas than the other two euphausiid species. This apparent succession from larger, cold water species to smaller warm water species through the year was mirrored in the annual biomass cycles of copepods on the Patagonian shelf considered in the studies of Ramirez (1966,1981). Larger cold water copepods, *Calanus* spp. dominated the Spring biomass peak whereas smaller, warm water copepods *Paracalanus parvus* and *Centropages brachiatus* were dominant during the Summer and Autumn. In a review of temperate zooplankton cycles by Davis (1987) this apparent succession was found to be

common of a number of areas (*N. Atlantic + North Sea*: Wiborg, 1954; Colebrook, 1982, 1984; *Sea of Japan*: Meshcheryakova, 1960; Morioka and Komaki, 1978; *Georges Bank*: Riley, 1947; Sherman et al., 1987; O'Reilly et al., 1987). Vidal (1980a,b,c) showed that the small copepod species *Pseudocalanus* spp. required a lower food concentration for maximum growth than the larger *Calanus pacificus*. It was also found that growth efficiency of the larger species decreased with increasing temperature (8°C to 15°C) and body size (5 to 175μg). Considering the lower and potentially limiting food availability during periods after the phytoplankton bloom, it is possible that this pattern of succession is a result of size and temperature efficiency factors affecting physiological rates, assuming that the findings of Vidal (1980a,b,c) are applicable to other zooplankton groups. However, these findings were disputed by Huntley and Boyd (1984) who found that the critical food concentration for growth of *Calanus* sized animals were lower during warmer months whereas the opposite was true for smaller animals. Nevertheless, the contention that seasonal patterns in zooplankton biomass are influenced by physiological rates and environmental fluxes as opposed to density dependent factors is one supported by Colebrook (1982, 1984). Overall though, it is clear that a study with greater temporal resolution is required before the euphausiid community in this region could be conclusively considered to adhere to any hypothesis on annual biomass patterns in temperate regions.

Caution must also be exercised when comparing absolute biomass values found in the present study to other euphausiid biomass estimates in the literature. Sampling methods differ in both the type of net used and the sampling interval fished. In the Continuous Plankton Surveys for instance, on which the work of Lindley is based (see review - Lindley, 1982), sampling depth was between 0 and 10m. The effect of diurnal

vertical migration most probably has a profound effect on the density and age composition of specimens caught in this restricted sampling interval. By contrast, other studies such as Mauchline (1985) integrate biomass values over 2000m and so include a considerable part of the water column in which many species are not found. Averaging over such a depth would make density and biomass estimates much lower than would normally be obtained if only the normal depth ranges of euphausiid populations were considered. Therefore, a fair comparison between studies can only be achieved in cases where sampling depths are comparable. Even so, it is still not certain that the normal vertical distributions of species do not differ between the respective study areas.

The effect of mesh size and sampling speed may also be profound and small stages or fast swimming adults may well be underestimated. Samples used in the present reanalysis were collected by a bongo net with a mesh size of 300μm and the sampling interval was from 0 to 100m or maximum shelf depth. Two other studies are reported where sampling equipment and fishing technique were similar to the present study, Ritz and Hosie (1982) for *Nyctiphanes australis* in south-east Tasmania and Stuart and Pillar (1988) for *E.lucens* in the southern Benguela current. Ritz and Hosie (1982) calculated a mean annual biomass of between 5.389 mg DW m^{-3} and 6.388 mg DW m^{-3} depending on the calculation method used. Stuart and Pillar (1988) found that mean annual biomass ranged between 9.58 mg DW m^{-3} offshore and 70.69 mg DW m^{-3} inshore. Averaging over sample groups, the mean annual biomass values in the present study were 1.36 mg DW m^{-3} for *E.vallentini*, 0.92 mg DW m^{-3} for *E.lucens* and 0.17 mg DW m^{-3} for *T.gregaria.* It is apparent that the mean annual biomass of euphausiids on the Patagonian shelf is considerably lower than in south-east Tasmania or the Benguela current.

9.5.2 Seasonal and geographic patterns in PR and P:B d^{-1}

It is evident that there is a considerable difference between seasonal trends in PR and P:B d^{-1}. Whereas PR considers the rate of biomass produced daily, P:B d^{-1} essentially considers daily weight specific growth rate of a population which is affected by the rates of physiological processes. According to the Ikeda-Motoda model, which principally considers respiration, physiological rates are determined by the weight of the individual and the habitat temperature. Therefore, the Summer and Autumn peaks in P:B d^{-1} principally reflect the fact that the size distribution and habitat temperature in these months resulted in higher physiological rates. PR on the other hand is determined both by P:B d^{-1} and the biomass of the population. The seasonal difference between P:B d^{-1} and PR is therefore one mainly influenced by biomass levels and shows that the rate of physiological processes and biomass fluctuate differently through the year. The fact that seasonal trends in PR of euphausiid species in this investigation mainly reflect biomass levels further indicates that the rate of production is principally driven by biomass changes rather than fluctuations in habitat temperature or the size distribution of the population.

These findings differ from those of other production models such as Davis (1987) who reconsidered the Riley (1947) and Huntley-Boyd (1984) models in terms of predicting production cycles of copepods and chaetognaths in temperate regions. Although, as in the present investigation, weight specific growth rates (or P:B d^{-1}) were higher in Autumn compared to Spring, seasonal trends in PR values were found to differ from those of biomass, with the Autumn rise in PR being much higher than the equivalent rise in biomass. Such a discrepancy can partially be explained if the absolute values of P:B d^{-1}, are considered, since the Davis (1987) and Huntley-Boyd (1984)

values were almost 10 times higher (0.1 d^{-1} on average) than those calculated in the present study. Also seasonal fluctuations in biomass differ only by a factor of 4 in Davis (1987) and so resulting PR values are unlikely to be as dominated by biomass as in the present investigation.

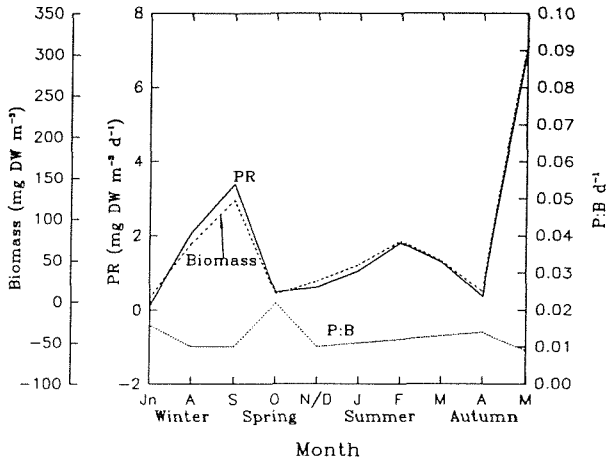
It is difficult to make further comparisons to other euphausiid studies with respect to seasonal fluctuation in P:B d^{-1} and daily PR because most euphausiid production studies measure annual production through population dynamic methods where such parameters are not calculated. In fact, the only comparison that can be made is with the findings of Stuart and Pillar (1988) who studied growth and production of *E.lucens* in the southern Benguela Current. Stuart and Pillar (1988) measured biomass for each monthly period of field data from inshore, intermediate and offshore regions. Daily production rate (PR) and P:B were estimated from a combination of population dynamic and laboratory methods. In fig 9.5b, biomass, PR and P:B are compared for each region and it can be seen that whereas in inshore regions, PR closely matches biomass, in intermediate and offshore regions, PR varies considerably from trends in biomass. These PR variations are reflected in corresponding changes in P:B, showing that, unlike the present study region, weight specific growth rate is important in determining PR in Benguela region euphausiids.

With respect to absolute values of PR reported in Stuart and Pillar (1988), it is evident that although there are some comparable values, especially in the offshore regions, most PR values for *E.lucens* in the Benguela are between one and two orders of magnitude greater than calculated for *E.lucens* on the Patagonian shelf. The same conclusion holds if the comparison is extended to *E.vallentini* and *T.gregaria* on the Patagonian shelf although in the case of the latter, the difference would be closer to 3

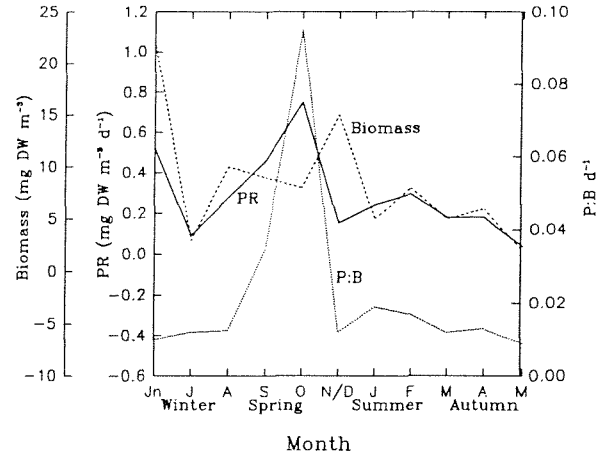
Seasonal fluctuation of biomass, production rate and P:B d^{-1} for *E.lucens* in the Benguela region

(from Stuart & Pillar, 1988)

Inshore



Intermediate



Offshore

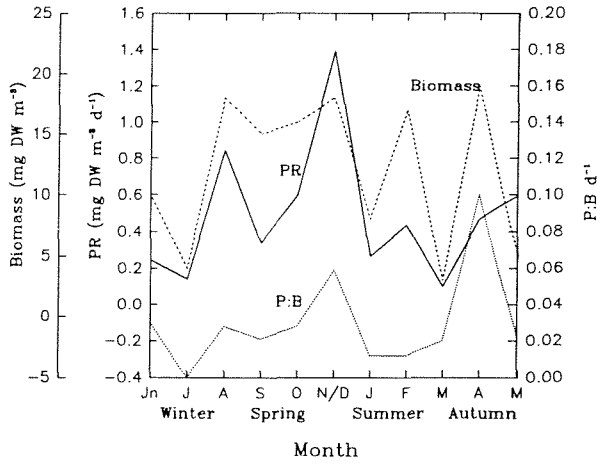


Figure 9.5b

orders of magnitude. In terms of P:B d^{-1}, both studies found similar values which generally fell between 0.01 and 0.04 d^{-1}. In a limited number of instances in the Benguela study however, values were found to rise to 0.09 or 0.1 d^{-1}, which is well above those found in the present study for any species. These high values probably correspond to peak spawning periods.

Overall then, P:B d^{-1} in the present study was generally found to be largest in either Summer or Autumn but the increase in weight specific growth rate in these seasons did not appear to greatly influence PR, which appeared to be more closely related to the large oscillations in biomass. Comparisons to other studies show that PR levels are comparatively low in euphausiid species in the Patagonian shelf. However the similarity in present P:B d^{-1} to values for *E.lucens* in the Benguela region values indicate that physiological rates are very similar to those in a region with warmer, more productive waters.

9.5.3 IP and P/B yr^{-1} in relation to other studies

One of the major inaccuracies in calculating IP is the uncertainty about whether the range in PR values is representative of PR fluctuations throughout the year. For instance, in *E.vallentini*, although a peak was found in PR in Winter, it is possible that PR continued to rise within the Winter-Spring sampling interval and IP would be underestimated as a result. However, the most empirical solution to this problem is to carry out a survey with greater temporal resolution so that fluctuations in PR could be more accurately traced. It is nevertheless possible to try and establish whether IP and P/B yr^{-1} are within the broad range of expected values for temperate euphausiid populations through comparison with other studies that have estimated these parameters.

Values obtained by various euphausiid studies for P/B yr^{-1} and IP are presented in Table 9.5(i) along with mean biomass, temperature and latitudinal position. Through comparing the values in this table to the IP and P/B yr^{-1} values obtained by present analysis in Table 9.4(i), it can be seen that the results of the present analysis fall within the broad range of values from other studies. However, it can also be seen that values within Table 9.5(i) have an extensive range, especially with respect to IP yr^{-1}, so making comparisons to values obtained by the present analysis does little more than establish whether results are within an order of magnitude of what would be expected.

Another approach to determining the accuracy of the results of the present investigations is to establish whether there are any relationships between production parameters and abiotic parameters in the studies included in Table 9.5(i) and subsequently predicting values for the present investigations from any significant regressions that are found. Lindley (1982), for instance, when considering results for the euphausiid community in the North Atlantic and North Sea, found that there was a clear relationship between P/B yr^{-1} and surface temperature and so if this broad trend extends to studies in other regions, P/B yr^{-1} values could be predicted for the present study region through just knowing average surface temperature values. Furthermore, considering the distinct relationship between latitude and temperature (Svedrup et al., 1942), if the findings of Lindley (1982) hold for euphausiids in general, it should follow that there would be a trend between latitude and P/B yr^{-1} on a global scale such that a P/B yr^{-1} value could be predicted for the present study region through simply knowing the latitude. In Table 9.5(i), the P/B yr^{-1} IP and biomass values for a number of euphausiid species are given, along with the latitude and respective.

Values from Table 9.5(i) were used to regress latitude and temperature against

Study/Region	Species	Mean Biomass (mg DW m^{-3} yr^{-1})	P/B yr^{-1}	IP yr^{-1} (mg DW m^{-3} yr^{-1})	Number cohorts	Lat. °N/ °S	Temp. °C
Stuart & Pillar (1988) *Benguela current*	*Euphausia lucens*	9.580-12.090	10.10-16.01	142.28-479.39	cont.[1]	32	20
Ritz & Hosie (1982) *SE Tasmania*	*Nyctiphanes australis*	5.389	13.30-14.50	78.29-84.79	cont.	43	14
Lindley (1980) *N.Atlantic*	*Thysanoessa inermis*	0.635-1.231	2.30-4.89	2.667-2.875	2	45	22
Lindley (1982a) *N.Atlantic*	*Euphausia krohnii*	0.2275	6.07	1.378	cont.	45-55	16
	Nematoscelis megalops	0.065	5.71	0.383	1	45-55	16
	Thysanoessa gregaria	0.020	4.50	0.105	cont.	45-55	16
Berkes (1977) *Gulf St. Lawrence*	*Thysanoessa raschii*	0.470	3.80	1.800	1	48	17
Mauchline (1985) *Rockall Trough*	*Thysanopda acutifrons*	1.153	2.3	-	1	55	13
	Nematobranchion boopis	0.201	1.2	-	1-2	55	13
	Stylocheiron maximum	0.1325	2.5	-	cont.	55	13
Lindley (1982b) *N.Sea + N.Atlantic*	*Meganyctiphanes norvegica*	6.978 (av.)	3.25 (av.)	4.080 (av.)	2	64-66	10
		4.993 (av.)	2.93 (av.)	1.800 (av.)	2	58-64	12
		1.210 (av.)	6.00 (av.)	0.200 (av.)	2	50-59	13
	Nyctiphanes couchii	1.025 (av.)	5.00 (av.)	0.200 (av.)	cont.	55-59	12.5
		4.780 (av.)	4.00 (av.)	1.200 (av.)	cont.	50-55	16

[1] cont. - continuous reproduction over an extended period through the year

Table 9.5(i) *continued overleaf*

Lindley (1980) *N.Sea + N.Atlantic*	*Thysanoessa longicaudata*	1.420 (av.)	3.35 (av.)	0.39 (av.)	2	64-66	10
		2.840 (av.)	2.79 (av.)	1.04 (av.)	4	58-64	12
Lindley (1980) cont.	*Thysanoessa longicaudata*	4.514 (av.)	5.21 (av.)	1.09 (av.)	4	55-59	13
		5.580 (av.)	2.85 (av.)	1.94 (av.)	2.5	50-55	14
		1.040 (av.)	1.95 (av.)	0.825 (av.)	2	45-50	17
		1.960 (av.)	4.2 (av.)	1.135 (av.)	2	40-45	21
Allen (1971) *Antarctica*	*E.superba*	-	1.8	-	1	63	0
Siegel (1992) *Antarctica*	*E.superba*	$9x10^4$-$12.26x10^4$	1.6	-	1	63	0

Table 9.5(i): Values for annual mean biomass, P/B yr^{-1} and number of generations per year of euphausiids from a range of latitudes and Summer temperatures from Svedrup et al. (1942)

P/B yr^{-1} values. IP was not regressed against latitude and temperature because the depths over which values were integrated differed between studies, making an inter study comparison unsuitable. P/B yr^{-1} is a relative term and does not depend factors such as the depth range that was fished. It was found that there was a distinct relationship between P/B yr^{-1} and both latitude and temperature. The fact that latitude but not temperature was significant at the $p=0.05$ level is possibly a reflection of the fact that temperatures were crudely obtained from a general surface thermocline map in Svedrup et al. (1942) because most studies did not include data on temperature. The fact that despite these crude approximations that there was still a relationship with $p=0.089$ is strong evidence that a significant relationship exists between temperature and P/B yr^{-1} in euphausiid species on a global scale.

Applying these regressions to the present investigation investigation, regressions relating latitude/temperature and P/B yr^{-1} were applied to the surface temperatures and latitudes of the present study area. For euphausiid populations at 45°S, the P/B yr^{-1} was predicted to be 6.554 by the Latitude-P/B regression and 4.304 by the Temperature-P/B regression. These match well with the corresponding P/B yr^{-1} values found by this study which ranged between 6.5317 for *T.gregaria* and 4.1306 for *E.vallentini* although there was not such a good match at 53°S where values found by this study were approximately 20% higher than those predicted by the regressions. Nevertheless, the regressions illustrate that the production rate estimates of the present study are within the range of what would be expected for this region.

In terms of body size there is a definite correspondence to the prediction that species in this region have a body size that is intermediate between Antarctic species and sub-Tropical/Tropical species. The body size of *E.vallentini* ranges between 15 and

28mm, of *E.lucens* between 10 and 18mm and *T.gregaria* between 11 and 20mm. Typical herbivorous Antarctic euphausiids are *E.superba* which has a body size ranging between 45 and 65mm and *Thysanoessa macrura* which has a body size between 18 and 31mm. Herbivorous euphausiid species common to sub-Tropical waters to the north of the Patagonian shelf are *Euphausia tenera*, 7-9mm body size, *E.recurva*, 10-17mm body size and *E.brevis* 8-10mm (Baker et al., 1990). The number of generations would be expected to be intermediate between sub-tropical populations that continuously reproduce and polar populations which produce one generation per year. This study showed that the average number of broods on the Patagonian shelf was 2 to 3 per year in *E.lucens*, 2 per year in *E.vallentini* and 4 per year in *T.gregaria* (see Chapt. 8) which, in each case, is approximately mid-way between sub-tropical and polar levels. However, some caution must be exercised when simply considering the number of generations per year as a measure of reproductive output, since there may be greater investment per brood in cases where the number of generations per year is relatively small (Clarke and Gore, 1990).

To determine annual production, it is also necessary to be able to accurately estimate biomass which unfortunately is not as predictable as P/B yr^{-1} or individual body size. Certain latitudinal trends were found by Ikeda (1985), who determined biomass values at each 10° latitude along 170°W, using data from a number of different studies. Two standing stock peaks were apparent, the largest between 50° and 70° and the other at the equator. In latitudes between 10° and 50°, biomass levels were generally low. In a similar earlier study, Foxton (1956) compared displacement volumes taken by a single type of net for latitudes between 0 and 70° at 5° intervals. Although the number of samples at low latitudes was considerably less than at higher latitudes, it was clearly shown that displacement volume was substantially greater at higher latitudes and peaked

between 50° and 55°S.

One of the dangers with analyses based purely on latitude is that oceanographic features which could greatly influence plankton volumes may vary considerably at different longitudes along the same latitude. For instance, a further analysis by Foxton (1956) showed that volumes were greatly influenced by the position of the Antarctic convergence, which has a latitudinal position that varies considerably with longitude. Any generalisation in terms of sample volume must therefore take prevailing conditions into account. Water depth is also a major influence on plankton biomass. In a study of a temperate region in the north-west Atlantic, Grice and Hart (1962) showed that the mean biomass found on the shelf was 4 times greater than that on the slope, which was in turn, 3 to 4 times greater than oceanic regions (ie. Gulf Stream and Sargasso Sea). This trend is common to a number of northern Atlantic regions (Raymont, 1983) and is probably applicable to most other coastal regions in other oceans.

Considering all these trends, total zooplankton biomass for the Patagonian shelf would be expected to be relatively high, especially towards the higher latitudes of the survey. The total zooplankton biomass values given in Ciechomski and Sanchez (1983) are certainly comparable to studies on other temperate studies such as Grice and Hart (1962), with peak annual values of approximately 32 g DW m^{-3} in the former study and 128 g DW m^{-3} in the latter[1]. However, these values are merely equivalent to the average biomass of the Antarctic euphausiid species *E.superba* alone, with values estimated at 122.6 g DW m^{-3} yr^{-1} (Siegel, 1992)[2]. The average annual biomass of euphausiids on the Patagonian shelf is miniscule by comparison with values 0.2 and 1.4 mg DW m^{-3} yr^{-1}

[1] Assuming a volume to dry weight conversion of 1ml to 0.16 g DW (Cushing et al. 1958)

[2] Assumuing wet weight to dry weight conversion of 0.1

integrated over 100m for species in this study.

One of the major outstanding problems in measuring euphausiid production is the accurate determination of biomass. The schooling behaviour and excellent swimming abilities of krill (Hamner, 1984; Kils, 1979) make finding krill unpredictable and hard to sample quantitatively using nets. Alternative methods such as the use of acoustic techniques also have their problems since estimating the target strength of a backscatter signal so that the *in situ* biomass can be determined is a difficult procedure (Ross and Quetin, 1988). Combined with the added difficulty of accounting for seasonal and interannual variability on the scale of orders of magnitude (Siegel, 1988), there is still much ground to cover before reliable IP and yield estimates for euphausiids can be made.

9.6 Conclusions

1, Annual mean biomass was considerably smaller in *T.gregaria* (0.102 to 0.262 mg DW m^{-3} yr^{-1}) than in *E.vallentini* (0.463 to 2.502 mg DW m^{-3} yr^{-1}) and *E.lucens* (0.381 to 2.708 mg DW m^{-3} yr^{-1}).

2, *E.vallentini* exhibited peak biomass levels during the Winter, mainly through elevated abundances of adults and sub-adulys, followed by low levels for the rest of the year. *E.lucens* and *T.gregaria* showed peak biomass during Summer and Autumn.

3, Seasonal trends in production rate (PR) closely complied with trends in biomass with *E.vallentini* peaking in Winter and *E.lucens* and *T.gregaria* peaking in Summer and Autumn.

4, Peak PR values were highest in *E.vallentini* (0.12 mg DW d^{-1}) with comparable peak values found in *E.lucens* (0.10 mg DW d^{-1}). Peak PR values were considerably lower in *T.gregaria* (<0.02 mg DW d^{-1}).

5, P:B d^{-1} values were comparable in all 3 species and generally ranged between 0.0015 and 0.0030 d^{-1}.

6, Highest P:B d^{-1} was found in either Summer or Autumn in all species and in each sample group.

7, Integrated production (IP) was substantially lower in *T.gregaria* (0.663 to 1.642 mg DW m^{-3} yr^{-1}) than in *E.vallentini* (3.338 to 12.772 mg DW m^{-3} yr^{-1}) and *E.lucens* (2.182 to 10.195 mg DW m^{-3} yr^{-1}).

8, P/B yr^{-1} was comparable in all species with *T.gregaria* having the highest average value (6.35 yr^{-1}), followed by *E.lucens* (5.65 yr^{-1}) and then *E.vallentini* (5.13 yr^{-1}).

9, There were no apparent common geographic trends between species in any of the calculated parameters and typically there was an apparently random oscillating sequence of high and low values from sample groups 1 to 4 in all species.

10, P:B d^{-1} values were comparable to those found for *E.lucens* in the Benguela region. P/B yr^{-1} for each of the 3 species fitted in with the general trend observed in other euphausiid studies of increasing values with higher temperature and lower latitude. PR and IP were substantially lower than those estimated for *E.superba* in the Antarctic but were within expected levels for a temperate shelf region.

9.7 Overview of euphausiid life cycles and production on the Patagonian shelf.

One of the aims of investigating the population ecology and production of euphausiids on the Patagonian shelf was to consider their potential as a fishery resource. *Euphausia superba* in the Antarctic region has been fished by a number of nations, including Russia, Japan and Poland. However, as remarked by Everson (1984), exploiting resources in the Antarctic is limited by its remoteness from recognised markets. The advantage of exploiting euphausiid resources on the Patagonian shelf is their vicinity to mainland South America and its large population centres. When comparing respective biomass levels however, it is evident that levels are considerably lower on the Patagonian shelf than typical levels found in Antarctica. Considering the problems experienced in making such a huge krill resource as found in the Antarctic an economic and efficient operation (Everson, 1984), it would seem that exploiting the euphausiid resource found on the Patagonian shelf is not economically viable. Furthermore, the potential implications of such exploitation on the shelf ecosystem are completely unknown.

A further reason for investigating the population ecology of euphausiids in this region was their potential importance as a food resource for the local squid fishery (*Illex argentinus* and *Loligo gahi*) (Ivanovic and Brunetti, 1994). There are a number of other potential euphausiid predators in the shelf region, such as the rockhopper penguin (*Eudyptes chrysocome chrysocome*) (Croxall et al., 1985), the albatross (Thompson, 1992) and fish (*Benguela region*: James, 1987). Therefore, it is hard to make a direct estimate of the potential euphausiid biomass available as food for the commercial squid

species without greater knowledge of food webs and levels of predatory consumption. However, considering that euphausiid biomass shows marked seasonality in this region, one aspect which may reveal the importance of the euphausiid stock to squid populations is evidence that the population dynamics of the respective species show some seasonal correspondence.

Correspondence between the timing of spawning by commercial fish stocks and the seasonal cycle has been extensively considered by Cushing (1975) in northern temperate regions. The larval phase of the fishes life cycle is believed to be the major limiting phase with respect to the size of the new generation. This is because the newly spawned fish exploit the carrying capacity of the environment and, at this time, food is the limiting factor. Matching spawning to the seasonal outbursts of planktonic production means that food limitation is reduced or absent and recruitment is more successful. Different parts of the temperate region exhibit different seasonality patterns and accordingly, the adult populations show corresponding differences in their spawning cycles. Cushing (1975) distinguished 3 types of spawning cycle:

1, Autumn spawners - these adults are linked to temperate regions where there are Spring and Autumn peaks of equal amplitude in plankton populations. Here the larval spawning ends at or near the peak of the Autumn outburst. As the larvae drift, food is available for approximately 3 months.

2, Winter spawners - these adults are linked to regions where the Spring peak is of much greater magnitude than the Autumn peak. Here the larvae are released into an early Spring production cycle.

3, Spring spawners - these adults are linked to offshelf regions where the seasonal cycle consists of either a late Spring peak of high amplitude and an early low Autumn peak or

a single outburst in mid-Summer. Here the adults release their larvae around April or May into a production cycle that persists for approximately 3 months.

The fish spawn at positions that are fixed from year to year and the period of larval drift is of great biological importance, both in establishing a geographical base for the stock and as a phase during which natural regulation takes place.

One of the commercial squid species in the area of the present study, *Illex argentinus*, exhibits a life cycle consisting of adult migration to spawning grounds followed by period of larval drift and then a return to feeding grounds. The species is found over the Patagonian shelf, shelf break and around the Falkland Islands at depths of between 80 and 800m. The life cycle is poorly understood (Rodhouse and Hatfield, 1990) but it is believed that most of the population spawns in Winter within the Brazil Current. Juveniles appear over the northern part of the shelf in the austral Spring and then spread outwards and offshore. They then move back over the shelf during the Summer and in Autumn, they move eastwards towards the edge of the shelf and northwards towards the spawning area. According to Cushing's scheme, Winter spawning should reflect a temperate production cycle that involves a large Spring peak and an Autumn peak of lower amplitude. The total zooplankton biomass data of Ciechomski and Sanchez (1983) (see Section 9.5) corresponds to this pattern in the northern region where the spawning grounds are presumed to lie.

The second commercial squid species in this region, *Loligo gahi*, is a neritic species which lives and spawns in shallow waters to depths of about 400m. A model of its life cycle was initially put forward by Patterson (1988) and subsequently supported by analyses carried out by Hatfield (1991). There are essentially two periods of recruitment arising from two separate spawning episodes in Spring and Autumn. The species is

semelparous so each spawning episode is produced from one of two distinct groups within the population. The Spring spawners recruit into the fishery in March and spawn and die in September/October. The Autumn spawners recruit into the fishery in November and spawn and die in April/May. Hatfield (1991) did show however that spawning times may deviate from this model because of interannual variation. Juvenile squid migrate from presumed spawning grounds in shallow water, down the continental shelf and slope to deeper waters as they grow and mature (Hatfield et al., 1990). The main fishery for this species is in and around the Falkland Islands and at these latitudes, the total zooplankton biomass pattern (Ciechomski and Sanchez, 1983) showed a single and persistent peak in Summer. Therefore, the life cycle of *Loligo gahi* in this region only partially complies with the seasonal zooplankton cycle since, firstly, a supposedly offshore Summer peak seasonal cycle was found on a shelf region and secondly, in addition to Spring spawning, there was also an Autumn spawning period. Overall, it is evident that the spawning periods of the two commercial squid species are not the same and that these dissimilarities correspond in differing degrees to the different seasonal plankton cycles at distinct parts of the shelf.

In the previous discussion, it was shown that the seasonal cycle of euphausiid biomass in this region did not correspond with the seasonal pattern seen in the total zooplankton biomass. While biomass peaked in Winter for *E. vallentini* and Summer in *E. lucens*, total zooplankton biomass peaked in Spring in the northerly part of the shelf. Some compliance was shown in the southerly shelf region with both *E. lucens* and total zooplankton biomass peaking in the Summer, but the timing of peak *E. vallentini* biomass was again asynchronous in that it again occurred in the Winter. It would therefore seem that euphausiids, or more correctly, their larvae, may not be the most important dietary

component of squid paralarvae during what is probably the major limiting phase of squid recruitment.

Nevertheless there are certain anomalies associated with the migrating life cycle of *Illex argentinus* that may point to the importance of the Winter appearance of *E.vallentini* pre-spawn adults. For most marine invertebrates, reproduction is one of the most energy intensive periods of their life and achieving an optimum balance between competing demands such as activity, growth and reproduction is critical to fitness (Calow, 1981). Biochemical analyses and estimated power budgets calculated for *Illex argentinus* (Clarke et al., 1994), showed that in the final days of feeding, before migrating to the spawning grounds, a typical animal consumed 4-5% of body energy content per day. This substantial intake would be taking place during late Autumn/early Winter, which is a period of limited total zooplankton biomass, according to Ciechomski and Sanchez (1983), although pre-spawn *E.vallentini* adults are one of the major zooplankton components during this period. In addition to gut content analyses which show that euphausiids are a major component of adult *I.argentinus* diets (Ivanovic and Brunetti, 1994), the biochemical evidence of Clarke et al. (1994) also point to importance of euphausiid adults as a dietary component. Prior to migration, there is a large build up of lipid in the digestive gland which is believed to act as a reserve in fuelling migration activity. Euphausiids, especially pre-spawn adults, are significantly rich in lipid (3-20% of fresh weight, Clarke, 1984). Although it is possible that *I.argentinus* may synthesise lipid *de novo*, it is more energetically efficient to derive such components directly from their diet and pre-spawn adult euphausiids would present a suitable dietary source of lipid. Therefore the presence of prespawn *E.vallentini* adults during Winter is possibly very important with respect to the ability of *I.argentinus* to

migrate to its northerly spawning grounds.

Loligo gahi does not make such a migration and so the build-up of energetic reserves is probably not as crucial a part of the life cycle in this species. Nevertheless, it is likely that energetic demands would increase towards the time of reproduction. It is possible that the Spring spawning population may rely on the appearance of pre-spawn *E.vallentini* adults in Winter to meet the reproductive demands of Spring spawning. Similarly, the Summer peak in pre-spawn *E.lucens* may be a major resource for the Autumn spawners.

There is another major resource around the Falkland Islands which may supplant the reliance on euphausiids as a major dietary component of adult *L.gahi*. The post-larvae of the benthic galatheid crab *Munida gregaria* are present in substantial numbers around the Falkland Islands during Spring (pers. observ.). Although it is not known whether these animals form a dietary component of *L.gahi*, if they are consumed their large biomass would sufficiently meet the energetic demands of the Spring spawning population. Seasonal studies on *Munida gregaria* have not been carried out in the Falkland region but studies on populations around New Zealand (Zeldis, 1985) show that the post-larvae persist until the Autumn and so it is also possible that the species could be a major dietary component of the Autumn spawning population. However, dietary studies on *L.gahi* are obviously needed to confirm that adult squid around the Falkland Islands exploit this significant component of the Falkland Island zooplankton community.

Chapter 10 Conclusions

In introducing this thesis, it was established that there was a clear need to gain a greater understanding of the zooplankton ecology of the south-west Atlantic both for applied purposes such as the management of commercial fisheries and for theoretical purposes, since the region has been little studied compared with other regions such as the North Atlantic and western Pacific. Within this obvious need for greater understanding, it was further established that least was known about the mesoscale community ecology of the region despite the fact that this is one of the most important spatial scales at which zooplankton processes take place, especially with respect to the influence of environmental variability and also the impact zooplankton distribution has on higher trophic levels (Haury et al., 1978). This thesis therefore primarily concentrated on the mesoscale ecology of the region through analysing the species composition and abundance of zooplankton caught during RMT8 and Bongo net surveys in 1990 and 1991.

The RMT8 used in 1990 caught mostly macrozooplankton which were found to have distribution patterns that were most greatly influenced by a combination of water mass and latitude such that distinct faunas were found in different water masses. Water masses were not found to be as influential on distribution patterns observed in the surface dwelling mesozooplankton caught by the 1990 Bongo nets but the effect of a combination of sea surface temperature and latitude was found to be more important such that different species assemblages occurred in exclusive temperature ranges which were arranged in a north-south pattern. Nevertheless, despite the different influences on the distribution patterns between the surface-dwelling mesozooplankton and the deeper

living macrozooplankton, there were distinct similarities in some of the distribution patterns. For instance, both sample sets had a pattern concentrated in the northern part of the survey grid, corresponding with the location of the STZ and highest temperatures. There was also another common pattern associated with the Falkland shelf. However, there were differences between sample sets both in the distributional patterns and species composition of the mid-latitude stations with the RMT8 samples mostly consisting of species that exhibited strong vertical migrations whilst the Bongo samples were dominated by larvae. What is more, the larvae found in the Bongo samples were principally of species whose adults showed strongest associations to the Falkland Shelf. This may reflect the reduced ability of larvae to counteract expatriating forces such as the Falkland Current compared with adults and also stands to illustrate the profound influence of mesoscale environmental features such as the Falkland Current on community distribution patterns.

Another feature that was suggested by the 1990 Bongo and RMT8 analyses was that the nature of the boundary between species assemblages in the north and in the south of the survey were different, with the northern (STZ/SAZ) boundary being one defined by species composition whilst the boundaries to the south (ie. SAZ/PFZ and PFZ/Falkland Shelf in the case of the RMT8 and Offshore intermediate/Falkland Shelf in the case of the Bongo) being defined by differences in the abundance of ubiquitous species. This was underlined by the comparison of 1990 and 1991 Bongo sample sets where it was also possible to distinguish some of the more important causal factors behind the observed distribution patterns. Analyses showed that the STZ/SAZ boundary was defined by the 17.3°C isotherm in both years despite of the strong influence of expatriating mesoscale phenomena in this region, suggesting that organisms found close

to this boundary region were at the edge of their physiological limits. This is because it is likely that organisms found in this region are commonly expatriated and the fact that none are found in the other region indicates that rapid and extensive mortality of expatriates is taking place. By contrast, in the PFZ region, although distributional patterns were similar between years, there was a considerable difference in local sea surface temperature. Temperature tolerance does not appear to be as important in this region therefore and it is more likely that mesoscale advective forces such as the Falkland Current principally determine community distribution patterns. Warm-core eddies, which are another mesoscale feature, were seen to be influential in the Transition region especially through their expatriating effect which created a mixed sub-tropical/sub-Antarctic fauna. The larger geographic range of the Transition group in 1991 corresponded with the greater prevalence of warm-core eddies within the study region during that year.

With respect to the findings of previous studies on zooplankton distribution in the south-west Atlantic, the results of the present analysis represent, to a certain extent, a consolidation of the pieces of information that already exist. Nevertheless, many aspects of the present analysis, such as the fact that it was aimed at the community level and at mesoscale spatial resolution were unique and much of the detail that has been gained represents a considerable advance in present knowledge of the nature of zooplankton distribution in the region. In terms of the relevance of this information to more applied topics such as fishery management, the above approach is fundamental to understanding wider processes that impinge on the recruitment and maintenance of stocks. For instance, the variable influence of the Falkland Current in expatriating zooplankton larvae into the Transition region may prove to be very important in determining the carrying capacity of

the shelf environment, especially since some of these groups, such as the euphausiid, are one of the main dietary components of both commercially exploited squid species (Ivanovic and Brunetti, 1994; Collins et al., 1994). Furthermore, the penetration of mesoscale eddies into the Transition region may have considerable influence on both species composition and the productivity of the region as a whole and knowing the extent of zooplankton expatriation by these features and their frequency of penetration is crucial in assessing the success of commercial species that migrate through this region such as *Illex argentinus* (Rodhouse et al., 1992).

Studying the population ecology of main zooplankton species of the region is beneficial both in terms of fishery management as well as in understanding the structuring community level distribution patterns. From the analyses carried out in the present investigation, it was evident that the dominance of the adults and larvae of different euphausiid species in the water column changed through the year, with *E.vallentini* adults and larvae being dominant during Spring, *E.lucens* adults and larvae being dominant during Summer and to a lesser extent, Autumn and *T.gregaria* being present in small but constant proportions during every season. In terms of community distribution therefore, patterns would be expected to vary considerably through the year according to stages of euphausiid life cycles. Furthermore, considering the profound influence of features such as the Falkland Current on shelf communities, it is likely that the success of various cohorts is a function of seasonal variability in prevailing conditions and it would be interesting to further examine what effect larval expatriation from the shelf environment has on euphausiid populations in this region.

As well as examining different patterns of spawning and recruitment, the productivity and biomass of euphausiid populations on the Patagonian shelf was

calculated to determine whether their apparent importance as a food resource for commercial squid (Ivanovic and Brunetti, 1994) was reflected in their prevalence and rate of turnover. It was found that, compared to total zooplankton biomass (Ciechomski and Sanchez, 1983), the relative amount of euphausiids in the water column through the year was low, although they were proportionally more significant during Winter as a result of pre-spawn *E.vallentini* adults being prevalent in the surface layers. Nevertheless, the weight specific growth rate (P:B d^{-1}) was comparable to species found in much warmer waters (Stuart, 1986) showing that euphausiids were a very productive part of the zooplankton community in this region despite their relatively low annual biomass.

Another aim of this investigation was to examine some of the wider aspects of pelagic biogeography both in terms of general patterns and investigative methods. Community parameters such as displacement volume, abundance, species richness, diversity and equitability were related to various geographic and hydrographic variables from which one of the most stroking patterns was the significant linear relationship between species richness (S) and latitude. It was found that neither the location of water mass boundaries nor surface thermal fronts had any significant effect on this pattern despite the profound influence of both these features on the distribution of species assemblages. Such linear relationships between species richness and latitude have been widely reported on global scales (Boltovskoy, 1982; Rohde, 1992), but its occurrence at the mesoscale level has not been so widely noted and would be contrary to the expectations of most pelagic biogeographers, such as Angel who, in the recent 2nd Pelagic Biogeography Conference (1995), predicted steps in the levels of species richness when looking between water masses. The linear, unstepped pattern found by the present

investigation would otherwise show that latitudinal species richness patterns have fractal qualities since mesoscale patterns mirror the linear relationships seen at global scales. This suggests that mechanisms which affect pelagic diversity are somewhat more complex than simple circulation derived phenomena.

Most of the investigative methods used in Pelagic Biogeography are slow and labour intensive and there is a great need to try and establish methods that can map biogeographic patterns quickly and inexpensively. Satellite imagery has emerged as a powerful tool in investigating surface temperature patterns over a range of spatial scales and given the profound influence of temperature on zooplankton distribution in this region, its potential use as a quick and easy device for mapping community distribution patterns is attractive. Although limited in their scope, studies carried out by this investigation showed that the feasibility of this approach was nevertheless somewhat limited. The use of thermal features to define community distribution relies on the fact that absolute relationships between these two parameters can be defined. This was possible with respect to the sub-tropical/sub-Antarctic transition but other relationships appeared to be vague with thermal features in satellite images appearing to be poor tracers of community distribution patterns between years in the Polar Frontal Zone region. However, satellite images were very useful in highlighting principal factors that regulate faunal assemblage patterns and they also allowed the confounding effect of temporal intervals between sampling stations to be better accommodated for. However, along with the many other approaches that have been tried, satellite imagery does not, as yet, appear to be a substitute for labour intensive *in situ* sampling.

The discussions within this thesis have emphasised the complexity of the field of pelagic biogeography and, given the fact that scientific method is so difficult to apply,

any conclusions that are drawn are better viewed as working hypotheses rather than empirical statements. Nevertheless what this study has shown is that environmental variables, especially factors related to temperature and water mass, are a dominant influence on the distribution of species assemblages in this region. The biological component was also shown to be influential with, for instance, physiological limitation being instrumental in producing a marked transition between sub-tropical and sub-Antarctic fauna across the STF. The life cycles of important zooplankton species also play a major role in community distribution patterns and the displacement of larvae from the shelf dwelling adult populations is a further illustration of the intimate relationship between environmental factors such as advection and biological factors such as ontogenetic and vertical migration. The findings of the present analysis represent a primary step to understanding the mesoscale ecology of the region. A fuller understanding will not only require similar information from further research cruises to build up both spatial detail and temporal coverage but also the incorporation of different, novel techniques because many of the still outstanding problems can only be tackled by an integrated, multi-disciplinary approach.

Chapter 11 Future Work

The production of a pelagic biogeography thesis very rarely represents the neat completion of study into a particular topic because most insights are gained through successive refinements of available information rather than directly testing preset hypotheses. This means that numerous questions will remain unanswered irrespective of the success of the research undertaken. For this reason it was believed necessary to give a brief overview of the problems that remain outstanding and possible ways they can be addressed in the future.

The most immediate goal of any future planktonic research on the Patagonian and Falkland Shelves would be to study the population and trophic ecology of *Munida gregaria*. The total amount of research carried out on this organism has been lamentable despite the fact that, from personal observation, the biomass of the post-larvae dominate the shelf ecosystem by orders of magnitude in the Austral Spring and possibly other seasons. One of the first things that needs to be established is the importance this organism as a food source to commercially exploited squid and fish species if not to the wider South Atlantic ecosystem. Gut-content studies carried out by Thompson (pers. comm.) have shown that these organisms are consumed by penguins and albatross but similar studies on commercially fished species are urgently required. Estimating the biomass of this organism may be made easier by its monospecific swarming behaviour (pers. observ.) which may lend itself well to studies by Acoustic Doppler Current Profilers (ADCP). However, determining the life history of this species can only be obtained through regular nets trawls which need to be as quantitative as possible so that the rate at which pelagic post-larvae sink to start the adult benthic stage can be

monitored accurately.

A common problem faced by many marine studies is defining the geographic limits of populations. This is especially important in pelagic biogeography when trying to monitor the dispersion of species through interaction with hydrographic features because it is often inferred that single populations exist where distribution patterns are broadly continuous and multiple populations exist where there is little apparent inter-connection between several major zones of concentration. Inferences are often based on vague information and the almost arbitrary way in which the geographic limits of populations are defined belies its fundamental importance to biogeographic schemes. The problem extends to the current investigation with respect to the dispersion of euphausiid larvae from the shelf regions into the oceanic Transition zone. Here it is inferred that the larvae that are found within the Transition zone derive from the Shelf adult population because the larvae are found in the direction of prevailing currents and there is no accompanying adult population. However, it is possible that the larvae are members of a different euphausiid population either resident in the Transition region or originate from a different source and without further information it is difficult to refute any semi-plausible hypothesis that is put forward.

Recently developed genetic techniques have possibly provided the solution to such problems. The techniques rely on choosing areas of the genome with mutation rates that have a time scale equivalent to the divergence of populations. Differences between representatives from the chosen areas can then be measured to determine whether they comprise the same population. The technique has been applied by Bucklin (in press) on copepods in the Gulf Stream and has provided illuminating results, some of which contrary to accepted wisdom about the status of populations in the region. The system

can not only be applied to populations but also to species or even families depending on the nature of the region on the genome being investigated. Most interesting of all, recent evidence has pointed to the possibility of using specimens that have been preserved in formalin for such investigations (Bucklin, pers. comm.), which may make obtaining such information cost effective as well as very profound in its implications towards biogeographic theory.

One of the main conclusions from the modelling of production in Chapter 10 was that the accurate estimation of biomass was the major source of variance in any estimate that was made. The history of marine ecology research has shown this parameter to be particularly difficult to measure in zooplankton, both spatially and temporally. There have been many attempts to invent a economical means of measuring biomass distribution such as ADCP, optical sensors and video-cameras but there have been difficulties with each method and none has stood out as a solution to this fundamental problem. Some of the most revealing results in this field have been obtained through long-term monitoring programmes such as the Continuous Plankton Recorder (CPR) Survey in the North Atlantic and the CALCOFI programme in the California Current region. Both have revealed that decadal variability is considerable and that there may be climate driven fluctuations consistent with patterns seen on land. There is also evidence of long term periodicity in fishery stocks in, for instance, sardine and anchovies, where 50-75 year oscillations were found over the last 1700 year period (Baumgartner et al., 1994). The *Discovery* and *William Scoresby* samples taken during the earlier part of the 20th Century in the south-west Atlantic cover a period of approximately 30 years and analysis of these samples may give a number of insights into decadal variance in zooplankton and icthyoplankton biomass in this region which can both be tied in with

other long term studies and give a context to the findings of the present investigation. Furthermore, such data can be incorporated into the diffusion based modelling studies, such as have been advocated in Olson and Hood (1994) to gain an idea of expected variability in species composition as well as fluctuations in biomass.

One of the disappointing aspects of the present investigation was the inconsistent manner in which surface thermal features detected by satellite images were correlated with the distribution of faunal assemblages. This does not nevertheless eliminate the possibility of using remotely sensed data to monitor *in situ* distribution patterns since there are a number of further parameters in addition to surface temperature which can now be measured from satellites. For instance, the new TOPEX/POSEIDON satellite can obtain data on the heat content of the ocean's mixed layer by measuring sea surface height, and thermal processes in the mixed layer have already been demonstrated to be more dynamic than previously supposed. It is possible that the more sophisticated the measuring ability of satellites become, the greater their ability to predict *in situ* distribution patterns and this may, in turn, make the continued study of biogeography more economically viable. This does not suggest that the study of pelagic biogeography is not economically important as was outlined extensively by Krause and Angel (1994), but does point to the incompatibility of the long-term nature of biogeographic investigation and the short-term conditions of scientific funding. It is hoped that the benefits of at least one of the potential future investigations outlined above will be able to bridge this gap.

Bibliography

Allison, S. K. and K. F. Wishner (1986). Spatial and temporal patterns of zooplankton biomass across the Gulf Stream. - Mar. Ecol. Prog. Ser. 31: 233-244.

Alvarino, A. (1969). Los Quetognatos del Atlantico distribucion y notas esenciales de sistematica. - Trabajos del Instituto espanol de oceanografia 37: pp. 1-290.

Alvarino, A. (1981). Siphonophorae. In: D. Boltovskoy (ed.). Atlas del Zooplankton del Atlantico sudoccidental. - INIDEP, Mar del Plata, Argentina: 383-390.

Angel, M. V. (1977). Windows in a sea of confusion. In: N. R. Anderson and B. J. Zahuranec (ed.). Oceanic Sound Scattering Prediction. - Plenum Press, New York: 217-248.

Angel, M. V. (1979). Zoogeography of the Atlantic. In: S. Van der Spoel and A. C. Pierrot-Bults (ed.). Zoogeography and diversity of plankton. - Edward Arnold, London: 160-190.

Angel, M. V. (1986). Vertical distribution: study and implications. In: A. C. Pierrot-Bults, S. v. d. Spoel, B. J. Zahuranec and R. K. Johnson (ed.). Pelagic Biogeography. - UNESCO, Paris: 3-13.

Angel, M. V. and M. J. R. Fasham (1975). Analysis of the vertical and geographic distributions of the abundant species of planktonic ostracods in the north-east Atlantic. - J. Mar. Biol. Ass. U.K. 55: 709-737.

Antezana, T. and E. Brinton (1981). Euphausiacea. In: D. Boltovsky (ed.). Atlas del zooplankton del Atlantico sudoccidental. - INIDEP, Mar del Plata: 681-694.

Atkinson, A. (1990). Ecology and distribution of zooplankton around the island of South Georgia, Antarctica. Ph.D Thesis. Council for Academic Awards (C.N.A.A.), London.

Atkinson, A. (1991). Life cycles of *Calanoides acutus*, *Calanus simillinus* and *Rhincalanus gigas* within the Scotia Sea. - Marine Biology 109: 79-91.

Atkinson, A. and J. M. Peck (1990). The distribution of zoooplankton in relation to the South Georgia shelf. In: K. R. Kerry and G. Hempel (ed.). Antarctic Ecosystems Ecological change and conservation. - Springer-Verlag, Berlin:

Backus, R. H. (1986). Biogeographic boundaries in the open ocean. - In: A. C. Pierrot-Bults, B. J. Zahuranec and A. K. Johnson (eds.). Proceedings of the International conference on pelagic biogeography. - UNESCO, Paris: 9-14

Badcock, J. and N. R. Merrett (1977). On the distribution of midwater fishes in the eastern north Atlantic. In: N. R. Andersen and B. J. Zahuranec (ed.). Oceanic Sound Scattering Prediction. - Plenum Press, New York: 249-282.

Baker, A. d. C. (1959). Distribution and life history of *Euphausia triacantha*. - Discovery Reports XXIX: 309-340.

Baker, A. d. C., B. P. Boden and E. Brinton (1990). A practical guide to the euphausiids of the world. - British Museum (Natural History), London: pp.96

Ball, I. R. (1976). Nature and formulation of biogeographical hypotheses. - Syst. Zool. 24: 407-430.

Barange, M. (1990). Vertical migration and habitat partitioning of 6 euphausiid species in the northern Benguela upwelling system. - J. Plank. Res 12: 1223-1237.

Barnard, K. H. (1932). Amphipoda. - Discovery Reports V: 1-326.

Bary, B. M. (1956). Notes on ecology, systematics and development of some Mysidacea and Euphausiacea (Crustacea) from New Zealand. - Pac. Sci. 10: 431-467.

Bary, B. M. (1963). Temperature, salinity and plankton in the eastern north Atlantic and coastal waters of Britain, 1957 II. The relationships between species and water bodies. - J. Fish. Res. Bd. Canada 20(4): 1031-1065.

Bastida, R., M. Bertolotti, S. Bezzi, N. Brunetti, J. Ciechomski, C. Gregorio, H. Otero, et al. (1986). Impacto ecologico y economico de las capturas aldredor de las Malvinas despues de 1982. - Mar del Plata, Argentina: pp.154

Beaufort, L. F. d. (1943). Zoogeographie. - J. Noordom and Zoon, Gorinchem.

Berkes, F. (1973). Production and comparative ecology of euphausiids in the Gulf of St. Lawrence. Ph.D. Thesis. McGill Univ., Montreal.

Bernhard, M., F. Moller, A. Nassogue and A. Zattera (1973). Influence of pore size of plankton nets and towing speed on the sampling performance of two high speed samplers. - Mar. Biol. 20: 109-136.

Boden, B. (1951). The eggs and larval stages of *Nyctiphanes simplex*, a euphausiid crustacean from California. - Proc. London 121(3): 515-527.

Boden, B. P. (1950). The post-naupliar stages of the crustacean *Euphausia pacifica*. - Trans. of American Microscopy Society 69(4): 373-386.

Bogdanov, D. V. (1961). Map of the natural zones of the ocean. - Okeanologiya 1: 941-943.

Bollens, S. M., B. W. Frost and T. S. Lin (1992). Recruitment, growth and diel vertical migration of *Euphausia pacifica* in a temperate fjord. - Mar. Biol. 114: 219-228.

Boltovskoy, D. (1975). Some biometrical, ecological, morphological and distributional aspects of Chaetognatha. - Hydrobiologia 46(4): 515-534.

Boltovskoy, D. (1979). Zooplankton of the south-western Atlantic. - S. Afr. J. Sci. 75: 541-545.

Boltovskoy, D., Ed. (1981a). Atlas del zooplankton del Atlantico sudoccidental. Mar del Plata, INIDEP.

Boltovskoy, D. (1981b). Chaetognatha. In: D. Boltovskoy (ed.). Atlas del Zooplankton del Atlantico sudoccidental. - INIDEP, Mar del Plata, Argentina: 759-774.

Boltovskoy, D. (1982). Variacion latitudinal de la diversidad zooplankton en el atlantico sudoccidental. - Physis (Buenos Aires) Secc A. 41(100): 1-6.

Boltovskoy, D. (1986). Biogeography of the south-western Atlantic: current problems and prospects. In: A. C. Pierrot-Bults, B. J. Zahuranec and A. K. Johnson (ed.). Proceedings of the International conference on pelagic biogeography. - UNESCO, Paris: 14-25

Boltovskoy, D. (1989). Las zonas de transicion en la pelagial biogeografica y paleogiogeografia. In: F. P. Brandini (ed.). Memorias do III Encontro de Placton. - Curitiba:

Boltovskoy, D. and W. R. Riedel (1987). Polycystine Radiolaria of the California current region: seasonal and geographic patterns. - Mar. Micropal. 12: 65-104.

Boltovskoy, E. (1981). Foramanifera. In: D. Boltovksoy (ed.). Atlas del zooplankton del Atlantico Sudoccidental. - INIDEP, Mar del Plata: 317-352.

Boschii, E. E., M. I. Iorio and K. Fischbach (1981). Distribucion y abundancia de los crustaces decapodos capturas en las campanas de los B/I "Walter Herwig" y "Shankai Maru" en el Mar Argentino, 1978-1979. - Contrib. Inst. Nac. Inv. Des. Pesq. (Mar del Plata) 383: 233-252.

Boucher, J. (1984). Localization of zooplankton populations in the Ligurian marine front: role of ontogenetic migration. - Deep Sea Res. 31(5): 469-484.

Boucher, J., F. Ibanez and L. Prieur (1987). Daily and seasonal variations in the spatial distribution of zooplankton populations in relation to the physical structure in the Ligurian Sea Front. - J. Mar. Res. 45: 133-173.

Bowman, T. E. (1960). The pelagic amphipod genus *Parathemisto* in the north Pacific and adjacent Arctic ocean. - Proc. U.S. Nat. Mus. 112(3439)

Bowman, T. E. (1978). Revision of the pelagic amphipod genus *Primno*.

Bowman, T. E. and H. E. Gruner (1973). The familiea and genera of Hyperiidea (Crustacea: Amphipoda). - Smithsonian Contrib. Zool. 146: pp1-64.

Boyd, S. H., P. H. Wiebe and J. L. Cox (1978). Limits of *Nematoscelis megalops* in the NW Atlantic in relation to Gulf Stream cold-core rings. II. Physiological and

biochemical effects of expatriation. - J. Mar. Res. 36: 143-159.

Bray, J. R. and J. T. Curtis (1957). An ordination of the upland forest communities of Southern Wisconsin. - Ecol. Monog. 27: 325-349.

Briggs, J. C. (1974). Marine Zoogeography. - McGraw-Hill, New York: pp.475

Brinton, E. (1962). The distribution of Pacific Euphausiids. - Bull. Scripps. Inst. Oceanogr. 8(2): 51-270.

Brinton, E. (1976). Population biology of *Euphausia pacifica* off Southern California. - Fish. Bull. 74(4): 733-763.

Brinton, E. and J. L. Reid (1986). On the effects of interannual variations in circulation and temperature upon euphausiids of the California Current. In: A. C. Pierrot-Bults, S. v. d. Spoel, B. J. Zahuranec and R. K. Johnson (ed.). Pelagic Biogeography. - UNESCO, Paris: 25-35.

Browne, E. T. and P. L. Kramp (1939). Hydromedusae of the Falkland Islands. - Discovery Report XVII: 265-322.

Bushing, M. and D. Fiegenbaum (1984). Feeding by an expatriate population of *Sagitta enflata*. - Bull. Mar. Sci. 34: 240-243.

Calow, P. (1981). Resource utilization and reproduction. In: C. R. Townsend and P. Calow (ed.). Physiological ecology. - Blackwell, Oxford: 245-270.

Casanova, B. (1974). Les euphausiaces de Mediteranee (systematique et developpement larvaire. Biogeographie et biologie). Ph.D Thesis. Univ. Provence.

Cassie, R. M. (1954). Some uses of probability paper in the analysis of size frequency distributions. - Aust. J. Mar. Freshwat. Res. 5: 513-522.

Cassie, R. M. (1972). Fauna and sediments of an intertidal mud flat: an alternative multivariate analysis. - J. exp. mar. Biol. Ecol. 9: 55-64.

Chiu, T. S. and Y. H. Hsyu (1994). Interannual variation of ichthyoplankton density and species composition in the waters off northeastern Taiwan. - Mar. Biol. 119(3): 441-448.

Ciechomski, J. D. d. and R. P. Sanchez (1983). Relation between ichthyoplankton abundance and associated zooplankton biomass in the shlef waters off Argentina. - Biol. Ocean. 3(1): 77-101.

Clarke, A. (1984). The lipid content and composition of some Antarctic macrozooplankton. - Br. Antarct. Surv. Bull. 63: 57-70.

Clarke, A. (1992). Is there a latitudinal diversity cline in the sea? - TREE 7(9): 286-287.

Clarke, A. and D. J. Gore (1992). Egg size and composition in *Ceraserolis* (Crustacea, Isopoda) from the Weddell Sea. - Polar Biol. 12(1): 129-134.

Clarke, A., P. G. Rodhouse and D. J. Gore (1994). Biochemical composition in relation to the energetics of growth and sexual maturation in the Ommastrephid squid *Illex argentinus*. - Phil. Trans. R. Soc. Lond. Ser. B 344(1308): 201-212.

Clarke, G. A., W. T. Edmondson and W. E. Ricker (1946). Appendix: Mathematical formulation of biological productivity. - Ecol. Monog. 16: 336-337.

Clarke, K. R. and M. Ainsworth (1993). A method of linking multivariate community structure to environmental variables. - Mar. Ecol. Prog. Ser. 92: 205-213.

Clarke, M. R. (1969). A new mid-water trawl for sampling discrete depth horizons. - J. mar. biol. Ass. U.K. 49: 945-960.

Clifford, H. T. and W. Stephenson (1975). An introduction to numerical classification. - Academic Press, New York.

Clutter, R. I. and M. Anraku (1966). Avoidance of samplers. In: Zooplankton Sampling. UNESCO monographs in oceanographi methodology. 2: 57-76.

Cohen, D. M. (1973). Zoogeography of the fishes of the Indian Ocean. In: B. Zeitschel and S. A. Gerlach (ed.). The biology of the Indian Ocean. - Springer-Verlag, Berlin: 451-464.

Cole, L. C. (1954). The population consequences of life history phenomena. - Q. Rev. Biol. 29: 103-137.

Colebrook, J. M. (1978). Continuous Plankton Records: zooplankton and environment, North-East Atlantic and North Sea, 1948-1975. - Oceanol. Acta 1(1): 9-23.

Colebrook, J. M. (1982). Continuous plankton records: seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. - J. Plank. Res. 41: 435-462.

Colebrook, J. M. (1984). Continuous plankton records: relationship between species of phytoplankton and zooplankton in the seasonal cycle. - Mar. Biol. 83: 313-323.

Collins, M. A., S. Degrave, C. Lordan, G. M. Burnell and P. G. Rodhouse (1994). Diet of the squid *Loligo forbesi* Steenstrup (Cephalopoda, Loliginidae) in Irish waters. - J. Mar. Sci. 51(3): 337-344.

Crosnier, A. and J. Forest (1973). Les Crevettes Profondes de l'Atlantique Oriental Tropical. - ORSTOM, Paris: pp.409

Croxall, J. P., P. A. Prince, A. Baird and P.Ward (1985). The diet of the Southern Rockhopper penguin *Eudyptes chrysocome chrysocome* at Beauchene Island, Falkland Islands. - J. Zool. London 206: 485-496.

Csirke, J. (1987). The Patagonian fishery resources and the offshore fisheries in the south-west Atlantic. - FAO Fish. tech. Pap. 286

Curtolo, L. M., J. R. Dadon and H. E. Mazzoni (1990). Distribution and abundance of euphausiids off Argentina in Spring 1978. - Neritica 5(1): 1-14.

Cushing, D. H. (1975). Marine ecology and fisheries. Pages. - Cambridge University Press, Cambridge, U. K.

Cushing, D. H., G. F. Humphrey, K. Banse and T. Laevastu (1958). - Rapp. P-v Reun. Cons. Perm. Int. Explor. Mer. 144: 15-16.

Cuzin-Roudy, J. (1987). Gonad history of Antarctic krill *Euphausia superba* Dana during its breeding season. - Polar Biology 7: 237-244.

Cuzin-Roudy, J. (1993). Reproductive strategies of the Mediterranean krill, *Meganyctiphanes norvegica* and the Antarctic krill *Euphausia superba* (Crustacea: Euphausiacea). - Invertebrate Reproduction and Development 23(2): 105-114.

Cuzin-Roudy, J. and M. O. Amsler (1991). Ovarian development and sexual maturity staging in Antarctic krill, *Euphausia superba* Dana (Euphausiacea). - J. Crust. Biol. 11(2): 236-249.

Dadon, J. R. (1989). Pterapoda, Euthecosomata del mar epicontinental Argentino y adyencias. Ph.D. thesis. Universidad Buenos Aires.

Dadon, J. R. and D. Boltovsky (1982). Zooplankton recurrent groups (Pteropoda, Euphausiasea, Chaetognatha) in the south-western Atlantic Ocean. - PHYSIS (Buenos Aires) Secc A. 41(100): 63-83.

Dahiya, R. C. (1980). Estimating the population sizes of different types of organisms in a plankton sample. - Biometrics 36: 437-446.

David, P. M. (1958). The distribution of the chaetognatha of the Southern Ocean. - Discovery Report XXIX: 199-228.

Davies, C. S. (1987). Components of the zooplankton production cycle in the temperate ocean. - J. Mar. Res. 45: 947-983.

Davies, W. K. D. (1982). Factorial ecology. - Gower, Aldershot.

Davis, C. S. (1987). Components of the zooplankton production cycle in the temperate ocean. - J. Mar. Res. 45: 947-983.

Davis, C. S. and P. H. Wiebe (1985). Macrozooplankton biomass in a warm-core Gulf Stream Ring: Time series changes in size structure, taxonomic composition and vertical distribution. - J. Geophys. Res. 90(5): 8871-8884.

Day, J. H., J. G. Field and M. P. Montgomery (1971). The use of numerical methods

to determine the distribution of the benthic fauna across the continental shelf of North Carolina. - J. Anim. Ecol 40: 93-126.

Deacon, G. E. R. (1933). A general account of the hydrology of the South Atlantic Ocean. - Discovery Reports VII: 171-238.

Dilwyn-John, D. (1936). The southern species of the genus *Euphausia.* - Discovery Reports XIV: 193-324.

Einarsson, H. (1945). Euphausiacea I. Northern Atlantic Species. - Dana Report 27: pp. 184.

Ekman, S. (1953). Zoogeography of the sea. -Edward Arnold, London.

El-Sayed, S. Z. and L. H. Weber (1982). Spatial and temporal variations in phytoplankton biomass and primary production in the south-west Atlantic and the Scotia sea. - Polar Biol. 1: 83-90.

Esnal, G. B. (1981). Thaliacea: Salpidae. In: D. Boltovskoy (ed.). Atlas del zooplankton del Atlantico sudoccidental. - INIDEP, Mar del Plata, Argentina: 793-803.

Everson, I. (1984). Zooplankton. - Antarct. Ecol. 2: 463-490.

Fager, E. W. (1957). Determination and analysis of recurrent groups. - Ecology 3: 460-496.

Fager, E. W. (1963). Communities of organisms. In: M. N. Hill (ed.). *The sea.* - 415-437.

Fager, E. W. and J. A. McGowan (1963). Zooplankton species groups in the north Pacific. - Science 140: 453-460.

Fasham, M. J. R. and M. V. Angel (1975). The relationship of the zoogeographic distributions of the planktonic ostracods in the north-east Atlantic to the water masses. - J. mar. biol. Ass. U.K. 55: 739-757.

Field, J. G., K. R. Clarke and R. M. Warwick (1982). A practical strategy for analysing multispecies distribution patterns. - Mar. Ecol. Prog. Ser. 8: 37-52.

Fisher, A. G. (1981). Climatic oscillations in the biosphere. In: M. H. Nitecki (ed.). Biotic crises in ecological and evolutionary time. - Academic Press, New York: 103-131.

Fleminger, A. (1975). Geographical distribution and morphological divergence in American coastal-zone planktonic copepods of the genus *Labidocera.* In: L. E. Cronin (ed.). Estuarine research I. Chemistry, biology and estuarine system. - Academic Press, New York: 319-348.

Fleminger, A. and K. Hulsemann (1974). Systematics and distribution of four sibling

species comprising the genus *Pontellina* Dana (Copepoda, Calanoida). - Fish. Bull. 72(1): 63-120.

Fleminger, A. and K. Hulsemann (1977). Geographical range and taxonomic divergence in the North Atlantic *Calanus* (*C. helgoglandis, C. finmarchicus, C. glacialis*). - Mar. Biol. 40: 233-248.

Foxton, P. (1956). The distribution of the standing crop of zooplankton in the Southern ocean. - Disovery Report XXVII: 191-236.

Foxton, P. (1966). The distribution and life history of *Salpa thompsoni* with observation on a related species *Salpa gerlachei*. - Discovery Report XXXIV: 1-116.

Foxton, P. (1972). Observations of the vertical distribution of *Acanthaphyra* (Crustacea: Decapoda) in the eastern North Atlantic, with particular reference to species of the *purpurea* group. - Proc. Roy. Soc. Edinb. B, 73: 301-313.

France, R., J. Holmes and A. Lynch (1991). Use of size-frequency data to estimate the age composition of crayfish populations. - Can. J. Fish. Aquat. Sci. 48: 2324-2332.

Fraser, F. C. (1936). On the development of the young stages of krill (*Euphausia superba*). - Discovery Reports XIV: 1-192.

Fraser, J. H. (1967). Siphonophora in the plankton to the north and west of the British Isles. - Proc. R. Soc. Edin. (B) 70: 1-30.

Frost, W. E. (1935). Larval stages of the euphausiids *Nematoscelis megalops* (G.O. Sars) and *Stylocheiron longicorne* (G.O. Sars) taken off the south-west coast of Ireland. - Procs. of the Royal Irish Academy 42(B): 443-458.

Fulton, J. and R. LeBrasseur (1984). Euphausiids of the continental shelf and slope of the Pacific coast of Canada. La Mer. - Bull. Soc. franco-jap. Oceanogr., Tokyo 22: 268-276.

Garzoli, S. L. and A. Bianchi (1987). Time-space variability of the local dynamics of the Malvinas-Brazil Confluence as revealed by inverted echo sounders. - J. Geophys. Res. 92(C2): 1914-1922.

Gauch, H. G. (1982). Multivariate analysis in community ecology. - Cambridge University Press, Cambridge, U.K: pp.298

George, R. Y. (1985). Metabolism of Antarctic Krill, *Euphausia superba*, and its tropho-dynamic implications. In: W. R. Siegfried, P. R. Condy and R. M. Laws (ed.). Antarctic nutrient cycles and food webs. - Springer-Verlag, Berlin: 324-329.

Giguere, L. A., J. St-Pierre, B. Bernier, A. Vezina and J. Rondeau (1989). Can we estimate the true weight of zooplankton samples after chemical preservation? - Can. J. Fish. Aquat. Sci. 46: 522-527.

Gopalakrishnan, K. (1975). Biology and taxonomy of the genus *Nematoscelis* (Crustacea, Euphausiacea). - Fish. Bull. 73(4): 797-814.

Gordan, A. L., D. T. Georgi and H. W. Taylor (1977). Antarctic polar frontal zone in the western Scotia sea - summer 1975. - J. Phys. Oceanog. 7: 309-328.

Gordan, A. L. and C. L. Greengrove (1986). Geostrophic circulation of the Brazil-Falkland confluence. - Deep Sea Res. 33(5): 573-585.

Grant, A. (1989). The use of graphical methods to estimate demographic paramters. - J. Mar. Biol. Assoc. U.K. 69: 367-371.

Grant, A., P. J. Morgan and P. J. W. Olive (1987). Use made in marine ecology of methods for estimating demographic parameters from size/frequency data. - Mar. Biol. 95: 201-208.

Grice, G. D. and A. D. Hart (1962). The abundance and seasonal occurence and distribution of the epizooplankton between New York and Bermuda. - Ecol. Monog. 32(4): 287-307.

Griffiths, F. B., G. H. Brown, D. D. Reid and R. R. Parker (1984). Estimation of sample zooplankton abundance from Folsom splitter sub-samples. - J. Plankton Res. 6: 721-731.

Gurney, R. (1947). Some notes on the development on the Euphausiacea. - Proc. Zool. Soc. Lond. 117: 49-64.

Haedrich, R. L. and D. C. Judkins (1979). Macrozooplankton and its environment. In: S. Van der Spoel and A. C. Peirrot-Bults (ed.). Zoogeography and diversity of plankton. - Edward-Arnold, London: 4-29.

Hamner, W. M. (1984). Aspects of schooling in *Euphausia superba*: chemoreception, feeding, schooling and molting. - Science 220: 433-435.

Harbison, G. R., D. C. Biggs and L. P. Madin (1977). The associations of Amphipoda Hyperiidae with gelatinous zooplankton. II. Associations with Cnidaria, Ctenophora and Radiolaria. - Deep Sea Res. 24: 465-488.

Harding, J. P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. - J. Mar. Biol. Assoc. U.K. 28: 141-153.

Hargreaves, P. M. (1985). The vertical distribution of Decapoda, Euphausiacea and Mysidacea at 42°N 17°W. - Biol. Ocean 3(4): 431-464.

Hatfield, E. M. C. (1991). Post-recruit growth of the Patagonian squid *Loligo gahi*. - Bull. Mar. Sci. 49(1-2): 349-361.

Hatfield, E. M. C. (1992). Recruitment, demography and growth of the Patagonian squid *Loligo gahi* (d, Orbigny, 1835) in the Falkland Island waters. - Ph.D Thesis,

Council for National Academic awards (C.N.A.A.), London.

Hatfield, E. M. C., P. G. Rodhouse and J. Porebski (1990). Demography and distribution of the Patagonian squid (*Loligo gahi* d'Orbigny) during the austral winter. - J. Cons. int. Explor. Mer 46: 306-312.

Haury, L. R., J. A. McGowan and P. H. Wiebe (1978). Patterns and processes in the time-space scales of plankton distributions. In: J. H. Steele (ed.). Spatial patterns in plankton communities. - Plenum Press, New York: 277-327.

Hayward, T. and J. A. McGowan (1979). Pattern and structure in an oceanic zooplankton community. - Am. Zool. 19: 1045-1055.

Heath, W. A. (1977). The ecology and harvesting of euphausiids in the Strait of Georgia. Ph.D Thesis. Univ. British Columbia, B.C. Canada.

Hentschel, E. (1938). Das Netzplankton des Sudatlantischen Ozeans. Eine Zusammenfassung. - Wiss.Ergbn.dt.Atl.Exped. "Meteor" 1925-1927 13: 245-308.

Hesse, R. (1924). Tiergeographiee. - Fisher Verlag, Jena: pp.613

Hirche, H. (1984). Temperature and metabolism of plankton-I. Respiration of Antarctic zooplankton at different temperatures with a comparison of Antarctic and Nordic krill. - Comp. Biochem. Physiol. 77A: 361-368.

Hirota, Y., T. Nemoto and R. Marumo (1984). Vertical distribution of larvae of *Euphausia nana* and *Euphausia similis* in Sagami bay and Suruga bay, Central Japan. - Mar. Biol. 81: 131-137.

Hopkins, T. L., D. M. Milliken, L. M. Bell, E. J. McMichael, J. J. Hefferman and R. V. Cano (1981). The landward distribution of oceanic plankton and micronekton over the west Florida continental shelf as related to their vertical distribution. - J. Plankton Res. 3: 645-658.

Horwood, J. W. and R. M. Driver (1976). A note on theoretical sub-sampling distribution of macroplankton. - J. Cons. Int. Explor. Mer 36: 274-276.

Hulsizer, E. (1971). A study of the reproductive cycle of *Euphausia pacifica* at two stations in Puget Sound. M.Sc. Thesis. Univ. Washington.

Huntley, M., E. Brinton (1991). Mesoscale variation in growth and early development of *Euphausia superba* Dana in the western Bransfield Strait region. - Deep Sea Res. 38(8/9): 1213-1240.

Huntley, M. and C. Boyd (1984). Food limited growth of marine zooplankton. - Amer. Nat. 124(4): 455-478.

Huntley, M. E., M. D. G. Lopez (1992). Temperature dependent production of marine

copepods: a global synthesis. - Am. Nat. 140 (2): 201-242

Hurley, D. E. (1969). Amphipoda, Hyperiidea. - Antarctic Map Folio Series Distribution of selected groups of marine invertebrates in waters south of 35°S latitude(Folio 11): 32-34.

Ikeda, T. (1974). Nutritional ecology of marine zooplankton. - Mem. Fac. Fish. Hokkaido Univ. 22: 1-97.

Ikeda, T. (1984). Sequences in metabolic rates and elemental composition (C, N, P) during the development of *Euphausia superba* Dana and estimated food requirements during its life span. - J. Crust. Biol. 4(1): 273-284.

Ikeda, T. (1985). Metabolic rates of epipelagic marine zooplankton as aa function of body mass aand temperature. - Mar. Biol. 85: 1-11.

Ikeda, T. and S. Motoda (1978). Estimated zooplankton production and their ammonia excretion in the Kuroshio and adjacent seas. - Fish. Bull. 76(2): 357-367.

Ikeda, Y., G. Siedler and M. Zwierz (1989). On the variability of Southern Ocean fron locations between southern Brazil and the Antarctic peninsula. - J. Geophys. Res. 83(C9): 4501-4522.

Ivanovic, M. L. and N. E. Brunetti (1994). Food and feeding of *Illex argentinus*. - Antarct. Sci. 6(2): 185-193.

James, A. G. (1987). Feeding ecology, diet and field-based studies on feeding selectivity of the cape anchovy *Engraulis capensis* (Gilchrist). - S. Afr. J. mar. Sci. 5: 673-692.

Jerde, C. W. and R. Lasker (1966). Moulting of euphausiid shrimps: shipboard observations. - Limnol. Oceanog. 11: 120-124.

Jespersen, P. (1923). On the quantity of macroplankton in the Mediterranean and the Atlantic. - Rep. Danish Oceanogr. Exped. 1908-1910 III, 3.

Jespersen, P. (1935). Quantitative investigations on the distribution of macroplankton in the different oceanic regions. - Dana reports II: pp.44

Johnson, E. A. (1977). A multivariate analysis of the niches of plant populations in raised bogs I. Niche dimensions. - Can. J. Bot. 55: 1201-1210.

Johnson, M. W. and E. Brinton (1963). Biological species, water masses and currents. In: M. N. Hill (ed.). The Sea. - 381-403.

Jones, J. B. (1981). Growth of 2 species of freshwater crayfish (*Paranephrops spp.*) in New Zealand. - N. Z. J. Mar. Freshwater Res. 15: 15-20.

Jongman, R. H. G., C. F. J. T. Braak and O. F. R. v. Tongeren (1987). Data analysis in community and landscape ecology. - Pudoc, Washington.

Kane, J. (1993). Variability of zooplankton biomass and dominant species abundance on Georges Bank, 1977-1986. - Fish. Bull. 91(3): 464-474.

Kemp, S. and A. G. Bennet (1929). Discovery Investigations: Objects, Equipment and Methods. - Discovery Reports I: 1-151.

Kensley, B. F. (1972). Shrimps and Prawns of South Africa. - South African Museum: pp.65

Kikuno, T. and A. Kawamura (1983). Observations of the ovarian eggs and spawning habit in *Euphausia superba* Dana. Ed. T. Nemoto and T. Matsuda. Proceedings of the BIOMASS coloquium. special issue 27. 104-121. Memoirs of the National Institute of Polar Research, Tokyo.

Kils, U. (1979). Swimming speed and escape capacity of Antarctic krill, *Euphausia superba*. - Meeresforschung 27: 264-266.

Kimmerer, W. J. (1987). The theory of secondary production calculations for continuously reproducing populations. - Limnol. Oceanog. 32(1): 1-13.

Klinkenberg, L. (1994). The vertical partitioningof 3 co-occurring euphausiid species on the Falkland Shelf, south-west Atlantic. Undergraduate Thesis. Southampton Univ.

Kramp, P. L. (1959). The hydromedusae of the Atlantic ocean and adjacent waters. - Dana Report 46: pp. 284.

Krause, D. C. and M. V. Angel (1994). Marine biogeography, climate change and societal needs. - Prog. Oceanog. 34: 221-235.

Kulka, D. W. and S. Corey (1978). The life history of *Thysanoessa inermis* (Kroyer) in the Bay of Fundy. - Can. J. Zool. 56: 492-506.

Lacroix, G. (1968). Les fluctuations quantitatives du zooplankton de la Baie-des-Chaleurs (Golfe Saint Laurent). D.Sc. Thesis. Universite Laval, Quebec.

Lasker, R. (1966). Feeding, growth, respiration and carbon utilization of a euphausiid crustacean. - J. Fish. Res. Bd. Can. 23(9): 1291-1317.

Laval, P. (1980). Hyperiid amphipod as crustacean parasitoids associated with gelatinous zooplankton. - Ocean. Mar. Biol. Ann. Rev 18: 11-56.

Lebour, M. V. (1924). The Euphausiidae in the neighbourhood of Plymouth and their importance as herring food. - J. Mar. Biol. Assoc. U.K. 13: 402-431.

Legeckis, R. and A. L. Gordon (1982). Satellite observations of the Brazil and Falkland currents- 1975 to 1976 and 1978. - Deep Sea Res. 29(3A): 375-401.

Lindley, J. A. (1978). Population dynamics and production of euphausiids. I. *Thysanoessa longicaudata* in the north Atlantic ocean. - Mar. Biol. 46: 121-130.

Lindley, J. A. (1982). Continuous plankton records: Geographical variations in numerical abundance, biomass and production of euphausiids in the North Atlantic Ocean and the North Sea. - Mar. Biol. 71(7): 7-10.

Lopez, R. B. (1964). Problemas de la distribucion geografica de los peces marinos sudamericanos. - Bol. Inst. Biol. Mar. (Mar del Plata) 7: 57-63.

Macdonald, P. D. M. and T. J. Pitcher (1979). Age-groups from size-frequency data: a versatile and efficent method of analysing distribution mixtures. - J. Fish. Res. Bd. Can. 36: 987-1001.

Macdonald, R. (1927). Irregular development in the larval history of *Meganyctiphanes norvegica*. - J. Mar. Biol. Assoc. U.K. 14: 785-794.

Mackintosh, N. A. (1934). Distribution of the macroplankton in the Atlantic sector of the Antarctic. - Discovery Report IX: 65-160.

Madin, L. P. and G. R. Harbison (1977). The associations of Amphipoda Hyperiidea with gelatinous zooplankton I. Associations with Salpidae. - Deep Sea Res. 24: 449-463.

Makarov, R. R. (1974). Dominance of larval forms of euphausiid (Crustacea: Eucarida) ontogenesis. - Mar. Biol. 26(1): 45-56.

Makarov, R. R. and C. J. Denys (1980). Stages of sexual maturity of *Euphausia superba*. BIOMASS Handbook: pp.11.

Mardia, K. V., J. T. Kent and J. M. Bibby (1979). Multivariate analysis. - Academic Press, London.

Mauchline, J. (1959). The development of the Euphausiacea (Crustacea) especially that of *Meganyctiphanes norvegica* (Sars). - Proc. Zool. Soc. Lond. 132: 627-639.

Mauchline, J. (1960). The biology of the euphausiid crustacean, *Meganyctiphanes norvegica* Sars. - Proc. R. Soc. Edin. B 67: 141-179.

Mauchline, J. (1965). The larval development of the euphausiid *Thysanoessa raschii* (Sars). - Crustaceana 9: 31-40.

Mauchline, J. (1971). Euphausiacea larvae. Zooplankton. - Cons. Internat. Explor. Mer. 135/137: 1-16.

Mauchline, J. (1977). Growth and moulting of crustacea, especially euphausiids. In: N. R. Andersen and B. J. Zahuranec (ed.). Oceanic Sound Scattering and Prediction. - 401-422.

Mauchline, J. (1980). The biology of mysids and euphausiids. - Adv. Mar. Biol. 18: 1-681.

Mauchline, J. (1985). Growth and production of Euphausiacea (Crustacea) in the

Rockall Trough. - Mar. Biol. 90: 19-26.

Mauchline, J. and L. R. Fisher (1969). The biology of euphausiids. - Adv. Mar. Biol. 7: 1-454.

Mazzoni, H. E. (1990). Chaetognatha del Mar Argentino ciclos estancionales de la distribucion espacial y otros aspectos ecologicas. Ph.D. thesis. Universidad de Buenos Aires.

McCarthy, J. J. and J. L. Nevins (1986). Sources of nitrogen for primary production in warm-core rings 79-E and 81-D. - Limnol. Oceanog. 31: 690-700.

McClaren, I. A. and C. J. Corkett (1986). Life cycles and production of two copepods on the Scotian Shelf, eastern Canada. In: G. Shriever, H. K. Schminke and C. T. Shih (eds.). Proceedings of the Second International Conference on Copepoda. 58. 362-368. Syllogeus.

McGowan, J. A. (1971). Oceanic biogeography of the Pacific. In: B. M. Funnell and W. R. Riedel (ed.). The micropaleotology of oceans: 1-74.

McGowan, J. A. (1974). The nature of oceanic ecosystems. In: C. B. Miller (ed.). The biology of the oceanic Pacific: 9-28.

McGowan, J. A. &. F. (1966). The relationship between the size of net used and estimates of zooplankton diversity. - Limnol. Oceanogr. 11: 456-469.

McIntyre, A. and A. W. H. Be (1967). Modern coccolithophoridae of the Atlantic Ocean I. Placoliths and Cyrtoliths. - Deep Sea Res. 14: 561-597.

McLaughlin, P. (1965). A rediscription of the Euphausiid Crustacean, *Nematoscelis difficilis*. - Crustaceana 9(1): 41-44.

Menni, R. C. and H. L. Lopez (1984). Distributional patterns of Argentina marine fishes. - Physis A 42(103): 71-85.

Mertz, D. B. and D. E. McCauley (1980). The domain of laboratory ecology. - Sythese 43: 95-110.

Mesenheimer, J. (1905). Die tiergeographischen Regionen des Pelagias, auf Grund der Verbreitung der Pteropoden. - Zool. Anz. 29: 153-163.

Mills, E. L. (1969). The community concept in marine zoology, with some comments on continua and instability in some marine communities: A review. - J. Fish. res. Bd. Can. 26(6): 1415-1428.

Montu, M. (1977). Eufausidos de la plataforma Argentina y adyacencias I. Distribucion estacional en al sector Patagonico. - Ecosur 4(8): 187-225.

Montu, M. (1982). Reproduccion y ciclos de vida en cuatro especies en eufausidos

patagonicos (Crustacea, Eucarida). - Arq. Biol. Tecnol. 25(2): 247-259.

Morioka, Y. and Y. Komaki (1978). Seasonal and vertical distribution of zooplankton biomass in the Japan Sea. - Bull. Jap. Sea Reg. Fish. Res. Lab. 29: 255-267.

Nafpaktitis, B. G. (1977). Fishes of the N. W. Atlantic. Sears Foundation for Marine Research. Memoir 1, part 7.

Nelson, G. and L. Hutchings (1987). Passive transportation of pelagic system components in the southern Benguela area. - S. Afr. J. Mar. Sci 5: 223-234.

Nepgen, C. S. D. V. (1957). The euphausiids of the west coast of South Africa. - Invest. Rep. Div. Fish. S. Afr. 28:

Nesis, N. K. (1974). Okeanicheskie golovonogie mollyuski yugo-zapadnol Atlantiki. - Trudy Inst. Okeanol. 98: 51-75.

O'Reilly, J. E., C. Evans-Zetlin and D. A. Busch (1987). Primary production. In: R. H. Backus (ed.). Georges Bank. - MIT Press, Cambridge, MA: 220-233.

Olson, D. B. (1986). Transtion zones and faunal boundaries in relationship to physical properties of the ocean. In: A. C. Pierrot-Bults, S. v. d. Spoel, B. J. Zahuranec and R. K. Johnson (ed.). Pelagic Biogeography. - UNESCO, Paris: 219-226.

Olson, D. B., G. P. Podesta, R. H. Evans and O. B. Brown (1988). Temporal variations in the separation of the Brazil and Malvinas currents. - Deep Sea Res. 35(12): 1971-1990.

Omori, M. and W. M. Hamner (1982). Patchy distribution of zooplankton: behaviour, population assessment and sampling problems. - Mar. Biol. 72: 193-200.

Omori, M. and T. Ikeda (1984). Methods in marine zooplankton ecology. - John Wiley & sons: pp.299.

Pakhomov, E. A., R. Perrissinotto and C. D. McQuaid (1994). Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. - Mar. Ecol. Prog. Ser. 111: 155-169.

Paranjape, M. A. (1967). Moulting and respiration of euphausiids. - J. Fish. Res. Bd. Can. 24(6): 1229-1240.

Patterson, K. R. (1988). Life history of Patagonian squid *Loligo gahi* and growth parameter estimates using least square fits to von Bertalanffy models. - Mar. Ecol. Prog. Ser. 47: 65-74.

Pearcy, W. G. and L. F. Small (1968). Effects of pressure on the respiration of vertically migrating crustaceans. - J. Fish. Res. Bd. Can. 25: 1311-1316.

Pearcy, W. G., G. H. Theilacker and R. Lasker (1969). Oxygen consumption of

Euphausia pacifica: the lack of diel rhythm or light-dark effect, with a comparsion of experimental techniques. - Limnol. Oceanog. 14: 219-223.

Pearcy, W. G. &. R. M. L. (1966). Vertical migration and distribution of mesopelagic fishes off Oregon. - Deep Sea Res. 13(2): 153-165.

Pedersen, G., K. S. Tande and E. M. Nilssen (1995). Temporal and regional variation in the copepod community in the central Barents Sea during Spring and early Summer, 1988 and 1989. - J. Plank. Res. 17(2): 263-282.

Peterson, R. G. and I. T. Whitworth (1989). The sub-Antarctic and Polar fronts in relation to deep water masses through the south-western Atlantic. - J. Geophys. Res. 94(C4): 10817-10838.

Pickford, G. (1946). *Vampyroteuthis infernalis* Chun, an archaic dibranchiate cephalopod. I. Natural history and distribution. - Dana Report 29: 1-40.

Pierrot-Bults, A. C. (1974). Taxonomy and zoogeography of certain members of the "*Sagitta serrodentata* group" (Chaetognatha). - Bijdragen tot der Diekunde 44(2): 215-234.

Pillar, S. C. (1984a). A comparison of the performance of four zooplankton samplers. - S. Afr. J. mar. Sci. 2: 1-18.

Pillar, S. C. (1984b). Laboratory studies on the larval growth and development of *Euphausia lucens* (Euphausiacea). - S. Afr. J. mar. Sci. 2: 43-48.

Pillar, S. C. (1986). Temporal and spatial variations in copepod and euphausiid biomass off the southern and south-western coasts of South Africa in 1977/78. - S. Afr. J. mar. Sci. 4: 219-229.

Pillar, S. C., D. A. Armstrong and L. Hutchings (1989). Vertical migration, dispersal and transport of *Euphausia lucens* in the southern Benguela Current. - Mar. Ecol. Prog. Ser. 53: 179-190.

Pillar, S. C., M. Barange and L. Hutchings (1991). Influence of the frontal system on the cross shelf distribution of *Euphausia lucens* and *Euphausia recurva* in the southern Benguela system. - S. Afr. J. mar. Sci. 11: 475-481.

Pillar, S. C. and V. Stuart (1988). Population structure, reproductive biology and maintenance of *Euphausia lucens* in the southern Benguela current. - J. Plank. Res. 10(6): 1083-1098.

Piola, A. R. and A. L. Gordon (1989). Intermediate waters in the south-west South Atlantic. - Deep Sea Res. 36(1): 1-16.

Podesta, G. P., O. B. Brown and R. H. Evans (1991). The annual cycle of satellite-derived sea surface temperature in the southwestern Atlantic Ocean. - J. Climate 4(4): 457-467.

Pommeranz, T., C. Herrmann and A. Kuhn (1982). Mouth angles of the RMT1+8 during paying out and hauling. - Ber. dt. wiss. Kommn. Meeresforschung 29: 267-274.

Ponomareva, L. A. (1966). The euphausiids of the North Pacific, their distribution, ecology and mass species. Pages. - Inst. Okeanol. Akad. Sci. U.S.S.R, Moscow, 1963. Israel Program Sci. Transl., 1966.

Poore, M. E. D. (1955). The use of phytosociological methods in ecological investigations I. The Braun-Blanquet system. - J. Ecol 43: 226-244.

Pugh, P. R. (1975). The distribution of siphonophores in a transect across the north Atlantic ocean at 32°N. - J. exp. mar. biol. Ecol. 20: 77-97.

Ramirez, F. C. (1966). Copepodos Calanoidos marinos del area de Mar del Plata con la descipcion de *Pontella marplantensis* n. sp. - Bolletin del Instituto del biologia marina Mar del Plata 11: 1-24.

Ramirez, F. C. (1981). Zooplankton y produccion sedundaria. Parte I. Distribucion y variacion estancional de los copepodos. In: V. Angelescu (ed.). Campanas de investigacion pesquera realizados en el Mar Argentino por los B/I Shinkai Maru y Walter Herwig y el P/P Marburg, anos 1978 y 1979. Resultados de la Part Argentina. - INIDEP, Mar del Plata: 202-212.

Ramirez, F. C. and C. Dato (1983). Seasonal changes in population structure and gonadal development of three euphausiid species. - Oceanol. Acta 6(4): 427-433.

Rao, C. R. (1964). The use and interpretation of principal component analysis in applied research. - Sankhya A 26: 329-358.

Raymont, J. E. G. (1983). Plankton and the productivity of the oceans. - Pergamon Press, Oxford: pp.824.

Redfield, A. C. (1958). In: A. Buzzati-Traverso (ed.). Perspectives in Marine Biology. - Univ. Calif. Press, Berkeley: 17-23.

Reid, J. L., E. Brinton, A. Fleminger, E. L. Venrick and J. McGowan (1978). Ocean circulation and marine life. In: H. Charnock and G. E. R. Deacon (ed.). Advances in oceanography. - Plenum Publishing Corporation, New York: 65-130.

Reid, J. L., J. W. D. Nowlin and W. C. Patzert (1977). On the characteristics and circulation of the southwestern Atlantic Ocean. - J. Phys. Oceanog. 7: 62-91.

Ridoux, V. (1988). Subantarctic krill, *Euphausia vallentini* Stebbing, preyed upon by penguins around Crozet Islands (Southern Indian Ocean): population structure and annual cycle. - J. Plank. Res. 10(4): 675-690.

Rigler, F. H. and J. A. Downing (1984). The calculation of secondary production. In: J. A. Downing and F. H. Rigler (ed.). Secondary productivity in fresh waters 2nd ed. - Blackwell, 19-58.

Riley, G. A. (1947). A theoretical analysis of the zooplankton population on Georges Bank. - J. Mar. Res. 6: 54-73.

Ring-Group (1981). Gulf Stream cold-core rings: Their physics, chemistry and biology. - Science 212: 1092-1100.

Ritz, D. A. and G. W. Hosie (1982). Production of the euphausiid *Nyctiphanes australis* in Storm Bay, south-eastern Tasmania. - Mar. Biol. 68: 103-108.

Roden, G. (1986). Thermohaline fronts and baroclinic flow in the Argentine basin during the austral spring of 19984. - J. Geophys. Res. 91(C4): 5075-5093.

Rodhouse, P. G. (1990). Cephalopod fauna of the Scotia Sea at South Georgia: potential for commercial exploitation and possible consequences. In: K. Kerry and G. Hempel (ed.). Ecological change and the conservation of Antarctic ecosystems. Proc. 5th SCAR Symp. Antarct. Biol. - Springer-Verlag, Berlin: 289-298.

Rodhouse, P. G. and E. M. C. Hatfield (1990). Dynamics of growth and maturation in the cephalopod *Ilex argentinus* (de Catellannos, 1960), (Teuthoidea: Ommastrephidae). - Phil. Trans. R. Soc. Lond. Ser. B. 329: 229-241.

Rodhouse, P. G., C. Symon and E. M. C. Hatfield (1992). Early life cycle of cephalopods in relation to the major oceanographic features of the south-west Atlantic ocean. - Mar. Ecol. Prog. Ser. 89: 183-195.

Roe, H. S. J. (1972). The vertical distribution and diurnal migration of calanoid copepods collected on the SOND Cruise 1965 1. The total population and general discussion. - J. Mar. Biol. Ass. U.K. 52: 277-314.

Roe, H. S. J. (1974). Observations on the diurnal vertical migrations of an oceanic community. - Mar. Biol. 28: 99-113.

Roger, C. (1973). Biological investigations of some important species of Euphausiacea (Crustacea) from the equatorial and south tropical Pacific. In: R. Fraser (ed.). Oceanography of the South Pacific. - New Zealand National Commission for UNESCO, 449-456.

Rohde, K. (1986). Differences in species diversity of Monogenea between the Pacific and the Atlantic Oceans. - Hydrobiologia 137: 21-28.

Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. - OIKOS 65: 514-527.

Rohde, K., M. Heap and D. Heap (1993). Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. - Am. Nat. 142: 1-16.

Roman, M. R., A. L. Gauzens and T. J. Cowles (1985). Temporal and spatial changes in epipelagic microzooplankton and mesozooplankton biomass in a warm-core Gulf

Stream ring 82-B. - Deep Sea Res. 32: 1007-1022.

Ross, R. M. (1981). Laboratory culture and development of *Euphausia pacifica*. - Limnol. Oceanog. 26(2): 235-246.

Ross, R. M. (1982). Energetics of *Euphausia pacifica* I. Effects of body Carbon and Nitrogen and temperature on measured and predicted production. - Mar. Biol. 68: 1-13.

Ross, R. M., K. L. Daly and T. S. English (1982). Reproductive cycle and fecundity of *Euphausia pacifica* in Puget Sound, Washington. - Limnol. Oceanog. 27(2): 304-314.

Ross, R. M. and L. B. Quetin (1983). Spawning frequency and fecundity of the Antarctic krill *Euphausia superba*. - Mar. Biol. 77: 201-205.

Ross, R. M. and L. B. Quetin (1988). *Euphausia superba*: a critical review of estimates of annual production. - Comp. Biochem. Physiol. 90B(3): 499-505.

Russel, F. S. (1935). On the value of certain planktonic animals as indicators of water movements in the English Channel and North Sea. - J. mar. biol. Ass. U.K. 20: 309-332.

Ruud, J. T. (1927). Zooplankton of the coast of More. - Rapp. P. -V. Reun. Cons. Int. Explor. Mer 41: 120-124.

Ruud, J. T. (1928). Fluctuations in the larval stages of Euphausiids off More, 1926-1927. - J. Cons. Int. Explor. Mer 1

Ruud, J. T. (1932). On the biology of southern Euphausiidae. - Hvalrad Skr. 2: 1-105.

Sabates, A., J. H. Gill and F. Pages (1989). Relationship between zooplankton distribution, geographic characteristics and hydrographic patterns off the Catalan coast. - Mar. Biol. 103: 153-159.

Sameoto, D. D. (1976). Respiration rates, energy budgets and molting frequencies of three species of euphausiid found in the Gulf of St. Lawrence. - J. Fish. Res. Bd. Can. 33: 2568-2576.

Saprykina, M. I. and G. M. Mukhina (1987). Morphological and cytological characteristics of *Euphausia superba* oogenesis. In: R. R. Makarov (ed.). Biological and oceanographic investigations of the Pacific sector of Antarctica. - Vsesoiuznogo Nauchno-Issledovatel'skogo Instituta Rybnogo Okeanografi (VNIRO), Moscow, USSR: 135-151.

Saville, A. (1958). Mesh selection in plankton nets. - J. Cons. perm. int. Explor. Mer 23(2): 192-201.

Semenov, V. N. and I. S. Berman (1977). Biogeographic aspects of the distribution and dynamics of water masses off the South American coast. - Oceanol. 17: 1073-1084.

Shannon, C. E. and W. Weaver (1963). The mathematical theory of communication. Pages. - University Illinois Press, Urbana.

Sheard, K. (1953). Taxonomy, distribution and development of the Euphausiacea (Crustacea). - B.A.N.Z.A.R.E. Reports, Series B VIII(1): 1-72.

Sheard, K. (1964). Species groups in the zooplankton of eastern Australian slope waters. - Aust. J. Mar. Fresh. Res. 16(2): 219-254.

Sherman, K., W. G. Smith, J. R. Green, E. Cohen, M. S. Berman, K. A. Marti and J. R. Goulet (1987). Zooplankton production and fisheries of the northeast shelf. In: R. H. Backus (ed.). Georges Bank. - MIT Press, Cambridge, MA: 268-282.

Shih, C.-t. (1969). The systematics and biology of the Family Phronimidae (Crustacea: Amphipoda). - Dana Report 14(74): 1-100.

Siegel, V. (1988). In: D. Sahrhage (ed.). Antarctic ocean and resources variability. - Springer, Berlin: 219-230.

Siegel, V. (1992). Assessment of the krill (*Euphausia superba*) spawning stock off the Antarctic peninsula. - Arch. Fisch. 41(2): 101-130.

Simpson, E. H. (1949). Measurement of diversity. - Nature 163(688):

Small, L. F. and J. F. Hebard (1967). Respiration of a vertically migrating marine crustacean, *Euphausia pacifica*, Hansen. - Limnol. Oceanog. 12: 212-280.

Small, L. F., J. F. Hebard and C. D. McIntire (1966). Respiration in euphausiids. - Nature 211: 1210-1211.

Smiles, M. C. J. and W. G. Pearcy (1971). Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. - Fish. Bull. 69(1): 79-86.

Smith, M. M. and P. C. Heemstra (1986). Smith's Sea Fishes. - Springer-Verlag, Berlin.

Soulier, B. (1965). Essai d'harmonisation de la nomenclature des larves d'euphausiaces. - Rev. Trav. Inst. Peches marit. 29(2): 191-195.

Steedman, H. F. (1976). General and applied data on formaldehyde fixation and preservation of marine organisms. In: H. F. Steedman (ed.). Zooplankton fixation and preservation. - UNESCO, Paris: 103-154.

Steur, A. (1933). Zur planmassigen Erforschung der geographischen Verbreitung des Haliplanktons, besonders der Copepoden. - Zoogeographica 1: 269-302.

Strauss, R. E. (1982). Statistical significance of species clusters in association analysis. - Ecology 63(3): 634-639.

Stuart, V. (1986). Feeding and metabolism of *Euphausia lucens* in the southern Benguela current. - Mar. Ecol. Prog. Ser. 30: 117-125.

Stuart, V. (1992). Fecundity of *Euphausia lucens* (Hansen) - laboratory evidence for multiple broods. - J. Exp. Mar. Biol. Ecol. 160: 221-228.

Stuart, V. and S. C. Pillar (1988). Growth and production of *Euphausia lucens* in the southern Benguela Current. - J. Plank. Res. 10(6): 1099-1112.

Stuart, V. and S. C. Pillar (1990). Diel grazing patterns of all the ontogenetic stages of *Euphausia lucens* and *in situ* predation rates on copepods in the southern Benguela upwelling region. - Mar. Ecol. Prog. Ser. 64: 227-241.

Svedrup, H. U., M. W. Johnson and R. H. Fleming (1942). The Oceans. - Prentice-Hall, New York.

Thiel, M. E. (1938). Die Chaetognathed Bevolkerung des Sudatlantischen Ozeans. - Wiss. Ergbn. Deuthsch. Atl. Exped. "Meteor", 1925-1927. 13(1): 1-110

Thomas, A. C. (1992). Spatial patterns of zooplankton community composition and satellite measured surface temperature. - Cont. Shelf Res. 12(5/6): 753-777.

Thomas, A. C. and W. J. Emery (1988). Relationships between near-surface plankton concentrations and satellite measured sea surface temperature. - J. Geophys. Res. 95(C12): 15,733-15,748.

Thomas, P. and T. Ikeda (1987). Sexual regression, shrinkage, rematuration and growth in spent females *Euphausia superba* in the laboratory. - Mar. Biol. 95: 357-363.

Thompson, K. R. (1992). Quantitative analysis of the use of discards from squid trawler by Black-browed Albatross *Diomedea melanophris* in the vicinity of the Falkland Islands. - IBIS 134: 11-21.

Thurston, M. H. (1976). Vertical distribution and diurnal migration of the Crustacea Amphipoda collected during the SOND cruise, 1965. II. The Hyperiidea and general discussion. - J. Mar. Biol. Ass. U.K. 56: 359-382.

Totton, A. K. and M. E. Bargman (1965). A synopsis of the Siphonophorae: pp1-230.

Tranter, D. J., R. R. Parker and G. R. Cresswell (1980). Are warm-core eddies unproductive? - Nature 284: 540-542.

Tranter, D. J. and P. E. Smith (1966). Filtration performance. In: (ed.). Zooplankton sampling. - 27-57.

Tranter, D. J., D. J. Tafe and R. L. Sandland (1983). Some zooplankton charcteristics of warm-core eddies by the East Australian Current, with particular reference to copepods. - Aust. J. Mar. Freshw. Res. 34: 587-607.

Trathan, P. N., I. Everson, D. G. M. Miller, J. L. Watkins and E. J. Murphy (1995). Krill biomass in the Atlantic. - Nature 373(6511): 201-202.

Tremblay, M. J. and J. C. Roff (1983). Community gradients in the Scotian shelf zooplankton. - Can. J. Fish. Aqu. Sci. 40: 598-611.

Unesco (1966). Zooplankton sampling. Uneso monographs in oceanographic methodology. vol.2. Unesco, Paris.

Uye, S., H. Kuwata and T. Endo (1987). Standing stocks and production rates of phytoplankton and planktonic copepods in the inland Sea of Japan. - J. Oceanog. Soc. Japan 42: 421-434.

Van der Spoel, S. (1994a). History, progress and future of theory in pelagic biogeography. - Prog. Oceanog. 34: 101-107.

Van der Spoel, S. (1994b). The basis for boundaries in pelagic biogeography. - Prog. Oceanog. 34: 121-133.

Van der Spoel, S., A. C. Pierrot-Bults and P. H. Schalk (1990). Probable Mesozoic vicariance in the biiogeography of Euphausiacea. - Bijdragen tot de Dierkunde 60(3/4): 155-162.

Van Guelpen, L., D.F. Markle & D.J. Duggan (1982). An evaluation of accuracy, precision and speed of several zooplankton sub-sampling techniques. - J. Cons. Int. Explor. Mer 40: 226-236.

Vanucci, M. (1966). Loss of organisms through the meshes. In: Zooplankton Sampling. Unesco monographs in oceanographic methodology. 2: 77-86.

Venrick, E. L. (1971). The statistics of sub-sampling. - Geol. Ocean. 16: 811-818.

Vidal, J. (1980a). Physioecology of zooplankton I. Effects of phytoplankton concentration, temperature and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* spp. - Mar. Biol. 56: 111-134.

Vidal, J. (1980b). Physioecology of zooplankton II. Effects of phytoplankton concentration, temperature and body size on the development aand molting rates of *Calanus pacificus* and *Pseudocalanus* spp. - Mar. Biol. 56: 135-146.

Vidal, J. (1980c). Physioecology of zooplankton IV. Effects of phytoplankton concentrations, temperature and body size on the net production efficiency in *Calanus pacificus*. - Mar. Biol. 56: 203-211.

Vidal, J. and S. L. Smith (1986). Biomass, growth and devlopment of populations of herbivorous zooplankton in the south-eastern Bering Sea during spring. - Deep Sea Res. 33: 523-556.

Vinogradov, M. (1982). Hyperiid amphipods.

Walker, H. A., S. B. Saila and E. L. Anderson (1979). Exploring data structure of the New York Bight benthic data using post collection stratification of samples and linear discriminant analysis of species composition comparisons. - Estuar. coast. mar. Sci 9: 101-120.

Weber, L. H. and S. Z. El-Sayed (1985). Spatial variability of phytoplankton and the distribution and abuundance of krill in the Indian sector of the Southern Ocean. In: W. R. Siegfried, P. R. Condy and R. M. Laws (ed.). Antarctic Nutrient Cycles and Food Webs. - Springer-Verlag, Berlin

Whittaker, R. H. (1962). Classification of natural communities. - Botan. Rev. 28: 1-239.

Wiborg, K. F. (1954). Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway. - Fish. Dir. Skr. Ser. HavUndrs. 11: 1-246.

Wiborg, K. F. (1966). Undersokelser av krill (lyskreps) i Hardanger-fjorden og tilstotende omrader. samt pa stasjon M i Norskehavet. - Fisk. Gang. 52: 754-761.

Wiborg, K. F. (1971). Investigations in euphausiids in some fjords on the west coast of Norway in 1966-1977. - Fiskeridr. Skr. Ser. Havunders 16: 10-35.

Wickett, W. B. (1967). Ekman transport and zooplankton concentration in the North Pacific Ocean. - J. Fish. Res. Bd. Can. 24(3): 581-594.

Wiebe, P. H. and S. H. Boyd (1978). Limits of *Nematoscelis megalops* in the north-western Atlantic in relation to Gulf Stream cold core rings. I. Horizontal and vertical distribution. - J. Mar. Res. 36: 119-142.

Wiebe, P. H. and G. R. Flierl (1983). Euphausiid invasion/dispersal in Gulf Stream cold-core rings. - Aust. J. Mar. Fresw. Res 34: 625-652.

Williams, R. and N. Frangopoulou (1985). Vertical distribution and nocturnal migration of *Nyctiphanes couchii* in relation to the summer thermocline in the Celtic Sea. - Mar. Biol. 89: 257-262.

Williams, R. and J. A. Lindley (1982). Variability in abundance, vertical distribution and ontogenetiic migrations of *Thysanoessa longicaudata* (Crustacea:Euphausiacea) in the north-eastern Atlantic Ocean. - Mar. Biol. 69: 321-330.

Williamson, M. H. (1961). An ecological survey of the Scottish herring fishery.Part IV:changes in the plankton during the period 1949 to 1959.Appendix: a method for studying the relations of plankton variations to hydrography. - Bull. Mar. Ecol. 5: 207-209.

Winberg, G. G. (1971). Methods for the estimation of production of aquatic animals. Academic Press, London.

Wishner, K. F. and S. K. Allison (1986). The distribution and abundance of copepods in

relation to the physical structure of the Gulf Stream. - Deep Sea Res. 33(6): 705-731.

Yentsch, C. S. and D. A. Phinney (1985). Rotary motions and convection as a means of regulating primary production in warm core rings. - J. Geophys. Res. 90(C2): 3237-3248.

Young, J. W. (1989). The distribution of hyperiid amphipods (Crustacea:Peracarida) in relation to warm-core eddy J in the Tasman Sea. - J. Plank. Res 11: 711-728.

Zeldis, J. R. (1985). Ecology of *Munida gregaria - distribution and abundance, population dynamics and fisheries*. - Mar. Ecol. Prog. Ser. 22(1): 77-99.

Appendix I

1990 Phase 1

RMT8 (mesh diameter 4.5mm; 0-200 oblique)
Bongo (mesh diameter 335μm; surface tow)

Station 29:	RMT8 - 51°33.5'S 57°47.0'W - 51°34.2'S 57°52.3'W; 7/10/90; 16.56-17.56
(st. code 28)	Bongo - 51°34.1'S 57°48.4'W - 51°34.2'S 57°50.8'W; 7/10/90; 18.43-19.13
Station 30:	RMT8 - 51°59.5'S 58°00.0'W - 51°56.7'S 58°00.5'W; 7/10/90; 22.39-23.39
(st.code 34)	Bongo - 51°56.1'S 58°00.5'W - 51°54.6'S 58°00.7'W; 8/10/90; 00.10-00.40
Station 31:	RMT8 - 51°59.2'S 56°59.0'W - 51°56.7'S 57°00.6'W; 8/10/90; 04.17-05.17
(st.code 35)	Bongo - 51°59.7'S 56°58.1'W - 51°58.5'S 56°58.6'W; 8/10/90; 06.27-06.57
Station 32:	RMT8 - 52°58.5'S 57°02.9'W - 52°56.5'S 57°05.4'W; 8/10/90; 13.50-14.50
(st.code 51)	Bongo - 52°55.4'S 57°05.6'W - 52°55.5'S 57°07.5'W; 8/10/90; 15.27-15.57
Station 33:	RMT8 - 53°00.0'S 58°58.0'W - 53°01.3'S 59°01.5'W; 8/10/90; 22.24-23.24
(st.code 49)	Bongo - 53°00.5'S 59°00.4'W - 53°00.4'S 59°02.4'W; 9/10/90; 00.06-00.36
Station 34:	RMT8 - 53°00.2'S 59°59.6'W - 53°00.2'S 60°02.9'W; 9/10/90; 03.48-04.48
(st.code 48)	Bongo - 53°00.3'S 59°59.3'W - 53°00.3'S 60°01.3'W; 9/10/90; 05.30-06.00
Station 35:	RMT8 - 52°59.5'S 61°59.9'W - 53°00.9'S 62°04.5'W; 10/10/90; 13.05-14.05
(st.code 46)	Bongo - 53°00.1'S 62°00.4'W - 53°00.2'S 62°02.1'W; 10/10/90; 14.50-15.20
Station 36:	RMT8 - 52°00.1'S 62°59.2'W - 51°57.1'S 62°59.5'W; 10/10/90; 21.50-22.50
(st.code 31)	Bongo - 52°00.0'S 62°59.8'W - 51°58.5'S 63°00.9'W; 10/10/90; 23.36-00.06
Station 37:	RMT8 - 52°04.4'S 60°05.2'W - 52°02.9'S 60°08.0'W; 11/10/90; 09.57-10.57
(st.code 33)	Bongo - 52°04.6'S 60°04.7'W - 52°03.9'S 60°06.1'W; 11/10/90; 12.10-12.40
Station 38:	RMT8 - 50°59.6'S 60°00.7'W - 50°58.3'S 60°04.6'W; 21/10/90; 11.14-12.21
(st.code 20)	Bongo - 51°00.0'S 60°00.0'W - 50°59.4'S 60°02.5'W; 12/10/90; 12.59-13.31
Station 39:	RMT8 - 50°00.4'S 59°59.6'W - 50°01.6'S 60°02.5'W; 12/10/90; 19.08-20.08
(st.code 4)	Bongo - 50°00.1'S 59°59.8'W - 50°00.6'S 60°00.9'W; 12/10/90; 20.38-21.08
Station 40:	RMT8 - 51°30.1'S 61°00.2'W - 51°30.3'S 61°03.4'W; 15/10/90; 06.20-07.20
(st.code 27)	Bongo - 51°29.6'S 61°00.9'W - 51°30.0'S 61°02.3'W; 15/10/90; 07.53-08.23
Station 41:	RMT8 - 50°00.1'S 62°00.4'W - 49°57.6'S 62°02.3'W; 5/11/90; 18.48-19.52[1]
(st.code 2)	Bongo - 49°59.8'S 61°59.9'W - 49°58.6'S 62°01.6'W; 5/11/90; 20.30-21.00
Station 42:	RMT8 - 51°00.3'S 62°59'W - 51°02.1'S 63°00.2'W; 6/11/90; 03.48-04.50
(st.code 11)	Bongo - 51°00.1'S 62°59.9'W - 51°01.3'S 63°41.1'W; 6/11/90; 05.25-05.55
Station 43:	RMT8 - 49°59.6'S 57°00.2'W - 49°59.1'S 57°04.0'W; 7/11/90; 04.18-05.27
(st.code 7)	Bongo - 50°00.1'S 57.00.0'W - 50°00.0'W 57°02.4'W; 7/11/90; 06.07-06.37
Station 44:	RMT8 - 51°00.2'S 57°00.1'W - 51°01.0'S 57°03.6'W; 7/11/90; 13.02-14.02
(st.code 23)	Bongo - 51°00.0'S 57°00.2'W - 51°00.2'S 57°02.1'W; 7/11/90; 14.30-15.00

[1] All times are given as local time

1990 Phase 2

RMT8 (mesh diameter 4.5mm; 0-300m oblique)
Bongo (mesh diameter 335μm; surface tow)

Station 1:	RMT8 - 33°00.0'S 46°59.8'W - 34°01.2'S 46°59.7'W; 22/10/90; approx.09.30-11.00
(st.code 106)	Bongo - 33°00.0'S 46°59.8'W - 34°01.2'S 46°59.7'W; 22/10/90; 11.32-12.32
Station 2:	RMT8 - 35°59.6'S 48°00.0'W - 36°01.5'S 48°05.8'W; 22/10/90; 22.25-00.31
(st.code 113)	Bongo - 36°00.0'S 48°00.0'W - 36°00.5'S 48°01.7'W; 23/10/90; 01.26-02.02
Station 3:	RMT8 - 36°00.1'S 48°60.0'W - 36°00.4'S 49°05.4'W; 23/10/90; 06.26-07.55
(st.code 112)	Bongo - 36°00.3'S 48°59.9'W - 36°01.5'S 49°00.8'W; 23/10/90; 08.40-09.10
Station 4:	RMT8 - 37°59.7'S 50°00.0'W - 37°55.1'S 49°59.1'W; 26/10/90; 23.31-01.08
(st.code 120)	Bongo - 38°00.0'S 49°59.6'W - 37°58.4'S 49°59.5'W; 27/10/90; 01.56-02.29
Station 5:	RMT8 - 38°00.6'S 49°00.0'W - 37°57.0'S 49°00.5'W; 27/10/90; 06.50-08.20
(st.code 121)	Bongo - 38°00.0'S 48°59.8'W - 37°58.5'S 48°59.9'W; 27/10/90; 09.01-09.31
Station 6:	RMT8 - 39°60.0'S 52°00.6'W - 40°02.7'S 52°05.1'W; 28/10/90; 01.34-03.09
(st.code 127)	Bongo - 40°00.0'S 52°00.0'W - 40°01.5'S 52°00.7'W; 28/10/90; 03.53-04.28
Station 7:	RMT8 - 40°00.6'S 53°00.4'W - 40°05.6'S 53°00.7'W; 28/10/90; 08.43-10.13
(st.code 126)	Bongo - 40°00.1'S 52.59.8'W - 40°02.2'S 52°59.4'W; 28/10/90; 11.24-11.54
Station 8:	RMT8 - 42°00.2'S 54°00.3'W - 42°00.2'S 54°06.3'W; 28-29/10/90; 22.40-00.43
(st.code 133)	Bongo - 42°00.4'S 53°59.0'W - 42°00.0'S 54°01.8'W; 29/10/90; 01.27-02.03
Station 9:	RMT8 - 41°60.0'S 55°00.3'W - 41°56.0'S 54°59.5'W; 29/10/90; 06.01-07.40
(st.code 132)	Bongo - 41°59.9'S 54°59.7'W - 41°58.7'S 54°59.6'W; 29/10/90; 08.26-08.56
Station 10:	RMT8 - 42°00.1'S 56°00.1'W - 41°59.9'S 55°55.8'W; 29/10/90; 12.44-14.14
(st.code 131)	Bongo - 41°59.9'S 55°59.9'W - 41°59.8'S 55°58.1'W; 29/10/90; 16.15-16.45
Station 11:	RMT8 - 42°00.2'S 57°00.3'W - 41°59.6'S 56°55.7'W; 29/10/90; 21.10-22.44
(st.code 130)	Bongo - 42°00.4'S 57°00.0'W - 41°60.0'S 56°57.8'W; 29/10/90; 23.30-00.00
Station 12:	RMT8 - 44°00.2'S 54°59.4'W - 43°55.5'S 54°59.1'W; 30/10/90; 12.07-13.37
(st.code 139)	Bongo - 44°00.2'S 55°00.6'W - 43°59.5'S 55°00.4'W; 30/10/90; 14.26-14.56
Station 13:	RMT8 - 44°00.1'S 56°00.0'W - 43°59.3'S 55°57.4'W; 30/10/90; 19.00-20.40
(st.code 138)	Bongo - 43°59.9'S 56°00.2'W - 43°59.5'S 55°59.1'W; 30/10/90; 21.10-21.40
Station 14:	RMT8 - 44°00.7'S 57°00.4'W - 43°57.0'S 56°57.4'W; 31/10/90; 01.47-03.30
(st.code 137)	Bongo - 43°60.0'S 59°59.9'W - 43°58.9'S 56°59.0'W; 31/10/90; 04.22-04.52
Station 15:	RMT8 - 44°00.0'S 58°00.2'W - 43°56.8'S 57°57.8'W; 31/10/90; 08.51-10.21
(st.code 136)	Bongo - 44°00.0'W 58°00.3'W - 43°58.9'W 57°59.3'W; 31/10/90; 11.05-11.35
Station 16:	RMT8 - 43°59.6'S 59°00.3'W - 43°54.0'S 58°57.4'W; 31/10/90; 16.00-17.30
(st.code 135)	Bongo - 44°00.1'S 59°00.4'W - 43°59.6'S 59°02.5'W; 31/10/90; 18.42-19.12
Station 17:	RMT8 - 46°00.0'S 59°00.2'W - 45°59.1'S 59°06.1'W; 1/11/90; 06.50-08.30
(st.code 142)	Bongo - 46°00.2'S 59°00.2'W - 46°00.0'S 59°01.9'W; 1/11/90; 09.20-09.50
Station 18:	RMT8 - 46°00.2'S 57°59.6'W - 46°00.1'S 57°54.2'W; 1/11/90; 13.57-15.27
(st.code 143)	Bongo - 46°00.0'S 58°00.0'W - 46°00.3'S 57°57.5'W; 1/11/90; 16.13-16.43

Station 19:	RMT8 - 45°59.8'S	56°59.7'W - 46°02.0'S 57°04.1'W; 1/11/90; 20.19-21.50
(st.code 144)	Bongo - 46°00.2'S	56°59.9'W - 46°01.4'S 57°02.0'W; 1/11/90; 22.40-23.10
Station 20:	RMT8 - 45°59.6'S	56°00.0'W - 45°57.3'S 56°03.1'W; 2/11/90; 03.25-05.03
(st.code 145)	Bongo - 46°00.2'S	56°00.3'W - 45°59.3'S 56°01.0'W; 2/11/90; 05.50-06.20
Station 21:	RMT8 - 45°59.7'S	54°59.4'W - 45°56.7'S 55°00.5'W; 2/11/90; 10.07-11.37
(st.code 146)	Bongo - 45°59.9'S	54°59.9'W - 45°58.5'S 54°59.4'W; 2/11/90; 12.14-12.44
Station 22:	RMT8 - 48°00.5'S	54°00.1'W - 48°02.7'S 54°01.7'W; 3/11/90; 23.23-00.58
(st.code 155)	Bongo - 48°00.3'S	54°00.4'W - 48°01.1'S 54°01.1'W; 3/11/90; 01.50-02.20
Station 23:	RMT8 - 47°59.9'S	55°00.3'W - 47°58.8'S 55°03.9'W; 3/11/90; 06.40-08.10
(st.code 154)	Bongo - 47°59.9'S	55°00.1'W - 47°59.4'S 55°01.4'W; 3/11/90; 08.47-09.17
Station 24:	RMT8 - 47°59.9'S	56°00.9'W - 47°57.0'S 56°04.8'W; 3/11/90; 13.27-14.57
(st.code 153)	Bongo - 47°59.8'S	55°59.9'W - 47°58.9'S 56°01.6'W; 3/11/90; 15.46-16.16
Station 25:	RMT8 - 48°00.1'S	57°00.7'W - 48°03.0'S 57°04.4'W; 3/11/90; 19.40-21.20
(st.code 152)	Bongo - 48°00.1'S	57°00.0'W - 48°01.4'S 57°00.0'W; 3/11/90; 22.15-22.45
Station 26:	RMT8 - 48°00.1'S	58°00.5'W - 48°03.2'S 58°01.8'W; 4/11/90; 02.21-03.55
(st.code 151)	Bongo - 48°00.1'S	58°00.0'W - 48°00.7'S 58°00.8'W; 4/11/90; 04.43-05.13
Station 27:	RMT8 - 48°00.7'S	58°59.7'W - 48°03.7'S 59°00.0'W; 4/11/90; 20.00-21.30
(st.code 150)	Bongo - 48°00.0'S	58°59.8'S - 48°01.5'S 59°00.0'W; 4/11/90; 22.25-22.55
Station 28:	RMT8 - 48°00.9'S	60°01.1'W - 48°04.1'S 59°59.9'W; 5/11/90; 03.10-04.43
(st.code 149)	Bongo - 48°00.0'S	59°59.7'W - 48°01.3'W 59°59.6'W; 5/11/90; 05.35-06.05

1991

Bongo (mesh diameter - 500μm; 0-50m oblique)

Station 1: 33°59.9'S 48°29.7'W - 33°58.6'S 48°28.1'W; 5/11/91; 05.30-06.04

Station 2: 33°59.8'S 47°29.8'W - 34°00.0'S 47°28.1'W; 5/11/91; 10.38-11.10

Station 3: 33°59.9'S 46°30.2'W - 33°59.0'S 46°28.0'W; 5/11/91; 16.05-16.30

Station 4: 35°00.4'S 49°19.1'W - 35°00.0'S 49°16.4'W; 6/11/91; 09.05-09.35

Station 5: 34°59.7'S 48°20.1'W - 34°58.4'S 49°19.3'W; 6/11/91; 03.32-04.10

Station 6: 35°00.0'S 47°19.5'W - 34°59.7'S 47°17.9'W; 5/11/91; 22.44-23.14

Station 7: 35°59.8'S 49°55.8'W - 35°58.9'S 49°55.1'W; 6/11/91; 15.17-15.47

Station 8: 36°00.0'S 48°56.3'W - 35°59.4'S 48°55.2'W; 6/11/91; 20.06-20.36

Station 9: 36°00.1'S 47°55.6'W - 35°58.9'S 47°54.9'W; 7/11/91; 01.20-01.50

Station 10: 36°59.9'S 50°50.0'W - 36°58.7'S 50°49.7'W; 7/11/91; 16.37-17.07

Station 11: 36°59.9'S 49°50.1'W - 36°59.5'S 49°48.9'W; 7/11/91; 12.02-12.33

Station 12: 36°59.5'S 48°50.2'W - 36°58.4'S 48°49.7'W; 7/11/91; 07.45-08.17

Station 13: 37°59.9'S 51°59.5'W - 38°00.3'S 51°57.8'W; 8/11/91; 00.34-01.07

Station 14: 38°00.0'S 50°59.2'W - 38°01.3'S 50°58.8'W; 9/11/91; 17.29-17.59

Station 15: 38°00.1'S 49°59.0'W - 38°01.4'S 49°57.4'W; 9/11/91; 11.20-11.50

Station 16: 39°00.4'S 52°49.8'W - 39°02.1'S 52°49.4'W; 9/11/91; 13.56-14.26

Station 17: 38°59.8'S 51°49.2'W - 39°00.2'S 51°49.5'W; 9/11/91; 08.44-09.16

Station 18: 38°59.7'S 50°49.7'W - 39°00.2'S 50°50.0'W; 9/11/91; 02.49-03.19

Station 19: 39°59.5'S 53°45.1'W - 40°01.1'S 53°44.2'W; 9/11/91; 20.45-21.15

Station 20: 40°00.3'S 52°45.4'W - 39°59.9'S 52°43.4'W; 10/11/91; 00.47-01.27

Station 21: 40°00.4'S 51°46.1'W - 40°01.4'S 51°47.3'W; 10/11/91; 05.12-05.37

Station 22: 41°00.0'S 54°57.0'W - 41°01.2'S 54°57.1'W; 10/11/91; 20.49-21.20

Station 23: 41°00.5'S 53°59.9'W - 41°02.3'S 53°59.3'W; 10/11/91; 16.22-16.52

Station 24: 41°00.1'S 52°57.4'W - 41°00.3'S 52°59.0'W; 10/11/91; 12.24-12.53

Station 25: 42°00.1'S 57°24.8'W - 42°00.7'S 57°24.7'W; 11/11/91; 17.17-17.46

Station 26: 42°00.1'S 56°25.0'W - 42°01.3'S 56°24.9'W; 11/11/91; 12.30-13.01

Station 27: 42°00.4'S 55°24.8'W - 42°01.7'S 55°24.6'W; 12/11/91; 01.07-01.36

Station 28: 42°59.7'S 58°33.3'W - 42°58.2'S 58°32.8'W; 12/11/91; 16.40-17.10

Station 29: 43°00.2'S 57°33.2'W - 43°00.9'S 57°33.8'W; 12/11/91; 12.25-12.55

Station 30: 43°00.3'S 56°33.2'W - 43°02.2'S 56°33.5'W; 12/11/91; 08.12-08.43

Station 31: 44°00.0'S 59°04.9'W - 43°58.3'S 59°03.5'W; 12/11/91; 23.15-23.45

Station 32: 44°00.0'S 58°04.9'W - 43°58.5'S 58°05.1'W; 13/11/91; 03.27-04.00

Station 33: 44°00.0'S 57°05.2'W - 43°59.0'S 57°05.4'W; 13/11/91; 07.32-08.05

Station 34: 44°59.2'S 59°47.4'W - 44°56.9'S 59.46.7'W; 13/11/91; 22.10-22.40

Station 35: 44°59.9'S 58°53.9'W - 44°58.1'S 58°54.0'W; 13/11/91; 17.53-18.23

Station 36: 45°00.1'S 57°54.3'W - 44°59.0'S 57°54.5'W; 13/11/91; 13.38-14.09

Station 37: 45°59.9'S 60°30.1'W - 45°58.7'S 60°30.8'W; 14/11/91; 05.13-05.42

Station 38: 45°59.4'S 59°29.8'W - 45°57.6'S 59°29.8'W; 14/11/91; 09.23-09.52

Station 39: 45°59.2'S 58°30.6'W - 45°58.1'S 58°31.8'W; 14/11/91; 13.25-13.55

Appendix IIa
RMT8 1990

Species	tot.rel.abund. no.ind./sample	occurrence freq. no.occ./sample	station code no.ind./sample	106	113	112	120	121	127	126	133	132	131	130	139	138	137	136	135	142	143	144	145	146	155	154
			station no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
		displ.vol. ml/m3		0.0027	0.0112	0.0051	0.0125	0.0062	0.0138	0.0027	0.0138	0.0054	0.0077	0.0124	0.0023	0.0073	0.0115	0.0101	0.0117	0.0040	0.0058	0.0102	0.0139	0.0033	0.0073	0.0099
Scypholanceola spp.	1.3	2.0	0.0	0.7	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cystisoma cf. magna	2.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.7
Vibilia spp.	37.3	10.0	1.3	0.0	0.0	5.3	4.0	0.0	14.7	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Hyperoche medusarem	3.3	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemityphis tenuimanus	37.3	8.0	12.0	1.3	7.3	9.3	3.3	0.0	1.3	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cranocephalus scleroticus	1.3	1.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Cyllopus magellanicus	19.3	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eupronoe minuta	5.3	2.0	0.7	0.0	0.0	0.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0
Brachyscelus crusculum	32.0	3.0	4.0	2.7	0.0	25.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sympronoe spp.	0.7	1.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhabdosoma spp.	2.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scina spp.	14.7	3.0	0.0	6.7	0.0	5.3	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phrosina semilunata	16.0	5.0	2.0	1.3	2.7	9.3	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paraphronima gracilis	8.7	1.0	5.3	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Platyscelus serratulus	3.3	3.0	0.0	1.3	0.0	1.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Platyscelus armatus	15.3	7.0	6.7	0.0	4.0	0.7	2.0	0.7	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxycephalus clausi	2.0	1.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxycephalus cf.piscator	8.7	3.0	0.7	2.7	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Streetsia challengeri	16.0	5.0	6.0	4.0	2.0	2.7	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Streetsia cf.piscator	5.3	1.0	0.0	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calamorhyncus pellucidus	1.3	2.0	0.7	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paraphronima gracilis	4.7	3.0	0.7	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Themisto gaudichaudii	12260.7	40.0	0.0	0.0	0.0	8.0	110.7	104.0	128.7	56.0	853.3	81.3	20.0	29.3	269.3	76.0	44.7	87.3	124.0	242.7	312.0	225.3	24.7	74.7	185.3
Primno macropa	386.0	33.0	0.7	1.3	0.0	0.0	4.0	2.7	5.3	0.0	12.0	11.3	4.0	0.7	2.7	10.0	58.0	28.0	9.3	85.3	13.3	1.3	1.3	8.0	18.7
Phrosina semilunata	72.7	17.0	7.3	6.0	22.7	10.7	0.0	0.0	7.3	1.3	1.3	1.3	4.0	0.0	0.0	2.0	2.0	0.0	2.7	0.0	0.0	0.0	0.7	0.0	0.0
Phronima cf.bucephala	16.7	3.0	4.7	0.0	4.0	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematoscelis megalops	4500.3	30.0	2.7	74.7	4.7	58.7	130.7	104.0	54.7	384.0	2.7	5.3	42.7	15.3	810.7	32.0	0.0	0.0	4.0	4.0	125.3	2197.3	24.0	117.3	0.0
Nematoscelis tenella	32.0	1.0	0.0	0.0	0.0	32.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematoscelis atlantica	14.0	3.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	10.7	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematoscelis microps	282.0	8.0	0.0	0.0	0.0	128.0	32.0	56.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thysanopoda monocantha	52.0	4.0	22.7	22.7	1.3	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	42.7	0.0	0.0	21.3	0.0
Nematobranchion boopis	2.0	1.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematobranchion sexspinosum	2.7	1.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematobranchion flexipes	54.0	4.0	2.7	8.0	38.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphausia longirostris	408.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. gibboides	1.3	1.0	0.0	0.0	0.0	0.0	0.0	18.7	0.0	42.7	9.3	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	74.7	0.0	0.0
E. spinifera	89.3	7.0	1.3	12.0	2.0	58.7	0.0	0.0	9.3	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0
E. recurva	308.7	6.0	46.7	224.0	2.7	26.7	0.0	2.7	0.0	0.0	0.0	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0
E. gibba	12.0	3.0	0.0	2.7	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. similis	1422.7	20.0	0.0	0.0	0.0	16.0	16.0	56.0	0.0	309.3	37.3	0.0	0.0	1.3	117.3	26.7	1.3	42.7	0.0	14.7	29.3	0.0	37.3	176.0	5.3
E. similis (armata)	19.3	3.0	0.0	0.0	0.7	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.0	0.0
E. vallentini	59598.0	36.0	0.0	0.0	0.0	0.0	50.7	29.3	1.3	704.0	14.7	21.3	917.3	8.7	320.0	37.3	28.0	50.0	22.7	6.7	258.7	0.0	10.7	10.7	186.7
E. lucens	19912.3	36.0	5.3	0.0	3.3	21.3	8.0	98.7	33.3	586.7	8.0	242.7	96.0	8.0	53.3	224.0	52.0	234.7	10.7	5.3	32.0	0.0	52.0	176.0	0.0
E. triacantha	1491.3	20.0	0.0	0.0	0.0	5.3	10.7	2.7	0.0	0.0	13.3	42.7	85.3	2.0	0.0	288.0	13.3	21.3	60.0	153.3	10.7	0.0	8.7	0.0	490.7
Stylocheiron abbreviatum	118.7	7.0	21.3	26.7	20.0	10.7	0.0	0.0	0.0	0.0	0.0	0.0	32.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0
Stylocheiron maximum	1177.3	30.0	6.7	1.3	8.7	13.3	18.7	90.7	17.3	64.0	25.3	37.3	42.7	7.3	64.0	0.0	42.7	48.3	50.7	33.3	50.7	0.0	58.7	53.3	21.3
Thysanoessa gregaria	9230.3	35.0	21.3	74.7	1.3	133.3	53.3	240.0	0.0	309.3	8.0	442.7	42.7	32.0	32.0	837.3	24.0	3.3	5.3	12.0	122.7	0.0	9.3	58.7	90.7
Salpa thompsoni (aggregate)	1608.3	22.0	0.0	0.0	0.0	0.0	0.0	5.3	2.7	24.0	20.7	30.7	40.0	0.0	0.0	0.7	0.0	35.3	1.3	12.0	74.7	24.0	0.0	0.0	212.0
Salpa thompsoni (solitary)	98.3	15.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.7	0.0	5.3	0.0	0.7	0.0	0.0	2.0	1.3	0.0	0.0	0.7	0.0	0.0	9.3
Salpa maxima	2.0	2.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ihlea magahlanica	5.0	2.0	2.3	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Iasis zonaria	72.7	7.0	0.0	40.0	10.7	5.3	0.0	0.0	0.0	3.3	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tethys vagina	0.7	1.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	1.3	0.0	0.0	0.0
Acanthaphyra spp.	8.7	3.0	0.0	2.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Systellapsis dibilis	11.3	4.0	0.0	7.3	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0
Funcalia spp.	2.0	1.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.3	0.0	0.0	0.0
Chelophyes appendiculata	4542.0	16.0	5.3	1205.3	858.7	650.0	26.7	181.3	5.3	426.7	186.7	64.0	0.0	112.0	149.3	0.0	0.0	0.0	0.0	0.0	80.0	213.3	116.0	261.3	0.0
Hippopodus hippopus	277.3	9.0	0.0	37.3	48.0	58.7	10.7	42.7	61.3	10.7	0.0	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0
Ceratocymba sagittata	56.0	4.0	0.0	16.0	26.7	10.7	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Abylopsis tetragamna	309.3	5.0	0.0	90.7	64.0	141.3	2.7	0.0	10.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rosacea plicata	265.3	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lensia cf.	72.0	1.0	0.0	0.0	0.0	0.0	72.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	85.3	1.3	21.3	0.0	0.0	0.0	0.0
Eudoxoides spiralis	29.0	3.0	0.0	0.0	0.0	0.0	13.3	10.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vogtia spinosa	2.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diphyes antarctica	2.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Physophora/Pyrostephos cf.	23.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Stegacephalidae	128.7	11.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0	4.0	0.0	0.0	10.7	0.0	18.7	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lysianissadae	22.0	7.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	1.3	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	25.3	0.0	0.0	8.7	0.0
Gammarid (misc.)	112.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0	0.0	4.0	0.0
Munida gregaria	190.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sergestes henseni	156.0	8.0	0.0	116.7	0.0	5.3	0.0	0.7	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. diapontis	32.7	7.0	0.0	12.7	1.3	2.7	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	2.7	19.3	0.0	5.3	0.0
S. arcticus	130.0	11.0	0.0	4.0	0.0	16.7	0.0	68.7	0.0	11.3	0.0	0.0	6.0	0.0	5.3	2.0	0.0	0.0	0.0	0.0	0.7	9.3	0.0	3.3	0.0
S. cf. guineensis	8.7	3.0	0.0	2.7	0.0	2.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	3.3	0.0
S. splendens	0.7	1.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. prehensilis	38.7	3.0	0.0	25.3	0.0	12.7	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gennadus gilchristi	44.0	6.0	0.0	1.3	0.0	10.0	0.0	10.0	0.0	8.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
G. tinayrei	25.3	8.0	0.0	3.3	0.0	8.0	0.0	4.7	0.0	0.0	0.0	0.0	0.7	0.0	1.3	1.3	0.0	0.0	0.0	0.0	3.3	0.0	0.0	4.7	0.0

Species	tot.rel.abund. no.ind./sample	occurrence freq. no.occ./sample	station no. 1 no.ind./sample	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Sagitta gazellae	37644.7	43.0	34.7	8.0	104.0	138.7	2304.0	1578.7	192.0	853.3	725.3	1301.3	810.7	1141.3	800.0	1173.3	2965.3	924.7	1568.0	874.7	1813.3	938.7	896.0	1450.7	1354.7
Eukrohnia hamata	384.0	11.0	0.0	0.0	0.0	0.0	192.0	42.7	0.0	10.7	5.3	21.3	10.7	42.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.7	32.0	0.0
Sagitta bipunctata	29.3	3.0	0.0	0.0	0.0	0.0	0.0	21.3	2.7	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagitta hexaptera	360.0	9.0	24.0	26.7	69.3	74.7	64.0	21.3	5.3	0.0	0.0	0.0	0.0	64.0	10.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagitta planctonis	809.3	11.0	0.0	26.7	85.3	176.0	170.7	42.7	56.0	32.0	0.0	0.0	0.0	80.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.3	74.7	64.0	0.0
Pterosagitta draco	1.3	1.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sio nordenskjoldii	15.3	7.0	0.0	8.0	0.0	1.3	0.0	1.3	0.0	2.7	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scopelosaurus spp.	19.3	5.0	0.0	12.7	0.7	4.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.7	0.0
Scopelosaurus meadi	5.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scopelosaurus ahlstromi	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0	0.0	0.0
Bathylagus spp.	11.3	6.0	0.0	3.3	0.0	1.3	0.0	0.0	0.0	2.0	0.0	0.0	2.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
Diplopluus taenia	0.7	1.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Melanonus gracilis	6.0	3.0	0.0	2.7	0.0	0.0	0.0	2.7	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corcorella atlantica	0.7	1.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lyconodes	0.7	1.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
anguilliform larvae	4.0	2.0	0.0	0.7	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Argyropelecus aculeatus	24.7	8.0	0.0	4.0	6.0	10.7	0.7	1.3	0.0	0.7	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Argyropelecus hemigymnus	44.0	15.0	0.0	6.0	1.3	10.7	0.7	0.7	0.7	6.0	0.0	0.0	0.0	0.7	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Valiencienellus tripunctulatus	11.3	6.0	0.0	0.0	4.7	3.3	0.0	0.7	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	5.3	2.7	4.0	0.0
Trachopteridae	0.7	1.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Pseudoichthys spp.	0.7	1.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paralepididae	0.7	1.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vinciguerria poweriae	15.3	6.0	0.0	4.0	0.0	4.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	2.0	0.0
Pollinichthys spp.	0.7	1.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melanostomias niger	0.7	1.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gnathopus spp.	0.7	1.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ariosoma mellissi	0.7	1.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Symblophorus boops	3.3	3.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bathophilus nigerrimus	1.3	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
Nansenia	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
Congridae	1.3	1.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Avocettina paucipira	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Derichthys cf. serpentinus	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stomias boa boa	2.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Photoichthydae	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0
Gempylidae	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Argentinidae	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Idiacanthus atlanticus	2.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Howella sherboni	9.3	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Gymnoscopelus braueri	119.3	12.0	0.0	2.7	0.0	0.7	0.0	6.0	0.0	0.0	0.0	0.0	18.7	1.3	7.3	38.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0
Gymnoscopelus bolini	44.3	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.0	2.7	0.0	0.7	0.0
Gymnoscopelus larvae	223.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.0	0.7	1.3	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Gymnoscopelus (n) cf. fraseri	14.3	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gymnoscopelus (Nasolynchus)	2.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	4.0	0.0
Gymnoscopelus spp.	6.7	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lobiancha spp.	1.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Diogenichthys atlanticus	1.3	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hygophum hygomii	16.0	4.0	0.0	9.3	0.0	0.0	0.0	2.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Hygophum reinhradtii	7.3	3.0	0.0	3.3	0.0	1.3	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0
Lepidophanes guentheri	126.0	7.0	0.0	27.3	0.0	4.7	0.0	0.0	0.0	38.7	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	3.3	45.3	0.0	5.3	0.0
Centroscopelus warmingli	18.0	6.0	0.0	6.0	0.0	0.7	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampandena notialis	2.7	2.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	6.7	0.0	2.0	0.0
Scopelopsis multipunctatus	1.3	1.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bollinichthys longipes	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampanyctus pulsilus	36.0	6.0	0.0	16.7	0.0	8.7	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Lampanyctus cf. alatus	2.7	3.0	0.0	1.3	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	2.0	0.0
Lampanyctus australis	13.3	5.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0
Lampanyctus lepidolynchus	6.0	3.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	4.0	0.0
Lampanyctus spp.	3.3	4.0	0.0	1.3	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.0
Lampanyctus Intricans	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.0	0.0
Diaphus moltis	4.7	1.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
Dipahus lucidus	6.7	2.0	0.0	6.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphus effulgens	1.3	1.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphus taaningi	1.3	2.0	0.0	0.7	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphus hudsoni	41.3	5.0	0.0	0.0	0.0	4.0	0.0	2.7	0.0	24.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	6.7	0.0	0.0	0.0
Diaphus cf. meadi	39.3	4.0	0.0	13.3	0.0	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.0	0.0	3.3	0.0
Diaphus subtilis	2.7	2.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0
Bollinichthys longipes	10.0	2.0	0.0	9.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Lampichthys procens	9.3	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	7.3	0.0	0.0	0.0
Protomyctophum andriashevi	14.7	6.0	0.0	0.0	0.0	0.0	0.0	8.7	0.0	2.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Protomyctophum bolini	186.7	18.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.0	2.0	9.3	16.0	0.0	6.7	29.3	12.7	16.7	0.0	19.3	15.3	4.7	0.7	4.0	0.0
Protomyctophum tenisoni	19.3	7.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0	0.0	2.7	0.0	0.7	0.0	0.0	2.0	0.0	0.0	0.0	0.0
Protomyctophum spp.	2.7	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.7	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0
Mauralian mueller	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Electrona antarctica	5.3	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Electrona cf.	3.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0
Metaelectrona ventralis	1.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kreffichthys spp.	84.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	70.0	7.3	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0

Station no.	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
displ.vol. ml/m3	0.0057	0.0085	0.0085	0.0049	0.0055	0.002742	0.001261	0.003071	0.003592	0.004113	0.002468	0.00181	0.020731	0.009872	0.013711	0.00713	0.006252	0.016041	0.012614	0.009735	0.016179
Station code	153	152	151	150	149	28	34	35	51	49	48	46	31	33	20	4	27	2	11	7	23
Species																					
Scypholanceola spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cystisoma cf. magna	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vibilia spp.	6.7	0.0	0.0	0.7	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hyperoche medusarem	1.3	0.7	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemityphis tenuimanus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cranocephalus scleroticus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyllopus magellanicus	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eupronoe minuta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brachyscelus crusculum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sympronoe spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhabdosoma spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scina spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phrosina semilunata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paraphronima gracilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Platyscelus serratulus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Platyscelus armatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxycephalus clausi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxycephalus cf.piscator	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Streetsia challengeri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Streetsia cf.piscator	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calamorhyncus pellucidus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paraphronima gracilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Themisto gaudichaudii	44.7	47.3	93.3	50.7	5.3	462.0	22.0	2.0	16.0	148.0	109.0	310.0	968.0	0.0	2160.0	424.0	1800.0	168.0	2320.0	26.0	26.0
Primno macropa	6.7	7.3	5.3	4.0	0.7	0.0	0.0	0.0	10.0	1.0	4.0	12.0	1.0	0.0	0.0	4.0	0.0	20.0	32.0	0.0	0.0
Phrosina semilunata	0.0	0.7	1.3	0.0	0.7	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phronima cf.bucephala	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematoscelis megalops	0.0	0.0	2.7	53.3	10.7	2.0	0.0	148.0	8.0	56.0	16.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematoscelis tenella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	1.0	
Nematoscelis atlantica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematoscelis microps	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thysanopoda monocantha	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematobranchion boopis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematobranchion sexspinosum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematobranchion flexipes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphausia longirostris	10.7	112.0	64.0	74.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. gibboides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. spinifera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. recurva	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. gibba	0.0	0.0	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. similis	21.3	154.7	66.7	266.7	26.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. similis (armata)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. vallentini	576.0	42.7	88.0	85.3	709.3	122.0	16.0	176.0	604.0	776.0	1120.0	944.0	17152.0	0.0	4.0	616.0	176.0	8320.0	7168.0	1072.0	17152.0
E. lucens	32.0	0.0	32.0	0.0	0.0	66.0	3360.0	340.0	36.0	456.0	992.0	144.0	3200.0	0.0	4.0	472.0	0.0	704.0	4283.0	128.0	3712.0
E. triacantha	106.7	58.7	72.0	42.7	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stylocheiron abbreviatum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stylocheiron maximum	64.0	90.7	45.3	90.7	37.3	0.0	0.0	0.0	0.0	8.0	0.0	8.0	0.0	0.0	4.0	72.0	0.0	0.0	0.0	0.0	0.0
Thysanoessa gregaria	448.0	112.0	133.3	26.7	69.3	0.0	0.0	0.0	0.0	304.0	994.0	128.0	2176.0	0.0	5.0	400.0	0.0	64.0	1600.0	216.0	0.0
Salpa thompsoni (aggregate)	7.3	45.3	394.7	12.7	18.0	0.0	0.0	216.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	202.0	228.0
Salpa thompsoni (solitary)	10.7	1.3	8.0	0.7	1.3	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	54.0	0.0
Salpa maxima	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ihlea magahlanica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Iasis zonaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tethys vagina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acanthaphyra spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Systellapsis dibilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Funcaiia spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chelophyes appendiculata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hippopodus hippopus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceratocymba sagittata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Abylopsis tetragamna	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rosacea plicata	77.3	20.7	18.7	26.7	4.0	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lensia cf.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eudoxoides spiralis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vogtia spinosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diphyes antarctica	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Physophora/Pyrostephos cf.	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	3.0	1.0	14.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stegacephalidae	0.0	2.0	2.0	1.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lysianissadae	0.0	2.7	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gammarid (misc.)	0.0	0.0	0.0	0.0	0.0	0.0	8.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	1.0	0.0	0.0	3.0	97.0	0.0	0.0
Munida gregaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	167.0	9.0	0.0	9.0	0.0	0.0	0.0	0.0
Sergestes henseni	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. diapontis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. arcticus	0.0	0.0	6.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. cf. guineensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. splendens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. prehensilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gennadus gilchristi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
G. tinayrei	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Station no. Species	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Sagitta gazellae	442.7	60.0	661.3	1344.0	261.3	58.0	11.0	412.0	532.0	59.0	448.0	112.0	240.0	0.0	2896.0	2176.0	688.0	52.0	1472.0	296.0	1472.0
Eukrohnia hamata	10.7	0.0	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagitta bipunctata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagitta hexaptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagitta planctonis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pterosagitta draco	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sio nordenskjoldii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scopelosaurus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scopelosaurus meadi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scopelosaurus ahlstromi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bathylagus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diplophus taenia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melanonus gracilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corcorella atlantica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lyconodes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
anguilliform larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Argyropelecus aculeatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Argyropelecus hemigymnus	0.0	0.7	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Valiencienellus tripunctulatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trachopteridae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudoichthys spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paralepididae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vinciguerria poweriae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pollinichthys spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melanostomias niger	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gnathopus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ariosoma mellissi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Symblophorus boops	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bathophilus nigerrimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nansenia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Congridae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Avocettina paucipira	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Derichthys cf. serpentinus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stomias boa boa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Photoichthydae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gempylidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Argentinidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Idiacanthus atlanticus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Howella sherboni	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gymnoscopelus braueri	0.0	2.0	27.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gymnoscopelus bollini	0.0	2.7	4.7	0.0	24.0	0.0	0.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gymnoscopelus larvae	0.0	0.0	0.0	0.0	0.0	146.0	0.0	4.0	0.0	41.0	16.0	0.0	16.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gymnoscopelus (n) cf. fraseri	0.0	0.0	0.0	7.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gymnoscopelus (Nasolynchus) sp	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Gymnoscopelus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lobiancha spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diogenichthys atlanticus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hygophum hygomii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hygophum reinhradtii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepidophanes guentheri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Centroscopelus warmingii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampandena notialis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scopelopsis multipunctatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bollinichthys longipes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampanyctus pulsillus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampanyctus cf. alatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampanyctus australis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampanyctus lepidolynchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampanyctus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampanyctus intricans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphus mollis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dipahus lucidus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphus effulgens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphus taaningi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphus hudsoni	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphus cf. meadi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphus subtilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bollinichthys longipes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lampichthys procera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Protomyctophum andriashevi	0.0	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Protomyctophum bolini	12.0	2.0	6.0	2.0	22.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Protomyctophum tenisoni	0.0	2.0	4.7	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Protomyctophum spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mauralian mueller	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Electrona antarctica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Electrona cf.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metaelectrona ventralis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kreffichthys spp.	0.0	0.7	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix IIb	Station No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Bongo 1990	Displac.vol. ml/m3	0.00191	0.683644	0.036283	0.221516	1.859971	5.152159	0.343732	1.021647	0.441123	0.269257	0.183324	0.366647	0.261618	0.45258	0.074475	0.175685	0.267347	0.525146	1.995554	0.429665	0.204329	0.223426	0.381924	1.584986
	Station code	106	113	112	120	121	127	126	133	132	131	130	139	138	137	136	135	142	143	144	145	146	155	154	153
Species																									
Euphausia vallentini(adult)	no.ind/sample	0	0	0	0	0	0	0	0	0	64	19	0	6	96	1	0	0	0	4	0	0	1	0	0
E.vallentini(calyptopes I)		0	0	0	0	0	0	0	1792	0	0	0	0	0	0	512	0	0	0	0	0	0	0	0	0
E vallentini(c II)		0	0	0	0	0	0	0	3200	0	0	0	0	0	0	832	4480	0	0	0	0	0	0	64	0
E.vallentini(c III)		0	0	0	0	0	0	256	1280	0	0	0	0	768	0	576	3456	0	0	0	0	0	256	128	0
E.vallentini(furcilia I)		0	0	0	0	0	0	512	0	0	0	0	0	0	0	384	5760	0	0	0	0	0	64	32	64
E.vallentini(f II)		0	0	0	0	0	0	128	0	0	0	0	0	0	0	320	5248	0	0	0	0	0	0	96	0
E.vallentini(f III)		0	0	0	0	0	0	0	0	0	128	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.vallentini(f IV)		0	0	0	0	0	0	0	0	0	256	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.vallentini(f V)		0	0	0	0	0	0	0	0	0	256	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.vallentini(f VI)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.vallentini(post-larvae)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(adult)		0	224	0	64	176	3392	0	672	0	64	18	64	136	1184	15	21	0	4	80	29.84	16	20	0	0
E.lucens(c I)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(c II)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(c III)		0	0	0	512	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(f I)		0	0	0	0	0	0	128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(f II)		0	0	0	0	0	0	1792	0	0	0	0	16	0	0	128	0	0	0	0	0	0	0	0	0
E.lucens(f III)		0	0	0	0	0	0	1664	32	0	0	0	48	96	0	0	0	0	0	256	0	0	0	0	0
E.lucens(f IV)		0	0	0	0	0	0	6272	0	0	0	0	16	0	0	128	0	0	0	1280	0	0	0	0	0
E.lucens(f V)		0	0	0	0	0	0	8832	0	0	0	0	0	0	0	0	0	0	0	0	37.29	0	0	0	0
E.lucens(f VI)		0	0	0	0	0	0	7424	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(post-larvae)		0	0	0	1792	0	12032	1536	1536	0	0	0	16	680	464	0	0	0	4	4172	193.95	0	0	0	0
Thysanoessa gregaria(adult)		4	1344	3216	896	368	0	3072	256	256	3520	11	0	0	0	81	9	1	92	12	2563	0	1349	118	348
T.gregaria(c I)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(c II)		0	0	0	0	0	0	128	128	0	0	0	0	512	64	0	0	0	0	0	0	0	0	0	0
T.gregaria(c III)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	256	0	0	0	0	0	576	0	0
T.gregaria(f I)		0	0	0	2560	0	0	0	640	192	1536	0	208	3072	832	832	256	2240	0	0	208	112	0	288	1920
T.gregaria(f II)		0	0	0	512	0	0	0	128	96	6912	448	416	512	2368	640	640	1472	0	2312	16	64	0	64	0
T.gregaria(f III)		0	0	0	1536	0	0	0	256	85.32	1536	0	32	1792	512	128	0	0	0	0	0	64	0	0	0
T.gregaria(post-larvae)		428	0	0	4608	0	0	896	128	74.66	0	0	0	640	0	192	0	0	0	1792	0	0	0	0	0
Nematoscelis megalops(adult)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
N.megalops(c II)		0	0	0	4864	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2112	0	0
N.megalops(c III)		0	0	0	2816	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N.megalops(f I)		0	0	0	0	0	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	512	0	0
N.megalops(f III)		0	0	0	0	0	320	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stylocheiron maximum		0	0	0	0	0	0	166	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nematoscilis atlantica		0	0	0	0	0	3044	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia spinifera		0	6308	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0
E.spinifera(calyptopes)		0	0	0	256	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.spinifera(f I)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.spinifera(f II)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	0	0	0	0
E.spinifera(f III)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	512	0	0	0	0	0
Euphausia similis(adult)		0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	256	0	0	0	0	0
E.similis(c III)		0	0	0	0	0	0	0	0	0	0	64	0	0	0	0	0	0	0	0	0	0	0	0	0
E.similis(f II)		0	0	0	0	0	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0
E.similis(f III)		0	0	0	0	0	0	0	0	0	0	96	0	0	0	0	0	0	0	0	0	0	0	0	0
E.similis(post-larvae)		0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0
Euphausia longirostris(adult)		0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.longirostris(f VII)		0	0	0	256	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.longirostris(post-larvae)		0	0	0	256	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia triacantha(c II)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.triacantha(c III)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.triacantha(f I)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.triacantha(f II)		0	0	0	0	0	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia recurva		0	2816	0	1472	0	16	0	32	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Stylocheiron spp.		0	64	0	2560	0	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Euphausia gibba		0	0	0	0	0	0	0	192	0	0	0	0	37	0	0	0	0	0	0	0	0	0	0	0
Euphausia tenera		0	0	0	0	0	0	0	512	0	0	0	0	0	0	15	0	0	0	6220	276	16	2	0	0
Euphausia sibogae		0	0	0	0	0	0	0	0	0	0	0	0	72	0	0	0	0	0	0	0	0	0	0	0
Thysanopoda spp.		8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species \ Station No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Cyllopus magellanicus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hyperietta spp.	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anchylomera blossevillei	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperiella spp.	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vibilia spp.	0	192	6	206	0	0	0	0	0	0	13	0	0	48	0	0	0	0	0	0	0	0	0	0
Calamorhyncus pellucidus	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Scina spp.	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phronomella elongata	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phronima sedentaria	0	92	33	128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycaeopsis spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperoche medusarem	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phrosina semilunata	0	52	77	320	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenoscina spp.	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platyscelus spp.	0	0	4	644	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemityphis tenuimanus	0	0	118	704	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxycephalus spp.	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphityrus spp.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paralycaea	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperionyx spp.	0	0	5	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primno macropa(adult)	1	0	30	0	48	0	16	0	171	0	384	32	0	0	3	2	16	12	0	32	2	0	12	8
Primno macropa(juvenile)	0	0	0	0	0	0	0	0	160	0	0	0	0	0	384	0	0	8	0	0	384	192	0	0
Themisto gaudichaudii(adult)	7	104	8	128	128	64	3200	32	1525	52	2	0	39	32	16	18	1424	8	48	368	0	0	628	144
Themsito gaudichaudii(juvenile)	0	0	0	0	0	0	0	0	1216	0	269	176	0	336	576	256	0	156	0	0	656	0	0	704
Eupronoe minuta	85	40	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta gazellae	0	4	0	0	0	0	0	288	75	132	22244	992	72	1200	18	248	832	76	68	180	56	400	680	576
S.tasmanica	0	0	0	0	736	304	336	1472	6144	0	608	2048	1348	16	13	128	304	20	1536	112	280	80	0	0
S.planctonis	0	0	0	0	0	0	144	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S.lyra	0	0	0	0	0	0	0	0	0	0	32	0	0	0	0	0	16	48	0	0	0	0	0	0
S.bipunctata	124	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	64	0	0
Eukrohnia hamata	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	136	0	0	0	2448	120	296
Sagitta hexaptera	0	44	0	260	384	206	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S.serrodentata	0	56	98	1600	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chelophyes appendiculata	5	96	0	42	0	0	16	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0
Ceratocymba sagitatta	1	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
Eudoxoides spiralis	0	100	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abylopsis tetragona	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	64	0	0
Pyrostephos cf.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalia longicauda	0	5280	0	820	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ihlea maghalanica	0	0	0	18	0	0	112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salpa aspera	0	0	0	4	0	0	0	0	0	0	0	0	0	16	3	0	0	0	0	0	0	0	0	0
Salpa thompsoni(aggregate)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salpa thompsoni(solitary)	0	0	0	0	0	0	0	0	0	0	0	49	83	0	0	0	0	0	0	0	0	0	0	53
Sergestiid larvae	103	4	29	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	4
Acanthaphyra larvae	0	15	0	0	0	0	0	0	0	0	4	0	0	0	5	0	0	0	0	0	0	0	0	64
Decapod larvae	0	32	0	48	0	0	128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Munida gregaria(larvae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	192	0	0
Miscellaneous fish larvae	3	11	38	990	18	0	0	0	0	528	0	386	0	32	16	0	90	272	12	0	32	0	232	32
Myctophiid larvae	0	4	0	3	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Station No.	25	26	277	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Displac.vol ml/m3	0.429665	0.129854	0.20242	0.129854	1.657551	0.343732	0.028644	0.003819	0.024825	0.00993	0.003246	0.15277	0.080204	0.036283	0.190962	0.011458	0.110758	0.021006	0.076385	0.026735

Station code	152	151	150	149	28	34	35	51	49	48	46	31	33	20	4	27	2	11	7	23
Species																				
Euphausia vallentini(adult)	36	0	20	21	2	0	8	0	2	11	0	168	0	1	59	12	300	0	100	0
E.vallentini(calyptopes I)	0	0	0	96	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1408	0
E.vallentini(c II)	0	0	3840	96	0	0	0	0	0	0	0	0	0	16	0	0	20	0	3040	0
E.vallentini(c III)	0	0	1920	0	0	0	0	0	0	0	0	0	0	4	0	0	52	0	1536	0
E.vallentini(furcilia I)	0	0	1280	352	0	0	0	0	0	0	0	0	0	0	0	0	36	0	0	0
E.vallentini(f II)	256	0	512	160	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0
E.vallentini(f III)	0	0	0	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.vallentini(f IV)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.vallentini(f V)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.vallentini(f VI)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.vallentini(post-larvae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(adult)	75	0	3	10	8	5216	2	0	117	33	0	592	23	6	84	88	360	0	160	0
E.lucens(c I)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(c II)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(c III)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(f I)	768	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(f II)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(f III)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(f IV)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(f V)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(f VI)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(post-larvae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thysanoessa gregaria(adult)	777	40	20	41	0	96	0	3	5	0	10	32	0	26	28	28	124	30	264	0
T.gregaria(c I)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(c II)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(c III)	0	0	0	224	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(f I)	320	0	2176	512	0	0	0	0	0	0	0	0	0	0	0	0	0	0	96	0
T.gregaria(f II)	192	0	128	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(f III)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(post-larvae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nematoscelis megalops(adult)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N.megalops(c II)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N.megalops(c III)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N.megalops(f I)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N.megalops(f III)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stylocheiron maximum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nematoscis atlantica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia spinifera	19	0	55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.spinifera(calyptopes)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.spinifera(f I)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.spinifera(f II)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.spinifera(f III)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia similis(adult)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.similis(c III)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.similis(f II)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.similis(f III)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.similis(post-larvae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia longirostris(adult)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.longirostris(f VII)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.longirostris(post-larvae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia triacantha(c II)	256	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.triacantha(c III)	320	0	128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.triacantha(f I)	1792	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.triacantha(f II)	64	0	384	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia recurva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stylocheiron spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia gibba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia tenera	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia sibogae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thysanopoda spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Station No. Species	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Cyllopus magellanicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperietta spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anchylomera blossevillei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperiella spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vibilia spp.	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calamorhyncus pellucidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scina spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phronomella elongata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phronima sedentaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycaeopsis spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperoche medusarem	79	5	130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phrosina semilunata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenoscina spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platyscelus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemityphis tenuimanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxycephalus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphityrus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paralycaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperionyx spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primno macropa(adult)	0	2	256	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primno macropa(juvenile)	0	0	0	0	0	0	0	0	0	0	4	0	0	17	0	5	0	2	0	0
Themisto gaudichaudii(adult)	113	69	1776	134	99	168	1	3	3	7	5	196	5	5	6	15	148	157	12	0
Themsito gaudichaudii(juvenile)	192	0	0	0	0	0	0	0	0	0	412	12	80	576	0	585	1192	35	20	12
Eupronoe minuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta gazellae	1568	1345	1216	144	188	40	163	121	44	2	44	0	5	156	100	10	4	3	72	16
S.tasmanica	0	0	0	8	818	176	5	0	404	4	13	156	7	63	21	6	22	32	52	88
S.planctonis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S.lyra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S.bipunctata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Eukrohnia hamata	0	2240	3136	456	2	0	1	17	0	0	0	0	15	6	0	20	0	0	0	4
Sagitta hexaptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S.serrodentata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chelophyes appendiculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratocymba sagitatta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eudoxoides spiralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abylopsis tetragona	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Pyrostephos cf.	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalia longicauda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Ihlea maghalanica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salpa aspera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salpa thompsoni(aggregate)	1	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salpa thompsoni(solitary)	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sergestiid larvae	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthaphyra larvae	1	0	0	0	608	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Decapod larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Munida gregaria(larvae)	0	0	75900	0	96	0	0	0	0	0	0	0	1760	222	0	0	188	0	0	0
Miscellaneous fish larvae	288	23	192	34	12	16	0	0	0	0	0	2	1	0	0	0	0	0	41	0
Myctophiid larvae	0	0	0	0	0	0	0	1	5	0	0	0	0	0	0	0	0	1	0	0

Appendix IIIa	Station no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Bongo 1990 (restricted data)	displac. vol.(ml/mm3)	0.00191	0.683644	0.036283	0.221516	1.859971	5.152159	0.343732	1.021647	0.441123	0.269257	0.183324	0.366647	0.261618	0.45258	0.074475	0.175685
	Station code	106	113	112	120	121	127	126	133	132	131	130	139	138	137	136	135
Species																	
E.vallentini(total calyptopes)	LN(1+no.ind./sample)	0	0	0	0	0	0	5.549076	8.74401	0	4.174387	2.995732	0	6.652863	4.574711	7.561122	8.979291
E.vallentini(total furcilia)		0	0	0	0	0	0	6.463029	0	0	6.463029	0	0	0	0	6.558198	9.306468
E.lucens(total calyptopes)		0	0	0	6.240276	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(post-larvae)		0	0	0	7.491645	0	9.395408	7.337588	7.337588	0	0	0	2.833213	6.523562	6.142037	0	0
Thysanoessa gregaria(adult)		1.609438	7.204149	8.076205	6.799056	5.910797	0	8.03041	5.549076	5.549076	8.1665	2.484907	0	0	0	4.406719	2.302585
T.gregaria(total calyptopes)		0	0	0	0	0	0	4.859812	4.859812	0	0	0	0	6.240276	4.174387	0	5.549076
T.gregaria(fucilia I)		0	0	0	7.848153	0	0	0	12.70331	9.437077	13.80062	6.033086	9.917045	12.89022	11.58485	11.58485	5.549076
T.gregaria(f II)		0	0	0	6.240276	0	0	0	4.859812	4.574711	8.841159	6.107023	6.033086	6.240276	7.770223	6.463029	6.463029
T.gregaria(f III)		0	0	0	19.281	0	0	4.859812	11.32284	9.058603	13.29018	3.496508	7.809947	6.799056	19.16183	8.348775	0
T.gregaria(post-larvae)		6.061457	0	0	8.435766	0	0	6.799056	4.859812	4.32625	0	0	0	6.463029	0	5.26269	0
Euphausia recurva		0	7.943428	0	7.295056	0	2.833213	0	3.496508	0	0	0	0	1.386294	0	0	0
Stylocheiron spp.		0	4.174387	0	7.848153	0	4.174387	0	0	0	0	0	0	0	0	0	0
Phronima sedentaria		0	4.532599	3.526361	4.859812	0	0	0	0	0	0	0	0	0	0	0	0
Phrosina semilunata		0	3.970292	4.356709	5.771441	0	0	0	0	0	0	0	0	0	0	0	0
Themisto gaudichaudii		2.079442	4.65396	2.197225	4.859812	4.859812	4.174387	8.071219	3.496508	7.330405	3.970292	1.098612	0	3.688879	3.496508	2.833213	2.944439
Sagitta gazellae		0	1.609438	0	0	0	0	0	5.666427	4.330733	4.890349	10.00987	6.900731	4.290459	7.09091	2.944439	5.517453
Sagitta tasmanica		0	0	0	0	6.602588	5.720312	5.820083	7.295056	8.723394	0	6.411818	7.625107	7.207119	2.833213	2.639057	4.859812
Sagitta hexaptera		0	3.806662	0	5.56452	5.953243	5.332719	2.833213	0	0	0	0	0	0	0	0	0
Sagitta serrodentata		0	4.043051	4.59512	7.378384	0	0	0	0	0	0	0	0	0	0	0	0

		Station no.	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
		displac. vol.(ml/mm3)	0.267347	0.525146	1.995554	0.429665	0.204329	0.223426	0.381924	1.584986	0.429665	0.129854	0.20242	0.129854	1.657551	0.343732	0.028644
		Station code	142	143	144	145	146	155	154	153	152	151	150	149	4	2	7
Species																	
E.vallentini(total calyptopes)	LN(1+no.ind./sample)		0	0	1.609438	0	0	5.55296	5.26269	0	3.610918	0	8.662332	5.365976	4.094345	5.921578	8.713582
E.vallentini(total furcilia)			0	0	0	0	0	4.174387	4.859812	4.174387	5.549076	0	7.491645	6.357842	0	3.89182	0
E.lucens(total calyptopes)			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(post-larvae)			0	1.609438	8.33639	5.272743	0	0	0	0	0	0	0	0	0	0	0
Thysanoessa gregaria(adult)			0.693147	4.532599	2.564949	7.849324	0	7.20786	4.779123	5.855072	6.656727	3.713572	3.044522	3.73767	3.367296	4.828314	5.57973
T.gregaria(total calyptopes)			0	0	0	0	0	6.357842	0	0	0	0	0	5.4161	0	0	4.574711
T.gregaria(fucilia I)			14.58265	0	0	5.342334	11.11258	6.932448	11.69951	15.08732	11.03413	0	16.00371	13.07438	0	0	0
T.gregaria(f II)			7.295056	0	7.746301	2.833213	4.174387	0	4.174387	0	5.26269	0	4.859812	4.174387	0	0	0
T.gregaria(f III)			0	0	6.932448	0	3.496508	0	0	0	0	0	0	0	0	0	0
T.gregaria(post-larvae)			0	0	7.491645	0	0	0	0	0	0	0	0	0	0	0	0
Euphausia recurva			0	0	0	0	0	1.098612	0	0	0	0	0	0	0	0	0
Stylocheiron spp.			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phronima sedentaria			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phrosina semilunata			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Themisto gaudichaudii			7.261927	2.197225	3.89182	5.910797	0	0	6.444131	4.976734	4.736198	4.248495	7.482682	4.905275	1.94591	5.003946	2.564949
Sagitta gazellae			6.725034	4.343805	4.234107	5.198497	4.043051	5.993961	6.523562	6.357842	7.358194	7.204893	7.104144	4.976734	4.615121	1.609438	4.290459
Sagitta tasmanica			5.720312	3.044522	7.337588	4.727388	5.638355	4.394449	0	0	0	0	0	2.197225	3.091042	3.135494	3.970292
Sagitta hexaptera			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta serrodentata			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix IIIb
Bongo 1991

Species	Station no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	displac.vol(ml/m3)	0.03972	0.007638	0.003055	0.366647	0.137493	0.096245	0.007638	0.270402	0.116105	0.064163	0.426228	0.045831	0.226099	0.122216	1.836292	0.071802	1.370344	0.786764	0.218461	1.243545
	LN(1+no.ind/sample)																				
T.gregaria(adult)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(calyptopes)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(furcilia I)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(furcilia II)		2.639057	0	2.639057	4.369448	2.484907	1.386294	5.105945	0	3.713572	2.397895	0	3.713572	2.833213	0	6.385194	5.509388	5.4161	6.411818	0.693147	5.888878
T.gregaria(furcilia III)		0.693147	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(post-larvae)		4.394449	1.609438	1.94591	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(post-larvae)		0	0	0.693147	0	0	0	0	0	5.866468	0	7.560601	0	0	0	0	0	0	0	6.932448	0
E.vallentini(furcilia)		4.174387	1.94591	1.386294	0	4.394449	4.859812	3.367296	0	5.4161	6.816736	6.932448	0	0	8.27614	6.240276	4.488636	6.602588	8.636397	0	7.943428
E.vallentini(calyptopes)		4.234107	1.609438	1.386294	0	5.303305	7.728856	4.65396	7.896925	4.859812	4.859812	0	5.288267	0	8.565793	6.916715	0	6.834109	7.491645	0	7.943428
Stylocheiron spp.		0	0	0	6.948897	3.89182	0	0	4.859812	0	0	7.987864	0	7.057037	0	6.645091	0	6.645091	8.253488	0	8.110427
Euphausia recurva(adult)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10.55584	0
Euphausia recurva(larvae)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.625107	0
Sagitta serrodentata		3.367296	2.639057	2.772589	0.693147	2.564949	4.26268	0	0	4.890349	0	0	0	3.806662	0	0	0	0	0	0	0
Sagitta tasmanica		3.73767	1.94591	1.94591	2.833213	5.749393	4.430817	3.970292	4.867534	7.084226	0	0	3.465736	6.124683	0	0	2.197225	0	0	0	0
Sagitta gazellae		2.197225	0	0	0	3.89182	6.511745	0	0	6.558198	0	0	0	8.702344	0	0	0	0	0	0	6.240276
Sagitta hexaptera		4.394449	0	0	2.833213	2.890372	4.442651	0	6.932448	4.574711	0	0	0	0	0	0	0	0	0	0	0
Phronima sedentaria		0	0	0	0	4.394449	3.988984	6.25575	0	5.081404	5.484797	6.263398	3.218876	7.25347	6.224558	4.859812	5.303305	6.602588	4.174387	2.197225	0
Phrosina semilunata		6.175867	1.609438	1.609438	6.042633	3.295837	2.944439	0	5.549076	0	3.73767	4.174387	2.197225	4.532599	5.081404	5.081404	4.919981	0	5.081404	3.89182	2.197225
Themisto gaudichaudii		4.574711	2.944439	2.944439	2.302585	1.791759	4.430817	1.609438	5.616771	7.848153	3.713572	1.609438	0.693147	5.609472	4.394449	0	3.713572	3.89182	0	0	0

	Station no.	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
	displac.vol(ml/m3)	0.018332	0.274985	0.771487	0.210822	0.412478	0.649271	0.511779	0.213878	0.190962	0.297901	0.129854	0.186379	1.102997	0.339149	1.495616	0.534694	0.224571	0.293318	0.659965
Species	LN(1+no.ind/sample)																			
T.gregaria(adult)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(calyptopes)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(furcilia I)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(furcilia II)		2.944439	2.833213	2.639057	1.791759	4.110874	5.003946	0	2.197225	3.89182	2.70805	2.564949	1.386294	6.013715	2.833213	5.720312	2.397895	0	1.609438	5.129899
T.gregaria(furcilia III)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T.gregaria(post-larvae)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.lucens(post-larvae)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E.vallentini(furcilia)		3.433987	0	4.983607	8.254269	7.155396	6.558198	7.316548	8.435766	7.640604	1.098612	6.932448	8.577912	6.463029	8.723394	5.97381	6.411818	9.41646	7.568896	9.182866
E.vallentini(calyptopes)		2.484907	4.859812	1.609438	0	5.843544	5.937536	6.300786	3.496508	6.803505	2.397895	0	5.26269	6.175867	0	5.129899	5.568345	0	3.610918	8.844625
Stylocheiron spp.		0	7.050123	5.572154	8.031385	6.529419	3.367296	6.240276	5.910797	0	5.129899	0	4.174387	6.033086	0	3.218876	0	4.394449	2.197225	0
Euphausia recurva(adult)		0	0	0	0	8.091627	0	5.26269	10.42825	5.771441	2.639057	9.11482	7.770223	0	10.94787	5.796058	5.924256	10.84437	8.292298	8.110427
Euphausia recurva(larvae)		0	0	0	0	0	0	6.240276	7.629004	0	0	8.515792	6.107023	0	9.99957	0	0	9.901936	4.859812	0
Sagitta serrodentata		0.693147	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta tasmanica		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta gazellae		3.555348	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta hexaptera		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phronima sedentaria		0	0	0	1.098612	2.197225	2.995732	6.124683	2.833213	3.218876	0	0	1.609438	0	2.890372	0	0	3.806662	0	0
Phrosina semilunata		0	4.442651	2.197225	4.59512	6.781058	8.076205	5.693732	5.820083	5.283204	3.044522	5.433722	5.484797	5.820083	2.995732	4.488636	6.240276	5.666427	4.828314	6.033086
Themisto gaudichaudii		3.433987	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix IVa

Extraction of temperature values from temperature/depth plots given in Montu (1977)

Profile values at 0, 25, 50, 75 and 100m were taken. Where the profiles ended at depths shallower than 100m (eg 25m or 50m), values below the last measured depth were marked as missing.

Although the sampling grid of each of the 4 surveys was very similar, the match between stations was not exact and there were cases where stations in one season did not have equivalents in other seasons. To overcome this problem, the Spring survey was arbitrarily chosen as the model sampling grid and stations in other seasons were matched to the nearest station in the Spring season. In situations where a station in one season had no match to an equivalent Spring station (eg. where there were 2 stations in Spring but 3 in the other season) the station in that season was not included in the multivariate analysis.

Appendix IVb

Defining statistical characters of temperature factor 1 and 2 from the analysis of temperature data from Montu (1977)

1, Average temperature difference - A Mann-Whitney rank sum test was used to compare the mean temperature (averaged over depth and season) of factor 1 and factor 2 stations. A significant difference was found ($P < 0.001$). The mean temperature of each factor region averaged over depth and season was:

factor 1 = 8.915°C (st.dev. 1.600°C)
factor 2 = 7.522°C (st.dev. 0.555°C)

2, Average depth difference - A test to determine whether there was a significant depth difference between factor 1 and factor 2 stations was carried out. This was to assess whether the average temperatures were biased by the greater inclusion of bottom (75m and 100m) readings with colder temperatures in one factor group compared to the other. The analysis compared the fraction of readings taken to the maximum amount expected (ie. the maximum number of readings for a station would be 4 seasons x 5 depths, but this would be less if temperatures at bottom depths were not read because the waters were too shallow).

Using a Mann-Whitney rank sum test, it was found that there was a significant difference ($P < 0.001$), with factor 1 stations having a median of 16/20 stations and factor 2 stations having a median of 20/20 stations. Cold 75m and 100m temperatures are therefore less common among the factor 1 stations. Therefore, the warmer mean temperatures of factor 1 stations are, to certain extent, an artifact of shallower sampling depths.

3, To overcome the above problem, it was necessary to cover each depth and each season separately. The mean and standard deviation of temperature with depth in each season is given in Table IV(i). A t-test or Mann-Whitney rank sum test was carried out, depending on whether the data had a normal distribution, in order to test for significant differences between factor 1 and 2 at each depth and season. The majority were significantly different at the $P = 0.05$ level. The following were not significant:

Spring 100m	P=0.068
Summer 0m	P=0.762
Summer 25m	P=0.116
Summer 100m	P=0.953
Autumn 75m	P=0.063
Autumn 100m	P=0.754
Winter 100m	P=0.362

It can be seen that in Spring, Autumn and Winter, it was the upper levels that show significant differences in temperature between the factor regions. Noticeably, the difference between the surface temperatures in Summer were not significant. The bottom layer in all seasons does not differ significantly between seasons.

4, From the data presented in Table IV(i), it is evident there was a thermocline. This was especially seen in Summer where the mean surface temperatures were approximately 6°-7°C higher than the temperature at 100m . A further test was therefore carried out to determine whether the strength of the thermocline differed between factor regions. The thermocline was measured by taking the bottom most temperature from the surface temperature. A Mann-Whitney test was used on values obtained for each season. No significant differences were found between the strength of the thermoclines in factor 1 and 2 in Autumn (P=0.620) and Winter (P=0.703). As shown in Table IV(i), the thermocline was quite weak in Winter, although there was an average difference of approximately 6°C between top and bottom temperatures in Autumn. Significant differences were found between factors in Spring (P=0.024) and Summer (P=0.008). The thermocline was stronger in the factor 2 stations (mean 6.474°C, st.dev. 1.318°C) compared to factor 1 stations (mean 4.929°C, st.dev. 2.510°C). In Spring, factor 1 had the strongest thermocline, although the thermoclines in both regions were relatively small, 0.5°C on average.

Appendix IVc

Sort methods used in the analysis of adults from the *Discovery/William Scoresby* samples

(i) Adult sort methods - Adults and post-larvae were caught in both the Nansen 70 and Nansen 100 nets. Because of their different mesh and mouth diameter sizes, the size selectivities of the nets were likely to be different. To consider just one mesh size would ignore the potentially different size/maturity frequencies caught by the other net and neither could justifiably be considered to obtain a more representative sample of the adult population. It was therefore decided to analyse an equal amount of N70 and N100 samples wherever possible.

The target number of adults of each species to be sorted from a sample was set at 50, and the target number of samples to be processed for each season/temperature factor was 4 (to be balanced between N70 and N100 nets). If the number of adults in a sample did not reach 50, further samples were considered. If there were less than 4 samples, it was aimed to obtain a total of 200 individuals in equal proportion from the number of samples that were available. Samples with survey dates closest to those of Montu (1977) were given priority and samples with dates further away from this target were only processed when no other, more suitable, samples were present.

Separated individuals were subsequently sexed and staged according to the scale given by Makarov and Denys (1980) with slight modofications as explained in Section

Season/Depth	factor 1 mean (°C)	factor 1 st.dev. (°C)	factor 1 no. stations missing	factor 2 mean (°C)	factor 2 st.dev. (°C)	factor 2 no. stations missing
Spring 0m	6.915	1.062	0	6.325	0.531	0
Spring 25m	6.813	1.083	0	6.175	0.471	0
Spring 50m	6.804	1.105	4	5.999	0.454	0
Spring 75m	6.376	0.892	14	5.838	0.456	1
Spring 100m	5.898	0.432	23	5.597	0.411	6
Summer 0m	13.138	2.458	0	13.016	1.213	0
Summer 25m	12.134	2.508	0	11.189	1.633	0
Summer 50m	8.569	1.856	3	7.405	1.339	0
Summer 75m	7.578	1.483	9	6.585	0.591	2
Summer100m	6.250	0.941	26	6.270	0.677	7
Autumn 0m	12.420	2.404	0	9.606	0.843	0
Autumn 25m	12.192	2.459	0	9.395	0.879	0
Autumn 50m	10.439	1.825	3	8.750	0.725	0
Autumn 75m	8.305	1.696	9	7.405	0.918	0
Autumn 100m	6.776	1.145	24	6.656	0.779	8
Winter 0m	7.525	1.641	0	6.451	0.694	0
Winter 25m	7.500	1.644	0	6.467	0.727	0
Winter 50m	7.641	1.549	3	6.451	0.707	0
Winter 75m	7.446	1.495	12	6.435	0.690	0
Winter 100m	6.583	1.192	23	6.257	0.578	5

Table IV(i): Mean and standard deviations of seasonal temperature with depth in the factor 1 and factor 2 regions

8.2.3. One problem with all proposed euphausiid developmental schemes is that none put forward a method for separating large post-larvae from small immature adult specimens. The defining characteristics for separating *Euphausia vallentini* and *E.lucens* adults from their respective post-larvae are completely contradictory in Lebour (1926), Dilwyn-John (1936) and Bary (1956). The transition between post-larvae and adult was therefore marked on the basis of size at points that were reasonably midway between the smallest post-larvae and medium sized immature adults. For *E.vallentini*, the division between post-larvae and adult was made at 13mm, in *E.lucens*, at 10mm and in *T.gregaria*, at 8mm. In *E.vallentini* and *E.lucens* the range in post-larval size was considerable compared to the larval stages. A target number of 50 specimens from each season/temperature factor was therefore obtained to assess the size frequency distribution of the post-larval population.

The length of every individual identified was measured from rostrum tip to telson tip with SIGMASCAN electronic digitising apparatus fitted to a Wild 308700 microscope. The apparatus had a measured accuracy of +/-0.05mm.

Dry weight analysis was carried out for each species using Female C/D, 10 male with spermatophores and 10 immature specimens of known length. Each specimen was rinsed in distilled water and placed on an aluminium foil disk of known weight. The disk was carefully folded to enclose the specimen. All specimens were then placed in a fan assisted oven at 70°C for 36 hours before being reweighed. All weights were measured on a Mettler MT5 electronic balance.