THE ROLE OF THE EUTHECOSOME PTEROPOD, *LIMACINA RETROVERSA*, IN THE POLAR FRONTAL ZONE, SOUTHERN OCEAN

Thesis submitted in fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

at

RHODES UNIVERSITY

by

KIM SARAH BERNARD

November 2006

ABSTRACT

The aim of the present study was to assess the ecological role of the euthecosome pteropod, *Limacina retroversa*, in particular, and the mesozooplankton community, in general, in the pelagic ecosystem of the Polar Frontal Zone (PFZ), Southern Ocean. Data were collected from four oceanographic surveys to the Indian sector of the PFZ during austral autumn 2000, 2002, 2004 and 2005.

Copepods, mainly *Calanus simillimus*, *Oithona similis*, *Clausocalanus* spp. and *Ctenocalanus* spp., typically dominated total mesozooplankton counts, accounting for, on average, between 75.5 % and 88.1 % (Mean = 77.4 %; SD = 13.4 %) of the total, during the present investigation. Results of the study indicate that *L. retroversa* may, at times, contribute substantially to total mesozooplankton abundances. During the study, *L. retroversa* contributed between 0.0 and 30.0 % (Mean = 5.3 %; SD = 7.1 %) to total mesozooplankton numbers. Significant small-scale variability in abundance and size structure of *L. retroversa* and abundance of copepods was minimal. Inter-annual variability, on the other hand, was significant between some years. Total pteropod numbers were greatest during April 2002 and 2004, while copepods exhibited greatest abundances during April 2004 only. Pearson's Correlation analysis suggested that *L. retroversa* abundances were positively correlated to total surface chlorophyll-*a* (chl-*a*) concentrations. The significantly lower chl-*a* concentrations recorded during April 2005 may explain the reduced pteropod numbers observed during that survey.

The size class structure of *L. retroversa* comprised mainly small and medium-sized individuals during all four surveys. This corresponds well with records from the northern hemisphere (sub-Arctic and Arctic waters) where *Limacina* spp. are reported to exhibit maximum spawning during mid to late-summer. Higher abundances of large individuals only occurred during April 2005, when chl-*a* concentrations were very low; possibly the result of delayed spawning, due to reduced food availability.

Ingestion rates of the four most abundant copepods, determined using the gut fluorescence technique, ranged between 159.32 ng (pigm) ind^{-1} day^{-1} and 728.36 ng (pigm) ind^{-1} day^{-1} (Mean = 321.01 ng (pigm) ind^{-1} day^{-1}; SD = 173.91 ng (pigm) ind^{-1}

day^{-1}). Ingestion rates of *L. retroversa* were much higher, ranging from an average of 4 28.68 ng (pigm) ind^{-1} day^{-1} in April 2002 to 4 196.88 ng (pigm) ind^{-1} day^{-1} in April 2005 (Mean = 4157.36 ng (pigm) ind^{-1} day^{-1}; SD = 35.37 ng (pigm) ind^{-1} day^{-1}). Average daily grazing rates for the pteropod varied between 0.39 mg (pigm) m^{-2} day^{-1} in April 2005 and 17.69 mg (pigm) m^{-2} day^{-1} in April 2004 (Mean = 6.13 mg (pigm) m^{-2} day^{-1}; SD = 11.04 mg (pigm) m^{-2} day^{-1}); corresponding average daily grazing impacts ranged between 8.4 % and 139.8 % of the phytoplankton standing stock in April 2005 and 2004, respectively (Mean = 48.5 %; SD = 84.5 %). Average daily grazing rates of the four copepods ranged from 4.58 mg (pigm) m^{-2} day^{-1} to 8.77 mg (pigm) m^{-2} day^{-1}, during April 2002 and 2004, respectively (Mean = 6.28 mg (pigm) m^{-2} day^{-1}; SD = 5.94 mg (pigm) m^{-2} day^{-1}). Collectively, the copepods removed an average of between 31.6 % and 89.8 % of the phytoplankton standing stock per day, during April 2002 and 2004, respectively (Mean = 70.8 %; SD = 86.7 %). The daily grazing impact of the copepods accounted for an average of between 40.4 % and 87.8 % of the total zooplankton grazing impact, during April 2004 and 2005, respectively (Mean = 75.0 %; SD = 65.5 %). *L. retroversa* was responsible for an average of 52.4 % and 59.5 % of the total zooplankton grazing impact, during April 2002 and 2004, respectively. However, during April 2005, when *L. retroversa* numbers were significantly lower than previous years, the pteropod contributed an average of only 7.5 % to the total zooplankton grazing impact. Thus, during the present investigation, the pteropod was responsible for removing a mean of 48.9 % of the available phytoplankton (SD = 74.9 %).

The predation impact of the dominant carnivorous macrozooplankton and micronekton in the PFZ was determined during April 2004 and 2005 using daily ration estimates obtained from the literature. Additionally, gut content analysis was used to determine the contribution of *L. retroversa* to the diet of the dominant predators. Average predation impact ranged from 1.1 % and 5.7 % of the total mesozooplankton standing stock during April 2004 and 2005, respectively (Mean = 3.8 %; SD = 12.3 %). Chaetognaths and euphausiids dominated total carnivore numbers and made the greatest contributions to total predation impact during both years. Copepods appeared to be the main prey item of the dominant carnivorous macrozooplankton-micronekton in the region. *L. retroversa* was only detected in the gut contents of the amphipod, *Themisto gaudichaudi*, but not in either of the

chaetognath species (*Eukrohnia hamata* and *Sagitta gazellae*) or the myctophid fish (*Electrona* spp.). The pteropod was found in 19 % of amphipod guts dissected. Pearson's Correlation analyses showed that the four major predatory zooplankton groups found in the PFZ (chaetognaths, euphausiids, amphipods and myctophid fish) were positively correlated to abundances of *L. retroversa*, suggesting that the pteropod might be an important prey item for many of the carnivorous macrozooplankton/micronekton in the PFZ.

To conclude, *L. retroversa* may play an important role in the pelagic ecosystem of the PFZ, in austral autumn. However, ocean acidification and calcium carbonate undersaturation (as a result of increased anthropogenic carbon dioxide emissions), that is predicted to occur within the next 50 – 100 years, will most likely have significant implications for the Sub-Antarctic pelagic ecosystem if *L. retroversa* cannot adapt quickly enough to the changes.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PREFACE

Data used in the present study were collected during four oceanographic surveys to the Polar Frontal Zone of the Southern Ocean. These surveys included: (1) the fifth Marion Island Offshore Survey (MIOS V), April 2000; (2) the second Marion Offshore Ecosystem Variability Survey (MOEVS II), April 2002; (3) the fourth Marion Offshore Ecosystem Variability Survey (MOEVS IV), April 2004; and (4) the fifth Marion Offshore Ecosystem Variability Survey (MOEVS V), April 2005.

Data from MOEVS II and MOEVS IV have been published:

Bernard KS, Froneman PW (2003) Mesozooplankton community structure and grazing impact in the Polar Frontal Zone of the south Indian Ocean during austral autumn 2002. Polar Biology 26: 268-275

Bernard KS, Froneman PW (2005) Trophodynamics of selected mesozooplankton in the west-Indian sector of the Polar Frontal Zone, Southern Ocean. Polar Biology 28: 594-606

Raw data from MOEVS II and MOEVS IV have, however, been re-analysed using more suitable methods for the purpose of this study.

ACKNOWLEDGMENTS

I would like to thank the South African Departments of Environmental Affairs and Tourism (DEAT) and Science and Technology (DST), as well as the National Research Foundation (NRF), for providing funding for my PhD over the last three years. Also, to the various captains and crew members of the *MV SA Agulhas*, during my voyages to the Southern Ocean, my sincere thanks for your hard work and patience in helping us get the samples we needed. Thanks must also go to the Department of Zoology and Entomology, Rhodes University, for providing me with the necessary space and equipment to carry out my research.

Professor William Froneman, Will, thank you for your dedicated and enthusiastic supervision throughout my PhD. Thanks for letting me see my ideas through and, when I thought I'd never finish, thanks for re-assuring me and reminding me to stay positive. I really appreciate all that you have done for me in the past and the opportunities you have given me.

There are a number of other people who have helped me tremendously over the past three years. Dr. Isabelle Ansorge, Issi, thanks for the fantastic company and endless cups of tea on the helideck, you really made the voyages so much fun. Thanks also to Issi for providing the oceanographic data used in this study and for teaching me how to use ODV. To my brother, Ant Bernard, thanks for being so supportive during the cruises that we went on together, I always know I can count on you for anything. I hope you know how much I value your opinion. I would also like to thank Professor Evgeny Pakhomov who has offered me advice and assistance on a number of occasions, thank you for taking the time to help. To all the various students from Rhodes University and the University of Cape Town (especially Paula, Louise A., Tara and Albert), who assisted in some way during the cruises to the Southern Ocean, thank you all for your help; the cups of coffee you brought to wake me up; the plates of supper you got for me when I couldn't get to the dining room because the net was still in the water; the silly songs and jokes that made me laugh. Also thanks to Louise Lange for all her hard work and long hours spent behind the computer, monitoring the nets, during the 2005 voyage. I would also like to thank Professor Mike Davies-Coleman, who, although I could tell really wanted to control the winch for the nets, let me do it anyway so that I could learn. Liv and Paul, thanks

for the weekends away, runs, dinners and chats that helped me keep my mind off the stress.

To Mum, Dad, Ant and Kelly, my family, thanks so much for the love and support that you have given me throughout my life, and especially throughout these last three years. Kell, thanks for the beautifully hand-drawn welcome-home pictures you made me every time I got back from a cruise (I'll bring them out at your 21st!), I'll treasure them forever. Ant, I've already thanked you for your help at sea, but as my brother, thanks for reminding me not to stress too much and especially not to care (although I still do) about what other people think. Mum, thanks for getting so excited every time I finished a chapter and for telling me how proud you are, it really helped me get through. Dad, thank you for letting me get on with it, but for also letting me know that you were proud of what I was doing and that if I ever needed your help you'd be there. Thanks, also, to Tanah and Chutney for dragging me out to Mountain Drive for walks!

Finally, thanks to my wonderful partner, Mike. You have supported me in all my crazy endeavours and have been there to share my ups and downs. Thank you for your unconditional love and friendship and for never giving up on me.

DECLARATION

The following thesis has not been submitted to any university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author, unless otherwise stated.

"…throw off the bowlines.
Sail away from the safe harbour.
Catch the trade winds in your sails.
Explore. Dream. Discover."

Mark Twain

CHAPTER ONE:

GENERAL INTRODUCTION

1.1 UNDERSTANDING THE BIOLOGICAL PUMP IN THE OCEANIC ENVIRONMENT

In light of the impacts of global warming and the increase in anthropogenic emissions of the greenhouse gases, including carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), scientists from various backgrounds are focusing their efforts on determining a global carbon budget. In order to do so, it is essential to understand how carbon is sequestered or stored and how it is released back into the atmosphere. Since the world's oceans are the largest carbon reservoirs on earth, removing between 1 and 3 Pg C y^{-1} (Pg = 10^{15} g) of the 5 – 7 Pg of anthropogenic carbon produced annually (Sarmiento *et al.* 2000; Rivkin & Legendre 2002), extensive research has been carried out in selected regions or "hotspots" of the global oceans (for example the World Ocean Circulation Experiment and the Joint Global Ocean Flux Study programmes) in an attempt to better understand the impacts the oceans have on the global carbon cycle.

In the oceanic environment, carbon is exported via two main pathways: (1) the *solubility pump* involves the transfer of dissolved inorganic carbon (DIC) from surface waters to depth by means of physical processes, such as movement along a concentration gradient, and by the downward movement of water masses to the ocean depths and is, by far, the greatest form of carbon flux in the oceans (Longhurst 1991); (2) the *biological pump* involves the transfer of dissolved and particulate organic carbon (DOC and POC, respectively) through the pelagic food web. For the interest of this study, the biological pump will be discussed in further detail.

1.1.1 The biological pump

Through the process of photosynthesis, CO_2 in the surface waters is absorbed by phytoplankton cells. The biogenic carbon will then either be remineralized through respiration, exported to the pelagic food web, via grazing and predation, or transferred to the ocean depths (Le Fèvre *et al.* 1998). Biogenic carbon can be exported to the deep ocean through a number of mechanisms, including aggregates of fast-sinking particles of ungrazed, dead or senescent phytoplankton cells (Le Fèvre *et al.* 1998); large, fast-sinking faecal pellets, some with high carbon contents (Le Fèvre *et al.* 1998); organic debris and carcasses (Le Fèvre *et al.* 1998); vertical migrations of zooplankton (Longhurst *et al.* 1990); and planktonic metabolism at depth (Cho &

Azam 1988). Biological processes play an important role in sustaining the gradient of CO_2 between the surface and the deep ocean (Rivkin & Legendre 2002).

Legendre & Le Fèvre (1992) proposed that three pools of biogenic carbon exist in the pelagic ecosystem: (1) short-lived organic carbon; (2) long-lived organic carbon; and (3) sequestered biogenic carbon. They based these pools on the time elapsed between the photosynthetic uptake of CO_2 by phytoplankton and the release of carbon into either the surface waters or the atmosphere. Short-lived organic carbon travels mainly through the microbial food web and is generally recycled in the upper water column within a few days. Long-lived organic carbon exists mainly in top predators, including exploited fish, whales and sea birds, where it can remain for varying lengths of time ranging from a few days to one hundred years. Some of this carbon may even be transported to depth through the sinking of carcasses where it will enter the sequestered biogenic carbon pool. Sequestered biogenic carbon is carbon that has been trapped in the deep ocean, where it can remain for hundreds or even thousands of years depending on the movement of the deep water and the activities of man. Sequestered biogenic carbon includes organic remains buried in the sediments (e.g. oil), inorganic deposits of biological origin (e.g. carbonates), refractory dissolved organic matter and dissolved CO_2 from oxidation of organic compounds at depth (Le Fèvre *et al.* 1998). It is an understanding of the magnitude of sequestered biogenic carbon that is of importance in determining a global carbon budget for the oceans. In order to do this, research has focused on the partitioning of biogenic carbon within pelagic ecosystems, mainly through the analyses of trophic structures and food webs. The separation of biogenic carbon between the two major pelagic food webs, namely the *microbial* and *classical* food webs, determines the fate of the carbon and therefore the efficiency of the biological pump (Sherr & Sherr 1988; Longhurst 1991; Fortier *et al.* 1994; Froneman 1995).

The microbial food web (different from the *microbial loop* in that it includes phytoplankton) is most common in oligotrophic systems where phytoplankton biomass is low and dominated by picophytoplankton (0.45 – 2.0 µm) (Legendre & Le Fèvre 1992; Fortier *et al.* 1994; Froneman *et al.* 1997). Picophytoplankton cells and heterotrophic bacteria are grazed on by protozoans, which are, in turn, preyed upon by mesozooplankton (Legendre & Le Fèvre 1992). As Legendre & Le Fèvre (1992)

suggest, carbon that enters the microbial food web is generally recycled within a few days in the upper water column, where it may be re-used by phytoplankton or released into the atmosphere. Mesozooplankton feeding on protozoans are, in some instances, able to prolong the life of biogenic carbon within the food web by transferring it to the top predators. There is very little opportunity for biogenic carbon in the microbial food web to be transferred to depth through vertical flux and enter the sequestered biogenic carbon pool; microzooplankton (< 200 µm) produce mini-faecal pellets that remain in suspension for extended periods resulting in the majority of the carbon being decomposed or recycled by bacteria in the euphotic zone (Azam *et al.* 1983). Additionally, due to their small size, most microzooplankton carcasses are unlikely to leave the euphotic zone, and instead will be recycled within the upper water column. An exception to this is presented by the foraminifera, the outer shells of which sink to the ocean depths transporting carbon in the form of calcium, where they collect in the sediments, eventually forming what is known as foraminiferan oozes (Auras-Schudnagies *et al.* 1989; Eguchi *et al.* 1999; Gooday 2002; and references therein). Another exception to this general rule is when large microphagous zooplankton, such as salps, doliolids, appendicularians and pteropods are numerous (Fortier *et al.* 1994). Microphagous zooplankton can ingest small particles (down to approximately 1 µm in diameter for salps), thereby enhancing carbon flux through the production of large, fast-sinking faecal pellets and respiration and egestion at depth (Fortier *et al.* 1994).

The classical food web dominates in eutrophic regions, where phytoplankton biomass is high and dominated by microphytoplankton (> 20 µm) such as diatoms. In these systems, herbivorous meso- (200 – 2000 µm) and macrozooplankton (> 2000 µm) grazing on the phytoplankton are, in turn, preyed upon by carnivorous macrozooplankton, which are themselves preyed upon by the top predators, including whales, fish, seals and sea birds. According to Legendre & Le Fèvre (1992), biogenic carbon that enters the classical food web will remain in the system for up to one hundred years and possibly longer if transported to depth. Macrozooplankton are most efficient at transporting biogenic carbon to depth through the production of large, fast-sinking faecal pellets with high carbon contents (Fortier *et al.* 1994). For example, salp (tunicate) faecal pellets have been reported to have sinking rates of up to 2700 m day^{-1} (Fortier *et al.* 1994) and a carbon content of up to 37 % (Bruland & Silver 1981). Macrozooplankton also undergo extensive diel vertical migrations,

which further contribute to carbon flux through respiration and egestion at depth (Longhurst 1991; Fortier *et al.* 1994). In contrast, the majority of mesozooplankton produce relatively small, slow-sinking faecal pellets, with reported sinking rates of approximately 100 m day^{-1} (Fortier *et al.* 1994). Additionally, copepods, which dominate the mesozooplankton community, demonstrate coprophagy (re-ingestion of faecal pellets) and coprohexy (mechanical disintegration of faecal pellets), thereby greatly reducing the amount of faecal material that reaches the deep ocean (Paffenhöfer & Knowles 1979; Lampitt *et al.* 1990; Noji *et al.* 1991). Mesozooplankton do, however, undergo diel vertical migrations (Atkinson *et al.* 1992a, b; Atkinson & Sinclair 2000), and in this way enhance their contribution to carbon flux through respiration and egestion at depth.

It follows, therefore, that in eutrophic regions, where microphytoplankton dominate, and consequently where meso- and macrozooplankton represent the primary grazers, the biological pump will be most efficient (Longhurst & Harrison 1989; Fortier *et al.* 1994). More biogenic carbon will reach the deep oceans and enter long-lived organic carbon pools. It is important to point out, however, that in eutrophic regions where abundances of macrozooplankton are low, for example due to predation by top predators, the efficiency of the biological pump will be reduced (Froneman *et al.* 2004). Conversely, oligotrophic regions, dominated by picophytoplankton and the microbial food web, exhibit a relatively inefficient biological pump (Longhurst & Harrison 1989), with the exception of those regions where either foraminifera or large microphagous zooplankton are abundant. Generally, these oligotrophic regions trap much of the carbon in the short-lived organic carbon pools, releasing it back into the atmosphere (Fortier *et al.* 1994).

1.2 THE SOUTHERN OCEAN

The Southern Ocean is the largest continuous body of water on earth, covering an expanse of approximately 38 million km^2 (Tomczak & Godfrey 1994). The role of the Southern Ocean in the global carbon cycle is, however, still debated (Caldeira & Duffy 2000; and references therein). Although extensive research has been carried out in the Southern Ocean, these studies have focussed, almost entirely, on regions of high productivity, including the Marginal Ice Zone (MIZ) (Bathmann *et al.* 1993;

Froneman *et al.* 1997), the neritic waters of Antarctica (Pakhomov & Perissinotto 1997), the vicinity of the major oceanic fronts (Froneman & Perissinotto 1996; Dubischar & Bathmann 1997; Pakhomov & Perissinotto 1997) and in the waters surrounding the Antarctic and sub-Antarctic islands (Perissinotto 1992; Atkinson 1994; Ward *et al.* 1995; Atkinson *et al.* 1996; Pakhomov *et al.* 1997). Apart from these regions of high productivity, the majority of the Southern Ocean is far less productive. The extreme environment of the Southern Ocean is the main cause of low productivity; the region experiences very low temperatures, low to nil light availability for much of the year and persistent high winds, which reduce water column stability and generate a deep mixed layer depth, all of which are limiting factors for phytoplankton production (Laubscher *et al.* 1993; Dafner 1997; Balarin 1999; Froneman *et al.* 2001).

1.2.1 Oceanographic environment

The Southern Ocean consists of the southern regions of the Indian, Pacific and Atlantic Oceans, and includes, among others, the Ross, Weddell and Scotia Seas (Tomczak & Godfrey 1994). The Antarctic continent represents the southern boundary of the Southern Ocean, while the northern boundary, although not geographically fixed, coincides with the location of the Subtropical Convergence (STC) (Lutjeharms 1985). Two major currents exist in the Southern Ocean, the "East Wind Drift", which is a narrow current bordering the Antarctic continent, and the "West Wind Drift", commonly known as the Antarctic Circumpolar Current (ACC) (Deacon 1937).

The ACC consists of a series of cores of varying intensities (Nowlin *et al.* 1977; Hoffman & Whitworth 1985), two of which are the high-speed Sub-Antarctic Front (SAF) and Antarctic Polar Front (APF), which represent the northern and southern boundaries, respectively, of the region known as the Polar Frontal Zone (PFZ) (Emery 1977; Hoffman 1985) see Figure 1.1. Combined, these fronts are responsible for approximately 75 % of the baroclinic transport within the ACC (Nowlin & Klinck 1986). As a result of the high flow velocities and temperature gradients associated with the SAF and APF, these fronts represent important biogeographic boundaries to the distribution of planktonic species (Backus 1985;

Boden *et al.* 1988; Pakhomov *et al.* 1994; Froneman *et al.* 1995b; Tarling *et al.* 1995; Pakhomov & Froneman 1999a). Both fronts can be identified by sub-surface measurements of temperature and/or salinity. At 200 m, the axial water temperature of the SAF is around 6 ºC while the salinity is approximately 34.3 $^{o}/_{oo}$. At the APF, the axial water temperature at 200 m is around 2 ºC (Ansorge *et al.* 2005).

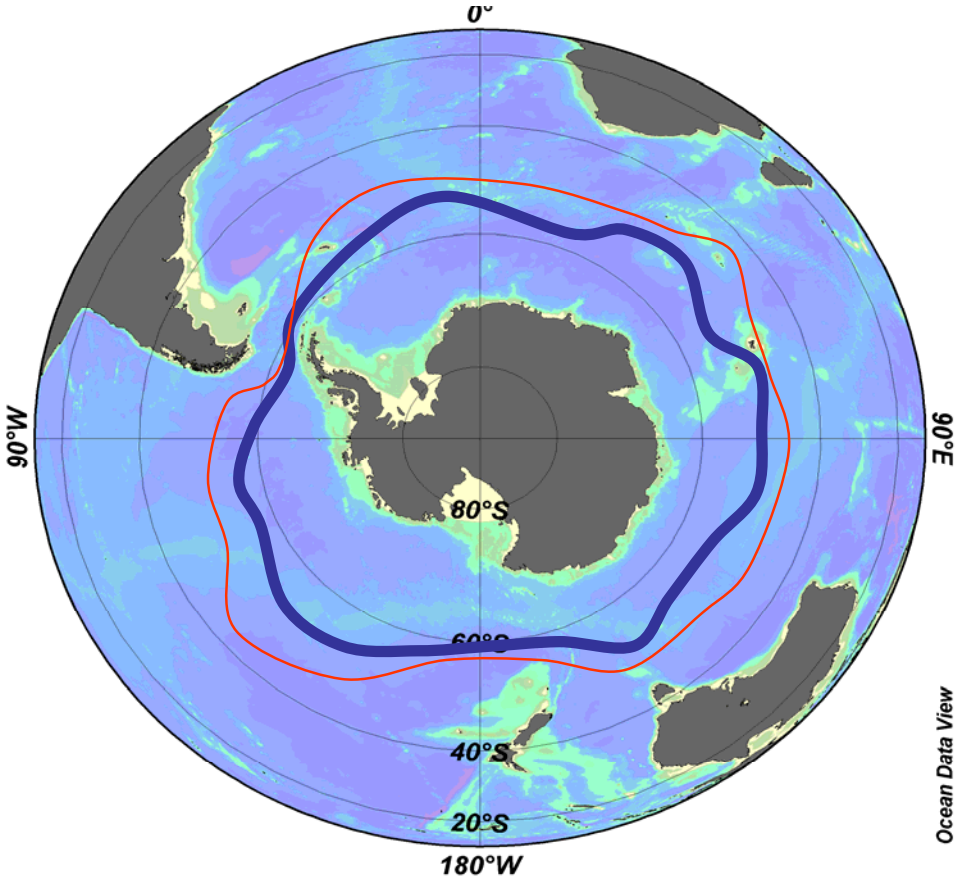

Figure 1.1 Circumpolar map of the Southern Ocean. The blue line represents the average geographic position of the Antarctic Polar Front (APF); the red line represents the approximate geographic position of the Sub-Antarctic Front (SAF). Figure drawn in the Ocean Data View computer package.

The PFZ is a region of transition between the warmer, less-productive Sub-Antarctic Surface Waters (SASW), north of the SAF, and the colder, more-productive Antarctic Surface Waters (AASW), south of the APF (Belkin & Gordon 1996; Ansorge *et al.* 1999; Froneman *et al.* 1999). The position of the PFZ varies on a temporal scale (Hoffman & Whitworth 1985) and is affected by the local bathymetry and wind patterns (Nowlin & Klinck 1986; Ansorge *et al.* 1999). The SAF and APF,

marking the boundaries of the PFZ, exhibit a high degree of spatial and temporal mesoscale variability (Lutjeharms & Valentine 1984; Lutjeharms 1990), including eddies (Bryden 1983; Ansorge *et al.* 1999; Froneman *et al.* 1999) and meanders in both fronts (Legeckis 1977; Lutjeharms 1990; Ansorge *et al.* 1999; Froneman *et al.* 1999). These mesoscale features facilitate the mixing of the SASW and AASW within the PFZ, resulting in the intrusion of foreign water bodies from the north and south as extensions of the SAF and APF, respectively (Ansorge *et al.* 1999; Perissinotto *et al.* 2000).

1.2.2 Primary production

Phytoplankton biomass and productivity in the Southern Ocean exhibits a high degree of both spatial and temporal variability (Table 1.1) (Laubscher *et al.* 1993; van Leeuwe *et al.* 1998; Pakhomov *et al.* 2001; Dafner 1997). Although most of the Southern Ocean is relatively un-productive, ranging from 0.1 to 0.5 g C m^{-2} day^{-1} (El-Sayed 1988; Bradford-Grieve *et al.* 1997; Dafner 1997), certain regions of the Southern Ocean are highly productive with primary productivity exceeding 1 g C m^{-2} day^{-1} (Bradford-Grieve *et al.* 1997; Dafner 1997). These regions include the MIZ (Froneman *et al.* 1997; Froneman *et al.* 2001), the vicinity of the major oceanic frontal systems (El-Sayed 1988; Laubscher *et al.* 1993; Froneman *et al.* 1999; Froneman *et al.* 2001), the waters surrounding the oceanic islands (Perissinotto & Duncombe Rae 1990) and the neritic waters of Antarctica (Arrigo *et al.* 1997; Dafner 1997). Periodic open ocean blooms may also occur (El-Sayed 1988; Smetacek *et al.* 1997). The high productivity in these regions is strongly associated with physical factors, including water column stability (Laubscher *et al.* 1993; Dafner 1997; Balarin 1999), increased availability of trace metals, particularly iron (De Baar *et al.* 1995; Pakhomov & Froneman 1999a), macronutrient availability (El-Sayed 1988; Pakhomov & Froneman 1999a) and seawater temperatures (Laubscher *et al.* 1993; Froneman *et al.* 2001). Primary production also exhibits seasonal variability, with elevated primary production levels observed during spring and summer when light availability and water column stability are high, favouring the production of phytoplankton blooms (Laubscher *et al.* 1993; Xiuren *et al.* 1996; Dafner 1997; Bracher *et al.* 1999; Balarin 1999; Froneman *et al.* 1999; Froneman *et al.* 2001).

The phytoplankton size structure, which is strongly linked to phytoplankton biomass and productivity, also exhibits spatial and temporal variability in the Southern Ocean (Laubscher *et al.* 1993; Froneman *et al.* 2001). Microphytoplankton (> 20 µm), typically colonial and chain-forming diatoms, such as *Nitzchia* spp. and *Chaetoceros* spp. (Priddle 1990), generally dominate in regions of enhanced productivity and phytoplankton biomass (El-Sayed 1988; Laubscher *et al.* 1993; Kang & Fryxell 1993; Froneman *et al.* 1995a, b; Froneman & Pakhomov 2000; Froneman *et al.* 2001). Conversely, in the less productive open waters of the Southern Ocean, small nano- (2.0 – 20 µm) and picophytoplankton (0.45 – 2.0 µm) contribute most to total phytoplankton biomass and production (Laubscher *et al.* 1993; Xiuren *et al.* 1996; Froneman *et al.* 2001). Nanophytoplankton consist mostly of unicellular green flagellates and small diatoms (Jacques & Panouse 1991), while picophytoplankton communities are made up of cyanobacteria and green flagellates (Knox 1994). The predominance of small phytoplankton cells in the open ocean regions is likely due to environmental conditions that limit the growth of larger cells, such as high wind stress that results in deep mixed layers, and low macro- and micronutrient availability (Laubscher *et al.* 1993; Dafner 1997; Balarin 1999; Froneman *et al.* 2001). In such conditions, pico- and nanophytoplankton cells, due to their large surface area-to-volume ratio, are capable of using the available light and nutrients more efficiently than microphytoplankton (Fogg 1991). During winter, when wind stress is high and light availability dramatically reduced, production is almost entirely dominated by picophytoplankton (Laubscher *et al.* 1993; Xiuren *et al.* 1996; Dafner 1997; Lancelot *et al.* 2000; Ansorge *et al.* 1999; Bracher *et al.* 1999; Balarin 1999; Froneman *et al.* 1999; Froneman *et al.* 2001).

Table 1.1 Surface phytoplankton biomass (PB; µg L^{-1}), integrated phytoplankton biomass (IPB; mg m^{-2}), primary production (PP; mg C m^{-2} day^{-1}) and dominant phytoplankton size fraction (DSF) in different regions of the Southern Ocean, from the literature.

Region	Season	PB	IPB	PP	DSF	Source
STFZ	ND	ND	ND	250 – 500	ND	Dafner 1997
SAF	Summer	ND	18.1 – 33.0	45 – 178	Nano- & Pico-	Froneman *et al.* 2001
SAZ	Winter	0.12 – 0.13	ND	71 - 121	Micro-	Bradford-Grieve *et al.* 1998
SAZ	Spring	0.19 – 0.22	ND	471 - 565	Micro-	Bradford-Grieve *et al.* 1998
PFZ	ND	ND	ND	250 – 500	ND	Dafner 1997
Sub-Antarctic islands	ND	ND	ND	500 – 750	ND	Dafner 1997
NPFZ	Summer	ND	67.3	701	Micro-	Tremblay *et al.* 2002
SPFZ	Summer	ND	47.0	649	Micro-	Tremblay *et al.* 2002
APF	Summer	ND	10.4 – 34.7	77 – 266	Variable	Froneman *et al.* 2001
POOZ	Summer	ND	28.3	440	Pico-	Tremblay *et al.* 2002
POOZ	Summer	ND	12.0 – 18.3	60 – 112	Nano-	Froneman *et al.* 2001
POOZ	ND	4.5	ND	ND	ND	Dafner 1997
SIZ (non-bloom)	Summer	ND	31.0	239	Nano-	Tremblay *et al.* 2002
SIZ (bloom)	Summer	ND	69.6	630	Micro-	Tremblay *et al.* 2002
MIZ	Summer	ND	19.2 – 58.3	126 – 442	Micro-	Froneman *et al.* 2001
Antarctic Shelf	ND	ND	ND	> 3000	ND	Dafner 1997

STFZ – Sub-Tropical Frontal Zone
PFZ – Polar Frontal Zone
APF – Antarctic Polar Front
POOZ – Permanently Open Ocean Zone
SIZ – Seasonal Ice Zone
SPFZ – Southern PFZ
NPFZ – Northern PFZ
MIZ – Marginal Ice Zone
SAF – Sub-Antarctic Front
SAZ – Sub-Antarctic Zone
ND – No Data

1.2.3 Zooplankton

The majority of research carried out on the community structure and trophodynamics the zooplankton of the Southern Ocean has focused on the regions of high productivity, including the MIZ (Boysen-Ennen *et al.* 1991; Atkinson 1995; Atkinson & Shreeve 1995; Hansen *et al.* 1996; Hernández-León *et al.* 1999; Atkinson & Sinclair 2000; Hernández-León *et al.* 2000; Li *et al.* 2001), the frontal regions, for example, the APF (Hansen *et al.* 1990; Brown & Landry 2001; Urban-Rich *et al.* 2001; Dubischar *et al.* 2002) and in the waters surrounding the various oceanic islands within the Southern Ocean, for example, South Georgia (Atkinson *et al.* 1992a, b; Øresland & Ward 1993; Atkinson 1994; Atkinson *et al.* 1996; Atkinson & Snÿder 1997; Atkinson *et al.* 1999; Ward *et al.* 2002), Kerguelen Island (e.g. Razouls *et al.* 1996, 1998) and the Prince Edward Archipelago (Grindley & Lane 1979; Miller 1982; Perissinotto & Boden 1989; Perissinotto *et al.* 1990a, b; Perissinotto 1992; Froneman & Pakhomov 1998a, b; Ansorge *et al.* 1999; Froneman *et al.* 1999; Pakhomov & Froneman 1999a; Pakhomov & Froneman 2000; Pakhomov *et al.* 2000b; Hunt *et al.* 2001; Gurney *et al.* 2002). Recent surveys have begun to investigate the open ocean regions of the Southern Ocean, such as the PFZ (Bernard & Froneman 2002). Major zooplankton grazers in the Southern Ocean are copepods, euphausiids and salps (Perissinotto 1992; Atkinson 1996; Atkinson *et al.* 1996; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Froneman *et al.* 2000a; Gurney *et al.* 2002; Pakhomov & Froneman 2004b), while the dominant carnivorous taxa include chaetognaths, amphipods and some euphausiids (Grindley & Lane 1979; Voronina 1984; Øresland 1990; Hosie 1994; Voronina *et al.* 1994; Tarling *et al.* 1995; Froneman *et al.* 1998; Froneman & Pakhomov 1998b; Pakhomov *et al.* 1999; Pakhomov & Froneman 2000; Froneman *et al.* 2002a).

Copepods

Copepods are, by far, the most abundant mesozooplankton group in the Southern Ocean, accounting for between 40 and 98 % of total mesozooplankton densities (Conover & Huntley 1991; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Froneman & Pakhomov 1998a; Pakhomov & Froneman 1999a; Pakhomov *et al.* 2000a; Bernard & Froneman 2002; Hunt & Pakhomov 2003; Pakhomov &

Froneman 2004a). Their numerical dominance remains constant throughout most of the region (see Perissinotto 1992; Atkinson *et al.* 1996; Hansen *et al.* 1996; Froneman & Pakhomov 1998a; Froneman *et al.* 1999; Pakhomov *et al.* 1997, 2000a; Bernard & Froneman 2002). Among the copepods, the small cyclopoid copepods of the genus *Oithona* typically dominate total zooplankton numbers, contributing up to 80 % to the total (Gallienne & Robins 2001; Dubischar *et al.* 2002; Bernard & Froneman 2002). A number of grazing studies have been conducted on copepods in the past, focusing mainly on the larger species due to the difficulties that arise using smaller animals. There have, however, been a few studies that have focused on the smaller, numerically dominant copepods, particularly of the cyclopoid family (Atkinson 1994, 1995, 1996; Atkinson *et al.* 1996; Bernard & Froneman 2002). Although copepods do not have exceptionally high individual daily ingestion rates (ranging from 4.71 to 812.4 ng (pigm) ind^{-1} day^{-1}) (Perissinotto 1992; Atkinson 1996; Atkinson *et al.* 1996; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Urban-Rich *et al.* 2001; Pakhomov & Froneman 2004b), they often make the greatest contribution to total grazing impact due to their numerical dominance. For instance, Pakhomov & Froneman (2004b) estimated that, in the Atlantic sector south of the APF, copepods contributed up to 73.4 % of the total grazing impact.

Euphausiids

Euphausiids may, at times, dominate zooplankton communities, but this is usually localised and highly patchy. *Euphausia superba* (Antarctic krill) and to a lesser extent *Thysanoessa macrura*, tend to dominate the total zooplankton biomass (up to 80 % of the total) in the region of the Permanently Open Oceanic Zone (POOZ), between the MIZ and the APF (Pakhomov *et al.* 2000a). North of the APF, euphausiids (mainly *E. frigida*, *E. triacantha*, *E. recurva* and *Thysanoessa* spp.) generally contribute no more than 30 % of the total biomass (Pakhomov *et al.* 2000a; Bernard & Froneman 2006). Euphausiids tend to exhibit greater individual daily ingestion rates than copepods, ranging from 3.2 ng (pigm) ind^{-1} day^{1} for furcilia to as much as 12 512 ng (pigm) ind^{-1} day^{-1} for adult *E. triacantha* south of the APF (Perissinotto 1992; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Gurney *et al.* 2002; Pakhomov & Froneman 2004b; Bernard & Froneman 2006).

The euphausiids *Nematoscelis megalops*, *T. macrura* and *E. longirostris* are considered to be carnivorous species (Hopkins 1985; Hopkins & Torres 1989; Perissinotto *et al.* 1996; Pakhomov *et al.* 1999; Gurney 2000; Froneman *et al.* 2002a). In fact, these species may make substantial contributions to total predation on the mesozooplankton standing stock, feeding predominantly on the most abundant copepods (Pakhomov *et al.* 1999; Froneman *et al.* 2002a).

Tunicates

Tunicates exhibit a highly patchy distribution (Perissinotto & Pakhomov 1998a, b; Pakhomov *et al.* 2002; and references therein). Pakhomov *et al.* (2000a) found dense swarms of *Salpa fusiformis* near the Subtropical Convergence (STC), where the species accounted for up to 96 % of the total zooplankton numbers. Swarms of the tunicate, *S. thompsoni*, were also encountered between the APF and the northern expansion of the zero degree isotherm, contributing up to 30 % of total zooplankton densities (Pakhomov *et al.* 2000a). Outside of these regions, however, tunicates were virtually absent, particularly in the MIZ (Pakhomov *et al.* 2000a). This is likely due to the apparent spatial segregation between krill and salps (Loeb *et al.* 1997; Pakhomov *et al.* 2002), and the high densities of the former in the region. Salps can be considered to be microphagous, capable of consuming a far wider range of particle sizes than most pelagic crustaceans, ranging from 1 to 1000 µm (Fortier *et al.* 1994). *E. superba*, on the other hand, consumes food particles mainly between 10 and 50 µm in diameter (Meyer & El-Sayed 1983; Opalinski *et al.* 1997, cited in Pakhomov *et al.* 2002). Additionally, salps exhibit very high filtration rates (Fortier *et al.* 1994; Perissinotto & Pakhomov 1998a, b), and can therefore consume large quantities of food. Using *in situ* chl-*a* concentrations, Perissinotto & Pakhomov (1998b) estimated salp clearance rates to average 430 mL h^{-1} for small-medium sized individuals (1 – 5 cm) and 5400 mL h^{-1} for larger individuals (5 – 12 cm). *S. thompsoni* has exceptionally high individual daily ingestion rates, which increase with increase in salp size, ranging from 704 ng (pigm) ind^{1} day^{-1} for individuals < 1 cm to 124 923 ng (pigm) ind^{-1} day^{-1} for individuals 7 to 13 cm in length (Perissinotto & Pakhomov 1998a, b; Pakhomov & Froneman 2004b).

Chaetognaths

Chaetognaths, primarily *Sagitta gazellae* and *Eukrohnia hamata*, are the most abundant carnivorous zooplankton group in the Southern Ocean, at times contributing up to 92 % of the total zooplankton biomass (Perissinotto & McQuaid 1992; Pakhomov *et al.* 1994; Froneman & Pakhomov 1998b; Froneman *et al.* 1998; Pakhomov *et al.* 1999; Pakhomov *et al.* 2000a; Pakhomov & Froneman 2000; Froneman *et al.* 2002a). Chaetognaths feed predominantly on copepods, but tintinnids, euphausiids, cladocerans, other chaetognaths, appendicularians, molluscs, ostracods and fish larvae have also been reported in chaetognath stomach contents (Feigenbaum 1979; Baier & Purcell 1997; Froneman *et al.* 1998; Froneman & Pakhomov 1998b). The chaetognaths, *E. hamata* and *S. gazellae*, have been reported to consume between 0.01 and 141.5 % of the available mesozooplankton standing stock within the Southern Ocean (Pakhomov *et al.* 1999; Froneman *et al.* 2002a) Chaetognaths are therefore considered an important link between the mesozooplankton community and the top predators (Sameoto 1988; Pakhomov *et al.* 1996), thereby assisting in the transfer of carbon from the short-lived pool to the long-lived pool.

Amphipods

The most abundant pelagic amphipod in the PFZ is the hyperiid amphipod, *Themisto gaudichaudi*. Although its distribution is patchy, it has been recorded in large numbers in the PFZ (Pakhomov & McQuaid 1996). *T. gaudichaudi* is considered an obligate carnivore, feeding predominantly on mesozooplankton (Hopkins 1985; Pakhomov & Perissinotto 1996); in some areas the species has been successful in controlling the mesozooplankton standing stock (Gibbons *et al.* 1992, cited in Pakhomov & Perissinotto 1996). However, *T. gaudichaudi* typically only consumes between 0.0 and 1.2 % of the available mesozooplankton standing stock in the Southern Ocean (Pakhomov *et al.* 1999; Froneman *et al.* 2002a). As a major food source for many of the Southern Ocean top predators, including fish, squid, birds and whales (Rodhouse *et al.* 1992; Bost *et al.* 1994; Kock *et al.* 1994, all cited in Pakhomov & Perissinotto 1996), *T. gaudichaudi* provides an important link between mesozooplankton and the top consumers. In addition to aiding the transfer of carbon from the short-lived pool to the long-lived pool, *T. gaudichaudi* contributes to carbon

sequestration through diel vertical migrations (Everson & Ward 1980, cited in Pakhomov & Perissinotto 1996) and the production of large, fast-sinking faecal pellets (Fortier *et al.* 1994).

1.3 EUTHECOSOME PTEROPODS

As discussed earlier in this chapter, the role of the Southern Ocean in the global carbon cycle is, as yet, still undefined (Caldeira & Duffy 2000; and references therein). Since zooplankton communities play an important role in the biological flux of carbon to depth, it is essential to study all components of a community. A great deal of research has already been conducted on what have been termed "major" zooplankton grazers, including copepods, euphausiids and salps (Voronina 1998). There are, however, a number of other zooplankton taxa that are recorded in high numbers in the Southern Ocean, yet have not been considered in terms of their grazing impact and contribution to biologically mediated carbon flux. Pteropods, although relatively understudied in the Southern Ocean, can account for a large proportion of total zooplankton numbers (Table 1.2). For example, Bernard (2002) recorded an average abundance of 108.37 ind. m^{-3} for *Limacina retroversa* in regions south of the SAF, within the Indian sector of the Southern Ocean. The only species contributing more to total numbers in this region was the cyclopoid copepod, *Oithona similis*. Pteropods may also contribute substantially to total zooplankton biomass (Pakhomov & Froneman 2004a). Pakhomov & Froneman (2004a) found that at the Spring Ice Edge during December 1997 to January 1998, the pteropod, *Clio sulcata*, contributed 13.1 % to total biomass.

1.3.1 Pteropod biology

Thecosome pteropods are pelagic gastropod molluscs and the name *pteropod* literally means *winged foot* (Lalli & Gilmer 1989). Thecosomes have unique adaptations to their planktonic mode of life, including the foot being modified to function as wings. Additionally, thecosome pteropods are typically small with thin, delicate, external shells. Most species have developed mechanisms to retain buoyancy when swimming has ceased. Furthermore, thecosomes are the only opisthobranchs that employ a free-floating mucous web, which they use to trap food

particles from the water column (Lalli & Gilmer 1989). Thecosome pteropods can be divided into two groups: euthecosomes and pseudothecosomes (Lalli & Gilmer 1989). For the purpose of the present study, euthecosome pteropods will be discussed in further detail.

Euthecosome pteropods posses an external shell made of calcium in the form of aragonite. They exist throughout the world's oceans, from Antarctica to the Arctic, with greatest abundances at the high latitudes and greatest diversity in the warmer, equatorial waters (Lalli & Gilmer 1989). The majority of euthecosome species exist in the surface waters, down to approximately 200 m, but mesopelagic and bathypelagic species do occur. Euthecosomes can occur in such high numbers in certain areas that they form a substantial food source for commercial fish species (Lalli & Gilmer 1989).

There are 34 known species of euthecosomes, which are classified according to their shell morphology. The most primitive genus, *Limacina* (Family Limacinidae), contains only seven species, all with spirally coiled shells (spiralled sinistrally, as opposed to dextrally as in prosobranch snails). The shells of Cavoliniidae do not exhibit spiral coiling, instead they are bilaterally symmetrical. Shapes of cavoliniid shells vary from straight and pointed (*Creseis*) to pyramidal (*Clio*) (Lalli & Gilmer 1989). The dominant species in the Southern Ocean are *Limacina retroversa*, in the PFZ, and *L. helicina* forma *antarctica* and *Clio pyrimidata* forma *sulcata*, in the waters south of the APF (Boltovskoy 1999).

1.3.2 Swimming

Limacina spp. swim by means of paired muscular wings that extend upwards out of the shell aperture (Lalli & Gilmer 1989). Upward motion of the pteropod is a result of downward strokes of the wings. Sinking is very rapid, due to the weight of the shell, and occurs when the animal holds its wings vertically above the body. Sinking rates of 25 cm $sec.^{-1}$ for live adult pteropods have been recorded in the Norwegian Sea (Noji, unpublished data cited in Bathmann *et al.* 1991). Euthecosomes are able to sink slowly (0.5 cm $sec.^{-1}$) and reach neutral buoyancy by spreading their wings horizontally (Lalli & Gilmer 1989). Neutral buoyancy occurs

concurrently with feeding, as the animals extend a mucous web to capture food particles (Gilmer & Harbison 1986). Since active swimming is energetically costly, pteropods restrict swimming largely to escaping from predators and to diurnal vertical migrations (Lalli & Gilmer 1989).

Table 1.2 Average abundances (ind. m^{-3}) and percentage contribution of *Limacina* spp. to total mesozooplankton numbers (% of Total) in sectors of the Southern Ocean. Data obtained from a selection of the available literature.

Season	Region	Species	Av. Abund.	% of Total	Source
Summer	Atlantic sector	*Limacina helicina*	0.67	0.3	Pakhomov & Froneman 2004a
Winter	STC	*Limacina* spp.	0.36	1.2	Pakhomov & Perissinotto 1997
Summer	SAZ	*Limacina* spp.	0.70	0.2	Ward *et al.* 2003
Summer	PFZ	*Limacina* spp.	175	13	Ward *et al.* 2003
Autumn	PFZ	*Limacina retroversa*	66.91	17	Bernard (2001) *unpub. data*
Autumn	PEI	*Limacina* sp.	5.58	ND	Froneman & Pakhomov 1998a
Autumn	PEI	*Limacina* sp.	150	3.5	Perissinotto 1992
Autumn	PEI	Pteropods	4.28	5	Hunt & Pakhomov 2003
Summer	AAZ	*Limacina* spp.	166	11	Ward *et al.* 2003
Summer	AAZ	*Limacina* spp.	0.30	1.1	Ward *et al.* 2003
Summer	South Georgia	*Limacina* spp.	28.01	13	Pakhomov *et al.* 1997
Summer	South Georgia	Pteropods	ND	~ 35	Atkinson *et al.* 1996
Summer	South Georgia	*Limacina helicina*	15.47	ND	Ward *et al.* 2002
Summer	South Georgia	*Limacina helicina*	54.7	ND	Ward et al. 2005
Summer	Scotia Sea	*Limacina* spp.	< 0.01	ND	Ward *et al.* 2004
Autumn	Norwegian Sea	*Limacina retroversa*	> 13600	ND	Bathmann *et al.* 1991

SAZ – Sub-Antarctic Zone
PFZ – Polar Frontal Zone
AAZ – Antarctic Zone
PEI – Prince Edward Islands (Sub-Antarctic)
STC – Subtropical Convergence
ND – No Data

1.3.3 Feeding and carbon transfer

Euthecosome pteropods capture planktonic food particles by means of an external mucous web that can be many times the size of their bodies (Lalli & Gilmer 1989). Gilmer & Harbison (1986) recorded web diameters for *L. helicina* ranging between 40 and 55 mm for animals with a shell length of approximately 11 mm. Web diameters for *L. retroversa* were estimated at approximately 20 mm (Gilmer & Harbison 1986). Particles trapped within the webs are transferred to the mouth via ciliary pathways. The mantle lining and the palial gland are the sites of mucous production; ciliary pathways used in web deployment and the collection of food are positioned on the mantle lining, footlobes and wings (Lalli & Gilmer 1989). Web deployment and retraction is very rapid, and if the animal is disturbed during feeding, the entire web will be discarded. Euthecosomes feed typically on phytoplankton, but small zooplankton also form a substantial portion of their diets. During a survey conducted at the Spring Ice Edge over the period December 1997 to January 1998, *C. sulcata* exhibited daily ingestion rates of up to 27 757 ng (pigm) ind^{-1} day^{-1}, representing a contribution of as much as 52.5 % of the total grazing impact in the region (Pakhomov & Froneman 2004b).

Euthecosomes are preyed upon by a wide variety of zooplanktonic predators, fish, marine mammals and sea birds (Perissinotto & McQuaid 1992; Pakhomov *et al.* 1996; Pakhomov & Perissinotto 1996; Froneman & Pakhomov 1998b; Froneman *et al.* 1998; Armstrong *et al.* 2005; Bushula *et al.* 2005). Carnivorous zooplankton feeding on euthecosome pteropods include chaetognaths, heteropods, ctenophores, medusae, siphonophores, gymnosome pteropods and some pseudothecosomes (Lalli 1970; Conover & Lalli 1972; Lalli & Gilmer 1989; Foster & Montgomery 1993, cited in Seibel & Dierssen 2003; Pakhomov & Perissinotto 1996; Pakhomov *et al.* 1996; Froneman & Pakhomov 1998b; Böer *et al.* 2005). Fish predators include herring, mackerel, cod larvae, redfish larvae, salmon, yellowfin tuna, small myctophids and nototheniids among others (Lalli & Gilmer 1989; Pakhomov *et al.* 1996; Armstrong *et al.* 2005; Bushula *et al.* 2005).

The production of pseudofaeces and faecal pellets, as well as the abandonment of mucous webs, provide feeding surfaces for small zooplankton grazers, including

copepods (Lalli & Gilmer 1989). Additionally, these aggregations serve as a substrate and nutrient source for bacteria.

Large faecal pellets and mucous webs that are heavily loaded with particles may sink to the ocean depths, contributing to carbon sequestration (Lalli & Gilmer 1989; Meinecke & Wefer 1990; Bathmann *et al.* 1991; Noji *et al.* 1997). Indeed, there is evidence of mucous webs in sediment traps (Bathmann *et al.* 1991; Noji *et al.* 1997). Bruland and Silver (1981) reported sinking rates of 440 – 1 800 m day^{-1} for faecal pellets of the pteropod *Corolla spectabilis*, while Yoon *et al.* (2001) recorded faecal pellet sinking rates for *Clio* spp. of between 65 and 205.7 m day^{-1}. In addition to the sinking of mucous webs and faecal pellets, pteropod shells (of dead individuals) are transferred to the ocean depths on a seasonal basis (Meinecke & Wefer 1990; Bathmann *et al.* 1991; Collier *et al.* 2000; Gardner *et al.* 2000; Accornero *et al.* 2003). Meinecke & Wefer (1990) recorded the sedimentation of *L. helicina* and *L. retroversa* in the Norwegian Sea. The results of their study indicated that sedimentation occurred only from early autumn to winter when the pteropods were reportedly exhibiting high reproduction rates (Meinecke & Wefer 1990). In agreement with these findings, Bathmann *et al.* (1991) note that the high autumn sedimentation rates observed in the eastern Norwegian Sea are coincident with the annual maximum abundance of the *L. retroversa*. In the Norwegian Sea, *L. retroversa* occurs in considerable numbers only in August (Noji 1989, cited in Bathmann *et al.* 1991), with the majority of individuals being in the smallest size fraction, reflecting population development and growth. This period, however, was also associated with considerable mortality towards the end of the month, resulting in the enhanced sedimentation of pteropod shells (Bathmann *et al.* 1991). In the Ross Sea, during 1996 – 1997, the largest flux of organic carbon occurred in late autumn and was due almost entirely to the pteropod, *L. helicina* (Collier *et al.* 2000; Gardner *et al.* 2000). Additionally, a separate study in the Terra Nova Bay polynya, Ross Sea, *L. helicina* constituted a major component of the carbon flux during late autumn (Accornero *et al.* 2003).

1.3.4 Reproduction

Euthecosome pteropods are all protandrous hermaphrodite, in other words, they mature first as males and then as females. Reproduction in the family Limacinidae has been described on a number of occasions (see Lalli & Gilmer 1989). *L. retroversa*, the Sub-Antarctic/Sub-Arctic species, exhibits seasonal patterns in its reproduction. In the northern hemisphere, egg production peaks in the summer months, but may also coincide with spring and autumn phytoplankton blooms (Lalli & Gilmer 1989; Gannefors *et al.* 2005). In the Argentine Sea, *L. retroversa* exhibits a life cycle of two generations per year, with different strategies of development occurring according to the season of birth (Dadon & de Cidre 1992). Individuals that are born in spring mature early, reproducing before the end of summer, while those born in summer delay sexual maturity until after the winter, reproducing the following spring (Dadon & de Cidre 1992). *L. helicina*, the Antarctic/Arctic species, spawns primarily during summer in the northern hemisphere, with a life-cycle of approximately 1.5 – 2 years (Kobayashi 1974). There is much less information regarding *L. helicina* in the Antarctic, but specimens are largest during summer and spawning occurs during late summer (Massy 1920, cited in Lalli & Gilmer 1989).

1.3.5 Ecological indicators

A number of species of euthecosome pteropods are sensitive to environmental conditions, including temperature and salinity; and can be used as indicators of environmental change (Lalli & Gilmer 1989). In the Atlantic sector of the Southern Ocean, *L. retroversa* is primarily concentrated in the Sub-Antarctic waters, north of the Antarctic Polar Front (APF), where water temperatures range between 3 and 6 ºC, and can therefore be considered an indicator of Sub-Antarctic water masses (Lalli & Gilmer 1989). South of the APF, *L. helicina* signifies the presence of Antarctic water (Lalli & Gilmer 1989). Due to the mixing of these two water masses, however, it is possible that either species may be transported out of their water mass of origin.

The availability of phytoplankton may impact substantially on some pteropod populations. For example, Seibel & Dierssen (2003) noted that reduced phytoplankton biomass in McMurdo Sound, Antarctica, strongly affected the occurrence and metabolic rates of *L. helicina*, which in turn had an impact on the

presence and metabolism of *Clione antarctica*, the gymnosome pteropod that feeds exclusively on *L. helicina* (Gilmer & Lalli 1990, cited in Seibel & Dierssen 2003). Both *L. helicina* and *C. antarctica* are important components of the pelagic ecosystem, potentially capable of influencing phytoplankton biomass (Pakhomov & Froneman 2004b) and carbon flux (Meinecke & Wefer 1990; Bathmann *et al.* 1991; Noji *et al.* 1997). Seibel & Dierssen (2003) suggest that the state of pteropod populations may in fact be indicative of the overall health of the pelagic ecosystem in the region.

Euthecosome pteropods may be affected by changes in CO_2 levels in the world's oceans (Feely *et al.* 2004; Orr *et al.* 2005). A recent survey on the impact of anthropogenic CO_2 on the calcium carbonate ($CaCO_3$) system of the oceans indicates that increasing CO_2 levels may result in the reduction of the $CaCO_3$ saturation depth and a corresponding increase in the acidity of the oceans. These changes would cause an increase in the dissolution rates of $CaCO_3$ particles from the shells of pteropods and other organisms (including coccolithophorids and foraminifera), further increasing CO_2 concentrations, resulting in a negative feedback loop (Feely *et al.* 2004). Orr *et al.* (2005) hypothesise that undersaturated conditions of $CaCO_3$ will occur over much of the high-latitude surface oceans during the 21st century and that thecosome pteropods will not be able to adapt quickly enough to these changes. What impact this might have on the structure, biodiversity and trophic interactions of polar ecosystems is unclear (Orr *et al.* 2005).

1.4 AIMS

Despite the evidence suggesting that euthecosome pteropods may potentially play a large role in the oceanic carbon cycle, very little data on Southern Ocean pteropods exist. Furthermore, in order to fully understand the impact continued increases in atmospheric CO_2 concentrations and corresponding changes in ocean pH and chemistry have on euthecosome pteropods in the PFZ, it is essential to gain more insight into the ecology of the dominant euthecosome species in the region.

The objective of this study was to investigate the ecological role of the dominant euthecosome pteropod, *L. retroversa*, (Gastropoda: Mollusca) in the PFZ of the Southern Ocean (See Figure 1.2 for information on survey areas). The aims of this work were two-fold:

1. To describe the distribution and size structure of *L. retroversa* in the PFZ, Southern Ocean.
2. To assess the role of *L. retroversa* in the pelagic food web and, therefore, in the oceanic carbon cycle.

The research formed part of the South African National Antarctic Programme (SANAP). Unfortunately, due to logistical constraints, the study of the ecological role of *L. retroversa* was restricted to the PFZ in the Indian sector of the Southern Ocean during austral autumn (see Figure 1.2).

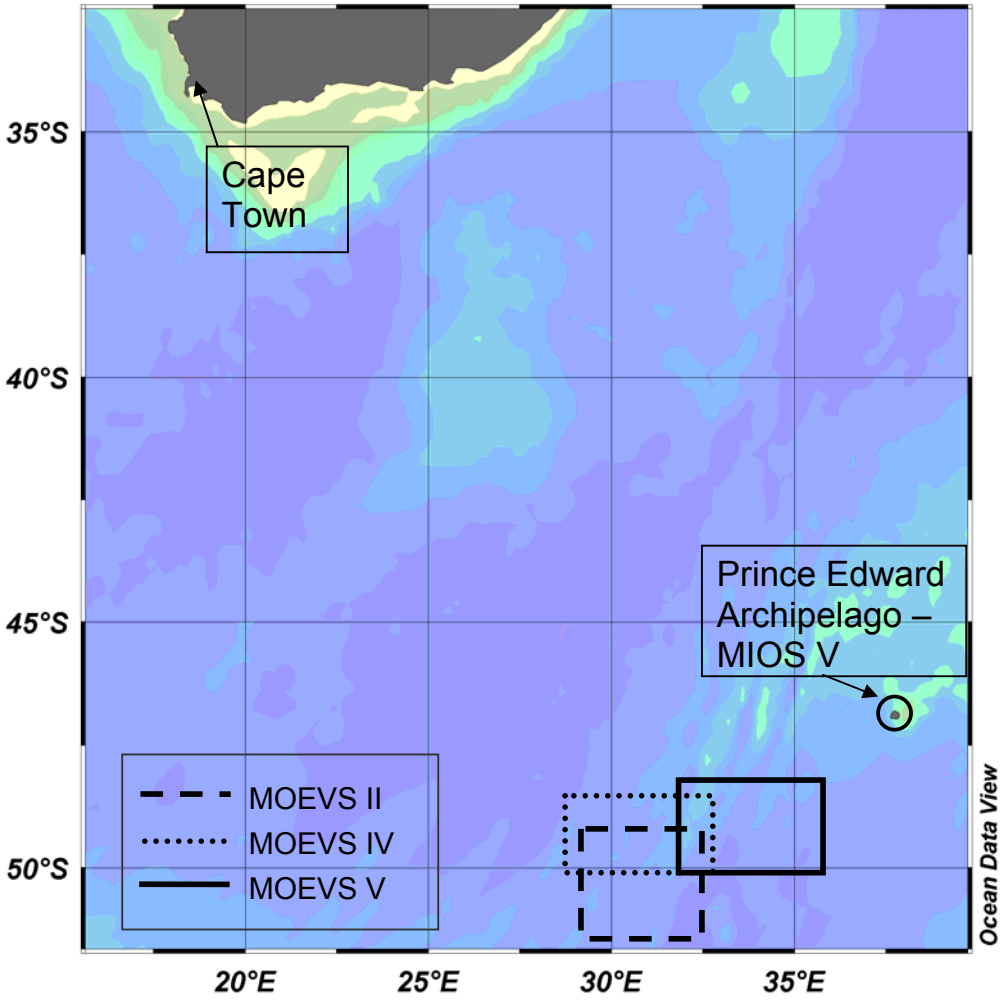

Figure 1.2 Map indicating the positions of the various surveys undertaken during the present study. MIOS V = the fifth Marion Island Offshore Survey conducted in April 2000; MOEVS II = the second Marion Offhsore Ecosystem Variability Study conducted in April 2002; MOEVS IV = the fourth Marion Offshore Ecosystem Variability Study conducted in April 2004; MOEVS V = the fifth Marion Offshore Ecosystem Variability Study conducted in April 2005.

CHAPTER TWO:

INTER-ANNUAL VARIABILITY IN THE MESOZOOPLANKTON COMMUNITY STRUCTURE IN THE POLAR FRONTAL ZONE, WITH EMPHASIS ON *LIMACINA RETROVERSA*

2.1 INTRODUCTION

The Polar Frontal Zone (PFZ) in the Southern Ocean is a transition zone that separates the two high-speed cores of the Antarctic Circumpolar Current (ACC), namely the Sub-Antarctic Front (SAF), to the north, and the Antarctic Polar Front (APF), to the south (Emery 1977). The region is typically characterised by a high degree of physical variability, with eddies (Bryden 1983; Ansorge *et al.* 1999; Froneman *et al.* 1999) and meanders (Legeckis 1977; Lutjeharms 1990; Ansorge *et al.* 1999; Froneman *et al.* 1999) in both fronts. In the region south-east of southern Africa, high flow variability within the PFZ appears to be focussed around the region of the South-West Indian Ridge and the Andrew Bain Fracture Zone, at approximately 30 ºE (Ansorge & Lutjeharms 2005; Froneman *et al.* 2002b). As the SAF and APF are forced through the Andrew Bain Fracture Zone, disturbances in the frontal systems are generated on the eastern side of the ridge, resulting in the formation of both cyclonic and anti-cyclonic eddies (Ansorge & Lutjeharms 2005.).

Eddies formed through the interaction of the ACC with the South-West Indian Ridge facilitate the transfer of plankton across the main frontal systems. As a consequence, the zooplankton species composition in the PFZ is highly variable with communities generally comprising species from a variety of origins; including sub-tropical (e.g. *Ctenocalanus vanus*; *Pleuromamma abdominalis*), sub-Antarctic (e.g. *Metridia lucens*; *Scolecithricella minor*; *Calanus simillimus*; *Limacina retroversa*) and Antarctic species (e.g. *Oithona frigida*; *Rhincalanus gigas*; *Clausocalanus laticeps*; *Ctenocalanus citer*) (Ansorge *et al.* 1999; Froneman *et al.* 1999; Pakhomov & Froneman 1999a).

Studies conducted in the various regions of the Southern Ocean have shown that the mesozooplankton community is dominated, both numerically and by biomass, by copepods of the genera *Oithona*, *Ctenocalanus*, *Calanus* and *Clausocalanus* (Hopkins 1985; Conover & Huntley 1991; Perissinotto 1992; Atkinson & Shreeve 1995; Atkinson 1996; Atkinson *et al.* 1996; Pakhomov *et al.* 2000a; Bernard & Froneman 2002; Pakhomov & Froneman 2004a). Although copepods predominate, other taxa are also a common feature of the PFZ zooplankton community. The euthecosome pteropod, *Limacina retroversa*, can reach relatively high numbers and

can, at times, contribute substantially to total mesozooplankton numbers and biomass (See for example Perissinotto 1992; Pakhomov *et al.* 1997; Froneman & Pakhomov 1998a; Bernard & Froneman 2002; Ward *et al.* 2003). Detailed studies of the variability of the abundance and distribution patterns of *L. retroversa* in the PFZ are, however, lacking.

The aim of the present chapter was, therefore, to evaluate the inter-annual variability in abundance and size structure of *L. retroversa* populations within different water masses in the Indian sector of the Southern Ocean, north of 52 ºS.

2.2 METHODS

Data were collected during three research expeditions on board the MV *SA Agulhas* to the Indian sector of PFZ during austral autumn. The expeditions were: (1) Marion Offshore Ecosystem Variability Survey II (MOEVS II, April 2002); (2) MOEVS IV (April 2004); and (3) MOEVS V (April 2005). Additionally, data collected during four previous surveys to the same region were included in multiple regression analyses to test for potential correlation between total chlorophyll-*a* (chl-*a*) concentrations and *L. retroversa* numbers. These surveys were: (1) Marion Island Offshore Study II (MIOS II, April 1997); (2) MIOS IV (April 1999); (3) MIOS V (April 2000); and (4) MOEVS I (April 2001). See Appendix, Tables A.1 to A.8, for details of each voyage.

2.2.1 Survey details

Thirteen stations were occupied in the west-Indian sector of the Southern Ocean, during MOEVS II, conducted in April 2002 (Figure 2.1). MOEVS IV consisted of an intense oceanographic survey within the PFZ between 29 ° and 33 °E and 48 ° and 50 °S (Figure 2.2). Fifteen biological stations were occupied during MOEVS IV (Figure 2.2). A multidisciplinary oceanographic survey was conducted during MOEVS V in April 2005, with the aim of investigating the physical and biological characteristics of a mesoscale negative anomaly (-40 cm sea surface height) identified within the PFZ, east of the South-West Indian Ridge, between 32 º and 36 ºE and between 47.5 º and 49.5 ºS (Figure 2.3). The anomaly, a cold core eddy,

was identified using merged geophysical data records from JASON-1 and TOPEX/Poseidon products (I.J. Ansorge, Cape Town, personal communication). Mesozooplankton samples were collected at 23 stations within and around the eddy.

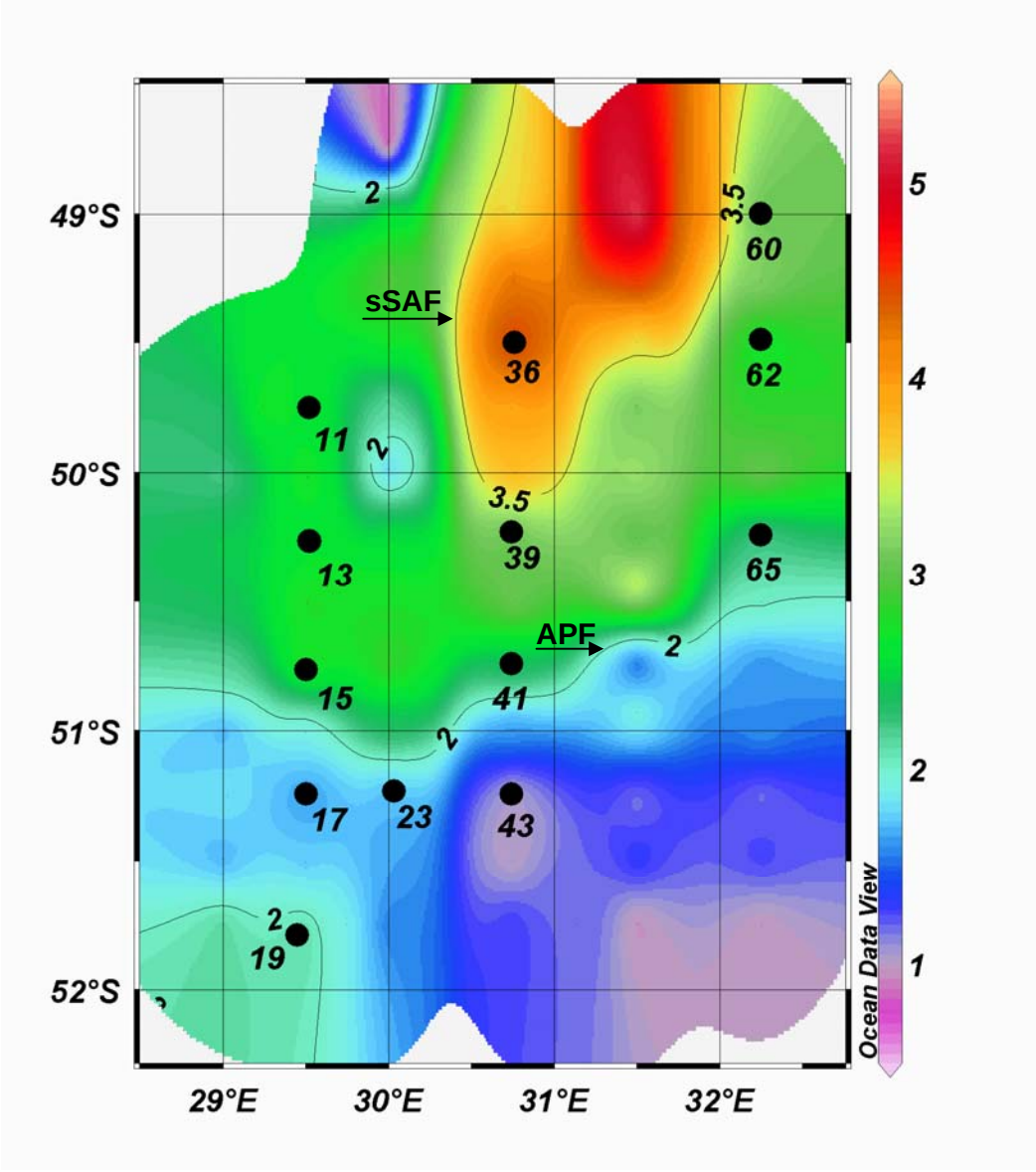

Figure 2.1 MOEVS II cruise track with station numbers of mesozooplankton net tows, superimposed over sub-surface temperature (200 m), austral autumn, 2002. Two major fronts are represented: the southern Sub-Antarctic Front (sSAF; 3.5 ºC isotherm); and the Antarctic Polar Front (APF; 2 ºC isotherm).

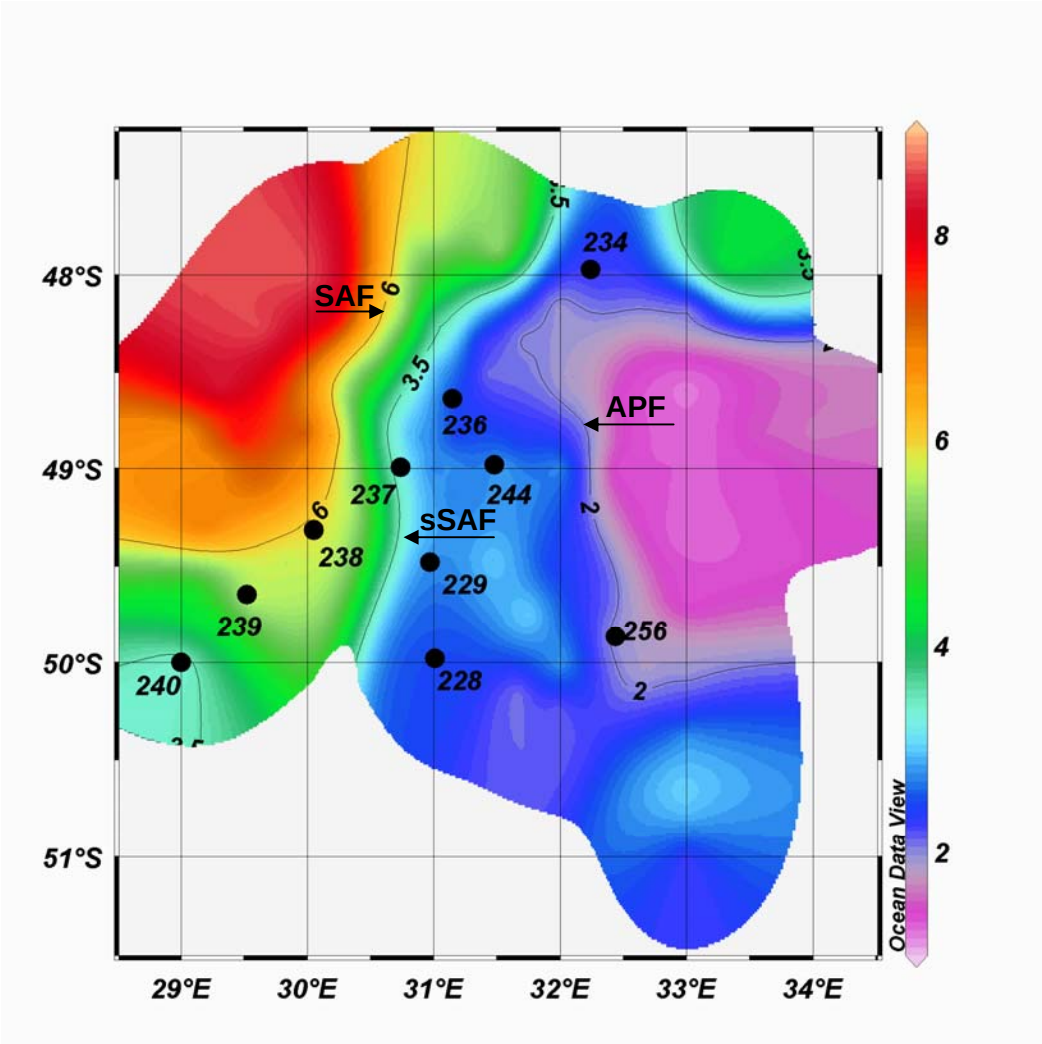

Figure 2.2 MOEVS IV cruise track with station numbers of mesozooplankton net tows, superimposed over sub-surface temperature (200 m), austral autumn, 2004. Three major fronts are represented: the Sub-Antarctic Front (SAF; 6 ºC isotherm); the southern Sub-Antarctic Front (sSAF; 3.5 ºC isotherm); and the Antarctic Polar Front (APF; 2 ºC isotherm).

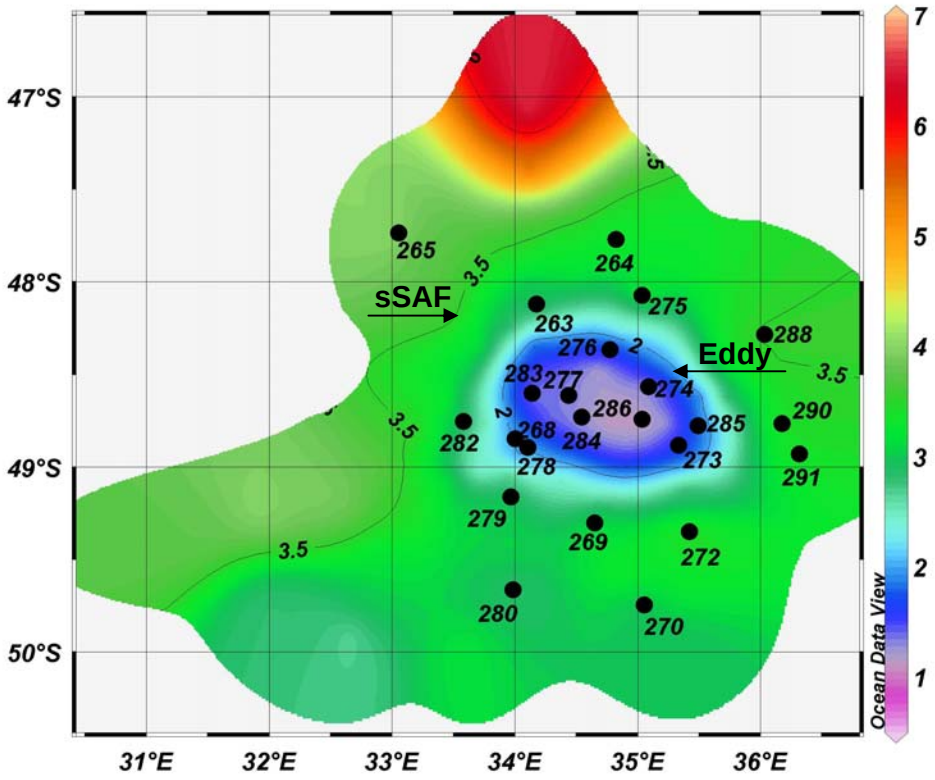

Figure 2.3 MOEVS V cruise track with station numbers of mesozooplankton net tows, superimposed over sub-surface temperature (200 m), austral autumn, 2005. The southern Sub-Antarctic Front (sSAF; 3.5 ºC isotherm) is presented. The eddy has been outlined using the 2 ºC isotherm, typically representing the Antarctic Polar Front (APF).

2.2.2 Physical oceanography

During each survey, sub-surface (200 m) temperatures were recorded at each station with a Neil Brown MK III conductivity, temperature and depth (CTD) probe. Sub-surface temperatures (200 m) were used to detect major oceanic fronts: 6 ºC for the SAF; 3.5 ºC for the southern SAF (sSAF); 2 ºC for the APF (Ansorge *et al.* 2005).

2.2.3 Phytoplankton biomass

During each survey, total surface chl-*a* concentrations were measured at each station by gently passing (< 5 cm Hg) a 250 mL aliquot of surface seawater, obtained from the scientific seawater supply, through a GF/F filter. Total chl-*a* concentrations

were then measured fluorometrically, using a Turner Fluorometer after 24 hours of extraction at -20 ºC in 90 % acetone after the method of Holm-Hansen & Riemann (1978). Size-fractionated chl-*a* concentrations were estimated during MOEVS IV and V only. A 250 mL aliquot of surface seawater was gently filtered through a serial filtration unit, separating the phytoplankton into pico- (0.45 – 2.0 µm), nano- (2.0 – 20 µm) and micro- (> 20 µm) size fractions.

2.2.4 Mesozooplankton community

During MOEVS II and V, mesozooplankton samples were collected by vertical tows using a WP-2 net fitted with a 200 µm mesh net and a 1.5 L cod-end. During MOEVS IV, mesozooplankton were collected at each station by oblique tows using a Bongo net fitted with 200 µm and 300 µm mesh nets. A Universal Underwater Unit (U^3, Robertson *et al.* 1981) was attached to the Bongo to monitor temperature and depth throughout the tow. Tows were conducted to depths of 300 m during the day and 200 m at night, to compensate for the diel vertical migrations of the zooplankton. Towing speeds varied from 0.8 to 2.5 knotts. Volume filtered during each tow was calculated by multiplying mouth area of the net (0.25 m^2 for both net types) by distance of tow. Samples were immediately fixed in 6 % buffered formalin (hexamine). In the laboratory, sub-samples (1/64 to 1/32) from each station were sorted, identified and abundance and total biomass measured. The keys of Boltovskoy (1999) were used for zooplankton identification. Abundances were expressed as the number of individuals per cubic meter (ind. m^{-3}). Additionally, the pteropod, *Limacina retroversa*, was separated into three size classes: (1) small (< 500 µm); (2) medium (500 – 1 500 µm); and (3) large (> 1 500 µm) and counted. These size classes were selected based on the findings of Dadon & de Cidre (1992). Their study of the reproductive cycle of *L. retroversa* in the Argentine Sea placed life stages of the species into the following categories: (1) immature individuals with non-developed gonads were < 500 µm; (2) immature to fully developed males were between 500 µm and 1 500 µm; and (3) individuals > 1 500 µm represented hermaphrodites with increasing female components (Dadon & de Cidre 1992). The size classes selected for the present study can therefore be categorised as the following: (1) < 500 µm (juveniles); (2) 500 – 1 500 µm (males); and (3) > 1 500 µm (females).

Total mesozooplankton biomass at each station was determined from 1/8 sub-samples. Sub-samples were retained on pre-weighed GF/F filters and oven-dried at 60 ºC for at least 24 hours, after which filters were re-weighed. Dry weights (biomass) were determined by subtracting the final weights from the initial weights. Biomass values were expressed as milligrams of dry weight per cubic metre (mg Dwt. m^{-3}). Accurate measurements of total pteropod biomass were not possible due to the varying degrees of disintegration of shells at many stations.

2.2.5 Statistical analyses

Hierarchical cluster analysis

In order to assess spatial patterns in the mesozooplankton community structure during each survey, hierarchical cluster analysis and multidimensional scaling were used in conjunction with the Bray-Curtis similarity index (Bernard & Froneman 2002; Pakhomov & Froneman 2004a). Species abundance data were log transformed [$\log_{10}(x + 1)$] in order to reduce bias due to the occurrence of highly abundant species (Legendre & Legendre 1983). The similarity programmes ANOSIM and SIMPER, of the Plymouth Routines in Multivariate Ecological Research 5 (PRIMER-E Ltd. 2005) computer package (Clarke & Warwick 1994), were used to test the significance levels and sources of difference (respectively) between the mesozooplankton communities associated with the different groupings identified by hierarchical cluster analysis (Field *et al.* 1982).

Analysis of variance

Factorial ANOVAs (StatSoft, Inc. 2004) were used to test for any significant variability between year and water mass for the following variables: total surface chl-*a* concentrations; total mesozooplankton abundances; total and size-fractionated *L. retroversa* abundances; and total copepod abundances. Post-Hoc analyses were done using Fisher's LSD tests. All variables were log-transformed.

Correlation analysis

Pearson's Correlation (Linear Correlation) analyses were used to determine whether any relationship existed between total chl-*a* biomass and *L. retroversa* numbers and between percentage contribution of micro-, nano- and picophytoplankton and *L. retroversa* numbers. Total surface chl-*a* and *L. retroversa* data used in the analysis were obtained from surveys conducted during austral autumn 1997 (MIOS II), 1999 (MIOS IV), 2000 (MIOS V) and 2001 (MOEVS I) as well as the surveys conducted during 2002 (MOEVS II), 2004 (MOEVS IV) and 2005 (MOEVS V). Data for the percentage contribution of the three size classes of phytoplankton were obtained from surveys conducted during austral autumn 2001 (MOEVS I), 2004 (MOEVS IV) and 2005 (MOEVS V).

2.3 RESULTS

2.3.1 Physical oceanography

Marion Offshore Ecosystem Variability Study (MOEVS) II – April 2002

Two oceanographic fronts were encountered during the investigation. The APF lay within a narrow band, centred on 50.75 °S and the southern branch of the SAF (sSAF) appeared to demonstrate substantial meandering (Froneman *et al.* 2002b). See Figure 2.1.

Marion Offshore Ecosystem Variability Study (MOEVS) IV – April 2004

The survey area was divided into two distinct regions, separated by an intense frontal feature, represented by the close proximity of the SAF, the sSAF and the APF. Two stations were occupied between the SAF and sSAF, with the remaining stations being situated between the sSAF and APF (Figure 2.2).

Marion Offshore Ecosystem Variability Study (MOEVS) V – April 2005

A cold core eddy was identified between 48 º and 49.25 ºS and between 33 º and 36 ºE, with a diameter of approximately 120 nautical miles and a depth exceeding 900 m (Figure 2.3). A subsurface (250 – 300 m) temperature minimum of < 0.4 ºC at

stations within the eddy suggest that the water mass originated from south of the APF (I.J. Ansorge, Cape Town, personal communication). The surrounding Sub-Antarctic water mass was between 3 and 5 ºC warmer than the centre of the eddy.

2.3.2 Phytoplankton biomass

Marion Offshore Ecosystem Variability Study (MOEVS) II – April 2002

Total surface chlorophyll-*a* (chl-*a*) concentrations ranged from 0.105 to 0.364 µg L^{-1} (Mean = 0.19 µg L^{-1}; SD = 0.07 µg L^{-1}) (Table 2.1). There was no significant relationship between total chl-*a* concentration and sea surface temperature (Pearson's Correlation: $r^2 = 0.01$; r = 0.10; p = 0.73).

Table 2.1 Total surface phytoplankton biomass (chl-*a*), MOEVS II, April 2002.

Station	Date	Time (GMT)	Longitude (ºE)	Latitude (ºN)	Surface chl-*a* (µg L^{-1})
11	04/08/02	01:25:00	29.500	-49.750	0.13
13	04/08/02	07:15:00	29.497	-50.253	0.12
15	04/08/02	13:20:00	29.517	-50.817	0.13
17	04/08/02	16:13:00	29.500	-51.250	0.11
19	04/08/02	20:25:00	29.483	-51.750	0.19
23	04/09/02	06:00:00	30.006	-51.287	0.15
36	04/11/02	11:15:00	30.744	-49.521	0.34
39	04/12/02	05:11:00	30.787	-50.246	0.20
41	04/12/02	10:05:00	30.752	-50.752	0.29
43	04/12/02	15:13:00	30.750	-51.250	0.36
60	04/14/02	06:00:00	32.310	-48.976	0.16
62	04/14/02	11:19:00	32.202	-49.464	0.13
65	04/14/02	18:46:00	32.274	-50.249	0.18

Marion Offshore Ecosystem Variability Study (MOEVS) IV – April 2004

Total surface chl-*a* concentrations during the survey ranged between 0.03 and 0.26 µg L^{-1} (Mean = 0.14 µg L^{-1}; SD = 0.06 µg L^{-1}) (Table 2.2). The picophytoplankton (< 2.0 µm) fraction dominated total chl-*a* biomass at all stations, contributing on average 64.3 % (SD = 13.2 %) to the total pigment. Nanophytoplankton (2.0 – 20.0 µm) contributed up to 56.0 % to the total, with a mean contribution of 28.8 % (SD = 14.2 %). Microphytoplankton (> 20.0 µm) contributed, on average, < 10 % to the total pigment at all stations (Table 2.2). Chl-*a* biomass was

not significantly correlated to sea surface temperature (Pearson's Correlation: r^2 = 0.06; r = 0.25; p = 0.26).

Table 2.2 Total surface and size-fractionated phytoplankton biomass (chl-*a*), MOEVS IV, April 2004.

Station	Date	Time (GMT)	Latitude (°N)	Longitude (°E)	Micro- (%)	Nano- (%)	Pico- (%)	Surface chl-*a* (µg L^{-1})
228	15.04.2004	01:16	-49.989	31.058	ND	ND	ND	0.26
229	15.04.2004	06:20	-49.499	31.016	4.6	20.7	74.7	0.16
234	16.04.2004	06:18	-48.007	32.299	5.2	30.3	64.5	0.11
236	16.04.2004	16:58	-48.668	31.166	2.2	43.1	54.7	0.08
237	16.04.2004	21:37	-48.989	30.636	15.7	20.8	63.5	0.03
238	17.04.2004	02:36	-49.326	30.090	9.0	34.7	56.3	0.16
239	17.04.2004	07:20	-49.673	29.534	3.6	11.8	84.5	0.13
240	17.04.2004	12:03	-50.002	29.001	2.2	27.3	70.5	0.13
244	18.04.2004	10:20	-48.998	31.528	5.0	56.0	39.0	0.21
256	23.04.2004	10:56	-49.852	32.453	14.9	14.2	70.9	0.10

ND = No Data

Marion Offshore Ecosystem Variability Study (MOEVS) V – April 2005

Total surface chl-*a* biomass ranged from 0.06 to 0.14 µg L^{-1} (Mean = 0.09 µg L^{-1}; SD = 0.018 µg L^{-1}) (Table 2.3). The phytoplankton community was dominated by the pico- (< 2.0 µm) and nanophytoplankton (2.0 – 20.0 µm) fractions, which contributed between 30.9 and 84.3 % (Mean = 54.8 %; SD = 12.9 %) and between 14.1 and 66.4 % (Mean = 42.4 %; SD = 12.2 %) to total phytoplankton biomass, respectively. Microphytoplankton (> 20.0 µm) contributed no more than 10 % to total biomass at all stations, with an average of 2.8 % (SD = 2.0 %). No correlation was found between sea surface temperature and total surface chl-*a* (Pearson's Correlation: r^2 = 0.01; r = -0.08; p = 0.69).

Table 2.3 Total surface and size-fractionated phytoplankton biomass (chl-*a*), MOEVS V, April 2005.

Station	Date	Time (GMT)	Latitude (ºN)	Longitude (ºE)	Micro- (%)	Nano- (%)	Pico- (%)	Surface chl-*a* (µg L^{-1})
263	04/17/05	11:24:00	-48.123	34.149	0.0	36.5	63.4	0.08
264	04/17/05	18:07:00	-47.788	34.750	3.6	54.1	42.3	0.06
265	04/18/05	04:50:00	-47.767	33.006	5.1	58.3	36.6	0.09
268	04/18/05	22:08:00	-48.877	34.077	2.6	21.4	76.0	0.07
269	04/19/05	03:31:00	-49.318	34.652	2.6	41.2	56.3	0.12
270	04/19/05	08:43:00	-49.747	35.077	3.4	30.6	66.0	0.11
272	04/19/05	18:03:00	-49.406	35.377	3.1	51.2	45.7	0.07
273	04/19/05	23:19:00	-48.914	35.325	3.8	33.8	62.4	0.09
274	04/20/05	05:59:00	-48.573	35.084	2.8	66.4	30.9	0.08
275	04/20/05	13:32:00	-48.087	35.036	10.0	49.2	40.8	0.08
276	04/20/05	19:12:00	-48.362	34.781	2.0	59.1	38.9	0.07
277	04/21/05	00:08:00	-48.626	34.467	2.3	47.4	50.4	0.10
278	04/21/05	04:38:00	-48.915	34.112	3.2	37.6	59.2	0.07
279	04/21/05	09:38:00	-49.165	33.945	4.0	42.0	54.0	0.10
280	04/21/05	14:34:00	-49.671	34.015	1.8	41.1	57.1	0.08
282	04/22/05	01:18:00	48.773	33.576	3.6	49.1	47.4	0.10
283	04/22/05	06:10:00	48.765	33.980	0.7	29.6	69.8	0.14
284	04/22/05	11:11:00	48.726	34.527	1.6	14.1	84.3	0.07
285	04/22/05	15:10:00	48.752	35.030	1.4	51.3	47.3	0.09
286	04/22/05	19:06:00	48.778	35.488	1.9	44.2	53.8	0.10
288	04/23/05	04:47:00	48.132	35.916	2.6	39.7	57.8	0.08
290	04/23/05	13:55:00	48.768	36.201	3.0	42.9	54.1	0.10
291	04/24/05	09:00:00	48.944	36.335	0.0	34.1	65.9	0.10

2.3.3 Mesozooplankton community

Marion Offshore Ecosystem Variability Study (MOEVS) II – April 2002

Total mesozooplankton numbers during the survey ranged between 19.06 and 657.53 ind. m^{-3} (Mean = 250.35 ind. m^{-3}; SD = 221.91 ind. m^{-3}). Total mesozooplankton numbers were dominated by copepods (*Calanus simillimus*, *Oithona similis*, *Clausocalanus* spp. and *Ctenocalanus* spp.), which contributed an average of 79.4 % to the total numbers (SD = 11.0 %) (Table 2.4). Total mesozooplankton biomass ranged between 1.31 and 33.22 mg Dwt. m^{-3} (Mean = 7.03 mg Dwt. m^{-3}; SD = 8.55 mg Dwt. m^{-3}) (Table 2.4).

Limacina retroversa were recorded in numbers reaching up to 71.58 ind. m^{-3} (Mean = 17.82 ind. m^{-3}; SD = 23.35 ind. m^{-3}) during the survey (Table 2.4). The pteropod, however, only contributed between 0.4 and 20.7 % to total mesozooplankton numbers (Mean = 8.4 %; SD = 6.9 %). Small and medium

individuals were most common during the survey, contributing an average of 45.2 % (SD = 30.7 %) and 45.4 % (SD = 27.3 %) to the total pteropod numbers, respectively (Figure 2.4). Large individuals only accounted for an average of 9.4 % (SD = 12.6 %) of the total (Figure 2.4).

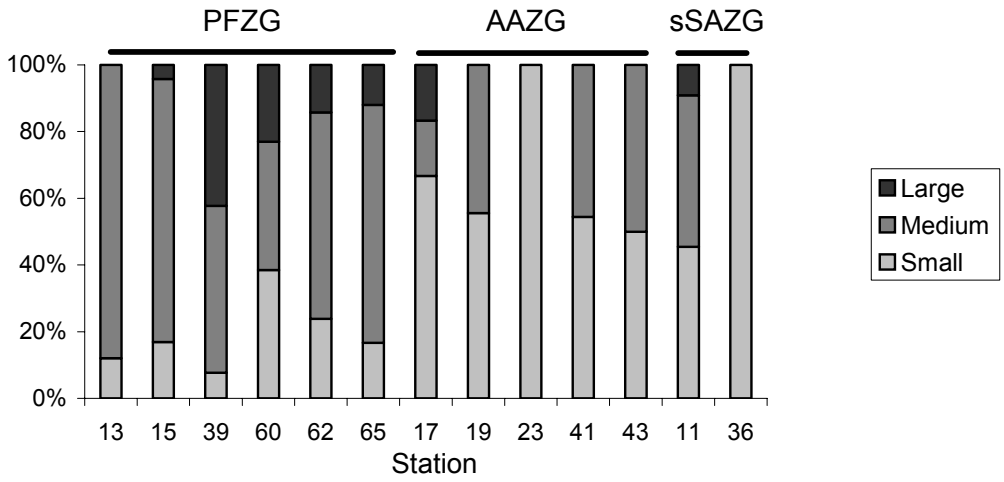

Figure 2.4 Size class structure of *L. retroversa* during MOEVS II, April 2002. Stations have been separated into groups identified by hierarchical cluster analysis. PFZG = Polar Frontal Zone Group; AAZG = Antarctic Zone Group; sSAZG = southern Sub-Antarctic Zone Group.

Table 2.4 Total mesozooplankton and dominant species abundances (ind. m^{-3}) and total biomass (mg Dwt. m^{-3}), MOEVS II, April 2002. Groupings identified by hierarchical cluster analysis.

	PFZG						AAZG					sSAZG	
Station numbers	**13**	**15**	**39**	**60**	**62**	**65**	**17**	**19**	**23**	**41**	**43**	**11**	**36**
Calanus simillimus	144.86	34.40	5.44	7.06	1.97	1.76	10.36	24.03	13.35	4.75	1.76	117.81	4.99
Oithona similis	111.63	218.23	10.55	20.55	3.94	70.79	58.38	279.02	350.86	86.48	39.64	156.25	30.82
Clausocalanus spp.	9.37	3.23	1.76	5.65	2.25	5.96	7.53	17.36	31.15	6.25	4.40	17.55	0.89
Ctenocalanus spp.	13.63	12.90	4.69	14.75	2.54	22.50	128.52	216.27	186.87	6.92	49.77	32.59	4.28
Limacina retroversa	71.58	52.68	3.77	5.49	2.68	29.77	5.18	41.39	4.45	7.20	4.63	1.67	1.25
Ostracods	0.85	2.15	1.42	5.02	1.27	0.44	0.00	2.67	0.00	0.00	0.66	0.84	0.53
Appendicularians	19.60	1.08	0.08	1.41	0.70	0.00	0.94	12.02	41.32	0.68	1.32	55.15	0.00
Sagitta gazellae	0.85	0.00	0.08	0.47	0.00	0.22	0.00	0.00	0.00	0.14	0.00	0.84	1.96
Eukrohnia hamata	5.11	1.08	0.75	11.77	1.69	1.54	0.00	4.01	2.54	1.77	0.66	21.73	17.64
Total abundance	388.71	351.81	30.92	80.60	19.06	143.58	219.27	657.53	650.71	118.71	114.33	407.76	71.55
Total biomass	8.38	33.22	1.31	5.92	3.48	3.57	3.19	13.95	5.12	2.31	3.66	5.42	1.80

Marion Offshore Ecosystem Variability Study (MOEVS) IV – April 2004

Total mesozooplankton abundance during the survey was highly variable, ranging from 51.07 to 870.83 ind. m^{-3} (Mean = 352.00 ind. m^{-3}; SD = 238.48 ind. m^{-3}). Copepods dominated total mesozooplankton numbers, contributing an average of 75.5 % to the total (SD = 13.5 %). The chaetognaths, *Eukrohnia hamata* and *Sagitta gazellae*, on average, accounted for < 5.5 % of the total, with the exception of station 239, where they contributed up to 22.4 % to the total numbers (Table 2.5). Total mesozooplankton biomass values were highly variable, ranging from 2.61 to 38.42 mg Dwt. m^{-3} (Mean = 16.62 mg Dwt. m^{-3}; SD = 10.62 mg Dwt. m^{-3}) (Table 2.5).

L. retroversa was recorded in numbers of up to 107.42 ind. m^{-3} (Mean = 43.02 ind. m^{-3}; SD = 38.60 ind. m^{-3}), contributing an average of 11.8 % to total numbers (SD = 8.7 %) (Table 2.5). Total pteropod numbers were dominated entirely by medium-sized individuals, accounting for, on average, 82.4 % (SD = 5.5 %) of the total (Figure 2.5). Small and large individuals only contributed an average of 7.6 % (SD = 5.8 %) and 10.0 % (SD = 5.5 %), respectively (Figure 2.5).

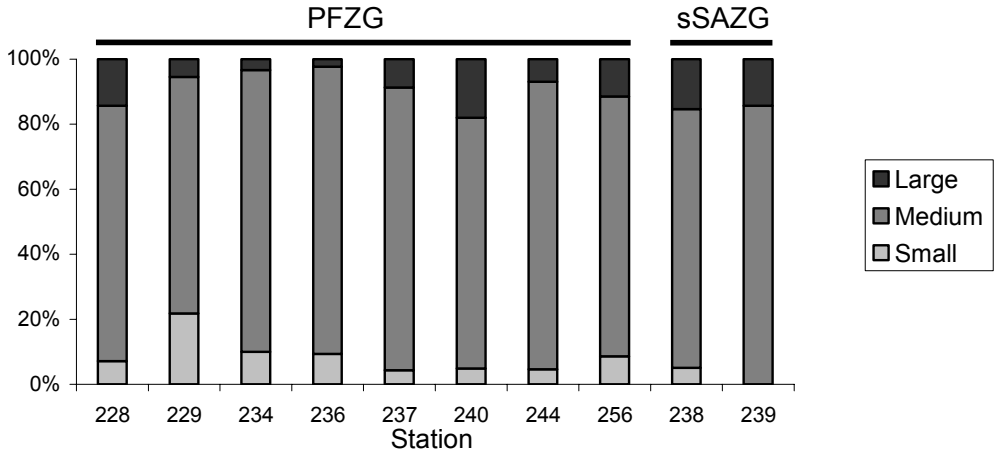

Figure 2.5 Size class structure of *L. retroversa* during MOEVS IV, April 2004. Stations have been separated into groups identified by hierarchical cluster analysis. PFZG = Polar Frontal Zone Group; sSAZG = southern Sub-Antarctic Zone Group.

Table 2.5 Total mesozooplankton and dominant species abundances (ind. m^{-3}) and total biomass (mg Dwt. m^{-3}), MOEVS IV, April 2004. Groupings identified by hierarchical cluster analysis.

	PFZG								sSAZG	
Station numbers	**228**	**229**	**234**	**236**	**237**	**240**	**244**	**256**	**238**	**239**
Calanus simillimus	149.10	69.55	76.49	99.50	107.00	145.14	290.04	33.39	0.78	1.58
Oithona similis	213.77	31.68	23.80	73.01	10.26	18.75	19.26	59.37	18.30	5.27
Clausocalanus spp.	77.25	26.85	8.50	23.26	14.66	14.68	16.05	29.68	30.81	5.53
Ctenocalanus spp.	174.25	77.12	27.20	69.13	80.62	75.83	69.57	82.56	14.54	5.80
Ostracods	37.72	13.08	17.00	6.46	22.72	10.60	39.60	13.91	4.69	10.14
Limacina retroversa	70.06	107.42	26.06	83.34	30.78	4.08	80.27	19.48	1.56	7.11
Sagitta gazellae	14.37	1.38	2.27	1.29	2.20	3.26	6.42	1.86	1.25	0.92
Eukrohnia hamata	1.80	2.75	6.23	3.88	15.39	20.39	23.55	7.42	1.09	10.54
Total abundance	870.83	357.90	206.62	396.74	319.09	322.95	595.43	302.93	96.41	51.06
Total biomass	21.74	17.90	13.03	18.22	23.53	19.00	38.42	8.63	2.61	3.08

Marion Offshore Ecosystem Variability Study (MOEVS) V – April 2005

Total mesozooplankton abundances during MOEVS V were highly variable, ranging from 16.75 to 605.27 ind. m^{-3} (Mean = 161.77 ind. m^{-3}; SD = 155.08 ind. m^{-3}). The mesozooplankton community was numerically dominated by copepods, mainly *Calanus simillimus*, *Clausocalanus* spp., *Ctenocalanus citer* and *Oithona* spp., which collectively accounted for up to 98.1 % of total numbers (Mean = 88.1 %; SD = 8.2 %). Other major contributors to total mesozooplankton numbers were chaetognaths (*Sagitta gazellae* and *Eukrohnia hamata*), which contributed up to 17.9 % to the total (Mean = 5.5 %; SD = 5.1 %) (Table 2.6). Total mesozooplankton biomass ranged between 0.76 and 32.26 mg Dwt. m^{-3} (Mean = 6.05 mg Dwt. m^{-3}; SD = 6.49 mg Dwt. m^{-3}) (Table 2.6).

The pteropod, *L. retroversa*, was very scarce during the entire survey, with an average abundance of 0.92 ind. m^{-3} (SD = 1.15 ind. m^{-3}) (Table 2.6). *L. retroversa* contributed between 0.0 and 3.6 % to total mesozooplankton abundance (Mean = 0.9 %; SD = 1.0 %). Medium-sized individuals made the greatest contribution to total pteropod numbers during the survey, reaching up to 100.0 % of the total (Mean = 46.9 %; SD = 33.7 %) (Figure 2.6). Small and large individuals accounted for approximately 16.6 % (SD = 23.1 %) and 14.8 % (SD = 17.0 %) of the total, respectively, during the survey (Figure 2.6).

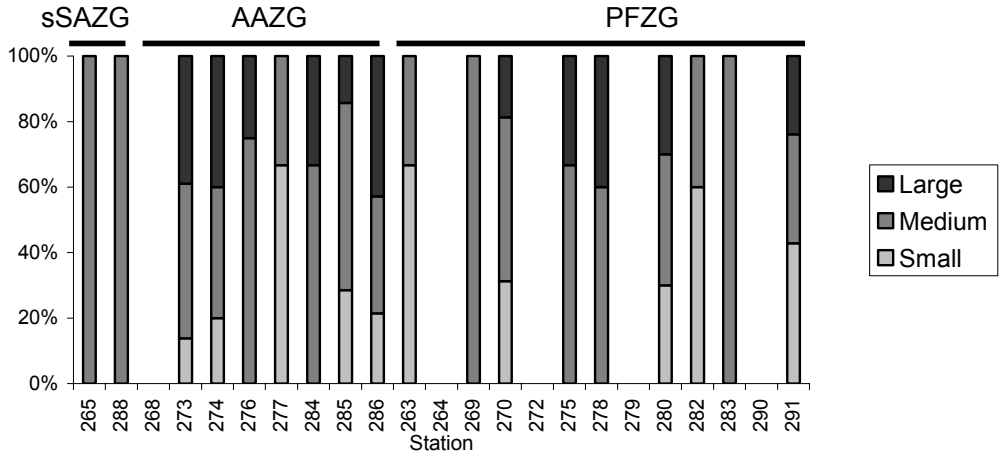

Figure 2.6 Size class structure of *L. retroversa* during MOEVS V, April 2005. Stations have been separated into groups identified by hierarchical cluster analysis. sSAZG = southern Sub-Antarctic Zone Group; AAZG = Antarctic Zone Group; PFZG = Polar Frontal Zone Group.

Table 2.6 Total mesozooplankton and dominant species abundances (ind. m^{-3}) and total biomass (mg Dwt. m^{-3}), MOEVS V, April 2005. Groupings identified by hierarchical cluster analysis.

	sSAZG		AAZG							
Station numbers	**265**	**288**	**268**	**273**	**274**	**276**	**277**	**284**	**285**	**286**
Calanus simillimus	25.333333	115.071	46.667	230.603	28.381	43.022	15.333	4.286	123.077	19.710
Clausocalanus spp.	6.5641026	3.556	16.000	40.635	3.810	13.867	9.556	0.524	18.051	5.797
Ctenocalanus spp.	0	4.848	104.000	111.746	27.619	129.067	70.667	1.952	101.744	26.435
Oithona spp.	2.4615385	3.232	135.556	164.571	80.762	113.778	43.111	13.857	180.513	67.478
Chaetognaths	1.6410256	5.172	1.778	1.016	1.143	1.067	1.111	0.286	1.641	0.000
Ostracods	2.2564103	2.909	1.778	2.032	0.571	1.067	0.000	0.238	3.282	0.696
Limacina retroversa	0.6153846	0.646	0.000	4.063	0.190	1.067	0.222	0.810	1.641	0.232
Total abundances (ind. m^{-3})	39.355311	138.354	320.848	605.267	148.025	311.180	146.044	22.698	451.997	131.710
Total biomass (mg Dwt. m^{-3})	4.912	10.027	9.920	32.256	3.029	8.960	2.112	0.768	8.960	4.096

Table 2.6 Continued…

	PFZG												
Station numbers	**263**	**264**	**269**	**270**	**272**	**275**	**278**	**279**	**280**	**282**	**283**	**290**	**291**
Calanus simillimus	69.333	22.538	35.200	15.583	41.978	5.333	47.238	55.188	35.171	23.200	31.429	3.368	4.310
Clausocalanus spp.	32.762	3.269	0.533	0.167	1.720	0.202	6.857	3.246	4.036	1.867	1.524	3.789	0.186
Ctenocalanus spp.	144.762	14.452	2.400	2.500	10.667	1.939	52.190	15.304	42.667	34.667	11.048	7.018	1.457
Oithona spp.	99.810	2.581	14.533	17.500	19.613	5.051	62.095	22.725	2.595	33.333	24.000	22.035	5.736
Chaetognaths	28.190	5.849	3.333	3.000	8.774	2.263	4.952	19.478	5.189	10.400	3.048	10.947	2.016
Ostracods	10.667	1.204	1.333	1.333	3.097	1.576	6.857	12.986	5.477	2.400	1.714	5.614	1.395
Limacina retroversa	3.810	0.000	0.933	0.083	0.000	0.525	2.286	0.000	2.018	1.067	0.762	0.000	0.279
Total abundances (ind. m^{-3})	407.293	63.644	62.305	42.060	91.502	17.657	196.068	144.621	105.284	117.248	79.555	61.313	16.755
Total biomass (mg Dwt. m^{-3})	8.021	4.000	2.640	1.536	6.176	1.099	6.272	9.216	4.281	4.256	4.715	0.757	1.088

2.3.4 Statistical analyses

Hierarchical cluster analysis

Marion Offshore Ecosystem Variability Study (MOEVS) II – April 2002

Hierarchical cluster analysis separated the stations into three groups. Group 1 consisted of six stations (stations 13, 15, 39, 60, 62 and 65), which were situated primarily within the PFZ waters and is named the PFZ Group (PFZG). Group 2 was made up of five stations (stations 17, 19, 23, 41 and 43), situated mainly in the Antarctic Zone (AAZ) waters and has thus been designated the AAZ Group (AAZG). Finally, Group 3 consisted of only two stations (stations 11 and 36), which were positioned in or near the southern Sub-Antarctic Zone (sSAZ), and was therefore named the sSAZ Group (sSAZG) (Figure 2.7). ANOSIM tests indicated that the three groups were significantly different from each other ($p < 0.05$ in all cases). Taxa responsible for the similarity within groups and dissimilarity between groups are presented in Table 2.7. The copepods, *O. similis*, *Ctenocalanus* spp. and *C. simillimus* and the pteropod, *L. retroversa* were responsible for most of the similarity within the groups (Table 2.7). The distinction of the three groupings identified with the hierarchical cluster analysis was largely due to shifts in the relative abundances of the numerically dominant species, rather than the presence or absence of individual species.

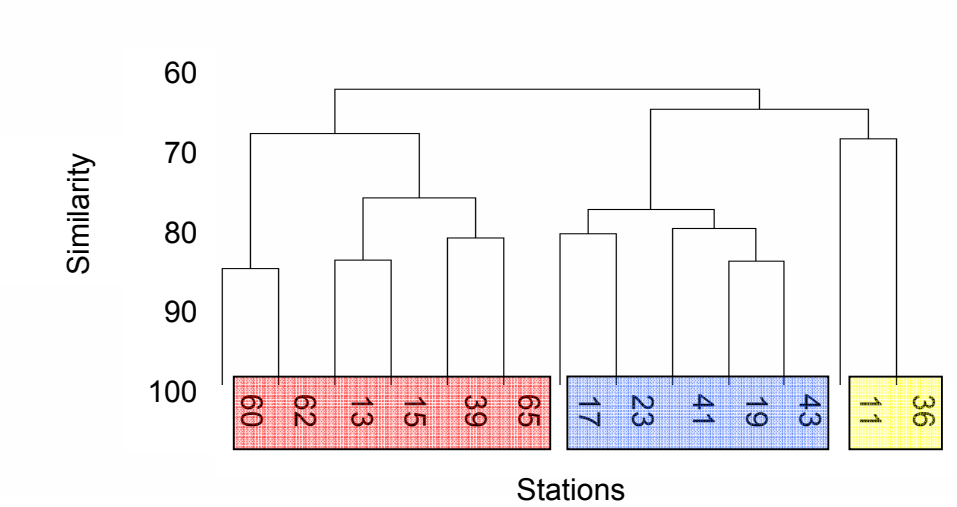

Figure 2.7 Results of the hierarchical cluster analysis (Primer-E, Ltd. 2005) for mesozooplankton communities encountered during MOEVS II, April 2002. Red box = Group 1 (PFZG); Blue box = Group 2 (AAZG); Yellow box = Group 3 (sSAZG).

Table 2.7 Species responsible for similarity within groups identified using hierarchical cluster analysis, MOEVS II, April 2002 (SIMPER, PRIMER-E, Ltd. 2005). PFZG = Polar Frontal Zone Group; AAZG = Antarctic Zone Group; sSAZG = southern Sub-Antarctic Zone Group.

Group 1 (PFZG)		**Group 2 (AAZG)**		**Group 3 (sSAZG)**	
Average Similarity: 76.8 %		**Average Similarity: 79.7 %**		**Average Similarity: 68.0 %**	
Taxon	**Average abundance (ind. m^{-3})**	**Taxon**	**Average abundance (ind. m^{-3})**	**Taxon**	**Average abundance (ind. m^{-3})**
O. similis	72.62	*O. similis*	162.87	*O. similis*	93.54
L. retroversa (total)	27.66	*Ctenocalanus* spp.	117.67	*C. simillimus*	61.40
Ctenocalanus spp.	11.83	*C. simillimus*	10.85	*Ctenocalanus* spp.	18.43
L. retroversa (medium)	21.90	*L. retroversa* (total)	12.57	*E. hamata*	19.68
C. simillimus	32.58	*C. laticeps*	6.19	*C. laticeps*	4.86
L. retroversa (small)	4.25	*L. retroversa* (small)	7.42		
C. laticeps	2.53	*C. brevipes*	7.14		
E. hamata	3.66	*Paraeuchaeta* spp.	3.19		
Paraeuchaeta spp	2.15	Appendicularians	11.25		
C. brevipes	2.17				
Nauplii	1.83				

Marion Offshore Ecosystem Variability Study (MOEVS) IV – April 2004

Hierarchical cluster analysis, carried out on the entire mesozooplankton community at each station, identified two distinct, significantly different groupings of mesozooplankton during the survey (ANOSIM: $p < 0.05$) (Figure 2.8). The first group consisted of eight stations found within the PFZ (stations 228, 229, 234, 236, 237, 240, 244 and 256), and was thus termed the PFZ Group (PFZG). The second group included only two stations found in the southern sSAZ (stations 238 and 239) and was thus designated the sSAZ Group (sSAZG). Differences between the two groupings could be ascribed to shifts in the relative contribution of the numerically dominant species as opposed to the presence or absence of individual species. The average abundances of the most numerous zooplankton taxa, accounting for < 70 % of the similarity within the two groupings identified with the numerical analysis is shown in Table 2.8.

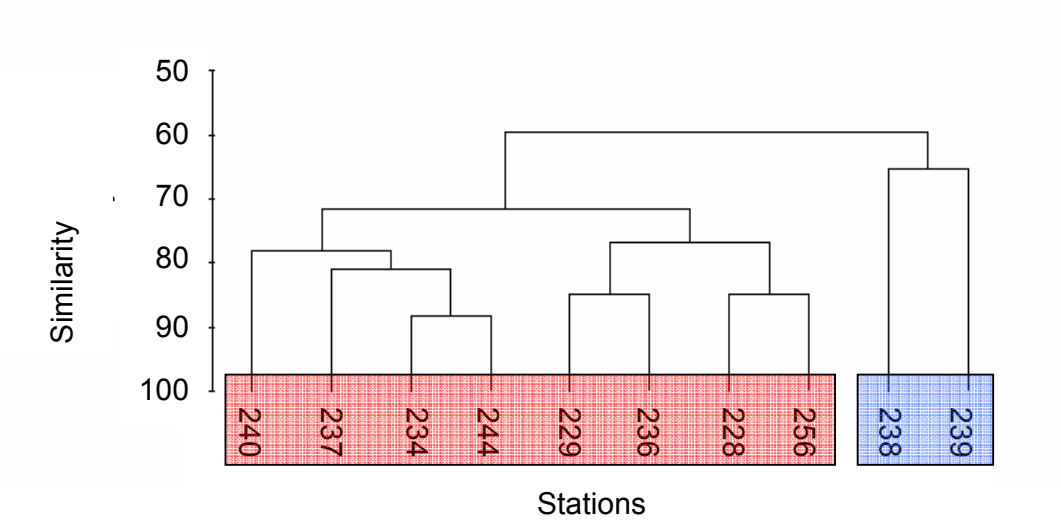

Figure 2.8 Results of the hierarchical cluster analysis (Primer-E, Ltd. 2005) for mesozooplankton communities encountered during MOEVS IV, April 2004. Red box = Group 1 (PFZG); Blue box = Group 2 (sSAZG).

Table 2.8 Species responsible for similarity within groups identified using hierarchical cluster analysis, MOEVS IV, April 2004 (SIMPER, PRIMER-E, Ltd. 2005). PFZG = Polar Frontal Zone Group; sSAZG = southern Sub-Antarctic Zone Group.

Group 1 (PFZG)		**Group 2 (sSAZG)**	
Average Similarity: 78.4 %		**Average Similarity: 65.3 %**	
Taxon	**Average abundance (ind. m^{-3})**	**Taxon**	**Average abundance (ind. m^{-3})**
C. simillimus	360.37	*Ctenocalanus* spp.	39.15
Ctenocalanus spp.	232.02	*C. brevipes*	71.04
L. retroversa (total)	160.31	*O. similis*	45.97
O. similis	161.76	Ostracods	12.34
C. laticeps	38.49	*S. minor*	5.23
M. lucens	50.23	*Orthoconcheocia* spp.	7.07
L. retroversa (medium)	43.24	*M. lucens*	26.13
C. brevipes	35.50	*L. retroversa* (total)	14.72
Paraconchoecia spp.	30.62	*S. gazellae*	4.05
E. hamata	28.85	*E. hamata*	19.31
O. frigida	27.70	*Paraconchoecia* spp.	6.62
S. minor	16.52	*C. simillimus*	4.16
Ostracods	17.18		
S. gazellae	11.83		

Marion Offshore Ecosystem Variability Study (MOEVS) V – April 2005

Results of the hierarchical cluster analysis identified three significantly different groupings of mesozooplankton during MOEVS V (ANOSIM: $p < 0.05$ in all cases) (Figure 2.9). Group 1 consisted of only two stations (stations 265 and 288) that were positioned within the southern sSAZ, and have been named the sSAZ Group (sSAZG). Group 2 consisted of those stations within the eddy (stations 268, 273, 274, 276, 277, 284, 285 and 286), and were designated the name Eddy Group. Group 3 consisted of stations occupied in the surrounding PFZ waters (stations 263, 264, 269, 270, 272, 275, 278, 279, 280, 282, 283, 290 and 291) and was therefore given the name PFZ Group (PFZG). Again, the differences between the three groups were ascribed to changes in the relative contribution of the more ubiquitous dominant mesozooplankton in the region, rather than the presence/absence of individual species (Table 2.9). The main species responsible for the dissimilarity between the three groupings were *Calanus simillimus*, *Oithona* spp., *Ctenocalanus* spp. and *Clausocalanus* spp. (Table 2.9). All four copepod species are fairly widespread, occurring in both the sub-Antarctic and Antarctic waters (Boltovskoy 1999). As a result, these species cannot be employed as indicator species of specific water masses encountered during the study.

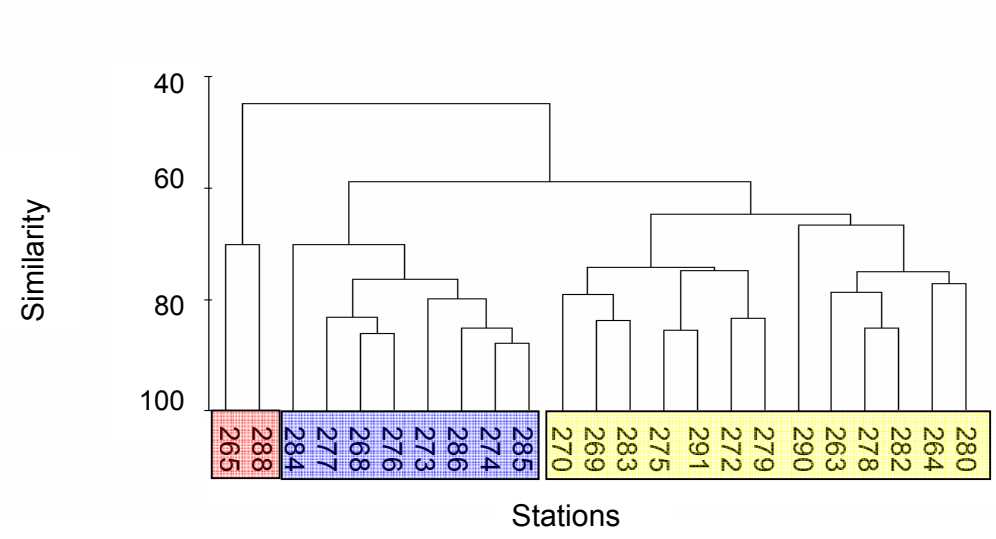

Figure 2.9 Results of the hierarchical cluster analysis (Primer-E, Ltd. 2005) for mesozooplankton communities encountered during MOEVS V, April 2005. Red box = Group 1 (sSAZG); Blue box = Group 2 (Eddy Group); Yellow box = Group 3 (PFZG).

Table 2.9 Species responsible for similarity within groups identified using hierarchical cluster analysis, MOEVS V, April 2005 (SIMPER, PRIMER-E, Ltd. 2005). sSAZG = southern Sub-Antarctic Zone Group; PFZG = Polar Frontal Zone Group.

Group 1 (sSAZG)		**Group 2 (Eddy Group)**		**Group 3 (PFZG)**	
Average Similarity: 70.2 %		**Average Similarity: 81.1 %**		**Average Similarity: 75.8 %**	
Taxon	**Average abundance (ind. m^{-3})**	**Taxon**	**Average abundance (ind. m^{-3})**	**Taxon**	**Average abundance (ind. m^{-3})**
C. simillimus	95.71	*Oithona* spp.	126.17	*C. simillimus*	38.06
Chaetognaths	4.69	*Ctenocalanus* spp.	96.70	*Oithona* spp.	29.79
Oithona spp.	4.05	*C. simillimus*	77.13	*Ctenocalanus* spp.	31.84
Ostracods	3.68	*Clausocalanus* spp.	12.16	Chaetognaths	9.87
Clausocalanus spp.	2.19	*C. laticeps*	5.33	Ostracods	4.95
C. laticeps	5.28	*M. lucens*	6.07	*M. lucens*	3.30
		Nauplii	2.47	*Clausocalanus* spp.	3.88
				S. minor	1.09
				P. abdominalis	1.25

Analysis of variance

Total surface chl-*a* concentrations exhibited no significant variability between the various water masses encountered during any of the three surveys (Table 2.10). Surface chl-*a* concentrations in the sSAZ, PFZ and AAZ waters showed inter-annual variability, with values in all three water masses being significantly greater during MOEVS II than MOEVS V (Table 2.10). No significant inter-annual variability was detected in any of the water masses between MOEVS II and IV and MOEVS IV and V (Table 2.10).

Table 2.10 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Total surface chlorophyll-*a*.

	MOEVS II	MOEVS IV	MOEVS V	sSAZ	PFZ	AAZ
sSAZ – PFZ	p = 0.30	p = 0.44	p = 0.93			
sSAZ – AAZ	p = 0.87		p = 0.88			
PFZ – AAZ	p = 0.24		p = 0.68			
II – IV				p = 0.35	p = 0.20	
II – V				p = 0.03 (II > V)	p = 0.01 (II > V)	p < 0.001 (II > V)
IV – V				p = 0.19	p = 0.16	

Total mesozooplankton numbers showed no significant variability between water masses during MOEVS II (Table 2.11). Mesozooplankton abundances during MOEVS IV, however, were significantly greater in the PFZ than in the sSAZ (Table 2.11), while during MOEVS V, numbers were greater in the AAZ than the PFZ, with values in the sSAZ being intermediate between the two (Table 2.11). Both the sSAZ and AAZ water masses showed no significant variability in total mesozooplankton numbers between the years, while the PFZ water mass exhibited significantly greater mesozooplankton abundances during MOEVS IV than either MOEVS II or MOEVS V (Table 2.11).

Table 2.11 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Total mesozooplankton abundance.

	MOEVS II	MOEVS IV	MOEVS V	sSAZ	PFZ	AAZ
sSAZ – PFZ	p = 0.47	p = 0.02 (sSAZ < PFZ)	p = 0.96			
sSAZ – AAZ	p = 0.57		p = 0.19			
PFZ – AAZ	p = 0.08		p = 0.03 (PFZ < AAZ)			
II – IV				p = 0.33	p = 0.01 (II < IV)	
II – V				p = 0.36	p = 0.57	p = 0.54
IV – V				p = 0.96	p < 0.001 (IV > V)	

L. retroversa numbers were significantly greater in the PFZ waters than in the sSAZ during MOEVS II and IV, but showed no significant variability between water masses during MOEVS V (Table 2.12). In the PFZ and AAZ waters, abundances of *L. retroversa* were significantly greater during MOEVS II and IV than during MOEVS V (Table 2.12). Total copepod abundances showed significant variability between water masses during all three surveys (Table 2.13). During MOEVS II and MOEVS V, copepods were most abundant in the AAZ waters, while during MOEVS IV, copepods were most numerous in the PFZ water mass (Table 2.13). No inter-annual variability in copepod numbers occurred in either the sSAZ or AAZ water masses (Table 2.13). However, in the PFZ, numbers of copepods were greatest during MOEVS IV (Table 2.13).

Table 2.12 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): *L. retroversa* abundance.

	MOEVS II	**MOEVS IV**	**MOEVS V**	**sSAZ**	**PFZ**	**AAZ**
sSAZ – PFZ	p = 0.02 (sSAZ < PFZ)	p = 0.01 (sSAZ < PFZ)	p = 0.77			
sSAZ – AAZ	p = 0.08		p = 0.96			
PFZ – AAZ	p = 0.44		p = 0.72			
II – IV				p = 0.47	p = 0.11	
II – V				p = 0.47	p < 0.001 (II > V)	p < 0.001 (II > V)
IV – V				p = 0.15	p < 0.001 (IV > V)	

Table 2.13 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Copepod abundance.

	MOEVS II	**MOEVS IV**	**MOEVS V**	**sSAZ**	**PFZ**	**AAZ**
sSAZ – PFZ	p = 0.47	p = 0.01 (sSAZ < PFZ)	p = 0.94			
sSAZ – AAZ	p = 0.41		p = 0.19			
PFZ – AAZ	p = 0.04 (PFZ < AAZ)		p = 0.01 (PFZ < AAZ)			
II – IV				p = 0.27	p = 0.01 (II < IV)	
II – V				p = 0.52	p = 0.82	p = 0.62
IV – V				p = 0.64	p < 0.001 (IV > V)	

The percentage contribution of small individuals of *L. retroversa* to total *L. retroversa* numbers did not vary significantly between water masses during either MOEVS IV or MOEVS V (Table 2.14). However, during MOEVS II, the percentage contribution of small pteropods was significantly greater in the AAZ water mass than in the PFZ waters (Table 2.14). Significant inter-annual variability in the percentage contribution of small *L .retroversa* was observed in all three water masses with values in the sSAZ and AAZ waters being greatest during MOEVS II, while those in the PFZ water mass were greatest during MOEVS II and V (Table 2.14). During MOEVS II, the percentage contribution of medium-sized *L. retroversa* was greatest in the sSAZ and PFZ waters (Table 2.15). However, no significant variability between water masses was observed during either MOEVS IV or V (Table 2.15). In the sSAZ waters, no inter-annual variability was exhibited for the relative contribution of medium-sized pteropods. In the PFZ, however, the percentage of medium-sized individuals was significantly greater during MOEVS IV than either MOEVS II or V (Table 2.15). In the AAZ waters the percentage contribution of medium-sized pteropods was significantly higher during MOEVS V than MOEVS II (Table 2.15). The percentage contribution of large *L. retroversa* did not exhibit any significant variability between water masses during any of the three surveys (MOEVS II, IV and V) (Table 2.16). Inter-annual variability in percentage contribution of large individuals only occurred in the PFZ water mass, with values being greatest during MOEVS V (Table 2.16).

Table 2.14 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Percentage contribution of small individuals to total *L. retroversa* abundance.

	MOEVS II	**MOEVS IV**	**MOEVS V**	**sSAZ**	**PFZ**	**AAZ**
sSAZ – PFZ	p = 0.10	p = 0.44				
sSAZ – AAZ	p = 0.58					
PFZ – AAZ	p = 0.03 (PFZ < AAZ)		p = 0.18			
II – IV				p = 0.01 (II > IV)	p = 0.01 (II > IV)	
II – V					p = 0.09	p = 0.04 (II > V)
IV – V					p < 0.001 (IV < V)	

Table 2.15 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Percentage contribution of medium individuals to total *L. retroversa* abundance.

	MOEVS II	**MOEVS IV**	**MOEVS V**	**sSAZ**	**PFZ**	**AAZ**
sSAZ – PFZ	p = 0.25	p = 0.87				
sSAZ – AAZ	p = 0.002 (sSAZ > AAZ)					
PFZ – AAZ	p < 0.001 (PFZ > AAZ)		p = 0.55			
II – IV				p = 0.05	p = 0.01 (II < IV)	
II – V					p = 0.02 (II > V)	p < 0.001 (II < V)
IV – V					p < 0.001 (IV > V)	

Table 2.16 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Percentage contribution of large individuals to total *L. retroversa* abundance.

	MOEVS II	**MOEVS IV**	**MOEVS V**	**sSAZ**	**PFZ**	**AAZ**
sSAZ – PFZ	p = 0.52	p = 0.31				
sSAZ – AAZ	p = 0.54					
PFZ – AAZ	p = 0.87		p = 0.60			
II – IV				p = 0.59	p = 0.08	
II – V					p = 0.35	p = 0.42
IV – V					p = 0.02 (IV > V)	

Correlation analysis

A positive linear relationship was found to exist between total surface chl-*a* concentrations and total *L. retroversa* numbers (Figure 2.10: $r^2 = 0.49$; $r = 0.70$; $p < 0.001$). Pearson's Correlation analyses using percentage contribution of surface size-fractionated chl-*a* and total *L. retroversa* numbers indicated a positive linear relationship between the percentage contribution of microphytoplankton and total pteropod numbers (Figure 2.11: $r^2 = 0.58$; $r = 0.76$; $p < 0.001$). Conversely, negative correlations were found to exist between relative contribution of nanophytoplankton to total chl-*a* concentrations and total pteropod numbers (Figure 2.12: $r^2 = 0.34$; $r = -0.58$; $p < 0.001$) and between the relative contribution of picophytoplankton and total *L. retroversa* numbers (Figure 2.13: $r^2 = 0.31$; $r = -0.56$; $p < 0.001$).

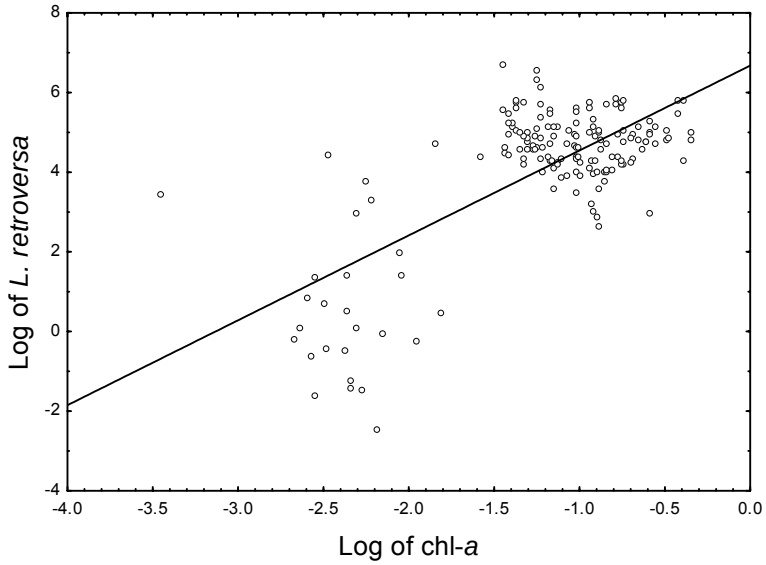

Figure 2.10 Results of Pearson's Correlation analysis: *L. retroversa* abundances (ind. m^{-3}) versus total surface chl-*a* concentrations (µg L^{-1}) ($r^2 = 0.49$; $r = 0.70$; $p < 0.001$). Data used for the analysis were collected during MIOS II, IV and V and MOEVS I, II, IV and V.

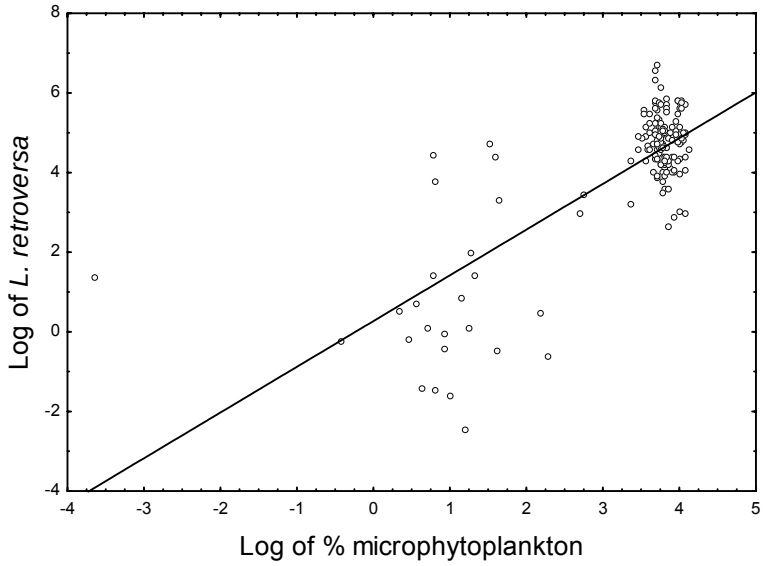

Figure 2.11 Results of Pearson's Correlation analysis: *L. retroversa* abundances (ind. m^{-3}) versus percentage contribution of microphytoplankton ($r^2 = 0.58$; $r = 0.76$; $p < 0.001$). Data used for the anlaysis were collected during MOEVS I, IV and V.

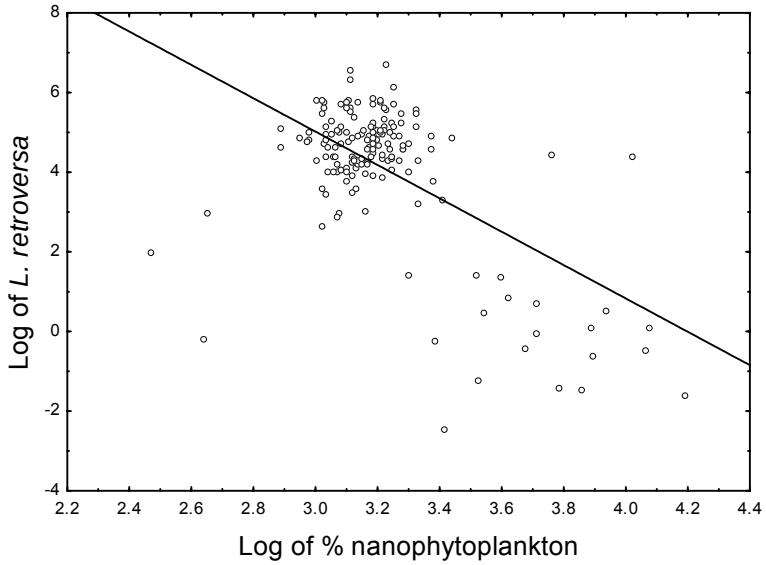

Figure 2.12 Results of Pearson's Correlation analysis: *L. retroversa* abundances (ind. m^{-3}) versus percentage contribution of nanophytoplankton ($r^2 = 0.34$; $r = -0.58$; $p < 0.001$). Data used for the anlaysis were collected during MOEVS I, IV and V.

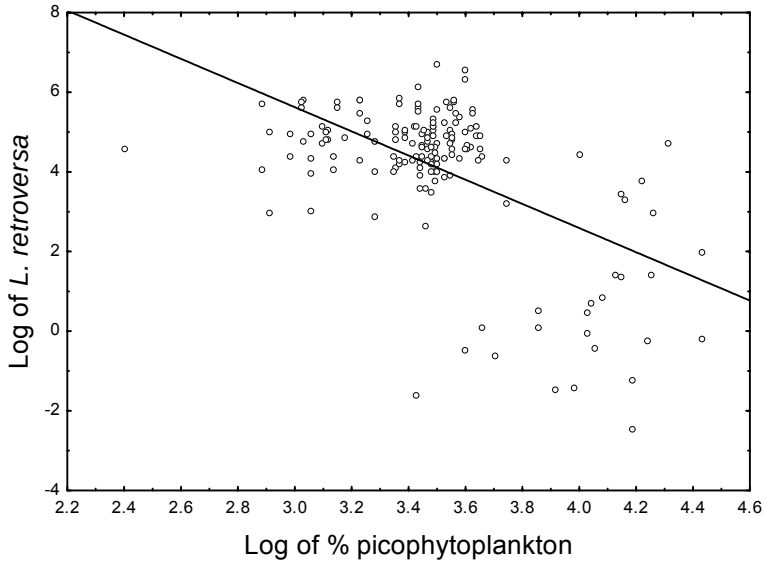

Figure 2.13 Results of Pearson's Correlation analysis: *L. retroversa* abundances (ind. m^{-3}) versus percentage contribution of picophytoplankton ($r^2 = 0.31$; $r = -0.56$; $p < 0.001$). Data used for the analysis were collected during MOEVS I, IV and V.

2.4 DISCUSSION

MOEVS II was occupied in the vicinity of the Antarctic Polar Front (APF; 2 ºC at 200 m depth), which lay between 50.5 º and 51.25 ºS. At 30.5 ºE, a tongue of warmer water intruded to about 50.25 ºS, representing a meander in the southern Sub-Antarctic Front (sSAF; 3.5 ºC at 200 m depth), which was most likely caused by topographic steering through the Andrew Bain Fracture Zone on the South-West Indian Ridge (Froneman *et al.* 2002b; Ansorge & Lutjeharms 2005). During MOEVS IV, an intense frontal feature was observed flowing in a northward direction between 30.5 º and 31.5 ºE and represented the coincidence of three fronts: the SAF, sSAF and APF. As for MOEVS II, the northward movement and near-joining of these fronts was probably due to the interaction of the Antarctic Circumpolar Current (ACC) and the Andrew Bain Fracture Zone (Ansorge & Lutjeharms 2005). A cold core eddy of Antarctic Zone (AAZ) origin was the main focus of the investigation during MOEVS V. The eddy has been outlined using the 2 ºC sub-surface (200 m) isotherm, which is typically used to identify the APF (Ansorge *et al.* 2005). The waters surrounding the eddy were typical of the PFZ. The sSAF (3.5 ºC at 200 m) was also present in the survey region.

During all three surveys, total chlorophyll-*a* (chl-*a*) concentrations were highly variable (Tables 2.1 to 2.3) and did not show any significant correlation with sea surface temperatures. There was, however, a significant difference in total chl-*a* concentration between the years, with concentrations being greater during MOEVS II than MOEVS V and values during MOEVS IV being intermediate between the two. Total chl-*a* values during MOEVS II and IV were in the range of those recorded during previous surveys in the region during the same season (Pakhomov *et al.* 2000b; Froneman *et al.* 2001; Bernard & Froneman 2002). Chl-*a* concentrations during MOEVS V, on the other hand, were substantially lower than expected for the region, which could be the result of grazing pressure by zooplankton (see Chapter Four). Interestingly, no variation in total chl-*a* occurred between the various water masses encountered during any of the three surveys. Total phytoplankton biomass was dominated by the nanophytoplankton fraction during MOEVS IV and both pico- and nanophytoplankton during MOEVS V. The predominance of small phytoplankton is common for the region (Laubscher *et al.* 1993; Xiuren *et al.* 1996; Froneman *et al.*

2001) and is the result of a combination of factors including low light availability, low water column stability (i.e. deep mixed-layer depths), low surface temperatures and low trace metal (particularly iron) availability (Laubscher *et al.* 1993; Dafner 1997; Lancelot *et al.* 2000; Bracher *et al.* 1999; Balarin 1999; Froneman *et al.* 2001). Small phytoplankton (< 20 µm) are better able to grow and reproduce in these conditions due to their small surface area-volume ratio (Fogg 1991).

Total mesozooplankton abundances recorded during all three surveys are within the range of those reported in the literature (Perissinotto 1992; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Froneman & Pakhomov 1998a; Froneman *et al.* 2000a; Pakhomov & Froneman 2004b). In agreement with numerous previous investigations conducted in different sectors of the Southern Ocean, the mesozooplankton communities during the present surveys exhibited variability in total numbers and biomass and were strongly dominated by copepods, particularly *Oithona similis*, *Calanus simillimus*, *Ctenocalanus* spp. and *Clausocalanus* spp. (Conover & Huntley 1991; Pakhomov & Perissinotto 1997; Froneman & Pakhomov 1998a; Pakhomov & Froneman 1999a; Pakhomov *et al.* 2000a; Bernard & Froneman 2002; Pakhomov & Froneman 2004a). The chaetognaths, *Eukrohnia hamata* and *Sagitta gazellae*, were the most abundant carnivorous zooplankton during all three surveys, which is not uncommon for the region (Perissinotto & McQuaid 1992; Pakhomov *et al.* 1994; Froneman & Pakhomov 1998b; Froneman *et al.* 1998; Pakhomov *et al.* 2000a; Pakhomov & Froneman 2000). Abundances of the euthecosome pteropod, *L. retroversa*, ranged between 0.0 and 107.42 ind. m^{-3} during the study, which is within the range reported in previous investigations in the PFZ (Perissinotto 1992; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Hunt & Pakhomov 2003; Ward *et al.* 2003).

The distinct separation of mesozooplankton assemblages by hierarchical cluster analysis was associated with water mass during all three surveys. During MOEVS II (April 2002), the survey was occupied within two major water masses, namely the Polar Frontal Zone (PFZ) and the Antarctic Zone (AAZ). The PFZ was further separated by the presence of the southern Sub-Antarctic Front (sSAF) and the region north of this front was named the southern Sub-Antarctic Zone (sSAZ). Stations occupied during the survey were separated into three significantly different

groups that were associated with the three water masses (AAZ, PFZ and sSAZ). Stations situated within each water mass generally fell into the same group (as identified by hierarchical cluster analysis). There was, however, some degree of mixing between water masses, with station 41 from the AAZG being situated in the PFZ water mass, in close proximity to the APF, and station 11 from the sSAZG lying within the PFZ waters close to the sSAF. This is not surprising however, as substantial cross-frontal mixing has been reported on numerous occasions in the region (Pakhomov & Perissinotto 1997; Pakhomov *et al.* 2000a; Perissinotto *et al.* 2000; Ward *et al.* 2003). The separation of stations into their respective groups was not a result of the presence or absence of indicator species, but rather the relative abundances of certain species. It should be noted that there was no significant variability in total mesozooplankton numbers between any of the water masses encountered during MOEVS II. The most abundant copepod species, *O. similis* and *Ctenocalanus* spp., were most numerous in the AAZ waters. Conversely, *Limacina retroversa* was more numerous in the PFZ water mass than in the AAZ, which is likely due to the fact that *L. retroversa* is considered a Sub-Antarctic species (Boltovskoy 1999) and would therefore be more abundant north of the APF. Interestingly, the numbers of *L. retroversa* in the sSAZ waters were the lowest recorded throughout the survey.

During MOEVS IV (April 2004), the majority of the stations occupied fell within the region of the PFZ, between the APF and the sSAF. Two stations, however, were grouped separately from the rest, these lay within the sSAZ. The separation of these stations into their respective groups was not due to the presence or absence of certain indicator species, but rather due to the relative abundances of dominant mesozooplankton taxa. Indeed, total mesozooplankton numbers as well as total copepod numbers were significantly greater in the PFZ water mass than in the sSAZ waters. These results reiterate previous perceptions that different water masses have different levels of productivity and plankton standing stock (Pakhomov & Perissinotto 1997; Pakhomov *et al.* 2000a; Ward *et al.* 2003). *L. retroversa* numbers were significantly greater in the PFZ than in the sSAZ waters during MOEVS IV.

During MOEVS V (April 2005), a cold core eddy, of AAZ origin, was encountered in a region of the PFZ. Stations were separated into three groups

associated with the eddy, the surrounding PFZ waters and the sSAZ waters. The sSAZG consisted of only two stations, both of which lay in the sSAZ waters. Although most stations in the PFZG were situated within their corresponding water mass, some were not, and this suggests a degree of mixing between the eddy and the surrounding waters. Interestingly, mixing of stations only seemed to occur on the upstream side of the eddy (western boundary). Total mesozooplankton and total copepod numbers were greatest within the eddy (AAZ waters).

It is generally accepted that the APF represents a significant barrier to the distribution of planktonic organisms (Deacon 1982; Pakhomov & McQuaid 1996; Errhif *et al.* 1997; Pakhomov *et al.* 2000a; Ward *et al.* 2003). However, in most studies (e.g. Pakhomov *et al.* 2000a; Ward *et al.* 2003), including the present study, there is some degree of mixing between water masses, with the result that some Antarctic species may be found in the PFZ, while certain Sub-Antarctic species may occur south of the APF. In fact, many authors report that the different zooplankton communities associated with the various water masses are often determined by changes in the relative abundances of certain taxa, and not necessarily by fundamental differences in faunal composition (Siegel & Piatkowski 1990; Pakhomov & Perissinotto 1997; Ward *et al.* 2003).

The abundance of the pteropod, *L. retroversa*, showed significant inter-annual variability. Total *L.* retroversa numbers were high during MOEVS II and IV, but significantly lower during MOEVS V. This was most likely due to the reduced phytoplankton biomass observed throughout that survey. Seibel & Dierssen (2003) suggest that *L. helicina* (the Arctic/Antarctic species) may be strongly affected by regional phytoplankton concentrations. Indeed, Pearson's Correlation analysis on the present data indicates that there is a positive correlation between total chl-*a* concentrations and *L. retroversa* numbers, suggesting a dependency of the pteropod on available phytoplankton. Indeed, Kobayashi (1974) reported that, in the Arctic, the availability of food is very important for *Spiratella ("Limacina") helicina* as the pteropod requires a continuous source of nutritive particulate organic matter in order to sustain the growth cycle. *L. retroversa* numbers also appear to be positively correlated to the relative abundances of microphytoplankton and negatively correlated to nano- and picophytoplankton. However, this may be due to the fact that

microphytoplankton and total chl-*a* concentrations are also positively correlated (Froneman & Pakhomov 1998a; Froneman *et al.* 2001). Lalli & Gilmer (1989) report that the main food items for *L. retroversa* include diatoms, dinoflagellates, coccolithophorids and tintinnids. It is important to note, however, that these items were identified using gut contents analysis, which relies on food items being easily recognisable, the more readily digestible bacteria, detritus and naked flagellates would not have been identified (Lalli & Gilmer 1989).

Medium-sized *L. retroversa* dominated total pteropod numbers during MOEVS IV and V (Figures 2.4 and 2.5), indicating that the majority of spawning had taken place in early-mid summer. During MOEVS II, both medium and small-sized individuals were abundant, suggesting that in some communities, spawning had occurred in late summer. Both sets of results are in agreement with a study conducted in the northern hemisphere on a similar species (Gannefors *et al.* 2005). Gannefors *et al.* (2005) found that *L. helicina* exhibited its main spawning period during the summer months, peaking in late summer, with juveniles and veligers dominating total pteropod communities during autumn. The percentage contribution of small and medium-sized *L. retroversa* varied significantly between water masses during MOEVS II. This result suggests that there is possible variability in the spawning periods of *L. retroversa* within the different water masses. This requires further investigation.

CHAPTER THREE:

SMALL-SCALE TEMPORAL AND SPATIAL VARIABILITY IN ABUNDANCES AND SIZE STRUCTURE OF *LIMACINA RETROVERSA* AT THE SUB-ANTARCTIC PRINCE EDWARD ISLANDS

3.1 INTRODUCTION

The sub-Antarctic, Prince Edward Archipelago (47 ºS, 38 ºE) is situated in the Indian sector of the Southern Ocean, within the Polar Frontal Zone (PFZ). The archipelago consists of two islands, namely Marion and Prince Edward that are separated by a shallow (200 m) inter-island shelf (Pakhomov & Froneman 1999a). The Prince Edward Islands (PEIs) lie directly in the path of the easterly flowing Antarctic Circumpolar Current and are bordered to the north and south by the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF), respectively (Lutjeharms & Valentine 1984; Nowlin & Klinck 1986; Nowlin *et al.* 1987). As a result of its position, the archipelago acts as an obstacle to the prevailing currents, resulting in extreme spatial and temporal mesoscale variability in the local hydrology (Ansorge *et al.* 1999; Pakhomov & Froneman 1999a), with eddies and meanders occurring in both fronts (Legeckis 1977; Bryden 1983; Lutjeharms 1990; Ansorge *et al.* 1999).

Oceanographic surveys conducted in the waters surrounding the PEIs indicate that the positions of both the APF and SAF exhibit a high degree of latitudinal variability (Lutjeharms & Valentine 1984; Lutjeharms 1990; Duncombe-Rae 1989a, b). Furthermore, it has been suggested that the physical environment in the vicinity of the archipelago may be strongly influenced by the proximity of the SAF relative to the islands (Pakhomov & Froneman 1999a; Ansorge & Lutjeharms 2002; Pakhomov *et al.* 2000b; Perissinotto *et al.* 2000). When the SAF is positioned to the north of the PEIs, an island-mass effect is observed, with water mass retention occurring between the islands, over the inter-island shelf. Conversely, when the SAF is situated further south, sometimes even flowing between the islands, a flow-through system predominates, with little to no retention taking place within the inter-island region (Ansorge & Lutjeharms 2002; Pakhomov *et al.* 2000b; Hunt & Pakhomov 2003). During a retention system, increased water column stability and macronutrient availability, resulting from freshwater runoff from the islands, promotes the development of phytoplankton blooms, the so-called *island-mass effect*, in the inter-island region (El-Sayed 1988; Laubscher *et al.* 1993; Dafner 1997; Balarin 1999; Pakhomov & Froneman 1999a). It has been suggested that, during a retention system, mesozooplankton may become entrained over the inter-island region, providing an abundant food source for the land-based predators (Pakhomov & Froneman 1999a).

The fluctuation between the retention and flow-through systems results in a high degree of variability in both primary and secondary production in the waters surrounding the PEIs. Considering that the position of the SAF can exhibit a high degree of variability (Valentine & Lutjeharms 1983; Nagata *et al.* 1988; Duncombe Rae 1989; Lutjeharms 1990), it is likely that productivity in the vicinity of the PEIs may vary considerably, both spatially and temporally, on a reasonably small scale.

In the previous chapter (Chapter Two) inter-annual variability in abundance and size structure of the euthecosome pteropod, *Limacina retroversa* was discussed. It is important, however, to establish the small-scale variability of the species. The aim of the present chapter was thus to determine the small-scale spatio-temporal variability in the mesozooplankton community, with particular emphasis on the abundance and size structure of *L. retroversa*.

3.2 METHODS

3.2.1 Survey details

The fifth Marion Island Offshore Survey (MIOS V) was conducted at two stations (A and B) within the inter-island region of the PEI archipelago, during April 2000 (Figure 3.1). Station A was located around 46.8 ºS, 37.9 ºE, while station B was in the vicinity of 46.9 ºS, 38 ºE (Figure 3.1). Between 1 and 3 zooplankton tows were conducted at each station every evening for 18 consecutive days, from 10 to 27 April 2000. A total of 34 zooplankton tows were conducted at station A and 36 at station B. During each zooplankton tow, sea surface temperature was recorded using an on-board sensor.

3.2.2 Phytoplankton biomass

Surface size-fractionated and total chlorophyll-*a* (chl-*a*) concentrations were measured during each zooplankton tow by gently passing (< 5 cm Hg) a 250 mL aliquot of surface seawater, obtained from the scientific seawater supply, through a serial filtration unit, separating the phytoplankton into pico- (0.45 – 2.0 µm), nano- (2.0 – 20 µm) and microphytoplankton (> 20 µm) size fractions. Chl-*a* concentrations were then measured fluorometrically using a Turner Fluorometer after 24 hours of

extraction in 90 % acetone, after the method of Holm-Hansen & Riemann (1978). Total chl-*a* concentrations were calculated as the sum of size-fractionated chl-*a* concentrations.

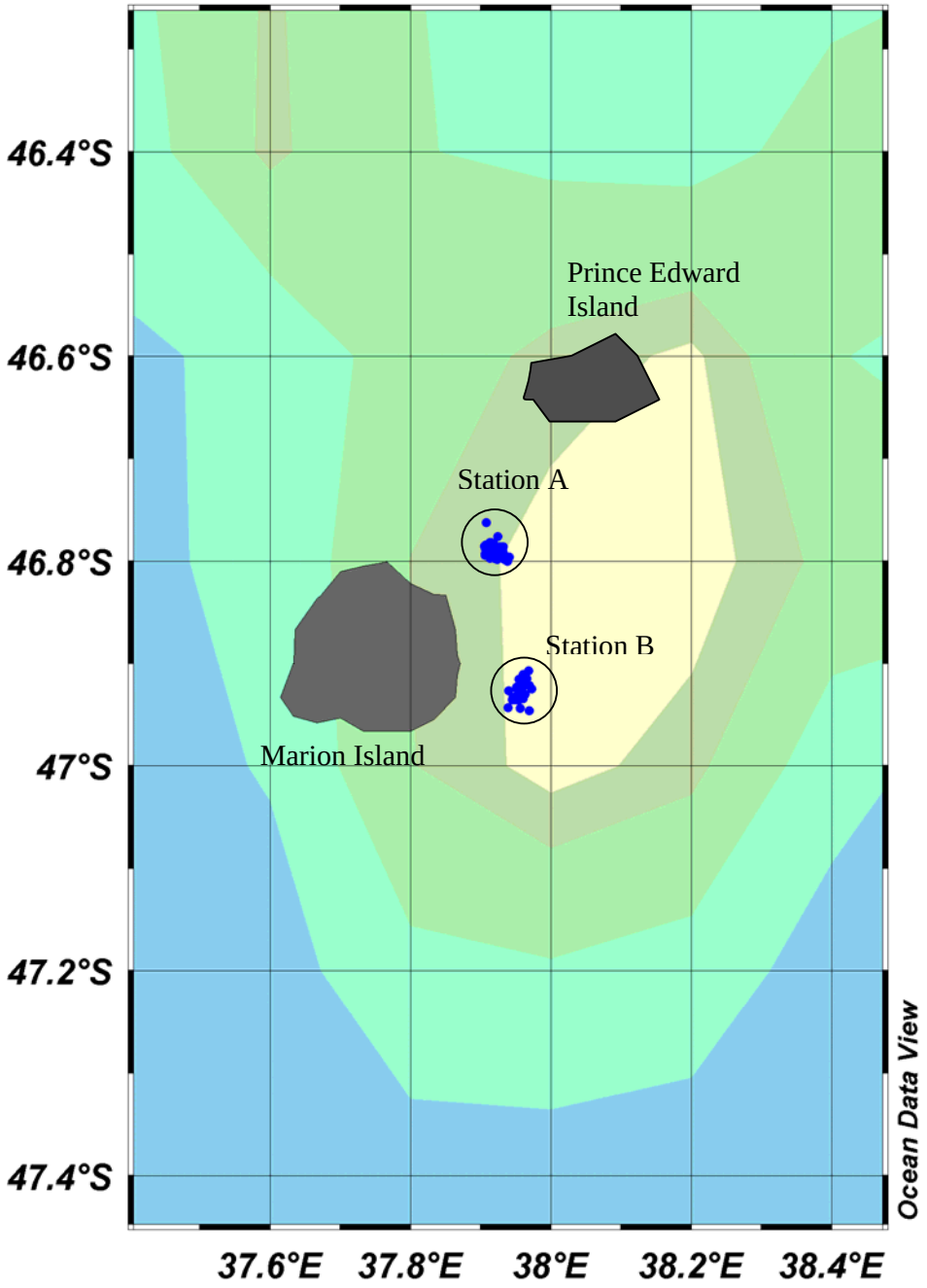

Figure 3.1 Positions of stations A and B on the inter-island shelf between Marion and Prince Edward Islands, Sub-Antarctic. MIOS V, April 2000. The contours represent the bathymetry.

3.2.3 Mesozooplankton community

Mesozooplankton were collected at each station by oblique tows using a Bongo net fitted with 300 µm mesh nets. The Bongo net was fitted with a Universal Underwater Unit (U^3; Robertson *et al.* 1981) that measured volume filtered and depth attained for each tow. Tows were conducted to 200 m during the evening. Samples from both nets were preserved in a 6 % buffered (hexamine) formalin solution. In the laboratory, mesozooplankton were counted and identified using the keys of Boltovskoy (1999). *L. retroversa* was further sorted into three size classes: (1) small (< 500 µm); (2) medium (500 – 1 500 µm); and (3) large (> 1 500 µm) and numbers within each size class were estimated (Dadon & de Cidre 1992). For the purpose of this study, samples collected from each net during one tow were assumed to come from the same community. An average abundance was therefore obtained from both nets for every tow.

3.2.4 Statistical analyses

Hierarchical cluster analysis

In order to identify different mesozooplankton assemblages at each station over the period of 18 days, hierarchical cluster analysis and multidimensional scaling were used in conjunction with the Bray-Curtis similarity index (Bernard & Froneman 2002; Pakhomov & Froneman 2004a). Species abundance data were log transformed [$\log_{10}(x + 1)$] and standardised in order to reduce bias due to the occurrence of highly abundant species (Legendre & Legendre 1983). The similarity programmes ANOSIM and SIMPER, of the Plymouth Routines in Multivariate Ecological Research 5 (PRIMER-E Ltd. 2005) computer package (Clarke & Warwick 1994), were used to test the significance levels and sources of difference (respectively) between the mesozooplankton assemblages associated with the different groupings identified by hierarchical cluster analysis (Field *et al.* 1982).

Analysis of variance

Factorial ANOVAs (StatSoft, Inc. 2004) were used to determine the variability in total and size-fractionated chl-*a*, total mesozooplankton numbers, copepod numbers and total and size-fractionated *L. retroversa* numbers between the two stations and

over the period of 18 days. Fisher's LSD tests were used for Post-Hoc analyses (StatSoft, Inc. 2004). In addition, factorial ANOVAs and Fisher's LSD tests were used to test for significant variability of total mesozooplankton numbers, total and size-fractionated *L. retroversa* numbers and total copepod numbers between the different groups identified at each station by hierarchical cluster analysis.

3.3 RESULTS

3.3.1 Sea surface temperature

Sea surface temperatures at station A ranged from 5.95 to 6.59 ºC (Mean = 6.31 ºC; SD = 0.16 ºC) (Figure 3.2), while those at station B ranged between 5.86 and 6.59 ºC (Mean = 6.25 ºC; SD = 0.17 ºC) (Figure 3.3).

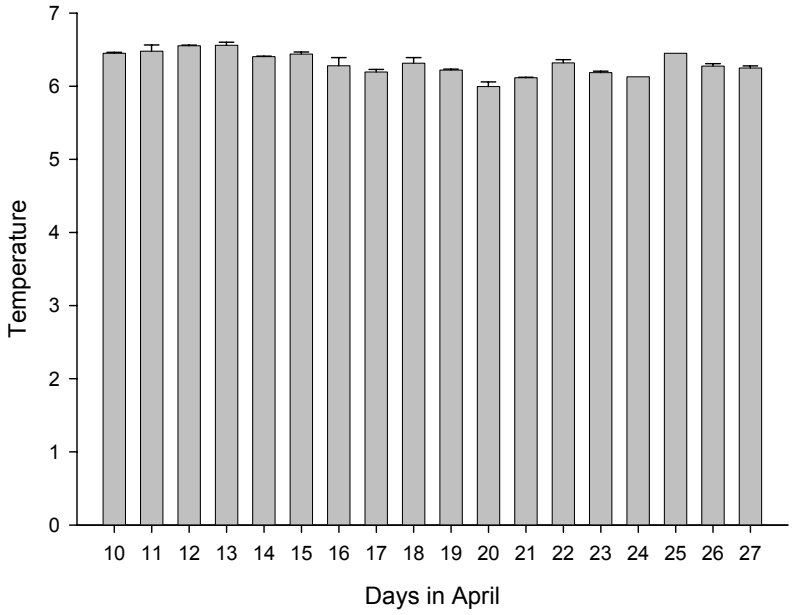

Figure 3.2 Average sea surface temperature (ºC) over a period of 18 days (10 to 27 April 2000) at station A, during MIOS V. Error bars represent standard deviation.

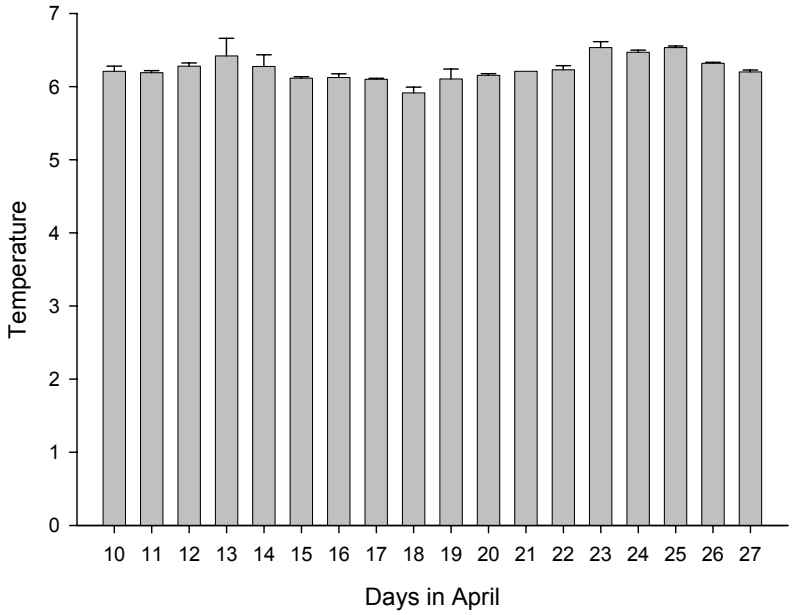

Figure 3.3 Average sea surface temperature (ºC) over a period of 18 days (10 to 27 April 2000) at station B, during MIOS V. Error bars represent standard deviation.

3.3.2 Phytoplankton biomass

Total surface chl-*a* concentrations at station A ranged between 0.29 and 0.68 µg L^{-1} (Mean = 0.42 µg L^{-1}; SD = 0.11 µg L^{-1}) (Figure 3.4). Total surface chl-*a* concentrations showed significant small-scale variability during the survey (see 3.3.4, below). Microphytoplankton contributed between 29.6 and 62.2 % to the total phytoplankton biomass (Mean = 46.1 %; SD = 7.1 %) (Figure 3.5). Nanophytoplankton contributed up to 29.3 % (Mean = 23.7 %; SD = 2.5 %) to total chl-*a*, while picophytoplankton contributed between 11.1 and 42.5 % of the total (Mean = 30.2 %; SD = 6.1 %) (Figure 3.5).

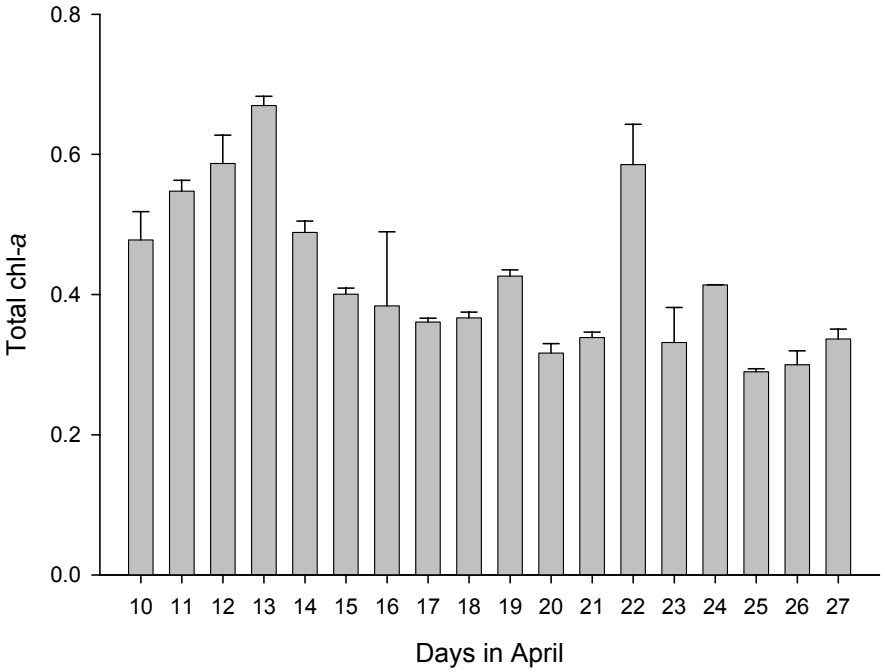

Figure 3.4 Average total surface chl-*a* (µg L^{-1}) over a period of 18 days (10 to 27 April 2000) at station A, during MIOS V. Error bars represent standard deviation.

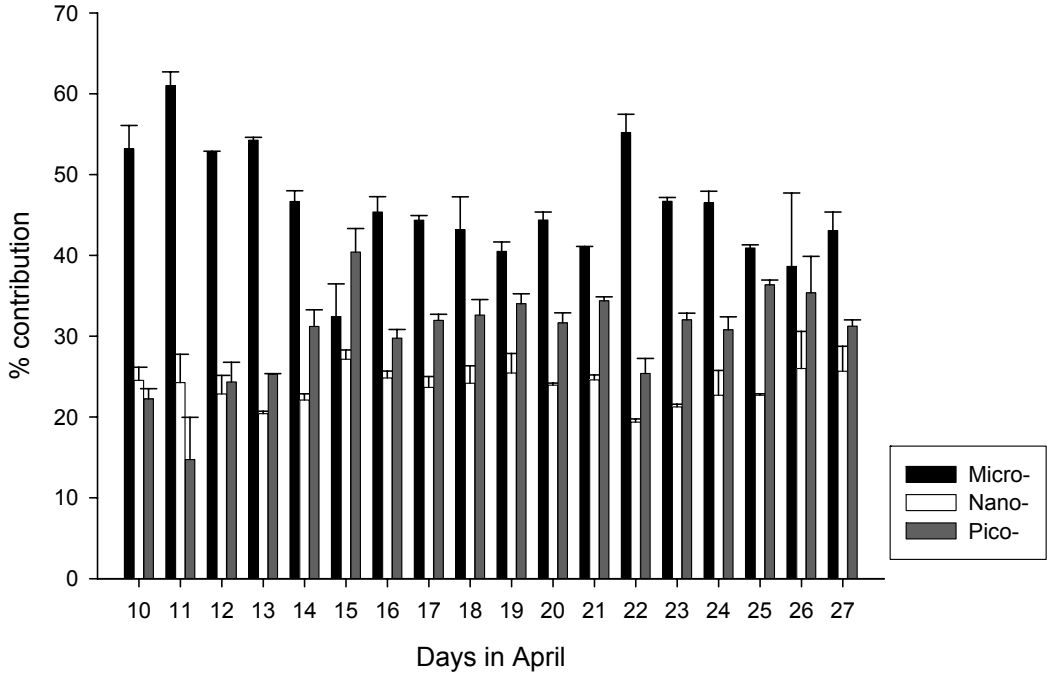

Figure 3.5 Average percentage contribution of surface size-fractionated chl-*a* to total chl-*a* over a period of 18 days (10 to 27 April 2000) at station A, during MIOS V. Error bars represent standard deviation.

Total surface chl-*a* concentrations at station B ranged from 0.24 to 0.71 µg L^{-1} (Mean = 0.36 µg L^{-1}; SD = 0.11 µg L^{-1}) (Figure 3.6). As for station A, total surface chl-*a* concentrations at station B exhibited significant small-scale variability throughout the survey (see 3.3.4, below). Microphytoplankton contributed up to 60.1 % of total chl-*a* biomass (Mean = 46.2 %; SD = 7.5 %) (Figure 3.7). Nanophytoplankton was responsible for between 18.1 and 31.2 % of the total phytoplankton biomass (Mean = 23.6 %; SD = 2.5 %), while picophytoplankton contributed up to 38.2 % of the total (Mean = 30.3 %; SD = 5.8 %) (Figure 3.7).

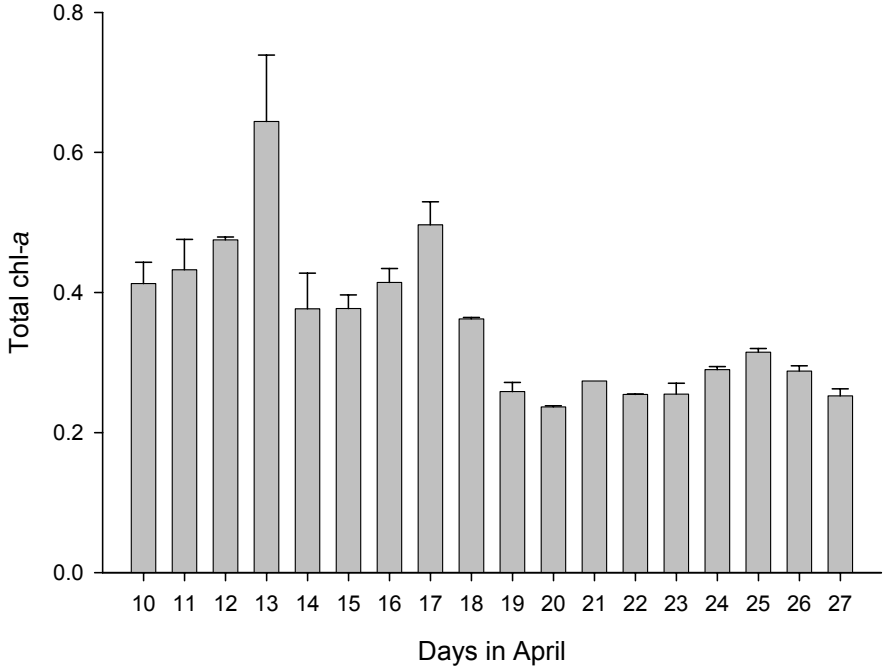

Figure 3.6 Average total surface chl-*a* (µg L^{-1}) over a period of 18 days (10 to 27 April 2000) at station B, during MIOS V. Error bars represent standard deviation.

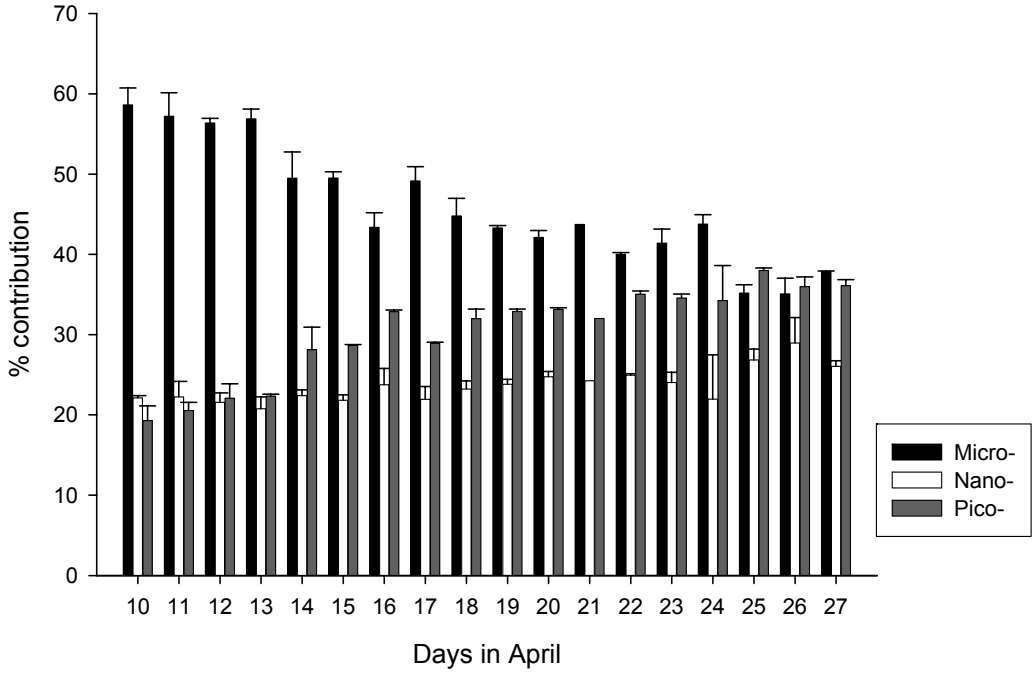

Figure 3.7 Average percentage contribution of surface size-fractionated chl-*a* to total chl-*a* over a period of 18 days (10 to 27 April 2000) at station B, during MIOS V. Error bars represent standard deviation.

3.3.3 Mesozooplankton community

Total mesozooplankton abundance at station A ranged from 229.53 to 1003.65 ind. m^{-3} (Mean = 472.46 ind. m^{-3}; SD = 163.70 ind. m^{-3}) (Figure 3.8). Copepod abundances ranged between 91.94 and 510.03 ind. m^{-3} (Mean = 237.42 ind. m^{-3}; SD = 86.75 ind. m^{-3}), while the euthecosome pteropod, *L. retroversa*, reached numbers as high as 618.58 ind. m^{-3} (Mean = 127.56 ind. m^{-3}; SD = 102.62 ind. m^{-3}) (Figure 3.9). Chaetognath abundances ranged from 32.02 to 137.87 ind. m^{-3} (Mean = 63.61 ind. m^{-3}; SD = 22.48 ind. m^{-3}) (Figure 3.9). Other mesozooplankton groups, including ostracods, salps, appendicularians and polychaetes exhibited an average combined abundance of 43.86 ind. m^{-3} (SD = 20.96 ind. m^{-3}) (Figure 3.9).

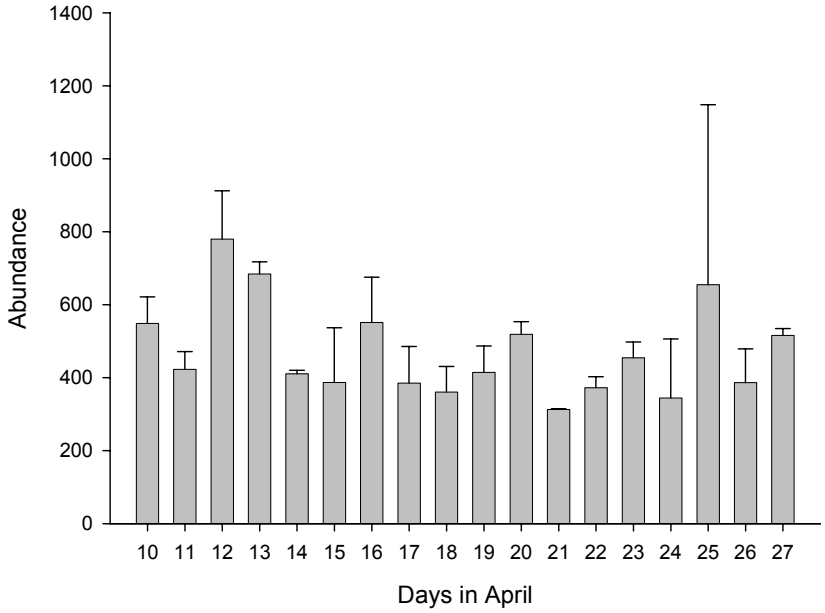

Figure 3.8 Average total mesozooplankton numbers (ind. m^{-3}) at station A, during MIOS V, April 2000. Error bars represent standard deviation.

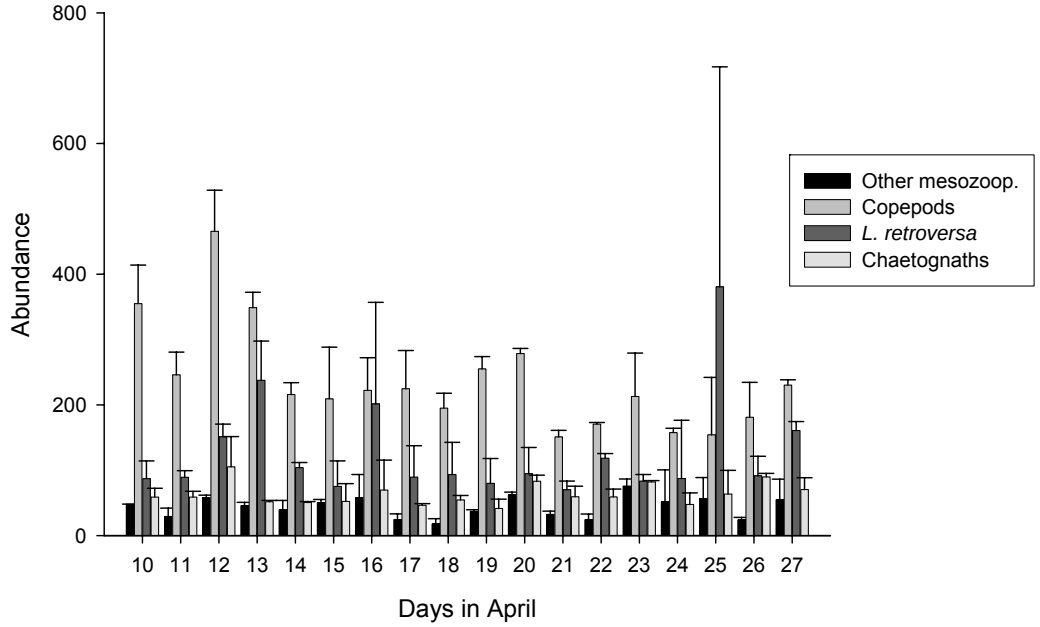

Figure 3.9 Average contribution of dominant groups to total mesozooplankton numbers (ind. m^{-3}) over a period of 18 days (10 to 27 April 2000) at station A, during MIOS V. Error bars represent standard deviation.

Total mesozooplankton numbers at station B ranged between 144.73 and 1046.05 ind. m^{-3} (Mean = 522.49 ind. m^{-3}; SD = 179.44 ind. m^{-3}) (Figure 3.10). Abundances of up to 546.84 ind. m^{-3} (Mean = 259.78 ind. m^{-3}; SD = 97.02 ind. m^{-3}) were recorded for copepods and *L. retroversa* numbers ranged between 35.39 and 530.52 ind. m^{-3} (Mean = 162.92 ind. m^{-3}; SD = 104.74 ind. m^{-3}) (Figure 3.11). Chaetognath numbers ranged from 14.98 to 146.22 ind. m^{-3} (Mean = 63.06 ind. m^{-3}; SD = 25.67 ind. m^{-3}) (Figure 3.11). Other mesozooplankton (ostracods, salps, appendicularians and radiolarians) were recorded in numbers averaging 36.74 ind. m^{-3} (SD = 22.35 ind. m^{-3}) (Figure 3.11).

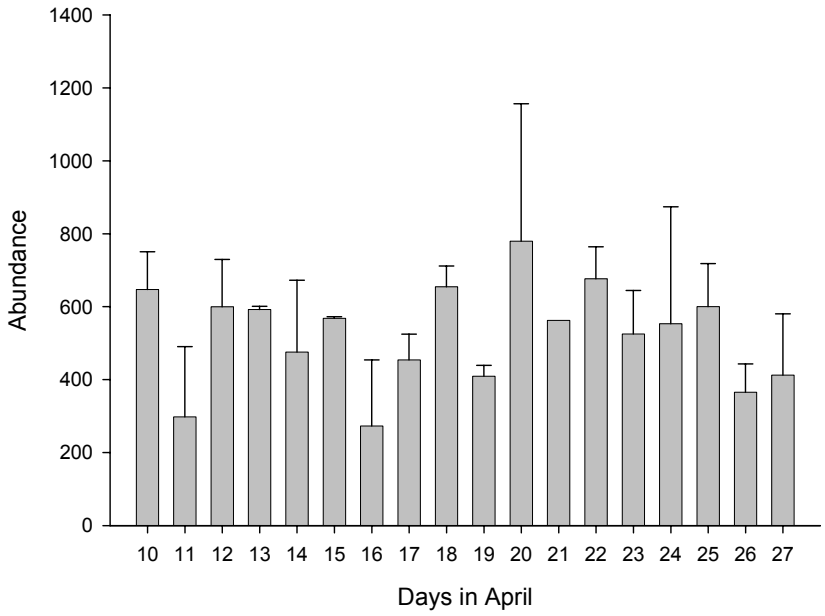

Figure 3.10 Average total mesozooplankton numbers (ind. m^{-3}) at station B, during MIOS V, April 2000. Error bars represent standard deviation.

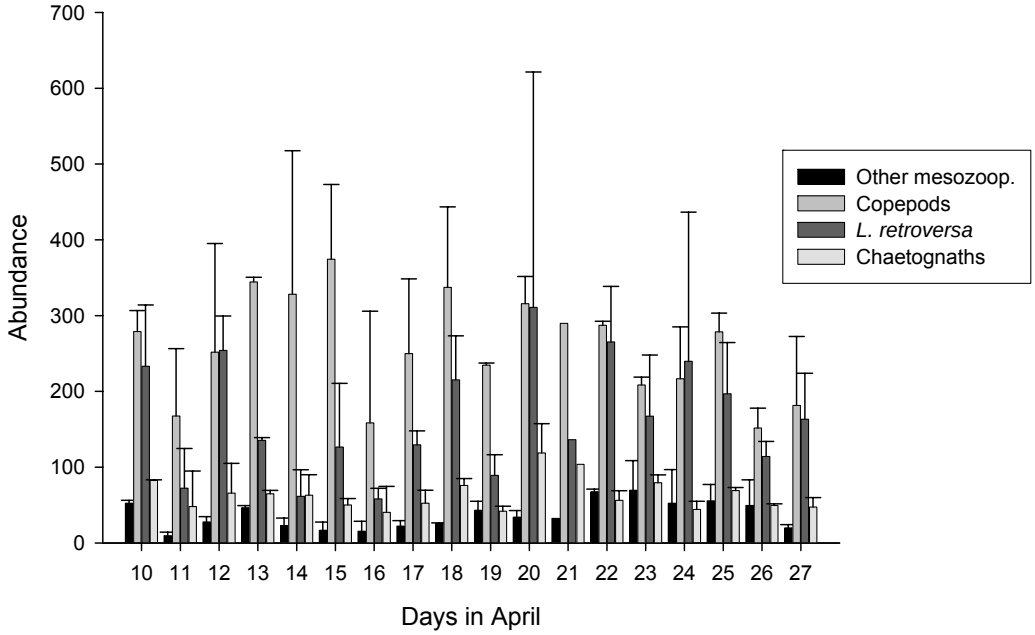

Figure 3.11 Average contribution of dominant groups to total mesozooplankton numbers (ind. m^{-3}) over a period of 18 days (10 to 27 April 2000) at station B, during MIOS V. Error bars represent standard deviation.

At station A, the percentage contribution of the small size class for *L. retroversa* ranged between 10.6 and 73.5 % (Mean = 42.8 %; SD = 16.3 %) of the total pteropod numbers (Figure 3.12). The medium size class contributed up to 56.7 % of the total (Mean = 37.9 %; SD = 9.3 %) (Figure 3.12). Large individuals of *L. retroversa* ranged between 0.5 and 59.8 % of the total (Mean = 19.3 %; SD = 15.1 %) (Figure 3.12). Small individuals of *L. retroversa* contributed between 18.6 and 73.1 % of the total pteropod numbers at station B (Mean = 39.6 %; SD = 14.0 %) (Figure 3.13). Medium sized individuals were responsible for up to 65.8 % of the total (Mean = 43.0 %; SD = 12.1 %), while large *L. retroversa* contributed between 2.1 and 47.6 % (Mean = 17.4 %; SD = 10.7 %) to the total (Figure 3.13).

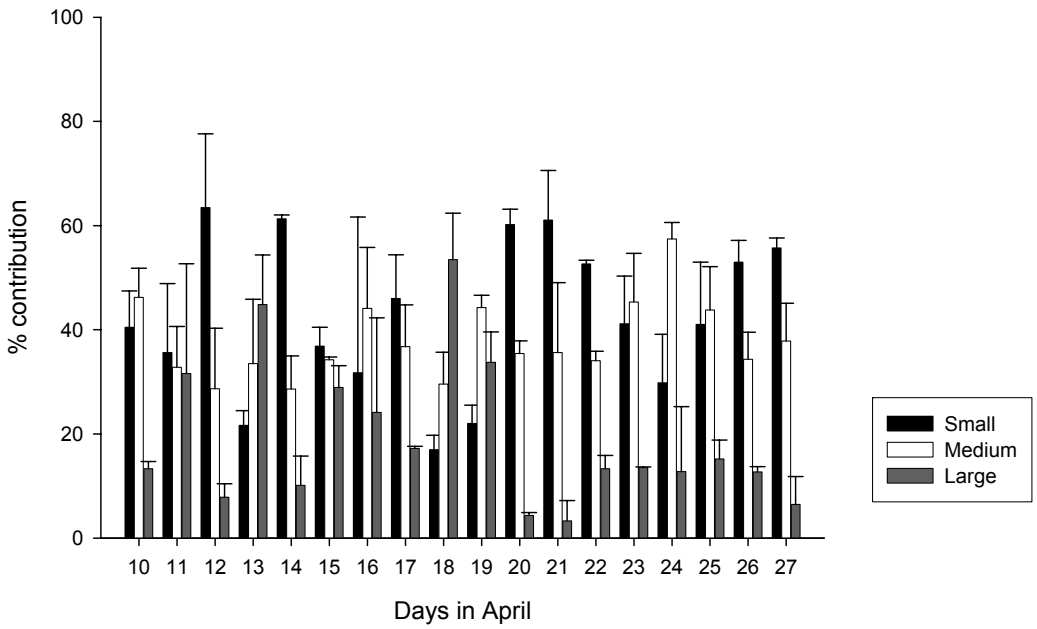

Figure 3.12 Average percentage contributions of the three size classes of *L. retroversa* to total *L. retroversa* numbers over a period of 18 days (10 to 27 April 2000) at station A, during MIOS V. Error bars represent standard deviation.

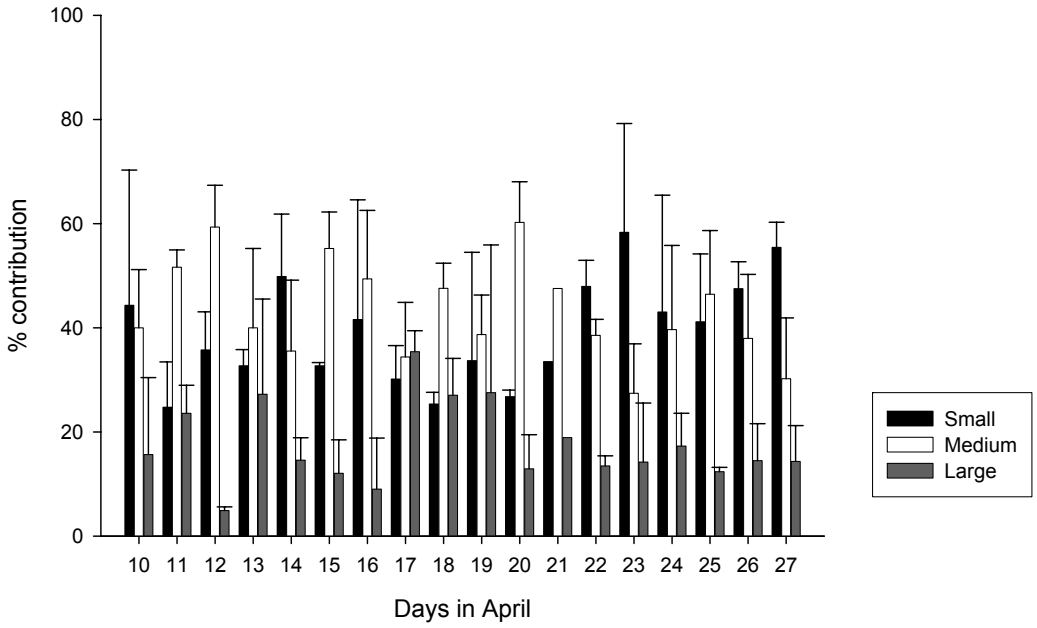

Figure 3.13 Average percentage contributions of the three size classes of *L. retroversa* to total *L. retroversa* numbers over a period of 18 days (10 to 27 April 2000) at station B, during MIOS V. Error bars represent standard deviation.

3.3.4 Statistical analyses

Hierarchical cluster analysis

Two distinct, significantly different mesozooplankton assemblages were identified by hierarchical cluster analysis at station A (ANOSIM: p = 0.002). The predominant mesozooplankton community (Group 1) was encountered on 13 out of the 18 days surveyed, while a second community (Group 2) was encountered on the 21, 23, 24, 25 and 26 of April 2000 (Figure 3.14). Species responsible for the similarity within each of the two groups included *L. retroversa* (total numbers and size-fractionated numbers), *Calanus simillimus*, *Eukrohnia hamata*, ostracods, *Ctenocalanus* spp. and *Paraeuchaeta* spp. (Table 3.1). The difference between the two groupings identified by hierarchical cluster analysis was due to the relative abundances of dominant mesozooplankton species, and not the presence or absence of individual species.

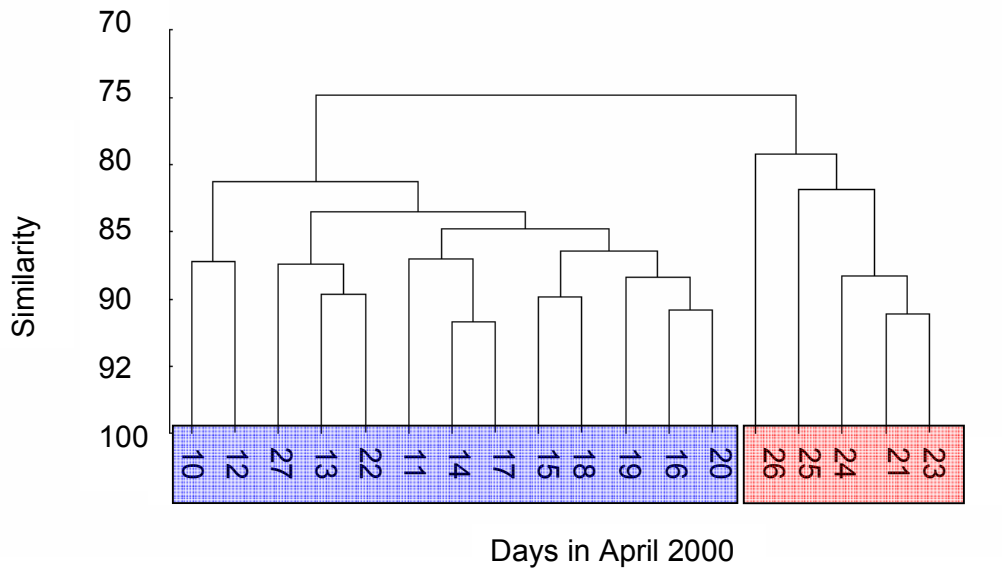

Figure 3.14 Results of hierarchical cluster analysis for mesozooplankton assemblages at station A, during MIOS V, April 2000. Blue box = Group 1; Red box = Group 2.

Table 3.1 Species responsible for up to 90 % of the similarity within groups at station A, during MIOS V, April 2000.

Group 1		**Group 2**	
Average similarity: 86.3 %		**Average similarity: 84.6 %**	
Taxon	**Average abundance (ind. m^{-3})**	**Taxon**	**Average abundance (ind. m^{-3})**
Total mesozooplankton	487.43	Total mesozooplankton	434.92
L. retroversa	121.40	*L. retroversa*	144.03
C. simillimus	61.95	*C. simillimus*	69.39
E. hamata	56.40	*L. retroversa* – medium	77.88
Ctenocalanus spp.	55.72	*L. retroversa* – small	66.49
M. lucens	44.31	*E. hamata*	63.45
L. retroversa – small	41.35	Ostracods	39.11
L. retroversa – medium	39.38	*Ctenocalanus* spp.	28.44
Ostracods	36.60	*L. retroversa* – large	25.34
L. retroversa – large	29.72	*M. lucens*	11.26
C. brevipes	19.21	*C. brevipes*	9.40
O. similis	15.65	Nauplii	8.37
Paraeuchaeta spp.	13.54	*E. longiceps*	7.88
S. minor	11.83		
E. longiceps	9.98		

Two significantly different mesozooplankton assemblages were identified at station B by hierarchical cluster analysis (ANOSIM: p = 0.001). Group 1 comprised the predominant mesozooplankton community that was encountered on 16 out of the 18 days of the survey. A second mesozooplankton community (Group 2) was encountered on 14 and 15 April 2000 (Figure 3.15). Species responsible for the similarity within each of the groups included *L. retroversa* (total and size-fractionated numbers), *C. simillimus*, *E. hamata*, *Metridia lucens*, *Ctenocalanus* spp., *Paraeuchaeta* spp., ostracods and *Clausocalanus brevipes* (Table 3.2). Changes in the relative abundances of these species, and not the presence or absence of certain species, resulted in the distinction of the two different mesozooplankton assemblages identified by hierarchical cluster analysis.

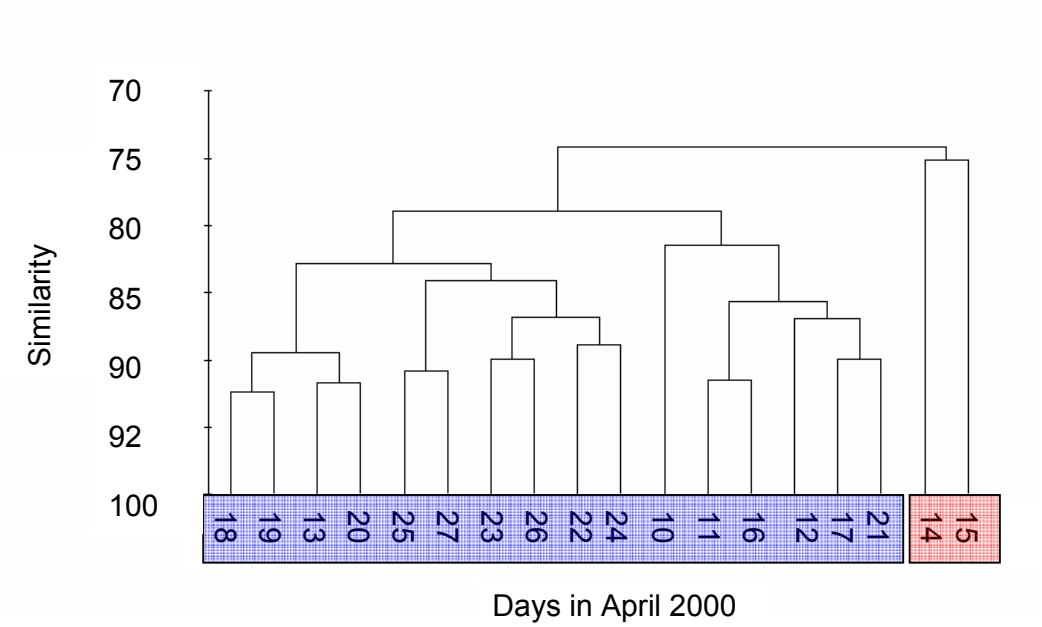

Figure 3.15 Results of hierarchical cluster analysis for mesozooplankton assemblages at station B, during MIOS V, April 2000. Blue box = Group 1; Red box = Group 2.

Table 3.2 Species responsible for up to 90 % of the similarity within groups at station B, during MIOS V, April 2000.

Group 1		**Group 2**	
Average similarity: 86.3 %		**Average similarity: 75.1 %**	
Taxa	**Average abundance (ind. m^{-3})**	**Taxa**	**Average abundance (ind. m^{-3})**
Total mesozooplankton	529.97	Total mesozooplankton	498.18
L. retroversa	177.83	*C. simillimus*	108.43
C. simillimus	110.79	*M. lucens*	95.18
L. retroversa – medium	67.24	*Ctenocalanus* spp.	68.98
E. hamata	57.96	*L. retroversa*	63.03
L. retroversa – small	57.47	*E. hamata*	53.90
Ctenocalanus spp.	39.76	*L. retroversa* – small	48.17
Ostracods	29.70	*C. brevipes*	19.58
L. retroversa – large	25.57	Ostracods	14.42
Paraeuchaeta spp.	23.01	*O. similis*	13.05
M. lucens	19.11	*Paraeuchaeta* spp.	12.12
C. brevipes	13.11	*C. laticeps*	7.31
Nauplii	9.03	*S. minor*	6.52
E. longiceps	8.22	Nauplii	4.67

Analysis of variance

Significant small-scale temporal variability (i.e. 24 hours) in sea surface temperature was observed 35 % of the time (i.e. 6 out of the possible 17 times during the survey) at both stations A and B (Table 3.3). Significant small-scale spatial variability (i.e. between stations A and B) in sea surface temperature occurred on 50 % of the days sampled, in other words, on 9 of the 18 possible days during the survey (Table 3.4).

Table 3.3 Daily variability at stations A and B for sea surface temperature, total surface chl-*a* and percentage contribution of microphytoplankton, nanophytoplankton and picophytoplankton, during MIOS V, April 2000.

Day	Temperature (°C)		Total chl-*a* (µg L^{-1})		% Microphytoplankton		% Nanophytoplankton		% Picophytoplankton	
	A	B	A	B	A	B	A	B	A	B
10-11	NS	NS	S	NS	S	NS	NS	NS	S	NS
11-12	NS	NS	NS	NS	S	NS	NS	NS	S	NS
12-13	NS	NS	S	S	NS	NS	NS	NS	NS	NS
13-14	S	S	S	S	S	S	NS	NS	S	S
14-15	NS	S	S	NS	S	NS	S	NS	S	NS
15-16	S	NS	NS	NS	S	S	NS	NS	S	S
16-17	NS	NS	NS	S	NS	S	NS	NS	NS	S
17-18	NS	S	NS	S	NS	NS	NS	NS	NS	NS
18-19	NS	S	NS	S	NS	NS	NS	NS	NS	NS
19-20	S	NS	S	NS	NS	NS	NS	NS	NS	NS
20-21	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
21-22	S	NS	S	NS	S	NS	S	NS	S	NS
22-23	NS	S	S	NS	S	NS	NS	NS	S	NS
23-24	NS	NS	S	NS	NS	NS	NS	NS	NS	NS
24-25	S	NS	S	NS	S	S	NS	S	S	NS
25-26	S	S	NS	NS	NS	NS	NS	NS	NS	NS
26-27	NS	NS	NS	NS	NS	NS	NS	NS	S	NS

NS = Not significant ($p > 0.05$)
S = Significant ($p < 0.05$)

Table 3.4 Spatial variability between stations A and B on days 10 to 27 for sea surface temperature, total surface chl-*a* and percentage contribution of microphytoplankton, nanophytoplankton and picophytoplankton, during MIOS V, April 2000.

Day	Temperature (°C)	Total chl-*a* (μg L^{-1})	% Microphytop.	% Nanophytop.	% Picophytop.
10	S	NS	S	NS	NS
11	S	S	NS	NS	S
12	S	S	NS	NS	NS
13	NS	NS	NS	NS	NS
14	NS	S	NS	NS	NS
15	S	NS	S	S	S
16	S	NS	NS	NS	NS
17	NS	S	NS	NS	NS
18	S	NS	NS	NS	NS
19	NS	S	NS	NS	NS
20	S	S	NS	NS	NS
21	NS	NS	NS	NS	NS
22	NS	S	S	S	S
23	S	S	S	NS	NS
24	S	S	NS	NS	NS
25	NS	NS	S	S	NS
26	NS	NS	NS	NS	NS
27	NS	S	S	NS	S

NS = Not significant ($p > 0.05$)
S = Significant ($p < 0.05$)

At station A, small-scale temporal variability in total surface chl-*a* concentrations was observed 53 % of the time (i.e. 9 times out of a possible 17), while at station B, small-scale temporal variability in surface chl-*a* concentrations occurred 29 % of the time (i.e. 5 times out of a possible 17; see Table 3.3). Small-scale spatial variability in total surface chl-*a* concentrations was seen on 10 of the days sampled, or 56 % of the time (Table 3.4).

Significant variation in the percentage contribution of microphytoplankton to total chl-*a* biomass occurred on a small temporal scale 47 % of the time at station A, and only 24 % of the time at station B (Table 3.3). Significant small-scale temporal variability in the relative contribution of nanophytoplankton was observed 12 % of the time at station A and only 6 % of the time at station B (Table 3.3). While that of picophytoplankton occurred 53 % of the time at station A and 18 % of the time at station B (Table 3.3). Significant small-scale spatial variability in the percentage contribution of size-fractionated phytoplankton to total phytoplankton biomass was

observed 33 % of the time for microphytoplankton, 17 % of the time for nanophytoplankton and 22 % of the time for picophytoplankton (Table 3.4).

Significant small-scale temporal variability in total mesozooplankton numbers occurred 6 % of the time at station A and 12 % of the time at station B (Table 3.5). There was no significant small-scale spatial variability in total mesozooplankton numbers during the entire survey (Table 3.6). Significant small-scale temporal variability in total copepod numbers was observed only 6 % of the time at both stations A and B (Table 3.5). Significant small-scale spatial variability in total copepod numbers occurred 11 % of the time (Table 3.6). Significant small-scale temporal variations in *L. retroversa* numbers occurred 12 % of the time at station A, but not at station B (Table 3.5). Significant small-scale spatial variability in *L. retroversa* numbers was observed only 6 % of the time (Table 3.6).

Significant small-scale temporal variability in the percentage contribution of small individuals of *L. retroversa* to total pteropod numbers occurred 35 % of the time at station A, but was not observed at station B (Table 3.5). Significant small-scale temporal variability in the relative contribution of medium-sized *L. retroversa* to total pteropod numbers was not observed at station A, while at station B variability occurred 6 % of the time (Table 3.5). Significant small-scale temporal variability in the percentage contribution of large individuals of *L. retroversa* occurred 29 % of the time at station A and only 18 % of the time at station B (Table 3.5). Significant small-scale spatial variability in the relative contribution of the three size classes of *L. retroversa* to total pteropod numbers occurred 11 % of the time for small individuals, 22 % of the time for medium-sized pteropods and 6 % of the time for large individuals (Table 3.6).

Table 3.5 Daily variability at stations A and B for total mesozooplankton numbers, copepod numbers, *L. retroversa* numbers and percentage contribution of small, medium and large size classes of *L. retroversa*, during MIOS V, April 2000.

Day	Total mesozoop. (Ind. m^{-3})		Copepods (Ind. m^{-3})		*L. retroversa* (Ind. m^{-3})		Small *L. retroversa* (%)		Medium *L. retroversa* (%)		Large *L. retroversa* (%)	
	A	B	A	B	A	B	A	B	A	B	A	B
10-11	NS	S	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
11-12	S	NS	S	NS	NS	NS	S	NS	NS	NS	S	S
12-13	NS	NS	NS	NS	NS	NS	S	NS	NS	NS	S	S
13-14	NS	NS	NS	NS	NS	NS	S	NS	NS	NS	S	NS
14-15	NS	NS	NS	NS	NS	NS	S	NS	NS	S	NS	NS
15-16	NS	NS	NS	S	NS	NS	NS	NS	NS	NS	NS	NS
16-17	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	S
17-18	NS	NS	NS	NS	NS	NS	S	NS	NS	NS	NS	NS
18-19	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
19-20	NS	S	NS	NS	NS	NS	S	NS	NS	NS	S	NS
20-21	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
21-22	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	NS
22-23	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
23-24	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
24-25	NS	NS	NS	NS	S	NS	NS	NS	NS	NS	NS	NS
25-26	NS	NS	NS	NS	S	NS	NS	NS	NS	NS	NS	NS
26-27	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS = Not significant ($p > 0.05$)
S = Significant ($p < 0.05$)

Table 3.6 Spatial variability between stations A and B on days 10 to 27 for total mesozooplankton numbers, copepod numbers, *L. retroversa* numbers and percentage contribution of small, medium and large size classes of *L. retroversa*, during MIOS V, April 2000.

Day	Total Mesozooplankton (Ind. m^{-3})	Copepods (Ind. m^{-3})	*L. retroversa* (Ind. m^{-3})	Small *L.r.* (%)	Medium *L.r.* (%)	Large *L.r.* (%)
10	NS	NS	NS	NS	NS	NS
11	NS	NS	NS	NS	S	NS
12	NS	S	NS	S	S	NS
13	NS	NS	NS	NS	NS	NS
14	NS	NS	NS	NS	NS	NS
15	NS	S	NS	NS	S	NS
16	NS	NS	NS	NS	NS	NS
17	NS	NS	NS	NS	NS	NS
18	NS	NS	NS	NS	NS	NS
19	NS	NS	NS	NS	NS	NS
20	NS	NS	S	S	S	NS
21	NS	NS	NS	NS	NS	S
22	NS	NS	NS	NS	NS	NS
23	NS	NS	NS	NS	NS	NS
24	NS	NS	NS	NS	NS	NS
25	NS	NS	NS	NS	NS	NS
26	NS	NS	NS	NS	NS	NS
27	NS	NS	NS	NS	NS	NS

NS = Not significant ($p > 0.05$)
S = Significant ($p < 0.05$)

No significant variability was observed for total mesozooplankton numbers between the groups identified by hierarchical cluster analysis at each station ($p = 0.37$ and $p = 0.89$, for stations A and B, respectively). Total copepod numbers varied significantly between the groups identified at both stations A and B. At station A, copepod numbers were greater in Group 1 than Group 2 ($p = 0.01$), while at station B, numbers were higher in Group 2 than Group 1 ($p = 0.02$). Total *L. retroversa* numbers did not show any significant variability between groups at either of the stations ($p = 0.59$ and $p = 0.08$, for stations A and B, respectively). Similarly, the percentage contribution of small ($p = 0.56$ and $p = 0.59$, for stations A and B, respectively) and medium ($p = 0.07$ and $p = 0.93$, for stations A and B, respectively) *L. retroversa* did not vary significantly between groups at each station. The percentage contribution of large individuals, however, was significantly greater in Group 1 at station A ($p = 0.03$), but no variability was observed between Groups 1 and 2 at station B ($p = 0.76$).

3.4 DISCUSSION

Oceanographic surveys in the vicinity of the Prince Edward Archipelago have shown that prevailing hydrodynamic conditions in the waters surrounding the archipelago may by strongly influenced by the proximity of the SAF (Perissinotto & Duncombe Rae 1990; Ansorge & Lutjeharms 2002; Pakhomov *et al.* 2000b; Perissinotto *et al.* 2000). During the present investigation sea surface temperatures at both stations (A and B) remained within the narrow range of between 5.95 and 6.59 ºC at station A and 5.86 and 6.59 ºC at station B (Figures 3.2 and 3.3). This suggests that the investigation was conducted in PFZ waters, with the position of the SAF likely being to the north of the islands, as the PFZ water mass has a surface temperature of approximately 6 ºC (IJ Ansorge, *personal communication*). Furthermore, surface chl-*a* concentrations recorded *en route* to the Prince Edward Archipelago showed that the SAF lay to the north of the islands, at 45 ºS, while measurements made during the return trip to Cape Town indicated that the SAF was positioned at 45.5 ºS (EA Pakhomov, *unpublished data*). These results suggest that the prevailing hydrodynamic condition at the time of investigation was that of a retention system (Perissinotto *et al.* 2000). It should be noted that although significant small-scale temporal variability was shown to occur in sea surface temperature, this was most likely the result of freshwater input from the islands. Another possible reason for sea surface temperature variation is the effect of advection of parcels of water, with variable physical characteristics, from the upstream region to the area between the islands (Pakhomov *et al.* 2000c).

Total chl-*a* concentrations recorded at both stations during the 18 day survey are also indicative of a retention system, with enhanced phytoplankton biomass occurring on some of the days. Although total chl-*a* values are not as high as those reported in other studies for blooms in the Southern Ocean (Saggiomo *et al.* 1998; Pakhomov *et al.* 1997; Froneman *et al.* 2001; Pakhomov *et al.* 2001; Tremblay *et al.* 2002), they are higher than those typically reported in other open water regions of the PFZ (Bernard & Froneman 2002; Froneman *et al.* 2000a; see also Chapter Two) and are similar to those reported in the waters surrounding the PEIs and other Sub-Antarctic islands (Pakhomov *et al.* 1997; Bradford-Grieve *et al.* 1998; Froneman & Balarin 1998; Froneman & Pakhomov 1998a; Froneman *et al.* 1999). Enhanced

nutrient levels (El-Sayed 1988; Pakhomov & Froneman 1999a) and increased water column stability (Laubscher *et al.* 1993; Dafner 1997; Balarin 1999), due to freshwater run-off, are the basis for phytoplankton blooms during a retention system at the Prince Edward Archipelago (Perissinotto *et al.* 1990a, b; Perissinotto & Duncombe Rae 1990). Total and size-fractionated chl-*a* concentrations varied significantly over short periods of time and also, on some occasions, between stations A and B. Variability on such a small spatio-temporal scale is an important factor to consider when examining the pelagic ecosystem (Pakhomov *et al.* 2000c).

Average total mesozooplankton numbers at both stations A and B (472.46 ind. m^{-3} and 522.49 ind. m^{-3}, respectively) were higher than those recorded in most previous surveys at the Prince Edward Archipelago (Allanson *et al.* 1985; Perissinotto 1992; Froneman & Pakhomov 1998a; Pakhomov *et al.* 1998; Froneman *et al.* 1999; Pakhomov & Froneman 1999a; Hunt *et al.* 2001; Hunt & Pakhomov 2003). The mesozooplankton community during the survey was dominated by copepods (mainly *C. simillimus*, *Ctenocalanus* spp., *O. similis* and *C. brevipes*), chaetognaths (*E. hamata* and *S. gazellae*) and the thecosome pteropod, *L. retroversa*. This result is in agreement with numerous other investigations in the vicinity of the Prince Edward Archipelago and indeed the PFZ (Perissinotto 1992; Froneman & Pakhomov 1998a; Bernard & Froneman 2002; Hunt & Pakhomov 2003; see also Chapter Two). Total mesozooplankton numbers did not vary significantly over short distances, but on a few occasions did vary significantly over 24 hours. Small-scale variability of copepods and pteropods was not particularly frequent, with both groups maintaining fairly uniform densities. It is important to note, however, that while variability was not common, both copepod and pteropod numbers were shown to vary significantly over 24 hour periods and between stations A and B.

The size class structure of *L. retroversa* was generally dominated by the small (< 500 µm) and medium-sized (500 – 1500 µm) individuals, which accounted for an average of 42.8 % and 37.9 %, respectively, at station A; and for an average of 39.6 % and 43.0 %, respectively, at station B. Large individuals (> 1500 µm) made substantial contributions to total *L. retroversa* numbers (> 45 %) on days 13 and 18 at station A and on day 20 at station B, but on average, this size class contributed < 20 % at both stations. The predominance of small and medium sized individuals

during autumn suggests that *L. retroversa* exhibits a similar spawning pattern in the Southern Ocean to that of *L. helicina* in the Arctic waters (Gannefors *et al.* 2005), with the main spawning period being late summer to early autumn, resulting in elevated numbers of juveniles (small and medium sized individuals) in late autumn and spring (Gannefors *et al.* 2005). Gannefors *et al.* (2005) reported that the highest numbers of females (large individuals) occurred in summer in the Arctic waters, but by early autumn, their numbers had significantly decreased. During the present survey, although large females were encountered in early autumn, their low abundance is similar to that reported by Gannefors *et al.* (2005). Statistical analysis conducted on the present data indicates that small-scale spatio-temporal variability in the size structure of *L. retroversa* was observed on a few occasions, but on the whole, the size structure remained relatively constant.

Hierarchical cluster analyses separated mesozooplankton assemblages into two different groups at each station. The mesozooplankton assemblages associated with each group at each station may indicate the presence of pockets of different water masses within the general PFZ waters flowing past the islands at the time. Indeed, previous investigations at the Prince Edward Archipelago suggest that pockets of differing water masses are frequently pulsed through the inter-island region (Perissinotto & McQuaid 1992; Pakhomov *et al.* 2000c). According to Perissinotto & McQuaid (1992), zooplankton may be advected from upstream of the islands to the inter-island region, thereby replenishing the zooplankton stocks, depleted by predation of land-based predators. Pakhomov *et al.* (2000c) suggest that a parcel of colder, more saline water passed between the inter-island region during their investigation; bringing with it, distinctly Antarctic species, such as the euphausiid, *Thysanoessa macrura* (Pakhomov *et al.* 2000c). Total copepod numbers appeared to be the main factor responsible for the variability between groups identified at each station. Interestingly, total *L. retroversa* numbers, as well as the percentage contribution of small and medium sized individuals did not exhibit any variability between groups at either of the stations. The percentage contribution of large *L. retroversa*, on the other hand, did vary significantly between groups at station A, but not at station B. At station A, the percentage contribution of large individuals was higher during the initial 13 days of the survey, and then dropped off significantly. While it is possible that the different mesozooplankton assemblages identified at each

station might represent different water mass pockets, the lack of oceanographic data makes it difficult to be certain. If, indeed, pulsing of different water masses did occur during the present investigation, it is interesting to note that even on a small spatial scale, two stations can experience entirely different water masses.

The results of the present study stress the importance of understanding small-scale variability in such an unpredictable environment. They also highlight the fact that sea surface temperature and total and size-fractionated chl-*a* concentrations are highly erratic and may frequently vary significantly over short distances and periods of time. Although copepods and the pteropod, *L. retroversa*, were not as frequently variable as chl-*a* was during the present survey, both taxa have been shown to be positively correlated to total chl-*a* concentrations (see Chapter Two). Interestingly, enhanced levels of chl-*a* at both stations A and B appear to be followed 3 – 5 days later by increased numbers of *L. retroversa*. It is not clear, however, whether this is due to a response by the pteropods to increased phytoplankton concentrations or simply the result of the presence of a different water mass due to pulsing.

CHAPTER FOUR:

INTER-ANNUAL VARIABILITY IN THE GRAZING IMPACT OF DOMINANT ZOOPLANKTON TAXA IN THE POLAR FRONTAL ZONE AND SURROUNDING WATER MASSES, SOUTHERN OCEAN, WITH SPECIFIC REFERENCE TO *LIMACINA RETROVERSA*

4.1 INTRODUCTION

The role of the Southern Ocean in the global carbon cycle is still being debated. Although extensive research has been carried out in the Southern Ocean, these studies focussed largely on the more productive regions, including the Marginal Ice Zone (Froneman *et al.* 1997), the vicinity of the major oceanic fronts (Froneman & Perissinotto 1996; Dubischar & Bathmann 1997; Pakhomov & Perissinotto 1997), the neritic waters of Antarctica (Pakhomov & Perissinotto 1997) and in the waters surrounding the oceanic islands (Perissinotto 1992; Atkinson 1994; Atkinson *et al.* 1996; Pakhomov *et al.* 1997). The expanse of open ocean north of the Antarctic Polar Front (APF), which typically exhibits relatively low productivity (Laubscher *et al.* 1993; Froneman *et al.* 2001), has largely been ignored. In order to understand the role of this region in the Southern Ocean carbon cycle, it is essential that studies examining biologically mediated carbon flux be conducted.

The Antarctic Circumpolar Current (ACC) is bound by two major fronts, namely the Sub-Antarctic Front (SAF), to the north, and the APF, to the south. The region between the two fronts is a transition zone known as the Polar Frontal Zone (PFZ). It is a region of intense physical and biological variability, with meanders and eddies being common in both the SAF and APF (Legeckis 1977; Bryden 1983; Lutjeharms 1990; Ansorge *et al.* 1999; Froneman *et al.* 1999), facilitating the transfer of plankton across the frontal systems. Consequentially, the zooplankton community in the PFZ is highly variable and comprised of species from a variety of origins, including sub-tropical (e.g. *Ctenocalanus vanus*; *Pleuromamma abdominalis*), sub-Antarctic (e.g. *Metridia lucens*; *Scolecithricella minor*; *Calanus simillimus*) and Antarctic (e.g. *Oithona frigida*; *Rhincalanus gigas*; *Clausocalanus laticeps*; *Clausocalanus citer*) (Ansorge *et al.* 1999; Froneman *et al.* 1999; Pakhomov & Froneman 1999a). The mesozooplankton community of the PFZ, although highly variable, is dominated by copepods mainly of the genera *Oithona*, *Ctenocalanus*, *Calanus* and *Clausocalanus* (Hopkins 1985; Conover & Huntley 1991; Perissinotto 1992; Atkinson & Shreeve 1995; Atkinson 1996; Atkinson *et al.* 1996; Pakhomov *et al.* 2000a; Bernard & Froneman 2002; Pakhomov & Froneman 2004a).

Estimates of the grazing impact of copepods within the PFZ range from < 1 % to 50 % of the available chlorophyll-*a* (chl-*a*) biomass (Morales *et al.* 1991; Perissinotto 1992; Atkinson *et al.* 1996; Razouls *et al.* 1998; Froneman *et al.* 2000a; Li *et al.* 2001; Urban-Rich *et al.* 2001) and between 2 % and 70 % (Hansen *et al.* 1990; Morales *et al.* 1991; Atkinson & Shreeve 1995; Atkinson 1996; Dubischar & Bathmann 1997; Razouls *et al.* 1998; Li *et al.* 2001) in the water column. Although copepods generally dominate total mesozooplankton numbers and biomass in the region, previous research suggests that euthecosome pteropods, of the genus *Limacina*, may at times contribute up to 10 % to total numbers (Bernard & Froneman 2002) and up to 35 % of the total standing stock (Pakhomov & Froneman 2004a). In a study at the sub-Antarctic Prince Edward Archipelago, Perissinotto (1992) reported that the pteropod, *Limacina* sp., exhibited daily ingestion rates that were higher than any of the large copepods or euphausiid species in the region. More recently, Pakhomov & Froneman (2004b) showed that during summer in the Spring Ice Edge Zone in the Atlantic sector of the Southern Ocean, pteropods (*L. helicina* and *Clio sulcata*) were responsible for up to 53 % of the total grazing impact. These findings suggest that pteropods may represent important consumers of phytoplankton in the region of the PFZ. At present, there is insufficient evidence to suggest any seasonality in grazing impact of *L. retroversa* in the region.

The aim of this chapter is, therefore, to assess the variability in the autumn grazing rates of *L. retroversa* and its contribution to total zooplankton grazing impact in the PFZ and surrounding water masses.

4.2 METHODS

The grazing impacts of the dominant zooplankton taxa were estimated during the Marion Offshore Ecosystem Variability Studies (MOEVS) II, IV and V, during April 2002, 2004 and 2005, respectively. Details of the physical environment, surface chl-*a* concentrations, phytoplankton size class structure and mesozooplankton community structure are available in Chapter Two. Details of voyages are presented in the Appendix, Tables A.6 to A.8. For the purpose of determining grazing variability between water masses, station groupings determined by hierarchical cluster analysis for each survey (see Chapter Two) have been used as indicators of water

mass. Station groupings for MOEVS II are: southern Sub-Antarctic Zone Group (sSAZG: stations 11 and 36); Polar Frontal Zone Group (PFZG: stations 13, 15, 39, 60, 62 and 65); and Antarctic Zone Group (AAZG: stations 17, 19, 23, 41 and 43). Station groupings for MOEVS IV are: PFZG (stations 228, 229, 234, 236, 237, 240, 244 and 256); and sSAZG (stations 238 and 239). Station groupings for MOEVS V are: sSAZG (stations 265 and 288); PFZG (stations 264, 269, 270, 272, 275, 279, 280, 283, 290 and 291); and Eddy Group/AAZG (stations 262, 263, 268, 273, 274, 276, 277, 278, 282, 284, 285 and 286). Note that during MOEVS V, the eddy encountered was of AAZ origin, and will thus be denoted AAZG water mass for the purpose of the present study.

4.2.1 Integrated chlorophyll-*a* (chl-*a*)

For the purpose of the grazing study, chl-*a* concentrations were integrated over the top 100 m of the water column. At each station from each survey (see Chapter Two for station details), seawater samples were collected at five standard depths (0, 5, 20, 50 and 100 m) in the upper 100 m of the water column using a 12 x 8 L Niskin bottle rosette attached to a CTD (conductivity, temperature, depth) probe. Chl-*a* concentrations at each depth were determined by gently passing (< 5 cm Hg) a 250 mL aliquot of seawater through a GF/F filter. Chl-*a* was then extracted from the filter in 8 mL of 90 % acetone and stored at -20 ºC for at least 24 hours. After centrifugation (5000 rpm), the chl-*a* concentration was measured using a Turner Designs 10AU Fluorometer, after the method of Holm-Hansen & Riemann (1978). Chl-*a* concentrations from the selected depths were integrated over the top 100 m of the water column by trapezoidal integration. Integrated chl-*a* concentrations were expressed as mg m^{-2}.

4.2.2 Integrated zooplankton abundances

Mesozooplankton were collected using either a Bongo or WP2 net as described in Chapter Two. Macrozooplankton were collected from the same nets during MOEVS IV. During MOEVS V, macrozooplankton samples were collected using an RMT-8 net with a mesh size of 0.45 cm and a mouth area of 8 m^2. Samples collected with the RMT-8 net were treated in a similar manner to those collected with

the Bongo and WP2 nets, as described previously. Total zooplankton abundances, expressed as number of individuals per cubic meter (ind. m^{-3}), were integrated over the top 100 m of the water column so as to be comparable with integrated chl-*a* values and have been expressed as number of individuals per square meter (ind. m^{-2}).

4.2.3 Zooplankton ingestion rates and grazing impact

The grazing impacts of the dominant zooplankton taxa in the PFZ and surrounding water masses were investigated using the gut fluorescence technique (Mackas & Bohrer 1976). The taxa selected for the study included the four most abundant copepod species (*Calanus simillimus*, *Clausocalanus* spp., *Ctenocalanus* spp. and *Oithona similis*), the most abundant euphausiid species (*Euphausia vallentini*, *Thysanoessa macrura* and euphausiid furcilia), the tunicate, *Salpa thompsoni*, and the euthecosome pteropod, *Limacina retroversa*. Ingestion rates for the dominant copepods and *L. retroversa* were estimated during MOEVS II and IV. Regression equations obtained from ingestion rates and integrated chl-*a* values measured during MOEVS II and IV were used to estimate ingestion rates of the copepods and pteropod for MOEVS V (see Appendix, Table A.9). Gut evacuation and gut pigment degradation rates for *L. retroversa* were only estimated during MOEVS IV. The gut evacuation and gut pigment degradation rates obtained during that survey were then used to estimate the ingestion rate of *L. retroversa* for MOEVS II. Copepod gut evacuation rates were estimated during MOEVS II and IV.

Note that due to time constraints at sea, only ingestion rates of the copepods and pteropod were determined by the author, while ingestion rates for the tunicate and dominant euphausiids were estimated by others, assisted by the author. Only the final values for daily ingestion rates of *S. thompsoni* and the euphausiids are presented and used here. Ingestion rates for *S. thompsoni* were estimated during MOEVS II (PW Froneman), while those for the dominant euphausiids were estimated during MOEVS V (ATF Bernard, MSc thesis).

Collectively, the taxa used to investigate total zooplankton grazing impact contributed up to 95.9 %, 88.1 % and 96.7 % of the total zooplankton numbers during MOEVS II, IV and V, respectively (MOEVS II: Mean = 84.0 %; SD = 11.4 %;

MOEVS IV: Mean = 76.4 %; SD = 10.8 %; MOEVS V: Mean = 84.6 %; SD = 10.5 %) (Tables 4.1 – 4.3).

The estimation of the daily consumption of phytoplankton by the selected zooplankton requires the following variables: integrated gut pigment over 24 hours (G, ng (pigm) ind^{-1}), gut evacuation rate (k, h^{-1}) and gut pigment destruction rate (b^1, non-dimensional). Due to size constraints, the gut pigment destruction rate was only estimated for *L. retroversa*, *S. thompsoni* and the euphausiids. An average value of 50 % gut pigment destruction was assumed for all the copepod species (Perissinotto 1992; Froneman *et al.* 2000a).

Integrated gut pigment concentrations (G) were obtained by assessing the diel variability in gut pigment contents of the selected mesozooplankton. Animals were collected in either Bongo or WP2 nets (see Chapter Two for details) at approximately 4 hour intervals over a 24 hour period. For small taxa (i.e. all copepods and the pteropod), samples collected were immediately anaesthetized in a solution of soda: seawater (1:5, v/v), after Morales *et al.* (1991), retained on a 200 µm mesh sieve and frozen at -20 °C in the dark for later analysis. In the laboratory, samples were thawed and individuals were quickly sorted under low light conditions using a Wild M5A Heerbrugg dissecting microscope, operated at 50 x magnification. For the larger specimens (i.e. salps and euphausiids), individuals were picked directly from the catch. Once a sufficient number of individuals for each species were collected (40 x *O. similis*; 20 x *C. simillimus*, *Clausocalanus* spp. and *Ctenocalanus* spp.; 5 – 10 x *L. retroversa*; 1 x *S. thompsoni* and 1-5 x euphausiids) they were placed into plastic centrifuge tubes (10 mL) with 8 mL of 90 % acetone and stored at -20 °C for 24 hours. After centrifugation (5000 rpm), pigment content of the acetone extract was measured, before and after acidification using a Turner Designs 10AU Fluorometer (Mackas & Bohrer 1976). Gut pigment contents were calculated according to the method of Båmstedt *et al.* (2000). It is important to note that only adult copepods were examined, while predominantly medium-sized individuals of *Limacina retroversa* were selected to estimate pteropod ingestion rates.

The calculation of gut evacuation rate (k, h^{-1}) required that freshly caught zooplankton be gently placed into a 10 L plastic bucket filled with particle-free water

(passed through 0.2 µm filters) to which non-fluorescent charcoal powder had been added (Perissinotto 1992). Experiments were carried out on deck at ambient seawater temperatures. Sub-samples were collected every 10 minutes for the first hour and every 20 minutes thereafter, and treated as described in the previous paragraph. Total incubation time was 2 hours. The gut evacuation rate was derived from the slope of the regression of the natural logarithm of gut pigments versus time (Dam & Peterson 1988).

The gut pigment destruction rate (b^1) of *L. retroversa*, *S. thompsoni* and the euphausiid species was determined using independent measurements of gut pigment loss. Active individuals were gently placed into a 10 L bucket of particle-free water (as described in the previous paragraph for gut evacuation rates) and allowed to empty their guts for 24 hours. A two-compartment pigment budget approach was employed by comparing the decrease in pigment content in the grazing bottles with the increase in gut pigment levels of animals incubated in these bottles (Perissinotto 1992). The experiment required that 1 L of natural seawater be placed into a plastic bottle. A 500 mL sub-sample was then removed and the chl-*a* concentration assessed. A single pteropod, salp or euphausiid was placed into the remaining 500 mL and incubated for 1 hour, after which the chl-*a* concentration of the water and the gut pigment content of the animal were estimated. A total of ten replicates were prepared per taxa. Loss of pigment due to destruction was calculated using the following equation (Perissinotto 1992):

$$b = \{[(Gt - Pb)/P]^{-1}\} \times 100 \quad (1)$$

Where *Gt* is gut content per individual, *Pb* is background fluorescence per individual and *P* is total amount of pigment ingested per individual (calculated from the difference between control and experimental water assemblages).

Daily ingestion rates of selected zooplankton [*I*, ng (pigm) ind^{-1} day^{-1}] were estimated using the following equation (Perissinotto 1992):

$$I = kG/(1-b^1) \quad (2)$$

Taxon-specific grazing rates [mg (pigm) m^{-2} day^{-1}] were calculated as the product of abundance and individual ingestion rates. Community grazing impact was

then expressed as a percentage of the integrated phytoplankton biomass consumed per day.

4.2.4 Statistical analyses

Analysis of variance

Factorial ANOVAs (StatSoft, Inc. 2004) were used to test for any significant variability between either year or water mass for the following variables: total integrated chl-*a*; total mesozooplankton grazing rates and grazing impact; *L. retroversa* grazing rates and grazing impact; and copepod grazing rates and grazing impact. Post-Hoc analyses were done using Fisher's LSD tests. All variables were log-transformed.

Correlation analysis

Pearson's Correlation (Linear Correlation) analysis (StatSoft, Inc. 2004) was used to test for significant correlations between integrated chl-*a* and the following variables: total mesozooplankton grazing impact; *L. retroversa* grazing rates and grazing impact; and copepod grazing rates and grazing impact. Pearson's Correlation was also used to test for significant correlations between sea surface temperature and integrated chl-*a*.

4.3 RESULTS

4.3.1 Integrated chlorophyll-*a* (chl-*a*)

Marion Offshore Ecosystem Variability Study (MOEVS) II – April 2002

Chl-*a* concentrations, integrated over the top 100 m of the water column, during the survey ranged from 10.97 to 28.34 mg m^{-2} (Mean = 15.38 mg m^{-2}; SD = 4.79 mg m^{-2}) (Figure 4.1). There was no significant relationship between integrated chl-*a* and sea surface temperature (Pearson's Correlation: $r^2 = 0.04$; $r = 0.20$; $p = 0.52$).

Marion Offshore Ecosystem Variability Study (MOEVS) IV – April 2004

Total chl-*a* concentrations, integrated for the top 100 m of the water column, ranged from 4.15 mg m^{-2} to 25.70 mg m^{-2} (Mean = 13.22 mg m^{-2}; SD = 5.86 mg m^{-2}) during the survey, with no distinct spatial trends being observed (Figure 4.2). Indeed, total integrated chl-*a* concentrations were not significantly correlated to surface seawater temperature (Pearson's Correlation: $r^2 = 0.09$; $r = 0.30$; $p = 0.40$).

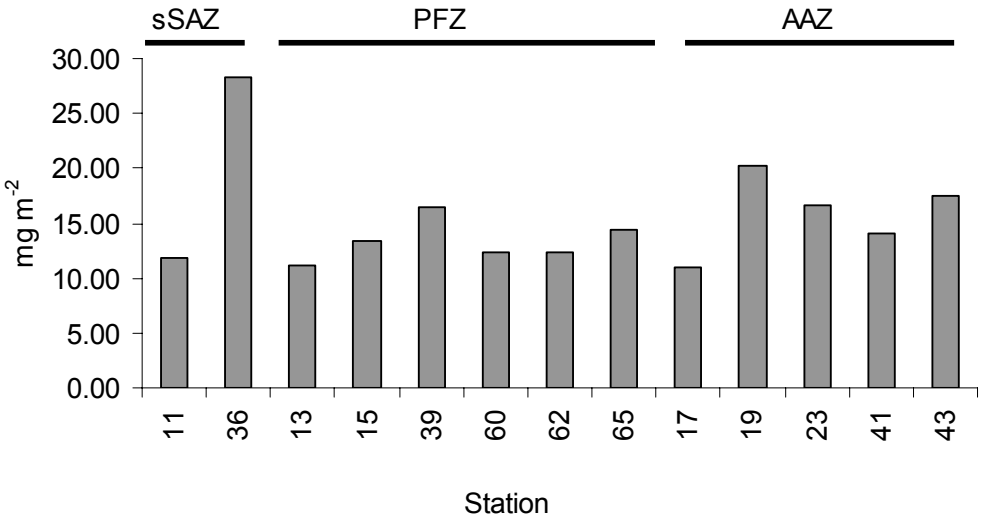

Figure 4.1 Integrated chlorophyll-*a* values in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ) during MOEVS II, April 2002.

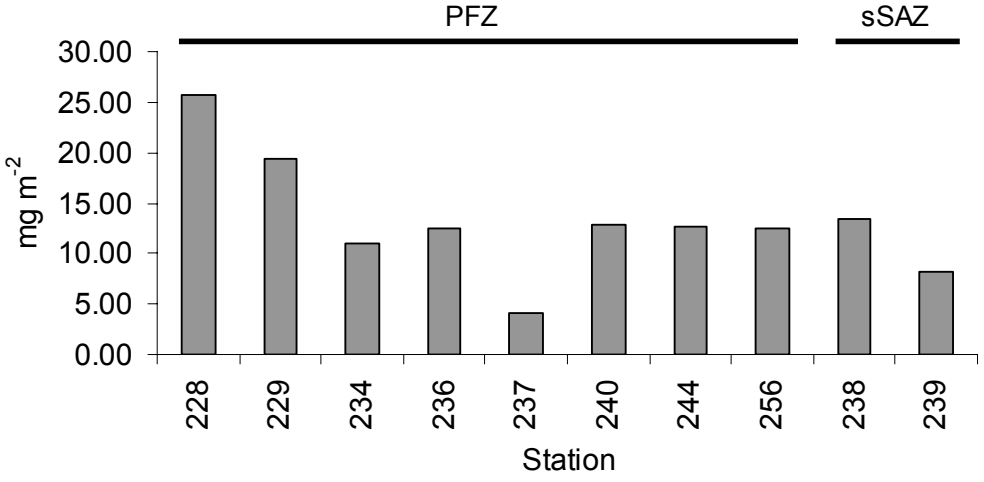

Figure 4.2 Integrated chlorophyll-*a* values in the Polar Frontal Zone (PFZ) and southern Sub-Antarctic Zone (sSAZ) during MOEVS IV, April 2004.

Marion Offshore Ecosystem Variability Study (MOEVS) V – April 2005

Integrated chl-*a* values for the top 100 m of the water column ranged between 4.43 and 11.37 mg m^{-2} (Mean = 7.95; SD = 1.97) (Figure 4.3). There was no significant correlation between integrated chl-*a* and sea surface temperature (Pearson's Correlation: $r^2 = 0.0004$; r = 0.02; p = 0.92) and no spatial trends were observed for integrated chl-*a* in the survey area.

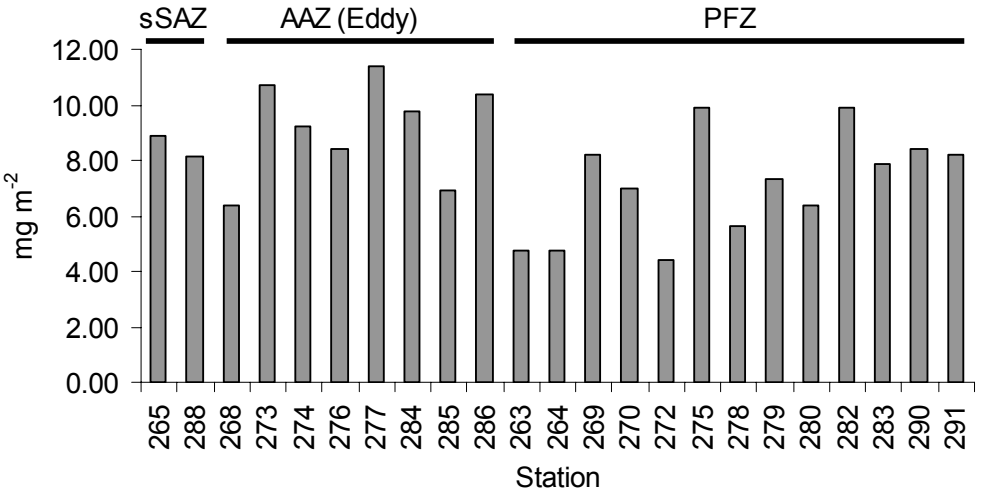

Figure 4.3 Integrated chlorophyll-*a* values in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ or Eddy) during MOEVS V, April 2005.

4.3.2 Integrated zooplankton abundances

Marion Offshore Ecosystem Variability Study (MOEVS) II – April 2002

Total integrated zooplankton abundances within the top 100 m of the water column ranged from 1 906.04 to 65 752.53 ind. m^{-2} during MOEVS II (Mean = 25 035.02 ind. m^{-2}; SD = 22 190.88 ind. m^{-2}) (Table 4.1). Copepods accounted for up to 93.4 % of the total zooplankton counts (Mean = 75.4 %; SD = 12.2 %) (Figure 4.4), with an average abundance of 20 148.11 ind. m^{-2} (SD = 18 962.65 ind. m^{-2}) (Table 4.1). *L. retroversa* only contributed between 0.4 and 20.7 % (Mean = 8.4 %; SD = 6.9 %) (Figure 4.4) to the total numbers, averaging 1 782.42 ind. m^{-2} (SD = 2 335.05

ind. m^{-2}) (Table 4.1). Other grazers, including *S. thompsoni* and euphausiid furcilia, accounted for less than 0.8 % of the total numbers throughout the survey (Figure 4.4).

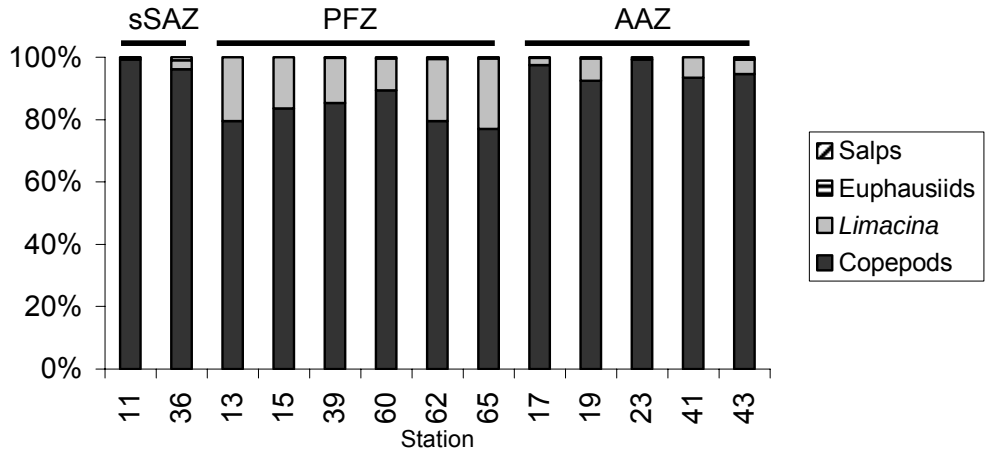

Figure 4.4 Percentage contributions of major herbivorous zooplankton groups to total zooplankton abundances in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ), during MOEVS II, April 2002.

Marion Offshore Ecosystem Variability Study (MOEVS) IV – April 2004

The average total integrated zooplankton abundance for the top 100 m of the water column during MOEVS IV was 35 199.61 ind. m^{-2} (SD = 23 847.72 ind. m^{-2}) (Table 4.2). Copepods were responsible for between 35.6 and 78.8 % (Mean = 64.2 %; SD = 11.3 %) (Figure 4.5) of the total zooplankton numbers, with an average abundance of 23 699.17 ind. m^{-2} (SD = 16 961.75 ind. m^{-2}) (Table 4.2). *L. retroversa* numbers ranged from 156.38 ind. m^{-2} to 10 741.99 ind. m^{-2} (Mean = 4 301.71 ind. m^{-2}; SD = 3 859.76 ind. m^{-2}) (Table 4.2), which corresponds to between 1.3 and 30.0 % (Mean = 11.8 %; SD = 8.7 %) of the total numbers (Figure 4.5). Euphausiids were not present in very high numbers, accounting for an average of only 0.4 % (SD = 0.5 %) of the total (Figure 4.5).

Marion Offshore Ecosystem Variability Study (MOEVS) V – April 2005

Total integrated zooplankton numbers for the top 100 m of the water column during MOEVS V ranged between 1 675.45 and 60 526.68 ind. m^{-2} (Mean = 16

117.31 ind. m^{-2}; SD = 15 508.48 ind. m^{-2}) (Table 4.3). Copepods accounted for up to 96.3 % of the total (Mean = 83.7 %; SD = 10.5 %) (Figure 4.6), with numbers ranging from 1 168.99 to 54 755.56 ind. m^{-2} (Mean = 14 243.24 ind. m^{-2}; SD = 14 393.49 ind. m^{-2}) (Table 4.3). *L. retroversa* contributed substantially less to total zooplankton numbers during MOEVS V, with an average of 0.9 % (SD = 1.0 %) of the total (Figure 4.6). *L. retroversa* numbers varied between 0.00 and 406.35 ind. m^{-2} (Mean = 92.39 ind. m^{-2}; SD = 114.93 ind. m^{-2}) (Table 4.3). Combined, *S. thompsoni* and *E. vallentini* (the remaining dominant grazers), accounted for less than 0.2 % (Mean = 0.02 %; SD = 0.03 %) of the total zooplankton numbers throughout the survey (Figure 4.6).

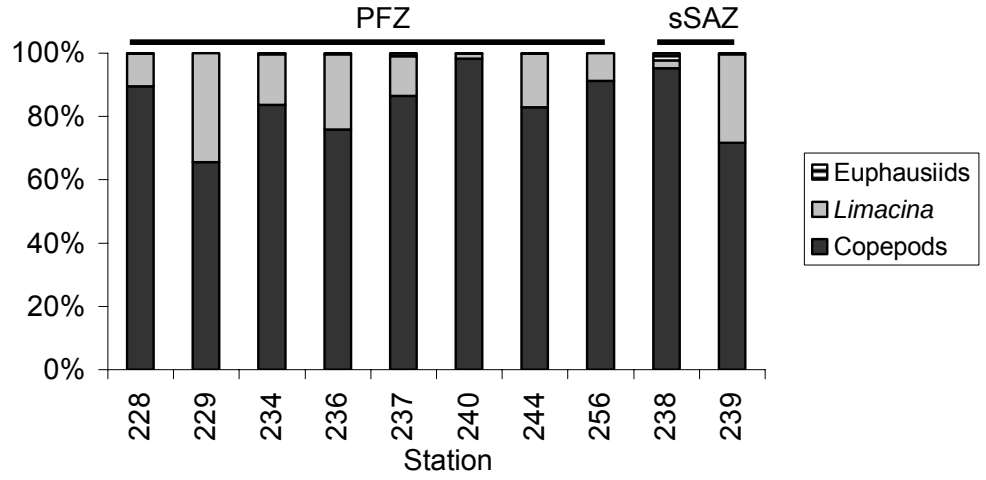

Figure 4.5 Percentage contributions of major herbivorous zooplankton groups to total zooplankton abundances in the Polar Frontal Zone (PFZ) and southern Sub-Antarctic Zone (sSAZ), during MOEVS IV, April 2004.

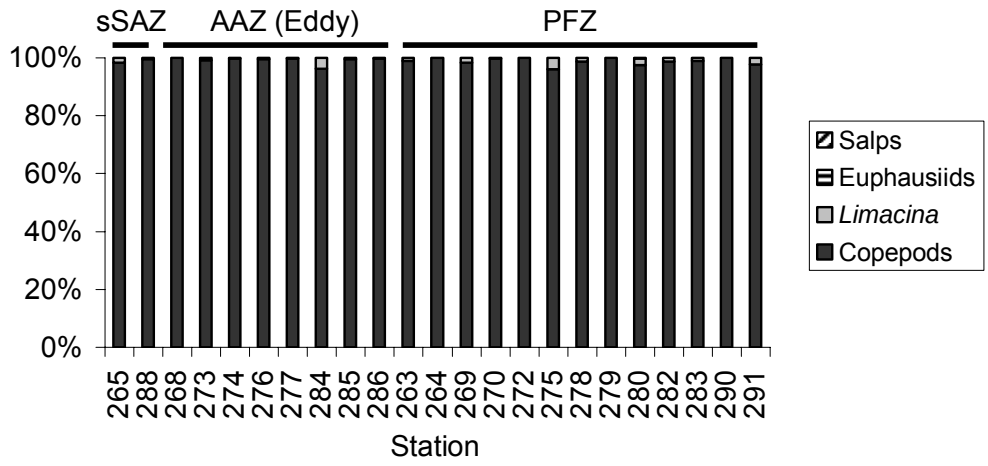

Figure 4.6 Percentage contributions of major herbivorous zooplankton groups to total zooplankton abundances in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ or Eddy), during MOEVS V, April 2005.

Table 4.1 Integrated abundances (ind. m^{-2}) of selected zooplankton at stations occupied within the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ) during MOEVS II, April 2002.

	sSAZ		PFZ						AAZ				
Station numbers	**11**	**36**	**13**	**15**	**39**	**60**	**62**	**65**	**17**	**19**	**23**	**41**	**43**
Calanus simillimus	11781.45	498.86	14486.39	3439.99	544.42	706.06	197.19	176.43	1035.71	2403.00	1334.79	475.16	176.18
Oithona similis	15625.04	3082.23	11163.04	21822.46	1055.33	2055.41	394.38	7079.26	5837.65	27901.54	35085.91	8647.91	3963.94
Clausocalanus spp.	1754.68	89.08	937.35	322.50	175.89	564.84	225.36	595.45	753.25	1735.50	3114.51	624.50	440.44
Ctenocalanus spp.	3258.70	427.59	1363.42	1290.00	469.04	1474.87	253.53	2249.48	12852.26	21627.03	18687.06	692.38	4976.95
Limacina retroversa	167.11	124.71	7157.98	5267.49	376.90	549.15	267.62	2977.26	517.86	4138.51	444.93	719.53	462.46
Euphausiid furcilia	73.69	41.38	10.74	13.54	6.70	24.29	7.27	48.38	23.72	218.65	40.04	3.50	22.73
Salpa thompsoni (< 20mm)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	50.46	0.00	0.00	62.51
Total zooplankton	40776.17	7155.29	38871.02	35181.21	3092.29	8060.17	1906.04	14358.42	21927.16	65752.53	65071.39	11870.68	11432.91

Table 4.2 Integrated abundances (ind. m^{-2}) of selected zooplankton at stations occupied within the Polar Frontal Zone (PFZ) and southern Sub-Antarctic Zone (sSAZ) during MOEVS IV, April 2004.

	PFZ								sSAZ	
Station numbers	**228**	**229**	**234**	**236**	**237**	**240**	**244**	**256**	**238**	**239**
Calanus simillimus	14910.09	6954.75	7648.73	9949.65	10700.26	14514.18	29003.95	3339.43	78.19	158.07
Oithona similis	21377.12	3167.51	2379.60	7300.72	1026.05	1875.43	1926.46	5936.77	1829.60	526.91
Clausocalanus spp.	7724.51	2685.50	849.86	2325.89	1465.79	1467.73	1605.38	2968.38	3080.61	553.26
Ctenocalanus spp.	17425.05	7712.20	2719.55	6913.07	8061.84	7583.25	6956.67	8255.82	1454.30	579.60
Limacina retroversa	7005.95	10741.99	2606.23	8334.45	3078.16	407.70	8026.92	1948.00	156.38	711.33
Euphausia vallentini	47.72	5.65	0.00	45.43	21.76	0.00	0.00	0.00	17.59	2.47
Thysanoessa macrura	117.89	13.99	55.77	94.01	229.03	42.04	123.75	17.39	142.69	6.17
Total zooplankton	87083.27	35789.52	20662.26	39673.81	31908.87	32295.40	59543.19	30292.70	9640.64	5106.48

Table 4.3 Integrated abundances (ind. m^{-2}) of selected zooplankton at stations occupied within the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ) during MOEVS V, April 2005.

	sSAZ		AAZ							
Station numbers	**265**	**288**	**268**	**273**	**274**	**276**	**277**	**284**	**285**	**286**
Calanus simillimus	2533.33	11507.07	4666.67	23060.32	2838.10	4302.22	1533.33	428.57	12307.69	1971.01
Clausocalanus spp.	656.41	355.56	1600.00	4063.49	380.95	1386.67	955.56	52.38	1805.13	579.71
Ctenocalanus spp.	0.00	484.85	10400.00	11174.60	2761.90	12906.67	7066.67	195.24	10174.36	2643.48
Oithona similis	246.15	323.23	13555.56	16457.14	8076.19	11377.78	4311.11	1385.71	18051.28	6747.83
Limacina retroversa	61.54	64.65	0.00	406.35	19.05	106.67	22.22	80.95	164.10	23.19
Salpa thompsoni (< 20 mm)	0.00	0.00	ND	15.73	0.00	7.07	0.46	0.00	0.13	4.60
Salpa thompsoni (> 20 mm)	0	0.055147	ND	1.62755707	0	1.381579	0.061275	0	0.025067	0.027574
Euphausia vallentini	0.00	0.06	7.02	0.86	4.56	0.67	0.25	0.00	0.23	0.77
Total zooplankton	3935.53	13835.39	32084.81	60526.68	14802.54	31117.99	14604.44	2269.84	45199.67	13171.01

Table 4.3 Continued…

	PFZ												
Station numbers	**263**	**264**	**269**	**270**	**272**	**275**	**278**	**279**	**280**	**282**	**283**	**290**	**291**
Calanus simillimus	6933.33	2253.76	3520.00	1558.33	4197.85	533.33	4723.81	5518.84	3517.12	2320.00	3142.86	336.84	431.01
Clausocalanus spp.	3276.19	326.88	53.33	16.67	172.04	20.20	685.71	324.64	403.60	186.67	152.38	378.95	18.60
Ctenocalanus spp.	14476.19	1445.16	240.00	250.00	1066.67	193.94	5219.05	1530.43	4266.67	3466.67	1104.76	701.75	145.74
Oithona similis	9980.95	258.06	1453.33	1750.00	1961.29	505.05	6209.52	2272.46	259.46	3333.33	2400.00	2203.51	573.64
Limacina retroversa	380.95	0.00	93.33	8.33	0.00	52.53	228.57	0.00	201.80	106.67	76.19	0.00	27.91
Salpa thompsoni (< 20 mm)	0.00	0.21	ND	0.03	ND	ND	0.00	0.00	9.17	0.52	0.00	0.17	0.00
Salpa thompsoni (> 20 mm)	0	0.139085	ND	0.130064	ND	ND	0.091912	0	2.277813	0.061275	0	0.137868	0
Euphausia vallentini	7.30	0.05	0.00	1.06	0.00	0.00	0.00	0.00	2.05	1.96	0.00	1.86	0.03
Total zooplankton	40729.25	6364.44	6230.48	4205.95	9150.19	1765.66	19606.76	14462.09	10528.44	11724.78	7955.46	6131.33	1675.45

4.3.3 Zooplankton ingestion rates

Analysis of diel variability of gut pigment contents indicated that during MOEVS II the copepods, *C. simillimus* and *Clausocalanus* spp. (Figure 4.7) exhibited statistically significant differences in gut pigment content between day and night samples, with gut pigments concentrations being higher at night (One-Way ANOVA: $p < 0.05$ in both cases). The cyclopoid copepod, *O. similis*, and the calanoid copepod, *Ctenocalanus* spp. (Figure 4.7), showed no significant variation in gut pigment content over a 24 hour period (One-Way ANOVA: $p > 0.05$ in both cases). *C. simillimus* and *Clausocalanus* spp. exhibited similar trends in diel variability during MOEVS IV, with significantly different gut pigment contents for day and night samples (One-Way ANOVA: $p < 0.05$ in both cases) (Figure 4.8). *Ctenocalanus* spp. also exhibited significant diel variability in gut pigment contents during MOEVS IV, with pigment concentrations being greatest during the night (One-Way ANOVA: $p < 0.05$) (Figure 4.8). In contrast, the cyclopoid copepod, *O. similis*, and the pteropod, *L. retroversa*, showed no significant variation in gut pigment concentrations between day and night samples (One-Way ANOVA: $p > 0.05$ in both cases) (Figure 4.8).

Negative linear models provided the best fit for the decline in gut pigment contents during MOEVS II for *Clausocalanus* spp., *Ctenocalanus* spp. and *O. similis*, while a negative exponential model was most suitable to measure the decline in gut pigment contents for *C. simillimus*. Gut evacuation rates (k) of the copepods ranged from 0.32 h^{-1} for *C. simillimus* to 1.43 h^{-1} for *Ctenocalanus* spp., which corresponds to a gut passage time ($1/k$) of 3.15 hours and 0.70 hours, respectively (Table 4.4). *Clausocalanus* spp. exhibited a gut evacuation rate of 0.44 h^{-1} (2.25 hour gut passage time), while *O. similis* displayed a gut evacuation rate of 0.77 h^{-1}, or a 1.30 hour gut passage time (Table 4.4).

During MOEVS IV, negative exponential models provided the best fit for the decline in gut pigment contents for all four copepod species and *L. retroversa*. Gut evacuation rates (k) of the copepods ranged from 0.34 h^{-1} for *Ctenocalanus* spp. to 0.57 h^{-1} for *O. similis*, which corresponds to a gut passage time ($1/k$) of 2.94 hours to 1.75 hours, respectively (Table 4.4). *C. simillimus* exhibited a gut evacuation rate of 0.50 h^{-1}, i.e. 2.00 hour gut passage time, while *Clausocalanus* spp. had a gut

evacuation rate of 0.35 h^{-1}, or 2.86 hour gut passage time (Table 4.4). *L. retroversa* had a gut evacuation rate of 1.33 h^{-1}, which corresponds to a gut passage time of 0.75 hours (Table 4.4). Results of the two-compartmental approach for gut pigment destruction indicated that *L. retroversa* exhibited a mean destruction rate of 58 % (SD = 7 %; n = 30).

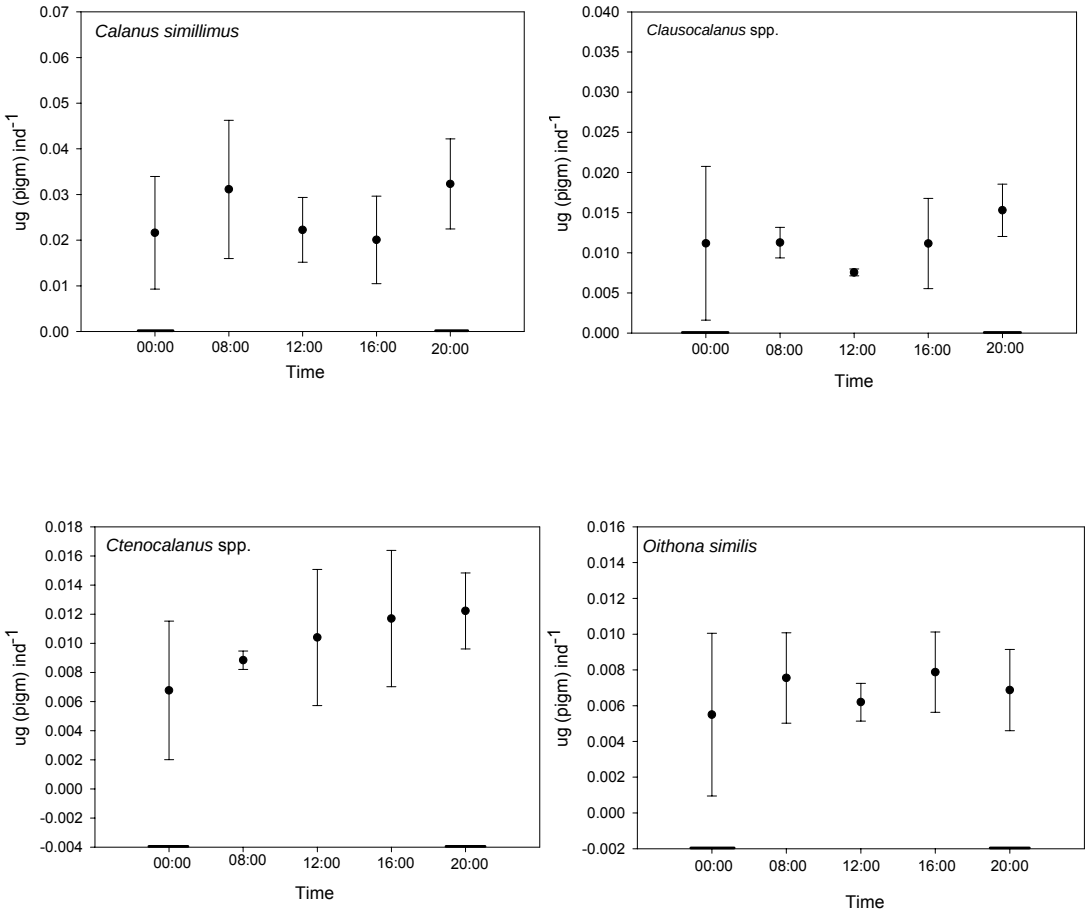

Figure 4.7 Diel variability in gut pigment contents for the dominant copepod species (*Calanus simillimus*, *Clausocalanus* spp, *Oithona similis* and *Ctenocalanus vanus*) during MOEVS II, April 2002. Thickened sections along x-axis represent times of darkness.

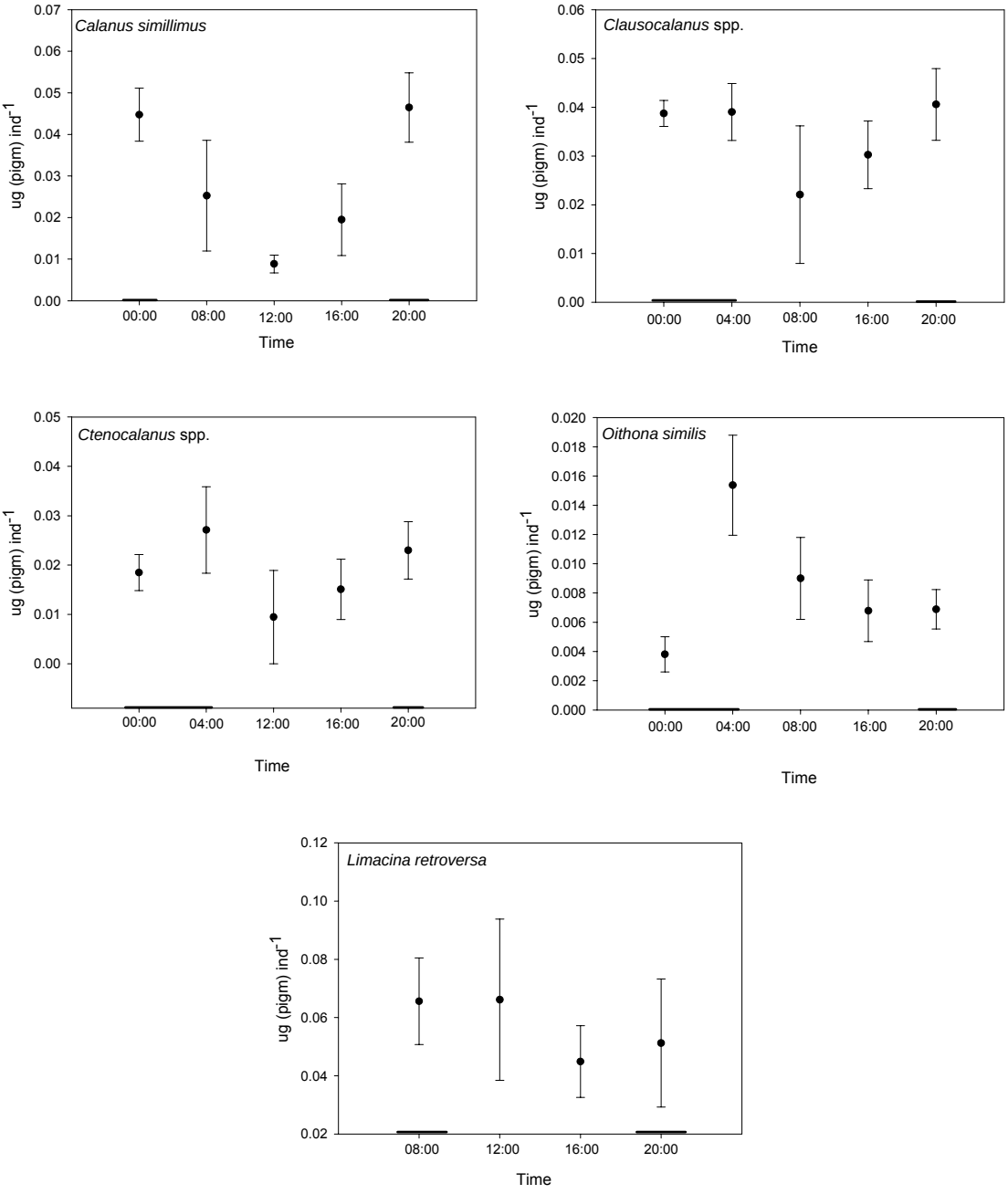

Figure 4.8 Diel variability in gut pigment contents for the dominant copepod species (*Calanus simillimus*, *Clausocalanus* spp, *Oithona similis* and *Ctenocalanus vanus*) and *L. retroversa* during MOEVS IV, April 2004. Thickened sections along x-axis represent times of darkness.

During MOEVS II, daily individual ingestion rates of the copepods ranged from an average of 180.05 ng (pigm) ind^{-1} day^{-1} for *Clausocalanus* spp. to 321.95 ng (pigm) ind^{-1} day^{-1} for *C. simillimus* (Table 4.4). *L. retroversa* exhibited an average individual daily ingestion rate equivalent to 4 146.51 ng (pigm) ind^{-1} day^{-1} (Table 4.4). During MOEVS IV, average daily individual ingestion rates of the copepods varied between 159.32 ng (pigm) ind^{-1} day^{-1} for *O. similis* and 728.36 ng (pigm) ind^{-1} day^{-1} for *C. simillimus* (Table 4.4). Average daily ingestion rates for *L. retroversa* were estimated at 4 128.68 ng (pigm) ind^{-1} day^{-1} (Table 4.4). Average individual daily ingestion rates for the four dominant copepods and *L. retroversa* were estimated for MOEVS V from regressions using integrated chl-*a* concentrations and individual ingestion rates measured for each taxon during MOEVS II and IV. See Appendix, Table A.9 for regression equations for each taxon. Estimated individual daily ingestion rates for the copepods during MOEVS V ranged from 177.98 ng (pigm) ind^{-1} day^{-1} for *O. similis* to 579.28 ng (pigm) ind^{-1} day^{-1} for *C. simillimus* (Table 4.4). The estimated average individual daily ingestion rate for *L. retroversa* during MOEVS V was 4 196.88 ng (pigm) ind^{-1} day^{-1} (Table 4.4).

Ingestion rates for the euphausiids, *E. vallentini* and *T. macrura*, were estimated at 906.00 and 57.21 ng (pigm) ind^{-1} day^{-1}, respectively, while daily ingestion rates of euphausiid furcilia were 312.43 ng (pigm) ind^{-1} day^{-1}. Average daily ingestion rates calculated for *S. thompsoni* were 150 414.27 ng (pigm) ind^{-1} day^{-1} for individuals smaller than 20 mm in length, and 705 714.32 ng (pigm) ind^{-1} day^{-1} for those larger than 20 mm (Table 4.4).

Table 4.4 Gut evacuation rate constants (k, h^{-1}); gut passage time ($1/k$, hours); and average daily ingestion rates (I, ng (pigm) ind^{-1} day^{-1}) of selected zooplankton. Standard deviation in parenthesis.

Taxon	Gut evacuation rate (k, h^{-1})	Gut passage time ($1/k$, hours)	Average daily ingestion rate (I, ng (pigm) ind^{-1} day^{-1})	Survey
L. retroversa	1.33	0.75	4 146.51 (1 296.82)	MOEVS II
			4 128.68 (892.23)	MOEVS IV
			4 196.88 (8.56)	MOEVS V
C. simillimus	0.32	3.15	321.95 (108.10)	MOEVS II
	0.50	2.00	728.36 (644.03)	MOEVS IV
			579.28 (30.84)	MOEV V
Clausocalanus spp.	0.44	2.25	180.05 (44.00)	MOEVS II
	0.35	2.86	454.16 (194.97)	MOEVS IV
			356.61 (20.30)	MOEVS V
Ctenocalanus spp.	1.43	0.70	182.10 (68.41)	MOEVS II
	0.34	2.94	265.37 147.50)	MOEVS IV
			264.80 (2.95)	MOEVS V
O. similis	0.77	1.30	182.10 (68.41)	MOEVS II
	0.57	1.75	159.32 (84.98)	MOEVS IV
			177.98 (2.82)	MOEVS V
S. thompsoni (< 20 mm)	0.77	1.31	150 414.27 (81 914.96)	MOEVS II (PW Froneman)
S. thompsoni (> 20 mm)	0.97	1.03	705 714.32 (1 053 080.50)	MOEVS II (ATF Bernard)
Euphausiid furcilia			312.43 (189.72)	MOEVS V (ATF Bernard)
E. vallentini			906.00 (758.23)	MOEVS V (ATF Bernard)
T. macrura			57.21	MOEVS V (ATF Bernard)

4.3.4 Grazing impact

Marion Offshore Ecosystem Variability Study (MOEVS) II – April 2002

During the survey, total daily grazing rate of zooplankton averaged 13.29 mg (pigm) m^{-2} day^{-1} (SD = 12.82 mg (pigm) m^{-2} day^{-1}) (Table 4.5), which corresponds to an average of 93.0 % (SD = 94.3 %) of the available phytoplankton standing stock consumed per day (Table 4.6). The combined daily grazing rate of the four numerically dominant copepods ranged from 0.24 to 12.41 mg (pigm) m^{-2} day^{-1} (Mean = 4.58 mg (pigm) m^{-2} day^{-1}; SD = 4.18 mg (pigm) m^{-2} day^{-1}) (Table 4.5). Collectively these copepods were responsible for consuming an average of 31.6 % (SD = 26.8 %) of the phytoplankton biomass per day (Table 4.6). *L. retroversa* was responsible for consuming an average of 54.3 % (SD = 78.9 %) of the available

phytoplankton standing stock (Table 4.6), the average grazing rate for the species was 7.39 mg (pigm) m^{-2} day^{-1} (SD = 9.68 mg (pigm) m^{-2} day^{-1}) (Table 4.5). *L. retroversa* accounted for up to 84.4 % of the total daily grazing impact during the survey (Mean = 52.4 %; SD = 28.6 %), while copepods were responsible for, on average, 40.9 % (SD = 26.6 %) of the total grazing impact (Figure 4.9). Euphausiid furcilia made the smallest contribution to total grazing impact, with an average of 0.2 % (SD = 0.3 %) (Figure 4.9). *S. thompsoni* (only individuals < 20 mm in length were encountered during MOEVS II) made substantial contributions to the total grazing impact at the only two stations where it occurred (stations 19 and 43), where it was responsible for up to 64.7 % of the total grazing impact (Figure 4.9). The average contribution of *S. thompsoni* to the total grazing impact, however, was 6.6 % (SD = 18.4 %). The average grazing rate of *S. thompsoni* was estimated at 1.31 mg (pigm) m^{-2} day^{-1} (SD = 3.21 mg (pigm) m^{-2} day^{-1}) (Table 4.5), corresponding to an average daily grazing impact of 7.0 % (SD = 17.4 %) of the available phytoplankton biomass (Table 4.6).

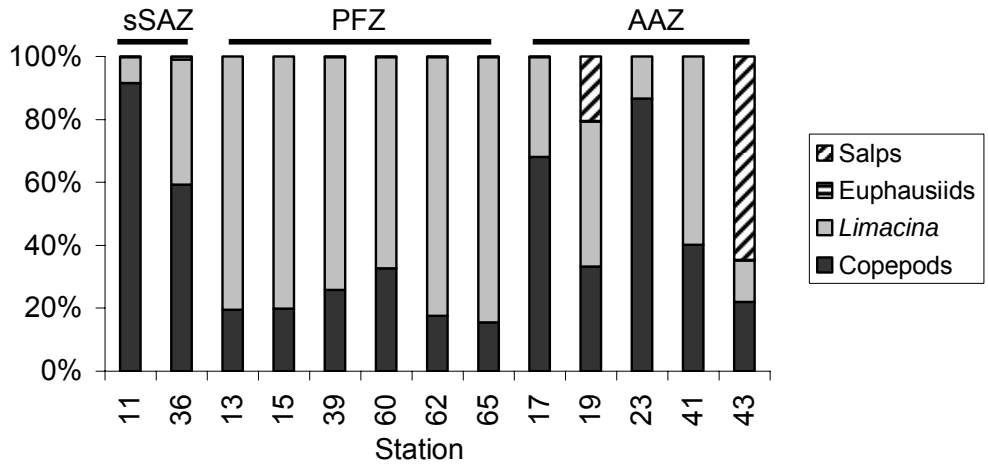

Figure 4.9 Percentage contributions of herbivorous groups to total grazing impact in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ), during MOEVS II, April 2002.

Table 4.5 Grazing rates (mg (pigm) m^{-2} day^{-1}) of selected zooplankton and integrated chlorophyll-*a* in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ) during MOEVS II, April 2002.

	sSAZ		PFZ						AAZ				
Station numbers	**11**	**36**	**13**	**15**	**39**	**60**	**62**	**65**	**17**	**19**	**23**	**41**	**43**
Calanus simillimus	3.79	0.09	4.66	1.11	0.15	0.32	0.06	0.06	0.33	0.85	0.53	0.15	0.09
Oithona similis	2.85	0.56	2.03	3.97	0.25	0.33	0.07	1.57	1.06	6.41	6.23	1.57	1.10
Clausocalanus spp.	0.32	0.01	0.17	0.06	0.03	0.11	0.04	0.12	0.14	0.23	0.80	0.11	0.10
Ctenocalanus spp.	0.77	0.10	0.32	0.31	0.11	0.35	0.06	0.53	3.05	4.93	4.43	0.16	1.91
Limacina retroversa	0.69	0.52	29.68	21.84	1.56	2.28	1.11	12.35	2.15	17.16	1.84	2.98	1.92
Euphausiid furcilia	0.02	0.01	0.00	0.00	0.00	0.01	0.00	0.02	0.01	0.07	0.01	0.00	0.01
Salpa thompsoni (< 20 mm)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.59	0.00	0.00	9.40
Total grazing rates	8.44	1.30	36.87	27.29	2.11	3.39	1.35	14.64	6.74	37.23	13.85	4.99	14.53
Integrated chl-a	11.82	28.34	11.19	13.39	16.54	12.40	12.32	14.35	10.97	20.31	16.70	14.10	17.54

Table 4.6 Grazing impact (%) of selected zooplankton on phytoplankton standing stock in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ) during MOEVS II, April 2002.

	sSAZ		PFZ						AAZ				
Station numbers	**11**	**36**	**13**	**15**	**39**	**60**	**62**	**65**	**17**	**19**	**23**	**41**	**43**
Calanus simillimus	32.1	0.3	41.7	8.3	0.9	2.6	0.5	0.4	3.0	4.2	3.2	1.1	0.5
Oithona similis	24.1	2.0	18.2	29.7	1.5	2.6	0.6	10.9	9.7	31.6	37.3	11.2	6.3
Clausocalanus spp.	2.7	0.0	1.5	0.4	0.2	0.9	0.3	0.8	1.2	1.1	4.8	0.8	0.6
Ctenocalanus spp.	6.5	0.4	2.9	2.3	0.7	2.8	0.5	3.7	27.8	24.3	26.6	1.2	10.9
Limacina retroversa	5.9	1.8	265.3	163.1	9.4	18.4	9.0	86.1	19.6	84.5	11.0	21.2	10.9
Euphausiid furcilia	0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.3	0.1	0.0	0.0
Salpa thompsoni (< 20 mm)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	37.4	0.0	0.0	53.6
Total	71.5	4.6	329.6	203.8	12.8	27.3	10.9	102.0	61.4	183.3	83.0	35.4	82.8

Marion Offshore Ecosystem Variability Study (MOEVS) IV – April 2004

Total daily grazing rate of zooplankton during the study ranged between 3.54 and 52.31 mg (pigm) m^{-2} day^{-1} (Mean = 26.48 mg (pigm) m^{-2} day^{-1}; SD = 18.30 mg (pigm) m^{-2} day^{-1}) (Table 4.7) or between 28.0 and 768.2 % (Mean = 229.7 %; SD = 213.6 %) of the available chl-*a* per day (Table 4.8). The collective daily grazing rates of the copepods ranged between 0.60 and 22.40 mg (pigm) m^{-2} day^{-1} (Mean = 8.77 mg (pigm) m^{-2} day^{-1}; SD = 7.23 mg (pigm) m^{-2} day^{-1}) (Table 4.7) or between 7.4 and 461.0 % (Mean = 89.8 %; SD = 133.6 %) of the total phytoplankton standing stock per day (Table 4.8). The combined daily grazing impact of the copepods accounted for an average of 40.4 % (SD = 28.7 %) of the total daily grazing impact (Figure 4.10). The largest contribution to total grazing impact, however, was exhibited by *L. retroversa*, which contributed an average of 59.5 % (SD = 28.8 %) to total grazing impact (Figure 4.10). Daily grazing rates of *L. retroversa* ranged from 0.65 to 44.35 mg (pigm) m^{-2} day^{-1} (Mean = 17.69 mg (pigm) m^{-2} day^{-1}; SD = 15.78 mg (pigm) m^{-2} day^{-1}) (Table 4.8), which corresponded to between 4.8 and 307.4 % (Mean = 139.8 %; SD = 115.1 %) of the available phytoplankton standing stock per day (Table 4.8). The euphausiids, *E. vallentini* and *T. macrura*, consumed an average of only 0.2 % of the available phytoplankton (SD = 0.3 %) (Table 4.8).

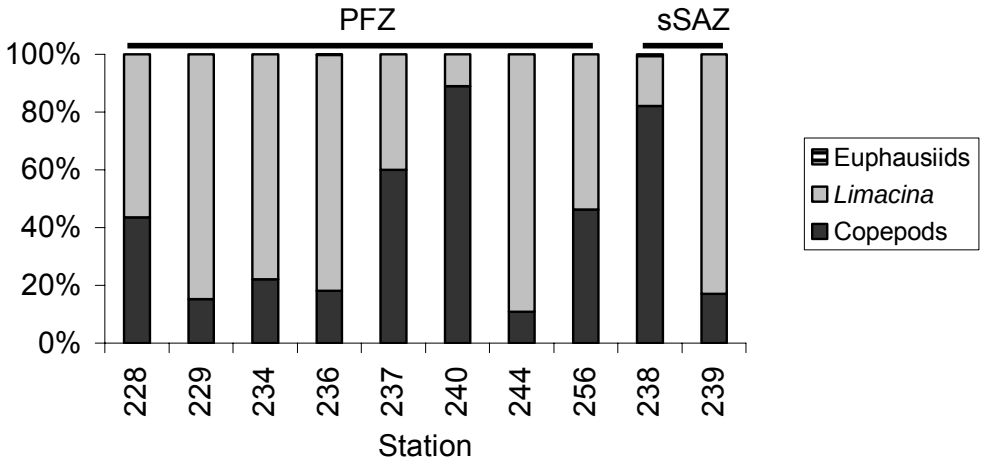

Figure 4.10 Percentage contributions of herbivorous groups to total grazing impact in the Polar Frontal Zone (PFZ) and southern Sub-Antarctic Zone (sSAZ), during MOEVS IV, April 2004.

Table 4.7 Grazing rates (mg (pigm) m^{-2} day^{-1}) of selected zooplankton and integrated chlorophyll-*a* in the Polar Frontal Zone (PFZ) and southern Sub-Antarctic Zone (sSAZ) during MOEVS IV, April 2004.

	PFZ								sSAZ	
Station numbers	**228**	**229**	**234**	**236**	**237**	**240**	**244**	**256**	**238**	**239**
Calanus simillimus	10.86	5.07	2.32	3.10	14.96	10.57	3.08	2.43	0.06	0.12
Oithona similis	3.41	0.50	0.38	1.01	0.16	0.30	0.31	0.95	0.59	0.08
Clausocalanus spp.	3.51	0.33	0.39	0.71	0.75	0.67	0.73	1.35	1.79	0.25
Ctenocalanus spp.	4.62	2.05	0.72	0.76	3.25	2.01	0.60	2.19	0.65	0.15
Limacina retroversa	28.93	44.35	13.52	25.27	12.71	1.68	38.84	8.04	0.65	2.94
Euphausia vallentini	0.04	0.01	0.00	0.04	0.02	0.00	0.00	0.00	0.02	0.00
Thysanoessa macrura	0.01	0.00	0.00	0.01	0.01	0.00	0.01	0.00	0.01	0.00
Total grazing rate	51.37	52.31	17.33	30.89	31.86	15.24	43.57	14.96	3.75	3.54
Integrated chl-a	25.70	19.42	10.96	12.58	4.15	12.77	12.64	12.42	13.42	8.19

Table 4.8 Grazing impact (%) of selected zooplankton on phytoplankton standing stock in the Polar Frontal Zone (PFZ) and southern Sub-Antarctic Zone (sSAZ) during MOEVS IV, April 2004.

	PFZ								sSAZ	
Station numbers	**228**	**229**	**234**	**236**	**237**	**240**	**244**	**256**	**238**	**239**
Calanus simillimus	42.3	26.1	21.2	24.6	360.7	82.8	24.4	19.6	0.4	1.4
Oithona similis	13.3	2.6	3.5	8.0	3.9	2.3	2.4	7.6	4.4	1.0
Clausocalanus spp.	13.7	1.7	3.5	5.6	18.0	5.2	5.8	10.9	13.3	3.1
Ctenocalanus spp.	18.0	10.5	6.6	6.0	78.3	15.8	4.8	17.6	4.8	1.9
Limacina retroversa	112.5	228.3	123.3	200.9	306.5	13.2	307.4	64.8	4.8	35.9
Euphausia vallentini	0.2	0.0	0.0	0.3	0.5	0.0	0.0	0.0	0.1	0.0
Thysanoessa macrura	0.0	0.0	0.0	0.0	0.3	0.0	0.1	0.0	0.1	0.0
Total grazing impact	199.9	269.3	158.1	245.6	768.2	119.3	344.8	120.5	28.0	43.3

Marion Offshore Ecosystem Variability Study (MOEVS) V – April 2005

During MOEVS V, total daily grazing rate ranged between 0.66 and 30.99 mg (pigm) m^{-2} day^{-1} (Mean = 6.99 mg (pigm) m^{-2} day^{-1}; SD = 6.99 mg (pigm) m^{-2} day^{-1}) (Table 4.9). On average, 95.4 % (SD = 89.5 %) of the available phytoplankton standing stock was consumed per day (Table 4.10). Copepods contributed to an average of 87.8 % (SD = 11.3 %) of the total daily grazing impact (Figure 4.11). The combined grazing rates of the copepods during the survey ranged from 0.54 to 25.78 mg (pigm) m^{-2} day^{-1} (Mean = 6.17 mg (pigm) m^{-2} day^{-1}; SD = 6.07 mg (pigm) m^{-2} day^{-1}) (Table 4.9), removing an average of 84.7 % (SD = 80.1 %) of the available phytoplankton biomass per day (Table 4.10). The average daily grazing rate of *L. retroversa* was 0.39 mg (pigm) m^{-2} day^{-1} (SD = 0.48 mg (pigm) m^{-2} day^{-1}) (Table 4.9), which corresponded to an average daily grazing impact of 8.4 % (SD = 10.4 %) of the available phytoplankton biomass (Table 4.10). Although *L. retroversa* made a substantial contribution to total daily grazing impact at station 263 (33.8 %), on average, the species was accountable for only 7.5 % (SD = 8.7 %) of the total (Figure 4.11). During the survey, *S. thompsoni* had a grazing impact reaching up to 46.9 % of the available phytoplankton biomass, however, on average, the species consumed only 5.2 % (SD = 12.2 %) of the phytoplankton standing stock per day during the survey (Table 4.10). *E. vallentini* contributed less than 0.2 % to total daily grazing impact at all stations throughout the survey (Figure 4.11).

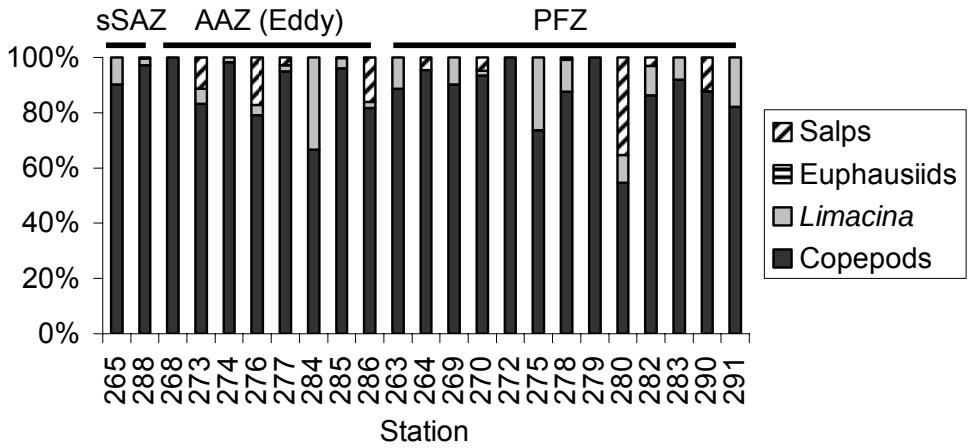

Figure 4.11 Percentage contributions of herbivorous groups to total grazing impact in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ or Eddy), during MOEVS V, April 2005.

Table 4.9 Grazing rates (mg (pigm) m^{-2} day^{-1}) of selected zooplankton and integrated chlorophyll-*a* in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ, or Eddy) during MOEVS V, April 2005.

	sSAZ		AAZ							
Station numbers	**265**	**288**	**268**	**273**	**274**	**276**	**277**	**284**	**285**	**286**
Calanus simillimus	1.43	6.62	2.82	12.33	1.58	2.46	0.80	0.24	7.33	1.06
Clausocalanus spp.	0.88	4.08	1.74	7.54	0.97	1.51	0.49	0.14	4.52	0.65
Ctenocalanus spp.	0.00	0.13	2.78	2.91	0.73	3.41	1.83	0.05	2.71	0.69
Oithona similis	0.04	0.06	2.38	3.00	1.45	2.03	0.79	0.25	3.19	1.23
Limacina retroversa	0.26	0.27	0.00	1.70	0.08	0.45	0.09	0.34	0.69	0.10
Salpa thompsoni (< 20 mm)	0.00	0.00	ND	2.37	0.00	1.06	0.07	0.00	0.02	0.69
Salpa thompsoni (> 20 mm)	0.00	0.04	ND	1.15	0.00	0.98	0.04	0.00	0.02	0.02
Euphausia vallentini	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total grazing rates	2.61	11.20	9.72	30.99	4.82	11.89	4.12	1.02	18.48	4.44
Integrated chl-a	8.88	8.14	6.38	10.71	9.25	8.43	11.37	9.78	6.88	10.37

Table 4.9 Continued…

	PFZ												
Station numbers	**263**	**264**	**269**	**270**	**272**	**275**	**278**	**279**	**280**	**282**	**283**	**290**	**291**
Calanus simillimus	4.37	1.42	2.02	0.93	2.66	0.29	2.91	3.25	2.12	1.27	1.82	0.19	0.25
Clausocalanus spp.	2.70	0.88	1.25	0.57	1.65	0.18	1.80	2.00	1.31	0.78	1.12	0.12	0.15
Ctenocalanus spp.	3.90	0.39	0.06	0.07	0.29	0.05	1.40	0.41	1.14	0.91	0.29	0.19	0.04
Oithona similis	1.73	0.04	0.26	0.31	0.34	0.09	1.08	0.40	0.05	0.60	0.43	0.39	0.10
Limacina retroversa	1.60	0.00	0.39	0.04	0.00	0.22	0.96	0.00	0.85	0.45	0.32	0.00	0.12
Salpa thompsoni (< 20 mm)	0.00	0.03	ND	0.00	ND	ND	0.00	0.00	1.38	0.08	0.00	0.03	0.00
Salpa thompsoni (> 20 mm)	0.00	0.10	ND	0.09	ND	ND	0.06	0.00	1.61	0.04	0.00	0.10	0.00
Euphausia vallentini	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total grazing rates	14.32	2.86	3.98	2.00	4.94	0.83	8.22	6.06	8.46	4.13	3.99	1.01	0.66
Integrated chl-a	4.74	4.74	8.17	7.01	4.43	9.88	5.61	7.34	6.38	9.89	7.85	8.44	8.17

Table 4.10 Grazing impact (%) of selected zooplankton on phytoplankton standing stock in the southern Sub-Antarctic Zone (sSAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AAZ or Eddy) during MOEVS V, April 2005.

	sSAZ		AAZ (Eddy)							
Station numbers	**265**	**288**	**268**	**273**	**274**	**276**	**277**	**284**	**285**	**286**
Calanus simillimus	16.1	81.4	44.2	115.0	17.1	29.1	7.1	2.4	106.5	10.3
Clausocalanus spp.	9.9	50.1	27.3	70.4	10.5	17.9	4.3	1.5	65.7	6.3
Ctenocalanus spp.	0.0	1.6	43.6	27.2	7.8	40.4	16.1	0.5	39.4	6.7
Oithona similis	0.5	0.7	37.4	28.0	15.7	24.1	6.9	2.6	46.3	11.8
Limacina retroversa	2.9	3.3	0.0	15.9	0.9	5.3	0.8	3.5	10.0	0.9
Salpa thompsoni (< 20 mm)	0.0	0.0	ND	22.1	0.0	12.6	0.6	0.0	0.3	6.7
Salpa thompsoni (> 20 mm)	0.0	0.5	ND	10.7	0.0	11.6	0.4	0.0	0.3	0.2
Euphausia vallentini	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	29.4	137.5	152.5	289.3	52.1	141.1	36.3	10.4	268.4	42.8

Table 4.10 Continued…

	PFZ												
Station numbers	**263**	**264**	**269**	**270**	**272**	**275**	**278**	**279**	**280**	**282**	**283**	**290**	**291**
Calanus simillimus	92.1	30.0	24.8	13.2	60.1	3.0	51.9	44.3	33.3	12.9	23.2	2.3	3.0
Clausocalanus spp.	57.0	18.5	15.2	8.1	37.2	1.8	32.1	27.3	20.6	7.9	14.3	1.4	1.9
Ctenocalanus spp.	82.3	8.2	0.8	0.9	6.5	0.5	25.0	5.5	17.9	9.2	3.7	2.2	0.5
Oithona similis	36.5	0.9	3.2	4.4	7.6	0.9	19.3	5.5	0.7	6.1	5.4	4.7	1.3
Limacina retroversa	33.8	0.0	4.8	0.5	0.0	2.2	17.1	0.0	13.3	4.5	4.1	0.0	1.4
Salpa thompsoni (< 20 mm)	0.0	0.7	ND	0.1	ND	ND	0.0	0.0	21.6	0.8	0.0	0.3	0.0
Salpa thompsoni (> 20 mm)	0.0	2.1	ND	1.3	ND	ND	1.2	0.0	25.2	0.4	0.0	1.2	0.0
Euphausia vallentini	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
Total	301.9	60.4	48.7	28.6	111.5	8.4	146.6	82.6	132.7	41.8	50.8	12.0	8.1

4.3.5 Statistical analyses

Analysis of variance

Integrated chl-*a* did not show any significant variation between water masses for any of the surveys (Table 4.11). However, within a water mass, integrated chl-*a* varied significantly between the years. In the sSAZ and AAZ, integrated chl-*a* values during MOEVS II were significantly higher than those measured during MOEVS V (Table 4.11). In the PFZ, integrated chl-*a* concentrations during MOEVS II and IV were significantly higher than those recorded during MOEVS V (Table 4.11).

Neither total zooplankton grazing rates nor grazing impact varied significantly between water masses during any of the three surveys (Tables 4.12 and 4.13). Inter-annual variability in total zooplankton grazing rates occurred within the sSAZ and PFZ waters, with values being greatest in both water masses during MOEVS IV (Table 4.12). Inter-annual variability in total zooplankton grazing impact occurred only in sSAZ waters, where values were significantly greater during MOEVS IV than MOEVS V (Table 4.13).

Table 4.11 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Integrated chlorophyll-*a*.

	MOEVS II	**MOEVS IV**	**MOEVS V**	**sSAZ**	**PFZ**	**AAZ**
sSAZ – PFZ	p = 0.24	p = 0.52	p = 0.46			
sSAZ – AAZ	p = 0.56		p = 0.75			
PFZ – AAZ	p = 0.42		p = 0.46			
II – IV				p = 0.10	p = 0.72	
II – V				p = 0.03 (II > V)	p < 0.001 (II > V)	p < 0.001 (II > V)
IV – V				p = 0.53	p < 0.001 (IV > V)	

Table 4.12 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Total zooplankton grazing rates.

	MOEVS II	**MOEVS IV**	**MOEVS V**	**sSAZ**	**PFZ**	**AAZ**
sSAZ – PFZ	p = 0.25	p = 0.66	p = 0.23			
sSAZ – AAZ	p = 0.30		p = 0.34			
PFZ – AAZ	p = 0.90		p = 0.65			
II – IV				p = 0.07	p = 0.29	
II – V				p = 0.45	p = 0.14	p = 0.10
IV – V				p = 0.01 (IV > V)	p = 0.01 (IV > V)	

Table 4.13 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Total zooplankton grazing impact.

	MOEVS II	MOEVS IV	MOEVS V	sSAZ	PFZ	AAZ
sSAZ – PFZ	p = 0.44	p = 0.73	p = 0.19			
sSAZ – AAZ	p = 0.43		p = 0.29			
PFZ – AAZ	p = 0.95		p = 0.62			
II – IV				p = 0.09	p = 0.14	
II – V				p = 0.65	p = 0.92	p = 0.58
IV – V				p = 0.03 (IV > V)	p = 0.07	

Grazing rates of *L. retroversa* did not vary significantly between water masses during any of the three surveys (Table 4.14). Lowest grazing rates for *L. retroversa* were observed during MOEVS V in each of the water masses (Table 4.14). Grazing rates of copepods showed no significant variability between water masses during any of the surveys (Table 4.15). There was no significant inter-annual variability in copepod grazing rates in any of the water masses encountered (Table 4.15).

Table 4.14 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): *L. retroversa* grazing rates.

	MOEVS II	MOEVS IV	MOEVS V	sSAZ	PFZ	AAZ
sSAZ – PFZ	p = 0.19	p = 0.85	p = 0.92			
sSAZ – AZZ	p = 0.12		p = 0.74			
PFZ – AAZ	p = 0.68		p = 0.53			
II – IV				p = 0.09	p = 0.15	
II – V				p = 0.49	p = 0.01 (II > V)	p < 0.001 (II > V)
IV – V				p = 0.02 (IV > V)	p < 0.001 (IV > V)	

Table 4.15 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Copepod grazing rates.

	MOEVS II	MOEVS IV	MOEVS V	sSAZ	PFZ	AAZ
sSAZ – PFZ	p = 0.37	p = 0.69	p = 0.18			
sSAZ – AAZ	p = 0.44		p = 0.29			
PFZ – AAZ	p = 0.89		p = 0.60			
II – IV				p = 0.12	p = 0.36	
II – V				p = 0.84	p = 0.85	p = 0.94
IV – V				p = 0.08	p = 0.40	

Grazing impact of *L. retroversa* did not vary significantly between water masses during MOEVS II, IV or V (Table 4.16). Inter-annual variability in *L. retroversa* grazing impact was significant in the PFZ and AAZ water masses, where values were lowest during MOEVS V (Table 4.16). The grazing impact of copepods

exhibited no significant variation between water masses during any of the present surveys (Table 4.17). No significant inter-annual variability in the grazing impact of copepods was observed for any of the water masses encountered during the surveys (Table 4.17).

Table 4.16 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): *L. retroversa* grazing impact.

	MOEVS II	MOEVS IV	MOEVS V	sSAZ	PFZ	AAZ
sSAZ – PFZ	p = 0.33	p = 0.81	p = 0.94			
sSAZ – AAZ	p = 0.19		p = 0.86			
PFZ – AAZ	p = 0.59		p = 0.71			
II – IV				p = 0.12	p = 0.08	
II – V				p = 0.67	p = 0.06	p = 0.003 (II > V)
IV – V				p = 0.05	p = 0.001 (IV > V)	

Table 4.17 Results of Factorial ANOVA and Fisher's LSD test (StatSoft, Inc. 2004): Copepod grazing impact.

	MOEVS II	MOEVS IV	MOEVS V	sSAZ	PFZ	AAZ
sSAZ – PFZ	p = 0.58	p = 0.76	p = 0.15			
sSAZ – AAZ	p = 0.57		p = 0.25			
PFZ – AAZ	p = 0.97		p = 0.58			
II – IV				p = 0.16	p = 0.18	
II – V				p = 0.96	p = 0.16	p = 0.38
IV – V				p = 0.18	p = 0.99	

Correlation analysis

Results of Pearson's Correlation analyses indicated that, while no significant correlation existed between copepod grazing rates and integrated chl-*a* (Figure 4.13: $r^2 = 0.04$; r = -0.20; p = 0.19), there was a positive linear correlation between *L. retroversa* grazing rates and integrated chl-*a* (Figure 4.12: $r^2 = 0.18$; r = 0.42; p = 0.01). No correlation was found to exist between total zooplankton grazing impact and integrated chl-*a* (Figure 4.14: $r^2 = 0.02$; r = -0.13; p = 0.40) or between *L. retroversa* grazing impact and integrated chl-*a* (Figure 4.15: $r^2 = 0.08$; r = 0.28; p = 0.07). A weak, negative correlation, however, existed between copepod grazing impact and integrated chl-*a* (Figure 4.16: $r^2 = 0.17$; r = -0.41; p = 0.004).

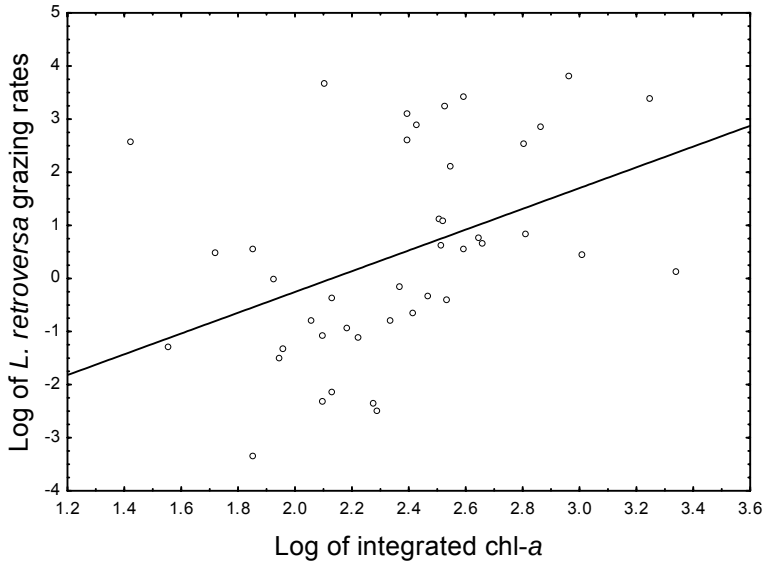

Figure 4.12 Results of Pearson's Correlation analysis: *L. retroversa* grazing rates (mg (pigm) m^{-2} day $^{-1}$) versus integrated chl-*a* (mg (pigm) m^{-2}) (r^2 = 0.18; r = 0.42; p = 0.01). Data used for the analysis were collected during MOEVS II, IV and V.

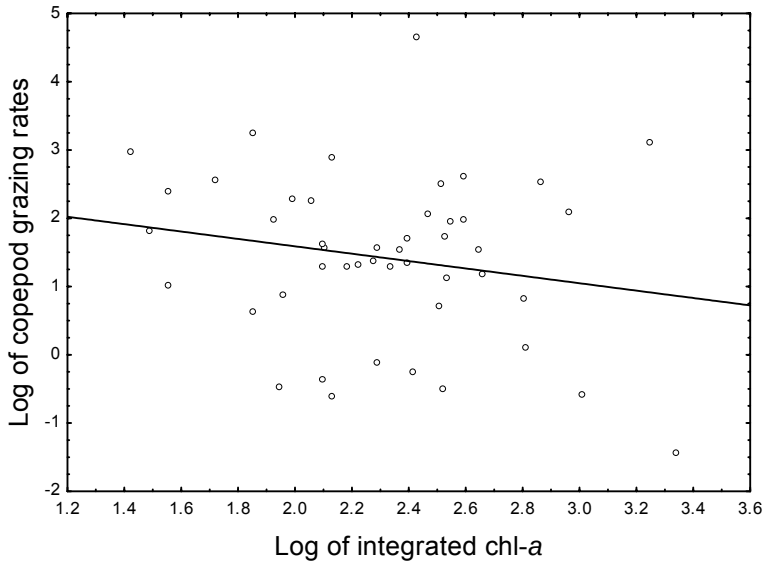

Figure 4.13 Results of Pearson's Correlation analysis: Copepod grazing rates (mg (pigm) m^{-2} day^{-1}) versus integrated chl-*a* (mg (pigm) m^{-2}) (r^2 = 0.04; r = -0.20; p = 0.19). Data used in the anlaysis were collected during MOEVS II, IV and V.

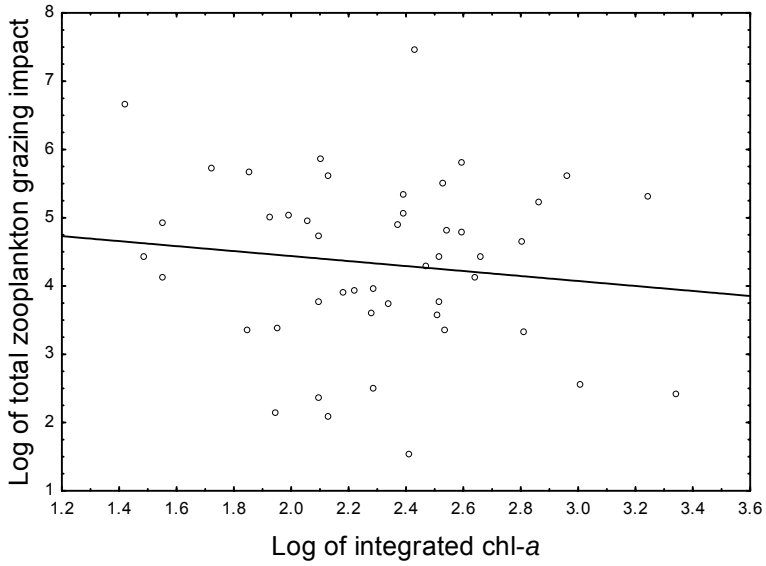

Figure 4.14 Results of Pearson's Correlation analysis: Total zooplankton grazing impact (% phytoplankton standing stock) versus integrated chl-*a* (mg (pigm) m^{-2}) (r^2 = 0.02; r = -0.13; p = 0.40). Data used in the anlaysis were collected during MOEVS II, IV and V.

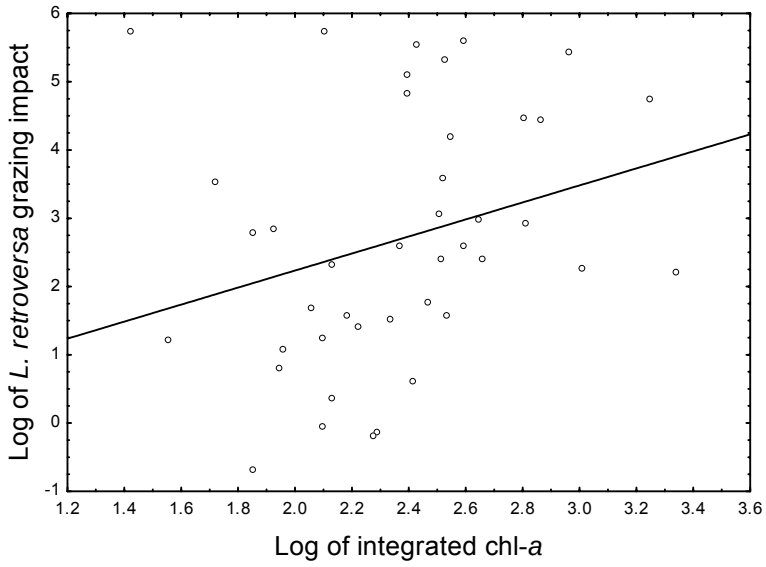

Figure 4.15 Results of Pearson's Correlation analysis: *L. retroversa* grazing impact (% phytoplankton standing stock) versus integrated chl-*a* (mg (pigm) m^{-2}) (r^2 = 0.08; r = 0.28; p = 0.07). Data used in the analysis were collected during MOEVS II, IV and V.

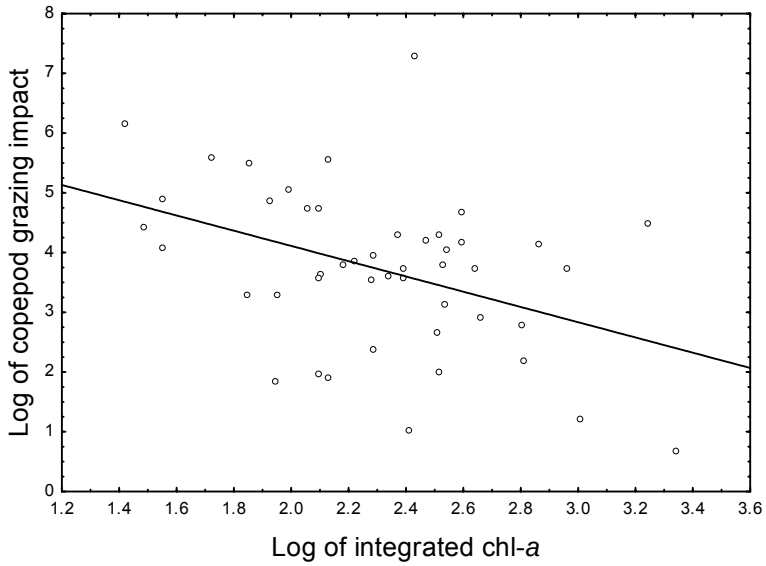

Figure 4.16 Results of Pearson's Correlation analysis: Copepod grazing impact (% phytoplankton standing stock) versus integrated chl-*a* (mg (pigm) m^{-2}) (r^2 = 0.17; r = -0.41; p = 0.004). Data used in the analysis were collected during MOEVS II, IV and V.

4.4 DISCUSSION

Integrated chl-*a* values for MOEVS II and IV were typical of those reported for the region (Bradford-Grieve *et al.* 1998; Froneman *et al.* 2001). Chl-*a* concentrations during MOEVS V, on the other hand, were significantly lower, with values never exceeding 12 mg (pigm) m^{-2} and averaging 8 mg (pigm) m^{-2}. Such low chl-*a* concentrations could be attributed to high zooplankton grazing pressures (to be discussed). Integrated chl-*a* concentrations did not vary significantly between the water masses during any of the three surveys. However, within the Polar Frontal Zone (PFZ) water mass, integrated chl-*a* values were greatest during MOEVS II and IV. In the southern Sub-Antarctic Zone (sSAZ) and Antarctic Zone (AAZ) water masses chl-*a* biomass was greatest during MOEVS II.

Total zooplankton abundances recorded during the present investigation ranged between 1 675.45 ind. m^{-2} (MOEVS V) and 87 083.27 ind. m^{-2} (MOEVS IV). These values are within the range reported in previous investigations throughout the Southern Ocean (Perissinotto 1992; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Froneman & Pakhomov 1998a; Froneman *et al.* 2000a; Pakhomov & Froneman

2004b). For example, during winter, in the region of the Subtropical Convergence, total mesozooplankton abundances ranged from 1 446.1 ind. to 25 332.8 ind. m^{-2} (Pakhomov & Perissinotto 1997), while at South Georgia, during austral summer, total mesozooplankton numbers ranged between 15 698.0 and 46 907.0 ind. m^{-2} (Pakhomov *et al.* 1997). Copepods numerically dominated the zooplankton counts throughout the three surveys, accounting for up to 96 % of all zooplankton counted. This result is consistent with those of previous studies conducted in various regions of the Southern Ocean during different seasons (Hopkins 1985; Conover & Huntley 1991; Perissinotto 1992; Atkinson & Shreeve 1995; Atkinson 1996; Atkinson *et al.* 1996; Pakhomov *et al.* 2000a; Bernard & Froneman 2002; Pakhomov & Froneman 2004a). As is typical of the PFZ, the copepod community consisted primarily of *C. simillimus*, *Clausocalanus* spp., *Ctenocalanus* spp. and *O. similis* (Bernard & Froneman 2002). Other grazers included the pteropod, *L. retroversa*; the tunicate, *S. thompsoni*; and the euphausiids, *E. vallentini* and *T. macrura*, as well as euphausiid furcilia. *L. retroversa* generally contributed around 10 % to total zooplankton numbers during MOEVS II and IV, but an average of < 1 % during MOEVS V. *S. thompsoni* and the euphausiids never contributed to more than 1.6 % of the total zooplankton numbers during any of the three surveys.

Diel variability in gut pigment content was only observed for two of the calanoid copepods, *C. simillimus* and *Clausocalanus* spp. during MOEVS II and for all three calanoid copepods (*C. simillimus*, *Clausocalanus* spp. and *Ctenocalanus* spp.) during MOEVS IV. These results reflect the diel vertical migration patterns of the species commonly reported in other studies in the region (Atkinson *et al.* 1992a, b; Perissinotto 1992). The absence of any significant diel variability in gut pigment contents for the cyclopoid copepod, *O. similis*, and the pteropod, *L. retroversa*, during the investigation can thus likely be ascribed to these species exhibiting less pronounced diel vertical migrations. Unfortunately, no data were collected during the present study to support this hypothesis. It is worth noting that Atkinson *et al.* (1996) reported that both *O. similis* and an unidentified pteropod remained in the upper 40 m of the water column during both the day and night.

Gut evacuation rates estimated for the copepods during MOEVS II and IV are within the range reported in the literature (Perissinotto 1992; Atkinson 1996;

Atkinson *et al.* 1996; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Froneman *et al.* 2000a; Pakhomov & Froneman 2004b). However, very few reports on the gut evacuation rate of *Limacina* spp. exist in the literature. Pakhomov & Perissinotto (1997) found that in the Subtropical Convergence during austral winter, *Limacina* spp. exhibited a gut evacuation rate of 0.36 h^{-1}. The gut evacuation rate reported in the present study, 1.33 h^{-1}, is substantially more rapid with the evacuation of the gut contents being completed in just over 45 minutes. The discrepancy between the two values may be due to spatial or temporal differences between the studies or simply due to the fact that different species may exhibit varying gut evacuation rates. Indeed, it is well documented that the gut passage time and pigment destruction in copepods may reflect variable food concentrations (Wang & Conover 1986; Dagg & Walser 1987; Peterson *et al.* 1990, all cited in Pasternak 1994), seawater temperature (Dam & Peterson 1988) and feeding history (Head 1988).

Perissinotto (1992) measured gut evacuation rates for *Limacina* sp. in the vicinity of the Prince Edward Archipelago (PFZ) during austral autumn and recorded a value of 0.98 h^{-1}, which is closer to the value that was recorded during the present study. It is possible that the differences between the gut evacuation rate during the present study and that presented by Perissinotto (1992) might be the result of variable food concentrations during the studies (Pasternak 1994; and references therein). Indeed, Perissinotto (1992) recorded chl-*a* concentrations that were much higher than those measured during the present study. The gut pigment destruction rate of 58 % for the pteropod, *L. retroversa*, appears to be the first estimate made for this species. Perissinotto (1992) assumed a gut pigment destruction rate of 60 % for *L. retroversa*, which was obtained by averaging the destruction rates, estimated for large copepods and euphausiids.

Daily individual ingestion rates of the calanoid copepods (*C. simillimus*, *Clausocalanus* spp. and *Ctenocalanus* spp.), the euphausiids and salps are within the range reported by previous investigations (Perissinotto 1992; Atkinson 1996; Atkinson *et al.* 1996; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Froneman *et al.* 2000a; Gurney *et al.* 2002; Pakhomov & Froneman 2004b). *L. retroversa*, however, exhibited a substantially greater daily individual ingestion rate during the present study than any other previous reports (Perissinotto 1992;

Pakhomov & Perissinotto 1997; Pakhomov & Froneman 2004b). It is important to point out, however, that two of the aforementioned investigations were conducted in different regions of the Southern Ocean at different times of the year (Pakhomov & Perissinotto 1997; Pakhomov & Froneman 2004b).

Perissinotto (1992) estimated daily ingestion rates for *Limacina* sp. during austral autumn in the vicinity of the Prince Edward Archipelago in the PFZ and recorded values an order of magnitude less than those of the present study. Perissinotto (1992) reported that *Limacina* sp. preferentially grazed on particles < 5 μm, and suggested that the ingestion of larger cells might be limited by the dimensions of the ciliated grooves through which the food enters the mouth (Perissinotto 1992). During the study conducted by Perissinotto (1992), nano- (2.0 – 20.0 μm) and microphytoplankton (> 20.0 μm) composed up to 86 % of the total pigment. In contrast, the phytoplankton biomass during the present study was almost entirely dominated by pico- (< 2.0 μm) and nanophytoplankton. The elevated ingestion rates obtained for the pteropod during the present study might therefore be the result of an abundance of preferentially-sized food particles. Variability in ingestion rates might also be due to varying food concentrations, which may result in differing gut evacuation rates between the two surveys (Wang & Conover 1986; Dagg & Walser 1987; Peterson *et al.* 1990, all cited in Pasternak 1994).

Total zooplankton grazing rates during previous investigations in the Southern Ocean have been highly variable, ranging from < 1 to 72 mg (pigm) m^{-2} day^{-1} (Perissinotto 1992; Froneman *et al.* 1997; Pakhomov *et al.* 1997; Pakhomov & Perissinotto 1997; Froneman *et al.* 2000a; Li *et al.* 2001; Pakhomov & Froneman 2004b). Average zooplankton grazing rates during the present study fall within this range, between 0.66 mg (pigm) m^{-2} day^{-1} (for MOEVS V) and 51.97 mg (pigm) m^{-2} day^{-1} (for MOEVS IV). There was no effect of water mass on the total zooplankton grazing rates observed during any of the surveys conducted in the present study. Interestingly, zooplankton grazing rates in the AAZ waters did not vary between the years. Grazing rates in the sSAZ and PFZ water masses, on the other hand, were greater during MOEVS IV than MOEVS V, possibly as a result of the enhanced productivity associated with the intense frontal feature present during MOEVS IV.

Total zooplankton grazing impact ranged from 4.6 to 768.2 % of the available phytoplankton standing stock throughout the three surveys combined, with averages of 93.0 %, 229.7 % and 95.4 % for MOEVS II, IV and V, respectively. These values are the highest reported for the Southern Ocean (Perissinotto 1992; Froneman *et al.* 1997; Pakhomov *et al.* 1997; Pakhomov & Perissinotto 1997; Li *et al.* 2001; Urban-Rich *et al.* 2001; Froneman *et al.* 2000a; Pakhomov & Froneman 2004b). However, in most previous investigations the grazing impact of the pteropod, *L. retroversa*, was not included (Froneman *et al.* 1997; Froneman *et al.* 2000a; Li *et al.* 2001; Urban-Rich *et al.* 2001). If we ignore the impact of *L. retroversa* in the present study, then the average daily grazing impact of the numerically dominant zooplankton is equivalent to 38.6 %, 89.9 % and 89.9 % of the phytoplankton biomass for MOEVS II, IV and V, respectively. The majority of these values now fall within the range reported in previous investigations. This result highlights the importance of studying all major zooplankton taxa, and not only those that are most abundant. Stations where grazing impact on phytoplankton is still excessively high (> 100 %) after pteropods have been removed tend to be those with low integrated chl-*a* concentrations or high grazer abundances (particularly *C. simillimus*). The most likely scenario at these stations is that, at the time of sampling, the zooplankton community had already consumed much of the available phytoplankton standing stock, but was still present in high abundances, resulting in possibly biased grazing impact estimates. It should be noted that the present study does not consider the potential influence of biological interactions (e.g. interspecific competition and predation) in mediating the grazing impact of the herbivorous zooplankton. For example, a trophic cascading study, conducted by Froneman & Bernard (2004) in the PFZ, demonstrated that the addition of carnivorous zooplankton to incubation bottles coincided with a decreased impact of the herbivorous zooplankton on the phytoplankton standing stocks.

The taxa that contributed the most to total daily grazing impact were the four dominant copepods (*C. simillimus*, *Clausocalanus* spp., *Ctenocalanus* spp. and *O. similis*) and the pteropod, *L. retroversa*. During MOEVS II and IV, *L. retroversa* accounted for an average of 52 % and 60 % of the total daily grazing impacts, respectively; this, despite the fact that during these two surveys the pteropod contributed on average 8 % and 12 % to the total zooplankton counts, respectively.

Conversely, during MOEVS V, *L. retroversa* contributed an average of only 8 % of the total grazing impact. A Factorial ANOVA and Fisher's LSD test showed that in the sSAZ, PFZ and AAZ water masses, the grazing rates of *L. retroversa* were, in fact, significantly lower during MOEVS V, while in the PFZ and AAZ waters, pteropod grazing impact was significantly reduced during MOEVS V. This is most likely due to the fact that during MOEVS V the integrated and surface chl-*a* concentrations were significantly lower than the previous years, resulting in lower abundances of *L. retroversa*. As discussed in Chapter Two, a positive linear relationship existed between *L. retroversa* and surface chl-*a*, suggesting that the pteropod might be reliant on high food concentrations. Indeed, Pearson's Correlation analysis of data from the present chapter indicated that a positive linear relationship existed between *L. retroversa* grazing rates (a product of pteropod numbers) and integrated chl-*a*. No correlation, however, was observed between *L. retroversa* grazing impact and integrated chl-*a*.

L. retroversa grazing rates and grazing impact did not vary significantly between water masses during any of the three surveys conducted in the present study. The grazing rates and grazing impact of the four dominant copepods, combined, showed no significant variability between water mass or years.

Euphausiids did not make substantial contributions to total grazing impact in any of the three surveys. *S. thompsoni* was responsible for up to 64.7 % of the total grazing impact during MOEVS II and 35.3 % of the total during MOEVS V, although, on average, the tunicate did not make any major contributions to total grazing impact throughout the study. In general, grazing was dominated by *L. retroversa* and the copepods.

CHAPTER FIVE:

PREDATION IMPACT OF CARNIVOROUS MACROZOOPLANKTON AND MYCTOPHID FISH IN THE POLAR FRONTAL ZONE, WITH EMPHASIS ON THE ROLE OF *LIMACINA RETROVERSA* AS A POTENTIAL PREY SOURCE

5.1 INTRODUCTION

While there is now considerable data on the role of selected herbivorous zooplankton in the transfer of carbon to the ocean depths (Pakhomov *et al.* 1997; Froneman *et al.* 1997, 2000), the role of carnivorous zooplankton has largely been neglected due to methodological constraints (Gibbons *et al.* 1992; Froneman *et al.* 2002a). Carnivorous macrozooplankton and nekton facilitate the transfer of carbon both to the sea floor – by means of extensive vertical migrations and the production of large, fast-sinking faecal pellets (Dilling & Alldredge 1993; Fortier *et al.* 1994) – and to the top predators, including flying seabirds, penguins, seals, fish and whales (Brown & Klages 1987; Joiris *et al.* 1996; Cherel & Kooyman 1998; Cherel *et al.* 2002).

In the Polar Frontal Zone (PFZ), organisms preying on mesozooplankton include carnivorous macrozooplankton, consisting largely of chaetognaths, euphausiids, amphipods and gelatinous taxa; and myctophid fish, all of which exhibit highly patchy distribution (Pakhomov *et al.* 1999; Pakhomov & Froneman 2000a; Froneman *et al.* 2002a). Previous investigations in the PFZ during both summer and autumn suggest that a seasonal trend in predation impact exists in the PFZ, with predation impacts being < 1.5 % of the mesozooplankton standing stock in summer (Pakhomov *et al.* 1999) and averaging 5 % in autumn, with values as high as 44 % (Froneman *et al.* 2002a). Chaetognaths and euphausiids typically dominate total carnivorous macrozooplankton/micronekton numbers, and appear to contribute the most to total predation impact in the region (Froneman *et al.* 1998; Froneman & Pakhomov 1998b; Pakhomov *et al.* 1999; Pakhomov *et al.* 2000c; Froneman *et al.* 2002a).

The euthecosome pteropod, *Limacina retroversa*, is an important grazer in the PFZ food chain (see for example Chapter Four), and it has been suggested that the species may make substantial contributions to the downward flux of carbon through the sedimentation of shells, diel vertical migrations and the sinking of abandoned mucous webs and faecal pellets (Lalli & Gilmer 1989; Meinecke & Wefer 1990; Bathmann *et al.* 1991; Noji *et al.* 1997). *L. retroversa* thus has the potential to play a major role in the transfer of carbon from the short-lived organic carbon pool, in the

surface waters, to the sequestered biogenic carbon pool in the deep sea (Legendre & Le Fèvre 1992; see also Chapter One). *L. retroversa* may also provide a link between autotrophic carbon and the higher trophic levels and top predators in the region, assisting in the transfer of carbon from the short-lived pool to the long-lived organic carbon pool (Legendre & Le Fèvre 1992; see also Chapter One). Indeed, numerous studies in both the northern and southern hemispheres suggest that *Limacina* spp. may be an important prey item for many carnivorous macrozooplankton and fish species, including the amphipod, *Themisto gaudichaudi* (Pakhomov & Perissinotto 1996); the chaetognath, *Sagitta gazellae* (Froneman & Pakhomov 1998b; Froneman *et al.* 1998); myctophid fish (Perissinotto & McQuaid 1992; Pakhomov *et al.* 1996); nototheniid fish (Bushula *et al.* 2005); and, in the Gulf of Alaska, juvenile pink salmon (Armstrong *et al.* 2005). Additionally, the gymnosomatous pteropod, *Clione limacina*, feeds exclusively on *Limacina* spp. and will thus be strongly affected by the distribution and abundances of the euthecosome species (Lalli 1970; Conover & Lalli 1972; Siebel & Dierssen 2003; Böer *et al.* 2005).

Thus, the aims of the present chapter were: (1) to determine the carnivorous macrozooplankton and myctophid fish standing stock in the PFZ during 2004 and 2005; (2) to provide an estimate of the predation impact of the dominant carnivores for both years; and (3) to assess the role of *L. retroversa* as a potential prey item for the carnivorous macrozooplankton and myctophid fish.

5.2 METHODS

Macrozooplankton and myctophid fish samples were collected at selected stations during the fourth and fifth Marion Offshore Ecosystem Variability Studies (MOEVS IV and V), during April 2004 and 2005, respectively (Figures 5.1 & 5.2). Details of the voyages are available in the Appendix. Physical oceanography for each voyage has been described in detail in Chapter Two (See also Figures 5.1 & 5.2).

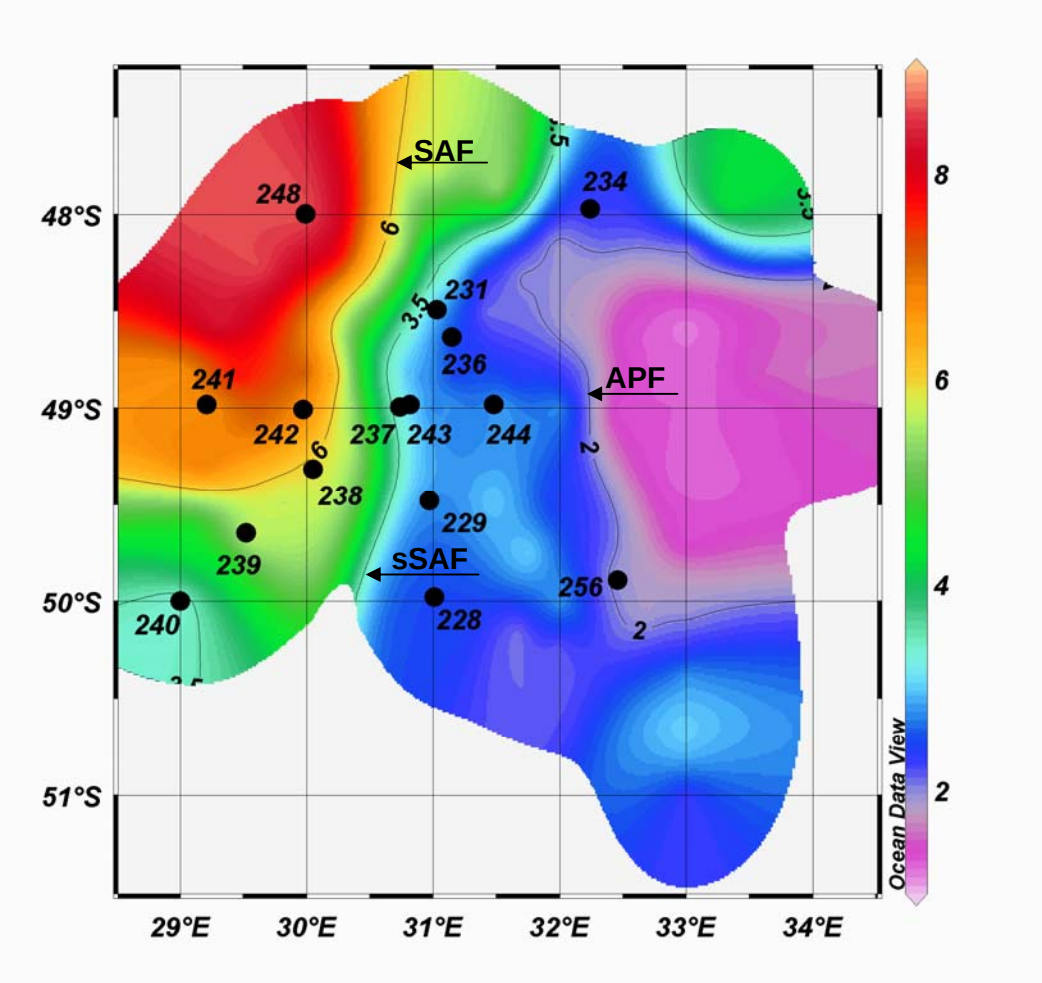

Figure 5.1 Sub-surface temperature plot with carnivore station positions for MOEVS IV, April 2004. The SAF (Sub-Antarctic Front) is represented by the 6 °C isotherm; the sSAF (southern Sub-Antarctic Front) is represented by the 3.5 °C isotherm; the APF (Antarctic Polar Front) is represented by the 2 °C isotherm.

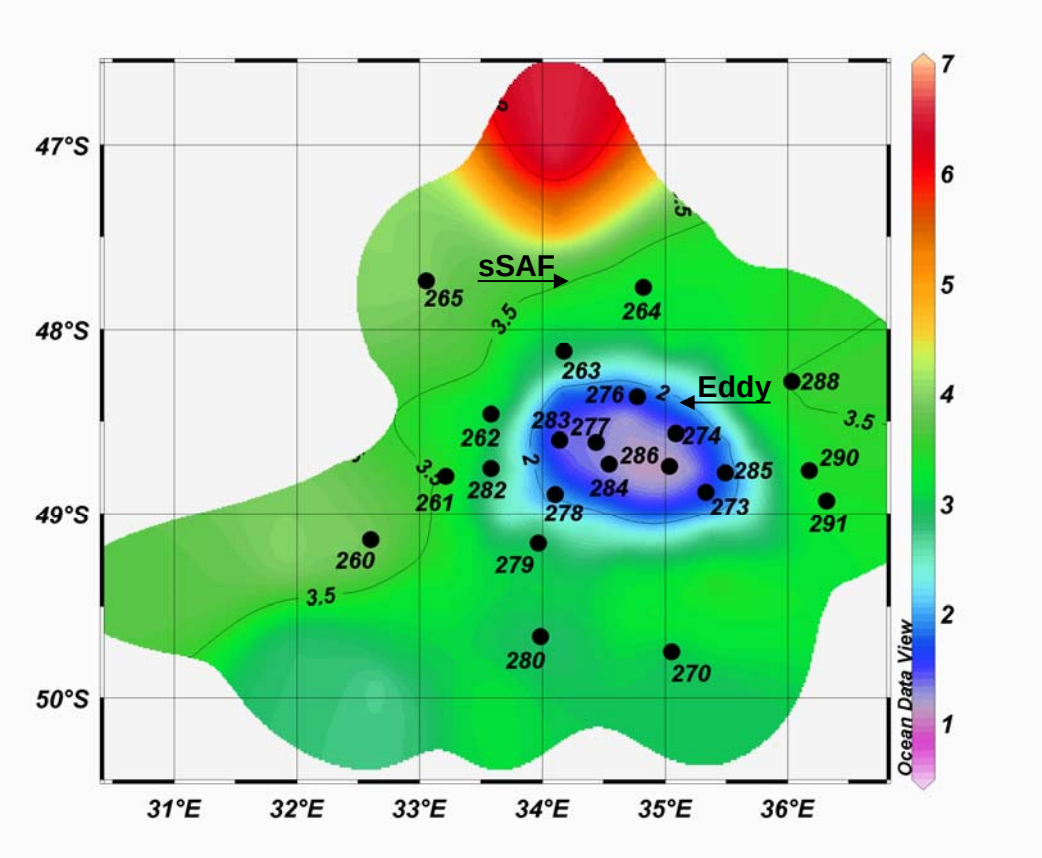

Figure 5.2 Sub-surface temperature plot with carnivore station positions for MOEVS V, April 2005. The sSAF is represented by the 3.5 °C isotherm; the eddy is outlined by the APF, represented by the 2 °C isotherm.

5.2.1 Predator abundance and biomass

Macrozooplankton and myctophid fish samples were collected using a Bongo net during MOEVS IV and an RMT-8 net during MOEVS V. The Bongo net was fitted with one 200 µm mesh net and one 300 µm mesh net. Tows were conducted to depths of 300 m during the day and 200 m at night, to compensate for diel vertical migration. The RMT-8 net had a mesh size of 0.45 cm and a mouth area of 8 m^2 and tows were conducted in a similar manner to those using the Bongo net. All samples were immediately fixed in 6 % buffered formalin (hexamine). Carnivorous taxa were identified to species (for the chaetognaths, euphausiids and amphipods) or genus (for the myctophid fish) and counted. Abundances were expressed as number of individuals per cubic meter (ind. m^{-3}). Biomass for each of the dominant carnivore groups was determined by oven-drying sub-samples of chaetognaths, carnivorous

euphausiids, amphipods and myctophid fish from each station at 60 ºC for at least 24 hours (48 hours in the case of larger specimens). Biomass was expressed as milligrams of dry weight per cubic meter (mg Dwt. m^{-3}). Mesozooplankton samples were collected using a Bongo net during MOEVS IV and a WP2 net during MOEVS V (See Chapter Two for further details). Mesozooplankton biomass was obtained by oven-drying a sub-sample (1/32) from each station at 60 °C for 24 hours. Mesozooplankton biomass was expressed as milligrams of dry weight per cubic meter (mg Dwt. m^{-3}).

5.2.2 Predation impact

Predation impact of the numerically dominant macrozooplankton and myctophid fish taxa on mesozooplankton during MOEVS IV and V was estimated following the approach of Froneman *et al.* (2002a). The taxa considered for investigation include the chaetognaths, *Sagitta gazellae* and *Eukrohnia hamata*, the amphipod, *Themisto gaudichaudi*, the euphausiids, *Nematocelis megalops*, *Thysanoessa macrura* and *Euphausia longirostris*, and the myctophid fish, *Electrona* spp., all of which have been demonstrated in previous investigations to be carnivorous (Øresland 1990; Pakhomov & Perissinotto 1996; Pakhomov *et al.* 1996; Perissinotto *et al.* 1996; Froneman & Pakhomov 1998b; Froneman *et al.* 1998; Gurney 2000; Froneman *et al.* 2000a, b). Average daily rations for the dominant carnivorous macrozooplankton and myctophid fish during the investigation were obtained from the literature (see Table 5.1). Predation impact has been restricted to the mesozooplankton component only as previous investigations suggest that carnivorous macrozooplankton and myctophid fish feed predominantly on mesozooplankton (Froneman *et al.* 1998, 2000a, b; Pakhomov *et al.* 1999; Gurney 2000). Daily predation rate of carnivorous zooplankton was estimated as the product of carnivore biomass at each station and average daily ration for each predator; and was expressed as milligrams of dry weight consumed per cubic meter per day (mg Dwt. m^{-3} day^{-1}). Total daily predation impact was calculated as the percentage of mesozooplankton biomass consumed per day (Data for mesozooplankton biomass were obtained from Chapter Two).

Table 5.1 Daily rations of major carnivorous macrozooplankton and micronekton in the Polar Frontal Zone, Southern Ocean.

Carnivores	Daily ration (% dry body mass)	Methods	Source
Euphausiids	12.43	Egestion rates, energy budget, gut fullness index	Perissinotto *et al.* 1996, Gurney 2000
Amphipods			
T. gaudichaudi	14.05	Gut contents, energy budget, *in vitro* incubations	Pakhomov & Perissinotto 1996, Froneman *et al.* 2000a, b
Chaetognaths			
E. hamata	8.00	*In situ* gut contents	Øresland 1990, Froneman & Pakhomov 1998b, Froneman *et al.* 1998
S. gazellae	9.00	*In situ* gut contents	Froneman & Pakhomov 1998b, Froneman *et al.* 1998
Myctophids	1.93	Gut content analysis, energy budget	Pakhomov *et al.* 1996

5.2.3 Gut content analysis

The gut contents of chaetognaths (*E. hamata* and *S. gazellae*), amphipods (*T. gaudichaudi*) and myctophid fish (*Electrona* spp.), were examined by dissection of the stomach. Prey inside the stomach were identified, where possible, to group and counted. In addition, unidentifiable or digested matter was recorded. Specimens used for gut content analysis were randomly selected from both MOEVS IV and V samples, with the exception of myctophid fish that were only captured during MOEVS V. Data collected from gut content analysis were expressed as frequency of occurrence (%) of different prey taxa in the stomachs of carnivorous macrozooplankton and myctophid fish. Due to low abundances (< 0.01 ind. m^{-3}) of the carnivorous euphausiids, *E. longirostris*, *T. macrura* and *N. megalops*, gut content analysis was not carried out on these species.

5.2.4 Statistical analyses

Hierarchical cluster analysis

In order to determine spatial trends within the carnivorous macrozooplankton and myctophid fish assemblages during MOEVS IV and V, hierarchical cluster

analysis and multidimensional scaling were used in conjunction with the Bray-Curtis similarity index (Bernard and Froneman 2002; Pakhomov and Froneman 2004a). Species abundance data were normalised by log-transformation [$\log_{10}(x + 1)$] (Legendre & Legendre 1983). The similarity programmes ANOSIM and SIMPER, of the Plymouth Routines in Multivariate Ecological Research 5 (PRIMER-E Ltd. 2005) computer package (Clarke & Warwick 1994), were used to test the significance levels and sources of difference (respectively) between the macrozooplankton and myctophid fish assemblages associated with the different groups identified by hierarchical cluster analysis (Field *et al.* 1982).

Analysis of variance

One-Way ANOVAs (StatSoft, Inc. 2004) were used to determine the significance of inter-annual variability in total carnivore abundances and biomass, as well as abundances and biomass of the separate predator taxa (i.e. chaetognaths, amphipods, euphausiids and myctophid fishes). A One-Way ANOVA was also used to test for significant inter-annual variability in total and taxon-specific predation impacts.

Correlation analysis

Pearson's Correlations (Linear Correlations; StatSoft, Inc. 2004) were used to identify possible relationships in predator-prey abundances, comparing numbers of chaetognaths, amphipods, euphausiids and myctophid fishes against those of copepods and the pteropod, *L. retroversa*.

5.3 RESULTS

5.3.1 Predator abundance and biomass

During MOEVS IV, total carnivorous macrozooplankton and myctophid fish abundances attained levels of up to 31.39 ind. m^{-3} (Mean = 11.63 ind. m^{-3}; SD = 8.40 ind. m^{-3}) (Table 5.2; Figure 5.3) and comprised mainly the chaetognaths, *S. gazellae* and *E. hamata*, which were recorded in numbers averaging 3.10 ind. m^{-3} (SD = 3.76

ind. m^{-3}) and 7.33 ind. m^{-3} (7.24 ind. m^{-3}), respectively (Table 5.2). The percentage contribution of carnivorous macrozooplankton and myctophid fish to total zooplankton biomass was highly variable (Figure 5.5). With the exception of station 238 where carnivorous biomass contributed 46.7 % to the total, carnivorous biomass generally contributed < 10 % (Mean = 6.7 %; SD = 12.0 %) to the total zooplankton biomass (Figures 5.3 & 5.5). The chaetognaths made up an average of 0.31 mg Dwt. m^{-3} (SD = 0.33 mg Dwt. m^{-3}) in biomass (Figure 5.7; Table 5.2). Euphausiids were found in abundances averaging 1.17 ind. m^{-3} (SD = 1.07 ind. m^{-3}) (Table 5.2), their average biomass (Mean = 0.45 mg Dwt. m^{-3}; SD = 0.81 mg Dwt. m^{-3}) exceeding that of the chaetognaths (Figure 5.7; Table 5.2). Abundance and biomass of the amphipod, *T. gaudichaudi*, never exceeded 0.2 ind. m^{-3} and 0.4 mg Dwt. m^{-3} (Table 5.2). Myctophid fish of the genus *Electrona* spp. were not recorded during the entire survey (Table 5.2).

During MOEVS V, predatory zooplankton abundances ranged from 0.06 to 17.06 ind. m^{-3} (Mean = 3.66 ind. m^{-3}; SD = 4.53 ind. m^{-3}) (Table 5.3; Figure 5.4). Percentage contribution of carnivorous macrozooplankton and myctophid fish to total zooplankton biomass was highly variable, with values ranging from 0.0 to 86.8 % (Mean = 22.5 %; SD = 23.0 %) of the total zooplankton biomass (Figures 5.4 & 5.6). As in MOEVS IV, the chaetognaths, *S. gazellae* and *E. hamata*, again dominated total carnivore counts, with average abundances of 0.91 ind. m^{-3} (SD = 2.79 ind. m^{-3}) and 2.69 ind. m^{-3} (SD = 3.21 ind. m^{-3}), respectively (Table 5.3). The average combined chaetognath biomass during the survey was 0.22 mg Dwt. m^{-3} (SD = 0.29 mg Dwt. m^{-3}) (Figure 5.8; Table 5.3). The euphausiids and *T. gaudichaudi* exhibited average abundances of 0.03 ind. m^{-3} (SD = 0.05 ind. m^{-3}) and 0.01 ind. m^{-3} (SD = 0.04 ind. m^{-3}), respectively (Table 5.3). While the average biomass of *T. gaudichaudi* was low (Mean = 0.04 mg Dwt. m^{-3}; SD = 0.08 mg Dwt. m^{-3}), that of the euphausiids was much higher, at 1.03 mg Dwt. m^{-3} (SD = 2.17 mg Dwt. m^{-3}) (Figure 5.8; Table 5.3). Although myctophid fish (*Electrona* spp.) accounted for an average of only 0.001 ind. m^{-3} (SD = 0.001 ind. m^{-3}) (Table 5.3), their biomass reached up to 2.89 mg Dwt. m^{-3} (Mean = 0.53 mg Dwt. m^{-3}; SD = 0.78 mg Dwt. m^{-3}) (Figure 5.8; Table 5.3).

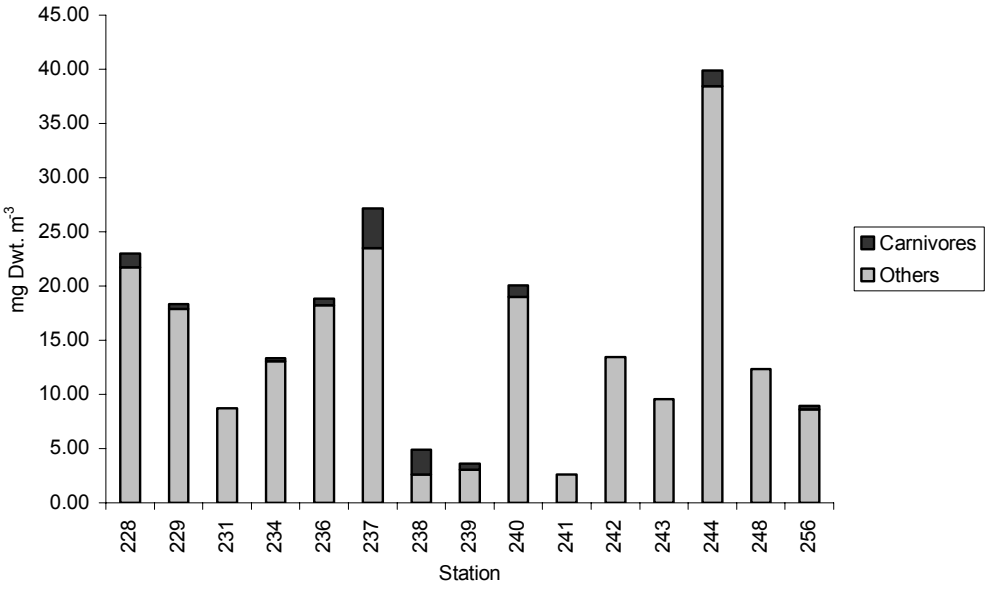

Figure 5.3 Total zooplankton and carnivore biomass during MOEVS IV, April 2004.

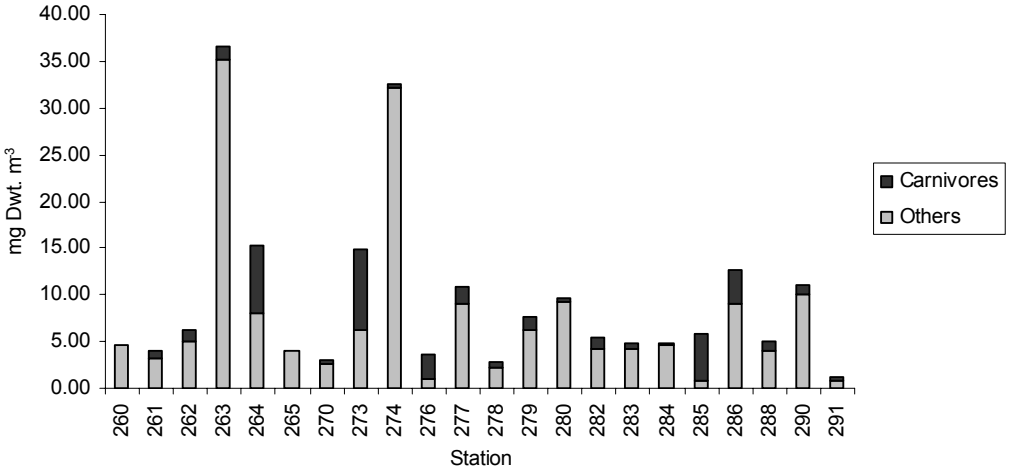

Figure 5.4 Total zooplankton and carnivore biomass during MOEVS V, April 2005.

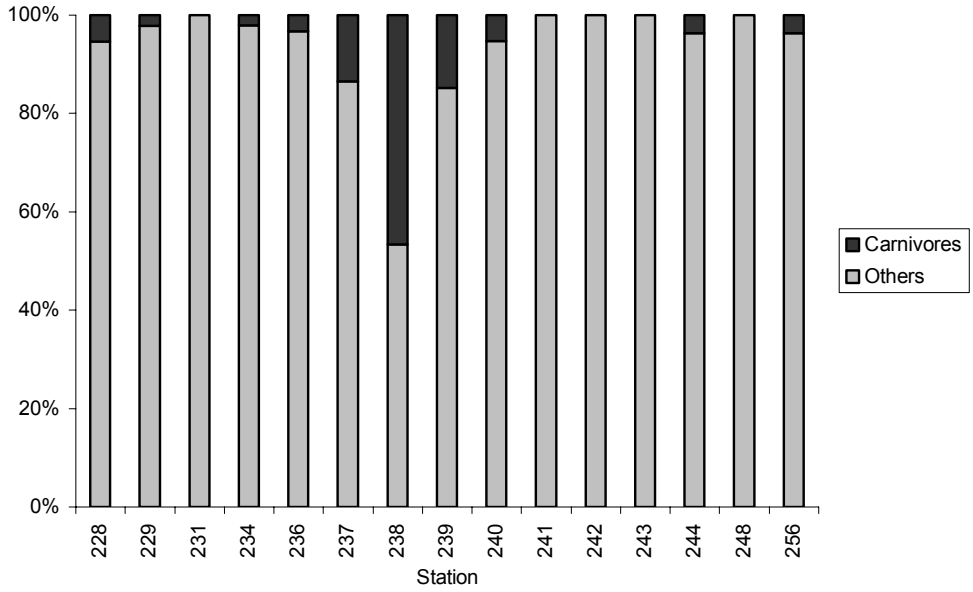

Figure 5.5 Percentage contribution of carnivores to total zooplankton biomass during MOEVS IV, April 2004.

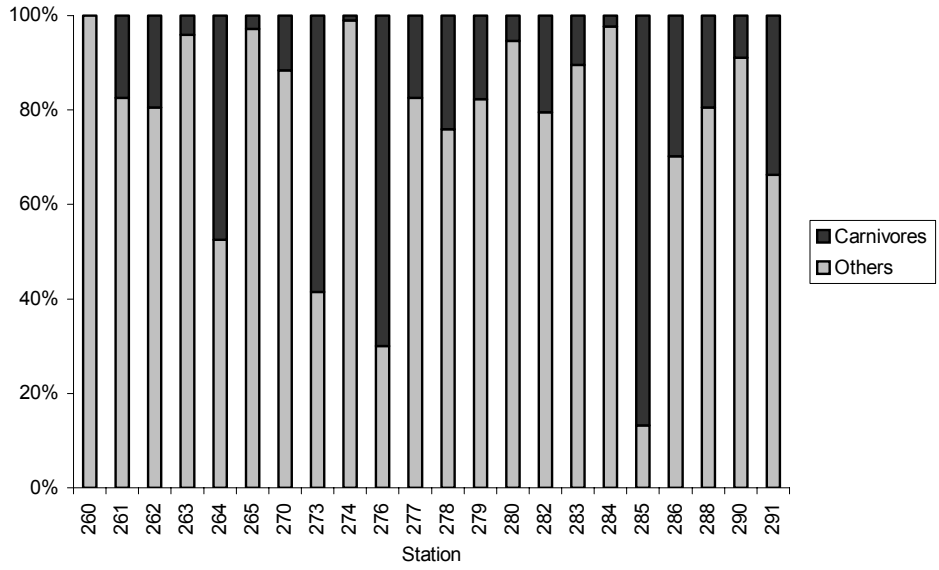

Figure 5.6 Percentage contribution of carnivores to total zooplankton biomass during MOEVS V, April 2005.

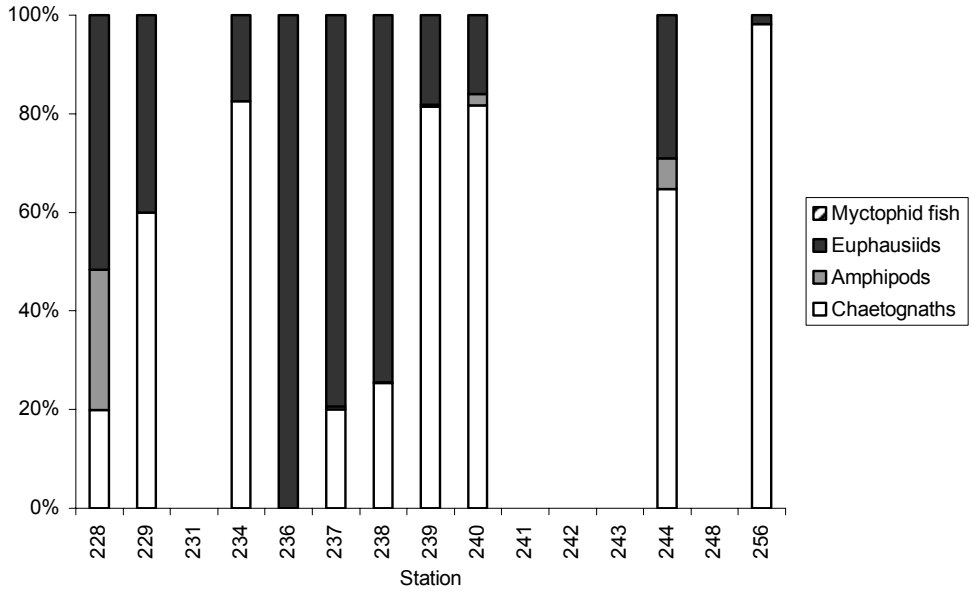

Figure 5.7 Percentage contributions of the major carnivore groups to total carnivore biomass during MOEVS IV, April 2004.

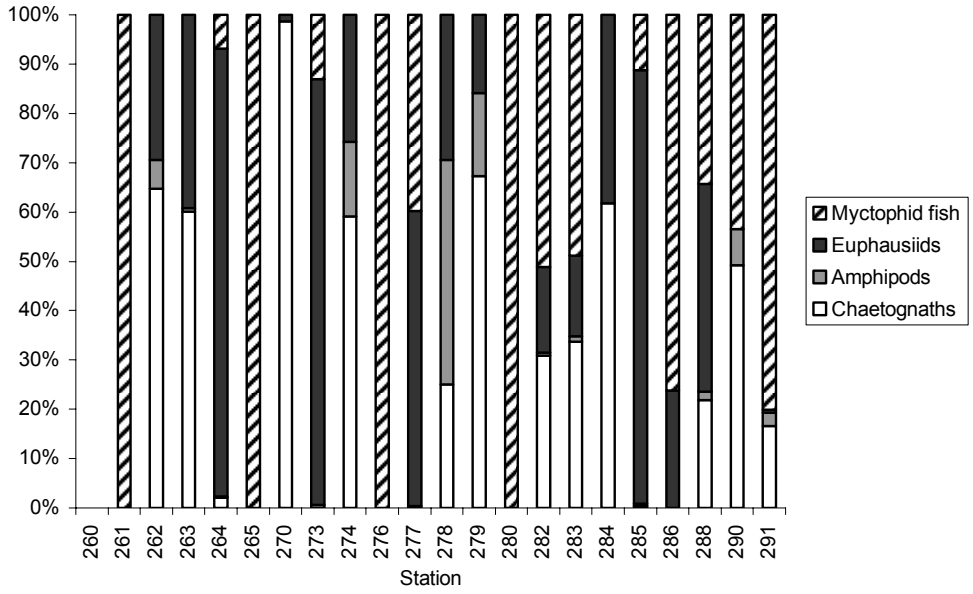

Figure 5.8 Percentage contributions of the major carnivore groups to total carnivore biomass during MOEVS V, April 2005.

Table 5.2 Abundance (A; ind. m^{-3}) and biomass (B; mg Dwt. m^{-3}) of numerically dominant carnivorous macrozooplankton and myctophid fish taxa during MOEVS IV, April 2004.

Stations	Chaet.		Amph.		Euph.		Total	
	A	B	A	B	A	B	A	B
228	16.17	0.25	0.11	0.35	1.66	0.64	17.94	1.24
229	4.13	0.25	0.01	0.00	0.22	0.16	4.36	0.41
231	8.66	0.00	0.03	0.00	2.91	0.00	11.60	0.00
234	8.50	0.23	0.04	0.00	0.56	0.05	9.10	0.28
236	5.17	0.00	0.08	0.00	1.44	0.61	6.69	0.61
237	17.59	0.73	0.00	0.02	2.65	2.90	20.24	3.65
238	2.34	0.58	0.15	0.00	1.90	1.70	4.39	2.29
239	11.46	0.44	0.01	0.00	0.15	0.10	11.62	0.54
240	23.65	0.86	0.01	0.03	0.45	0.17	24.11	1.06
241	1.17	0.00	0.00	0.00	0.22	0.00	1.39	0.00
242	0.86	0.00	0.00	0.00	3.10	0.00	3.96	0.00
243	6.25	0.00	0.01	0.00	0.50	0.00	6.76	0.00
244	29.97	0.95	0.02	0.09	1.40	0.43	31.39	1.46
248	11.31	0.00	0.05	0.00	0.13	0.00	11.49	0.00
256	9.28	0.32	0.01	0.00	0.18	0.01	9.47	0.33

Chaet. = Chaetognaths (*Sagitta gazellae* and *Eukrohnia hamata*)
Amph. = Amphipods (*Themisto gaudichaudi*)
Euph. = Euphausiids (*Thysanoessa macrura*, *Euphausia longirostris* and *Nematocelis megalops*)

Table 5.3 Abundance (A; ind. m^{-3}) and biomass (B; mg Dwt. m^{-3}) of numerically dominant carnivorous macrozooplankton and myctophid fish taxa during MOEVS V, April 2005.

Station	Chaet.		Amph.		Euph.		Mycto.		Total	
	A	B	A	B	A	B	A	B	A	B
260	2.08	0.00	0.00	0.00	0.01	0.00	< 0.01	0.00	2.09	0.00
261	1.92	0.00	0.01	0.00	0.10	0.00	< 0.01	0.70	2.02	0.70
262	17.06	0.79	0.00	0.07	0.00	0.36	< 0.01	0.00	17.06	1.21
263	14.50	0.89	0.00	0.01	0.00	0.58	< 0.01	0.00	14.50	1.48
264	5.12	0.15	0.00	0.02	0.09	6.59	< 0.01	0.49	5.21	7.25
265	1.64	0.00	0.00	0.00	0.00	0.00	< 0.01	0.11	1.64	0.11
270	1.39	0.34	0.00	0.00	0.00	0.00	< 0.01	0.00	1.39	0.35
273	0.00	0.00	0.00	0.05	0.05	7.53	< 0.01	1.14	0.06	8.72
274	0.85	0.20	0.00	0.05	0.00	0.09	< 0.01	0.00	0.85	0.34
276	0.32	0.00	0.00	0.00	0.04	0.00	< 0.01	2.55	0.37	2.55
277	0.40	0.01	0.00	0.00	0.24	1.14	< 0.01	0.75	0.64	1.90
278	6.65	0.17	0.00	0.30	0.00	0.20	< 0.01	0.00	6.65	0.67
279	8.96	0.91	0.00	0.23	0.00	0.22	< 0.01	0.00	8.96	1.35
280	1.94	0.00	0.00	0.00	0.03	0.00	< 0.01	0.52	1.97	0.52
282	5.12	0.34	0.00	0.01	0.03	0.19	< 0.01	0.57	5.15	1.11
283	1.50	0.17	0.00	0.01	0.00	0.08	< 0.01	0.24	1.50	0.50
284	0.84	0.07	0.00	0.00	0.00	0.04	< 0.01	0.00	0.84	0.11
285	0.04	0.02	0.20	0.02	0.02	4.43	< 0.01	0.56	0.26	5.03
286	2.85	0.00	0.00	0.00	0.03	0.90	< 0.01	2.89	2.88	3.79
288	2.19	0.22	0.00	0.02	0.00	0.42	< 0.01	0.34	2.19	0.99
290	3.35	0.48	0.00	0.07	0.04	0.00	< 0.01	0.42	3.39	0.98
291	0.87	0.06	0.00	0.01	0.00	0.00	< 0.01	0.31	0.87	0.39
295	3.28	0.00	0.00	0.00	0.06	0.00	< 0.01	0.11	3.34	0.11

Chaet. = Chaetognaths (*Sagitta gazellae* and *Eukrohnia hamata*)
Amph. = Amphipods (*Themisto gaudichaudi*)
Euph. = Euphausiids (*Thysanoessa macrura*, *Euphausia longirostris* and *Nematocelis megalops*)
Mycto. = Myctophid fish (*Electrona* spp.)

5.3.2 Potential predation impact

Average mesozooplankton biomass of 14.19 mg Dwt. m^{-3} (SD = 9.50 mg Dwt. m^{-3}) and 7.58 mg Dwt. m^{-3} (SD = 8.90 mg Dwt. m^{-3}) were recorded during MOEVS IV and V, respectively (Figures 5.3 & 5.4; Tables 5.4 & 5.5). The mesozooplankton assemblages encountered during the two surveys are described in detail in Chapter Two.

During MOEVS IV, total estimated predation rate ranged between 0.00 and 0.43 mg Dwt. m^{-3} day^{-1} (Mean = 0.09 mg Dwt. m^{-3} day^{-1}; SD = 0.12 mg Dwt. m^{-3} day^{-1}), which corresponded to a predation impact of between 0.0 and 10.0 % (Mean = 1.1 %; SD = 2.5 %) of the mesozooplankton standing stock per day (Table 5.4). Euphausiids exhibited potential daily predation rates averaging 0.06 mg Dwt. m^{-3} day^{-1} (SD = 0.10 mg Dwt. m^{-3} day^{-1}) (Table 5.4). Average daily predation rates of the chaetognaths and amphipods were estimated at 0.03 mg Dwt. m^{-3} day^{-1} (SD = 0.03 mg Dwt. m^{-3} day^{-1}) and 0.005 mg Dwt. m^{-3} day^{-1} (SD = 0.01 mg Dwt. m^{-3} day^{-1}), respectively (Table 5.4). Chaetognaths and euphausiids contributed the most to total daily predation impact, up to 97.4 % (Mean = 47.7 %; SD = 33.6 %) and 100.0 % (Mean = 47.6 %; SD = 32.0 %), respectively (Figure 5.9). Amphipods contributed an average of 4.7 % (SD = 10.3 %) to the total daily predation impact (Figure 5.9).

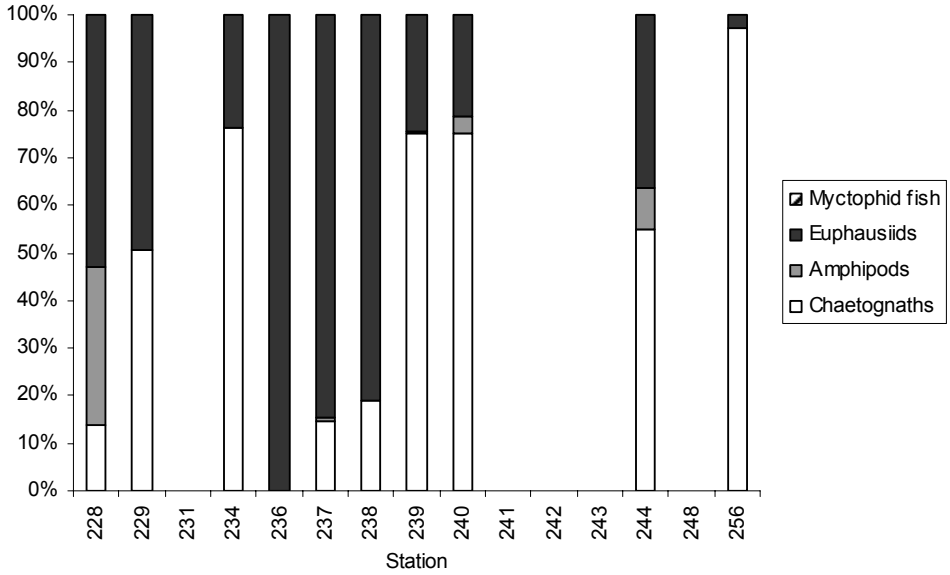

Figure 5.9 Percentage contributions of the major carnivore groups to total predation impact during MOEVS IV, April 2004.

Table 5.4 Predation impact of the major carnivorous macrozooplankton and myctophid fish during MOEVS IV, April 2004.

Station	Mesozooplankton biomass (mg Dwt. m^{-3})	Food consumption (mg Dwt. m^{-3} d^{-1})				Standing stock
		Chaet.	Amph.	Euph.	Total	(%)
228	21.74	0.02	0.05	0.08	0.15	0.7
229	17.90	0.02	0.00	0.02	0.04	0.2
231	8.72	0.00	0.00	0.00	0.00	0.0
234	13.03	0.02	0.00	0.01	0.03	0.2
236	18.22	0.00	0.00	0.08	0.08	0.4
237	23.53	0.06	0.00	0.36	0.43	1.8
238	2.61	0.05	0.00	0.21	0.26	10.0
239	3.08	0.04	0.00	0.01	0.05	1.6
240	19.00	0.07	0.00	0.02	0.10	0.5
241	2.60	0.00	0.00	0.00	0.00	0.0
242	13.44	0.00	0.00	0.00	0.00	0.0
243	9.56	0.00	0.00	0.00	0.00	0.0
244	38.42	0.08	0.01	0.05	0.15	0.4
248	12.36	0.00	0.00	0.00	0.00	0.0
256	8.63	0.03	0.00	0.00	0.03	0.3

Chaet. = Chaetognaths (*E. hamata*, *S. gazellae*)
Amph. = Amphipods (*T. gaudichaudi*)
Euph. = Euphausiids (*T. macrura*, *E. longirostris*, *N. megalops*)

The average total daily predation rate of carnivorous macrozooplankton and myctophid fish during MOEVS V was 0.16 mg Dwt. m^{-3} day^{-1} (SD = 0.27 mg Dwt. m^{-3} day^{-1}), corresponding to an average daily predation impact of 5.7 % (SD = 15.6 %) of the available mesozooplankton standing stock (Table 5.5). The highest predation rates were estimated for the euphausiids, with an average of 0.13 mg Dwt. m^{-3} day^{-1} (SD = 0.27 mg Dwt. m^{-3} day^{-1}) (Table 5.5). Chaetognaths and myctophid fish consumed an average of 0.02 mg Dwt. m^{-3} day^{-1} (SD = 0.03 mg Dwt. m^{-3} day^{-1}) and 0.01 mg Dwt. m^{-3} day^{-1} (SD = 0.01 mg Dwt. m^{-3} day^{-1}), respectively (Table 5.5). Amphipods exhibited the lowest predation rates, with an average of 0.006 mg Dwt. m^{-3} day^{-1} (SD = 0.01 mg Dwt. m^{-3} day^{-1}) (Table 5.5). During the survey, chaetognaths, euphausiids and myctophid fish all made substantial contributions to the total daily predation impact. Chaetognaths and myctophid fish contributed an average of 29.0 % (SD = 29.7 %) and 26.1 % (SD = 38.6 %) to total daily predation impact, respectively (Figure 5.10). Euphausiids were responsible for an average of 38.2 % (SD = 35.6 %) of total predation impact (Figure 5.10). Although amphipods contributed up to 52.6 % to total daily predation impact, their average contribution was 6.8 % (SD = 12.8 %) (Figure 5.10).

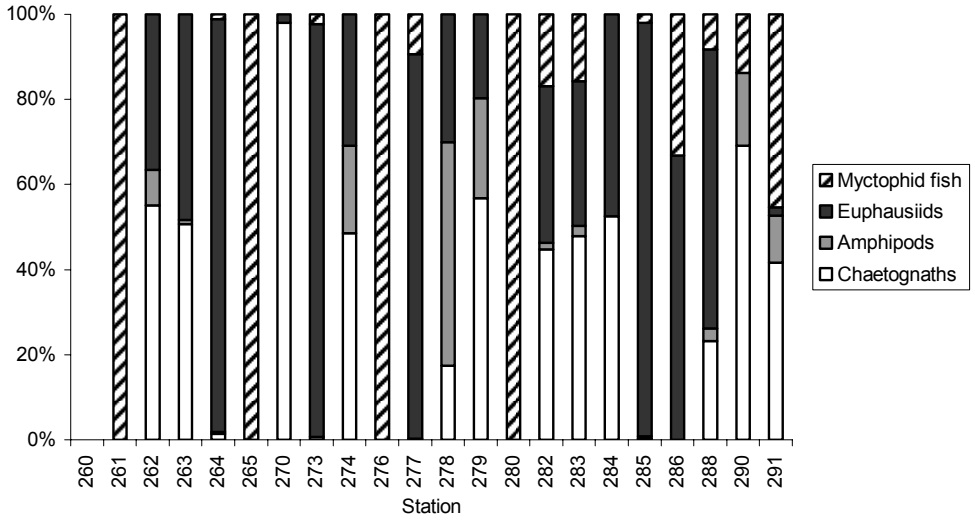

Figure 5.10 Percentage contributions of the major carnivore groups to total predation impact during MOEVS V, April 2005.

Table 5.5 Predation impact of the major carnivorous macrozooplankton and myctophid fish during MOEVS V, April 2005.

Station	Mesozooplankton	Food consumption (mg Dwt. m^{-3} d^{-1})					Standing stock
	biomass (mg Dwt. m^{-3})	Chaet.	Amph.	Euph.	Myct.	Total	(%)
260	4.61	0.00	0.00	0.00	0.00	0.00	0.0
261	3.31	0.00	0.00	0.00	0.01	0.01	0.4
262	5.01	0.07	0.01	0.04	0.00	0.12	2.4
263	35.16	0.08	0.00	0.07	0.00	0.15	0.4
264	8.02	0.01	0.00	0.82	0.01	0.84	10.5
265	4.00	0.00	0.00	0.00	0.00	0.00	0.1
270	2.64	0.03	0.00	0.00	0.00	0.03	1.1
273	6.18	0.00	0.01	0.94	0.02	0.97	15.6
274	32.26	0.02	0.01	0.01	0.00	0.03	0.1
276	1.10	0.00	0.00	0.00	0.05	0.05	4.5
277	8.96	0.00	0.00	0.14	0.01	0.16	1.6
278	2.11	0.01	0.04	0.02	0.00	0.08	3.9
279	6.27	0.08	0.03	0.03	0.00	0.14	2.2
280	9.22	0.00	0.00	0.00	0.01	0.01	0.1
282	4.28	0.03	0.00	0.02	0.01	0.06	1.5
283	4.26	0.01	0.00	0.01	0.00	0.03	0.7
284	4.71	0.01	0.00	0.01	0.00	0.01	0.2
285	0.77	0.00	0.00	0.55	0.01	0.57	73.6
286	8.96	0.00	0.00	0.11	0.06	0.17	1.9
288	4.10	0.02	0.00	0.05	0.01	0.08	1.9
290	10.03	0.04	0.01	0.00	0.01	0.06	0.6
291	0.76	0.01	0.00	0.00	0.01	0.01	1.7
295	1.09	0.00	0.00	0.00	0.00	0.00	0.2

Chaet. = Chaetognaths (*E. hamata*, *S. gazellae*)
Amph. = Amphipods (*T. gaudichaudi*)
Euph. = Euphausiids (*T. macrura*, *E. longirostris*, *N. megalops*)
Mycto. = Myctophid fish (*Electrona* spp.)

5.3.3 Gut content analysis

Results of gut content analysis indicate that copepods constituted the main food source of the dominant carnivorous macrozooplankton and myctophid fish in the PFZ during the two surveys (Table 5.6). Although copepods were only found in 2 % of *E. hamata* (n = 1612) stomachs and 20 % of *S. gazellae* (n = 270) stomachs, the majority of chaetognath stomachs dissected consisted mainly of digested, unidentifiable matter. *L. retroversa* was not detected in the stomach contents of either of the chaetognath species (Table 5.6). Copepods were encountered in 91 % of amphipod stomachs dissected (n = 60). In addition to copepods, *L. retroversa* was recorded in 19 % of amphipod guts, representing the second-most common food item for the amphipods (Table 5.6). Copepods were recorded in 64 % of myctophid fish stomachs dissected, while euphausiids (mainly furcilia) were encountered in 57 % of myctophid gut contents (n = 28). Ostracods and amphipods occurred relatively frequently (21 % and 11 %, respectively) in the stomachs of myctophids, while *L. retroversa* was not encountered in any of the myctophid stomach contents (Table 5.6).

Table 5.6 Frequency of occurrence (%) of prey taxa in the stomachs of selected carnivorous macrozooplankton and myctophid fish.

Prey	Frequency of occurrence (%)			
	E. ham. (n = 1612)*	S. gaz. (n = 270)*	Amph. (n = 60)**	Mycto. (n = 28)
Copepod	2	20	91	64
Chaetognaths	1	3	9	0
Amphipods	0	4	8	11
Euphausiids	0	10	0	57
Ostracods	0	0	0	21
Pteropods	0	0	19	0
Polychaetes	0	0	6	0
Crust. Eggs	33	15	0	0
Unidentified	64	46	3	25

E. ham. = *Eukrohnia hamata*
S. gaz. = *Sagitta gazellae*
Amph. = Amphipods (*Themisto gaudichaudi)*
Mycto. = Myctophid fishes (*Electrona* spp.)
Crust. = Crustacean

* Data for *E. hamata* and *S. gazellae* courtesy of Miss D Lukáč (MSc 2005).
** Data for *T. gaudichaudi* courtesy of Miss L Lange (MSc 2005).

5.3.4 Statistical analyses

Hierarchical cluster analysis

Stations occupied during MOEVS IV were separated into three groups by hierarchical cluster analysis (Figure 5.11). Group 1 consisted of only one station (station 242) and was not significantly different from either Group 2 or Group 3 (ANOSIM; p = 0.1 and p = 0.167, respectively). Group 2 consisted of stations 229, 231, 234, 237, 239, 240, 243, 244 and 256, while Group 3 was made up of stations 228, 236, 238, 241 and 248. Groups 2 and 3 were significantly different from each other (ANOSIM; p = 0.002). Results of a SIMPER analysis indicate that the difference between the groups was not due to the presence or absence of certain indicator species, but was rather the result of varying abundances of a few dominant species. The separation of stations into the above mentioned groups did not show any association with the water masses encountered during the survey.

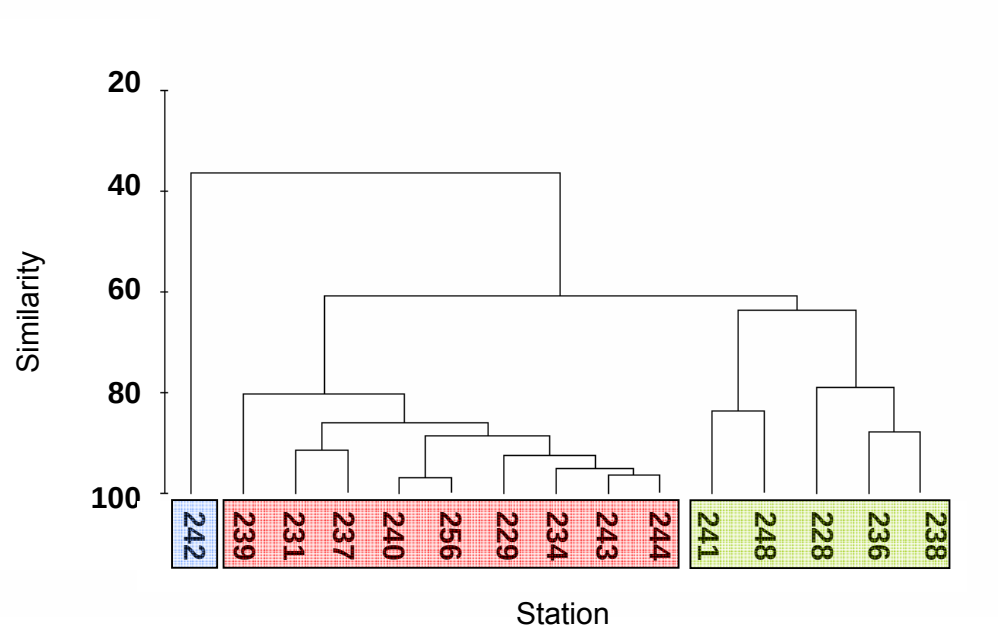

Figure 5.11 Results of hierarchical cluster analysis for MOEVS IV, April 2004. Blue box = Group 1; Red box = Group 2; Green box = Group 3.

Hierarchical cluster analysis separated stations occupied during MOEVS V into four groups (Figure 5.12). Groups 1 and 4 consisted of only one station each, namely stations 273 and 285, respectively. Group 2 constituted stations 270, 274, 276, 277 and 282, while Group 3 was made up of stations 260, 261, 262, 263, 264,

265, 278, 279, 280, 283, 284, 286, 288, 290 and 291. Groups 1, 2 and 4 were not significantly different from each other (ANOSIM; $p > 0.05$). Group 3, however, was significantly different from Groups 1, 2 and 4 (ANOSIM; $p = 0.001$ in each instance). As for MOEVS IV, the difference between the groups was due to the relative abundances of common species, and not to the presence or absence of indicator species. In addition, there was no association between groups identified by hierarchical cluster analysis and the water masses encountered during the investigation.

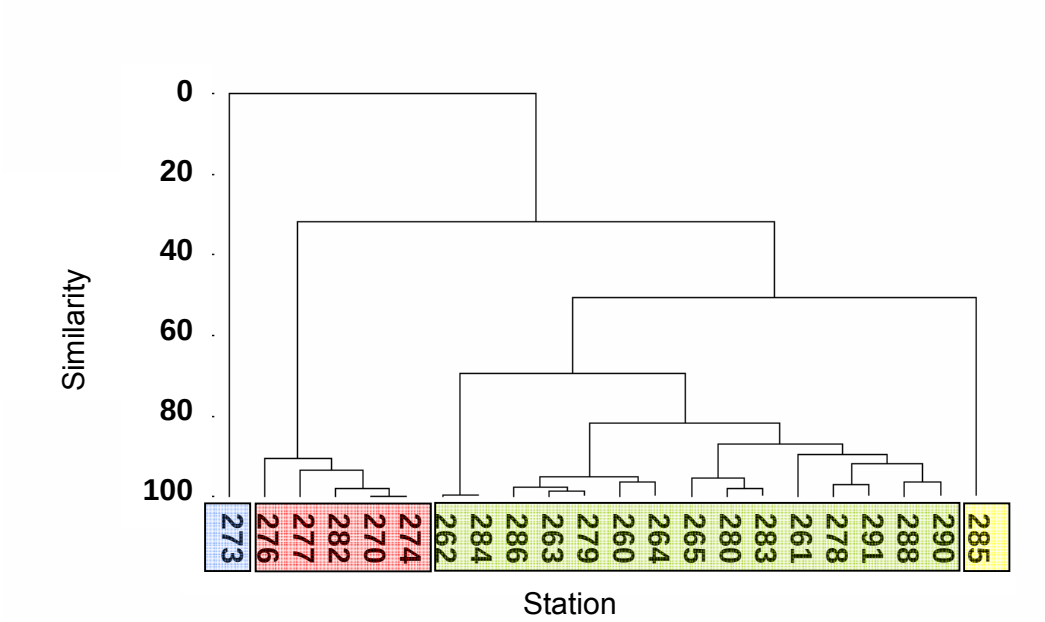

Figure 5.12 Results of hierarchical cluster analysis for MOEVS V, April 2005. Blue box = Group 1; Red box = Group 2; Green box = Group 3; Yellow box = Group 4.

Analysis of variance

Results of a series of One-Way ANOVAs and Fisher's LSD tests (StatSoft, Inc. 2004) indicated that total carnivorous macrozooplankton and myctophid fish numbers were significantly higher during MOEVS IV than MOEVS V ($p < 0.001$). However, no significant variability in total carnivore biomass was observed between the years ($p = 0.50$). Euphausiid numbers were significantly higher during MOEVS IV ($p < 0.001$), as were the abundances of the chaetognaths, *S. gazellae* and *E. hamata* ($p = 0.003$ and $p = 0.004$, respectively). The biomass values recorded for both the euphausiids and chaetognaths did not vary significantly between the surveys

($p = 0.43$ and $p = 0.08$, respectively). The amphipod, *T. gaudichaudi*, did not exhibit significant inter-annual variation in terms of abundances ($p = 0.43$) or biomass ($p = 0.84$). Statistical analyses were not carried out on the myctophid fish as no specimens were collected during MOEVS IV.

There was no significant inter-annual variability for the predation impacts of chaetognaths, amphipods or euphausiids ($p > 0.05$ in all cases). In addition, total predation impact did not exhibit any variation between the years ($p = 0.54$).

Correlation analysis

Pearson's Correlation analyses indicated that there were significant positive correlations between *L. retroversa* abundances and abundances of chaetognaths (Figure 5.13: $r^2 = 0.51$; $r = 0.71$; $p < 0.001$), carnivorous euphausiids (Figure 5.15: $r^2 = 0.46$; $r = 0.68$; $p < 0.05$) and myctophid fish (Figure 5.16: $r^2 = 0.54$; $r = 0.74$; $p < 0.001$). There was also a significant, but very weak, positive correlation between abundances of *L. retroversa* and amphipod numbers (Figure 5.14: $r^2 = 0.08$; $r = 0.29$; $p < 0.001$). Significant positive correlations were also observed between copepod numbers and those of chaetognaths (Figure 5.17: $r^2 = 0.26$; $r = 0.51$; $p < 0.001$) and myctophid fish (Figure 5.20: $r^2 = 0.30$; $r = 0.55$; $p < 0.001$). A much weaker, but still significant, positive correlation was also observed between copepod abundances and numbers of amphipods (Figure 5.18: $r^2 = 0.09$; $r = 0.29$; $p < 0.001$). No significant correlation was found to exist between copepod abundances and that of carnivorous euphausiids (Figure 5.19: $r^2 = 0.06$; $r = 0.25$; $p > 0.05$).

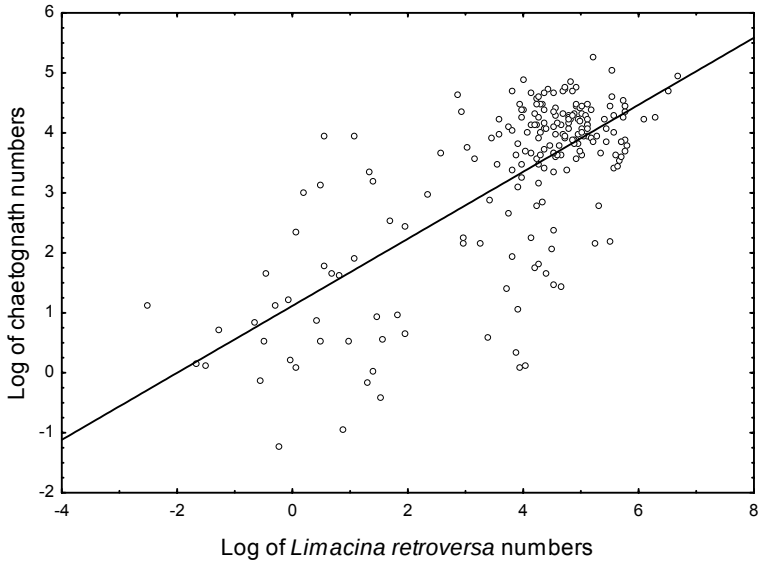

Figure 5.13 Pearson's Correlation results: *L. retroversa* numbers (ind. m^{-3}) versus chaetognath numbers (ind. m^{-3}) ($r^2 = 0.51$; $r = 0.71$; $p < 0.001$). Data used in the analysis were collected during MOEVS IV and V.

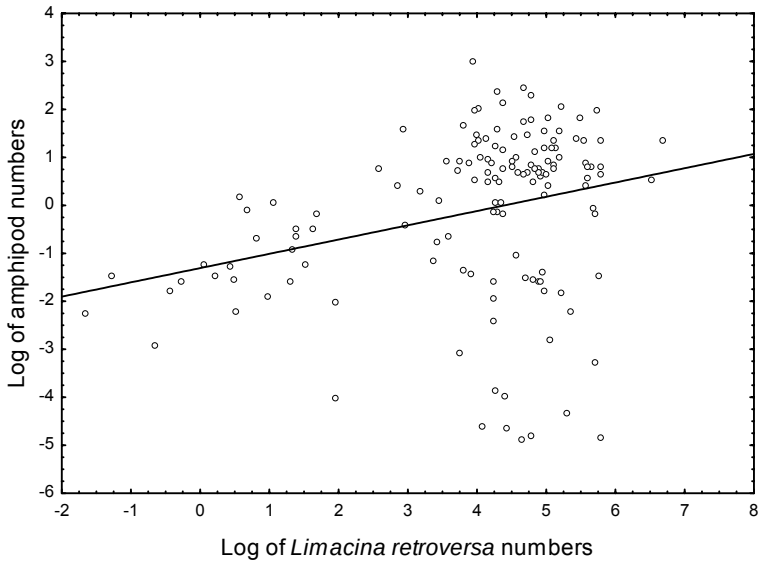

Figure 5.14 Pearson's Correlation results: *L. retroversa* numbers (ind. m^{-3}) versus amphipod numbers (ind. m^{-3}) ($r^2 = 0.08$; $r = 0.29$; $p < 0.001$). Data used in the anlaysis were collected during MOEVS IV and V.

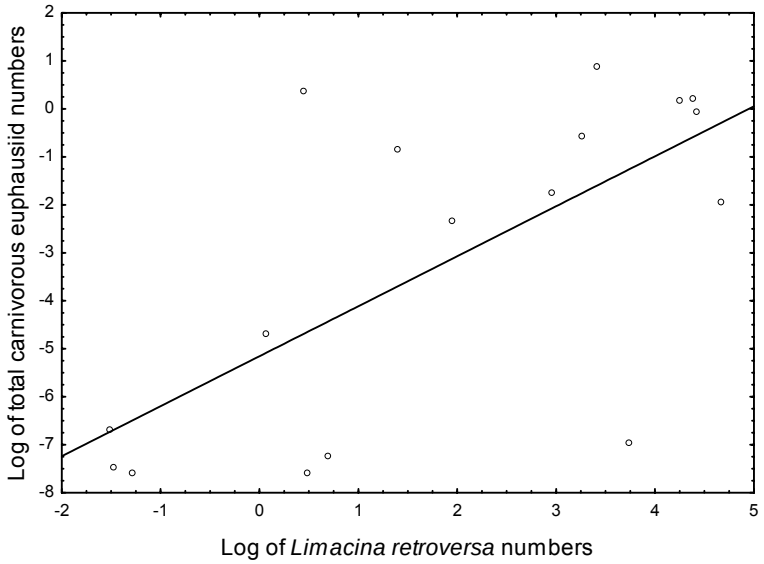

Figure 5.15 Pearson's Correlation results: *L. retroversa* numbers (ind. m^{-3}) versus carnivorous euphausiid numbers (ind. m^{-3}) ($r^2 = 0.46$; $r = 0.68$; $p = 0.003$). Data used in the analysis were collected during MOEVS IV and V.

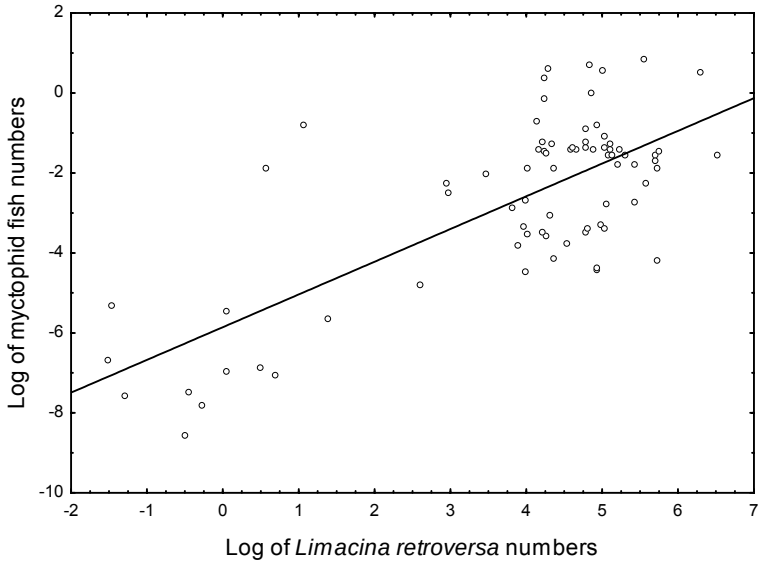

Figure 5.16 Pearson's Correlation results: *L. retroversa* numbers (ind. m^{-3}) versus myctophid fish numbers (ind. m^{-3}) ($r^2 = 0.54$; $r = 0.74$; $p < 0.001$). Data used in the analysis were collected during MOEVS V.

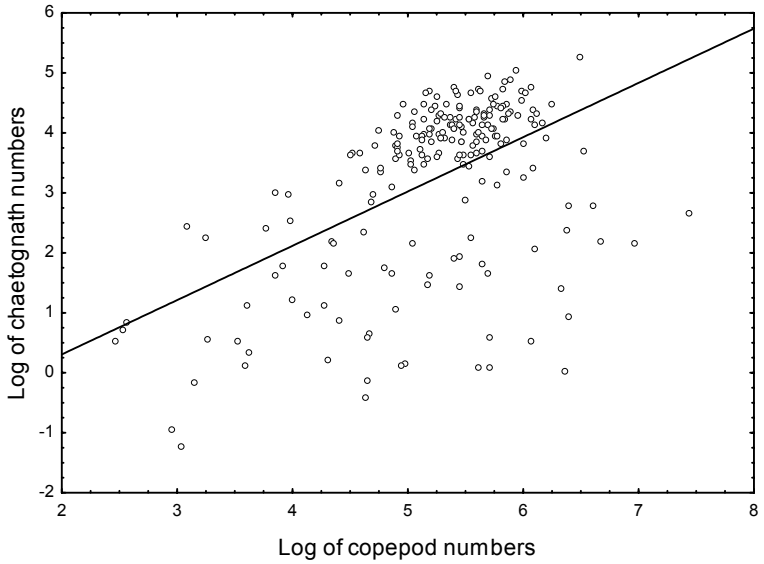

Figure 5.17 Pearson's Correlation results: copepod numbers (ind. m^{-3}) versus chaetognath numbers (ind. m^{-3}) ($r^2 = 0.26$; $r = 0.51$; $p < 0.001$). Data used in the analysis were collected during MOEVS IV and V.

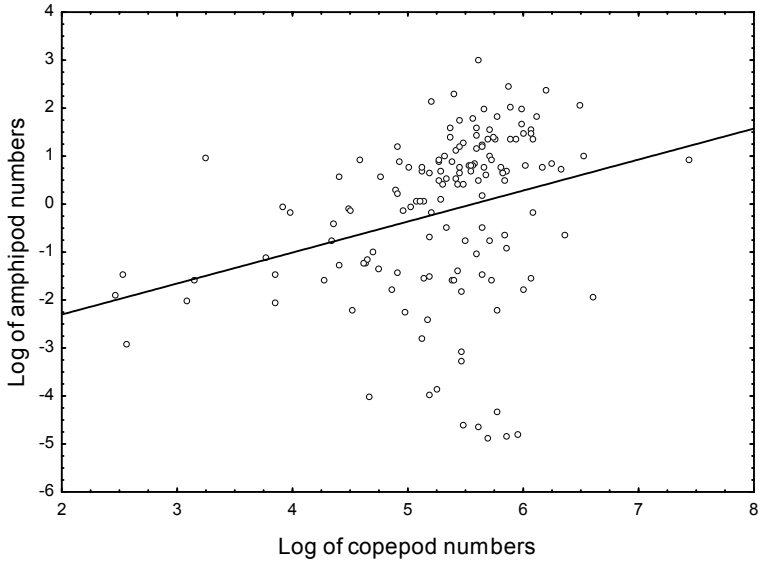

Figure 5.18 Pearson's Correlation results: copepod numbers (ind. m^{-3}) versus amphipod numbers (ind. m^{-3}) (r2 = 0.09; $r = 0.29$; $p < 0.001$). Data used in the analysis were collected during MOEVS IV and V.

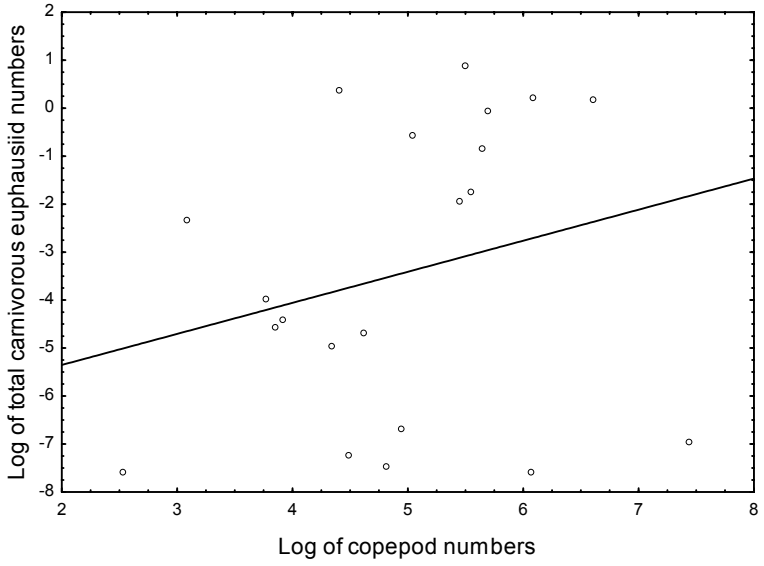

Figure 5.19 Pearson's Correlation results: copepod numbers (ind. m^{-3}) versus total carnivorous euphausiid numbers (ind. m^{-3}) ($r^2 = 0.06$; $r = 0.25$; $p = 0.28$). Data used in the analysis were collected during MOEVS IV and V.

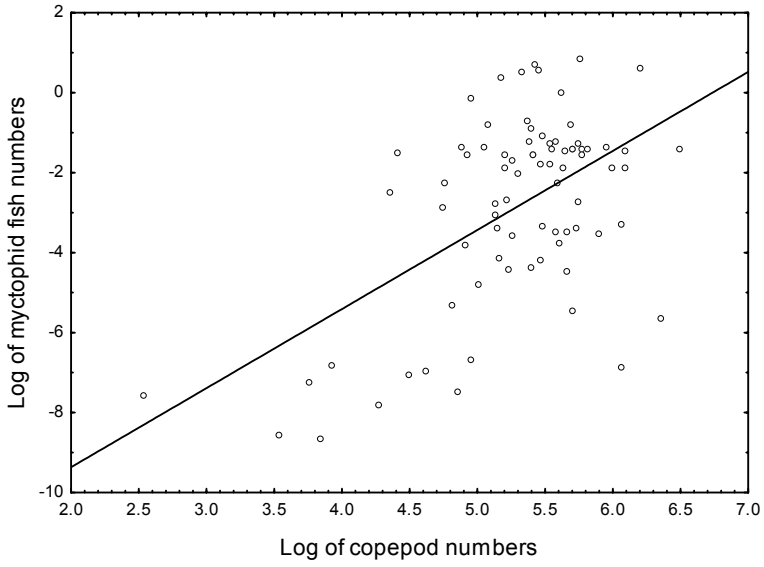

Figure 5.20 Pearson's Correlation results: copepod numbers (ind. m^{-3}) versus myctophid fish numbers (ind. m^{-3}) ($r^2 = 0.30$; $r = 0.55$; $p < 0.001$). Data used in the anlaysis were collected during MOEVS V.

5.4 DISCUSSION

The percentage contribution of carnivorous macrozooplankton and myctophid fish to total zooplankton biomass was highly variable throughout both surveys, ranging from 0.0 to 46.7 % during MOEVS IV and 0.0 to 86.8 % during MOEVS V. This result is consistent with previous investigations in the region and reflects the variable nature of the oceanographic environment and its effect on the biology of the PFZ (Pakhomov *et al.* 1999; Froneman *et al.* 2002a). Carnivorous macrozooplankton and myctophid fish abundances and biomass during MOEVS IV and V were typical of the PFZ for autumn (Froneman *et al.* 1999; Pakhomov & Froneman 1999a; Pakhomov & Froneman 2000).

It has been suggested that while a seasonal trend exists in the PFZ with regard to total zooplankton densities (Froneman *et al.* 1998; Pakhomov *et al.* 1999; Pakhomov & Froneman 2000; Froneman *et al.* 2002a), species composition does not vary significantly throughout the year. Indeed, total predator biomass was broadly similar between both years investigated, with chaetognaths and euphausiids dominating total predator biomass during MOEVS IV; and chaetognaths, euphausiids and myctophid fish contributing the most to total predator biomass during MOEVS V. These results are congruent with those from previous investigations in the PFZ as well as other regions of the Southern Ocean (Grindley & Lane 1979; Voronina 1984; Øresland 1990; Hosie 1994; Voronina *et al.* 1994; Tarling *et al.* 1995; Pakhomov *et al.* 1998, 1999a, 2000a; Froneman *et al.* 2002a).

Amphipods, although capable of swarming to great densities (Bocher *et al.* 2001; Pakhomov & Perissinotto 1996; Pakhomov & Froneman 1999b), were not encountered in large numbers during either MOEVS IV or V. The lack of myctophid fish in samples collected during MOEVS IV is probably due to net avoidance as a Bongo net, with only a small mouth area, was used to collect samples during that survey. Similarly, it is important to note that the Bongo net used during MOEVS IV would also likely have under-sampled the larger euphausiids. On the other hand, an RMT-8 net, with a wide mouth area, was used to collect macrozooplankton and myctophid fish during MOEVS V.

Significant inter-annual variability in total carnivore abundance was evident, with values being greater during MOEVS IV. This, combined with the lack of variability in total carnivore biomass between the two surveys, suggests that individuals were larger during MOEVS V; hence, while numbers were significantly lower, biomass values remained uniform. The same trend was observed for both chaetognaths and euphausiids, with numbers being greater during MOEVS IV, but biomass remaining constant between the years. The presence of large predators during MOEVS V cannot be explained by enhanced prey standing stocks since, at the time of the survey, mesozooplankton numbers recorded within the eddy were not very high.

During both surveys, macrozooplankton and myctophid fish assemblages, as identified by hierarchical cluster analyses, were not restricted to specific water masses (Figures 5.11 and 5.12). This finding suggests that the boundaries created by the fronts and the eddy during the present studies were not strong enough to restrict the movement of macrozooplankton and myctophid fish, thereby resulting in mixed communities. Although previous investigations have found that frontal systems in the Southern Ocean may act as barriers to macrozooplankton and myctophid fish communities (e.g. Pakhomov *et al.* 1999), other authors have reported highly mixed communities with an apparent lack of association to water mass (e.g. Froneman *et al.* 2002a; Bernard & Froneman 2006). Indeed, a detailed study on the distribution of euphausiids in the Indian sector of the PFZ conducted concurrently with the present investigation, suggests that the distribution of many of the euphausiid species common to the Sub-Antarctic waters was not limited by frontal systems in the region (Bernard & Froneman 2006).

Total predation impact of the carnivorous zooplankton during MOEVS IV ranged from 0 to 10 % of the available mesozooplankton standing stock, with an average daily predation impact of 1 %. Average daily predation impact during MOEVS V was 6 % of the mesozooplankton standing stock, but values as high as 74 % were recorded (station 285). At this station (285), euphausiids were responsible for 65.5 % of total daily predation impact (See Table 5.5). It is important to note, however, that due to the omnivorous feeding behaviour of the euphausiids, *Thysanoessa* spp. and *Nematocelis megalops*, which were considered for this study,

the results of predation impact should be viewed with caution as it is possible that the values for euphausiid predation rates may have been over-estimated (Mayzaud *et al.* 2003; Perissinotto *et al.* 1998; Pakhomov *et al.* 1998; Froneman *et al.* 2002a). Results of gut content analyses of *T. macrura* in the high Antarctic showed that diatoms occurred in 21 – 59 % of the stomachs (Hopkins 1985; Hopkins & Torres 1989). The predation impact estimates reported here are in the range reported during previous investigations in the PFZ for autumn (Froneman *et al.* 2002a), but were substantially higher than those recorded during summer within the same region (Pakhomov *et al.* 1999). Øresland (1995) suggested that the combined predation impact of carnivorous macrozooplankton may be substantial during the colder months when most of the prey taxa are less active, which may explain the high predation impact estimates recorded during the present study. No significant inter-annual variability was observed for either taxon-specific predation impacts (i.e. predation impacts of chaetognaths, amphipods and euphausiids) or total predation impact. It is important to point out the potential for error that might exist by employing data published in the literature. Predation rates and daily rations of predators are known to demonstrate a high degree of spatial and temporal variability and may be determined by both physico-chemical (e.g. temperature) and biological (e.g. prey availability and species composition) variables (Øresland 1995; Pakhomov *et al.* 1999; Froneman *et al.* 2002a). The predation impacts presented here should, therefore, be regarded with caution. Nonetheless, the data do indicate that carnivorous zooplankton within the PFZ may, at times, play an important role in structuring the mesozooplankton community during austral autumn.

Results of gut content analyses during the present study indicate that copepods are the dominant prey type for the majority of carnivorous macrozooplankton and myctophid fish in the PFZ during austral autumn (Table 5.3). Previous investigations in the region suggest that most predatory zooplankton are opportunistic feeders, generally consuming prey that is most abundant, i.e. copepods (Hopkins 1985; Hopkins & Torres 1989; Perissinotto & McQuaid 1992; Pakhomov & Perissinotto 1996; Pakhomov *et al.* 1996; Froneman & Pakhomov 1998b; Froneman *et al.* 1998; Froneman *et al.* 2000b). In fact, copepods (including copepod fragments) have been found in 26.5 % and 80 % of the stomach contents of the chaetognaths, *E. hamata* and *S. gazellae*, respectively (Froneman & Pakhomov 1998b); in 49 % of the guts of the

amphipod, *T. gaudichaudi* (Froneman *et al.* 2000b); and, in myctophid fish species, copepods were found in the stomach contents of 27 % *Electrona antarctica*, 23 % *Gymnoscopelus braueri*, 64 % *G. nicholsi* and 97 % *Protomyctophum bolini* (Pusch *et al.* 2004). Positive correlations between copepod abundances and those of chaetognaths, amphipods and myctophid fish from the present survey, suggest that as copepod numbers increase, so do some predator numbers. This finding reinforces the importance of copepods in the diets of major carnivorous macrozooplankton and myctophid fish in the region. Interestingly, similar positive correlations were found to exist between numbers of *L. retroversa* and abundances of chaetognaths, amphipods, myctophid fish and carnivorous euphausiids, suggesting that the pteropod may be a more important component in the diets of selected carnivorous taxa than was indicated by the gut content analyses from the present investigation. Indeed, gut content analysis has a fundamental flaw in that it does not account for soft-bodied organisms that are easily digested (Mauchline 1980; Gurney 2000). Since the aragonite shell of *L. retroversa* is readily dissolved in acidic solutions, the digestive enzymes in the stomach of a predator might dissolve the shell, leaving the soft body tissues to be digested beyond recognition.

Although *L. retroversa* did not frequently occur in the stomach contents of the major carnivorous zooplankton and myctophid fish during the present survey, previous investigations show that the pteropod can, at times, comprise a substantial component of the diets of some carnivorous taxa (Pakhomov & Perissinotto 1996; Froneman & Pakhomov 1998b; Froneman *et al.* 1998; Perissinotto & McQuaid 1992; Pakhomov *et al.* 1996; Armstrong *et al.* 2005; Bushula *et al.* 2005). In fact, *Limacina* spp. are the only prey consumed by the gymnosomatous pteropod, *Clione limacina* (Lalli 1970; Conover & Lalli 1972; Böer *et al.* 2005). There is potential, therefore, for *L. retroversa* to provide a link between primary production and the higher trophic levels, assisting in the transfer of carbon from the short-lived organic carbon pool to the long-lived organic carbon pool (Legendre & Le Fèvre 1992).

CHAPTER SIX:

FINAL DISCUSSION

Anthropogenic emissions of carbon dioxide (CO_2) have resulted in increased atmospheric CO_2 concentrations from 200 parts per million (ppm), during the 400 000 years before the industrial revolution, to almost 380 ppm, at present (Feely *et al.* 2004). It has been suggested that 30 % of total anthropogenic atmospheric CO_2 has been absorbed by the world's oceans over the last few decades (Sabine *et al.* 2004). When CO_2 dissolves in the ocean it reduces the pH of the water, increasing the acidity. Caldeira & Wickett (2003) propose that continued, unabated CO_2 emissions over the next few centuries might result in changes in ocean pH levels that far exceed any experienced in the past 300 million years. Our understanding of the implications of such changes is limited due to the scarcity of relevant data. However, recent studies predict that changes in seawater chemistry occurring during the present century could have severe consequences for calcifying organisms, especially thecosome (*shelled*) pteropods (Feely *et al.* 2004; Orr *et al.* 2005). These investigations have found that even the shells of live pteropods dissolved rapidly in surface waters that were undersaturated with respect to aragonite (Feeling *et al.* 2004; Orr *et al.* 2005). Orr *et al.* (2005) suggest that thecosome pteropods will not be able to adapt quickly enough to survive changes in seawater chemistry that will occur over a large portion of the high-latitude surface oceans during the twenty-first century. The implications are likely to be far-reaching, effecting the structure, biodiversity and tropho-dynamics of polar ecosystems (Orr *et al.* 2005).

In the Polar Frontal Zone (PFZ) of the Southern Ocean, thecosome pteropods, primarily the euthecosome, *Limacina retroversa*, are relatively abundant members of the mesozooplankton community (Perissinotto 1992; Pakhomov *et al.* 1997; Pakhomov & Perissinotto 1997; Froneman & Pakhomov 1998a; Bernard & Froneman 2002; Ward *et al.* 2003; Pakhomov & Froneman 2004a). A lack of sufficient data examining the general ecology of *L. retroversa* in the Indian sector of the PFZ prompted the present investigation.

Total mesozooplankton abundances recorded during the present investigation ranged between 16.75 ind. m^{-3} and 870.83 ind. m^{-3}; and are within the range of those reported in the literature (Perissinotto 1992; Pakhomov & Perissinotto 1997; Pakhomov *et al.* 1997; Froneman & Pakhomov 1998a; Froneman *et al.* 2000a; Pakhomov & Froneman 2004b). The mesozooplankton community during the

investigation was numerically dominated by copepods, primarily of the genera *Calanus*, *Oithona*, *Clausocalanus* and *Ctenocalanus*, which is typical of the region (Conover & Huntley 1991; Pakhomov & Perissinotto 1997; Froneman & Pakhomov 1998a; Pakhomov & Froneman 1999a; Pakhomov *et al.* 2000a; Bernard & Froneman 2002; Pakhomov & Froneman 2004a). On average, the copepods accounted for between 75.5 % and 88.1 % of the total mesozooplankton numbers during all three surveys. The contribution of *L. retroversa* to total mesozooplankton numbers was highly variable. The average contribution of the pteropod ranged from 0.9 % to 11.8 % of the total mesozooplankton abundances.

Total abundances of *L. retroversa* varied significantly in the PFZ between the years investigated and appeared to be directly related to total surface chlorophyll-*a* (chl-*a*) concentrations. Total surface chl-*a* biomass was greatest during the second Marion Offshore Ecosystem Variability Study (MOEVS II), corresponding with enhanced pteropod numbers during that survey. Seibel & Dierssen (2003) suggest that *L. helicina* (the Antarctic/Arctic species) may be strongly affected by regional phytoplankton concentrations. During austral summer 2000 – 2001, reduced phytoplankton stocks in the Ross Sea noticeably impacted on abundances of *L. helicina* (Seibel & Dierssen 2003). In addition, oxygen consumption rates of *L. helicina* measured during that study were lower than those recorded during previous years by the same authors; and was possibly a result of food deprivation (Seibel & Dierssen 2003). Furthermore, Kobayashi (1974) has reported that, in the Arctic, *Spiratella ("Limacina") helicina*, relies on high quality food availability throughout the year in order to sustain their continuous growth cycle.

During MOEVS II and IV, *L. retroversa* abundances were significantly greater in the PFZ than in either the Antarctic Zone (AAZ) or southern Sub-Antarctic Zone (sSAZ) water masses. *L. retroversa* is generally considered a Sub-Antarctic species (Boltovskoy 1999), thus elevated abundances in the PFZ would be expected. The lack of variability in *L. retroversa* numbers between water masses during MOEVS V is likely due to the extremely low chl-*a* concentrations encountered in all three water masses (PFZ, AAZ and sSAZ) during that survey. The size class structure of *L. retroversa* varied between the years and between water masses. The percentage contribution of small individuals to total pteropod numbers was significantly lower in

two of the water masses (sSAZ and AAZ) during MOEVS V, which might indicate regional delayed spawning during MOEVS V as a result of low food availability. In fact, relatively short delays in food supply have been shown to effect reproductive success, resulting in failed metamorphosis of some larval zooplankton (Ross & Quetin 1989, cited in Seibel & Dierssen 2003). Furthermore, large individuals of *L. retroversa* contributed significantly more to total pteropod numbers during MOEVS V than during the other surveys, reinforcing the hypothesis that spawning had been delayed. Typically, most adult females die after spawning (Kobayashi 1974; Gannefors *et al.* 2005). The presence of high numbers of large individuals of *L. retroversa* during MOEVS V, therefore suggests that they had not yet spawned. The over-all predominance of medium and small individuals during the three surveys suggests that the life cycle of *L. retroversa* in the PFZ is similar to that of *L. helicina* in the Arctic (Kobayashi 1974; Gannefors *et al.* 2005). In *L. helicina*, spawning occurs primarily during summer, peaking in late summer, with some spawning still occurring until late autumn (Gannefors *et al.* 2005). Similarly, the results of the present investigation suggest that spawning had occurred during early to late summer in all three years.

An investigation into the small-scale spatio-temporal variability of *L. retroversa* numbers and size structure and total copepod numbers (MIOS V; see Chapter Three) showed little significant spatial or temporal variability. Generally, the size structure of *L. retroversa* during MIOS V was made up primarily of small and medium-sized individuals, which is in agreement with results from investigations conducted in the Arctic Ocean by Gannefors *et al.* (2005) as well as results from MOEVS II, IV and V from the present investigation.

Average grazing rates of the dominant herbivorous zooplankton during the present investigation ranged between 6.99 mg (pigm) m^{-2} day^{-1} and 26.48 mg (pigm) m^{-2} day^{-1}, corresponding to an average daily grazing impact of between 93.0 % and 229.7 % of the available phytoplankton standing stock. Average grazing rates of the four most abundant copepods (*Calanus simillimus, Oithona similis, Clausocalanus* spp. and *Ctenocalanus* spp.) varied from 4.58 mg (pigm) m^{-2} day^{-1} to 8.77 mg (pigm) m^{-2} day^{-1}. Collectively, average copepod grazing impact accounted for between 40.4 % and 87.8 % of the total zooplankton grazing impact during the three surveys.

Grazing rates of *L. retroversa* reported during the present study were highly variable, ranging between 0.39 mg (pigm) m^{-2} day^{-1} and 17.69 mg (pigm) m^{-2} day^{-1} during the three surveys. During MOEVS II and IV, *L. retroversa* accounted on average for > 50 % of the total daily grazing impact, representing the most important grazer among those investigated during those surveys. Their contribution to total grazing impact during MOEVS II and IV is substantial, considering that *L. retroversa* contributed an average of only 8 % and 12 % to total zooplankton numbers during MOEVS II and IV, respectively. On the other hand, during MOEVS V, the pteropod made a significantly lower average contribution to the total daily grazing impact of only 8 %. Grazing rates of *L. retroversa* were also significantly reduced during MOEVS V, most likely the result of diminished abundances of *L. retroversa* during that survey.

L. retroversa appears to be a major contributor to total zooplankton grazing impact in the PFZ of the Southern Ocean during austral autumn. *L. retroversa* abundances appear to be strongly affected by the availability of phytoplankton. In contrast to the tunicate, *S. thompsoni*, that is limited in number by phytoplankton standing stock, abundance of *L. retroversa* increases with elevated phytoplankton biomass. Although *S. thompsoni* has an exceptionally high grazing rate, it is unable to modify its filtration rate and thus, at high chl-*a* concentrations, the filtration system becomes clogged by phytoplankton cells and the animal dies (Perissinotto & Pakhomov 1997; Perissinotto & Pakhomov 1998b). *L. retroversa*, on the other hand, has more control over its feeding behaviour. The pteropod feeds by means of a mucous web that it deploys into the water column, trapping food particles (Lalli & Gilmer 1989). At the end of a feeding period *L. retroversa* is able to discard the web and any remaining food particles that may still be attached (Lalli & Gilmer 1989). Additionally, it appears that *L. retroversa* is able to feed selectively on certain food particles and discard those that are less palatable (Lalli & Gilmer 1989). In the Arctic, *Spiratella ("Limacina") helicina* requires a continuous, high quality supply of food in order to sustain its growth cycle (Kobayashi 1974). The energy required for locomotion, particularly swimming up the water column, would also likely demand a high carbon intake (Lalli & Gilmer 1989). Unfortunately no metabolic rates were determined during the present study to verify this. However, Seibel & Dierssen (2003) have reported that oxygen consumption rates of *L. helicina* in the Ross Sea are reduced during periods of low phytoplankton biomass.

The relatively high abundances and grazing rates of *L. retroversa* suggest that the pteropod may play an important role in the transfer of carbon, from surface waters to depth, in the PFZ. There is evidence that euthecosome pteropods contribute substantially to regional carbon flux, thereby enhancing the efficiency of the biological pump (Bruland & Silver 1981; Lalli & Gilmer 1989; Meinecke & Wefer 1990; Bathmann *et al.* 1991; Noji *et al.* 1997; Collier *et al.* 2000; Gardner *et al.* 2000; Yoon *et al.* 2001; Accornero *et al.* 2003). Pteropods contribute to the downward flux of carbon in the oceans through the production of large faecal pellets with sinking rates that range from 65 m day^{-1} for *Clio* spp. to 1 800 m day^{-1} for *Corolla spectabilis* (Bruland & Silver 1981; Yoon *et al.* 2001). Abandoned mucous webs that are heavily laden with autotrophic and heterotrophic particles have been recorded in sediment traps in the Norwegian Sea (Bathmann *et al.* 1991; Noji *et al.* 1997). Noji *et al.* (1997) reported sinking rates of approximately 300 m day^{-1} for *L. retroversa* mucous aggregates. Mass sedimentation of empty shells of dead *Limacina* spp. has also been recorded on a number of occasions in both the northern and southern hemispheres (Meinecke & Wefer 1990; Bathmann *et al.* 1991; Collier *et al.* 2000; Gardner *et al.* 2000; Accornero *et al.* 2003). In all of the aforementioned investigations maximum sedimentation of *Limacina* spp. occurred during autumn or winter. These findings suggest that *L. retroversa* may enhance localised carbon flux in the PFZ.

While euthecosome pteropods may play an important role in the sequestration of carbon in the PFZ, results from the present study, as well as numerous previous investigations, suggest that *L. retroversa* might also constitute an important component of the diet of carnivorous macrozooplankton and micronekton, as well as top vertebrate predators (Perissinotto & McQuaid 1992; Pakhomov *et al.* 1996; Pakhomov & Perissinotto 1996; Froneman & Pakhomov 1998b; Froneman *et al.* 1998; Armstrong *et al.* 2005; Bushula *et al.* 2005). While results of gut content analyses during the present study did not identify *L. retroversa* as a major prey item for most of the dominant carnivorous taxa examined, the positive predator-prey relationships between abundances of *L. retroversa* and those of carnivorous euphausiids (*Nematocelis megalops*, *Thysanoessa macrura* and *Euphausia longirostris*), chaetognaths (*Sagitta gazellae* and *Eukrohnia hamata*), amphipods (*Themisto gaudichaudi*) and myctophid fish (*Eletrona* spp.) suggest that the pteropod

may be an important food source for these predators. The main problem associated with gut content analysis is that soft-bodied taxa are rapidly digested and therefore not easily identified (Mauchline 1980; Gurney 2000). Although pteropods possess a shell, it is made of aragonite (Lalli & Gilmer 1989) and therefore would likely be dissolved rapidly in the stomach acids of the predators, leaving only the soft body behind. Most of the carnivorous zooplankton examined during the present investigation are opportunistic predators, feeding largely on the most abundant prey (Hopkins 1985; Perissinotto & McQuaid 1992; Pakhomov *et al.* 1996; Froneman *et al.* 1998; Froneman *et al.* 2000b). Thus, when *L. retroversa* is abundant it would most likely constitute an important prey item.

While it has been suggested that predation by carnivorous zooplankton may control mesozooplankton standing stocks, average daily predation during the present investigation removed 1 % and 6 % of the mesozooplankton standing stocks during MOEVS IV and V, respectively. It is therefore likely that during the present investigation, *L. retroversa* played a more important role in sequestering carbon to the sea floor than in providing a link between primary producers and top predators in the region.

6.1 CONCLUSION

Results of the present study highlight the role that the euthecosome pteropod, *L. retroversa*, plays in the PFZ ecosystem in the Indian sector of the Southern Ocean. *L. retroversa* can, at times, contribute substantially to total mesozooplankton numbers and can be considered a major grazer in the zooplankton community. Additionally, the pteropod may also provide an important prey source to the higher trophic levels, including the top vertebrate predators in the region. Euthecosome pteropods enhance the sequestration of carbon to the sea floor, through the sinking of large faecal pellets and abandoned mucous webs; and, in death, the mass sedimentation of empty shells.

Continued anthropogenic emissions of CO_2 will result in an increase in the acidity of the surface waters of the world's high-latitude oceans, with a corresponding decrease in the calcium carbonate ($CaCO_3$) saturation depth (Caldeira & Wickett 2003; Feely *et al.* 2004; Orr *et al.* 2005). The consequences of which will be dire for

calcareous, shell-forming organisms, particularly euthecosome pteropods, as aragonite dissolves far more readily than other forms of $CaCO_3$ (Feely *et al.* 2004). If the acidity of high-latitude oceans increases and the waters become undersaturated with regard to $CaCO_3$, then it is predicted that euthecosome pteropods in the high-latitude regions will not survive (Orr *et al.* 2005). This will have far-reaching affects on the entire pelagic ecosystem of the high-latitudes, the extent of which cannot accurately be predicted due to a scarcity of relevant data.

6.2 RECOMMENDATIONS FOR FUTURE RESEARCH

1. In order to fully understand the life cycle of *L. retroversa* in the Southern hemisphere, investigations into the seasonal variability of *L. retroversa* abundances, vertical distribution patterns and size class structure are required. Kobayashi (1974) recorded that the vertical distribution patterns of *Spiratella ("Limacina") helicina* in the Arctic varied according to pteropod size and season.
2. Since peak spawning tends to occur during summer, it is likely that pteropod numbers and therefore grazing impact would demonstrate a high degree of seasonality with highest values coinciding with a peak in reproductive output. There is, however, a lack a seasonal data for the Indian sector of the Polar Frontal Zone (PFZ) and, indeed, in other regions of the Southern Ocean. It is therefore important that seasonal investigations of the mesozooplankton grazing impact, and particularly the grazing impact of *L. retroversa* be conducted.
3. It has been suggested that the Antarctic/Arctic euthecosome pteropod, *L. helicina*, requires a continuous supply of high quality food particles in order to sustain its high metabolic requirements (Kobayashi 1974; Seibel & Dierssen 2003). Metabolic rate studies in the PFZ are needed in order to determine the energy budget for *L. retroversa* and to ascertain the dependence of species on phytoplankton standing stocks.
4. The contribution of pteropods to carbon flux in the Indian sector of the PFZ is largely unknown. It is possible that during austral autumn, following the peak in spawning, mass sedimentation of *L. retroversa* may occur over parts of the Southern Ocean. Carbon flux studies using sediment traps are therefore necessary.

REFERENCES

ACCORNERO A, Manno C, Esposito F, Gambi MC (2003) The vertical flux of particulate matter in the polynya of Terra Nova Bay. Part II. Biological components. *Antarctic Science* 15: 175-188

ALLANSON BR, Boden BP, Parker L (1985) A contribution to the oceanology of the Prince Edward Islands. In: Siegfried WR, Condy PR, Laws RM (Eds) *Antarctic nutrient cycles and food webs*. Springer, Berlin Heidelberg New York, pp38-45

ANSORGE IJ, Froneman PW, Pakhomov EA, Lutjeharms JRE, Perissinotto R, Ballegooyen RC van (1999) Physical-biological coupling in the waters surrounding the Prince Edward Islands (Southern Ocean). *Polar Biology* 21: 135-145

ANSORGE IJ, Lutjeharms JRE (2002) The hydrography and dynamics of the ocean environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* 37: 107-127

ANSORGE IJ, Lutjeharms JRE (2005) Direct observations of eddy turbulence at a ridge in the Southern Ocean. *Geophysical Research Letters* 32: unknown page numbers

ANSORGE IJ, Speich S, Lutjeharms JRE, Göni GJ, de W Rautenbach CJ, Froneman PW, Rounault M, Garzoli S (2005) Monitoring the oceanic flow between Africa and Antarctica: Report of the first GoodHope cruise. *South African Journal of Science* 101: 29-35

ARMSTRONG JL, Boldt JL, Cross AD, Moss JH, Davis ND, Myers KW, Walker RV, Beauchamp DA, Haldorson LJ (2005) Distribution, size, and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon, *Oncorhynchus gorbuscha*. *Deep-Sea Research II* 52: 247-265

ARRIGO KR, Worthen DL, Lizotte MP, Dixon P, Dieckmann G (1997) Primary production in Antarctic Sea Ice. *Science* 276: 394-397

ATKINSON A, Ward R, Williams R, Poulet SA (1992a) Diel vertical migration and feeding of copepods at an oceanic site near South Georgia. *Marine Biology* 113: 583-593

ATKINSON A, Ward P, Williams R, Poulet SA (1992b) Feeding rates and diel vertical migration of copepods near South Georgia: comparison of shelf and oceanic sites. *Marine Biology* 114: 49-56

ATKINSON A (1994) Diets and feeding selectivity among the epipelagic copepod community near South Georgia in summer. *Polar Biology* 14: 551-560

ATKINSON A (1995) Omnivory and feeding selectivity in five copepod species during spring in the Bellingshausen Sea, Antarctica. *ICES Journal of Marine Science* 52: 000-000

ATKINSON A, Shreeve RS (1995) Response of the copepod community to a spring bloom in the Bellingshausen Sea. *Deep-Sea Research II* 42: 1291-1311

ATKINSON A (1996) Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. *Marine Ecology Progress Series* 130: 85-96

ATKINSON A, Shreeve RS, Pakhomov EA, Priddle J, Blight SP, Ward P (1996) Zooplankton response to a phytoplankton bloom near South Georgia, Antarctica. *Marine Ecology Progress Series* 144: 195-210

ATKINSON A, Snÿder R (1997) Krill-copepod interactions at South Georgia, Antarctica, I. Omnivory by *Euphausia superba*. *Marine Ecology Progress Series* 160: 63-76

ATKINSON A, Ward P, Hill A, Brierley AS, Cripps GC (1999) Krill-copepod interactions at South Georgia, Antarctica, II. *Euphausia superba* as a major control on copepod abundance. *Marine Ecology Progress Series* 176: 63-79

ATKINSON A, Sinclair JD (2000) Zonal distribution and seasonal vertical migration of copepod assemblages in the Scotia Sea. *Polar Biology* 23: 46-58

AURAS-SCHUDNAGIES A, Kroon D, Ganssen G, Hemleben C, van Hinte JE (1989) Distributional pattern of planktonic foraminifers and pteropods in surface waters and top core sediments of the Red Sea, and adjacent areas controlled by the monsoonal regime and other ecological factors. *Deep-Sea Research* 36: 1515-1533

AZAM F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water column microbes in the sea. *Marine Ecology Progress Series* 10: 257-263

BACKUS RH (1985) Biogeographic boundaries in the open ocean. In: Pierrot-Bults AC, van der Spoel S, Zahuranec BJ, Johnson RK (Eds) *Pelagic Biogeography*. Unesco, France, pp. 9-14

BAIER CT, Purcell JE (1997) Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic Bight. *Marine Ecology Progress Series* 146: 43-53

BALARIN MG (1999) Size-fractionated phytoplankton biomass and primary production in the Southern Ocean. MSc thesis. Rhodes University, Grahamstown, 137 pp

BÅMSTEDT U, Gifford DJ, Irigoien X, Atkinson A, Roman M (2000) Feeding. In: Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (Eds) *ICES Zooplankton methodology manual*. Academic Press. UK, pp. 230 – 231

BATHMANN UV, Noji TT, van Bodungen B (1991) Sedimentation of pteropods in the Norwegian Sea in autumn. *Deep-Sea Research* 38: 1341-1360

BATHMANN UV, Makarov PR, Spiridonov VA, Rhohardt G (1993) Winter distribution and overwintering strategies of the Antarctic copepod species *Calanoides*

acutus, *Rhincalanus gigas* and *Calanus propinquus* (Crustacea, Calanoida) in the Weddell Sea. *Polar Biology* 13: 333-346

BELKIN IM, Gordon AL (1996) Southern Ocean fronts from the Greenwich meridian to Tasmania. *Journal of Geophysical Research* 101: 3675-3696

BERNARD KS (2002) Mesozooplankton community structure and grazing impact in the Polar Frontal Zone of the Southern Ocean. MSc thesis, Rhodes University, South Africa.

BERNARD KS, Froneman PW (2002) Mesozooplankton community structure in the Southern Ocean upstream of the Prince Edward Islands. *Polar Biology* 25: 597-604

BERNARD ATF, Froneman PW (2006) Euphausiid population structure and grazing in the Antarctic Polar Frontal Zone – austral autumn 2004. *African Journal of Marine Science* 28: pages not available at time of printing

BOCHER P, Cherel Y, Labat J-P, Mayzaud P, Razouls S, Jouventin P (2001) Amphipod-based food web: *Themisto gaudichaudi* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. *Marine Ecology Progress Series* 223: 261-276

BODEN BP, Duncombe Rae CM, Lutjeharms JRE (1988) The distribution of the diatoms of the south-west Indian Ocean surface waters between Cape Town and the Prince Edward archipelago. *South African Journal of Science* 84: 811-818

BÖER M, Gannefors C, Kattner G, Graeve M, Hop H, Falk-Petersen S (2005) The Arctic pteropod *Clione limacina*: seasonal lipid dynamics and life-strategy. *Marine Biology* 147: 707-717

BOLTOVSKOY D (Ed) *South Atlantic Zooplankton*; Volumes 1 & 2; Backhuys Publishers, Leiden; 1999

BOYSEN-ENNEN E, Hagen W, Hubold G, Piatkowski U (1991) Zooplankton biomass in the ice-covered Weddell Sea, Antarctica. *Marine Biology* 111: 227-235

BRACHER AU, Kroon BMA, Lucas MI (1999) Primary production, physiological state and composition of phytoplankton in the Atlantic Sector of the Southern Ocean. *Marine Ecology Progress Series* 190: 1-16

BRADFORD-GRIEVE JM, Chang FH, Gall M, Pickmere S, Richards F (1997) Size fractionated phytoplankton standing stocks and primary production during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31: 210-224

BRADFORD-GRIEVE JM, Murdoch R, James M, Oliver M, McLeod J (1998) Mesozooplankton biomass, composition, and potential grazing pressure on phytoplankton during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. *Deep-Sea Research I* 45: 1709-1737

BROWN CR, Klages NT (1987) Seasonal and annual variation in diets of Macaroni (*Eudyptes chrysolophus chrysolophus*) and Southern rockhopper (*E. chrysocome chrysocome*) penguins at sub-Antarctic Marion Island. *Journal of Zoology, London* 212: 7-28

BROWN SL, Landry MR (2001) Microbial community structure and biomass in surface waters during a Polar Front summer bloom along 170ºW. *Deep-Sea Research II* 48: 4039-4058

BRULAND KW, Silver MW (1981) Sinking rates of faecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). *Marine Biology* 63: 295-300

BRYDEN HL (1983) The Southern Ocean In: Robinson AR (ed) *Eddies in marine science*. Springer, Berlin Heidelberg New York, pp 265-277

BUSHULA T, Pakhomov EA, Kaehler S, Davis S, Kalin RM (2005) Diet and daily ration of two nototheniid fish on the shelf of the sub-Antarctic Prince Edward Islands. *Polar Biology* 28: 585-593

CALDEIRA K, Duffy PB (2000) The role of the Southern Ocean in uptake and storage of anthropogenic carbon dioxide. *Science* 287: 620-622

CALDEIRA K, Wickett ME (2003) Anthropogenic carbon and ocean pH. *Nature* 425: 365

CHEREL Y, Kooyman GL (1998) Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica. *Marine Biology* 130: 335-344

CHEREL Y, Pütz K, Hobson KA (2002) Summer diet of king penguins (*Aptenodytes patagonicus*) at the Falkland Islands, southern Atlantic Ocean. *Polar Biology* 25: 898-906

CHO BC, Azam F (1988) Major role of bacteria in biogeochemical fluxes in the ocean's interior. *Nature* 332: 441-443

CLARKE KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Environmental Research Council, Cambridge

COLLIER R, Dymond J, Honjo S, Manganini S, Francois R, Dunbar R (2000) The vertical flux of biogenic and lithogenic material in the Ross Sea: moored sediment trap observations 1996-1998. *Deep-Sea Research II* 47: 3491-3520

CONOVER RJ, Lalli CM (1972) Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusc. *Journal of Experimental Marine Biology and Ecology* 9: 279-302

CONOVER RJ, Huntley M (1991) Copepods in ice-covered seas – Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *Journal of Marine Systems* 2: 1-41

DADON JR, de Cidre LL (1992) The reproductive cycle of the Thecosomatous pteropod *Limacina retroversa* in the western South Atlantic. *Marine Biology* 114: 439-442

DAFNER E (1997) Primary production and development of phytoplankton in the Atlantic sector of the Southern Ocean. *GeoJournal* 41: 5-14

DAM HG, Peterson WT (1988) The effect of temperature on the gut clearance rate constant of planktonic copepods. *Journal of Experimental Marine Biology and Ecology* 123: 1-14

DE BAAR HJW, de Jong JTM, Bakker DCE, Lascher BM, Veth C, Bathmann U, Smetacek V (1995) Importance of iron for phytoplankton blooms and carbon dioxide drawdown in the Southern Ocean. *Nature* 373: 412-415

DEACON GER (1937) The hydrology of the Southern Ocean. *Discovery Report* 15: 1-124

DEACON GER (1982) Physical and biological zonation in the Southern Ocean. *Computers & Geosciences: An International Journal* 1-15

DILLING L, Alldredge AL (1993) Can chaetognath fecal pellets contribute significantly to carbon flux? *Marine Ecology Progress Series* 92: 51-58

DUBISCHAR CD, Bathmann UV (1997) Grazing impact of copepods and salps on phytoplankton in the Atlantic sector of the Southern Ocean. *Deep-Sea Research II* 44: 415-433

DUBISCHAR CD, Lopes RM, Bathmann UV (2002) High summer abundances of small pelagic copepods at the Antarctic Polar Front – implications for ecosystem dynamics. *Deep-Sea Research II* 49: 3871-3887

DUNCOMBE RAE CM (1989) Frontal systems encountered between southern Africa and the Prince Edward Islands during April/May 1987. *South African Journal of Antarctic Research* 19: 21-25

EGUCHI NO, Kawahata H, Taira A (1999) Seasonal response of planktonic foraminifera to surface ocean condition: sediment trap results from the Central North Pacific Ocean. *Journal of Oceanography* 55: 681-691

EL-SAYED SZ (1988) Productivity of the Southern Ocean: a closer look. *Computational Biochemistry and Physiology* 90: 489-49

EMERY WJ (1977) Antarctic Polar Frontal Zone from Australia to the Drake Passage. *Journal of Physical Oceanography* 7: 811-822

ERRHIF A, Razouls C, Mayzaud P (1997) Composition and community structure of pelagic copepods in the Indian sector of the Antarctic Ocean during the end of the austral summer. *Polar Biology* 17: 418-430

FEELY RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* 305: 362-366

FEIGENBAUM D (1979) Daily ration and specific daily ration of the chaetognath *Sagitta enflata*. *Marine Biology* 54: 75-82

FIELD JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multi species distribution patterns. *Marine Ecology Progress Series* 8: 37-52

FOGG GE (1991) The phytoplanktonic ways of life. *New Phytology* 118: 191-232

FORTIER L, Le Fevere J, Legendre L (1994) Export of biogenic carbon to fish and the deep ocean: the role of planktonic macrophages. *Journal of Plankton Research* 16:809-839

FRONEMAN PW (1995) The role of microzooplankton in carbon cycling in the Southern Ocean. PhD thesis. Rhodes University, Grahamstown

FRONEMAN PW, Perissinotto R, McQuaid CD, Laubscher RK (1995a) Summer distribution of netphytoplankton in the Atlantic sector of the Southern Ocean during austral summer. *Polar Biology* 15: 77-84

FRONEMAN PW, McQuaid CD, Perissinotto R (1995b) Biogeographic structure of the microphytoplankton assemblages of the south Atlantic and Southern Ocean during austral summer. *Journal of Plankton Research* 17: 1791-1802

FRONEMAN PW and Perissinotto R (1996) Structure and grazing of the microzooplankton communities of the Subtropical Convergence and a warm-core eddy in the Atlantic sector of the Southern Ocean. *Marine Ecology Progress Series* 135: 237-245

FRONEMAN PW, Pakhomov EA, Perissinotto R, Laubscher RK, McQuaid CD (1997) Dynamics of the plankton communities during seasonal ice melt in the Lazarev Sea during austral summer 1994-95. *Marine Ecology Progress Series* 149: 201-214

FRONEMAN PW, Balarin MG (1998) Structure and grazing impact of the protozooplankton community in the waters surrounding the Prince Edward Islands (Southern Ocean). *Polar Biology* 20: 198-205

FRONEMAN PW, Pakhomov EA (1998a) Biogeographic study of the plankton communities of the Prince Edward Islands. *Journal of Plankton Research* 20: 653-669

FRONEMAN PW, Pakhomov EA (1998b) Trophic importance of the chaetognaths *Eukrohnia hamata* and *Sagitta gazellae* in the pelagic system of the Prince Edward Islands (Southern Ocean). *Polar Biology* 19: 242-249

FRONEMAN PW, Pakhomov EA, Perissinotto R, Meaton V (1998) Feeding and predation impact of two chaetognath species, *Eukrohnia hamata* and *Sagitta gazellae*, in the vicinity of Marion Island (Southern Ocean). *Marine Biology* 131: 95-101

FRONEMAN PW, Ansorge IJ, Pakhomov EA, Lutjeharms JRE (1999) Plankton community structure in the physical environment surrounding the Prince Edward Islands (Southern Ocean). *Polar Biology* 22: 145-155

FRONEMAN PW, Pakhomov EA (2000) Spatial and temporal variability in chlorophyll-*a* and diatom distribution in the south-east Indian Ocean. *Vie et Milieu* 50: 275-288

FRONEMAN PW, Pakhomov EA, Perissinotto R, McQuaid CD (2000a) Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993. Part 2. Biochemical zonation. *Deep-Sea Research I* 47: 1687-1702

FRONEMAN PW, Pakhomov EA, Treasure A (2000b) Trophic importance of the hyperiid amphipod, *Themisto gaudichaudi*, in the Prince Edward Archipelago (Southern Ocean) ecosystem. *Polar Biology* 23: 429-436

FRONEMAN PW, Laubscher RK, McQuaid CD (2001) Size-fractionated primary production in the south Atlantic and Atlantic sectors of the Southern Ocean. *Journal of Plankton Research* 23: 611-622

FRONEMAN PW, Pakhomov EA, Gurney LJ, Hunt BPV (2002a) Predation impact of carnivorous macrozooplankton in the vicinity of the Prince Edward Island archipelago (Southern Ocean) in austral autumn 1998. *Deep-Sea Research II* 49: 3243-3254

FRONEMAN PW, Ansorge IJ, Vumazonke L, Gulekana K, Bernard K, Webb AM, Leukes W, Risien CM, Thomalla S, Hermes J, Knott M, Anderson D, Hargey N, Jennings M, Veitch J, Lutjeharms JRE, McQuaid CD (2002b) Physical and biological variability in the Antarctic Polar Frontal Zone: report on research cruise 103 of the MV *SA Agulhas*. *South African Journal of Science* 98: 1-3

FRONEMAN PW, Bernard KS (2004) Trophic cascading in the Polar Frontal Zone of the Southern Ocean during austral autumn 2002. *Polar Biology* 27: 112-118

FRONEMAN PW, Pakhomov EA, Balarin MG (2004) Size-fractionated phytoplankton biomass, production and biogenic carbon flux in the eastern Atlantic sector of the Southern Ocean in late austral summer 1997-1998. *Deep-Sea Research II* 51: 2715-2729

GALLIENNE CP, Robins DB (2001) Is *Oithona* the most important copepod in the world's oceans? *Journal of Plankton Research* 23: 1421-1432

GANNEFORS C, Böer M, Kattner G, Graeve M, Eiane K, Gulliksen B, Hop H, Falk-Petersen S (2005) The Arctic sea butterfly *Limacina helicina*: lipids and life strategy. *Marine Biology* 147: 169-177

GARDNER WD, Richardson MJ, Smith WO Jr (2000) Seasonal patterns of water column particulate organic carbon and fluxes in the Ross Sea, Antarctica. *Deep-Sea Research II* 47: 3423-3449

GIBBONS MJ, Stuart V, Verheye HM (1992) Trophic ecology of carnivorous zooplankton in the Benguela. *South African Journal of Marine Science* 12: 421-437

GILMER RW, Harbison GR (1986) Morphology and field behaviour of pteropod molluscs: feeding methods in the families Cavoliniidae, Limacinidae and Peraclididae (Gastropoda: Thecosomata). *Marine Biology* 91: 47-57

GRINDLEY JR, Lane SB (1979) Zooplankton around Marion and Prince Edward Islands. *CNFRA* 4: 111-125

GOODAY AJ (2002) Biological responses to seasonally varying fluxes of organic matter to the ocean floor: A review. *Journal of Oceanography* 58: 305-332

GURNEY LJ (2000) Feeding ecology of three principal euphausiid species in the waters surrounding the Prince Edward Archipelago. MSc Thesis, Rhodes University, South Africa. Pages 1-135

GURNEY LJ, Froneman PW, Pakhomov EA, McQuaid CD (2002) Diel feeding patterns and daily ration estimates of three subantarctic euphausiids in the vicinity of the Prince Edward Islands (Southern Ocean). *Deep-Sea Research II* 49: 3207-3227

HANSEN B, Berggreen UC, Tande KS, Eilertsen HC (1990) Post-bloom grazing by *Calanus glacialis, C. finmarchicus* and *C. hyperboreus* in the region of the Polar Front, Barents Sea. *Marine Biology* 104: 5-14

HANSEN B, Christiansen S, Pedersen G (1996) Plankton dynamics in the marginal ice zone of the central Barents Sea during spring: carbon flow and structure of the grazer food chain. *Polar Biology* 16: 115-128

HEAD EJH (1988) Copepod feeding behaviour and the measurement of grazing rates *in vivo* and *in vitro*. *Hydrobiologia* 167/168: 31-41

HERNÁNDEZ-LEÓN S, Torres S, Gómez M, Montero I, Almeida C (1999) Biomass and metabolism of zooplankton in the Bransfield Strait (Antarctic Peninsula) during austral spring. *Polar Biology* 21: 214-219

HERNÁNDEZ-LEÓN S, Almeida C, Portillo-Hahnefeld A, Gómez M, Montero I (2000) Biomass and potential feeding, respiration and growth of zooplankton in the Bransfield Strait (Antarctic Peninsula) during austral summer. *Polar Biology* 23: 679-690

HOFFMAN EE (1985) The large scale horizontal structure of the Antarctic Circumpolar Current from FGGE drifters. *Journal of Geophysical Research* 90: 7087-7097

HOFFMAN EE, Whitworth T (1985) A synoptic description of the flow at the Drake Passage from year long measurements. *Journal of Geophysical Research* 90: 7177-7187

HOLM-HANSEN O, Riemann B (1978) Chlorophyll-a determination: improvements in methodology. *Oikos* 30: 438-447

HOPKINS TL (1985) Food web of an Antarctic midwater ecosystem. *Marine Biology* 89: 197-212

HOPKINS TL, Torres JJ (1989) Midwater food web in the vicinity of a marginal ice zone in western Weddell Sea. *Deep-Sea Research* 36: 543-560

HOSIE GW (1994) The macrozooplankton communities in the Prydz Bay region, Antarctica. In: El-Sayed SZ (Ed) *Southern Ocean Ecology: the biomass perspective*. Cambridge University Press, United Kingdom, pp. 93-123

HUNT BPV, Pakhomov EA, McQuaid CD (2001) Short-term variation and long-term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology* 138: 369-381

HUNT BPV, Pakhomov EA (2003) Mesozooplankton interactions with the shelf around the sub-Antarctic Prince Edward Islands archipelago. *Journal of Plankton Research* 25: 885-904

JACQUES G, Panouse M (1991) Biomass and composition of size-fractionated phytoplankton in the Weddell Sea Confluence area. *Polar Biology* 11: 315-328

JOIRIS CR, Tahon J, Holsbeek L, Vancauwenberghe M (1996) Seabirds and marine mammals in the eastern Barents Sea: late summer at-sea distribution and calculated food intake. *Polar Biology* 16: 245-256

KANG S-H, Fryxell GA (1993) Phytoplankton in the Weddell Sea, Antarctica: composition, abundance and distribution in water-column assemblages of the marginal ice-edge during autumn. *Marine Biology* 116: 335-348 (Abstract only)

KNOX GA (1994) *The Biology of the Southern Ocean*. Cambridge University Press, United Kingdom

KOBAYASHI HA (1974) Growth cycle and related vertical distribution of the thecosomatous pteropod *Spiratella ("Limacina") helicina* in the Central Arctic Ocean. *Marine Biology* 26: 295-301

LALLI CM (1970) Structure and function of the buccal apparatus of *Clione limacina* (Phipps) with a review of feeding in gymnosomatous pteropods. *Journal of Experimental Marine Biology and Ecology* 4: 101-118

LALLI CM, Gilmer RW (1989) *Pelagic Snails. The Biology of Holoplanktonic Gastropod Mollus*ks. Stanford University Press, California. Pages 58-166

LAMPITT R, Noji RR, von Bodungen B (1990) What happens to zooplankton faecal pellets? Implications for material flux. *Marine Biology* 104: 15-23

LANCELOT C, Hannon E, Becquevort S, Veth C, De Baar HJW (2000) Modeling phytoplankton blooms and carbon export production in the Southern Ocean: dominant controls by light and iron in the Atlantic sector in Austral spring 1992. *Deep-Sea Research I* 47: 1621-1662

LAUBSCHER RK, Perissinotto R, McQuaid CD (1993) Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology* 13: 471-481

LE FÈVRE J, Legendre L, Rivkin RB (1998) Fluxes of biogenic carbon in the Southern Ocean: roles of large microphagous zooplankton. *Journal of Marine Systems* 17: 325-345

LEGECKIS R (1977) Oceanic Polar front in the Drake Passage – satellite observations during 1976. *Deep-Sea Research* 24: 701-704

LEGENDRE L, Legendre P (1983) *Numerical ecology*. Elsevier, Amsterdam

LEGENDRE L, Le Fèvre J (1992) Interactions between hydrodynamics and pelagic ecosystems: relevance to resource exploitation and climate change. *South African Journal of Marine Science* 12: 477-486

LI C, Sun S, Zhang G, Ji P (2001) Summer feeding activities of zooplankton in Prydz Bay, Antarctica. *Polar Biology* 24: 892-900

LOEB V, Siegel V, Holm-Hansen O, Hewitt R, Fraser W, Trivelpiece S (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387: 897-900

LONGHURST AR, Harrison WG (1989) The biological pump: profiles of plankton production and consumption in the upper ocean. *Progress in Oceanography* 22: 47-123

LONGHURST AR, Bedo AW, Harrison WG, Head EJH, Sameoto DD (1990) Vertical flux of respiratory carbon by oceanic diel migrant biota. *Deep-Sea Research* 37: 685-694

LONGHURST AR (1991) Role of the marine biosphere in the global carbon cycle. *Limnology and Oceanography* 36: 1507-1526

LUTJEHARMS JRE, Valentine HR (1984) Southern Ocean thermal fronts south of Africa. *Journal of Physical Oceanography* 18: 761-774

LUTJEHARMS JRE (1985) Location of frontal systems between Africa and Antarctica: some preliminary results. *Deep-Sea Research* 32: 1499-1509

LUTJEHARMS JRE (1990) Temperature profile of the upper ocean layer in the region between Cape Town and Marion Island (In Afrikaans with English abstract). *South African Journal of Antarctic Research* 20: 21-32

MACKAS D, Bohrer R (1976) Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *Journal of Experimental Marine Biology and Ecology* 25: 77-85

MAUCHLINE J (1980) The biology of mysids and euphausiids. *Advances in Marine Biology* 18: 1-681

MAYZAUD P, Boutoute M, Alonzo F (2003) Lipid composition of the euphausiids *Euphausia vallentini* and *Thysanoessa macrura* during summer in the Southern Indian Ocean. *Antarctic Science* 15: 463-475

MEINECKE G, Wefer G (1990) Seasonal pteropod sedimentation in the Norwegian Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 79: 129-147

MILLER DGM (1982) Results of a combined hydro acoustic and midwater trawling survey of the Prince Edward Island group. *South African Journal of Antarctic Research* 12: 3-10

MORALES CE, Bedo A, Harris RP, Tranter PRG (1991) Grazing of copepod assemblages in the north-east Atlantic: the importance of the small size fraction. *Journal of Plankton Research* 13: 455-472

NAGATA Y, Michida Y, Umimura Y (1988) Variation of positions and structures of the oceanic fronts in the Indian Ocean sector of the Southern Ocean in the period from 1965 to 1987. In Sahrhage D (Ed) *Antarctic Ocean and Resources Variability*. Springer-Verlag. Berlin, Heidelberg

NOJI TT, Estep KW, MacIntyre F, Norrbin F (1991) Image analysis of faecal material grazed upon by three species of copepods: evidence for coprohexy, coprophagy and coprochaly. *Journal of the Marine Biological Association of the United Kingdom* 71: 465-480

NOJI TT, Bathmann UV, von Bodungen B, Voss M, Antia A, Krumbholz M, Klein B, Peeken I, Noji CIM, Rey F (1997) Clearance of picoplankton-sized particles and formation of rapidly sinking aggregates by the pteropod, *Limacina retroversa*. *Journal of Plankton Research* 19: 863-875

NOWLIN WD, Whitworth T, Pillsbury RB (1977) Structure and transport of the Antarctic Circumpolar Current at the Drake Passage from short-term measurements. *Journal of Physical Oceanography* 7: 788-802

NOWLIN WD Jr, Klinck JM (1986) The physics of the Antarctic Circumpolar Current. *Revised Geophysics* 24: 469-491

ØRESLAND V (1990) Feeding and predation impact of the chaetognath *Eukrohnia hamata* and the copepod *Euchaeta antarctica* in Gerlache Strait, Antarctic Peninsula. *Marine Ecology Progress Series* 119: 77-86

ØRESLAND V, Ward P (1993) Summer and winter diet of four carnivorous copepod species around South Georgia. *Marine Ecology Progress Series* 98: 73-78

ORR JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar G, Plattner G-K, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig M-F, Yamanaka Y, Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437: 681-686

PAFFENHÖFER GA, Knowles SC (1979) Ecological implications of faecal pellet size, production and consumption by copepods. *Journal of Marine Research* 37: 35-49

PAKHOMOV EA, Perissinotto R, McQuaid CD (1994) Comparative structure of the macrozooplankton / micronekton communities of the Subtropical and Antarctic Polar Fronts. *Marine Ecology Progress Series* 111: 155-169

PAKHOMOV EA, McQuaid CD (1996) Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biology* 16: 271-286

PAKHOMOV EA, Perissinotto R (1996) Trophodynamics of the hyperiid amphipod *Themisto gaudichaudi* in the South Georgia region during late austral summer. *Marine Ecology Progress Series* 134: 91-100

PAKHOMOV EA, Perissinotto R, McQuaid CD (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Marine Ecology Progress Series* 134: 1-14

PAKHOMOV EA, Verheye HM, Atkinson A, Laubscher RK, Taunton-Clark J (1997) Structure and grazing impact of the mesozooplankton community during late summer 1994 near South Georgia, Antarctica. *Polar Biology* 18: 180-192

PAKHOMOV EA, Perissinotto R (1997) Mesozooplankton community structure and grazing impact in the region of the Subtropical Convergence south of Africa. *Journal of Plankton Research* 19: 675-691

PAKHOMOV EA, Froneman PW, Ansorge I (1998) Prince Edward Island Offshore oceanographic study: a report on research cruise April/May 1997. *South African Journal of Science* 94: 153-157

PAKHOMOV EA, Froneman PW (1999a) The Prince Edward Islands pelagic ecosystem, Southern Ocean: a review of achievements. *Journal of Marine Systems* 18: 355-367

PAKHOMOV EA, Froneman PW (1999b) Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean). *Marine Biology* 134: 501-515

PAKHOMOV EA, Perissinotto R, Froneman PW (1999) Predation impact of carnivorous macrozooplankton and micronekton in the Atlantic sector of the Southern Ocean. *Journal of Marine Systems* 19: 47-64

PAKHOMOV EA, Froneman PW (2000) Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone of the Indian Ocean during austral autumn 1997. *Polar Biology* 23: 410-419

PAKHOMOV EA, Perissinotto R, McQuaid CD and Froneman PW (2000a) Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993. Part I. Ecological zonation. *Deep-Sea Research I* 47: 1663-1686

PAKHOMOV EA, Froneman PW, Ansorge IJ, Lutjeharms JRE (2000b) Temporal variability in the physico-biological environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* 26: 75-95

PAKHOMOV EA, Ansorge IJ, Froneman PW (2000c) Variability in the inter-island environment of the Prince Edward Islands (Southern Ocean). *Polar Biology* 23: 593-603

PAKHOMOV EA, Ratkova T, Froneman PW, Wassmann P (2001) Phytoplankton dynamics at the ice-edge zone of the Lazarev Sea (Southern Ocean) during the austral summer 1994/1995 drogue study. *Polar Biology* 24: 422-431

PAKHOMOV EA, Froneman PW, Perissinotto R (2002) Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. *Deep-Sea Research II* 49: 1881-1907

PAKHOMOV EA, Froneman PW (2004a) Zooplankton dynamics in the eastern Atlantic sector of the Southern Ocean during the austral summer 1997/1998. Part 1. Community structure. *Deep-Sea Research II* 51: 2599-2616

PAKHOMOV EA, Froneman PW (2004b) Zooplankton dynamics in the eastern Atlantic sector of the Southern Ocean during the austral summer 1997/1998. Part 2. Grazing impact. *Deep-Sea Research II* 51: 2617-2631

PASTERNAK AF (1994) Gut fluorescence in herbivorous copepods: an attempt to justify the method. *Hydrobiologia* 292/293: 241-248

PERISSINOTTO R, Boden BP (1989) Zooplankton-phytoplankton relationships at the Prince Edward Islands during April/May 1985-1986. *South African Journal of Antarctic Research* 19: 26-30

PERISSINOTTO R, Allanson BR, Boden BP (1990a) Trophic relations within the island seas of the Prince Edward archipelago, Southern Ocean. In Barnes M, Gibson RN (Eds) *Proceedings to the 24th European Marine Biology Symposium*. Aberdeen University Press. UK

PERISSINOTTO R, Duncombe Rae CM, Boden BP, Allanson BR (1990b) Vertical stability as a controlling factor of the marine phytoplankton production at the Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series* 60: 205-209

PERISSINOTTO R and Duncombe Rae CM (1990) Occurrence of anticyclonic eddies on the Prince Edward Plateau (Southern Ocean): effects on phytoplankton biomass and production. *Deep-Sea Research* 37: 777-793

PERISSINOTTO R (1992) Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of the Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series* 79: 243-258

PERISSINOTTO R, McQuaid CD (1992) Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. *Marine Ecology Progress Series* 80: 15-27

PERISSINOTTO R, Pakhomov EA, Froneman PW, Laubscher RK (1996) *The Antarctic marine ecosystem and global climate change: climate change and the oceanic carbon cycle*. South African National Antarctic Research Programme (SANARP), Final Project Report. FRD-CSIR, Pretoria, South Africa. Pages 1-35

PERISSINOTTO R, Pakhomov EA (1997) Feeding association of the copepod *Rhincalanus gigas* with the tunicate *Salpa thompsoni* in the Southern Ocean. *Marine Biology* 127: 469-483

PERISSINOTTO R, Pakhomov EA (1998a) Contribution of salps to carbon flux of marginal ice zone of the Lazarev Sea, southern ocean. *Marine Biology* 131: 25-32

PERISSINOTTO R, Pakhomov EA (1998b) The trophic role of the tunicate *Salpa thompsoni* in the Antarctic marine ecosystem. *Journal of Marine Systems* 17: 361-374

PERISSINOTTO R, Lutjeharms JRE, van Ballegooyen RC (2000) Biological-physical interactions and pelagic productivity at the Prince Edward Islands, Southern Ocean. *Journal of Marine Systems* 24: 327-341

PRIDDLE J (1990) Antarctic planktonic ecosystem. In Mullins BM, Priddle J (Eds) *Polar Marine Diatoms*. Cambridge British Antarctic Survey. Natural Environmental Research Council. Cambridge, pp. 25-34

PRIMER-E, Ltd. (2001). PRIMER 5 for Windows (version 5.2.4)

PUSCH C, Hulley PA, Kock K-H (2004) Community structure and feeding ecology of mesopelagic fishes in the slope waters of King George Island (South Shetland Islands, Antarctica). *Deep-Sea Research I* 51: 1685-1708

RAZOULS S, Koubbi P, Mayzaud P (1996) Spatio-temporal distribution of mesozooplankton in a sub-Antarctic coastal basin of the Kerguelen Archipelago (southern Indian Ocean). *Polar Biology* 16: 581-587

RAZOULS S, Du Réau G, Guillot P, Maison J, Jeandel C (1998) Seasonal abundance of copepod assemblages and grazing pressure in the Kerguelen Island area (Southern Ocean). *Journal of Plankton Research* 20: 1599-1614

RIVKIN RB, Legendre L (2002) Roles of food web and heterotrophic microbial processes in upper ocean biogeochemistry: Global patterns and processes. *Ecological Research* 17: 151-159

ROBERTSON AA, Alexander DGW, Miller DGM (1981) Modified collapsible opening and closing midwater trawls (RMT-8 and RMT-20). *Fisheries Bulletin of South Africa* 14: 103-113

SABINE CL, Feely RA, Gruber N, Key RM, Lee K, Bullister JL, Wanninkhof R, Wong CS, Wallace DWR, Tilbrook B, Millero FJ, Peng T-H, Kozyr A, Ono T, Rios AF (2004) The oceanic sink for anthropogenic CO_2. *Science* 305: 367-371

SAGGIOMO V, Carrada GC, Mangoni O, Ribera d'Alcalà M, Russo A (1998) Spatial and temporal variability of size-fractionated biomass and primary production in the Ross Sea (Antarctica) during austral spring and summer. *Journal of Marine Systems* 17: 115-127

SAMEOTO DD (1988) Feeding of lantern fish *Benthosema glaciale* off the Nova Scotia Shelf. *Marine Ecology Progress Series* 44: 113-129

SARMIENTO JL, Monfray P, Maier-Reimer E, Aumount O, Murmane RJ, Orr JC (2000) Sea-air CO_2 fluxes and carbon transport: A comparison of three ocean general circulation models. *Global Biogeochemical Cycles* 14: 1267-1281

SEIBEL BA, Dierssen HM (2003) Cascading trophic impacts of reduced biomass in the Ross Sea, Antarctica: Just the tip of the iceberg? *Biological Bulletin* 205: 93-97

SHERR B, Sherr B (1988) Role of microbes in pelagic food webs: a revised concept. *Limnology and Oceanography* 33: 1225-1227

SIEGEL V, Piatkowski U (1990) Variability in the Macrozooplankton community of the Antarctic Peninsula. *Polar Biology* 10: 373-386

SMETACEK V, de Bar HJW, Bathmann UV, Lochte K, Rutgers van der Loeff MM (1997) Ecology and biogeochemistry of the Antarctic Circumpolar Current during austral spring: a summary of Southern Ocean JGOFS cruise ANT X/6 of RV Polarstern. *Deep-Sea Research II* 44: 1-21

STATSOFT INC. (2004) STATISTICA (data analysis software system), version 7. www.statsoft.com

TARLING GA, Ward P, Sheader M, Williams JA, Symon C (1995) Distribution patterns of the macrozooplankton assemblages in the southwest Atlantic. *Marine Ecology Progress Series* 120: 29-40

TOMCZAK M, Godfrey JS (1994) *Regional oceanography: An introduction.* Pergamon, Elsevier Science Ltd., UK

TREMBLAY JE, Lucas MI, Kattner G, Pollard R, Strass, VH, Bathmann U, Bracher A (2002) Significance of the Polar Frontal Zone for large-sized diatoms and new production during summer in the Atlantic sector of the Southern Ocean. *Deep-Sea Research II* 49: 3793-3881

URBAN-RICH J, Dagg M, Peterson J (2001) Copepod grazing on phytoplankton in the Pacific sector of the Antarctic Polar Front. *Deep-Sea Research II* 48: 4223-4246

VALENTINE HR, Lutjeharms JRE (1983) Oceanic thermal fronts in the Southern Ocean. *CSIR Research Report* 558. CSIR, Stellenbosch

VAN LEEUWE MA, de Baar HJW, Veldhuis MJW (1998) Pigment distribution in the Pacific region of the Southern Ocean (autumn 1995). *Polar Biology* 19: 348-353

VORONINA NM (1984) *Pelagic ecosystems of the Southern Ocean*. Nauka Press, Moscow. Pages 1-206

VORONINA NM, Kosobokova KN, Pakhomov EA (1994) Composition and biomass of summer metazoan plankton in the 0-200m layer of the Atlantic sector of the Antarctic. *Polar Biology* 14: 91-95

VORONINA NM (1998) Comparative abundance and distribution of major filter-feeders in the Antarctic pelagic zone. *Journal of Marine Systems* 17: 375-390

WARD P, Atkinson A, Murray AWA, Wood AG, Williams R, Poulet SA (1995) The summer zooplankton community at South Georgia: biomass, vertical migrations and grazing. *Polar Biology* 15: 195-208

WARD P, Whitehouse M, Meredith M, Murphy E, Shreeve R, Korb R, Watkins J, Thorpe S, Woodd-Walker R, Brierley A, Cunningham N, Grant S, Bone D (2002) The Southern Antarctic Circumpolar Current Front: physical and biological coupling at South Georgia. *Deep-Sea Research I* 49: 2183-2202

WARD P, Whitehouse M, Brandon M, Shreeve R, Woodd-Walker R (2003) Mesozooplankton community structure across the Antarctic Circumpolar Current to the north of South Georgia: Southern Ocean. *Marine Biology* 143: 121-130

WARD P, Grant S, Brandon M, Siegel V, Sushin V, Loeb V, Griffiths H (2004) Mesozooplankton community structure in the Scotia Sea during the CCAMLR 2000 survey: January-February 2000. *Deep-Sea Research II* 51: 1351-1367

WARD P, Shreeve R, Whitehouse M, Korb B, Atkinson A, Meredith M, Pond D, Watkins J, Goss C, Cunningham N (2005) Phyto- and zooplankton community structure and production around South Georgia (Southern Ocean) during Summer 2001/02. *Deep-Sea Research I* 52: 421-441

XIUREN N, Zilin L, Genhai Z, Junxian S (1996) Size-fractionated biomass and productivity of phytoplankton and particulate carbon in the Southern Ocean. Polar *Biology* 16: 1-11

YOON W, Kim S, Han K (2001) Morphology and sinking velocities of fecal pellets of copepod, molluscan, euphausiid, and salp taxa in the northeastern tropical Atlantic. *Marine Biology* 139: 923-928

APPENDIX

Table A.1 Station details for the MIOS II voyage to the Prince Edward Archipelago, April 1997.

Station number	Date (m/d/y)	Time (GMT)	Latitude (ºN)	Longitude (ºE)	Temp. ºC	Net type	Mesh size (µm)
1	04/30/97	17:43:00	-47.307	37.003	8.41	Bongo	300
2	04/30/97	20:08:00	-46.966	36.995	6.48	Bongo	300
3	04/30/97	22:37:00	-46.657	37.001	6.86	Bongo	300
4	05/01/97	0:45:00	-46.344	36.999	6.74	Bongo	300
5	05/01/97	2:48:00	-46.045	37.001	7.89	Bongo	300
6	05/01/97	4:57:00	-46.197	37.244	7.53	Bongo	300
8	05/01/97	6:11:00	-46.387	37.486	7.41	Bongo	300
9	05/01/97	16:45:00	-46.727	37.962	6.89	Bongo	300
14	05/02/97	15:59:00	-46.684	38.246	6.78	Bongo	300
16	05/03/97	15:58:00	-47.088	37.885	6.69	Bongo	300
17	05/03/97	18:46:00	-46.918	37.955	6.70	Bongo	300
18	05/03/97	20:25:00	-46.784	37.973	6.65	Bongo	300
19	05/03/97	22:10:00	-46.687	30.040	6.59	Bongo	300
20	05/03/97	0:00:00	-46.559	30.100	6.58	Bongo	300
21	05/04/97	3:03:00	-46.758	37.832	6.58	Bongo	300
22	05/04/97	15:52:00	-46.918	38.536	6.44	Bongo	300
23	05/04/97	17:28:00	-46.875	38.334	5.87	Bongo	300
24	05/04/97	20:16:00	-46.846	38.196	6.20	Bongo	300
25	05/04/97	21:55:00	-46.806	37.992	6.44	Bongo	300
26	05/04/97	23:12:00	-46.767	37.809	6.76	Bongo	300
27	05/05/97	0:19:00	-46.735	37.664	6.79	Bongo	300
28	05/05/97	2:00:00	-46.688	37.431	6.59	Bongo	300

Table A.2 Station details for the MIOS IV voyage to the Prince Edward Archipelago, April 1999.

Station number	Date (m/d/y)	Time (GMT)	Latitude (ºN)	Longitude (ºE)	Temp. ºC	Net type	Mesh size (µm)
1	04/05/99	18:12	-46.50	37.01	8.68	Bongo	300
2	04/05/99	19:50	-46.50	37.07	8.60	Bongo	300
3	04/05/99	20:40	-49.38	37.03	8.68	Bongo	300
4	04/05/99	23:06	-46.50	37.31	8.74	Bongo	300
5	04/06/99	19:57	-47.33	37.16	7.23	Bongo	300
6	04/07/99	22:05	-47.17	37.18	7.06	Bongo	300
7	04/07/99	23:00	-47.06	37.13	7.15	Bongo	300
8	04/07/99	22:17	-46.82	38.06	7.91	Bongo	300
9	04/08/99	17:24	-46.88	38.32	7.50	Bongo	300
10	04/08/99	19:07	-46.89	38.14	7.49	Bongo	300
11	04/08/99	20:40	-46.81	38.00	8.00	Bongo	300
12	04/08/99	21:39	-46.76	37.87	7.80	Bongo	300
13	04/08/99	22:47	-46.75	37.72	8.11	Bongo	300
14	04/09/99	1:18	-46.59	38.09	7.39	Bongo	300
15	04/09/99	2:00	-46.71	38.05	7.46	Bongo	300
16	04/09/99	16:42	-46.92	37.99	7.55	Bongo	300
17	04/09/99	18:20	-47.00	37.92	6.95	Bongo	300
33	04/26/99	14:24	-46.85	38.08	6.27	Bongo	300
34	04/26/99	17:50	-46.84	38.17	6.14	Bongo	300
35	04/25/99	20:27	-46.73	38.25	6.14	Bongo	300
36	04/26/99	21:10	-46.69	38.30	6.00	Bongo	300
37	04/26/99	22:10	-46.71	38.24	6.12	Bongo	300
38	04/27/99	0:45	-46.75	38.13	6.19	Bongo	300
39	04/27/99	2:18	-46.74	38.20	6.12	Bongo	300
40	04/27/99	4:49	-46.75	38.13	6.20	Bongo	300
42	04/27/99	8:22	-46.75	38.13	6.29	Bongo	300
43	04/27/99	17:45	-46.72	38.04	6.56	Bongo	300
44	04/27/99	19:16	-46.74	37.90	6.31	Bongo	300
45	04/27/99	20:13	-46.81	37.94	6.56	Bongo	300
50	04/28/99	18:17	-46.73	37.81	6.40	Bongo	300
51	04/28/99	19:26	-46.67	37.76	6.12	Bongo	300
52	04/28/99	20:34	-46.70	37.67	6.35	Bongo	300
53	04/28/99	21:50	-46.72	37.71	6.38	Bongo	300
54	04/28/99	23:24	-46.80	37.87	6.58	Bongo	300

Table A.3 Station details for point A of the MIOS V voyage to the Prince Edward Archipelago, April 2000.

Station number	Date (m/d/y)	Time (GMT)	Latitude (ºN)	Longitude (ºE)	Temp. ºC	Net type	Mesh size (µm)
9	04/10/2000	19:10	-46.79	37.93	6.44	Bongo	300
10	04/10/2000	19:35	-46.80	37.91	6.46	Bongo	300
15	04/11/2000	18:07	-46.79	37.93	6.42	Bongo	300
16	04/11/2000	18:32	-46.78	37.92	6.54	Bongo	300
20	04/12/2000	18:44	-46.78	37.91	6.55	Bongo	300
21	04/12/2000	19:03	-46.79	37.93	6.56	Bongo	300
27	04/13/2000	17:56	-46.79	37.92	6.59	Bongo	300
28	04/13/2000	18:17	-46.78	37.91	6.53	Bongo	300
32	04/14/2000	17:45	-46.79	37.93	6.40	Bongo	300
33	04/14/2000	18:01	-46.79	37.91	6.41	Bongo	300
35	04/15/2000	19:51	-46.80	37.93	6.42	Bongo	300
36	04/15/2000	20:10	-46.79	37.91	6.46	Bongo	300
44	04/16/2000	18:59	-46.80	37.94	6.36	Bongo	300
45	04/16/2000	19:16	-46.79	37.93	6.20	Bongo	300
48	04/17/2000	18:13	-46.80	37.94	6.22	Bongo	300
49	04/17/2000	18:31	-46.80	37.93	6.17	Bongo	300
56	04/18/2000	17:57	-46.80	37.93	6.26	Bongo	300
57	04/18/2000	18:13	-46.79	37.93	6.37	Bongo	300
60	04/19/2000	18:07	-46.79	37.93	6.23	Bongo	300
61	04/19/2000	18:24	-46.78	37.92	6.21	Bongo	300
65	04/20/2000	17:40	-46.80	37.93	6.04	Bongo	300
66	04/20/2000	17:59	-46.80	37.92	5.95	Bongo	300
69	04/21/2000	17:47	-46.80	37.92	6.11	Bongo	300
70	04/21/2000	18:05	-46.79	37.92	6.12	Bongo	300
75	04/22/2000	17:43	-46.80	37.93	6.29	Bongo	300
76	04/22/2000	18:02	-46.79	37.93	6.35	Bongo	300
81	04/23/2000	17:55	-46.80	37.92	6.17	Bongo	300
82	04/23/2000	18:14	-46.79	37.93	6.20	Bongo	300
86	04/24/2000	17:50	-46.80	37.92	6.13	Bongo	300
87	04/24/2000	18:06	-46.79	37.91	6.13	Bongo	300
90	04/25/2000	17:56	-46.79	37.92	6.45	Bongo	300
91	04/25/2000	18:15	-46.79	37.91	6.45	Bongo	300
95	04/26/2000	17:41	-46.78	37.92	6.25	Bongo	300
96	04/26/2000	18:01	-46.79	37.93	6.30	Bongo	300
99	04/27/2000	17:50	-46.78	37.92	6.23	Bongo	300
100	04/27/2000	18:10	-46.78	37.91	6.27	Bongo	300

Table A.4 Station details for point B of the MIOS V voyage to the Prince Edward Archipelago, April 2000.

Station number	Date (m/d/y)	Time (GMT)	Latitude (ºN)	Longitude (ºE)	Temp. ºC	Net type	Mesh size (µm)
7	04/10/2000	17:24	-46.92	37.96	6.16	Bongo	300
8	04/10/2000	17:47	-46.94	37.94	6.26	Bongo	300
13	04/11/2000	16:16	-46.93	37.96	6.17	Bongo	300
14	04/11/2000	16:41	-46.94	37.94	6.21	Bongo	300
18	04/12/2000	17:00	-46.92	37.96	6.31	Bongo	300
19	04/12/2000	17:26	-46.91	37.97	6.25	Bongo	300
25	04/13/2000	16:21	-46.93	37.96	6.25	Bongo	300
26	04/13/2000	16:40	-46.92	37.96	6.59	Bongo	300
30	04/14/2000	16:11	-46.94	37.95	6.20	Bongo	300
31	04/14/2000	16:33	-46.92	37.96	6.17	Bongo	300
34	04/14/2000	19:22	-46.76	37.83	6.46	Bongo	300
38	04/15/2000	22:02	-46.95	37.97	6.13	Bongo	300
39	04/15/2000	22:20	-46.94	37.96	6.10	Bongo	300
42	04/16/2000	17:29	-46.92	37.97	6.09	Bongo	300
43	04/16/2000	17:49	-46.91	37.96	6.16	Bongo	300
46	04/17/2000	16:34	-46.92	37.97	6.09	Bongo	300
47	04/17/2000	16:50	-46.93	37.96	6.11	Bongo	300
54	04/18/2000	16:23	-46.92	37.97	5.97	Bongo	300
55	04/18/2000	16:40	-46.93	37.96	5.86	Bongo	300
58	04/19/2000	16:33	-46.93	37.94	6.20	Bongo	300
59	04/19/2000	16:54	-46.92	37.95	6.01	Bongo	300
63	04/20/2000	16:25	-46.92	37.95	6.14	Bongo	300
64	04/20/2000	16:42	-46.91	37.96	6.17	Bongo	300
67	04/21/2000	16:43	-46.92	37.96	6.21	Bongo	300
73	04/22/2000	16:15	-46.93	37.95	6.27	Bongo	300
74	04/22/2000	16:34	-46.92	37.96	6.19	Bongo	300
79	04/23/2000	16:16	-46.93	37.95	6.59	Bongo	300
80	04/23/2000	16:36	-46.92	37.96	6.48	Bongo	300
84	04/24/2000	16:13	-46.94	37.95	6.45	Bongo	300
85	04/24/2000	16:30	-46.92	37.95	6.49	Bongo	300
88	04/25/2000	16:13	-46.92	37.95	6.52	Bongo	300
89	04/25/2000	16:31	-46.94	37.95	6.55	Bongo	300
93	04/26/2000	16:13	-46.94	37.95	6.31	Bongo	300
94	04/26/2000	16:30	-46.93	37.95	6.33	Bongo	300
97	04/27/2000	16:13	-46.92	37.96	6.18	Bongo	300
98	04/27/2000	16:29	-46.92	37.96	6.22	Bongo	300

Table A.5 Station details for the MOEVS I voyage to the Polar Frontal Zone, April 2001.

Station number	Date (m/d/y)	Time (GMT)	Latitude (ºN)	Longitude (ºE)	Temp. ºC	Net type	Mesh size (µm)
B01187099	04/18/2001	7:15	-49.53	32.56	4.43	Bongo	200
B01188099	04/18/2001	13:55	-49.05	33.00	4.10	Bongo	200
B01189099	04/18/2001	18:20	-48.15	33.00	5.37	Bongo	200
B01190099	04/18/2001	22:35	-47.25	32.59	7.73	Bongo	200
B01191099	04/19/2001	2:58	-46.35	32.59	8.57	Bongo	200
B01192099	04/19/2001	7:06	-46.34	34.14	8.34	Bongo	200
B01193099	04/19/2001	11:18	-47.25	34.15	8.44	Bongo	200
B01194099	04/19/2001	15:30	-48.14	34.15	6.70	Bongo	200
B01195099	04/19/2001	20:09	-49.05	34.15	3.99	Bongo	200
B01196099	04/22/2001	12:17	-49.54	34.15	4.14	Bongo	200
B01197099	04/22/2001	17:23	-49.54	35.30	4.20	Bongo	200
B01198099	04/22/2001	22:26	-49.04	35.29	4.33	Bongo	200
B01199099	04/23/2001	3:04	-48.15	35.30	7.27	Bongo	200
B01200099	04/23/2001	7:01	-47.24	35.30	7.60	Bongo	200
B01201099	04/23/2001	11:00	-46.34	35.29	7.61	Bongo	200
B01202099	04/23/2001	15:25	-46.34	36.44	6.82	Bongo	200
B01203099	04/23/2001	20:14	-47.24	36.45	6.00	Bongo	200
B01204099	04/24/2001	0:35	-48.14	36.44	4.92	Bongo	200
B01205099	04/24/2001	4:57	-49.04	36.44	5.40	Bongo	200
B01206099	04/24/2001	9:58	-49.55	36.46	5.38	Bongo	200
B01207099	04/24/2001	13:43	-49.54	38.00	5.37	Bongo	200
B01208099	04/24/2001	17:57	-49.04	37.59	5.33	Bongo	200
B01209099	04/25/2001	0:55	-48.15	38.00	5.76	Bongo	200
B01210099	04/25/2001	7:37	-47.25	38.00	5.96	Bongo	200
B01211099	04/25/2001	11:48	-46.34	37.59	6.38	Bongo	200

Table A.6 Station details for the MOEVS II voyage to the Polar Frontal Zone, April 2002.

Station number	Date (m/d/y)	Time (GMT)	Latitude (ºN)	Longitude (ºE)	Temp. ºC	Net type	Mesh size (µm)
11	04/08/02	1:25	-49.75	29.50	6.20	WP2	200
13	04/08/02	7:15	-50.25	29.50	5.43	WP2	200
15	04/08/02	13:20	-50.82	29.52	5.01	WP2	200
17	04/08/02	16:13	-51.25	29.50	3.80	WP2	200
19	04/08/02	20:25	-51.75	29.48	3.60	WP2	200
23	04/09/02	6:00	-51.29	30.01	6.10	WP2	200
36	04/11/02	11:15	-49.52	30.74	6.57	WP2	200
39	04/12/02	5:11	-50.25	30.79	5.90	WP2	200
41	04/12/02	10:05	-50.75	30.75	4.47	WP2	200
43	04/12/02	15:13	-51.25	30.75	3.30	WP2	200
60	04/14/02	6:00	-48.98	32.31	4.00	WP2	200
62	04/14/02	11:19	-49.46	32.20	5.10	WP2	200
65	04/14/02	18:46	-50.25	32.27	4.80	WP2	200

Table A.7 Station details for the MOEVS IV voyage to the Polar Frontal Zone, April 2004.

Station number	Date (m/d/y)	Time (GMT)	Latitude (ºN)	Longitude (ºE)	Temp. ºC	Net type	Mesh size (µm)
228	04/15/2004	01:16	-49.99	31.06	4.05	Bongo	200
229	04/15/2004	06:20	-49.50	31.02	4.48	Bongo	200
231	04/15/2004	17:11	-48.49	31.00	4.58	Bongo	200
234	04/16/2004	06:18	-48.01	32.30	4.28	Bongo	200
236	04/16/2004	16:58	-48.67	31.17	4.46	Bongo	200
237	04/16/2004	21:37	-48.99	30.64	5.20	Bongo	200
238	04/17/2004	02:36	-49.33	30.09	7.40	Bongo	200
239	04/17/2004	07:20	-49.67	29.53	6.53	Bongo	200
240	04/17/2004	12:03	-50.00	29.00	5.27	Bongo	200
241	04/17/2004	19:54	-49.01	29.23	7.37	Bongo	200
242	04/17/2004	00:34	-49.00	29.98	7.61	Bongo	200
243	04/18/2004	05:27	-48.98	30.75	4.98	Bongo	200
244	04/18/2004	10:20	-49.00	31.53	4.82	Bongo	200
248	04/20/2004	07:31	-48.02	30.01	8.47	Bongo	200
251	04/21/2004	14:30	-49.12	31.47	4.38	Bongo	200
256	04/23/2004	10:56	-49.85	32.45	3.76	Bongo	200

Table A.8 Station details for the MOEVS V voyage to the Polar Frontal Zone, April 2005.

Station number	Date (m/d/y)	Time (GMT)	Latitude (ºN)	Longitude (ºE)	Temp. ºC	Net type	Mesh size (µm)
259	04/16/05	05:51	-49.33	31.03	3.40	WP2	200
260	04/16/05	16:58	-49.14	32.60	3.50	WP2	200
261	04/16/05	23:08	-48.80	33.22	3.30	WP2	200
262	04/17/05	06:43	-48.46	33.62	4.20	WP2	200
263	04/17/05	11:24	-48.12	34.15	5.30	WP2	200
264	04/17/05	18:07	-47.79	34.75	5.20	WP2	200
265	04/18/05	04:50	-47.77	33.01	6.20	WP2	200
266	04/18/05	10:15	-48.02	33.44	5.90	WP2	200
267	04/18/05	14:38	-48.54	34.05	6.30	WP2	200
268	04/18/05	22:08	-48.88	34.08	5.00	WP2	200
269	04/19/05	03:31	-49.32	34.65	3.30	WP2	200
270	04/19/05	08:43	-49.75	35.08	2.40	WP2	200
271	04/19/05	13:59	-49.93	35.37	3.80	WP2	200
272	04/19/05	18:03	-49.41	35.38	2.80	WP2	200
273	04/19/05	23:19	-48.91	35.32	5.50	WP2	200
274	04/20/05	05:59	-48.57	35.08	4.70	WP2	200
275	04/20/05	13:32	-48.09	35.04	6.20	WP2	200
276	04/20/05	19:12	-48.36	34.78	3.90	WP2	200
277	04/21/05	00:08	-48.63	34.47	4.10	WP2	200
278	04/21/05	04:38	-48.91	34.11	4.10	WP2	200
279	04/21/05	09:38	-49.16	33.95	5.60	WP2	200
280	04/21/05	14:34	-49.67	34.01	4.70	WP2	200
282	04/22/05	01:18	-48.77	33.58	3.80	WP2	200
283	04/22/05	06:10	-48.76	33.98	5.10	WP2	200
284	04/22/05	11:11	-48.73	34.53	4.90	WP2	200
285	04/22/05	15:10	-48.75	35.03	5.00	WP2	200
286	04/22/05	19:06	-48.78	35.49	2.30	WP2	200
287	04/23/05	01:46	-48.45	35.75	2.40	WP2	200
288	04/23/05	04:47	-48.13	35.92	2.80	WP2	200
290	04/23/05	13:55	-48.77	36.20	6.40	WP2	200
291	04/24/05	09:00	-48.94	36.34	0.60	WP2	200

Table A.9 Regression equations used to estimate average daily individual ingestion rates for the four dominant copepods and *L. retroversa*, during MOEVS V.

Taxon	Equation
Calanus simillimus	$y = 705.668 - 15.9723 * x$ ($p > 0.05$)
Oithona similis	$y = 166.4085 + 1.4623 * x$ ($p > 0.05$)
Clausocalanus spp.	$y = 439.8211 - 10.5155 * x$ ($p > 0.05$)
Ctenocalanus spp.	$y = 276.9065 - 1.5299 * x$ ($p > 0.05$)
Limacina retroversa	$y = 4\ 231.9551 - 4.4327 * x$ ($p > 0.05$)

y = individual daily ingestion rate

x = integrated chl-*a* concentration