MESOZOOPLANKTON COMMUNITY STRUCTURE AND GRAZING IMPACT IN THE POLAR FRONTAL ZONE OF THE SOUTHERN OCEAN

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ABSTRACT

Mesozooplankton community structure and grazing impact in the Polar Frontal Zone (PFZ) of the Southern Ocean were investigated during two cruises of the South African National Antarctic Programme (SANAP), the Marion Offshore Ecosystem Variability Study I & II (MOEVS).

During the first cruise (MOEVS I), a meso-scale oceanographic grid survey was conducted in the upstream region of the Prince Edward Islands (PEI) in austral autumn (April) 2001. Mesozooplankton samples, collected using a Bongo net (fitted with 200 and 300?m mesh nets) at depths between 200 and 300 m, were separated into three size fractions: 200-500 ?m; 500-1000 ?m; 1000-2000 ?m by reverse filtration. Total surface (depth <5 m) chlorophyll-*a* (chl-*a*) concentration (measured fluorometrically) during the study ranged between 0.11 and 0.34 ?g l^{-1} and was always dominated by picophytoplankton (<2.0 ?m). Total mesozooplankton abundance and biomass during the survey ranged between 49 and 1512 ind. m^{-3} and between 0.7 and 25 mg Dwt. m^{-3}, respectively. Throughout the survey, the 200-500 ?m class numerically dominated the mesozooplankton community, comprising an average of ~ 69% (SD = ? 12.3%). The dominant species in the 200-500 ?m size fraction were the copepods *Oithona similis, Calanus simillimus* and *Metridia lucens* and the pteropod, *Limacina retroversa*. However, in terms of biomass, the 1000-2000 ?m group was predominant, with dry weight values constituting an average of ~ 66% (SD = ? 10.2%). Biomass was dominated by carnivorous zooplankton, particularly the euphausiids, *Euphausia vallentini* and *Thysanoessa vicina* and the chaetognaths, *Sagitta gazellae* and *Eukrohnia hamata*. Three distinct groupings of stations were identified by multivariate analysis. The different station groupings identified reflect changes in the relative contributions of the dominant species rather than different species assemblages.

During the second cruise (MOEVS II), conducted in April 2002 (austral autumn), mesozooplankton community structure and grazing impact were investigated at 13 stations in the west Indian sector of the PFZ. Total integrated chl-*a* biomass ranged between 11.17 and 28.34 mg chl-*a* m^{-2} and was always dominated by nano- and picophytoplankton (<20 µm). Throughout the study, small copepods, mainly *Oithona similis* and *Ctenocalanus vanus*, numerically dominated the mesozooplankton community comprising up to 85% (range 30 to 85%) of the total abundance. Grazing activity of the four most abundant copepods (*O. similis*, *C. vanus*, *Calanus simillimus* and *Clausocalanus* spp.), which comprised up to 93% of total mesozooplankton abundance, was investigated using the gut fluorescent technique. Results of gut fluorescence analyses indicated that *C. simillimus*, *Clausocalanus* spp. and *Ctenocalanus vanus* exhibited diel variability in gut pigments, with maximum values at various stages of the night. In contrast, O. *similis* did not demonstrate diel variation in gut pigment contents. Ingestion rates of the four copepods ranged from 23.23 to 1462.02 ng (pigm.) ind^{-1} day^{-1}, depending on the species. The combined grazing impact of the four copepods, ranged between 1 and 36% of the phytoplankton standing stock per day, with the highest daily impact (~ 35.86%) occurring at stations in the vicinity of the Antarctic Polar Front. Among the copepods, *O. similis* and *C. vanus* were generally the most important consumers of phytoplankton biomass; together they were responsible for up to 89% (range 15 to 89%) of the total daily grazing impact. Carbon specific ingestion rates of the copepods varied between 42 and 320% body carbon per day, depending on the species.

The study highlights the importance of small copepods in terms of both their significant contribution to total mesozooplankton numbers and their grazing impact on the phytoplankton standing stocks in the PFZ during austral autumn.

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PREFACE

This work has been divided into two investigations:

1. The mesozooplankton community structure survey, conducted during the first Marion Offshore Ecosystem Variability Study (MOEVS I), April 2001.
2. The mesozooplankton grazing study, conducted during the second Marion Offshore Ecosystem Variability Study (MOEVS II), April 2002.

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DECLARATION

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

CHAPTER ONE: GENERAL INTRODUCTION

1.1. THE GLOBAL CARBON CYCLE: THE ROLE OF THE OCEANS

Increasing anthropogenic emissions of the greenhouse gases, such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), and their role in global warming are currently cause for great concern (Siegenthaler & Sarmiento 1993). The world's oceans act as a carbon pump by transporting carbon from the surface waters to the ocean bottom, through both physico-chemical (solubility pump) and biological (biological pump) processes (Longhurst 1991). The oceans represent the largest carbon reservoirs on earth, containing ~ 95% of the total circulating carbon within the biosphere, thereby controlling atmospheric CO_2 concentrations (Siegenthaler & Sarmiento 1993).

The biological pump involves the production of particulate and dissolved organic carbon (POC and DOC respectively) by marine organisms through the processes of: photosynthesis by phytoplankton; the sinking of dead/senescent cells and animal debris; and the grazing and migratory behaviour of zooplankton (Fig. 1.1.) (Longhurst 1991; Fortier et al. 1994; Falkowski et al. 1998). The overall effect of these biological processes is a reduction in the partial pressure of carbon dioxide (CO_2) in surface waters, thereby resulting in the draw-down of atmospheric CO_2, along a concentration gradient from the atmosphere to the surface water (Longhurst 1991; Siegenthaler & Sarmiento 1993). The rate of oceanic uptake of carbon via the biological pump is determined by the rate and magnitude of the downward flux of POC and DOC from surface waters to depth (Longhurst & Harrison 1989; Longhurst 1991). Within the biological pump, the sinking of dead/senescent phytoplankton cells (von Bodungen et al. 1986) and the feeding activity (herbivory or carnivory) of zooplankton (Longhurst & Harrison 1989; Longhurst 1991) represent the major pathways for the transfer of carbon to depth. The contribution of dead/senescent cells to total carbon flux is thought, however, only to be substantial in areas of dense phytoplankton blooms (Pakhomov et al. 2002) or during ice-melt, when algae trapped in sea ice is released en mass in summer as the ice melts (Fischer et al. 1988). Active grazing by zooplankton is, therefore, regarded as the most important mechanism for transporting carbon from the surface waters to depth (Longhurst 1991; Fortier et al. 1994).

The separation of phytogenic carbon between the two major pelagic food webs, namely the "microbial" and the "classical" food webs, determines the amount of carbon flux to depth, and thus the efficiency of the biological pump (Sherr & Sherr 1988; Longhurst 1991; Fortier et al. 1994; Froneman 1995). Macrozooplankton (>2000 ?m) produce large, dense faecal pellets, which have a relatively high carbon content and are fast-sinking (Fortier et al. 1994). For example, salp (tunicate) faecal pellets have a sinking rate of up to 2700 m d^{-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 contributes to carbon flux through respiration and egestion at depth (Fig. 1.1.) (Longhurst 1991; Fortier et al. 1994). In contrast, mesozooplankton (200–2000 ?m) produce relatively small, slow-sinking faecal pellets, with sinking rates of ~ 100 m d^{-1} (Fortier et al. 1994). In addition, copepods demonstrate coprophagy (re-ingestion of faecal pellets) and coprohexy (disintegration of faecal pellets), thereby greatly reducing the amount of faecal material that reaches the ocean bottom (Paffenhöfer & Knowles 1979; Lampitt et al. 1990; Noji et al. 1991). Mesozooplankton do, however, undergo diel vertical migrations, and in this way enhance their contribution to carbon flux through respiration and egestion at depth (Fig. 1.1.).

The microbial loop, comprising microheterotrophs (<200 ?m), phytoplankton and bacteria, contribute little to carbon flux. They generally produce mini-faecal pellets which remain in suspension for extended periods resulting in the majority of the carbon in the pellets being decomposed/ recycled by bacterioplankton in the euphotic zone (Azam et al. 1983). In addition, microheterotrophs generally have high assimilation efficiencies, which result in faecal pellets with a low carbon content. Finally, microheterotrophs do not undertake extensive diel migrations, still further restricting their role in the transport of carbon to depth (Fig. 1.1.).

It can be assumed, therefore, that in regions where macrozooplankton represent the most important consumers of phytoplankton, the efficiency of the biological pump will be high (Fortier et al. 1994). Carbon flux is reduced in regions where mesozooplankton represent the dominant consumers of phytoplankton production, and in a system dominated by microheterotrophs, it would be minimal (Fahnenstiel et al. 1995). The partitioning of carbon between large, intermediate and small heterotrophs is largely determined by the size structure of the phytoplankton assemblages. A notable exception is tunicates, which are able to consume particles in the size range 0.2 to 200 ?m (Fortier et al. 1994; Dubischar & Bathmann 1997; Pakhomov et al. 2002). Several studies in the Southern Ocean have demonstrated that microheterotrophs represent the dominant consumers of phytoplankton production in regions where small picophytoplankton (0.45 – 2.0 ?m) dominate total chlorophyll-*a* (chl-*a*) (Garrison et al. 1993; Lutjeharms et al. 1994; Burkill et al. 1995; Froneman 1995; Froneman et al. 1996; Froneman & Perissinotto 1996; Froneman et al. 1997). Omnivorous and herbivorous macrozooplankton, e.g. euphausiids, contribute the most to total grazing impact in regions where microphytoplankton (>20 ?m) dominate total chl-*a* (Gurney et al. 2002; Pakhomov et al. 2002). Under circumstances where nanophytoplankton dominate total chl-*a*, partitioning between the microheterotrophs and metazoans (mainly crustaceans) is broadly similar.

The size structure of phytoplankton cells in the Southern Ocean is highly seasonal (Laubscher et al. 1993). During the winter months, when there is a high degree of instability in the water column and low light availability, pico- and nanophytoplankton typically dominate total chl-*a* (Jacques 1989; Laubscher et al. 1993; Ansorge et al. 1999; Froneman et al. 1999). Micro- and mesozooplankton represent the dominant phytoplankton grazers during winter and it is likely that the carbon flux to depth would be minimal during this period (Froneman 1995; Froneman & Perissinotto 1996; Froneman et al. 1996; Pakhomov et al. 1997a). In contrast, during austral summer, the better light environment and reduced mixing (less wind activity), favour microphytoplankton, which make a more substantial contribution to total chl-*a* during this period. This is particularly true for those regions characterised by high water column stability, such as the waters surrounding oceanic islands, the vicinity of the fronts, the Marginal Ice Zone and the neritic waters of Antarctica (see below). Since macrozooplankton are efficient grazers of microphytoplankton, these will be regions of enhanced carbon flux. Data on the zooplankton community structure and grazing impacts, although important in improving our understanding of trophic interactions, are thus also fundamental to an understanding of the role of zooplankton in the oceanic carbon cycle (Froneman et al. 2000; Pakhomov et al. 2000).

1.2. THE SOUTHERN OCEAN: THE LARGEST CONTINUOUS BODY OF WATER ON EARTH

The Southern Ocean, covering an expanse of ~ 38 million km^2 of open ocean, is the largest continuous body of water on Earth, and is therefore likely to play a major role in the global carbon cycle (Tomczak & Godfrey 1994). The Southern Ocean is made up of the southern regions of the Indian, Pacific and Atlantic Oceans and includes the Ross, Weddell and Bellingshausen Seas among others. The southern boundary of the Southern Ocean is represented by the Antarctic continent and the northern boundary, although not geographically fixed, coincides with the location of the Subtropical Convergence (STC) (Lutjeharms 1985). Two major currents exist within the Southern Ocean, the "East Wind Drift", a narrow current bordering the Antarctic continent, and the "West Wind Drift", commonly referred to as the Antarctic Circumpolar Current (ACC) (Deacon 1937).

The ACC is made up of a series of cores of varying intensities (Nowlin et al. 1977; Hoffman & Whitworth 1985). The Polar Frontal Zone (PFZ), situated within the ACC, is bounded by two high-speed cores, namely the Sub-Antarctic Front (SAF), to the north, and the Antarctic Polar Front (APF), to the south (Emery 1977; Hoffman 1985) (Fig. 1.3.). Together these fronts are responsible for approximately 75% of the baroclinic transport within the ACC (Nowlin & Klink 1986). The two fronts are generally considered to be regions of steep meridional gradients of temperature, salinity and nutrients (Emery 1977; Deacon 1982; Lutjeharms 1985; Nowlin & Klinck 1986) and, therefore, 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 1999).

1.3. THE POLAR FRONTAL ZONE

The PFZ is a transition zone in which the surface waters are gradually altered from the warmer Sub-Antarctic Surface Waters (SASW) north of the SAF, to the colder 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 with time (Hoffman & Whitworth

1985) and is strongly affected by the local bathymetry (Nowlin & Klink 1986; Ansorge et al. 1999). The boundaries of the PFZ, the SAF and APF, demonstrate a high degree of 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 result in increased mixing of SASW and AASW within the PFZ, with foreign bodies of water intruding from the north and south as extensions of the SAF and APF, respectively (Perissinotto et al. 2000).

1.4. PHYTOPLANKTON IN THE PFZ

Phytoplankton biomass and productivity in the PFZ are closely correlated and exhibit a strong degree of spatial and temporal variability (Laubscher et al. 1993). The open waters of the PFZ typically exhibit low productivity year-round, with chl-*a* concentrations ranging from 0.12 to 0.42 mg (chl-*a*) m^{-3} (Smith & Nelson 1985; El-Sayed 1988; Jacques 1989; Laubscher et al. 1993; Froneman et al. 2001; Froneman et al. 2002b) and productivity ranging between 0.1 and 0.3 mg C m^{-2} day^{-1} (El-Sayed 1988; Jacques 1989; Comiso et al. 1993; Sullivan et al. 1993; Froneman et al. 2001). Enhanced levels of phytoplankton biomass (>1.5 mg Chl-*a* m^{-3}) and productivity (>1 g C m^{-2} day^{-1}) have, however, been documented during austral spring and summer in the vicinity of the major oceanic fronts (Allanson et al. 1981; Lutjeharms et al. 1985; El-Sayed 1988; Jacques 1983; Laubscher et al. 1993; Bradford-Grieve et al. 1997; Froneman et al. 1999; Froneman et al. 2001) and in the waters surrounding several sub-Antarctic oceanic islands (Perissinotto & Duncombe Rae 1990; El-Sayed & Jitts 1973; Mandelli & Burkholder 1966). Periodic phytoplankton blooms have also been recorded in the open waters of the PFZ (Froneman et al. 1995b). The factors responsible for an increase in phytoplankton biomass and productivity in these regions include increased water-column stability (Jacques 1989; Laubscher et al. 1993; Balarin 1999), the availability of trace metals (de Baar et al. 1995; Pakhomov & Froneman 1999), macronutrient availability (Jacques 1983; El-Sayed 1988; Pakhomov & Froneman 1999) and seawater temperature (Neori & Holm-Hansen 1982; Laubscher et al. 1993; Froneman et al. 2001).

Phytoplankton community size structure in the PFZ exhibits distinct spatial and temporal variability and is generally strongly linked to phytoplankton biomass and production (Laubscher et al. 1993; Froneman et al. 2001). In regions of enhanced phytoplankton biomass and productivity, (e.g. frontal regions and the waters surrounding oceanic islands), large microphytoplankton make a substantial contribution or dominate total phytoplankton biomass (El-Sayed 1988; Jacques 1989; Laubscher et al. 1993; Froneman & Pakhomov 2000; Froneman et al. 2001). In contrast, in the open waters of the PFZ where phytoplankton biomass and productivity are generally low, small nano- and picophytoplankton dominate chl-*a* biomass and production (Jacques 1989; Laubscher et al. 1993). The predominance of small phytoplankton cells in the open waters of the PFZ is thought to be due to a combination of low macronutrient availability and the high wind activities in the region, resulting in deep mixed layer depths (Laubscher et al. 1993; Balarin 1999; Froneman et al. 2001). Such conditions are particularly suited to the production of small pico- and nanophytoplankton cells, which, due to their large surface area: volume ratio, are capable of using available light and nutrients more efficiently than their larger counterparts (Fogg 1991).

It is important to note that during winter, when wind stress is high, production is almost entirely dominated by picophytoplankton throughout the PFZ (Ansorge et al. 1999; Froneman et al. 1999). Microphytoplankton assemblages are generally dominated by colonial and chain-forming diatoms, such as *Chaetoceros* spp. (Priddle 1990). Nanophytoplankton consist mostly of unicellular green flagellates and small diatoms (Jacques & Panouse 1991). Picophytoplankton communities are comprised of cyanobacteria and green flagellates (Knox 1994).

1.5. ZOOPLANKTON IN THE PFZ

1.5.1 COMMUNITY STRUCTURE

Most research on the zooplankton communities of the Southern Ocean and the grazing impacts of such communities has been restricted to regions of enhanced productivity and zooplankton biomass (e.g. Siegel & Piatkowski 1990; Tuker & Burton 1990; Boysen-Ennen et al. 1991; Perissinotto & McQuaid 1992; Siegel et al. 1992; Hopkins et al. 1993; Pakhomov 1993; Hosie 1994; Pakhomov et al. 1994; Pakhomov & Perissinotto 1997; Bathmann et al. 1993; Froneman et al. 1997; Perissinotto 1992; Atkinson 1994; Ward et al. 1995; Atkinson et al. 1996; Pakhomov et al. 1997; Froneman & Perissinotto 1996; Dubischar & Bathmann 1997).

The zooplankton community in the PFZ (specifically in the region of the sub-Antarctic Prince Edward Islands, see Fig. 1.3.) has been described on several occasions (Grindley & Lane 1979; Miller 1982; Boden & Parker 1986; Boden 1988; Perissinotto 1992; Froneman & Pakhomov 1998; Ansorge et al. 1999; Froneman et al. 1999; Pakhomov & Froneman 1999; Pakhomov et al. 2000 a, b; Perissinotto et al. 2000; Hunt et al. 2001; Dubischar et al. in press). The results of these studies have demonstrated that zooplankton abundance and biomass are highly variable, reflecting the variable oceanographic environment (Table 1.1. and references therein). Deacon (1983) suggests that the varying intensities of the SAF and APF may result in an increase in the interchange of Antarctic Surface Water (AASW) and Sub-Antarctic Surface Water (SASW), within the PFZ. The temporal variability in the oceanographic conditions in the PFZ is reflected in the zooplankton community. Species of either sub-tropical (e.g. *Ctenocalanus vanus*; *Pleuromamma abdominalis*), sub-Antarctic (e.g. *Metridia lucens*; *Scolecithricella minor*; *Calanus simillimus*) or Antarctic (e.g. *Oithona frigida*; *Rhincalanus gigas*; *Limacina* spp.; *Clausocalanus laticeps*) origin may predominate locally within the region (Ansorge *et al.* 1999; Froneman *et al.* 1999; Pakhomov & Froneman 1999). The contribution of Antarctic and sub-Antarctic species is determined largely by their position within the PFZ; closer to the APF the zooplankton community is well represented by Antarctic species, while sub-Antarctic species typically dominate in the vicinity of the SAF (Ansorge et al. 1999; Froneman et al. 1999; Pakhomov & Froneman 1999).

Previous studies indicate that mesozooplankton, comprising mainly copepods (including *Calanus simillimus*, *Rhincalanus gigas*, *Metridia* spp., *Oithona* spp., *Calanoides* spp. and *Clausocalanus* spp.), dominate the zooplankton community in the PFZ in terms of both abundance and biomass. Among the larger zooplankton (>2000 ?m), chaetognaths (*Eukrohnia hamata* and *Sagitta gazellae*), amphipods (*Themisto gaudichaudi*), euphausiids (*Euphausia vallentini*, *E. longirostris*, *Nematocelis megalops* and *Thysanoessa macrura*) and tunicates (*Salpa thompsoni* and *Phrononema segentaria*) numerically dominate (Ansorge et al. 1999; Froneman et al. 1999; Pakhomov & Froneman 1999; Pakhomov & Froneman 2000). However, the contribution of these larger zooplankton to total zooplankton abundance and biomass is generally <10% (Pakhomov et al. 1994; Froneman et al. 1999; Pakhomov & Froneman 1999). Exceptions occur during intense active swarming of euphausiids, amphipods and chaetognaths. Under these conditions, the contribution of the larger zooplankton to total zooplankton biomass can be as high as 60% (Pakhomov & Froneman 1999).

In terms of spatial variation, enhanced zooplankton abundance and biomass values have been documented in the vicinity of the fronts (the APF and SAF) and in the waters surrounding the sub-Antarctic islands (Froneman & Pakhomov 1998; Ansorge et al. 1999; Froneman et al. 1999; Pakhomov & Froneman 1999; Pakhomov et al. 2000 a, b). The elevated zooplankton biomass/ abundance values in such regions are presumed to be the result of the high food availability (chl-*a*) generally recorded in these areas. Species composition generally varies because of differing levels of abundances and biomasses of eurytypic species (Vervoort 1951; Foxton 1966; Park 1980; Deacon 1982) rather than the presence or absence of stenotypic species (Fasham & Angel 1975; Backus 1985; Gibbons 1997). There are, unfortunately, limited seasonal studies in the PFZ. Preliminary data suggest, however, that a strong seasonal pattern in zooplankton biomass exists, with maximum values in summer and minimum values in winter (Pakhomov et al. 2000b; Hunt et al. 2001)

Unfortunately, studies in the PFZ have employed sampling gear with a mesh size >300 ?m. According to Gallienne & Robins (2001), this mesh size undersamples mesozooplankton numbers by up to 99%, while biomass values are underestimated by approximately 50%. The small, highly abundant cyclopoid copepods (e.g. *Oithona* spp.) are very rarely retained by this mesh size, and juveniles of larger species may also pass through 300 ?m nets (Gallienne & Robins 2001). Recent studies in the PFZ (Dubischar et al. in press), employing a Multinet with a mesh of 100 ?m, estimated abundance values (of copepods only) to range between 21 000 and 97 000 ind. m^{-2}, with *Oithona similis* generally contributing >70% of the total numbers (Table 1.1.) (Dubischar et al. in press). This finding is in agreement with Schnack et al. (1985) who found that cyclopoid copepods (including *O. similis* and *Oncaea* spp.) may account for between 40 – 80% of total copepod numbers in Antarctic waters (Bellingshausen and Scotia Seas). Based on these findings, it is likely that a significant component of the mesozooplankton community has not been investigated in the PFZ due to the sampling gear employed.

1.5.2. FEEDING ECOLOGY

Zooplankton play an essential role in the carbon cycle of the Antarctic marine ecosystem, forming a link between the primary producers and the higher trophic consumers, such as fish, seabirds and whales (Swadling et al. 1997). It is therefore important to gain an understanding of the zooplankton grazing potential. Numerous grazing studies have been conducted within the Southern Ocean (Table 1.2.). Many of these studies have, however, been influenced in a combination of the following ways:

1) they have been restricted to the High Antarctic region of the Southern Ocean (e.g. Schnack 1985; Atkinson & Shreeve 1995; Pakhomov et al. 1997);
2) studies have focussed largely on the larger zooplankton species, such as *Euphausia superba*, *Calanus propinquus*, *Calanoides acutus*, *Rhincalanus gigas*, *Metridia gerlachei* and *Salpa thompsoni* (e.g. Conover & Huntley 1991; Atkinson et al. 1992 a, b; Lopez & Huntley 1995; Dubischar & Bathmann 1997; Li et al. 2001);
3) investigations have largely been restricted to the austral summer months (e.g. Atkinson 1996; Froneman et al. 2000; Hernández-León et al. 2000).

There have been very few grazing studies conducted in the PFZ, and those that have been undertaken were limited to euphausiids (*Euphausia vallentini*, *E. longrostris*, *E. superba* and *Nematocelis megalops*, see Perissinotto 1992; Froneman et al. 2000; Gurney et al. 2002) and the larger copepods (*Rhincalanus gigas*, *Metridia gerlachei*, *Calanoides acutus*, *Calanus* *propinquus* and *C. simillimus*, see Perissinotto 1992; Froneman et al. 2000). Data on the grazing impact of smaller copepods on the phytoplankton of the PFZ are thus lacking.

Research conducted on small zooplankton suggests that the mass-specific ingestion rates of small copepods (200–500 ?m) are greater than those of larger zooplankton species (>500 ?m), with cyclopoid copepods ingesting around 200% of their body carbon per day (e.g. Swadling et al. 1997). In contrast, the euphausiid *Euphausia superba* is estimated to consume between 0.02 and 28% of their body carbon per day (Pakhomov et al. 2002 and references therein). Hernández-León et al. (2000) showed that about 60 – 80% of total mesozooplankton (200–1400 ?m) ingestion was due to the smaller organisms (200–500 ?m), comprising mainly copepods. In the research presented by Swadling et al. (1997), cyclopoid copepods (particularly *Oncaea curvata*, *Oithona similis* and cyclopoid nauplii) always accounted for the greatest proportion of total grazing. These results suggest that, although large species (copepods, amphipods and euphausiids) may dominate the biomass, the numerically dominant smaller species may contribute more to grazing pressure and thus to carbon turnover within the PFZ. Indeed, Morales et al. (1991) found that daily consumption of phytoplankton by the small mesozooplankton fraction (200-500 ?m) was up to 4x that of the medium size fraction (500-1000 ?m) and up to 11x that of the large size class (1000-2000 ?m).

These findings suggest that the attention of grazing studies needs to be re-focussed on seasonal investigations of the feeding ecology of smaller zooplankton species (copepods) in the open waters of the Southern Ocean. In this way, we will gain a more accurate understanding of the ecological role that zooplankton play in the Southern Ocean.

1.5.3. PREDATION

Small copepods, although possibly very important grazers of phytoplankton production in the PFZ (see *1.4.2.* above), are likely to contribute very little to vertical carbon flux (Fortier et al. 1994; also see *1.1. The Global Carbon Cycle* above). However, predation of mesozooplankton by large carnivorous zooplankton in the PFZ is now fairly well-documented (see for example Froneman et al. 1998; Pakhomov et al. 1999; Froneman et al. 2000; Froneman et al. 2002a) and may represent an important source of carbon flux to depth.

Five major groups of carnivorous macrozooplankton occur in the PFZ; decapods, amphipods, gelatinous zooplankton, euphausiids and chaetognaths, as well as nektonic myctophid fishes (Froneman et al. 1998; Froneman & Pakhomov 1998; Pakhomov et al. 1999; Froneman et al. 2000; Froneman et al. 2002a). The combined impact of these predators on mesozooplankton standing stock within the PFZ ranges from 0.5 to 44% per day (Pakhomov et al. 1999; Froneman et al. 2002a). The dominant predators in the west Indian sector of the PFZ include the chaetognaths (*Eukrohnia hamata* and *Sagitta gazellae*), euphausiids (*Thysanoessa macrura*, *Nematocelis megalops* and *Euphausia longirostris*) and amphipods (*Themisto gaudichaudi*) (Pakhomov et al. 1999; Froneman et al. 2002a). Froneman et al. (2002a) estimated the total daily predation rate of chaetognaths to range from 0.11 to 18.09 mg Dwt. m^{-2} day^{-1} and that of the euphausiids to range from 0 to 105.9 mg Dwt. m^{-2} day^{-1}. Myctophid mesopelagic fishes (e.g. *Electrona carlsbergi*) and the swarming hyperiid amphipod (*T. gaudichaudi*) are also important predators in the Southern Ocean, and are capable of controlling the mesozooplankton standing stock (Pakhomov et al. 1996; Froneman et al. 2002a).

Gut content analyses of the dominant carnivorous macrozooplankton indicate that the major predators of the PFZ are opportunistic, generally consuming the numerically dominant mesozooplanktonic groups within the region, including the copepods, *Oithona similis*, *Clausocalanus* spp. and *Metridia lucens* (Froneman et al. 1998; Pakhomov et al. 1999; Froneman et al. 2000). The presence of carnivorous macrozooplankton is thus likely to enhance the efficiency of the biological pump in the PFZ.

1.5. AIMS

The main aims of this study were as follows:

?? To describe the mesozooplankton community in the west Indian sector of the Polar Frontal Zone, and to relate changes in structure to the physical environment.

?? To estimate the feeding ecology of the dominant components of the mesozooplankton community.

The study was conducted during two cruises of the South African National Antarctic Programme (SANAP), during April 2001 and 2002, in the south-west Indian Ocean (Fig. 1.3.).

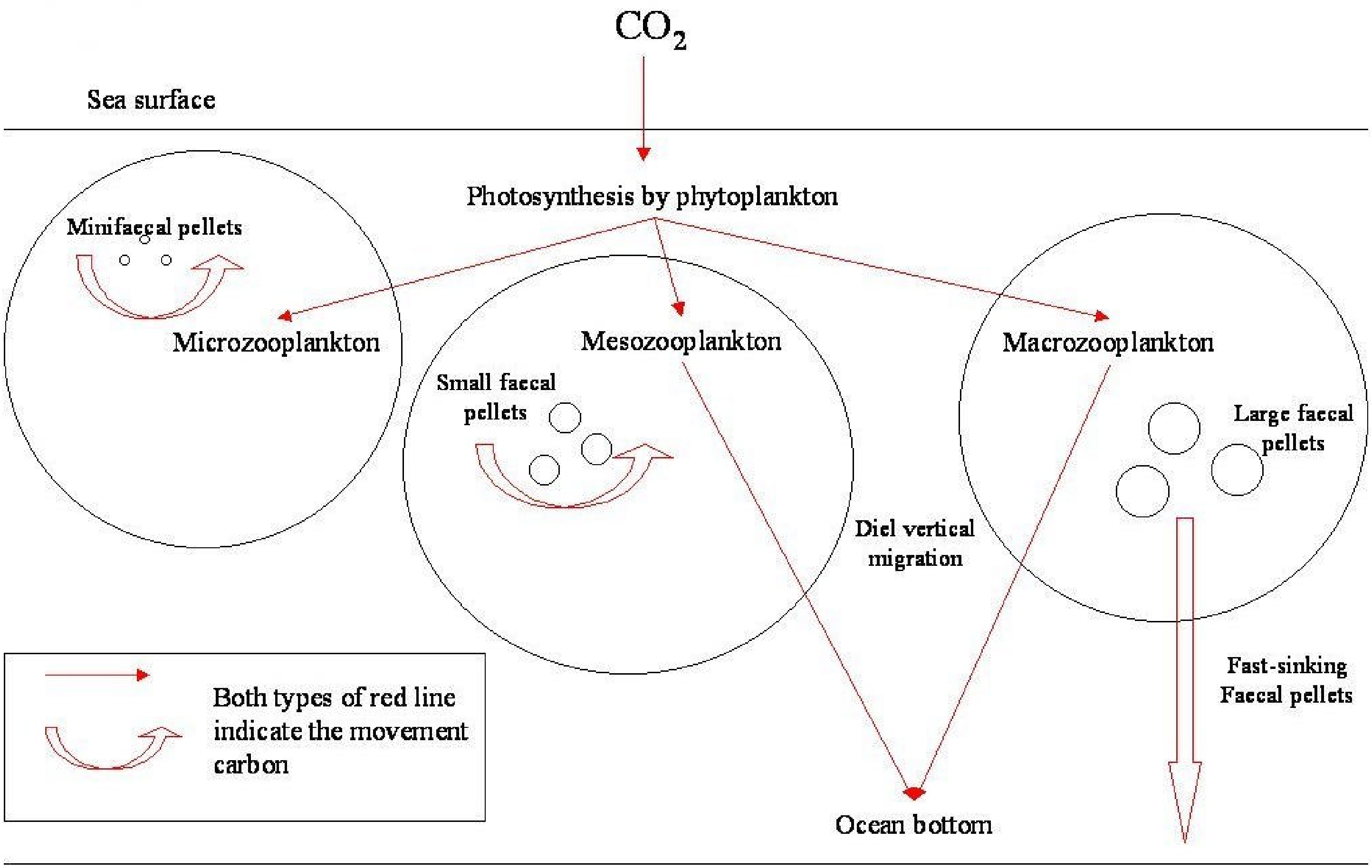

Figure 1.1. A simplified illustration of the biological pump.

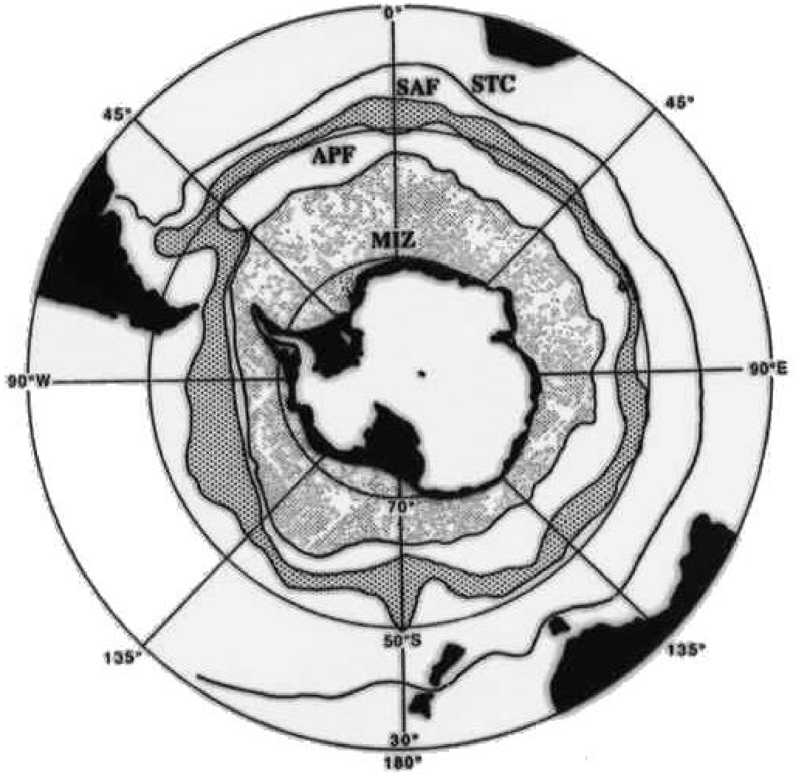

Figure 1.2. A map of the Southern Ocean, showing the Marginal Ice Zone (MIZ) and the oceanic frontal systems, the Antarctic Polar Front (APF); Sub-Antarctic Front (SAF); and Sub-Tropical Convergence (STC) (Hunt 2001).

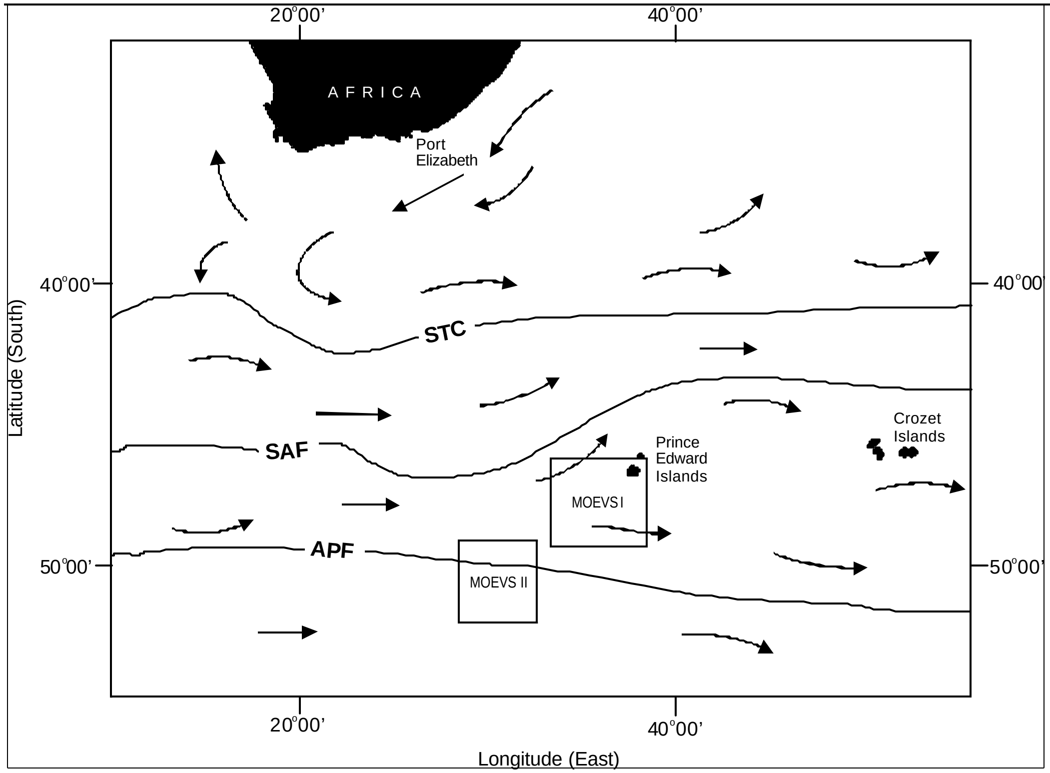

Figure 1.3. A map of the west Indian Sector of the Southern Ocean, showing the position of the surveys conducted during the first and second Marion Offshore Ecosystem Variability Studies (MOEVS I and II).

Table 1.1. Mean abundance and biomass values (with either range or standard deviation, depending on what was provided) of mesozooplankton in the Polar Frontal Zone, within the general study area indicated in Fig. 1.3. ND = no data.

Period	Abundance (ind. m^{-3})		Biomass (mg Dwt. m^{-3})		Average sampling depth (m)	Net,mesh (?m)	Source
	Mean	Range/Standard Deviation	Mean	Range/Standard Deviation			
March, 1976	2137	400-4850	17.2	8.7-28.4	0-130	WP-2, ?	Grindley & Lane, 1979
November, 1976	1715	1575-1854	24.8	14.6-34.9	0-68	WP-2, ?	Grindley & Lane, 1979
May, 1983	255	22-594	29.1	13-53	0-100	N70V, 200	Boden & Parker, 1986
April, 1985	190	150-229	23.7	17.4-30	0-300	Bongo, 200	Perissinotto, 1992
May, 1987	ND	ND	40.0	ND	0-250	WP-2, ?	Boden, 1988
April/May, 1989	ND	ND	7.7	1.04-62.70	0-300	Bongo, 300	Ansorge et al,. 1999
April, 1989	160	130-191	44.5	32.3-56.8	0-300	Bongo, 300	Perissinotto, 1992
April, 1989	ND	ND	0.14	0.05-0.3	0-300	Bongo, 300	Perissinotto et al., 2001
Feb/March, 1994	26	16-47	8.02	4.3-11.5	0-200	Bongo, 300	Pakhomov et al., 1997
Feb/March, 1994	35	ND	4.1	ND	0-200	WP-2, 200	Pakhomov et al., 1997
April/May, 1996	96	25-192	2.8	0.6-7.75	0-300	Bongo, 300	Froneman & Pakhomov, 1998
April/May, 1989	ND	10-490	ND	<4-63	0-300	Bongo, 300	Pakhomov et al. 2000 a
April/May, 1997	ND	7–274	ND	0.6–15.9	0-300	Bongo, 300	Pakhomov et al. 2000 a
Jan/Feb, 1993	84.2	47.8–128.7	47.2	21.6–91.5	0-300	Bongo, 300	Pakhomov et al. 2000 b
April/May, 1997	73	43	7.5	4.3	0-300	Bongo, 300	Hunt et al., 2001
April/May, 1997	ND	ND	3.2	0.33-15.69	0-300	Bongo, 300	Froneman et al., 1999

April/May, 1997	153	72	8.0	2.4	0-300	Bongo, 300	Hunt et al., 2001
April/May, 1998	73	73	10.3	11.7	0-300	Bongo, 300	Hunt et al., 2001
April/May, 1999	65	25	8.7	5.5	0-300	Bongo, 300	Hunt et al., 2001
April/May, 1999	97	31	12.0	4.6	0-300	Bongo, 300	Hunt et al., 2001
Dec/Jan, 1995/1996	55500	21000-97000	ND	ND	0-300	Multinet, 100	Dubischar et al. in press

Table 1.2. Comparison of grazing studies conducted in the Southern Ocean, with reference to region, season, species (size range in brackets) and percentage phytoplankton biomass (% PB) and phytoplankton production (% PP) consumed per day. Small = 200-500 ? m; medium = 500-800 ?m; large = >800 ?m.

Author	Region	Season	Species (size range)	% PB	% PP
Schnack (1985)	Antarctica	Summer	Copepodids (small); *Euphausia superba, Metridia gerlachei, Calanoides acutus, Rhincalanus gigas, Calanus propinquus* (medium – large)	ND	ND
Conover & Huntely (1991)	Polar Seas	Year round	*C. propinquus, C. acutus, R. gigas, M. gerlachei* (medium – large)	ND	ND
Atkinson et al. (1992 a & b)	South Georgia (Antarctica)	Summer	*C. acutus, Calanus simillimus, C. propinquus, R. gigas* (medium – large)	ND	ND
Perissinotto (1992)	Prince Edward Islands (sub-Antarctic)	Autumn	*C. simillimus, Clausocalanus brevipes, M. gerlachei, Euphausia vallentini, Conchoecia* spp., *Limacina* spp. (medium – large)	24 (4.9 – 47.7)	46 (8.8 – 81.3)
Atkinson & Shreeve (1995)	Bellingshausen Sea (Antarctica)	Spring	*Oithona* spp. (small); *R. gigas, M. gerlachei, C. propinquus, C. acutus* (large)	0.09 (0.0064 – 0.31)	1.04 (0.012 – 2.9)
Lopez & Huntely (1995)	Antarctica	Summer	*M. gerlachei* (large)	ND	ND
Atkinson (1996)	Near South Georgia (Open ocean Polar Frontal Zone)	Summer	*Oithona* spp. (small); *C. simillimus, Metridia* spp., *Pseudocalanus* spp., *Clausocalanus laticeps, Metridia lucens, Neocalanus tonsus, Pleuromamma robusta* (medium – large)	ND	ND
Atkinson et al. (1996)	South Georgia (Antarctica)	Summer	Copepodites of small spp. (small); *C. acutus, C. propinquus, C. simillimus, M. lucens, R. gigas, M. gerlachei, P. robusta* (medium – large)	ND	ND
Dubischar & Bathmann (1997)	Atlantic Sector	Summer	*C. acutus, C. propinquus, R. gigas, Salpa thompsoni* (large)	ND	ND
Pakhomov & Perissinotto (1997)	Sub-Tropical Convergence (and south)	Winter	Small copepods (small); *R. gigas, Calanus* spp., *Pleuromamma* spp., *Metridia* spp., *Euphausia* spp., *Limacina* spp. (medium – large)	8 (0.8 – 18)	75 (20 – 165)
Pakhomov et	South Georgia	Summer	Small copepods, cyclopoid	4 (0.5 –	36 (5 –

al. (1997)	(Antarctica)		copepods (small); pteropods, *R. gigas, C. acutus, C. simillimus, Thysanoessa* spp., *Euphausia frigida, E. triacantha* (medium – large)	8)	102)
Swadling et al. (1997)	Antarctic coastal waters	Summer	*Oncaea curvata, Oithona similis*, nauplii (small); *Stephos longipes, Paralabidocera antarctica,* harpacticoids (medium); *Calanoides acutus* (large)	ND	2.3 (0.9 – 4.4)
Razouls et al. (1998)	Kerguelen Island (Sub-Antarctic)	Year round	*Oithona* spp. (small); *C. simillimus, Metridia* spp., *C. acutus, R. gigas* (medium – large)	ND	ND
Froneman et al. (2000)	PFZ (Atlantic Sector)	Summer	*R. gigas, M. gerlachei, C. acutus, Thysanoessa macrura, C. propinquus, E. superba, C. simillimus, Thysanoessa* spp. (medium – large)	12.4 (3.9 – 18.3)	66.5 (53 – 89)
Hernández-León et al. (2000)	Bransfield Strait (Antarctica)	Summer	Small, medium and large spp. (names not provided)	ND	ND
Li et al. (2001)	Prydz Bay (Antarctica)	Summer	*C. acutus, M. gerlachei* (large)	0.15 (<0.1 – 0.4)	8 (3.8 – 12.5)

CHAPTER TWO: MATERIALS AND METHODS

For clarity, this study has been divided into two major investigations. The first was an analysis of the mesozooplankton community structure, conducted during the first Marion Offshore Ecosystem Variability Study (MOEVS I), in April 2001. The second investigation was a study of the feeding ecology of the dominant mesozooplankton species, conducted during the second Marion Offshore Ecosystem Variability Study (MOEVS II), in April 2002. Both studies were conducted as a part of the South African National Antarctic Programme (SANAP).

2.1. MARION OFFSHORE ECOSYSTEM VARIABILITY STUDY I – APRIL 2001

2.1.1. SURVEY DETAILS

The MOEVS I survey consisted of a grid of 5 north-south transects extending across the PFZ, between 49º55' and 46º35'S and between 33º and 38ºE upstream of the Prince Edward Islands (Fig. 2.1.). Along each transect, 10 hydrographic stations, 25 nautical miles apart, were occupied. At these stations, sea-surface temperature and size-fractionated chlorophyll-*a* (chl-*a*) concentrations were recorded. Sea surface temperature readings were taken using the ship's temperature sensor, calibrated with a Crawford bucket (Crawford 1972). At every second station (50 nautical mile intervals), mesozooplankton samples were collected (Fig. 2.1.). The surface position of the SAF during the survey was determined from the position of the 7 ºC surface isotherm (Fig. 2.1.) (Froneman et al. 1999).

2.1.2. CHLOROPHYLL-A

Surface size-fractionated chl-*a* concentrations were determined by gently passing (<5 cm Hg) 250 ml of surface seawater, obtained from a shipboard pump, through a serial filtration unit, separating the chl-*a* into pico- (<2.0 ? m), nano- (2.0 - 20 ? m) and micro- (>20

?m) size fractions. Chl-*a* concentrations were determined fluorometrically (Turner Designs 10 AU) after 24 hours of extraction in 90% acetone (Holm-Hansen & Riemann 1978).

2.1.3. ZOOPLANKTON SAMPLING

Mesozooplankton samples were collected using a Bongo net fitted with 200 ?m and 300 ?m mesh nets. The Bongo net was fitted with a Universal Underwater Unit (U^3, Robertson et al. 1981), which monitored temperature and depth throughout the tow. An electronic flow meter was used to calculate the volume of water filtered during each tow. Tows were conducted to a depth of 200 m at night and 300 m during the day, in order to compensate for diel vertical migration. Towing speeds during the survey ranged between 0.4 and 1.9 knots. The samples collected were fixed in 6% buffered formalin (hexamine).

2.1.4. ZOOPLANKTON COMMUNITY STRUCTURE

In order to determine size-fractionated abundances, sub-samples (ranging from 1/32 to 1/256 of the total sample) of the 200 ?m net sample from each station were separated by reverse filtration into three size categories (200-500 ?m; 500-1000 ?m; 1000-2000 ?m), according to the method of Hernández-León et al. (1999, 2000). The species composition and numbers of zooplankton in each size class were then recorded, and abundances were expressed as number of individuals per cubic metre (ind. m^{-3}). Species were identified using the keys of Boltovskoy (1999). Size-fractionated biomass was determined using 1/8 sub-samples from each station, separated by reverse filtration into the same three size categories, retained on pre-weighed GF/F filters and oven-dried at 60 ºC for 24 to 36 hours, after which the filters were re-weighed. Dry weights were determined by subtracting the final weights from the initial weights. Biomass values were expressed as milligrams of dry weight per cubic meter (mg Dwt. m^{-3}).

2.1.5. *ZOOPLANKTON NUMERICAL ANALYSIS*

In order to compare mesozooplankton communities at the various stations, hierarchical cluster analysis (q-type) and multidimensional scaling were used in conjunction with the Bray-Curtis similarity index (Plymouth Routines in Multivariate Ecological Research, PRIMER, computer package; Clarke & Warwick 1994). Species abundance data were log transformed [$\log_{10}(x+1)$] in order to reduce bias due to highly abundant species (Legendre & Legendre 1983). The PRIMER program, ANOSIM, a multivariate analogue of a one-way ANOVA (Clarke & Warwick 1994), was used according to the procedure described by Field et al. (1982), to test the significance levels and sources of difference between zooplankton assemblages associated with the different groupings identified in the hierarchical cluster analysis. Cluster analysis provided merely a data summary, indicating community structure patterns, but not those species responsible for such patterns. The PRIMER program, SIMPER (Clarke & Warwick 1994), was used to determine the percentage contribution of certain species to within-group similarity. This analysis was based on station abundance levels. For the purpose of this study, species responsible for up to 80% of the similarity measured were used in the analysis, as these species contributed the most to each measure. Mackas (1984) found that SIMPER analysis was well suited to mesoscale surveys where differences in zooplankton communities were largely the result of variable abundance and biomass values, as is the case in the PFZ, rather than differences in species composition.

2.1.6. *STATISTICAL ANALYSIS*

Pearson's Correlation analysis was used to determine the relationships between the physico-chemical (temperature and salinity) and biological (chl-*a*) parameters and mesozooplankton abundance and biomass. All values were corrected following the Bonferroni adjustment.

2.2. MARION OFFSHORE ECOSYSTEM VARIABILITY STUDY II – APRIL 2002

2.2.1. SURVEY DETAILS

Integrated chl-*a*, mesozooplankton abundance and copepod grazing were estimated at 13 stations in the west-Indian sector of the Southern Ocean, during the second Marion Offshore Ecosystem Variability Study (MOEVS II) conducted in April 2002 (Fig. 2.2.). Sub-surface (200 m) temperatures were recorded with a Neil Brown MK III conductivity, temperature and depth (CTD) probe. Grazing activity of the numerically dominant copepods was investigated using the gut fluorescence technique (Mackas & Bohrer 1976).

2.2.2. INTEGRATED CHLOROPHYLL-A

Seawater samples were collected at 5 depths (0, 20, 50, 75 and 100 m) using a 12 x 8L Niskin bottle rosette attached to the Neil Brown MK III CTD probe. Chl-*a* concentrations at each depth were determined from a 250 ml seawater sample obtained from the rosette bottle and filtered (vacuum <5 cm Hg) through a GF/C filter. Filters were then placed in 8 ml of 90% acetone and stored at – 20 ?C for 24 hours. After centrifugation (5000 rpm) the chl-*a* concentration was measured using a Turner Designs 10AU Fluorometer, according to the method of Holm-Hansen & Riemann (1978). Chl-*a* concentrations were integrated for the top 100 m of the water column by trapezoidal integration (Froneman et al. 2002b) and were expressed as milligrams of chl-*a* pigment per square meter [mg (pigm) m^{-2}].

2.2.3. ZOOPLANKTON COMMUNITY STRUCTURE

Mesozooplankton samples were collected by vertical tows using a WP-2 net fitted with a 200 ?m mesh and a 1.5 l cod-end. Sampling depths were determined by employing the following equation (see Sameoto et al. 2000):

$$Zf = \text{wire out} / \cos \text{angle of wire}$$

Nets were raised at speeds ranging between 0.15 and 0.23 m s^{-1}. Tows were conducted to a depth of between 229 to 243 m during the day and 142 to 156 m at night. Volume filtered during each tow was calculated by multiplying mouth area of the net by depth of tow. Samples were immediately fixed in 6% buffered formalin (hexamine). In the laboratory, samples were sorted and analysed for taxonomic identification and numerical abundance (Boltovskoy 1999). Zooplankton abundance was expressed as individuals per cubic metre (ind. m^{-3}) for comparison with MOEVS I values and as individuals per square metre (ind. m^{-2}) in order to calculate the grazing impact on integrated chl-*a*. Biomass was determined using 1/8 sub-samples from each station, retained on pre-weighed GF/F filters and oven-dried at 60 ºC for 24 to 36 hours, after which filters were re-weighed. Dry weights were determined by subtracting the final weights from the initial weights. Biomass values were expressed as milligrams of dry weight per cubic meter (mg Dwt. m^{-3}).

2.2.4. ZOOPLANKTON FEEDING ECOLOGY

The feeding rates of the four most abundant copepods (*Calanus simillimus*, *Clausocalanus* spp., *Ctenocalanus vanus* and *Oithona similis*), which formed up to 93% of total mesozooplankton abundance, were investigated using the gut fluorescence technique (Mackas & Bohrer 1976).

In order to assess variability in feeding activity, animals were collected at 5 to 7 hour intervals over 24 hours using the sampling gear described above. Samples were immediately anaesthetised in a solution of soda: seawater (1:5, v/v; Morales et al. 1991), before being filtered (vacuum <1 cm Hg) onto GF/C filters, placed in petri dishes and frozen for later analysis. In the laboratory, filters were thawed and individuals of the copepod species quickly sorted under low light conditions using a Nikon dissection microscope, operated at 100x magnification. Once sufficient individuals were collected for each species (10 individuals of *Calanus simillimus*; 20 - 25 individuals of *Clausocalanus* spp.; 25 individuals of *Ctenocalanus vanus*; and 30 - 40 individuals of *Oithona similis*) they were placed in plastic centrifuge tubes (10 ml) with 8 ml of 90% acetone and stored at – 20 ?C for 24 hours. It must be noted at this point, that only adults and copepodites of the selected species were chosen. After centrifugation (5000 rpm) the pigment content of the acetone extract was measured, before and after acidification, using a Turner Designs 10AU Fluorometer (Mackas & Bohrer 1976). Pigment contents were expressed as chl-*a* equivalents per individual [ng (pigm) ind^{-1}] and calculated according to the method of Strickland & Parsons (1968), as modified by Conover et al. (1986).

In order to calculate the gut evacuation rate (k, h^{-1}), freshly caught zooplankton were gently placed into a 20 l plastic bucket filled with filtered seawater (0.2 ? m) to which non-fluorescent charcoal powder was added (Perissinotto 1992; Perissinotto & Pakhomov 1996). Experiments were carried out on deck at ambient seawater temperatures (approximately 5°C). Sub-samples of zooplankton were collected according to the procedure described above, every 10 minutes for the first hour and every 20 minutes thereafter. Animals were then stored as described above. The 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 vs. time (Dam & Peterson 1988).

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

$$I = kG/(1-b?)$$

Where k is the gut evacuation rate (h^{-1}), G is an integrated value (over 24 hours) of gut pigment contents [ng (pigm) ind^{-1}] and b? is a non-dimensional index of pigment destruction. Due to the difficulty of separating different copepod species, an average value of 30% gut pigment destruction was assumed for all copepods (Dam & Peterson 1988). Community grazing impact was then expressed as a percentage of the integrated phytoplankton standing stock consumed per day. To estimate community grazing impact, abundance data of the four copepod species were combined with individual ingestion rates. Grazing impact was then expressed as the percentage integrated chl-*a* biomass consumed per day.

Carbon specific daily rations, expressed as percentage body carbon consumed per day, were calculated by determining the dry weight of individual copepods and assuming a carbon content of 40% dry weight and a chl-*a* : carbon ratio of 50 (Atkinson 1994). In order to calculate individual dry weights, 10 to 20 individuals of each species were placed on pre-weighed GF/C filters and oven-dried at 60 ?C for 36 hours. Dry weights of species were then calculated by subtracting the initial weight of the filter from the final. Weights were determined using a Sartorius microbalance with a precision of 0.01 mg.

2.2.5. STATISTICAL ANALYSIS

Regression analysis was used to test for correlations between mesozooplankton abundance and integrated chl-*a*, between mesozooplankton biomass and integrated chl-*a* and between copepod grazing and integrated chl-*a*. Independent t-tests were used to test for diel variations in gut pigment content for each of the four copepod species investigated. Analyses were conducted using the statistical computer package, SigmaPlot (Jandel Scientific).

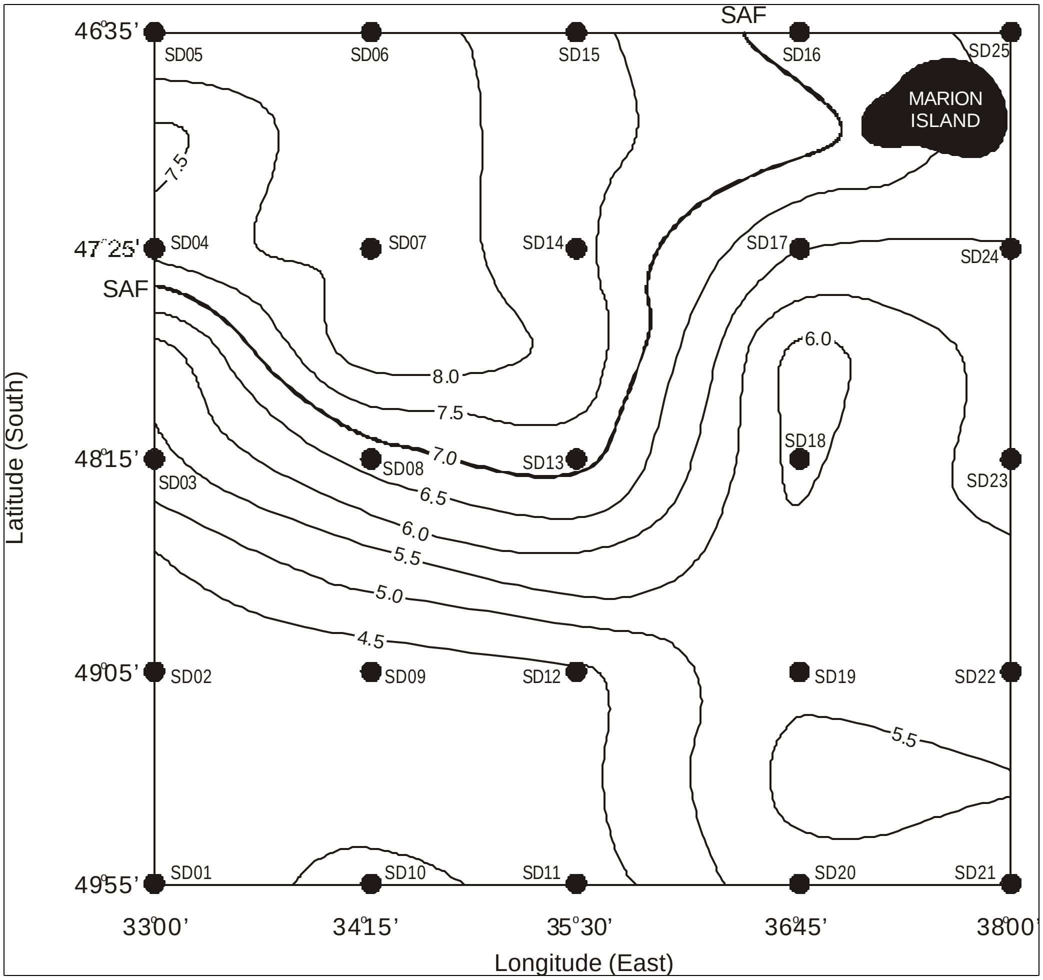

Figure 2.1. Mesozooplankton sampling stations occupied during the first Marion Offshore Ecosystem Variability Study (MOEVS I, April 2001) superimposed on surface temperature isotherms. The thickened isotherm represents the surface expression of the Sub-Antarctic Front (SAF).

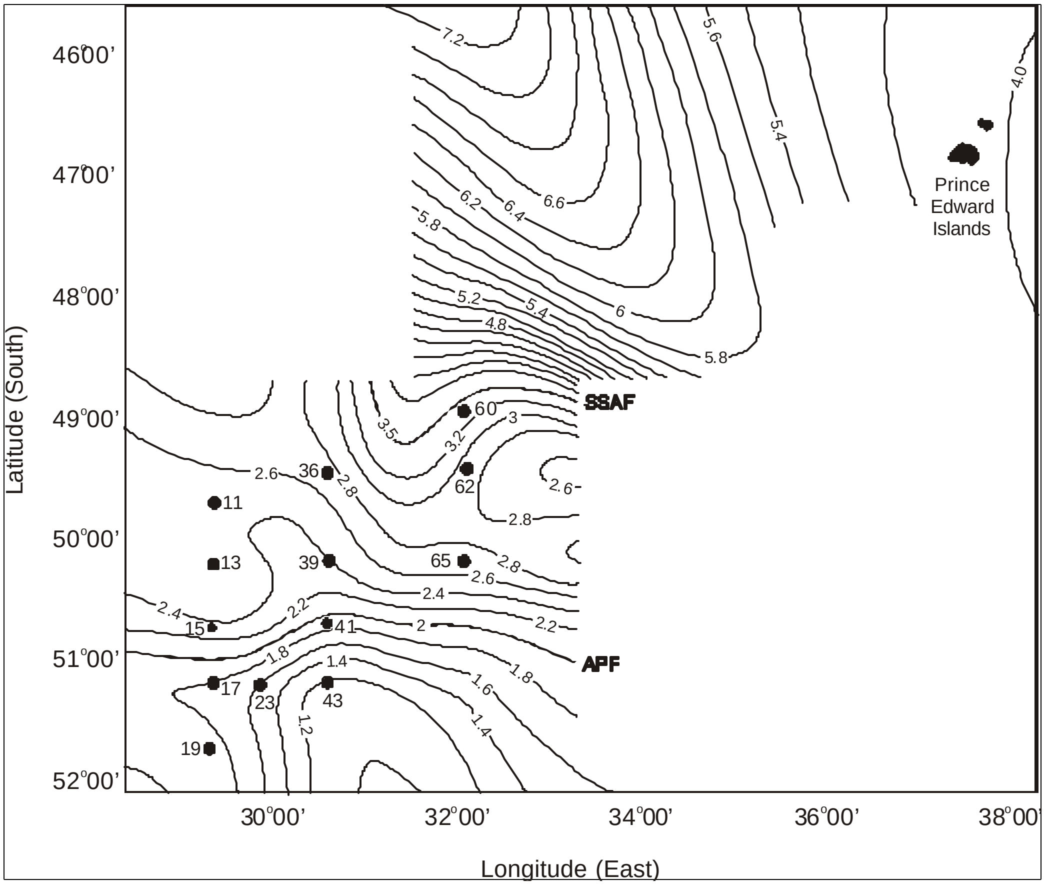

Figure 2.2. Grazing stations occupied during the second Marion Offshore Ecosystem Variability Study (MOEVS II, April 2002) superimposed on sub-surface (200 m) temperature isotherms. The thickened isotherms represent the Antarctic Polar Front (APF) and the southern Sub-Antarctic Front (SSAF).

CHAPTER THREE: RESULTS

3.1. MARION OFFSHORE ECOSYSTEM VARIABILITY STUDY I - APRIL 2001

3.1.1. OCEANOGRAPHY

Surface temperature readings collected during the survey indicate that between 33º and 35º30'E, the Sub-Antarctic Front (SAF) lay at ~ 47º25'S (Fig. 2.1.). At ~ 35º30'E the SAF veered northwards to 47ºS, possibly the result of topographical deflection upstream of the area of investigation (Fig. 2.1.). South of the SAF, there was a gradual decrease in water temperature from north to south.

3.1.2. CHLOROPHYLL-A

Total chlorophyll-*a* (chl-*a*) concentrations exhibited no clear spatial patterns throughout the investigation, with values ranging from 0.11 to 0.34 ?g l^{-1} (Table 3.1.). Pico- (<2.0 ?m) and nanophytoplankton (2.0-20 ?m) dominated total chl-*a*, contributing up to 98% of the total (Fig. 3.1.). An exception was recorded at station SD 09, where microphytoplankton (>20 ?m) contributed over 50% of the total (Fig. 3.1.). Two other stations, SD 02 and SD 11, had relatively high microphytoplankton concentrations, contributing 35% and 41% of the total pigment, respectively. In general, however, microphytoplankton contributed <20% of the total chl-*a* (Fig. 3.1.).

3.1.3. ZOOPLANKTON ABUNDANCE AND SPECIES COMPOSITION

Total mesozooplankton abundance was greatest in the south-western sector of the grid, south of the SAF, with abundances ranging from 367 to 1512 ind. m^{-3} (mean ~ 858 ind. m^{-3}) (Table 3.1.). The zooplankton abundances in the warmer waters to the north of the SAF were significantly lower (One Way Analysis of Variance; P <0.05), ranging from

49 to 287 ind. m^{-3} (Table 3.1.). The south-eastern section of the grid had intermediate abundance values ranging from 104 to 428 ind. m$^{?3}$. Total mesozooplankton abundance was not significantly correlated to either chl-*a* (Pearson's Correlation Analysis; r = 0.2; P >0.05) or temperature (r = 0.624; P >0.05).

Throughout the investigation, the smallest size class (200-500 ?m) had the highest abundance values (Fig. 3.2.), comprising an average of 69% (SD = ± 12.3%) of all mesozooplankton counted. Exceptions were noted at six stations at which the dominant size class was the 500-1000 ?m group (Fig. 3.2.). Generally, however, the intermediate size fraction comprised <25% of total zooplankton counts. The contribution of the 1000-2000 ?m size class to total zooplankton counts was always <18%.

The 200-500 ?m size fraction was dominated by the cyclopoid copepod, *Oithona similis*, which comprised an average of 59% (SD = ? 10.4%) of total mesozooplankton counts. Also well-represented in this fraction were the small individuals of the pteropod *Limacina retroversa* and the calanoid copepods *Ctenocalanus vanus* (stages IV and V), *Metridia lucens* (stages III and IV) and *Clausocalanus brevipes*. The contribution of these species was, however, always <10% of total mesozooplankton counted in the 200-500 ?m size class. The 500-1000 ?m fraction comprised mainly of adult stages of *Ctenocalanus vanus*, *M. lucens* (stages III - V), *Calanus simillimus* (adults and stages IV and V) and *L. retroversa*. Collectively, these species accounted for between 63 and 78% of zooplankton within the 500-1000 ?m fraction. Also found in this fraction were adult *O. similis*, *Pleuromamma abdominalis* and *M. lucens*. The combined contribution of these species to total mesozooplankton counted was, however, always <5%. Finally, the 1000-2000 ?m fraction was dominated almost entirely by euphausiid furcilia and chaetognaths (*Eukrohnia* *hamata* and *Sagitta gazellae*). See Fig. 3.3. for the contribution of the seven most abundant species/taxa throughout the investigation.

3.1.4. ZOOPLANKTON BIOMASS

In congruence with the total abundance values, total mesozooplankton biomass was greatest at stations located in the south-western sector of the grid and ranged from 5.68 to 25.72 mg Dwt. m^{-3} (Table 3.1.). With one exception, station SD 13, the lowest mesozooplankton biomass (range between 0.71 and 5.65 mg Dwt. m^{-3}) was recorded at stations north of the SAF (Table 3.1.). At stations in the south-eastern sector of the grid survey, average total mesozooplankton biomass was 7.73 mg Dwt. m^{-3} (range from 4.92 to 12.74 mg Dwt. m^{-3}). Total mesozooplankton biomass was not significantly correlated to chl-*a* ($r = 0.3$; $P > 0.05$), but was significantly correlated to temperature ($r = 0.728$; $n = 25$; $P < 0.05$). In contrast to the size-fractionated abundance values, the 1000-2000 ?m size class generally yielded the highest biomass values (Fig. 3.4.), constituting on average 66% (SD = ??10.2%) of the total mesozooplankton biomass. Exceptions were recorded at stations SD 07 and SD 14 where the 500-1000 ?m fraction dominated total mesozooplankton biomass. The 500-1000 ?m size class was the second largest contributor to total mesozooplankton biomass, comprising between 9 and 68% (mean = 24%) of total mesozooplankton biomass. The contribution of the 200-500 ?m size class to total mesozooplankton biomass was always <15%. Exceptions were recorded at stations SD 07 and SD 15 where the 200-500 ?m size fraction comprised 18 and 34% of total biomass, respectively (Fig. 3.4.).

3.1.5. NUMERICAL ANALYSIS

Three distinct, significantly different groupings of mesozooplankton ($P > 0.05$; ANOSIM, PRIMER) were identified during the survey (Fig. 3.5.). The average abundances of the most numerous zooplankton species accounted for as much as 80% of the similarity within the groupings identified with the hierarchical cluster analysis (Table 3.2.). The first zooplankton group comprised those stations found north of, or in the immediate proximity of, the SAF (Fig. 3.6.). This group is, therefore, designated the Sub-Antarctic Zone Group (SAZG). The SAZG was characterised by the presence of warmer water zooplankton species, including *Clausocalanus brevipes* and *Pleuromamma abdominalis* (Boltovskoy 1999) (Table 3.2.). The remaining two groupings, designated groups 2 and 3, were not restricted to any specific water mass or hydrological feature. Group 2 was characterised by the presence of Antarctic zooplankton species, such as *Oithona frigida*, *Rhincalanus gigas* and *Limacina retroversa* (Boltovskoy 1999) (Table 3.2.). Group 3 comprised a combination of species both Antarctic and sub-Antarctic in origin (Table 3.2.), with *C. brevipes* from the warmer waters, and *L. retroversa* from the colder waters. The main reason for the differences between the three groupings was not the presence/absence of certain species, but rather the relative contributions of different zooplankton species to the groups.

3.2. MARION OFFSHORE ECOSYSTEM VARIABILITY STUDY II - APRIL 2002

3.2.1. GENERAL OCEANOGRAPHY

Results of the hydrographic survey indicate that within the region of investigation, two oceanographic fronts were encountered, the Antarctic Polar Front (APF) and the southern branch of the Sub-Antarctic Front (SSAF). The positions of both fronts were identified according to sub-surface features. The APF lay within a narrow band, centred around 50?45`S (Froneman et al. 2002b). In contrast, the SSAF appeared to demonstrate substantial meandering, which appears to be the result of topographic steering through the Andrew Bain Fracture Zone (Froneman et al. 2002b) (Fig. 2.2.).

3.2.2. INTEGRATED CHL-A

Total integrated chl-*a* values during the study ranged from 11.17 to 28.34 mg (pigm) m^{-2} (Fig. 3.7.). There were no spatial trends observed for the integrated chl-*a* concentration during the investigation (Fig. 3.7.).

3.2.3. ZOOPLANKTON COMMUNITY STRUCTURE

Total mesozooplankton abundances during the investigation varied from 41.4 to 1372 ind. m^{-3} (Table 3.3.) (integrated values ranged from 3732 to 74667 ind. m^{-2}; Table 3.4.). The main peaks in zooplankton abundance (up to 75 000 ind. m^{-2}) were recorded at stations (SD 17, 23 and 41) occupied in the vicinity of the APF (Fig. 3.8.), while the lowest values were recorded in the PFZ waters, north of the APF. The copepods, *Calanus simillimus*, *Clausocalanus* spp., *Ctenocalanus vanus* and *Oithona similis* dominated total mesozooplankton numbers throughout the survey, contributing up to 93% of the total abundance (Table 3.4.; Fig. 3.8.). Other copepods recorded include *Rhincalanus gigas*, *Paraeuchaeta biloba*, *Scolecithricella minor*, *Oncaea antarctica* and *Pleuromamma abdominalis*. The contribution of these species to total mesozooplankton abundance was, however, always <2%. Among the copepods, *O. similis* and *C. vanus*, were the most numerous, together contributing up to 85% (range 30 to 85%) of the total mesozooplankton abundances.

Among the larger zooplankton, the chaetognaths, *Eukrohnia hamata* and *Sagitta gazellae*, and the amphipod, *Themisto gaudichaudi* numerically dominated (Table 3.4.). The contribution of these species to total abundance was, however, generally <10%. Exceptions were recorded at stations SD 15, 36 and 60 where the combined contribution of chaetognaths and amphipods was up to 28% of the total abundance (range 15 – 28%). There was no significant correlation between total mesozooplankton abundance and integrated chl-*a* biomass ($r = 0.128$; $P > 0.05$).

Total mesozooplankton biomass during the investigation ranged from 1.31 to 33.22 mg Dwt. m^{-3} (Table 3.3.). The greatest mesozooplankton biomass (33.22 mg Dwt. m^{-3}) occurred at station SD 15, which corresponds to the unusually high numbers of amphipods observed at this station (Table 3.3.; Fig. 3.8.). The lowest biomass values were observed in the PFZ waters north of the APF. There was no significant correlation between total mesozooplankton biomass and integrated chl-*a* ($r = 0.136$; $P > 0.05$).

3.2.4. ZOOPLANKTON FEEDING ECOLOGY

Of the four copepod species investigated, *Calanus simillimus*, *Clausocalanus* spp. and *Ctenocalanus vanus* exhibited diel variation in their feeding behaviour ($P < 0.05$ for all three species, t-test), with maximum gut pigment content values at 21h00 and 04h00 (local time) for *C. simillimus*, at 21h00, 04h00 and 09h00 (local time) for *Clausocalanus* spp. and at 21h00 (local time) for *Ctenocalanus vanus* (Fig. 3.9.). *Oithona similis* showed no significant difference in gut pigment content over 24 hours ($P > 0.05$, t-test) (Fig. 3.9.). With the exception of *Calanus simillimus*, negative linear models provided the best fit to the decline in gut pigment contents for the gut evacuation experiments (Table 3.5.). For *C. simillimus*, a negative exponential model provided the best fit (Table 3.5.). Gut evacuation rates (k) ranged from 0.318 to 1.428 h^{-1} (Table 3.5.). Average individual ingestion rates were highest for *C. simillimus* at ~ 618.61 ng (pigm) ind^{-1} day^{-1} (range 241.33 – 1462.02; SD = 312.78) and lowest for *O. similis* at ~ 39.37 ng (pigm) ind^{-1} day^{-1} (range 23.23 – 61.60; SD = 9.81). Average ingestion rates for *Ctenocalanus vanus* and *Clausocalanus* spp. were

~ 81.34 ng (pigm) ind^{-1} day^{-1} (range 62.02 – 104.52; SD = 16.62) and 123.66 ng (pigm) ind^{-1} day^{-1} (range 55.79 – 397.31; SD = 86.52), respectively (Table 3.5.).

The combined grazing impact of the four copepod species ranged from 1 to 36% of the phytoplankton standing stock per day (Table 3.6.). Generally, the highest impact occurred at stations in the vicinity of the APF. An exception was recorded at station SD 13, located in the PFZ, where the second highest grazing impact during the entire study was recorded. With three exceptions (stations SD 11, 13 and 39), copepods <1000 μm (*Oithona similis* and *Ctenocalanus vanus*) represented the most important consumers of phytoplankton biomass (Table 3.6.). Collectively, these species were responsible for up to 91% (range 15 to 91%) of the phytoplankton grazing per day. There was no significant correlation between copepod grazing and integrated chl-*a* biomass ($r = 0.384$; $P > 0.05$).

The average individual dry weights of the copepods ranged from 1.54 to 92.5 μg, depending on the species (Table 3.5.), it must be noted at this point, that dry mass values for *Oithona similis* were obtained from Atkinson (1996). The mass specific ingestion rates of the four copepods ranged from 42 to 320% of body carbon per day, depending on the species (Table 3.5.). Generally, the highest mass specific ingestion rates were obtained for the smaller copepods (*Oithona similis* and *Ctenocalanus vanus*), where >100% body carbon was consumed per day. For the larger copepods (*Calanus simillimus* and *Clausocalanus* spp.), carbon derived from phytoplankton generally contributed <90% of body carbon.

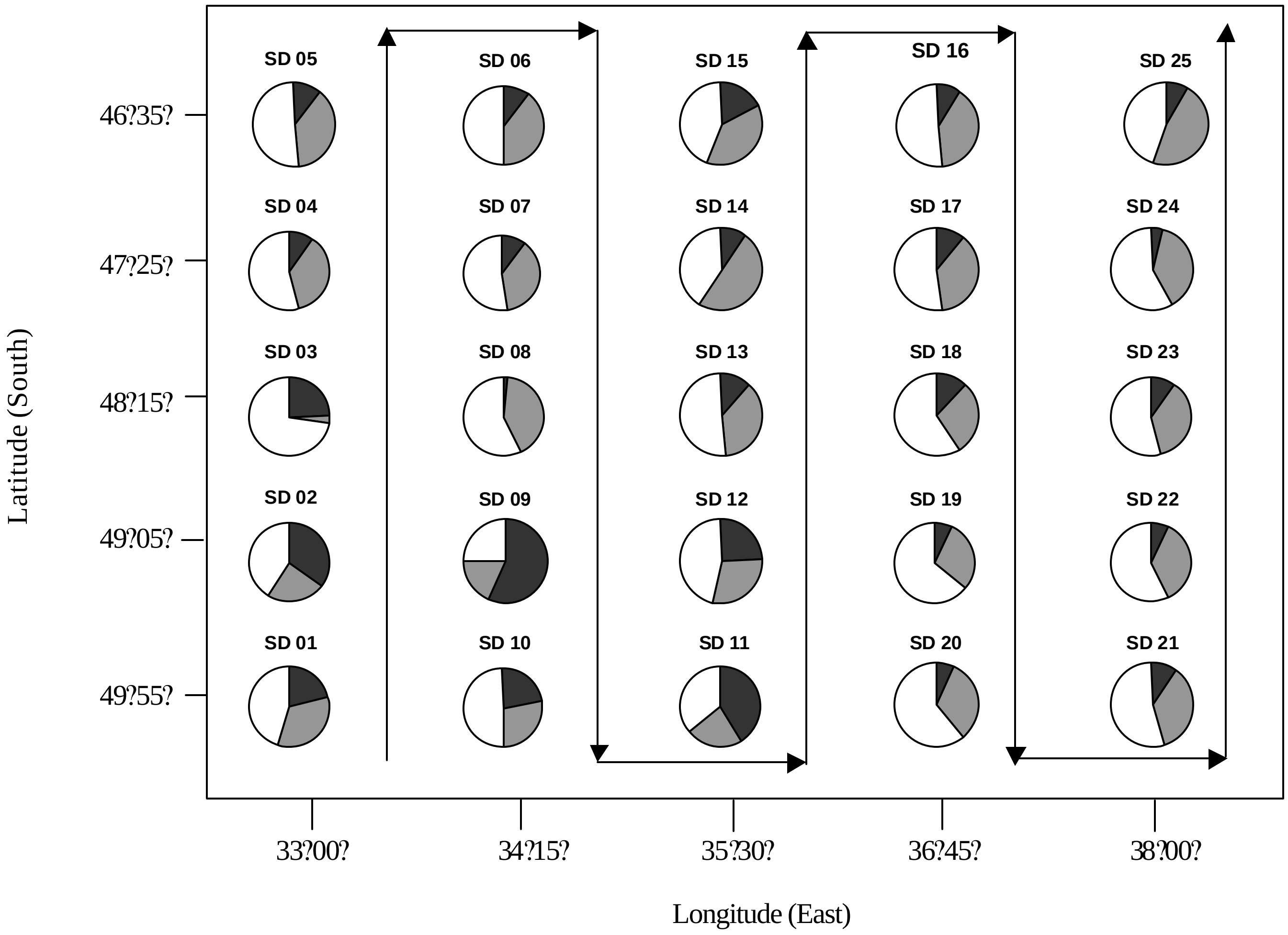

Figure 3.1. Size-fractionated chlorophyll-*a* concentrations at the mesozooplankton sampling stations, occupied during the first Marion Offshore Ecosystems Variability Study (MOEVS I), April 2001. White = picophytoplankton; grey = nanophytoplankton; black = microphytoplankton.

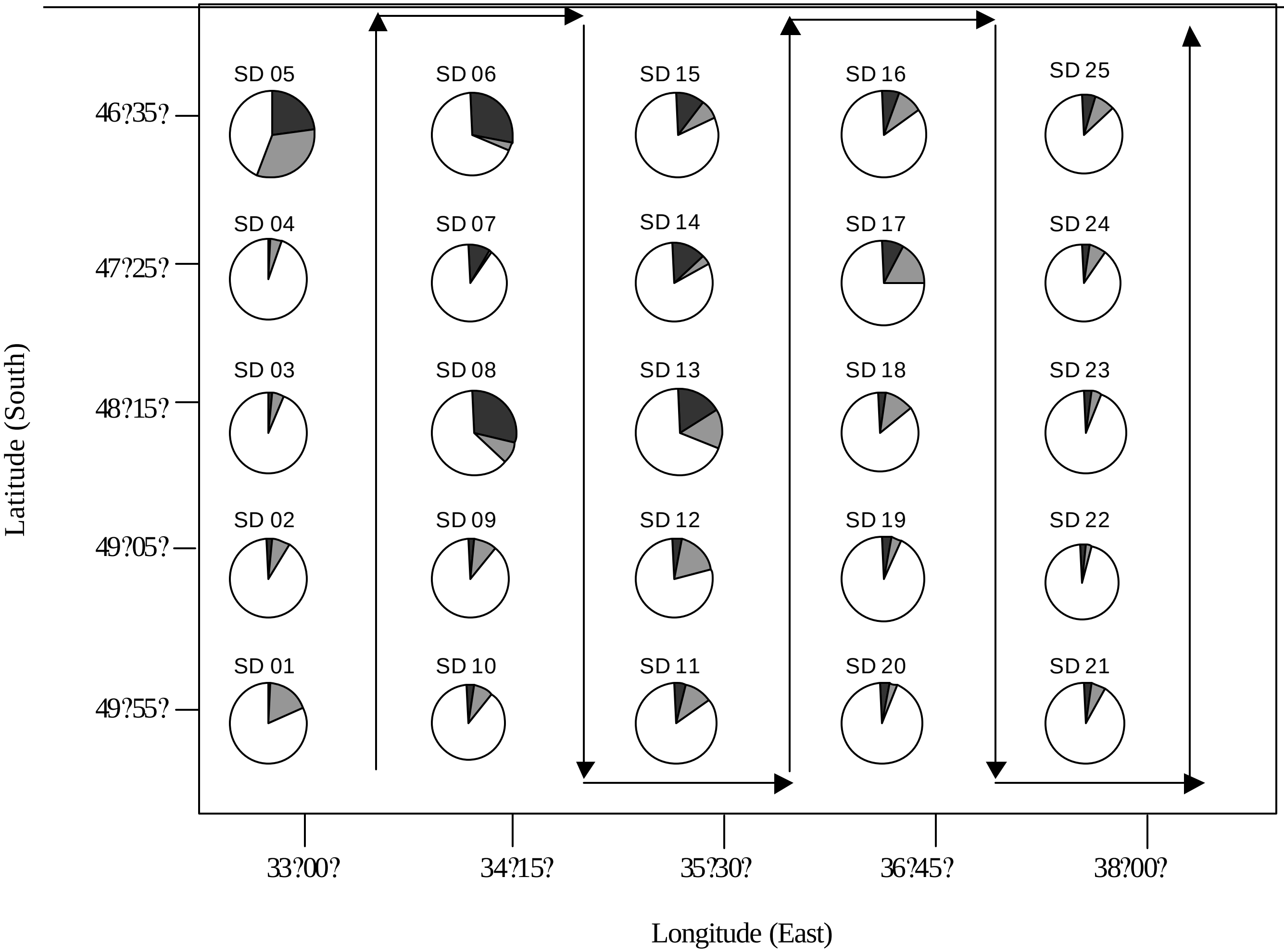

Figure 3.2. Mesozooplankton size-fractionated abundance at sampling stations occupied during the first Marion Offshore Ecosystems Variability Study (MOEVS I), April 2001. White = 200-500 ?m; grey = 500-1000 ?m; black = 1000-2000 ?m.

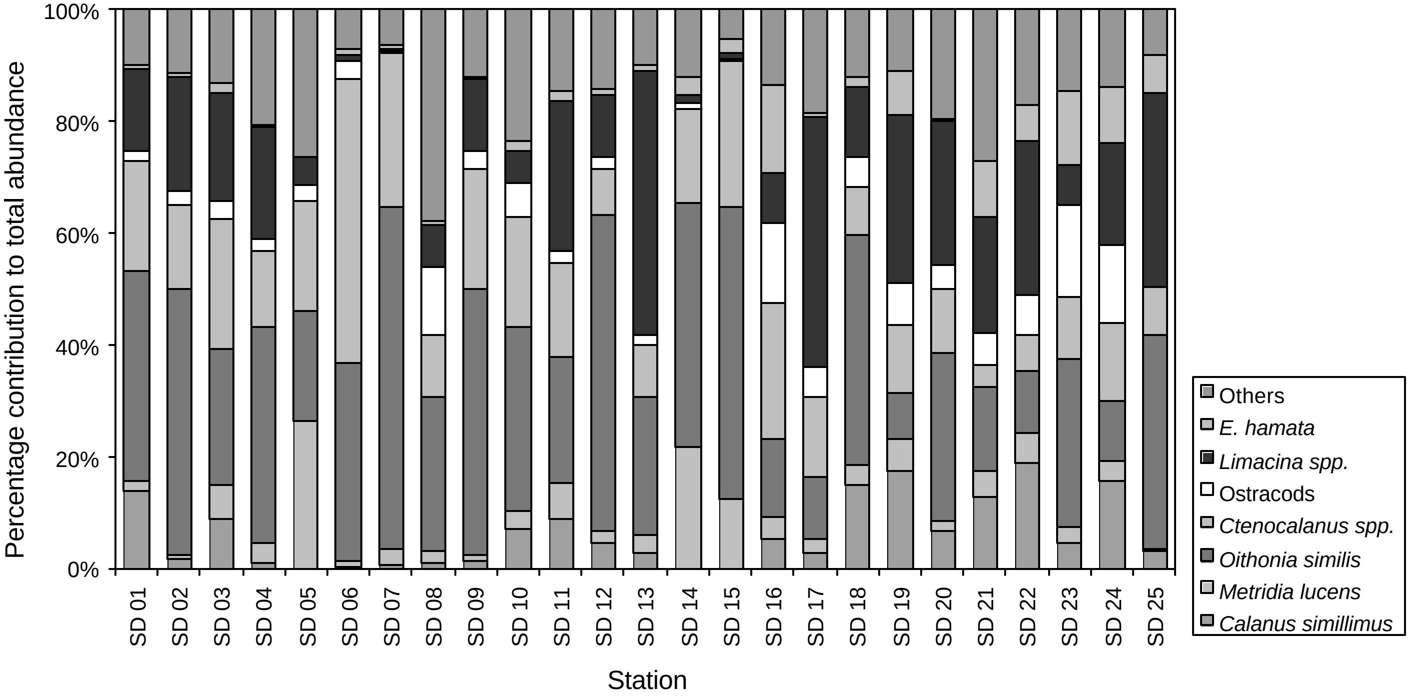

Figure 3.3. Contribution of the seven most abundant mesozooplankton taxa at the stations occupied during the first Marion Offshore Ecosystems Variability Study (MOEVS I), April 2001.

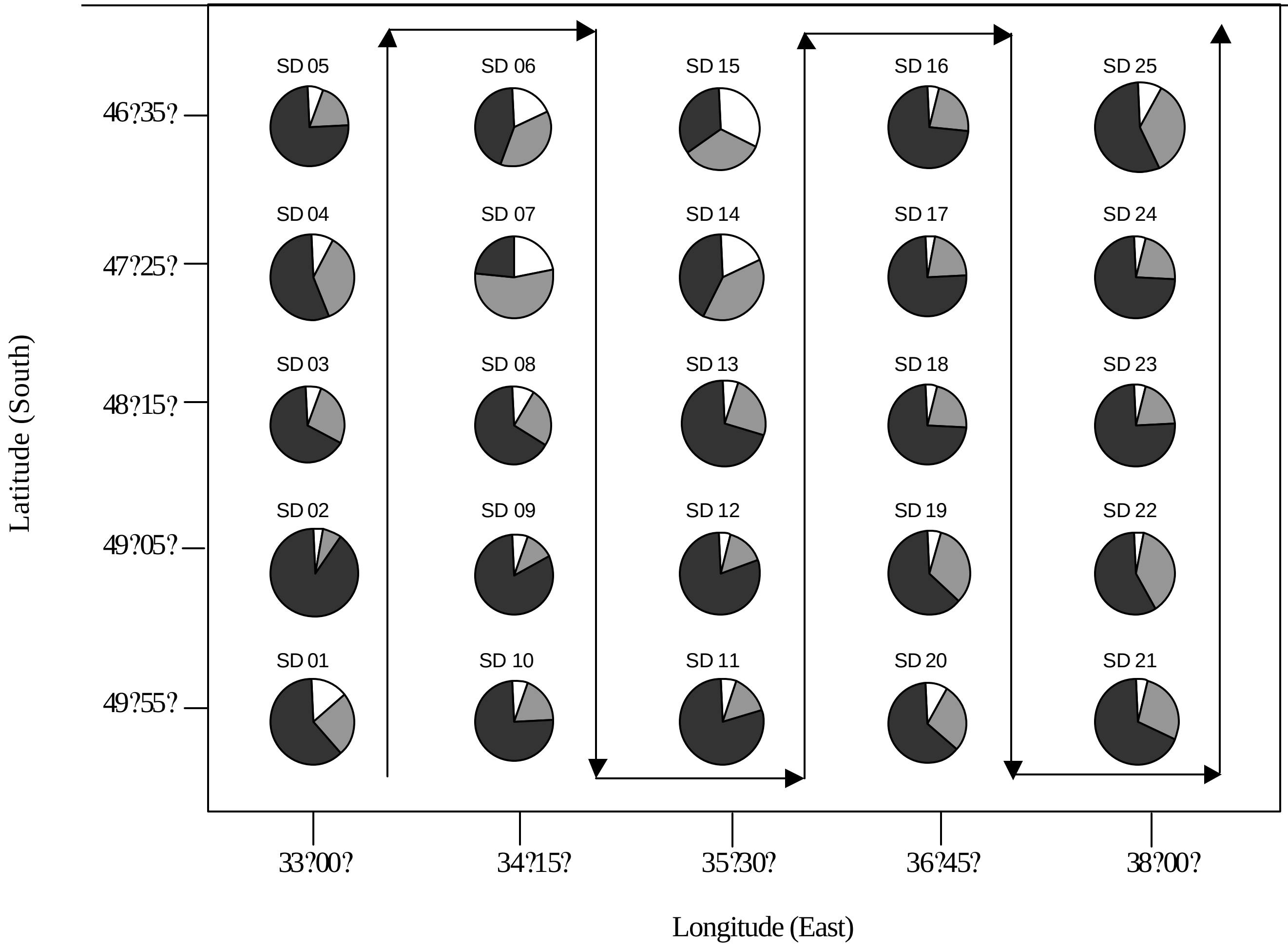

Figure 3.4. Mesozooplankton size-fractionated biomass at sampling stations occupied during the first Marion Offshore Ecosystems Variability Study (MOEVS I), April 2001. White = 200-500 ? m; grey = 500-1000 ?m; black = 1000-2000 ? m.

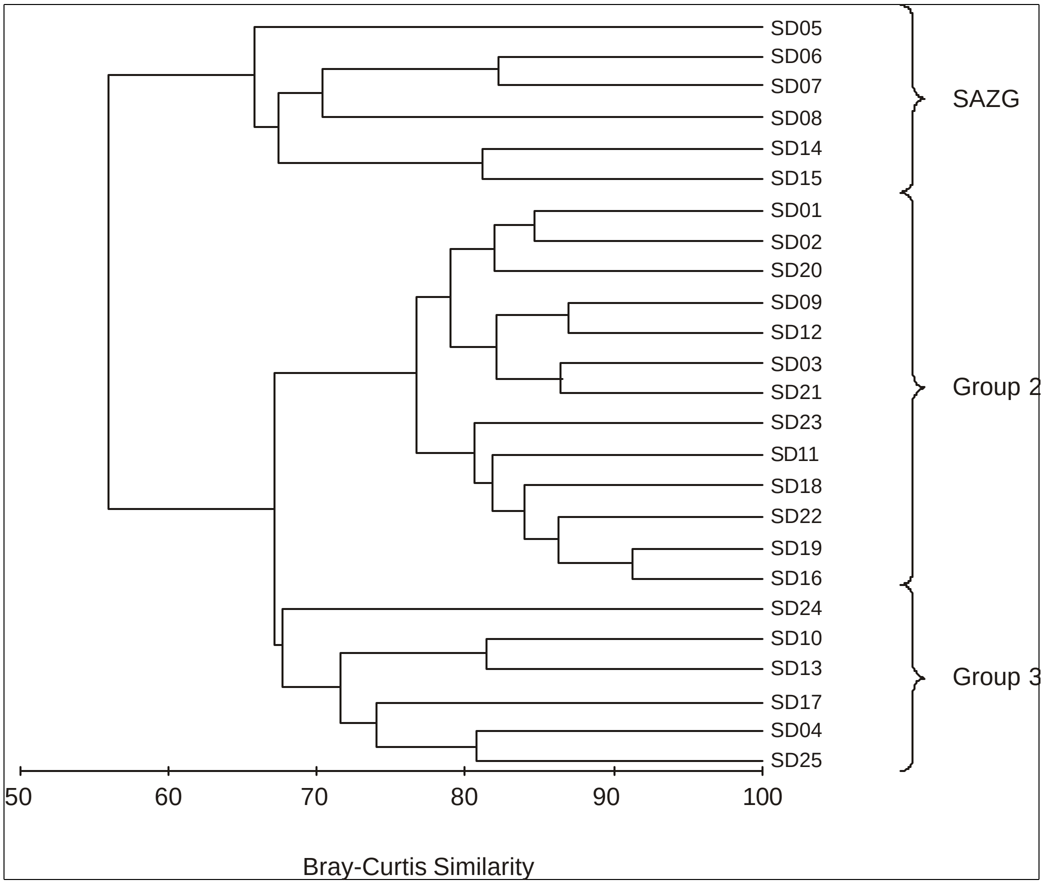

Figure 3.5. Dendrogram showing the classification of mesozooplankton data collected during the first Marion Offshore Ecosystem Variability Study (MOEVS I), April 2001 (PRIMER Computer Package). SAZG – Sub-Antarctic Zone Group.

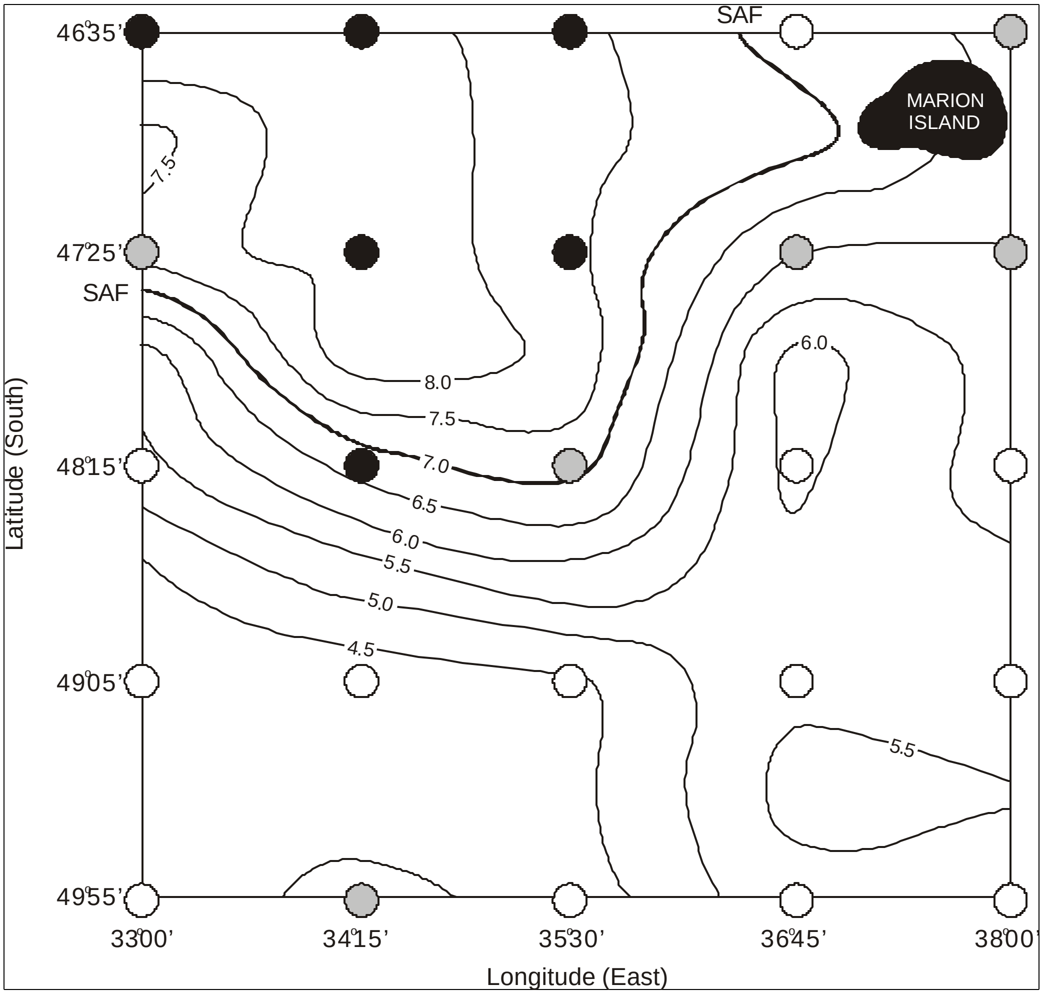

Figure 3.6. Station clusters, as identified with hierarchical cluster analysis (PRIMER Computer Package), superimposed on surface temperature isotherms. Black = SAZG; white = Group 2; grey = Group 3.

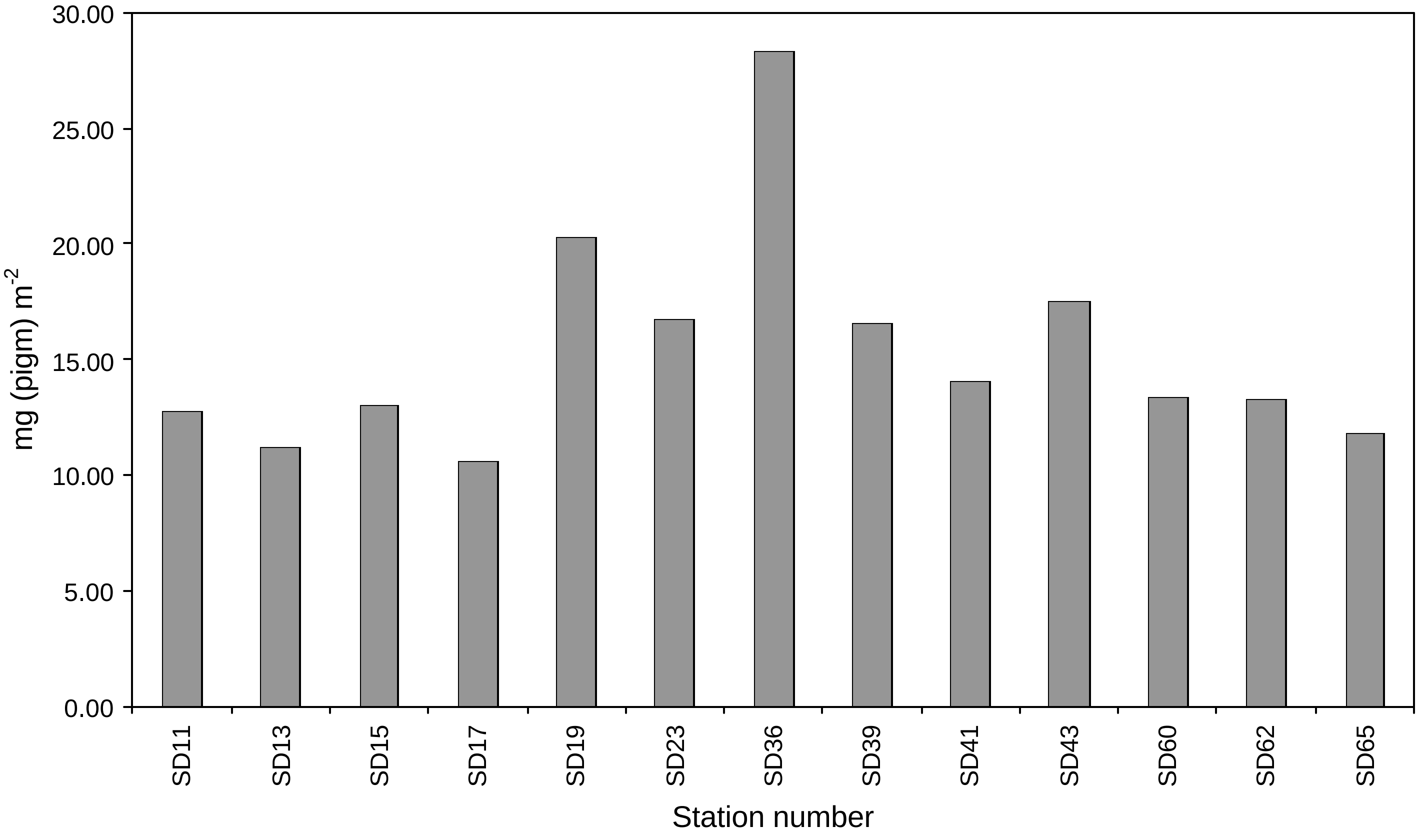

Figure 3.7. Integrated chlorophyll-*a* concentrations (top 100 m) at selected stations occupied during the second Marion Offshore Ecosystem Variability Study (MOEVS II), April 2002.

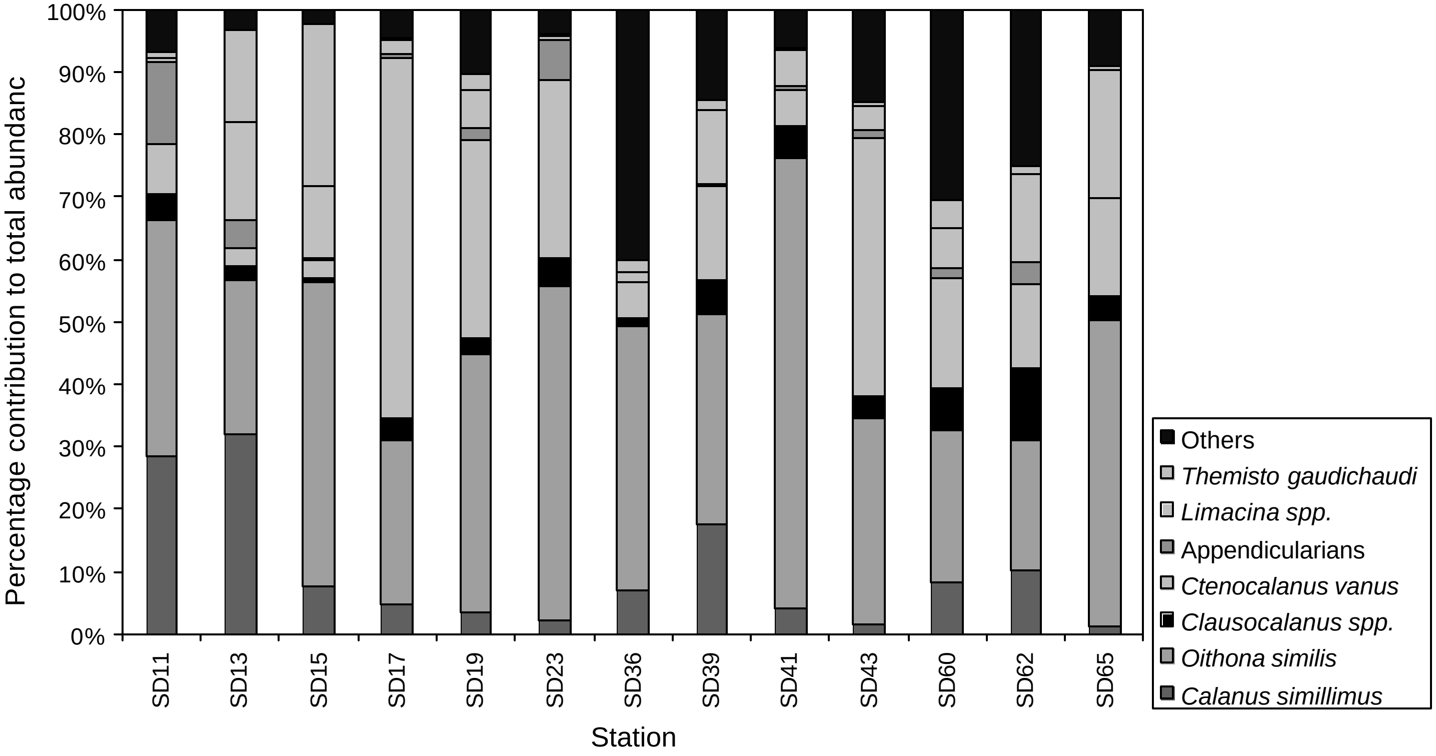

Figure 3.8. Contribution of the seven most abundant taxa to total mesozooplankton abundance during the second Marion Offshore Ecosystem Variability Study (MOEVS II), April 2002.

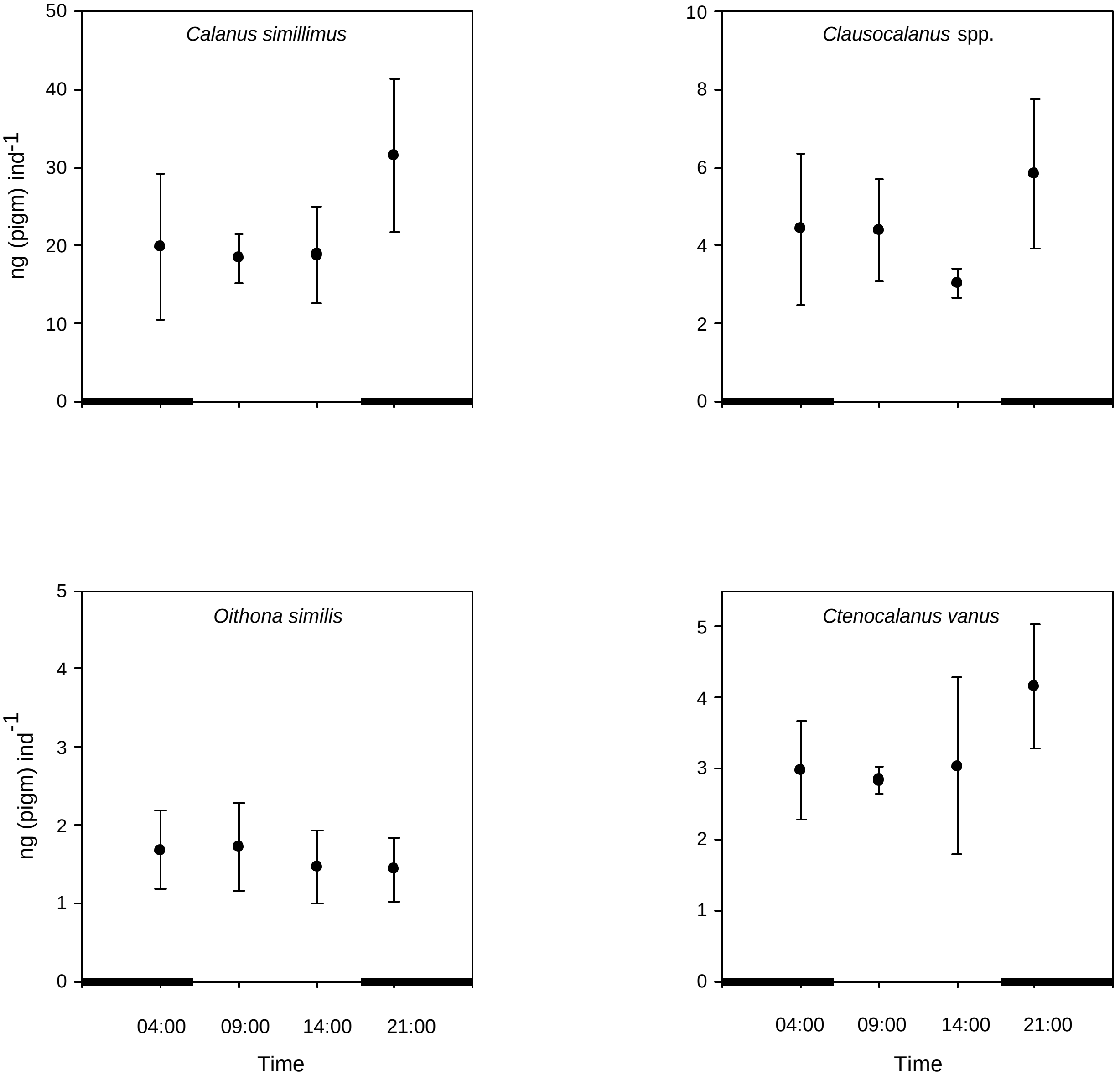

Figure 3.9. Diel variation in gut pigment contents of four species of copepod, during the second Marion Offshore Ecosystem Variability Study (MOEVS II), April 2002. Thickened parts of the x-axis represent night-time values.

Table 3.1. Total chlorophyll-*a* concentration (?g l^{-1}), mesozooplankton abundance (ind. m^{-3}) and biomass (mg Dwt. m^{-3}) values at stations occupied during the first Marion Offshore Ecosystem Variability Study (MOEVS I), April 2001.

Station number	Total chlorophyll-*a* (?g l$^{?1}$)	Total mesozooplankton abundance (ind. m$^{?3}$)	Total mesozooplankton biomass (mg Dwt. m$^{?3}$)
SD 01	0.122	629	7.468
SD 02	0.139	1222	25.717
SD 03	0.113	1063	11.726
SD 04	0.201	251	2.727
SD 05	0.197	49	2.172
SD 06	0.231	86	0.707
SD 07	0.289	118	0.831
SD 08	0.156	66	2.339
SD 09	0.248	1512	25.197
SD 10	0.144	104	6.752
SD 11	0.180	254	10.139
SD 12	0.124	848	16.809
SD 13	0.193	103	6.649
SD 14	0.184	120	1.771
SD 15	0.338	287	1.877
SD 16	0.208	121	6.937
SD 17	0.187	130	4.848
SD 18	0.143	366	6.122
SD 19	0.187	312	5.584
SD 20	0.208	367	6.325
SD 21	0.226	219	5.677
SD 22	0.151	253	11.243
SD 23	0.149	296	12.741
SD 24	0.146	428	6.026
SD 25	0.136	424	4.919

Table 3.2. Average abundances of the eight most abundant mesozooplankton species accounting for up to 80% of the similarity within each grouping identified with the cluster analysis. Data obtained during the first Marion Offshore Ecosystem Variability Study (MOEVS I), April 2001.

SUBANTARCTIC ZONE GROUP (SAZG) 69.00% similarity		GROUP 2 78.89% similarity		GROUP 3 71.88% similarity	
Species	Average abundance (ind. m^{-3})	Species	Average abundance (ind. m^{-3})	Species	Average abundance (ind. m^{-3})
Oithona similis	55.37	*O. similis*	219.23	*O. similis*	45.50
Ctenocalanus vanus	31.35	*L. retroversa*	108.37	*L. retroversa*	41.72
Clausocalanus brevipes	4.05	*C. vanus*	93.94	*C. vanus*	21.80
Metridia lucens	13.44	*Calanus simillimus*	47.04	*C. simillimus*	4.9
Limacina retroversa	2.27	*M. lucens*	17.55	*M. lucens*	4.15
Eukrohnia hamata	2.16	*E. hamata*	16.89	*C. brevipes*	6.11
Pleuromamma abdominalis	1.75	*Oithona frigida*	13.83	*E. hamata*	6.41
Scolecithricella minor	1.17	*Rhincalanus gigas*	10.42	*S. minor*	2.16

Table 3.3. Total mesozooplankton abundance (ind. m^{-3}) and biomass (mg Dwt. m^{-3}) values at grazing stations during the second Marion Offshore Ecosystem Variability Study (MOEVS II), conducted in April 2002.

Station	Total abundance (ind. m^{-3})	Total biomass (mg Dwt. m^{-3})
SD 11	431.15	5.42
SD 13	461.01	8.38
SD 15	452.57	33.22
SD 17	229.27	3.19
SD 19	869.42	13.95
SD 23	1372.93	5.12
SD 36	91.98	1.80
SD 39	41.35	1.31
SD 41	252.24	2.31
SD 43	155.80	3.66
SD 60	180.12	5.92
SD 62	42.82	3.48
SD 65	188.28	3.57

Table 3.4. Numerical abundance (ind. m^{-2}) of selected mesozooplankton species at grazing stations occupied during the second Marion Offshore Variability Ecosystem Study (MOEVS II), April 2002.

Taxon	Station number												
	SD11	SD13	SD15	SD17	SD19	SD23	SD36	SD39	SD41	SD43	SD60	SD62	SD65
Copepoda													
Calanus simillimus	4746.6	9596.2	1785.9	1078.5	567.4	1526.8	449.1	659.1	1003.5	59.8	1347.8	414.0	98.9
Clausocalanus spp.	706.9	620.9	167.4	764.4	409.8	3562.5	80.2	212.9	1318.9	149.6	1078.3	473.1	333.7
Ctenocalanus vanus	1312.9	903.2	669.7	13383.6	5106.2	21375.0	385.0	567.8	1462.3	1690.5	2815.5	532.2	1260.7
Oithona similis	6295.2	7394.7	11329.0	6079.0	6587.7	40132.6	2774.9	1277.6	18264.1	1346.4	3923.7	827.9	3967.6
Chaetognatha													
Sagitta gazellae	33.7	56.4	-	-	-	-	176.4	10.1	28.7	-	89.9	-	12.4
Eukrohnia hamata	875.3	338.7	55.8	-	94.6	290.8	1588.0	91.3	372.7	22.4	2246.4	354.8	86.5
Amphipoda													
Themisto gaudichaudi	84.2	2173.2	3041.5	24.5	204.9	145.4	28.1	15.2	21.5	9.4	179.7	14.8	12.4
Total	16529.0	27716.0	20286.2	22918.7	15712.7	74667.0	6424.0	3731.5	25123.8	3904.6	15417.8	3954.7	8006.2

Table 3.5. Coefficient of variance for gut evacuation rate value (r^2 values; $P < 0.05$ in all cases), gut evacuation rate (k, h^{-1}), average daily ingestion rates [ng (pigm) ind^{-1} day^{-1}] and carbon specific ingestion rates of selected copepod species during the second Marion Offshore Variability Ecosystem Study (MOEVS II), April 2002. Values in brackets are standard deviation.

Taxon	r^2	k (h^{-1})	Average daily ingestion rate [ng (pigm) ind^{-1} day^{-1}]	Individual dry weight (?g)	Carbon ration (% body C day^{-1})
Calanus simillimus	0.236	0.318	618.61 (312.78)	92.5 (12.87)	83.5 (42.2)
Clausocalanus spp.	0.0213	0.444	123.66 (86.52)	36.8 (13.69)	42.0 (29.4)
Ctenocalanus vanus	0.2297	1.428	81.34 (16.62)	6.1 (0.65)	166.7 (34.1)
Oithona similis	0.3741	0.768	39.37 (9.81)	1.54 (Atkinson 1996)	319.6 (79.6)

Table 3.6. Integrated phytoplankton biomass, zooplankton ingestion rates and grazing impact at grazing stations occupied during the second Marion Offshore Variability Ecosystem Study (MOEVS II), April 2002.

	Phytoplankton biomass	Daily ingestion rates [mg (pigm) m $^{-2}$]				Daily grazing impact
Station	[mg (Chl-a) m^{-2}]					% phytoplankton biomass
		Calanus simillimus	*Clausocalanus spp.*	*Ctenocalanus vanus*	*Oithona similis*	
SD11	12.75	1.33	0.06	0.22	0.27	18.59
SD13	11.17	2.7	0.05	0.15	0.32	28.79
SD15	12.99	0.5	0.01	0.11	0.49	8.59
SD17	10.57	0.3	0.06	2.22	0.26	26.94
SD19	20.31	0.16	0.03	0.85	0.28	6.52
SD23	16.7	0.43	0.28	3.55	1.73	35.86
SD36	28.34	0.13	0.01	0.06	0.12	1.12
SD39	16.54	0.19	0.02	0.09	0.06	2.12
SD41	14.06	0.28	0.1	0.24	0.79	10.08
SD43	17.54	0.02	0.01	0.28	0.06	2.09
SD60	13.38	0.38	0.08	0.47	0.17	8.22
SD62	13.29	0.12	0.04	0.09	0.04	2.09
SD65	11.77	0.03	0.03	0.21	0.17	3.69

CHAPTER FOUR: DISCUSSION

4.1. MARION OFFSHORE ECOSYSTEM VARIABILITY STUDY I - APRIL 2001

The position of the surface expression of the Sub-Antarctic Front (SAF) between 47 ? and 47?25? S is in agreement with previous investigations (Lutjeharms & Valentine 1984; Ansorge et al. 1999; Froneman et al. 1999; Pakhomov et al. 2000 a).

In contrast to the majority of previous studies conducted in the Polar Frontal Zone (PFZ) during austral summer and autumn (Froneman et al. 1995a, b; Pakhomov & Froneman 1999), no enhancement of chlorophyll-*a* (chl-*a*) concentration was found at stations occupied in the region of the SAF. This result is, however, in agreement with Froneman et al. (1999), highlighting the variability in the biology of the region. Generally, pico- (0.45–2.0 ? m) and nanophytoplankton (2.0–20 ? m) dominated total chl-*a* throughout the survey, which is consistent with previous investigations conducted in the PFZ during different seasons (Jacques 1989; Laubscher et al. 1993; Froneman et al. 2001). The predominance of pico- and nanophytoplankton appears to be related to high wind activity and low macro-nutrient concentrations, which favour the growth of small phytoplankton cells (Laubscher et al. 1993; Froneman et al. 2001). Exceptions were recorded in the southern vicinity of the SAF, where microphytoplankton (>20 ? m) dominated total chl-*a*, a finding common to many investigations in the region (e.g. El-Sayed 1988; Jacques 1989; Laubscher et al. 1993; Froneman & Pakhomov 2000; Froneman et al. 2001). Since microphytoplankton dominated in the vicinity of the front, one would expect the region to exhibit elevated levels of phytoplankton biomass (Allanson et al. 1981; Laubscher et al. 1993; Froneman et al. 2001), this, however, was not the case and may be the result of zooplankton grazing.

The estimates of mesozooplankton abundance and biomass during this study are substantially higher than those reported in previous studies conducted in both the inshore and off-shore environments of the Prince Edwards Islands (PEI) during austral autumn (Allanson et al. 1985; Froneman & Pakhomov 1998; Pakhomov & Froneman 1999; Pakhomov et al. 1998; Froneman et al. 1999). For example, Hunt et al. (2001), summarising data collected over the period 1996 to 1999, estimated that zooplankton abundances ranged between 57.48 and 139.92 ind. m^{-3} and biomass between 4.23 and 10.33 mg Dwt. m^{-3} (Table 4.1.). During the present study, mesozooplankton abundances ranged between 49 and 1512 ind. m^{-3} and biomass between 5.68 and 25.72 mg Dwt. m^{-3} (Table 4.1.). Although differences in the results between the various studies may reflect inter-annual variability, it is more likely that the higher biomass and abundance values recorded here can be related to the sampling gear employed (Table 4.1.). Previous studies employed Bongo nets fitted with 300 and 500 ?m nets that would not have sampled the smaller copepods or the early developmental stages of mesozooplankton species efficiently (Gallienne & Robins 2001). Indeed, during this study, the small copepod *Oithona similis* (which would have been missed by the coarser mesh sizes of previous surveys) contributed most to the total mesozooplankton numbers at all stations, constituting, on average, 59% of the total. It should be noted, however, that the zooplankton abundance and biomass recorded during the present study are themselves likely to have been underestimated, as a recent study conducted by Gallienne & Robins (2001) suggests that a mesh size of 200 ?m may result in an underestimation of up to 70% of the smaller mesozooplankton biomass.

Total abundance and biomass estimates showed similar spatial trends, with the greatest values occurring in the colder waters south of the SAF and the lowest values north of the front where warmer waters were encountered. Intermediate values in both abundance and biomass were recorded in the transition zone between the cold and warm waters. Similar patterns in zooplankton abundance and biomass have been observed during previous investigations in the PFZ (Froneman & Pakhomov 1998; Ansorge et al. 1999; Froneman et al. 1999; Pakhomov & Froneman 2000; Pakhomov et al. 2000 a, b). The mesozooplankton species composition comprised mainly the copepods, *Calanus simillimus*, *Metridia lucens*, *Oithona similis* and *Ctenocalanus* spp., the pteropod *Limacina* spp., and ostracods. As is typical for the PFZ, the community structure consisted of a mixture of species of sub-Tropical, sub-Antarctic and Antarctic origins (Ansorge et al. 1999; Froneman et al. 1999; Pakhomov & Froneman 1999). A distinct shift in mesozooplankton species composition was observed across the SAF, complementing previous studies that highlight the importance of this front as a biogeographical boundary to the distribution of plankton species (Froneman et al. 1995a, b; Pakhomov & McQuaid 1996). The major differences between the communities were due to the relative abundances of species, rather than the presence/absence of stenotypic zooplankton. Copepods were, by far, the most numerous of all mesozooplankton groups, comprising up to 89% of total numbers, a finding which is common to many investigations in a variety of oceanic regions (e.g. Conover & Huntley 1991; Pakhomov & Perissinotto 1997; Froneman & Pakhomov 1998; Voronina 1998; Pakhomov & Froneman 1999; Pakhomov et al. 2000a; Auel & Hagen 2002).

The 200-500 ?m size fraction dominated total mesozooplankton numbers throughout the survey, with the cyclopoid copepod, *Oithona similis*, being the most abundant species. Fairly recent evidence, noting the numerical dominance of small copepod species (particularly the cyclopoid species) in many oceanic environments, supports this finding (e.g. Turner & Dagg 1983; Turner 1994; Atkinson 1996; Errhif et al. 1997; Gallienne & Robins 2001; Auel & Hagen 2002; Dubischar et al. in press). Total mesozooplankton biomass was, on the other hand, dominated by the 1000-2000 ?m fraction. This finding, although not always observed in the Southern Ocean (e.g. Hernández-León et al. 1999; Pakhomov et al. 2000a), is in agreement with many previous investigations in the region (Bradford-Grieve et al. 1998; Pakhomov et al. 1999; Hernández-León et al. 2000).

Pakhomov et al. (1999) showed that the zooplankton biomass in the region between the SAF and the Subtropical Convergence (STC) was dominated by carnivores, comprising chaetognaths, amphipods and euphausiids. Analysis of the zooplankton community composition within the 1000-2000 ?m size class during the present investigation agreed with this observation; with chaetognaths and euphausiids numerically dominating the samples. It appears therefore, that the zooplankton community encountered during this survey was similar in composition to that recorded in the region between the SAF and STC in austral summer 1993 (Pakhomov et al. 1999). This result is hardly surprising, as the PFZ is considered as a transition zone between the Antarctic and the sub-Antarctic Zones. According to Pakhomov et al. (1999), the high abundances of predators found between the SAF and STC reflect relative stability in food resources. Estimates of the predation impact of carnivorous zooplankton on the mesozooplankton in the PFZ during autumn range between 5 and >100% of the standing stock (Froneman et al. 1998; Froneman & Pakhomov 1998; Pakhomov et al. 1999; Froneman et al. 2000; Froneman et al. 2002a). Gut content analyses indicate that small copepods, particularly *Oithona*, *Clausocalanus* and *Calanus* spp., are the main prey items in the guts of the dominant carnivorous zooplankton in the PFZ (Froneman et al. 2002b). These data suggest that the size structure of the mesozooplankton in the PFZ is likely to be determined by the predatory effects of the large number of carnivorous zooplankton in the region.

4.2. MARION OFFSHORE ECOSYSTEM VARIABILITY STUDY II - APRIL 2002

It has been documented during previous oceanographic investigations that complex fracture zones in the south-west Indian Ridge significantly affect the flow of the Antarctic Circumpolar Current (ACC) (Hoffmann 1985; Pollard & Read 2001; Park et al. 2001). During the present study, the Andrew Bain Fracture Zone (50?S, 30?E) functioned as an important choke point to the flow of the ACC, resulting in the convergence of the Antarctic Polar Front (APF) and the southern branch of the SAF (SSAF). East of 32?E, the APF/SSAF separated, with the APF meandering eastwards across the Enderby Plain, while the SSAF was deflected northwards where it converged with the SAF at ~ 48?S (Froneman et al. 2002b).

The values of integrated phytoplankton biomass obtained during the present study are in the same range as previous investigations conducted in the Polar Frontal Zone (PFZ) during austral autumn (Pakhomov & Froneman 1999, and references therein). Integrated chl-*a* values ranged from 11.17 – 28.34 mg (pigm) m^{-2} and showed no particular spatial trends. Surprisingly, no enhancement of chl-*a* biomass was recorded in the vicinity of the SSAF or APF. The absence of a peak in chl-*a* concentrations in the vicinity of these two fronts highlights the temporal variability in the biology of the Southern Ocean, or alternatively, may reflect the grazing activity of the herbivorous zooplankton in the region. Throughout the investigation, pico- and nanophytoplankton (<20 ?m) dominated total integrated chl-*a* biomass (Froneman et al. 2002b). This finding is in agreement with previous studies conducted in the PFZ during austral autumn (Bernard & Froneman 2002; Gurney et al. 2002) and can be related to the high wind activity and low macronutrient concentrations in the region, which favour the production of small phytoplankton cells (Laubscher et al. 1993; Froneman et al. 2001).

Abundances and biomass of mesozooplankton during the investigation ranged from 41.35 to 1372.93 ind. m^{-3} and from 1.31 to 33.22 mg Dwt. m^{-3} respectively (Table 4.1.). These values are in agreement with those obtained during the MOEVS I cruise. The highest concentrations of mesozooplankton were generally observed at stations near the APF, supporting previous findings that biological enhancement occurs close to oceanic fronts (Pakhomov & Perissinotto 1997; Smetacek et al. 1997; Froneman et al 2000). The elevated zooplankton abundances recorded in the region of the APF support recent suggestions that the front represents an important feeding ground for the top predators found on the Prince Edward Islands (Nel et al. 2001). The lowest abundances of mesozooplankton were observed within the transitional waters of the PFZ. Total mesozooplankton biomass values were also very similar to those obtained during MOEVS I, ranging from 1.31 to 33.22 mg Dwt. m^{-3} (Table 4.1.). Peaks in biomass did not, however, correspond to peaks in abundance. This is probably due to the fact that smaller copepods with low biomasses contributed most to total abundance. The greatest biomass was observed at station SD 15, where very high numbers of the amphipod *Themisto gaudichaudi* were recorded. The lowest biomass values were observed north of the APF, corresponding to the low abundances in that region. Of interest is the fact that the station with the highest abundance (SD 23) exhibited a below-average biomass, due to the predominance of *Ctenocalanus vanus* and *Oithona similis.*

The species composition of the mesozooplankton community and the numerical dominance of the small calanoid copepods, *Calanus simillimus*, *Clausocalanus* spp., *Ctenocalanus vanus* and the cyclopoid copepod, *Oithona similis*, during MOEVS II are in agreement with the findings of MOEVS I, (Bernard & Froneman 2002; see also section *3.1.* above). It should be noted that estimates of zooplankton abundance should be regarded with caution, as the sampling gear employed is likely to have underestimated the contribution of smaller copepods and copepodite stages, particularly *Oithona* spp., to total mesozooplankton abundance (Gallienne & Robins 2001). Swarms of predatory zooplankton, comprising the amphipod *Themisto gaudichaudi* and the chaetognaths *Eukrohnia hamata* and *Sagitta gazellae*, were occasionally observed during the study. Recent studies indicate that these carnivores prey preferentially on the dominant copepods in the PFZ (Froneman et al. 1998; Froneman & Pakhomov 1998; Pakhomov et al. 1999; Froneman et al. 2000; Froneman et al. 2002a). It is, therefore, likely that the presence of such predators, although patchy, will play an important role in structuring the local mesozooplankton community of the PFZ (see also section *4.1.* above).

The gut evacuation rates (k, h^{-1}) and average daily ingestion rates of the four copepod species investigated during this study are similar to estimates for the same species or copepods of similar size obtained in previous studies (see Table 4.2. and references therein). As expected, the largest of the four copepods, *Calanus simillimus*, exhibited the highest average daily ingestion rate [~ 618.61 ng (pigm.) ind^{-1} day^{-1}], while *Oithona similis*, the smallest, showed the lowest average daily ingestion rate [~ 39.37 ng (pigm.) ind^{-1} day^{-1}]. Carbon derived from the consumption of phytoplankton was equivalent to between 42 and 320% body carbon per day, depending on species. The mass specific carbon ingestion rates reported here are substantially higher than those reported in other regions of the Southern Ocean (Atkinson 1994, 1996; Swadling et al. 1997). Analysis of the literature indicates that copepods preferentially consume particles in the nano- (2 to 20 ?m) size class (Fortier et al. 1994). Throughout the present study, pico- and nanophytoplankton dominated total chl-*a* concentrations. The high mass specific ingestion rates of the four copepod species therefore probably reflect the favourable size structure of the phytoplankton community. The high carbon specific ingestion rates of the four copepods measured during the study suggest that carbon derived from the consumption of phytoplankton was sufficient to meet their basic metabolic requirements. The need for a contribution from alternative carbon sources (e.g. protozooplankton and faecal material) to the total daily carbon ration of the four copepod species appears, therefore, to be minimal. However, the possibility cannot be excluded that alternative sources of carbon are consumed during austral summer, when large microphytoplankton tend to dominate total chl-*a* (Froneman et al. 2001).

The combined daily grazing impact of the four copepod species, which comprised up to 93% of the total mesozooplankton abundance, ranged between 1 and 36% of the phytoplankton biomass (Table 4.1.). These estimates are within the range previously reported for the PFZ during the same season (Perissinotto 1992). On the other hand, the estimates of grazing impact presented here are substantially higher than those carried out in the same region in austral summer, where the zooplankton community impact was equivalent to <10% of the phytoplankton biomass (Dubischar & Bathmann 1997; Froneman et al 2000). Studies conducted in the PFZ during austral summer indicate that microphytoplankton (>20 ?m), comprising mainly chain forming diatoms of the genus *Chaetoceros*, may contribute up to 40% of total phytoplankton biomass (Froneman et al. 2001). The lower grazing impact of the copepods during summer probably reflects the inability of small copepods to feed on large microphytoplankton (Fortier et al. 1994). These data suggest that a seasonal pattern in the grazing impact of copepods exists within the PFZ, with maximum rates recorded during winter when small phytoplankton cells dominate total chl-*a*. The levels of grazing by the copepods presented here are in the range reported for other regions of the Southern Ocean (Atkinson & Shreeve 1995; Pakhomov & Perissinotto 1997; Pakhomov et al. 1997; Froneman et al. 2000).

Table 4.1. Comparison of average abundance and biomass values from investigations employing 300 ?m and 200 ? m mesh nets.

Net, mesh (? m)	Mean abundance (range/standard deviation)	Mean biomass (range/standard deviation)	Source
300	ND	7.7 (1.04-62.70)	Ansorge et al. 1999
300	160 (130-191)	44.5 (32.3-56.8)	Perissinotto 1992
300	ND	0.14 (0.05-0.3)	Perissinotto et al. 2001
300	96 (25-192)	2.8 (0.6-7.75)	Froneman & Pakhomov 1998
300	(10-490)	(<4-63)	Pakhomov et al. 2000 a
300	(7-274)	(0.6-15.9)	Pakhomov et al. 2000 a
300	73 (43)	7.5 (4.3)	Hunt et al. 2001
300	ND	3.2 (0.33-15.69)	Froneman et al. 1999
300	153 (72)	8.0 (2.4)	Hunt et al. 2001
300	73 (73)	10.3 (11.7)	Hunt et al. 2001
300	65 (25)	8.7 (5.5)	Hunt et al. 2001
300	97 (31)	12.0 (4.6)	Hunt et al. 2001
200	**385 (49-1512)**	**8.0 (0.71-25.72)**	**MOEVS I**
200	**367 (41-1373)**	**7.03 (1.31-33.22)**	**MOEVS II**

Table 4.2. Estimates of gut evacuation rates (k, h^{-1}) and ingestion rates (IR) of selected copepod species compared with results from the present study (MOEVS II, April 2002).

Source	Size/species	k (h^{-1})	IR ($ng.ind^{-1} day^{-1}$)	Season
Perissinotto (1992)	*Calanus simillimus*	1.96	ND	Autumn
	Clausocalanus brevipes	1.41	ND	
Pakhomov et al. (1997)	*C. simillimus*	ND	213.2	Summer
Pakhomov & Perissinotto (1997)	*Calanus* spp.	3.674	383.6	Winter
	Small copepods	4.573	ND	
	Metridia spp.	1.289	115.0	
Froneman et al. (2000)	*Calanus propinquus*	1.020	ND	Summer
	C. simillimus	2.359	ND	
Atkinson (1996)	*Oithona* spp.	1.46	ND	Summer
	C. simillimus	1.07	ND	
	Clausocalanus laticeps	0.856	ND	
	Metridia lucens	0.46	ND	
Atkinson et al. (1992 b)	*C. simillimus*	1.12	82	Summer
	Calanoides acutus	2.56	775	
MOEVS II	*C. simillimus*	0.318	618.61	Autumn
	Clausocalanus spp.	0.444	123.66	
	Ctenocalanus vanus	1.428	81.34	
	Oithona similis	0.768	39.37	

CHAPTER FIVE: SYNTHESIS

In the Polar Frontal Zone (PFZ), during austral autumn of 2001 and 2002, phytoplankton biomass (chl-*a*) was generally low, ranging between 0.11 and 0.34 ?g l^{-1} (surface chl-*a*) and between 11.17 and 28.34 mg m^{-2} (integrated chl-*a*). During both periods, the phytoplankton community was dominated by pico- (0.45–2.0 ?m) and nanophytoplankton (2.0–20 ?m), which formed up to 95% of the total phytoplankton biomass. Exceptions existed in the vicinity of the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF), where microphytoplankton (>20 ?m) comprised a significant proportion (up to 35%) of total pigment. The dominance of microphytoplankton in these regions did not always correspond with enhanced phytoplankton biomass, which probably reflects grazing by zooplankton assemblages within these regions. Indeed, it is worth noting that the highest zooplankton grazing impact during 2002 was recorded at stations occupied in the vicinity of the APF.

During both investigations (MOEVS I and II), the total mesozooplankton abundance and biomass values were highly variable, ranging from 41 to 1512 ind. m^{-3} and from 0.7 to 33.2 mg Dwt. m^{-3}, respectively, this range, however, did not change substantially from one year to the next. Elevated values of both abundance and biomass were observed in the vicinity of the SAF and APF, highlighting the importance of these regions as areas of enhanced biological productivity. Size-fractionated studies of the mesozooplankton community structure, conducted during the MOEVS I study (April 2001), indicated that the 200-500 ?m fraction dominated total mesozooplankton numbers, comprising approximately 69% (SD ? 12.3%) of the total. This size class consisted primarily of small copepods, particularly the cyclopoid, *Oithona similis.* In contrast, total mesozooplankton biomass was dominated by the 1000-2000 ?m fraction, contributing an average of 66% (? 10.2%) to the total dry weight. Carnivorous zooplankton, mainly chaetognaths (*Eukrohnia hamata* and *Sagitta gazellae*), euphausiids (*Euphausia vallentini*, *Thysanoessa vicina* and *E. longirostris*) and amphipods (*Themisto gaudichaudi*) dominate this size class. The predominance of carnivores within the 1000-2000 ?m size class suggests that these organisms are likely to play an important role in structuring the mesozooplankton community of the region. Indeed, it has previously been documented that these predators feed on the most abundant mesozooplanktonic species in the PFZ (Pakhomov et al. 1999; Froneman et al. 2002a), consuming up to 44% of the mesozooplankton standing stock per day.

The results of the grazing studies of the four dominant copepod species (*Calanus simillimus*, *Clausocalanus* spp., *Ctenocalanus vanus* and *Oithona similis*) within the PFZ during the MOEVS II study suggests that these species have a significant impact on the phytoplankton biomass in the region. Together, they were capable of removing up to 36% (1 – 36%) of the phytoplankton standing stock per day, with the highest grazing impact occurring in the vicinity of the APF. Among the four copepods, *C. vanus* and *O. similis* were responsible for the majority (up to 89%) of the total daily grazing impact. Carbon specific ingestion rates of these two copepods (>100% body carbon per day) suggested that both species were consuming sufficient phytoplankton-derived carbon to meet their daily metabolic requirements.

5.1. FUTURE RESEARCH INITIATIVES

5.1.1. Indirect evidence suggests that the numerically dominant mesozooplankton (small copepods) exhibit a seasonal grazing impact, with the strongest feeding effects being recorded during winter (Perissinotto 1992) and the weakest during summer (Pakhomov et al. 1997; Froneman et al. 2000). Since few grazing studies have been conducted on the small copepods in the PFZ during austral spring, summer and winter, it would be essential to undertake investigations during these periods in order to assess the seasonal variation in grazing pressure.

5.1.2. It has been suggested that alternative carbon sources (e.g. protozoans and microheterotrophs) play an important role in the diet of small copepods during the warmer months in the Southern Ocean, when microphytoplankton dominate total chl-*a* (Atkinson 1996). It is likely, therefore, that the small copepods in the PFZ might also consume alternative sources of carbon during austral summer. Future research should thus aim to assess the seasonal role of alternative sources of carbon (protozooplankton) in the diets of the small copepods in other regions of the Southern Ocean, particularly the PFZ.

5.1.3. Predation of mesozooplankton by omnivorous macrozooplankton (e.g. euphausiids) appears also to exhibit seasonal variation (Gurney et al. 2002). It is likely that during austral autumn and winter, when small phytoplankton cells dominate, macrozooplankton prey preferentially on mesozooplankton. During austral spring and summer, when microphytoplankton make a more substantial contribution to total chl-*a* concentration, the herbivorous feeding mode is likely to prevail. Thus, seasonal investigations need to be conducted in order to examine the effect of predators on the mesozooplankton community structure of the PFZ.

5.1.4. It can be assumed, when mesozooplankton represent the most important consumers of phytoplankton, that the transfer of carbon to depth is relatively inefficient (Fortier et al. 1994). However, predatory macrozooplankton feeding on mesozooplankton is likely to enhance the local efficiency of the biological pump. During periods when macrozooplankton represent the dominant grazers of phytoplankton, the relative efficiency of the biological pump within the PFZ will probably be substantially enhanced. It is, therefore, important that seasonal studies examining the vertical flux of carbon in the PFZ be undertaken to assess the role of this region in the Southern Ocean carbon cycle.

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APPENDIX

Table A.1. Species list for the Marion Offshore Ecosystem Variability Study I, April 2001.

Species or taxa	Species or taxa
Copepoda (Calanoida)	Copepoda (Cyclopoida)
Rhincalanus gigas	*Oithona similis*
Subeucalanus longiceps	*Oithona frigida*
Candacia maxima	Copepoda (Harpacticoida)
Candacia spp.	*Microsetella rosea*
Microcalanus spp.	Copepoda (Poecilostomatoida)
Calanoides acutus	*Oncaea antarctica*
Calocalanus spp.	Ostracoda
Gaetanus minor	Appendicularia
Metridia lucens	Pteropoda
Paraeuchaeta biloba	*Limacina* spp.
Paraeuchaeta exigua	Tunicata
Paraeuchaeta spp.	*Salpa thompsoni*
Heterorhabdus austrinus	Nauplii
Aetideus spp.	Chaetognatha
Clausocalanus laticeps	*Sagitta gazellae*
Ctenocalanus spp.	*Eukrohnia hamata*
Pleuromamma abdominalis	*Eukrohnia marri*
Pleuromamma gracilis	
Scaphocalanus spp.	
Scolecithricella minor	
Racovitzanus spp.	

Table A.2. Mesozooplankton sampling stations during the Marion Offshore Ecosystem Variability Study I, April 2001.

Station	Date	Time (GMT)	Latitude (South)	Longitude (East)	Depth of tow
SD 01	18 April 2001	07h15	49:53	32:56	300 m
SD 02	18 April 2001	13h55	49:05	33:00	300 m
SD 03	18 April 2001	18h20	48:15	33:00	200 m
SD 04	18 April 2001	22h35	47:25	32:59	200 m
SD 05	19 April 2001	02h58	46:35	32:59	200 m
SD 06	19 April 2001	07h06	46:34	34:14	300 m
SD 07	19 April 2001	11h18	47:25	34:15	300 m
SD 08	19 April 2001	15h30	48:14	34:15	200 m
SD 09	19 April 2001	20h09	49:05	34:15	200 m
SD 10	22 April 2001	12h17	49:54	34:15	300 m
SD 11	22 April 2001	17h23	49:54	35:30	200 m
SD 12	22 April 2001	22h26	49:04	35:29	200 m
SD 13	23 April 2001	03h04	48:15	35:30	200 m
SD 14	23 April 2001	07h01	47:24	35:30	300 m
SD 15	23 April 2001	11h00	46:34	35:29	300 m
SD 16	23 April 2001	15h25	46:34	36:44	200 m
SD 17	23 April 2001	20h14	47:24	36:45	200 m
SD 18	24 April 2001	00h35	48:14	36:44	200 m
SD 19	24 April 2001	04h57	49:04	36:44	300 m
SD 20	24 April 2001	09h58	49:55	36:46	300 m
SD 21	24 April 2001	13h43	49:54	38:00	300 m
SD 22	24 April 2001	17h57	49:04	37:59	200 m
SD 23	25 April 2001	00h55	48:15	38:00	200 m
SD 24	25 April 2001	07h37	47:25	38:00	300 m
SD 25	25 April 2001	11h48	46:34	37:59	300 m

Table A.3. Species list for the Marion Offshore Ecosystem Variability Study II, April 2002.

Species or taxa	Species or taxa
Copepoda (Calanoida)	Copepoda (Poecilostomatoida)
Rhincalanus gigas	*Oncaea antarctica*
Eucalanus longiceps	Ostracoda
Eucalanus sewelli	Polychaeta
Calanus simillimus	Appendicularia
Candacia spp.	Pteropoda
Calanoides acutus	*Limacina* spp.
Metridia lucens	Nauplii
Haloptilus oxycephalus	Chaetognatha
Paraeuchaeta biloba	*Sagitta gazellae*
Paraeuchaeta spp.	*Eukrohnia hamata*
Heterorhabdus austrinus	Euphausiids
Aetideus armatus	*Euphausia longirostris*
Clausocalanus laticeps	*Euphausia vallentini*
Clausocalanus brevipes	*Thysanoessa vicina*
Ctenocalanus vanus	Euphausiid furcilia
Pleuromamma abdominalis	Amphipoda
Racovitzanus spp.	*Themisto gaudichaudi*
Scolecithricella minor	*Cyllopus lucasi*
Copepoda (Cyclopoida)	Tunicata
Oithona similis	*Salpa thompsoni*
Oithona frigida	

Table A.4. Grazing study stations during the Marion Offshore Ecosystem Variability Study II, April 2002.

Station	Date	Time (GMT)	Latitude (South)	Longitude (East)
SD 11	08 April 2002	01h25	49:45	29:30
SD 13	08 April 2002	07h15	50:15	29:29
SD 15	08 April 2002	13h20	50:49	29:31
SD 17	08 April 2002	16h13	51:15	29:30
SD 19	08 April 2002	20h25	51:45	29:29
SD 23	09 April 2002	06h00	51:17	30:00
SD 36	11 April 2002	11h15	49:31	30:44
SD 39	12 April 2002	05h11	50:14	30:47
SD 41	12 April 2002	10h05	50:45	30:45
SD 43	12 April 2002	15h13	51:14	30:45
SD 60	14 April 2002	06h00	48:58	32:18
SD 62	14 April 2002	11h19	49:27	32:12
SD 65	14 April 2002	18h46	50:14	32:16