TROPHODYNAMICS OF MESOZOOPLANKTON IN THE VICINITY OF THE SUBTROPICAL CONVERGENCE IN THE INDIAN SECTOR OF THE SOUTHERN OCEAN

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ABSTRACT

The trophodynamics of the numerically dominant mesozooplankton (200-2000µm) in the vicinity of the Subtropical Convergence (STC) in the Indian sector of the Southern Ocean during austral autumn (April / May) 2007 were investigated as part of the Southern Ocean Ecosystem Variability Study. The survey consisted of six north-south transects each bisecting the STC between 38º to 43ºS and 38º to 41º45'E. In total, 48 stations situated at 30 nautical mile intervals were occupied over a period of ten days. Hydrographic data revealed a well defined surface and sub-surface expression of the STC, which appeared to meander considerably between 41ºS and 41º15'S. Surface chlorophyll-*a* (chl-*a*) concentrations were low, ranging between 0.08 and 0.68 mg chl-*a*.m^{-3} and were generally dominated by the picophytoplankton (<2µm) which made up 66.6% (SD±17.6) of the total pigment. Chl-*a* concentrations integrated over the top 150m of the water column ranged between 11.97 and 40.07 mg chl-*a*.m^{-2} and showed no significant spatial patterns ($p>0.05$). Total integrated mesozooplankton abundance and biomass during the study ranged between 3934.9 and 308521.4 ind.m^{-2} (mean = 47198.19; SD±62411.4 ind.m^{-2}) and between 239.8 and 4614.3 mg Dwt.m^{-2} (mean = 1338.58; SD ±1060.5), respectively. Again, there were no significant spatial patterns in the total mesozooplankton abundance or biomass within the region of study ($p>0.05$). No significant correlations were found between biological (chlorophyll-*a* concentrations and zooplankton abundance) and physico-chemical variables (temperature and salinity) ($p>0.05$). The total mesozooplankton community was numerically dominated by copepods of the genera *Pleuromamma, Calanus, Oncaea* and *Oithona.* Other important representatives of the mesozooplankton community included the tunicate, *Salpa thompsoni,* and the pteropod, *Limacina retroversa.* At the 40% similarity level, numerical analysis identified five distinct mesozooplankton groupings within the survey area. Differences between the groupings were associated

with changes in the relative contribution of numerically dominant species rather than the presence or absence of individual species. No groupings were associated with any specific feature of the front within the survey area.

The feeding rates of the six most numerically abundant mesozooplankton species (*Calanus simillimus, Limacina retroversa, Pleuromamma abdominalis, Clausocalanus breviceps, Oncaea conifera, Salpa thompsoni)* accounting for on average 39% of the total mesozooplankton counts, were investigated using the gut fluorescence technique. For all species, the total gut pigment contents during the night time were significantly higher than the daytime values ($p<0.05$ for all species). The gut evacuation rates (k) for selected mesozooplankton ranged between 0.14 and 0.81 h^{-1}. The ingestion rates ranged between 147.8 and 5495.4 ng(pigm)$ind^{-1}.day^{-1}$ which corresponded to a daily ration of between 2.4 and 10.9% body carbon. The combined grazing impact of the selected species on the daily phytoplankton standing stock was highly variable and ranged between 1.2 and 174.1% with an average of 27.3% (SD±38.78%) within the survey area. The highest grazing impact (>60%) was typically associated with those stations where the pteropod, *L. retroversa,* and the tunicate, *S. thompsoni,* contributed more than 5% of the total mesozooplankton counts. No significant differences were found in the grazing impact of any or all selected species situated either north, south or in the immediate vicinity of the front ($p>0.05$ in all cases).

The lack of defined spatial patterns in the mesozooplankton abundance and community structure suggests that the STC did not act as a significant biogeographic barrier to the distribution of mesozooplankton during the study. It is presumed that the large scale mixing event caused by a storm prior to this study was responsible for the observed lack of elevated biological activity within the region of the STC.

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Lastly I am indebted to my parents for the motivation, understanding and financial support which got me to this point and which keeps me going.

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 PHYSICAL AND BIOLOGICAL OCEAN PROCESSES

The world's oceans play a vital role in maintaining the correct balance of CO_2 in the earth's atmosphere by acting as a significant sink and reservoir for CO_2 (Longhurst 1991; Siegenthaler and Sarmiento 1993). Approximately one third of all anthropogenic CO_2 emissions are sequestered into the world's oceans which contain ~95% of the circulating carbon within our biosphere (Siegenthaler and Sarmiento 1993). The surface layer of the oceans is in equilibrium with earth's atmosphere while the deep ocean is oversaturated with CO_2 and therefore prevents excess CO_2 from being released into the atmosphere (Longhurst 1991). The importance of the world's oceans in maintaining the correct equilibrium of CO_2 in our atmosphere is becoming increasingly important due to significantly increasing atmospheric concentrations of the greenhouse gases (mainly CO_2) which may be the primary driving force behind the observed global climate change (Gille 2002). Since 1750 atmospheric CO_2 levels have risen from ~278ppm to ~378ppm at the end of 2004 (Hamwey 2005). This highlights the need to understand the role of the world's oceans in determining the global carbon budget and how this in turn affects our environment.

In the ocean, carbon is exported from the surface waters to the deep ocean via two main pathways. Firstly, there is the physical solubility pump which involves the transfer of dissolved inorganic carbon from the surface waters to depth via physical processes such as the thermohaline circulation (Fig. 1.1.) (Fortier *et al*. 1994). The formation and sinking of CO_2 rich water masses is the primary mechanism for the downward flux of CO_2 in the ocean (Fortier *et al*. 1994). This process is necessary to allow surface CO_2 laden water to reach the deep ocean so as to reduce the partial pressure of CO_2 in surface waters which then results in further atmospheric CO_2 drawdown (Siegenthaler and Sarmiento 1993; Rivkin and

Legendre 2001; Froneman *et al*. 2004). The secondary mechanism for CO_2 drawdown in the ocean is through biologically mediated carbon flux (Longhurst 1991). This process is known as the "biological pump".

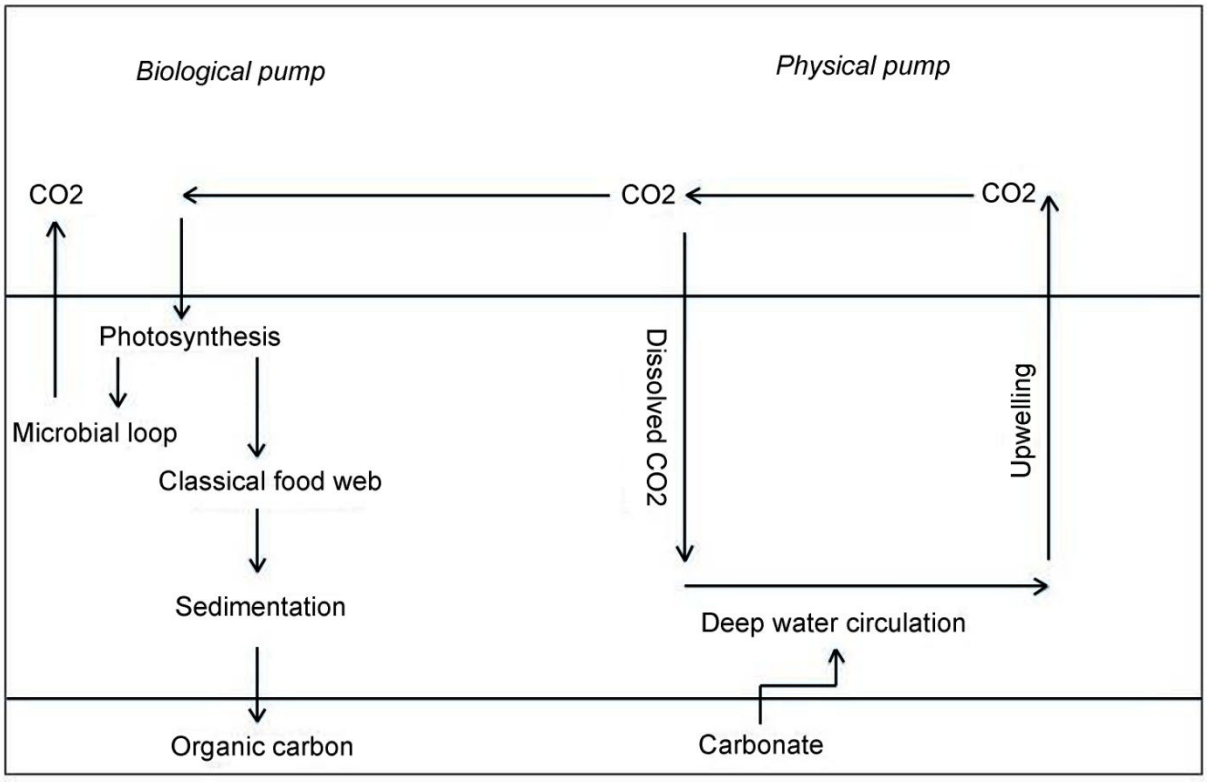

Figure 1.1. A simplified illustration of the biological and physical pumps (Adapted from Fortier *et al*. 1994).

Through the process of photosynthesis, atmospheric CO_2 in the surface waters of the ocean is absorbed by phytoplankton (Rivkin and Legendre 2001). This biogenic carbon can then either be assimilated by respiration or exported to depth. In the open ocean the main pathways for the biological pump to transport organic carbon from the surface to depth is through sedimentation of dead or senescent phytoplankton and the heterotrophic activity of zooplankton (Fig. 1.1.) (Longhurst 1991).

The magnitude of carbon flux to depth is determined by which food web phytogenic carbon enters, namely the microbial or classical food web (Longhurst 1991).

The classical food web predominates in those regions where primary production is dominated by large phytoplankton size classes (e.g. microphytoplankton) (Fortier *et al*. 1994). The large zooplankton are able to transport biogenic carbon to depth through the production of large, fast sinking faecal pellets and respiration at depth due to their diel vertical migrations (Shnack 1985; Fortier *et al*. 1994). This, coupled with the fact that large zooplankton represent an important carbon source for larger predators results in biogenic carbon sinking to depth through vertical flux, thus contributing to an efficient biological pump which may account for up to 30% of the total sinking flux across the thermocline (Longhurst 1991).

The microbial food web represents the net sink for primary production in ecosystems where primary production is low and dominated by small phytoplankton size classes (e.g. picophytoplankton) which are grazed on by protozoans, which are in turn, grazed on by small zooplankton size classes (e.g. microzooplankton) (Legendre and Le Fevre 1992). Carbon which enters the microbial food web is usually maintained and recycled in the upper layers of the water column because the associated small size classes of zooplankton do not respire at depth, have high assimilation efficiencies, do not produce fast sinking faecal pellets and do not transfer carbon to higher trophic levels (Legendre and Le Fevre 1992; Fortier *et al*. 1994). This means that biogenic carbon is not efficiently transferred to depth which in turn does not contribute to an efficient biological pump.

1.2. The Southern Ocean

The Southern Ocean is the largest continuous body of water on earth and covers an area of approximately 38 million km^2 (Tomczak and Godfrey 1994, Froneman *et al*. 2004). The Southern Ocean comprises the Indian, Pacific and Atlantic Oceans, as well as several seas (Ross, Weddell and

Scotia). The northern boundary of the Southern Ocean is defined by the Subtropical Convergence (Lutjeharms *et al*. 1985) and its southern boundary is defined by the Antarctic continent (Fig. 1.2.). The two major currents in the Southern Ocean are the East Wind Drift, which flows in an anti-clockwise direction bordering the Antarctic continent, and the Antarctic Circumpolar Current (ACC) which dominates the rest of the Southern Ocean, flowing in a clockwise direction around Antarctica (Deacon 1988). The flow of the ACC is concentrated at three major oceanic fronts (Fig. 1.2.). The most southerly front is the Antarctic Polar Front (APF) which forms the southern boundary of a region known as the Polar Frontal Zone (PFZ) which stretches northwards until the Sub-Antarctic Front (SAF) which forms the northern boundary (Hoffman 1985). The third major front is the Subtropical Convergence (STC). All of the fronts have relatively steep temperature gradients and flow rates associated with them, the STC having the highest (up to $0.15^{o}C.km^{-1}$ and 10^{6} $m^{3}.s^{-1}$, respectively, associated with the STC south of Africa) (Boden *et al*. 1988; Stramma 1992; Pakhomov *et al*. 1994).

The Southern Ocean plays a major role in the global oceanic thermohaline circulation as it links all major ocean basins at their southern extents (Deacon 1982; Gille 2002). This allows for the circumglobal transport of heat and salt between the Indian, Pacific and Atlantic Oceans which plays a vital role in regulating the global climate (Fyfe 2006). Knowledge of the impacts that exchange and modifications of water masses in the Southern Ocean have on climate systems are of critical importance considering that some physical characteristics of the Southern Ocean may be changing in response to human induced climate change. Between the 1950's and 1980's the mid-depth temperatures in the Southern Ocean have risen by ~ 0.17ºC (Gille 2002; Fyfe 2006). According to Gille (2002), the majority of the warming in the Southern Ocean is concentrated around the Antarctic Circumpolar Current which is critically important in mediating water mass exchanges between the different ocean basins. The impact of increasing ocean temperatures on the biology of the region remains poorly understood.

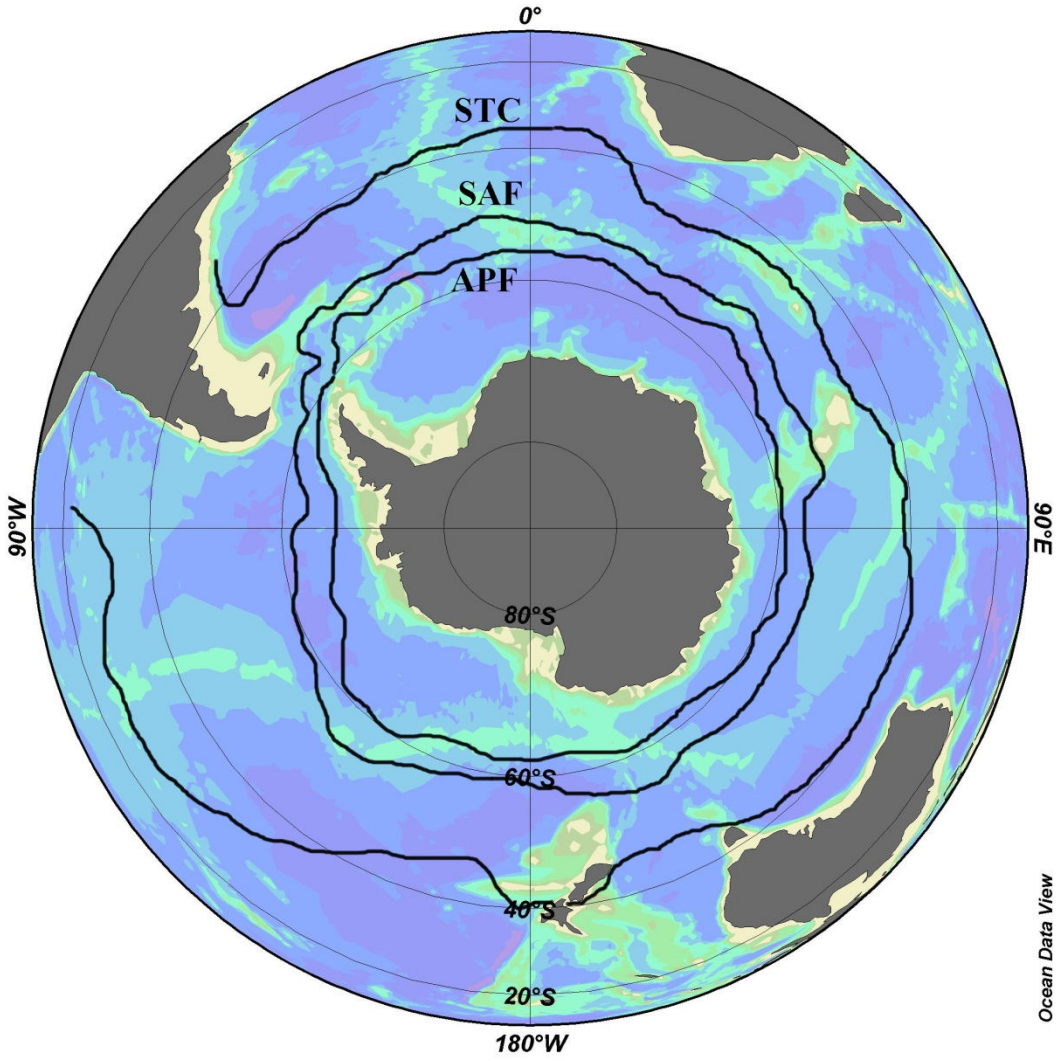

Figure 1.2. A map of the Southern Ocean showing the approximate positions of major oceanic fronts, namely the Subtropical Convergence (STC), the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF) (Adapted from Tomczak and Godfrey 1994).

1.2.1. Primary production in the Southern Ocean

Primary production in the Southern Ocean exhibits a high degree of both spatial and temporal variability (El-Sayed 1988; Laubscher *et al*. 1993; Pakhomov *et al*. 2000). Despite the abundant supply of nutrients derived from continuous upwelling centered around the Antarctic Divergence, total primary production within the region is generally low, ranging between 0.1 and 0.3 g $C.m^{-2}day^{-1}$ (Atkinson 1998;

Siegenthaler and Sarmiento 1993; Froneman *et al*. 2001 and references therein). Factors that contribute to low productivity, generally most prevalent during winter months, include an unfavorable light environment conferred by an unstable water column and the poor availability of trace metals (mainly iron) (El-Sayed 1988, Froneman 1995; Schultes *et al*. 2006). Recent studies indicate that iron availability and water column stability act synergistically to control primary production in high Antarctic regions (Fielding *et al.* 2007; Bakker *et al.* 2007). North of the Antarctic Polar Front, total primary production may also be limited by silicate availability (Laubscher *et al*. 1993). Phytoplankton in these unproductive regions are usually dominated by the small nano- (2-20µm) and picophytoplankton (<2µm) (Fogg 1991; Laubscher *et al*. 1993; Froneman and Perissinotto 1996). There are however, areas of relatively high production including the circumpolar frontal regions; the marginal ice zone (MIZ) and waters surrounding various oceanic islands that demonstrate the so called "Island mass effect" of increased phytoplankton biomass (Fogg 1977; Boden 1988; El-Sayed 1988; Froneman *et al*. 2004; Arrigo *et al*. 2008). Additionally, phytoplankton blooms may also occur within open waters of the Southern Ocean (El-Sayed 1988). Within these relatively productive regions, total phytoplankton production is typically dominated by the larger microphytoplankton (>20µm) comprising mainly diatoms (El-Sayed 1988; Laubscher *et al*. 1993; Froneman *et al*. 2001).

1.3. The Subtropical Convergence

The Subtropical Convergence (STC) is one of the major fronts in the world's oceans forming a boundary between relatively cold (<13ºC) and fresh (<34.3 psu) Sub-Antarctic surface water to the south and warm (>20ºC) and saline (>35.4 psu) Subtropical surface water to the north (Deacon 1982; Lutjeharms and Valentine 1984). The front has a mean middle temperature of approximately 14.3ºC in the sector south of Africa (Lutjeharms and Valentine 1984) and is characterized by sharp temperature and salinity gradients which can exceed 0.15ºC.km^{-1} and 0.06 psu.km^{-1}, respectively (Lutjeharms and Ansorge 2001). Barange *et al*. (1998) and Lutjeharms *et al*. (1993) showed that the STC exhibits

substantial latitudinal variability in position and intensity with some regions, such as south of South Africa, exhibiting a well defined consistent temperature gradient whereas other regions, such as the mid-Atlantic, are less defined and more ephemeral. Shannon *et al*. (1990) suggested that the mean position of the STC south of Africa lies between 40º35' and 41º40' S, however, further east and west of South Africa the position of the STC shifts considerably (Fig. 1.3.). Latitudinal shifts of up to 600km have been reported in the mid-Atlantic while south of Africa, the position of the front may vary up to 225km (Smythe-Wright *et al*. 1998 and references therein).

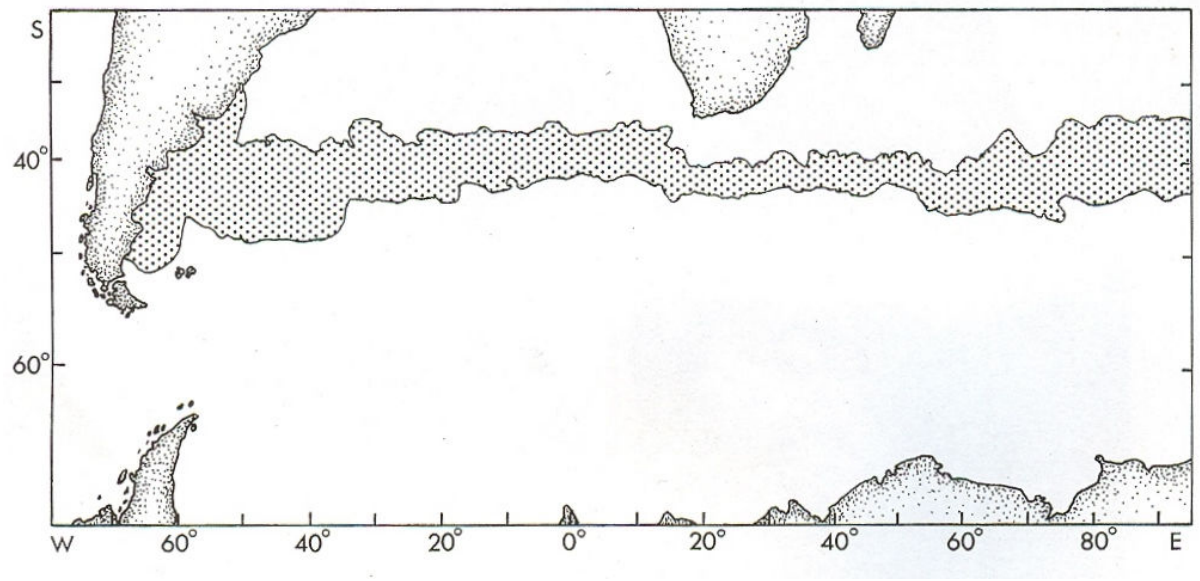

Figure 1.3. Latitudinal variation in the position of the STC (represented by the speckled area) shown by the weekly surface expression of the STC (represented by the 13ºC surface isotherm) throughout the year of 1983 (after Shannon *et al*. 1990).

1.3.1. Primary production in the region of the STC

A key feature of the STC is that it generally displays elevated levels of chlorophyll-*a* (chl-*a*) throughout its circumglobal extent which is thought to reflect increased localized primary production (Fig. 1.4.) (Froneman and Perissinotto 1996; Weeks and Shillington 1996; Froneman *et al*. 1997;

Pakhomov and Perissinotto 1997; Barange *et al*. 1998; Bradford-Grieve *et al*. 1998; James and Hall 1998; Read *et al*. 2000; Llido *et al*. 2005; Delizo *et al*. 2007). Due to enhanced primary production, the STC has some of the lowest pCO_2 values in the southern hemisphere and is as a consequence, one of the largest potential sinks for atmospheric CO_2 (Takahashi and Azevedo 1982). Mechanisms responsible for high levels of production in the vicinity of the STC include increased water column stability and horizontal advection of macro-nutrients or surface divergence (Lutjeharms *et al*. 1985; El-Sayed 1988; Laubscher *et al*. 1993; Froneman *et al.* 2002). Previous studies found the STC to exhibit enhanced primary production in the Atlantic (Froneman and Perissinotto 1996; Barange *et al*. 1998), south of Africa (Weeks and Shillington 1996; Froneman *et al*. 1997; Pakhomov and Perissinotto 1997), Indian (Read *et al*. 2000; Llido *et al.* 2005) and New Zealand (Bradford-Grieve *et al*. 1998; James and Hall 1998; Delizo *et al*. 2007) sectors. Typical values in the region of the STC in these different sectors ranged between 0.4 and 2.49 mg chl-*a*.m^{-3} (Table 1.1.).

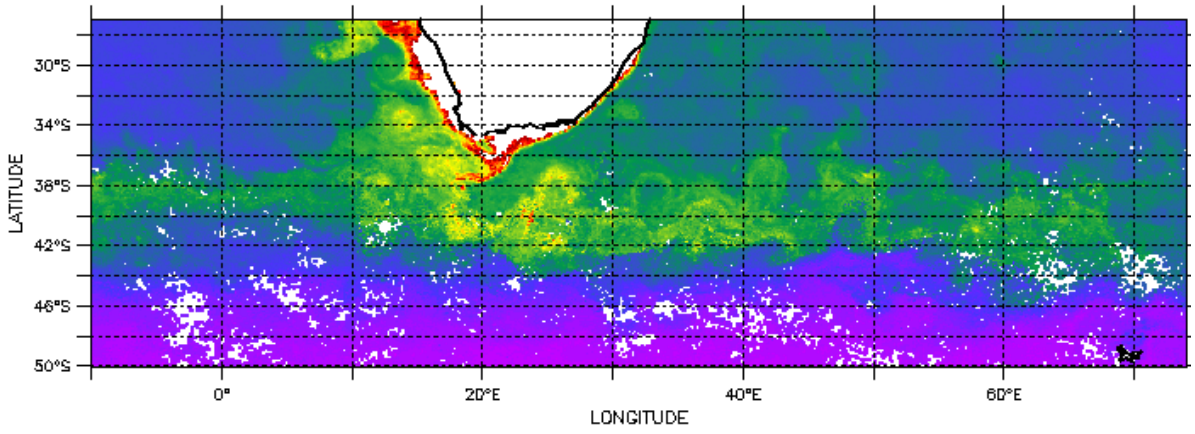

Figure 1.4. Satellite altimetry image showing chl-*a* concentrations south of Africa. The lighter green colour generally indicates relatively high levels of chl-*a* in the region of the STC (after Ansorge 2007).

Table 1.1. Total chl-*a* concentrations (mg chl-*a*.m^{-3}) in the vicinity of the STC in different sectors of the Southern Ocean during different seasons.

Range of chl-*a* concentrations (mg chl-*a*.m^{-3})	**Sector**	**Season**	**Source**
0.5 – 0.16	Atlantic sector	Winter	Froneman and Perissinotto 1996
0.4 - 0.75	Atlantic sector	Summer	Barange *et al*. 1998
0.75 - 1.04	south of Africa	Summer	Allanson *et al*. 1981
0.23 - 0.57	south of Africa	Summer / Autumn	Weeks and Shillington 1996
0.4 - 0.7	south of Africa	Winter	Froneman *et al*. 1997
0.35 - 0.85	south of Africa	Winter	Barange *et al*. 1998
0.5 – 0.8	Indian sector	Summer	Read *et al*. 2000
0.4 – 1.05	Indian sector	Spring / Summer	Llido *et al*. 2005
0.52 - 2.49	New Zealand sector	Winter / Spring	Bradford-Grieve *et al*. 1998
0.385 - 0.584	New Zealand sector	Winter / Spring	James and Hall 1998
0.39 - 2.84	New Zealand sector	Spring	Delizo *et al*. 2007

The phytoplankton size structure in the region of the STC has generally been shown to be dominated by the small pico- and nanophytoplankton in regions where the front is less defined (e.g. in the Atlantic sector) and by larger microphytoplankton where the front is more stable (e.g. south of Africa) (Barange *et al*. 1998). Various studies have suggested that enhanced biological activity in the vicinity of the front is a permanent feature (Allanson *et al*. 1981; Lutjeharms *et al*. 1985; Pakhomov *et al*. 1994). More recently, however, Llido *et al*. (2005) suggested that primary production in the region of the STC takes place as episodic bloom events which have typical chl-*a* concentrations of between 0.85 and 1.05 mg chl-*a*.m^{-3}. The bloom events are shown to occur more frequently in spring and summer due to increased water column stability and light availability. We can presume during bloom events when the front is stable that the phytoplankton size structure would be dominated by larger microphytoplankton (Fogg 1991). On the other hand during a non-bloom period, the phytoplankton size structure will be dominated by the smaller pico- and nanophytoplankton (Fogg 1991).

1.3.2. Zooplankton in the region of the STC

The zooplankton community structure in the region of the STC is highly diverse largely due to the presence of species from sub-tropical and Sub-Antarctic waters which border either side of the front (Pakhomov and Perissinotto 1997; Barange *et al*. 1998; Bradford-Grieve *et al*. 1998). Throughout this region, mesozooplankton (200-2000µm) are the most abundant size class of zooplankton with the grazers comprising mainly copepods, euphausiids, tunicates and pteropods whilst the carnivorous zooplankton usually include chaetognaths, mysids and amphipods (Pakhomov and Perissinotto 1997; Barange *et al*. 1998; Bradford-Grieve *et al*. 1998). Copepod species which have been found to be most abundant in the vicinity of the STC include *Metridia* spp, *Pleuromamma* spp, *Clausocalanus* spp, *Oithona* spp and *Oncaea* spp (Pakhomov and Perissinotto 1997; Barange *et al*. 1998; Bradford-Grieve *et al*. 1998). The contribution of these species to total counts however, demonstrates a high degree of both spatial and temporal variability.

Due to the sharp temperature gradient at the STC (Deacon 1982; Lutjeharms and Valentine 1984), it has been demonstrated that the front may act as a strong biogeographic barrier to the distribution of plankton and nekton (Deacon 1982; Boden *et al*. 1988; Pakhomov *et al*. 1994; Froneman *et al*. 1995; Barange *et al*. 1998). Studies conducted in the vicinity of the front have demonstrated that distinct zooplankton communities can be identified in the waters to the north and south of the STC (Pakhomov and Perissinotto 1997; Barange *et al*. 1998; Bradford-Grieve *et al*. 1998). However, a number of investigations have highlighted the importance of physical processes, such as meandering and eddies in the region of the STC which facilitate the movement of zooplankton across the front (Lutjeharms and Gordon 1987; Lutjeharms and Valentine 1988; Duncombe Rae 1991).

Zooplankton abundance values at the STC have been shown to generally decrease from north to south with values peaking in the centre of the front (Pakhomov and Perissinotto 1997; Barange *et al*. 1998). In the vicinity of the STC, total mesozooplankton abundance and biomass values have been found to be highly variable, ranging from 10^{-1} to 10^{-3} ind.m^{-3} and ~3 to >100 mg Dwt.m^{-3}, respectively (Table 1.2.). Abundance and biomass values were also found to peak in sectors of the STC where the front is more intense and defined including the region south of Africa and near New Zealand (Barange *et al*. 1998; Bradford-Grieve *et al*. 1998). In contrast, in those sectors where the front is less intense, such as in the mid-Atlantic Ocean, the zooplankton abundance and biomass values are generally 10-20% lower (Barange *et al*. 1998).

Table 1.2. Range of abundance (ind.m^{-3}) and biomass (mg Dwt.m^{-3}) values for mesozooplankton found in the vicinity of the STC in different seasons and sectors from the published literature (- No data).

Abundance (ind.m^{-3})	**Biomass (mg Dwt.m^{-3})**	**Season**	**Sector**	**Source**
10 - 150	-	Summer	Mid-Atlantic	Barange *et al*. 1998
10 - 250	-	Winter	South of Africa	Barange *et al*. 1998
13.3 – 81.9	-	Winter	South of Africa	Pakhomov and Perissinotto 1997
-	2.8 – 5.3	Winter	New Zealand	Bradford-Grieve *et al*. 1998
-	7.5 – 102.3	Spring / Summer	New Zealand	Bradford-Grieve *et al*. 1998

1.4. FEEDING ECOLOGY OF MESOZOOPLANKTON

Zooplankton form an important link between the phytoplankton and higher trophic level consumers in their respective marine ecosystems and it is therefore important to understand and assess zooplankton grazing potential (Swadling *et al*. 1997). Furthermore, CO_2 flux within the marine environment is driven, in part, by biological processes responsible for the creation and removal of organic material from surface waters (Bradford-Grieve *et al*. 1998). In order to quantify the amount of CO_2 flux due to organic particulate matter sedimentation it is necessary to measure the grazing impact

zooplankton may have on phytoplankton standing stock (Parsons and Lalli 1988, Bradford-Grieve *et al*. 1998).

The grazing impact of mesozooplankton on phytoplankton standing stock throughout the world's oceans is highly variable, ranging from <1% to 48% of the phytoplankton biomass (Table 1.3.). In some regions however, mesozooplankton may consume more than the locally produced primary production (Bathmann *et al*. 1990, Hansen *et al*. 1990, Ward *et al*. 1995). Variations in the grazing impact of mesozooplankton on phytoplankton can be related to numerous factors including zooplankton abundance, distribution and species composition and the size of the local phytoplankton community (Laubscher *et al*. 1993; Froneman and Perissinotto 1996; Pakhomov and Perissinotto 1997). In those regions where mesozooplankton are not able to meet their metabolic carbon requirements by feeding on phytoplankton alone, they may consume alternative carbon sources, including protozooplankton or indeed other copepods (Atkinson *et al*. 1996; Froneman *et al*. 1996; Pakhomov *et al*. 2002).

The grazing impact of the smaller size classes of mesozooplankton (200-500μm) has been shown in some cases to have a larger impact on phytoplankton standing stock than the larger size classes, mainly due to their higher ingestion rates and high numerical abundances (Morales *et al*. 1991). Previous studies (Morales *et al*. 1991; Swadling *et al*. 1997; Hernandez-Leon *et al*. 2000) showed that these smaller size classes consisting mainly of cyclopoid copepods accounted for the greatest proportion of total grazing impact of the herbivorous zooplankton. However, it has been demonstrated that some larger size classes of mesozooplankton (1000 - 2000μm) do have relatively high ingestion rates and can be responsible for a high proportion of the total grazing (Bernard and Froneman 2005).

Table 1.3. Spatial and temporal estimates of the grazing impact of mesozooplankton on phytoplankton standing stock, with reference to region, season and the percentage phytoplankton biomass consumed per day (% PB).

% PB	Season	Region	Source
<0.01 – 0.31%	Spring	Bellingshausen Sea	Atkinson and Shreeve 1995
1 – 29%	Autumn	Polar Frontal Zone	Bernard and Froneman 2005
2%	Spring	North Atlantic	Dam *et al*. 1993
3.9 – 18.3%	Summer	Polar Frontal Zone	Froneman *et al*. 2000
6 – 18%	Autumn / Winter	Southern California Bight	Landry 1994
<1%	Summer	North-east Atlantic	Morales *et al*. 1991
1 – 18%	Winter	STC South of Africa	Pakhomov and Perissinotto 1997
4.9 – 47.7%	Autumn	Prince Edward Islands	Perissinotto 1992
1 -5%	Spring	Benguela region	Peterson *et al*. 1990
0.5 – 7.7%	Spring	Central Pacific	Zhang *et al*. 1995

Results of studies that have examined the trophodynamics of zooplankton in the region of the STC suggest that the mesozooplankton are the dominant consumers of phytoplankton and that grazing impact in the region of the STC is moderate to low, generally accounting for <20% of the available phytoplankton standing stock (Froneman and Perissinotto 1996; Pakhomov and Perissinotto 1997; Bradford-Grieve *et al*. 1998). Grazing by zooplankton may, however, demonstrate a high degree of spatial and temporal variability due to the highly variable phytoplankton size structure usually associated with the STC (Pakhomov and Perissinotto 1997). The main aim of this study was to investigate the trophodynamics of the numerically dominant mesozooplankton in the region of the STC in the Indian Ocean sector of the Southern Ocean. These data will contribute to our understanding of the control on primary production imposed by grazers in the vicinity of the STC in the Indian sector of the Southern Ocean.

1.5. AIMS

The main objectives of this study were as follows:

i. Assess the role of the STC in the Indian sector of the Southern Ocean as a biogeographic barrier to the distribution of mesozooplankton during austral autumn, 2007.

ii. Investigate the trophodynamics of mesozooplankton in the vicinity of the STC in the Indian sector of the Southern Ocean during austral autumn.

The study was conducted during the first cruise of the Southern Ocean Ecosystem Variability Study during April / May 2007, in the Indian sector of the Southern Ocean.

CHAPTER TWO: MATERIALS AND METHODS

2.1. SURVEY DETAILS

All data for this study were obtained during the first Southern Ocean Ecosystem Variability Study aboard the MV 'S.A. Agulhas' (Voyage 132) in austral autumn (April 2nd to May 14th, 2007) in the Indian Sector of the Southern Ocean. The grid survey consisted of 6 north-south transects each bisecting the Subtropical Convergence (STC) between 38º to 43ºS and 38º to 41º45'E (Fig. 2.1.). In total, 48 stations situated at ~30 nautical mile intervals were occupied over a period of ten days within the survey area. Shortly before sampling began, a large storm was encountered within the survey area.

2.2. ENVIRONMENTAL VARIABLES

At all stations, a vertical profile of salinity and temperature was obtained to a depth of 1500m using a Seabird SBE 9/11 CTD (Conductivity, Temperature and Depth) probe. Water samples were collected at variable depths within the upper 150m of the water column (0, 25, 50, 75, 100 and 150m) using a 12 x 8L Niskin bottle rosette attached to the CTD. The position of the STC was determined using the characteristic subsurface 10ºC isotherm at 200m (Ansorge *et al*. 2005).

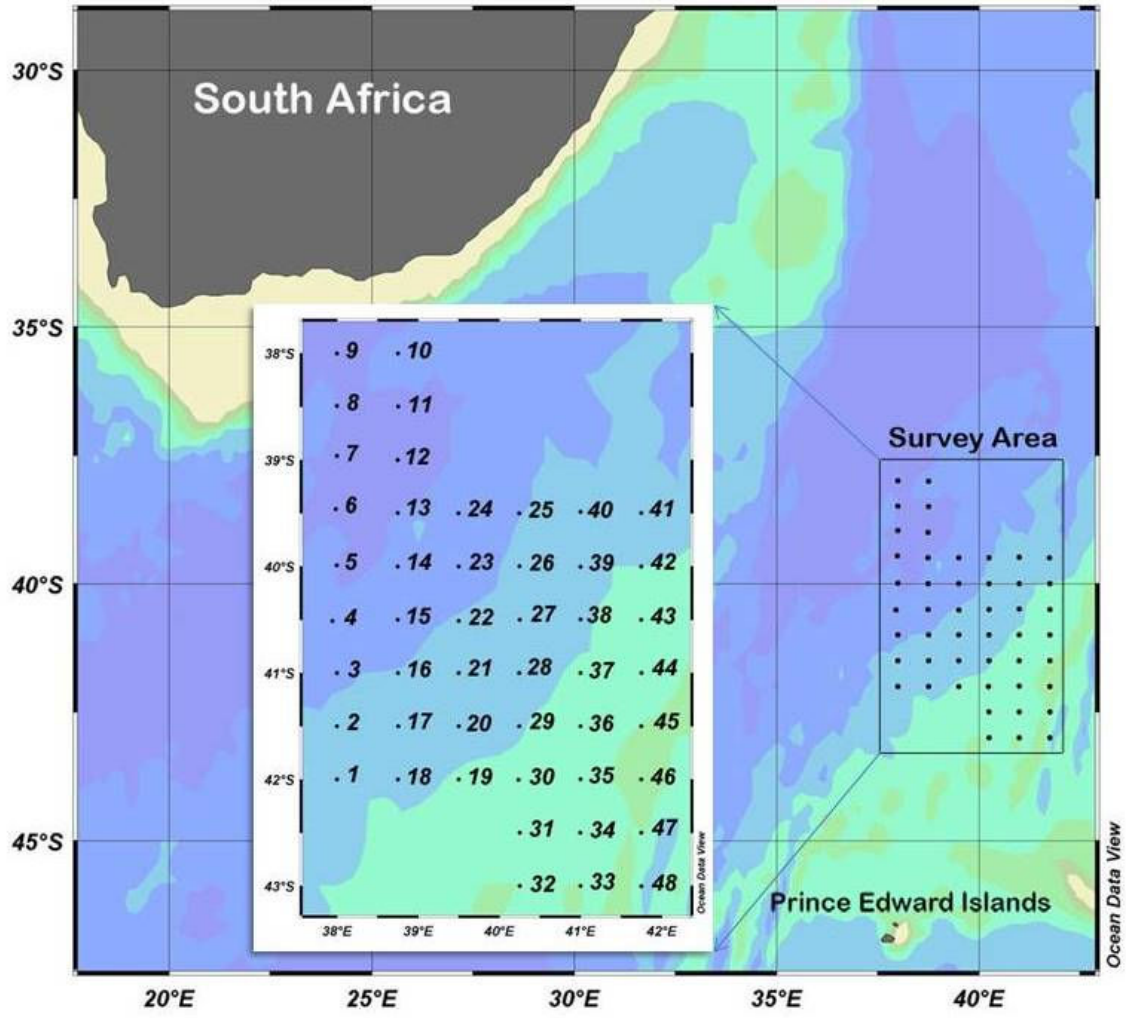

Figure 2.1. A map of the survey area and station positions (numbered) occupied in the Indian Sector of the Southern Ocean during first Southern Ocean Ecosystem Variability Study aboard the MV 'S.A. Agulhas' during austral autumn (May) 2007.

2.3. CHLOROPHYLL-*A* (CHL-*A*)

Size fractionated surface chl-*a* concentrations at each station were determined from a 250ml water sample collected from the surface using a Crawford bucket which was passed through a serial filtration unit (Hg <5cm) which separated the pico- (<2µm), nano- (2-20µm) and microphytoplankton (>20µm) size fractions. Integrated chl-*a* concentrations at each station were determined from a 250ml water sample collected from each Niskin bottle which was gently filtered (Hg <5cm) through a GF/F

filter. All filters were then placed in 8ml of 90% acetone and stored at -20ºC for at least 24 hours in the dark and then centrifuged at 5000rpm for 5 minutes. The chl-*a* concentrations were determined using a Turner Designs 10AU Fluorometer following the method of Holm-Hansen and Riemann (1978). The surface chl-*a* concentrations were expressed as milligrams of chl-*a* per unit volume (mg chl-*a*.m^{-3}). The chl-*a* concentrations for each station were then integrated for the top 150m of the water column by trapezoidal integration according to Bernard and Froneman (2002). Integrated chl-*a* concentrations were expressed as milligrams of chl-*a* pigment per unit area (mg chl-*a*.m^{-2}).

2.4. ZOOPLANKTON SAMPLING

Mesozooplankton samples were collected using a Bongo net fitted with 200µm mesh nets and a Universal Underwater Unit (U^3) which continuously measured temperature and depth during net tows. A digital flowmeter was used to calculate the volume of water filtered during each tow. Net tows were conducted to a depth of 300m during the day and to 200m at night to compensate for diel vertical migrations of zooplankton in accordance with several previous studies in the Southern Ocean (Bernard and Froneman 2002, 2005). Samples collected were immediately preserved in 6% buffered formalin (hexamine). In the laboratory, subsamples (1/4 to 1/32) obtained using a Folsom plankton sampler from each station were used for taxonomic identification, numerical abundance and biomass determination. These results were then integrated over the depth of the water column (200 or 300m) by trapezoidal integration (Bernard and Froneman 2002) and expressed as individuals per unit area (ind.m^{-2}). Biomass was determined using a 1/16 subsample from each station which was retained on pre-weighed GF/C filters that were oven-dried at 60ºC for 24 hours. The filters were then re-weighed using a Sartorius microbalance and the total dry weights determined by subtracting the final weights from the initial weights. These results were then integrated over the depth of the water column (200 or 300m) by trapezoidal integration according to Bernard and Froneman (2002) and expressed as milligrams of dry

weight per meter squared (mg Dwt.m^{-2}). No correction factor was applied for the loss of tissue due to preservation of the samples in formalin.

2.5. GRAZING RATES

The feeding rates of 6 of the most numerically abundant mesozooplankton species (*Pleuromamma abdominalis*, *Calanus simillimus*, *Oncaea conifera*, *Clausocalanus breviceps*, *Limacina retroversa* and *Salpa thompsoni*), accounting for on average 39.3% (SD±17.3) of the total mesozooplankton counts, were investigated using the gut fluorescence technique (Mackhas and Bohrer 1967). The gut fluorescence technique has been widely employed to estimate the grazing activity of zooplankton in a variety of aquatic habitats (Mackas and Bohrer 1978; Dam 1986; Dam and Peterson 1988; Takatsuji *et al*. 1997; Bernard and Froneman 2003). The principle behind the technique is that pigments from the ingested algae can be quantitatively extracted from the organism using organic solvents (Mackas and Bohrer 1978). Uncertainty regarding the amount of gut pigment destruction during the process of digestion (Mayzaud and Razouls 1992; Pasternak 1994) and its restriction to chlorophyll-*a* bearing prey only (does not consider the contribution of non-fluorescent food sources) are the main weakness of the technique (Bamstedt *et al*. 2000). Nonetheless, because of its analytical simplicity, the gut fluorescence technique remains one of the most widely employed techniques to estimate the zooplankton herbivorous activity in aquatic ecosystems.

At selected stations throughout the survey area, mesozooplankton samples collected using the Bongo net were incubated in particle free water, to which charcoal was added, for a period of 2 hours. Representative samples were taken immediately to determine the initial gut pigment contents and thereafter samples were taken at intervals of 15 minutes for the first hour and 20 minute intervals for the second hour. After removal from incubation, animals were immediately anesthetised using CO_2 gas (Morales *et al*. 1991) before being gently filtered (vacuum <1cm Hg) onto GF/C filters and frozen for later analysis in the laboratory. In the laboratory, the filters were thawed and the individual taxa rapidly

sorted under low light conditions using a Nikon dissecting microscope, operated at 100x magnification. Once sufficient individuals (only adults) were collected for each species (30 individuals for all copepods and *L. retroversa* and between 5 and 10 individual *S. thompsoni* per sample) they were placed in 10ml test tubes containing 8ml of 90% acetone and stored in the dark at -20ºC for 24 hours. The test tubes were then centrifuged at 5000rpm for 5 minutes after which the pigment content of the acetone extract was measured using a Turner Designs 10AU Fluorometer (Mackas and Bohrer 1976). Gut pigment contents were then determined according to the method of Strickland and Parsons (1968), as modified by Conover *et al.* (1986) and were expressed as chl-*a* equivilents per individual (ng chl-*a*.ind^{-1}). The gut evacuation rate (k) per taxon was derived from the exponential slope of change in gut pigment contents over time (Dam and Peterson 1988). Daily ingestion rates [ng(pigm)ind^{-1}.day^{-1}] were then estimated employing the following equation, after 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 inconspicuous species, an average value of 50% gut pigment destruction was assumed for all taxa (Mayzaud *et al*. 1992; Perissinotto 1992; Bernard and Froneman 2003). To estimate community grazing impact, abundance data of the six investigated taxa were combined with individual ingestion rates. Grazing impact was then expressed as the percentage of total integrated phytoplankton standing stock consumed per day.

2.6 DAILY RATIONS

To estimate the carbon specific daily rations, the dry weight of individuals was determined and a carbon content of 40% dry weight and a carbon : chl-*a* ratio of 50 was assumed (Atkinson 1994; Bernard and Froneman 2003). To calculate individual dry weights, 40 individuals per species were

placed on pre-weighed GF/C filters and oven dried at 60ºC for 36 hours. The filters were then weighed using a Sartorius microbalance with a precision of 0.001 mg and individual weights were calculated by subtracting the final weight from the initial weight of the filter and then dividing by the number of individuals weighed. Results were then expressed as percentage body carbon consumed per day (% body C day^{-1}).

2.7. ZOOPLANKTON COMMUNITY ANALYSIS

Physical and biological data collected during the survey were plotted using Ocean Data View (ODV) 3.2.0, (Schlitzer 2006). Spatial patterns in the total mesozooplankton abundance data were analysed using the statistical package, PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke and Warwick 1994). To evaluate potential groupings in community structure between stations, a hierarchical cluster analysis was employed according to the methods of Field *et al*. (1982). Species data were log transformed in order to reduce the bias due to highly abundant species (Legendre and Legendre 1983) and the Bray-Curtis similarity measure applied after which a dendrogram was plotted using complete linkage. To test for differences between observed groupings, the one-way ANOSIM procedure (a program of PRIMER) was employed, after Field *et al*. (1982). To identify which species were responsible for the observed groupings, the SIMPER analysis was used and species which contributed 5% or more to observed groups were listed. Finally, the BIO-ENV procedure of the PRIMER computer package was employed to determine which physico-chemical variables (temperature, salinity) and biological variables best grouped the sample sites in a manner consistent with the zooplankton groupings identified with the hierarchical cluster analysis (Clarke and Ainsworth 1993).

2.8. STATISTICAL ANALYSIS

To test for significant correlations between variables (temperature, salinity and integrated chl-*a*), a multiple regression analysis was employed. Independent t-tests were used to test for significant patterns in diel vertical variations in gut pigment content of mesozooplankton. Regression analysis was used to test for correlations between integrated chl-*a* and mesozooplankton abundance, the grazing impact of the investigated species and integrated chl-*a* and sea surface temperature. To test for any significant differences between integrated chl-*a*, mesozooplankton abundance and the grazing impact of mesozooplankton situated north, in the immediate vicinity and south of the front on phytoplankton standing stock, a one-way ANOVA with a post hoc Tukey test for different N was employed. All analyses were done using the statistical computer package, Statistica version 7.

CHAPTER THREE: RESULTS

3.1. PHYSICAL ENVIRONMENT

The STC within the study area was well defined and characterised by a strong frontal surface temperature gradient (up to 0.29ºC per Nautical Mile) as well as a well defined boundary throughout the entire water column (Froneman *et al*. 2007). Typical north-south transitions across the STC were from warm (>20ºC), saline (>35.4psu) water masses typical of Subtropical water, to cool (<13ºC), fresh (<34.3psu) water masses typical of Sub-Antarctic water (Froneman *et al*. 2007). From transect one to six, both the surface and subsurface expression (represented by the 200m 10ºC isotherm) of the STC exhibited considerable meandering between 41ºS and 42º15'S (Fig. 3.1.). From transects three to six, evidence of the southern boundary of the Agulhas Return Current was also identified (represented by water >20ºC) in the north-eastern sector of the survey area (Froneman *et al*. 2007).

3.2. CHLOROPHYLL-*A* (CHL-*A*)

Surface chl-*a* concentrations within the survey area were generally low, ranging between 0.08 and 0.68 mg chl-*a*.m^{-3} and were typically dominated by the picophytoplankton (<2µm) which made up 66.6% (SD±17.6) of the total pigment at all stations (Fig. 3.2a,b.). Exceptions were recorded at stations 11, 12 and 43 along transects 2 and 6 where the nanophytoplankton (2-20µm) and microphytoplankton (>20µm) were identified as the dominant contributor to the total surface chl-*a*. The nano- and microphytoplankton fractions contributed on average 28.0% (SD±16.5) and 5.4% (SD±8.4) to total pigment, respectively. There were no significant spatial correlations between the different size classes of phytoplankton and any region of the area under investigation related sea surface temperature or salinity (ANOVA p>0.05). The chl-*a* concentrations integrated over the top 150m of the water column ranged between 11.97 and 40.07 mg chl-*a*.m^{-2} (mean = 21.1 (SD±7.5) mg chl-*a*.m^{-2}) and again, did not

exhibit any trends in spatial distribution related to sea surface temperature or salinity (regression analysis $p>0.05$) (Fig. 3.3. original data presented in appendix).

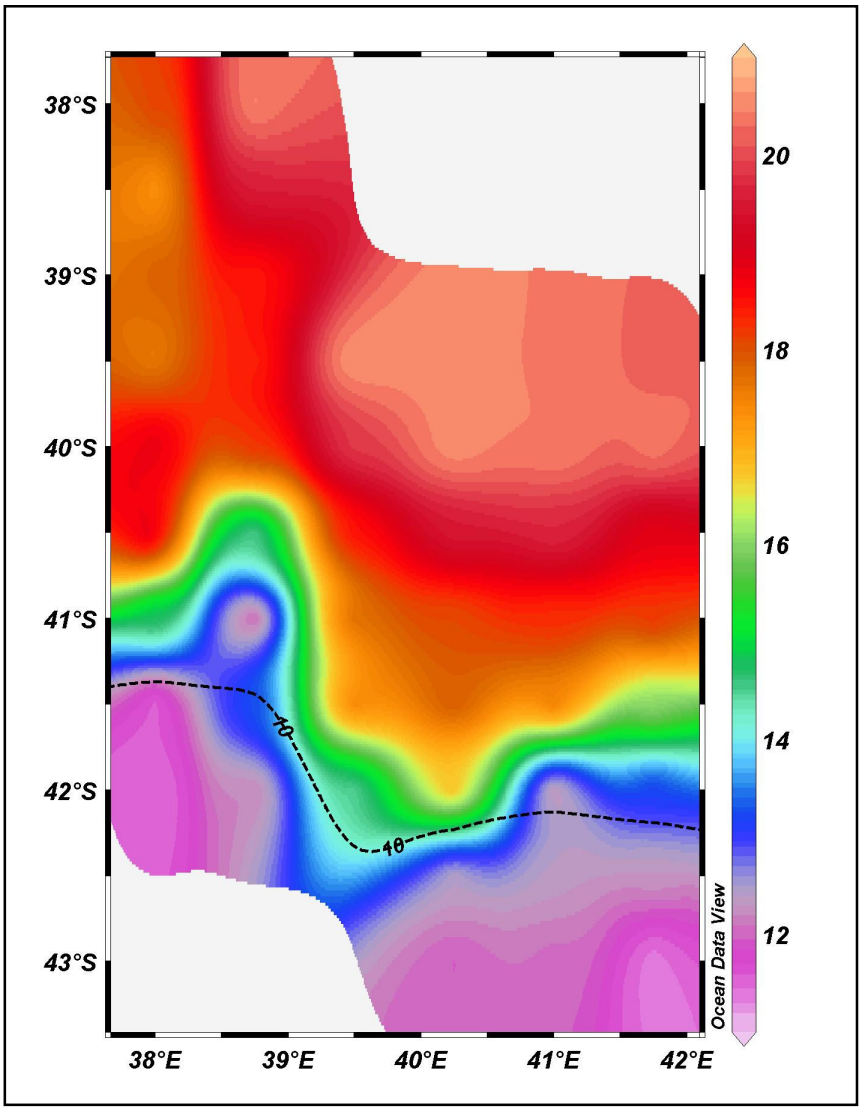

Figure 3.1. Sea surface temperature within the survey area showing the surface (represented by the 13ºC isotherm; Shannon *et al*. 1990) and subsurface expression (represented by the 10ºC 200m isotherm seen as the dotted line; Ansorge *et al*. 2005) of the Subtropical Convergence during the first Southern Ocean Ecosystem Variability Study, May 2007.

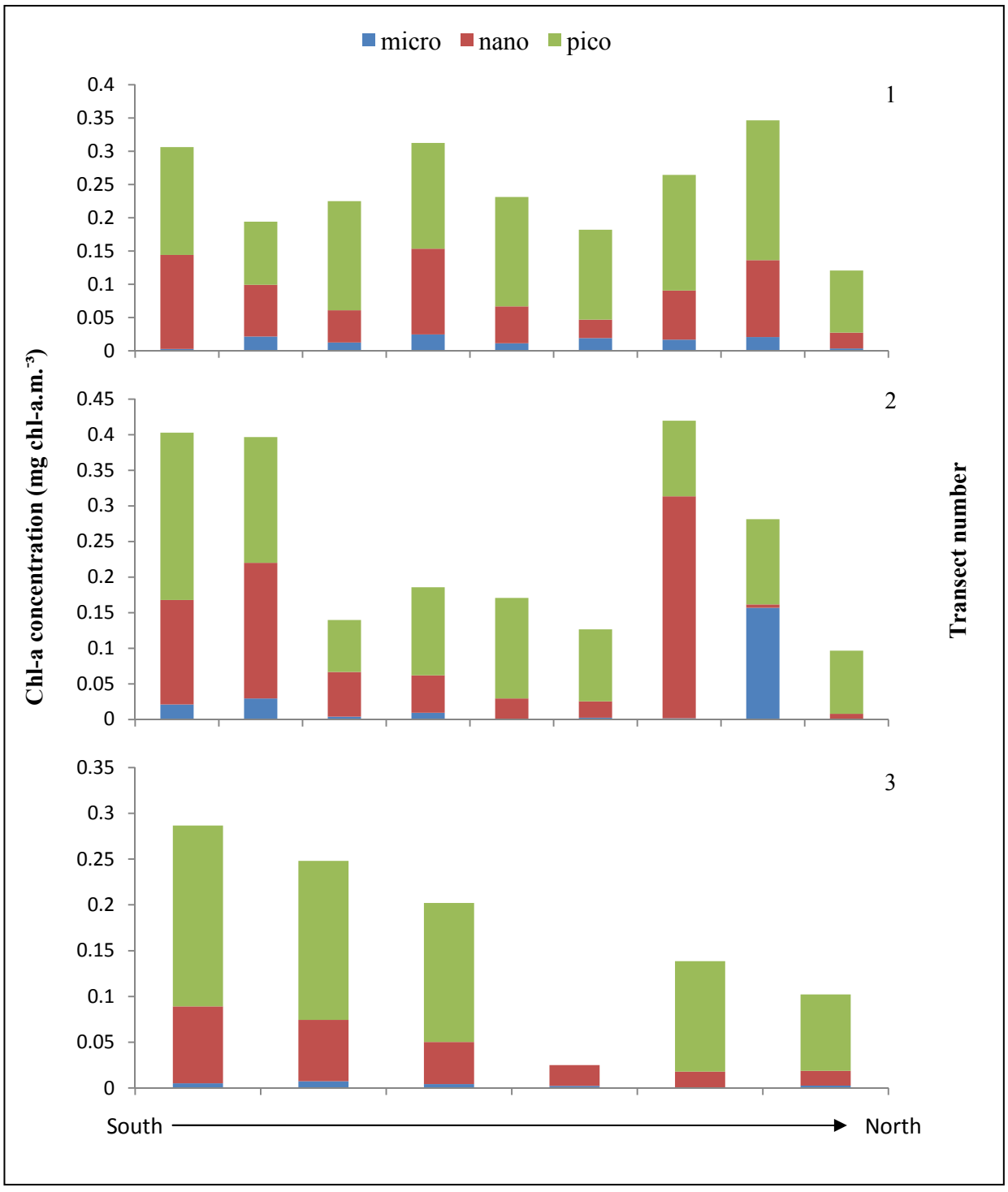

Figure 3.2a. Size fractionated (micro-, nano-, and picophytoplankton) surface chl-*a* concentrations within the survey area during the first Southern Ocean Ecosystem Variability Study, May 2007. Data are presented along south – north transects (transect numbers 1-3).

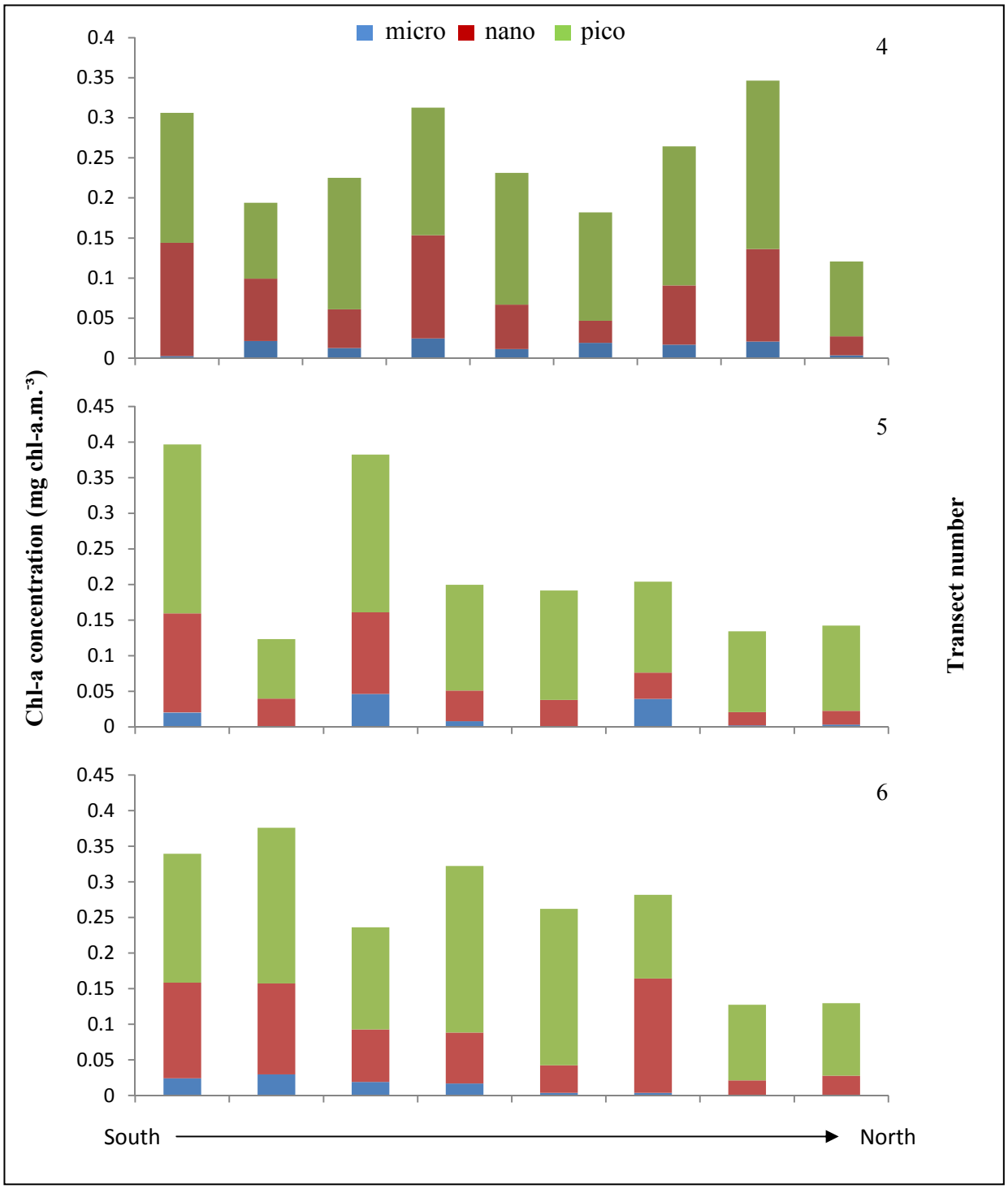

Figure 3.2b. Size fractionated (micro-, nano-, and picophytoplankton) surface chl-*a* concentrations within the survey area during the first Southern Ocean Ecosystem Variability Study, May 2007. Data are presented along south – north transects (transect numbers 3-6).

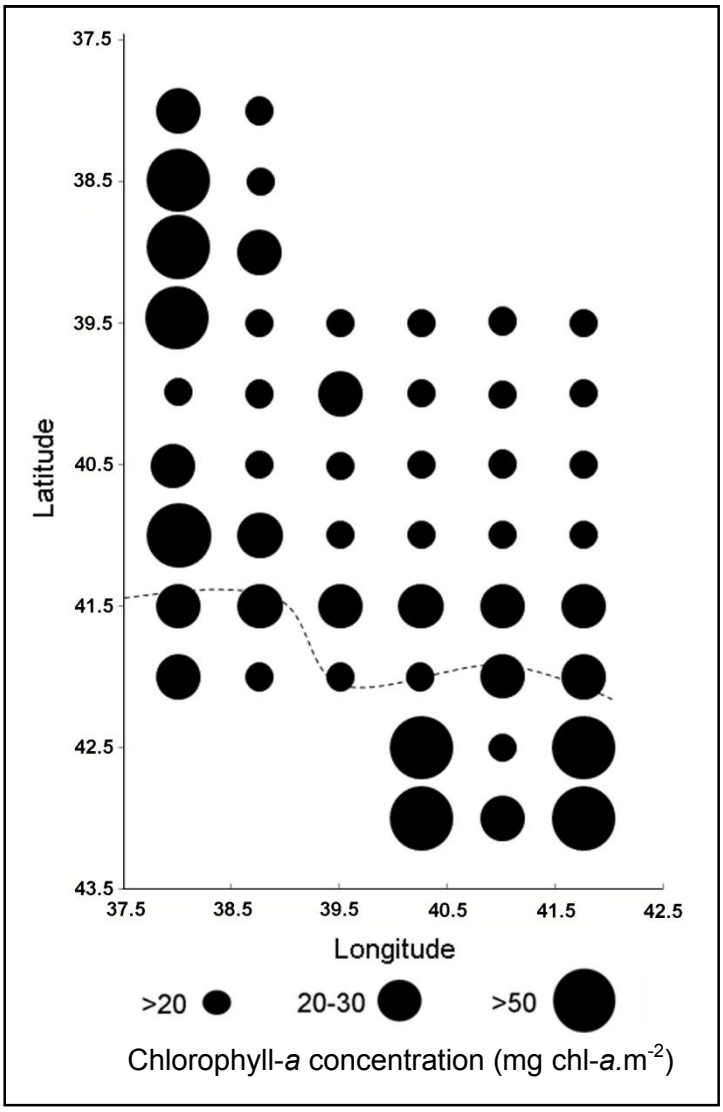

Figure 3.3. Total areal chlorophyll-*a* concentration (mg chl-*a*.m^{-2}) within the survey area during the first Southern Ocean Ecosystem Variability Study, May 2007. Dotted line indicates the subsurface expression of the STC according to Ansorge *et al*. (2005).

3.3. MESOZOOPLANKTON ABUNDANCE AND BIOMASS

Total integrated mesozooplankton abundance and biomass during the study ranged between 3934.9 and 308521.4 ind.m^{-2} (mean = 47198.19; SD±62411.4 ind.m^{-2}) and between 239.8 and 4614.3 mg Dwt.m^{-2} (mean = 1338.58; SD±1060.5), respectively (Fig. 3.4 and 3.6., original data are presented in Table A.2.). There was no evidence of enhanced mesozooplankton abundance or biomass at those

stations occupied in the immediate vicinity of the front nor were there any significant spatial patterns of mesozooplankton abundance and biomass north and south of the STC (ANOVA $p<0.05$). Multiple regression analysis between physico-chemical variables (temperature and salinity) and biological variables (integrated chl-*a* and mesozooplankton abundance and biomass) revealed no significant correlations ($p>0.05$ in all cases) (Fig. 3.5.).

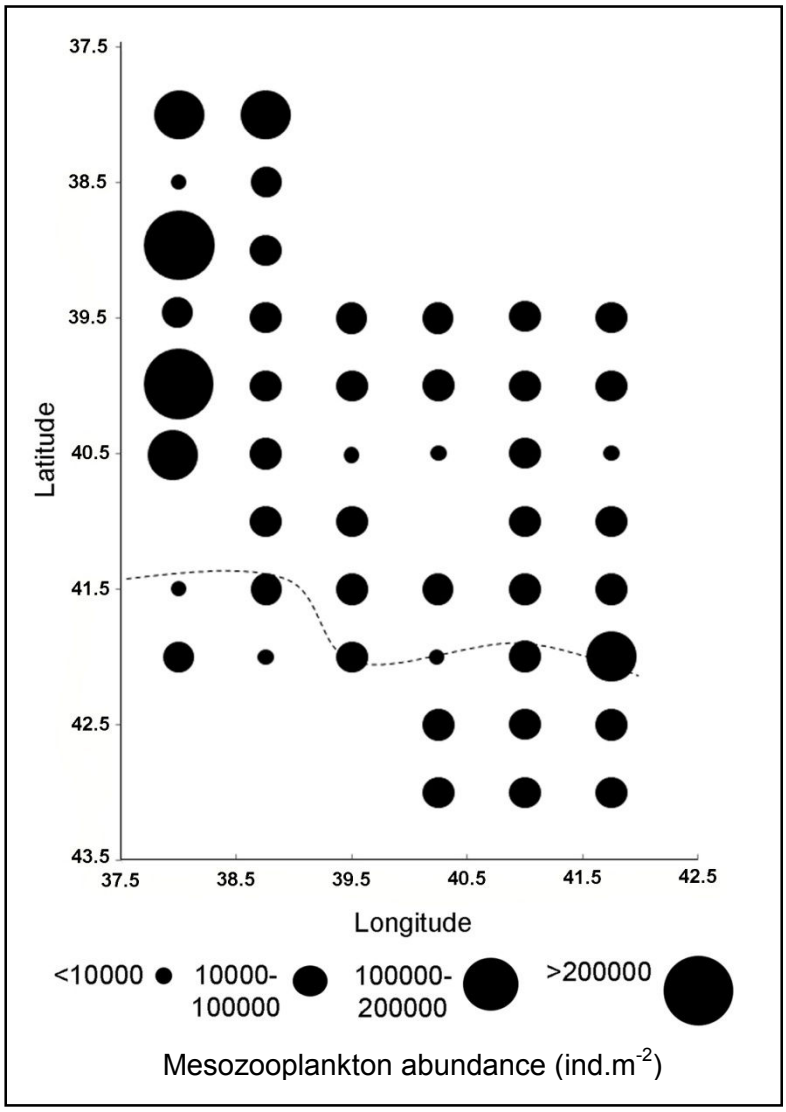

Figure 3.4. Integrated mesozooplankton abundance (ind.m^{-2}) within the survey area during the first Southern Ocean Ecosystem Variability Study, May 2007. Dotted line indicates the subsurface expression of the STC according to Ansorge *et al*. (2005).

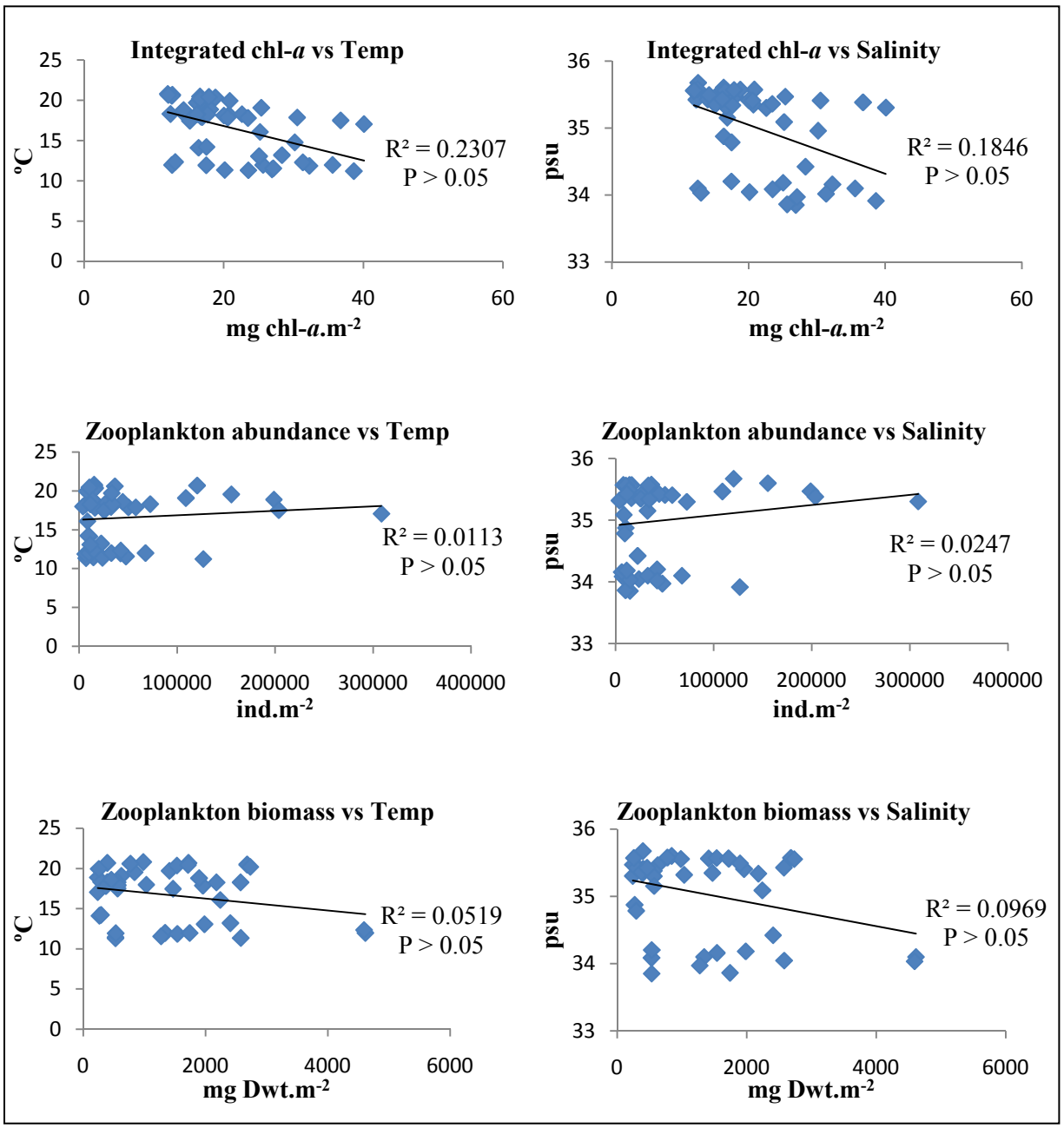

Figure 3.5. Regression analysis of integrated chl-*a* (mg chl-*a*.m^{-2}), mesozooplankton abundance (ind.m $^{-2}$) and biomass (mg Dwt.m^{-2}) against temperature (ºC) and salinity (psu) within the survey area during the first Southern Ocean Ecosystem Variability Study, May 2007.

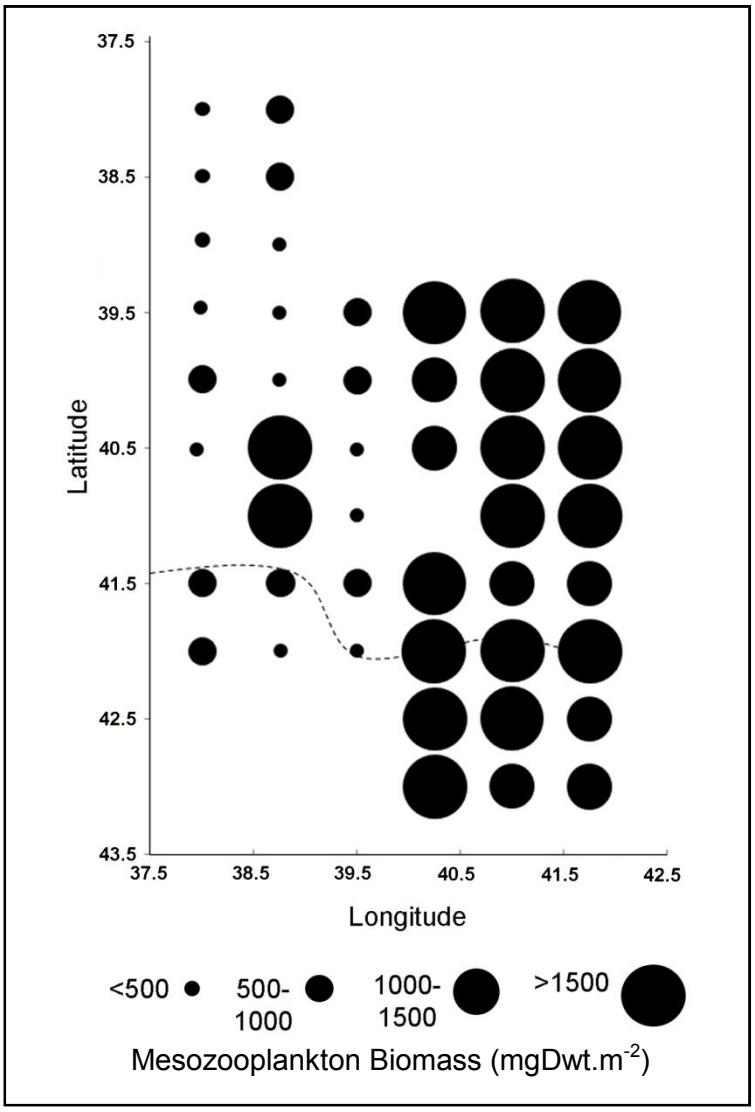

Figure 3.6. Integrated mesozooplankton biomass (mg Dwt.m^{-2}) within the survey area during the first Southern Ocean Ecosystem Variability Study, May 2007. Dotted line indicates the subsurface expression of the STC according to Ansorge *et al*. (2005).

Throughout the study area, the total mesozooplankton abundance was numerically dominated by copepods which comprised on average 68% (SD±27.1) of the total mesozooplankton counts (Fig. 3.7. original data in appendix Table A.3.). Exceptions were recorded at stations 2 to 11 and station 34 where euphausiid furcilia, the pteropod, *L. retroversa* and the tunicate, *S. thompsoni* were important contributors to the total mesozooplankton abundance.

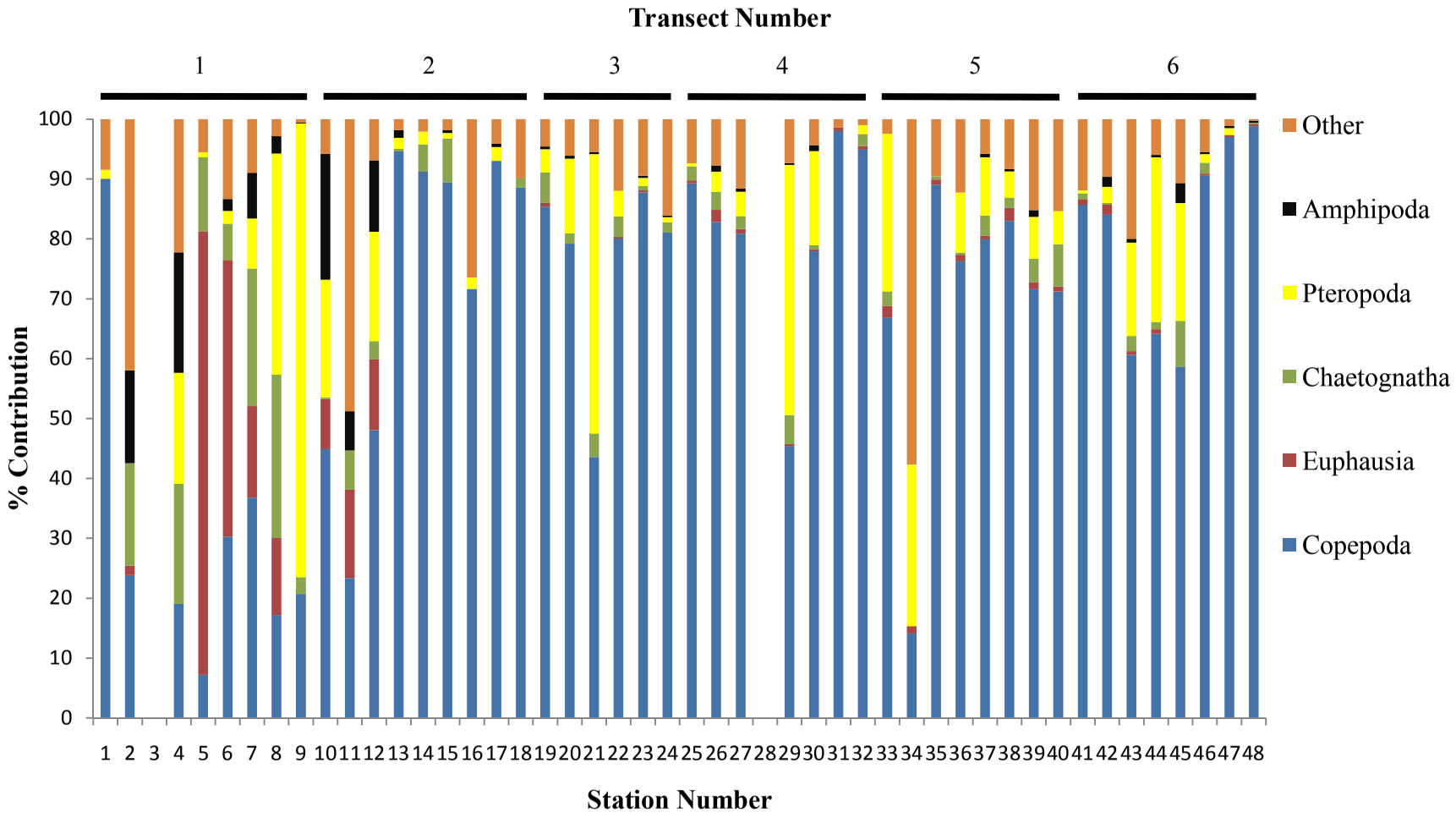

Figure 3.7. The contribution of the different taxa to the total mesozooplankton counts within the survey area during the first Southern Ocean Ecosystem Variability Study, May 2007. Note: Due to logistical constraints, no tows were conducted at stations 3 and 28.

The contribution of these groups to the total mesozooplankton counts was, however generally <10% of the total counts at all stations. Among the copepods, the numerically dominant species were (in order of highest total abundance) *Pleuromamma abdominalis, Oithona similis, Metridia lucens, Oncaea conifera, Clausocalanus breviceps* and *Calanus simillimus*. Collectively these six copepod species accounted for between 1 and 67% (mean= 42%) of the total mesozooplankton counts within the survey area. The carnivorous component of the mesozooplankton community structure was dominated by the chaetognaths (*Eukrohnia hamata, Sagitta gazellae* and *Sagitta zetesios*), amphipods (*Themisto gaudichaudi* and *Phrononema segentaria*) and the euphausiids (*Euphausia megalops, Euphausia similis, Euphausia erostris* and *Longicaudata thysanoessa*) (Sterley 2008). The contribution of the carnivorous mesozooplankton to the total zooplankton counts was, however, always less than 10% (Sterley 2008).

3.4. MESOZOOPLANKTON COMMUNITY ANALYSIS

At the 40% similarity level, the hierarchical cluster analysis identified five distinct, significantly different groupings of stations (ANOSIM $p<0.05$), designated Groups 1 to 5, within the survey area (Fig. 3.8.). The 5 groupings were, however, not associated with any specific water mass or feature within the survey area. The spatial distribution of the different stations within the five groupings identified with the hierarchical cluster analysis is shown in Figure 3.9. SIMPER analysis indicated that the different zooplankton groupings identified with the numerical analysis could be ascribed to changes in the relative abundances of the numerically dominant species within each grouping (mainly copepods from the genera *Oithona, Metridia and Pleuromamma*) rather than the presence or absence of individual species. Species which contributed at least 5% similarity to the designated groupings are listed in Table 3.1. The Bio-Env statistical procedure of the PRIMER package indicated that the environmental variables which best grouped the sample sites in a manner consistent with the zooplankton community

structure groupings was, in order of importance, integrated chl-*a* (37.9% in agreement), salinity (36.5% in agreement) and temperature (26.6% in agreement).

Table 3.1. Station groupings identified using hierarchical cluster analysis, average abundance of mesozooplankton within groupings and species responsible for at least 5% similarity within groups using the SIMPER procedure of the statistical package, PRIMER (Clark and Warwick 1994).

Group	**No. of Stations**	**Average abundance (ind.m^{-2})**	**Species in order of importance which contributed at least 5% similarity to observed groupings.**
1	7	54223.6 (SD±39119.9)	*Metridia lucens*, *Oithona similis*, *Pleuromamma abdominalis*, *Clausocalanus breviceps*, *Oncaea conifera*.
2	13	97648.9 (SD±85330.9)	*Limacina retroversa*, *Pleuromamma abdominalis*, *Oithona similis*, Euphausiid furcilia, *Calanus simillimus*, *Themisto gaudichaudi*, *Oncaea conifera*.
3	3	6937.8 (SD±6012.9)	*Limacina retroversa*, *Pleuromamma abdominalis*, *Calanus simillimus*, *Oithona similis*.
4	14	18916.6 (SD±9263.5)	*Calanus simillimus*, *Oncaea conifera*, *Pleuromamma abdominalis*, *Oithona similis*, Ostracods, *Limacina retroversa*, *Corycaeus* spp.
5	8	11057.2 (SD±3583.3)	*Oithona similis*, *Pleuromamma abdominalis*, *Metridia lucens*, *Calanus simillimus*, *Limacina retroversa*.

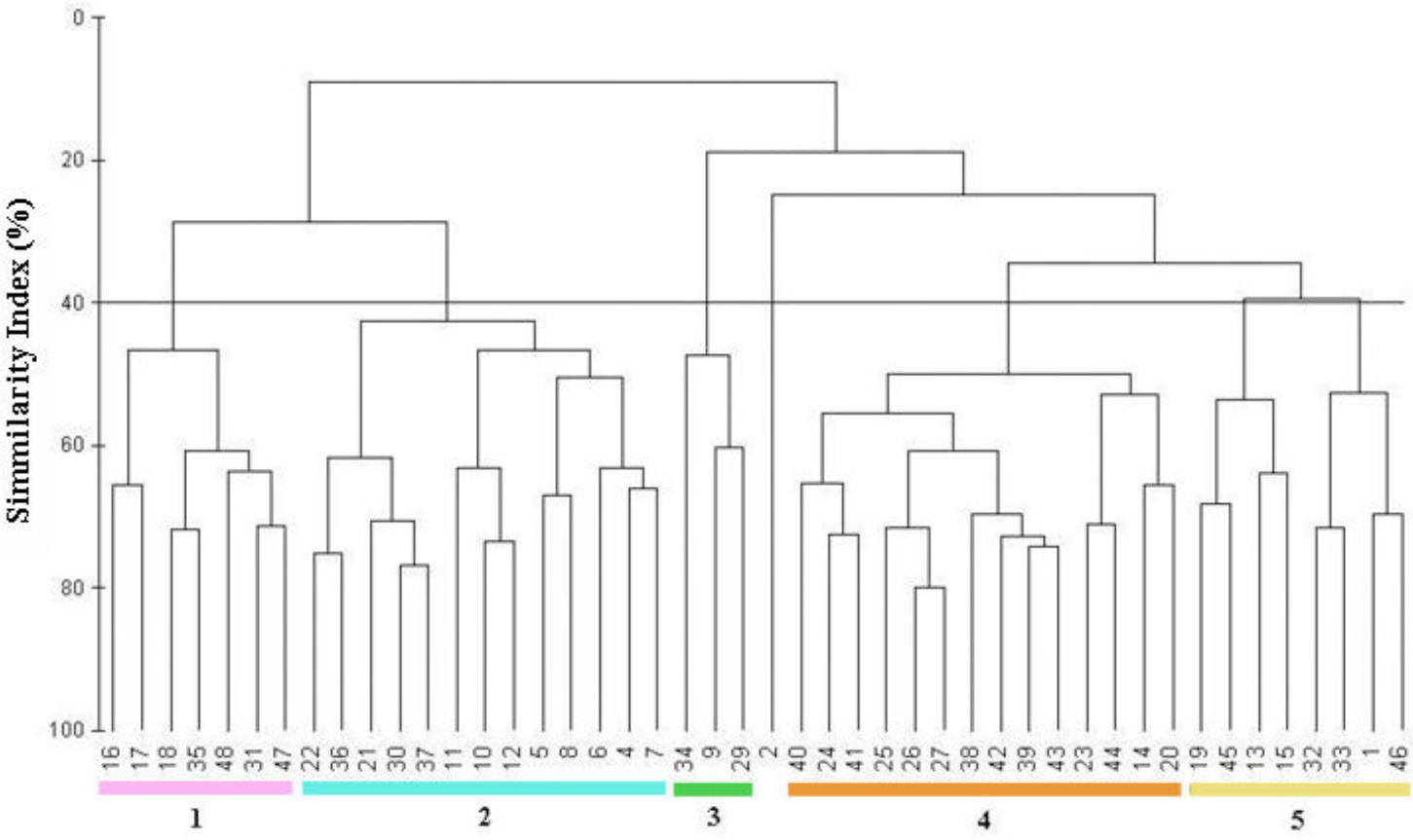

Figure 3.8. Dendrogram displaying the classification of mesozooplankton data collected during the first Southern Ocean Ecosystem Variability Study, May 2007 (PRIMER Computer Package). Five major groupings were identified at a 40% similarity level.

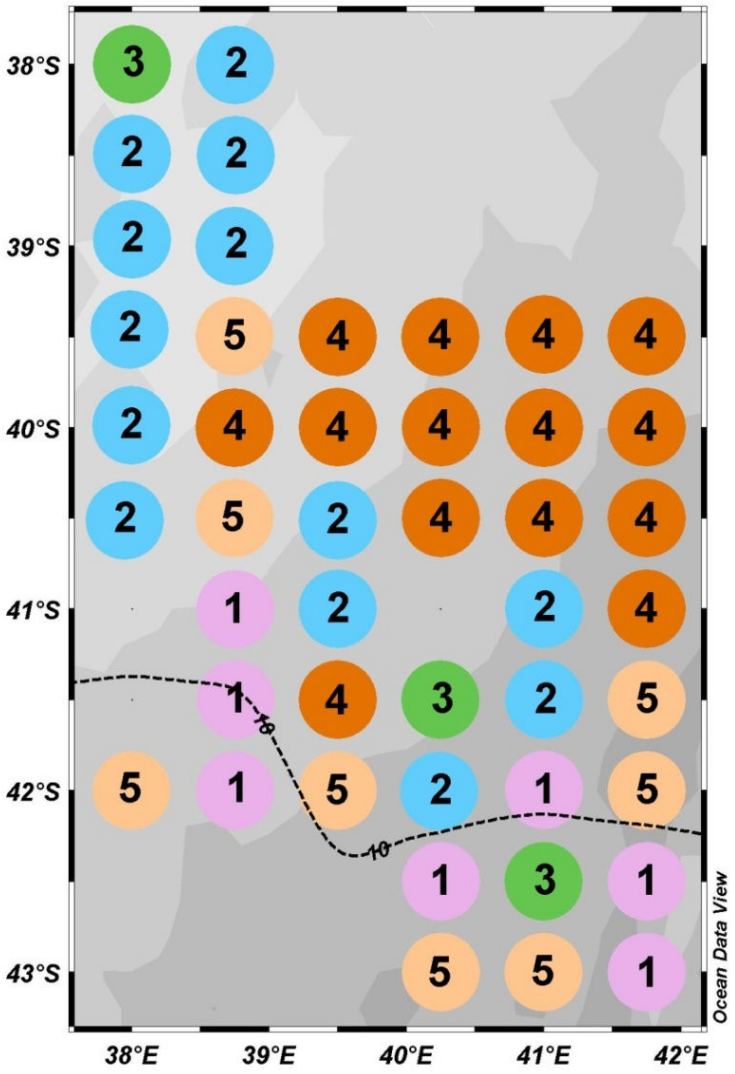

Figure 3.9. Spatial distribution of stations within the 5 groupings identified with the hierarchical cluster analysis (PRIMER Computer Package). Numbers and colours correspond to Figure 3.8. Dotted line indicates the subsurface expression of the STC according to Ansorge *et al*. (2005).

3.5. MESOZOOPLANKTON GRAZING

3.5.1. Diel variability in gut pigment contents

For five out of six species investigated for diel variability in gut contents, gut pigment contents during the nighttime were significantly higher than daytime gut pigment contents ($p<0.05$ for all species; Fig. 3.10.). No daytime samples of *S. thompsoni* were collected. Gut pigment contents for *C. breviceps, O. conifera, P. abdominalis, C. simillimus* and *L. retroversa* during the day ranged between 0.15 and 0.36, 0.12 and 0.26, 0.15 and 0.42, 0.14 and 0.46 and 0.07 and 0.23 ng(pigm)ind^{-1} and between 0.37 and 0.59, 0.21 and 0.29, 0.23 and 0.45, 0.25 and 0.60 and 0.27 and 0.53 ng(pigm)ind^{-1} at night, respectively.

3.5.2. Gut evacuation rates

A total of 14 gut evacuation experiments were conducted during the survey. Negative exponential models provided the best fit for the decline in gut pigment contents over time for all species. The gut evacuation rates (k) for six of the copepods ranged between 0.14 and 0.81 h^{-1}. The gut evacuation rate of *P. abdominalis* ranged between 0.44 and 0.71 (n=5), between 0.63 and 0.81 h^{-1} for *C. simillimus* (n=3), between 0.91 and 1.25 h^{-1} for *O. conifera* (n=2). Finally the gut evacuation rate of *C. breviceps* (n=1) was estimated at 0.14 h^{-1}. The gut evacuation rate for the pteropod, *L. retroversa,* ranged between 0.70 and 0.73 h^{-1} (n=2) and for the salp, *S. thompsoni,* a value of 0.53 h^{-1} (n=1) was recorded (Table 3.2.).

3.5.3. Ingestion rates

Ingestion rates were highest for the tunicate *S. thompsoni* and the copepod *C. simillimus* (5495.4 and 605.5 ng(pigm)ind^{-1}.day^{-1}, respectively) and lowest for the small copepod species *C. breviceps* and

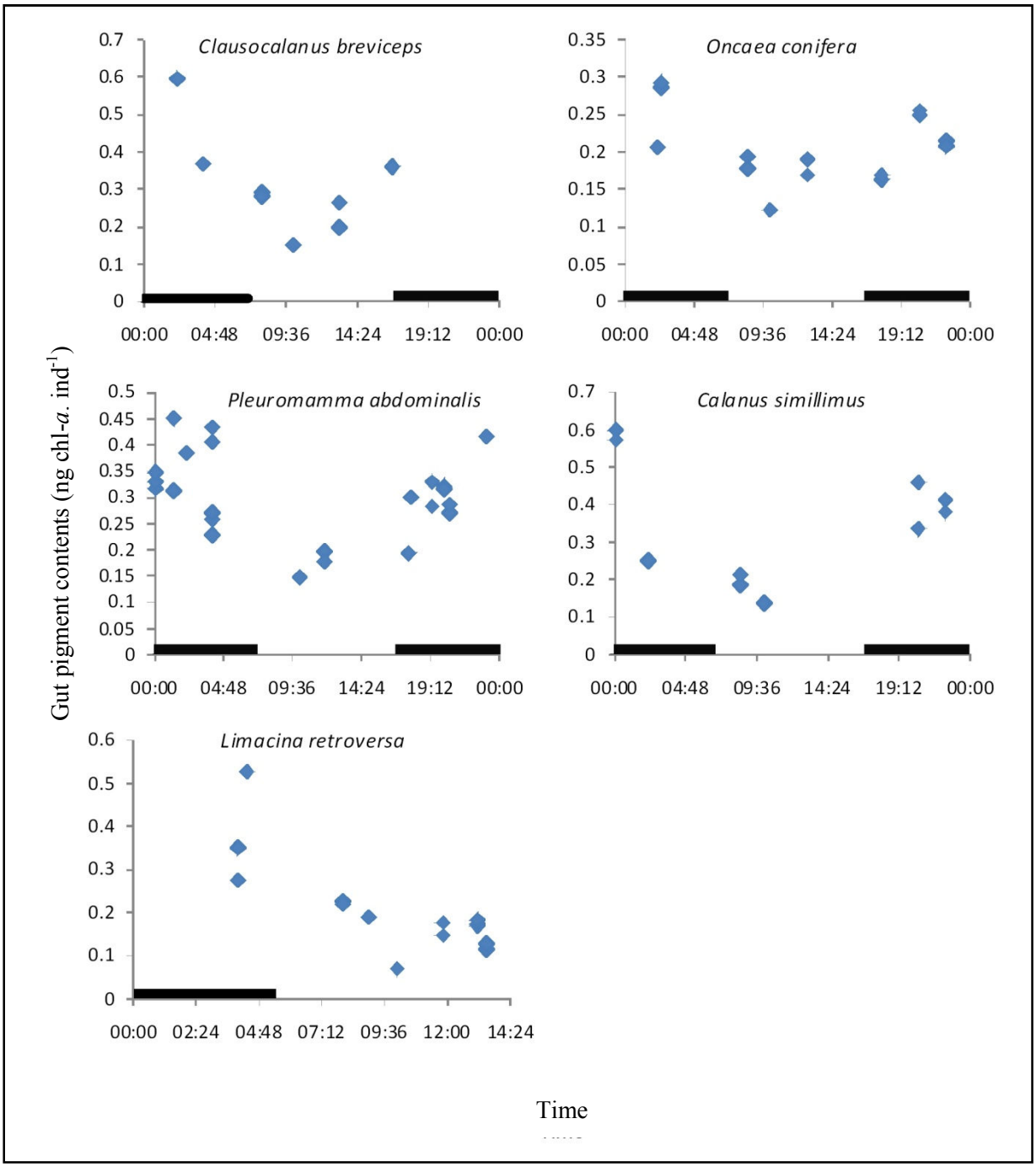

Figure 3.10. Diel variation in gut pigment contents of selected copepod species (*C. breviceps, O. conifera, P. abdominalis* and *C. simillimus*) and the pteropod, *L. retroversa*, during the first Southern Ocean Ecosystem variability Study, May 2007. Thickened sections of the x-axis represent nighttime.

O. conifera (147.8 and 207.5 ng(pigm)ind^{-1}.day^{-1}, respectively). The mean ingestion rate for the pteropod, *L. retroversa,* was calculated at 318.2 ng(pigm)ind^{-1}.day^{-1} and that of *P. abdominalis,* 437.1 ng(pigm)ind^{-1}.day^{-1} (Table 3.2.). Assuming a chl-*a* : carbon ratio of 50:1, these ingestion rates correspond to a daily carbon ration equivalent of between 2.4 and 10.9% body carbon for the selected mesozooplankton species investigated during this study (Table 3.2.).

3.5.4. Grazing impact

The combined grazing impact of the selected mesozooplankton species on the phytoplankton standing stock during the study ranged between 1.17 and 174.08% with an average of 27.3% (SD±38.78%) (Table 3.3., Fig. 3.11.). The grazing impact of individual species on integrated phytoplankton standing stock is represented in Table 3.3. The highest grazing impact (>60%) was typically associated with those stations (6, 10, 16, 34 and 35) where the tunicate, *S. thompsoni,* and the pteropod, *L. retroversa,* contributed to more than 5% of the total mesozooplankton counts. At those stations where the total zooplankton community was dominated by copepods (>60% of total counts), the grazing impact on the total phytoplankton standing stock was moderate, accounting for less than 30% of the integrated phytoplankton biomass (mean = 26%). Exceptions were recorded at stations 16, 18, 35 and 36 where the grazing impact ranged between 46 and 139% of the integrated phytoplankton standing stock. There were no significant correlations found between the total abundance of mesozooplankton or total phytoplankton biomass and total grazing impact on the phytoplankton standing stock (regression analysis, $p>0.05$). No significant differences were found in the grazing impact of any or all selected species situated either north, south or in the immediate vicinity of the front ($p>0.05$ in all cases).

Table 3.2. Coefficient of variance (R^2 values; $p<0.05$ in all cases), gut evacuation rate constants (k), average daily ingestion rates [ng(pigm)$ind^{-1}.day^{-1}$] and carbon specific ingestion rates of selected mesozooplankton species during the first Southern Ocean Ecosystem Variability Study, May 2007. Values in parenthesis are standard deviations.

Species	**R^2**	**k (h^{-1})**	**Average daily ingestion rate [ng(pigm)$ind^{-1}.day^{-1}$]**	**Ind. dry weight (ng)**	**Carbon ration (% body C day^{-1})**
Copepods					
Calanus simillimus	0.65	0.7 (±0.1)	605.5	125.0	8.3
Pleuromamma abdominalis	0.80	0.57 (±0.1)	437.1	80.0	7.3
Clausocalanus breviceps	0.70	0.14	147.8	27.5	7.4
Oncaea conifera	0.78	0.35 (±0.08)	207.5	12.5	2.4
Pteropods					
Limacina retroversa	0.72	0.49 (±0.01)	318.2	87.5	10.9
Tunicates					
Salpa thompsoni	0.69	0.53	5495.4	1160	8.4

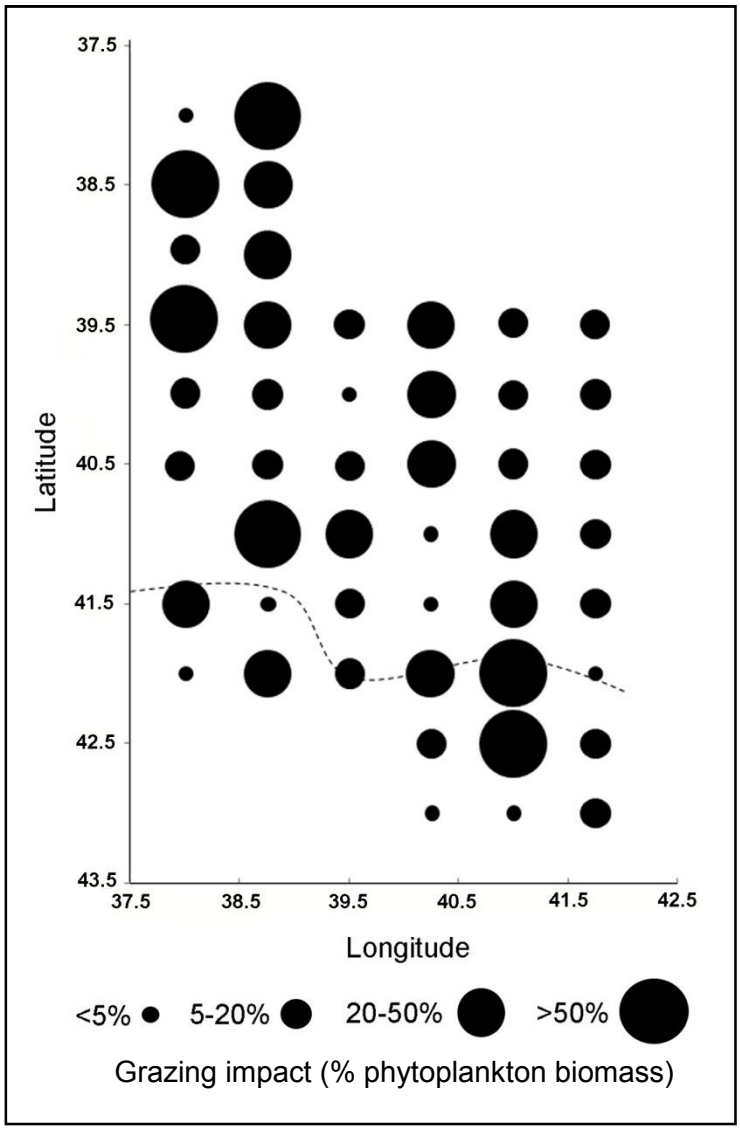

Figure 3.11. Mesozooplankton grazing impact (as a percentage of total integrated phytoplankton biomass consumed by selected mesozooplankton species) on phytoplankton standing stock within the survey area during the first Southern Ocean Ecosystem Variability Study, May 2007. Dotted line indicates the subsurface expression of the STC according to Ansorge *et al*. (2005).

Table 3.3. Integrated phytoplankton biomass, zooplankton ingestion rates and grazing impact of mesozooplankton at stations occupied during the first Southern Ocean Ecosystem Variability Study, May 2007. Note: Due to logistical constraints, no net tows were conducted at stations 3 and 28. – Not present.

Station number	**Phytoplankton Biomass (mg chl-*a*.m^{-2})**	**Daily ingestion rates [mg(pigm)m^{-2}]**						**Daily grazing impact (% phytoplankton biomass)**
		Calanus simillimus	***Pleuromamma abdominalis***	***Clausocalanus breviceps***	***Oncaea conifera***	***Limacina retroversa***	***Salpa thompsoni***	
1	26.89	-	0.00	0.09	0.07	0.03	0.12	1.17
2	23.51	-	0.01	0.01	0.01	-	7.19	30.72
4	25.36	0.39	-	0.10	0.39	3.21	-	16.14
5	18.05	0.29	1.63	0.01	0.64	0.40	5	16.47
6	36.73	0.81	9.98	0.79	0.68	1.04	50.63	174.08
7	30.51	0.08	-	0.17	0.07	1.00	0.25	5.15
8	40.07	2.05	2.02	0.05	0.04	18.14	-	55.68
9	20.71	0.06	0.04	0.00	0.00	0.73	-	4.03
10	12.62	2.80	1.62	0.15	0.65	2.76	-	63.30
11	16.36	1.16	5.37	0.16	0.47	-	-	43.76
12	22.59	2.33	5.01	0.06	0.06	3.16	-	47.03
13	14.61	2.00	0.85	0.02	-	0.05	-	20.00
14	12.35	0.63	1.11	0.12	0.03	0.09	-	16.06
15	16.37	0.17	0.36	0.01	-	0.02	0.40	5.81
16	20.13	-	1.76	0.11	0.12	0.11	25.94	139.34
17	28.32	0.18	0.43	0.16	0.14	0.12	-	3.44
18	17.48	0.10	0.58	0.34	0.17	-	7.26	48.34

Table 3.4. continued

19	17.51	0.17	0.47	0.01	0.02	0.06	0.71	8.17
20	23.45	0.57	0.16	0.13	0.03	0.32	-	5.18
21	16.88	0.94	0.74	0.04	0.04	2.42	-	24.79
22	14.04	0.77	1.27	0.13	0.32	0.30	-	19.84
23	20.84	0.17	0.50	0.02	0.07	0.02	-	3.72
24	11.97	0.68	0.34	0.02	0.15	0.02	-	10.03
25	12.54	1.47	1.27	0.09	0.82	0.03	-	29.32
26	12.05	1.47	0.60	0.04	0.37	0.12	-	21.58
27	12.58	1.78	0.69	0.04	0.25	0.21	-	23.61
29	16.7	0.05	0.06	0.01	0.01	0.26	-	2.32
30	15.13	0.82	1.63	0.03	0.16	0.96	-	23.72
31	35.57	0.21	2.15	0.93	1.16	-	-	12.51
32	32.25	0.21	0.14	0.01	0.05	0.02	-	1.39
33	25.63	0.20	0.05	0.00	0.04	0.43	0.11	3.23
34	13.04	0.05	0.14	-	0.05	0.63	20.01	160.13
35	27.08	0.30	2.63	0.16	0.52	-	13.21	62.14
36	20.56	1.51	4.56	0.14	0.42	1.39	-	38.99
37	17.65	2.18	1.67	0.03	0.19	0.80	-	27.64
38	16.11	0.62	0.45	-	1.04	0.23	-	14.49
39	16.59	0.26	0.14	0.01	0.33	0.16	-	5.47
40	18.79	0.50	0.07	0.01	0.13	0.14	1.06	10.19
41	16.57	0.56	0.07	0.05	0.57	0.02	-	7.66
42	17.87	0.24	0.47	-	0.29	0.07	-	5.95
43	14.22	0.58	0.17	-	0.36	0.51	-	11.39
44	16.16	0.36	0.30	0.01	0.01	0.50	-	7.29
45	25.19	0.02	0.30	0.01	0.01	0.26	1.01	6.37
46	25.04	0.09	0.39	-	0.11	0.04	-	2.53
47	31.33	0.79	0.47	0.05	0.49	0.11	0.65	8.19
48	38.62	0.34	0.49	1.57	0.23	-	-	6.79

CHAPTER FOUR: DISCUSSION

In contrast to previous studies conducted in the region of the Subtropical Convergence in the Atlantic Ocean (Froneman and Perissinotto 1996; Barange *et al*. 1998), south of Africa (Weeks and Shillington 1996; Froneman *et al*. 1997; Pakhomov and Perissinotto 1997), the Indian Ocean (Read *et al*. 2000; Llido *et al*. 2005) and near New Zealand (Bradford-Grieve *et al*. 1998; James and Hall 1998; Delizo *et al*. 2007) no biological enhancement (total chl-*a* concentrations and mesozooplankton abundance) was recorded at those stations occupied in the vicinity of the front during the present study (Fig. 3.3. and 3.4.). Llido *et al*. (2005) suggested that biological enhancement in the region of the STC takes place as episodic chl-*a* bloom events interspersed by non-bloom periods. The development of a stable water column appeared largely to promote such bloom events and wind driven water column mixing appeared to result in the expansion of the mixed layer depth and the dissipation of the phytoplankton bloom (Llido *et al*. 2005). The absence of any biological enhancement during this study appears to reflect a non-bloom period due to the influence of a large storm, which occurred in the area under investigation prior to this study, on the biology of the region. Indeed, it is worth noting that the results of size-fractionated chl-*a* during this investigation showed that the phytoplankton size community was dominated by picophytoplankton (<2µm), which is consistent with observations recorded in highly turbulent areas of the world's oceans (Laubscher *et al*. 1993; Froneman 1999; Schultes *et al*. 2006). The estimates of the total integrated phytoplankton biomass reported here are in the range published for the region of the front (Pakhomov and Perissinotto 1997; Barange *et al*. 1998; Bradford-Grieve *et al*. 1998).

The estimates of total mesozooplankton abundance during this study are in the range reported in the literature for the region of the STC during different seasons (Pakhomov and Perissinotto 1997; Barange *et al*. 1998; Bradford-Grieve *et al*. 1998). These data suggest that mesozooplankton abundance demonstrates little seasonality in the region of the front. The highly variable distribution of

mesozooplankton abundance observed during this study can most likely be explained by the diffuse distribution of chl-*a* in the study area as well as the effects of the substantial mixing event caused by the storm prior to the study. Indeed, the results of the PRIMER Bio-Env analysis showed that integrated chl-*a* concentration was the most important factor determining mesozooplankton distribution. This result is in agreement with previous studies (Froneman *et al*. 2000; Schultes *et al*. 2006), which have shown that zooplankton preferentially feed on and congregate around concentrated distributions of large phytoplankton cells. Also in agreement with the published literature (Perissinotto 1992; Pakhomov and Perissinotto 1997; Barange *et al*. 1998; Bradford-Grieve *et al*. 1998; Bernard and Froneman 2002), the mesozooplankton community was numerically dominated by copepods, which comprised on average 68% (SD±27.1) of the total zooplankton counts.

Numerical analysis failed to identify any distinct mesozooplankton groupings associated with any of the water masses or frontal region during the study (Fig. 3.9.). Indeed, the SIMPER analysis indicated that the differences between groups identified with the numerical analysis were ascribed to changes in the relative abundance of the dominant species rather than the presence or absence of individual species (Table 3.1.). There appeared to be a slight west-east gradient in mesozooplankton abundance and biomass with higher abundance in the north-west area of the survey and higher biomass in the eastern area of the survey, however spatial differences were not significant. The absence of any significant differences in the mesozooplankton community structure north and south of the front suggests that the STC did not act as a biogeographic barrier to the distribution of mesozooplankton during the study. This result is in contrast to previous studies conducted in different sectors of the STC during different seasons (Deacon 1982; Boden *et al*. 1988; Pakhomov *et al*. 1994; Froneman *et al*. 1995; Pakhomov and Perissinotto 1997; Barange *et al*. 1998), which have highlighted the importance of the STC as a biogeographic barrier to the distribution of plankton and nekton species. Further evidence to suggest that the front did not represent a strong biogeographic barrier was the presence of species found outside of their natural biogeographic range. The pteropod, *Limacina retroversa,* was widely distributed in Subtropical waters north of the front, although according to Lalli and Gilmer (1989), this species is

considered to be an indicator species of Sub-Antarctic water masses. Other notable species found outside their natural biogeographic distributions included the copepods *Ctenocalanus vanus* (Sub-Antarctic species found in Subtropical water) and *Oithona nana* (tropical species found in Sub-Antarctic water) (Boltovskoy 1999). The presence of Subtropical and Sub-Antarctic species beyond their natural distribution ranges during this study can likely be ascribed to horizontal transport as a result of cross frontal mixing due to an intense storm in the region under investigation prior to the survey. Other cross frontal transport mechanisms in the region of the front could include eddies formed due to the strong shear at the front which has been shown to transport large water masses across the STC in this region (Froneman *et al.* 1997; Froneman and Perissinotto 1996). During the period that this study took place, there was no physical oceanographic evidence to suggest the presence of a recent eddy.

In agreement with previous studies conducted within the same geographic region (Pakhomov and Perissinotto 1997; Bernard 2002), all selected mesozooplankton species showed unimodal diel feeding rhythms with a peak in gut pigment contents recorded at night (Fig. 3.10.). The observed patterns can be attributed to marked diel vertical migration patterns exhibited by mesozooplankton (Longhurst 1991; Fortier *et al*. 1994; Bernard 2002; Froneman *et al*. 2002). The estimates of gut pigment content, gut evacuation rate, and ingestion rates obtained for the mesozooplankton during this study were in the range reported in the published literature for different regions of the Southern Ocean during different seasons (Perissinotto 1992; Atkinson *et al*. 1996; Pakhomov and Perissinotto 1997; Bradford-Grieve *et al*. 1998; Bernard 2002; Froneman *et al*. 2002).

The daily rations of phytoplankton carbon for the selected mesozooplankton species during this study ranged from 2.4 to 10.9% body carbon (Table 3.2.). These estimates are in the range reported for copepods in a low chl-*a* environment (Atkinson 1996; Gaudy *et al*. 2003). The daily carbon requirements for mesozooplankton are highly variable. According to Dagg *et al*. (1982), copepods respire ~ 6% body carbon per day, which would suggest that these organisms need to consume substantially more carbon to cover their excretory and assimilation losses. If we assume that the copepods require 10% body carbon

per day to meet all of their metabolic requirements, results from grazing studies would suggest that the copepods are consuming alternative carbon sources. It is worth noting that preliminary data from a lipid analysis study conducted in parallel to this investigation confirmed the importance of heterotrophic carbon sources in the diets of the plankton within the region of study (Richoux and Froneman, unpublished data). Interestingly, the highest daily carbon rations were obtained for the pteropod and salp (Table 3.2.). The elevated daily rations obtained for these two organisms can likely be attributed to the fact that they feed by means of a mucous mesh, which allows them to feed on a wide range of particle sizes (Fortier *et al*. 1994; Bernard and Froneman 2005). The low daily rations obtained for the copepods can likely be attributed to the inability of these organisms to feed on picophytoplankton, which was the dominant component of the phytoplankton assemblages within the region of investigation (Fig. 3.2a,b.).

The grazing impact of the selected mesozooplankton species during this investigation ranged from 1.2 to 174.1% of the available phytoplankton (mean = 27.3%). Estimates of the grazing impact of mesozooplankton on phytoplankton are highly variable ranging from <1 up to 48% of total standing stock (Peterson *et al*. 1990; Morales *et al*. 1991; Perissinotto 1992; Dam *et al*. 1993; Atkinson and Shreeve 1995; Pakhomov and Perissinotto 1997; Froneman *et al*. 2000). The elevated grazing impact (>100% of integrated phytoplankton biomass) recorded at selected stations within the survey area during this study can probably be attributed to the presence of *Salpa thompsoni* and *L. retroversa.* Recent studies indicate that both salps and pteropods have among the highest ingestion rates recorded for mesozooplankton (Pakhomov and Froneman 2004; Bernard and Froneman 2005). The high ingestion rates for these species can be attributed to their feeding ecology (see above) (Fortier *et al*. 1994; Bernard and Froneman 2005). Overall however, the grazing impact of the selected mesozooplankton species generally accounted for <30% of the available phytoplankton standing stock (Table 3.3.). This result is in agreement with the published literature (Table 1.3.) and highlights the importance of the mesozooplankton as consumers of phytoplankton in the open ocean.

CHAPTER FIVE: SYNTHESIS

Analysis of the zooplankton community data indicates that the STC did not act as a biogeographic barrier to the distribution of mesozooplankton during this study (chapter 3). The absence of this barrier can likely be attributed to the intense storm prior to this investigation, which would have contributed to cross frontal mixing. The turbulence generated by the storm contributed to the absence of any biological enhancement (chl-*a* and mesozooplankton abundance and biomass) at those stations in the vicinity of the front and the predominance of picophytoplankton (<2μm) throughout the region of investigation. Although the physical parameters (temperature and salinity) showed a well defined front, it is likely that the biology within the region of the front lagged behind the re-establishment of a strong frontal zone.

This study provides evidence, supporting Llido *et al*. (2005), to suggest that biological enhancement in the vicinity of the STC takes place episodically with limited temporal and spatial scales. We can presume that the STC periodically acts as a strong biogeographic barrier when the front intensifies during a bloom event but in between such events substantial cross-frontal mixing does occur. The relative instability of the STC in the Indian sector of the Southern Ocean (compared to the sector of the STC south of Africa which is intensified by the presence of the Agulhas Return Current (Lutjeharms and Ansorge 2001)) is also presumed to make this region of the STC more prone to cross frontal mixing events during storms thus contributing to the region acting as a weak biogeographic barrier to the distribution of mesozooplankton.

The estimated grazing impact of selected mesozooplankton species in this study are in the range reported in the published literature (Table 1.3.). Results from grazing studies indicate that the numerically dominant components of the mesozooplankton were not able to meet their basic metabolic

requirements by feeding on phytoplankton alone. As a consequence, it is suggested that these organisms feed on alternative carbon sources. The vertical carbon flux during this study may have been minimal, particularly where copepods were the most important consumers of phytoplankton as they produce small, slow sinking faecal pellets with a low carbon content (Fortier *et al*. 1994). Copepods also demonstrate coprohexy and coprophagy which would have further reduced vertical carbon flux (Fortier *et al*. 1994). The contribution of the macrozooplankton to vertical carbon flux is also likely to have been minimal as they generally occurred in low abundances throughout the region of study area (Sterley 2008). It is possible however, that at selected stations where the salp, *Salpa thompsoni,* and the pteropod, *Limacina retroversa,* were the dominant consumers of phytoplankton standing stock, the mesozooplankton may have had a greater contribution to vertical carbon flux. This is due to the ability of these organisms to produce large, fast sinking faecal pellets with a high carbon content (Fortier *et al*. 1994). Due to the patchy nature of the zooplankton community structure and the apparent instability of the STC within the Indian Ocean sector, we can expect to find that this region of the front acts as an unpredictable and erratic net sink for atmospheric CO_2.

5.1. FUTURE RESEARCH INITIATIVES

5.1.1. This study provides *in situ* evidence, supporting Llido *et al*. (2005), to suggest that biological enhancement in the vicinity of the STC takes place episodically in the form of phytoplankton blooms with limited temporal and spatial scales rather than with a defined seasonal scale. Therefore, the implications of bloom and non-bloom periods and the frequency thereof on zooplankton-mediated carbon flux needs to be taken into account when assessing the role of the STC as a potential sink of atmospheric CO_2. Thus, further *in situ* studies should be conducted over a period of time in which a phytoplankton bloom and non-bloom period is observed so as to assess the potential variation in the zooplankton community structure and grazing impact on phytoplankton biomass to estimate how zooplankton-mediated carbon flux may vary.

5.1.2. It has been suggested by Gallienne and Robins (2001) that zooplankton sampling nets with a mesh size of 200μm or larger may substantially under estimate the contribution of the early developmental stages of copepods and the smaller copepod species (such as *Oithona* and *Oncaea* spp) as well as dramatically under estimate the mesozooplankton abundance and biomass by up to 90% and 33%, respectively. Future studies should consider using nets with a smaller mesh size or at least take into account the potential implications (such as under estimating the role of zooplankton mediated carbon flux) of under sampling certain components of the zooplankton community.

5.1.3. This study supports previous studies (Atkinson 1996; Froneman *et al*. 1996) which have indicated that alternative carbon sources (e.g. protozoans and microheterotrophs) play an important role in the diets of numerically dominant zooplankton in the Southern Ocean, particularly during winter. The low daily carbon rations of selected mesozooplankton recorded during this investigation suggest that alternative food sources were an important carbon source to mesozooplankton. Future research should thus aim to assess the role of alternative food sources in the diets of mesozooplankton in the Indian sector of the STC, particularly during bloom and non-bloom events.

5.1.4. Overall, the variability of the STC in the region under investigation together with the challenges of limited temporal studies make it difficult to characterize the community structure and trophodynamics of mesozooplankton in the Indian sector of the STC. The use of satellite altimetry data could be employed more to add to our understanding but there is a need to consider the complex subsurface physical dynamics at the frontal zone and how this varies over time. Thus, further *in situ* studies should look at broader temporal and spatial scales which, together with satellite data, may give further insight into factors responsible for the characteristics of the STC observed in this study and thus improve our understanding of this region of the Ocean.

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APPENDIX

Table A.1. Species list for the first Southern Ocean Ecosystem Variability Study, May 2007.

Species or taxa	Species or taxa
Copepods	**Amphipods**
Aetideus spp	*Themisto gaudichaudi*
Calanus simillimus	
Calocalunus spp	**Chaetognaths**
Candacia spp	*Eukrohnia hamata*
Clausocalanus breviceps	*Sagitta gazellae*
Corycaeus spp	*Sagitta maxima*
Ctenocalanus spp	*Sagitta zetesios*
Euchirella rostrata	
Gaetanus spp	**Pteropods**
Halopticus oxycephalus	*Limacina retroversa*
Heterorhabdus spp	
Lucicutia spp	**Tunicates**
Metridia lucens	*Salpa thompsoni*
Microsetella rosea	
Oithona similis	**Other**
Oncaea conifera	Appendicularians
Paraeuchaeta biloba	Eggs
Paraeuchaeta spp	Euphausiid furcilia
Pleuromamma abdominalis	Fish
Rhincalanus nastus	Naupli
Sapphirina spp	Ostracods
Scaphocalanus spp	Polychaetes
Scolecithricella minor	Siphonaria
Subeucalanus longiceps	

Table A.2. Dates and positions of mesozooplankton sampling stations, including integrated chl-*a,* mesozooplankton biomass and abundance and the depth of the net tows during the first Southern Ocean Ecosystem Variability Study, May 2007. Note: No net tows were conducted at stations 3 and 28 due to technical difficulties.

Station	Date	Longitude (degrees east)	Latitude (degrees north)	Chl-*a* (mg chl-*a*.m^{-2})	Abundance (ind.m^{-2})	Biomass (mg Dwt.m^{-2})	Depth of tow
1	4/17/2007	37.9999	-42.0008	26.89	14555.89824	530.2211	300
2	4/17/2007	38.0008	-41.5001	23.51	7017.906828	529.4151	300
3	4/18/2007	38.0033	-40.9997	30.16	-	-	-
4	4/18/2007	37.9483	-40.5107	25.36	198787.8866	241.9136	300
5	4/18/2007	37.9987	-39.9887	18.05	203725.4179	563.7912	200
6	4/19/2007	37.9872	-39.4612	36.73	50303.49545	345.8928	200
7	4/19/2007	38.0008	-38.9632	30.51	308521.3841	239.7511	200
8	4/19/2007	38.0008	-38.494	40.07	6076.139695	394.5702	300
9	4/19/2007	38.0008	-38.0005	20.71	120405.5957	396.263	300
10	4/19/2007	38.7518	-38.0025	12.62	155303.0196	840.8817	200
11	4/19/2007	38.7567	-38.4993	16.36	72592.34469	565.6816	200
12	4/20/2007	38.7505	-39.0005	22.59	17723.62368	396.5761	200
13	4/20/2007	38.7505	-39.499	14.61	26310.36741	295.4961	300
14	4/20/2007	38.7505	-40.0008	12.35	10449.91075	267.6509	300
15	4/20/2007	38.7505	-40.5	16.37	23800.45342	2577.879	300
16	4/20/2007	38.7518	-41.0013	20.13	22476.13999	2407.871	200
17	4/20/2007	38.7568	-41.5	28.32	42271.72209	532.7176	200
18	4/21/2007	38.7528	-42.001	17.48	9386.434589	292.7543	200
19	4/21/2007	39.5	-42.001	17.51	16146.51315	372.7003	300
20	4/21/2007	39.5	-41.5001	23.45	32560.03778	568.4795	300
21	4/21/2007	39.5	-41.0001	16.88	44403.68489	460.2585	300
22	4/22/2007	39.5	-40.5113	14.04	7956.768593	255.4795	300
23	4/22/2007	39.5013	-39.9997	20.84	15180.31136	983.4661	300
24	4/22/2007	39.4987	-39.5003	11.97	36426.0473	773.6326	300
25	4/22/2007	40.2453	-39.501	12.54	15464.07954	1722.313	300

26	4/23/2007	40.2503	-39.9992	12.05	32861.51454	1341.488	200
27	4/23/2007	40.252	-40.5003	12.58	3934.871205	1034.242	300
28	4/23/2007	40.2455	-41.0003	16.70	-	-	-
29	4/23/2007	40.2455	-41.5003	20.00	67689.8827	4614.294	300
30	4/23/2007	40.2367	-42.0025	15.13	6317.868168	1540.407	200
31	4/23/2007	40.252	-42.5003	35.57	10221.06436	1741.635	200
32	4/24/2007	40.252	-43	32.25	14656.94039	4593.358	200
33	4/24/2007	41	-43	25.63	47690.41051	1274.369	300
34	4/24/2007	40.9987	-42.4992	13.04	57728.70486	1958.715	300
35	4/24/2007	41.0015	-41.9973	27.08	34296.76054	2180.948	200
36	4/24/2007	41.0007	-41.5008	20.56	33317.46678	1412.399	200
37	4/25/2007	41.0005	-40.9993	17.65	14042.48197	2681.687	200
38	4/25/2007	41.0005	-40.4975	16.11	16283.74544	1534.867	300
39	4/25/2007	41.0005	-40.0033	16.59	15197.97844	2734.64	300
40	4/25/2007	41.0005	-39.4872	18.79	10473.27554	1715.803	300
41	4/25/2007	41.748	-39.499	16.57	13775.59449	1896.293	200
42	4/26/2007	41.7495	-39.9997	17.87	11396.4877	2575.664	200
43	4/26/2007	41.75	-40.5	14.22	8451.409892	2241.813	200
44	4/26/2007	41.7512	-41.0002	16.16	11351.44723	1985.211	300
45	4/26/2007	41.75	-41.5	25.19	42393.83053	1133.425	300
46	4/26/2007	41.75	-42	25.04	126709.8092	2441.928	200
47	4/26/2007	41.75	-42.5	31.33	47198.19122	1332.309	200
48	4/27/2007	41.75	-43.0017	38.62	62411.41869	1053.463	200

Table A.3. Identified taxa integrated abundance per station during the first Southern Ocean Ecosystem Variability Study, May 2007. Note: Due to technical difficulties there are no data for stations 3 and 28.

Station→	1	2	4	5	6	7	8	9
Taxa↓	**ind.m^{-2}**							
Copepods								
1. Aetideus spp	72.4	0.0	85.6	0.0	0.0	0.0	0.0	0.0
2. Calanus simillimus	0.0	0.0	641.7	479.4	1343.7	135.2	3386.5	99.5
3. Calocalunus spp	217.3	0.0	770.0	0.0	255.9	60.1	0.0	21.3
4. Candacia spp	0.0	0.0	85.6	127.8	255.9	0.0	138.2	0.0
5. Clausocalanus breviceps	579.3	54.5	684.4	95.9	5374.7	1171.9	345.6	7.1
6. Corycaeus spp	0.0	0.0	256.7	127.8	0.0	0.0	0.0	14.2
7. Ctenocalanus spp	144.8	0.0	2053.3	383.5	5886.5	1682.8	0.0	0.0
8. Euchirella rostrata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9. Gaetanus spp	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10. Halopticus oxycephalus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11. Heterorhabdus spp	0.0	0.0	0.0	383.5	0.0	60.1	138.2	0.0
12. Lucicutia spp	0.0	13.6	85.6	0.0	0.0	0.0	0.0	0.0
13. Metridia lucens	5214.1	231.7	1026.7	255.7	1279.7	120.2	0.0	7.1
14. Microsetella rosea	0.0	0.0	0.0	127.8	0.0	0.0	0.0	7.1
15. Oithona similis	5069.2	1062.9	8983.3	2173.2	2815.3	4747.9	13408.0	412.2
16. Oncaea conifera	325.9	61.3	1882.2	3068.1	3263.2	315.5	207.3	7.1
17. Paraeuchaeta biloba	0.0	0.0	0.0	255.7	767.8	0.0	138.2	0.0
18. Paraeuchaeta spp	0.0	0.0	256.7	255.7	767.8	8774.6	0.0	0.0
19. Pleuromamma abdominalis	1.9	27.3	0.0	3739.3	22842.3	0.0	4630.6	88.8
20. Rhincalanus nastus	0.0	0.0	0.0	127.8	0.0	0.0	0.0	0.0
21. Sapphirina spp	0.0	0.0	171.1	0.0	0.0	60.1	0.0	0.0
22. Scaphocalanus spp	0.0	0.0	256.7	0.0	0.0	60.1	0.0	0.0
23. Scolecithricella minor	0.0	54.5	85.6	0.0	0.0	0.0	0.0	0.0
24. Subeucalanus longiceps	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphipods								
25. Themisto gaudichaudi	0.0	1090.2	21902.1	0.0	4095.0	3846.4	8846.5	7.1
Pteropods								
26. Limacina retroversa	108.6	0.0	10095.5	1246.4	3263.2	3155.2	57018.4	2302.5
Tunicates								
27. Salpa thompsoni	21.1	1308.2	0.0	0.0	9213.7	45.1	0.0	0.0
Other								
28. Appendicularians	0.0	109.0	21902.1	2045.4	12284.9	3846.4	0.0	0.0
29. Chaetognaths	0.0	1199.2	21902.1	24544.9	12284.9	11539.2	84041.7	170.6
30. Eggs	0.0	109.0	0.0	0.0	0.0	0.0	0.0	21.3
31. Euphausiid furcilia	0.0	109.0	0.0	147269.2	94184.6	7692.8	39809.2	0.0
32. Fish	0.0	0.0	0.0	8181.6	0.0	0.0	8846.5	7.1
33. Naupli	0.0	0.0	85.6	0.0	511.9	60.1	0.0	0.0
34. Ostracods	1231.1	0.0	2224.4	767.0	2047.5	540.9	0.0	0.0
35. Polychaetes	0.0	109.0	0.0	0.0	0.0	0.0	0.0	0.0
36. Siphonaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table A.3. Continued.

	10	11	12	13	14	15	16	17	18	19	20
	ind.m^{-2}										
1	0.0	0.0	135.2	0.0	110.1	0.0	0.0	0.0	0.0	0.0	0.0
2	4631.0	1909.5	3852.7	3298.3	1045.8	287.6	0.0	196.0	165.1	278.6	947.5
3	0.0	159.1	135.2	79.5	0.0	0.0	0.0	0.0	0.0	0.0	79.0
4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	79.0
5	1042.0	1074.1	405.5	159.0	825.6	71.9	772.4	1078.1	2311.7	64.3	868.5
6	308.7	477.4	135.2	0.0	0.0	0.0	114.4	130.7	0.0	0.0	157.9
7	154.4	318.2	0.0	238.4	660.5	239.7	1258.7	392.0	880.7	0.0	0.0
8	0.0	0.0	135.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11	154.4	0.0	0.0	0.0	110.1	0.0	0.0	0.0	0.0	42.9	79.0
12	308.7	159.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	1080.6	795.6	540.7	0.0	0.0	47.9	1258.7	1176.1	7705.8	235.7	0.0
14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	2315.5	1591.2	1081.5	2622.8	6715.2	3834.8	801.0	8493.9	7705.8	1778.7	1342.3
16	3125.9	2267.5	304.2	0.0	165.1	0.0	600.7	686.0	825.6	75.0	138.2
17	0.0	318.2	135.2	0.0	110.1	95.9	228.9	130.7	0.0	42.9	0.0
18	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
19	3704.8	12292.2	11456.6	1947.2	2532.0	814.9	4033.5	980.1	1321.0	1082.2	375.0
20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
22	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
23	154.4	0.0	0.0	0.0	110.1	47.9	114.4	0.0	440.3	107.2	39.5
24	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
25	12349.3	10183.8	8651.6	238.4	0.0	47.9	0.0	130.7	0.0	42.9	79.0
26	8683.1	0.0	9935.8	159.0	275.2	47.9	343.3	392.0	0.0	182.2	1006.7
27	0.0	0.0	0.0	0.0	0.0	71.9	4720.0	0.0	1321.0	128.6	0.0
28	0.0	2546.0	0.0	0.0	220.2	0.0	0.0	0.0	440.3	21.4	39.5
29	61746.5	10183.8	2162.9	79.5	1210.9	767.0	0.0	0.0	660.5	471.5	276.3
30	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
31	4939.7	22913.6	8651.6	0.0	0.0	0.0	0.0	0.0	0.0	64.3	0.0
32	0.0	5091.9	0.0	0.0	0.0	0.0	0.0	0.0	220.2	0.0	0.0
33	154.4	0.0	0.0	0.0	110.1	0.0	0.0	392.0	660.5	21.4	39.5
34	2624.2	1909.5	675.9	79.5	0.0	47.9	0.0	522.7	880.7	64.3	276.3
35	154.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	39.5
36	463.1	5091.9	4325.8	159.0	0.0	0.0	0.0	0.0	220.2	42.9	197.4

Table A.3. Continued.

	21	22	23	24	25	26	27	29	30	31	32
	ind.m^{-2}										
1	0.0	0.0	0.0	0.0	86.7	0.0	0.0	0.0	0.0	0.0	31.4
2	1558.4	1265.1	278.2	1114.9	2428.4	2421.1	2935.6	78.0	1346.8	339.6	353.6
3	111.3	0.0	0.0	42.9	0.0	0.0	87.6	12.0	85.5	0.0	0.0
4	111.3	126.5	0.0	0.0	86.7	0.0	87.6	0.0	85.5	0.0	0.0
5	278.3	885.5	125.2	107.2	607.1	273.4	262.9	78.0	192.4	6282.3	94.3
6	167.0	632.5	278.2	1243.6	780.6	468.6	1139.2	96.0	256.5	0.0	0.0
7	222.6	1265.1	0.0	0.0	0.0	0.0	0.0	24.0	85.5	452.8	0.0
8	0.0	0.0	0.0	42.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.0	0.0	0.0	0.0
11	0.0	0.0	0.0	85.8	0.0	0.0	0.0	0.0	0.0	0.0	62.9
12	55.7	0.0	0.0	0.0	0.0	104.1	175.3	0.0	0.0	0.0	0.0
13	55.7	253.0	0.0	0.0	520.4	0.0	0.0	0.0	1197.2	28977.6	471.5
14	0.0	0.0	0.0	0.0	86.7	0.0	0.0	0.0	0.0	0.0	0.0
15	1614.1	6957.8	945.9	1157.8	2254.9	728.9	6484.7	108.0	1795.8	1584.7	2420.3
16	194.8	1518.1	319.9	729.0	3946.2	1796.3	1226.8	60.0	769.6	5603.1	259.3
17	167.0	379.5	111.3	171.5	86.7	52.1	0.0	12.0	85.5	1131.9	0.0
18	0.0	0.0	0.0	0.0	1127.5	208.3	175.3	0.0	0.0	0.0	0.0
19	1697.6	2909.6	1154.6	771.9	2905.4	1366.8	1577.4	126.0	3719.8	4923.9	330.0
20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21	111.3	0.0	0.0	0.0	0.0	0.0	0.0	12.0	0.0	0.0	0.0
22	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
23	0.0	0.0	27.8	0.0	86.7	104.1	0.0	0.0	0.0	226.4	220.0
24	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.0	0.0	0.0	0.0
25	111.3	0.0	27.8	42.9	0.0	156.2	175.3	12.0	256.5	0.0	0.0
26	7597.3	948.8	55.6	64.3	86.7	390.5	657.2	821.8	3014.3	0.0	70.7
27	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
28	389.6	1518.1	333.9	257.3	433.6	52.1	2541.3	36.0	85.5	0.0	0.0
29	1280.1	1518.1	55.6	257.3	867.3	468.6	1051.6	191.9	171.0	0.0	125.7
30	222.6	0.0	0.0	42.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
31	0.0	126.5	27.8	0.0	173.5	312.4	262.9	12.0	85.5	452.8	31.4
32	0.0	0.0	0.0	42.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
33	55.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
34	612.2	1391.6	389.5	1715.3	2168.2	676.9	1051.6	239.9	684.1	905.6	62.9
35	0.0	0.0	0.0	128.6	0.0	104.1	0.0	0.0	85.5	0.0	0.0
36	55.7	126.5	0.0	85.8	86.7	312.4	87.6	0.0	85.5	0.0	0.0

Table A.3. Continued.

	33	34	35	36	37	38	39	40	41	42	43
	ind.m^{-2}										
1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	72.4	0.0	43.7
2	331.0	89.9	500.9	2491.9	3596.5	1018.4	437.1	833.4	922.7	391.4	951.2
3	248.3	0.0	0.0	0.0	104.2	436.5	54.6	0.0	0.0	0.0	43.7
4	0.0	0.0	0.0	415.3	104.2	145.5	54.6	64.1	72.4	0.0	0.0
5	20.7	0.0	1102.1	934.5	234.6	0.0	54.6	96.2	325.7	0.0	0.0
6	0.0	0.0	0.0	415.3	417.0	872.9	874.2	705.2	651.3	174.0	131.2
7	0.0	0.0	0.0	0.0	0.0	436.5	273.2	192.3	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0	104.2	0.0	0.0	0.0	0.0	0.0	0.0
9	0.0	0.0	0.0	0.0	104.2	0.0	0.0	0.0	0.0	0.0	0.0
10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	34.8	0.0
11	0.0	0.0	0.0	0.0	0.0	0.0	0.0	64.1	0.0	0.0	0.0
12	0.0	0.0	0.0	415.3	0.0	291.0	0.0	64.1	0.0	0.0	0.0
13	1117.3	0.0	7347.3	1245.9	104.2	291.0	109.3	0.0	0.0	139.2	87.5
14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	1986.3	269.8	10686.9	7683.3	5420.8	1163.9	655.7	577.0	651.3	1009.1	656.0
16	186.2	224.8	2504.7	2024.7	938.2	5019.4	1611.9	609.0	2768.2	1409.2	1738.3
17	0.0	0.0	133.6	207.7	104.2	0.0	109.3	0.0	217.1	69.6	174.9
18	0.0	0.0	0.0	0.0	0.0	0.0	0.0	128.2	0.0	0.0	0.0
19	103.5	314.7	6011.4	10434.8	3831.0	1018.4	327.8	160.3	162.8	1069.9	393.6
20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
22	0.0	0.0	0.0	0.0	0.0	145.5	0.0	64.1	0.0	0.0	0.0
23	206.9	89.9	0.0	0.0	0.0	0.0	163.9	0.0	72.4	34.8	0.0
24	0.0	89.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
25	0.0	0.0	0.0	0.0	208.5	145.5	163.9	0.0	0.0	174.0	87.5
26	1344.9	1978.2	0.0	4360.8	2501.9	727.5	491.8	448.8	54.3	208.8	1607.2
27	20.7	3641.8	2404.6	0.0	0.0	0.0	0.0	192.3	0.0	0.0	0.0
28	0.0	89.9	133.6	2907.2	729.7	436.5	874.2	320.5	361.9	347.9	1005.8
29	248.3	0.0	267.2	207.7	1146.7	582.0	546.4	1154.0	144.7	34.8	349.9
30	0.0	0.0	0.0	207.7	0.0	0.0	163.9	0.0	0.0	34.8	43.7
31	206.9	179.8	400.8	623.0	208.5	727.5	163.9	128.2	144.7	174.0	87.5
32	0.0	0.0	0.0	0.0	0.0	0.0	109.3	64.1	0.0	0.0	0.0
33	41.4	0.0	0.0	415.3	104.2	0.0	0.0	0.0	72.4	69.6	0.0
34	124.1	1079.0	667.9	1038.3	1042.5	2327.9	983.5	1666.8	1013.2	452.3	1224.5
35	41.4	0.0	0.0	207.7	0.0	0.0	0.0	0.0	289.5	69.6	43.7
36	0.0	0.0	133.6	0.0	0.0	0.0	0.0	64.1	72.4	34.8	306.1

Table A.3. Continued.

	44	45	46	47	48
	ind.m^{-2}				
1	45.4	0.0	0.0	0.0	0.0
2	590.3	28.2	154.8	1305.0	557.4
3	45.4	112.7	0.0	0.0	0.0
4	0.0	0.0	41.3	0.0	0.0
5	68.1	84.5	0.0	355.9	10590.1
6	590.3	0.0	0.0	0.0	0.0
7	0.0	0.0	0.0	0.0	27868.7
8	0.0	0.0	0.0	0.0	0.0
9	0.0	0.0	0.0	0.0	0.0
10	0.0	0.0	0.0	0.0	0.0
11	0.0	0.0	0.0	0.0	0.0
12	0.0	28.2	0.0	0.0	0.0
13	0.0	56.3	3095.8	21829.7	20065.5
14	0.0	0.0	0.0	0.0	0.0
15	771.9	1380.4	2394.1	4587.4	13748.6
16	68.1	42.3	526.3	2372.8	1114.7
17	90.8	0.0	0.0	316.4	0.0
18	0.0	28.2	82.6	0.0	0.0
19	681.1	676.1	897.8	1067.8	1114.7
20	0.0	0.0	0.0	0.0	0.0
21	0.0	0.0	0.0	0.0	0.0
22	0.0	0.0	0.0	0.0	0.0
23	45.4	28.2	41.3	316.4	743.2
24	0.0	0.0	0.0	0.0	0.0
25	45.4	281.7	41.3	158.2	371.6
26	1566.4	831.1	123.8	355.9	0.0
27	0.0	183.1	0.0	118.6	0.0
28	317.8	225.4	165.1	0.0	371.6
29	136.2	647.9	206.4	0.0	371.6
30	90.8	197.2	0.0	0.0	0.0
31	90.8	0.0	41.3	158.2	371.6
32	0.0	0.0	0.0	0.0	0.0
33	0.0	0.0	0.0	0.0	0.0
34	227.0	84.5	454.1	316.4	0.0
35	0.0	0.0	0.0	0.0	0.0
36	0.0	28.2	0.0	0.0	0.0