Trophodynamics of Carnivorous Zooplankton in the Region of the Subtropical Convergence within the Indian Sector of the Southern Ocean, with Particular Emphasis on Chaetognaths

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ABSTRACT

Trophodynamics of carnivorous zooplankton in the region of the Subtropical Convergence (STC) in the Indian sector of the Southern Ocean was investigated during austral autumn (April 2007) as part of the first cruise of the Southern Ocean Ecosystem Variability Study. Within the region of the study, the STC was well defined by the 14°C surface isotherm which separated the Agulhas Return Current and Subtropical water in the north from Sub-Antarctic waters to the south. Total average abundance (3.89 ± 5.46ind 100m^{-3}) and biomass (0.14 ± 0.27mg Dwt 100m^{-3}) of carnivorous zooplankton south of the front were significantly higher than the total average abundance (1.33 ± 1.81ind 100m^{-3}) and biomass (0.03 ± 0.05mg Dwt 100m^{-3}) north of the front ($p<0.001$). There were no significant correlations between the selected physico-chemical (temperature and salinity) and the biological (mesozooplankton abundance and biomass) variables and the total abundance and biomass of the carnivorous zooplankton during the investigation ($p>0.05$ in all cases). There was no evidence of enhanced biomass and abundance values at stations occupied in the immediate vicinity of the front. Total average carnivorous zooplankton abundance was dominated by chaetognaths (*Eukrohnia hamata* Möbius 1875, *Sagitta gazellae* Ritler-Záhony 1909 and *S. zetesios* Fowler 1905) and euphausiids (*Nematoscelis megalops* Sars 1883, *Euphausia longirostris* Hansen 1908 and *E. spinifera* Sars 1883), which contributed up to $86.58 \pm 32.91\%$ of the total counts. The total average biomass was dominated by euphausiids and amphipods (*Themisto gaudichaudii* Guérin-Méneville 1825, *Phronima sedentaria* Forsskål 1775 and *Vibilia armata* Bovallius 1887) which contributed up to $71.45 \pm 34.85\%$ of the total counts. In general the populations of both the euphausiids and amphipods were dominated by females while the chaetognaths were dominated by juveniles. Numerical analysis identified two major zooplankton groupings within the survey area which did not coincide with the water masses within the survey area. The SIMPER procedure of the PRIMER package indicated differences between the groups were mainly attributed to changes in the abundance of the numerically dominant species rather than the presence or absence of individual species. The absence of any significant spatial patterns in the distribution of the carnivorous zooplankton suggests that the STC did not act as a biogeographical barrier during the present study.

The mean feeding rates of the chaetognaths *E. hamata*, *S. gazellae* and *S. zetesios* were 1.82 ± 0.85prey d^{-1}, 3.63 ± 2.08prey d^{-1} and 2.18 ± 0.59prey d^{-1}, respectively. These rates correspond to a combined predation impact equivalent to $<5\%$ of the mesozooplankton standing stock or $<10\%$ of the mesozooplankton secondary production. Mesozooplankton, comprising mainly copepods was the dominant prey in the guts of the three chaetognath species. Total predation impact of the

euphausiids, chaetognaths and amphipods, estimated using published daily ration data, on the mesozooplankton standing stock and secondary production ranged from 0.01% to 1.53% and from 0.03% to 30.54%, respectively. Among the carnivorous zooplankton, chaetognaths were generally identified as the dominant predators of mesozooplankton. Low predation impact of selected carnivorous zooplankton suggested that these organisms contributed little to the vertical carbon flux within the region of investigation during the study.

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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 is that of the author.

*"In loving memory of my dad for being
my inspiration and my biggest fan"*

CHAPTER ONE

GENERAL INTRODUCTION

1.1   THE SIGNIFICANCE OF THE OCEANS IN THE GLOBAL CARBON CYCLE

As a result of human activities (burning of fossil fuels, deforestation and agricultural practices) atmospheric concentrations of the greenhouse gas, carbon dioxide (CO_2), have risen dramatically over the past century (Siegenthaler and Sarmiento 1993, Pakhomov *et al*. 2000). The oceans are considered the largest carbon reservoirs and sinks, as they contain approximately 95% of the total circulating carbon within the biosphere, and are therefore essential in regulating the global carbon cycle (Siegenthaler and Sarmiento 1993, Pakhomov *et al*. 2000, Froneman *et al*. 2000a). The oceans are responsible for the sequestration of surface carbon to depth, either by means of physico-chemical (solubility pump) or biological (biological pump) processes (Longhurst 1991, Froneman *et al*. 2000a). The solubility pump is a passive method of transport, which relies on a concentration gradient for the diffusion of atmospheric CO_2 to the surface water and then to depth via the thermohaline circulation (Longhurst and Harrison 1989, Longhurst 1991).

The biological pump relies on the production of particulate (POC) and dissolved (DOC) organic carbon which is subsequently exported to the deeper layers of the ocean (Siegenthaler and Sarmiento 1993, Froneman *et al*. 2000a). POC and DOC are products of biological processes such as photosynthesis by phytoplankton, the sinking of dead or senescent cells and animal waste, as well as the grazing and migratory behaviour of zooplankton (Longhurst 1991, Pakhomov *et al*. 1994, Fortier *et al*. 1994, Froneman *et al*. 2000a). The removal rate of atmospheric CO_2 from the surface layers of the ocean is highly dependant on the quantity, as well as the rate at which POC and DOC are produced and transported to depth (Longhurst and Harrison 1989, Longhurst 1991). Photosynthesis and the sinking of dead cells contribute significantly to carbon flux but only during phytoplankton blooms where between 10% and 20% of primary production is transported to depth (Longhurst 1991, Pakhomov *et al*. 2000, Froneman *et al*. 2000a, Bernard 2002). Heterotrophic activity and vertical migration by zooplankton, therefore, plays an important role in establishing the efficiency of the biological pump, particularly in the open waters of the world oceans (Longhurst and Harrison 1989, Longhurst 1991, Pakhomov *et al*. 2000, Froneman *et al*. 2000a).

Phytogenic carbon within the marine ecosystem can be partitioned into two major pelagic food webs; the so called "microbial loop" and the "classical food web" (Longhurst and Harrison 1989, Longhurst 1991, Siegenthaler and Sarmiento 1993, Fortier *et al*. 1994, Froneman *et al*.

2000a). The "microbial loop" which is controlled by microheterotrophs (<200µm) (Fortier *et al*. 1994, Froneman *et al*. 2000a, Bernard 2002) produce faecal pellets which are too small to have a significant contribution to vertical carbon flux as they remain in suspension for extended periods of time (Fortier *et al*. 1994, Froneman *et al*. 2000a, Bernard 2002) (Fig 1.1). In addition, the close association between microheterotrophs and bacteria within the microbial loop contribute to the recycling of carbon in the surface layers (Perissinotto 1995). Additionally, the faecal pellets which do sink to depth contribute little to carbon flux as microheterotrophs have high assimilation efficiencies, producing faecal pellets low in carbon content (Fortier *et al*. 1994, Froneman *et al*. 2000a, Bernard 2002). Lastly, organisms of this size class do not undergo diel vertical migration and are largely restricted to the surface waters (Froneman *et al*. 2000a). As a consequence, in the regions where the microbial loop represents the net sink for primary production, the magnitude of vertical carbon flux is low, contributing to a relatively inefficient biological pump (Froneman *et al*. 2000a). However, the utilization of organic matter, the base of the microbial loop, by bacteria is important as it creates a major pathway for the transfer of energy through the different food webs as bacteria form part of the first trophic level within the classical food web (Perissinotto 1995). Bacteria, therefore, represent a vital link between the microbial loop and the classical food web as they form an important food source for the second and third trophic levels within the classical food web (Perissinotto 1995).
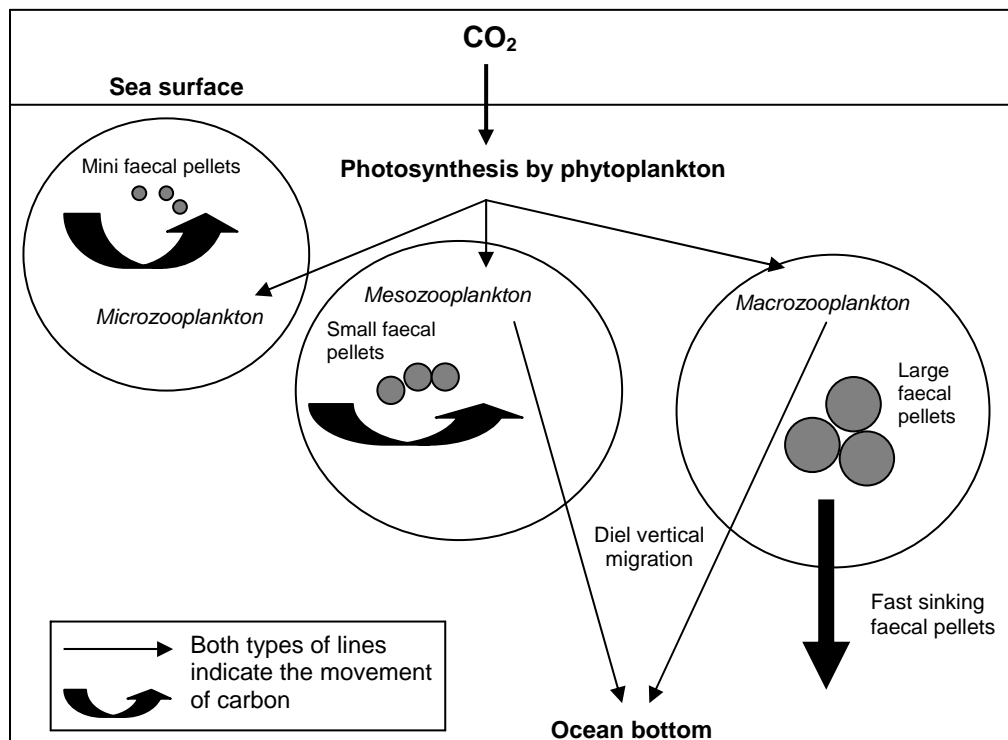
FIGURE 1.1 A simplified illustration of the biological pump (Bernard 2002).

The second food web, commonly known as the "classical food web", can have a significant influence on the efficiency of the biological pump. However, the efficiency of the biological pump is strongly mediated by the zooplankton community size structure. Faecal pellets produced by mesozooplankton (200-2000μm) contribute little to the carbon flux as they are small and have relatively slow sinking rates (Longhurst and Harrison 1989, Longhurst 1991, Pakhomov *et al.* 2000, Froneman *et al.* 2000a, Bernard 2002). Additionally, the mesozooplankton community is generally dominated by copepods which readily graze on their own faecal pellets (Fortier *et al.* 1994). As a result the re-ingestion (coprophagy) or disintegration (coprorhexy) of the faecal pellets substantially reduces the rate of carbon flux to depth thereby reducing the efficiency of the biological pump (Fortier *et al.* 1994) (Fig 1.1). Mesozooplankton are, however, able to contribute to vertical carbon flux through respiration and egestion at depth as they undergo diel vertical migration (Fortier *et al.* 1994, Froneman *et al.* 2000a, Bernard 2002).

Macrozooplankton (<2000μm) on the other hand, contribute significantly to carbon flux by producing large faecal pellets, with relatively high carbon content, which have fast sinking rates (Longhurst and Harrison 1989, Longhurst 1991, Fortier *et al.* 1994, Pakhomov *et al.* 1999, Froneman *et al.* 2000a, Bernard 2002, Froneman *et al.* 2002, Lukác 2005) (Fig 1.1). Macrozooplankton also undergo extensive diel vertical migrations, up to 800m, which contribute to carbon flux through respiration and egestion at depth (Longhurst and Harrison 1989, Pakhomov *et al.* 1999, Froneman *et al.* 2000a, Froneman *et al.* 2002, Lukác 2005). It can therefore be assumed that where the large macrozooplankton are the dominant consumers of primary production, the biological pump will be efficient (Froneman *et al.* 2000a, Bernard 2002, Froneman *et al.* 2002). Thus to understand the role of zooplankton within the Southern Ocean carbon cycle, one needs to understand the structure of the zooplankton community and its dynamics (Pakhomov *et al.* 2000).

1.2   *PHYSICAL OCEANOGRAPHY OF THE SOUTHERN OCEAN*

The Southern Ocean is the largest continuous body of water on the Earth and links the southern regions of the Indian, Atlantic and Pacific Oceans (Lutjeharms and Valentine 1984, Lutjeharms 1985, Bernard 2002, Lukác 2005). The Antarctic continent forms the southern boundary of this vast ocean while the northern limit is established by the Subtropical Convergence (STC) (Lutjeharms and Valentine 1984, Lutjeharms 1985, Froneman *et al.* 1997, Pakhomov and Perissinotto 1997, Bernard 2002, Lukác 2005). The Southern Ocean south of Africa is characterised by four major fronts; the Agulhas Front (AF), the STC, the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF), which ultimately form part of the Antarctic Circumpolar Current (ACC) (Fig 1.2) (Lutjeharms and Valentine 1984, Lutjeharms 1985, Bernard 2002, Lukác 2005). As

a result these fronts divide the Southern Ocean into sub-regions with distinct physical and biological properties (Pakhomov *et al*. 1994, Froneman and Perissinotto 1996, Johnson and Terazaki 2004, Lukác 2005, Froneman *et al*. 2007).
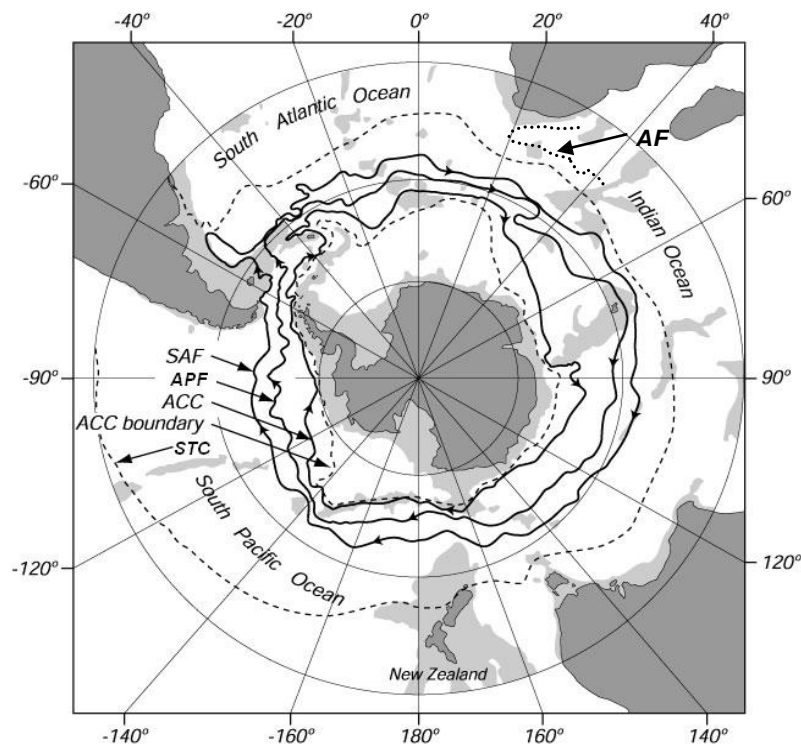
FIGURE 1.2 The circumpolar currents of the Southern Ocean: Agulhas Front (AF); Subtropical Convergence (STC); Subantarctic Front (SAF); Antarctic Polar Front (APF) and the Antarctic Circumpolar Current (ACC) (Modified from Orsi *et al*. 1995).

The APF is identified as the region where Antarctic surface water subducts below the less dense Sub-Antarctic water and is positioned south of the SAF (Lutjeharms and Valentine 1984, Lutjeharms 1985, Lukác 2005) (Fig 1.2). The SAF is predominantly a subsurface front identified by changes in the vertical structure of the water column and is positioned south of the STC (Fig 1.2) (Lutjeharms and Valentine 1984, Barange *et al*. 1998, Lukác 2005). The AF formed by the Agulhas Return Current (ARC) is situated north of the STC and is identified by an average middle temperature of 18.4°C (Lutjeharms and Valentine 1984) (Fig 1.2). This front becomes a prominent feature when its interaction with the STC is minimal but it forms an intricate part of the meridional heat flux due to the shedding of warm core eddies (Lutjeharms and Valentine 1984, Pakhomov and Perissinotto 1997, Barange *et al*. 1998).

The STC originates off the coast of Argentina, as the southern boundary of the Brazil Current, and may separate into multiple quasipermanent frontal features within some regions of the Southern Ocean (Tomczak *et al*. 2004) (Fig 1.2). It then extends across the Atlantic Ocean at about

40°S passing south of Africa and continuing through the Indian and Central Pacific Oceans where it shifts northward arriving at the coast of Chile (Fig 1.2) as far north as 30°S (Tomczak *et al*. 2004). Between Africa and Antarctica, the STC is the most prominent surface frontal system with an estimated width of 225km (Lutjeharms and Valentine 1984). Within this region, denser Sub-Antarctic surface water subducts north, beneath Subtropical surface water, thus characterising this front with strong horizontal temperature and salinity gradients which separates water masses of different physico-chemical properties (Lutjeharms and Valentine 1984, Lutjeharms 1985, Barange *et al*. 1998, Pollard *et al*. 2002, Lukác 2005). The front can be identified by an average middle surface temperature of 14.3°C or by a substantial drop in temperature from north to south of about 8.4°C (Lutjeharms and Valentine 1984, Lutjeharms 1985). Within the Indian sector of the Southern Ocean, the STC lies between approximately 40°S - 42°S while south of Africa its position is highly variable but is estimated at 42°S (Lutjeharms and Valentine 1984, Lutjeharms 1985, Barange *et al*. 1998, Lukác 2005). According to Tomczak *et al*. (2004) this frontal feature demonstrates a high degree of seasonality in its location and adds that the velocity of this front east of South Africa reduces from 30sv to 10sv as it approaches Australia. Tomczak *et al*. (2004) thus conclude that the STC is highly variable in its strength and position throughout the Oceans resulting in an increase in its latitudinal variability.

The STC is strongly associated with the ARC south of Africa. According to Lutjeharms (1985), this results in a single feature consisting of two fronts, the AF and the STC, with the first stronger front occurring at approximately 39°S. The second front is situated at approximately 43°S and is considered to be the STC as the surface saline value illustrates properties of the true STC (Lutjeharms 1985). In this instance, the northern most front is thus considered the AF. In a study conducted by Lutjeharms and Valentine (1984), a separate AF was detected as the average middle temperature of the STC on that occasion was 12.1°C, but in a later study the average middle temperature of the STC was recorded at 16.7°C. In the latter study the AF had merged with the STC thus causing the increase in temperature. Lutjeharms (1985) also states that although the fronts may merge south of Africa, east of 19°E they diverge, thus creating two separate fronts, the AF and the STC. The interaction of the two fronts also causes a variation in the position of the STC with the average location of the STC east of 20°E being to the south of the average location of the STC west of 20°E (Lutjeharms 1985). This southward deflection of the STC east of the 20°E is due to the influence of eddies within the system (Lutjeharms 1985). Lutjeharms (1985), states that the STC should rather be called the Subtropical Frontal Zone due to its dynamic and irregular behaviour creating a band rather than a single front.

The STC is considered a major biogeographical boundary to the distribution of both plankton and nekton due to the sharp transition in temperature and salinity between Sub-Antarctic water and Subtropical waters (Deacon 1982, Butler *et al*. 1992, Pakhomov *et al*. 1994, Froneman *et al*. 1995, Tarling *et al*. 1995, Froneman *et al*. 1997, Pakhomov and Perissinotto 1997, Barange *et al*. 1998, Bernard 2002, Tomczak *et al*. 2004). In the zone were the STC and AF converge, a distinct boundary is formed which limits the distribution of Sub-Antarctic species to the north and Subtropical species to the south (Pakhomov *et al*. 2000). The area between the STC and the AF is characterised by a number of meanders which generally break off and form eddies. Interactions between the AF and the STC thus intensifies the level of dynamic variability which results in further shedding of eddies (Lutjeharms and Valentine 1984, Lutjeharms 1985, Froneman *et al*. 1997, Pakhomov and Perissinotto 1997). Within these areas, eddies play a vital role in the mixing of communities as the plankton communities associated with eddies are similar to the communities in which the eddies originate (Pakhomov and Froneman 2004a). Due to the ability of eddies to move independently of the surrounding water currents they are therefore able to transport these communities across biogeographical boundaries (Froneman *et al*. 1997, Pakhomov and Perissinotto 1997, Pakhomov *et al*. 1999, Pakhomov *et al*. 2000, Lukác 2005). Eddies are also associated with increased abundance and biomass levels of plankton, usually occurring on the edge, due to increased water column stability and nutrient availability (Froneman *et al*. 1995). The production of eddies indicates that the STC demonstrates a high degree of latitudinal variability as the strength or velocity of the front varies along the latitude (Tomczak *et al*. 2004).

The interaction of the STC with the AF, the reduction in velocity and the increase in frontal meandering and the production of eddies suggests that within areas of the STC were there is a high degree of variability, with regard to the hydrodynamics, the potential of cross frontal mixing is increased as well as being highly variable in occurrence and intensity (Lutjeharms and Valentine 1984, Lutjeharms 1985, Lutjeharms *et al*. 1993, Pakhomov *et al*. 1994, Pakhomov *et al*. 1999). Data on the hydrodynamics of the STC within in the Indian Ocean is minimal, however, and therefore the degree of variability within this area cannot be established.

1.3   BIOLOGICAL STUDIES

1.3.1   COMMUNITY STRUCTURE

The zooplankton community structure, including abundance, biomass and distribution, is strongly linked to the hydrography on both temporal and spatial scales (Froneman *et al*. 1995, Gibbons 1997, Lukác 2005). In a study within the Antarctic Polar Frontal zone, Hunt *et al*. (2002)

demonstrated that plankton species were strongly correlated to the physico-chemical properties of the water masses. The study also concluded that differences within community structures were not necessarily due to variations in species composition but rather to the variations in abundance and biomass of the numerically dominant species. Within the south west Atlantic, Tarling *et al.* (1995) identified four distinct zooplankton groupings: the Polar Frontal Zone, the Sub-Antarctic zone, the Sub-tropical zone and the Falkland shelf. Tarling *et al.* (1995) stated that these results indicated a clear relationship between the faunal zones and the position of the water masses. Similarly, Froneman *et al.* (1995) identified eight distinct phytoplankton groupings namely: Continental water boundary, Marginal ice zone, Antarctic zone, APF group, Polar Frontal Zone, Sub-Antarctic zone, Subtropical zone and the ARC group, along a transect between southern Africa and Antarctica. These findings indicate that fronts represent biogeographic boundaries in the distribution of plankton species. However, fronts are also considered as transition zones as within these areas there is a convergence of different plankton communities and water properties which results in a new ecotone that sustains a unique community (Pakhomov and Perissinotto 1997, Bernard 2002, Pakhomov and Froneman 2004a).

Studies conducted in different sectors of the Southern Ocean during different seasons have demonstrated that the total zooplankton community is numerically and by biomass, dominated by mesozooplankton (200 - 2000μm) comprising mainly copepods, pteropods and ostracods. (Lutjeharms and Valentine 1984, Lutjeharms 1985, Butler *et al.* 1992, Lutjeharms *et al.* 1993, Pakhomov *et al.* 1994, Tarling *et al.* 1995, Froneman and Perissinotto 1996, Pakhomov and Perissinotto 1997, Froneman *et al.* 1998, Barange *et al.* 1998, Froneman and Pakhomov 1998, Pakhomov *et al.* 1999, Froneman *et al.* 2000a, Froneman *et al.* 2000b, Perissinotto *et al.* 2001, Bernard 2002, Hunt *et al.* 2002, Gurney *et al.* 2002, Froneman *et al.* 2002, Johnson and Terazaki 2004, Tomczak *et al.* 2004, Lukác 2005, Froneman *et al.* 2007). Locally, however, the total zooplankton biomass may be dominated by the macrozooplankton (>2000μm) which may comprise up to 30% of the total zooplankton biomass but generally contribute <10% to the total abundance (Froneman *et al.* 1998, Pakhomov *et al.* 1999, Pakhomov and Froneman 2000, Bernard 2002, Froneman *et al.* 2002). Estimates of mesozooplankton abundance and biomass are highly variable ranging from 10^1 to 10^5ind m^{-3} and from <1 to 25mg Dwt m^{-3}, respectively (Froneman *et al.* 1997, Barange *et al.* 1998, Bernard 2002, Mayzaud *et al.* 2002). Maximum zooplankton biomass is typically recorded in those regions characterised by elevated phytoplankton biomass including; oceanic frontal systems, marginal ice zones and in waters surrounding the various oceanic islands which demonstrate the so-called "island mass effect" (Butler *et al.* 1992, Pakhomov *et al.* 1994, Tarling *et al.* 1995, Froneman and Perissinotto 1996, Pakhomov and Perissinotto 1997, Froneman *et al.* 1998, Barange *et al.* 1998, Froneman and Pakhomov 1998, Pakhomov *et al.* 1999, Froneman *et*

al. 2000a, Froneman *et al*. 2000b, Perissinotto *et al*. 2001, Bernard 2002, Hunt *et al*. 2002, Gurney *et al*. 2002, Froneman *et al*. 2002, Johnson and Terazaki 2004, Tomczak *et al*. 2004, Lukác 2005, Froneman *et al*. 2007).

Macrozooplankton are usually dominated by tunicates, chaetognaths, euphausiids and amphipods which also form the main component of the carnivorous zooplankton assemblage (Pakhomov *et al*. 1994, Froneman *et al*. 2002). In a study conducted by Pakhomov *et al*. (1994) in the region of the APF during austral autumn, macrozooplankton abundance and biomass ranged from 0.3ind m^{-2} to 29.9ind m^{-2} and from 2mg Dwt m^{-2} to 495mg Dwt m^{-2}, and were dominated by tunicates and euphausiids. In the same study, during austral winter, the macrozooplankton community in the region of the STC was dominated by chaetognaths with an abundance ranging from 0.2ind m^{-2} to 6.9ind m^{-2} and a biomass ranging from 3mg Dwt m^{-2} to 1227mg Dwt m^{-2}.

Carnivorous zooplankton form an important component of the zooplankton community within the Southern Ocean, accounting for at times up to 20% of the total standing stock (Pakhomov *et al*. 1999). According to Froneman *et al*. (2002), the carnivorous zooplankton community consists of five major groups namely: decapods, gelatinous zooplankton, chaetognaths, amphipods and euphausiids, of which the euphausiids and chaetognaths are generally the most abundant. The contribution of these groups to the total carnivore abundance and biomass demonstrates a high degree of both spatial and temporal variability reflecting among others, reproductive patterns, behavioural activities such as swarming and availability of food (mainly zooplankton) (Froneman *et al*. 2002).

Like the other components of the zooplankton community, maximum abundance of macrozooplankton is associated with those areas of increased food availability including oceanic frontal systems, marginal ice zones and in the waters surrounding the various oceanic islands, for example the Prince Edward Islands in the Sub-Antarctic region. Pakhomov *et al*. (2000) shows that major frontal systems situated in the far south of the Southern Ocean, such as the APF, are associated with higher abundance (84.2 ± 21.9 ind m^{-3}) and biomass (47.22 ± 24.28 mg Dwt m^{-3}) values than those situated further north such as the STC (69.2 ± 80.1 ind m^{-3} and 25.4 ± 32.42 mg Dwt m^{-3}, respectively). The observed pattern is thought to reflect changes in food availability. According to Tarling *et al*. (1995) species with a wide spread distribution pattern, including *Themisto gaudichaudii, Sagitta gazellae* and some *Euphausiids*, tend to have higher abundances. Froneman *et al*. (2002) argue that seasonality is responsible for the variation in abundance and biomass of species but not in the composition of the community. Regardless of this variation, fronts are generally associated with increased abundance and biomass levels due to their increased water

column stability and nutrient availability as a result of cross frontal mixing (Froneman *et al.* 1995, Froneman *et al.* 1997, Pakhomov and Perissinotto 1997, Hunt *et al.* 2002, Pakhomov and Froneman 2004a).

1.3.2   FEEDING ECOLOGY AND PREDATION IMPACT

The bulk of studies that have examined the heterotrophic activity of zooplankton in the Southern Ocean have focussed on copepods and euphausiids (Barange *et al.* 1991, Froneman and Perissinotto 1996, Pakhomov and Perissinotto 1997, Pakhomov *et al.* 2000, Perissinotto *et al.* 2001, Hunt *et al.* 2002, Gurney *et al.* 2002, Pusch *et al.* 2004, Pakhomov and Froneman 2004a, Pakhomov and Froneman 2004b, Schultes *et al.* 2006). Few studies have thus examined the trophodynamics of carnivorous zooplankton within the Southern Ocean. In a study conducted by Froneman *et al.* (2002) within the vicinity of the Prince Edward Islands, carnivorous macrozooplankton (chaetognaths, euphusiids, amphipods, decapods and gelatinous species) formed a significant component of the zooplankton assemblage and were suggested to play an important role in increasing the localised efficiency of the biological pump due to their high predation impact on the local zooplankton standing stock (up to 15%). Carnivorous zooplankton are typically non-selective predators generally feeding on the most abundant prey, mainly mesozooplankton comprising largely copepods (Oresland 1990, Barange *et al.* 1991, Froneman *et al.* 1998, Froneman *et al.* 2000b, Perissinotto *et al* 2001, Gurney *et al.* 2002, Johnson and Terazaki 2004, Lukác 2005). Although cannibalism has been observed, it is generally restricted to the chaetognaths (Feigenbaum and Maris 1984, Froneman *et al.* 1998). Estimates of the total predation impact of the carnivorous zooplankton are, not surprisingly, highly variable accounting for 0.1 to 99% of the mesozooplankton standing stock and >100% of the secondary production (Pakhomov *et al.* 1999, Froneman *et al.* 2000a). The variation in the predation impact reflects amongst others, prey abundances, community composition of carnivorous zooplankton and seasonality. Among the carnivorous zooplankton chaetognaths have been identified as the dominant carnivore (Froneman and Pakhomov 1998).

The study of trophodynamics of carnivorous zooplankton have largely been restricted to the Atlantic sector of the Southern Ocean, and in the waters surrounding the Prince Edward Islands in the Sub-Antarctic region (Froneman and Perissinotto 1996, Pakhomov *et al.* 1999). Data on the role of carnivorous zooplankton in other sectors of the Southern Ocean, particularly within the Indian Ocean sector of the STC, remain poor.

1.4   AIMS

The main aims of this study were:

1. To describe the carnivorous zooplankton community in the Indian Ocean sector of the STC.
2. To asses the role of the STC as a biogeographical barrier to the distribution of carnivorous zooplankton.
3. To estimate the predation impact of the numerically dominant carnivorous species on the mesozooplankton.

CHAPTER TWO

MATERIALS AND METHODS

2.1   SURVEY DETAILS

Zooplankton samples were collected aboard the research vessel *SA Agulhas* during the first Southern Ocean Ecosystem Variability Study to the region of the Subtropical Convergence (STC) in the Indian sector of the Southern Ocean during austral autumn (April) 2007. The survey consisted of a grid of six north–south transects extending across the STC between 38°S - 43°S and 38°E - 42°E. A total of 48 stations were occupied within the grid survey (Fig 2.1). At each station vertical profiles of salinity, temperature and depth up to 1500m were recorded using a Neil Brown CTD (conductivity-temperature-depth). Sea surface temperature and salinity readings were taken using the ship's thermosalinograph. Zooplankton samples were collected at every station within the study area. The surface expression of the STC during the study was determined from the position of the 14°C surface isotherm (Lutjeharms and Valentine 1984, Lutjeharms 1985, Lutjeharms *et al*. 1993) (Fig 2.1).
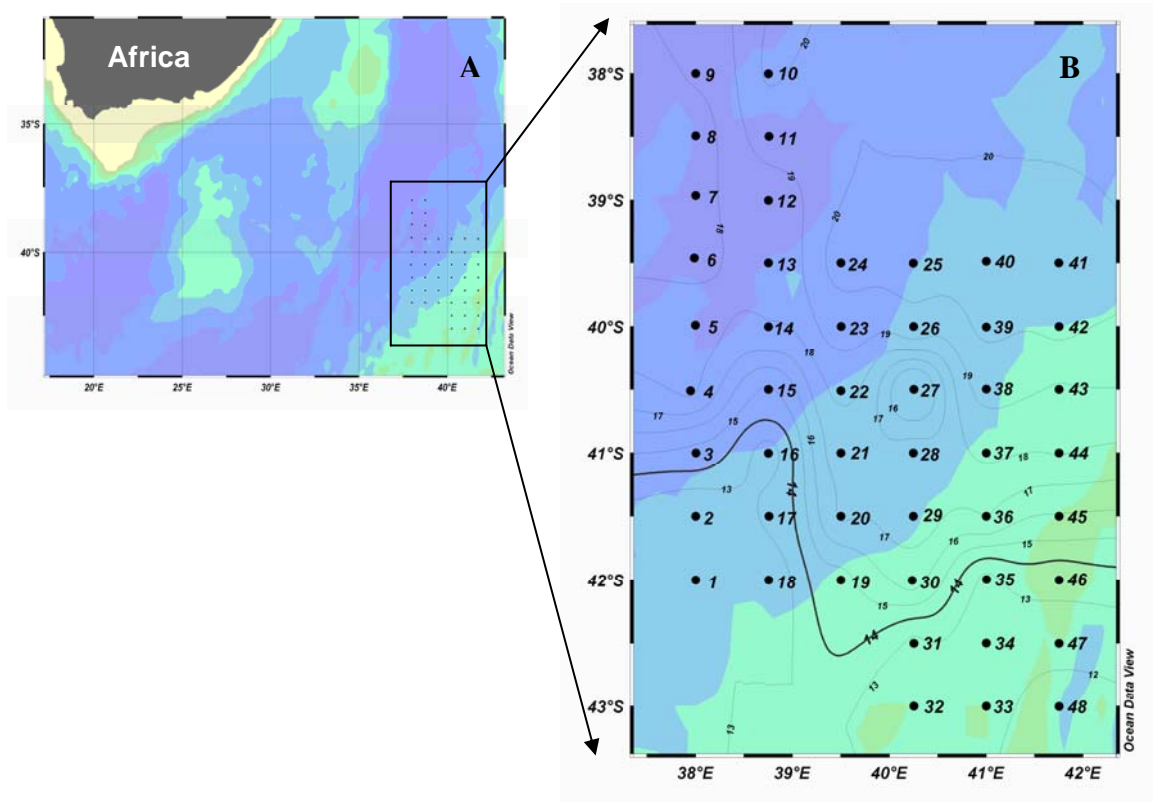
FIGURE 2.1 **A**) The study site in relation to Africa. **B**) Zooplankton sampling stations occupied during the study superimposed on surface temperature isotherms. The thickened 14°C isotherm represents the surface expression of the Subtropical Convergence (STC) (Lutjeharms and Valentine 1984, Lutjeharms 1985, Lutjeharms *et al*. 1993).

2.2   CHLOROPHYLL-a ANALYSIS

Surface size-fractionated chlorophyll-*a* (chl-*a*) concentrations were determined at each station by gently passing (<2cm Hg) 250ml of surface seawater, collected using a Crawford bucket, through a series of filters thus separating the chl-*a* into the pico- (<2.0μm), the nano- (2.0 – 20μm) and the micro-phytoplankton (>20μm) fractions. In order to determine integrated chl-*a* concentrations, total chl-*a* was determined at each station at five standard depths (25m, 50m, 75m, 100m and 150m) by passing 250ml of water through a GF/F filter. Depth samples were collected using Niskin bottles attached in a rosette fastened to the CTD. In both instances filters were placed in 8ml of 90% acetone and stored in the dark for 24h at -20°C before concentrations were determined fluorometrically (Turner Designs 10 AU) according to the method of Holm-Hansen and Riemann (1978).

2.3   ZOOPLANKTON

2.3.1   ZOOPLANKTON SAMPLING

Zooplankton samples were collected using a Bongo net (200μm mesh) fitted with a Universal Underwater Unit (U^3) which monitored temperature and depth throughout the tow. An electronic flow meter was used to calculate the volume of water filtered during each tow. Towing speeds ranged between 1 and 3 knots while tows were conducted to a depth of 200m at night and 300m during the day to account for patterns of diel vertical migration among the zooplankton (Froneman *et al*. 1998, Froneman and Pakhomov 1998, Froneman *et al*. 2002, Lukác 2005). The sampling procedure adopted during this study is in agreement with several previous studies within the Southern Ocean (Oresland 1990, Barange *et al*. 1991, Pakhomov *et al*. 1994, Froneman *et al*. 1998, Barange *et al*. 1998, Froneman and Pakhomov 1998, Pakhomov *et al*. 1999, Froneman *et al*. 2000a, Froneman *et al*. 2000b, Bernard 2002, Gurney *et al*. 2002, Froneman *et al*. 2002, Lukác 2005) and will therefore allow for comparisons with these studies. Collected samples were preserved in fixed 6% buffered (hexamine) formalin and later examined in the laboratory.

Zooplankton were identified where possible to the species level using keys of Boltovskoy (1999) and Baker *et al*. (1990) using a Nikon dissecting microscope operated at 100X and 500X magnification. A detailed analysis of the mesozooplankton (200 - 2000μm) community during the survey was undertaken in parallel to this study by Daly (2008). Samples where then separated into the following groups: amphipods, euphausiids, chaetognaths, decapods and mysids. Gelatinous zooplankton species were disregarded as their contribution was minimal (<1% of the total

abundance) and damage to specimens was too extensive to allow for identification. Total abundance and biomass were determined from the entire sample. Biomass was determined after samples were dried at 60°C for 24h. Abundance is expressed as ind $100m^{-3}$ while biomass is expressed as mg Dwt $100m^{-3}$.

2.3.2   ZOOPLANKTON COMMUNITY SIZE STRUCTURE AND SEX RATIOS

Individuals were measured in millimetres (mm), using callipers, and sexed under a Nikon dissecting microscope operated at 100X and 500X magnification (Boltovskoy 1999) in order to determine the size structure of selected components of the carnivorous zooplankton community. Euphausiids were measured from the tip of the carapace to the end of the tail (Baker *et al*. 1990), the amphipods from the most end point of the head to the tail end (Boltovskoy 1999) and chaetognaths, from the tip of the head to the end of the tail, excluding the tail fin (Oresland 1990). Male euphausiids were identified by the modification of the first pleopod as a reproductive organ while male amphipods were identified by the reduced size of the first pair of antenna (Boltovskoy 1999). Due to the hermaphroditic nature of chaetognaths, sexual maturity was grouped into three stages based on the development of the ovaries and the seminal vesicles using a modification of Johnson and Terazaki (2004) classification system.

Stage I.   Ovaries and seminal vesicles not developed or are barely visible.

Stage II.   Ovaries and seminal vesicles moderately developed. Ovaries slender with possible ova, seminal vesicles empty.

Stage III.   Ovaries and seminal vesicles fully mature. Ovaries are swollen with conspicuous ova. Seminal vesicles filled with sperm or partly discharged. Tail segment is opaque.

2.3.3   ZOOPLANKTON NUMERICAL ANALYSIS

Hierarchical cluster analysis and multidimensional scaling were used in conjunction with the Bary-Curtis similarity index in order to compare carnivorous zooplankton communities at the various stations (Field *et al*. 1982). Prior to the analysis, abundance data were log transformed [$\log_{10}(x + 1)$] to reduce the influence of species with particularly high abundance values (Field *et al*. 1982). The ANOSIM procedure from the PRIMER (Plymouth Routine In Multivariate Ecological Research) program (Clarke and Warwick 1994), was used to test the significance levels and sources of difference between zooplankton assemblages associated with the different groupings identified with the hierarchical cluster analysis. The SIMPER procedure from the PRIMER program (Clarke and Warwick 1994), was then employed to determine which species contributed most to the

observed groupings identified with the hierarchical cluster analysis. Finally the BIO-ENV procedure (Clarke and Warwick 1994), was employed to determine the environmental factors (temperature, salinity and mesozooplankton abundance) which best explained the different groupings identified with the hierarchical cluster analysis (Hunt *et al.* 2002).

2.3.4   STATISTICAL ANALYSIS

Pearson's correlation analysis was used to determine the relationships between the total carnivorous zooplankton abundance and biomass, surface temperature, salinity, mesozooplankton abundance and biomass and total integrated and total surface chlorophyll-*a* concentrations. Correlations were also used to determine the relationships of abundance and biomass levels for the orders Amphipoda and Euphausiacea as well as for the phylum Chaetognatha, with the physical (surface temperature and salinity) and the biological variables (mesozooplankton and chlorophyll-*a*). In order to determine if there was a difference in total abundance and biomass levels, as well as the grouped (Amphipoda, Euphausiacea and Chaetognatha) abundance and biomass levels, between stations as well as north and south of the front, a one-way ANOVA was used. A one-way ANOVA was also used to determine differences between lengths of males and females and then pooled (if no significant difference was found) for differences north and south of the front within the numerically dominant species. The Fisher LSD post hoc test was used to explain any significant differences. An ANCOVA, using temperature as a covariant, was used to determine whether there was a difference between the lengths of the specific chaetognathas at the various stages of maturity. Once again the Fisher LSD post hoc test was used to explain any significant differences. In all cases standard deviation is represented as ±. All statistical analyses were conducted using the computer package STATISTICA 8.0. The computer program Ocean Data View 3.2.0 was used to map total abundance and biomass values, grouped abundance and biomass values, surface temperature and the study site.

2.3.5   GUT CONTENT ANALYSIS AND FEEDING RATES

Gut content analysis and feeding rates were calculated only for the numerically dominant chaetognaths (*Sagitta gazellae, S. zetesios, and Eukrohnia hamata*) as they are strictly carnivorous (Feigenbaum and Maris 1984). All individuals of each species were dissected and their gut contents examined under a Nikon dissecting microscope operated at 100X to 500X magnification. Prey found in the forward part of the digestive tract were omitted from counts in order to account for cod-end feeding (Feigenbaum and Maris 1984). Due to the advanced state of digestion of prey generally recorded during the study the prey in the guts of selected chaetognath species was separated into the following groups; Amphipoda, Euphausiacea, Copepoda and "other". "Other"

was that prey which was unidentifiable and items were assumed to represent the remains of a single prey item only (Barange *et al.* 1998, Froneman *et al.* 2002).

The feeding rates (Fr, prey d^{-1}) of the chaetognaths were then calculated using the equation of Oresland (1995):

$$Fr = (mean\ NPC\ /\ Dt)\ x\ 24$$

where NPC is the mean number of prey per chaetognath, Dt is the digestion time in hours and the multiplication by 24 is to provide a daily feeding rate.

The Dt value for *S. gazellae* was estimated using the empirical equation (Froneman *et al.* 1998):

$$Dt = 10.96e^{-0.086\ T}$$

where T is the water temperature (°C). An average sea water temperature of 16.56°C was assumed during the cruise in order to standardise chaetognath digestive times. The Dt for *E. hamata* was estimated by Oresland (1995) to be 5h while that of *S. zetesios* was estimated by Dilling and Alldredge (1993) to be 3h. As copepods accounted for the vast majority of the prey items in all three species of chaetognaths, calculation of mean NPC includes only the copepods, thus Fr reflects consumption of only the copepods. Predation impact of the chaetognaths; *E. hamata, S. gazellae* and *S. zetesios,* were estimated using the calculated Fr, by combining the respective chaetognath Fr with their densities (ind 100m^{-3}) (Froneman and Pakhomov 1998). Data were expressed as a percentage of the mesozooplankton standing stock and mesozooplankton secondary production consumed per day. To estimate the predation impact on the mesozooplankton secondary production a production rate of 5% for the entire community was assumed (Froneman and Pakhomov 1998).

2.3.6 TOTAL ZOOPLANKTON PREDATION IMPACT

The predation impact of the carnivorous macrozooplankton was restricted to the mesozooplankton (copepods) fraction as previous studies (Oresland 1987, Oresland 1990, Oresland 1995, Froneman *et al.* 1998, Froneman *et al.* 2000a, Froneman *et al.* 2002) have shown this fraction to be their main food source. The daily predation impact was restricted to the species considered to be carnivorous according to published literature, which includes the Chaetognaths (*S. gazellae, S. zetesios* and *E. hamata*), Euphausiids (*Nematoscelis megalops* and *Euphausia longirostris*) and the Amphipod, *Themisto gaudichaudii* (Froneman and Pakhomov 1998, Froneman *et al.* 2000b, Gurney *et al.* 2002). Table 2.1 provides a list of the published daily rations used during this study to

estimate the predation impact of the carnivorous zooplankton on the mesozooplankton standing stock. The daily predation impact of each species on the mesozooplankton standing stock and secondary production was calculated by multiplying the biomass (mg Dwt $100m^{-3}$) of each species by the percentage of daily ration (calculated using dry body weight) consumed for that taxon (Froneman *et al*. 1998, Froneman *et al*. 2002). Data were expressed as a percentage of the copepod standing stock consumed per day or as a percentage of the secondary production consumed per day.

TABLE 2.1 Published daily rations (% dry body weight) of selected carnivorous zooplankton used to estimate the percentage of mesozooplankton standing stock and secondary production consumed per day.

Species	Daily ration	Source
AMPHIPODA		
Themisto gaudichaudii	11.5	Froneman *et al*. (2000a), Froneman *et al*. (2000b)
CHAETOGNATHA		
Eukrohnia hamata	6	Froneman and Pakhomov (1998)
Sagitta gazellae	8	Froneman and Pakhomov (1998)
Sagitta zetesios	2	Dilling and Alldredge (1993)
EUPHAUSIACEA		
Nematoscelis megalops	7.8	Gurney *et al*. (2002)
Euphausia longirostris	19.9	Gurney *et al*. (2002)

CHAPTER THREE

RESULTS

3.1   OCEANOGRAPHY

Sea surface temperatures during the survey ranged from 11.22°C to 20.80°C (Fig 3.1). The Subtropical Convergence front (STC), indicated by the 14°C surface isotherm (Lutjeharms *et al.* 1993), separating warmer water in the north from colder water in the south, occurred between 40.6°S and 41.5°S west of 39°E (Fig 3.1). East of 39°E, the STC occurred further south and was situated between 42°S and 42.5°S (Fig 3.1). The exception to this occurred at station 27 (40.5°S 40.3°E) which had a temperature of 15°C (Fig 3.1). The occurrence of a warm water mass (18-20°C) north of the frontal feature indicated the presence of the Agulhas Return Current (ARC) (Lutjeharms and Valentine 1984, Lutjeharms 1985, Froneman *et al.* 2007).
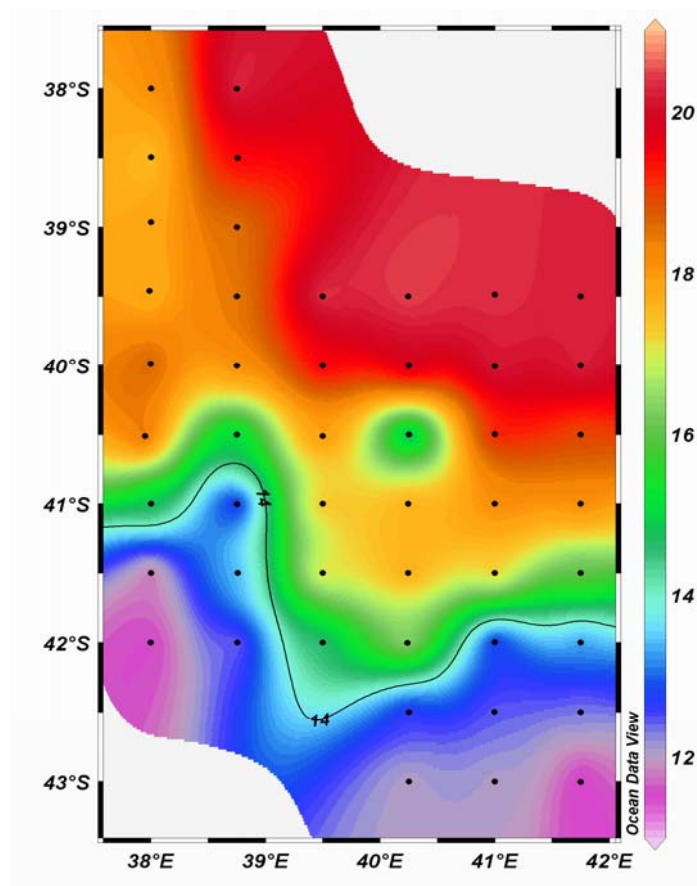
FIGURE 3.1 Surface temperatures (°C) within the survey area during April 2007. Dots represent stations while the thickened line represents the position of the Subtropical Convergence (14°C isotherm) (Lutjeharms and Valentine 1984).

3.2 CHLOROPHYLL-A

Total surface chlorophyll-*a* (chl-*a*) concentration ranged from 0.03mg chl-*a* m^{-3} to 0.42mg chl-*a* m^{-3} and indicated a distinct spatial pattern with the highest concentrations recorded at the stations located south of the front (Fig 3.2A). Indeed, total surface chl-*a* concentrations at stations south of the front were significantly higher than the stations to the north of the STC (ANOVA, F = 11.74; df = 46; p<0.001). There was no evidence of enhanced chl-*a* concentrations at those stations associated with the front (3, 16, 17, 19, 30, 35 & 46) (Fig 3.2A). Integrated chl-*a* concentrations, over depth, ranged from 11.97mg chl-*a* m^{-2} to 40.07mg chl-*a* m^{-2}, and demonstrated no significant spatial patterns (p>0.05) (Fig 3.2B).
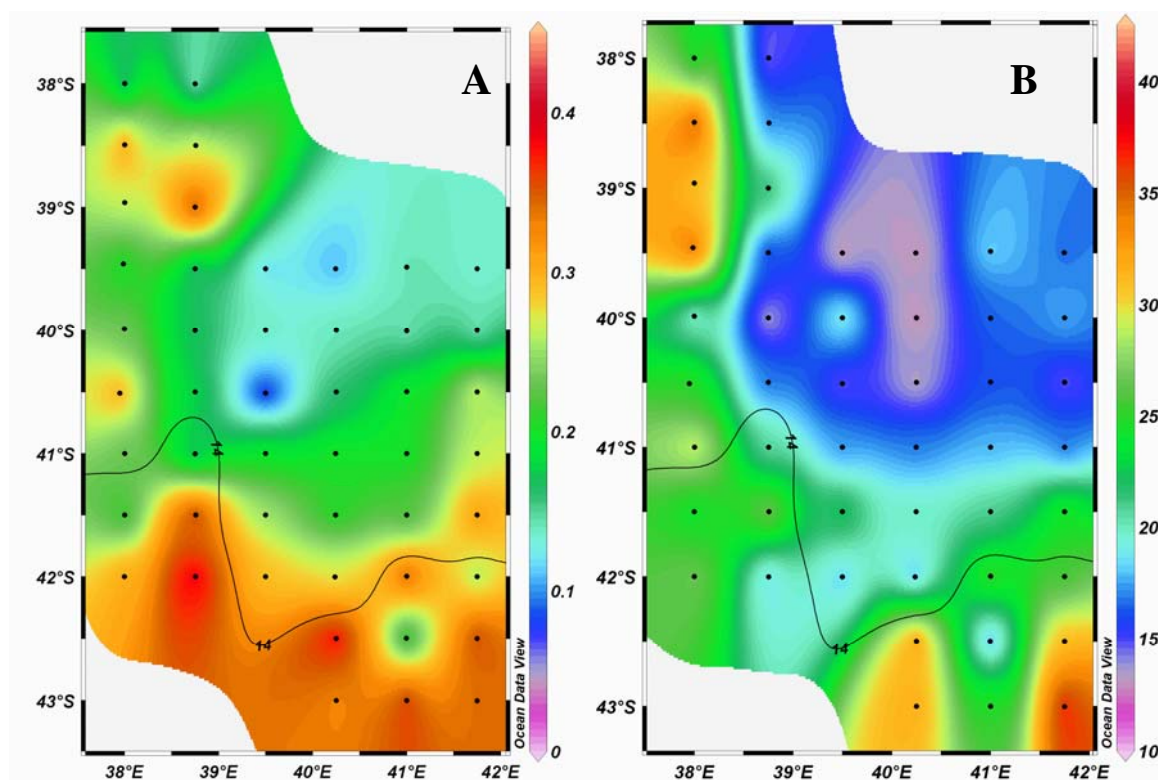
FIGURE 3.2 Total surface chlorophyll-*a* (mg m^{-3}) (**A**) and integrated chlorophyll-*a* (mg m^{-2}) (**B**) within the survey area during April 2007. Dots represent the stations while the thickened line represents the surface expression (14°C isotherm) of the Subtropical Convergence (Lutjeharms and Valentine 1984).

Total chl-*a* concentration throughout the survey area was dominated by the pico- (<2.0μm) and the nanophytoplankton (2.0 – 20μm) which contributed up to 98% of the total chl-*a* concentration (Fig 3.3). Exceptions occurred at station 11 and 22 where the microphytoplankton (>20μm) accounted for 55% and the nanophytoplankton (2.0 - 20 μm) accounted for 90% of the total surface pigment, respectively (Fig 3.3). In general, however, microphytoplankton contributed less than 20% to the total surface chl-*a* concentration. Picophytoplankton concentrations ranged between 0.01mg chl-*a* m^{-3} and 0.16mg chl-*a* m^{-3} while nanophytoplankton concentrations ranged between 0.01mg chl-*a* m^{-3} and 0.31mg chl-*a* m^{-3}.
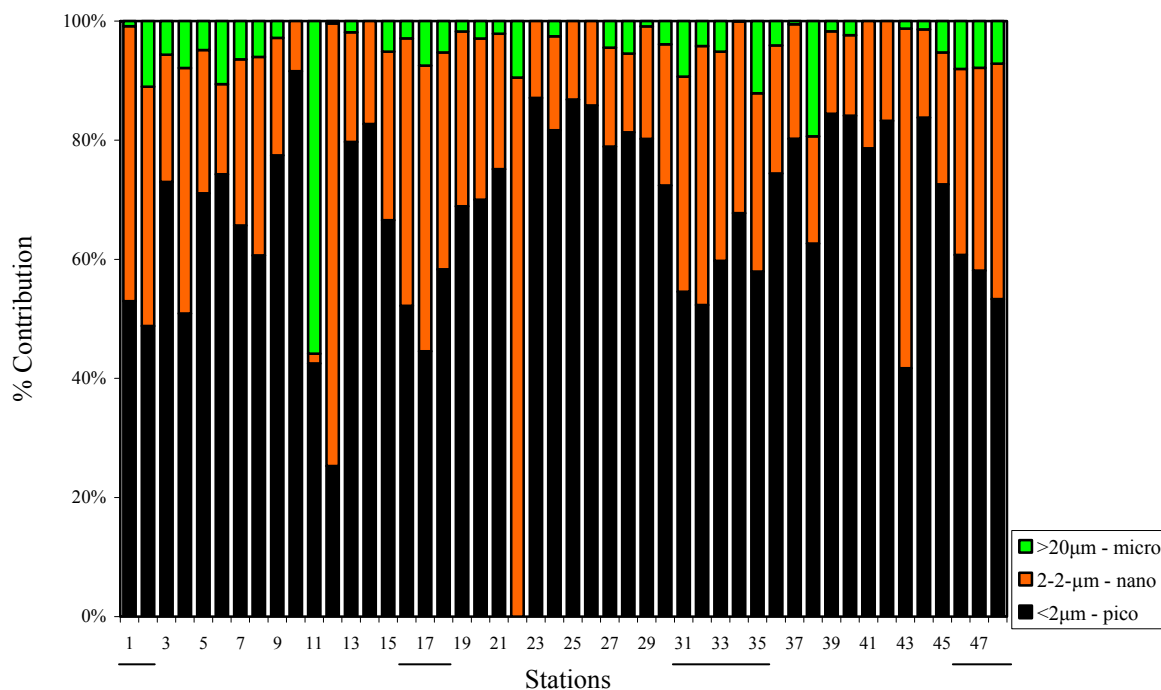
FIGURE 3.3 Percentage contribution of the different size classes to the total chlorophyll-*a* concentrations within the survey area during April 2007. (Lines represent stations south of the Subtropical Convergence)

3.3 COMMUNITY STRUCTURE AND SPATIAL TRENDS

3.3.1 SPATIAL DISTRIBUTION

3.3.1.1 TOTAL MESOZOOPLANKTON

A detailed description of the mesozooplankton community is described by Daly (2008). Here a brief account of the mesozooplankton community is provided. Total mesozooplankton abundance and biomass during the study ranged from 13.12ind m^{-3} to 1028.40ind m^{-3} (average of 198.14 ± 270.51ind m^{-3}) and from 0.80mg Dwt m^{-3} to 23.07mg Dwt m^{-3} (average of 5.55 ± 4.84mg Dwt m^{-3}), respectively (Daly 2008). The mesozooplankton community was in terms of abundance and by biomass, dominated by copepods; *Pleuromamma abdominalis*, *Oithona similus*, *Metridia lucens*, *Oncaea conifera*, *Clausocalanus breviceps*, *Calanus simillimus* and *Canonicle jajonicle*, which accounted for between 1% and 67% (42% mean) of the total mesozooplankton abundance (Daly 2008). Also well represented among the mesozooplankton community was the pteropod, *Limacina retroversa*, the tunicate, *Salpa thompsoni* and euphausiid furcilia. The contribution of these taxa to the total mesozooplankton counts and biomass were, however, always <10% (Daly 2008). Abundance and biomass values north and south of the frontal feature were not significantly different (p>0.05) (Daly 2008). There were no significant correlations between the mesozooplankton abundance and biomass values and the selected physical (temperature and

salinity) and biological (chl-*a*) variables evident during the study (Daly 2008). Also, there were no significant spatial patterns in the total mesozooplankton abundance and biomass evident during the study (p>0.05 in both cases) (Daly 2008).

3.3.1.2 TOTAL CARNIVOROUS ZOOPLANKTON

Total average carnivorous zooplankton abundance and biomass during the study ranged from 0.28 ± 0.62ind $100m^{-3}$ to 5.36 ± 6.47ind $100m^{-3}$ and from 0.04 ± 0.08mg Dwt $100m^{-3}$ to 22.34 ± 42.20mg Dwt $100m^{-3}$, respectively (Fig 3.4 and Appendix 1). Total carnivorous zooplankton abundance and biomass demonstrated a distinct spatial pattern with the values south of the front being significantly higher than those recorded north of the frontal feature (ANOVA, F = 19.68 & 19.48, respectively; df = 46; p<0.001) (Fig 3.5). There was no evidence of biological enhancement with regard to abundance and biomass at the stations occupied in the immediate vicinity of the STC (p>0.05).
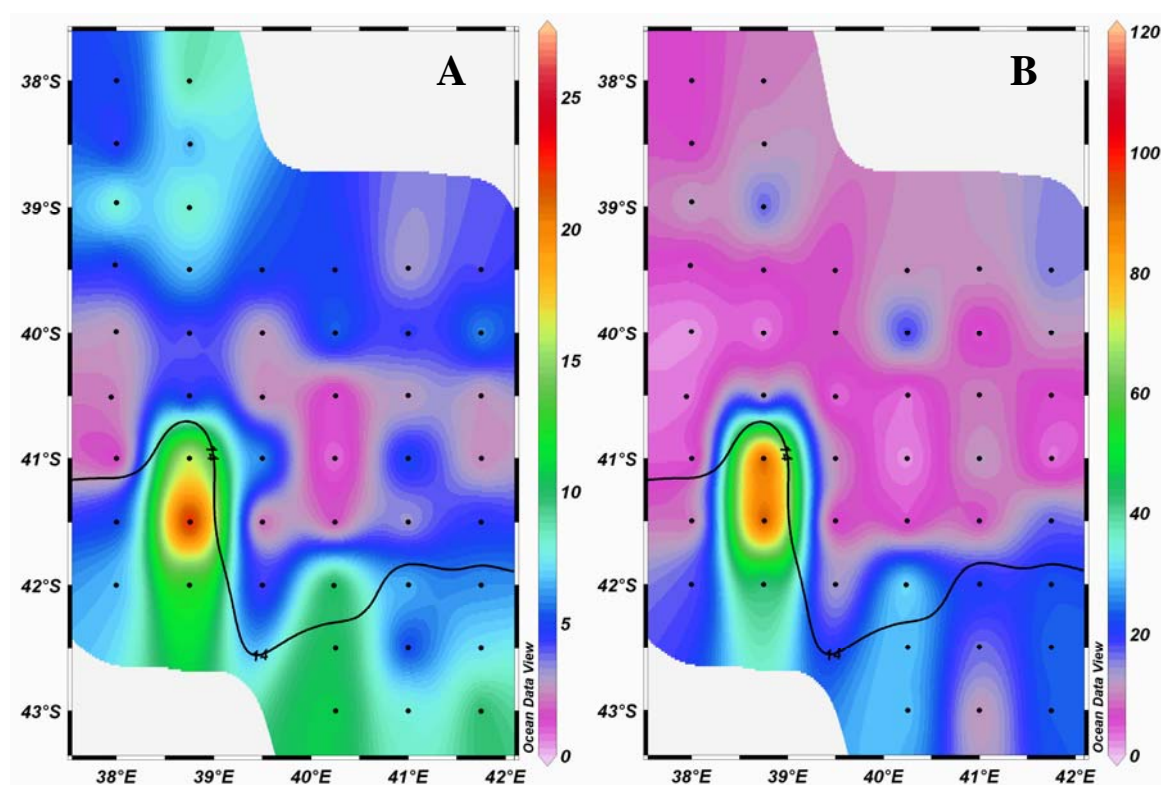
FIGURE 3.4 Total average carnivorous zooplankton abundance (ind $100m^{-3}$) (**A**) and biomass (mg Dwt $100m^{-3}$) (**B**) within the survey area during April 2007. Dots represent the stations while the thickened line represents the surface expression (14°C isotherm) of the Subtropical Convergence (Lutjeharms and Valentine 1984).
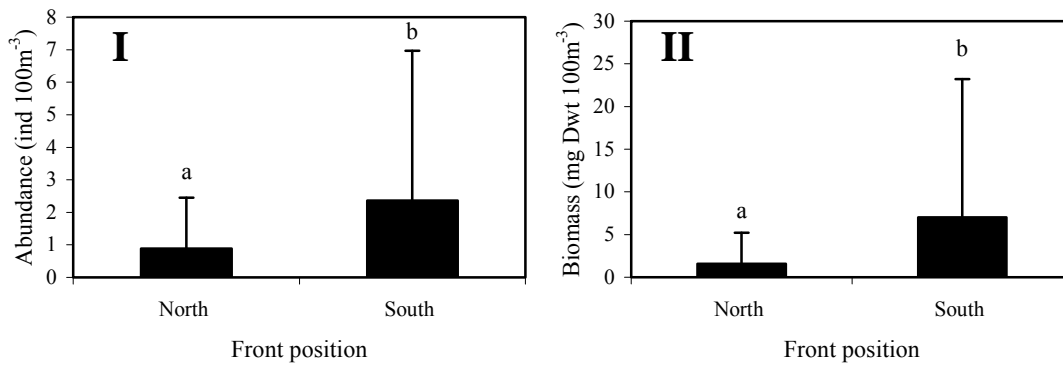
FIGURE 3.5 Total average carnivorous zooplankton abundance (ind 100m^{-3}) (**I**) and biomass (mg Dwt 100m^{-3}) (**II**) north and south of the Subtropical Convergence during April 2007. Error bars indicate standard deviation. Different letters indicate statistical differences (ANOVA).

Total carnivorous zooplankton abundance during the study was dominated by the chaetognaths and euphausiids, which combined, accounted for $87 \pm 33\%$ of the total abundance (Fig 3.6). An exception was recorded at station 17 where amphipods accounted for $\approx 55\%$ of the total abundance (Fig 3.6). Biomass, however, was dominated by the euphausiids and the amphipods, throughout the study area, which together accounted for $72 \pm 35\%$ of the total biomass (Fig 3.7).
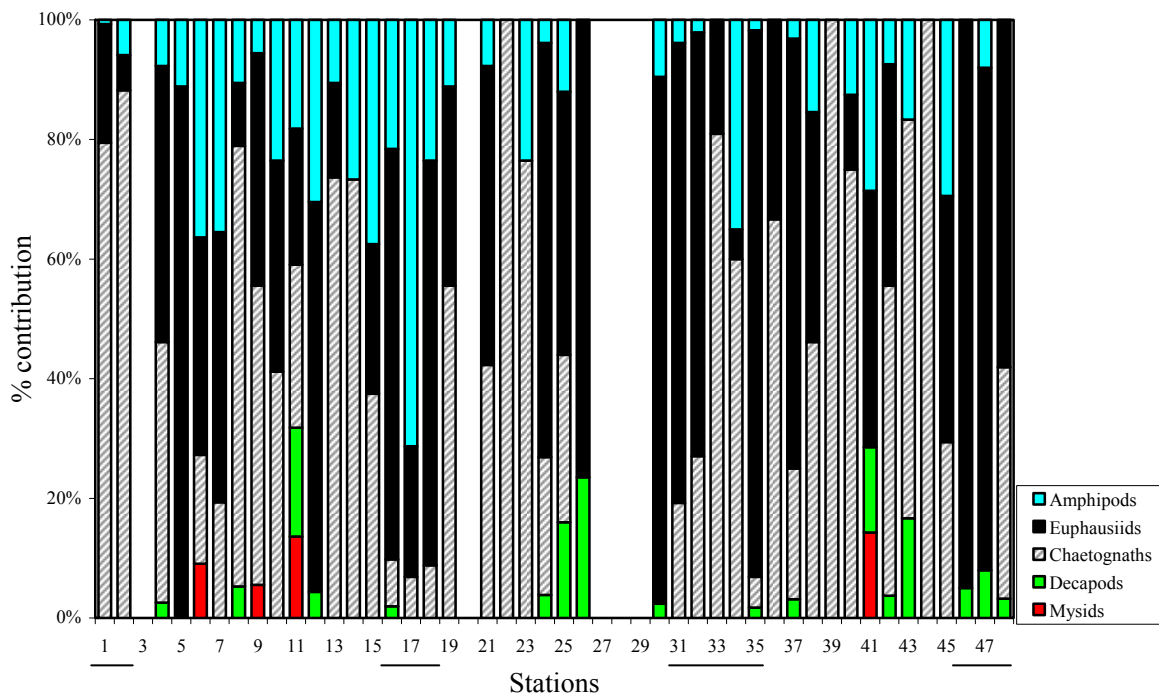
FIGURE 3.6 Percentage contribution of the different taxonomic groups to the total carnivorous zooplankton abundance (ind 100m^{-3}) within the survey area during April 2007. (Lines represent stations south of the Subtropical Convergence while no samples were collected at stations 27 to 29 due to logistical constraints)
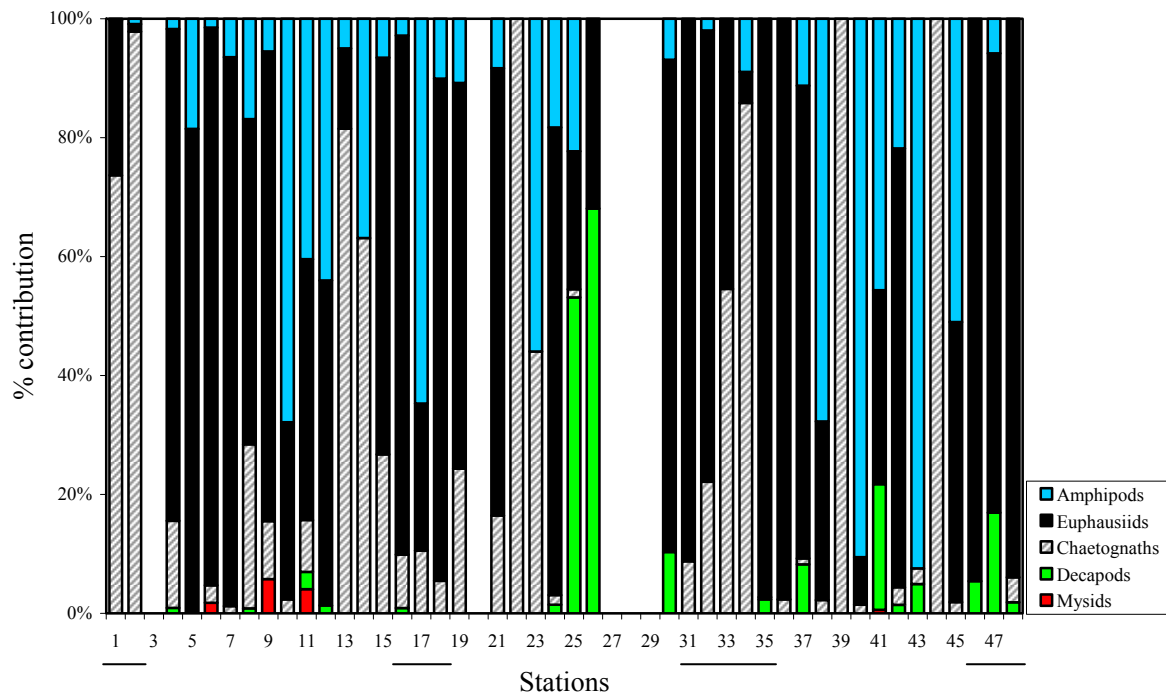
FIGURE 3.7 Percentage contribution of the different taxonomic groups to the total carnivorous zooplankton biomass (mg Dwt100m^{-3}) within the survey area during April 2007. (Lines represent stations south of the Subtropical Convergence while no samples were collected at stations 27 to 29 due to logistical constraints)

Both abundance and biomass values of the euphausiids were significantly higher south of the STC (ANOVA, F = 18.10 & 18.56, respectively; df = 46; p<0.001), while only the biomass values of the chaetognaths were significantly higher south of the frontal feature (ANOVA, F = 17.46; df = 46; p<0.001) (Fig 3.8). There were no significant correlations between the selected physico-chemical (temperature and salinity) and biological (mesozooplankton abundance and biomass and chl-*a*) variables, and the total abundance and biomass of the carnivorous zooplankton (p>0.05, in all cases). The spatial patterns in community structure of the numerically dominant groups; amphipods, euphausiids and chaetognaths are discussed in detail below.
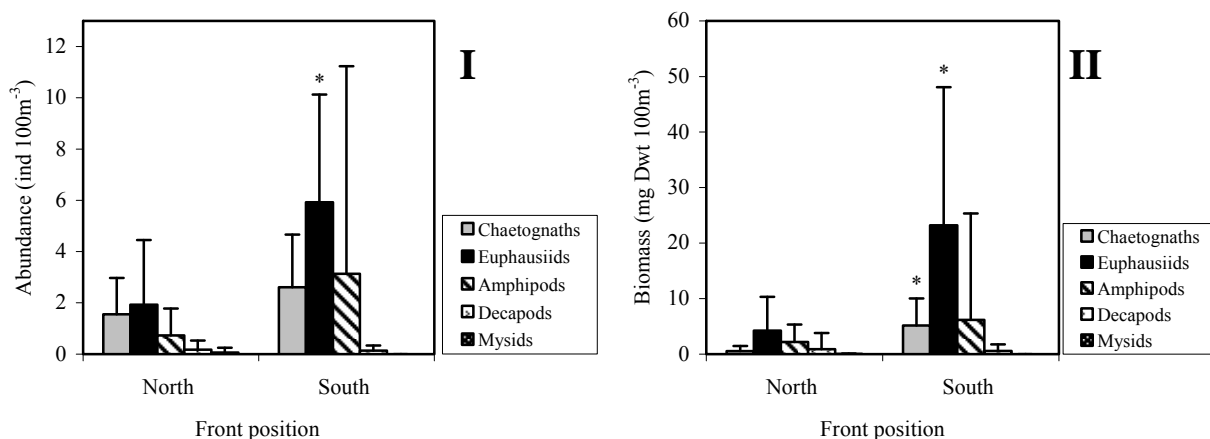
FIGURE 3.8 Total average abundance (ind 100m^{-3}) (**I**) and biomass (mg Dwt 100m^{-3}) (**II**) for the different taxonomic groups north and south of the Subtropical Convergence during April 2007. Error bars indicate standard deviation. *****Indicates statistical differences within each taxonomic group (ANOVA).

3.3.1.3 ORDER: AMPHIPODA

Total average amphipod abundance and biomass values during the study ranged from 0.04 ± 0.01ind 100m^{-3} to 14.84 ± 20.31ind 100m^{-3} and from 0.02 ±0.03mg Dwt 100m^{-3} to 69.78 ± 97.27mg Dwt 100m^{-3}, respectively (Fig 3.9). Total amphipod abundance and biomass spatial patterns were similar to those of the total carnivorous zooplankton values, where higher values were generally recorded in the waters south of the front (Fig 3.9). Differences in the estimated abundance and biomass values of the amphipods north and south of the front were, however, not significant (p>0.05) (Fig 3.8). There was no evidence of any increased abundance or biomass values of amphipods at the stations occupied in the region of the STC (Fig 3.9).
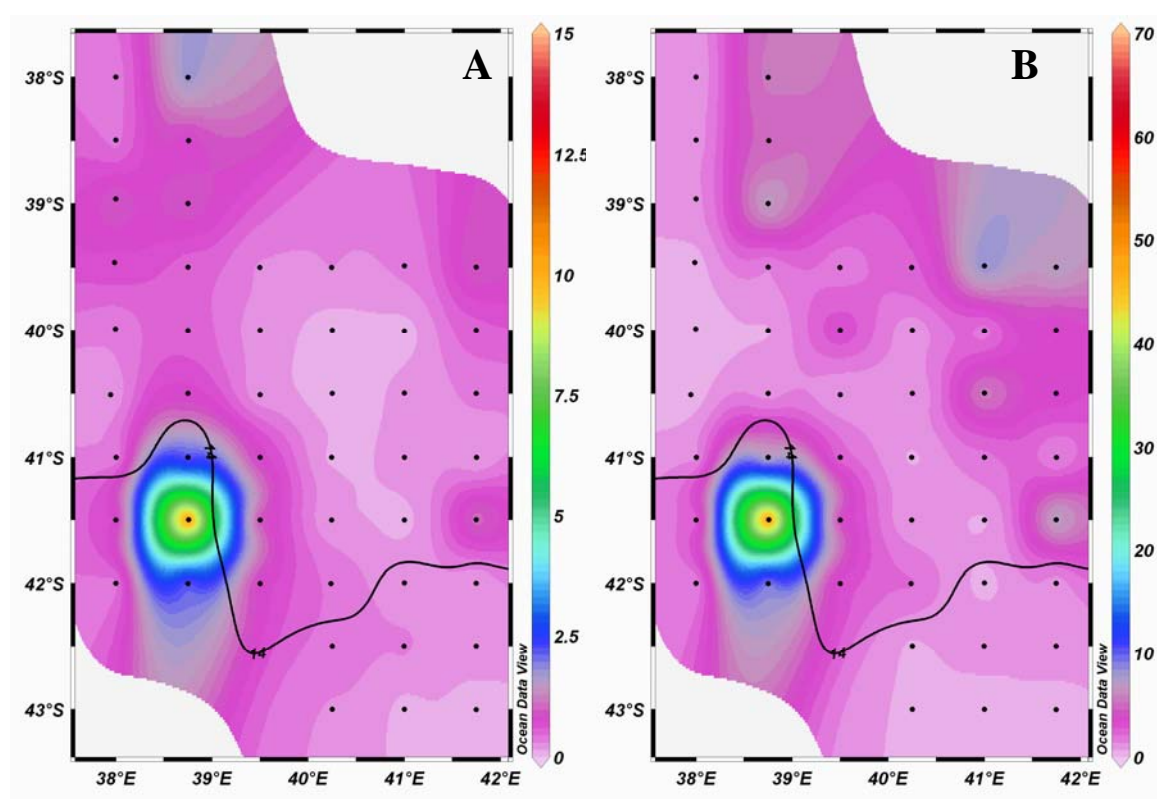
FIGURE 3.9 Total average amphipod abundance (ind 100m^{-3}) (**A**) and biomass (mg Dwt 100m^{-3}) (**B**) within the survey area (April 2007). Dots represent the stations while the thickened line represents the surface expression (14°C isotherm) of the Subtropical Convergence (Lutjeharms and Valentine 1984).

A total of 15 species of amphipod were identified within the survey area. Of the amphipod species, *Themisto gaudichaudii* (Guérin-Méneville 1825 in Boltovskoy 1999)*, Phronima sedentaria* (Forsskål 1775 in Boltovskoy 1999) and *Vibilia armata* (Bovallius 1887 in Boltovskoy 1999) accounted for 55%, 16% and 16%, respectively, of the total amphipod abundance and 55%, 26% and 7% of the total amphipod biomass, respectively (Table 3.1). The contribution of the remaining amphipod species to the total abundance and biomass was <3% at all stations (Table 3.1).

TABLE 3.1 Total percentage contribution of each amphipod species to total amphipod abundance (ind 100m^{-3}) and biomass (mg Dwt 100m^{-3}) during April 2007.

Amphipod	Abundance %	Biomass %
Themisto gaudichaudii	55.18	54.91
Vibilia armata	16.31	6.70
Phronima sedentaria	15.75	25.66
Phrosinia semilunata	2.42	7.32
Platyscelus armatus	2.14	0.36
Phronima atlantica	1.75	0.03
Vibilia propinqua	1.42	0.32
Dairella latissima	1.10	0.03
Hyperiella antarctica	1.04	0.02
Cyllopus magellanicus	0.85	0.18
Cyphocaris challengeri	0.58	0.02
Paralycaea gracilis	0.44	1.07
Phronima curvipes	0.43	0.05
Pronoe capito	0.41	0.01
Cystisoma fabricii	0.20	3.34

Of the amphipod species only *T. gaudichaudii* demonstrated significantly (ANOVA, F = 3.70 & 3.40, respectively; df = 46; p<0.05) higher abundance and biomass values at stations south of the front (Table 3.2). There were no significant correlations between the abundance and biomass values of *T. gaudichaudii* and any of the physical (temperature and salinity) or biological (chl-*a* and mesozooplankton abundance and biomass) variables (p>0.05, in all cases). In addition, the total amphipod and species abundance and biomass values did not significantly correlate with any of the physical or biological variables (p>0.05, in all cases).

TABLE 3.2 Average abundance and biomass, of the dominant amphipod species, north and south of the Subtropical Convergence during April 2007. Values in brackets represent standard deviation. (* significantly higher values, ANOVA, p<0.05).

SPECIES	ABUNDANCE (ind 100m^{-3})		BIOMASS (mg Dwt 100m^{-3})	
	North	South	North	South
Phronima sedentaria	0.25 (±0.04)	0.12 (±0.23)	1.99 (±4.17)	0.67 (±1.25)
Themisto gaudichaudii	0.07 (±0.01)	2.63 (±8.01)*	0.34 (±1.58)	11.97 (±38.12)*
Vibilia armata	0.22 (±0.01)	0.24 (±0.60)	0.50 (±1.69)	0.22 (±0.76)

3.3.1.4 ORDER: EUPHAUSIACEA

A total of 24 euphausiid species were identified during the survey, however, only five species (*Nematoscelis megalops*, *Thysanoessa longicaudata, T. parva, Euphausia longirostris* and *E. spinifera*) contributed to the bulk of the abundance (>70%) and biomass (>85%). Total average

euphausiid abundance and biomass values during the study ranged from 0.13 ± 0.01ind 100m^{-3} to 2.45 ± 2.75ind 100m^{-3} and from 0.03 ± 0.01mg Dwt 100m^{-3} to 16.25 ± 24.37mg Dwt 100m^{-3}, respectively (Fig 3.10). Total abundance and biomass values south of the front were significantly higher than those obtained in waters north of the front (ANOVA, F = 18.10 & 18.56, respectively; df = 46; p<0.001) (Fig 3.8). There was no evidence of any enhanced euphausiid abundance and biomass values at the stations occupied in the region of the front (p>0.05) (Fig 3.10). The abundance and biomass distributions could not be explained by the environmental conditions as there were no significant correlations between the physico-chemical (temperature and salinity) and biological (chl-*a* and mesozooplankton abundance and biomass) variables and the total euphausiid abundance and biomass values (p>0.05 in all cases).
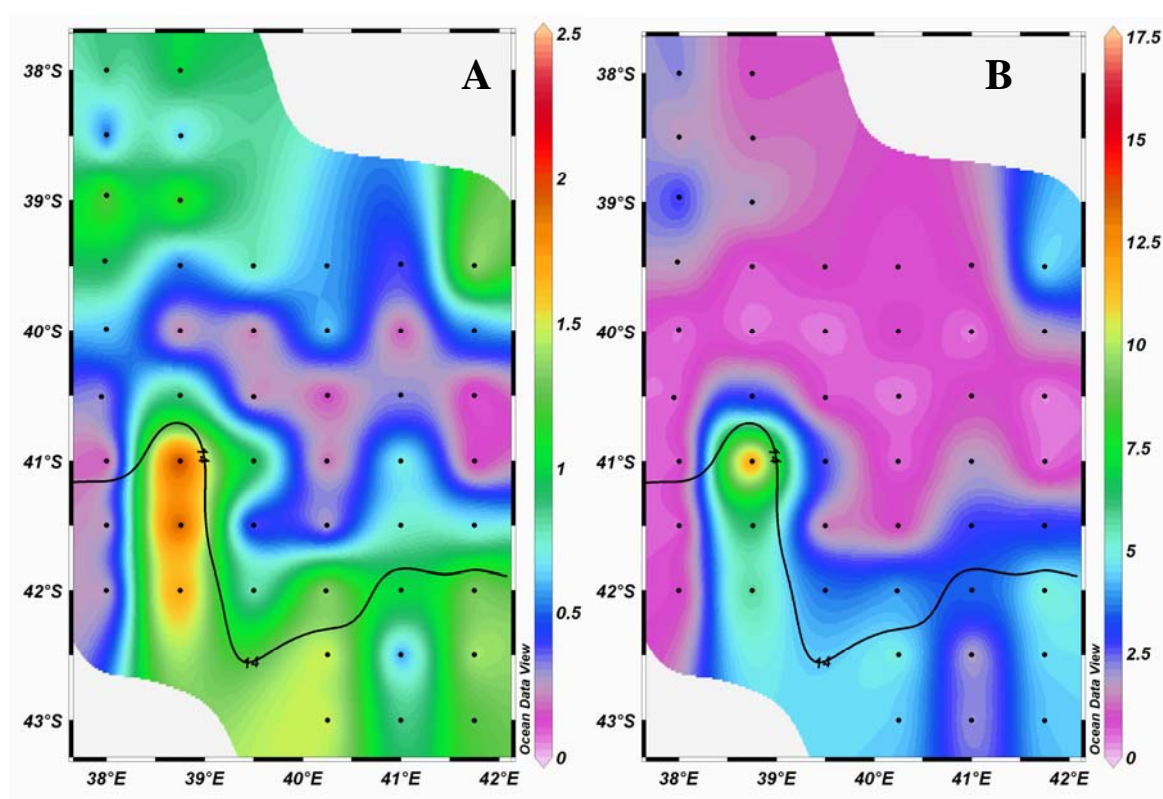
FIGURE 3.10 Total average euphausiid abundance (ind 100m^{-3}) (**A**) and biomass (mg Dwt 100m^{-3}) (**B**) within the survey area (April 2007). Dots represent the stations while the thickened line represents the surface expression (14°C isotherm) of the Subtropical Convergence (Lutjeharms and Valentine 1984).

The abundance and biomass values, of individuals of the genus *Euphausia*, north of the STC (0.94 ± 1.57ind 100m^{-3} and 2.18 ± 3.91mg Dwt 100m^{-3}, respectively), were significantly lower than the mean abundance (3.75 ± 3.90ind 100m^{-3}) and biomass (17.19 ± 25.41mg Dwt 100m^{-3}) values south of the STC (ANOVA, F = 15.48 & 12.34, respectively; df = 46; p<0.05) (Fig 3.11). There were no significant correlations between the estimated abundance and biomass values of the *Euphausia* genus and the selected physico-chemical and biological variables during the study (p>0.05 in all cases).
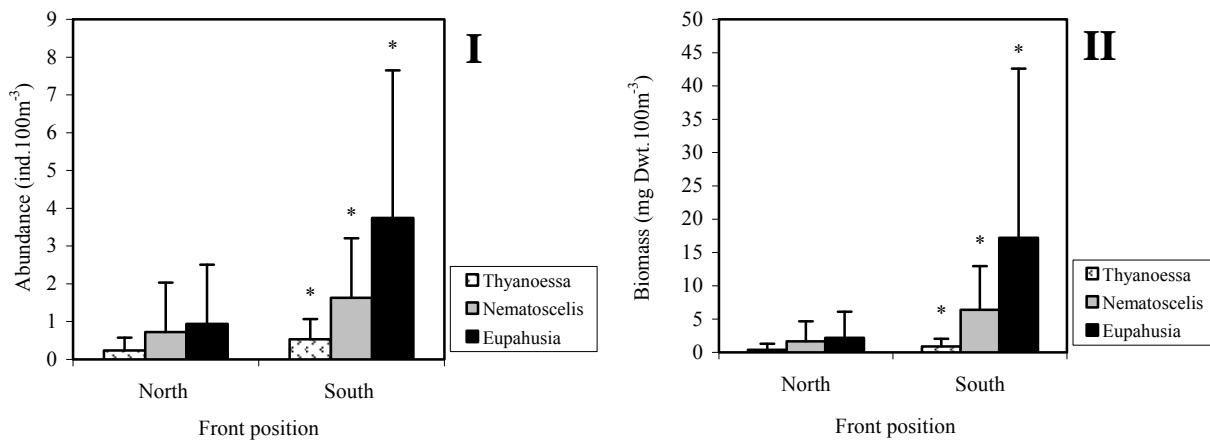
FIGURE 3.11 Total average abundance (ind 100m^{-3}) (**I**) and biomass (mg Dwt 100m^{-3}) (**II**) for each euphausiid genus north and south of the Subtropical Convergence during April 2007. Error bars indicate standard deviation. ***** Indicates statistical differences within each genus (ANOVA).

The *Euphausia* genus dominated the total euphausiid abundance and biomass and accounted for 34 ± 35% of the abundance and for 35 ± 37% of the biomass (Fig 3.12 & 3.13). Among the euphausiids, *E. longirostris* (Hansen 1908 in Boltovskoy 1999) accounted for ≈ 24% of the total *Euphausia* genus abundance (Table 3.3) and a total of 17% of the total euphausiid abundance, while *E. spinifera* (Sars 1883 in Boltovskoy 1999) accounted for ≈ 32% of the total *Euphausia* genus biomass (Table 3.3) and ≈ 20% of the total euphausiid biomass.
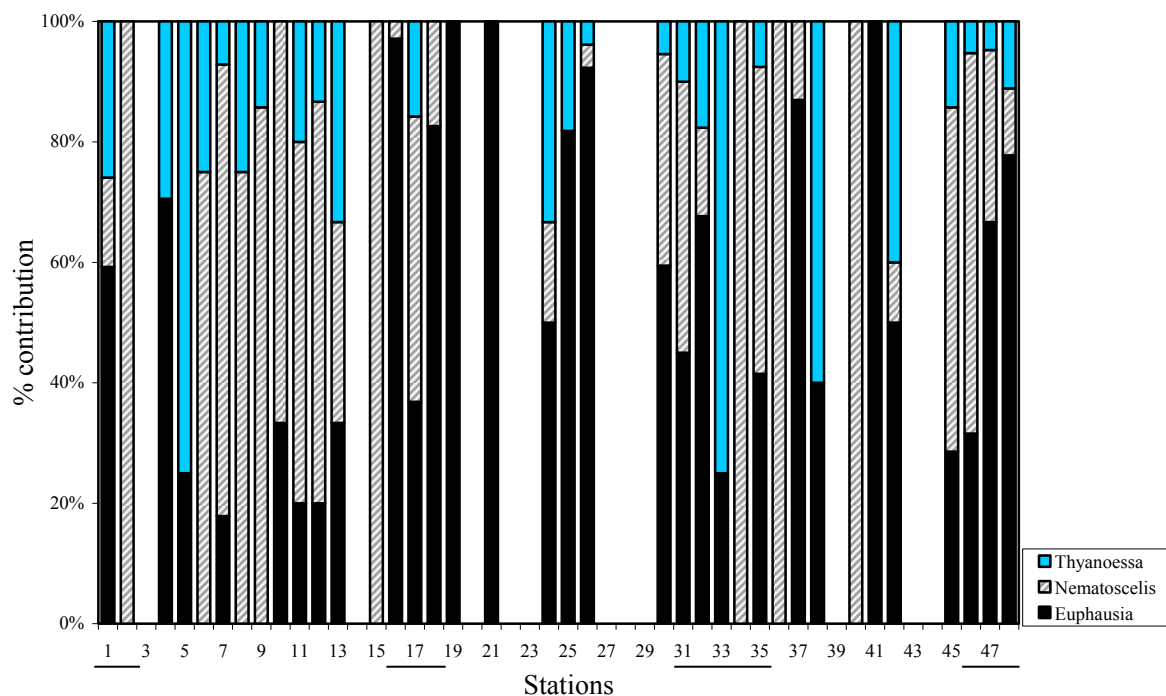
FIGURE 3.12 Percentage contribution of each genus to the total euphausiid abundance (ind 100m^{-3}) within the survey area during April 2007. (Lines represent stations south of the Subtropical Convergence while no samples were collected at stations 27 to 29 due to logistical constraints)
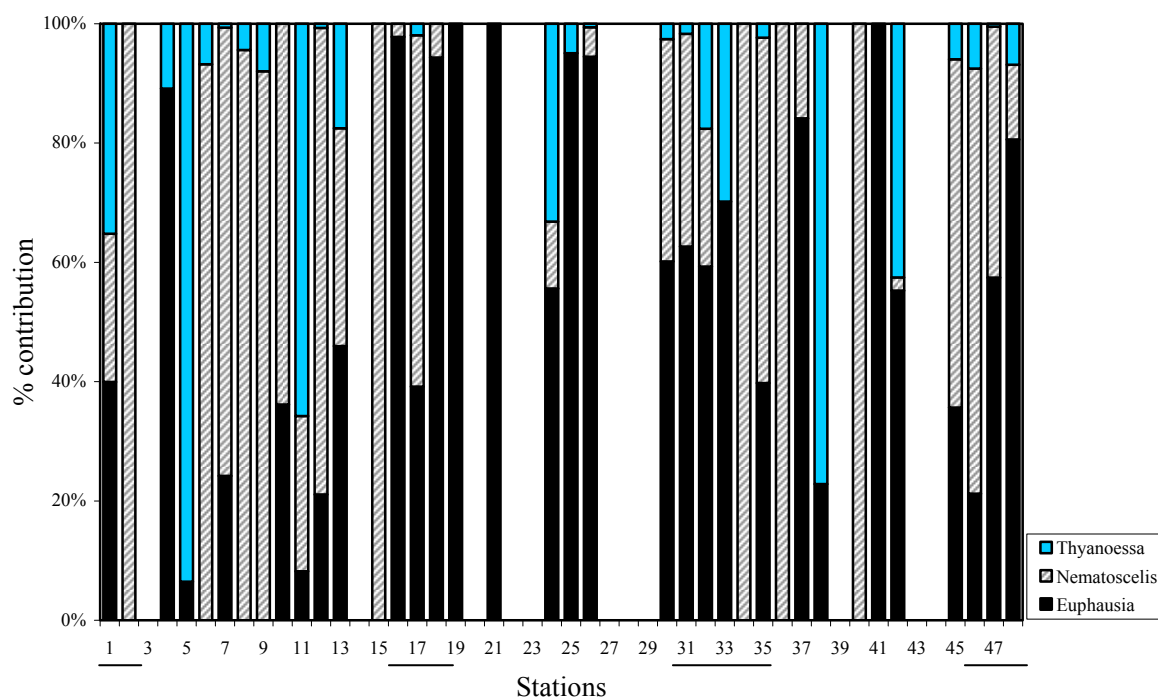
FIGURE 3.13 Percentage contribution of each genus to the total euphausiid biomass (mg Dwt 100m^{-3}) within the survey area during April 2007. (Lines represent stations south of the Subtropical Convergence while no samples were collected at stations 27 to 29 due to logistical constraints)

The *Nematoscelis* genus total abundance and biomass values during the study ranged from 0.18ind 100m^{-3} to 4.95ind 100m^{-3} and from 0.05mg Dwt 100m^{-3} to 16.10mg Dwt 100m^{-3}, respectively. Both the abundance and biomass values south of the frontal feature were significantly higher (ANOVA, F = 4.14 & 11.85, respectively; df = 46; p<0.05) than those north of the front (Fig 3.11). Similarly to the *Euphausia* genus, the abundance and biomass values of the *Nematoscelis* genus did not significantly correlate to the physical and biological variables. The percentage contribution of this genus to total euphausiid abundance was 31 ± 36% (Fig 3.12) while the biomass accounted for 32 ± 38% of the total (Fig 3.13) euphausiid biomass. Of the *Nematoscelis* species, *N. megalops* (Sars 1883 in Boltovskoy 1999) accounted for ≈ 90% and a total of 96% of the genus abundance and biomass, respectively (Table 3.3). *N. megalops* comprised a total of 63% and a total of 30% of the total euphausiid abundance and biomass, respectively.

TABLE 3.3 Total percentage contribution of each species to total respective euphausiid genus abundance (ind 100m^{-3}) and biomass (mg Dwt 100m^{-3}) during April 2007.

	Abundance	Biomass		Abundance	Biomass
Euphausia			*Nematoscelis*		
E. longirostris	23.83	18.92	N. megalops	89.96	96.36
E. recurva	20.52	9.00	N. atlantica	9.21	2.08
E. similis	19.94	19.35	N. difficilis	0.83	1.56
E. spinifera	12.93	31.69			
E. lamelligera	8.11	5.78	*Thysanoessa*		
E. armata	6.43	10.39	T. longicaudata	51.30	57.36
E. superba	2.98	2.18	T. parva	39.64	37.41
E. pacifica	2.06	0.10	T. gregaria	5.64	3.01
E. tricicantha	1.49	2.27	T. longipes	1.89	1.49
E. fallax	0.77	0.08	T. inspinata	0.60	0.26
E. mucroata	0.48	0.09	T. raschi	0.57	0.39
E. brevis	0.29	0.01	T. vicina	0.36	0.08
E. hanseni	0.11	0.12			
E. lucens	0.05	0.03			

Representations of the genus *Thysanoessa* total abundance and biomass values during the study were significantly (ANOVA, F = 5.28 & 5.87, respectively; df = 46; p<0.05) higher south of the front than those recorded in the waters north of the STC (Fig 3.11) and ranged from 0.08ind 100m^{-3} to 1.44ind 100m^{-3} and from 0.05mg Dwt 100m^{-3} to 4.06mg Dwt 100 m^{-3}, respectively. Abundance and biomass values at stations within the immediate vicinity of the front were, however, not significantly (p>0.05) higher than the values at all other stations. Correlation analysis indicated that there was no significant relationship between the biological and physical data and the total *Thysanoessa* abundance and biomass values. The percentage contribution of this genus to the total abundance and biomass values of the euphausiids was lower than those of *Nematoscelis* and *Euphausia* and only accounted for 12 ± 19% of the total euphausiid abundance (Fig 3.12) and 10 ± 21% of the total euphausiid biomass (Fig 3.13). Within the *Thysanoessa* genus, *T. longicaudata* (Krøyer 1846 in Boltovskoy 1999) accounted for a total of 51% and 57% of the total *Thysanoessa* genus abundance and biomass, respectively (Table 3.3), but accounted for a total of 29% of the total euphausiid abundance and less than 4% of the total euphausiid biomass.

3.3.1.5 PHYLUM CHAETOGNATHA

Total average chaetognath abundance and biomass during the study ranged from 0.18 ± 0.09ind 100m^{-3} to 3.44 ± 1.43ind 100m^{-3} and from 0.04 ± 0.01mg Dwt 100m^{-3} to 10.03 ± 0.01mg Dwt 100m^{-3}, respectively (Fig 3.14). There were no significant spatial difference in the estimates of total chaetognath abundance and biomass values evident during the study (p>0.05) (Fig 3.14). Also,

abundance and biomass values at stations within the immediate vicinity of the front were not significantly higher than the values at stations further north and south of the STC ($p > 0.05$). The total chaetognath abundance and biomass values were not significantly correlated to the physical or biological data ($p > 0.05$).
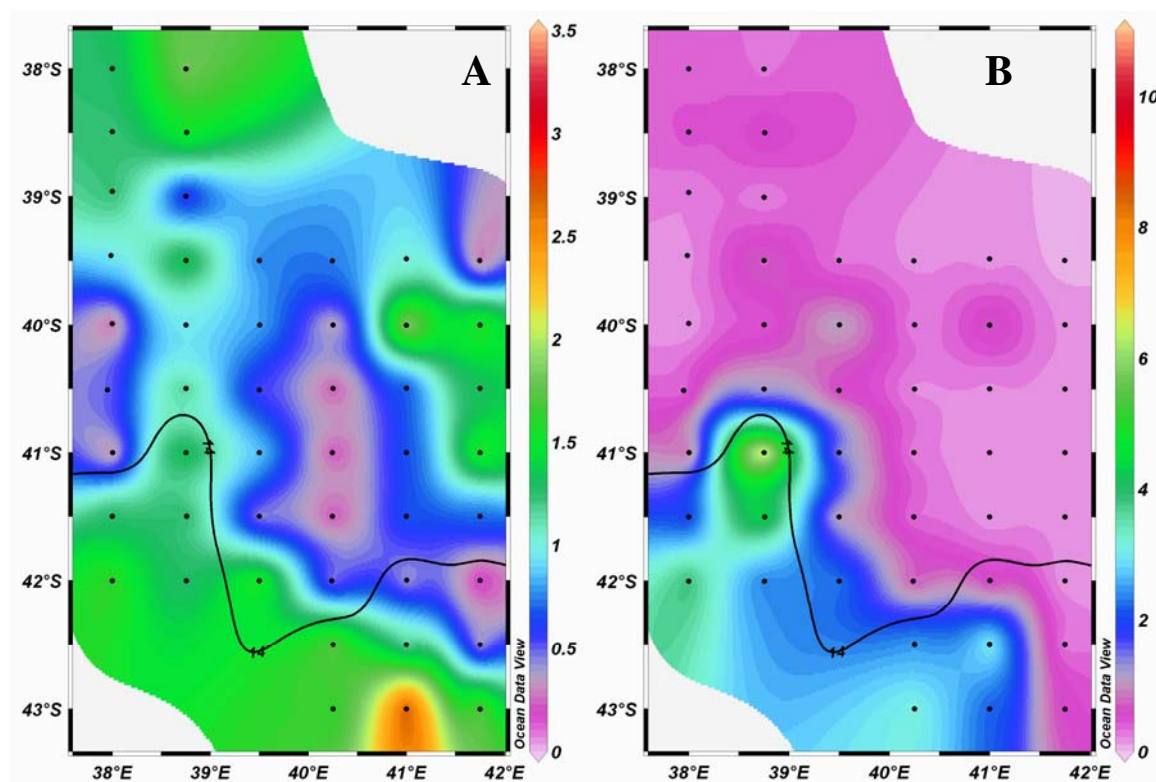
FIGURE 3.14 Total average chaetognath abundance (ind100m^{-3}) (**A**) and biomass (mg Dwt 100m^{-3}) (**B**) within the survey area (April 2007). Dots represent the stations while the thickened line represents the surface expression (14°C isotherm) of the Subtropical Convergence (Lutjeharms and Valentine 1984).

Four species of chaetognaths were identified within the survey area: *Eukrohnia hamata* (Möbius 1875 in Boltovskoy 1999), *Sagitta gazellae* (Ritler-Záhony 1909 in Boltovskoy 1999), *S. zetesios* (Fowler 1905 in Boltovskoy 1999) and *S. maxima* (Conant 1896 in Boltovskoy 1999). Of these species, the latter was disregarded as it accounted for less than 1% of the total chaetognath abundance and biomass values within the survey area (Appendix 2). Total abundance values for *E. hamata* ranged from 0.12ind 100m^{-3} to 4.27ind 100m^{-3}, those of *S. gazellae* from 0.15ind 100m^{-3} to 4.45ind 100m^{-3} while *S. zetesios* ranged from 0.22ind 100m^{-3} to 2.43ind 100m^{-3}. Biomass values ranged from 0.01mg Dwt 100m^{-3} to 4.4mg Dwt 100m^{-3}, from 0.003mg Dwt 100m^{-3} to 11.68mg Dwt 100m^{-3} and from 0.03mg Dwt 100m^{-3} to 2.48mg Dwt 100m^{-3}, respectively. Total abundance values of *E. hamata* and *S. zetesios* indicated no significant difference ($p > 0.05$) north and south of the frontal feature however, the biomass values of *S. zetesios* were significantly higher south of the front (ANOVA, F = 7.48; df = 46; $p < 0.05$) (Fig 3.15). The total average abundance and biomass values of *S. gazellae* were, however, significantly higher south of the STC (ANOVA, F = 22.15 & 35.70, respectively; df = 46; $p < 0.05$) (Fig 3.15).
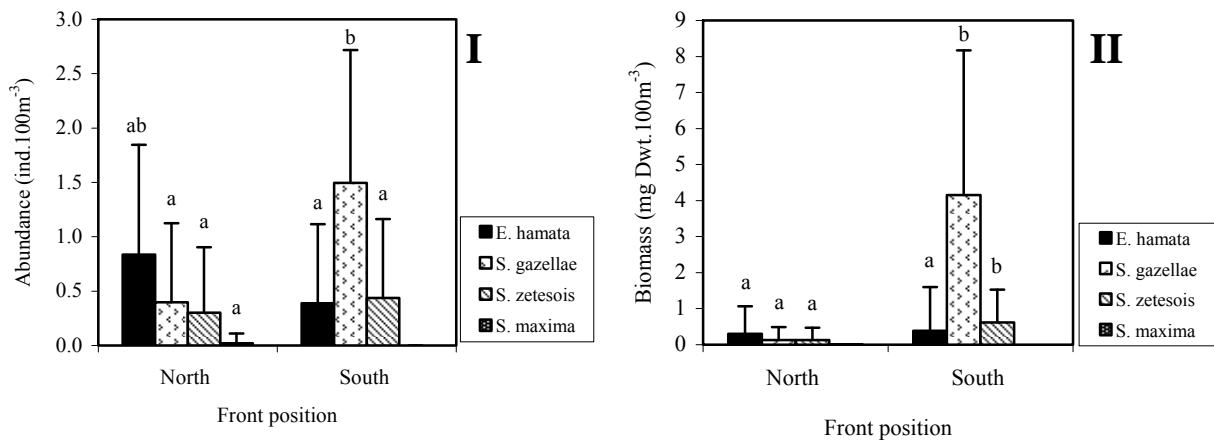
FIGURE 3.15 Total average abundance (ind 100m^{-3}) (**I**) and biomass (mg Dwt 100m^{-3}) (**II**) of the four chaetognath species north and south of the Subtropical Convergence during April 2007. Error bars indicate standard deviation. Different lettering indicates statistical differences within each species (ANOVA).

Of the three chaetognath species *S. gazellae* accounted for $29 \pm 35\%$ of the total chaetognath abundance while *E. hamata* and *S. zetesios* accounted for $31 \pm 36\%$ and $14 \pm 25\%$ of the total chaetognath abundance, respectively (Fig 3.16). Individually, the three species accounted for $32 \pm 39\%$, $28 \pm 36\%$ and $14 \pm 28\%$, respectively, to the total chaetognath biomass (Fig 3.17). The distribution patterns of each species, with regard to abundance and biomass, were however not a result of the environmental factors due to the lack of the physical (temperature and salinity) and biological (mesozooplankton abundance and biomass and chl-*a*) factors significantly correlating with the abundance and biomass values ($p > 0.05$, in all cases).
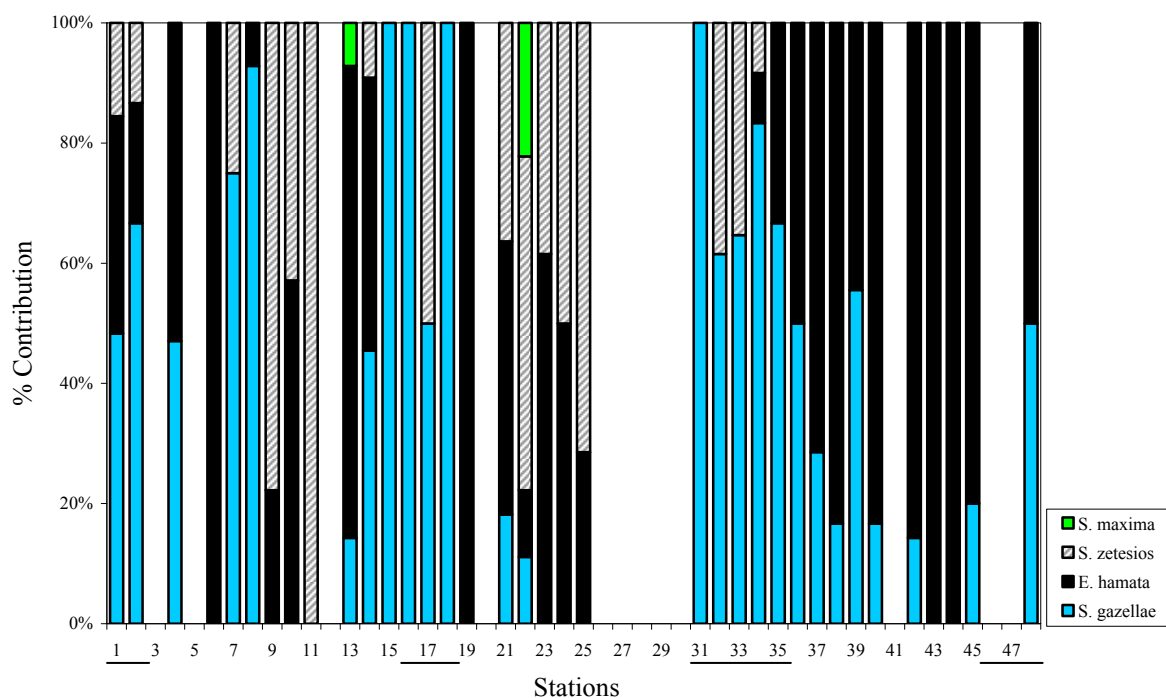
FIGURE 3.16 Percentage contribution of different chaetognath species to the total chaetognath abundance (ind 100m^{-3}) within the survey area during April 2007. (Lines represent stations south of the Subtropical Convergence while no samples were collected at stations 27 to 29 due to logistical constraints)
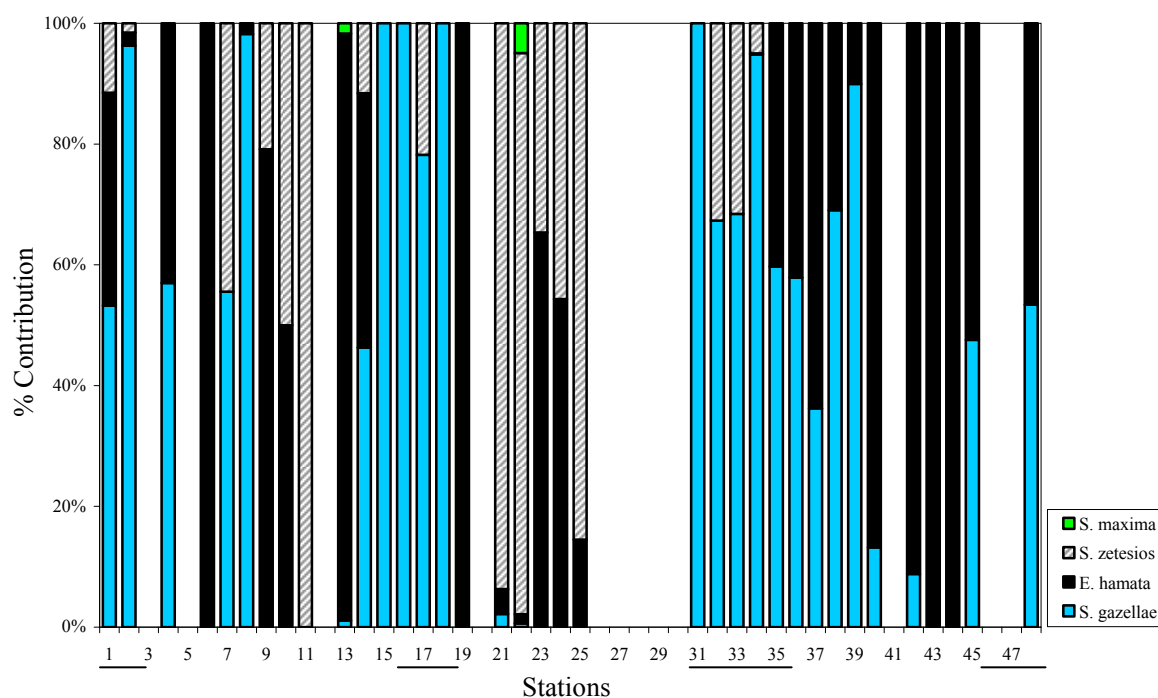
FIGURE 3.17 Percentage contribution of different chaetognath species to the total chaetognath biomass (mg Dwt 100m^{-3}) within the survey area during April 2007. (Lines represent stations south of the Subtropical Convergence while no samples were collected at stations 27 to 29 due to logistical constraints)

3.3.2 SIZE STRUCTURE AND SEX RATIOS

Length and sex analysis was restricted to the most abundance species within each group and included the following species *Phronima sedentaria, Themisto gaudichaudii* and *Vibilia armata* of the amphipoda order, *Euphausia longirostris, E. recurva* (Hansen 1905 in Boltovskoy 1999)*, E. similis* (Sars 1883 in Boltovskoy 1999)*, Nematoscelis megalops* and *Thysanoessa longicaudata* of the euphausiacea order and the three species of chaetognaths, *Eukrohnia hamata, Sagitta gazellae* and *S. zetesios*.

3.3.2.1 ORDER: AMPHIPODA

P. sedentaria was dominated by females which accounted for ≈ 80% of the total counts. Average male lengths ranged from 9.50 ± 0.71mm to 15.00 ± 0.01mm while the average female lengths ranged from 10.00 ± 0.01mm to 34.00 ± 0.01mm (Fig 3.18). A one-way ANOVA indicated that the females were significantly larger than the males ($F = 11.28$; $df = 32$; $p<0.05$). There was no significant difference in lengths of males and females north and south of the frontal feature ($p>0.05$).
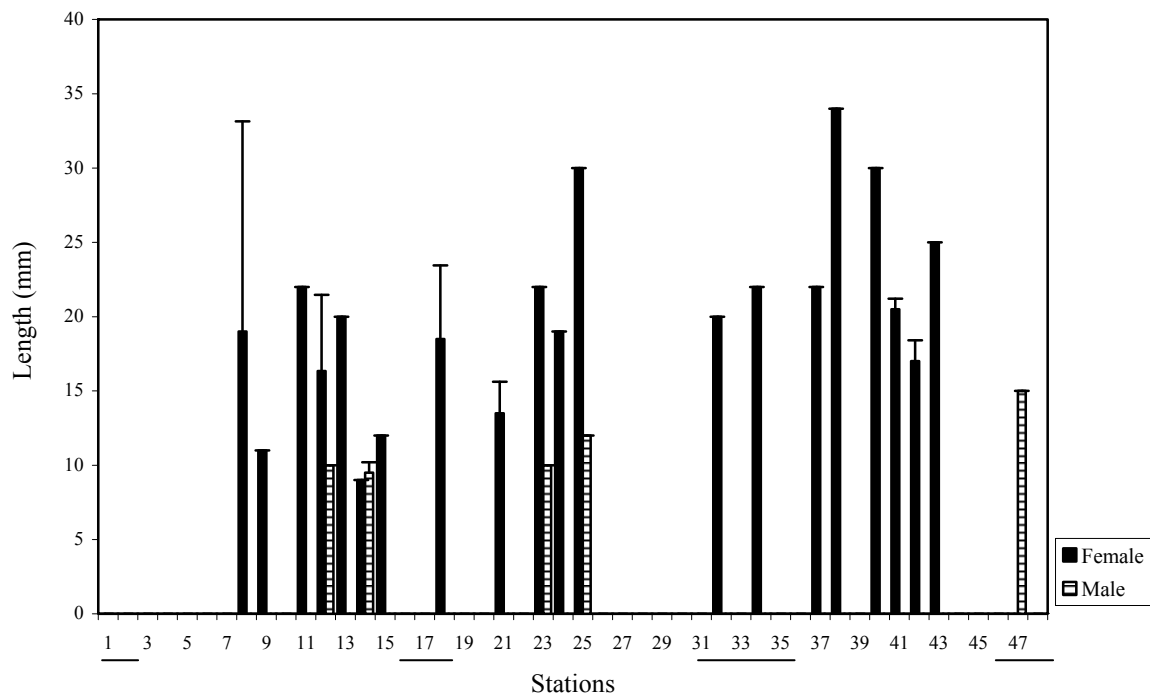
FIGURE 3.18 Average lengths (mm) of male and female *Phronima sedentaria* within the survey area (April 2007). Error bars represent standard deviation. (No data indicates the absence of this species at the station while the lines represent stations south of the Subtropical Convergence)
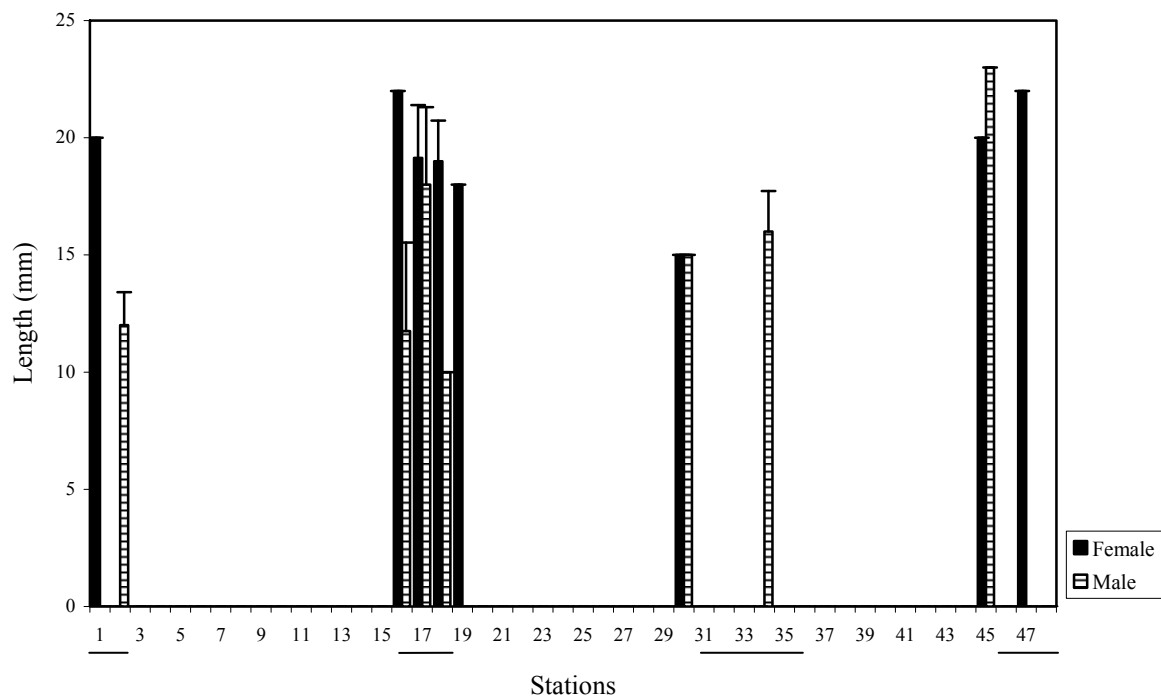
FIGURE 3.19 Average lengths (mm) of male and female *Themisto gaudichaudii* within the survey area (April 2007). Error bars represent standard deviation. (No data indicates the absence of this species at the station while the lines represent stations south of the Subtropical Convergence)

Males dominated the *T. gaudichaudii* population throughout the survey area and accounted for approximately 70% of the total counts. Average female lengths were significantly larger than the average male lengths and ranged from 15.00 ± 0.01mm to 22.00 ± 0.01mm, while average male lengths ranged from 10.00 ± 0.01mm to 23.00 ± 0.01mm (ANOVA, F = 7.14; df = 83; p<0.05) (Fig 3.19). There were no significant spatial patterns in the size distribution of *T. gaudichaudii* evident during the study (p>0.05).

Within the *V. armata* population, females occurred in a ratio of $\approx$ 1:2, male to female. Average female lengths ranged from 8.00 ± 0.01mm to 10.00 ± 0.01mm while those of the males ranged from 9.00 ± 1.55mm to 11.00 ± 1.41mm (Fig 3.20). There were no significant differences in the length of male and female *V. armata* (p>0.05). In addition there was no significant spatial pattern in the size distribution of *V. armata* evident during the survey (p>0.05).
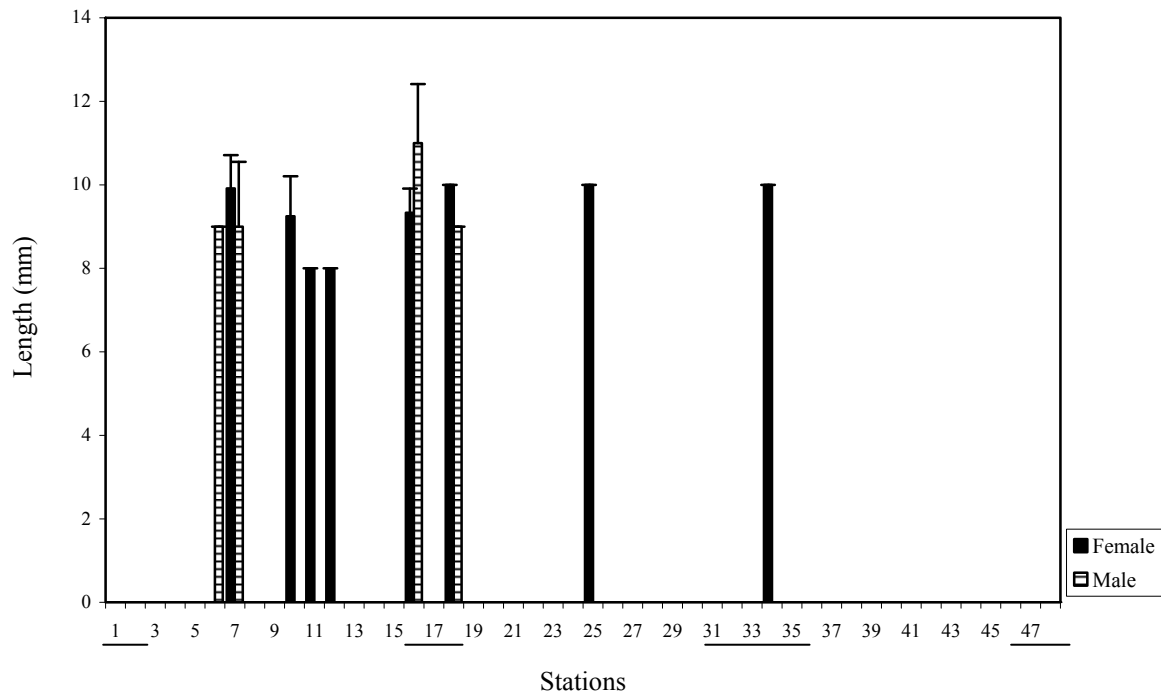
FIGURE 3.20 Average lengths (mm) of male and female *Vibilia armata* within the survey area (April 2007). Error bars represent standard deviation. (No data indicates the absence of this species at the station while the lines represent stations south of the Subtropical Convergence)

3.3.2.2 ORDER: EUPHAUSIACEA

E. longirostris was dominated by females, which accounted for $\approx$ 93% of the total counts. Average female lengths ranged from 13.50 ± 2.12mm to 26.00 ± 0.01mm, while the lengths of the males ranged from 23.00 ± 0.01mm to 25.00 ± 0.01mm (Fig 3.21). Statistical analysis indicated that there was no significant difference (p>0.05) between male and female lengths or between average sizes of *E. longirostris* north and south of the STC.
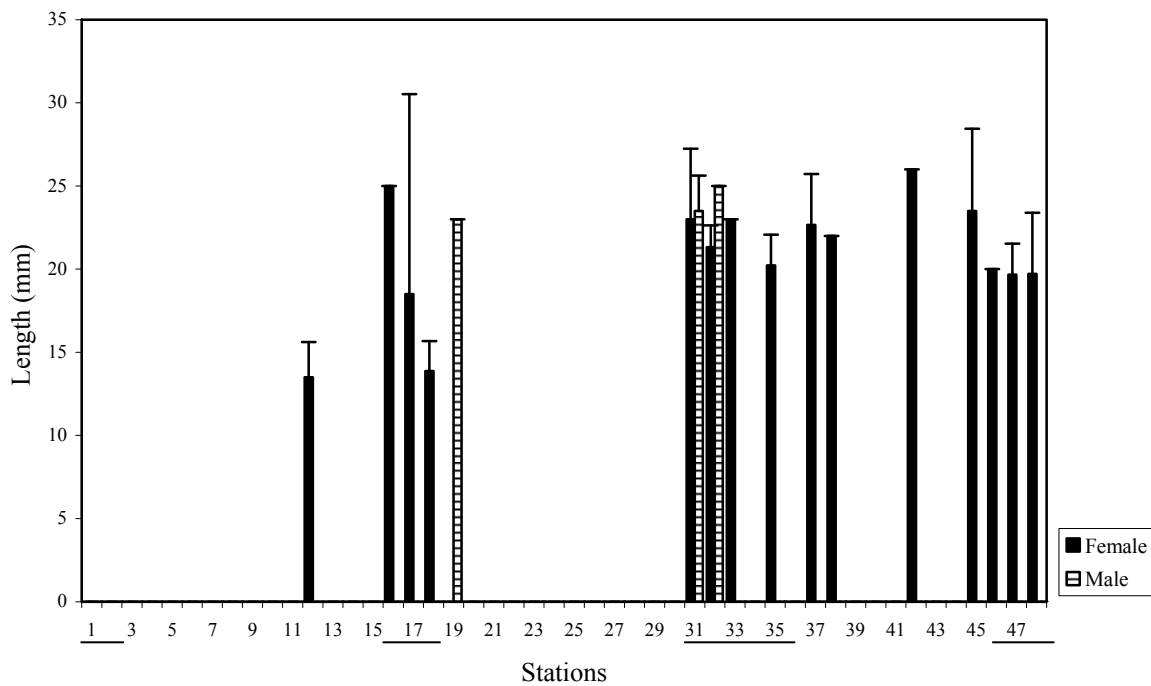
FIGURE 3.21 Average lengths (mm) of male and female *Euphausia longirostris* within the survey area (April 2007). Error bars represent standard deviation. (No data indicates the absence of this species at the station while the lines represent stations south of the Subtropical Convergence)

Males dominated the total *E. recurva* counts, and accounted for a total of 57% of the total counts. The average male and female lengths ranged from 14.00 ± 0.01mm to 17.67 ± 1.97mm and from 13.00 ± 0.01mm to 20.00 ± 0.01mm, respectively (Fig 3.22). Again there were no significant differences in sizes between the males and the females ($p>0.05$) and there were no significant spatial patterns in the size distribution of *E. recurva* evident during the study ($p>0.05$) (Fig 3.22).

Females dominated the *E. similis* counts which accounted for $\approx 98\%$ of the total. Average male lengths were 25.00 ± 0.01mm while the mean length of females ranged from 17.00 ± 0.01mm to 24.00 ± 1.41mm (Fig 3.23). The average lengths of the males and females were not significantly different ($p>0.05$) from one another. Similarly, the total lengths north and south of the front were not significantly different ($p>0.05$) from one another.
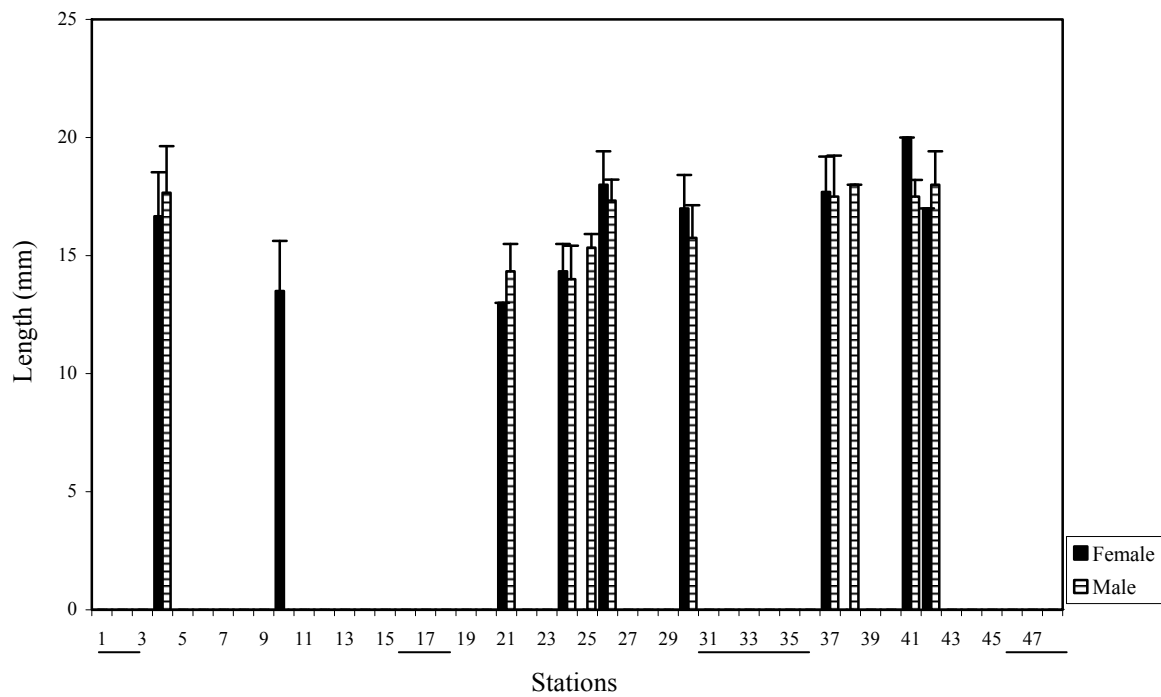
FIGURE 3.22 Average lengths (mm) of male and female *Euphausia recurva* within the survey area (April 2007). Error bars represent standard deviation. (No data indicates the absence of this species at the station while the lines represent stations south of the Subtropical Convergence)
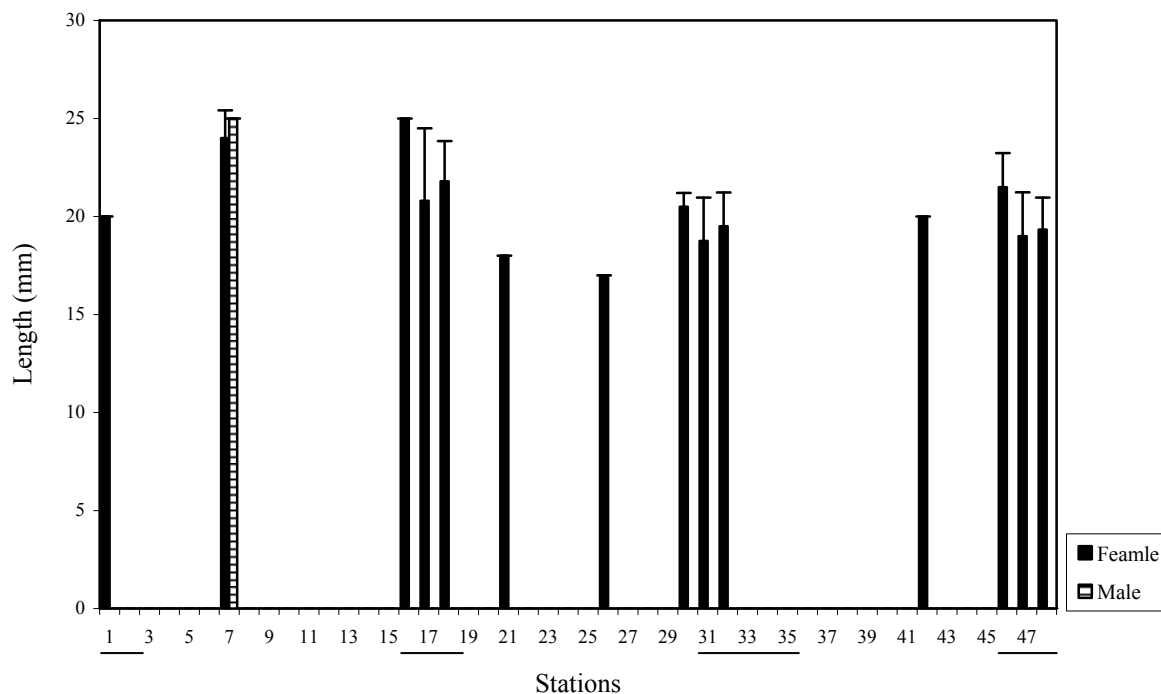
FIGURE 3.23 Average lengths (mm) of male and female *Euphausia similis* within the survey area (April 2007). Error bars represent standard deviation. (No data indicates the absence of this species at the station while the lines represent stations south of the Subtropical Convergence)

Females accounted for a total of 98% of all *N. megalops* counted during the survey. Average female lengths ranged from 18.00 ± 2.65mm to 25.33 ± 0.58mm while average male lengths were 25.00 ± 0.01mm (Fig 3.24). Male and female lengths were not significantly ($p>0.05$) different from one another, however, significantly larger individuals occurred south of the frontal feature (ANOVA, $F = 72.14$; $df = 142$; $p<0.001$). Total lengths were also negatively correlated ($r = -0.7$) with temperature where larger individuals occurred at colder temperatures.
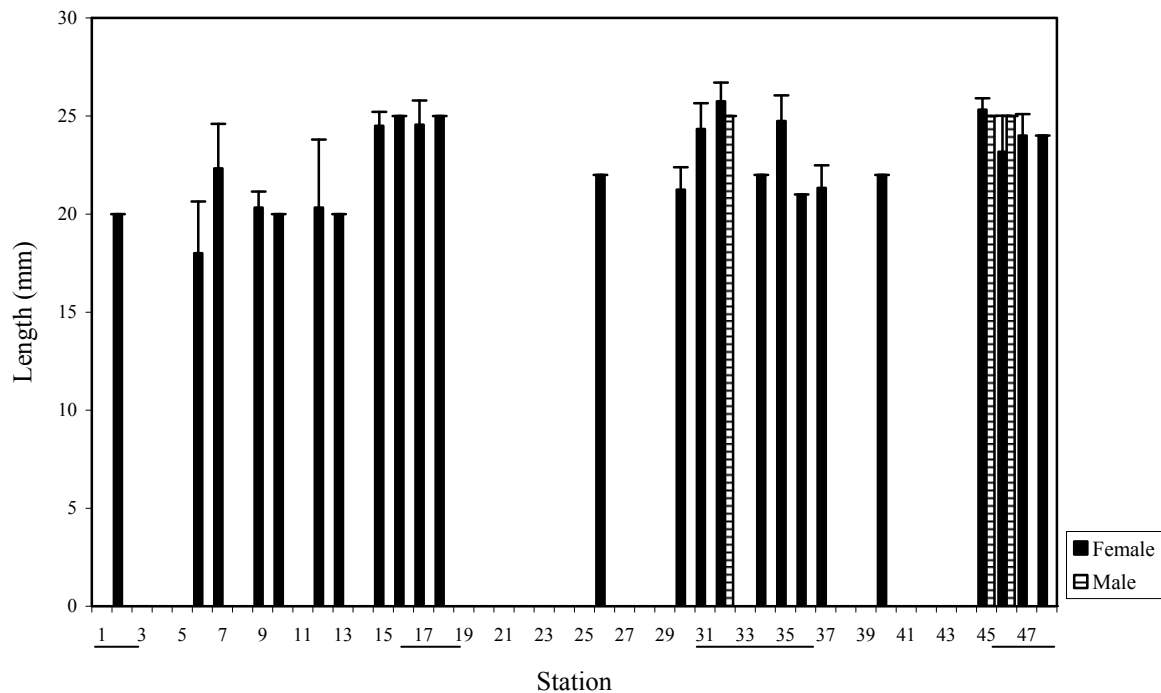
FIGURE 3.24 Average lengths (mm) of male and female *Nematoscelis megalops* within the survey area (April 2007). Error bars represent standard deviation. (No data indicates the absence of this species at the station while the lines represent stations south of the Subtropical Convergence)

Female *T. longicaudata*, again, dominated the population and accounted for approximately 95% of the total counts. Average lengths were not significantly different where average female lengths ranged from 10.00 ± 0.01mm to 26.00 ± 5.03mm while average male lengths ranged from 15.00 ± 0.01mm to 20.00 ± 0.01mm ($p>0.05$) (Fig 3.25). However, individuals occurring south of the STC were significantly larger than those occurring north of the frontal feature (ANOVA, $F = 10.31$; $df = 37$; $p<0.05$) yet there were no significant correlations between the average lengths and any of the physical or biological data ($p>0.05$).
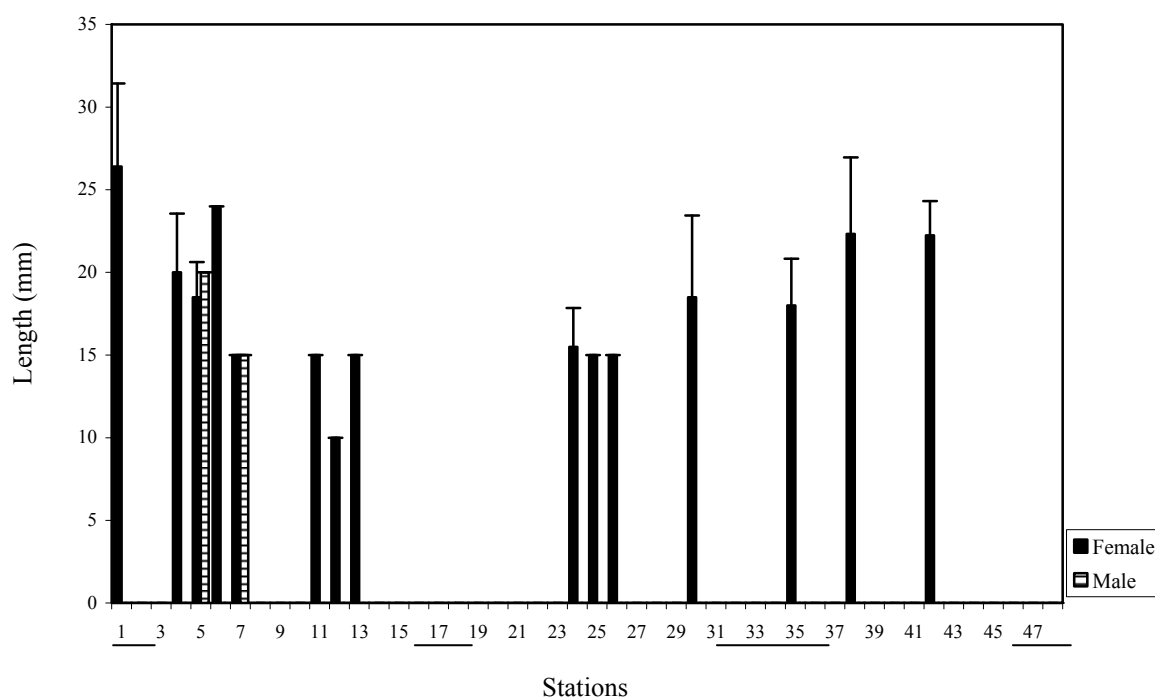
FIGURE 3.25 Average lengths (mm) of male and female *Thysanoessa longicaudata* within the survey area (April 2007). Error bars represent standard deviation. (No data indicates the absence of this species at the station while the lines represent stations south of the Subtropical Convergence)

3.3.2.3 PHYLUM: CHAETOGNATHA

The three stages of maturity within the *E. hamata* population occurred in a ratio of 1**:**5**:**14, III: II: I, and accounted for a total of 5%, 23% and 72%, respectively, of the total counts. Juveniles were thus numerically dominant within the *E. hamata* population. Lengths for each stage (I, II and III) ranged from 21.00 ± 0.01mm to 38.00 ± 6.20mm, from 24.00 ± 0.01mm to 48.64 ± 3.11mm and from 30.75 ± 7.27 to 48.50 ± 0.71mm, respectively (Fig 3.26). The average lengths of stages II and III were not significantly different from one another ($p>0.05$). Stage I individuals were, however, significantly smaller than the average lengths of individuals from stages II and III (ANOVA, F = 34.73; df =153; $p<0.001$) (Fig 3.26).

The number of *E. hamata* individuals per stage of maturity that occurred north or south of the STC varied, with 92 individuals recorded in the waters north of the front and 66 individuals recorded south of the STC (Fig 3.29). North of the front, 68 individuals were identified as stage I maturity, 20 individuals as stage II maturity and 5 individuals as stage III maturity. South of the front, 45, 20 and 3 individuals were identified as stage I, II and III maturity, respectively (Fig 3.29). Regardless of this, the juvenile counts within the *E. hamata* species were significantly more numerous than both the counts of stages II and III irrespective of the position north or south of the STC (ANOVA, $p<0.05$).
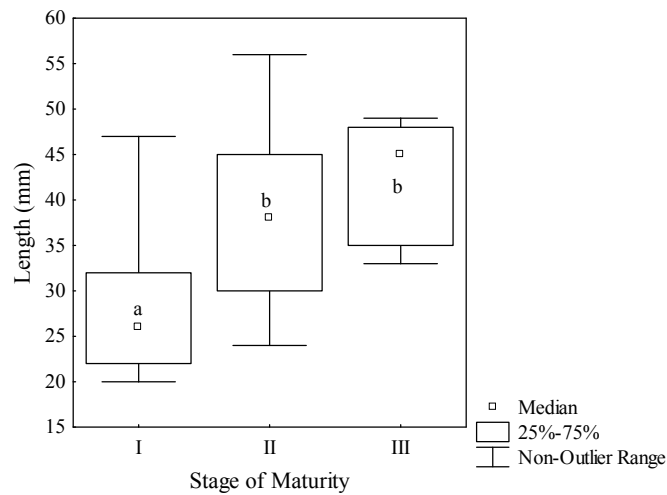
FIGURE 3.26 Total length (mm) of the different maturity stages of the chaetognath, *Eukrohnia hamata*, during April 2007. (Lettering indicates statistical differences between stages of maturity lengths, ANOVA)
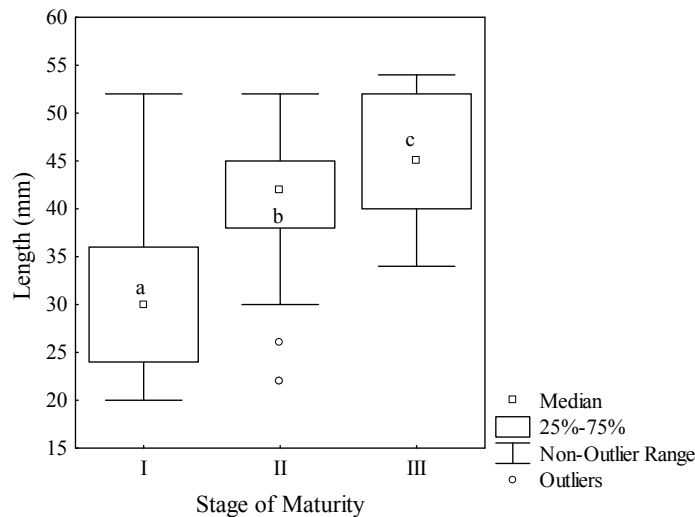
FIGURE 3.27 Total length (mm) of the different maturity stages of the chaetognath, *Sagitta gazellae*, during April 2007. (Lettering indicates statistical differences between stages of maturity lengths, ANOVA)

The population of *S. gazellae* during this study was also dominated by juveniles as stage I accounted for a total of 67% of the total count while stages II and III accounted for a total of 25% and 8% of the total count, respectively. The ratio of the different developmental stages was thus 1:3:9, III: II: I. The average lengths of stage I ranged from 20.00 ± 1.00mm to 40.71 ± 7.62mm, while those of stages II and III ranged from 22.00 ± 0.01 to 49.00 ± 3.61mm and from 35.50 ± 2.12mm to 52.00 ± 0.01mm, respectively (Fig 3.27). The average lengths of each stage of maturity within this species were significantly different from each other where stage I had the smallest individuals (ANOVA, F = 47.39; df = 195; p<0.001) (Fig 3.27).

Within the *S. gazellae* population, a total of 132 individuals occurred south of the front while 66 individuals occurred north of the frontal feature (Fig 3.29). North of the front, 57 individuals were identified as stage I maturity, 8 individuals as stage II maturity and 1 individual as stage III maturity, while south of the front, 76, 42 and 14 individuals were identified as stage I, II and III maturity, respectively (Fig 3.29). Once again the number of juveniles within the *S. gazellae* species was significantly more numerous than the number of individuals that occurred within stages II and III irrespective of the position north or south of the STC (ANOVA, $p < 0.05$).

Juveniles also numerically dominated the *S. zetesios* counts and accounted for 67% of the total counts. The individuals of stages II and III contributed 28% and 5%, respectively, of the total counts of *S. zetesios* within the survey area. The ratio of stage I:II:III was therefore calculated at 1:6:13. The average lengths of each stage (I, II and III) ranged from 20.00 ± 0.01mm to 42.00 ± 0.01mm, from 29.00 ± 0.01mm to 48.00 ± 0.01mm and from 37.00 ± 0.01 to 43.00 ± 4.24mm, respectively (Fig 3.28). The average individual length of stages II and III were not significantly ($p > 0.05$) different, however, the average individual length of stage I were significantly (ANOVA, $F = 25.17$; $df = 76$; $p < 0.001$) smaller than the average individuals length from both stages II and III (Fig 3.28).
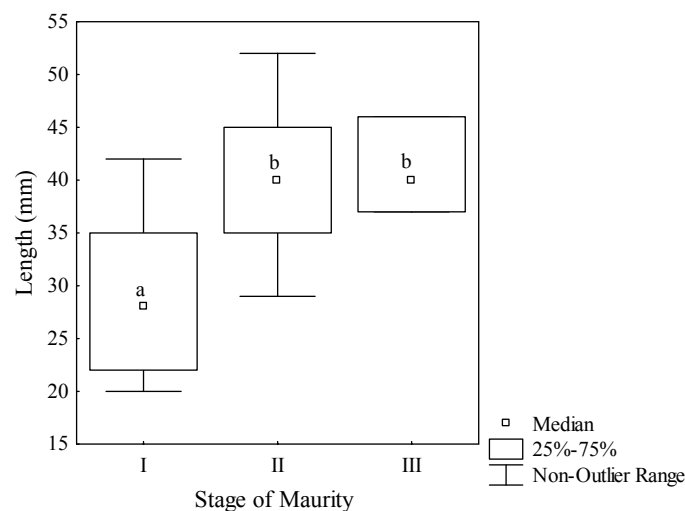
FIGURE 3.28 Total length (mm) of the different maturity stages of the chaetognath, *Sagitta zetesios*, during April 2007. (Lettering indicates statistical differences between stages of maturity lengths, ANOVA)

A total of 42 individuals of *S. zetesios* occurred north of the frontal feature while 37 individuals occurred south of the front (Fig 3.29). There were no significant ($p > 0.05$) differences in the contribution of the different stages to the total counts north and south of the front however, the juveniles were numerically dominant (Fig 3.29).
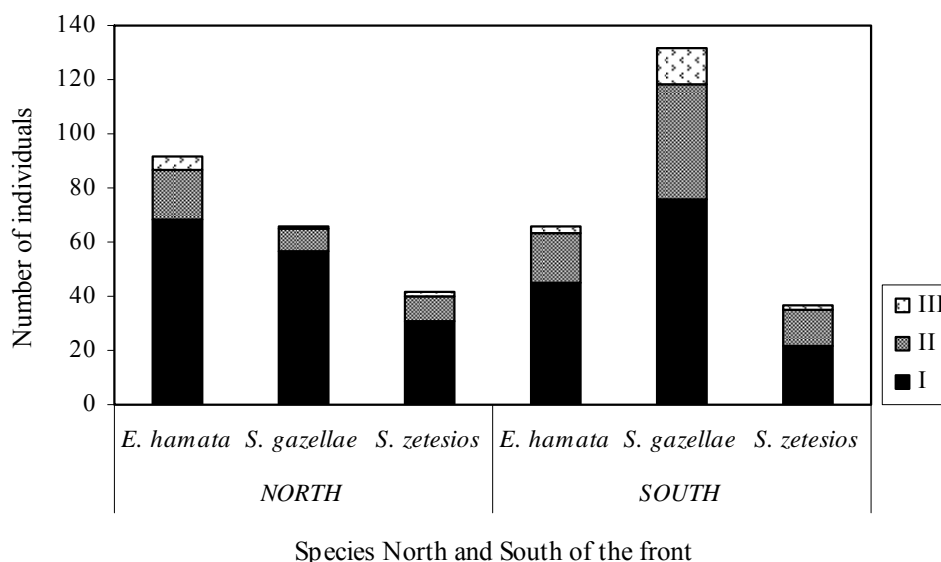
FIGURE 3.29 Number of individuals per maturity stage north and south of the Subtropical Convergence for the three chaetognath species during April 2007.

The integration of temperature as a co-factor within the analyses of length and stage of maturity indicated that temperature was not a factor with regard to stage of maturity, so that stage of maturity was dependent on the length of an individual. Again, when temperature was used as a co-factor, ANOVA indicated that individuals of stage I were smaller than those of stages II and III, except in the case of *S. gazellae* were individuals of stage II were also smaller than those of stage III.

3.3.3   COMMUNITY STRUCTURE

Hierarchical cluster analyses identified three groups, designated Groups 1 to 3, of stations at the 20% level of similarity within the survey area (Fig 3.30). The spatial distribution of the stations within the various groupings identified with the hierarchical cluster analysis is indicated in Figure 3.31. Group 1 consisted of station 5 (Fig 3.30 & 3.31) which was situated north of the frontal feature, and included three species with a total average abundance of 0.02 ± 0.11ind 100m^{-3} (Table 3.4). This group was thus considered an outlier and therefore disregarded in further analysis. Group 2 (n=11) included the stations that occurred south of the frontal feature, with the exception of stations 7 and 12 which were north of the STC (Fig 3.30 & 3.31). This group comprised 28 species with a total average abundance of 0.27 ± 1.39ind 100m^{-3} (Table 3.4). Group 3, incorporated those stations situated north of the frontal feature, with the exception of stations 1, 2, 33 and 34, which occurred south of the front (Fig 3.30 & 3.31), and consisted of 48 species with a total average abundance of 0.09 ± 0.37ind 100m^{-3} (Table 3.4). ANOSIM indicated that Groups 2 and 3 were significantly different from one another ($p<0.05$).
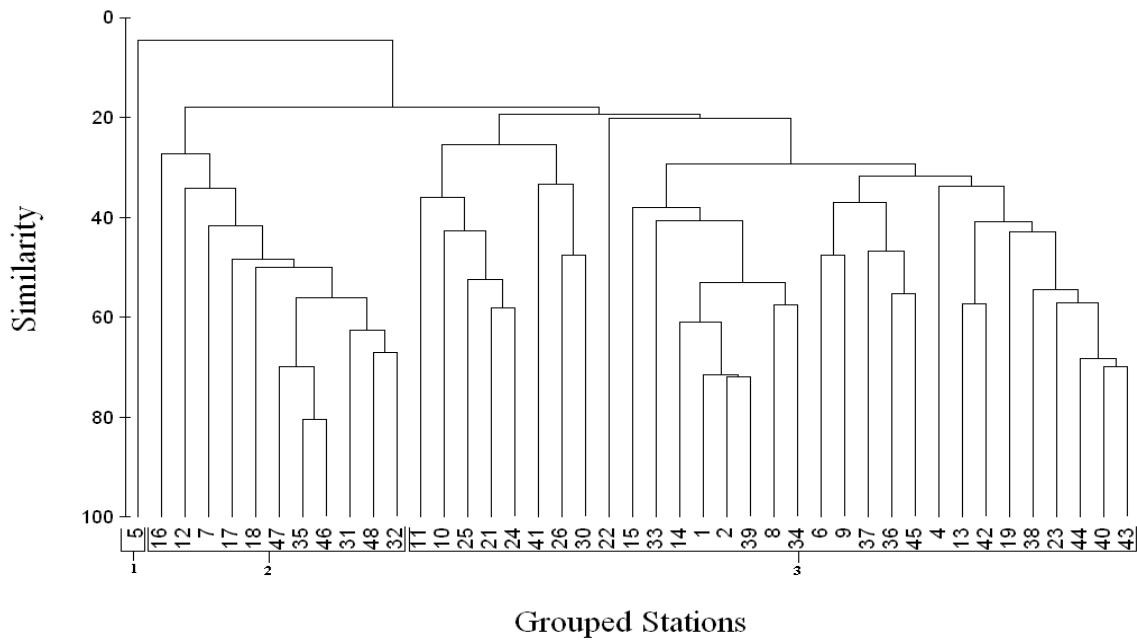
FIGURE 3.30 Hierarchical cluster analyses indicating station groupings according to total abundances (ind 100m^{-3}) per carnivorous species within the survey area during April 2007.
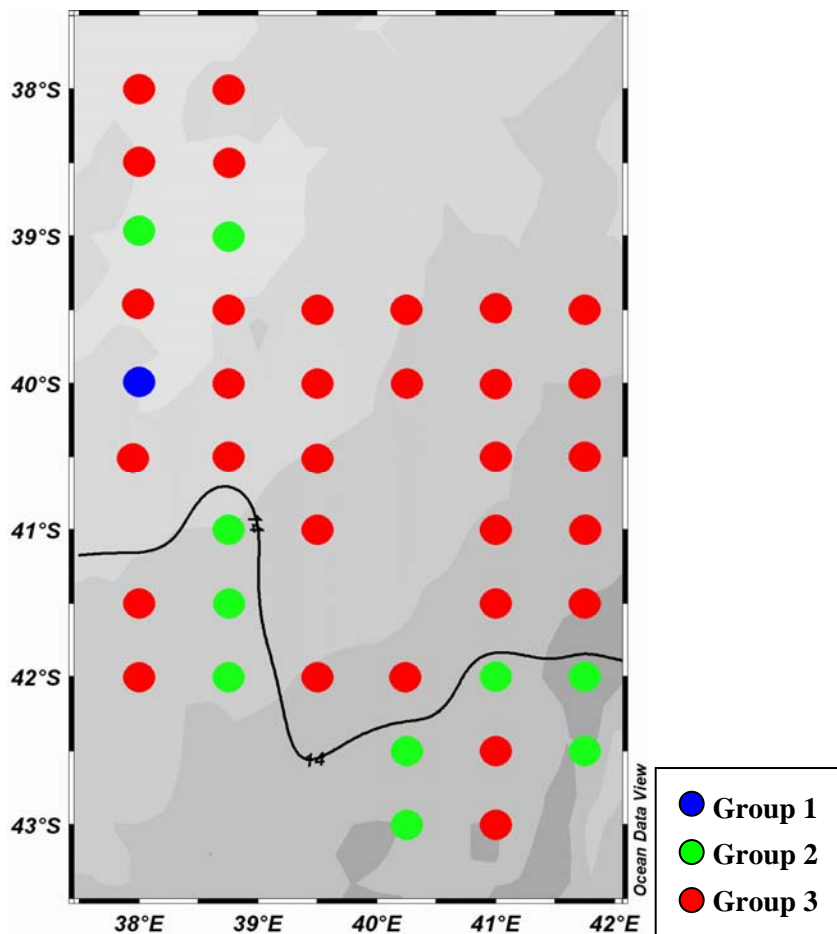
FIGURE 3.31 The spatial distribution of the various groupings identified with the hierarchical cluster analysis, according to total abundances (ind 100m^{-3}) per carnivorous species, during the survey (April 2007). The thickened line represents the surface expression (14°C isotherm) of the Subtropical Convergence (Lutjeharms and Valentine 1984)

TABLE 3.4 Composition and average abundance (ind 100m^{-3}) of the carnivorous zooplankton per grouping identified by the hierarchal cluster analysis within the survey area (April 2007). (Euphausiid distribution: *Sub-Antarctic/Antarctic; †Subtropical/Agulhas Return Current).

Taxa	Group 1 (n = 1)	Group 2 (n = 11)	Group 3 (n = 31)
EUPHAUSIACEA			
Euphausia			
E. armata†		5.03	0.19
E. brevis†	0.23		
E. fallax†			0.63
E. hanseni†			0.09
E. lamelligera†		2.59	4.00
E. longirostris†		17.16	2.20
E. lucens†			0.04
E. mucroata†			0.39
E. pacifica†		1.68	
E. recurva†			16.68
E. similis†		14.11	2.09
E. spinifera*†		7.92	2.59
E. superba*		0.50	1.92
E. triacantha*		1.21	
Nematoscelis			
N. atlantica†		0.50	3.79
N. difficilis†			0.39
N. megalops†		29.65	12.17
Thysanoessa			
T. gregaria*†		0.83	
T. inspinata†			0.09
T. longicaudata†	0.70	1.68	5.16
T. longipes*			0.28
T. parva†		4.33	1.49
T. raschii†			0.08
T. vicina*			0.05
CHAETOGNATHA			
Eukrohnia hamata		2.16	32.14
Sagitta gazellae		12.50	23.71
Sagitta zetesios		3.25	13.86
Sagitta maxima			0.70
AMPHIPODA			
Cyllopus magellanicus		0.12	0.44
Cyphocaris challengeri			0.39
Cystisoma fabricii			0.14
Dairella latissima		0.41	0.31
Hyperiella antarctica		0.22	0.47
Paralycaea gracilis			0.29
Phronima atlantica		0.22	0.94
Phronima curvipes	0.23		0.05
Phronima sedentaria		3.80	6.64

TABLE 3.4 CONTINUED

Phrosinia semilunata		0.50	1.11
Platyscelus armatus		0.48	0.94
Pronoe capito			0.27
Themisto gaudichaudii		33.20	3.39
Vibilia armata		7.36	3.45
Vibilia propinqua		0.86	0.08
DECAPODA			
Decapod larva			0.05
Brachyura larva		0.50	
Gennadas			0.51
Lucifer			0.58
Plesiopenagus			0.08
Posiphae			0.38
Sergestes		1.76	3.00
Sicyonia			0.71
Stomatopoda larva			0.45
MYSIDACAE			
Siriella thompsoni			2.15
Total Average	0.02	0.27	0.09
Std	0.11	1.39	0.37
No. species	3	28	48

Results from the PRIMER procedure SIMPER, indicated that the average similarity between stations within Group 2 was 28%. Within this group *Eukrohnia hamata* (45%), *Sagitta gazellae* (18%), *S. zetesios* (8%), *Phronima sedentaria* (8%), *Nematoscelis megalops* (6%) and *Euphausia recurva* (6%) collectively, accounted for ≈ 92% of the total similarity of stations within the group. The average similarity between stations in Group 3 was 45%. Here, *N. megalops* (34%), *E. longirostris* (21%), *E. similis* (20%), *S. gazellae* (12%), *Thysanoessa parva* (Hansen 1905 in Boltovskoy 1999) (3%) and *E. lamelligera* (Hansen 1911 in Boltovskoy 1999) (2%) combined, accounted for ≈ 92% of the total similarity of stations within the group. *N. megalops, E. longirostris, E. similis, E. hamata* and *S. gazellae* together accounted for 51% of the total dissimilarity (82%) between Groups 2 and 3. Although some species were group specific, the numerically dominant species occurred in both groups but at different abundance levels. Differences between the groupings thus reflected the variation in the numerical abundance of the dominant species rather than the presence or absence of individual species. Results from the BIO-ENV procedure of PRIMER indicated that 23% of the clustering was due to temperature, 20% due to salinity, 8% due to the mesozooplankton abundance and only 15% when temperature, salinity and the mesozooplankton abundance were considered together.

3.4   CHAETOGNATH FEEDING RATES

A total of 155 stomachs of *E. hamata,* 198 of *S. gazellae* and 70 of *S. zetesios* were examined for the presence of prey items in their guts. Of the total stomach contents examined, only 65 stomachs of *E. hamata* contained prey while only 100 and 20 stomachs of *S. gazellae* and *S. zetesios*, respectively, contained prey items. No oil droplets were recorded in the guts of the three chaetognath species. Gut content analysis indicated that copepods were the preferred prey species for the three chaetognaths accounting for >75% of all prey identified (Fig 3.32). The second most frequently recorded prey in the gut content of the chaetognaths were the amphipods although their contribution was always <15% of all prey identified (Fig 3.32). Chaetognaths were recorded in the guts of *E. hamata* and *S. gazellae* although their contribution to the total prey consumed was <10% (Fig 3.32).

Mean number of prey per chaetognath (NPC) and the feeding rates of the three dominant species of chaetognaths are presented in Table 3.5. The mean NPC for *E. hamata* ranged from 0.27prey ind^{-1} to 0.58prey ind^{-1} while that of *S. gazellae* and *S. zetesios* ranged from 0.16prey ind^{-1} to 0.78prey ind^{-1} and from 0.19prey ind^{-1} to 0.35prey ind^{-1}, respectively. Of the three species, *S. gazellae* had an average feeding rate of 3.63 ± 2.08prey d^{-1} while the average feeding rates of *S. zetesios* and *E. hamata* were 2.18 ± 0.59prey d^{-1} and 1.82 ± 0.85prey d^{-1}, respectively. NPC and feeding rates of the three chaetognath species did not differ significantly between day and night nor were there any significant differences in feeding rates north and south of the STC (ANOVA, p>0.05, in both cases). The average percentage of mesozooplankton standing stock and secondary production removed by the three chaetognaths employing the feeding rates were as follows; *E. hamata* 0.09 ± 0.01% and 1.87 ± 0.27% respectively, *S. gazellae* 0.20 ± 0.22% and 4.08 ± 4.05% respectively, and *S. zetesios* 0.08± 0.13% and 1.61 ± 2.54% respectively (Table 3.5).
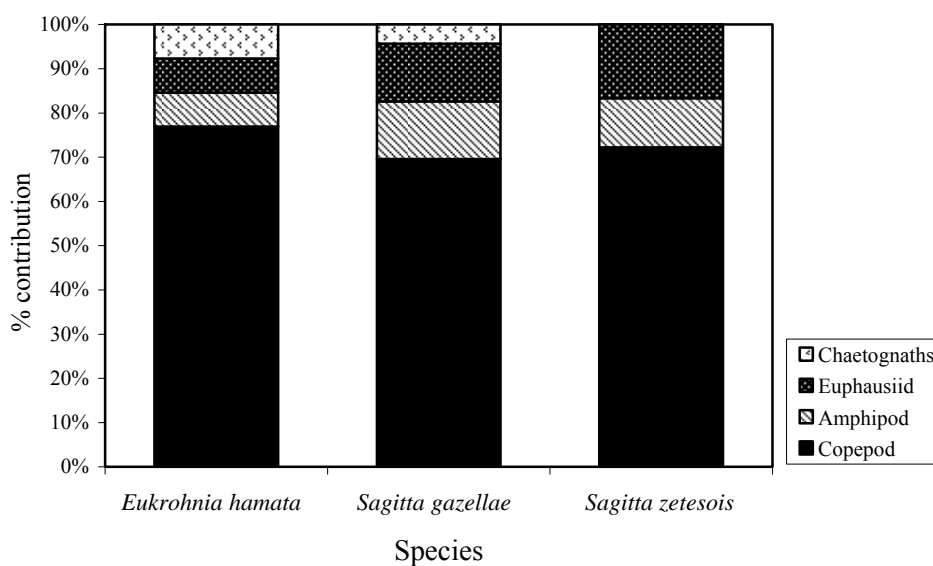
FIGURE 3.32 Total percentage contribution of prey items to chaetognath gut content during the survey (April 2007) in the Indian Ocean in the region of the Subtropical Convergence.

TABLE 3.5 Mean number of prey (NPC) prey ind^{-1}, daily feeding rates (Fr) prey d^{-1}, and predation impact expressed as a percentage of the mesozooplankton standing stock (%S.S.) and secondary production (%S.P.) consumed per day, of the three chaetognath species at stations with feeding individuals. (Dt represents digestive time).

Station	E. hamata (Dt 5hrs)				S. gazellae (Dt 2.64hrs)				S. zetesios (Dt 3hrs)			
	NPC	Fr	% S.S.	% S.P.	NPC	Fr	% S.S.	% S.P.	NPC	Fr	% S.S.	% S.P.
1	0.58	2.80	0.11	2.14	0.78	7.07	0.36	7.21				
2					0.56	5.05	0.58	11.50	0.24	1.88	0.04	0.86
4					0.33	3.03	<0.01	0.07				
7									0.19	1.50	<0.01	0.08
9									0.35	2.80	0.27	5.37
11									0.32	2.53	0.01	0.11
13	0.27	1.29	0.09	1.86								
18					0.16	1.44	0.01	0.16				
32					0.33	3.03	0.18	3.53				
39					0.24	2.16	0.10	1.98				
42	0.29	1.37	0.08	1.60								
Average	0.38	1.82	0.09	1.87	0.40	3.63	0.20	4.08	0.27	2.18	0.08	1.61
Stdev	0.18	0.85	0.01	0.27	0.23	2.08	0.22	4.05	0.07	0.59	0.13	2.54

3.5   TOTAL PREDATION IMPACT

The predation impact of the species considered here to be feeding upon the mesozooplankton standing stock and secondary production, mainly copepods, were calculated per station, using published daily rations (Table 2.1). The combined grazing impact of the selected carnivorous zooplankton within the region of investigation ranged from 0.01mg Dwt 100m^{-3}d^{-1} to 18.38mg Dwt 100m^{-3}d^{-1} (Table 3.6). These rates corresponded to a predation impact between <1% and 1.53% of the mesozooplankton standing stock or between 0.03% and 30.54% of the total mesozooplankton secondary production (Table 3.6). With the exception of station 17, chaetognaths and euphausiids were identified as the dominant consumers of mesozooplankton and accounted for between 1% and 98% (43.87 ± 44.31% and 48.69 ± 43.71%, respectively) of the total consumption of mesozooplankton standing stock and secondary production per day, respectively (Fig 3.33). The remaining group, the amphipods, generally accounted for less than 10% of the total predation impact. Total predation impact of the carnivorous zooplankton on both the mesozooplankton standing stock and secondary production was significantly higher south of the STC (ANOVA, p<0.05, in both cases).
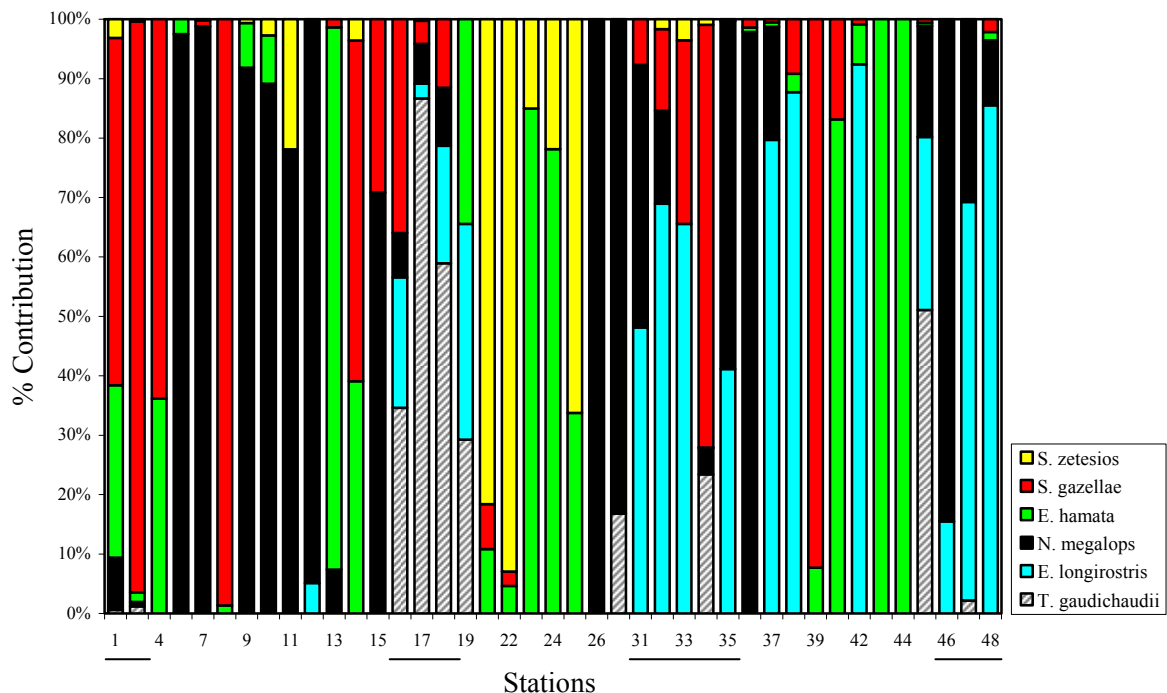
FIGURE 3.33 Percentage contribution of the numerically dominant species to total predation impact on the mesozooplankton standing stock and secondary production, per station, during the survey (April 2007). (Lines represent stations south of the Subtropical Convergence)

TABLE 3.6 Predation impacts of the numerically dominant carnivorous zooplankton species on the mesozooplankton standing stock and the secondary production of mesozooplankton, per station, within the Subtropical Convergence front in the Indian sector of the Southern Ocean.

Station Number	Mesozooplankton Biomass (mg Dwt 100m⁻³)		Food Consumption (mg Dwt 100m⁻³ d⁻¹)							% Mesozooplankton Consumed d⁻¹	
	Standing Stock	Secondary Production	*T. gaudichaudii*	*E. longirostris*	*N. megalops*	*E. hamata*	*S. gazellae*	*S. zetesios*	Total	Standing Stock	Secondary Production
1	176.74	8.84	0.01	0.00	0.08	0.26	0.53	0.03	0.91	0.52	10.30
2	176.47	8.82	0.00	0.00	0.00	0.01	0.34	0.00	0.35	0.20	4.00
4	208.97	10.45	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.01	0.13
6	281.90	14.09	0.00	0.00	0.25	0.01	0.00	0.00	0.26	0.09	1.83
7	172.95	8.65	0.00	0.00	0.79	0.00	0.01	0.00	0.80	0.46	9.26
8	79.92	4.00	0.00	0.00	0.00	0.00	0.09	0.00	0.09	0.11	2.28
9	131.52	6.58	0.00	0.00	0.34	0.03	0.00	0.00	0.37	0.28	5.65
10	198.13	9.91	0.00	0.00	0.07	0.01	0.00	0.00	0.08	0.04	0.76
11	420.44	21.02	0.00	0.00	0.06	0.00	0.00	0.02	0.08	0.02	0.39
12	282.84	14.14	0.00	0.04	0.69	0.00	0.00	0.00	0.73	0.26	5.16
13	132.19	6.61	0.00	0.00	0.02	0.19	0.00	0.00	0.20	0.15	3.10
14	98.50	4.92	0.00	0.00	0.00	0.01	0.01	0.00	0.02	0.02	0.34
15	89.22	4.46	0.00	0.00	0.17	0.00	0.07	0.00	0.24	0.27	5.31
16	1288.94	64.45	0.77	0.49	0.17	0.00	0.80	0.00	2.23	0.17	3.46
17	1203.94	60.20	15.93	0.46	1.22	0.00	0.71	0.05	18.38	1.53	30.54
18	266.36	13.32	0.82	0.28	0.14	0.00	0.16	0.00	1.39	0.52	10.45
19	97.58	4.88	0.14	0.17	0.00	0.16	0.00	0.00	0.48	0.49	9.76
21	189.49	9.47	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.02	0.36
22	153.42	7.67	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.13
23	85.16	4.26	0.00	0.00	0.00	0.14	0.00	0.02	0.16	0.19	3.81
24	327.82	16.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
25	257.88	12.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
26	861.16	43.06	0.00	0.00	0.03	0.00	0.00	0.00	0.03	0.00	0.07
30	735.23	36.76	0.19	0.00	0.92	0.00	0.00	0.00	1.10	0.15	3.00
31	2307.15	115.36	0.00	1.36	1.25	0.00	0.22	0.00	2.83	0.12	2.46
32	770.20	38.51	0.00	1.82	0.42	0.00	0.36	0.04	2.65	0.34	6.87
33	580.55	29.03	0.00	0.45	0.00	0.00	0.21	0.02	0.69	0.12	2.37
34	1531.12	76.56	0.31	0.00	0.06	0.00	0.93	0.01	1.31	0.09	1.72
35	637.18	31.86	0.00	0.72	1.03	0.00	0.00	0.00	1.76	0.28	5.51
36	979.36	48.97	0.00	0.00	0.24	0.00	0.00	0.00	0.24	0.02	0.49
37	1090.47	54.52	0.00	0.55	0.13	0.01	0.00	0.00	0.70	0.06	1.28
38	470.80	23.54	0.00	0.13	0.00	0.00	0.01	0.00	0.15	0.03	0.63
39	893.90	44.69	0.00	0.00	0.00	0.01	0.13	0.00	0.15	0.02	0.33
40	511.62	25.58	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.04
42	857.90	42.90	0.00	0.26	0.00	0.02	0.00	0.00	0.28	0.03	0.66
43	948.15	47.41	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.01
44	858.55	42.93	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.02
45	747.27	37.36	1.06	0.60	0.39	0.01	0.01	0.00	2.08	0.28	5.56
46	992.61	49.63	0.00	0.23	1.26	0.00	0.00	0.00	1.49	0.15	2.99
47	566.71	28.34	0.04	1.37	0.63	0.00	0.00	0.00	2.05	0.36	7.23
48	1220.96	61.05	0.00	1.70	0.22	0.03	0.04	0.00	1.99	0.16	3.25

CHAPTER FOUR

DISCUSSION

4.1   OCEANOGRAPHY

The Subtropical Convergence (STC) within the survey area was well defined with a drop in temperature of up to 6°C observed over ≈ 100 nautical miles. The observed temperature gradient is consistent with the published literature (Lutjeharms and Valentine 1984). The presence of the Agulhas Return Current (ARC) in the north eastern sector of the survey area was also in accordance with the published literature (Lutjeharms and Valentine 1984). The frontal system created a boundary between cold, Sub-Antarctic water in the south and warm, Subtropical water in the north. The establishment of the steep temperature gradient across the front has been demonstrated to represent an important biogeographic barrier to the distribution of plankton. (Froneman and Perissinotto 1996, Froneman *et al*. 1997, Pakhomov and Perissinotto 1997, Barange *et al*. 1998). However, meanders in the flow of the STC, either due to topographic steering or due to the interaction of the two water masses, as seen during this survey, contributes to cross frontal mixing (Lutjeharms and Valentine 1984, Lutjeharms *et al*. 1993). Additionally, the storm prior to the survey being conducted would have further contributed to the exchange of surface waters across the STC. These factors combined would likely have contributed to a highly complex hydrology within the region of investigation, which would have had a large influence on the biology of the region.

4.2   CHLOROPHYLL-A

Mean surface chlorophyll-*a* (chl-*a*) (0.23 ± 0.10mg m^{-3}) and integrated chl-*a* (21.14 ± 7.53mg m^{-2}) concentrations within the survey area fell within the lower range reported in the literature for the region of the STC during different seasons (Froneman and Perissinotto 1996, Pakhomov and Perissinotto 1997, Barange *et al*. 1998, Pakhomov *et al*. 2000, Froneman *et al*. 2000b, Llido *et al*. 2005). There was no evidence of elevated chl-*a* concentrations at those stations occupied in the immediate vicinity of the front, nor was there any significant spatial pattern evident to the north and south of the front (Fig 3.2). The absence of any biological enhancement in the vicinity of the front can likely be linked to the intense storm prior to the survey being conducted, which would have facilitated vertical movement/mixing of the water column. Although the temperature data indicated a strong presence of a frontal feature, the lack of a correlation between the chlorophyll data and the temperatures suggested that there might be a lag phase in the biological response to a disturbance within the water column. The increased turbulence generated by the storm

would have favoured the growth of picophytoplankton (< 2.0μm) within the survey area (Fogg 1991, Froneman *et al*. 1995). Smaller cells are able to respond faster to the re-stabilizing of the water column due to their favourable surface area: volume rations and their lower nutrient requirements (Fogg 1991). This result is in accordance with Llido *et al*. (2005) who suggested that the STC is associated with episodic bloom events, occurring mainly during spring and summer, but which are limited spatially and temporally which results in patchy production.

4.3   COMMUNITY STRUCTURE AND SPATIAL TRENDS

4.3.1   SPATIAL TRENDS

The mesozooplankton comprising mainly copepods, numerically and by biomass dominated the total zooplankton community within the region of investigation (Daly 2008). This result is consistent with numerous studies conducted in different sectors of the Southern Ocean, which have highlighted the importance of copepods in the plankton assemblages of the region with regard to the functioning of the ecosystem as well as their contribution to vertical carbon flux (Froneman and Perissinotto 1996, Pakhomov and Perissinotto 1997, Barange *et al*. 1998). The total mesozooplankton abundance (ranged from 13.12ind m^{-3} to 1028.40ind m^{-3}) and biomass (ranged from 0.80mg Dwt m^{-3} to 23.07mg Dwt m^{-3}) values obtained during this study were, however, lower than previously observed in the region of the Subtropical Convergence (STC) south of Africa and in the Atlantic Ocean (Froneman and Perissinotto 1996, Pakhomov and Perissinotto 1997, Barange *et al*. 1998, Froneman *et al*. 2000a). Again, in contrast to previous studies, there was no evidence of increased mesozooplankton abundance and biomass values at those stations occupied in the immediate vicinity of the front (Froneman and Perissinotto 1996, Pakhomov and Perissinotto 1997, Barange *et al*. 1998, Froneman *et al*. 2007). The absence of any peaks in the mesozooplankton abundance and biomass at those stations occupied in the region of the front has been suggested to be the result of the storm prior to the survey being conducted and the low food availability (mainly phytoplankton) within the study region (Daly 2008).

The contribution of carnivorous zooplankton to the total zooplankton abundance and biomass during the present study was generally <10% (range 2% to 12%). This result is in agreement with previous studies conducted in the Southern Ocean (Pakhomov *et al*. 1994, Pakhomov and Perissinotto 1997, Barange *et al*. 1998, Pakhomov *et al*. 1999). The estimates of the total carnivorous zooplankton abundance and biomass during this study were, however, lower than those reported by Pakhomov *et al*. (1994) and Pakhomov and Perissinotto (1997) for the region of the STC south of Africa. The reduced values obtained during this study may be due to seasonality,

which influences food availability, or the result of the underestimation of the carnivorous zooplankton community due to gear employed during the study. Many studies suggest that net avoidance is the main reason for the underestimation of the carnivorous zooplankton community due to their superior swimming abilities (Oresland 1987, Oresland 1990, Oresland 1995, Froneman *et al.* 1998, Pakhomov *et al.* 1999, Pakhomov *et al.* 2000, Froneman *et al.* 2000a, Froneman *et al.* 2002, Johnson and Terazaki 2004, Pakhomov and Froneman 2004a, Pakhomov and Froneman 2004b). During this survey the compounded effect of net avoidance and sampling technique (bongo net sampling restricted to the upper 300m) may have resulted in a significant underestimation of carnivorous zooplankton. Studies in the region of the STC which have employed a RMT-8 net generally recorded carnivorous zooplankton abundance values (ranges from 5.30 ± 5.7ind m^{-3} to 14.0 ± 10.7ind m^{-3}) ≈ 3 times higher than those where bongo nets (ranges from 2.24 ± 1.66ind m^{-3} to 4.39 ± 2.29ind m^{-3}) have been employed (Pakhomov *et al.* 1994, Pakhomov and Perissinotto 1997, Barange *et al.* 1998, Pakhomov *et al.* 1999, Pakhomov *et al.* 2000, Pakhomov and Froneman 2000, Froneman *et al.* 2000a, Pakhomov and Froneman 2004a, Pakhomov and Froneman 2004b, Lukác 2005). Although the chaetognath abundance and biomass values fell within the range reported for the region of the STC (Pakhomov *et al.* 1994, Froneman *et al.* 1998, Barange *et al.* 1998, Froneman and Pakhomov 1998, Pakhomov *et al.* 1999, Froneman *et al.* 2002, Pakhomov and Froneman 2004a, Pakhomov and Froneman 2004b, Lukác 2005), the underestimation of carnivorous zooplankton during this survey may also be due to the lack of gelatinous species contribution along with the low abundance and biomass values of amphipods and euphausiids.

There was no evidence of any enhancement in the abundance and biomass values of the total carnivorous zooplankton or indeed of the different taxa, at those stations occupied in the immediate vicinity of the STC (Fig 3.4). This result is in contrast to previous studies, which have shown that the frontal region is typically associated with increased levels of carnivorous zooplankton abundances and biomass (Pakhomov *et al.* 1994, Barange *et al.* 1998, Pakhomov *et al.* 1999, Pakhomov *et al.* 2000, Pakhomov and Froneman 2000, Froneman *et al.* 2000a, Mayzaud *et al.* 2002, Johnson and Terazaki 2004, Pakhomov and Froneman 2004a, Pakhomov and Froneman 2004b). A study conducted in parallel to this investigation showed that the mesozooplankton distribution demonstrated no significant spatial patterns (Daly 2008). Therefore, the absence of any carnivorous zooplankton enhancement can likely be attributed to the diffuse distribution of their preferred prey, mainly copepods, throughout the region of investigation.

The domination of the carnivorous zooplankton abundance by the chaetognaths and euphusiids during this study, is in accordance with previous studies within the different sectors of the Southern Ocean during different seasons (Froneman *et al.* 1998, Froneman and Pakhomov 1998,

Pakhomov *et al*. 1999). Both the euphausiids and the chaetognaths had significantly higher biomass values south of the frontal feature, which was mainly attributed to the presence of larger individuals within the respective populations. There are two possible explanations for this result; the first is related to the size of the individuals while the second is linked to phyla adaptability to water column mixing and turbulence. The former implies that larger individuals were able to maintain their position within the water column despite disturbances, thus explaining the presence of larger individuals south of the frontal feature particularly within the cold waters (stations 16 to18). According to Genin *et al*. (2005) and Gallager *et al*. (2004) increasing stratification of the water column decreases the turbulence velocity, allowing the congregation of zooplankton as their swimming speeds become greater than that of the flow velocity. They also state that larger zooplankton are capable of swimming independently of the local flow more often than smaller individuals as their swimming speeds are generally greater than the local turbulence or flow velocity. This would suggest that larger individuals during this survey were able to re-establish themselves within the disturbed water column faster than smaller individuals due to their superior swimming capabilities (Gallager *et al*. 2004, Genin *et al*. 2005).

The second scenario implies that these two taxonomic groups were able to respond faster to the stabilizing of the water column after disturbances than other groups, and thus were able to re-establish themselves within the water column (Tarling *et al*. 1995, Johnson and Terazaki 2004). According to Genin *et al*. (2005) and Gallager *et al*. (2004) aggregation of specific species of zooplankton or the transport of these individuals by the water flow is directly related to the swimming speed of the individual species. This suggests that both the euphausiids and the chaetognaths had swimming capabilities superior to all other groups within the survey. The ability to adapt to conditions of increased disturbances or the ability to respond faster to the re-stabilizing of a water column, adds to the point that these groups would be more successful in areas prone to storms.

4.3.2   SIZE STRUCTURE AND SEX RATIOS

The life history of amphipods within the Southern Ocean is not a well-studied phenomenon and therefore information of their reproductive strategies, sex ratios and breeding success is lacking. However, within this survey, numerically dominant amphipod species demonstrated sexual dimorphism with females being significantly larger than males. A notable exception was *Vibilia armata,* which displayed no sexual dimorphism. These results are in accordance with Boltovskoy (1999). Female size is linked to reproduction, where larger individuals are able to produce larger numbers of eggs and are therefore more fecund (Boltovskoy 1999). *Phronima sedentaria* is

interesting in that the females live within a "barrel" (which is a hollowed out salp) which they use as a breeding nest (Boltovskoy 1999). Females are therefore larger in order to maintain themselves and their "barrels" within the water column. As females were generally larger, it suggests that their ability to withstand environmental disturbances may be superior to the smaller males, with the exception of *Themisto gaudichaudii.* Within the amphipod species females were generally the dominant sex with the exception of *T. gaudichaudii* were males where the dominant sex. Due to the lack of a significant correlation with the physical and biological data, these findings were not explained by the tested environmental characteristics. The increased number of females within the amphipod population during this survey may have marked the end of the breeding season where the male mortality rate was higher than the females (Tarling 2003).

The reproductive strategies of the euphausiids are highly diverse and are not necessarily species specific (Siegel 2000). The euphausiids are unique in that they are able to adapt their reproductive strategies according to their ambient environment and are thus able to maximize their breeding success when conditions are favourable (Siegel 2000). The euphausiids during this survey were generally dominated by the females and demonstrated no sexual dimorphism. This result is in accordance with Boltovskoy (1999) and Siegel (2000). According to Tarling (2003) female euphausiids require more energy due to the high energy cost of egg production. As a result females tend to congregate in the surface waters where maximum food availability occurs. Males on the other hand are generally recorded at deeper depths (Tarling 2003). The predominance of females among the euphausiid samples may therefore reflect the spatial variations in the distribution of male and female euphausiids within the region.

Few studies have considered the life history strategies and population dynamics of chaetognaths within the Southern Ocean. The size structure and the percentage contribution of individuals to each stage of maturity within this chaetognath community is, however, in accordance with previous studies on chaetognaths in the Southern Ocean (Oresland 1987, Oresland 1990, Oresland 1995, Johnson and Terazaki 2004, Lukác 2005). On the whole the chaetognath population was dominated by immature individuals throughout the study area. The high contribution of immature individuals within the chaetognath population during this survey suggests that breeding took place during summer. However, a number of studies suggest that chaetognaths breed at low rates throughout the year with increased breeding rates under favourable conditions thus maintaining the high contribution of juveniles in the population year round (Oresland 1987, Oresland 1990, Oresland 1995, Johnson and Terazaki 2004).

Other explanations for the high contribution of immature individuals to the chaetognath population within this study are related to size distribution within the water column and survival rate of larger individuals. Some studies suggest that larger or mature individuals congregate at greater depths (>500m) than smaller or immature individuals (Feigenbaum and Maris 1984, Oresland 1987, Oresland 1990, Oresland 1995, Johnson and Terazaki 2004, Tomczak *et al.* 2004, Lukác 2005). The sampling protocol employed during this survey may thus have under-sampled the larger individuals as sampling never exceeded 300m (Johnson and Terazaki 2004). The low contribution of larger and therefore mature individuals to the chaetognath population may be due to higher mortality rates than immature individuals due to increased predation by other chaetognaths and fish (Oresland 1987, Oresland 1990, Pakhomov *et al.* 1994, Oresland 1995, Johnson and Terazaki 2004).

4.3.3 COMMUNITY STRUCTURE

Numerical analysis identified three distinct zooplankton groupings (designated Groups 1 to 3) within the survey area (Fig 3.30). Of the three groups identified, Group 1, consisted of a single station (Station 5), and was therefore, regarded as an outlier. Groups 2 and 3 comprised stations located to the north and south of the STC, which suggests that the STC did not act as a biogeographical barrier to the distribution of carnivorous zooplankton during the present study. This result was consistent with the findings of a parallel study which showed that the front did not act as a barrier to the distribution of mesozooplankton (Daly 2008). Results of the SIMPER analysis indicated that the distinction of the two groupings could be associated with changes in the contribution of the numerically dominant species rather than the presence or absence of individual species (Table 3.4). A further indication that the STC did not act as a biogeographical barrier was the presence of several euphausiid species, Sub-Antarctic in origin (*Euphausia superba* and *E. spinifera*), being recorded in the waters north of the front. Similarly several Subtropical species (*E. longirostris, E. similis* and *Nematoscelis megalops*), were also recorded south of the frontal feature. Further evidence to suggest the inefficiency of the STC as a biogeographical barrier was provided by the BIO-ENV analysis, which suggested that temperature and salinity combined accounted for less than 20% of the observed groupings. The main findings of the numerical analysis during this investigation is in contrast to previous studies which identified the STC as an important biogeographical barrier to the distribution of plankton (Deacon 1982, Pakhomov *et al.* 1994, Froneman and Perissinotto 1996, Froneman *et al.* 1997, Pakhomov and Perissinotto 1997, Pakhomov *et al.* 1999, Perissinotto *et al.* 2001, Froneman *et al.* 2007).

Several possible factors may have contributed to the STC not acting as a biogeographical barrier to the distribution of carnivorous zooplankton during this study. The intense storm one week prior to the survey may have facilitated the transfer of surface waters across the frontal region. Additionally, it is well documented that the intensity of the STC demonstrates a high degree of latitudinal variability (Lutjeharms 1985, Butler *et al*. 1992, Lutjeharms *et al*. 1993, Johnson and Terazaki 2004, Tomczak *et al*. 2004) so that within the mid-oceans the biogeographical barrier may be intermittent or weak resulting in the increased distributions of species (Lutjeharms *et al*. 1993, Tomczak *et al*. 2004).

4.4   FEEDING RATES AND PREDATION IMPACT

4.4.1   CHAETOGNATHS

Results of gut content analyses indicated that copepods were the most important prey item consumed by the chaetognaths, *E. hamata*, *S. gazellae* and *S. zetesios* (Fig 3.32). This result is consistent with the published literature which has demonstrated that chaetognaths can be regarded as non-selective predators generally consuming the most abundant prey, mainly copepods (Oresland 1995, Froneman *et al*. 1998, Lukác 2005). Cannibalism has been documented for a number of chaetognath species (Oresland 1987, Oresland 1990, Froneman *et al*. 1998, Froneman and Pakhomov 1998, Froneman *et al*. 2002, Johnson and Terazaki 2004). The low frequency of occurrence (<10% of all prey identified) of chaetognaths in the gut contents of selected chaetognaths during this investigation, suggests that cannibalism by chaetognaths did not represent an important source of mortality for the chaetognaths. In contrast to previous studies conducted both in the high Antarctic (Oresland 1990) and in the Sub-Antarctic regions of the Southern Ocean (Froneman and Pakhomov 1998, Froneman *et al* 1998), no oil droplets were recorded in the guts of the three chaetognath species (Fig 3.32). Oresland (1990) suggested that oil droplets in the guts of chaetognaths might function as a buoyancy mechanism or as energy reserve to cope with the high seasonal variability in food availability within the high Antarctic region. The absence of oil droplets in the guts of the chaetognaths may therefore reflect the lack of any seasonal pattern in food availability in the region of investigation. It is worth noting that the study by Daly (2008) demonstrated that the total mesozooplankton abundance and biomass during the present study was in range reported in the region of the STC during different seasons.

According to Feigenbaum and Maris (1984) and Johnson and Terazaki (2004), feeding success and predation impact of chaetognaths is largely determined by prey encounters. The estimates of mesozooplankton abundance and biomass during this survey were approximately 10%

to 20% lower than those recorded by Froneman and Pakhomov (1998) in the vicinity of the Prince Edward Islands, and Lukác (2005) in the Polar Frontal Zone. Despite the reduced prey availability, the mean number of prey (NPC) and daily feeding rates (Fr) of the chaetognaths, *E. hamata* and *S. gazellae*, during this study were higher than those found by Froneman *et al*. (1998), Froneman and Pakhomov (1998) and Lukác (2005) in the Polar Frontal Zone of the Southern Ocean during the same season. The feeding rates recorded during this study can likely be attributed to an average water temperature during the survey being higher ($\approx 2°C$ higher) than previous studies which have shown that chaetognath feeding rates are positively correlated to seawater temperature (Oresland 1987, Oresland 1990, Oresland 1995, Gurney *et al*. 2002).

The predation impact of selected chaetognaths on mesozooplankton abundances and biomass during this study was estimated employing two different techniques, the gut content analyses approach and the daily ration values published in the literature. For both *E. hamata* and *S. zetesios*, the predation impact estimated using published daily ration data far exceeded that obtained using the gut content analysis approach. On the other hand, the estimates of mesozooplankton standing stock and secondary production removed by *S. gazellae*, employing the gut content analysis approach, was ≈ 2 times higher than those obtained using daily ration values. The discrepancy in the results obtained using the different approaches highlights the need for survey specific studies to be conducted on selected taxa as the feeding rates of chaetognaths vary according to, amongst others, seawater temperature, prey availability, reproductive status and condition (Feigenbaum and Maris 1984, Oresland 1987, Oresland 1990, Oresland 1995, Froneman *et al*. 1998, Froneman and Pakhomov 1998, Froneman *et al*. 2002, Johnson and Terazaki 2004)

4.4.2 TOTAL CARNIVOROUS ZOOPLANKTON

The estimated predation impact of the carnivorous zooplankton on the mesozooplankton during this survey (0.01 – 18.38mg Dwt 100m^{-3}d^{-1}) fell within the range reported by Pakhomov *et al*. (1999), during austral summer, in the Atlantic sector of the Southern Ocean (2.33 – 48.33mg Dwt 100m^{-3}d^{-1}) and a study by Froneman *et al*. (2002), during austral winter, in the vicinity of the Prince Edward Archipelago (0.27 – 36.37mg Dwt 100m^{-3}d^{-1}). Among the various groups, the chaetognaths and the euphausiids were generally identified as the most important consumers of mesozooplankton (Fig 3.33 & Table 3.6). This result is consistent with the published literature and highlights the importance of these organisms as predators of mesozooplankton in the Southern Ocean (Pakhomov *et al*. 1994, Oresland 1995, Froneman *et al*. 1998, Barange *et al*. 1998, Froneman and Pakhomov 1998, Pakhomov *et al*. 1999, Froneman *et al*. 2000a, Gurney *et al*. 2002, Froneman *et al*. 2002, Pakhomov and Froneman 2004a, Pakhomov and Froneman 2004b). It is

worth noting that the amphipod, *Themisto gaudichaudii*, was on two occasions (Stations 16 and 18) identified as the dominant consumer of mesozooplankton biomass and secondary production (Table 3.6). The observed pattern could be related to the fact that *T. gaudichaudii* has been demonstrated to swarm which coincides with localised elevated densities of the amphipods. Thus, during swarming events, the predation impact of amphipods on the mesozooplankton standing stock, and particularly the secondary production, may be increased when mesozooplankton productivity is low as was observed in this survey (Gibbons 1997, Froneman *et al*. 2000b).

The estimates of predation impact of the carnivorous zooplankton on the mesozooplankton should be viewed with caution, as there are several potential sources of error. Firstly, there may have been an underestimation of the abundances of the euphausiids, due to net avoidance. Secondly, the study was restricted to the upper 300m of the water column which may have further contributed to the underestimation of larger zooplankton abundance and biomass (Johnson and Terazaki 2004). Lastly, the use of published daily rations, which demonstrate a high degree of variability reflecting amongst other, the influence of temperature, prey availability and the condition of individual species may have also introduced errors in the estimation of feeding impacts of the carnivorous zooplankton on the mesozooplankton (Dilling and Alldredge 1993, Froneman *et al*. 1998, Froneman *et al*. 2000a, Froneman *et al*. 2000b, Gurney *et al*. 2002). Despite these potential sources of error, the present data provides some insight into the ecological importance of carnivorous zooplankton as consumers of mesozooplankton within the region of investigation.

CHAPTER FIVE

CONCLUSION

During this survey the Subtropical Convergence (STC) was well defined and the water masses of cold Sub-Antarctic water to the south and the warmer Subtropical water to the north were clearly evident. The Agulhas Return Current was also observed and the influence of this current on the hydrodynamics of the STC was evident in the presence of a meander in the front. Despite the well-defined front, the STC did appear not to act as an effective biogeographical barrier to the distribution of the carnivorous zooplankton. This result is in agreement with a study conducted in parallel to this investigation by Daly (2008). The inability of the front to limit the distribution of the zooplankton can likely be due to three factors.

The first is linked to the horizontal mixing of the water column generated by a storm prior to the study. Water column disturbances, or increased turbulence, intensify mixing within a water column which increases the variability in zooplankton distribution, creating a more homogenised distribution of the carnivorous zooplankton within the survey area (Sullivan *et al*. 1993, Tarling *et al*. 1995, Barange *et al*. 1998, Gallager *et al*. 2004, Genin *et al*. 2005). Although the water column may have re-established there may be a lag phase in the response of the biology so that during sampling, the carnivorous zooplankton distribution would have been highly variable. The second explanation relates to the variability of the front's hydrodynamics. Within this area of investigation, the STC is highly influenced by the Agulhas Return Current and the reduction in water velocity which results in the meandering of the front, contributing to increase cross frontal mixing (Lutjeharms and Valentine 1984, Lutjeharms 1985, Butler *et al*. 1992, Lutjeharms *et al*. 1993, Lutjeharms *et al*. 2001, Tomczak *et al*. 2004). These interactions also influence the distribution of zooplankton as it allows for the movement of zooplankton species, which may be restricted by specific water masses, across fronts. The third explanation suggests that the area sampled may have been more of a transition zone between the different water masses rather than the sampling of two distinct water masses north and south of the STC. This is due to the distribution of specific euphausiid species (*Euphausia superba*, *E. spinifera*, *E. longirostris, E. similis* and *Nematoscelis megalops*), which are suggested to be indicator species of the Subtropical and sub-Antarctic water masses (Gibbons 1997), occurring throughout the sampling area and not restricted to the specific water masses north and south of the frontal feature. It could therefore be said that within areas were the STC has increased hydrodynamic variability, which allows for the mixing of the different water masses, its effectiveness as a biogeographical barrier is inconsistent.

The total abundance and biomass values of the carnivorous zooplankton during this study were lower than the observed values in previous studies within the STC south of Africa (Pakhomov *et al*. 1994, Barange *et al*. 1998, Pakhomov *et al*. 1999, Pakhomov and Froneman 2000, Froneman *et al*. 2000a). The low abundance and biomass levels may be attributed to a number of factors. The first may be linked to the low availability of food resources, mainly mesozooplankton, within the area. The lower values may be attributed to seasonality in reproduction as evident from the low contribution of juveniles to the total counts with the exception of the chaetognaths. Alternatively, the reduced values could be attributed to net avoidance, particularly by larger individuals. Net avoidance is a common phenomenon within the zooplankton community and contributes substantially to the underestimation of zooplankton abundance and biomass values (Oresland 1990, Pakhomov *et al*. 1994, Froneman *et al*. 1998, Pakhomov *et al*. 1999, Gurney *et al*. 2002, Froneman *et al*. 2002). Lastly, the sampling strategy employed may also contribute to the underestimation of zooplankton communities, as bongo net sampling was restricted to the upper 300m of the water column.

The absence of enhanced abundance and biomass values at those stations occupied in the region of the front, during the study, is in contrast to previous studies conducted within the STC south of Africa and in the Atlantic sector of the Southern Ocean (Pakhomov *et al*. 1994, Pakhomov and Perissinotto 1997, Pakhomov *et al*. 1999, Mayzaud *et al*. 2002, Pakhomov and Froneman 2004a, Pakhomov and Froneman 2004b). The absence of biological enhancement at the front substantiates the findings of Froneman and Perissinotto (1996) and Llido *et al*. (2005) who suggest that the STC is associated with patchy productivity which is not necessarily linked to seasonal changes.

The carnivorous zooplankton community during this survey generally accounted for <10%, (range 2% to 12%) of the total zooplankton community, which is in accordance with previous studies on zooplankton communities within the Southern Ocean, during different seasons (Pakhomov *et al*. 1994, Barange *et al*. 1998, Pakhomov *et al*. 1999, Pakhomov *et al*. 2000, Pakhomov and Froneman 2000, Pakhomov and Froneman 2004a, Pakhomov and Froneman 2004b, Lukác 2005). The carnivorous zooplankton community during this study consisted mainly of chaetognaths and euphausiids, which was also consistent with previous studies (Pakhomov *et al*. 1994, Barange *et al*. 1998, Pakhomov *et al*. 1999, Pakhomov *et al*. 2000, Pakhomov and Froneman 2000, Pakhomov and Froneman 2004a, Pakhomov and Froneman 2004b, Lukác 2005). The homogenous distribution, or wide spread distribution, of these two groups within the Southern Ocean, substantiates that they are highly adaptable, as those species that are able to tolerate a wide

variety of environmental conditions would naturally be more successful, particularly within an environment that is highly dynamic as found within this study.

The intensity of feeding, and therefore predation impact of the carnivorous zooplankton, is highly dependant on prey encounters. Areas of increased food availability (zooplankton) provide favourable conditions for prey encounters which would result in an increase in predation (Feigenbaum and Maris 1984, Barange *et al*. 1991, Pakhomov *et al*. 1994, Oresland 1995, Froneman *et al*. 1998, Barange *et al*. 1998, Froneman and Pakhomov 1998, Pakhomov *et al*. 1999, Froneman *et al*. 2000b, Froneman *et al*. 2002, Johnson and Terazaki 2004). During this study, the combined predation impact of carnivorous zooplankton was low as prey encounters would have been low due to low food availability. Exceptions to this, however, did occur at three stations south of the frontal feature where the samples were dominated by the amphipod *Themisto gaudichaudii*. The low predation impact, however, may also be due to a combination of low abundance values of carnivorous zooplankton, as a result of net avoidance, and the use of published daily rations, which in themselves are highly variable. Regardless of this, productivity and feeding by zooplankton affect the efficiency of the biological pump functioning and determine whether or not fronts, like the STC, are important to carbon sequestration (Longhurst and Harrison 1989, Longhurst 1991, Fogg 1991, Froneman *et al*. 2000a, Froneman *et al*. 2002, Falkowski 2003). The generally low predation impact of the carnivorous zooplankton on the mesozooplankton during this study suggests that these organisms would have contributed little to vertical carbon flux. It is worth noting that a study conducted in parallel to this study indicated that grazing impact of the herbivorous zooplankton on phytoplankton accounted for <5% of the standing stock (Daly 2008). As a consequence one could assume that the zooplankton mediated vertical carbon flux within the region was low contributing to an inefficient biological pump.

Further research within in this area is essential. Undertaking studies that would examine the seasonality in productivity, or the lack there of, is vital to the understanding of the biological pump and it effectiveness in the drawdown of atmospheric carbon, especially when solutions to slow the rate of global warming are ineffective. Studies determining whether the STC is in fact an effective biogeographical barrier, particularly within the mid-oceans are also important in understanding the spatial distributions of species and the potential ocean warming or cooling. A complete understanding of the reproductive strategies of the pelagic zooplankton, particularly within a highly unpredictable environment such as this one, is also necessary to fully understand their contribution to the Southern Ocean ecosystem.

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APPENDIX

APPENDIX 1. Average carnivorous zooplankton abundance and biomass at selected stations within the survey area during April 2007. (Values in brackets represent standard deviation)

Station Number	Location		Total Average Abundance (n = 5) (ind 100m^{-3})		Total Average Biomass (n = 5) (mg Dwt 100m^{-3})	
1	38.00°E	42.00°S	1.29	(± 2.21)	3.39	(± 5.43)
2	38.00°E	41.50°S	0.91	(± 1.73)	0.90	(± 1.96)
3	38.00°E	41.00°S	0.00	(± 0.00)	0.00	(± 0.00)
4	37.95°E	40.51°S	0.39	(± 0.48)	0.27	(± 0.47)
5	38.00°E	39.99°S	0.42	(± 0.82)	0.15	(± 0.27)
6	37.99°E	39.46°S	0.78	(± 0.70)	0.74	(± 1.52)
7	38.00°E	38.96°S	2.00	(± 2.57)	2.92	(± 5.92)
8	38.00°E	38.49°S	0.60	(± 0.99)	0.83	(± 0.93)
9	38.00°E	38.00°S	1.00	(± 1.14)	1.20	(± 1.99)
10	38.75°E	38.00°S	1.92	(± 1.86)	1.74	(± 2.58)
11	38.76°E	38.50°S	1.11	(± 0.56)	2.05	(± 2.09)
12	38.75°E	39.00°S	1.82	(± 3.17)	4.19	(± 5.67)
13	38.75°E	39.50°S	1.40	(± 2.30)	0.79	(± 1.37)
14	38.75°E	40.00°S	0.70	(± 1.28)	0.08	(± 0.12)
15	38.75°E	40.50°S	0.61	(± 0.61)	0.64	(± 0.91)
16	38.75°E	41.00°S	3.66	(± 6.20)	22.34	(± 42.20)
17	38.76°E	41.50°S	5.36	(± 6.47)	21.57	(± 29.09)
18	38.75°E	42.00°S	2.31	(± 3.93)	7.31	(± 13.27)
19	39.50°E	42.00°S	0.75	(± 0.91)	2.25	(± 3.03)
20	39.50°E	41.50°S	0.00	(± 0.00)	0.00	(± 0.00)
21	39.50°E	41.00°S	1.41	(± 1.71)	1.83	(± 2.89)
22	39.50°E	40.51°S	0.28	(± 0.62)	0.10	(± 0.22)
23	39.50°E	40.00°S	0.39	(± 0.77)	1.60	(± 2.21)
24	39.50°E	39.50°S	1.09	(± 1.58)	1.20	(± 2.02)
25	40.25°E	39.50°S	1.00	(± 0.93)	1.89	(± 2.04)
26	40.25°E	40.00°S	1.30	(± 2.15)	4.76	(± 7.20)
27	40.25°E	40.50°S	0.00	(± 0.00)	0.00	(± 0.00)
28	40.25°E	41.00°S	0.00	(± 0.00)	0.00	(± 0.00)
29	40.25°E	41.50°S	0.00	(± 0.00)	0.00	(± 0.00)
30	40.24°E	42.00°S	2.46	(± 5.10)	7.65	(± 13.54
31	40.25°E	42.50°S	2.16	(± 3.53)	6.20	(± 12.37)
32	40.25°E	43.00°S	2.21	(± 3.38)	6.08	(± 9.91)
33	41.00°E	43.00°S	1.70	(± 2.98)	1.42	(± 1.96)
34	41.00°E	42.50°S	0.65	(± 1.12)	2.87	(± 5.31)
35	41.00°E	42.00°S	1.42	(± 2.83)	4.68	(± 10.11)
36	41.00°E	41.50°S	0.46	(± 0.68)	0.62	(± 1.34)
37	41.00°E	41.00°S	1.22	(± 1.85)	2.69	(± 4.52)
38	41.00°E	40.50°S	0.43	(± 0.51)	2.22	(± 3.29)
39	41.00°E	40.00°S	0.96	(± 2.15)	0.37	(± 0.83)
40	41.00°E	39.49°S	0.50	(± 0.79)	2.28	(± 4.51)
41	41.75°E	39.50°S	0.74	(± 0.60)	3.28	(± 3.27)
42	41.75°E	40.00°S	1.38	(± 1.59)	2.35	(± 3.68)
43	41.75°E	40.50°S	0.38	(± 0.53)	0.83	(± 1.68)
44	41.75°E	41.00°S	0.36	(± 0.79)	0.04	(± 0.08)
45	41.75°E	41.50°S	0.94	(± 0.88)	3.62	(± 4.81)
46	41.75°E	42.00°S	1.21	(± 2.54)	4.78	(± 9.97)
47	41.75°E	42.50°S	1.39	(± 2.63)	4.97	(± 8.14)
48	41.75°E	43.00°S	2.11	(± 2.83)	4.72	(± 9.76)

APPENDIX 2. Total chaetognath abundance (ind 100m^{-3}) and biomass (mg Dwt 100m^{-3}) per species at selected stations within the survey area during April 2007.

Station Number	Eukrohnia hamata		Sagitta gazellae		Sagitta zetesios		Sagitta maxima	
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
1	1.86	4.40	2.48	6.65	0.80	1.44	0.00	0.00
2	0.80	0.10	2.66	4.24	0.53	0.07	0.00	0.00
3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	0.47	0.08	0.42	0.11	0.00	0.00	0.00	0.00
5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.94	0.11	0.00	0.00	0.00	0.00	0.00	0.00
7	0.00	0.00	1.98	0.10	0.66	0.08	0.00	0.00
8	0.17	0.02	2.19	1.12	0.00	0.00	0.00	0.00
9	0.56	0.46	0.00	0.00	1.94	0.12	0.00	0.00
10	2.26	0.10	0.00	0.00	1.70	0.10	0.00	0.00
11	0.00	0.00	0.00	0.00	1.75	0.89	0.00	0.00
12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
13	4.27	3.11	0.78	0.03	0.00	0.00	0.39	0.05
14	1.34	0.11	1.34	0.12	0.27	0.03	0.00	0.00
15	0.00	0.00	1.41	0.86	0.00	0.00	0.00	0.00
16	0.00	0.00	1.68	10.03	0.00	0.00	0.00	0.00
17	0.00	0.00	1.44	8.92	1.44	2.48	0.00	0.00
18	0.00	0.00	1.21	2.00	0.00	0.00	0.00	0.00
19	2.09	2.73	0.00	0.00	0.00	0.00	0.00	0.00
20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
21	1.36	0.06	0.54	0.03	1.09	1.41	0.00	0.00
22	0.15	0.01	0.15	0.00	0.77	0.47	0.31	0.02
23	1.09	2.30	0.00	0.00	0.68	1.22	0.00	0.00
24	0.63	0.05	0.00	0.00	0.63	0.04	0.00	0.00
25	0.42	0.02	0.00	0.00	1.06	0.11	0.00	0.00
26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
31	0.00	0.00	2.07	2.72	0.00	0.00	0.00	0.00
32	0.00	0.00	1.84	4.53	1.15	2.20	0.00	0.00
33	0.00	0.00	4.45	2.66	2.43	1.23	0.00	0.00
34	0.22	0.02	2.20	11.68	0.22	0.61	0.00	0.00
35	0.12	0.04	0.24	0.05	0.00	0.00	0.00	0.00
36	0.76	0.03	0.76	0.04	0.00	0.00	0.00	0.00
37	0.95	0.08	0.38	0.05	0.00	0.00	0.00	0.00
38	0.89	0.08	0.18	0.17	0.00	0.00	0.00	0.00
39	2.14	0.19	2.67	1.68	0.00	0.00	0.00	0.00
40	1.56	0.14	0.31	0.02	0.00	0.00	0.00	0.00
41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
42	3.06	0.32	0.51	0.03	0.00	0.00	0.00	0.00
43	1.28	0.11	0.00	0.00	0.00	0.00	0.00	0.00
44	1.78	0.18	0.00	0.00	0.00	0.00	0.00	0.00
45	1.10	0.18	0.28	0.16	0.00	0.00	0.00	0.00
46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
48	2.04	0.47	2.04	0.53	0.00	0.00	0.00	0.00