Community structure and predation impact of carnivorous macrozooplankton in the Polar Frontal Zone (Southern Ocean), with particular reference to chaetognaths

by

Danica Lukáč

Submitted in fulfillment of the requirements for the degree of

Masters of Science at Rhodes University

Supervisors:

Professor P.W. Froneman

&

Professor C.D. McQuaid

December 2005

Contents

List of Figures

Chapter 1 – Introduction

Chapter 2 – Materials and methods

Chapter 3 – Results

Figure 3.14. Dendogram of cluster analysis comparing the zooplankton abundance of selected carnivorous macrozooplankton at each RMT-8 station occupied during the survey. Stations in group 1 were located south-east of the frontal feature, stations in group 2 were located north-west of the feature and stations in group 3 were located within/in the vicinity of the frontal feature. The dashed line represents the cut-off level used to delimit assemblages.

Figure 3.15. Position of the RMT-8 sampling stations occupied during late austral summer (April/May) 2004. Groups identified by cluster analysis have been circled. The diagonal lines indicate the position of the frontal feature (combined Subantarctic and Antarctic Polar Fronts).

Figure 3.16. Dendogram of cluster analysis comparing the zooplankton abundance of selected carnivorous macrozooplankton at each Bongo station occupied during the survey. Group 1 (station 242) was located within the frontal feature. The remaining stations were located throughout the survey area. The dashed line represents the cut-off level used to delimit assemblages.

Figure 3.17. Dendogram of cluster analysis comparing the zooplankton abundance of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2005. Group 1: all stations located inside eddy; Group 2: nine stations in the Polar Frontal Zone, three stations at eddy edge, two stations in Antarctic Surface Water; Group 3: five stations at eddy edge, three stations in the Polar Frontal Zone. Groups 4 and 5 were omitted from the analysis. The dashed line represents the cut-off level used to delimit assemblages.

Figure 3.18. Dendogram of cluster analysis comparing the zooplankton biomass of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2001. Stations in blocks were located in the Subantarctic Surface Water. The remaining stations were located in the Polar Frontal Zone. The dashed line represents the cut-off level used to delimit assemblages.

Figure 3.19. Dendogram of cluster analysis comparing the zooplankton biomass of selected carnivorous macrozooplankton at RMT-8 net stations occupied in he vicinity of the Prince Edward Islands during late austral summer (April/May) 2004. The dashed line represents the cut-off level used to delimit assemblages.

Figure 3.20. Dendogram of cluster analysis comparing the zooplankton biomass of selected carnivorous macrozooplankton at bongo stations occupied in he vicinity of the Prince Edward Islands during late austral summer (April/May) 2004. The dashed line represents the cut-off level used to delimit assemblages.

Figure 3.21. Dendogram of cluster analysis comparing the zooplankton biomass of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2005. The dashed line represents the cut-off level used to delimit assemblages.

Figure 3.33. Population structure of *Sagitta gazellae* in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005.

Figure 3.34. Population structure of *Eukrohnia hamata* at the eddy edge of an eddy observed in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005.

Figure 3.35. Population structure of *Eukrohnia hamata* in the Antarctic Surface Water in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005.

Figure 3.36. Population structure of *Eukrohnia hamata* in the Subantarctic Surface Water in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005.

Figure 3.37. Proportions of maturity stages of *Eukrohnia hamata* in the Polar Frontal Zone, Antarctic Surface water and eddy edge occurring in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005. Bars indicate standard deviation.

List of Tables

Chapter 1 – Introduction

Chapter 2 – Materials and methods

Chapter 3 – Results

Table 3.7. Composition and average biomass (mg wwt m-3) of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2005. Groupings were identified with cluster analysis.

Table 3.8. Predation impact of carnivorous macrozooplankton at selected stations occupied during the survey conducted in the surrounding waters if the Prince Edward Islands in late austral summer (April/May) 2001 Mesozooplankton data were obtained from Bernard and Froneman (2002).

Table 3.9. Predation impact of carnivorous macrozooplankton at selected stations occupied during the survey conducted in the waters surrounding the Prince Edward Islands in late austral summer (April/May) 2004. Mesozooplankton data were obtained from Bernard and Froneman (2004).

Table 3.10. Predation impact of carnivorous macrozooplankton at selected stations occupied during the survey conducted in the surrounding water of the Prince Edward Islands in late austral summer (April/May) 2005. Mesozooplankton data were obtained from Bernard and Froneman (2005).

Table 3.11. Abundance (ind. m^{-3}) and biomass (mg wwt m^{-3}) of selected chaetognath species at stations occupied in the waters surrounding the Prince Edward Islands during late austral summer (April/May) 2001.

Table 3.12. Abundance (ind. m^{-3}) and biomass (mg wwt m^{-3}) of selected chaetognath species at stations occupied in the waters surrounding the Prince Edward Islands during late austral summer (April/May) 2004. Only data obtained from bongo nets are represented here.

Table 3.13. Abundance (ind. m^{-3}) and biomass (mg wwt m^{-3}) of selected chaetognath species at stations occupied in the waters surrounding the Prince Edward Islands during late austral summer (April/May) 2005.

Table 3.14. Gut contents (% contribution by number) of *Eukrohnia hamata* and *Sagitta gazellae* in the waters surrounding the Prince Edward Islands during the late austral summers (April/May) of 2001, 2004 and 2005. Digits in italics represent the number of chaetognath guts inspected, “n” is the number of chaetognaths with food items in their guts.

Table 3.15. Mean number of prey (NPC), daily feeding rate (Fr), number of copepods consumed (m^{-3} d^{-1}) and predation impact of two chaetognath species on mesozooplankton standing stock during the survey conducted in the waters surrounding the Prince Edward Islands in late austral summer (April/May) 2001.

Table 3.16. Mean number of prey (NPC), daily feeding rate (Fr), number of copepods consumed ($m^{-3}\ d^{-1}$) and predation impact of two chaetognath species on mesozooplankton standing stock during the survey conducted in the waters surrounding the Prince Edward Islands in late austral summer (April/May) 2004.

Table 3.17. Mean number of prey (NPC), daily feeding rate (Fr), number of copepods consumed ($m^{-3}\ d^{-1}$) and predation impact of two chaetognath species on mesozooplankton standing stock during the survey conducted in the waters surrounding the Prince Edward Islands in late austral summer (April/May) 2005.

Appendix

List of Tables

Acknowledgements

My most sincere thanks goes to William Froneman who not only came up with the idea for this research, who gave advice on how to proceed with the work and helped with identifying species that were totally new to me, but who also introduced me to a life at sea and gave me constant encouragement throughout these last two years. William, thank you for your patience and for the many times you had to explain the concepts of fronts meandering, converting m^2 to m^3, working out predation impacts and countless other things that boggled my mind.

Two other people deserve much thanks. Firstly, Christopher McQuaid for providing insight and reading the final manuscript, and for giving both scientific advice and life-long knowledge. Christopher, thank you for always gently nudging me to expect better of myself, to ask questions and to learn more. Secondly, Martin Villet without whose statistical expertise this work would not have been completed. Martin, thank you for your tremendous patience in explaining and re-explaining the basics of statistics.

I also need to thank Isabelle Ansorge, the Chief-Scientist during the 2004 cruise, and her UCT team for the collection of oceanographic data. Thanks is also due to the students of both Rhodes and UCT who made my 2004 cruise a memorable and enjoyable one, and the officers and crew of the *SA Agulhas* who contributed towards a save and pleasant trip.

Finally, the greatest thanks are for my family who let me have two more years of student life. Mum and dad, I am so grateful for your support, both financial and emotional. Stan and Mands, thank you for giving me time and space. Then, more thanks than I could ever write on a page, to my best friend, Louise Lange, for constant and steady support especially when times got tough, for talking and/or complaining about our masters work, for sharing office space, for many mugs of coffee, and definitely for hours of laughing and dancing. Lastly, to someone who has only been part of the process in the last three months but who made the final haul so much easier, I am grateful to Christopher Marlin

for support, constant encouragement and his excitement towards my work. Thank you, my babe.

The Department of Environmental Affairs and Tourism (DEAT) and the National Research Foundation (NRF) provided funding for this project. Thank you.

Abstract

The community structure and predation impact of carnivorous macrozooplankton (>2 cm; chaetognaths, medusae, ctenophores and mysids), with particular emphasis on the chaetognaths *Eukrohnia hamata* and *Sagitta gazellae*, were investigated during three surveys conducted in late austral summer (April/May) of 2001, 2004 and 2005 in the Polar Frontal Zone in the vicinity of the Prince Edward Islands (46º45'S, 37º50'E), Southern Ocean. The 2001 survey formed part of the Marion Offshore Variability Ecosystem Study (MOVES II), while the 2004 and 2005 surveys formed part of the Dynamics of Eddy Impacts on Marion's Ecosystem study (DEIMEC III and IV respectively). Macrozooplankton samples were collected using WP-2, RMT-8 and Bongo nets. Results of the hydrographic survey indicated that the region of investigation, the Polar Frontal Zone (PFZ), is an area of high mesoscale variability. During the 2004 survey the Antarctic Polar Front (APF) and the Subantarctic Front (SAF) merged to form an intense frontal feature with subsurface temperature and salinity ranging from 8.5-7.5ºC and 34.15-33.88, respectively. A cyclonic cold core eddy, believed to have been spawned from the APF, was observed during the 2005 survey. Macrozooplankton abundance and biomass ranged from 0 to 43.731 ind. m^{-3}, and from 0 to 41.55 mg wwt m^{-3} respectively, during the three surveys. Among the carnivorous macrozooplankton, chaetognaths (*Eukrohnia hamata* and *Sagitta gazellae*) were most prominent, contributing up to 85% of the total biomass during all three surveys. Elevated biomass values were found near and within the frontal feature during the 2004 survey, and also along the eddy edge during the 2005 survey. However, hierarchical cluster analysis did not reveal the presence of distinct zooplankton groupings associated with the various water masses encountered during the surveys and this is probably due to the high mesoscale variability in oceanographic conditions that are characteristic of the PFZ. The total average predation impact of the selected carnivorous macrozooplankton during the 2001, 2004 and 2005 surveys accounted for 4.93 ± 6.76%, 0.55 ± 0.51% and 4.88 ± 4.45 of the mesozooplankton standing stock, respectively. *S. gazellae* had the highest consumption rate in all three surveys, consuming up to 800 g Dwt $1000m^{-3}d^{-1}$ during the study.

Of the two chaetognaths, *E. hamata* dominated the chaetognath standing stock. The combined abundance and biomass values of *E. hamata* and *S. gazellae* ranged from 0 to 43.73 ind. m^{-3} and from 0 to 41.551 mg wwt m^{-3} respectively, during the three surveys. Inter-annual variability in the chaetognath densities was apparent. Highest abundances and biomasses tended to be associated with specific water masses, confirming the existence of a relationship between zooplankton community structure and hydrographic conditions. Generally, about 90% of the chaetognaths contained no food in their guts. *S. gazellae* consumed a wider variety of prey. Oil droplets occurred in the guts of ≈ 51% of *E. hamata*. Cannibalism was low in both species, but greater in *S. gazellae* than *E. hamata*. During the three surveys, the feeding rate values of *E. hamata* and *S. gazellae* went up to 0.48 and 2.099 prey d^{-1} respectively. *S. gazellae* also had a greater predation impact on the mesozooplankton standing stock than *E. hamata*. The mean predation impact of the chaetognaths combined was 0.31 ± 0.291%, 0.52 ± 0.28% and 0.53 ± 0.56% of the mesozooplankton standing stock during the 2001, 2004 and 2005 surveys, respectively. During all three surveys, the majority of individuals (≈ 76%) of the chaetognaths were at stage I maturity, suggesting that during the time of study the chaetognaths were not reproducing. In both species a significant difference (log-linear analysis, $p < 0.05$) in maturities between the years investigated was observed. In general, there were no differences in lengths and maturities between the different water masses encountered during the surveys. The lengths of *E. hamata* and *S. gazellae* ranged from 5 to 24 mm and from 9.4 to 63.6 mm, respectively.

Chapter 1

Introduction

1.1 Physical oceanography

The Southern Ocean forms a link between the south Atlantic, Pacific and Indian Oceans and is generally considered to extend from the Antarctic continent in the south, to the Subtropical Convergence in the north (Foster and Middleton, 1984). The Southern Ocean has thus been estimated to cover approximately 22% of the total world ocean area (Tomczak and Godfrey in El-Sayed, 2005). Due to its immense size and intense interaction with the atmosphere, it is recognized as having an important role in the global carbon cycle (Deacon, 1983; Abbott *et al*., 2000; Lutjeharms *et al*., 2001). The circulation of the Southern Ocean is dominated by three principle circumpolar fronts. From north to south these are the Subtropical Convergence (STC), the Sub-Antarctic Front (SAF), and the Antarctic Polar Front (APF) (Belkin and Gordon, 1996; Froneman *et al*., 1999; Pollard *et al*., 2002) (Figure 1.1). As the fronts demonstrate a high degree of latitudinal variability and may move hundreds of km north or south, the Southern Ocean may include most of the ocean up to the coastal waters of South America, southern Africa and Australia (Foster and Middleton, 1984).

The STC is the broadest frontal system between Africa and Antarctica and forms the boundary between Subtropical Surface Waters and the Sub-Antarctic Surface Waters (Lutjeharms and Emery, 1983; Pollard *et al*., 2002). The front is marked by a sudden temperature increase of ~4ºC (Pollard *et al*., 2002). In the Indian Ocean sector of the Southern Ocean, at 40-42ºE, Pollard *et al*. (2002) found the STC to lie between 41º and 42ºS. Similarly, Lutjeharms and McQuaid (1986) found the STC to lie at 41ºS south of Africa.

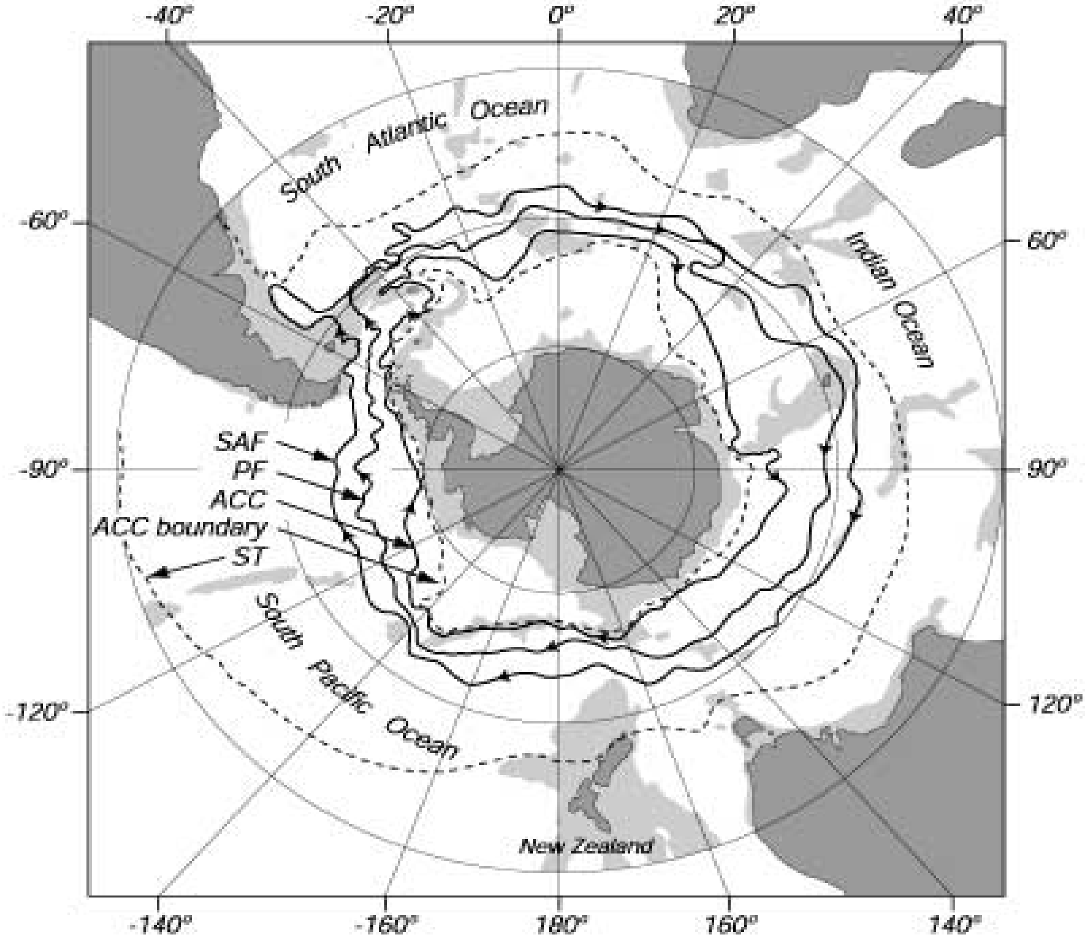

Fig. 1.1. The circumpolar currents of the Southern Ocean: Subtropical Convergence (ST); Subantarctic Front (SAF), Polar Front (PF) and the Antarctic Circumpolar Current (ACC). Picture taken from www.oceanworld.tamu.edu

The SAF is predominantly a subsurface front and is identified by changes in the vertical structure of the water column (Ansorge *et al*., 1999; Pollard *et al*., 2002), specifically a gradient between 3ºC and 5ºC (Lutjeharms and Emery, 1983; Ansorge *et al*., 1999), with a subsurface salinity minimum north of the front, and lowest salinity water in the surface layer south of the front (Pollard *et al*., 2002). In the Indian sector of the Southern Ocean, the mean position of the SAF is ≈ 48ºS (Lutjeharms and McQuaid, 1986).

The APF has a steep temperature gradient and marks the transition between the cold Antarctic Surface Water and the warmer Sub-Antarctic waters (Foster and Middleton, 1984; but see below). It is most often identified by the north-most extent of the 2ºC subsurface temperature minimum (Ansorge *et al*., 1999; Pollard *et al*., 2002). On average, the APF lies at 50ºS to 51ºS south of Africa (Lutjeharms and Valentine, 1984; Lutjeharms and McQuaid, 1986).

Together, the three frontal systems form one of the major current systems in the world – the easterly-flowing Antarctic Circumpolar Current (ACC) (Belkin, 1989), and divide the Southern Ocean into sub-regions that have distinct physical and biological properties (Ward *et al*., 2003; Johnson and Terazaki, 2004). The ACC surrounds the entire Antarctic continent and is unique because it is almost unobstructed by land masses (Foster and Middleton, 1984). The flow of the ACC is influenced by friction resulting from bottom topography (Foster and Middleton, 1984; Nowlin and Klinck, 1986). A number of regions in the Southern Ocean have been identified as “choke points” in the flow of the ACC. For example, the deep Andrew Bain Fructure Zone located at 50ºS, 30ºE in the South-west Indian Ridge has been found to deflect and intensify the ACC (Pollard and Read, 2001), often causing the APF and the SAF either to merge into a single intensive band or to meander to form a double front (Read and Pollard, 1993; Park *et al*., 2001). Similarly, oceanic islands of the Southern Ocean act as obstacles to the ACC, substantially modifying the oceanography and biology of the surrounding environment (Pakhomov *et al*., 1998; Pakhomov *et al*., 2000). The ACC has two main zones of transport, the Polar Frontal Zone (PFZ) and the Antarctic Zone (AAZ) (Pollard *et al*., 2002), which are separated by the three fronts mentioned above. The AAZ lies between the Antarctic continent and the APF, and the PFZ lies between the APF and the SAF (Lutjeharms and Valentine, 1984; Ansorge *et al*., 1999).

The Prince Edward Islands (PEI), comprising Prince Edward Island and Marion Island, are located south-east of the southern tip of Africa (47ºS, 38ºE), and lie directly in the path of the ACC, between the SAF to the north and the APF to the south (Lutjeharms and Valentine, 1984). The islands thus lie within the PFZ. Due to the seasonal presence of enormous numbers of top predators, the surrounding waters of the PEI have been the focus of numerous hydrographic and biological studies. Variability in the oceanographic environment of the PEI includes meanders in the frontal systems that delimit the PFZ, and the presence of both cold- and warm-core features. These features are thought to be generated largely by the interaction of the ACC with prominent bottom topography, and result in increased zooplankton biomass and complex zooplankton communities (Ansorge *et al*., 1999; Froneman *et al.*, 1999; Pakhomov *et al*., 2000).

Many extensive studies have been conducted in the region of the PEI. In the last 9 years these studies have included the Marion Island Oceanographic Survey (MIOS) which took place in April/May 1996 – 1999 (Hunt, 2000), and the Marion Offshore Variability Ecosystem Study (MOVES) which took place in April/May 2001 – 2002 (Bernard and Froneman, 2002, 2003). The most recent study was conducted during April/May 2002 – 2005, and falls under the Dynamics of Eddy Impact on Marion's Ecosystem Study (DEIMEC), which aims to understand the importance of the oceanic environment upstream of the PEI (Pakhomov *et al*., 2003). In general, the broad findings of the above studies have shown that the zooplankton community in the vicinity of the PEI is highly variable due to the variability in oceanographic conditions (Froneman and Pakhomov, 1998; Hunt, 2000). The frontal systems to the north and south of the islands generally act as biogeographic boundaries to the distribution of plankton (Pakhomov *et al*., 1999; Ansorge *et al*., 2004). However, both warm and cold core eddies that are produced far afield can transport plankton communities across the frontal boundaries (Pakhomov and McQuaid, 1996; Froneman *et al.*, 1999; Pakhomov and Froneman, 2000).

On closer inspection, the PFZ forms a unique water mass that separates the SAF (to the north) from the APF (to the south) (Lutjeharms and Valentine, 1984). While some authorities describe the APF as separating the cold and productive Antarctic Surface Waters (ASW) from the warm but less-productive Sub-Antarctic Surface Waters (SASW) (Foster and Middleton, 1984), this role can be considered to be fulfilled by the PFZ (Lutjeharms, 1985). The zooplankton community structure and biomass within the PFZ are strongly linked to hydrography on both temporal and spatial scales (Piatkowski, 1989; Pakhomov and McQuaid, 1996; Pakhomov and Froneman, 2000). The PFZ is an area of high oceanographic variability and this influences the biology, so that plankton species of sub-tropical, sub-Antarctic and Antarctic origin all occur within the region (Boden and Parker, 1986; Perissinotto and Boden, 1989; Froneman and Pakhomov, 1998). As mentioned earlier, the variability in oceanography results from the changing positions of fronts and from eddies detaching from meandering fronts, with both the oceanic fronts and eddies recently having been recognized as areas of increased biological productivity (Froneman and Perissinotto, 1996; Pakhomov *et al*., 1994; Pakhomov *et al*., 1996). On spatial scales, Ansorge *et al*. (1999) found that the PFZ around the PEI was characterized by a uniform distribution of total zooplankton abundance and biomass. On a temporal scale, Hunt *et al*. (2001) found that variability in the zooplankton community structure observed between months was greater than the variability observed between years.

The zooplankton community in the vicinity of the PEI demonstrates a high degree of inter-annual variability. For example, Froneman *et al.* (1999) found that macrozooplankton species contributed <5% to the total zooplankton abundance, while Ansorge *et al.* (1999) found that the macrozooplankton species could contribute up to 25% to the total abundance. Generally, however, the zooplankton community in terms of both abundance and biomass tends to be dominated by mesozooplankton, especially copepods, ostracods and small chaetognaths (Perissinotto and Boden, 1989; Ansorge *et al*. 1999; Froneman *et al*., 1999). The macrozooplankton is mainly represented by euphausiids, amphipods and large chaetognaths, with the chaetognaths often comprising >50% of the total macrozooplankton abundance and standing stock (Ansorge *et al*., 1999; Pakhomov *et al*., 2000; Froneman *et al*., 2002).

1.2 Biological studies

Most studies have focused on herbivorous micro- and mesozooplankton as key components of the biological pump in the Southern Ocean (Froneman and Perissinotto, 1996; Froneman *et al*., 2000; Bernard and Froneman, 2003; Ward *et al*., 2003). Recent studies have shown, however, that carnivorous macrozooplankton and micronekton play a potentially important role in the transportation of carbon to depth (Pakhomov *et al*., 1994; Pagès *et al*., 1996; Froneman *et al*., 1997; Pakhomov *et al*., 1999; Froneman *et al*., 2000; Froneman *et al*., 2002) because of their distinct vertical migrations (Perissinotto and McQuaid, 1992; Ward *et al*., 1995; Pakhomov and Froneman, 1999; Steinberg *et al*., 2000; Fleddum *et al*., 2001, Froneman *et al*., 2002; King and LaCasella, 2003) and the production of fast-sinking fecal pellets (Fortier *et al*., 1994; Pakhomov *et al*., 1999; Froneman *et al*., 2002) (see Figure 1.2). In a study off the coast of California, Dilling and Alldredge (1993) found that the sinking of chaetognath fecal pellets could contribute between 4-6% to carbon flux in the euphotic zone and 6-60% at depth. Fortier *et al*. (1994) also point out that in certain cases an increase by an order of magnitude in the size ratio of a consumer and its food particle results in biogenic carbon being kept within the ocean for a longer period of time. Carnivorous macrozooplankton may therefore increase the localized efficiency of the biological pump.

Predation by zooplankton in pelagic waters has a great influence on the species composition and abundance of zooplankton (Fancett and Jenkins, 1988). In the cold waters of the Southern Ocean, mesozooplankton tends to be dominated in numbers by copepods, which often account for >75% of total mesozooplankton abundance (Froneman *et al*., 1997; Froneman *et al*., 2002). Because of their numerical abundance, copepods are the major constituents in the diets of a variety of carnivorous macrozooplankton including amphipods, chaetognaths, euphausiids and decapods, as well as myctophid fish (Lancraft *et al*., 1991; Øresland, 1995; Froneman and Pakhomov, 1998; Pakhomov *et al*., 1999; Johnson and Terazaki, 2004). Of the true carnivorous macrozooplankton in the Southern Ocean, chaetognaths and siphonophores are the most abundant (Piatkowski, 1989; Park and Wormuth, 1993; Pakhomov *et al*., 1994; Ward *et al*., 1995; Froneman *et al*., 2002; Kaufman *et al*., 2003). The feeding rate of the chaetognath *Eukrohnia hamata* alone (between 0 – 0.5 prey day^{-1}) may be equal to a daily loss of up to 6% of copepod standing stock (Øresland, 1995; Froneman and Pakhomov, 1998; Froneman *et al*., 1998). Although not abundant numerically, other important carnivorous macrozooplankton in terms of biomass are mysids and gelatinous zooplankton such as medusae and siphonophores (Pakhomov *et al*., 1994; Froneman *et al*., 2002). The predation impact of carnivorous gelatinous zooplankton on small copepods was so great (2-12% biomass removed daily) in the Humboldt Current off

Chile, that Gonzalés *et al*. (2004) suggested that carnivorous gelatinous zooplankton may control the abundance of copepods as well as the size structure of the copepod community.

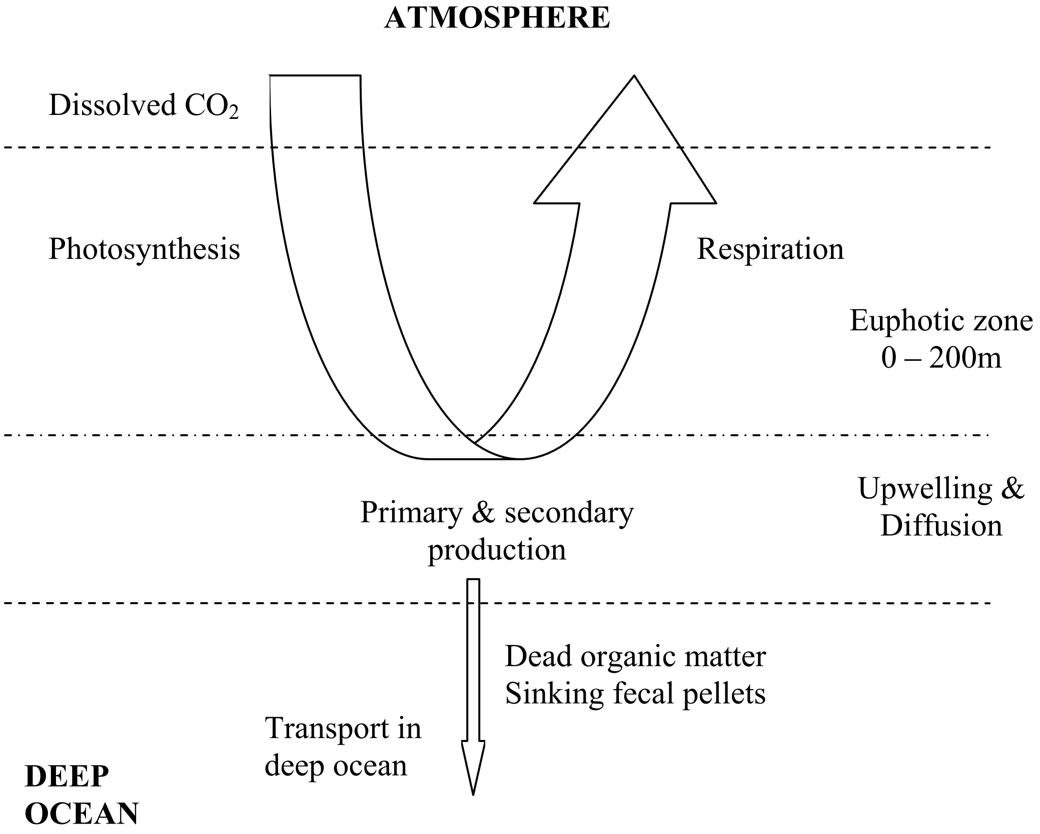

Fig. 1.2. The biological pump showing the pathways of the carbon cycle in the marine environment, with sequestration of organic carbon into the ocean interior.
(Modified from Perissinotto, 1995)

1.3 Chaetognath biology

In terms of species numbers, chaetognaths, commonly known as arrow worms, form one of the smallest phyla in the animal kingdom with ≈ 100 described species (Davis, 1955; Casanova, 1999). They are, however, extremely abundant throughout the world's oceans; their biomass may attain levels of 5-15% of total zooplankton biomass (Welch *et al.*, 1996), and has been estimated to be 10-30% of that of copepods (Casanova, 1999; Johnson and Terazaki, 2004). Because chaetognaths are both prey for numerous large carnivores (Sameoto, 1988; Pakhomov *et al.*, 1996; Go *et al.*, 1998), as well as being predators themselves (Feigenbaum, 1979, 1982; Pearre, 1982; Øresland, 1995; Kehayias *et al.*, 1996; Froneman and Pakhomov, 1998; Froneman *et al.*, 1998; Casanova, 1999), they form an integral component of marine food webs.

The vertical distribution of chaetognaths differs from region to region, since chaetognaths tend to be associated with specific temperatures, not necessarily with specific depths (Casanova, 1999). For example, *Eukrohnia hamata* and *Sagitta maxima* occur at depths below 300m in the tropical Atlantic but are found in surface waters in colder regions, while juveniles occur in shallower waters than adults (Casanova, 1999).
All chaetognaths are strictly carnivorous (Feigenbaum and Maris, 1984), feeding primarily on copepods (Feigenbaum, 1982; Øresland, 1995; Froneman *et al.*, 1998; Geisecke and Gonzalés, 2004). The predominance of copepods in the diets of chaetognaths can be ascribed to their numerical dominance in marine ecosystems (Feigenbaum and Maris, 1984; Kehayias *et al.*, 1996; Baier and Purcell, 1997a; Froneman and Pakhomov, 1998). The feeding rates of chaetognaths generally range from 0 to 4.23 prey day^{-1} (see Table 1.1). For example, in the vicinity of the PEI the feeding rate of *Eukrohnia hamata* ranged from 0 to 0.5 prey day^{-1}(Froneman and Pakhomov, 1998) while in the South Atlantic Bight the feeding rate of *Sagitta hispida* is 0.83 to 4.23 prey day^{-1}(Baier and Purcell, 1997a). Tintinnids, euphausiids, cladocerans and larval fish are also commonly found in chaetognath guts (Feigenbaum and Maris, 1984; also see Table 1.1).

Chaetognaths are non-selective feeders and will typically feed on the most abundant prey (Feigenbaum and Maris 1984). Their diet thus varies seasonally and annually, reflecting seasonal and annual trends in the zooplankton community structure (Feigenbaum and Maris, 1984; Kehayias *et al*., 1996). Prey size depends on chaetognath size, with the minimum prey size determined by the ability of the hooks on the head to grasp the prey. The maximum prey size is determined by the mouth opening (Sullivan, 1980; Pearre, 1980).

Chaetognaths are protandrous hermaphrodites, and cross-fertilization is the most common mode of reproduction (Casanova, 1999). Maturity stages are determined by the visibility and/or fullness of ovaries and seminal vesicles (Dunbar, 1962; Pearre, 1981; Kehayias *et al*., 1996). Because only a few studies within the Southern Ocean have examined chaetognath reproduction over a 12-month period, it is difficult to determine whether chaetognaths reproduce seasonally or throughout the year. In a study conducted at the Antarctic Peninsula, Øresland (1995) found all stages of maturity of *Eukrohnia hamata* in both winter and summer, suggesting breeding throughout the year. Pearre (1981) observed a similar pattern for *Sagitta elegans* in Nova Scotia, Canada. Segregation of the different developmental stages at different depths was observed in *E. hamata* by Johnson and Terazaki (2004). Sexually mature adults spawned at depth, while developing juveniles migrated into shallower water and return to depth as they matured.

Despite the ecological importance of chaetognaths, little is known about their abundances, diet or predation impact in the Southern Ocean (Froneman *et al*., 1998). Most studies on chaetognath ecology have been conducted north of the equator, specifically off the coasts of California (Baier and Purcell, 1997a; Dilling and Alldredge, 1993); Florida (Feigenbaum, 1979); Massachusetts (Feigenbaum, 1982); Nova Scotia (Pearre, 1982); Greece, (Kehayias *et al*., 1996); and in the subarctic Pacific (Sullivan, 1980); in the Canadian high Arctic (Welch *et al*., 1996); and even a saline lake connected to Tokyo Bay (Nagasawa, 1985).

Chaetognath studies within the Southern Ocean have largely been restricted to the Antarctic Peninsula (Øresland, 1995); the Australian sector of the Antarctic Ocean (Johnson and Terazaki, 2004); and in the immediate vicinity of the Prince Edward Islands (Froneman and Pakhomov, 1998; Froneman *et al*., 1998). Around the PEI, chaetognath abundance may be as high as 15 ind. m^{-3}, although they are typically <5 ind. m^{-3} (Froneman *et al*., 1999). Estimates of chaetognath biomass and abundance in the PFZ in the vicinity of the PEI demonstrate a high inter-annual variability (see Table 1.2). For example, the abundances of *Sagitta gazellae* ranged from 0.2 to 7.8 ind. m^{-3} in April/May 1996, but only ranged from 0.46 to 1.63 ind.m^{-3} in April/May 1986 (Table 1.2). Similarly, the biomass of *S. gazellae* was estimated at 157.32 mg DW 1000m^{-3} in April 1998, but at 32.6 mg DW 1000m^{-3} in April 1997 (Table 1.2). Such extreme variability in biomass and abundance suggests strong temporal variation in the predation impact of chaetognaths on the mesozooplankton standing stock. This variability in biomass, and thus feeding activity in the PFZ, may in turn influence the biologically mediated carbon flux.

Previous studies in the PFZ have examined the feeding trophodynamics of amphipods, euphausiids, and chaetognaths while the role of other carnivorous macrozooplankton, specifically the gelatinous macrozooplankton, has generally been ignored. This study examines the community structure of selected carnivorous macrozooplankton during three cruises in 2001, 2004 and 2005, of the South African National Antarctic Program (SANAP) and focuses on chaetognath biology. The main aims are to describe inter-annual variability in the selected carnivorous macrozooplankton community structure within the PFZ, with special emphasis on the population structure, reproduction and feeding ecology of the two numerically dominant chaetognaths *Eukrohnia hamata* (Mobius, 1975) and *Sagitta gazellae* (Ritter-Záhony, 1910).

Table 1.1. Predation impact and gut contents of chaetognath species from published data.

Species	**Location and season**	**Feeding rate (prey day^{-1} chaetognath^{-1})**	**Daily predation impact on total mesozooplankton standing stock (%)**	**General gut content**	**Comment**	**Reference**
Sagitta enflata	Mejillones Bay (northern Chile) Spring Winter	1.2	6 0.4	Small copepods (<1500mm)	Feeding rate decreased with depth.	Geisecke & Gonzalés (2004)
Eukrohnia hamata	Antarctic Peninsula Winter		0.2	Copepods *Oncaea* spp.		Øresland (1995)
E. hamata *S. gazellae*	Prince Edward Islands (Southern Ocean) Late summer	0 – 0.5 0 – 0.9	5.2 3.2	Copepods Chaetognaths Crustacean eggs		Froneman & Pakhomov (1998)
E. hamata *S. gazellae*	Prince Edward Islands (Southern Ocean) Late summer	0.05 – 0.14 0.15 – 0.76 0 – 0.17	0.2 – 1.21 0.01 – 0.35	Copepods Copepods Chaetognaths	Chaetognath distribution significantly correlated to copepod densities. Chaetognath abundance decreased with depth.	Froneman *et al*. (1998)
S. enflata	Vineyard Sound (Massachusetts)	0.53 – 1.33		Copepods Chaetognaths Appendicularians	Feeding rate increased with chaetognath size.	Feigenbaum (1982)
S. enflata	Gulf Stream, Florida Winter	1.7 – 2.9		Copepods Chaetognaths	Feeding rate increased with chaetognath size and was independent of time of day.	Feigenbaum (1979)
S. enflata *S. helenae* *S. hispida*	South Atlantic Bight (North Carolina) Winter	0.41 – 1.14 0.91 – 4.21 0.83 – 4.23		Copepods Tintinnids Molluscs Ostracods	Density of prey determined predation impact.	Baier & Purcell (1997a)

Table 1.2. Estimates of biomass and/or abundance of chaetognaths commonly found in the Polar Frontal Zone in the vicinity of the Prince Edward Islands.

Species of chaetognath	**Time of study**	**Biomass**	**Abundance**	**Source**
Sagitta sp.	April/May 1989		49.6 ind. m^{-3}	Perissinotto & McQuaid (1992)
Chaetognaths combined	Jan – Feb, June - July 1993	0.64 mg DW m^{-2}	0.12 ind. m^{-2}	Pakhomov *et al* (1994)
Eukrohnia hamata *Sagitta gazellae*	April/May 1996		0.8 – 18.7 ind. m^{-3} 0.2 – 7.8 ind. m^{-3}	Froneman & Pakhomov (1998)
E. hamata *S. gazellae*	April/May 1986		5.1 – 19.4 ind. m^{-3} 0.46 – 1.63 ind. m^{-3}	Froneman *et al* (1998)
S. gazellae *S. maxima* *E. hamata*	April 1998	157.32mg DW $1000m^{-3}$ 1.98mg DW $1000m^{-3}$ 1.24mg DW $1000m^{-3}$	20 ind. $1000m^{-3}$ 2.8 ind. $1000m^{-3}$ 5.6 ind. $1000m^{-3}$	Pakhomov *et al* (2000)
S. gazellae *E. hamata*	April/May 1997	32.6mg DW $1000m^{-3}$ 0.1mg DW $1000m^{-3}$	5.7 ind. $1000m^{-3}$ 0.9 ind. $1000m^{-3}$	Pakhomov & Froneman (2000)

Chapter 2

Materials and methods

2.1. Survey scheme

Zooplankton samples were collected during three annual relief voyages to the Prince Edward Islands (PEI) (Voyages 99, 116 and 117; years 2001, 2004 and 2005 respectively) aboard the research vessel *SA Agulhas* in late austral summer (April/May). Figure 2.1 shows the geographic positions of the three surveys. During voyage 99, the survey was largely restricted to the upstream region of the islands in the open waters of the Polar Frontal Zone (PFZ) between 46º 34.18S - 49º 55.03S and 32º 56.80E - 38º 00.39E; during voyage 116, the survey was restricted to the immediate vicinity of the Andrew Bain fracture zone at between 47º 44.60S - 49º 59.32S and 29º 13.93E - 34º 01.78E. Finally, during voyage 117 the survey was conducted in the vicinity of a cold core eddy generated by the interaction of the Antarctic Polar Front (APF) with the South-West Indian Ridge at 47º 46.27S - 49º 46.83S and 31º 01.68E - 36º 22.71E. Details of the position of stations occupied during the surveys are presented in Appendix 1 (Tables 3.18 – 3.20). The sampling methods employed during the three surveys were broadly similar.

2.2. Oceanography

At each station, a Neil Brown Instrument was used to determine conductivity-temperature-depth (CTD) to a depth of 1500m. For the purpose of this study the Antarctic Polar Front (APF) was defined by the position of the 2°C isotherm at 200m (Lutjeharms and Emery, 1984), and the Subantarctic Front (SAF) by the position of the 7°C isotherm at 100m (Nagata *et al*., 1988).

2.3. Chlorophyll-*a* analysis

At each station, the chlorophyll-*a* concentration of the upper 100m of the water column was determined at 5 depths (0, 20, 50, 75 and 100m) from a 250ml water sample, obtained from rosettes attached to the CTD, that had been passed through a GF/F filter. Filters were then placed in 8ml of 90% acetone and stored for 24 h at -20ºC, after which the chl-*a* concentration was measured fluorometrically using a Turner Designs 10AU Fluorometer (Holm-Hansen and Riemann, 1978). Integrated chlorophyll-*a* concentrations were determined by trapezoidal integration (Bernard and Froneman, 2003).

2.4 Zooplankton

2.4.1. Zooplankton sampling

To collect zooplankton samples, a WP-2 net (200µm mesh size) was used in 2001, a Rectangular Midwater Trawl (RMT-8) net (5mm mesh size) and Bongo nets (200µm and 300µm mesh sizes) were used in 2004, and Bongo nets only were used in 2005. An electronic flowmeter was fitted into the WP-2 and Bongo nets to calculate the volume of water filtered during each tow during the 2001 and 2004 surveys. The RMT-8 net employed during the 2004 survey had a nominal mouth area of $8m^2$ (Baker *et al.*, 1973). The volume filtered by the RMT-8 net trawl was determined by multiplying the mouth area of the trawl by the distance travelled. The distance was calculated by the ship's average speed and the duration of the trawl. All net types were towed obliquely at a speed of 1 to 3 knots and were conducted to a depth of 200m at night and 300m during the day to account for diel vertical migrations. Samples were preserved in 6% buffered formalin and examined in the laboratory. No correction for the loss of tissue due to preservation in formalin was made. Total volume of water filtered during net tows ranged between 150 and $860m^3$.

When possible, zooplankton were identified to the lowest possible taxon using the keys of Boltovskoy (1981, 1999) and Razouls (1994). Total abundances and wet weights of the carnivorous macrozooplankton species sampled were determined either from the entire sample or from sub-samples (1/2 to 1/64 aliquots) obtained using a Folsom plankton splitter. Individual animals from the selected species, taken from either the entire sample or sub-samples, were dabbed dry using paper towel and then weighed to the nearest 0.001g using a Sartorius Micro MC1 electronic microbalance. Zooplankton abundance and biomass data were expressed as individuals per cubic meters ($ind.m^{-3}$) and as mg of wet weight per cubic meters ($mg\ wwt\ m^{-3}$), respectively. Although euphausiids are omnivorous (Price *et al*., 1988; Atkinson and Snÿder, 1997; Atkinson *et al*., 1999), their preferred diet is phytoplankton (Atkinson *et al*., 1999) and they were therefore excluded from this study.

2.4.2. Zooplankton analysis

The zooplankton community structure was analyzed separately for each cruise. Prior to the analysis, all data (biomass and abundance) were log transformed [$\log_{10}(x + 1)$] to reduce the influence of species with particularly high abundance or biomass (Field *et al*., 1982). To compare zooplankton communities, hierarchical cluster analysis and multidimensional scaling were used based on the Bray-Curtis similarity index (Field *et al*., 1982). The similarity analysis programs ANOSIM and SIMPER of the Plymouth Routine In Multivariate Ecological Research computer package (PRIMER) were used to test significance levels and sources of difference between zooplankton assemblages associated with different groups of stations (Clarke and Warwick, 1994). Based on station abundance and biomass levels, SIMPER analysis determined the percentage contribution of species to within-group similarity and between-group dissimilarity. Similarity levels were not fixed but were adjusted to obtain meaningful groupings (Siegel and Piatkowski, 1990). The level of similarity used as a cut of point to determine station clusters thus varied among years. The abundance and biomass data obtained from the RMT-8 and Bongo nets used in the 2004 survey were analysed separately since *t*-tests showed significant differences ($p < 0.05$) between the two net types.

For each survey, Pearson correlation was used to determine the relationships of macrozooplankton abundance and biomass levels to surface temperature and salinity level at each station. Pearson correlation analysis was also used to identify significant relationships between the total carnivorous macrozooplankton and mesozooplankton densities. Mesozooplankton were counted and analysed by Bernard and Froneman for 2002, 2004 and 2005. Only significant relationships are presented in the results. The computer package Statistica 6 was used for this analysis.

2.5. Macrozooplankton predation impact

The daily predation impact of the different carnivorous groups on mesozooplankton during each survey was estimated by multiplying the biomass (dry weight) value of each carnivore taxon at each station (excluding RMT-8 stations) by published values of the % of daily ration of dry body weight consumed for that taxon (Froneman *et al*., 2002). Data were expressed as a percentage of the mesozooplankton standing stock (obtained from Bernard and Froneman 2002, 2005; Bernard *et al*., 2006) consumed per day. The predation impact of the carnivorous macrozooplankton was restricted to the mesozooplankton fraction only, as previous investigations have shown this fraction to be the main food-source of the taxa investigated in the present study (Froneman *et al*., 1998, 2000; Pakhomov *et al*., 1999). Predation impact was only calculated at stations where data of mesozooplankton were available. Ctenophores were excluded from the analysis in this case, since we assumed that they fed on fish larvae or other ctenophores (Froneman pers comm., 2004). Although mysids are omnivorous, they tend to prefer animal-matter food and were therefore included in the predation impact analysis (Murano, 1999). Dry weights of chaetognaths (n = 10) and mysids (n = 4) were determined from a subsample of the 2004 survey after oven drying at 60ºC for 24 hours. The water content was estimated to be 93% (±2%) of total body weight for chaetognaths, and 83% (±2%) for mysids. The water content of the remaining gelatinous zooplankton was assumed to be 96% of the wet weight (Froneman pers comm., 2004).

2.6. Chaetognath analysis

The size structure, stages of development and gut contents of the numerically dominant chaetognaths (*Sagitta gazellae* and *Eukrohnia hamata*) were investigated for each survey. Where four or more stations were sampled in each water mass encountered during the survey, at least four stations from each water mass were selected to conduct the analysis, thus not all stations that were sampled during a survey were necessarily used in the chaetognath analysis. Table 2.1 shows the stations used for the chaetognath analysis for each survey and in the different water masses encountered.

2.6.1. Chaetognath community size structure

The size structure of the numerically dominant chaetognaths was assessed by determining the length of at least 200 individuals from each water mass. Body length was measured (to the nearest mm) from the tip of the head to the end of the tail, excluding the tail fin, using Vernier callipers (Øresland, 1995). Length measurements were not corrected for shrinkage due to preservation in fomalin. Wet weight (to the closest 0.001g) was obtained using a Sartorius Micro MC1 electronic microbalance.

2.6.2. Gut content analysis and feeding rates

Individuals of *Sagitta gazellae* and *Eukrohnia hamata* were dissected and their gut contents examined under a dissecting microscope at 100x and 500x magnification. For each of the three surveys, a minimum of 15 stomachs of each species were selected randomly from at least 2 stations in each water mass were examined. Prey found in the upper quarter of the gut were omitted from counts in order to account for cod-end feeding (Feigenbaum and Maris, 1984). Prey were sorted into three stages of digestion, according to Øresland (1987) as follows: (a) undigested; (b) digested but identifiable; (c) unidentifiable. Unidentifiable prey items were assumed to represent the remains of a single prey item only.

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

$$Fr = (\text{mean } NPC / Dt) \times 24$$

Where NPC is the mean number of prey per chaetognath and Dt is the digestive time. The Dt value for *S. gazellae* was estimated using the empirical equation $Dt = 10.96e^{-0.086T}$ (Stuart and Verheye, 1991), where T is the water temperature (ºC). A mean sea water temperature of 5ºC was assumed during the cruises. Øresland (1995) has estimated the Dt value for *E. hamata* to be 10h. Since mesozooplankton accounts for >80% of prey in stomachs of the two study species (Froneman *et al*., 1998), only the predation impact on the mesozooplankton community was calculated. Predation impact was calculated by combining daily feeding rates with the chaetognath densities. Results were expressed as a percentage of the mesozooplankton standing stock consumed per day.

2.6.3. Maturity stages

The maturity stages of *Sagitta gazellae* and *Eukrohnia hamata* were determined by examining at least 200 individuals from each water mass encountered during the surveys. Chaetognaths were examined under a Wild Heerbrugg dissecting microscope at 100x and 500x magnification. Maturity stages were based on the development of the ovaries and seminal vesicles, using a modification of Furnestin's (1957) classification: Stage I: ovaries and seminal vesicles not developed or barely visible; Stage II: seminal vesicles and ovaries moderately developed, ovaries slender with possible ova, seminal vesicles empty; Stage III: ovaries and vesicles fully mature, ovaries swollen with conspicuous ova, vesicles filled with sperm or partly discharged, tail segment opaque. Maturity stages were expressed as a frequency (%) of the total number of chaetognaths examined within each water mass.

The lengths of chaetognaths were compared among the different water masses using a one-way ANOVA, while the distribution of specimens in three maturity stages was compared using log linear analysis. Significant results were further examined using Tukey's post-hoc test. The feeding rates of the two species were compared between the species and amongst the different water masses using a two-way ANOVA, followed by the Newman-Keuls post-hoc test where necessary (Zar, 1996).

Finally, all three surveys were combined for inter-annual analysis. One-way ANOVAs were used to separately compare abundances, biomasses and predation impacts of carnivorous macrozooplankton between the three years investigated. Tukey's post-hoc test was used to examine significant results. Chaetognath lengths and feeding rates of *Sagitta gazellae* and *Eukrohnia hamata* were compared separately using two-way ANOVAs, followed by the Newman-Keuls post-hoc test where necessary. Log linear analyses were used to compare the distribution of specimens in the three maturity stages.

Where data are given as an average amount, they are represented as the average ± standard deviation.

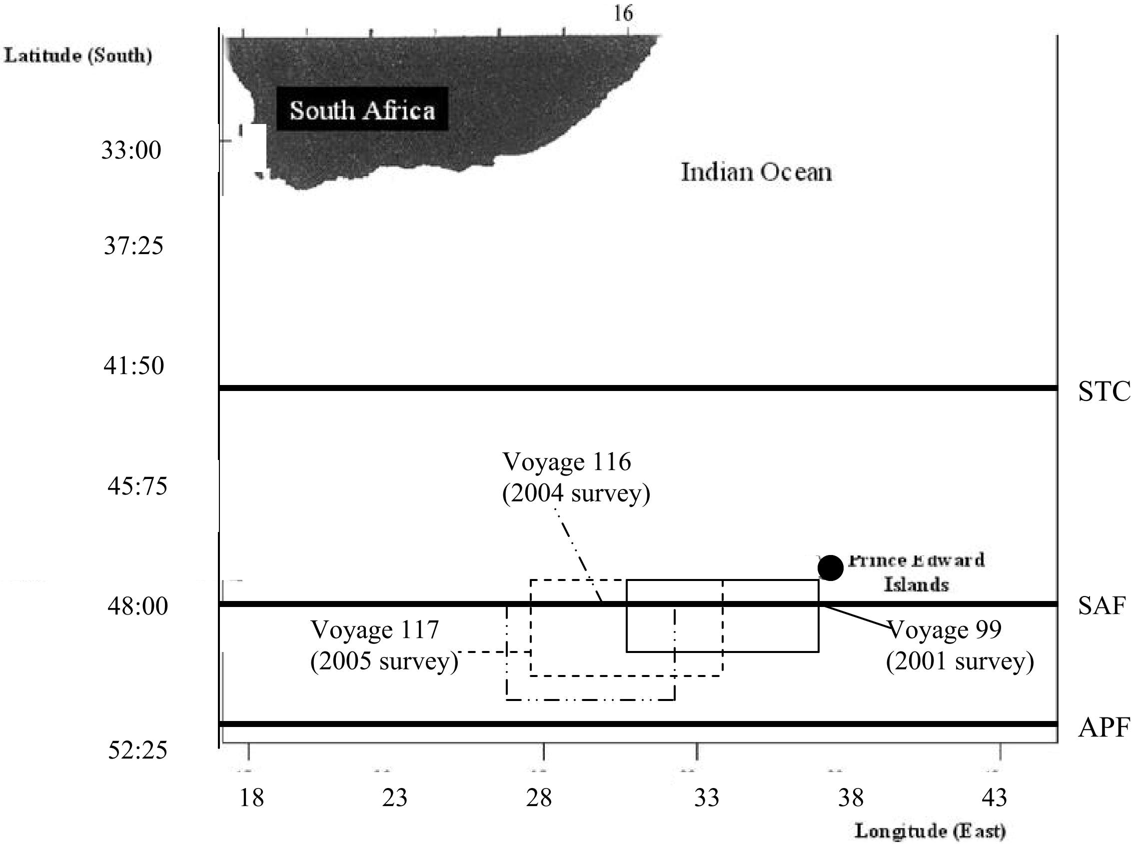

Fig. 2.1. Geographic positions of the three surveys conducted during late austral autumn of 2001, 2004 and 2005 in the Indian Ocean sector of the Southern Ocean. The average positions of fronts as derived from literature are indicated.

Table 2.1. Stations used for the chaetognath analysis showing their occurrence in the different water masses encountered during the three surveys.

2001		2004			2005		
SASW	**PFZ**	**SASW**	**PFZ**	**ASW**	**SASW**	**Eddy edge**	**ASW**
192	203	238	237	228	259	262	274
190	206	239	243	234	260	263	276
193	207	240		244	261	268	277
201	208	241		256	264	269	283
	209	248			265	275	284
					270	278	285
					272	279	286
					280	282	
					288		
					290		
					291		
					295		

Chapter 3

Results

3.1. Physical environment

2001 Survey

The majority of the survey was conducted within the Polar Frontal Zone (PFZ) where the surface temperature ranged between 4.14ºC and 7.6 ºC, and corresponded to salinity values of 33.69-33.91. North of the PFZ the water was warmer and less fresh, with surface temperatures ranging between 8.44 ºC and 7.61 ºC, and salinities of 33.81-34.06; these values are typical of Subantarctic Surface Water (SASW). The Subantarctic Front (SAF) lay at about 47º25'S at between 33º and 35º30'E. At 35º30'E the SAF then turned northwards towards 47ºS, which may have resulted from topographic deflection caused by the South West Indian Ridge (Figure 3.1). A steady decrease in water temperature from north to south was observed south of the SAF (Bernard and Froneman, 2002).

2004 Survey

A detailed description of the oceanographic conditions in the study area is published in Ansorge *et al.* (2004). Here, I describe the position of the SAF and Antarctic Polar Front (APF) as they relate to the plankton distribution. During the survey, the SAF and APF appeared to merge into a distinct frontal feature. Water masses identified in the study area showed a distinct separation in properties between the north-western and south-eastern sectors of the grid (Figure 3.2). In the north-western region waters were distinctly Subantarctic in origin (>8.5ºC, >34.2), suggesting that the SAF lay extremely far to the south compared to previous surveys (DEIMEC I and II). In the south-eastern corner water masses were typical of the Antarctic zone showing a distinct subsurface temperature minimum of <2.5ºC. The north-eastern extension of the SAF/APF at 30º30'E may explain the northward intrusion of these water masses, which would be more commonly found to the south of the APF (see further Ansorge *et al*., 2004). Of particular interest was the subsurface temperature distribution in the far eastern edge of the survey grid, which may suggest the presence of a cold core eddy (Figure 3.2). In this feature temperatures were <1.5ºC and are typical of the remnants of Winter Water, suggesting that this water mass may have been entrained by a cyclonic eddy spawned at the APF.

2005 Survey

Ansorge *et al.* (2005) presents a detailed description of the oceanographic conditions of the study area. Here, a brief description of water masses encountered during the survey is given. A cold core eddy was identified between 48º-49º15'S and 33º-36ºE (Figure 3.3). The eddy was approximately 120nm in diameter and extended to a depth of >1000m., with a very strong subsurface expression. Prior to the survey, successive altimetry images showed the eddy detaching from the APF at 50ºS, 32º30'E and moving in a north to north-east direction. The eddy exhibited a relatively warm subsurface temperature minimum layer of 4.2 - 4.4ºC, and a fresh salinity layer of 33.777 - 33.831. At 250 – 300m depth the eddy temperature minimum was <0.4ºC, corresponding to salinity values of 34.121 – 34.135, which confirmed the source of the eddy as being from south of the APF. At 200m the surrounding water was between 3 - 5ºC warmer than the cold core of the eddy. The water mass characteristics of the eddy were that of Antarctic Surface Water (ASW). The SAF, denoted by its 6ºC subsurface expression, lay north of the eddy at 47º15'S.

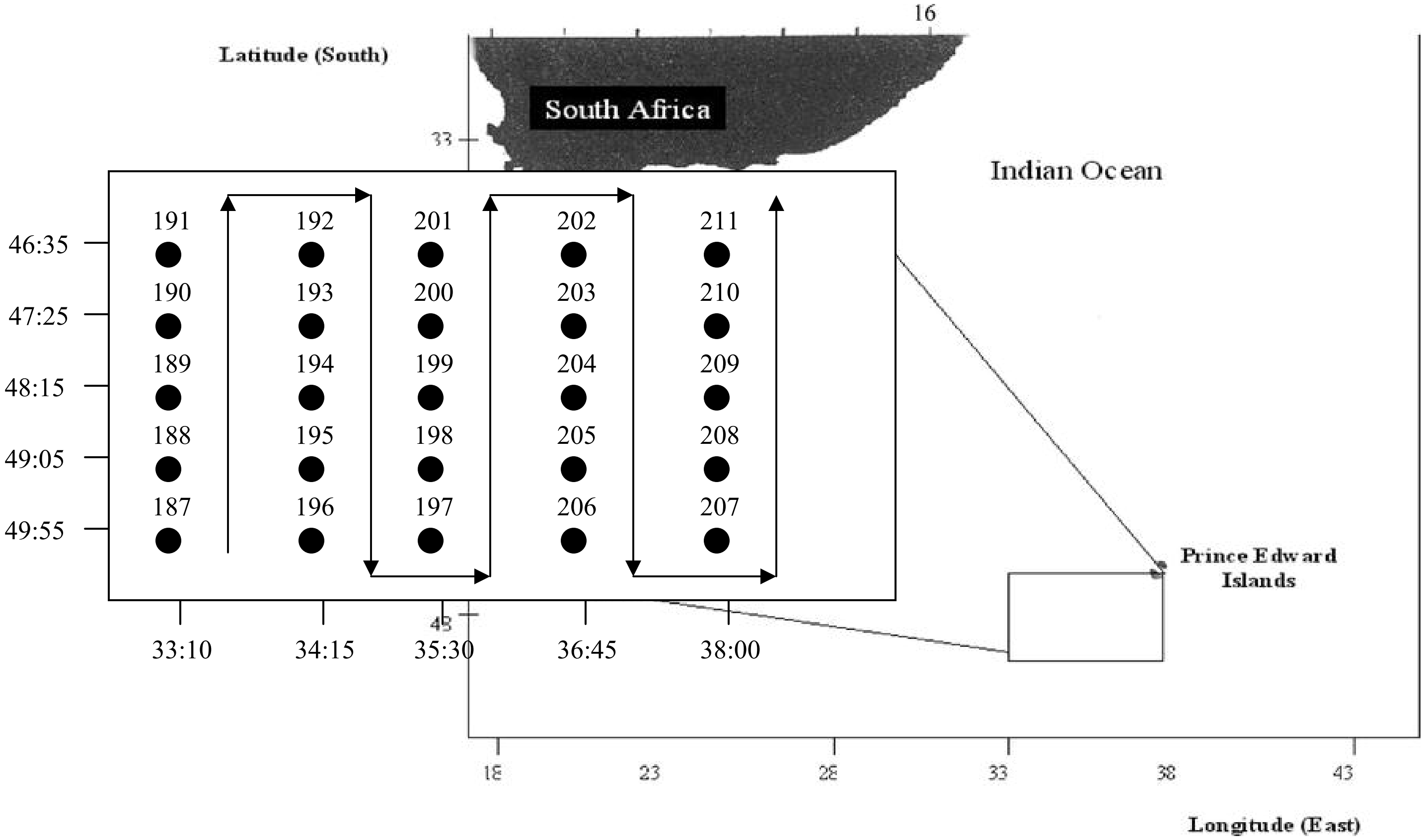

Fig. 3.1. Positions of the sampling stations occupied during the MOVES I survey conducted in the upstream region of the Prince Edward Islands in April/May, 2001.Arrows indicate the cruise track. Station positions are indicated by dark circles and station numbers are shown above the station positions.

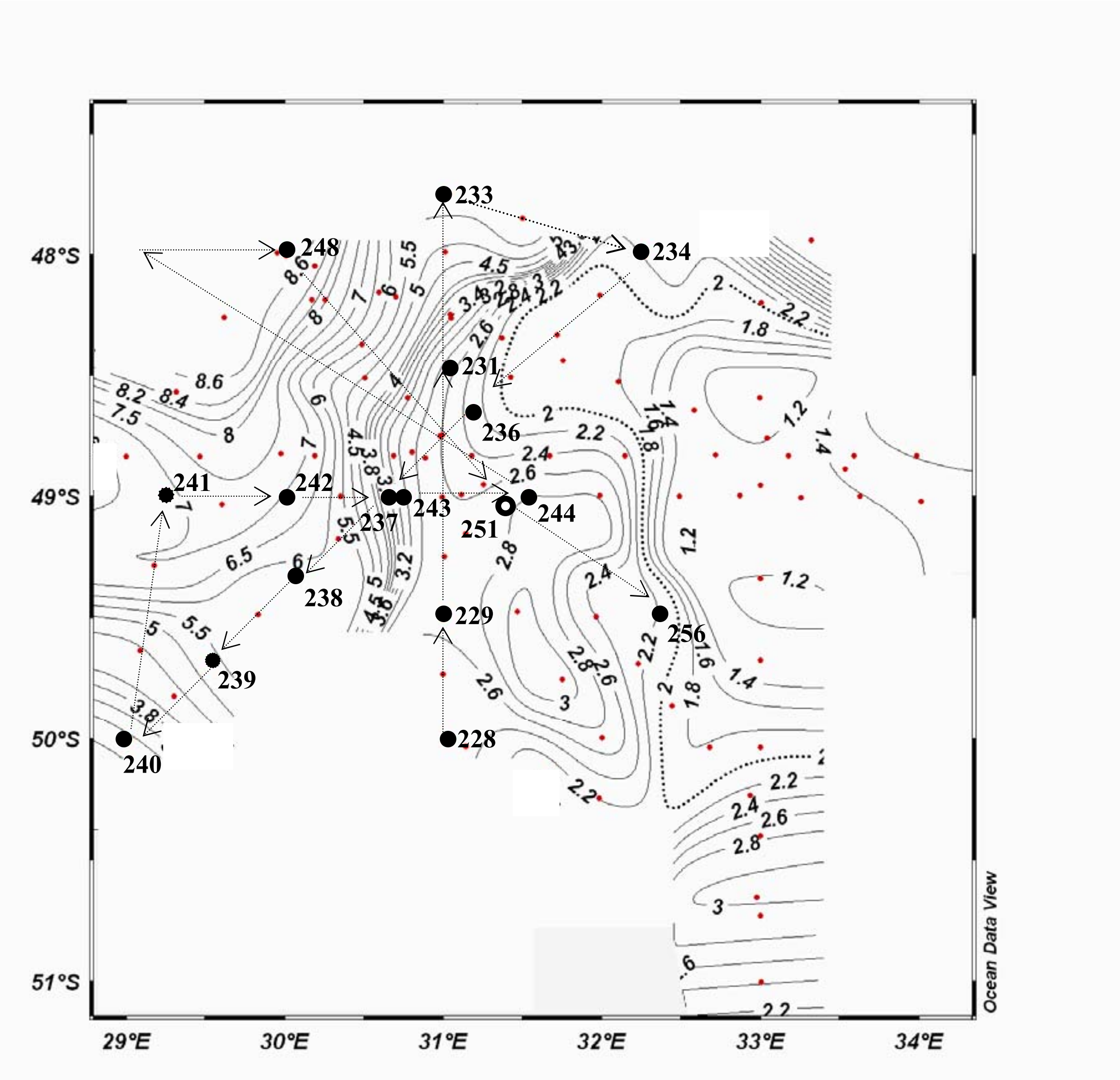

Fig. 3.2. Positions of the sampling stations occupied during the DEIMEC III survey conducted at the Antarctic Polar Frontal Zone, Southern Ocean, in April 2004. Arrows indicate the cruise track. Station positions are indicated by dark circles and station numbers are shown next to the station positions. Subsurface temperature (200m) isotherms are shown.

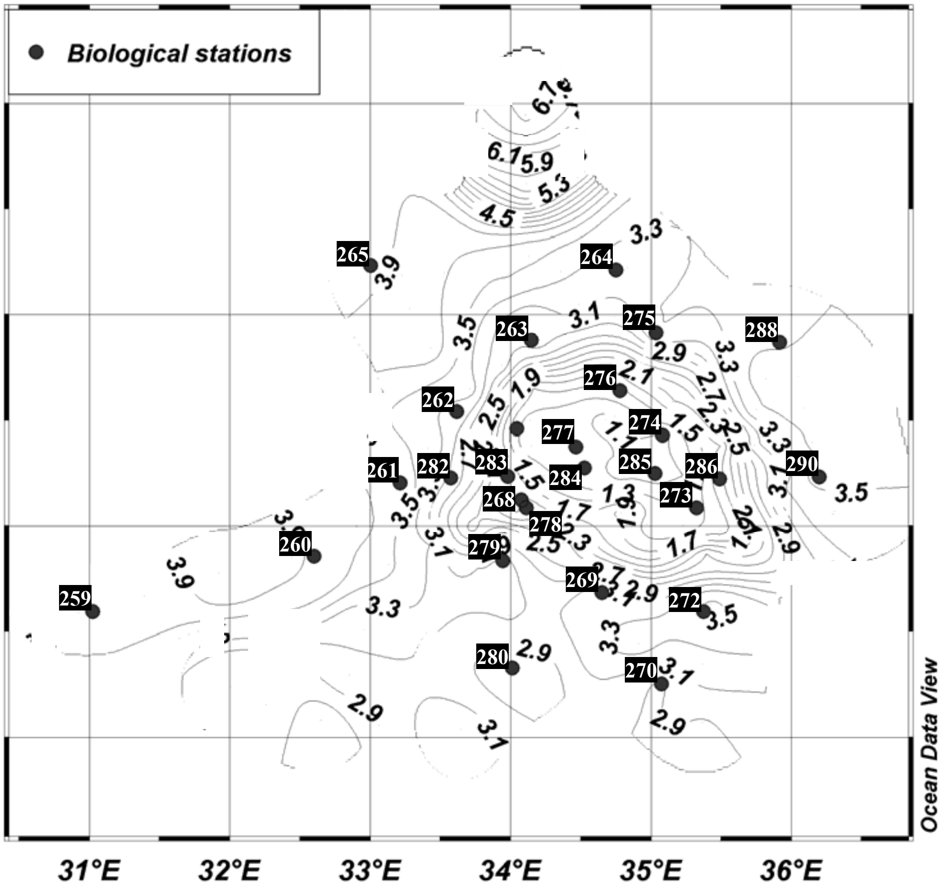

Fig. 3.3. Positions of the sampling stations occupied during the DEIMEC IV survey conducted at the Antarctic Polar Frontal Zone, Southern Ocean, in April 2005. Station positions are indicated by dark circles and station numbers are shown in dark blocks next to the station positions. Subsurface temperature (200m) isotherms are shown.

3.2. Macrozooplankton distribution

2001 Survey

The total biomass and abundance of the selected macrozooplankton during the survey varied between 0 and 0.18 mg wwt m^{-3} (mean 0.041 ±0.043 mg wwt m^{-3}) and between 0.379 and 43.731 $ind.m^{-3}$ (mean 12.543 ±13.26 $ind.m^{-3}$), respectively. The spatial distribution of macrozooplankton was quasi-uniform throughout the study area, with patchy low biomass values (Figure 3.4). The mean biomass of stations occupied in the Subantarctic Surface Water (SASW) (0.0293 ±0.0411 mg wwt m^{-3}) was lower than the mean biomass of stations in the PFZ (0.0474 ±0.046 mg wwt m^{-3}). The elevated biomasses (>0.1 mg wwt m^{-3}) were mainly associated with chaetognaths and ctenophores (stns. 190, 198, 208 and 210).

Pearson correlation analysis between densities (both abundance and biomass) and sea surface temperature showed weak correlations ($r^2 = 0.096$ for abundance; $r^2 = 0.013$ for biomass). A slightly stronger correlation was observed between densities and salinity ($r^2 = 0.411$ for abundance; $r^2 = 0.161$ for biomass). The correlation between densities of macrozooplankton and mesozooplankton was also poor ($r^2 = 0.002$ for abundances; $r^2 = 0.002$ for biomasses; $p > 0.05$ in all cases).

2004 Survey

The total biomass of the selected macrozooplankton during the survey varied between 0.55 and 41.55 mg wwt m^{-3} (mean 10.88 ± 11.69 mg wwt m^{-3}). The total abundance for the RMT-8 net and bongo nets varied between 0 and 0.017 $ind.m^{-3}$ (mean 0.004 ± 0.005 $ind.m^{-3}$), and between 0.866 and 29.97 $ind.m^{-3}$ (mean 10.435 ± 8.076 $ind.m^{-3}$), respectively. The spatial distribution of macrozooplankton was not uniform throughout the study area, with biomass being greatest between 29 and 32ºE, specifically at stations occupied within or near the frontal feature (Figure 3.5). The average biomass was much lower to the east (downstream region) than to the west of the fronts (Figure 3.5). The elevated biomass (>10 mg wwt m^{-3}) of macrozooplankton near and within the frontal feature was mainly associated with chaetognaths (stns. 237, 242, 244, 250).

Pearson correlation analysis between densities (both abundance and biomass) and sea surface temperature, and between densities and salinity, showed weak correlations (for correlation with temperature $r^2 = 0.008$ for abundance and $r^2 = 0.114$ for biomass; for correlation with salinity $r^2 = 0.054$ for abundance and $r^2 = 0.025$ for biomass; $p > 0.05$ in all cases). Similarly, there was a poor correlation between densities of mesozooplankton and macrozooplankton ($r^2 = 0.118$ for abundance and $r^2 = 0.117$ for biomass; $p > 0.05$ in both cases).

2005 Survey

The total biomass and abundance of the selected macrozooplankton during the survey varied between 0.0002 and 0.256 mg wwt m^{-3} (mean 0.072 ± 0.062 mg wwt m^{-3}) and between 0.04 and 17.066 ind.m^{-3} (mean 3.456 ±3.974 ind.m^{-3}), respectively. Generally, stations with low abundances all occurred outside the eddy (PFZ) (Figure 3.6) and had a mean biomass of 0.042 ±0.034 mg wwt m^{-3}. Stations inside the eddy (ASW) had the mean biomass of 0.17 ±0.417 mg wwt m^{-3}, while stations along the eddy edge had a mean biomass of 0.091 ±0.083 mg wwt m^{-3}. As with the other two surveys, the elevated biomass (>1 mg wwt m^{-3}) of macrozooplankton was mainly associated with chaetognaths.

Pearson correlation analysis showed a significant correlation between sea surface temperature and macrozooplankton biomass only ($r^2 = 0.288$; $p < 0.05$). The correlation between salinity and densities was poor ($r^2 = 0.026$ for biomass and $r^2 = 0.064$ for abundance; $p > 0.05$ in both cases). In contrast to the other two surveys, there was a strong correlation between macrozooplankton biomass and mesozooplankton biomass ($r^2 = 0.494$; $p < 0.05$), as well as between macrozooplankton abundance and mesozooplankton abundance ($r^2 = 0.386$; $p < 0.05$).

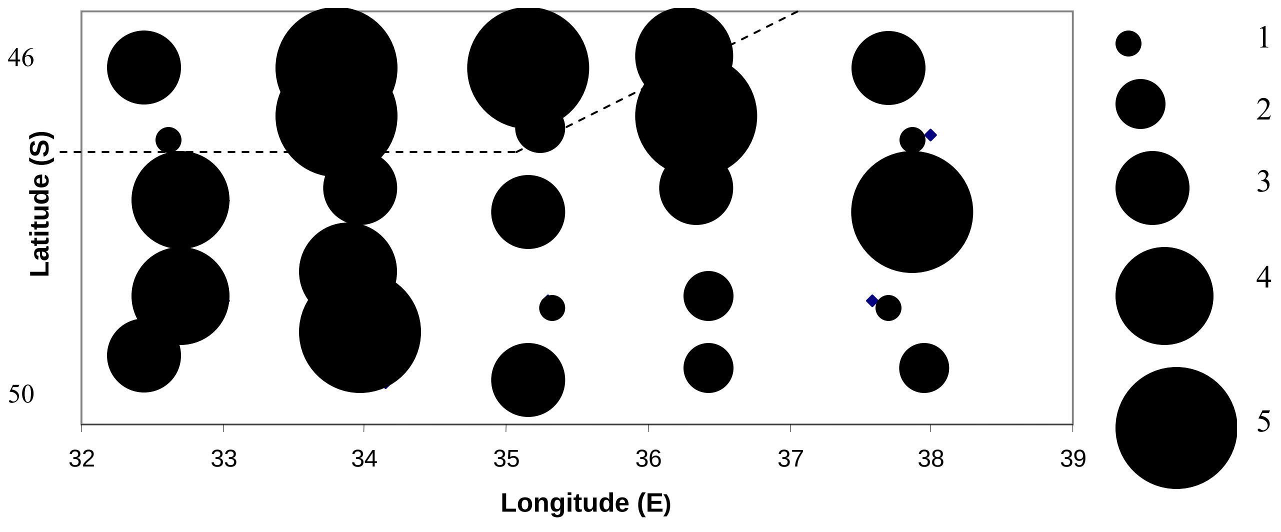

Fig. 3.4. Spatial distribution of the biomass of selected macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2001. The dotted line indicates the position of the Subantarctic Front.
1 = 0-0.005; 2 = 0.0051-0.009; 3 = 0.0091-0.015; 4 = 0.0159-0.1; 5 = 0.11-0.2 mg wwt m^{-3}.

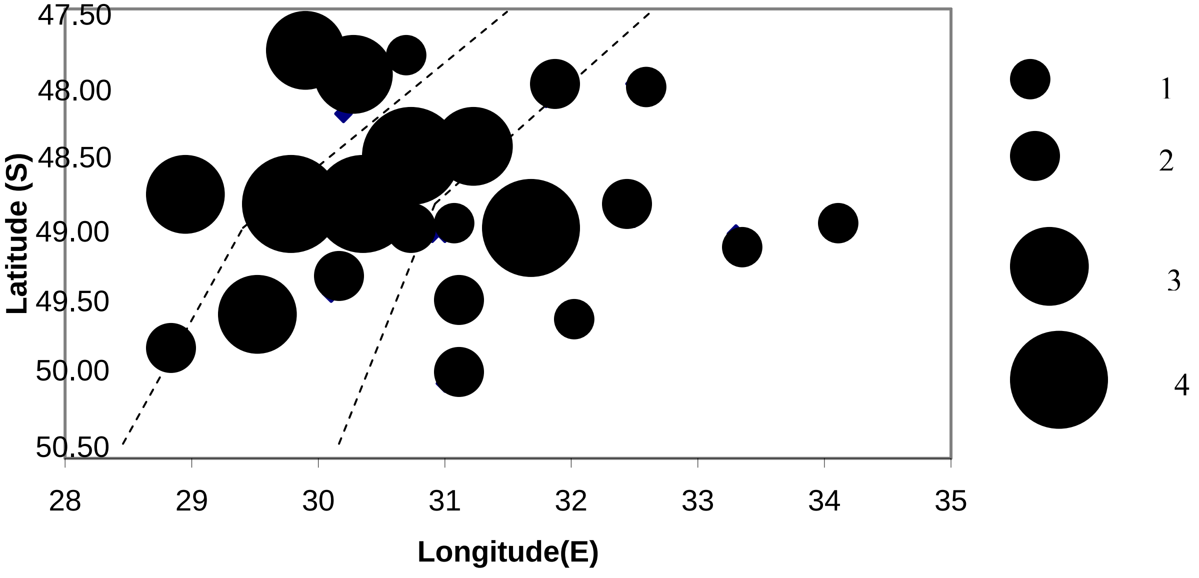

Fig. 3.5. Spatial distribution of the biomass of the selected macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2004. The diagonal lines indicate the position of the frontal feature (Subantarctic Front and Antarctic Polar Front). 1< 1; 2 = 1-4.99; 3 = 5-9.99; 4 > 10 mg wwt m^{-3}.

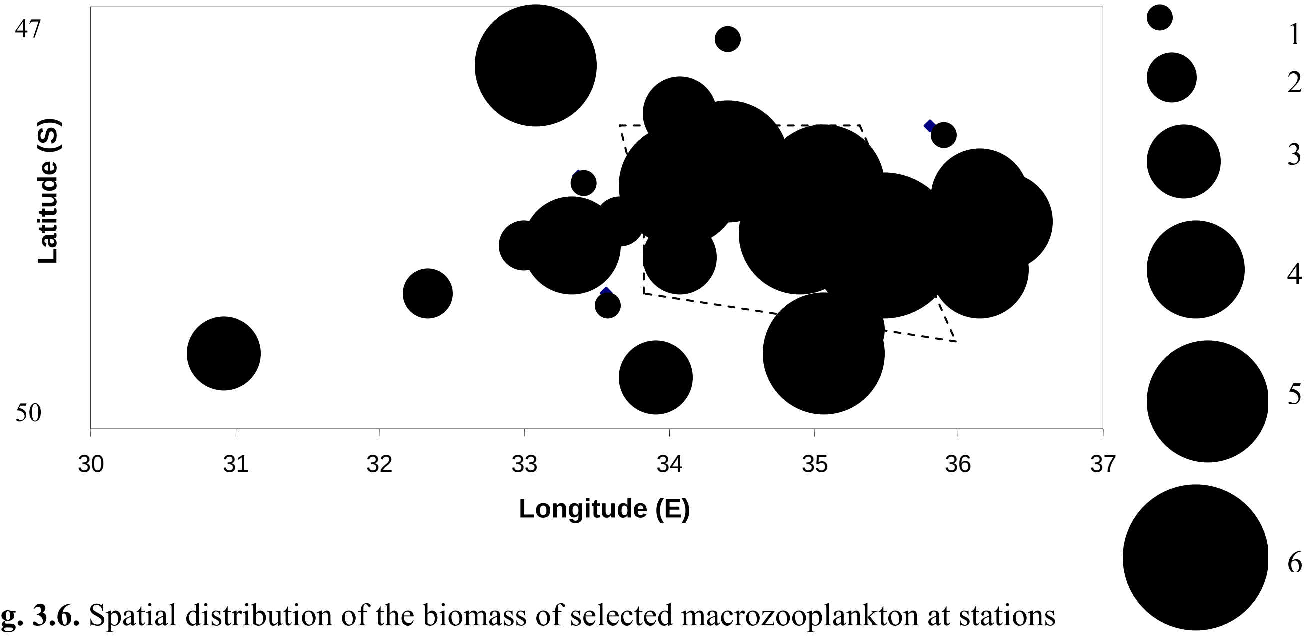

Fig. 3.6. Spatial distribution of the biomass of selected macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2005. The dotted line indicates the eddy edge.1 = 0-0.001; 2 = 0.0011-0.005; 3 = 0.0051-0.009; 4 = 0.0091-0.015; 5 = 0.00159-0.1; 6 = 0.11-0.26 mg wwt m^{-3}.

3.3. Plankton community structure

2001 Survey

A total of seven selected macrozooplankton species were collected during the 2001 survey (Table 3.1). The highest number of species (4) was recorded at stations 198 and 203, located in the Polar Frontal Zone (PFZ), south-west of the Subantarctic Front (SAF). The chaetognath group had the highest number of species (3), followed by hydromedusae (2 species) (Table 3.1). Most of the macrozooplankton were subantarctic species, such as the three chaetognaths *Eukrohnia hamata*, *Sagitta gazellae* and *Sagitta marri*, although a subtropical species of ctenophore, *Beroe cucumis*, was also observed (Table 3.1). Numerically, chaetognaths dominated, accounting for 99.65% (±11.97%) of the total average abundance (Figure 3.7). Ctenophores contributed < 0.63% (±0.98%) to the total average abundance. Chaetognaths dominated the wet weight, contributing 88.11% (±21.33%) to the total average biomass. *S. gazellae* alone contributed 52.32% (±30%) to the total average biomass. *Beroe cucumis* accounted for 8.57% (±17.77%) of the total average biomass while the remaining groups contributed < 2.03% (±5.87%) (Figure 3.8).

2004 Survey

A total of 15 and 5 selected macrozooplankton species were collected in the RMT-8 and bongo nets respectively (Table 3.2). The highest number of species (7) was recorded at station 233, west of the frontal feature. The chaetognaths had the highest number of species (4), followed by cephalopods (3 species) and medusae (3 species) (Table 3.2). Most of the macrozooplankton were subantarctic species e.g. chaetognaths *E. hamata*, *S. gazellae*, *Sagitta maxima*, and ctenophora, *Pleurobrachiidae* spp. There were, however, several species of subtropical origin, including the medusae *Heterotiara anonyma* and *Oceania armata*, and the cephalopod *Illex argentinus* (Table 3.2). Numerically, chaetognaths were the most prominent group in the RMT-8 net, accounting for 83% (±14.55%) of the total average abundance. They were followed by fragments of unidentified gelatinous zooplankton (5 ±1.3%), ctenophores (2 ±0.4%) and medusae (1.7

±0.7%). Unidentified gelatinous zooplankton (a), (b) and (c) were clearly different from each other, but have been analyzed together since individually they contribute little to the abundance. Similarly, chaetognaths were the most prominent group numerically in the bongo nets, accounting for 95% (±5.3%) of the total average abundance. No unidentified gelatinous zooplankton were sampled by the bongo nets. *Pleurobrachiidae* spp. were the next prominent group numerically, but only accounted for <1% (±0.001%) of the total abundance (Figure 3.9) When the biomasses of the RMT-8 and bongo nets were combined, chaetognaths again dominated the samples, contributing 85% (±6.3%) of total wet weight. *S. gazellae* alone contributed 58% (±4.8%) to total biomass. These were followed by ctenophores and the unidentified gelatinous zooplankton which accounted for 10% (±1.9%) and 3% (±0.5%) to the total biomass respectively. The remaining groups contributed <3% (±0.12%) (Figure 3.10).

2005 Survey

Only five carnivorous macrozooplankton species were collected during the survey, namely four species of chaetognaths and one species of ctenophore (Table 3.3). At the majority of stations only *E. hamata* and *S. gazellae* occurred. All the species were subantarctic in origin, although the ctenophore *B. cucumis* may also occur in subtropical regions (Mianzan, 1999). As in the other two surveys, chaetognaths dominated numerically, accounting for 96.04% ±8.57% of the total average abundance. *E. hamata* alone contributed 75.79% ±25.71% to the total average abundance while *B. cucumis* only contributed 4.1% ±18.9% (Figure 3.11). Chaetognaths contributed 94.2% ±17.37% to the wet weight, thus dominating the macrozooplankton biomass. *S. gazellae* alone contributed 50.03 ±39.33% to the total biomass, while *B. cucumis* contributed 10.41 % ±27.26% (Figure 3.12).

In the appendix, table 3.21 lists all the selected carnivorous macrozooplankton species collected during the three surveys and table 3.22 gives the abundance and biomass values of stations sampled during the three surveys.

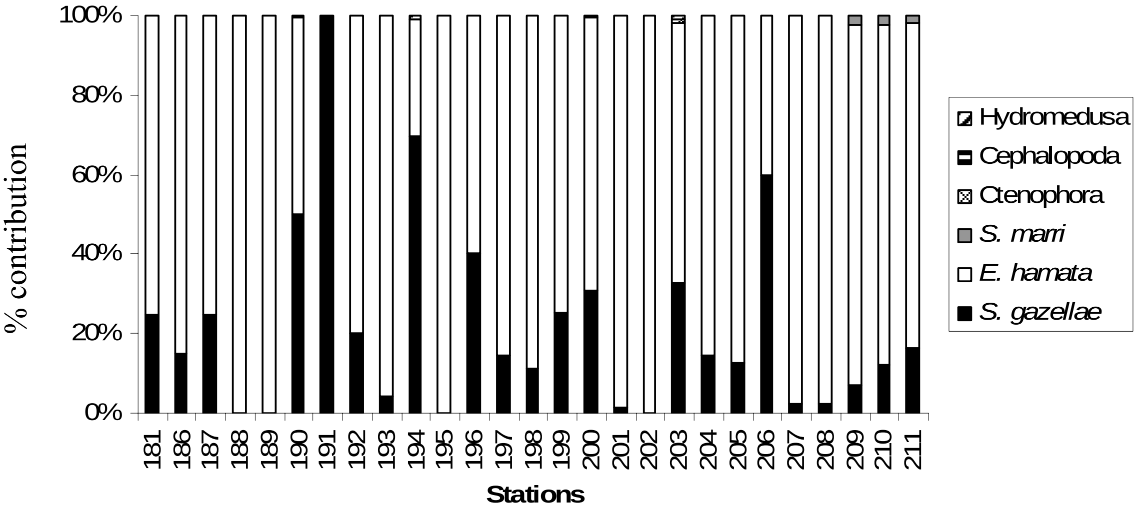

Fig. 3.7. Percentage contribution of selected carnivorous macrozooplankton to the total carnivorous macrozooplankton abundance at stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2001.

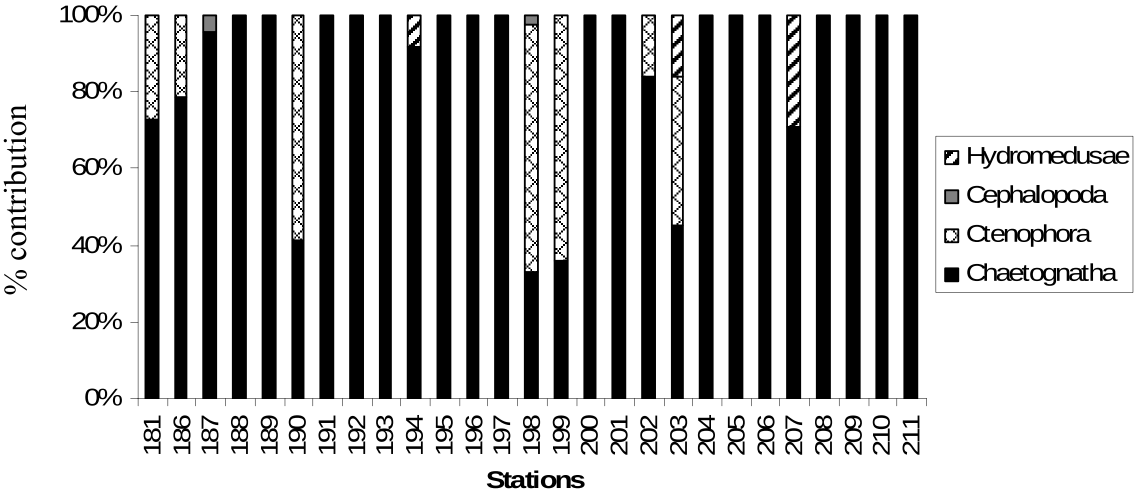

Fig. 3.8. Percentage contribution of selected carnivorous macrozooplankton to the total carnivorous macrozooplankton biomass at stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2001.

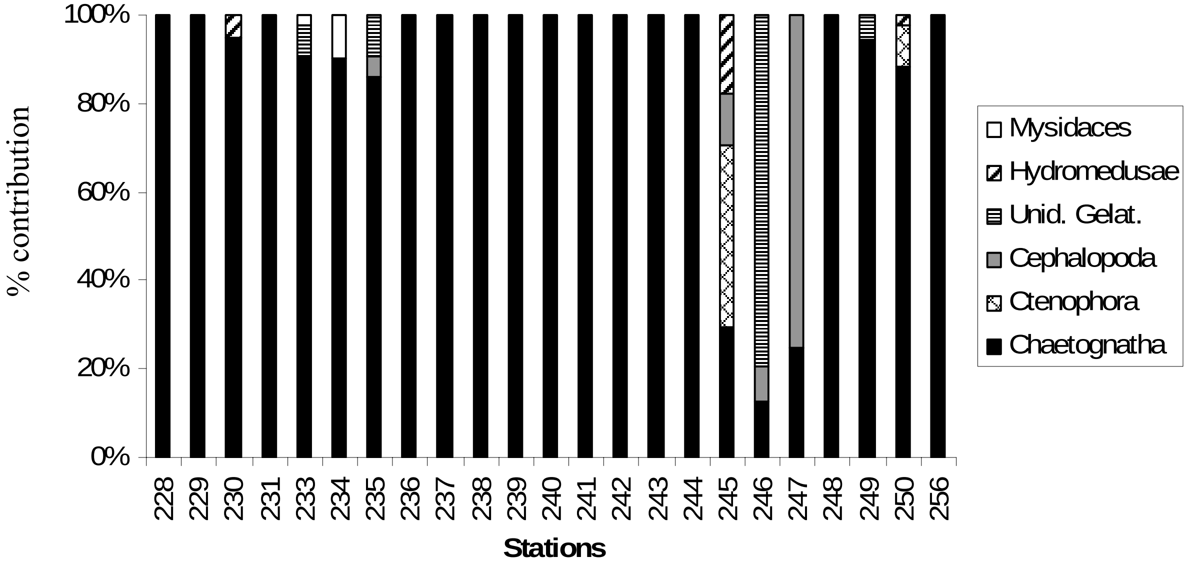

Fig. 3.9. Percentage contribution of selected carnivorous macrozooplankton to the total carnivorous macrozooplankton abundance at stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2004.
Unid. Gelat = Unidentified gelatinous zooplankton (probably ctenophores)

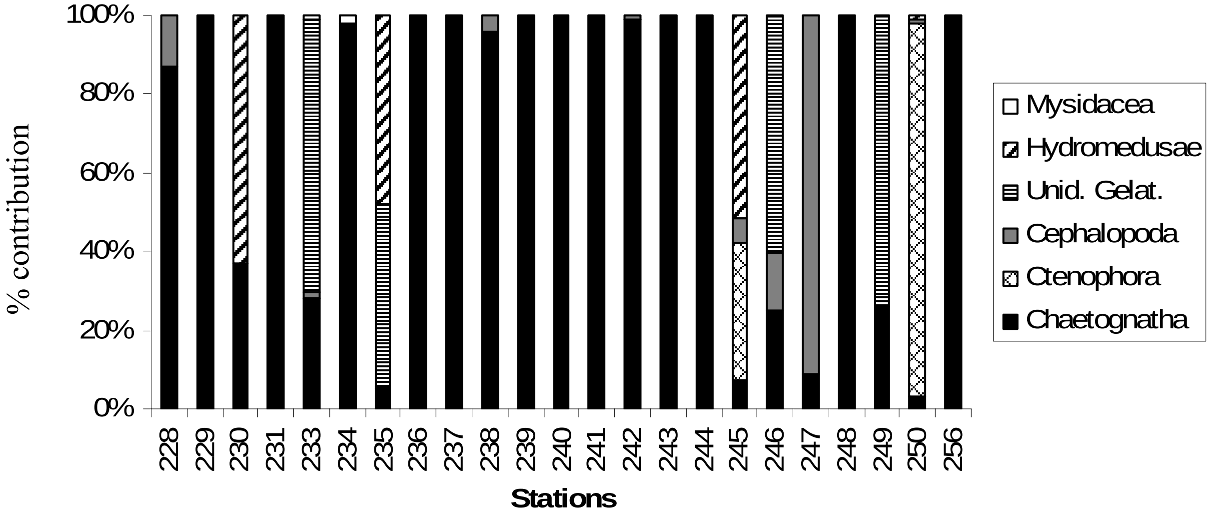

Fig. 3.10. Percentage contribution of the selected carnivorous macrozooplankton to the total carnivorous macrozooplankton biomass at all stations occupied in the survey area at the Antarctic Polar Frontal Zone in late austral summer (April/May) 2004.
Unid. Gelat. = Unidentified gelatinous zooplankton (probably ctenophores)

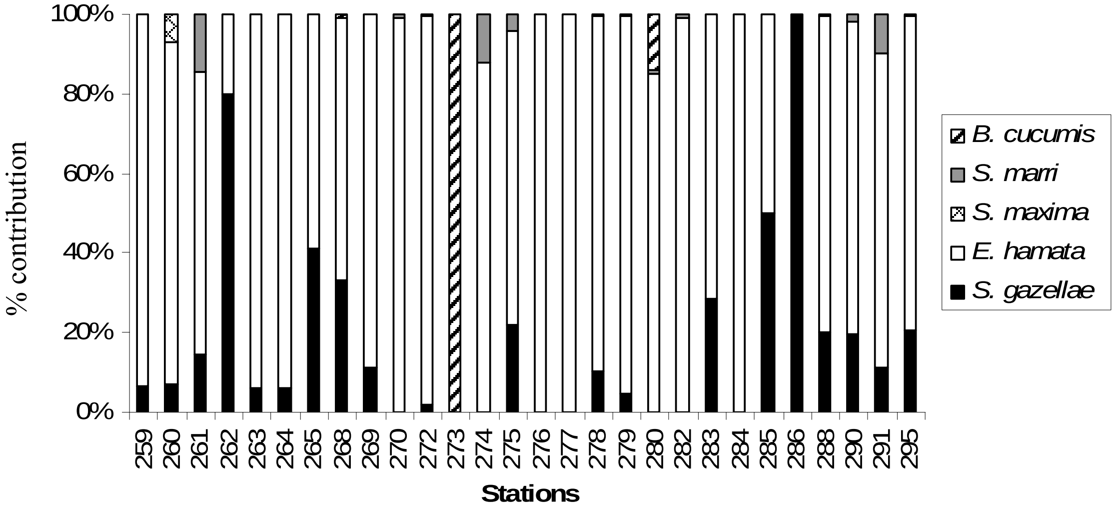

Fig. 3.11. Percentage contribution of selected carnivorous macrozooplankton to the total carnivorous macrozooplankton abundance at stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2005.

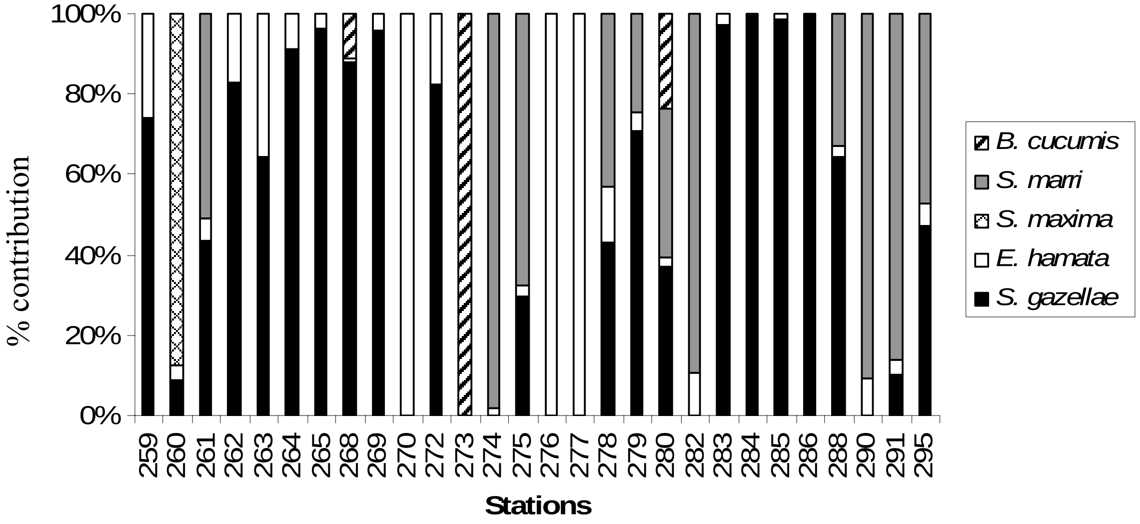

Fig. 3.12. Percentage contribution of selected carnivorous macrozooplankton to the total carnivorous macrozooplankton biomass at stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2005.

3.3.1. Numerical analyses

2001 Survey

Hierarchical cluster analysis revealed the presence of three major groups of stations at approximately the 35% level of similarity (Figure 3.13). The first group consisted of one station only, situated north-west of the Subantarctic Front (SAF). The second group comprised of eighteen stations all but one (stn. 101) of which were located south of the SAF. Group 3 combined eight stations which were dispersed throughout the survey region. Group 2 had the highest number of species (n = 7), while group 1 had the lowest number of species (n = 2) (Table 3.1).

The highest overall between-group average dissimilarity (95.46%) was found between groups 1 and 2, with *Eukrohnia hamata* being absent from group 1. *E. hamata* was also responsible for 69.13% and 49.23% of the average dissimilarity index between groups 2 and 3 (77.31% average dissimilarity) and between groups 1 and 3 (71.93% average dissimilarity) respectively.

Average macrozooplankton densities are given in Table 3.1. Group 2 had the highest average abundance (17.86 ind.m^{-3}), followed by group 3 (2.01 ind.m^{-3}). A significant difference in average abundance was found between groups 2 and 3 only ($p < 0.05$). Taxonomic composition between groups differed. Group 2 contained all three of the chaetognath species observed during the survey, and it was also the only group containing the cephalopod *Brachioteuthis riisei*. Chaetognaths dominated all groups.

SIMPER analysis showed the average similarity among stations of group 3 to be the highest (64.42%) and this was attributed to the presence of *E. hamata* and *Sagitta gazellae*. The similarity among stations of group 2 was 59.49% and was attributed to the presence of *E. hamata*.

2004 Survey

RMT-8 net data

Hierarchical cluster analysis revealed the presence of three major groups of stations at approximately the 10% level of similarity (Figure 3.14). The first group combined three stations located east of the frontal feature. The second group comprised two stations located west of the frontal feature and group three combined three stations found within or near the frontal feature (Figure 3.15). Groups 2 and 3 had a higher number of species ($n = 8$) than group 1($n = 6$) (Table 3.2). The highest overall dissimilarity (96.77%) was found between groups 2 and 1, with *S. gazellae* being responsible for >80% of the between-group average dissimilarity index. Unidentified gelatinous zooplankton (a) and (c) were each responsible for <5% of the average dissimilarity. *S. gazellae* also accounted for 76.80% of the average dissimilarity index between groups 3 and 1. *Eukrohnia hamata* was another major contributor to the dissimilarity index between groups 3 and 1, being responsible for >19% of the average dissimilarity. The dissimilarity between the groups of stations could be attributed to changes in the contribution of individual species to the total abundance rather than species presence or absence.

Average macrozooplankton densities of different groups are given in Table 3.2. Group 2 had the highest average abundance (13.2 ind.m^{-3}), while groups 1 and 3 had lower abundances (3.2 ind.m^{-3} and 2.7 ind.m^{-3} respectively). No significant difference in average abundance was found between groups ($p > 0.5$). Taxonomic composition among groups differed. The zooplankton community of group 2 and group 3 was dominated by chaetognaths (91 and 68% respectively). In group 1 the zooplankton community was dominated by unidentified gelatinous zooplankton (43%).

SIMPER analysis showed the average similarity between stations to be highest (59%) within group 2. Group 1 was the least homogenous community with the average similarity among stations being 16%. Interestingly, *E. hamata* was absent in both group 1 and group 2. Mysids occurred in group 2 only, whereas cephalopods occurred in groups 1 and 3. Abundance of medusae was 0.0004 ind.m^{-3} in group 3 and 0.0002 ind.m^{-3} in group 1 with no medusae in group 2 (Figure 3.14).

Bongo nets data

Hierarchical cluster analysis revealed the presence of only two groups of stations at approximately the 10% level of similarity (Figure 3.16). The first group consisted of station 242 only, which was located west of the frontal feature and had a macrozooplankton abundance of 0.866 ind.m^{-3}. The second group comprised of the remaining bongo nets stations (n = 14) and had an average abundance of 11.118ind.m^{-3}. The overall dissimilarity between the two groups was 77% with *E. hamata* and *S. gazellae* accounting for 78 and 99% of the between-group average dissimilarity index. Average macrozooplankton densities of the different groups are given in Table 3.2. Even though group 1 comprised of only one station, there was no significant difference in average abundance between the groups ($p > 0.05$). Taxonomic composition between the two groups differed only in the respect that station 242 was the only station where *E. hamata* was absent.

SIMPER analysis showed the average similarity among stations of group 2 to be 49%, with *S. gazellae* being responsible for 100% of the similarity.

2005 Survey

Five major groups of stations were revealed by hierarchical cluster analysis at approximately the 18% level of similarity. Group 4 consisted of a single station, and group 5 consisted of two stations, but only a single species occurred at each of these stations, and they were therefore omitted from further analysis (Figure 3.17). Group 1 combined three stations, all of which were located inside the eddy. Group 2 combined twelve stations, nine of which were located in the Polar Frontal Zone (PFZ), while three and two stations were located at the eddy edge and in the Antarctic Surface Water (ASW) inside the eddy, respectively. Eight stations comprised group 3, five of which were located along the eddy edge and the remaining three were located in the PFZ.

Ignoring groups 4 and 5, the highest between-group average dissimilarity index was found between groups 3 and 1 (80.12%), while the between-group average dissimilarity index between groups 3 and 2, and between groups 2 and 1 was 42.11% and 63.68% respectively. *E. hamata* and *S. gazellae* were responsible for the dissimilarity between all the groups analyzed. At the highest dissimilarity (between groups 3 and 1), *E. hamata* and *S. gazellae* accounted for 77.82% and 99.03% of the dissimilarity, respectively. Between groups 2 and 1, *E. hamata* and *S. gazellae* accounted for 65.76% and 91.81% of the dissimilarity respectively, while between groups 3 and 2 they accounted for 67.55% and 95.02% respectively. Group 2 was the only group in which *Beroe cucumis* occurred. Table 3.3 shows the average macrozooplankton abundance of the different groups. The average abundances for groups 1,2 and 3 were 0.52 ind.m^{-3}, 1.81 ind.m^{-3} and 8.14 ind.m^{-3}, respectively. ANOSIM found a significant difference among the average abundances of all of the groups analyzed ($p < 0.05$).

SIMPER analysis showed the average similarity among stations of group 1 to be 73.77%, with *E. hamata* being responsible for 100% of the similarity. The average similarity among stations of groups 2 and 3 was 73.87% and 75.97% respectively. In group 3 *E. hamata* was responsible for 90.4% of the similarity, while in group 2 both *E. hamata* and *S. gazellae* were responsible for the similarity, accounting for 83.84% and 98.56% of the average similarity respectively.

Different nets were used in different years, but there was no significant effect of net type (see above). When the abundances of macrozooplankton were compared among the three years investigated, it was found that the total average abundances of 2005 was significantly different from those recorded in 2001 (Tukey's test; $p = 0.002$). The total average abundances of macrozooplankton in 2001, 2004 and 2005 were 12.54 ±13.26 ind. m^{-3}, 10.43 ±8.36 ind. m^{-3} and 3.31 ±4.12 ind. m^{-3}, respectively.

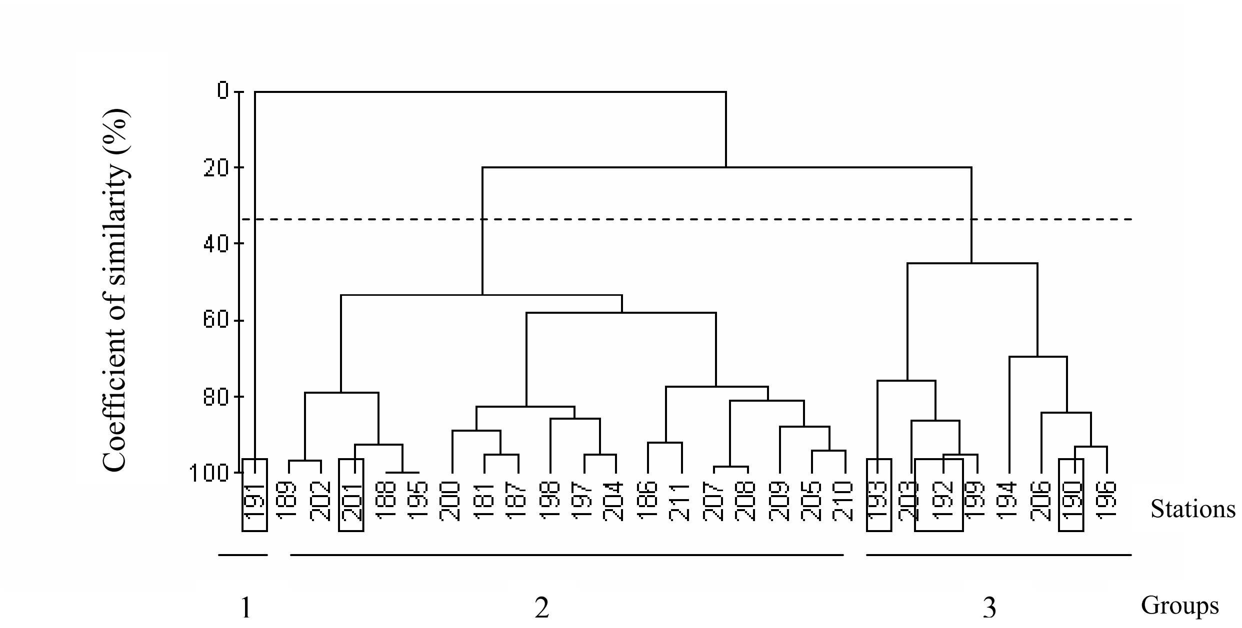

Fig. 3.13. Dendrogram of cluster analysis comparing the zooplankton abundance of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2001. Stations in blocks were located in Subantarctic Surface Waters. The remaining stations were located in the Polar Frontal Zone waters. The dashed line represents the cut-off level used to delimit assemblages.

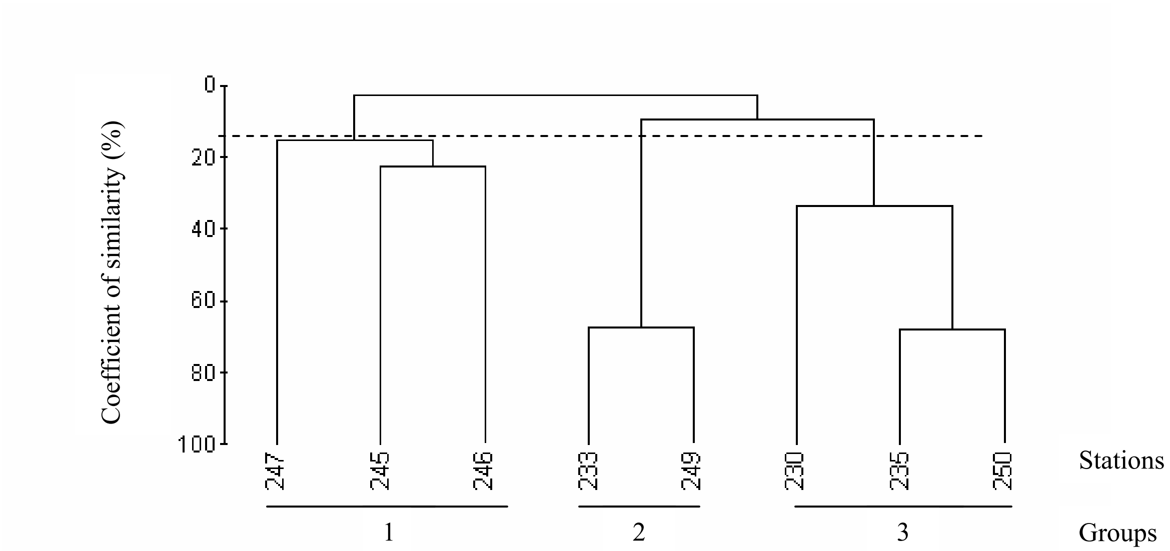

Fig. 3.14. Dendrogram of cluster analysis comparing the zooplankton abundance of selected carnivorous macrozooplankton at each RMT-8 station occupied during late austral summer (April/May) 2004. Stations of group 1 were located south-east in the frontal feature, stations in group 2 were located north-west in the feature and stations of group 3 were located within/in the vicinity of the frontal feature. The dashed line represents the cut-off level used to delimit assemblages.

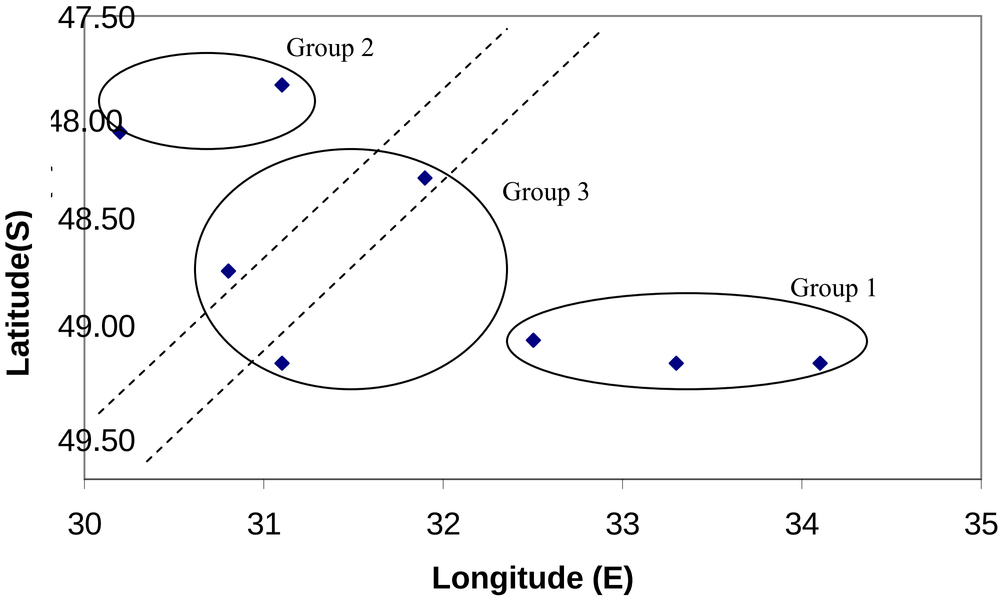

Fig. 3.15. Position of the RMT-8 sampling stations occupied during late austral summer (April/May) 2004. Groups identified by cluster analysis have been circled. The diagonal lines indicate the position of the frontal feature (combined Subantarctic and Antarctic Polar Fronts).

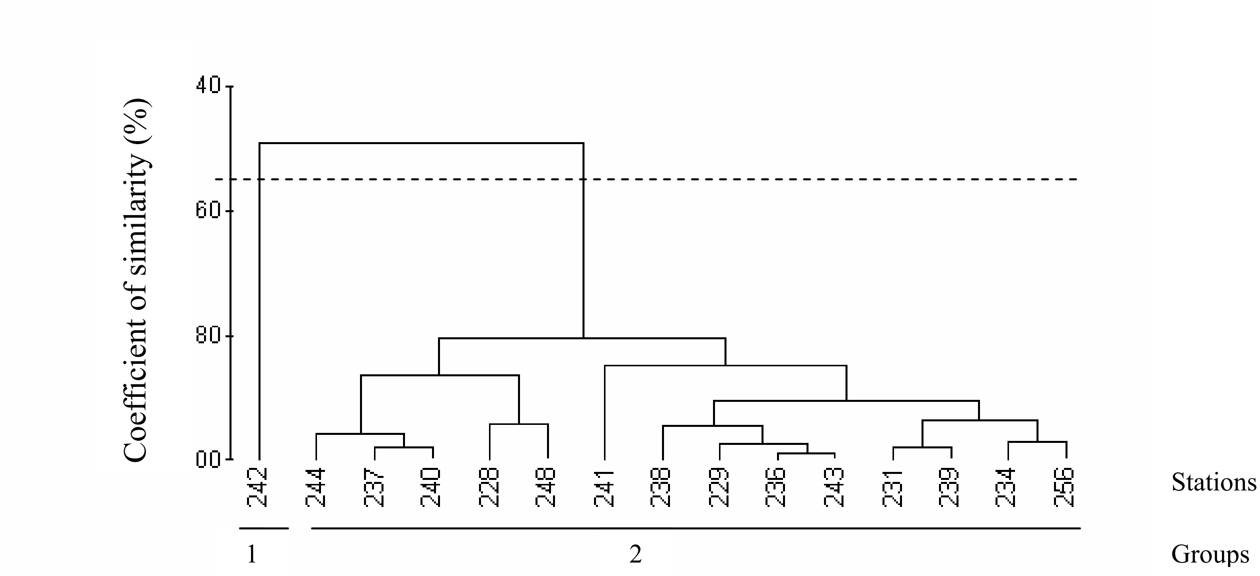

Fig. 3.16. Dendrogram of cluster analysis comparing the zooplankton abundance of selected carnivorous macrozooplankton at each Bongo station occupied during late austral summer (April/May) 2004. Group 1 (station 242) was located within the frontal feature. The remaining stations were located throughout the survey area. The dashed line represents the cut-off level used to delimit assemblages.

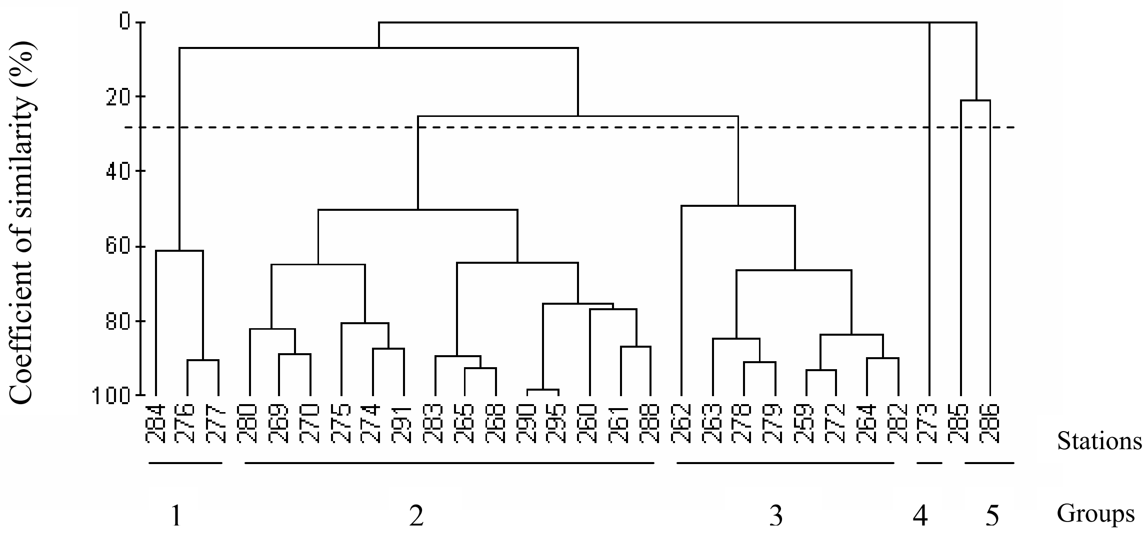

Fig. 3.17. Dendrogram of cluster analysis comparing the zooplankton abundance of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2005. Group 1: all stations located inside eddy; Group 2: nine stations in the Polar Frontal Zone, three stations at eddy edge, two stations inside the eddy; Group 3: five stations at eddy edge, three stations in the Polar Frontal Zone. Groups 4 and 5 were omitted from the analysis. The dashed line represents the cut-off level used to delimit assemblages.

3.3.2. Biomass

2001 Survey

Four major groups were revealed by hierarchical cluster analysis at approximately the 18% level of similarity (Figure 3.18). Group 1 combined two stations, 198 and 199, which were located south of the front. Group 2 consisted of sixteen stations, two of which were located north of the front in the Subantarctic Surface Water (SASW). Groups 3 and 4 consisted of three and six stations respectively. Only groups 2 and 4 had certain stations located in the SASW.

The average dissimilarity between groups was relatively high: the between-group average dissimilarity index between groups 2 and 3, between groups 2 and 4, and between groups 3 and 4 was 85.85%, 83.46% and 62.64% respectively. *Eukrohnia hamata* was responsible for >90% of the dissimilarity between groups 2 and 3, and between groups 2 and 4, while *Sagitta gazellae* was responsible for >90% of the dissimilarity between groups 3 and 4. The dissimilarity between groups 2 and 1, and between groups 4 and 1, was attributed not only to *S. gazellae* and *E. hamata*, but also to *Beroe cucumis* which accounted for >68% of the dissimilarity between both groups 3 and 1 (average dissimilarity index = 83.48%), and between groups 4 and 1 (average dissimilarity index = 83.69%) The group average dissimilarity index between groups 2 and 1 was 65.09%, and was primarily due to *E. hamata* which was responsible for 96.86% of the dissimilarity. The average macrozooplankton biomass of the different groups is given in Table 3.4. There was a significant difference found in the average biomass between groups 2 and 3, and between groups 2 and 4 ($p < 0.05$).

SIMPER analysis showed the average similarity between stations of groups 2 and 4 to be 58.62% and 60.70% respectively, and this similarity was attributed to the presence of both *S. gazellae* and *E. hamata*. The similarity between stations of group 3 was 76.13%, of which 100% was attributed to *E. hamata*. The similarity between stations of group 1 was 42.41%, with *B. cucumis, E. hamata* and *S. gazellae* being responsible for 63.99%, 87.98% and 100% of the similarity, respectively.

2004 Survey

RMT-8 net data

Total biomass of the carnivorous macrozooplankton investigated was highly variable, ranging from 0.05 to 16.12 mg wwt m^{-3}. *Pleurobrachiidae* spp. contributed >55% (±29.7%) to the total average biomass. However, *Pleurobrachiidae* spp. were only found at stations 245 and 250. The next most prominent groups contributing to the total average biomass were unidentified gelatinous zooplankton (a) and chaetognaths, accounting for 13% (±31.4%) and 12% (±12%), respectively.

Two major groups of stations were revealed within the region of investigation by hierarchical cluster analysis at approximately the 10% level of similarity (Figure 3.19). The first group combined four stations which were dispersed throughout the survey area. The second group also combined four stations, three of which were located east of the frontal feature. Group 1 only had one species more than group 2. The overall dissimilarity between the groups was 78.48%, with *Oceania armata* and *Teuthida* spp. accounting for most of the dissimilarity, being responsible for 90.14% and 86.51% of the between-group average dissimilarity index respectively. Generally, the average dissimilarity could be attributed to the presence or absence of individual species. Average macrozooplankton biomass of the groups is given in Table 3.5. No significant difference in average biomass was found between groups ($p > 0.05$).

SIMPER analysis showed the average similarity among stations of group 1 to be 31.64%. The following species were responsible for the similarity: *Pleurobrachiidae* spp. (94.26%), *Heterotiara anonyma* (85.08%), unidentified gelatinous zooplankton (b) (75.24%), and *S. gazellae* (59.41%). In group 2, the average similarity between stations was lower than in group 1, namely 26.17%, with *Sagitta maxima* accounting for 100% of the similarity. Other species responsible for the similarity between stations of group 2 were, in order of importance, unidentified gelatinous zooplankton (c) (89.58%), *Illex argentinus* (75.59%) and *S. gazellae* (45.58%).

Bongo nets data

The total biomass of the carnivorous macrozooplankton investigated was also highly variable in the bongo nets as it was in the RMT-8 net. The total biomass ranged from 0 to 41.55 mg wwt m^{-3}. The chaetognaths *E. hamata* and *S. gazellae* contributed the most to the total average biomass, namely 72% (±32.4%) and 33% (±33.2%) respectively. Hierarchical cluster analysis revealed four major groups of stations at approximately the 48% level of similarity (Figure 3.20). Groups 1, 2 and 3 comprised of single stations only, namely stations 242, 234 and 236 respectively, all of which were located in close proximity to the frontal feature. Group 4 combined the remaining twelve bongo stations, which were dispersed throughout the survey area. The between-group average dissimilarity was exceptionally high. The dissimilarity between groups 4 and 3, 2 and 3, 2 and 1, 3 and 1 was 100% and could be attributed to the absence of individual species. The average dissimilarity between groups 4 and 2 was 96.64%, with *S. gazellae* and *Eucopia* spp. being responsible for 73.69% and 97.95% of the dissimilarity respectively. The average dissimilarity between groups 4 and 1 was only 57.92% and *S. gazellae* and *Pleurobrachiidae* spp. were responsible for 22.92% and 17.31% of the dissimilarity respectively. Generally, the average dissimilarity could be attributed to the contribution and/or the presence or absence of individual species. Table 3.6 shows the average macrozooplankton biomass of the different groups. As in the RMT-8 net, no significant difference in biomass was found between groups ($p > 0.05$).

SIMPER analysis showed the average similarity among stations of group 4 to be 83.33% with *E. hamata* and *S. gazellae* being responsible for 50.84% and 100% of the similarity, respectively.

It is important to note that, although the bongo nets collected fewer species than the RMT-8 net, the biomass values obtained from stations sampled by either of the two net types were not significantly different (*t*-test; $p > 0.05$).

2005 Survey

Hierarchical cluster analysis revealed six major groups of stations at approximately the 10% level of similarity (Fig. 3.21). Group 5 consisted of a single station only (stn. 273) in which only *Beroe cucumis* occurred, and it was therefore excluded from further analysis. Group 1 combined three stations, two of which were located inside the eddy (Antarctic Surface Water (ASW)), and one was located outside the eddy (Polar Frontal Zone (PFZ)). Group 2 combined nine stations, the majority of which were in the PFZ. Stations 260 formed group 3 in which three species occurred, and it was located in the SASW. Group 4 combined twelve stations, two of which were located in the ASW, and five each were located in the PFZ and along the eddy edge. The final group, group 6, combined two stations which were located inside the eddy (ASW).

Ignoring group 5, which was 100% dissimilar from all the other groups, the highest between-group average dissimilarity index was 98.9% between groups 1 and 6 where *S. gazellae* and *E. hamata* were responsible for 67.72% and 100% of the dissimilarity respectively. Groups 4 and 2 were the least dissimilar from each other, with *S. gazellae* and *Sagitta marri* contributing 48.14% and 91.02% to a between-group average dissimilarity index of 67.06%. *Sagitta maxima* was the most responsible for the dissimilarity between group 3 and the other groups. *S. gazellae* was the only species that contributed to the dissimilarity between all the groups. Table 3.7 shows the average macrozooplankton biomass of the different groups. Significant differences in the average biomass were found between the following groups: Groups 4 and 2; groups 4 and 1; groups 4 and 6; groups 2 and 1; and groups 2 and 6 ($p < 0.05$).

SIMPER analysis showed the average similarity between stations of group 2 to be the highest (73.42%), with *S. marri* and *S. gazellae* contributing 81.94% and 95.28% to the average similarity respectively. The lowest average similarity (18.01%) was found between stations of group 6 where *S. gazellae* was responsible for 100% of the similarity. The average similarity between stations of groups 4 and 1 was 57.13% and 62.97%, respectively.

There were no significant differences in the total average biomasses of macrozooplankton among the three years investigated (Tukey’s test; $p > 0.05$ for all three years).

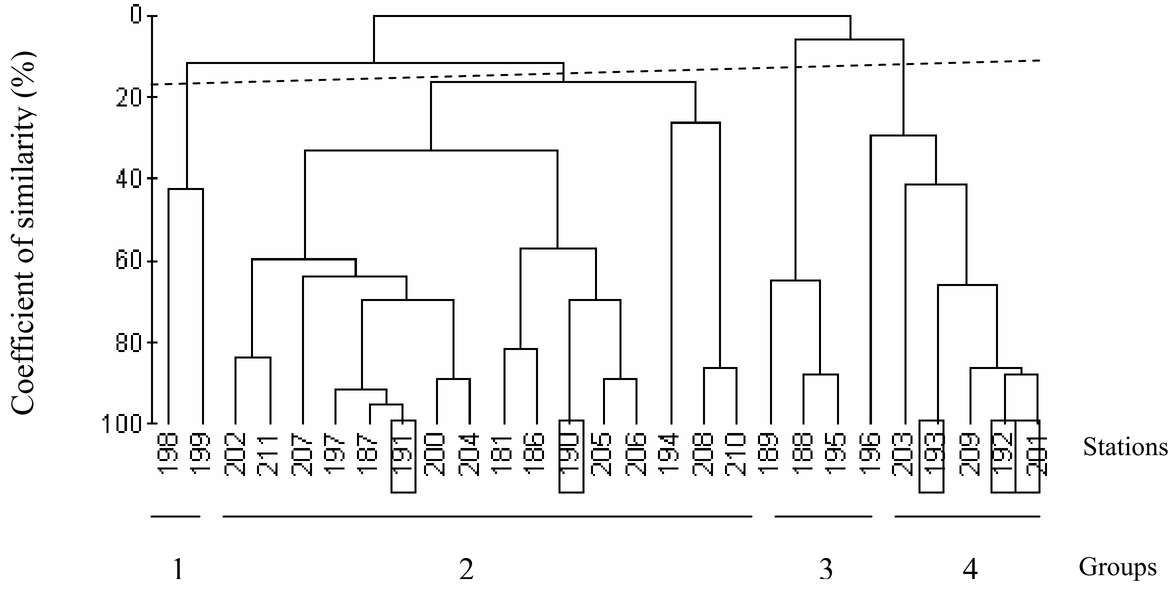

Fig. 3.18. Dendrogram of cluster analysis comparing the zooplankton biomass of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2001. Stations in blocks were located in the Subantarctic Surface Water. The remaining stations were located in the Polar Frontal Zone. The dashed line represents the cut-off level used to delimit assemblages.

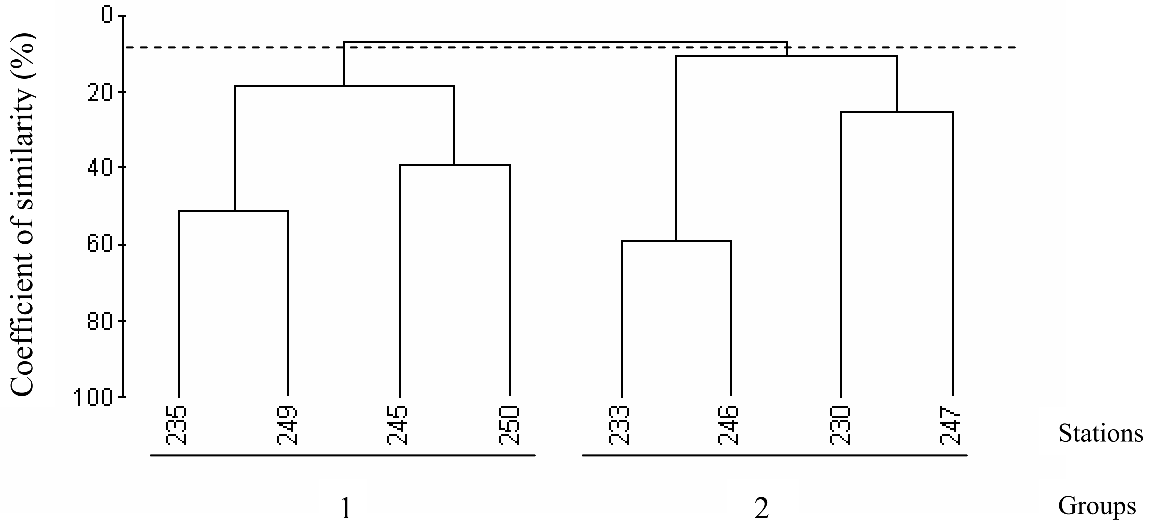

Fig. 3.19. Dendrogram of cluster analysis comparing the zooplankton biomass of selected carnivorous macrozooplankton at RMT-8 net stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2004. The dashed line represents the cut-off level used to delimit assemblages.

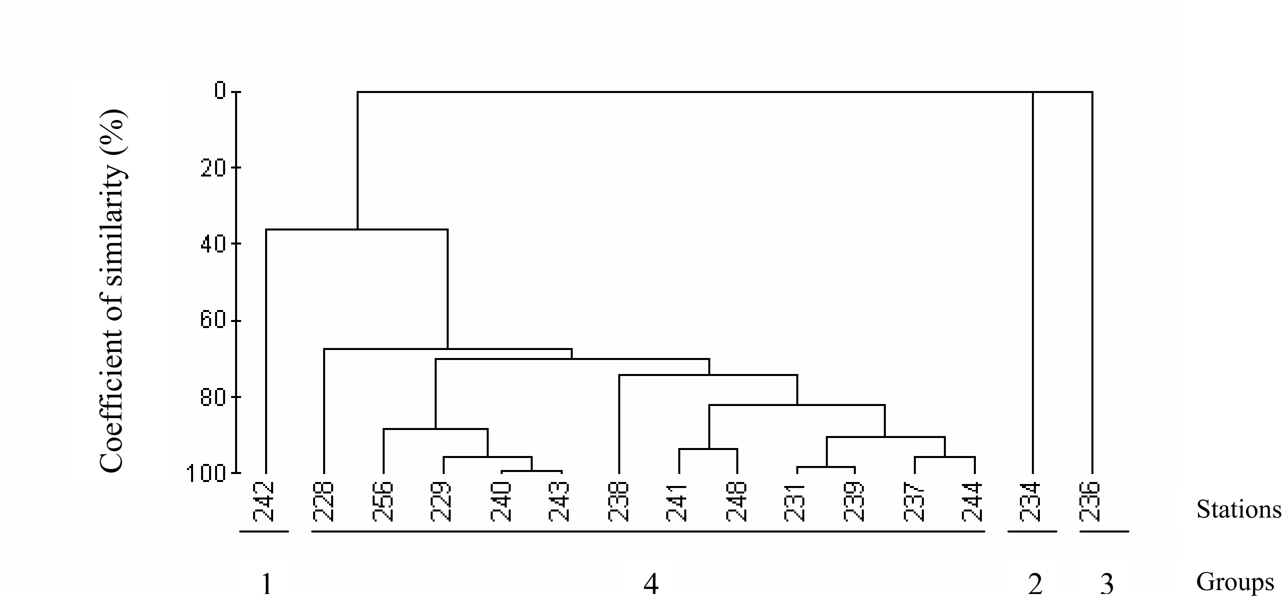

Fig. 3.20. Dendrogram of cluster analysis comparing the zooplankton biomass of selected carnivorous macrozooplankton at bongo stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2004. The dashed line represents the cut-off level used to delimit assemblages.

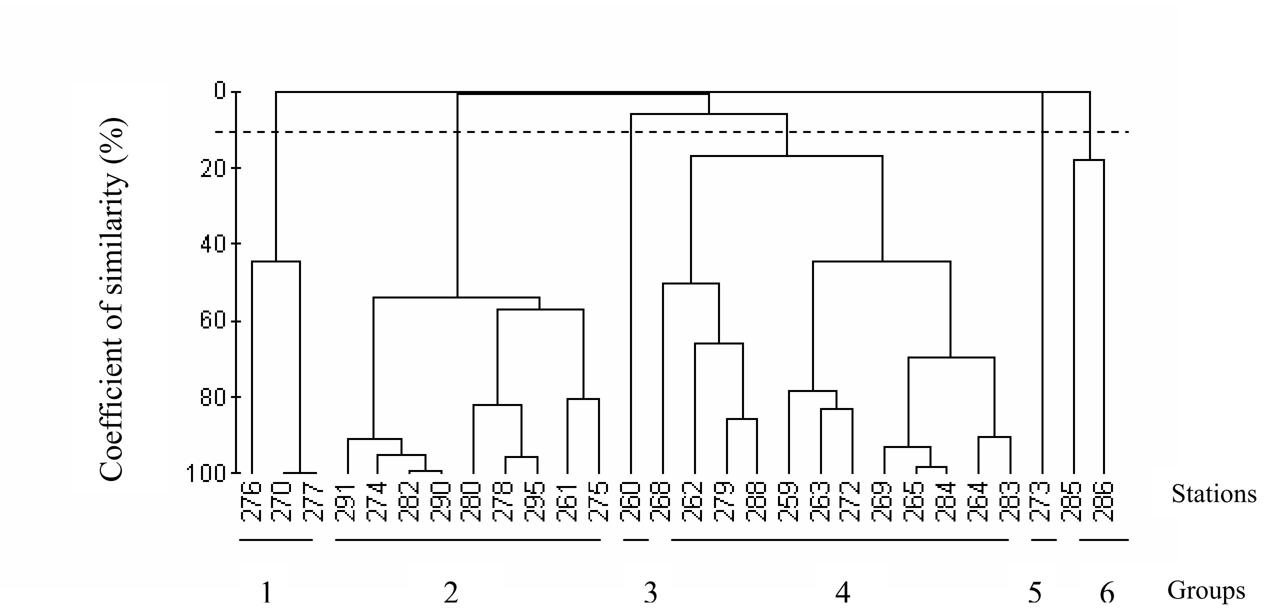

Fig. 3.21. Dendrogram of cluster analysis comparing the zooplankton biomass of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2005. The dashed line represents the cut-off level used to delimit assemblages.

3.4. Predation impact

2001 Survey

The total predation impact estimates of the five groups of carnivores on the mesozooplankton standing stock are given in Table 3.8. The combined predation impact of macrozooplankton ranged between 0.05% and 27.72% of the mesozooplankton standing stock. The highest predation impact was recorded at stations where chaetognaths dominated numerically (stns. 192, 200, 210, Table 3.8). An extremely high predation impact was recorded at station 192, where the mesozooplankton biomass was much lower compared to the biomass at the other stations. Chaetognaths were generally the most important consumers of mesozooplankton standing stock (Figure 3.22). The total daily predation impact of *Eukrohnia hamata* and *Sagitta gazellae* ranged from 0 to 150 g Dwt $1000m^{-3}d^{-1}$ and from 0 to 800 g Dwt $1000m^{-3}d^{-1}$ respectively (Table 3.8). The total daily predation impact of medusae ranged from 0 to 10 g Dwt $1000m^{-3}d^{-1}$, respectively (Table 3.8).

2004 Survey

Estimates of the total predation impact of six groups of carnivores on mesozooplankton standing stock are given in Table 3.9. The combined predation impact of macrozooplankton ranged from 0.03% to 1.54% of mesozooplankton standing stock. The highest impact was recorded at stations where chaetognaths numerically dominated the carnivorous macrozooplankton (stations 239, 241 and 242; Table 3.9). Chaetognaths were identified as the most important consumers of mesozooplankton standing stock (Figure 3.23). Total daily predation impact of the chaetognaths *E. hamata* and *S. gazellae* ranged from 0.44 to 77.53 mg Dwt $1000m^{-3}d^{-1}$ and from 0.67 to 191.87 mg Dwt $1000m^{-3}d^{-1}$ respectively (Table 3.9). Predation impact of the remaining groups was always <3% of the total predation impact, except at station 234 where mysids were the only carnivores found. Predation impact of the remaining groups generally responded to <1 mg Dwt $1000m^{-3}d^{-1}$ (Table 3.9).

2005 Survey

Table 3.10 shows the estimates of the total predation impact of the five carnivore groups on mesozooplankton standing stock. The combined predation impact of macrozooplankton ranged between 0% and 13.89% of the mesozooplankton standing stock. The chaetognath S. *gazellae* was the most important consumer of the mesozooplankton standing stock, except at station 273 where only ctenophores were found (Figure 3.24). The total daily predation impacts of S. *gazellae* from 2.24 to 728 mg Dwt 1000m^{-3}d^{-1} (Table 3.10). *Sagitta maxima* was only found at station 260 where it consumed 397.6 mg Dwt 1000m^{-3}d^{-1}, which corresponded to 87.14% of the total predation impact at that station. *E. hamata* contributed 22.63% ±27.91% to the total predation impact.

A comparison of the total average predation impact of macrozooplankton on the mesozooplankton standing stock between the three years investigated showed a significant difference between the predation impact of 2004 and the other two years (Tukey's test; $p = 0.035$ for 2001; $p = 0.015$ for 2005). The total average predation impacts in 2001, 2004 and 2005 were 4.93 ± 6.76%, 0.55 ± 0.51% and 4.88 ± 4.45% of the mesozooplankton standing stock, respectively.

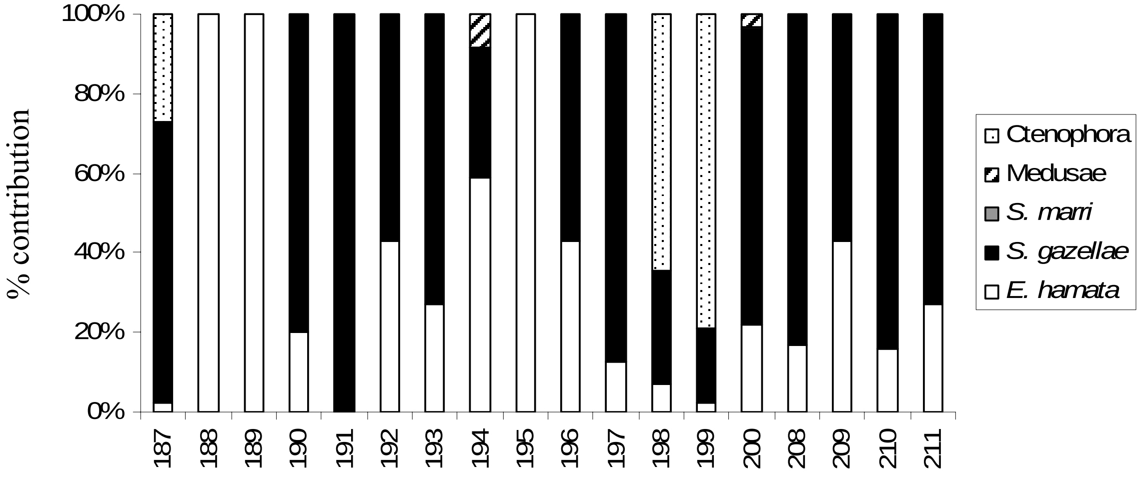

Fig. 3.22. Percentage contribution of five major carnivores to the total predation impact of selected carnivorous macrozooplankton on the mesozooplankton standing stock at certain stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2001. Mesozooplankton data were obtained from Bernard and Froneman (2002).

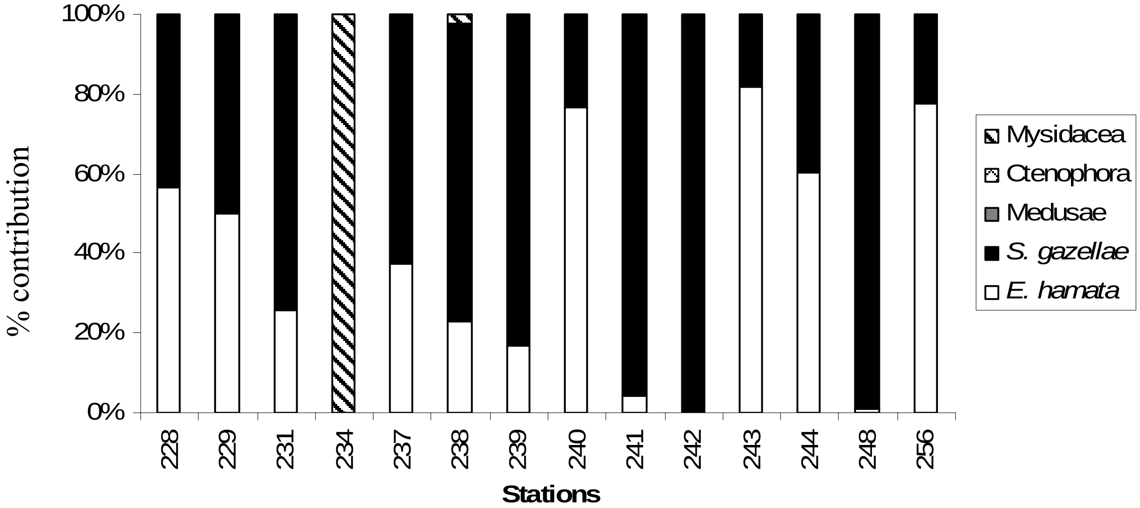

Fig. 3.23. Percentage contribution of six major carnivore groups to the total predation impact of selected carnivorous macrozooplankton at Bongo net stations occupied in the survey area at the Antarctic Polar Frontal Zone in April 2004. The predation impact of ctenophores was low and therefore does not show on the graph. Mesozooplankton data were obtained from Bernard and Froneman (2004).

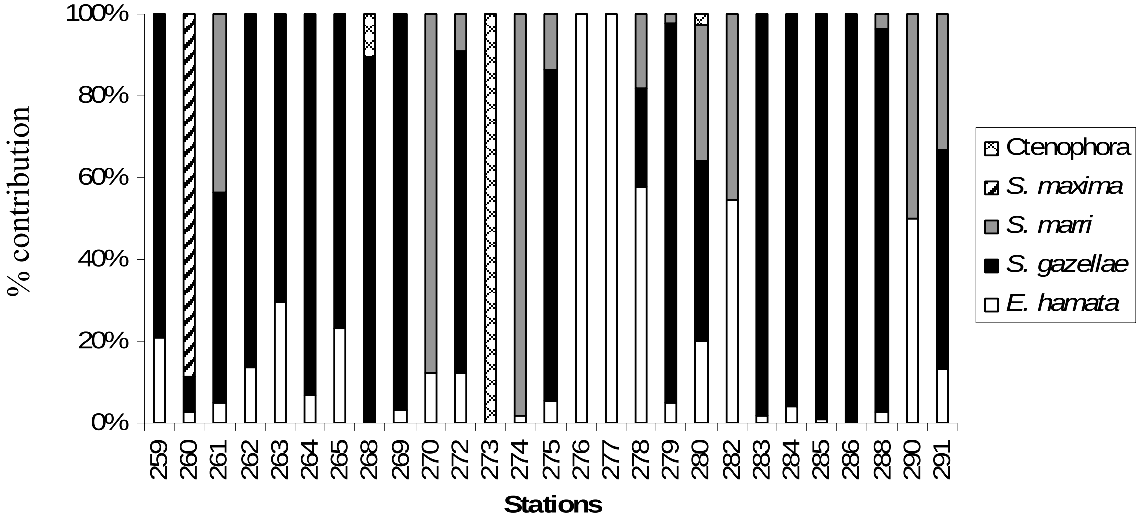

Fig. 3.24. Percentage contribution of five major carnivores to the total predation impact of selected carnivorous macrozooplankton on the mesozooplankton standing stock at stations occupied in the vicinity of the Prince Edward Islands in late austral summer (April/May) 2005. Mesozooplankton data were obtained from Bernard and Froneman (2005).

Table 3.1. Composition and average abundance (ind. m^{-3}) of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2001. Groups were identified using cluster analysis.

Taxa	**Group 1 (n = 1)**	**Group 2 (n = 18)**	**Group 3 (n = 8)**
Chaetognatha			
Eukrohnia hamata **	< 0.05	16.31	1.10
Sagitta gazellae **		1.46	0.91
Sagitta marri **		0.12	
Medusae			
Pegantha martagon **		< 0.05	< 0.05
Arctapodema ampla **			< 0.05
Cephalopoda			
Brachioteuthis riisei ***		< 0.05	
Ctenophora			
Beroe cucumis */**		< 0.5	< 0.05
Total	< 0.05	17.86	2.01
Standard deviation		7.34	0.1
No. of species	1	7	6

Species origin: *subtropical, **Antarctic/Subantarctic, ***Subantarctic

Table 3.2. Composition and average abundance (ind.m^{-3}) of selected carnivorous macrozooplankton at RMT-8 stations (A) and bongo stations (B) occupied during late austral summer (April/May) 2004. Groups were identified using cluster analysis.

	(A)			**(B)**	
Taxa	**Group 1 (n=3)**	**Group 2 (n=2)**	**Group 3 (n=3)**	**Group 1 (n=1)**	**Group 2 (n=14)**
Chaetognatha					
Eukrohnia hamata**			0.4		7.854
Sagitta gazellae**	0.1	12	2	0.86	3.264
Sagitta maxima**	<0.05	<0.05			
_Pterosagitta draco_*			<0.05		
Medusae					
_Heterotiara anonyma_*			0.1		
_Oceania armata_*			<0.05		
Calycopsis borchgrevinki**					
Mysidacea					
Eucopia grimaldii		<0.05			
Eucopia spp.		<0.05			<0.0001
Cephalopoda					
_Illex argentinus_*	0.1	<0.05			
_Abralia (Pygmabralia) redfieldi_*			<0.05		<0.0001
Teuthida spp.	<0.05				
Ctenophora					
Pleurobrachiidae spp.***	1		0.1	0.006	
Unidentified gelatinous zooplankton (a)		1			
Unidentified gelatinous zooplankton (b)		0.1	0.1		
Unidentified gelatinous zooplankton (c)	2	0.1			
Total	3.2	13.2	2.7	0.866	11.118
Standard deviation	0.07	0.5	0.1	0.0006	2.295
No. of species	6	8	8	2	4
			8		

Species origin: *subtropical, **Antarctic/Subantarctic, ***Subantarctic

Table 3.3. Composition and average abundance (ind.m^{-3}) of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2005. Groups were identified using cluster analysis.

Taxa	**Group 1 (n = 3)**	**Group 2 (n = 14)**	**Group 3 (n = 8)**
Chaetognatha			
Eukrohnia hamata **	0.29	1.45	6.09
Sagitta gazellae **	0.23	0.32	2.03
Sagitta marri **		0.03	0.02
Sagitta maxima **		0.01	
Ctenophora			
Beroe cucumis */**		0.02	
Total	0.52	1.81	8.14
Standard deviation	0.03	0.55	2.52
No. of species	2	5	3

Species origin: *subtropical, **Antarctic/Subantarctic, ***Subantarctic
Stations 273, 285 and 286 were outliers and therefore not included in the table.

Table 3.4. Composition and average biomass (mg wwt m^{-3}) of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2001. Groups were identified using cluster analysis.

Taxa	**Group 1 (n = 2)**	**Group 2 (n = 16)**	**Group 3 (n = 3)**	**Group 4 (n = 6)**
Chaetognatha				
Eukrohnia hamata **	0.01	0.01	< 0.005	< 0.005
Sagitta gazellae **	0.02	0.05		< 0.005
Sagitta marri **				< 0.005
Medusae				
Pegantha martagon **		< 0.005		
Arctopodema ampla **		< 0.005		< 0.005
Cephalopoda				
Brachioteuthis riisei ***	< 0.005	< 0.005		
Ctenophora				
Beroe cucumis */**	0.05	0.01		< 0.005
Total	0.08	0.15	< 0.005	< 0.025
Standard deviation	0.02	0.02		0
No. of species	4	6		5

Species origin: *subtropical, **Antarctic/Subantarctic, ***Subantarctic

Table 3.5. Composition and average biomass (mg wwt m^{-3}) of selected carnivorous macrozooplankton at RMT-8 stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2004. Groups were identified using cluster analysis.

Taxa	**Group 1 (n=4)**	**Group 2 (n=4)**
Chaetognatha		
*Eukrohnia hamata***	0.001	<0.0005
*Sagitta gazellae***	0.32	0.371
*Sagitta maxima***	0.006	0.068
*Pterosagitta draco**	0.01	
Medusae		
*Heterotiara anonyma**	0.223	
*Oceania armata**		0.008
*Calycopsis borchgrevinki***	0.126	
Mysidacea		
Eucopia grimaldii		0.011
Eucopia spp.		0.004
Cephalopoda		
*Illex argentinus**	0.015	0.048
*Abralia (Pygmabralia) redfieldi**	0.002	
Teuthida spp.		0.013
Ctenophora		
Pleurobrachiidae spp.***	0.989	
Unidentified gelatinous zooplankton (a)	0.368	0.516
Unidentified gelatinous zooplankton (b)	0.302	
Unidentified gelatinous zooplankton (c)		0.534
Total	2.362	1.574
Standard deviation	0.281	0.216
No. of species	11	10

Species origin: *subtropical, **Antarctic/Subantarctic, ***Subantarctic

Table 3.6. Composition and average biomass (mg wwt m^{-3}) of selected carnivorous macrozooplankton at bongo stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2004. Groups were identified using cluster analysis.

Taxa	**Group 1 (n = 1)**	**Group 2 (n = 1)**	**Group 3 (n = 1)**	**Group 4 (n = 12)**
Chaetognatha				
*Eukrohnia hamata***	4.943	7.397	7.397	5.158
*Sagitta gazellae***		3.412	3.412	3.697
*Sagitta maxima***				
*Pterosagitta draco**				
Medusae				
*Heterotiara anonyma**				
*Oceania armata**				
*Calycopsis borchgrevinki***				
Mysidacea				
Eucopia grimaldii				
Eucopia spp.		0.178		0.014
Cephalopoda				
*Illex argentinus**				
*Abralia (Pygmabralia) redfieldi**				0.041
Teuthida spp.				
Ctenophora				
Pleurobrachiidae spp.***	0.233			
Unidentified gelatinous zooplankton (a)				
Unidentified gelatinous zooplankton (b)				
Unidentified gelatinous zooplankton (c)				
Total	5.176	10.987	10.809	8.91
Standard deviation	2.355	2.952	1.993	2.26
No. of species	2	3	2	4

Species origin: *subtropical, **Antarctic/Subantarctic, ***Subantarctic

Table 3.7. Composition and average biomass (mg wwt m-3) of selected carnivorous macrozooplankton at stations occupied in the vicinity of the Prince Edward Islands during late austral summer (April/May) 2005. Groups were identified using cluster analysis.

Taxa	**Group 1 (n = 3)**	**Group 2 (n = 9)**	**Group 3 (n = 1)**	**Group 4 (n = 12)**	**Group 5 (n = 2)**
Chaetognatha					
Eukrohnia hamata **	< 0.0005	0.007	0.003	0.01	< 0.0005
Sagitta gazellae **		0.02	0.01	0.08	0.002
Sagitta marri **		0.05			
Sagitta maxima **			0.07		
Ctenophora					
Beroe cucumis */**	< 0.0005			0.002	
Total	< 0.001	0.077	0.083	0.092	0.002
Standard deviation		0.02	0.03	0.04	
No. of species	2	3	3	3	2

Species origin: *subtropical, **Antarctic/Subantarctic, ***Subantarctic

Group 5 was excluded from the table since it consisted of an outlier (station 273).

Table 3.8. Predation impact of carnivorous macrozooplankton at selected stations occupied during the survey conducted in the surrounding waters if the Prince Edward Islands in late austral summer (April/May) 2001. Mesozooplankton data were obtained from Bernard and Froneman (2002).

Station	Mesozooplankton Biomass (mg Dwt $1000m^{-3}$)	Food consumption (g Dwt $1000m^{-3}d^{-1}$)					Standing stock
		Chaet *E. hamata* (6%)	Chaet *S. gazellae* (8%)	Chaet *S. marri* (6%)	Med (5%)	Total	(%)
187	7 468	6	168			174	2.33
188	25 717	18				18	0.07
189	11 726	30				30	0.26
190	2 727	12	48			60	2.20
191	2 172	0	168			168	7.73
192	707	84	112			169	27.72
193	831	12	32			44	5.29
194	2 339	72	40		10	122	5.22
195	25 197	12				12	0.05
196	6 752	6	8			12	0.18
197	10 139	24	168			192	1.89
198	16 809	42	168			210	1.25
199	5 649	3	24			27	0.48
200	1 771	66	224	1.2	10	301.2	17.01
201	1 877	6	16			22	1.17
203	4 848	1.68	15.12			16.8	0.35
206	6 325	41.58	303.52			345.1	5.46
207	5 677	47.08	147.28		76.5	270.86	4.77
208	11 243	120	592			712	6.42
209	12 741	12	16			28	0.22
210	6 026	150	800			950	15.77
211	4 919	36	96			132	2.68

Values in brackets indicate daily ration as a percentage of dry body weight, obtained from Froneman *et al.* (2002)
Chaet = Chaetognaths; Med = Medusae

Table 3.9. Predation impact of carnivorous macrozooplankton at selected stations occupied during the survey conducted in the waters surrounding the Prince Edward Islands in late austral summer (April/May) 2004. Mesozooplankton data were obtained from Bernard and Froneman (2004).

Station	Mesozooplankton Biomass (mg Dwt 1000m^{-3})	Food consumption (g Dwt 1000m^{-3}d^{-1})					Standing stock
		Chaet *E. hamata* (6%)	Chaet *S. gazellae* (8%)	Med (5%)	Mysids (2%)	Total	(%)
228	21 740	8.66	6.62			15.28	0.07
229	17 900	3.11	2.87			5.98	0.03
231	8 720	11.11	32.33			43.44	0.50
234	13 030	31.08	19.12		0.60	50.8	0.39
237	23 530	77.53	129.30			206.33	0.88
238	2 610	4.80	15.50		0.55	20.85	0.80
239	3 080	8.12	39.25			47.37	1.54
240	19 000	7.58	2.36			9.94	0.05
241	2 600	1.36	27.68			29.04	1.12
242	13 440		191.87			191.87	1.43
243	9 560	8.87	2.27			11.14	0.12
244	38 420	52.98	35.27			88.25	0.23
248	12 360	0.44	52.64			53.08	0.43
256	8 650	2.41	0.67			3.08	0.04

Values in brackets indicate daily ration as a percentage of dry body weight, obtained from Froneman *et al*. (2002)
Chaet = Chaetognaths; Med = Medusae

Table 3.10. Predation impact of carnivorous macrozooplankton at selected stations occupied during the survey conducted in the surrounding waters of the Prince Edward Islands in late austral summer (April/May) 2005. Mesozooplankton data were obtained from Bernard and Froneman (2005).

Station	Mesozooplankton biomass (mg Dwt $1000m^{-3}$)	Food consumption	(g Dwt $1000m^{-3}d^{-1}$)				Standing stock
		Chaet *E. hamata* (6%)	Chaet *S. gazellae* (8%)	Chaet *S. marri* (6%)	Chaet *S. maxima* (8%)	Total	(%)
259	4 608	29.4	112			141.4	3.07
260	3 312	12.6	39.2		397.6	449.4	13.59
261	5 008	12.6	134.4	113.4		260.4	5.20
262	35 157	113.4	728			841.4	2.39
263	8 021	63	151.2			214.2	2.67
264	4 000	33.6	459.2			492.8	12.32
265	4 912	8.4	*28*			288.4	5.87
268	9 920	8.4	1260			1268.4	12.79
269	2 640	8.4	252			260.4	9.86
270	1 536	2.94		*21*		23.94	1.56
272	6 176	29.4	184.8	*21*		235.2	3.81
273	32 256						0
274	3 029	0.42		*21*		21.24	0.70
275	1 099	8.4	123.2	*21*		152.6	13.89
276	8 960	0.42				0.42	0.01
277	2 112	2.94				2.94	0.14
278	6 272	67.2	*28*	*21*		116.2	1.85
279	9 216	42	812	*21*		875	9.49
280	4 281	12.6	*28*	*21*		61.6	1.44
282	4 256	25.2		*21*		46.2	1.09
283	4 715	8.4	403.2			411.6	8.73
284	768	1.26	*28*			29.26	3.81
285	8 960	0.21	22.4			22.61	0.25
286	4 096		2.24			2.24	0.05
288	10 027	16.8	548.8	*21*		586.6	5.85
290	757	21		*21*		42	5.55
291	1 088	8.4	33.6	*21*		63	5.79

Values in brackets indicate daily ration as a percentage of dry body weight, obtained from Froneman *et al*. (2002). Values in italics indicate where the average biomass was used to work out food consumption. Chaet = Chaetognaths

3.5. Chaetognath population structure

3.5.1 Chaetognath standing stock and distribution

2001 survey

Abundances (ind.m^{-3} ±SD) of chaetognaths were generally lower at stations occupied in the Subantarctic Surface Water (SASW) (1.2 ±1.97) than at stations occupied in the Polar Frontal Zone (PFZ) (7.37 ±11.0). *Eukrohnia hamata* dominated the chaetognath standing stock numerically, comprising up to 78.1 ±24.36% of the total. *Sagitta gazellae* only dominated numerically at stations 91 (located in SASW), 94 and 106 (both located in the PFZ). Densities of *E. hamata* ranged from 0 to 42.67 ind.m^{-3} and for *S. gazellae* densities ranged between 0 and 3.59 ind.m^{-3} (Table 3.11). Densities of *Sagitta marri* ranged from 0 to 1.04 ind.m^{-3}. *S. marri* thus contributed <1% to the chaetognath standing stock and was therefore not included in further analyses.

As with the abundances, the biomass (mg wwt m^{-3} ±SD) values of chaetognaths were generally lower at stations occupied in the SASW (0.009 ±0.022) than at stations occupied in the PFZ (0.014 ±0.025). However, in terms of the contribution to the chaetognath standing stock, *S. gazellae* dominated by biomass, comprising 64.49 ±29.88% of the total. *E. hamata* only dominated the biomass at stations 88, 89 and 95 (all located in the PFZ). The biomass values of *S. gazellae* and *E. hamata* ranged from 0 to 0.143 mg wwt m^{-3} and from 0 to 0.036 mg wwt m^{-3} respectively (Table 3.11). The biomass of *S. marri* ranged between 0 and 0.001 mg wwt m^{-3}, and this contributed <1% to the total chaetognath biomass.

2004 survey

Densities of *E. hamata* and *S. gazellae* ranged between 0 and 23.55 ind.m^{-3} and from 0.67 to 14.37 ind.m^{-3}, respectively (Table 3.12). No other chaetognath species were recorded in 2004. Abundances (ind.m^{-3} ± SD) of chaetognaths were greatest at stations occupied in the Antarctic Surface Water (ASW) (7.99 ±7.53) and lowest at stations occupied in the

Polar Frontal Zone (PFZ) (4.18 ±4.53). Stations occupied in the Subantarctic Surface Water (SASW) had a mean chaetognath abundance of 4.23 ±6.04 ind.m^{-3}. *E. hamata* again dominated the chaetognath standing stock numerically, comprising up to 62.2 ±30.12% of the total. Exceptions were recorded at stations 228, 241, 242 and 248 where *S. gazellae* dominated numerically.

In contrast to the abundances, the chaetognath biomass values (mg wwt m^{-3} ± SD) were greatest at stations occupied in the PFZ (6.45 ±9.58) but lowest at stations occupied in the ASW (4.19 ±4.319). Stations in the SASW had a mean chaetognath biomass of 5.34 ±9.58 mg wwt m^{-3}. Unlike the 2001 survey, *E. hamata* generally dominated the biomass, comprising 57.97 ±28.81% of the chaetognath standing stock, while *S. gazellae* dominated the biomass at stations 228, 229, 240, 243, 244 and 256. The biomass values of *S. gazellae* and *E. hamata* ranged from <0.0005 to 18.461 mg wwt m^{-3} and from 0 to 23.09 mg wwt m^{-3} respectively (Table 3.12).

2005 survey

Abundances (ind.m^{-3} ± SD) of chaetognaths were greatest at stations occupied along the eddy edge (3.55 ±4.64), followed by abundances at stations occupied in the Subantarctic Surface Water (SASW) (1.3 ±1.3). Stations occupied in the Antarctic Surface Water (ASW) had the lowest abundances (0.26 ±0.34). With the exceptions of stations 262, 284 and 286, *E. hamata* again dominated chaetognath standing stock numerically, composing up to 76.12 ±26.29% of the total. Densities of *E. hamata* ranged from 0 to 13.65 ind.m^{-3} and *S. gazellae* densities also ranged between 0 and 13.65 ind.m^{-3} (Table 3.13). Densities of *Sagitta marri* and *Sagitta maxima* ranged between 0 and 0.16 ind.m^{-3} and from 0 to 0.32 ind.m^{-3}, respectively. *S. marri* and *S. maxima* contributed <0.5% to the chaetognath standing stock and were therefore ignored from further analysis.

As with the abundances, the biomass of chaetognaths (mg wwt m^{-3} ± SD) were greatest at stations occupied along the eddy edge (0.042 ±0.066), followed by the biomass at stations occupied in the PFZ (0.014 ±0.026). Similarly to the biomass values observed in 2004, the biomass was lowest at stations occupied inside the eddy in the ASW (0.006 ±0.019). As in 2001, *S. gazellae* dominated by biomass, comprising 55.57 ±41.91% of the total chaetognath standing stock. *E. hamata* dominated the chaetognath biomass at stations 265, 270, 274, 276, 277, 278, 280, 282 and 290. The biomass values of *S. gazellae* and *E. hamata* ranged from 0 to 0.225 mg wwt m^{-3} and from 0 to 0.027 mg wwt m^{-3} respectively (Table 3.13).

Overall, *E. hamata* dominated the chaetognath standing stock numerically during all the three surveys. Of the three years investigated, 2001 had the highest densities of *E. hamata* but the lowest densities of *S. gazellae*. Only the densities of *E. hamata* differed significantly between the three years (Newman-Keuls test; p = 0.049 for 2001 vs. 2004; p = 0.0001 for 2001 vs. 2005; and p = 0.042 for 2004 vs. 2005). When the densities of the two species were combined, the densities between 2001 and 2005 were significantly different (Tukey's test; p = 0.003). The chaetognath densities in 2005 were much lower (mean 1.69 ±2.87 ind.m^{-3}) than in 2001 (mean 6.23 ±10.23 ind.m^{-3}) and 2004 (mean 5.22 ±6.07 ind.m^{-3}).

In terms of biomass, *S. gazellae* dominated in 2004 (mean 10.14 ±25.64 mg wwt m^{-3}) and 2005 (mean 24.39 ±41.02 mg wwt m^{-3}), but *E. hamata* dominated in 2001 (mean 3.75 ±19.44 mg wwt m^{-3}). The biomass values of *S. gazellae* were significantly different between 2001 and 2005 (Newman-Keuls test; p = 0.04). When the biomass values of the two species were combined, the biomass values of 2001 differed significantly from those of 2005 (Tukey's test; p = 0.002). The chaetognath biomass in 2001 (mean 1.89 ±13.74 mg wwt m-3) was lower than in 2004 (mean 7.63 ±18.47 mg wwt m^{-3}) and 2005 (mean 19.41 ±38.56 mg wwt m^{-3}).

Table 3.11. Abundance (ind. m^{-3}) and biomass (mg wwt m^{-3})of selected chaetognath species at stations occupied in the waters surrounding the Prince Edward Islands during late austral summer (April/May) 2001.

Stations	***E. hamata***		***S. gazellae***		***S. marri***	
	Abundance	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**
181	6.94	0.002	2.31	0.03	0	0
186	12.23	0.006	2.16	0.043	0	0
187	5.77	0.002	1.93	0.03	0	0
188	8.69	0.004	0	0	0	0
189	16.1	0.008	0	0	0	0
190	1.44	0.003	1.44	0.085	0	0
191	0	0	0.38	0.03	0	0
192	0.98	0.002	0.25	0.002	0	0
193	0.87	0.003	0.04	0.005	0	0
194	0.52	0.018	1.22	0.008	0	0
195	8.59	0.003	0	0	0	0
196	1.55	0.001	1.04	0.001	0	0
197	4.91	0.006	0.82	0.03	0	0
198	9.46	0.01	1.18	0.03	0	0
199	1.02	0.008	0.34	0.004	0	0
200	4.02	0.016	1.79	0.041	0.01	< 0.0005
201	6.58	0.002	0.09	0.003	0	0
202	19.44	0.006	0	0.02	0	0
203	0.73	< 0.0005	0.37	0.003	0	0
204	5.91	0.015	0.99	0.03	0	0
205	24.43	0.005	3.49	0.064	0	0
206	1.72	0.01	2.59	0.054	0	0
207	42.69	0.011	1.04	0.026	0	0
208	38.91	0.029	0.95	0.106	0	0
209	39.58	0.003	3.13	0.003	1.04	< 0.0005
210	25.11	0.036	3.59	0.143	0.72	0.001
211	14.26	0.008	2.85	0.018	0.36	< 0.0005

Table 3.12. Abundance (ind. m^{-3}) and biomass (mg wwt m^{-3}) of selected chaetognath species at stations occupied in the waters surrounding the Prince Edward Islands during late austral summer (April/May) 2004. Only data obtained from Bongo nets are represented here.

Stations	***E. hamata***		***S. gazellae***	
	Abundance	**Biomass**	**Abundance**	**Biomass**
228	1.8	1.182	14.37	2.063
229	2.75	0.485	1.38	0.74
231	7.99	5.773	0.67	2.644
234	6.23	7.397	2.27	3.413
236	3.88	7.397	1.29	3.413
237	15.39	23.09	2.2	18.461
238	1.09	2.768	1.25	1.142
239	10.54	7.009	0.92	1.932
240	20.39	0.421	3.26	1.805
241	0.39	4.943	0.78	0.323
242	0	0	0.86	< 0.0005
243	5.06	0.406	1.19	2.111
244	23.55	6.298	6.42	12.613
248	3.48	9.401	7.83	0.104
256	7.42	0.12	1.86	0.43

Table 3.13. Abundance (ind. m^{-3}) and biomass (mg wwt m^{-3}) of selected chaetognath species at stations occupied in the waters surrounding the Prince Edward Islands during late austral summer (April/May) 2005.

Stations	***E. hamata***		***S. gazellae***	
	Abundance	Biomass	Abundance	Biomass
259	3.41	0.007	0.23	0.02
260	1.92	0.003	0.16	0.007
261	1.6	0.003	0.32	0.023
262	3.41	0.027	13.65	0.13
263	13.65	0.015	0.85	0.027
264	4.8	0.008	0.32	0.082
265	0.96	0.002	0.68	< 0.0005
268	1.28	0.002	0.64	0.225
269	1.28	0.002	0.16	0.045
270	1.39	0.001	0	0
272	3.84	0.007	0.08	0.033
273	0	0	0	0
274	0.85	0.001	0	0
275	0.91	0.002	0.28	0.022
276	0.32	< 0.0005	0	0
277	0.4	0.001	0	0
278	5.97	0.016	0.68	< 0.0005
279	8.53	0.01	0.43	0.145
280	1.26	0.003	0.68	< 0.0005
282	5.12	0.006	0	0
283	1.07	0.002	0.43	0.072
284	0.16	< 0.0005	0.68	< 0.0005
285	0.02	< 0.0005	0.02	0.004
286	2.69	< 0.0005	0.16	< 0.0005
288	1.71	0.004	0.48	0.098
290	2.67	0.005	0.68	< 0.0005
291	0.75	0.002	0.12	0.006
295	2.6	0.006	0.68	< 0.0005

3.5.2. Gut-content analysis

All prey items found in the foregut of the two chaetognath species were omitted from the analysis because of the possibility of cod-end feeding. Many of the prey items could not be identified due to the advanced state of digestion, and have been referred to as "unidentifiable prey". Oil droplets were not considered as prey items for the purpose of the analysis.

2001 survey

Of the 326 stomachs of *Eukrohnia hamata* and the 92 stomachs of *Sagitta gazellae* examined, only 14 and 5 guts contained prey items respectively. Thus, of the total chaetognaths examined during this investigation, 95% *E. hamata* and 95% *S. gazellae* contained no food in their guts. Table 3.14 shows the variety of food items found in the guts of the chaetognaths examined. The guts of both species contained mostly unidentifiable food items, which accounted for ≈58% of the prey in *E. hamata* and ≈44.5% of the prey in *S. gazellae*. Crustacean eggs were also an important component of the diets of both species, however, *S. gazellae* consumed a wider variety of prey (Figure 3.25). Multiple prey were found in the gut of only one *S. gazellae* while only single prey items were found in the guts of *E. hamata*. Oil droplets were found in the guts of *E.hamata* only. Up to 30% of the *E. hamata* examined contained oil droplets, with often >2 oil droplets found in a single gut.

2004 survey

A total of 407 stomachs of *E. hamata* and 90 stomachs of *S. gazellae* were examined for the presence of prey in their guts. Food items were found in the guts of only 18 *E. hamata* and 8 *S. gazellae*. Therefore, of the total chaetognaths examined during this investigation, 96% *E. hamata* and 91% *S. gazellae* contained no food items in their guts. The variety of food items found in the guts of the chaetognaths examined is shown in table 3.14. Crustacean eggs were the most important prey item in the diet of *E. hamata*, contributing

≈54% to the gut contents. Unidentifiable prey items, most likely copepods, were recorded in 44.5% of *S. gazellae* guts. *S. gazellae* again consumed a greater variety of prey (Figure 3.25). Cannibalism was observed in *E. hamata* only, but the contribution of chaetognaths to the total number of prey items in *E. hamata* guts was only ≈2.5% (Table 3.14). Again, oil droplets were found in the guts of *E. hamata* only, with up to 49% of the *E. hamata* examined containing oil droplets in their guts. Often >2 oil droplets were found in a single gut.

2005 survey

Of the 879 stomachs of *E. hamata* and 88 stomachs of *S. gazellae* examined, only 42 and 12 guts contained prey items respectively. Thus, no food items were found in the guts of 95% *E. hamata* and 86% *S. gazellae* examined. Table 3.14 shows the variety of food items in the guts of the chaetognaths examined. Unidentifiable prey items were the most important component of the diet of both species, contributing up to 92% and 50% to the gut contents of *E. hamata* and *S. gazellae*, respectively. *S. gazellae* again consumed a greater variety of prey, including euphausiid fragments and radiolarians (Figure 3.25). In contrast to the 2004 study, cannibalism was only observed in *S. gazellae*, with chaetognaths contributing up to 8.3% to the total number of prey items found in the guts of *S. gazellae* (Table 3.14). Oil droplets were found in ≈74% of the *E. hamata* guts examined, with often >2 oil droplets being found in a single gut. No oil droplets were found in the guts of *S. gazellae.*

Overall, the two major differences in the gut contents of the two chaetognath species in all the years investigated were that *S. gazellae* consumed a greater variety of prey than *E. hamata*, and that oil droplets were found in the guts of *E. hamata* only (Figure 3.25).

Table 3.14. Gut contents (% contribution by number) of *Eukrohnia hamata* and *Sagitta gazellae* in the waters surrounding the Prince Edward Islands during the late austral summers (April/May) of 2001, 2004 and 2005. Digits in italics represent the number of chaetognath guts inspected, "n" is the number of chaetognaths with food items in their guts.

	2001		**2004**		**2005**	
Food item	*E. hamata* (n = 14) *326*	*S. gazellae* (n = 5) *92*	*E. hamata* (n = 28) *407*	*S. gazellae* (n = 10) *90*	*E. hamata* (n = 43) *879*	*S. gazellae* (n = 9) *88*
Copepoda						
Oithona spp.	-	-	-	-	2	25
Metridia spp.	-	11	2.5	22.5	2	-
Euphausiacea						
Thysanoessa spp.	-	11	-	11	-	-
Euphausiid fragments	-	-	-	-	-	8.3
Chaetognatha						
Eukrohnia hamata	-	-	2.5	-	-	8.3
Sagitta gazellae	-	-	-	-	-	-
Amphipoda						
Themisto gaudichaudii	-	-	-	11	-	-
Radiolaria	-	-	-	-		8.3
Crustacean eggs	42	33.5	54	11	4	-
Unidentifiable (digested)	58	44.5	41	44.5	92	50

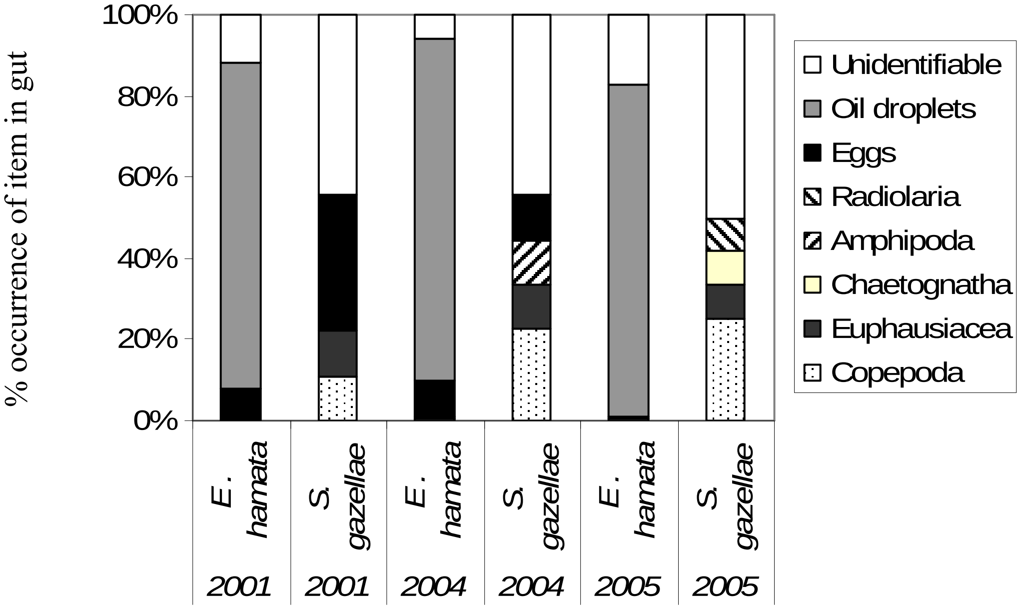

Fig. 3.25. Percentage contribution, by number, of various items found in the guts of *E. hamata* and *S. gazellae* collected from the vicinity of the Prince Edward Islands in late austral summers (April/May) of years 2001, 2004 and 2005.

3.5.3. Predation impact

The mean number of prey consumed per chaetognath (NPC), daily feeding rate (Fr) and predation impact of *Eukrohnia hamata* and *Sagitta gazellae* on mesozooplankton standing stock for 2001, 2004 and 2005 are shown in Tables 3.15 – 3.17. Since the contribution of chaetognaths as prey items was small, cannibalism has been ignored and the predation impact of chaetognaths on the chaetognath standing stock was not assessed.

2001 survey

The Number of Prey per Chaetognath (NPC) and Feeding rate (Fr) values for both species were not significantly different between the Subantarctic Surface Water (SASW) and Polar Frontal Zone (PFZ) (ANOVA, $p > 0.05$). For *E. hamata* the NPC values in the SASW and PFZ were 0.083 ± 0.012 prey ind^{-1} and 0.106 ± 0.025 prey ind^{-1} respectively, and the feeding rates were 0.218 ± 0.048 prey day^{-1} and 0.249 ± 0.059 prey day^{-1} respectively. *S. gazellae* had an NPC value of 0.199 ± 0.088 prey ind^{-1} and a feeding rate of 0.669 ± 0.295 prey day^{-1} in the PFZ, while in the SASW the single NPC value was 0.111 prey ind^{-1} and the single Fr was 0.374 prey day^{-1}.The NPC values for *E. hamata* ranged from 0 to 0.128 prey ind^{-1}, and between 0 and 0.286 prey ind^{-1} for *S. gazellae*. These rates corresponded to a feeding rate of up to 0.307 prey day^{-1} (range 0 – 0.307) for *E. hamata* and up to 0.964 prey day^{-1} (range 0 – 0.964) for *S. gazellae*. When combined with the abundance estimates the Fr values of *E. hamata* and *S. gazellae* corresponded between 0.13 – 3.12% and between 0.01 – 0.96% of the mesozooplankton standing stock, respectively (Table 3.15).

Generally, both the NPC and Fr rates were higher in *S. gazellae* than in *E. hamata* (Table 3.15). In *S. gazellae* the NPC value was 0.169 ± 0.082 prey ind^{-1} and the Fr rate was 0.571 ± 0.278 prey d^{-1}, while for *E. hamata* the NPC value was 0.093 ± 0.022 prey ind^{-1} and the Fr rate was 0.233 ± 0.052 prey d^{-1}.

2004 survey

For both species the NPC and Fr values were not significantly different between the Subantarctic Surface Water (SASW), Antarctic Surface Water (ASW) and Polar Frontal Zone (PFZ) (ANOVA, $p > 0.05$), although generally the PFZ had slightly higher values. The NPC values for *E. hamata* in the SASW, PFZ and ASW were 0.066 ± 0.001 prey ind^{-1}, 0.047 ± 0.027 prey ind^{-1} and 0.054 ± 0.024 prey ind^{-1}, respectively and the feeding rates were 0.157 ± 0.011 prey day^{-1}, 0.112 ± 0.066 prey day^{-1} and 0.13 ± 0.058 prey day^{-1}, respectively (Table 3.18). In the SASW *S. gazellae* had NPC and Fr values of 0.136 ± 0.052 prey ind^{-1} and 0.333 ± 0.199 prey day^{-1}, respectively (Table 3.18). In The PFZ the single NPC and Fr values for *S. gazellae* were 0.125 prey ind^{-1} and 0.3 prey day^{-1} respectively. In the ASW no *S. gazellae* were observed with prey in their gut. The NPC values for *E. hamata* ranged from 0 to 0.073 prey ind^{-1}, and between 0 and 0.188 prey ind^{-1} for *S. gazellae*. These rates corresponded to a feeding rate of up to 0.192 prey day^{-1} (range 0 – 0.192) for *E. hamata* and up to 0.451 prey day^{-1} (range 0 – 0.451) for *S. gazellae*. When combined with the abundance estimates the Fr values of *E. hamata* and *S. gazellae* corresponded between 0.01 – 6.69% and between 0.13 – 1.13% of the mesozooplankton standing stock, respectively (Table 3.15).

As in 2001, *S. gazellae* generally had higher NPC and Fr rates than *E. hamata* (Table 3.16). The mean NPC and Fr rates were 0.134 ± 0.041 prey ind^{-1} and 0.327 ± 0.098 prey day^{-1} for *S. gazellae* respectively, while for *E. hamata* the mean NPC and Fr rates were 0.055 ± 0.023 prey ind^{-1} and 0.132 ± 0.054 prey day^{-1} respectively.

2005 survey

The NPC and Fr values for both species were not significantly different between the Polar Frontal Zone waters (PFZ), Antarctic Surface Water (ASW) and water at the eddy edge (ANOVA, $p > 0.05$). The NPC values for *E. hamata* in the ASW, at the eddy edge and SASW were 0.112 ± 0.067 prey ind^{-1}, 0.069 ± 0.048 prey ind^{-1} and 0.044 ± 0.017 prey ind^{-1}, respectively, and the feeding rates were 0.27 ± 0.16 prey day^{-1}, 0.166 ± 0.115

prey day^{-1} and 0.098 ± 0.038 prey day^{-1}, respectively. In the SASW *S. gazellae* had NPC and Fr values of 0.314 ± 0.155 prey ind^{-1} and 0.891 ± 0.609 prey day^{-1}, respectively. In the ASW the single NPC and Fr values were 0.33 prey ind^{-1} and 1.122 prey day^{-1}, respectively and the single NPC and Fr values were 0.286 prey ind^{-1} and 0.964 prey day^{-1} at the eddy edge, respectively. NPC values of *E. hamata* ranged from 0 to 0.2 prey ind^{-1} and ranged between 0 and 0.5 prey ind^{-1} for *S. gazellae* (Table 3.17). These rates corresponded to a feeding rate of up to 0.48 prey day^{-1} (range 0 – 0.48) for *E. hamata* and up to 1.685 prey day^{-1} (range 0 – 1.685) for *S. gazellae*. When combined with the abundance estimates the Fr values of *E. hamata* and *S. gazellae* corresponded between 0.001 – 0.48% and between 0.02 – 2.49% of the mesozooplankton standing stock, respectively (Table 3.17).

As in the other two years investigated, *S. gazellae* generally had higher NPC and FR rates than *E. hamata* (Table 3.17). In *S. gazellae* the mean NPC and FR rates were 0.303 ± 0.12 prey ind^{-1} and 0.934 ± 0.521 prey day^{-1}, respectively, while for *E. hamata* the mean NPC and FR rates were 0.066 ± 0.05 prey ind^{-1} and 0.159 ± 0.119 prey day^{-1}, respectively.

Overall, the NPC and Fr rates were lower for *E. hamata* than for *S. gazellae* in all the years investigated, and this was reflected in the greater predation impact of *S. gazellae* over *E. hamata* on the mesozooplankton standing stock. The mean % (±SD) predation impact of *S. gazellae* on mesozooplankton standing stock during the 2001, 2004 and 2005 surveys was 0.31 ±0.29; 0.52 ±0.28 and 0.53 ±0.55, respectively, and for *E. hamata* it was 0.77 ±0.97; 1.07 ±1.86 and 0.36 ±0.52, respectively. The predation impact of *S. gazellae* was significantly different between 2001 and 2004 survey (two-way ANOVA followed by Newman-Keuls test; p = 0.005). There was also a significant difference in the predation impact between the two species during the 2001 survey (Newman-Keuls test; p = 0.035). When the predation impacts of the two species were combined, there was a significant difference between the 2001 and 2004 surveys (Tukey's test; p = 0.012). The combined mean % (±SD) predation impacts of the two species on mesozooplankton standing stock during the 2001, 2004 and 2005 surveys were 0.31 ± 0.29, 0.52 ± 0.28 and 0.53 ± 0.56, respectively.

Table 3.15. Mean number of prey (NPC), daily feeding rate (Fr), number of copepods consumed (m^{-3} d^{-1}) and predation impact of two chaetognath species on mesozooplankton standing stock during the survey conducted in the waters surrounding the Prince Edward Islands in late austral summer (April/May) 2001.

Station	*Eukrohnia hamata*				*Sagitta gazellae*			
	NPC	Fr	No. copepods consumed m^{-3} d^{-1}	% mesozooplankton standing stock consumed d^{-1}	NPC	Fr	No. copepods consumed m^{-3} d^{-1}	% mesozooplankton standing stock consumed d^{-1}
190	0.094	0.226	0.32	0.13	0.111	0.374	0.539	0.22
192	0.071	0.17	0.16	0.19	0	0	*0.822*	0.96
193	0	0	*0.203*	0.17	0	0	*0.023*	0.02
201	0	0	*1.533*	0.53	0.111	0.374	0.034	0.01
203	0	0	*0.17*	0.13	0.286	0.964	0.35	0.27
206	0.128	0.307	0.53	0.14	0	0	*1.479*	0.40
207	0	0	*9.947*	0.79	0	0	*0.594*	0.14
208	0.079	0.19	7.39	1.73	0	0	*0.542*	0.13
209	0	0	*9.222*	3.12	0	0	*1.787*	0.60

* Values in italics were obtained by employing the mean Fr (mean Fr E. hamata = 0.233, mean Fr S. gazellae = 0.571) of each of the chaetognath species.

Table 3.16. Mean number of prey (NPC), daily feeding rate (Fr) , number of copepods consumed (m^{-3} d^{-1}) and predation impact of two chaetognath species on mesozooplankton standing stock during the survey conducted in the waters surrounding the Prince Edward Islands in late austral summer (April/May) 2004.

Station	*Eukrohnia hamata*				*Sagitta gazellae*			
	NPC	Fr	No. copepods consumed m^{-3} d^{-1}	% mesozooplankton standing stock consumed d^{-1}	NPC	Fr	No. copepods consumed m^{-3} d^{-1}	% mesozooplankton standing stock consumed d^{-1}
228	0.022	0.053	0.095	0.01	0	0	*4.7*	0.64
234	0	0	*0.822*	0.55	0	0	*0.742*	0.5
237	0.073	0.175	2.693	1.15	0.125	0.3	0.66	0.28
238	0	0	*0.144*	0.18	0.188	0.451	0.564	0.71
239	0.07	0.168	1.771	6.69	0	0	*0.3*	1.13
240	0.061	0.146	2.977	1.07	0	0	*1.066*	0.38
241	0	0	*0.051*	0.02	0	0	*0.255*	0.08
243	0.02	0.048	0.243	0.29	0	0	*0.389*	0.46
244	0.06	0.144	3.391	0.79	0	0	*2.099*	0.49
248	0	0	*0.459*	0.21	0.089	0.214	1.676	0.77
256	0.08	0.192	1.425	0.57	0	0	*0.608*	0.25

* Values in italics were obtained by employing the mean Fr (mean Fr *E. hamata* = 0.132, mean Fr *S. gazellae* = 0.327) of each of the chaetognath species.

Table 3.17. Mean number of prey (NPC), daily feeding rate (Fr), number of copepods consumed (m^{-3} d^{-1}) and predation impact of two chaetognath species on mesozooplankton standing stock during the survey conducted in the waters surrounding the Prince Edward Islands in late austral summer (April/May) 2005.

Station	*Eukrohnia hamata*				*Sagitta gazellae*			
	NPC	Fr	No. copepods consumed m^{-3} d^{-1}	% mesozooplankton standing stock consumed d^{-1}	NPC	Fr	No. copepods consumed m^{-3} d^{-1}	% mesozooplankton standing stock consumed d^{-1}
259	0	0	*0.542*	0.9	0.2	0.059	0.014	0.02
260	0.048	0.115	0.221	0.69	0.125	0.421	0.067	0.21
261	0.067	0.161	0.258	0.34	0	0	*0.299*	0.39
262	0.077	0.185	0.633	0.03	0	0	*12.749*	0.59
263	0.023	0.055	0.751	0.17	0	0	*0.794*	0.18
264	0.023	0.055	0.264	0.24	0.429	1.446	0.463	0.43
265	0	0	*0.153*	0.25	0	0	*0.635*	1.04
268	0.077	0.185	0.237	0.05	0	0	*0.598*	0.13
269	0.048	0.115	0.147	0.2	0.286	0.964	0.154	0.21
270	0.021	0.05	0.07	0.13	-	-	-	-
272	0.064	0.154	0.591	0.35	0	0	*0.075*	0.05
274	0.073	0.175	0.149	0.09	-	-	-	-
275	0	0	*0.145*	0.63	0	0	*0.262*	1.14
276	0.149	0.358	0.115	0.02	-	-	-	-
277	0	0	*0.064*	0.03	-	-	-	-
278	0.022	0.053	0.316	0.15	0	0	*0.635*	0.29
279	0.174	0.418	3.566	2.71	0	0	*0.402*	0.31
280	0	0	*0.2*	0.14	0.25	0.843	0.573	0.39
282	0.064	0.154	0.788	0.57	-	-	-	-
283	0.027	0.065	0.07	0.08	0.33	1.122	0.482	0.54
284	0.2	0.48	0.077	0.30	0	0	*0.635*	2.49
285	0	0	*0.003*	0.001	0	0	*0.019*	0.01
286	0	0	*0.428*	0.24	0	0	*0.448*	0.25
288	0.023	0.055	0.094	0.05	0.5	1.685	0.809	0.44
290	0.045	0.108	0.288	0.62	0	0	*0.635*	1.37
291	0.047	0.113	0.085	0.3	0	0	*0.112*	0.4
295	0.054	0.13	0.338	0.43	0	0	*0.635*	0.81

* Values in italics were obtained by using the employing the mean Fr (mean Fr *E. hamata* = 0.159, mean Fr *S. gazellae* = 0.934) of each of the chaetognath species. – indicated where mesozooplankton biomass data was unavailable.

3.5.4. Size distribution and maturity

For each of the years investigated, the size distribution and maturity were plotted simultaneously to show the relationship between size and maturity development. Where either the size distribution or maturity of the chaetognaths differed significantly ($p < 0.05$) between the water masses, the data were analyzed separately for each water mass unless otherwise stated. In cases where no significant difference in size or maturity was observed between the water masses, data were pooled.

2001 survey

No significant differences were found in the average sizes (*t*-test; $p > 0.05$) and maturities (log-linear analysis; $p > 0.05$) of *Sagitta gazellae* in the two water masses, Polar Frontal Zone (PFZ) and Subantarctic Surface Water (SASW). *S. gazellae* had a wide size distribution and the majority of individuals ($n = 16$) measured between 20.1 and 25mm in length (Figure 3.26). The mean length was 35.21 ±10.18mm. No *S. gazellae* of < 10.1mm and >55mm were found. Overall, the *S. gazellae* population shows a platykurtic size distribution with stage II and III individuals being restricted to the larger sizes (Figure 3.26). Individuals in stage I contributed 65.68 ±17.09% to the total *S. gazellae* population examined, while only 25.53 ±13.33 and 9.1 ±11.46 of *S. gazellae* were in developmental stages II and III, respectively (Figure 3.27).

The lengths and maturities of *Eukrohnia hamata* were significantly different between the PFZ and SASW (*t*-test and log-linear analysis respectively, $p < 0.05$). The majority of *E. hamata* examined measured between 14.1 and 16mm in the PFZ ($n = 45$) and between 12.1 and 14mm in the SASW ($n = 53$) (Figures 3.28 and 3.29). The mean lengths of *E. hamata* were 14.22 ±2.96mm and 13.21 ±2.6mm in the PFZ and SASW, respectively. Overall, the *E. hamata* populations in both water masses had a normal size distribution (Figures 3.28 and 3.29). Individuals in stage I were numerically dominant in both the PFZ and SASW, contributing 84.4 ±12.34% and 95.5 ±4.43% to the total *E. hamata* population, respectively (Figure 3.30). No *E. hamata* of stage III development were found in the SASW (Figure 3.30).

2004 survey

The lengths of *S. gazellae* were significantly different between all three water masses i.e. Subantarctic Surface Water (SASW), Polar Frontal Zone (PFZ) and Antarctic Surface Water (ASW) (Newman-Keuls test; $p < 0.0001$ between all three surveys). The mean lengths were 35.53m ±8.17mm, 49.53 ±12.63mm and 23.45 ±8.2mm for the SASW, PFZ and ASW, respectively. However, because only a few of *S. gazellae* individuals that were examined were found at stations occupied in the PFZ and ASW, the size and maturity data from all three water masses were pooled. The majority of *S. gazellae* examined (n = 20) were found in the 40.1 – 45mm size class, and no individuals measured <10.1mm or >65mm (Figure 3.31). The *S. gazellae* population had a skewed size distribution, with most of the chaetognaths occurring in the lower size classes (Figure 3.31). The maturity stages of *S. gazellae* were not significantly different between the three water masses (log-linear analysis; $p > 0.05$). Stage I *S. gazellae* were again numerically dominant, contributing 54 ±27.63% to the total population examined, while only 10.38 ±19.11% and 2.06 ±4.22% of the *S. gazellae* were in stages II and III, respectively (Figure 3.31). Surprisingly, stage III *S. gazellae* occurred in both small and large size classes. There was no significant difference in the sizes and maturities of *E. hamata* between the three water masses (Newman-Keuls test and log-linear analysis respectively, $p > 0.05$). The majority of *E. hamata* (n = 104) measured between 10.1 and 12mm in length, and fewer than 10 individuals were >18.1mm in length (Figure 3.32). The *E. hamata* population had a normal size distribution (Figure 3.32). *E. hamata* in stage I were again the most dominant numerically, contributing 90.17 ±7.54% to the total population examined. Stage II *E. hamata* contributed 9.83 ±7.55% to the population while no stage III individuals were observed (Figure 3.32).

2005 survey

The sizes and maturities of *S. gazellae* were not significantly different between the three water masses i.e. Antarctic Surface Water (ASW), eddy edge and the Polar Frontal Zone (PFZ) (Newman-Keuls test and log-linear analysis respectively; $p > 0.05$). *S. gazellae* of lengths between 10.1 and 15mm (n = 13), and also between 45.1 and 50mm (n = 13) were numerically dominant, showing bimodality in the size distribution (Figure 3.33). The majority of the *S.*

gazellae examined were in stage I development, contributing 62.64 ±40.43% to the total population, and *S. gazellae* in stages II and III contributed 14.9 ±18.54% and 22.46 ±30.82% to total numbers, respectively (Figure 3.33).

The lengths of *E. hamata* were not significantly different between the three water masses (Newman-Keuls test; $p > 0.05$ between all three masses). The mean length of *E. hamata* at the eddy edge was 12.04 ±2.52mm, while in the ASW and PFZ the mean lengths were 11.14 ±3.18mm and 11.49 ±2.67mm respectively. At the eddy edge *E. hamata* of lengths between 10.1 and 14mm were the most common ($n = 166$) (Figure 3.34), while in the ASW the majority of *E. hamata* measured between 8.1 and 10mm in length ($n = 27$) (Figure 3.35) and in the PFZ the majority of *E. hamata* were in the 10.1 – 12mm size class ($n = 156$) (Figure 3.35). No *E. hamata* of >18mm in length were observed at the eddy edge while *E. hamata* >18mm in length were found in the other two water masses. Overall, the size distributions of the *E. hamata* populations in all three water masses were normal, with the ASW population being slightly skewed towards the lower size classes (Figs 3.34, 3.35 and 3.36). In terms of maturities of *E. hamata* there were no significant differences between the water masses (log-linear analysis; $p > 0.05$). *E. hamata* in stage I were numerically dominant, contributing 85.31 ±13.95% to the total population examined, while individuals in stages II and III contributed only 11.25 ±11.82% and 3.44 ±5.8% respectively (Figure 3.37).

An analysis of the lengths of the two chaetognath species between the three years investigated showed no significant difference in the lengths of *S. gazellae* (Tukey's test; $p > 0.05$ among all three years), but there were significant differences in the lengths of *E. hamata* (Tukey's test; $p < 0.001$ 0 for 2001 vs. 2004; $p < 0.001$ for 2001 vs. 2005; and $p = 0.107$ for 2004 vs. 2005). The mean lengths of the *E. hamata* for years 2001, 2004 and 2005 were 13.8 ±2.86mm, 12.02 ±3.4mm and 11.66 ±2.7mm, respectively.

Log-linear analysis revealed a significant difference in the maturities of the chaetognath species among the three years investigated, and this was attributed to the variability of stage III chaetognaths in the two species ($p < 0.001$ for both species). Log-linear analysis also revealed a difference in maturities between the two species, and this was attributed to the greater number of stage III *S. gazellae* than *E. hamata* and also a greater number of stage I *E. hamata* than *S. gazellae* ($p < 0.001$).

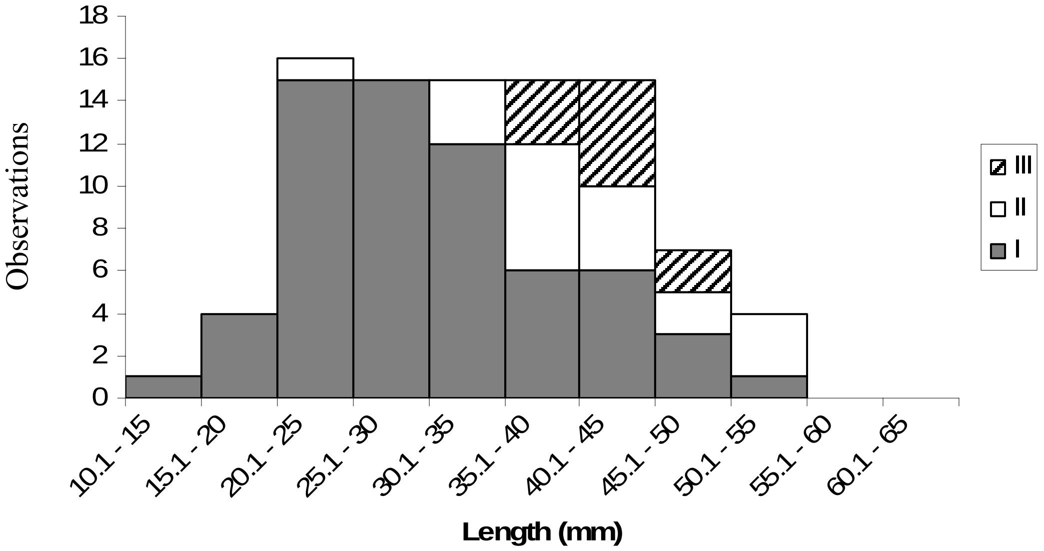

Fig. 3.26. Population structure of *Sagitta gazellae* in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2001.

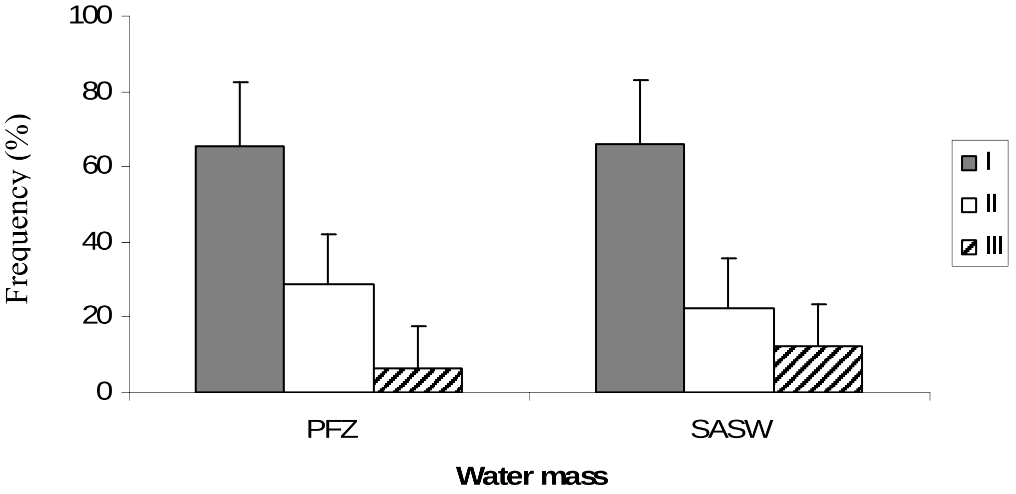

Fig. 3.27. Proportions of maturity stages of *Sagitta gazellae* in the Polar Frontal Zone and Subantarctic Surface Water in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2001. Bars indicate standard deviation.

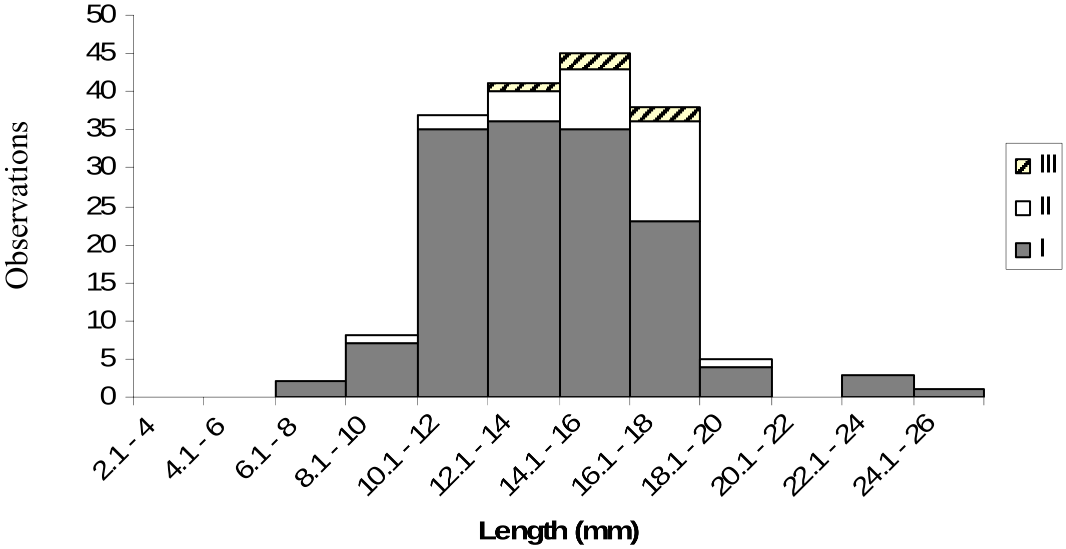

Fig. 3.28. Population structure of *Eukrohnia hamata* at the Polar Frontal Zone in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2001.

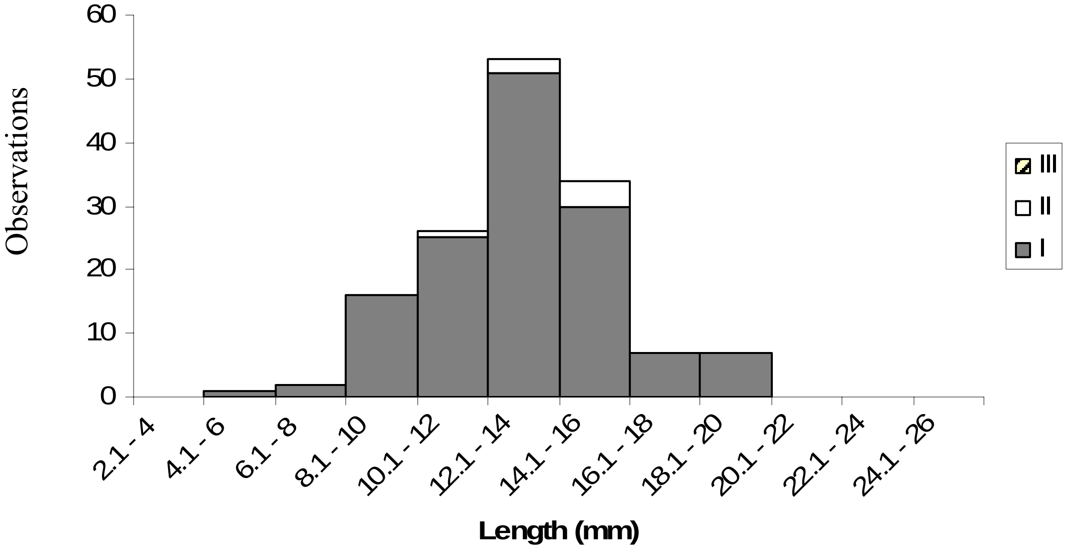

Fig. 3.29. Population structure of *Eukrohnia hamata* in the Subantarctic Surface Water in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2001.

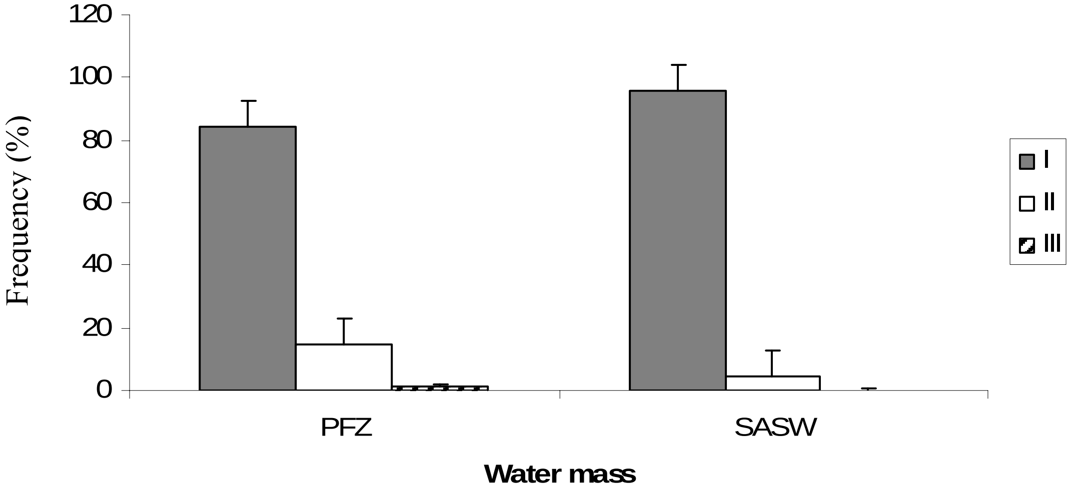

Fig. 3.30. Proportions of maturity stages of *Eukrohnia hamata* in the Polar Frontal Zone and Subantarctic Surface Water in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2001. Bars indicate standard deviation.

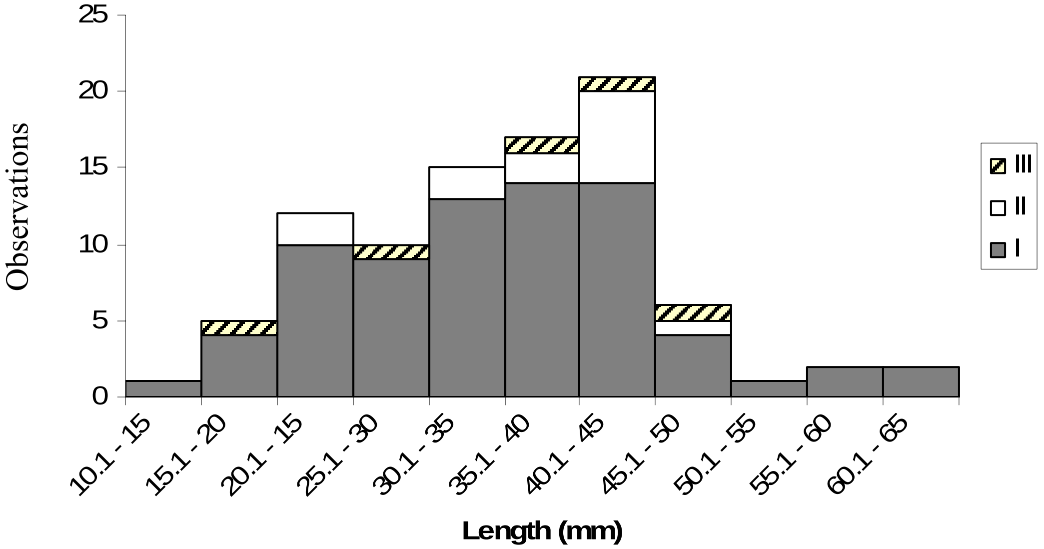

Fig. 3.31. Population structure of *Sagitta gazellae* in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2004.

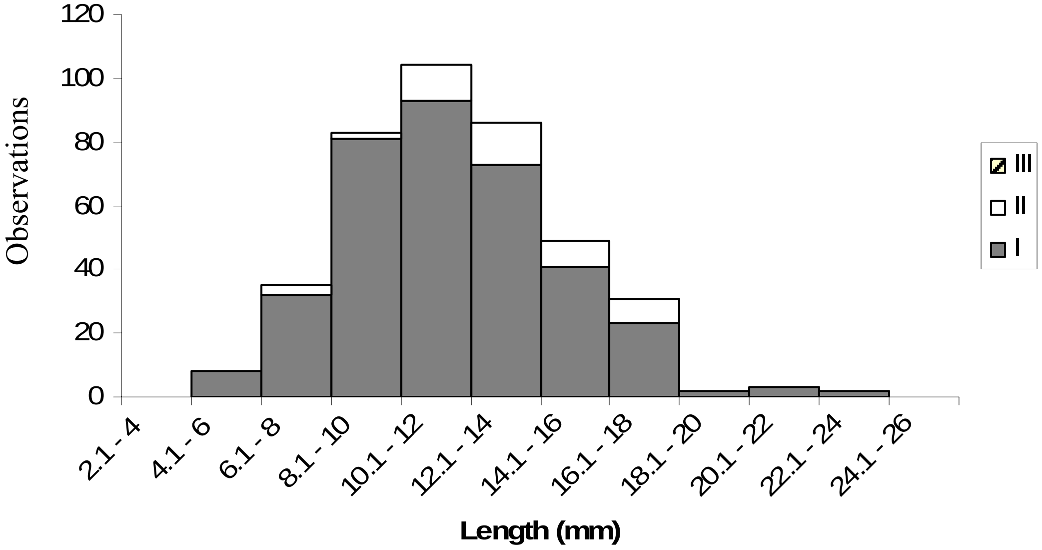

Fig. 3.32. Population structure of *Eukrohnia hamata* in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2004.

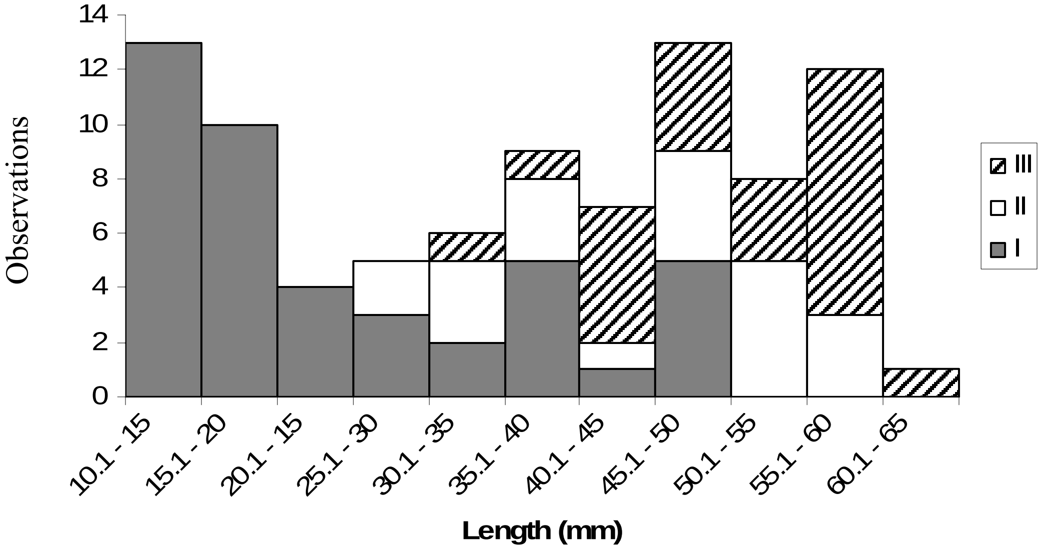

Fig. 3.33. Population structure of *Sagitta gazellae* in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005.

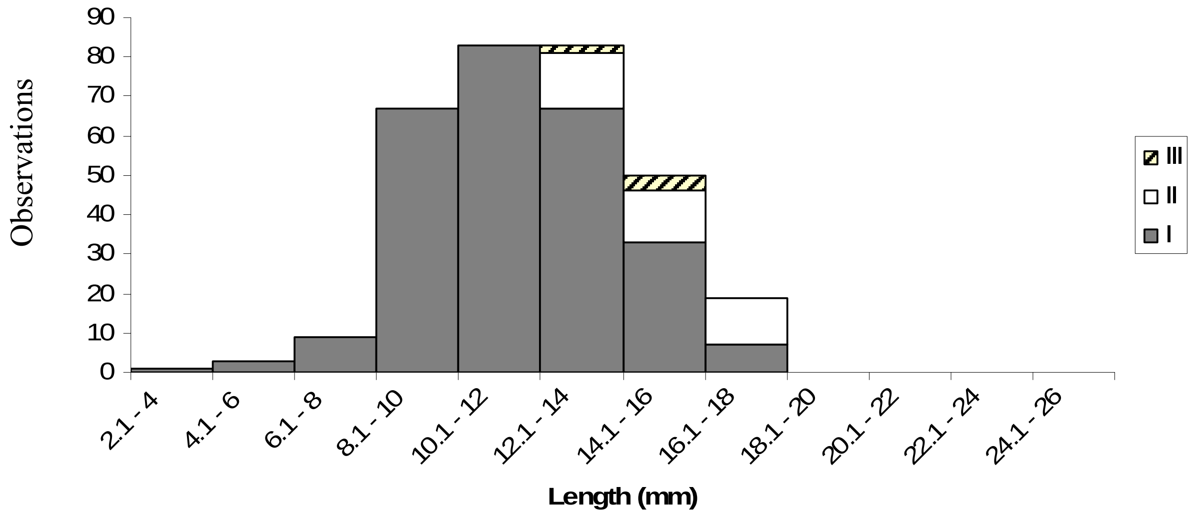

Fig. 3.34. Population structure of *Eukrohnia hamata* at the eddy edge of an eddy observed in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005.

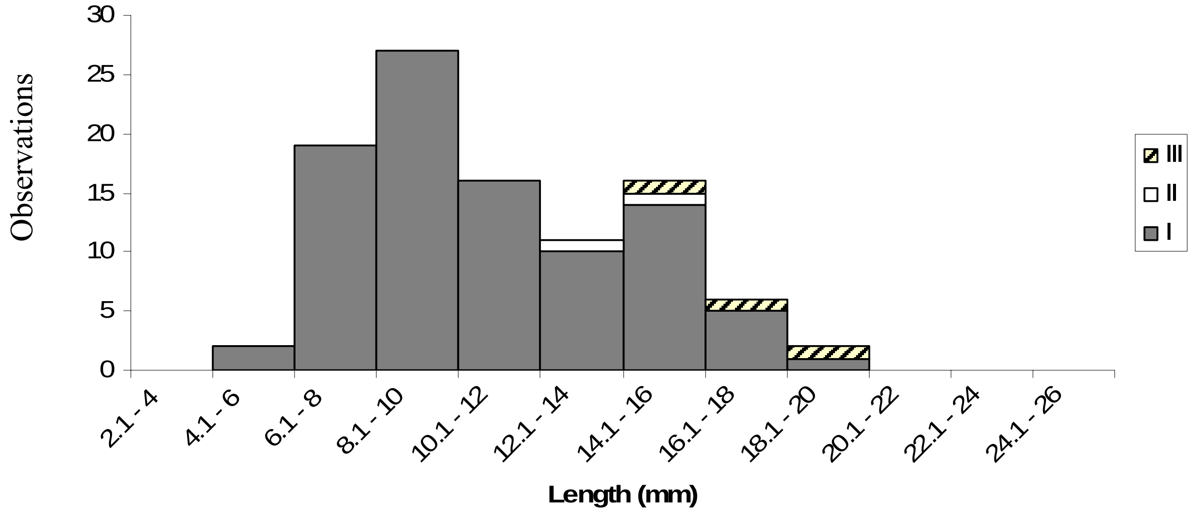

Fig. 3.35. Population structure of *Eukrohnia hamata* in the Antarctic Surface Water in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005.

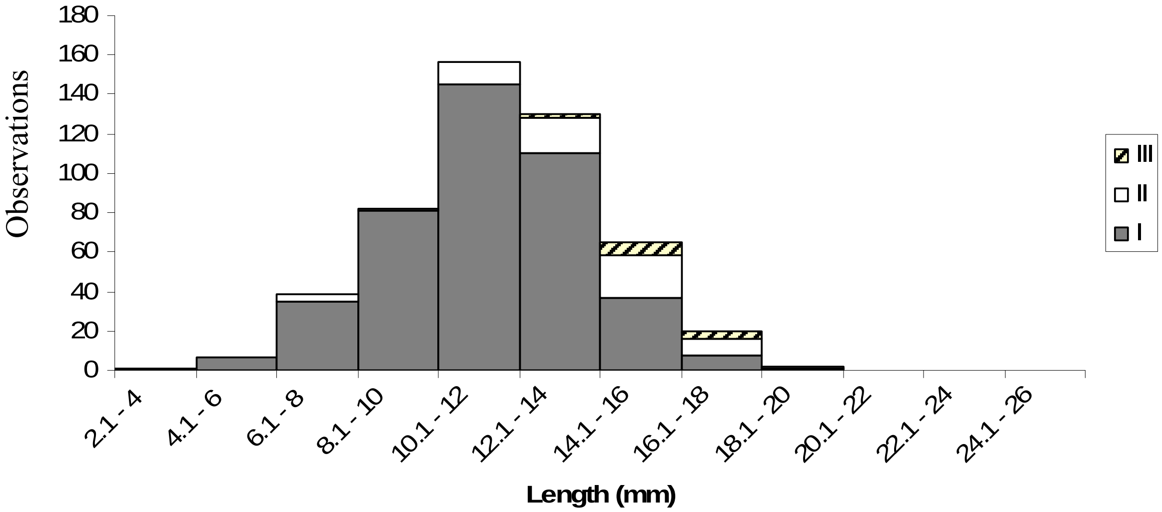

Fig. 3.36. Population structure of *Eukrohnia hamata* in the Subantarctic Surface Water in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005.

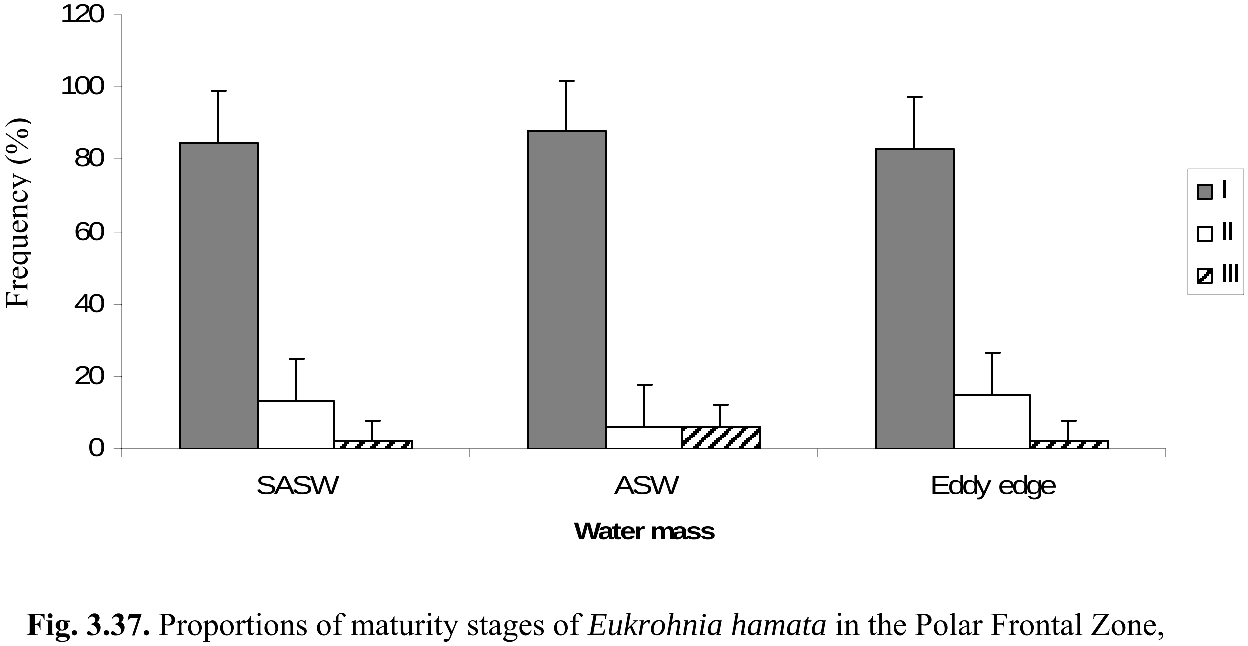

Fig. 3.37. Proportions of maturity stages of *Eukrohnia hamata* in the Polar Frontal Zone, Antarctic Surface water and eddy edge occurring in the vicinity of the Prince Edward Islands, late austral summer (April/May) 2005. Bars indicate standards deviation.

Chapter 4

Discussion

4.1. Physical environment

Previous studies have demonstrated that the positions of the Subantarctic Front (SAF) and the Antarctic Polar Front (APF) are not stationary, and that the fronts may in fact meander over a distance greater than 1° latitude (Foster and Middleton, 1984; Lutjeharms and McQuaid, 1986; Read and Pollard, 1993; Pakhomov and Froneman, 1999; Park *et al*., 2001). In the present study, the high variability in the positions of the fronts was evident during the three surveys (see further Bernard and Froneman, 2002; Ansorge *et al*., 2004; Ansorge and Bernard, 2005). The movement in fronts was largely the result of the interaction between the hydrology and prominent topography, mainly the south-Indian Ridge (Ansorge *et al*., 1999). The interaction of the frontal systems with the prominent topography facilitated the formation of the cold-core eddy during the 2005 survey.

Although previous studies have shown a strong relationship between sea temperature and the distribution of zooplankton, creating distinct zooplankton communities (Piatkowski, 1989; Froneman *et al*., 1997; Hosie *et al*., 2000), numerical analyses did not identify any distinct spatial patterns in the carnivorous macrozooplankton assemblages during the surveys conducted in 2001 and 2004. Similarly, in 2005 there was a poor positive correlation between sea surface temperature and macrozooplankton biomass. Also, during the 2001 and 2004 surveys, there was a poor correlation between meso- and macrozooplankton abundance, while there was a positive correlation during the 2005 survey. The absence of any distinct spatial pattern in macrozooplankton abundance during the 2001 and 2004 surveys can likely be attributed to the high degree of mesoscale flow variability of the Antarctic Circumpolar Current (ACC), which translocates species across biogeographic boundaries represented by the frontal systems (Boden and Parker, 1986; Ansorge *et al*., 1999; Froneman *et* al., 1999; Pakhomov and Froneman, 2000). The variability facilitated the advection of characteristic water bodies in various directions which transported zooplankton across the main frontal systems represented by the SAF and APF. It is also worth noting that Johnson and Terazaki (2004) did not find a correlation between chaetognath abundance and the thermocline or halocline, suggesting that hydrographic features in the water column do not necessarily influence the distribution of all zooplankton species.

4.2. Macrozooplankton distribution

Studies conducted in the vicinity of the Prince Edward Islands (PEI) have shown that the biogeographic origins of the zooplankton community in the Polar Frontal Zone (PFZ) demonstrate a high degree of inter-annual variability. Miller (1982) and Allanson *et al.* (1985) found the zooplankton community to be of subantarctic origin. On the other hand, Grindley and Lane (1979) found Antarctic species to be most prominent, whereas Pakhomov and Froneman (2000) found that subtropical species contributed substantially to the zooplankton community. In the present study, the macrozooplankton community structure during the three surveys was comprised of species from all three origins, with species of subantarctic origin being poorly represented (Tables 3.1 – 3.3). It is interesting to note from the abundance data of the RMT-8 net in the 2004 survey (Table 3.2), that carnivorous macrozooplankton abundances were greatest north-west of the frontal feature (0.012 ± 0.005ind.m^{-3}) in the subantarctic water but were low within the feature (0.002 ± 0.001 ind.m^{-3}) and south-east of the feature (0.005 ± 0.002 ind.m^{-3}) in the cooler Antarctic water (Figure 3.11). Together with the fact that species numbers were lowest south-east of the frontal feature, these findings suggest that the fronts act as biogeographic barriers to zooplankton. This is in agreement with previous studies (Brandt and Wadley, 1981; Piatkowski, 1989; Pakhomov *et al*., 1994; Pakhomov *et al*., 1999). Also important to note is the distribution of macrozooplankton abundance during the 2005 survey where greatest abundances were found in groups that contained stations located along the eddy edge (Table 3.3). Group 3 had five stations located at the eddy edge and had a total average abundance of 8.19 ± 2.52 ind.m^{-3}, while group 1 contained stations located inside the eddy only (Antarctic Surface Water), and had a total average abundance of 0.52 ±0.03 ind.m^{-3}. This suggests that the mixing of water masses along an eddy edge supports larger macrozooplankton abundances.

4.3. Plankton community structure

Total carnivorous macrozooplankton abundances and biomasses in all three surveys were in the range found in studies conducted in this region of the Southern Ocean during the same season (Pakhomov *et al*., 1994; Ansorge *et al*., 1999; Pakhomov and Froneman, 2000; Froneman *et al*., 2002). During the 2001 survey, the abundances of carnivorous macrozooplankton ranged between 0.379 and 43.731 ind.m^{-3}, and were found to be significantly higher (Tukey's test, $p = 0.0018$) than the abundances of the 2005 survey which ranged between 0.04 and 17.066 ind.m^{-3}. From the Bongo nets used in the 2004 survey, the abundance of carnivorous macrozooplankton was estimated to range between 0.865 to 29.97 ind.m^{-3}. These estimates are lower than those reported by Froneman *et al* (2002) within the same region (see Appendix 1, table 1). However, the abundance estimates obtained from the RMT-8 net during the 2004 survey are in the range reported by Pakhomov *et al* (1994) and Pakhomov and Froneman (2000) who also used the RMT-8 net. The total biomass of carnivorous macrozooplankton during the 2001, 2004 and 2005 surveys ranged from 0 to 0.18mg wwt m^{-3}, from 0 to 41.55mg wwt m^{-3}, and from 0.0002 to 1.271mg wwt m^{-3} respectively. These autumn values are lower than the summer values reported in Froneman *et al* (2002) within the Polar Frontal Zone (PFZ).The difference in biomass values between the studies can likely be attributed to the seasonality of zooplankton dynamics. Total carnivorous macrozooplankton biomass estimated from bongo nets during the 2004 survey is in the range 0.07 to 3.42mg Dwt m^{-3} reported by Froneman *et al*. (2002) using the same net type (Appendix 1, table 1). The total carnivorous macrozooplankton biomass estimated from the RMT-8 net was lower than the range 20 to 91000mg Dwt m^{-3} reported by Pakhomov and Froneman (2000), but the previous study included fish in the biomass estimates, whereas the present study did not. Estimated mean biomass values using the RMT-8 net were not significantly different from those of the Bongo nets (*t*-test; $p > 0.05$). This suggests that net avoidance, if it occurs at all, is not variable between the two net types. It is also important to mention, however, that estimates of macrozooplankton biomass are often underestimated due to tissue loss caused by preservation of samples in formalin (Froneman *et al*., 2002).

The carnivorous macrozooplankton community was dominated numerically and by biomass by the chaetognaths *Eukrohnia hamata* and *Sagitta gazellae* during the three surveys. The importance of chaetognaths to zooplankton communities is now well documented (Veronina *et al*., 1994; Pakhomov *et al*., 2000; Froneman *et al*., 2002; Johnson and Terazaki, 2004). Among the chaetognaths, *S. gazellae* had the greatest biomass values in all the three years investigated. The total biomass values of *S. gazellae* during the 2001, 2004 and 2005 surveys ranged from 0 to 0.106mg wwt m^{-3}, from 0.012 to 34.261mg wwt m^{-3}, and from 0 to 0.225mg wwt m^{-3}, respectively. The dominance of *S. gazellae* is in agreement with Pakhomov and Froneman (2000) but differs from Froneman *et al*. (1999) who found that *E. hamata* contributed more to macrozooplankton biomass than the other chaetognaths. Perissinotto and Boden (1989) in a two-year study found that chaetognaths contributed ≈12 per cent to the total zooplankton catch in 1985, but only ≈ 2 per cent in 1986. Such extreme variability in the contribution of different groups to total carnivore biomass has been attributed to the variability in oceanography in a region, prey availability, swarming behavior of various groups and the stage of the lifecycle of a species at the time of sampling (Froneman *et al*., 2002; Johnson and Terazaki, 2004). In general, the total carnivorous macrozooplankton biomass values during the 2001 survey were evenly distributed, with stations situated along the 34ºE transect displaying somewhat higher values (Figure 3.4).

4.4. Predation impact

Estimates of the predation impact of the selected carnivores during the 2001, 2004 and 2005 surveys ranged from 0.05 to 27.72%, from 0.01 to 1.54%, and from 0.01 to 19.7% of the total mesozooplankton standing stock, respectively. The 2004 predation impact estimates were significantly lower than those for the 2001 and 2005 surveys (Tukey's test, $p = 0.036$ for 2001; $p = 0.016$ for 2005). The 2004 estimates, however, are in the range 0.1 – 6.5% reported by Pakhomov *et al* (1999), while the 2001 and 2005 estimates are in the range 0.4 – 40% reported by Froneman *et al* (2002) in the Polar Frontal Zone (PFZ). The studies of Pakhomov *et al* (1999) and Froneman *et al* (2002) included euphausiids and amphipods as part of the carnivorous macrozooplankton. It is worth noting that during the three years investigated in the present study, euphausiids and amphipod densities generally contributed <10% of the total macrozooplankton standing stock. Euphausiids are known to dominate total carnivore biomass and their impact on mesozooplankton is considered to be substantial (Froneman *et al*., 2002).

The absence of euphausiids may account for the lower predation estimates recorded during the present study. The predation impacts observed in the present study are similar to the 2 – 12% copepod biomass removed by carnivorous gelatinous zooplankton in the northern Humboldt Current off Chile (González *et al*., 2004). In agreement with Pakhomov *et al* (1999) and Froneman *et al* (2002), chaetognaths were identified as the most important predators of mesozooplankton in the PFZ (Figures 3.19 – 3.21). The high predation pressure of chaetognaths can largely be attributed to their numerical dominance of the carnivorous macrozooplankton abundance during the three surveys. It should be noted that the estimates of predation impact should be regarded with caution as there are several potential sources of error. For example, many of the carnivores investigated in the present study exhibit cannibalism (Pearre, 1982; Dilling and Alldredge, 1993). On the other hand, estimates of the predation impact of mysids may have been underestimated due to net avoidance. Although not investigated in the present study, it is important to mention that carnivorous macrozooplankton are prey to myctophid fish (Pakhomov *et al*., 1996), and land-based predators e.g. birds from the Prince Edward Islands (Pakhomov and Froneman, 1999; Pagés *et al*., 1996; Perissinotto and McQuaid, 1992). Predation on the carnivorous macrozooplankton may thus reduce their impact on the mesozooplankton. The relatively low daily predation estimates recorded during the three years investigated here suggest that carnivorous macrozooplankton would not have increased the localized efficiency of the biological pump during the late austral summers of 2001, 2004 and 2005, and especially not in 2004 where predation impact was estimated to be the lowest.

4.5. Chaetognath population structure

4.5.1. Chaetognath standing stock and distribution

The results of the present study show the dominance of the chaetognaths *Sagitta gazellae* and *Eukrohnia hamata* in the carnivorous component of macrozooplankton in the waters in the vicinity of the Prince Edward Islands (PEI). The dominance of chaetognaths in carnivorous zooplankton assemblages is widely reported throughout the world’s oceans, including waters surrounding the PEI (Froneman and Pakhomov, 1998; Froneman *et al*., 1998), eastern Atlantic sector of the Southern Ocean (Pakhomov and Froneman, 2004), Georges Bank in the North Atlantic Ocean (Sullivan and Meise, 1996), northern Californian Current (Reese *et al.*, 2005), and across the Australian sector of the Antarctic Ocean (Johnson and Terazaki, 2004).

During the three surveys, the densities of chaetognaths varied among the different water masses, suggesting that their distribution was related to hydrographic features. The relationship between hydrography and zooplankton distribution has been shown in previous studies (Piatkowski, 1989; Ulloa *et al.*, 2000; Youssara and Gaudy, 2001; Fernández de Puelles *et al.*, 2004; Giesecke and González, 2004; Johnson and Terazaki, 2004; Reese *et al.*, 2005). Similarly, Sullivan and Meise (1996) found that the abundance of chaetognaths at Georges Bank decreased with a rise in temperature. Although there was a high degree of overlap in chaetognath densities between the three surveys, there was also substantial inter-annual variability. This was especially evident in the densities of *Eukrohnia hamata*, which were significantly different among the three surveys (ANOVA; $p < 0.05$). Inter-annual variability also existed between the densities of chaetognaths occurring in the same water mass but in different years. For example, during the 2001 survey stations in the Polar Frontal Zone (PFZ) had highest chaetognath abundances, while during the 2004 survey stations in the PFZ had the lowest abundances. The findings of the 2004 survey are in agreement with Ansorge *et al.* (1999) who found that the contribution of macrozooplankton to total dry weight was significantly lower in the PFZ than in the Subantarctic Front (SAF).

The numerical dominance of *E. hamata* to the chaetognath standing stock during the three years investigated in the present study is in agreement with previous studies conducted in the vicinity of the PEI (Boden and Parker, 1986; Froneman and Pakhomov, 1998; Froneman *et al.*, 1998), but is in contrast with other studies (Pakhomov *et al.*, 1994; Pakhomov and Froneman, 2000). The variability in the dominance of a species to the zooplankton community structure has been reported in previous studies and has been attributed to variability in physical and biological dynamics (Perissinotto and Boden, 1989; Kaufmann *et al.*, 2003). The combined total abundance and biomass values of *S. gazellae* and *E. hamata* during the three surveys in the present study (0.38 – 43.73 ind. m^{-3} and 0.004 – 0.179 mg wwt m^{-3} in 2001; 0.86 – 29.97 ind.m^{-3} and 0.005 – 41.55 mg wwt m^{-3} in 2004; and 0 – 14.5 ind.m^{-3} and 0 – 0.157 mg wwt m^{-3} in 2005) are in the range reported for previous studies within the same geographical region (Boden and Parker, 1986; Froneman and Pakhomov, 1998; Froneman *et al.*, 1998; Pakhomov and Froneman, 2000).

4.5.2. Gut-content analysis and feeding rate

In agreement with Froneman and Pakhomov (1998) and Froneman *et al.* (1998), gut-content analysis revealed that *Sagitta gazellae* fed on a wider variety of prey than *Eukrohnia hamata* in the three surveys (Table 3.14). It must be noted, however, that much of the prey found in *Eukrohnia hamata* was not identifiable due to its advanced state of digestion. The ability of *S. gazellae* to consume a wider variety of prey can be attributed to the greater size of *S. gazellae* over *E. hamata*, since maximum prey size is delimited by the size of the chaetognath mouth opening (Pearre, 1980; Sullivan, 1980; Pearre, 1982; Kehayias *et al.*, 1996). However, the importance of copepods and unidentifiable prey items in the diets of both the species is clearly evident in the present study (Figure 3.22).

Roughly 51% of the *E. hamata* examined contained oil droplets in their guts (Figure3.22). The presence of oil droplets in the guts of *E. hamata* has been reported in previous studies (Sameoto, 1987; Øresland, 1990; Froneman and Pakhomov, 1998; Froneman *et al.*, 1998). The reason for the occurrence of oil droplets, as well as their function, remains unknown. Sameoto (1987) suggested that the oil droplets may represent the final part of copepod prey to be digested, since copepods such as *Calanus* spp. are rich in oil. If oil droplets are in fact the remains of prey, their exclusion as prey items may severely underestimate the daily feeding rate of *E. hamata*. Øresland (1990) suggested that oil droplets may function as a buoyancy mechanism or as food reserves. Interestingly, Båmstedt (1978) found highest concentrations of oil droplets in *E. hamata* to occur during winter. In the present study, no oil droplets were found in the guts of *S. gazellae*. Since *S. gazellae* consume a wider variety of prey, it is unlikely that this species would need to store oil droplets as food reserves.

Cannibalism was observed in *E. hamata* during the 2004 survey, contributing up to 2.5% to the total number of prey items, while during the 2005 survey *S. gazellae* displayed cannibalistic behaviour with prey chaetognaths contributing up to 8.3% to the total number of prey items identified. These rates are in agreement with Froneman and Pakhomov (1998) and Froneman *et al*. (1998) in studies conducted during the same time of year and in the same region of the Southern Ocean. Cannibalism in chaetognaths is not uncommon and has been observed in *Sagitta enflata* (Feigenbaum, 1979; Pearre, 1982; Kehayias *et al.*, 1996), *S. serratodentata* (Kehayias *et al.*, 1996), *S. bipunctata* (Kehayias *et al.*, 1996), and *S. elegans* (Feigenbaum, 1982). Pearre (1982) found that larger chaetognaths displayed a higher degree of cannibalism than smaller chaetognaths. Cannibalism, both inter- and intra-specific, is an important source of carbon in chaetognath diets (Feigenbaum, 1982; Pearre, 1982). Since the contribution of chaetognath prey to the diets of *S. gazellae* and *E. hamata* was low in the present study, it is likely that other prey items were sufficient to sustain the two species during the time of study. In the present study, multiple prey were only observed during the 2001 survey and only in a single *S. gazellae*. This observation is rather low when compared to the multiple prey found in seven *S. gazellae* in a study by Froneman and Pakhomov (1998). Also, 1.7% of *S. enflata* examined by Feigenbaum (1979), and 14.6% of *S. enflata* examined by Kehayias *et al.* (1996) contained multiple prey in their guts. The frequency of multiple prey in other chaetognath species is reported in Feigenbaum and Maris (1984).

The daily feeding rates (Fr; prey d^{-1}) of *E. hamata* and *S. gazellae* varied from 0 to 0.307 and from 0 to 0.964 during the 2001 survey, from 0 to 0.192 and from 0 to 0.451 during the 2004 survey, and from 0 to 0.418 and from 0 to 1.685 in the 2005 survey, respectively (Tables 3.15 – 3.17). The Fr values of *E. hamata* in the present study are similar to those of Froneman and Pakhomov (1998) and Froneman *et al.* (1998), as well as to studies conducted in the high Antarctic region (Øresland, 1990, 1995). The Fr values of *S. gazellae* reported here are, however, somewhat higher than those reported in Froneman and Pakhomov (1998) and Froneman *et al*. (1998).

4.5.3. Predation impact

The combined predation impact of the two chaetognaths during the 2001, 2004 and 2005 surveys was estimated at 3.63%, 0.23% and 2.26% of the mesozooplankton standing stock, respectively (Tables 3.15 – 3.17). These values are in the range reported by Froneman and Pakhomov (1998) and Froneman *et al.* (1998). There was a significant difference in the predation impact of *S. gazellae* between the 2001 and 2004 surveys (Newman-Keuls test; p = 0.005). Such variability is not surprising since inter-annual variability in chaetognath abundances, which are likely to affect the impact of chaetognaths on mesozooplankton standing stock, has been reported in previous studies and this study (Allanson *et al.*, 1985; Perissinotto and Boden, 1989; Sullivan and Meise, 1996). There was also a significant difference between the predation impacts of the two species during the 2001 survey (Newman-Keuls test, p = 0.035), with *Eukrohnia hamata* having a much lower impact (1.82 ±3.57%) than *S. gazellae* (5.39 ±5.18%). Although not examined in the present study, other factors that may influence the impact of chaetognaths on mesozooplankton standing stock are the abundance of prey (Sullivan, 1980; Sullivan and Meise, 1996, Kehayias *et al.*, 1996; Baier and Purcell, 1997a; Tönnesson and Tiselius, 2005), and competition with other carnivores (Baier and Purcell, 1997a). In the present study, the correlations between chaetognath densities and mesozooplankton densities were poor during all three surveys (Pearson correlation analysis; $r^2 < 0.38$ and $p > 0.05$ for the three surveys). This is in contrast with Froneman *et al.* (1998) who found that chaetognath abundances were significantly correlated to copepod densities in the same geographical region as the present study. Similarly, at Georges Bank in the North Atlantic Ocean, Sullivan and Meise (1996) found that chaetognath numbers increased following an increase in copepod abundance. However, the relationship between the abundances of chaetognaths and mesozooplankton during the 2005 survey in the present study was good unless extreme values were removed from the data set. This suggests that the greater the abundance of mesozooplankton, the stronger the correlation between chaetognath and mesozooplankton abundances. It is possible that strong relationships between chaetognaths and their prey exist, but that the strength of the relationships is variable between years. It is also possible that previous studies have not excluded extreme values and/or outliers from their analyses. However, it is important to note that the Polar Frontal Zone, the geographic region of investigation in the present study, is a transition zone between Subantarctic and Antarctic waters, and as such does not generally exhibit any distinct zooplankton communities.

There are a number of limitations when employing gut-content analysis for the estimation of predation impact and these are likely to underestimate the importance of chaetognaths in marine food webs. Firstly, chaetognaths are soft-bodied and fragile and many are damaged during net tows, so that their abundances may be underestimated (Feigenbaum and Maris, 1984; Froneman *et al*., 1998). In terms of feeding rates, the regurgitation of prey during sampling and cod-end feeding cannot be ignored (Feigenbaum and Maris, 1984). Also, Baier and Purcell (1977a) found that net tows of longer than 2 minute duration resulted in as much as 50% prey loss from chaetognath guts. In the present study, net tows were conducted for no less than 20 minutes, thus potentially underestimating the number of prey in chaetognath guts. In addition, the digestion times (Dt) of the chaetognaths investigated in the present study were derived from the literature and these values may vary with conditions such as water temperature (Feigenbaum, 1982; Pearre, 1982; Nagasawa, 1985; Baier and Purcell, 1997a). Lastly, it was assumed that unidentifiable prey items in the chaetognath guts were the remains of single prey items only, and as stated above, the occurrence of multiple prey in the guts of chaetognaths is well documented (Feigenbaum and Maris, 1984; Øresland, 1995; Kehayias *et al*., 1996).

4.5.4. Size distribution and maturity

The lengths of *Sagitta gazellae* and *Eukrohnia hamata* varied from 12.2 to 52.2mm and from 6 to 18.8mm during the 2001 survey; from 13.8 to 63.6mm and from 5 to 24mm during the 2004 survey; from 9.4 to 62.6mm and from 5 to 20mm during the 2005 survey, respectively. The lengths of *E. hamata* are in the range reported by Øresland (1995) at the Antarctic Peninsula during the same season. The maximum lengths of *S. gazellae* during this study are similar to those given by Casanova (1999). No other studies to date have been done on *S. gazellae* population structure in the vicinity of the Prince Edward Islands (PEI). *E. hamata* showed significant differences in lengths between the three surveys (Newman-Keuls test; $p < 0.05$). This may be a reflection of the variable characteristics of the different water masses encountered during the surveys, since temperature has a direct effect on the growth of chaetognaths (Welch *et al*., 1996). Also, the length of chaetognaths has been found to increase with an increase in prey density (Feigenbaum and Maris, 1984). Chaetognaths are opportunistic ambush predators and their feeding success is determined mostly in prey encounters, which increase as abundances of prey increase (Johnson and Terazaki, 2004). In the present study, the lengths and maturities of *E. hamata* were significantly different (ANOVA; $p < 0.05$) between the Polar Frontal Zone (PFZ) and the Subantarctic Surface Water (SASW) during the 2001 survey only, while the lengths of *S. gazellae* were only significantly different (ANOVA; $p < 0.05$) between the three water masses encountered during the 2004 survey. As mentioned earlier, the PFZ is a transition area and is characterized be high mesoscale variability so that distinct populations are not common. However, Johnson and Terazaki (2004) suggested that differing lengths may be explained by differences in breeding periodicity during sampling.

Very little is known about the reproduction of chaetognaths, especially in the Southern Ocean. In a study conducted in the Antarctic Ocean during summer (December/January), Johnson and Terazaki (2004) found *E. hamata* at stage I maturity to be most common and mature individuals to be less common. During winter (July/August) at the Antarctic Peninsula, Øresland (1995) also found *E. hamata* at stage I maturity to be most common. Similarly, in the present study, both chaetognath species had most individuals at stage I maturity. It would thus seem that the species were not reproducing during the time of study (April/May). However, Øresland (1995) suggested that *E. hamata* breeds at a low rate throughout the year. On the other hand, Johnson and Terazaki (2004) found that large and mature *E. hamata* tended to occur in deeper water (> 500m), and Welch *et al* (1996) found larger individuals of *Parasagitta elegans* in deeper water than smaller individuals. It is thus possible that during the present study mature chaetognaths were not sampled simply because of the depth of sampling (generally not > 300m). What is also clear from the present study is that the larger individuals of both the species were always the most mature, suggesting that *S. gazellae* and *E. hamata* reach maturity after a specific body length. This is in agreement with a study on the *E. hamata* population structure by Øresland (1995), and a study on the *S. elegans* population structure by Pearre (1981). Pearre (1981) found small and immature *S. elegans* numerically dominant in the Bedford Basin, Nova Scotia, during both July and December. Another possible explanation for the dominance of stage I chaetognaths during the present study is that few chaetognaths survive to adulthood due to predation by predators such as the poecilostomatoid copepod *Oncaea* spp. (Go *et al.*, 1998), other chaetognaths (Pearre, 1982), and fish (Pakhomov *et al.*, 1996; Schabetsberger *et al.*, 2000). In the present study, the mean level of maturity of both the species differed significantly among the three years investigated. This could again be explained by the variable temperatures encountered during the three surveys. However, Johnson and Terazaki (2004) found that breeding was unaffected by hydrography.

In general, both *E. hamata* and *S. gazellae* displayed populations with normal size distribution in the present study. This is in agreement with a study on *E. hamata* (Øresland, 1995) but is in contrast with the strongly bimodial size distribution displayed by *S. elegans* (Pearre, 1981).

Chapter 5

Conclusion

5.1. General conclusion

Oceanic fronts and eddy edges are characterized by increased zooplankton biomass, and frontal systems may form biogeographic boundaries for many zooplankton species in such a way as to affect zooplankton abundances and community structure. During the present study, however, the fronts did not act as boundaries to zooplankton due to the high mesoscale variability in oceanography. For example, the formation of an eddy during the 2005 survey, which was able to transport species across fronts. Carnivorous gelatinous macrozooplankton play an important role in the Southern Ocean ecosystem and potentially have a great influence on mesozooplankton standing stock. However, in the present study the predation impact of the macrozooplankton was not sufficient to increase the localized efficiency of the biological pump.

Chaetognaths, specifically *Eukrohnia hamata*, are the dominant carnivorous gelatinous macrozooplankton in the waters in the vicinity of the Prince Edward Islands. Densities of *E. hamata* and *Sagitta gazellae* are variable among years, and even among water masses, confirming the relationship between zooplankton distribution and hydrographic conditions. Although *S. gazellae* consume a wider variety of prey, copepods are the major food source of both the species. The predation impact of the two species on mesozooplankton is relatively high, and is likely to have been underestimated due to the various limitations in methods used to obtain estimates. From the results it would seem that both the species mature at a certain size, and it is possible that both size and maturity are affected by water temperature and food availability.

5.2. Suggestions for future research

1. Previous studies have found that different net types and of differing mesh size sample at different efficiencies (Baier and Purcell, 1997b). It is thus important that the sampling abilities of different nets are examined so that results of different studies are comparable. This would also examine which nets are highly avoided by zooplankton, and should therefore not be used for zooplankton collection.

2. Preservation in formalin has been known to shrink and distort specimens, and it is advisable to identify, measure and weigh specimens as soon after collection as possible.

3. Most studies in the Southern Ocean, particularly those conducted in the Polar Frontal Zone in the vicinity of the Prince Edward Islands, have taken place during late austral summer. There is therefore a lack of year-round information on zooplankton dynamics. It is thus suggested that, if possible, studies are conducted during all seasons of the year so that data on the seasonality of zooplankton densities and community structure is established. This would also resolve the issue as to whether chaetognaths such as *Eukrohnia hamata* and *Sagitta gazellae* reproduce seasonally or continuously throughout the year, and whether they mature with size.

4. Since many zooplankton species undergo ontogenic migrations, tows should be conducted to depths that cover the entire population depth range of the species being studied. This would give more insight into the population structures of zooplankton species.

5. Although a number of published works have used live chaetognaths in their feeding rates experiments (Dilling and Alldredge, 1993; Nagasawa, 1985, Feigenbaum (unpubl.) in Feigenbaum and Maris, 1984), for the most part, because of their fragility, chaetognaths are difficult to collect in a condition that allows them to be kept alive in the laboratory. Net tows tend to damage chaetognaths, and thus it would be ideal if chaetognaths were

collected by hand using SCUBA or snorkeling. This may be difficult in the cold and rough waters of the Southern Ocean, but the possibility should at least be considered.

6. Longhurst (1991) is of the opinion that the uptake of carbon by the marine biosphere is likely to weaken rather than strengthen, and thus enhance the rate of increase of atmospheric carbon. If the question of whether and to what extend carnivorous macrozooplankton contributes to carbon flux in the Southern Ocean is to be answered beyond doubt, more experiments on digestion time, prey selection and production of fecal pellets need to be conducted. Experiments should focus on chaetognaths since numerically they are the most important component of carnivorous macrozooplankton in the Southern Ocean.

References

Abbott, M.R., Richman, J.G., Letelier, R.M. and Bartlett, J.S. 2000. The spring bloom in the Antarctic Polar Frontal Zone as observed from a mesoscale array of bio-optical sensors. *Deep-Sea Research II*. 47: 3285-3314.

Allanson, B.R., Boden, B., Parker, L. and Duncombe Rae, C. 1985. A contribution to the oceanology of the Prince Edward Islands. In: *Antarctic nutrient cycles and food webs*. Siegfried, W.R., Condy, P.R. and Laws, R.M. (Eds). Springer, Berlin, pp. 38-45.

Ansorge, L.J., Froneman, P.W., Pakhomov, E.A., Lutjeharms, J.R.E., Perissinotto, R. and van Ballegooyen, R.C. 1999. Physical-biological coupling in the waters surrounding the Prince Edward Islands (Southern Ocean). *Polar Biology*. 21: 135-145.

Ansorge, I.J., Froneman, P.W., Lutjeharms, J.R.E., Bernard, K., Bernard, A., Lange, L., Lukáč, D., Backeburg, B., Blake, J., Bland, S., Burls, N., Davies-Coleman, M., Gerber, R., Gildenhuys, S., Hayes-Foley, P., Ludford, A., Manzoni, T., Robertson, E., Southey, D., Swart, S., Van Rensburg, D., and Wynne, S. 2004. An interdisciplinary cruise dedicated to understanding ocean eddies upstream of the Prince Edward Islands. *South African Journal of Science*. 100: 319-322.

Ansorge, I.J. and Bernard, K.S. 2005. *DEIMEC IV: Hydrographic and biological data report*. University of Cape Town, Cape Town, pp. 32.

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

Atkinson, A., Ward, P., Hill, A., Brierley, A.S. and Cripps, G.C. 1999. Krill-copepod interactions at South Georgia, Antarctica, II. *Euphausia superba* as a major control on copepod abundance. *Marine Ecology Progress Series*. 176: 63-79.

Baier, C.T. and Purcell, J.E. 1997a. Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic Bight. *Marine Ecology Progress Series*. 146: 43-53.

Baier, C.T. and Purcell, J.E. 1997b. Effects of sampling and preservation on apparent feeding by chaetognaths. *Marine Ecology Progress Series*. 146: 37-42.

Baker, A. de C., Clarke, M.R. and Harris, M.J. 1973. The N.I.O. combination net (RMT 1+8) and further developments of rectangular midwater trawls. *Journal of the Marine Biology Association of the United Kingdom*. 53: 167-184.

Båmstedt, U. 1987. Studies of the deep water pelagic community of Korsfjorden, Western Norway: seasonal variation in weight and biochemical composition of *Chiridius armatus* (Copepoda), *Boreomysis arctica* (Mysidacea) and *Eukrohnia hamata* (Chaetognatha) in relation to their biology. *Sarsia*. 63: 145-154.

Belkin, I.M. 1989. Alternation of the front distributions in the Southern Ocean near the Corzet Plateau. Transactions of the USSR Academy of Science: Earth sciences section. 308: 265-268. (Published in English in 1991)

Belkin, I.M. and Gordon, A.L. 1996. Southern Ocean fronts from Greenwich meridian to Tasmania. *Journal of Geophysical Research*. 101: 3675-3696.

Bernard, K.S. and Froneman, P.W. 2002. Mesozooplankton community structure in the Southern Ocean upstream of the Prince Edward Islands. *Polar Biology*. 25: 597-604.

Bernard, K.S. and Froneman, P.W. 2003. Mesozooplankton community structure and grazing impact in the Polar Frontal Zone of the south Indian Ocean during austral autumn 2002. *Polar Biology*. 26: 268-275.

Bernard, K.S. and Froneman, P.W. 2005. Trophodynamics of selected mesozooplankton in the west-Indian sector of the Polar Frontal Zone, Southern Ocean. *Polar Biology*. 28: 594-606.

Bernard, K.S., Froneman, P.W., Bernard, A.T.F. and Lange, L. 2006. Mesozooplankton community associated with a cold-core eddy in the Polar Frontal Zone. *Polar Biology* (submitted).

Boden, B.P. and Parker, L.D. 1986. The plankton of the Prince Edward Islands. *Polar Biology*. 5: 81-93.

Boltovskoy, D. 1999. (Ed). South Atlantic zooplankton, vols 1, 2. Backhuys, Leiden.

Boltovskoy, D. 1981. (Ed). Atlas del zooplancton del Atlàntico Sudoccidental y métodos de trabajo con el zooplancton marino, Publicación especial del INIDEP, Mar del Plata, Argentina.

Brandt, S.B. and Wadley, V.A. 1981. Thermal fronts as ecotones and zoogeographic barriers in marine and freshwater systems. *Proceedings of the Ecological Society of Australia.* 11: 13-26.

Casanova, J-P. 1999. Chaetognatha. In: *South Atlantic zooplankton*, vol. 2.Boltovskoy, D. (Ed). Backhuys, Leiden, pp. 1353-1374.

Clarke, K.R. and Warwick, R.M. 1994. *Change in marine communities: an approach to statistical analysis and interpretation.* National Environmental Research Council, Cambridge, pp. 138.

Davis, C.C. 1955. *The Marine and Freshwater Plankton*. Michigan State University Press, Michigan. pp. 562.

Deacon, G.E.R. 1983.Kerguelen, Antarctic and Subantarctic. *Deep-Sea Research*. 20: 77-81.

Dilling, L. and Alldredge, A.L. 1993. Can chaetognath fecal pellets contribute significantly to carbon flux? *Marine Ecology Progress Series*. 92: 51-58.

Dunbar, M.J. 1962. The life cycle of *Sagitta elegans* in arctic and Antarctic seas, and the modifying effects of hydrographic differences in the environment. *Journal of Marine Research*. 20: 76-91.

El-Sayed, S. 2005. History and evolution of primary productivity studies of the Southern Ocean. *Polar Biology*. 23: 423-438.

Fancett, M.S. and Jenkins, G.P. 1988. Predatory impact of scyphomedusae on ichthyoplankton and other zooplankton in Port Phillip Bay. *Journal of Experimental Marine Biology and Ecology* 116: 63-77.

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

Feigenbaum, D. 1982. Feeding by the chaetognath, *Sagitta elegans*, at low temperatures in Vineyard Sound, Massachusetts. *Limnological Oceanography*. 27: 699-706.

Feigenbaum, D. L. and Maris, R.C. 1984. Feeding in the chaetognatha. *Oceanography and Marine Biology Annual Review*. 22: 343-392.

Fernández de Puelles, M.L., Valencia, J., Jansá, J. and Morillas, A. 2004. Hydrographical characteristics and zooplankton distribution in the Mallorca channel (Western Mediterranean): spring 2001. *Journal of Marine Science*. 61: 654-666.

Field, J.G., Clarke, K.R. and Warwick, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*. 8: 37-52.

Fleddum, A., Kaartvedt, S. and Ellertsen, B. 2001. Distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica* in habitats of shallow prey assemblages and midnight sun. *Marine Biology*. 139: 719-726.

Fortier, L., Le Fèvre, J. and Legendre, L. 1994. Export of biogenic carbon to fish and to the deep ocean: the role of large plankton microphages. *Journal of Plankton Research*. 16: 809-839.

Foster, T.D. and Middleton, J.H. 1984. The oceanographic structure of the Eastern Scotia Sea. I. Physical oceanography. *Deep-Sea Research*. 31: 529-550.

Froneman, P.W. and Perissinotto, R. 1996. Structure and grazing of the microzooplankton communities of the Subtropical Convergence and a warm-core eddy in the Atlantic sector of the Southern Ocean. *Marine Ecology Progress Series*. 135: 237-235.

Froneman, P.W., Pakhomov, E.A., Perissinotto, R., Laubscher, R.K. and McQuaid, C.D. 1997. Dynamics of the plankton communities of the Lazarev Sea (Southern Ocean) during seasonal ice melt. *Marine Ecology Progress Series*. 149: 201-214.

Froneman, P.W. and Pakhomov, E.A. 1998. Trophic importance of the chaetognaths *Eukrohnia hamata* and *Sagitta gazellae* in the pelagic system of the Prince Edward Islands (Southern Ocean). *Polar Biology*. 19: 242-249.

Froneman, P.W., Pakhomov, E.A., Perissinotto, R. and Meaton, V. 1998. Feedings and predation impact of two chaetognath species, *Eukrohnia hamata* and *Sagitta gazellae*, in the vicinity of Marion Island (southern ocean). *Marine Biology*. 131: 95-101.

Froneman, P.W., Ansorge, I.J., Pakhomov, E.A. and Lutjeharms, J.R.E. 1999. Plankton community structure in the physical environment surrounding the Prince Edward Islands (Southern Ocean). *Polar Biology*. 22: 145-155.

Froneman, P.W., Pakhomov, E.A. and Treasure, A. 2000. Trophic importance of the hyperiid amphipod, *Themisto gaudichaudi*, in the Prince Edward Archipelago (Southern Ocean) ecosystem. *Polar Biology*. 23: 429-436.

Froneman, P.W., Pakhomov, E.A., Gurney, L.J. and Hunt, B.P.V. 2002. Predation impact of carnivorous macrozooplankton in the vicinity of the Prince Edward Islands archipelago (Southern Ocean) in austral autumn 1998. *Deep-Sea Research II*. 29: 3243-3254.

Furnestin, M.-L. 1957. Chaetognathes et zooplancton du secteur atlantique marocain. Rev. Trav. Pêches. Marit., 21: 1-356. *Analysis of the biological cycle and seasonal relationships with hydrology of the species off Morocco, based on 7 years of data.*

Giesecke, R. and González, H.E. 2004. Feeding of *Sagitta enflata* and vertical distribution of chaetognaths in relation to low oxygen concentrations. *Journal of Plankton Research*. 26: 475-486.

Go, Y-B., Oh, B-C. and Terazaki, M. 1998. Feeding behavior of the poecilostomatoid copepods *Oncaea* spp. on chaetognaths. *Journal of Marine Systems*. 15: 1-4.

González, H.E., Giesecke, R., Vargas, C.A., Pavez, M., Iriarte, P.J., Santibáñez, P., Castro, L., Escribano, R. and Pagès, F. 2004. Carbon cycling through the pelagic foodweb in the northern Humboldt Current off Chile (23ºS). *Journal of Marine Science*. 61: 572-584.

Grindley, J.R. and Lane, S.B. 1979. Zooplankton around Marion and Prince Edward Islands. C.N.F.R. 44: 111-125.

Holm-Hansen, O. and Riemann, B. 1978. Chlorophyll-a determination: improvements in methodology. *Oikos*. 30: 438-447.

Hosie, G.W., Schultz, M.B., Kitchener, J.A., Cochran, T.G. and Richards, K. 2000. Macrozooplankton community structure off East Antarctica (80 - 150ºE) during the Austral summer of 1995/1996. *Deep-Sea Research II*, 47: 2437-2463.

Hunt, B.P.V. 2000. Mesozooplankton community structure in the vicinity of the Prince Edward Islands (Southern Ocean) 37º50'E, 46º45'S. MSc thesis, Rhodes University, Grahamstown, pp 180.

Hunt, B.P.V., Pakhomov, E.A. and McQuaid, C.D. 2001. Short-term variation and long-term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology*. 138: 369-381.

Johnson, T.B. and Terazaki, M. 2004. Chaetognath ecology in relation to hydrographic conditions in the Australian sector of the Antarctic Ocean. *Polar Biology.* 17: 1-15.

Kaufmann, R.S., Fisher, E.C., Gill, W.H., King, A.L., Laubacher, M. and Sullivan, B. 2003. Temporal patterns in the distribution, biomass and community structure of macrozooplankton and micronekton within Port Foster, Deception Island, Antarctica. *Deep-Sea Research II*. 50: 1765-1785.

Kehayias, G., Lykakis, J. and Fragopoulu, N. 1996. The diets of the chaetognaths *Sagitta enflata, S. serratodentata atlantica* and *S. bipunctata* at different seasons in Eastern Mediterranean coastal waters. *Journal of Marine Science*. 53: 837-846.

King, A. and LaCasella, E.L. 2003. Seasonal variation in abundance, diel vertical migration, and population structure of *Metridia gerlachei* at Port Foster, Deception Island, Antarctica. *Deep-Sea Research II*. 50: 1753-1763.

Lancraft, T.M., Hopkins, T.L., Torres, J.J. and Donnely, J. 1991. Oceanic micronekton/ macrozooplankton community structure and feeding in the ice covered Antarctic waters during the winter (AMERIEZ 1998). *Polar Biology*. 9: 225-233.

Longhurst, A.R. 1991. Role of marine biosphere in the global carbon cycle. *Limnological Oceanography*. 36: 1507-1526.

Lutjeharms, J.R.E. and Emery, W.J. 1983. The detailed thermal structure of the upper ocean layers between Cape Town and Antarctica during the period Jan.-Feb. 1978. *South African Journal of Antarctic Research.* 13: 3-14.

Lutjeharms, J.R.E. and Valentine, H.R. 1984. Southern Ocean Thermal fronts south of Africa. *Journal of Physical Oceanography*. 18: 761-774.

Lutjeharms, J.R.E. 1985. Location of frontal systems between Africa and Antarctica: some preliminary results. *Deep-Sea Research*. 32: 1499-1509.

Lutjeharms, J.R.E. and McQuaid, L.H. 1986. Changes in the structure of thermal ocean fronts south of Africa over a three-month period. *South African Journal of Science*. 82: 470-476.

Lutjeharms, J.R.E., Monteiro, P.M.S., Tyson, P.D. and Obura, D. 2001. The oceans around southern Africa and regional effects of global change. *South African Journal of Science*. 97: 119-130.

Mianzan, H.W. 1999. Ctenophora. In: Boltovskoy, D. (Ed.), South Atlantic Zooplankton. Backhuys, Leiden, pp. 561-573.

Miller, D.G.M. 1982. Results of a combined hydroacoustic and midwater trawling survey of the Prince Edward Islands group. *South African Journal of Antarctic Research*. 12: 17-22.

Murano, M. 1999. Mysidacea. In: Boltovskoy, D. (Ed.), South Atlantic Zooplankton. Backhuys, Leiden, pp. 1099-1140.

Nagasawa, S. 1985. The digestive efficiency of the chaetognath *Sagitta crassa* Tokioka, with observations on the feeding process. *Journal of Experimental Marine Biology and Ecology*. 87: 271-281.

Nagata, Y., Michida, Y. and Unimura, Y. 1988. Variation of positions and structures of the oceanic fronts in the Indian Ocean sector of the Southern Ocean in the period from 1965 to 1987. In: Sahrhage, D. (Ed.), Antarctic Ocean and Resources Variability. Springer-Verlag, Berlin, pp. 92-98.

Nowlin, W.D. Jr. and Klinck, J.M. 1986. The physics of the Antarctic Circumpolar Current. *Review of Geophysics*. 24: 469-491.

Øresland, V. 1987. Feeding of the chaetognaths *Sagitta elegans* and *S. setosa* at different seasons in Gullmarsfjorden, Sweden. *Marine Ecology Progress Series*. 39: 69-79.

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

Øresland, V. 1995. Winter population structure and feeding of the chaetognath *Eukrohnia hamata* and the copepod *Euchaeta antarctica* in Gerlache Strait, Antarctic Peninsula. *Marine Ecology Progress Series*. 119: 77-86.

Pagès, F., White, M.G. and Rodhouse, P.G. 1996. Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Frontal Zone in summer 1994. *Marine Ecology Progress Series*. 141: 139-147.

Pakhomov, E.A., Perissinotto, R. and McQuaid, C.D. 1994. Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Marine Ecology Progress Series*. 111: 155-169.

Pakhomov, E.A. and McQuaid, C.D. 1996. Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biology*. 16: 271-286.

Pakhomov, E.A., Perissinotto, R. and McQuaid, C.D. 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Marine Ecology Progress Series*. 134: 1-14.

Pakhomov, E.A., Froneman, P.W. and Ansorge, I. 1998. Prince Edward Islands' offshore oceanographic study: report of research cruise April-May 1997. *South African Journal of Science*. 94: 1-6.

Pakhomov, E.A. and Froneman, P.W. 1999. The Prince Edward Islands pelagic ecosystem, south Indian Ocean: a review of achievements, 1976-1990. *Journal of Marine Systems*. 18: 355-367.

Pakhomov, E.A., Perissinotto, R. and Froneman, P.W. 1999. Predation impact of carnivorous macrozooplankton and micronekton in the Atlantis sector of the Southern Ocean. *Journal of Marine Systems*. 19: 47-64.

Pakhomov, E.A. and Froneman, P.W. 2000. Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone in the Indian Ocean during austral autumn 1997. *Polar Biology*. 23: 410-419.

Pakhomov, E.A., Ansorge, I.J. and Froneman, P.W. 2000. Variability in the inter-island environment of the Prince Edward Islands (Southern Ocean). *Polar Biology*. 23: 593-603.

Pakhomov, E.A., Ansorge, I.J., Kaehler, S., Vumazonke, L.U., Gulekana, K., Bushula, T., Balt, C., Paul, D., Hargey, N., Stewart, H., Chang, N., Furno, L., Mkatshwa, S., Visser, C., Lutjeharms, J.R.E. and Hayes-Foley, P. 2003. Studying the impact of ocean eddies on the ecosystem of the Prince Edward Islands: DEIMEC II. *South African Journal of Science*. 99: 187-190.

Pakhomov, E.A. and Froneman, P.W. 2004. Zooplankton dynamics in the eastern Atlantic sector of the Southern Ocean during the austral summer 1997/1998 – Part 1: Community structure. *Deep-Sea Research II*. 51: 2599-2616.

Park, Y-H. and Wormuth, J.H. 1993. Distribution of Antarctic zooplankton around Elephant Island during austral summers of 1988, 1989 and 1990. *Polar Biology*. 13: 215-225.

Park, Y-H., Charriaud, E., Craneguy, P. and Kartavtseff, A. 2001. Fronts, transport and Weddell Gyre at 30ºE between Africa and Antarctica. *Journal of Geophysical Research*. 106: 2857-2879.

Pearre, S., Jr. 1980. Feeding by chaetognatha: the relation of prey size to predator size in several species. *Marine Ecology Progress Series*. 3: 125-134.

Pearre, S., Jr. 1981. Feeding by Chaetognatha: energy balance and importance of various components of the diet of *Sagitta elegans*. *Marine Ecology Progress Series*. 5: 45-54.

Pearre, S., Jr. 1982. Feeding by Chaetognatha: Aspects of Inter- and Intra-Specific Predation. *Marine Ecology Progress Series*. 7: 33-45.

Perissinotto, R. and Boden, B.P. 1989. Zooplankton-phytoplankton relationships at the Prince Edward Islands during April/May 1985 and 1986. *South African Journal of Antarctic Research*.. 19: 26-30.

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

Perissinotto, R. 1995. Marine Productivity. In: *Encyclopedia of Environmental Biology*. Vol. 2. Nierenberg, W.A. (Ed). Academic Press, San Diego, 507-521.

Piatkowski, U. 1989. Macroplankton communities in Antarctic surface waters: spatial changes related to hydrography. *Marine Ecology Progress Series*. 55: 251-259.

Pollard, R.T. and Read, J.F. 2001. Circulation pathways and transport of the Southern Ocean in the vicinity of the Southwest Indian Ridge. *Journal of Geophysical Research*. 106: 2881-2898.

Pollard, R.T., Mucas, M.I. and Read,J.F. 2002. Physical controls on biogeochemical zonation in the Southern Ocean. *Deep-Sea Research II*. 49: 3289-3305.

Price, H.J., Boyd, K.R. and Boyd, C.M. 1988. Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*. *Marine Biology*. 97: 67-77.

Razouls, C. 1994. Manual d'identifiaction des principlaes especes de copepodes pelaquies antarctiques et subanatrctiques. Ann Inst Oceanogr, Paris, 1-204.

Read, J.F. and Pollard, R.T. 1993. Structure and transport of the Antarctic Circumpolar Current and Agulhas Return Current at 40ºE. *Journal of Geophysical Research*. 98: 12281-12295.

Reese, D.C., Miller, T.W. and Brodeur, R.D. 2005.Community structure of near-surface zooplankton in the California Current in relation to oceanographic conditions. *Deep-Sea Research II*. 52: 29-50.

Sameoto, D.D. 1987. Vertical distribution and ecological significance of chaetognaths in the Arctic environment of Baffin Bay. *Polar Biology*. 7: 317-328.

Sameoto, D.D. 1988. Feeding of lantern fish *Benthosema glaciale* off the Nova Scotia Shelf. *Marine Ecology Progress Series*. 44: 113-129.

Schabetsberger, R., Broduer, R.D., Ciannelli, L., Napp, J.M. and Swartzman, G.L. 2000. Diel vertical migration and interaction of zooplankton and juvenile walleye Pollock (*Theragra chalcogramma*) at a frontal region near the Pribilof Islands, Bering Sea. *Journal of Marine Science*. 57: 1283-1295.

Siegel, V. and Piatkowski, U. 1990. Variability in the macrozooplankton community structure of the Antarctic Peninsula. *Polar Biology*. 10: 373-386.

Steinberg, D.K., Carloson, C.A., Bates, N.R., Goldthwain, S.A., Madin, L.P. and Michaels, A.F. 2000. Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep-Sea Research*. 47: 137-158.

Stuart, V. and Verheye, H.M. 1991. Diel migration and feeding patterns of the chaetognath, *Sagitta friderici*, off the west coast of South Africa. *Journal of Marine Research*. 49: 493-515.

Sullivan, B.K. 1980. In situ feeding behavior of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at Ocean Station “P”. *Limnological Oceanography*. 25: 317-326.

Sullivan, B.K. and Meise, C.J. 1996. Invertebrate predators of zooplankton on Georges Bank, 1977-1987. *Deep-Sea Research II*. 43: 1503-1519.

Tönnesson, K. and Tiselius, P. 2005. Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. *Marine Ecology Progress Series*. 289: 177-190.

Ulloa, R., Palma, S. and Silva, N. 2000. Bathymetric distribution of chaetognaths and their association with water masses off the coast of Valparaíso, Chile. *Deep-Sea Research*. 47: 2009-2027.

Veronina, N.M., Kosobokova, K.N. and Pakhomov, E.A. 1994. Composition and biomass of summer metazoan plankton in the 0-200 m layer of the Atlantic sector of the Antarctic. *Polar Biology*. 14: 91-95.

Ward, P., Atkinson, A., Murray, A.W.A., Wood, A.G., Williams, R. and Poulet, S.A. 1995. The summer zooplankton community at South Georgia: biomass, vertical migration and grazing. *Polar Biology*. 15: 195-208.

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

Welch, H.E., Siferd, T.D. and Bruecker, P. 1996. Population densities, growth, and respiration of the chaetognath *Parasagitta elegans* in the Canadian high Arctic. *Canadian Journal of Fisheries and Aquatic Science*. 53: 520-527.

Youssara, F. and Gaudy, R. 2001. Variations of zooplankton in the frontal area of the Alboran sea (Mediterranean sea) in winter 1997. *Oceanologica Acta*. 24: 361-376.

Zar, J.H. 1996. *Biostatical analysis*. Prentice-Hall, Inc., pp. 908.

Appendix

Table 3.18. Details of net tows conducted in austral summer (April/May) 2001 (MOVES I) including station position, date, net type used, depth (m) of sampling, and sea surface temperature (ºC) and salinity.

Station	Latitude	Longitude	Date	Net type	Depth	Temperature	Salinity
181	46º 52.56S	37º 53.46E	12-Apr	Bongo	80	6.56	33.82
186	49º 52.56S	32º 59.51E	18-Apr	Bongo	300	4.43	33.88
187	49º 53.95S	32º 56.80E	18-Apr	Bongo	300	4.36	33.91
188	49º 05.22S	33º 00.40E	18-Apr	Bongo	300	4.46	33.88
189	48º 15.04S	35º 00.40E	18-Apr	Bongo	200	5.37	33.83
190	47º 25.24S	32º 59.93E	18-Apr	Bongo	200	7.73	33.81
191	46º 35.44S	32º 59.46E	19-Apr	Bongo	200	8.57	33.96
192	46º 34.18S	34º 14.03E	19-Apr	Bongo	300	8.34	34.06
193	47º 25.11S	34º 15.48E	19-Apr	Bongo	300	8.44	34.03
194	48º 14.95S	34º 15.90E	19-Apr	Bongo	200	6.7	33.87
195	49º 05.10S	34º 14.93E	19-Apr	Bongo	200	3.99	33.90
196	49º 54.78S	34º 15.00E	22-Apr	Bongo	300	4.14	33.89
197	49º 54.84S	35º 30.56E	22-Apr	Bongo	200	4.2	33.89
198	49º 04.91S	35º 29.92E	22-Apr	Bongo	200	4.33	33.83
199	48º 15.17S	35º 30.07E	23-Apr	Bongo	200	7.27	33.83
200	47º 24.95S	35º 30.22E	23-Apr	Bongo	300	7.6	33.93
201	46º 34.87S	35º 29.98E	23-Apr	Bongo	300	7.61	33.89
202	46º 34.73S	36º 44.68E	23-Apr	Bongo	200	6.82	33.78
203	47º 24.73S	36º 45.10E	23-Apr	Bongo	200	6	33.73
204	48º 14.43S	36º 44.62E	24-Apr	Bongo	200	4.92	33.76
205	49º 04.92S	36º 44.92E	24-Apr	Bongo	300	5.4	33.77
206	49º 55.03S	36º 46.12E	24-Apr	Bongo	300	5.38	33.82
207	49º 54.97S	38º 00.21E	24-Apr	Bongo	300	5.37	33.74
208	49º 04.93S	37º 59.45E	24-Apr	Bongo	200	5.33	33.77
209	48º 15.13S	38º 00.18E	25-Apr	Bongo	200	5.76	33.71
210	47º 25.18S	38º 00.39E	25-Apr	Bongo	300	5.96	33.69
211	46º 34.85S	37º 59.84E	25-Apr	Bongo	300	6.38	33.82

Table 3.19. Details of net tows conducted in austral summer (April/May) 2004 (DEIMEC III) including station position, date, net type used, depth (m) of sampling, and sea surface temperature (ºC) and salinity.

Station	**Latitude**	**Longitude**	**Date**	**Net type**	**Depth**	**Temperature**	**Salinity**
228	49º 59.32S	31º 03.48E	15-Apr	Bongo	200	4.05	33.77
229	49º 29.96S	31º 00.94E	15-Apr	Bongo	300	4.48	33.80
230	49º 00.29S	31º 00.56E	15-Apr	RMT-8	400	4.57	33.76
231	48º 29.21S	31º 83.67E	15-Apr	Bongo	200	4.58	33.76
233	47º 44.60S	31º 01.70E	16-Apr	RMT-8	350	6.81	33.83
234	48º 00.40S	32º 17.96E	16-Apr	Bongo	300	4.28	33.77
235	48º 20.00S	31º 41.00E	16-Apr	Bongo	350	4.19	33.72
236	48º 40.06S	31º 09.98E	16-Apr	Bongo	300	4.46	33.76
237	48º 59.36S	30º 38.15E	16-Apr	Bongo	>1000	5.2	33.78
238	49º 19.45S	30º 05.42E	17-Apr	Bongo	200	7.4	33.64
239	49º 40.37S	29º 32.02E	17-Apr	Bongo	300	6.53	33.80
241	49º 00.60S	29º 13.93E	17-Apr	Bongo	>1000	7.37	33.89
242	49º 00.00S	29º 59.07E	17-Apr	Bongo	200	7.61	33.81
243	48º 59.00S	30º 45.00E	18-Apr	Bongo	300	4.98	33.72
244	48º 59.85S	31º 31.68E	18-Apr	Bongo	300	4.82	33.82
245	48º 59.94S	32º 29.71E	18-Apr	RMT-8	>1000	3.91	33.77
246	49º 00.49S	33º 16.32E	18-Apr	RMT-8	350	3.82	33.74
247	49º 00.83S	34º 01.78E	20-Apr	RMT-8	350	4.1	33.65
248	48º 01.18S	30º 00.07E	20-Apr	Bongo	302	8.47	34.20
249	48º 22.17S	30º 29.77E	21-Apr	RMT-8	453	6.87	33.80
250	48º 45.11S	30º 58.79E	21-Apr	RMT-8	300	5.46	33.76
256	49º 51.13S	32º 27.17E	23-Apr	Bongo	300	3.76	33.80

Table 3.20. Details of net tows conducted in austral summer (April/May) 2005 (DEIMEC IV) including station position, date, net type used, depth (m) of sampling, and sea surface temperature (ºC) and salinity.

Station	Latitude	Longitude	Date	Net type	Depth	Temperature	Salinity
259	49º 20.06S	31º 01.68E	16-Apr	Bongo	300	5.33	33.68
260	49º 08.62S	32º 36.12E	16-Apr	Bongo	200	5.38	33.69
261	48º 47.76S	33º 12.91E	16-Apr	Bongo	200	5.28	33.69
262	48º 27.63S	33º 37.09E	17-Apr	WP-2	300	4.71	33.71
263	48º 07.48S	34º 11.50E	17-Apr	WP-2	300	4.24	33.74
264	47º 47.27S	34º 45.54E	18-Apr	WP-2	200	4.24	33.74
265	47º 46.06S	33º 00.34E	18-Apr	WP-2	300	5.78	33.69
268	48º 52.62S	34º 04.73E	18-Apr	WP-2	200	4.31	33.81
269	49º 19.06S	34º 39.10E	19-Apr	WP-2	200	4.9	33.71
270	49º 46.83S	35º 01.12E	19-Apr	WP-2	300	4.72	33.72
272	49º 24.33S	35º 22.61E	19-Apr	WP-2	200	4.49	33.74
273	48º 54.82S	35º 19.48E	19-Apr	WP-2	200	3.11	33.71
274	48º 34.35S	35º 05.04E	20-Apr	WP-2	300	4.34	33.78
275	48º 05.19S	35º 02.14E	20-Apr	WP-2	300	4.24	33.83
276	48º 21.73S	34º 46.84E	20-Apr	WP-2	200	4.33	33.81
277	48º 37.58S	34º 28.02E	21-Apr	WP-2	200	4.2	33.84
278	48º 54.87S	34º 06.71E	21-Apr	WP-2	300	4.61	33.71
279	49º 09.98S	33º 56.95E	21-Apr	WP-2	300	4.96	33.71
280	49º 40.20S	34º 01.29E	21-Apr	WP-2	300	4.21	33.75
282	48º 46.29S	33º 34.48E	22-Apr	WP-2	200	4.93	33.71
283	48º 45.89S	33º 58.81E	22-Apr	WP-2	300	4.36	33.75
284	48º 43.77S	34º 31.61E	22-Apr	WP-2	300	4.26	33.83
285	48º 45.06S	35º 01.84E	22-Apr	WP-2	200	4.29	33.82
286	48º 46.70S	35º 29.34E	22-Apr	WP-2	200	4.4	33.78
288	48º 07.88S	35º 55.01E	23-Apr	WP-2	300	5.3	33.69
290	48º 46.05S	36º 12.02E	23-Apr	WP-2	300	5.08	33.70
291	48º 56.04S	36º 20.14E	24-Apr	WP-2	300	5.11	33.69
295	48º 56.95S	36º 22.71E	24-Apr	WP-2	200	-	-

Table 3.21. Carnivorous macrozooplankton species collected during all surveys (MOVES I, DEIMEC II and DEIMEC III).

TAXA

Cephalopoda
Illex argentinus
Brachioteuthis riisei
Teuthida spp.

Chaetognatha
Eukrohnia hamata
Pterosagitta draco
Sagitta gazellae
Sagitta maxima
Sagitta marri

Ctenophora
Beroe cucumis
Pleurobrachiidae spp.

Medusae
Heterotiara anonyma
Arctapodema ampla
Oceania armata
Pegantha martagon

Mysidacea
Eucopia grimaldii
Eucopia spp.

Table 3.22. Total abundance (ind. m^{-3}) and biomass (mg ww m^{-3}) at stations sampled during the three surveys (MOVES I, DEIMEC II and DEIMEC III).

2001 (MOVES I)			2004 (DEIMEC II)			2005 (DEIMEC III)		
Station	**Abundance**	**Biomass**	**Station**	**Abundance**	**Biomass**	**Station**	**Abundance**	**Biomass**
181	9.261	0.043	**228**	16.171	3.739	**259**	3.644	0.027
186	14.404	0.063	**229**	4.13	1.224	**260**	2.24	0.081
187	7.702	0.033	***230***	0.936	0.053	**261**	2.24	0.053
188	8.694	0.004	**231**	8.66	8.417	**262**	17.066	0.157
189	16.098	0.007	***233***	16.762	5.461	**263**	14.506	0.042
190	2.883	0.021	**234**	8.5	10.987	**264**	5.12	0.09
191	0.379	0.03	***235***	3.065	1.561	**265**	1.636	0.052
192	1.22	0.004	**236**	5.17	10.809	**268**	1.94	0.256
193	0.93	0.008	**237**	17.59	41.551	**269**	1.44	0.047
194	1.76	0.028	**238**	2.34	4.072	**270**	1.4	0.001
195	8.591	0.003	**239**	11.46	8.941	**272**	3.933	0.04
196	2.59	0.002	**240**	23.65	2.226	**273**	0.64	0.029
197	5.724	0.035	**241**	1.17	5.266	**274**	0.973	0.051
198	10.665	0.121	**242**	0.866	34.494	**275**	1.227	0.074
199	1.363	0.032	**243**	6.25	2.516	**276**	0.32	0.0002
200	5.823	0.056	**244**	29.97	18.912	**277**	0.4	0.001
201	6.669	0.004	***245***	0.923	1.011	**278**	6.689	0.116
202	19.446	0.031	***246***	0.847	0.712	**279**	9	0.205
203	1.12	0.007	***247***	0.153	0.069	**280**	1.482	0.135
204	6.897	0.045	**248**	11.31	9.504	**282**	5.18	0.056
205	27.92	0.069	***249***	7.46	2.633	**283**	1.494	0.074
206	4.31	0.064	***250***	3.02	16.119	**284**	0.16	0.05
207	43.731	0.053	**256**	9.28	0.55	**285**	0.04	0.004
208	39.861	0.135				**286**	0.16	0.0004
209	43.75	0.005				**288**	2.147	0.152
210	29.413	0.18				**290**	3.41	0.055
211	17.466	0.026				**291**	0.947	0.058
						295	3.296	0.106

***** In the 2004 survey, stations in italics represent stations sampled with Bongo nets.