Feeding dynamics and distribution of the hyperiid amphipod, *Themisto gaudichaudii* (Guérin, 1828) in the Polar Frontal Zone, Southern Ocean.

By

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Submitted in fulfilment of the requirements for the degree of Master of Science at Rhodes University

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December 2005

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ACKNOWLEDGEMENTS

I am grateful to Prof. Will Froneman for his guidance and constant encouragement during the entire process of sampling and writing up a master's thesis. I would also like to thank Prof. Christopher McQuaid for his suggestions and guidance during my study.

I am indebted to the honours and post graduate students of Rhodes University's Southern Oceans Group, without whom I would have no data! Thank you to Kim, Ant, Albert, Tara, Louise and Paula. You guys made the work worthwhile and lots of fun.

I would also like to thank my best friend, Danica, for all her suggestions and encouragement. Thank you! Her positive outlook on life made doing masters more fun than I would have ever imagined.

I am most grateful to my parents. Thanks mom and dad! Who without fail kept believing in me and kept me looking ahead throughout the entire two years of studying and writing up. I am also grateful to the rest of my family, especially Max, René, Meyer and Henrietta, for their support throughout the study.

Finally, I would like to thank the Department of Environmental Affairs and Tourism, and Rhodes University for providing funds and facilities for this study. I would also like to thank Isabelle Ansorge (University of Cape Town) for sharing oceanographic data, and the officers and crew of the marine vessel *SA Agulhas* for their assistance at sea. I am grateful to the technicians from the Sea fisheries Research Institute for their assistance during both cruises and to Mrs. Valerie Meaton for enumeration and identification of zooplankton species.

PREFACE

Work from this study has been published in the South African Journal of Science.
Ansorge I.J., Froneman, P.W., Lutjehars, J.R.E., Bernard, K., Bernard, A., Lange, L., Lukác, 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 S. Wynne (2004) *South African Journal of Science* 100: 319-322

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

DECLARATION

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

ABSTRACT

The population structure and feeding dynamics of the hyperiid amphipod, *Themisto gaudichaudii*, was investigated during two cruises of the South African National Antarctic Programme conducted in the Indian sector of the Polar Frontal Zone during austral autumn (April) 2004 and 2005. During the 2004 cruise the frontal features that delimit the PFZ converged to form a single distinctive feature. In 2005, the research cruise was conducted in the vicinity of a cold-core eddy which was spawned from the Antarctic Polar Front. Total mesozooplankton abundance and biomass during the 2004 study ranged from 55.19 to 860.57 ind. m^{-3}, and from 2.60 to 38.42 mg dwt m^{-3}, respectively. In 2005 the abundance and biomass ranged from 23.1 to 2160.64 ind. m^{-3}, and from 0.76 to 35.16 mg dwt m^{-3}, respectively. The mesozooplankton community was numerically dominated by copepods, pteropods, and ostracods during both surveys. The abundance and biomass of *Themisto gaudichaudii* in the region of investigation was < 0.2 ind. m^{-3} (range 0.01 to 0.15 ind. m^{-3}) and < 0.06 mg dwt m^{-3} (range 0.02 to 0.06 mg dwt m^{-3}) during 2004, while in 2005 the abundance and biomass of the amphipod ranged from < 0.01 to 0.2 ind. m^{-3} and <0.01 to 0.04 mg dwt m^{-3}, respectively. These values correspond to < 1% of the total mesozooplankton abundance and biomass during both surveys. *T. gaudichaudii* exhibited no significant spatial patterns in abundance, biomass and total length during both 2004 and 2005 ($p > 0.05$ in all cases). A key feature of the two investigations was the virtual absence of juveniles (total length < 15 mm) among the amphipod population, supporting the suggestion that they exhibit strong seasonal patterns in reproduction. Gut content analysis during both years indicated that for both the male and female amphipods', copepods were the most prevalent prey species found in stomachs, followed by chaetognaths and pteropods. Results of electivity studies indicate that *T. gaudichaudii* is an opportunistic predator, generally feeding on the most abundant mesozooplankton prey. Results of *in vitro* incubations indicated that the total daily feeding rate of *T. gaudichaudii* during 2004 ranged from 11.45 to 20.90 ind. m^{-3} d^{-1}, which corresponds to between 0.12 and 1.64% of the total mesozooplankton standing stock. In 2005, the feeding rate ranged between 0.1 and 1.73% of the total mesozooplankton standing stock. The low predation impact of *T. gaudichaudii* during this study can be related to their low abundances and high interannual variability throughout the region of investigation.

CHAPTER ONE - INTRODUCTION

1.1 Biological Pump

Understanding the physical and biological processes that influence the vertical transport of organic material is critical to our understanding of the sequestration of carbon to the oceans' interior (Steinberg *et al.,* 2002; Dandonneau *et al.*, 2004). The "biological pump" refers to the various biological processes that mediate the transfer of carbon from surface waters to the deep ocean (Longhurst and Harrison, 1989; Longhurst, 1991; Fortier *et al.,* 1994; Legendre, 1996; Pakhomov *et al.,* 1999; Froneman *et al.,* 2002; Steinberg *et al.*, 2002; Tréguer, 2002). A critical element in the cycling of carbon in the oceans is the flux of photosynthetically fixed carbon out of the photic zone (Broecker and Peng, 1982; Berger *et al.*, 1989; Falkowski *et al.*, 1998; Priddle *et al.*, 1992). The "biological pump" decreases the partial pressure of CO_2 in surface waters resulting in the sinking or draw-down of atmospheric CO_2 (Huntley *et al.,* 1991; Longhurst 1991; Wefer and Fisher, 1991; Siegenthaler and Sarmiento, 1993). Most important to climate change is the organic matter that sinks into the deep ocean before it decays (Falkowski, 2002). When it is transported to a depth below the pycnocline, CO_2 remains at depth for a longer period, because the colder temperature and higher density of this water prevent it from mixing with the warmer waters above (Falkowski, 2002). Within a few hundred years most of the nutrients released in the deep sea return via upwelling and other ocean currents back to sunlit surface waters, where they stimulate additional phytoplankton growth (Falkowski, 2002). This cycle keeps the biological pump at natural equilibrium, where the concentration of CO_2 in the atmosphere is approximately 200 parts per million lower than it would otherwise be (Falkowski, 2002).

The rate of carbon transfer to depth defines the efficiency of the biological pump, and this is mainly a function of the partitioning of phytogenic carbon among the various size classes of grazers in the zooplankton community structure (Longhurst, 1991; Legendre *et al.*, 1993; Fortier *et al.*, 1994; Froneman *et al.*, 1996, 1997; Froneman *et al.*, 2004). Phytoplankton production is channelled into either the "microbial loop", comprising phytoplankton, bacteria and autotrophic organisms of < 200 µm; or into the classical food web (Longhurst, 1991; Siegenthaler and Sarmiento, 1993; Legendre and Michaud, 1998).

Recycling is rapid in the microbial loop, but the system does not export organic matter to the deep layers of the ocean very well (Longhurst and Harrison, 1989; Fahnenstiel *et al.*, 1995). In contrast, the classical food web, dominated mainly by metazooplankton, is characterised by carbon being exported to depth through the sinking of phytoplankton cells, the production of large fast-singing faecal pellets with a high carbon content and diel vertical migration patterns (Longhurst and Harrison, 1989; Fortier *et al.*, 1994). Extensive research over the past several decades has shown that the biological carbon pump has a variable efficiency (e.g. export ration; Eppley and Peterson, 1979; Karl *et al.*, 2001; Figure 1) depending upon the particular oceanic ecosystem being investigated (Lomas and Bates, 2004).

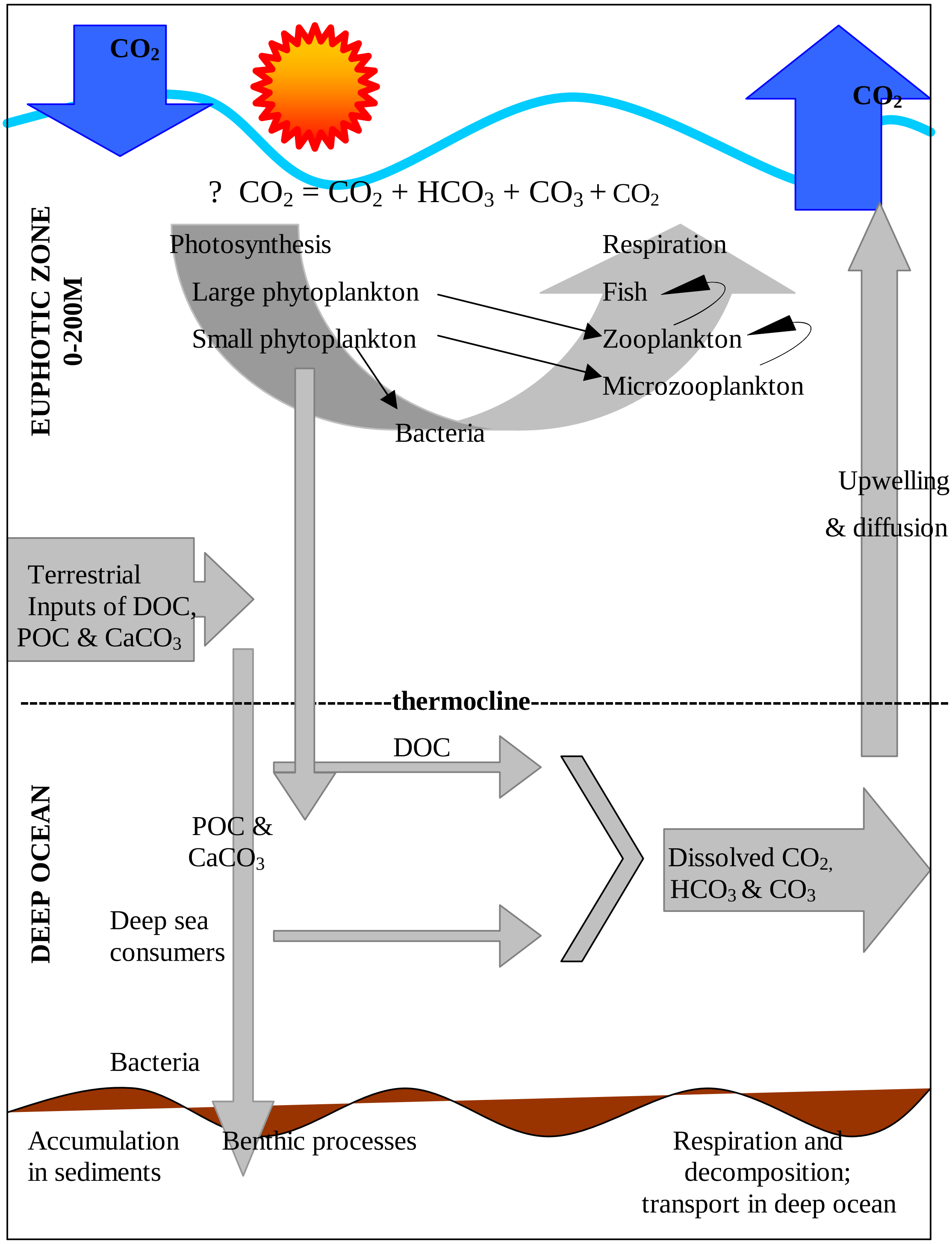

Figure 1.1 Schematic diagram depicting the biological pump. (CO_2 = Carbon dioxide; DOC = dissolved organic carbon; POC = particulate organic carbon; $CaCO_3$ = calcium carbonate) (From www.nature.com. and www.sd-commission.org.uk/)

1.2 Southern Ocean

The Southern Ocean's role in the global carbon cycle is presently a primary concern for oceanographers and marine biologists alike (Takahashi and Azevedo, 1982; Legendre and Michaud, 1998; Metzl *et al.*, 1991; Murphy *et al.*, 1991). The Southern Ocean encompasses an area of approximately 38 million km^2 of open water. Due to its large size and its profuse supply of nutrients, it is thought that this ocean plays an important role in the global carbon cycle (Falkowski, 2002). The surface waters of the Southern Ocean are characterised by an abundant supply of nutrients, however, the total phytoplankton production in the open waters of the Southern Ocean is typically low, <0.5g Cm^{-2}d^{-1} (Allanson *et al.*, 1981; Hayes *et al.*, 1984; El-Sayed, 1988; Jacques 1989; Laubscher *et al.*, 1993; Jochem *et al.*, 1995). Consequently, the Southern Ocean is regarded as a high-nutrient low-chlorophyll (HNLC) region. There are, however, areas of elevated production, including the vicinity of frontal regions (Laubscher *et al.*, 1993; Bradford-Grieve *et al.*, 1997), the Marginal Ice zone (Froneman *et al.*, 2004) and the waters surrounding the various oceanic islands that are found dispersed throughout the region (Pakhomov and Froneman, 1999).

1.3 Polar Frontal Zone

The Polar Frontal Zone (PFZ) separates the two high speed centres of the Antarctic Circumpolar Current (ACC), namely the Sub-antarctic Front (SAF) to the north and the Antarctic Polar Front (APF) to the south (Figure 1.2; Lutjeharms and Valentine, 1984). The region represents a transition in surface waters from the warmer, less productive Sub-antarctic Surface Waters (SASW) in the north, to the colder, more productive Antarctic Surface Waters (AASW) in the south (Deacon, 1983; Lutjeharms, 1985). Oceanographic surveys have indicated that the Polar Frontal Zone exhibits a high degree of spatial and temporal variability, including eddies and meanders in these frontal systems (Lutjeharms, 1990; Ansorge *et al.*, 1999; Pakhomov and Froneman, 1999). In the region south of Africa, this results partly from the interaction of the ACC with prominent topography, including the south-west Indian Ridge (Ansorge *et al.*, 1999).

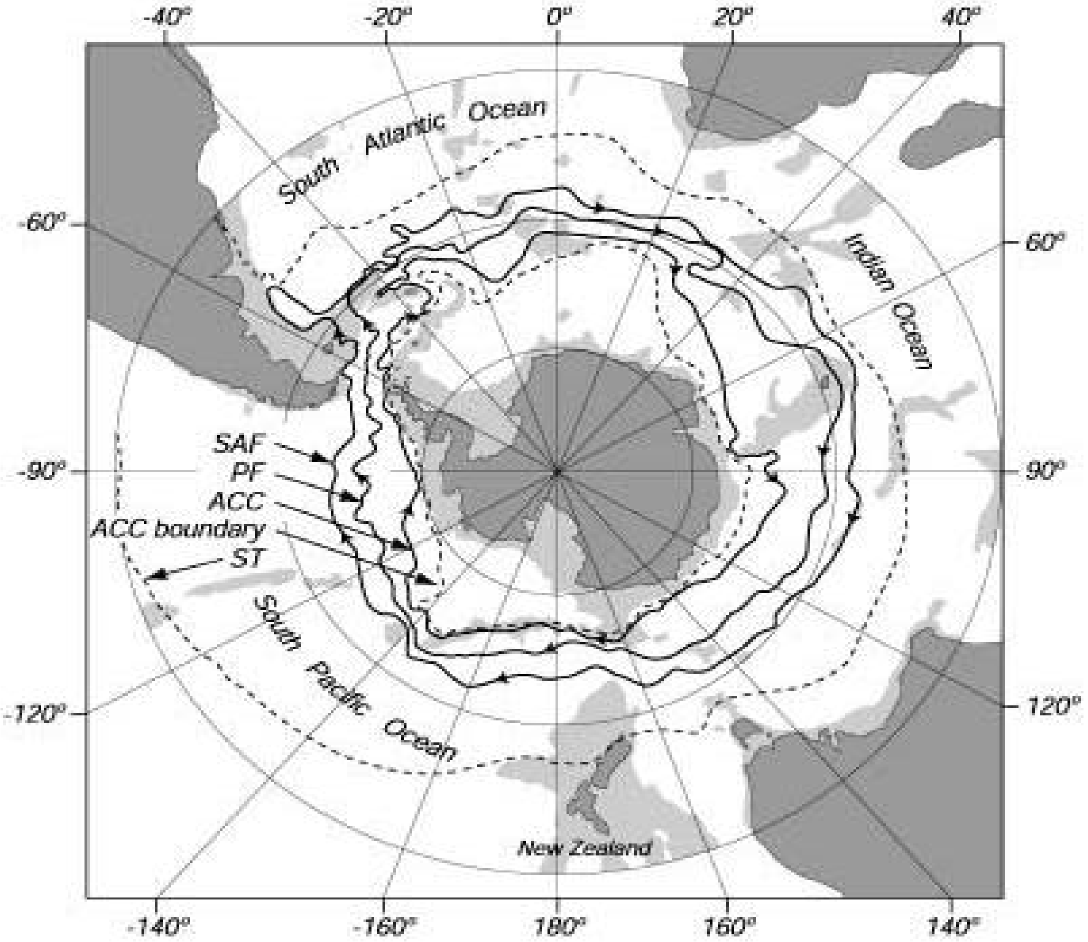

Figure 1.2 The Southern Ocean with the various zones and frontal systems highlighted (SAF = Sub-antarctic front; PF = Polar Front; ACC = Antarctic Circumpolar Current; ST = Subtropical Convergence) From www.oceanworld.tamu.edu/.

1.4 Biology of the Polar Frontal Zone

The highly variable oceanographic environment of the Polar Frontal Zone is reflected in the biology, with the plankton community comprising a mixture of Antarctic, sub-Antarctic and sub-tropical species (Boden and Parker, 1986; Perissinotto and Boden, 1989; Froneman and Ansorge, 1998; Froneman and Pakhomov, 1998). The phytoplankton community of the Polar Frontal Zone is typically dominated by picoplankton (<2.0 µm) and nanophytoplankton (2-20 µm), reflecting the high wind activity and low macronutrient concentrations that prevail within the region (Froneman *et al.*, 2001; Gurney *et al.*, 2002). Chlorophyll-a concentrations within the Polar Frontal Zone are highly variable ranging from 0.03 mg.m^{-3} to 3.4 mg.m^{-3} (Table 1). The highest chlorophyll-a concentrations are typically recorded in the vicinity of the frontal systems that delimit the Polar Frontal Zone and the waters surrounding the oceanic islands, which demonstrates the so-called “island mass effect” (Pakhomov and Froneman, 1999; Froneman *et al.*, 2001).

The zooplankton community in the Polar Frontal Zone is numerically and by biomass dominated by mesozooplankton, comprising mainly copepods (e.g. *Oithona similis, Calanus simillimus* and *Metridia lucens*) (Hopkins, 1985; Conover and Huntley 1991; Atkinson and Shreeve 1995; Atkinson 1996; Atkinson *et al.*, 1996; Bernard and Froneman, 2002). Bernard and Froneman (2002) recorded mesozooplankton abundances ranging from 49 to 1512 ind.m^{-3} in the Indian sector of the Polar Frontal Zone. Similarly, Hunt *et al.,* (2001) estimated mesozooplankton abundances within the Polar Frontal Zone to range between 57.48 to 139.92 ind.$^{-3}$, for the period 1996-1999. The total zooplankton biomass in the Polar Frontal Zone ranged from <1 to 25 mg. Dwt. m^{-3} in the vicinity of the Prince Edward Islands, with copepods (mainly *Oithona frigida* and *Clausocalanus brevipes*) contributing >70 % to the total biomass (Froneman *et al.,* 2000, 2002; Bernard and Froneman 2003, 2005). Locally, however, the total zooplankton biomass may be dominated by euphausiids or gelatinous zooplankton, or amphipods, which may at times contribute up to 60 % of the total biomass.

Table 1.1 Mean values of total chlorophyll-a concentration and mesozooplankton abundance recorded during different seasons within the Polar Frontal Zone of the Southern Ocean.

Season	Chl-a	Mesozooplankton abundance	Author
Summer	2.5 mg.m^{-3} (1998)		Korb *et al.*, 2005
	4.3 mg.m^{-3} (1999)		Korb *et al.*, 2005
	2.7 mg.m^{-3} (2001)		Korb *et al.*, 2005
	223.3 mg.m$^{-2\ (total)}$		Laubscher *et al.*, 1993
	47 mg.m$^{-2\ (total)}$		Tremblay *et al.*, 2002
	63.3 mg.m$^{-2\ (total)}$		Tremblay *et al.*, 2002
	15.3 mg.m$^{-2\ (integrated)}$		Tremblay *et al.*, 2002
	26.5 - 554.7 mg m^{-2}	12 553 - 304 312 ind.m^{-2} (total copepods)	Ward *et al.*, 2002
	40 - 218 mg.m^{-2}	50 135 - 276 129 ind.m^{-2}	Ward *et al.*, 2005
		188 ind.m^{-3}	Bernard and Froneman, 2003
	0.1 - 1.5 mg.m^{-3}		Hiscock *et al.*, 2003
	123.7 mg.m$^{-2\ (total)}$		Laubscher *et al.*, 1993
		60.7 ind.m^{-3}	Froneman *et al.*, 2000
		36.8 ind.m^{-3}	Froneman *et al.*, 2002
	18 - 163 mg.m^{-2}		Korb and Whitehouse, 2004
	0.3 - 0.4 mg.m^{-3}		Hunt and Hosie, 2005

Summer	0.4 - 3.4 mg.m^{-3}		Korb *et al.*, 2005
		2981 - 39 080 ind.m^{-3}	Pakhomov and Froneman, 2000
		13 - 167 ind.m^{-3}	Pakhomov and Froneman, 2000
Autumn	13.2 mg.m$^{-2 \text{ (integrated)}}$ Sub-antarctic zone group	1106.3 ind.m^{-2}	Bernard and Froneman, 2005
	13.4 mg.m$^{-2 \text{ (integrated)}}$ Antarctic zone group	492.7 ind.m^{-2}	Bernard and Froneman, 2005

1.5 Carnivorous Zooplankton

A key feature of the zooplankton community of the Polar Frontal Zone is the high contribution of carnivorous zooplankton, including chaetognaths (mainly *Eukrohnia hamata* and *Sagitta gazellae*) and amphipods (mainly *Themisto gaudichaudii),* to the total mesozooplankton abundance and biomass (Froneman and Ansorge, 1998; Froneman and Pakhomov, 1998; Pakhomov and Froneman, 2000). In the vicinity of the Prince Edwards Islands, during austral autumn 2002, the carnivorous zooplankton comprised between 4 and 72 % of the total zooplankton biomass and consisted of 5 major groups: decapods, gelatinous zooplankton (including jellyfish, siphonophores and ctenophores), chaetognaths, amphipods, and euphausiids (Froneman *et al.,* 2002). The contribution of these groups to total carnivore biomass and abundance was, however, highly variable, reflecting the complex environment and its influence on the biology (Froneman *et al.,* 2002; Bernard and Froneman, 2005).

Among the carnivorous zooplankton within the Polar Frontal Zone, chaetognaths (mainly *Eukrohnia hamata* and *Sagitta gazellae*) and the hyperiid amphipod, *Themisto gaudichaudii* are numerically the most abundant (Pakhomov and Froneman, 2000). The elevated abundances of the chaetognaths and amphipods within the Polar Frontal Zone suggest that these organisms play an important ecological role within the region.

1.6 *Themisto gaudichaudii*

1.6.1 Distribution

Hyperiid amphipods form an important component of epi- and mesopelagic communities in both polar cold-water regions (Vinogradov, 1999). Members of the genus *Themisto* (a senior synonym of *Parathemisto)* (Bowman *et al.,* 1982) overwhelmingly dominate the cooler epipelagic amphipod fauna, and their importance in the north Atlantic is well documented (Dunbar, 1957, 1964; Dalpadado *et al.,* 2001). Among the mesozooplankton, it is secondary in abundance only to copepods, euphausiids, chaetognaths, and gelatinous species (Vinogradov, 1999).

The majority of *T. gaudichaudii* are found in the upper 100-300m of the water column (Bowman *et al.*, 1982). A marked diurnal vertical migration takes place within the upper 100-200m, away from the surface during daylight and towards the surface at night (Hardy & Gunther, 1935; Bary, 1959; Kane, 1966; Everson & Ward, 1980). Vertical migration has an ontogenetic component, with juveniles restricted to shallower depths (<100m) than adults (Bigelow, 1926; Bousfield, 1951).

Kane (1966) reported that spawning occurs mainly in September and December, but juveniles may be found in samples taken as late in the season as March. Based on monthly length frequencies of the amphipods (measured from the head to the longest uropod, Figure 1.3) Kane (1966) suggested that the normal life-cycle is one year from hatching to breeding, and some adults, which reach an unusually large size, may survive another season of breeding.

1.6.2 Feeding/Prey selection

Amphipods of the genus *Themisto* are regarded as obligate carnivores (Kane, 1967; Sheader & Evans, 1975; Hopkins, 1985). Siegfried (1965) determined that *T. gaudichaudii* was an indiscriminate, carnivorous feeder, its gut contents reflecting the composition of the plankton in the surrounding waters. Amphipod conditioning, size differences and the size and structure of their grasping and holding appendages influence prey selection. The type of prey taken by *Parathemisto gaudichaudii* was found to depend on season and on the body size of specimens (Sheader and Evans, 1975). In a study conducted by Pakhomov & Perissinotto (1996) in the vicinity of South Georgia, *T. gaudichaudii's* diet was found to consist mainly of copepods such as *Calanus simillimus, Calanoides acutus* and *Metridia* spp. Prey in the size range of 1-4 mm were preferentially consumed by *T. gaudichaudii* adults (Pakhomov & Perissinotto, 1996).

1.6.3 Daily rations and predation impact

Feeding activity of *T. gaudichaudii* peaks at sunrise and sunset, corresponding to their diel vertical migration patterns (Froneman *et al.,* 2000). Using both *in vitro* incubation and the gut fullness index approach, Froneman *et al.,* (2000) determined that the daily ration of *T. gaudichaudii* in the Polar Frontal Zone was equivalent to 1.2 and 19.8 % of body dry weight. The predation impact of *T. gaudichaudii* over the upper 300 m of the water column was low, accounting for <0.4 % of the mesozooplankton biomass (Froneman *et al.,* 2000). The low values could be attributed to the low abundance of *T. gaudichaudii* during the study. Similarly, in the South Georgia region, the estimated daily ration of *T. gaudichaudii* was equal to 6.3 % of body dry weight (Pakhomov and Perissinotto, 1996). Pakhomov and Perissinotto (1996) found that the predation impact of *T. gaudichaudii* adults in the high Antarctic region never exceeded 2.1 % of mesozooplankton standing stock per day, but accounted for ˜ 70 % of the daily secondary production.

Froneman *et al.,* (2000) have suggested that *T. gaudichaudii's* importance as a secondary production consumer in the Polar Frontal Zone exhibits a high degree of spatio-temporal variability. *Themisto gaudichaudii* is known to be a swarming crustacean, and at times these swarms can reach densities of up to several hundred individuals per cubic meter (Gibbons *et al.,* 1992). Hence, the amphipod may have a substantial predation impact on local zooplankton assemblages.

Themisto gaudichaudii has a high energy content (Williams & Robins, 1979; Torres *et al.*, 1994) and is one of the primary sources of food for predators including fish, squid, birds and whales (Nemoto & Yoo, 1970; Permitin & Tarverdieva, 1972; Rodhouse *et al.*, 1992; Bost *et al.*, 1994; Kock *et al.,* 1994). According to Gibbons *et al.,* (1992) *T. gaudichaudii* represents an important ecological link between small zooplankton and top consumers and, in certain areas, may effectively control the mesozooplankton standing stock, thereby affecting the population dynamics of higher predators such as penguins (Bost *et al.*, 1994) and fish (Kock *et al.,* 1994).

1.7 AIMS

Themisto gaudichaudii exhibits a high degree of spatial and temporal variability in abundance and biomass within the Polar Frontal Zone. The amphipod is thought be an important component of the zooplankton community, and a potentially important consumer of secondary production; at times controlling the mesozooplankton standing stock, (Pakhomov *et al.*, 1999a, b) thereby having a significant contribution to the downward flux of carbon.

The main aim of this study was to investigate the trophodynamics of *T. gaudichaudii* in the Indian sector of the Polar Frontal Zone, during austral autumn 2004 and 2005. The study was carried out during two cruises of the South African National Antarctic Programme (SANAP), during the annual relief voyages to the Prince Edward Islands.

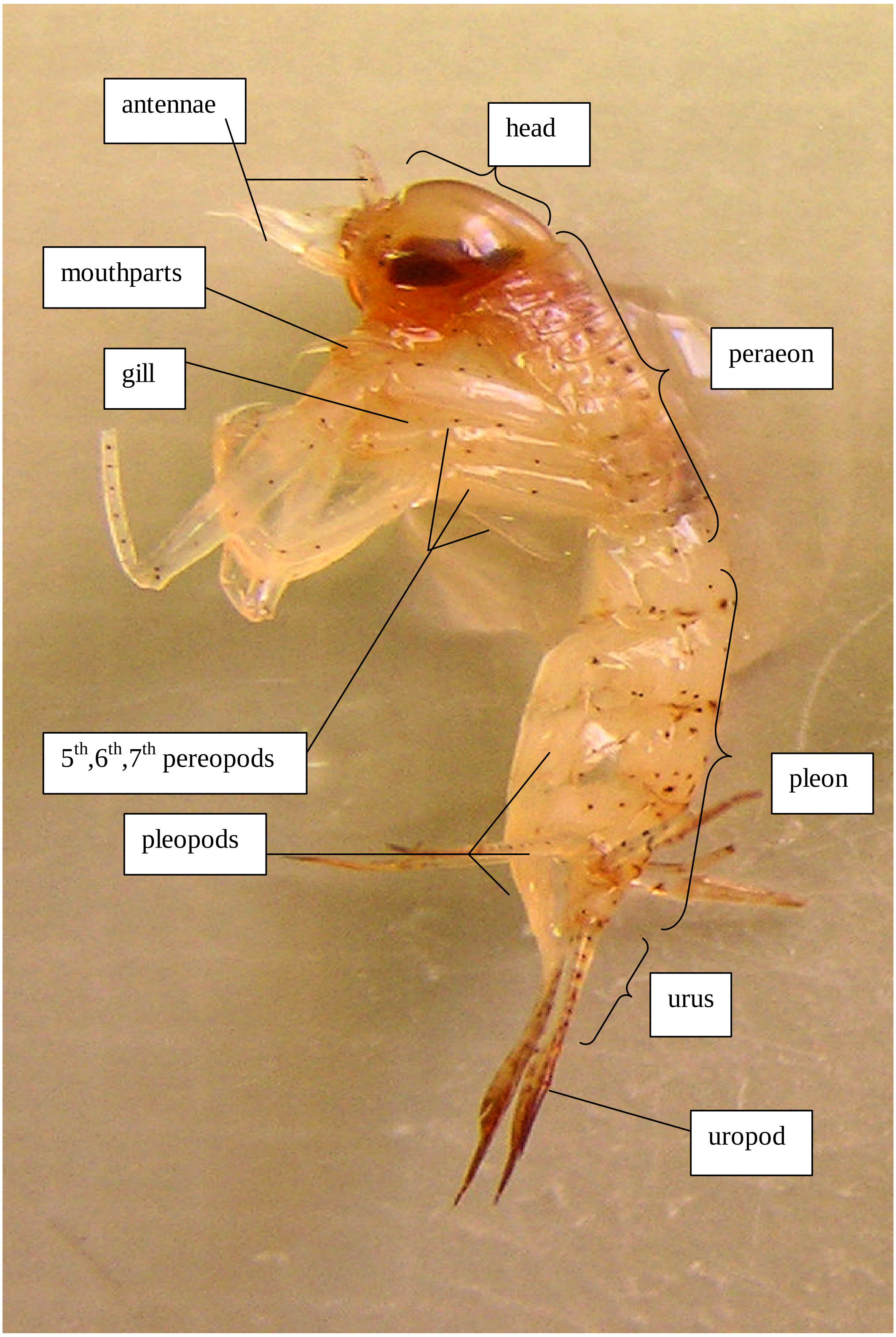

Figure 1.3 Digital photograph of *Themisto gaudichaudii*.

CHAPTER TWO – MATERIALS AND METHODS

2.1 Sampling Region

The trophodynamics of the hyperiid amphipod, *T. gaudichaudii,* in the PFZ waters was investigated in the Indian sector of the Southern Ocean during two cruises (voyage 116 and 123) conducted on board the supply and research vessel *SA Agulhas* in 2004 and 2005. The 2004 cruise consisted of an intense oceanographic survey in the vicinity of a mesoscale anomaly identified within the Antarctic Circumpolar Current, between 29°-33°E, 48°-50°S. A detailed cruise track is presented in Figure 2.1. Sub-surface temperatures were recorded using a Neil Brown MK III conductivity, temperature, and depth probe at each of the 15 sampling stations.

During the second cruise (from 7 April to 12 May 2005) an interdisciplinary oceanographic survey was conducted upstream of the islands, to investigate the physical and biological characteristics of an intense mesoscale negative anomaly, a cold core eddy, spawned from the Antarctic Polar Front (Figure 2.2). This anomaly was identified prior to the cruise from Merged Geophysical Data records collected using a combination of JASON-1 and TOPEX/Poseidon products, and was pinpointed to be within the ACC between 32°- 36°E, 47°30-49°30S (I.J. Ansorge, personal communication). The physical environment was assessed using an Expendable Bathythermograph (XBT) and a Conductivity-Temperature-Depth probe (CTD).

2.2 Zooplankton 2004 and 2005

Zooplankton samples were collected at stations during both cruises using a Bongo net fitted with 200 and 300µm nets. The net was fitted with a Universal Underwater Unit (U^3) to measure depth and temperature continuously during each tow. The nets were towed to a depth of 300m during the day and 200m during the night. Due to mechanical failure of the flow meter, the volume filtered by the bongo net was determined by multiplying the mouth area by the distance sampled (estimated from the average speed of the ship, and the duration of the tow). After each tow, samples collected in the 200µm mesh were immediately fixed in 4-6% buffered hexamine formalin for later analysis of the zooplankton community structure in the laboratory.

All the amphipods from all the stations were measured with Vernier callipers to the nearest 0.01mm, from the top of the head to the end of the longest uropod (Figure 1.3). In the laboratory species, composition, abundance and biomass of mesozooplankton were determined from sub-samples (½ or $^1/_{64}$), obtained using a Folsom plankton splitter and abundance was expressed as number of individuals per meter cubed (ind. m^{-3}). Total dry weight of *Themisto gaudichaudii* was determined for each station by oven drying the sub-samples (½ and ¼) at 60°C for 24h. The biomass measured was expressed as milligrams dry weight per meter cubed (mg dwt m^{-3}). No corrections were made for a loss of tissue for the samples preserved in formalin.

2.3 Gut Content Analysis 2004 and 2005

Thirty *Themisto gaudichaudii* (total length range 16 – 25 mm) were examined for prey items in their guts during each of the two cruises. To assess diel variability in prey items, 15 individuals from day and night time were analysed. Guts were dissected out and the prey identified using a Heerenburg dissecting microscope operated at 300 – 250x magnification. Due to the advanced state of digestion, prey items in the guts of *T. gaudichaudii* were separated into the following groups: Copepoda, Euphaussiacea, Chaetognatha, Pteropoda and other (including polychaetes and fish larvae). Results of the gut content analysis were expressed as frequency of occurrence (%) of each prey item found in all the stomachs.

2.4 Selective Feeding

To assess if *T. gaudichaudii* selected particular prey, an index of electivity was calculated according to Ivlev (1961). This index has been successfully used to determine prey selectivity for a wide range of marine and freshwater fishes (Kim, 1991; Ushakumari and Aravindan, 1992; Alwany *et al.,* 2003) as well as invertebrates (Tolomeyev, 2002).

The Ivlev index is defined as:

$$E_i = (r_i - p_i)/(r_i + p_i)$$

Where r_i is the proportion of food type consumed and p_i is the proportion of this food type that is available in the environment. The E values range from – 1.0 to +1.0, with preference indicated by values between 0 and + 1.0, while values between 0 and – 1.0 indicate inaccessibility of prey item or avoidance, and values equal 0 indicating no selection (Ivlev 1961; Tolomeyev, 2002). Known densities of copepods (4 – 16 ind.l^{-1}) were incubated in 5*l* containers, filled with filtered seawater from the seawater supply, each containing a single healthy undamaged amphipod. Only copepods were considered as previous studies have shown that these organisms account for >80% of the identified prey in the guts of *T. gaudichaudii* (Froneman *et al.*, 2000). At the end of 24 hours, the amphipods were removed and the water was filtered through 200µm mesh to isolate the remaining copepod species. This study was only conducted during the 2004 cruise.

2.5 In Vitro Incubations 2004

The feeding rate of *T. gaudichaudii* under varying prey densities was estimated by *in vitro* incubations. Five-liter polyethylene containers were filled with seawater from the scientific seawater supply. Immediately after capture a single undamaged hyperiid (total length 18 - 24 mm) was placed into the carboy. The animals were allowed to acclimate for 24h. Known densities (1 – 30 ind l^{-1}) of the most abundant copepods at each station were then added to the containers using a micropipette. Densities of prey in the containers were within an order of magnitude of the average natural assemblages (K.S. Bernard, personal communication), and they comprised the same species present in the natural assemblages (predominantly copepods, Table 2.1), thereby keeping the feeding patterns of the amphipods as natural as possible. After 24h the amphipods from each container were preserved in 4-6% buffered formalin, and the remaining prey in each container counted. This procedure was replicated a total of 40 times. The incubations were carried out on deck under ambient conditions.

The amphipod's feeding rate (estimated by the difference between the number of copepods before and after the experiments) was then plotted against initial copepod density. A second order regression analysis ($p < 0.05$) was then fitted to the data using the computer programme Statistica in order to derive a predictive equation of feeding rate of the amphipod at varying densities of copepods.

2.6 Predation Impact

To estimate the predation impact of *T. gaudichaudii* on the mesozooplankton standing stock during the two cruises, the estimated daily feeding rate at each station was combined with the abundance estimates of the amphipod at each station. Results were then expressed as a percentage of total mesozooplankton standing stock consumed per day.

2.7 Data Analysis

Using the computer program STATISTICA version 6, the abundance and biomass data for the mesozooplankton and amphipods were compared among the water masses for each cruise. T-tests ($p < 0.05$) were then carried out to compare the densities and biomass of *T. gaudichaudii* in the various water masses encountered during each survey. Variables were tested for normality using the Shapiro-Wilks test. Where the variables were not normally distributed, the data was log transformed to stabilise the variances. Subsequently Levene's T-test was performed. Relationships between the abundance and biomass of *T. gaudichaudii* with those of its mesozooplankton prey, were estimated using Pearson's correlation analysis.

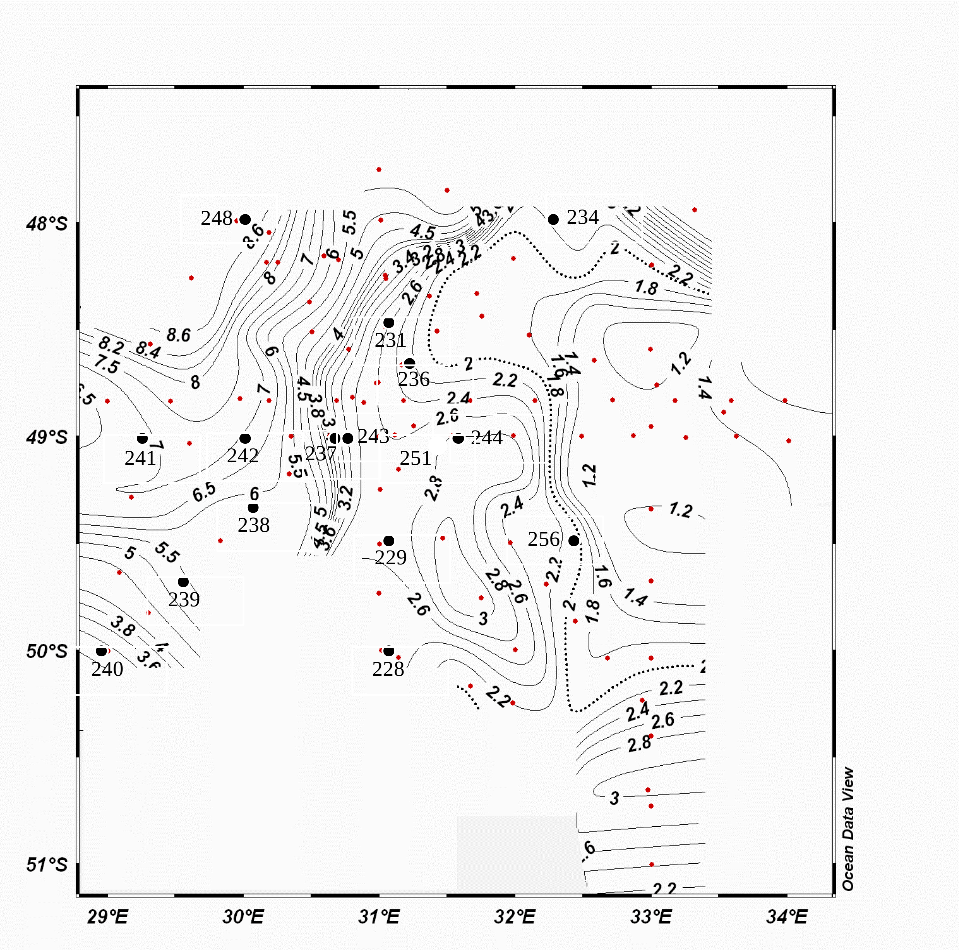

Figure 2.1. Sampling stations superimposed over the sub-surface temperatures during the April 2004 DEIMEC III cruise to the Polar Frontal Zone.

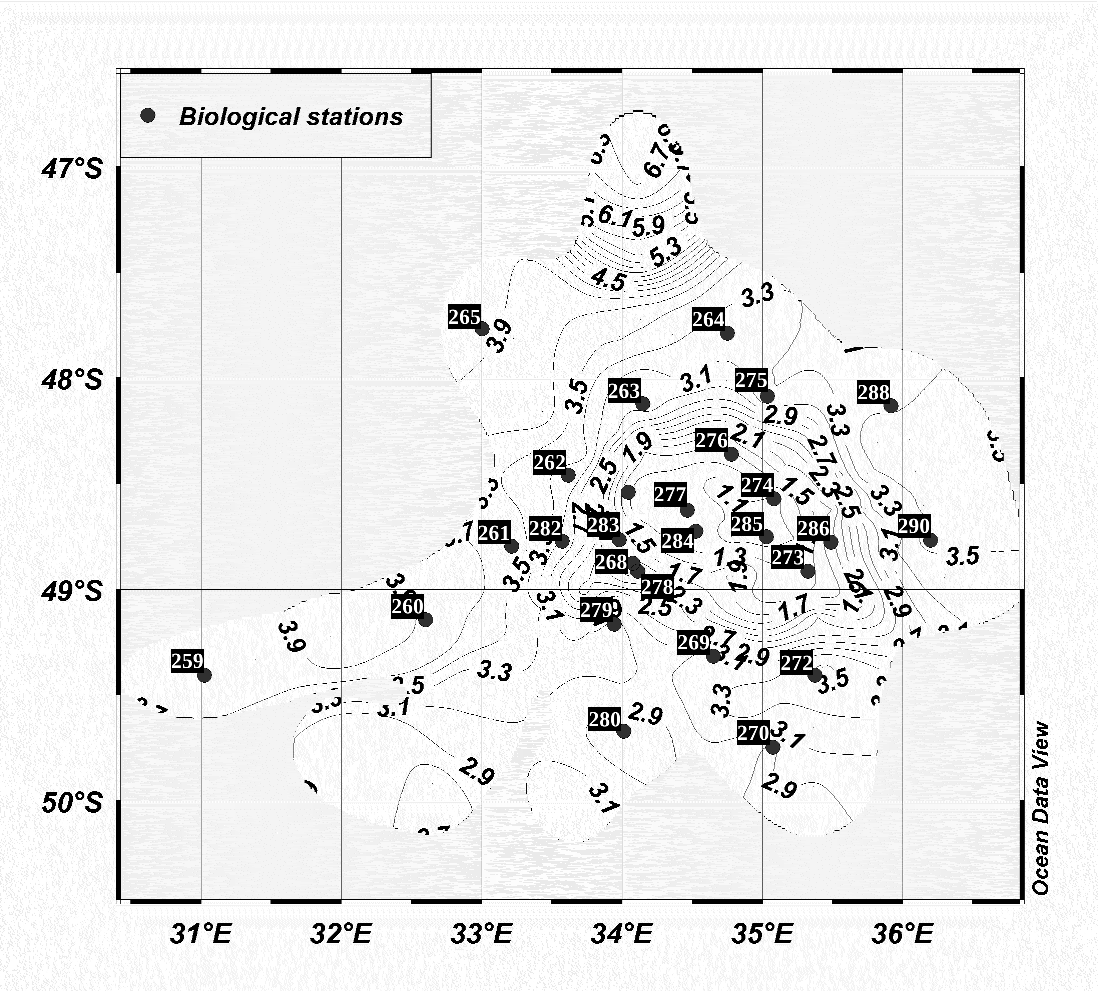

Figure 2.2. Biological stations super-imposed over sub-surface temperature (200 m) isotherms. DEIMEC IV research cruise to the Polar Frontal Zone, Southern Ocean, April 2005.

Table 2.1 Copepod species used during the *in vitro* incubation experiments in 2004 and 2005. Collectively these species accounted for more than 90% of the total mesozooplankton abundance at all stations during both cruises (Bernard and Froneman, 2004; submitted).

Species	**Developmental Stage**
Calanus simillimus	*III – V*
Metridia lucens	*II - III*
Oithona similis	*IV – V*
O. frigida	*IV – V*
Clausocalanus laticeps	*V*
C. brevipes	*II – IV*
Ctenocalanus spp	*III – V*

CHAPTER THREE - RESULTS

3.1 Hydro-Physical Environment

During the 2004 survey, it appeared that the SAF and the APF had merged into a single distinctive feature. This feature separated the area of investigation into two distinct regions (Figure 2.1). In the north-western region the water mass was distinctly Sub-antarctic, with sub-surface temperatures >8.5 and salinity at >34.2, suggesting that the SAF lay much further to the south than normal, or that an eddy had become detached from north of the SAF, resulting in the advection of warmer, more salty water southwards. The south-eastern corner water mass had a subsurface temperature of <2.5 °C, characterising it as Antarctic surface waters (Ansorge *et al.*, 2004).

During the 2005 survey (Figure 2.2), a cold core eddy was identified within the Polar Frontal Zone, between 48º-49º15'S and 33º-36ºE. Its size and shape corresponded closely to that of a negative anomaly SSH observed from altimetry data (I.J. Ansorge, personal communication). The feature was pronounced throughout the entire observed depth range exhibiting a very strong subsurface expression. Its diameter was approximately 120 nautical miles and it extended to depths >1000 m (I.J. Ansorge, personal communication). Successive altimetry images taken prior to the research cruise showed the eddy to have been detached from the APF at 50ºS and 32º30'E, it then moved in a north and north-eastward direction. Typical upper-layer profiles of temperature and salinity across the cold core eddy showed a well-developed subsurface temperature minimum layer, which was capped between 77 –101 m by a relatively warm 4.2 – 4.4 ºC and fresh 33.7 – 33.8 layer. In this region, a subsurface temperature minimum <0.4 ºC and corresponding salinity values between 34.1 and 34.1 at 250 –300 m at stations occupied within the eddy feature further confirmed the source of this eddy from south of the APF (Figure 2.2). At 200 m the cold core eddy was between 3 –5 ºC cooler than the surrounding Polar Frontal Zone waters. Water masses were typical of Winter Water, a remnant of the previous winter mixed layer capped by seasonal warming and freshening (Park *et al.*, 1998). Water mass characteristics of the eddy were typical of Antarctic Surface Water and further confirm its generation from the region of the APF. Hence, the eddy's core was made up of cold Antarctic surface waters, with warmer Sub-Antarctic surface waters surrounding it.

3.2 Mesozooplankton Community Structure 2004

A detailed description of the mesozooplankton community within the region of investigation is presented in Bernard and Froneman (2004). Here a brief summary of the research findings is presented. The total mesozooplankton community abundance and biomass ranged from 55.19 – 860.57 ind. m^{-3} and from 2.60 – 23.53 mg dwt m^{-3}, respectively (Table 3.1). Total mesozooplankton abundance (Levene’s t-test; t-value = 2.7; df = 13; p-value = 0.02) and biomass (Levene’s t-test; t-value = 1.7; df = 13; p-value = 0.12) were significantly higher ($p< 0.05$) at stations in the Sub-antarctic surface waters, than at stations within the Antarctic waters. Among the mesozooplankton, copepods were identified as the single most important group, collectively comprising ˜ 76 % (ranging from < 0.1 to 36 %) of the total mesozooplankton counted (Figure 3.1). Among the copepods *Calanus simillimus*, *Ctenocalanus* spp. and *Oithona similis* were the most well represented. Collectively these three copepod species made up 60.6 % of all the copepods counted. Also well represented among the mesozooplankton was the teropods *Limacina retroversa*, which contributed 11 % (SD = 33.6) of the total zooplankton counted. Ostracods made up 5 % (SD = 9.82) of the total mesozooplankton counts. *Sagitta gazellae* and *Eukrohnia hamata* were the most abundant chaetognaths identified; however, they made up < 1 % of the total mesozooplankton counts (Table 3.1).

3.3 *Themisto gaudichaudii* 2004

Abundances of *T. gaudichaudii* during the study ranged from 0 to 0.15 ind. M^{-3}, and biomass between 0 and 0.63 mg dwt m^{-3} (Figure 3.2). There were weak correlations between the biomass of mesozooplankton prey and the abundance ($r = 0.38$; $p<0.05$) and biomass ($r = 0.44$; $p<0.05$) of *T. gaudichaudii* (Figure 3.3 and 3.4). *T. gaudichaudii* made up <1 % of the total mesozooplankton community biomass and abundance during the survey. There were no apparent spatial patterns in its distribution during the study. Indeed the abundance (Levene's t-test; t-value = 2.2; df = 10; p-value = 0.05; $p > 0.05$) and biomass (Student's t-test; t-value = 0.1; df = 13; p-value = 0.9; $p > 0.05$) of *Themisto gaudichaudii* on either side of the frontal feature displayed no significant difference (Figure 3.5 and 3.6). Again, there were no significant spatial differences in the total length of *T. gaudichaudii* between the Sub-antarctic and Antarctic surface waters (Student's t-test; t-value = 0.7; df = 21; p-value = 0.5; $p > 0.05$; Figure 3.7). The total length of *T. gaudichaudii* within the study region ranged between 15 and 21 mm.

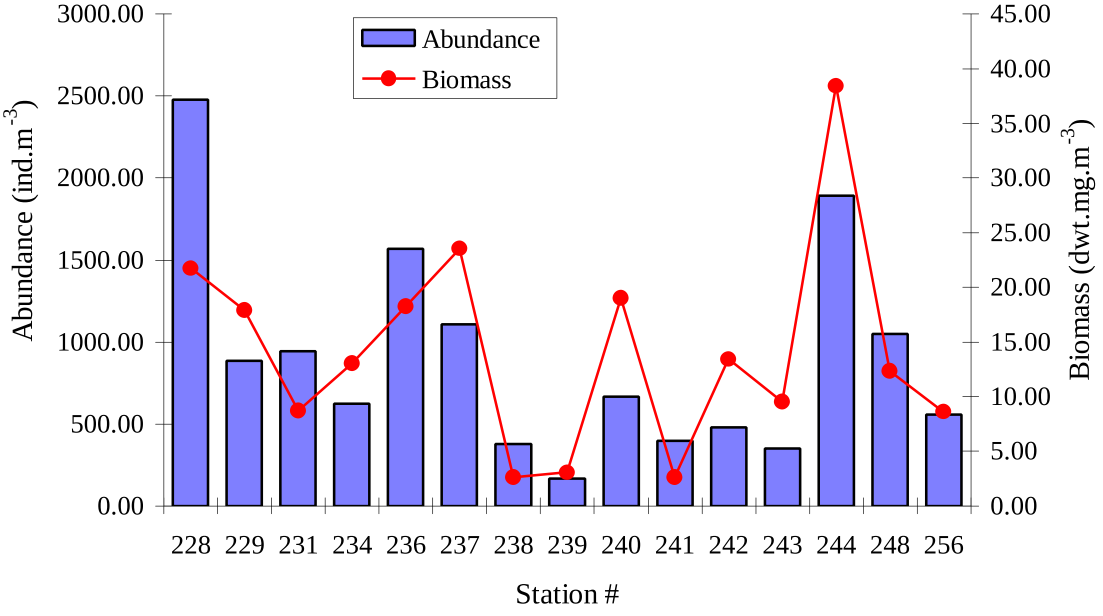

Figure 3.1 Total mesozooplankton biomass and abundance during the DEIMEC III cruise conducted during austral autumn 2004.

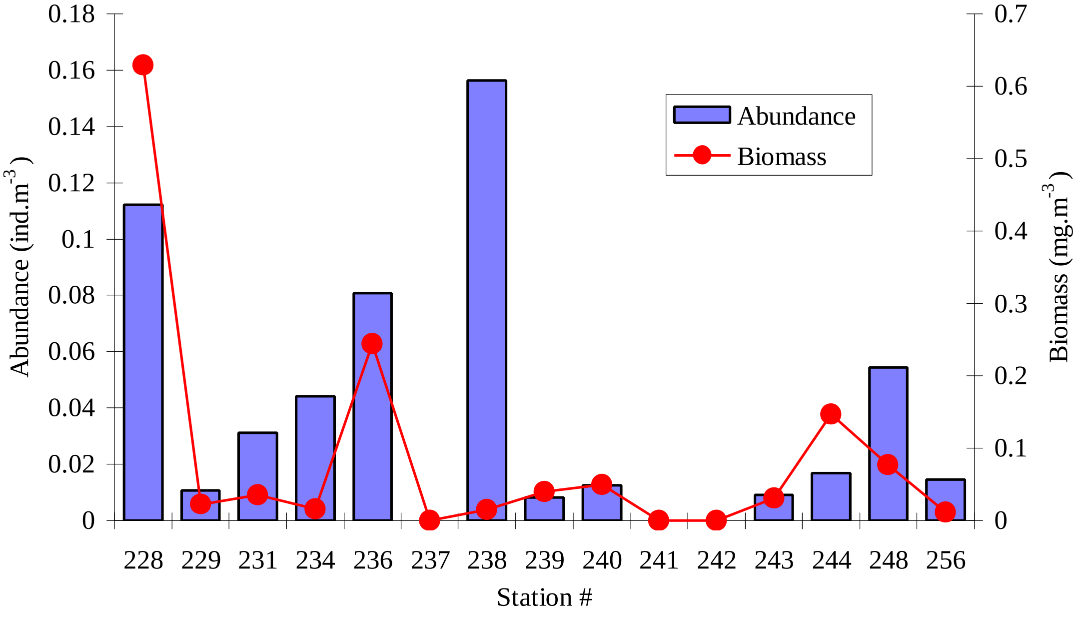

Figure 3.2 Total biomass and abundance of *Themisto gaudichaudii* at selected stations occupied during the third DEIMEC survey, conducted in April 2004.

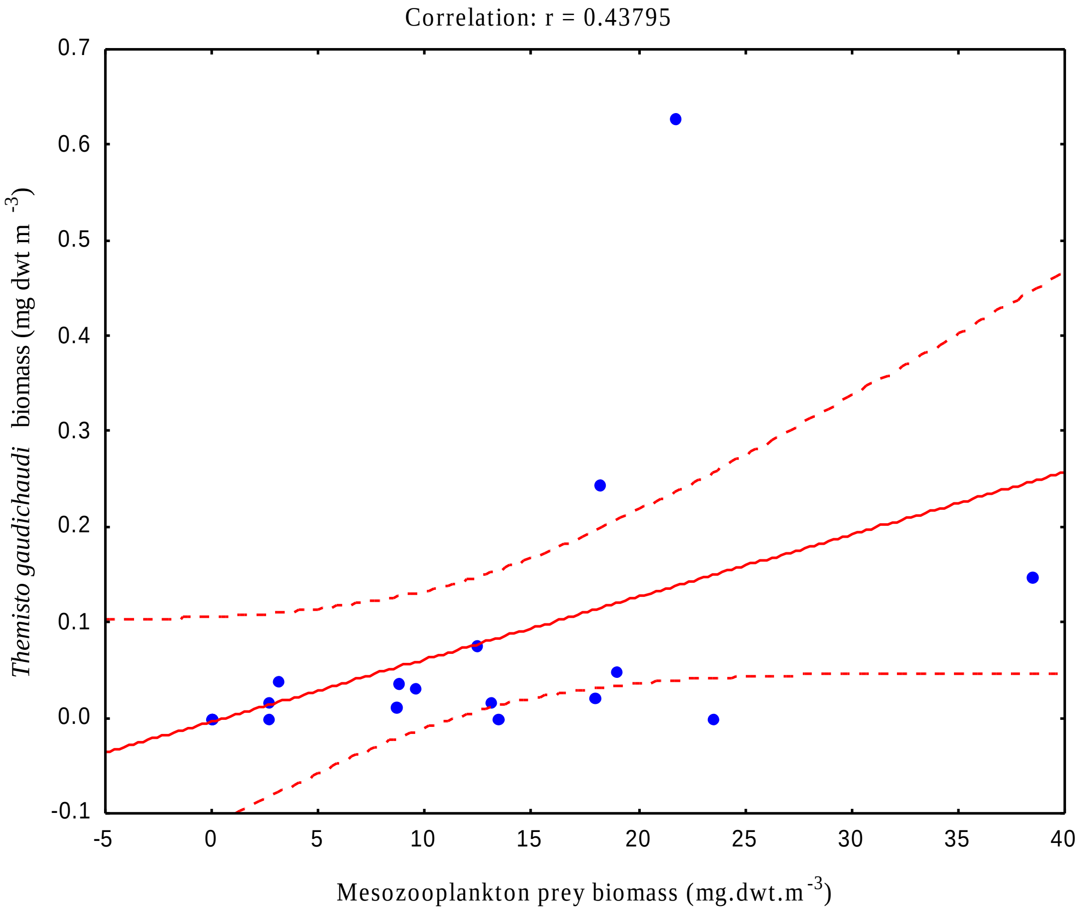

Figure 3.3 The relationship between the biomass of *T. gaudichaudii* and mesozooplankton prey.

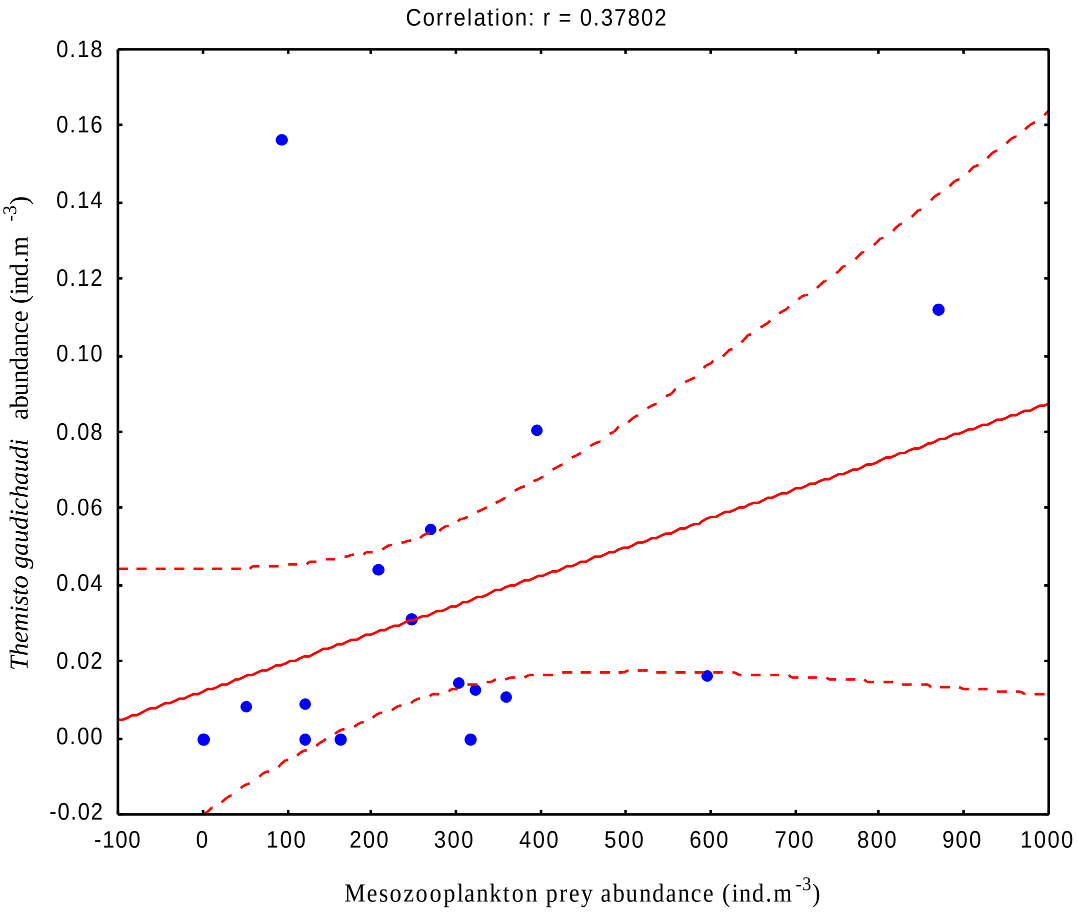

Figure 3.4 The relationship between *T. gaudichaudii* abundance and its mesozooplankton prey abundance.

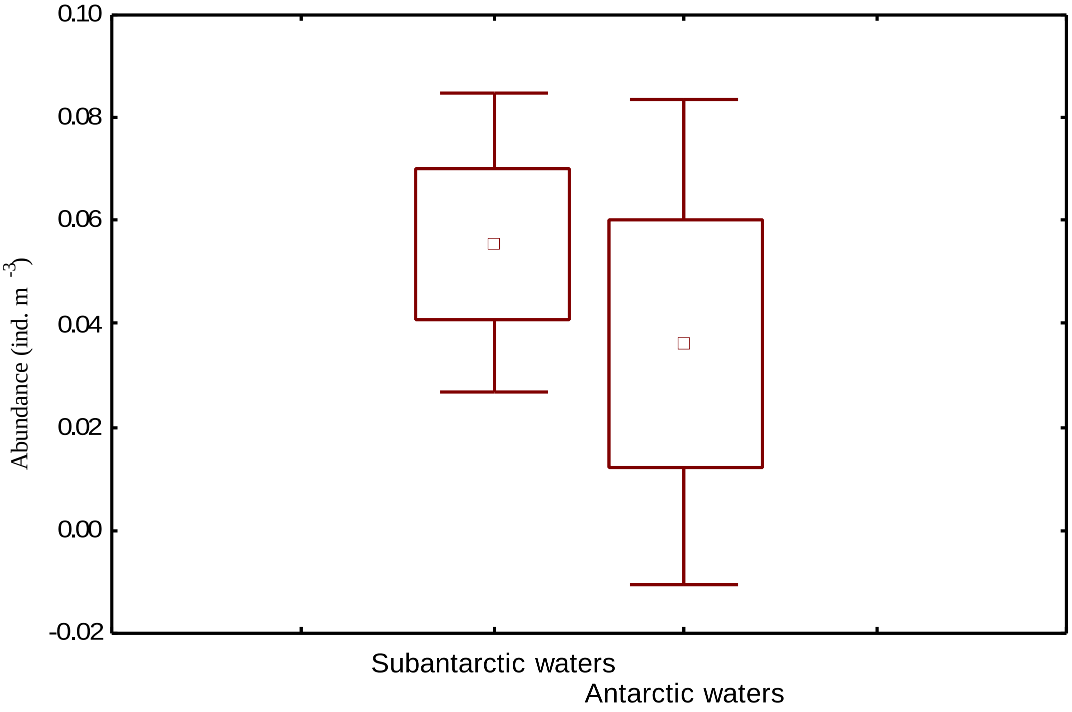

Figure 3.5 Mean abundance (ind.m^3) of *T. gaudichaudii* within the two water masses encountered during the 2004 research cruise.With mean, standard deviation and error bars.

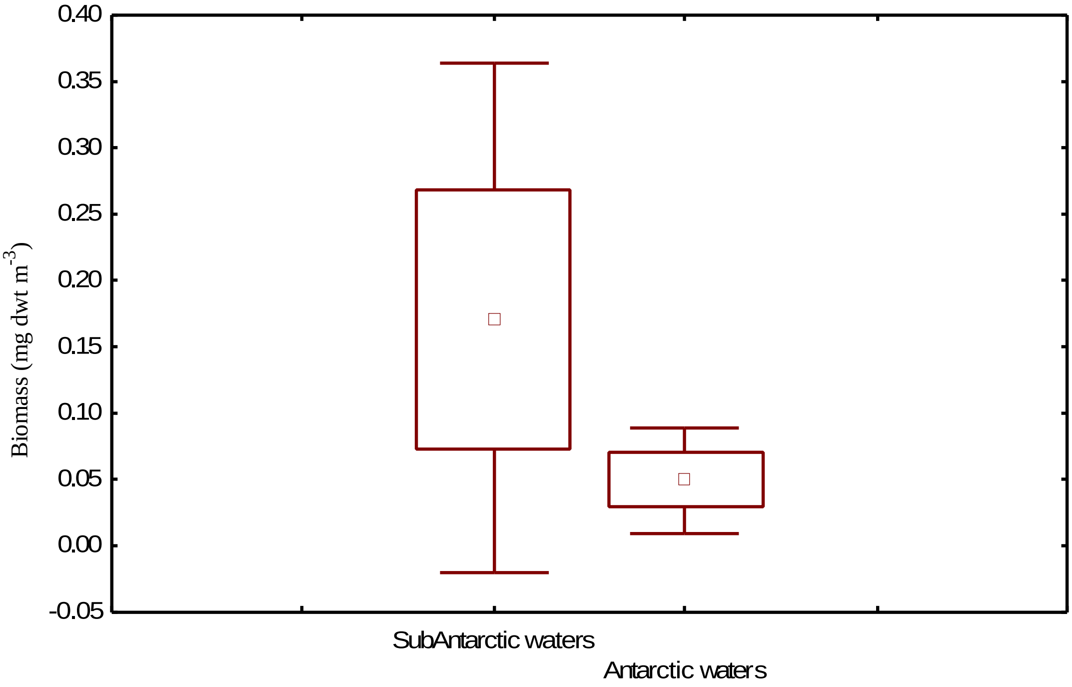

Figure 3.6 Mean biomass (mg dwt m^3) of *T. gaudichaudii* within the two water masses encountered during the 2004 research cruise.Displaying the mean, standard deviation and error bars.

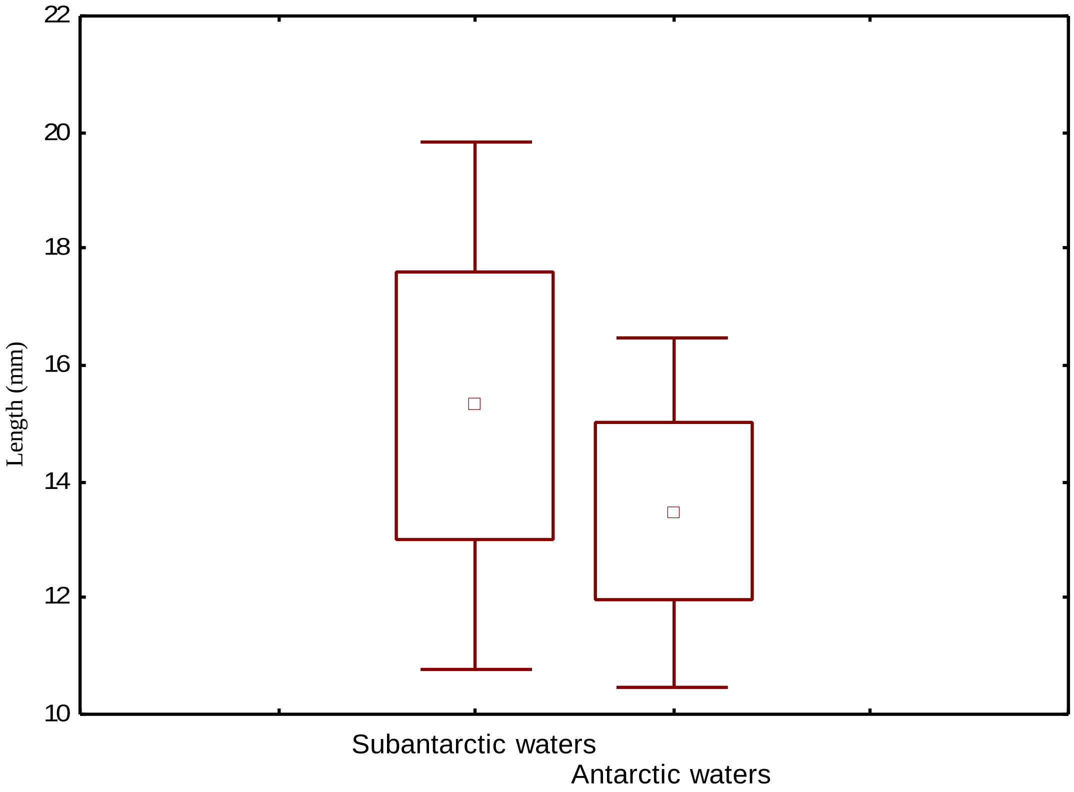

Figure 3.7. Total length (mm) of *T. gaudichaudii* in Antarctic and Sub-antarctic waters, encountered during the 2004 research cruise.With the mean, standard deviation and y-error bars.

3.4 Mesozooplankton Community Structure 2005

A detailed description of the mesozooplankton community during the study is presented elsewhere (Bernard *et al.,* in press). The total mesozooplankton abundance ranged from 25.09 to 2160.64 ind. m^{-3}, and the biomass between 0.75 and 35.16 mg dwt m^{-3} (Table 3.2). There was a significant spatial difference in the total mesozooplankton biomass (t-value = -0.7; df = 17; p-value = 0.05) and abundance (t-value = -2.5; df = 17; p-value = 0.02) between stations occupied in the core of the eddy and in the PFZ waters ($p<0.05$) (Figure 3.8). The total mesozooplankton abundances at stations occupied within the eddy were significantly higher than those recorded at the periphery of the feature and in the surrounding PFZ waters. The mesozooplankton community was numerically dominated by the copepods *Calanus simillimus*, *Oithona* spp and *Ctenocalanus* spp at all stations. Combined, these three copepod species made up 85 % of the total mesozooplankton standing stock, with *Calanus simillimus* contributing 36 % to the total. Bernard *et al.,* (in press) found that the total mesozooplankton abundance were higher at stations occupied within the core/center of the eddy and at the edge of the eddy, than they were at station within the PFZ (outside the eddy).

3.5 *Themisto gaudichaudii* 2005

Abundance and biomass values of *T. gaudichaudii* within the region of investigation ranged from <0.001 to 0.2 ind. m^{-3} and from <0.01 to 0.04 mg dwt m^{-3}, respectively (Figure 3.9). The total abundance (t-value = -0.6; df = 17; p-value = 0.5) and biomass (t-value = -0.3; df = 14; p-value = 0.7) of *T. gaudichaudii* was highly variable and exhibited no spatial difference between the eddy core, eddy edge and surrounding PFZ waters ($p>0.05$). The total length of amphipods within the region, ranged between 10 mm and 25.9 mm, with a median size of 16.5 mm. There was no significant difference (t-value = 1.9; df = 14; p-value = 0.1; $p>0.05$) in the total length of the animals sampled in the different water masses encountered during the survey (Figure 3.10).

There was no correlation between the abundance and biomass of *T. gaudichaudii* and its mesozooplankton prey (r=-0.06, p>0.05) (Figure 3.11). Highest abundances of *Themisto gaudichaudii* typically co-occurred with the lowest abundances of its mesozooplankton prey (Figure 3.12).

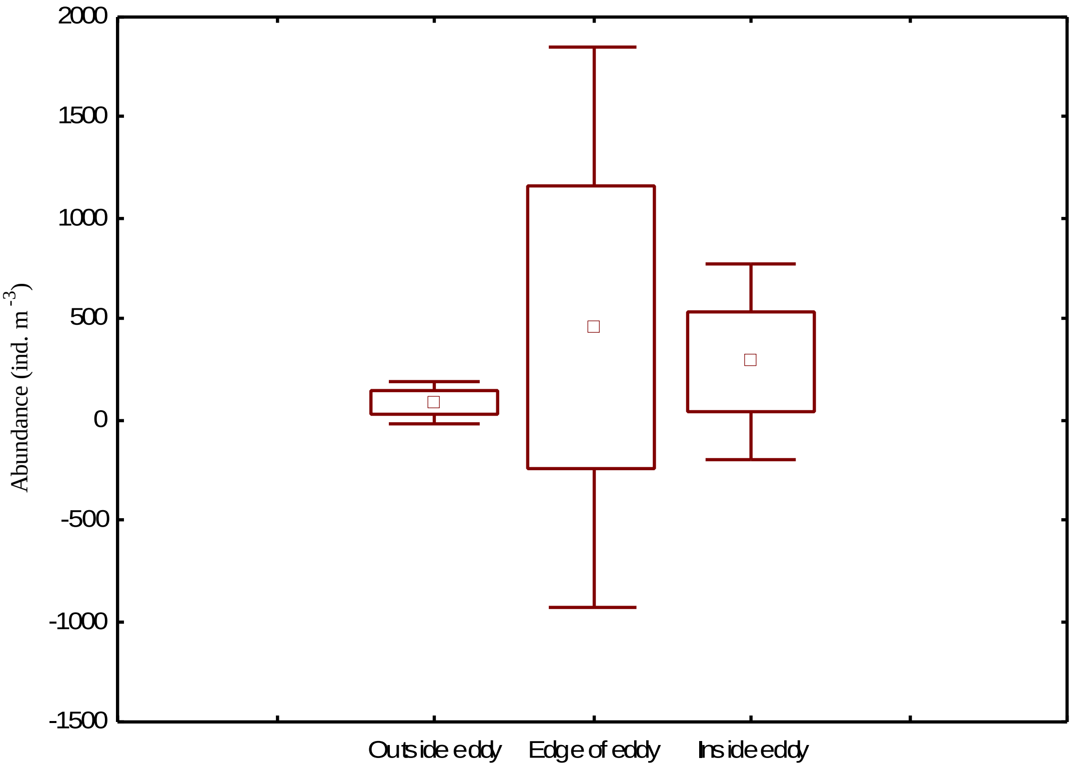

Figure 3.8 Total abundance of mesozooplankton encountered outside, on the edge, and inside the cold core eddy, sampled during the 2005 research cruise. With the mean, standard deviation and y-error bars.

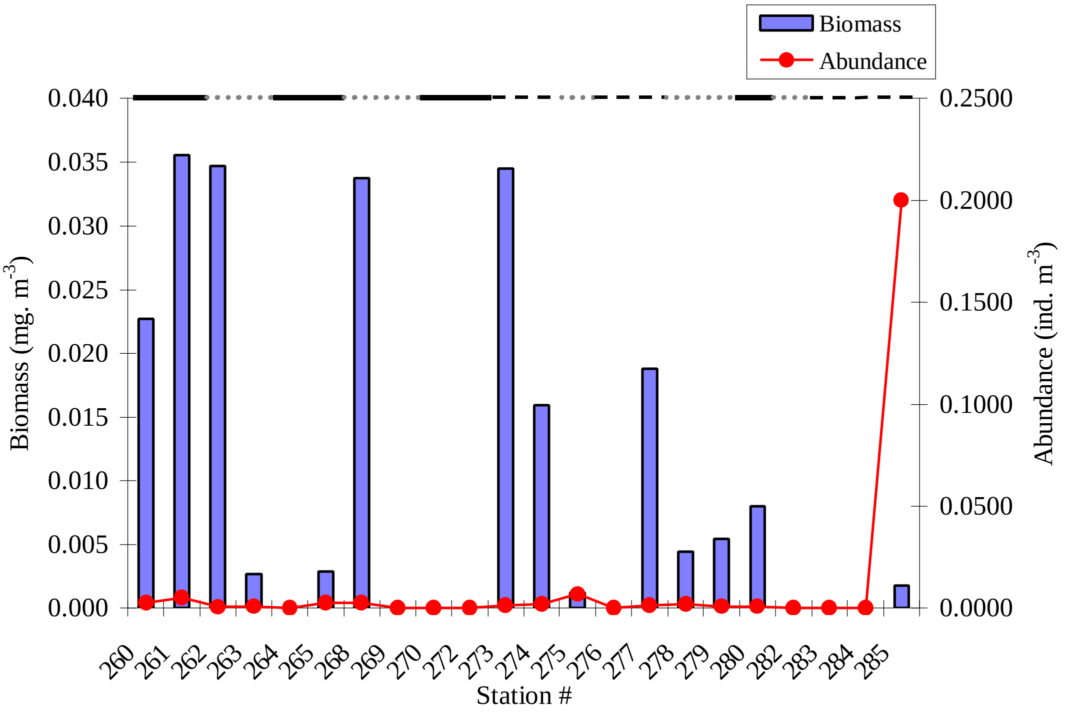

Figure 3.9 Abundance and biomass of *T. gaudichaudii* during the 2005 DEIMEC IV survey. (▬ refers to station occupied outside of the eddy, · stations occupied on the edge of the eddy, and — stations occupied inside of the eddy.)

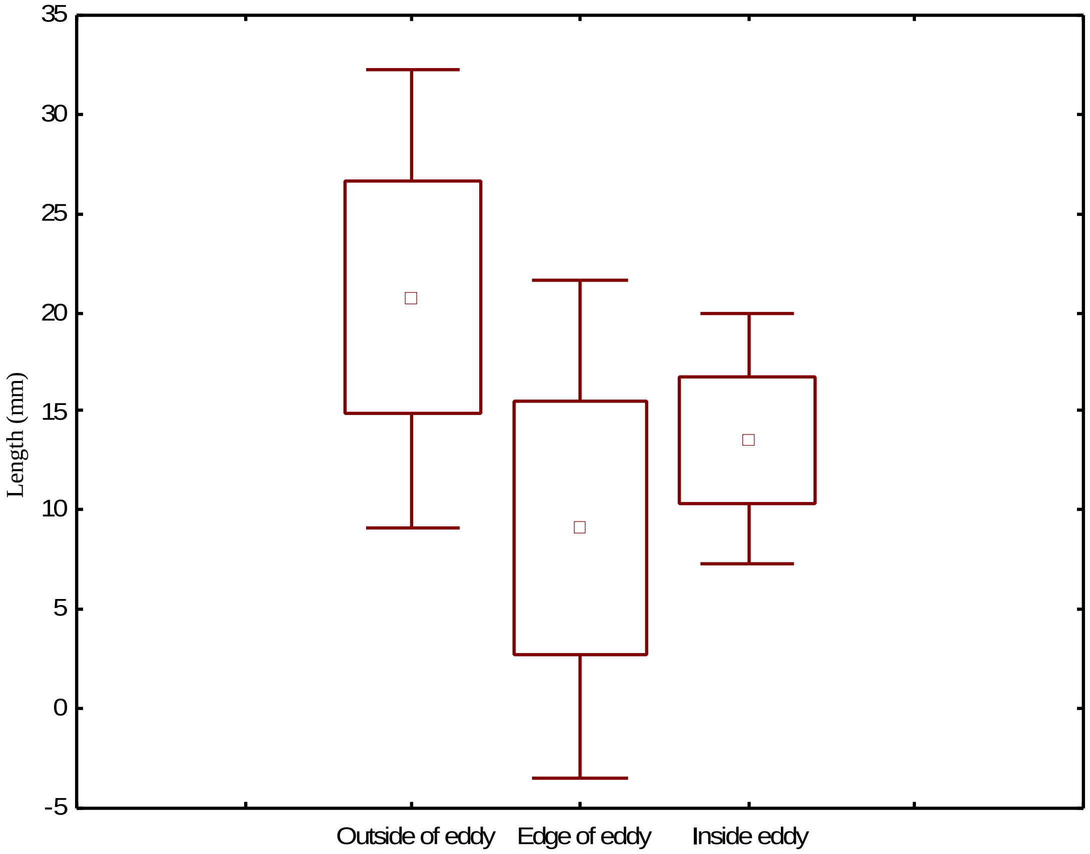

Figure 3.10 Length (mm) of *T. gaudichaudii* within the various regions of the eddy encountered during the 2005 research cruise. Displaying mean, standard deviation and error bars.

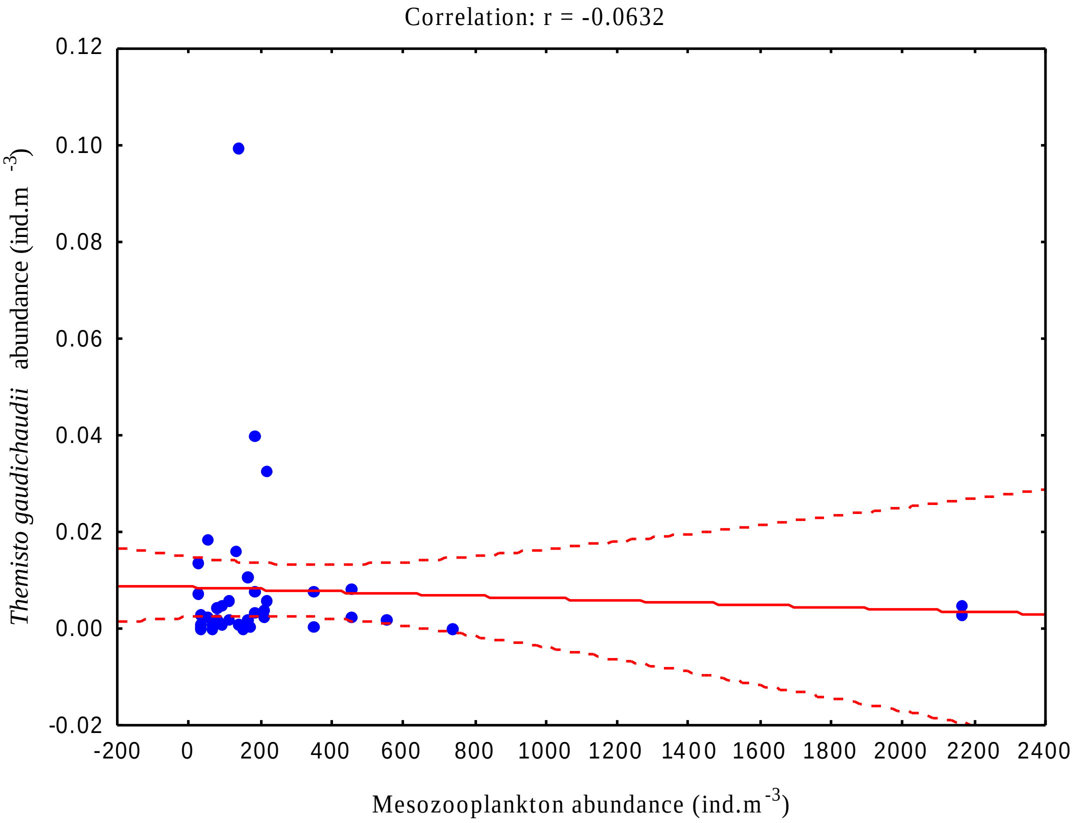

Figure 3.11. Relationship between *T. gaudichaudii* abundance and mesozooplankton prey abundance during the 2005 research cruise.

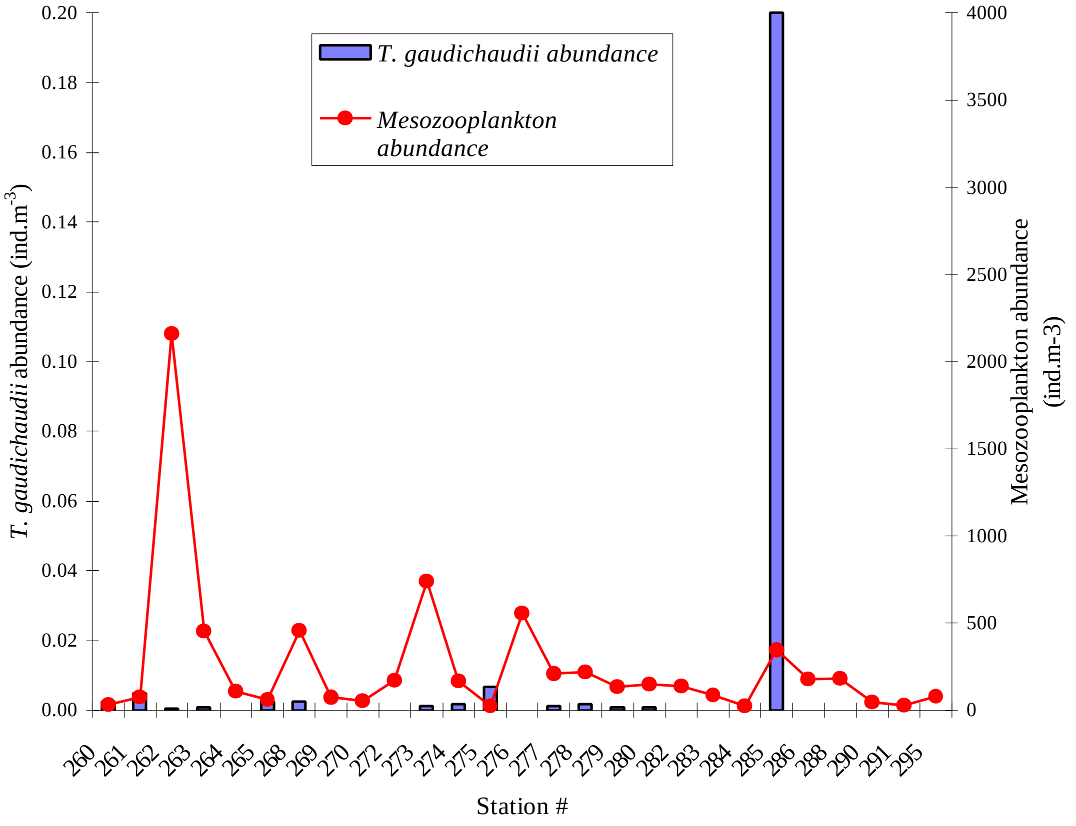

Figure 3.12 Abundances of T. gaudichaudii and its mesozooplankton prey during the 2005 study.

3.6 Gut Content Analysis 2004

The total length of amphipods used in this analysis ranged from 17 to 25 mm. The gut content analysis results indicated that for both male and female *T. gaudichaudii*, copepods were found in between 86 % and 93 % of all guts examined during the day and between 93 % and 100 % of guts during the night (Table 3.3). Also well represented among the prey were chaetognaths and pteropods, which were recorded in up to 27 % of all the stomachs examined.

3.7 Gut Content Analysis 2005

The total length of the animals examined for prey in their guts in 2005 ranged between 19 and 29 mm. Of the 30 stomachs that were analysed, during the day copepods were found in 80 % and 93 % of the males and females' guts respectively; while at night they were found in 93 % of male and 87 % of the female guts. During the night pteropods were found in 40 % of the male *T. gaudichaudii* stomachs and 26 % of the female stomachs (Table 3.3). These results are similar to those of 2004.

3.8 Electivity Indices 2004

Electivity indices of *T. gaudichaudii* during the *in vitro* experiments conducted in 2004 ranged between 0 and –1 (? = 0.04) (Figure 3.13), suggesting that the amphipod can be considered as an opportunistic predator generally feeding on the most abundant prey at each station.

3.9 In Vitro Incubations 2004

The feeding rate of *T. gaudichaudii* during *in vitro* incubations increased with an increase in prey density. However, at prey densities of >20 ind. l^{-1}, no further increase in the feeding rate of the amphipod was observed. A second order non-linear regression analysis provided the best fit in the change in feeding rate of *T.*

gaudichaudii with an increase in the prey abundance (r^2= 0.83) (Figure 3.14). The derived equation was:

$y = 2.8561 \, Ln(x) - 0.4713$

Where: y is the feeding rate (number of copepods ind.d^{-1}) and x is the copepod density (ind.l^{-1}).

3.10 Predation Impact 2004

The predation impact of *T. gaudichaudii* on the mesozooplankton prey was estimated by combining the estimated feeding rate of the amphipod at each station with their abundance estimates (figure 3.14). The total estimated feeding rate of *T. gaudichaudii* during the survey ranged between 11.5 and 20.9 copepod ind. l^{-1} d^{-1} (Figure 3.15), corresponding to a loss of between 0.12 and 1.64 % of the total mesozooplankton standing stock. There were no significant spatial patterns in the predation impact of *T. gaudichaudii* (t-value = 0.9; df = 10; p-value = 0.3; $p > 0.05$).

3.11 Predation Impact 2005

As the size classes of the amphipods were similar in 2004 and 2005 (Figure 3.16), and no juveniles were present, we were able to compare the results. Given that the mean size of *T. gaudichaudii* during the 2005 cruise corresponded to that recorded in 2004, the estimated predation impact of *T. gaudichaudii* on the mesozooplankton standing stock was estimated (Figure 3.17) employing the predictive equation ($y = 2.8561Ln(x) – 0.4713$) derived during the previous year, 2004. The individual feeding rate of *T. gaudichaudii* during the study ranged between 8.6 and 21.1 copepods d^{-1} l^{-1}. When combined with the abundance data, the estimated predation impact of *T. gaudichaudii* ranged from <0.01 and 3.25 copepods m^{-3}, which corresponds to a daily loss of between <0.01 to 1.73 % of the total mesozooplankton standing stock. During 2005 no significant spatial patterns were evident (t-value = -0.8; df = 8; p-value = 0.5; $p > 0.05$).

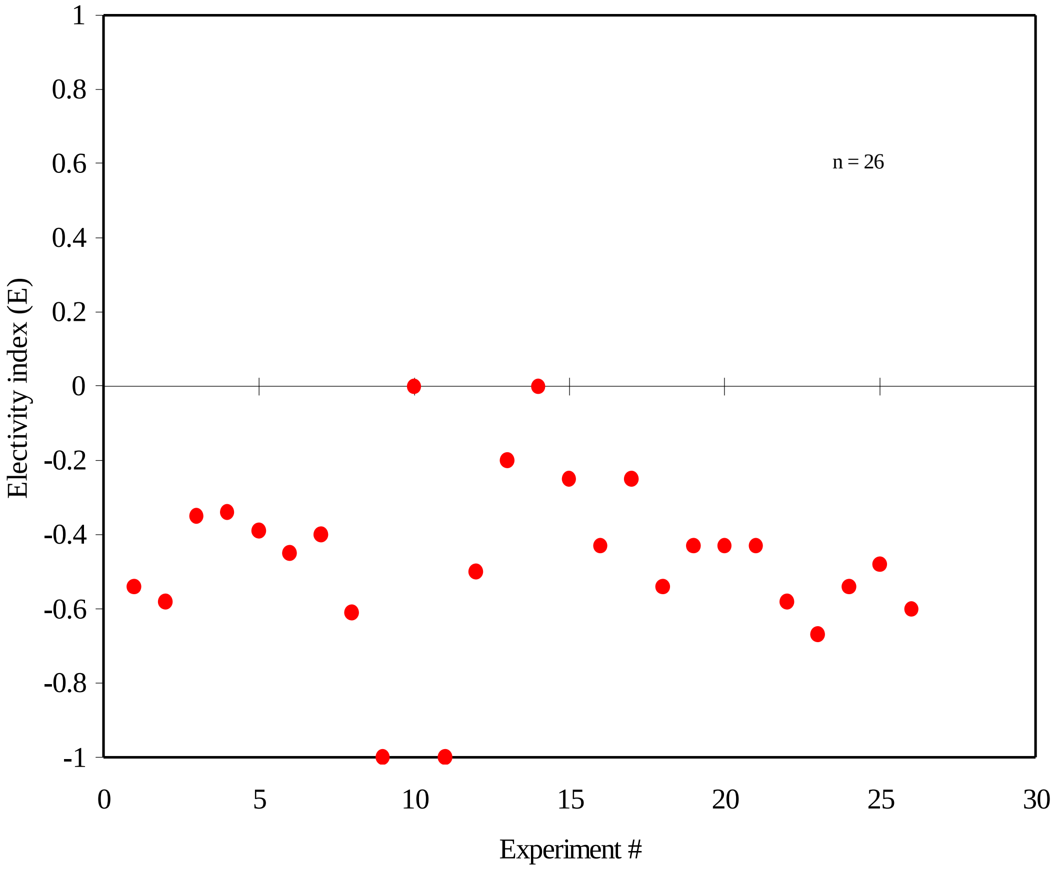

Figure 3.13. The mean electivity index (E) values from *in vitro* experiments conducted with *Themisto gaudichaudii* in the Polar Frontal Zone region. Values <1 indicate no selection for a particular type of prey (n=26).

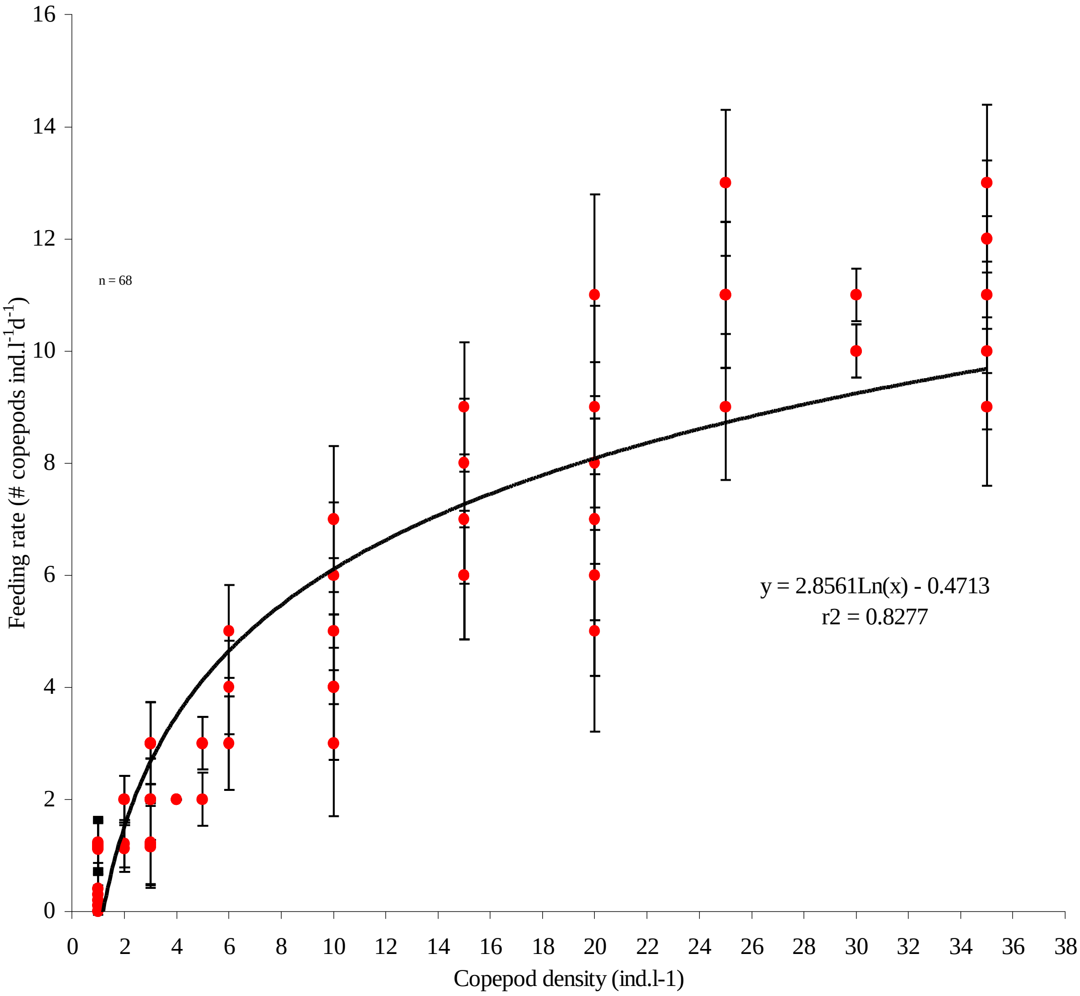

Figure 3.14. The predicted feeding rate of *Themisto gaudichaudii* at densities of mesozooplankton (copepods), during the *in vitro* experiment conducted in 2004. Values are means ± standard deviation.

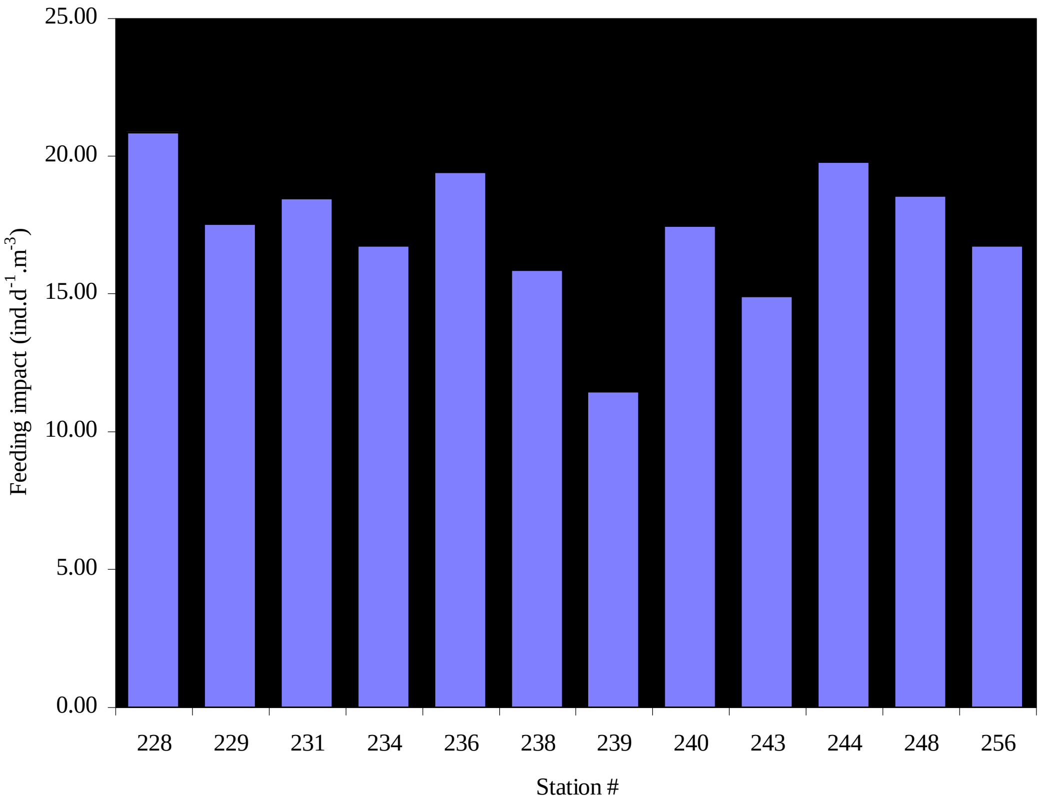

Figure 3.15 Estimated feeding rate of *T. gaudichaudii* at selected sampling stations occupied during the 2004 survey.

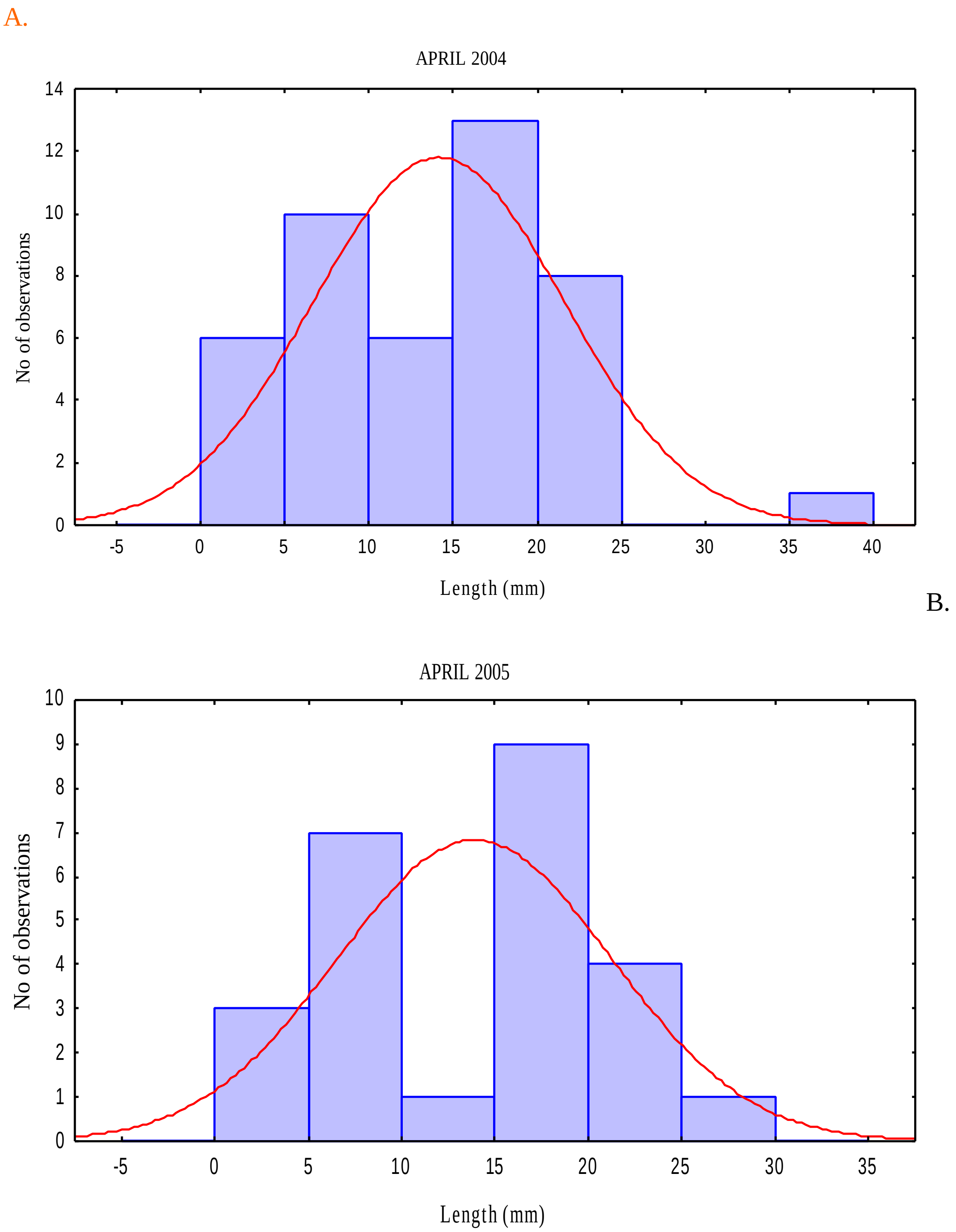

Figure 3.16. Length classes of *T. gaudichaudii* during the a) 2004 and b) 2005 survey.

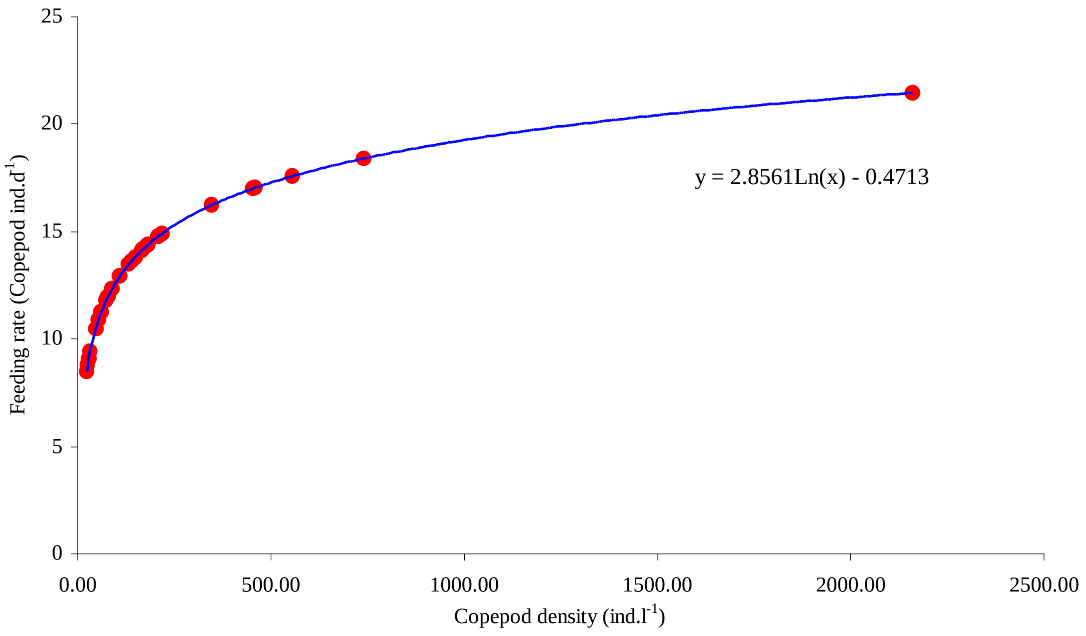

Figure 3.17 Feeding rate of *T. gaudichaudii* during the 2005 survey. Estimated using the predictive equation developed in 2004, from *in vitro* studies.

Table 3.1 Abundance (ind. m^{-3}) of selected mesozooplankton species at the stations occupied during the third DEIMEC survey, April 2004. Data from Bernard and Froneman (2005)

Taxon	**Station number**						
	228	**229**	**231**	**234**	**236**	**237**	**238**
Copepoda							
Calanus simillimus	149.10	69.55	37.95	76.49	99.50	107.00	0.78
Metridia lucens	61.08	13.08	13.98	2.85	23.26	5.13	12.04
Oithona similis	213.77	31.68	61.25	23.80	73.01	10.26	18.30
Oithona frigida	25.15	1.38	9.99	7.93	4.52	0.73	0.63
Clausocalanus laticeps	28.74	17.90	5.33	3.97	14.86	8.79	0.47
Clausocalanus brevipes	48.50	8.95	8.65	4.53	8.40	5.86	30.34
Ctenocalanus spp.	174.25	77.12	58.58	27.20	69.13	80.62	14.54
Pleuromamma abdominalis	23.35	6.89	2.00	1.70	1.29	8.79	1.56
Scolecithricella minor	12.57	6.89	9.32	1.13	2.58	8.06	1.09
Ostracoda	37.72	13.08	20.64	17.00	6.46	22.72	4.69
Pterapoda							
Limacina retroversa	70.06	107.42	0.00	26.06	83.34	30.78	1.56
Chaetognatha							
Sagitta gazellae	14.37	1.38	0.67	2.27	1.29	2.20	1.25
Eukrohnia hamata	1.80	2.75	7.99	6.23	3.88	15.39	1.09
Amphipoda							
Themisto gaudichaudii	0.11	0.01	0.03	0.04	0.08	0.00	0.15
Total	860.57	358.08	236.38	201.20	391.60	306.33	88.49

Table 3.1 Continued.

239	**240**	**241**	**242**	**243**	**244**	**248**	**256**
1.58	145.14	0.00	1.72	36.03	290.04	0.00	33.39
0.92	4.89	10.49	59.46	2.98	10.70	26.11	17.62
5.27	18.75	23.32	10.34	11.61	19.26	17.41	59.37
0.66	13.05	1.17	0.00	3.87	12.84	2.61	18.55
5.53	7.34	0.00	0.00	1.79	8.56	0.00	20.41
5.53	7.34	6.61	17.23	1.79	7.49	19.15	9.28
5.80	75.83	45.47	27.57	21.44	69.57	151.43	82.56
0.13	0.00	9.33	12.06	3.28	5.35	0.00	2.78
1.05	5.71	2.72	0.00	1.49	6.42	0.87	2.78
10.14	10.60	10.49	9.48	6.55	39.60	10.44	13.91
7.11	4.08	3.89	14.65	20.84	80.27	23.50	19.48
0.92	3.26	0.78	0.86	1.19	6.42	7.83	1.86
10.54	20.39	0.39	0.00	5.06	23.55	3.48	7.42
0.01	0.01	0.00	0.00	0.01	0.02	0.05	0.01
55.19	316.39	114.66	153.37	117.93	580.09	262.88	289.42

Table 3.2 Total mesozooplankton abundance (ind/m^{-3}) found during the 2005 survey.

Species/station number	259	260	261	262	263	264	265	268	269	270
Calanus simillimus	38.83	9.28	55.84	1122.99	77.65	41.92	39.52	67.20	42.24	19.95
Clausocalanus spp.	1.07	2.56	2.40	64.85	24.75	4.80	0.96	10.88	0.32	0.21
C. laticeps	0.00	0.48	0.32	27.31	11.95	1.28	9.28	12.16	0.32	0.00
Ctenocalanus spp.	1.71	3.36	8.96	303.79	162.13	26.88	0.00	149.76	2.88	3.20
Metridia lucens	1.92	0.32	0.00	58.03	3.41	8.64	0.00	4.48	1.60	0.96
Paraeuchaeta biloba	0.43	0.32	0.00	0.00	0.85	0.00	0.00	0.00	0.00	0.00
Paraeuchaeta spp.	0.00	0.00	0.00	3.41	0.85	0.32	0.00	0.00	0.00	0.00
P. barbata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Heterorhabdus spp.	0.00	0.00	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.21
Oithona spp.	4.69	4.48	1.12	474.45	111.79	4.80	3.84	195.20	17.44	22.40
Scolecithricella minor	0.00	0.64	0.16	10.24	1.71	0.96	0.00	0.64	0.32	0.11
Pleuronamma abdominalis	0.00	0.00	0.00	3.41	0.85	5.12	0.00	0.64	0.48	0.11
Haloptilus spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Candacia spp.	0.00	0.00	0.00	0.00	0.85	0.00	0.00	0.64	0.00	0.00
Rhincalanus gigas	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aetideus armatus	0.00	0.00	0.00	3.41	0.00	0.00	0.00	0.00	0.00	0.00
Eucalanus sewelli	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00
Subeucalanus longiceps	0.00	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00	0.11
Euchirella rostrata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Medusa	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Siphonaria	0.00	0.00	0.32	3.41	0.85	0.32	0.00	0.00	0.00	0.00
Salps	0.00	0.00	0.16	0.00	0.00	0.00	0.00	2.56	0.00	0.00
Polychaetes	0.21	0.16	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.32
Eggs	0.00	0.32	0.00	0.00	2.56	0.00	0.00	0.00	0.00	0.00
Nauplii	0.21	0.00	0.00	0.00	3.41	0.32	0.16	8.32	0.96	0.11
Chaetognaths	6.19	8.16	6.40	17.07	31.57	10.88	2.56	2.56	4.00	3.84
Ostracods	4.69	1.92	0.32	27.31	11.95	2.24	3.52	2.56	1.60	1.71
Limacina spp.	0.43	0.00	0.16	40.96	5.12	0.32	0.64	0.00	1.12	0.11
Isopods	0.00	0.00	0.16	0.00	0.00	0.00	0.16	0.00	0.00	0.00
Amphipods	0.00	0.0025	0.0050	0.0004	0.0008	0.00	0.0025	0.0025	0.00	0.00
Appendicularians	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.28	0.16	0.32
Total (ind.m^{-3}) abundance	**60.59**	**32.00**	**76.97**	**2160.64**	**453.12**	**108.80**	**60.80**	**458.88**	**73.44**	**53.65**

Table 3.2 continued.

272	**273**	**274**	**275**	**276**	**277**	**278**	**279**	**280**	**282**	**283**	**284**
78.08	290.56	31.79	7.04	77.44	22.08	52.91	50.77	51.20	27.84	35.20	4.80
2.56	37.12	3.41	0.16	17.92	12.16	5.55	2.13	5.04	1.28	0.64	0.43
0.64	14.08	0.85	0.11	7.04	1.60	2.13	0.85	0.84	0.96	1.07	0.16
19.84	140.80	30.93	2.56	232.32	101.76	58.45	14.08	62.11	41.60	12.37	2.19
1.92	30.72	2.56	0.05	1.28	3.84	8.11	3.41	2.52	6.72	2.77	0.27
0.96	3.84	0.00	0.00	1.28	0.64	0.00	2.13	1.26	0.00	0.21	0.00
0.32	0.00	0.00	0.16	0.64	0.00	0.00	0.00	0.00	0.32	0.43	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.32	0.00	0.43	0.16	0.64	0.00	1.71	0.00	0.00	0.00	0.21	0.05
36.48	207.36	90.45	6.67	204.80	62.08	69.55	20.91	3.78	40.00	26.88	15.52
1.92	3.84	0.64	0.11	1.28	0.00	0.85	2.56	2.10	0.64	0.85	0.16
0.32	2.56	1.07	0.00	0.00	0.00	1.71	2.99	1.68	1.92	0.43	0.05
0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.64	0.00	0.21	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.21	0.05	0.00	0.00	0.85	1.28	0.42	0.32	0.00	0.05
0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	1.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.64	0.00	0.00
0.00	0.00	0.00	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00
0.32	0.00	0.00	0.00	0.00	0.00	0.43	0.00	0.84	0.32	0.43	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.21	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.92	0.00	0.64	0.11	1.92	1.60	0.00	0.43	0.42	0.00	0.43	0.21
16.32	1.28	1.28	2.99	1.92	1.60	5.55	17.92	7.55	12.48	3.41	0.32
5.76	2.56	0.64	2.08	1.92	0.00	7.68	11.95	7.97	2.88	1.92	0.27
0.00	3.84	0.64	0.69	0.64	0.32	2.13	0.00	0.84	0.64	0.85	1.01
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.0013	0.0017	0.0067	0.00	0.0013	0.0017	0.0008	0.0008	0.00	0.00	0.00
0.00	0.00	0.00	0.00	2.56	0.32	0.00	0.43	0.00	0.32	0.00	0.00
168.32	**739.84**	**165.76**	**23.10**	**554.88**	**208.00**	**217.60**	**131.84**	**148.56**	**139.20**	**88.53**	**25.49**

Table 3.2 continued.

285	286	288	290	291	295	TOTAL
96.00	27.20	151.89	2.56	7.41	5.92	2536.11
9.60	5.76	3.41	2.67	0.32	4.64	227.60
4.48	2.24	1.28	0.21	0.00	0.80	102.44
79.36	36.48	6.40	5.33	2.51	20.80	1532.56
2.56	2.88	1.71	2.45	0.32	3.84	157.29
0.00	0.64	0.00	0.11	0.00	0.00	12.67
0.00	0.32	0.00	0.00	0.16	0.32	7.25
0.00	0.32	0.00	0.00	0.00	0.00	0.32
0.00	0.32	0.00	0.21	0.48	0.00	5.07
140.80	93.12	4.27	16.75	9.87	25.76	1915.24
2.56	1.28	1.28	1.71	0.37	1.60	38.53
1.28	0.32	0.00	0.64	0.05	4.16	29.79
0.00	0.00	0.00	0.00	0.00	0.00	0.05
0.64	0.64	0.00	0.00	0.00	0.00	4.27
0.64	0.00	0.00	0.00	0.05	0.00	3.89
0.00	0.00	0.43	0.11	0.11	0.00	4.11
0.00	0.00	0.00	0.21	0.00	0.00	0.37
0.00	0.00	0.00	0.00	0.00	0.00	0.96
0.00	0.00	0.00	0.00	0.05	0.00	1.97
0.00	0.00	0.00	0.00	0.00	0.00	0.85
0.00	0.00	0.00	0.00	0.00	0.00	5.17
0.00	0.00	0.00	0.00	0.00	0.00	5.05
0.00	0.00	0.00	0.11	0.05	0.00	1.71
0.00	0.00	0.00	0.11	0.00	0.00	2.99
1.28	5.76	0.00	0.11	0.11	0.32	28.74
1.28	0.00	6.83	8.32	3.47	7.20	192.94
2.56	0.96	3.84	4.27	2.40	3.04	120.51
2.56	0.64	0.85	0.00	0.53	0.00	65.05
0.00	0.00	0.00	0.00	0.00	0.00	0.32
0.2000	0.00	0.00	0.00	0.00	0.00	0.23
0.64	0.64	0.00	0.43	0.11	0.00	7.20
346.44	**179.52**	**182.19**	**46.29**	**28.37**	**78.40**	**7011.25**

Table 3.3 Frequency of occurrence of various prey items recorded in the gut of *Themisto gaudichaudii* during two cruises in the Polar Frontal Zone during austral autumn (April 2004/2005).

Taxa	**Frequency of occurrence (%)**							
	2004				**2005**			
	DAY		NIGHT		DAY		NIGHT	
Prey	Male	Female	Male	Female	Male	Female	Male	Female
Copepoda	86	93	100	93	80	93	93	87
Chaetognatha	20	27	7	0	0	0	7	13
Polychaeta	0	13	27	0	0	0	0	7
Amphipod	0	7	0	0	13	47	0	0
Pteropod	7	13	27	33	7	0	40	26
Other	0	13	0	7	0	0	7	0
Total number of stomachs	**30 exmained**				**30 examined**			

CHAPTER FOUR – DISCUSSION

4.1 General Discussion

Previous studies conducted in the region of the Prince Edward Islands have demonstrated close coupling between the physical environment and the plankton species composition and distribution (Froneman and Pakhomov, 1998; Ansorge *et al.*, 1999; Froneman *et al.,* 1999; Pakhomov and Froneman, 1999). The role of the frontal systems as regions of increased biological activity and as biogeographic barriers to the distribution of phytoplankton and zooplankton in the Polar Frontal Zone of the Southern Ocean has also received considerable attention (Pakhomov and Perissinotto, 1997; Smetacek *et al.,* 1997; Pakhomov *et al.,* 1999a, b; Froneman *et al.,* 2000; Bernard and Froneman, 2003). Furthermore, the results of several studies have demonstrated that the frontal systems that delimit the Polar Frontal Zone, the Sub-antarctic Front and Antarctic Polar Front are characterised by increased biological activity (Pakhomov and Perissinotto, 1997; Smetacek *et al.,* 1997; Froneman *et al.,* 2000).

The Polar Frontal Zone has on a number of occasions been demonstrated to be an area of high mesoscale variability, including meanders in frontal systems and the presence of both warm and cold core eddies (Lutjeharms, 1990). The position of the Sub-antarctic Front and the Antarctic Polar Front demonstrate a high degree of latitudinal variability, as these are both dynamic regions with high vertical and horizontal instability, and exhibit “extensive” north-south meandering (Lutjeharms and Valentine, 1984; Nagata *et al.,* 1988; Duncombe Rae, 1989; Lutjeharms, 1990). Vertical mixing in the Antarctic Circumpolar Current is recognized as an important process involved in the overturning circulation of the global ocean (Rintoul and Trull, 2001; Wunsch and Ferrari, 2004). The mixing regime of the upper ocean also influences biological processes by regulating the vertical supply of nutrients and by moving phytoplankton along the exponential daylight profile (Cisewski *et al.*, 2005). During April/May 1997, eddies created a front-like structure in the downstream of the Prince Edward Island region, which subsequently increased the spatial heterogeneity in the zooplankton distribution pattern (Froneman *et al.,* 1999).

Transient eddies play a role in transferring salt or freshwater across the polar fronts (Morrow *et al.,* 2004). It has been reported that cold-core eddies transport cool, low salinity polar water across the polar and Subantarctic fronts (SAF's) into the Subantarctic Zone; consequently mixing of core waters can contribute to cooling and lowering the salinity of the ambient subantarctic water (Morrow *et al.,* 2004). Counter rotating eddies, generated from SAF and APF instabilities, have been observed in the downstream region of the Prince Edward Islands (Pakhomov and Froneman, 2000). In addition, observations south of Australia have also shown that eddies may enhance the associated zonal flow (Emery, 1977). Originating from nearby frontal systems, mesoscale eddies have been hypothesized to advect aliens into the Prince Edward Island region (Boden and Parker, 1986). The extreme mesoscale variability in the physical environment of the Polar Frontal Zone was clearly evident during the 2004 and 2005 surveys. During 2004, as a result of topographic steering of the Antarctic Circumpolar Current through the Andrew Bain fracture zone of the south-Indian ridge, the Antarctic Polar Front and Sub-antarctic Front appeared to merge into a single distinct feature (Figure 2.1; Ansorge *et al.,* 2004). The cold core feature appeared to have its origin from the region of the Antarctic Polar Front (Ansorge *et al.,* 2004).

The variable physical environment observed during these two cruises plays a significant role in determining the plankton species composition and distribution within the region. There was a distinct shift in the mesozooplankton community structure across the fronts during the 2004 survey (Bernard and Froneman, 2005). Numerical analysis identified two mesozooplankton communities, distinct from each other, separated by the frontal feature, named the Antarctic and the Subantarctic Zone Groups. The total mesozooplankton abundance and biomass during the 2004 survey ranged between 55.19 and 860.57 ind. m^{-3} and between 2.60 to 38.42 mg dwt m^{-3}, respectively. These values are in the range reported in previous studies within the same geographical region during the same season. For example, Bernard and Froneman (2002) in the upstream region of the Prince Edward Islands recorded mesozooplankton abundances ranging from 49 to 1,512 ind. m^{-3}. Similarly, Hunt *et al.*, (2001) estimated mesozooplankton abundances to range between 57.48 to 139.92 ind. m^{-3}, for the period 1996-1999.

During the 2005 study the general zooplankton composition and biomass agreed well with previous investigations conducted in the same geographical region (Boden and Parker, 1986; Froneman and Pakhomov, 1998; Pakhomov and Froneman, 1999; Bernard and Froneman, 2002, 2003;). Copepod abundances followed the same trend as recorded by previous studies in the Southern Ocean (Hernandez-Leon *et al.*, 1999; Froneman *et al.*, 2000; Pakhomov and Froneman, 2000; Bernard and Froneman, 2002, 2003) contributing approximately 85 % to the total zooplankton abundance. In agreement with numerous other studies conducted in various regions of the Southern Ocean (Hernandez-Leon *et al.*, 1999; Pakhomov and Froneman, 2000; Bernard and Froneman, 2003) the total mesozooplankton abundance was numerically dominated by copepods of the genera *Oithona,* and *Clausocalanus,* which contributed up to 93 % of the total mesozooplankton abundance. There was no evidence to suggest that the eddy was responsible for transporting mesozooplankton species across the biogeographic barrier represented by the Antarctic Polar Front. Consequently the mesozooplankton community composition within the Polar Frontal Zone is highly variable and made up of taxa from a variety of origins, including the Antarctic and the Subantarctic Zones (Ansorge *et al.*, 1999; Pakhomov and Froneman, 1999; Bernard and Froneman, 2003).

The contribution of the carnivorous component of the mesozooplankton community during both cruises was small, as both chaetognaths and amphipods each made up < 10 % of the total mesozooplankton abundance (This study, Lukac, 2005). This result is in contrast to previous studies conducted in the region where carnivores were found to contribute up to 25 % to the total mesozooplankton abundance (Hernandez-Leon *et al.*, 1999). The marked variability in the contribution of the carnivorous zooplankton to total zooplankton standing stock can be attributed to extreme variability in the oceanographic environment. According to Bowman (1960) amphipods are generally ranked third in numerical zooplankton abundance and the genus *Themisto* dominates the colder epipelagic amphipod fauna (Bowman *et al.,* 1982). During the 2004 and 2005 surveys *T. gaudichaudii* made up <1 % of the total counts of the mesozooplankton community.

Total abundance and biomass of *T. gaudichaudii* during the 2004 study ranged between 0.01 and 0.014 ind. m^{-3} and between 0.01 and 0.62 mg dwt m^{-3}, respectively (Figure 3.2). During the survey conducted in 2005, *T. gaudichaudii* abundance never exceeded 0.2 ind. m^{-3}, and the biomass was always <0.04 mg dwt m^{-3}. *T. gaudichaudii* contributed <1 % of the total mesozooplankton abundance and biomass during both the surveys. The estimates presented here are substantially lower than those recorded in the region of the Prince Edwards Island during previous investigations using the same sampling gear and mesh size (Boden and Parker, 1986; Froneman *et al.,* 2000). For example, Froneman *et al.,* (2000) reported that the abundance of *T. gaudichaudii* attained levels of up to 0.4 ind. m^{-3} with values of 0.2 ind. m^{-3} not uncommon in the vicinity of the Prince Edward Island. The elevated abundances of *T. gaudichaudii* in the waters surrounding the Prince Edward Islands are thought to be attributable to the concentration of the zooplankton in the shallow shelf waters around the islands (Froneman *et al.,* 2000). It should be noted that the zooplankton community structure, abundance and biomass within the Polar Frontal Zone region typically displays a high degree of inter-annual variability reflecting a variable oceanographic environment and its effect on the zooplankton population dynamics (Froneman *et al.,* 2000).

Recent studies conducted in the high Antarctic region have demonstrated that different water mass within the region were characterised by different development stages of the same chaetognaths species (Johnson and Terazaki, 2004). During this study, there were no significant differences in the mean abundance and biomass, and the size composition of *T. gaudichaudii* within the different water masses encountered during both 2004 and 2005 surveys ($p > 0.05$ in all cases). The absence of any difference can likely be ascribed to the fact that the Polar Frontal Zone represents a transitional zone between the warmer Subantarctic waters to the north and the colder Antarctic surface waters to the south.

A key feature of the study during both years was the virtual absence of juvenile amphipods within the two regions of investigation (Figure 3.16). During 2004 and 2005 the contribution of juveniles (<10 mm total length) to the total number of amphipods was < 10 % during both years. The absence of smaller individuals cannot be linked to the sampling methodology employed, as a mesh size of 200 µm was used during both surveys. The absence of juveniles indicates that these animals exhibit a strong seasonal pattern in their reproduction within the Polar Frontal Zone. Indeed, field studies in the high Antarctic region suggest that *T. gaudichaudii* release their young during the mid summer months (Kane, 1966). The low abundances and biomass of *T. gauidichaudii* during the present study can therefore, in part also be attributed to the seasonal reproductive patterns exhibited by the amphipod.

4.2 Feeding Ecology

As in other studies in the Southern Ocean, for example in South Georgia (Pakhomov and Perissinotto, 1996) and in the waters surrounding the Prince Edward Islands (Froneman *et al.*, 2000), copepods were the dominant component of *Themisto gaudichaudii's* diet, during both surveys. The results of gut content analysis also showed a close relationship between the structure of the local zooplankton community and the diet of *Themisto gaudichaudii;* as did the results of gut content analysis by Pakhomov and Perissinotto, (1996) and Froneman *et al.*, (2000). Froneman *et al.*, (2000) stated that *T. gaudichaudii* feeds on the most abundant copepod and chaetognaths species. The results of gut content analyses and *in vitro* incubations during both 2004 and 2005 indicated that *T. gaudichaudii* displayed no specific prey selection, as Ivlev's mean result value was – 0.4. This result is consistent with studies conducted in the high Antarctic region which showed that *T. gaudichaudii* is an opportunistic predator capable of consuming prey of an appropriate size and taxonomy (Hopkins, 1985; Pakhomov & Perissinotto, 1996). There was no evidence of diel variability in the prey consumed by the amphipods, which is consistent with the study conducted by Froneman *et al.,* (2000) within the same geographic region during the same season. It should be noted that the results of the in vitro incubations should be considered with caution due to a number of experimental artefacts including bottling effects (may have altered the escape response of the copepods) and the lack of acclimation of *T.gaudichaudi* to the experimental conditions. Furthermore, the incubation experiments only considered the predation of the amphipod on copepods. The absence of other prey may have modified the predation impact of the amphipod on the total mesozooplankton. Nonetheless the results of the experiments provide the first predictive equation of the response of the amphipod to changes in prey availability.

The daily ration of *T. gaudichaudii* in different sections of the Southern Ocean has traditionally been estimated using the gut fullness index approach (Pakhomov and Perissinotto, 1996; Froneman *et al.,* 2000). To compare results obtained during the *in vitro* incubations during this study with those studies undertaken using the gut fullness index approach, daily ration of *T. gaudichaudii* was estimated. The daily rates were estimated assuming a mean dry weight of 0.0273 mg for three numerically dominant copepods during the 2004 survey and combining it with the estimated feeding rate at selected stations (see above). Using this approach the estimated daily ration of *T. gaudichaudii* ranged between 1.2 and 5.9 % body dwt. (mean ˜ 1.8 % body dwt.) during the study. Froneman *et al.,* (2000) calculated that the daily ration of *T. gaudichaudii* near the Prince Edward Islands ranged between 1.2 and 8.7 % body dwt. Similarly, in the South Georgia region, the daily ration of *T. gaudichaudii* was estimated at 6.3 % body dwt (Pakhomov and Perissinotto, 1996). The similar daily rations obtained using the various approaches suggest that the estimated feeding rate of *T. gaudichaudii* obtained using the derived predictive equation, can be used to estimate the feeding and predation impact of *T. gaudichaudii.*

4.3 Predation Impact

The estimated daily impact of *T. gaudichaudii* during the 2004 study corresponded to <0.1 to 1.64 % of the mesozooplankton standing stock daily, and between <0.1 and 1.73 % of the mesozooplankton standing stock during 2005. These estimates are in the range reported by Pakhomov and Perissinotto, (1996) in the South Georgia region where *T. gaudichaudii* was estimated to consume <0.4 % and <13 % of mesozooplankton standing stock and secondary production, respectively. The estimates reported here are also in the range reported for previous studies within the Polar Frontal Zone during austral autumn (Froneman *et al.*, 2000; Froneman *et al.*, 2002). For example, Froneman *et al.*, (2002) reported that *T. gaudichaudii* consumed < 5 % of the total mesozooplankton stock, with values of < 1 % not uncommon. The low impact of *T. gaudichaudii* reported during the two studies, can be attributed to the low abundance of *T. gaudichaudii* throughout the region of investigation (see above). Generally, the predation impact of *T. gaudichaudii* was highest where the highest densities of *T. gaudichaudii* co-occurred with the lowest zooplankton abundances (Pakhomov and Perissinotto, 1996). Froneman *et al.*, (2000) suggested that *T. gaudichaudii's* importance as a secondary production consumer in the waters surrounding the Prince Edward Archipelago exhibits a high degree of spatio-temporal variability. It is likely that during the summer months when *T. gaudichaudii* abundances are elevated due to reproduction, the predation impact of the amphipod on mesozooplankton standing stock will be substantial.

CHAPTER FIVE - CONCLUSION

During this study the biomass and abundance values of *T. gaudichaudii* were highly variable and generally lower than those reported in previous studies undertaken within the Polar Frontal Zone during the same season (Boden and Parker, 1986; Froneman *et al.*, 2000). The high degree of interannual variability in the biomass and abundance values of *T. gaudichaudii* can in all likelihood be ascribed to the variable oceanography in the Polar Frontal Zone environment and its influence on the biology of the region. *Themisto gaudichaudii* exhibited no significant spatial pattern in biomass, abundance and total length ($p > 0.05$) within the different water masses encountered during the two surveys. The absence of any spatial pattern can be linked to the fact that the Polar Frontal Zone represents a transition zone between the warmer Sub-antarctic surface waters to the north, and the colder Antarctic surface waters to the south. Furthermore, the region is characterised by mesoscale variability including the presence of cold and warm core features and cross frontal mixing which facilitates the transfer of species across the frontal systems. The lack of any spatial patterns in abundance and biomass is therefore, not surprising.

A key feature of the investigation was the virtual absence of juveniles throughout the region of investigation. The absence of juveniles was not an artefact of the sampling gear that was employed, as nets with a small mesh size (200 µm), were employed. It is known that the hyperiids release their broods in the high Antarctic region during of summer (Kane, 1966; Labat *et al.*, 2005). No recent studies have been conducted on the reproductive biology of *T. gaudichaudii* in the Polar Frontal Zone. The absence of any juveniles within the samples may partially account for the lower abundance and biomass estimates of *T. gaudichaudii* during this study. Preliminary data suggest that the abundance and biomass of zooplankton with the Polar Frontal Zone during summer was 25 – 50 % higher than recorded within the region during winter. The reduced abundances of *T. gaudichaudii* within the two regions of investigation contributed to the low predation impact of the amphipods on the mesozooplankton (generally < 1 % of the standing stock). On the basis of these findings it is apparent that carnivory by *T. gaudichaudii* would not contribute to a localised increase in the efficiency of the biological pump. However, it is likely that during the summer months, the expected increase in the abundance and biomass of *T. gaudichaudii* resulting from the reproductive activities of the amphipod will dramatically increase their predation impact on the mesozooplankton within the Polar Frontal Zone. Under these conditions, the amphipod may locally increase the efficiency of the biological pump.

5.1 Future Research Initiatives

i) It has also been suggested that juvenile *T. gaudichaudii* feeds on phytoplankton (Siegfreid, 1965; Nemoto and Yoo, 1970; Hopkins, 1985), however the evidence is not conclusive. Further investigations need to focus on the feeding ecology of juvenile *T.gaudichaudii* and whether the pigments within the guts of juvenile *T. gaudichaudii* are derived from secondary sources (*i.e.* consumed prey) is not clear. Also this study only focussed on the feeding activity of adult *T. gaudichaudii*. Therefore, it is important that further feeding studies be conducted on both juveniles and adults. This will be linked to studies on the vertical distribution of both adults and juveniles, as they may occur at different depths due to different feeding requirements.

ii) Comparing the results of this study with those conducted in other seasons strongly suggests a strong seasonal pattern in the population structure of the amphipod within the Polar Frontal Zone (as evident from the virtual absence of juveniles). Studies conducted in the high Antarctic region suggest that *T. gaudichaudii* breeds mainly in late spring, early summer. It is unclear whether a similar pattern exists within the Polar Frontal Zone. Also, there are no studies/information on the ontogenetic migration patterns of the amphipods.

iii) Hyperiid amphipods have been found to be an important prey item for many pelagic predators (fish, squid and whales) and terrestrial predators (flying birds) (Nemoto and Yoo, 1970; Permitin and Tarverdieva, 1972; Rodhouse *et al.*, 1992; Bost *et al.*, 1994; Kock *et al.*, 1994). Consequently, the amphipod can be seen as an important link between the pelagic and terrestrial ecosystems, particularly in the vicinity of the oceanic islands within the PFZ. In order to understand *T. gaudichaudii's* role in the PFZ carbon cycle, it is essential that future studies examine the role of the amphipod in the diets of the top predators, particularly those flying seabirds and penguins found on the various oceanic islands within the PFZ.

CHAPTER SIX - REFERENCES

Allanson B.R., Hart R.C. and J.R.E. Lutjeharms (1981) Observations on the nutrients, chlorophyll and primary production of the Southern Ocean south of Africa. South Africa. *Journal of Antarctic Research* 10/11: 3-14

Alwany M., Thaler E. and M. Stachowitsch (2003) Food selection in two corallivorous butterflyfishes, *Chaetodon austriacus* and *C. trifascialis,* in the Northern Red Sea. *Marine Ecology* 24: 165-177

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

Ansorge I.J., Froneman P.W., Lutjehars J.R.E., Bernard K., Bernard A., Lange L., Lukác 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 S. Wynne (2004) *South African Journal of Science* 100: 319-322

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

Atkinson A. and R.S. Shreeve (1995) Response of the copepod community spring bloom in the Bellingshausen Sea. *Deep Sea Research II* 42: 1291-1311

Atkinson A., Shreeve R.S., Pakhomov E.A., Priddle J., Blight S.P. and P. Ward (1996) Zooplankton response to a phytoplankton bloom near south Georgia, Antarctica. *Marine Ecology Progress Series* 144: 195-210

Bary B.M. (1959) Ecology and distribution of some pelagic Hyperiidae (Crustacea Amphipods) from New Zealand water. *Pacific Science XIII* (4): 317-334

Berger W.H., Smetacek V.S. and G. Wefer (1989) Ocean productivity and paleoproductivity – an overview. In: Berger W.H., Smetacek V., Wefer G. (Eds.) *Productivity of the ocean: Present and past.* Wiley, New York. Pp. 1-34

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

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

Bernard K.S. and P.W. Froneman (2005) Trophodynamics of selected mesozooplankton in the west Indian sector of the Polar Frontal Zone, Southern ocean. *Polar Biology* 28: 594-604

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

Bigelow H.B. (1926) Plankton of the offshore waters of the Gulf of Maine. *Bulletin of the United States Bureau of Fisheries* 40: 1-509

Boden B.P. and L.D. Parker (1986) Plankton of the Prince Edward Islands. *Polar Biology* 5: 81-93

Bost C.A., Koubbi P.I., Genevois F., Ruchon L. and V. Ridox (1994) Gentoo penguin *Pygoscelis papua* diet as an indicator of Planktonic availability in the Kerguelen Islands. *Polar Biology* 114: 147-153

Bousfied E.L. (1951) Pelagic Amphipoda of the Belle Isle Strait Region. *Journal of the Fisheries Research Board of Canada* 8: 134 -163

Bowman T.E. (1960) The pelagic amphipod genus *Parathemisto* (Hyperidea: Hyperidae) in the north Pacific and adjacent Arctic ocean. *Proceedings of the United States National Museum.* Smithsonian Institution, Washington, DC, 112: 343-392

Bowman T.E., Cohen A.C. and M.M. McGuiness (1982) Vertical distribution of *Themisto gaudichaudii* (Amphipoda: Hyperiidea) in deepwater dumpsite 106 off the Delaware Bay. *Smithsonian Contributions to Zoology,* Smithsonian Institution Press, Washington, 351: 1-24

Bradford-Grieve J.M., Chang F.H., Gall M., Pickmeres S. and F. Richards (1997) Size-fractionated phytoplankton standing stock and primary production during astral winter and spring 1993 in the Subtropical Convergence Region near New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31: 201-224

Broecker W.S. and T.H. Peng (1982) *Tracers and the sea*. Eldigio Press, New York

Cisewski B., Strass V.H. and H. Prandke (2005) Upper-ocean vertical mixing in the Antarctic Polar Front Zone. *Deep-sea Research II* 52: 1087-1108

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

Dalpadado P., Borkner N., Bogstad, B. and S. Mehl (2001) Distribution of *Themisto* (Amphipoda) species in the Barents Sea and predator-prey interactions. *ICES Journal of Marine Science* 58: 876-895

Dandonneau Y., Deschamps P., Nicolas J., Loisel H., Blanchot J., Montel Y., Thieuleux F. and G. Bécu (2004) Seasonal and interannual variability of ocean colour and composition of phytoplankton communities in the North Atlantic, equatorial Pacific and South Pacific. *Deep-sea Research II* 51: 303-318

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

Ducombe Rae C.M. (1989) Data report of the first cruise of the Marion Offshore Ecological Study (MOES I) *CSIR*, Pretoria, 385pp

Dunbar M..J. (1957) The determinants of production in Northern Seas: a study of the biology of *Themisto libellula* (Mandt.). *Canadian Journal of Research* 35: 797-819

Dunbar M.J. (1964) Euphausiids and pelagic amphipods; distribution in North Atlantic and Arctic waters. *Ser. Atlas, Marine Environ Folio* 6

El-Sayed S.Z. (1988) Seasonal and interannual variability's in Antarctic phytoplankton with reference to krill distribution. In: Sahrhage, D. (ed.) *Antarctic Ocean and resources variability*. Springer-Verlag, Berlin, p 101-119

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

Eppley R.W. and B.J. Peterson (1979) particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282: 677-680

Everson I. and P. Ward (1980) Aspects of Scotia Seas zooplankton. *Zoological Journal of the Linnean Society* 14: 93-101

Fahnenstiel G.L., McCormick M.J., Lang G.A., Radalje D.G., Lohrenz S.E., Marcowitz M., Wagoner B. and H.J. Garrick (1995) Taxon specific growth and loss rates for dominant phytoplankton populations from the northern Gulf of Mexico. *Marine Ecology Progress Series* 117: 229-239

Falkowski P.G. (2002) The Ocean’s invisible forest. *Scientific America* 287: 54-62

Falkowski P.G., Barber R.T. and V. Smetacek (1998) Biochemical controls and feedbacks on ocean primary production. *Science* 281: 200-206

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

Froneman P.W. and Ansorge I.J. (1998) The third Marion Island Oceanographic Study (MIOS III) conducted during April/May 1998. *South African Journal of Science* 94: 437-439

Froneman P.W. and E.A. Pakhomov (1998) Biogeographic study of the Planktonic communities of the Prince Edward Islands. *Journal of Plankton Research* 20: 653-669

Froneman P.W., Pakhomov E.A., Perissinotto R. and C.D. McQuaid (1996) Role of microplankton in the diet and daily ration of Antarctic zooplankton species during austral summer. *Marine Ecology Progress Series* 143: 15-23

Froneman P.W., Pakhomov E.A., Perissinotto R., Laubsher R.K. and C.D. McQuaid (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., Ansorge I.J., Pakhomov E.A. and J.R.E. Lutjeharms (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 A. Treasure (2000) Trophic importance of the hyperiid amphipod, *Themisto gaudichaudii*, in the Prince Edward Archipelago (Southern Ocean) ecosystem. *Polar Biology* 23: 429-436

Froneman P.W., Laubscher R.K. and C.D. McQuaid (2001) Size-fractionated primary production in the south Atlantic and Atlantic sectors of the Southern Ocean. *Journal of Plankton Research* 23: 611-622

Froneman P.W., Pakhomov E.A., Gurney L.J. and B.P.V. Hunt (2002) Predation impact of carnivorous macrozooplankton in the vicinity of the Prince Edward Island archipelago (Southern Ocean) in austral summer 1998. *Deep-Sea Research II* 49: 3243-3254

Froneman P.W., Pakhomov E.A. and M.G. Balarin (2004) Size-fractionated phytoplankton biomass, production and biogenic carbon flux in the eastern Atlantic sector of the Southern Ocean in late austral summer 1997-1998. *Deep-sea Research II* 51: 2715-2729

Gibbons M.J., Stuart V. and H.M. Verheye (1992) Trophic ecology of carnivorous zooplankton in the Benguela. *South African Journal of Marine Science* 12: 421-437

Gurney L.S., Froneman P.W., Pakhomov E.A. and C.D. McQuaid (2002) Diel feeding patterns and daily ration estimates of 3 Subantarctic euphausiids in the vicinity of the Prince Edward Islands (Southern Ocean). *Deep-sea Research II* 49: 3207-3227

Hardy A.C. and E.R. Gunther (1935) The plankton of the South Georgia whaling grounds and adjacent waters: 1926-27. *Discovery Report XI*: 1-456

Hayes P.K., Whitaker T.M. and G.E. Fogg (1984) The distribution and nutrient status of phytoplankton in the Southern Ocean between 20º and 70º W. *Polar Biology* 3: 153-165

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

Hiscock M.R., Marra J., Smith Jr. W.O., Goericke R., Meaures C., Vink S., Olsen R.J., Sosik H.M. and Barber R.T. (2003) Primary productivity and its regulation in the Pacific sector of the Southern Ocean. *Deep-sea Research II* 50: 533-558

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

Hopkins T.L. (1985) Food web of an Antarctic midwater ecosystem. *Marine Biology* 89: 197-212

Hunt B.P.V. and G.W. Hosie (2005) Zonal structure of zooplankton communities in the Southern Ocean south of Australia: results from a 2150 km continuous plankton recorder transect. *Deep-sea Research I* 52: 1241-1271

Hunt B.P.V., Pakhomov E.A. and C.D. McQuaid (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

Huntley M.E., Lopez M.D.G. and D.M. Karl (1991) Top predators in the Southern Ocean: a major leak in the biological carbon pump. *Science* 353: 64-66

Ivlev V.W. (1961) *Experimental ecology of the feeding of fishes*. Yale University Press. New Haven, Connecticut. 302pp

Jacques G. (1989) Primary production in the open Antarctic Ocean during the austral summer. A review. *Vie milieu* 39: 1-17

Jochem F.J., Mathot S. and B. Quéguiner (1995) Size-fractionated primary production in the open Southern Ocean in austral spring. *Polar Biology* 15: 381-392

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

Kane J.E. (1966) The distribution of *Parathemisto gaudichaudii* (Guer.), with observations on its life-history in the 0º to 20º E sector of the Southern Ocean. *Discovery Report* 34: 163-198

Kane J.E. (1967) Observations on the moulting and feeding of a hyperiid amphipod. *Crustaceana* 6: 129-132

Karl D.M., Dore J., Lukas R., Michaels A.F., Bates N. and A.H. Knap (2001) Building the long-term picture: The US JGOFS time-series programs. *Oceanography* 14: 6-17

Kim Y.S. (1991) Review of methods for measurement of ecological energy conversion rate by herbivores in offshore and adjacent sea. *Bulletin of the Korean Fisheries Society* 24: 266-271

Kock K.H., Wilhelms H., Everson I. and J. Gröger (1994) Variations in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic). *Marine Ecology Progress Series* 108: 43-57

Korb E. and M. Whitehouse (2004) Contrasting primary production regimes around South Georgia, Southern Ocean: large blooms versus high nutrient, low chlorophyll waters. *Deep-sea Research I* 51: 721-738

Korb R.E., Whitehouse M.J., Thorpe S.E. and M. Gordon (2005) Primary production across the Scotia Sea in relation to the physico-chemical environment. *Journal of Marine Science* 57: 231-249

Labat J., Mayzaud P. and S. Sabini (2005) Population dynamics of *Themisto gaudichaudii* in Kerguelen Islands waters, Southern Indian Ocean. *Polar Biology* 28: 776 - 783

Laubscher R.K., Perrisinotto R. and C.D. McQuaid (1993) Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology* 13: 471-481

Legendre L. (1996) The biological CO_2 pump in seasonally ice-covered waters. Proc. NIPR Symp. *Polar Biol*. 9: 61-74

Legendre L., Gossilin M., Hirche H.J., Kattner G. and G. Rosenberg (1993) Size-fractionated phytoplankton production in the Greenland Sea (75ºN). *Marine Ecology Progress Series* 98: 297-313

Legendre L. and J. Michaud (1998) Flux of biogenic carbon in oceans: size dependant regulation by pelagic food webs. *Marine Ecology Progress Series* 164: 1-11

Lomas M.W. and N.R. Bates (2004) Potential controls on interannual partitioning of organic carbon during the winter/spring phytoplankton bloom at the Bermuda Atlantic time-series study (BATS) site. *Deep-sea Research I* 51: 1619-1636

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

Longhurst A.R. and W.R. Harrison (1989) The biological pump: profiles of Plankton production and consumption in the upper ocean. *Progress in Oceanography* 22: 47-123

Lutjeharms J.R.E. (1985) Location of frontal systems between Africa and Antarctica: some preliminary results. *Deep-sea Research* 32: 1459-1509

Lutjeharms J.R.E. (1990) Temperature profile of the upper ocean layer in the region between Cape Town and Marion Island. *South African Journal of Antarctic Research* 20: 21-32

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

Metzl N., Beauverger C., Brunet C., Goyet C. and A. Poisson (1991) Surface water carbon dioxide in the Southwest Indian sector of the Southern Ocean: highly variable CO_2 source/sink region in summer. *Marine Chemistry* 35: 85-96

Morrow R., Donguy J., Chaigneau A. and S.R. Rintoul (2004) Cold-core anomalies at the Subantarctic front, south of Tasmania. *Deep-sea Research I* 51: 1417-1440

Murphy P.P., Feely R.A., Gammon R.H., Harrison D.E., Kimberley C.K. and L.S. Waterman (1991) Assessment of air-sea exchange of CO_2 in the South Pacific during austral autumn. *Journal of Geophysical Research* 96: 20 455- 20 465

Nagata Y., Michida Y. and Y. Umimura (1988) Variations of positions and structures of the oceanic fronts in the Indian ocean sector of the Southern Ocean in the period from 1965 to 1987. *Antarctic Ocean and resources variability.* Springer, Berlin Heidelberg New York

Nemoto T. and K.I. Yoo (1970) An amphipod *Parathemisto gaudichaudii* as a food of the Antarctic Sei whales. *Scientific Report. Whales Research Institute* 22: 153-158

Pakhomov E.A. and P.W. Froneman (1999) Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean): a new concept for the biomass build up for higher trophic levels. *Marine Biology* 134: 501-515

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

Pakhomov E.A. and R. Perissinotto (1996) Trophodynamics of the hyperiid amphipod *Themisto gaudichaudii* in the South Georgia region during late austral summer. *Marine Ecology Progress Series* 134: 91-100

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

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

Pakhomov E.A., Froneman P.W., Kuun P.J. and M. Balarin (1999b) Feeding dynamics and respiration of the bottom dwelling caridean shrimp *Nauticaris marionis* Bate, 1888 (Crustacea: Decapoda) in the vicinity of Marion Island (Southern Ocean). *Polar Biology* 21: 112-121

Park Y. –H., Charriaud E. and M. Fieux (1998) Thermohaline structure of the Antarctic Surface Water/Winter Water in the Indian sector of the Southern Ocean. *Journal of Marine Systems* 17: 5-23

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

Permitin Y.E. and M.I. Tarverdieva (1972) The food of some Antarctic fish in the South Georgia area. *Journal of Ichthyology* 12: 104-114

Priddle J., Smetacek V. and U. Bathmann (1992) Antarctic marine primary productivity, biochemical carbon cycles and climatic change. *Philosophical Transactions of the Royal Society of London B* 338: 289297

Rintoul S.R. and T.W. Trull (2001) Seasonal evolution of the mixed layer in the Subantarctic Zone south of Australia. *Journal of Geophysical Research* 106: 31 447-31 462

Rodhouse P.G., White M.G. and M.R.R. Jones (1992) Trophic relations of the cephalapod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Front, Scotia Sea. *Marine Biology* 114: 415-421

Sheader M. and F. Evans (1975) Feeding and gut structure of *Parathemisto gaudichaudii* (Guerin) (Amphipoda, Hyperiidea). *Journal of Marine Biological Association, UK.* 55: 641-656

Siegenthaler U. and J.L. Sarmiento (1993) Atmospheric carbon dioxide and the ocean. *Nature* 365: 119-125

Siegfried W.R. (1965) Observations of the amphipod *Parathemisto gaudchaudii* (Guér.) off the West coast of South Africa. *Zoologica Africana* 1: 339-352

Smetacek V., De Bar H.J.W., Bathmann U.V., Lochte K. and M.M. Rugters van der Loeff (1997) Ecology and biogeochemistry of the Antarctic Circumpolar Current during austral spring: a summary of Southern Ocean JGOFS cruise ANTX/6 of RV Polarstern. *Deep Sea Reasearch II* 44: 1-21

Steinberg D.K., Goldthwait S.A. and D.A.H. Hansell (2002) Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. *Deep-sea Research I* 49: 1445-1461

Takahashi T. and A.E.G. Azevedo (1982) The oceans as a CO_2 reservoir. In: Reck R.A., Hummerl J.R. (Eds.) *Interpretation of climate and photochemical models, ozone and temperature measurements.* American Institute of Physics, New York, pp 83-109

Tolomeyev A.P. (2002) Phytoplankton diet of *Arctodiaptomus salinus* (Copepoda,Calanoida) in Lake Shira (Khakasia). *Aquatic Ecology* 36: 229-234

Torres J.J., Aarset A.V., Donnelly J., Hopkins T.L., Lancraft T.M. and D.G. Ainley (1994) Metabolism of Antarctic micronenktonic crustacea as a function of depth of occurrence and season. *Marine Ecology Progress Series* 113: 207-219

Tremblay J.E., Lucas M.I., Kattner G., Pollard R., Strauss V.H., Bathmann U. and A. Bracher (2002) Significance of the Polar Frontal Zone for large-sized diatoms and new production during summer in the Atlantic sector of the Southern Ocean. *Deep-sea Research II* 49: 3793-3811

Tréguer P. (2002) Silica and the cycle of carbon in the ocean. *C.R. Geoscience* 334: 3-11

Ushakumari V.S. and C.M. Aravindan (1992) food selection and feeding habits of the Asian Cichlid, *Etroplus surantensis* (Bloch), in a tropical lake. *Journal of Aquaculture Tropics* 7: 15-19

Vinogradov G. (1999) Amphipoda In: *South Atlantic Zooplankton.* D. Boltovskoy (Ed) Backuys Publishers, Leiden, The Netherlands. Pp 1141-1240

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

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

Ward P., Shreeve R., Whitehouse M., Korb B., Atkinson A., Meredith M., Pond D., Watkins J., Goss C. and N. Cunningham (2005) The summer zooplankton community at South Georgia: biomass, vertical migration and grazing. *Polar Biology* 15: 195-208

Wefer G. and G. Fisher (1991) Annual primary production and export flux in the Southern ocean from sediment trap data. *Marine Chemistry* 35: 597-613

Williams R. and D. Robins (1979) Caloric, ash, carbon and nitrogen content in relation to length and dry weight of *Parathemisto gaudichaudii* (Amphipoda: Hyperiidea) in the north east Atlantic Ocean. *Marine Biology* 52: 247-252

Wunsch C. and R. Ferrari (2004) Vertical mixing, energy, and the general circulation of the oceans. *Annual Review of Fluid Mechanics* 36: 281-314

APPENDIX

Table A1. Mesozooplankton sampling stations during the DEIMEC III survey, April 2004.

Station #	**Sampling date**	**Sampling depth**	**Latitude**	**Longitude**
B00228	15-04-2004	200 m	48°5	30°11
B00229	15-04-2004	300 m	48°08	29°58
B00231	15-04-2004	200 m	49°59	31°03
B00234	16-04-2004	300 m	49°29	31°
B00236	16-04-2004	200 m	49°	31°
BOO237	16-04-2004	200 m	48°29	31°83
B00238	17-04-2004	200 m	48°	32°17
B00239	17-04-2004	300 m	48°4	31°09
B00240	17-04-2004	303 m	48°59	30°38
B00241	17-04-2004	200 m	49°19	30°05
B00242	17-04-2004	200 m	49°4	29°32
B00243	18-04-2004	300 m	50°	29°
B00244	18-04-2004	300 m	49°	29°13
B00248	20-04-2004	302 m	49°	29°59
B00256	23-04-2004	200 m	49°51	32°27

Table A2. Mesozooplankton sampling stations during the DEIMEC iv study, April 2005

Stat #	Latitude	Longitude	Area within Eddie	Surface waters
259	49.25.03	30.55.56	out	Sub-antarctic surface H2O
260	49.08.62	32.36.12	out	Sub-antarctic surface H2O
261	48.47.76	33.12.91	out	Sub-antarctic surface H2O
262	48.27.63	33.37.06	edge	MIX
263	48.07.40	34.08.91	edge	MIX
264	47.47.27	34.45.45	out	Sub-antarctic surface H2O
265	47.46.04	33.00.34	out	Sub-antarctic surface H2O
266	48.09.78	33.26.23	edge	Mix
267	48.32.49	34.02.99	edge	Mix
268	48.52.62	34.04.73	edge	Mix
269	49.19.06	34.30.10	edge	Mix
270	49.44.83	35.04.62	out	Sub-antarctic surface H2O
271	49.56.06	35.22.34	out	Sub-antarctic surface H2O
272	49.24.33	35.22.61	out	Sub-antarctic surface H2O
273	48.54.82	35.19.48	in	Antarctic surface H2O
274	48.34.35	35.05.04	in	Antarctic surface H2O
275	48.05.19	35.02.14	edge	Mix
276	48.21.73	34.46.84	in	Antarctic surface H2O
277	48.37.58	34.28.02	in	Antarctic surface H2O
278	48.54.87	34.06.71	edge	Mix
279	49.09.87	33.56.95	edge	Mix
280	49.40.24	34.00.89	out	Sub-antarctic surface H2O
282	48.46.35	33.34.58	edge	Mix
283	48.45.87	33.58.77	in	Antarctic surface H2O
284	48.43.78	34.31.61	in	Antarctic surface H2O
285	45.45.09	35.01.81	in	Antarctic surface H2O
286	48.46.65	35.29.27	in	Antarctic surface H2O
288	48.07.91	35.54.96	out	Sub-antarctic surface H2O
290	48.46.05	36.12.03	out	Sub-antarctic surface H2O
291	48.56.65	36.20.36	out	Sub-antarctic surface H2O

Table A3. The feeding impact of the amphipod *Themisto gaudichaudi* at each of the stations occupied during the 2004 DEIMEC III survey.

Station Number	**Feeding rate (ind.d-1)**	**Abundance of *T. gaudichaudii (ind.m-3)***	**Abundance of mesozooplankton (ind.m-3)**	**Daily impact (individual copepods.d-1. l-1)**
228	20.90	0.11	869.46	0.02
229	17.57	0.01	357.38	<0.01
231	18.46	0.03	244.99	<0.01
234	16.76	0.04	206.23	<0.01
236	19.42	0.08	394.76	0.02
238	15.84	0.16	91.32	0.03
239	11.45	0.01	50.58	<0.01
240	17.43	0.01	321.27	<0.01
243	14.94	0.01	121.26	<0.01
244	19.80	0.02	593.99	<0.01
248	18.54	0.05	268.91	<0.01
256	16.71	0.01	302.40	<0.01