Euphausiid population structure and grazing in the Indian sector of the Antarctic Polar Frontal Zone, during austral autumn

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Abstract

The trophodynamics of the numerically dominant euphausiid species within a region of high mesoscale oceanographic variability in the southwest Indian sector of the Antarctic Polar Frontal Zone (PFZ) were investigated during the austral autumns April/May) of 2004 and 2005.

During the 2004 survey, sub-surface (200 m) temperature profiles indicated that an intense frontal feature, formed by the convergence of the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF) bisected the survey area into two distinct zones, the Sub-Antarctic Zone (SAZ) and the Antarctic Zone (AAZ). Total integrated chlorophyll-*a* (chl-*a*) biomass was typical for the region (< 25 mg chl-*a* m^{-2}), and was dominated by picophytoplankton. Total euphausiid abundance and biomass ranged from 0.1 to 3.1 ind m^{-3} and 0.1 to 8.1 mg dwt m^{-3}, respectively, and did not differ significantly between the stations occupied in the SAZ and AAZ ($p > 0.05$). The multivariate analysis identified two interacting mechanisms controlling the distribution patterns, abundance and biomass of the various euphausiid species, namely (1) diel changes in abundance and biomass, (2) and restricted distribution patterns associated with the different water masses. Ingestion rates were determined for five euphausiid species. *E. triacantha* was found to have the highest daily ingestion rate ranging from 1 226.1 to 6 029.1 ng pigm $ind^{-1}d^{-1}$, while the lowest daily ingestion rates were observed in the juvenile *Thysanoessa* species (6.4 to 943.0 ng pigm $ind^{-1}d^{-1}$). The total grazing impact of the selected euphausiids ranged from < 0.1 to 20.1 µg pigm $m^{-2}d^{-1}$, corresponding to < 0.15 % of the areal chl-*a* biomass. The daily ration estimates of autotrophic carbon for the euphausiids suggested that phytoplankton represented a minor component in their diets, with only the sub-adult *E. vallentini* consuming sufficient phytoplankton to meet their daily carbon requirements.

A cyclonic cold-core eddy spawned from the region of the APF located in the southwest Indian sector of the PFZ was the dominant feature during the 2005 survey. The total areal chl-*a* biomass throughout the region was low, ranging between 5.6 and 11.4 mg chl-*a* m^{-2}, and was significantly higher within the core of the eddy compared to the surrounding waters ($p < 0.05$). RMT-8 and WP-2 total euphausiid abundance and biomass estimates were high, and ranged from 0.004 to 0.36 ind m^{-3} and 0.065 to 1.21 mg dwt m^{-3}, and from 0.01 to 18.2 ind m^{-3} and 0.01 to 15.7 mg dwt m^{-3}, respectively. A distinct spatial pattern in the euphausiid community was evident with the Antarctic species, *Euphausia frigida*, *E. triacantha* and *E. superba* predominating within the core of the eddy, while the PFZ waters were characterized by the sub-Antarctic species, *E. longirostris*, *Stylocheiron maximum*, *Nematoscelis megalops* and *Thysanoessa gregaria*. The eddy edge acted as a transition zone where species from both regions co-occurred. Within the survey area the combined ingestion rate of the six numerically dominant euphausiid species ranged between 0.02 and 5.31 µg pigm $m^{-2}d^{-1}$, which corresponded to a loss of between < 0.001 and 0.11 % of the available chl-*a* biomass. *E. triacantha* and juvenile *T. macura* were identified as the dominant grazers. There was no apparent spatial pattern in the grazing activity of the euphausiids within the region of investigation. The average daily rations of the euphausiids examined were < 2 % of their body carbon. The low daily ration of the euphausiids could be ascribed to the predominance of small picophytoplankton in the region of investigation, which are too small to be grazed efficiently by larger zooplankton. The marked spatial patterns in species composition and the elevated abundance and biomass of euphausiids, suggest that the mesoscale eddies contribute to the spatial and temporal heterogeneity of the planktonic community of the PFZ and may represent important foraging regions for many of the apex predators within the region.

Chapter 1: Introduction

General introduction

The biological pump

The world oceans, due to their large size, are thought to play a critical role in regulating the global carbon cycle (Siegenthaler and Sarmiento, 1993). Carbon taken up in the surface waters by phytoplankton is transported to the bottom of the ocean by the biological and solubility pumps (Longhurst, 1991; Le Fevre *et al*., 1998). Although the solubility pump (the transport of carbon to depth via rapidly sinking surface water) is thought to represent the major source of carbon flux, it is limited to regions of downwelling at oceanic fronts and close to the poles, where formation of dense fast sinking water, such as Antarctic Bottom Water and North Atlantic Deep Water occurs (Le Fevre *et al*., 1998).

The biological pump involves the production and export of dissolved and particulate organic carbon to depth through the processes of photosynthesis by phytoplankton, the sinking of dead and senescent phytoplankton and the grazing and migratory behaviour of zooplankton (Longhurst, 1991; Fortier *et al*., 1994). The sinking of dead or senescent phytoplankton cells is thought to contribute to vertical carbon flux in areas of high productivity, including the oceanic fronts, the marginal ice zone and the waters surrounding the oceanic islands (Longhurst, 1991). Within the open waters of the ocean, the active grazing of phytoplankton by larger zooplankton is considered the most important mechanism for transporting carbon to depth (Longhurst, 1991; Fortier *et al*., 1994; Le Fevre *et al*., 1998).

The efficiency of the biological pump is determined by the rate at which carbon is transferred from the surface waters to depth, generally below the pycnocline (Longhurst, 1991; Fortier *et al*., 1994; Le Fevre *et al*., 1998). Biogenic carbon within the oceans can be grouped into three pools according to the amount of time that the carbon is removed form the atmosphere (Fig 1.1) (Fortier *et al*., 1994).

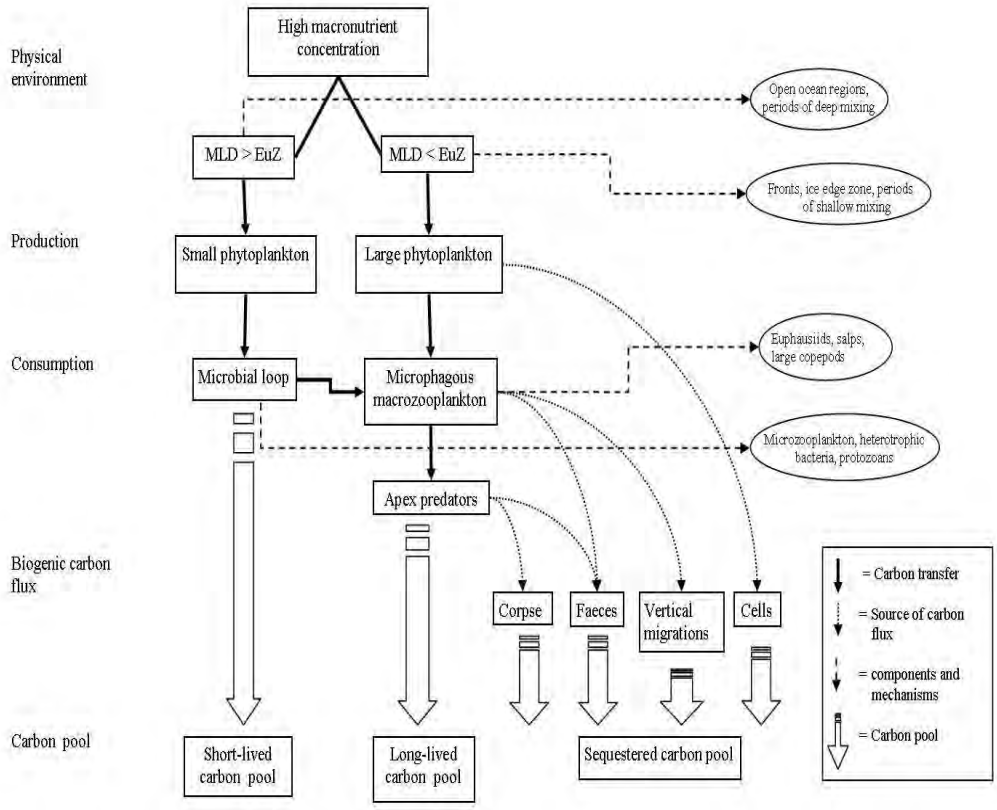


Figure 1.1: Schematic flow diagram reflecting selected pathways of carbon flow through the oceanic food webs of the Southern Ocean. The major sources of carbon flux and the partitioning of carbon amongst the different carbon pools are indicated. MLD = mixed layer depth, EuZ = euphotic zone

The short-lived (< 10^{-2} years) carbon pool transits mainly through small phytoplankton cells (< 5 µm) and the microbial food web (Longhurst, 1991; Fortier *et al*., 1994). Long-lived organic carbon (10^{-2} to 10^{2} years) flows through large phytoplankton cells (> 5 µm) and the

associated primary and secondary consumers (i.e. macrozooplankton and fish and birds) that make up the classical oceanic food web (Fortier *et al*., 1994). The carbon incorporated into the sequestered carbon pool (> 10^2 years) can take on various forms, including organic remains buried in the sediment and inorganic deposits of biological origin such as coral reefs (Fortier *et al*., 1994). In the microbial loop, cycling of organic material is finite because all the organisms involved rematerialize the organic carbon obtained from the local primary production of pico- and nano sized phytoplankton cells (Fig 1.1) (Le Fevre *et al*., 1998). As a result, the export of biogenic carbon to depth and larger organisms is restricted to meso- (200 – 2000 μm) and macrozooplankton (> 2000 μm) feeding on the heterotrophic components of the microbial loop, i.e. microzooplankton (Le Fevre *et al*., 1998).

In the classical food web, large phytoplankton cells are actively grazed by meso- and macrozooplankton, which are in turn are food for apex predators such as birds, fish, seals and whales (Le Fevre *et al*., 1998). Under conditions where the classical food web predominates, flux of biogenic carbon to depth is expected to be high due to the relatively faster sinking rates of the large phytoplankton cells together with the extensive vertical migrations that the macrozooplankton undertake and the production of large fecal pellets with quick sinking rates (Fortier *et al*., 1994; Le Fevre *et al*., 1998). Accordingly the partitioning of available carbon between the different size classes of phytoplankton and more importantly the associated food webs that these carbon sources support, plays an integral role in determining efficiency of the biological pump (Fig 1.1) (Longhurst, 1991; Fortier *et al*., 1994; Le Fevre *et al*., 1998; Froneman; 1995).

Physical structure of the Southern Ocean

Within the Southern Ocean, frontal boundaries separate distinct physical environments and planktonic assemblages (Deacon, 1982; Froneman *et al*., 1995; Pakhomov and McQuaid, 1996; Pakhomov *et al*., 2000). At the northern limit of the Southern Ocean lies the sub-Tropical Convergence (STC). South of the STC, the Antarctic Circumpolar Current (ACC) flows eastward unabated around the globe (Deacon, 1982; Orsi *et al*., 1995). The ACC itself can be divided into regions of intensified flow, or current cores, associated with three major frontal systems, the sub-Antarctic Front (SAF), the Antarctic Polar Front (APF) and the Southern ACC front (Deacon, 1982- although SF referred to as Weddell-Scotia Front; Orsi *et al*., 1995). From a biological perspective the fronts are of particular importance because they often represent biogeographic boundaries to the distribution of plankton species and are associated with elevated productivity and biological activity that is reflected in the biomass of all the trophic levels of the pelagic food web (Pakhomov and McQuaid, 1996; Pakhomov *et al*., 2000). In contrast, the regions between the fronts are characterized by reduced flow, with episodic mesoscale disturbances including eddies and meanders generated from the frontal regions, creating a highly dynamic oceanographic environment (Ansorge and Lutjeharms, 2002; Read *et al*., 2002; Ansorge and Lutjeharms, 2003; Ansorge *et al*., 2004).

Antarctic Polar Frontal Zone (PFZ)

The PFZ is an inter-frontal region within the ACC, and is bounded by the SAF to the north and the APF to the south (Deacon, 1982; Orsi *et al*., 1995). The PFZ is characteristic of a transition zone blending water masses and plankton from the sub-Antarctic waters to the

north with the Antarctic water to the south (Ansorge and Lutjeharms, 2003; Ansorge *et al.*, 2004).

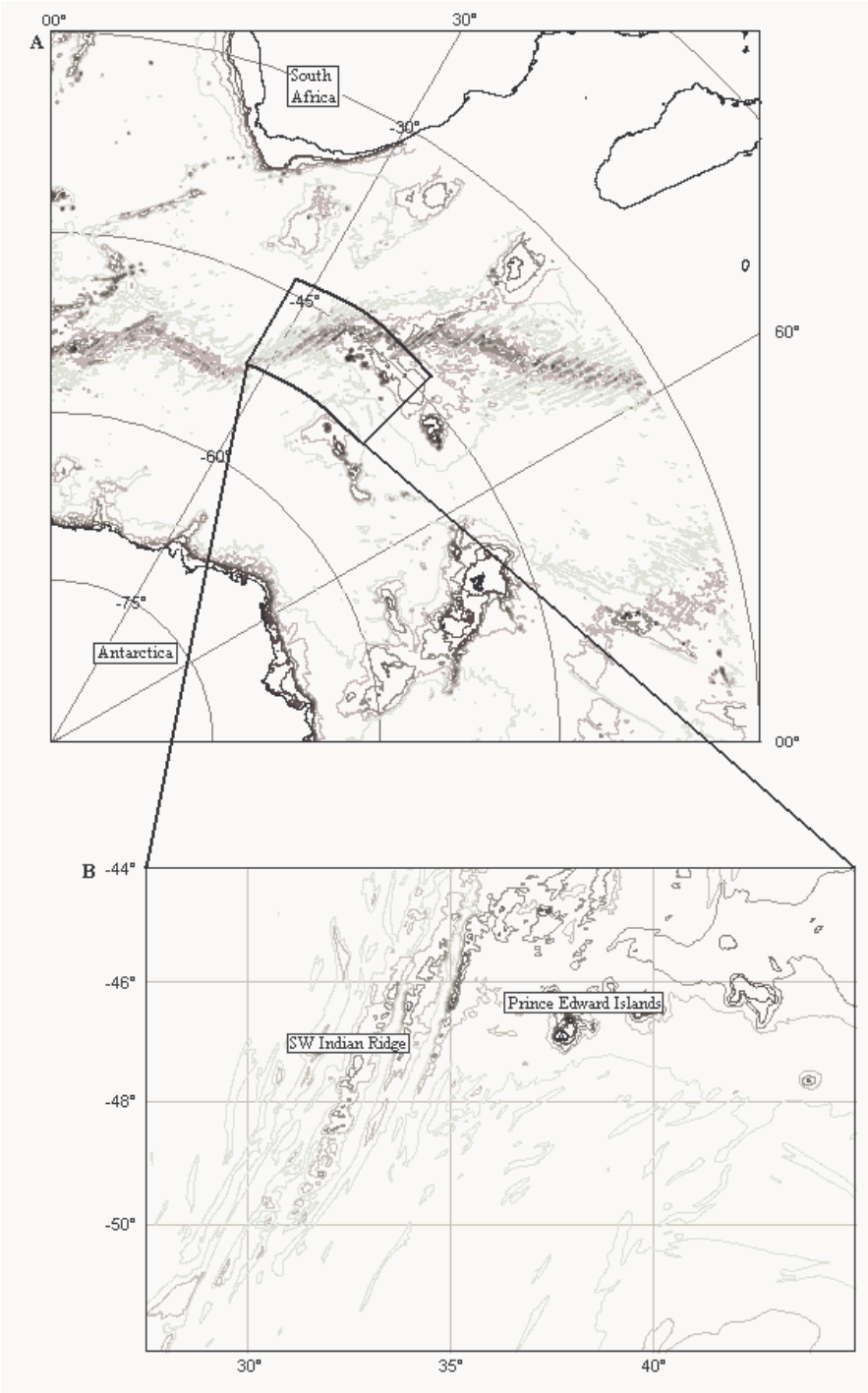


Figure 1.2: A – Map showing the bathymetry (0 – 3000 m) of the Indian sector of the Southern Ocean. B – Location of the Prince Edward Islands in relation to the South West Indian Ridge.

It has long been established that the path of the ACC is strongly influenced by prominent topographic features, including the Southwest Indian Ridge (SWIR) (Fig 1.2) and the Pacific-Antarctic Ridge (Gordon *et al.*, 1978; Deacon, 1979; Orsi *et al.*, 1995). Not only is the ACC topographically steered around or between fracture zones in the ridges, the disturbance in flow caused by the currents intensification, and the bunching of the SAF and APF, results in the formation of meanders and eddies in the lee of the ridges (Pollard and Read, 2001; Ansorge and Lutjeharms, 2003). Downstream of the SWIR the position of the SAF and the APF are particularly variable, often merging into a single feature for short periods (Read and Pollard, 1993; Park and Gamberoni, 1995; Ansorge and Lutjeharms, 2003; Ansorge *et al.*, 2004). Recent hydrographic and altimetric studies have provided evidence that this region represents an area of enhanced eddy, both cyclonic (cold-core) and anti-cyclonic (warm-core), formation (Ansorge and Lutjeharms, 2003; Ansorge *et al.*, 2004). Once formed the cyclonic eddies originating from the APF and anti-cyclonic eddies originating from the SAF are advected into the PFZ (Ansorge and Lutjeharms, 2003).

Productivity in the Southern Ocean

Within the open waters of the Southern Ocean the Antarctic paradox exists whereby productivity is greatly reduced in relation to the availability of major plant nutrients (Strass *et al.*, 2002). A number of potentially interacting factors are thought to contribute to the apparent pattern, including light limited phytoplankton growth due to wind induced deep mixing (Falkowski *et al.*, 1998), low concentrations of trace metals such as iron (Boyd *et al.*, 2000; Strass *et al.*, 2002), as well as zooplankton grazing (Dubischar and Bathmann, 1997). On the other hand, the elevated levels of phytoplankton biomass in the fronts of the ACC have been attributed to advection and accumulation of phytoplankton cells in the region of

the front (Pollard *et al.*, 1995), isopycnal advection of nutrients into the surface waters (Garcon *et al.*, 2001), and increased water column stability (Strass *et al.*, 2002). As with frontal regions, oceanic eddies are associated with upwelling of nutrients along sloping isopycnal surfaces, termed "eddy pumping" (Falkowski *et al.*, 1991; McGillicuddy Jn *et al.*, 1998; Garcon *et al.*, 2001; Uz *et al.*, 2001). The geostrophic flow patterns within eddies and fronts share a number of common properties and as a result it is thought that the eddies may demonstrate higher levels of production compared to the surrounding waters (Read *et al.*, 2002). Although oceanic eddies have been observed on a number of occasions in the Southern Ocean (Peterson *et al.*, 1982; Gouretski and Danilov, 1993; Read *et al.*, 2002; Ansorge and Lutjeharms, 2003) the controls of productivity within the cold and warm core features has not been satisfactorily addressed.

Plankton of the Polar Frontal Zone

The PFZ is characterized by low levels of chlorophyll biomass (generally < 25 mg chl-*a* m^{-2}), and zooplankton communities that display a high degree of spatial and temporal variability in biomass and species composition, which is inherently linked to the mesoscale disturbances in the frontal jets that delineate the region (Perissinotto, 1992; Pakhomov and McQuaid, 1996; Froneman and Pakhomov, 1998; Ansorge *et al.*, 1999; Hunt *et al.*, 2001; Bernard and Froneman, 2005). The representative plankton community of the PFZ is not endemic to the region with sub-tropical, sub-Antarctic and Antarctic species of origin being present at any one time (Frost *et al.*, 1976; Lutjeharms and Vallentine, 1984; Allanson *et al.*, 1985; Perissinotto and Boden, 1989; Froneman and Ansorge, 1998; Froneman and Pakhomov, 1998; Pakhomov and Froneman, 1999). In general, small phytoplankton cells, the pico- and nanophytoplankton (< 20 µm), predominate throughout the PFZ (80 – 90 % of total surface

chl-*a*), which can be attributed to the persistence of a wind induced deep mixed layer depth, restricting microphytoplankton growth rates and increasing the relative contribution of small cells to the total phytoplankton community (Atkinson, 1996; Froneman *et al*., 1999; Strass *et al*., 2002; Bernard and Froneman, 2003; Bernard and Froneman, 2005). The occurrence of large phytoplankton cells (> 20 µm) is spatially and temporally limited to regions where nutrient upwelling and a shallowing of the mixed layer depth create more favorable conditions for growth, such as the frontal systems that delimit the PFZ and in the vicinity of the oceanic islands which demonstrate the so called "island mass effect" (Deacon, 1982; Perissinotto and Duncombe Rae, 1990; Pakhomov and Froneman, 2000; Pakhomov *et al*., 2000). In these regions, the large cells can contribute in excess of 50 % to the total surface phytoplankton concentration (Pakhomov *et al*., 1997; Perissinotto *et al*., 1997; Froneman *et al*., 1999).

The mesozooplankton, comprising mainly copepods, pteropods and chaetognaths, are numerically and by biomass the dominant component of the zooplankton assemblage within the PFZ (Pakhomov *et al*., 2000; Bernard and Froneman, 2005). Although the macrozooplankton and micronekton in general contribute little to the total zooplankton abundance (generally <10 %; Pakhomov and Froneman, 1999), by virtue of their size their contribution to the total zooplankton biomass can often be considerable (Pakhomov and Froneman, 1999; Pakhomov and Froneman, 2000). This, for example is particularly evident in the frontal regions where the contribution of macrozooplankton (mainly euphausiids) and micronekton to the total zooplankton biomass ranges between 30 and 40 %, while in the open waters of the PFZ macrozooplankton and micronekton generally contribute < 20 % to the total zooplankton biomass (Pakhomov *et al*., 1999; Pakhomov and Froneman, 2000; Pakhomov *et al*., 2000).

Euphausiids

Euphausiids are considered to be an integral component of the macrozooplankton community of the PFZ and indeed the Southern Ocean (Pakhomov and Froneman, 1999; Hosie *et al*., 2000; Pakhomov and Froneman, 2000; Fisher *et al*., 2004). A considerable number of publications have addressed various aspects of euphausiid trophodynamics within the more productive regions of the Southern Ocean, particularly around the oceanic islands such as South Georgia (Ward *et al*., 2003; Pakhomov *et al*., 1994) and the Prince Edward Islands (Perissinotto, 1992; Gurney *et al*., 2002; Hunt and Pakhomov, 2003), the marginal ice zone (Perissinotto *et al*., 1997) and the waters off the Antarctica (Pakhomov and Perissinotto, 1996; Hosie *et al*., 2000; Fisher *et al*., 2004; Pakhomov *et al*., 2004). Only recently have studies begun to investigate the role of euphausiids in the less productive open waters of the Southern Ocean (see for example, Pakhomov and Froneman, 2004), while no research has specifically addressed the trophodynamics of euphausiids in the mesoscale oceanographic features, such as meanders in the fronts of the ACC and the eddies that propagate into the inter-frontal regions.

As with the majority of zooplankton in the Southern Ocean, the horizontal distribution patterns of euphausiids is related to the presence of strong biogeographic boundaries represented by the main frontal features, most notably the APF (Mauchline and Fisher, 1969; Deacon, 1982; Pakhomov *et al*., 2000). The view that the PFZ represents a transition zone between the water masses and plankton communities of the sub-Antarctic and Antarctic waters is again reflected in the euphausiid community with species of sub-tropical, sub-Antarctic and Antarctic origin co-occurring at any one time (Pakhomov and Froneman, 2000; Gurney *et al*., 2002; Hunt and Pakhomov, 2003). Thus although the euphausiid community

within the PFZ is generally dominated by *Euphausia vallentini* (Stebbing, 1990) and *Thysanoëssa vicina* (Hansen, 1911) and/or *T. macura* (GO Sars, 1883), species such as *E. longirostris* (Hansen, 1908), *E. similis* (GO Sars, 1883), *T. gregaria* (GO Sars, 1883), *Nematoscelis megalops* (GO Sars 1883) and *Stylocheiron maximum* (Hansen, 1908) periodically occur at high densities within the region (Fig 1.3) (Froneman *et al*., 1999; Pakhomov and Froneman, 2000; Gurney *et al*., 2002).Similarly, the abundance and biomass estimates of euphausiids within the PFZ displays a high degree of spatial (*c*. 0.1 – 5.9 ind m^{-3}; Froneman *et al*., 2002) and temporal (1999 – *c*. 0.6 ind m^{-3}, 1998 = *c*. 2.2 ind m^{-3}; Gurney, 2000) variability.

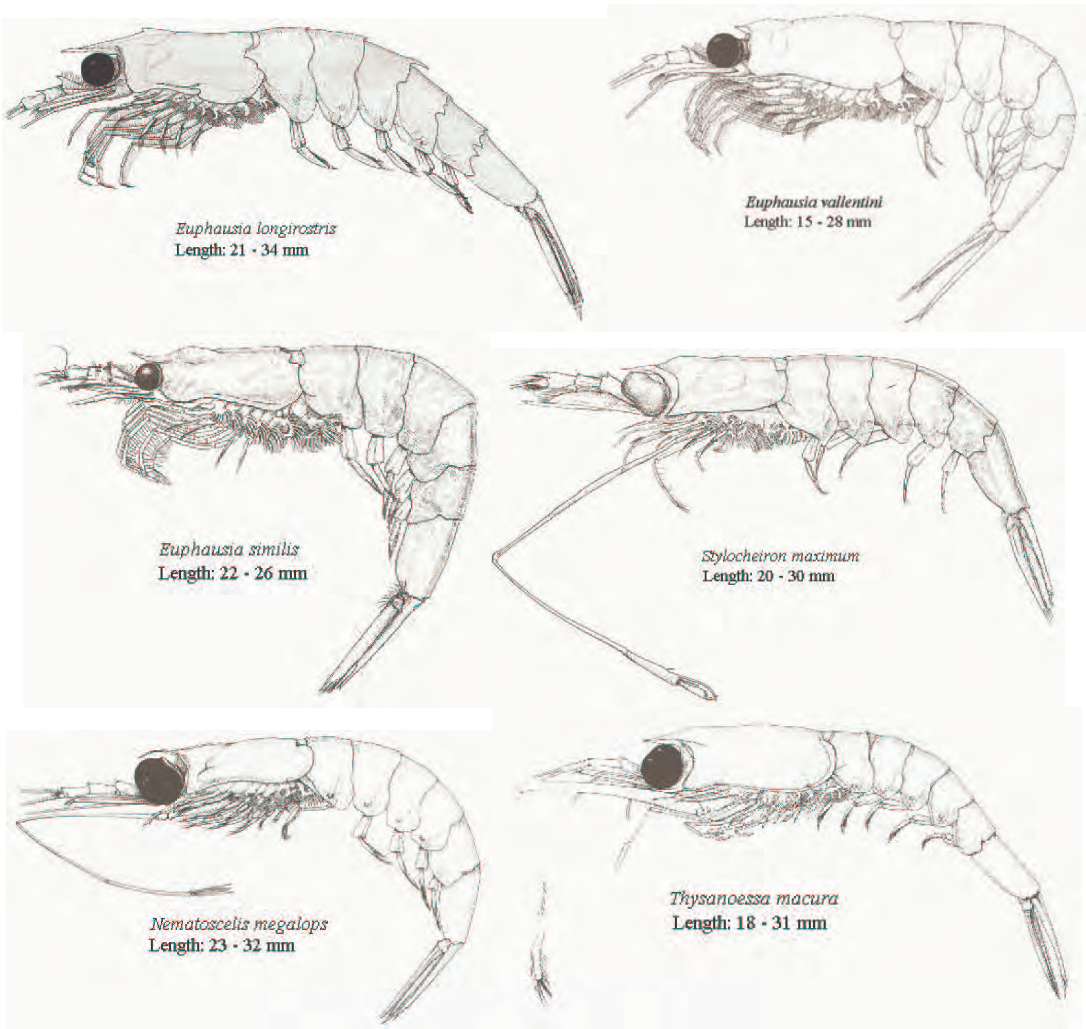


Figure 1.3: Sketches of the dominant species of euphausiid found in the Indian sector of the Antarctic Polar Frontal Zone (After Baker *et al*., 1990).

Most euphausiids are thought to be opportunistic omnivores (Mauchline and Fisher, 1969; Pilditch and McClatchie, 1994) and are the key prey items for many of the top marine predators, such as birds, seals, whales, fish and squid (Brown *et al*., 1990; Cooper and Brown, 1990; Kear, 1992; Perissinotto and McQuaid, 1992; Bost *et al*., 1994, Watanuki *et al*., 1994). Euphausiids are maxillary feeders and make use of highly setose mouthparts as well as the first and second thoracic limbs, together termed the feeding basket, to collect food particles, drawn toward the animal by feeding currents created by the pleopods (Mauchline and Fisher, 1969). It is possible to infer food preferences by the structure of the mouth parts of different species of euphausiid, with species in the genera of *Euphausia* and *Thysanoëssa* being characterized by heavily setose mouthparts and therefore suited to filter feeding (Mauchline, 1967; Mauchline and Fisher, 1969). On the other hand mouthparts of species in the genera of *Nematoscelis* and *Stylocheiron* are less setose and thus not as well adapted to filter feeding (Mauchline, 1967; Mauchline and Fisher, 1969). In addition species in the genera *Thysanoëssa*, *Nematoscelis* and *Stylocheiron* have greatly elongated second thoracic limbs together with bilobed eyes, and it has been suggested that these modifications are for a carnivorous feeding mode (Mauchline, 1980).

The ingestion rates of euphausiids show a high degree of seasonal and inter-species variability, ranging between 0.15 and 12.51 µg pigm $ind^{-1}d^{-1}$, while the grazing impact on the phytoplankton biomass seldom exceeds 5 % (Table 1.1) (Pakhomov and Perissinotto, 1996; Pakhomov *et al*., 1997;Perissinotto *et al*., 1997;Perissinotto *et al*., 2001; Gurney *et al*., 2002; Pakhomov *et al*., 2004; Pakhomov and Froneman, 2004). Feeding studies have shown that phytoplankton rarely constitutes a major component in the diet of euphausiids in the PFZ (< 5 % of body carbon per day), due partly to the unfavorable size structure of phytoplankton

(pico- and nanophytoplankton), which predominates within the region (Perissinotto, 1992; Pakhomov *et al*., 1997; Gurney *et al*., 2002; Pakhomov and Froneman, 2004).

Table 1.1: Estimates of euphausiid ingestion rates and grazing impacts taken from the literature for selected regions in the Southern Ocean. Asterix (*) = grazing impact under swarm conditions.

Author	Chl-*a* biomass (mg chl-*a* m^{-2})	Euphausiid ingestion rate (mg pigm $m^{-2}d^{-1}$)	Grazing impact %	Species
Pakhomov and Perissinotto, 1996	90.0 - 520.0	/	0.002 - 0.28, max 5 %*	*E. crystallorophias*
Pakhomov *et al*., 1997	32.8 - 333.2	0.09 - 0.324	0.08 - 1.23	*E. triacantha, E. frigida, Thysanoessa spp.*
Perissinotto *et al*., 1997	/	/	0.01 - 2.68	*E. superba*
Pakhomov and Froneman, 2004	20.0 - 53.9	/	0.02 - 0.61	*Thysanoessa* and *Euphausia spp*

On the other hand, under conditions where large microphytoplankton contribute most to the total areal biomass, euphausiids such as *E. superba* and *E. vallentini* adults and juveniles appear to be able to meet their daily food requirements on an autotrophic diet (5 – 45 % of body carbon per day) (Perissinotto *et al*., 1997; Gurney *et al*., 2002; Pakhomov *et al*., 2004). These findings are supported by isotope analysis, which show juvenile *E. vallentini* to be mainly herbivorous, while the diets of adult *E. vallentini* and *E. longirostris* appear to contain a significant heterotrophic component (Gurney *et al*., 2001).

Islands and Predators

Within the Southern Ocean numerous isolated oceanic islands are seasonally home to several million marine foraging top predators, including penguins, flying seabirds and several species of piniped (Ridoux, 1988; Pakhomov and Froneman, 1999). The Prince Edward Island (PEI) archipelago, consisting of Marion and Prince Edward, are situated downstream from the

SWIR (Fig 1.1B) at the northern border of a region of high mesoscale oceanographic variability in the PFZ. A number of past studies have identified the inter-island region (Allanson *et al*., 1985; Boden, 1988; Perissinotto and Duncombe Rae, 1990), as well as the SAF and APF to the north and south of the islands (Pakhomov *et al*., 2000; Perissinotto *et al*., 2000), as important foraging grounds for top predators on the islands due to the elevated zooplankton and nekton stocks within the regions. Recently, eddies spawned from the APF and the SAF have drawn attention for their possible role of advecting large volumes of plankton biomass from the region of the fronts to the PEI. Indeed, these features have been identified as foraging grounds for grey-headed Albatross that nest on the islands (Nell *et al*., 2001).As yet no research has investigated the biological characteristics of these features in relation to the surrounding water mass in the PFZ.

Motivations and aims

Euphausiids have been identified as key components of the zooplankton assemblages of the PFZ. Furthermore they not only appear to be an important food source for many marine and terrestrial predators, they also have the ability to feed on the basal trophic level, the phytoplankton, in the pelagic food web of the Southern Ocean. This has a number of important implications, firstly it creates an efficient means of carbon transfer to the apex predators, and in addition it has the potential to enhance the localized efficiency of the biological pump, as euphausiid are microphagous, produce fast sinking fecal material and undertake extensive diel vertical migrations.

Meanders in fronts and eddies appear to have the ability to enhance productivity on a local scale. Thus, in a region where productivity is limited, such as the PFZ, these features may

represent localized “oases” that not only contribute to the habitat and species heterogeneity, but also have the potential to augment carbon transfer to predators and flux to depth.

This thesis provides a report on various aspects of the population structure, distribution patterns and feeding biology of the dominant component of the macrozooplankton community, the euphausiids, together with the chlorophyll-*a* and oceanographic environments encountered during two surveys of the South African National Antarctic Program (SANAP) conducted during the austral autumns of 2004 and 2005.

The main aims of the research are to:

1 – Determine the influence of mesoscale oceanographic variability in the form of meanders and eddies on the species distribution patterns of the numerically dominant euphausiids within the PFZ.

2 – To investigate the herbivorous feeding dynamics of the numerically dominant euphausiids recorded within the regions of mesoscale oceanographic variability.

Analytical techniques

Environmental parameters

For the purpose of this study, univariate and multivariate analytical methods were employed to determine the extent to which samples differed in terms of (1) total euphausiid abundance and biomass and (2) euphausiid species composition and species-specific abundance and

biomass. For the statistical analysis two grouping parameters were placed on the euphausiid data. Samples were grouped according to (1) their geographic location within the different water masses encountered during the two surveys, and (2) whether the samples were collected during the daytime or the nighttime.

The present study was conducted in a region of high mesoscale oceanographic variability in the PFZ, which is known to be a strong biogeographic boundary to many of the plankton species, including euphausiids (Deacon, 1982; Pakhomov and McQuaid, 1996). Moreover euphausiids are known to undertake extended diel vertical migrations, which significantly affect the observed distribution patterns in the oceanic environment (Mauchline and Fisher, 1969; Mauchline, 1980; Vinogradov, 1997). Although it is possible that a number of variables, including physiological restrictions and biological interactions, which could influence the distribution patterns of euphausiids at a local scale may have been overlooked, the parameters selected, namely region and period, appear to be dominant factors affecting patterns in plankton abundance and biomass on a broad scale, and are thus deemed suitable and sufficient to meet the aims of this study stipulated above.

Multivariate analyses are an effective method of extracting valuable biological information from complex data sets and are widely used to investigate the distribution patterns of plankton in the Southern Ocean (Atkinson *et al*., 1990; Froneman *et al*., 1999; Pakhomov *et al*., 2000; Hunt *et al*., 2002; Ward *et al*., 2003; Ward *et al*., 2004; Bernard and Froneman, 2005). Multivariate analyses base their comparisons of two or more samples on the extent to which the samples share particular species at similar levels of abundance and/or biomass (Clarke and Warwick, 1994). This allows a matrix of similarity coefficients to be constructed that can either be clustered in the form of a dendogram or mapped in the form of an

ordination plot which reflect the relative dissimilarity of species composition (Clarke and Warwick, 1994). Following this, differences between site and conditions can be identified using "non-classical hypothesis testing" as it is invalid to make the standard assumption of normality when performing a multivariate analysis (see Clarke and Warwick, 1994 for detailed description of the statistical methods involved in multivariate analyses).

Euphausiid ingestion rates and grazing impact

At present there are a number of methods available that allow the ingestion rates of zooplankton to be estimated. These include gut fluorescence (Mackas and Bohrer, 1976; Conover *et al*., 1986), fecal pellet production (Clarke *et al*., 1988; Dilling *et al*., 1998), radioactive tracer (Ellis and Small, 1989) and *in vitro* incubation (Stuart, 1986) techniques.

The gut fluorescence technique is a quick and inexpensive method of accurately estimating the gut evacuation rate of herbivorous and omnivorous species of zooplankton (Bamstedt *et al*., 2000). In addition it has been widely used on many species of euphausiid, including *E. superba* (Perissinotto *et al*., 1997; Pakhomov and Froneman, 2004; Pakhomov *et al*., 2004), *E. vallentini* (Perissinotto, 1992; Gurney *et al*., 2002), *E. longirostris* and *N. megalops* (Gurney *et al*., 2002), as well as *E. triacantha*, *T. macura* and *E. frigida* (Pakhomov *et al*., 1997; Pakhomov and Froneman, 2004). The gut fluorescence technique further allows the grazing impact and daily ration of autotrophic carbon of the selected zooplankton species to be calculated (Gurney *et al*., 2002), thus providing valuable information on the contribution of autotrophic food to the diets of the species.

A limitation of the gut fluorescence technique is that the method only addresses the herbivorous component in the diet of zooplankton. As a result, the method often draws criticism when investigating the feeding patterns of omnivorous zooplankton, such as euphausiids. In these situations it is recommended that a combination of analytical techniques be used to investigate the feeding biology of zooplankton, one that investigates the herbivorous component (i.e. gut fluorescence) and the other the carnivorous component (i.e. in vitro incubations) of the diets (Bamstedt *et al*., 2000). However, as the major goal of the feeding study was to investigate the contribution of phytoplankton to the diets of the euphausiids, it was decided that the gut fluorescence technique was sufficient alone.

Chapter 2: Methods

Marion Offshore Ecological Variability Survey (MOEVS)

MOEVS was a suite of biological and oceanographic surveys (2002 – 2005) designed to investigate the various processes that influence the delivery of food (mainly macrozooplankton and micronekton) to the large numbers of top predators that inhabit the Prince Edward Islands.

Survey details

This study was conducted as a part of the MOEVS IV and V surveys, carried out on board the *RV SA Agulhas* in the austral autumns 2004 and 2005, respectively. During both cruises altimetry data (TOPEX/Poseidon) were used to identify regions of high mesoscale oceanographic variability if the form of negative sea-surface height anomalies in the Polar Frontal Zone (PFZ), upstream of the Prince Edward Islands (PEI). Both surveys were conducted in the vicinity of the Southwest Indian Ridge (SWIR) between 30° and 35˚ E and 47° and 50˚ S (Fig. 1.2, 3.1 and 4.1). The survey areas were designed around star shaped grids with transects cutting through the anomalies and into the surrounding water masses. Along each transect, stations were occupied every 20 nautical miles. At each station the physical environment, integrated chlorophyll-*a* (chl-*a*), size fractionated chl-*a* and zooplankton community structure were investigated. In addition

the grazing activity of the numerically dominant species of euphausiid was assessed at selected stations.

Environmental variables

Conductivity, Temperature and Depth (CTD) profiles were collected using a Neil Brown MK III probe at each station, to a depth of 1000 m. At each station integrated chl-*a* concentrations were determined for the upper 100 m of the water column. For this purpose 250 mL seawater samples, collected from 5 standard depths (0, 5, 20, 50, 100 m) using the Niskin bottles attached to the CTD probe, were gently filtered (< 5 cm Hg) through GF/F filter paper. Chl-*a* was then extracted in 8 ml of 90 % acetone and stored at – 20 °C in the dark for 24 hours (h). Following centrifugation (5000 rpm), chl-*a* concentrations were measured before and after acidification using a Turner designs 10AU Fluorometer, after the method of Holm-Hansen and Riemann (1978). The integrated chl-*a* concentration for the top 100 m of the water column was then calculated by trapezoidal integration and expressed as mg chl-*a* m^{-2}. Surface size fractionated chl-*a* concentrations were determined by filtering a 250 mL surface seawater sample through a serial filtration unit, that separated the phytoplankton into pico- (< 2.0 µm), nano- (2.0 – 20.0 µm) and microphytoplankton (> 20 µm) size fractions. The chl-*a* concentrations were then calculated as described above and expressed as µg chl-*a* L^{-1}.

Euphausiid community structure

During MOEVS IV euphausiid samples were collected using a Bongo net (Mouth area: 0.25 m², mesh sizes = 200 and 300 µm) to which a Universal Underwater Unit (U^3, Robertson *et al.* 1981) was attached to monitor the depth and temperature throughout the tow. The Bongo nets were fitted with two L PVC cod-ends to limit the damage to the euphausiids. Towing speed varied from 0.8 – 2.5 knots, while the duration of each tow varied from 15 to 25 minutes. Oblique tows were conducted to 300 m during the daytime while at nighttime the net was restricted to the top 200 m of the water column. This sampling method was employed to account for diel vertical migrations that zooplankton undertake (Gurney *et al*., 2002; Bernard and Froneman, 2005). Due to software problems that prevented the use of an electronic flow meter, the volume of water sampled during each tow was calculated by multiplying the mouth area of the net (0.25 m^2) by the duration and speed of the tow. In addition to the Bongo net tows, 8 Rectangular Mid-water Trawl (RMT-8, mouth area: 8 m^2, mesh size: 0.45 cm) tows were conducted to collect specimens for the euphausiid feeding experiments.

During MOEVS V two nets were employed to sample the euphausiid community structure within the region of investigation. Juvenile and sub-adult stages of the euphausiid species were collected using a WP-2 net fitted with a PVC cod-end (Mouth area: 0.25 m², mesh diameter: 300 µm) towed vertically from a depth of 200 m during the night and 300 m during the day, to account for diel vertical migrations (Gurney *et al*., 2002; Bernard and Froneman, 2005). The larger developmental stages and adult

euphausiids were collected using an open and closing RMT-8 (mouth area: 8.0 m², mesh size: 0.45 cm) fitted with a fine mesh cod-end, towed obliquely between 500 – 5 m at each station. A Universal Underwater Unit (U^3, Robertson *et al.*, 1981) was attached to the net to monitor the temperature and depth throughout the tow.

During both cruises samples collected were preserved in 6 % buffered (hexamine) formalin for later analysis in the laboratory. Species-specific abundance (individuals m^{-3}) and biomass (mg dry weight m^{-3}) were then calculated using whole samples (where $n < 100$) or sub-samples ($\leq {}^{1}/_{32}$ when $n > 100$). The euphausiid species were identified, according to the keys of Boden (1951), Baker *et al.* (1990) and Gibbons *et al.* (1999), sexed by the presence or absence of a petasmae on the first and second pleopods, and their carapace length (CL) measured under a Nikkon dissecting microscope (50 x magnification) fitted with a macrometer. To calculate the biomass, CL to dry weight regression formulae (see below) were applied to the CL data for the dominant euphausiid species. For the least abundant species all individuals were weighed (Sauter microbalance) after oven drying at 60 °C for 24 h.

Morphometric analysis

The morphometric analysis was carried out in order to determine the relationships between carapace length (CL) and dry weight of the dominant species of euphausiid collect during both the MOEVS IV and V cruises. Due to the brittle nature of the rostral spine in certain species of euphausiid (Mauchline and Fisher, 1969; Baker *et al.*, 1990)

two measures of carapace length were collected. The first measure of CL was defined as the region from the anterior tip of the rostrum to the dorsal posterior margin of the carapace, and is the measure of CL that was used during this study. The second measure (CL2) excluded the rostral spine and was defined as the region between the post-ocular (anterior) margin of the carapace to the dorsal posterior margin of the carapace. Individual dry weight was measured after oven drying at 60 ˚C for > 24 h. Following this, regression analyses (Sigma Stat, version 1.0) were preformed on the data to calculate the significance of the relationships and the regression equations. The results of the morphometric analysis can be found in 'Appendix 1'.

Statistical analysis

The total euphausiid abundance and biomass data were analyzed using factorial design and one-way analyses of variance (ANOVA), followed by post-hoc tests (Fishers LSD) employing the statistical analysis program, Statistica (version 6.0). Where necessary the data were first $\log_{10}$ transformed to meet the assumptions of parametric statistics, namely normality and equality of variance. The degree of association between chl-*a* biomass and total euphausiid and species specific abundance and biomass was assessed using non-parametric Spearman Rank correlation analyses (Statistica version 6.0).

Multivariate analysis was performed using the Plymouth Routines In Marine Multivariate Ecological Research (PRIMER) computer package (Clarke and Warwick, 1994), after the method of Field *et al.* (1982). To assess if there were any significant spatial patterns in

euphausiid abundance and species composition, hierarchical cluster analysis (q-type) and non-metric multidimensional scaling (MDS) were employed with the Bray-Curtis similarity index (Bernard and Froneman, 2002; Hunt *et al*., 2002; Pakhomov and Froneman, 2004). For this purpose the abundance and biomass data were log transformed [$\log_{10}(x+1)$] to weight the contribution of common and rare species (Legendre and Lengendre, 1983). To test for the significance levels and sources of difference between the *a priori* determined euphausiid groupings, the non-parametric two-way crossed analysis of similarity (ANOSIM) was employed. The euphausiid species that contributed most to the intra-group similarity and inter-group dissimilarity were then determined using the PRIMER program SIMPER (Similarity percentages).

Although comparisons between the samples collected during the daytime and nighttime periods may be confounded due to the sampling procedure implemented for the WP-2 and Bongo nets, by taking the time of sampling (period) and region into account in the statistical analyses, the effect of period and sampling strategy on the population structure of the euphausiids can be separated from the effect of region.

Euphausiid ingestion rates and grazing impact

The gut pigment concentrations (ng pigm ind^{-1}) of euphausiids from selected stations during the MOEVS IV and V surveys were calculated using the fluorescence technique (Mackas and Boher, 1976; Conover *et al*., 1896). The euphausiids were grouped into three size classes, with juveniles, sub-adults and adults being studied separately. Immediately after capture the animals were placed in test tubes with 8 mL 90 % acetone

and stored at – 20 °C for 24 h. For the juvenile and sub-adult euphausiid stages, 2 – 10 individuals were combined per tube, while the gut pigments of single adult euphausiids were extracted. For each station 3 – 10 replicates per species were analyzed. Following this, chl-*a* and phaeopigments were measured before and after acidification using a Turner 10AU fluorometer, as described above. The gut pigment contents (*G*) were then calculated according to Strickland and Parsons (1968) modified by Conover *et al.* (1986), and expressed as ng pigm ind^{-1}.

In order to assess the diel variability in gut pigment content a single 24 h station was occupied during both the 2004 and 2005 surveys. Over this period, Bongo, WP-2 and RMT-8 net tows were conducted every four hours, and where possible euphausiid were removed and their gut pigment content measured as described above.

Gut evacuation rate (*k*) experiments were performed on the numerically dominant species of euphausiid. Freshly caught individuals were placed in 20 L plastic containers filled with 0.2 μm filtered seawater, to which non-fluorescent charcoal particles were added to stimulate continuous feeding (Willason and Cox, 1987; Perissinotto and Pakhomov, 1996). The incubations were carried out on deck during the nighttime to simulate ambient light and temperature conditions. The experiments were run for 2 to $2^1/_2$ h periods with 3 – 5 individuals being removed every 10 minutes for the first hour and every 20 min thereafter and their gut pigments extracted. Gut evacuation rates (*k*, h^{-1}) were then derived from the slope of the regression of the natural logarithm of gut pigments versus time (Dam and Peterson, 1988). Where possible, the gut evacuation experiments were

terminated when the change in gut pigment over the change in time was greater than 2 (Perissinotto and Pakhomov, 1996). Although there is little consensus on the duration of gut evacuation rate experiments (see for example Dam and Peterson, 1988; Peterson *et al*., 1990; Atkinson, 1996), the model formulated by Perissinotto and Pakhomov (1996) represents a non-subjective cut off point for zooplankton under continuous feeding conditions. In addition it has been widely applied to euphausiid gut evacuation rate experiments (Perissinotto *et al.*, 1997;Gurney *et al*., 2002; Pakhomov and Froneman, 2004; Pakhomov *et al*., 2004).

Two-compartment pigment budget experiments were run in an attempt to determine the gut pigment degradation efficiency of the selected euphausiid species (Mayzaud and Razouls, 1992; Perissinotto, 1992). The animals were first starved for 24 h in 0.2 µm filtered seawater containing charcoal powder. A one-liter sample of natural seawater was then split between two 500 mL incubation bottles. A single euphausiid was placed into the treatment bottle, while the other acted as the control. The experiments were run for 2 h under ambient light and temperature conditions. Subsequent to this the chl-*a* concentration of the water from the treatment and control bottles and the gut pigment content of the euphausiid were measured using the fluorescence techniques already described. In addition the background fluorescence of the remaining euphausiids that were starved for 24 h was measured. The pigment degradation (*b'*) was then calculated using the equation:

$$b'(\%) = \left({(Gt - Pb)}/{P} \right)^{-1} \times 100$$

where *Gt* is the gut pigment content after time *t*, *Pb* is the background fluorescence per individual, and *P* is the total amount of pigment ingested, calculated from the difference in chl-*a* concentration between the control and treatment bottles. Any loss of pigment was assumed to be the result of gut pigment destruction.

The daily ingestion rates (*I*, ng pigm $ind^{-1}d^{-1}$) were estimated using the equation:

$$I = kG\left(1 \big/ (1 - b') \right)$$

Where *G* is the gut pigment content integrated over 24 h (ng pigm ind^{-1}), *k*, is the gut evacuation rate constant (h^{-1}), and *b'* is the non-dimensional index of pigment loss during digestion (Mayzaud and Razouls, 1992; Perissinotto, 1992; Pakhomov and Froneman, 2004).

The euphausiid community and species-specific ingestion rates were estimated by combining the abundance data (ind m^{-2}) with the individual ingestion rates for each species and expressed as µg pigm $m^{-2}d^{-1}$. The total euphausiid grazing impact was then calculated by expressing the community ingestion rate as a percentage of the total areal chl-*a* biomass. The daily rations of autotrophic carbon were calculated by converting the individual daily pigment ingested to carbon ingested assuming a carbon to chl-*a* ratio of 50:1 (Atkinson, 1996). Although a number of carbon to chlorophyll ratios for the Southern Ocean are available ($C = 80Chl^{0.6}$ – Hewes *et al*., 1990; C = 37.5x pigment (chl-*a* + phaeopigments) – Pakhomov *et al*., 2004), the ration of 50:1 is the most widely used allowing for comparisons between this study and past work (see for example Pakhomov *et al*., 1997; Gurney *et al*., 2002; Pakhomov and Froneman, 2004; Bernard and

Froneman, 2005). A carbon to dry weight ratio of 0.45:1 was assumed to calculate the carbon content of the selected euphausiid species (Ikeda and Mitchell, 1982; Ikeda and Bruce, 1986). The contribution of autotrophic carbon to the daily carbon requirements was then calculated and expressed as a percentage of the individual's body carbon.

Chapter 3:

Marion Offshore Ecological Variability Survey IV

Results

Physical environment

Analysis of the sub-surface (200 m) temperature data indicated that an intense frontal feature, thought to be the product of the convergence of the SAF and APF, bisected the survey region into two distinct zones (Fig 1).

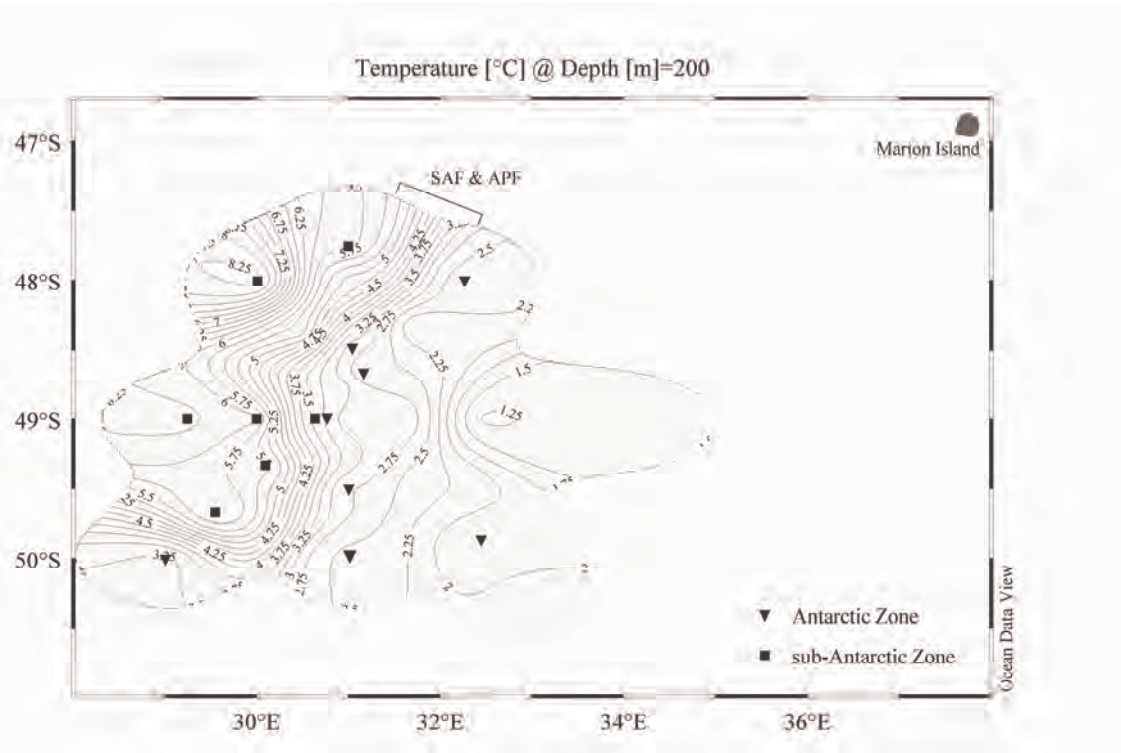


Figure 3.1: Sub-surface (200 m) temperature (°C) contour plot of the MOEVS IV survey area. The position of the biological stations occupied in the SAZ and AAZ are indicated. SAF = sub-Antarctic Front, APF = Antarctic Polar Front

The zone to the northwest of the front was characterized by warm (4 – 8 ˚C) sub-Antarctic water, while the zone to the southeast of the front was characterized by cold (< 2.0 ˚C) Antarctic surface water (Ansorge *et al.* 2004). For the purpose of further analysis the biological stations occupied to the northwest of the front are considered to lie within the sub-Antarctic zone (SAZ), while the stations occupied to the southeast are positioned within the Antarctic zone (AAZ) waters.

Chlorophyll-a

The areal (integrated) chl-*a* concentrations were determined at 23 stations, with thirteen stations being occupied in the AAZ and ten in the SAZ. Throughout the survey area areal chl-*a* biomass ranged between 4.2 and 22.8 mg chl-*a* m^{-2} (mean ± SD = 13.2 ± 4.3 mg chl-*a* m^{-2}) (Fig 3.2 B). Total surface chl-*a* varied between < 0.1 and 0.3 µg chl-*a* L^{-1} (0.1 ± 0.03 µg chl-*a* L^{-1}) (Fig 3.2 A). Both measures of chl-*a* differed little between the stations occupied in the waters of the AAZ and SAZ (Mann-Whitney U test, $p > 0.05$ in both cases). Picophytoplankton (<2.0 µm) were the dominant component of the phytoplankton community contributing from 52 to 87 % (mean ± SD = 65 ± 11 %) to the total surface chl-*a* concentration. The nanophytoplankton (2.0-20.0 µm) contributed on average 27 % (SD = ± 18 %), while the microphytoplankton (>20 µm) contributed little (<10 %) to the total surface chl-*a* concentration (Fig 3.2 A).

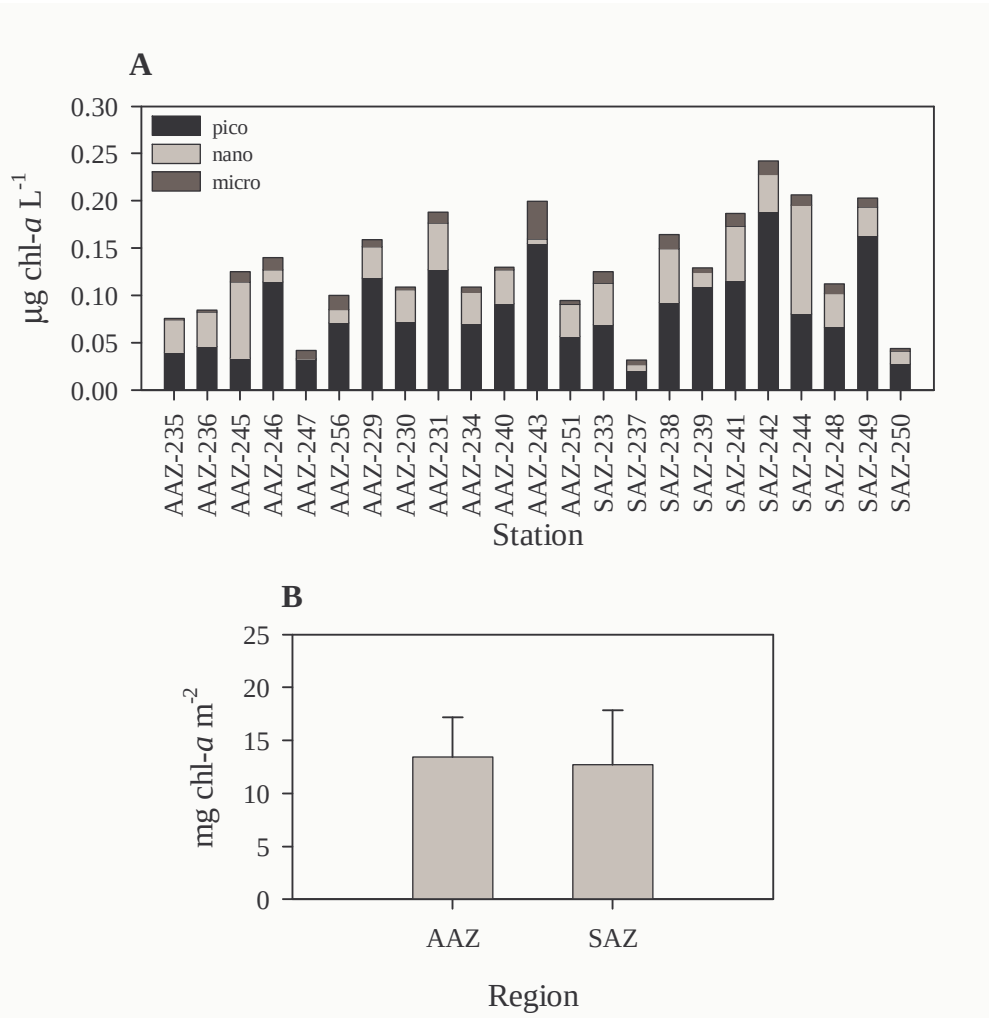


Figure 3.2: A – Contribution of the pico-, nano- and microphytoplankton to the total surface chl-*a* concentration within the AAZ and SAZ regions of the MOEVS IV survey area. B – Mean (± SD) areal chl-*a* biomass (mg chl-*a* m^{-2}) recorded in the different regions of the survey area.

Euphausiid size composition

Euphausiids were grouped according to their mean carapace length (CL) into juvenile (CL < 2.0 mm), sub-adult (CL 2.0 – 4.0 mm) and adult (CL > 4.0 mm) size classes (Mauchline and Fisher, 1969). The size constraints were fitted according to the maximum recorded lengths of the dominant species of euphausiid, namely *Thysanoessa* species and *E. vallentini*, taken

from previous publications (Mauchline, 1969; Baker *et al.*, 1990). The results indicate that the populations of *E. similis*, *E. triacantha* (Holt and Tattersall, 1906), *E. longirostris*, *N. megalops* and *T. gregaria* were predominantly adult individuals, while the populations of *E. vallentini*, *E. frigida* (Hansen, 1911 and *S. maximum* fell into the sub-adult size class (Table 3.1). Two distinct cohorts of *Thysanoessa* species were identified with one cohort being identified as sub-adults and the other juveniles.

Table 3.1: Mean (± SD) carapace length (mm) and dry weight (mg) for all the species of euphausiid recorded during the MOEVS IV survey.

	Carapace length (mm)					Dry weight (mg)	
Species	n	Mean	SD	min	max	mean	SD
E. vallentini	123	3.50	1.09	1.76	7.04	2.31	0.76
E. similis	14	5.17	1.00	2.96	7.20	6.67	1.29
E. triacantha	11	7.46	2.07	2.56	8.00	20.39	5.66
E. longirostris	18	6.75	0.99	4.40	8.09	15.76	2.17
E. frigida	9	3.22	0.63	2.56	4.32	2.15	0.42
T. spp. (sub-adults)	166	2.89	0.45	2.00	4.24	1.77	0.28
T. spp. (juveniles)	345	1.61	0.27	0.80	1.92	1.01	0.17
S. maximum	33	2.27	0.87	0.80	4.16	1.66	0.63
N. megalops	23	5.51	0.62	4.36	6.37	7.61	0.86
T. gregaria	9	4.36	1.00	2.80	5.60	2.16	0.50

Euphausiid community structure

A total of 15 bongo tows were conducted within the region of investigation, with eight located in the AAZ and seven in the SAZ (Fig 1). A total of nine species of euphausiid were recorded within the survey area (Table 2), with the total Abundance and Biomass being dominated by juvenile and sub-adult stages of the *Thysanoessa* species, *T. macrura* and *T. vicina* (mean ± SD = A: 66.4 ± 34.4 %, B: 51.4 ± 36.5 %) and to a lesser extent sub-adult *Euphausia vallentini* (A: 14.3 ± 14.6 %, B: 19.6 ± 22.0 %). Larger size classes of the

euphausiids recorded, namely *E. longirostris*, *E. triacantha*, *E. similis* and *Nematoscelis megalops*, contributed considerably less to the total abundance (< 5 %) and biomass (<20 %) (Table 3.2).

Univariate analysis

Diel changes in total euphausiid abundance and biomass were significant in both the SAZ and AAZ (Mann-Whitney U test, $p < 0.05$, $Z > 2.5$ in both cases). The total euphausiid abundance and biomass did not differ significantly between the stations occupied in the SAZ and the AAZ (Factorial ANOVA, $p > 0.05$ in both cases). Throughout the region of investigation total euphausiid abundance and biomass ranged between 0.1 and 1.4 ind m^{-3} and 0.1 and 1.2 mg dwt m^{-3} during the daytime and 0.2 and 3.1 ind m^{-3} and 1.2 and 8.1 mg dwt m^{-3} during the nighttime. Total euphausiid biomass interacted significantly with time of day and zone (Factorial ANOVA, $p < 0.05$, $F = 11.7$), reflecting an influx of large euphausiids, including *E. triacantha* and *E. frigida*, into the surface waters of the AAZ during the nighttime (Table 3.2).

Multivariate analysis

The juvenile and sub-adult stages of the *Thysanoessa* spp. were excluded from the multivariate analysis as the data likely represented a combination of *T. macrura* and *T. vicina* individuals. The abundance and biomass estimates of *Thysanoessa* spp. did not differ significantly between the stations occupied in the AAZ and SAZ waters Mann-Whitney U test, $p > 0.05$).

Table 3.2: Abundance (ind m^{-3}) and Biomass (mg dwt m^{-3}) estimates for all euphausiids recorded with the Bongo net in the AAZ and SAZ regions of the survey area during the MOEVS IV survey.

			Species									
			E. vallentini		*E. similis*		*E. triacantha*		*E. longirostris*		*E. frigida*	
	station		A	B	A	B	A	B	A	B	A	B
AAZ	B00256	13:56	0	0	0	0	0.007	0.005	0	0	0	0
	B00236	19:58	0.454	0.992	0	0	0.038	0.230	0	0	0	0
	B00229	9:20	0.056	0.057	0	0	0.003	0.003	0	0	0	0
	B00234	9:18	0	0	0	0	0	0	0	0	0	0
	B00240	15:03	0	0	0	0	0	0	0	0	0	0
	B00243	8:27	0.019	0.017	0	0	0	0	0	0	0	0
	B00228	4:16	0.477	0.917	0	0	0.007	0.121	0	0	0	0
	B00231	20:11	1.165	5.244	0	0	0.416	0.509	0	0	0.749	1.669
SAZ	B00239	10:20	0.025	0.055	0	0	0	0	0	0	0	0
	B00244	13:20	0	0	0	0	0	0	0	0	0	0
	B00248	10:31	0	0	0	0	0	0	0.068	1.148	0	0
	B00237	0:37	0.218	0.561	0.011	0.105	0	0	0.034	0.660	0	0
	B00238	5:36	0.176	0.180	0.006	0.078	0	0	0.004	0.015	0	0
	B00241	22:54	0.085	0.155	0.038	0.245	0.008	0.123	0.023	0.115	0	0
	B00242	3:34	0.377	0.308	0.094	0.408	0	0	0.007	0.021	0	0

Table 3.2: continued

			Species									
			Thysanoessa spp		*S. maximum*		*N. megalops*		*T. gregaria*		Total	
Region	Station	Time	A	B	A	B	A	B	A	B	A	B
AAZ	B00256	13:56	0.174	0.114	0	0	0	0	0	0	0.181	0.119
	B00236	19:58	0.940	0.485	0	0	0	0	0	0	1.432	1.708
	B00229	9:20	0.140	0.091	0	0	0	0	0	0	0.199	0.151
	B00234	9:18	0.568	0.313	0	0	0	0	0	0	0.568	0.313
	B00240	15:03	0.420	0.143	0.025	0.026	0	0	0	0	0.446	0.168
	B00243	8:27	0.465	0.165	0.019	0.006	0	0	0	0	0.503	0.187
	B00228	4:16	1.179	0.954	0	0	0	0	0	0	1.663	1.992
	B00231	20:11	0.499	0.398	0	0	0	0	0.083	0.234	2.913	8.054
SAZ	B00239	10:20	0.072	0.033	0.016	0.010	0.042	0.285	0.012	0.044	0.168	0.427
	B00244	13:20	1.269	0.431	0.167	0.045	0	0	0	0	1.436	0.476
	B00248	10:31	0	0	0.065	0.050	0	0	0	0	0.133	1.198
	B00237	0:37	2.290	0.942	0	0	0	0	0	0	2.554	2.267
	B00238	5:36	1.464	0.798	0.078	0.013	0	0	0.037	0.099	1.764	1.183
	B00241	22:54	0.006	0.003	0	0	0.070	0.710	0.012	0.013	0.241	1.364
	B00242	3:34	2.585	1.113	0	0	0.027	0.218	0.013	0.035	3.103	2.103

The results from the multivariate analysis performed on the abundance and biomass data were very similar and as a result only the abundance results are presented below. Results from the clustering and ordination analysis identified three distinct groups of stations separating at approximately 30 % similarity (Fig 3.3 A, B).

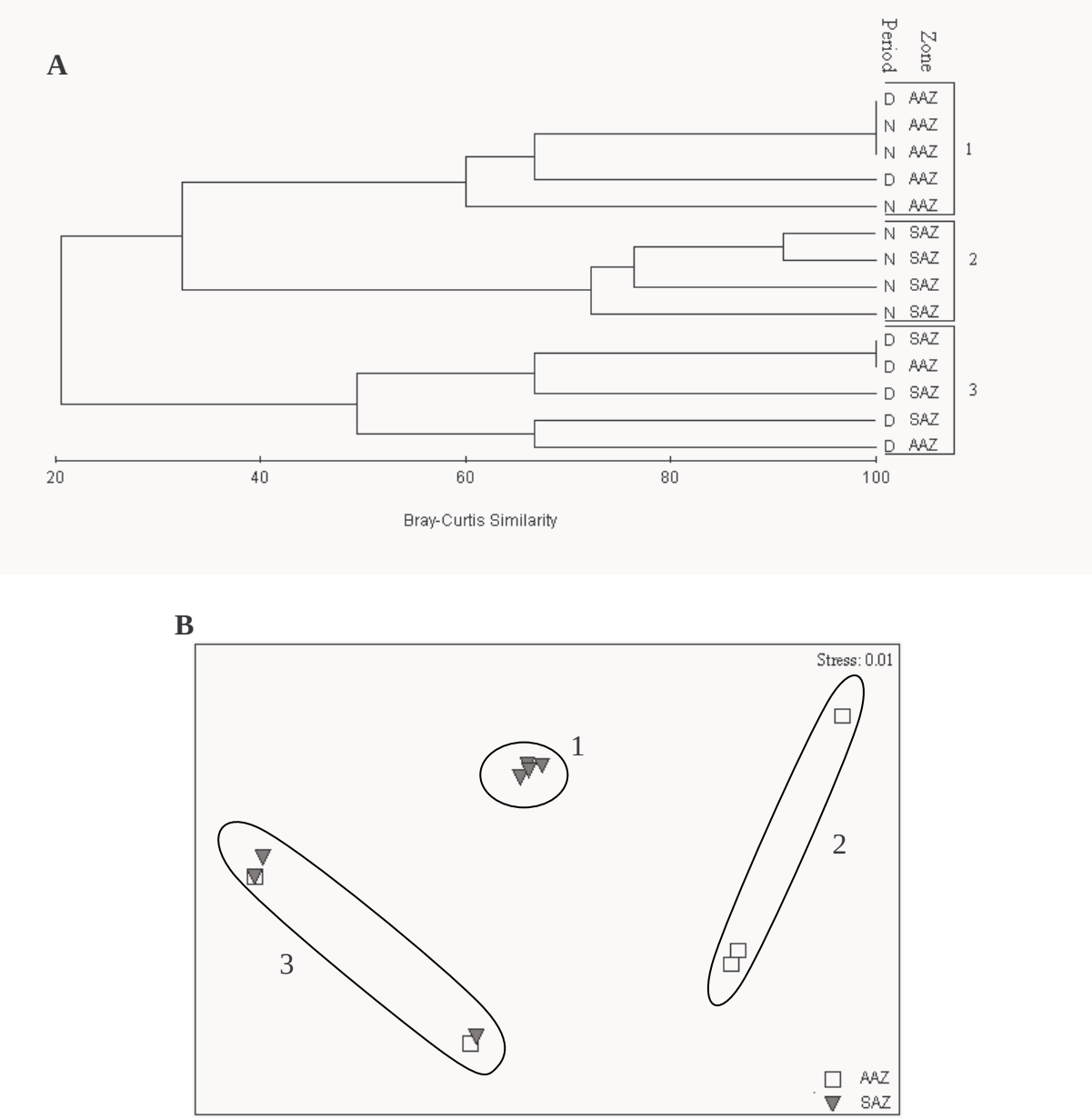


Figure 3.4: Results from the cluster (A) and ordination (B) analysis performed on the euphausiid abundance data collected with the Bongo net during the MOEVS IV survey. 1 = AAZ group; 2 = SAZ group; 3 = daytime group.

Two groupings, consisting of nighttime stations, were geographically consistent with the distribution of the SAZ and AAZ water masses. The third station grouping consisted of daytime stations from both the SAZ and AAZ. The results of the two-way crossed ANOSIM identified significant differences between the stations occupied in the SAZ and the AAZ ($p < 0.05$, $R = 0.5$) and the daytime and nighttime stations ($p < 0.05$, $R = 0.4$).

Table 3.3: Average abundances (ind m^{-3}) of the predominant euphausiid species within the waters of the AAZ and SAZ identified by the similarity percentages procedure SIMPER. Values in parentheses indicate the % contribution to the within group similarity. The dash indicates that the species did not contribute to the within group similarity.

	Average abundance of individuals m^{-3}	
Species	AAZ	SAZ
E. triacantha	0.06 (18.4)	—
Thysanoessa spp.	0.55 (62.4)	1.10 (27.7)
E. vallentini	0.27 (17.1)	0.13 (15.9)
E. longirostris	—	0.02 (18.6)
S. maximum	—	0.05 (15.4)
E. similis	—	0.02 (9.3)
T. gregaria	—	0.01 (8.8)

The similarity percentage procedure (SIMPER) was used to determine which species contributed to the similarities and differences between the SAZ and AAZ groupings (Table 3.3). In order to demonstrate the prevalence of the *Thysanoessa* spp. within the survey region all species of euphausiid were included in the SIMPER analysis. Few similarities in taxonomic composition existed between the SAZ and AAZ stations, with only *Thysanoessa* spp. and *E. vallentini* contributing significantly (> 15 %) to the within group similarity in both regions. The SAZ appeared more specious than the AAZ with six species of euphausiid contributing to the total within group similarity of 54.2, while only three species accounted for the within group similarity of 62.8 in the AAZ (Table 3.3).

Ingestion rates

Ingestion rates were calculated for *E. vallentini* (sub-adults), *E. similis* and the *Thysanoessa* spp. (juveniles and sub-adults), while diel patterns in gut pigment concentrations were determined for the above mentioned species as well as *E. longirostris* and *E. triacantha*.

Differences between the day and nighttime gut pigment contents were only significant for *E. vallentini* sub-adults (Mann-Whitney U test, $p < 0.05$, $U = 49.0$) and *E. similis* ($p < 0.05$, $U = 60.0$), with the nighttime measurements being higher than the daytime values (Fig 3.4). A total of six gut evacuation rate experiments were conducted on three species of euphausiid (Fig 3.5), with the gut evacuation rate constant (k) ranging between 0.55 and 0.94 h^{-1}, corresponding to a gut passage time ($^1/_k$) of between 1.83 and 1.06 h, respectively.

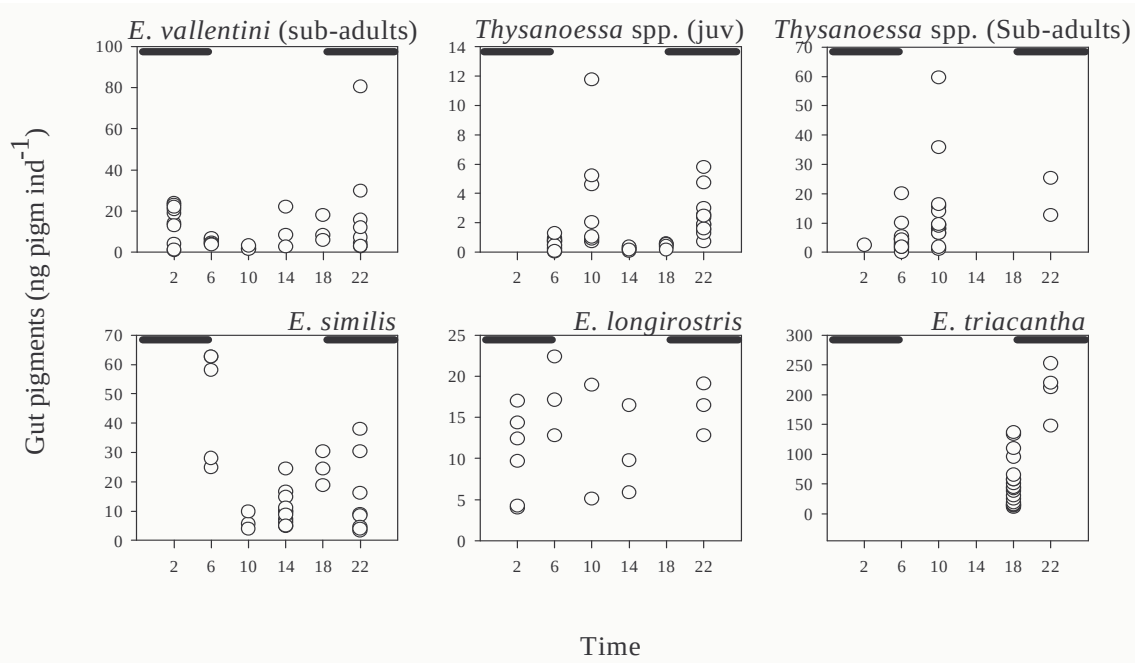


Figure 3.4: Diel variation in gut pigment content (ng pigm ind^{-1}) of the selected species of euphausiid recorded during the MOEVS IV survey. The thickening of the x-axis indicates period of darkness.

No gut evacuation rate experiments were preformed on *E. longirostris* and *E. triacantha*. As a consequence *k* values of 0.75 h^{-1} for *E. longirostris* and 1.10 h^{-1} for *E. triacantha*, determined during the MOEVS V survey from the same geographic region, were employed.

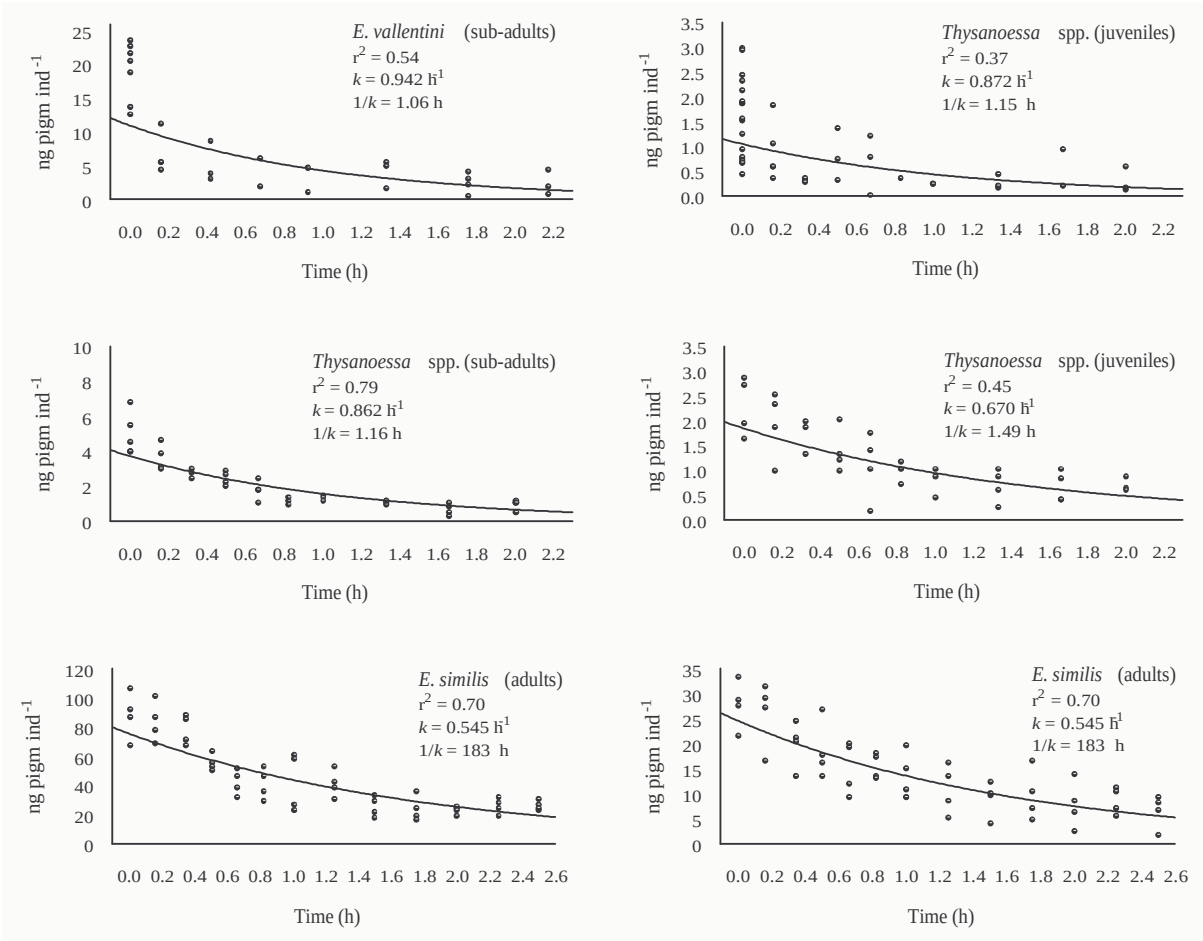


Figure 3.5: Dynamics of the decline in gut pigment, together with the results of the negative exponential regression analyses for the selected species of euphausiid analyzed during MOEVS IV. The gut evacuation rate (*k*) and gut passage time ($^{1}/_{k}$) are provided for each species.

Gut pigment destruction levels were determined for *E. vallentini* sub-adults (mean ±SD = 52.8 ±16.6 %, n = 5), *E. similis* (56.8 ± 9.8 %, n = 3), *E. longirostris* (70.0 ± 15.2 %, n = 3)

and juvenile and sub-adult *Thysanoessa* spp. (50.3 ± 19.2 %, n = 7). No gut pigment destruction level was calculated for *E. triacantha*, as a result a 23.1 % pigment degradation level was assumed (see chapter 4).

Daily individual ingestion rates for the selected species of euphausiid ranged between 7.85 and 228.83 ng pigm $ind^{-1}d^{-1}$ for juvenile *T. macura*, and 1 226.07 and 6 029.05 ng pigm $ind^{-1}d^{-1}$ for *E. triacantha* (Table 3.4). *E. vallentini* and *E. similis* exhibited individual ingestion rates of between 65.4 and 3 005.5 ng pigm $ind^{-1}d^{-1}$ and 366.1 and 4 316.7 ng pigm $ind^{-1}d^{-1}$, respectively (Table 3.4). The individual daily ingestion rate calculated for the sub-adult *Thysanoessa* spp. ranged between 111.46 and 1 144.64 ng pig $ind^{-1}d^{-1}$.

Table 3.4: Individual ingestion rates (ng pigm $ind^{-1}d^{-1}$) for the numerically dominant species of euphausiid recorded in the different regions of the survey area during the MOEVS IV survey. The asterix (*) identifies samples collected with the RMT-8 net.

Region	Station	Species					
		E. vallentini (sub-adults)	*E. similis*	*T.* spp (sub-adults)	*T.* spp. (juveniles)	*E. longirostris*	*E. triacantha*
AAZ	B00235*	3005.51					6029.05
	B00245*	643.43					1226.07
	B00246*	1296.63					4711.51
	B00256				15.29		
	B00234				228.83		
SAZ	B00237	65.37		111.46		498.85	
	B00238		4316.72	234.16	13.54	847.76	
	B00239			551.72	32.93		
	B00241		366.09	876.76		784.68	5077.41
	B00244				7.85		
	B00248				194.39		
	B00249*		969.57	1144.64			
	B00250*	1129.95	1882.35			1483.79	

Grazing impact

The total euphausiid grazing impact recorded during the study ranged from 0.04 to 20.09 µg pigm $m^{-2}d^{-1}$, equivalent to < 0.15 % of the areal chl-*a* biomass (Table 3.5). There were no significant differences in the euphausiid community grazing levels and grazing impact between the SAZ and AAZ waters (Mann-Whitney U test, $p > 0.05$ in both cases). The juvenile and sub-adult *Thysanoessa* spp. and *E. vallentini* accounted for the majority of the grazing activity (> 60 %) throughout the survey area.

Table 3.5: Euphausiid community ingestion rates (µg pigm $m^{-2}d^{-1}$) and the total grazing impact of the dominant species of euphausiid recorded in the different regions of the survey area during the MOEVS IV survey.

	AAZ		SAZ	
	mean	SD	mean	SD
Euphausiid community ingestion rate				
µg pigm $m^{-2}d^{-1}$	2.36	3.01	2.14	2.98
µg C $m^{-2}d^{-1}$	117.97	3.01	106.91	148.78
Chl-a biomass (mg m^{-2})	10.96	2.45	12.72	5.10
% of chl-a biomass	0.02	0.02	0.02	0.02
% Contribution to grazing impact				
Thysanoessa spp. (juveniles)	31.4	39.2	43.2	44.4
E. vallentini **(**sub-adults**)**	33.5	41.3	22.3	30.9
E. triacantha	35.1	41.3	4.5	9.8
E. similis			15.4	27.3
E. longirostris			14.6	30.3

The dry weight used to determine the daily rations of the selected species of euphausiid was determined from the carapace lengths of the euphausiids used for the gut pigment analysis. The daily ration estimates for the different size classes of the *Thysanoessa* spp. ranged between 1.01 and 10.36 % body carbon (mean = 5.28 ± 3.91 %) for the sub-adults and between 0.13 and 3.74 % body carbon (mean = 1.34 ± 1.66 %) for the juveniles (Table 3.6).

E. vallentini sub-adults had a mean daily ration estimate equivalent to 5.29 ± 4.75 % of their body carbon content. The daily ration estimates for *E. similis* and *E. triacantha* ranged between 0.61 and 7.19 % and 0.90 and 4.42 % body carbon, respectively. Finally the daily ration estimates for *E. longirostris* corresponded to < 1 % of its body carbon content (Table 3.6).

Table 3.6: Mean ingestion rates (µg C $ind^{-1}d^{-1}$) and daily ration estimates for the selected species of euphausiid used for the grazing experiment during the MOEVS IV survey.

		Ingestion rate (µg C $Ind^{-1}d^{-1}$)		Daily ration (% Body carbon $ind^{-1}d^{-1}$)			
	Dwt (mg ind^{-1})	mean	SD	mean	SD	min	max
E . longirostris	14.02	45.19	20.77	0.72	0.33	0.40	1.18
E. triacantha	15.17	195.96	98.57	3.12	1.54	0.90	4.42
E. vallentini (sub-adults)	2.58	43.86	54.09	5.29	4.75	0.28	12.94
E. similis	6.67	63.49	73.27	2.47	2.47	0.61	7.19
T. macura (sub-adults)	1.23	29.19	21.60	5.28	3.91	1.01	10.36
T. macura (juveniles)	0.68	4.11	5.06	1.34	1.66	0.13	3.74

Discussion

Oceanographic environment

It has long been established that the path of the Antarctic Circumpolar Current (ACC) is strongly influenced by prominent bottom topographic features, including the Southwest Indian Ridge (SWIR) (Gordon *et al.* 1978, Deacon 1979, Orsi *et al.* 1995). Not only is the ACC topographically steered around or between fracture zones in the SWIR, the disturbance in flow caused by the currents intensification, and the bunching of the SAF and APF, results

in the formation of meanders and eddies in the lee of the ridges (Pollard and Read 2001, Ansorge and Lutjeharms 2003). As the survey region was situated just downstream from the SWIR it is likely that the confluence of the SAF and APF observed during this study resulted from the interaction between the ACC and the SWIR (Ansorge *et al*. 2004).

Chlorophyll-a

The open waters of the PFZ are generally characterized by low levels of areal chl-*a* biomass, for example phytoplankton seldom reach densities greater than 25 mg chl-*a* m^{-2}, while the pico- and nanophytoplankton dominate the phytoplankton assemblage (Perissinotto 1992, Atkinson 1996, Froneman *et* al. 1999, Pakhomov *et al*. 2000, Bernard and Froneman 2003, Pakhomov and Froneman 2004). The chl-*a* environment encountered during the present study is thus typical for the region of investigation. On the other hand the fronts of the ACC are often associated with elevated productivity ascribed to increased water column stability (Strass *et al*. 2002), advection and accumulation of phytoplankton cells in the region of the front (Pollard *et al*. 1995) and isopycnal advection of nutrients into the surface waters (Garcon *et al*. 2001). In contrast, the front encountered during the present survey was not associated with high chl-*a* biomass. The absence of a localized ecological response by the phytoplankton may reflect the continuous wind activity that typifies the PFZ during the autumn and winter months, resulting in a deeper mixed layer depth. Alternatively, low concentrations of trace metals, such as iron, may have limited the growth of the phytoplankton throughout the survey area (Boyd *et al*. 2000). Trace metals, such as iron, are essential for phytoplankton growth and occur at very low concentrations in the open waters of the Southern Ocean, including the PFZ (Boyd *et al*. 2000).

Euphausiid population characteristics

The bulk of the research effort on euphausiids within the PFZ has been limited to waters surrounding the oceanic islands, such as the Prince Edward Island (PEI) archipelago (Perissinotto, 1992; Froneman *et al.*, 2002; Gurney *et al.*, 2002; Hunt and Pakhomov, 2003). As a result, little is known of euphausiids ecological role within the pelagic ecosystems of Antarctic Polar Frontal Zone.

During the present study, the total euphausiid abundance estimates were within the range reported for the PFZ on a number of occasions using similar sampling gear during the same season (Froneman *et al.*, 1999; Froneman *et al.*, 2002; Hunt and Pakhomov, 2003). It is generally accepted that larger nets are more efficient at catching large zooplankton than smaller nets. From the analysis of the carapace lengths of the euphausiids, it is apparent that the juvenile and sub-adult stages of *Thysanoessa* spp. and *E. vallentini*, dominated the euphausiid community. The adult stages of the larger species of euphausiid were poorly represented. This was most evident from the daytime samples, where the euphausiid species that were predominantly adults, such as *E. triacantha*, *E. longirostris* and *E. similis*, were almost always absent. These species are known to undertake extended vertical migrations, occupying a depth of between 250 – 500 m during the day light hours (Mauchline and Fisher 1969). Consequently the majority of the populations would not have been sampled during this period, as the net tows were restricted to the top 300 m of the water column. During the nighttime period the abundance estimates of the various euphausiid species were within the range previously reported using a variety of net types (Froneman *et al*. 2000, Hosie *et al*. 2000, Hunt and Pakhomov 2003, Fisher *et al*, 2004).

In terms of abundance, euphausiids represented a minor component of the zooplankton community during the present survey contributing < 10 % (0.2 – 7.2 %) to the total zooplankton abundance. However, the importance of euphausiids within the open waters of the PFZ is emphasized when one looks at the biomass data where euphausiids often contributed > 50 % (5.7 – 89.8 %) to the total zooplankton biomass (see Bernard and Froneman 2005).

Although the total number of euphausiids differed little between the SAZ waters to the northwest (1.34 ± 0.1.21 ind m^{-3}) and the AAZ waters to the southeast (0.99 ± 0.95 ind m^{-3}) of the front, the species composition demonstrated marked differences. The Antarctic species *E. frigida* and *E. triacantha* (Mauchline and Fisher 1969, Deacon 1982) were restricted to the waters of the AAZ, while the waters of the SAZ were characterized by *E. similis*, *E. longirostris*, *N. megalops* and *T. gregaria*, all of which are of sub-Antarctic origin (Mauchline and Fisher 1969). Juvenile and sub-adult *Thysanoessa* spp. and *E. vallentini* occurred at high densities in both the SAZ and AAZ. As *E. vallentini* is considered to be sub-Antarctic in origin (Mauchline and Fisher 1969), the cross frontal distribution pattern suggests that the front was not a biogeographic boundary to all the species of euphausiid recorded. *E. vallentini* is known to exhibit shallow vertical distribution pattern (Mauchline and Fisher 1969) and as a result may have been exposed to stronger mixing and advection forces caused by Ekman transport and wind driven inertial currents (Mackas *et al*. 2005).

Euphausiid grazing

Among the euphausiids examined during this study, *E. vallentini* and *E. similis* showed pronounced diel patterns in gut pigment content, suggesting that these species show increased

grazing activity during the nighttime (Fig 3.5). It is probable that this pattern is associated with the diel vertical migrations displayed by these euphausiids (Gurney *et al.*, 2002; Pakhomov and Froneman, 2004) with the daytime period being occupied at a depth below the chl-*a* maximum. There was little variability between the daytime and nighttime gut pigment contents of the *Thysanoessa* spp. (juveniles and sub-adults) possibly reflecting a continuous feeding behaviour.

The estimated gut evacuation rate of *E. vallentini* (0.94 h^{-1}) during this study, is greater than that reported by Perissinotto (1992), 0.59-0.81 h^{-1}, while within the upper range of what Gurney *et al.* (2002) reported, 0.45-0.99 h^{-1}, within the same geographic region. Similarly, the gut evacuation rates for *Thysanoessa* spp. sub-adults (0.86 h^{-1}) and juveniles (0.77 h^{-1}) were similar to previous findings (Pakhomov *et al*., 1997; Pakhomov and Froneman, 2004).

Gut pigment destruction efficiency in various species of euphausiid, although variable, tend to be greater than 50 % of the total pigment ingested (Perissinotto, 1992; Perissinotto and Pakhomov, 1996; Gurney *et al*., 2002; Pakhomov and Froneman, 2004). The mean gut pigment destruction levels reported for *E. vallentini* (52.8 ± 16.6 %), *E. similis* (56.8 ± 9.8 %) and the sub-adult (57.2 ± 13.6 %) and juvenile (44.9 ± 18.6 %) *Thysanoessa* spp. are thus, not atypical from previous findings. The gut pigment destruction levels reported for *E. longirostris* (70.2 ± 15.1 %) are in the upper range reported for euphausiid in the literature (Perissinotto, 1992; Perissinotto and Pakhomov, 1996; Gurney *et al*., 2002; Pakhomov and Froneman, 2004). Variability in gut pigment destruction effeciency of zooplankton are thought to reflect a variety of factors including feeding history, prey type, quality of food and temperature (Frost, 1972; Dagg and Walser, 1987).

In agreement with previous studies conducted within the open waters of the PFZ, the cumulative grazing impact of the euphausiid species investigated during this study corresponded to < 0.15 % of the areal chl-*a* biomass (Pakhomov and Froneman 2004). In recent years it has become increasingly evident that euphausiid play a relatively minor role in the removal of autotrophic carbon from the surface waters of the Southern Ocean, with the notable exception of *E. superba* during phytoplankton bloom conditions (Perissinotto *et al*. 1997). A number of factors could contribute to the low grazing impact of euphausiid within the region. Euphausiids in the PFZ seldom occur in high enough densities for their grazing activity to significantly impact the phytoplankton biomass, and when swarms of euphausiids do occur in the region, the spatial extent is generally limited and the resultant grazing impact is restricted to a local scale and does not reflect the pattern in the PFZ as a whole. In addition, a number of authors have suggested that the low grazing impact of euphausiids in the PFZ can be attributed to the unfavourable size structure of the phytoplankton assemblage that predominates within the region (Perissinotto 1992, Gurney *et al*. 2002). Thus, the low grazing impact of the selected euphausiids examined during this study could reflect the predominance of picophytoplankton throughout the region of investigation, which is not efficiently filtered by euphausiids (Perissinotto 1992). It is worth noting that the results of a study conducted in parallel to this investigation showed that the grazing impact of the five numerically dominant mesozooplankton species, comprising 79 % of the total mesozooplankton community, ranged between 0.125 and 2.828 mg pigm m^{-2}, or between 1 and 29 % of the available chl-*a* per day (Bernard and Froneman 2005). The high grazing impact of the mesozooplankton during this period was largely attributed to the grazing activity of the pteropod, *Limacina retroversa*, which has been shown to feed efficiently on picophytoplankton (Noji *et al.* 1997). These findings suggest that the bulk of the chl-*a* may not have been available for the euphausiid community, and reaffirms the understanding that the mesozooplankton are the dominant link

between autotrophic production and the pelagic food webs of the PFZ during the unproductive autumn period.

The contribution of phytoplankton to the daily carbon requirements of euphausiids, particularly *E. superba*, has received considerable scientific attention (Perissinotto and Pakhomov 1996, Atkinson and Snÿder 1997, Perissinotto *et al.* 1997, Ross *et al.* 1998, Gurney *et al.* 2002). Past research has demonstrated that for Antarctic krill to meet their basic daily metabolic requirements, they must consume between 0.8 and 2.8 % of their body carbon per day (Clarke *et al.* 1988, Huntley *et al.* 1994). On the other hand, Perissinotto *et al.* (1997) suggested that when the energetic costs of growth, molting and reproduction are taken into account, the daily ration of *E. superba* would generally range between 5 and 15 % of the body carbon during the summer months. As this study was conducted during austral autumn when the reproductive demand and growth is reduced, it is assumed a daily ration estimate of between 5 and 10 % would be sufficient to meet the euphausiid energetic demands. Considering this, it is apparent that only the sub-adult *Thysanoessa* spp. and *E. vallentini* would have been able to meet their energetic demands on a herbivorous diet. Assuming that smaller size classes of euphausiids are able to filter out small phytoplankton cells more efficiently than large euphausiids it is possible that the pico- and nanophytoplankton which predominated throughout the region of investigation would have been available to the juvenile and sub-adult stages of the euphausiids encountered. On the other hand, the daily ration estimates for *E. triacantha* (3.12 ± 1.54 % body carbon d^{-1}) and *E. similis* (2.47 ± 2.47 % body carbon d^{-1}) suggest that these species would have been principally omnivorous during the study period, as their daily ration estimates of autotrophic carbon would have been insufficient to meet their daily food requirements. Equally the low daily ration estimates for

E. longirostris suggest that it would have had to make use of alternative carbon sources, e.g. protozooplankton or mesozooplankton, to meet their daily food requirements.

Conclusions

Although the observed distribution pattern in total euphausiid abundance and biomass showed no significant variability between the sub-Antarctic and Frontal regions, the species specific distribution patterns were marked, and suggested that the frontal feature formed by the convergence of the SAF and APF acted as an biogeographic boundary to the distribution of euphausiids. Indeed the sub-Antarctic euphausiids *E. similis*, *E. longirostris* and *N. megalops* were restricted to the sub-Antarctic waters of the survey region, while the Antarctic species *E. triacantha* and *E. frigida* were only recorded in the frontal and Antarctic waters. On the other hand, cross frontal distribution patterns were displayed by the dominant components of the euphausiid community, *Thysanoessa* spp. and *E. vallentini*.

The results from the grazing studies suggest that only the sub-adult *Thysanoessa* spp and *E. vallentini* would have been able to meet their theoretical daily food requirements on an autotrophic diet. The low daily ration estimates for the adult euphausiids appears to be related to the unfavourable size structure of the phytoplankton assemblage, and suggests that their diet would have been supplemented by an heterotrophic food source during the survey. Finally the grazing impact of euphausiids on the phytoplankton was negligible, generally corresponding to < 0.15 % of the total areal phytoplankton biomass.

Chapter 4:

Marion Offshore Ecological Variability Survey V

Results

Physical environment

The physical oceanographic data within the region of investigation correlated strongly with the altimetry data, with a negative anomaly or cyclonic cold-core eddy being situated to the north of the APF, within the PFZ between 48° and 50° S and 31° and 36° E (Fig 4.1).

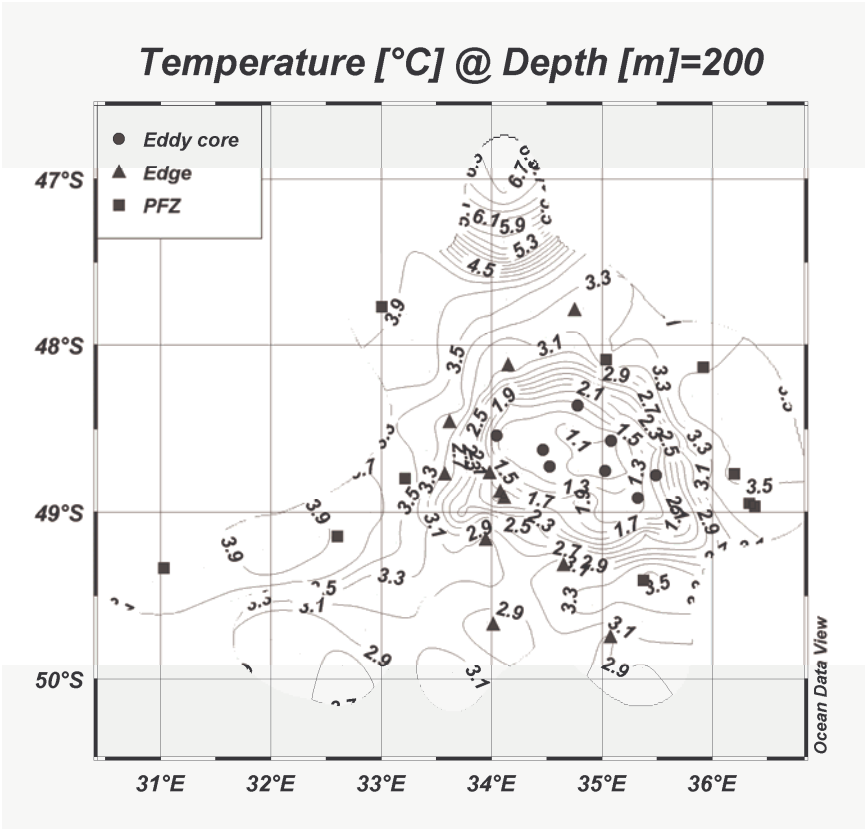


Figure 4.1: Sub-surface (200 m) temperature (°C) contour plot of the MOEVS V survey area. The position of the biological stations occupied in the Core of the eddy, the Edge of the eddy and the PFZ waters are indicated.

From the subsurface temperature data (200, 300, 400 m) the region of investigation could broadly be divided into three distinct zones. The water mass in the core of the eddy was typical of the Antarctic Zone with a subsurface (200 m depth) minimum of < 2.0 °C, while the surrounding water was typical of the PFZ, 4 – 6 °C (Ansorge and Lutjeharms, 2002). A transition zone between the Core and the PFZ, the eddy Edge, was identified as the region where the subsurface temperature expression lay between 2.75 and 3.75 °C. A total of 29 biological stations were occupied within the vicinity of the feature, with 8 occupied in the Core of the eddy, 11 along the Edge of the eddy, and 10 within the PFZ waters. Throughout the results and discussion the data will be discussed in relation to the Core, Edge and PFZ regions of the survey area.

Chlorophyll-a

Surface chl-*a* concentrations were very low throughout the region, and showed no distinct spatial pattern between the three zones (One way ANOVA, $p>0.05$). The highest mean chl-*a* concentration was recorded at the Edge of the feature (0.10 ± 0.02 µg chl-*a* L^{-1}), while the Core and the PFZ regions had almost identical mean chl-*a* concentrations (0.09 ± 0.01 µg chl-*a* L^{-1}) (Fig 4.2A). The percentage contribution of the pico-, nano- and microphytoplankton size classes to the total surface chl-*a* showed no distinct spatial pattern between the different zones ($p > 0.05$). Total surface chl-*a* concentration at all the stations, was dominated by the nano- (2 – 20 µm) and picophytoplankton (< 2 µm) size classes, contributing on average between 50 – 60 % and 35 – 45 % of the total, respectively (Fig 4.2A). The microphytoplankton size fraction (> 20 µm) always contributed less than 5 % of the total pigment

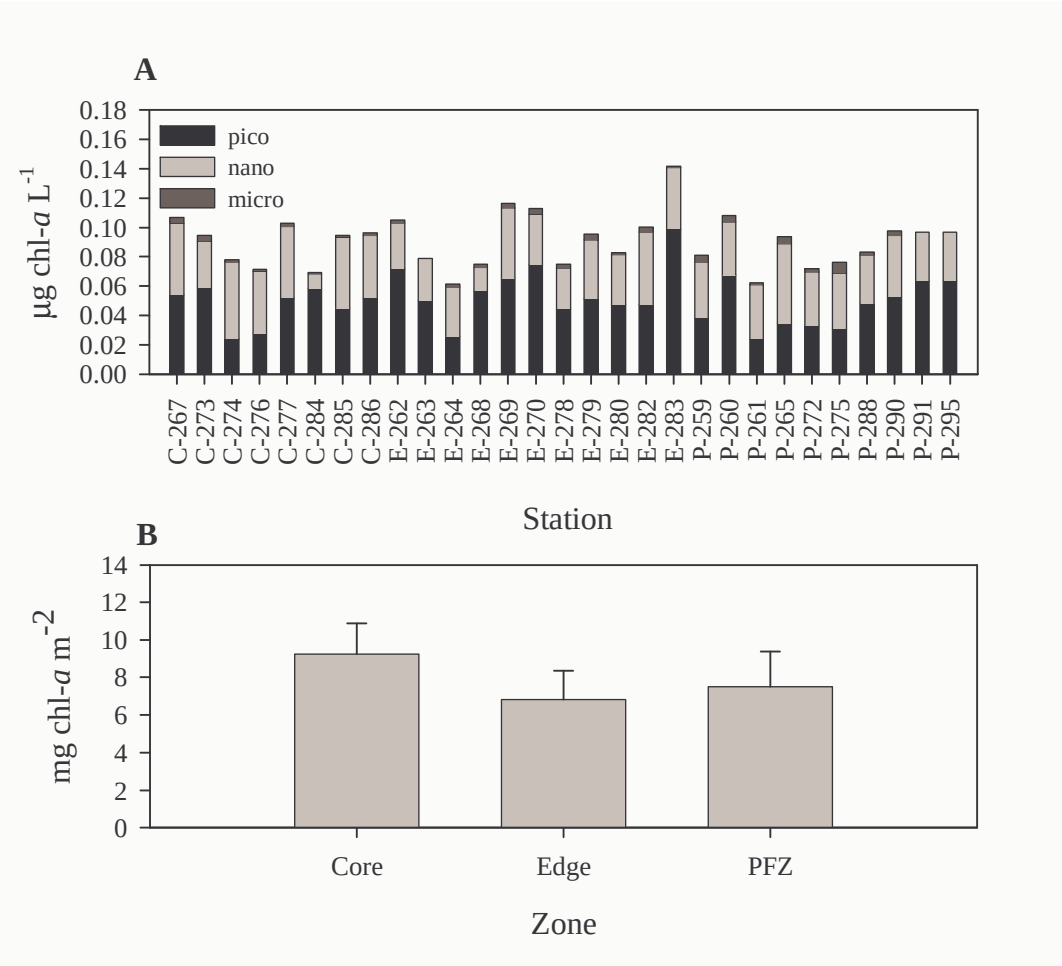


Figure 4.2: A – Contribution of the pico-, nano- and microphytoplankton to the total surface chl-*a* concentration within the Core (C), Edge (E) and PFZ (P) regions of the MOEVS V survey area. B – Mean (± SD) areal chl-*a* biomass (mg chl-*a* m^{-2}) recorded in the different regions of the survey area.

Integrated chl-*a* concentrations (Fig 4.2B) showed a marked spatial pattern with the Core region being characterized by significantly higher chl-*a* concentrations (mean = 9.26 ±1.62 mg chl-a m^{-2}) than the Edge (mean = 6.83 ± 1.52 mg chl-*a* m^{-2}) and PFZ (mean = 7.52 ± 1.87 mg chl-*a* m^{-2}) waters (One-way ANOVA, df = (2, 26), F = 4.96, $p < 0.05$).

Euphausiid size composition

Euphausiids were grouped according to their mean carapace length (CL) into juvenile (CL < 2.0 mm), sub-adult (CL 2.0 – 5.0 mm) and adult (CL > 4.0 mm) classes (Mauchline and Fisher, 1969). The results from the euphausiids collected with the RMT-8 net indicated that the individuals from the populations of *E. vallentini*, *E. triacantha*, *E. longirostris* and *S. maximum* were predominantly adult (i.e. CL > 4.0 mm). The mean carapace lengths of *T. macura* and *E. frigida* fell within the range stipulated for sub-adults (Table 4.1).

Table 4.1: Mean (± SD) carapace length (mm) and dry weight (mg) of the numerically dominant species of euphausiid encountered during MOEVS V – RMT-8 data.

	Carapace length (mm)					Dry weight (mg)	
	n	mean	SD	min	max	mean	SD
E. vallentini	716	4.47	0.80	2.24	7.76	4.73	0.85
E. frigida	456	3.02	0.81	0.64	6.32	1.86	0.50
E. triacantha	317	6.78	1.74	2.48	9.20	15.34	3.94
E. longirostris	285	7.68	0.65	6.00	9.93	21.32	1.80
S. maximum	170	5.92	1.75	2.40	10.65	5.33	1.58
T. macura	172	2.55	2.19	1.20	9.60	1.53	1.31

The populations of euphausiid sampled with the WP-2 net were considerably smaller than those collected with the RMT-8 net, with the majority of individuals from the populations of *E. longirostris*, *S. maximum* and *E. vallentini* falling within the adult size class (Table 4.2). The mean carapace lengths of *E. triacantha* and *E. frigida* fell within the sub-adult size class. The mean CL of the *T. macura* was < 2.00 mm, and as a result they were categorized as juveniles. The broad size range of all the dominant species of euphausiid from both the WP-2 and RMT-8 nets, except *E. longirostris*, suggests that more than one cohort was present in the different populations during the 2005 survey (Table 4.1 and 4.2).

Table 4.2: Mean (± SD) carapace length (mm) and dry weight (mg) of the numerically dominant species of euphausiid encountered during MOEVS V – WP-2 data.

	Carapace length (mm)					Dry weight (mg)	
	n	mean	SD	min	max	mean	SD
E. vallentini	51	4.07	1.00	1.36	6.00	3.84	0.94
E. frigida	135	2.47	0.31	1.44	3.44	1.24	0.16
E. triacantha	3	3.74	1.27	2.64	5.12	4.30	1.46
E. longirostris	14	7.64	0.88	6.00	9.68	21.05	2.42
S. maximum	3	5.04	2.01	3.76	7.36	4.02	1.60
T. macura	474	1.77	0.58	0.96	6.41	1.01	0.36

Euphausiid community structure

RMT-8

A total of 26 RMT-8 tows were conducted within the region of investigation, with the average tow filtering *c.* 9000 m^{-3}. Nine species of euphausiid were recorded within the survey area, with six species (*Euphausia vallentini, E. frigida, E. triacantha, E. longirostris, Stylocheiron maximum* and *Thysanoessa macura*) consistently contributing > 95 % to the total euphausiid abundance and biomass (Fig 4.3B, D). The species present varied between the different zones identified during the study. Two species of Antarctic euphausiid, *E. frigida* and *E. superba* (Dana, 1850), were found in the Core of the eddy, but were absent from the PFZ. A number of euphausiid species of sub-Antarctic origin that occurred in the PFZ waters were not recorded in the core of the feature, namely *E. longirostris*, *S. maximum*, *T. gregaria* and *Nematoscelis megalops* (Table 4.3). The Antarctic and sub-Antarctic euphausiid species recorded co-occurred within the Edge region of the eddy, although *E. superba* and *T. gregaria* were absent.

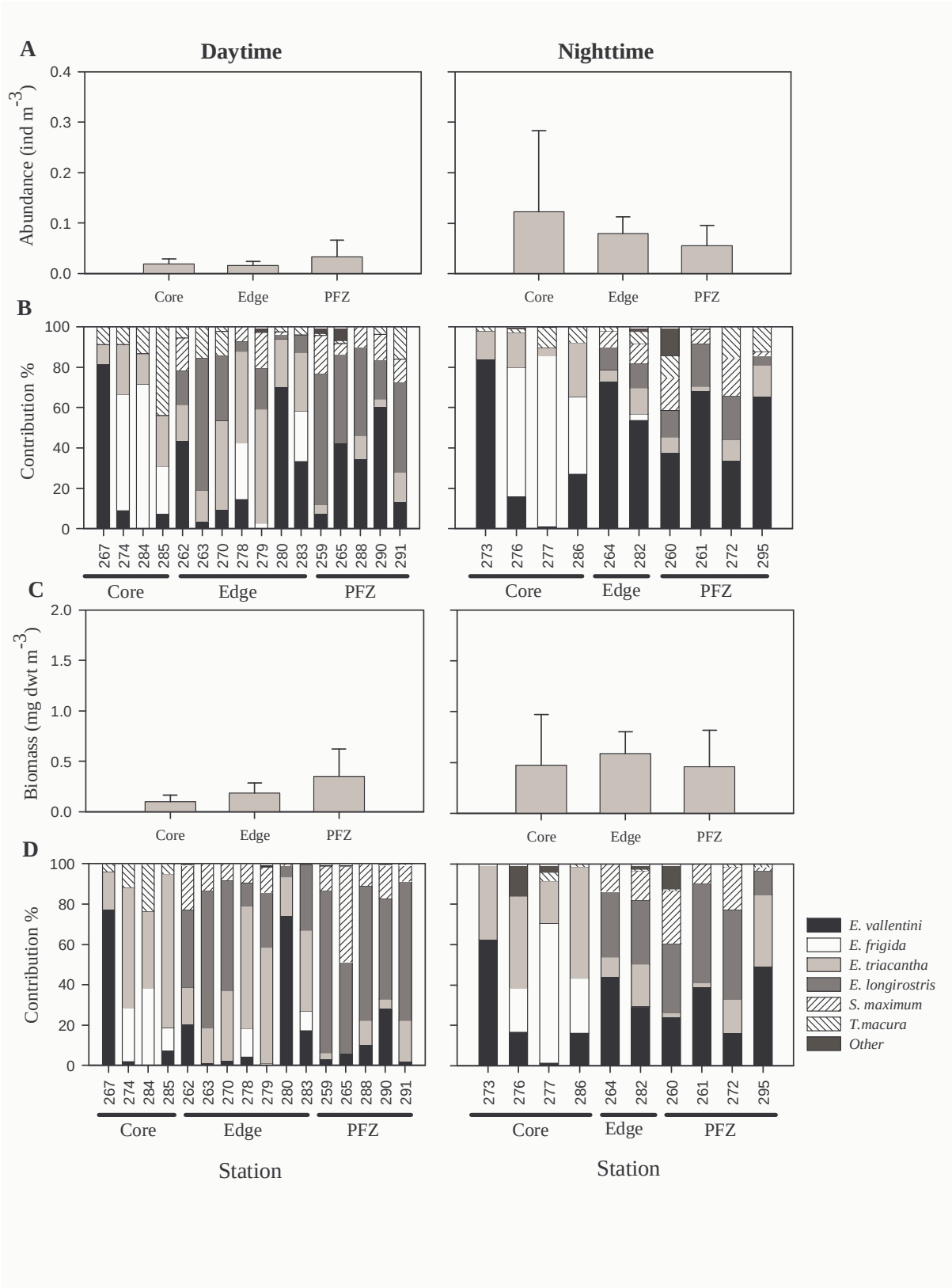


Figure 4.3: Mean (± SD) total euphausiid daytime and nighttime abundance (A) and biomass (C) values, together with the % contribution of the dominant euphausiid species (B, D) collected with the RMT-8 sampling gear, within the Core, Edge and PFZ regions of the MOEVS V survey area.

Throughout the region of investigation total euphausiid abundance and biomass from the RMT-8 samples ranged between 0.004 and 0.091 ind m^{-3} and 0.054 and 0.769 mg dwt m^{-3} during the daytime, and 0.019 and 0.364 ind m^{-3} and 0.123 and 1.211 mg dwt m^{-3} during the nighttime (Table 4.3).

Univariate analysis

The total euphausiid abundance (A) and biomass (B) data ($\log_{10}$ transformed) collected with the RMT-8 net showed no significant interaction effect between zone and time of day (Factorial ANOVA, $p > 0.05$ in both cases). Total euphausiid abundance and biomass did not differ significantly between the Core, Edge and PFZ waters ($p > 0.05$ in both cases) (Fig 4.3A, C). While diel variability was marked (A: df = (1, 20), $F = 13.587$, $p < 0.05$; B: df = (1, 20), $F = 10.47$, $p < 0.05$) with the nighttime total euphausiid abundance and biomass recorded in the Core of the eddy (A = 0.12 ± 0.16 ind m^{-3}, B = 0.47 ± 0.50 mg dwt m^{-3}) being significantly greater than the daytime values recorded in the Core (A = 0.02 ± 0.01 ind m^{-3}, B = 0.10 ± 0.06 mg dwt m^{-3}). Similarly and the nighttime abundance estimates from the Edge of the eddy (0.08 ± 0.03 ind m^{-3}) were significantly greater than that recorded during the daytime at the Edge (0.02 ± 0.01 ind m^{-3}) (Fishers LSD, $p < 0.05$ in all cases). Of the species that occurred in all the regions investigated, namely *E. triacantha*, *E. vallentini* and *T. macura*, only the abundance data for *E. triacantha* showed a marked interaction between zone and time of day (df = (3, 20), $F = 3.91$, $p < 0.05$). In addition the nighttime abundance of *E. triacantha* in the Core of the eddy (0.010 ± 0.004 ind m^{-3}) was significantly greater than that recorded in the PFZ (0.004 ± 0.004 ind m^{-3}) waters (df = (2, 20), $F = 3.94$, $p < 0.05$). While *E. vallentini* and *E. triacantha* showed significant diel patterns in abundance and biomass (Fishers LSD, $p < 0.05$ in both cases).

Table 4.3: Abundance (ind m^{-3}) and Biomass (mg dwt m^{-3}) estimates for all euphausiids recorded with the RMT-8 net within the different regions of the survey area during the MOEVS V survey.

			Species									
			E. vallentini		*E. frigida*		*E. triacantha*		*E. longirostris*		*S. maximum*	
Zone	Station	Time	A	B	A	B	A	B	A	B	A	B
Core	B00267	17:38	0.017	0.051	0	0	0.002	0.012	0	0	0	0
	B00273	2:19	0.046	0.117	0	0	0.008	0.069	0	0	0	0
	B00274	8:59	0.001	0.001	0.007	0.020	0.003	0.046	0	0	0	0
	B00276	21:12	0.007	0.047	0.028	0.062	0.008	0.130	0	0	0	0
	B00277	3:08	0.002	0.016	0.309	0.844	0.015	0.259	0	0	0	0
	B00284	14:11	0	0	0.009	0.028	0.002	0.028	0	0	0	0
	B00285	18:10	0.002	0.014	0.008	0.022	0.008	0.148	0	0	0	0
	B00286	22:06	0.008	0.032	0.011	0.054	0.008	0.110	0	0	0	0
Edge	B00262	9:43	0.011	0.042	0	0	0.005	0.037	0.004	0.079	0.004	0.045
	B00263	14:24	0	0.003	0	0	0.002	0.043	0.008	0.168	0.002	0.033
	B00264	21:07	0.075	0.324	0	0	0.006	0.075	0.012	0.238	0.008	0.100
	B00270	11:43	0.001	0.003	0	0	0.003	0.040	0.002	0.062	0.001	0.009
	B00278	7:38	0.003	0.007	0.005	0.025	0.008	0.105	0.001	0.020	0.001	0.016
	B00279	12:38	0	0	<0.001	0.001	0.004	0.069	0.002	0.033	0.001	0.015
	B00280	17:34	0.021	0.276	0	0	0.007	0.073	0.001	0.020	<0.001	0.003
	B00282	4:18	0.030	0.125	0.002	0.001	0.007	0.091	0.007	0.138	0.005	0.063
	B00283	9:10	0.004	0.013	0.003	0.008	0.004	0.031	0.001	0.025	0	0
PFZ	B00259	8:51	<0.001	0.002	0	0	<0.001	0.002	0.003	0.043	0.001	0.007
	B00260	19:58	0.007	0.030	0	0	0.001	0.003	0.002	0.042	0.003	0.033
	B00261	2:08	0.075	0.373	0	0	0.003	0.022	0.023	0.475	0.008	0.092
	B00265	7:50	0.012	0.027	0	0	0	0	0.013	0.203	0.001	0.211
	B00272	21:03	0.010	0.049	0	0	0.003	0.050	0.007	0.132	0.006	0.064
	B00288	7:47	0.008	0.029	0	0	0.003	0.035	0.010	0.188	0.002	0.031
	B00290	16:55	0.055	0.220	0	0	0.004	0.033	0.017	0.384	0.011	0.127
	B00291	12:00	0.002	0.004	0	0	0.002	0.039	0.007	0.131	0.002	0.016
	B00295	2:01	0.041	0.215	0	0	0.010	0.156	0.003	0.052	0.001	0.008

Table 4.3: continued

			Species									
			T. macura		*N. megalops*		*T. gregaria*		*E. superba*		Total	
Zone	Station	Time	A	B	A	B	A	B	A	B	A	B
Core	B00267	17:38	0.002	0.003	0	0	0	0	0	0	0.021	0.065
	B00273	2:19	0.001	0.001	0	0	0	0	0	0	0.054	0.187
	B00274	8:59	0.001	0.009	0	0	0	0	0	0	0.013	0.076
	B00276	21:12	0.001	0.001	0	0	0	0	<0.001	0.044	0.043	0.283
	B00277	3:08	0.036	0.050	0	0	0	0	0.001	0.042	0.364	1.211
	B00284	14:11	0.002	0.017	0	0	0	0	0	0	0.013	0.074
	B00285	18:10	0.014	0.010	0	0	0	0	0	0	0.032	0.194
	B00286	22:06	0.002	0.003	0	0	0	0	0	0	0.029	0.199
Edge	B00262	9:43	0.001	0.002	0	0	0	0	0	0	0.025	0.204
	B00263	14:24	0	0	0	0	0	0	0	0	0.012	0.246
	B00264	21:07	0.002	0.002	0	0	0	0	0	0	0.103	0.738
	B00270	11:43	<0.001	<0.001	0	0	0	0	0	0	0.007	0.114
	B00278	7:38	0	0	0	0	0	0	0	0	0.017	0.173
	B00279	12:38	0	0	<0.001	0.002	0	0	0	0	0.008	0.120
	B00280	17:34	<0.001	<0.001	0	0	0	0	0	0	0.029	0.374
	B00282	4:18	0.003	0.003	0.001	0.011	0	0	0	0	0.056	0.433
	B00283	9:10	0.001	<0.001	0	0	0	0	0	0	0.012	0.077
PFZ	B00259	8:51	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0	0	0.004	0.054
	B00260	19:58	0.002	0.001	0.002	0.015	<0.001	<0.001	0	0	0.019	0.123
	B00261	2:08	0	0	0	0	0.001	<0.001	0	0	0.110	0.963
	B00265	7:50	<0.001	<0.001	<0.001	0.004	0.001	<0.001	0	0	0.029	0.446
	B00272	21:03	0.005	0.004	0	0	0	0	0	0	0.030	0.298
	B00288	7:47	0	0	0	0	0	0	0	0	0.023	0.282
	B00290	16:55	0.003	0.006	0	0	0	0	0	0	0.091	0.769
	B00291	12:00	0.003	0.001	0	0	0	0	0	0	0.016	0.191
	B00295	2:01	0.008	0.007	0	0	0	0	0	0	0.062	0.438

The results of the Spearman Rank correlation analysis agreed with the distribution patterns of the specific species of euphausiid and areal chl-*a* biomass between the different regions identified. The abundance and biomass of *E. frigida* were found to have a significant positive correlation to the distribution of the integrated chl-*a* biomass (A: $R = 0.45$, $t = 2.45$, $p < 0.05$; B: $R = 0.43$, $t = 2.32$, $p < 0.05$). While the abundance and biomass estimates of *E. longirostris* (A: $R = -0.38$, $t = -2.03$, $p = 0.05$; B: $R = 0.40$, $t = 2.12$, $p < 0.05$) and *S. maximum* (A: $R = -0.50$, $t = 2.45$, $p < 0.05$; B: $R = -0.42$, $t = -2.28$, $p < 0.05$) displayed a significant negative relationship with the integrated chl-*a* biomass.

WP-2

A total of 28 WP-2 tows were conducted within the region of investigation. Eight species of euphausiid were recorded, largely reflecting the same species composition as the RMT-8 data. An exception was presented by *E. superba*, which was absent from the WP-2 net samples. Similarly the larger species of euphausiid (*E. triacantha*, *E. longirostris* and *S. maximum*) were absent from the majority of the samples collected (Table 4.4). Daytime abundance and biomass was dominated by juvenile and sub-adult stages of *T. macura* contributing > 95 % of the total at most stations (Fig 4.4B, D). The nighttime samples showed an increase in the contribution of *E. vallentini* and *E. frigida*, which together with *T. macura* accounted for more than 90 % of the total abundance and 80 % of the total biomass (Fig 4.4B, D). The distribution patterns of euphausiids obtained with the WP-2 net were similar to those of the RMT-8, with *E. frigida* only occurring in the Core of the eddy, while *E. longirostris*, *N. megalops* and *T. gregaria* were only recorded at stations occupied within PFZ and Edge waters. Stations occupied at the Edge of the eddy were again characterized by the presence of Antarctic and sub-Antarctic euphausiid species (Table 4.4).

Table 4.4: Abundance (ind m^{-3}) and Biomass (mg dwt m^{-3}) estimates for all euphausiids recorded with the WP-2 net within the different regions of the survey area during the MOEVS V survey.

			Species									
			E. vallentini		*E. frigida*		*E. triacantha*		*E. longirostris*		*S. maximum*	
Zone	Station	Time	A	B	A	B	A	B	A	B	A	B
Core	B00273	2:19	0.480	3.426	5.920	6.345	0	0	0	0	0.040	0.022
	B00274	8:59	0	0	0.027	0.020	0	0	0	0	0	0
	B00276	21:12	0	0	3.840	3.891	0	0	0	0	0	0
	B00277	3:08	0	0	2.240	2.538	0	0	0	0	0	0
	B00284	14:11	0	0	0	0	0	0	0	0	0	0
	B00285	18:10	0	0	0.160	0.222	0	0	0	0	0	0
	B00286	22:06	0	0	0.640	0.689	0	0	0	0	0	0
Edge	B00262	9:43	0	0	0	0	0	0	0	0	0	0
	B00263	14:24	0	0	0	0	0	0	0	0	0	0
	B00264	21:07	1.840	6.753	0	0	0	0	0.040	0.312	0	0
	B00268	1:08	0	0	0.800	0.606	0	0	0	0	0	0
	B00269	6:31	0.080	0.087	0	0	0	0	0	0	0	0
	B00270	11:43	0	0	0	0	0	0	0	0	0	0
	B00278	7:38	0	0	0.013	0.008	0	0	0	0	0	0
	B00279	12:38	0	0	0	0	0	0	0	0	0.040	0.002
	B00280	17:34	0.039	0.048	0	0	0	0	0	0	0	0
	B00282	4:18	0.140	0.196	0	0	0.020	0.066	0	0	0	0
	B00283	9:10	0	0	0	0	0	0	0	0	0	0
PFZ	B00259	8:51	0	0	0	0	0	0	0	0	0	0
	B00260	19:58	0.070	0.248	0	0	0	0	0.180	3.311	0	0
	B00261	2:08	0.220	0.636	0	0	0	0	0.080	1.718	0	0
	B00265	7:50	0	0	0	0	0	0	0	0	0	0
	B00272	21:03	0.160	0.301	0	0	0	0	0	0	0.040	0.218
	B00275	16:32	0	0	0	0	0	0	0	0	0	0
	B00288	7:47	0	0	0	0	0	0	0	0	0	0
	B00290	16:55	0	0	0	0	0	0	0	0	0	0
	B00291	12:00	0	0	0	0	0	0	0	0	0	0
	B00295	2:01	0.060	0.218	0	0	0.060	0.221	0	0	0.020	0.037

Table 4.4: continued

			Species							
			T. macura		*N. megalops*		*T. gregaria*		Total	
Zone	Station	Time	A	B	A	B	A	B	A	B
Core	B00273	2:19	11.840	5.374	0	0	0	0	18.240	15.167
	B00274	8:59	0.147	0.050	0	0	0	0	0.173	0.070
	B00276	21:12	2.160	1.608	0	0	0	0	6.240	5.499
	B00277	3:08	0.020	0.370	0	0	0	0	2.880	2.908
	B00284	14:11	0.013	0.010	0	0	0	0	0.013	0.010
	B00285	18:10	7.680	6.180	0	0	0	0	7.840	6.403
	B00286	22:06	3.680	2.754	0	0	0	0	4.800	3.443
Edge	B00262	9:43	0.413	0.464	0	0	0	0	0.413	0.464
	B00263	14:24	3.840	1.523	0	0	0	0	3.840	1.523
	B00264	21:07	2.880	1.823	0	0	0	0	4.760	8.888
	B00268	1:08	0.320	0.112	0	0	0	0	1.120	0.718
	B00269	6:31	1.080	0.576	0	0	0	0	1.160	0.663
	B00270	11:43	0.027	0.013	0	0	0	0	0.027	0.013
	B00278	7:38	0.507	0.362	0	0	0	0	0.520	0.370
	B00279	12:38	0.187	0.100	0	0	0	0	0.227	0.102
	B00280	17:34	0.787	0.312	0	0	0	0	0.826	0.360
	B00282	4:18	0.240	0.119	0	0	0	0	0.420	0.380
	B00283	9:10	0.107	0.063	0	0	0	0	0.107	0.063
PFZ	B00259	8:51	0.640	0.087	0	0	0	0	0.640	0.087
	B00260	19:58	1.950	0.956	0.160	1.606	0.020	0.056	2.380	6.176
	B00261	2:08	0.260	0.120	0	0	0	0	0.560	2.474
	B00265	7:50	0.080	0.138	0	0	0	0	0.080	0.138
	B00272	21:03	1.480	0.606	0	0	0	0	1.680	1.126
	B00275	16:32	0.027	0.003	0	0	0	0	0.027	0.003
	B00288	7:47	0.133	0.093	0	0	0	0	0.133	0.093
	B00290	16:55	0.053	0.015	0	0	0	0	0.053	0.015
	B00291	12:00	0.107	0.036	0	0	0	0	0.107	0.036
	B00295	2:01	0.660	0.371	0	0	0	0	0.800	0.846

Univariate analysis

Total euphausiid abundance and biomass collected with the WP-2 net ranged between 0.013 and 3.840 ind m^{-3} and 0.010 and 1.523 mg dwt m^{-3} during the daytime, and between 0.420 and 18.240 ind m^{-3} and 0.380 and 15.167 mg dwt m^{-3} during the nighttime. The Core region had the highest abundance and biomass, with nighttime mean values of 8.04 ± 6.94 ind m^{-3} and 6.75 ± 5.72 mg dwt m^{-3}, respectively (Fig 4.4A, C). The Edge (mean: 1.87 ± 1.96 ind m^{-3}, 2.66 ± 4.15 mg dwt m^{-3}) and the PFZ (mean: 1.31 ± 0.76 ind m^{-3}, 2.66 ± 2.45 mg dwt m^{-3}) waters were characterized by considerably lower abundance and biomass values (Table 4.4, Fig 4.4A, C).

As with the RMT-8 data, the total abundance (A) and biomass (B) data ($\log_{10}$ transformed) collected with the WP-2 net showed no significant interaction effect of zone and time of day (Factorial ANOVA, $p > 0.05$ in both cases). A strong diel pattern in abundance and biomass was evident, with the nighttime total euphausiid abundance and biomass from the Core of the eddy (A = 8.04 ± 6.94 ind m^{-3} and B = 6.75 ± 5.72 mg dwt m^{-3}) and PFZ (A = 1.31 ± 0.76 ind m^{-3} and B = 2.66 ± 2.45 mg dwtm^{-3}) waters being significantly greater than that recorded during the daytime (Core: A = 2.68 ± 4.47 ind m^{-3} and B = 2.16 ± 3.67 mg dwt m^{-3}; PFZ: A = 0.17 ± 0.23 ind m^{-3} and B = 0.06 ± 0.05 mg dwt m^{-3}) (Fishers LSD, $p < 0.05$ in all cases). The pattern appears to be the result of an influx of larger species of euphausiid, namely *E. frigida*, *E. vallentini* and *E. longirostris*, into the surface waters at night (Table 4.4, Fig 4.4C, D). The abundance of the dominant species of euphausiid recorded in the WP-2 net, namely *T. macura*, showed no significant interaction between zone and time of day ($p > 0.05$).

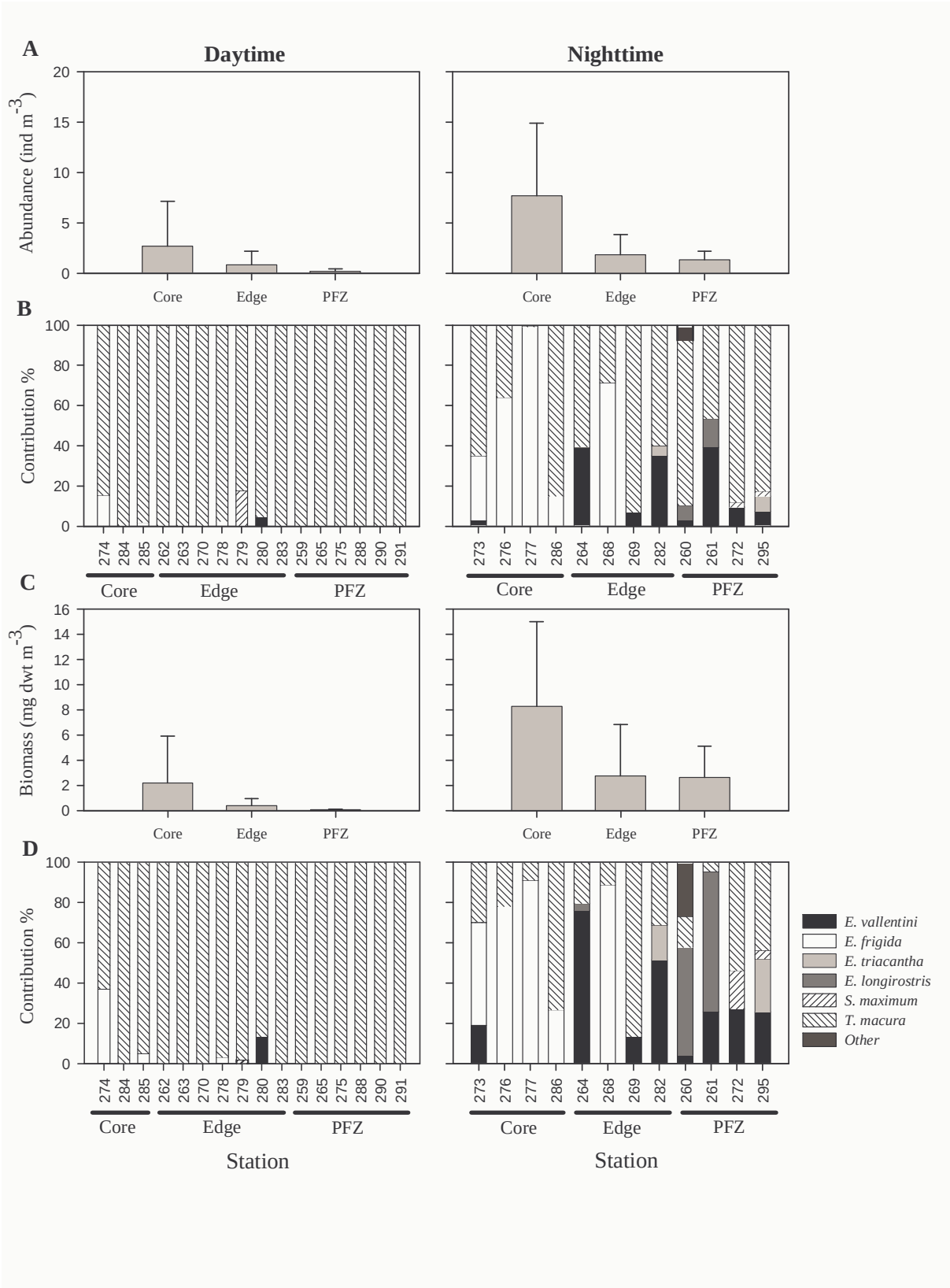


Figure 4.4: Mean (± SD) total euphausiid daytime and nighttime abundance (A) and biomass (C) values, together with the % contribution of the dominant euphausiid species (B, D) collected with the WP-2 sampling gear, within the Core, Edge and PFZ regions of the MOEVS V survey area.

There were no significant correlations between the abundance and biomass estimates of euphausiid from the WP-2 net and any of the measures of chl-*a* concentration recorded during the survey (Spearman Rank correlation: $p > 0.05$ in all cases).

Multivariate analysis

For the multivariate analysis of the RMT-8 data, the day and nighttime samples were combined. The results of the two-way crossed analysis of similarity (ANOSIM) performed on the abundance and biomass data showed a significant difference between the different zones for both the daytime and nighttime samples (A: $R = 0.30$, $p < 0.05$, and B: $R = 0.38$, $p < 0.05$). The pairwise test revealed significant separation between the Core and the Edge groups (A: $R = 0.40$, $p < 0.05$, and B: $R = 0.42$, $p < 0.05$) and the Core group and the PFZ group (A: $R = 0.48$, $p < 0.05$, and B: $R = 0.62$, $p < 0.05$). The analysis was, however, unable to distinguish between the Edge group and the PFZ group for both abundance ($R = 0.08$, $p > 0.05$) and biomass ($R = 0.15$, $p > 0.05$). The test for differences between the daytime and nighttime groups showed a significant difference for the abundance data ($R = 0.27$, $p < 0.05$), but not for the biomass data ($R = 0.15$, $p > 0.05$). The result of the cluster analysis on the abundance data indicated three groups separating at *c.* 35 % similarity level (Fig 4.5A). Group A1 consisted of an even mixture of stations from the Edge of the eddy and PFZ waters, while the stations from the Core of the eddy were predominant in Group A3 (Fig 4.5A). The ordination analysis produced similar results (Fig 4.5B), showing a strong separation between the stations occupied in the Core of the eddy and PFZ waters. The results from the cluster analysis on the biomass data appear relatively complex (Fig 4.6A), and reflect the interactive effects of period and zone on the euphausiid species composition and biomass.

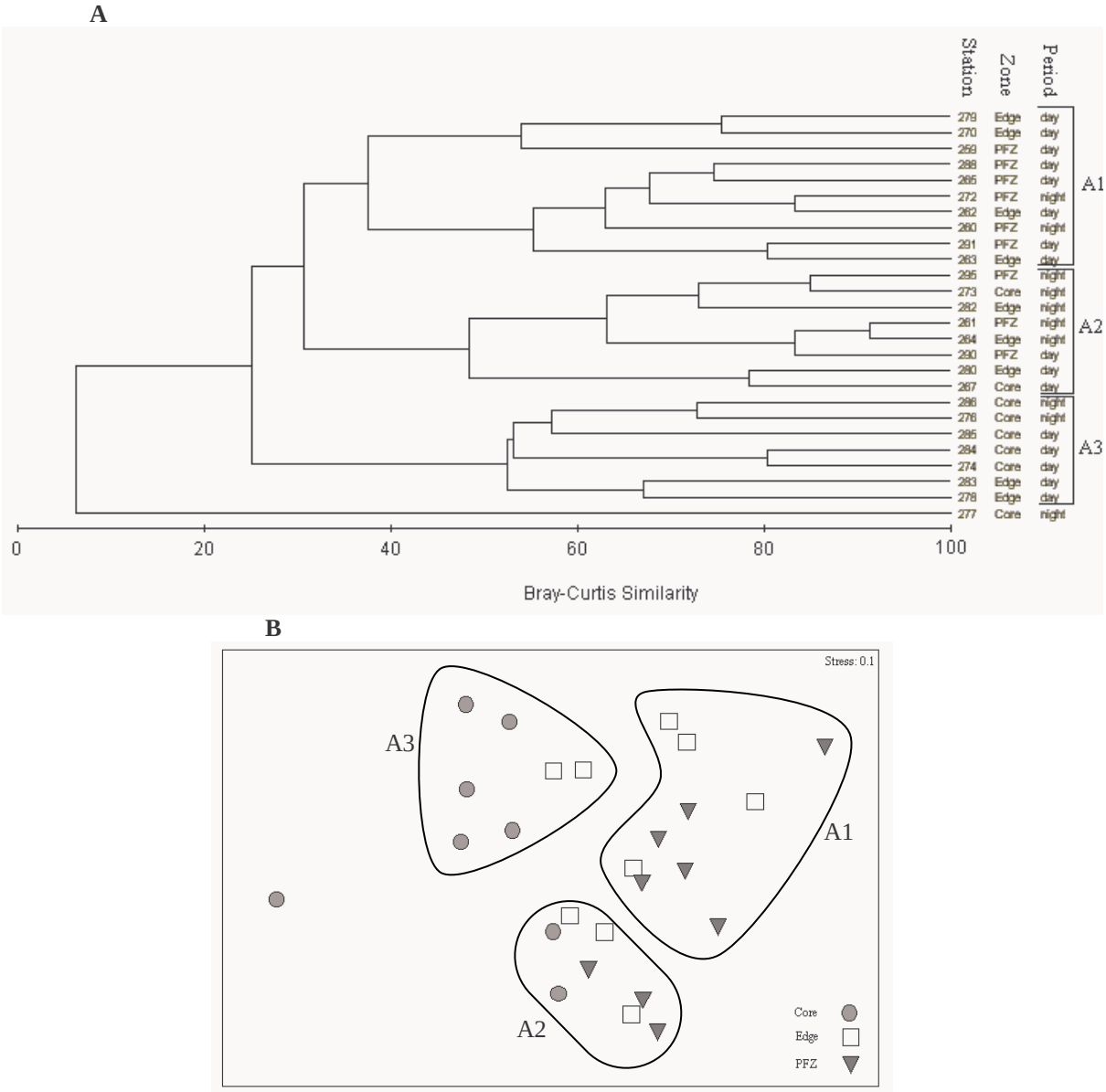
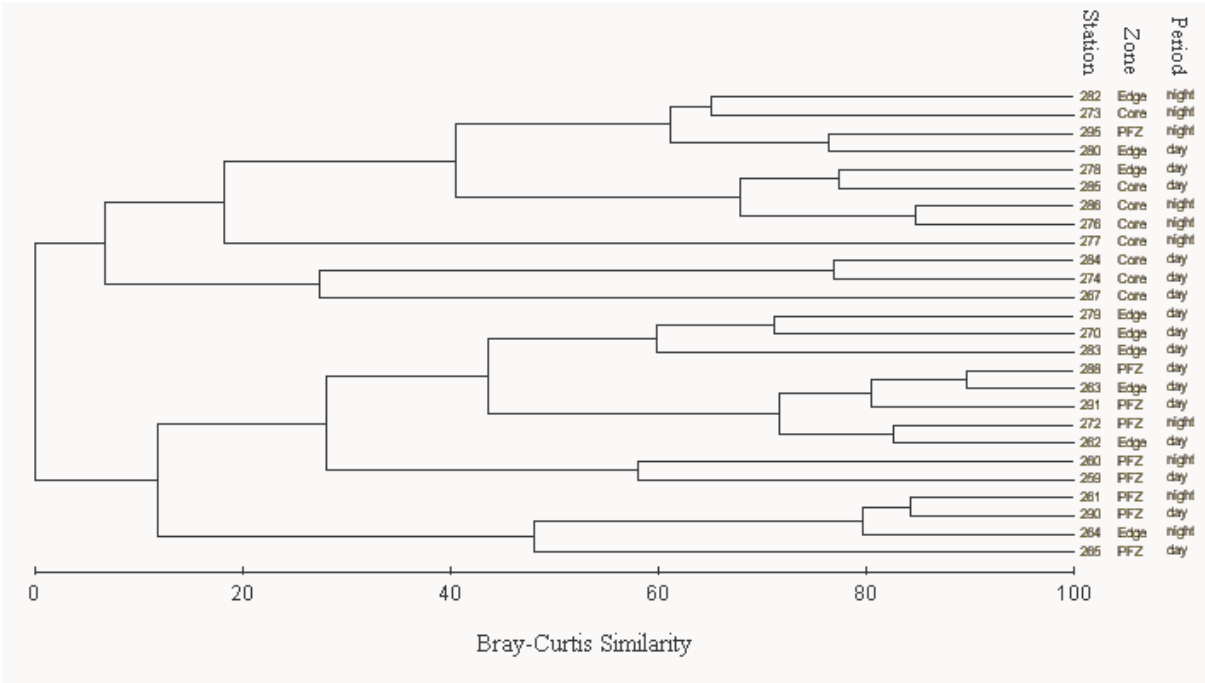


Figure 4.5: Results from the cluster (A) and ordination (B) analysis performed on the euphausiid abundance data collected with the RMT-8 net during the MOEVS V survey. A1 = Edge and PFZ group; A2 = Core, Edge and PFZ group; A3 = Core group.

A



B

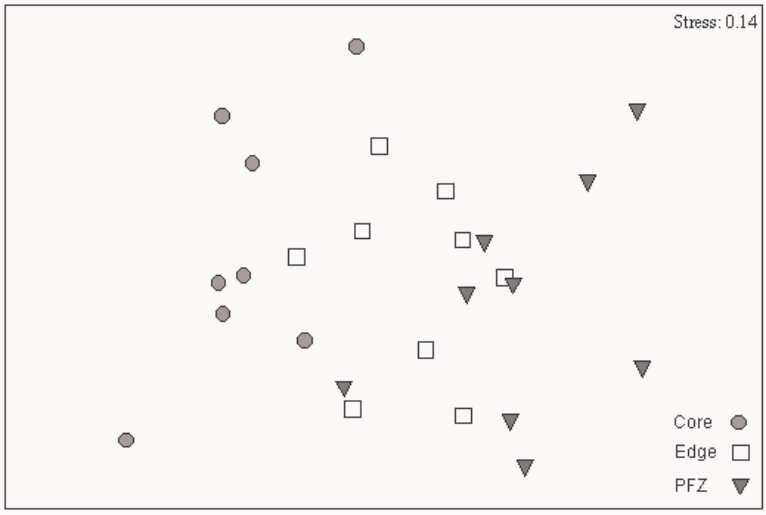


Figure 4.6: Results from the cluster (A) and ordination (B) analysis performed on the euphausiid biomass data collected with the RMT-8 net during the MOEVS V survey.

This complex pattern is resolved, to a large degree, in the MDS plot, with the stations occupied in the Core of the eddy and the PFZ water showing the greatest separation (Fig 4.6B). The location of the Edge samples in between the Core and PFZ samples in the MDS plot, further suggests that this region acts as a transition zone between the Core of the eddy and the surrounding water mass (Fig 4.6B).

Table 4.5: Contribution (%) of the dominant species of euphausiid to the within group similarity for the RMT-8 Abundance and Biomass data from the different regions of the MOEVS V survey area. Results acquired from the PRIMER program SIMPER.

		Species					
		T. macura	*E. frigida*	*E. triacantha*	*E. vallentini*	*E. longirostris*	*S. maximum*
Core	A	11.77	38.03	28.99	21.19		
	B		12.5	70.86	12.5		
Edge	A			42.03	24.24	19.4	10.07
	B			55.01	9.41	27.37	
PFZ	A			8.19	39.65	33.87	12.31
	B			13.52	15.8	54.81	15.31

The similarity percentages procedure (SIMPER) showed relatively low within group similarities for both the abundance and biomass data, with the samples in the Core of the eddy showing a 35 % and 43 % similarity level in the species of euphausiid present, respectively. The stations occupied in the Edge of the eddy and the PFZ waters showed a 41 % and a 43 % species similarity level for the abundance data, and a 52 % and 44 % species similarity level for the biomass data, respectively. The within group similarity showed a succession of dominant species from the Core to the PFZ waters (Table 4.5). In terms of abundance, *E. frigida* (contribution to the within group similarity = 38 %) was the most important species in the Core of the eddy. *E. triacantha* (42 %) contributed most to the within group similarity at the Edge of the eddy, while *E. vallentini* (40 %) was the dominant species in the PFZ waters. In terms of species contribution to the biomass of euphausiids

within the different zones *E. triacantha* contributed most in the Core (71 %) and Edge (55 %) regions of the eddy, while *E. longirostris* contributed most within the water of the PFZ (55 %).

Due to the strong diel variability in abundance and biomass of the euphausiids collected with the WP-2 net, only the nighttime samples were used for the multivariate analyses. The one-way analysis of similarities (ANOSIM) was used to determine whether the predetermined groupings (Core, Edge and PFZ) placed on the data agreed with the observed distribution patterns of the euphausiids. The test for differences between groups was significant for both abundance ($R = 0.3$, $p < 0.05$) and biomass ($R = 0.4$, $p < 0.05$). The pairwise tests produced similar results for abundance and biomass with only the Core and PFZ groups demonstrating a significant separation (A: $R = 0.71$, $p < 0.05$; B: $R = 0.97$, $p < 0.05$). The degree of separation between the Core and the Edge group, and the Edge and the PFZ group was insignificant for the abundance and biomass data ($p > 0.05$ in all cases).

The ordination analysis and cluster analysis showed a similar pattern with three groups separating at the 45 % similarity level for abundance and biomass (Fig 4.7, 4.8). Groups A3 and B3 were dominated by stations within the Core of the eddy for both abundance and biomass, respectively. The remaining groups consisted of a mixture of Edge and PFZ stations (Fig 4.7, 4.8). For the abundance data the stations within the Core and the PFZ both had a within group similarity of *c.* 55 %, while the edge region had a lower similarity of *c.* 35 % (SIMPER).

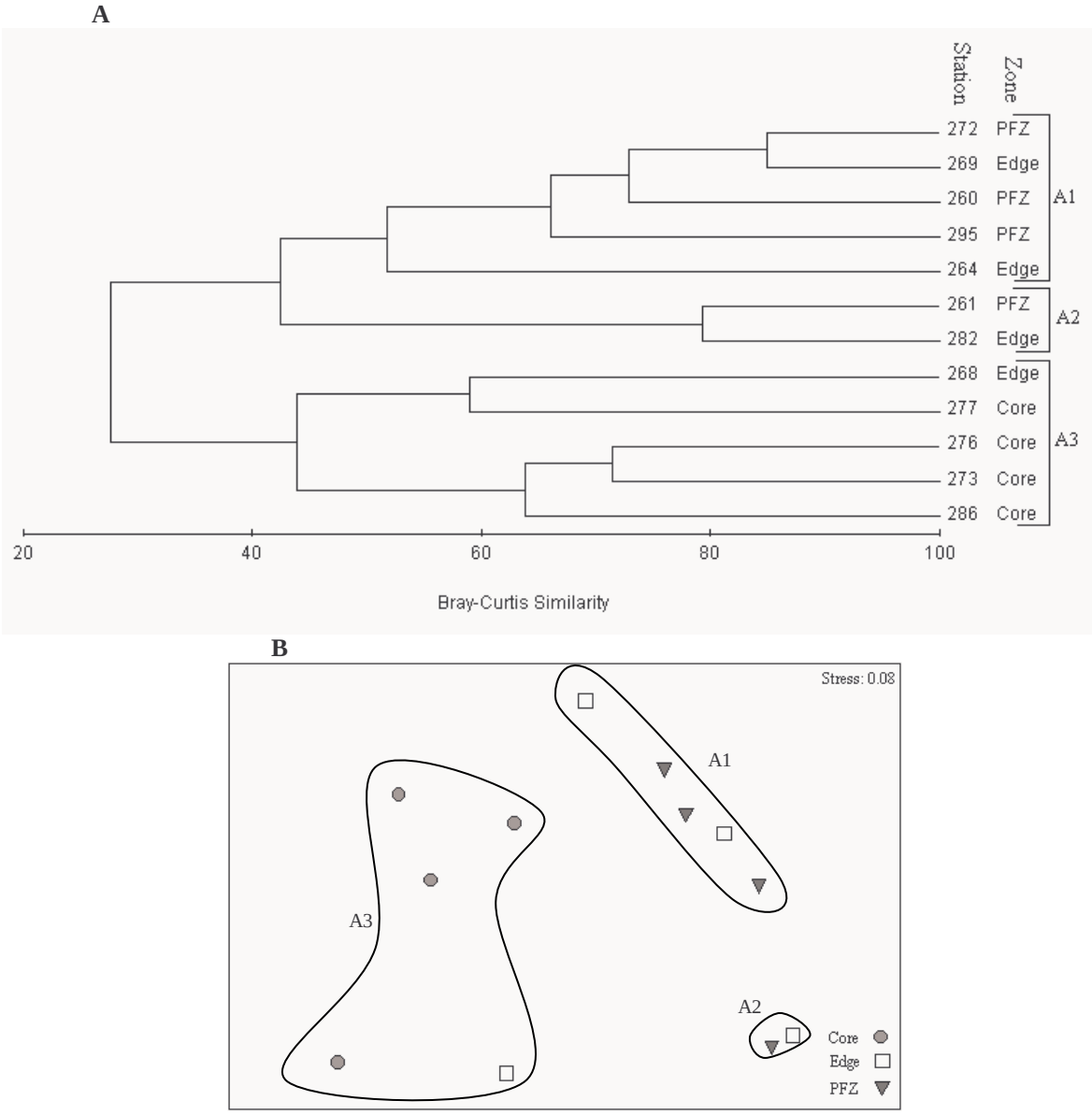


Figure 4.7: Results from the cluster (A) and ordination (B) analysis performed on the euphausiid abundance data collected with the WP-2 net during the MOEVS V survey. A1, A2 = PFZ and Edge group; A3 = Core group.

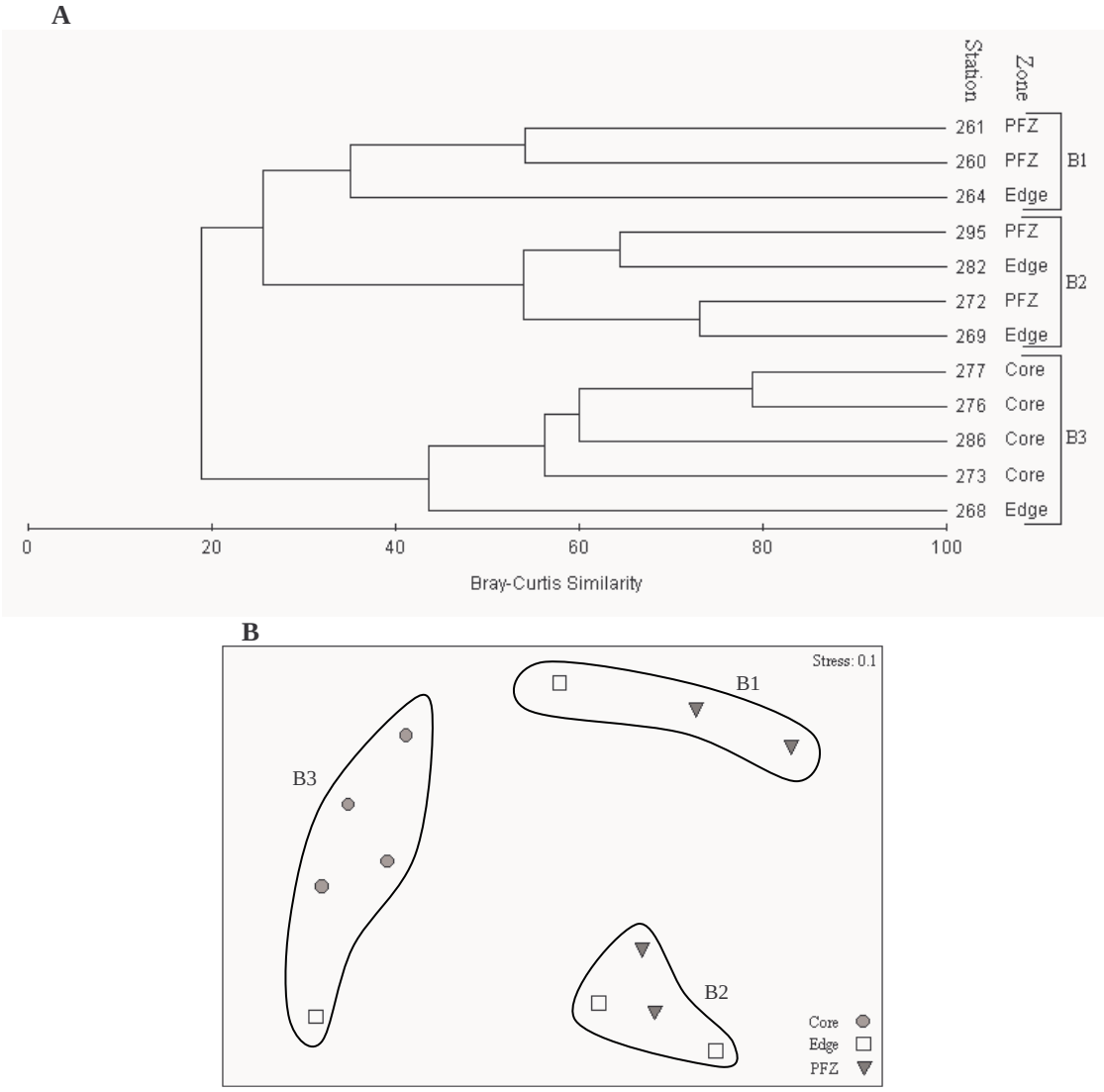


Figure 4.8: Results from the cluster (A) and ordination (B) analysis performed on the euphausiid biomass data collected with the WP-2 net during the MOEVS V survey. B1, B2 = PFZ and Edge group; B3 = Core group.

For the biomass results, the Core of the eddy had the highest within group similarity level of 61 %, while the similarity levels for the Edge (21 %) and the PFZ (3 %) were considerably lower. *E. frigida* (A = 62 %, B = 64 %) and *T. macura* (A = 38 %, B = 36 %) accounted for all the similarity within the Core group, while, *T. macura* (A = 87 %, B 75 %) and *E. vallentini* (A =13 %, B = 25 %) were responsible for the similarity in the Edge region of the eddy. The PFZ region was dominated by *T. macura* (A = 81 %, B = 42 %) and *E. vallentini* (A = 16 %, B = 39 %) for both abundance and biomass, although *E. longirostris* did contribute substantially to the within group similarity for the biomass data (17 %).

Ingestion rates

Only the numerically dominant euphausiid species (listed above) were used for the calculation of ingestion rates and grazing impact. Although all species showed pronounced variability in gut pigment levels over a 24 h period (Fig 4.9), differences between daytime and nighttime pigment contents were only significant for *E. vallentini* (Mann-Whitney U test, $U = 145.0$, $p < 0.001$). Ten gut evacuation rate experiments were performed on 5 of the numerically dominant euphausiid species, with the gut evacuation rate constant (k) varying between 0.40 and 1.69 h^{-1} (Fig 4.10). Due to its scarcity at the stations where feeding experiments were conducted, no k value was determined for *E. frigida* during the study. As a result a value of 0.29 h^{-1} determined by Pakhomov and Froneman (2004) in the Atlantic sector of the PFZ was employed.

Gut pigment destruction rates were determined for *E. vallentini* (mean: 47.5 ± 28.1 %, n = 4), *E. triacantha* (mean: 23.1 ± 13.5 %, n = 3), *E. longirostris* (mean: 29 ± 3.8 %, n = 3) and *T. macura* juveniles (mean: 44.9 ± 18.6 %, n = 3). No gut pigment destruction rates were

determined for *E. frigida* and *S. maximum*. As a result values of 35.8 % (Pakhomov and Froneman, 2004) and 50 % of the total pigment ingested were assumed, respectively.

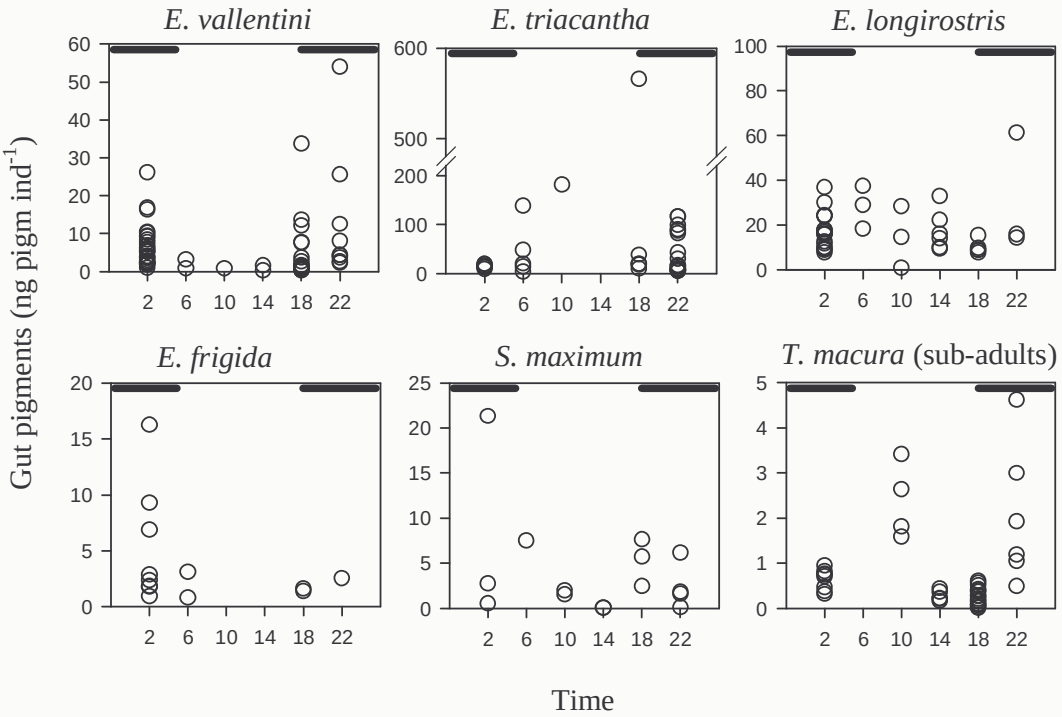


Figure 4.9: Diel variation in gut pigment content (ng pigm ind^{-1}) of the selected species of euphausiid during the MOVES V survey. The thickening of the *x-axis* indicates period of darkness.

Ingestion rates were determined using mean *k* values obtained for each species (Fig 4.10). *E. triacantha* and to a lesser extent *E. longirostris* had the highest daily ingestion rates of the euphausiids studied (Table 4.6), consuming between 717.1 – 6332.2 ng pigm ind^{-1}d^{-1} and 208.3 – 1655.2 ng pigm ind^{-1}d^{-1}, respectively. The lowest daily ingestion rates were recorded for *E. frigida*, ranging between 18.5 and 41.1 ng pigm ind^{-1}d^{-1}. Daily ingestion rates for *E. vallentini* were low, ranging between 30.6 and 977.9 ng pigm ind^{-1}d^{-1}.

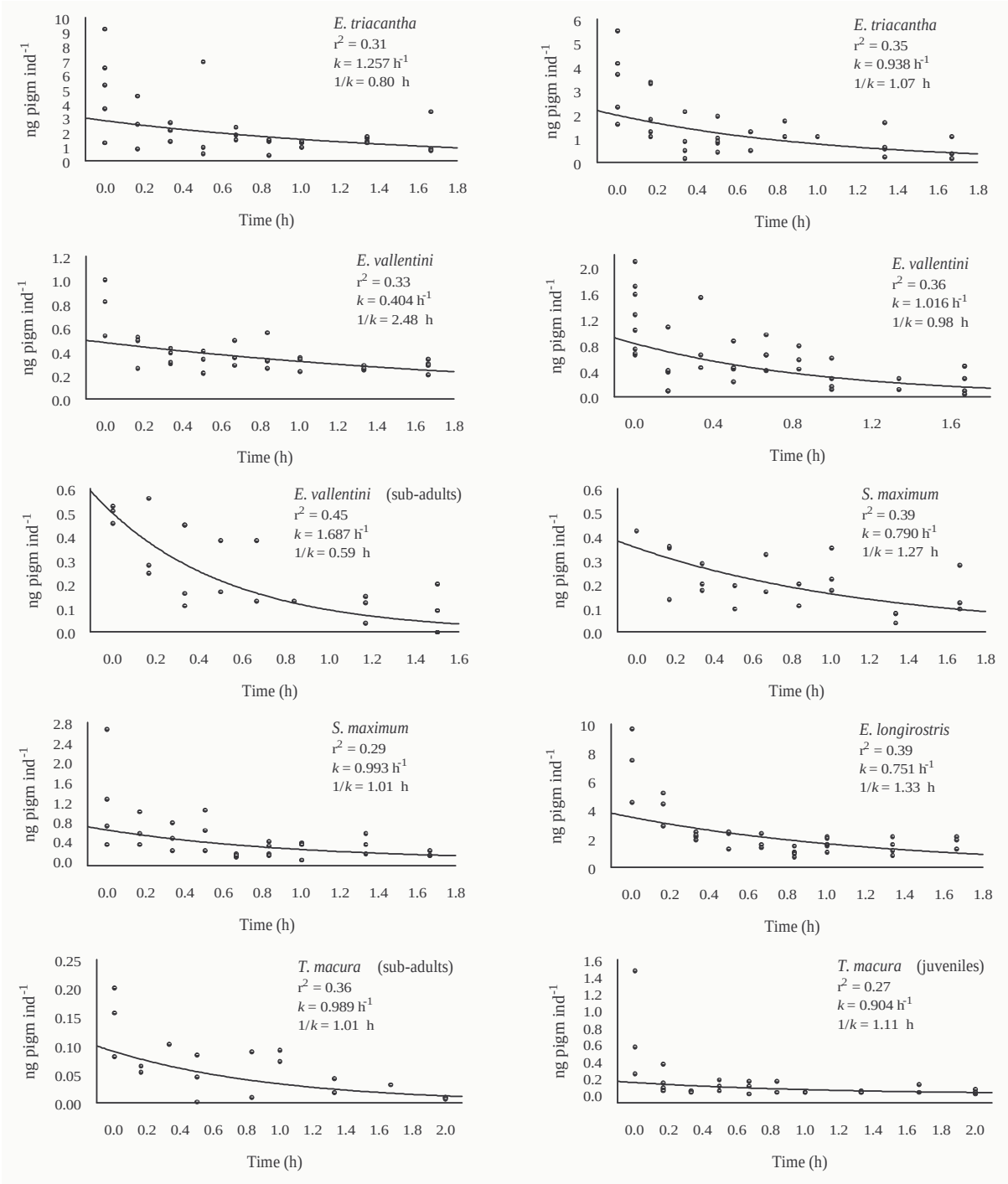


Figure 4.10: Dynamics of the decline in gut pigment, together with the results of the negative exponential regression analyses for the selected species of euphausiid analysed during MOEVS V. The gut evacuation rate (k) and gut passage time ($^1/_k$) are provided for each species.

Table 4.6: Individual ingestion rates (ng pigm $ind^{-1}d^{-1}$) of the dominant euphausiid species recorded in the different regions of the survey area during the MOEVS V survey.

		Species					
Zone	Station	*E. longirostris*	*E. triacantha*	*E. vallentini*	*S. maximum*	*E. frigida*	*T. macura* (juv)
Core	B00273			137.2			17.7
	B00277					28.5	
	B00285		717.1	139.8			8.6
	B00286		2239.8	351.7		18.5	
Edge	B00262	373.1	6250.4	39.3	303.1		
	B00263						8.9
	B00264		1470.9	102.4			105.9
	B00268						38.4
	B00278	732.3	1560.6	96.8	93.2	41.1	
	B00279	1655.2					
	B00280		1953.9	977.9			14.0
	B00283						100.6
PFZ	B00260	208.3		53.6	262.0		6.2
	B00261	425.9	6332.2	172.0			
	B00265						57.2
	B00272	1187.9	2225.0	834.0	31.8		
	B00290				320.9		
	B00291	270.7		30.6			

Grazing impact

To calculate the euphausiid community ingestion rates, RMT-8 abundance data (ind m^{-2}) were applied to the individual ingestion rates calculated for *E. longirostris*, *E. triacantha*, *E. vallentini*, *S. maximum* and *E. frigida*. The abundance data from the WP-2 net were applied to the individual ingestion rate of *T. macura* (juveniles). Community ingestion rates ranged between 0.02 and 5.31 µg pigm $m^{-2}d^{-1}$, with the highest community ingestion rates recorded at the stations occupied in the Core of the eddy (mean: 1.71 ± 1.74 µg pigm $m^{-2}d^{-1}$) (Table 4.7). The euphausiid community ingestion rate was lowest at the stations occupied in the PFZ waters (mean: 0.76 ± 0.69 µg pigm $m^{-2}d^{-1}$). A mean community ingestion rate of 1.09 ± 1.45

Table 4.7: Euphausiid community ingestion rates (µg pigm $m^{-2}d^{-1}$) and the total grazing impact of the dominant species of euphausiid recorded in the different regions of the survey area during the MOEVS V survey.

	Core		Edge		PFZ	
	mean	SD	mean	SD	mean	SD
Euphausiid community ingestion rate						
µg pigm $m^{-2}d^{-1}$	1.71	1.74	1.09	1.45	0.76	0.69
µg C $m^{-2}d^{-1}$	85.45	87.19	54.54	72.66	38.17	34.48
Chl-a biomass (mg pigm m^{-2})	9.26	1.62	6.83	1.52	7.52	1.87
Grazing impact (%)	0.02	0.02	0.02	0.03	0.01	0.01
% Contribution to grazing impact						
E. longirostris			4.3	4.4	17.3	15.5
E. triacantha	43.9	31.7	30.3	25.1	23.6	18.9
E. vallentini	4.5	8.8	6.0	15.1	8.8	9.4
S. maximum			0.7	0.8	2.4	2.9
E. frigida	2.7	5.5	0.1	0.1		
T. macura (juv)	48.9	38.2	58.5	33.3	47.9	28.4

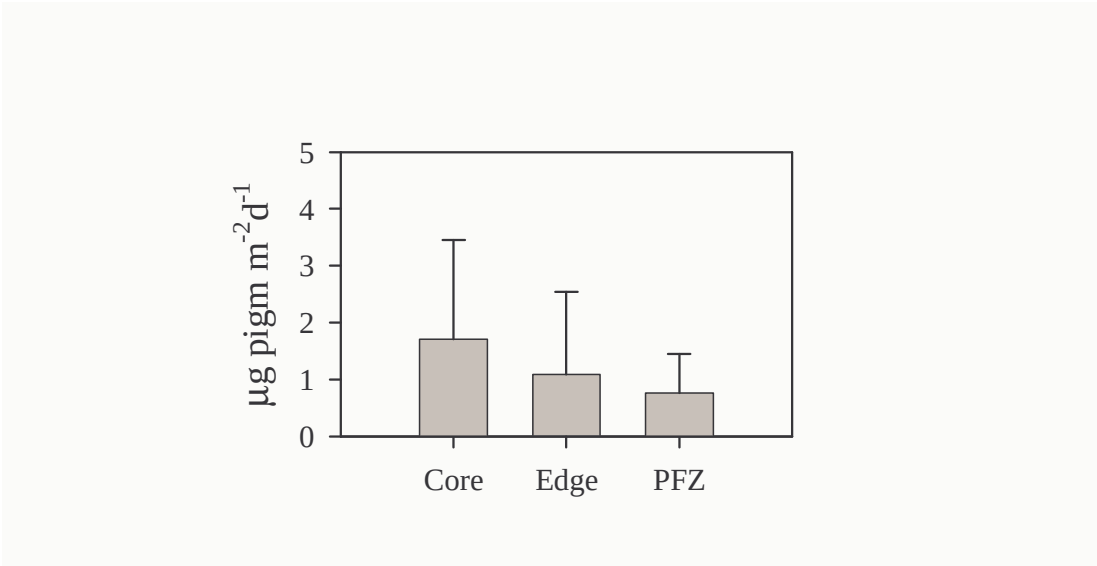


Figure 4.11: Mean (± SD) euphausiid community ingestion rates (µg pigm $m^{-2}d^{-1}$) for the Core, Edge and PFZ regions of the MOEVS V survey area.

µg pigm $m^{-2}d^{-1}$ was recorded within the edge of the eddy (Table 4.7). There were no significant spatial patterns in the euphausiid community grazing rates during the study (Fig 4.11) (Kruskal-Wallis ANOVA, $p > 0.05$).

The combined grazing impact of the euphausiids was very low, with the total euphausiid grazing impact never exceeding 0.2 % (range = < 0.001 – 0.11 %) of the total areal chl-*a* biomass. The combined grazing impact was similar between the Core and the Edge, *c.* 0.02 %, while lowest in the PFZ waters (0.01 ± 0.01 %) (Table 4.7). Again there was no significant difference between the grazing impacts of the six dominant species of euphausiid in the different zones ($p > 0.05$). In terms of the percentage chl-*a* biomass consumed, *T. macura* (juv) and *E. triacantha* were the dominant grazers, accounting for *c.* 54.1 ± 31.3 and 36.9 ± 23.9 % of the total euphausiid grazing activity, respectively (Table 4.7).

Table 4.8: Mean ingestion rates (µg C $ind^{-1}d^{-1}$) and daily ration estimates for the selected species of euphausiid used for the grazing experiment during the MOEVS V survey.

		Ingestion rate (µg C $Ind^{-1}d^{-1}$)		Daily ration (% Body carbon $ind^{-1}d^{-1}$)			
	Dwt (mg)	mean	SD	mean	SD	min	max
E. longirostris	20.28	34.67	27.07	0.38	0.30	0.11	0.91
E. triacantha	17.82	142.19	109.17	1.77	1.36	0.45	3.95
E. vallentini	3.97	13.34	16.47	0.75	0.92	0.09	2.73
S. maximum	10.50	8.82	6.66	0.19	0.14	0.03	0.34
E. frigida	4.57	1.47	0.57	0.07	0.03	0.05	0.10
T. macura (juv)	0.72	1.99	1.98	0.62	0.62	0.10	1.65

The dry weight estimates from the CL's of the euphausiids used in the gut pigment analysis were used to calculate the body carbon content of the selected euphausiids. Due the lack of any significant spatial variability in grazing activity, the species-specific ingestion rates from the Core, Edge and PFZ regions were combined to calculate the autotrophic daily ration

estimates of the selected euphausiids (Table 4.8). *E. triacantha* had the highest daily ration estimate, with an autotrophic carbon ingestion rate equivalent to between 0.45 and 3.95 % (mean = 1.77 ± 1.36 %) of their body carbon content (Table 4.8). The remaining species of euphausiid, namely *E. longirostris*, *E. vallentini*, *S. maximum*, *E. frigida* and *T. macura* (juveniles) had very low daily ration estimates, equivalent to < 1 % of their body carbon content (Table 4.8).

Discussion

Physical environment

The water column characteristics of the cold-core feature investigated during this study suggest that the eddy would have originated at the APF (Ansorge and Lutjeharms, 2003). Recent observations by Ansorge and Lutjeharms (2003) suggest that the mesoscale turbulence generated by the interaction of the ACC with the South-West Indian Ridge result in large eddies being formed. These eddies are subsequently advected into the PFZ where they contribute to the mesoscale variability in the oceanographic environment (Ansorge and Lutjeharms, 2003). To date, no biological studies have been conducted in the vicinity of these features.

Chlorophyll-a

The surface and integrated chl-*a* concentrations recorded during this study were lower than that previously reported for this region during austral autumn (Gurney *et al.*, 2002; Bernard

and Froneman, 2003; Ansorge *et al.*, 2004). This aside, the marked increase in areal chl-*a* biomass within the Core of the eddy suggests that the feature showed enhanced accumulation of areal chl-*a* biomass. Previous studies have shown that the Core region of an eddy is associated with the highest chl-*a* concentrations and biomass (Garcon *et al.*, 2001). Reasons for this have been ascribed mainly to factors that increase the nutrient concentrations within the eddy environment, including elevated nutrient concentrations at the eddies origin (Garcon *et al*., 2001) and eddy pumping (Falkowski *et al*., 1991; McGillicuddy Jr. *et al.*, 1998).

Trends in euphausiid population characteristics

The total abundance and biomass of euphausiids recorded within the three regions of the survey area using the RMT-8 net are considerably greater than what has previously been reported for the Indian sector of the PFZ using the same sampling gear (Pakhomov and Froneman, 2000). Indeed, the estimates of abundance and biomass fall within the upper range of what has previously been reported for the entire macroplankton and micronekton assemblage in the PFZ (Pakhomov and Froneman, 2000). Furthermore, the euphausiid abundance estimates are within the range of the total macrozooplankton community of the Northwest Weddell Sea, except when large swarms of *E. superba* were encountered (MOCNESS, Fisher *et al.*, 2004). Similarly the Core abundance estimates of *E. triacantha*, *E. frigida* and *T. macura* are considerably greater than summer estimates from the region to the east of Prydz Bay for the same species (RMT-8, Hosie *et al.* 2000). The results from the WP-2 data show a similar trend, with the total euphausiid abundance estimates, particularly in the Core of the feature, falling within the total macrozooplankton range reported for the PFZ (Bongo net, Froneman *et al*., 1999; Froneman *et al*., 2002). Also, the WP-2 abundances of *T. macura*, reported here, are comparable to *Thysanoessa* species recorded during the summer

months in the Scotia Sea (Ward *et al.*, 2004). A number of studies have demonstrated that the APF is characterized by elevated abundance and biomass of macrozooplankton and micronekton (Pakhomov *et al.*, 1999; Pakhomov and Froneman, 2000; Pakhomov *et al.*, 2000). The elevated abundance and biomass of euphausiids in the Core of the eddy could therefore be related to the fact that the feature appeared to have originated from the APF.

Past studies on zooplankton dynamics within eddies and the surrounding waters have shown that distinct community assemblages exist within the distinguishable regions of the features, and that these communities change as the eddy ages, reflecting entrainment of zooplankton species that show seasonal variability in abundances and different communities associated with different zoogeographic regions (Mackas and Galbraith, 2002; Endo and Wiebe, 2005; Mackas *et al.*, 2005). Both the RMT-8 and WP-2 data sets showed distinct spatial patterns in euphausiid population characteristics associated with the *a priori* determined regions. The euphausiids of the PFZ region were typical of those previously recorded in the PFZ during the same season (Pakhomov and Froneman, 2000; Froneman *et al.*, 2002; Gurney *et al.*, 2002; Hunt and Pakhomov, 2003). On the other hand, the euphausiids of the Core region comprised mainly of vagrants (*E. triacantha*, *E. superba* and *E. frigida*) that are rarely recorded within the PFZ (Pakhomov and Froneman, 2000; Froneman *et al.*, 2002; Gurney *et al.*, 2002; Hunt and Pakhomov, 2003), and are typically associated with the region to the south of the APF (Mauchline and Fisher, 1969; Deacon, 1982). Mackas and Galbraith (2002) suggested that the zooplankton found in the Core of an eddy reflect the area where the eddy formed. The presence of Antarctic species, and the characteristics of the seawater within the Core of this eddy, suggests that the feature was formed in the region of the APF and that eddy was able to retain, to some degree, the euphausiid species that were distinctive of the front.

The multivariate analysis conducted on the RMT-8 and WP-2 data sets were in general agreement. In both cases ANOSIM suggested that although the separation, in terms of community structure and abundance estimates, between the PFZ region and the Edge region were blurred, the Core region was in fact a separate entity to its surrounding waters, particularly the PFZ. The absence of any distinct differences between the PFZ and the eddy Edge can be attributed to the fact that the eddy edge represents a transition zone between the cold-core feature and the surrounding waters (Mackas *et al*., 2005). Only *E. vallentini* and *T. macura* were recorded in each of the zones for both the WP-2 and RMT-8 data. *T. macura* is known to occur in the Antarctic Polar Frontal Zone (Pakhomov and Froneman, 2000; Froneman *et al.*, 2002) and within Antarctic waters (Mauchline and Fisher, 1969; Pakhomov *et al.*, 1999; Pakhomov *et al.*, 2000; Fisher *et al.*, 2004). On the other hand, *E. vallentini* is usually only associated with the PFZ (Mauchline and Fisher, 1969). The presence of this species in the Core of the eddy suggests that it is likely to have been entrained into the feature once it had been spawned from the region of the front. While the opposite could be proposed for *E. triacantha*, whose presence in the PFZ could reflect the loss of individuals from the eddy (Table 4.3, Figure 5.3). It is possible that the deep vertical distribution pattern of *E. triacantha* reduced its exposure to surface wind driven inertial currents and ekman transport, allowing the species to retain its position in the eddy (Mackas *et al*., 2005).

Correlations between zooplankton densities and phytoplankton biomass have been reported on a number of occasions, and have been attributed to aggregation of zooplankton around rich feeding grounds (Pakhomov and McQuaid, 1996; Pakhomov *et al*., 2000; Gurney *et al*., 2002). Although it is possible that the correlations between chl-*a* biomass and *E. frigida* (positive correlation), *E. longirostris* and *S. maximum* (negative correlation) from the RMT-8 data are linked to feeding habits of the specific species, it is likely that the associations are

not causative and merely reflect the predominance of *E. frigida* within the Core of the eddy, where the highest ($p < 0.05$) areal chl-*a* biomass was recorded, and the restricted distributions of *E. longirostris* and *S. maximum* to the PFZ and Edge regions that were characterized by reduced areal chl-*a* biomass. This result again reaffirms the role of the Edge region of the eddy as a biological boundary to selected species of euphausiid.

Euphausiid grazing

The gut pigment contents of all species of euphausiid analyzed were very low, with the exception of *E. triacantha*, and fell below the range of previous findings for the same species (Gurney *et al*., 2002; Pakhomov and Froneman, 2004). A diel pattern in gut pigment content was only evident for *E. vallentini*, while the gut pigment concentrations of *E. longirostris*, *E. triacantha*, *E. frigida*, *T. macura* and *S. maximum* varied to a greater or lesser degree throughout the 24 hour period. Diel variability in gut pigment concentrations of euphausiids has been reported by a number of authors (Gurney *et al*., 2002; Pakhomov and Froneman, 2004), and can been attributed to the diel vertical migrations undertaken by the zooplankton. The absence of clear trends in gut pigment is thought to be a result of a continuous feeding behaviour (Gurney *et al*., 2002).

A number of studies have calculated gut evacuation rates and gut pigment degradation coefficients for *E. vallentini* and *E. longirostris* (Gurney *et al*., 2002) and *E. triacantha* and *T. macura* (Pakhomov and Froneman, 2004). Of these, only the gut evacuation rate of *T. macura*, $k = 0.55\ h^{-1}$ (Pakhomov and Froneman, 2004), showed considerable deviation of from that reported here, $k = 0.95\ h^{-1}$. The gut evacuation rates reported for *S. maximum* are the first reported for this region.

Various factors are though to contribute to the variability in gut pigment destruction rates commonly observed for zooplankton, including the degree of starvation or the level of feeding activity (Head, 1992), prey type and trophic history (Mayzaud and Rayzouls, 1992). Past studies have reported fairly high pigment degradation rates for euphausiids, > 50 % (Perissinotto, 1992; Perissinotto and Pakhomov, 1996; Perissinotto *et al.*, 2001; Gurney *et al.*, 2002). Although there was considerable variability in the estimates, the mean gut pigment destruction rate estimates reported here were generally < 50 % of the total pigment ingested. Due to the fact that the starvation and acclimation period for the various species was standardized, coupled with the fact that the euphausiids were incubated at similar food concentrations, the observed variability in gut pigment destruction rates can likely be attributed to the condition of the individual experimental animals.

The individual ingestion rates of the selected euphausiid species during this investigation were below or within the lower range of ingestion rates previously reported for the same species within the PFZ and indeed in other regions of the Southern Ocean (see for example: Perissinotto, 1992; Pakhomov *et al.*, 1997; Gurney *et al.*, 2002; Pakhomov and Froneman, 2004). Perissinotto (1992) demonstrated that the sub-Antarctic euphausiids, *E. vallentini* and *T. vicina*, actively select food particles in the micro- (20 – 200 µm) and to a lesser extent nanophytoplankton (2 – 20 µm) size classes. During the present study, the total chl-*a* concentrations were dominated by picophytoplankton, which are generally considered to be too small to be grazed efficiently by the large euphausiid species (Fortier *et al.*, 1994). The low chl-*a* biomass together with the unfavourable size structure of the phytoplankton community within the region of investigation may have accounted for the low ingestion rates and grazing impact of the numerically dominant euphausiids. Although euphausiid grazing

impact seldom exceeds 5 % of the total areal chl-*a* biomass (see table 1.1), the values reported here (< 0.15 %) fall well below the range of values presented in the literature (Perissinotto, 1992; Pakhomov *et al*., 1997; Perissinotto *et al.*, 1997; Pakhomov and Froneman, 2004).

It is generally assumed that for krill to meet their daily basic metabolic and energetic costs during the summer months, they need to consume between 5 and 15 % of their body carbon weight in food (Clarke *et al.*, 1988; Huntly *et al.*, 1994; Perissinotto *et al.*, 1997). As this study was conducted during the austral autumn, when reproductive demand and growth is reduced, it is assumed that the daily ration of the euphausiids should range between 5 and 10 % of their body carbon. The mean daily rations of all the species of euphausiid examined were generally equivalent to < 2 % of body carbon. The low daily ration of autotrophic carbon reported for *S. maximum* (0.03 – 0.3 %) is not surprising as it demonstrates morphological adaptations for carnivory (Mauchline and Fisher 1969). The daily rations reported for *E. vallentini* (0.09 – 2.73 %) and *E. longirostris* (0.1 – 0.9 %) from this study are considerably lower than what has previously been reported for these species within the PFZ during autumn (Gurney *et al.*, 2002). It is worth noting that during the study conducted by Gurney *et al.* (2002) the total chl-*a* concentrations were more than double that recorded during the present study, and the nano- and microphytoplankton size classes contributed most to the total chl-*a* concentration. Thus the higher daily rations reported by Gurney *et al.* (2002) may be attributed to a more favourable phytoplankton community structure that was encountered during their study. Due to the low daily ration estimates recorded during this study, it is proposed that the selected euphausiid species examined would have had to make use of alternate food sources, such as protozooplankton and mesozooplankton to meet their daily carbon requirements.

Conclusion

The results reported here indicate that the abundance and biomass estimates of the euphausiids associated with the cold-core eddy were considerably greater than previously reported for the PFZ during austral autumn (Pakhomov and Froneman, 2000; Froneman *et al.*, 1999), and indeed are comparable to the more productive regions of the Southern Ocean, e.g. the NW Weddell Sea, the Scotia Sea and Prydz Bay, during summer (Hosie *et al.*, 2000; Fisher *et al.*, 2004; Ward *et al.*, 2004).

The ability of the eddy investigated during this study to transport large numbers of vagrant species into the PFZ (*E. triacantha*, *E. frigida* and *E. superba*) suggests that these features contribute to the spatial heterogeneity of the zooplankton community composition within the PFZ. In addition, the elevated euphausiid abundance and biomass values within the feature suggest that eddies generated by the interaction of the ACC with the South-west Indian ridge may represent important foraging grounds for the apex predators found on the various oceanic islands in the PFZ.

The results from the grazing studies suggest that all of the euphausiid species examined would have had to make use of alternate carbon sources to meet their daily energetic demands. The observed pattern appears to be related to the low biomass and unfavorable size structure of the phytoplankton assemblage that is a characteristic of the PFZ during the unproductive autumn and winter months.

Summary and conclusions

The results of this study indicate that the region where the ACC interacts with the Southwest Indian Ridge is characterized by extreme spatial and inter-annual mesoscale variability in both physico-chemical and biological variables. During 2004, the frontal systems that delimit the PFZ converged to form a single intense feature, which separated the area of investigation into two distinct regions. During 2005 a cyclonic geostrophic circulation cell, consisting of a core of Antarctic surface water, was nested within the waters of the PFZ.

The total surface chlorophyll-*a* concentrations and areal chl-*a* biomass encountered during the survey conducted during 2004 (0.03 to 0.26 µg chl-*a* L^{-1}; 4.15 to 22.18 mg chl-*a* m^{-2}, respectively) were considerably greater than that recorded in 2005 (0.06 to 0.14 µg chl-*a* L^{-1}; 4.13 to 11.37 mg chl-*a* m^{-2}, respectively). The elevated phytoplankton biomass that was observed in the core of the cold-core eddy investigated during 2005 can be ascribed to the fact that the feature was spawned from the APF which is well documented to be an area of elevated biological activity. Assuming that these features are also formed during summer, it is not unreasonable to suggest that during more favourable growth conditions, these features will produce a more substantial chl-*a* response.

During both surveys it was evident that the distributions of certain species of sub-Antarctic and Antarctic euphausiids were limited by biogeographic boundaries in the form of the frontal feature encountered during the 2004 survey, and the eddy in 2005. Although the euphausiid species composition was similar between the two surveys, the Core of the eddy encountered during 2005 had a greater representation of Antarctic species, with the notable

inclusion of *E. superba*. Indeed this result represents the most northerly record of this species in the Indian sector of the Southern Ocean (Mauchline and Fisher, 1969; Mauchline, 1980; Deacon, 1982; Baker *et al*., 1990). Moreover the abundance and biomass estimates recorded in the Core of the eddy (A = 0.01 to 18.24 ind m^{-3}, and B = 0.01 to 15.17 mg dwt m^{-3}), were twice as high as those recorded throughout the 2004 survey (A = 0.16 to 3.10 ind m^{-3}, and B = 0.15 to 8.05 mg dwt m^{-3}) (comparing Bongo and WP-2 net samples). The eddies ability to maintain, to some degree, the euphausiid populations from the APF and transport the elevated abundances and biomass into the PFZ not only increased the species heterogeneity in the region, but also suggests that these features may represent important foraging grounds for top predators found on the Prince Edward Islands. Similarly the front encountered in 2004 was characterized by elevated biomass estimates of euphausiids compared to the surrounding waters, suggesting that it may also represent an important foraging ground. These findings are supported by observations of grey-headed albatross and satellite tracking of elephant seals, which demonstrated that the predators often linger within the areas of mesoscale oceanographic variability in the PFZ (Nell *et al*., 2001, M. Bester, *pers comm*.).

The results from the grazing experiments conducted during both 2004 and 2005 agreed with the bulk of the literature on euphausiid feeding behaviour, which suggests that phytoplankton represent a minor component in the diets of euphausiids in the open waters of the PFZ, during the austral autumn and winter. It is likely that the low chl-*a* biomass and the predominance of the small phytoplankton, particularly picophytoplankton throughout both regions of investigation played a major role in the observed low ingestion rates and daily ration estimates of the selected species of euphausiid. Although the daily ration estimates for the majority of the species used in the feeding experiments were insufficient to meet their daily carbon requirements (< 5 %), exceptions were noted with the smaller size classes of

euphausiid, such as the sub-adult *E. vallentini* and *Thysanoessa* spp. (MOEVS IV), which had daily rations of autotrophic carbon sufficient to meet their theoretical daily carbon demands (> 5 % of their body carbon content). Interestingly *E. triacantha*, one of the larger species of euphausiid encountered during both surveys, was characterized by having relatively high ingestion rates (717.1 to 6332.2 ng pigm $ind^{-1}d^{-1}$) and daily ration estimates (0.45 to 4.42 %). The feeding basket of *E. triacantha* is known to be more highly setose than that for example *E. longirostris*, and thus could account for the observed high gut pigment concentrations (Mauchline, 1967; Mauchline and Fisher, 1969).

Seasonality within the Southern Ocean is marked, with the summer months seeing an influx of millions of top predators into the region to exploit the greatly elevated macrozooplankton and micronekton stocks (Pakhomov and Froneman, 1999). The current study was conducted during the unproductive autumn months and as a result the data presented is expected to reflect the basal level of phytoplankton concentrations, euphausiid abundance and biomass and grazing activity for the region. Nonetheless this data characterizes important aspects of the ecological response by euphausiids to the presence of mesoscale oceanographic features in the ACC. Although it appears that a response reflecting elevated euphausiid abundance and biomass in the regions of mesoscale variability occurs, the feeding by euphausiids on autotrophic production is limited due to the low biomass and unfavourable size structure of the phytoplankton assemblage, that characterizes the PFZ during the autumn and winter months. The next step would be to observe the response of the phytoplankton and in turn the euphausiids and other zooplankton populations within the mesoscale features during the productive summer months.

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Appendix 1:

Morphometric analysis

Only the dominant species of euphausiid that were represented by a wide range of size classes, namely *E. vallentini*, *E. triacantha*, *E. longirostris*, *S. maximum* and *T. macura*, were used for the morphometric analysis. The male and female *S. maximum* were analyzed separately as the species is known to have a number of sexual dimorphic traits (Mauchline and Fisher, 1969). Regressions were run using polynomial, exponential growth and power equations to determine the best fit of the data (Sigma Stat 8.0). The results of the regression analysis between the different measures of carapace length (CL) produced strong correlations ($R^2 > 0.97$), using polynomial quadratic and linear equations (Fig A1.1 – A1.6) for all except *E. longirostris*. Indeed *E. longirostris* were the exception throughout the analysis with the relationships between the sets of CL data and between the CL and weight data best described by fitting polynomial regression equations, at relatively low R^2 estimates (Fig A1.2). The CL to weight regressions performed on the remainder of the species of euphausiid used in the study were strong (i.e. $R^2 > 0.90$) and best described by power and exponential growth equations.

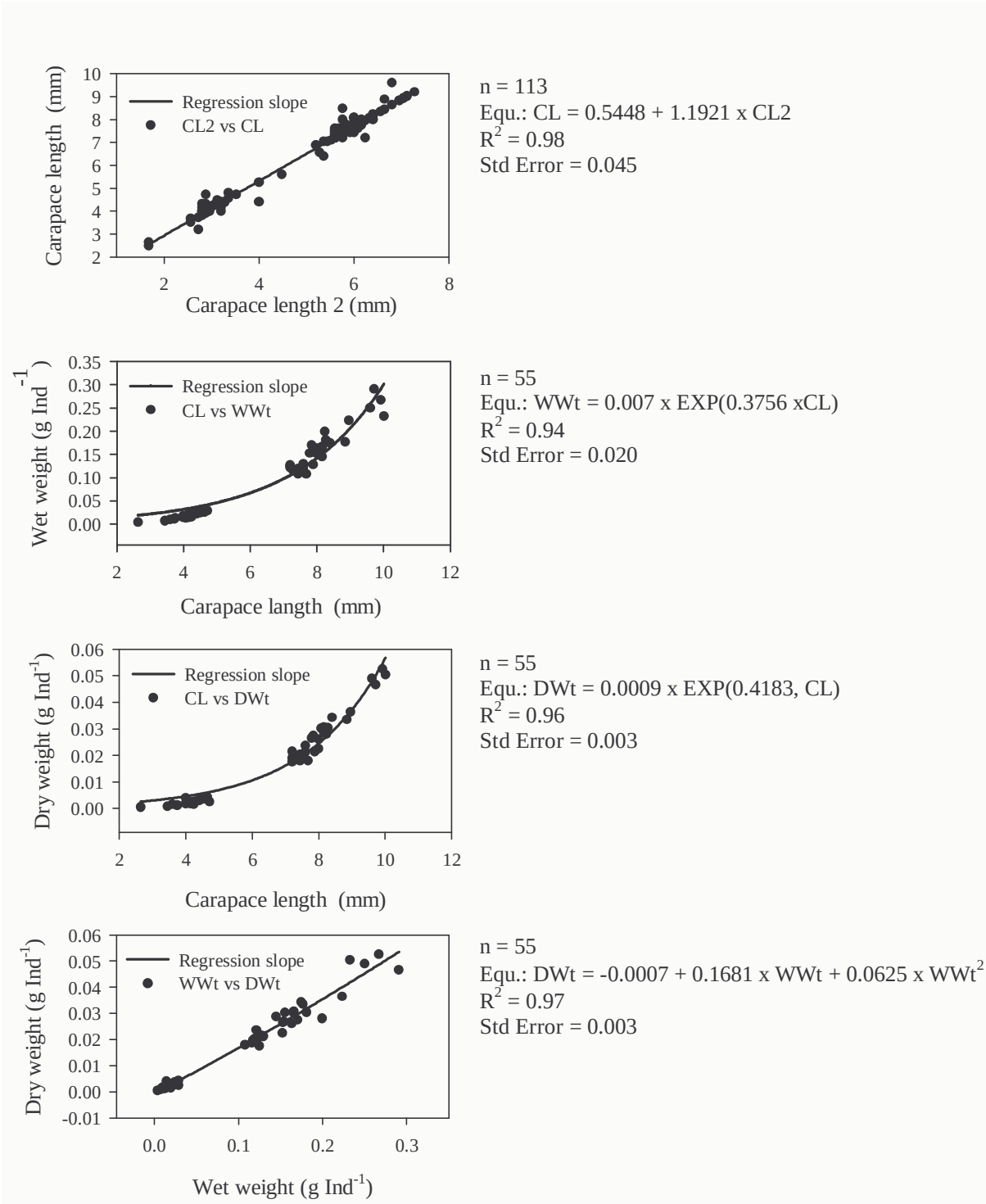

Figure A1.1: Morphometric relationships calculated for *E. triacantha*.

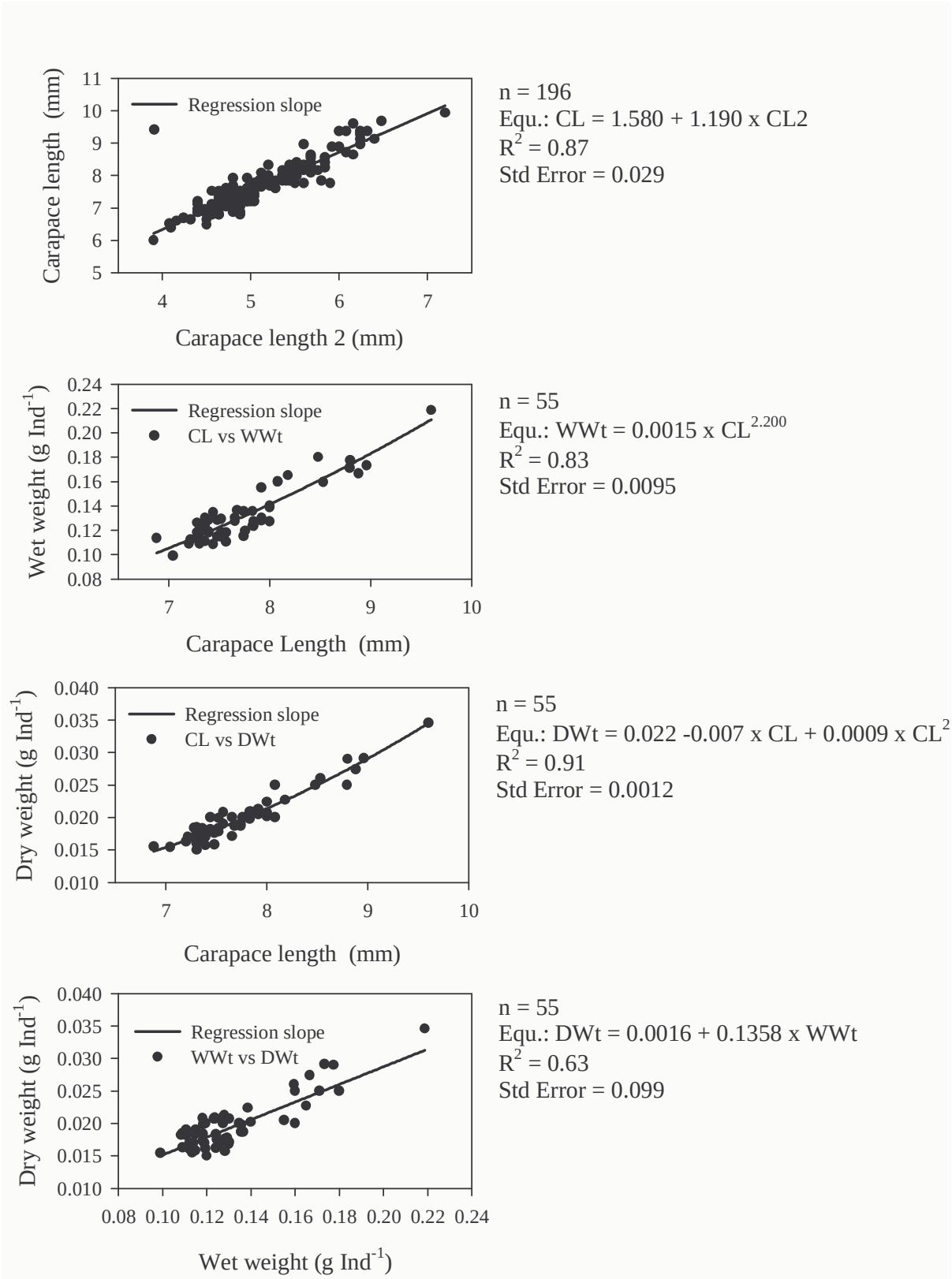

Figure A1.2: Morphometric relationships calculated for *E. longirostris*.

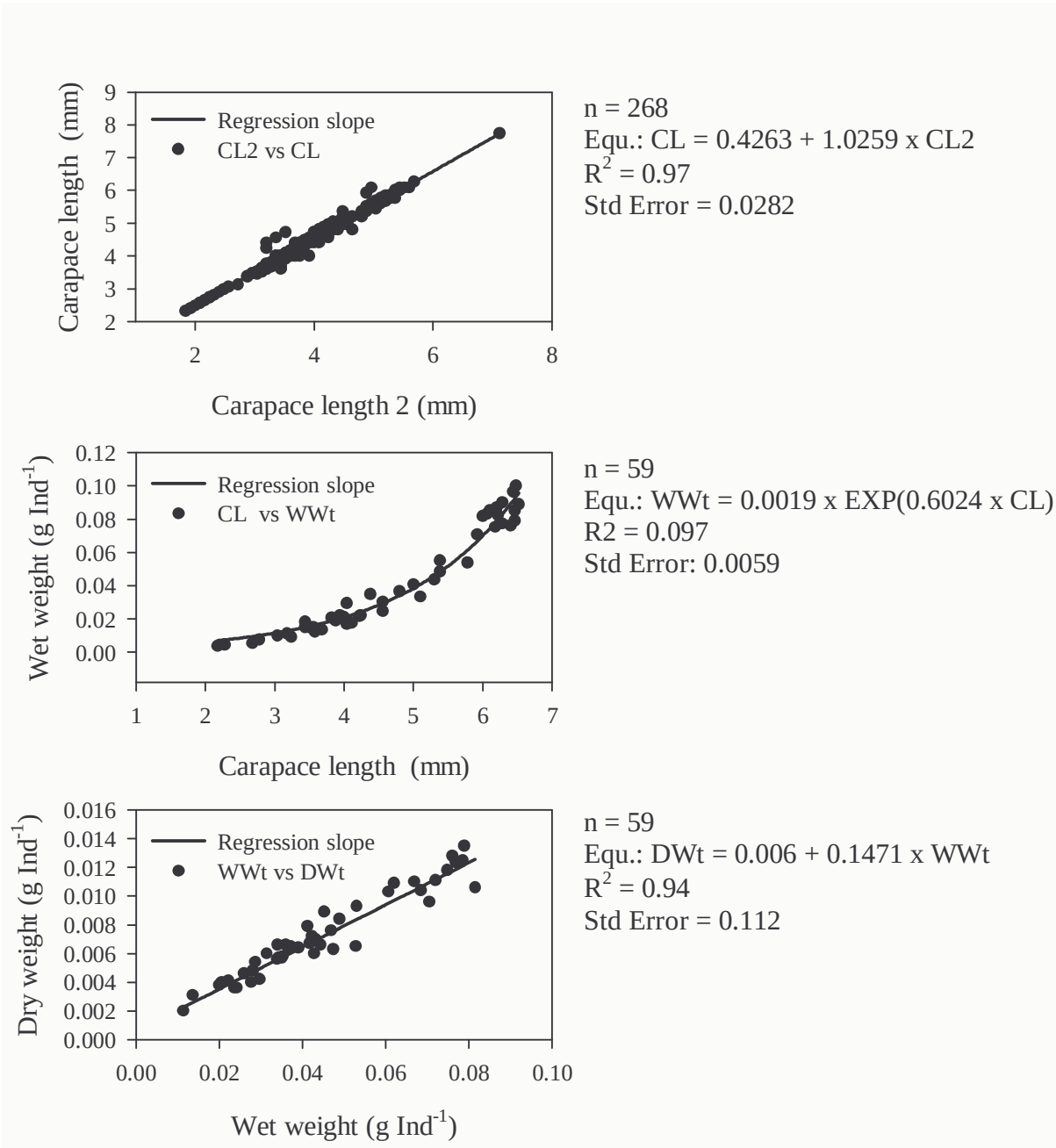

Figure A1.3: Morphometric relationships calculated for *E. vallentini*.

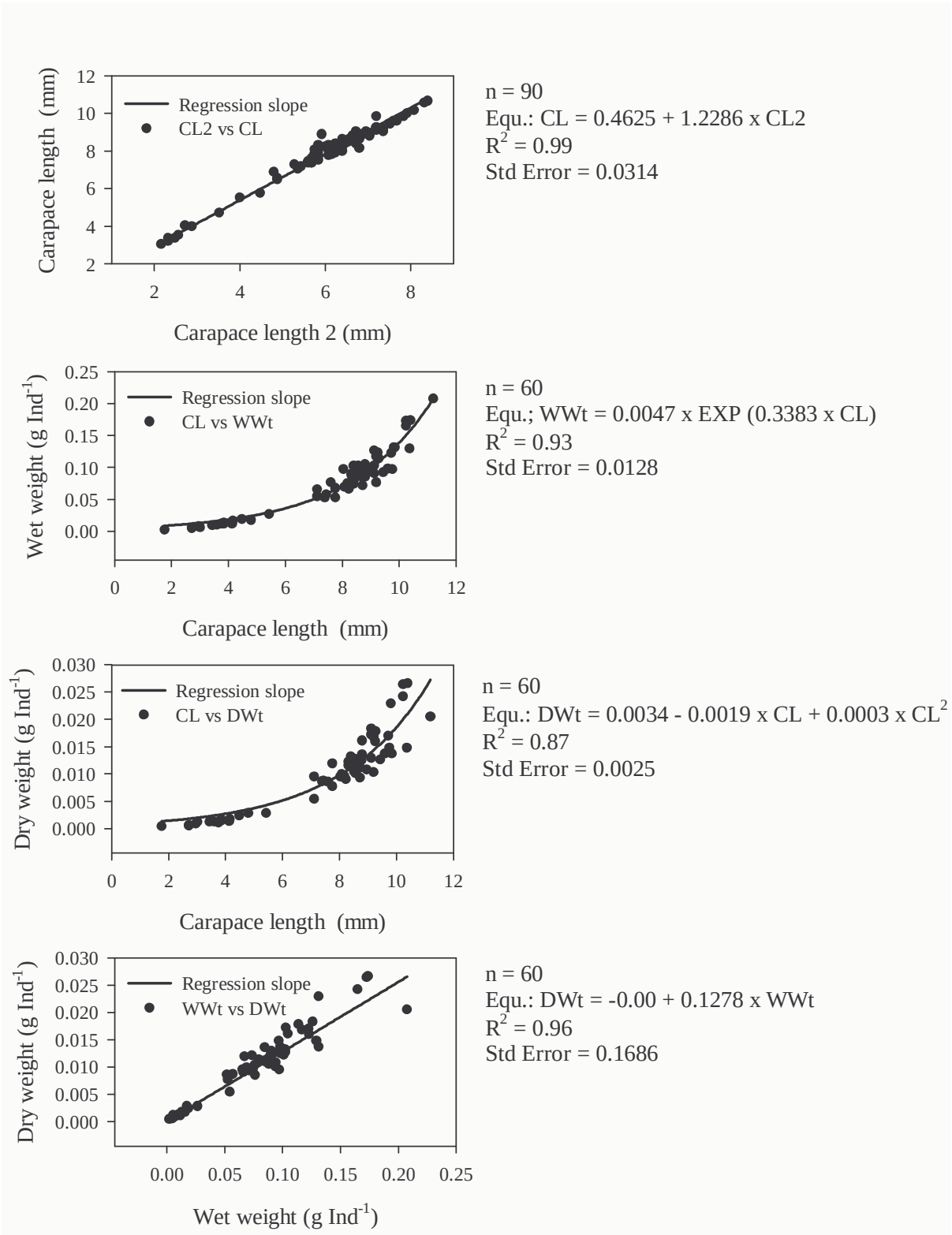

Figure A1.4: Morphometric relationships calculated for *S. maximum* females.

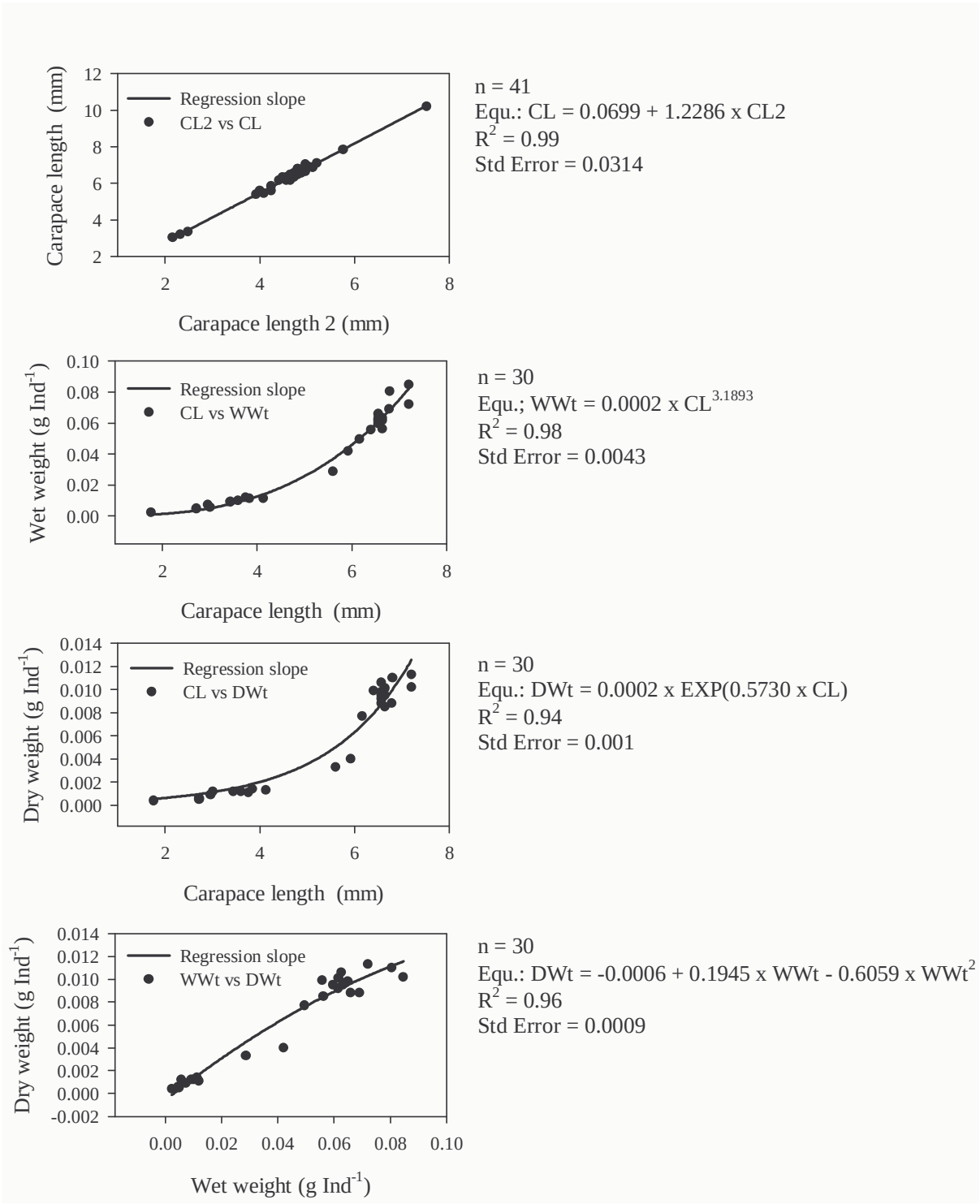

Figure A1.5: Morphometric relationships calculated for *S. maximum* males.

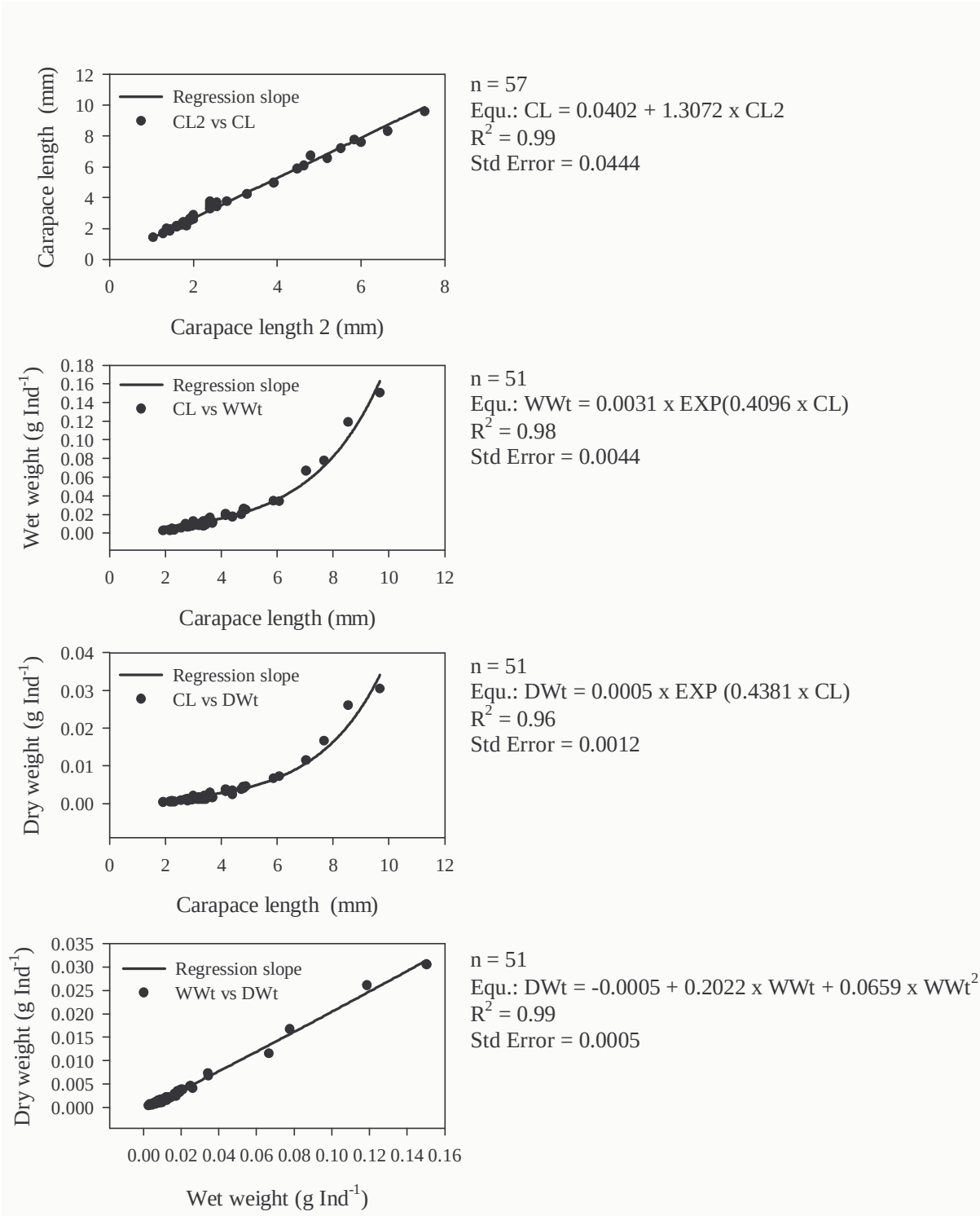

Figure A1.6: Morphometric relationships calculated for *T. macura*.

Table A1.1: Biological station details for the MOEVS IV survey conducted in April 2004. Asterix (*) = no sample collected.

Station	date	Time GMT)	Latitude (South)	Longitude (East)	Depth of tow Bongo	RMT-8
B00228	April 15, 2004	1:36 AM	49.9887	31.0580	200	*
B00229	April 15, 2004	6:20 AM	49.4993	31.0157	300	*
B00230	April 15, 2004	11:35 AM	49.0048	31.0093	*	400
B00231	April 15, 2004	5:11 PM	48.4868	31.0012	200	*
B00233	April 16, 2004	12:26 AM	47.7433	31.0283	*	300
B00234	April 16, 2004	6:18 AM	48.0067	32.2993	300	*
B00235	April 16, 2004	11:36 AM	48.3333	31.6833	*	400
B00236	April 16, 2004	4:58 PM	48.6677	31.1663	200	*
B00237	April 16, 2004	9:37 PM	48.9893	30.6358	200	*
B00238	April 17, 2004	2:36 AM	49.3257	30.0903	200	*
B00239	April 17, 2004	7:20 AM	49.6728	29.5337	300	*
B00240	April 17, 2004	12:03 PM	50.0023	29.0008	300	*
B00241	April 17, 2004	7:54 PM	49.0100	29.2322	200	*
B00242	April 17, 2004	12:34 AM	49.0000	29.9845	200	*
B00243	April 18, 2004	5:27 AM	48.9833	30.7500	300	*
B00244	April 18, 2004	10:20 AM	48.9975	31.5280	300	*
B00245	April 18, 2004	3:54 PM	48.9990	32.4952	*	300
B00246	April 18, 2004	10:44 PM	49.0082	33.2720	*	300
B00247	April 19, 2004	1:14 AM	49.0138	34.0297	*	300
B00248	April 20, 2004	7:31 AM	48.0197	30.0145	300	*
B00249	April 21, 2004	5:40 AM	48.3695	30.4962	*	400
B00250	April 21, 2004	10:31 AM	48.7518	30.9783	*	400
B00251	April 21, 2004	2:30 PM	49.1245	31.4697	300	*
B00256	April 22, 2004	10:56 AM	49.8522	32.4528	300	*

Table A1.2: Biological station details for the MOEVS V survey conducted in April 2005.

Asterix (*) = no sample collected.

Station	date	Time GMT)	Latitude (South)	Longitude (East)	Depth of tow	
					WP-2	RMT-8
B00259	April 16, 2005	5:51 AM	49.3343	31.0280	300	500
B00260	April 16, 2005	4:58 PM	49.1437	32.6020	200	500
B00261	April 16, 2005	11:08 PM	48.7960	33.2152	200	500
B00262	April 17, 2005	6:43 AM	48.4605	33.6177	300	500
B00263	April 17, 2005	11:24 AM	48.1233	34.1485	300	500
B00264	April 17, 2005	6:07 PM	47.7878	34.7500	200	500
B00265	April 18, 2005	4:50 AM	47.7673	33.0057	300	500
B00267	April 18, 2005	2:38 PM	48.5415	34.0458	*	500
B00268	April 18, 2005	10:08 PM	48.8770	34.0768	200	*
B00269	April 19, 2005	3:31 AM	49.3177	34.6517	200	*
B00270	April 19, 2005	8:43 AM	49.7472	35.0770	300	500
B00272	April 19, 2005	6:03 PM	49.4055	35.3768	200	500
B00273	April 19, 2005	11:19 PM	48.9137	35.3247	200	500
B00274	April 20, 2005	5:59 AM	48.5725	35.0840	300	500
B00275	April 20, 2005	1:32 PM	48.0865	35.0357	300	500
B00276	April 20, 2005	7:12 PM	48.3622	34.7807	200	500
B00277	April 21, 2005	12:08 AM	48.6263	34.4670	200	500
B00278	April 21, 2005	4:38 AM	48.9145	34.1118	300	500
B00279	April 21, 2005	9:38 AM	49.1645	33.9452	300	500
B00280	April 21, 2005	2:34 PM	49.6707	34.0148	300	500
B00282	April 22, 2005	1:18 AM	48.7725	33.5763	200	500
B00283	April 22, 2005	6:10 AM	48.7645	33.9795	300	500
B00284	April 22, 2005	11:11 AM	48.7257	34.5268	300	500
B00285	April 22, 2005	3:10 PM	48.7515	35.0302	300	500
B00286	April 22, 2005	7:06 PM	48.7775	35.4878	200	500
B00288	April 23, 2005	4:47 AM	48.1318	35.9160	300	500
B00290	April 23, 2005	1:55 PM	48.7675	36.2005	300	500
B00291	April 24, 2005	9:00 AM	48.9442	36.3353	300	500
B00295	April 24, 2005	11:01 PM	48.9638	36.3845	200	500