Micronekton and Macrozooplankton of the Western Antarctic Peninsula and the Eastern Ross Sea: Contrast Between Two Different Thermal Regimes

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Micronekton and Macrozooplankton of the Western Antarctic Peninsula and the Eastern Ross Sea: Contrast Between Two Different Thermal Regimes

by

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A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy
College of Marine Science
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ABSTRACT

Micronekton and macrozooplankton were sampled from the Western Antarctic Peninsula (WAP) and eastern Ross Sea regions. Samples were collected over the course of six research cruises to the Southern Ocean. Four of those cruises were conducted in the Marguerite Bay region of the WAP during the austral fall and winter of 2001 and 2002. A fifth cruise sampled faunal assemblages at nine sites, ranging from Joinville Island at the northern tip of the WAP to Charcot Island near the southern extent of the WAP, during austral fall 2010. A sixth cruise was conducted in the pack ice within the offshore, continental slope, and continental shelf zones of the Eastern Ross Sea during austral summer 1999/2000. The purpose of this dissertation was to describe the macrozooplanktonic/micronektonic faunal assemblages present in each of those regions and relate differences in species composition and distribution patterns to local bathymetry, hydrography, and physical conditions. A variety of multivariate techniques were used to identify unique multispecies assemblages and to quantify the contributions of both oceanic and neritic species to the assemblages within each study region.

The invertebrate micronekton/macrozooplankton communities found in the Marguerite Bay region of the WAP during the 2001/2002 cruises were a mixture of oceanic and neritic fauna: a direct result of local hydrographic conditions. Near the shelf break and in the outer reaches of the Marguerite Trough, a deep canyon transecting the
shelf in a south-southeast direction, the communities were more diverse, dominated by oceanic species such as the euphausiid, *Euphausia triacantha*, the salp, *Salpa thompsoni*, and an amphipod, *Themeisto gaudichaudii*. The assemblages present in the nearshore fjords exhibited lower diversity and were dominated by neritic species such as the euphausiids, *E. crystallorophias*, and the mysid, *Antarctomysis ohlinii*. At the mid-shelf and mid-trough locations, the assemblages were composed of a variable mixture of oceanic and neritic fauna. The faunal mixing and overall species composition in those areas is the result of episodic Circumpolar Deep Water (CDW) intrusions onto the shelf via deep bathymetric features such as the Marguerite Trough.

Distinct multispecies assemblages were identified at Joinville, Croker Passage, Marguerite Bay, Charcot Island, and from a region that included samples from sites near Anvers Island, Renaud Island and the Marguerite Trough. Assemblages at Joinville and Croker Passage were both dominated by *E. superba* and *S. thompsoni*, but hydrographic conditions at Joinville favored a neritic assemblage, underscored by the substantial numbers of the nototheniid fish, *Pleuragramma antarcticum*. The assemblage at Croker Passage was more oceanic in nature with major inputs from the myctophid fish, *Electrona antarctica* and the amphipod, *T. gaudichaudii*.

Marguerite Bay and Charcot Island were well-mixed assemblages with strong representation by both neritic and oceanic fauna. The mid-peninsula assemblage was also oceanic in character, being overwhelmingly dominated by the euphausiid, *Thysanoessa macrura*, and *T. gaudichaudii*. *Pleuragramma antarcticum* were captured at five sites: Joinville, Croker Passage, Marguerite Bay, and the two sites near Charcot
Island. They were completely absent at the two sites near Anvers Island, at Renaud Island, and in the Marguerite Trough.

In the eastern Ross Sea, cluster analyses identified three primary groups, which were characterized as oceanic, mixed, and neritic assemblages due partly to their geographical location, but mostly to their faunal composition. The oceanic assemblage contained the highest number of taxa and was dominated by oceanic fauna, such as the hydrozoans *Diphyes antarctica* and *Calycopsis borchgrevinki*, and the scyphozoan *Atolla wyvillei*. Top contributors in the mixed assemblage included those species that dominated in the oceanic assemblage as well as substantial contributions from *E. superba* and the tunicate, *Ihlea racovitzai*. The neritic assemblage was overwhelmingly dominated by *E. crystallorophias* and *E. superba*. The physical environment strongly impacted micronektonic/ macrozooplanktonic distributions and densities in the eastern Ross Sea. Changes in faunal composition were directly related to temperature differences encountered at the shelf break and the subsequent filtering out of oceanic fauna from cold, shelf waters where endemic fauna were most prevalent.
CHAPTER ONE
INTRODUCTION TO THE SOUTHERN OCEAN AND THE STUDY SITES IN THE
WESTERN ANTARCTIC PENINSULA AND THE EASTERN ROSS SEA

The Southern Ocean

Zooplankton distributions in the Antarctic marine ecosystem are largely
influenced by the physical features and environmental conditions of the region. Major
physical characteristics, such as circulation patterns and frontal regions, combine to
create an ecosystem that is essentially isolated from the rest of the world (Laws, 1985).
Water temperatures are always cold, but sea ice extent and irradiance levels change
throughout the year. High nutrient concentrations in the austral spring support rich
phytoplankton blooms in coastal upwelling and ice edge regions. All of these
characteristics make the Southern Ocean one of the most unique and productive regions
of the world.

One distinct physical characteristic of the Southern Ocean is the Antarctic
Convergence or Polar Front. This is the zone where cold Antarctic surface waters
flowing northward meet warmer sub-Antarctic waters flowing southward (Laws, 1985).
Waters south of this zone, which is centered near a latitude of 50° S, are much colder,
exhibiting temperatures ranging from -2°C to 4°C (Laws, 1985; Huntley and Niiler, 1995;
Larsson, 2004). This boundary encircles the Antarctic continent essentially creating a semi-closed ecosystem, which contains many endemic and uniquely adapted species (Hempel, 1985; Knox, 1994).

Circulation patterns are one of the strongest influences on distributions of zooplankton in the Southern Ocean (Deacon, 1937; Stein and Heywood, 1994; Huntley and Niiler, 1995). The driving force behind Southern Ocean circulation is the surface wind field (Foster, 1984). Near the continent, surface currents are pushed by easterly winds to create the Antarctic Coastal Current (Knox, 1994). Farther offshore, both surface and deeper currents are forced northward by the Antarctic Peninsula and then driven clockwise around the continent by westerly winds (Laws, 1985). This clockwise circulation, the Antarctic Circumpolar Current (ACC), is the only oceanic current that fully encircles the globe (Knox, 1994). Between those two well-defined currents exists a series of irregular eddies and gyres that may act to either disperse or retain local zooplankton populations (Foster, 1984; Quetin et al., 1996).

Sea ice is another dominant and distinguishing characteristic of the Southern Ocean. Within a single year, sea ice extent can vary from a minimum area of $4 \times 10^6 \text{ km}^2$ during the austral summer to approximately five times that area during the austral winter (Stammerjohn and Smith, 1996). The duration of the sea ice season can also vary from year to year and has been reported to be decreasing in some regions of the Southern Ocean over the past 50 years (Smith et al., 2003a, b). Those variations in sea ice extent and duration both directly and indirectly influence abundance and distributions of zooplankton populations. Sea ice directly impacts zooplankton by providing habitat, a
feeding site or source, refuge from predators, and a breeding ground (Stammerjohn and Smith, 1996). Sea ice indirectly affects zooplankton by impacting phytoplankton concentrations and primary productivity rates. The formation of sea ice increases surface water salinities, which decrease water column stability and phytoplankton abundances (Foster, 1984). Sea ice, and the overlying snow cover, further inhibits primary productivity by decreasing light penetration into surface waters. Conversely, melting of sea ice decreases surface salinities, thus increasing water column stability and allowing phytoplankton to thrive in a high-light, high-nutrient environment (Knox, 1994).

Phytoplankton abundance and distribution is highly variable in the Southern Ocean. While most oceanic waters exhibit very low phytoplankton biomass, waters near ice-edge zones, frontal zones, and coastal regions are highly productive (El-Sayed, 1988; Moline and Prezlin, 1996). Hart (1934) first reviewed the factors limiting phytoplankton production in the Southern Ocean and stated that physical features, such as those discussed in the previous paragraph, were most likely to influence production rates. More recent studies (Heywood and Whitaker, 1984; Hempel, 1985; El-Sayed, 1988; Knox, 1994; Moline and Prezlin, 1996; Larsson, 2004) suggest that zooplankton grazing, vertical mixing, and micro-nutrient limitations, especially iron, may be more important limiting factors.

The abundant, albeit patchy and seasonal, phytoplankton distributions found in the Southern Ocean support a large and diverse zooplankton community (Everson, 1984; Knox, 1994). Copepods, euphausiids, and salps are dominant herbivorous taxa, while amphipods, ostracods, and pelagic molluscs are secondary contributors (Knox, 1994).
The predatory component of the zooplankton assemblage includes chaetognaths, copepods, polychaetes, medusa, siphonophores, and larval fishes (Knox, 1994). Although the community is diverse, most descriptions of the pelagic ecosystem have focused on the Antarctic krill, *Euphausia superba*. Due to its overwhelming abundance and widespread distribution, *E. superba* serves as a primary food source for many higher trophic level predators including seabirds, penguins, seals, and whales (Marr, 1962; Laws, 1985; Knox, 1994). Although the importance of *E. superba* cannot be discounted, the zooplankton community as a whole plays a pivotal role in the ecology of the Antarctic ecosystem, functioning as a link between primary producers and upper trophic level predators (Piatkowski, 1985; Lancraft et al., 2004; Lawson et al., 2004).

**Study Sites**

Annual primary production rates are higher in the Ross Sea than in any other region of the Southern Ocean (Arrigo and van Dijken, 2004). The magnitude of the annual phytoplankton bloom is probably only limited by sea-ice dynamics and the availability of iron (Arrigo and van Dijken, 2004). However, this high phytoplankton biomass is coupled with relatively low zooplankton biomass (Tagliaabue and Arrigo, 2003). Diebel and Daly (2007) reported that zooplankton biomass in the Ross Sea was similar to that found on the Weddell Sea shelf, but an order of magnitude lower than that found on the Western Antarctic Peninsula shelf. Zooplankton biomass was lowest in the Indian Ocean sector. Community diversity in the Ross Sea is also low with *E. crystallorophias* and *E. superba* representing the majority of the macrozooplankton.
(Hecq et al., 2000). Because there have been very few studies on zooplankton
distribution and abundance in the Ross Sea, especially in the eastern Ross Sea, the factors
influencing zooplankton communities in this part of the Southern Ocean are not yet fully
understood.

In contrast to the Ross Sea, the coastal zone of the Western Antarctic Peninsula
(WAP) is considered one of the most productive and biologically rich areas in the
Southern Ocean (Marr, 1962; Huntley et al., 1991; Lascara et al., 1999). Krill abundance
is unusually high in this area and as a result densities of apex predators are also high
(Hofmann et al., 2002; Diebel and Daly, 2007). The WAP shelf region is characterized
by several physical factors thought to enhance winter survival of krill (Hofmann et al.,
2002; Ashijan et al., 2004). First, there is a gyral circulation pattern over the shelf in that
region that may act as a retention mechanism for krill and other zooplankton (Hofmann et
al., 2002). Second, the consistent presence of winter sea ice not only provides protection,
but may provide food for overwintering larval krill (Daly, 1990). Lastly, subsurface
intrusions of warm, nutrient-rich Circumpolar Deep Water (CDW) onto the shelf provide
essential heat and nutrients for several physical and biological processes. Specifically,
heat associated with CDW is considered important for maintaining subsurface water
temperatures on the shelf (Dinniman et al., 2011), as well as for influencing annual sea
ice formation (Dinniman and Klinck, 2004). In addition, upwelling of CDW near the
shelf break brings nutrients into the upper water column, which enhances primary
productivity (Prezelin et al., 2000).
Summary of the Dissertation

The purpose of this dissertation was to describe the macrozooplanktonic/micronektonic faunal assemblages present at several sites along the Western Antarctic Peninsula (WAP) and in the Eastern Ross Sea and relate differences in species composition and distribution patterns to local bathymetry, hydrography and physical conditions. Each of Chapters 2 through 4 represents a separate study and includes all relevant tables, figures, and references. Chapter 2 presents findings from a series of four cruises conducted in the Marguerite Bay region of the WAP during the austral fall and winter of 2001 and 2002. Chapter 3 compares faunal assemblages sampled from nine different sites, ranging from Joinville Island at the northern tip of the WAP to Charcot Island near the southern extent of the WAP, during the austral fall of 2010. Chapter 3 also focuses on distribution and abundance of the Antarctic silverfish, Pleuragramma antarcticum, and how its disappearance from some Antarctic regions may be related to climate change. Chapter 4 compares faunal assemblages captured from the pack ice within the offshore, continental slope, and continental shelf zones in the eastern Ross Sea during the austral summer of 1999/2000. The final chapter presents a summary of conclusions from each of the previous three chapters.

References


CHAPTER TWO
INVERTEBRATE MICRONEKTON AND MACROZOOPLANKTON IN THE
MARGUERITE BAY REGION OF THE WESTERN ANTARCTIC
PENINSULA

Note to Reader
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Abstract
Invertebrate micronekton and macrozooplankton in the Marguerite Bay region of
the Western Antarctic Peninsula (WAP) were sampled using a 10-m² MOCNESS as part
of the Southern Ocean Global Ecosystem Dynamics (SO GLOBEC) program. A total of
62 trawls were completed during four separate cruises in the austral fall (April - June)
and winter (July - September) of 2001 and 2002. Crustaceans dominated the system in
both seasons, accounting for 32 of the 55 species captured in the fall and 30 of the 48
species captured in winter. In both seasons, a very few species made up the majority of
the catch. In the fall, the euphausiids, *Euphausia crystallorophias*, *E. superba*, and
*Thysanoessa macrura*, and the mysid, *Antarctomysis ohlinii*, numerically dominated the
assemblage, contributing over 85% of the total. In the winter, the same three euphausiids
and the chaetognath, *Pseudosagitta gazellae*, were the numerical dominants, comprising
over 90% of the catch. A significant increase in total abundance and biomass was
observed from 2001 to 2002.

The invertebrate micronekton/macrozooplankton communities found in the
Marguerite Bay region of the WAP were a mixture of oceanic and neritic fauna: a direct
result of local hydrographic conditions. Near the shelf break and in the outer reaches of
the Marguerite Trough, a deep canyon transecting the shelf in a south-southeast direction,
the communities were more diverse, dominated by oceanic species such as *Euphausia
triacantha*, *Salpa thompsoni*, and *Themisto gaudichaudii*. The assemblages present in the
nearshore fjords exhibited lower diversity and were dominated by neritic species such as
*E. crystallorophias* and *A. ohlinii*. At the mid-shelf and mid-trough locations, the
assemblages were composed of a variable mixture of oceanic and neritic fauna. The
faunal mixing and overall species composition in those areas is the result of episodic
Circumpolar Deep Water (CDW) intrusions onto the shelf via deep bathymetric features
such as the Marguerite Trough.

Species diversity and integrated abundance for the upper 200 m of the water
column were similar between seasons in the WAP study region, but integrated biomass
was nearly three times greater in fall than in winter. Integrated estimates from the WAP
study region were similar to those from other studies conducted in the Scotia and
Weddell Seas, but were orders of magnitude lower than estimates from a study in Croker
Passage, primarily due to a large catch of *E. superba*. In contrast, species diversity in the
WAP was higher than recorded in any of the previously mentioned studies, which is due
to the mixing of typical oceanic fauna with endemic nearshore fauna.

**Introduction**

The continental shelf in the Marguerite Bay region of the Western Antarctic
Peninsula (WAP) comprises a varying mixture of oceanic and neritic fauna. The mixture
is a result of at least three physical properties of the WAP shelf that removes barriers to
shelfward movement of open ocean species. First, its depth, though typical of the
Antarctic continental shelf (200-500 m; Eastman, 1993), is far greater than that found in
more temperate systems (200 m maximum; Sverdrup et al., 1942), resulting in an
environment with little to no depth limitation on distributions of open ocean fauna
(Eastman, 1993). Second, and unique to the WAP shelf, is the absence of a steep
temperature and salinity gradient, or slope front, at the shelf break (Klinck et al., 2004),
further increasing the potential for faunal mixing. Many species, especially fish, are
sensitive to the sharp temperature gradients encountered at the shelf break in most
Antarctic coastal systems (cf. Cullins et al., 2011) and, as a result, there is a clear
demarcation between oceanic and coastal assemblages in other Antarctic regions. A third
prominent physical feature of the WAP shelf region is the proximity of the Antarctic
Circumpolar Current (ACC), which flows in a northeasterly direction near the shelf
break. Many cross-shelf troughs and depressions are found on the WAP shelf, providing a route for intrusions of warm, oceanic Circumpolar Deep Water (CDW) and yet another mechanism for mixing open ocean and coastal assemblages (Hofmann et al., 1996; Smith et al., 1999; Klinck et al., 2004).

CDW is a nutrient-rich water mass associated with the ACC, characterized by temperatures ranging from 1.0 to 2.0 °C and salinities from 34.6 to 34.74. CDW intrusions onto the shelf occur when the ACC is deflected by changes in topography (Dinniman and Klinck, 2004). CDW typically resides at depths below 200 m, resulting in a water mass structure at depth that is nearly oceanic in character. In our study area, the Marguerite Trough, a deep canyon transecting the shelf in a south-southeast direction near Adelaide Island, enhances the extent of CDW intrusions by providing a deep connection between the outer shelf and inner reaches of Marguerite Bay. In 2001, Klinck et al. (2004) identified two to three CDW intrusions onto the shelf near Marguerite Bay, leading them to estimate a possible 4 – 6 intrusions per year in this region.

The importance of those CDW intrusions is three-fold. First, they may serve as an integral part of the life history of many species. For example, the presence or absence of CDW can greatly influence the success or failure of larval hatching in Antarctic krill (*Euphausia superba*). *E. superba* embryos sink after release in the water column, hatch at depth and then ascend to the surface during larval development (Marr, 1962). The fairly shallow depth and warm temperature of the CDW allow the larvae in turn to hatch at shallower depths and develop faster thus increasing their chances of survival (Hofmann et al., 1992; Hofmann and Husrevoglu, 2003). Second, the influx of nutrients into
surface waters via upwelling of CDW onto the shelf can create areas of enhanced
biological production (Prezelin et al., 2004). Finally, as CDW moves shelfward the
diffusion of heat and nutrients into cooler surface waters will influence annual sea ice
formation (Dinniman and Klinck, 2004).

Due to its unique physical properties, the WAP shelf region is one of the most
productive areas in the Southern Ocean and also serves as an important nursery ground
for the Antarctic krill, *Euphausia superba* (Marr, 1962; Siegel, 1988; Atkinson et al.,
2001). Most descriptions of the Antarctic pelagic ecosystem have focused on *E. superba*
due to its overwhelming abundance and widespread distribution, and its ecological
importance as a primary food source for fishes, seabirds, penguins, seals, and whales
(Marr, 1962; Laws, 1985, Knox, 1994). However, there are not only three other abundant
species of euphausiid, but also an entire suite of micronektonic and macrozooplanktonic
species that play a role in the ecology of the WAP ecosystem (Piatkowski, 1985; Lancraft
et al., 1989, 1991, 2004). By describing the contributions of all species present in the
study area and relating their distributions to the local hydrography, we will approach a
more complete understanding of the WAP shelf ecosystem.

As part of the Southern Ocean Global Ecosystem Dynamics (SO GLOBEC)
program, the present study examined the invertebrate micronekton/macrozooplankton
communities found in the Marguerite Bay region of the WAP including the taxonomic
composition, interannual variability, and distribution patterns of those communities
during the fall and winter in 2001 and 2002. Multivariate techniques were used to
identify unique multispecies assemblages and to quantify the contributions of both
oceanic and neritic species to those assemblages. Finally, we compared the integrated abundance and biomass of the WAP pelagic community to other regions within the Southern Ocean.

Methods

Study Area

The present study took place during four cruises to the Marguerite Bay region of the Western Antarctic Peninsula. Cruises 1 and 3 sampled during the austral fall aboard the Antarctic Support Research Vessel (A.S.R.V.) *Laurence M. Gould* (April – June 2001 and 2002 inclusive) and cruises 2 and 4 were aboard the Research Vessel Ice Breaker (R.V.I.B.) *Nathaniel B. Palmer* during the winter season (July – September 2001 and 2002 inclusive). Fall cruises had a process sampling strategy, occupying six sites for 5-6 days at each of six locations within the study region. Winter cruises aboard the *RVIB Palmer* sampled along a predetermined survey grid comprised of stations at 20 km intervals along 12-14 across-shelf transects (Hofmann et al., 2004).

Each general process site was sampled at multiple locations (Figure 2.1). For purposes of discussion, each general process site will be termed “site” and the sampling stations within the site will be termed “stations”. Process site 1 was located near the shelf break at the mouth of the Marguerite Trough. Samples were collected from four stations (1a-1d) within site 1. Process site 2 was located approximately mid-shelf within the Marguerite Trough and included stations 2a and 2b. Process site 3 was a generic mid-shelf designation that included several
different stations located on the continental shelf outside of Marguerite Bay. Stations 3a, 3b, 3d, 3e, 3g, and 3h were shallow, with bottom depths less than 350 m while stations 3c, 3f, and 3i had bottom depths of greater than 470 m. Process site 4 was located at the southern end of the Marguerite Trough in George VI Sound. Stations within site 4 (4a and 4b) were only sampled in fall 2001. Process site 5 was in northern Marguerite Bay and included four stations (5a – 5d) located southeast of Adelaide Island. Process site 7 was northeast of Adelaide Island in Crystal Sound and included stations 7a and 7b. The missing process site 6, originally located south of Marguerite Bay, was not sampled during any of the four cruises due to heavy ice conditions.

Specimen Collection

Macrozooplankton and micronekton were collected with a 10-m$^2$ Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) outfitted with six 3-mm mesh nets (Wiebe et al., 1976, 1985). Towing speed for all trawls was 1.5-2.2 knots. During those trawls, the first net fished obliquely from surface to depth with each subsequent net fishing a discrete depth layer upward to the surface. Trawls reaching depths of 400 meters or less sampled depth strata of 0-50 m, 50-100 m, 100-150 m, 150-200 m, and 200-400 m. Trawls reaching depths between 400 and 500 m sampled depth strata of 0-50 m, 50-100 m, 100-200 m, 200-300 m, and 300-400 or 500 m. Trawls reaching depths between 700 and 1000 m sampled depth strata of 0-50 m, 50-100 m, 100-200 m, 200-500 m, and 500-700 or 1000 m. A total of 62 trawls were completed during the four cruises with 22 occurring during each fall cruise and 9 per winter cruise (Table
2.1). Most trawls (49 of 62) were conducted at night, or dusk, with only a few occurring during the day (13 of 62).

Specimens collected during each cruise were preserved in a 5-10% buffered formaldehyde solution and shipped to the laboratory for analysis. All invertebrate micronektonic and macrozooplanktonic specimens were sorted, counted, identified to lowest possible taxon, and weighed (g wet mass). Numerically abundant species, three euphausiids and one mysid, were first sorted into 20 mm size classes (0-20 mm, 21-40 mm, and 41-60 mm) and then enumerated and weighed. Large collections of euphausiids at times required subsampling. Those were initially sorted to remove any non-euphausiid taxa, which were then enumerated and weighed. The remaining euphausiids were then subsampled using a Motoda splitter (Motoda, 1959). Counts and weights of the subsampled euphausiids were used to estimate the total number and wet mass of euphausiids in the sample. The larval furcilia stage of *Euphausia superba* was considered independently from adult *E. superba* in all analyses except for the size class distributions. After processing, samples were transferred to 50% isopropanol for long-term storage. All fish collected in the samples were processed and analyzed by Donnelly and Torres (2008).

**Data Analyses**

Volumetric abundance and biomass values from each trawl were obtained by dividing the raw number or wet mass by the water volume filtered during each trawl (# or g WM $10^4$ m$^{-3}$). Those standardized values were then used to compute the mean
abundance and biomass of each individual taxon per cruise as well as the mean overall
abundance and biomass for each cruise. Statistical comparisons between cruises were
performed on the volumetric data (\# or g WM $10^4$ m$^{-3}$) using generalized linear mixed

Seasonal vertical distributions for 10 common species were compiled from nets
that fished within the following depth strata: 0-50 m, 50-100 m, 100-200 m, 200-500 m,
and 500-1000 m. For vertical distributions, standardized volumetric values were
calculated from total abundances and total volumes filtered per depth stratum. Those
values were used to determine vertical ranges for each species. The peak range was
chosen as the stratum with the highest recorded abundance.

Invertebrate macrozooplankton/micronekton assemblage structure was analyzed
by multivariate techniques using the PRIMER v6 software package (Clarke and Gorley,
2006). Volumetric abundance and biomass data were log (x+1) transformed to allow for
a more even contribution from both common and rare taxa in each analysis (Clarke,
1993). For each cruise, mean volumetric abundance and biomass at each sampled station
were used to calculate Bray-Curtis similarity matrices that were subsequently used to
generate hierarchical cluster analysis dendrograms and MDS ordination plots. Because
many stations were only sampled with one trawl during the cruises, significant
differences in multispecies assemblages were determined by the SIMPROF procedure.
The SIMPROF (similarity profile permutation test) procedure assumes no a priori
structure to the data and tests the null hypothesis that there is no meaningful structure.
When SIMPROF is conducted in conjunction with cluster analysis, it creates a
dendrogram that displays statistically significant structure in the data. Those groups denoted by a solid dark line are found to have significant structure ($P < 0.05$), while those denoted by lighter dashed lines are found to have no further significant structure ($P > 0.05$) and may simply represent a clustering of random variability (Clarke et al., 2008). The SIMPER (analysis of similarity percentages) procedure was used to identify those taxa contributing most to the similarities within each resultant cluster group. Shannon’s diversity index ($H'$) and Pielou’s evenness ($J'$) were also calculated for the fall and winter abundance cluster groups (Shannon and Weaver, 1949; Pielou, 1966).

For regional comparisons, each taxon’s integrated abundance ($\# \text{ m}^{-2}$) and biomass (g WM m$^{-2}$) for the 0-200 m strata in both fall and winter were calculated by dividing the total number or wet mass by the water volume filtered for the depth stratum sampled by each net. Those values were then multiplied by the vertical range, in meters, for each depth stratum and summed. Because there were so few daytime trawls, those data were omitted from this analysis.

**Results**

**Taxonomic Composition**

A total of 58 taxa (55 in the fall, 48 in the winter) belonging to sixteen different taxonomic groups were collected during this study (Tables 2.2 and 2.3). Although the catch was fairly diverse, only a few species accounted for the majority of the total abundance and biomass. Three euphausiids, *Euphausia crystallorophias*, *E. superba*, and *Thysanoessa macrura*, and one mysid, *Antarctomysis ohlinii*, ranked as the most abundant taxa in each individual cruise, with the only exceptions occurring during the
2002 winter cruise when both *E. crystallorophias* and *A. ohlinii* were outnumbered by the chaetognath, *Pseudosagitta gazellae*, and the amphipod, *Epimeriella macronyx*. Interannual differences were observed in taxon contributions to total abundance. In fall 2001, the numerically dominant species was *A. ohlinii*, but that shifted to *E. crystallorophias* in fall 2002. Abundance rankings also differed between winter cruises, with *T. macrura* and *E. superba* serving as the ranking species in 2001 and 2002, respectively.

With respect to biomass, *E. superba* was the dominant species in three of the four cruises (not in winter 2001) contributing from 41% to 73% of the catch. The other numerically dominant species’ (*E. crystallorophias*, *T. macrura*, and *A. ohlinii*) also contributed substantially to total biomass, but were occasionally out-ranked by the large scyphozoans, *Atolla wyvillei* and *Periphylla periphylla*. Removal of the scyphozoans from the analyses revealed that the four numerically dominant species accounted for no less than 78% of the captured biomass during any individual cruise. Biomass rankings were nearly identical during both fall cruises, but there was a shift from winter 2001 to 2002. In winter 2001, *E. crystallorophias*, *T. macrura*, and *E. superba* all supplied similar contributions to biomass, ranging from 10% to 13% of the catch. However, in winter 2002, *E. superba* dominated and accounted for more than 70% of the captured biomass.

Size distributions of the dominants during each of the four cruises are presented in Figure 2.2. *A. ohlinii* and *T. macrura* had fairly consistent size class breakdowns throughout the four cruises with the majority of individuals captured
falling into the small (0-20 mm) size class. However, both *E. crystallorophias* and *E. superba* exhibited a different pattern. In fall and winter 2001 (cruises 1 and 2), the majority (>88%) of captured *E. crystallorophias* were in the 21-40 mm size class. In 2002, the number of individuals in the small size class increased and this shifted the size class distributions to a nearly equal spread between 0-20 and 21-40 mm individuals. *E. superba* exhibited a similar pattern, shifting from a large size class dominated distribution in 2001 to a small to intermediate size class dominated distribution in 2002.

**Interannual Comparisons**

The total volume filtered during each fall cruise (1,737,762 vs. 1,406,961 m³) was similar, but both the mean number of specimens (300.209 vs. 1289.075 individuals $10^4$ m$^{-3}$; $P<0.01$) and the mean biomass (102.775 vs. 268.128 g WM $10^4$ m$^{-3}$; $P<0.01$) were significantly higher in 2002 (Table 2.2). Although mean abundances of most individual taxa were also higher in fall 2002, there were significant differences in only a few of those taxa due to a high variability in numbers per catch. The amphipods *E. macronyx*, *Eusirus microps*, and *Orchomene plebs*, and the leptomedusae all exhibited significant increases in both abundance and biomass in fall 2002 ($P<0.05$). Three species, a cephalopod, *Alluroteuthis antarcticus*, the amphipod, *Cyphocarus richardi* and the ostracod, *Gigantocypris muelleri*, significantly increased in number only ($P<0.05$). Several other species significantly increased in biomass only and included *E. superba*, the amphipods, *Cyllopus lucasii* and *Eusirus properdentatus*, the mysid,
A. maxima, and the chaetognath, P. gazellae ($P < 0.05$). In contrast, the furcilia stages of E. superba showed a significant decrease in abundance and biomass from fall 2001 to 2002 ($P < 0.04$), which is due to the fact that none were captured in the fall 2002 trawls.

Clearly, the trend within the fall data was that first, similar volumes were sampled in each year. Second, if the entire suite of samples were compared between years, the totals in numbers and biomass were far higher in 2002. Yet, for the majority of individual species, no significant differences were observed between years in either mean numbers or mean biomass. In order to address this conundrum, all trawls that were conducted at a station that was only sampled in either 2001 or 2002 were removed from the data set for further comparisons. Six stations (1a, 1b, 2a, 2b, 5a and 5c) were sampled in both 2001 and 2002 during the fall cruises (Table 2.4) for a total of thirty-one trawls (14 in 2001 and 17 in 2002). As with the total data set, the marked increase in total numbers and biomass from 2001 to 2002 remained significant. When catches from duplicate stations were compared between years, there were also significant increases in both total numbers and biomass at stations 2b and 5a ($P < 0.01$), and in numbers at stations 1a and 5c ($P < 0.04$). It was concluded that the high variability in abundance and biomass per catch was the reason for the large, statistically significant interannual difference when total abundance and biomass were compared without being mirrored by a similar significant change in individual species numbers, even though large interannual differences were observed in individual species’ means.

During the winter cruises, total volumes filtered in 2001 and 2002 were similar (543,635 vs. 511,192 m$^3$). Although the mean total abundance (280.078 vs. 856.683
individuals $10^4$ m$^{-3}$; $P = 0.01$) was significantly higher in winter 2002, there was no significant effect of year in mean total biomass (66.073 vs. 166.424 g WM $10^4$ m$^{-3}$; $P = 0.26$; Table 2.3). Looking at individual species, the euphausiids, *E. crystallorophias*, *E. superba*, and *E. triacantha*, the tunicate, *Salpa thompsoni*, the amphipods, *Hyperia macrocephala* and *O. plebs*, and the hydrozoan, *Diphyes antarctica*, all exhibited significant increases in abundance from winter 2001 to 2002 ($P < 0.05$). Both *E. properdentatus* and *P. gazellae* also had significantly higher biomass in winter 2002 ($P < 0.02$). Two stations (1a and 1d) were each sampled once in winter 2001 and winter 2002 (Table 2.4). Because there was only one sample per station, no statistical comparisons between years were conducted.

Although fewer trawls were completed during the winter cruises, statistical comparisons between cruises that occurred during the same year, i.e., fall 2001 vs. winter 2001 and fall 2002 vs. winter 2002, revealed no significant differences in either total abundance or biomass ($P > 0.05$). Four stations were sampled in both seasons (1a, 1b, 2a and 5a) in 2001, and two stations were sampled in both seasons (1a and 7b) in 2002 (Table 2.4). As with the total data set, there were no statistical differences between stations that were sampled in both seasons within each year.

**Vertical Distributions**

Seasonal discrete depth distributions were compiled for 10 common species by pooling data from each of the fall cruises and each of the winter cruises (Figure 2.3). The euphausiids, *E. crystallorophias*, *E. superba*, *E. triacantha*, and *T. macrura*, were found
throughout the sampled water column, but peak abundances differed among the species. During the fall cruises, *E. crystallorophias* and *E. superba* were most abundant between 100-200 m during the day, but both species ascended at night with peak *E. superba* abundances at the surface (0-50 m) and *E. crystallorophias* peaking between 50-100 m. *E. triacantha* also ascended at night, moving from a peak range of 200-500 m during the day to 100-200 m at night. In contrast, *T. macrura* descended from a peak range of 50-100 m during the day to 100-200 m at night. In the winter, all four euphausiids were again found throughout the water column with the exception of *E. crystallorophias*, which was only found from the surface to 200 m at night. Winter daytime peak distributions of both *E. crystallorophias* and *E. superba* were deeper than in the fall, with the majority of *E. crystallorophias* found between 200-500 m and *E. superba* between 500-1000 m. *E. superba* was still concentrated at the surface at night, but *E. crystallorophias* peaked at 100-200 m in the winter. Peak distributions of *E. triacantha* and *T. macrura* were nearly the same in winter as in fall, with *E. triacantha* concentrated at 200-500 m and *T. macrura* concentrated at 50-100 m in both day and night trawls.

Other common species exhibited similar peak distributions during both day and night, and fall and winter. *A. ohlinii*, *E. macronyx*, and *E. properdentatus* were concentrated between 200-500 m, with the only major exception being slightly higher abundances of *E. macronyx* between 100-200 m at night in the fall. No winter nighttime values for *A. ohlinii* are shown in Figure 2.3, since it was not captured in any of those corresponding trawls. Both *S. thompsoni* and *T. gaudichaudii* were concentrated at the surface with the only exception occurring
during the daytime in winter when peak distributions of both were found deeper in the water column.

**Multispecies Assemblages**

Cluster and SIMPROF analyses of fall abundance (Figure 2.4) and biomass (Figure 2.5) divided the 12 sampled stations from 2001 and 2002 into two primary groups: an offshore group that included trawls occurring at the off-shelf, shelf-edge, and outer trough sites (stations 1a, 1b, and 2a) and an inshore group that included the trawls from the bay and fjord sites (stations 4a, 5a-d, and 7a-b). Trawls from station 2b were split, with trawls from fall 2001 clustering with the offshore group and those from fall 2002 clustering with the inshore group. On the abundance dendrogram (Figure 2.4), the offshore group further divided into two significant clusters that were defined as an oceanic and a transitional cluster. The oceanic cluster included trawls that were conducted seaward of the shelf break (station 1a) while the transitional cluster included trawls conducted on the shelf within the Marguerite Trough (stations 2a and 2b). Trawls from station 1b were split between the two offshore clusters with those from 2001 falling into the transitional cluster and those from 2002 falling into the oceanic cluster.

Unlike the abundance data, with biomass there were no significant sub-groups within the offshore cluster (Figure 2.5). MDS ordination plots calculated from the similarity matrices show the same group structure for both abundance and biomass with resultant stress levels of <0.1 (Figures 2.6 and 2.7). In fall 2001, one trawl was conducted at station 4b deep within George VI Sound near the permanent ice-shelf. Both abundance and biomass data from that trawl clustered as an outlier, which is likely due to
the unusual nature of the catch. It was dominated by the neritic euphausiid *E. crystallorophias* (82%), yet also had several oceanic species underscoring the connection between ocean and shelf provided by the Marguerite Trough.

A SIMPER analysis conducted on the fall abundance data identified the taxa that contributed the most to similarities within each cluster group. The species *E. triacantha* and *Salpa thompsoni* were most abundant in the oceanic cluster and contributed over 20% each to the similarity within that group. In the neritic cluster, *E. superba*, *T. macrura*, *E. crystallorophias*, and *A. ohlinii* were the most numerous species and contributed nearly 50% to the similarity within that cluster. Dominant taxa in the transitional cluster included several species (*E. superba*, *T. macrura*, *T. gaudichaudii* and *P. gazellae*) that were present to varying degrees in each of the three cluster groups (Table 2.5). The remainder of the taxa in the transitional cluster included species that were also present in either the oceanic or the neritic cluster, with the only exceptions being *E. frigida* and *E. superba furcilia*. Abundance and distribution of several dominant species and how they relate to the three major clusters are shown in Figure 2.8 as bubble plot overlays of the fall abundance MDS ordination.

During the winter cruises, 16 stations were sampled, each with one trawl per cruise. Site 3, which was only sampled during the winter cruises, included several stations (3a-3i) that were found at various locations on the continental shelf. Due to the presence of sea ice, only two trawls were completed at the more inshore sites during the winter cruises: one at station 5a in 2001 and one at station 7b in 2002. The rest of the samples were collected from site 1 at the shelf break and include the samples from
stations 1a and 1d that occurred in both years. Cluster and SIMPROF analyses of winter abundance and biomass divided the samples into four and five significant groups, respectively. Like fall abundance, winter abundance clustered into an offshore and inshore group, with the offshore group further dividing into oceanic and transitional clusters. However, the addition of site 3 created another significant cluster group within the offshore branch that was defined as a mid-shelf cluster (Figure 2.9). The oceanic cluster included all samples from site 1, the transitional cluster included the trawls completed at station 2a as well as two of the mid-shelf trawls completed in 2001 (stations 3g and 3i), and the mid-shelf cluster contained the rest of the site 3 trawls. Not surprisingly, those samples collected from stations 5a and 7b formed the inshore group (neritic cluster).

Results from winter biomass were less clear than those from winter abundance. Overall the samples still divided into an offshore and inshore group, however in this case the transitional group divided into its own significant cluster rather than nesting within the offshore group, and the mid-shelf cluster fell into the inshore group (Figure 2.10). Removal of several jellyfish species (*A. wyvillei, C. borchgrevinki,*, and *P. periphylla*) from the cluster analysis yielded a slightly less complex clustering pattern with those stations that clustered originally as oceanic and transitional combining into one offshore group and the mid-shelf and neritic group clustering within the inshore group (Figure 2.11). The MDS ordination plots of winter abundance and biomass (without jellyfish) are presented in Figures 2.12 and 2.13.
Results of the SIMPER analysis of winter abundance revealed that *T. macrura* dominated in three of the four clusters, contributing from 25% to nearly 40% of the similarity within each cluster group (Table 2.6). Several other taxa (*E. macronyx, E. superba, E. crystallorophias, P. macropa, P. gazellae, and S. thompsoni*) were also present in either 3 or 4 of the cluster groups suggesting that there was more species overlap in the winter samples as compared to the fall samples. Figure 2.14 shows the bubble plots of the abundance and distribution of four euphausiid species captured in the winter trawls.

Diversity indices for fall and winter were calculated with abundance data from each sampled station. Mean values for each significant cluster are presented in Table 2.7. In both fall and winter, more species were collected from the oceanic clusters, but the highest diversity and evenness indices occurred in the fall transitional cluster and in the winter neritic cluster.

*Integrated Abundance and Biomass*

A total of 37 taxa were present in the upper 200 meters of the water column during the cruises. In the fall, *E. crystallorophias* and *E. superba* contributed both the highest numbers and the most biomass to the upper 200 meters of the water column (Table 2.8). Other species such as *S. thompsoni, A. ohlinii, T. macrura, E. triacantha,* and *T. gaudichaudii* also supplied a substantial proportion of the total catch in the 0-200 m layer while *P. periphylla* and *A. wyvillei* contributed to total biomass. During the
winter, *E. superba* and *T. macrura* were the dominant taxa, contributing over 94% in number and 85% in biomass. Total densities in each season were similar, but total biomass was approximately three times greater in fall than in winter.

**Discussion**

**Dominant Species and Interannual Differences**

A total of 58 invertebrate taxa were collected during the four cruises to the Marguerite Bay region of the WAP in 2001 and 2002. Of those, four species, *E. crystallorophias*, *E. superba*, *T. macrura*, and *A. ohlinii*, accounted for the vast majority of the total abundance and biomass, contributing from 74% to 92% of the total number during each individual cruise. Many previous studies have also reported *E. superba* and *T. macrura* as dominant species throughout the WAP region (Kittel and Stepnik, 1983; Kittel et al., 1985; Lancraft et al., 1989, 1991, 2004; Nordhausen, 1992, 1994a and b) with others listing *E. crystallorophias* and *A. ohlinii* as dominants in nearshore environments (Lancraft et al., 2004; Ross et al., 1996). Interestingly, each of the dominants ranked as the top numerical contributor in only one cruise. In the fall, *A. ohlinii* dominated in 2001 and *E. crystallorophias* dominated in 2002, while in the winter, *T. macrura* dominated in 2001 and *E. superba* dominated in 2002. Biomass contributions from the four dominants were also high, ranging from 37% to 84% of the total during each of the cruises. In winter 2002, their biomass contributions were diminished (37%) due to the capture of several large scyphozoans, *A. wyvillei* and *P. periphylla*. When the
scyphozoans were removed from consideration, biomass contributions from the four dominants increased and ranged from 75% to 87%.

Contributions by fish taxa to total abundance and biomass in the SO GLOBEC study were described by Donnelly and Torres (2008) and were relatively low in the fall and winter seasons. Although fishes comprised approximately two-thirds of the species found in the study, their contribution to total abundance in fall and winter ranged from only 1.5 – 3% (Donnelly and Torres, 2008). However, fish constituted a larger proportion of the biomass, contributing between 16 and 19% in both seasons (Donnelly and Torres, 2008).

Despite the fact that there were few significant differences in abundance or biomass of the dominant euphausiids, there was nearly an order of magnitude increase in both measures in 2002. Interannual comparisons of mean abundance and biomass of each dominant revealed that while all four species increased in number and wet mass between fall cruises, that was not the case between winter cruises. In winter 2002, both *E. crystallorophias* and *A. ohlinii* decreased in abundance and were outranked by *P. gazellae* and *E. macronyx*. In fact, the numerical catches of those two species decreased by more than 20-fold from winter 2001 to 2002. Winter distributions of those two species (Figure 2.14) show that catches of *A. ohlinii* were limited to stations where the deep, nearshore fjords are located. *E. crystallorophias* was also present at the fjord stations, but there were also substantial catches in the transitional cluster as well as at some of the stations in the oceanic cluster. This suggests that *E. crystallorophias* distributions tend to spread out onto the shelf during the winter when ice extent has
increased. It is likely then that *P. gazellae* and *E. macronyx* outnumbered *A. ohlinii* and *E. crystallorophias* in winter 2002 for two reasons: 1) the more ubiquitous distributions of *P. gazellae* and *E. macronyx* allowed for greater numbers to be captured and 2) the decreased number of trawls that were completed in sites 5 and 7 reduced the chances of catching *A. ohlinii* and to some degree *E. crystallorophias*.

Sea ice coverage and formation differed in both timing and extent during the cruises in 2001 and 2002. In fall 2001, much of the study region, including portions of Marguerite Bay, remained open and free of ice until late June. In contrast, the ice edge extended well past the islands west of the Antarctic Peninsula in 2002 and this is echoed in the more offshore distribution of sample stations during those cruises (Perovich et al., 2004). The delayed sea ice formation in 2001 may have reduced spawning and recruitment success leading to the dearth of larval krill in the 2002 trawls. However, the abundance of larval krill in 2001 is reflected in the size increment data for both years. In fall 2001, the majority of captured *E. superba* were large (41-60 mm), but that decreased steadily over the following cruises such that large krill represented less than 10% of the total catches in 2002. The decrease in large *E. superba* was accompanied by an increase in small (0-20 mm) and intermediate (21-40 mm) sized individuals in 2002, which implies that a substantial number of larvae from 2001 survived and overwintered in the local region (Daly, 2004). *E. crystallorophias* exhibited similar size distribution patterns, with the occurrence of small-sized individuals increasing to over 50% in 2002. This suggests that the dramatic increase in both *E. superba* and *E. crystallorophias* abundance/biomass in 2002 is the result of a successful spawning and recruitment season in 2001.
Although mean abundance and biomass were higher in fall than in winter within each year, there were no significant differences detected between seasons. However, several other studies conducted in this region (Lascara et al., 1999; Ashijan et al., 2004; Lawson et al., 2004), noted a substantial decrease in both density and biomass captured in the winter when compared to the fall. Because of the nature of the present study and the differences in sampling sites/stations between seasons, a rigorous assessment of seasonal variations in taxon abundance and biomass is not possible.

Distributions and Hydrographic Influences

The invertebrate micronekton/macrozooplankton assemblages found in the Marguerite Bay region of the WAP were composed of a varying mixture of oceanic and neritic species: a product of the local hydrography. In most oceanic regions, the continental shelf is less than 200 m deep and the subsequent change in depth at the shelf break acts as a natural barrier between oceanic and shelf fauna. However, the Antarctic, specifically the WAP continental shelf, is much deeper, ranging in depth from 200-500 m (Dinniman and Klinck, 2004). As a result there is less filtering out of oceanic species from the shelf community (Eastman, 1993).

The proximity of the ACC to the shelf break is another unique attribute of the WAP region that enhances species mixing (Dinniman and Klinck, 2004). Oceanic fauna located near the shelf break are associated with the warmer waters of the ACC and when ACC-associated CDW intrudes onto the shelf, it potentially carries those oceanic fauna
along with it. Those sub-surface CDW intrusions typically occur near anomalous bathymetric features such as the Marguerite Trough and are estimated to happen from 4-6 times per year (Klinck et al., 2004). As the CDW moves farther onto the shelf, it becomes slightly cooler and fresher, referred to as modified CDW (Hofmann and Klinck, 1998), as it mixes with shelf waters containing resident neritic fauna. Donnelly and Torres (2008), who described the fish assemblages from these same trawls, reported that modified CDW was present throughout the study region in both seasons.

Cluster analysis of the fall and winter samples identified three primary groups, defined as oceanic, transitional, and neritic assemblages, primarily due to their geographic location. In the Antarctic, the oceanic region is typically found in the deeper waters (>2000 m) offshore of the continental shelf; the neritic region is located on the continental shelf in coastal regions (Ross et al., 1996). The transitional zone is defined as the area between and represents a region of mixing between oceanic and neritic waters rather than a distinctly different physical or biological environment. Siegel and Piatkowski (1990) identified and described three similar assemblages in a more northerly region of the WAP during fall, winter, and spring seasons in the 1980’s and concluded that differences between the assemblages were not due to differences in species composition, but rather due to changes in abundances of those species. This was borne out by the ubiquitous distributions of many of the taxa encountered in the present study. As a result, there were very few species that served as ideal indicators for any particular assemblage. Instead, those species that contributed most to similarities within an assemblage as well as those that have been typically characterized as either oceanic or neritic fauna were most useful in describing the assemblages and the degree of mixing
within each assemblage. Species such as the ice krill, *E. crystallorophias*, along with the deep, fjord-favoring mysids, *A. ohlinii* and *A. maxima*, and the gammarid amphipods, *E. properdentatus* and *E. macronyx*, were most abundant at nearshore stations, while the oceanic euphausiid, *E. triacantha* and salp, *S. thompsoni*, were most common at the shelf break/off-shelf stations.

Fish taxa collected during the SO GLOBEC study exhibited distribution patterns similar to those of the invertebrate micronekton/microzooplankton component. Oceanic genera such as *Electrona*, *Gymnoscopelus*, *Protomyctophum*, *Bathylagus*, *Cyclothone*, and *Notolepsis* dominated at the offshore stations, while the notothenioids such as the Antarctic silverfish, *Pleuragramma antarcticum*, were most abundant nearshore (Donnelly and Torres, 2008).

For simplicity, only those species listed in Tables 2.5 and 2.6 will be discussed with respect to their distributions and contributions to each assemblage. In the fall, faunal mixing was maximal in the transitional assemblage and included samples collected primarily from site 2, located approximately 150-200 km shoreward of the shelf break within the trough near the mouth of Marguerite Bay. Within that assemblage, there was a nearly even mix of neritic and oceanic taxa contributing to the structure of that group. The oceanic assemblage, collected near the shelf break at site 1, contained the largest number of taxa but was dominated by oceanic species such *E. triacantha*, *S. thompsoni*, and *T. gaudichaudii*. In contrast, the assemblage present at the nearshore sites (sites 4, 5 and 7) had the lowest species number and diversity and evenness indices. *E. superba*
dominated in that assemblage along with the neritics, *A. ohlinii* and *E. crystallorophias*, with *T. gaudichaudii* being the only oceanic species present.

During the winter, faunal mixing was prevalent in both the mid-shelf and transitional clusters, but species distributions, especially those of the four abundant euphausiids, were much broader than in the fall. While *E. crystallorophias* was confined to nearshore sites in the fall, its distribution extended across the shelf reaching the shelf break in the winter (Figures 2.8 and 2.14). In fact, average *E. crystallorophias* abundances in the transitional and neritic zones were nearly identical in the winter.

Siegel and Piatkowski (1990) reported a similar pattern for *E. crystallorophias* in the spring, when distributions extended into the transitional zone. In the opposite extreme, the CDW-associated euphausiid, *E. triacantha*, was also more widespread in winter and present in all assemblages suggesting that CDW, or modified CDW, was indeed present on the inner shelf during the winter, corroborating the findings of Donnelly and Torres (2008). In the fall, *E. superba* occurred predominantly at nearshore sites, a pattern reported by Lancraft et al. (2004) in the Croker Passage, but during the winter abundances were more evenly distributed among all assemblages. *T. macrura* exhibited wide-ranging distributions not only in winter, but throughout the study. This species is commonly described as having a uniform and ubiquitous distribution (Kittel et al., 1985; Nordhausen, 1994a; Piatkowski, 1985) and was abundant in each of the described assemblages serving as a top contributor in both the fall and winter transitional groups.

Water column depth also influences distributions, especially the prevalence and persistence of oceanic fauna as CDW moves across the shelf. Several deeper dwelling
oceanics, such as the decapods, *Gennadus kempi* and *Pasiphea scotiae*, were captured, although in low densities, at the offshore station, but were completely absent at any of the shelf stations. Those species are most likely limited in horizontal extent by the depths encountered as they move shelfward. In contrast, oceanic fauna with shallower distributions, such as *Salpa thompsoni* and *Themisto gaudichaudii* were more widespread across the shelf and were present in nearly all assemblages.

Vertical depth ranges for most species in this study were fairly broad and encompassed the entire sampled water column (surface to 1000 m). Of the common species, only the euphausiids demonstrated marked diel vertical migrations (DVM). Both *E. crystallorophias* and *E. superba* migrated during both seasons, while *E. triacantha* migrations were only evident during the fall. Studies by Lancraft et al. (1989, 2004) in the Scotia Sea and Croker Passage during the fall, and by Nordhausen (1994a) in Gerlache Strait and Crystal Sound during the winter, found no evidence of DVM by any of those species. However, Lancraft et al. (1991) found that *E. superba* did vertically migrate during the winter in the Scotia Sea. Several species also exhibited seasonal differences in vertical distribution patterns. Maximum densities of *E. crystallorophias* were deeper during both the day and night in the winter. Peak daytime abundances of *E. superba* were also deeper in the winter, but nighttime peaks were still at the surface. In fact, *E. superba* comprised nearly 80% of the catch in surface waters, with *T. macrura* being the only other major contributor. *T. macrura* exhibited no diel vertical migration patterns during the winter.
Regional Comparisons

Invertebrate species diversity in the WAP study region was relatively high (55 taxa in the fall; 48 taxa in the winter) due to the mixing of typical Antarctic oceanic fauna with endemic nearshore fauna. In comparison, species lists for invertebrate micronekton/macrozooplankton collected from oceanic regions in the Scotia and Weddell Seas ranged from only 27 to 29 species (Lancraft et al., 1989). However, a winter study in the Scotia Sea in the vicinity of the Weddell-Scotia Confluence, an area of faunal mixing, reported a total of 40 species, a number more similar to the WAP study (Lancraft et al., 1991). Hydrographic conditions in the Confluence are comparable to those of the WAP shelf in that there is mixing of the colder and warmer water masses of the Weddell Gyre and the ACC, and their associated fauna, which enhances local diversity (Lancraft et al., 1991). Diversity in Croker Passage (32 species), which like the WAP study region included a mixture of both oceanic and nearshore fauna, was also lower than that seen in the present study (Lancraft et al., 2004) and may arise from the lack of a well developed CDW layer, thus excluding deeper dwelling oceanic fauna such as Euphausia triacantha (Lancraft et al., 2004). A summer study in the permanent ice zone of the Ross Sea reported a total of 31 species, which is also lower than the present study, but similar to species counts in the Scotia Sea, Weddell Sea, and Croker Passage (Hopkins, 1987).

Fish diversity in the SO GLOBCEC study region was also high when compared to other studies. Donnelly and Torres (2008) reported a total of 34 and 22 species for the fall and winter, while numbers in the Weddell Sea and Croker Passage reached only about a third to half of that total (Lancraft et al., 1989, 2004). Fish diversity in the Scotia
Sea, which is heavily influenced by the ACC, was again more similar to the WAP study region with 15 and 17 species reported in the fall and winter (Lancraft et al., 1989, 1991).

Mean total integrated abundance and biomass for the upper 200 m of the water column were calculated for purposes of comparison to other regional studies. Because direct comparisons between studies can be misleading due to differences in sampling design and gear, we have chosen to compare data only from studies that reported nighttime integrated values for the 0-200 m stratum. For that reason, comparisons will be limited to results presented by Lancraft et al. (1989, 1991, 2004).

Integrated biomass of invertebrate micronekton and macrozooplankton from the WAP study region (Table 2.8) was nearly three times greater in the fall than in the winter (9.11 vs. 3.02 g WM m$^{-2}$), which was likely due to a reduced catch of *E. crystallorophias* in the winter (2.61 vs. 0.005 g WM m$^{-2}$). Total fall integrated biomass from the WAP was also greater than the value reported from the Scotia Sea in the fall (9.11 vs. 4.58 g WM m$^{-2}$; Lancraft et al., 1989). However, the WAP winter biomass was only half that reported in the Scotia Sea in winter (3.02 vs. 7.65 g WM m$^{-2}$; Lancraft et al., 1991) and can be attributed to a smaller *E. superba* catch. Integrated biomass in Croker Passage during the fall (187.64 g WM m$^{-2}$; Lancraft et al., 2004) was two orders of magnitude higher than that seen in the WAP study region during the fall. This was due to an inordinately large catch of *E. superba*, which was almost 50 times greater (3.78 vs. 174.81 g WM m$^{-2}$; Lancraft et al., 2004) than the catch in the WAP study region.

Invertebrate micronekton and macrozooplankton integrated abundances were more similar than biomass estimates for the WAP study region in fall and winter (37.96
vs. 29.72 individuals m$^{-2}$). Abundances reported in the Weddell Sea (11.56 individuals m$^{-2}$) and in both the winter and fall Scotia Sea studies (12.95 and 21.63 individuals m$^{-2}$) were also similar, but, like the biomass estimate, abundance in the Croker Passage (801.28 individuals m$^{-2}$) was substantially higher than in the WAP study region (Lancraft et al., 1989, 1991, 2004). *E. superba* alone supplied 98% of the catch in Croker Passage. During fall in the WAP study region, *E. crystallorophias* dominated, though not to the same extent as *E. superba* in Croker Passage, which underscores the strong neritic influence on the WAP community.

When compared to other oceanic ecosystems, there were notable differences in species assemblages. In most oceanic regions, decapod species are both diverse and abundant (Hopkins and Lancraft, 1984), but in the WAP region there were only four species present; three oceanic and one neritic species found in the fjords (*Notocrangon antarcticus*). The reduced presence of decapods in Antarctic pelagic communities has been noted in several other studies (Piatkowski, 1985; Lancraft et al., 1989, 1991, 2004). Amphipods are another group that differs in relative abundance and diversity in Antarctic communities. In fact, in some Antarctic regions amphipods may occasionally contribute a substantial portion of the overall abundance and biomass. In the WAP study, there were a total of 8 gammarid and 10 hyperiid amphipods represented throughout the cruises. *Themisto gaudichaudii* was present in sufficient densities to serve as a major contributor in nearly all identified assemblages while *Epimeriella macronyx* served that purpose in the nearshore assemblages. In contrast, amphipods are much less common in subtropical regions, like the eastern Gulf of Mexico, where only 25 individuals were collected during a summer study (Hopkins and Lancraft, 1984).
Total species diversity in the WAP region was low in comparison to diversities found in mid-latitude oceanic regions. For example, in the eastern Gulf of Mexico, the number of identified invertebrate micronekton and macrozooplankton species, as well as the number of fish species, was nearly double that found in the WAP study region (Hopkins and Lancraft, 1984; Donnelly and Torres, 2008). In contrast, total integrated abundance and biomass in the WAP region was high compared to the Gulf of Mexico and Hawaii (Hopkins and Lancraft, 1984; Maynard et al., 1975). In the pelagic community as in most others, species diversity, abundance, and biomass all tend to scale with temperature in that diversity increases when moving from polar to equatorial regions, while abundance and biomass decline.

Conclusions

In both seasons, crustaceans dominated the system accounting for 35 of the 58 taxa encountered during the four cruises. However, a very few species made up a majority of the catch in either season. In the fall, the euphausiids, *Euphausia crystallorophias*, *E. superba*, and *Thysanoessa macrura*, and the mysid, *A. ohlinii*, numerically dominated the assemblage while in the winter, the same three euphausiids and the chaetognath, *P. gazellae*, were the numerical dominants. A significant increase in total abundance and biomass was also observed from 2001 to 2002.

Three broad groupings of invertebrate micronektonic/macrozooplanktonic taxa were identified in the waters of the WAP shelf, an oceanic, neritic, and mixed or
transitional assemblage. The change in faunal composition was a cross-shelf gradient rather than a sharp boundary at the shelf break and was largely due to changes in relative species abundance with some changes in species composition.

Species diversity and integrated abundance for the upper 200 m of the water column were similar between seasons in the WAP study region, but integrated biomass was nearly three times greater in fall than in winter. Integrated estimates from the WAP study region were similar to those from other studies conducted in the Scotia and Weddell Seas, but were orders of magnitude lower than estimates from a study in Croker Passage, primarily due to a large catch of *E. superba*. In contrast, species diversity in the WAP was higher than recorded in any of the previously mentioned studies, which is due to the mixing of typical oceanic fauna with endemic nearshore fauna.

Results of the present study show that abundance and distribution of invertebrate micronekton and macrozooplankton in the WAP shelf region are highly variable in both space and time. Siegel (2000) described three categories of factors that potentially influence distributions of euphausiids, which can likely be applied to all taxa in the WAP shelf ecosystem. These categories include behavioral factors such as vertical or ontogenetic migrations, life history-related factors such mortality and recruitment success or failure, and physical factors such as temperature and circulation patterns. Only through a better understanding of all of these factors can we hope to gain a complete understanding of the WAP shelf ecosystem.
References


Nordhausen, W., 1994b. Winter abundance and distribution of *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura* in Gerlache Strait and Crystal Sound, Antarctica. Marine Ecology Progress Series 109, 131-142.


Table 2.1: 10-m$^2$ MOCNESS trawl data from the four SO GLOBEC cruises conducted in 2001 and 2002 near the Marguerite Bay region of the Western Antarctic Peninsula. Trawls are organized by season and station. Local time = GMT – 4 hours, TOD = Time of Day

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<th>Trawl</th>
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<th>Time (GMT)</th>
<th>TOD</th>
<th>Latitude (°S)</th>
<th>Longitude (°S)</th>
<th>Trawl Depth (m)</th>
<th>Bottom Depth (m)</th>
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Table 2.2: Mean volumetric abundance (# individuals $10^4$ m$^{-3}$) and biomass (g WM $10^4$ m$^{-3}$) of each taxon during fall 2001 and 2002. 
$n = $ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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<td># (10^4 , m^3) SD gWM (10^4 , m^3) SD</td>
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<td>0.017 0.05</td>
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<td>0.0041 0.02</td>
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\(^a\)No weights were recorded for these specimens.
Table 2.3: Mean volumetric abundance (# individuals $10^4$ m$^{-3}$) and biomass (g WM $10^4$ m$^{-3}$) of each taxon during winter 2001 and 2002. $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

<table>
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<tr>
<th>Taxonomic Group</th>
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<th>WINTER 2002 ($n = 9$)</th>
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<td>VF = 511,192 m$^3$</td>
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<td>gWM 10$^4$m$^{-3}$</td>
<td>SD</td>
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^aNo weights were recorded for these specimens.
Table 2.4: Total number of trawls completed at each station during each of the four cruises

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Table 2.5: Results of SIMPER analysis on fall volumetric abundance data showing the taxa contributing the most to similarity within each significant cluster. Values in parentheses represent the overall similarity among samples within a cluster group. % Contribution = percentage contribution to the overall similarity among samples within a cluster group. Only those taxa that contributed 1% or more to overall group similarity are listed.

<table>
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<tr>
<th>Oceanic (68.47% Similarity)</th>
<th>Transitional (71.53% Similarity)</th>
<th>Neritic (69.90% Similarity)</th>
</tr>
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<td>% Contribution</td>
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<td>% Contribution</td>
</tr>
<tr>
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<td><em>Salpae thompsoni</em></td>
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<td><em>Themisto gaudichaudii</em></td>
<td>17.56</td>
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<td><em>Euphausia superba</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Leptomedusa</em></td>
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<tr>
<td></td>
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<td><em>Primno macropa</em></td>
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</table>
Table 2.6: Results of SIMPER analysis on winter volumetric abundance data showing the taxa contributing the most to similarity within each significant cluster. Values in parentheses represent the overall similarity among samples within a cluster group. % Contribution = percentage contribution to the overall similarity among samples within a cluster group. Only those taxa that contributed 1% or more to overall group similarity are listed.

<table>
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<tr>
<th>Oceanic (70.66% Similarity)</th>
<th>Transitional (61.45% Similarity)</th>
<th>Neritic (73.78% Similarity)</th>
<th>Mid-Shelf (60.44% Similarity)</th>
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<td>% Contribution</td>
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<td>% Contribution</td>
<td>% Contribution</td>
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<td>Euphausia superba</td>
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<td>Primno macropa</td>
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<td>Atoll wyvillei</td>
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<tr>
<td>Periphylla periphylla</td>
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<td>Themisto gaudichaudii</td>
<td>3.27</td>
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<tr>
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<td>Orcomene plebs</td>
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<td>Petalidium foliaceum</td>
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Table 2.7: Diversity ($H'$) and evenness ($J'$) for fall and winter abundance cluster groups. SD = standard deviation

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<th>Cluster</th>
<th>Diversity ($H'$)</th>
<th>Evenness ($J'$)</th>
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<td>Outlier</td>
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<td><strong>Winter</strong></td>
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<tr>
<td>Oceanic</td>
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<td>Mid-Shelf</td>
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Table 2.8: Mean integrated abundance (# individuals m\(^{-2}\)) and biomass (g WM m\(^{-2}\)) of taxa collected from discrete night tows within the 0-200 meter depth stratum during the fall and winter cruises. \(n\) = number of trawls.

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<td></td>
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<td>Winter ((n = 6))</td>
<td>gWM m(^{-2})</td>
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<tr>
<td></td>
<td># m(^{-2})</td>
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</tbody>
</table>

Total                        | 37.96              | 9.11  | 29.72              | 3.02  |       |       |       |       |
Figure 2.1: Trawl locations for fall and winter SO GLOBEC cruises. Large rectangles represent sampled sites while smaller rectangles represent sampled stations within each site. Red squares = Fall 2001, Green circles = Winter 2001, Orange squares = Fall 2002, Purple circles = Winter 2002.
Figure 2.2: Size distributions of dominant species collected during the four SO GLOBEC cruises.
Figure 2.3: Vertical distributions of 10 common species collected during the four SO GLOBEC cruises. $n =$ number of individuals.
Figure 2.3: Continued.
Figure 2.3: Continued.
Figure 2.4: Percent similarity cluster dendrogram of fall invertebrate micronekton/macrozooplankton abundance (# individuals $10^4$ m$^{-3}$). Numbers along the abscissa represent the cruise and station number (Ex. Cruise 3, station 1a is designated as 3-1a).
Figure 2.5: Percent similarity cluster dendrogram of fall invertebrate micronekton/macrozooplankton biomass (g WM $10^4$ m$^{-3}$). Numbers along the abscissa represent the cruise and station number (Ex. Cruise 3, station 1a is designated as 3-1a).
Figure 2.6: MDS ordination plot of fall abundance ((# individuals $10^4 \text{ m}^3$) data.
Figure 2.7: MDS ordination plot of fall biomass (g WM $10^4$ m$^{-3}$) data.
Figure 2.8: Bubble plot overlays of the fall abundance MDS ordination plot representing the relative abundance of several common species. The larger the bubble, the greater the number of individuals were captured at that station. Please note that bubble sizes are not consistent among species.
Figure 2.9: Percent similarity cluster dendrogram of winter invertebrate micronekton/macrozooplankton abundance (# individuals $10^4$ m$^{-3}$). Numbers along the abscissa represent the cruise and station number (Ex. Cruise 2, station 1a is designated as 2-1a).
Figure 2.10: Percent similarity cluster dendrogram of winter invertebrate micronekton/macrozooplankton biomass (g WM $10^4$ m$^{-3}$). Numbers along the abscissa represent the cruise and station number (Ex. Cruise 2, station 1a is designated as 2-1a).
Figure 2.11: Percent similarity cluster dendrogram of winter invertebrate micronekton/macrozooplankton biomass (g WM $10^4$ m$^{-3}$) minus the jellyfish taxa. Numbers along the abscissa represent the cruise and station number (Ex. Cruise 2, station 1a is designated as 2-1a).
Figure 2.12: MDS ordination plot of winter abundance (# individuals $10^4 \text{ m}^{-3}$) data.
Figure 2.13: MDS ordination plot of winter biomass (g WM $10^4$ m$^{-3}$) data minus the jellyfish taxa.
Figure 2.14: Bubble plot overlays of the winter abundance MDS ordination plot representing the relative abundance of several common species. The larger the bubble, the greater the number of individuals were captured at that station. Please note that bubble sizes are not consistent among species.
CHAPTER THREE
MICRONEKTONIC FISHES AND INVERTEBRATES IN A GRADIENT OF REGIONAL WARMING: THE WESTERN ANTARCTIC PENINSULA

Abstract

Micronektonic fishes and invertebrates were sampled with 32 midwater trawls at nine sites along the Western Antarctic Peninsula (WAP) in the austral fall (March – April) of 2010. Study sites were located within four hydrographic regions: near Joinville Island in Region I, at Croker Passage, near Anvers Island, and near Renaud Island in Region II, within Marguerite Bay and the Marguerite Trough in Region III, and near Charcot Island in Region IV. A total of 62 taxa representing 12 taxonomic groups of pelagic invertebrates and 9 families of fish were captured, but assemblages were dominated by only a few species. The most numerically abundant taxa were the euphausiids, *Thysanoessa macrura*, *Euphausia superba*, and *E. crystallorophias*, combining to contribute nearly 79% of the total catch. Biomass dominants included *E. superba*, which contributed more than 44% of the total catch, the notothenioid *Pleuragramma antarcticum*, and the salp, *Salpa thompsoni*. A comparison of total catches among sites revealed that the largest volumetric abundances and biomasses were captured at the Marguerite Bay site where mean values reached 1176 individuals $10^4$ m$^{-3}$ and 530 g WM $10^3$ m$^{-3}$ ($P <0.01$).
Cluster analysis identified distinct multispecies assemblages at Joinville Island, Croker Passage, Marguerite Bay, and Charcot Island, and an assemblage that included samples from sites near Anvers Island, Renaud Island, and the Marguerite Trough.

Assemblages at Joinville Island and Croker Passage were both dominated by *E. superba* and *S. thompsoni*, but hydrographic conditions at Joinville Island favored a neritic assemblage, underscored by the substantial numbers of *P. antarcticum*. The assemblage at Croker Passage was more oceanic in nature with major inputs from the myctophid, *Electrona antarctica* and the hyperiid amphipod, *Themisto gaudichaudii*. Marguerite Bay and Charcot Island were well-mixed assemblages with strong representation by both neritic and oceanic fauna. The mid-peninsula assemblage was also oceanic in character, being overwhelmingly dominated by *Thysanoessa macrura* and *T. gaudichaudii*.

*Pleuragramma antarcticum* were captured at five sites: Joinville Island, Croker Passage, Marguerite Bay, and the two sites near Charcot Island. They were completely absent at the two sites near Anvers Island, at Renaud Island, and in the Marguerite Trough. One fish was captured in Croker Passage. The majority of fish captured in Marguerite Bay were larger than 150 mm SL, with very few fish of smaller size present. If resident populations reproduce and recruit locally rather than being sustained by larval advection, those populations will be highly susceptible to local extinction and this may be the causative factor behind the disappearance of *Pleuragramma* from the mid-peninsula region. Continued warming and subsequent sea ice reductions may not only cause *Pleuragramma* population collapses in the Marguerite Bay and Charcot Island regions, but may also change the character of the faunal assemblages along the WAP to those of an oceanic system.
Introduction

Several unique physical properties of the Western Antarctic Peninsula (WAP) shelf make it one of the most productive and diverse regions in the Southern Ocean. The bathymetry of the Antarctic shelf, which is much deeper than in other oceanic systems (200-500 m vs. <200 m; Dinniman and Klinck, 2004), enhances faunal mixing by effectively removing a natural barrier to deeper dwelling oceanic fauna (Eastman, 1993). Another attribute, which is unique to the WAP shelf, is the absence of a slope front zone and its associated steep temperature and salinity gradients. In other Antarctic coastal regions, water column temperatures are uniformly cold (-2 °C), and oceanic species are excluded from the shelf (DeWitt, 1970; Donnelly et al., 2004). The WAP is the only region of the Antarctic where oceanic fishes are prevalent on the shelf despite their lack of biological antifreezes (Cullins et al., 2011). Hydrographic conditions on the WAP shelf are also influenced by the proximity of the Antarctic Circumpolar Current (ACC) to the shelf break. As the ACC flows northeasterly along the shelf break, it encounters deep cross-shelf troughs and depressions that allow intrusions of warm, nutrient-rich Circumpolar Deep Water (CDW) onto the shelf (Smith et al., 1999; Dinniman and Klinck, 2004; Klinck et al., 2004) providing yet another mechanism for enhanced faunal mixing in that region.

Faunal assemblages are also influenced by local circulation patterns in the WAP region. Large-scale circulation on the shelf is clockwise, driven by the northeasterly flowing ACC at the shelf break and the southward flowing coastal current (Hofmann et al., 1996). Smaller sub-gyres also exist along the WAP shelf (Figure 3.1) which may
limit advection and locally retain fauna, especially in inner shelf regions (Piñones et al.,
2011; Murphy et al., 2012). For those reasons, it is predicted that a continuum of distinct
hydrographic regimes exists along the WAP shelf. These regimes may be differentiated
by hydrographic properties such as water column temperature and salinity profiles or the
presence of CDW and sea ice. Each regime may be further classified by its faunal
composition and the presence or absence of key species such as the ice-associated
nototheniid fish, *P. antarcticum*.

Most notothenioids are benthic as adults, but *Pleuragramma* has a completely
pelagic life history and is primarily found in the midwaters over the continental shelf
from the surface to 500 m, and deeper in the coastal canyons (Cullins et al., 2011).
Because the depth of the Antarctic continental shelf makes bottom fauna inaccessible to
many higher trophic level predators, *Pleuragramma* are an important prey source for
flighted seabirds (Ainley et al., 1991), penguins (Bengtson et al., 1993; Williams, 1995;
Ainley, 2002), and seals (Oritsland, 1977; Lowry et al., 1988; Fuiman et al., 2002; La
Mesa et al., 2004). Several species of fishes feed principally on *Pleuragramma* as well
(Eastman, 1985), indicating that it represents a critical trophic link in the coastal system.
However, in recent years a marked change has been detected in diet compositions of
several predators in the vicinity of Anvers Island. Prior to the late 1980s, *Pleuragramma*
was a key component in diets of Adelie penguins, south polar skuas (*Catharacta
lonnbergi*), and kelp gulls (*Larus dominicanus*) but this is no longer the case (Neilson,
1983; Fraser, 1989, unpublished data). This suggests that *Pleuragramma* have
disappeared from the foraging ranges of Anvers Island seabirds.
The Antarctic Peninsula has been identified as one of the most rapidly warming regions in the world (Vaughan et al., 2003). Annual air temperatures have increased by 2-3°C (Turner et al., 2005) and sea surface temperatures have increased by more than 1°C (Meredith and King, 2005) over the past 50 years, resulting in decreased sea ice extent in the WAP, specifically in the vicinity of Anvers Island (Ducklow et al., 2007). Reductions in sea ice could directly impact population dynamics of fauna such as *Pleuragramma* which appear to have life history stages that rely on the presence of sea ice (Vacchi et al., 2004; Clarke et al., 2007). Freshwater inputs from increased glacial meltwater may impact phytoplankton assemblages by shifting dominance from diatoms to smaller cryptophytes (Moline et al., 2004). This in turn may impact grazing efficiencies of zooplankton causing further shifts in faunal composition and distribution, e.g. the encroachment of salps and other oceanic fauna into regions previously dominated by neritic species (Atkinson et al., 2004).

The present study examined the macrozooplanktonic/micronektonic faunal assemblages at several sites along the WAP shelf including taxonomic composition and distribution patterns in relation to local bathymetry and hydrography. One objective of this study was to test the hypothesis that four distinct hydrographic regimes exist from north to south along the WAP continental shelf and that the faunal assemblages within those regimes could be biologically discriminated. Multivariate techniques were used to identify unique multispecies assemblages and to quantify the contributions of both oceanic and neritic species to each assemblage. Abundance and biomass of *Pleuragramma* in the WAP shelf region were compared to densities recorded by previous studies.
Methods

Study Sites and Sample Collection

Samples were collected at nine different sites located within four hydrographic regions along the Western Antarctic Peninsula (Figure 3.1) aboard the Research Vessel Ice Breaker (R.V.I.B.) *Nathaniel B. Palmer* during the austral fall (March – April) of 2010. Region I included the northernmost sampling site, which was located in Antarctic Sound near Joinville Island. Four sites were sampled in Region II. Those sites consisted of Croker Passage near the northern boundary of the region; Palmer located south of Anvers Island; Palmer Deep offshore of Anvers Island; and the pass to the east of Renaud Island. Sampling in Region III occurred at two sites in Marguerite Bay, one near the southern tip of Adelaide Island and one located mid-shelf within the Marguerite Trough. In Region IV, sampling occurred at two sites in the vicinity of Charcot Island, one nearshore (Charcot Island) and one offshore within a cross-shelf canyon (Charcot Deep).

Hydrographic data were collected at or near each site using a CTD. Characteristic water masses such as Antarctic Surface Water (AASW; temperature -1.8 to 1.0 °C, salinity 33.0 to 33.7), Winter Water (WW; temperature -1.5 °C, salinity 33.8 to 34.0), and Circumpolar Deep Water (CDW; temperature 1.0 to 2.0 °C, salinity 34.6 to 34.74) as defined by Smith et al. (1999) were denoted on plots when present.

Macrozooplankton and micronekton were collected at each site with a 10-m² Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) outfitted with six 3-mm mesh nets (Wiebe et al., 1976, 1985). A total of 32 trawls were
successfully completed with seven conducted during the day and 25 at night, or dusk (Table 3.1). For each trawl, the first net fished obliquely from surface to depth and each subsequent net fished a discrete depth layer up towards the surface. Most trawls fished to depths of 500 m and sampled depth strata of 0-50, 50-100, 100-200, 200-300, and 300-500 m. Three trawls fished to a depth of 1000 m and sampled depth strata of 0-100, 100-200, 200-300, 300-500, and 500-1000 m. One trawl fished to a depth of 331 m and sampled depth strata of 0-50, 50-100, 100-170, 170-225, and 225-331 m.

Specimens collected in the trawls were either preserved in a 10% buffered formalin solution or frozen and shipped to the laboratory for analysis. All micronektonic and macrozooplanktonic specimens were sorted, counted, identified to lowest possible taxon, and weighed (g wet mass). Standard length (mm SL) was measured for all fish specimens. After processing, samples were transferred to 50% isopropanol for long term storage.

Data Analyses

Volumetric abundance and biomass values from each trawl were obtained by dividing the raw number or wet mass by the water volume filtered during each trawl (# or g WM x 10$^4$ m$^{-3}$). Those standardized values were then used to compute the mean abundance and biomass of each individual taxon per site as well as the mean overall abundance and biomass for each site. Statistical comparisons between sites were
performed on the volumetric data (# or g WM x 10^4 m^3) using generalized linear mixed models in SAS version 9.2 (SAS Institute Inc., Cary, NC, USA).

Vertical distributions for four common invertebrate species and two common fish species were compiled from nets that fished within the following depth strata: 0-50, 50-100, 100-200, 200-300, 300-500, and 500-1000 m. Median and mean volumetric abundance was calculated for each depth stratum and those values were used to determine the vertical range for each species. The peak range for each species was chosen as the stratum with the highest mean volumetric abundance for daytime and nighttime trawls. There were a total of seven daytime trawls and 25 nighttime trawls completed during the cruise.

Macrozooplankton/micronekton assemblage structure was analyzed by multivariate techniques using the PRIMER v6 software package (Clarke and Gorley, 2006). Volumetric abundance and biomass data were log (x+1) transformed to allow for a more even contribution from both common and rare taxa in each analysis (Clarke, 1993). Transformed data were then used to calculate Bray-Curtis similarity matrices, which were subsequently used to perform an analysis of similarities (ANOSIM) and generate hierarchical cluster analysis dendrograms and MDS ordination plots. The ANOSIM procedure is a non-parametric permutation/randomization test that functions as an analogue to a standard univariate ANOVA test (Clark and Green, 1988). The test produces a global R value (which usually ranges from 0 to 1, where 0 indicates no differences) and an associated significance level. The SIMPER (analysis of similarity
percentages) procedure was used to identify those taxa contributing most to the similarities within each resultant cluster group.

Median and mean integrated abundance (\( \# \text{ m}^{-2} \)) and biomass (g WM m\(^{-2} \)) for the 0-200 m stratum were determined by first selecting those nets from each trawl that sampled within 0-200 m. Integrated values were then calculated by dividing the total number or wet mass from each net by the water volume filtered by that net, multiplied by the vertical range, in meters, trawled by that net, and summed for each trawl. Mean integrated abundance and biomass were calculated for the 0-200 m stratum at each site. Because there were so few daytime trawls, those data were omitted from this analysis.

**Results**

*Hydrography*

Water column properties varied markedly among the sites (Figures 3.2A – 3.2I). At Joinville Island, Croker Passage, and Palmer, the water column was nearly isothermal and isohaline from the surface to 500 m depth; however, temperature and salinity ranges varied among the three sites. Joinville Island had the coldest water column with temperatures ranging from only -1.8 to -1.4 °C and salinities from 34.3 to 34.4. Salinity profiles were similar at Croker Passage and Palmer, ranging from approximately 33.8 at the surface to 34.6 at depth, but temperatures at Palmer were substantially warmer (0.6 to 1.0 °C) than those at Croker Passage (-0.5 to 0.1 °C). In addition, CDW was present at depths below 375 m at Palmer.
The water column was stratified at the remaining six sites. At Palmer Deep and Marguerite Bay, a temperature minimum occurred between 90 and 200 m with coldest temperatures recorded at approximately 140 m. A similar temperature minimum occurred at Renaud Island and Marguerite Trough, but was slightly shallower and instead extended from 50 to either 150 or 200 m. At Charcot Island and Charcot Deep, the coldest temperatures occurred near the surface (<100 m) and were associated with AASW. WW was also present between 100 and 200 m at those two sites. CDW was present at all six stratified sites and first appeared between depths of 340 to 375 m at most sites. The only exception occurred in the Marguerite Trough where CDW was detected at the much shallower depth of 230 m.

**Taxonomic Composition**

A total of 62 taxa representing 12 taxonomic groups of pelagic invertebrates and 9 families of fish were collected during this study (Tables 3.2A – 3.2I). The gammarid amphipods were the most diverse taxonomic group overall with eight taxa, followed by the hyperiid amphipods and the nototheniid fish, each with six taxa. Diversity was greatest at the Croker Passage and Marguerite Bay sites, each with 39 taxa. Gammarids were also among the most diverse taxonomic groups at the majority of study sites, the exceptions being at the Palmer and Palmer Deep sites where numbers of euphausiid, hyperiid, and/or mysid taxa were greater. The myctophids were the most diverse fish family at all sites except Joinville Island, Charcot Island, and Charcot Deep. At Joinville Island, no myctophids were collected and the nototheniid family Channichthyidae was
most diverse. At Charcot Island, myctophids and nototheniids were equally diverse whereas nototheniids were the most diverse fish family at Charcot Deep.

The most numerically abundant taxa included the euphausiids, *Thysanoessa macrura*, *Euphausia superba*, and *E. crystallorophias*, combining to contribute nearly 79% of the total catch. Those three species were also the most abundant taxa at all sites, except Croker Passage where the tunicate, *Salpa thompsoni*, was the numerical dominant. Among the fishes, the myctophid, *Electrona antarctica*, was the dominant fish species at the Croker Passage, Palmer, Renaud Island, Marguerite Trough, and Charcot Island sites. Another myctophid, *Protomyctophum bolini*, was dominant at Palmer Deep. Two nototheniids were numerical dominants at the remaining sites; *Pleuragramma antarcticum* at Joinville Island and Marguerite Bay and *Trematomus* sp. at Charcot Deep.

With respect to biomass, *E. superba* was the dominant species, contributing more than 44% of the total catch. Other dominant biomass contributors included *P. antarcticum* and *S. thompsoni*, which supplied 16% and 11% of the catch, respectively. Biomass dominants at each of the sites were similar to numerical dominants with the exception of Charcot Island, where *P. antarcticum* contributed the most biomass overall. Among the fishes, *P. antarcticum* was also the dominant biomass contributor at Joinville Island and Marguerite Bay. Other dominant fish taxa included the myctophids at five sites: *E. antarctica* at Palmer, Marguerite Trough, and Charcot Deep, *P. bolini* at Palmer Deep, and *Gymnoscopelus nicholsi* at Renaud Island. The paralepidid, *Notolepis coatsi*, contributed the most fish biomass at Croker Passage.
Discrete depth distributions were compiled for four common invertebrate and two common fish species by pooling data from all sites (Figure 3.3). It should be noted that there were far fewer daytime trawls than nighttime trawls conducted during the cruise. In addition, total numbers of individuals captured during the daytime trawls were often substantially lower than total numbers captured during the nighttime trawls, suggesting daytime net avoidance. A day-night disparity in total catch is a common shortcoming of net-based studies and may result in an underestimate of daytime abundance; however, day-night shifts in population maxima remain accurate. Because so little data are available on vertical distribution patterns for the species addressed in the present study, results from daytime trawls were included and contrasted with nighttime abundances.

Four species, *E. superba*, *T. macrura*, *S. thompsoni*, and *E. antarctica*, were found throughout the sampled water column (surface to 1000 m). The remaining common species, *E. crystallorophias* and *P. antarcticum*, were only present from the surface to 500 m. Peak daytime ranges were similar between the two fish species (300 - 500 m) but *E. antarctica* had nighttime peaks at 100 - 200 m as well as 300 - 500 m while *P. antarcticum* was concentrated between 100 - 300 m. The euphausiids *E. crystallorophias* and *E. superba* were most abundant at the surface (0 - 50 m) at night but both descended during the day with peak abundances of *E. crystallorophias* at 200 - 300 m and *E. superba* at 50 - 100 m. In contrast, the majority of *T. macrura* ascended from 200 - 300 m at night to 50 - 100 m in the day. The salp, *S. thompsoni*, behaved similarly, with the
majority ascending from a peak nighttime distribution of 500 - 1000 m to the surface during the day.

Site Comparisons

A comparison of total catches among sites showed that the largest volumetric abundances were captured at Marguerite Bay where the mean exceeded 1000 individuals $10^4$ m$^{-3}$ ($P = 0.01$; Tables 3.2A-3.2I). At the Marguerite Trough site, mean abundances were an order of magnitude lower with only 146 individuals $10^4$ m$^{-3}$ captured. Although only one trawl was completed at Marguerite Trough, the total volume filtered was similar to that of Palmer Deep (147,439 vs. 195,705 m$^3$) where the mean abundance of 626 individuals $10^4$ m$^{-3}$ was significantly higher. Mean abundances among the remaining sites were similar, ranging from approximately 300 to 800 individuals $10^4$ m$^{-3}$. Mean volumetric biomass was also highest at the Marguerite Bay site (530 g WM $10^4$ m$^{-3}$), but the lowest biomasses were captured at the Marguerite Trough, Palmer, and Palmer Deep sites where mean values ranged from 17 to 41 g WM $10^4$ m$^{-3}$ ($P < 0.01$). Renaud Island had slightly higher mean biomass (73 g WM $10^4$ m$^{-3}$) and the remaining sites, Joinville Island, Croker Passage, Charcot Island and Charcot Deep, all had means near or slightly higher than 200 g WM $10^4$ m$^{-3}$.

Comparisons of total catches of dominant invertebrate and fish revealed that there were differences in abundance and biomass among sites for most of those taxa. *E. superba* was present at all sites but was most prevalent at Joinville Island, Marguerite
Bay, and Charcot Deep where mean volumetric abundances (ranging from 235 to 496 individuals $10^4$ m$^{-3}$; $P<0.01$) and biomasses (ranging from 140 to 355 g WM $10^4$ m$^{-3}$; $P<0.01$) were similar. Abundance and biomass of *E. superba* was one to two orders of magnitude lower at the remaining sites. The greatest quantities of *E. crystallorophias* were captured at the Marguerite Bay and Charcot Island sites where means of 507 individuals $10^4$ m$^{-3}$ and 172 individuals $10^4$ m$^{-3}$, respectively, were significantly higher than measures at the other sites ($P<0.01$). The greatest biomasses of *E. crystallorophias* were also captured at those sites, but biomass was significantly higher at Marguerite Bay than at Charcot Island (102 vs. 29 g WM $10^4$ m$^{-3}$; $P<0.01$). Very few *E. crystallorophias* were captured at Croker Passage, Palmer, and Renaud Island, while none were captured at Palmer Deep. Total catches of *T. macrura* were highest at the Palmer, Palmer Deep, and Renaud Island sites where mean abundances exceeded 386 individuals $10^4$ m$^{-3}$ ($P<0.01$) and mean biomasses ranged from 14 to 23 g WM $10^4$ m$^{-3}$ ($P<0.01$). The salp, *S. thompsoni*, was captured in greatest quantities at Croker Passage (203 individuals $10^4$ m$^{-3}$; 145 g WM $10^4$ m$^{-3}$; $P<0.01$), in moderate quantities at Joinville Island, and in relatively low quantities at the Palmer, Palmer Deep, Marguerite Trough, and Charcot Island sites. No *S. thompsoni* were captured at Renaud Island, Marguerite Bay, and Charcot Deep.

The lanternfish, *E. antarctica*, was present at all sites except Joinville Island but the largest catches were at the Charcot Island site where the means were 5 individuals $10^4$ m$^{-3}$ and 36 g WM $10^4$ m$^{-3}$ ($P<0.01$). As mentioned earlier, *P. antarcticum* was absent from the Palmer, Palmer Deep, Renaud Island, and Marguerite Trough sites. The largest *P. antarcticum* abundances, with means between 3 and 4 individuals $10^4$ m$^{-3}$, were
captured at Joinville Island and Charcot Island ($P < 0.01$); however, average biomass was significantly higher at the Charcot Island site (163 vs. 44 g WM $10^4$ m$^{-3}$; $P < 0.01$). No differences in abundance or biomass among sites were detected for other prevalent fishes such as $G. nicholsi$, $G. braueri$, $N. coatsi$ or $P. bolini$ ($P > 0.16$).

**Multispecies Assemblages**

One-way ANOSIM analyses of volumetric abundance and biomass revealed that there were significant differences in multispecies assemblages among sites (Abundance: Global $R = 0.938$, $P < 0.01$; Biomass: Global $R = 0.805$, $P < 0.01$). Cluster analysis of abundance data separated trawls from the nine sites into five distinct clusters at the 60% similarity level (Figure 3.4). Groups A and B were more similar and comprised of trawls conducted at Joinville Island and Croker Passage, respectively. Group D included the trawls conducted in Marguerite Bay and Group E included the trawls from Charcot Island and Charcot Deep. Group C was composed of the remaining trawls which were from the Palmer, Palmer Deep, Renaud Island, and Marguerite Trough sites. At the 49% similarity level, biomass cluster groups were very similar to those on the abundance dendrogram, with the only differences occurring in Groups D and E (Figure 3.5). Instead of comprising one cluster group, the nearshore Charcot Island trawls clustered with Marguerite Bay in Group D, leaving only the Charcot Deep trawls in Group E. The MDS ordination plots show the 2-dimensional structure of the abundance and biomass data with resultant stress levels of 0.12 and 0.15, respectively (Figures 3.6 and 3.7).
SIMPER analysis of the abundance data identified the taxa that contributed the most to similarities within each resultant cluster group. Although most dominant taxa were present in all clusters, each contributed to the similarity within the clusters to varying degrees. In Group C, *T. macrura* and the oceanic hyperiid, *Themisto gaudichaudii*, were the two most abundant species combining to contribute more than 50% of the similarity within that group (Table 3.3). The euphausiid *T. macrura* was also the dominant species in Group E but, in contrast, the secondary contributors were the euphausiids *E. crystallorophias* and *E. superba*. Species composition in Group D was similar to that of Group C, but instead *E. crystallorophias* was the ranking species contributing 19% to the similarity within the group. Groups A and B were similar in that the top two contributors were either *E. superba* or the oceanic *S. thompsoni*; however, in Group B, *S. thompsoni* contributed nearly twice that of *E. superba* (30% vs. 16%) whereas in Group A, percent contributions from each species were similar (14% vs. 18%). Bubble plot overlays of the MDS ordination plot show the abundance and distribution of the dominant invertebrate and fish species and how they relate to the abundance cluster groups (Figure 3.8).

Results from SIMPER analysis on biomass were similar to that of abundance with the major differences arising from the greater influence of species that were less numerous but larger in size (Table 3.4). In Group A, *P. antarcticum* increased from contributing less than 4% to the similarity within the abundance cluster to nearly 15% of the similarity within the biomass cluster. The influence of *E. antarctica* also increased, especially in Group B where it was the second ranked contributor. The composition of Cluster Groups D and E was slightly different for biomass than for abundance (placement
of Charcot Island trawls), and as a result *E. crystallorophias* rather than *T. macrura* was the ranking species in Group E. Figure 3.9 shows the bubble plot overlays of biomass and distribution of six common species.

*Integrated Abundance and Biomass*

A total of 31 invertebrate and 12 fish taxa were captured in the upper 200 m of the water column during the cruise. Of those taxa, 18 contributed 1% or more to either the total integrated abundance or biomass at a minimum of one site (Tables 3.5A – 3.5I). The euphausiids *T. macrura* and *E. superba* were dominant contributors of abundance and biomass in the 0-200 m layer at the majority of sites. The ice krill, *E. crystallorophias*, was the top contributor at Charcot Island and *S. thompsoni* was the top contributor at Croker Passage. Other taxa such as *T. gaudichaudii*, *E. antarctica*, *G. nicholsi*, and *P. antarcticum* also supplied a substantial proportion of the catch among the sites. Mean total densities in the upper 200 m ranged from approximately 6 individuals m⁻² at the Marguerite Trough site to 63 individuals m⁻² at Marguerite Bay. Densities at the remaining sites fell between 15 and 30 individuals m⁻². Biomass estimates showed a similar pattern, with the lowest mean recorded at Marguerite Trough (0.4 g WM m⁻²) and the highest at Marguerite Bay (33 g WM m⁻²).
Pleuragramma antarcticum Size Distributions

Size distributions of *P. antarcticum* captured from each site are presented in Figure 3.10. Standard lengths of all fishes captured ranged from 19 to 213 mm with three modal peaks occurring at the 45 mm (small), 115 mm (medium), and 155 mm (large) size class intervals. The small and medium modal groups were primarily composed of fish captured from Joinville Island, while those in the large modal group were dominated by fish captured at Marguerite Bay. The large modal group also included all of the fish captured at Charcot Island. Fewer fish were captured at Charcot Deep and those all fell into the small modal group. No fish from Charcot Island or Charcot Deep fell into the medium modal group. One fish, falling into the medium modal group, was captured from Croker Passage. No *P. antarcticum* were captured from the Palmer, Palmer Deep, Renaud Island, or Marguerite Trough sites.

Discussion

Faunal Composition and Hydrographic Influences

A total of 62 taxa were collected during the present study, but four species, *E. crystallorophias, E. superba, T. macrura,* and *S. thompsoni,* accounted for the majority of the catch, contributing more than 84% of the total abundance and 69% of the total biomass captured. Those species have previously been characterized as dominant taxa in various regions along the WAP including Bransfield Strait (Piatkowski, 1985; Witek et al., 1985; Brinton and Townsend, 1991; Nordhausen, 1992), Croker Passage (Lancraft et
al., 2004), Gerlache Strait (Nordhausen, 1994a, 1994b), the region extending from Anvers to Adelaide Island (Ross et al., 2008), and Marguerite Bay (Parker et al., 2011). Fishes constituted more than one-third of the taxa captured, but contributions to overall abundance were negligible totaling to less than 1% of the catch. However, two important pelagic fish species, the Antarctic silverfish, *P. antarcticum*, and the myctophid, *E. antarctica*, contributed substantial biomass accounting for 16% and 4% of the total catch, respectively.

Vertical depth ranges for most dominant species encompassed the entire sampled water column, but neither *E. crystallorophias* nor *P. antarcticum* were captured at depths greater than 500 m. This may be an artifact of the trawling effort since the few deep trawls (surface to 1000 m) were conducted at sites (Croker Passage and Palmer) where both species were either absent or present at very low densities. However, a study in the Marguerite Bay region during 2001/2002 yielded similar results (Donnelly and Torres, 2008; Parker et al., 2011), suggesting that the coastal distributions of both species may preclude their presence below 500 m at most of the present study sites. Deeper distributions of *P. antarcticum* were recorded at Croker Passage in 1983 (Lancraft et al., 2004), but since only one fish was captured at that site in the present study (as well as being captured in a net that fished obliquely from the surface to depth) a valid comparison cannot be made. It should be noted that the WAP is the only region of the Antarctic whose temperature profile allows the intrusion of oceanic fishes into shelf waters. The lanternfishes, dominated by *E. antarctica*, are well established despite their lack of biological antifreezes (Cullins et al., 2011). In coastal regions where low temperature (-2.0 °C) ice-shelf water is present, e.g. the Ross Sea (Dinniman et al., 2003),
oceanic species are excluded (DeWitt, 1970; Donnelly et al., 2004); their presence in the water column ends at the shelf break.

Micronektonic/macrozooplanktonic faunal assemblages along the WAP continental shelf were composed of a varying mix of neritic and oceanic species. The extent of mixing between the two assemblages as well as changes in the relative abundances of dominant species among sites was directly related to the unique bathymetry and hydrographic conditions present on the WAP shelf. Faunal mixing is maximized as CDW moves onto the shelf and mixes with cooler, fresher shelf waters (Donnelly and Torres, 2008; Parker et al., 2011). This was illustrated by the balance of oceanic and neritic fauna in assemblages at sites in the Marguerite Bay region and near Charcot Island. For example, taxonomic diversity was high at Charcot Deep, a site that was located nearshore but within a deep trench where fauna associated with cold, shelf waters mixed with oceanics transported onto the shelf within the warm, deep CDW layer. Although that assemblage was dominated by the euphausiid, *E. superba*, there was almost even representation by neritic and oceanic fauna. The assemblage in the Marguerite Trough was also well mixed, but instead the ubiquitous euphausiid *T. macrura* was the predominant species. The character of the fauna suggests there was a weaker neritic influence at the Trough site, which was reflected in the warmer water column temperatures and the much shallower presence of CDW at that site. Conversely, the assemblages at the most nearshore sites, Marguerite Bay and Charcot Island, were dominated by *E. crystallorophias* and *P. antarcticum*, both of which are coastal species most commonly found in cold shelf waters (Smith and Schnack-Schiel, 1990; Hubold, 1984).
At the two northernmost sites, Joinville Island and Croker Passage, the absence of a CDW layer strongly influenced the assemblages. Near Joinville Island, circulation is driven by cold surface waters moving westward from the Weddell Sea (Stein, 1986; Thompson et al., 2009) resulting in a water column more typical of higher latitude Antarctic shelf regions where temperatures are near freezing (-2 °C) from the surface to depth (Dinniman et al., 2003). Those cold temperatures effectively excluded many oceanics from the Joinville Island assemblage, especially those fishes such as *E. antarctica* which lack antifreezes (Cullins et al., 2011). Instead, silverfish were not only abundant at Joinville Island, but captured at densities comparable to those recorded in Marguerite Bay and near Charcot Island. The water column at Croker Passage was also well mixed, but temperatures were slightly warmer with an average near 0 °C. The resulting assemblage at Croker Passage consisted primarily of oceanic fauna and was overwhelmingly dominated by *S. thompsoni*, which is becoming increasingly more common in the northern WAP region (Atkinson et al., 2004).

At Renaud Island and the two Palmer sites, temperatures were even warmer than those at Croker Passage, generally exceeding 0 °C throughout the water column. Not surprisingly, oceanic fauna were most prevalent in those assemblages but *T. macrura* dominated, as observed in the Marguerite Trough assemblage. In fact, *T. macrura* contributed more than 83% of the total number of individuals captured at the two Palmer sites and just over 65% at Renaud Island. Diversity at the Palmer Deep site was the lowest recorded in the study and contributions by the few neritic fauna present in the assemblage totaled less than 1%. Despite the fact that the Palmer and Renaud Island sites
were located nearshore, *E. crystallorophias* was present only at very low densities and *P. antarcticum* was completely absent from the assemblages.

**Hydrographic Regimes and Multispecies Assemblages**

One of the goals of the present study was to investigate the existence of several distinct hydrographic regimes occurring along the WAP shelf. Physical factors such as the presence of persistent gyral circulation patterns, which act to retain fauna, and the extent and duration of seasonal sea ice were used to define different regions. In addition, the expected composition of the faunal assemblages and the prevalence of ice-associated fauna like *E. crystallorophias* and *P. antarcticum* were used to characterize those regions. Prior to this study, we hypothesized that there were four such regions occurring from north to south along the WAP (Figure 3.1). The northernmost region (Region I), which extends from Joinville Island to just north of Brabant Island, was delineated by its lack of gyral circulation and the strong influence of coldwater flow from the Weddell Sea (Hofmann et al., 1996). Assemblages in this region were expected to contain high densities of *P. antarcticum* and other neritic fauna. Region II was characterized by the existence of a clockwise gyral circulation pattern that encompassed the area from north of Brabant Island to just south of Renaud Island (Hofmann et al., 1996; Smith et al., 1999). In addition, regional warming in this area has led to a substantial decrease in sea ice extent primarily due to earlier ice retreat in the spring (Ducklow et al., 2007). Assemblages in Region II were predicted to be composed almost exclusively of oceanic fauna.
The Marguerite Bay system, which included Adelaide Island to the north and Alexander Island to the south, comprised Region III and was defined by a second cyclonic gyre that extended from Lavoisier Island to the southern extent of Lazarev Bay (Klinck et al., 2004). Lastly, Region IV was designated by an area extending from Lazarev Bay in the north to an as yet undefined boundary south of Charcot Island. Fewer studies have been conducted in this region, but it has been hypothesized that there is a third gyral circulation pattern just north of Charcot Island (Hofmann, unpublished data) and that this region is the southernmost WAP shelf area exposed to CDW intrusions. In Regions III and IV, the presence of cold shelf waters and warm CDW is expected to generate assemblages composed of both oceanic and neritic fauna.

Cluster analysis of the assemblages from each site identified five primary groups, which corresponded closely with the hypothesized regions and their expected faunal compositions. Distinct assemblages were identified at Joinville Island, Marguerite Bay, and Charcot Island, which coincided with Regions I, III and IV, respectively. Assemblages from the two Palmer sites, Renaud Island, and the Marguerite Trough clustered together and, with the exception of the Marguerite Trough site, fit within the geographical constraints of Region II. The Croker Passage assemblage grouped independently rather than within Regions I or II most likely due to the overwhelming abundance of *S. thompsoni* in those samples. Because most taxa were captured throughout the study region, there were no apparent indicator species for any particular assemblage. Instead, changes in the relative abundance and biomass of major taxa were instrumental in determining differences among the multispecies assemblages (Siegel and
Piatkowski, 1990). In addition, those species that have been typically classified as either oceanic or neritic fauna were useful in characterizing the multispecies assemblages.

The assemblages at Joinville Island and Croker Passage were more similar to each other than to the other three cluster groups. Although *E. superba*, *S. thompsoni*, and *T. macrura* were dominant contributors in both northern groups, hydrographic conditions at Joinville Island favored a neritic assemblage as evidenced by the substantial contributions from *P. antarcticum* and the deep dwelling mysid, *Antarctomysis maxima*. In contrast, the assemblage at Croker Passage was more oceanic in nature with major inputs from *E. antarctica* and *T. gaudichaudii*. Assemblages at Marguerite Bay and Charcot Island grouped more closely due to strong neritic and oceanic influences, which functioned to maximize faunal mixing at those sites. This is demonstrated by the prevalence of the neritics, *E. crystallorophias* and *P. antarcticum*, as well as the oceanics, *T. gaudichaudii* and *E. antarctica* in those assemblages. The final cluster assemblage included samples collected from several sites in the mid-peninsula region, roughly corresponding to Region II, and was overwhelmingly dominated by two species, *T. macrura* and *T. gaudichaudii*. Although *T. macrura* is not considered an oceanic species, but rather a ubiquitously distributed species (Kittel and Stepnik, 1983; Kittel et al., 1985; Nordhausen, 1994a, 1994b; Piatkowski, 1985), abundances were an order of magnitude higher at most sites in Region II. Very few neritic fauna were present in the Region II assemblage. Most notable was the complete absence of *P. antarcticum*.

Although samples for this study were collected over a two month period and thus only present a snapshot of the multispecies assemblages present at each of the study sites,
results from cluster analyses provide support for the presence of distinct hydrographic regimes along the WAP. The unique hydrography of the WAP creates complex cross-shelf circulation processes that increase retention at inner shelf locations (Piñones et al., 2011; Murphy et al., 2012), effectively limiting connectivity between the regions. However, there is evidence suggesting that flow from the Antarctic coastal current connects the Marguerite Bay region to areas further south, such as Charcot Island (Piñones et al., 2011). Microchemical analyses of otolith nuclei were conducted on fish captured during this study and revealed that there were no significant differences in isotopic ratios between fish captured in Marguerite Bay and near Charcot Island, but that ratios in those fish were significantly different than ratios from fish captured in the Ross Sea (Ferguson et al., unpublished data). This suggests that Pleuragramma from Marguerite Bay and Charcot Island are part of the same population. Genetic analyses were also performed on fish captured in this study and yielded similar results, with the Marguerite Bay and Charcot Island fish comprising a single, panmictic population that was differentiated from the Joinville Island fish (Patarnello and Agostini, unpublished data). Results of these studies provide three lines of evidence, based on cluster analyses, otolith microchemical analyses, and genetic analyses, that there is little to no connectivity between the northernmost region at Joinville Island and the southernmost regions at Marguerite Bay and Charcot Island.
Disappearance of Pleuragramma antarcticum from the WAP Shelf

Extensive sampling of larval and adult *P. antarcticum* has occurred in the waters of the WAP shelf region. Consecutive sampling programs such as FIBEX and SIBEX (First and Second International Biomass EXperiments, respectively), RACER (Research on Antarctic Coastal Ecosystem Rates), and AMLR (Antarctic Marine Living Resources) have provided consistent information on *P. antarcticum* distributions on the WAP since 1976 (Rembiszewski et al., 1978; Slosarczyk and Rembiszewski, 1982; Skora and Sosinski, 1983; Slosarczyk and Cielniaszek, 1985; Kellerman, 1986, 1987, 1989; Slosarczyk, 1986; White and North, 1987; Kellerman and Kock, 1988; Loeb, 1991). There have also been several individual studies that, when taken collectively with the sampling programs provide a fairly good description of historical *P. antarcticum* distributions on the WAP shelf (Daniels, 1982; Daniels and Lipps, 1982; Hubold and Tomo, 1989; Kellerman and Schadwinkel, 1991; Morales-Nin et al., 1998; Lancraft et al., 2004; Donnelly and Torres, 2008). Among those studies, juvenile and adult silverfish have been definitively captured in nets deployed in Croker Passage (Lancraft et al., 2004), northwest of Adelaide Island (Skora and Sosinski, 1983) and in the Marguerite Bay region (Donnelly and Torres, 2008). In addition, schools of several thousand *Pleuragramma* were reported by a diver under the ice near Palmer Station, Anvers Island (Daniels, 1982).

Most life history information on *Pleuragramma* comes from samples collected from the Ross and Weddell Seas, as well as from the Antarctic Peninsula region. Size at birth ranged between 8-10 mm in the Weddell Sea (Hubold, 1990) and averaged 9.3 mm
in the Ross Sea (Vacchi et al., 2004), suggesting that there is little variability in hatching size among regions. In Terra Nova Bay near the Ross Sea, *Pleuragramma* eggs were found floating in the platelet ice underneath 1.3 m thick sea ice, where they began hatching in mid-November (Vacchi et al., 2004). This was a crucial finding since it suggests that sea ice cover is important to *Pleuragramma* early life history. In addition, it confirmed that *Pleuragramma* have pelagic eggs, a conclusion first reported by Faleyeva and Gerasimchuk (1990) in a histological study on *Pleuragramma* gonads. Like size-at-hatching, timing of hatching was found to occur consistently in the November-December period in the Ross Sea, Weddell Sea, and in the Peninsula region (Kellerman, 1986; Hubold and Tomo, 1989; Kellerman and Kock, 1988; Vacchi et al., 2004). It is believed that spawning takes place in late winter (August - September) and that embryos develop over a period of 60-75 days before hatching (Kellerman and Kock, 1988).

*Pleuragramma* remain in the larval stage until their third year of life when they are at standard lengths (SL) of 60-90 mm (Hubold, 1985). Data on length-at-age obtained using annular rings of otoliths (sagittae) suggested that *Pleuragramma* reach a size of approximately 200 mm SL in their fourteenth year and that the largest sized fishes (245-250 mm SL) were approximately 21 years old (Hubold and Tomo, 1989; Reisenbichler, 1993). Data on length-at-age obtained reading otolith microincrements (daily rings) with a scanning electron microscope suggested that *Pleuragramma* were far older: a 205 mm fish was determined to be 33.5 years of age (Radtké et al., 1993). Despite the differences, it is relatively clear that *Pleuragramma* is a slow-growing, long-lived fish, even when considered among other Antarctic fishes.
Visual and histological studies suggest that *Pleuragramma* collected from the Mawson Sea spawned for the first time at sizes of approximately 130-160 mm SL (Faleyeva and Gerasimchuk, 1990). Hubold (1985) reported that *Pleuragramma* in the Weddell Sea first showed gonadal development at a size of 125 mm SL and Reisenbichler (1993) reported that *Pleuragramma* from McMurdo Sound showed gonadal development at 160 mm SL. Agreement between the three studies is reasonably good, with a consensus figure of 130-160 mm SL. If the size at sexual maturity, 130-160 mm SL, is applied to the Hubold and Tomo (1989) growth curve, *Pleuragramma* reaches sexual maturity at an age of 7-9 years, or at about 55% of its maximum size (Kock and Kellerman, 1990).

There is little information on the spawning behavior of *Pleuragramma* but several studies provide suggestions. Daniels (1982) observed thousands of *Pleuragramma* underneath land-fast sea ice near Anvers Island during the months of June through October suggesting that *Pleuragramma* may form spawning aggregations under coastal sea ice in the winter or, at the very least, that *Pleuragramma* behavior may change during winter months. The recent observations by Vacchi et al. (2004) confirm that *Pleuragramma* lay pelagic eggs and that reproduction occurs nearshore (Kellerman, 1986). Follow up studies by Vacchi et al. (2012) substantiated the importance of Terra Nova Bay as a nursery area for *Pleuragramma* and that eggs and newly hatched larvae were widely distributed throughout the area. In addition, Vacchi et al. (2012) found that hatching occurred predominantly in November. However, present data still do not provide a sufficient estimate of egg development time and thus, the timing of spawning.
Silverfish were captured at five sites during the present study: Joinville Island, Croker Passage, Marguerite Bay, and the two sites near Charcot Island. They were completely absent at the two Palmer sites, at Renaud Island, and in the Marguerite Trough. They were nearly absent in Croker Passage (one fish was captured), where they were previously considered a dominant fish species (Reisenbichler, 1993) and where Lancraft et al., (2004) measured an integrated abundance of 88 individuals $10^3$ m$^{-2}$ in the upper 200 m of the water column in 1983. In Marguerite Bay, volumetric abundances of *P. antarcticum* were also much lower with a mean of approximately 1 individual $10^4$ m$^{-3}$ compared to 45 individuals $10^4$ m$^{-3}$ in 2001 and 2002 (Donnelly and Torres, 2008). Biomass estimates in Marguerite Bay were more similar, at approximately 50 g WM $10^4$ m$^{-3}$ (Donnelly and Torres, 2008), suggesting that the fish caught in 2010 were substantially larger than those from the 2001/2002 study. In fact, the majority of fish captured from Marguerite Bay in 2010 were larger than 150 mm SL (age class 10; Hubold and Tomo, 1989) compared to a majority of fishes sized 30-53 mm SL (age class 1) in 2001 and 55-72 mm SL (age class 2) in 2002 (Donnelly and Torres, 2008; Figure 3.11). Comparison of the 2001, 2002, and 2010 *Pleuragramma* size distributions show what appears to be the progression of a single year class of fish.

There are several potential causes for the disappearance of *Pleuragramma antarcticum* from the WAP shelf. Circulation is a major factor that can influence populations of any marine organism and lead to advection out of a local area. This is a plausible explanation for the absence of *Pleuragramma* in Region II, but the presence of larger adult fish in Marguerite Bay suggests advection is not the primary factor in that area. Another potential cause may be related to predation pressure. *Pleuragramma* are
considered a key prey source in Antarctic coastal regions for many upper trophic level predators (O’Driscoll et al., 2011). Therefore, it is possible that predation is a direct cause of the disappearance of *Pleuragramma* from Region II, where they were previously found to be a key component of Adelie penguin diets (Fraser, 1989, unpublished data). In the Marguerite Bay region, predators may be principally feeding on larvae and smaller sized adults, thus explaining the prevalence of larger fish in 2010.

The physical environments of the local regions may be impacting *Pleuragramma* populations by limiting recruitment success. Over the past 50 years, mid-winter air temperatures in the Palmer region (Region II) of the WAP have increased by nearly 6 °C, producing an overall decrease in the presence of sea ice over a range of spatial and temporal scales (Fraser et al., 1992; Smith et al., 2003a, b). During the last decade, sea ice has been forming later and retreating earlier, resulting in a nearly two week decrease in the duration of the sea ice season when compared to prior conditions (Smith et al., 2003a, b). Recent findings (Vacchi et al., 2004, 2012) suggest that the early life history of *Pleuragramma* has an obligate tie to the sea-ice canopy. Studies by Emslie et al. (1998) and Emslie and McDaniel (2002) found a link in the paleoecological record between the regional presence of silverfish and Adelie penguins during past warming and cooling episodes in the WAP. Specifically, warming periods were associated with the disappearance of both species, while cooling periods were associated with their presence. The life history of Adelie penguins is also critically dependent on winter sea ice (Fraser et al., 1992), and in the Palmer region their populations have decreased by 70% over the past three decades (Fraser and Patterson, 1997; Smith et al., 2003a, b). If *Pleuragramma* are dependent on sea ice for recruitment success and resident populations are reproducing
and recruiting locally, those populations will be highly susceptible to local extinction in
the face of continued regional warming and subsequent sea ice reductions.

Conclusions

Subtle changes in faunal composition and shifts in dominant taxa demonstrated
the importance and influence of local hydrography on micronektonic fish and
invertebrate distributions. On-shelf circulation patterns and identification of five
different multispecies assemblages, as well as results from otolith microchemical
analyses and genetic analyses, provide substantial support for the existence of distinct
hydrographic regimes along the WAP shelf. Along with those findings, the
disappearance of *Pleuragramma* from Region II and the absence of younger year classes
in Marguerite Bay suggests that populations within each region are primarily being
sustained by local reproduction rather than larval advection.

Mid-winter air temperatures in the vicinity of Region II have increased by nearly
6 °C over the past 50 years, resulting in an overall decrease in the extent and duration of
the winter sea ice season (Fraser et al., 1992; Smith et al., 2003a, b). If resident
populations reproduce and recruit locally, those populations will be highly susceptible to
local extinction. If *Pleuragramma* are dependent on sea ice during their early life history,
this may be the causative factor behind the disappearance of *Pleuragramma* from Region
II. Continued warming and subsequent sea ice reductions may not only cause
*Pleuragramma* population collapses in the Marguerite Bay and Charcot Island regions,
but may also change the character of the faunal assemblages along the WAP to those of an oceanic system.

References


Nordhausen, W., 1994b. Winter abundance and distribution of *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura* in Gerlache Strait and Crystal Sound, Antarctica. Marine Ecology Progress Series 109, 131-142.


Table 3.1: 10-m$^2$ MOCNESS trawl data from nine sites sampled along the Western Antarctic Peninsula in 2010. Local time = GMT – 4 hours, TOD = Time of Day

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<th>Region</th>
<th>Site</th>
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<th>Time (GMT)</th>
<th>TOD</th>
<th>Latitude ($^\circ$S)</th>
<th>Longitude ($^\circ$S)</th>
<th>Trawl Depth (m)</th>
<th>Bottom Depth (m)</th>
<th>Volume Filtered (m$^3$)</th>
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Table 3.2A: Volumetric abundance (\# individuals $10^4 \text{ m}^{-3}$) and biomass (g WM $10^4 \text{ m}^{-3}$) of each taxon at the Joinville Island site in 2010. $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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Joinville Island ($n = 3$)

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*No weights were recorded for these specimens.
Table 3.2B: Volumetric abundance (\# individuals 10^4 m^{-3}) and biomass (g WM 10^4 m^{-3}) of each taxon at the Croker Passage site in 2010. \( n \) = number of trawls, VF = total volume filtered (m^3), SD = standard deviation

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*a*No weights were recorded for these specimens.
Table 3.2C: Volumetric abundance (# individuals $10^4$ m$^{-3}$) and biomass (g WM $10^4$ m$^{-3}$) of each taxon at the Palmer site in 2010. 
$n = \text{number of trawls}, VF = \text{total volume filtered (m}^3), SD = \text{standard deviation}

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gWM $10^4$ m$^{-3}$
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*aNo weights were recorded for these specimens.*
Table 3.2D: Volumetric abundance (# individuals $10^4$ m$^{-3}$) and biomass (g WM $10^4$ m$^{-3}$) of each taxon at the Palmer Deep site in 2010. 

$n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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Mean Total                   | 625.91 |     | 32.93|
Number of Taxa               | 18     |     |      |

*No weights were recorded for these specimens.*
Table 3.2E: Volumetric abundance (# individuals $10^4 \text{ m}^3$) and biomass (g WM $10^4 \text{ m}^3$) of each taxon at the Renaud Island site in 2010. *n* = number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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Mean Total: 843.04  Number of Taxa: 33

*aNo weights were recorded for these specimens."
Table 3.2F: Volumetric abundance (\# individuals $10^4$ m$^{-3}$) and biomass (g WM $10^4$ m$^{-3}$) of each taxon at the Marguerite Bay site in 2010. \( n \) = number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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Mean Total 1176.48 529.657
Number of Taxa 39

*aNo weights were recorded for these specimens.*
Table 3.2G: Volumetric abundance (# individuals $10^4 \text{m}^{-3}$) and biomass (g WM $10^4 \text{m}^{-3}$) of each taxon at the Marguerite Trough site in 2010. $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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\*No weights were recorded for these specimens.
Table 3.2H: Volumetric abundance (# individuals $10^4$ m$^{-3}$) and biomass (g WM $10^4$ m$^{-3}$) of each taxon at the Charcot Island site in 2010. *n* = number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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*a* No weights were recorded for these specimens.
Table 3.2I: Volumetric abundance (# individuals $10^4$ m$^{-3}$) and biomass (g WM $10^4$ m$^{-3}$) of each taxon at the Charcot Deep site in 2010. 
$n$ = number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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Charcot Deep ($n = 4$)  
VF = 250965

145
Table 3.2I: Continued

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Table 3.2i: Continued

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Mean Total 370.31 173,797
Number of Taxa 38

*a* No weights were recorded for these specimens.
Table 3.3: Results of SIMPER analysis on volumetric abundance data showing the taxa contributing the most to similarity within each cluster group. Values in parentheses represent the overall similarity among samples within a cluster group. \% Contribution = percentage contribution to the overall similarity among samples within a cluster group. Only those taxa that contributed 1% or more to overall group similarity are listed.

<table>
<thead>
<tr>
<th>Group A (85.39% similarity)</th>
<th>Group B (71.14% similarity)</th>
<th>Group C (70.09% similarity)</th>
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<tbody>
<tr>
<td>Joinville Island trawls</td>
<td>Croker Passage trawls</td>
<td>Palmer, Palmer Deep, Renaud Island, and Marguerite Trough trawls</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>% Contribution</th>
<th>% Contribution</th>
<th>% Contribution</th>
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<tbody>
<tr>
<td>Euphausia superba</td>
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<tr>
<td>Salpa thompsoni</td>
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<tr>
<td>Antarctomysis maxima</td>
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<td>Thysanoessa macrura</td>
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<td>Orchestomene plebs</td>
<td>9.38</td>
<td>Orchestomene plebs</td>
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<tr>
<td>Euphausia crystallorophias</td>
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<td>Cyphocaris richardi</td>
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<td>Mysidetes sp.</td>
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<td>Pseudosagitta gazellae</td>
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<td>Electrona antarctica</td>
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Table 3.3: Continued

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<th>Group D (83.11% similarity)</th>
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<td>% Contribution</td>
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<td>Antarctomysis maxima</td>
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<tr>
<td>Trematomus sp.</td>
<td>1.07</td>
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</table>
Table 3.4: Results of SIMPER analysis on volumetric biomass data showing the taxa contributing the most to similarity within each cluster group. Values in parentheses represent the overall similarity among samples within a cluster group. % Contribution = percentage contribution to the overall similarity among samples within a cluster group. Only those taxa that contributed 1% or more to overall group similarity are listed.

<table>
<thead>
<tr>
<th>Group A (79.52% similarity)</th>
<th>Group B (59.01% similarity)</th>
<th>Group C (53.99% similarity)</th>
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</thead>
<tbody>
<tr>
<td>Joinville Island trawls</td>
<td>Croker Passage trawls</td>
<td>Palmer, Palmer Deep, Renaud Island, and Marguerite Trough trawls</td>
</tr>
<tr>
<td>% Contribution</td>
<td>% Contribution</td>
<td>% Contribution</td>
</tr>
<tr>
<td>Euphausia superba</td>
<td>19.62 Salpa thompsoni</td>
<td>41.88 Thysanoessa macrura</td>
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<td>14.59 Euphausia superba</td>
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<td>3.40 Euphausia triacantha</td>
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<td>1.40 Calycopsis borchgrevinki</td>
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<td>1.28 Chaetognath</td>
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<td>Group D (66.01% similarity)</td>
<td>Group E (63.61% similarity)</td>
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<td>-----------------------------</td>
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<td><strong>Marguerite Bay and Charcot Island trawls</strong></td>
<td><strong>Charcot Deep trawls</strong></td>
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<td><strong>% Contribution</strong></td>
<td><strong>% Contribution</strong></td>
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<td>Euphausia superba</td>
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<td>Cyphocarus richardi</td>
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<td>Orchomene plebs</td>
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Table 3.5A: Integrated abundance (# individuals m$^{-2}$) and biomass (g WM m$^{-2}$) of taxa collected from discrete night tows within the 0-200 meter depth stratum at the Joinville Island site in 2010. $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation.

Joinville Island ($n = 3$)

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<th>Taxa</th>
<th># m$^{-2}$</th>
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<th>Mean</th>
<th>SD</th>
<th>gWM m$^{-2}$</th>
<th>Median</th>
<th>Mean</th>
<th>SD</th>
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<td>0.128</td>
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<td>0.001</td>
<td>0.002</td>
<td>0.000</td>
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<tr>
<td>Themisto gaudichaudii</td>
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<tr>
<td>Thysanoessa macrura</td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Tomopteris carpenteri</td>
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<tr>
<td>Edentoliparis terraenovae</td>
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<tr>
<td>Electrona antarctica</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Gymnoscopelus braueri</td>
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<tr>
<td>Gymnoscopelus nicholsi</td>
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<td>Melanostigma gelatinosum</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Pleuragramma antarcticum</td>
<td>0.041</td>
<td>0.048</td>
<td>0.051</td>
<td>0.396</td>
<td>0.562</td>
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<tr>
<td>Mean Total</td>
<td>22.839</td>
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</tbody>
</table>
Table 3.5B: Integrated abundance (# individuals m\(^{-2}\)) and biomass (g WM m\(^{-2}\)) of taxa collected from discrete night tows within the 0-200 meter depth stratum at the Croker Passage site in 2010. \(n\) = number of trawls, VF = total volume filtered (m\(^3\)), SD = standard deviation

<table>
<thead>
<tr>
<th>Taxa</th>
<th># m(^{-2}) Median</th>
<th># m(^{-2}) Mean</th>
<th># m(^{-2}) SD</th>
<th>gWM m(^{-2}) Median</th>
<th>gWM m(^{-2}) Mean</th>
<th>gWM m(^{-2}) SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alluroteuthis antarcticus</em></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Chaetognath</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Euphausia crystallophias</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Euphausia superba</td>
<td>1.035</td>
<td>1.035</td>
<td>0.719</td>
<td>0.288</td>
<td>0.288</td>
<td>0.303</td>
</tr>
<tr>
<td>Euphausia triacantha</td>
<td>0.015</td>
<td>0.015</td>
<td>0.003</td>
<td>0.002</td>
<td>0.002</td>
<td>0.000</td>
</tr>
<tr>
<td>Orchomene plebs</td>
<td>0.069</td>
<td>0.069</td>
<td>0.002</td>
<td>0.009</td>
<td>0.009</td>
<td>0.007</td>
</tr>
<tr>
<td>Primno macropa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudosagitta gazellae</td>
<td>0.014</td>
<td>0.014</td>
<td>0.019</td>
<td>0.006</td>
<td>0.006</td>
<td>0.008</td>
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<tr>
<td>Themisto gaudichaudi</td>
<td>0.660</td>
<td>0.660</td>
<td>0.129</td>
<td>0.055</td>
<td>0.055</td>
<td>0.021</td>
</tr>
<tr>
<td>Thysanoessa macrura</td>
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<td>0.734</td>
<td>0.881</td>
<td>0.026</td>
<td>0.026</td>
<td>0.031</td>
</tr>
<tr>
<td>Tomopteris carpenteri</td>
<td>0.007</td>
<td>0.007</td>
<td>0.010</td>
<td>0.004</td>
<td>0.004</td>
<td>0.006</td>
</tr>
<tr>
<td>Edentoliparis terraenovae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Electrona antarctica</td>
<td>0.035</td>
<td>0.035</td>
<td>0.050</td>
<td>0.373</td>
<td>0.373</td>
<td>0.527</td>
</tr>
<tr>
<td>Gymnoscopelus braueri</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Gymnoscopelus nicholsi</td>
<td>0.014</td>
<td>0.014</td>
<td>0.020</td>
<td>0.585</td>
<td>0.585</td>
<td>0.827</td>
</tr>
<tr>
<td>Melanostigma gelatinosum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pleuragramma antarcticum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Mean Total                  | 15.780               | 13.481            |                 |                       |                     |                   |
Number of Taxa              | 10                   |                   |                 |                       |                     |                   |
Table 3.5C: Integrated abundance (# individuals m$^{-2}$) and biomass (g WM m$^{-2}$) of taxa collected from discrete night tows within the 0-200 meter depth stratum at the Palmer site in 2010. $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

<table>
<thead>
<tr>
<th>Taxa</th>
<th># m$^{-2}$</th>
<th>gWM m$^{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median</td>
<td>Mean</td>
</tr>
<tr>
<td>Alluroteuthis antarcticus</td>
<td>0.026</td>
<td>0.026</td>
</tr>
<tr>
<td>Chaetognath</td>
<td>1.236</td>
<td>1.236</td>
</tr>
<tr>
<td>Euphausia crystallorophias</td>
<td>0.019</td>
<td>0.019</td>
</tr>
<tr>
<td>Euphausia superba</td>
<td>0.002</td>
<td>0.002</td>
</tr>
<tr>
<td>Euphausia triacantha</td>
<td>0.007</td>
<td>0.007</td>
</tr>
<tr>
<td>Orchoomene plebs</td>
<td>0.049</td>
<td>0.049</td>
</tr>
<tr>
<td>Primno macropa</td>
<td>0.027</td>
<td>0.027</td>
</tr>
<tr>
<td>Pseudosagitta gazellae</td>
<td>0.846</td>
<td>0.846</td>
</tr>
<tr>
<td>Salpa thompsoni</td>
<td>16.904</td>
<td>16.904</td>
</tr>
<tr>
<td>Themisto gaudichaudii</td>
<td>0.002</td>
<td>0.002</td>
</tr>
<tr>
<td>Thysanoessa macrura</td>
<td>0.032</td>
<td>0.032</td>
</tr>
<tr>
<td>Tomopteris carpenteri</td>
<td>19.151</td>
<td>1.898</td>
</tr>
</tbody>
</table>

Palmer ($n = 2$)
VF = 62061
Table 3.5D: Integrated abundance (# individuals m\(^{-2}\)) and biomass (g WM m\(^{-2}\)) of taxa collected from discrete night tows within the 0-200 meter depth stratum at the Palmer Deep site in 2010. \(n\) = number of trawls, VF = total volume filtered (m\(^3\)), SD = standard deviation

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Palmer Deep ((n = 2))</th>
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<th></th>
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<tr>
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<td>VF = 21187</td>
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<td></td>
</tr>
<tr>
<td></td>
<td># m(^{-2})</td>
<td>Median</td>
<td>Mean</td>
<td>SD</td>
<td>gWM m(^{-2})</td>
<td>Median</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td><em>Alluroteuthis antarcticus</em></td>
<td></td>
<td>0.085</td>
<td>0.085</td>
<td>0.010</td>
<td>0.007</td>
<td>0.007</td>
<td>0.003</td>
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</tr>
<tr>
<td><em>Chaetognath</em></td>
<td></td>
<td>0.049</td>
<td>0.049</td>
<td>0.069</td>
<td>0.047</td>
<td>0.047</td>
<td>0.066</td>
<td></td>
</tr>
<tr>
<td><em>Euphausia crystallorophias</em></td>
<td></td>
<td>0.008</td>
<td>0.008</td>
<td>0.012</td>
<td>0.001</td>
<td>0.001</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td><em>Euphausia superba</em></td>
<td></td>
<td>0.031</td>
<td>0.031</td>
<td>0.043</td>
<td>0.006</td>
<td>0.006</td>
<td>0.009</td>
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<tr>
<td><em>Euphausia triacantha</em></td>
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<td>0.658</td>
<td>0.658</td>
<td>0.931</td>
<td>0.057</td>
<td>0.057</td>
<td>0.081</td>
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<tr>
<td><em>Orchomene plebs</em></td>
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<td>2.129</td>
<td>2.129</td>
<td>1.727</td>
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<tr>
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<td>7.437</td>
<td>0.563</td>
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<tr>
<td><em>Pseudosagitta gazellae</em></td>
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<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td><em>Salpa thompsoni</em></td>
<td></td>
<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td><em>Thysanoessa macrura</em></td>
<td></td>
<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td><em>Tomopteris carpenteri</em></td>
<td></td>
<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td><em>Edentoliparis terraenovae</em></td>
<td></td>
<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td><em>Electrona antarctica</em></td>
<td></td>
<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
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</tr>
<tr>
<td><em>Gymnoscopelus braueri</em></td>
<td></td>
<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
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<tr>
<td><em>Gymnoscopelus nicholsi</em></td>
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<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
<td></td>
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<tr>
<td><em>Melanostigma gelatinosum</em></td>
<td></td>
<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td><em>Pleuragramma antarcticum</em></td>
<td></td>
<td>0.015</td>
<td>0.015</td>
<td>0.022</td>
<td>0.023</td>
<td>0.023</td>
<td>0.033</td>
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<tr>
<td><strong>Mean Total</strong></td>
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<td>0.822</td>
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<tr>
<td><strong>Number of Taxa</strong></td>
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</tbody>
</table>
Table 3.5E: Integrated abundance (# individuals m\(^{-2}\)) and biomass (g WM m\(^{-2}\)) of taxa collected from discrete night tows within the 0-200 meter depth stratum at the Renaud Island site in 2010. \(n\) = number of trawls, VF = total volume filtered (m\(^3\)), SD = standard deviation.

<table>
<thead>
<tr>
<th>Taxa</th>
<th># m(^{-2})</th>
<th>Median</th>
<th>Mean</th>
<th>SD</th>
<th>Median</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alluroteuthis antarcticus</td>
<td>0.000</td>
<td>0.001</td>
<td>0.002</td>
<td>0.000</td>
<td>0.029</td>
<td>0.066</td>
<td></td>
</tr>
<tr>
<td>Chaetognath</td>
<td>0.087</td>
<td>0.103</td>
<td>0.099</td>
<td>0.002</td>
<td>0.003</td>
<td>0.003</td>
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</tr>
<tr>
<td>Euphausia crystallorophias</td>
<td>0.139</td>
<td>0.134</td>
<td>0.133</td>
<td>0.014</td>
<td>0.017</td>
<td>0.019</td>
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</tr>
<tr>
<td>Euphausia superba</td>
<td>0.251</td>
<td>0.290</td>
<td>0.241</td>
<td>0.163</td>
<td>0.216</td>
<td>0.178</td>
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<tr>
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<td>0.223</td>
<td>0.327</td>
<td>0.001</td>
<td>0.049</td>
<td>0.070</td>
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</tr>
<tr>
<td>Orchestomene plebs</td>
<td>0.003</td>
<td>0.006</td>
<td>0.008</td>
<td>0.000</td>
<td>0.002</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td>Primno macropa</td>
<td>0.015</td>
<td>0.012</td>
<td>0.009</td>
<td>0.000</td>
<td>0.001</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>Pseudosagitta gazellae</td>
<td>0.056</td>
<td>0.047</td>
<td>0.023</td>
<td>0.007</td>
<td>0.007</td>
<td>0.005</td>
<td></td>
</tr>
<tr>
<td>Salpa thompsoni</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Themisto gaudichaudi</td>
<td>6.893</td>
<td>5.930</td>
<td>4.637</td>
<td>0.385</td>
<td>0.345</td>
<td>0.274</td>
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</tr>
<tr>
<td>Thysanoessa macrura</td>
<td>20.273</td>
<td>19.611</td>
<td>8.107</td>
<td>0.761</td>
<td>0.691</td>
<td>0.302</td>
<td></td>
</tr>
<tr>
<td>Tomopteris carpenteri</td>
<td>0.000</td>
<td>0.007</td>
<td>0.014</td>
<td>0.000</td>
<td>0.002</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td>Edentoliparis terraenovae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Electrona antarctica</td>
<td>0.005</td>
<td>0.021</td>
<td>0.028</td>
<td>0.023</td>
<td>0.153</td>
<td>0.238</td>
<td></td>
</tr>
<tr>
<td>Gymnoscopelus braueri</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gymnoscopelus nicholsi</td>
<td>0.000</td>
<td>0.009</td>
<td>0.021</td>
<td>0.000</td>
<td>0.368</td>
<td>0.824</td>
<td></td>
</tr>
<tr>
<td>Melanostigma gelatinosum</td>
<td>0.000</td>
<td>0.004</td>
<td>0.007</td>
<td>0.000</td>
<td>0.039</td>
<td>0.071</td>
<td></td>
</tr>
<tr>
<td>Pleuragramma antarcticum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Mean Total                  | 26.397       | 1.921  |
| Number of Taxa              | 14           |

Renaud Island (\(n = 5\))
VF = 136255
Table 3.5F: Integrated abundance (# individuals m^{-2}) and biomass (g WM m^{-2}) of taxa collected from discrete night tows within the 0-200 meter depth stratum at the Marguerite Bay site in 2010. \( n \) = number of trawls, VF = total volume filtered (m^{3}), SD = standard deviation.

<table>
<thead>
<tr>
<th>Taxa</th>
<th># m^{-2}</th>
<th>gWM m^{-2}</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median</td>
<td>Mean</td>
</tr>
<tr>
<td><em>Alluroteuthis antarcticus</em></td>
<td>0.005</td>
<td>0.009</td>
</tr>
<tr>
<td>Chaetognath</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Euphausia crystallorophias</em></td>
<td>23.522</td>
<td>20.531</td>
</tr>
<tr>
<td><em>Euphausia triacantha</em></td>
<td>0.005</td>
<td>0.004</td>
</tr>
<tr>
<td><em>Orchomene plebs</em></td>
<td>0.051</td>
<td>0.053</td>
</tr>
<tr>
<td><em>Primno macropa</em></td>
<td>0.000</td>
<td>0.001</td>
</tr>
<tr>
<td><em>Pseudosagitta gazellae</em></td>
<td>0.008</td>
<td>0.012</td>
</tr>
<tr>
<td><em>Salpa thompsoni</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Themisto gaudichaudi</em></td>
<td>0.640</td>
<td>1.115</td>
</tr>
<tr>
<td><em>Thysanoessa macrura</em></td>
<td>4.146</td>
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</tr>
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<td><em>Tomopteris carpenteri</em></td>
<td>0.000</td>
<td>0.002</td>
</tr>
<tr>
<td><em>Edentoliparis terraenovae</em></td>
<td>0.002</td>
<td>0.004</td>
</tr>
<tr>
<td><em>Electrona antarctica</em></td>
<td>0.000</td>
<td>0.007</td>
</tr>
<tr>
<td><em>Gymnoscopelus braueri</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gymnoscopelus nicholsi</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Melanostigma gelatinosum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pleuragramma antarcticum</em></td>
<td>0.068</td>
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</table>

Marguerite Bay (\( n = 4 \))
VF = 170964

Mean Total

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<th>62.599</th>
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</thead>
<tbody>
<tr>
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</table>
Table 3.5G: Integrated abundance (# individuals m$^{-2}$) and biomass (g WM m$^{-2}$) of taxa collected from discrete night tows within the 0-200 meter depth stratum at the Marguerite Trough site in 2010. $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

<table>
<thead>
<tr>
<th>Taxa</th>
<th># m$^{-2}$</th>
<th>gWM m$^{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median</td>
<td>Mean</td>
</tr>
<tr>
<td>Alluroteuthis antarcticus</td>
<td>0.054</td>
<td>0.054</td>
</tr>
<tr>
<td>Chaetognath</td>
<td>0.032</td>
<td>0.032</td>
</tr>
<tr>
<td>Euphausia crystallorophias</td>
<td>0.042</td>
<td>0.042</td>
</tr>
<tr>
<td>Euphausia superba</td>
<td>0.013</td>
<td>0.013</td>
</tr>
<tr>
<td>Euphausia triacantha</td>
<td>0.031</td>
<td>0.031</td>
</tr>
<tr>
<td>Orchomene plebs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primno macropa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudosagitta gazellae</td>
<td>0.095</td>
<td>0.095</td>
</tr>
<tr>
<td>Salpa thompsoni</td>
<td>0.005</td>
<td>0.005</td>
</tr>
<tr>
<td>Themisto gaudichaudii</td>
<td>0.442</td>
<td>0.442</td>
</tr>
<tr>
<td>Thysanoessa macrura</td>
<td>5.569</td>
<td>5.569</td>
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<tr>
<td>Tomopteris carpenteri</td>
<td>0.011</td>
<td>0.011</td>
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<tr>
<td>Edentoliparis terraenovae</td>
<td>0.009</td>
<td>0.009</td>
</tr>
<tr>
<td>Electrona antarctica</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gymnoscopelus braueri</td>
<td>0.003</td>
<td>0.003</td>
</tr>
<tr>
<td>Gymnoscopelus nicholsi</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Melanostigma gelatinosum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pleuragramma antarcticum</td>
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<td>Mean Total</td>
<td>6.306</td>
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<tr>
<td>Number of Taxa</td>
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Table 3.5H: Integrated abundance (# individuals m$^{-2}$) and biomass (g WM m$^{-2}$) of taxa collected from discrete night tows within the 0-200 meter depth stratum at the Charcot Island site in 2010.  $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Charcot Island ($n = 2$)</th>
<th>VF = 26137</th>
<th># m$^2$ Median</th>
<th># m$^2$ Mean</th>
<th># m$^2$ SD</th>
<th>gWM m$^2$ Median</th>
<th>gWM m$^2$ Mean</th>
<th>gWM m$^2$ SD</th>
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<tbody>
<tr>
<td>Alluroteuthis antarcticus</td>
<td></td>
<td></td>
<td>0.058</td>
<td>0.058</td>
<td>0.026</td>
<td>0.003</td>
<td>0.003</td>
<td>0.003</td>
</tr>
<tr>
<td>Chaetognath</td>
<td></td>
<td></td>
<td>12.784</td>
<td>12.784</td>
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<td>2.133</td>
<td>2.133</td>
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<tr>
<td>Euphausia crystallorophias</td>
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<td>1.036</td>
<td>1.036</td>
<td>1.124</td>
<td>0.233</td>
<td>0.233</td>
<td>0.060</td>
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<tr>
<td>Euphausia superba</td>
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<td></td>
<td>0.053</td>
<td>0.053</td>
<td>0.028</td>
<td>0.016</td>
<td>0.016</td>
<td>0.011</td>
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<tr>
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<td>0.007</td>
<td>0.007</td>
<td>0.009</td>
<td>0.001</td>
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<td>Orchomene plebs</td>
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<td>0.022</td>
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<td>0.013</td>
<td>0.002</td>
<td>0.002</td>
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<tr>
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<td>0.061</td>
<td>0.087</td>
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<tr>
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<td>0.241</td>
<td>0.241</td>
<td>0.019</td>
<td>0.013</td>
<td>0.013</td>
<td>0.000</td>
</tr>
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<td>Salpa thompsoni</td>
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<td>0.604</td>
<td>0.186</td>
<td>0.027</td>
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<tr>
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<td>0.076</td>
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<td>Tomopteris carpenteri</td>
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<tr>
<td>Edentoliparis terraenovae</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>Electrona antarctica</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gymnoscopelus braueri</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>Gymnoscopelus nicholsi</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Melanostigma gelatinosum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pleuragramma antarcticum</td>
<td></td>
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<tr>
<td>Mean Total</td>
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Table 3.5I: Integrated abundance (# individuals m$^{-2}$) and biomass (g WM m$^{-2}$) of taxa collected from discrete night tows within the 0-200 meter depth stratum at the Charcot Island site in 2010. $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

<table>
<thead>
<tr>
<th>Taxa</th>
<th># m$^{-2}$</th>
<th>Charcot Deep ($n = 3$)</th>
<th>gWM m$^{-2}$</th>
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<tbody>
<tr>
<td></td>
<td>Median</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td><em>Alluroteuthis antarcticus</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chaetognath</td>
<td>0.218</td>
<td>0.337</td>
<td>0.247</td>
</tr>
<tr>
<td><em>Euphausia crystallorophias</em></td>
<td>2.900</td>
<td>3.020</td>
<td>2.531</td>
</tr>
<tr>
<td><em>Euphausia triacantha</em></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>Orchomene plebs</em></td>
<td>0.000</td>
<td>0.006</td>
<td>0.010</td>
</tr>
<tr>
<td><em>Primno macropa</em></td>
<td>0.022</td>
<td>0.028</td>
<td>0.019</td>
</tr>
<tr>
<td><em>Pseudosagitta gazellae</em></td>
<td>0.058</td>
<td>0.077</td>
<td>0.032</td>
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<td><em>Salpa thompsoni</em></td>
<td>2.380</td>
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<td><em>Themisto gaudichaudii</em></td>
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<tr>
<td><em>Thysanoessa macrura</em></td>
<td></td>
<td></td>
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<tr>
<td><em>Tomopteris carpenteri</em></td>
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<tr>
<td><em>Edentoliparis terraenovae</em></td>
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<tr>
<td><em>Electrona antarctica</em></td>
<td></td>
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<tr>
<td><em>Gymnoscopelus braueri</em></td>
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<tr>
<td><em>Gymnoscopelus nicholsi</em></td>
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<tr>
<td><em>Melanostigma gelatinosum</em></td>
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</tr>
<tr>
<td><em>Pleuragramma antarcticum</em></td>
<td>0.013</td>
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</table>
Figure 3.1: Trawl and site locations along the Western Antarctic Peninsula in 2010. Arrows indicate general water circulation patterns within the four regions (Hofmann et al., 1996, unpublished data).
Figure 3.2A: Temperature (solid line) and salinity (dashed line) to 500 m depth at Joinville Island during the 2010 cruise.
Figure 3.2B: Temperature (red solid line) and salinity (blue dashed line) to 500 m depth at Croker Passage during the 2010 cruise.
Figure 3.2C: Temperature (red solid line) and salinity (blue dashed line) to 500 m depth at Palmer during the 2010 cruise. Box denotes general temperature and salinity ranges for CDW.
Figure 3.2D: Temperature (red solid line) and salinity (blue dashed line) to 500 m depth at Palmer Deep during the 2010 cruise. Box denotes general temperature and salinity ranges for CDW.
Figure 3.2E: Temperature (red solid line) and salinity (blue dashed line) to 456 m depth at Renaud Island during the 2010 cruise. Box denotes general temperature and salinity ranges for CDW.
Figure 3.2F: Temperature (red solid line) and salinity (blue dashed line) to 500 m depth at Marguerite Bay during the 2010 cruise. Box denotes general temperature and salinity ranges for CDW.
Figure 3.2G: Temperature (red solid line) and salinity (blue dashed line) to 500 m depth at Marguerite Trough during the 2010 cruise. Box denotes general temperature and salinity ranges for CDW.
Figure 3.2H: Temperature (red solid line) and salinity (blue dashed line) to 500 m depth at Charcot Island during the 2010 cruise. Boxes denote general salinity and temperature ranges for AASW, WW, and CDW.
Figure 3.2I: Temperature (red solid line) and salinity (blue dashed line) to 500 m depth at Charcot Deep during the 2010 cruise. Boxes denote general salinity and temperature ranges for AASW, WW, and CDW.
Figure 3.3: Vertical distributions of common invertebrate and fish species collected during the 2010 cruise. $n =$ number of individuals.
Figure 3.4: Percent similarity cluster dendrogram of 2010 micronekton/macrozooplankton volumetric abundance (\# individuals $10^4$ m$^{-3}$). Roman numerals along the abscissa represent hydrographic regions. Brackets represent cluster groups at the 60% similarity level.
Figure 3.5: Percent similarity cluster dendrogram of 2010 micronekton/macrozooplankton volumetric biomass (g WM $10^4$ m$^{-3}$). Roman numerals along the abscissa represent hydrographic regions. Brackets represent cluster groups at the 60% similarity level.
Figure 3.6: MDS ordination plot of 2010 abundance (# individuals $10^4$ m$^{-3}$) data.
Figure 3.7: MDS ordination plot of 2010 biomass (g WM $10^4$ m$^{-3}$) data.
Figure 3.8: Bubble plot overlays of the 2010 abundance MDS ordination plot representing the relative abundance of several common species. The larger the bubble, the greater the number of individuals were captured at that site. Please note that bubble sizes are not consistent among species.
Figure 3.9: Bubble plot overlays of the 2010 biomass MDS ordination plot representing the relative abundance of several common species. The larger the bubble, the greater the number of individuals were captured at that site. Please note that bubble sizes are not consistent among species.
Figure 3.10: Size distributions of *Pleuragramma antarcticum* collected from each site during the 2010 cruise.
Figure 3.11: Size distributions of *Pleuragramma antarcticum* captured during the 2001 and 2002 SO GLOBEC cruises in the Marguerite Bay region of the Western Antarctic Peninsula (Donnelly et al., 2008).
CHAPTER FOUR

INVERTEBRATE MICRONEKTON AND MACROZOOPLANKTON OF THE

EASTERN ROSS SEA

Abstract

Invertebrate micronekton and macrozooplankton were sampled with a total of 36 midwater trawls in the eastern Ross Sea in austral summer (December – February) 1999/2000 as part of the Antarctic Pack Ice Seal (APIS) program. Sampling occurred in three different zones: offshore in water depths exceeding 2500 m, at the continental slope in depths ranging from 500 - 2000 m, and on the continental shelf in waters ≤500 m depth. A total of 41 taxa representing 14 different taxonomic groups of pelagic invertebrates were captured, but assemblages were dominated by only a few taxa. The ice krill, *Euphausia crystallorophias*, was the numerical dominant and contributed nearly 59% of the total volumetric catch. Dominant biomass contributors included the coronate scyphozoan, *Atolla wyvillei*, and the Antarctic krill, *E. superba*, contributing 36% and 31% of the volumetric biomass, respectively. Comparisons of total catches among the three zones revealed that volumetric abundances and biomasses were similar in the offshore and continental slope zones, but higher than catches in the continental shelf zone. However, the total abundance and biomass of pelagic invertebrates captured in the eastern Ross Sea was quite low compared to other Antarctic regions. Cluster analyses
identified three primary groups, which were characterized as oceanic, mixed, and neritic assemblages due partly to their geographical location but mostly to their faunal composition. The oceanic assemblage contained the highest number of taxa and was dominated by oceanic fauna such as hydrozoans, *Diphyes antarctica* and *Calycopsis borchgrevinki*, and the scyphozoan, *Atolla wyvillei*. Top contributors in the mixed assemblage included those species that dominated in the oceanic assemblage as well as substantial contributions from the euphausiid, *Euphausia superba* and the tunicate, *Ihlea racovitzai*. The neritic assemblage was overwhelmingly dominated by the euphausiids, *E. crystallorophias* and *E. superba*. The physical environment strongly influenced micronektonic/macrozooplanktonic distributions and densities in the eastern Ross Sea. Changes in faunal composition were directly related to the presence of a strong slope front and/or temperature differences encountered at the shelf break, resulting in the filtering out of many oceanic fauna from cold, shelf waters where endemic fauna were most prevalent. Persistent ice cover resulted in low phytoplankton concentrations, which limited zooplankton densities.

**Introduction**

Few studies have focused on the micronekton and macrozooplankton assemblages of the eastern Ross Sea. The area is of interest because it is one of the few regions that retain dense concentrations of pack ice throughout the summer, when sea ice is receding around the rest of the Antarctic continent (Gloersen et al., 1992), potentially providing habitat and/or a food source for zooplankton, fishes and upper trophic level predators.
including crabeater, leopard, Ross and Weddell seals (Daly and Macaulay, 1988; Laws, 1985). The summer expansion of the Ross Sea polynya, which is located in the western Ross Sea, produces three residual ice fronts that increase the thickness and complexity of the pack ice in the eastern Ross Sea. Those ice fronts are found at the northern extent of the ice pack, along the eastern side of the polynya, and at the southern expanse of the ice pack near the continent (Ackley et al., 2003). No front is present at the eastern extent of the Ross Sea where the pack ice continues into the Amundsen Sea. The nature and quantity of sea ice in the eastern Ross Sea makes access difficult and has limited the number of biological studies conducted in the region.

Micronekton and macrozooplankton distributions are strongly influenced by the physical factors of the local environment. The eastern Ross Sea is characterized by its relatively narrow, but deep (500-700 m) continental shelf and the presence of a subsurface front near the continental slope (Ackley et al., 2003). This Antarctic Slope Front is a region where cold shelf waters mix with warmer, oceanic waters creating steep temperature and salinity gradients (Jacobs, 1991), which may enhance biological productivity (Pages and Schnack-Schiel, 1996). The front may also function as a barrier preventing oceanic fauna from moving onto the shelf (DeWitt, 1970). In a study of fishes from the same region, Donnelly et al. (2004) found that oceanic species were present seaward of the shelf break, but absent on the shelf. This is most likely due to the temperature structure of the water column. In high latitude Antarctic shelf regions like the Ross Sea, temperatures are near freezing (-2 °C) from surface to depth (Dinniman et al., 2003). Those cold temperatures exclude many oceanics, especially fishes which lack biological antifreezes (Cullins et al., 2011).
The present study examined the invertebrate macrozooplanktonic/micronektonic faunal assemblages present in the offshore, continental slope, and continental shelf waters of the eastern Ross Sea including the taxonomic composition and distribution patterns in relation to several physical attributes of the local environment. Multivariate techniques were used to identify unique multispecies assemblages and to quantify the contributions of both oceanic and neritic species to each assemblage. We also compared volumetric and integrated abundance and biomass of the eastern Ross Sea pelagic assemblages to other regions within the Southern Ocean.

**Methods**

*Study Area and Sample Collection*

Invertebrate micronekton and macrozooplankton were collected from the eastern Ross Sea during austral summer (December – February) 1999/2000 as part of the Antarctic Pack Ice Seal (APIS) program. Midwater trawls were conducted from the Research Vessel Ice Breaker (R.V.I.B) *Nathaniel B. Palmer* using a 4-\(m^2\) Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) outfitted with five 4-mm mesh nets (Wiebe et al., 1976, 1985) and a 9-\(m^2\) Tucker trawl with a 4-mm mesh net tapering to a 1-mm mesh tail section. A total of 36 daytime trawls (22 MOCNESS and 14 Tucker) were completed and the majority sampled from the surface to either 500 m or 1000 m depth (Table 4.1). For MOCNESS trawls, the first net fished obliquely from surface to depth and each subsequent net fished a discrete depth layer up
towards the surface. Volumes filtered for MOCNESS and Tucker trawls were estimated from TSK flowmeters. Sampling occurred in three different zones; offshore in water depths exceeding 2500 m, at the continental slope in depths ranging from 500-2000 m, and on the continental shelf in waters \( \leq 500 \) m depth. Sea ice was present at all trawl sites with the exception of trawl M-10 which occurred in open water in the offshore zone (Figure 4.1).

Specimens were preserved in a 5-10% buffered formaldehyde solution and shipped to the laboratory for analysis. All invertebrate micronektonic and macrozooplanktonic specimens were sorted, identified to lowest possible taxon, counted and weighed (g wet mass). After processing, all samples were transferred to 50% isopropanol for long term storage. All fish present in the samples were processed and analyzed by Donnelly et al. (2004).

Data Analyses

Raw abundance and biomass values were standardized by dividing their number or wet mass by the water volume filtered during each trawl (\( \# \) or g WM \( 10^4 \) m\(^{-3} \)). Those volumetric values were then used to calculate mean abundance and biomass of each individual taxon within each of the three zones as well as the median and mean overall abundance and biomass captured within the three zones. Statistical comparisons among zones were performed using generalized linear mixed models in SAS version 9.2 (SAS Institute Inc., Cary, NC, USA).
Median and mean integrated abundance (# m\(^{-2}\)) and biomass (g WM m\(^{-2}\)) were calculated for each taxon within the 0-200 m stratum in the offshore, continental slope, and continental shelf zones. Integrated values were determined by first selecting those nets from each trawl that sampled within the 0-200 m depth stratum. Integrated values were then calculated by dividing the number or wet mass from each net by the water volume filtered by that net, then multiplying by the vertical range, in meters, trawled by that net, and summing for each trawl.

Multispecies assemblage structure was analyzed by multivariate techniques using the PRIMER (Plymouth Routines In Multivariate Ecological Research) v6 software package (Clarke and Gorley, 2006). Volumetric abundance and biomass data were log (x+1) transformed to allow for a more even contribution from common and rare taxa in the analyses (Clarke, 1993). Bray-Curtis similarity matrices were then generated from the transformed data, which were subsequently used to perform an analysis of similarities (ANOSIM) on assemblages present in each of the three zones. The ANOSIM procedure is a non-parametric permutation/randomization test that functions as an analogue to a standard univariate ANOVA test (Clarke and Green, 1988). The test produces a global R statistic (which usually ranges from 0 to 1, where 0 indicates no differences) and an associated significance level. Post hoc pairwise comparisons also produce an R statistic and p-value for each pair, but because p-values are highly dependent on the number of replicates in the comparison, the R statistic is most useful in determining differences (Clarke and Gorley, 2006). The Bray-Curtis similarity matrices were also used to generate hierarchical cluster analysis dendrograms and MDS ordination plots. The SIMPER (analysis of similarity percentages) procedure was used to identify those taxa
contributing the most to the similarities within each resultant cluster group. Shannon’s
diversity index \( (H') \) and Pielou’s evenness \( (J') \) were calculated for the resultant
abundance and biomass cluster groups (Shannon and Weaver, 1949; Pielou, 1966).

**Results**

*Taxonomic Composition*

A total of 41 taxa representing 14 different taxonomic groups were collected
during this study (Tables 4.2A – 4.2C). The gammarid and hyperiid amphipods were the
most diverse groups, each represented by seven taxa. Diversity was greatest in the
offshore zone, where 39 of the 41 taxa were present, but decreased shoreward dropping to
18 taxa at the continental slope and to only 8 taxa on the shelf. Despite the relatively
diverse catch, only a few species accounted for the majority of the total abundance and
biomass. The ice krill, *Euphausia crystallorophias*, was the numerical dominant and
contributed nearly 59% of the total volumetric catch. Dominant biomass contributors
included the scyphozoan, *Atolla wyvillei*, and the Antarctic krill, *E. superba*, contributing
36% and 31% of the volumetric biomass, respectively. Other prevalent biomass
contributors included the chaetognath, *Pseudosagitta gazellae*, the hydrozoan, *Diphyes
antarctica*, and the tunicate, *Ihlea racovitzai*. Those three species, along with *E.
crystallorophias* and *E. superba*, were the only taxa present in all three zones and each,
with the exception of *I. racovitzai*, contributed considerably to the overall catch as well as
to the catches within each zone. Although absent from the shelf and present only at low
densities near the continental slope, another euphausiid, *Thysanoessa macrura*, was relatively abundant in the offshore zone and as a result ranked as the fifth most abundant species. It should be noted that due to its large size, specimens of the scyphozoan, *Stygomedusa gigantea*, were not preserved and therefore their wet weights are not included in biomass estimates.

Comparisons of total catches among the three zones revealed that the mean number of specimens in the offshore and continental slope zones were similar (107.64 vs. 85.98 individuals $10^4$ m$^{-3}$) but significantly higher ($P = 0.02$) than densities in the continental shelf zone (17.16 individuals $10^4$ m$^{-3}$). Mean volumetric biomasses were also higher ($P < 0.01$) in the offshore and continental slope zones (56.17 and 28.66 g WM $10^4$ m$^{-3}$) than on the shelf (3.43 g WM $10^4$ m$^{-3}$). Total catches of *E. crystallorophias* were similar in all three zones with mean abundances ranging from 14.56 to 58.40 individuals $10^4$ m$^{-3}$ ($P = 0.71$) and mean biomasses ranging from 2.43 to 7.09 g WM $10^4$ m$^{-3}$ ($P = 0.80$). However, abundances and biomasses of *E. superba* in the offshore and continental slope zones (ranging from 19.53 to 26.18 individuals $10^4$ m$^{-3}$ and from 10.02 to 17.26 g WM $10^4$ m$^{-3}$) were significantly higher ($P < 0.02$) than in the continental shelf zone (0.62 individuals $10^4$ m$^{-3}$ and 0.22 g WM $10^4$ m$^{-3}$). Mean abundances of *P. gazellae, D. antarctica*, and *T. macrura* were greatest in the offshore zone ($P < 0.01$) but no differences in biomass were detected among zones for any of the three species.
Vertical Distributions

Discrete depth distributions were compiled for eight common species by pooling data from MOCNESS trawls conducted in the offshore and continental slope zones (Figure 4.2). Because the cruise was conducted during the austral summer, all tows occurred in daylight. Four species, *E. superba, T. macrura, P. gazellae*, and the hydrozoan *Calycopsis borchgrevinki*, were found from the surface to 1000 m. *E. crystallorophias* was only found in the upper 200 m and *D. antarctica* was within the upper 500 m. The two scyphozoans, *A. wyvillei* and *S. gigantea*, were only found below 200 m and 100 m, respectively. Both *E. crystallorophias* and *E. superba* were most abundant at the surface (0-50 m), while *T. macrura, P. gazellae* and the two hydrozoans were most abundant between 50 and 200 m. The scyphozoans were most abundant at deeper depths; *A. wyvillei* below 500 m and *S. gigantea* between 200 and 500 m.

Multispecies Assemblages

One-way ANOSIM analyses of volumetric abundance and biomass indicated that there were significant differences in the assemblages present in each zone (Abundance: Global R = 0.587, *P* <0.01; Biomass: Global R = 0.636, *P* <0.01). Post-hoc analyses revealed that differences were primarily due to offshore assemblages and that the continental slope and shelf assemblages were similar (Abundance: R = 0.294; Biomass: R = 0.132). Cluster analysis of abundance data separated trawls into three primary clusters at the 40% similarity level (Figure 4.3): an oceanic assemblage comprised exclusively of
trawls conducted in the offshore zone, a mixed assemblage comprised of trawls conducted in all three zones near the eastern extent of the study area, and a neritic assemblage comprised of trawls conducted in all three zones in the central and western portions of the study area. Biomass cluster groups at the 40% similarity level were similar to those generated from abundance data (Figure 4.4). Although four cluster groups resulted, three of those groups corresponded closely with the composition of the oceanic, mixed, and neritic assemblages from the abundance analysis. The fourth group was composed of only two trawls, one of which was conducted in the offshore zone and the other in the continental slope zone, which were dominated by *C. borchgrevinki*. In the cluster dendrograms for both abundance and biomass, four trawls, one in the continental slope zone and three in the continental shelf zone, clustered independently. In three of those trawls (trawls M-9, T-2 and T-4), the independent clustering was due primarily to the prevalence of various gammarid and hyperiid amphipod species. Trawl T-7 clustered independently due a catch that was composed of only one *E. crystallorophia*. One additional trawl (M-8) clustered independently on the biomass dendrogram due also to an overall small catch that was dominated by *E. crystallorophias*. MDS ordination plots show the 2-dimensional structure of the abundance and biomass clusters, each with resultant stress levels of 0.14 (Figures 4.5 and 4.6).

SIMPER analysis of abundance data identified taxa that contributed most to the similarities within each cluster group (Table 4.3). Most dominant taxa were present in all three of the clusters but each contributed in varying degrees to cluster similarities. In the oceanic assemblage, *D. antarctica*, *T. macrura*, *P. gazellae*, and *C. borchgrevinki* were the most abundant, combining to contribute over 66% of the similarity within that group.
Although the top contributors in the mixed assemblage also included *D. antarctica* and *P. gazellae*, there were also substantial contributions from *E. superba* and the tunicate, *Ihlea racovitzai*. The neritic assemblage was overwhelmingly dominated by *E. crystallorophias*, which contributed over 50% alone to the total similarity in the cluster group.

Results from SIMPER analysis on biomass data were largely influenced by the presence of gelatinous zooplankton including the scyphozoans, hydrozoans, and tunicates (Table 4.4). In the oceanic assemblage, *A. wyvillei* accounted for more than 55% of the similarity within the cluster group. Similarly, *I. racovitzai* was the dominant biomass contributor (41%) in the mixed assemblage, with secondary contributions from *D. antarctica* (31%) and *P. gazellae* (22%). The neritic assemblage differed in that the top contributors were the euphausiids, with *E. crystallorophias* and *E. superba* contributing 46% and 37%, respectively.

Removal of several gelatinous species (scyphozoans, hydrozoans, and tunicates) from ANOSIM analyses revealed that there were still significant differences between assemblages within each zone but, resultant R values were lower, suggesting that those differences were less pronounced without the gelatinous fauna (Abundance: Global R = 0.455, *P* < 0.01; Biomass: Global R = 0.304, *P* < 0.02). In addition, removal of those species from abundance and biomass cluster analyses increased the complexity of the resultant dendrograms, producing five to seven primary groups rather than three or four at the 40% similarity level. This suggests that it is more appropriate to retain the gelatinous species in the analyses.
Mean diversity and evenness indices were calculated for the resultant abundance and biomass cluster groups (Table 4.5). Diversity and evenness were lowest in the neritic assemblage and highest in the mixed assemblage. The only exception was a slightly higher diversity index for the oceanic assemblage associated with the abundance data.

Integrated Abundance and Biomass

A total of 25 taxa were present in the upper 200 m of the water column within the offshore and continental slope zones during the cruise. All of those taxa, with the exception of the gammarid amphipod, *Epimeriella macronyx*, were present in the offshore zone but only 11 taxa were present in the continental slope zone. The euphausiid, *E. crystallorophias*, was the overwhelmingly dominant contributor of abundance and biomass in the 0 - 200 m layer in both the offshore and continental slope zones (Tables 4.6A and 4.6B). *E. crystallorophias* densities were similar in the offshore and continental slope zones (3.030 vs. 3.909 individuals m$^{-2}$). Mean total densities in the offshore zone were also similar to those in the continental slope zone (4.742 vs. 5.025 individuals m$^{-2}$) but mean total biomasses were higher in the offshore zone (1.069 g WM m$^{-2}$) than in the continental slope zone (0.699 g WM m$^{-2}$). No 200 m stratum data were compiled for the continental shelf since all net tows conducted in that zone used the Tucker trawl, which fished one net from surface to depth.
Discussion

A total of 41 invertebrate taxa were captured from the eastern Ross Sea during the 1999/2000 austral summer cruise. The ice krill, *E. crystallorophias*, accounted for the vast majority of the catch, contributing more than half of the total abundance. However, the scyphozoan, *A. wyvillei*, and the Antarctic krill, *E. superba*, contributed greater percentages of the total biomass (36% and 31%, respectively) due to their larger sizes. *E. crystallorophias* was the most abundant species in all three zones and was also the top biomass contributor on the shelf. Previous studies have described *E. crystallorophias* as the dominant micronektonic/ macrozooplanktonic species in the shelf waters of McMurdo Sound (Hopkins, 1987) and the western Ross Sea (Sala et al., 2002), as well as in coastal regions within Prydz Bay (Thomas and Green, 1988), the Lazarev Sea (Pakhomov and Perissinotto, 1996), and Marguerite Bay (Parker et al., 2011). *E. superba* was also present in each zone, but densities were greater in the offshore and continental slope zones. Both euphausiids were most abundant in surface waters just below the sea ice.

A comparison of assemblages revealed that those from the continental slope and continental shelf zones were more similar than those from offshore. Subsequent cluster analyses reinforced those results and identified three primary groups, which were characterized as oceanic, mixed, and neritic assemblages due partly to their geographical location but mostly to their faunal composition. The oceanic assemblage was composed primarily of samples collected from the offshore zone in water depths exceeding 2500 m, while the mixed and neritic assemblages included a combination of trawls from all three
zones. Although most dominant taxa were present to varying degrees within each assemblage, changes in the relative abundance and biomass of those taxa (Siegel and Piatkowski, 1990), as well as the presence of species that are typically characterized as either oceanic or neritic fauna, were key determinants for describing the assemblages. The oceanic assemblage contained the highest number of taxa and was dominated by oceanic fauna such as *D. antarctica*, *A. wyvillei*, and *C. borchgrevinki*. The euphausiid *T. macrura*, although not considered an oceanic species but rather a ubiquitously distributed species (Kittel et al., 1985; Nordhausen, 1994; Piatkowski, 1985) was also abundant in the oceanic assemblage. In the mixed assemblage, greater faunal mixing was demonstrated by the presence of species that dominated in the oceanic assemblage as well as two neritic species, *I. racovitzai* and *E. crystallorophias*, and *E. superba*. In contrast, diversity and evenness were lowest in the neritic assemblage due to the overwhelming dominance of *E. crystallorophias* and *E. superba*.

The composition of the faunal assemblages in the eastern Ross Sea was strongly influenced by the physical properties of the region. One of those features is the relatively narrow and deep (500 - 700 m) continental shelf where, at the shelf break, water depths increase rapidly to more than 3000 m (Ackley et al., 2003). The extreme changes in topography encountered within the continental slope zone enhance mixing of cold, shelf waters with warmer, oceanic waters, creating a subsurface front that is characterized by steep temperature and salinity gradients (Jacobs, 1991). This Antarctic slope front is often associated with increased biological productivity but it also functions as a strong boundary between oceanic and shelf fauna (Pages and Schnack-Schiel, 1996).
Temperature profiles reported by Jacobs et al. (2002) show the striking differences between the three zones. In the offshore zone, a cold surface layer extended to a depth of approximately 100 m where temperatures rapidly increased before reaching a maximum near 300 m (Donnelly et al., 2004). The temperature profile was similar in the continental slope zone, with the primary difference being a deepening of the surface layer and the temperature maximum. On the shelf, temperatures were cold (< -1.5 °C) and nearly isothermal from the surface to depth. Those cold ice-shelf waters exclude many oceanic species and as a result their distributions do not extend beyond the shelf break (DeWitt, 1970). This was demonstrated by the substantial decrease in the number of taxa present in the offshore and continental shelf zones (39 vs. 8 taxa, respectively). In addition, Donnelly et al. (2004) found that among the fishes, oceanic genera such as *Electrona, Gymnoscopelus, Bathylagus, Cyclothone*, and *Notolepis* were prevalent in the offshore zone, but absent on the shelf where they were replaced by the notothenioid *Pleuragramma antarcticum*.

The total abundance and biomass of pelagic invertebrates and fishes (Donnelly et al., 2004) captured in the eastern Ross Sea was quite low. A similar study in the ice-covered regions of the Bellingshausen and Amundsen Seas also found that zooplankton distributions were patchy and that overall biomass was lower compared to other Antarctic regions (Siegel and Harm, 1996). Diebel and Daly (2007) reported that zooplankton biomass in the Ross Sea was similar to that found on the Weddell Sea shelf, but an order of magnitude lower than that found on the Western Antarctic Peninsula shelf. Abundance and biomass in the Marguerite Bay region of the Western Antarctic Peninsula (WAP) ranged from 280-1289 individuals $10^4$ m$^{-3}$ and 66-268 g WM $10^4$ m$^{-3}$ (Parker et
al., 2011) compared to a mean of 70 individuals $10^4$ m$^{-3}$ and 29 g WM $10^4$ m$^{-3}$ for the entire study area. Studies conducted in the marginal ice zone of the Scotia and Weddell Seas reported integrated abundances and biomasses for the 0-200 m stratum that ranged from 12-22 individuals m$^{-2}$ and 5-20 g WM m$^{-2}$ (Lancraft et al., 1989, 1991) compared to 6-9 individuals m$^{-2}$ and 1 g WM m$^{-2}$ recorded in the offshore and continental slope zones of this study. Densities of individual taxa in the eastern Ross Sea were also substantially lower than those from the other studies. In the Scotia and Weddell Seas, integrated abundances and biomasses of *E. superba* ranged from 3-11 individuals m$^{-2}$ and 0.6-3 g WM m$^{-2}$ (Lancraft et al., 1989, 1991) versus 0.4-1 individual m$^{-2}$ and <1 g WM m$^{-2}$. However, integrated abundance and biomass of *E. crystallorophias* from this study (4-7 individuals m$^{-2}$ and 0.4-0.6 g WM m$^{-2}$) fell within the range measured in Marguerite Bay in 2001 and 2002 (0.04-19 individuals m$^{-2}$ and 0.005-3 g WM m$^{-2}$; Parker et al., 2011).

Another physical factor may have indirectly influenced micronekton/macrozooplankton densities in the study area by impacting phytoplankton concentrations. That factor is a unique attribute of the eastern Ross Sea; it is one of the few areas that remain covered by sea ice throughout the summer, when sea ice is retreating around the rest of the continent (Gloersen et al., 1992). For the duration of the cruise, the majority of the study area was covered by ice, especially along the southern and eastern boundaries (Ackley et al., 2003). A potential consequence of the persistent sea ice in this region is a decrease in phytoplankton productivity. Measurements taken during the cruise show that the majority of the study area had very low phytoplankton biomass and that phytoplankton blooms, when present, were small and infrequent (Ackley et al., 2003). This is in stark contrast to the southwestern Ross Sea, which is
considered to be the most productive region in the Southern Ocean (Arrigo et al., 1998a, 1998b). However, in that highly productive area, the seasonal phytoplankton bloom is triggered by sea ice retreat and associated increases in irradiance and water column stability (Smith et al., 2000).

Conclusions

The physical environment strongly impacted micronektonic/macrozooplanktonic distributions and densities in the eastern Ross Sea. Three broad groupings of invertebrate fauna were identified from trawls conducted in the offshore, continental slope, and continental shelf zones; an oceanic, mixed, and neritic assemblage. Changes in faunal composition were directly related to temperature differences encountered at the shelf break and the subsequent filtering out of oceanic fauna from cold, shelf waters where endemic fauna were most prevalent. Persistent ice cover resulted in low phytoplankton concentrations, which likely limited zooplankton densities. Despite the low invertebrate biomass, higher trophic level predators such as crabeater, Weddell, and Ross seals were abundant in the pack ice of the region suggesting that this area serves as an important platform for molting and foraging during the summer months (Ackley et al., 2003).
References


Table 4.1: 4-m$^2$ MOCNESS and 9-m$^2$ Tucker trawl data from the APIS cruise conducted in the eastern Ross Sea during austral summer 1999/2000. Local time = GMT – 4 hours, TOD = Time of Day

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Table 4.2A: Volumetric abundance (# individuals $10^4$ m$^{-3}$) and biomass (g WM $10^4$ m$^{-3}$) of each taxon captured within the offshore zone during austral summer 1999/2000. $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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| Mean Total      | 185.48                              | 131.73 |
| Number of Taxa  | 33                                  |       |

*aNo weights were recorded for these specimens.*
Table 4.2B: Volumetric abundance (# individuals 10^4 m^-3) and biomass (g WM 10^4 m^-3) of each taxon captured within the continental slope zone during austral summer 1999/2000. n = number of trawls, VF = total volume filtered (m^3), SD = standard deviation

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Table 4.2B: Continued

Continental Slope ($n = 7$)

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Mean Total: 117.14
Number of Taxa: 23

$^a$No weights were recorded for these specimens.
Table 4.2C: Volumetric abundance (# individuals $10^4$ m$^{-3}$) and biomass (g WM $10^4$ m$^{-3}$) of each taxon captured within the continental shelf zone during austral summer 1999/2000. $n =$ number of trawls, VF = total volume filtered (m$^3$), SD = standard deviation

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*aNo weights were recorded for these specimens.*
Table 4.3: Results of SIMPER analysis on volumetric abundance data showing the taxa contributing the most to similarity within each cluster group. Values in parentheses represent the overall similarity among samples within a cluster group. % Contribution = percentage contribution to the overall similarity among samples within a cluster group. Only those taxa that contributed 1% or more to overall group similarity are listed.

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<th>Mixed (60.25% similarity)</th>
<th>Neritic (61.50% similarity)</th>
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<td>Calycopsis borchgrevinki</td>
<td>11.05</td>
<td>Euphausia superba</td>
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<td>Euphausia superba</td>
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<td>Clio pyramidata</td>
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<tr>
<td>Cyllopus lucasii</td>
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Table 4.4: Results of SIMPER analysis on volumetric biomass data showing the taxa contributing the most to similarity within each cluster group. Values in parentheses represent the overall similarity among samples within a cluster group. % Contribution = percentage contribution to the overall similarity among samples within a cluster group. Only those taxa that contributed 1% or more to overall group similarity are listed.

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<th>Neritic (52.56% similarity)</th>
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Table 4.5: Diversity ($H'$) and evenness ($J'$) for abundance and biomass cluster groups. SD = standard deviation

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<th>Evenness ($J'$)</th>
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Table 4.6A: Integrated abundance (# individuals m$^{-2}$) and biomass (g WM m$^{-2}$) of taxa collected from discrete tows within the 0-200 meter depth stratum from the offshore zone during austral summer 1999/2000. $n =$ number of trawls

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<td>0.003</td>
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</tr>
<tr>
<td>Vanadis antarctica</td>
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<td>0.008</td>
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Mean Total                  | 4.742   | 1.069     |
Number of Taxa              | 24      |           |

*No weights were recorded for these specimens.*
Table 4.6B: Integrated abundance (# individuals m\(^{-2}\)) and biomass (g WM m\(^{-2}\)) of taxa collected from discrete tows within the 0-200 meter depth stratum from the continental slope zone during austral summer 1999/2000. \(n = \) number of trawls

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Continental Slope ((n = 7)), VF = 32715</th>
<th># m(^2)</th>
<th></th>
<th>gWM m(^{-2})</th>
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<tr>
<td></td>
<td>Median</td>
<td>Mean</td>
<td>SD</td>
<td>Median</td>
<td>Mean</td>
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<tr>
<td>Alluroteuthis antarcticus</td>
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<td></td>
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<td>Atolla wyvillei</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beroe sp.</td>
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<td>Calycopsis borchgrevinki</td>
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<td>0.069</td>
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<td>Clio pyramidata</td>
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<td>Cylopus lucasii</td>
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<td>0.011</td>
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<td>Eusirus antarcticus</td>
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<td>Eusirus microps</td>
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<td>0.004</td>
<td>0.009</td>
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<td>0.000</td>
</tr>
<tr>
<td>Hyperoche medusarum</td>
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</tr>
<tr>
<td>Limacina antarctica</td>
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<td>0.017</td>
<td>0.035</td>
<td>0.000</td>
<td>0.002</td>
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<td>Nematocarcinus lanceopes</td>
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<td></td>
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<td></td>
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<td>Primno macropa</td>
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<td></td>
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<td>Pseudosagitta gazellae</td>
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<td>0.153</td>
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<td>Thysanoessa macrura</td>
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<tr>
<td>Tomopteris carpenteri</td>
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<tr>
<td>Vanadis antarctica</td>
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</tbody>
</table>

Mean Total                      | 5.025  |          | 0.699      |
Number of Taxa                  | 11     |          |            |

\(^a\)No weights were recorded for these specimens.
Figure 4.1: Trawl locations in the eastern Ross Sea during austral summer 1999/2000.
Figure 4.2: Vertical distributions of eight common species collected during the 1999/2000 cruise. $n =$ number of individuals.
Figure 4.3: Percent similarity cluster dendrogram of 1999/2000 micronekton/macrozooplankton volumetric abundance (# individuals $10^4$ m$^{-3}$). Numbers along the abscissa represent the gear and trawl number (Ex. MOCNESS trawl 14 is designated as M14). Brackets represent cluster groups at the 40% similarity level.
Figure 4.4: Percent similarity cluster dendrogram of 1999/2000 micronekton/macrozooplankton volumetric biomass (g WM $10^4$ m$^{-3}$). Numbers along the abscissa represent the gear and trawl number (Ex. MOCNESS trawl 14 is designated as M14). Brackets represent cluster groups at the 40% similarity level.
Figure 4.5: MDS ordination plot of 1999/2000 abundance (# individuals $10^4$ m$^{-3}$) data.
Figure 4.6: MDS ordination plot of 1999/2000 biomass (g WM 10^4 m^-3) data.
CHAPTER FIVE
SUMMARY OF CONCLUSIONS

In the WAP region, three broad groupings of invertebrate taxa were identified in the waters near the vicinity of Marguerite Bay: an oceanic, neritic, and mixed or transitional assemblage. The degree of faunal mixing in the assemblages was facilitated by the absence of a subsurface slope front and its associated sharp temperature and salinity gradients and the presence of warm Circumpolar Deep Water (CDW) below 200 m on the shelf (Dinniman and Klinck, 2004). As a result, change in faunal composition in the Marguerite Bay region was a cross-shelf gradient rather than a sharp boundary at the shelf break. In contrast, the presence of a strong Antarctic Slope Front near the upper continental slope considerably altered the faunal composition on the shelf in the eastern Ross Sea. Water temperatures on the shelf were near freezing (-2 °C) from the surface to depth, effectively excluding most oceanic fauna, as demonstrated by the substantially lower faunal abundances and species diversity found on the shelf. Three primary assemblages were also identified in the eastern Ross Sea, but instead of a cross-shelf gradient, the major distinctions occurred at the shelf break.

Overall abundance and biomass of captured invertebrates also differed between regions. Total densities in the Marguerite Bay region were 3 to 12 times higher than the
highest densities, which were captured from the offshore zone, in the eastern Ross Sea. When compared to shelf densities in the Ross Sea, the total catch from Marguerite Bay was one to two orders of magnitude higher. Differences in total biomass were less pronounced, but that may be attributable to greater numbers of large, heavy scyphozoans captured from the Ross Sea. The lower catches in the Ross Sea may be a result of the pack ice that was present throughout the study site. One potential consequence of heavy ice coverage is decreased phytoplankton productivity, which ultimately limits zooplankton densities. In the Marguerite Bay region, faunal densities were enhanced by the presence of nutrient-rich CDW and a persistent cyclonic gyre, which acts to retain fauna (Klinck et al., 2004).

A comparison of assemblages from sites along the WAP shelf revealed several distinct faunal assemblages, which corresponded closely with hydrographic regions that were defined by characteristics such as local circulation patterns and sea ice extent and duration. The faunal compositions within each assemblage were closely linked to on-shelf circulation patterns and the thermal regimes of each region. Along with those findings, the disappearance of the Antarctic silverfish, *Pleuragramma antarcticum*, from the mid-peninsula region and the absence of younger year classes in Marguerite Bay suggests that populations in most regions are being sustained by local reproduction rather than larval advection. Over the past 50 years, a warming trend in that mid-peninsula region has resulted in warmer air temperatures and a decrease in the duration of the sea ice season (Smith et al., 2003a, b). Many endemic species, such as *Pleuragramma antarcticum*, have life histories, which are critically dependant on winter sea ice. If resident populations of zooplankton and fishes reproduce and recruit locally, those
populations will be highly susceptible to local extinctions. Continued warming and subsequent sea ice reductions may not only cause *Pleuragramma* population collapses in the Marguerite Bay and Charcot Island regions, but may also change the character of the faunal assemblages along the WAP to those of an oceanic system.

Distributions of macrozooplankton and micronekton in the Western Antarctic Peninsula (WAP) and eastern Ross Sea regions were influenced by local bathymetry, hydrography and physical conditions. Subtle changes in faunal composition and shifts in dominant taxa demonstrated the importance these factors have on macrozooplanktonic/micronektonic fish and invertebrate assemblages. An improved understanding of physical and biological interactions is essential for predicting marine ecosystem responses to the increasing threat of global climate change.

**References**

