6-30-2008

Characterization of the Western Antarctic Peninsula Ecosystem: Environmental Controls on the Zooplankton Community

Marina Marrari
University of South Florida

Characterization of the Western Antarctic Peninsula Ecosystem:

Environmental Controls on the Zooplankton Community

by

Marina Marrari

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

Major Professor: Kendra L. Daly, Ph.D.
Chuanmin Hu, Ph.D.
Gary Mitchum, Ph.D.
Luis García-Rubio, Ph.D.
Meng Zhou, Ph.D.

Date of Approval:
June 30, 2008

Keywords: Southern Ocean, Marguerite Bay, SeaWiFS chlorophyll, krill, *Euphausia superba*

DEDICATION

to my husband, Christian

my daughter, Valentina

and my parents Juan and Marcela

ACKNOWLEDGEMENTS

NOTE TO THE READER

The original of this document contains color that is necessary for understanding the data.

The original dissertation is on file with the USF library in Tampa, Florida.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Characterization of the Western Antarctic Peninsula Ecosystem: Environmental

Controls on the Zooplankton Community

Marina Marrari

ABSTRACT

The zooplankton community of Marguerite Bay, western Antarctic Peninsula, was

investigated in relation to variability in chlorophyll concentrations and sea ice dynamics,

using a combination of satellite remote sensing techniques and plankton net data.

SeaWiFS chlorophyll data were validated with concurrent *in situ* data measured by HPLC

and fluoromentric methods, and results indicate that SeaWiFS chlorophyll is an accurate

measure of *in situ* values when HPLC data are used as ground truth.

Climatology data of SeaWiFS chlorophyll west of the Antarctic Peninsula showed

that the Bellingshausen Sea and Marguerite Bay usually had higher and more persistent

chlorophyll concentrations compared with northern regions. These predictable

phytoplankton blooms could provide the Antarctic krill, *Euphausia superba*, with the food

required for successful reproduction and larval survival. Unusually high krill

reproduction in 2000/2001 was coincident with above-average chlorophyll concentrations

throughout the study area and was followed by the largest juvenile recruitment since

1981. High larval densities at the shelf break along the Antarctic Peninsula may have

resulted, in part, from krill spawning in the Bellingshausen Sea. Interannual differences in sea ice also probably contributed to the variability in larval krill abundances.

Interannual differences were observed in the species composition of the zooplankton of Marguerite Bay during fall, and these were linked to variability in the environmental conditions. *Thysanoessa macrura* was the most abundant euphausiid in 2001, while *Euphausia crystallorophias* dominated in 2002, and *E. superba* had intermediate densities during both years. Copepods were more abundant in 2001 by a factor of 2.6. Copepods and *T. macrura* showed a rapid population response to unusually high chlorophyll concentrations in the Bellingshausen Sea and Marguerite Bay during spring-summer 2000/2001, whereas *E. superba* and *E. crystallorophias* had a longer term response and showed increased recruitment in fall 2002. There were no clear associations between the distribution of zooplankton and environmental conditions in fall; however there was a significant relationship between chlorophyll concentrations in the Bellingshausen Sea during the preceding spring and zooplankton patterns during fall.

CHAPTER ONE

THE WESTERN ANTARCTIC PENINSULA: PHYSICAL AND BIOLOGICAL
SETTING

The Southern Ocean covers approximately 10% of the world's ocean,

supporting large concentrations of zooplankton and higher trophic level organisms. The

region plays an important role in the world's ocean biogeochemical cycle (Sarmiento et

al., 1998) and has a profound influence on global circulation by connecting the Atlantic,

Pacific, and Indian Ocean basins, and through deep water formation. Based on

biogeography, three main zones have been described for the Southern Ocean: (1) an ice-

free zone rich in nutrients, but relatively poor in primary production, with a zooplankton

community dominated by copepods, salps and small euphausiids, (2) a productive

seasonal pack-ice zone that includes the area covered by sea ice during winter, but mostly

ice-free during summer and fall, where zooplankton may be dominated by the Antarctic

krill, *Euphausia superba*, and (3) a permanent pack ice zone, with generally low

zooplankton biomass, where *E. superba* is often replaced by the neritic euphausiid,

Euphausia crystallorophias (Hempel, 1985).

Within the Atlantic sector of the Southern Ocean, the continental shelf along the

western Antarctic Peninsula (WAP) includes waters of the seasonal and permanent pack

ice zones (Fig. 1.1). This region supports high concentrations of zooplankton and

predators, and is considered one of the most productive areas in Antarctic waters (Deibel and Daly, 2007). The Antarctic Peninsula region also is of interest as it is warming more rapidly than almost any other place on the planet. A considerable increase in atmospheric and upper-ocean temperatures has occurred in the last 50 years, while ice shelves have retreated (King, 1994; Smith et al., 1996b; Vaughan and Doake, 1996; Vaughan et al., 2003). In addition, there have been marked changes in winter sea ice extent and duration (Parkinson 2002). These changes have important implications for Antarctic organisms that rely directly on sea ice for reproduction, such as Adèlie penguins (Trivelpiece and Fraser, 1996), as well as for others that will suffer indirect effects through changes in prey populations (Costa and Crocker, 1996).

The Antarctic krill, *E. superba*, is a relatively large pelagic crustacean (up to 65 mm in length) and a keystone species in the Antarctic ecosystem, acting as a primary grazer on phytoplankton and prey for a variety of higher trophic level predators. Most Antarctic predators, including species of fish, seals, whales, penguins, and many seabirds, rely on zooplankton for survival, and in particular Antarctic krill (Lowry et al., 1988; Ainley and DeMaster, 1990; Costa and Crocker, 1996; Murase et al., 2002). *E. superba* has a circumpolar distribution, with highest concentrations in the Atlantic sector of the Southern Ocean (Marr, 1962). It is believed that krill originated in the WAP region are the source of large populations observed downstream in the Scotia Sea and at South Georgia Island (Fach and Klinck, 2006; Thorpe et al., 2007).

Since the *Discovery* expeditions in the 1920-30s, which surveyed almost the entire Southern Ocean and resulted in a large amount of information regarding the distribution, biology and ecology of Antarctic krill (Marr, 1962), research in the vicinity

of the WAP has been mostly restricted to northern waters along the continental shelf and

downstream in the Scotia Sea.
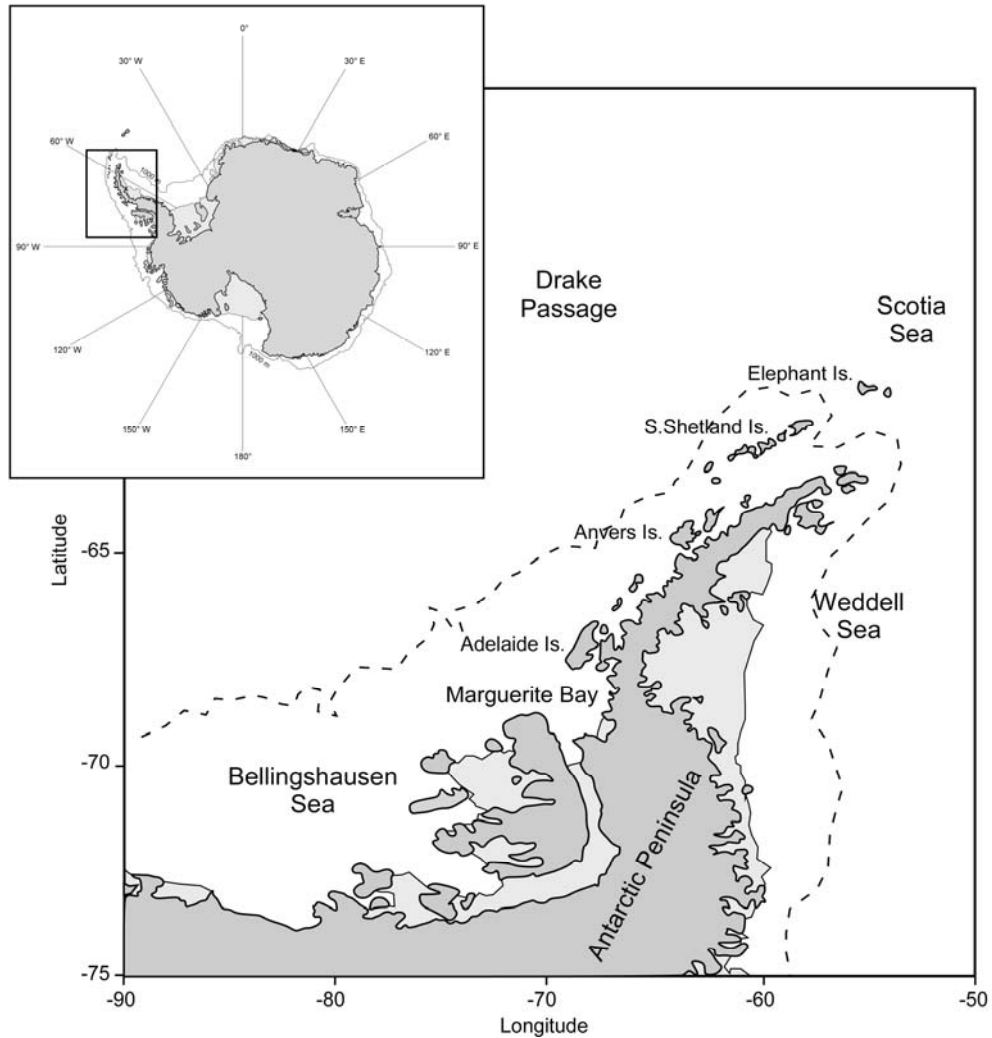
Figure 1.1. Map of the western Antarctic Peninsula (WAP) region and geographic references. The dotted line indicates the 1000 m isobath.

Some interdisciplinary programs that investigated the structure and dynamics of

the marine ecosystem from the mid- to northern sectors of the WAP include BIOMASS

Program (Biological Investigations of Marine Antarctic Systems and Stocks) in 1985/86

3

(El-Sayed, 1994), RACER (Research on Antarctic Coastal Ecosystem Rates) (Huntley et al., 1991), Palmer LTER (Long Term Ecological Research), which since the early 1990s has been dedicated to studying how physical forcing affects the structure and function of the ecosystem (Ross et al., 1996), and AMLR (Antarctic Marine Living Resources Program), established in 1990 to assess resources in the area around Elephant Island (e.g., Loeb et al., 1997; Siegel et al., 2002; Watkins et al., 2004). The information resulting from these efforts, as well as from other field expeditions from the United Kingdom, Germany, Argentina, Poland, Russia, and Chile, among others, has greatly improved our understanding of the processes controlling populations in the area, and has provided insight into the dominant physical components, such as circulation, hydrography, nutrient distributions, and sea ice dynamics. However, in spite of the significant amount of information available for the northern sectors, there have been few studies in southern regions of the WAP (Marguerite Bay and the eastern Bellingshausen Sea) (Atkinson, 1995; Siegel and Harm, 1996; Lascara et al., 1999; Meyer et al., 2003).

The Southern Ocean Global Ocean Ecosystem Dynamics Program (SO GLOBEC) field efforts were focused in the vicinity of Marguerite Bay, as limited information suggested that it was an important overwintering site for upper trophic level predators and, therefore, probably of their food source, Antarctic krill (Hoffman et al., 2004). The primary goal of the U.S. SOGLOBEC Program was to investigate the physical and biological factors that influence the growth, recruitment, and overwintering survival of *E. superba* in the vicinity of Marguerite Bay as well as the associated predators and prey of krill (Hoffman et al., 2004).

Initial results of the US SOGLOBEC Program have described the general

circulation in Marguerite Bay. There are two major currents: the wind-driven westerly

Antarctic Circumpolar Current (ACC) that flows northward along the continental shelf

break, and the buoyancy-driven Antarctic Peninsula Coastal Current (APCC), which

flows southward along the coast (Moffat et al., 2008) (Fig. 1.2). The APCC enters

Marguerite Bay at the south end of Adelaide Island, flows clockwise along the coast and

exits around the north end of Alexander Island. Mesoscale circulation features, such as

gyres on the outer shelf and eddies within inner Marguerite Bay, contribute to making

Marguerite Bay a favorable retention area for phyto- and zooplankton (Beardsley et al.,

2004; Klinck et al., 2004; Dorland and Zhou, 2008)

Marguerite Bay encompasses a relatively wide and deep continental shelf, with

mean depths of ~ 400 m (Bolmer et al., 2004). The bathymetry is influenced by

Marguerite Trough, a deep canyon up to 1600 m deep, which intersects the continental

shelf off Marguerite Bay, crosses the shelf, and extends into George VI Sound (Fig. 1.3).

In addition, the area is characterized by numerous seamounts and depressions that result

in a variable and complicated topography, particularly in the northern sectors, such as

Laubeuf Fjord and Crystal Sound north of Marguerite Bay. Intrusions of Upper

Circumpolar Deep Water (UCDW), found at depths greater than 500 m in oceanic areas,

have been observed on the continental shelf, supplying Marguerite Bay with warm and

nutrient rich waters at depth. These intrusions occur through Marguerite Trough, as well

as in other shelf break areas such as those off Crystal Sound and west of Alexander Island

(Fig. 1.2) (Dinniman and Klinck, 2004).

The hydrographic structure of continental shelf waters along the Antarctic Peninsula has

been previously described (Smith et al., 1999; Klinck et al., 2004). The primary water

masses include Antarctic Surface Water (ASSW), characterized by temperatures and
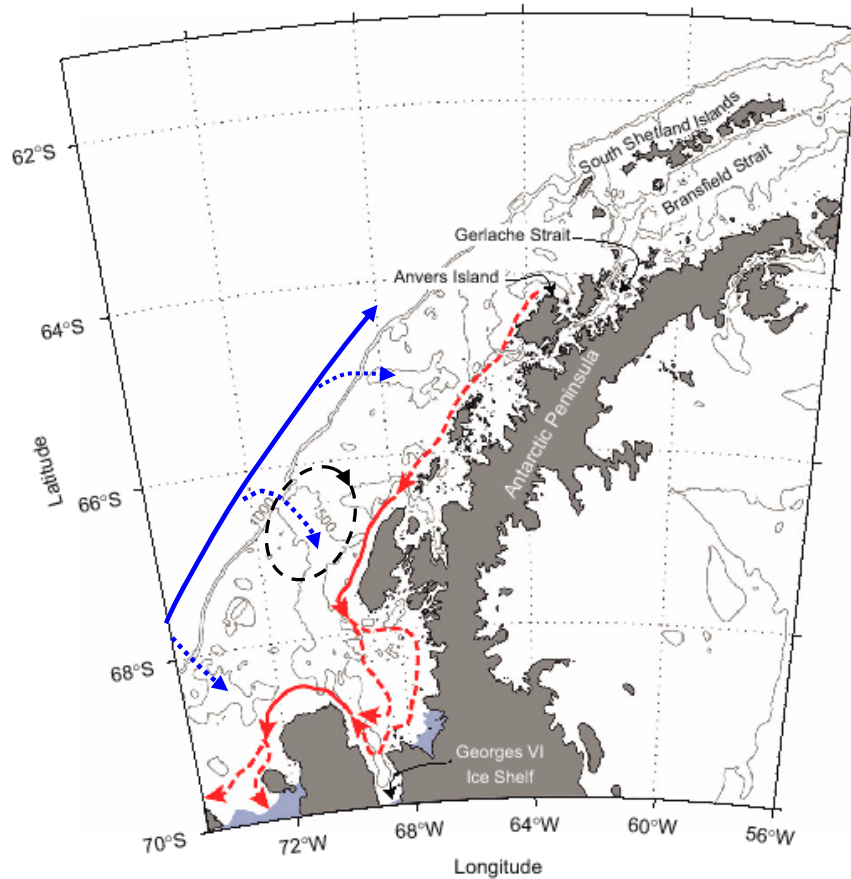
Figure 1.2. General circulation in Marguerite Bay, and schematic paths of the Antarctic Circumpolar Current (ACC) (blue) and Antarctic Peninsula Coastal Current (APCC) (red). The dotted blue line represents the approximate location of intrusions of Upper Circumpolar Deep Water (UCDW) onto the continental shelf (Dinniman and Klinck, 2004). Sections of broken red line represent suggested paths of the APCC, not derived from observations (adapted from Moffat et al., 2008). The approximate location of a mesoscale clockwise gyre is indicated by the broken black line (Klinck et al., 2004)

salinity ranges between -1.8 and 1 °C and 33.0 and 33.7, respectively. Beneath a

pycnocline, generally established at ~ 100 - 120 m, is warm (1.5 °C) and salty (34.6 –

34.73) water derived from Circumpolar Deep Water (CDW), which is typically present in

waters over the outer shelf of the WAP at depths of 200 - 600 m. During late fall, surface

heat loss and wind forcing result in a deep winter mixed layer occupied by near-freezing

(< -1 °C) Winter Water (WW). This surface layer is partially restratified in spring and a

remnant layer of cold WW is normally observed at ~ 80 - 100 m between the AASW and

modified CDW layers.
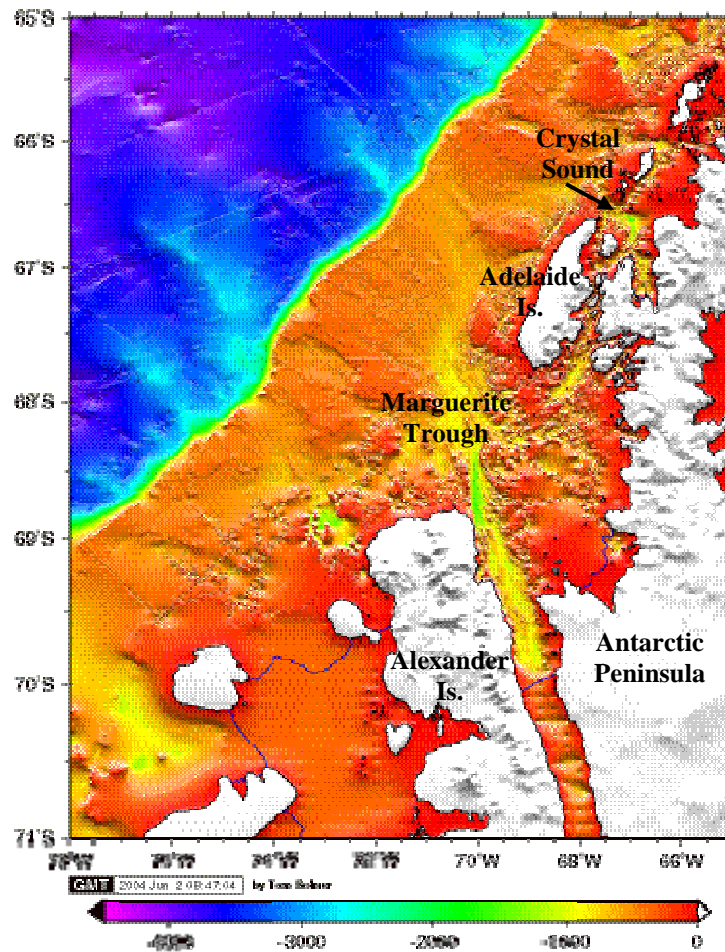
Figure 1.3. Bathymetric map of Marguerite Bay and adjacent waters of the western
Antarctic Peninsula. Bathymetry in meters (m). Reproduced from Bolmer et al. (2004).

A major physical characteristic of the Southern Ocean is the annual advance

and retreat of sea ice. During summer most of the WAP continental shelf is ice-free,

allowing dense phytoplankton blooms to develop. During winter, sea ice cover can

completely cover the continental shelf. In recent years, however, a dramatic decline in sea

ice extent has been observed in the WAP, resulting in areas of the northern WAP which

may remain ice-free throughout the year. However, in southern sectors, such as

Marguerite Bay and the eastern Bellingshausen Sea, winter sea ice generally extends over

most of the continental shelf and, thus, can be considered an important factor influencing

marine organisms. Extensive sea ice reduces the penetration of radiant heat into the

water column during spring, summer, and fall, limiting phytoplankton growth and, thus,

food available to zooplankton.

To summarize, the Marguerite Bay region is characterized by a complex

seafloor topography, extreme variability in seasonal sea ice conditions, and circulation

features, which include opposite flowing currents, intrusions of oceanic waters onto the

shelf, and mesoscale gyres and eddies. Given the rapidly changing conditions of this

region and the potential effects on Antarctic organisms, understanding zooplankton

population dynamics and their response to environmental variability is critical to

predicting the effects of climate change on the Antarctic ecosystem as a whole.

This dissertation aims to investigate the effects of environmental variability on

the population dynamics of phytoplankton and zooplankton in the vicinity of Marguerite

Bay, with special emphasis on *E. superba*. For this purpose, I use a combination of ocean

color remote sensing techniques, zooplankton net data, and environmental information.

The main objective of Chapter 2 is to evaluate the performance of the SeaWiFS satellite

sensor (Sea-Viewing Wide Field-of-View Sensor) in estimating chlorophyll

concentrations in the Southern Ocean. Chapter 3 focuses on using SeaWiFS data to

describe the temporal and spatial dynamics of chlorophyll distributions along the WAP

during spring and summer, and relate the interannual variability observed in chlorophyll dynamics to changes in the reproduction and recruitment success of *E. superba*. Chapter 4 investigates the patterns of abundance and distribution of the dominant zooplankton groups in Marguerite Bay, in relation to variability in environmental conditions, and a summary of the major findings and future direction is presented in Chapter 5.

CHAPTER TWO

VALIDATION OF SEAWIFS CHLOROPHYLL A CONCENTRATIONS IN THE SOUTHERN OCEAN: A REVISIT

INTRODUCTION

Since the launch of the Sea-viewing Wide Field-of-view Sensor (SeaWiFS, McClain et al., 1998) onboard the Orbview-II satellite in August 1997, ocean color data products, in particular concentrations of chlorophyll a (C_a, mg m^{-3}) in the surface ocean, have been used to investigate a wide variety of fundamental topics including ocean primary productivity, biogeochemistry, coastal upwelling, eutrophication, and harmful algal blooms (e.g., Hu et al., 2005; Muller-Karger et al., 2004). Other ocean color missions, such as the ongoing MODerate-resolution Imaging Spectroradiometer (MODIS, Esaias et al., 1998; Terra satellite for morning pass since 1999 and Aqua satellite for afternoon pass since 2002) or the future National Polar-Orbiting Operational Environmental Satellite System (NPOESS), assure the continuity of remotely sensed ocean color in assessing the long-term global change in several key environmental parameters, including C_a. Quantitative use of ocean color data products requires a high level of accuracy. During algorithm development, the errors in the C_a data products after logarithmic transformation were about 0.2 or less (O'Reilly et al., 2000), which corresponds to roughly 50% root mean square (RMS) relative error. Global validation efforts show that in most ocean basins C_a errors are about 0.3 (Gregg and Casey, 2004)

although in regions such as the Southern Ocean, reported errors are significantly larger.

The Southern Ocean was defined by the International Hydrographic Organization in 2000 to encompass waters between the northern coast of Antarctica and 60° S. Oceanographers, however, traditionally have defined the northern limit of the SO as the Subtropical Front (at approximately 40º S) (Orsi et al., 1995). Typical chlorophyll concentrations in the Southern Ocean range between 0.05 and 1.5 mg m^{-3} (Arrigo et al., 1998; El-Sayed, 2005). It is believed that the interaction of light and deep mixing, iron, and grazing limit phytoplankton growth throughout the Southern Ocean, in addition to low silicate concentrations which can limit diatom production north of the Polar Front (Moline and Prézelin, 1996; Daly et al., 2001; Boyd, 2002). However, elevated chlorophyll concentrations (1 to > 30 mg m^{-3}) are characteristic of many regions, including continental shelf and ice edge areas (Holm-Hansen et al., 1989; Moore and Abbott, 2000; El-Sayed, 2005), and even values of up to 190 mg m^{-3} have been reported (El-Sayed, 1971). The Antarctic Peninsula region, in particular, supports large concentrations of phytoplankton, zooplankton, seabirds, seals and whales, and is considered one of the most productive areas of the Southern Ocean, for reasons that are not fully understood (Deibel and Daly, 2007).

Several studies have relied on ocean color data to investigate phytoplankton spatial patterns (Moore and Abbott, 2000; Holm-Hansen et al., 2004a), interannual variability during summer (Smith et al., 1998a; Korb et al., 2004) and primary productivity (Dierssen et al., 2000; Smith et al., 2001) west of the Antarctic Peninsula and in the adjoining Scotia Sea. These studies used *in situ* C_a determined from water samples using fluorometric methods (C_a^{Fluor}) to validate monthly/weekly averages of

11

SeaWiFS C_a ($C_a{}^{SWF}$) data product at ~ 9 x 9 km^2 or ~ 4 x 4 km^2 resolution and concluded

that in the Southern Ocean, $C_a{}^{SWF}$ values are significantly lower than those estimated

from *in situ* water samples. For example, Dierssen and Smith (2000) applied *in situ* bio-

optical data measured between 1991 and 1998 to the OC2v2 algorithm to test its

applicability west of the Antarctic Peninsula in the Southern Ocean. They concluded that

C_a derived from the OC2v2 algorithm using *in situ* reflectance was 60% lower than *in*

situ C_a (C_a between 0.7 and 43 mg m^{-3}, median ~ 1 mg m^{-3}). Korb et al. (2004) reported

that $C_a{}^{SWF}$ values were only 87% of $C_a{}^{Fluor}$ for concentrations lower than 1 mg m^{-3} and

only 30% for concentrations above 5 mg m^{-3} in the South Georgia area (54.5º S, 37º W).

In addition, Moore et al. (1999) found a strong linear relationship between $C_a{}^{SWF}$ and

$C_a{}^{Fluor}$ ($R^2 = 0.72$, n = 84) in the Ross Sea, although they noted that SeaWiFS tended to

underestimate C_a values between 0.1 and 1.5 mg m^{-3}.

The previous validation methods may present several limitations. First, *in situ*

samples are point measurements while satellite pixels cover a larger area (up to 9 x 9

km^2). Patchiness within a pixel will affect the comparison of results between areas and

over time (e.g., Hu et al., 2004). Second, the *in situ* and satellite measurements are not

strictly concurrent and the time differences can be large (up to a month). Finally, and

most importantly, previous validation studies used *in situ* C_a from fluorometric

measurements, while it is now widely recognized that High Performance Liquid

Chromatography (HPLC) may yield more accurate results in determining C_a from water

samples. Fluorometric methods may result in biased results, particularly in the presence

of certain accessory pigments (Lorenzen, 1981; Welschmeyer, 1994).

In a study that included three different areas of the world's oceans, Trees et al.

(1985) reported that errors in the C_a^{Fluor} ranged between -68 and 53% with a mean of 39%. In addition, Bianchi et al. (1995) found that C_a^{Fluor} in the northern Gulf of Mexico was approximately 30% lower than C_a^{HPLC}, except in near coastal areas. It is believed that the presence of significant amounts of chlorophyll b (C_b), characteristic of chlorophytes, prochlorophytes and prasinophytes, causes fluorometric techniques to underestimate C_a. On the other hand, high concentrations of chlorophyll c (C_c), typically found in diatoms, dinoflagellates, cryptophytes, and haptophytes, lead to an overestimation of C_a with respect to fluorometric measurements. The fluorescence emission spectra of degradation products (phaeopigments) of C_a and C_b overlap considerably, causing an overestimation of C_a phaeopigments and, thus, an underestimation of C_a. On the other hand, C_a and C_c have partially overlapping fluorescence spectra, causing an overestimation of C_a and subsequent underestimation of phaeopigments a (Gibbs, 1979; Jeffrey et al., 1997). The filters used in the standard fluorometric method (Lorenzen, 1981) cannot effectively discriminate between C_a, C_b, C_c and their degradation products; thus, depending on the type of phytoplankton present and their associated pigments, C_a may be overestimated or underestimated by fluorometric methods.

Herein, I use concurrent HPLC and fluorometric data collected between 1998 and 2002 in waters west of the Antarctic Peninsula, as well as high-resolution SeaWiFS data, to re-examine whether SeaWiFS C_a is underestimated in the Southern Ocean as reported in previous studies. I also discuss possible explanations for the observed results and investigate the effects of different accessory pigments on C_a estimations.

13

METHODS

SeaWiFS daily Level 2 data between December 1997 and December 2004 were

obtained from NASA Goddard Space Flight Center. These data were derived from the

high-resolution (~ 1 km/pixel near nadir) Level 1 data collected by ground stations, as

well as occasional satellite onboard recording over the area using the most current

algorithms and software package (SeaDAS4.8). A total of 6606 data files were obtained

and mapped to a rectangular projection with approximately 1 km^2/pixel for the area

between 45 - 75° S and 50 - 80° W west of the Antarctic Peninsula (Fig. 1.1). The data

product used in this study is the surface C_a estimated with the OC4v4 empirical algorithm

(O'Reilly, 2000):

$$C_a = 10^{0.366 - 3.067R + 1.93R^2 + 0.649R^3 - 1.532R^4} \tag{1}$$

where R = log$_{10}$[(max(R$_{rs443}$, R$_{rs490}$, R$_{rs510}$))/R$_{rs555}$)] and R$_{rs}$ is the remote sensing

reflectance, a data product after atmospheric correction.

Chlorophyll fluorescence and HPLC pigment data were collected and analyzed

by Drs Raymond Smith (University of California Santa Barbara) and Maria Vernet

(University of California San Diego) as part of the Palmer Long Term Ecological

Research (LTER) program during cruises west of the Antarctic Peninsula (see

http://pal.lternet.edu/data/ for detailed methods). The location of the LTER chlorophyll

sampling stations between 1998 and 2002 are shown in figure 2.1. Most of the samples

were collected within the 2000 m isobath, although two transects were conducted across

Drake Passage in January-February 1999 and 2000 to measure C_a^{Fluor}. At each station, water column samples were collected at discrete depths for both fluorometric and HPLC measurements. C_a, C_b and C_c were obtained by HPLC from samples collected at fixed stations during January-February 1998 and 1999 following the methods of Wright et al. (1991), and during January-February 2000 and 2001 following the methods of Zapata et al. (2000).

C_a and phaeopigment concentrations also were obtained by fluorometric methods by measuring total fluorescence and subtracting phaeopigments after acidification from samples collected during January - February 1998, 1999, 2000, 2001 and 2002 following Smith et al. (1981, 1996a, 1998). Welschmeyer's (1994) method, which effectively measures fluorescence from C_a only and reduces interference from C_b or its phaeo-derivatives, was not applied (M. Vernet, *pers. comm.*).

Because the signal detected by the satellite sensor is an optically-weighted function of signals at all depths (up to 50 - 60 m for clear waters), the method of Gordon (1992) was used to calculate a depth-weighted chlorophyll concentration, <C>, to compare with satellite estimates:

$$< C >= \frac{\int_0^z g(z')C(z')dz'}{\int_0^z g(z')dz'} \qquad (2)$$

where $g(z) = \exp[-2\int_0^z K(z')dz']$ and z is the depth. K is the diffuse attenuation coefficient that is approximated by $K(z) \approx 0.121\ C(z)^{0.428}$ (Morel, 1988). The integration was from 0 to 50 m and included 5 or 6 vertical samples at most stations, although in some cases only 3 - 4 samples were available for the calculations. A total of 189 HPLC

and 775 fluorometric C_a values were used in these analyses. Because the weighting

function, $g(z)$, decreases exponentially with increasing depth, $<C>$ is not very different

from the surface value, at least for fluorometric C_a (ratio = 1.02 ± 0.15, p = 0.841). For

the HPLC samples, the differences between $<C>$ and surface C_a are significant (ratio =

1.05 ± 0.99, p = 0.022). The daily, high-resolution SeaWiFS C_a data were queried to

compare with the *in situ* data in the following manner. To reduce errors caused by

digitization and random noise, for each *in situ* data point, all valid satellite data from a 5

x 5 pixel box covering the *in situ* location (except those cloud and land adjacent pixels)

were used to compute the median value (Hu et al., 2001). A rigorous comparison

between satellite and *in situ* data should limit the time difference between the two

measurements to within $\pm$ 2 - 3 hours. Due to extended cloud coverage and the

occasional presence of sea ice, however, only a small number of HPLC data points were

obtained under such rigorous criteria, leading to statistically meaningless results.

Therefore, the time difference between satellite and *in situ* measurements was relaxed to

$\pm$ 3 days.

Estimating uncertainty in a satellite-derived parameter with log-normal

distribution is not trivial, as discussed in Campbell (submitted). Here, two estimates were

used to assess the differences between the *in situ* and satellite-derived data. First, the root

mean square (RMS) and the mean difference (bias) in percentage were defined as:

$$RMS = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(x_i)^2} \times 100$$

$$bias = \bar{x} = (\frac{1}{n}\sum_{i=1}^{n}x_i) \times 100 \qquad (3)$$

$$x = \frac{S-I}{I}$$

where S is satellite data, I is *in situ* data, and n is the number of data pairs. For a

normally distributed x, RMS should equal the standard deviation. Further, because the

natural distribution of C_a is lognormal (Campbell, 1995), error estimates were also made

on the logarithmically transformed (base 10) data:

$$log\_RMS = \sqrt{\frac{\sum[(\log(S)-\log(I)]^2}{n}}$$

$$log\_bias = \frac{\sum[\log(S)-\log(I)]}{n} \qquad (4)$$

These error estimates have been used in recent publications to describe the performance

of the ocean color algorithms (O'Reilly et al., 2000) and to validate SeaWiFS global and

regional estimates of C_a (Darecki and Stramski, 2004; Gregg and Casey, 2004; Zhang et

al., 2006). Note that these latter error estimates cannot be expressed as percentages

because they are logarithmically transformed (Campbell, submitted).
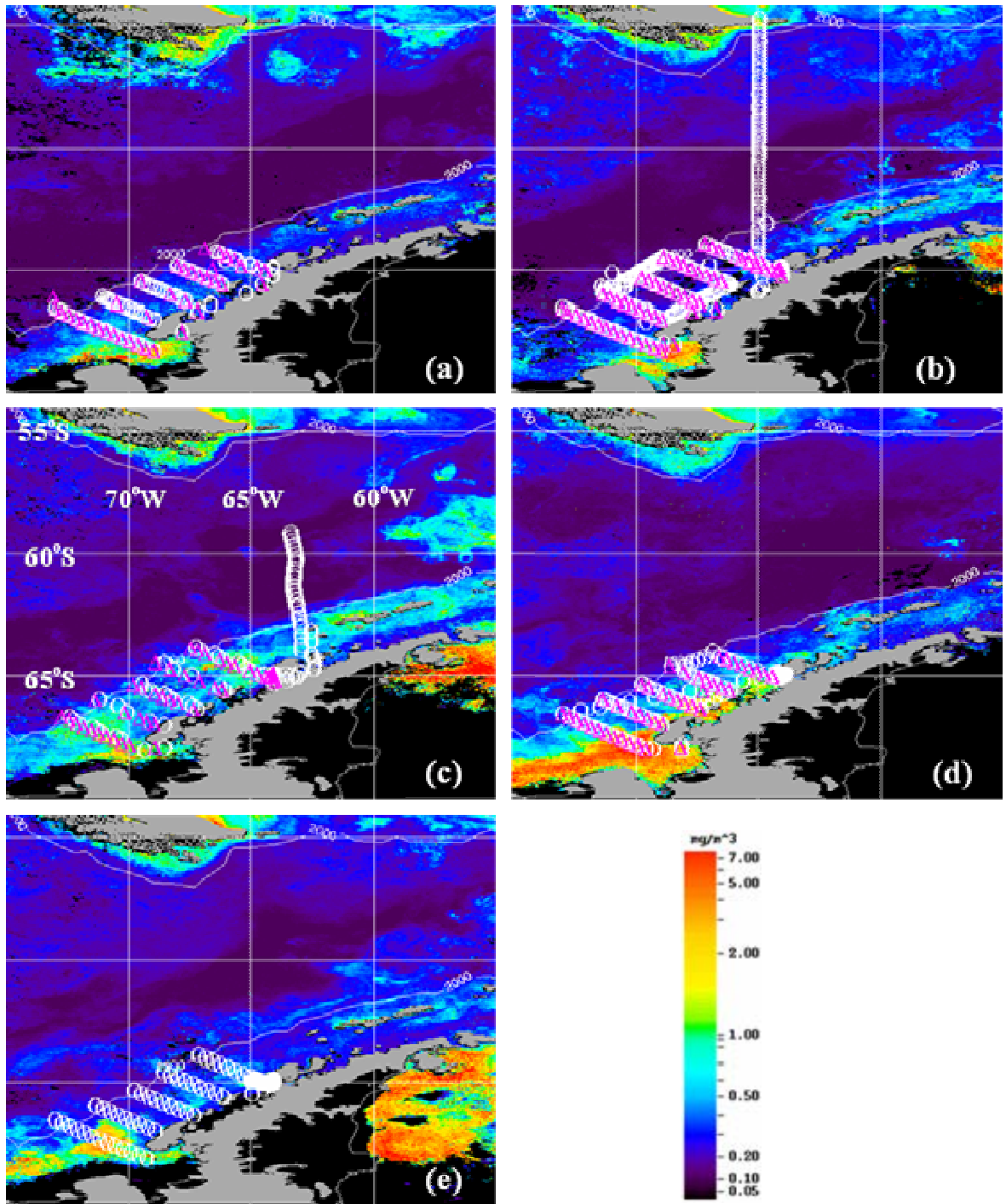
Figure 2.1. Sampling stations overlaid on SeaWiFS images of mean C_a for January (a)
1998, (b) 1999, (c) 2000, (d) 2001 and (e) 2002. White circles: fluorometric samples,
pink triangles: HPLC samples, white line: 2000 m isobath.

RESULTS

Typical C_a^{Fluor} and C_a^{HPLC} distributions during austral summer are presented for January-February 1999 (Fig. 2.2). In all years, C_a^{Fluor} ranged from 0.052 to 27.6 mg m^{-3}, with a median of 0.86 mg m^{-3}. C_a^{HPLC} was typically lower and ranged from 0.017 to 14.6 mg m^{-3} with a median of 1.04 mg m^{-3}. In general, the lowest C_a values (<0.1 mg m^{-3}) were consistently found offshelf in Drake Passage. Elevated C_a values (>1 mg m^{-3}) were detected throughout the continental shelf, with the highest values (>10 mg m^{-3}) always observed in Marguerite Bay.
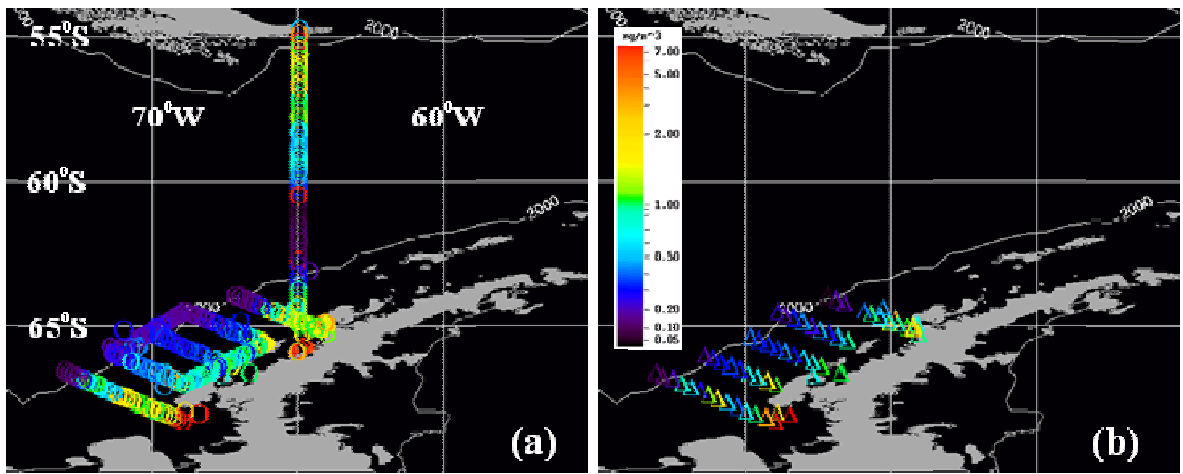
Figure 2.2. Distribution of *in situ* depth-weighted (a) C_a^{Fluor} and (b) C_a^{HPLC} during January-February 1999. White line: 2000 m isobath.

A total of 96 C_a^{SWF}-C_a^{HPLC} matching pairs and 307 C_a^{SWF}-C_a^{Fluor} matching pairs were obtained using the method described above. Table 2.1 lists the statistics of these comparisons. In general, C_a^{SWF} is significantly lower than C_a^{Fluor} (Fig. 2.3), with a ratio of 0.55 ± 0.63 between the two (Table 2.1). The inverse ratio, i.e., the ratio of C_a^{Fluor}/C_a^{SWF}, is 2.73 ± 2.19, consistent with previous observations in the Southern Ocean

where $C_a{}^{\text{Fluor}}$ was used to validate $C_a{}^{\text{SWF}}$ and the same pattern of underestimation was observed (Moore et al., 1999; Dierssen and Smith, 2000; Korb et al., 2004). In contrast, $C_a{}^{\text{HPLC}}$ showed a more satisfactory agreement with $C_a{}^{\text{SWF}}$ over a wide dynamic range (0.1 – 4 mg m^{-3}) (Fig. 2.3). The mean ratio of $C_a{}^{\text{SWF}}/C_a{}^{\text{HPLC}}$ is close to 1 (i.e. 1.12), in contrast to the lower ratio of 0.55 for $C_a{}^{\text{SWF}}/C_a{}^{\text{Fluor}}$.

Table 2.1. Statistics for the comparisons between $C_a{}^{\text{SWF}}$ and *in situ* C_a ($C_a{}^{\text{Fluor}}$, $C_a{}^{\text{HPLC}}$). *n* is the number of matching pairs, RMS is root mean square error, SD is standard deviation

Parameter	$C_a{}^{\text{SWF}}$ vs. $C_a{}^{\text{Fluor}}$	$C_a{}^{\text{SWF}}$ vs. $C_a{}^{\text{HPLC}}$
n	307	96
Ratio ± SD	0.55 ± 0.63	1.12 ± 0.91
RMS	77.2%	91.4%
Bias	-45.2%	12%
log_RMS	0.44	0.34
log_bias	-0.36	-0.07

Although the RMS errors for the two comparisons are comparable (Table 2.1), $C_a{}^{\text{HPLC}}$ is nearly equally scattered around the 1:1 line (Fig. 2.3), suggesting that the bias errors in $C_a{}^{\text{SWF}}/C_a{}^{\text{HPLC}}$ are significantly smaller than those in $C_a{}^{\text{SWF}}/C_a{}^{\text{Fluor}}$. Clearly, the agreement between $C_a{}^{\text{SWF}}$ and $C_a{}^{\text{HPLC}}$ is much improved over that between $C_a{}^{\text{SWF}}$ and $C_a{}^{\text{Fluor}}$.

Similar results were also obtained from the algorithm perspective. By using the spectral remote sensing reflectance data (R_{rs}) derived from satellite measurements (Fig. 2.4), the OC4v4 algorithm yielded comparable results to those obtained from HPLC measurements. In contrast, $C_a{}^{\text{Fluor}}$ values are significantly higher than those predicted by the OC4v4 algorithm for the entire range considered.

Are these results representative of the entire Southern Ocean? Due to cloud cover, satellite data were not available for all pixels every day. This reduced the number of C_a^{SWF} data points, which resulted in a limited number of matching pairs for comparing satellite and *in situ* data (307 for fluorometric and 96 for HPLC). However, the *in situ* data itself comprised a much larger dataset that included 832 concurrent fluorometric and HPLC measurements. When this *in situ* dataset was used to compare C_a^{Fluor} and C_a^{HPLC}, similar results were obtained, i.e., the mean ratio of C_a^{Fluor}/C_a^{HPLC} is 2.43 ± 3.37 (Fig. 2.5). The ratio of C_a^{Fluor}/C_a^{HPLC} appears to decrease with increasing concentrations (Table 2.2), although for C_a^{HPLC} <0.05 mg m^{-3} and C_a^{HPLC} >3.0 mg m^{-3} the statistical results may not be reliable because of the few matching pairs available and the scatter of the data (Fig. 2.5). For C_a^{HPLC} between 1.5 and 3.0 mg m^{-3}, the bias is small (15%) and the mean ratio of C_a^{Fluor}/C_a^{HPLC} is close to unity (1.15 ± 0.73). Between 0.05 and 1.5 mg m^{-3}, however, C_a^{Fluor} is much higher than Ca^{HPLC} (mean $C_a^{Fluor}/C_a^{HPLC} = 2.48 \pm 2.23$, n = 647). This difference is believed to be due to errors in the Ca^{Fluor} measurements as described above. Because most (> 90%) of the waters in the Southern Ocean have surface C_a^{SWF} values between 0.05 and 1.5 mg m^{-3} (Fig. 2.6), this assessment can be generalized and applied to most regions.
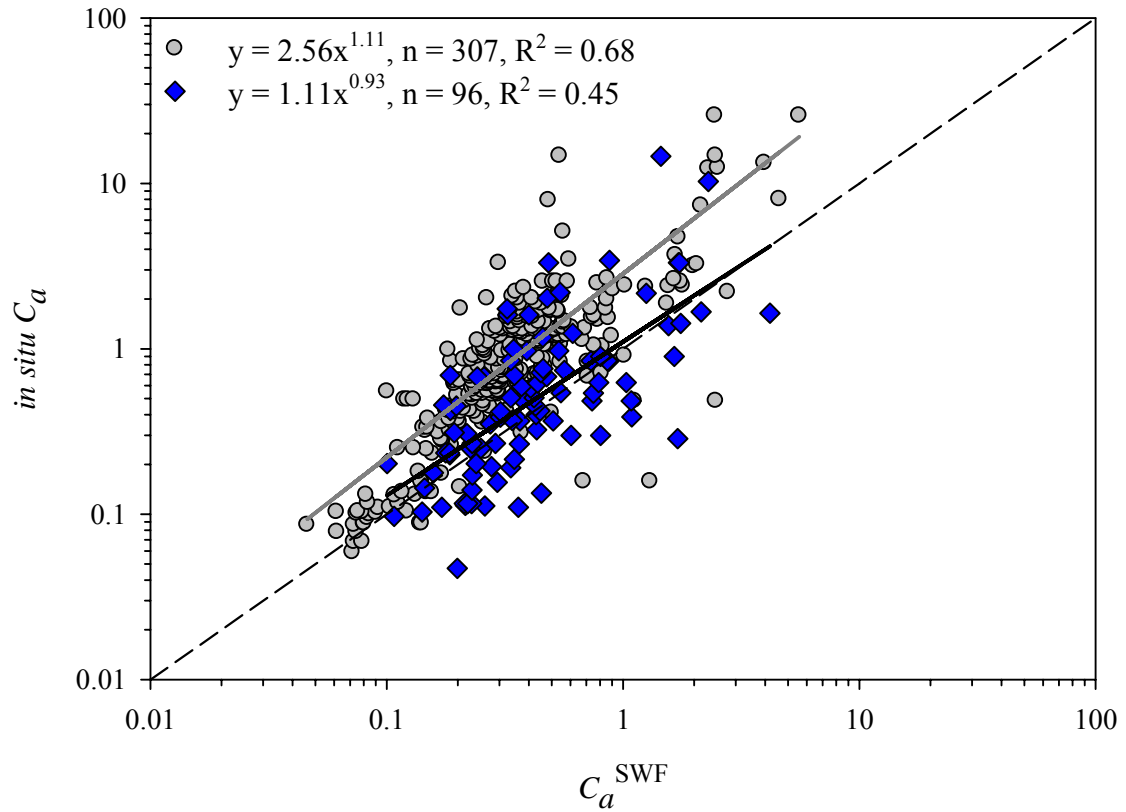
Figure 2.3. Comparison between C_a^{SWF} (mg m^{-3}, SeaDAS4.8, OC4v4 algorithm) and *in situ* C_a (mg m^{-3}). Grey circles and line: C_a^{Fluor}, blue diamonds and black solid line: C_a^{HPLC}. The dashed line shows the 1:1 relationship. The statistics of the comparisons are listed in Table 1.
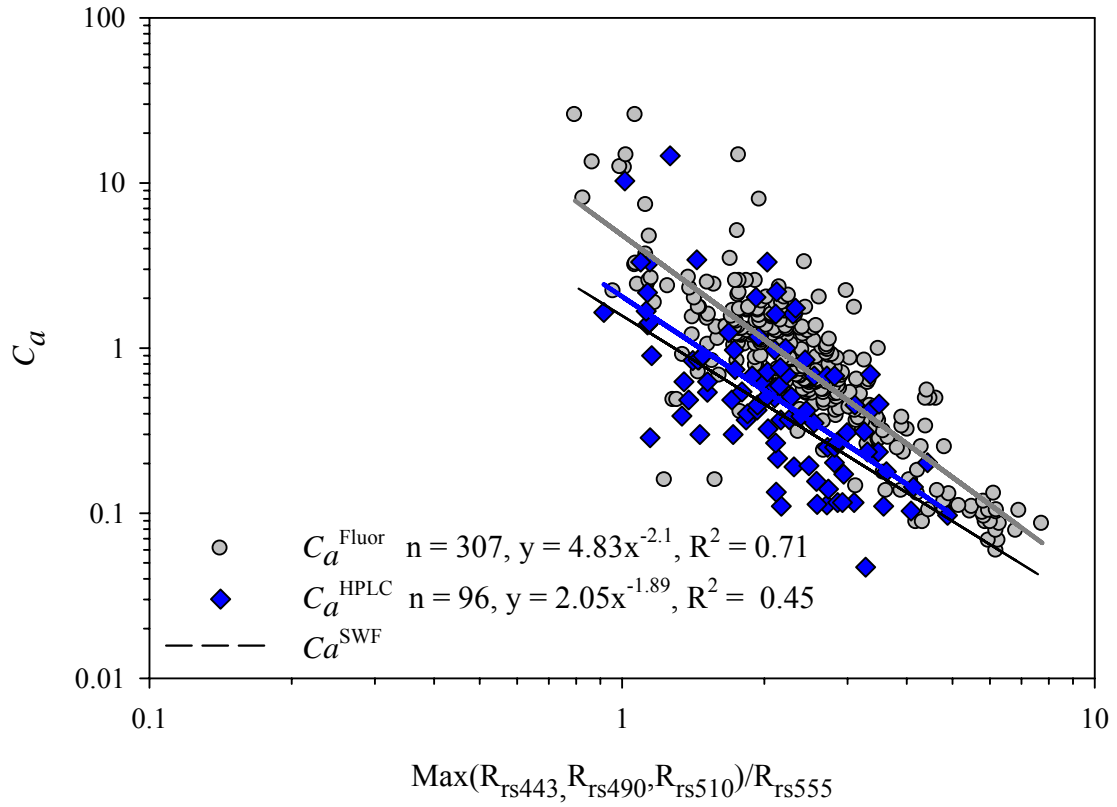
Figure 2.4. Comparison between C_a predicted by the OC4v4 algorithm (using SeaWiFS-derived R_{rs} as input) and measured *in situ* C_a (mg m^{-3}). Black broken line: OC4v4 prediction (C_a^{SWF}); grey circles and solid line: C_a^{Fluor}, blue diamonds and thick line: C_a^{HPLC}.

Table 2.2. Statistics for the comparisons between C_a^{Fluor} and C_a^{HPLC} (mg m^{-3}) for data shown in Figure 2.5. a_0 and a_1 are the power fitting coefficients in the form of $C_a^{Fluor} = a_0 \times (C_a^{HPLC})^{a1}$, R^2 is the corresponding coefficient of determination, *n* is the number of matching pairs, RMS is root mean square error, SD is standard deviation.

C_a^{HPLC} range	0.01 - 15	< 0.05	0.05 – 1.5	1.5 – 3.0	> 3.0
n	832	21	647	96	68
a_0, a_1	1.40, 0.66	0.28, 0.14	1.34, 0.63	1.01, 0.96	2.15, 0.55
R^2	0.67	0.01	0.49	0.11	0.14
$C_a^{Fluor}/C_a^{HPLC} \pm SD$	2.43 ± 3.37	10.06 ± 15.21	2.48 ± 2.23	1.15 ± 0.73	1.37 ± 1.04
RMS	366%	1739%	268%	74%	110%
bias	143%	905%	148%	15%	37%
log_RMS	0.40	0.87	0.40	0.23	0.34
log_bias	0.25	0.79	0.29	-0.01	0.02
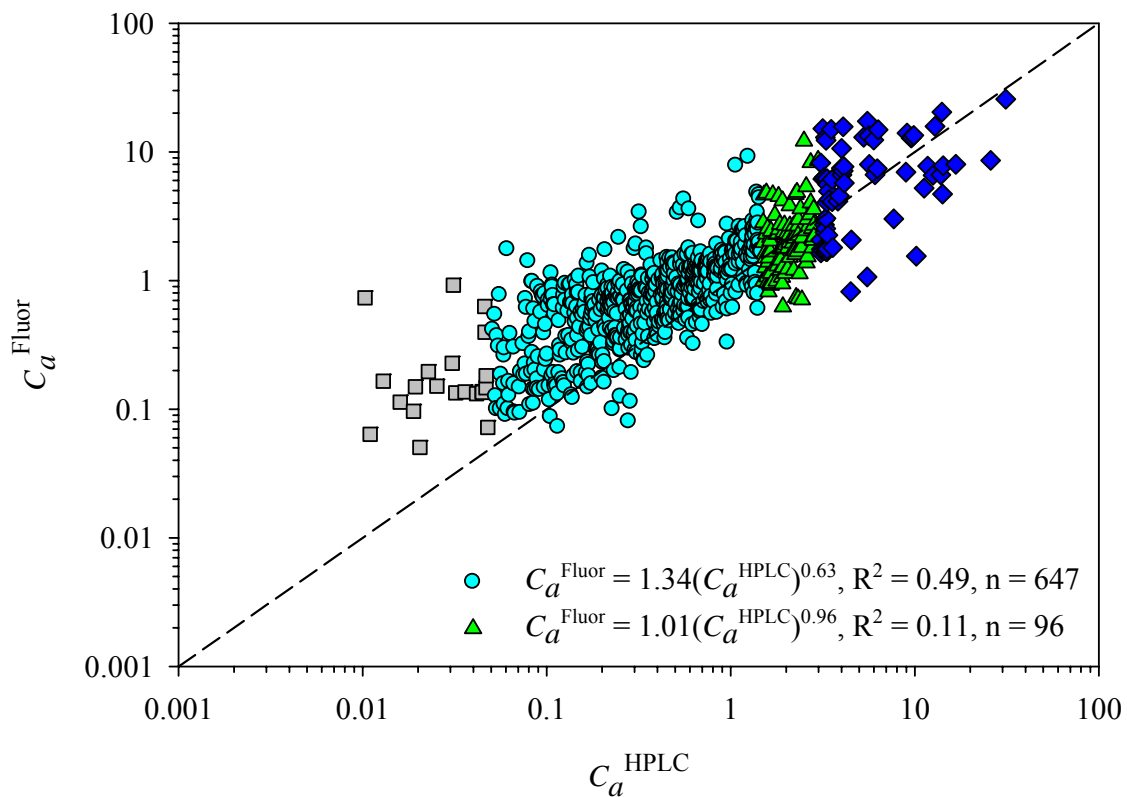
Figure 2.5. Comparison between C_a^{HPLC} and C_a^{Fluor} (mg m^{-3}) between January and February 1998 - 2001 (n = 832). Grey squares: C_a < 0.05 mg m^{-3}, cyan circles: C_a between 0.05 - 1.5 mg m^{-3}, green triangles: C_a between 1.5 - 3 mg m^{-3}, blue diamonds: C_a > 3 mg m^{-3}. The dashed line shows the 1:1 relationship. Statistics for the comparison are listed in Table 2.2.
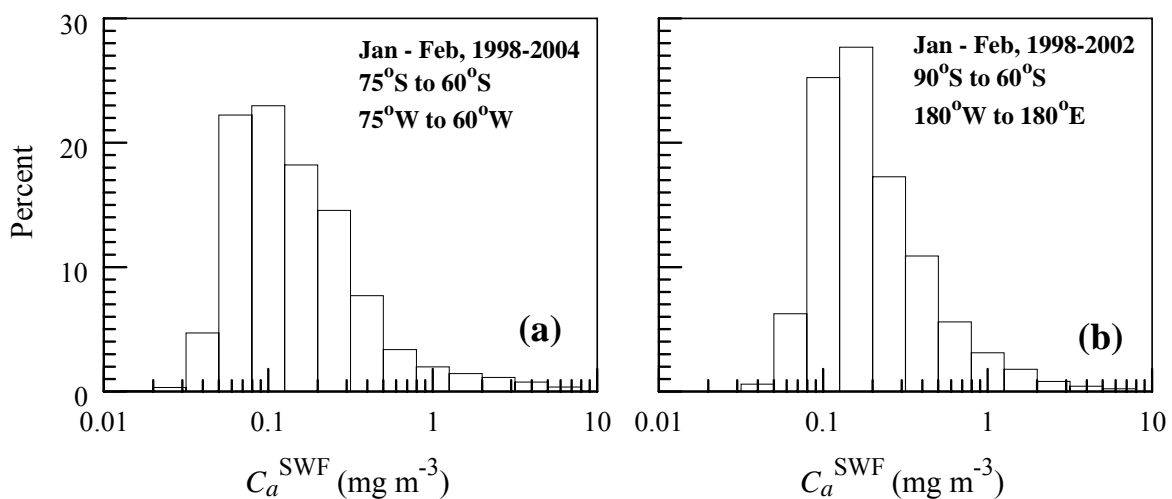
Figure 2.6. Normalized histogram of C_a^{SWF} distributions (mg m^{-3}) in the Southern Ocean during austral summer. (a) For the study region (Fig. 1.1) bound by $75 - 60^o$ S and $75 - 60^o$ W; (b) for the entire Southern Ocean (south of 60^oS). The y-axis shows the percentage surface area. 91% and 96% of the surface waters for (a) and (b), respectively, fall within the range of 0.05 to 1.5 mg m^{-3}.

DISCUSSION

Although HPLC has been recommended as the most reliable method to determine C_a (e.g. Trees et al., 1985), most cruise surveys still use the fluorometric method because it is faster, requires less technical expertise and is less expensive than HPLC. The C_a data originally used in the development of the OC4v4 algorithm (O'Reilly et al., 2000) included 2,853 *in situ* measurements from a variety of oceanic environments (but not the Southern Ocean), of which 72% were fluorometric and 28% were HPLC measurements. Therefore, the predicted C_a satellite measurements should naturally lean toward the fluorometric values. However, this was not observed in the present study, suggesting that the species composition and their associated pigment absorption characteristics in waters west of the Antarctic Peninsula region may be different from the "mean" composition and absorption on which the original algorithm was based.

26

The large difference observed between C_a^{Fluor} and C_a^{HPLC} from the same water

samples was likely due, in part, to interference of the fluorescence signal by chlorophyll

accessory pigments (C_b, C_c and their degradation products). In this study, C_b only

occurred in low concentrations compared to C_a (mean ratio $C_b/C_a = 0.023$, n = 486);

however, C_c was relatively high (mean ratio $C_c/C_a = 0.25$, n = 486) (Fig. 2.7). The

presence of significant amounts of C_c is known to cause an overestimation of C_a by the

fluorometric method (Gibbs, 1979; Lorenzen, 1981).

C_b is an accessory pigment in prochlorophytes, chlorophytes and prasinophytes,

while C_c is generally present in diatoms, dinoflagellates, cryptophytes and haptophytes

(Parsons et al., 1984). Diatoms are the dominant phytoplankton in waters west of the

Antarctic Peninsula, with dinoflagellates being very abundant at times (Prézelin et al,

2000, 2004). Prochlorophytes, a type of cyanobacteria first identified in the late 1980s

(Chisholm et al., 1988), have not yet been observed in the Southern Ocean, while

chlorophytes can be abundant (Prézelin et al, 2000, 2004). Similarly, cryptophytes are

usually scarce in the water column, but can be very abundant in coastal surface melt

water during spring and summer (Moline and Prézelin, 1996). Alloxanthin, the

biomarker pigment for cryptophytes (Prézelin et al, 2000), occurred in 91% (n = 516) of

the pigment samples. Hence, chlorophytes were probably the dominant source of C_b

during our study period, while the dominant sources of C_c appear to be diatoms,

dinoflagellates and cryptophytes, identified by the presence of fucoxanthin, peridinin, and

alloxanthin in 99.5%, 53% and 91% of the samples, respectively.

C_b and C_c vary widely throughout the world's ocean (Jeffrey, 1976; Lorenzen,

1981; Trees et al., 1985; Bidigare et al. 1986; Goericke and Repeta, 1993; Bianchi et al.,

1995). Overall, these studies found that C_b can cause an underestimation of C_a by the fluorometric method with ratios of C_b/C_a ranging from 0.15 to 0.51, while the presence of significant amount of C_c can lead to an overestimation of C_a. Typical ratios of C_c/C_a for assemblages dominated by phytoplankton containing chlorophyll c range from 0.15 to 0.44 (Bidigare et al., 1986; Bianchi et al., 1995; Lohrenz et a., 2003). Results reported here are consistent with these previous findings.

Can the presence of significant amount of C_c lead to overestimation of C_a when the latter is derived from remote sensing reflectance data? The inversion of remote sensing reflectance to C_a is an implicit (e.g., OC4v4) or explicit (e.g., Maritorena et al., 2002) function of phytoplankton pigment absorption. Lohrenz et al. (2003) reported that even if the amount of accessory pigments (sum of carotenoids and $C_b + C_c$) is equal to C_a, the perturbation to the pigment absorption is < 30%, suggesting a relatively small error in the satellite-retrieved C_a. Hence, the large differences between C_a^{SWF} and C_a^{Fluor} observed here cannot be explained by the additional absorption of accessory pigment, but can be explained by the interference of these accessory pigments to the fluorescence peak when C_a is determined using the fluorometric method.
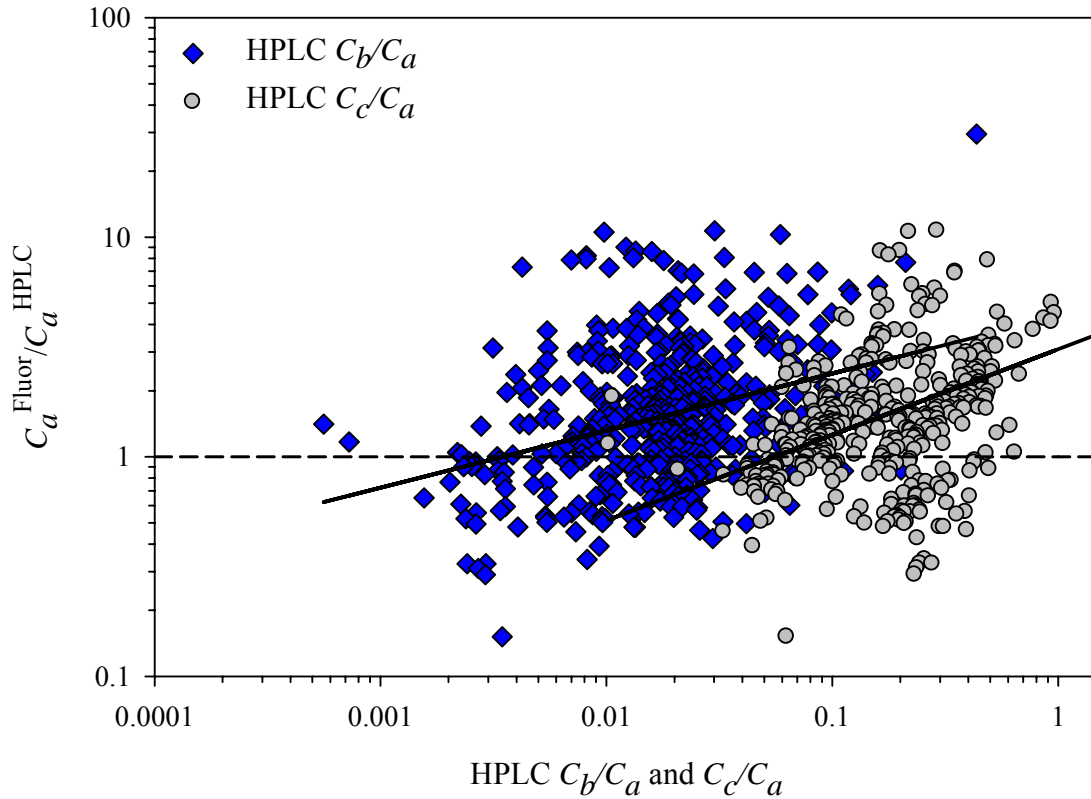
Figure 2.7. Relationship between HPLC C_b/C_a and C_a^{Fluor}/C_a^{HPLC} (y = 4.36 $x^{0.26}$, R^2 = 0.11, n = 482), and between HPLC C_c/C_a and C_a^{Fluor}/C_a^{HPLC} (y = 3.09 $x^{0.39}$, R^2 = 0.19, n = 482). Note that the slope for the latter (0.39) is significantly larger than for the former (0.26). Here C_b/C_a = 0.023 ± 0.034 (n = 482) and C_c/C_a = 0.25 ± 0.59 (n = 482).

In summary, contrary to previous reports that estimates of C_a^{SWF} in the Southern Ocean were significantly lower than those measured *in situ*, satellite estimates reported here agree with those determined from water samples for C_a between 0.05 and 1.5 mg m^{-3} for January-February between 1998 and 2001. This is primarily because the *in situ* C_a data were determined by HPLC (C_a^{HPLC}) rather than by fluorometric methods (C_a^{Fluor}), which are known to introduce significant errors in C_a estimates in the presence of certain accessory pigments.

CHAPTER THREE

SPATIAL AND TEMPORAL VARIABILITY OF SEAWIFS CHLOROPHYLL A

DISTRIBUTIONS WEST OF THE ANTARCTIC PENINSULA: IMPLICATIONS

FOR KRILL PRODUCTION

INTRODUCTION

Chlorophyll distributions in the Southern Ocean show high spatial and temporal variability. Most Antarctic open waters have relatively low chlorophyll concentrations despite the availability of nutrients and, thus, the Southern Ocean is generally considered to be a High-Nutrient Low-Chlorophyll region (Holm-Hansen et al., 1977). Nevertheless, large phytoplankton blooms do occur during spring and summer, particularly in waters associated with ice edges, polynyas, islands, and continental shelves (e.g., Smith and Nelson, 1985; Sullivan et al., 1993; Moore and Abbott, 2000; Arrigo and van Dijken, 2003). Some of the largest blooms develop in the marginal ice zone (MIZ), in waters associated with the seasonal advance and retreat of sea ice. As the ice edge recedes, low salinity meltwater produces a low density surface lens that reduces vertical mixing and shallows the mixed layer; consequently, phytoplankton are able to grow in a high irradiance stable environment. This phenomenon is common in the MIZ of the Weddell and Ross Seas, as well as in other regions around Antarctica (El-Sayed, 1971; El-Sayed and Taguchi, 1981; Smith and Nelson, 1985; Sedwick and DiTullio, 1997), with reported chlorophyll concentrations up to 190 mg m^{-3} (El-Sayed, 1971).

Polynyas are areas of open water surrounded by sea ice, usually characterized by elevated surface chlorophyll concentrations. Arrigo and van Dijken (2003) examined surface chlorophyll concentrations in 37 Antarctic polynyas and report values ranging from 0.24 to 7 mg chl m^{-3} during summer. Maximum chlorophyll concentrations occurred in the Amundsen and Ross Seas, in agreement with previous reports of up to 40 mg m^{-3} in the Ross Sea polynya (Arrigo and McClain, 1994). Antarctic islands can also be surrounded by chlorophyll-rich waters. For example, the region around South Georgia has been characterized as highly productive, with high densities of phytoplankton and zooplankton, as well as large colonies of seals and seabirds (Atkinson et al., 2001). Phytoplankton blooms in this area have been observed from November to April with chlorophyll concentrations reaching 30 mg m^{-3}. The high productivity at South Georgia has been attributed to a combination of factors including enhanced supply of iron and rapid recycling of nitrogen, favorable temperatures, and a shallow stable inshore water column (reviewed in Atkinson et al., 2001).

The continental shelf waters west of the Antarctic Peninsula (55 - 75 ºS, 50 - 80 ºW) (Fig. 3.1) in particular, are considered to be one of the most productive regions of the Southern Ocean, supporting high densities of phytoplankton, zooplankton, and upper trophic level predators (e.g., Fraser and Trivelpiece, 1996; Arrigo et al. 1998; Deibel and Daly, 2007). Chlorophyll concentrations in the northern sectors along the Antarctic Peninsula shelf have been reported to reach values up to 38 mg chl m^{-3} during December and January (Holm-Hansen and Mitchell, 1991; reviewed in Smith et al., 1996a; Rodriguez et al., 2002). More recently, Arrigo and van Dijken (2003) reported that SeaWiFS chlorophyll in a phytoplankton bloom related to the Marguerite Bay polynya

averaged 2.30 mg chl m^{-3}, while Garibotti et al. (2003) and Meyer et al. (2003) observed summer chlorophyll concentrations up to 17.86 mg m^{-3} in 1997 and 25 mg m^{-3} in 2000, respectively, within Marguerite Bay. These findings suggest that the southern sector of the Antarctic Peninsula also may support large phytoplankton blooms.

Studies of the spatial and temporal dynamics of phytoplankton along the northern part of the Peninsula reveal a pattern of chlorophyll accumulation in coastal areas over the summer, with lower concentrations offshore (Smith et al., 1998a; Garibotti et al., 2003). These studies also identify an alongshore gradient with higher biomass in the northern sectors of the Antarctic Peninsula earlier in the productive season, which later progresses to the southeast as the sea ice retreats in the same direction. Most studies to date, however, have only dealt with chlorophyll distributions north of Marguerite Bay and, thus, information on phytoplankton dynamics in the vicinity of Marguerite Bay and to the south in the Bellingshausen Sea is scarce.

The Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) program investigated the physical and biological factors that influence the growth, recruitment, and overwintering survival of Antarctic krill, *Euphausia superba,* in the vicinity of Marguerite Bay (Fig. 3.1), west of the Antarctic Peninsula, during austral fall and winter of 2001 and 2002. Krill play a key role in the Antarctic ecosystem as one of the primary pelagic herbivores and prey for many predators. The large krill population west of the Antarctic Peninsula appears to be maintained by occasional strong year classes, with often poor recruitment in the intervening years (Siegel and Loeb, 1995; Hewitt et al., 2003; Quetin and Ross, 2003). The suite of physical and biological factors that govern krill reproduction and recruitment, however, remain poorly known.

During the GLOBEC study, large differences in abundances of larval and juvenile krill were observed between the two years (Daly, 2004). During fall 2001, larvae were very abundant ($< 0.01 - 132$ ind m^{-3}), with younger stages dominant offshelf and older stages dominant onshelf (Fig. 3.2, see Fig. 3.1 for station locations). Offshore larval densities (up to 132 ind m^{-3}) are amongst the highest reported for the area and are comparable to those reported by Rakusa-Suszczewski (1984) for 1981. Few juveniles were observed anywhere in 2001. During fall 2002, relatively high concentrations of young larvae were again detected in oceanic waters ($< 0.01 - 211$ ind m^{-3}), although average abundances were significantly lower than in 2001 and all larval stages were scarce in coastal areas (Fig. 3.2). In contrast, juveniles were relatively abundant on the middle and inner shelf in the vicinity of Marguerite Bay ($< 0.01 - 2.37$ ind. m^{-3}), indicating a successful recruitment from the 2001 larval population. These results led me to investigate the environmental conditions that contributed to the large krill reproduction during austral spring and summer 2000/2001, and subsequent high larval densities.

Herein, I investigate chlorophyll dynamics west of the Antarctic Peninsula using SeaWiFS ocean color data between 1997 and 2004, with special emphasis on the Marguerite Bay region, to better understand the conditions that make it a suitable habitat for krill. I also examine the effects of the retreat of the ice edge on the timing and location of phytoplankton blooms west of the Antarctic Peninsula. Finally, I discuss the environmental mechanisms that potentially support successful krill reproduction and recruitment in this area.

METHODS

The study area consisted of the coastal waters west of the Antarctic Peninsula, adjacent deep waters in the Drake Passage, and coastal and oceanic waters of the Bellingshausen Sea (55 - 75 °S and 50 - 80 °W), as chlorophyll concentrations in these areas are most likely to influence regional krill populations (Fig. 3.1).

Krill were collected aboard the R.V. *Lawrence M. Gould* during austral autumn between 23 April and 6 June 2001 and between 7 April and 20 May 2002 as part of the US SO GLOBEC program. A total of 18 and 16 net tows were done at several stations during 2001 and 2002 respectively. Individuals were collected at eight discrete depth intervals using a 1-m^2 MOCNESS (Multiple Opening-Closing Net and Environmental Sensing System) net system, with a 333 μm mesh. Krill were identified for stages of larvae (calyptopis I - III, furcilia I - VI), juveniles, or adults (males or females) after Makarov (1980) and measured for total length (from the base of the eye to the tip of the telson, excluding setae). Herein, the distribution of krill stage abundances are compared at two representative stations; one offshelf (Sta. 1) and one onshelf (Sta. 5) (Fig. 3.2). Abundances are the mean of four onshelf and two offshelf net tows in 2001, and three onshelf and two offshelf net tows in 2002. Stage abundances (A, ind m^{-3}) were calculated as a weighted mean for the sampling depth using:

$$A = \frac{(\sum_{i=1}^{8} x_i * z_i)}{\sum_{i=1}^{8} z_i}$$

where i represents each of the eight nets (collections from different depth strata) in each

34

cast, x is the abundance of each krill stage in each net (ind m^{-3}), and z is the depth interval of each stratum (m).

A recruitment index (R_1) for *E. superba* was calculated as the proportion of one year-old krill compared to age-class one plus all older age classes from all net samples for fall 2001 and 2002. Age-class one was defined as juvenile krill with total length ranging from 20 - 30 mm following Siegel et al. (1998). The total abundance (ind m^{-3}) of juveniles 20 - 30 mm and of juveniles 20 - 30 mm plus all older stages was estimated for each net and summed over the entire cruise to estimate a recruitment index for each cruise. Offshelf net tows (Sta. 1), which did not contain any juvenile or adult krill, were excluded from the recruitment calculation. All except one of the onshelf stations were located in inner coastal waters; therefore, recruitment estimates were not biased as a result of migration of large krill to the inner shelf in late summer and fall (Siegel et al., 2003; Hewitt et al., 2003).

The chlorophyll dataset includes 6606 SeaWiFS daily Level 2 files (~ 1 km/pixel near nadir) between September 1997 and December 2004 obtained from NASA Goddard Space Flight Center. These data were collected by ground stations, as well as occasional satellite onboard recording over the area using the most recent algorithms and software package (SeaDAS4.8). The level 2 data were mapped to a rectangular projection with approximately 1 km^2/pixel for the western Antarctic Peninsula region (Fig. 3.1). The parameter used in this study is the surface chlorophyll concentration derived from the OC4v4 empirical band-ratio (blue versus green) algorithm (O'Reilly et al., 2000). SeaWiFS chlorophyll estimates are biased toward surface values as the sensor only "sees" the first few meters of the water column. Nevertheless, SeaWiFS chlorophyll provides a

35

good assessment of water column concentrations in the Southern Ocean, as maximum

chlorophyll concentrations are near surface and surface chlorophyll is well correlated with

depth integrated chlorophyll (Holm-Hansen and Mitchell, 1991; Holm-Hansen et al.,

2004a; Korb et al., 2004).

The accuracy of the SeaWiFS algorithm in the Southern Ocean is being debated.

Several studies using *in situ* chlorophyll fluorescence determined that the SeaWiFS

algorithm underestimates chlorophyll *a* concentrations in the Southern Ocean (e.g.,

Dierssen and Smith, 2000; Korb et al., 2004). However, recent results from more accurate

in situ HPLC (High Performance Liquid Chromatography) values demonstrated that

SeaWiFS chlorophyll *a* estimates are accurate (bias = 12%) for chlorophyll concentrations

between 0.1 and ~ 4 mg m^{-3}, which include > 90% of the waters in the Southern Ocean

(Chapter 2; Marrari et al., 2006). The mean ratio between SeaWiFS chlorophyll and *in*

situ HPLC chlorophyll was close to unity (i.e., 1.12) (n = 96), indicating good agreement

between the two sets of data. Although these previous results could not verify the

SeaWiFS algorithm for chlorophyll concentrations greater than ~ 4 mg m^{-3}, here I use the

algorithm to estimate a larger range of chlorophyll concentrations in order to investigate

relative changes in chlorophyll spatial and temporal dynamics. In addition, because

colored dissolved organic matter (CDOM) may introduce significant errors to the

estimation of surface chlorophyll *a* from ocean color remote sensing data (e.g., Carder et

al., 1989), I measured CDOM absorption from 10 surface water samples collected in the

study area between April 4 and May 10, 2002. Absorbance spectra were obtained at 1 nm

intervals from 200 to 750 nm with a Hitachi U-3300 double-beam spectrophotometer with

10-cm quartz cells. MilliQ water was used in the reference cell. Three scans were run for
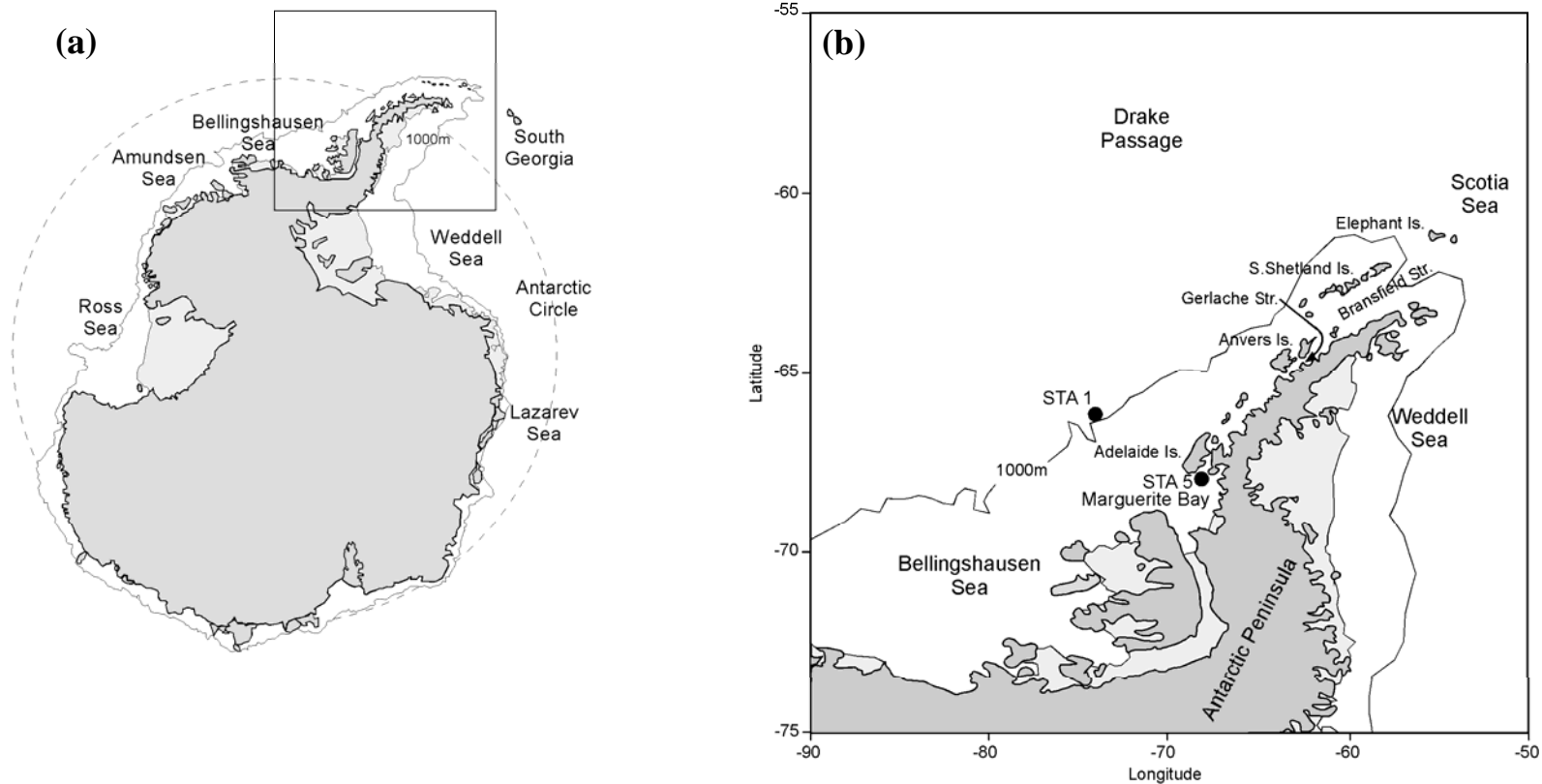
Figure 3.1. (a) Map of the Antarctic continent showing the location of the study area and other geographic references. The solid line represents the 1000 m isobath and the dashed line indicates the Antarctic Circle (66.3ºS). (b) Details of the Antarctic Peninsula region and location of the US Southern Ocean GLOBEC offshelf (Sta. 1) and onshelf (Sta. 5) net sampling stations (●) represented in Fig. 2.

each sample and the resulting spectra were averaged to reduce noise. Data were corrected for scattering by subtracting absorbance at 700 nm from all measurements. Absorbance values were converted to absorption coefficients (Kirk, 1983). The absorption coefficient at 375 nm, $a_{(375)}$, was used as an index of CDOM concentration. Because $a_{(375)}$ was low in all samples (0.02 - 0.148 m^{-1}), I conclude that the accuracy of the SeaWiFS chlorophyll estimates is not affected by the presence of significant levels of CDOM.

The Southern Ocean daily satellite images normally have missing data due to a relatively high percentage of cloud cover; therefore, at least weekly composites of data typically are needed to obtain good spatial coverage (e.g., Holm-Hansen et al., 2004a). In this study, biweekly composites of SeaWiFS chlorophyll data are used. A seven-year climatology of biweekly chlorophyll *a* concentrations (mean chlorophyll concentration at each pixel) was generated from the mapped Level 2 data from September 1997 through December 2004 and biweekly composite images were produced. When calculating the mean value in either the climatology or the biweekly data, only valid data were used. Suspicious data identified by various quality flags associated with each pixel (for example cloud contamination, large solar/view angle, etc.) were excluded from the calculations.

The study area was divided into fourteen subregions, each representing different oceanographic conditions in order to (1) investigate the initiation and progression of phytoplankton blooms, and (2) analyze the relative differences in chlorophyll concentrations between regions along the coastal Antarctic Peninsula and offshore areas. Regions 1 - 6 represent offshelf oceanic regimes with depths greater than 2000 m, while regions 7 and 8 are located over the continental shelf slope, defined as the area between 500 and 2000 m. Regions 9, 10 and 11 represent coastal waters along the Antarctic

Peninsula shelf and regions 13 and 14 are located in Marguerite Bay. Region 12 includes both coastal and oceanic waters in the Scotia-Weddell confluence area. The biweekly geometric mean chlorophyll concentrations between September - March 1997 to 2004 were calculated for each region and the results plotted over time in relation to the climatology. Although values up to 55 mg m^{-3} were estimated from SeaWiFS for Marguerite Bay during summer, concentrations lower than 0.01 mg m^{-3} and greater than 20 mg m^{-3} were excluded from the geometric mean calculations, since the accuracy of these values could not be verified with concurrent *in situ* data. However, as most of the SeaWiFS chlorophyll concentrations during the study period were within the 0.01 - 20 mg m^{-3} range, the geometric mean calculations were not significantly affected by excluding the few extreme values. Gaps in the time series occurred when the available data points were < 10% of the total number of pixels within each region during the biweekly period of maximum spatial coverage.

The mean location of the ice edge within the study area during October, November, and December of 2000 and 2001 was determined using a two-dimensional linear interpolation of monthly ice concentration on a 25 km resolution grid. Monthly averaged gridded ice concentrations generated using the NASA Team algorithm and Nimbus-7 SMMR and DMSP SSM/I passive microwave data were obtained from the National Snow and Ice Data Center (Cavalieri et al., 2005). The ice edge was considered to be the location where sea ice concentration was ≤ 15% (Gloersen et al., 1992). The mean location of the ice edge during these months was superimposed over the concurrent biweekly SeaWiFS chlorophyll images. In addition, the mean location of the ice edge during the preceding month also was plotted in order to evaluate changes in chlorophyll

concentrations within the region of ice edge retreat. To examine whether there was a relationship between the retreat of the ice edge and the formation of phytoplankton blooms, chlorophyll concentrations along the location of the ice edge in September, October, and November 2000 and 2001 were extracted from the satellite data. The chlorophyll values at the same locations were extracted for the subsequent 6-biweekly periods (three months). Thus, at the September location of the ice edge, chlorophyll concentrations were analyzed during September - November and at the November ice edge location, chlorophyll was analyzed during December - January. The median chlorophyll concentration for each biweekly period was estimated and plotted over time to generate a time series of chlorophyll concentrations at the ice edge location.

The daily area free of sea ice (km^2) in the northern and southern sections of Marguerite Bay was estimated from satellite data following the methods described in Arrigo and van Dijken (2003). A daily climatology from 1997 through 2004 was calculated as the mean daily ice-free area within each subregion. A running average was applied to reduce the daily variability (bandwidth = 9.1 days). The time series of daily ice-free area from 1997 to 2004 were plotted in relation to the 8-year climatology with special emphasis on 2001 and 2002.
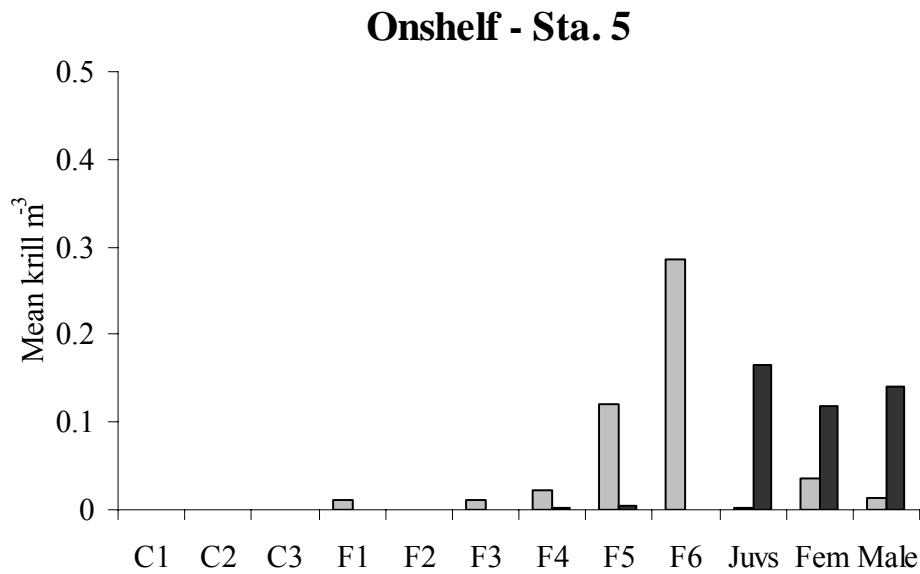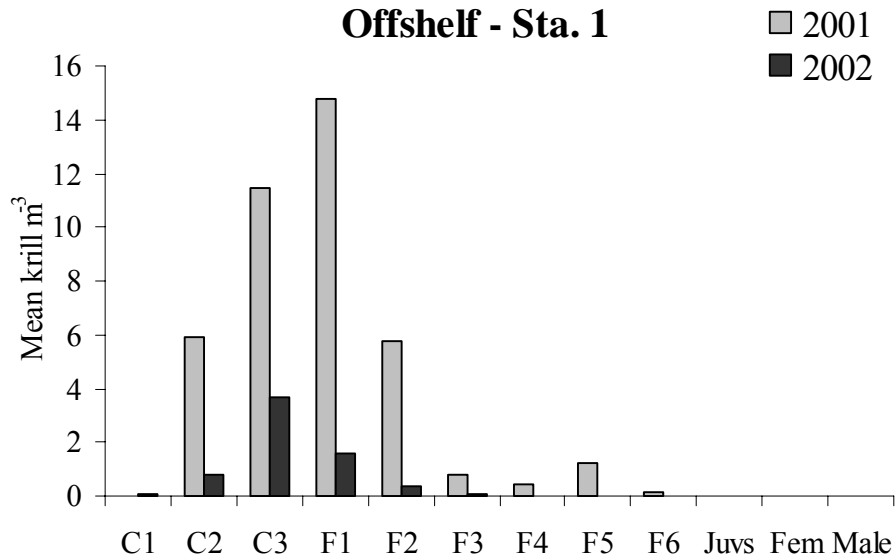
Figure 3.2. Mean abundance (ind m^{-3}) of development stages of *Euphausia superba* in offshelf waters (Sta. 1) west of the Antarctic Peninsula and coastal waters (Sta. 5) of Marguerite Bay during fall 2001 (light grey) and 2002 (dark grey). CI - CIII = calyptopis 1 - 3; FI - FVI = furcilia 1 - 6; juvs = juveniles ; males = adult males; females = adult females.

41

RESULTS

Biweekly climatological patterns of chlorophyll *a* indicate that oceanic and coastal areas in the Bellingshausen Sea and coastal Marguerite Bay had persistently high chlorophyll concentrations (0.1 - > 7 mg m^{-3}) during spring and summer in comparison with any other area west of the Antarctic Peninsula between September and March 1997 - 2004 (Fig. 3.3). Oceanic waters offshore of the northern Antarctic Peninsula typically had relatively low concentrations (0.1 - 0.2 mg m^{-3}). Intermediate values (0.1 - ~ 2 mg m^{-3}) were generally observed over the more northern continental shelf regions west of the Antarctic Peninsula and downstream in the Scotia Sea, although small, short-lived blooms with chlorophyll values greater than 2 mg m^{-3} occurred nearshore in this region.

The spatial and temporal changes in chlorophyll patterns suggest that biomass accumulations initially occurred during October and November in offshelf waters, mainly in the Bellingshausen Sea and to a lesser extent near the shelf break in the vicinity of the Shetland Islands at the northern end of the Antarctic Peninsula (Fig. 3.3). As the season progressed (mid-December), phytoplankton blooms developed onshore, especially in the vicinity of Marguerite Bay and the coastal Bellingshausen Sea, where they remained well established until early April. In contrast, there didn't appear to be a significant seasonal increase in chlorophyll in northern Peninsula waters, except near some of the islands such as the South Shetlands and a few short-lived blooms nearshore.

A cross-shelf gradient in chlorophyll concentrations (higher values in coastal areas to lower values at the shelf break) was observed for Marguerite Bay and to the south during summer (January - March). Between Anvers and Adelaide islands, there was a similar cross-shelf gradient in January, but by late February maximum chlorophyll

42

concentrations had shifted to mid-shelf and outer shelf areas near Anvers Island. At the northern end of the Peninsula, there was no apparent cross-shelf gradient. Instead, maximum chlorophyll values occurred in the vicinity of the Shetland Islands and Elephant Island near the outer shelf.

The geometric mean chlorophyll concentrations for the 14 subregions defined in the study area (Fig. 3.4a) illustrate the interannual (1997 - 2004) variability in patterns of chlorophyll distribution west of the Antarctic Peninsula. Variations from the climatology were relatively small (maximum $\pm$ 0.4 mg m^{-3}) in offshelf regions of the Antarctic Circumpolar Current (ACC), Drake Passage, and the Scotia Sea (regions 1 - 6), with the Bellingshausen and Scotia Sea regions having higher variability than the Drake Passage regions (Fig. 3.4b). Regions 1 - 2 and 4 - 5 had a small chlorophyll peak in early November (year day 315), whereas the Scotia Sea generally sustained higher levels of chlorophyll for longer periods (until early April). Variability in waters at the tip of the Peninsula (region 12) was influenced by the large chlorophyll concentrations to the east of the Antarctic Peninsula in the Weddell Sea. Shelf slope waters (regions 7 and 8) had similar interannual ranges in chlorophyll, although the years with chlorophyll concentrations greater than climatology were not necessarily the same. For waters over the continental shelf (regions 9 - 11), the southern Bellingshausen and Marguerite Bay shelf region had the highest chlorophyll concentrations and variability, with declining values to the northeast.
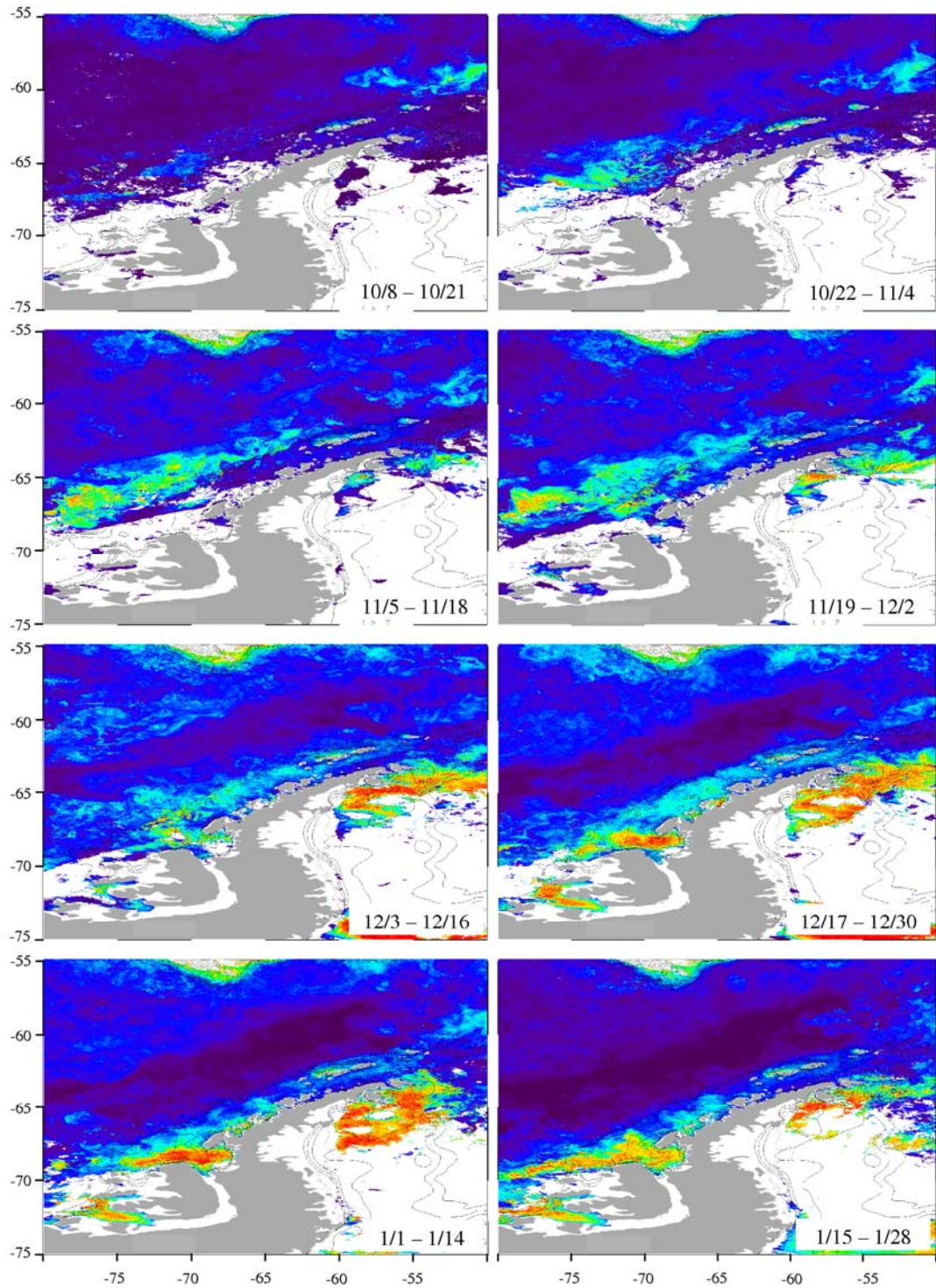
Figure 3.3. Biweekly climatology (1997 - 2004) of SeaWiFS chlorophyll concentrations (mg m^{-3}) between October and March. The date range included in each image is indicated on the lower right hand corner. White areas indicate no data due to the presence of clouds and/or sea ice. The white thin line represents the 1000 m isobath.
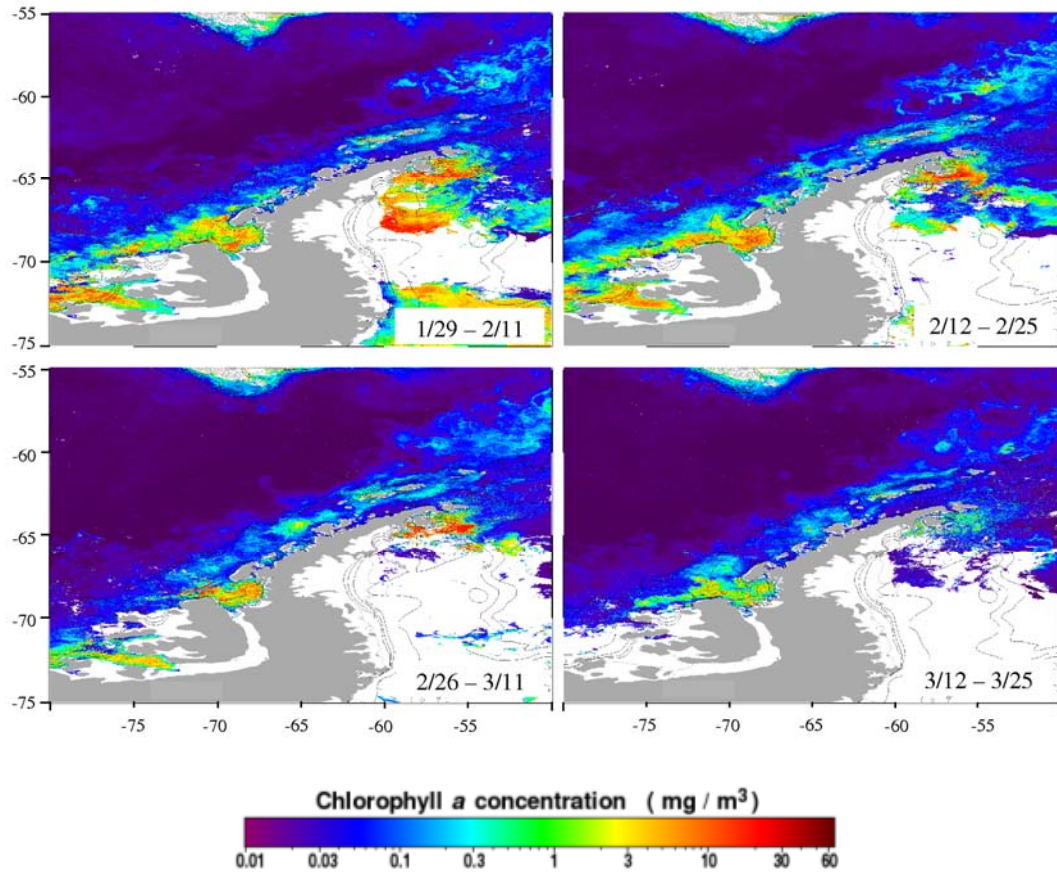
Figure 3.3. (Continued)

The highest chlorophyll concentrations at the northern tip of the Peninsula (regions 3, 6, and 12) occurred during 1999/2000. Elsewhere, 2000/2001 had substantially higher chlorophyll concentrations during summer (December - February) compared with most of the other years analyzed, particularly in the Bellingshausen Sea (regions 1, 4, 7 and 9) and Marguerite Bay (regions 13 and 14). In waters over the continental shelf of the Bellingshausen Sea (regions 7 and 9), chlorophyll was generally elevated during the spring and summer seasons of both 2000/2001 and 2001/2002, with high variability observed both between and within years. During 2001/2002, however, these chlorophyll peaks did not occur for as extended a period of time as in 2000/2001. Shelf break and

45

coastal regions along the Antarctic Peninsula (regions 8, 10 and 11) had elevated mean chlorophyll concentrations relative to offshore areas, although the variations (up to 0.41 mg m^{-3}) with respect to the climatology were less evident than in the Bellingshausen Sea (region 9, up to 0.97 mg m^{-3}) or Marguerite Bay (up to 3.72 mg m^{-3}), and mean values never exceeded 0.72 mg m^{-3} (note the different y-axis scales between plots). Marguerite Bay had the highest chlorophyll concentrations in comparison with any other region analyzed. In northern Marguerite Bay, average values during January for all years were 1.24 - 1.31 mg m^{-3}. However, during January 2001, mean chlorophyll reached 4.95 mg m^{-3}, whereas 2002 values were consistently near or below the 7-year average. In southern Marguerite Bay, 2000/2001 showed high mean values of up to 2.76 mg chl m^{-3} from late December through February, a factor of 2.5 higher than average (1.09 mg chl m^{-3}) conditions. The presence of sea ice prevented satellite chlorophyll data collection during most of the 2001/2002 summer.

The location, timing, and extent of sea ice during 2000/2001 and 2001/2002 were examined in relation to chlorophyll concentrations to better understand the relationship between sea ice and phytoplankton blooms (Fig. 3.5). Chlorophyll concentrations were highly variable in relation to the receding ice edge in our study area. During September 2000 and 2001, the ice edge was located in oceanic waters of the ACC. By October, the ice margin had retreated considerably and occurred closer to the coast at its eastern extent, but chlorophyll had not increased significantly at the September ice edge locations (Fig. 3.5a and 3.5b, top 2 panels). This suggests that October was too early in the productive season for any significant chlorophyll accumulations to occur within the ice edge zone. In November, the ice edge had receded onshelf in the mid-Antarctic Peninsula, but in the

46

Bellingshausen Sea the ice edge remained offshore in 2000 and approximately at the shelf

break in 2001. Chlorophyll concentrations increased significantly in this region, reaching

~ 5 mg m^{-3} (Fig. 3.5a and 3.5b, center panels). Although ice edge blooms appear to have

occurred in some parts of the Bellingshausen Sea during November and December, most

of this region of enhanced chlorophyll was presumably too far from the ice edge to have

been influenced by ice melt processes.
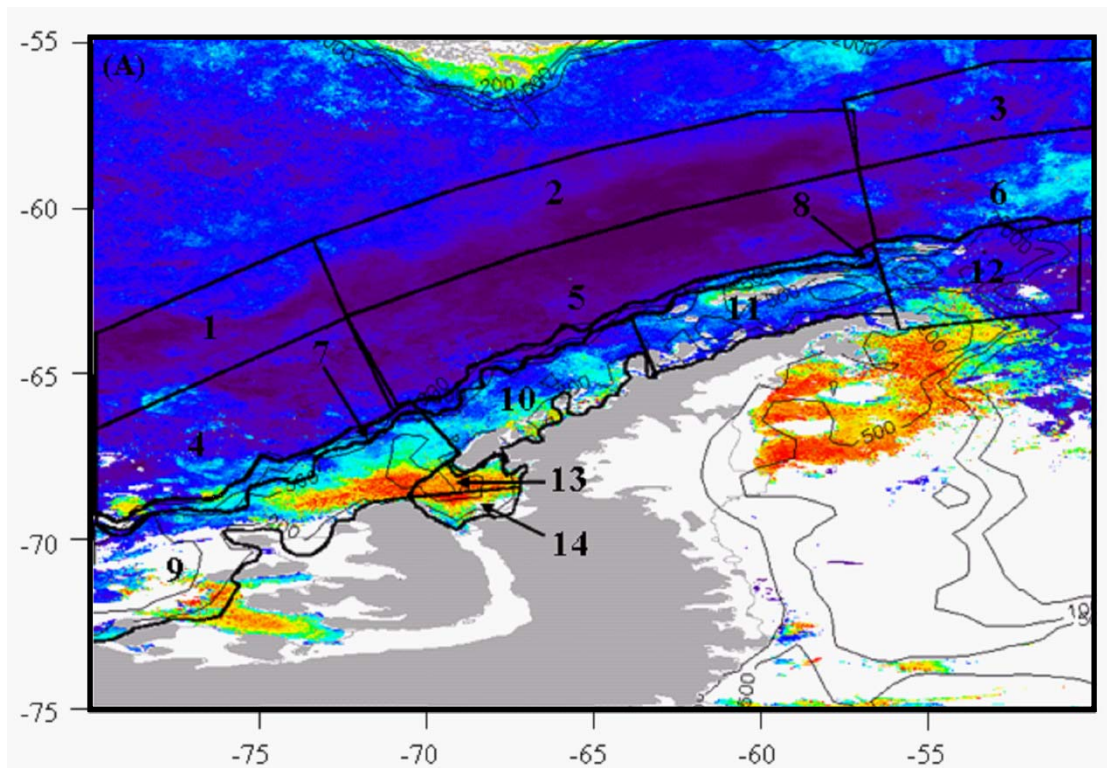
Figure 3.4a. Location of the 14 subregions along the western Antarctic Peninsula
superimposed over the climatology (1998 - 2004) of SeaWiFS chlorophyll concentrations
(mg m^{-3}) for January 1 - 14.
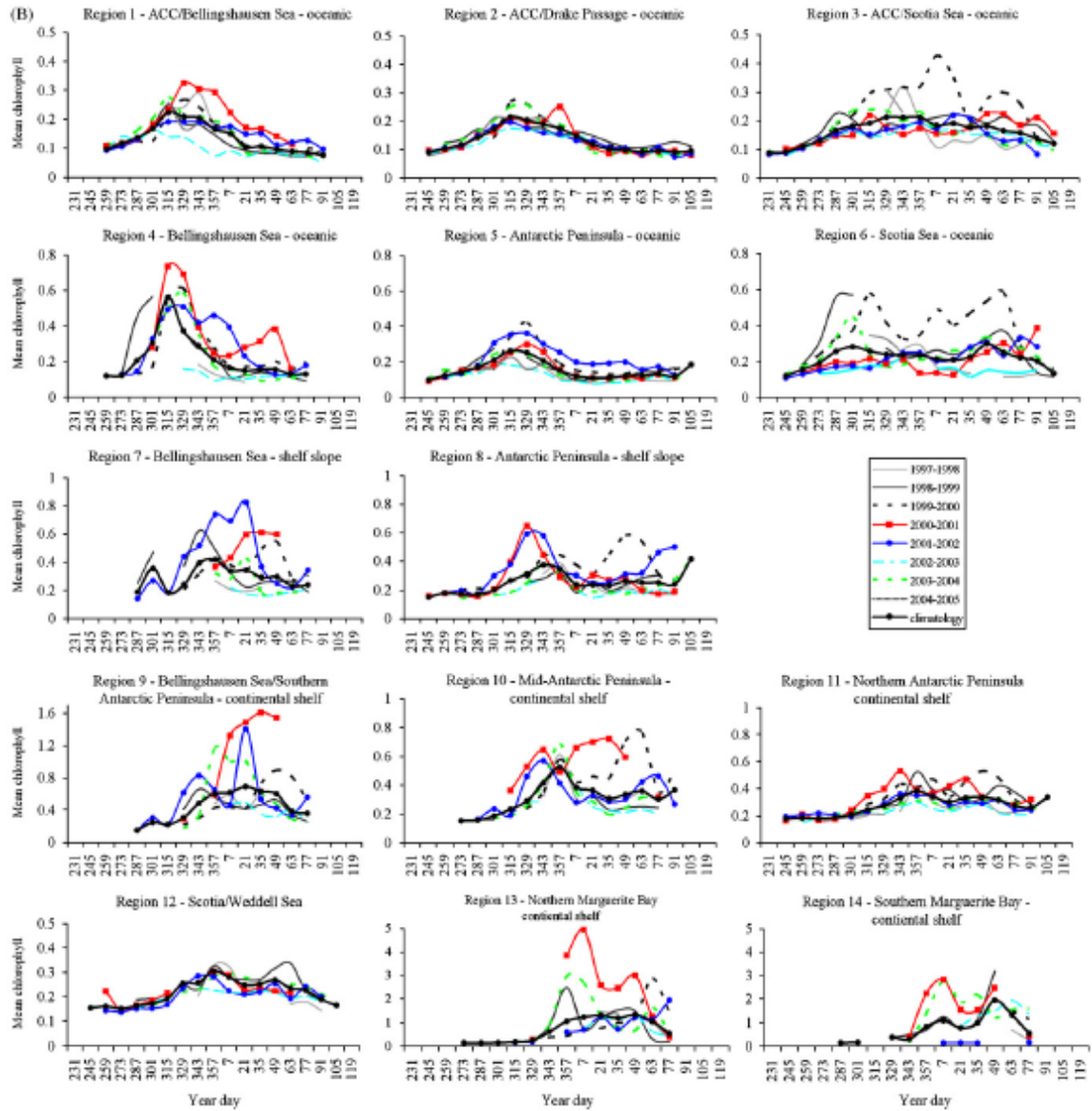
Figure 3.4b. Time series of geometric mean chlorophyll concentrations in each subregion for each biweekly period during 1997 - 2004. The 7-year climatology is also included for each region (thick black line with circles). Note the difference in scale of the y-axis for the different regions. The 2000/2001 (red squares), 2001/2002 (blue circles), 2002/2003 (cyan broken line), and 2003/2004 (green dotted line) spring-summer seasons are highlighted in color.

48
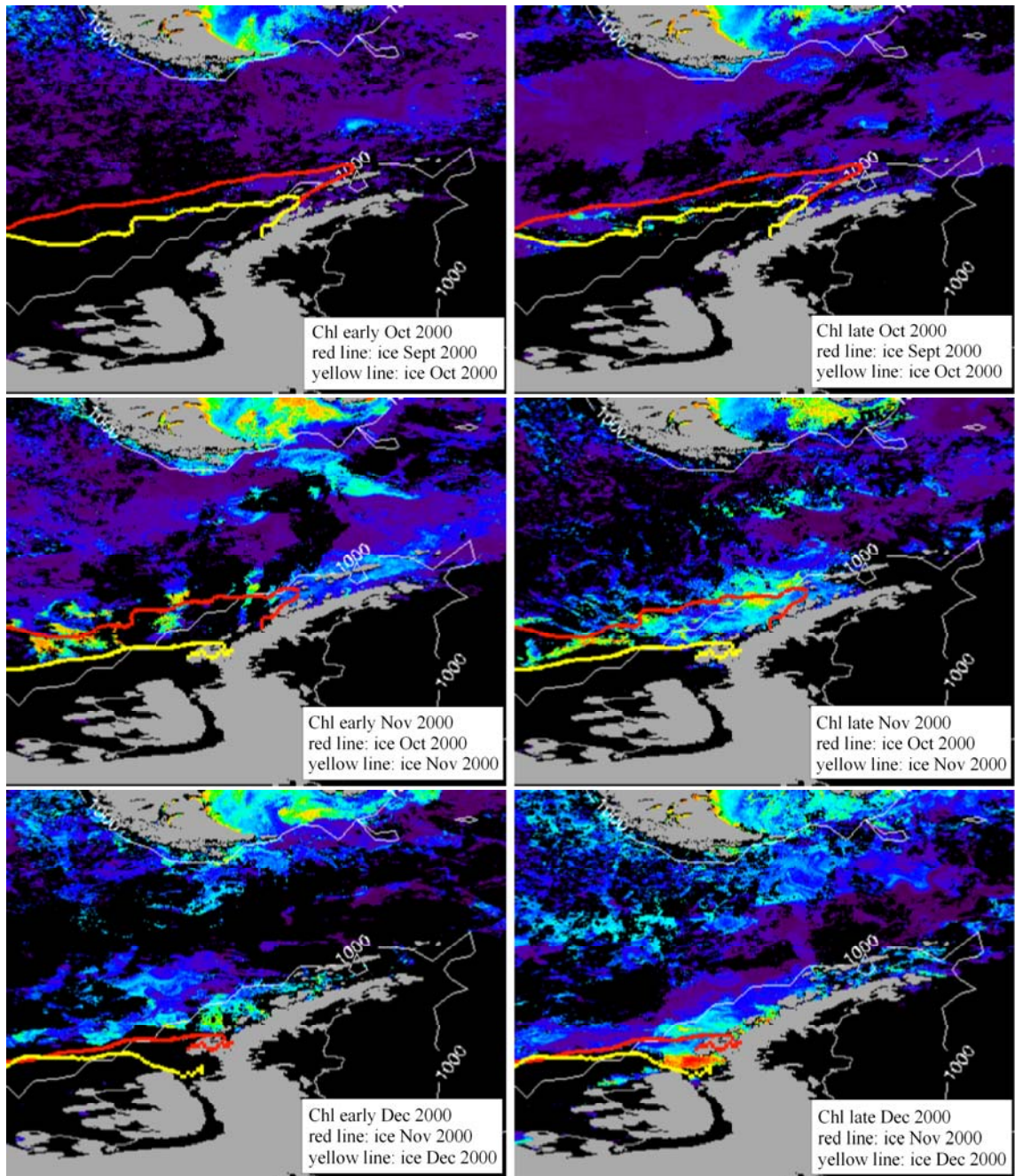
Figure 3.5a. Biweekly SeaWiFS chlorophyll concentrations (Chl, mg m^{-3}) in October
(Oct), November (Nov) and December (Dec) of 2000. The mean monthly location of the
ice edge is also shown: the red line indicates the location of the ice edge during the
preceding month, the yellow line represents the current month. The 1000 m isobath is
indicated by the white line.
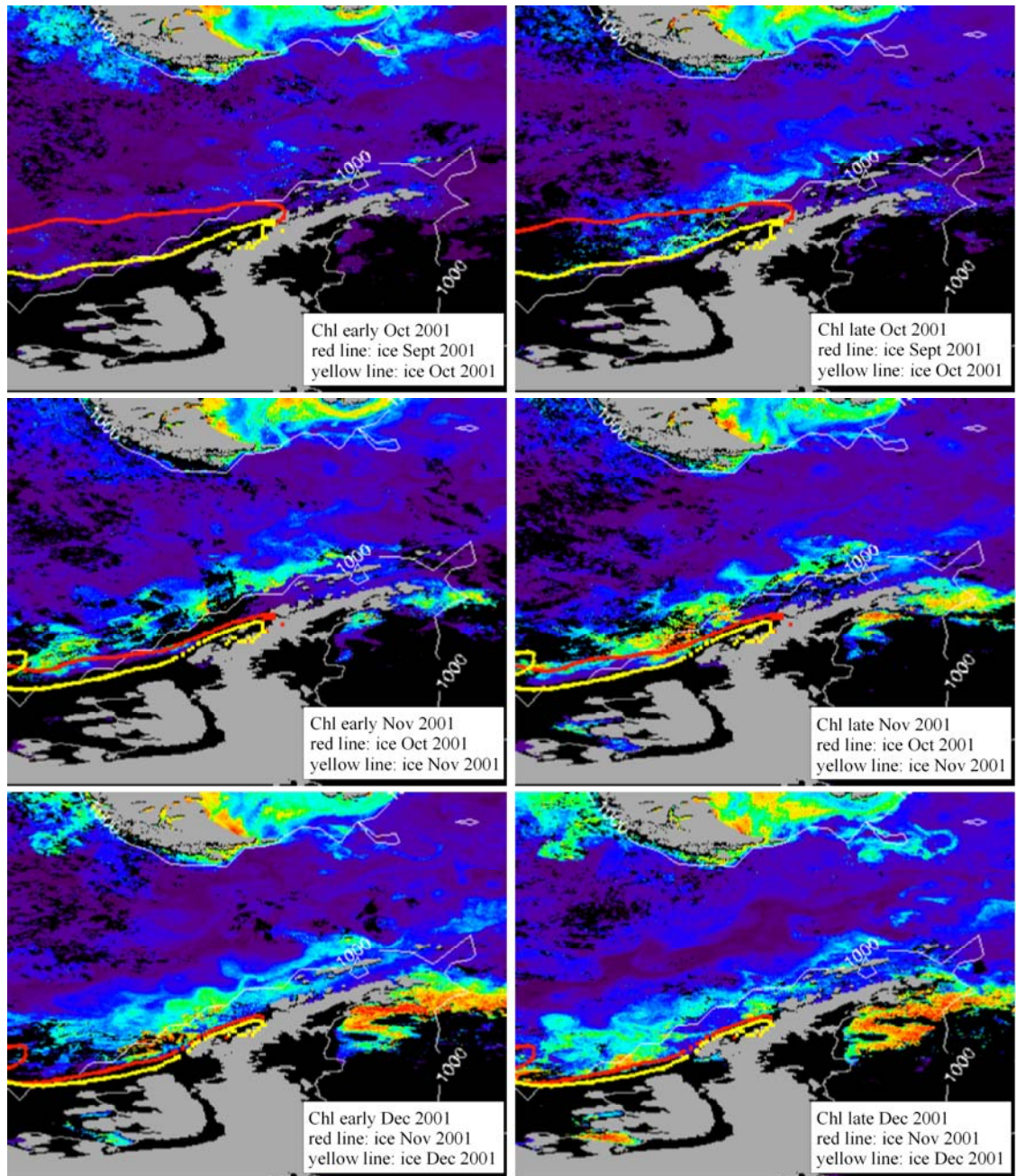
Figure 3.5b. Biweekly SeaWiFS chlorophyll concentrations (Chl, mg m^{-3}) in October (Oct), November (Nov) and December (Dec) of 2001. The mean monthly location of the ice edge is also shown: the red line indicates the location of the ice edge during the preceding month, the yellow line represents the current month. The 1000 m isobath is indicated by the white line.

The analysis of chlorophyll buildup during the weeks following the retreat of the ice edge reveals an increase in chlorophyll concentrations in the vicinity of the October and November ice edge locations, both in 2000 and 2001; however, values usually reached a maximum 4 - 6 weeks after the ice had receded (Fig. 3.6). In addition, other areas along the Antarctic Peninsula that were never influenced by sea ice also showed a similar increase during our study period. For example in November and December of 2001 (Fig. 3.5b), the ice edge occupied coastal areas of the Bellingshausen Sea and along the Antarctic Peninsula to Anvers Island (see Fig. 3.1 for site locations). Even though ice never occupied the northern end of the Peninsula, elevated chlorophyll concentrations were observed along the shelf break and in coastal areas. Thus, processes other than the retreat of the ice edge likely influenced phytoplankton dynamics in this more northern area.
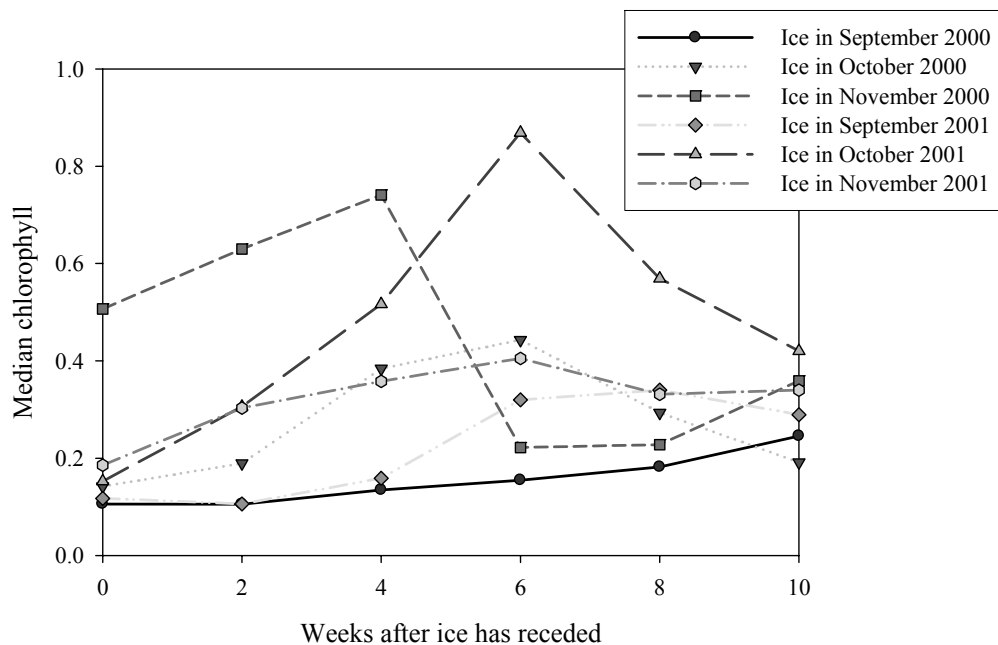
Figure 3.6. Biweekly time series of chlorophyll accumulation after the ice had receded at the September, October, and November 2000 and 2001 locations of the ice edge shown in figure 3.5.

Sea ice coverage in Marguerite Bay also showed strong variability between the years analyzed and these differences are particularly marked between 2000/2001 and 2001/2002. During summer and early fall (January - April), typical values of ice-free areas range from approximately 9,000 to 11,000 km^2 in northern Marguerite Bay and from ~ 4,500 to 7,500 km^2 in southern Marguerite Bay (Fig. 3.7c). A comparison of the climatology and 2001 and 2002 daily ice-free areas (km^2) indicates that 2002 had above average sea ice in both the northern and southern sectors throughout the spring, summer, and fall (Fig. 3.7a and 3.7b). In addition, ice formed earlier in 2002 than in 2001. In contrast, 2001 had sea ice values significantly below the 8-year mean, particularly from January through July, as indicated by the unusually large ice-free areas observed both in the northern and southern sectors. In 2001 these values reached approximately 12,000 and 11,500 km^2 in the northern and southern regions respectively. On the other hand, the areas free of ice only reached 6,000 - 9,000 km^2 in the northern and 0 - 2,000 km^2 in southern sectors during the same months in 2002, suggesting an especially extensive sea ice cover. During winter (starting in mid-July or year day ~ 200), sea ice conditions were similar for both years, although, as mentioned above, ice occupied both the northern and southern sectors considerably earlier in 2002. Other years with above-average sea ice cover were 1997/1998 and 1999/2000, while during 1998/1999 and 2003/2004 sea ice was lower than normal.

Recruitment indices (R_1) for *E. superba* collected during fall in the GLOBEC study area were 0 for 2001 and 0.4 for 2002, representing no juvenile recruitment from the 1999/2000 larval year class and significant recruitment from the 2000/2001 larval year class, respectively. Published krill recruitment index values for years of elevated

52

recruitment west of the Antarctic Peninsula between 1975 and 2002 are provided for

comparison (Table 3.1).
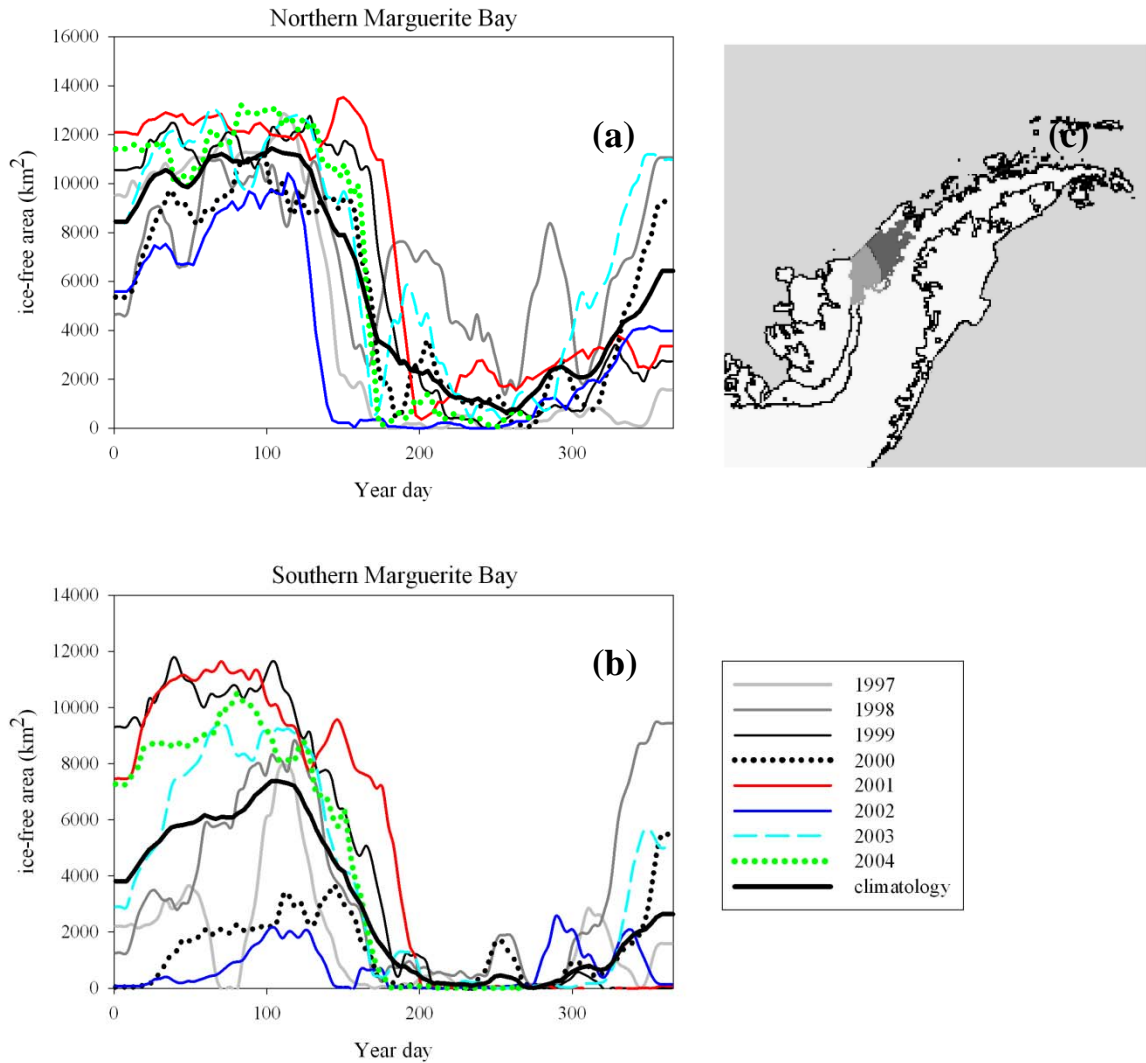
Figure 3.7. Daily ice-free area (km^2) in (a) northern and (b) southern Marguerite Bay during 1997 - 2004. The 8-year climatology also is shown (black thick line). (c) Location of the northern (dark grey) and southern (light grey) Marguerite Bay regions.

Table 3.1. Years of elevated krill recruitment between 1975 and 2002. Source publications are designated by symbols in the table. Recruitment indices (R_1) were estimated from the proportion of one year-old krill compared to age-class one plus all older age classes. Year class is the year larvae were produced; whereas recruitment to the juvenile stage occurs the following year. All krill were collected during austral summer (January - March) in waters west of the Antarctic Peninsula, except this study when krill were collected during austral fall (April - June). Only years of high recruitment ($R_1 > 0.5$) are shown

Year class	R_1	Location	Study period
1979/1980	0.559	Elephant Island area *	1975 - 1996
1980/1981	0.757	Elephant Island area *	1975 - 1996
1987/1988	0.651	Elephant Island area *	1977 - 1997
1994/1995	0.622	Elephant Island area *	1975 - 1996
	0.639	Western Antarctic Peninsula [#]	1985 - 2002
1999/2000	0.573	Elephant Island area *	1975 - 2000
	0	Western Antarctic Peninsula [#]	1985 - 2002
	0	Marguerite Bay region [§]	2001 - 2002
2000/2001	0.748	Western Antarctic Peninsula [#]	1985 - 2002
	0.400	*Marguerite Bay region* [§]	2001 - 2002

* Siegel et al. (2002); [#] Siegel et al. (2003); [§] this study

DISCUSSION

Chlorophyll concentrations showed considerable temporal and spatial variability in waters west of the Antarctic Peninsula during austral spring and summer between 1997 and 2004, with the largest and most persistent phytoplankton blooms consistently occurring in Marguerite Bay and the Bellingshausen Sea areas. The climatology showed a cross-shelf chlorophyll gradient in early summer in the middle and southern regions of the Peninsula. Investigators from the Palmer Long Term Ecological Research (LTER) program have reported a similar gradient in chlorophyll concentrations for January 1991 - 1995 (Smith et al., 1998a) and January 1997 (Garibotti et al., 2003) between Anvers and Adelaide islands, suggesting that this pattern of chlorophyll distribution has remained relatively constant in this area for about two decades. In 1997, average chlorophyll concentrations in coastal areas were an order of magnitude greater than those in the vicinity of the shelf break (4.38 mg m^{-3} vs. 0.22 mg m^{-3}) and corresponded to a shallower mixed layer and greater vertical stability of the water column in coastal waters (Garibotti et al., 2003). Climatology results presented here indicate that these environmental conditions may usually change by mid- February in the middle region of the Peninsula (Anvers to Adelaide islands) as this cross-shelf pattern was no longer present, except in Marguerite Bay and to the south.

The above mentioned studies also describe an alongshore gradient in chlorophyll concentrations with higher values in the northern sectors of the Peninsula earlier in the season possibly associated to the seasonal alongshore retreat of the sea ice and/or to latitudinal differences between areas. Present results, however, indicate that chlorophyll concentrations in the southern sectors are consistently higher than in any other area

55

analyzed west of the Antarctic Peninsula. In addition, chlorophyll accumulations in these areas occur earlier in the spring and persist longer throughout the summer than most areas in the northern regions. Thus, the southern areas are vitally important to the Antarctic Peninsula ecosystem in terms of overall chlorophyll standing stock and the phytoplankton blooms are likely to play an important role in supporting higher trophic level dynamics.

Few studies provide information on phytoplankton dynamics in the Bellingshausen Sea (Savidge et al., 1995; Barlow et al., 1998). SeaWiFS images of the circumpolar distribution of mean annual chlorophyll concentrations show that the Bellingshausen and Amundsen Seas support large phytoplankton blooms (Fig. 1 in El-Sayed, 2005). Satellite derived estimates of primary productivity also indicate that the Bellingshausen/Amundsen Sea area is one of the most productive in Antarctic waters, only exceeded by the Ross and Weddell Seas (Arrigo et al., 1998). Typically, ice edge blooms are tightly coupled to spring ice edge retreat in Antarctic waters (Sullivan et al., 1993; Arrigo and McClain, 1994; Garibotti et al., 2005), where blooms develop within about two weeks after the ice recedes from a particular location. During austral spring 1992, investigators from the UK STERNA Program observed elevated chlorophyll concentrations in oceanic waters of the Bellingshausen Sea in late November (up to > 7 mg m^{-3}) and early December (up to 2.4 mg m^{-3}), but reported that they were not related to sea ice retreat (Savidge et al., 1995; Barlow et al., 1998). During the present study, some blooms appeared to occur along the ice edge in the Bellingshausen Sea; however, most blooms occurred with approximately a 4 - 6 week lag and, therefore, probably were not related to the ice retreat, in agreement with the STERNA Program observations. Clearly, there is a need for future phytoplankton studies in the Bellingshausen Sea in order to elucidate the factors that

control the formation and persistence of spring blooms in the region.

Ice edge blooms have been suggested to be an important feature in the northern Antarctic Peninsula region (e.g., Siegel and Loeb, 1995; Smith et al., 1998b). In contrast, findings reported herein indicate that the formation of spring blooms was not necessarily coupled to the retreat of the ice edge in the vicinity of the northern Peninsula between 1997 - 2004. Instead, blooms first appeared near the shelf break and gradually progressed to more coastal areas, suggesting that shelf break processes were likely an important factor influencing phytoplankton growth in the northern Peninsula region. The strong currents of the eastward flowing ACC interact with the bathymetry when it encounters the shelf break, generating meanders that usually can be detected at the surface. Antarctic surface waters are rich in macronutrients; however, iron deficiency has been proposed as a factor limiting phytoplankton growth (De Baar et al., 1995; Holm-Hansen et al., 2004b; 2005). The importance of upwelled iron-rich deep ACC waters to chlorophyll aggregations has been described for several regions of the Southern Ocean, including the Scotia Sea, the Polar Front region downstream of South Georgia, the Ross Sea, and the Antarctic Peninsula shelf break (De Baar et al., 1995; Measures and Vink, 2001; Prézelin et al., 2000; 2004; Holm-Hansen et al., 2005). Hence, upwelling of iron-rich deep water, rather than the retreat of the ice edge, may be a major factor controlling phytoplankton bloom development during spring and summer in the vicinity of the shelf break, and in coastal waters along the northern Antarctic Peninsula.

Although sea ice extent and duration in the Bellingshausen Sea and along the Antarctic Peninsula has decreased over the past 25 years (Parkinson, 2002; Ducklow et al., 2006), high interannual variability in sea ice is still observed. Ducklow et al. (2006)

analyzed 14 years (1991 - 2004) of sea ice extent data near Palmer Station in the vicinity

of Anvers Island, and found that 2001 had the lowest (69,932 km^2) winter sea ice extent

of all years analyzed, while 2002 had the highest (109,936 km^2) (mean = 91,112 km^2).

The early retreat of sea ice in Marguerite Bay in spring of 2001 resulted in large

phytoplankton blooms in ice-free waters during summer. In contrast, the persistent

presence of sea ice in Marguerite Bay during summer - fall 2002 resulted in overall lower

chlorophyll concentrations in coastal surface waters. The positive relationship between

sea ice cover and chlorophyll concentrations is further supported by observations during

other years of this study. For example in 2003/2004, peaks of above-average chlorophyll

concentration in northern and southern Marguerite Bay during January (Fig. 4b; regions

13 and 14) coincided with an early retreat of the sea ice in late 2003 and lower than

normal sea ice extent during late 2003 - early 2004, particularly in the northern region

(Fig. 3.7). In addition, the ice-free area in northern Marguerite Bay during late 1998 -

early 1999 was larger than average, concurrent with high chlorophyll concentrations in the

region during December - January 1998/1999.

Several investigations have suggested that sea ice extent and duration are the

primary environmental factors influencing krill recruitment in the northern regions of the

Antarctic Peninsula, as spring - summer ice edge blooms were believed to support krill

reproduction and winter sea ice biota to provide food for overwintering larvae

(Kawaguchi and Satake, 1994; Siegel and Loeb, 1995; Quetin and Ross, 2003). Results

from this study, however, indicate that ice edge blooms are not prevalent in this region

and, thus, may not be a primary source of food for reproducing krill. In addition during

both winters of the GLOBEC study, sea ice biota concentrations were very low (0.05 -

0.07 mg chl m^{-3}) at the ice-water interface where larval krill feed (Daly, 2004). Indeed, a large percentage of larvae were not even associated with the undersurface of sea ice and instead remained in the water column, particularly in 2002. Also in both winters, larvae showed evidence of food limitation, as indicated by delayed development, decrease in growth rates, increased intermolt period, and decrease in dry weight, body carbon, and nitrogen (Daly, 2004). Hence, the presence of extensive sea ice during winter is not necessarily a good predictor of food availability for overwintering larvae and, environmental factors other than winter sea ice conditions must play an important role in recruitment.

Krill typically reproduce during late spring and summer (November - March) west of the Antarctic Peninsula (Siegel, 1988). Results from net samples suggest that the majority of the females migrate near the vicinity of the shelf break where they spawn in oceanic waters (e.g., Siegel, 1992; Hoffman et al., 1992), possibly owing to the predictable shelf break blooms that occur early in the productive season as observed in the climatology (Fig. 3.3). Successful krill reproduction and larval survival require an adequate food supply (Ross and Quetin, 1983; 1989). Adult females may require above average phytoplankton concentrations (1 - 5 mg chl m^{-3}) to initiate reproduction (Ross and Quetin, 1986) and relatively high chlorophyll concentrations (> 0.5 mg chl m^{-3}) to sustain multiple spawning throughout the summer (Nicol et al., 1995). It also is critical for the first-feeding larvae (calyptopis I) to encounter an adequate food supply in the euphotic zone within 10 - 14 days, otherwise they will not survive (Ross and Quetin, 1986). Hence, knowledge about differences in the timing, extent, and evolution of phytoplankton blooms is critical for understanding the interannual variability observed in krill

59

recruitment success.

The recruitment indices in Table 1 indicate that only six out of 27 years had successful recruitment. Our fall (April - May) estimated recruitment ($R_1 = 0.4$) for 2000/2001 is lower than the 0.748 reported for summer by Siegel et al. (2003) (Table 3.1). A decrease in krill recruitment indices is commonly observed between summer and fall (Siegel and Loeb, 1995), owing to the seasonal decline in krill population abundance (Lascara et al. 1999). The lower fall indices correlate with summer values and, therefore, can still serve as a relative indicator of recruitment. The two highest recruitment years resulted from high reproduction in 1980/1981 and 2000/2001. Elevated recruitment from 2000/2001 larvae also was observed downstream at South Georgia (Siegel et al., 2003). In contrast, conditions during 2001/2002 were not as favorable for a successful reproduction, as evidenced by the lower number of larvae recorded during fall 2002 (this study; Daly, 2004) and the subsequent low numbers of krill observed during January 2003 along the Peninsula (Ducklow et al., 2006).

Results reported herein suggest that seasonal persistence of elevated food concentrations from phytoplankton blooms during spring and summer likely were a strong influence on krill reproduction and recruitment, particularly in 2001. Recruitment also may vary along the Peninsula depending on the location of phytoplankton blooms. For example during 1999/2000, higher chlorophyll concentrations occurred in the Elephant Island - Scotia Sea areas relative to any other year analyzed (Fig. 3.4b: regions 3, 6, and 12). Published krill recruitment index values indicate that elevated recruitment occurred in 2001 from the 1999/2000 larvae ($R_1 = 0.573$) in this area (Siegel et al., 2002). On the other hand, chlorophyll concentrations in the southern sectors of the western Antarctic

Peninsula were average or below-average in coastal waters including Marguerite Bay early in the season (regions 7, 8, 9, 10, 11, 13), although by February an increase could be observed in most regions along the continental shelf. Consistent with the lower availability of food during the critical early reproductive period, recruitment indices in the southern part of the study area for the 1999/2000 larvae were low [R_1 = 0.076 in summer; (Siegel et al., 2003) and R_1 = 0 in fall (this study)].

Chlorophyll concentrations in the Bellingshausen may have influenced downstream densities of larval krill in the vicinity of Marguerite Bay, especially at the offshelf station in the ACC. Recent modeling studies suggest that krill spawned in the Bellingshausen Sea are transported downstream to the Western Antarctic Peninsula area and into the Scotia Sea (e.g., Thorpe et al., 2007). The wide range of larval stages observed in offshelf waters during fall 2001 indicated that krill reproduction started relatively early in the season and continued for an extended period. The dominant larval modes included CIII, FI, and FII, in addition to considerable numbers of late stage furcilia. Based on experimentally determined growth rates (Ikeda, 1984), these larvae represent a range of spawning episodes between mid-December (FVIs: ~ 127 days old) and early to late-March (CIIs: ~ 44 days old). Assuming that most reproducing adult females released eggs in the vicinity of the shelf break (Siegel, 1988), the approximate location of the spawning population upstream in the ACC may be estimated from the age of larvae and the transport rate of the current. For example, the dominant FI mode in 2001 is estimated to be about 63 days old and, therefore, likely originated from a late February - early March reproductive event. Surface velocities in the ACC reach 0.25 - 0.4 m sec^{-1}, but decrease monotonically with depth (Klinck and Nowlin, 2001). Mesoscale

meanders and eddies also may act to reduce the transport rate. Assuming an average

eastward current velocity of the ACC of ~ 0.1 - 0.2 m sec^{-1}, the spawning location

possibly occurred in offshelf waters of the Bellingshausen Sea between 83 - 94 °W (Fig.

3.8; white box). Although this spawning location is west of our study area, larger scale

ocean color imagery (Fig. 3.8a) shows large blooms in this region in 2001, which would

provide adequate food for an early and extended reproduction by adults and provide food

for larvae transported to the east. In contrast during 2002 chlorophyll concentrations

during summer were relatively low (Fig. 3.8b) and, thus, there was less food available for

reproduction or larval growth.

The results obtained during the present study indicate that spring and summer

phytoplankton blooms appear to be a significant factor influencing krill recruitment in the

vicinity of the Antarctic Peninsula. Clearly, further studies of the factors controlling

phytoplankton blooms in waters adjacent to the southern Antarctic Peninsula and in the

Bellingshausen Sea are warranted, especially since this area may play a major role in krill

reproduction and influence other components of the Antarctic food web. In addition,

further physiological-based krill studies are needed to better understand the relative

impact of summer phytoplankton blooms versus winter sea ice cover in governing

recruitment, particularly in light of the regional decline in sea ice.
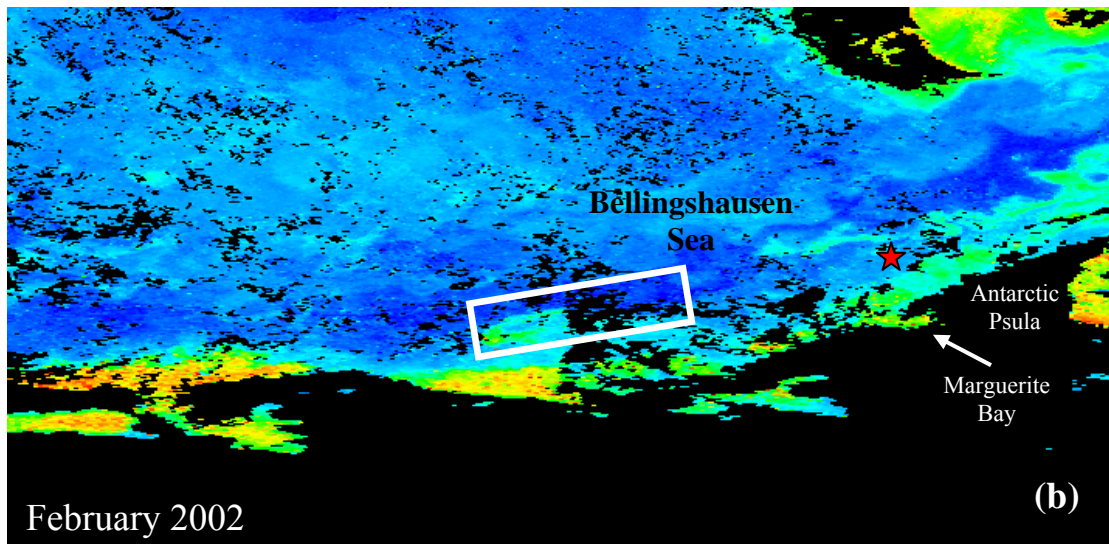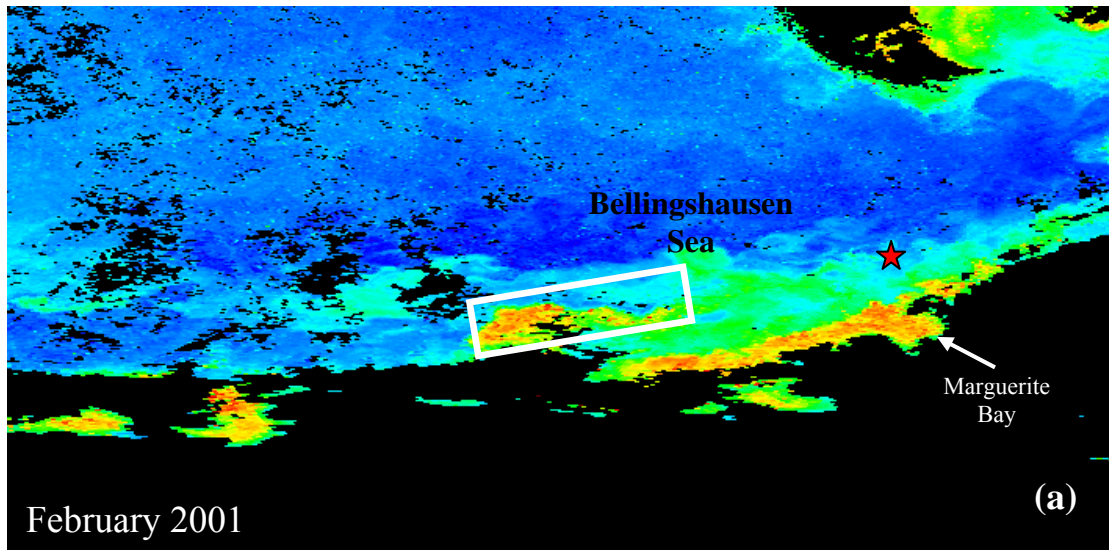
Figure 3.8. Monthly mean SeaWiFS chlorophyll concentrations in the Bellingshausen Sea during February (a) 2001 and (b) 2002. The white box represents the area of potential krill spawning. The red star indicates the location of the US SO GLOBEC sampling Station 1 where krill were collected. Images correspond to the level-3 standard mapped images (resolution of 9 km/pixel) and were obtained from the global ocean color imagery (http://oceancolor.gsfc.nasa.gov/cgi/level3.pl).

CHAPTER 4

PHYSICAL AND BIOLOGICAL CONTROLS ON INTERANNUAL
VARIABILITY OF ZOOPLANKTON IN MARGUERITE BAY, WESTERN
ANTARCTIC PENINSULA, AUSTRAL FALL 2001 AND 2002

INTRODUCTION

Zooplankton are a key component of marine ecosystems, acting as the link
between primary producers and higher trophic levels. In the Southern Ocean, the
Antarctic krill, *Euphausia superba*, often dominates zooplankton biomass and is
considered a keystone species. It is a relatively large euphausiid, up to 65 mm in length,
and an important phytoplankton grazer, particularly during spring and summer, and prey
for many upper trophic level predators, including fish, penguins, seals, and whales. *E.
superba* has a circumpolar distribution and in deep water can often be observed in dense
aggregations over the continental shelf. Due to its vital role in the Antarctic ecosystem,
the zooplankton literature is dominated by studies of this species. Extensive research has
focused on examining the distribution and abundance of *E. superba* (e.g., Marr, 1962;
Siegel, 1992), its reproduction and growth (Ross and Quetin, 1983; Brinton et al., 1986;
Daly, 1990; Quetin et al., 2003), behavior (e.g., Hamner et al., 1983; Marschall, 1988)
and role in the Antarctic foodweb (Hempel, 1985; Laws, 1985). In addition to this
species, other zooplankton, including other euphausiid species and copepods, are

important components of the Antarctic ecosystem. Nonetheless, the information

available on their role in the ecosystem, population dynamics, and ecology is limited

compared to that of *E. superba*.

Thysanoessa macrura, an omnivorous euphausiid up to ~ 29 mm in length

(Nordhausen, 1992), is broadly distributed in coastal and oceanic waters of the Southern

Ocean and at all temperature and salinity ranges (Hempel and Marschoff, 1980). Its

distribution overlaps that of *E. superba* and both species often co-occur. The larvae of *T.*

macrura are herbivorous and graze on phytoplankton during spring and summer, whereas

the adults prey mainly on copepods (Hopkins, 1985). *E. crystallorophias* is another

relatively small euphausiid (up to ~ 36 mm) found exclusively in neritic waters, where it

either co-exists or replaces *E. superba* (Daly and Zimmerman, 2004). *E. crystallorophias*

is mainly herbivorous throughout its life cycle. Both *E. cyrstallorophias* and *T. macrura*

can be a significant food item for higher trophic level predators, including penguins, fish

and whales and, thus, are also important members of the Antarctic foodweb (Croxall,

1984; Nemoto and Nasu, 1958; Ainley and DeMaster, 1990).

Copepods dominate zooplankton abundance in many regions of the Southern

Ocean and their biomass may exceed that of krill at times (Schnack-Schiel and Mujica,

1994). The dominant species include the herbivore *Calanoides acutus* and several

omnivorous species, including *Metridia gerlachei*, *Calanus propinquus* and

Ctenocalanus spp. Several studies have analyzed the patterns of distribution and

abundance of the dominant copepods in different areas of the Southern Ocean and have

emphasized their critical role in the zooplankton community, both as prey for carnivorous

zooplankton and fish, and also as predators of phytoplankton and microzooplankton (e.g.

65

Hopkins, 1985; Conover and Huntley, 1991; Schnack-Schiel et al., 1991; Lopez and

Huntley, 1995; Atkinson, 1998; Voronina, 1998; Schnack-Schiel, 2001). In addition,

other zooplankton, such as *E. superba*, have been observed to rely on copepods during

fall and winter when phytoplankton is scarce in the water column (Hopkins, 1985; Daly,

pers. comm.).

The western Antarctic Peninsula (WAP) is one of the most productive areas of the

Southern Ocean, supporting high concentrations of phytoplankton, zooplankton and

upper trophic level predators (Deibel and Daly, 2007). This area also is of interest due to

its rapid warming relative to any other area in the world's ocean (Vaughan and Doake,

1996) and the dramatic decline in sea ice cover observed in recent decades (Parkinson,

2002), which in turn has important implications for Antarctic organisms. Although

elevated chlorophyll concentrations have been observed along the continental shelf of the

northern WAP during austral spring and summer (Moline et al., 1997; Smith et al.,

1998a; Garibotti et al., 2003), recent results have shown that phytoplankton blooms are

particularly large and persistent in the southeastern sectors, including Marguerite Bay and

the western Bellingshausen Sea (Chapter 3; Marrari et al., 2008). The factors that

contribute to the relatively high productivity of this region include its northern location

relative to other Antarctic shelf areas, a relatively wide continental shelf, and the

intrusion onto the shelf of nutrient-rich Upper Circumpolar Deep Water (UCDW) (Deibel

and Daly, 2007). Numerous studies also have examined zooplankton in the WAP region,

which have improved our understanding of the patterns of abundance, distribution and

reproduction of the dominant taxa (e.g. Hopkins, 1985; Siegel, 1988; 1992; Mujica, 1989;

Schnack-Schiel and Mujica, 1994; Ross et al., 1996; Siegel and Harm, 1996; Loeb et al.,

1997). However, these studies almost exclusively took place in the northernmost sectors of the Peninsula, from Adelaide Island toward the northeast, and only a few extended further south to the outer shelf off Marguerite Bay (Lascara et al., 1999, Meyer et al., 2003). Despite the critical role of the southern sector in the ecosystem of the WAP, studies of zooplankton from Marguerite Bay and the Bellingshausen Sea have been scarce (Atkinson, 1995; Siegel and Harm, 1996; Meyer et al., 2003).

The Southern Ocean Global Ocean Ecosystem Dynamics Program (SO GLOBEC) focused its study in the vicinity of Marguerite Bay, as this region was believed to be an important overwintering habitat for *E. superba* based on observations of predators during winter (Hofmann et al., 2004). The main objective of SO GLOBEC was to investigate the physical and biological factors that influence the growth, recruitment and overwintering survival of *E. superba* (Hoffman et al., 2004). The program supported two ships operating simultaneously during two fall and winter cruises in the vicinity of Marguerite Bay in 2001 and 2002. In addition to krill data, an extensive dataset involving other important zooplankton groups was generated from net samples.

Marguerite Bay should be a favorable environment for zooplankton owing to persistent elevated concentrations of phytoplankton, the availability of protected areas such as fjords and bays that serve as refuge from advection out of the area, and the intrusion of UCDW onto the shelf through Marguerite Trough, a deep canyon (> 500 m) that intercepts the continental shelf break off Marguerite Bay. In addition, the flow of the Antarctic Peninsula Coastal Current (APPC) (Beardsley et al., 2004; Klinck et al., 2004; Moffat et al., 2008) in this area involves a gyre-like feature that contributes to making Marguerite Bay a favorable retention area for both phyto- and zooplankton, and thus a

potentially favorable feeding ground for predators.

Understanding the dynamics of zooplankton populations and how they respond to environmental change is critical to assessing the impact that these changes will have on the Antarctic ecosystem as a whole, and in particular on upper trophic level predators that rely on zooplankton as a food source. Herein, I investigate the patterns of abundance and distribution of dominant zooplankton in Marguerite Bay during austral fall 2001 and 2002 in relation to the interannual variability of environmental conditions, and examine possible ecological relationships within and between groups.

METHODS

The study area consisted of coastal waters in the vicinity of Marguerite Bay along the western Antarctic Peninsula region between 66 - 70 °S and 67 - 73 °W. Zooplankton and environmental data were collected between 23 April and 6 June 2001 and 7 April and 20 May 2002 during process cruises onboard the R.V. *Lawrence M. Gould*, as part of the SO GLOBEC Program. The process cruises occupied six coastal stations and samples from a total of 12 zooplankton net hauls were obtained during each cruise (Fig. 4.1). In addition, Video Plankton Recorder data of zooplankton were obtained aboard the R.V. *Nathaniel B. Palmer* during survey cruises along 13 transects spaced 40 km apart on the mid to outer shelf off Marguerite Bay (Ashjian et al., 2008). Results reported here are derived from net samples obtained suring survey cruises.

Zooplankton samples were collected at eight discrete depth intervals using a 1m^2 Multiple Opening-Closing Net System and Environmental Sensing System (MOCNESS), having 333 μm mesh. Maximum sampling depths ranged between 200 and 800 m,

depending on bathymetry. Samples were preserved in 10% formalin and stored for

analysis in the laboratory. Samples were initially split to include approximately 100

individuals of the dominant euphausiid species. For copepod counts and identification,

samples were split further to include approximately 100 individuals of the dominant

copepod. All zooplankton taxa present in the subsamples were identified and counted.

Euphausiids were identified to species and developmental stage (larval stages, juveniles,

adult females and adult males) after Makarov (1981) and Mauchline (1981), and

measured for total length to the nearest half mm (from the base of the eye to the tip of the

telson, excluding setae). For plotting purposes, length data were grouped in 1 mm length

bins. Only data for juveniles > 20 mm total length and adults are included in this study.

Copepods were identified for species and enumerated. For Euchaetidae, the designation

of Park (1994) was followed, who ascribed the Antarctic species to the genus

Paraeuchaeta. All other zooplankton groups were identified, counted, measured, and

classified into > 15 mm or < 15 mm total length; however, analyses in this study

combined the abundances of these size categories.
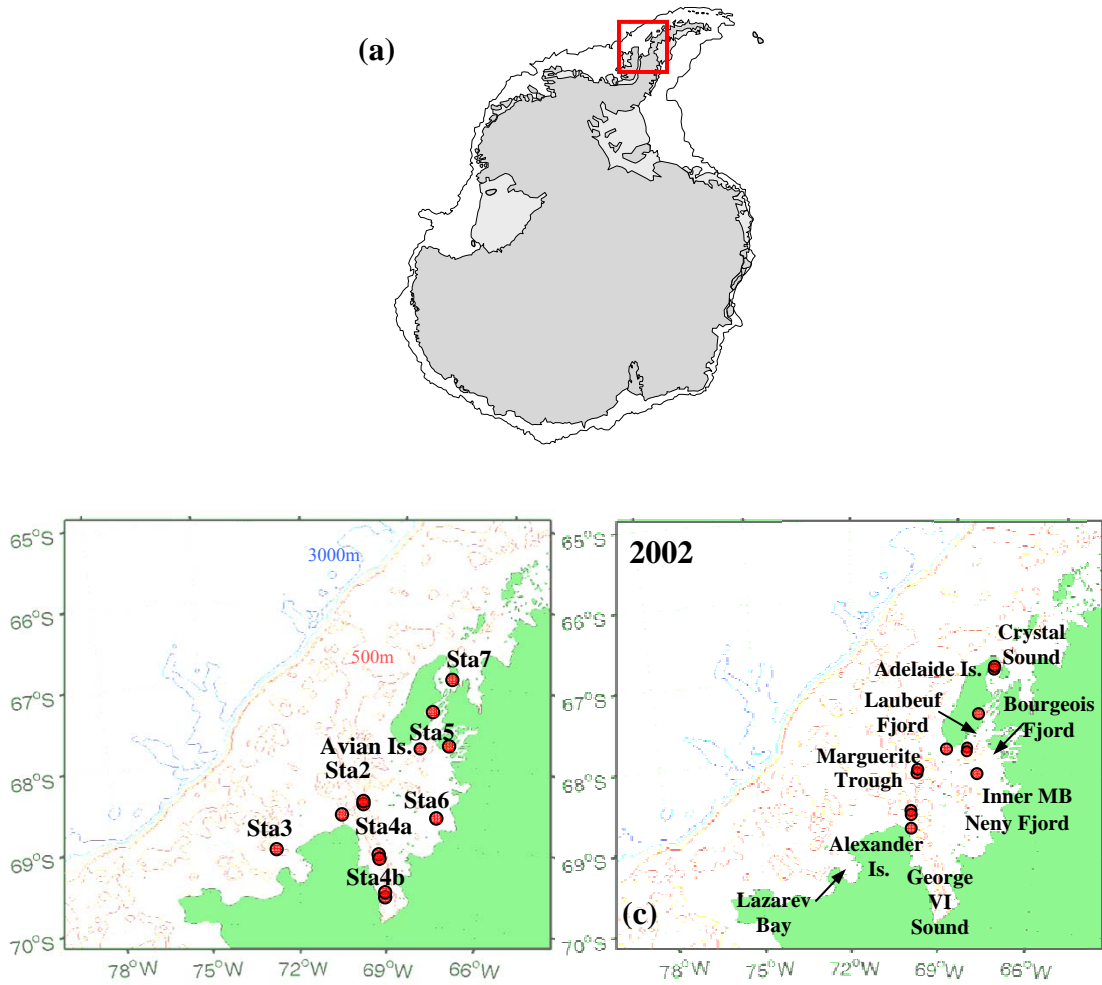
Figure 4.1. (a) Location of the study area (red rectangle) and MOCNESS net hauls (circles) during fall of (b) 2001 and (c) 2002. General station locations and geographic references are also indicated. MB is Marguerite Bay.

Water column integrated abundance (A, ind m^{-2}) was calculated for each taxa in all net hauls using:

$$A = \sum_{i=1}^{8} n_i z_i$$

where n is abundance (ind m^{-3}) in net i, and z is the depth interval (m) of the stratum sampled by net i, calculated as the difference between the depth at which the net was

closed and the depth at which it was opened (e.g., if stratum sampled was 100 - 150 m, z is 50 m). A mean water column integrated abundance was estimated for each taxa during each year (n = 12). In addition, a mean integrated abundance was calculated for all taxa at each station, when multiple net hauls were done at a station.

The depth of maximum abundance (Z) was obtained for each taxa in each net haul by calculating the center-depth of the stratum with the highest abundance at a given location. A mean depth of maximum abundance was calculated for each taxa during each year.

Abundances and depth distributions for all taxa were tested for normality (Shapiro-Wilk W Test) (Shapiro et al., 1968). Abundances (A) and depths of maximum abundance (Z) for all dominant copepod species followed a normal distribution; therefore, statistical analyses for copepod parameters included arithmetic means, Student's t-Test, and one-way ANOVA at $\alpha = 0.05$ (Zar, 1984). Abundances and vertical distributions of all other groups, including euphausiids, were not normally distributed; thus, statistical analyses reported here are nonparametric and included geometric means, Mann-Whitney U Test, and Kruskall-Wallis ANOVA at $\alpha = 0.05$ (Zar, 1984).

Vertical profiles of conductivity, temperature, and density were obtained with a CTD mounted on the MOCNESS during all net hauls. In addition, water column chlorophyll samples were collected at several CTD stations in proximity to the MOCNESS locations. A total of 15 and 6 casts are available for fall 2001 and 2002, respectively. At each CTD station, chlorophyll samples for 4 - 9 depths were collected using 10-L Niskin bottles mounted on a rosette. Water was filtered onto GF/F filters and pigments were extracted in 90% acetone at -20 °C in the dark for at least 24 hours.

71

Chlorophyll fluorescence was measured on a Turner Design Digital 10-AU-05 fluorometer calibrated prior to each cruise. MOCNESS tows were matched to the geographically closest CTD cast for comparisons between zooplankton and environmental data (Fig. 4.1). Spearman rank order correlations were calculated between the vertically integrated abundance of all zooplankton taxa and several environmental variables: vertically integrated pigment concentrations (chlorophyll + phaeopigment; mg m^{-2}), bottom depth (m), and salinity at 10 m.

In addition to the concurrent environmental variables measured during fall, monthly mean chlorophyll concentrations between 45 - 75 °S and 50 - 80 °W were obtained from SeaWiFS for the preceding summer season. More detail on the processing of SeaWiFS data are presented in Chapters 2 and 3. Analyses in this chapter include five of the subregions defined in Chapter 3 (Fig. 3.4a), which represent oceanic and coastal waters of the Bellingshausen Sea and Marguerite Bay. The geometric mean chlorophyll for the five subregions was calculated for each biweekly period from October - April during spring-summer 2000/2001 and 2001/2002. Data are presented in relation to the seven-year climatology calculated as the geometric mean for 1997 - 2004 at each subregion.

RESULTS

Abundance and Percent Contribution

The zooplankton of Marguerite Bay comprised 13 major taxonomic groups,

72

including 12 species of copepods, three species of euphausiids, and 10 other taxa (Tables 4.1 and 4.2). The dominant copepods included *Calanoides acutus*, *Metridia gerlachei*, *Ctenocalanus* spp., and *Paraeuchaeta* spp. *Oithona* spp., *Oncaea* spp., *Calanus propinquus*, *Rhincalanus gigas*, *Gaidius tenuispinus* and *Scolecithricella minor* were present in generally lower numbers. *Aetidopsis antarctica* and *Metridia curticauda* were present only occasionally in low abundances and, therefore, were excluded from the remaining analyses. Overall, copepods were significantly more abundant in fall 2001 (24,362 ± 11,948 ind m^{-2}) than 2002 (9,496 ± 6,450 ind m^{-2}) (Student's t-Test; p < 0.001) (Fig. 4.2a). During 2001, abundances were highest in Laubeuf Fjord (Sta. 5), at the northern end of Alexander Island (Sta. 4a), George VI Sound (Sta. 4b), Lazarev Bay (Sta. 3), and Neny Fjord (Sta. 6). In 2002, copepods were most abundant in the vicinity of Alexander Island and southern Laubeuf Fjord. Densities were lowest in Crystal Sound (Sta. 7), Bourgeois Fjord (Sta. 5), and at the southern end of Adelaide Island (Avian Island). Abundances also were low in northern Laubeuf Fjord during 2002. In addition, copepod species percent composition showed interannual differences (Fig. 4.2b). In 2001, *C. acutus* and *M. gerlachei* dominated the community (mean = 52 and 38% of the total copepod abundance, respectively), followed by *Paraeuchaeta* spp. (5%). In contrast, during 2002 the number of relatively abundant species (> 5%) was higher and included *M. gerlachei* (32%) *Ctenocalanus* spp. (27%), *C. acutus* (18%), *Oithona* spp. (10%), and *Paraeuchaeta* spp. (8%*)*. *C. propinquus* and *R. gigas*, two relatively large species frequently found in high abundances in the Southern Ocean, only accounted for < 3% of total copepod abundance during both years. *Oncaea* spp., a frequently dominant small copepod (< 1 mm) was generally present in low abundances throughout the study

73

area, and only accounted for 1.4% and 2.6% of total copepods during 2001 and 2002,

respectively.

Table 4.1. Copepod abundance (ind m^{-2}) in the vicinity of Marguerite Bay during austral fall 2001 and 2002. Mean = arithmetic mean, SD = standard deviation, n = number of net hauls in which a species was present

	Fall 2001			Fall 2002		
Taxonomic group	**Mean**	**SD**	**n**	**Mean**	**SD**	**n**
Copepods						
Aetidopsis antarctica	10.9	37.9	1	6.29	21.8	1
Calanoides acutus	13358	7979	12	1909	1891	12
Calanus propinquus	145	121	10	173	174	11
Ctenocalanus spp.	263	174	12	2497	1856	11
Gaidius tenuispinus	79.8	75.9	9	32.9	36	7
Metridia curticauda	0	0	0	7.87	27.3	1
Metridia gerlachei	8883	5487	12	3153	2390	12
Oithona spp.	55.2	55.9	12	908	994	12
Oncaea spp.	274	286	12	239	264	10
Paraeuchaeta spp.	1165	696	12	560	440	12
Rhincalanus gigas	58.6	67.0	10	12.4	30.0	7
Scolecithricella minor	67.7	121	4	13.2	39.6	3

Table 4.2. Zooplankton abundance (ind m^{-2}) in the vicinity of Marguerite Bay during austral fall 2001 and 2002. Geo mean = geometric mean, Range = minimum - maximum, n = number of net hauls in which a taxon was present

| Taxonomic group	Fall 2001			Fall 2002		
	Geo mean	Range	n	Geo mean	Range	n
Ostracods	775	32.4 - 4728	12	788	83.6 - 2517	12
Euphausiids						
Euphausia crystallorophias	2.78	0.24 - 13.2	10	18.5	1.93 - 137	12
Euphausia superba	6.22	0.24 - 72.6	11	14.8	1.63 - 117	11
Thysanoessa macrura	45.9	7.19 - 266	12	16.2	4.27 - 51.9	12
Amphipods	15.11	5.63 - 91.5	12	12.7	6.77 - 86.6	12
Mysids	1.73	0.23 - 34.9	11	4.26	0.75 - 29.8	10
Medusae	13.3	0.27 - 520	9	0.39	0.12 - 1.47	6
Siphonophores	present	-	12	present	-	11
Polychaetes	136	0.65 - 1110	10	11.9	0.48 - 279	11
Pteropods	254	2.33 - 2119	12	273	7.63 - 1556	11
Chaetognaths	57.0	3.05 - 687	12	31.3	4.23 - 161	12
Appendicularians	4.46	0.78 - 32.3	3	1447	147 - 5693	4
Salps	3.22	0.61 - 43.9	3	0.22	0.15 - 0.27	3
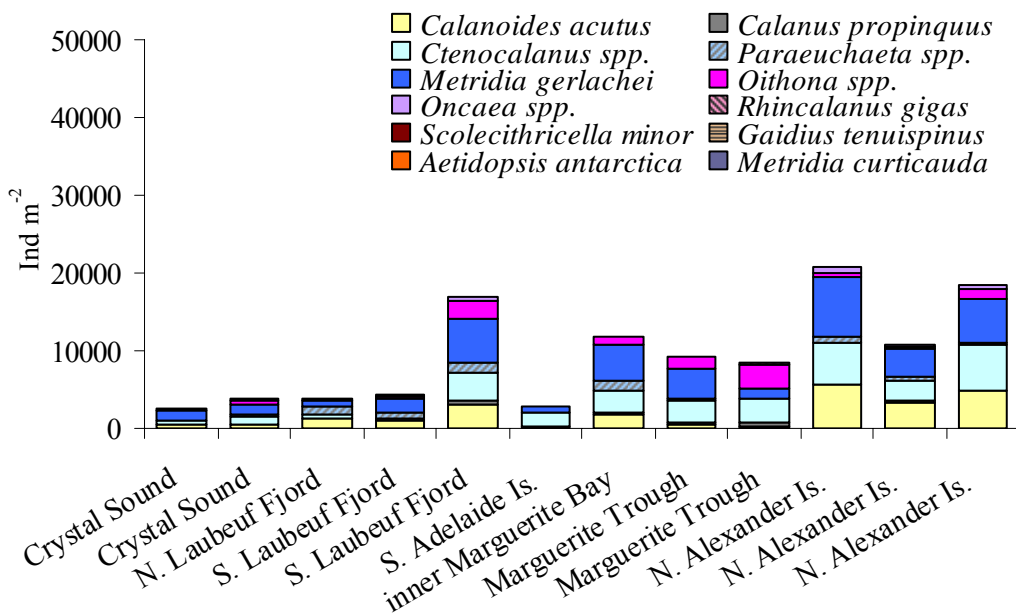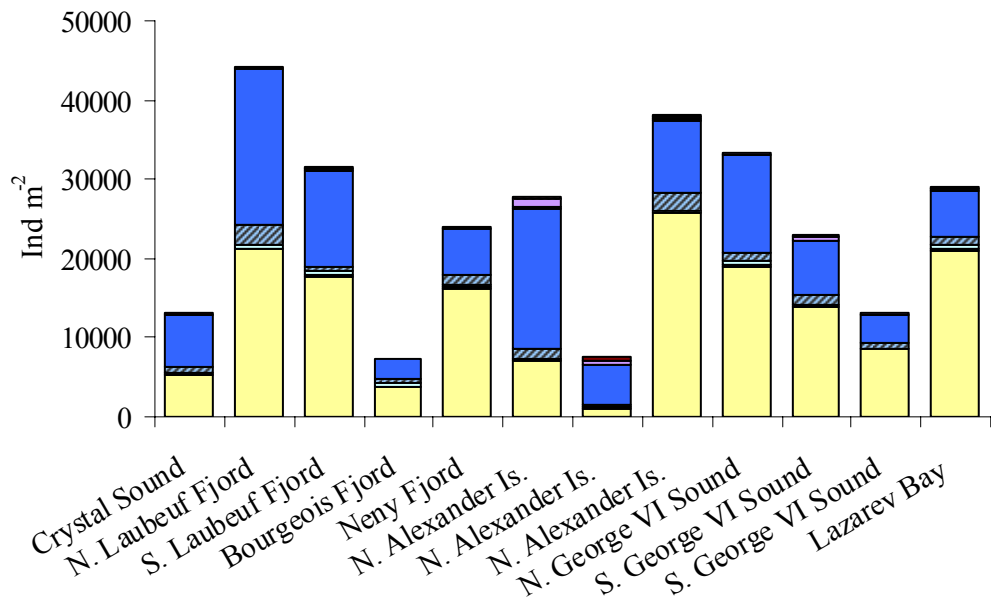
Figure 4.2a. Water column integrated abundance (ind m^{-2}) of copepods from net hauls in the vicinity of Marguerite Bay during austral fall 2001 (top) and 2002 (bottom).
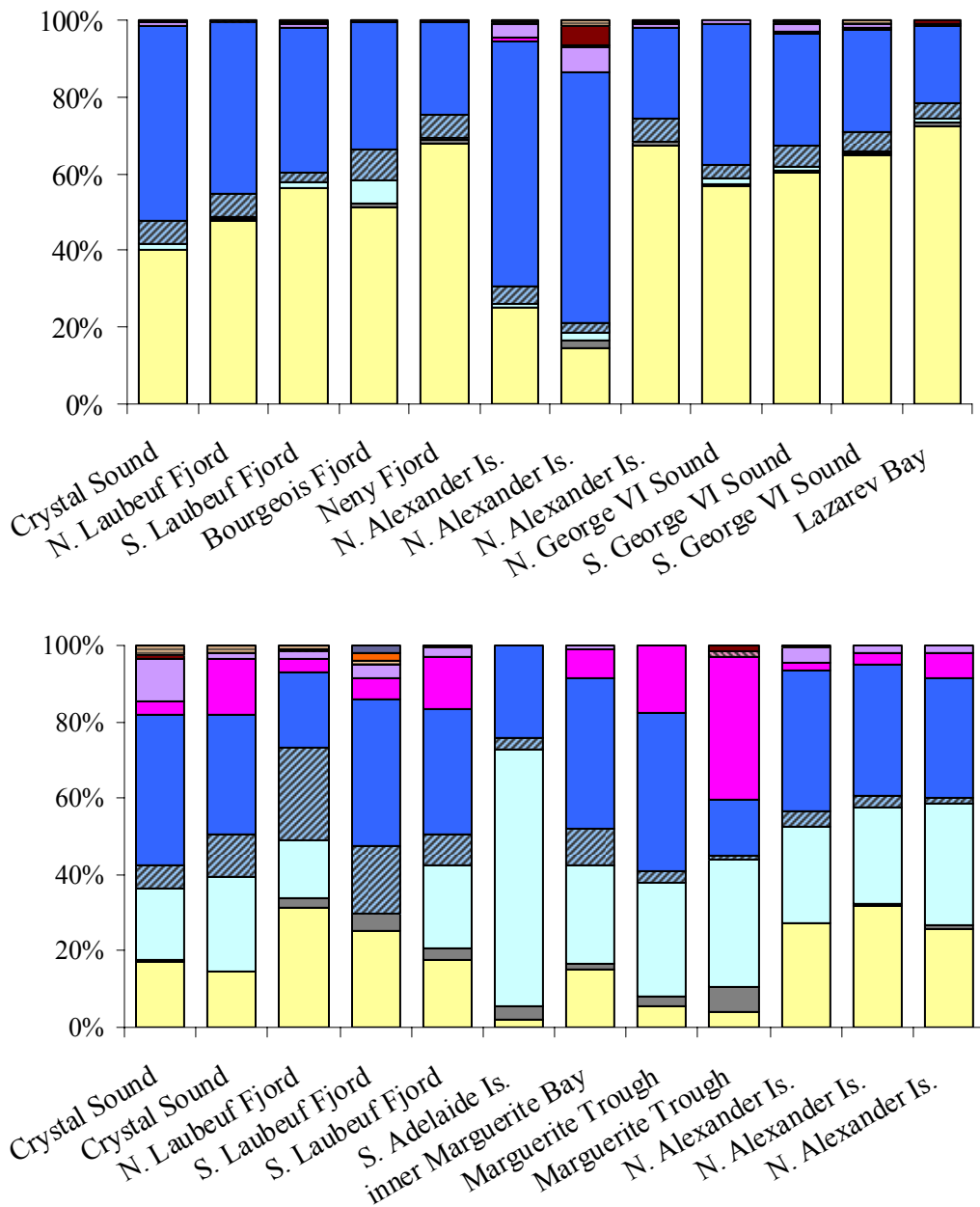
Figure 4.2b. Percent composition of copepods at coastal stations in Marguerite Bay during austral fall 2001 (top) and 2002 (bottom). Color legend as in Figure 4.2a.

The overall geometric mean abundance of total euphausiids was very similar during both years: 66.3 and 66.8 ind m^{-2} in 2001 and 2002, respectively (Mann Whitney U; p = 1.00) (Fig. 4.3a). Although abundances were variable within sampling locations and over the study area, distribution patterns were consistent between years. Northern areas, such as Laubeuf Fjord and Crystal Sound, consistently had the highest integrated total euphausiid abundances. The southern sectors, including Neny Fjord, inner Marguerite Bay and near Alexander Island, had relatively lower euphausiid abundances during both years. George VI Sound and Lazarev Bay were only sampled during 2001 and had the lowest abundances of all areas surveyed.

Despite the similarity in total euphausiid abundance and distribution between years, there were significant interannual differences in species percent composition (Fig. 4.3b). *T. macrura* was the most abundant species during 2001 with a geometric mean abundance of 45.9 ind m^{-2}, whereas *E. crystallorophias* had overall low abundances (2.78 ind m^{-2}), and *E. superba* had intermediate values (6.22 ind m^{-2}). During fall 2002, abundances were similar among species, with *E. crystallorophias* having the highest mean value (18.5 ind m^{-2}), followed by *T. macrura* (16.2 ind m^{-2}), and finally *E. superba* with the lowest abundance (14.8 ind m^{-2}). Interannual differences in abundances of *T. macrura* (Mann Whitney U; p = 0.020) and *E. crystallorophias* (Mann Whitney U; p = 0.004) were significant, whereas values for *E. superba* were not significantly different between years (Mann Whitney U; p = 0.200).
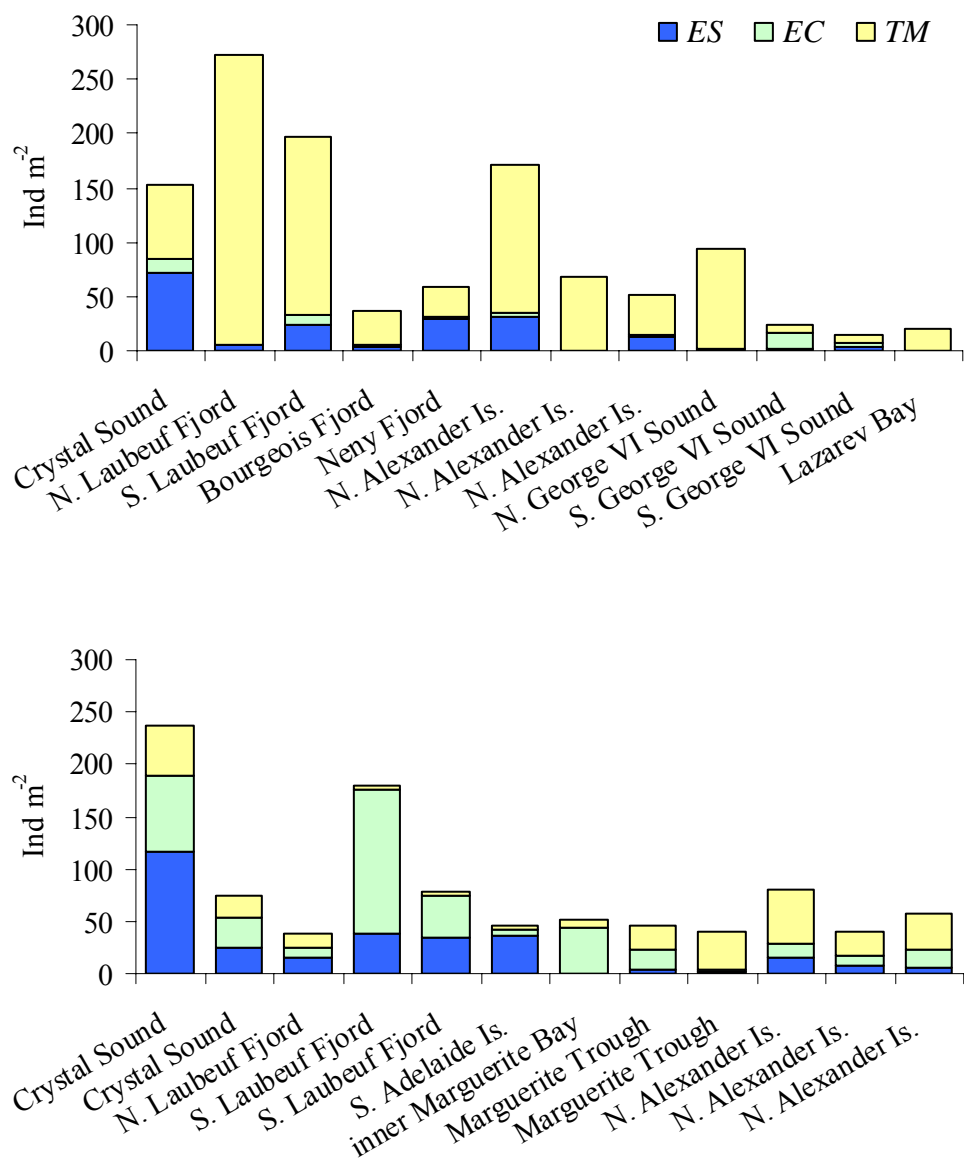
Figure 4.3a. Water column integrated abundances of euphausiids (ind m^{-2}) from net hauls in the vicinity of Marguerite Bay during austral fall 2001 (top) and 2002 (bottom).
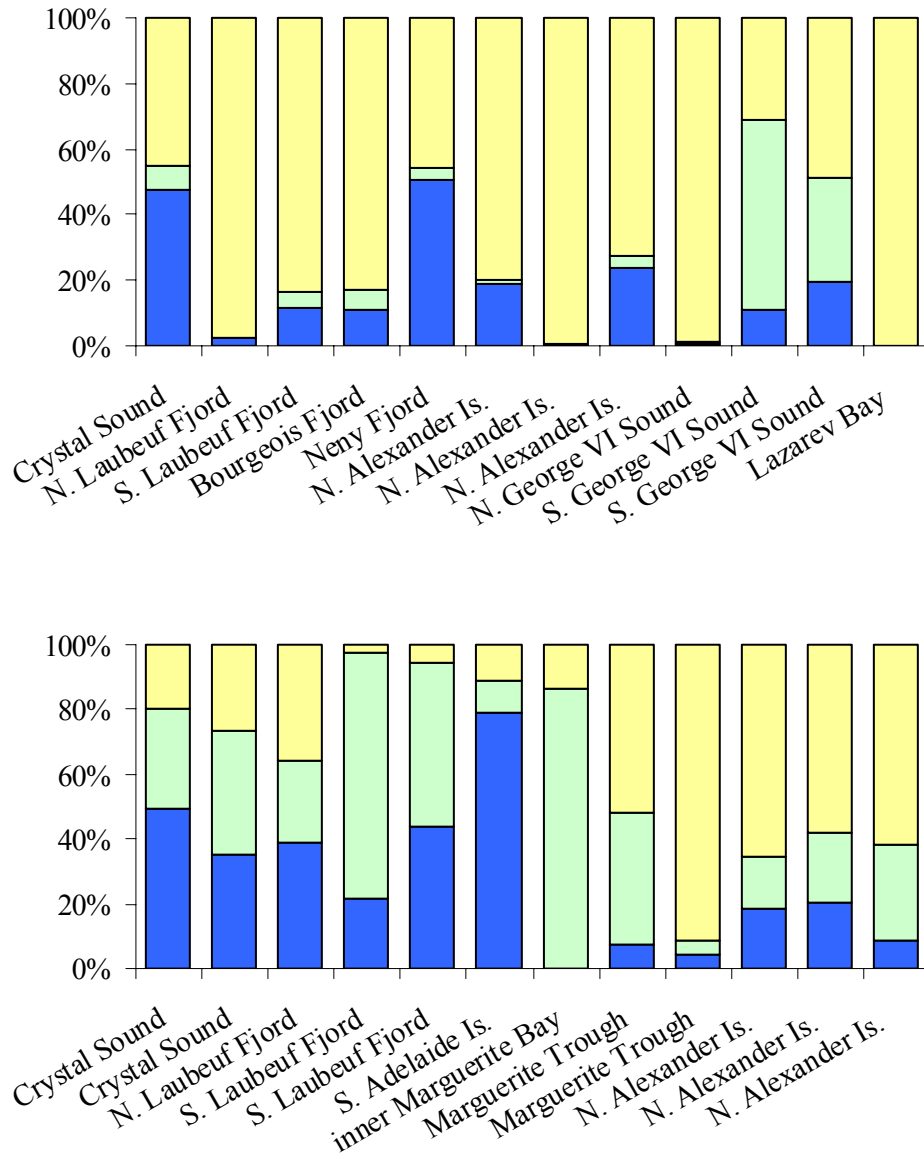
Figure 4.3b. Percent composition of euphausiids from net hauls in the vicinity of Marguerite Bay during austral fall 2001 (top) and 2002 (bottom). Color legend as in Figure 4.3a.

Even though abundances of *E. superba* were comparable between years, there were key interannual differences in developmental stage composition (Fig. 4.4). During 2001, non-larval *E. superba* were almost exclusively adult males and females and juveniles were essentially absent. Only a few year-two juveniles, 34 mm total length (TL), were observed at one station in Laubeuf Fjord (0.08 ind m^{-3}). Overall, juveniles accounted for only ~ 2% of the postlarval *E. superba* densities in 2001. In contrast, year-one juveniles were abundant and constituted ~ 41% of the populations in 2002, suggesting a successful recruitment from 2001 larvae. Postlarval *T. macrura* were mostly juveniles 8 - 10 mm TL during 2001 and 2002 (Fig. 4.5). Juveniles comprised 91% of individuals in fall 2001, and ~ 69% in 2002, when the remaining 31% were adults ranging primarily between 16 - 20 mm TL. During 2001, *E. crystallorophias* juveniles (10 - 18 mm TL) comprised 11% of the population, while the remaining fraction (89%) included adults 20 - 36 mm TL (mode: 29 mm TL) (Fig. 4.6). In 2002, juveniles were a larger fraction of the population (28%), while the adults had a bimodal distribution, with a larger mode at 20 mm TL, and lower proportions of larger individuals between 29 - 33 mm TL. Even though the percent composition of postlarval *E. crystallorophias* was comparable between years, larval abundances showed marked interannual differences, with higher values in 2001 throughout the study area. Maximum abundances in 2001 were 829 ind m^{-2} in Neny Fjord, whereas the highest values recorded in 2002 were ~ 18 ind m^{-2} in northern Laubeuf Fjord (data not shown).

In addition to copepods and euphausiids, other dominant zooplankton groups included ostracods, pteropods, polychaetes, chaetognaths, appendicularians, amphipods, and mysids (Fig. 4.7a and b). Ostracods and pteropods were numerically dominant

81

during both years and showed no significant interannual differences (Mann Whitney U test, p = 1.00 for ostracods, p = 0.805 for pteropods). Appendicularians were more abundant during 2002 (geometric mean = 1447 ind m^{-2}) although their distribution was very patchy and they were present in only four net hauls. During 2001, they were present at three locations, but in very low abundances. Polychaetes and chaetognaths were relatively abundant during 2001, but had lower densities in 2002. Abundances for amphipods and mysids were not significantly different between years (Mann Whitney U test, p = 0.32 for amphipods, p = 0.204 for mysids). Gelatinous zooplankton were generally rare. Siphonophores could not be numerically quantified due to the presence of only fragments of colonies in the samples; however, fragments were classified as "few" or "numerous" and were frequent throughout the water column at most locations during both years, particularly in the upper 300 m.

Laubeuf Fjord had the highest abundances of these groups of zooplankton, followed by the areas in the vicinity of Alexander Island and Neny Fjord/inner Marguerite Bay (Sta. 6) during both years (Fig. 4.7a). In 2001, abundances were lowest in Bourgeois Fjord, one station in southern George VI Sound, and Lazarev Bay, while during the following fall, densities were lowest in Crystal Sound and south of Adelaide Island. In terms of percent composition, during 2001 ostracods, pteropods and polychaetes dominated at all stations except in Lazarev Bay. At this location, these groups were scarce or absent, and the community was composed primarily of medusae, chaetognaths, and salps (Fig. 4.7b). Although ostracods dominated the zooplankton numerically at most locations in 2001, their percent contribution varied among stations. Their contribution was maximum in Crystal Sound, Laubeuf Fjord, and George VI

Sound, and minimum in the vicinity of Alexander Island and Lazarev Bay. In 2002,

ostracods again dominated numerically at most locations, but were only a minor fraction

of zooplankton in some net hauls in Laubeuf Fjord, Adelaide Island, and Marguerite

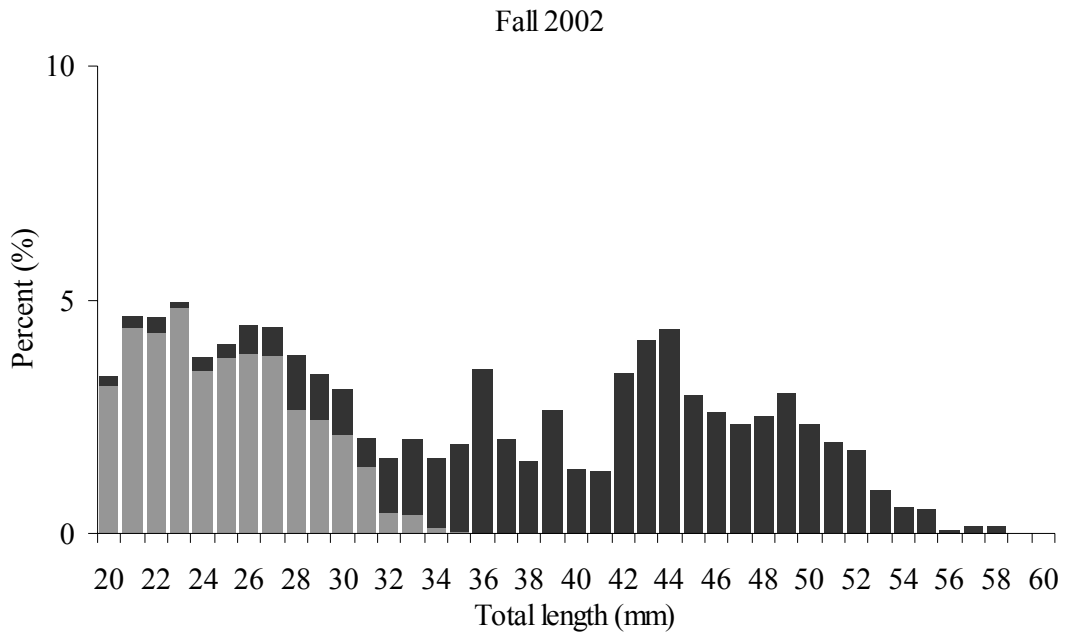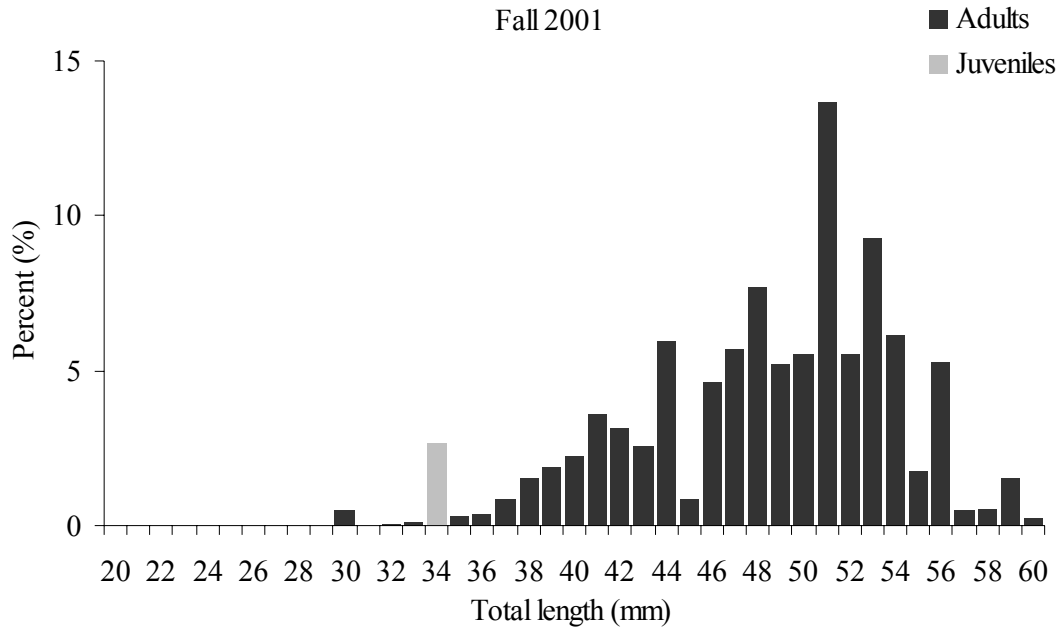Trough, where appendicularians were most important.

Figure 4.4. Length-frequency of *E. superba* juveniles and adults during fall 2001 (top) and 2002 (bottom). Data represent all coastal net hauls for each year. Only juveniles ≥ 20 mm are included.
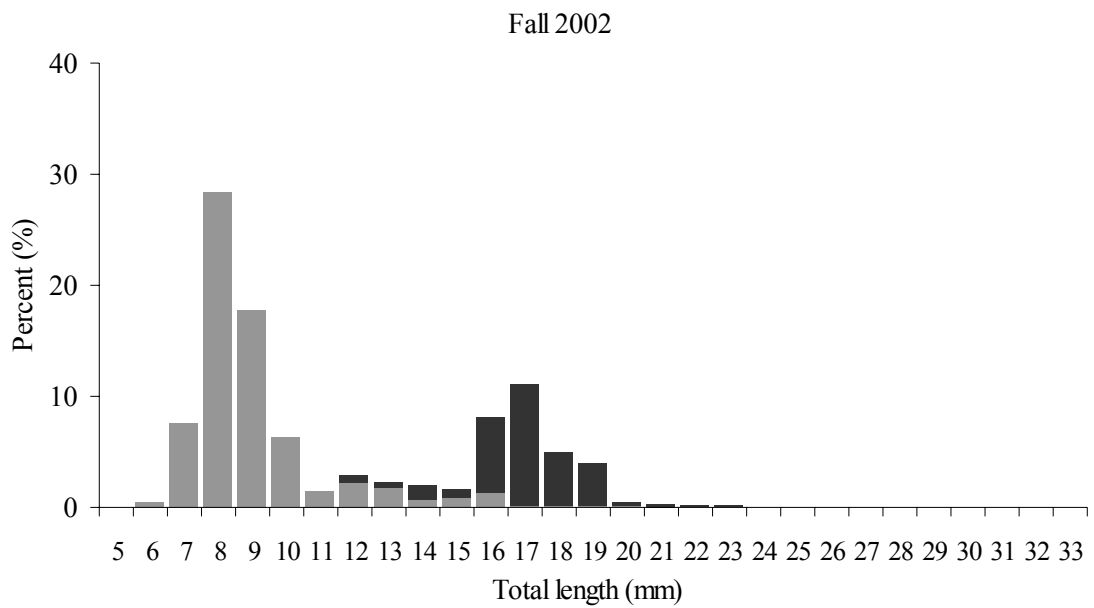
84

Figure 4.5. Length-frequency of *T. macrura* juveniles and adults during fall 2001 (top) and 2002 (bottom). Data represent all coastal net hauls for each year.

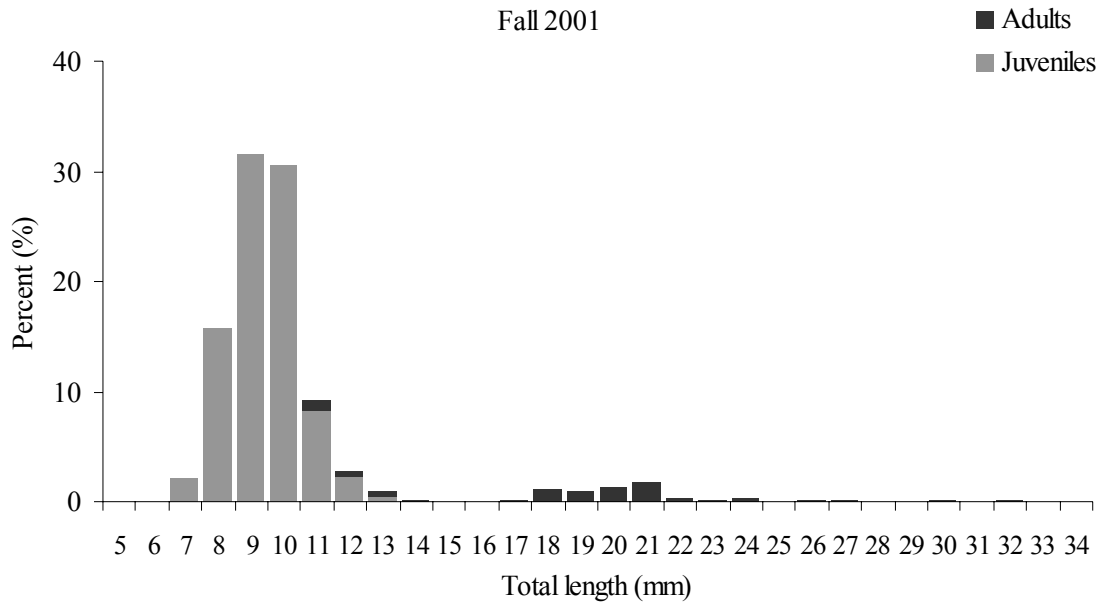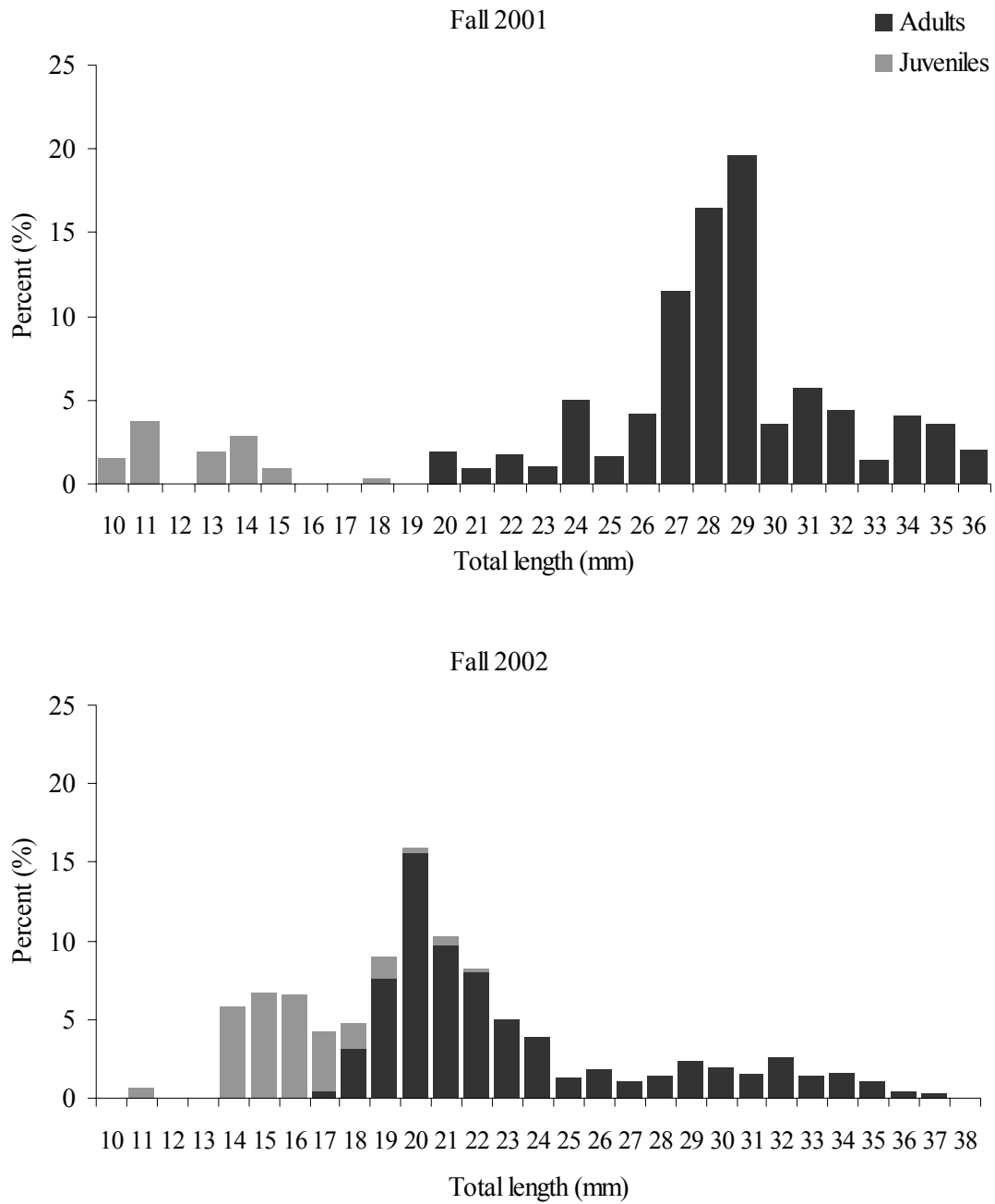Figure 4.6. Length-frequency of *E. crystallorophias* juveniles and adults during fall 2001 (top) and 2002 (bottom). Data represent all coastal net hauls for each year.

Figure 4.7a. Water column integrated abundances of zooplankton other than copepods and euphausiids (ind m^{-2}) from net hauls in the vicinity of Marguerite Bay during austral fall 2001 (top) and 2002 (bottom).

Figure 4.7b. Percent composition of zooplankton other than copepods and euphausiids from net hauls in the vicinity of Marguerite Bay during austral fall 2001 (top) and 2002 (bottom). Color legend as in Figure 4.5a.

Vertical Distribution

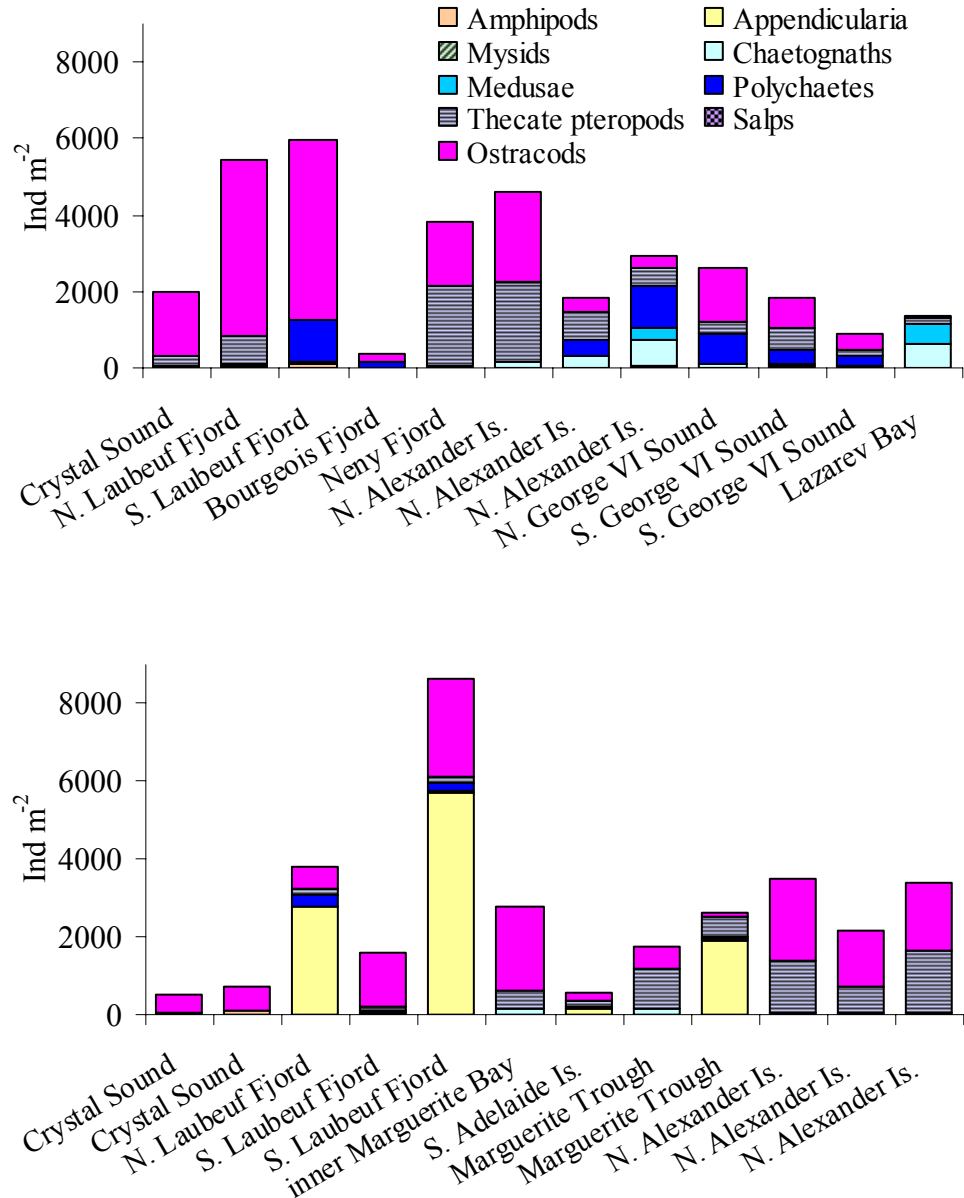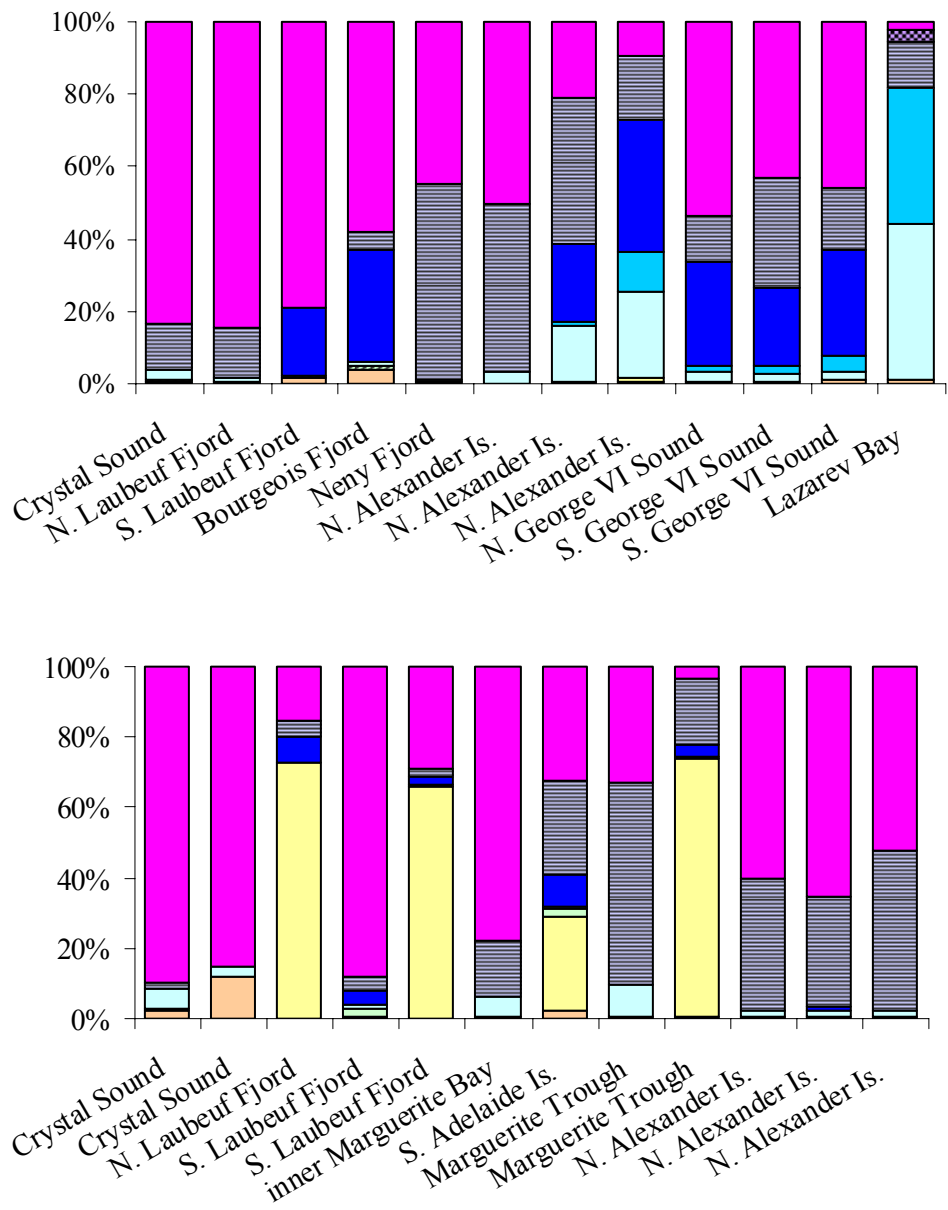Overall, the mean depth of maximum abundance for all copepods was significantly deeper in the water column during May - June 2001, than in April - May 2002 (2001: 252 m; 2002: 75 m; Student's t-Test; $p < 0.001$) (Fig. 4.8). Looking at individual species, only depths of *Paraeuchaeta* spp., *Oithona* spp., and *R. gigas* were significantly different between years (ANOVA, $p < 0.05$), although other species such as *M. gerlachei*, *Oncaea* spp., and *S. minor* also had somewhat shallower distributions in 2002. Copepod species occurred within three depth ranges: shallow (0 - 100 m), intermediate (100 - 150 m), and deep (> 150 m) water groups (Table 4.3). In 2001, shallow species included *Ctenocalanus* spp. and *C. propinquus*, while *Oithona* spp., *S. minor, Paraeuchaeta* spp., *M. gerlachei, C. acutus, G. tenuispinus* and *Oncaea* spp. were identified as deep species. Only *R. gigas* was intermediate during the first year. In contrast, *Oithona* spp., *R. gigas*, and *Paraeuchaeta* spp. were grouped as shallow species during 2002, while *M. gerlachei* and *S. minor* were intermediate. *Oncaea* spp., *C. acutus*, and *G. tenuispinus* remained deep species during fall 2002.

The vertical distributions of euphausiids were similar within and between years (Table 4.4) and geometric mean depths of maximum abundance for all species were in the upper 100 m (65 - 84 m). Mysids were distributed the deepest during 2001 (249 m) and 2002 (224 m), while amphipods were located at intermediate depths in 2001 (125 m) and represented the shallowest group during 2002 (55 m). The depths of maximum abundance for *E. superba, E. crystallorophias*, and *T. macrura* were not significantly different within or between years (Kruskall-Wallis ANOVA; $p = 0.882$ in 2001, and $p = 0.873$ in 2002). However, even though their general depth ranges overlapped throughout

Table 4.3. Mean depth of maximum abundance (Z, m) of copepods in 2001 and 2002. Species in bold indicate those that were classified in the same depth category during both years. The range represents the shallowest and deepest depth (m) at which each species was present. Depth categories were based on the general hydrography of the area. At most net hauls, the upper mixed layer ranged between 0 - ~100 m, with a thermocline/pycnocline generally between ~100 - 150 m, and warmer saltier water below ~150 m

Fall 2001								
Shallow	**Z**	**Range**	**Intermediate**	**Z**	**Range**	**Deep**	**Z**	**Range**
Ctenocalanus **spp.**	51	0 - 500	*R. gigas*	147	0 - 800	*Oithona* spp.	162	0 - 525
C. propinquus	80	0 - 525				*S. minor*	184	0 - 350
						Paraeuchaeta spp.	201	0 - 800
						M. gerlachei	213	0 - 800
						C. acutus	213	0 - 800
						G. tenuispinus	249	0 - 800
						Oncaea **spp.**	348	0 - 800

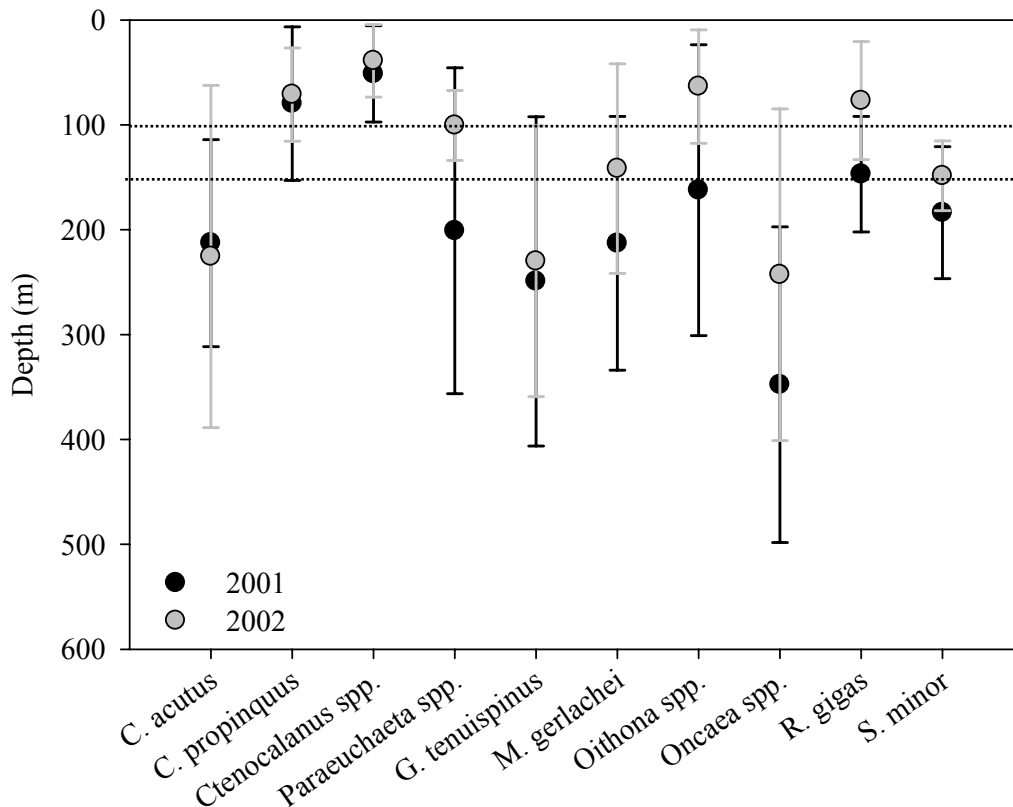| Fall 2002								
Shallow	**Z**	**Range**	**Intermediate**	**Z**	**Range**	**Deep**	**Z**	**Range**
Ctenocalanus **spp.**	39	0 - 500	*M. gerlachei*	142	0 - 500	*C. acutus*	226	0 - 500
Oithona spp.	63	0 - 500	*S. minor*	149	100 - 200	*G. tenuispinus*	230	0 - 500
C. propinquus	71	0 - 460				*Oncaea* **spp.**	243	0 - 500
R. gigas	77	0 - 200						
Paraeuchaeta spp.	100	0 - 500						

Figure 4.8. Mean depth of maximum abundance (m) of copepods during 2001 (black) and 2002 (grey). Values represent the arithmetic mean of the depth of maximum abundance of a species for all net hauls. Vertical bars represent 1 standard deviation. Dotted horizontal lines represent the limits of the 0 - 100, 100 - 150, and > 150 m depth ranges.

the study area, the depths of maximum abundance of species usually did not overlap at any given location (Fig. 4.8). For example in Crystal Sound during 2001, the maximum abundances of *E. superba* occurred at 50 m, while *T. macrura* primarily occurred at 100 m (Fig. 4.9a). In 2002, the depth of maximum abundance for *E. superba* was 150 m, *E. crystallorophias* was primarily found at 50 m, and *T. macrura* was at 75 m. In Laubeuf Fjord, *E. superba* and *T. macrura* had peaks at 100 m in 2001, while *E. crystallorophias* was observed at 50 m, and a second mode for *T. macrura* occurred at 400 - 500 m (Fig. 4.9b). In 2002, *E. superba* had peaks of maximum abundance at 75 m and 150 m, while

E. crystallorophias occurred primarily at 100 m. In the vicinity of Alexander Island

during fall 2001, *E. superba* could be found mostly at 50 m, while *T. macrura* was

mainly at 100 m (Fig. 4.9c). Finally, south of Adelaide Island, elevated abundances of *E.*

superba were located at shallow depths in 2002 (0 - 100 m, maximum at 50 m), while *T.*

macrura showed a smaller peak at 150 m, and *E. crystallorophias* was not present in

significant numbers.

The geometric mean depths of maximum abundances of all euphausiid species

ranged between 65 - 73 m in 2001, while the majority of copepods were located at 252 m

during the same year. Looking at individual net hauls for 2001, the maximum

abundances of both groups did not overlap at almost any location, with the bulk of the

copepod community located consistently deeper than the mode of the euphausiids

(Appendix 1). On the other hand, during 2002, euphausiids were observed at similar

depths as the previous fall, with maximum abundances between 70 - 84 m (Table 4.4),

while copepods were significantly shallower than in 2001, mostly at 75 m (Appendix 2).

Table 4.4. Mean depth of maximum abundance (m) of euphausiids, amphipods, and
mysids during fall 2001 and 2002. Data include all coastal stations for each cruise.
Values represent the geometric mean depth of maximum abundance of each group for all
net hauls during each year (n = 12). The range (m) represents the range of depths in the
water column that were occupied by each taxon

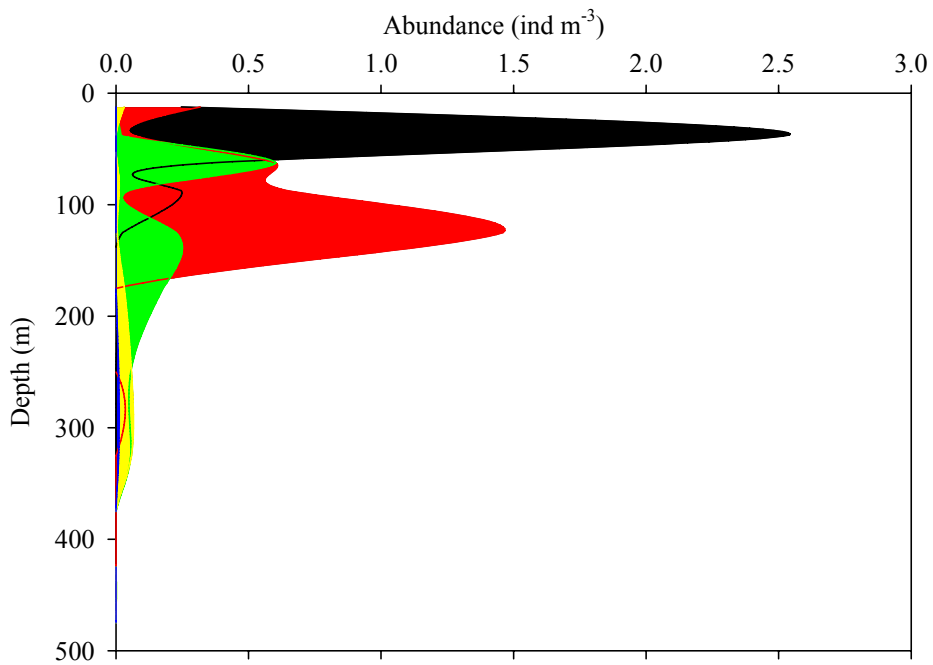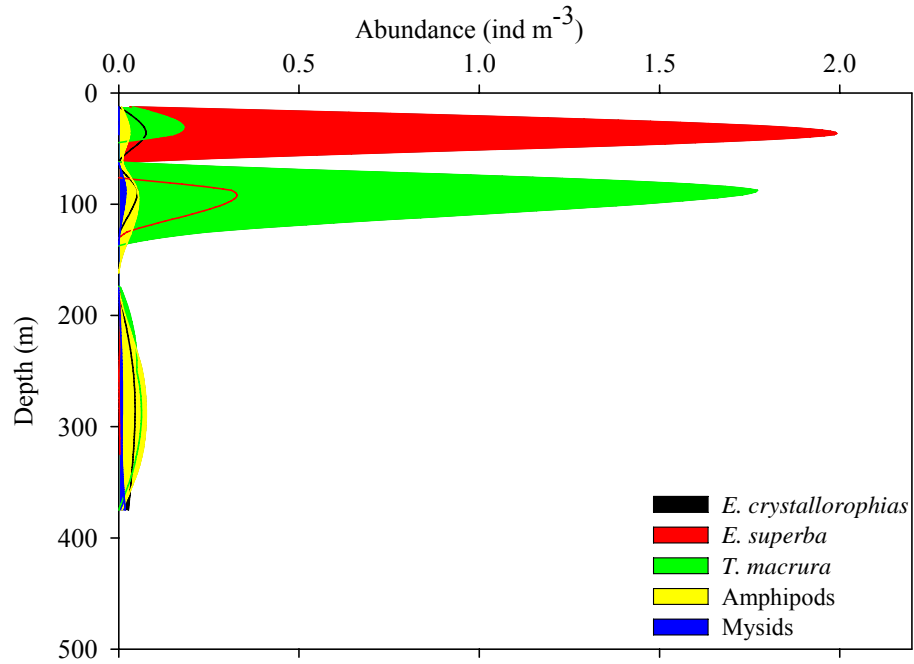|	Fall 2001		Fall 2002	
	Depth (m)	**Range**	**Depth (m)**	**Range**
E. crystallorophias	65	0 - 500	70	0 - 500
E. superba	73	0 - 500	78	0 - 500
T. macrura	68	0 - 800	84	0 - 500
Amphipods	125	0 - 800	55	0 - 500
Mysids	249	0 - 500	224	0 - 500

Figure 4.9a. Vertical distribution of euphausiids, amphipods, and mysids (ind m^{-3}) in Crystal Sound during austral fall 2001 (top) and 2002 (bottom).
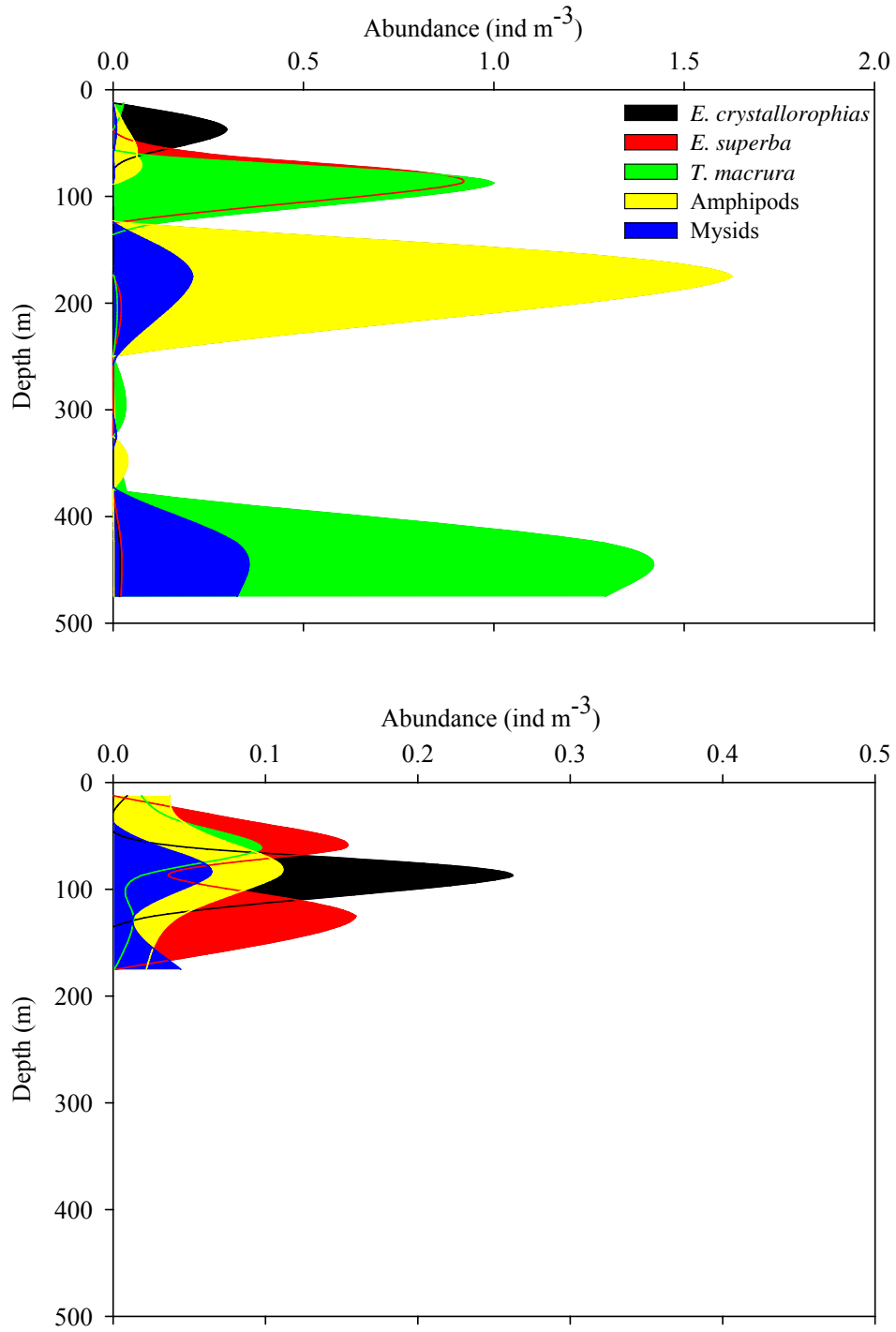
Figure 4.9b. Vertical distribution of euphausiids, amphipods, and mysids (ind m^{-3}) in Laubeuf Fjord during austral fall 2001 (top) and 2002 (bottom).
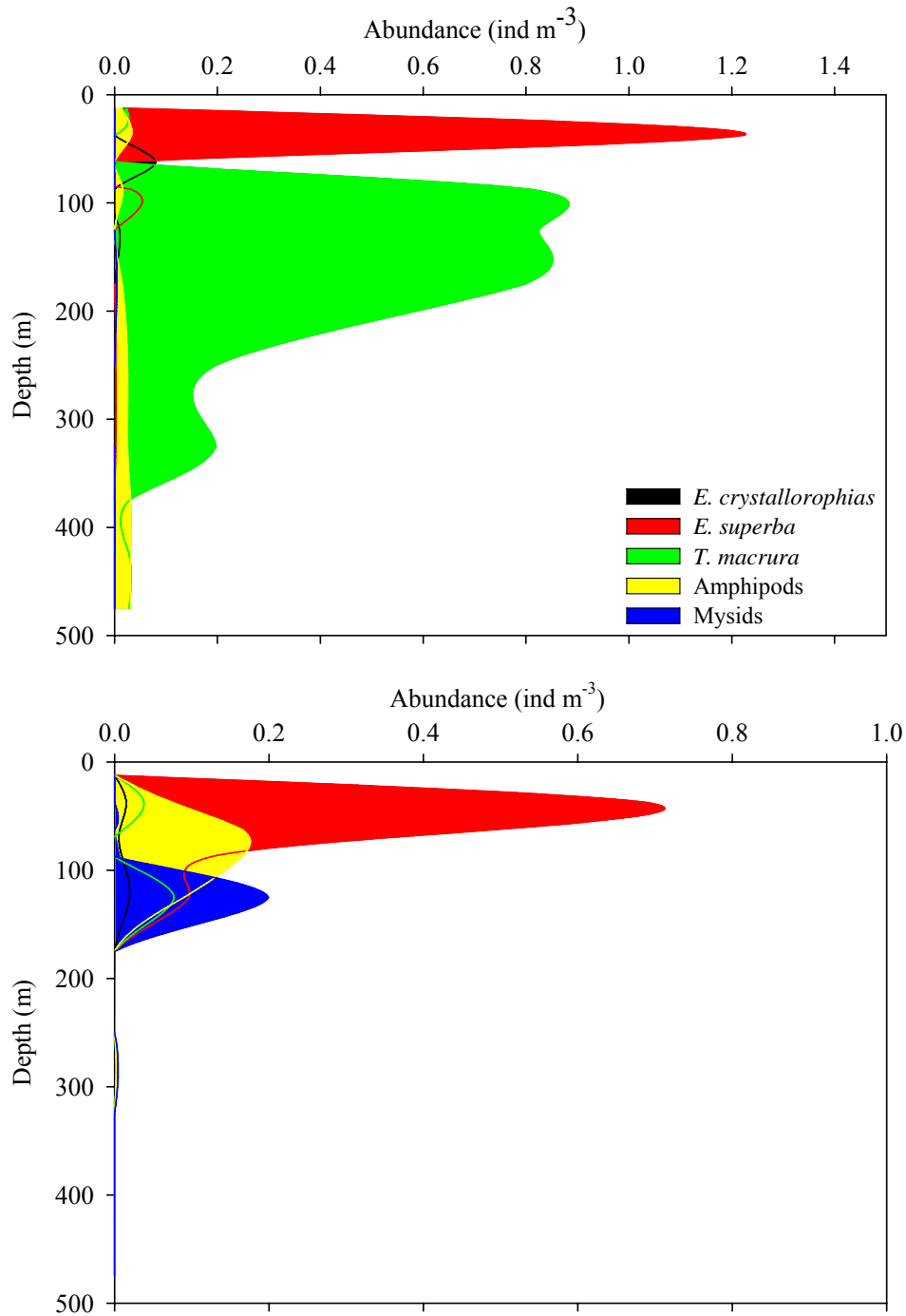
Figure 4.9c. Vertical distribution of euphausiids, amphipods, and mysids (ind m^{-3}) in the vicinity of Alexander Island during austral fall 2001 (top) and south of Adelaide Island in fall 2002 (bottom).

Horizontal Distribution

  The horizontal distribution of zooplankton varied within the study area. In general, in areas where euphausiids, amphipods, and mysids (i.e. macrozooplankton) were abundant, copepod densities were low, and vice versa (Fig. 4.10a). Macrozooplankton were most abundant in northern sectors, whereas copepod abundances were highest in southern sectors, such as inner Marguerite Bay, the vicinity of Alexander Island, George VI Sound and Lazarev Bay (Fig. 4.10b). Exceptions to this pattern were observed in fall 2001 in northern Laubeuf Fjord, where copepods and macrozooplankton were highly abundant, in Bourgeois Fjord, where all zooplankton were scarce, and south of Adelaide Island in 2002, where copepod and macrozooplankton abundances were low.
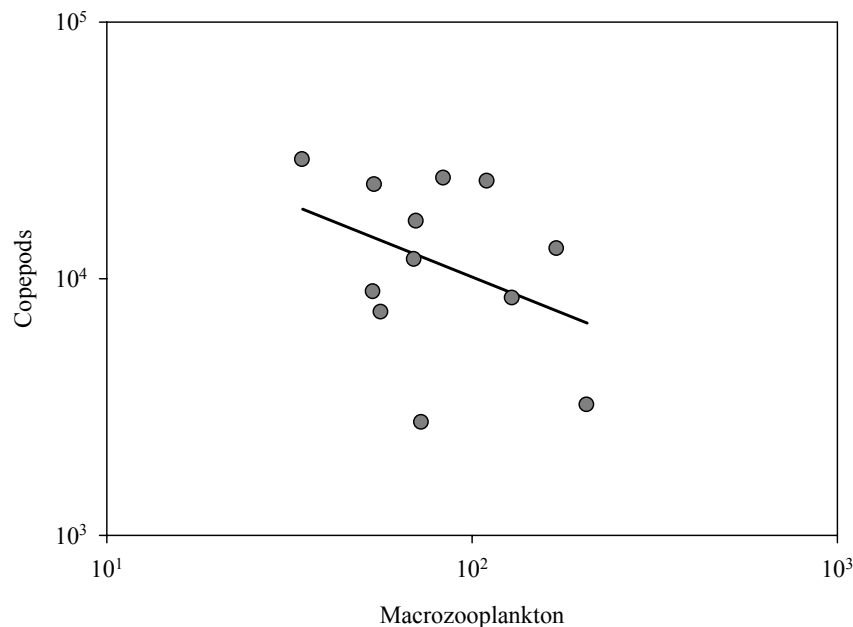

Figure. 4.10a. Linear correlation between integrated abundances (ind m^{-2}) of total macrozooplankton (euphausids, amphipods, and mysids) and copepods at different stations during fall 2001 and 2002 (n = 12; r = -0.39; p = 0.208). When multiple net hauls were sampled, values represent the mean. Plot includes data for stations in Crystal Sound (Sta. 7), Laubeuf and Bourgeois fjords (Sta. 5), Neny Fjord/inner Marguerite Bay (Sta. 6), Marguerite Trough (Sta. 2), S. Adelaide Island (Avian Is.), Alexander Island (Sta. 4a), George VI Sound (Sta. 4b), and Lazarev Bay (Sta. 3). Data for Laubeuf Fjord in 2001 were excluded (outlier).
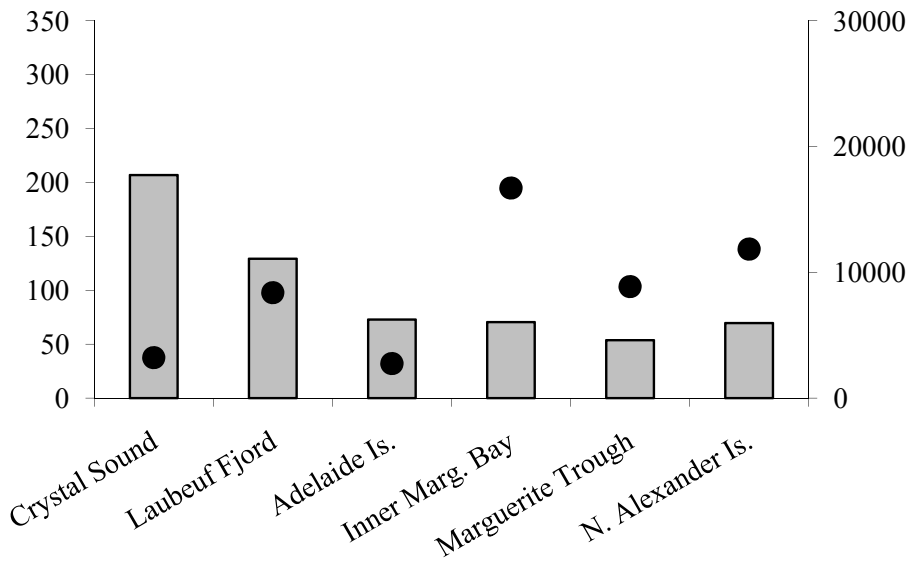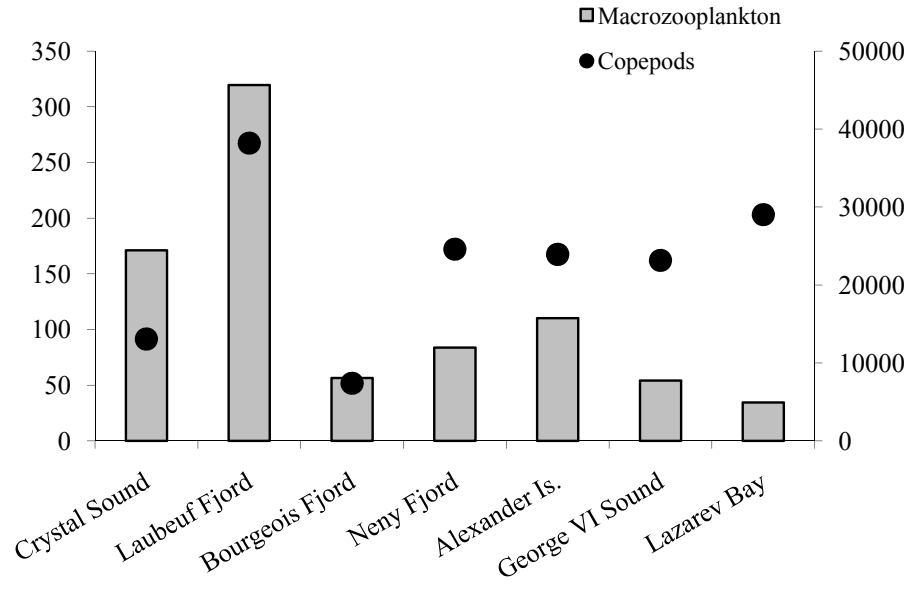
Figure 4.10b. Mean water column integrated abundance (ind m^{-2}) of macrozooplankton (euphausiids, amphipods, and mysids) (grey bars, left axis) and copepods (black circles, right axis) at different stations within Marguerite Bay during fall 2001 (top) and 2002 (bottom).

97

Fall Environmental Parameters

The environmental parameters investigated here were chosen based on their potential influence on zooplankton distributions: vertically integrated pigment concentrations (chlorophyll + phaeopigment, mg m^{-2}), surface salinity, and bottom depth. Integrated pigment represents food availability, while surface salinity is an indicator of sea ice formation and melting, and the presence of glacial meltwater nearshore, which affects the type of phytoplankton present in the water column. Relationships between zooplankton and bottom depth potentially indicate concentration of organisms nearshore or in association with Marguerite Trough, or deep shelf depressions. Fall integrated pigment concentrations in Marguerite Bay ranged between 9.6 - 33 mg m^{-2} in 2001, and 72.4 - 236 mg m^{-2} in 2002. Maximum pigment concentrations were located in Laubeuf Fjord during both years, while lowest values were observed in the in George VI Sound during fall 2001, in Crystal Sound during fall 2002, as well as in the vicinity of Alexander Island during both years. Even though pigment concentrations were lowest in Crystal Sound during 2002, values were more than double those observed in the same area during the previous year. Surface salinity values were similar between years and ranged between 33.04 - and 33.55. The shallowest stations had bottom depths of ~ 300 - 400 m and were located near the coast of Alexander Island, the northern edge of Marguerite Trough in central Marguerite Bay, southern Adelaide Island, and inner Marguerite Bay, while the deepest areas, with bottom depths > 800 m, were in northern George VI Sound, Lazarev Bay, and a location in the vicinity of Alexander Island.

Overall, there were no clear associations between the horizontal distribution of zooplankton (ind m^{-2}) and concurrent environmental variables, including vertically

integrated pigment concentrations (chlorophyll + phaeopigment, mg m^{-2}), surface salinity, and bottom depth (Table 4.5). In general, only a few copepods showed a significant correlation with environmental variables. During 2001, *Ctenocalanus* spp. showed a positive correlation with pigment concentrations, *Oithona* spp. showed a negative relationship, and *G. tenuispinus* was positively correlated with bottom depth. During fall 2002, *Paraeuchaeta* spp. showed a positive correlation with pigment concentrations, while *C. acutus* and *Oncaea* spp. were positively correlated with bottom depth. Only two other zooplankton taxa showed significant relationships with pigment concentrations: *T. macrura* in 2001 and mysids in 2002. Only two groups, *E. superba* and the copepod *R. gigas*, showed significant relationships with surface salinity, and these were only observed during 2002. Of the 138 relationships examined between zooplankton abundance and environmental variables, 11 were significant, which is only slightly higher than the number that would be expected with 95% confidence if all relationships were statistically insignificant (i.e., seven).

At many locations there was a negative trend between the vertical distribution of macrozooplankton (i.e., euphausiids, amphipods, and mysids) and gradients in temperature, salinity, and density (examples in Appendix 3). *E. superba* was located either above or below the thermocline/pycnocline in 92% of the net hauls in which the species was present, while corresponding values for *E. crystallorophias* and *T. macrura* were 77% and 60% respectively (Table 4.6). However, euphasuiids coincided with physical gradients at 8 - 23% of the locations sampled (examples in Appendix 4). Most amphipods and mysids were located primarily deeper than the thermocline/pycnocline, with only smaller fractions present at the depth of the temperature/density gradient. In

general, no patterns were observed in the vertical distribution of zooplankton in relation to fall pigment concentrations.

Table 4.5. Spearman rank order correlations between integrated abundance of zooplankton (ind m^{-2}) and vertically integrated pigment concentrations (chlorophyll + phaeopigment; mg m^{-2}), salinity at 10 m (S_{10}), and bottom depth (bottom Z). Significant correlations ($p < 0.05$) are in bold

	Fall 2001			Fall 2002		
Taxonomic group	**Pigment**	**S_{10}**	**Z**	**Pigment**	**S_{10}**	**Z**
Copepods						
C. acutus	0.415	-0.021	-0.147	0.262	-0.161	**0.630**
C. propinquus	0.085	0.385	-0.403	0.582	0.301	-0.144
Ctenocalanus spp.	**0.799**	-0.063	0.028	0.000	0.210	0.256
G. tenuispinus	-0.257	0.211	**0.641**	0.077	-0.500	0.004
M. gerlachei	0.427	-0.126	-0.077	0.211	0.049	0.441
Oithona spp.	**-0.701**	0.266	0.182	0.143	0.189	0.014
Oncaea spp.	-0.463	-0.161	0.280	0.152	-0.378	**0.635**
Paraeuchaeta spp.	-0.018	0.154	-0.336	**0.743**	-0.223	0.217
R. gigas	-0.300	0.413	-0.039	0.536	**0.609**	0.004
S. minor	-0.173	0.295	-0.033	-0.081	0.037	0.221
TOTAL copepods	0.543	-0.049	-0.147	0.397	0.203	0.497
Ostracods	0.341	-0.126	-0.049	0.379	-0.132	0.382
Euphausiids						
E. crystallorophias	-0.355	-0.487	0.249	0.110	**-0.657**	-0.060
E. superba	0.220	-0.273	-0.427	0.110	-0.582	-0.109
T. macrura	**0.707**	-0.133	-0.287	-0.633	0.217	0.193
Amphipods	0.628	-0.035	-0.517	0.008	-0.356	-0.199
Mysids	0.567	-0.028	-0.028	**0.802**	-0.347	-0.091
Medusae	-0.300	0.099	0.218	0.206	-0.250	0.411
Polychaetes	0.122	-0.553	0.039	0.649	-0.189	0.466
Pteropods	-0.311	0.434	-0.301	0.253	**0.580**	0.311
Chaetognaths	-0.280	0.203	-0.028	-0.084	0.308	-0.045
Appendicularians	-0.165	0.340	-0.119	0.556	0.104	-0.025
Salps	0.009	0.431	-0.211	-0.055	-0.257	0.354

Table 4.6. Percentage of net hauls in which macrozooplankton were located primarily shallower, deeper, or at the same depth as the thermocline/pycnocline. Percentage of net hauls with widespread vertical distributions are also indicated. *n* is the total number of net hauls in which a taxon was present during 2001 and 2002 combined. A total of seven net hauls were excluded from the calculations due to a vertically uniform water column (four net hauls in 2001) or lack of concurrent CTD data (three net hauls in 2002)

	Shallower (%)	Deeper (%)	Same depth (%)	Widespread (%)	n
Euphausiids					
E. crystallorophias	54	23	23	0	13
E. superba	58	33	8	0	12
T. macrura	33	27	13	27	15
Amphipods	19	56	6	19	16
Mysids	0	89	11	0	9

Summer Chlorophyll Concentrations and Krill Recruitment

Surface chlorophyll concentrations in the Bellingshausen Sea and Marguerite Bay during the spring and summer influenced the abundance and composition of the zooplankton during fall (Fig. 4.11a). In oceanic waters of the Bellingshausen Sea (Fig. 4.11b and c), chlorophyll concentrations were above average during austral spring-summer 2000/2001 (November - January). As the summer progressed, phytoplankton blooms moved onshore and above average chlorophyll concentrations were observed in the coastal Bellingshausen Sea during January - March 2001 (Fig. 4.11d). During the 2001/2002 season, conditions offshore were average between November and January (Fig. 4.11b and c), while in coastal waters, above normal chlorophyll concentrations were primarily observed by late February (Fig. 4.11d). Within Marguerite Bay, the interannual differences were even more striking, with extremely high chlorophyll concentrations during austral summer - fall 2001 and below average conditions in 2002 (Fig. 4.11e - f).

There was a strong correlation (Spearman R = 0.81, p < 0.05) between geometric mean chlorophyll concentrations in the Bellingshausen Sea during November and summer recruitment indices for *E. superba* previously reported for the western Antarctic Peninsula region (Fig. 4.12a). Geometric mean chlorophyll concentrations for November 1997 - 2004 in oceanic waters of the Bellingshausen Sea were highest during the spring - summer 2000/2001 season (n = 8), coincident with the highest recruitment index (R_1) observed for *E. superba* during all years for which data are available (1997/1998 - 2002/2003) (Fig. 4.12b). Relatively low chlorophyll concentrations were registered during November 1997, 1998, and 2002, when low recruitment values also were recorded.
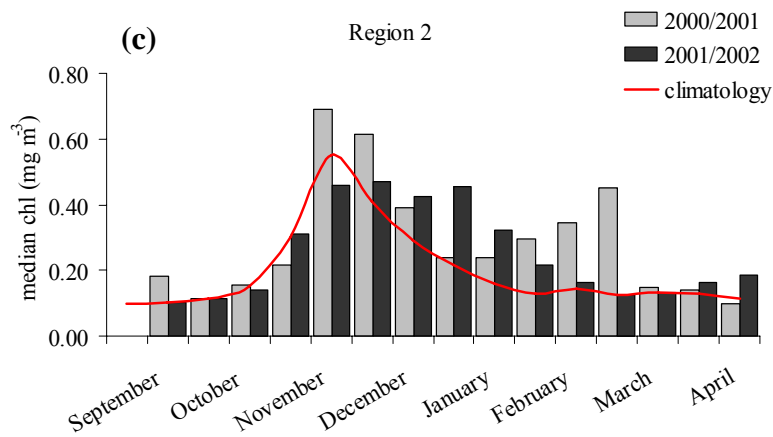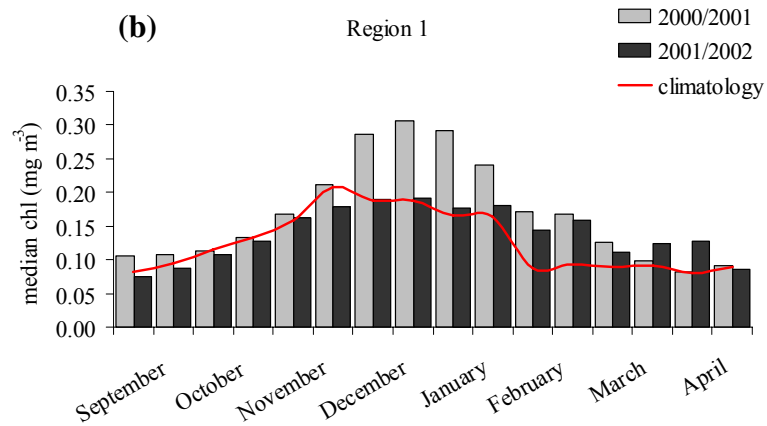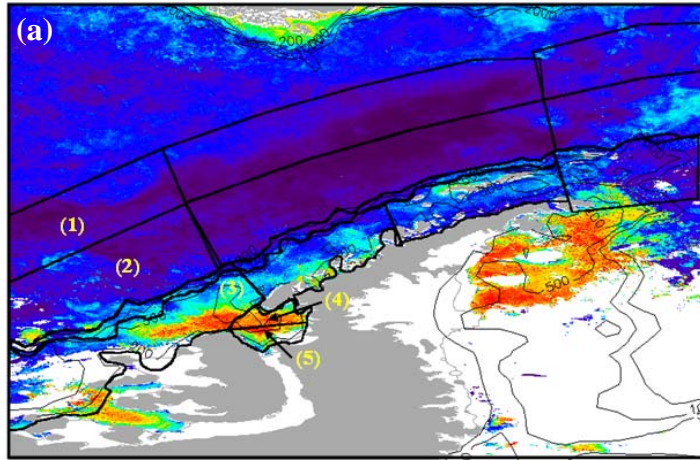
Figure 4.11. (a) Location of the subregions analyzed for median SeaWiFS chlorophyll concentrations (chl, mg m^{-3}) in (b, c) oceanic and (d) coastal waters of the Bellingshausen Sea, (e) northern, and (f) southern Marguerite Bay in spring/summer 2000/2001 (grey) and 2001/2002 (black). A climatology for spring/summer 1997/1998 - 2003/2004 is represented by the red line and corresponds to the median chlorophyll in each subregion for the seven seasons analyzed.
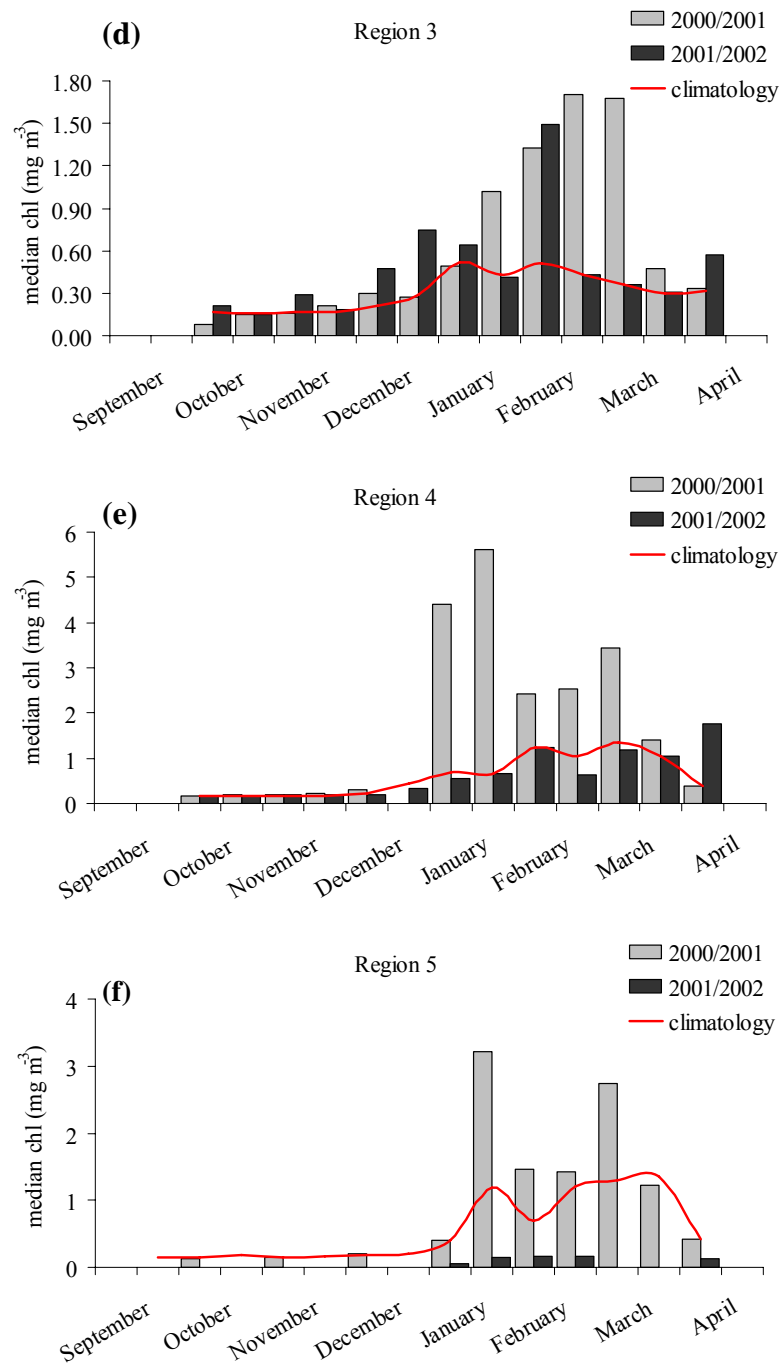
103

(d) Region 3

(e) Region 4

(f) Region 5
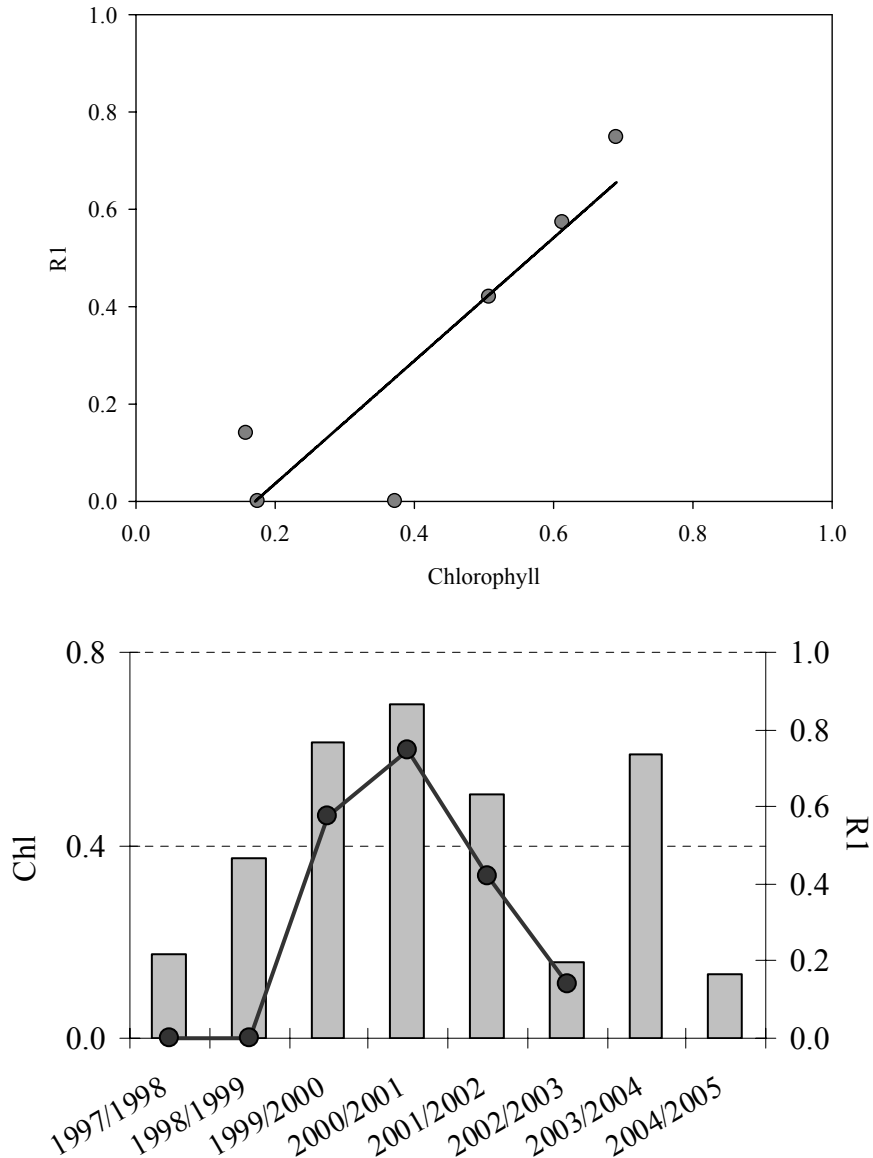
Figure 4.11. (Continued)

104

Figure 4.12. (a) Spearman R correlation between geometric mean chlorophyll concentrations (Chl, mg m^{-3}) in oceanic waters of the Bellingshausen Sea during November 1997 - 2004 and recruitment of *E. superba* (R_1) in waters west of the the Antarctic Peninsula, for the period 1997/1998 - 2002/2003; n = 6; R = 0.81; p < 0.05). (b) Time series of geometric mean chlorophyll concentration in oceanic waters of the Bellingshausen Sea during November 1997 - 2004 (grey bars) and recruitment of *E. superba* (R_1) (black circles) in waters west of Antarctic Peninsula. Chlorophyll estimated as geometric mean SeaWiFS chlorophyll concentration during late November in subregion 2 of Fig. 4.11a. Recruitment indices (R_1) for 1997/1998 - 1999/2000 from Siegel et al. (2002); for 2000/2001 from Siegel et al. (2003); and for 2001/2002 and 2002/2003 from the Palmer LTER DataZoo database (data provided by L. Quetin and R. Ross).

DISCUSSION

Composition and Abundance of Zooplankton in Marguerite Bay

Total zooplankton abundances in the WAP, and Marguerite Bay in particular, are generally higher than those reported for other areas of the Southern Ocean. Deibel and Daly (2007) summarized zooplankton abundance data for continental shelf regions around Antarctica and report that values in Marguerite Bay and Crocker Passage are one or two orders of magnitude higher than in any other area considered, including the Weddell and Ross seas. Copepods numerically dominated the zooplankton community of Marguerite Bay during fall, with a mean abundance of 24,362 ind m^{-2} in 2001, and values up to 44,135 ind m^{-2} in Laubeuf Fjord. Also during SO GLOBEC, Ashjian et al. (2008) investigated zooplankton on the outer continental shelf of Marguerite Bay using Video Plankton Recorder (VPR) data, and estimated copepod mean integrated abundances of 2,832 ± 2,983 ind m^{-2} for fall 2001, only ~ 10% of the estimates reported here for coastal waters in Marguerite Bay. In comparison, near South Georgia in the Scotia Sea, total copepod abundances during summer 1994 - 1996 were up to an order of magnitude higher than those calculated here for fall, with median values ranging between 66,684 and 235,793 ind m^{-2} for the upper 200 m of the water column (Atkinson et al., 1999).

Copepod species composition in Marguerite Bay was comparable to that described for other Antarctic areas, including waters west of the Antarctic Peninsula (e.g., Hopkins, 1985; Schnack-Schiel and Mujica, 1994), the Bellingshausen Sea (Atkinson, 1995; Siegel and Harm, 1996), and western Weddell Sea (Hopkins and Torres, 1988). However, during SO GLOBEC, *C. acutus*, *M. gerlachei*, *Ctenocalanus* spp., and *C.*

propinquus dominated total copepod abundance and, the smaller *Oncaea* spp. and *Oithona* spp. did not represent a major fraction of the community, in contrast to previous results. A study in Crocker Passage, on the northern Antarctic Peninsula shelf, reported a similar fall copepod species composition, but observed that *Oncaea curvata* comprised over half of the total abundance (Hopkins, 1985). Other results from the WAP also indicate that these smaller copepods generally outnumber larger species (Schnack-Schiel and Mujica, 1994; Cabal et al., 2002). In contrast to the relatively finer mesh used during these previous studies (162 - 200 μm), zooplankton were sampled with 333 μm mesh during SO GLOBEC; thus, it is possible that abundances of smaller cyclopods, including *Oncaea* spp. (0.6 - 1.1 mm in length) and *Oithona* spp. (0.7 - 1.2 mm), were underestimated.

T. macrura was the most abundant euphausiid in 2001, with integrated abundances up to 266 ind m^{-2}. These values are higher than maximum integrated abundances of 78 ind m^{-2} reported during spring 1989 for Gerlache Strait, at the northern end of the WAP (Nordhausen, 1994). Mean abundances of *T. macrura* during fall in Marguerite Bay (2001: 45.9 ind m^{-2}; 2002: 16.2 ind m^{-2}) also were higher than average spring values in the Weddell Sea, which ranged between 0.75 and 2.98 ind m^{-2} in the upper 200 m (Donnelly et al., 2006). *E. superba* is often a major fraction of the macrozooplankton community, comprising up to 95% of the larger zooplankton in waters along the northern WAP (Lancraft et al., 2004). This species was observed at almost every location surveyed during the present study; however, abundances did not exceed those of other euphausiids and macrozooplankton groups, particularly during 2001. The distribution of *E. superba* is patchy, with post larval individuals usually aggregated in

compact and dense swarms that can often be undersampled by plankton nets (Wiebe et al., 2004); thus, the relatively low abundances reported here should be interpreted with caution. Densities of *E. superba* estimated from acoustic surveys during the fall survey cruises in Laubeuf Fjord and Crystal Sound were approximately an order of magnitude higher than those from net samples in the same area, and the difference was attributed, in part, to krill net avoidance (Lawson et al., 2008). *T. macrura* forms more diffuse aggregations and is more evenly distributed throughout the water column, which allows for more accurate abundance estimates from net data. Despite being likely undersampled, *E. superba* still comprised a major fraction of the fall zooplankton biomass in Marguerite Bay (see estimates below). Mean integrated abundances of juvenile and adult *E. superba* in Marguerite Bay were 6.22 and 14.8 ind m^{-2} in 2001 and 2002, respectively, with maximum values up to 117 ind m^{-2} in Crystal Sound during 2002. These abundances are in the same order of magnitude as values reported for other areas of the WAP. In a review of data for Elephant Island between 1977 and 2004, Siegel (2005) reports abundances ranging between 1.4 and 336 ind m^{-2} (median for all years = 9.1 ind m^{-2}), while Lancraft et al. (2004) estimated fall abundances of 788 ind m^{-2} for the upper 200 m of the water column in Crocker Passage.

Although *T. macrura* may at times outnumber *E. superba*, the latter is generally more important in terms of biomass. For the present study, biomass data are not available; however, some simple calculations can provide useful estimates of interspecific biomass differences. During 2001, the overall geometric mean abundance of *T. macrura* in Marguerite Bay was 45.9 ind m^{-2}, with most individuals at 9 - 10 mm TL (Fig. 4.5). In the case of *E. superba*, the average abundance was 6.22 ind m^{-2} during

108

the same year, with a mode at 51 mm TL (Fig. 4.4). The mean biomass for *T. macrura* in 2001 was 0.68 g WW m^{-2}, while the corresponding value for *E. superba* was 9.11 g WW m^{-2}, based on the length frequency distributions for both species during fall 2001 and a length-wet weight relationship from Ashjian et al. (2004) (wet weight = 0.0054 x Length$^{3.214}$). These biomass estimates are within the range of values reported for euphausiids in other Antarctic areas. In the western Antarctic Peninsula shelf region, mean fall biomass of krill estimated from acoustic data was 12 g m^{-2} (Lascara et al., 1999), whereas summer estimates for krill around Elephant Island in 1978 - 2004 ranged between 0.76 and 75.2 g m^{-2} (Siegel, 2005). In addition, Voronina (1998) summarized published biomass estimates for *E. superba* from plankton nets in different areas of the northern WAP and reported values generally ranging between 0.2 and 54 g WW m^{-2}, although biomass at Crocker Passage during fall 1983 reached 229 g WW m^{-2}. In the Weddell Sea, average spring biomass for *E. superba* ranged from 0.54 g WW m^{-2} in open waters, to 1.2 g WW m^{-2} in the vicinity of the ice edge, while corresponding values for *T. macrura* were 0.57 and 1.4 g WW m^{-2}, respectively (Donnelly et al., 2006). Despite the rapid population response to elevated food concentrations and numerical dominance of *T. macrura* during fall 2001, *E. superba* was still the dominant euphausiid in terms of biomass.

Other numerically important taxa observed in Marguerite Bay during fall 2001 and 2002, such as ostracods, pteropods, polychaetes, and chaetognaths, are common members of the zooplankton of the WAP (Schnack-Schiel and Mujica, 1994; Siegel and Harm, 1996). Pteropods and ostracods constituted the most abundant non-copepod zooplankton in the study area during both years analyzed. Pteropod abundances recorded

109

during this study did not vary interannually, and are similar to other SO GLOBEC values reported for the outer shelf off Marguerite Bay, which reached ~ 1200 ind m^{-2} in the vicinity of Marguerite Trough (Ashjian et al., 2008). Small pteropods (< 15 mm), which dominated numerically in Marguerite Bay with values up to 2,119 ind m^{-2}, are mostly herbivores (Hopkins, 1985). Ostracods abundances reached 4,728 ind m^{-2} in southern Laubeuf Fjord during 2001, which comprised ~ 76% of the non-copepod zooplankton at this location. Ostracods are generally omnivores and feed primarily on debris of *E. superba*, phytoplankton, and copepods (Hopkins, 1985). To the author's knowledge, other ostracod integrated abundances have not been reported for the Marguerite Bay area, and VPR results indicated that they were not a dominant component of the zooplankton of the mid and outer shelf of Marguerite Bay (C. Ashjian, *pers. comm.*). A study in the Weddell Sea observed that ostracods comprised 5.4% of total zooplankton biomass under the ice, and 2.6% in open waters (Hopkins and Torres, 1988).

Chaetognaths were more abundant in Marguerite Bay than in other Antarctic areas, with mean integrated abundances of 57 and 31.3 ind m^{-2} in 2001 and 2002 respectively, although values reached 687 ind m^{-2} in the vicinity of Alexander Island during 2001. Donnelly et al. (2006) report mean values of 1.75 ind m^{-2} for the Weddell Sea, while Lancraft et al. (2004) estimated mean integrated abundances of 6.37 ind m^{-2} for Crocker Passage during fall. During SO GLOBEC, chaetognaths comprised, on average, 8% of the non-copepod zooplankton during 2001, with values up to 42% in Lazarev Bay, and 23% around Alexander Island. The mean percent composition reported here agrees well with values from the Weddell Sea ranging between 3.8 and 29.3% (Hopkins and Torres, 1988; Donnelly et al., 2006). Chaetognaths are predators and feed

mostly on copepods, although the larger species also have been observed to prey on

mysids and amphipods (Hopkins, 1985). Thus, high abundances of chaetognaths in

copepod-rich waters near Alexander Island are not surprising.

Polychaetes were more abundant in fall 2001 relative to 2002. This group

includes mostly herbivorous species in Antarctic waters (Hopkins, 1985) and, thus,

higher densities in fall 2001, when chlorophyll concentrations were higher, are expected.

Vertically integrated abundances reported for the outer shelf off Marguerite Bay reached

~ 2,300 ind m^{-2} west of Alexander Island in 2001 (Ashjian et al., 2008), more than double

the maximum values of 1,110 ind m^{-2} estimated here in coastal Marguerite Bay during

the same year.

Variability in Euphausiid Life History Strategies

Variability in life history strategies between euphasuiid species resulted in

interannual differences in species percent composition. During the chlorophyll-rich 2001

season, the ubiquitous *T. macrura* dominated the euphausiid community, followed by *E.*

superba, and *E. crystallorophias*. The numerical dominance of *T. macrura* has been

previously reported as well for other areas of the Southern Ocean (e.g., Atkinson and

Peck, 1988; Mujica, 1989). There exist marked differences in the timing of the onset of

reproduction between species of Antarctic euphausiids. *T. macrura* is the first species to

start reproducing, with spawning as early as September (Makarov, 1979). Later in

spring, *E. crystallorophias* reproduction begins, followed by *E. superba*, which spawns

mainly between November and March (Marr, 1962).

Most individuals of *T. macrura* observed during fall 2001 were juveniles between

8 - 11 mm TL (87% total) (Fig. 4.5). *T. macrura* has a more rapid development than the *Euphausia* species. Although information on larval growth rates is available for *T. macrura* (Nordhasuen, 1992, Siegel, 1987), juvenile development has not been described. Nordhausen (1992) reports that it takes 90 days for calyptopis II (C2) to develop into the last larval stage, furcilia VI (F6). In addition, Makarov (1979) estimates that it takes 15 - 20 days for eggs to change into C2, indicating a total larval development time of 105 - 110 days. Siegel (1987) estimated age and growth of *T. macrura* in the Weddell Sea from length-frequency data and suggested that larvae can first develop into juveniles at 8 mm in length, during the second half of their first year of life. If reproduction of *T. macrura* along the western Antarctic Peninsula starts in September - October, individuals observed during fall could be up to seven or eight months old. Development estimates suggest that the *T. macrura* juveniles observed during fall 2001 originated from a reproductive event(s) during spring-summer 2000/2001 (age-class 0+), when chlorophyll concentrations were above climatology values.

Development of *E. superba* and *E. crystallorophias* is slower and, therefore, populations take longer to respond to environmental changes. In contrast to the 105 - 110 days estimated for larval development of *T. macrura*, laboratory experiments indicate that *E. superba* can develop from an egg to F6 in approximately 127 days (Ikeda, 1984), while the larval development time for *E. crystallorophias* is even longer (Ikeda, 1986; Brinton and Townsend, 1991). This longer development coupled with a later onset of reproduction in November - March suggest that juveniles of *E. superba* and *E. crystallorophias* will not be present in the water column of the western Antarctic Peninsula region until the spring of their second year (age class 1+), which is supported

112

by field observations (Daly 2004; Daly and Zimmerman, 2004). During SO GLOBEC, elevated chlorophyll concentrations in 2001 supported a successful reproduction of *E. superba* and *E. crystallorophias* during spring-summer 2000/2001, as evidenced by the presence of numerous larvae in fall 2001 and juveniles during 2002. Hence, *T. macrura* had a rapid population response to elevated chlorophyll concentrations, demonstrated by the large numbers of juveniles present in fall 2001 (Fig. 4.5), whereas *E. superba* and *E. crystallorophias* showed a slower population response, supported by the scarcity of juveniles of either species during fall 2001 and the high proportion of juveniles present during fall 2002 (Figs 4.4 and 4.6).

E. superba females are believed to spawn offshore in the vicinity of the shelf-break (Marr, 1962; Siegel, 1988; 1992). Because eggs are denser than seawater, they sink and hatch at depths of 800 - 1000 m. The young larvae then swim to the surface before turning into the first feeding stage, calyptopis I (Marr, 1962), at which point they need to find food within approximately 10 days or otherwise will not survive (Ross and Quetin, 1986). This life strategy is hypothesized to have several ecological advantages, including preventing the eggs from reaching the seafloor and becoming unviable or eaten by benthic organisms. In addition, the larvae produced at these depths will develop in warmer (> 1 °C) Circumpolar Deep Water (CDW) found below 500 m, thus reducing the risk of predation by epi- and mesopelagic fauna. The developmental ascent described by Marr (1962) for *E. superba* also has been reported for larvae of *T. macrura* (Makarov, 1979). These two species share several ecological characteristics, such as a common widespread distribution, a similar reproductive strategy involving deep hatching of eggs and larval ascent, and a primarily herbivorous larval phase. Their similar life strategies

113

would indicate that these euphausiids are strong competitors; however, it has been suggested that the two month separation between the onset of reproduction is an adaptation to avoid competition for food between their larvae (Makarov, 1979). In addition, during the postlarval stages, when both species coexist, *E. superba* are mainly herbivores during spring and summer, while adult *T. macrura* have been described as omnivores, feeding mostly on large copepods, such as *C. acutus* and *M. gerlachei* (Hopkins, 1985). Additionally, their depths of maximum abundances in the water column generally do not overlap. In summary, although *E. superba* and *T. macrura* share a common distribution and similar life history strategies, they have developed individual adaptations to minimize competition between them, allowing them to coexist as widespread, successful, Antarctic species.

Summer Chlorophyll and Zooplankton Population Response

Interannual variability in chlorophyll concentrations strongly influences zooplankton populations. Population responses for *T. macrura*, *E. crystallorophias*, and *E. superba* were described above. In addition, the influence of spring/summer chlorophyll concentrations is demonstrated by the strong correlation observed between November chlorophyll concentrations in the Bellingshausen Sea and recruitment of *E. superba* along the WAP during the following year. Previous studies reported correlations between sea ice extent during winter and successful juvenile recruitment of *E. superba* during the following spring (Kawaguchi and Satake, 1994; Siegel and Loeb, 1995; Hewitt et al., 2003). Sea ice biota on the undersurface of sea ice constitutes an alternative food source for overwintering larval krill, while sea ice provides refuge from predators, which

114

further reduces winter larval mortality (Daly 1990; Daly and Macaulay, 1991). During

SO GLOBEC, there were interannual differences in the extent and timing of the advance

and retreat of sea ice (Chapter 3; Parkinson, 2002; Marrari et al., 2008); however, winter

sea ice conditions were similar in 2001 and 2002, and sea ice biota concentrations were

low at the ice-water interface during both years (0.05 - 0.07 μg l^{-1}) (Daly, 2004). Despite

similar winter sea ice, krill recruitment showed marked interannual differences,

suggesting that other processes influence recruitment of *E. superba* in this area. It is here

hypothesized that the early and persistent availability of phytoplankton in offshore waters

of the Bellingshausen Sea supports early and repeated reproductive events during spring

and summer and results in a high reproductive output. In addition, high concentrations of

phytoplankton in offshore and coastal areas during summer and fall will lead to faster

growth and development of larvae, which will be in better condition to survive

overwinter. Low food conditions or the late onset of blooms will lead to late and/or poor

reproduction and smaller/weaker larvae which may not be able survive overwinter.

Although phytoplankton blooms in the Bellingshausen Sea and Marguerite Bay were

spatially variable, spring chlorophyll concentrations exceeded minimum values (1 - 5 mg

m^{-3}) required to initiate reproduction of *E. superba* (Ross and Quetin, 1986) during both

SO GLOBEC years. It is the variability in the timing and persistence of these blooms,

rather than the absolute chlorophyll concentrations, what will influence the reproduction

and recruitment success of euphausiids.

The composition of the copepod community also showed marked interannual

differences, which appear to be related to variability in food availability. During the

chlorophyll-rich 2001 season, *C. acutus* dominated, comprising 52% of the total

115

copepods. *C. acutus* has been described as the only true herbivore in Antarctic waters

(Conover and Huntley, 1991; Atkinson, 1998), feeding mainly on phytoplankton during

spring and summer. This species spawns over a short time and produces one distinct

cohort. Maximum densities can be observed in the surface layer during summer, when

the population reaches stage copepodid V (C5). In areas of deep bathymetry, *C. acutus*

undergoes a seasonal ontogenetic migration, moving to deep waters during the fall and

winter, where individuals do not feed (Schnack-Schiel and Mujica, 1994), whereas in

shallower coastal areas, *C. acutus* moves to intermediate depths. *M. gerlachei*, the

second numerically dominant species during 2001 and most abundant copepod in 2002, is

primarily omnivorous and its success does not rely heavily on high phytoplankton

concentrations. This species starts to spawn in December and continues during summer.

M. gerlachei does not undergo a seasonal ontogenetic migration and is more widely

distributed throughout the water column (Atkinson and Peck, 1988; Schnack-Schiel and

Hagen, 1995). The elevated phytoplankton concentrations observed in Marguerite Bay

throughout the summer of 2001 likely favored the reproduction of *C. acutus*, which

reached relatively high abundances and dominated the copepod community during fall.

Lower chlorophyll concentrations during 2002 resulted in lower abundances of copepods.

The copepod community was dominated by omnivorous species, such as *M. gerlachei*

and *Ctenocalanus* spp., which together accounted for ~ 60% of total copepods, whereas

C. acutus had an 85% population reduction relative to 2001.

Controls on Zooplankton Spatial Patterns in Marguerite Bay

Copepods and macrozooplankton showed opposite horizontal distributions in

Marguerite Bay, with higher abundances of macrozooplankton in the northern sectors of the study area, and greatest densities of copepods in southern areas. These distinct distributions are likely the result of a combination of circulation features and seasonal predation. The general circulation in Marguerite Bay (Fig. 1.2) involves a coastal current (APCC) that enters Marguerite Bay at the northern end, flows along the coast in a clockwise direction (Moffat et al., 2008), and exits Marguerite Bay along the outer coast of Alexander Island. In addition, drifter data revealed a clockwise gyre-like circulation in the central areas of Marguerite Bay during fall 2001 and 2002 (Beardsley et al., 2004), while ADCP results showed the presence of two eddies in George VI Sound during fall 2001 (Dorland and Zhou, 2008). These features, in combination with the general circulation of the APCC, contribute to creating a favorable retention habitat for zooplankton in Marguerite Bay. These circulation features can transport zooplankton within coastal Marguerite Bay, particularly smaller taxa such as copepods, which are unable to swim against currents. The northern sectors of the study area, such as southern Crystal Sound, had a more sluggish flow than that observed for the APCC (Zhou et al., 2004). Given the capabilities of euphasuiids to swim at cruising speeds of 10 - 15 cm sec^{-1} (Hamner et al., 1983; Zhou and Dorland, 2004), it is likely that these larger organisms are able to maintain their distributions preferentially in these quieter northern areas, resulting in the higher abundances observed relative to the southern sectors. In a study from the Crystal Sound area using Acoustic Doppler Current Profiler (ADCP) data, Zhou and Dorland (2004) demonstrate that the swimming capabilities of *E. superba* can determine the maintenance of aggregations in the mesoscale circulation field of the area.

The effects of predation are cumulative over the summer productive period and

may have contributed to the different spatial distributions observed between copepods and euphausiids in Marguerite Bay during fall. Predation during fall was likely not strong enough to significantly reduce copepod abundances in the northern sectors, particularly given that the much of the euphausiid and copepod populations occurred at different depths in the water column. A negative correlation between abundances of copepods and euphausiids was reported for summer in waters around South Georgia, where predation pressure of euphausiids was found to determine, at least in part, copepod distributions (Atkinson et al., 1999). In summary, the combined effects of currents and retention features, seasonal predation, and behavior of macrozooplankton, likely determined the distinct spatial distributions observed for these taxa during fall in Marguerite Bay.

Vertical distribution of euphausiids and other zooplankton, including copepods, amphipods and mysids, rarely overlapped throughout Marguerite Bay during 2001. All euphausiids were consistently shallower than the most abundant copepods species, *C. acutus* and *M. gerlachei*, and these vertical distributions are consistent with other results for euphausiids of the continental shelf of Marguerite Bay (e.g., Lawson et al., 2008; Ashjian et al., 2008). Considering that the fall 2001 cruise took place during May - June, after *C. acutus* has normally started its seasonal descent into deeper waters, the vertical separation of the two groups could be attributed to differing winter behaviors. However, the omnivore *M. gerlachei*, which also comprised a major fraction of total copepods, does not undergo seasonal vertical migrations and is known to feed throughout the year. Thus, the deep distribution of this species relative to euphausiids could be the result of accumulated predation pressure. In contrast to the vertical depth partitioning observed in

2001, euphasuiids and copepods had an overlapping distribution during 2002. The overall shallower distribution of copepods in 2002 could have resulted from a combination of factors, including (1) an earlier fall cruise (April - May) relative to 2001 (May - June), (2) a smaller contribution of *C. acutus* to the total copepod abundance with higher proportions of surface-dwelling species such as *Ctenocalanus* spp and *Oithona* spp., and (3) reduced predation pressure during fall 2002, a consequence of *E. superba* not feeding on copepods (K. Daly, *pers. comm.*), as well as lower densities of other omnivorous and carnivorous zooplankton, such as *T. macrura*, chaetognaths and medusae.

Studies of mysids from the Southern Ocean are few; however, Brandt et al. (1998) described 37 species of Antarctic mysids, 19 of which are endemic, and reviewed information on their biogeography and vertical distributions. Mysids are generally hyperbenthic or bathypelagic, and prefer an omnivorous diet, feeding on phytoplankton and a variety of zooplankton, including copepods, coelenterates, and euphausiid molts (Hopkins, 1985). During our study, mysids were located consistently deeper than euphausiids and amphipods, with some individuals recorded at depths of up to 800 m, the maximum depth sampled during SO GLOBEC. These distributions are consistent with previous coastal studies, while in deep-waters, Antarctic species have been recorded at depths of up to 4500 m (Torres and Hopkins, 1988; Brandt et al, 1998). Although depths in Marguerite Bay reach ~ 1,600 m at a few locations, the mean depth of the area is ~ 400 m (Bolmer et al., 2004) (Fig. 1.1). In deeper areas of the WAP, such as the vicinity of the shelf break, vertical distributions of mysids may extend to greater depths than those reported herein.

Amphipods were located at intermediate depths between euphausiids and mysids in 2001, but were shallower than both groups during 2002. Although data on the species composition of the amphipod community during SO GLOBEC are not currently available, the distinct vertical distributions observed could be related to interannual variability in the percent contribution of different species. For example, in 2001 deeper living large gammarid amphipods appear to have dominated, while smaller hyperiid amphipods, such as *Themisto gaudichaudii*, which are known to inhabit shallower waters (Hopkins, 1985; Torres and Hopkins, 1988), may have been more important in 2002.

Relationship between zooplankton and fall environmental parameters

There were no clear trends between zooplankton spatial distributions and fall environmental variables in Marguerite Bay. The positive correlation observed in 2001 between pigment concentrations and abundances of *Ctenocalanus* spp. could be the result of the mainly herbivorous diet of this species (Hopkins, 1985); however, no other herbivores had positive correlations with this parameter. The positive relationship between the carnivore *Paraeuchaeta* spp. and pigment concentrations during 2002 is even less evident. *Paraeuchaeta* spp. are raptorial predators, feeding primarily on smaller copepods, such as *Oncaea* spp. and copepodites of *M. gerlachei* (Hopkins 1985), which are omnivores and may ingest significant amounts of phytoplankton. However, these prey species did not show positive relationships with pigment concentrations. Moreover, only a weak positive trend (not statistically significant) was observed between *Paraeuchaeta* spp. and their main prey, *Oncaea* spp. ($r = 0.39$; $p = 0.216$) and *M. gerlachei* ($r = 0.32$; $p = 0.308$) during 2002. The overall lack of relationship between

120

pigment concentrations and grazers is likely due to the fact that herbivorous/omnivorous copepods may not have been feeding on phytoplankton during mid to late fall. Among the macrozooplankton, only the omnivores *T. macrura* and mysids showed positive correlations with pigment concentrations in 2001 and 2002 respectively, but these relationships were not consistent interannually.

Relationships between copepod abundances and bottom depth are consistent for some copepod species (Table 4.4). For example, *G. tenuispinus*, *C. acutus*, and *Oncaea* spp. were classified as deep species during both years, and also showed a significant tendency for higher abundances at locations of deeper bathymetry, such as those in the vicinity of Marguerite Trough and southern Laubeuf Fjord (Fig. 1.3).

Summary

The variability observed in total abundance and percent composition of the zooplankton of Marguerite Bay during fall can be linked directly to the contrasting environmental conditions that prevailed during the preceding spring-summer seasons. During spring-summer 2000/2001 a combination of warmer sea surface temperatures, higher than normal chlorophyll concentrations, and low sea ice cover resulted in a favorable environment for zooplankton reproduction and larval growth, which led to the distinctive composition and overall higher abundances observed during fall 2001. Above average concentrations of chlorophyll in many areas, including the Bellingshausen Sea and Marguerite Bay, led to high concentrations of copepods, juvenile *T. macrura*, and larval *Euphausia* spp. during fall 2001, and subsequent elevated numbers of juvenile and adult *E. superba* and *E. crystallorophias* in fall 2002. On the other hand, lower surface

temperatures, extensive and persistent sea ice cover and, consequently, lower than normal chlorophyll concentrations during spring-summer 2001/2002, resulted in lower plankton abundances in Marguerite Bay during fall 2002, particularly copepods, larval euphausiids, herbivorous macrozooplankton and juvenile *T. macrura*. For other groups that do not rely heavily on phytoplankton for reproduction and survival, such as ostracods, pteropods, chaetognaths, amphipods and mysids, the interannual environmental variability did not have as large an impact on their populations, which is evidenced by the smaller interannual differences observed in their abundances.

CHAPTER FIVE

SUMMARY AND CONCLUDING REMARKS

Validated satellite chlorophyll data offer great insight into the temporal and spatial variability of phytoplankton dynamics in remote and difficult to access areas, such as the Southern Ocean. The high resolution and synoptic nature of these datasets are unattainable using traditional ship-based measurements. Validation results confirm that SeaWiFS surface chlorophyll concentrations derived for the Southern Ocean are an accurate measure of *in situ* values between 0.05 - 1.5 mg m^{-3}. These findings contradict previous results that report an underestimation of SeaWiFS chlorophyll in Antarctic waters. The good agreement between SeaWiFS and *in situ* chlorophyll concentrations reported here was based on the use of chlorophyll data determined by HPLC as ground truth, instead of chlorophyll concentrations estimated from fluorescence, which has been shown to introduce significant errors when certain accessory pigments are present in the water column. Because more than 90% of the Southern Ocean has chlorophyll values in the 0.05 - 1.5 mg m^{-3} range, it is not necessary to develop an alternative bio-optical algorithm for this region. However, if computer models (e.g., to estimate primary production or eutrophic depth) have been developed using fluorometric methods as input, then the satellite estimates of chlorophyll concentrations will need adjustment to be consistent with these models.

A major finding of this dissertation is the presence of predictable and persistent

123

phytoplankton blooms in the Bellingshausen Sea and Marguerite Bay areas between 1997 and 2004, and the strong influence that environmental variability in these areas has on the zooplankton community of the WAP. The lack of field sampling in this region may partly explain why the magnitude of phytoplankton aggregations has been previously overlooked. Chlorophyll concentrations in the southern sectors are consistently higher than in any other part of the WAP. The climatology of chlorophyll concentrations for the period between 1997 and 2004 indicated that chlorophyll values were elevated during 2001 in comparison to all other years, particularly in the vicinity of Marguerite Bay.

Zooplankton composition in the vicinity of Marguerite Bay was similar to that reported for previous WAP studies, and included 12 species of copepods, three species of euphausiids, and ten other groups. The observed variability in total abundance and percent composition of the zooplankton during fall was strongly influenced by the contrasting environmental conditions that prevailed during the preceding spring-summer seasons. During spring-summer 2000/2001 warmer sea surface temperatures, higher than normal chlorophyll concentrations, and low sea ice cover created a favorable environment for zooplankton reproduction and larval growth. Above average chlorophyll concentrations in 2001 led to high concentrations of copepods, juvenile *T. macrura*, and larval *Euphausia* spp. during fall 2001, and subsequent elevated abundances of juvenile and adult *E. superba* and *E. crystallorophias* during fall 2002. In contrast, lower surface temperatures, extensive and persistent sea ice cover, and consequently lower than normal chlorophyll concentrations during spring-summer 2001/2002 resulted in lower plankton abundances in Marguerite Bay during fall 2002, particularly copepods, larval euphausiids, herbivorous macrozooplankton and juvenile *T. macrura*. For other groups

124

that do not rely heavily on phytoplankton for reproduction and survival such as ostracods, pteropods, chaetognaths, amphipods and mysids, environmental variability did not have a large impact on their populations, which is evidenced by the small interannual differences observed in their abundances.

Zooplankton, particularly *E. superba*, originating in the Bellingshausen Sea and southern areas along the WAP may be a significant source for populations found downstream in shelf waters of the northern Antarctic Peninsula, the Scotia Sea, and South Georgia (Fach and Klinck, 2006; Thorpe et al, 2007). Thus, variability in the timing and persistence of phytoplankton in the southern WAP will not only affect local zooplankton and predators, but ultimately may impact the entire ecosystem of the WAP and adjacent Scotia Sea. The pivotal role that environmental variability in Marguerite Bay and the Bellingshausen Sea plays in structuring the zooplankton community is demonstrated by the results presented here. Given the few datasets currently available, and the poor understanding of the processes than control environmental variability in these regions, particularly chlorophyll dynamics, future studies of ecosystem dynamics along the WAP should include the Marguerite Bay and Bellingshausen Sea regions.

REFERENCES CITED

Ainley, D.G., and Demaster, D.P. 1996. The upper trophic levels in polar marine ecosystems. In: Smith, W.O. (Ed.), Polar Oceanography, Part B: Chemistry, Biology, and Geology. Academic Press, Inc., San Diego, pp 599-629.

Arrigo, K.R., and McClain, C.R. 1994. Spring phytoplankton production in the western Ross Sea. Science 266, 261-263.

Arrigo, K.R., and van Dijken, G.L. 2003. Phytoplankton dynamics within 37 Antarctic coastal polynya systems. Journal of Geophysical Research 108, 3271.

Arrigo, K.R., Worthen, D., Schnell, A., and Lizotte, M.P. 1998. Primary production in Southern Ocean waters. Journal of Geophysical Research 103, 15587-15600.

Ashjian, C.J., Davis, C.S., Gallager, S.M., Wiebe, P.H., and Lawson, G.L. 2008. Distribution of larval krill and zooplankton in association with hydrography in Marguerite Bay, Antarctic Peninsula, in austral fall and winter 2001 described using the Video Plankton Recorder. Deep Sea Research II 55: 455-471.

Ashjian, C.J., Rosenwaks, G.A., Wiebe, P.H., Davis, C.S., Gallager, S.M., Copley, N.J., Lawson, G.L., and Alatalo, P. 2004. Distribution of zooplankton on the continental shelf off Marguerite Bay, Antarctic Peninsula during austral fall and winter, 2001. Deep-Sea Research II 51: 2073-2098.

Atkinson, A. 1995. Omnivory and feeding selectivity in five copepod species during spring in the Bellingshausen Sea, Antarctica. ICES Journal of Marine Science 52: 385-396.

Atkinson, A. 1998. Life cycle strategies of epipelagic copepods in the Southern Ocean. Journal of Marine Systems 15: 289-311.

126

Atkinson. A., and Peck, J.M. 1988. A summer-winter comparison of zooplankton in the oceanic area around South Georgia. Polar Biology 8: 463-473.

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

Atkinson, A., Whitehouse, M.J., Priddle, J., Cripps, G.C., Ward, P., Brandon, M.A., 2001. South Georgia, Antarctica: a productive, cold water, pelagic ecosystem. Marine Ecology Progress Series 216, 279-308.

Barlow, R.G., Mantoura, R.F.C., and Cummings, D.G. 1998. Phytoplankton pigment distributions and associated fluxes in the Bellingshausen Sea during the austral spring 1992. Journal of Marine Systems 17, 97-113.

Beardsley, R.C., Limeburner, R., and Owens, W.B. 2004. Drifter measurements of surface currents near Marguerite Bay on the western Antarctic Peninsula shelf during austral summer and fall, 2001 and 2002. Deep-Sea Research II 51: 1947-1964.

Bianchi, T.S., Lambert, C., and Biggs, D.C. 1995. Distribution of chlorophyll a and phaeopigments in the northwestern Gulf of Mexico: A comparison between fluorometric and high-performance liquid chromatography measurements. Bulletin of Marine Science 56, 25-32.

Bidigare, R.R., Frank, T.J., Zastrow, C., and Brooks, J.M. 1986. The distribution of algal chlorophylls and their degradation products in the Southern Ocean. Deep-Sea Research 33, 923-937.

Bolmer, S.T., Beardsley, R.C., Pudsey, C., Morris, P., Wiebe, P., Hofmann, E.E., Anderson, J., and Maldonado, A. 2004. A high-resolution bathymetric map from Marguerite Bay and adjacent west Antarctic Peninsula shelf from the southern ocean GLOBEC program. Woods Hole Oceanographic Institution Technical Report, WHOI-2004-02, 78pp.

Boyd, P.W. 2002. Environmental factors controlling phytoplankton processes in the Southern Ocean. Journal of Phycology 38, 844-861.

Brandt, A., Mühlenhardt-Siegel, U., and Siegel, V. 1998. An account of the Mysidacea (Crustacea, Malacostraca) of the Southern Ocean. Antarctic Science 10(1): 3-11.

Brinton. E., and Townsend, A.W. 1991. Development rates and habitat shifts in the Antarctic neritic euphausiid *Euphausia crystallorophias*. Deep-Sea Research 38: 1195-1211.

Brinton, E., Huntley, M., and Townsend, A.W. 1986. Larvae of *Euphausia superba* in the Scotia Sea and Bransfield Strait in March 1984 – development and abundance compared with 1981 larvae. Polar Biology 5: 221-234.

Cabal, J.A., Alvarez-Marqués, F., Acuña, J.L., Quevedo, M., Gonzalez-Quirós, R., Huskin, I., Fernández, D., Rodríguez del Valle, C., and Anadón, R. 2002. Mesozooplankton distribution and grazing during the productive season in the Northwest Antarctic Peninsula (FRUELA cruises). Deep-Sea Research II 49: 869-882.

Campbell, J.W. 1995. The lognormal distribution as a model for bio-optical variability in the sea. Journal of Geophysical Research 100: 13,237-13,254.

Campbell, J.W. Methods for quantifying the uncertainty in a chlorophyll algorithm as demonstrated for the SeaWiFS algorithm. Remote Sensing of Environment (submitted).

Carder, K.L., Steward, R.G., Harvey, G.R., and Ortner, P.B. 1989. Marine humic and fulvic acids: their effects on remote sensing of ocean chlorophyll. Limnology and Oceanography 34: 68-81.

Cavalieri, D., Parkinson, C., Gloersen, P., and Zwally, H.J. 1996, updated 2005. Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I passive microwave data, June to September 2001. Boulder, CO, USA: National Snow and Ice Data Center. Digital media.

Chisholm, S.W., Olson, R.J., Zettler, E.R., Goericke, R., Waterbury, J., and Welschmeyer, N. 1988. A novel free living prochlorophyte abundant in the oceanic euphotic zone. Nature 334: 340-343.

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

Costa, D.P., and Crocker, D.E. 1996. Marine mammals of the Southern Ocean. Foundations for Ecological Research West of the Antarctic Peninsula. Antarctic Research Series 70: 287-301.

Croxall, J.P. 1984. Seabirds. In: Laws, R.M. (Ed.), Antarctic Ecology. Academic Press, London, 533-619 pp.

Daly, K.L. 1990. Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. Limnology and Oceanography 35(7): 1564-1576.

Daly, K.L. 2004. Overwintering growth and development of larval *Euphausia superba*: an interannual comparison under varying environmental conditions west of the Antarctic Peninsula. Deep-Sea Research II 51: 2119-2138.

Daly, K.L., and Macaulay, M.C. 1991. The influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the antarctic marginal ice zone. Marine Ecology Progress Series 79: 37-66.

Daly, K.L., and Zimmerman, J. 2004. Comparisons of morphology and neritic distributions of *Euphausia crystallorophias* and *Euphausia superba* furcilia during autumn and winter west of the Antarctic Peninsula. Polar Biology 28: 72-81.

Daly, K.L., Smith, W.O., Johnson, G.C., DiTullio, G.R., Jones, D.R., Mordy, C.W., Feely, R.A., Hansell, D.A., and Zhang, J. 2001. Hydrography, nutrients, and carbon pools in the Pacific sector of the Southern Ocean: Implications for carbon flux. Journal of Geophysical Research 106: 7107-7124.

Darecki, M., and Stramski, D. 2004. An evaluation of MODIS and SeaWiFS bio-optical algorithms in the Baltic Sea. Remote Sensing of Environment 89: 326-350.

De Baar, H.J., De Jong, J.T.M., Bakker, D.C.E., Löscher, B.M., Veth, C., Bathmann, U., and Smetacek, V. 1995. Importance of iron for plankton blooms and carbon dioxide drawdown in the Southern Ocean. Nature 373: 412-415.

Deibel, D., and Daly, K.L. 2007. Zooplankton processes in Arctic and Antarctic polynyas. In: Smith, W.O., Jr., Barber, D., (Eds.), Polynyas: Windows into Polar Oceans. Elsevier Oceanography Series 74: 271-321.

Dierssen, H.M., and Smith, R. 2000. Bio-optical properties and remote sensing ocean color algorithms for Antarctic Peninsula waters. Journal of Geophysical Research 105: 26,301-26,312.

Dierssen, H.M., Vernet, M., and Smith, R.C. 2000. Optimizing models for remotely estimating primary production in Antarctic coastal waters. Antarctic Science 12: 20-32.

Dinniman, M.S., and Klinck, J.M. 2004. A model study of circulation and cross-shelf exchange on the west Antarctic Peninsula continental shelf. Deep-Sea Research II 51: 2003-2022.

Donnelly, J., Sutton, T.T., and Torres, J.J. 2006. Distribution and abundance of micronekton and macrozooplankton in the NW Weddell Sea: relation to a spring ice-edge bloom. Polar Biology 29: 280-293.

Dorland, R.D., and Zhou, M. 2008. Circulation and heat fluxes during the austral fall in George VI Sound, Antarctic Peninsula. Deep-Sea Research II 53: 294-308.

Ducklow, H.W., Fraser, W., Karl, D.M., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M., and Daniels, R.M., 2006. Water-column processes in the West Antarctic Peninsula and the Ross Sea: interannual variations and foodweb structure. Deep-Sea Research II 53: 834-852.

El-Sayed, S.Z., 1971. Observations on phytoplankton bloom in the Weddell Sea. In: Llano, G.A., Wallen, I.E. (Eds.), Biology of the Antarctic Seas IV vol. 17, pp 301-312.

El-Sayed, S.Z. 1994. Southern Ocean ecology: the BIOMASS perspective. Cambridge University Press. 421pp.

El-Sayed, S.Z. 2005. History and evolution of primary productivity studies of the Southern Ocean. Polar Biology 28: 423-438.

El-Sayed, S.Z., and Taguchi, S., 1981. Primary production and standing crop of phytoplankton along the ice-edge in the Weddell Sea. Deep-Sea Research 28A: 1017-1032.

Esaias, W.E., Abbott, M.R., Barton, I., Brown, O.B., Campbell, J.W., Carder, K.L., Clark, D.K., Evans, R.H., Hoge, F.E., Gordon, H.R., Balch, W.M., Letelier, R., and Minnett, P.J. 1998. An overview of MODIS capabilities for ocean science observations. IEEE Transactions on Geoscience and Remote Sensing 36: 1250-1265.

Fach, B.A., and Klinck, J.M. 2006. Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea. Part I: Circulation and particle tracking simulations. Deep-Sea Research I 53: 987-1010.

Fraser, W.R., and Trivelpiece, W.Z. 1996. Factors controlling the distribution of seabirds: winter-summer heterogeneity in the distribution of Adélie penguin populations. Antarctic Research Series 70: 257-272.

Garibotti, I.A., Vernet, M., and Ferrario, M.E. 2005. Annually recurrent phytoplanktonic assemblages during summer in the seasonal ice zone west of the Antarctic Peninsula (Southern Ocean). Deep-Sea Research I 52: 1823-1841.

Garibotti, I.A., Vernet, M., Ferrario, M.E., Smith, R.C., Ross, R.M., and Quetin, L.B. 2003. Phytoplankton spatial distribution patterns along the western Antarctic Peninsula (Southern Ocean). Marine Ecology Progress Series 261: 21-39.

Gibbs C.F. 1979. Chlorophyll *b* interference in the fluorometric determination of chlorophyll *a* and 'phaeo-pigments'. Australian Journal of Marine and Freshwater Research 30: 597-606.

Gloersen, P., Campbell, W.J., Cavalieri, D.J., Comiso, J.C., Parkinson, C.L., and Zwally, H.J. 1992. Arctic and Antarctic Sea ice, 1978-1987: Satellite Passive Microwave Observations and Analysis. NASA Special Publication 511.

Goericke, R., and Repeta, D.J. 1993. Chlorophylls a and b and divinyl chlorophylls a and b in the open subtropical North Atlantic Ocean. Marine Ecology Progress Series 101: 307-313.

Gordon, H.R. 1992. Diffuse reflectance of the ocean: influence of nonuniform phytoplankton pigment profile. Applied Optics 31: 2116-2129.

Gregg, W.W., and Casey, N.W. 2004. Global and regional evaluation of the SeaWiFS chlorophyll dataset. Remote Sensing of Environment 93: 463-479.

Hamner, W.M., Hamner, P.P., Strand, S.W., and Gilmer, R.W. 1983. Behavior of Antarctic krill *Euphausia superba*: chemoreception, feeding, schooling, and molting. Science 220: 433-435.

Hempel, G. 1985. Antarctic marine food webs. In: Siegfried, W.R., Condy, P.R., and Laws, R.M. (Eds.), Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, pp 266-270.

Hempel, I., and Marschoff, E. 1980. Euphausiid larvae in the Atlantic sector of the Southern Ocean. Meeresforschung 28: 32-47.

Hewitt, R.P., Demer, D.A., Emery, J.H. 2003. An 8-year cycle in krill biomass density inferred from acoustic surveys conducted in the vicinity of the South Shetland Island during the austral summers of 1991 - 1992 through 2001 - 2002. Aquatic Living Resources 16: 205-213.

Hoffman, E.E., Capella, J.E., Ross, R.M., and Quetin, L.M. 1992. Models of the early life history of *Euphausia superba* - Part I. Time and temperature dependence during the descent-ascent cycle. Deep-Sea Research 39: 1177-1200.

Hofmann, E.E., Wiebe, P.H., Costa, D.P., and Torres, J.J. 2004. An overview of the Southern Ocean Global Ocean Ecosystems Dynamics program. Deep-Sea Research II 51: 1921-1924.

Holm-Hansen, O., El-Sayed, S.Z., Franceschini, G.A., and Cuhel, R.L. 1977. Primary production and the factors controlling phytoplankton growth in the Southern Ocean. Adaptations within Antarctic ecosystems: proceedings of the Third SCAR Symposium on Antarctic Biology. pp 11-50.

Holm-Hansen, O., Kahru, M., and Hewes, C.D. 2005. Deep chlorophyll a maxima (DCMs) in pelagic Antarctic waters. II. Relation to bathymetric features and dissolved iron concentrations. Marine Ecology Progress Series 297: 71-81.

Holm-Hansen, O., Kahru, M., Hewes, C.D., Kawaguchi, S., Kameda, T., Sushin, V.A., Krasovski, I., Priddle, J., Korb, R., Hewitt, R.P., and Mitchell, B.G. 2004a. Temporal and spatial distribution of chlorophyll-a in surface waters of the Scotia Sea as determined by both shipboard measurements and satellite data. Deep-Sea Research I 51: 1323-1331.

Holm-Hansen, O., Mitchell, B.G. 1991. Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. Deep-Sea Research 38: 961-980.

Holm-Hansen, O., Mitchell, B.G., Hewes, C.D., and Karl, D.M. 1989. Phytoplankton blooms in the vicinity of Palmer Station, Antarctica. Polar Biology 10: 49-57.

Holm-Hansen, O., Naganobu, M., Kawaguchi, S., Kameda, T., Krasovski, I., Tchernyshkov, P., Priddle, J., Korb, R., Brandon, M., Demer, D., Hewitt, R.P., Kahru, M., and Hewes, C.D. 2004b. Factors influencing the distribution, biomass, and productivity of phytoplankton in the Scotia Sea and adjoining waters. Deep-Sea Research II 51: 1333-1350.

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

Hopkins, T.L., and Torres, J.J. 1988. The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986. Polar Biology 9: 79-87.

Hu, C., Carder, K.L., and Müller-Karger, F.E. 2001. How precise are SeaWiFS ocean color estimates? Implications of digitization-noise errors. Remote Sensing of Environment 76: 239-249.

Hu, C., Muller-Karger, F.E., Taylor, C., Carder, K.L., Kelble, C., Johns, E., and Heil, C. 2005. Red tide detection and tracing using MODIS fluorescence data: A regional example in SW Florida coastal waters. Remote Sensing of Environment 97: 311-321.

Hu, C., Nababan, B., Biggs, D.C., and Müller-Karger, F.E. 2004. Variability of bio-optical properties at sampling stations and implications for remote sensing. A case study in the NE Gulf of Mexico. International Journal of Remote Sensing 25: 2111-2120.

Huntley, M., Karl, D.M., Niiler, P., and Holm-Hansern, O. 1991. Research on Antarctic Coastal Ecosystem Rates: an interdisciplinary field experiment. Deep-Sea Research 38: 911-942.

Ikeda, T. 1984. Development of the larvae of the Antarctic krill (*Euphausia superba* Dana) observed in the laboratory. Journal of Experimental Marine Biology and Ecology 75: 107-117.

Ikeda, T. 1986. Preliminary observations on the development of the larvae of *Euphausia crystallorophias* Holt and Tattersall in the laboratory. Mem. Natl. Inst. Polar Res., Special Issue 40: 183-186.

Jeffrey, S.W. 1976. A report of green algal pigments in the Central North Pacific Ocean. Marine Biology 37: 33-37.

Jeffrey, S.W., Mantoura, R.F.C., and Bjornland, T. 1997. Data for the identification of 47 key phytoplankton pigments. In: Jeffrey, S.W., Mantoura, R.F.C., and Wright, S.W. (Eds.), Phytoplankton pigments in oceanography. UNESCO Publishing, Paris, 661pp.

Kawaguchi, S., and Satake, M. 1994. Relationship between recruitment of the Antarctic krill and the degree of ice cover near the South Shetland Islands. Fisheries Science 60, 123-124.

King, J.C. 1994. Recent climate variability in the vicinity of the Antarctic Peninsula. International Journal of Climatology 14: 357-369.

Kirk, J.T.O. 1983. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Cambridge, pp 49-50.

Klinck, J.M., Hofmann, E.E., Beardsley, R.C., Salihoglu, B., and Howard, S. 2004. Water-mass properties and circulation on the west Antarctic Peninsula continental shelf in austral fall and winter 2001. Deep-Sea Research II 51: 1925-1946.

Klinck, J.M., and Nowlin, W.D., Jr. 2001. Antarctic Circumpolar Current. In: Steele, J., Thorpe, S., and Turekian, K., (Eds.), Encyclopedia of Ocean Sciences. Academic Press, pp 151-159.

Korb, R.E., Whitehouse, M.J., and Ward, P. 2004. SeaWiFS in the Southern Ocean: spatial and temporal variability in phytoplankton biomass around South Georgia. Deep-Sea Research II 51: 99-116.

Lancraft, T.M., Reisenbichler, K.R., Robison, B.H., Hopkins, T.L., and Torres, J.J. 2004. A krill-dominated micronekton and macrozooplankton community in Crocker Passage, Antarctica, with an estimate of fish predation. Deep-Sea Research II 51: 2247-2260.

Lascara, C.M., Hofmann, E.E., Ross, R.M., and Quetin, L.B. 1999. Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. Deep-Sea Research 46: 951-984.

Laws, R.M. 1985. The ecology of the southern ocean. American Scientist 73: 26-40.

Lawson, G.L., Wiebe, P.H., Ashjian, C.J., and Stanton, T.K. 2008. Euphasuiid distribution along the Western Antarctic Peninsula - Part B: Distribution of euphasuiid aggregations and biomass, and associations with environmental features. Deep-Sea Research II 53: 432-454.

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., and Trivelpiece, S. 1997. Effects of sea ice extent and krill or salp dominance on the Antarctic food web. Nature 387: 897-900.

Lohrenz, S.E., Weidemann, A.D., and Tuel, M. 2003. Phytoplankton spectral absorption as influenced by community size structure and pigment composition. Journal of Plankton Research 25: 35-61.

Lopez, M.D.G., and Huntley, M. 1995. Feeding and diel vertical migration cycles of *Metridia gerlachei* (Giesbrecht) in coastal waters of the Antarctic Peninsula. Polar Biology 15: 21-30.

Lorenzen, C.J. 1981. Chlorophyll b in the eastern North Pacific Ocean. Deep-Sea Research 28: 1049-1056.

Lowry, L.F., Ward Testa, J., and Clavert, W. 1988. Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. Polar Biology 8: 475-478.

Makarov, R.R. 1979. Larval distribution and reproductive ecology of *Thysanoessa macrura* (Crustacea: Euphausiacea) in the Scotia Sea. Marine Biology 52: 377-386.

Makarov, R.R. 1981. Larval development of the Antarctic euphausiids. BIOMASS Handbook No.3.

Maritorena, S., Siegel, D.A., and Peterson, A.R. 2002. Optimization of a semianalytical ocean color model for global-scale application. Applied Optics 41: 2705-2714.

Marr, J.W.S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba*). 'Discovery' Report 32: 33-464.

Marrari, M., Daly, K.L., and Hu, C. 2008. Spatial and temporal variability of SeaWiFS chlorophyll *a* distributions west of the Antarctic Peninsula: Implications for krill production. Deep-Sea Research II 55: 377-392.

Marrari, M., Hu, C., and Daly, K.L., 2006. Validation of SeaWiFS chlorophyll *a* concentrations in the Southern Ocean: A revisit. Remote Sensing of Environment 105: 367-375.

Marschall, H. 1988. The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. Polar Biology 9: 129-135.

Mauchline, J. 1981. Key for the identification of Antarctic euphausiids. BIOMASS Handbook No.5.

McClain, C.R., Cleave, M.L., Feldman, G.C., Gregg, W.W., Hooker, S.B., and Kuring, N. 1998. Science quality SeaWiFS data for global biosphere research. Sea Technology 39: 10-16.

Measures, C.I., and Vink, S. 2001. Dissolved Fe in the upper waters of the Pacific sector of the Southern Ocean. Deep-Sea Research II 48: 3913-3941.

Meyer, B., Atkinson, A., Blume, B., and Bathmann, U. 2003. Feeding and energy budgets of larval Antarctic krill *Euphausia superba* in summer. Marine Ecology Progress Series 257: 167-177.

Moffat, C., Beardsley, R.C., Owens, B., and van Lipzig, N. 2008. A first description of the Antarctic Peninsula Coastal Current. Deep-Sea Research II 55: 276-293.

Moline, M., and Prézelin, B.B. 1996. Long-term monitoring and analyses of physical factors regulating variability in coastal Antarctic phytoplankton biomass, *in situ* productivity, and taxonomic composition over subseasonal, seasonal and interannual time scales. Marine Ecology Progress Series 145: 143-160.

Moline, M.A., Prèzelin, B., Schofield, O., and Smith, R.C. 1997. Temporal dynamics of coastal Antarctic phytoplankton: environmental driving forces and impact of a 1991/92 summer diatom bloom on the nutrient regimes. In: Battaglia, B., Valencia, J., and Walton, D.W.S. (Eds.), Antarctic communities species structure and survival. Cambridge University Press, pp 67-72.

Moore, J.K., and Abbott, M.R. 2000. Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. Journal of Geophysical Research 105: 28,709-28,722.

Moore, J.K., Abbott, M.R., Richman, J.G., Smith, W.O., Cowles, T.J., Coale, K.H., Gardner, W.D., and Barber, R.T. 1999. SeaWiFS satellite ocean color data from the Southern Ocean. Geophysical Research Letters 26: 1465-1468.

Morel, A. 1988. Optical modeling of the upper ocean in relation to its biogenous matter content (case 1 waters). Journal of Geophysical Research 93: 10,749-10,768.

Mujica, A. 1989. Distribución del Orden Euphausiacea en el Estrecho Bransfield y zonas adyacentes (SIBEX-INACH, Enero-Frebrero, 1984). Pesq. Antart. Bras. 1(1): 35-44.

Müller-Karger, F.E., Varela, R., Thunell, R., Astor, Y., Zhang, H., Luerssen, R., and Hu, C. 2004. Processes of coastal upwelling and carbon flux in the CARIACO basin. Deep Sea Research 51: 927-943.

Murase, H., Matsuoka, K., Ichii, T., and Nishiwaki, S. 2002. Relationahip between the distribution of euphausiids and baleen whales in the Antarctic (35°E - 145°W). Polar Biology 25: 135-145.

Nemoto, T., and Nasu, K. 1958. *Thysanoessa macrura* as a food of baleen whales in the Antarctic. Sci. Rep. Whales Re. Inst. 13: 193-199.

Nicol, S., De la Mare, W.K., and Stolp, M. 1995. The energetic cost of egg production in Antarctic krill (*Euphusia superba* Dana). Antarctic Science 7: 25-30.

Nordhasuen, W. 1992. Distribution and growth of larval and adult *Thysanoessa macrura* (Euphausiacea) in the Bransfield Strait region, Antarctica. Marine Ecology Progress Series 83: 185-196.

Nordhausen, W. 1994. Distribution and diel vertical migration of the euphausiid *Thysanoessa macrura* in Gerlache Strait, Antarctica. Polar Biology 14: 219-229.

O'Reilly J.E., Maritorena, S., O'Brien, M.C., Siegel, D.A., Toole, D., Menzies, D., Smith, R.C., Mueller, J.L., Mitchell, B.G., Kahru, M., Chavez, F.P., Strutton, P., Cota, C.F., Hooker, F.B., McClain, C.R., Carder, K.L., Müller-Karger, F.E., Harding, L., Magnuson, A., Phinney, D., Moore, G.F., Aiken, J., Arrigo, K.R., Letelier, R., and Culver, M. 2000. SeaWiFS postlaunch calibration and validation analyses: Part 3. SeaWiFS postlaunch technical report series, 11. In: Hooker, S.B., and Firestone, E.R. (Eds.), NASA Technical Memorandum 2000-206892, 49pp.

Orsi, A.H., Whitworth III, H., and Nowlin, W.D. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep-Sea Research 42: 641-673.

Park, T. 1994. Taxonomy and distribution of the marine calanoid copepod family Euchaetidae. Bulletin of the Scripps Institution of Oceanography University of California, San Diego v. 29, University of California Press, Berkeley, CA. 203pp.

Parkinson, C.L. 2002. Trends in the length of the Southern Ocean sea-ice season, 1979-1999. Annals of Glaciology 34: 435-440.

Parsons, T.R., Takahashi, M., and Hargrave, B. 1984. Biological Oceanographic Processes. Pergamon Press, Oxford. 330pp.

Prézelin, B.B., Hofmann, E.E., Mengelt, C., and Klinck, J.M. 2000. The linkage between Upper Circumpolar Deep Water (UCDW) and phytoplankton assemblages on the west Antarctic Peninsula continental shelf. Journal of Marine Research 58: 165-202.

Prézelin, B.B., Hofmann, E.E., Moline, M., and Klinck, J.M. 2004. Physical forcing of phytoplankton community structure and primary production in continental shelf waters of the Western Antarctic Peninsula. Journal of Marine Research 62: 419-460.

Quetin, L.B, and Ross, R.M. 2003. Episodic recruitment in Antarctic krill, *Euphausia superba*, in the Palmer LTER study region. Marine Ecology Progress Series 259: 185-200.

Quetin, L.B., Ross, R.M., Frazer, T.K., Amsler, M.O., Wyatt-Evens, C., and Oakes, S.A. 2003. Growth of larval krill, *Euphausia superba*, in fall and winter west of the Antarctic Peninsula. Marine Biology 143: 833-843.

139

Rakusa-Suszczewski, S. 1984. Krill larvae in the Atlantic sector of the Southern Ocean during FIBEX 1981. Polar Biology 3: 141-147.

Rodriguez, F., Varela, M., and Zapata, M. 2002. Phytoplankton assemblages in the Gerlache and Bransfield Straits (Antarctic Peninsula) determined by light microscopy and CHEMTAX analysis of HPLC pigment data. Deep-Sea Research II 49: 723-747.

Ross, R.M., and Quetin, L.B. 1983. Spawning frequency and fecundity of the Antarctic krill *Euphausia superba*. Marine Biology 77: 201-205.

Ross, R.M., and Quetin, L.B. 1986. How productive are Antarctic krill? BioScience 36: 264-269.

Ross, R.M., and Quetin, L.B. 1989. Energetic cost to develop to the first feeding stage of *Euphausia superba* Dana and the effect of delays in food availability. Journal of Experimental Marine Biology and Ecology 133: 103-127.

Ross, R.M., Hofmann, E.E., and Quetin, L.B. 1996. Foundations for Ecological Research West of the Antarctic Peninsula. American Geophysical Union, Washington, DC. 448pp.

Sarmiento, J.L., Hughes, T.M.C., Stouffer, R.J., and Manabe, S. 1998. Simulated response of the ocean carbon cycle to anthropogenic climate warming. Nature 393: 245-249.

Savidge, G., Harbour, D., Gilpin, L.C., and Boyd, P.W. 1995. Phytoplankton distributions and production in the Bellingshausen Sea, Austral spring 1992. Deep-Sea Research II 42: 1201-1224.

Schnack-Schiel, S.B. 2001. Aspects of the study of the life cycles of Antarctic copepods. Hydrobiologia 453/454: 9-24.

Schnack-Schiel, S.B., and Hagen, W. 1995. Life cycle strategies of *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* (Copepoda: Calanoida) in the eastern Weddell Sea, Antarctica. ICES Journal of Marine Science 52: 541-548.

Schnack-Schiel, S.B., and Mujica, A. 1994. The zooplankton of the Antarctic Peninsula region. In: El-Sayed (Ed.), Southern Ocean Ecology: the BIOMASS prespective. Cambridge University press, pp 79-92.

Schnack-Schiel, S.B., Hagen, W., and Mizdalski, E. 1991. Seasonal comparison of *Calanoides acutus* and *Calanus propinquus* (Copepoda: Calanoida) in the southeastern Weddell Sea, Antarctica. Marine Ecology Progress Series 70: 17-27.

Sedwick, P.N., and DiTullio, G.R. 1997. Regulation of algal blooms in Antarctic shelf waters by the release of iron from melting sea ice. Geophysical Research Letters 24: 2515-2518.

Shapiro, S.S., Wilk, M.B., and Chen, H. J. 1968. A comparative study of various tests of normality. Journal of the American Statistical Association 63: 1343-1372.

Siegel, V. 1987. Age and growth of Antarctic Euphausiacea (crustacean) under natural conditions. Marine Biology 96: 483-495.

Siegel, V, and Harm, U. 1996. The composition, abundance, biomass and diversity of the epipelagic zooplankton communities of the Southern Bellingshausen Sea (Antarctic) with special reference to krill and salps. Arch. Fish. Mar. Res. 44: 115-139.

Siegel, V. 1992. Assessment of the krill (*Euphausia superba*) spawning stock off the Antarctic Peninsula. Arch. Fisch. Wiss. 41: 101-130.

Siegel, V. 2005. Distribution and population dynamics of *Euphausia sup*erba: summary of recent findings. Polar Biology 29: 1-22.

Siegel, V. 1988. A concept of seasonal variation of krill (*Euphausia superba*) distribution and abundance west of the Antarctic Peninsula. In: Sahrhage, D., (Ed.), Antarctic Ocean and Resources Variability. Springer, Berlin, pp 219-230.

Siegel, V., Bergstrom, B., Mühlenhardt-Siegel, and U., Thomasson, M. 2002. Demography of krill in the Elephant Island area during summer 2001 and its significance to stock recruitment. Antarctic Science 14: 162-170.

141

Siegel, V., and Loeb, V. 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. Marine Ecology Progress Series 123: 45-56.

Siegel, V., Loeb, V., and Gröger, J. 1998. Krill (*Euphausia superba*) density, proportional and absolute recruitment and biomass in the Elephant Island region (Antarctic Peninsula) during the period 1977 to 1997. Polar Biology 19: 393-398.

Siegel, V., Ross, R.M., and Quetin, L.B. 2003. Krill (*Euphausia superba*) recruitment indices from the western Antarctic Peninsula: are they representative of larger regions? Polar Biology 26: 672-679.

Smith, D.A., Hofmann, E.E., Klinck, J.M., and Lascara, C.M. 1999. Hydrography and circulation of the west Antarctic Peninsula continental shelf. Deep-Sea Research I 46: 925-949.

Smith, R.C., Baker, K.S., and Dustan, P. 1981. Fluorometric techniques for the measurement of oceanic chlorophyll in the support of remote sensing. SIO Ref. 81-17.

Smith, R.C., Baker, K.S., Byers, M.L., and Stammerjohn, S.E. 1998b. Primary productivity of the Palmer Long Term Ecological Research Area and the Southern Ocean. Journal of Marine Systems 17: 245-259.

Smith, R.C., Baker, K.S., Dierssen, H.M., Stammerjohn, S.E., and Vernet, M. 2001. Variability of primary production in an Antarctic marine ecosystem as estimated using a multi-scale sampling strategy. American Zoologist 41: 40-56.

Smith, R.C., Baker, K.S., and Vernet, M. 1998a. Seasonal and interannual variability of phytoplankton biomass west of the Antarctic Peninsula. Journal of Marine Systems 17: 229-243.

Smith, R.C., Dierssen, H. and Vernet, M. 1996b. Phytoplankton biomass and productivity in the Western Antarctic Peninsula region. In: Ross, R.M., Hofmann, E.E. and Quetin, L.B. (Eds.), Foundations for Ecological Research West of the Antarctic Peninsula. AGU Antarctic Research Series 70, 233-256.

Smith, R.C., Stammerjohn, S.E., and Baker, K.S. 1996a. Surface air temperature variations in the western Antarctic Peninsula region. In: Ross, R.M., Hofmann, E.E., and Quetin, L.B. (Eds.), Foundation for Ecological Research West of the Antarctic Peninsula. AGU Antarctic Research Series 70, 105-121.

Smith, W.O., and Nelson, D.M. 1985. Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. Science 227: 163-166.

Sullivan, C.W., Arrigo, K.R., McClain, C.R., Comiso, J.C., and Firestone, J. 1993. Distribution of phytoplankton blooms in the Southern Ocean. Science 262: 1832-1837.

Thorpe, S.E., Murphy, E.J., and Watkins, J.L. 2007. Circumpolar connections between Antarctic krill (*Euphausia superba* Dana) populations: Investigating the roles of ocean and sea ice transport. Deep-Sea Research I 54: 792-810.

Trees, C.C., Kennicutt, M.C., and Brooks, J.M. 1985. Errors associated with the standard fluorometric determination of chlorophylls and phaeopigments. Marine Chemistry 17: 1-12.

Trivelpiece, W.Z., and Fraser, W.R. 1996. The breeding biology and distribution of Adélie penguins: adaptations to environmental variability. Antarctic Research Series 70: 273-285.

Vaughan, D.G., Marshall, G.J., Connelley, W.M., Parkinson, C., Mulvaney, W., Hodgson, D.A., King, J.C., Pudsey, C.J., and Turner, J. 2003. Recent rapid regional climate warming on the Antarctic Peninsula. Climate Change 60: 243-274.

Vaughan, D.G., and Doake, C.S.M. 1996. Recent atmospheric warming and retreat if ice shelves on the Antarctic Peninsula. Nature 379: 328-331.

Voronina, N.M. 1998. Comparative abundance and distribution of major filter-feeders in the Antarctic pelagic zone. Journal of Marine Systems 17: 375-390.

143

Watkins, J.L., Hewitt, R., Naganobu, M., and Sushin, V. 2004. The CCAMLR 2000
    Survey: a multinational, multi-ship biological oceanography survey of the
    Atlantic sector of the Southern Ocean. Deep-Sea Research II 51: 1205-1213.

Welschmeyer, N. 1994. Fluorometric analysis of chlorophyll a in the presence of
    chlorophyll b and phaeopigments. Limnology and Oceanography 39: 1985-1992.

Wiebe, P.H., Ashjian, C.J., Gallager, S.M., Davis, C.S., Lawson, G.L., and Copley, N.J.
    2004. Using a high powered strobe light to increase the catch of Antarctic krill.
    Marine Biology 144: 493-502.

Wright, S.W., Jeffrey, S.W., Mantoura, R.F.C., Llewellyn, C.A., Bjorland, T., Repeta D.,
    and Welschmeyer, N. 1991. Improved HPLC method for the analysis of
    chlorophylls and carotenoids from marine phytoplankton. Marine Ecology
    Progress Series 77: 183-196.

Zapata, M., Rodriguez, F., and Garrido J.L. 2000. Separation of chlorophylls and
    carotenoids from marine phytoplankton: a new HPLC method using a reversed
    phase C8 column and pyridine-containing mobile phases. Marine Ecology
    Progress Series 195: 29-45.

Zar, J.H. 1984. Biostatistical Analysis. Prentice Hall Inc., New Jersey. 717pp.

Zhang, C., Hu, C., Shang, S., Müller-Karger, F.E., Li, Y., Dai, M., Huang, B., Ning, X.,
    and Hong, H. 2006. Bridging between SeaWiFS and MODIS for continuity of
    chlorophyll a concentration assessments off Southeastern China. Remote Sensing
    of Environment 102: 250-263.

Zhou, M., and Dorland, R. 2004. Aggregation and vertical migration behavior of
    Euphausia superba. Deep-Sea Research II 51: 2119-2138.

Zhou, M., Zhu, Y., and Peterson, J.O. 2004. In situ growth and mortality of
    mesozooplankton during the austral fall and winter in Marguerite Bay and its
    vicinity. Deep-Sea Research II 51: 2009-2118.

APPENDICES

Appendix 1. Vertical distribution of euphausiids (left column) and copepods (ind m^{-3}) (right column) in Marguerite Bay during fall 2001. The black broken line indicates the maximum sampling depth when a net haul was sampled to depths shallower than 500 m.

Crystal Sound

Northern Laubeuf Fjord


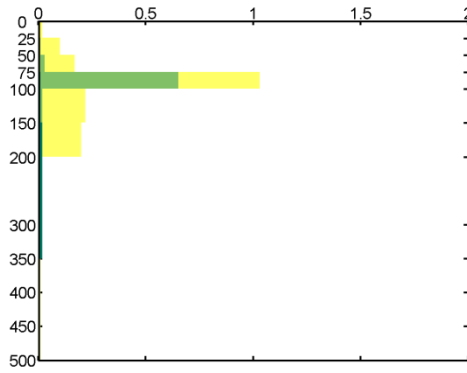
Southern Laubeuf Fjord

146
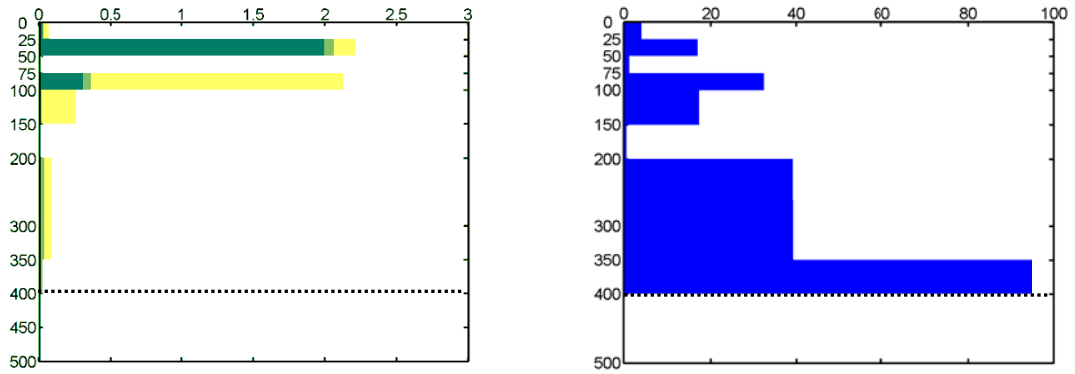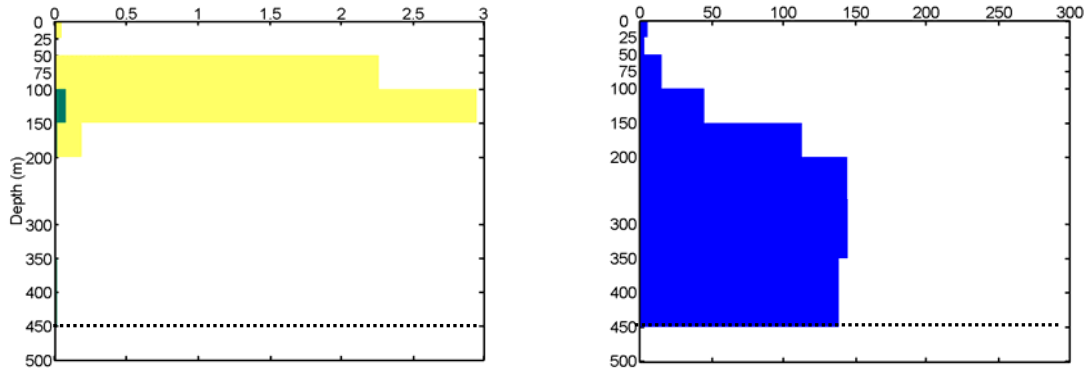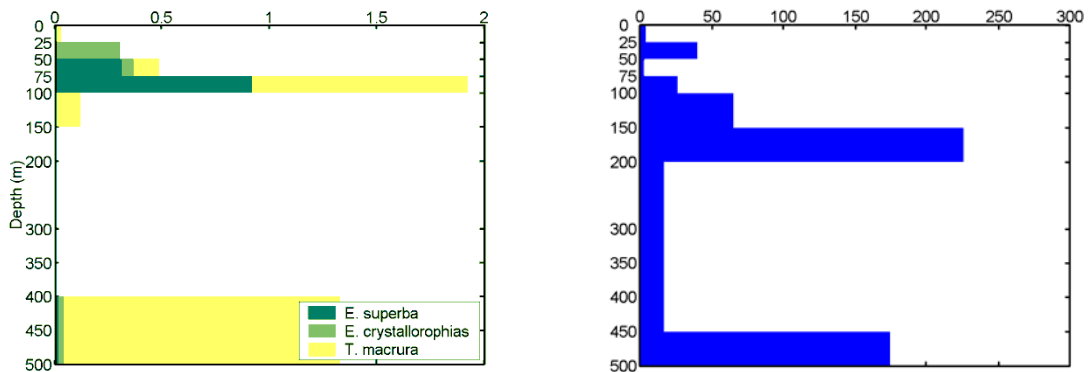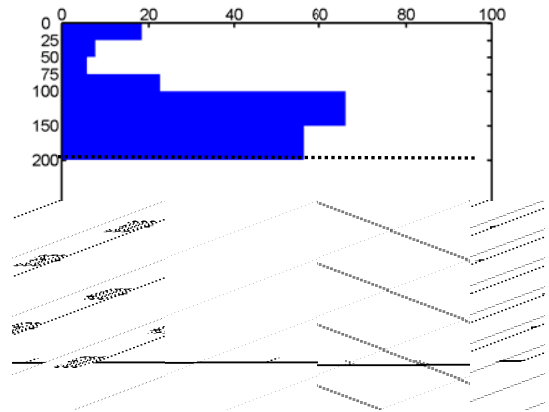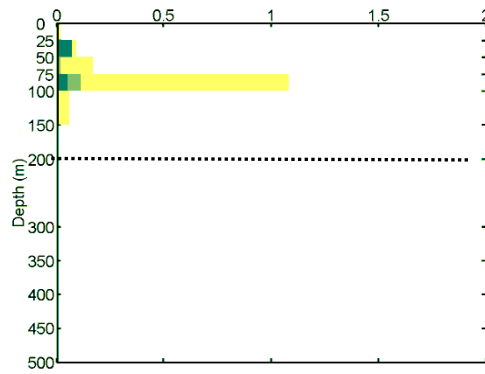
Bourgeois Fjord
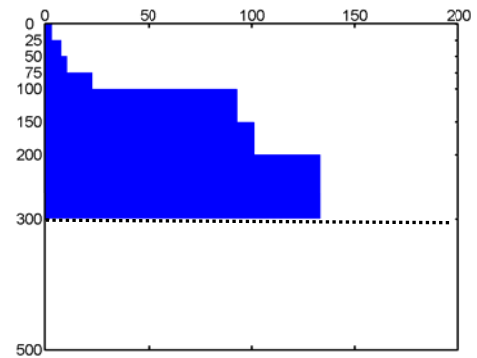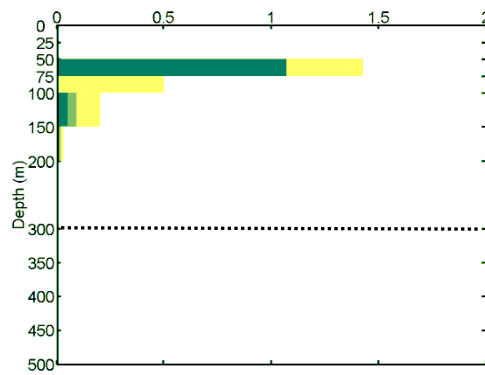
Neny Fjord
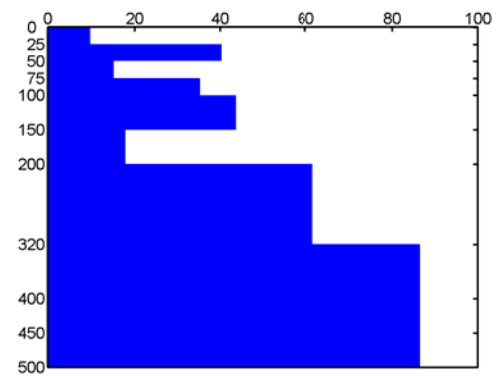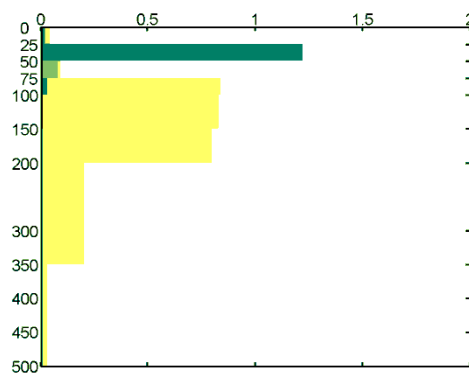
Northern Alexander Island

Appendix 1. (Continued)
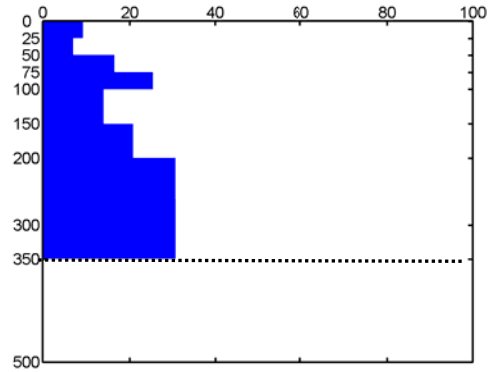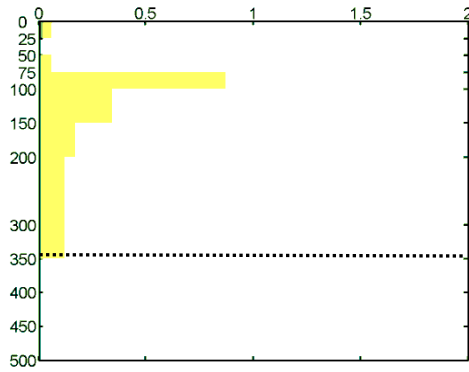
Northern Alexander Island
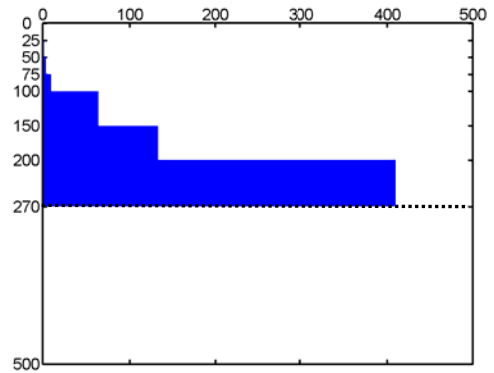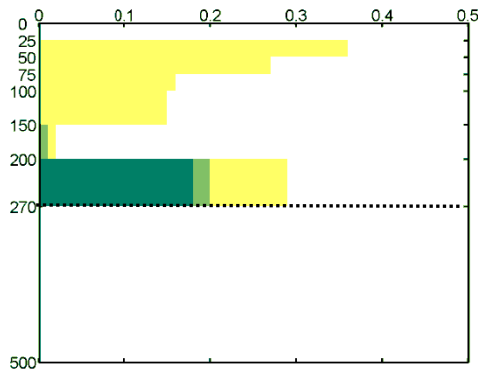
Northern Alexander Island

Lazarev Bay

148
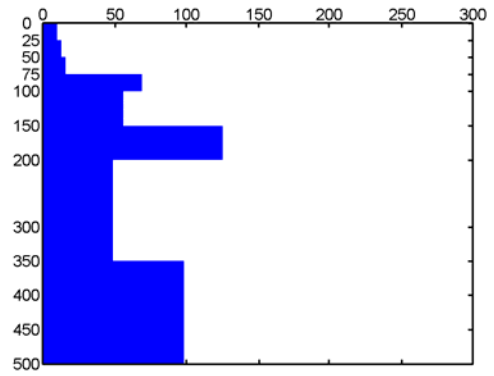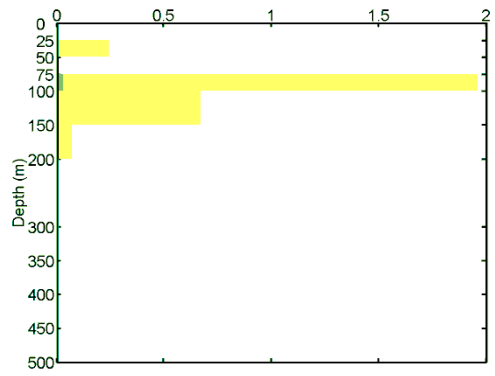
Northern George VI Sound
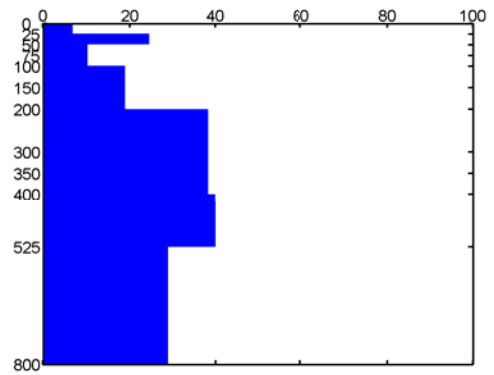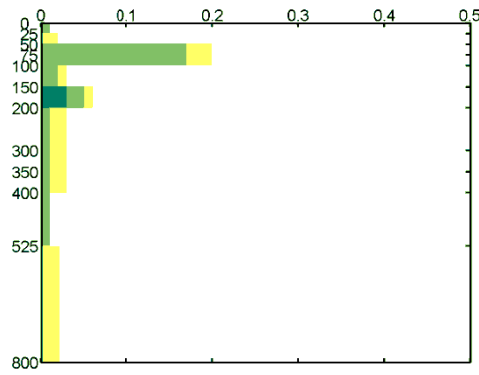
Southern George VI Sound
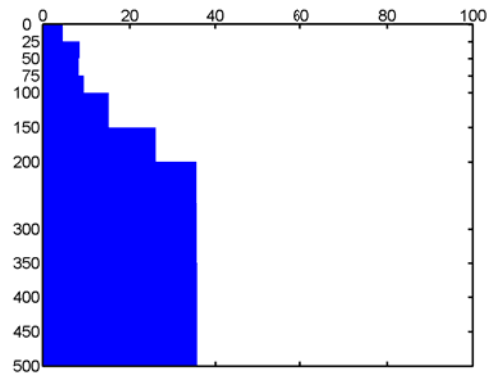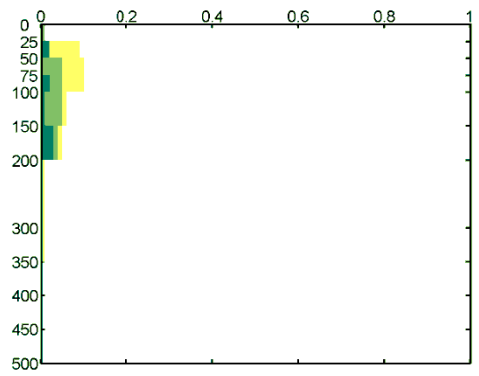
Southern George VI Sound

Appendix 2. Vertical distribution of euphausiids (left column) and copepods (ind m^{-3}) (right column) in Marguerite Bay during fall 2002. The black broken line indicates the maximum sampling depth when a net haul was sampled to depths shallower than 500 m. Color legend as in Appendix 1.
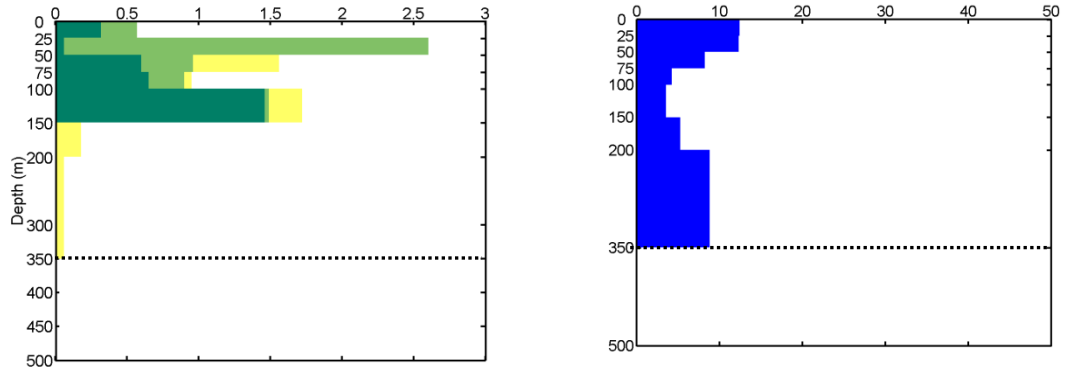
Crystal Sound

Crystal Sound

Northern Laubeuf Fjord
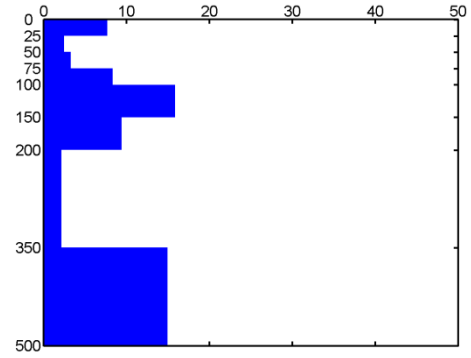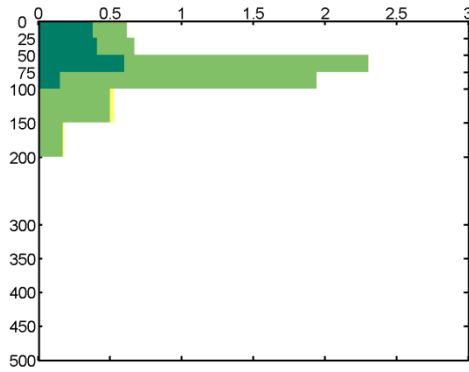
Southern Laubeuf Fjord

Southern Laubeuf Fjord

Northern Alexander Island

Appendix 2. (Continued)
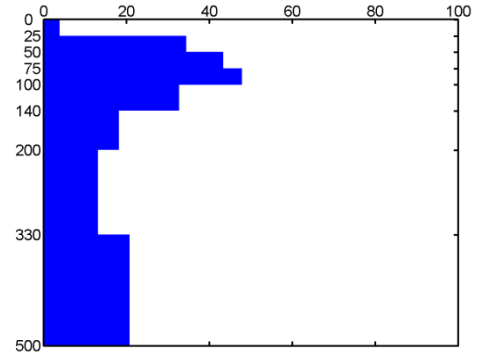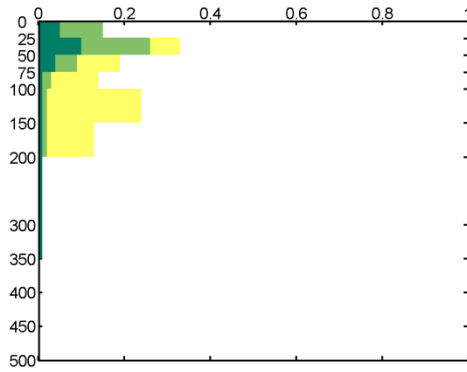
Northern Alexander Island
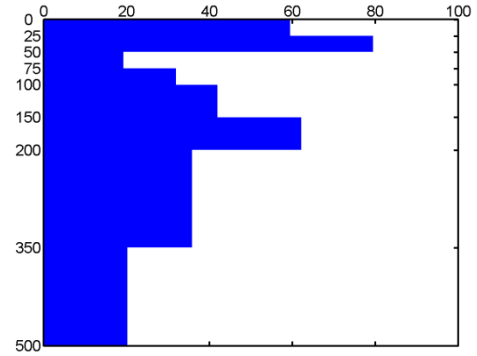
Northern Alexander Island
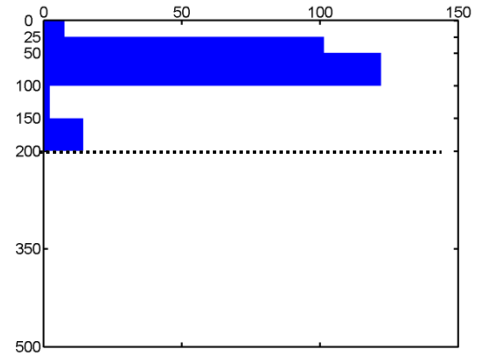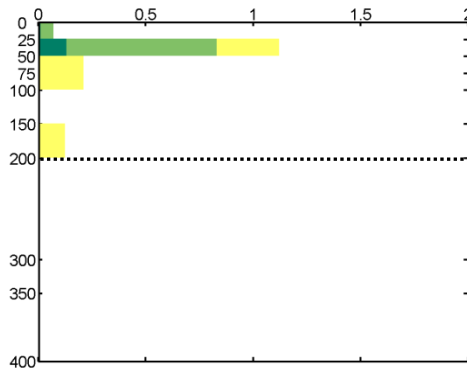
Marguerite Trough

Appendix 2. (Continued)
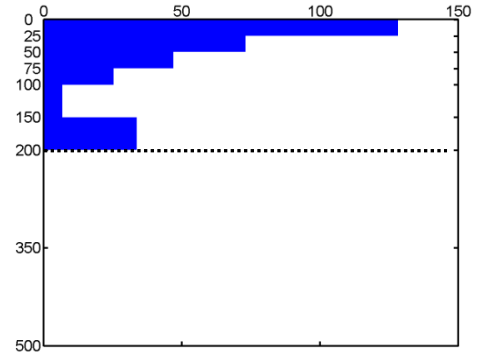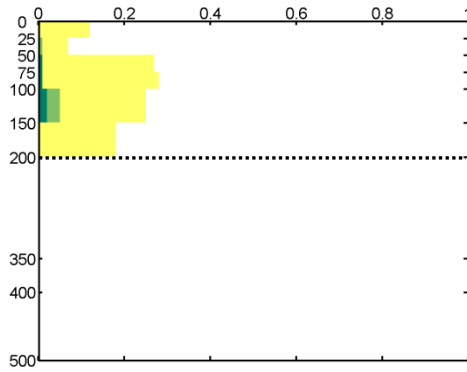
Marguerite Trough
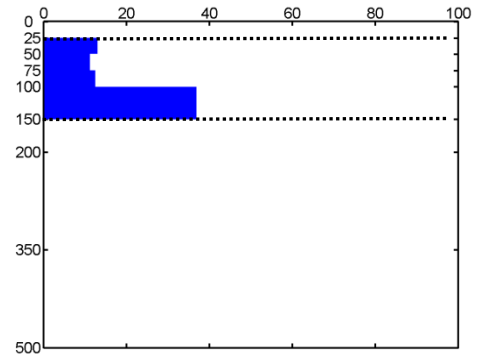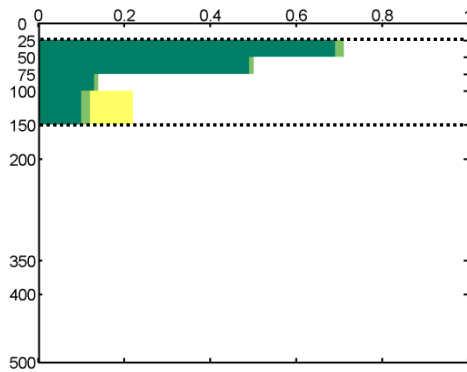
Southern Adelaide Island

Inner Marguerite Bay

153
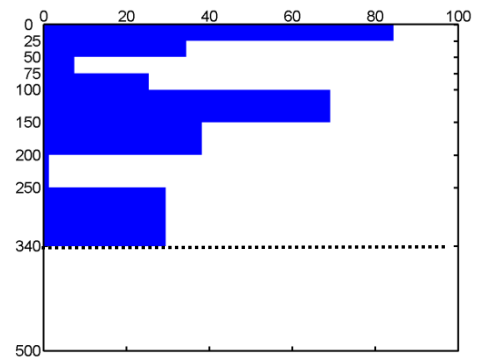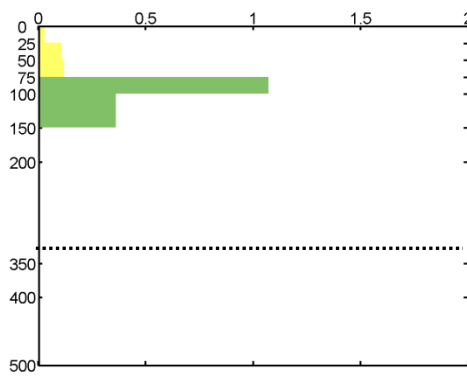
Appendix 3. Vertical distribution of macrozooplankton (ind m^{-3}) in Marguerite Bay, in relation to environmental parameters. Pigment (mg m^{-3}) represents chlorophyll + phaeopigment concentrations.

Southern Laubeuf Fjord, fall 2001

154

Bourgeois Fjord, fall 2001
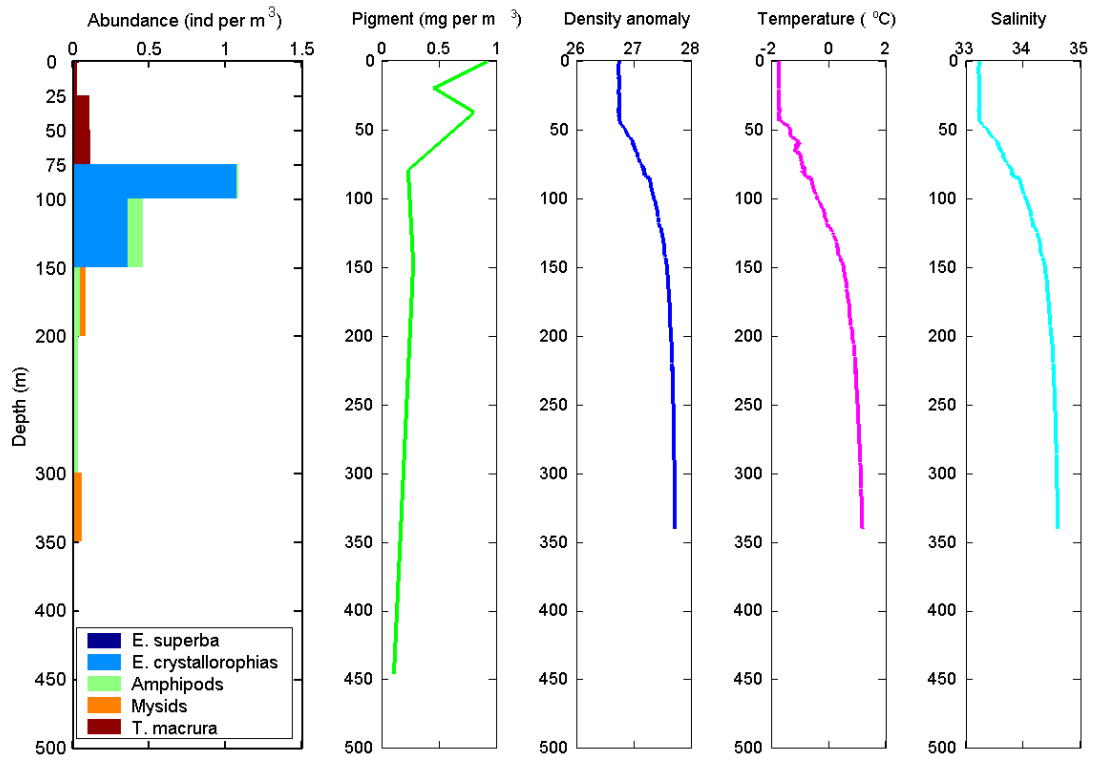
Southern George VI Sound, fall 2001
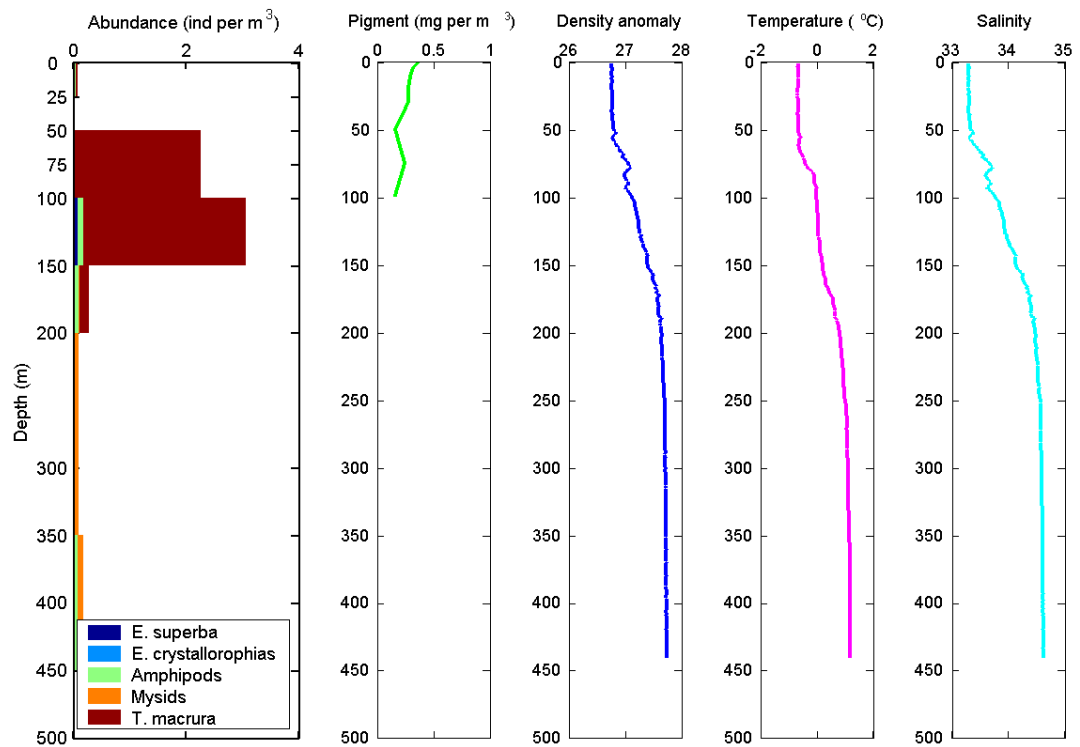
Appendix 3. (Continued)
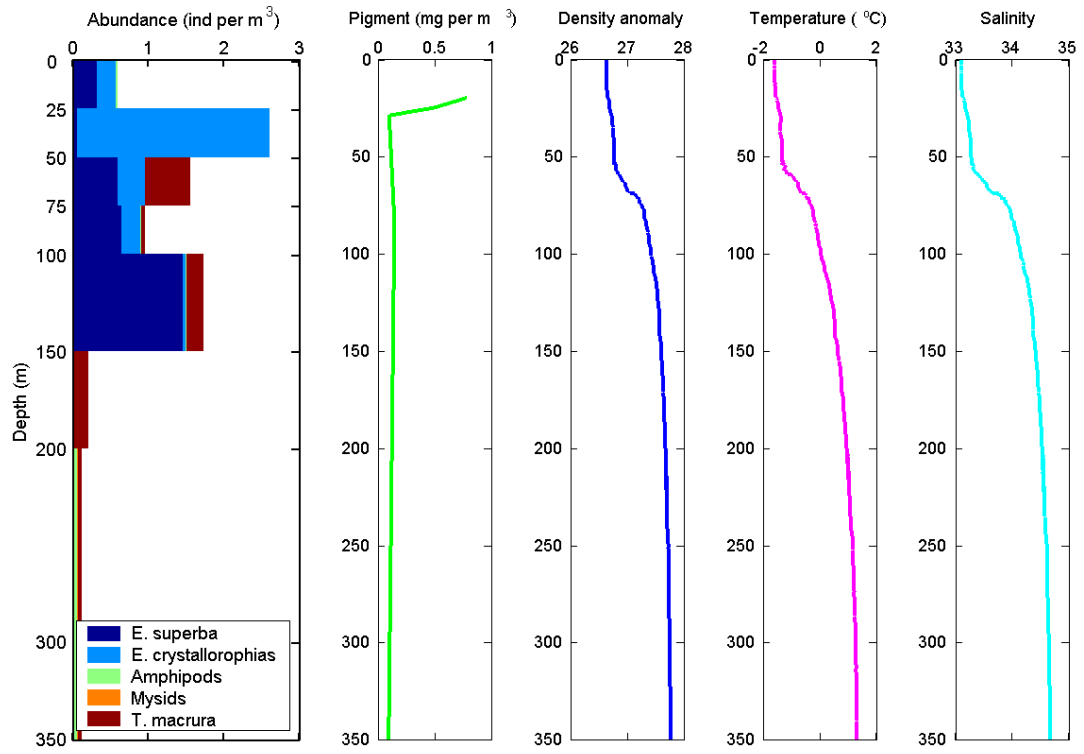
Crystal Sound, fall 2002

Appendix 3. (Continued)
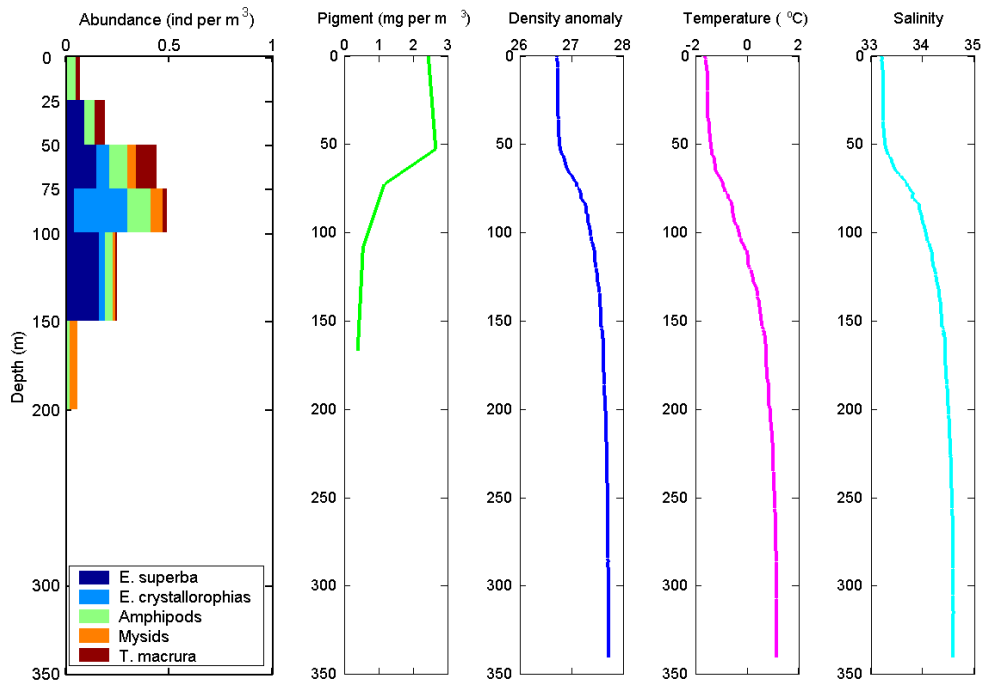

Southern Laubeuf Fjord, fall 2002

Inner Marguerite Bay, fall 2002

Appendix 4. Vertical distribution of macrozooplankton (ind m^{-3}) in Marguerite Bay, in relation to environmental parameters. Pigment (mg m^{-3}) represents chlorophyll + phaeopigment concentrations.

Northern Laubeuf Fjord, fall 2001

Northern Laubeuf Fjord, fall 2002

ABOUT THE AUTHOR

Marina Marrari received a degree in Biological Sciences from the Universidad Nacional de Mar del Plata, Argentina, in 2001. She did her thesis research at the Zooplankton Laboratory of the Instituto Nacional de Investigación in Desarrollo Pesquero (INIDEP) under the guidance of Dr. María Delia Viñas, and later worked at Scripps Institution of Oceanography for several months in 2002. During this time, Marina participated in numerous research cruises in continental shelf waters off the coast of Argentina and California.

Marina came to the College of Marine Science of the University of South Florida as a Fulbright Scholar in the fall of 2002, and joined the Zooplankton Ecology Laboratory led by Dr. Kendra Daly. While in the Ph.D. program, she participated in several international research meetings and coauthored four publications in peer-reviewed scientific journals.