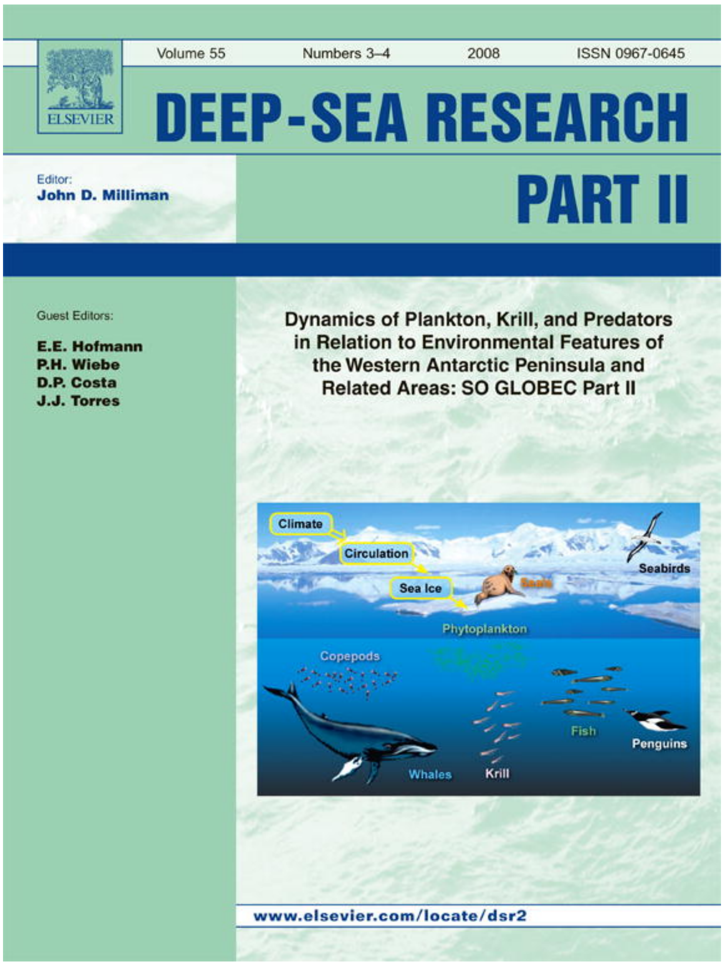

Volume 55 Numbers 3–4 2008 ISSN 0967-0645

DEEP-SEA RESEARCH
PART II

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Dynamics of Plankton, Krill, and Predators in Relation to Environmental Features of the Western Antarctic Peninsula and Related Areas: SO GLOBEC Part II

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DEEP-SEA RESEARCH
PART II
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Spatial and temporal variability of SeaWiFS chlorophyll *a* distributions west of the Antarctic Peninsula: Implications for krill production

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Accepted 7 November 2007
Available online 27 December 2007

Abstract

SeaWiFS chlorophyll *a* distributions between 1997 and 2004 were investigated in relation to sea-ice dynamics for waters west of the Antarctic Peninsula (55–75°S, 50–80°W) in order to better understand the reproductive patterns and recruitment success of the Antarctic krill, *Euphausia superba*. Climatology patterns showed that the Bellingshausen Sea and Marguerite Bay region usually had higher chlorophyll *a* concentrations, which persisted throughout austral spring and summer, compared with more northern regions along the Antarctic Peninsula and the western Scotia Sea. These predictable and long-lasting phytoplankton accumulations could provide krill with the food levels required for successful reproduction and larval survival. Unusually high krill reproduction in 2000/2001 was coincident with above-average chlorophyll *a* concentrations throughout most of the study area and resulted in the largest juvenile recruitment (in 2001/2002) since 1981. High larval densities (up to 132 ind m^{-3}) at the shelf break along the Antarctic Peninsula may have resulted, in part, from krill spawning in the Bellingshausen Sea. In general, ice-edge blooms were only a significant feature in the southern sectors of our study area, particularly in the Bellingshausen Sea and, thus, may not support krill reproduction in the northern Peninsula region as previously believed. Instead, phytoplankton blooms during spring in the northern region appeared to be governed by shelf-break processes, such as upwelling of iron-rich deep water. Interannual differences in sea ice also probably contributed to the variability in larval krill abundances observed in Marguerite Bay. Sea ice melted early in 2000/2001, allowing elevated phytoplankton blooms to develop. In contrast, sea ice persisted throughout spring and summer 2001/2002 limiting phytoplankton accumulation, particularly in southern Marguerite Bay. Thus, the early and extended availability of elevated chlorophyll *a* concentrations during spring and summer 2000/2001, particularly in the vicinity of Marguerite Bay and to the south in the Bellingshausen Sea, as well as reduced sea ice in coastal areas, likely supported the unusually high densities of larval krill observed during fall in waters west of the Antarctic Peninsula.

Keywords: Chlorophyll *a*; Climatology; SeaWiFS; Antarctic krill; *Euphausia superba*; Sea ice; Southern Ocean; Antarctic Peninsula; Bellingshausen Sea

Regional Index terms: Antarctic; Southern Ocean; Antarctic Peninsula; Marguerite Bay; Drake Passage; Bellingshausen Sea

1. Introduction

Chlorophyll *a* 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 austral 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

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doi:10.1016/j.dsr2.2007.11.011

around Antarctica (El-Sayed, 1971; El-Sayed and Taguchi, 1981; Smith and Nelson, 1985; Sedwick and DiTullio, 1997), with reported chlorophyll *a* 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 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 also can 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°S, 50–80°W) (Fig. 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 (Fraser and Trivelpiece, 1996; Arrigo et al., 1998; Deibel and Daly, 2007). Chlorophyll *a* concentrations in the northern sectors along the Antarctic Peninsula shelf have been reported to reach values up to 38 mg m^{-3} during December and January (Holm-Hansen and Mitchell, 1991; reviewed in Smith et al., 1996; Rodriguez et al., 2002). More recently, Arrigo and van Dijken (2003) reported that Sea-viewing Wide Field-of-view Sensor (SeaWiFS) chlorophyll *a* concentrations in a phytoplankton bloom related to the Marguerite Bay polynya averaged 2.30 mg m^{-3}, while Garibotti et al. (2003) and Meyer et al. (2003) observed summer chlorophyll *a* 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

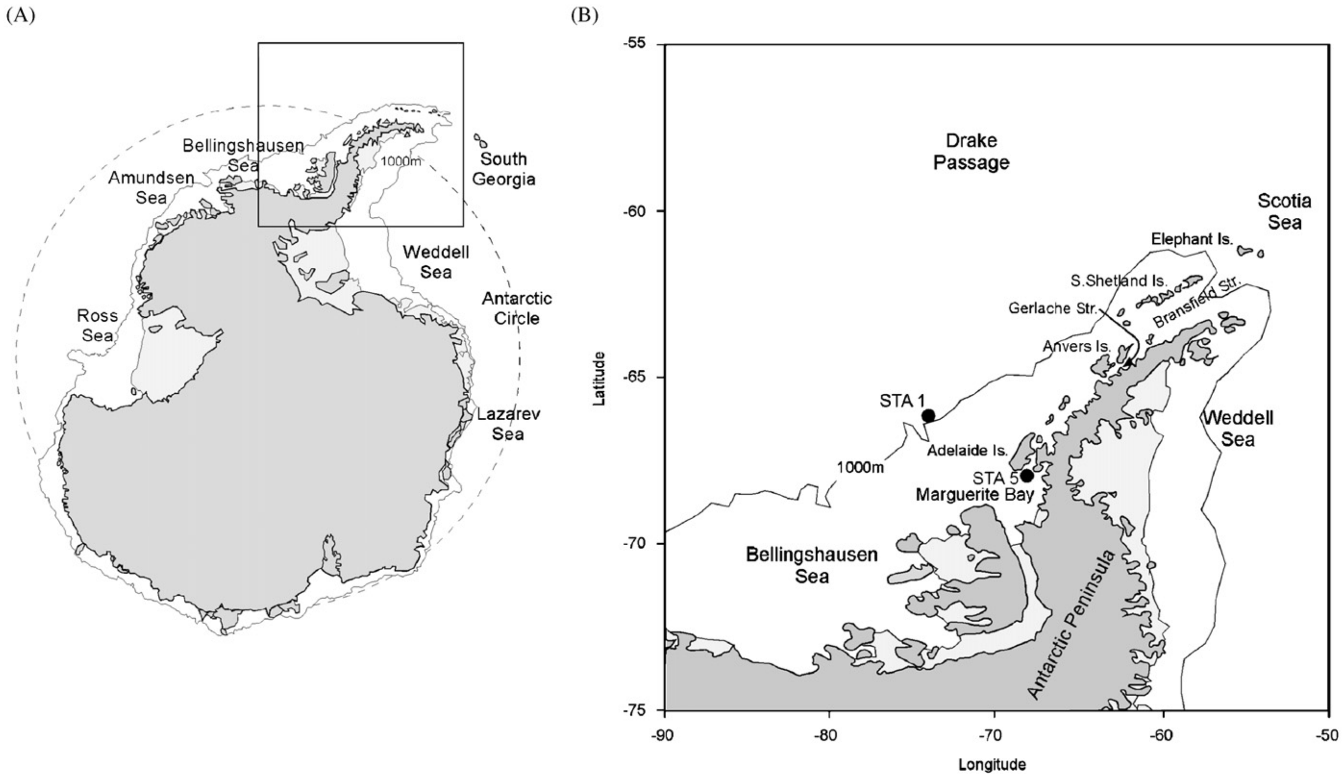

Fig. 1. (A) Map of the Antarctic continent showing the location of the study area and other geographic references. The solid line represents the 1000-m isobath, and the dashed line indicates the Antarctic Circle (66.3°S). (B) Details of the Antarctic Peninsula region and location of the US Southern Ocean GLOBEC offshelf (Sta. 1) and onshelf (Sta. 5) net sampling stations (●) represented in Fig. 2.

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. 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 2 years (Daly, 2004). During austral fall 2001, larvae were very abundant (<0.01 to $132\,\mathrm{ind\,m^{-3}}$), with younger stages dominant offshelf and older stages dominant onshelf (Fig. 2, see Fig. 1 for station locations). Offshore larval densities (up to $132\,\mathrm{ind\,m^{-3}}$) 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 to $211\,\mathrm{ind\,m^{-3}}$), although average abundances were significantly lower than in 2001 and all larval stages were scarce in coastal areas (Fig. 2). In contrast, juveniles were relatively abundant on the middle and inner shelf in the vicinity of Marguerite Bay (<0.01 to $2.37\,\mathrm{ind\,m^{-3}}$), indicating a successful recruitment from the 2001 larval population. These results prompted us to investigate the environmental conditions that contributed to the large krill reproduction during austral spring and summer 2000/2001, and subsequent high larval densities.

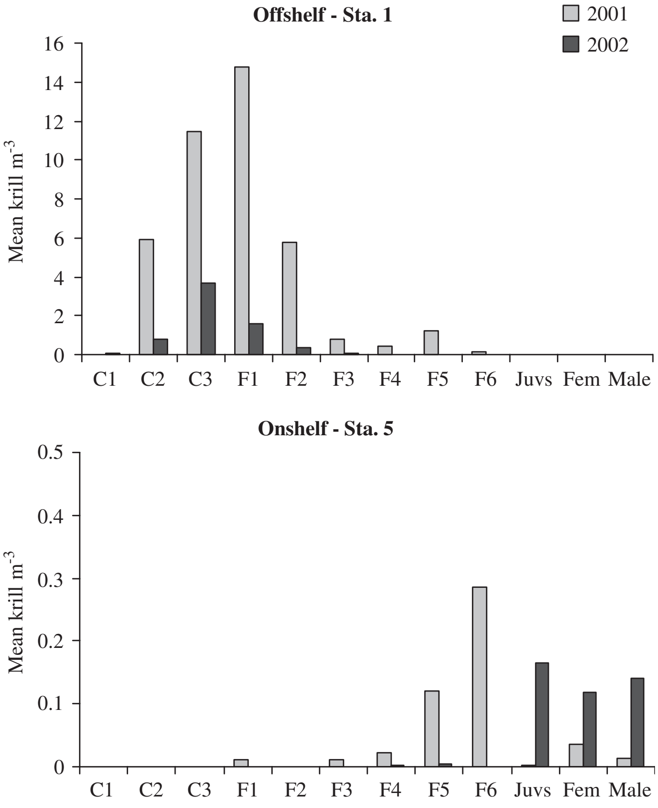

Fig. 2. Mean abundance ($\mathrm{ind\,m^{-3}}$) of development stages of *Euphausia superba* in offshelf waters (Sta. 1) west of the Antarctic Peninsula and coastal waters (Sta. 5) of Marguerite Bay during fall 2001 (light gray) and 2002 (dark gray). CI–CIII = calyptopis 1–3; FI–FVI = furcilia 1–6; juvs = juveniles; males = adult males; females = adult females.

Herein, we 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. We also investigate the effects of the retreat of the ice edge on the timing and location of phytoplankton blooms west of the Antarctic Peninsula. Finally, we discuss the environmental mechanisms that potentially support successful krill reproduction and recruitment in this area.

2. 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. 1).

Krill were collected aboard the R.V. *Lawrence M. Gould* during austral fall 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 Multiple Opening-Closing Net and Environmental Sensing System (MOCNESS) 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 were compared at two representative stations; one offshelf (Sta. 1) and one onshelf (Sta. 5) (Fig. 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, $\mathrm{ind\,m^{-3}}$) were calculated as a weighted mean for the sampling depth using

$$A = \frac{\sum_{i=1}^{8} x_i \times z_i}{\sum_{i=1}^{8} z_i},$$

where i represents each of the eight nets (collections from different depth strata) in each cast, x is the abundance of each krill stage in each net (ind m^{-3}), and z is the depth of each stratum (m).

A recruitment index (R_1) for *E. superba* was calculated as the proportion of 1-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 to 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 calculations. 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 *a* dataset includes 6606 SeaWiFS daily Level 2 files (~1 km pixel^{-1} near nadir) between September 1997 and December 2004 obtained from NASA Goddard Space Flight Center (http://oceancolor.gsfc.nasa.gov). These data were collected by ground stations, as well as occasional satellite onboard recording over the area, and processed 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^{-1} for the western Antarctic Peninsula region (Fig. 1). The parameter used in this study is the surface chlorophyll *a* concentration derived from the OC4v4 empirical

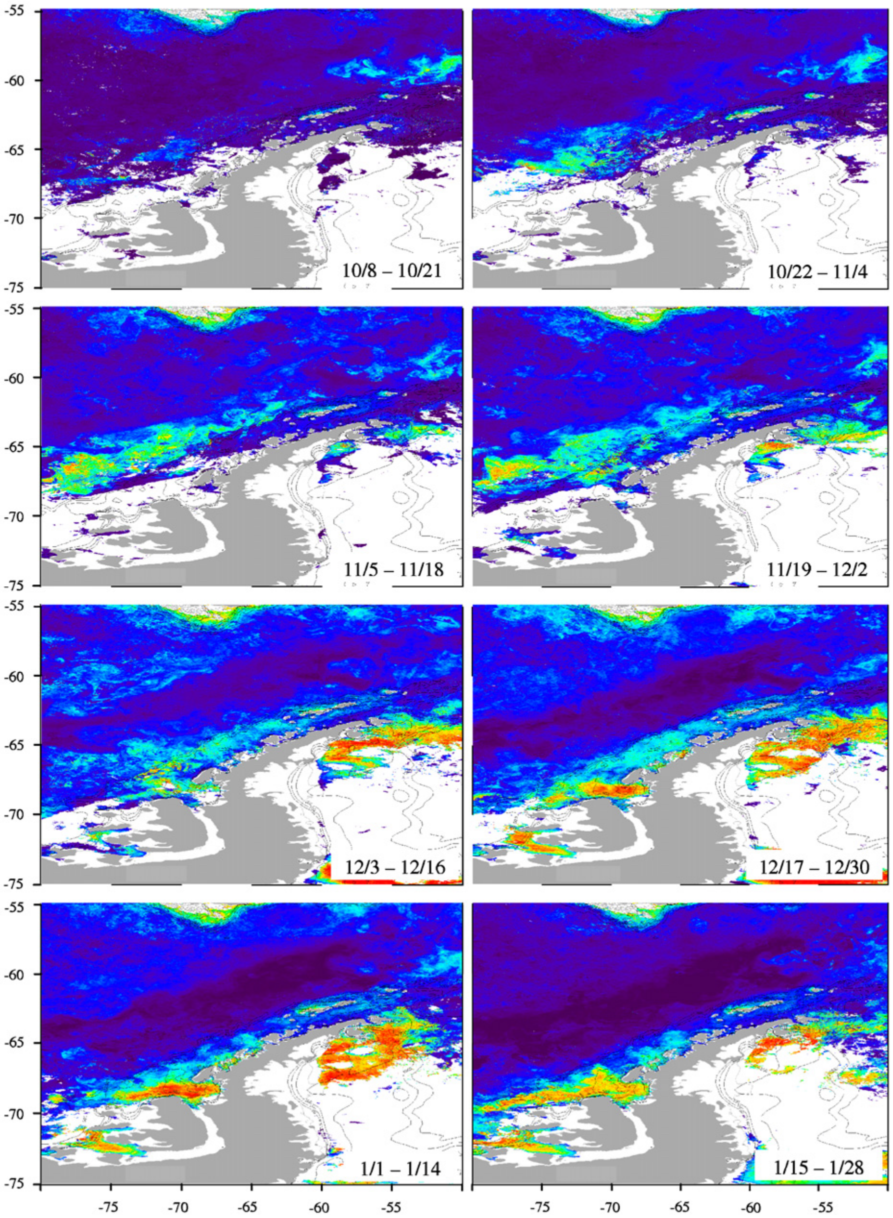

Fig. 3. Biweekly climatology (1997–2004) of SeaWiFS chlorophyll *a* concentrations (mg m^{-3}) between October and March. White areas indicate no data due to the presence of clouds and/or sea ice.

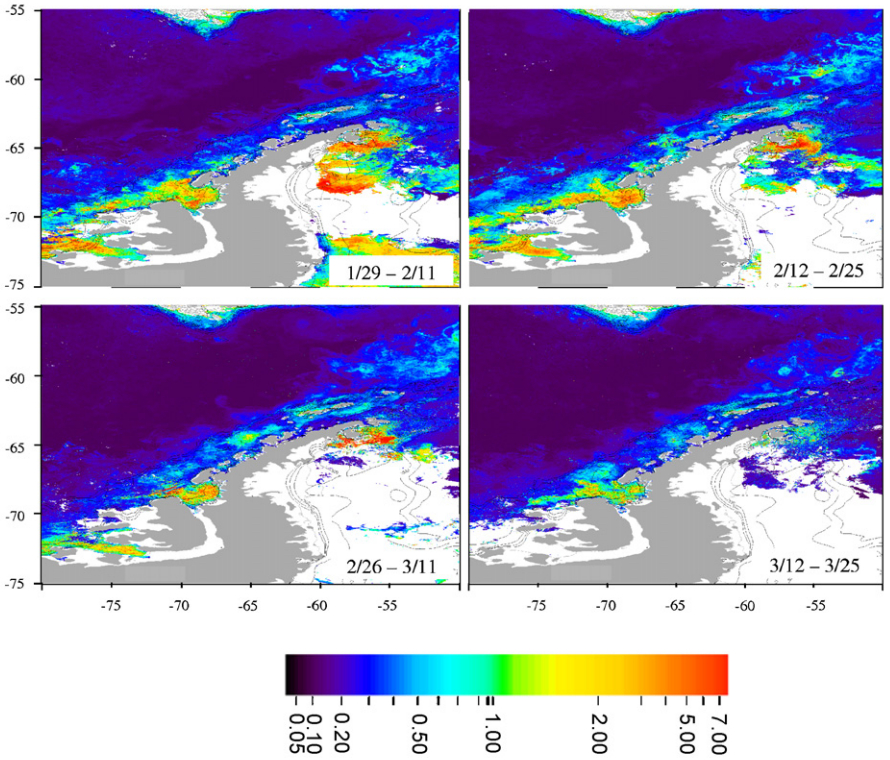

Fig. 3. (*Continued*)

band-ratio (blue versus green) algorithm (O'Reilly et al., 2000). Because the ocean-color signal is an integrated signal from the surface to about one optical depth (corresponding to about 37% of the surface irradiance), SeaWiFS chlorophyll *a* provides a good assessment of water column concentrations in the Southern Ocean, as maximum chlorophyll *a* 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 SeaWiFS chlorophyll *a* 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, a recent study using 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 $\sim$4 mg m^{-3}, which include $>$90% of the waters in the Southern Ocean (Marrari et al., 2006). The mean ratio between SeaWiFS chlorophyll *a* and *in situ* HPLC chlorophyll *a* was close to unity (i.e., 1.12, $n = 96$), indicating good agreement between the two sets of data. Although Marrari et al. (2006) could not verify the accuracy of SeaWiFS chlorophyll *a* concentrations greater than $\sim$4 mg m^{-3}, here we use a larger range of chlorophyll concentrations 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 (Carder et al., 1989), we measured CDOM absorption from 10 surface water samples collected in our study area between 4 April and 10 May 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 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 (Hu et al., 2002). 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}), we conclude that the accuracy of the SeaWiFS chlorophyll estimates is likely 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, typically at least weekly composites are needed to obtain good spatial coverage (Holm-Hansen et al., 2004a). For our study, we generated biweekly composites of SeaWiFS chlorophyll *a* data. A 7-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 (Fig. 3). 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 (e.g., cloud contamination, large solar/view angle, etc.) were excluded from the calculations.

The study area was divided into 14 subregions (Fig. 4A), 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 *a* 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 9–11 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 *a* concentrations between September–March 1997 and 2004 were calculated for each region and the results were plotted over time in relation to the climatology (Fig. 4B). 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 we could not verify the accuracy of these values with concurrent *in situ* data. However, as most of the SeaWiFS chlorophyll *a* concentrations during our 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 (Fig. 5A and B). 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 (approximately 3 months). Thus, at the September location of the ice edge, chlorophyll concentrations were analyzed during September–November and at the

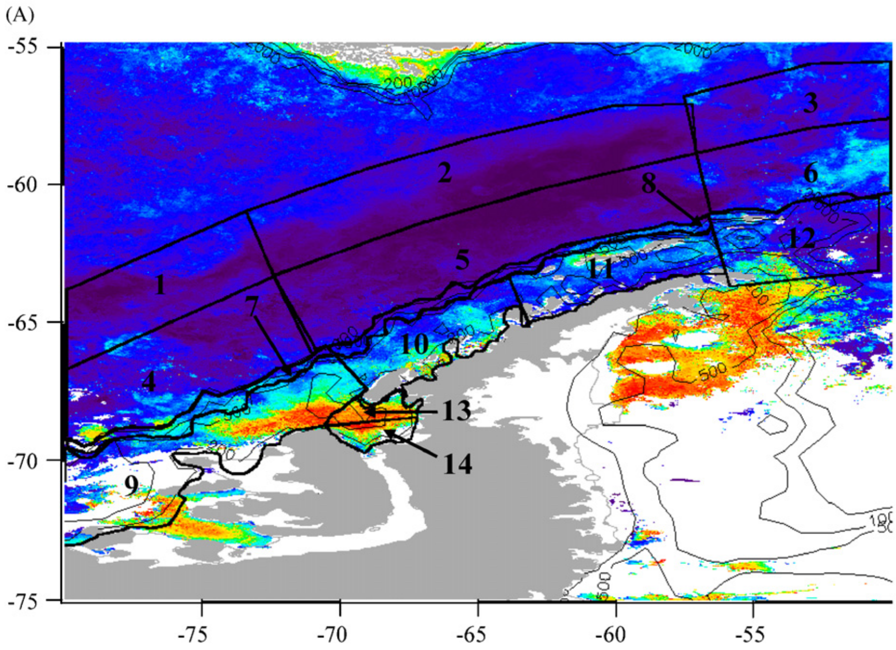

Fig. 4. (A) Location of the 14 subregions along the western Antarctic Peninsula superimposed over the climatology (1998–2004) of SeaWiFS chlorophyll *a* concentrations (mg m^{-3}) for 1–14 January. (B) Time series of geometric mean chlorophyll concentrations in each subregion for each biweekly period 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.

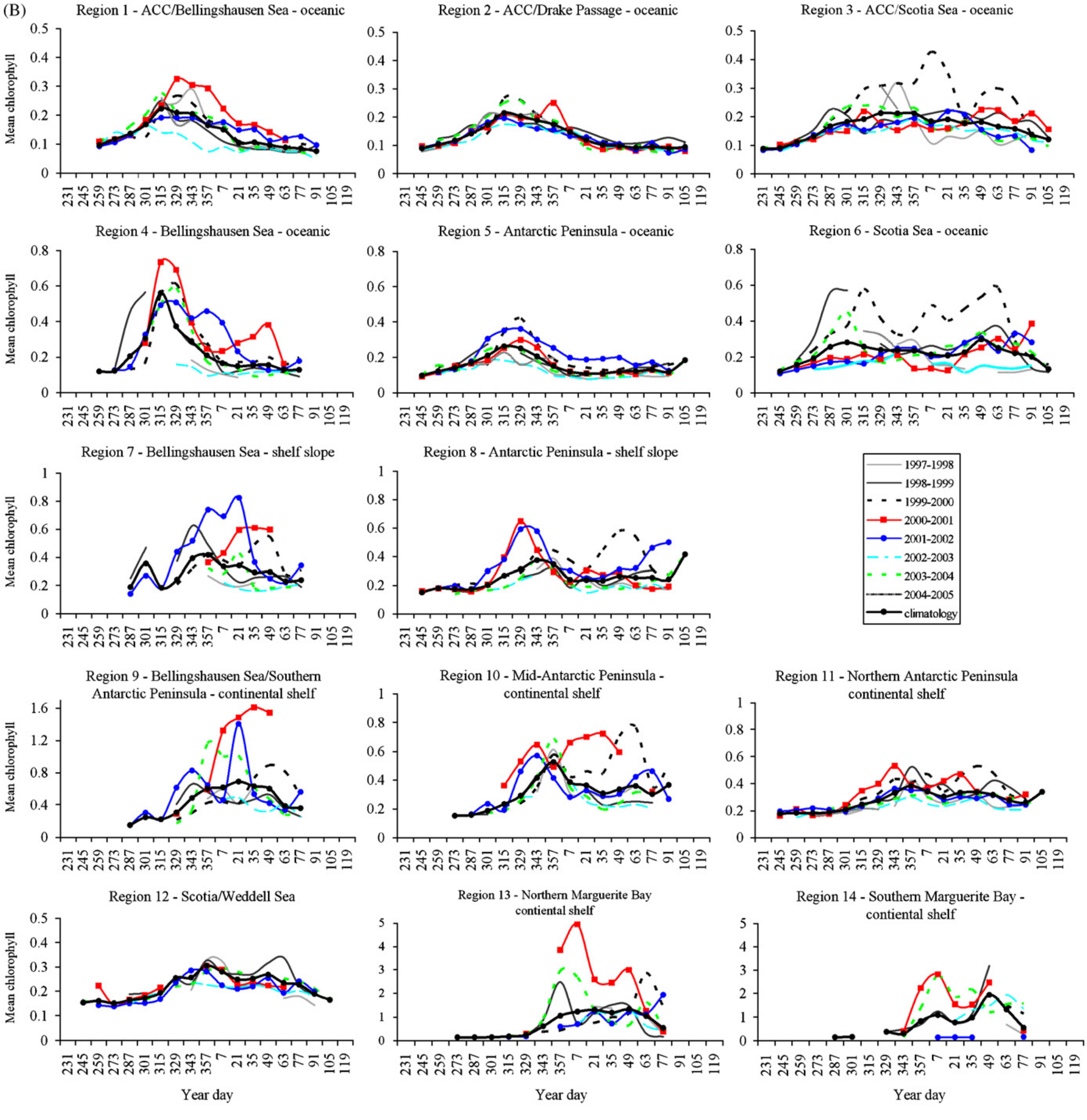

Fig. 4. (*Continued*)

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 (Fig. 6).

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) (Fig. 7). 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 (Fig. 7).

3. 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 to $>7\,\mathrm{mg\,m^{-3}}$) during spring and summer in comparison with any other area west of the Antarctic Peninsula between September and March 1997–2004 (Fig. 3). Oceanic waters offshore of the northern Antarctic Peninsula typically had relatively low concentrations (0.1–0.2 mg m^{-3}). Intermediate values (0.1 to ~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). 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 did not 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 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. 4) illustrate

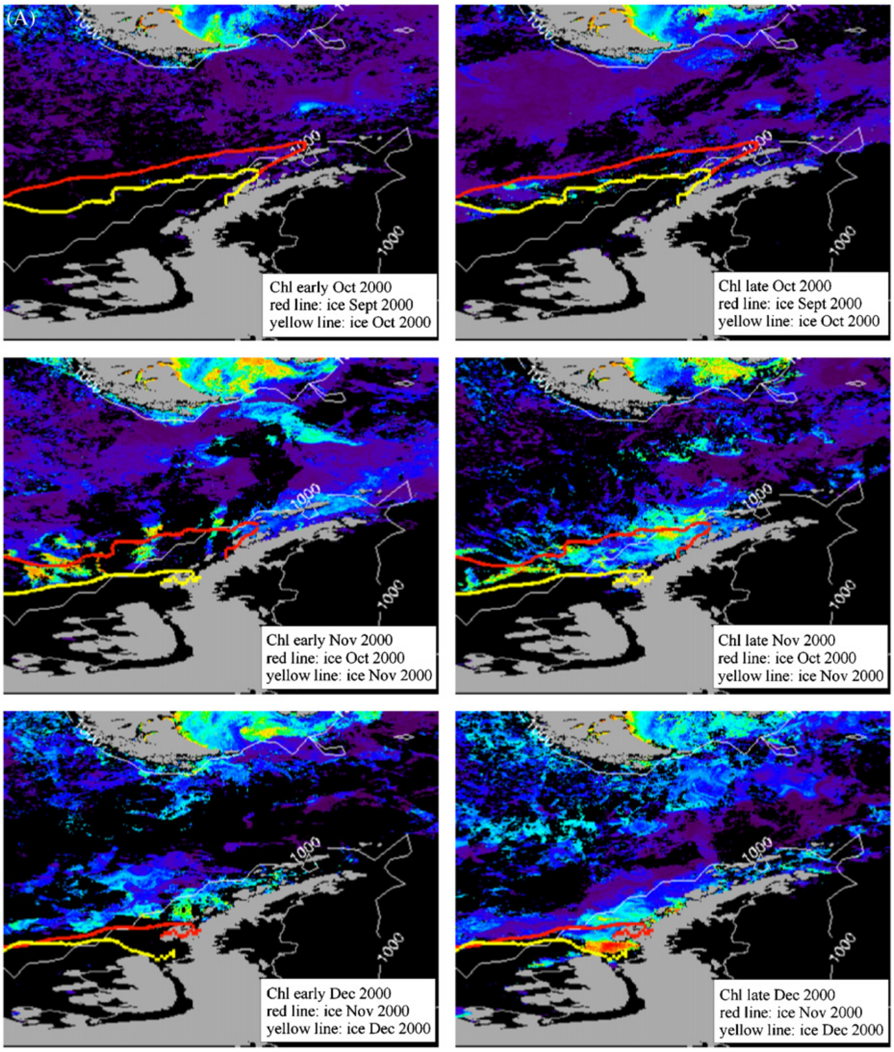

Fig. 5. Biweekly SeaWiFS chlorophyll *a* concentrations (Chl, mg m^{-3}) in October (Oct), November (Nov) and December (Dec) of (A) 2000 and (B) 2001. The mean monthly location of the ice edge is also shown: the red line indicates the location of the ice edge during the preceding month, the yellow line represents the current month. The 1000-m isobath is indicated by the white line.

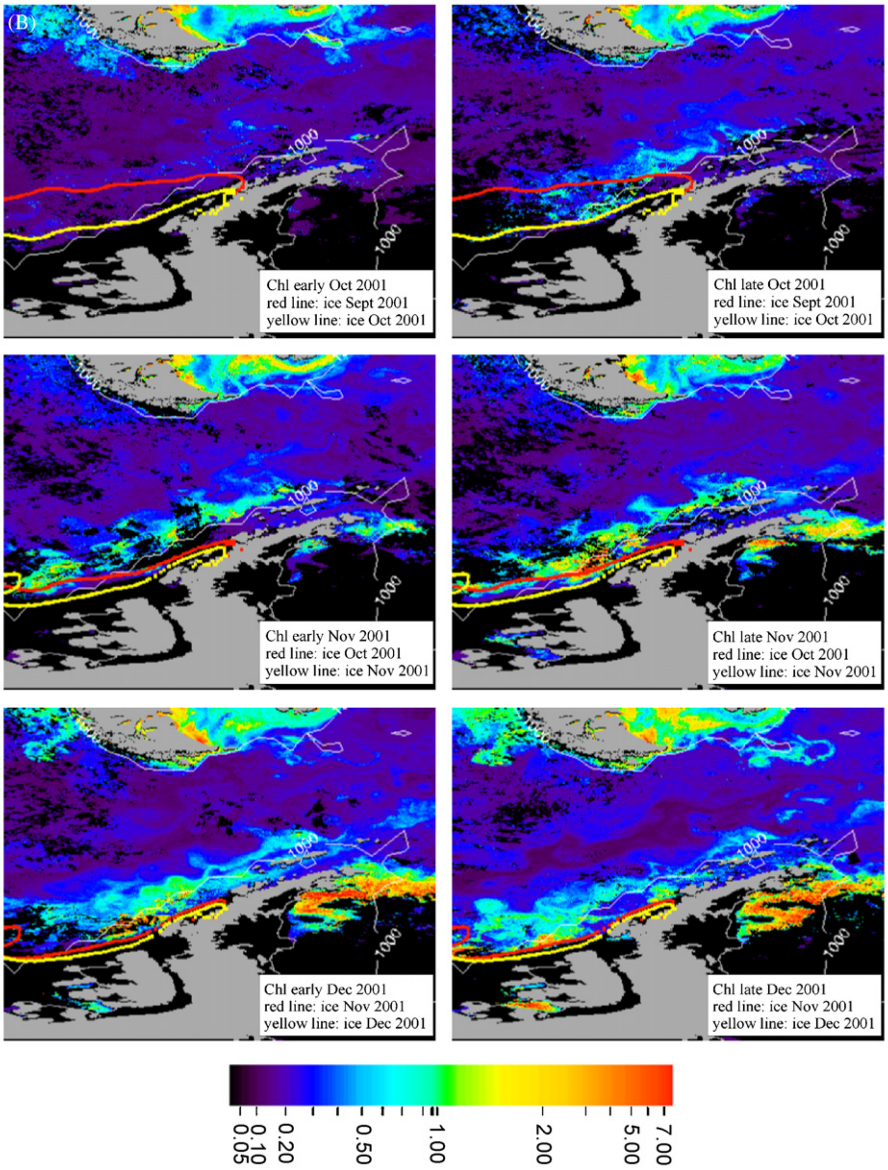

Fig. 5. (*Continued*)

the interannual (1997–2004) variability in patterns of chlorophyll distribution west of the Antarctic Peninsula. Variations from the climatology were relatively small (maximum ± 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. 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.

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

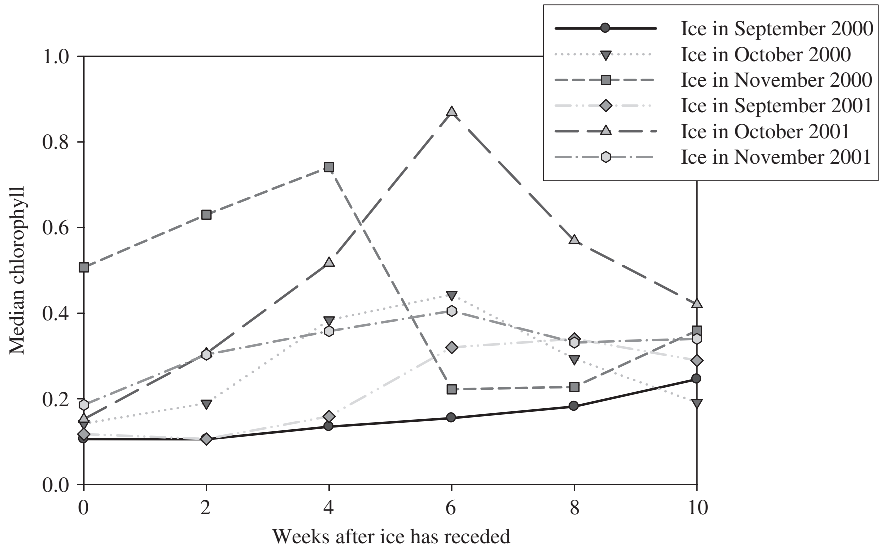

Fig. 6. Biweekly time series of chlorophyll *a* accumulation after the ice had receded at the September, October, and November 2000 and 2001 locations of the ice edge shown in Fig. 5A and B.

period of time as in 2000/2001. Shelf break and 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 understand better the relationship between sea ice and phytoplankton blooms (Fig. 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. 5A and B, top two 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 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. 5A and B, 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.

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. 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. 5B), the ice edge occupied coastal areas of the Bellingshausen Sea and along the Antarctic Peninsula to Anvers Island (see Fig. 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.

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 9000 to 11,000 km^2 in northern Marguerite Bay and from ~4500 to 7500 km^2 in southern Marguerite Bay (Fig. 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

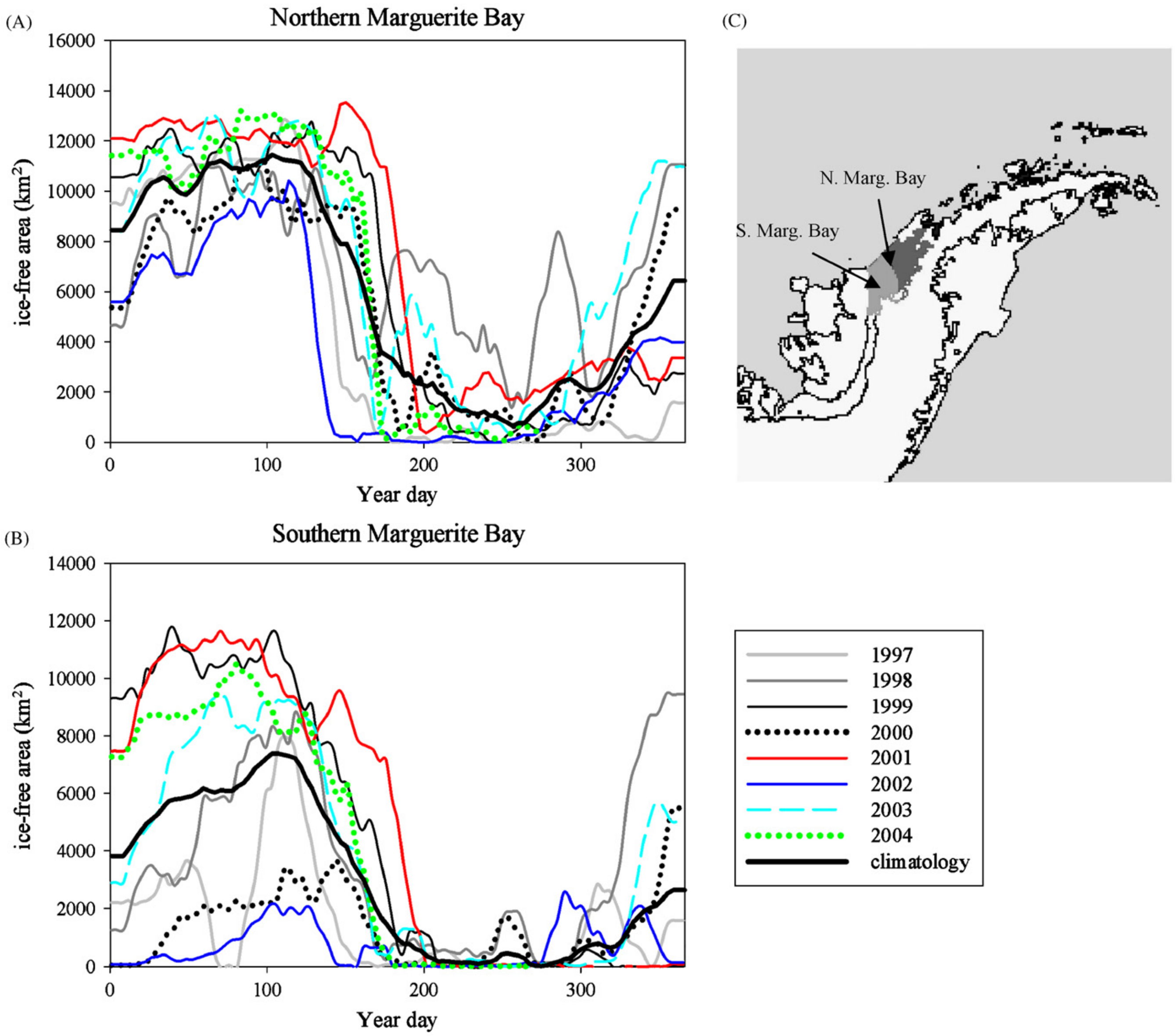

Fig. 7. Daily ice-free area (km^2) in (A) northern and (B) southern Marguerite Bay during 1997–2004. The 8-year climatology also is shown (black thick line). (C) Location of the northern (dark gray) and southern (light gray) Marguerite Bay regions.

the spring, summer, and fall (Fig. 7A and B). 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 6000–9000 km^2 in the northern and 0–2000 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 recruitment west of the Antarctic Peninsula between 1975 and 2002 are provided for comparison (Table 1).

4. Discussion

Chlorophyll concentrations showed considerable temporal and spatial variability in waters west of the Antarctic Peninsula during austral spring and summer between 1997

Table 1
Years of elevated krill recruitment between 1975 and 2002

Year class	R_1	Location	Study period
1979/1980	0.559	Elephant Island area[a]	1975–2000
1980/1981	0.757	Elephant Island area[a]	1975–2000
1987/1988	0.651	Elephant Island area[a]	1975–2000
1994/1995	0.622	Elephant Island area[a]	1975–2000
	0.639	Western Antarctic Peninsula[b]	1985–2002
1999/2000	0.573	Elephant Island area[a]	1975–2000
	0.076	Western Antarctic Peninsula[b]	1985–2002
	0	Marguerite Bay region[c]	2001–2002
2000/2001	0.748	Western Antarctic Peninsula[b]	1985–2002
	0.400	Marguerite Bay region[c]	2001–2002

Source publications are designated by symbols in the table. Recruitment indices (R_1) were estimated from the proportion of 1-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.

[a] Siegel et al. (2002).

[b] Siegel et al. (2003).

[c] This study.

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} versus 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). Our climatology indicates 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 with the seasonal alongshore retreat of the sea ice and/or with latitudinal differences between areas. Our results, however, indicate that chlorophyll concentrations in the southern sectors are consistently higher than in any other area 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; 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 2 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 our 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, our findings 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 and 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. This relationship between sea-ice cover and chlorophyll concentrations is further supported by observations during other years of our 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. 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). Our results, 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 sea ice is not necessarily a good predictor of food availability for overwintering larvae and environmental factors other than winter sea ice 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; Hofmann 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). 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 ($>0.5\,mg\,m^{-3}$) 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 recruitment success.

The recruitment indices in Table 1 indicate that only 6 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 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).

Our results 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. 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 7–11, 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 Sea 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 s^{-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 s^{-1}, the spawning location possibly occurred in offshelf waters of the Bellingshausen Sea between 83°W and 94°W (Fig. 8:

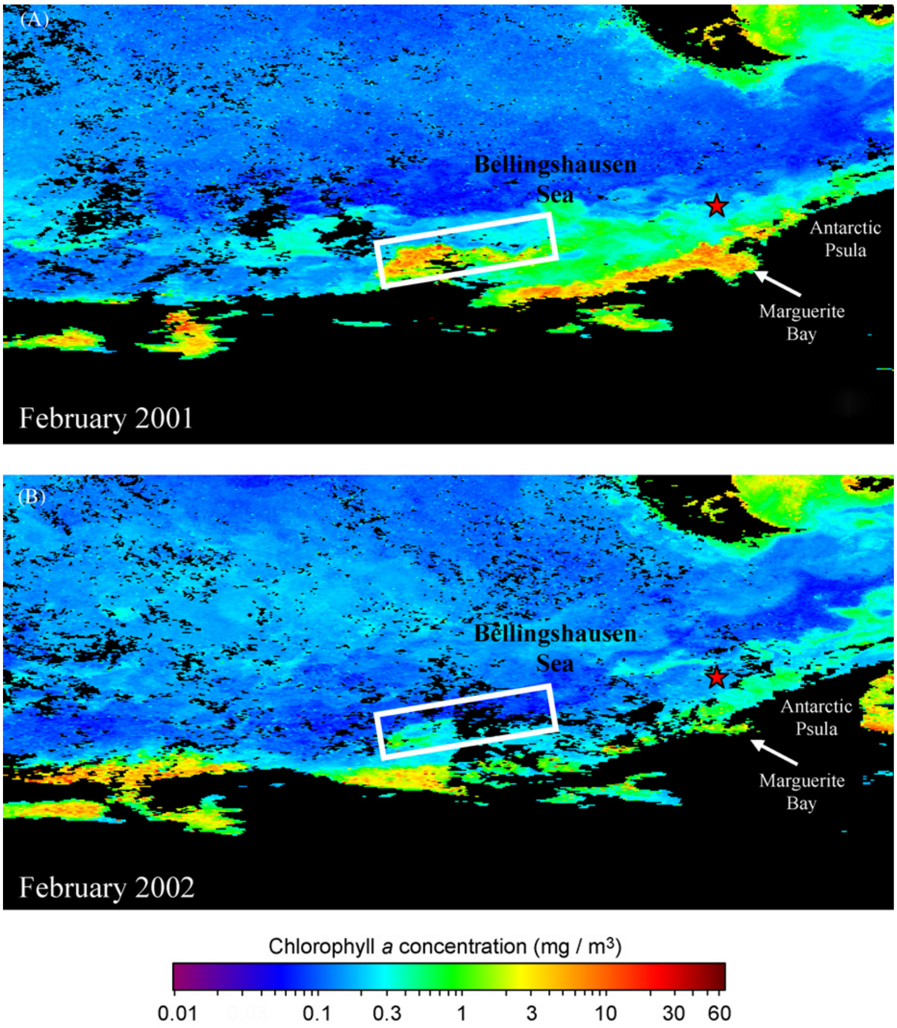

Fig. 8. Monthly mean SeaWiFS chlorophyll *a* concentrations in the Bellingshausen Sea during February (A) 2001 and (B) 2002. The white box represents the area of potential krill spawning. The red star indicates the location of the US SO GLOBEC sampling Station 1 where krill were collected. Images correspond to the level-3 standard mapped images (resolution of 9 km pixel^{-1}) and were obtained from NASA (http://oceancolor.gsfc.nasa.gov/cgi/level3.pl).

white box). Although this spawning location is west of our study area, larger-scale ocean-color imagery (Fig. 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. 8B), and thus there was less food available for reproduction or larval growth.

Our results indicate that spring and summer phytoplankton blooms are 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.

Acknowledgments

This study was supported by the US National Science Foundation (NSF) Grants OPP-9910610 and OPP-196489 to K. Daly, and by US NASA Grant NNS04AB59G to C. Hu. We thank M. Zhou, Y. Wu, R. Dorland, D. Mertes and J. Smith for collecting the MOCNESS net samples and A. Timonin and T. Semenova for help with zooplankton analyses. We are grateful to K. Arrigo and G.L. van Dijken for providing the daily sea-ice data in Marguerite Bay and to E. Chapman for the ice-edge location data. We also thank J. Smith for collecting the CDOM samples and R. Conmy for her assistance with sample processing. B. Murch of USF/IMaRS provided assistance in obtaining and processing the SeaWiFS satellite data. This publication represents IMaRS contribution no. 121 and US GLOBEC contribution no. 560.

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