Southern Ocean productivity in relation to spatial and temporal variation in the physical environment

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[1] The physical factors that have been reported to affect primary and secondary production in the Southern Ocean are examined and critically reviewed. Long time series of physical measurements from the Southern Ocean are available and there is a theoretical base from which models can be constructed. In contrast, there are few large-scale measurements of biological parameters and a paucity of long-term biological data sets for the Antarctic region. The absence of predictive models for the biological systems of the region is underpinned by the absence of theoretical understanding of the variations in the physical environment and their effects on primary, secondary, or tertiary production. To further this understanding, we have examined some of the major seasonal and interannual physical data available for the region (sea ice extent and retreat rate, wind stress, and surface ocean circulation patterns) and have examined their relationship to spatial and temporal variation in satellite-derived proxies of primary productivity (Sea-viewing Wide Field-of-view Sensor (SeaWiFS) ocean color data). The results indicate that there are regional differences in the dominant physical forcings and that simple models will fail to replicate the observed patterns of primary production. We have also used the dynamics of Antarctic krill in the South Atlantic as an example to develop a model and explore the various hypotheses that have been put forward to explain interannual variability in this region. Results from this model indicate that the physical system may change in ways that cause periodic shifts in the relative importance of the factors that affect secondary production. The implications for the design of future research programs are explored. *INDEX TERMS:* 4207 Oceanography: General: Arctic and Antarctic oceanography; 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; 4805 Oceanography: Biological and Chemical: Biochemical cycles (1615); 4504 Oceanography: Physical: Air/sea interactions (0312); 4540 Oceanography: Physical: Ice mechanics and air/sea/ice exchange processes; *KEYWORDS:* Antarctic ecosystem, biological-physical coupling, air-sea interactions, krill dynamics, ecosystem modeling

1. Introduction

[2] The Southern Ocean is a significant component of the global marine ecosystem. It covers approximately 10% of the world's oceans, consisting of distinct physical and biological regimes separated from other oceans by the Polar Front (PF). Interest in the biological productivity of the Southern Ocean has arisen because of its role in global carbon fluxes [*Sarmiento et al.*, 1998], its status as one of the major oceanic High Nitrate-Low Chlorophyll (HNLC) regions [*Falkowski et al.*, 1998], its capacity to support large populations of vertebrates (e.g., baleen whales) [*Marr*, 1962] and the ecological consequences of harvesting [*Murphy*, 1995].

[3] The Southern Ocean comprises two major current systems: the eastward flowing Antarctic Circumpolar Current (ACC) and the westward flowing Antarctic Coastal Current. The other major physical feature of this system is the annual advance and retreat of sea ice. The pelagic ecosystem of the Southern Ocean can be divided into distinct environments using a number of different criteria. Biogeochemical provinces have been defined according to physical features and include the PF zone (PFZ), the permanently open ocean zone (POOZ), the marginal ice zone (MIZ), and the coastal and continental shelf zone [*Arrigo et al.*, 1998]. These zones have been put in a wider ecological context by *Longhurst* [1998] who identified a Subantarctic Water Ring Province, an open ocean Antarctic Province and an Austral Polar Province essentially corresponding to the three previously identified biogeochemical zones. The significant physical and ecological differences

between the biogeochemical provinces [*Tréguer and Jacques*, 1992; *Arrigo et al.*, 1998; *Longhurst*, 1998] illustrate the ecological heterogeneity of the Southern Ocean, such that the early view of a single and simple "Antarctic marine ecosystem" [*Murphy*, 1962] is no longer generally accepted.

1.1. Large-Scale Research

[4] The Southern Ocean has been the focus of several major research initiatives such as Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) and the Joint Global Ocean Flux Study (JGOFS). There have also been initiatives associated with the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), including long-term studies [*Hewitt and Demer*, 1994a] and large-scale krill biomass surveys in the Indian [*Nicol*, 2000a] and Atlantic [*CCAMLR*, 2000] sectors. Other long-term or large-scale research in the Antarctic Peninsula region has included the Palmer Long-Term Ecological Research (LTER) Program [*Smith et al.*, 1995], the Research on Antarctic Coastal Ecosystem Rates (RACER) Program [*Huntley et al.*, 1991], and the Southern Ocean Global Ocean Ecosystem Dynamics (GLOBEC) winter study [*GLOBEC*, 1999]. The primary region of interest has been the Atlantic sector [*El-Sayed*, 1994; *Smetacek et al.*, 1997] with more recent attention being given to the Bellingshausen Sea [*Turner and Owens*, 1995], and the Indian sector [*Gaillard*, 1997; *Nicol et al.*, 2000c]. The U.S. Southern Ocean JGOFS has focused heavily on the biogeochemical cycling at the PF near 170°W and the Ross Sea [*Smith et al.*, 2000a]. As a result of programs like these, a more complete understanding is now emerging regarding the factors controlling primary productivity and the major ecosystem linkages in the Southern Ocean, but large sectors of this globally important region remain poorly sampled and understood.

[5] Large-scale ocean-wide examination of the physical mechanisms that influence southern ocean productivity is difficult because of

1. the varying spatial scales at which many studies are undertaken,

2. the paucity of long-term data sets,

3. the accuracy and precision of the methods/tools available for these studies.

[6] The large-scale physical characteristics of the region and their dynamics are the most straightforward to measure through remote sensing, instrument arrays or oceanographic surveys. Long-term data sets on features such as sea ice extent [*Murphy et al.*, 1995; *Jacka*, 1997] and drift [*Heil and Allison*, 1999], currents [*Hofmann and Klinck*, 1998] and the position of frontal systems [*Orsi et al.*, 1995] have permitted the construction of models which describe features such as the general circulation [*Webb et al.*, 1991] and sea ice dynamics.

[7] Quantifying the dynamic relationship between primary and secondary producers is much more difficult. Few regional synoptic surveys have collected the information on a range of variables that allows the development of comprehensive ecosystem models [*Huntley et al.*, 1991; *El-Sayed*, 1994; *Smith et al.*, 1995; *Nicol et al.*, 2000c]. Most often, measurement of key biological variables occurs over a range of spatial and temporal scales [*Murphy et al.*, 1988]. In addition, most studies are directed at the distribution and abundance of organisms rather than at estimates of production. Remotely sensed ocean color has been used extensively as an indicator of surface chlorophyll concentration [*Comiso et al.*, 1993; *Sullivan et al.*, 1993; *Moore and Abbott*, 2000] but direct measurements of primary productivity are still dependent on water samples collected from hydrographic casts. Fast repetition rate fluorometry (FRRF) [*Kolber and Falkowski*, 1993; *Strutton et al.*, 1997; *Behrenfeld and Kolber*, 1999] and satellite primary productivity algorithms have been developing rapidly [*Behrenfeld and Falkowski*, 1997], including specialized algorithms for Antarctic regions [*Dierssen and Smith*, 2000; *Dierssen et al.*, 2000]. These techniques, in conjunction with the increasing quantity and quality of ocean color data that is now becoming available, should improve quantification of global and regional primary productivity.

[8] Abundance and distribution of secondary producers is assessed using nets for the smaller categories of metazoan organisms and acoustics for larger ones. Both techniques have limitations, especially for patchily distributed organisms [*Watkins*, 2000]. Fisheries data have also been used to relate the biological status of harvested species to environmental conditions [*Ichii et al.*, 1998b; *Kawaguchi et al.*, 1998]. Determining rate processes of secondary producers in relation to their environment is more difficult still [*Ross et al.*, 2000] and there are no standard methodologies [*Nicol*, 2000b].

[9] Production of high trophic level consumers is also problematic. The production of land-based vertebrates can be estimated for the portion of their life cycle that they are on land [*Croxall*, 1989]. However, for many entirely marine vertebrates it is extremely difficult to obtain even the most basic population information [*Croxall*, 1992] other than distribution and abundance [*Woehler*, 1997; *Thiele et al.*, 2000]. Information on the production of fish can come from fisheries data for commercially harvested species but for invertebrates there are few data.

1.2. Biological–Physical Coupling

[10] Sea ice has a number of ecological roles [*Nicol and Allison*, 1997]; as a platform for larger animals to rest; as a substrate on which communities can develop; as a major production zone and a source of phytoplankton for the spring bloom, Its melting can enhance stability in the neighboring surface waters and it can act as a collector for airborne nutrients which can be released upon its melt in spring. Sea ice also acts as a physical, chemical and biological barrier between the atmosphere and the ocean. The increased realization of the ecological importance of sea ice has resulted in the development of a number of conceptual models that have used sea ice as a major forcing factor [*Loeb et al.*, 1997].

[11] Other conceptual models have related Southern Ocean productivity to various features of the ACC [*de Baar et al.*, 1995; *Tynan*, 1998; *Nicol et al.*, 2000d]. Most models have used a variety of specifically collected and historical data rather than developing the models from first principles Developing productivity models for the Southern Ocean requires matching the scales of the studies, the scales of the processes being studied and the scale of the problem, which in this case is identifying the processes that influence the large-scale patterns of production. The development of

these models has been largely a passive process taking years to refine a model based on sequential developments. Even then, the efficacy of the model for purposes such as fisheries management may still be open to question because of its largely untested application to future circumstances. An alternative approach is to establish monitoring or experimental work that will actively discriminate between competing models. This process reduces uncertainty and determines more quickly the set of plausible models that may best describe the behavior of the system.

1.3. Aims

[12] In this paper, we review the various conceptual models that have been proposed to account for the large-scale spatial distribution and interannual variability of primary and secondary production. Our aims are:

1. To investigate the relationship between sea ice dynamics, climatological wind stress and primary productivity at spatial scales of the order of thousands of kilometers.

2. To review the processes that have been proposed to account for spatial and temporal changes in krill populations, with particular attention to the South Atlantic.

3. To develop a simple model of krill productivity, mortality and advection, and to relate the results of the model to empirical data.

4. To describe how large-scale changes in physical processes may impact primary and secondary productivity.

[13] We conclude with some comments on sampling and modeling strategies, and the way in which these strategies can be adversely affected by large-scale physical oceanographic perturbations.

2. Mechanisms Influencing Production

2.1. Factors Influencing Southern Ocean Primary Productivity

[14] *Ackley and Sullivan* [1994] have described the characteristics and significance of phytoplankton communities within and beneath sea ice, but here we wish to focus on ice edge and open ocean productivity to investigate the influence of ice retreat rates and wind stress on the formation of blooms. The dominant paradigm regarding summer primary productivity in Antarctic waters is that ice retreat (1) seeds the upper ocean with phytoplankton cells growing in or on the ice and (2) leads to the formation of a low salinity, stable surface layer [*Smith and Nelson*, 1985]. Antarctic sea ice coverage is either at or near its maximal extent in September each year, retreats slowly through October and November, thereafter more rapidly, reaching minimal extent in January and February, after which new ice begins to form. The stable surface water layer created by melting sea ice represents a favorable environment for bloom development, as it can prevent deep mixing of cells away from optimum light levels. Near-surface blooms may significantly deplete upper water column nutrients, and retention near the surface can prevent the community from utilizing deeper nutrient sources. In reality, wind-induced mixing erodes the stable upper water column over a time period of weeks to months, such that phytoplankton productivity later in the Austral summer is often limited by micronutrients and/or light availability [*Smith et al.*, 2000b; *Strutton et al.*, 2000]. Meltwater-induced blooms are not a ubiquitous feature

[*Savidge et al.*, 1995; *Bathmann et al.*, 1997] and their absence may be related to a rapid rate of ice retreat. There are few observations of the processes occurring in the lee of the retreating ice during the full development and decay of a spring bloom, so it is difficult to place these isolated observations in a more general context.

[15] The major physical mechanism opposing springtime meltwater stratification in the euphotic zone is wind stress. The Southern Ocean, particularly from approximately $0°E$ to $150°E$, $40°-60°S$, experiences the greatest oceanic wind stresses in the world [*Trenberth et al.*, 1990; *da Silva et al.*, 1994], primarily during Austral winter, but also during other seasons. Deep wind-induced mixed layers and low integrated daily irradiance may combine to limit primary productivity in the Southern Ocean [*Holm-Hansen et al.*, 1977; *Smith and Nelson*, 1985]. During summer, polar regions may receive total daily integrated irradiance equal to that of tropical oceans [*Campbell and Aarup*, 1989; *Sakshaug and Slagstad*, 1991] but that this is rarely the case due to extensive cloud cover [*Bishop and Rossow*, 1991; *Comiso et al.*, 1993]. A comprehensive account of the relationship between irradiance, water column stability, and bloom formation, based on the work of *Sverdrup* [1953], is given by *Nelson and Smith* [1991].

### 2.2. Large-Scale Temporal and Spatial Variability of Primary Production

[16] As an overview, we begin by examining the large-scale distribution and interannual variability of Southern Ocean phytoplankton biomass using satellite ocean color data. Figure 1a shows individual seasonal composite images of Sea-viewing Wide Field-of-view Sensor (SeaWiFS) chlorophyll spanning the four Austral summers for which the instrument has been in orbit: December, January, and February (DJF) 1997–2001. These months represent the peak periods of primary productivity in Antarctic waters [*Abbott et al.*, 2000; *Smith et al.*, 2000b]. Figure 1b combines these four summer composites into one "climatology" (albeit only from the 4 years of available data). Together these data illustrate regions of consistently high and low productivity, as well as regions of significant interannual variability south of the PF.

[17] The Ross and Weddell Seas exhibit high chlorophyll levels when ice-free, as do most of the near-coastal regions and the area north of the Weddell Sea, from about $0°W$ to $60°W$, between $50°S$ and $70°S$. These high chlorophyll areas are often associated with bathymetric features. An analysis of the interannual variance in chlorophyll (data not shown) reveals that these regions also exhibit the greatest variability in chlorophyll concentration (Figures 2 and 3). However, the total area over which this variability occurs is small relative to the vast area that experiences moderate variability in chlorophyll. The Indian Ocean sector of the Southern Ocean (approximately $0°-70°E$ or $80°E$) and the SE Pacific are often low in chlorophyll, particularly in the open ocean areas. These general patterns were also identified by *Moore and Abbott* [2000] based on 1997–1998 data. In the SE Pacific sector, approximately $60°-150°W$, this region of low chlorophyll was bounded to the north by the PF in 1997–1998, 1998–1999, and 1999–2000.

[18] Substantial interannual variability is apparent from this time series. Figure 1a suggests that the 1999–2000
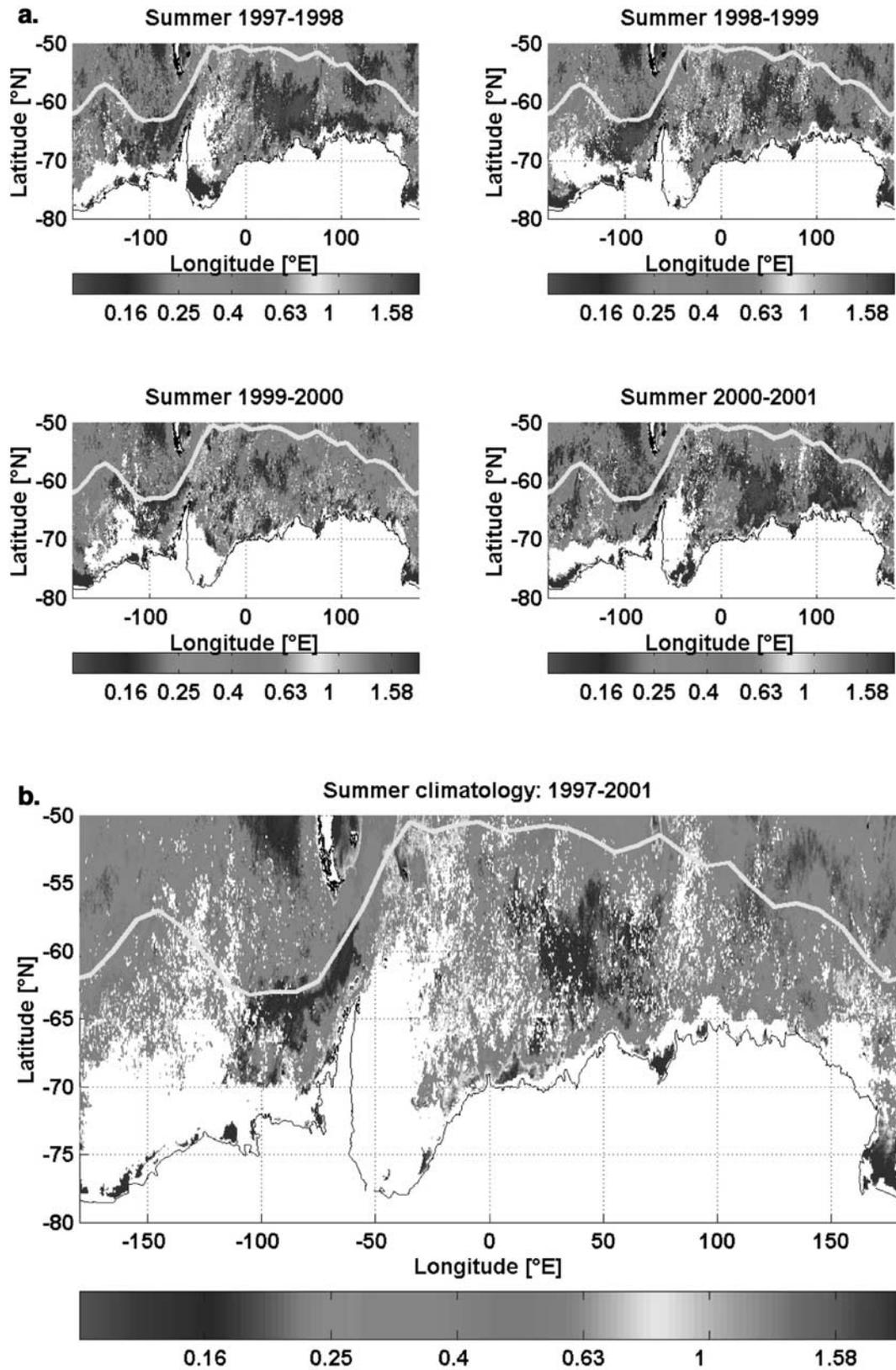
Figure 1.   (a) Mean SeaWiFS chlorophyll concentration [mg m^{-3}] for the Austral summers (DJF) of 1997–1998, 1998–1999, 1999–2000, and 2000–2001. The PF, as described by *Moore et al.* [1999], is plotted in yellow. (b) SeaWiFS chlorophyll [mg m^{-3}] climatology for DJF 1997–2001. Mean chlorophyll was calculated using only pixels that contained valid data for all four summers depicted in Figure 1a. Color bar is chlorophyll [mg m^{-3}], and the PF is plotted in yellow.
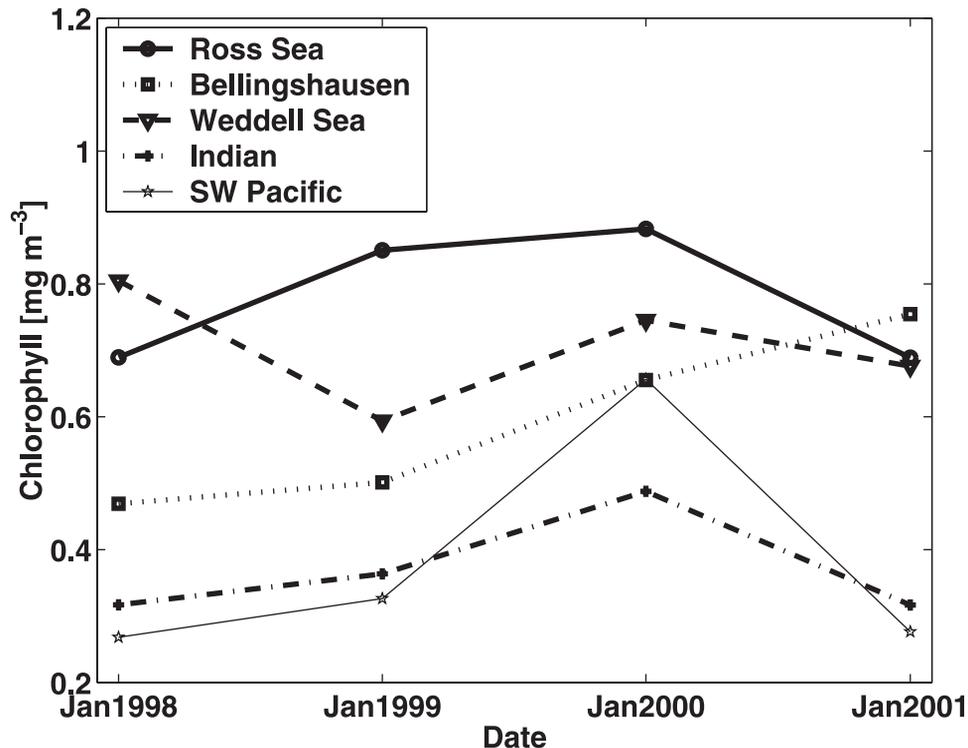
Figure 2. Mean DJF SeaWiFS chlorophyll concentration [mg m^{-3}] between the coast and PF in five regions defined by longitude [*Arrigo et al.*, 1998; *Gloersen et al.*, 1992]: The Ross Sea sector (160°E to 130°W), the Bellingshausen/Amundsen Sea sector (130°−60°W), the Weddell Sea sector (60°W to 20°E), the south Indian Ocean sector (20°−90°E), and the SW Pacific sector (90°−160°E).

summer exhibited higher chlorophyll concentrations throughout much of the Southern Ocean. This observation is confirmed by a time series of mean chlorophyll concentrations (Figure 2). These means were calculated to quantify regional, interannual variability in five areas surrounding the Antarctic continent [*Gloersen et al.*, 1992; *Arrigo et al.*, 1998]: The Ross Sea sector (160°E to 130°W), the Bellingshausen/Amundsen Sea sector (130°−60°W), the Weddell Sea sector (60°W to 20°E), the south Indian Ocean sector (20°−90°E) and the SW Pacific sector (90°−160°E). Within these areas, the mean chlorophyll concentration was calculated from all valid SeaWiFS pixels between the coast and the PF (as defined by *Moore et al.* [1999]). The Indian, SW Pacific, and Bellingshausen/Amundsen sectors do experience generally lower chlorophyll than the Weddell and Ross Seas (Figure 1), and in almost all regions, the 1999−2000 summer was highly productive, despite exhibiting no obvious differences in total ice coverage. In the SW Pacific and Indian sectors, the region of high chlorophyll conforms to the productive area already described [*Nicol et al.*, 2000d]. Elevated productivity in the 80°−150°E region has also been identified from long-term surface chlorophyll records (summarized by *Savidge et al.* [1996]), and larger-scale Antarctic ocean color data sets [*Moore and Abbott*, 2000]. Sea ice data sets (http://www.antcrc.utas.edu.au/~jacka/seaice.html) describe recurrent greater northward extent of winter ice coverage in this region, a phenomenon that has been explained by the existence of a partially closed, cyclonic gyre [*Worby et al.*, 1998; *Bindoff et al.*, 2000].

[19] The interannual variability in chlorophyll concentrations is also depicted in Figure 3. The data are as described above and plotted as mean chlorophyll concentration for each sector in Figure 2. The number of pixels at each chlorophyll concentration is represented as a proportion of the total number of valid SeaWiFS pixels with chlorophyll <1.0 mg m^{-3}. Chlorophyll concentrations of >1.0 mg m^{-3} (50−70% of the pixels) were excluded from the presentation because the interannual variability (data not shown) in the high chlorophyll areas (>1.0 mg m^{-3}) is small relative to the low chlorophyll areas (<1.0 mg m^{-3}). The data illustrate some regional and interannual features. The Ross Sea and Weddell Sea plots are clearly skewed toward higher chlorophyll concentrations, with more pixels at >0.5 mg m^{-3} and less at ~0.2 mg m^{-3}. These productive regions exhibit reduced interannual variability, except during the 2000−2001 summer, which is characterized by slightly lower chlorophyll. For the Weddell sea, this decline in 2000−2001 is due to reduced offshore chlorophyll concentrations, whereas in the Ross Sea, the 2000−2001 nearshore bloom appears to be much reduced in spatial extent and intensity. For the Indian, SW Pacific and Bellingshausen sectors, the majority of the <1.0 mg m^{-3} pixels are centered around 0.2 mg m^{-3}, or closer to 0.1 mg m^{-3} for the Indian sector. The Bellingshausen shows a strong skewing toward higher chlorophyll during 2000−2001, the same time period for which the Ross and Weddell Seas, which neighbor this region, shifted toward lower chlorophyll. For the Indian and SW Pacific sectors, the shift toward higher chlorophyll in 1999−2000 is clearly visible.
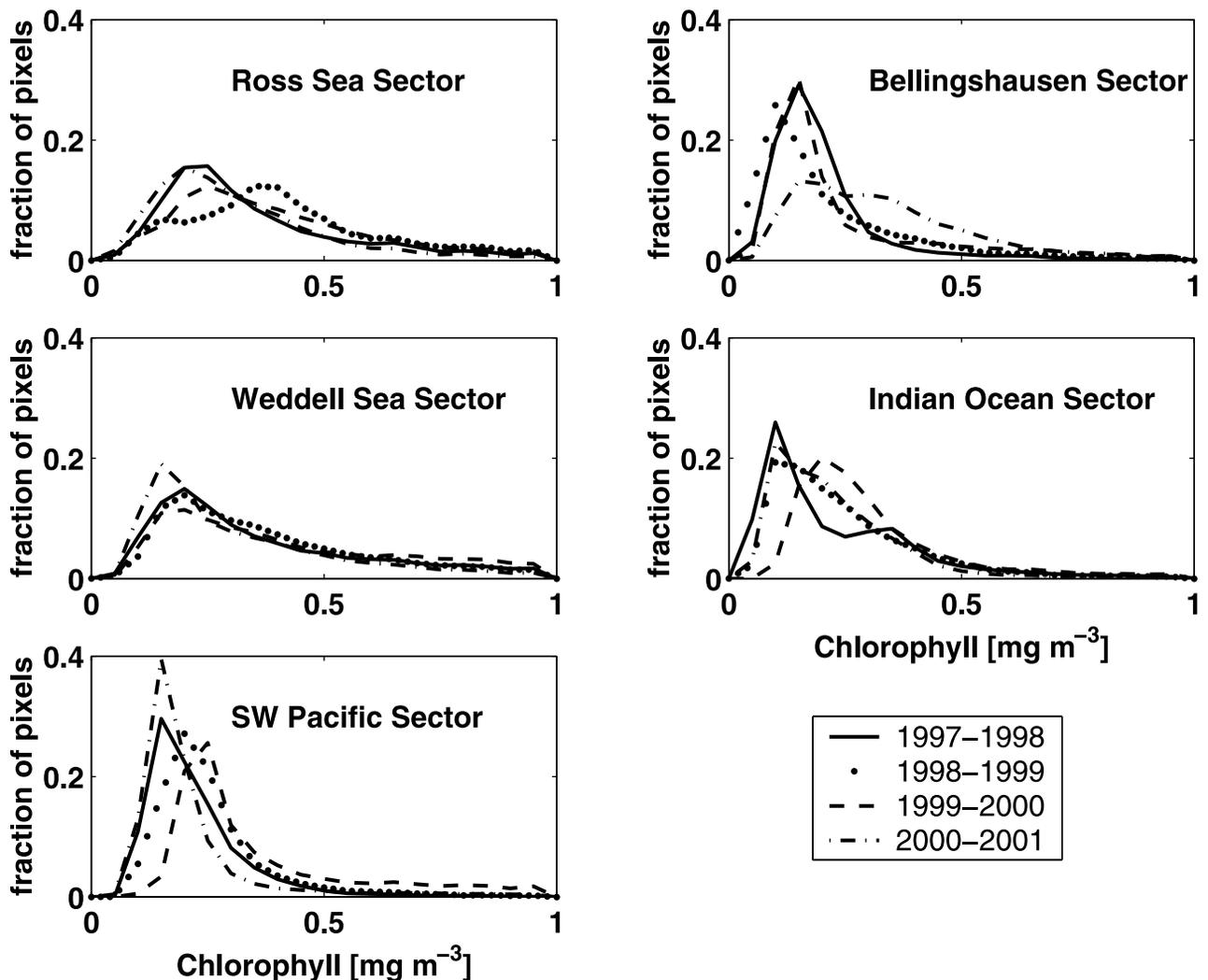
Figure 3. Frequency distribution of DJF SeaWiFS chlorophyll pixels in the five regions described above. Frequency distributions are quantified as a proportion (0–1) of all pixels in each region with chlorophyll <1.0 mg m^{-3}.

[20] *Savidge et al.* [1995] suggested that the lack of an ice edge bloom during their study to the west of the Antarctic Peninsula was a result of very rapid ice retreat. We examined the relationship between the rate of ice retreat and the development of an ice edge bloom using the ocean color data summarized in Figures 1, 2, and 3, in conjunction with data describing the northern extent of sea ice by month. Sea ice coverage was calculated using data from the Special Sensor Microwave/Imager (SSM/I). For monthly data from September 1997 (start of SeaWiFS) to March 2001, the northern extent of Antarctic sea ice was determined in bins of 10° longitude and then interpolated onto an 8-day grid to correspond with SeaWiFS 8-day data. The rate of change in sea ice area (in km^2 d^{-1}: advancing = +ve, retreating = −ve) was then calculated. We acknowledge a potential problem with this method in that the pixel sizes for the ice and chlorophyll data do not match, however, our interest is in comparing seasons and regions, over which any biases in the method will be constant. For periods of ice retreat, the rate of retreat was then compared with the mean chlorophyll concentration in ice-free pixels between the coast and the

PF, from the same 10° longitude bin (Figure 4). The results were compared with geographical and oceanographic features (Figure 4a). Figure 4b summarizes the mean DJF SeaWiFS chlorophyll concentration and mean rate of ice retreat for 1997–2001 as a function of longitude, and the correlations in each longitude bin are represented as a function of longitude in Figure 4c.

[21] A negative correlation between chlorophyll and ice retreat rate indicates that bloom formation is associated with quickly retreating ice, and vice versa for a positive correlation. There are considerable regional differences in this relationship (Figure 4c). High chlorophyll is associated with rapid summer ice retreat in the Weddell and Ross Seas, as well as in the Prydz Bay area (∼75°E) and eastern Australian sector, near 140°E. A physical–biological coupling mechanism to explain the favoring of blooms by rapid ice retreat is not immediately apparent. This correlation may simply be because these coastal regions, particularly the embayments are sites of intense blooms due to geography, bathymetry, and circulation, and are also regions where the annual difference between maximum and minimum ice
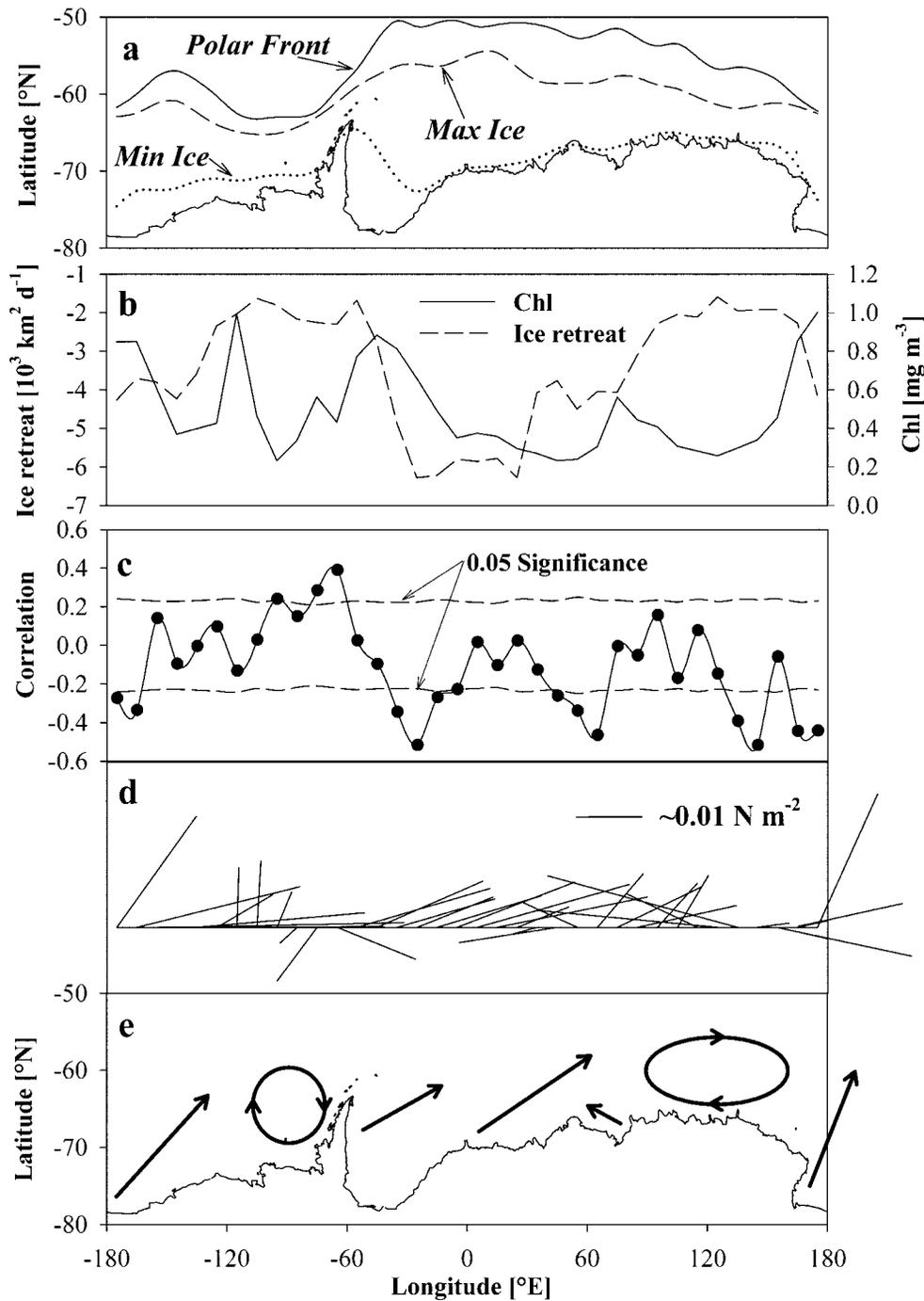
Figure 4. (a) The Antarctic coastline, the position of the PF (solid line), and the climatological maximum (dashed line) and minimum (dotted line) ice extent. (b) Mean DJF SeaWiFS chlorophyll concentration from 1997 to 2001 (solid line) compared to estimates of mean ice retreat (dashed line) as a function of longitude. (c) Correlation between rate of ice retreat and mean DJF SeaWiFS chlorophyll concentration as a function of longitude. A negative correlation implies that rapid ice retreat is correlated with high chlorophyll concentrations. The 0.05 significance level is plotted as a dashed line. The significance line is not straight because the number of observations varies as a function of longitude. (d) Climatological wind vectors, wind "sticks" point in the direction of the wind and the size of each stick is proportional to wind strength (scale indicates 0.01 N m^{-2}). (e) Representation of climatological winds around Antarctica as large-scale wind patterns.

extent is large, thus requiring rapid retreat. However, this does not explain the correlation observed near 140°E where there is a regional minimum in sea ice extent and is a region of relatively low productivity [*Strutton et al.*, 2000]. A positive correlation between high chlorophyll and slow ice retreat was observed near 70°W, close to the Bellingshausen Sea, similar to field observations [*Savidge et al.*, 1995].

[22] Investigation of ice dynamics with regard to the high chlorophyll observed in the Indian and Australian Sectors during the 1999–2000 summer did not reveal any clear relationship between retreat rates and bloom development. However, there was evidence of greater northward extent of ice during the preceding winter. Relative to the 1997, 1998, and 2000 winters, winter ice was observed approximately 0.5°–1.5° latitude further north between 50°E and 90°E during winter 1999. Increased ice extent during winter could lead to higher chlorophyll concentrations in the following summer simply by increasing the area over which meltwater stability is induced, or the area which is seeded by released ice algae. Alternatively, iron released from melting sea ice may increase phytoplankton productivity [*Sedwick and DiTullio*, 1997] in "high" sea ice years, by increasing the opportunity for the atmospheric deposition of iron onto the ice surface, for subsequent release.

[23] As bloom development and dispersion is related to water column stability, which is itself related to wind stress, we have analyzed the climatological wind fields for the Southern Ocean [*da Silva et al.*, 1994] in relation to the available SeaWiFS chlorophyll data. The wind data span the period 1945–1989 and are available at ftp://niteroi.gsfc. nasa.gov/pub/uwm_coads/1x1/data/coards_clm. While the time period of the wind climatology is different to that of the SeaWiFS chlorophyll record, these data can still be compared, assuming that no large-scale changes have occurred in seasonal wind patterns over the last decade (Figure 4d). Wind stress was calculated using only the data from the latitudinal range of sea ice retreat, for DJF each summer, the period corresponding to the chlorophyll data in Figure 1. Combining the data presented in Figure 4, it becomes clear that high chlorophyll, increased winter sea ice extent and prevailing southwesterly winds are observed in the vicinity of the Ross Sea, Weddell Sea and Prydz Bay (~75°E). Conversely, weak north or NE winds, reduced winter sea ice extent and lower chlorophyll are observed near 80°W and 130°E. This relationship between wind stress and productivity was also supported by investigating the relationship between the wind vectors and SeaWiFS chlorophyll. Significant positive correlations (0.05 significance level, n = 36, r = 0.373 for zonal winds, r = 0.428 for meridional winds, CV = 0.329) were observed between the zonal and meridional component of the climatological wind and mean chlorophyll, but not between the scalar wind (i.e., total magnitude of the wind stress) and chlorophyll. To summarize, at large spatial scales of the order of 10° of longitude, the direction of the wind field is important to the formation of blooms: westerlies and southerlies co-occur with enhanced chlorophyll, while northeasterlies do not.

[24] Our analysis of winds, ice dynamics, and chlorophyll explains some observed phenomena, but also raises further questions. Our main conclusions are as follows:

1. There is no consistent relationship between ice retreat rates and chlorophyll concentrations (Figure 4c). Depending on location we observed enhanced chlorophyll associated with rapid ice retreat (Ross Sea, Weddell Sea, and Prydz Bay) slower ice retreat (Bellingshausen Sea) or no correlation at all. Large-scale (~10^3 km) spatial variability of chlorophyll is perhaps best explained by factors such as proximity to fronts and localized upwelling [*Bathmann et al.*, 1997; *Moore and Abbott*, 2000], coastline morphology, bathymetric features, large-scale ocean circulation [*Strutton et al.*, 2000] and perhaps release of iron from sea ice [*Sedwick and DiTullio*, 1997].

2. There is no simple relationship between productivity in an area and the average annual coverage of sea ice (Figures 4a and 4b), which might be predicted from an extension of hypotheses developed at single locations [*Loeb et al.*, 1997].

3. Coastal regions are characteristically the most productive waters. Movement of this production offshore could occur as a result of large-scale physical processes such as gyres, coastal currents and prevailing winds (Figures 4d and 4e). The large-scale relationship between enhanced production in the coastal waters and its offshore transport in a gyre has been illustrated for the 80°–150°E region [*Nicol et al.*, 2000d].

4. Localized upwelling, associated with bathymetric features, is likely to be responsible for increased oceanic productivity as has been shown in the region of the Kerguelen Plateau at approximately 85°E in Figure 2 and also demonstrated by *Moore and Abbott* [2000].

[25] Future analysis could investigate these processes, in conjunction with contemporary wind stress data (perhaps from satellite scatterometers, as opposed to climatological data), at greater spatial and temporal resolution. As the length of the SeaWiFS time series increases, it will become possible to investigate the spatial variability of productivity at longer timescales. Specifically, the influence of the Antarctic circumpolar wave (ACW) identified by *White and Peterson* [1996] should be quantified. The ACW, which perturbs surface pressure, winds, ocean temperature and sea ice extent has been shown to take of the order of 8–10 years to circumnavigate the Antarctic continent. The SeaWiFS data we have used span 4 summers, and some of the observed variability, such as the increase in chlorophyll in the SW Pacific and Indian sectors in 1999–2000, may be related to ACW propagation. Preliminary investigations of this phenomenon [*Le Quéré*, 2000] have suggested that the impact on chlorophyll is small (changes of 0.02–0.06 mg m^{-3}) and varies in sign spatially. It would be of great interest to revisit and expand the analysis presented here in 5 years.

2.3. Distribution and Magnitude of Secondary Production

[26] The key secondary producers (herbivores) in the Southern Ocean are thought to be salps, copepods, and krill [*Ross et al.*, 1996; *Voronina*, 1998]. The dynamics of a population and its productivity at a given time and place is governed by its reproductive, growth and mortality rates. Studies of such rate processes are mostly limited to those on Antarctic krill and generalizations about the production of other herbivorous species come largely from observations of distribution and abundance, although detailed studies in restricted areas have examined other species such as copepods around South Georgia [*Atkinson et al.*, 2001].

Table 1. Summary of Primary Production and Dominant Herbivores in Four Biogeographic Zones in the Southern Ocean

Biogeographic Zone	Primary Productivity	Dominant Herbivores
Coastal zone	Seasonally high	*Euphausia crystallarophias*, Copepods
Marginal ice zone	Seasonally very high	*Euphausia superba*, Copepods
Permanently open ocean zone	Low	*Salpa thomsonii*, Copepods
Polar frontal zone	High	*Euphausia valentinii, Euphausia frigida, Euphausia triacantha*

[27] The distribution of the major herbivores is assumed to be related to the distribution of phytoplankton. However, the abundance of secondary producers and the level of secondary productivity may not necessarily coincide with the distribution of chlorophyll or the level of primary production (see for example the variation in this relationship among copepod species at South Georgia [*Atkinson et al.*, 2001]). This may result from factors that introduce spatial or temporal lags into the system, differences in the production to biomass ratios between trophic levels or the responsiveness of secondary producers to factors other than chlorophyll *a*. A number of large-scale conceptual models have been developed to account for changes observed in the distribution and abundance of krill:

1. There is a close relationship between krill abundance and ice cover [*Loeb et al.*, 1997; *Nicol et al.*, 2000d].

2. There is competition between krill and salps [*Loeb et al.*, 1997].

3. There is a close association of phytoplankton, zooplankton and higher-order predators with the Southern Boundary of the ACC [*Tynan*, 1998].

4. The abundance of krill outside the sea ice zone is predominantly the product of transport of krill, the "krill conveyor belt" from the Antarctic Peninsula to South Georgia [*Murphy et al.*, 1998].

[28] This section examines these concepts further by reviewing the mechanisms that may influence secondary production, its distribution, and the processes that may influence the structure of pelagic assemblages, drawing on examples of species other than krill where possible.

2.3.1. General Distributions of Secondary Producers

[29] There is surprisingly little direct evidence of the effects of temporal or spatial variations in primary productivity on secondary production. In fact, early studies made much of the lack of correlation between the abundance of species such as krill in an area and the abundance of phytoplankton [*Hardy*, 1936]. Even recent studies have found no obvious or direct relationships despite finding some correlations at different spatial scales between the distribution of krill and the abundance of phytoplankton [*Weber and El-Sayed*, 1985]. Some of the uncertainty in the relationship may be due to methodological problems: krill distribution and abundance are generally estimated on different horizontal and depth scales from phytoplankton abundance or primary productivity. However, there are also likely to be different timescales of response between phytoplankton and herbivores to changes in the physical environment which would tend to make simple relationships unlikely [*Murphy et al.*, 1988]. For example, copepods can respond very quickly to phytoplankton blooms, although this may vary between species [*Atkinson et al.*, 2001].

[30] The distribution of the major groups of herbivorous animals has been related to the distribution of primary production and to geographic areas [*Ross et al.*, 1996; *Le Fèvre et al.*, 1998; *Voronina*, 1998]. At larger scales, there is an apparent relationship between the circumpolar distribution of secondary producers, notably krill, from historical data and the distribution of chlorophyll from satellite data [*Tynan*, 1998]. Large-scale surveys have also shown such a relationship [*Nicol et al.*, 2000d]. The distribution of herbivores can be related to biogeographic zones (Table 1).

[31] The boundaries of these biogeographic zones are neither fixed in time and space nor are they impermeable, so the relative extents of each of these zones can vary interannually and regionally. Although the communities of secondary producers may vary throughout the region, their distribution generally follows that of primary production. The greatest abundance of herbivores is found in the coastal/shelf and frontal regions while lower abundances are observed in the open ocean.

2.3.2. Relationship Between Secondary Producers and Sea Ice

[32] Despite the long recognition of some relationship between krill and sea ice [*Mackintosh*, 1972], the exact nature of that relationship has only recently been investigated, largely through the recognition of the importance of the sea ice algal community. Krill feeding on algae under sea ice has now been recorded many times [*O'Brien*, 1987; *Marschall*, 1988; *Stretch et al.*, 1988], however, most of the recorded observations are for austral spring, the period when the sea ice algal community is most developed. Observations of krill feeding during the food shortage of midwinter suggest carnivory [*Huntley et al.*, 1994], detrital feeding [*Kawaguchi et al.*, 1986], or reduction in physiological energy demands through shrinkage [*Ikeda and Dixon*, 1982] or reduced metabolism [*Quetin and Ross*, 1991]. Krill larvae are the life stage most vulnerable to food shortage and the ice algal community is the most obvious source [*Ross et al.*, 2000]. A comprehensive 6-year SCUBA study at the Palmer Long-Term Ecological Research site [*Quetin et al.*, 1996] showed that the sea ice habitat was mostly utilized by subadult krill and the association between these krill and the underside of the ice was largely evident in late winter (September).

[33] Given the obvious logistic constraints it is difficult to see how the degree of dependency of krill on the sea ice community during winter can be quantified. Simple correlations between annual sea ice extent and recruitment are potentially confounded by other factors (see below) and assume a closed system. If there is a simple relationship between the extent of winter sea ice and the recruitment of krill then regions with the greatest extent of winter sea ice might be expected to yield the greatest recruitment and those with least, would contribute least to the global krill population. Regionally, areas with a higher biomass of krill have been found to coincide with areas of greater annual extent of sea ice [*Nicol et al.*, 2000d] but this does not appear to be a circumpolar phenomenon. In

fact, the regions with the greatest krill biomass include those with least extent of sea ice: the Antarctic Peninsula region and South Georgia where there is rarely any sea ice [*Mackintosh*, 1972, 1973]. The relationship is thus not simple.

[34] Sea ice is also thought to contribute to the spatial separation of krill and salps; krill are thought to be an ice adapted species whereas salps are thought to be adapted to life in the open ocean. Variations in the relative abundance of Antarctic krill and salps off the western Antarctic Peninsula have been attributed to interannual variations in the amount of winter sea ice [*Siegel and Loeb*, 1995; *Loeb et al.*, 1997]. Following years with above average winter sea ice cover, krill were found to be more abundant and the observed proportion of age 1 krill in the population was greater but salps were scarce. The converse of each of these conditions was observed following years with below average sea ice. This inverse correlation has been thought to arise because of the winter sea ice habitat being the feeding ground for the krill population, whereas salps, it is supposed, are excluded by the increased sea ice because of their more pelagic habit. The relative abundance of these two species in summer is thus viewed as a combination of the result of the physical conditions favoring one over the other in the previous winter combined with the competition between them during spring and summer.

[35] Conditions for competitive exclusion to arise between the two taxa seem unlikely [*Le Fèvre et al.*, 1998] as competitors need to potentially co-occur, require the same resources and those resources must be limited. Recent assessments of why these taxa may be segregated did not find any quantitative evidence for competition for food [*Nishikawa et al.*, 1995; *Kawaguchi et al.*, 1998]. Mutual exclusion between adult krill and salps seems unlikely to arise from salps preying on krill eggs and larvae [*Huntley et al.*, 1989], or krill preying on salps [*Kawaguchi and Takahashi*, 1996]. Most large-scale studies appear to show that salps are oceanic creatures which may be more adapted to oligotrophic waters [*Nishikawa et al.*, 1995]. Antarctic krill, on the other hand, are found mainly in the shelf and slope areas, and in the vicinity of fronts and ice edges where primary productivity is generally higher [*Ichii et al.*, 1998a; *Lascara et al.*, 1999; *Pauly et al.*, 2000].

[36] The spatial segregation of salps and krill seems more likely to be driven by variation in the location and strengths of the major ocean water masses, which in turn influence the extent of sea ice in a given year. Within the marginal sea ice zone, it is likely that Antarctic krill play a critical ecological role and have a very high circumpolar biomass [*Nicol et al.*, 2000a]. In the permanently open ocean zone, salps may dominate as consumers of primary production. The greater variation observed in the interaction between these water masses around the Antarctic Peninsula compared with other areas may be a product of the latitudinal extent of different biogeographic zones [*Arrigo et al.*, 1998]. Near the tip of the Antarctic Peninsula, the three zones south of the ACC are compressed into $10°−15°$ of latitude, whereas in areas such as the eastern Weddell Sea and the western Ross Sea, they extend over more than $30°$. Future studies into the relationship between krill dynamics and the extent of winter sea ice might usefully examine the factors that cause there to be a

greater extent of sea ice in 1 year than in others, which might provide clues as to the ultimate causes of variation in krill recruitment.

2.3.3. Relationship Between Secondary Production and the ACC

[37] *Tynan* [1998] argued that production in the Southern Ocean is aggregated around the Southern Boundary of the ACC. This analysis depended on the accumulation of data from a variety of sources, studies that were undertaken over widely different timescales, which did not overlap. Off eastern Antarctica direct measurements of the relationship between the Southern Boundary and biological productivity suggested that productivity, at all levels, was actually bounded to the north by the Southern Boundary [*Nicol et al.*, 2000d] in contrast to Tynan's analysis of historical data which suggested that the Southern Boundary was the site of higher production.

2.3.4. Distribution and Abundance of Krill

[38] The distribution of krill is a product of both their behavior and of the circulation patterns. Younger, nonreproductive krill are found on the shelf whereas reproductive adults are generally found offshore of the shelf break in summer [*Lascara et al.*, 1999; *Nicol et al.*, 2000b]. In addition, the number and sizes of aggregations in an area can change over the course of a year, with fewer, but larger, aggregations being found in winter [*Lascara et al.*, 1999]. These changes are thought to be behaviorally induced with many small, widely dispersed, foraging aggregations in summer coalescing into the smaller number of larger onshore wintering aggregations [*Ross et al.*, 1996]. These patterns and their seasonal changes are unlikely to result simply from the circulation patterns in the areas studied [*Lascara et al.*, 1999]. Spatial distributions on a number of scales could be influenced by active vertical [*Ross et al.*, 1996] and/or horizontal migration [*Kanda et al.*, 1982]. Further studies are required to identify the mechanisms that underpin these spatial separations.

[39] On a larger scale (>1000 km), there are regions around the Antarctic where quasi-permanent, large-scale concentrations of krill are thought to exist [*Mackintosh*, 1972, 1973; *Lubimova et al.*, 1982]. Many of these concentrations are related to environmental features but there are persistent populations of krill in certain areas which exhibit both demographic [*Lascara et al.*, 1999] and genetic [*Zane et al.*, 1998] continuity but appear different to other areas. Nevertheless, the prevailing view is that these populations are the product of physical retention mechanisms which allow the build up of local populations from a moving stream of krill in the ACC [*Murphy et al.*, 1998]. Direct observations of krill aggregations being passively transported by currents [*Everson and Murphy*, 1987] or of krill schools actively travelling over long distances are rare [*Kanda et al.*, 1982] but few studies have set out to examine the phenomenon of krill flux.

[40] Reconciling the potential for physical transport of krill and the apparent differentiation of krill stocks on a large scale is a priority topic for research on the dynamics of krill populations. One of the few detailed analyses of the interaction between the dynamics of pelagic populations and physical processes [*Huntley and Niiler*, 1995] concluded that mesoscale oceanographic processes influencing resident time of zooplankton in an area play a crucial role in

keeping zooplankton and krill in areas of high primary productivity. The results of that study indicate the great potential for movement from one region to another over the generation time (7–10 years) of a population but that individuals were likely to be retained within a region over the course of a season yielding high secondary production in areas of high primary production. This is evident for a number of zooplankton species around South Georgia where secondary production of krill and copepods may be able to meet the demand of consumers by having rapid growth rates while retained in this area [*Atkinson et al.*, 2001]. Although the boundaries to mostly closed populations of krill in the Southern Ocean are difficult to determine at this stage, it appears likely that the abundance of secondary producers will be correlated with primary production of a region.

2.3.5. Rate Processes for Krill

[41] The key rate processes for krill are growth, reproduction, recruitment, and mortality, which together with immigration and emigration determine the abundance of krill in a particular area. Off the western Antarctic Peninsula region, a good relationship has been found between the growth rate of juvenile krill and the average level of chlorophyll *a* in a given year [*Ross et al.*, 2000]. In this study, maximum growth rates of krill were only observed in years with extensive diatom blooms, indicating food quality rather than absolute measures of primary productivity or phytoplankton biomass was a key factor in determining growth rates. *Hofmann and Lascara* [2000] have developed a physiological growth model for Antarctic krill based on the relationships between krill, primary production, and sea ice. Recruitment of Age 1 krill has been related to a number of biotic and abiotic factors [*Siegel et al.*, 1997]. The key intrinsic factors that can affect recruitment in a season are the spawning success the previous year and the overwintering success of the cohort that is entering the adult population. Spawning success appears related to the availability of food; krill require considerable food intake to support spawning, can only produce more than one brood if food supplies are high [*Nicol et al.*, 1995] and also depend on the long-term feeding history [*Quetin et al.*, 1994]. The number of broods that krill can produce is also related to the length of the productive season [*Ross and Quetin*, 1983] and the length of the spawning season can vary considerably between seasons and regions depending on environmental conditions [*Ross and Quetin*, 2000].

[42] Mortality occurs through consumption by predators. Estimates of the annual consumption of krill by land-based predators and some fish species have been acquired for some locations [*Croxall and Prince*, 1987]. Reliable estimates for most fish and cetaceans remain elusive. Much less attention has been given to estimating natural mortality rates in krill populations than has been devoted to estimating recruitment and consumption. Values of annual natural mortality (M) for the postlarval krill may range between 0.66 and 1.35 yr^{-1} [*Siegel and Nicol*, 2000]. Regional, seasonal and interannual differences in mortality can be attributed to different predator demands, as well as short-term variability or long-term trends of environmental parameters. There may also be ontogenetic differences in natural mortality. *Pakhomov* [1995] estimated that the natural mortality rate for *E. superba* during the first year

is relatively high (M = 1.11–1.12 yr^{-1}), it decreases thereafter during the maturation period (M = 0.52–0.65 yr^{-1}) and increases slowly for older age groups, reaching a maximum during the last year of life (M = 1.29–2.41 yr^{-1}).

[43] For a given area, observed rates of population growth will also be influenced by the rates of immigration to and emigration from an area. The large-scale patterns described in this paper provide some foundation for considering a S-N connection in some areas, particularly in the Scotia Arc region. The concept of "krill flux" has been a dominant paradigm in Antarctic ecology. The basic underlying theme is that of a "krill conveyor belt" which carries krill in the ACC along the western Antarctic Peninsula past the South Orkneys and South Sandwich Islands to South Georgia [*Hofmann et al.*, 1998]. Krill are, to a large extent, viewed as passive drifters in the flow field, though regions with consistently high biomass within the general area are viewed as having extended residence times which are oceanographically determined [*Murphy et al.*, 1998].

[44] Krill appear to be concentrated in the inner shelf area in the western Antarctic Peninsula region when compared to the outer shelf area in all seasons [*Lascara et al.*, 1999]. Further to the north, west of the South Shetlands, krill were an order of magnitude more abundant in the inner shelf region (138 g m^{-2}) when compared to oceanic waters (8 g m^{-2}) [*Ichii et al.*, 1998a]. In these locations, the observed geostrophic flows have been described as sluggish, and tend to have a southwesterly direction with limited exchange along the shelf either north or south [*Ichii and Naganobu*, 1996; *Smith et al.*, 1999] in contrast to the models of large-scale geostrophic flows in the region, which indicate a W-E flow toward South Georgia [*Hofmann et al.*, 1998].

[45] There are two important aspects that remain to be determined to understand the importance of a "krill conveyor belt" to the dynamics of krill at South Georgia: the magnitude of immigration required to sustain the krill population and its predators at South Georgia and evidence for the transport of krill from a source population. In the case of the latter, there is little direct evidence for large-scale transport of krill in the ACC (see above). However, one of the key reasons that krill flux has had to be inferred is the mismatch between the demand for krill at South Georgia, estimated from predator diet analysis, and the biomass of krill in the waters around South Georgia, estimated by acoustics. At South Georgia, the average density of krill is generally among the highest measured anywhere around the Antarctic [*Brierley et al.*, 1999], although there are years when krill appear to be nearly absent [*Heywood et al.*, 1985]. Despite this, acoustic estimates of density have failed to approach the estimated requirements for krill from land-based predators in the South Georgia area [*Croxall et al.*, 1985] although recent analyses have suggested that the mismatch may not be as great as first envisaged [*Atkinson et al.*, 2001]. This, however, is not a unique problem to South Georgia. Recent global estimates of krill abundance using acoustic data from around the continent fall considerably short of that required to support the global requirements of land-based and pelagic predators of krill [*Nicol et al.*, 2000a]. It is difficult to envisage an import-driven production system at South Georgia when the global population of krill is unable to provide the level of export required.
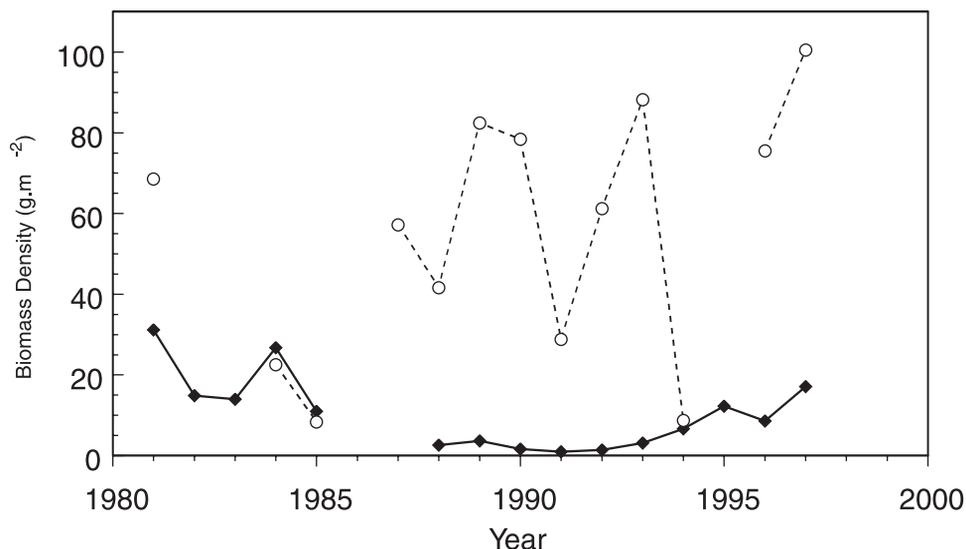
Figure 5. Observed biomass densities (g m^{-2}) at Elephant Island (Antarctic Peninsula) from net-haul surveys (filled diamonds) [*Siegel et al.*, 1998] and acoustic surveys (open squares) [*Brierley et al.*, 1999; *Hewitt and Demer*, 1994a].

[46] Part of the problem in matching supply and demand for krill in regions such as South Georgia may come from an underestimation of in situ production [*Atkinson et al.*, 2001]. Estimated production to biomass ratios for krill range from 0.53 to 2.77 yr^{-1} [*Miller and Hampton*, 1989; *Voronina*, 1998]. There is also evidence that there is not a fixed P/B ratio for krill and that in certain areas it may be close to zero [*Ross and Quetin*, 1988]. Standing stock estimates at South Georgia of 1.5 million tons [*Trathan et al.*, 1992] could thus generate production of between 0.8 and 4.2 million tons, depending on which estimate of P/B is used. This compares to estimated predator demand in the same area of 9.76 million tons [*Everson*, 1995]. Obviously, the degree to which flux must be implied to support consumption depends on the level of production as well as on realistic estimates of abundance and distribution of krill, and consumption by predators.

[47] There has always been some uncertainty concerning the self sustaining nature of the krill population at South Georgia [*Marr*, 1962; *Mackintosh*, 1972]. Krill larvae have been found in this area [*Marr*, 1962] but some studies do report their absence [*Ward et al.*, 1990]. Large reproductive females are sometimes found in high abundance in South Georgia waters [*Marr*, 1962]. It is likely that they spawn there, but whether the eggs are retained in the locality or lost to the east through the prevailing water flow is unknown. Other organisms with planktonic larvae that populate the waters around South Georgia such as fish or copepods appear to have self sustaining populations, or at least are assumed to have residence times which are significant in terms of their overall life spans. Similarly, other island groups in the ACC also appear to have resident populations of organisms which are either planktonic or which have planktonic phases in their life cycles so the mere existence of a strong prevailing current is not sufficient to require the concept of flux to explain the existence of a persistent population around an island group. There is also evidence from other oceanic regions that distinct populations of pelagic organisms can arise, despite the homogenizing effect of ocean currents, e.g., various species of krill in the North Atlantic [*Bucklin et al.*, 1997; *Zane et al.*, 2000]. Also, other oceanic, and even truly holoplanktonic organisms can display genetic heterogeneity between populations [*Aoyama et al.*, 1999], site fidelity [*Swearer et al.*, 1999] and self-recruitment [*Jones et al.*, 1999]. Thus, the separation of krill into distinct local populations in the Southern Ocean is not easy to dismiss without direct evidence [*Ayala and Valentine*, 1979].

3. Examining the Role of Sea Ice and Advection on the Dynamics of Krill

[48] The concepts discussed above raise a number of issues concerning the dynamics of krill populations. Most work relating the dynamics of krill populations to interannual variation in the environment has emanated from long-term monitoring studies of the Antarctic Peninsula. The longest time series of abundance surveys come from Elephant Island, extending back to 1978. In this case, there are two sets of data. The first is a series of random net-haul surveys, which provides estimates of density and age structure of krill and has been used to estimate biomass densities and to derive indices of recruitment, notably the abundance of 1-year-old krill in the region [*Siegel et al.*, 1998]. The second is a series of acoustic estimates of biomass over the last two decades [*Hewitt and Demer*, 1994b; *Brierley et al.*, 2000].

[49] It is noteworthy that the estimates of biomass densities from the two different types of survey yield very different results (Figure 5). Despite the expected differences arising from the known methodological differences, the shapes of the time series are very different. Results of the net-haul series have been used to conclude that a significant decrease in krill biomass has occurred from the 1980s to the 1990s [*Siegel et al.*, 1997]. In contrast, the acoustic series has been used to conclude that the krill biomass varies in a predictable way according to complex cyclical phenomena
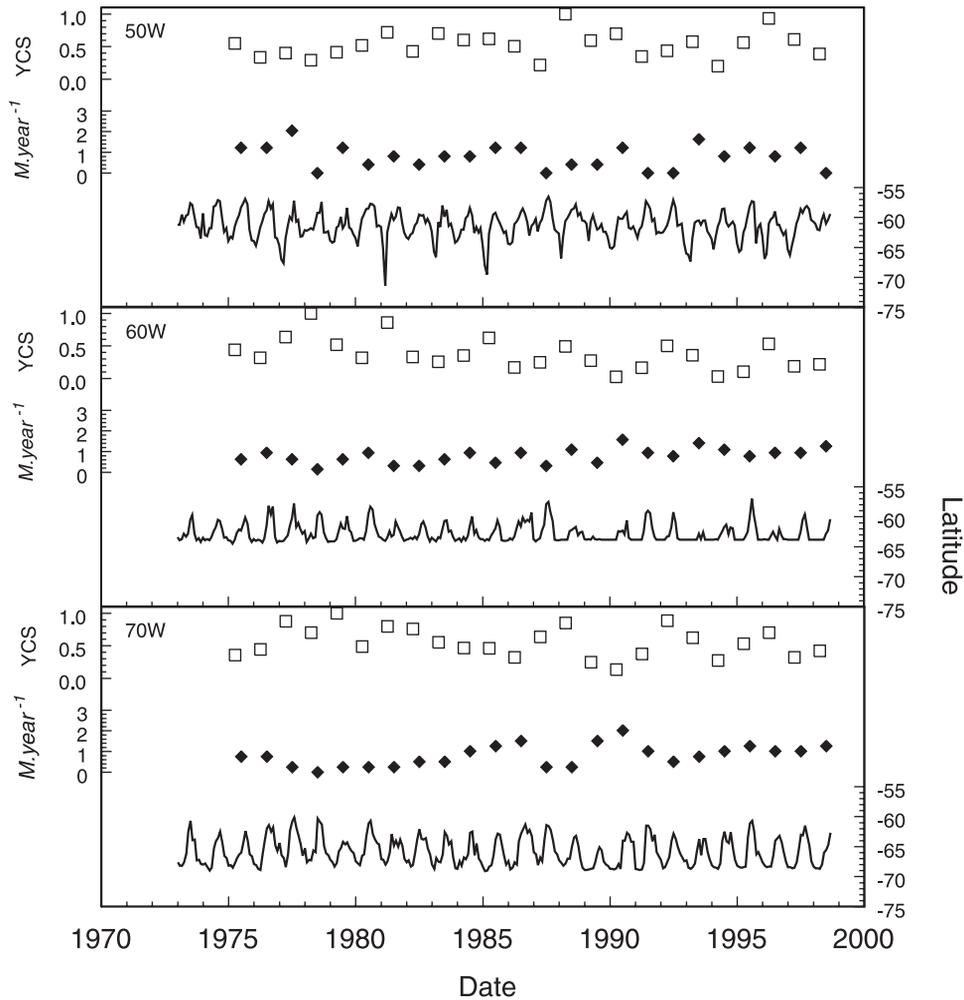
Figure 6. Ice extent (solid lines) at different longitudes: Weddell Sea (50°W), Elephant Island (60°W), and western Antarctic Peninsula (70°W) along with year class strength (YCS) (open squares) and mortality (filled diamonds) time series estimated from the ice data. Year class strength was translated directly to represent recruitment in the following year.

[*Brierley et al.*, 2000]. In both cases, the researchers have argued that (1) krill recruitment arises predominantly from the western Antarctic Peninsula and recruits and adult krill from the Weddell Sea periodically contribute to the Elephant Island local population but this is not regular [*Brierley et al.*, 2000], (2) variation in recruitment is driven by the extent and density of sea ice in the spawning year [*Siegel and Loeb*, 1995], (3) mortality rate is around 0.8 yr^{-1} [*Siegel and Nicol*, 2000], and (4) a large proportion of the biomass is exported toward South Georgia [*Murphy et al.*, 1998].

[50] Here, we explore whether the hypotheses posed above may contribute to influencing the dynamics of the local krill population at Elephant Island and, in particular, evaluate whether the seasonal and interannual variation in ice extent may be a primary force governing krill in the region. We use a simple population model for krill driven by the variation in the extent of sea ice in the region, which is derived from the ice climatology described above. Two other areas considered to have varying degrees of influence on the Elephant Island area were the Weddell Sea and the west Antarctic Peninsula. The major current flows in this area are illustrated by *Siegel and Loeb* [1995]. The charac-

teristics of sea ice for each of these regions were approximated using average ice extent in the 10° longitude bins at 60°W for Elephant Island, 50°W for the Weddell Sea and 70°W for the Antarctic Peninsula (Figure 6).

[51] For each area, the local population is modeled as a simple closed population where the numbers at age, a, at the beginning of a year, t, are given by

$$N_{a,t} = N_{a-1,t-1}e^{-M(a-1,t-1)} \qquad (1)$$

where $M(a - 1, t - 1)$ is the rate of age-specific natural mortality in the previous year. In this model, recruitment occurs at age 1 [*Siegel and Loeb*, 1995]. In order to estimate biomass, the length-at-age model of *Rosenberg et al.* [1986] is used without interannual variation in growth in this simple case, such that

$$L(a,t) = 60\,\text{mm}\left[1 - e^{-0.45\,yr^{-1}\left(a+\frac{t}{0.33}\right)}\right] \qquad \text{when } t \le g \quad (2)$$

$$L(a,t) = 60\,\text{mm}\left[1 - e^{-0.45\,yr^{-1}(a+1)}\right] \qquad \text{when } t > g$$

where a is the age class of the animal, t is the time in a year and g is the fraction of the year in which growth occurs. These lengths (mm) are converted to mass (mg) using the usual equation

$$W(a, t) = 0.00128 L(a, t)^{3.449} \qquad (3)$$

Interannual variation in the progression of sea ice was summarized from the ice climatology data into a number of state variables considered to underpin the hypotheses above: the maximum and minimum sea ice extent were determined for each year as well as the beginning of summer and the duration of summer.

[52] Following the discussion above, the spawning success of adults may be governed by the amount of sea ice available in spring time. A simple model of ice conditions for spawning is to integrate the ice extent (relative to the extent at the beginning of summer) from the time of the winter maximum to the beginning of summer, called here the spring ice condition. Recruitment at age one was scaled from 0 to 1.0 according to the spring ice condition in the previous year, ranging from no ice retreat (0) to the maximum spring ice condition (1.0). The resultant year class strengths arising from the spring ice conditions for each area are given in Figure 6.

[53] Natural mortality (M yr^{-1}) was varied each year according to the length of summer, which is considered the primary feeding period on Antarctic krill. The length of summer (months) was defined according to the extent of sea ice; the longer the period when sea ice was absent from the area the greater the access for krill predators generally. The beginning and end of summer was determined as the first and last month in the year when sea ice was regularly south of a "summer" latitude in that area. In some years, the ice did not retreat south of the summer latitude. Natural mortality in those years was assumed to be zero for this simulation. For an area, the summer latitude was determined by first determining the average cycle of ice extent (average extent in each month over the full time series) and then by finding the series of 4 months (considered to be sufficient to estimate the average summer extent in the area) for which the average ice extent over that period was the lowest of all sets of 4 months in the average cycle. The extent of sea ice in the first month of that 4-month period was considered to be the "summer" latitude.

[54] There is no basis for establishing the relative rates of natural mortality in the different regions. While other models could have been developed, a simple model of natural mortality was chosen that provided the same average annual rate of natural mortality, $\hat{M}$, in each area over the course of the time series. Natural mortality would vary from one year to the next according to the ice model above but within a year the mortality rate would remain constant during the months in which predation could occur. Consequently, for a given area, A, the natural mortality rate per month, $\overline{M}_A$, was calculated to be

$$\overline{M}_A = \frac{\hat{M}}{\overline{S}_A} \qquad (4)$$

where $\overline{S}_A$ is the mean length of summer in the area. The natural mortality for a given year in an area was estimated as

$$M_{A,y} = x\overline{M}_A S_y \qquad (5)$$

where S_y is the length of summer in year, y, and x is a scaling factor, which was adjusted so that the average mortality over the time series was the same for each area. The resultant natural mortality series for each area are given in Figure 6.

[55] The model includes migration of a portion of each population out of the respective areas in each year. This proportion per year was fixed for each area. According to many of the current theories of movement of krill in the South Atlantic, the western Peninsula and the Weddell Sea populations provide input into the Elephant Island local population but not the reverse [*Siegel and Loeb*, 1995]. In addition, a proportion of the Elephant Island population is moved each year in a northeasterly direction toward South Georgia. The model captured these potential properties of the system.

[56] The last aspect of the model was to estimate biomass density in the month in which the actual surveys took place. This is a critical aspect of reporting the results due to natural mortality being constrained to the summer period. The model population at Elephant Island was sampled in February in simulation years when no survey was undertaken.

[57] The aim of this modeling exercise was to examine the relative importance of the three different areas coupled with migration out of the Elephant Island area in generating a time series that resembled the observed time series. Three scenarios were explored in the main simulation: (1) interannual variation in both recruitment and mortality, (2) recruitment was varied each year while mortality was kept constant at the average mortality, and (3) mortality was varied each year while recruitment was kept constant. All the results were then standardized using standard normal deviates in order to compare the relative shapes of the time series against the observed biomass densities. In addition, the proportion of recruits in the population in each year was compared to the proportions reported by *Siegel et al.* [1998].

[58] A deterministic age structure at equilibrium was used to seed the model beginning in 1973. The effects of this age structure were not apparent by 1981. Hence, the time series for the comparisons extended from 1981 to 1998. A number of methods were explored to estimate the values of the parameters (average annual natural mortality and the contribution of the different populations to the Elephant Island population) needed to give the best fit of the model data to the observed data. However, there were too few data points to do this effectively. As well, the changes in sampling strategies in both programs during the time series meant that the observed data did not necessarily conform to a single relative index of the status of the population. Thus, this preliminary evaluation was only approximately fitted by eye. The primary simulations used an average annual rate of natural mortality of $M = 0.8$ yr^{-1}, consistent with the range of natural mortality reviewed by *Siegel and Nicol* [2000].

[59] Comparisons with the biomass density series from net-haul surveys provided the best fit using this simple model structure when approximately 20% of the western Antarctic Peninsula local population and 50% of the Weddell Sea local population migrated to the Elephant Island area, and 40% of the accumulated Elephant Island local population migrated out of the area each year. The results
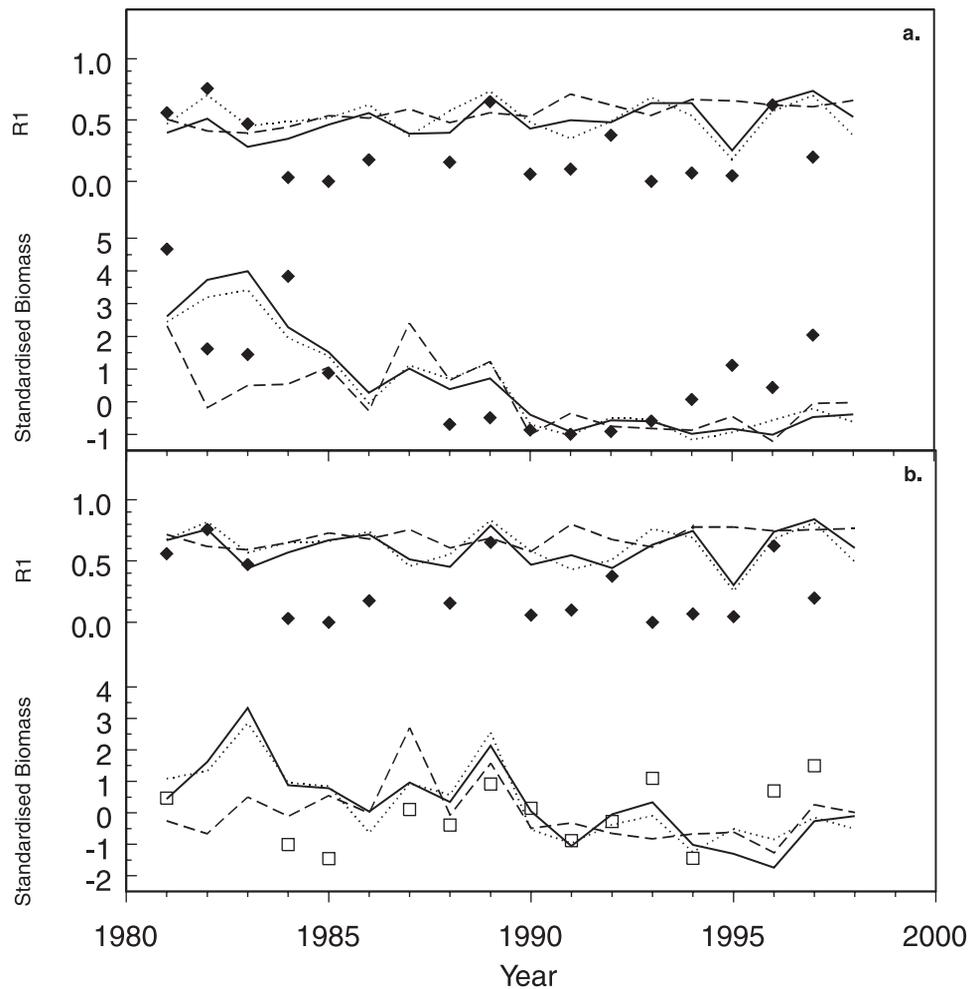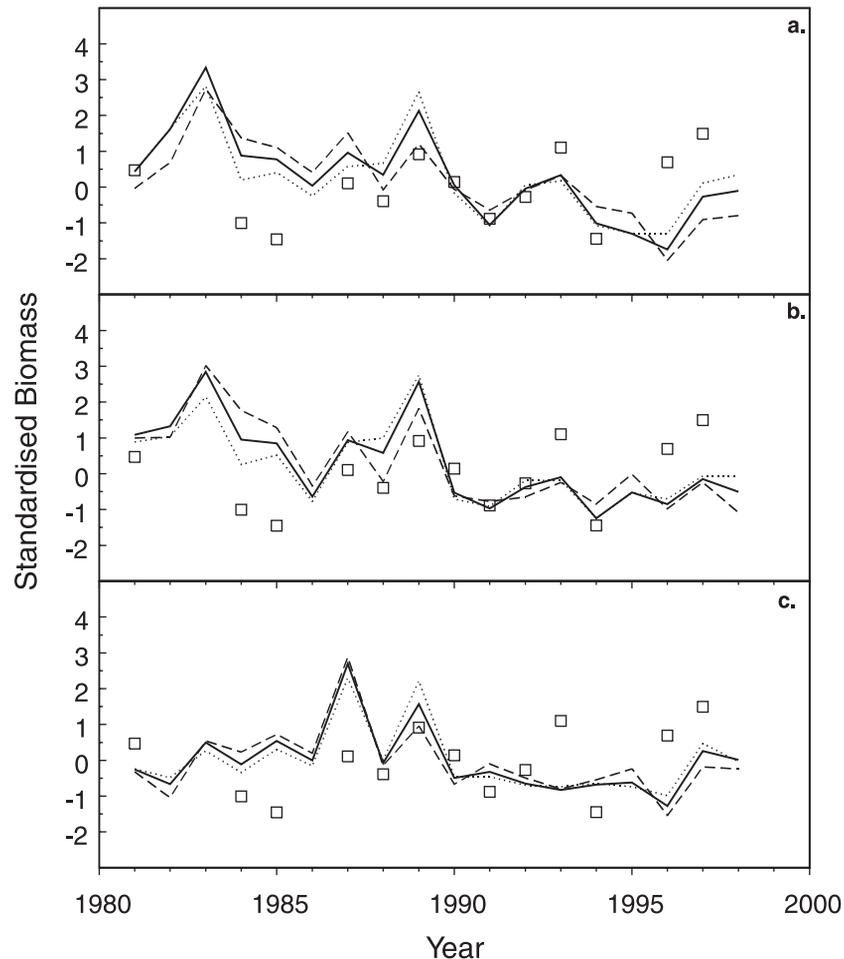
Figure 7. Standardized biomass densities and recruitment strengths (R1) for Elephant Island from model simulations using the recruitment and mortality time series shown in Figure 6 and fitting the time series to (a) the net-haul time series and (b) the acoustic time series. Fits were made by adjusting the migration patterns from the western Antarctic Peninsula and Weddell Sea into the Elephant Island area coupled with emigration from the area. Filled diamonds are observations from net-haul surveys. Open squares are observations from acoustic surveys. Solid lines are model with interannual variation in both recruitment and mortality. Dotted line is model with constant recruitment and interannual variation in mortality. Dashed line is model with constant mortality and interannual variation in recruitment.

for this migratory pattern are shown in Figure 7a. In this case, the shape of the time series for the model with interannual variability in mortality and constant recruitment provides the best fit of the three models; the time series for the model with interannual variation in both recruitment and mortality appears dominated by the variable mortality time series. Until 1994, the shape is consistent with the conclusion of *Siegel et al.* [1997] that the period in the early 1980s had greater abundances of krill than in the subsequent years. In that study, the errors in the biomass estimates were such that the variation between 1981 and 1985 was not significant. After 1994, the time series is flatter than indicated by the observed biomass densities. Following 1994, there may have been a shift toward a pattern dominated by recruitment variability. This result can be expected given the shift to a much lower ice cover since 1990.

[60] The biomass density time series from the acoustic surveys was most closely approximated when there was no migration from the western Antarctic Peninsula and approx-imately 30% of the Weddell Sea local population migrated into the area and 70% of the accumulated Elephant Island population migrated out of the area each year (Figure 7b). The relative contributions of the models of interannual variation in mortality and recruitment described for the other data set are applicable to this model, whereby variation in mortality is a dominant forcing variable in the population trajectory prior to 1994, and recruitment variation is the dominant feature after that time.

[61] An interesting result is that the time series of recruitment strengths (R1) are almost identical for the two different migration models (Figures 7a and 7b). There does not appear to be a close association between the model results and the observed values of R1. This would suggest that the model scenarios presented here may be unlikely or that the spatial location of recruits may have varied between the years when the surveys were undertaken. Some evidence discussed above suggested that the local distributions of krill may vary from one year to the next, such that recruits may not always

Figure 8. Standardized biomass densities for Elephant Island from simulations comparing model outputs with the acoustic time series, following Figure 7b. Sensitivity of the models to different rates of average annual natural mortality: (a) model with interannual variation in recruitment and interannual variation in mortality, (b) model with constant recruitment and interannual variation in mortality, and (c) model with constant mortality and interannual variation in recruitment. Open squares are observations from acoustic surveys. Solid lines, M = 0.8; dashed lines, M = 0.4; dotted lines, M = 1.2.

appear in surveys in fixed areas. Also, changes in sampling regimes during the time series may have affected each of the programs [*Siegel and Bergström*, 2002].

[62] The sensitivity of the models to different average annual mortality rates was explored in comparison with the acoustic time series. The model inputs were the same as those discussed above except the average annual mortality rate was varied to 0.4 and 1.2 yr^{-1}, a similar range to that given by *Siegel and Nicol* [2000]. These results are presented in Figure 8. The results discussed above seem relatively insensitive to this range of average annual natural mortality.

[63] With respect to the hypotheses put forward above, the general results indicate that variability in ice extent and rates of ice retreat will be important factors influencing krill populations, if the linkages between these characteristics and recruitment and mortality have been correctly identified in this model. However, local ice conditions are likely to be insufficient to explain the dynamics of local krill stocks; the migration of krill from other populations will be important as well. Nevertheless, the model results suggest that the rate of migration into and out of areas in this region

may be less than originally thought. As well, the western Antarctic Peninsula seems much less important than the Weddell Sea. The latter region may provide a constant contribution to the Elephant Island area, rather than being irregular. Last, the biomass at Elephant Island appears to have been driven primarily by interannual variation in mortality rather than recruitment until 1994, after which time the biomass appears more greatly affected by variations in recruitment.

[64] The degree to which krill migrate out of the Elephant Island area is not clear from these results. The models required at least 40% of the population migrating out of the area each year. This analysis has been made difficult by the different biomass time series. Such differences need to be explained before conclusions can be reached on the factors influencing krill populations. Although the total biomass densities observed may be explained by net-hauls underestimating the abundance of krill compared to acoustics, the difference in shapes of the time series needs to be explored. Were the surveys sampling different parts of the population? Is it possible that

the acoustic surveys were sampling that part of the population that was more likely to migrate compared to the samples of the net-haul surveys?

[65] The Elephant Island acoustic surveys covered widely different areas (17,338–43,474 km^2) [*Hewitt and Demer*, 1994a]. Experience from conducting surveys of very large areas (873,000 km^2) has shown that the mean density obtained can be greatly influenced by the areas included in the averaging process [*Pauly et al.*, 2000]. Antarctic krill are known to concentrate close to the shelf front zone [*Ichii et al.*, 1998a] so the more tightly a survey focuses on this area the higher the mean density is likely to be. Additionally, the latitudinal width of the band of krill-rich waters can change considerably between regions [*Nicol et al.*, 2000d] so average densities of krill can vary depending on the relative amounts of krill-rich and krill-poor water surveyed. Thus, the estimation of krill densities for comparing between areas and between seasons will require careful stratification and standardization before valid comparisons can be made.

[66] These results may in part explain the unresolved aspects of the population dynamics of krill in this area reported by E. J. Murphy et al. (Modelling the dynamics of krill populations in the Antarctic Peninsula region, submitted to *Marine Biology*). The dominance of interannual variation of mortality in these results is counter to the emphasis on recruitment described by other authors. The models of recruitment and mortality presented here result in an inverse relationship between the two parameters, though not a perfect one. This exercise illustrates that more detailed field work is required to disentangle the importance of postrecruitment mortality from the importance of recruitment in explaining interannual variation in the abundance of krill. In particular, there has been insufficient attention given to determining sources of variation in mortality.

[67] The models also show that the progression of ice advance and retreat may go a long way to explaining the dynamics of the population. However, the interplay between recruitment and mortality may not provide a predictable lag in the system that would help with generating predictive statistical models relating variation in biomass to physical parameters. This needs to be explored further. A factor not considered here is the interannual and regional variability in growth rates. The physiological models of *Hofmann and Lascara* [2000] may provide further avenues for improving the fit of these models to observed data.

[68] While this exercise has provided the grounds for testing the relative importance of different processes (recruitment, mortality, and migration) to the dynamics of krill, further advancement of these models can only be achieved by taking account of the uncertainty in the observed time series of biomass densities. In addition to the problems of ensuring standard methods and survey designs between areas and years, many of the surveys are designed to monitor the availability of krill to predators rather than to monitoring the interannual variation in stock structure and its dynamics. While not necessarily mutually exclusive, these two aims require different forms of sampling in any given year. In order to better understand the latter, surveys may need to be designed in an adaptive way so that interannual variation in the spatial structure of the population is accounted for when endeavoring to survey the whole population of krill. As discussed above, this will require some consideration of the spatial limits of the population of interest.

4. A Proposed Conceptual Model of Production

[69] If production is concentrated to the south of the Southern Boundary or at the PF then why do some areas in the ACC have much higher abundances of primary and secondary producers than would be expected for oligotrophic waters? Similarly, why does production at the ice edge appear to be spatially variable around the continent?

[70] As discussed above in the analysis of primary production, the areas of greatest production are in the coastal waters to the south of the Southern Boundary. The northward extension of this production is at the western sides of the major gyral systems as a result of currents and winds. The reduced wind stress, presence of sea ice (and consequent ice melt) and nutrient-rich water provide for high rates of primary and secondary production. The northward extent of production appears to be related to sea ice extent in these areas but may instead be driven by the northward extension of the coastal current. This production may be retained, transported eastward in the ACC, and gradually depleted. It is in these areas where the relationship between biomass and ice extent breaks down. This process can be enhanced in areas without gyres as a result of a combination of the E-W coastal current, wind stress and ice formation causing an enhanced northward movement of ice and enhanced zone of ice melt, such as in eastern Antarctica [*Nicol et al.*, 2000d].

[71] As a consequence of this model, interannual variation in production would be driven by variation in the strength of the gyres, wind stress and the location of the ACC. Variation in these conditions would also provide for spatial changes in the relative distributions of the different assemblages, such as krill and salps. Krill, which are indicative of waters of the coastal current are found more widely distributed where this current is wider and vice versa. Salps on the other hand are more oceanic animals and thus covary with the distribution of the more oceanic water of the ACC. If the Southern Boundary of the ACC varies in its position, this would affect the width of the coastal current, the relative abundance of krill and salps and the amount of winter sea ice.

[72] Thus the changes observed in the Antarctic Peninsula region could be the result of oceanic changes rather than as a result of competition or differential responses of salps and krill to the presence of sea ice. Such oceanic changes have been indicated in the South Atlantic [*Priddle et al.*, 1988; *Ross et al.*, 1996] and it has been suggested that the variation in the exact location of the ACC relative to the shelf break in the western Antarctic Peninsula region influences the outer shelf circulation in this region [*Smith et al.*, 1999]. There are observations of onshore and offshore movements of the frontal systems in the Antarctic Peninsula region which have affected the strength of the coastal current [*Kim et al.*, 1998].

[73] The examination of geostrophic flows in that region would suggest that the western Antarctic Peninsula is likely not to be a source of krill for South Georgia, a point supported by the simple modeling exercise presented here and by some recent empirical data [*Watkins et al.*, 1999]. In

that exercise and consistent with the mechanisms we propose that drive the large-scale distributions of production generally, the Weddell Sea gyre may be an important source of production for the South Georgia region, although this is contrary to the evidence that these two areas are genetically distinct [*Zane et al.*, 1998].

4.1.   Implications for Monitoring the Status of the System

[74]   Observations at a single location which have a limited latitudinal extent can be severely affected by even small onshore–offshore regime shifts which may substantially affect biomass estimates of indicator species within a fixed survey area. Observed changes in relative abundance could thus be considered in terms of habitat shifts as a result of displacement of water masses caused by large-scale oceanographic or meteorological events. The consequences of this model is that a drop in relative abundance of krill (or salps) in one season may not be reflective of an overall drop in abundance; the krill (or salps) may have just been displaced out of the survey area. This could be reflected in the observed density of krill within its habitat; it should not vary greatly between years. The extent of the habitat is the key variable and this is what is reflected in the biomass (density per unit area) within the survey area. This model also would predict that because the relative abundance of krill and salps is determined by large-scale oceanographic processes, when these change so will the abundance of krill within the survey area. Consequently, the biomass of krill in an area can vary markedly from year to year, and even within a year, but the effects of a "bad krill year" may only be transitory.

5.   Concluding Remarks

[75]   There is no doubt that ice represents an important force in the ecology of the Southern Ocean, though it may act as a primary forcing function for some features and as a covariant for others. Our initial analysis of possible links between sea ice dynamics and primary productivity yielded mixed results, which we interpreted to be due to local circulation and bathymetry. This exercise illustrated the importance of satellite chlorophyll data for determining spatial and temporal changes in surface productivity. As this ocean color time series lengthens, further opportunities will arise for investigating biological–physical coupling on a range of timescales. Future analyses using contemporary wind stress data, in conjunction with other remotely sensed variables such as sea surface height, could elucidate the biological impact of processes such as the ACW [*White and Peterson*, 1996].

[76]   The results of the krill population model presented here indicate that shifts in the system may arise so that the relative importance of different factors influencing the abundance of krill may alter from time to time. We suggested that there may have been a shift in the relative importance of these factors around the Antarctic Peninsula from factors influencing mortality to factors influencing recruitment sometime in the early 1990s. The factors influencing mortality have not been quantitatively estimated and the factors influencing recruitment are only now being quantified. Given the potential for such shifts in relative

importance, statistical models of the system may not be sufficiently sensitive to use as predictive tools unless the causes for those shifts can be understood and incorporated in those models. Despite such uncertainties, it may be possible to further develop dynamic models of krill as presented here in such a way as to incorporate time series of factors considered to be of importance in the current statistical models, such as atmospheric conditions. For example, the use of wind stress is another factor which may be important and for which we can obtain a time series. The use of dynamic models such as these is an important component of understanding how statistical relationships may arise. In this case, results indicating that the Antarctic Peninsula may be less important to the krill population in the Scotia Arc than originally thought show that such models can provide counterintuitive insights to assist in discriminating between plausible hypotheses.

[77]   These analyses have highlighted that survey designs need to be updated to account for interannual variation in the spatial distribution of the populations of interest. In this context, repeated fixed spatial arrangements of survey areas may not help us further elaborate models on the relationships between biological production and the physical environment. Attention needs to be given to the design of sampling programs that will provide the data required to build effective quantitative models which can predict how productivity of various regions in the Southern Ocean might vary in the future.

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