Title: THE INFLUENCE OF SEA ICE ON PRIMARY PRODUCTION
IN THE SOUTHERN OCEAN: A SATELLITE PERSPECTIVE

AUTHORS: Walker O. Smith, Jr., Virginia Institute of Marine Sciences, College of William and
Mary, Gloucester Pt., VA 23062, and
Josefino C. Comiso, Cryospheric Sciences Branch, Code 614.1, NASA Goddard
Space Flight Center, Greenbelt, MD 27701

ABSTRACT: Sea ice in the Southern Ocean is a major controlling factor on phytoplankton productivity and growth, but the relationship is modified by regional differences in atmospheric and oceanographic conditions. We used the phytoplankton biomass (binned at 7-day intervals), PAR and cloud cover data from SeaWiFS, ice concentrations data from SSM/I and AMSR-E, and sea-surface temperature data from AVHRR, in combination with a vertically integrated model to estimate primary productivity throughout the Southern Ocean (south of 60°S). We also selected six areas within the Southern Ocean and analyzed the variability of the primary productivity and trends through time, as well as the relationship of sea ice to productivity. We found substantial interannual variability in productivity from 1997 – 2005 in all regions of the Southern Ocean, and this variability appeared to be driven in large part by ice dynamics. The most productive regions of Antarctic waters were the continental shelves, which showed the earliest growth, the maximum biomass, and the greatest areal specific productivity. In contrast, no large, sustained blooms occurred in waters of greater depth (> 1,000 m). We suggest that this is due to the slightly greater mixed layer depths found in waters off the continental shelf, and that the interactive effects of iron and irradiance (that is, increased iron requirements in low irradiance environments) result in the limitation of phytoplankton biomass over large regions of the Southern Ocean. Annual productivity of the Southern Ocean south of 60°S averages 23.65 g C m^{-2} y^{-1}, but yearly means ranged from 22.10 – 25.49 g C m^{-2} d^{-1} in 1998 and 2004, respectively. Annual primary productivity over the entire Southern Ocean appears to have increased significantly since 1998, and much of this increase was confined to the months of January and February. Causes for this trend remain unclear.

Popular Summary: Sea ice is of paramount importance in controlling phytoplankton productivity, growth and biomass in polar regions on all scales. At the small scale, sea ice can release epontic algae into the water, providing to the water column an inoculum of species that either continue their growth in the surface layer or rapidly sink through the water column to depth. Also, the production of melt water and the generation of a stratified surface layer can give rise to increased phytoplankton growth and accumulation within the marginal ice zone, and depending on how rapidly the ice edge retreats, can be a major site of autotrophic production for the entire Southern Ocean. On the large scale, ice is the major regulator of the availability of irradiance to phytoplankton, and hence controls the large-scale distribution of phytoplankton abundance and production. The Southern Ocean shows a significant amount of interannual variability in environmental and oceanographic features, such as ice concentration, distribution, and surface seawater temperatures, as well as in biological variables, such as pigment concentrations. During the nine-year study period (1997 – 2006) ice concentrations decreased slightly (ca. 2% per decade). Surface layer water temperatures were not correlated with phytoplankton pigments or productivity and showed the greatest variations in areas of the

Antarctic Circumpolar Current. Pigment concentrations were greatest in coastal regions, yet the maximum values were found on the continental shelf (in waters less than 800 m), but not in extremely shallow waters. Enhanced pigments were seldom observed in deep waters, which results from a deeper mixed layer and reduced iron concentrations, each of which by itself may not limit growth and accumulation, but the interactive effects might effectively preclude substantial phytoplankton growth. Productivity in the entire Southern Ocean showed a substantial and significant increase, and much of this increase was due to changes during the austral summer months. This suggests that changes in ice concentrations do not solely allow an accurate prediction of temporal trends in phytoplankton growth and photosynthesis, but that related oceanographic changes (such as in stratification, currents and iron supply) also may have a significant impact. No significant changes in the productivity of our selected regions was observed, largely due to the substantial variability of each region. Understanding the large-scale relationships over the entire Southern Ocean between phytoplankton growth/biomass and physical forcing are essential to a complete knowledge of the mechanisms controlling the food webs and biogeochemical cycles in the Antarctic.

Significant Findings: The Southern Ocean shows a significant amount of interannual variability in environmental and oceanographic features, such as ice concentration, distribution, and surface seawater temperatures, as well as in biological variables, such as pigment concentrations. During the nine-year study period (1997 – 2006) ice concentrations decreased slightly (ca. 2% per decade). Surface layer water temperatures were not correlated with phytoplankton pigments or productivity and showed the greatest variations in areas of the Antarctic Circumpolar Current. Pigment concentrations were greatest in coastal regions, yet the maximum values were found on the continental shelf (in waters less than 800 m), but not in extremely shallow waters. Enhanced pigments were seldom observed in deep waters, which results from a deeper mixed layer and reduced iron concentrations, each of which by itself may not limit growth and accumulation, but the interactive effects might effectively preclude substantial phytoplankton growth. Productivity in the entire Southern Ocean showed a substantial and significant increase, and much of this increase was due to changes during the austral summer months. This suggests that changes in ice concentrations do not solely allow an accurate prediction of temporal trends in phytoplankton growth and photosynthesis, but that related oceanographic changes (such as in stratification, currents and iron supply) also may have a significant impact. No significant changes in the productivity of our selected regions was observed, largely due to the substantial variability of each region. Understanding the large-scale relationships over the entire Southern Ocean between phytoplankton growth/biomass and physical forcing are essential to a complete knowledge of the mechanisms controlling the food webs and biogeochemical cycles in the Antarctic.

4

5

6

THE INFLUENCE OF SEA ICE ON PRIMARY PRODUCTION

IN THE SOUTHERN OCEAN: A SATELLITE PERSPECTIVE

9

10

11

12   Walker O. Smith, Jr.

13   Virginia Institute of Marine Sciences, College of William and Mary, Gloucester Pt., VA 23062

14   and

15   Josefino C. Comiso

16   NASA Goddard Space Flight Center, Code 614.1, Greenbelt, MD 27701
17
18

19

20

25 **ABSTRACT**

26   Sea ice in the Southern Ocean is a major controlling factor on phytoplankton productivity

27   and growth, but the relationship is modified by regional differences in atmospheric and

28   oceanographic conditions. We used the phytoplankton biomass (binned at 7-day intervals), PAR

29   and cloud cover data from SeaWiFS, ice concentrations data from SSM/I and AMSR-E, and sea-

30   surface temperature data from AVHRR, in combination with a vertically integrated model to

31   estimate primary productivity throughout the Southern Ocean (south of 60°S). We also selected

32   six areas within the Southern Ocean and analyzed the variability of the primary productivity and

33   trends through time, as well as the relationship of sea ice to productivity. We found substantial

34   interannual variability in productivity from 1997 – 2005 in all regions of the Southern Ocean,

35   and this variability appeared to be driven in large part by ice dynamics. The most productive

36   regions of Antarctic waters were the continental shelves, which showed the earliest growth, the

37   maximum biomass, and the greatest areal specific productivity. In contrast, no large, sustained

38   blooms occurred in waters of greater depth (> 1,000 m). We suggest that this is due to the

39   slightly greater mixed layer depths found in waters off the continental shelf, and that the

40   interactive effects of iron and irradiance (that is, increased iron requirements in low irradiance

41   environments) result in the limitation of phytoplankton biomass over large regions of the

42   Southern Ocean. Annual productivity of the Southern Ocean south of 60°S averages 23.65 g C

43    $m^{-2} y^{-1}$, but yearly means ranged from 22.10 – 25.49 g C $m^{-2} d^{-1}$ in 1998 and 2004, respectively.

44   Annual primary productivity over the entire Southern Ocean appears to have increased

45   significantly since 1998, and much of this increase was confined to the months of January and

46   February. Causes for this trend remain unclear.

47 **Introduction**

48   Sea ice is of paramount importance in controlling phytoplankton productivity, growth and

49   biomass in polar regions on all scales. At the small scale, sea ice can release epontic algae into

50   the water, providing to the water column an inoculum of species that either continue their growth

51   in the surface layer or rapidly sink through the water column to depth (Thomas, 2004).

52   Mesoscale processes, such as ice melt, also influence phytoplankton. For example, the

53   production of melt water and the generation of a stratified surface layer can give rise to increased

54   phytoplankton growth and accumulation within the marginal ice zone (MIZ: Smith and Nelson,

55   1985), and depending on how rapidly the ice edge retreats, can be a major site of autotrophic

56   production for the entire Southern Ocean (Smith and Nelson, 1986). On the large scale, ice is the

57   major regulator of the availability of irradiance to phytoplankton, and hence controls the large-

58   scale distribution of phytoplankton abundance and production.

59   However, because the physical forcing varies from region to region, the effects of melting ice

60   in the marginal ice zone are variable. For example, in the Ross Sea ice initially is reduced in its

61   ice cover via polynya expansion and ice advection, and continued expansion then is normally

62   determined by ice retreat to the east and west that is driven by in situ melting (Tremblay and

63   Smith, 2007). A stratified surface layer is generated that can vary in both space and time based

64   on the amount of melt water input (Smith et al., 2006). In the Bellingshausen Sea the zone of

65   enhanced biomass of phytoplankton was associated with a current-generated front, rather than

66   the melting ice (Boyd et al., 1995; Waldron et al., 1995), whereas in the Weddell Sea the MIZ

67   was correlated with enhanced phytoplankton accumulation, although variations along the ice

68   were observed (Nelson et al., 1987). Ice-edge phytoplankton blooms are not routinely observed

69   in the East Antarctica region (e.g., Strutton et al., 2000). Phytoplankton biomass over the broad

70 region in the Pacific sector of the Antarctic Convergence Current (ACC) was coupled to ice

71 retreat (Moore et al., 2000) and nutrient removal as modified by iron limitation (Hiscock et al.,

72 2003). While ice retreat undoubtedly introduces low density water to the surface layer, it does

73 not in all cases increase stratification for long enough to allow for a marked phytoplankton

74 growth stimulation and accumulation.

75 Smith and Nelson (1985) also suggested that the spatial extent of an ice-edge bloom would

76 be constrained by the wind-induced reduction in stratification away from the ice. This was based

77 on density determinations of sections that extended some 300 km from the ice edge, and was

78 supported by work of Alexander and Niebauer (1981) in the Bering Sea, who reported

79 phytoplankton blooms in the MIZ that were delineated by the extent of stratification. However,

80 longer sections in the Ross Sea have shown that sufficient stratification occurs within the entire

81 polynya during the ice-free period, although slightly deeper mixed layers routinely occur away

82 from the ice edge (Smith and Asper, 2001; Smith et al., 2006). Seasonal variations in the depth

83 of the mixed layer are far greater than the differences between the ice-edge and central region,

84 and it appears that the deepening of the mixed layer and the erosion of stratification is primary

85 driven by ice formation and brine rejection, rather than increases in winds (Tremblay and Smith,

86 2007). Therefore, the spatial extent of any ice-edge bloom likely varies as a function of regional

87 physical forcing.

88 Estimates of the productivity of the Southern Ocean, either regional or basin-wide, have

89 substantial uncertainty. Early estimates suggested that the overall productivity of the Southern

90 Ocean averaged 16 g C m^{-2} y^{-1} (Holm-Hansen et al., 1977), which is similar to rates in

91 subtropical oceans. Inclusion of the marginal ice zone productivity increased the estimate by

92 60% (Smith and Nelson, 1986), but all of the above estimates had extremely large uncertainties.

93   Arrigo et al. (1998b) used data from the SSM/I and CZCS satellite sensors and estimated that the

94   productivity of the Southern Ocean was some four times greater than had previously been

95   estimated, but the accuracy of the model results is compromised by errors in the CZCS

96   chlorophyll estimates, relatively poor spatial/temporal resolution, and substantial effects of

97   clouds. A similar approach was used by Moore and Abbott (2000), who estimated productivity

98   south of 50°S to be from 62-82 g C m^{-2} y^{-1}, depending on the assumptions used. However, these

99   were the first attempts to uniformly treat the productivity of the entire Southern Ocean and

100   estimate its productivity using remote sensing, similar to what had been attempted in other

101   oceanic regions (e.g., Behrenfield and Falkowski, 1997; Campbell et al., 2002; Behrenfeld et al.,

102   2007).

103   Here we use an approach similar to that of Arrigo et al. (1998b) and Moore and Abbott

104   (2000) to study the productivity of the Southern Ocean, in that we incorporate phytoplankton

105   pigment assessments, surface temperature estimates, modeled irradiance, and observed ice

106   concentrations, and incorporate them into a vertically integrated production model to estimate

107   productivity according to the technique of Behrenfield et al. (2002). We also select six regions to

108   assess the decadal changes in productivity at those sites, and also assess the relationship between

109   phytoplankton productivity with ice concentrations (a proxy for stratification) and bathymetry in

110   waters of the Antarctic. The resultant assessment of Southern Ocean productivity is the most

111   exhaustive ever compiled and provides an improvement in the quantitative role of carbon

112   fixation in Antarctic waters.

113   **Materials and Methods**

114   The key parameters used in this study are ice concentrations, sea surface temperatures,

115   phytoplankton pigment concentrations, photosynthetically active radiation (PAR), and cloud

116   cover, all of which are derived from satellite data. Ice concentrations and associated parameters

117   (e.g., ice extent and area) were derived using data from the Special Sensor Microwave Imager

118   (SSM/I) on the Defense Meteorological Satellite Program (DMSP) and mapped on a polar

119   stereographic grid at a 25 × 25 km resolution. Ice concentrations were derived from satellite

120   passive microwave data using the enhanced Bootstrap algorithm used for AMSR-E data and

121   adapted for SSM/I data (e.g., Comiso et al., 2003, Comiso, 2004). Sea surface temperatures

122   were derived from thermal infrared channels of the NOAA/Advanced Very High Resolution

123   Radiometer (AVHRR) as described in Comiso (2003). Pigment concentrations derived from

124   Sea-viewing Wide Field of View Sensor (SeaWiFS) data were provided by the NASA/Goddard

125   Earth Sciences (GES)/Distributed Active Archive Center (DAAC). Surface temperature and

126   pigment concentration data have been gridded in the same manner as the sea ice concentration

127   data but on a 6.25 × 6.25 km resolution. Daily, average pigment concentrations were estimated

128   using the standard SeaWiFS algorithm with OC4 (Version 4) calibration (Pat et al., 2003) and

129   used to generate weekly (7-day bins) and monthly data sets from 1997 to 2006. PAR data were

130   extracted as part of the SeaWiFS data and treated similarly. It is important to note that because

131   of cloud and ice masking the weekly and monthly averages do not reflect true averages, but are

132   averages of daylight data (for each data element) available during clear-sky, ice-free conditions

133   only.

134   Temperature, PAR and chlorophyll concentrations were used with a vertically generalized

135   production model (Behrenfeld and Falkowski, 1997) in which primary productivity (PP_{eu}, in

136   units of mg C m^{-2} d^{-1}) was calculated by the following equation:

137    $$PP_{eu} = 0.66125 \times P_{opt}^{B} \frac{E_o}{E_o + 4.1} C_{Sat} \times Z_{eu} \times D_{Irr}$$ (Eq. 1)

138   where P_{opt}^{B} is the optimal rate of photosynthesis within the water column (mg C (mg chl)$^{-1}$ h^{-1})

139   and is regulated by temperature, E_o is the surface daily PAR (mol photons m^{-2} d^{-1}), C$_{sat}$ is the

140   surface chlorophyll concentration (mg chl m^{-3}) determined by satellite, Z_{eu} is the depth of the

141   euphotic zone in meters, and D_{Irr} is the photoperiod (h). P_{opt}^{B} was estimated from sea surface

142   temperatures by the polynomial equation of Behrenfeld and Falkowski (1997), and all values at

143   temperatures less that -1.0°C were set to 1.13. Productivity was calculated on a daily basis, and

144   binned in a manner similar to that of chlorophyll. The gridding technique (the so called "drop in

145   a bucket" procedure) and the presence of clouds caused a large fraction of data elements (pixels)

146   in the daily maps to have missing data. In the case where a single empty or voided pixel is

147   surrounded by pixels with data, a simple interpolation technique is utilized to fill the empty

148   pixel. For slightly larger data gaps of a few pixels, a combination of spatial and temporal

149   interpolation was utilized. Such interpolation filled only a very small fraction of missing data in

150   the daily map, and for time-series studies weekly averages were produced as the basic product.

151   We recognize that regional algorithms have been developed for certain parts of the

152   Southern Ocean (e.g., Ross Sea: Arrigo et al., 1998b, Diersson and Smith, 2000), and that these

153   formulations provide a more accurate estimate of phytoplankton biomass in each area. We chose

154   to use the output from the standard global algorithm to simplify the comparison of regions and of

155   various years, to facilitate a comparison among all regions, and to avoid problems of defining

156   boundaries of optically different regions. While this approach may introduce error into absolute

157   estimates of productivity within a region, it provides a uniform basis to compute productivity

158   throughout the Southern Ocean, as regional algorithms (some of which need more rigorous

159   validation) are not available for all areas. We also chose specific regions for a more in-depth

160   analysis (Figure 1). These regions [Ross Sea I (RS I): the southern Ross Sea; Ross Sea II (RS

161   II), the central Ross Sea; the West Antarctic Peninsula (WAP), the South Georgia region in the

162   Antarctic Circumpolar Current (ACC); the Weddell Sea (WS); and the Indian Ocean (IO)], were

163   selected based on their large seasonal ice variations and enhanced productivity values measured

164   previously using discrete methods. The Indian Ocean study region was identified as a region

165   with consistently low pigment concentrations and included to assess how the variability of an

166   area that is a site of persistently deep, wind-induced mixed layers and low productivity compares

167   with the biomass and productivity of the other selected regions.

168   **Results**

169   *Irradiance*

170   Irradiance has two components: photoperiod and absolute irradiance impinging on the sea

171   surface. Photoperiod can be relatively easily modeled, as it is solely a function of latitude

172   (Figure 2a). Within the Southern Ocean, photoperiod varies from 0 – 24 h within one year, and

173   from 16.3 – 24 hours at the seasonal maximum (December 21). Surface PAR can be either

174   measured via satellite or modeled. Modeled irradiance was computed after the clear-sky model

175   of Watson and Gregg (1990); in addition, surface PAR was obtained from the SeaWiFS satellite

176   (Arrigo et al., 2004). Modeled PAR can, of course, be extended to any resolution, whereas

177   measured PAR is biased by cloud cover and is limited to the resolution of the sensor. Both

178   modeled and measured estimates of PAR were tested in the productivity model, and surprisingly

179   it was found that there was little difference between the two. As a result, we used the modeled

180   PAR for our full analysis, especially since the surface PAR data that are available were not

181   quality controlled (in terms of ice and ocean mask) in the polar regions. Modeled PAR ranged

182   from 0 – 70 mol photons m^{-2} d^{-1} within the year, and maxima ranged from 63 – 68 mol photons

183     $m^{-2} d^{-1}$ among the selected study regions (Figure 2a). PAR was the same as the scalar irradiance

184   calculated by others (e.g., Mitchell and Holm-Hansen, 1991).

185   *Ice Concentrations*

186   To show spatial variations in the distribution of ice concentration during late winter

187   through austral spring and summer (when blooms are most likely to occur) and autumn, multi-

188   year, monthly averages of ice concentrations were calculated for the years that SeaWiFS

189   provided data (Figure 3).   In October the ice cover is still fully consolidated throughout the

190   Antarctic region, but reduced concentrations are found in many coastal areas. Coastal polynyas

191   along most of these regions are more apparent in December, especially in the Ross Sea. In

192   February, much of the coastline becomes completely ice-free, with persistent ice cover being

193   prevalent in the Western Weddell Sea and the Amundsen/Bellingshausen Seas. In April, when

194   rapid ice growth in deeper water occurs, reduced concentrations along the coastlines continue.

195   The average concentration of the entire Antarctic sea ice cover in December (Figure 4) fluctuates

196   from about 55 to 65% from 1997 through 2006, with a majority of the fluctuations occurring

197   during the last five years. The trend in ice concentration also shows a decline of about 2% per

198   decade. In the selected study regions the average ice concentration varies seasonally (Figure 5),

199   except in the ACC and Indian Ocean, where little ice occurs throughout the year. In the Weddell

200   Sea and Ross Sea study areas, the ice cover is near 100% in winter but exhibits large variability

201   in the summer, while in the WAP the summer ice cover is almost zero, but exhibits large

202   variability in the winter. The percentage of open water (1 – ice cover percentage) varies in a

203   similar manner. Thus, in the Weddell Sea study area the average open-water percentage during

204   summer ranges from 30 - 100%, while in the Ross Sea study area II open water averages from 28

205   - 72%. The Ross Sea I study area averages open water concentrations of 10 - 20% in winter and

206   50 - 100% in summer, with 100% values occurring in 1997, 1999, 2000, 2002, 2005 and 2006.

207   *Surface Temperature*

208   While sea surface temperatures (SST) have been used to study oceanographic processes

209   in polar regions (e.g., Kwok and Comiso, 2002), they have not been used previously to evaluate

210   spatial variability of plankton concentrations in the region. In the Southern Hemisphere south of

211   60°S, the spatial distribution of SST is heavily influenced by the melting of sea ice during the

212   spring and summer. The data are thus useful to assess the degree to which temperatures are

213   correlated with phytoplankton growth and accumulation, but also the fate of the low density melt

214   water after sea ice melt. Monthly averages of SST in December from 1997 to 2005 (Figure 6)

215   provide the means to evaluate spatial distributions of SST and relationships with sea ice locations

216   (in white). The surfaces with near-freezing temperatures in the maps are likely the surfaces

217   influenced by sea ice, and it is apparent that the interannual variability of the extent and location

218   of these surfaces is large. In general the temperatures reflect the distribution of ice as well as the

219   north-south gradient in the surface heat budget. However, one area deviates substantially among

220   years: the ice edge at the Greenwich meridian. In some years (e.g., 1998, 2000, 2004) warm

221   water clearly is advected under the ice and initiates melting, opening large areas to the

222   atmosphere, and surface water temperatures are near 0°. The exact location of this intrusion, as

223   well as the strength of its surface signal, also varies substantially among years as well.

224   The seasonality and interannual variability of SST in the various study regions (Figure 7)

225   show that the regional as well as interannual variability is large. The warmest waters in all of the

226   study regions are in the ACC, although there were times (e.g., 1998 and 2001) when the Indian

227   Ocean study area was warmer during summer. There are no data in Weddell and Ross Sea study

228   areas during parts of the year when they are covered by sea ice, but the SST in these regions is

229   undoubtedly close to the freezing point of seawater. December sea surface temperatures ranged

230   from the freezing point (ca. -1.86°C in the Ross Sea, or 271.3°K) to more than 10°C (283.2°K) in

231   the ACC region (Figure 7). Seasonal ranges were greatest in the ACC (ca. 5.6°), followed by the

232   Indian Ocean and WAP study areas, while those in the ice covered regions show more moderate

233   seasonality (Figure 7). Specifically, Ross Sea I and II and Weddell Sea areas all had a range of

234   about 2°, while that of the WAP was about 3°.

235   *Pigment Distribution*

236   The distribution of chlorophyll *a* in the Southern Ocean was previously studied (Comiso

237   et al., 1993; Sullivan et al., 1993; Moore and Abbott, 2000); using Nimbus-7/CZCS data, but

238   spatial and temporal coverage was restricted and seasonally biased. This improved substantially

239   with the collection of SeaWiFS data (Moore and Abbott, 2000). The compendium presented in

240   Figure 8 is likely the most comprehensive representation of yearly and multiyear averages of

241   plankton concentration in the Southern Ocean. The data provide the means to identify regions

242   with persistently high chlorophyll *a* concentrations; similarly, they also indicate where the

243   persistently low concentrations occur. The composite also illustrates how the pigment

244   concentrations and distributions vary among years. The images show that maxima are largely

245   confined to continental shelf regions, and in particular to those polynyas where ice

246   concentrations become reduced during the growing season (Figure 8). Seasonal variations were

247   large at any single location, and could range from zero to greater than 20 μg L^{-1} in regions like

248   the Ross or Weddell Seas. Open ocean regions showed much smaller maxima, and only

249   occasionally exceeded 1 μg L^{-1}. The Pacific sector was an exception to this, and seemed to have

250   slightly greater chlorophyll levels than other areas of the Southern Ocean at a similar latitude and

251   depth.

252   Pigment concentrations in the selected study areas showed substantial variations among

253   themselves, as well as large interannual variations (Figure 9). The greatest concentration of

254   chlorophyll was found in the southern Ross Sea (RS I), followed by the central Ross Sea (RS II),

255   the ACC, the Weddell Sea, the West Antarctic Peninsula and the Indian Ocean. Mean annual

256   concentrations (calculated from all ice-free retrievals) and their standard deviations were $0.31 \pm$

257   0.02, 2.19 ± 0.98, 1.22 ± 0.29, 0.39 ± 0.17, 0.54 ± 0.17, 0.34 ± 0.06, and 0.14 ± 0.01 µg chl a L^{-1}

258   in the entire Southern Ocean, RS I, RS II, ACC, WS, WAP and IO, respectively.

259   *Primary Productivity*

260   Primary productivity of entire Southern Ocean south of 60°S was strongly correlated with

261   pigment concentrations (Figure 10). Annual productivity of the entire Southern Ocean (south of

262   60°S) equaled 23.65 ± 1.28 g C m^{-2} y^{-1} (Table 1). Means and standard deviations for the six

263   selected regions were 2.74 ± 0.98 for RS I, 2.26 ± 0.59 for RS II, 1.56 ± 0.50 for the WAP, 0.75

264   ± 0.28 for the WS, 2.83 ± 0.40 for the ACC, and 1.71 ± 0.16 g C m^{-2} d^{-1}, respectively. Monthly

265   (from November through March) mean productivity of the entire Southern Ocean showed

266   dramatic temporal and spatial variations (Figure 10), with the largest variations being associated

267   with the extreme maxima of coastal regions. The influence of the marginal ice zone is relatively

268   minor in this analysis, but the maximum chlorophyll concentration observed generally occurs

269   about six weeks after the disappearance of ice. There also is a notable lack of deep-water (>

270   1,000 m) blooms throughout the Southern Ocean, suggesting that productivity in these areas is

271   limited by irradiance, trace metal availability, other factors or by their interactive effects.

272   The temporal trends of primary productivity in the selected regions are shown in Figure 11.

273   One feature that becomes obvious is that polynyas (e.g., the Ross and Weddell Seas) bloom

274   much earlier than other regions of similar latitude, and even substantially before areas of similar

275   depth that are much farther north. For example, in RS I (ca. 77°S) chlorophyll *a* concentrations

276   reach 3 μg L^{-1} in November, while similar concentrations are rarely observed in the WAP (ca.

277   64°S) until mid-December. This suggests that for the spring phytoplankton assemblages of the

278   Ross and Weddell Seas the absolute requirement for irradiance for net photosynthesis is quite

279   low, or that stratification in the WAP is far weaker than in the polynyas. However, available

280   data do not support the latter hypothesis (e.g., Mitchell and Holm-Hansen, 1991; Palmer LTER

281   data, http://pal.lternet.edu/data/). Both polynyas also receive substantial amount of ice algae

282   released into the water column, providing an inoculum for the water column, and this input is

283   likely greater than in the WAP. However, it remains uncertain what factors might cause the

284   early bloom formation, but its appearance has a striking impact on regional productivity.

285   Productivity for the entire Southern Ocean shows a significant increase over the period of

286   this analysis (Figure 10). Monthly trends were also computed, and significant increases were

287   noted only for January and February (Figure 10). These two months are also the months of

288   minimum ice concentrations. We believe that this suggests that the summer increases are not

289   directly coupled to ice retreat, but are forced either by changing solar irradiance (and cloud

290   cover) available during these months, or by changing oceanographic conditions that bring iron

291   into the euphotic zone or change stratification. Discriminating among these possibilities is

292   beyond the scope of this analysis. Regardless, the highly significant increase in the productivity

293   of the entire Southern Ocean over the past decade implies that long-term changes in Antarctic

294   food webs and biogeochemical cycles are presently occurring.

295   **Discussion**

296   During the past two decades large amounts of satellite data from polar regions have been

297   collected, and this in turn has allowed concurrent observation and analysis of large-scale, long-

298   term patterns and trends in a variety of physical and biological features. For example, the spatial

299   and temporal trends in ice concentrations (Zwally et al., 2002; Comiso, 2003), teleconnections to

300   tropical regimes via the Annular Mode (Hall and Visbeck, 2002; Kwok and Comiso, 2003),

301   spatial variations in the location of the Polar Front (Moore and Abbott, 2004), and the

302   persistence and movement of a single patch of phytoplankton (Boyd et al., 2000) were all based

303   on satellite observations. This study represents the first attempt to combine satellite data on ice

304   concentrations, temperature, and SeaWiFS pigment levels for the entire Southern Ocean to

305   estimate, using a vertically integrated model, the primary production of the area south of 60°S.

306   Our annual estimate of primary productivity was 23.65 g C m^{-2} y^{-1} (Table 1). This is within the

307   range of previous estimates made using different techniques, data and approaches (Table 2), but

308   given the increased spatial and temporal of our analysis, likely represents the most accurate

309   assessment to date.

310   The estimates provide a good baseline for productivity studies in the Southern Oceans.

311   However, the estimates are not as accurate as we would like them to be because of a number of

312   reasons. For example, no productivity under the ice is included. While productivity is indeed

313   low under 100% ice due to irradiance limitation, it is not zero. Furthermore, while ice may be

314   present within one pixel, an ice concentration of 50%, for example, does not result in zero

315   productivity, but rather allows a substantial amount of irradiance into the water column to drive

316   production (Smith, 1996). Our present model is unable to account for this production, and hence

317   produces an underestimate in ice-covered waters. In addition, no attempt to include epontic

318   production is made (Arrigo et al., 1997), which has been estimated to range from 9-25% of

319   productivity in ice-covered waters.

320   Chlorophyll *a* concentrations are likely inaccurately estimated in some various regions by

321   the standard NASA global algorithm used in our procedures, which would lead to inaccuracies in

322   the overall estimate of productivity. Using CZCS data Moore and Abbott (2000) found that

323   changes in the algorithm used can result in a two-fold difference in chlorophyll estimates, which

324   in turn give rise to a large difference in productivity estimates. Regional models are unavailable

325   for the entire Southern Ocean; furthermore, there is a substantial variation among regions,

326   making the derivation of a generic Southern Ocean algorithm problematic (e.g., Arrigo et al.,

327   1998b; Diersson and Smith, 2000; Peloquin, 2006). Hence we used the standard algorithm,

328   despite the fact that it may not accurately represent the various sub-regions within the Southern

329   Ocean. But even assuming that there is a bias in the data generated by using the standard

330   algorithm, the temporal variability and the correlation analysis presented in this paper would still

331   be relevant.

332   One feature of the large-scale distribution of pigments and productivity is that a large

333   fraction of high productivity regions are confined to the continental shelf regions. This means

334   that the ocean depth may have a strong influence on the productivity observed. To quantitatively

335   assess this relationship, we analyzed December pigment concentrations in three separate years

336   (1998, 2003 and 2004) vs. depth; we found little relationship between the two, and the data

337   exhibited a tremendous amount of scatter (Figure 12). A distinct maximum occurred on the

338   continental shelf in all years, but somewhat surprisingly, at depths less than 250 m only modest

339   levels of pigments were observed. This may be an effect of strong winds from the continent that

340   advect the pigments offshore; it also might result from the fact that the coast often retains

341 significant ice cover during December (Figure 3), and even in areas where the ice had

342 disappeared, the water had been exposed to elevated irradiances for a relatively short period,

343 therefore restricting phytoplankton growth and accumulation. While a general negative

344 correlation between ice and chlorophyll has been observed previously (Comiso et al., 1993), it is

345 not immediately obvious why such a trend occurs, especially considering that the shelf break

346 around Antarctica occurs at ca. 800 m. Macronutrients (the concentrations of inorganic nitrogen,

347 phosphorus and silicic acid) are high throughout the Southern Ocean, and cannot explain this

348 trend. It is possible that micronutrients, such as iron, are added to the water as it flows over

349 sediments of the continental shelf and stimulate productivity and growth (Peloquin and Smith, in

350 press). However, it is uncertain that waters in contact with the sediments are indeed enriched

351 with micronutrients, although it has been shown that Modified Circumpolar Deep Waters are

352 elevated in [Fe] relative to waters above (Shorin et al., 2000; Boye et al., 2001). Stratification is

353 often greater on the shelf, but given the large amount of low density, fresh water introduced by

354 melting ice throughout the ice-covered waters at all depths of the Southern Ocean, it might be

355 expected that blooms would occur over much greater regions of the Antarctic than they

356 apparently do. Because shallower waters are unable to support populations of Antarctic krill

357 (Hofmann, 2003), it is possible that these coastal regions experience reduced grazing, but it

358 would not explain why other grazers such as copepods or *Euphausia crystallarophius* would not

359 remove phytoplankton at a similar rate in the absence of Antarctic krill. Colder waters tend to

360 de-couple production and grazing, but water temperatures off-shore and on the continental

361 shelves are not substantially different (Figure 6), and so the de-coupling would be expected to be

362 similar in both. Hence the extreme productivity of the continental shelves remains an enigma;

363   however, it may be more correct to say that the extreme lack of production in the deep water is

364   even more of an enigma.

365   One possible explanation for the deep-water's ultra-oligotrophic state might be the

366   interactive effects of iron and irradiance. Sunda and Huntsman (1997) showed in a series of

367   elegant experiments that at low irradiances the iron demand by phytoplankton increased. Thus,

368   while waters off the continental shelf are indeed often stratified by melt-water inputs, mean

369   mixed layers may be greater than those on the shelves. For example mixed layer depths in the

370   Pacific sector (from 60 – 68°S, in waters >2,500 m) during summer ranged from 5 – 89 m (mean

371   45.3 ± 20.4 m) in January – February (www.jgofs.whoi.edu). In contrast, mixed layers on the

372   continental shelf of the Ross Sea during the same period and year averaged 24.7 ± 14.4 m. Thus,

373   phytoplankton off the shelf would potentially require greater amounts of iron during growth

374   under lower irradiance. While these waters may have slightly greater inputs of aeolian Fe via

375   dust, surface layer concentrations are not dramatically different. Hence, we suggest that the

376   lower irradiances available to phytoplankton due to greater vertical mixing induce greater iron

377   requirements, and hence ultimately limit phytoplankton biomass and productivity in deep,

378   oceanic waters.

379   While the large-scale coupling between ice and primary productivity has been known for

380   some time, few data are available over appropriate time scales to adequately define the

381   relationship. We assessed the relationship between ice concentrations and derived monthly

382   productivity in the four ice-covered regions for all years (the West Antarctic Peninsula, the

383   Weddell Sea and the two sites of the southern Ross Sea; Figures 13, 14). Little correlation

384   between the ice and productivity was found in the WAP, either on an annual or monthly basis;

385   however, in both of the Ross Sea sites as well as in the Weddell Sea, a strong, negative

386   relationship was detected.   This suggests that the primary, causal mechanism behind the

387   interannual variability in the productivity of the WAP is *not* ice, whereas the large-scale patterns

388   of productivity in the more southerly, ice-covered areas are largely dependent on changes in ice

389   cover and hence irradiance availability on both annual and seasonal time scales.   This

390   furthermore suggests that if ice concentrations in the Ross Sea continue to increase, then

391   productivity would be expected to fall as well. However, changes in ice cover on the continental

392   shelf are far less pronounced that in other areas of the Ross Sea sector (i.e., the increases in ice

393   cover reported by Kwok and Comiso (2002) were largely driven by changes northwest of Cape

394   Adare, although some increases in the western Ross Sea on the continental shelf were also

395   observed). In addition, Comiso (this issue) has detected a *decrease* in ice concentrations in the

396   Pacific sector, so it remains problematic what, if any, ecosystem shifts might be occurring in

397   water structured by ice.

398   One of the more striking results of this work is the marked and significant increase in

399   primary productivity of the entire Southern Ocean (Figure 10a).   This change appears to be

400   driven by changes in January and February productivity (Figures 10d,e) and not by changes in

401   other months (although November, December and March also showed non-significant increases).

402   The trend also is not driven by limited, regional changes; that is, we did not detect changes in the

403   regions we selected for detailed analysis that contributed significantly to the overall trend we

404   found in the entire Southern Ocean. The changes in productivity we found could be related to a

405   number of environmental and oceanographic processes. For example, such changes could be

406   induced by large-scale, increased water column stratification. Such decreased mixing would

407   result in increased irradiance availability to phytoplankton and increased growth (and potentially

408   reduced iron demands as well). Assessing this change is impossible using the data available to

409   us, but it is noteworthy that models have predicted that the Southern Ocean will respond to

410   increased atmospheric changes through increased stratification induced by decreased salinity

411   (e.g., Sarmiento and le Quéré, 1996; Sarmiento et al., 1998). We are not suggesting that such

412   changes are occurring as a result of increased air temperatures, but such changes might be

413   contributing to this change. Increased productivity may also be due to enhanced iron inputs via

414   oceanographic changes; again, these could not be detected from the data available to us.

415   Behrenfeld et al. (2007), using a similar approach but on a global scale, found that since

416   1999 there has been a globally significant decrease in chlorophyll and productivity that was

417   driven in large part by changes in the lower latitudes. Their analysis did include the Southern

418   Ocean, and they found increased temperatures in the Pacific sector, but decreased temperatures

419   in the Atlantic. They also reported increased productivity in the deeper waters of the Pacific and

420   Atlantic south of the Subtropical Convergence, but did not attempt to assess any changes in

421   waters they did not consider permanently stratified (that is, south of the STC). However, their

422   results suggest that changes have indeed occurred in the Southern Ocean, but the physical

423   forcing for such changes remain uncertain at this time.

424   Decadal changes in ice concentrations have been observed for some time (e.g., Kwok and

425   Comiso, 2002), and long-term changes in ecosystem variables have also been observed (e.g.,

426   Laws, 1990; Atkinson et al., 2004). Specifically, we know that since 1979 ice concentrations

427   have greatly decreased in the West Antarctic Peninsula/Bellingshausen Sea region (ca. 7% per

428   decade), and those in the Ross Sea have increased by ca. 5.5% per decade (Kwok and Comiso,

429   2002). It would be expected that such changes in such a major physical forcing variable would

430   induce changes in primary productivity as well, but we were unable to discern any significant

431   temporal trend in either the WAP or Ross Sea. The Ross Sea has exhibited very strong

432   variability in the past decade, including a substantial change due to iceberg-driven ice

433   concentrations. In contrast, ice does not appear to be a major control of annual productivity in

434   the WAP, although it can impact regional food webs (Fraser and Trivelpiece, 1996). Further

435   analysis is needed to assess the environmental forcing of the large-scale changes we detected.

436   **Summary**

437   The Southern Ocean shows a significant amount of interannual variability in

438   environmental and oceanographic features, such as ice concentration, distribution, and surface

439   seawater temperatures, as well as in biological variables, such as pigment concentrations. We

440   have shown that during the nine-years (1997 – 2006) analyzed in this study that ice

441   concentrations decreased slightly (ca. 2% per decade). Surface layer water temperatures were

442   not correlated with phytoplankton pigments or productivity and showed the greatest variations in

443   areas of the Antarctic Circumpolar Current. Pigment concentrations were greatest in coastal

444   regions, yet the maximum values were found on the continental shelf (in waters less than 800 m),

445   but not in extremely shallow waters. Few periods of enhanced pigments were observed in deep

446   waters, and we suggest that this results from a deeper mixed layer and reduced iron

447   concentrations, each of which by itself may not limit growth and accumulation, but the

448   interactive effects might effectively preclude substantial phytoplankton growth.

449   Productivity in the entire Southern Ocean showed a substantial and significant increase,

450   and much of this increase was due to changes during the austral summer months. This suggests

451   that changes in ice concentrations do not solely allow an accurate prediction of temporal trends

452   in phytoplankton growth and photosynthesis, but that related oceanographic changes (such as in

453   stratification, currents and iron supply) also may have a significant impact. No significant

454   changes in the productivity of our selected regions was observed, largely due to the substantial

455   variability of each region. Understanding the large-scale relationships over the entire Southern

456   Ocean between phytoplankton growth/biomass and physical forcing are essential to a complete

457   knowledge of the mechanisms controlling the food webs and biogeochemical cycles in the

458   Antarctic.

459 **Literature Cited**

460 Alexander, V., and H.J. Niebauer, Oceanography of the eastern Bering Sea ice-edge zone in

461   spring, *Limnol. Oceanogr., 26,* 1111-1125, 1981.

462 Arrigo, K.R., and C.R. McClain, Spring phytoplankton production in the western Ross Sea,

463   *Science, 266,* 261-263, 1994.

464 Arrigo, K.R., and G.L. van Dijken, Annual cycles of sea ice and phytoplankton in the Cape

465   Bathurst polynya, southeastern Beaufort Sea, Canadian Arctic, *Geophys. Res. Letters, 31,*

466   [doi:10.1029/2003GL018978], 2004.

467 Arrigo, K.R., A. M. Weiss, and W.O. Smith, Jr., Physical forcing of phytoplankton dynamics in

468   the western Ross Sea, *J. Geophys. Res., 103,* 1007-1022, 1998a.

469 Arrigo, K.R., D.L. Worthen, M.P. Lizzote, P. Dixon, and G. Dieckmann, 1997, Primary

470   production in Antarctic sea ice, *Science, 276,* 394-397, 1997.

471 Arrigo, K.R., D.L. Worthen, A. Schnell, and M.P. Lizzote, Primary production in Southern

472   Ocean waters, *J. Geophys. Res., 103,* 15,587-15,600, 1998b.

473 Behrenfeld, M., and P. Falkowski, A consumer's guide to phytoplankton primary productivity

474   models, *Limnol. Oceanogr., 42,* 1-20, 1997.

475 Behrenfeld, M., J., R. T. O'Malley, D.A. Siegel, C.R. McClain, J.L. Sarmiento, G.C. Feldman,

476   A.J. Milligan, P.G. Falkoski, R.C. Letelier, and E.S. Boss, 2007. Climate-driven trends in

477   contemporary ocean productivity, *Nature, 444,* 752-755.

478 Behrenfield, M., E. Maranon, D.A. Siegel, S.B. Hooker, Photoacclimation and nutrient-based

479   model of light-saturated photosynthesis for quantifying ocean primary production, *Marine*

480   *Ecology Progress Series, 228,* 203-117, 2002.

481   Boyd, P.W., C. Robinson, G. Savidge, and P.J. leB. Williams, Water column and sea-ice primary

482   production during Austral spring in the Bellingshausen Sea, *Deep-Sea Res. II, 42,* 1225-

483   1252, 1995.

484   Boyd P.W., et al., A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by

485   iron fertilization, *Nature, 407,* 695-702, 2000.

486   Boye, M., C.M.G. van den Berg, J.T.M. de Jong, J. Leach, P. Croot, and H.J.W. de Baar,

487   Organic complexation of iron in the Southern Ocean, *Deep-Sea Res. I, 48,* 1477-1497, 2001.

488   Campbell, J., D. Antoine, R. Amstrong, K. Arrigo, W. Balch, R. Barber, M. Behrenfeld, R.

489   Bidigare, J. Bishop, M.E. Carr, W. Esaias, P. Falkowski, N. Hoepffner, R. Iverson, D. Kiefer,

490   S. Lohrenz, J. Marra, A. Morel, J. Ryan, V. Vedernikov, K. Waters, C. Yentsch, and J.

491   Yoder, Comparison of algorithms for estimating ocean primary production from surface

492   chlorophyll, temperature, and irradiance, *Global Biogeochem. Cycles, 16,* 105,

493   10.1029/2001GB001444, 2002.

494   Comiso, J.C., Warming trends in the Arctic, *J. Climate, 16,* 3498-3510, 2003.

495   Comiso, J.C., Sea ice algorithm for AMSR-E, *Rivista Italiana di Telerilevamento, 30/31,* 119-

496   130, 2004.

497   Comiso, J.C., C. McClain, C. Sullivan, J. Ryan, and C. L. Leonard, CZCS pigment

498   concentrations in the Southern Ocean and their relationships to some geophysical parameters,

499   *J. Geophys. Res., 98,* 2419-2451, 1993.

500   Comiso, J.C., D.J. Cavalieri, and T. Markus, Sea ice concentration, ice temperature, and snow

501   depth, using AMSR-E data, *IEEE TGRS, 41,* 243-252, 2003.

502   Dierssen, H.M., and R.C. Smith, Bio-optical properties and remote sensing ocean color

503   algorithms for Antarctic Peninsula waters, *J. Geophys. Res., 98,* 26,301-26,312, 2000.

504   El-Sayed, S.Z., Primary productivity and estimates of potential yield of the Southern Ocean, in

505   *Polar Research: To the present and to the future,* edited by M.A. McWhinnie, pp. 141-160,

506   Westview Press, Boulder, CO, 1978.

507   Fraser, W.R., and W.Z. Trivelpiece, Factors controlling the distribution of seabirds: winter-

508   summer heterogeneity in the distribution of Adélie penguin populations, in *Foundations for*

509   *Ecological Research West of the Antarctic Peninsula,* edited by R.M. Ross, E.E. Hofmann,

510   and L.B. Quetin, pp. 257-272, Ant. Res. Ser., American Geophysical Union, Washington,

511   DC, 1996.

512   Hall, A., and M. Visbeck, Synchronous variability in the Southern Hemisphere atmosphere, sea

513   ice, and ocean resulting from the annular mode, *J. Climate, 15,* 3043-3057, 2002.

514   Hiscock, M.R., J. Marra, W.O. Smith, Jr., R. Goericke, C. Measures, S. Vinke, R. Olson, H.

515   Sosik, and R.T. Barber, Primary productivity and its regulation in the Pacific Sector of the

516   Southern Ocean, *Deep-Sea Res. II,* 50, 533-558, 2003.

517   Hohn-Hansen, O., S.Z. El-Sayed, G.A. Francescini, and R.L. Cuhel, Primary production and

518   factors controlling phytoplankton growth in the Southern Ocean, in *Adaptations within*

519   *Antarctic Ecosystems,* edited by G.A. Llano, pp. 11-50, Gulf Publ., Houston, 1977.

520   Kwok, R., and J. C. Comiso, Spatial patterns of variability in Antarctic surface temperature:

521   Connections to the Southern Hemisphere Annular Mode and the Southern Oscillation,

522   *Geophys. Res. Lett., 29,* 10.1029/2002GL015415, 2002.

523   Moore, J.K., M.R. Abbott, J.G. Richman, W.O. Smith, Jr., T.J. Cowles, K.H. Coale, W.D.

524   Gardner, and R.T. Barber, SeaWiFS satellite ocean color data at the U.S. Southern Ocean

525   JGOFS line along 170°W, *Geophys. Res. Letters, 26,* 1465-1468, 1999.

526   Nelson, D.M., W.O. Smith, Jr., L.I. Gordon and B. Huber, Early spring distributions of nutrients

527   and phytoplankton biomass in the ice-edge zone of the Weddell/Scotia Sea, *J. Geophys.*

528   *Res.*, 92, 7181-7190, 1987.

529   Peloquin, J.A., Regulation and impact of the phytoplankton assemblage composition in the

530   Southern Ocean, Ph.D. Diss., VIMS, College of William and Mary, Williamsburg, VA, 169

531   pp.

532   Peloquin, J.A. and W.O. Smith, Jr., Phytoplankton blooms in the Ross Sea, Antarctica:

533   interannual variability in magnitude, temporal patterns, and composition, *J. Geophys. Res.* (in

534   press).

535   Sarmiento, J.L., and C. le Quéré, Oceanic carbon dioxide uptake in a model of century-scale

536   global warming, *Science, 274,* 1346 – 1350, 1996.

537   Sarmiento, J.L., T.M.C. Hughes, R.J. Stouffer, and S. Manabe, 1998, Simulated response of the

538   ocean carbon cycle to anthropogenic climate warming, Nature, 393, 245-249, 1998.

539   Shorin, Y., S. Iwamoto, M. Matsui, H. Obata, E. Nakayama, K. Suzuki, N. Handa, and M. Ishii,

540   The distribution of FE in the Australian sector of the Southern Ocean, *Deep-Sea I, 47,* 55-84,

541   2000.

542   Smith, W.O., Jr., and V.A. Asper, The influence of phytoplankton assemblage composition on

543   biogeochemical characteristics and cycles in the southern Ross Sea, Antarctica, *Deep-Sea*

544   *Res. I, 48,* 137-161, 2001.

545   Smith, W.O., Jr., and L.I. Gordon, Hyperproductivity of the Ross Sea (Antarctica) polynya

546   during austral spring, *Geophys. Res. Letters, 24,* 233-236, 1997.

547   Smith, W.O., Jr., and D.M. Nelson, Phytoplankton bloom produced by a receding ice edge in the

548   Ross Sea: Spatial coherence with the density field, *Science, 227,* 163-166. 1985.

549 Smith, W.O., Jr., and D.M. Nelson, The importance of ice-edge blooms in the Southern Ocean,

550 *BioScience, 36,* 251-257, 1986.

551 Smith, W.O., Jr., A.R. Shields, J.A. Peloquin, G. Catalano, S. Tozzi, M.S. Dinniman, and V.A.

552 Asper, Biogeochemical budgets in the Ross Sea: variations among years, *Deep-Sea Res. II,*

553 *53,* 815-833, 2006.

554 Sullivan, C.W., K.R. Arrigo, C.R. McClain, J.C. Comiso, and J. Firestone, Distributions of

555 phytoplankton blooms in the Southern Ocean, *Science, 262,* 1832-1837, 1993.

556 Sunda, W.G., and S.A. Huntsman, Interrelated influence of iron, light and cell size on marine

557 phytoplankton growth, *Nature, 390,* 389-392, 1997.

558 Strutton, P.G., F.B. Griffiths, R.L. Waters, S.W. Wright, and N.L. Bindoff, Primary productivity

559 of the coast of East Antarctica (80-150°E): January to March, 1996, *Deep-Sea Res. II, 47,*

560 2327-2362, 2000.

561 Thomas, D.N., 2004. *Frozen Oceans: The floating world of pack ice,* Natural History Museum,

562 224 pp.

563 Tremblay, J.-E., and W.O. Smith, Jr., Phytoplankton processes in polynyas, In *Polynyas:*

564 *Windows to the World's Oceans,* edited by W.O. Smith, Jr. and D.G. Barber, pp. 239-270,

565 Elsevier, Amsterdam, 2007.

566 Waldron, H.N., C.G. Attwood, T.A. Probyn, and M.I. Lucas, Nitrogen dynamics in the

567 Bellingshausen Sea during the Austral spring of 1992, *Deep-Sea Res. II, 42,* 1253-1276,

568 1995.

569 Zwally, H.J., J.C. Comiso, C. Parkinson, D. Cavalieri, and P. Gloersen, Variability of the

570 Antarctic sea ice cover, *J. Geophys. Res, 107,* 1029-1047, 2002.

571 **Figure Legends**

572 **Figure 1.** Location of regions within the Southern Ocean selected for detailed analysis. 1 = ACC

573   region; 2 = Indian Ocean; 3 = Weddell Sea; 4 = West Antarctic Peninsula (WAP); 5 =

574   Ross Sea I; 6 = Ross Sea II.

575 **Figure 2.** (a) Modeled photosynthetically active radiation impinging on the sea surface as

576   determined by the Watson-Gregg (1990) clear sky model, (b) Modeled photoperiod of the

577   Southern Ocean (between 55 - 80°S) over one year.

578 **Figure 3.** Mean ice concentrations for the Southern Ocean from 1997 – 2006 during a) October,

579   b) December, c) February, and d) April.

580 **Figure 4.** Mean ice concentrations in December for the years 1997-2006, showing the

581   magnitude and location of interannual variations throughout the Southern Ocean.

582 **Figure 5.** Variations of percentage of ice cover through time in a) the two Ross Sea selected

583   regions and the West Antarctic Peninsula, and b) the Weddell Sea and ACC areas.

584 **Figure 6.** Mean December sea surface temperature for the Southern Ocean for the years 1997 -

585   2006.

586 **Figure 7.** Variations of sea surface temperature through time in a) the two Ross Sea selected

587   regions and the West Antarctic Peninsula, and b) the Weddell Sea and ACC areas.

588 **Figure 8.** Mean austral growing season (November – March) chlorophyll concentration

589   throughout the entire Southern Ocean and that of each year from 1998-2006. Only ice-

590   free pixels are included in generating the mean.

591 **Figure 9.** Chlorophyll concentrations from 1997 – 2006 in the selected study regions. a) the

592   ACC, Indian Ocean and Weddell Sea areas, and b) the West Antarctic Peninsula and the

593   two selected regions from the Ross Sea.

594   **Figure 10.**   Annual (a) and mean monthly (November – March; b - f) primary productivity over

595   the entire Southern Ocean from 1997 - 2006. Annual values computed from computed

596   daily productivity and summed over the ice-free periods.

597   **Figure 11.** Primary productivity from 1997 – 2006 in the selected study regions. a) the two

598   Ross Sea selected regions and the West Antarctic Peninsula, and b) the Weddell Sea and

599   ACC areas.

600   **Figure 12.**   The relationship between depth and chlorophyll *a* concentrations in the Southern

601   Ocean during three years: a) 1998, b) 2003, and c) 2004.

602   **Figure 13.** The relationship between ice concentration and estimate annual primary productivity

603   from 1997 – 2006 in a) Ross Sea 1 study area, and b) Ross Sea 2 study area, (c) WAP

604   study area and (d) Weddell Sea Study area.

605   **Figure 14.**   The temporal changes in ice concentration and annual primary productivity in

606   November, December, Jauary, February and March from 1997 to 2006 in a) Ross Sea 1

607   study area, and b) Ross Sea 2 study area, (c) WAP study area and (d) Weddell Sea Study

608   area.

609   Table 1. Annual means (± standard deviations), minima and maxima of primary production in

610   the entire Southern Ocean and the selected subregions. Means are from the years 1997-2005.

611   Values in parentheses under minimum and maximum production represent the year of

612   occurrence.

Region	Mean Production $(g\,C\,m^{-2}\,y^{-1})$	Minimum Production $(g\,C\,m^{-2}\,y^{-1})$	Maximum Production $(g\,C\,m^{-2}\,y^{-1})$
Southern Ocean	23.65 ± 1.28 (22.10 – 25.49)	22.10 (1998)	25.49 (2004)
Ross Sea I	65.11 ± 24.98 (15.97 – 88.29)	15.97 (2003)	88.29 (2001)
Ross Sea II	54.14 ± 14.54 (25.63 – 80.10)	25.63 (2003)	80.10 (2004)
West Antarctic Peninsula	37.30 ± 11.83 (26.89 – 61.63)	26.89 (2004)	61.63 (2006)
Weddell Sea	18.17 ± 6.86 (6.68 – 30.87)	6.68 (2002)	30.87 (2005)
Antarctic Circumpolar Current	67.98 ± 9.61 (58.28 – 88.06)	58.28 (2006)	88.06 (2003)
Indian Ocean	41.12 ± 3.75 (35.79 – 45.39)	35.79 (2005)	45.39 (2001)

613

614   Table 2. Estimates of primary production of the Southern Ocean. All estimates are not

615   comparable, as they were derived as averages using different techniques and areas.

Area used in estimate	Primary Productivity $(g\ C\ m^{-2}\ y^{-1})$	Reference
38.1×10^6 km²; South of 50°S	16	Holm-Hansen et al. (1977)
38.1×10^6 km²; South of 50°S	43	El-Sayed (1977)
Weddell Sea marginal ice zone	30	Jennings et al. (1983)
Southern Ocean marginal ice zone	10	Smith and Nelson (1986)
Weddell Sea marginal ice zone	32.9	Smith and Nelson (1986)
Ross Sea marginal ice zone	45.6	Smith and Nelson (1986)
Ross Sea continental shelf	140	Arrigo and McLain (1994)
Ross Sea continental shelf	200	Smith and Gordon (1997)
South of 50°S	100	Arrigo et al. (1998a)
Ross Sea continental shelf	78.7 - 144	Arrigo et al. (1998b)
Southern Ocean (South of 50°S)	62.4; 82.2*	Moore and Abbott (2000)
Coastal polynyas	20 – 80	Arrigo and van Dijken (2004)
Southern Ocean (South of 60°S)	23.65 ± 1.28	This study
Ross Sea I	65.11 ± 24.98	This study
Ross Sea II	54.14 ± 14.54	This study
West Antarctic Peninsula	37.30 ± 11.83	This study
Weddell Sea	18.17 ± 6.86	This study
Antarctic Circumpolar Current	67.98 ± 9.61	This study
Indian Ocean	41.12 ± 3.75	This study

616   *: Values represent the entire region and only those waters with <70% ice cover
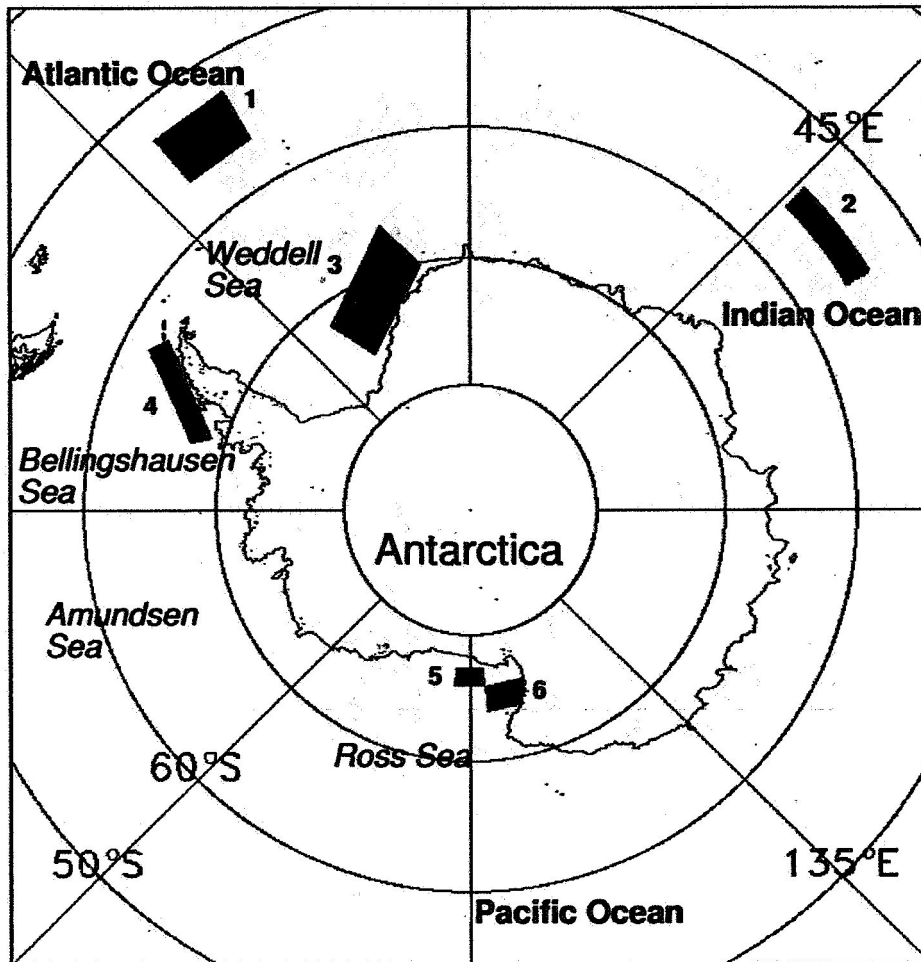
Figure 1. Location of regions within the Southern Ocean selected for detailed analysis.
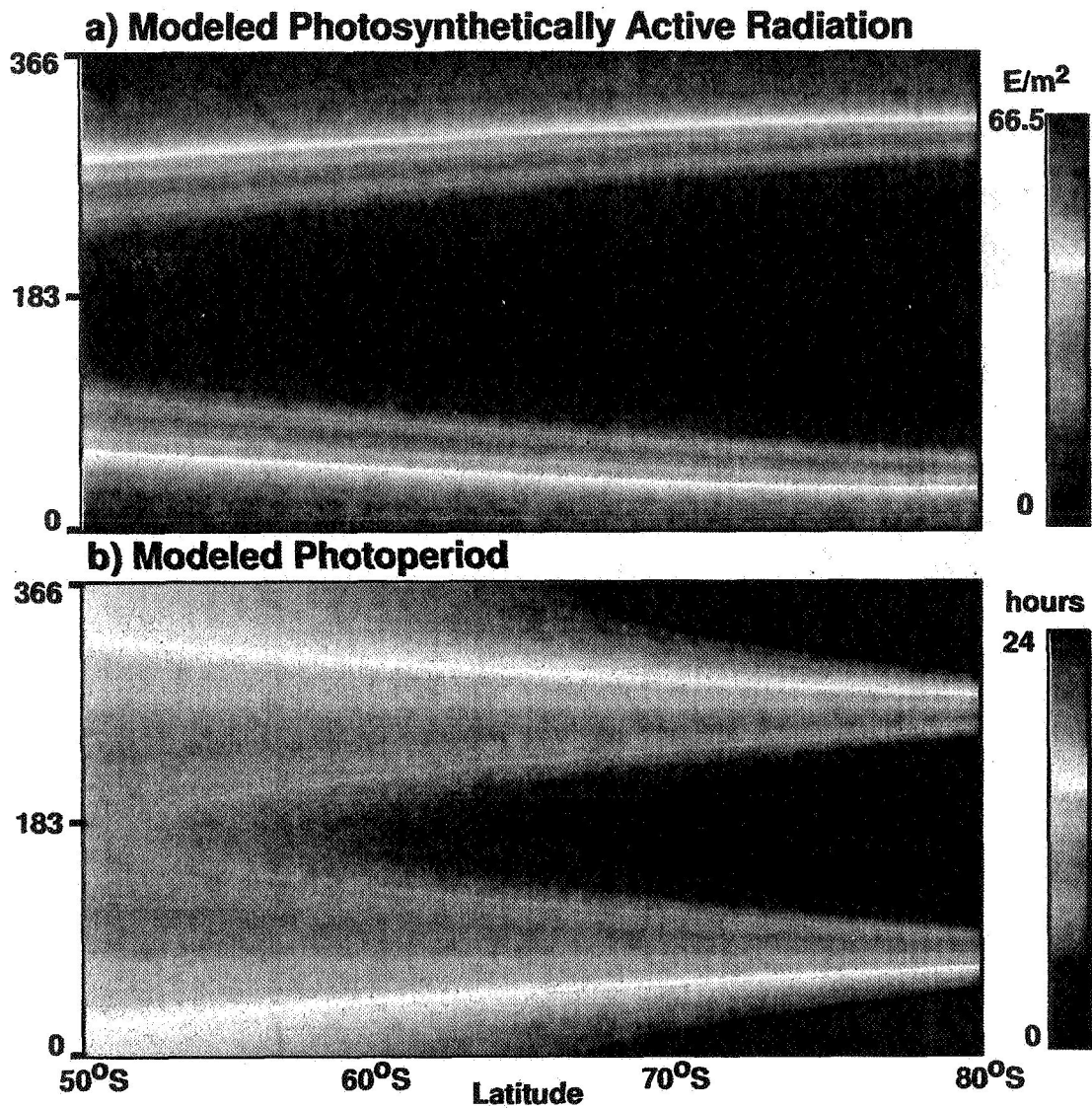
Figure 2. (a) Modeled photosynthetically active radiation impinging on the sea surface as determined by the Watson-Gregg (1990) clear sky model; (b) Modeled photoperiod of the Southern Ocean (between 55 and 80°S) over one year.
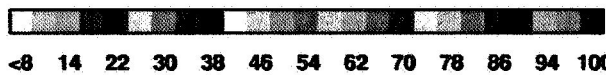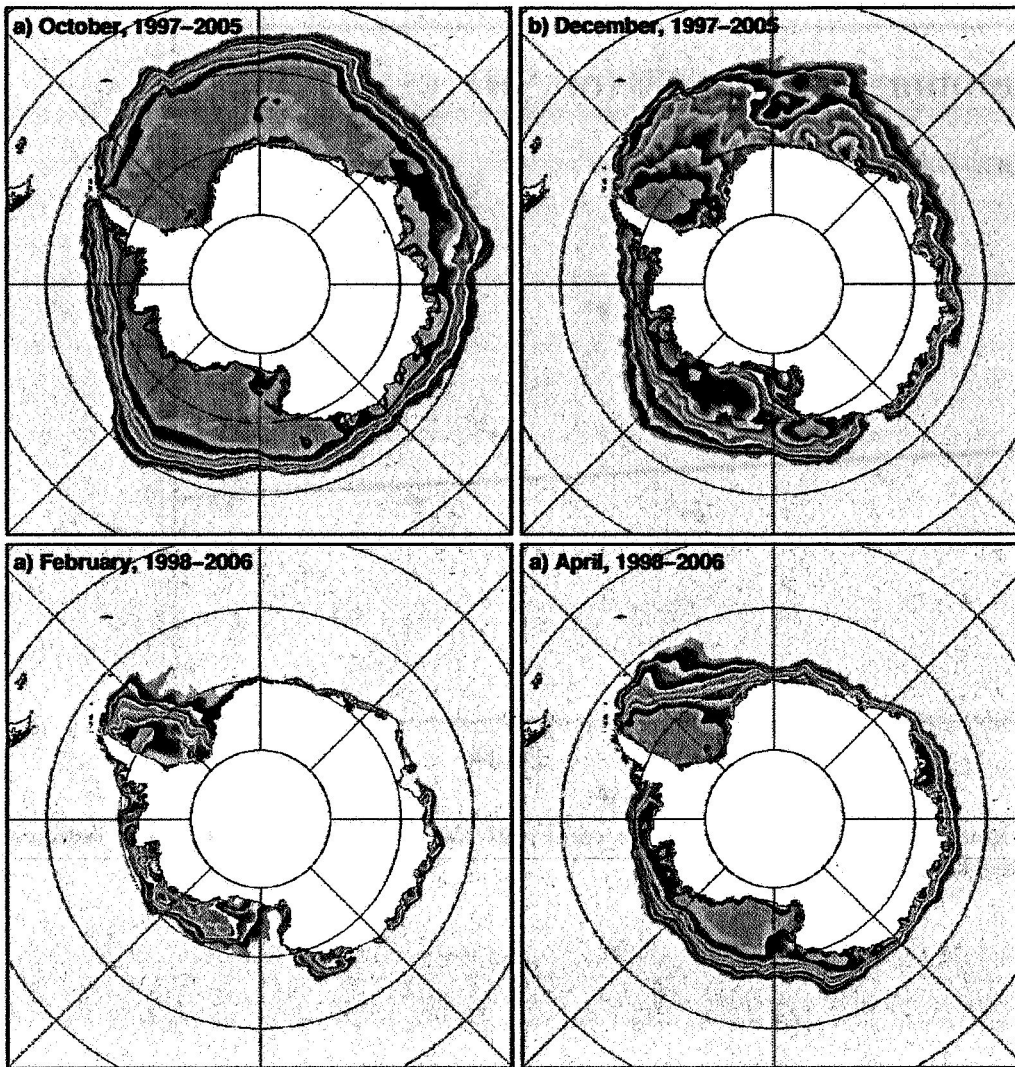
Figure 3. Mean ice concentrations over the Southern Ocean from 1997 – 2006 for a) October, b) December, c) February, and d) April.
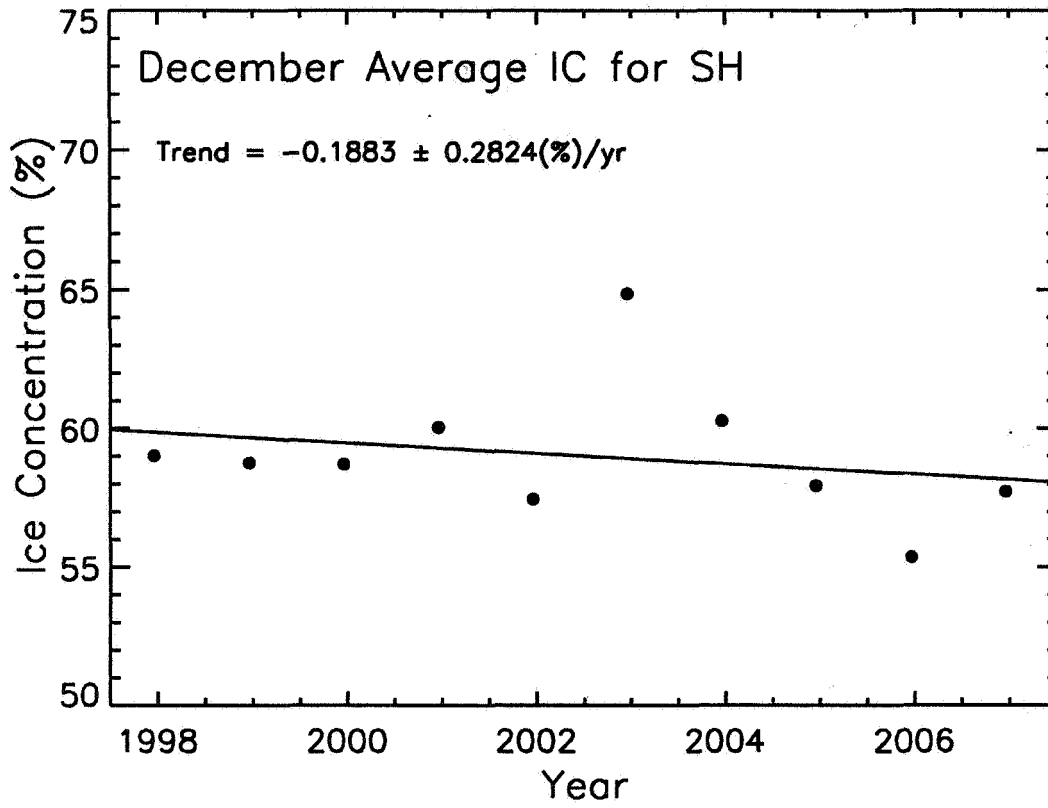
Figure 4. Mean ice concentrations in December for the years 1997-2006, showing the magnitude of interannual variations throughout the Southern Ocean.
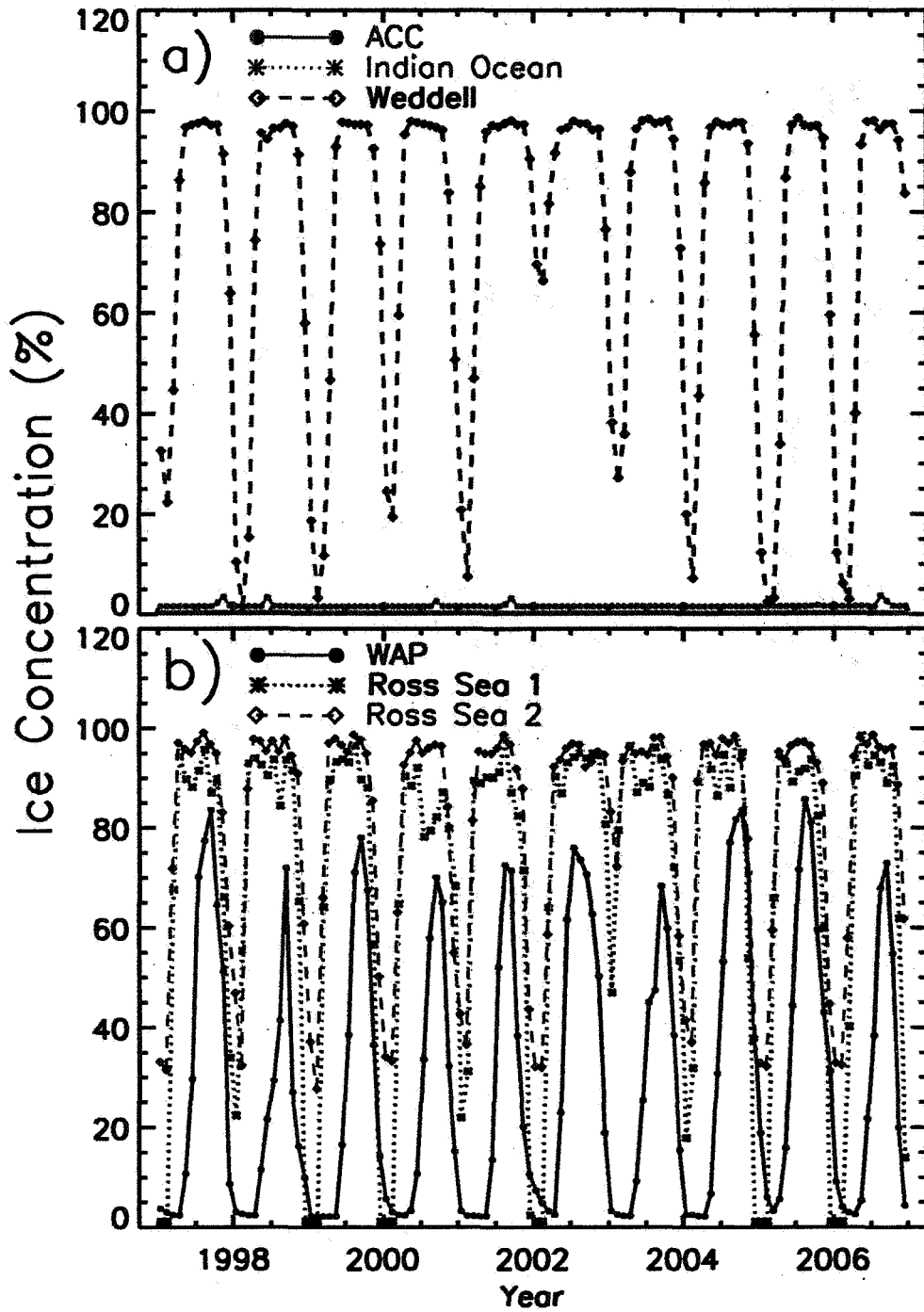
Figure 5. Variations of percentage of ice cover through time in a) the two Ross Sea selected regions and the West Antarctic Peninsula, and b) the Weddell Sea and ACC areas.
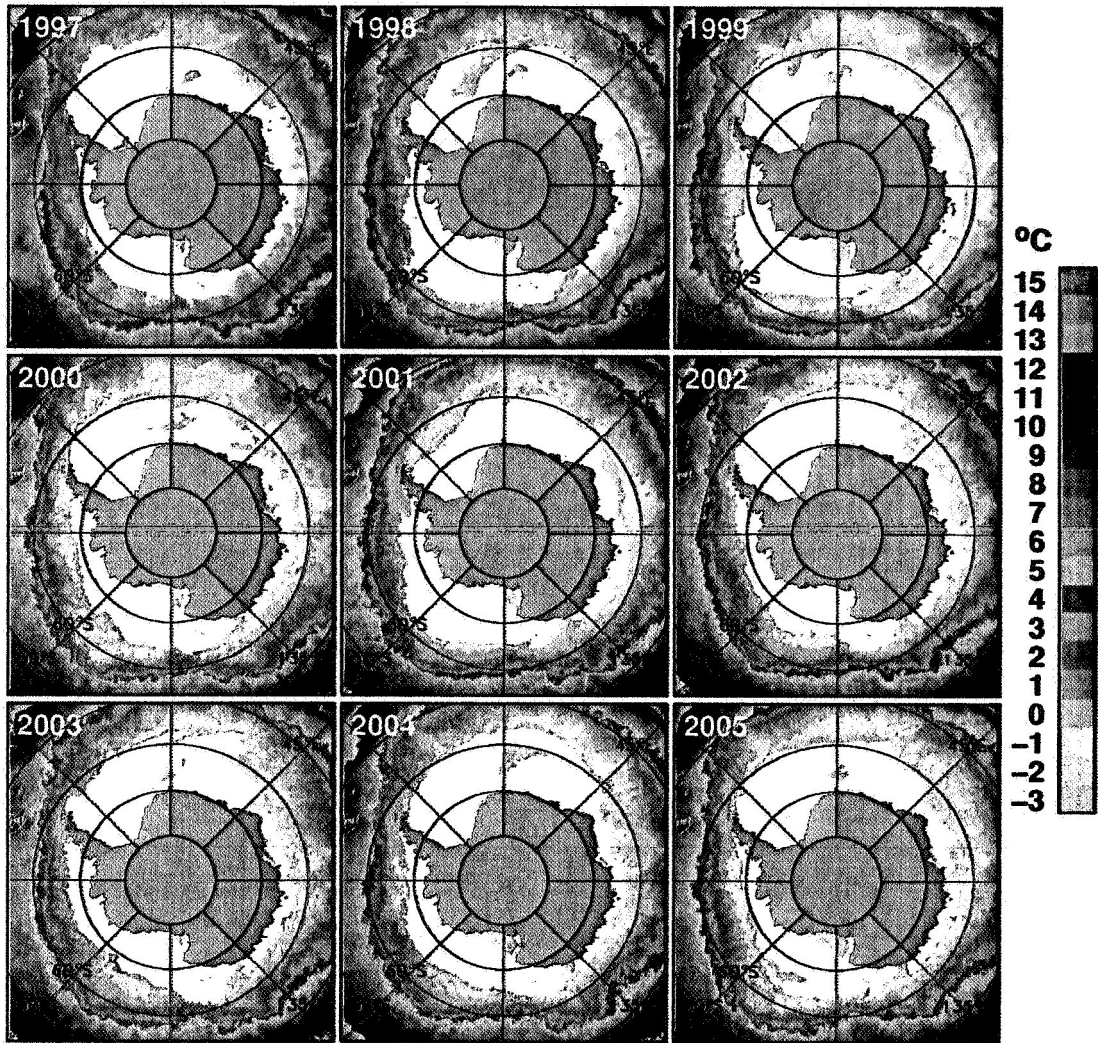
Figure 6. Mean December sea surface temperature for the Southern Ocean for the years 1997 - 2006.
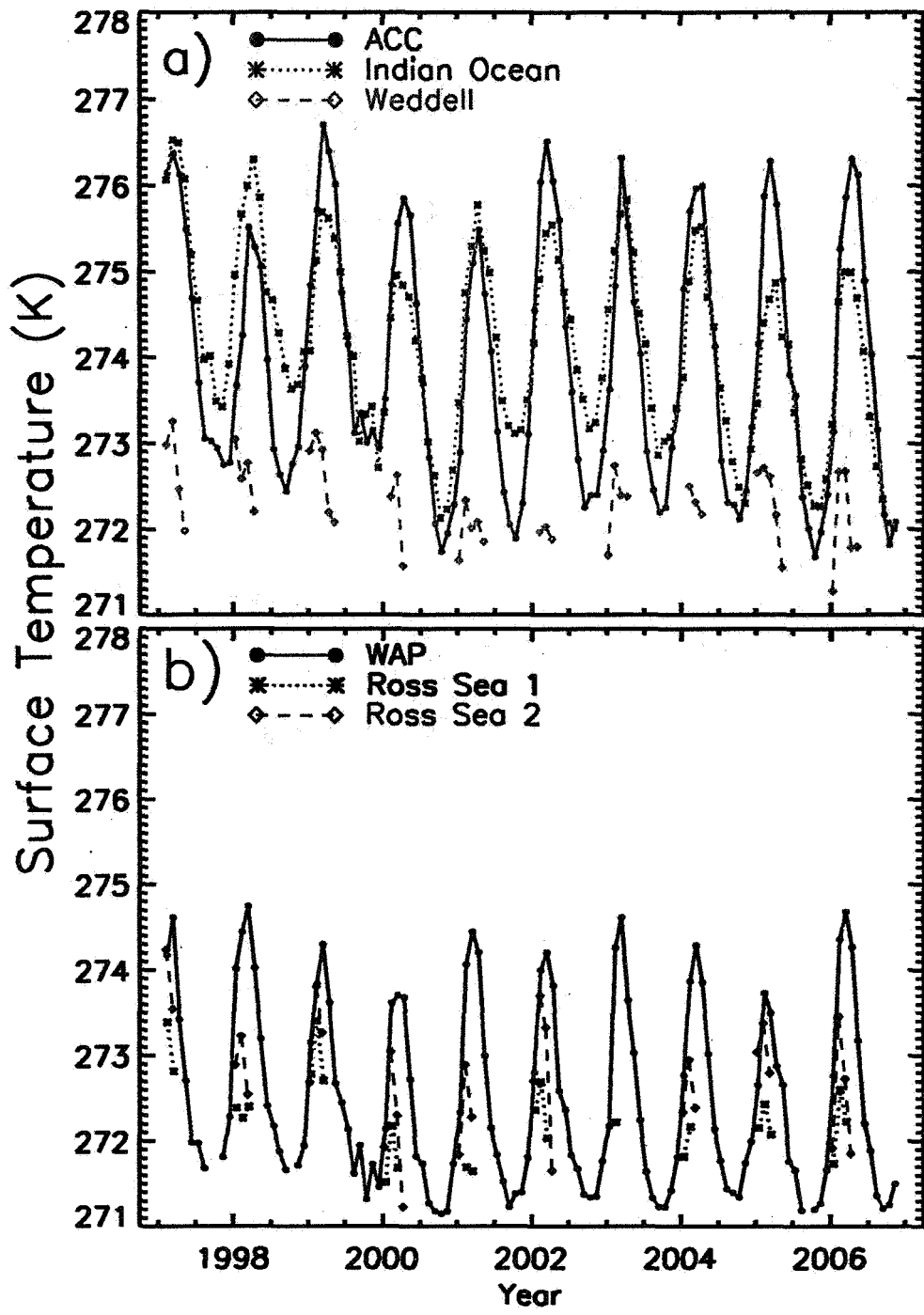
Figure 7. Variations of sea surface temperature through time in a) the ACC, Weddell Sea and Indian Ocean study areas and (b) the two Ross Sea selected regions and the West Antarctic Peninsula.
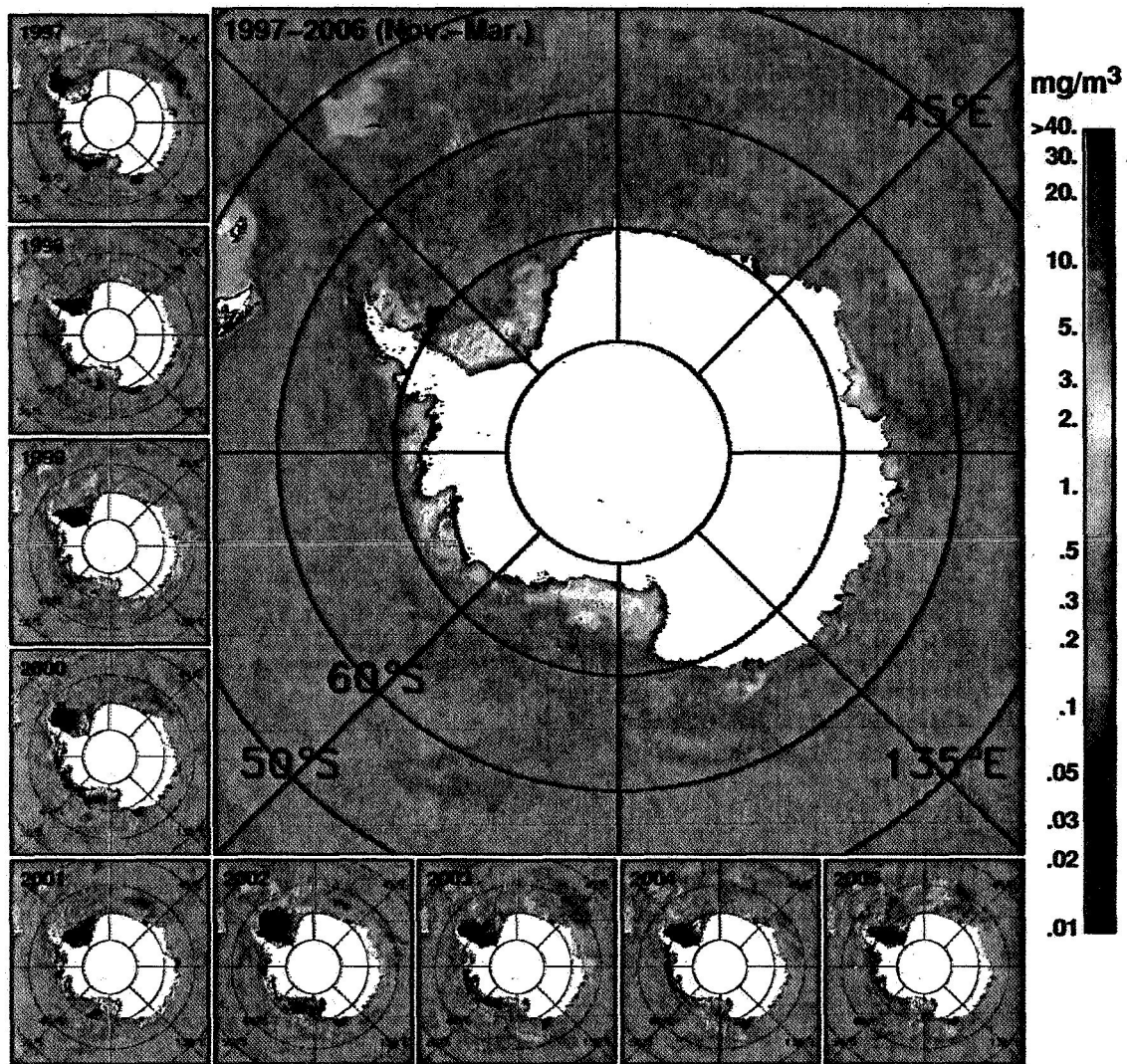
Figure 8. Mean austral growing season (November – March) chlorophyll concentration throughout the entire Southern Ocean and that of each year from 1998-2006. Only ice-free pixels are included in generating the mean.
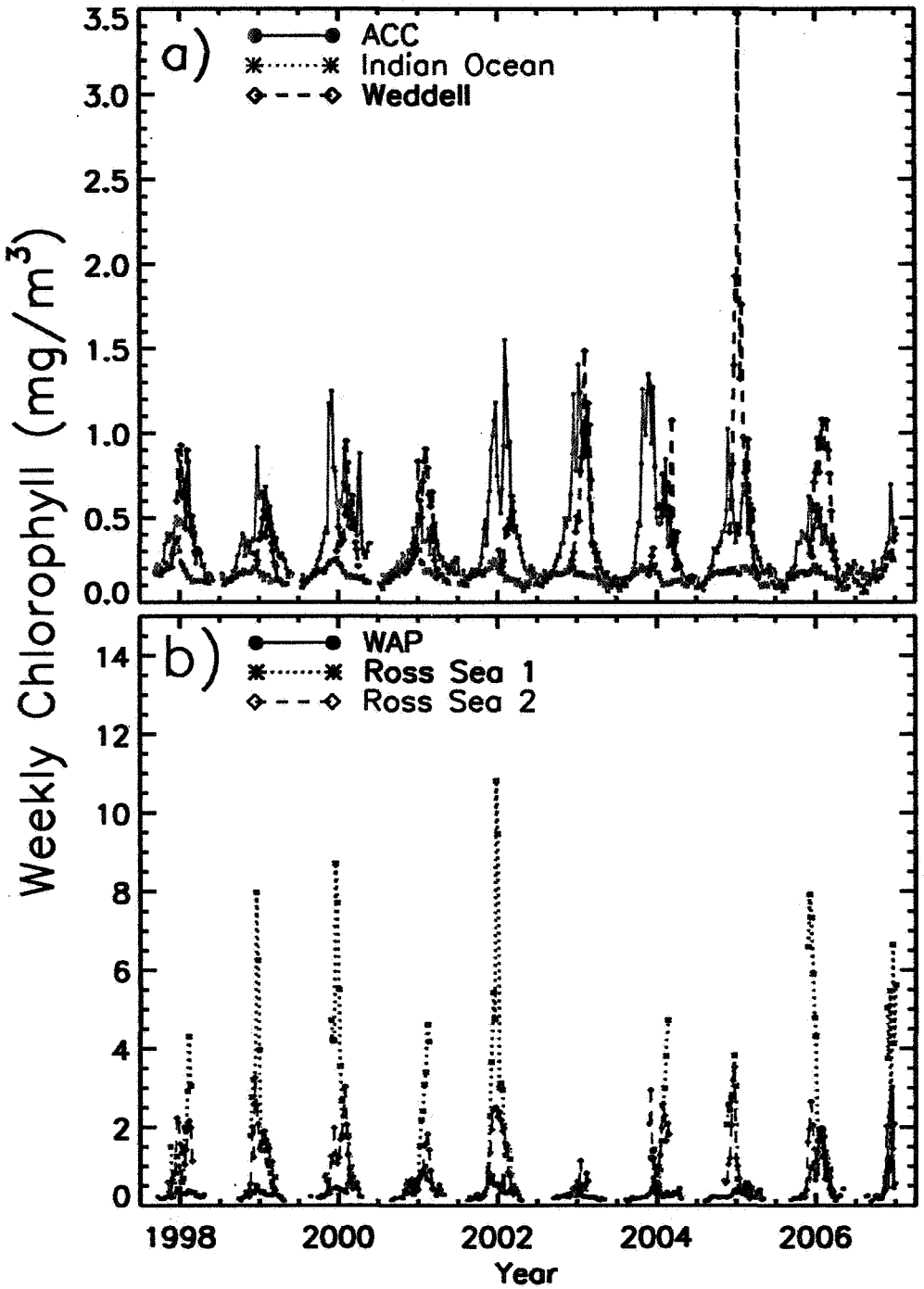
Figure 9. Chlorophyll concentrations from 1997 – 2006 in the selected study regions. a) the ACC, Indian Ocean and Weddell Sea areas, and b) the West Antarctic Peninsula and the two selected regions from the Ross Sea.
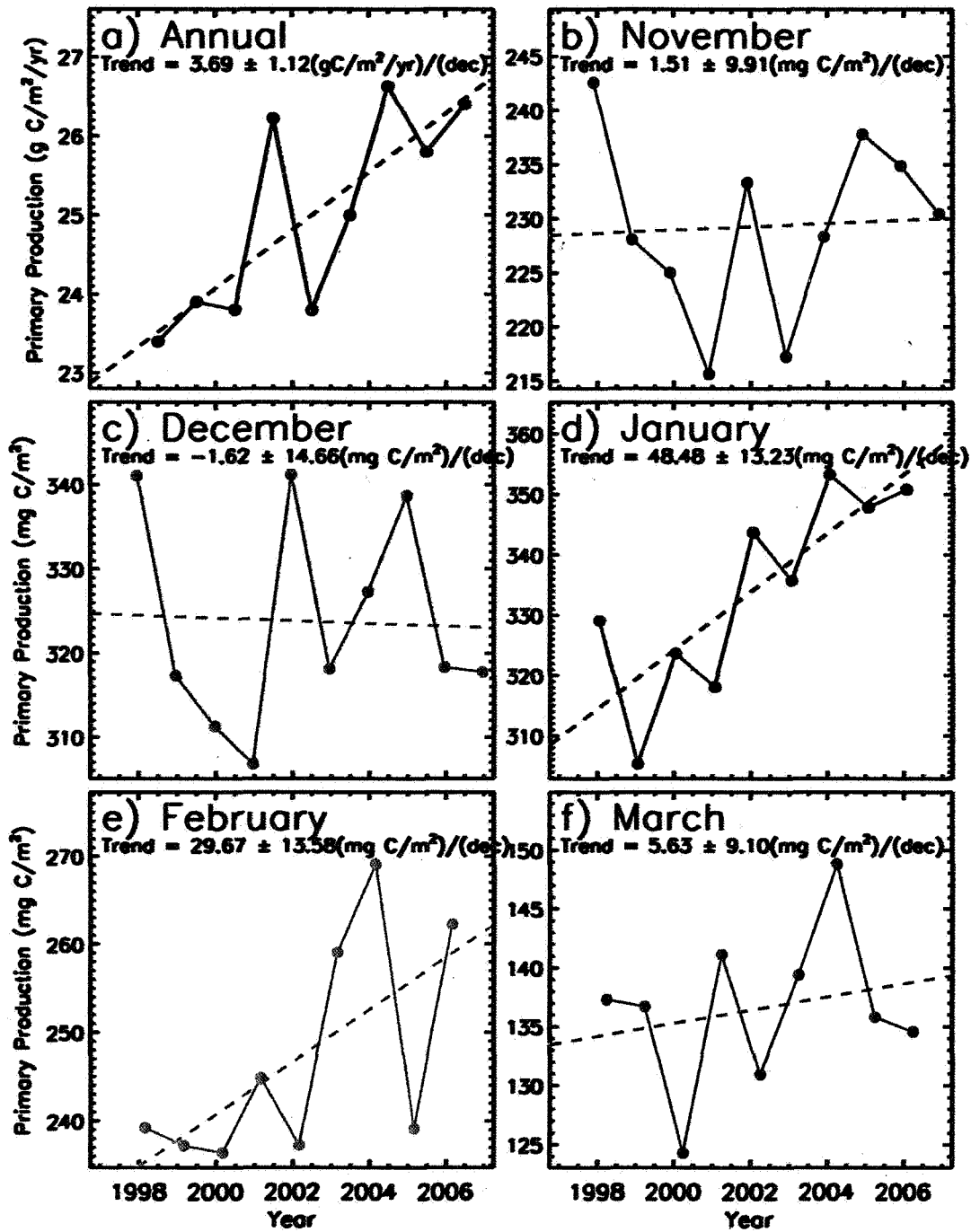
Figure 10. Annual (a) and mean monthly (November – March; b - f) primary productivity over the entire Southern Ocean from 1997 - 2006. Annual values computed from computed daily productivity and summed over the ice-free periods.
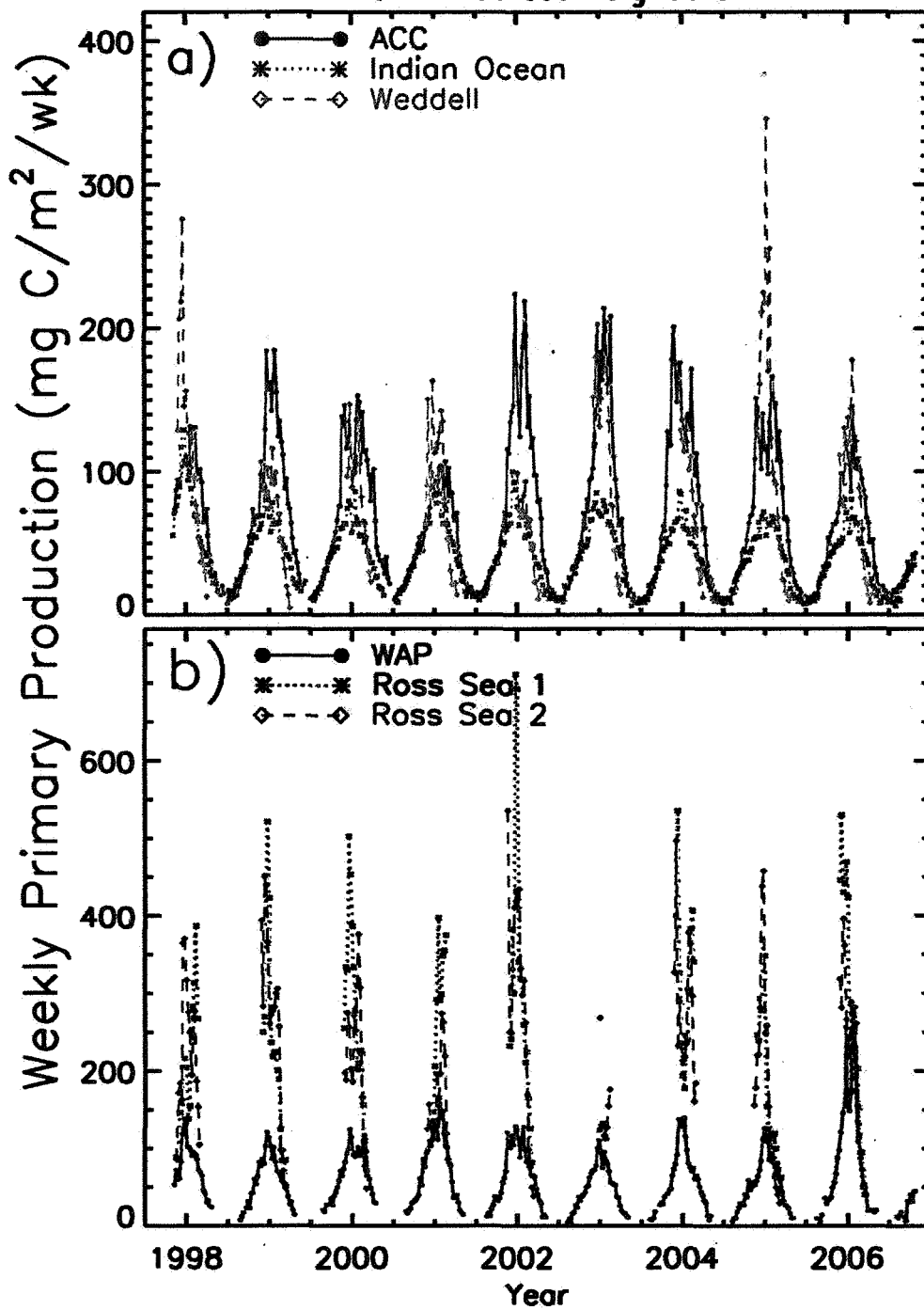
Figure 11. Primary productivity from 1997 – 2006 in the selected study regions. a) the two Ross Sea selected regions and the West Antarctic Peninsula, and b) the Weddell Sea and ACC areas.
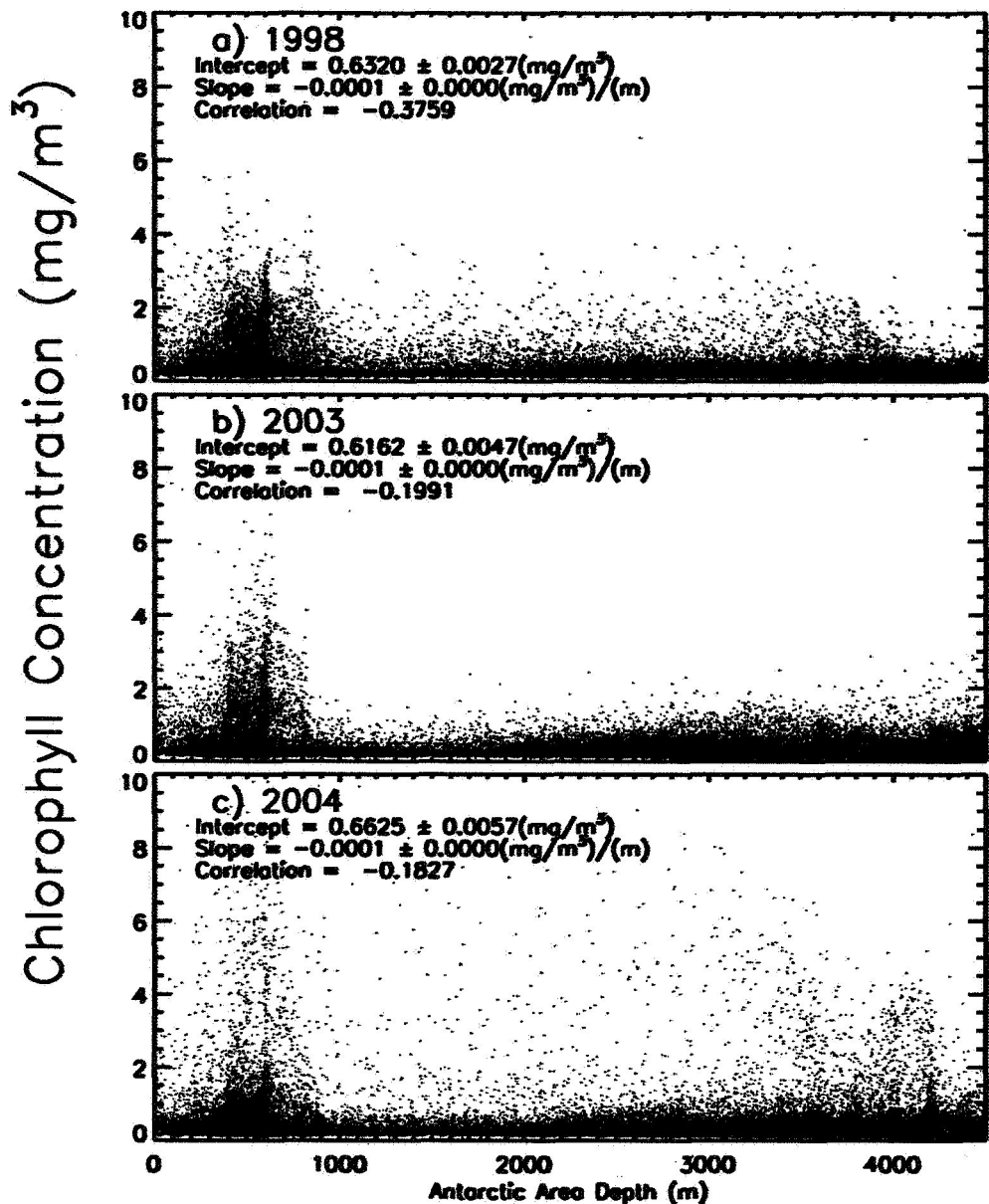
Figure 12. The relationship between depth and chlorophyll *a* concentrations in the Southern Ocean during three years: a) 1998, b) 2003, and c) 2004.
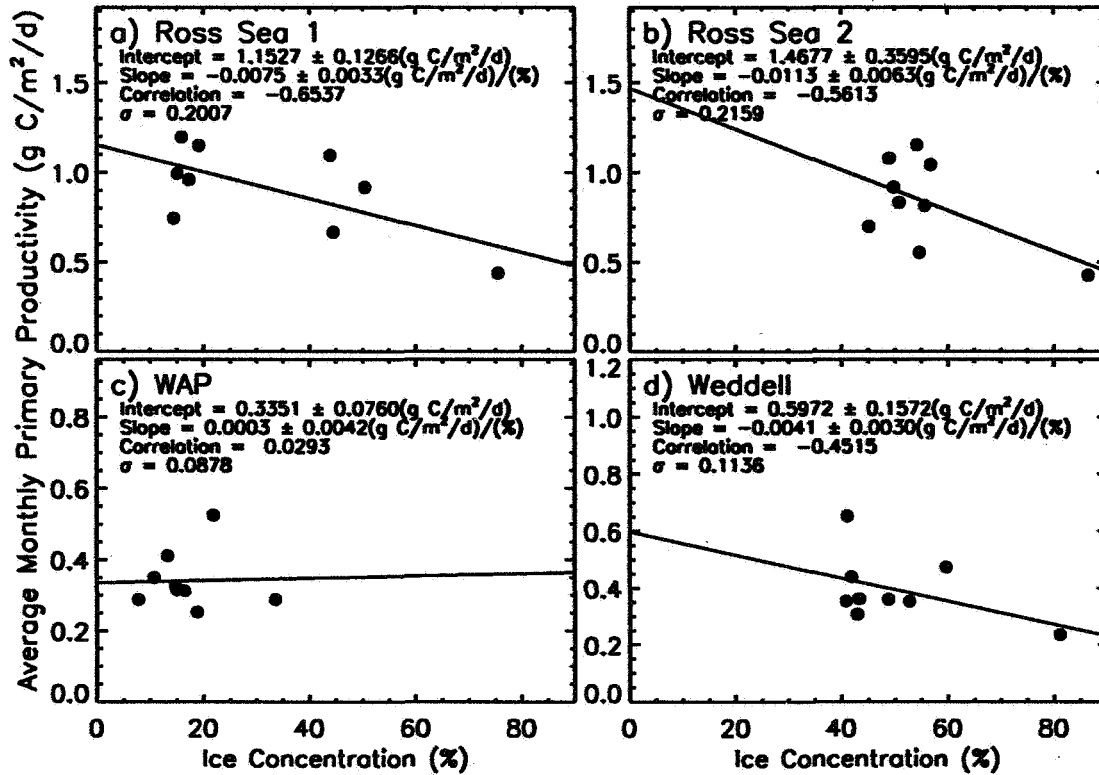
Figure 13. The relationship between ice concentration and estimate annual primary productivity from 1997 – 2006 in a) Ross Sea 1 study area, and b) Ross Sea 2 study area, (c) WAP study area and (d) Weddell Sea Study area.
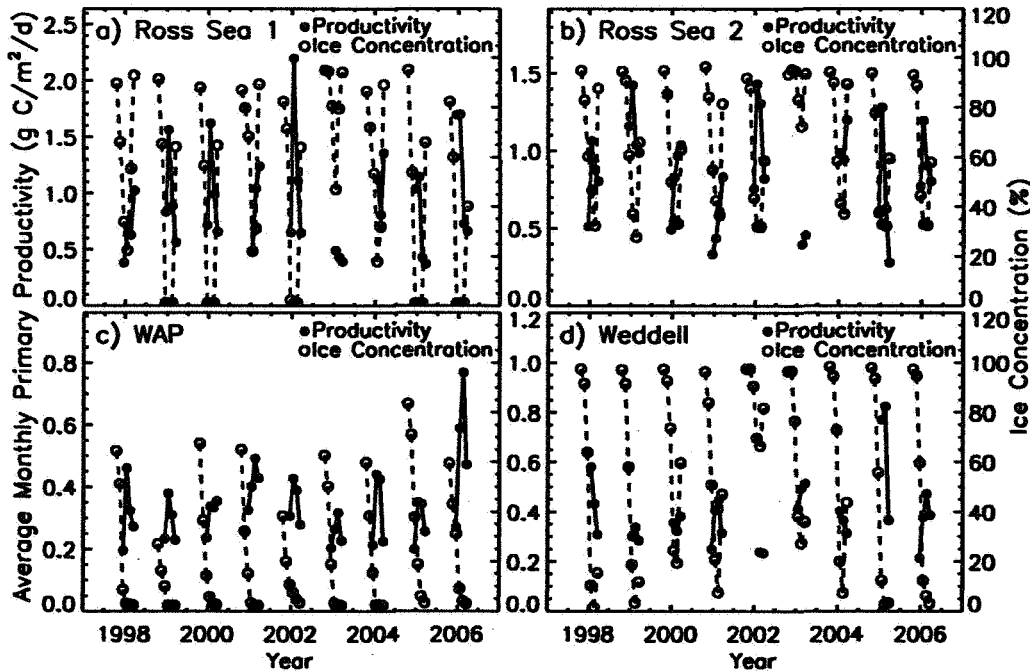

Figure 14. The temporal changes in ice concentration and annual primary productivity in November, December, Jauary, February and March from 1997 to 2006 in a) Ross Sea 1 study area, and b) Ross Sea 2 study area, (c) WAP study area and (d) Weddell Sea Study area.