Phytoplankton: Trophic modelling of the Ross Sea

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1 Introduction

The shelf waters of the Ross Sea are amongst the most biologically-productive areas of the Southern Ocean. Primary production may be as high as 180 gC m^{-2} y^{-1} with average sedimentation rates up to 97% (Fabiano et al. 1997, Saggiomo et al. 2000; Smith et al. 1996; Heilmayer et al. 2003). Growth of phytoplankton in the Ross Sea is characterised by localised, short-duration events of high productivity. These events occur especially in shallow coastal embayments, polynya, and in the vicinity of the retreating ice-edge. Phytoplankton blooms in the Ross Sea form a bimodal distribution: blooms of the prymnesiophyte *Phaeocystis antarctica* in late October/early November in unstratified waters, followed by diatom dominated blooms in December/January as the water stratifies (DiTullio & Smith 1997; Arrigo & van Dijken 2004; Kopczynska 1992; Reddy & Arrigo 2006).

A large number of studies have investigated why inorganic macronutrients are not exhausted in the Ross Sea (see: Lancelot et al. 2000; Arrigo et al. 2003 and references therein). It appears that the major factors limiting phytoplankton growth in the study region are light and iron, with the relative importance of these varying by region and season. Light intensities are generally insufficient for substantial phytoplankton growth except during the austral late spring, summer and early autumn period. The distribution of dissolved iron (and manganese) in the Ross Sea is such that there are relatively high (>0.5 nM) concentrations of dissolved iron during early spring compared with low concentrations in late spring and early summer (Sedwick et al. 2000). Light is hence the primary limiting environmental factor on phytoplankton growth early in the growing season. As mentioned above, light intensity experienced by phytoplankton depends significantly on water column structure and the depth of the thermocline, which, in turn, is affected by fresh water input due to ice melt. The observed seasonal differences in iron concentration are attributed to seasonal decreases in the upwelling of bottom waters, melting sea ice (see also Sedwick et al. 1997; Edwards & Sedwick 2001; Tagliabue & Arrigo 2006) that supplies iron into the upper water column, and the cumulative removal of iron from the water column due to biological uptake. Low dissolved iron concentrations become limiting on algal community growth in late summer, except in stratified, iron-rich waters near melting sea ice where diatoms are able to bloom.

The biomass (standing stock) of phytoplankton is affected by the balance between phytoplankton growth and loss, by grazing of zooplankton and through death and sinking of phytoplanktonic material. The relative importances of grazing of phytoplankton by zooplankton, and loss of phytoplankton due to sinking is seasonally and regionally heterogeneous. Fortunately, ocean colour remote sensing using satellite sensors gives us a method for estimating phytoplankton biomass in the surface waters of the Ross Sea.

2 Biomass

The model area defined in this study differs from areas considered by other studies of phytoplankton in the Ross Sea. For example, Arrigo & van Dijken (2004) considered the "Ross Sea area" to be bounded to the north by about 73.5°S whereas our area continues north to 69°S. Phytoplankton biomass and production is patchy, so the choice of area may significantly affect the average values for the region. For this reason, we focus here on estimating phytoplankton biomass and production from primary data sources, especially satellite observations of ocean colour, rather than taking values direct from the literature.

Satellite-borne ocean colour satellite sensors measure multispectral radiances at the top of the Earth's atmosphere which are then corrected for atmospheric scattering and absorption to estimate normalised water-leaving radiance (Gordon et al. 1988) for visible wavelengths (400–600 nm). A "bio-optical algorithm" is used to estimate the surface concentration of chlorophyll *a* from each ocean colour measurement (e.g., O'Reilly et al. 1998, 2000). Inaccuracies in satellite measurements of chlorophyll at the sea-surface arise from three main sources: (1) imperfect measurement of top-of-atmosphere radiances due to (for example) sensor degradation (Gordon et al. 1983); (2) imperfect correction for the optical effects of the atmosphere (Gordon & Wang 1994); (3) variations in the relationship between ocean colour and chlorophyll concentration (i.e. the chlorophyll algorithm) with location and season. It is also necessary to know the depth distribution of chlorophyll and how to convert chlorophyll to carbon to estimate water-column integrated phytoplankton biomass.

In this study we use ocean colour measurements from the NASA Sea Viewing Wide Field-of-view Sensor (SeaWiFS: Hooker et al. 1992) which began operation in September 1997 and was still operational a decade later. SeaWiFS full resolution data have a nadir pixel size of 1.1 x 1.1 km, and are subsampled on board the spacecraft to give Global Area Coverage (GAC) data (4.4 km resolution at nadir). Here, we used SeaWiFS Standard Mapped Image (SMI) products which are generated by averaging GAC data in time and space (Campbell et al. 1995). In the Ross Sea study area, the SMI cells have a resolution of approximately 2.7 km (longitude), 9.8 km (latitude) and areas of between 18 and 34 km^2 (median: 26 km^2). Data availability is limited by cloud cover and the present study uses monthly composite images where all valid data measured during a given month are combined. Monthly composite images are indicative of typical conditions, but do not necessarily give true mean monthly values because image pixels in different areas are composited from different quantities of data. Short-lived phytoplankton blooms (a few days) may have been missed completely or may disproportionately affect the composite value, especially when there were few cloud-free days (Comiso et al. 1993). By averaging data for each month over a number of years (1997–2004) we reduce likely biasing due to this effect, and reduce the significance of interannual variability. Concentrations of chlorophyll in this work were generated from SeaWiFS measurements of normalised water-leaving radiance using the SeaWiFS Ocean Chlorophyll-4 version 4 algorithm (OC4v4, O'Reilly et al. 2000) as implemented in SeaWiFS Data Analysis System (SeaDAS) version 4.3 (Fu et al. 1998). Some studies have shown that this algorithm for chlorophyll concentration tends to significantly under-estimate chlorophyll in the Southern Ocean by a factor of 1.6–2 or more (e.g., Mitchell & Holm-Hansen, 1991; Arrigo & McClain 1994; Dierssen & Smith 2000). However, a more recent study of remote sensing of chlorophyll by SeaWiFS in the Ross Sea (Arrigo & van Dijken 2004) did not show a large under-estimation. Instead, there was evidence of an under-estimation of chlorophyll by SeaWiFS relative to in situ measurements by ~13%. Here, we increase SeaWiFS SMI surface concentrations of chlorophyll by a factor of 1.13.

Low incident light prevented any data being collected by SeaWiFS in the Ross Sea between April and October each year. In the absence of light, primary production ceases, and phytoplankton concentrations are assumed to rapidly fall to trace concentrations (e.g., Knox 2007). We hence estimate an annual cycle of surface chlorophyll concentration indicated in Figure 1, which agrees closely with Arrigo & van Dijken (2004, their fig. 12). Our values are consistent with the results of Saggiomo et al. (1998, 2002), Mangoni et al. (2004), Vaillancourt et al. (2003). The range of interannual variation is approximately between a factor of 0.4 and 1.6 of our best estimate (Arrigo & van Dijken 2004), i.e. approximately ±60% (see Figure 1b).

To convert surface values of chlorophyll concentration to water column averages, we assumed that phytoplankton were well mixed between the surface and the seasonal thermocline or photic depth, whichever was shallower. Longhurst (1998, fig 10.5) gives this depth as approximately 30 m. This is consistent with previous results (Bender et al. 2000; Saggiomo et al. 2002; Smith et al. 2000; Hu & Smith 1998). Carbon-chlorophyll ratios for marine phytoplankton have been found to vary considerably between 20 to >200 gCg^{-1}Chl-*a* (Taylor et al. 1997; Lefevre et al. 2003). Data from SOIREE (Boyd 2002) and other experiments in iron-limited, subantarctic waters suggest a seasonally-invariate value of 80–100 gCg^{-1}Chl-*a* is reasonable, though Smith et al. (1996) found values between 126 and 228 gCg^{-1}Chl-*a* in the Ross Sea. DiTullio & Smith (1996) give an average value of 130 gCg^{-1}Chl-*a* for the Ross Sea. Arrigo (pers. com.) suggests using 90 gCg^{-1}Chl-*a*. Smith et al. (2000) indicate a seasonally-varying value for the ratio, with a summer value of ~150 gCg^{-1}Chl-*a*. Hewes et al. (1990) propose an empirical function that they state explains ~80% of the variance of C:Chl-*a* ratios in the Southern Ocean: $C=80\cdot[\text{Chl-a}]^{0.6}$. This relationship would suggest C:Chl-*a* values up to 116 gCg^{-1}Chl-*a* in the summer, and much higher values in the winter. We use a value in the middle of these literature values of 120 gCg^{-1}Chl-*a* in this work giving Figure 1c.

Finally, we calculated an equivalent phytoplankton density for the study area taking into account variations in the proportion of the study area that was ice free. Light levels are significantly reduced by sea ice (e.g., Knox 2007; Schwarz et al. 2005), especially if covered in snow, and this is likely to reduce phytoplankton growth below ice cover (Fritsen & Sullivan (1997). The magnitude of the reduction over large scales and in different seasons is not well known as the sea ice inhibits our ability to measure chlorophyll concentrations remotely. The model of Arrigo & van Dijken (2007) has negligible production in ice covered waters. Here, we assume that phytoplankton biomass is reduced by 90% in waters covered with sea ice.

The area of ice-free water in the study region changes seasonally as discussed in the document on the physical environment of the Ross Sea. We estimate about 88% of the study area is ice free (<10% ice concentration) in February, and only 12% is ice free in July. The average values of phytoplankton biomass and productivity for the Ross Sea area as a whole were adjusted to take this into account. Based on these considerations, the average phytoplankton biomass for the study region for the whole year was estimated to be 1.1 gC m^{-2} with a cycle as shown in Figure 1d. Note that this represents a typical or "average" year. The data from SeaWiFS, and published information (e.g., Arrigo & van Dijken 2004) show large variations in phytoplankton biomass for year to year. The variability may be of the order of -60% to +100% (i.e. factor of 0.4–2). This suggests that possible limits of phytoplankton biomass are 0.4–1.8 gC m^{-2} for a "typical" year.

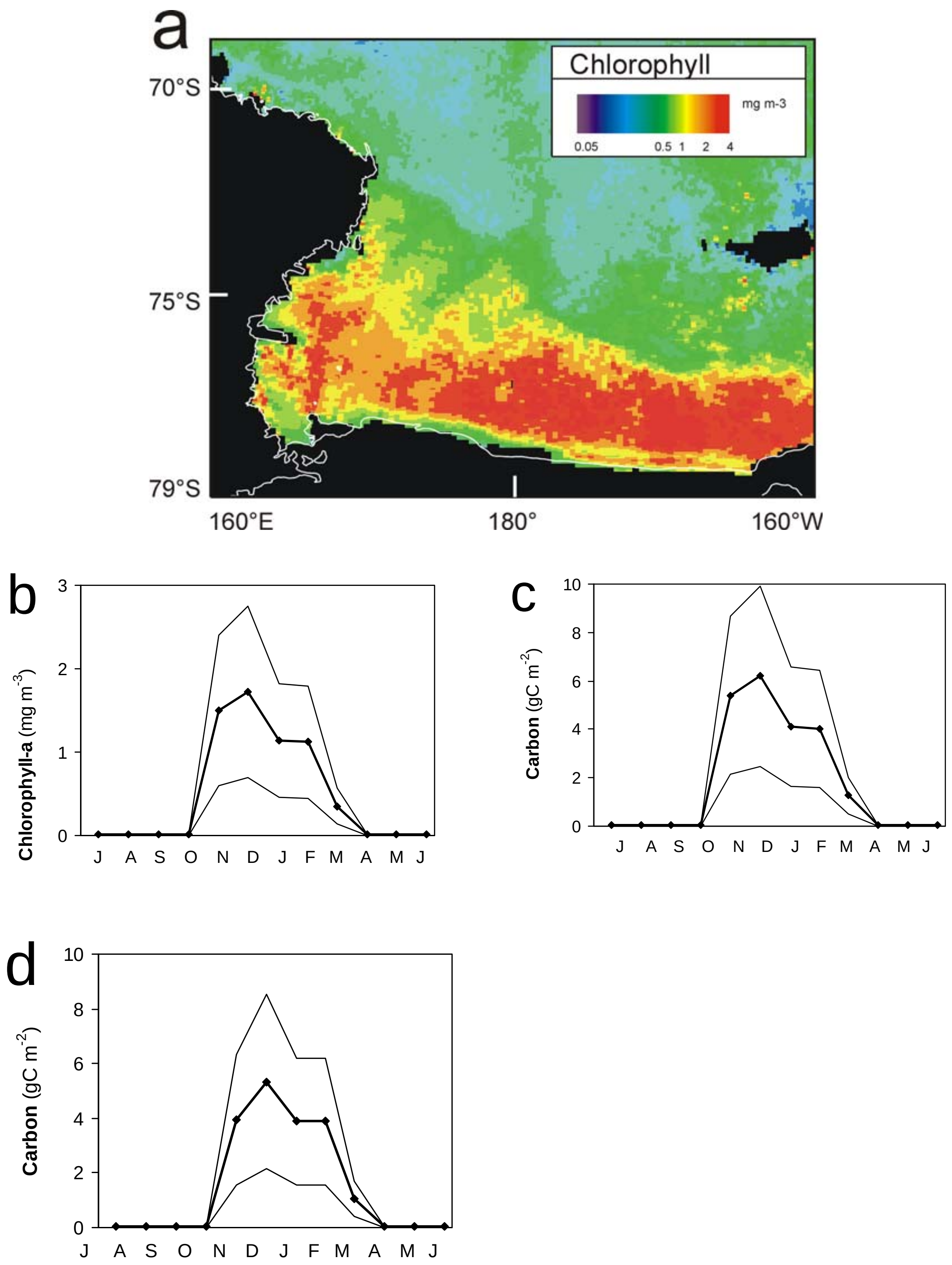

Figure 1. a: Average surface chlorophyll concentration for the study area measured by SeaWiFS between 1997–2004. **b**: Average surface chlorophyll-a concentration from SeaWiFS for the study area. **c**: Average

water column integrated carbon concentrations for study area. **d**: As (c) but taking into account variations in ice-free water over the year. The heavy centre lines indicate our best estimates of the values. The upper and lower lines indicate the approximate range of variation from year to year (Arrigo & van Dijken 2004).

3 Primary production by phytoplankton

Several studies present rates of primary productivity in the Ross Sea which may be >1.0 gC m^{-2} d^{-1} (Smith et al. 1996; Bates et al. 1998; Smith et al. 2000; Tagliabue & Arrigo 2003; Arrigo & van Dijken 2004). Arrigo & van Dijken (2004) relate sea ice to primary production on an areal basis, and indicate that the Ross Sea is the most productive sector of the Southern Ocean, with daily primary production rates often exceeding 2.0 gC m^{-2} d^{-1}. The magnitude of these values is consistent with earlier work by Smith & Gordon (1997). Nelson et al. (1996) used in situ data from a number of seasons to estimate an annual primary production on the Ross Sea shelf of 142 gC m^{-2} y^{-1}. Arrigo et al. (1998, 2000) estimated primary production for the Ross Sea shelf of 3.9 gC m^{-2} d^{-1} for December, and annual rates of production of 140–200 gC m^{-2} y^{-1}. Arrigo & van Dijken (2004) give primary production rates of c. 1–2 gC m^{-2} d^{-1} during the growing season. Bender et al. (2000) report average production rates of 2.2 gC m^{-2} d^{-1} for the Ross Sea growing season. Saggiomo et al. (1998; 2002) give integrated production values between 0.7–1.1 gC m^{-2} d^{-1} and 0.6–2.4 gC m^{-2} d^{-1} for the Ross Sea during the growing period. Vaillancourt et al. (2003) give an average of 0.4–1.2 gC m^{-2} d^{-1} for the Ross Sea during the summer. Smith et al. (2000) give production values which peak at about 2.5 gC m^{-2} d^{-1} in January.

In this work we estimated the net primary production based on the results of Arrigo & van Dijken (2004, 2007). We use their lower values from a normal ice year of 140 gC m^{-2} y^{-1} for their study area and adjust this to our study area as follows. Arrigo & van Dijken (2007) give average chlorophyll concentrations between December and February for their study area of about 1.1–3.1 mgChl-a m^{-3} for the years 1997–2003. Equivalent values from SeaWiFS for our study area are 0.25–1.9 mgChl-a m^{-3} for the same years. The average ratio of chlorophyll concentrations during the growing season in our area, compared to that of Arrigo & van Dijken (2007), is 0.42. We assume that the same ratio is applicable to primary production due to differences in phytoplankton biomass between the two areas. The ratio is less than unity due to the choice of study area: our area encompasses a relatively large area of the less productive waters to the north, whereas many modelling studies focus solely on the more productive waters of the southern Ross Sea. Hence, we estimate an annual net primary production for our study area of approximately 85 gC m^{-2} y^{-1} (43–71 gC m^{-2} y^{-1}). Our seasonal estimates are shown in Figure 2. Sweeney et al. (2000) give 35–80 gC m^{-2} y^{-1} for the smaller Ross Sea area bounded by the 1000 m isopleth. Smith et al. (2000) give an annual average value of 73 gC m^{-2} y^{-1} for the central part of the Ross Sea shelf. Nelson et al. (1996) used in situ data from a number of seasons to estimate an annual primary production on the Ross Sea shelf of 142 gC m^{-2} y^{-1} but this is for only the high production shelf area.

Our value for phytoplankton production is equivalent to a phytoplankton P/B of 53 y^{-1}. The low value of this (c.f. 248 y^{-1} for subantarctic water: Bradford-Grieve et al. 2003) reflects the short growing season in the Ross Sea (full darkness for almost a quarter of the year), and seasonal reduction of ice-free water.

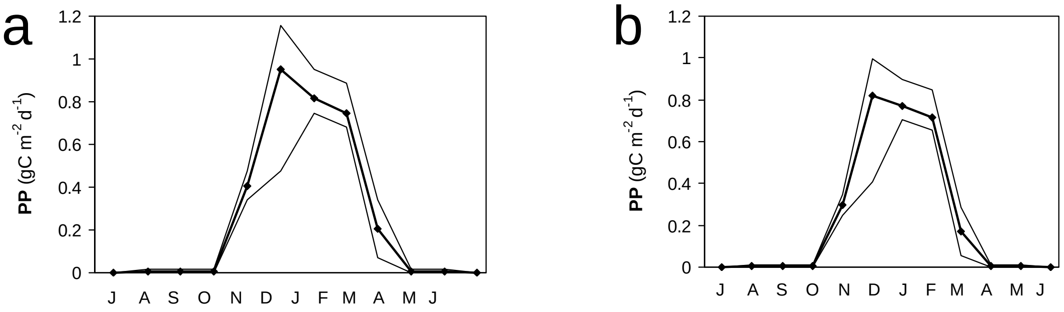

Figure 2. a: Average water column integrated net primary production for the study area. **b**: As (a) but taking into account variations in ice-free water over the year. The heavy centre lines indicate our best estimates of the values. The upper and lower lines indicate the approximate range of variation from year to year – see text for more details.

4 Ecotrophic efficiency

There is evidence that an unusually large proportion of the spring blooms of colonial *Phaeocystis antarctica* in the Ross Sea is ungrazed, sinking instead to the sea floor (Smith et al. 2003a, b). The evidence hence suggests an ecotrophic efficiency for phytoplankton significantly less than unity. Here, ecotrophic efficiciency (*E*) for phytoplankton in the Ross Sea is initially set to 0.50 following inverse modelling work (Ducklow et al. 2006) based on the November 1997 JGOFS research voyage to the region. Ducklow et al. (2006) concludes that sinking of ungrazed phytoplankton was high (0.5) in the Ross Sea.

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