

QUANTIFICATION OF SOUTHERN OCEAN PHYTOPLANKTON BIOMASS AND PRIMARY PRODUCTIVITY VIA SATELLITE OBSERVATIONS AND BIOGEOCHEMICAL MODELS

P.G. Strutton

Institute for Marine and Antarctic Studies
University of Tasmania
Private Bag 129
Hobart, Tasmania 7001
Australia

Email – peter.strutton@utas.edu.au

and

Australian Research Council Centre of Excellence
for Climate System Science

N.S. Lovenduski

Department of Atmospheric and Oceanic Sciences
University of Colorado
Campus Box 450,
Boulder, CO 80309, USA

M. Mongin and R. Matear

CSIRO Marine and Atmospheric Research
GPO Box 1538
Hobart, Tasmania 7001
Australia

Abstract

This paper reviews Southern Ocean primary productivity within the framework of satellite remote sensing and the development of food-web models. The satellite ocean colour (chlorophyll) data record is described, from the Coastal Zone Colour Scanner (CZCS) in the late 1970s through to the Ocean Colour and Temperature Scanner (OCTS), the Sea-viewing, Wide Field of view Sensor (SeaWiFS), the Moderate Resolution Imaging Spectroradiometer (MODIS) and the Medium Resolution Imaging Spectrometer (MERIS). The characteristics of these data and limitations, such as cloud cover and high solar zenith angle, are discussed with regard to their use in the Southern Ocean. A brief history of algorithms linking ocean colour to primary productivity is presented, focusing on the vertically generalised production model (VGPM) and more recent regional approaches. Using monthly climatologies of SeaWiFS chlorophyll, a phenology of phytoplankton blooms is presented for the major provinces surrounding Antarctica. Some of the published information regarding phytoplankton species composition and succession is summarised. A review of ecosystem and biogeochemical models for the Southern Ocean is presented, with a focus on those models that have been validated using satellite ocean colour data.

Introduction

Oceanic primary productivity supports food webs and contributes to the sequestration of carbon into the oceanic reservoir. The Southern Ocean (here mostly defined as south of 50°S) is a vast province with significant spatial and temporal variability in primary productivity. It is also the region of the global ocean where models and observations of air–sea CO₂ exchange differ most significantly, both in sign and magnitude (Gruber et al., 2009). This disagreement highlights the importance

of obtaining better estimates of all terms in the oceanic carbon budget, including primary productivity. In this paper, satellite and modelling techniques to estimate phytoplankton biomass and primary productivity in the Southern Ocean are reviewed.

The motivation for satellite productivity algorithm development comes at least in part from the two- to three-fold discrepancy between large-scale geochemical and more localised biological estimates of global primary productivity (Jenkins, 1988; Falkowski et al.,

1991). This field has developed by applying photosynthesis models, which relate primary productivity to light and chlorophyll, to satellite observations (Behrenfeld and Falkowski, 1997a; Schlitzer, 2002). More recently, Behrenfeld et al. (2005) proposed productivity models based on satellite carbon estimates, instead of chlorophyll. Satellite productivity algorithms are reviewed, then the phenology of Southern Ocean primary productivity is described. A summary of what is known about community composition and succession during Antarctic blooms, and a survey of some recent biogeochemical models of the Southern Ocean are provided. Future challenges for the field are discussed in conclusion.

Satellite ocean colour data and primary productivity algorithms

The term ‘ocean colour’ is used to describe satellite radiometric measurements in the visible spectrum, from which optical properties of the ocean are calculated. The main derived parameter of interest is chlorophyll concentration, as an index of phytoplankton biomass and precursor to primary productivity. Table 1 lists some of the properties of specific ocean colour sensors. Figures 1 and 2 show the Austral summer climatologies of pigment concentrations from the Coastal Zone Colour Scanner (CZCS) and the Sea-viewing, Wide Field of view Sensor (SeaWiFS). The products column of Table 1 focuses on chlorophyll, but the range of products is continually expanding. For example, for SeaWiFS and the Moderate Resolution Imaging Spectroradiometer (MODIS), NASA now disseminates particulate organic (POC) and inorganic carbon (PIC), photosynthetically available radiation (PAR), and a coloured dissolved organic matter (CDOM) index, among other products. MODIS and the Medium Resolution Imaging Spectrometer (MERIS) were specifically designed to provide a fluorescence channel as an indicator of phytoplankton physiology (Figure 3).

Throughout much of the literature, the terms ‘model’ and ‘algorithm’ are used interchangeably to refer to an equation or collection of equations that use chlorophyll (ocean colour) data and other inputs to calculate primary productivity, usually in units of mmolC m^{-2} or mgC m^{-2} per unit time (day or year). In this review, the term ‘model’ is reserved for biogeochemical simulations, and ‘algorithm’ is used to refer to (systems of) equations for deriving primary productivity.

The motivation for the development of a satellite algorithm stems from the global coverage afforded by satellite ocean colour data. Thousands of ^{14}C measurements of primary productivity have been made, and continue to be made, but they do not accurately scale to global totals (Jenkins, 1982, 1988; Falkowski et al., 1991). To achieve the most accurate possible picture

of global primary productivity, considerable effort has been directed towards the development of algorithms that take (surface) satellite data and (perhaps climatological) physical inputs, and provide integrated primary productivity as the output. This not only permits quantification of the global distribution of primary productivity, but also temporal changes at time scales from days to decades (e.g. Behrenfeld et al., 2006). The latter is one of the stated goals of NASA’s Ocean Biology and Biogeochemistry Program.

In general, ocean colour productivity algorithms are striving for daily, depth-integrated phytoplankton carbon fixation (PP_{eu} , where the subscript refers to the euphotic zone, typically defined as the 1% light level) as a function of satellite-based chlorophyll (C_{sat}). The earliest productivity algorithms parameterised PP_{eu} as some polynomial function of C_{sat} (Smith et al., 1982; Eppley et al., 1985). The next level of complexity was to add a dependence on the light field, that is $PP = f(\text{depth-integrated chlorophyll, daily PAR, constant})$, where the constant is the water-column-averaged quantum yield of photosynthesis (Morel, 1978; Falkowski, 1981; Platt, 1986; Morel, 1991). More recent algorithms have included the effects of photoadaptation (Balch et al., 1992) and spectral dependence (e.g. Platt, 1986; Morel, 1991). The latter accounts for the differential attenuation of wavelengths with depth in the water column, as well as variability in phytoplankton physiology (the photosynthesis vs irradiance parameters α , P_{max} and β ; Sakshaug et al. (1997)). It is probably fair to say that it is not yet clear how much the algorithms benefit from this added complexity.

In 1997, Behrenfeld and Falkowski developed what became known as the vertically generalised production model (VGPM; Behrenfeld and Falkowski, 1997b). The VGPM was validated using more than 11 000 global ^{14}C -based measurements of primary productivity, but coverage in the Southern Ocean was poor with less than a few hundred measurements. This algorithm’s key parameter is P_{opt}^B , the maximum level of biomass-normalised C fixation rate, in units of $\text{mgC (mg Chl)}^{-1} \text{hr}^{-1}$. It is a physiological parameter and is at least partially related to temperature, but Behrenfeld and Falkowski’s (1997b) relationship between P_{opt}^B and sea-surface temperature (SST) had error bars of about $\pm 100\%$ (their Figure 7). So, P_{opt}^B is crucial to the VGPM, but it is also the parameter with the most uncertainty. The algorithm also uses D_{irr} (photoperiod), C_{opt} (chlorophyll at the depth of P_{opt}^B), E_0 (daily PAR), and Z_{eu} (euphotic zone depth). D_{irr} can be accurately calculated based on location and day of year, C_{opt} can be fairly well estimated by C_{sat} (Behrenfeld and Falkowski, 1997b; their Figure 6), and the last two parameters (E_0 and Z_{eu}) are essentially disseminated by NASA, the latter as the diffuse attenuation coefficient at 490 nm, which may not describe Z_{eu} well where deep chlorophyll maxima occur.

Table 1: Summary of sensors, spatial resolution, mission dates, products relevant to this report and accuracy. The accuracy is defined as the median % difference between the satellite-derived and in situ estimates of chlorophyll. The sample size is larger for the Sea-viewing, Wide Field of view Sensor (SeaWiFS) because the database (<http://seabass.gsfc.nasa.gov>) was designed for the SeaWiFS era. The values reported here are for chlorophyll measured fluorometrically. For the high-performance liquid chromatography (HPLC) chlorophyll, the accuracy values are better (lower by as much as 12%) for each sensor, but the sample size is smaller. CZCS – Coastal Zone Colour Scanner; OCTS – Ocean Colour and Temperature Scanner; MODIS Aqua – Moderate Resolution Imaging Spectroradiometer; MERIS – Medium Resolution Imaging Spectrometer.

Sensor	Spatial resolution (km)	Mission dates	Chlorophyll-relevant products	Accuracy
CZCS	4	October 1978 to June 1986	pigment	61%, $n = 15$
OCTS	9	August 1996 to July 1997	chlorophyll- <i>a</i>	21%, $n = 17$
SeaWiFS	9	September 1997 to December 2010	chlorophyll- <i>a</i>	40%, $n = 1515$
MODIS Aqua	4 and 9	May 2002 to present	chlorophyll- <i>a</i> , fluorescence	44%, $n = 295$ for chlorophyll- <i>a</i>
MERIS	0.3	March 2002 to April 2012	chlorophyll- <i>a</i> , fluorescence	unknown

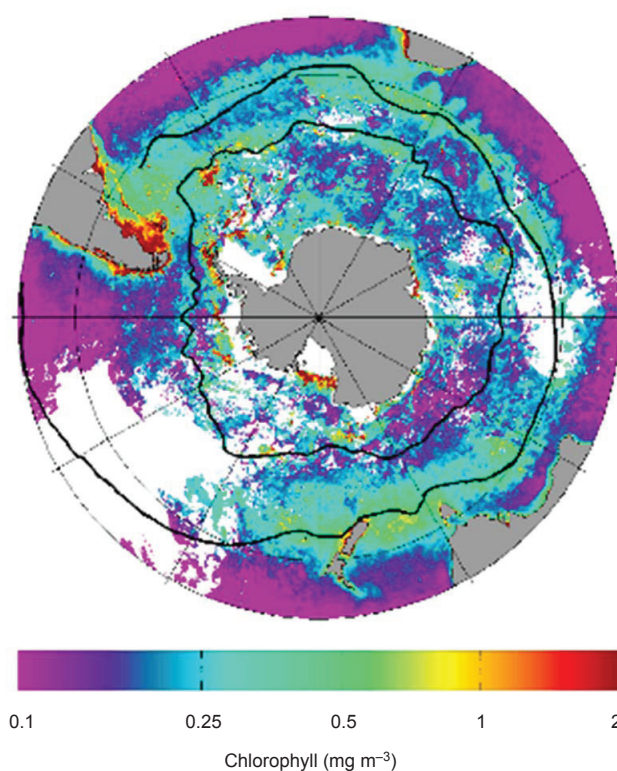


Figure 1: Austral summer ocean pigment concentrations from the Coastal Zone Colour Scanner (CZCS). The data are available at 4 km and 9 km (this image) spatial resolution. In all figures of this type, the northern and southern solid lines represent the subtropical front and the polar front respectively.

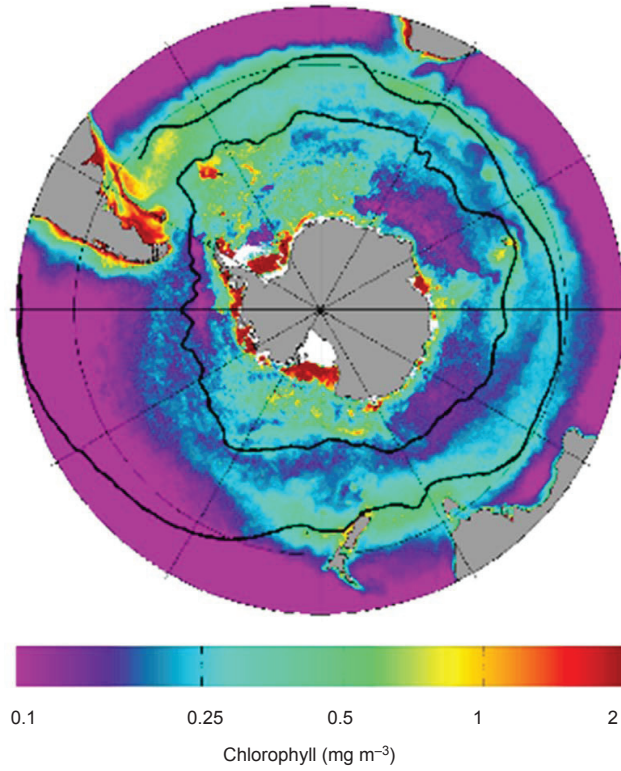


Figure 2: The Sea-viewing, Wide Field of view Sensor (SeaWiFS) Austral summer chlorophyll climatology.

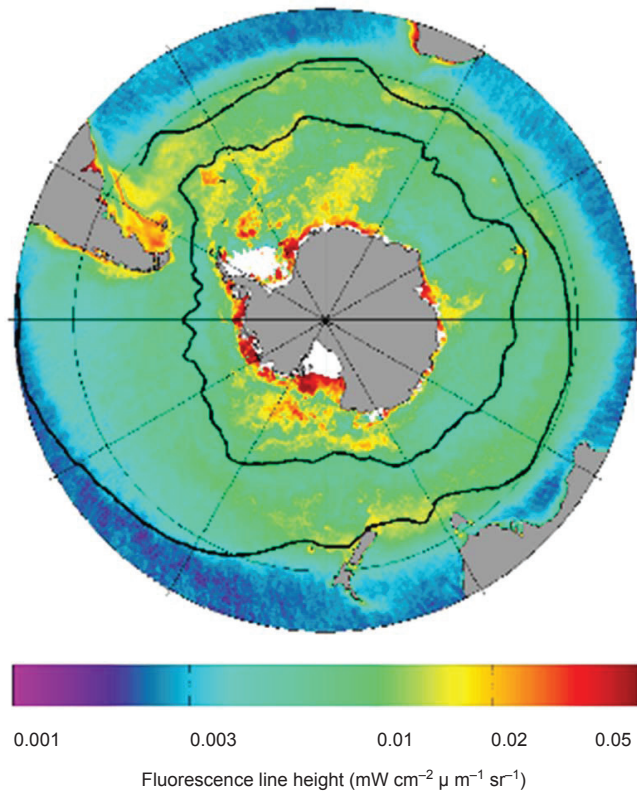


Figure 3: The Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua seasonal mean Fluorescence Line Height (FLH) for Austral summer 2007/08.

Despite the limitations of the VGPM imposed by the large errors in P^B_{opt} , it has become highly regarded because it works reasonably well in many places of interest to the community (although see discussion next paragraph) and its products are readily available. Behrenfeld and Falkowski (1997b) used it to arrive at a mean global annual phytoplankton carbon fixation of 43.5 GtC (43.5×10^{15} gC).

The development of productivity algorithms by the global oceanographic community continues. To evaluate the performance of the current range of techniques, Carr et al. (2006) compared the output of 31 satellite algorithms and biogeochemical models. When validated with observations, most of the algorithms did well in comparison with the data that were used to generate them, but did not compare well with other data. That is, many of the algorithms to date have been developed based on data from a relatively small region. If these algorithms are then applied globally, they do poorly in places where the physics, physiology or seasonal cycle are different from the region of input data. Some of the discrepancies may even be due to differences in the methods used to collect the data. Carr et al. (2006) found the largest discrepancies among the group of 31 algorithms/models in the Southern Ocean (and more generally for SST < 10°C and chlorophyll > 1 mg m⁻³). The Southern Ocean is likely particularly challenging because of spatial and temporal heterogeneity, the vast area and a lack of observations. They concluded that high-nutrient low-chlorophyll provinces (such as the Southern Ocean) are more difficult to accurately model, and that future progress in both satellite algorithms and biogeochemical models will require improved parameterisation of photosynthesis, including better understanding of the effect of temperature.

In an attempt to avoid the issues of the highly variable and uncertain parameters required in the VPGM class of algorithms, Behrenfeld et al. (2005) employed a new approach: a carbon-based, rather than a pigment-based, perspective. The premise here is that productivity algorithms are developed to derive C fixation, but satellites have to date mostly measured chlorophyll, so algorithms relate chlorophyll and phytoplankton physiology to light and then estimate net primary production (NPP). However, the carbon to chlorophyll ratio of phytoplankton (C: chlorophyll) is relatively well-parameterised in terms of changes due to nutrients and light (Geider, 1987). Therefore, if it is possible to quantify C: chlorophyll from remotely sensed and climatological data, it should also be possible to better represent the physiological status of phytoplankton, and use this information in NPP algorithms. Right now, mostly as a result of a limited in situ data foundation from which to work, this C-based class of algorithms is poorly constrained for the Southern Ocean, so they will not be discussed further.

In the section that follows, the application of several algorithms to derive estimates of Southern Ocean productivity will be described. In a global context, there are significant differences in both the spatial and temporal distribution of NPP between the algorithms. Improved parameterisations of algal physiology, and more advanced satellite ocean colour products (for example, no current productivity algorithms take into account satellite-measured fluorescence), may help this field to progress.

Application of satellite algorithms to derive Southern Ocean productivity

Satellite productivity algorithms have been applied to the Southern Ocean to derive (i) mean (per unit area) or total (spatially integrated) annual productivity estimates for the entire ocean, (ii) estimates of the productivity in subregions and (iii) measures of interannual variability in productivity. Here some of the work in this area is summarised and reasons for differences in the estimates are highlighted.

As described under ‘Satellite ocean colour data and primary productivity algorithms’, Figure 1 and Table 1, the spatial and temporal coverage of CZCS data in the Southern Ocean is poor. Nonetheless, until SeaWiFS, it remained the only satellite ocean color data product available. Arrigo et al. (1998) employed monthly climatological CZCS data with a regionally tuned Southern Ocean algorithm that was parameterised by irradiance, temperature, nutrients (nitrate or silicic acid) and chlorophyll. One of the most significant differences between this model and the VGPM is that it incorporated *spectral* attenuation of irradiance (Gregg and Carder, 1990). Nutrient and light limitation were incorporated via a resource limitation term. Light, and therefore light limitation, varied with depth, but nutrient limitation did not – it was parameterised according to annual climatological nutrients (Levitus et al., 1993) and a Monod nutrient uptake formulation. Primary productivity was set by the most limiting term. A correction was applied to the CZCS pigment data to account for the known issue of underestimation (Sullivan et al., 1993). Annual Southern Ocean primary productivity was estimated to be 4.41 GtC yr⁻¹, four to five times higher than estimates that had been made previously based on accumulated in situ observations. This new higher estimate was suggested as reconciling a paradox, in that previous productivity estimates were too low to support Southern Ocean grazers, including the keystone krill. Arrigo et al. (1998) were also probably the first of several subsequent authors to point out that the high productivity in the marginal ice zone contributes little to the overall Southern Ocean productivity, because the open ocean region is so much larger, although lower in productivity.

Probably the first paper to use SeaWiFS data to document mostly spatial variability in Southern Ocean chlorophyll and productivity (using the VGPM) was Moore and Abbott (2000). They identified three main regions of enhanced chlorophyll and productivity: the shelves/coasts, the marginal ice zone and open-ocean fronts. Their one-year time series of productivity confirmed that while the per unit area productivity might be high in these regions, their small spatial extent means that they contribute the least to overall Southern Ocean productivity. In fact, the highest monthly productivity number they calculated (based only on one year of data, 1997/98) was in their combined Weddell–Ross Sea region. They calculated Southern Ocean productivity (>50°S) to be 2.85 GtC yr⁻¹. This was almost identical to a version of the VGPM using corrected CZCS pigments, as Arrigo et al. (1998) used in their model. In an interesting validation, which few, if any, other papers emulated, they proposed that their estimated productivity was consistent with the seasonal cycle of southern hemisphere atmospheric O₂ (Bender et al., 1996).

As the time period of the SeaWiFS dataset increased, the focus of basin-scale productivity papers turned to interannual variability. Smith and Comiso (2008), using the VGPM, documented some aspects of spatial variability, noting that the shelves were the areas of highest productivity, and no sustained blooms occurred in waters deeper than 1 000 m. This last statement is curious, and may depend on each author's definition of a bloom; sustained, elevated chlorophyll concentrations do occur in the lee of small land masses in the Southern Ocean, such as Kerguelen Island (Blain et al., 2007). Nonetheless, Smith and Comiso (2008) observed a trend of increasing annual primary productivity, mostly in January and February, but did not offer a reason for the increase. Their mean annual rate of primary productivity was 23.65 gC m⁻² yr⁻¹, which is difficult to compare with other estimates in Table 2 (below), because their spatial area of interest was south of 60°S, not 50°S as for Arrigo et al. (1998) and Moore and Abbott (2000). If all calculations were converted to a per unit area estimate, the Smith and Comiso (2008) number would be one-quarter to one-third of the Arrigo et al. (1998) and Moore and Abbott (2000) estimates respectively. Smith and Comiso (2008) suggested that, compared to previous studies, their estimate was likely the most accurate to date because it used multiple years (1997 to 2005) of higher quality (SeaWiFS vs CZCS) ocean colour data.

Arrigo et al. (2008), in contrast to Smith and Comiso (2008), did not observe any secular trend in either ice coverage or primary productivity from 1997 to 2006. Their mean annual productivity estimate for the Southern Ocean was 1.95 GtC yr⁻¹, less than half of their previous estimate of 4.41 GtC yr⁻¹ based on a similar algorithm but with CZCS data (Arrigo et al., 1998).

What could be responsible for two studies, examining almost the same time period, finding a secular trend in productivity (Smith and Comiso, 2008) or not (Arrigo et al., 2008)? The most likely difference is the latitudinal scope of the calculations. Smith and Comiso (2008) were focused on the influence of sea-ice and so considered waters south of 60°S, whereas the northern boundary was 50°S for Arrigo et al. (2008). The former did not investigate the influence of the Southern Annular Mode (SAM) on their productivity time series but Arrigo et al. (2008) did. The correlation between the SAM and productivity (and chlorophyll) was positive but not significant at the 95% confidence level. The SAM accounted for only 31% of the variability in annual productivity. Using a shorter time series (1997–2004), Lovenduski and Gruber (2005) showed that the recent, predominantly positive, phase of the SAM was associated with a poleward contraction and strengthening of the circumpolar westerly winds, cool SST anomalies and positive chlorophyll anomalies, mostly south of 60°S. North of 60°S, the positive phase of the SAM is associated with negative chlorophyll anomalies centred around 45°S. By considering only south of 60°S, Smith and Comiso (2008) would have observed mostly the positive chlorophyll anomalies, but Arrigo et al. (2008) would have incorporated the region where the sign of the SAM–chlorophyll correlation changes, hence the weaker positive correlation.

Table 2 summarises the methods and results of the four Southern Ocean productivity studies discussed above (Arrigo et al., 1998; Moore and Abbott, 2000; Arrigo et al., 2008; Smith and Comiso, 2008). As the time series of satellite chlorophyll observations increases in length, it is becoming possible to better quantify trends, and attribute those trends to changes in physical forcing such as sea-ice or winds. To date the focus has been on identifying temporal trends, with some attention to temporal variability in certain subregions such as the Ross and Weddell Seas. The next frontier is a rigorous assessment of both spatial and temporal trends for the entire Southern Ocean.

The phenology of Southern Ocean primary productivity

The phenology of Southern Ocean productivity is relevant for understanding air–sea CO₂ exchange and the impacts on higher trophic levels, in particular krill. To gain some insight into the spatial and temporal variability of Southern Ocean productivity, monthly climatological maps of SeaWiFS chlorophyll during the Austral summer are presented (Figures 4 to 7), with some commentary regarding the seasonal cycle in prominent regions.

Table 2: Summary of the application of algorithms to derive mean annual Southern Ocean primary productivity (see ‘Application of satellite algorithms to derive Southern Ocean productivity’ in the text). Note different units and definition for what constitutes the Southern Ocean for Smith and Comiso (2008). CZCS – Coastal Zone Colour Scanner; SeaWiFS – Sea-viewing, Wide Field of view Sensor; VGPM – vertically generalised production model.

Authors	Region	Input data	Algorithm	Southern Ocean primary productivity
Arrigo et al. (1998)	>50°S	Corrected CZCS	Arrigo et al. (1998)	4.41 GtC yr ⁻¹
Moore and Abbott (2000)	>50°S	SeaWiFS	VGPM; Behrenfeld and Falkowski (1997b)	2.85 GtC yr ⁻¹
Smith and Comiso (2008)	>60°S	SeaWiFS	VGPM; Behrenfeld and Falkowski (1997b)	23.7 gC m ⁻² yr ⁻¹
Arrigo et al. (2008)	>50°S	SeaWiFS	Arrigo et al. (1998), modified	1.95 GtC yr ⁻¹

December (Figure 4): The Ross Sea bloom is intense (>2 mg m⁻³ chlorophyll) and separated by patchy ice from open ocean, less intense blooms to the north. Likewise, the Weddell Sea bloom is intense but patchy to the south and separated by sea-ice from a bloom trailing east off the northern tip of the Antarctic Peninsula. The Prydz Bay bloom is spatially small but ~2 mg m⁻³ (i.e. high biomass). Other coastal blooms are slightly separated from the coast, following retreating ice. Island wake blooms, such as South Georgia and Kerguelen, each span about 30° longitude.

January (Figure 5): The Ross Sea bloom is still intense, and oceanic blooms to the north are retreating south. The Weddell Sea bloom has expanded in the south, sea-ice is dissipating, and the bloom to the north, trailing off the peninsula, starts to contract. The Prydz Bay bloom is larger and more intense. Other coastal blooms are now closer to the coast. The South Georgia and Kerguelen blooms contract.

February (Figure 6): The Ross Sea bloom is declining but the southern Weddell Sea bloom is still large and intense. Sea-ice to the north of the Weddell Sea contracts, as does the trailing peninsula bloom. The Prydz Bay and other coastal blooms are in decline. The South Georgia bloom is smaller, as is the Kerguelen bloom, but the former is more intense.

March (Figure 7): Productivity begins to decline into winter. The Ross Sea bloom is absent and the Weddell Sea blooms are much reduced as new sea-ice forms. The Prydz Bay bloom contracts further and other coastal blooms are almost absent. The South Georgia bloom shrinks further and the Kerguelen bloom is minimal.

Antarctic phytoplankton community composition and species succession

East Antarctica: Cosmonaut Sea to Prydz Bay

In the Austral summer of 2005/06, an interdisciplinary survey was conducted of East Antarctica (30°E to 80°E). The suite of measurements included physical oceanography, primary productivity and phytoplankton species composition, krill biology and seabird and marine mammal distributions. Wright et al. (2010) used analysis of HPLC pigments to describe the phytoplankton community structure. Similar to the BROKE 1996 survey (see below) they observed differences in the phytoplankton communities separated by the southern boundary of the Antarctic Circumpolar Current (ACC). South of the southern boundary, there existed a dense bloom near the sea-ice, including both pelagic cells and cells released from melting ice. The bloom consisted of *Phaeocystis antarctica*, diatoms and cryptophytes. Chlorophyll inventories as high as 239 mg m⁻² were observed, declining to less than 100 mg m⁻² as large aggregates from sea-ice sunk out. One interesting aspect of this work was the evidence for grazing (presumably dominated by krill) in the pigment data. It was shown that an increase then decrease in *P. antarctica* following the disappearance of sea-ice was accompanied by increases in phaeophytin *a* and phaeophorbide *a*, which were interpreted as degradation products from grazing. This grazing and export (of fecal pellets) by krill swarms migrating south with the ice retreat was hypothesised to efficiently remove iron and carbon from the upper water column.

North of the productivity surrounding the retreating ice, nanoflagellates (haptophytes, dinoflagellates, prasinophytes and cryptophytes) dominated a subsurface peak (50–100 m) in biomass, with column-integrated chlorophyll inventories less than 50 mg m⁻². The hypothesis regarding phytoplankton productivity that emerged from

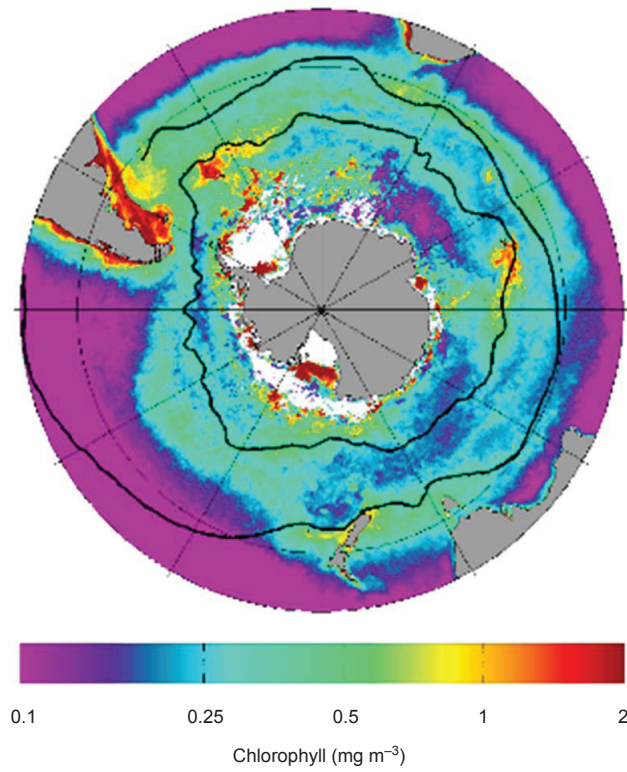


Figure 4: Climatological December chlorophyll for the Southern Ocean from the Sea-viewing, Wide Field of view Sensor (SeaWiFS).

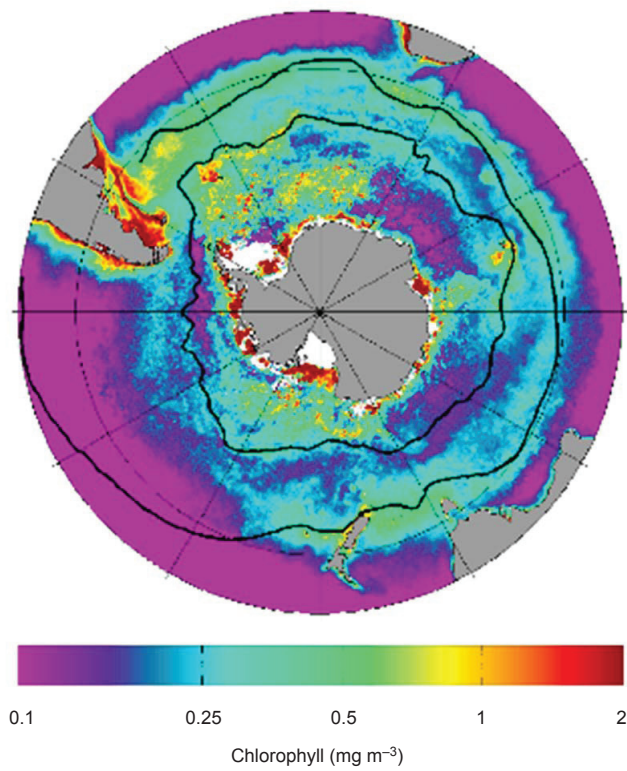


Figure 5: Climatological January chlorophyll for the Southern Ocean from the Sea-viewing, Wide Field of view Sensor (SeaWiFS).

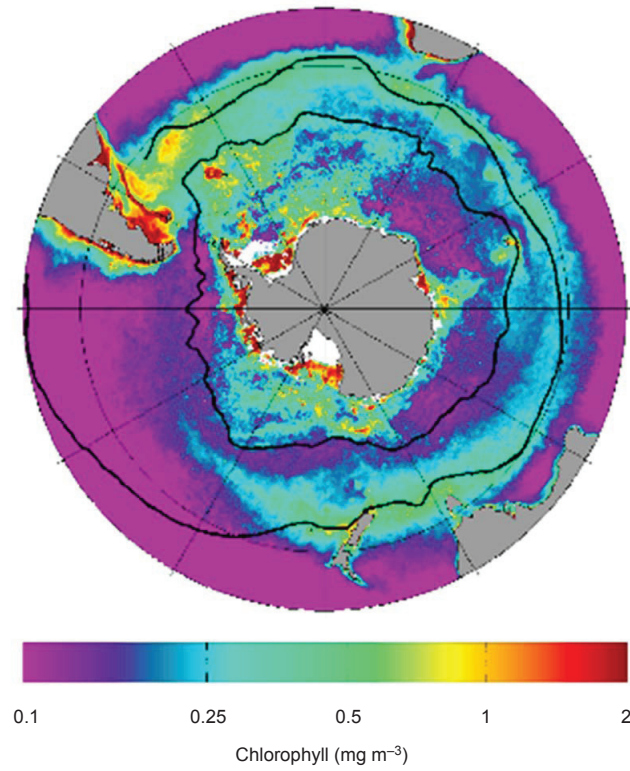


Figure 6: Climatological February chlorophyll for the Southern Ocean from the Sea-viewing, Wide Field of view Sensor (SeaWiFS).

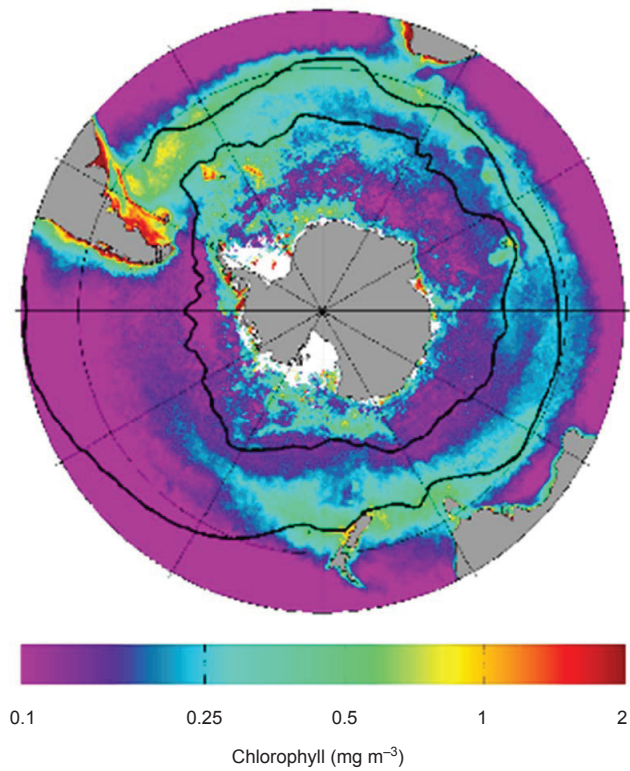


Figure 7: Climatological March chlorophyll for the Southern Ocean from the Sea-viewing, Wide Field of view Sensor (SeaWiFS).

this work is that iron is released from melting sea-ice (e.g. Sedwick and DiTullio, 1997) and fuels an intense bloom of *P. antarctica*, which is effectively grazed by krill. Later in the season to the north of the ice edge, a subsurface biomass maximum develops, possibly sustained by iron mixed towards the surface from below.

East Antarctica: Prydz Bay to Ross Sea

Across the region of Antarctic coastline south of Australia, the meridional extent of the ACC varies with longitude. It is closer to the coast in the east, near the Ross Sea, compared to the west, near Prydz Bay. During the BROKE survey in 1996 (Nicol et al., 2000a) the waters south of the southern boundary of the ACC were found to be dominated by diatoms (Waters et al., 2000) and characterised by higher productivity (Strutton et al., 2000), compared to the waters north of the southern boundary of the ACC (SBACC), which had low productivity and were picoplankton dominated. These observations and their impact on higher trophic levels are summarised in Nicol et al. (2000b). The waters south of the SBACC are more productive, diatom and krill dominated, with higher marine mammal and seabird abundance, compared to the waters north of the SBACC that are picoplankton/salp dominated with lower abundance at higher trophic levels.

The Ross Sea

The US Southern Ocean Joint Global Ocean Flux Study (JGOFS) program (Smith et al., 2000) extensively surveyed the biogeochemistry and ecology of the Ross Sea and the open ocean region to the north in the late 1990s. Selph et al. (2001), based on observations well north of the Ross Sea relatively early in the season (December), proposed a seasonal succession in the phytoplankton community. North of the retreating ice edge, centric diatoms dominated the community, while at the ice edge, *P. antarctica* was dominant. It was proposed that *P. antarctica* was characteristic of a younger, nascent bloom, immediately after ice melt and before vertical mixing of Si, while the diatoms represented the mature bloom after ice-free water has been sufficiently mixed. There has also been extensive work documenting the southward progression of the diatom bloom in association with depletion of abundant silicic acid (Hiscock et al., 2003). This gradient in silicon was central to the site selection for iron fertilisation during the Southern Ocean Iron Experiment (SOFeX) (Coale et al., 2004) and suggests that, as diatoms deplete silicic acid in the wake of retreating ice, non-silicified phytoplankton (flagellates) become dominant, such as at the SOFeX northern patch (Coale et al., 2004).

The progression of blooms from *P. antarctica* to diatoms is also observed in the Ross Sea itself, not just to the

north along the Southern Ocean JGOFS line. Here, dense *P. antarctica* blooms occur in poorly stratified waters north of the Ross Ice Shelf (Arrigo et al., 2000). Satellite data analysis suggests that these blooms regularly occur in late October or early November, and generally decline around mid-December (Arrigo and McClain, 1994). In December and January, diatom blooms occur in the strongly stratified western Ross Sea (Arrigo et al., 2000). Arrigo et al. (1998) suggested that these blooms cannot occur any earlier than they do because of wind mixing in Terra Nova Bay, which is eventually mitigated by solar heating and melting sea-ice. The lack of overlap, both spatial and temporal, between *P. antarctica* and diatoms was offered by Arrigo et al. (2000) as evidence for a physical, as opposed to a biological, succession mechanism for the separation of the two groups.

West Antarctic Peninsula

Prezelin et al. (2004) documented the importance of nutrient-rich upper circumpolar deep water (UCDW) intrusions onto the shelf of the west Antarctic Peninsula for stimulating diatom blooms. They proposed that when the SBACC flows along the boundary of the shelf, intrusions of UCDW are either upwelled onto the shelf, or mixed into the euphotic zone. When this occurs, diatoms bloom and NPP increases, and conversely, when there is no UCDW supply, diatom blooms are absent. This variability in diatom biomass reveals a clear link between physical forcing, productivity and phytoplankton community composition. Any process that alters the path or strength of the ACC, such as the SAM or changes in large-scale winds, will clearly modulate these UCDW intrusions with consequences for west Antarctic Peninsula productivity.

Biogeochemical models of the Southern Ocean

The previous algorithm discussion could be considered as one type of model, but ‘modelling’, as the term is most commonly used, represents another approach to explore biological–physical interactions and provide estimates of phytoplankton biomass, composition and NPP to link to higher trophic levels. The scale of common current models ranges from global 3-D to regional 3-D to 1-D. All three modelling scales have advantages and disadvantages. The following discussion reviews the present status of ocean models with respect to simulations of Southern Ocean NPP.

Global ocean circulation models coupled to a biogeochemical/ecosystem model

There exist a number of global numerical ocean general circulation models with incorporated

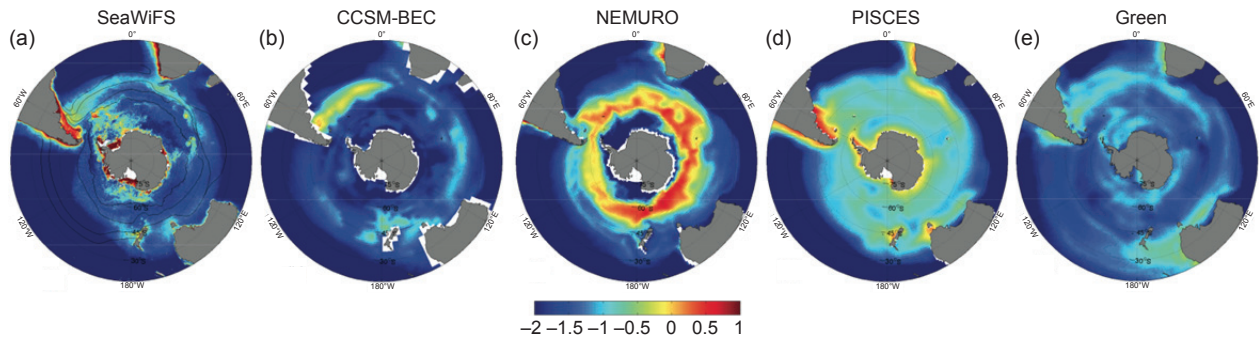


Figure 8: Annual-mean surface chlorophyll concentration ($\ln(\text{mg m}^{-3})$) from (a) the Sea-viewing, Wide Field of view Sensor (SeaWiFS), (b) the Community Climate System Model-Biogeochemical Elemental Cycling (CCSM-BEC) (Lovenduski et al., 2007), (c) the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) (Aita et al., 2006), (d) the Pelagic Integration Scheme for Carbon and Ecosystem studies (PISCES) (Aumont and Bopp, 2006), and (e) the Plankton Types Ocean Model/Dynamic Green Ocean Model (PlankTOM/DGOM) (Vogt et al., 2010). Model output represents the year 2006 (M. Vogt, pers. comm.)

biogeochemical/ecosystem components, which range in complexity from those with very simple parameterisations to those with multiple phytoplankton classes and complex parameterisations. The attraction of this modelling technique is that it provides a basin-scale approach to explore the biological–physical interactions. However, given the computational demands, the ability to replicate the complexity of the biological system is generally limited and the spatial resolution of the physics is not eddy-resolving.

Validation of these models is facilitated by the model-predicted surface chlorophyll field, which can be directly compared to the satellite record. Figure 8 shows a direct satellite-model comparison of surface chlorophyll in the Southern Ocean. The model output shown here was provided by the MARine Ecosystem Model Intercomparison Project (MAREMIP) (M. Vogt, pers. comm.), which aims to foster the development of models based on plankton functional types. This figure demonstrates that these models vastly differ in their estimates of surface chlorophyll concentration in the Southern Ocean. Furthermore, model estimates misrepresent both the magnitude and the spatial pattern of observed chlorophyll concentration in the Southern Ocean. These models vary greatly in their Southern Ocean mixed layer depths, often by as much as 100 m (M. Vogt, pers. comm.), and suffer from fairly coarse horizontal resolution. This chlorophyll inconsistency makes it difficult to justify the use of such a model for studies of Southern Ocean biological variability and trends, but considerable effort continues to be invested in the improvement of these models.

Models of physical/biogeochemical/ecological interactions at regional scale

Regional-scale models of provinces within the Southern Ocean, e.g. the Ross Sea or Antarctic Environment

and Southern Ocean Process Study (AESOPS) experimental area, have been successfully used to assess variability and trends in biological production. While regional models require information for their open ocean boundaries, their limited spatial extent permits the incorporation of fairly complex biological parameterisations and the simulation of phytoplankton taxa that are specific to the area of interest, e.g. *P. antarctica* in the Ross Sea. These models often explicitly predict surface chlorophyll and depth-integrated NPP and can therefore be validated against SeaWiFS estimates of chlorophyll and NPP algorithms. Figure 9 shows a comparison of annual primary production in the southwestern Ross Sea generated by the Coupled Ice Atmosphere Ocean (CIAO) model described in Arrigo and Van Dijken (2007) and a SeaWiFS-derived estimate. This figure demonstrates that the modelled estimates of production are within 20% of those obtained with satellite observations, indicating that biogeochemical models of the Southern Ocean on regional scales are producing realistic results (bearing in mind the errors associated with satellite algorithms) and providing a promising approach for understanding the variability and trends in Southern Ocean biology.

One-dimensional physical and biogeochemical models

Most of these models deal with the control of primary productivity in the Southern Ocean and the sensitivity to changes in nutrient supply, grazing pressure and light conditions. These models are suited to explore complex processes to improve our mechanistic understanding, rather than to provide realistic simulations of the Southern Ocean phytoplankton.

An example of the ‘classical’ biogeochemical framework used by many models is two classes of phytoplankton, diatoms and non-diatoms, two size classes of zooplankton, where the larger size fraction is able

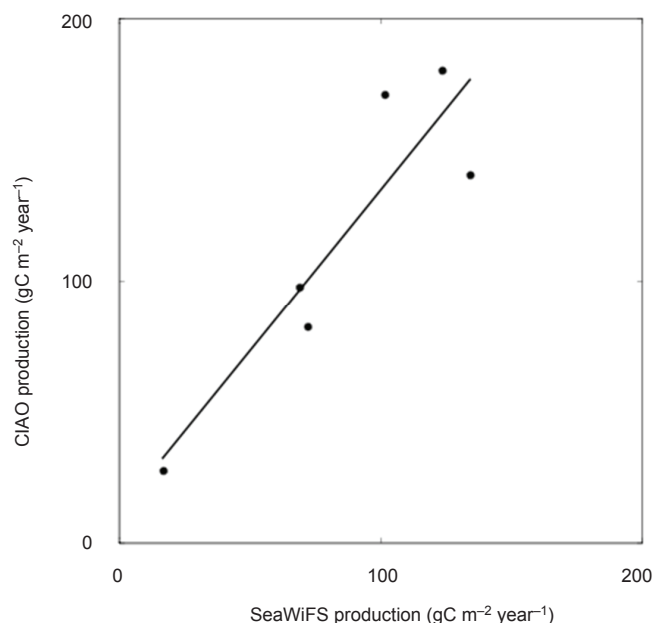


Figure 9: Comparing estimates of annual primary production in the southwestern Ross Sea generated by both the Coupled Ice Atmosphere Ocean (CIAO) model and independently using a productivity model that utilises the Sea-viewing, Wide Field of view Sensor (SeaWiFS) data as input. Note the close match in the modelled and observed estimates for each of the six years (1997–2003). Adapted from Arrigo and Van Dijken (2007). The linear fit is described by $y = 1.23x + 10.1$, $r^2 = 0.82$.

to graze both small zooplankton and phytoplankton, two detrital classes and cycling of carbon, nitrogen and silicon (Pondaven et al., 1998, 2000). Without iron, the Southern Ocean High Nitrate Low Chlorophyll (HNLC) condition was reproduced by artificially increasing the maximum grazing rate. This relatively simple model is able to capture most of the interannual variability in primary productivity, mostly due to variability in the mixed layer depth generated by the wind field.

Pasquer et al. (2005) used the Sea Water Microbial Community (SWAMCO-4) model (Lancelot et al., 2000; Hannon et al., 2001; Pasquer et al., 2005). The model explicitly described the processes driving the structure of a planktonic ecosystem composed of four taxonomic phytoplankton groups – diatoms, pico/nanophytoplankton, *P. antarctica* and coccolithophorids – and their forcing functions. Pasquer et al. (2005) presented the cross-application of this complex 1-D mechanistic ecosystem model in three oceanic provinces with contrasting key species dominances, and associated carbon fluxes, and evaluated its performance in reproducing the main regional characteristics (taxon dominance, primary production, export and air–sea CO₂ fluxes).

Mongin et al. (2006) used a non-Redfield biogeochemical model, including iron and more realistic grazing rates compared to Pondaven et al. (2000), who used up to 10 d⁻¹. Nutrient limitation, grazing, or light taken

alone could explain the HNLC conditions around the Kerguelen fixed time-series site (KERFIX, in the Indian Ocean sector of the Southern Ocean, 51°S 68°E, in the Permanently Open Ocean Zone (POOZ), just south of the Antarctic Polar Front). The KERFIX time-series shipboard observations revealed that C/N was slightly lower than Redfield due to iron and light co-limitation. Mongin et al. (2007) used the same model as in Mongin et al. (2006) to test the effects of dust input and mixed-layer depth. When aeolian Fe input was increased by a factor of 1 000 and mixed-layer depth was reduced at the same time, export of carbon increased by a factor of three. Light limitation prevented complete drawdown of nitrate, even if Fe limitation was removed and mixed-layer depth reduced. This set an upper limit on the primary production that can be achieved under the present meteorological conditions in this sector of the Southern Ocean.

Fennel et al. (2003) used a model similar to Pondaven et al. (2000), with the addition of implicit iron limitation, by imposing low growth rate and high Si/N ratio to diatoms. This model captured the general distribution of chlorophyll and nutrient from subsystems, including the low chlorophyll condition north of the Polar Front, and diatom blooms in the vicinity of the Polar Front.

The Kerguelen Ocean and Plateau compared Study (KEOPS) program (Jan–Feb 2005) examined the

phytoplankton bloom that forms annually in the vicinity of the Kerguelen Plateau. Shipboard observations revealed that the phytoplankton bloom was triggered by enhanced natural iron input from subsurface waters (Blain et al., 2007). For the KEOPS project, Mongin et al. (2008) used a slightly modified version of the Mongin et al. (2006) model and applied it in a two-dimensional framework, including horizontal diffusion. The aim was to recalculate the carbon sequestration efficiency of the KEOPS project on a seasonal scale, and perform some sensitivity analysis of the horizontal mixing. For a three-fold increase in sub-surface iron concentration, the 1-D biogeochemical model reproduced the off-plateau and on-plateau seasonal chlorophyll cycles. The 1-D model exhibited similar carbon, nitrogen and silicon concentrations to the KEOPS observations, but differed dramatically in terms of estimated seasonal iron budget. The work in this region continues; a second KEOPS research voyage was completed in late 2011, the results of which will be incorporated in further modeling work.

Conclusions and future directions

The coalescence of satellite estimates of primary productivity and biogeochemical models is advancing our understanding of Southern Ocean primary productivity and food webs. If $\sim 45 \text{ GtC yr}^{-1}$ is considered as the best current estimate of oceanic primary productivity (Behrenfeld and Falkowski, 1997b; Falkowski et al., 1998), then the summary values presented in Table 2 suggest that the Southern Ocean contributes between 5% and 10% of the global total. Arrigo et al. (2008) divided the Southern Ocean into five sectors which roughly correspond to the CCAMLR Statistical Reporting Areas: The Weddell Sea sector (Area 48), the South Indian and Southwest Pacific (together Area 58) and the Ross/Bellingshausen/Amundsen Seas (Area 88). Acknowledging that these sectors differ in their total area, Area 88 contributes the most annual primary productivity (895 TgC yr^{-1}), followed by Area 58 (587 TgC yr^{-1}) and Area 48 (477 TgC yr^{-1}). When normalised to ocean area, the ranking changes such that Area 48 is the most productive ($70.3 \text{ gC m}^{-2} \text{ yr}^{-1}$) followed by Area 88 ($61.1 \text{ gC m}^{-2} \text{ yr}^{-1}$) and Area 58 ($46.3 \text{ gC m}^{-2} \text{ yr}^{-1}$).

Used in isolation, the satellite data, although heavily compromised by clouds, provide important insights into the timing and intensity of blooms. The phenology section of this paper would not have been possible based only on in situ measurements, thus illustrating the power of satellite observations. However, there are, of course, areas where significant improvements need to be made. Firstly, the accuracy of satellite estimates of chlorophyll, and by extension primary productivity, are particularly poor in high-latitude oceans. The Carr et al. (2006) review of satellite and biogeochemical model estimates of primary productivity identified the Southern Ocean as one of the regions of poorest success. This is at least in

part due to the low density of validation data for such a vast ocean province, and by extension, poor parameterisation of phytoplankton physiology at low temperatures. But Dierssen et al. (2000), working in moderate-to-high productivity waters off the Western Antarctic Peninsula, found that surface chlorophyll explained 84% of the variability in euphotic zone integrated chlorophyll, which in turn explained 64% of the variability in integrated primary productivity. Only incremental improvements in the accuracy of productivity estimates were achieved by incorporating other parameters, such as the depth profile of irradiance. Few, if any, other papers have explicitly stated the degree to which surface chlorophyll can predict euphotic zone integrated productivity, but this result demonstrates the efficacy of satellite chlorophyll measurements for detecting spatial and temporal changes in productivity.

From a physical point of view, there is increasing evidence for the importance of eddies in driving vertical transports (Sokolov and Rintoul, 2007) and in controlling the Southern Ocean response to westerly wind variability (e.g. Boning et al., 2008; Sallee et al., 2010). Models that can adequately represent eddies are likely to better quantify nutrient fluxes and air–sea CO_2 exchange. However, increased spatial resolution will obviously require increased computing infrastructure, as well as detailed understanding of the physical processes.

This review has not discussed the rapidly developing field of data assimilation. This approach has the potential to improve the chlorophyll estimates of biogeochemical models and decrease the errors depicted in Figure 8. However, to date, Schlitzer (2002) is perhaps the only data-assimilation study that has focused on the Southern Ocean. Most data-assimilation efforts tend to be coastal or regional (see Gregg (2008) for a summary), and there has been relatively little emphasis on using data assimilation to improve estimates of productivity or other biogeochemical processes.

The satellite ocean colour data record is already long enough to investigate the response of Southern Ocean primary productivity to phenomena such as El Niño and the SAM, but a longer time series, perhaps as long as another decade, will be required to separately quantify the response of long interannual processes, such as the SAM, from secular trends due to climate change.

To improve estimation of primary productivity and air–sea CO_2 fluxes in the Southern Ocean, this paper concludes that the following are required:

- (i) expanded spatial and temporal coverage of productivity and pCO_2 measurements, and by extension, better calibration of NPP algorithms

- (ii) methods to fill gaps in observations and investigate seasonal to interannual variability in air-sea CO₂ fluxes, such as satellite-based proxies for pCO₂
- (iii) models of increasing spatial and temporal resolution, including better representation of the mixed-layer depth (critical for light/iron co-limitation)
- (iv) time series observations in the context of ocean observing systems, including moorings, gliders and expanded suites of parameters from profiling floats
- (v) ways to use the remotely sensed data to infer phytoplankton composition as well as concentration, and the supporting (in situ) data to assess such products
- (vi) modeling studies to probe the link between variability in climate, phytoplankton concentrations and NPP.

Acknowledgements

P. Strutton acknowledges support from the Australian Research Council Future Fellowship program and the Centre of Excellence for Climate System Science. N. Lovenduski is grateful for support from NSF (OCE-1155240) and NOAA (NA08OAR4320893). M. Mongin and R. Matear were supported by the CSIRO Wealth from Ocean Flagship and the Australian Commonwealth Cooperative Research Centres Program.

References

- Aita, M.N., Y. Yamanaka and M.J. Kishi. 2006. Interdecadal variation of the lower trophic ecosystem in the North Pacific between 1948 and 2002, in a 3-D implementation of the NEMURO model. *Ecol. Model.*, doi:10.1016/j.ecolmodel.2006.07.045.
- Arrigo, K.R. and C.R. McClain. 1994. Spring phytoplankton production in the western Ross Sea. *Science*, 265: 261–263.
- Arrigo, K.R. and G.L. Van Dijken. 2007. Interannual variation in air-sea CO₂ flux in the Ross Sea, Antarctica: a model analysis. *J. Geophys. Res.*, 112, doi: 10.1029/2006JC003492.
- Arrigo, K.R., D. Worthen, A. Schnell and M.P. Lizotte. 1998. Primary production in Southern Ocean waters. *J. Geophys. Res.*, 103: 15587–15600.
- Arrigo, K.R., G.R. DiTullio, R.B. Dunbar, M.P. Lizotte, D.H. Robinson, M. VanWoert and D.L. Worthen. 2000. Phytoplankton taxonomic variability and nutrient utilization and primary production in the Ross Sea. *J. Geophys. Res.*, 105: 8827–8846.
- Arrigo, K.R., G.L. Van Dijken and S. Bushinsky. 2008. Primary productivity in the Southern Ocean, 1997–2006. *J. Geophys. Res.*, 113: C08004, doi: 10.1029/2007JC004551.
- Aumont, O. and L. Bopp. 2006. Globalizing results from ocean in situ iron fertilization studies. *Global Biogeochem. Cycles*, 20: GB2017, doi: 10.1029/2005GB002591.
- Balch, W., R. Evans, J. Brown, G. Feldman, C. McClain and W. Esaias. 1992. The Remote Sensing of Ocean Primary Productivity: Use of a New Data Compilation to Test Satellite Algorithms. *J. Geophys. Res.*, 97: 2279–2293.
- Behrenfeld, M.J. and P.G. Falkowski. 1997a. A consumer's guide to phytoplankton primary productivity models. *Limnol. Oceanogr.*, 42: 1479–1491.
- Behrenfeld, M.J. and P.G. Falkowski. 1997b. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.*, 42: 1–20.
- Behrenfeld, M.J., E. Boss, D.A. Siegel and D.M. Shea. 2005. Carbon-based ocean productivity and phytoplankton physiology from space. *Global Biogeochem. Cycles*, 19: GB1006, doi: 10.1029/2004GB002299, 2005.
- Behrenfeld, M.J., R.T. O'Malley, D.A. Siegel, C.R. McClain, J.L. Sarmiento, G.C. Feldman, A.J. Milligan, P.G. Falkowski, R.M. Letelier and E.S. Boss. 2006. Climate-driven trends in contemporary ocean productivity. *Nature*, 444: 752–755.
- Bender, M., T. Ellis, P. Tans, R. Francey and D. Lowe. 1996. Variability in the O₂/N₂ ratio of southern hemisphere air, 1991–1994: implications for the carbon cycle. *Global Biogeochem. Cycles*, 10 (1): 9–21.
- Blain, S., B. Queguiner, L. Armand, S. Belviso, B. Bombled, L. Bopp, A. Bowie, C. Brunet, C. Brussaard, F. Carlotti, U. Christaki, A. Corbiere, I. Durand, F. Ebersbach, J.-L. Fuda, N. Garcia, L. Gerringa, B. Griffiths, C. Guigue, C. Guillermin, S. Jacquet, C. Jeandel, P. Laan, D. Lefevre, C. Lomonaco, A. Malits, J. Mosseri, I. Obernosterer, Y.-H. Park, M. Picheral, P. Pondaven, T. Remy, V. Sandroni, G. Sarthou, N. Savoye, L. Scouarnec, M. Souhaut, D. Thuiller, K. Timmermans, T. Trull, J. Uitz, P. van-Beek, M. Veldhuis, D. Vincent, E. Viollier, L. Vong and T. Wagener. 2007. Effect of natural iron fertilisation on carbon sequestration in the Southern Ocean. *Nature*, 446: 1070–1074.

- Boning, C.W., A. Dispert, M. Visbeck, S.R. Rintoul and F.U. Schwarzkopf. 2008. The response of the Antarctic Circumpolar Current to recent climate change. *Nature Geosci.*, 1: 864–869.
- Carr, M.-E., M.A.M. Friedrichs, M. Schmeltz, M.N. Aita, D. Antoine, K.R. Arrigo, I. Asanuma, O. Aumont, R. Barber, M. Behrenfeld, R. Bidigare, E.T. Buitenhuis, J. Campbell, A. Ciotti, H. Dierssen, M. Dowell, J. Dunne, W. Esaias, B. Gentili, W. Gregg, S. Groom, N. Hoepffner, J. Ishizaka, T. Kameda, C. Le Quere, S. Lohrenz, J. Marra, F. Melin, K. Moore, A. Morel, T.E. Reddy, J. Ryan, M. Scardi, T. Smyth, K. Turpie, G. Tilstone, K. Waters and Y. Yamanaka. 2006. A comparison of global estimates of marine primary production from ocean color. *Deep-Sea Res. II*, 53: 741–770.
- Coale, K.H., K.S. Johnson, F.P. Chavez, K.O. Buesseler, R.T. Barber, M.A. Brzezinski, W.P. Cochlan, F.J. Millero, P.G. Falkowski, J.E. Bauer, R.H. Wanninkhof, R.M. Kudela, M.A. Altabet, B.E. Hales, T. Takahashi, M.R. Landry, R.R. Bidigare, X. Wang, Z. Chase, P.G. Strutton, G.E. Friederich, M.Y. Gorbunov, V.P. Lance, A.K. Hiltling, M.R. Hiscock, M.H. Demarest, W.T. Hiscock, K.F. Sullivan, S.J. Tanner, R. M.Gordon, C.N. Hunter, V.A.F. Elrod, S.E. Fitzwater, J.L. Jones, S. Tozzi, M. Koblizek, A.E. Roberts, J. Herndon, J. Brewster, N. Ladizinsky, G. Smith, D. Cooper, D. Timothy, S.L. Brown, K.E. Selph, C.C. Sheridan, B.S.J. Twining and Z.I. Johnson. 2004. Southern Ocean iron enrichment experiment: carbon cycling in high- and low-Si waters. *Science*, 304: 408–414.
- Dierssen, H.M., R.C. Smith and M. Vernet. 2000. Optimizing models for remotely estimating primary production in Antarctic coastal waters. *Ant. Sci.*, 12: 20–32.
- Eppley, R.W., E. Stewart, M.R. Abbott and U. Heyman. 1985. Estimating ocean primary production from satellite chlorophyll. Introduction to regional differences and statistics for the Southern California Bight. *J. Plankton Res.*, 7: 57–70, doi: 10.1093/plankt/7.1.57.
- Falkowski, P.G. 1981. Light-shade adaptation and assimilation numbers. *J. Plankton Res.*, 3: 203–216, doi: 10.1093/plankt/3.2.203.
- Falkowski, P.G., D. Ziemann, Z.S. Kolber and P.K. Bienfang. 1991. Role of eddy pumping in enhancing primary production in the ocean. *Nature*, 352: 55–58.
- Falkowski, P.G., R.T. Barber and V. Smetacek. 1998. Biogeochemical controls and feedbacks on ocean primary production. *Science*, 281: 200–206.
- Fennel, K., M.R. Abbott, Y.H. Spitz, J.G. Richman and D.M. Nelson. 2003. Impacts of iron control on phytoplankton production in the modern and glacial Southern Ocean. *Deep-Sea Res. II*, 50: 833–851.
- Geider, R.J. 1987. Light and temperature dependence of the carbon to chlorophyll ratio in microalgae and cyanobacteria: implications for physiology and growth of phytoplankton. *New Phytologist*, 106: 1–34.
- Gregg, W.W. 2008. Assimilation of SeaWiFS ocean chlorophyll data into a three-dimensional global ocean model. *J. Mar. Sys.*, 69: 205–225.
- Gregg, W.W. and K.L. Carder. 1990. A simple spectral solar irradiance model for cloudless maritime atmospheres. *Limnol. Oceanogr.*, 35: 1657–1675.
- Gruber, N., M. Gloor, S.E. Mikaloff-Fletcher, S.C. Doney, S. Dutkiewicz, M.J. Follows, M. Gerber, A.R. Jacobson, F. Joos, K. Lindsay, D. Menemenlis, A. Mouchet, S.A. Muller, J.L. Sarmiento and T. Takahashi. 2009. Oceanic sources, sinks and transport of atmospheric CO₂. *Global Biogeochem. Cycles*, 23: doi: 10.1029/2008GB003349.
- Hannon, E., P.W. Boyd, M. Silviso and C. Lancelot. 2001. Modeling the bloom evolution and carbon flows during SOIREE: Implications for future in situ iron-enrichments in the Southern Ocean. *Deep-Sea Res. II*, 48: 2745–2773.
- Hiscock, M.R., J. Marra, W.O. Smith, R. Goericke, C.I. Measures, S. Vink, R.J. Olson, H.M. Sosik and R.T. Barber. 2003. Primary productivity and its regulation in the Pacific sector of the Southern Ocean. *Deep-Sea Res. II*, 50: 533–558.
- Jenkins, W.J. 1982. Oxygen utilization rates in North Atlantic subtropical gyre and primary production in oligotrophic systems. *Nature*, 300: 246–248.
- Jenkins, W.J. 1988. Nitrate flux into the euphotic zone near Bermuda. *Nature*, 331: 521–523.
- Lancelot, C., E. Hannon, S. Becquevort, C. Veth and H.J.W. de Baar. 2000. Modeling phytoplankton blooms and carbon export production in the Southern Ocean: dominant controls by light and iron in the Atlantic sector during Austral spring 1992. *Deep-Sea Res. I*, 47: 1621–1662.

- Levitus, S., M.E. Conkright, J.L. Reid, R.G. Najjar and A. Mantyla. 1993. Distribution of Nitrate, Phosphate and Silicate in the World Oceans. *Prog. Oceanogr.*, 31: 245–273.
- Lovenduski, N.S. and N. Gruber. 2005. Impact of the Southern Annular Mode on Southern Ocean circulation and biology. *Geophys. Res. Lett.*, 32: L11603, doi: 10.1029/2005GL022727.
- Lovenduski, N.S., N. Gruber, S.C. Doney and I.D. Lima. 2007. Enhanced CO₂ outgassing in the Southern Ocean from a positive phase of the Southern Annular Mode. *Global Biogeochem. Cycles*, 21: doi: 10.1029/2006GB002900.
- Mongin, M., D.M. Nelson, P. Pondaven and P. Treguer. 2006. Simulation of upper-ocean biogeochemistry with a flexible-composition phytoplankton model: C, N and Si cycling and Fe limitation in the Southern Ocean. *Deep-Sea Res. II*, 53: 601–619.
- Mongin, M., D.M. Nelson, P. Pondaven and P. Treguer. 2007. Potential phytoplankton responses to iron and stratification changes in the Southern Ocean based on a flexible-composition phytoplankton model. *Global Biogeochem. Cycles*, 21, doi: 10.1029/2007GB002972.
- Mongin, M., E. Molina and T.W. Trull. 2008. Seasonality and scale of the Kerguelen Plateau phytoplankton bloom: a remote sensing and modelling analysis of the influence of natural iron fertilization in the Southern Ocean. *Deep-Sea Res. II*, 55: 880–892.
- Moore, J.K. and M.R. Abbott. 2000. Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. *J. Geophys. Res.*, 105: 28709–28722.
- Morel, A. 1978. Available, usable, and stored radiant energy in relation to marine photosynthesis. *Deep-Sea Res.*, 25: 673–688.
- Morel, A. 1991. Light and marine photosynthesis: a spectral model with geochemical and climatological implications. *Prog. Oceanogr.*, 26: 263–306.
- Nicol, S., T. Pauly, N.L. Bindoff and P.G. Strutton. 2000a. “BROKE” a biological/oceanographic survey off the coast of East Antarctica (80–150°E) carried out in January–March 1996. *Deep-Sea Res. II*, 47: 2281–2297.
- Nicol, S., T. Pauly, N.L. Bindoff, S.W. Wright, D. Theile, G.W. Hosie, P.G. Strutton and E. Woehler. 2000b. Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature*, 406: 504–507.
- Pasquer, B., G. Laruelle, S. Becquevort, V. Schoemann, H. Goosse and C. Lancelot. 2005. Linking ocean biogeochemical cycles and ecosystem structure and function: results of the complex SWAMCO-4 model. *J. Sea Res.*, 53: 93–108.
- Platt, T. 1986. Primary production of the ocean water column as a function of surface light intensity: algorithms for remote sensing. *Deep-Sea Res. I*, 33: 149–163.
- Pondaven, P., C. Fravallo, D. Ruiz-Pino, P. Treguer, B. Queguiner and C. Jeandel. 1998. Modelling the silica pump in the permanently open ocean zone of the Southern Ocean. *J. Mar. Sys.*, 17: 587–619.
- Pondaven, P., D. Ruiz-Pino, C. Fravallo, P. Treguer and C. Jeandel. 2000. Interannual variability of Si and N cycles at the time-series station KERFIX between 1990 and 1995 – a 1-D modelling study. *Deep-Sea Res. I*, 47: 223–257.
- Prezelin, B.B., E.E. Hofmann, M. Moline and J.M. Klinck. 2004. Physical forcing of phytoplankton community structure and primary production in continental shelf waters of the Western Antarctic Peninsula. *J. Mar. Res.*, 62: 419–460.
- Sakshaug, E., A. Bricaud, Y. Dandonneau, P.G. Falkowski, D.A. Kiefer, L. Legendre, A. Morel, J. Parslow and M. Takahashi. 1997. Parameters of photosynthesis: definitions, theory and interpretation of results. *J. Plankton Res.*, 19: 1637–1670.
- Sallee, J.B., K.G. Speer and S.R. Rintoul. 2010. Zonally asymmetric response of the Southern Ocean mixed-layer depth to the Southern Annular Mode. *Nat. Geosci.*, 3, doi: 10.1038/NGEO812.
- Schlitzer, R. 2002. Carbon export fluxes in the Southern Ocean: results from inverse modeling and comparison with satellite-based estimates. *Deep-Sea Res. II*, 49: 1623–1644.
- Sedwick, P.N. and G.R. DiTullio 1997. Regulation of algal blooms in Antarctic shelf waters by the release of iron from melting sea ice. *Geophys. Res. Lett.*, 24: 2515–2518.
- Selph, K.E., M.R. Landry, C.B. Allen, A. Calbet, S. Christensen and R.R. Bidigare. 2001. Microbial community composition and growth dynamics in the Antarctic Polar Front and seasonal ice zone during late spring 1997. *Deep-Sea Res. II*, 48: 4059–4080.

- Smith, R.C., R.W. Eppley and K.S. Baker. 1982. Correlation of primary production as measured aboard ship in Southern California Coastal waters and as estimated from satellite chlorophyll images. *Mar. Biol.*, 66: 281–288.
- Smith, W.O. Jr. and J.C. Comiso. 2008. Influence of sea ice on primary production in the Southern Ocean: A satellite perspective. *J. Geophys. Res.*, 113: C05S93, doi: 10.1029/2007JC004251.
- Smith, W.O. Jr., R.F. Anderson, J.K. Moore, L.A. Codispoti and J.M. Morrison. 2000. The US Southern Ocean Joint Global Ocean Flux Study: an introduction to AESOPS. *Deep-Sea Res. II*, 47: 3073–3093.
- Sokolov, S. and S.R. Rintoul 2007. On the relationship between fronts of the Antarctic Circumpolar Current and surface chlorophyll concentrations in the Southern Ocean. *J. Geophys. Res.*, 112: C07030.
- Strutton, P.G., F.B. Griffiths, R.L. Waters, S.W. Wright and N.L. Bindoff. 2000. Primary productivity off the coast of East Antarctica (80–150°E): January to March 1996. *Deep-Sea Res. II*, 47: 2327–2362.
- Sullivan, C.W., K.R. Arrigo, C.R. McClain, J.C. Comiso and J. Firestone. 1993. Distributions of phytoplankton blooms in the Southern Ocean. *Science*, 262: 1832–1837.
- Vogt, M., S. Vallina, E. Buitenhuis, L. Bopp and C. Le Quere. 2010. Simulating the seasonal cycle of dimethylsulphide with the global multi-plankton functional type biogeochemistry model PlankTOM5. *J. Geophys. Res.-Oceans*, 115: C06021, doi: 10.1029/2009JC005529.
- Waters, R.L., R. van den Enden and H.J. Marchant. 2000. Summer microbial ecology off East Antarctica (80–150°E): protistan community structure and bacterial abundance. *Deep-Sea Res. II*, 47: 2401–2435.
- Wright, S.W., R.L. van den Enden, I. Pearce, A.T. Davidson, F.J. Scott and K.J. Westwood. 2010. Phytoplankton community structure and stocks in the Southern Ocean (30°E to 80°E) determined by CHEMTAX analysis of HPLC pigment signatures. *Deep-Sea Res. II*, 57: 758–778.

