A comparison of primary production models in an Antarctic mesoscale area

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Introduction

In the last decades remote sensing models to estimate ocean primary production (PP) have been developed in order to monitor large areas of the global ocean (i.e. Eppl ey et al., 1985; Behrenfeld and Falkowsky 1997; Mar ra et al., 2003; Behrenfeld et al., 2005; Westberry et al., 2008) as well as specific sites like the Southern Ocean (Dierssen et al., 2000; Arrigo et al., 2008). Several papers have focused on the comparison of the results obtained by these models (Campbell et al., 2002; Carr et al., 2006) and controversial results, in relation to the algorithms used, have been presented, especially for the Southern Ocean (Campbell et al., 2002; Carr et al. 2006; Shang et al. 2010). This region is a well known High Nutrient Low Chlorophyll area (HNLC), and it is generally assumed to be controlled by the supply of micronutrients (especially iron) and light that are needed for photosynthesis by primary producers. This type of bottom-up control suggests that the ecosystem will be sensitive to changes in physical forcing that influence the light and nutrient environment experienced by phytoplankton (e.g. upwelling, mixed layer depth, sea ice) (Rintoul et al., 2012).

Three kind of remote-sensing models and one based in the Metabolic Theory of Ecology (MTE) were applied to real data obtained during Coupling cruise (January 2010) in a mesoscale area of the Southern Ocean around the South Shetland Islands (SSI). The results obtained were compared and discussed to discern why they differ. The previous knowledge of the study area has allowed us to implement improvements in the selected models to achieve realistic results of PP based on the limitation by light, mixed layer depth and nutrient concentration.

Data collection and modelling

All the data used in this study were collected from RV BIO-Hesperides during Coupling cruise, 8th to 27th January 2010, using a rosette system of 24 oceanographic 12-L Niskin bottles operated with a CTD Seabird 911 plus. The survey was conducted around the SSI, with a main transect sampled from Drake Passage to Bransfield Strait (hereafter, Transect 1, Fig. 1). Sampling was performed at 6 depths (from 5 to 100 meters) including the depth of the fluorescence maximum (DFM). Chlorophyll a was measured fluorometrically following UNESCO (1994). Macronutrients concentration was measured by means of a Technicon TRAACS 800 System Autoanalyzers using standard protocols (Grasshoff et al., 1983). Phytoplankton composition and abundance was analysed by overlapping Flow cytometry and FlowCAM techniques to include the whole phytoplankton assemblage from 2 to 200 Em Equivalent spherical diameter (ESD). Plankton volume was then converted to carbon using Mender-Deue et al. (2000) equations. PP was measured on board only at 11 stations at two sampling depths, including surface and DFM, using the 14C method. We used the Si* tracer (calculated as the concentration of silicate minus nitrate concentration) defined by Sarmiento et al. 2004 as a proxy for iron limitation in the sampling area. The irradiance at the sea surface was monitored on deck with a Kipp & Zonen CM11 sensor. The average daily irradiance just below the sea surface (Io) was estimated considering 0.8 as the transmittance of silicate minus nitrate concentration defined by Sarmiento et al. 2004 as a proxy for iron limitation in the sampling area. The irradiance at the sea surface was monitored on deck with a Kipp & Zonen CM11 sensor. The average daily irradiance just below the sea surface (Io) was estimated considering 0.8 as the transmittance at the air–sea interface (Figueiras et al., 1999).

Five models based on data surveyed during the cruise were used to calculate PP. They can be classified into 3 groups:

1. Models based on Chl a: VGPM (Behrenfeld and Falkowsky 1997) and that of Dierssen et al. (2000) for the Western Antarctic Peninsula. Both models are not vertically resolved, in the sense that they estimate vertically integrated values from surface data.

VGPM: Net PP (NPP) (mgC/m²/d) = Chl a x Zeu x f(Io) x DL x PBopt ; f(Io) = 0.66125 x Io / (Io + 4.1) ; PBopt = -3.27 x 10⁻⁸ T⁷ + 3.4132 x 10⁻⁶ T⁵ – 1.348 x 10⁻⁴ T³ + 2.462 x 10⁻³ T² – 0.0205 x T + 0.0617 x T² + 0.2749 x T + 1.2956

Dierssen’s: NPP (mgC/m²/d) = Chl a x Zopt x F x DL x PBopt ; F = I/ (I + 11.77)

2. Models based on phytoplankton biomass: one based on Metabolic Theory of Ecology (MTE) developed by López-Urrutia et al., (2006) and that of Arrigo et al. (2008) for the whole Southern Ocean. As far as we know, this is the first time that a model based on the MTE is used for the calculation of PP in Antarctic waters. Arrigo et al. (2008) is in essence very similar to MTE, the main difference is that MTE calculates PP on an individual basis while

\[ F = \frac{I}{I_0 + 11.77} \]
Arrigo et al. (2008) uses the total biomass of the phytoplankton community.

López-Urrutia's: \(\ln (\text{NPP} \ (\text{mmol O}_2/\text{cell/d})) = -13.18 + 1.02 x \ln(M) - 0.28 x (1/\text{KT}) + \ln (I_p/(I_p + 1.52)) ; I_p = I_p \times \exp (-K_z \times Z)\), using a Photosynthetic quotient (PQ) of 1.25 for carbon conversion and the cell abundance (cells/m3) in each depth to express NPP in mgC/m3/d.

Arrigo's: NPP (mgC/m3/d) = \(\int C_{(0)} \times G_{(0)} \, dt ; G_{(0)} = \mu_{\text{max}}(0) \times L_{(0)}(0) \); \(\mu_{\text{max}}(0) = \mu_0 \times \exp \left[ r \times t_{(0)} \right] ; L_{(0)}(0) = 1 - \exp (-I_{(0)}/E_{(0)})\)

3. A model based on the Chl a/C ratio: CbPM (first described by Behrenfeld et al., 2005 and updated by Westberry et al., 2008). The primary processes which drive vertical changes in Chl a concentration in the CbPM are those associated with physiological, intracellular adjustments to ambient light and nutrient conditions:

\[ NPP (\text{mgC/m}^3/\text{d}) = \frac{\mu_{(0)} x C(z) ; \mu_{(0)} = \mu_{\text{max}} x f(\text{Nut}, T) x f(I) ; f(\text{Nut}, T) = (\text{Chl a/C})_{\text{max}}/(\text{Chl a/C})_{\text{max}} ; f(I) = 1 - \exp (-3 x I_1) ; (\text{Chl a/C})_{\text{max}} = 0.022 + (0.045 - 0.022) x \exp (-3 x I_1) ; \mu_{\text{max}} \text{ was calculated using Epplley's (1972) equation and the maximum temperature detected in the study area.} \]

The integration depth for the two latter groups was that of the photic layer in the stations where the depth of 1% of light was deeper than the upper mixed layer (Zml) and was Zml in the stations where the photic layer was shallower than the upper mixed layer. Zml was calculated for each station following Kara et al., (2000). To calculate the irradiance term in each model we took into consideration the median mixed layer light level for those depths over the Zml (I_{ml}) and I_{s} for deeper depths. To avoid the “fallacy of the averages” I_{ml} was calculated as:

\[ I_{ml} = \frac{\sum (I_p \times \exp (-K_z x Z))}{Zml} \]

Table 1. Symbols and units used.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Units</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\Phi_{\text{opt}})</td>
<td>mgC/mgChl/h</td>
<td>Maximum chlorophyll-normalized C fixation rate within a water column</td>
</tr>
<tr>
<td>(I_p)</td>
<td>mol photon/m²/day</td>
<td>Surface daily photosynthetically available radiation (PAR)</td>
</tr>
<tr>
<td>(I_{s})</td>
<td>mol photon/m²/day</td>
<td>Daily PAR at each depth</td>
</tr>
<tr>
<td>(Z_m)</td>
<td>m</td>
<td>Euphotic zone depth</td>
</tr>
<tr>
<td>(Z_{ml})</td>
<td>m</td>
<td>Mixed layer depth</td>
</tr>
<tr>
<td>(\text{Chl}_a)</td>
<td>mg/m³</td>
<td>Surface Chlorophyll a concentration</td>
</tr>
<tr>
<td>(\text{Chl}_a)</td>
<td>mg/m³</td>
<td>Chlorophyll a concentration</td>
</tr>
<tr>
<td>(\mu)</td>
<td>d⁻¹</td>
<td>Phytoplankton growth rate at 0°C, as in Epplley 1972</td>
</tr>
<tr>
<td>(\mu_{\text{opt}})</td>
<td>mgC/mgChl/h</td>
<td>Individual phytoplankton biomass</td>
</tr>
<tr>
<td>(C)</td>
<td>mg C/ m³</td>
<td>Phytoplankton biomass</td>
</tr>
<tr>
<td>(T)</td>
<td>°K</td>
<td>Temperature</td>
</tr>
<tr>
<td>t</td>
<td>°C</td>
<td>Temperature</td>
</tr>
<tr>
<td>(K_z)</td>
<td>m⁻¹</td>
<td>Diffusive attenuation coefficient</td>
</tr>
<tr>
<td>K</td>
<td>8.62x10⁻⁵ eV/k</td>
<td>Boltzman’s factor</td>
</tr>
<tr>
<td>(E_{(s)})</td>
<td>Emol photon/m²/s</td>
<td>Spectral photoacclimation parameter</td>
</tr>
</tbody>
</table>

Figure 1. Map of the study area and stations locations.
Results

The range of values for the input variables is roughly the range observed for our study period: for SST, -1.14 to 1.76°C reaching the highest temperatures in the Drake area and the lowest in the stations close to the Antarctic Peninsula; for mixed-layer depth, 12–362 m, with the deepest layers related with hydrographical fronts and subduction points; for surface daily PAR, 8–50 mol photon/m²/day; for euphotic depth, 36-144 m; for chlorophyll concentration, 0.04–2.39 mg/m³ reaching the highest values in the southern area and the lowest in the Drake Passage, and for phytoplankton biomass in each sampling depth, 32.90-278.95 mg C/m³. PP 13C values range from 0.52 to 19.32 (mg C/m³/d). For further details of physicochemical variables and water masses around the SSI see Hewes et al. (2009), SangraÁL et al. (2011). The results for discrete depths’ and integrated NPP of the different models are presented in Tables 2 and 3.

Table 2. Mean and standard deviation (Std) of NPP (mg C/m³/d).

<table>
<thead>
<tr>
<th></th>
<th>MTE</th>
<th>Arrigo’s</th>
<th>ChpM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>37.97</td>
<td>29.29</td>
<td>11.46</td>
</tr>
<tr>
<td>Std</td>
<td>40.42</td>
<td>29.31</td>
<td>16.09</td>
</tr>
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</table>

Table 3. Integrated mean and Std of NPP (mg C/m²/d)

<table>
<thead>
<tr>
<th></th>
<th>VGPM</th>
<th>Dierssen’s</th>
<th>MTE</th>
<th>Arrigo’s</th>
<th>ChpM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>684.56</td>
<td>601.07</td>
<td>2753.25</td>
<td>2172.45</td>
<td>775.93</td>
</tr>
<tr>
<td>Std</td>
<td>300.92</td>
<td>300.58</td>
<td>1097.09</td>
<td>758.87</td>
<td>480.75</td>
</tr>
</tbody>
</table>

The production estimated from ocean-color algorithms (1st group) based on Chl a was found to be highly correlated between them when using in situ data as the inputs of the algorithm, with a slope close to a 1:1 relationship. Models from the second group gave also similar results between them with higher correlations (R² = 0.943) (Fig.2). Biomass-based models gave significant higher NPP results than Chl a-based models (p-value < 0.05). In the case of the ChpM mean values were closer to group 1, but the overall trend in the study area was well defined between this 3rd group and the 2nd one with a power equation: ln Y = ln a + b ln X, Y = a X^b; NPP Arrigo’s = 4.145 x (NPP ChpM)⁰.⁹⁰³, R² = 0.957 (Fig. 3), ChpM vs MTE gave similar results (data not shown). There were no limitation for nitrate along the study area, neither phosphate but silicate distribution (Si* tracer) was selected as a reference for a possible iron limitation along the northern stations, as revealed by the strong silicate drawdown detected in the Drake Area (Fig. 4) summed to deep DFM and low Chl a values (Holm-Hansen et al., 2005).

![Table 2](image1)

![Table 3](image2)

![Figure 2](image3)

![Figure 3](image4)
Discussion

The overall conclusion obtained by those authors who estimate and compare PP using general models for areas as heterogeneous as the whole Southern Ocean, is the introduction of large errors (either overestimates or underestimates) due to the lack of punctual information (hydrographical fronts, subduction areas, eddies...). It is necessary to establish boundary conditions to obtain good results, especially at a mesoscale range. Carr et al. (2006) affirmed that the Southern Ocean is unquestionably the most challenging large basin, so it has been proven that the vertically integrated models such as those based just in surface Chl a (group 1, VGPM and derivatives) are too simple. Dierssen et al. (2000) comparing their results with data measured in situ, along Western Antarctic Peninsula (WAP), using $^{14}$C obtained high correlations explaining over 70% of the production variability. We must point out that they included few stations in the slope area underestimating the potential role of micro-nutrients (especially iron) in controlling the distribution, timing, and rates of primary production in this region (Seguret et al., 2012).

Although Coupling cruise was conducted at the end of the phytoplankton bloom, in some stations the biomass, specially nanophytoplankton, was still high. The use of 2nd group models seem to overestimate the NPP because the limiting terms do not include nutrients, they are based just in irradiance, temperature, vertical mixture limitations and body size of phytoplankton cells. In those stations situated in the Drake area, where the melting occurred much earlier in time and therefore the phytoplankton bloom, although a bulk of small size phytoplankton cells remained despite iron limitation, it did not achieve an optimal production yield. Arrigo’s theoretical model is simple in some assumptions because it uses constant ratios of C:Chla for the whole Southern Ocean and assumes that Chl a concentration is constant from surface to Zml. Our input data do not confirm these assumptions, therefore it is necessary to introduce a variable C:Chla ratio for each depth and station and study which physicochemical characteristics drive this variation. The high correlation found between MTE and Arrigo’s models highlights the potential uses of MTE in the Southern Ocean, making suitable the 3/4 allometric scaling theory in this area with and activation energy for autotrophic processes close to the reference value of $E_a = 0.32$ eV.

Behrenfeld et al. (2005) state that, at a global scale, surface nutrients decrease with increasing Sea Surface Temperature (SST). As nutrients can not be directly measured from space, they used SST to infer nutrient limitation from the term: $f$(Nut, T) = $\frac{(\text{Chl} a/C)_{m,nm}}{(\text{Chl} a/C)_{nm}}$. When in situ nutrient data from our survey are used, not only a common trend of Behrenfeld’s term, $f$(Nut, T), and SST is observed, but also a common trend with Si* tracer (Fig. 5, left). The power relationship found between CbPM and Arrigo’s models (Fig. 3) showed that differences were more pronounced in values below 40 mg C/m$^3$/d which agree with our conclusion of the overestimation of 2nd group models in those stations limited by nutrients. Although few stations were sampled for PP$_{in situ}$ experiments, and the scarce values at discrete depths are not comparable to those of integrated models, a similar spatial trend with the Si* tracer was detected (Fig. 5, right).

![Figure 4](image_url)  
**Figure 4.** Silicate (EM) distribution along Transect 1, north (left) to south (right)

![Figure 5](image_url)  
**Figure 5.** Scatter plot between Si* tracer and $f$(Nut, T) (left). Scatter plot between Si* tracer and PP$_{in situ}$ (mg C/m$^3$/d) (right). Red dots are stations situated in the Drake Area.
We did not include Westberry’s et al. (2008) nitracline depth consideration because nitrate was not limiting, taking constant values along the study area. Also we did not consider Chl/C = 0.0003 mg Chl/mg C when μ = 0, since the variation is negligible. Finally the update introduced by Westberry et al. (2008) in the irradiance term (Ig) = 1 – exp (-5 x Ig), was rejected because it was less restrictive than Behrenfeld’s one. Taking into account previous data of photosynthetic efficiency around the SSI, we observed photosaturation at surface layers in those stations sampled during sunny days. Only stations with deep Zml, or sampled in very cloudy days, may be experiencing light limitation. The improvements that we have introduced to CbPM have already been described in previous models as the original of Howard and Yoder (1997): the calculation of the maximum growth rate as a function of SST according to Eppley (1972) and the integration of NPP to the mixed-layer depth rather than to the euphotic depth.

In short, we consider that the results obtained with our updated version of CbPM (Fig. 6) fit with the real situation that was taking place during the austral summer of 2010. This conclusion could be extrapolated to other sites of the Southern Ocean, keeping in mind that each area of Antarctica is going to be limited by a specific variable. Shang et al. (2011) did not find good results using CbPM because they did not consider several aspects that we did.

Figure 6. Net Primary Production (NPP) output from CbPM along Transect 1.

Prior knowledge of the study area is essential, especially for mesoscale studies, but in this paper we have highlighted the ability of models developed from remote sensing data to calculate PP with real input data. The calculation of PP can be performed with good results through these indirect methods and avoid the tedious, and non always precise (i.e. Richardson, K. 1991; Aristegui et al. 1996), 14C or 13C incubations on board.

References


