Environmental controls of marine productivity hot spots around Antarctica

Kevin R. Arrigo¹, Gert L. van Dijken¹, and Aaron L. Strong²

¹Department of Earth System Science, Stanford University, Stanford, California, USA, ²Emmett Interdisciplinary Program in Environment and Resources, Stanford University, Stanford, California, USA

Abstract Antarctic coastal polynyas are biologically rich ecosystems that support large populations of mammals and birds and are globally significant sinks of atmospheric carbon dioxide. To support local phytoplankton blooms, these highly productive ecosystems require a large input of iron (Fe), the sources of which are poorly known. Here we assess the relative importance of six different environmental factors in controlling the amount of phytoplankton biomass and rates of net primary production (NPP) in 46 coastal polynyas around Antarctica. Data presented here suggest that melting ice shelves are a primary supplier of Fe to coastal polynyas, with basal melt rates explaining 59% of the between-polynya variance in mean chlorophyll a (Chl a) concentration. In a multiple regression analysis, which explained 78% of the variance in chlorophyll a (Chl a) between polynyas, basal melt rate explained twice as much of the variance as the next most important variable. Fe upwelled from sediments, which is partly controlled by continental shelf width, was also important in some polynyas. Of secondary importance to phytoplankton abundance and NPP were sea surface temperature and polynya size. Surprisingly, differences in light availability and the length of the open water season explained little or none of the variance in either Chl a or NPP between polynyas. If the productivity of coastal polynyas is indeed sensitive to the release of Fe from melting ice shelves, future changes in ice shelf melt rates could dramatically influence Antarctic coastal ecosystems and the ability of continental shelf waters to sequester atmospheric carbon dioxide.

1. Introduction

Antarctic coastal polynyas are areas of open water surrounded by sea ice that are maintained throughout the year either through the upwelling of warm water or as continental winds blow ice away from shore [Bromwich, 1989]. Because polynya waters are already ice-free in early spring when solar elevation is increasing rapidly, they often harbor extremely large phytoplankton concentrations compared to surrounding ice-covered waters. These blooms persist even after sea ice has disappeared in summer, generally maintaining the highest phytoplankton biomass on the relatively productive continental shelf [Arrigo and van Dijken, 2003]. This enhanced biological productivity is one of the factors that enables polynyas to support the highest densities of upper trophic level organisms in the Southern Ocean [Karnovsky et al., 2007] and increases the efficiency of the local biological pump, making areas like the Ross Ice Shelf polynya disproportionately large sinks of anthropogenic carbon dioxide [Arrigo et al., 2008a].

In these high-latitude environments, light availability controls the timing of phytoplankton blooms. When present, sea ice and its associated snow cover generally prevent sufficient light from penetrating into the surface ocean for net phytoplankton growth [Perovich, 1990; Arrigo et al., 2000]. Even after sea ice has retreated in spring, first from coastal polynyas and eventually from most other Southern Ocean waters, deep mixed layers may continue to reduce ambient light levels to values too low to promote a bloom. It is only after mixed-layer shoaling in the spring and summer that phytoplankton begin to grow rapidly and consume the available nutrients in surface waters [Smith and Gordon, 1997; Arrigo et al., 2000; Sambrotto et al., 2003]. Once blooms near their seasonal peak, the ultimate amount of phytoplankton biomass attainable in most Southern Ocean waters is limited by nutrient availability, usually of iron (Fe), which is often in short supply due to the lack of an efficient supply mechanism [Boyd et al., 2012]. While many parts of the global ocean receive large Fe fluxes through atmospheric dust deposition, the isolation of high latitude Antarctic waters from terrestrial Fe sources limits its supply by this means [Boyd et al., 2012]. Consequently, some of the most productive waters of the Southern Ocean are in the Scotia Sea, where Fe-limitation is relaxed when

© 2015. American Geophysical Union. All Rights Reserved.
dissolved Fe (dFe) from shallow shelves is mixed into surface waters during advection of the Antarctic Circumpolar Current [Ardelan et al., 2010; Chever et al., 2010; Planquette et al., 2011; Frants et al., 2013]. In other parts of the Southern Ocean, dFe is brought into surface waters through convective and turbulent mixing as well as upwelling [Fitzwater et al., 2000; Planquette et al., 2013; Measures et al., 2013], from melting of drifting icebergs [Smith et al., 2007; Raiswell et al., 2008; Lin et al., 2011], sea ice [Fitzwater et al., 2000; Grotti et al., 2005; Lannuzel et al., 2010], and floating ice shelves [Gerringa et al., 2012], and a small amount from atmospheric deposition [Boyd et al., 2012]. In waters receiving large inputs of exogenous Fe, the Fe limitation typical of Southern Ocean waters is ameliorated and phytoplankton can reach relatively high concentrations and significantly reduce local macronutrient concentrations.

Like the rest of the Southern Ocean, the growth of phytoplankton in coastal polynyas located on the continental shelf depends on the availability of dFe [Coale et al., 2005; Alderkamp et al., 2012; Gerringa et al., 2012]. However, despite the ecological and biogeochemical importance of coastal polynyas, little is known about the relative importance of the physical and chemical processes that facilitate the growth of local phytoplankton populations. Of the dozens of Antarctic coastal polynyas that have been identified [Arrigo and van Dijken, 2003], only a handful has been investigated in any detail. A recent study of polynyas in the Amundsen Sea showed that dFe introduced from melting at the base of the Pine Island Glacier was the dominant Fe pool on the continental shelf, despite relatively high concentrations of sediment-derived dFe [Gerringa et al., 2012]. This glacially derived Fe, produced both from release of particulate and dissolved Fe accumulated in glacial ice and as ice streams abrade continental crust while flowing to the coast [Shaw et al., 2011], was needed to satisfy the Fe requirement of the intense phytoplankton bloom that formed in the Pine Island Bay polynya [Gerringa et al., 2012; Alderkamp et al., 2012]. Bioassay experiments conducted in these waters demonstrated that, unlike other parts of the continental shelf, areas of the polynya receiving large amounts of Fe from ice sheet melt were not Fe-limited [Mills et al., 2012]. In contrast, in the Ross Ice Shelf polynya, sediment resuspension on the broad continental shelf is the primary source of dFe to phytoplankton, despite its proximity to the large Ross Ice Shelf [Sedwick et al., 2011].

In the present study, we attempt to better understand the factors controlling the magnitude of phytoplankton blooms in coastal polynyas by relating polynya size, polynya open water duration, local sea surface temperature (SST), light availability, continental shelf width, and for the first time, the basal melt rate of nearby ice shelves, to the amount of phytoplankton biomass and rates of net primary production (NPP) in 46 coastal polynyas around the Antarctic continent between 1998 and 2014 (Figure 1). The goal of this analysis is to provide a better understanding of how a wide suite of environmental variables interact to produce the large phytoplankton blooms observed in these important coastal biological oases.

2. Methods

2.1. Sea Ice

Daily sea ice distributions between 1 July 1997 and 30 June 2014 were computed from Special Sensor Microwave Imager (SSM/I) data obtained from the EOS Distributed Active Archive Center (DAAC) at the National Snow and Ice Data Center, University of Colorado, Boulder, CO [Maslanik and Stroeve, 2004]. SSM/I brightness temperatures were used as input to the enhanced resolution PSSM algorithm of Markus and Burns [1995]. Rather than producing maps of sea ice concentration at the usual 25 km resolution, this algorithm determines whether or not a given SSM/I subpixel (6.25 km) contains sea ice. If the ice cover is calculated to be greater than approximately 10%, then the subpixel is defined as being ice covered. Less than 10% ice cover and a given subpixel is identified as open water. The length of the open water season for each polynya was calculated as the number of days per year that the open water area exceeded 50% of the annual maximum open water area for that polynya. Because of the high degree of high-frequency variability in open water area, particularly in the smaller polynyas, this parameter was calculated from the mean open water area in each polynya (the solid black line in Figure 2).

2.2. Polynya Masks

The daily images of sea ice distribution were used to construct a spatial map of the number of days during the months of June through October (1997–2014) that each pixel location was ice-free. This map was used to identify the location of coastal polynyas based on the understanding that polynyas experience a greater
number of ice-free days than adjacent nonpolynya regions. A total of 46 recurring (at least 5 of 16 years) polynyas were identified during 1997–2014 (Figure 1). The maximum horizontal extent of phytoplankton blooms associated with summer polynyas is much larger than the wintertime polynya area. Therefore, spatial overlays were produced from SSM/I sea ice distributions and used to determine polynya location (from climatological open water area in November to December for the years 1997–2014), maximum summer polynya size (from climatological open water area in 15–31 December for the years 1997–2014), and ocean color-derived phytoplankton bloom areas (from SeaWiFS and MODIS/Aqua whole mission climatologies). These were used as a guide to assign pixels from all satellite imagery to each of the 46 polynyas.

2.3. Chlorophyll a, Sea Surface Temperature, and Net Primary Production

For the years 1997 through 2001, surface Chl a concentrations were determined from Level 3 (8 day binned, 9 km resolution) of the most recently reprocessed SeaWiFS ocean color data (Reprocessing R2010.0) using the OC4v6 algorithm, a modified version of the OC4v4 algorithm. For the years 2002 through 2014, surface Chl a concentrations were determined from Level 3 MODIS Aqua ocean color data (Reprocessing R2012.0 for the years 2002–2010, R2013.0 for 2011 to July 2012, R2013.1 for August 2012 to August 2013, and R2013.1.1 for September 2013 onward) using the OC3Mv6 algorithm. For the years 2002–2007, when both SeaWiFS and MODIS data are available, we verified that the calculated Chl a concentrations for the two sensors agreed to within 10%. Although there is some concern over the accuracy of Chl a algorithms based on satellite ocean color measurements in high-latitude waters, this is not a serious issue because our study focuses on the relative differences in Chl a between polynyas (that are all located at approximately the same latitude) rather than on absolute magnitudes. In addition, satellites cannot detect Chl a below the upper optical depth of the ocean, so biomass distributed deeper than this is not accounted for. There is a very high correlation between surface Chl a and depth-integrated Chl a within the mixed layer of the Southern Ocean [Arrigo et al., 1998a].

Figure 1. Location of the 46 coastal polynyas included in this study. Names of polynyas are given in Table 1.
Daily sea surface temperature (SST) is based on the Reynolds Optimally Interpolated SST (OISST) Version 2 product [Reynolds et al., 2007; Reynolds, 2009] obtained from NOAA (http://www.ncdc.noaa.gov/oisst).

The radiative transfer model of Gregg and Carder [1990] was used to compute clear-sky downwelling irradiance at each hour, which was subsequently corrected for fractional cloud cover according to the equation of Dobson.

![Figure 2. Annual cycles of open water area for the 46 coastal polynyas included in this study. Gray lines are for individual years and the solid black line is the mean for the 16 year time series.](image-url)
and Smith [1988]. Photosynthetically usable radiation (PUR) [Morel, 1978] at 1 m intervals within the water column was subsequently calculated at each pixel location as described in Arrigo et al. [1998b]. Chl a concentration, PUR, and SST were used to calculate the daily rate of NPP using the algorithm of Arrigo et al. [2008b]. The length of the phytoplankton bloom in each polynya was calculated as the number of days per year that NPP exceeded 50% of the annual maximum NPP for that polynya for that year. Because of the high degree of high-frequency variability in daily NPP, particularly in the smaller polynyas, the length of the phytoplankton bloom was calculated from an averaged annual cycle of NPP calculated for each polynya.

2.4. Other Data
At the centroid of each polynya location, we used bathymetric data from ETOPO2v2 (http://www.ngdc.noaa.gov) to calculate the width of the continental shelf, defined here as the shortest longitudinal distance between the local coastline and the 1000 m isobath.

Basal melt rates from the 39 of the 46 of Antarctic coastal polynyas that are adjacent to ice shelves were obtained from recent satellite-based estimates of the balance between ice accumulation and thinning [Rignot et al., 2013]. Input of basal meltwater was assumed to be zero for polynyas not located near ice shelves.

2.5. Statistics
To determine what environmental factors controlled phytoplankton abundance within the polynyas, we performed both single and multiple linear regression analysis. For the single linear regression, we regressed the 16 year mean satellite-derived polynya Chl a concentration (mg m$^{-2}$) during the average growing season (1 October to 31 March) for all 46 polynyas against the mean open water area of the polynya (km$^2$), the open water duration of each polynya (d a$^{-1}$), the mean SST of the polynya (°C), the incident downwelling PUR (mol photons m$^{-2}$ d$^{-1}$), and the mean annual basal meltwater input from the nearest ice shelf (Gt a$^{-1}$).

A multiple regression model was also created to understand the relative importance of each of the above six environmental variables in predicting both the satellite-derived mean polynya Chl a concentration (mg m$^{-2}$) and mean NPP (mg C m$^{-2}$ a$^{-1}$) during the growing season. The model form is

$$X_j \sim \beta_0 + \beta_1 V_1 + \beta_2 V_2 + \beta_3 V_3 + \ldots + \epsilon_j,$$

where $X_j$ is either the mean Chl a concentration or mean NPP in polynya $j$, $V_1$, $V_2$, and $V_3$, are the predictor variables 1–3, $\beta_0$ is the regression intercept, and $\beta_1$, $\beta_2$, and $\beta_3$ represent the estimated effects of each predictor variable. The residual error term, $\epsilon_j$, is assumed to have a mean of 0 and a variance $\sigma^2$. Inspection of model residuals showed that these assumptions about the distribution of $\epsilon_j$ were met for both Chl a and NPP.

Model selection was performed by iteratively removing nonsignificant predictor variables, and comparing model performance based on Akaike Information Criterion (AIC) to arrive at the maximum likelihood linear model to estimate mean Chl a concentration or NPP. The relative importance of each predictor variable in the final multiple regression model, quantified as the percent of $R^2$ explained, was assessed using the approach of Genizi [1993], operationalized in the relaimpo package in R [Groemping, 2006]. The potential for multicollinearity of predictor variables in the multiple regression model was assessed using the calculated variance inflation factor (VIF) for each variable using the vif function in R [Fox, 2008].

3. Results

3.1. Open Water
While coastal polynyas, by definition, have either reduced or no ice cover during winter, all 46 polynyas expanded greatly in size in October and November due to intensified rates of sea ice melt, and contracted in March as sea ice began to form again (Figure 2). The open water area of all polynyas showed a high degree of interannual variability between 1998 and 2014 (Figure 2), with some polynyas opening very little or not at all in the summer of a few years (e.g., polynyas 1, 9, 15, 19, 23, 29, 32, 35, and 37). These tended to be the smaller polynyas (<5000 km$^2$ at the summer peak), although that was not always the case. Some polynyas also exhibited highly anomalous years when the peak open water area in summer was greater than fourfold higher than the 16 year mean, although these were relatively few in number (e.g., polynyas 10 and 21). The mean open water area varied by approximately 3 orders of magnitude between polynyas, ranging from 954 ± 196 km$^2$ in the West Lazarev Sea polynya to 234,000 ± 39,000 km$^2$ in the Ross Ice Shelf.
Table 1. Mean (±SD) Statistics for 46 Antarctic Polytypes for the Years 1998–2014

<table>
<thead>
<tr>
<th>Polynya Name</th>
<th>Open Water Area</th>
<th>Mean Daily NPP</th>
<th>Annual NPP</th>
<th>Mean Total NPP</th>
<th>Shelf Width</th>
<th>Open Water Season Length of Bloom</th>
<th>Mean Daily PUR</th>
<th>Basal Melt Rate</th>
<th>Ice Shelf Name</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 Sulzberger Bay</td>
<td>6473 (1669)</td>
<td>372.6 (231.5)</td>
<td>33.0 (22.9)</td>
<td>0.236 (0.19)</td>
<td>0.68 (0.55)</td>
<td>163.5</td>
<td>90</td>
<td>69</td>
<td>−1.21 (0.19)</td>
</tr>
<tr>
<td>2 Hull Bay</td>
<td>6359 (828)</td>
<td>309.4 (160.4)</td>
<td>30.2 (15.8)</td>
<td>0.199 (0.12)</td>
<td>0.60 (0.45)</td>
<td>71.3</td>
<td>101</td>
<td>64</td>
<td>−1.17 (0.18)</td>
</tr>
<tr>
<td>3 Wringley Gulf</td>
<td>11100 (1151)</td>
<td>415.0 (169.4)</td>
<td>43.0 (19.1)</td>
<td>0.492 (0.26)</td>
<td>0.97 (0.61)</td>
<td>139.3</td>
<td>105</td>
<td>53</td>
<td>−1.03 (0.24)</td>
</tr>
<tr>
<td>4 Amundsen Sea</td>
<td>31844 (4679)</td>
<td>809.2 (165.7)</td>
<td>105.4 (21.9)</td>
<td>3.383 (0.90)</td>
<td>2.28 (0.63)</td>
<td>262.4</td>
<td>114</td>
<td>45</td>
<td>−0.77 (0.36)</td>
</tr>
<tr>
<td>5 Pine Island Bay</td>
<td>19688 (5486)</td>
<td>566.1 (198.8)</td>
<td>72.2 (28.2)</td>
<td>1.552 (0.96)</td>
<td>1.25 (0.60)</td>
<td>444.7</td>
<td>108</td>
<td>51</td>
<td>−0.83 (0.34)</td>
</tr>
<tr>
<td>6 Etlinor Bay</td>
<td>11265 (1483)</td>
<td>384.1 (89.2)</td>
<td>46.1 (14.1)</td>
<td>0.533 (0.22)</td>
<td>0.74 (0.25)</td>
<td>372.8</td>
<td>139</td>
<td>26</td>
<td>−0.78 (0.36)</td>
</tr>
<tr>
<td>7 Ronne Entrance</td>
<td>15120 (2968)</td>
<td>497.9 (136.6)</td>
<td>61.7 (18.3)</td>
<td>0.954 (0.38)</td>
<td>1.10 (0.47)</td>
<td>346.6</td>
<td>135</td>
<td>70</td>
<td>−0.53 (0.49)</td>
</tr>
</tbody>
</table>

Table 1. Mean (± SD) Statistics for 46 Antarctic Polytypes for the Years 1998–2014

- The basal melt rates and corresponding ice shelf names are from Rignot et al. (2013). SD is not available for the length of open water season and the length of the phytoplankton bloom because these two parameters were calculated from a single averaged seasonal cycle. Open water area, km²; mean daily net primary production, mg C m⁻² d⁻¹; annual net primary production, g C m⁻² a⁻¹; total annual net primary production, Tg C a⁻¹; mean chlorophyll a concentration (mg m⁻³); continental shelf width, km; length of open water season, days; length of bloom, days; sea surface temperature, °C; mean daily PUR, mol photons m⁻² d⁻¹; basal melt rate of ice shelf, Gt a⁻¹.

The length of time each year that each polynya remained ice-free was much less variable than polynya size, averaging 126 ± 32 d a⁻¹ across all 46 polynyas. The length of the open water season was shortest in the Ronne Ice Shelf polynya (64 d a⁻¹) and longest in the Amery Ice Shelf and adjacent Prydz Bay polynyas (217 d a⁻¹). Thirty-two of the 46 polynyas experienced open water seasons lasting between 100 and 150 d a⁻¹.

polynya (Table 1). The mean size of all polynyas was 14,000 ± 36,000 km², although most polynyas were substantially smaller than the mean, with 31 polynyas having mean open water areas < 10,000 km² and 19 with open water areas < 4000 km² (Figure 3a).

The length of time each year that each polynya remained ice-free was much less variable than polynya size, averaging 126 ± 32 d a⁻¹ across all 46 polynyas. The length of the open water season was shortest in the Ronne Ice Shelf polynya (64 d a⁻¹) and longest in the Amery Ice Shelf and adjacent Prydz Bay polynyas (217 d a⁻¹). Thirty-two of the 46 polynyas experienced open water seasons lasting between 100 and 150 d a⁻¹.

ARRIGO ET AL. PRODUCTIVITY HOT SPOTS AROUND ANTARCTICA 5550

Journal of Geophysical Research: Oceans

10.1002/2015JC010888

The length of each year that each polynya remained ice-free was much less variable than polynya size, averaging 126 ± 32 d a⁻¹ across all 46 polynyas. The length of the open water season was shortest in the Ronne Ice Shelf polynya (64 d a⁻¹) and longest in the Amery Ice Shelf and adjacent Prydz Bay polynyas (217 d a⁻¹). Thirty-two of the 46 polynyas experienced open water seasons lasting between 100 and 150 d a⁻¹.
There was no significant temporal trend in open water area for any of the 46 polynyas over the 16 year time series.

### 3.2. Chlorophyll a and Net Primary Production

Each year, surface Chl a concentrations in coastal polynyas began to increase in October and peaked around January. By March, low solar elevation and, presumably, deeper vertical mixing forced by intensifying winds, precluded net phytoplankton growth and Chl a concentrations fell back to prebloom levels. On average, phytoplankton blooms in coastal polynyas persisted for $62.2 \pm 12.4$ days each year (Table 1), much less than the average length of the open water season. The mean Chl a concentration calculated over the phytoplankton growing season in the 46 polynyas ranged from $0.17 \pm 0.10$ mg m$^{-3}$ (Lutzoh-Holm Bay polynya) to...

![Figure 3](image_url)
2.28 ± 0.63 mg m⁻³ (Amundsen Sea polynya), averaging 0.60 ± 0.42 mg m⁻³ across all polynyas (Table 1). Most (29 of 46) polynyas exhibited Chl a concentrations ranging from 0.2 to 0.6 mg m⁻³ (Figure 4a). The mean Chl a concentration for coastal polynyas was more than double the mean concentration in noncontinental shelf waters of the Southern Ocean [Arrigo et al., 2008b]. There was no significant temporal trend in Chl a concentration for any of the 46 polynyas over the 16 year time series.

Not surprisingly, the seasonal cycles of daily NPP (Figure 5) for all 46 polynyas were broadly similar to that of Chl a (mean Chl a concentration explained 91% of the variance in mean NPP between polynyas in this study). Most of the coastal polynyas exhibited similar degrees of interannual variability, with the magnitude of daily NPP of most polynyas ranging approximately fourfold between the least productive and most productive years (Figure 5). However, the annual rate of NPP varied by a factor of 16 between coastal polynyas, ranging from 6.7 ± 10.8 g C m⁻² a⁻¹ in the Lützow-Holm Bay polynya to 105.4 ± 21.9 g C m⁻² a⁻¹ in the Amundsen Sea polynya (Table 1 and Figure 4c). This is due for the most part to large differences in mean daily NPP between polynyas, which varied from 116 to 802 mg C m⁻² d⁻¹, although most polynyas (32 of 46) exhibited values within the range of 150–400 mg C m⁻² d⁻¹ (Figure 4b). Like polynya size and Chl a concentration, there was no significant temporal trend in mean annual NPP for any of the 46 polynyas over the 16 year time series.

Total NPP in each polynya, which is calculated as a product of the annual NPP rate per unit area and the open water area of each polynya, was far more variable between polynyas than mean annual NPP, owing to the large difference in size between polynyas. Total NPP varied by more than 4 orders of magnitude between polynyas, ranging from a mean of 0.011 ± 0.01 Tg C a⁻¹ (W. Lazarev Sea polynya) to 22.2 ± 6.73 Tg C a⁻¹ (Ross Ice Shelf polynya), although most polynyas were at the lower end of the frequency distribution (Figure 4d). Of the 46 polynyas studied here, 40 had total NPP values below 1.0 Tg C a⁻¹ and 20 had values below 0.1 Tg C a⁻¹ (Table 1). The Ross Ice Shelf polynya was somewhat of an anomaly, having an
average total NPP value fourfold higher than the next most productive polynya. This is due to the fact that the Ross Ice Shelf polynya is both a very large polynya (239,603 km² during the growing season) and one of the most productive polynyas per unit area (693 mg C m⁻² d⁻¹).
3.3. Environmental Controls on Chlorophyll $a$ and NPP

3.3.1. Mean Daily Photosynthetically Usable Radiation (PUR)
Because of differences in latitude and the amount of cloud cover between polynyas, the daily dose of incident PUR in a given polynya, averaged over the growing season, ranged from an average of 9.8 \pm 3.08 \text{ mol photons m}^{-2} \text{ d}^{-1} in the Lützow-Holm Bay polynya to 15.6 \pm 1.11 \text{ mol photons m}^{-2} \text{ d}^{-1} in the Wilson Hills polynya, averaging 3744 \pm 373.8 \text{ mol photons m}^{-2} \text{ d}^{-1} for all 46 polynyas. Mean daily PUR for most of the polynyas (39 of 46) was in the intermediate range of 13–16 mol photons m$^{-2}$ d$^{-1}$ (Figure 3c). Regression analysis showed that there was no statistically significant relationship between the mean daily PUR during each growing season and the corresponding mean Chl $a$ concentration for the 46 coastal polynyas (Figure 6a). The same was true for the relationship between mean daily PUR and mean annual NPP (Figure 7a).

3.3.2. Number of Open Water Days
Similarly, linear regression analysis demonstrated that the length of the phytoplankton growing season (number of open water days) in each polynya had no significant impact on local phytoplankton populations, explaining <1% of the variance in mean Chl $a$ concentration between polynyas (Figure 6b) and only 2% of the variance in mean annual NPP (Figure 7b). This result, coupled with that from mean daily PUR, demonstrates that incident light availability did not control phytoplankton abundance or productivity in Antarctic coastal polynyas.

3.3.3. Open Water Area
Because the Ross Ice Shelf polynya was so much larger than the other polynyas (Table 1), we analyzed the effect of open water area on Chl $a$ and NPP both with and without the Ross Ice Shelf polynya included in the analysis. Polynya size, quantified as the mean open water area during the growing season, was significantly correlated with Chl $a$ concentration (Figure 6c), with larger polynyas tending to contain higher phytoplankton biomass ($R^2 = 0.23$ with the Ross Ice Shelf polynya included and 0.43 without). This relationship was quite strong in the Indian Ocean sector of the Antarctic, and somewhat less so in the Pacific and Atlantic sectors (Figure 8a). Polynya size also explained 53% of the variance in mean annual NPP among polynyas (Figure 7c), and was the strongest predictor of NPP among all the variables tested when the Ross Ice Shelf polynya was excluded. However, polynya size explained only 31% of the variance in mean annual NPP when the Ross Ice Shelf polynya was included in the analysis.

3.3.4. Sea Surface Temperature (SST)
The mean SST of coastal polynyas during the growing season varied from a high of $-0.17 \pm 0.73^\circ C$ in the Marguerite Bay polynya to a low of $-1.27 \pm 0.17^\circ C$ in the W. Lazarev Sea and adjacent Breid Bay polynyas (Table 1). A little more than half (26 of 46) of coastal polynyas had a mean SST during the growing season above $-1.0^\circ C$ while the rest exhibited SSTs below that value (Figure 3d). The mean SST during the growing season explained 41% of the variance in Chl $a$ concentration (Figure 6d) and 51% of the variance in NPP for the 46 polynyas studied here (Figure 7d). The relationship between SST and Chl $a$ was strongest in the eastern Indian Ocean sector and western Pacific Ocean sector of the Antarctic (Figure 8b).

3.3.5. Continental Shelf Width
The width of the continental shelf where each polynya is located varied by more than a factor of 10 around the Antarctic continent. The shelf is broadest in the Ross Sea (>500 km), the Weddell Sea (450 km), and in the vicinity of the Antarctic Peninsula (200–450 km), including much of the Bellingshausen and Amundsen seas. However, these continental shelves account for only 13 of the 46 polynyas studied here. The rest of the polynyas around Antarctica are located on a relatively narrow continental shelf ranging in width from approximately 25–200 km (Figure 3e).

Using simple linear regression, the width of the continental shelf at the location of each polynya explained 40% of the variance in mean Chl $a$ concentration during the growing season (Figure 6e) and 42% of the variance in mean annual NPP between polynyas. The relationship between continental shelf width and Chl $a$ concentration was strongest in the western Pacific and western Indian sectors and weakest in the eastern Pacific sector of Antarctica (Figure 8c).

3.3.6. Basal Melt Rate
Of the 46 polynyas studied here, 39 were located in close proximity to an identified ice shelf. Basal melt rates for these ice shelves, obtained from Rignot et al. [2013] in units of Gt of meltwater per year, showed a high degree of spatial variability, ranging from approximately zero to 145 Gt a$^{-1}$ (Getz Ice Shelf). Because
some polynyas are associated with more than one ice shelf, their meltwater input was assumed to be the sum of all of the melting ice shelves in the immediate vicinity; these are indicated in Table 1. For example, the Amundsen Sea polynya is associated with the Dotson, Crosson, and Thwaites ice shelves, and is assumed to receive an aggregate meltwater input of 181 Gt a\(^{-1}\) (Table 1).

Simple linear regression analysis showed that 59% of the variance in mean Chl a concentration (Figure 6f) and 45% of the variance in NPP (Figure 7f) was explained by the basal melt rate of nearby ice shelves. The relationship between basal melt rate and Chl a was strongest in the Eastern Pacific sector, where basal melt rates were highest (Figure 8d), and weakest in the Indian sector, where all of the

Figure 6. Regression of mean annual Chl a concentration against (a) mean daily photosynthetically usable radiation (PUR, mol photons m\(^{-2}\) d\(^{-1}\)), (b) number of days of open water, (c) open water area (km\(^2\)) (Ross Ice Shelf polynya removed), (d) sea surface temperature (°C), (e) continental shelf width (km), and (f) basal melt rate of nearby ice shelves (Gt a\(^{-1}\)) for the 46 coastal polynyas included in this study.
polynyas without an associated ice shelf are located. The y-intercept of the regression of Chl \( a \) against basal melt rate (Figure 6f), which provides an estimate of the mean Chl \( a \) concentration to be expected under conditions of no basal melt, was 0.39 ± 0.37 mg m\(^{-3}\), indistinguishable from the mean Chl \( a \) concentration in the seven polynyas that are not located near an ice shelf (0.40 ± 0.13 mg m\(^{-3}\)). Even after removing the Amundsen Sea from the analysis (the largest contributor to the regression), basal melt rate still explained 41% of the variance in Chl \( a \) and 33% of the variance in annual NPP between polynyas.

**Figure 7.** Regression of annual NPP against (a) mean daily photosynthetically usable radiation (PUR, mol photons m\(^{-2}\) d\(^{-1}\)), (b) number of days of open water, (c) open water area (km\(^2\)) (Ross Ice Shelf polynya removed), (d) sea surface temperature (°C), (e) continental shelf width (km), and (f) basal melt rate of nearby ice shelves (Gt a\(^{-1}\)) for the 46 coastal polynyas included in this study.
Figure 8. Mean chlorophyll a concentration during the growing season for 46 polynyas plotted with (a) open water area (km²), (b) SST, (c) continental shelf width (km), and (d) basal melt rate of nearby ice shelves (Gt a⁻¹).
Several of the predictor variables were weakly ($R^2 = 0.15–0.20$), but significantly associated with each other (Table 2). Most of these associations involved continental shelf width, which was weakly associated with three of the other variables used in the multiple regression models. In addition, SST was also weakly associated with basal melt rate. The VIF of all predictor variables was below 1.75 (Tables 3 and 4), the threshold above which multicollinearity of predictor variables can be expected to significantly affect the multiple regression model [Fox, 2008].

### 3.4. Multiple Linear Regression Model

We performed a multiple regression analysis to determine which of the six environmental variables investigated here (polynya size, number of open water days, mean PUR, SST, continental shelf width, and basal melt rate of nearby ice shelves) were the most important factors controlling phytoplankton biomass in coastal Antarctic polynyas. The 16 year mean satellite-derived Chl $a$ concentration in Antarctic polynyas was strongly and positively associated with a combination of four predictor variables, which together explained 78% of the variance in mean annual Chl $a$ between polynyas ($p < 0.001$). These included the basal melt rate of nearby ice shelves, mean SST, the width of the continental shelf at the polynya location, and the size of the polynya (Table 3). The final model form is

$$\text{CHL}_j = \beta_0 + \beta_1 \text{BM}_j + \beta_2 \text{SST}_j + \beta_3 \text{SW}_j + \beta_4 \text{OW}_j,$$

where CHL$_j$ is mean Chl $a$ concentration in polynya $j$ (mg m$^{-3}$), $\beta_0$ is the intercept, $\beta_1$–$\beta_4$ represent the estimated effects of the four predictor variables on Chl $a$, BM$_j$ is the annual basal melt rate of ice shelf $j$ into polynya $j$ (Gt a$^{-1}$), SST$_j$ is the mean sea surface temperature of polynya $j$ ($^\circ$C), SW$_j$ is the width of the continental shelf at polynya $j$ (km), and OW$_j$ is the size (open water area) of polynya $j$ (km$^2$). For polynyas not associated with an ice shelf, BM was assumed to be zero. Because the $y$-intercept of the regression of Chl $a$ against basal melt rate was indistinguishable from the mean Chl $a$ concentration in the seven polynyas that are not located near an ice shelf, giving these polynyas a basal melt rate of zero had no impact on the amount of variance explained by the four predictor variables.

Of the four variables retained in the regression model for Chl $a$, the basal melt rate of nearby ice shelves was by far the most important factor controlling phytoplankton abundance in coastal polynyas (Table 3), explaining almost twice as much of the variance in mean Chl $a$ (43.9%) as the next most important variable (SST, Table 3). Again, even when the Amundsen Sea was removed from the analysis, basal melt rate remained a significant, albeit weaker, predictor of both Chl $a$ and total annual production in coastal polynyas. Interestingly, although continental shelf width was able to explain 40% of the variance in mean Chl $a$ when considered alone (Figure 6e), when included in the multiple regression model with the other three variables, its relatively large contribution (18.5%) was statistically significant only at the 90% confidence level. This unexpected result is due to the significant, albeit weak, association of continental shelf width

### Table 2. Significant Relationships Between Predictor Variables Used in the Multiple Regression Analyses for Both Chl $a$ and NPP

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Predictor</th>
<th>$R^2$</th>
<th>$p$ Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shelf width</td>
<td>SST</td>
<td>0.19</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>SST</td>
<td>Basal melt rate</td>
<td>0.15</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Shelf width</td>
<td>Basal melt rate</td>
<td>0.19</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Shelf width</td>
<td>Open water area</td>
<td>0.20</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

*aAll relationships are positive.*

### Table 3. Multiple Linear Regression Parameter Estimates (±Standard Error) and Relative Importance of Predictor Variables in Explaining the Variance in Mean Chlorophyll $a$ Concentration Among 46 Antarctic Polynyas

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate $\beta$</th>
<th>$p$ Value</th>
<th>VIF</th>
<th>Relative Importance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>$0.91 \pm 0.18$ (mg m$^{-3}$)</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal melt rate</td>
<td>$0.0054 \pm 0.00084$ (mg m$^{-3}$)(Gt a$^{-1}$)</td>
<td>&lt;0.001</td>
<td>1.36</td>
<td>43.9</td>
</tr>
<tr>
<td>SST</td>
<td>$0.01 \pm 0.01$ (mg m$^{-3}$)($^\circ$C)</td>
<td>&lt;0.01</td>
<td>1.36</td>
<td>24.5</td>
</tr>
<tr>
<td>Shelf width</td>
<td>$0.00050 \pm 0.000028$ (mg m$^{-3}$)(km)</td>
<td>&lt;0.10</td>
<td>1.66</td>
<td>18.5</td>
</tr>
<tr>
<td>Open water area</td>
<td>$0.0000025 \pm 0.0000009$ (mg m$^{-3}$)(km$^2$)</td>
<td>&lt;0.05</td>
<td>1.27</td>
<td>13.1</td>
</tr>
</tbody>
</table>

ARRIGO ET AL. PRODUCTIVITY HOT SPOTS AROUND ANTARCTICA 5558
we performed a similar multiple regression analysis to determine the factors that are most important in controlling mean annual NPP in coastal polynyas. This analysis differs from that performed for Chl $a$ because NPP is not directly measured but is calculated using an algorithm that includes Chl $a$, PUR, and SST as input. Like our results for Chl $a$, regression analysis showed that mean annual NPP was not related to the mean number of open water days of a given polynya, but unlike our results for Chl $a$, it was related to mean daily PUR. Because the mean number of open water days did not significantly improve the fit of the multiple linear regression model, it was removed from the analysis.

The 16 year mean annual NPP in Antarctic polynyas was highly significantly and positively associated with a combination of five predictor variables (adjusted $R^2 = 0.82$, $p < 0.001$) that included the basal melt rate of nearby ice shelves, mean SST, the width of the continental shelf at the polynya location, the size of the polynya, and mean daily PUR. The model form is

$$\text{NPP}_j = \beta_0 + \beta_1 \text{BM}_j + \beta_2 \text{SST}_j + \beta_3 \text{SW}_j + \beta_4 \text{OW}_j + \beta_5 \text{PUR}_j,$$

where NPP$_j$ is mean annual NPP in polynya $j$ (g C m$^{-2}$ yr$^{-1}$).

Unlike the case for Chl $a$, no single variable explained a preponderance of the variance in NPP between polynyas in the multiple regression (Table 4). SST had the greatest impact (34.9%), followed closely by the basal melt rate of nearby ice shelves (26.4%). The width of the continental shelf where the polynya was located and open water area each explained a similar proportion of the variance in NPP (17–19%). Although mean daily PUR was also a significant predictor variable in the multiple regression, it only accounted for 2.9% of the variance in NPP between polynyas.

### 4. Discussion

Polynyas are biologically important features within polar oceans due to their role as early and highly concentrated sources of primary production to coastal ecosystems [Arrigo and McClain, 1994; Smith and Gordon, 1997; Smith et al., 2000a; Arrigo et al., 2003; Tremblay and Smith, 2007], a critical breeding site for high concentrations of marine birds and mammals [Siniff et al., 1977; Ainley et al., 1991; Stirling, 1997], and because they have an unusually strong biological pump that facilitates high rates of carbon sequestration [Arrigo et al., 2008a]. However, the specific factors controlling these processes over the entirety of the Antarctic have received surprisingly little attention to date. This is primarily due to the difficulty in sampling coastal polynyas in situ during the spring when rates of biological productivity are at their peak. Even research icebreakers have only managed to sample a handful of Antarctic polynyas (e.g., Ross Sea, Amundsen, Pine Island, Prydz Bay, Mertz) during this critical time of year. As a result, satellite remote sensing is one of the few tools available for investigating polynya dynamics over time at a continental scale.

Fortunately, as the satellite data record lengthens, our ability to discern differences between polynyas has increased accordingly. In an early study of Antarctic coastal polynyas, Arrigo and van Dijken [2003] were able to identify 37 Antarctic polynya systems (a polynya system was either an individual polynya or a small group of small polynyas within a restricted geographic region) based on only 5 years of satellite data. This short time series made it impossible to determine the relative importance of different environmental factors in controlling phytoplankton biomass and production within individual polynyas. While many of these same
polynyas are included in the present study, the longer time series of available satellite data, particularly ocean color, allowed us to both to refine the original analysis by Arrigo and van Dijken [2003] and further separate their 37 identified polynya systems into the 46 individual polynyas investigated here, and to assess the relative importance of a suite of environmental factors on phytoplankton dynamics.

Despite the much larger data set now available, some of the essential polynya characteristics reported by Arrigo and van Dijken [2003] have not changed appreciably. These include both the mean open water area and the Chl a concentration of those polynyas that are common to both studies. For example, the Amundsen Sea polynya had a mean Chl a concentration of 2.18 mg m$^{-3}$ in the study of Arrigo and van Dijken [2003], within 5% of the concentration of 2.28 mg m$^{-3}$ estimated here. Similarly, the Lützow-Holm Bay polynya had the lowest phytoplankton biomass in both studies, with an identical mean Chl a concentration of 0.17 mg m$^{-3}$. This reflects the fact that phytoplankton abundance has changed very little in the decade separating the two studies.

4.1. What Controls Phytoplankton Abundance in Coastal Polynyas?

Although the 46 Antarctic coastal polynyas we identified varied greatly in size, they shared some important features in common. All of the polynyas exhibited a distinct seasonal cycle in open water area that included similar timing of open water area expansion and contraction and an annual peak open water area in January-February (Figure 2). This relatively uniform pattern of polynya development resulted in similar seasonal phytoplankton dynamics within the coastal polynyas, although the magnitude of phytoplankton biomass and NPP (Figure 5) varied greatly between polynyas.

We were surprised to find that 78 and 82% of the variability in Chl a and NPP, respectively, between polynyas was explained by the six environmental variables that were measured remotely by satellites, suggesting that processes not accounted for in our study likely played only a relatively minor role in controlling phytoplankton dynamics. Nevertheless, the specific combination of factors controlling phytoplankton abundance and productivity within polynyas varied regionally around the Antarctic continent, depending critically on local factors such as the width of the underlying continental shelf and the melt characteristics of nearby ice shelves and much less so on differences in surface downwelling irradiance and length of the open water season.

4.1.1. Light Availability

Our data clearly show that despite marked variability in mean daily incident PUR and the length of the open water season between polynyas, neither variable had any significant impact on either the mean Chl a concentration or mean annual NPP during the growing season (the same result was achieved when using seasonal peak Chl a and NPP). This weak relationship between incident light availability and both Chl a concentration and annual NPP is likely because coastal polynyas remain near their annual maximum size for an average of 126 days, more than twice as long as the lifetime of the average phytoplankton bloom (62 days). Thus, given the long photoperiod (up to 24 h) and extended open water season in these high latitude waters, it appears that factors other than incident light (e.g., nutrients, see below) controlled the magnitude of phytoplankton biomass and annual NPP within coastal polynyas.

It should be noted, however, that we were unable to assess the impact of mixed-layer depth, which controls the mean light level in the upper water column, on interpynya variability of either Chl a or NPP. Deep vertical mixing will reduce mean mixed-layer light levels and phytoplankton growth rates will decline accordingly.

4.1.2. Open Water Area

Our analysis showed that larger polynyas had higher Chl a concentrations and were more productive than smaller ones, although this relationship was markedly weakened when the enormous Ross Ice Shelf polynya was included. The mechanism underpinning this relationship is unclear. Polynya size itself would not be expected to exert any direct control on phytoplankton populations, unless it was somehow associated with

ARRIGO ET AL.  PRODUCIENCY HOT SPOTS AROUND ANTARCTICA 5560
another factor that controlled phytoplankton abundance. As we have already shown, incident light availability itself exerts no direct influence on phytoplankton abundance or productivity and there is only a weak association between open water area and mean daily PUR. In addition, there is no reason to believe that open water area is related to MLD, which could impact phytoplankton abundance. For example, MLDs in the relatively small Amundsen and Pine Island polynyas [Alderkamp et al., 2012] appear to be very similar to those in the much larger Ross Ice Shelf polynya [Arrigo et al., 1999] and Mertz polynya [Sambrotto et al., 2003; Vaillancourt et al., 2003; Tremblay and Smith, 2007; Beans et al., 2008]. Similarly, there is no obvious connection between polynya size and potential nutrient availability, which could also impact phytoplankton abundance (although other factors we investigated probably do control nutrient availability, as described below).

It is conceivable that the effect of open water area on phytoplankton abundance may be related to the fact that larger polynyas are likely to experience a greater amount of sea ice melt. Because sea ice can contain elevated concentrations of Fe [Sedwick and DiTullio, 1997; Fitzwater et al., 2000; Grottì et al., 2005; Lannuzel et al., 2010], a larger amount of melting sea ice could supply more dFe to surface waters, promoting greater phytoplankton abundance. However, polynya size is not just a function of the amount of sea ice melt. Sea ice can also be advected away from the coast by winds and local currents, creating coastal polynyas with very little dFe from melting sea ice. In the Ross Sea, the Terra Nova Bay polynya is characterized by large amounts of sea ice melt and elevated dFe concentrations in surface waters while the nearby Ross Ice Shelf polynya contains much less ice melt and reduced surface dFe concentrations [Arrigo et al., 2000; Sedwick et al., 2011]. Thus, the relationship between changes in sea ice area for a given polynya and the amount of ice melt needs to be explored further for a larger number of Antarctic polynyas.

Alternatively, the effect of open water area on phytoplankton abundance could be manifested through reduced phytoplankton loss rates, rather than enhanced growth rates, in larger polynyas. Large and highly productive polynyas often support a greater abundance of marine mammals and birds [Arrigo and van Dijken, 2003; Karnovsky et al., 2007; Paterson et al., 2015], whose high rates of predation on krill and other zooplankton could reduce the top-down control of phytoplankton populations. Still, the importance of top-down control in these ecosystems has not been conclusively demonstrated and requires further investigation.

4.1.3. SST
Surprisingly, despite the small SST differences between polynyas (Table 1), in simple linear regressions, SST was able to explain a large amount of the variance in both mean Chl $a$ (41%) and annual NPP (53%). There are two avenues by which temperature can impact phytoplankton abundance, one direct and one indirect. The direct pathway is physiological, related to the higher metabolic rates observed at higher temperatures. It has long been recognized that phytoplankton grow faster in warmer waters, up to the point where the temperature increase becomes detrimental to macromolecular structure [Eppley, 1972; Tilzer and Dubinsky, 1987]. However, the temperature differences we observed between coastal polynyas across the Antarctic averaged only about 1°C. Given the expected temperature sensitivity of marine phytoplankton ($Q_{10} = 1.88$) [Eppley, 1972], this small temperature difference would result in about a 5% increase in net growth rate at the higher temperature. Although this pattern is consistent with both the higher mean NPP we observed in warmer polynyas and the high amount of variance in NPP that was explained by SST (recall that SST is an input to the NPP algorithm), it probably cannot explain the higher Chl $a$ concentrations, since the maximum amount of biomass attained during a bloom is a function of nutrient availability, not phytoplankton growth rate (higher growth rates may allow phytoplankton to reach maximum biomass earlier, but nutrients control the ultimate attainable biomass level).

It is more likely that the relationship between temperature and Chl $a$ concentration is indirect, possibly mediated via the relationship between SST and MLD. In Antarctic polynyas that have been studied to date, increasing solar radiation during the late spring and summer heats surface waters, resulting in marked temperature stratification. When these mixed layers are relatively shallow, due to either reduced wind mixing or low freshwater input, surface heating is concentrated within a thin surface layer and SST is relatively high. Deeper mixed layers distribute this heat throughout a greater volume of water and surface warming is less, resulting in a lower SST. In this way, SST becomes negatively correlated with MLD. This pattern has been observed in both the Ross Ice Shelf polynya [Arrigo et al., 1999, 2000] and in polynyas in the Amundsen Sea [Alderkamp et al., 2012], where shallow mixed layers are associated with higher SST and greater...
concentrations of Chl a. Thus, the relatively high correlation between SST and Chl a may be more closely related to greater light availability in warmer, shallow mixed layers than to physiological enhancement of phytoplankton growth.

4.1.4. Continental Shelf Width
The strong relationship between continental shelf width and Chl a concentration is also most likely to be indirect, since the width of the shelf alone would not be expected to directly impact phytoplankton biomass. Instead, continental shelf width likely influences the amount of sediment-derived Fe that gets mixed into surface waters and becomes available to phytoplankton. It is well established that dFe availability controls phytoplankton growth in many parts of the Antarctic [de Baar et al., 1990; Martin et al., 1990], including on continental shelves [Coale et al., 2003, 2005; Arrigo et al., 2003; Sedwick and DiTullio, 1997]. Dissolved Fe concentrations increase with proximity to the Antarctic coast [Sedwick et al., 2008] and continental shelf waters are especially enriched in dFe due to their proximity to Fe-rich sediments [Fitzwater et al., 2000; Gerringa et al., 2012]. However, dFe concentrations in Antarctic shelf waters are still insufficient to promote complete utilization of macronutrients by phytoplankton [Smith and Gordon, 1997; Arrigo et al., 2000; Mills et al., 2012] so enhancing the supply of dFe on the continental shelf will generally increase phytoplankton abundance [Martin et al., 1990; de Baar et al., 1990; Fitzwater et al., 2000]. Thus, sediments are an important potential source of Fe in shallow continental shelf waters, but this Fe must be mixed to the surface.

It has been demonstrated in waters of the eastern Pacific Ocean near Peru that the transfer of sediment-derived Fe to the surface is much more efficient on broad continental shelves than on narrow ones [Biller and Bruland, 2013]. This is because wider continental shelves increase the amount of contact between Fe-rich sediments and waters that upwell onto the continental shelf. High water column concentrations of sediment-derived Fe have also been observed within polynyas located on Antarctic shelves, either driven by advection of water masses that rise to the surface during winter convection [Blain et al., 2008] or that intersect the seafloor as Circumpolar Deep Water impinges on the continental shelf in the Amundsen Sea [Gerringa et al., 2012] and along the west Antarctic Peninsula [Dinniman et al., 2011; Measures et al., 2013]. Thus, the higher Chl a concentrations we observed in Antarctic coastal polynyas associated with wider continental shelves are likely to result from the additional Fe entrained into surface waters that can support greater phytoplankton populations.

4.1.5. Basal Melt Rate
Our analyses showed that the basal melt rate of ice shelves adjacent to coastal polynyas was by far the most important environmental factor controlling local phytoplankton abundance. It is likely that the high correlation between basal melt rates and both phytoplankton biomass and NPP in Antarctic polynyas is associated with the release of Fe into coastal waters as ice shelves melt, with phytoplankton abundance scaling with the rate of melt and hence the amount of Fe released. Enhanced phytoplankton biomass has been reported previously in the vicinity of melting icebergs [Smith et al., 2007; Raiswell et al., 2008; Lin et al., 2011] so it is not surprising that melting ice sheets can have the same effect. However, the strength of the relationship between basal melt rate and Chl a is somewhat surprising given the potential differences between ice shelves in the quantity, origin, and chemical composition of the Fe released into the ocean during basal melt. Whether this Fe derives from ground-up bedrock from the base of the ice shelf or aeolian material accumulated in the ice over its long history is not known [Raiswell, 2011]. Despite these possible differences between ice sheets, the large amount of variance in phytoplankton biomass and NPP explained by basal melt rate suggests that the mechanisms of Fe release and incorporation by phytoplankton between polynyas are similar to the first order.

It should be noted, however, that our interpretation that the relationship between basal melt and phytoplankton biomass and NPP is due to glacial Fe supply may be confounded by the fact that intrusions of warm Circumpolar Deep Water onto the continental shelf can resuspend sediment Fe and also accelerate basal melting [Dinniman et al., 2012; Dutrieux et al., 2014]. Thus, high phytoplankton abundance in polynyas near ice shelves experiencing enhanced basal melting could be driven by increased upwelling rates and a greater flux of sediment-derived Fe, rather than a glacial Fe source. We consider this possibility unlikely given that melting ice shelves and icebergs are known sources of dFe to local waters [Smith et al., 2007; Gerringa et al., 2012; Planquette et al., 2013] and our observation that basal melt rates explained twice as much of the variance in Chl a between polynyas than did continental shelf width (Table 3).
Melting ice shelves could also reduce the density of local surface waters, increasing stratification and enhancing light availability, thereby increasing phytoplankton growth, irrespective of any additional dFe input. However, the limited available data for the Amundsen Sea suggest that as meltwater upwells at the face of the ice shelves, it promotes deep mixing, rather than stratification, and that phytoplankton abundance in these upwelled waters is very low [Alderkamp et al., 2012; Gerringa et al., 2012]. These waters eventually thermally stratify within 100 km the ice shelf face and the surface layer that forms is high in glacially derived Fe, both in particulate and dissolved form [Gerringa et al., 2012]. As surface waters continue to advect northward, they fuel high rates of phytoplankton NPP and concentrations of Chl a can exceed 10 mg m⁻³ [Alderkamp et al., 2012]. Binding by increased ligand concentrations keeps this Fe in bioavailable form so that the bloom can persist long distances from the Fe source [Thuróczy et al., 2012]. By contrast, in the Ross Sea, basal meltwater from the Ross Ice Shelf deepens as it advects away from the shelf face [Loose et al., 2009], so it contributes little or nothing to either surface stratification or surface dFe concentrations. Thus, the data from these two contrasting polynyas indicate that phytoplankton biomass and NPP in coastal polynyas is controlled largely by Fe availability, both released from melting ice shelves and resuspended from continental shelf sediments, rather than by surface stratification by ice sheet meltwater. Taken together, continental shelf width and basal melt rate explain 70% of the variance in mean Chl a concentration and 58% of the variance in mean annual NPP among the 46 Antarctic coastal polynyas. More field studies will be needed to confirm whether input of dFe is the basis for these relationships.

4.2. The Future

Annual rates of NPP in Antarctic coastal polynyas are among the highest in the Southern Ocean [Arrigo and van Dijken, 2003] due in large part to the relaxation of nutrient limitation by Fe released from melting ice shelves. Nevertheless, there is still an ample reservoir of unutilized macronutrients on Antarctic continental shelves and an additional Fe source would very likely result in enhanced phytoplankton production. Given the current rapid rate of ice shelf melting in west Antarctica [Rignot et al., 2013] and the expectation that the melt rate of Antarctic ice shelves is likely to increase in the future [Bell, 2008], rates of phytoplankton productivity are likely to increase as well. Thus, the ecological and biogeochemical importance of coastal polynyas is likely to increase as these regions become even more favorable for the growth of both phytoplankton and the higher trophic level organisms that rely on them as a food source.

References

Biller, D. V., and K. W. Bruland (2013), Sources and distributions of Mn, Fe, Co, Ni, Cu, Zn, and Cd relative to macronutrients along the central California coast during the spring and summer upwelling season, Mar. Chem., 155, 50–70, doi:10.1016/j.marchem.2013.06.003.


Chever, F., G. Sarthou, E. Bucciarelli, S. Blain, and A. R. Bowie (2010), An iron budget during the natural iron fertilisation experiment KEOPS (Kerguelen Islands, Southern Ocean), Biogeosciences, 7(2), 455–468.


Erratum
In the originally published version of this article, the results of a minor coding error were discovered. The errors have since been corrected and this version may be considered the authoritative version of record.