Ocean productivity south of Australia during spring and summer

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A B S T R A C T

We estimated mixed layer gross and net community production on a total of 20 crossings in the Australian sector of the Southern Ocean during the summer half-years (October–March) of 2007–2010. These estimates were calculated from measurements of O₂/Ar ratios and triple isotope compositions of O₂ in ~250 seawater samples collected underway. For comparison purposes, we also measured the seasonal drawdown of mixed layer NO₃ and SiO₂ concentrations during 2006–2007 and 2007–2008. Across all samples, average values of gross and net O₂ production (measured by O₂/Ar and O₂ isotopes), were about 86 ± 90 and 18 ± 17 mmol O₂ m⁻² day⁻¹, respectively. Gross production was highest at the Subtropical Front (up to ~230 mmol O₂ m⁻² day⁻¹), and decreased southward (to ~10 near the southern boundary of the Antarctic Circumpolar Current). In contrast, net community production showed little meridional variation. Net and gross O₂ production increased throughout the spring-to-fall period, although most SiO₂ drawdown occurred in December. Consistent with satellite chlorophyll estimates, we saw no evidence for an intense spring bloom (e.g. as has been observed in the North Atlantic). Volumetric net and gross O₂ production in the mixed layer, normalized to chlorophyll, increased with considerable scatter) with average irradiance in the mixed layer. These relationships provide a basis for estimating production from Argo float data and properties observed by satellite.

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1. Introduction

The Southern Ocean has long been identified as the largest High Nutrient Low Chlorophyll (HNLC) region in the global ocean. Variations in its status are important to nutrient delivery to other ocean basins (Sarmiento et al., 2004). They are also relevant to global carbon sequestration by the biological pump on decadal to at least interglacial timescales (Matear and Hirst, 1999; Sarmiento and Orr, 1991; Sigman and Boyle, 2000). The High Nutrient appellation is an over-simplification. Phosphate and nitrate remain abundant across the entire Southern Ocean throughout the year. However silica, an essential nutrient for diatoms, which are the dominant large phytoplankton group, becomes depleted in summertime waters between the Subantarctic Front and the Polar Front (Nelson et al., 2001; Treguer and Jacques, 1992; Trull et al., 2001a). Moreover, iron and light are actually the key limiting “nutrients”. Lack of iron, an essential element in enzymes, is now known to limit primary production essentially everywhere in the Southern Ocean except near localized sources such as islands, plateaus, and boundary currents (Boyd and Ellwood, 2010). Low light availability driven by both deep surface mixed layers and cloudiness also limits photosynthesis, including physiological interactions between Fe scarcity and the efficiency of light utilization (Hiscock et al., 2008; Mitchell et al., 1991; Strzepek et al., 2012; Sunda and Huntsman, 1997).

The Low Chlorophyll status is often linked to these limitations on primary production, but that is also an over-simplification, because loss by grazing and export is at least as strong a control on phytoplankton biomass accumulation (Cullen, 1995; Frost, 1991; Morel et al., 1991; Smith and Lancelot, 2004). Indeed, despite the LC status, Southern Ocean fluxes of organic carbon to the deep ocean in sinking particles are close to the global median (Honjo et al., 2008, 2000; Trull et al., 2001c). The efficiency of this grazing and export may be modulated as mixed layer [SiO₂] varies seasonally and meridionally.

Improving the understanding of the controls on the HNLC status of the Southern Ocean requires measurements of upper ocean carbon fluxes. In this context, we present a large set of paired estimates of gross primary production (GPP) and net community production (NCP) derived from gas tracers. The observations cover the north-south extent of Southern Ocean waters.
and the late spring to early autumn half-year that dominates annual production. As outlined in the Methods section, GPP estimates are based on the isotopic composition of dissolved oxygen, and the NCP estimates are based on the excess of dissolved oxygen concentrations relative to biologically inert argon concentrations. Conversion of these state variables to the GPP and NCP rate variables is achieved by calculation of gas exchange rates with the atmosphere. Both terms reflect productivities averaged over the gas exchange time of the mixed layer (=mixed layer depth/gas transfer velocity) or ~2 weeks.

The results are based on discrete samples collected from the underway clean seawater supply intake onboard the French Antarctic station resupply ship, ASTROLABE. ASTROLABE made three round-trip crossings of the Southern Ocean each year between Hobart, Tasmania, Australia and Dumont d'Urville, Adelie Land, Antarctica. These crossings made it possible to characterize GPP and NCP six times each season. We can thus evaluate spatial, seasonal, and interannual variations in the rate terms. Using supplementary surface seawater nutrient analyses, ARGO float data, and satellite observations, we can then also explore relationships with surface phytoplankton biomass, light levels, and mixed layer depths. Specifically, we focus on three questions:

1. Is there a spring phytoplankton bloom seen in primary production (as opposed to biomass accumulation) in the Australian sector of the Southern Ocean, and if so, what are its characteristics?
2. How does productivity vary with latitude in the Australian sector, and what factors mediate this relationship?
3. Is there a simple relationship between NCP and GPP and autonomously sensed properties, such as chlorophyll (Chl), sea-surface photosynthetically available radiation (PAR), and mixed layer depth (MLD)? If so, can it be used, in conjunction with ancillary data, to scale local estimates of NCP and GPP to broader regions?

As expanded on in the Discussion section, our study region south of Australia has the advantage of much background information. Material includes (a) a understanding of circulation from six repeats of the WOCE/CLIVAR SR3 hydrographic section from Tasmania to Antarctica (Rintoul and Trull, 2001; Sokolov and Rintoul, 2002; Sokolov and Rintoul, 2009; Trull et al., 2001a), (b) special volumes from two-month-long process studies of trace element (Fe, Mn, etc.) and macro-nutrient (N, P, Si) biogeochemistry and microbial tropho-dynamics in the SAZ (Bowie et al., 2011a, 2011b, 2009; Cassar et al., 2011, 2015; Sedwick et al., 2008, 1999; Trull et al., 2001b), and (c) an ongoing program, as part of Australia’s Integrated Marine Observing System (www.imos.org.au), of air to sea and surface to deep ocean carbon fluxes at the Southern Ocean Time Series site (Rigual-Hernández et al., 2015; Shadwick et al., 2015b; Trull et al., 2001c; Weeding and Trull, 2014). These efforts provide important context for our observations.

2. Experimental methods

2.1. Principles of the dissolved O2 tracer methods for GPP and NCP

The O2/Ar ratio of dissolved gases in the mixed layer, and the δ17O and δ18O of O2 can be used to constrain mixed layer NCP and GPP, respectively (Castro-Morales et al., 2013; Luz and Barkan, 2000; Prokopenko et al., 2011; Reuer et al., 2007). The O2/Ar ratio allows physical supersaturation (reflected in both O2 and Ar concentrations) to be removed from the total O2 supersaturation. O2/Ar measurements thus quantify that part of O2 supersaturation derived from photosynthesis in excess of respiration. Multiplying biological O2 supersaturation by the gas transfer velocity and saturation O2 concentration gives the sea-air flux of biological O2 (termed “net O2 bioflux” or just “net bioflux”). At steady state, and neglecting vertical mixing (see below), this flux must be sustained by photosynthesis in excess of respiration, and hence provides an estimate of NCP.

The estimation of GPP is based on recognition that there are two sources of dissolved O2 in the mixed layer, atmospheric O2, and O2 produced in situ by photosynthesis. Measuring both δ17O and δ18O of the dissolved O2 constrains the fraction deriving from each of these sources. The tracer quality of the two δ terms comes from the fact that O isotopes are mass-dependently fractionated by photosynthesis and respiration (for which the change in δ17O is ~0.5 times the change in δ18O). However, photochemical exchange in the stratosphere leads to non-mass-dependent fractionation, which in turn causes the global atmosphere to be depleted in 17O relative to 18O (Luz and Barkan, 2000; Luz et al., 1999). The relative proportions of atmospheric and photosynthetic O2 in the dissolved O2 pool can be computed from the magnitude of the 17O deficiency. Then, from the proportion of photosynthetic O2, the O2 concentration, and the gas transfer velocity, one can calculate the sea-air flux of photosynthetic O2 (“gross bioflux”). At steady-state, and again neglecting vertical mixing, this term provides an estimate of O2 gross primary production.

In the text that follows, we generally use the terms NCP and GPP to represent true values of production. We generally use the terms “net O2 bioflux” and “gross O2 bioflux” to represent the sea-air fluxes, calculated from observations, that approximate net and gross production.

The estimates of NCP and GPP from the O2 measurements rely on the assumptions of biological steady-state (constant NCP and GPP) and negligible mixing across the base of the surface mixed layer, as well as the parameterizations of air-sea gas exchange (as detailed below). Probable biases in net O2 bioflux estimates of NCP have been calculated in a model context (Jonsson et al., 2013). On average, when O2 is biologically supersaturated in the mixed layer, net O2 bioflux underestimates NCP by about 10%. Additional random errors are much larger, probably about ±40%, because of non-steady-state conditions, mixing across the base of the mixed layer, and analytical uncertainties. Experimental studies also show that net and gross bioflux can be influenced by upwelling, vertical mixing, and entrainment (e.g., Castro-Morales et al., 2013). We minimize these issues by excluding from our analysis samples that are undersaturated in O2 (which signifies upwelling). In any case, it is means and trends in our data that are robust, rather than individual excursions.

Nicholson et al. (2014) compared gross bioflux with GPP as simulated in a model context. In their simulations, gross bioflux underestimated GPP in spring. This discrepancy was associated with a modeled spring bloom that is not observed in our data. In summer and autumn, modeled gross bioflux was 2–3 times higher than simulated GPP in the mixed layer. This error derived largely from the entrainment and mixing of deeper euphotic zone waters into the mixed layer, a phenomenon unlikely to be important in our study area. In our data set, MLD was >40 m at 88% of XBT stations, and >30 m at 80% of stations. According to Westwood et al. (2011), most primary production in the Australian sector occurs above 30 m depth, and about 90% above 40 m depth. Therefore it is improbable that our data are seriously aliased by entrainment and mixing of deeper photosynthetic O2 into the mixed layer. There are additional errors associated with lateral advection and non steady-state conditions (Nicholson et al., 2014). Again, we need to focus on average values and trends rather than individual samples.
2.2. Dissolved O₂ sample collection and analysis

The water samples (Fig. 1) were collected from the underway clean seawater supply, which has its intake at about 3 m depth on the resupply ship Astrolabe. Water samples were collected into pre-evacuated and H₂Cl₂ pre-poisoned 500 ml bottles with Leuwers-Hapert O-ring valves, as described by Emerson et al. (1995) and Reuer et al. (2007). The gases equilibrated passively between the water and headspace before analysis in Princeton, and most of the water was removed by aspiration. Non-condensable gases (essentially O₂, N₂, and Ar) were frozen onto molecular sieve and then passed through a gas chromatographic column to separate O₂ and Ar from N₂. The O₂ and Ar were frozen into a cryo-cooler at ~ 15 K, warmed, and admitted to the Finnigan MAT 252 mass spectrometer as described by Reuer et al. (2007). ¹⁸O²O, ¹⁷O²O, and ¹⁶O₂ were measured by simultaneous collection for 3 cycles with 24 blocks per cycle. ¹²Δ of O₂ is defined by this equation:

\[ ¹²Δ = \ln(0.001 \times ³¹⁷O + 1) - 0.516 \times \ln(0.001 \times ³¹⁸O + 1) \]

The uncorrected ¹²Δ of O₂ was computed, using Eq. (1), from the raw data, based only on the observed ion current ratios. A number of factors can affect the raw values of ³¹⁷O and ³¹⁸O. We evaluated these factors by analyzing the variability of between 76 and 311 air standards measured during each of 5 analysis periods. In total, these extended from February 14, 2006, to January 1, 2011.

We rejected all samples where the mass 28 peak was greater than 0.3% of the mass 32 peak, because high N₂ leads to large errors in ³¹⁷O. We observed no dependence of ³¹⁷O and ³¹⁸O on the ratio of 28–32 ion currents for the remaining samples, or on the initial pressure imbalance between sample and reference sides (data not shown). We did not correct for the zero enrichment, which effectively cancels out when seawater is compared with water equilibrated in the laboratory.

The ¹²Δraw values were corrected for differential gas depletion between sample and reference sides during analysis (Stanley et al., 2010), according to the formula:

\[ \text{Imbalance term} = \left(1 - \frac{V_{2\text{sample}}-\text{end}}{V_{2\text{sample}}-\text{start}}\right) \times \left(1 - \frac{V_{2\text{reference}}-\text{end}}{V_{2\text{reference}}-\text{start}}\right) \]

The imbalance term registers the change in the ion current between sample and reference during 1 block. V is the voltage, and the subscripts “end” and “start” refer to the voltages read at the end of the first block by the interfering masses program and at the start of the first block by the standard Finnigan ion current acquisition software from which δ values are calculated.

¹²Δ data for a large number of equilibrated lab water samples analyzed in this way were higher than the equilibrium value (discussed below) by about 0.005‰. We therefore subtracted the average difference, calculated for each of our 5 analysis periods, from the corrected ¹²Δ value of O₂. Knowing ¹²Δ and ³¹⁸O, we then calculated ³¹⁷O from Eq. (1). Because of numerical issues, this approach is marginally more accurate than calculating ¹²Δ after correcting the measured ³¹⁷O and ³¹⁸O values independently. The choice of the coefficient (in Eq. (1)) is immaterial to the result: we calculate the same δ¹⁷O value if we use a coefficient of 0.518. We do not use ¹²Δ for any other purpose in the analysis of our results. ³¹⁸O of O₂ is fractionated by 0.1–0.3‰ during the process of sample preparation. A correction to the measured ³¹⁸O value is made which does not affect ¹²Δ. O₂/Ar ratios were normalized to air and a correction was applied for the residual gas in the water sample after equilibration with the headspace. Uncertainties are ±3‰ for the O₂/Ar ratio, ±0.1‰ for ³¹⁸O of O₂, and ±0.008‰ for ¹²Δ of O₂.

2.3. Calculation of net and gross production from the O₂ tracers

From ³¹⁷O and ³¹⁸O calculated as described above, the ratio of G/k[O₂]eq is calculated from Prokopenko et al. (2011, equation (7)), transformed to δ notation as described in their paper:

\[
\frac{G}{kO_2} = \frac{1 - \frac{10^{-3}δ^{18}O_{eq} + 1}{10^{-3}δ^{18}O_{eq} + 1}}{1 - \frac{10^{-3}δ^{18}O_{eq} + 1}{10^{-3}δ^{18}O_{eq} + 1}}
\]
identical to that of the substrate water. We note the discovery that
photosynthetic O₂ is fractionated inside cells by respiration before it
becomes part of the ambient O₂ pool (Luz and Barkan, 2011).
However, as long as the adopted parameters give a 17Δ value of
+0.249‰ for seawater with respect to air, calculated values of G/k
[O₂]eq will be insensitive to the exact values selected for the iso-
topic composition of photosynthetic O₂.

Finally we need to adopt values for δ17Oeq and δ18Oeq δ18Oeq was
accurately measured as a function of temperature (Benson and
Krause, 1980), and we use their temperature-dependent val-
ues. We adopt the 17Δ value for dissolved O₂ in equilibrium with
air, +0.008‰, measured by Reuer et al. (2007) and subsequently
by Stanley et al. (2010).

Gas transfer velocities between the ocean and atmosphere
were calculated as weighted-average values for the 60 days before
collection of the sample, using wind speeds from the NOAA/Sea-
winds blended product (Chin et al., 1998), and the gas transfer
parameterization of Sweeney et al. (2007). Gas transfer velocities
closer to days of collection were weighted more heavily (Bender
et al., 2011; Reuer et al., 2007). The sea-air biological O₂ flux (“net
O₂ bioflux”) was then simply calculated from the product of the
biological O₂ supersaturation, O₂ solubility (i.e. O₂ concentration
at saturation), and the gas transfer velocity (e.g., Reuer et al., 2007).
Gross O₂ bioflux was calculated from Prokopenko et al. (2011,
above equation).

The calculation of net and gross bioflux relies on the assump-
tion that there is negligible addition of air during the collection of
the water samples using the ship’s underway supply, e.g. from
either air forced under the hull by ship motions or exposure to air
in the pumping system. The relationship between δ18O of O₂ and
the O₂/Ar ratio provides an assessment of air injection during
collection. In the presence of only biological processes, these two
variables are anti-correlated along a line that passes slightly above
the atmospheric equilibrium point (at O₂/Ar~ −86 per mil relative
to air, and δ18O of O₂ about 0.8‰, in the Southern Ocean). This
occurs because the photosynthetic addition of O₂ raises O₂/Ar
while lowering δ18O of O₂ (since photosynthetic O₂ has the same
δ18O as seawater, around ~24‰ with respect to air O₂, which is
the standard). Conversely, respiration consumes O₂, lowering O₂/Ar
while raising δ18O of O₂ (because respiration discriminates
against the heavy isotope). The co-occurrence of gas exchange and
variable ratios of net/gross production complicates this correla-
tion. Nonetheless, a compact relationship between δ18O of O₂ and
the O₂/Ar ratio was observed (as shown in Supplementary material
Fig. S1). This suggests minimal addition of air to the samples, be-
cause air injection changes the O₂/Ar ratio while leaving δ18O
nearly unchanged. Based on this diagnostic, visual inspection in-
dicates that less than 5% of the samples may have experienced
significant air injection and only 3 points were sufficiently com-
promised to require removal from the dataset (Supplementary
material). We also assume that there is negligible removal of O₂ as
seawater flows through the ship’s line from the intake to the sampling
space (for a cautionary note see Jurak et al. (2010)).

Finally for this section, we note that either upwelling or net
heterotrophy (Hamme et al., 2012) can cause net O₂ bioflux to be
less than zero. We believe that upwelling is by far the dominant
cause, for two reasons. First, deep waters, undersaturated in O₂,
mix to the surface of the Southern Ocean, particularly south of the
Polar Front. Second, in the Southern Ocean as elsewhere, there is
not enough POC in the mixed layer to sustain net heterotrophy for
a large fraction of the summer half-year. We include samples with
negative bioflux in our data set (Supplementary material), but, to
keep the focus on productivity controls, we exclude biologically
under-saturated samples from the net bioflux values plotted in all
figures other than Fig. 3. The exception is samples that were bio-
logically undersaturated by < 0.3‰, which is the analytical

uncertainty. In contrast, we include all gross O₂ bioflux values in all
figures, (regardless of their associated O₂/Ar values). This is so
because gross bioflux is much less affected by upwelling than net
bioflux (since the oxygen isotopic gradient across the bottom of
the mixed layer is relatively much smaller than the O₂/Ar gradi-
ent). Exchange across the base of the mixed layer also impacts
NCP estimates based on nutrient depletions. From model calcu-
lations, the bias has been suggested to be up to 2-fold in spring
when mixed layer variability is large, and ~10% in summer when
stratification is well established (Wang and Matear, 2001; Wang
et al., 2001).

2.4. Additional data sources

Mixed layer macro-nutrient (nitrate, phosphate, and silicic
acid) samples were collected in parallel to the oxygen samples
(Fig. 2). Nutrient samples were frozen onboard and analyzed in
Hobart following WOCE protocols.

MLDs used in the interpretation of Astrolabe bioflux data were
estimated from XBT’s deployed by the ship. The base of the mixed
layer was identified using a temperature criterion (Tz was 0.2 °C
lower than Tsurf) (Montegut et al., 2004).

PAR and Chl were characterized by remote sensing (Arrigo
et al., 2008), and the extinction coefficient was parameterized in
terms of Chl (Morel and Maritorena, 2001). Average mixed layer
PAR was calculated from the following equation:

Average ML PAR = Sea surface PAR* \(\int \exp(-kz)dz/MLD\)

(4)

k is the light attenuation coefficient and z is depth below the
sea surface. The integral is evaluated from the sea surface to the
MLD.

We also computed chl-normalized net and gross O₂ bioflux, di-
viding bioflux by Chl as inferred from remote sensing. Specifically, we
used NASA MODIS/Aqua 2009b daily 4 km level 3 fields for remotely
sensed SST, PAR, and Chl (http://oceancolor.gsfc.nasa.gov).
For the purpose of calculating chl-normalized bioflux, the in-situ bioflux
observations are matched to the nearest available satellite data
points, and Chl is registered for the closest observation within a 1°
radius from the day of collection to 3 days before and after. The in-
clusion of such potentially distant matches is appropriate as the
waters we sample were likely mixed over a large area during the
period prior to sampling. We performed sensitivity tests that suggest
that the typical maximum error in Chl due to matching of distant
locations is less than ± 50%, which is within the acceptable range
for our application. However, the satellite chlorophyll retrievals add
scatter to the calculated values of chl-normalized production. We
also note that a number of papers discuss evidence that Southern
Ocean chlorophyll retrievals are aliased toward values lower than
in situ measurements (Johnson et al., 2013; Marrari et al., 2006;
Mitchell and Kahru, 2009; Szeto et al., 2011). This effect may alias our
calculations and can be addressed when the Southern Ocean chl al-
gorithm is better constrained.

The complete oxygen-based dataset is tabulated in the Sup-
plementary material.

3. Results

We first present contextual observations on the spatial and
seasonal variations of water column conditions. These come from
the in-situ discrete nutrient analyses (Section 3.1) and the ARGO
and satellite remote sensing estimates of mixed layer depth, in-
solation, and chlorophyll (Section 3.2). We then discuss net and
gross bioflux estimates (Section 3.3), and examine the relationship
between chl-normalized production and mixed layer irradiance.
and Zealand (e.g., Morrison et al., 2001; Smith Jr et al., 2000). There section (Trull et al., 2001a), and in the AESOPS study south of New along the nearby WOCE/CLIVAR SR3 north-south hydrographic upper water column, such as we 0.2 in Subtropical waters. High ratios for the Si/N decrease in the 2002). The uptake ratio under Fe limitation is near 4 vs. near 1 for there (Bowie et al., 2009; Cassar et al., 2011; Sosik and Olson, 2001; Wang et al., 2001). Keeping these caveats in mind, Model estimates suggest that these two transport modes double fluxes calculated from springtime nutrient drawdown (Wang and Matear, 2001; Wang et al., 2001). There are multiple contributing factors to these variations. In the AZ and PFZ, production is dominated by diatoms. Their Si uptake is known to increase with Si availability, and the Si/N uptake ratio is expected to be higher under the Fe limited conditions that prevail there (Bowie et al., 2009; Cassar et al., 2011; Sosik and Olson, 2002). The uptake ratio under Fe limitation is near 4 vs. near 1 for Fe replete growth, at least for some species (Brzezinski et al., 2002; Franck et al., 2000; Takeda, 1998). In the SAZ and especially Subtropical waters, non-siliceous organisms contribute significantly to NCP, lowering the Si/N drawdown ratio (Kopczynska et al., 2001; Trull et al., 2001c). In addition to these uptake-based controls on Si/N drawdown, remineralization is important. N is recycled more rapidly than Si, attenuating the ratio of NO₃/SiO₂ drawdown (Green and Sambrotto, 2006; Rubin, 2003). N/P drawdown stoichiometry also revealed zonal variations, with the median uptake ratio of N/P ranging from 13 to 19 in the Subtropical, Subantarctic, and Antarctic zones, but only ~9 in the PFZ. This result agrees well with (Lourey and Trull, 2001), who observed a ratio of 15.1 in the SAZ and 8.3 in the PFZ, but the cause remains unclear.

Calculation of NCP from the seasonal surface nitrate drawdown is difficult, because vertical distributions were not measured yet appear to be important, especially in the PFZ (Lourey and Trull, 2001; Parslow et al., 2001). As well, both vertical mixing and northward Ekman transport provide significant nutrient resupply (DiFio et al., 2006a; Green and Sambrotto, 2006; Rubin, 2003). Model estimates suggest that these two transport modes double fluxes calculated from springtime nutrient drawdown (Wang and Matear, 2001; Wang et al., 2001). Keeping these caveats in mind, we make approximate first estimates as follows. The seasonal [NO₃] decrease in the Subantarctic Zone was 3–4 µmol kg⁻¹, and about 2–3 µmol kg⁻¹ between the SAF and the SACCF (Fig. 2). For a summer MLD of ~40 m in the Subantarctic Zone and ~80 m to the south, and assuming C/N = 7, then seasonal NCP would be about 1 mol C m⁻² across the entire transect from the Subtropical Front to the SACCF. In comparison, depth resolved nitrate estimates suggest ~3–4 mol C m⁻² for the SAZ from October to March, a period over which mixed layer depth shoaled from 200 to ~50 m (DiFio et al., 2006a; Lourey and Trull, 2001).

There is considerable interannual variability in nutrient drawdown. As an example of interannual variability, October NO₃ and Fe replete growth, at least for some species (Brzezinski et al., 2002; Franck et al., 2000; Takeda, 1998). In the SAZ and especially Subtropical waters, non-siliceous organisms contribute significantly to NCP, lowering the Si/N drawdown ratio (Kopczynska et al., 2001; Trull et al., 2001c). In addition to these uptake-based controls on Si/N drawdown, remineralization is important. N is recycled more rapidly than Si, attenuating the ratio of NO₃/SiO₂ drawdown (Green and Sambrotto, 2006; Rubin, 2003). N/P drawdown stoichiometry also revealed zonal variations, with the median uptake ratio of N/P ranging from 13 to 19 in the Subtropical, Subantarctic, and Antarctic zones, but only ~9 in the PFZ. This result agrees well with (Lourey and Trull, 2001), who observed a ratio of 15.1 in the SAZ and 8.3 in the PFZ, but the cause remains unclear.

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Calculation of NCP from the seasonal surface nitrate drawdown is difficult, because vertical distributions were not measured yet appear to be important, especially in the PFZ (Lourey and Trull, 2001; Parslow et al., 2001). As well, both vertical mixing and northward Ekman transport provide significant nutrient resupply (DiFio et al., 2006a; Green and Sambrotto, 2006; Rubin, 2003). Model estimates suggest that these two transport modes double fluxes calculated from springtime nutrient drawdown (Wang and Matear, 2001; Wang et al., 2001). Keeping these caveats in mind, we make approximate first estimates as follows. The seasonal [NO₃] decrease in the Subantarctic Zone was 3–4 µmol kg⁻¹, and about 2–3 µmol kg⁻¹ between the SAF and the SACCF (Fig. 2). For a summer MLD of ~40 m in the Subantarctic Zone and ~80 m to the south, and assuming C/N = 7, then seasonal NCP would be about 1 mol C m⁻² across the entire transect from the Subtropical Front to the SACCF. In comparison, depth resolved nitrate estimates suggest ~3–4 mol C m⁻² for the SAZ from October to March, a period over which mixed layer depth shoaled from 200 to ~50 m (DiFio et al., 2006a; Lourey and Trull, 2001).

There is considerable interannual variability in nutrient drawdown. As an example of interannual variability, October NO₃ and
SiO$_2$ concentrations were meridionally constant across the AZ from the Polar Front (~56°S) south to about 61°S, in each year of our observations. However, [NO$_3$] seasonal drawdown was about 1 μM in 2006–7 but closer to 3 μM in 2007–8. In this same region, Si was almost fully depleted by January in 2007 but only about half depleted in 2008. The timing of SiO$_2$ depletion in our data set is similar to other observations, which also suggest that the seasonal consumption mainly occurs before the end of January (Green and Sambrotto, 2006; Morrison et al., 2001; Rubin, 2003).

3.2. Mixed layer depth, irradiance, and chlorophyll variations

In Hovmøller diagrams, Fig. 3 shows weekly estimates for mixed layer depth (MLD), euphotic depth (Z), Chlorophyll concentrations (Chl), and surface photosynthetically available radiation (PAR). Also shown is depth averaged PAR for the mixed layer, and the differences between the mixed layer and euphotic depths. Also shown are our sparser measurements of net O$_2$ bioflux, i.e. estimates of NCP.

There are clear seasonal cycles and considerable interannual variability in all these properties. MLD follows the well-known seasonal cycle: deep in winter and shallow in summer. The seasonality is at its largest in the Subantarctic Zone (Rintoul and Trull, 2001; Rintoul et al., 1997; Sokolov, 2008; Trull et al., 2001a). To generalize from 3 years’ data, mixed layers at the beginning of October are > 150 m deep north of the Polar Front, and shallower to the south. Mixed layers shoal in October in the north and November in the south. In the fall there is a slow transition back to deep wintertime values. Sea surface PAR values track the sun, with maximum values close to summer solstice. Average values of mixed layer PAR have greater variation in seasonal timing. In 2007–2008, mixed layer average PAR in the northern part of the study region was highest before summer solstice. In the next two years it was highest after. This pattern tracks MLD, and is a result of interannual variability in water column stratification. Shallower MLD’s were more prevalent in the early part of the growing season in 2007–2008, and more prevalent in the latter part the following 2 years.

In the northern part of the study area, Chl levels rose later in the growing season than the shoaling of MLD or the increase in mixed layer PAR. In other words, biomass (or at least chlorophyll) continued to increase after stratification. Highest Chl levels were not observed until the end of January, or February. During summer, Chlorophyll concentrations reached a maximum around the Subtropical Front, then decreased towards the south. There was a suggestion that Chl levels also increased at the southern end of the transect, as Antarctica was approached—a feature that is seen more strongly to the east of the Astrolabe transit in satellite data (Sokolov, 2008). Even the higher Chl accumulations that occurred in the SAZ were not large, rarely reaching more than 1 μg L$^{-1}$ (3). These levels are similar to those reached in the iron-limited sub-arctic North Pacific (Harrison et al., 2004) and can be contrasted with levels 3–5 times higher that develop in the more iron-rich (Ryan-Keogh et al., 2013) sub-arctic North Atlantic spring bloom (e.g. Mahadevan et al., 2012). During the mid-summer periods of highest Chl accumulations, the mixed layer was generally shallower than the euphotic zone (see citations in Section 2.1). Vertical mixing would cause our fluxes to overestimate ML production. The effect is strongest north of the subtropical front in summer (Fig. 3), and would cause us to overestimate summertime NCP between 43–46° south. This effect is unlikely to be important south of the Subtropical Front, where
only a small fraction of primary production takes place below the mixed layer (see Sections 2.1).

3.3. Spatial and temporal distributions of Gross and Net Community Production

Net O\textsubscript{2} bio\textsubscript{flux} (as an estimate of NCP) and gross O\textsubscript{2} bio\textsubscript{flux} (as an estimate of GPP) are plotted vs. latitude and averaged over 1\degree latitude bands in Fig. 4. In this and subsequent discussions of meridional variations, we exclude from the data set results from the Astrolabe cruise that is to the east of the other cruise tracks (Fig. 1). Net bio\textsubscript{flux} (averaged over all samples with biological O\textsubscript{2} supersaturation > -0.3\%) was 18 ± 17 mmol m\textsuperscript{-2} day\textsuperscript{-1} (1\sigma, n = 213). Gross O\textsubscript{2} bio\textsubscript{flux} was 91 ± 110. As discussed above, NCP is likely to be slightly higher than net bio\textsubscript{flux}, which is aliased low by vertical mixing. The ratio of both average and median net O\textsubscript{2} bio\textsubscript{flux}/gross O\textsubscript{2} bio\textsubscript{flux} was 0.20. These values are all similar to those of other studies of large domains in the Southern Ocean (Green and Sambrotto, 2006; Morrison et al., 2001; Reuer et al., 2007; Rubin, 2003).

Gross bio\textsubscript{flux} was highest from 43 to 48\degree S; in contrast, net bio\textsubscript{flux} showed no strong meridional trend (Fig. 4). This situation may be compared with that during the autumn SAZ-SENSE voyage (Feb. 2007). During this study, 14C production, gross O\textsubscript{2} bio\textsubscript{flux}, and net O\textsubscript{2} bio\textsubscript{flux} were all highest just to the south of the Subtropical Front near 45–46\degree S (Cassar et al., 2011). However, it is important to note that the SAZ-SENSE data did not show a monotonic southward decrease of net bio\textsubscript{flux}. Net bio\textsubscript{flux} was low in the southern part of the SAZ, then rose south of the Polar Front. In our Astrolabe data, gross bio\textsubscript{flux} was highest at the northern end of the transect, but not net O\textsubscript{2} bio\textsubscript{flux}. On the other hand, data from the New Zealand sector (Reuer et al., 2007) showed a persistent southward decrease in both net and gross bio\textsubscript{flux} from November or December through February.

Monthly average values (and standard errors) for gross and net bio\textsubscript{flux} are plotted vs. Southern Ocean Zone, from STZ to SACC, in Fig. 5. These data again illustrate the main temporal and meridional trends. There is a southward decrease in gross bio\textsubscript{flux} but little or no decrease in net bio\textsubscript{flux}. Maximum values of net bio\textsubscript{flux} come after the New Year. South of the Subtropical Front, maximum values of both net and gross bio\textsubscript{flux} occur in January. This feature may be linked to the rapid drawdown of SiO\textsubscript{2} in the December-January period.

The maintenance of high gross production into the beginning of March may be associated with elevated chlorophyll and shallow mixed layer depths during this time (Fig. 3). Iron is likely decreasing throughout the growing season (Bowie et al., 2009; Sedwick et al., 2008), but light and chlorophyll apparently win in our domain.

For the period from October to the beginning of March (~130 days), net O\textsubscript{2} bio\textsubscript{flux} averaged 17, 18, and 17 mmol m\textsuperscript{-2} day\textsuperscript{-1} for the Subtropical Zone, Subantarctic Zone, and Polar Front zone respectively. For a growing season of 130 days and $\Delta$CO\textsubscript{2}/$\Delta$O\textsubscript{2} = 117/170 (Sarmiento et al., 1998), NCP inferred from our O\textsubscript{2}/Ar data would be 1.5 mol C m\textsuperscript{-2} year\textsuperscript{-1}. Thus our estimates are in reasonably good agreement with estimates from a detailed seasonal
cycle study at 46° 56'S, 142° 15'E using hourly autonomous moored observations of O_{2} and pCO_{2} (≈ 2 mol C m^{-2}) (Shadwick et al., 2015a; Weeding and Trull, 2014). Estimates from NO_{2} drawdown are similar (Section 3.2). As with the Chl abundances, our NCP estimates are relatively low overall (< 20 mmol m^{-2} day^{-1}). These values are similar to sub-Arctic North Pacific waters (e.g. Harrison et al., 2004). They are about an order of magnitude below NCP values during the spring bloom in the sub-Arctic North Atlantic (Alkire et al., 2012; Bender et al., 1992; Quay et al., 2012). There, NCP can be as high as 1 mol C m^{-2} over a period of order 1 week, equivalent to net O_{2} bioflux values of about 200 mmol m^{-2} day^{-1}.

The seasonal cycle of NCP inferred here for the Subantarctic Zone is very different from that of Weeding and Trull (2014), who measured [O_{2}] and gas tension using a mooring. They diagnosed very high values of O_{2} NCP in early spring. These high values were required to explain the observed time series of [O_{2}], given evidence for rapid entrainment from deep mixed layers and highly variable mixed layer depths. This entrainment kept O_{2} undersaturated at the surface until the middle of December, after which time vertical mixing has little influence on the O_{2} balance of the mixed layer (their Fig. 5C). In contrast, the mixed layer was generally supersaturated in biological O_{2} during our cruises (Table S-1). Also, we calculated NCP only for waters that were biologically supersaturated in O_{2}. Thus biases from entrainment in our observations are likely to be small.

The difference between the two studies may also reflect spatial variations in the depth and intensity of late winter and early spring deep convection south of Australia. The Southern Ocean Time Series site southwest of Tasmania studied by Weeding and Trull (2014) exhibits deeper winter mixed layers than along our Astrolabe transects and the nearby WOCE/CLIVAR S3 line (Dong et al., 2008; Rintoul and Bullister, 1999; Rintoul and Trull, 2001). Interannual variability may also contribute to the difference. We observed biological supersaturation in the spring of 2007 and 2008, but mixed saturation status in spring, 2009. Significant interannual variability in biological O_{2} supersaturation and net O_{2} bioflux is hardly surprising given the large difference in Subantarctic Zone nitrate concentrations in October and November 2006, relative to 2007. Spatio-temporal variations may also explain high NCP inferred from nutrient and carbon dioxide observations in Drake Passage in springtime (Munro et al., 2015). Overall, these other observations of high springtime NCP do not invalidate our conclusion that, in O_{2}-supersaturated waters south of Australia, springtime productivity is not particularly high.

4. Discussion

4.1. Relationships between Chl, mixed layer PAR, and gross and net bioflux

The relationship between sea surface PAR, MLD, and production has been at the heart of attempts to understand seasonal and spatial variability in productivity back to at least the classic paper of Sverdrup (1953). It is also at the center of algorithms to calculate 14C production from remotely observed properties of the sea surface (e.g. Behrenfeld and Falkowski, 1997). Here we analyze the relationship between these properties using a simple approach that has basic mechanistic content. Our objectives are to identify a simple and transparent relationship between these properties, and to advance the possibility of simulating NCP from remotely sensed properties and Argo/BioARGO float data.

Specifically, we focus on the relationship between average volumetric production in the mixed layer normalized to Chl, and average irradiance in the mixed layer. One expects these terms to be related, because productivity increases as irradiance rises and as Chl rises. Our work follows, for example, the Vertically-Generalized Productivity Model of (Behrenfeld and Falkowski, 1997). Upon rearranging Eq. (10) of their paper, one gets an equation stating that the rate of Chl-normalized volumetric primary production in the euphotic zone scales with irradiance. Their irradiance term takes into account light saturation, and their model is more process- rich than ours (therefore also more complex), but the basic premises are similar.

In our model, the relevant terms are calculated as follows:

\[
\text{Chl-normalized volumetric gross bioflux in the ML} = \text{gross O}_{2}\text{bioflux}/(\text{MLD}\times\text{Chl})
\]  
\[
\text{Chl-normalized volumetric net bioflux in the ML} = \text{net O}_{2}\text{bioflux}/(\text{MLD}\times\text{Chl})
\]  

The equation for calculating average ML irradiance was presented earlier. Chl is in mg m^{-3}. The units of volumetric bioflux are mmol O_{2} mg Chl^{-1} day^{-1}. Average ML irradiance has the units of moles photons m^{-2} day^{-1}.

In evaluating the relationship between normalized bioflux and average ML irradiance, we exclude all samples with Chl < 0.10 mg m^{-3}, because at these low levels Chl retrieved from space may have large uncertainties (e.g. Johnson et al., 2013). As outlined above, we exclude samples from the net bioflux analysis that were biologically undersaturated in O_{2} by > 0.3‰. We also exclude two measurements of gross bioflux that were extreme outliers. We then plot normalized gross O_{2} bioflux and normalized net O_{2} bioflux vs. average ML irradiance (Fig. 6).

Chl-normalized volumetric gross and net O_{2} bioflux both rise with increasing values of average ML irradiance, albeit with considerable scatter. Out to a light flux of ~25 mol m^{-2} day^{-1}, there is no strong indication that irradiance is saturating. The R^2 is 0.44 for both normalized net bioflux and normalized gross bioflux plotted vs. average ML irradiance. This level of shared variance is remarkably high given errors in derived properties (satellite Chl observations, gas transfer velocity, mixed layer PAR, light attenuation coefficient) and the simplistic nature of the assumptions for calculating O_{2} bioflux (steady state, no water flux across the base of the mixed layer).

We analyzed the apparent absence of light saturation in the plots of normalized production vs. average ML irradiance using a simple model based on curves of 1-h 14C production vs. irradiance (Westwood et al., 2011), measured on the SAZ-SENSE cruise. According to Westwood et al., saturating irradiance during the SAZ-SENSE cruise averaged 56 µmol photons m^{-2} s^{-1} when evaluated for those stations where the MLD was within the euphotic zone. For a 16-hour day, this number corresponds to about 3 mol photons m^{-2} day^{-1}. It is approximately equal to the median value of average daily ML irradiance for our samples (Fig. 6). However, Fig. 6 shows that gross and net O_{2} bioflux continue to increase at higher irradiances, despite the fact that average daily ML irradiance is saturating. There are 2 reasons. First, light decreases exponentially with depth. Therefore, most of the mixed layer lies below the depth of average ML irradiance. Second, irradiance will be low, and production will be light-limited, towards the beginning and end of the photoperiod. For these 2 reasons, production during the photoperiod may be light-limited even if average irradiance in the mixed layer exceeds the light-saturated value.

In Fig. 7, we quantify these effects by plotting relative O_{2} production vs. irradiance for the case where saturating irradiance = 56 µmol photons m^{-2} s^{-1}. We assume that instantaneous production increases linearly with irradiance until it reaches the saturation value (at 56 µmol photons m^{-2} s^{-1}), and is constant thereafter. In our calculation, insolation decreases...
symmetrically about the noontime value along a hyperbolic curve that goes to zero at 4 AM and 8 PM (i.e., 16 h/8 h light/dark cycle). We calculate relative ML production for MLD from 1 to 100 m, in 1 m intervals. Corresponding values of average ML irradiance decrease from 45 to 6 mol photons m\(^{-2}\) s\(^{-1}\). The reason is that irradiance early in the day, late in the day, and lower in the mixed layer can be undersaturated even when average daily ML irradiance is much greater than the instantaneous saturating value.

Various factors complicate the relationship between light, Chl, and O\(_2\) production. Perhaps the most important is the iron sufficiency of the ecosystem, which also influences $\mu$. There are ample data suggesting that iron sufficiency changes in the study region (e.g., Cassar et al., 2011). Hiscock et al. (2008) argued that the effect of iron on the physiology of individual phytoplankton is to increase the initial slope of the P-I curve while leaving light-saturated production unchanged. In their experiments, the slope varied by about a factor of 2 between Fe-limited and Fe-sufficient phytoplankton. This variability would lead to scatter in the curve of gross O\(_2\) production (or bioflux) vs. average ML irradiance, but the basic relationship would be unchanged. In fact the greatest relevant effect of Fe is simply to cause a rise in the Chl. We implicitly acknowledge this effect by normalizing to Chl. Other obvious confounding factors include water temperature, light acclimation, and the changing nature of Southern Ocean ecosystems.

Despite these complications, our results show that there is a strong relationship between volumetric net and gross bioflux normalized to Chl, and average ML irradiance. These relationships can be exploited, using remotely sensed Chl values and MLD’s from ARGO floats and other sources, to scale local estimates of GPP and NCP to broader areas of the Southern Ocean. Scaled values can be used to achieve a better understanding of process-level controls on production, and to improve the simulation of biogeochemical cycles in models.

4.2. Net/gross bioflux variations

There are many possible controls on the overall trend of lower NCP/GPP ratios in the northern regions of the Southern Ocean observed here (Fig. 4). For example, zooplankton grazing and re-mineralization are both more effective in warmer waters (Laws et al., 2000; Steinberg et al., 2008). In addition, lower levels of SiO\(_2\) in the north may limit the growth of diatom micro-plankton, whose size allows them to more readily escape grazing pressure (Assmy et al., 2013; Morel et al., 1991). Importantly, the complexity of tropho-dynamics means that high NCP can still occur in small phytoplankton communities, as has been observed previously in this region (Cassar et al., 2015), including contributions to carbon export to the ocean interior (Richardson and Jackson, 2007).

5. Conclusions

Our data allow us to answer our three key research questions, outlined in the introduction, as follows:

**Fig. 6.** Net (left) and gross (right) O\(_2\) volumetric bioflux normalized to chlorophyll, plotted vs. average mixed layer irradiance. Net and gross O\(_2\) bioflux are calculated from mixed layer data and approximate O\(_2\) NCP and O\(_2\) GPP in the mixed layer. Normalized net bioflux is plotted only for samples where the biological O\(_2\) supersaturation is $> -0.3\%$ (within uncertainty of zero).

**Fig. 7.** Relative production vs. average daily irradiance in the mixed layer. Production is assumed to increase linearly up to saturating irradiance (taken as 56 \(\mu\)mol photons m\(^{-2}\) s\(^{-1}\)), and be constant at higher irradiances. This plot shows that daily production increases linearly with average mixed layer irradiance up to irradiances much higher than the instantaneous saturating irradiance, 3.2 mol m\(^{-2}\) day\(^{-1}\). The reason is that irradiance early in the day, late in the day, and lower in the mixed layer can be undersaturated even when average daily ML irradiance is much greater than the instantaneous saturating value.
1. In the Australian sector of the Southern Ocean there is no evidence of a spring bloom in the sense of very high rates of photosynthesis and carbon export.

2. The oxygen based GPP and NCP estimates (and the SiO₂ and NO₃ drawdowns) show considerable latitudinal and year to year variability, but with an overall trend of higher GPP in the north and little latitudinal variation in NCP.

3. Chl-normalized values of net and gross O₂ bioflux scale with average mixed layer irradiance, albeit with a high level of scatter. This relationship provides a useful check on models of productivity based on remote sensing, that can be evaluated further in future studies. The relationship also provides a basis for scaling GPP and NCP in the Southern Ocean based on Chl observed from satellites and mixed layer depths from ARGO floats and other sources.

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Appendix A. Supporting information

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References


