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- Vigorous NCP in the absence of diatoms
- Observed correlation of NCP to POC

Supporting Information:

- Readme
- Figure S1 and Tables S1–S4

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The relation of mixed-layer net community production to phytoplankton community composition in the Southern Ocean

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Abstract Surface ocean productivity mediates the transfer of carbon to the deep ocean and in the process regulates atmospheric CO₂ levels. A common axiom in oceanography is that large phytoplankton contribute disproportionately to the transfer of carbon to the deep ocean because of their greater ability to escape grazing pressure, build biomass, and sink. In the present study, we assessed the relationship of net community production to phytoplankton assemblages and plankton size distribution in the Sub-Antarctic Zone and northern reaches of the Polar Frontal Zone in the Australian sector of the Southern Ocean. We reanalyzed and synthesized previously published estimates of O₂/Ar net community oxygen production (NCP) and triple-O₂ isotopes gross primary oxygen production (GPP) along with microscopic and pigment analyses of the microbial community. Overall, we found that the axiom that large phytoplankton drive carbon export was not supported in this region. Mixed-layer-depth-integrated NCP was correlated to particulate organic carbon (POC) concentration in the mixed layer. While lower NCP/GPP and NCP/POC values were generally associated with communities dominated by smaller plankton size (as would be expected), these communities did not preclude high values for both properties. Vigorous NCP in some regions occurred in the virtual absence of large phytoplankton (and specifically diatoms) and in communities dominated by nanoplankton and picoplankton. We also observed a positive correlation between NCP and the proportion of the phytoplankton community grazed by microheterotrophs, supporting the mediating role of grazers in carbon export. The novel combination of techniques allowed us to determine how NCP relates to upper ocean ecosystem characteristics and may lead to improved models of carbon export.

1. Introduction

Nearly half of photosynthesis on Earth occurs in the oceans. When photosynthesis in the upper ocean exceeds respiration, carbon dioxide (CO₂) is drawn from the atmosphere and converted to organic carbon which settles to the ocean interior and ocean floor. There, it is respired as CO₂ or buried as organic carbon and isolated from the atmosphere for decades to millions of years [Volk and Hoffert, 1985]. The soft-tissue biological pump, the plankton-mediated transfer of carbon to the ocean interior, is a function of primary production, export of the unrespired carbon from the surface ocean, and attenuation of carbon flux at depth [Boyd and Trull, 2007]. The prevailing paradigm is that biological carbon export from the ocean surface is disproportionately driven by large phytoplankton, particularly diatoms, for reasons we detail in the next paragraph. We recently found evidence of considerable carbon export in a region dominated by picoplankton and nanoplankton with few diatoms—the Sub-Antarctic Zone (SAZ) south of Australia [Cassar *et al.*, 2011; de Salas *et al.*, 2011]. To investigate this apparent anomaly, we reanalyzed data from the SAZ-Sense cruise to explore how carbon export related to phytoplankton community composition, size structure, particulate organic carbon (POC) content, and grazing. Our results challenge the prevailing paradigm.

The precept that large cells drive export is based on both physical and ecological factors. Sinking rates of marine particles are expected to increase with their density and size, e.g., as the square of the radius for a sphere sinking under conditions of laminar flow, as described by Stokes' law, or linearly with size under

conditions of turbulence as occurs for most marine particles [e.g., *Allredge and Gotschalk, 1988*]. Thus, diatoms may sink faster than other phytoplankton because they are generally larger than other species and denser because of their silica frustules [*Armstrong et al., 2002; Boyd and Newton, 1995; Michaels and Silver, 1988*]. From an ecological perspective, larger phytoplankton are more likely to get exported because they can escape grazing pressure by zooplankton of similar or larger size, which have comparatively slower life cycles and cannot reproduce quickly to control a bloom [*Boyd and Newton, 1995; Buesseler, 1998; Michaels and Silver, 1988*]. Another factor for diatoms is that their silica frustules may protect their organic matter from remineralization [*Armstrong et al., 2002; Klaas and Archer, 2002; Passow, 2004*] in addition to acting as ballast, thus augmenting carbon export from the surface ocean. Small phytoplankton, such as cyanobacteria, are generally believed to contribute little to export because of their size and efficient population control by micrograzers [*Michaels and Silver, 1988*]. Export is also believed to be reduced in ecosystems dominated by small phytoplankton because of the greater number of trophic levels of consumption [*Laws et al., 2000*].

Not all analyses have found that large phytoplankton contribute disproportionately to export [*Henson et al., 2012; Le Moigne et al., 2012; Richardson and Jackson, 2007*]. Phytoplankton have evolved several mechanisms to reduce passive sinking by modifying their density (e.g., vacuoles and proportion of biomolecules with varying density) or shape (reviewed by *Reynolds [2006]*). Their physiology and sinking rates may be altered by several environmental factors, including nutrient and light availability and growth status [*Bienfang et al., 1982, 1983; Bienfang, 1981; Eppley et al., 1967; Muggli et al., 1996; Waite et al., 1997*]. Sinking rates of small cells may be increased by aggregation into larger particles by physical coagulation or by grazing. Larger zooplankton package organic matter into fecal pellets that sink on average 1–2 orders of magnitude faster than phytoplankton cells [*Small et al., 1979*] and are often a dominant contributor to carbon export [*Bishop et al., 1977; Manno et al., 2010*]. Grazers may also impact carbon export through their vertical migration [*Steinberg et al., 2000*], as previously observed in the SAZ [*Bradford-Grieve et al., 2001*]. In contrast, smaller grazers (i.e., microheterotrophs) are believed to promote retention of organic carbon within the surface ocean because of the slow sinking rate of fecal pellets produced [*Wassmann, 1998*].

In this study, we assess and characterize carbon export and carbon export efficiency in the Sub-Antarctic Zone by synthesizing previously published data from the SAZ-Sense cruise [*Cassar et al., 2011; de Salas et al., 2011*] to determine how export is related to phytoplankton cell size and community composition and whether export is inhibited by microheterotrophic grazing.

We estimated carbon export indirectly, via net community production (NCP, i.e., gross primary productivity minus community respiration), as determined by O_2/Ar mass spectrometry. Under steady state conditions (i.e., when there is no net gain or loss of organic carbon stocks), new production is balanced by and equals carbon export from the mixed layer [*Eppley and Peterson, 1979; Laws, 1991*]. We determined that carbon stocks approximated steady state and hence NCP approximated export. We also estimated gross primary production (GPP) via oxygen isotope analysis and hence could estimate the proportion of production exported. These measurements were compared with analyses of microbial community size and composition (using microscopy, flow cytometry, CHEMTAX pigment analysis, and filter fractionation), particulate organic carbon (POC) concentrations, and microheterotroph grazing.

2. Materials and Methods

2.1. Area of Study

The SAZ-Sense (Sub-Antarctic Sensitivity to Environmental Change) study was conducted on board the Australian icebreaker RSV *Aurora Australis* in the austral midsummer of 2007 (17 January to 20 February) in a region south of Tasmania (Figure 1). The SAZ-Sense campaign covered several major hydrographic provinces, including Subtropical, Sub-Antarctic, and Polar Frontal Zone waters, which are separated by the Subtropical and Sub-Antarctic Fronts. For a more thorough description of the studied region, see supporting information or the following references: *Bowie et al. [2011], Herraiz-Borreguero and Rintoul [2010], Mongin et al. [2011], Orsi et al. [1995], Rintoul et al. [1997], Sokolov and Rintoul [2007], and Trull et al. [2001]*.

2.2. Metabolic Rates and Derived Biogeochemical Fluxes: Theoretical Basis

At the ocean surface, an ecosystem has a positive internal energy change when the photosynthetic production of organic matter exceeds its oxidative loss. Through its pivotal role in biological redox reactions

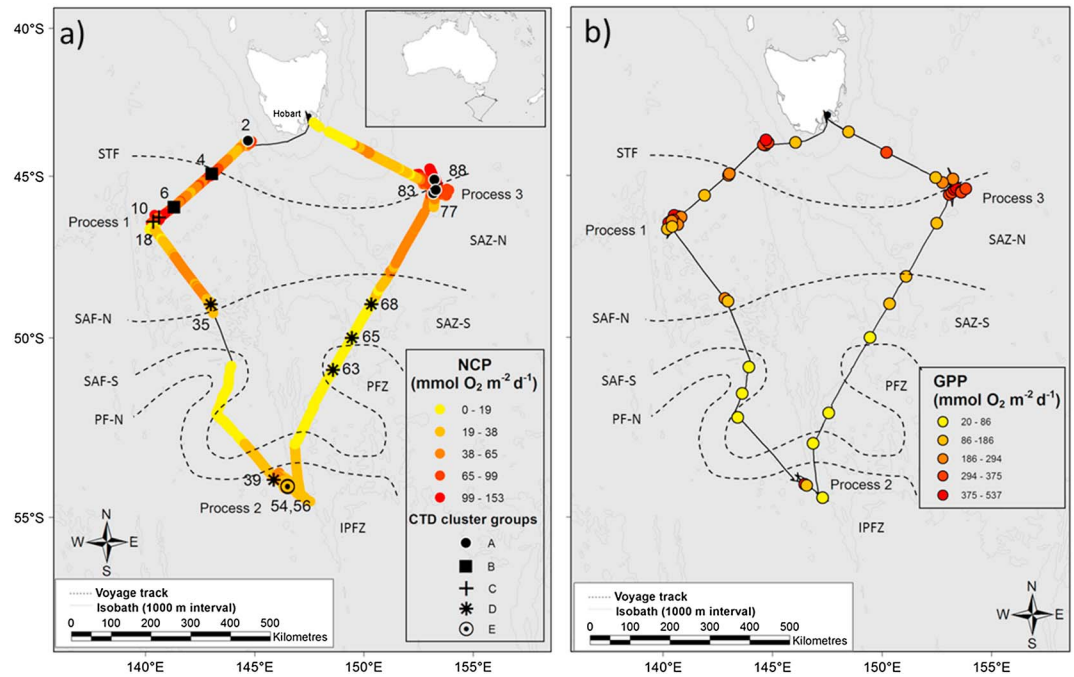


Figure 1. (a) O_2/Ar -NCP and (b) $^{17}\Delta$ -GPP estimates and microbial community composition along the cruise track. NCP and GPP are in $mmol\ O_2\ m^{-2}\ d^{-1}$, integrated over the mixed layer. NCP and GPP in carbon equivalents can be estimated by multiplying NCP and GPP estimates by 1.4 and 2.7, respectively [Bender *et al.*, 1999; Laws, 1991]. NCP observations and stations (2–88) grouped into five biogeographical clusters (A–E) according to CLUSTER and SIMPROF analyses of microbial community composition based on cell biomass from microscopy, flow cytometry, and CHEMTAX. Dash lines represent approximate positions of the Subtropical Front (STF), Sub-Antarctic Front (SAF), northern and southern branches of the Sub-Antarctic Front (SAF-N and SAF-S), and the northern branch of the polar front (PF-N), based on hydrographic underway and depth profile observations during the voyage [Bowie *et al.*, 2011]. The Interpolar Frontal Zone (IPFZ) lies to the south of the PF-N and a southern PF branch that is persistent in this sector of the Southern Ocean [Parslow *et al.*, 2001].

in surface waters, biological O_2 primarily reflects this net energetic balance. In addition, because biological oxygen and organic carbon are tightly coupled at the ocean surface, rates of productivity and export fluxes can be derived from mass spectrometric analyses of oxygen isotopes and argon in the mixed layer (see sections 2.3 and 2.4 for method description). Here we summarize the metabolic parameters relevant to this study and the logic and assumptions supporting calculations of the derived terms.

Metabolic rates considered are

$$GPP = \text{Gross Primary Production,}$$

$$NPP = \text{Net Primary Production}$$

$$= GPP - R_{\text{Autotrophic}}, \text{ where } R_{\text{Autotrophic}} = \text{respiration by autotrophs,}$$

$$NCP = \text{Net Community Production}$$

$$= GPP - R_{\text{Autotrophic}} - R_{\text{Heterotrophic}}, \text{ where } R_{\text{Heterotrophic}} = \text{respiration by heterotrophs}$$

2.3. GPP

GPP was derived from the triple-isotope anomaly of dissolved oxygen [Boering *et al.*, 2000; Lammerzahl *et al.*, 2002; Luz and Barkan, 2005; Luz *et al.*, 1999; Thiemens, 2001]. Oxygen in the surface ocean has two main sources, with distinct isotopic signatures: air and photosynthetic splitting of water. Atmospheric O_2 has a characteristic isotopic signature derived from a stratospheric reaction with a mass-independent fractionation between O_2 and CO_2 . Deviation from the mass-dependent relationship between $\Delta^{17}O$ and $\delta^{18}O$ is manifested in a nonzero value of $^{17}\Delta$, where $^{17}\Delta$ is generally defined as $^{17}\Delta = 10^6[\ln(10^{-3}\delta^{17}O + 1) - \lambda \ln(10^{-3}\delta^{18}O + 1)]$, where λ is the mass-dependent isotope fractionation factor (~ 0.518). GPP is calculated based on the dual delta method [Kaiser, 2011] with the constants and other factors described in Hamme *et al.* [2012]. Respiration

fractionates O_2 mass dependently and therefore does not change $^{17}\Delta$. GPP is the rate of photosynthetic O_2 production required to maintain the observed departure of $^{17}\Delta$ from atmospheric equilibrium against the equilibrating effect of gas exchange [Luz and Barkan, 2000]. Oxygen isotope measurements were performed following a method previously described by Reuer *et al.* [2007]. Factors for converting NCP and GPP from O_2 units to C units are provided for reference in the caption of Figure 1. Because of the uncertainty associated with O_2 to C conversion of GPP, all GPP measurements are presented in O_2 units. Other than Figure 1, all NCP observations are reported in carbon units unless presented in a ratio to GPP (i.e., Figures 5b, 5d, and 5f). See Juraneck and Quay [2013] for a detailed discussion of the discrepancies between O_2 - and C-based productivity measurements.

2.4. NCP

Net community production of carbon is accompanied by a stoichiometric release of biological oxygen and is proportional to the change in biological oxygen content in the mixed layer plus the loss across the surface. Thus, we can derive carbon-based NCP ($\text{mmol C m}^{-2} \text{d}^{-1}$) from measurements of oxygen.

$$\text{NCP} = \frac{1}{1.4} \left(\text{mld} \left[\frac{d[O_2]_{\text{bio}}}{dt} \right] + k[O_2]_{\text{bio}} \right)$$

where mld is the mixed-layer depth, $[O_2]_{\text{bio}}$ is the difference between the measured O_2 concentration and the saturation concentration that cannot be attributed to physical processes, the factor of 1.4 accounts for the stoichiometric ratio of carbon NCP to O_2 NCP associated with growth on nitrate [Laws, 1991], and k is the gas transfer velocity of oxygen (m d^{-1}). At steady state, NCP is balanced by a flux of biological oxygen to the atmosphere. Because the residence time of O_2 in the surface ocean is comparable to the turnover time of Southern Ocean planktonic ecosystems (1–2 weeks) [Falkowski and Raven, 2007], the method is well suited for the purpose of elucidating the physiological and food web structure controls over NCP and carbon export in the Southern Ocean. As they are based on gas exchange across the surface, and exchange across the base of the mixed layer is likely small in the region (see discussion below), such measurements are confined to the mixed layer. Results presented hereafter are integrated to the base of the mixed layer.

The method we use to estimate NCP has been described elsewhere [Craig and Hayward, 1987; Emerson *et al.*, 1995; Hendricks *et al.*, 2004; Spitzer and Jenkins, 1989]. Briefly, NCP can be derived from three terms: the biological O_2 supersaturation, a gas exchange coefficient, and the saturation concentration of O_2 . Because O_2 and the inert gas argon (Ar) have similar solubility properties, concurrent measurements of these two gases constrain the biological O_2 supersaturation [Craig and Hayward, 1987]. The O_2/Ar ratio was measured continuously by equilibrator inlet mass spectrometry, a method previously described by Cassar *et al.* [2009]. Seawater from the ship's underway system was pumped through a gas equilibrator, the headspace of which was connected to a quadrupole mass spectrometer for continuous analysis of the partial pressure ratio of the dissolved O_2 and Ar. Calibration of the O_2/Ar ion current ratio was performed with discrete samples collected every 6 h and measured on an isotope ratio mass spectrometer [Reuer *et al.*, 2007]. The gas exchange coefficient for O_2 was estimated based on the National Centers for Environmental Prediction wind data product [Kalnay *et al.*, 1996] and the wind speed parameterization of Wanninkhof [1992]. The gas transfer velocity was calculated taking into account the wind history, as described by Reuer *et al.* [2007]. The O_2 concentration at saturation was calculated based on Garcia and Gordon [1992]. This method harbors uncertainties associated with gas transfer velocity, mixing with water originating below the mixed layer, potential violation of the steady state assumption, and variability in mixed-layer depth and NCP in the period before sample collection [Cassar *et al.*, 2011; Castro-Morales *et al.*, 2013; Jonsson *et al.*, 2013; Reuer *et al.*, 2007].

2.5. Carbon Export Production

The net carbon produced via NCP must either increase the concentration of organic carbon in the mixed layer or be exported:

$$\text{NCP} = \text{mld} \left[\frac{d[\text{POC}]}{dt} + \frac{d[\text{DOC}]}{dt} \right] + \text{Export}_c$$

where Export_c represents carbon export production from the mixed layer ($\text{mmol C m}^{-2} \text{d}^{-1}$) and [POC] and [DOC] are the concentrations of particulate and dissolved organic carbon, respectively, in the mixed layer. Under steady state conditions in organic carbon, NCP is equal to new production (i.e., proportion of primary

production supported by allochthonous nutrients) and carbon export from the mixed layer [Dugdale and Goering, 1967; Eppley and Peterson, 1979]. Thus, $\text{Export}_c = \text{NCP}$. In the discussion below, we show that the assumption of steady state is reasonable for our study.

2.6. GPP- and POC-Normalized NCP

To distinguish whether any observed relationship between NCP and taxonomic composition or size structure was direct or resulting from a relation to primary production and total biomass, we examined two approaches to account for these effects: (i) we divided NCP by GPP which should be proportional to the export ratio under steady state (abbreviated “*ef*” ratio following Laws *et al.* [2000]) and (ii) we divided NCP by the POC concentration within the mixed layer to yield carbon export production per unit POC. Note that the export ratio (*ef*) under steady state is commonly defined as the proportion of NPP (here mixed-layer depth integrated) that is exported from the surface ocean, and for comparison purposes our ratio of NCP to GPP should be multiplied by a factor of ~ 2 to account for methodological aspects of these different measures (see Bender *et al.* [1999] and Juranek and Quay [2013] for detailed discussion).

Export is a function, among other things, of the POC concentration within the mixed layer and the average sinking rate of particles [D’Asaro, 2008; Jackson, 1990; Lande and Wood, 1987; Ruiz *et al.*, 1996; Serra *et al.*, 2003], provided that DOC production is a small component of NCP and assuming a uniform distribution of POC within the mixed layer [Ruiz, 1996]. We note that a 20% variation in DOC production is not likely to change our results as NCP varies by a factor of 500% over the region of study. When the conditions above are satisfied, the POC-normalized NCP should be equal to the effective sinking rate of particles out of the mixed layer (ψ_{ml}). Thus, $\psi_{\text{ml}} \propto \frac{\text{NCP}}{[\text{POC}]}$. Whereas the gas transfer velocity influences gas exchange at the ocean surface, ψ_{ml} is the piston pushing POC export at the base of the mixed layer. The GPP- and POC-normalized NCP relate to the *ef* ratio as follows: $ef = \frac{\text{NCP}}{\text{NPP}} = \frac{\psi_{\text{ml}} [\text{POC}]}{\text{NPP}} = \frac{\text{NCP}}{(\text{GPP} - R_{\text{autotrophic}})}$, with the important distinction that the *ef* ratio is generally integrated over the euphotic depth and our measurements are integrated over the mixed layer.

2.7. Community Composition

In order to assess the influence of the plankton community on NCP and derived properties NCP/GPP and NCP/POC, taxonomic analyses were performed using pigment, microscopic, and flow cytometric analyses.

2.7.1. CHEMTAX Matrix Factorization Analysis

Community composition was determined based on high-performance liquid chromatography (HPLC) pigment CHEMTAX and microscopic analyses. Pigments were collected and extracted as per Wright *et al.* [2010]. Briefly, 1–2 L of seawater were filtered onto Whatman GF/F filters in the dark. The blotted filters were frozen in liquid nitrogen for return to Australia and extracted by beadbeating (Biospec Products Mini-BeadBeater) in 300 μL dimethylformamide plus 50 μL methanol (containing 140 ng apo-8'-carotenal (Fluka) internal standard) using a modified method of Mock and Hoch [2005]. The extract was analyzed by HPLC [Zapata *et al.*, 2000]. Pigment data were interpreted using CHEMTAX software [Mackey *et al.*, 1996]. The pigment data set consisted of 509 samples with 15 pigments selected for CHEMTAX analysis. The data were broken into five strata to allow for pigment variation with depth due to light (supporting information Table S1). For each depth stratum, 40 CHEMTAX runs were performed from randomized starts [Higgins *et al.*, 2011]. Each was based on the matrix of pigment:chl *a* ratios presented in Table S2 in the supporting information. The initial matrix was randomly modified ± 0.7 -fold to generate 40 matrices as randomized starting points for CHEMTAX. These were run with wide limits (500%). Output ratios were collated for each run. The runs with the lowest root-mean-square residuals (amount of unexplained chlorophyll) were kept for each depth stratum. The pigment:chl *a* ratios for these runs were plotted versus depth. These profiles were smoothed manually to generate a new set of ratio matrices, which were the basis for a final round of optimization by CHEMTAX. This avoids the problem that less abundant pigments and taxa are not optimized as well as the major ones because they have less statistical weight and they introduce noise. The notional groups identified were prasinophytes, chlorophytes, cryptophytes, diatoms (groups A and B, containing Chl *c*1 + *c*2 or Chl *c*2 + *c*3, respectively), dinoflagellates (groups A and B, containing peridinin or fucoxanthin plus 19'-hexanoyloxyfucoxanthin, respectively), Haptophytes-8 (based on *Phaeocystis* sp.), and cyanobacteria. Pigment ratios for each group were based on average cultures, as summarized in Higgins *et al.* [2011], plus haptophytes (groups 6A and 6B based on *Emiliania huxleyi* morphotypes A and B/C), collected during the cruise [Cook *et al.*, 2011].

2.7.2. Microscopy and Flow Cytometry and Dilution Experiments

Surface seawater samples for light microscopy were fixed in Lugol's iodine and returned to Australia, where they were filtered, and the filters were mounted using the hydroxypropyl methacrylate (HPMA) [Crumpton and Wetzel, 1981]. Protistan cells were identified and counted by microscopy as detailed in *de Salas et al.* [2011]. Protistan taxa were identified to species level where possible; however, poor contrast from the HPMA preparations limited identification of lightly silicified diatoms, and Lugol's fixation prevented determination of the trophic status of some dinoflagellates [*de Salas et al.*, 2011]. A distinct group of unidentified nanoflagellates (UNAN, 2–5 μm diameter) was often abundant but lacked distinguishing features. Cyanobacteria, assumed to be *Synechococcus* sp., were enumerated using a Becton Dickinson FACScan flow cytometer equipped with a 488 nm argon laser and were discriminated by their phycoerythrin autofluorescence on bivariate scatterplots of orange versus red fluorescence [*Marie et al.*, 2001]. All counts were converted to biovolume and carbon biomass using values from the literature [*de Salas et al.*, 2011].

Whereas CHEMTAX provides a reasonably comprehensive interpretation of pigment categories, microscopy provides more reliable taxonomic identification but is very selective for large hard-shelled taxa. For example, fragile flagellates like haptophytes are underrepresented because of poor preservation. In the case of CHEMTAX analyses, although some groups are unambiguous (e.g., dinoflagellates A), some groups, such as haptophytes-8 and dinoflagellates B, overlap in their pigment characteristics in the Sub-Antarctic Zone. Hence, CHEMTAX and microscopy results are expected to diverge because of biases associated with both methods. However, we believe that differences in community composition between sites predicted by a given method are robust.

Grazing rates were determined by the grazing dilution method [*Landry and Hassett*, 1982]. Briefly, the microzooplankton grazing rate on phytoplankton is estimated based on a series of seawater incubations diluted to various extents with filtered seawater. As samples become increasingly diluted, the phytoplankton-grazer encounter rate decreases. Assuming that the grazing pressure is a function of the encounter rate, the influence of grazing on the phytoplankton growth rate (as measured by the chlorophyll change) becomes increasingly small at higher dilution ratios. Twenty five liters of seawater were 0.2 μm filtered with Supor (Gelman) filters at each station to provide a diluent that was used to create triplicate dilution gradients of 0, 30, 60, 90, and 100% of the seawater microbial community. The latter was filtered with 200 μm mesh to remove mesozooplankton. Triplicate bottles were incubated in a polythene deck incubator and exposed to ambient temperature and ~50% sunlight. Following incubation, size-fractionated chlorophyll (0.7–2.7 μm , 2.7–20 μm , and 20–200 μm) was determined by sequential filtration and HPLC analysis, numbers of cyanobacteria, bacteria, and heterotrophic nanoflagellates were determined by flow cytometry, while protists and microzooplankton were identified, sized, and counted by light microscopy [*Pearce et al.*, 2011; *de Salas et al.*, 2011].

2.7.3. Statistical Analyses

Protistan biomass was integrated over the mixed layer for each conductivity-temperature-depth (CTD) and analyzed using the statistical package PRIMER v6.1.12 [*Clarke*, 1993; *Clarke and Gorley*, 2006]. Biomass was $\log_{10}(x + 1)$ transformed, and a resemblance matrix was constructed using the Bray Curtis similarity index. Hierarchical cluster analysis (CLUSTER) was then performed to cluster CTD stations of similar protistan community composition, and similarity profile analysis (SIMPROF, $p = 5\%$, 999 permutations) identified significant differences in community composition between the clusters.

2.8. POC Concentration

Seawater was collected from six depths in the top 150 m at each station from the CTD-mounted Niskin bottles and transferred via precleaned tubing to completely fill weight-calibrated 2 L bottles. These bottles were inverted and the entire volume vacuum filtered (~150 mm Hg) through in-line 13 mm diameter glass fiber filters (Whatman GF/F, nominal pore size 0.7 μm , precombusted at 450°C for 4 h). Blanks were collected by carrying out all operations while filtering ~1 mL of seawater. The filters were transferred in a laminar flow bench to well trays and dried at 50°C in a clean oven for later analysis. On shore, filters were packed into silver cups, decarbonated by acidification with two 20 μL aliquots of 1N HCl followed by one of deionized water and redried at 50°C. Analysis was by combustion and gas chromatography a Fisons/Carlo Erba NC1500 elemental analyzer [*Gordon*, 1969; *Sharp*, 1974] calibrated with acetanilide standards. Blank corrections were typically less than 1% but ranged up to ~5% in the deeper samples.

3. Results and Discussion

A common view in oceanography is that carbon export is influenced by phytoplankton community composition because of differences in sinking rates, taxa-specific organic matter biodegradability, and trophic efficiencies of associated food webs. Diatoms have traditionally been thought to contribute disproportionately to carbon export due to their generally larger size, higher density, and limited top-down control by grazers with comparatively slower growth response. Further carbon export is believed to occur when diatoms are grazed upon by mesozooplankton, which egest rapidly sinking fecal pellets. In this section, previously published data from the SAZ-Sense cruise are reanalyzed and synthesized to test the hypotheses that carbon export is controlled by cell size, community composition, and microheterotroph grazing. We consider the relationships between geographical variations in production and export fluxes [Cassar *et al.*, 2011], microscopic analysis of protistan populations and vertical profiles of CHEMTAX data [de Salas *et al.*, 2011], and microheterotrophic grazing rates [Pearce *et al.*, 2010]. The original publications provide greater detail and context on each data set than is warranted in this synthesis.

3.1. Assumptions of Steady State and Negligible Vertical Mixing

Some of our conclusions rely on the assumption that oxygen and organic carbon stocks in the ecosystems studied are at steady state. This deserves further discussion. The biological oxygen flux varies about and approximates NCP [cf. Hamme *et al.*, 2012; Jonsson *et al.*, 2013; Martin *et al.*, 2013]. Over times of a week or longer, NCP is generally greater than the inventory change of POC and DOC in the mixed layer and must therefore be exported [Allison *et al.*, 2010; Brix *et al.*, 2006; Falkowski *et al.*, 2003; Lee, 2001]. However, carbon export may in some instances lag production [e.g., Buesseler *et al.*, 2001, 2004]. Considering that our measurements integrate NCP over approximately 10 days, the correlation of NCP to certain plankton groups could result from a lag of export. Before considering estimates of NCP and GPP, it was necessary to test the assumption that the organic carbon pool was essentially at steady state, i.e., NCP was balanced by carbon export. Below, we show that the assumption of steady state is reasonable for our study.

We estimate the change in autotrophic biomass at 17 stations along the cruise track based on the change in chlorophyll between the time of sampling and 8 days earlier as derived from 8 days composite satellite ocean color data. The average change in autotrophic biomass prior to our field observations was 1% (standard error of 2.5%) of the NCP measurements (maximum <10%), consistent with quasi steady state conditions in the organic carbon pool. Our calculations based on ocean color do not consider potential changes in community C/Chl ratio and do not provide information about DOC. However, DOC production is generally a small contribution of NCP in the Southern Ocean [e.g., Allison *et al.*, 2010; Hansell, 2002; Hansell and Carlson, 1998; Ishii *et al.*, 2002; Sweeney *et al.*, 2000]. Furthermore, it is possible that Chl may not be at steady state below the optical depth, although the infrequent occurrence of deep chlorophyll maxima and the generally homogeneous vertical distribution in the SAZ suggest that this is not likely to be of concern, in contrast to their common presence in the Polar Frontal Zone farther south [Parslow *et al.*, 2001]. Assessment of the steady state assumption would benefit from Lagrangian time series studies.

As mentioned in section 2.4, our NCP method assumes no entrainment of low oxygen waters into the mixed layer from below. This is of course an approximation, which makes our NCP estimates minimums. Importantly, the intensity of stratification was similar across much of the region (as estimated from the Brunt-Väisälä frequency), and vertical oxygen gradients between the mixed layer and the next 100 m of subsurface waters below the mixed layer were very small [Bowie *et al.*, 2011]. Thus, it is unlikely that interstation spatial variations in NCP are biased by spatial variations in exchange with subsurface waters. This perspective is consistent with previous simulations which estimated that less than 10% of NCP (based on nutrient depletion budgets) was sustained by vertical nutrient supply in the summer months, although significantly more in spring [Wang *et al.*, 2001].

3.2. Geographical Variability in Biology

Cell counting and CHEMTAX analysis provided different but complementary views of the protistan community composition, yet both agreed that there were five significantly different clusters of sites in the study area ($p < 0.05$). Although the techniques differed greatly in selectivity and precision, the 15 sites grouped by cluster analysis of cell count data fell into the same groups among the 50 sites grouped by cluster analysis of CHEMTAX data (summarized in Tables 1a and 1b). These clusters, labeled A–E from the north to the

Table 1a. Protist Community Composition in Regions Identified by Cluster Analysis of Data From Cell Counting (Microscopy Plus Flow Cytometry of Cyanobacteria)^a

Cluster	A	B	C	D	E	Average	Cell Size Range (μm) ^b
Location	STZ, Proc.3, SAZ-N	STF, Proc.1	SAZ-N, Proc.1	SAZ-S, IPFZ, Proc.2	IPFZ, Proc.2		
Cyanobacteria	30 ± 31	22	17	21 ± 18	0.3	20 ± 20	≤2
Diatoms	3 ± 5	1.3	60	6 ± 7	16.6	13 ± 21	15–200
Dinoflagellates ^c	47 ± 21	1.8	2.4	40 ± 9	9.8	27 ± 22	<10–50
Haptophytes	0.0	0.0	0.0	0.0	1.0	0.1 ± 0.4	≤8
Prasinophytes	0.1 ± 0.1	0.0	0.8	0.0	0.0	0.1 ± 0.3	≤8
Euglenoids	0.4 ± 0.3	0.3	0.4	0.6 ± 0.5	0.4	0.4 ± 0.3	20–30
Cryptophytes	0.7 ± 1.1	0.5	0.7	0.6 ± 0.4	0.8	0.7 ± 0.6	10–20
Unidentified <5 μm	3.9 ± 2.3	49	4	25 ± 16	44.4	22 ± 23	2–5
Protozoa ^d	13 ± 9	25	14	7 ± 4	26.7	15 ± 13	10–50
n ^e	4	2	2	5	2	15	

^aAll sites clustered based on cell count data fell into the same groups when clustered based on CHEMTAX data. Microscopy data only include those species/groupings that contributed up to 90% of community composition by biomass; thus, less abundant species are not represented. Data presented are averages for each cluster and standard deviations, where there were sufficient data points ($n > 2$). STZ = Subtropical Zone; STF = Subtropical Front; SAZ-N, SAZ-S = Sub-Antarctic Zone, north and south, respectively; and IPFZ = Interpolar Frontal Zone; Proc. = process station.

^bCell size range for SAZ-Sense taken from *de Salas et al.* [2011].

^cDinoflagellates include only autotrophic species.

^dProtozoa include heterotrophic dinoflagellates.

^en = number of sites in each cluster.

south, coincided with water masses from the Subtropical Zone to the Interpolar Frontal Zone (IPFZ) (defined in Figure 1). Cell size ranges for the protistan groups from microscopy observations in *de Salas et al.* [2011] are given in Table 1a.

CHEMTAX analysis does not provide size spectral information; however, it did confirm the importance of dinoflagellates through the study region, the importance of cyanobacteria (i.e., *Synechococcus* sp.), and the low stocks of diatoms in the north. It also suggested that there were significant stocks of haptophytes, probably accounting for the unidentified nanoflagellates seen by microscopy [*de Salas et al.*, 2011]. Important differences between the techniques should be noted in consideration of Tables 1a and 1b. Cell counting of cyanobacteria by flow cytometry is robust, with good precision. Cell counting of other groups via microscopy is strongly selective for large robust cells, principally diatoms and dinoflagellates, and generally has poor precision, yet it provides considerable taxonomic resolution of these groups (full data, supporting information Table S3). However, microscopy selects against small cells that lack identifiable features, while fragile cells may be lost completely from the analysis. Thus, the computed % POC of each taxon derived from

Table 1b. Protist Community Composition in Regions Identified by Cluster Analysis of Data From CHEMTAX Analysis^e

Cluster	A	B	C	D	E	Average
Location	STZ, Proc.3, SAZ-N	STF, Proc.1	SAZ-N, Proc.1	SAZ-S, IPFZ, Proc.2	IPFZ, Proc.2	
Cyanobacteria	13 ± 7	2.0 ± 0.4	2.8 ± 0.7	1.5 ± 1.5	0.9 ± 0.4	6.4 ± 7.1
Diatoms	3.1 ± 2.6	1.7 ± 1.0	18 ± 8	7.1 ± 5.5	28 ± 6	9 ± 11
Dinoflagellates ^a	29 ± 9	32 ± 5	21 ± 5	29 ± 5	14 ± 5	26 ± 9
Haptophytes	29 ± 9	49 ± 7	36 ± 9	46 ± 4	50 ± 7	39 ± 12
Prasinophytes	8.3 ± 2.7	6.2 ± 1.9	8.9 ± 2.3	6.4 ± 5.3	2.7 ± 4.5	6.7 ± 3.7
Chlorophytes	4.5 ± 3.0	3.7 ± 1.8	6.5 ± 2.3	4.7 ± 4.5	0.9 ± 1.0	3.8 ± 3.1
Euglenophytes	10.9 ± 4.4	4.7 ± 1.7	4.9 ± 2.6	4.3 ± 1.2	2.9 ± 0.7	6.9 ± 4.5
Cryptophytes	2.7 ± 2.6	0.5 ± 0.4	1.4 ± 0.3	1.0 ± 0.7	0.9 ± 0.6	1.7 ± 2.0
Total Chl <i>a</i> mg m ⁻²	29 ± 20	18 ± 9	39 ± 27	33 ± 17	25 ± 3	27 ± 17
Mixed-layer depth (m)	24 ± 17	59 ± 38	55 ± 36	68 ± 22	48 ± 12	43 ± 29
n ^c	21	11	3	7	8	50

^aAll sites clustered based on cell count data fell into the same groups when clustered based on CHEMTAX data. Microscopy data only include those species/groupings that contributed up to 90% of community composition by biomass; thus, less abundant species are not represented. Data presented are averages for each cluster and standard deviations, where there were sufficient data points ($n > 2$). STZ = Subtropical Zone; STF = Subtropical Front; SAZ-N, SAZ-S = Sub-Antarctic Zone, north and south, respectively; and IPFZ = Interpolar Frontal Zone; Proc. = process station.

^bDinoflagellates include only autotrophic species.

^cn = number of sites in each cluster.

microscopy (Table 1a) represents only its contribution to the microscopically recognizable biomass, and significant extra biomass has probably been ignored. CHEMTAX, on the other hand, captures the whole population of photosynthetic phytoplankton, particularly the nanoplankton, but is based on contribution to Chl *a* rather than POC; it ignores heterotrophs, lacks the taxonomic detail of microscopy, and is subject to uncertainties in interpretation (Table 1b). Results for cell counting and CHEMTAX differed in several ways, but a consistent picture emerged between the two techniques, revealing populations dominated by nanoplankton, picoplankton, and dinoflagellates, with diatoms normally being minor constituents (Tables 1a and 1b):

Cyanobacteria (*Synechococcus* sp., ≤ 2 μm diameter) contributed 20% of identified biomass across the SAZ on average, although in the IPFZ (cluster E), they contributed only 0.3%. The smaller contribution of cyanobacteria to Chl *a* determined by CHEMTAX reflects the small Chl *a*:Carbon ratio of *Synechococcus* [Liu *et al.*, 1999].

Nanoflagellate taxa (haptophytes, prasinophytes, euglenoids, and cryptophytes, 2–20 μm length) represented 23% of the microscopic biomass (including 22% unidentified cells), but they represented 58% of the CHEMTAX estimate, on average. These different estimates were probably due to the large proportion of cells unidentified by microscopy, coupled with the unknown, but likely significant, proportion of fragile cells lost altogether during microscopic fixation and preparation but captured by CHEMTAX analysis.

Diatoms (15–200 μm) were minor components of the populations according to both techniques, except in clusters C and E in the SAZ-N and IPFZ regions, respectively. In cluster C, diatoms represented 60% of the microscopically identifiable biomass and were dominated by *Thalassiosira* sp., although CHEMTAX estimated that the contribution was only 18% of total chlorophyll. In cluster E, the CHEMTAX estimate of diatoms (28%) was greater than the microscopic estimate (17%), which may be due to different species composition or an overestimation by CHEMTAX due to some contribution to fucoxanthin (the principal diatom carotenoid) from unidentified nanoplankton.

Autotrophic dinoflagellates (20–50 μm) were identified by microscopy as significant components of the populations only in clusters A and D (47%, 40%, respectively, with other clusters <10%). CHEMTAX suggested that dinoflagellates in regions B and C in particular contributed much greater proportions of Chl *a* (32% and 21%, respectively). It is unclear whether this is due to dinoflagellates that are microscopically unrecognizable or to a potential contribution of unrecognized haptophytes to the stocks of type 2 dinoflagellates, which have haptophyte pigmentation.

Protozoans (including heterotrophic dinoflagellates, 10–50 μm) averaged 15% of total biomass, with ~25% in clusters B and E, ~14% in clusters A and C, and only 7% in cluster D.

The biomass of microscopically unidentified cells did not correlate significantly with any CHEMTAX group, implying that the former did not consist of a single group of taxa.

Correlations between the techniques were generally not strong: estimates of diatom biomass were loosely, but significantly, correlated ($r = 0.58$, $p < 0.005$), dinoflagellates were better correlated ($r = 0.71$, $p < 0.001$), but other categories were poorer, attributable to contributions to CHEMTAX estimates from unidentified or lost cells by microscopy, as well as poor counting statistics for rarer cells. For cyanobacteria, the correlation between flow cytometric estimates (of POC) and CHEMTAX estimates (of Chl *a*) was stronger ($r = 0.93$, $p < 0.001$).

3.3. Net Community Production and Gross Primary Production and Relation to Taxonomy

The geographical variation in NCP during the SAZ-Sense cruise is overlain in Figure 1a. Briefly, most of the study region was net autotrophic with an average NCP of 31 $\text{mmol C m}^{-2} \text{d}^{-1}$ in the SAZ. There was a large meridional gradient, with highest NCP recorded at the Subtropical Front where the community composition of diatoms was small to negligible ($\leq 3\%$, clusters A and B) and where dinoflagellates and smaller cells such as *Synechococcus* sp. and nanoflagellates dominated. This trend in productivity was also reflected in our estimates of GPP based on triple isotopic composition of dissolved O_2 (Figure 1b). NCP/GPP varied between 0.06 and 0.54 (mean = 0.25, $s = 0.12$, and $N = 40$). No significant latitudinal trend in NCP/GPP was observed.

We found that NCP was not correlated to the proportion of the phytoplankton biomass accounted for by diatoms as determined by microscopic and CHEMTAX pigment analyses (Figure 2). Regions with communities dominated by diatoms variously exhibited high and low NCP (clusters C and E in SAZ-N and the IPFZ, respectively), while large NCP was observed in regions where diatoms contributed only a small fraction of the

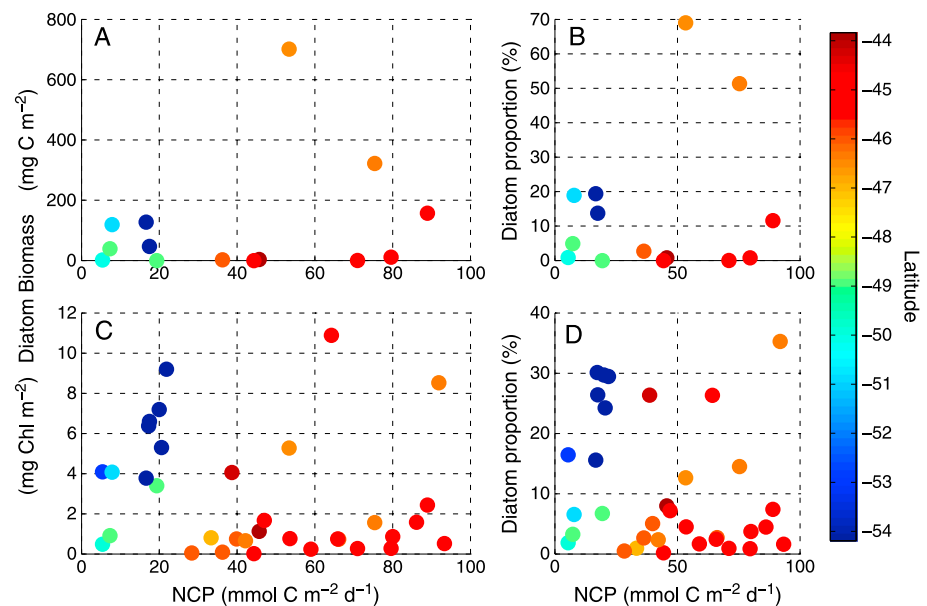


Figure 2. NCP as a function of diatom (a and c) biomass and (b and d) proportion within the mixed layer relative to community biomass as determined by microscopy (Figures 2a and 2b) and autotrophic biomass as determined by CHEMTAX analyses (Figures 2c and 2d). Points are color coded for latitude.

total community. Our results suggest that rapid carbon export in the Sub-Antarctic Zone may take place in the absence of vigorous diatom production, adding further evidence that the dogma that diatom production drives carbon export is not always true. A lack of correlation between NCP and the abundance of diatoms has also been recently reported at the Antarctic Peninsula [Huang *et al.*, 2012]. We point out that the contribution of a given group to total biomass may not necessarily reflect the contribution either to net primary production [e.g., Fernandez *et al.*, 2003; Stukel and Landry, 2010] or to net community production. Our objective was to relate plankton community to NCP, not to determine which group is actually exported, which can only be addressed with sediment traps or other measurements below the mixed layer.

Depending on the taxonomic composition of the upper trophic levels, grazing may enhance (classical food chain) or inhibit (microbial loop) the transfer of organic carbon to deeper waters [Legendre and Michaud, 1998]. In this study, we found a positive correlation of NCP with the proportion of primary productivity grazed upon by microheterotrophs ($r=0.62$, $n=11$, Figure 3) as determined by the dilution grazing method [Landry and Hassett, 1982]. This relationship suggested that NCP was strongly influenced by grazing of primary production through the classical food chain, with grazing being particularly important at lower latitudes (Figure 3). The greater grazing pressure at high NCP sites could also be explained by congregation of grazers at high production sites (see section 3.4). Our results are supported by the fact that fecal aggregates dominated carbon exported to traps at all process stations with negligible contribution from phytoplankton and phytoplankton aggregates [Ebersbach *et al.*, 2011].

Small phytoplankton, such as cyanobacteria, are generally believed to contribute little to export because of their size and efficient population control by micrograzers. However, cyanobacteria have been observed in deep fecal pellets and aggregates and are reported to contribute significantly to export in sub-Antarctic waters [Waite *et al.*, 2000]. Based on CHEMTAX pigment analyses, we found that NCP was significantly correlated to the mixed-layer-depth-integrated proportion of biomass attributable to cyanobacteria ($r=0.54$, $p=0.0009$), cryptophytes ($r=0.39$, $p=0.02$), euglenophytes ($r=0.49$, $p=0.004$), and negatively correlated to haptophytes ($r=-0.44$, $p=0.009$). Small cells such as cyanobacteria may contribute to carbon export through several putative pathways. Some mesozooplankton, such as salps, can graze in the $1\ \mu\text{m}$ size range of cyanobacteria. The poor digestibility [Gorsky *et al.*, 1999] and premature egestion of cyanobacteria such as *Synechococcus* sp. [Boenigk *et al.*, 2001] may further explain their contribution to NCP. Additionally, aggregation of cyanobacteria and other picoplankton may provide a vector for their sinking and grazing

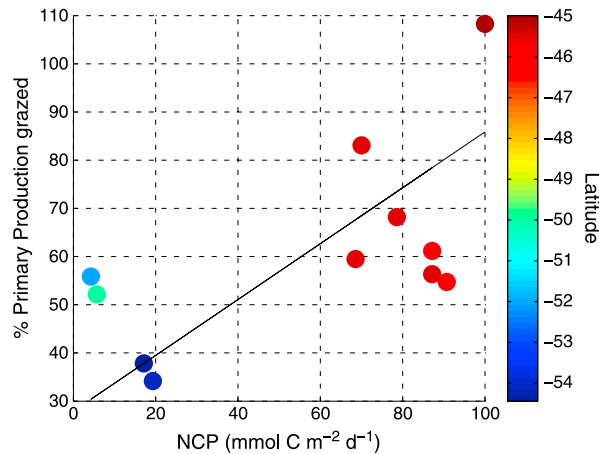


Figure 3. NCP versus proportion of primary production grazed, as determined by dilution experiments. The black line represents a model II least squares bisector regression analysis ($r = 0.62$, $p < 0.05$). Similar results were observed for volumetric NCP.

upon by mesozooplankton [e.g., Albertano et al., 1997; Jackson, 1990; Jackson et al., 2005; Olli and Heiskanen, 1999].

3.4. Influence of Bottom-Up Controls and Grazing on Export

The link between plankton community and carbon fluxes may be influenced by varying bottom-up controls on NCP. For example, higher availability of iron and/or light may explain the higher NCP observed in the northern regions of the SAZ [Cassar et al., 2011], with the relation to phytoplankton community being secondary or coincidental. In order to account for bottom-up controls,

we normalized our NCP measurements to calculate the carbon export per unit POC (NCP/POC, which, when the assumptions above are valid, is proportional to sinking rate) and the proportion of NCP exported (NCP/GPP). Our observations during the SAZ-Sense cruise support the theoretical prediction of a relationship between NCP and POC (Figure 4) with the slope of the regression line being significantly different from zero ($r = 0.75$, $p < 0.0001$, $n = 20$). If the relationship between NCP and POC holds in other regions, satellite estimates of POC may prove useful in constraining broad-scale patterns of NCP [Chang et al., 2014].

If the assumptions presented in section 2.6 hold, NCP/POC should reflect the average sinking rate of particles within the mixed layer. The average NCP/POC at our stations is 6 m d^{-1} (range of $1.8\text{--}19.5 \text{ m d}^{-1}$), consistent with modeled and measured (e.g., nuclide-based) sinking rates [Henderson et al., 1999; Lundsgaard and Olesen, 1997; Stramska, 2010; Tsunogai and Minagawa, 1978; Woods and Onken, 1982]. It should be noted that only some fraction of the POC within the mixed layer is actually sinking. Sinking rates of living and dead phytoplankton cells vary greatly from 0 to 30 and 60 m d^{-1} , respectively [Smayda, 1970, 1971]. Chlorophyll-based sinking rates are generally less than 1 m/d [Bienfang, 1984; Bienfang and Harrison, 1984; Jacques and Hoepffner, 1984; Johnson and Smith, 1986]. The proportion of POC within the mixed layer

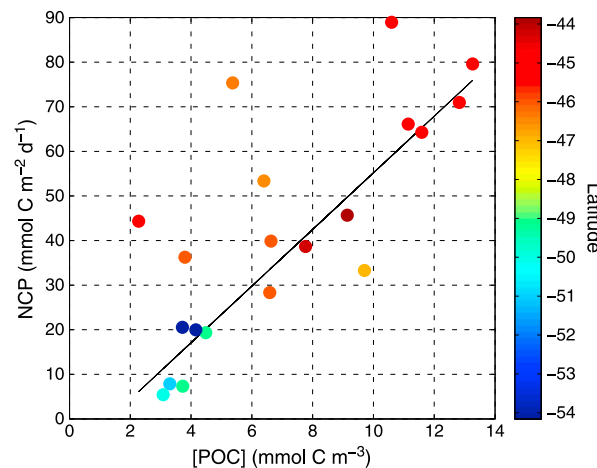


Figure 4. NCP as a function of POC concentration within the mixed layer during the SAZ-Sense cruise. Points are color coded for latitude. Line represents a robust (bisquare weight function) regression.

accounted for by living plankton varies greatly, from less than half to more than 70% [Eppley et al., 1977, 1983]. Hence, in addition to being maintained in suspension by turbulence and convection [Lande and Wood, 1987; Smayda, 1970], a significant proportion of POC within the mixed layer is living and may have some control over position within the water column through motility and buoyancy. The POC/Chl *a* ratios observed during our cruise (median = 96) suggest significant detrital and heterotrophic biomass, when compared to values for phytoplankton of $\sim 30\text{--}50$ [Geider, 1987]. Export is probably mediated by a fraction

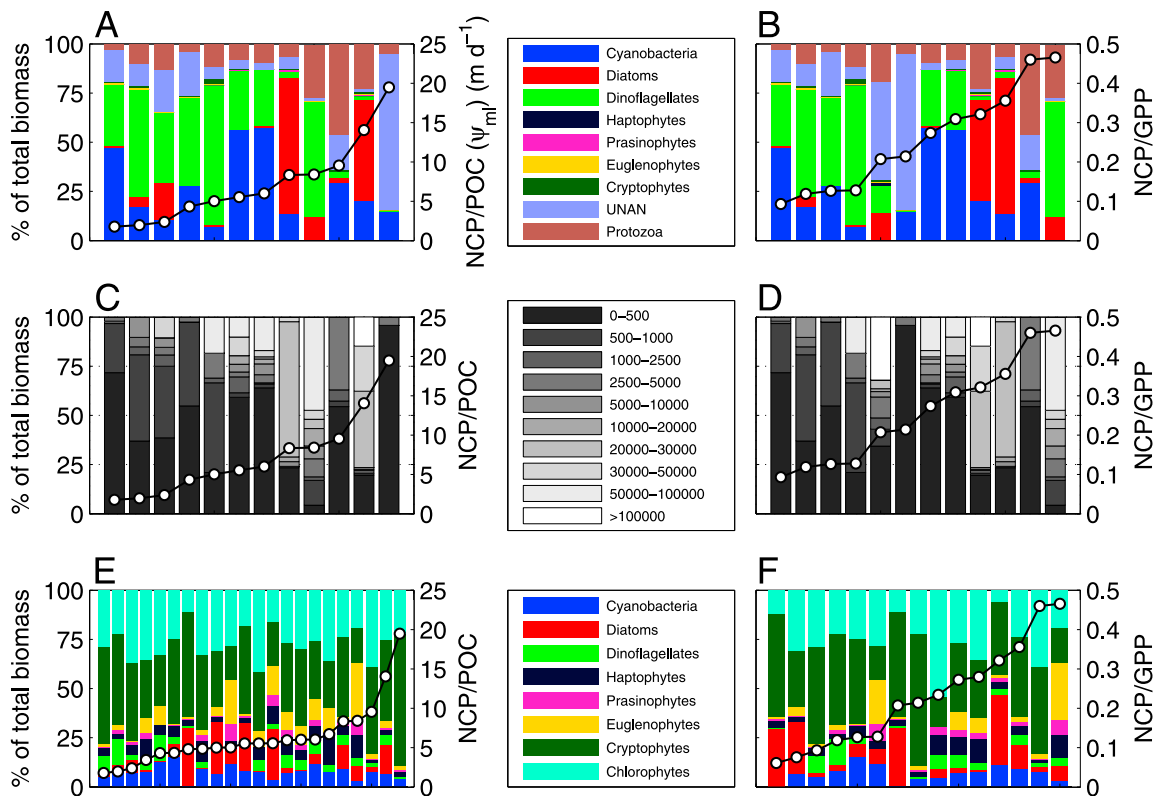


Figure 5. (a, c, and e) NCP/POC and (b, d, and f) NCP/GPP as a function of plankton community (Figures 5a–5d) and autotrophic community composition (Figures 5e and 5f). Community functional groups (Figures 5a and 5b) and group size distribution (in μm^3 , Figures 5c and 5d) were derived from microscopy. Autotrophic community functional groups (Figures 5e and 5f) were derived from CHEMTAX pigment analyses. The relative proportion of functional groups is represented by stacked bars. NCP/POC and NCP/GPP are represented by lines with circle symbols on the secondary ordinate axis. X axis represents individual stations “NCP/POC” (Figures 5a, 5c, and 5e) and “NCP/GPP” (Figures 5b, 5d, and 5f) circle, ranked in ascending order, with corresponding “community” stacked bar. UNAN stands for unidentified nanoflagellates. Biomass is in $\mu\text{g L}^{-1}$. Note that NCP in Figures 5a, 5c, and 5e is in $\text{mmol C m}^{-2} \text{d}^{-1}$. NCP and GPP in Figures 5b, 5d, and 5f are in $\text{mmol O}_2 \text{m}^{-2} \text{d}^{-1}$.

of the POC sinking at higher rates, consistent with the large particles observed in sediment traps during the SAZ-Sense study [Ebersbach et al., 2011]. The mean residence time of POC of 12 days in surface waters (supporting information Table S4), calculated from the ratio of MLD to NCP/POC, is consistent with observations in other regions of the world’s oceans [Eppley et al., 1992; Gardner et al., 2006; Karl et al., 1996; Laws et al., 1989; Pena et al., 1991; Raimbault et al., 2008].

The regression of NCP versus POC can be used to assess the impact of plankton composition and size distribution on carbon fluxes and identify “High Biomass Low Export” [Lam and Bishop, 2007] and similarly “Low Biomass High Export” regimes. Based on our microscopic analyses, there was no clear relationship between NCP/POC and functional groups or plankton size distribution at our study sites (Figure 5). Although low NCP/POC ratios were generally associated with communities dominated by smaller phytoplankton, high ratios were observed with such communities as well, such as the unidentified nanoplankton (UNAN, Figure 5a). High NCP/POC of communities with small cell sizes is likely to have been caused by aggregation of particles by coagulation or grazing. We did not find a clear relationship between NCP/POC and the presence of diatoms as determined by microscopy or pigment analyses. Interestingly, low NCP/POC was associated with communities dominated by dinoflagellates ($r = -0.65, p = 0.02$) (Figure 5a), particularly those observed by microscopy which include heterotrophic, autotrophic, and mixotrophic species (the trophic status of cells could not be confirmed following preservation). The same relationship was not evident from the HPLC biomass which accounts for only autotrophic and mixotrophic dinoflagellates (Figure 5e). As difference between the two is the heterotrophic status of the cells, it appears that the heterotrophic dinoflagellates are contributing significantly to grazing, remineralization, and O_2 consumption in surface waters.

Variability in NCP/POC may result from the association of nanoplankton with aggregate-forming processes, such as grazing and the associated packaging of organic matter into rapidly sinking fecal pellets. Grazing by ciliates may directly contribute to carbon export [Lundsgaard and Olesen, 1997; Nothig and Vonbodungen, 1989]. Alternatively, NCP/POC variability may stem from the correlation of protozoa with grazing by euphausiids and copepods and the associated packaging of organic matter into rapidly sinking fecal pellets. Copepods are believed to be a strong vector for carbon export in sub-Antarctic waters and in waters in the vicinity of the Subtropical Front [Bradford-Grieve *et al.*, 2001]. Oligotrich ciliates such as *Strombidium* spp., nauplii, and tintinnids plus heterotrophic dinoflagellates were observed in the region [Pearce *et al.*, 2011], and others have reported the presence of calanoid and cyclopoid copepods, euphausiids, and salps in the region [McLeod *et al.*, 2010]. Protozoa were mostly associated with phototrophic assemblages dominated by cyanobacteria, which may explain the strong correlation of NCP to cyanobacteria mentioned earlier. Other work showed that fecal aggregates dominated carbon exported to sediment traps at all process stations during this cruise and a negligible contribution from phytoplankton and phytoplankton aggregates [Ebersbach *et al.*, 2011], although we recognize that sediment traps may not be representative of mixed-layer NCP.

We did not find a clear relationship between NCP/Chl (NCP/POC data unavailable) versus the proportion of chlorophyll in various size fractions of the particulate matter. Our preliminary observations showed that low NCP/Chl is generally associated with chlorophyll in smaller size fractions and that larger NCP/Chl is associated with larger size fractions, but not all the time (supporting information Figure S1). The dominance of fecal export over cell settling may explain our lack of correlation between NCP/Chl and the proportion of chlorophyll in various size fractions. It should also be noted that our NCP/Chl observations do not strictly reflect NCP/POC and should be interpreted with caution.

Whereas NCP/POC and other derived variables give us some insight into the residence time and fractional loss rate of the organic matter within the mixed layer, NCP/GPP reflects the extent of recycling and the fractional loss within the mixed layer. Our observations suggest lower NCP/GPP when plankton communities are dominated by smaller plankton as determined by microscopy. Over a large meridional variation in taxa, we found that low NCP/POC and NCP/GPP were generally associated with smaller phytoplankton size assemblages (Figures 5c and 5d). Overall, pigment and microscopy analyses both show that high NCP/GPP can occur when diatoms do not represent a large proportion of the community. In summary, our data are broadly consistent with the view that low NCP often occurs in communities dominated by small cells, but this is not the same as stating that small cell communities cannot fuel high NCP, rather we observed that high NCP conditions occurred in both small and large cell-dominated communities, and moreover, the presence of large diatoms was not a sufficient condition to guarantee high NCP.

3.5. Caveats and Implications

Through a combination of mass spectrometric analysis and protistan community analysis, we were able to show that plankton cell size did not reliably predict export flux in our region of the Sub-Antarctic Zone, that vigorous (i.e., $>50 \text{ mmol C m}^{-2} \text{ d}^{-1}$) export occurred when diatoms were not dominant, and that microheterotrophs did not inhibit export. Several factors must be considered in relation to these results. First, diatoms are not equal when it comes to export [Assmy *et al.*, 2013]. The diatoms in these low-silica sub-Antarctic waters were lightly silicified, reducing their density compared with the more heavily silicified diatoms of the high Antarctic. Additional studies in regions with greater variability in community composition will provide further insight into the role of diatoms. Second, the size spectrum of particles in the water column is unlikely to relate to that of the individual protist cells in the population, as measured by microscopy, due to aggregation by coagulation or through ingestion and excretion as fecal pellets. Third, the correlation between taxonomy and export may not directly reflect the sinking rates of individual taxa but rather a relationship with higher community structure and processes such as grazing pressure that determine, or are determined by, community structure. Fourth, these results are based on the assumption of steady state in the POC pool, and although this assumption appears valid in this case, future work would benefit from Lagrangian time series studies. Fifth, the pigment and microscopy analyses, which are at this time the most commonly used taxonomic methods in oceanography, are both subject to uncertainties. Molecular tools should help reduce the uncertainty in the characterization of the plankton community as they become more available. Finally, we note that the overall biological pump is not a function of mixed-layer NCP alone and that our observations are not relevant to processes occurring below the mixed layer, such as

production below the mixed layer and mesopelagic flux attenuation [e.g., *Jacquet et al.*, 2011; *Lomas et al.*, 2009; *Martin et al.*, 2013].

Bottom-up and top-down controls shape phytoplankton assemblages, primary productivity, and carbon export. The latter is believed to be strongly governed by plankton and particle size, yet the dependence on size distribution is far from resolved, even below the mixed layer where a significant proportion of particles are inert [e.g., *Jouandet et al.*, 2011; *McDonnell and Buesseler*, 2010]. Predicting the future behavior of Earth's climate system will require an improved mechanistic understanding of the biological pump, including the influence of microbial community structure, aggregation, and grazing on carbon export production.

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