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Satellite estimates of net community production indicate predominance of net autotrophy in the Atlantic Ocean

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ABSTRACT

There is ongoing debate as to whether the oligotrophic ocean is predominantly net autotrophic and acts as a CO_2 sink, or net heterotrophic and therefore acts as a CO_2 source to the atmosphere. This quantification is challenging, both spatially and temporally, due to the sparseness of measurements. There has been a concerted effort to derive accurate estimates of phytoplankton photosynthesis and primary production from satellite data to fill these gaps; however there have been few satellite estimates of net community production (NCP). In this paper, we compare a number of empirical approaches to estimate NCP from satellite data with *in vitro* measurements of changes in dissolved O_2 concentration at 295 stations in the N and S Atlantic Ocean (including the Antarctic), Greenland and Mediterranean Seas. Algorithms based on power laws between NCP and particulate organic carbon production (POC) derived from ^{14}C uptake tend to overestimate NCP at negative values and underestimate at positive values. An algorithm that includes sea surface temperature (SST) in the power function of NCP and ^{14}C POC has the lowest bias and root-mean square error compared with *in vitro* measured NCP and is the most accurate algorithm for the Atlantic Ocean. Nearly a 13 year time series of NCP was generated using this algorithm with SeaWiFS data to assess changes over time in different regions and in relation to climate variability. The North Atlantic subtropical and tropical Gyres (NATL) were predominantly net autotrophic from 1998 to 2010 except for boreal autumn/winter, suggesting that the northern hemisphere has remained a net sink for CO_2 during this period. The South Atlantic subtropical Gyre (SATL) fluctuated from being net autotrophic in austral spring-summer, to net heterotrophic in austral autumn–winter. Recent decadal trends suggest that the SATL is becoming more of a CO_2 source. Over the Atlantic basin, the percentage of satellite pixels with negative NCP was 27%, with the largest contributions from the NATL and SATL during boreal and austral autumn–winter, respectively. Variations in NCP in the northern and southern hemispheres were correlated with climate indices. Negative correlations between NCP and the multivariate ENSO index (MEI) occurred in the SATL, which explained up to 60% of the variability in NCP. Similarly there was a negative correlation between NCP and the North Atlantic Oscillation (NAO) in the Southern Sub-Tropical Convergence Zone (SSTC), which explained 90% of the variability. There were also positive correlations with NAO in the Canary Current Coastal Upwelling (CNRY) and Western Tropical Atlantic (WTRA) which explained 80% and 60% of the variability in each province, respectively. MEI and NAO seem to play a role in modifying phases of net autotrophy and heterotrophy in the Atlantic Ocean.

1. Introduction

Marine photosynthesis and respiration mediate the exchange of CO_2 between the oceans and atmosphere. Gross primary production (GPP) equates to the amount of CO_2 taken up by marine autotrophic plankton, and net community production (NCP) is the difference between GPP and the organic carbon lost through autotrophic and heterotrophic respiration (R). NCP plays a key role in connecting trophic and biogeochemical dynamics of pelagic ecosystems, through metabolic balance between GPP and R and the subsequent fate of carbon through export or release to

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the atmosphere. There is ongoing debate as to whether the oligotrophic oceans are predominantly net autotrophic and acting as a CO_2 sink, or net heterotrophic and therefore acting as a CO_2 source to the atmosphere (Duarte, Regaudie-de-Gioux, Arrieta, Delgado-Huertas, & Agusti, 2013; Williams, Quay, Westberry, & Behrenfeld, 2013). Consensus is constrained by measurement capabilities and by the spatial and temporal frequency with which NCP can be determined (Ducklow & Doney, 2013).

Over the past several decades, the carbon fixation and metabolic balance of the Global Ocean has been largely derived from measurements of *in vitro* changes in cellular ^{14}C and dissolved O_2, respectively. These techniques rely on light-dark incubations to assess the incorporation of ^{14}C-labelled CO_2 into cells or production–consumption of O_2 over time and typically over 24 h. For *in vitro* changes in dissolved O_2, the samples are placed in borosilicate glass bottles and exposed to sunlight, either on-deck or on *in situ* floating buoys (Robinson et al., 2009), and the measured changes in O_2 are attributed to biological processes. The nature of these techniques means that ship borne measurements have limited spatial and temporal coverage. Over the past decade, geochemical methods have been developed; these are measurements of the O_2/Ar ratio and the triple isotopic composition of dissolved O_2 as a natural tracer of GPP and NCP. These measurements have been made on both research and commercial ships, such as ferries and container ships, to increase the spatial coverage of sampling (Juranek & Quay, 2013). The approach is based on *in situ* O_2 mass balance calculations, the triple oxygen isotope composition ($\delta(^{17}O)$ and $\delta(^{18}O)$) of dissolved O_2 and the O_2/Ar concentration ratio, which allow for longer time scale integration and extrapolation of measurements to dynamically changing conditions (Kaiser, 2011). Though the number of observations has increased, they describe the metabolic status over the mixed layer depth, rather than at discrete depths. Whilst *in vitro* methods provide an estimate of NCP over short time-scales (24 h), geochemical methods (O_2/Ar and the triple-oxygen-isotope method) integrate over longer time-scales (typically 1 to 3 weeks). *In vitro* methods suffer from potential substrate depletion and community changes and do not account for the effect of UV radiation (Agusti, Regaudie-de-Gioux, Arrieta, & Duarte, 2014; Regaudie-de-Gioux, Agusti, & Duarte, 2014). Geochemical methods are hampered by uncertainty over the parameterisation of O_2 exchange between the oceans and atmosphere. These approaches may also underestimate NCP because they do not account for O_2 photolysis (Kitidis et al., 2014). Neither of these approaches is able to fully resolve NCP at the global or even basin scales.

The debate continues as to which measurements of NCP are more representative of the metabolic state of the oceans (Duarte et al., 2013; Williams et al., 2013). From geochemical O_2-based estimates of NCP and ^{13}C enrichment of dissolved inorganic carbon (DIC) in surface waters, Williams et al. (2013) argue that the oligotrophic subtropical gyres of the open ocean are net autotrophic. They also suggest that lateral and vertical inputs of organic carbon are insufficient to sustain net heterotrophy. They conclude that *in vitro* measurements of changes in O_2 are erroneous in the oligotrophic gyres, which may be due to an underestimate of GPP (rather than an overestimate of R), as bottle incubations should represent a greater perturbation to natural light conditions for mixed-layer phytoplankton than they do to respiratory conditions for heterotrophs. By contrast, Duarte et al. (2013) counter argue that *in vitro* estimates of net heterotrophy in the oligotrophic gyres are correct because scaling relationships indicate that heterotrophic communities prevail in areas of low GPP, low chlorophyll *a* (Chla), and warm water, typical of the oligotrophic ocean. Heterotrophic metabolism can prevail where metabolic activity is subsidised by organic carbon inputs from the continental shelf or the atmosphere and from non-photosynthetic autotrophic and/or mixotrophic metabolic pathways. Duarte et al. (2013) reject the hypothesis that *in situ* measurements in oligotrophic regions indicate net autotrophy because both O_2/N_2 and O_2/Ar based methods only integrate over the mixed layer rather than the euphotic depth thus missing a substantial part of the plankton activity in the open ocean. These issues remain unresolved and the debate on whether the open ocean is net autotrophic or net heterotrophic, continues. Parallel to this, the oligotrophic regions are expanding (Polovina, Howell, & Abecassis, 2008) due to warming of the ocean, which could impact the metabolic balance of the Global Ocean.

There has been a concerted effort to derive both net primary production (NPP) and GPP from satellite ocean colour data, which has been driven by a series of model comparisons (Campbell et al., 2002; Carr et al., 2006; Friedrichs et al., 2009; Saba et al., 2010; Tilstone, Smyth, Poulton, & Hutson, 2009). Algorithms to predict NCP however, are in their infancy. Recently, empirical relationships between measured ^{14}C POC and NCP have been used with satellite-based estimates of POC

Table 1
Location and dates of cruises for the collection of *in vitro* net community production (NCP) data. BODC is British Oceanographic Data Centre. Data from AMT cruises 11 to 21 were used for calibration (C) and validation (V) of the algorithms. All other data were used for validation only.

Cruise Name	Vessel	Dates	Location	No. of Stations	Reference
CD046- BOFS	*RRS Charles Darwin*	01 May–14 June 1990	NADR	13	Williams (1998)
CD060- BOFS	*RRS Charles Darwin*	16–29 June 1991	N Atlantic	3	Holligan et al. (1993)
Bioantar 93	*RV BioHespérides*	05–14 February 1994	Antarctic	4	Aristegui, Montero, Ballesteros, Basterretxea, and vanLenning (1996)
CICYT AMB	*RV José Rioja*	01 March–01 September 1994	NAST-E	14	Serret, Fernandez, Sostres, and Anadon (1999)
CICYT AMB	*RV José Rioja*	01 October 1994–01 June 1995	NAST-E	21	Serret et al. (1999)
AMT4	*RRS James Clark Ross*	01 April 1997	NADR–SATL	13	Gonzalez, Anadon, and Maranon (2002)
AMT5	*RRS James Clark Ross*	01 September 1997	SATL - NADR	11	Gonzalez et al. (2002)
Bay of Biscay	*RV José Rioja*	01 April–03 August 1999	NADR	8	(Gonzalez et al. 2003)
POMME	*NO L'Atlante* *NO Thalassa*	28 September–03 October 2000, 07–23 March 2001, 02 May 2001, 20 September–03 October 2001.	NAST-E	23	Maixandeau, Lefevre, Fernandez, et al. (2005), Maixandeau, Lefevre, Karayanni, et al. (2005)
AMT12	*RRS James Clark Ross*	23 May–11 June 2003	SATL - NADR	C = 7; V = 12	Gist, Serret, Woodward, Chamberlain, and Robinson (2009)
AMT13	*RRS James Clark Ross*	18 September–7 October 2003	NADR - SATL	C = 9; V = 10	Gist et al. (2009)
AMT14	*RRS James Clark Ross*	5–29 May 2004	SATL - NADR	C = 8; V = 12	Gist et al. (2009)
AMT15	*RRS James Clark Ross*	21 September–24 October 2004	NADR - SATL	C = 7; V = 12	Gist et al. (2009)
AMT16	*RRS James Clark Ross*	26 May–24 June 2005	SATL - NADR	C = 8; V = 11	Gist et al. (2009)
AMT17	*RRS Discovery*	28 October–6 November 2005	NADR - SATL	7	Gist et al. (2009)
Threshold	*RV BioHespérides*	04 June–04 July 2006, 06 May–01 July 2007	Mediterranean Sea	8	Regaudie-de-Gioux, Vaquer-Sunyer, and Duarte (2009)
CARPOS	*RV BioHespérides*	14 October–21 November 2006	NAST-E	16	Aranguren-Gassis et al. (2011)
ATOS	*RV BioHespérides*	01–25 July 2007	Greenland Sea	8	Regaudie-de-Gioux and Duarte (2010)
AMT18	*RRS James Clark Ross*	16 September–21 October 2008	NADR - SATL	C = 7; V = 11	BODC
AMT21	*RRS Discovery*	02 October–08 November 2011	NADR - SATL	C = 15; V = 16	BODC
TOTAL				**295 (C = 61)**	