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 sub-tropical 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 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 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 et al. 2013; Williams et al. 2013). Consensus is constrained by measurement capabilities and by the spatial and temporal frequency with which NCP can be determined (Ducklow and 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 and 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 et al. 2014; Regaudie-de-Gioux et al. 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 subsidized 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 et al. 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 et al. 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 production to estimate NCP in specific regions of the Atlantic Ocean (Duarte et al. 2001; Serret et al. 2002; Serret et al. 2001), in the Southern Ocean (Nevison et al. 2014; Chang et al. 2014) and at global scales (Westberry et al. 2012). Serret et al. (2009) derived empirical relationships between measurements of *in vitro* O_2 based NCP and ^{14}C particulate organic carbon production (^{14}C POC) to predict NCP in either eutrophic or oligotrophic environments. Lopez-Urrutia et al. (2006) derived models to infer NCP from temperature and the size structure of the plankton community. Empirical relationships between R and a satellite based NPP model have been used to estimate global NCP (Westberry et al. 2012). Satellite models of NCP, based on net primary production and export, have also been proposed for the Southern Ocean (Nevison et al. 2012). Chang et al. (2014) developed a neural network approach based on self-organizing maps to construct weekly gridded maps of organic carbon export for the Southern Ocean. The maps were trained with *in situ* measurements of O_2/Ar to estimate NCP linked to potential predictors of NCP through statistical relationships with photosynthetically available radiation (PAR), Chla and mixed layer depth (MLD).

The objective of this paper is to develop and validate empirical satellite algorithms of NCP that can be applied to ocean colour satellite data, such as SeaWiFS and MODIS-Aqua, for the Atlantic Ocean. Using the SeaWiFS archive, the most accurate algorithms were used to analyse decadal trends in NCP, the extent of net heterotrophy in the Atlantic Ocean and the effect of climate forcing indices on this metabolic balance in different biogeochemical provinces.

2. Materials and Methods

2.1. Study area and sampling regime.

Water samples were collected from May 1990 to November 2011 using a SeaBird CTD on 26 cruises in the Atlantic Ocean, Mediterranean and Greenland Seas (Table 1). Sampling depths were determined by *in situ* fluorescence (WetLabs fluorometer), temperature, salinity (SBE) and / or PAR (Chelsea, SATLANTIC or Ocean Optics) profiles. Depth integrated *in vitro* NCP measurements were collected from 295 stations (Fig. 1A; Table 1). Of these, 61 stations from AMT 12, 13, 14, 15, 16, 18, 21 were used to calibrate the satellite algorithms (Fig. 2A, B) and data from AMT 4, 5, 12, 13, 14, 15, 16, 18, 21, other Atlantic Ocean cruises, Greenland and Mediterranean Seas (N=234; Table 1) were used to validate the algorithms (Fig. 3, 4, 5). Where calibration and validation data were used from the same cruises over similar time and spatial scales, there was no significant correlation between these data (r=0.059, P=0.653). Coincident *in vitro* NCP and ^{14}C POC were determined at 145 stations; 61 stations were used to calibrate new empirical algorithms of NCP, and 84 stations were used for algorithm validation.

2.2 Measured parameters.

2.2.1. In vitro ^{14}C Particulate Organic Carbon Production (POC).

Measurements of ^{14}C POC (N = 145) were made on seven AMT cruises (AMT 12, 13, 14, 15, 16, 18, 21; Table 1). Water samples were taken from 6 to 8 depths based on percentage surface irradiance and transferred from Niskin bottles to blacked-out carboys. Water from each sample was sub sampled into three 75-ml clear polycarbonate bottles and three black polycarbonate bottles. Each bottle was inoculated with between 185 and 740 kBq (5–20 mCi) $NaH^{14}CO_3$ according to the biomass of phytoplankton. They were then transferred to an on-deck, simulated *in situ* incubation system using neutral density and blue filters to reproduce sub-surface irradiance. The bottles were maintained at *in situ* temperature by pumping either sea surface water and / or refrigerated water through the system from dawn to sunset. Suspended material was filtered through 0.2 μm polycarbonate filters. The production of ^{14}C dissolved organic carbon (DOC) was not measured. ^{14}C POC measured at discrete depths was integrated over the sampling depth to 1% irradiance over daylight hours only, which means that integrated values are similar to NPP (Marra 2009). Further details of the protocols are given in (Poulton et al. 2006; Tilstone et al. 2009).

2.2.2. In vitro Net Community Production.

A dataset of NCP measurements was created from the database originally collated and maintained for Robinson and Williams (2005), supplemented with recently published data (Regaudie-de-Gioux and Duarte 2010; Regaudie-de-Gioux et al. 2009) and measurements made during recent AMT's (Table 1). The dataset is available at http://www.uea.ac.uk/environmental-sciences/people/People/Faculty+and+Research+Fellow/robinsonc#research and the AMT data are available from the British Oceanographic Data Centre (BODC). In order to ensure that the depth integrated data best approximates the NCP in the euphotic zone, data were only used when more than three depths were sampled and when the shallowest depth was <15m and the deepest was >50m. Photic zone integrated values were calculated by trapezoidal integration of the volumetric data from the surface to the 1% light depth. The details of the incubation and Winkler titration procedure used for each study are given in the cited references in Table 1. Determination of NCP on the AMT cruises followed the procedures described in Gist et al. (2009).

2.3. Satellite Estimates.

2.3.1. Satellite Algorithms of Net Community Production.

Four empirical relationships to derive NCP from *in vitro* ^{14}C POC were used and validated against independent *in vitro* O_2 NCP measurements. The first algorithm (Eq. 1) was derived from AMT6 data from three productive provinces and two unproductive areas of the East Atlantic, where net heterotrophy has been frequently measured. The second (Eq. 2) was derived from AMT11 data, which includes three productive provinces and one unproductive isolated regime in the South Atlantic, where net autotrophy prevailed (Serret et al. 2009). The algorithms are as follows:

$$NCP_A = 49.53 * \int {}^{14}C\ POC^{0.48} - 300 \qquad \text{Eq. 1 (AMT6 model).}$$

$$NCP_B = 212.01 * \int {}^{14}C\ POC^{0.15} - 300 \qquad \text{Eq. 2 (AMT11 model).}$$

To derive the power law, a value of 300 was added to each NCP measurement to make all the values positive. This value has then to be subtracted to derive the predicted NCP value in mmol O_2 m^{-2} d^{-1}.

For the third algorithm, half of the data from cruises AMT 12, 13, 14, 16, 18, 21 (N=61; referred to as calibration data) were used to derive a new empirical algorithm based on the power law between measured *in vitro* NCP and ^{14}C POC (Fig. 2A). To make it independent from the other algorithms, data from AMT6 and 11 were not included. For illustrative purposes, some data from AMT6 are indicated as outliers in Fig. 3. The algorithm is as follows:

$$NCP_C = 163.83 * \int \quad {}^{14}C\ POC^{0.2035} - 300 \qquad \text{Eq. 3.}$$

Similarly using the same AMT calibration data (N=61), a fourth algorithm was derived from the power law between measured *in vitro* O_2 NCP and ^{14}C POC & SST, as follows:

$$NCP_D = a * \int \quad {}^{14}C\ POC^{(b*SST-d)} - 300 \qquad \text{Eq. 4.}$$

where a = 179.86, b = -0.0036 and d = -0.2487 and POC is in mg C m^{-2} d^{-1} and SST in °C. The relationship between NCP and SST is given in Fig. 2B.

The performance of the four NCP algorithms ($NCP_{A,B,C,D}$) was assessed in four ways: firstly using 84 measurements of *in vitro* ^{14}C POC and SST from AMT 12, 13, 14, 15, 16, 18, 21 to model NCP (hereafter validation data Table 1), which were compared with *in vitro* NCP (Fig. 3, Table 2); secondly using satellite POC production generated from SeaWiFS OC4v6 Chla and AVHRR SST to calculate satellite NCP, which were compared with *in vitro* NCP (Fig. 4, Table 2) using the validation data listed in Table 1 (N = 234); thirdly using POC production generated from MODIS-Aqua OC3M and AVHRR SST to calculate satellite NCP which was then compared with *in vitro* NCP (Fig. 4, Table 2); and fourthly using mean monthly SeaWiFS data to derive NCP_C and NCP_D which were compared with mean monthly measured *in vitro* NCP using the validation data given in Table 1 (Fig. 5, 6, 7).

2.3.2. Satellite maps of Net Community Production.

Mean monthly satellite maps of NCP for the most accurate algorithm(s) were generated using NASA 9 km SeaWiFS OC4v6 Chla R2010 from 1998 to 2010. NCP was calculated from monthly satellite fields of POC production using the wavelength resolving model (WRM) of Morel (1991) implemented following Smyth et al. (2005) with SeaWiFS OC4v6 Chla and AVHRR SST data as follows:

$$\sum POC\,producion = 12\, a^{*}_{\max}\ \phi_m \int_0^D \int_0^{z_{eu}} \int_{400}^{700} Chla(z)\, PUR(z,t,\lambda)\ f\left(x(z,t)\right) d\lambda\ dz\ dt \quad \text{Eq 5.}$$

where a^*_{max} is the absorption cross section per unit of Chla, ϕ_m is the net growth rate in mol C (mol quanta)$^{-1}$ and PUR is the phytoplankton useable radiance. The WRM was calibrated using depth profiles such that surface values are a proxy for depth resolution to 1% of surface irradiance. The results from the WRM of Morel (1991) are equivalent to ^{14}C POC (Tilstone et al. 2009). Further details of how this WRM was run are given in Smyth et al. (2005). NCP was then calculated using the WRM POC production with SeaWiFS or MODIS-Aqua data using equation 3, and additionally with AVHRR or MODIS-Aqua SST data using equation 4.

2.4. Climate Indices.

Climatic indices are indicative of large-scale variability in physical parameters in the ocean. Trends in satellite estimates of NCP were compared with trends in the following climate indices: North Atlantic Oscillation (NAO) monthly indices were taken from www.cgd.ucar.edu/cas/; the multivariate ENSO index (MEI), which is representative of ENSO phases (Wolter and Timlin 2011), was downloaded from NOAA at www.esrl.noaa.gov/psd/enso/mei/; Northern Hemisphere Temperature (NHT), the weighted average of all grid-box measurements to derive SST and atmospheric anomalies (Jones et al. 2012), were obtained from the Climatic Research Unit, University of East Anglia and the Met Office Hadley Centre**.**

2.5. Statistical analyses.

Measured *in vitro* NCP within ± 3 hours of satellite overpass were used as the mean of a 1 km 3 x 3 pixel array around the sampling station following the procedures outlined in Bailey and Werdell (2006). Measured *in vitro* and satellite NCP were compared using model II linear regression analysis and the slope, intercept and percentage variability explained (r^2). The following statistics were used to evaluate model performance: the mean (M) and standard deviation (S) of the $\log_{10}$-difference error between measured *in vitro* and satellite or *in vitro* estimated NCP at each station and the $\log_{10}$ root-mean square ($\log_{10}$-RMS). We also used the inverse $\log_{10}$ transformed difference between satellite and measured values of M (F_{med}), M-S (F_{min}) and M+S (F_{max}) following (Campbell et al. 2002). To be able to $\log_{10}$ transform negative NCP values, which indicate net heterotrophy, the lowest NCP value (-215 mmol O_2 m^{-2} d^{-1}) was added to the entire data set. The F_{med}, F_{min} and F_{max} values therefore indicate relative rather than absolute differences. The unbiased (UPD) and absolute (APD) percentage difference were calculated to illustrate the uncertainty between measured *in vitro* and satellite NCP. The distribution of NCP was transformed until no significant difference was found between the expected and the observed distributions using the Kolmogrov - Smirnov with Lilliefors test to ensure homoscedasticity (Sokal and Rolf 1997). One way analysis of variance (ANOVA) was used to test whether there were significant differences between measured *in vitro* and satellite NCP. The ANOVA results are given as $F_{1,df} = x$, $p = y$ where F is the mean square to mean square error ratio, the sub-script numbers denote the degrees of freedom and p is the ANOVA critical significance value.

Mean monthly satellite NCP were extracted from 9 km maps in the following provinces, corresponding to the main regions from which the *in vitro* data were collected: North Atlantic Drift Province (NADR), North Atlantic Tropical Gyre (NATL), Canary Current Coastal upwelling (CNRY), Western Tropical Atlantic (WTRA), Eastern Tropical Atlantic (ETRA), South Atlantic Subtropical Gyre (SATL), Benguela Current Coastal (BENG) and South Subtropical Convergence (SSTC). The relationships between satellite NCP and climate indices were evaluated in three ways: 1.) Pearson correlation coefficients between mean monthly anomalies, 2.) Pearson correlation coefficients between mean annual values, and 3.) analysis of trends in cumulative sums of the monthly anomalies. For the first and latter analyses, mean monthly NCP anomalies were calculated by subtracting from each monthly value, the corresponding monthly average for the time series from 1998 to 2010. The correlations were run on anomalies so that temporal autocorrelation was reduced, since autocorrelation in the dataset may complicate statistical interpretation. For the correlation analyses, to further reduce any potential temporal autocorrelation between biological and physical data we also implemented the method of Pyper and Peterman (1998). This approach re-calculates the probability of significance of the correlation based on adjusted degrees of freedom to correct for temporal autocorrelation. This method was originally designed to account for temporal autocorrelation between fish and environmental data (Tzanatos et al. 2014), and is therefore ideal for analysing relationships between phytoplankton and climate variables.

The cumulative sums method was applied to the anomalies to further decompose the signal by reducing the high frequency variability to highlight major changes in monthly data values along the time-series (McQuatters-Gollop et al. 2008). Successive positive anomalies produce an increasing slope, whereas successive negative anomalies produce a decreasing slope. The area-averaged monthly cumulative sum of NCP was compared against the cumulative sum of each of the climate indices given in Section 2.4.

3. Results

3.1. Distribution of in vitro measurements of NCP.

The NCP measurements indicated predominantly positive NCP (i.e. GPP>R) in the NADR (N=79) and CNRY (N=6) during both boreal spring and autumn, though there were few measurements available in the CNRY (Fig. 1). Considering the high standard deviation in measured NCP, the NATL (N=99) tended to be in net balance in both boreal spring (mean NCP 17 ± 85 mmol O_2 m^{-2} d^{-1}) and autumn (mean NCP -29 ± 92 mmol O_2 m^{-2} d^{-1}). The standard deviation was high because the area of the NATL is large (290789 km^2), and different locations at different times of each year were sampled. During boreal autumn in the WTRA, some data indicated that GPP>R whilst others indicated R>GPP (Fig. 1C), and the mean NCP was -24 ± 106 mmol O_2 m^{-2} d^{-1} (N=29), similarly suggesting net balance. The SATL (N=48) also exhibited net balance in both austral autumn (mean NCP -32 ± 73 mmol O_2 m^{-2} d^{-1}) and winter (mean NCP 0 ± 65 mmol O_2 m^{-2} d^{-1}), considering the magnitude of the standard deviation. NCP data were only available in austral spring in the SSTC (N=11) and the mean was 79 ± 62 mmol O_2 m^{-2} d^{-1}, which is indicative of net autotrophy. There were too few measurements for a comprehensive evaluation of the metabolic status of this province. There were no measurements to evaluate the metabolic status of the ETRA and BENG. The other *in vitro* NCP data were from the North Atlantic (N=3), Antarctic (N=4), the Greenland (N=8) and Mediterranean (N=8) Seas (Table 1), but of these, there were also too few to assess the metabolic status of these regions.

3.2. Validation of satellite algorithms of NCP in the Atlantic Ocean.

NCP_D had the lowest *M*, *S*, RMS-E and $\log_{10}$-RMS, the highest r^2 (except using MODIS-Aqua) and F_{med} closest to 1 using both the measured and satellite POC production and SST data (Fig. 3D, 4D, Table 2). There was no significant difference between measured and modelled NCP_D estimated from measurements of ^{14}C POC and SST ($F_{1,167}$=1.34, p=0.249; Fig. 3D) and satellite POC production for both SeaWiFS ($F_{1,25}$=0.38, P=0.544) and MODIS-Aqua ($F_{1,35}$=0.01, P=0.905; Fig. 4D). The UPD and APD for NCP_D against *in vitro* measurements, using both measured ^{14}C POC and SST or satellite data, yielded the lowest difference of all of the algorithms tested, though APD of NCP_C for SeaWiFS was similar. NCP_C exhibited a similar accuracy, with low *M*, *S*, RMS-E, $\log_{10}$-RMS, UPD, APD and intercept, and F_{med} close to 1 using both measured and satellite data (Fig. 3C, 4C, Table 2). For NCP_C there was similarly no significant difference between NCP_C estimated from measurements of ^{14}C POC production and SST ($F_{1,167}$=0.34, P=0.559) and satellite derived POC production for both SeaWiFS ($F_{1,25}$=0.08, P=0.785) and MODIS-Aqua ($F_{1,35}$=0.51, p=0.478). For the mean monthly time series (Fig. 5), NCP_D was closer than NCP_C to the mean monthly measured NCP (Fig. 6, 7). In the NATL, the absolute percentage difference between measured *in vitro* values and NCP_C was 45 %, whereas for NCP_D it was 29 %. In the WTRA, the difference was 62 % for NCP_C and 27 % for NCP_D, and in the SATL it was 20 % for NCP_C and 17 % for NCP_D. NCP estimates using NCP_D were significantly higher in the NADR, CNRY, BENG and SSTC (P<0.0001); NCP_C were significantly higher in the NATL, ETRA, WTRA and SATL (P<0.0001; Fig. 5).

NCP_A generally had the highest *M*, *S*, RMS-E, $\log_{10}$-RMS and intercept, indicating a significant bias with a tendency to under-estimate NCP, as illustrated by the high F_{med} and F_{max} values. Using the independent dataset of ^{14}C POC measurements to validate the algorithm, there was a tendency for NCP_A to under-estimate NCP across the entire range of values, though the slope was parallel to the 1:1 (Fig. 3A). Using SeaWiFS and MODIS-Aqua data, the slope was between 1.5 and 2.0, and the UPD and APD were between 6 and 15% of measured values (Fig. 4A). There was a significant difference between measured *in vitro* NCP and NCP_A run using both measured ^{14}C POC and SST ($F_{1,167}=61.40$, $P<0.0001$) and satellite data from SeaWiFS ($F_{1,25}=11.18$, $P=0.003$) and MODIS-Aqua ($F_{1,35}=12.68$, $P=0.001$; Table 2). NCP_B generally improved the accuracy using both measured and satellite ^{14}C POC and SST (Fig. 3B, 4B, Table 2), though there were still significant differences between estimates derived from measured ($F_{1,167}=16.56$, $P<0.0001$) and MODIS-Aqua ($F_{1,35}=16.17$, $P<0.0001$). For SeaWiFS there was no significant difference between measured *in vitro* and satellite derived NCP_B ($F_{1,25}=3.85$, $P=0.061$; Fig. 4B), though this was just above the 5 % level of significance.

4. Discussion

4.1. Validation of satellite algorithms of net community production.

Remote sensing observations offer an attractive means of providing NCP data at a higher temporal and spatial resolution that can be achieved by *in vitro* and *in situ* observations, as long as accurate algorithms can be developed. The premise for using remote sensing data is that no area of the ocean is likely to be permanently autotrophic or heterotrophic, so it is necessary to have data at a high resolution to be able to adequately assess instances of net autotrophy or heterotrophy to accurately budget the metabolic state of specific provinces or regions. To this end, Westberry et al. (2012) converted satellite-derived NPP to O_2 equivalents using a photosynthetic quotient (PQ) of 1.4 or 1.1, depending on the primary nitrogen source for a given phytoplankton community following (Laws 1991). They applied empirical Photosynthesis-Respiration relationships to depth-resolved output from the Carbon based Production Model (CbPM) and then vertically integrated over the water column to yield euphotic-zone areal rates of GPP, R and NCP. For the Bermuda Atlantic Time Series site (BATS), Westberry et al. (2014) reported NCP of between 24 and 26 mmol O_2 m^{-2} d^{-1} for May, July, September and October. Similarly, our NCP_C algorithm yielded estimates of 23 mmol O_2 m^{-2} d^{-1} over the SeaWiFS time series for these months, though values from NCP_D were lower (11 mmol O_2 m^{-2} d^{-1}). Chang et al. (2014), using a neural network approach, reported mean area-integrated NCP south of 50 ºS in the Southern Ocean of 18 mmol C m^{-2} d^{-1}. For the SSTC region, they reported >30 mmol C m^{-2} d^{-1}, which is similar to our estimate of 33 mmol O_2 m^{-2} d^{-1} using NCP_C (assuming PQ=1.1), though this was double using NCP_D (which may account for higher PQ values).

We also compared the empirical solutions of NCP proposed by Serret et al. (2009) with these new algorithms (NCP_C and NCP_D) derived from a database comprised of *in vitro* O_2 NCP measurements in the Atlantic Ocean, Greenland and Mediterranean Seas. The rationale for using a power law is that at negative *in vitro* NCP values, a small increment in ^{14}C POC correlates with a large linear rise in NCP (Fig. 2A), which is controlled by both nutrient limitation, bacterial production and grazing. Beyond zero NCP, large increments in ^{14}C POC correlate with smaller increments in NCP (Fig. 2A) as the fixation of CO_2 reaches capacity under replete, nutrient conditions and high phytoplankton growth. The power law for the AMT6 model given in Serret et al. (2009) is constrained to the lower end of the range shown in Fig. 2A and the AMT11 model, to the upper end of the range. The slope of the AMT6 model (0.48), was higher than that of the AMT11 model (0.15) (Serret et al. 2009). The lower slope in the AMT11 model indicates that even though ^{14}C POC increases, there is no parallel increase in NCP, which suggests that R increases more than GPP in the AMT6 model. In the AM6 model ^{14}C POC and R are more tightly coupled. In both models, at negative NCP there is less coupling between ^{14}C POC and R, which implies that allochthonous organic matter subsidies are necessary at low ^{14}C POC. These subsidies are of minor importance at high ^{14}C POC.

We tested each of these relationships separately using an independent dataset to assess which of the algorithms best describes the spatial and temporal variability in NCP in the Atlantic Ocean. Though contrasting provinces may have different relationships between ^{14}C POC and NCP, the premise for this is that the relationship that best fits the *in vitro* measurements has the capacity to capture salient trends in metabolic state in the Atlantic Ocean. Of the *in vitro* measurements used for validation (N=234), ~54 % were collected from the oligotrophic gyres and ~80 % were collected during boreal autumn-winter. Due to the distribution of the data, theoretically, the relationship derived for the AMT6 model should be more accurate. The results of the algorithm validation however, indicated that the relationship derived for the AMT11 model consistently had a smaller bias and random error, a lower intercept RMS-E and $\log_{10}$-RMS and based on F_{med} (and F_{max}) was closer to 1, indicating more accurate estimates of NCP at median values where the majority of the data fell (Fig. 3). Using data from individual cruises to calibrate empirical algorithms can result in a strong bias, which limits their applicability in space and time, which proved to be the case for the AMT6 and 11 models. We therefore used a more comprehensive data set from the Atlantic Ocean to calibrate a further empirical algorithm for the basin (NCP_C; eq. 3). This was based on the same power law between ^{14}C POC and NCP (Fig. 2) as in Serret et al. (2009), but using different data and without differentiating between trophic or geographic regions. This improved the bias at the minimum and maximum range of the *in vitro* NCP measurements, but there was still an offset (Fig. 3C). We were able to reduce this offset further by introducing SST in the power law between ^{14}C POC and NCP (NCP_D; eq. 4) which in turn, improved each validation statistic metric (Fig. 3D, Table 2). The accuracy of the algorithms compared with the *in vitro* measurements was $NCP_D > NCP_C > NCP_A > NCP_B$. NCP_D was consistently more accurate than the other algorithms at low (negative NCP), high (positive NCP) and median (net balance) values (Fig. 3D, 4D, Table 2).

The temperature-size rule predicts that phytoplankton become smaller in a warmer, ocean (Finkel et al. 2010; Morán et al. 2010), at a rate of 2.5% decrease in cell volume per 1 °C (Atkinson et al. 2003). Seawater temperature is a driver of plankton community metabolism (Regaudie-de-Gioux and Duarte 2012). Lopez-Urrutia et al. (2006) showed that the balance between plankton production and respiration is affected by environmental temperature and that a differential response to temperature at the organism level determines the metabolic balance. In the sub-tropical North and South Atlantic, the activation energy that describes the temperature dependence of planktonic community metabolism is higher for R than for GPP (García-Corral et al. 2014). The real challenge in estimating NCP from satellite is to derive a robust proxy for R, which also exhibits an exponential temperature dependence at both subcellular and individual species levels (Gillooly et al. 2001). This suggests that the accuracy of NCP_D over the other algorithms is due to the fact that it captures more of the temperature dependency of GPP and R. Variability in the temperature dependence of R can be driven by a range of mechanisms that are contingent on temporal and spatial scales (Perkins et al. 2012). As long as sufficient data are used to capture these spatial and temporal changes, robust relationships between GPP and SST can be used to characterise the variation in GPP, R and thus NCP as we have shown here (Figs. 3, 4, Table 2). Since some of the data used were from the Antarctic, Greenland and Mediterranean Seas, these relationships may also be applicable to these regions and further validation data is needed to assess their applicability in these regions.

When the algorithms were applied to satellite POC production using the WRM, there was a consistent improvement in NCP_C with SeaWiFS data, such that the slope F_{med}, F_{min} and F_{max} were near to 1, the APD was high and the intercept small (Table 2, Fig. 4C). By comparison, NCP_D was more accurate with MODIS-Aqua than with SeaWiFS (Table 2, Fig. 4D). This bias between ocean colour sensors is not likely to be due to differences in sensor characteristics. There is good agreement between normalised water leaving radiance, the primary input to derive Chla, from both SeaWiFS and MODIS-Aqua which were within 0 to -2 and 1 to 7 % relative percentage difference from *in situ* values both at open ocean (Zibordi et al. 2006) and coastal sites (Melin et al. 2007). The number of match-ups for SeaWiFS and MODIS-Aqua were similar in the NATL, SATL and WTRA. The differences between algorithms applied to both SeaWiFS and MODIS-Aqua was probably because the match-ups with MODIS-Aqua covered a greater range of NCP than with SeaWiFS (Fig. 4), and over this range, NCP_D is potentially more accurate (Fig. 3). In addition, for MODIS-Aqua there were more match-up data from autumn in the NADR and NATL than for SeaWiFS. At these times of the year, in these provinces, and based on Fig. 4, we would expect NCP_D to perform better than NCP_C. For SeaWiFS, there were also more match-ups in the upwelling and eutrophic regions of the CNRY and NADR. Similarly, there were more SeaWiFS match-ups in spring in the NADR and NATL, when these provinces are net autotrophic. Since NCP_C was derived from the power law between ^{14}C POC alone and for the SeaWiFS match-ups predominantly GPP>R, which accounts for an improvement in the accuracy NCP_C with SeaWiFS data. By comparison, NCP_D reduced the scatter from *in vitro* measurements in the WTRA that the approach of Westberry et al. (2012) found challenging. We had no match-up data for the BENG, ETRA and SSTC, so we were not able to evaluate the performance of these algorithms in these provinces. Regional algorithms for the Atlantic Ocean may be more accurate than basin or global scale approaches (Serret et al. 2009). Though we collated a comprehensive data set of *in vitro* measurements for the Atlantic Ocean, 36 % of the data were from the NATL and 29 % from the NADR, in autumn (Fig. 1). Any regional differences in the relationships between GPP and R and NCP and ^{14}C POC are therefore likely to arise from differences in sampling times in the North and South Atlantic rather than differences between provinces per se. Future campaigns should aim to collect further data for satellite model validation in boreal spring-summer and austral autumn-winter, especially in South Atlantic provinces.

4.2. Metabolic state of the Atlantic Ocean.

Controversy still exists over whether the oligotrophic gyres in the global oceans are net autotrophic or heterotrophic. On the one hand, *in vitro* measurements of NCP overwhelmingly imply that the oligotrophic subtropical gyres of the open ocean are net heterotrophic or in net balance (Duarte et al. 1998; Duarte et al. 2001). Williams et al. (2013) looked at the possible sources of organic carbon and calculated that none of them were high enough to support net heterotrophy. From trends in *in situ* geochemical methods, Williams et al. (2013) deduced that the oligotrophic gyres are net autotrophic. Westberry et al. (2012) used satellite ocean colour estimates of NCP, reported a range from 630 to 2,800 Tmol C a^{-1} and from these observations, they estimated that 57 % of the global ocean surface area was net heterotrophic.

By way of comparison to these studies, we generated mean annual NCP images from the two most accurate algorithms (NCP_D and NCP_C) for the Atlantic Ocean using SeaWiFS data from 1998 to 2010 (Fig. 5) and the corresponding mean monthly time series data for eight Atlantic Provinces (Fig. 6, 7). NCP_C indicated that annually, GPP>R in all provinces, but that in NADR, NATL, SATL and SSTC there were periods when R>GPP. For NCP_C, the CNRY had the highest (mean ~121 ± 18 mmol O_2 m^{-2} d^{-1}) and the SATL had the lowest values (10 ± 6 mmol O_2 m^{-2} d^{-1}; Table 3). By comparison, for NCP_D, GPP>R in all provinces and there were periods in the NATL, SATL and WTRA when mean monthly values were just below 0 mmol O_2 m^{-2} d^{-1}, indicating net heterotrophy (Fig. 7). In the NATL during boreal autumn and in the SATL during austral autumn and winter, mean values were negative, but the standard deviation was greater than the negative NCP during austral and boreal autumn indicating net balance during these seasons (Table 3). Mean NCP_D for boreal spring, summer, autumn and winter from 1998 to 2010 in the Atlantic Ocean are given in Fig. 8 and indicate the seasonal extent of net autotrophy and net heterotrophy in the Atlantic Ocean. During boreal spring and summer the extent of negative NCP values in the NATL was low (Fig. 8). This increased to ~60 % by boreal autumn and winter (Fig. 9). Similarly during austral autumn and winter in the SATL, the spatial extent of negative NCP was larger (up to 70 % of pixels) than during austral spring and summer. In the WTRA during winter, there were 20 % negative NCP in boreal spring and winter, which extended towards the African coast, whereas during spring, summer and autumn this region was clearly net autotrophic (Fig. 8). Over the entire Atlantic Ocean basin from NADR to SSTC, 27 % of pixels had negative NCP (Fig. 9). For the Atlantic basin therefore, the contribution to net heterotrophy was principally due to the seasonal oscillation between the NATL in boreal autumn-winter as previously observed by Gist et al. (2009), and the SATL in austral autumn-winter (Fig. 9) also observed by González et al. (2002). When mean monthly values of NCP were used to derive seasonal estimates of NCP for individual provinces, net heterotrophy was only evident during boreal autumn-winter in the NATL and during austral autumn-winter in the SATL (Table 3). There was however considerable intra-regional variation as illustrated by the minimum and maximum range in Fig. 5 & 6. This variation illustrates that there are areas of the NATL and SATL that remain net heterotrophic for longer periods.

One of the key issues surrounding the existence and prevalence of net heterotrophy is whether there is any error or bias in *in vitro* bottle incubations over the 24 h incubation period (Williams et al. 2013). It has been argued that respiration rates measured from *in vitro* ‘dark bottle’ incubations in the oligotrophic gyres are fuelled by production that occurred *in situ*, under natural conditions, which is representative of very recent past conditions in these tightly coupled ecosystems. In contrast, the photosynthetic rate derived from ‘light bottle’ incubations reflects production on the day of the incubation maintained in a static and confined (bottle) environment, which can be very different from ambient *in situ* rates (Westberry et al. 2012). In addition, there may be a bias in these measurements since borosilicate bottles are opaque to UV radiation which can reduce NCP by 45 % (Agustí et al. 2014; Regaudie-de-Gioux et al. 2014).

To resolve this issue, Westberry et al. (2012) assumed that *in vitro* measurements between 10 to 40º N and -10 to -40º S were erroneous as they arise from bottle artefacts and therefore eliminated them from deriving any subsequent relationships for application to satellite data. They then inferred that the resulting relationships are in agreement with geochemical methods, which indicate net autotrophy globally. This is not surprising, because if it is assumed that all *in vitro* measurements from the oligotrophic gyres (that exhibit net heterotrophy) are erroneous, it is logical that the resulting GPP : R relationships will indicate net autotrophy in the global ocean. We chose not to make any assumptions on the debate between net autotrophy or heterotrophy in the oligotrophic gyres or pre-select the data used to constrain the relationships between ^{14}C POC and NCP (Fig. 1). The *in vitro* data from the NATL (between 10-40ºN) represented 36 % of the database and negative *in vitro* values, only recorded during boreal autumn (Fig. 1C), were 5 % of the total database. Some areas of the NATL are not strictly oligotrophic, however. Using data from AMT12-AMT21, when the DCM and thermocline were >100 m, 83 % of data in the NATL were negative (mean NCP -12.40 ± 2.95 mmolO_2 m^{-2}d^{-1}; Fig. 1).

The dilemma of whether to include these data or not is illustrated by the choice of selecting either algorithm NCP_A or NCP_B. When NCP_A is used (representative of net heterotrophy), it tends to under-estimate NCP (Fig. 4, 5). This resulted in 90 % of the resulting NCP satellite estimates using MODIS-Aqua to be net heterotrophic and 65 % using SeaWiFS. When NCP_B is used (representative of net autotrophy), only 3 and 6 % of MODIS-Aqua and SeaWiFS match-ups were net heterotrophic since this algorithm tends to slightly over-estimate NCP. Both NCP_C and NCP_D constrain the NCP estimates closer to the 1:1 and the net result is that 55 and 35 % of the predicted values are net heterotrophic, using MODIS-Aqua and SeaWiFS respectively.

4.3. Variation in NCP in the Atlantic Ocean in relation to climate indices.

Our objective was also to assess whether climate indices are correlated with phases of net autotrophy and heterotrophy. Satellite estimates of NPP have already been used to detect climate-induced responses in the marine biological carbon pump (Behrenfeld et al. 2006). A decrease in global NPP from 1998 to 2006 was coupled with an increase in global SST as a result of consecutive positive ENSO phases. These positive phases are associated with warmer SST, increased stratification, and a deeper nutricline (Martinez et al. 2009). During successive *El Niño* years (strong positive MEI), a deeper pycnocline in the eastern equatorial Pacific results in a diminished supply of nutrients to surface waters and a paralleled decrease in phytoplankton biomass (Pennington et al. 2006). For *La Niña* years (persistent negative MEI), phytoplankton biomass increases across the whole equatorial Pacific, due to a shoaling of the nutricline closer to the euphotic zone (Behrenfeld et al. 2006).

In our data, the trend in cumulative sums in NCP_D in the NADR was a net increase from 1998 to 2005, followed by a decrease from 2005 to 2008, then an increase again from 2008 to 2010 (Fig. 10A). In the NATL there was a net increase in the cumulative sums of NCP_D from 1998 to 2002, after which there was no change until 2006, when there was a decrease until 2010 (Fig. 10B). In the CNRY, there was a sharp rise in the cumulative sums of NCP from 1998 to 1999, which was followed by a gradual decrease until 2006, and an increase from

2006 to 2009 (Fig. 10C). The ETRA and WTRA exhibited a similar pattern from 1999 to 2010, with an increase in the cumulative sums of NCP$_D$ from 1999 to 2005, followed by a decrease from 2005 to 2010 (Fig. 10D, E). In the SATL, BENG and SSTC, there was a gradual decrease in NCP$_D$ from 1998 to 2009, followed by a sharp increase to 2010 (Fig. 10 F, G, H). These trends were largely reflected in the mean annual values (Fig. 10 I-P). Analysing both mean monthly anomalies and mean annual values of NCP$_D$ against a range of climate indices, the most significant and consistent relationships were negative correlations with MEI in the SATL and NAO in the SSTC, which explained 60 and 91 % of the annual variability in NCP$_D$ (Table 4; Fig. 10G, H). The cumulative sums of mean monthly anomalies further emphasise these trends; positive MEI coincided with decreasing cumulative sums in NCP$_D$ and negative MEI coincided with an increase in NCP$_D$ in the SATL (Fig. 10F, N). This implies that the magnitude of net heterotrophy during austral autumn and winter in this region could increase during successive positive MEI years. Statistical significance does not necessarily mean causality and therefore we do not demonstrate the mechanism behind these relationships. The scope of this analysis is not to provide a mechanistic link behind these relationships, but to gain further confidence that our modelled NCP$_D$ product is related to the broader climate variability.

For MEI during *El Niño* conditions for example, a warming in the mid- and east-Pacific causes convection to shift eastwards which weakens the convective circulation and reduces upwelling in the Eastern Pacific Ocean through a relaxation of the thermocline and warming of surface waters (Boyce et al. 2010). In the South Atlantic, this phenomenon has been linked to warmer temperatures (Ineson and Scaife 2009), which could enhance stratification and thus decrease NCP, which may explain the significant negative relationship we observed between NCP and MEI in the SATL. Using empirical orthogonal function analysis and k-means classification, Park et al. (2010) found that the periodicity in surface Chla was related to *El Niño* events. The ENSO phenomenon is also known to cause climate variability on inter-annual and decadal time-scales in the North Atlantic Ocean (Lau and Nath 2001). ENSO is usually correlated with variability in SST and salinity or water column stratification in the North Atlantic through changes in the wind-forcing (westerly and trade wind variability), as well as in oceanic circulation patterns (e.g., latitudinal or longitudinal displacements of Gulf, Azores or Canary Currents) (Curry and McCartney 2001). These processes can in turn cause anomalies in the temperature and salinity fields (Cianca et al. 2012). Recently it has been shown that MEI is significantly and positively correlated with Coccolithophore blooms in the North Atlantic (Shutler et al. 2012). During one of the strongest positive MEI (*El Niño*) events in 1998, the subarctic North Atlantic experienced unprecedentedly high sea-surface temperatures coinciding with the largest Coccolithophore bloom observed during the satellite era (Raitsos et al. 2006). ENSO has the potential to reduce the North Atlantic net sink of CO_2 by between 3–28 % by affecting the coverage of *E. huxleyi* (Shutler et al. 2012). By contrast to these studies, we did not find a significant correlation between NCP_D and MEI in North Atlantic Provinces. Although the values given in Table 4 are statistically significant ($p<0.05$), NCP_D and NAO in the WTRA and NHT in the SSTC are at the limit of significance. These relationships should therefore be treated with caution. The significant negative correlation that we observed between the MEI and NCP_D in the SATL suggests that in this region, persistent positive MEI may lead to enhanced stratification, lower nutrient availability and a reduction in NCP.

Over the past 30 years, there have been major fluctuations in atmospheric forcing in the North Atlantic which is reflected in the NAO (Hakkinen and Rhines 2004). A large positive NAO index is usually associated with strong westerly winds and low pressure around Iceland (Hurrell and Deser 2009). Bentsen et al. (2004) observed that convective mixing in the North Atlantic is linked to the NAO such that negative NAO leads to deeper vertical mixing in this region. The traditional view is that this will enhance the supply of nutrients to the photic zone for the onset of the spring bloom, which in turn affects the magnitude of GPP and possibly also NCP. Significant changes in the North East Atlantic have been documented across various trophic levels (Beaugrand et al. 2008; Edwards and Richardson 2004), which are strongly associated with different phases of the NAO index (Henson et al. 2009; Henson et al. 2012). During positive NAO years in the central North Atlantic, vertical mixing induced by strong westerly winds deepens the mixed layer. In the sub-Arctic and northern North Atlantic positive NAO years enhances the southerly transport of cold and fresh Arctic water which promotes strong stratification and a shoaling of the mixed layer (Zhai et al. 2012). Martinez et al. (2009) reported that although regions that have opposite patterns in Chla and SST account for 60 % of the global ocean, the North East Atlantic Ocean is characterized as an area of increasing SST and high phytoplankton abundance. This is because oceanic warming at higher North Atlantic temperate and Polar Regions contribute to reduce mixing, which may lead to increased phytoplankton growth due to accumulation of phytoplankton in the higher light environment of the surface ocean (Doney 2010; Richardson and Schoeman 2004). From the mean monthly anomalies in NCP_D and NAO we did not observe significant correlations in the NADR and NATL, though there was a strong positive correlations between mean annual NCP_D and NAO further south in the CNRY and WTRA. There were also significant, but negative correlations with NAO in the SSTC (Table 4B). The effect of the NAO on NCP in the South Atlantic, to our knowledge, has not previously been documented thus the mechanism for this is not understood.

In addition, we found significant negative correlations with NCP_D and NHT in the ETRA and a positive correlation in the SSTC. Li et al. (2012) showed that the NAO is a good predictor of NHT and that NAO precedes multi-decadal variability in NHT due to the thermal inertia associated with the relatively slow oceanic processes of the North Atlantic. Ocean colour anomalies of the NE Atlantic significantly parallel the NHT oscillation (Raitsos et al. 2014). The trend was reversed in the tropical Atlantic, because rising NHT causes thermal stratification to increase, which reduces vertical mixing and thus nutrient availability in the tropics (Doney 2006).

Conclusions

In this paper we compare a number of empirical approaches to estimating NCP from satellite data in the Atlantic Ocean. NCP was determined using *in vitro* measurements of changes in dissolved O_2 concentration at 295 stations from 26 cruises in the Atlantic Ocean, Greenland and Mediterranean Seas. Published algorithms based on power laws between NCP and ^{14}C POC tended to over-estimate NCP at negative values and under-estimate at positive values. By developing a relationship between remotely sensed POC production, SST and NCP, we were able to define a power law which explained >60 % of the variance in *in vitro* measurements of NCP, had the lowest bias and root-mean square error and was within 4 % of the *in vitro* measured values. Using this algorithm with SeaWiFS data, a 13 year time series of NCP was generated to assess spatial and temporal trends over the Atlantic Ocean. The North Atlantic sub-tropical and tropical Gyres remained predominantly net autotrophic from 1998 to 2010, suggesting that despite recent warming in the northern hemisphere, this region remains a net sink for CO_2. The South Atlantic sub-tropical Gyre and subtropical convergence zone fluctuated from net autotrophic in austral spring-summer to net heterotrophic in austral autumn-winter, suggesting that over the past decade these provinces are increasingly altering towards a CO_2 source in austral autumn-winter. Over the Atlantic basin from the NADR to SSTC, only ~27 % of the satellite pixels exhibited negative NCP which were mostly from the NATL in temperate autumn-winter and the SATL in austral autumn-winter. Variations in NCP in the northern and southern hemisphere were correlated with climate indices. There were consistent significant negative relationships between monthly and annual anomalies in NCP and MEI in the SATL and NAO in the SSTC. These relationships suggest that climate variability in the Pacific Ocean and North Atlantic may play a role in modifying phases of net autotrophy and heterotrophy in the South Atlantic.

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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 Feb 1994	Antarctic	4	(Aristegui et al. 1996)
CICYT AMB	*RV José Rioja*	01 March – 01 Sept 1994	NAST-E	14	(Serret et al. 1999)
CICYT AMB	*RV José Rioja*	01 Oct 1994 – 01 June 1995	NAST-E	21	(Serret et al. 1999)
AMT4	*RRS James Clark Ross*	01 April 1997	NADR – SATL	13	(Gonzalez et al. 2002)
AMT5	*RRS James Clark Ross*	01 Sept 1997	SATL - NADR	11	(Gonzalez et al. 2002)
Bay of Biscay	*RV José Rioja*	01 April – 03 Aug 1999	NADR	8	(Gonzalez et al. 2003)
POMME	*NO L'Atlante* *NO Thalassa*	28 Sept – 03 Oct 2000, 07 – 23 March 2001, 02 May 2001, 20 Sept – 03 Oct 2001.	NAST-E	23	(Maixandeau et al. 2005a; Maixandeau et al. 2005b)

AMT12	*RRS James Clark Ross*	23 May – 11 June 2003	SATL - NADR	C=7; V=12	(Gist et al. 2009)
AMT13	*RRS James Clark Ross*	18 Sept – 7 Oct 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 Sept – 24 Oct 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 Oct – 6 Nov 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 et al. 2009)
CARPOS	*RV BioHespérides*	14 Oct – 21 Nov 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 Sept – 21 Oct 2008	NADR - SATL	C=7; V=11	BODC
AMT21	*RRS Discovery*	02 Oct – 08 Nov 2011	NADR - SATL	C=15; V=16	BODC
TOTAL				**295 (C=61)**	

Table 2. Performance indices for relative errors in NCP algorithms using *in vitro*, MODIS and SeaWiFS data as input. Log-difference errors in measured and satellite estimates are given as Mean (*M*), Standard deviation (*S*), Root Mean Square Error (RMSE) and root-mean square (Log-RMS). The geometric mean and one-sigma range of the difference (F = Value_{meas} - Value_{alg}) are given by F_{med}, F_{min}, and F_{max}, respectively; values closer to 1 are more accurate. *N* is the number of data used. Percentage variability explained (r^2), slope and intercept are for log-log regression. The most accurate algorithm is highlighted in bold.

	Model	N	APD	UPD	Inter	Slope	R^2	M	S	RMSE	Log-RMS	F_{med}	F_{max}	F_{min}
In Situ data	NCP-A	84	3.4	-0.6	-89.81±5.78	**1.00**±0.10	0.53	0.29	0.29	103.43	0.41	1.96	3.81	**1.00**
	NCP-B	84	3.5	-1.2	29.80±2.83	0.43±0.05	0.46	-0.05	**0.08**	46.47	0.09	0.89	**1.06**	0.75
	NCP-C	84	**3.1**	1.0	**-1.00**±3.47	0.54±0.06	0.47	**0.01**	**0.08**	40.10	**0.08**	**1.02**	1.22	0.85
	NCP-D	84	3.1	**0.7**	-5.83±3.26	0.64±0.06	**0.58**	**0.02**	**0.07**	**35.60**	**0.07**	**1.04**	1.22	0.88
Sea WiFS (3 x 3 pixels)	NCP-A	13	10.9	5.8	-97.32±24.24	2.05±-0.65	0.48	0.47	0.46	103.63	0.70	2.93	8.37	**1.03**
	NCP-B	13	8.6	2.8	28.77±8.74	0.81±0.23	0.53	-0.06	**0.07**	34.48	0.10	0.86	**1.01**	0.74
	NCP-C	13	2.3	-1.2	**-2.78**±11.27	**1.03**±0.30	0.52	**0.01**	**0.02**	30.31	**0.08**	**1.03**	1.23	0.85
	NCP-D	13	**1.8**	**-0.9**	-4.89±9.67	**1.06**±0.26	**0.61**	**0.02**	**0.08**	**26.64**	**0.08**	**1.06**	1.26	0.89
MODIS-Aqua (3 x 3 pixels)	NCP-A	18	14.3	-13.6	-71.08±14.98	1.55±0.44	**0.25**	0.45	0.53	96.81	0.72	2.81	9.45	**0.83**
	NCP-B	18	5.3	2.6	38.10±6.09	0.61±0.18	0.21	-0.09	**0.08**	48.26	0.13	0.81	**0.97**	0.67
	NCP-C	18	3.8	-2.0	9.34±7.69	0.77±0.22	0.22	**-0.02**	**0.09**	34.04	**0.09**	**0.96**	1.17	0.78
	NCP-D	18	**3.7**	**0.9**	1.82±7.21	0.70±0.21	0.18	**0.00**	**0.09**	**29.70**	**0.09**	**0.99**	1.21	**0.82**

Table 3. Mean, standard deviation, minimum and maximum net community production from NCP_C and NCP_D for Atlantic Ocean provinces over all seasons (All) and boreal spring, summer, autumn and winter from 1998 to 2010.

NCP_C	**NADR**	**NATL**	**CNRY**	**ETRA**	**WTRA**	**BENG**	**SATL**	**SSTC**
All	42 ± 38 -22 - 107	23 ± 9 7 – 42	121 ± 18 87 – 167	75 ± 18 42 – 114	50 ± 9 28 – 76	80 ± 14 51 – 114	10 ± 6 0 – 38	33 ± 28 -10 – 89
Spring	64 ± 25 23 - 103	31 ± 4 27 – 42	142 ± 11 119 – 167	61 ± 9 42 – 79	44 ± 5 28 – 52	79 ± 10 62 - 99	4 ± 2 0 – 9	23 ± 17 1 – 68
Summer	80 ± 15 48 – 107	29 ± 4 20 – 40	122 ± 4 94 – 153	95 ± 12 73 – 114	60 ± 8 42 – 76	63 ± 6 51 – 82	10 ± 6 2 – 31	-1 ± 17 -10 – 37
Autumn	30 ± 18 2 – 62	15 ± 5 7 – 25	109 ± 12 89 – 155	80 ± 14 61 – 107	52 ± 7 37 – 66	88 ± 10 65 – 106	16 ± 6 8 – 38	44 ± 19 15 – 88
Winter	-8 ± 10 -22 – 12	17 ± 6 7 – 30	112 ± 13 87 – 142	63 ± 7 48 – 77	46 ± 6 33 – 59	91 ± 8 51 – 114	10 ± 3 3 – 14	65 ± 9 49 – 89
NCP_D								
All	64 ± 39 -2 -135	10 ± 12 -13 – 33	97 ± 26 48 – 150	39 ± 19 6 – 82	17 ± 8 -7 – 37	86 ± 13 62 – 116	4 ± 10 -12 – 34	68 ± 32 15 – 131
Spring	98 ± 25 56 – 135	25 ± 3 19 – 33	96 ± 19 55 – 124	20 ± 8 6 – 36	11 ± 5 -7 – 20	77 ± 7 63 – 96	-8 ± 2 -12 - -3	50 ± 16 26 – 88
Summer	93 ± 22 49 – 134	10 ± 6 0 – 23	96 ± 19 67 – 134	60 ± 15 21 – 82	24 ± 8 3 – 37	78 ± 8 62 – 98	8 ± 8 -6 – 26	31 ± 11 15 – 62
Autumn	43 ± 15 18 – 69	-4 ± 3 -13 - 0	70 ± 11 48 – 105	49 ± 14 30 – 76	18 ± 6 5 - 31	102 ± 7 86 - 116	16 ± 6 8 – 38	90 ± 21 59 – 131
Winter	17 ± 13 -2 – 42	7 ± 9 -11 - 24	96 ± 19 55 - 124	28 ± 8 14 – 46	14 ± 5 6 – 26	91 ± 8 74 - 114	-1 ± 5 -10 - 11	99 ± 33 75 – 131

Table 4. Significant pearson correlation coefficient between climate indices and mean monthly anomaly in satellite Net community Production (NCP_D) and mean annual NCP_D (N=12). North Atlantic Oscillation (NAO), multivariate ENSO index (MEI), and Northern Hemisphere Temperature (NHT), for different Atlantic provinces from 1998-2010. r is correlation coefficient and p is level of significance after correcting for temporal autocorrelation. * indicates significant correlation at the 5% level; ** is 0.5% level and *** is 0.05% level. For province descriptions see Fig. 1.

NCP_D	**Correlation coefficient**	**Monthly-NAO**	**Annual-NAO**	**Monthly-MEI**	**Annual-MEI**	**Monthly-NHT**	**Annual-NHT**
CNRY	r		0.802				
	P		0.001**				
ETRA	r						-0.676
	P						0.022*
WTRA	r		0.599				
	P		0.05*				
SATL	r			-0.385	-0.601		
	P			<0.0001***	0.039*		
SSTC	r	-0.180	-0.909			0.203	
	P	0.036*	<0.001***			0.06	

LEGENDS

Fig. 1. Sampling stations for *in vitro* measurements of net community production in the (a.) Atlantic Ocean, Antarctic, Mediterranean and Greenland Seas; (b.) *in vitro* measurements taken during April-May-June only and (c.) *in vitro* measurements taken during Sept-Oct-Nov. Bold open circles indicate stations with satellite match-ups from SeaWiFS; bold open squares indicate stations with satellite match-ups from MODIS-Aqua. NADR is North Atlantic Drift Province, NATL is North Atlantic Tropical Gyre, CNRY is Canary Current Coastal upwelling, WTRA is Western Tropical Atlantic, ETRA is Eastern Tropical Atlantic, SATL is South Atlantic Subtropical Gyre, BENG is Benguela Current Coastal, SSTC is South Subtropical Convergence.

Fig. 2. (a.) Power law between *in vitro* net community production (mmol O_2 m^{-2} d^{-1}) and ^{14}C POC (mmol C m^{-2} d^{-1}) used to parameterise NCP_C and (b.) additional relationship between *in vitro* net community production and sea surface temperature used to parameterise NCP_D.

Fig. 3. Comparison of *in vitro* measured and modelled (using measured ^{14}C POC and SST) net community production (mmol O_2 m^{-2} d^{-1}) for the Atlantic Ocean using half of the *in vitro* data shown in Fig. 1 to validate (a.) NCP_A (b.) NCP_B (c.) NCP_C (d.) NCP_D. For description of algorithms refer to Section 2. Solid line is the 1:1 line and dashed line is ordinary least squares regression. Open squares are data from AMT6, included for comparative purposes and were not used to calculate validation metrics given in Table 2.

Fig. 4. Comparison of *in vitro* measurements and satellite estimates of net community production for (a.) NCP_A (b.) NCP_B (c.) NCP_C (d.) NCP_D. Solid circles are SeaWiFS; open diamonds are MODIS-Aqua. Solid line is the 1:1 line, dashed line is the ordinary least squares regression for SeaWiFS and dotted line is the ordinary least squares regression for MODIS-Aqua.

Fig 5. Mean annual satellite maps of net community production (mmol O_2 m^{-2} d^{-1}) for the Atlantic Ocean from 1998 to 2010 using the NCP_C (left hand panel) and NCP_D (centre panel) with SeaWiFS data and difference between NCP_C-NCP_D (right hand panel). Bottom colour bar is NCP values for NCP_C and NCP_D. Top colour bar indicates extent of difference between NCP_C-NCP_D; positive values indicate NCP_C>NCP_D; negative values indicate NCP_D>NCP_C.

Fig. 6. Mean monthly variation in net community production (mmol O_2 m^{-2} d^{-1}) using NCP_C with SeaWiFS data from 1998 to 2010 in eight Provinces as described in Fig. 1. Dotted line represents metabolic net balance, grey shaded area represents maximum and minimum range; box whisker plots are mean, minimum and maximum range in mean monthly *in vitro* measurements of NCP.

Fig. 7. Mean monthly variation in net community production (mmol O_2 m^{-2} d^{-1}) using NCP_D with SeaWiFS data from 1998 to 2010 in eight Provinces as described in Fig. 1. Dotted line represents metabolic net balance, grey shaded area represents maximum and minimum range; box whisker plots are mean, minimum and maximum range in mean monthly *in vitro* measurements of NCP.

Fig. 8. Mean seasonal climatology in net community production (mmol O_2 m^{-2} d^{-1}) using NCP_D with SeaWiFS data from 1998-2010 for boreal (a.) Spring, (b.) Summer, (c.) Autumn and (d.) Winter. Pixels coloured dark blue indicate negative NCP (i.e. net heterotrophy).

Fig 9. Percentage of pixels with negative NCP from mean seasonal climatology given in Fig. 7 for Boreal Spring, Summer, Autumn and Winter in the NATL (a.), WTRA (b.), SATL (c.) and Atlantic Ocean from all provinces (d.). Bold symbols are mean values for SeaWiFS time series from 1998-2010; coloured lines and smaller symbols represent percentage values for individual years to indicate variation between years.

Fig. 10. Mean annual cumulative sums in the anomalies of net community production for NCP_D (open circles) and climate indices (crosses) in the (a.) NADR, (b.) NATL, (c.) CNRY, (d.) WTRA, (e.) ETRA, (f.) SATL, (g.) BENG and (h.) SSTC from 1998-2010. Mean annual NCP_D (solid circles) and climate mean annual indices (open squares) for the (i.) NADR, (j.) NATL, (k.) CNRY, (l.) WTRA, (m.) ETRA, (n.) SATL, (o.) BENG and (p.) SSTC. Significant correlations with climate indices are given after correction for temporal autocorrelation. The climate indices are; Multivariate ENSO Index (MEI), North Atlantic Oscillation Index (NAO) and Northern Hemisphere Temperature (NHT) . For definition of provinces refer to Fig. 1.