

1 **In-situ estimates of net primary production in the Western North Atlantic with Argo**
2 **profiling floats**

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20
21 **Key Points:**

- 22 • Net primary production derived from Argo-based bio-optical measurements was comparable
23 and complementary to ¹⁴C incubation and satellite estimates
- 24 • Both Carbon based Productivity Model and Photoacclimation Productivity Model have their
25 own advantages and limitations
- 26 • NPP profiles showed varying seasonal NPP distribution patterns along a North-South
27 transect in the Western North Atlantic Ocean
- 28

29 **Abstract**

30 The ^{14}C incubation method for Net Primary Production (NPP) has limited
31 spatial/temporal resolution, while satellite approaches cannot provide direct information at depth.
32 With chlorophyll-a and backscatter measurements from BGC-Argo floats, we quantified year-
33 round NPP in the western North Atlantic Ocean using both the Carbon-based Productivity Model
34 (CbPM) and Photoacclimation Productivity Model (PPM). Comparison with NPP profiles from
35 ^{14}C incubation measurements showed advantages and limitations of both models. CbPM
36 reproduced the magnitude of NPP in most cases. However, in the summer the CbPM-based NPP
37 had a large peak in the subsurface, which was an artifact from the subsurface chlorophyll
38 maximum caused by photoacclimation. PPM avoided the artifacts from photoacclimation, but the
39 magnitude of PPM-derived NPP was smaller than the ^{14}C result. Different NPP distribution
40 patterns along a North-South transect in the Western North Atlantic Ocean were observed,
41 including higher winter NPP/lower summer NPP in the south, timing differences in NPP
42 seasonal phenology, and different NPP depth distribution patterns in the summer months. Using
43 a 6-month record of concurrent oxygen and bio-optical measurements from two Argo floats, we
44 also demonstrated the ability of Argo floats to obtain estimates of the net community production
45 (NCP) to NPP ratio, ranging from 0.3 in July to -1.0 in December 2016. Our results highlight the
46 utility of float bio-optical profiles and indicate that environmental conditions (e.g. light
47 availability, nutrient supply) are major factors controlling the seasonality and spatial (horizontal
48 and vertical) distributions of NPP in the western North Atlantic Ocean.

49 **1 Introduction**

50 Biological productivity by upper-ocean phytoplankton communities is central to marine
51 biogeochemistry, carbon cycling, and ecosystem health. Phytoplankton net primary production
52 (NPP), defined as gross photosynthetic carbon fixation minus the carbon respired by
53 phytoplankton themselves, is a key metric of biological productivity. Traditional methods for
54 NPP measurements rely on ship-based discrete sampling and bottle incubations (e.g., ^{14}C
55 incubation), which introduce potential artifacts and limit the spatial and temporal coverage of the
56 global ocean. Over the past several decades, the establishment of operational ocean-observing
57 satellite networks made it possible to make reasonable estimates of large-scale ocean NPP
58 patterns. The global distribution of NPP has been estimated using satellite observations with the
59 Vertically Generalized Production Model (VGPM, *Behrenfeld and Falkowski, 1997*) and
60 Carbon-based Productivity Model (CbPM, *Behrenfeld et al., 2005; Westberry et al., 2008*).
61 However, the satellite remote sensing approach cannot provide direct information at depth, and
62 also lacks coverage in regions with high solar zenith angles or obscured by clouds.

63 The development of instruments/sensors on underway and autonomous platforms
64 provides a complementary approach to ship-based ^{14}C incubation and satellite remote sensing
65 methods. As an example of the application of underway surface measurements, *Burt et al.,*
66 [2018] combined underway bio-optical measurements and mass spectrometry to study spatial
67 distributions of NPP, net community production (NCP), and the NCP to NPP ratio in subarctic
68 Northeast Pacific surface waters during the spring/summer growth season (May to July). As for
69 previous depth-resolved studies using in-situ autonomous platforms, the 2008 North Atlantic
70 Bloom Experiment (NAB08) used Lagrangian floats and a Seaglider to obtain high-resolution
71 measurements within a single phytoplankton patch in the subarctic North Atlantic (59° N to 62°
72 N) during the spring bloom from April to May [*Alkire et al., 2012*]. During the NAB08
73 experiment, phytoplankton biological carbon production was studied in the context of NPP
74 (derived from bio-optical measurements [*Briggs et al., 2018*]), particulate organic carbon (POC,
75 derived from bio-optical measurements [*Alkire et al., 2012*]), and NCP (derived from oxygen and
76 nitrate mass balance [*Alkire et al., 2012*]). A similar experiment with autonomous floats was
77 conducted later in the subtropical North Atlantic near Bermuda Atlantic Time-Series (BATS)
78 stations from 2013 to 2014, in which a modified CbPM model was used for NPP estimation
79 [*Estapa et al., 2019*].

80 The western North Atlantic Ocean is an area with one of the most significant, open-ocean
81 phytoplankton seasonal blooms in the global ocean. From 2015 to 2018, a time-series study was
82 conducted in this region during the North Atlantic Aerosols and Marine Ecosystems Study
83 (NAAMES, <https://naames.larc.nasa.gov/>) funded by the National Aeronautics and Space
84 Administration (NASA). The objective of NAAMES was to study the key processes controlling
85 ocean system function, their influences on atmospheric aerosols, and their implications for
86 climate [*Behrenfeld et al., 2019*]. Four research cruises were conducted from 2015 to 2018, with
87 comprehensive shipboard sampling and measurements of biological production (including ^{14}C
88 incubation experiments for NPP). Biogeochemical Argo (BGC-Argo) floats were deployed
89 during these campaigns, thereby providing a unique opportunity for comparisons between
90 shipboard measurements and Argo float measurements. In our previous work, we used the
91 NAAMES BGC-Argo data to analyse the phytoplankton phenology in the context of
92 phytoplankton growth rate and carbon accumulation rate [*Yang et al., 2020*]. In this work, we use

93 the BGC-Argo data to derive depth-resolved NPP with two different bio-optical models. The
 94 Argo-based NPP is first evaluated against ^{14}C incubation NPP data from the NAAMES cruises,
 95 followed by an analysis of the spatial and temporal distributions of NPP in the western North
 96 Atlantic. We also demonstrate the possibility of obtaining in-situ seasonal NCP to NPP ratios,
 97 using a six-month concurrent record of bio-optical and oxygen measurements from two Argo
 98 floats.

99 2 Methods

100 2.1 Research area

101 This study utilized field data from the NASA North Atlantic Aerosol and Marine
 102 Ecosystem Study (NAAMES, *Behrenfeld et al.*, [2019]). Our research area, located in the North
 103 Atlantic Ocean between 39°N to 54°N and 36°W to 46°W (Figure 1), was divided into
 104 northern (more temperate) and southern (more subtropical) regions with the partition at 47°N ,
 105 roughly following the categorization by *Della Penna and Gaube* [2019].

106 2.2 In-situ bio-optical measurements

107 Chlorophyll-a concentration (*Chl*), phytoplankton carbon biomass (C_{phyto}), salinity (*S*),
 108 temperature (*T*), and pressure (*P*) data used for NPP calculation were obtained from five BGC-
 109 Argo floats (n0572, n0849, n0850, n0851, n0852, WMO number 5902460, 5903106, 5903107,
 110 5903108, and 5903109) deployed by the University of Maine (Figure 1). These five floats were
 111 chosen because each of them had several profiles nearby NAAMES cruise stations where ship-
 112 based ^{14}C NPP incubations were conducted, so that the performance of Argo float estimates of
 113 NPP could be evaluated. *Chl* was estimated from fluorometers on BGC-Argo floats, where the
 114 fluorometers were calibrated against discrete HPLC samples collected during NAAMES cruises.
 115 Float-measured particulate backscattering coefficients at 700 nm (*bbp* 700) were first converted
 116 to *bbp* at 470 nm using a power-law function with an exponent of 0.78 following *Boss et al.*,
 117 [2013] and assuming the particulate backscattering ratio to be wavelength invariant. And then
 118 C_{phyto} was calculated using *bbp* 470 with the algorithm from *Graff et al.* [2015]. It should be
 119 noted that a drawback of such approach is that a portion of the scattered light is due to non-algal
 120 particles. The floats operated with a profiling frequency from 1 to 5 days and had a depth
 121 resolution of $\sim 2\text{ m}$ in the upper 500 m and $\sim 4\text{ m}$ from 500 m to 1000 m. The BGC-Argo float
 122 data and documentation are available at <http://misclab.umeoce.maine.edu/floats/>.
 123

124 2.3 NPP calculation

125 2.3.1 Carbon based productivity model (CbPM)

126 The first NPP model used in this study is the original CbPM model [*Behrenfeld et al.*,
 127 2005]. In the CbPM, mixed layer NPP was calculated as the product of phytoplankton carbon
 128 (C_{phyto} , mg C m^{-3}) and phytoplankton specific growth rate (μ , d^{-1}) in the mixed layer:
 129

$$130 \quad NPP_{mld}^{CbPM} = C_{phyto} \cdot \mu \quad \text{mg C m}^{-3} \text{ d}^{-1} \quad (1)$$

where μ was calculated using the equation modified CbPM [*Westberry et al.*, 2008]:

$$131 \quad \mu = \frac{2 \cdot Chl / C_{phyto} \cdot (1 - \exp^{-5I_g})}{0.022 + (0.045 - 0.022) \cdot \exp^{-5I_g}} \quad \text{d}^{-1} \quad (2)$$

132 and where *Chl* is the chlorophyll concentration (mg m^{-3}), I_g is the median daily light level (mol
 133 photons $\text{m}^{-2} \text{ h}^{-1}$) in the mixed layer. The value of I_g was estimated using satellite-derived surface
 photosynthetically active radiation (*PAR*) at the ocean surface (I_0) following:

$$I_g = I_0 \cdot \exp^{-K_{PAR} \cdot MLD/2} \quad \text{mol photon m}^{-2} \text{ d}^{-1} \quad (3)$$

134 where the mixed layer depth (*MLD*) (m) was defined by a density offset from the value at 10 m
 135 with a threshold of 0.03 kg m⁻³ [*deBoyer Montégut et al.*, 2004] using float-measured *S* and *T*.
 136 K_{PAR} is the diffuse attenuation coefficient of PAR, which was calculated using Equations 4a and
 137 4b [*Morel et al.*, 2007].

$$K_{PAR} = 0.0864 + 0.884 \cdot K_{490} - 0.00137 \cdot K_{490}^{-1}, \text{ when } MLD \leq K_{490}^{-1} \quad \text{m}^{-1} \quad (4a)$$

$$K_{PAR} = 0.0665 + 0.874 \cdot K_{490} - 0.00121 \cdot K_{490}^{-1}, \text{ when } MLD > K_{490}^{-1} \quad \text{m}^{-1} \quad (4b)$$

138 where K_{490} is the 490 nm diffuse attenuation coefficient (m⁻¹), calculated from float-measured
 139 chlorophyll-a concentration [*Morel and Maritorena*, 2001]:

$$k_{490} = 0.0166 + 0.07242 \cdot Chl^{0.68955} \quad \text{m}^{-1} \quad (5)$$

140 It should be noted that for depth-resolved NPP, the CbPM calculation was performed using the
 141 full Argo *Chl* and C_{phyto} profiles, and the actual light level at each depth (I_z).

$$I_z = I_0 \cdot \exp(-K_{PAR} \cdot Z) \quad \text{mol photon m}^{-2} \text{ d}^{-1} \quad (6)$$

142

143 2.3.2 Photoacclimation productivity model (PPM)

144 The second model used in this study is the Photoacclimation Productivity Model (PPM)
 145 developed during the NAAMES project [*Fox et al.*, 2020]. Similar to the CbPM, this second
 146 approach computes depth-resolved NPP using an estimate of phytoplankton growth rate and
 147 biomass (Equation 1), but it also uses the photoacclimation model of *Behrenfeld et al.* [2016] to
 148 account for nuances of chlorophyll synthesis caused by dynamic exposure to light and darkness
 149 in the mixed layer. Accordingly, μ was calculated as:

$$\mu = \left[\left(\frac{1}{\theta_{DM}} (-16.80) + 1.57 \right) \cdot \left(\frac{1}{\theta_{PaM}} (47.03) + 0.0125 \right) \right] \cdot [1 - e^{(-5 \cdot I_z)}] \quad \text{d}^{-1} \quad (7)$$

150 where θ_{DM} represents a deep-mixing term that accounts for molecular signals regulating
 151 chlorophyll synthesis during exposure to darkness, such that chlorophyll synthesis abates:

$$\theta_{DM} = 19 \cdot e^{(0.038 I_0^{0.45}/k_{PAR})} \quad (8)$$

152 and θ_{PaM} implements a shallow-mixing correction for mixed layers less than 6 optical depths:

$$\theta_{PaM} = 19 \cdot e^{(0.038 I_0^{0.45}/k_{PAR})} \cdot \frac{1 + e^{(-0.15I_0)}}{1 + e^{(-3I_g)}} \quad (9)$$

153 The PPM assumes that dark conditions occur at depths greater than 6 optical depths and that the
 154 value of θ_{PaM} for mixing depths greater than this horizon are described by θ_{DM} . For depths below
 155 the mixed layer the shallow-mixing term is not applied in the second component of Equation 7
 156 (i.e. θ_{DM} is used instead of θ_{PaM}). The final term in Equation 7 describes the reduction in growth
 157 rate resulting from decreasing ambient light, which is estimated iteratively with depth. This
 158 decrease reflects the strength of the light limitation effect on μ and is characterized by the
 159 exponent (-5) [*Westberry et al.*, 2008]. As with the CbPM, I_z in equations 7-9 is the PAR value at
 160 depth of Z (m), which was estimated from surface PAR using Equation 6.

161

162 2.4 Evaluation of Argo-derived NPP with ¹⁴C incubation result

163 Ship-based ¹⁴C NPP incubation results are still the gold standard of NPP measurements in
 164 the field, recognizing that there might be some artifacts from ¹⁴C incubation experiments [*Morán*
 165 *et al.*, 2007; *Westberry et al.*, 2012] as well as potential uncertainties here from the
 166 temporal/spatial mismatches of Argo and incubation data. The ¹⁴C NPP data from nine stations
 167 (black stars in Figure 1) on three NAAMES cruises were used to evaluate the performance of the
 168 bio-optical-measurement-based Argo NPP estimates. Evaluations are presented in the context of

169 surface NPP (Section 3.1.1) and depth-resolved NPP (Section 3.1.2), respectively. When there
170 were multiple Argo profiles during the same 24-hour incubation experiment, the Argo-derived
171 NPP values were averaged and then compared with the ^{14}C incubation result. Type II linear
172 regression was used for the evaluation because both Argo-based NPP and ^{14}C -based NPP are
173 measured parameters with uncertainties and dependent on the same environmental conditions
174 and biological/physical processes.

175 NPP data from ^{14}C incubation experiments during NAAMES 1 to NAAMES 4 cruises
176 (stations shown in Figure 1) are available at <https://seabass.gsfc.nasa.gov/experiment/NAAMES>.
177 In brief, water collected by Niskin bottles pre-dawn were spiked with ^{14}C -bicarbonate and
178 incubated for 24 hours (dawn-to-dawn) at different light levels (corresponding to the sample
179 depth) in on-deck incubators to provide depth-resolved NPP (full details are provided in *Fox et*
180 *al.*, [2020]).

181

182 **2.5 Auxiliary data**

183 For comparison purposes, satellite-based estimates of surface NPP were compiled from
184 Moderate Resolution Imaging Spectroradiometer (MODIS) products (*Chl*, b_{bp} , *T*, *PAR*,
185 <http://sites.science.oregonstate.edu/ocean.productivity/1080.by.2160.8day.inputData.php>) and
186 using the same CbPM algorithm described in section 2.3.1. The MODIS dataset used here had a
187 spatial resolution of 0.167 by 0.167 degrees and a temporal resolution of 8 days. The *Chl* product
188 was derived using the Garver–Siegel–Maritorena model (GSM) algorithm [*Maritorena et al.*,
189 2002]. The gridded satellite product was interpolated to match the float data. A 1D interpolation
190 in time was applied first to match the time steps of Argo measurements and then a 2D
191 interpolation in space was applied to interpolate the gridded satellite data to the Argo location.
192 We also used MODIS derived surface *PAR* as I_0 for Argo NPP calculations because there were
193 no reliable Argo-based *PAR* data for NPP calculations. Monthly nitrate data used in our analysis
194 was taken from a 1 degree gridded global nitrate field from the World Ocean Atlas 2013 [*Garcia*
195 *et al.*, 2013], presented as the area mean of each region (northern region: 46 – 36°W, 47 – 54°N;
196 southern region: 46 – 36°W, 39 – 47°N).

197

198 **2.6 In-situ oxygen measurement and NCP calculation**

199 Oxygen data from the five NAAMES BGC-Argo floats lacked sufficient in-situ
200 calibration to assure adequate accuracy required for air-sea gas calculations as the floats did not
201 measure oxygen in air [*Bittig et al.*, 2018]. Therefore, the oxygen data used for NCP calculations
202 were obtained from a nearby Special Oxygen Sensor Argo float (9764, WMO number 5704770)
203 (Figure 1), together with the corresponding salinity, temperature, and depth data. Only 6-months
204 of data (from July to December 2016) were utilized for calculating NCP-to-NPP ratios,
205 corresponding to when the trajectory of SOS-Argo f9764 was close to the BGC-Argo n0572. It
206 should be noted that using NCP and NPP estimates from two different floats introduces more
207 uncertainties (e.g. spatial offsets) into the NCP-to-NPP ratio estimate. Oxygen was measured
208 using the air-calibrated Aanderaa optode O_2 sensors on the SOS-Argo float, with an accuracy
209 better than $\pm 0.2\%$ [*Bushinsky et al.*, 2016]. The profiling float operated at an interval of 5 days,
210 covering depths from the surface to ~ 1900 m. The vertical resolution in the top 200 m (where
211 most of the carbon production occurs) was 3-5 m. The SOS-Argo float data are available at
212 <https://sites.google.com/a/uw.edu/sosargo/home>.

213 NCP was calculated using a one-dimensional mixed layer O_2 mass-balance model,
214 simplified from a multi-layer model used in our previous studies [*Bushinsky and Emerson*, 2015;

215 *Yang et al.*, 2018, 2019]. Briefly, the time rate of change in the mixed layer oxygen inventory
 216 ($dh[O_2]/dt$, mol O₂ m⁻² d⁻¹, where h is the mixed layer depth) is the result of gas exchange (F_{A-W}),
 217 vertical advection (F_w), entrainment (F_E), diapycnal eddy diffusion (F_{Kz}) at the base of the mixed
 218 layer, and net biological oxygen production (F_{NCP}):

$$\frac{dh[O_2]}{dt} = F_{A-W} + F_w + F_E + F_{Kz} + F_{NCP} \quad \text{mmol m}^{-2} \text{ d}^{-1} \quad (10)$$

219 The net biological O₂ production (F_{NCP}) is evaluated as the difference between the measured O₂
 220 time rate of change ($d[hO_2]/dt$) and the calculated fluxes (F_{A-W} , F_w , F_E and F_{Kz}), and then
 221 converted to carbon production (NCP) with a constant oxygen to carbon molar ratio of 1.45
 222 [*Hedges et al.*, 2002]. The dominant term in the oxygen mass balance (other than F_{NCP}) is the air-
 223 sea gas exchange (F_{A-W}), which was derived with the Argo-measured O₂ and satellite-measured
 224 wind speed (U_{10} , from the advanced scatterometer, ASCAT,
 225 <http://apdrc.soest.hawaii.edu/las/v6/>) using an air-sea gas exchange model developed by *Liang et*
 226 *al.*, [2013] and improved by *Emerson et al.*, [2019].

227 **3 Results and Discussion**

228 **3.1 Evaluation of Argo-derived NPP**

229 **3.1.1 Evaluation of Surface NPP**

230 For surface NPP comparisons, ¹⁴C NPP data with sample/incubation depths shallower
 231 than 5 m were chosen and compared with the corresponding Argo NPP results. The CbPM model
 232 yielded surface NPP values close to the ¹⁴C NPP values (Figure 2a, with the slope of type II
 233 regression = 0.80, R = 0.93, RMSD = 0.41 mmol m⁻³ d⁻¹). The regression line for PPM NPP was
 234 further from the 1:1 line (grey solid line), with a slope of 0.44 (Figure 2b, R = 0.88, RMSD =
 235 0.29 mmol m⁻³ d⁻¹).

236 **3.1.2 Evaluation of Depth-resolved NPP**

237 A type II linear regression (Figure 3j, the green dotted line) showed good agreement
 238 between the CbPM-based Argo approach and ¹⁴C measurements of depth-resolved NPP (R =
 239 0.90, RMSD = 0.51 mmol m⁻³ d⁻¹), and the slope of 0.99 showed that the CbPM model
 240 performed well in reproducing the magnitude of NPP. The largest discrepancy between the ¹⁴C
 241 NPP and CbPM-based Argo NPP occurred at mid-depths during the NAAMES 3 cruise
 242 (September 2017, yellow triangles in Figure 3j). The mid-depth NPP maximum indicated by the
 243 Argo data (also consistent with the mid-depth Chl-a maximum, Figure S6) was not found in most
 244 of the ¹⁴C incubation profiles (except for the slightly elevated NPP at N3S2 around 50 m, see
 245 below), the most likely explanation for such a mismatch being elevated chlorophyll levels from
 246 subsurface photoacclimation. In the summer or early fall when surface and upper-ocean light
 247 intensity is high, phytoplankton decrease the concentration of light-harvesting pigments such as
 248 chlorophyll a, while the same pigments increase at mid-depth as the light level decreases. This
 249 cellular process likely causes the subsurface peak of Chl-a (Figure S6) observed in the
 250 September 2017 data. Because the CbPM model has limited capacity to account for
 251 photoacclimation below the mixed layer depth, the subsurface peak of Chl-a also led to artifacts
 252 of subsurface maximum in NPP (Figures 3e to 3h).

253 The correlation coefficient R and RMSD for PPM-based NPP were 0.81 and 0.37 mmol
 254 m⁻³ d⁻¹, respectively (Figure 4j). However, compared to the CbPM approach, the regression line
 255 (green dotted line in Figure 4j) between depth-resolved PPM-based NPP and ¹⁴C was also further

258 from the 1:1 line, with a slope of 0.50 (similar to the regression result in the surface: slope =
259 0.44, Figure 2b). There are several possible explanations for the underestimated NPP from PPM-
260 based Argo approach. First, it is possible that the above mentioned temporal/spatial mismatches
261 of the Argo and cruise data and the potential artifacts from ^{14}C incubation affected the
262 comparison of ^{14}C -based NPP and CbPM/PPM-based NPP. Second, the PPM algorithm used for
263 Argo NPP calculation might have some systematic biases that are not, as of yet, fully understood.
264 The PPM model used modeled θ_{PaM} rather than the measured Chl/C used in CbPM. Therefore,
265 the PPM model is less vulnerable to the high Chl/C caused by photoacclimation during the
266 summer months. As a result, the PPM-based Argo NPP did not have any large subsurface NPP
267 maximum for the NAAMES 3 cruise in September 2017 (Figures 4e to 4h). However, the PPM
268 result did show slightly elevated subsurface NPP (N3S1 near 30 m, N3S2 near 40 m, N3S3 and
269 N3S4 near 20 m), which was also captured by ^{14}C NPP profiles (i.e. N3S2 and N3S3, Figures 4f
270 and 4g) and was most likely due to the surface nutrient depletion (Figures S7, e-h).

271 Overall, our analysis showed that both the CbPM and PPM models generally performed
272 well in reproducing the NAAMES NPP data estimated with the state-of-the-art ^{14}C incubation-
273 based NPP measurements, with their own advantages and limitations. The CbPM model
274 reproduced the magnitude of NPP but had some artifacts when subsurface photoacclimation was
275 significant. The PPM model accounts for effects of subsurface photoacclimation, but the model-
276 estimated NPP was much lower than the ^{14}C NPP estimates. Our result indicates that it is critical
277 to choose an appropriate model for Argo-based NPP calculations under different circumstances
278 and that more efforts need to be invested to improve NPP estimates from bio-optical
279 measurements from profiling floats.

280

281 **3.2 Spatial and Temporal distribution of NPP in the Western North Atlantic**

282 3.2.1 Spatial and Temporal distribution of Surface NPP

283 First, we analyzed the spatial and temporal distribution of NPP in the western North
284 Atlantic in the context of an annual climatology of surface NPP derived from Argo float data.
285 The Argo results from the CbPM model (blue line in Figures 5a and 5c) were used here, because
286 our evaluation showed no artifacts of photoacclimation in the surface NPP with the CbPM model
287 and the magnitude of NPP from CbPM model agreed better with the ^{14}C NPP results.

288 For the northern region (Figure 5a), NPP was low ($\sim 1 \text{ mmol m}^{-3} \text{ d}^{-1}$) for the first three
289 months of the year (January - March), due to the lower light level (red line, Figure 5b) in the
290 wintertime. Phytoplankton concentrations notably increased from April forward, with NPP
291 increasing substantially through the spring and summer, reaching the peak of $17 \text{ mmol m}^{-3} \text{ d}^{-1}$ in
292 mid-May. By mid-June, NPP started decreasing toward a relatively low value around 1.3 mmol
293 $\text{m}^{-3} \text{ d}^{-1}$ in mid-August, which could have been due to nutrient limitation (grey bar in Figure 5b),
294 and over-grazing. These factors could also have explained the increasing NPP after mid-August
295 and a plateau with NPP of $3 \text{ mmol m}^{-3} \text{ d}^{-1}$ observed from late September to late November, as the
296 increasing mixed layer depth could have helped relieve stresses from nutrient limitation (by
297 mixing with nutrient-rich deep water) and grazing (by reducing the encounter rate of
298 phytoplankton and grazers). After late November, with worsening light condition, NPP
299 decreased fast and reached near-zero values by the end of the year, which aligned well with the
300 observations in January. Overall, this seasonal pattern of NPP was consistent with the
301 phytoplankton phenology reported in our previous work [Yang *et al.*, 2020] and can be explained
302 by the disturbance recovery hypothesis (DRH, [Behrenfeld and Boss, 2018]).

303 For the southern region, the overall seasonal pattern was similar but with several distinct
304 characteristics (Figure 5c). First, the timing for each stage of the NPP phenology was different.
305 In the southern region, the significant increase in NPP started in March (Figure 5c), about 1
306 month earlier than that in the northern region (Figure 5a), which could be related to the better
307 light condition. On the other hand, after the summer peak, NPP quickly dropped below 1 mmol
308 m^{-3} by the end of June in the southern region as surface nutrients were quickly depleted (Figure
309 5d), indicating that the difference in nutrient supply of the Northern and Southern Regions is also
310 an important factor that controls phytoplankton phenology. The low NPP values continued until
311 late September (much longer than that in the northern region), consistent with the depleted
312 nutrients shown in Figure 5d and indicating that nutrient limitation may have played a more
313 important role in the southern region. Second, NPP in January and February was higher in the
314 southern region, because the light condition was better at lower latitude in the winter (Figure 5b
315 and 5d).

316 On the other hand, the summer NPP maximum ($\sim 10 \text{ mmol m}^{-3} \text{ d}^{-1}$) was lower in the
317 southern region than in the northern region. Surface PAR at the southern region NPP climax
318 (close to $2 \text{ mol photon m}^{-2} \text{ h}^{-1}$, Figure 5d) was higher than that of the northern region NPP climax
319 (below $1.5 \text{ mol photon m}^{-2} \text{ h}^{-1}$, Figure 5b). Based on climatology, surface nutrient levels were
320 low, but not zero, during the climax for the southern region (Figure 5d). A possible explanation
321 for the lower NPP climax levels in the southern region is that the southern region has a weaker
322 over all bloom, due to the lower wintertime nutrient supply or summer macro- or micro-nutrient
323 limitation. Although NPP from October to January was slightly lower in the southern region than
324 that in the northern region, it actually represented a larger contribution to annual production,
325 since the summer NPP in the southern region was not as high as that in the northern region.

326 NPP estimates from satellite-based Chl and C_{phyto} (yellow line in Figures 5a and 5c) were
327 also compared to the Argo float results. For most of a year, the Argo and satellite estimates of
328 NPP were comparable. The largest differences occurred in the late spring and summer months
329 when NPP was high (Figures 5e and 5f), consistent with the fact that the Argo estimates of Chl
330 and C_{phyto} were also higher than satellite estimated for those months (Figure S8). Such mismatch
331 could be the result of spatial/temporal mismatch of Argo and satellite data and/or the systematic
332 offsets between the Argo and satellite measurements.

333

334 3.2.2 Spatial and Temporal distribution of Depth-resolved NPP

335 For the analysis of depth-resolved NPP, we present monthly climatologies of NPP from
336 the PPM model (Figure 6) because the PPM model did not have photoacclimation-related
337 artifacts (large subsurface NPP peak) in the summer. Although the NPP from the PPM model
338 might have underestimated the magnitude of NPP (as shown in section 3.1.2), this bias should
339 not affect the analysis on seasonal NPP variations. Monthly climatologies of nitrate
340 concentration ($[\text{NO}_3^-]$, Figure 8) and photosynthetically active radiation (PAR, Figure 7) were
341 also created to help with our analysis.

342 For the northern region (Figure 6, upper panel), the NPP profiles showed an exponential-
343 like shape with NPP decreasing with depth, similar to the PAR profiles (Figure 7, upper panel).
344 Such patterns indicate that the light condition was likely the major control of NPP distributions
345 at depth in the northern region. The seasonal pattern of depth-resolved NPP in the northern
346 region was similar to the seasonal pattern of surface NPP (Figure 5a), with NPP increasing from
347 spring to summer, NPP climax in June, low NPP in August, a second NPP peak in September
348 and October, and decreasing NPP in November and December.

349 For the southern region, the seasonal pattern of depth-resolved NPP (Figure 6, lower
350 panel) was also similar to the seasonal pattern of the surface NPP (Figure 5c). For most of the
351 year, the depth distribution of NPP in the southern region also followed an exponential-like
352 pattern similar to the PAR distribution, with the exception in the summer months (July, August,
353 and September). For these three summer months, the NPP profile was almost a straight line from
354 the surface to 15-40 m and was far from the exponential-like pattern of PAR (Figure 7),
355 indicating that the light condition was not the sole control of such NPP depth distribution. On the
356 other hand, nitrate was depleted from the surface to about 20 m and started increasing below 20
357 m (Figure 8), which likely explained the low NPP in the shallow water, and the slightly elevated
358 subsurface NPP observed by Argo float (July to September, lower panel of Figure 6) and the ^{14}C
359 result from NAAMES 3 (i.e. N3S2 and N3S3, Figures 4f and 4g). Overall, the depth-resolved
360 NPP revealed similar differences between the northern and southern region as suggested by the
361 surface NPP, including the higher winter NPP/lower summer NPP in the south, and timing
362 difference in NPP phenology. The more nutrient-controlled NPP depth distribution in the
363 southern region for summer months was distinct from the more light-controlled NPP depth
364 distribution in the north.

365 Comparison was also made with previous Argo NPP study in the North Atlantic [*Briggs*
366 *et al.*, 2018]. Although their research area was about 4-8 degrees north to our northern-most
367 location, the magnitude of observed NPP values were comparable. Their study yielded an
368 integrated NPP (surface to 60 m) of $\sim 84 \text{ mmol C m}^{-2} \text{ d}^{-1}$ during the spring bloom in an area from
369 58° N to 62° N [*Briggs et al.*, 2018], while our corresponding results in the upper 60 m during
370 the bloom period were $95 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (northern region, 47° N to 54° N) and 73 mmol C m^{-2}
371 d^{-1} (southern region, 39° N to 47° N), respectively.

372

373 **3.3 Estimate of mixed layer NCP to NPP ratio**

374 In steady state, the NCP to NPP ratio is equivalent to the f-ratio (the amount of
375 biologically produced carbon available for export) [*Eppley and Peterson*, 1979], which is a
376 useful metric for quantifying the strength of the biological carbon pump. The most widely used
377 estimates of the f-ratio are derived from an empirical relationship with temperature [*Laws et al.*,
378 2000, 2011]. However, these empirical equations are limited by the spatial and temporal
379 coverages of field-observed f-ratios. In this study, we demonstrate the ability of Argo profiling
380 floats in measuring f-ratios over large temporal and spatial scales by using concurrent
381 measurements of NCP and NPP on two Argo floats (BGC-Argo n0572 and SOS-Argo f9764)
382 from July to late December of 2016. Although the distance between these two floats were not
383 ideal (Figure S10), they roughly covered the same area (Figure 1) during this period of time and
384 could give us a big picture of NCP to NPP ratio in this area. The mixed layer-integrated NCP
385 (unit: $\text{mmol m}^{-2} \text{ d}^{-1}$) from Equation 10 was converted to mixed layer mean NCP (unit: mmol m^{-3}
386 d^{-1}). As shown in Figure 9a, the mixed layer depths (determined from salinity and temperature,
387 see the T-S plot in the Supporting Information) from these two floats were similar (except for
388 September), indicating they were measuring the same water mass and therefore that it was
389 reasonable to combine the NPP and NCP results from these two floats to estimate NCP/NPP
390 ratios. For these months, NPP decreased sharply from July to mid-August and then increased
391 slightly with a small peak in early September. Thereafter, NPP slowly decreased until late
392 December. The NCP trend generally followed the NPP variations, except for July. The highest
393 NCP/NPP ratio occurred between late August and early October, with peak values of 0.3. For
394 comparison, a higher NCP/NPP value (0.3 to 0.7) was observed by *Alkire et al.* [2012] in the

395 subarctic North Atlantic during the bloom season (April and May). NCP and the NCP/NPP ratio
396 turned negative in mid-October and continued decreasing, with the lowest NCP/NPP values
397 around -1.0 in December when both NPP and NCP were small. The negative winter NCP may
398 reflect ventilation of low O₂ water and net respiration that occurred earlier in the shallow aphotic
399 zone over the prior stratified season. Despite the potential spatial offsets between the two floats
400 and temporal offset between NPP and NCP (NPP is instantaneous while NCP reflects the
401 situation of several weeks prior in the mixed layer and longer in stratified subsurface waters), the
402 Argo results clearly show significant seasonal variations in NCP/NPP ratios that are quite
403 different than those derived from a traditional temperature-based empirical equation (purple line
404 in Figure 9c, calculated with Equation 3 in *Laws et al.*, [2011]).

405

406 **4 Summary and Implications**

407 In this study, we obtained for the first time year-round, in-situ estimates of NPP in the
408 western North Atlantic Ocean (39° N to 55° N, 30° W to 50° W) using the bio-optical
409 measurements on BGC-Argo floats from the NAAMES project. The BGC-Argo-measured NPP
410 was comparable and complementary to discrete-sampling-based ¹⁴C incubation measurements,
411 but it also filled the niche of temporal and spatial (both horizontally and vertically) coverage
412 limitations of the ship-based ¹⁴C and satellite remote sensing approaches. Evaluations against ¹⁴C
413 NPP incubation measurements showed advantages and limitations of both the CbPM and PPM
414 bio-optical models. Specifically, the CbPM reproduced the magnitude of NPP in most cases
415 (except those when subsurface photoacclimation was important), while PPM accounted for the
416 effects of subsurface photoacclimation but overall was biased low compared to ¹⁴C data. Overall,
417 our work demonstrates that Argo float data provides an important, complementary approach to ¹⁴C
418 and satellite remote sensing estimates of NPP, with the potential to provide more information on
419 the temporal and spatial distribution of phytoplankton carbon production. Our work also shows
420 the limitations of current NPP models, and emphasizes the need for improving the NPP estimates
421 using bio-optical measurements from Argo profiling floats.

422

423 **Acknowledgments**

424 In addition to the links included in the main text, the Argo data can also be obtained with
425 WMO number at <http://www.argodatamgt.org/Access-to-data/Description-of-all-floats2>. These
426 data were collected and made freely available by the International Argo Program and the national
427 programs that contribute to it (<http://www.argo.ucsd.edu>, <http://argo.jcommops.org>). The Argo
428 Program is part of the Global Ocean Observing System. The links for satellite-based NPP, PAR
429 and U₁₀ data were listed in the main text. Detailed data for each float were included in the
430 supporting information. Support for this work came from the National Aeronautics and Space
431 Administration (NASA) as part of the North Atlantic Aerosol and Marine Ecosystems Study
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433

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522

523 **Figure 1.** Trajectories of seven Argo profiling floats with the initial float deployment locations
524 denoted by filled symbols. The bar chart (right panel) indicates float deployment durations.
525 The dotted lines indicate the trajectory of SOS-Argo f9764 for NCP estimates, and all other
526 floats are BGC-Argo for NPP estimates. SOS-Argo data are available at
527 <https://sites.google.com/a/uw.edu/sosargo/home> and BGC-Argo data are available at
528 <http://misclab.umeoce.maine.edu/floats/>. The dash-line at 47° N divided the research area into
529 the northern (temperate) and southern (subtropical) regions. Stars (labeled with the station ID)
530 indicate ship stations where ¹⁴C NPP values were measured during NAAMES cruises (Fox et al.,
531 [2020]) and compared with NPP from nearby Argo floats. The circles and triangle indicate the
532 locations where BGC-Argo and SOS-Argo were first deployed.

533 **Figure 2.** Comparison of surface Net Primary Production (NPP, mmol m⁻³ d⁻¹) derived from ¹⁴C
534 approach and Argo estimates using CbPM (panel a) and PPM (panel b). The grey diagonal line is
535 1:1 line and the green dotted line presents Type II linear regression line. Type II linear regression
536 result for CbPM: $y = (0.80 \pm 0.08) x + (0.65 \pm 0.16)$, $R = 0.93$, $\text{RMSD} = 0.41 \text{ mmol m}^{-3} \text{ d}^{-1}$. Type
537 II linear regression result for PPM: $y = (0.44 \pm 0.06) x + (0.57 \pm 0.11)$, $R = 0.88$, $\text{RMSD} = 0.29$
538 $\text{mmol m}^{-3} \text{ d}^{-1}$.

539 **Figure 3.** (a - i): Net primary production (NPP, mmol m⁻³ d⁻¹) profiles derived from BGC-Argo
540 floats (blue line) on NAAMES ¹⁴C stations, using the Carbon-based Productivity Model (CbPM).
541 Black “x” indicates NPP results from onboard ¹⁴C incubation experiments during NAAMES1 to
542 NAAMES4 cruises (Fox et al., [2020]). The blue shading indicates the standard deviation of
543 multiple Argo profiles during the same 24-h incubation experiment. The red dotted line and
544 yellow dash line indicate mixed layer depth (MLD, m) and euphotic depth (Z_{1%}, m), respectively.
545 (j) The correlation between NPP estimates from Argo and ¹⁴C measurements. The grey diagonal
546 line in the background is the 1:1 line. The green dotted line is from a type II regression: $y = (0.99$
547 $\pm 0.07) x + (0.60 \pm 0.10)$, $R = 0.90$, $\text{RMSD} = 0.51 \text{ mmol m}^{-3} \text{ d}^{-1}$

548 **Figure 4.** (a - i): Net primary production (NPP, mmol m⁻³ d⁻¹) profiles derived from BGC-Argo
549 floats (blue line) on NAAMES ¹⁴C stations, using the PPM model from Fox et al., [2020]. Black
550 “x” indicates NPP results from onboard ¹⁴C incubation experiments during NAAMES1 to
551 NAAMES4 cruises (Fox et al., [2020]). The blue shading indicates the standard deviation of
552 multiple Argo profiles during the same 24-h incubation experiment. The red dotted line and
553 yellow dash line indicate mixed layer depth (MLD, m) and euphotic depth (Z_{1%}, m), respectively.
554 (j) The correlation between NPP estimates from Argo and ¹⁴C measurements. The grey diagonal
555 line in the background is the 1:1 line. The green dotted line is from a type II regression with all
556 data: $y = (0.50 \pm 0.05) x + (0.39 \pm 0.07)$, $R = 0.81$, $\text{RMSE} = 0.37 \text{ mmol m}^{-3} \text{ d}^{-1}$.
557

558 **Figure 5.** Climatologies of surface Net Primary Production (NPP) for the northern region (a) and
559 southern region (c) from Argo (blue line) and Satellite (yellow line) using CbPM model. Panels
560 (b) and (d) show surface photosynthetically active radiation (PAR_{surf} , red line) and the monthly
561 climatology of surface nitrate concentration ($[NO_3^-]$, grey bar) from World Ocean Atlas 2013
562 [Garcia *et al.*, 2013]. The shadings in panels (a-d) indicate one standard deviation. Correlation
563 analysis of panels (a) and (c) are presented in panels (e) to (f) with the grey diagonal line as 1:1
564 line and the black dash line as type II regression line. Type II linear regression result for
565 Northern Region: $y = (1.92 \pm 0.08) x + (-1.53 \pm 0.28)$, $R = 0.88$, $RMSD = 2.02 \text{ mmol m}^{-3} \text{ d}^{-1}$.
566 Type II linear regression result for Southern Region: $y = (2.44 \pm 0.10) x + (-1.95 \pm 0.21)$, $R =$
567 0.79 , $RMSD = 1.74 \text{ mmol m}^{-3} \text{ d}^{-1}$.

568 **Figure 6.** Monthly climatologies of net primary production (NPP, $\text{mmol m}^{-3} \text{ d}^{-1}$) profiles derived
569 from BGC-Argo measurements using the PPM model from Fox *et al.*, [2020]. The shadings
570 indicate one standard deviation. The red dotted line and yellow dash line indicate mixed layer
571 depth (MLD, m) and euphotic depth ($Z_{1\%}$, m), respectively.

572 **Figure 7.** Monthly climatologies of photosynthetically active radiation (PAR, $\text{mol photon m}^{-2} \text{ h}^{-1}$)
573 profiles derived from Satellite data
574 (<http://sites.science.oregonstate.edu/ocean.productivity/1080.by.2160.8day.inputData.php>). The
575 shadings indicate one standard deviation. The red dotted line and yellow dash line indicate mixed
576 layer depth (MLD, m) and euphotic depth ($Z_{1\%}$, m), respectively.

577 **Figure 8.** Monthly climatologies of nitrate ($[NO_3^-]$, $\mu\text{mol L}^{-1}$) profiles derived from World
578 Ocean Atlas 2013. The shadings indicate one standard deviation. The red dotted line and yellow
579 dash line indicate mixed layer depth (MLD, m) and euphotic depth ($Z_{1\%}$, m), respectively.

580 **Figure 9.** (a) Mixed layer depth from floats n0572 and f9764. (b) Mixed layer mean net primary
581 production (NPP) and net community production (NCP). (c) Mixed layer mean NCP to NPP
582 ratio (NCP/NPP). The purple dashed line indicates the NCP/NPP derived using temperature-
583 based empirical algorithm (Equation 3 in Laws *et al.*, [2011]). NPP was derived from BGC-Argo
584 n0572 using the Carbon-based Productivity Model (CbPM, Westberry *et al.*, [2008]). NCP was
585 calculated from oxygen mass balance using data from SOS-Argo float f9764. Both NCP and
586 NPP were converted to the mix layer mean (unit: $\text{mmol C m}^{-3} \text{ d}^{-1}$).

Figure 1.

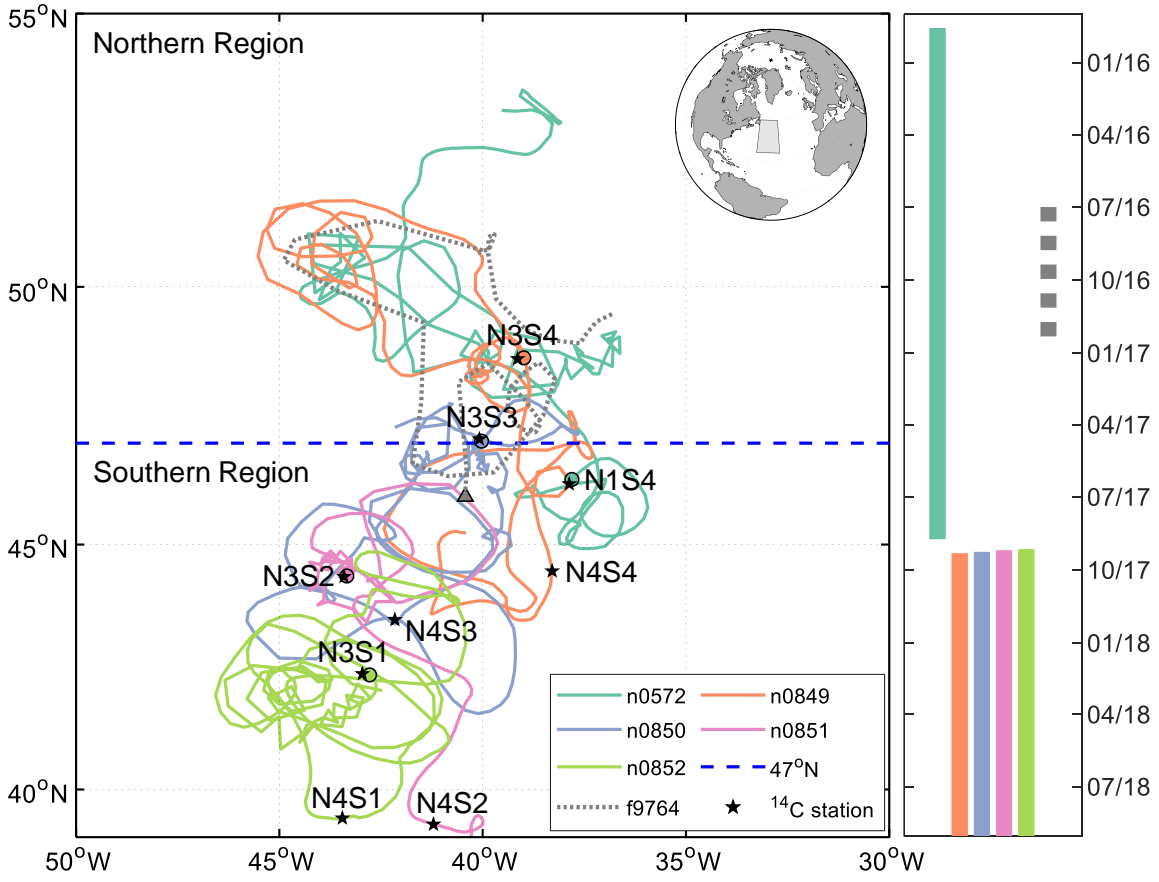


Figure 2.

○ Mar.2018 △ Sep.2017 □ Nov.2015 Type II Linear Regression

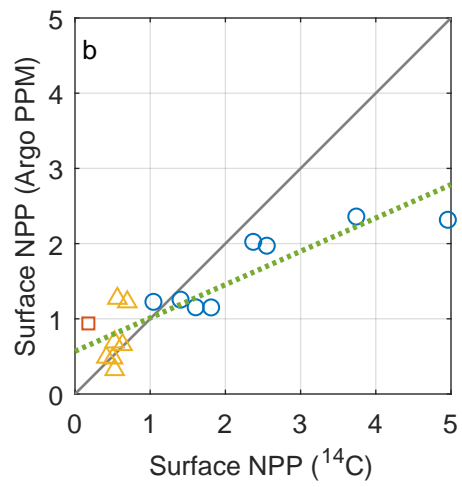
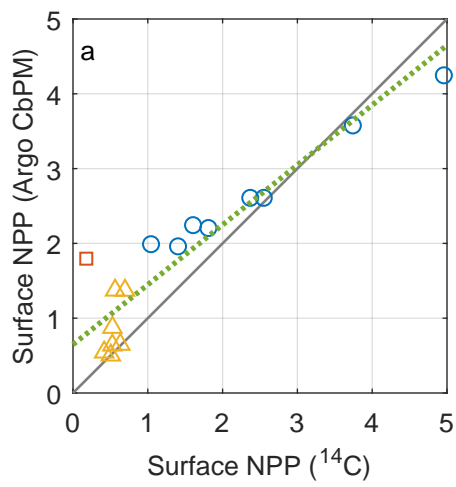


Figure 3.

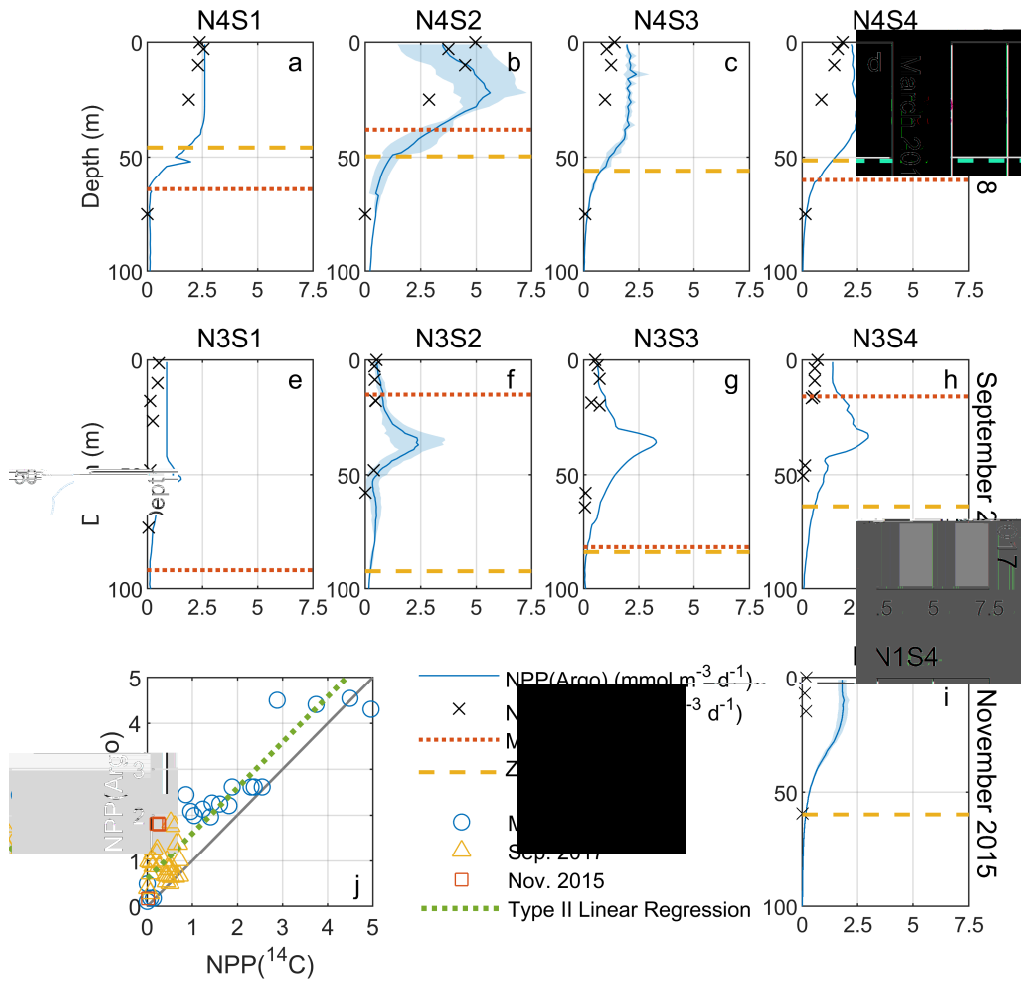


Figure 4.

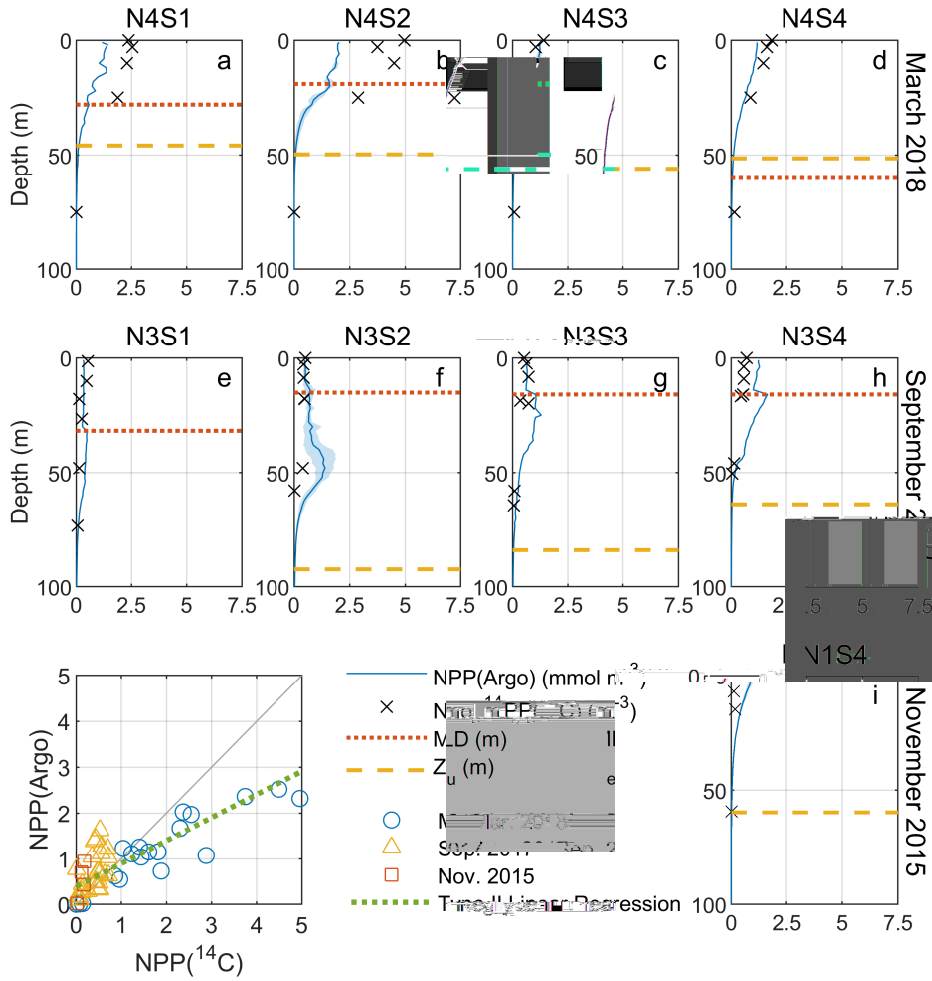


Figure 5.

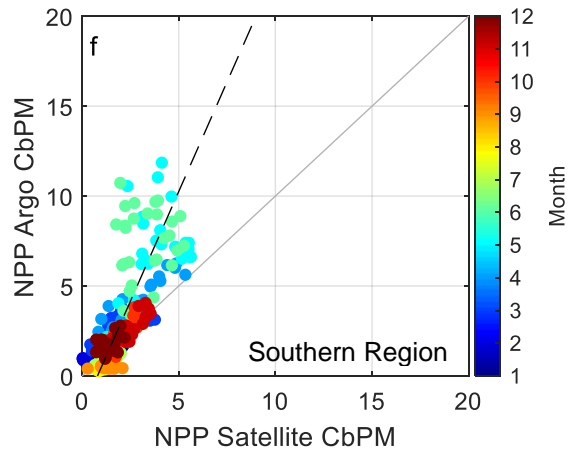
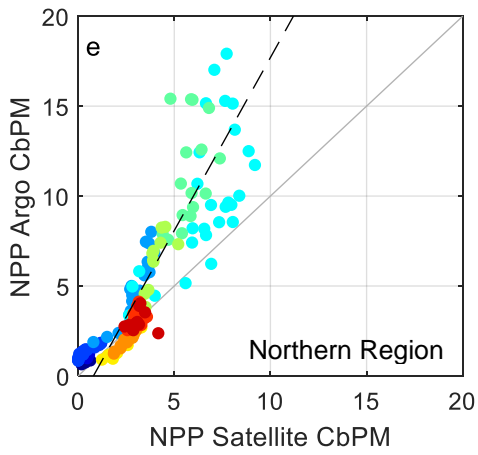
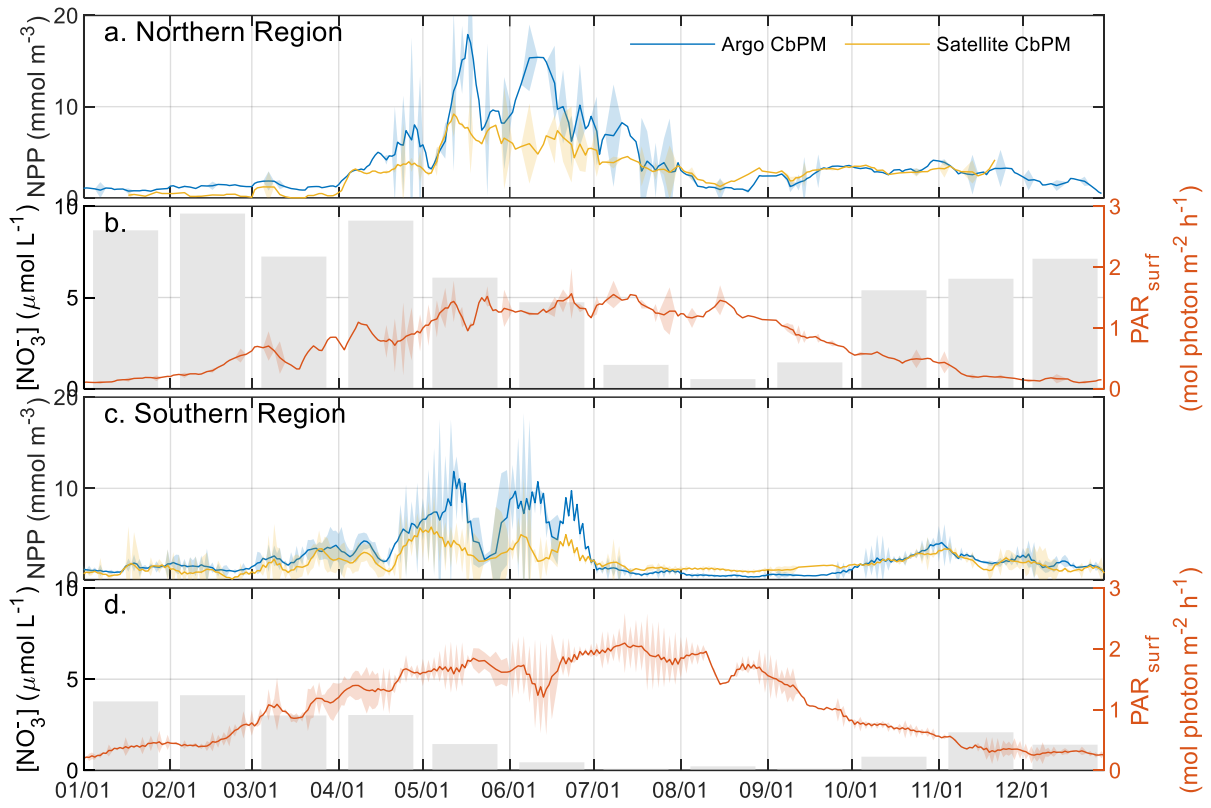


Figure 6.

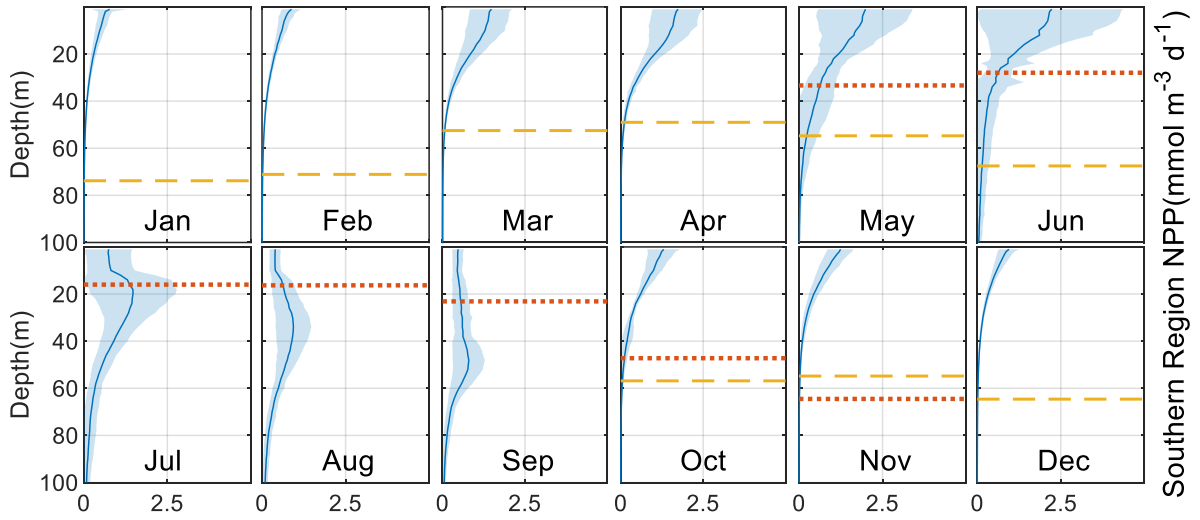
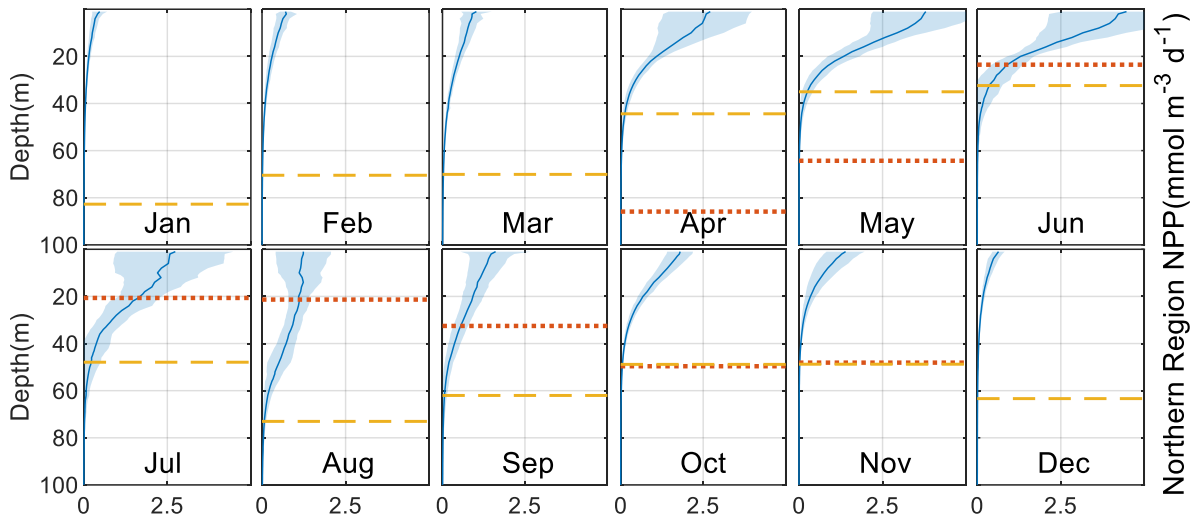
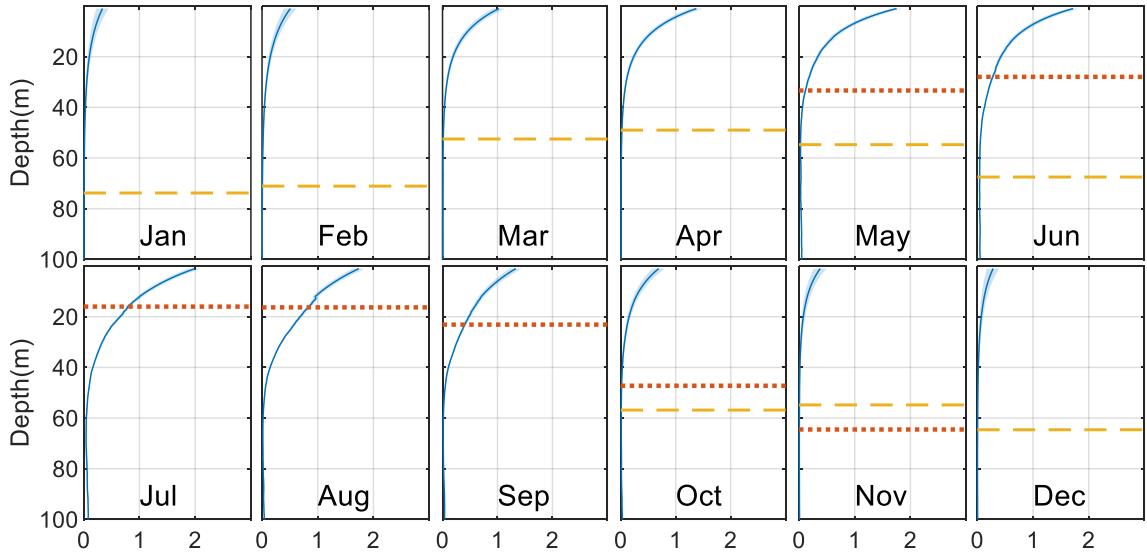
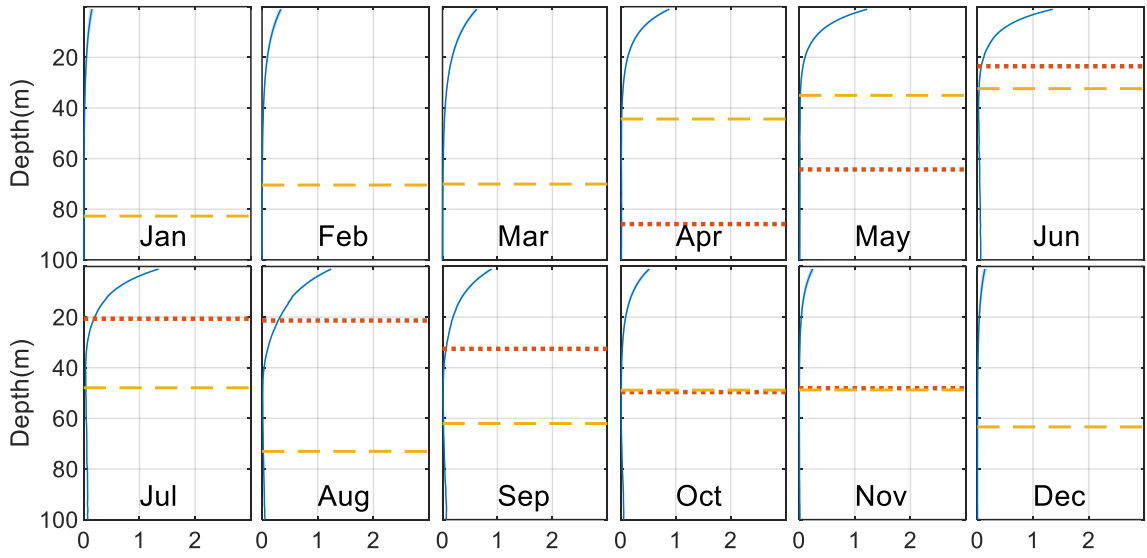


Figure 7.



Northern Region PAR (mol photon m⁻² h⁻¹)

Southern Region PAR (mol photon m⁻² h⁻¹)

Figure 8

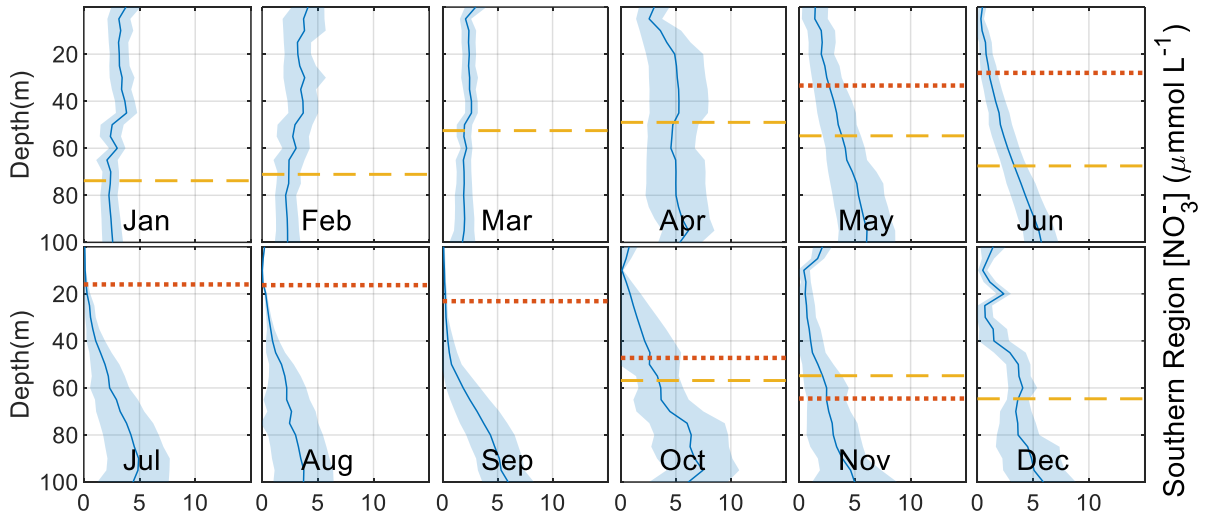
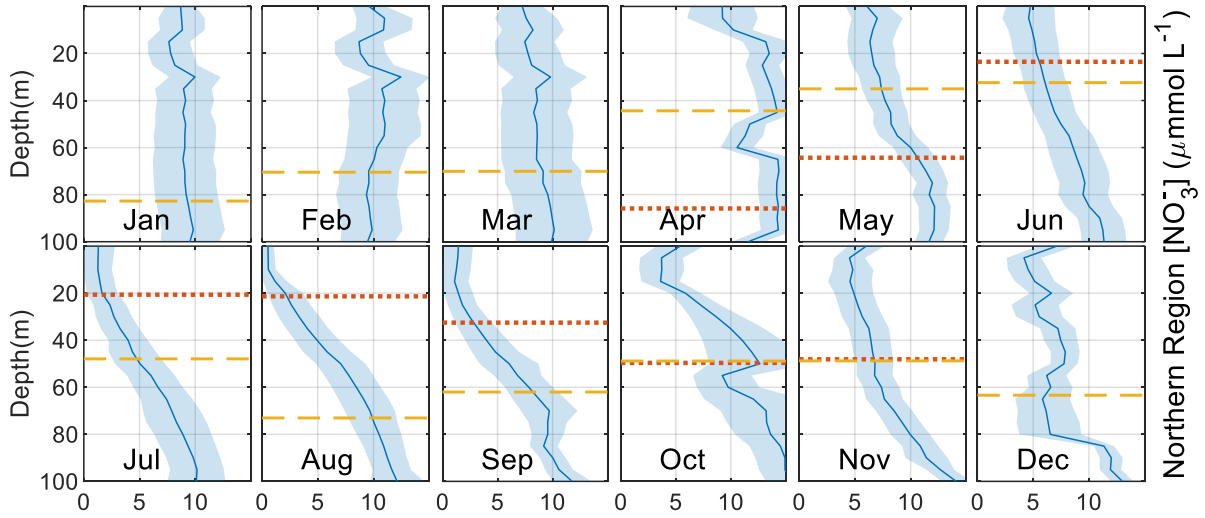


Figure 9.

