Global net community production and the putative net heterotrophy of the oligotrophic oceans

Toby K. Westberry, Peter J. le B. Williams, and Michael J. Behrenfeld

Received 17 April 2011; revised 1 October 2012; accepted 17 October 2012; published 22 December 2012.

1 Reconciling rates of organic carbon export from the euphotic zone with the consumption of organic material in the dark ocean remains one of the major quantitative uncertainties of the ocean carbon cycle. Euphotic zone net community production (NCP) provides one broad constraint on export flux and potential carbon drawdown. However, in vitro measurements of NCP consistently suggest that oligotrophic oceans are net heterotrophic, which is inconsistent with evidence of their carbon export to depth. Further, we have been unable to identify organic inputs on a scale to supplement the purported net heterotrophy. Here, we calculate global NCP rates using empirical relationships between in vitro photosynthesis (P) and respiration (R) and a satellite-based productivity model. A low value for global NCP (~139 ± 325 Tmol C a⁻¹) is found when a single P versus R (PvR) relation is derived from all in vitro data, with areas of net heterotrophy occupying 52% of the surface ocean. If a set of PvR relationships are instead derived by segregating the in vitro data into broad latitudinal zones associated with differing nutrient dynamics, we find a global NCP distribution in better agreement with independent model estimates of particulate carbon export, except in the 10°–40° latitudinal band where negative NCP values remain. Consistency between NCP and particulate export across all latitudes is achieved by applying a single PvR relationship derived using all in vitro data collected outside the 10°–40° latitudinal band. With this model, global NCP is estimated at ~781 ± 393 Tmol C a⁻¹ and modeled values at well-characterized field sites are in good agreement with non-incubation based in situ measurements. We infer from our results that in vitro NCP data from oligotrophic sites are too low, and suggest that this error is more likely the result of underestimated photosynthesis than overestimated respiration, although the precise physiological nature of the problem remains to be demonstrated.


1. Introduction

Major uncertainties exist in quantifying open ocean carbon cycling. One significant difficulty is reconciling the organic demand of the deep ocean with estimated rates of carbon export from the surface layer, the latter often being insufficient to sustain the former [Burd et al., 2010]. Surface export must broadly match deep water consumption when integrated over adequate space and time scales. Thus, the mismatch between current estimates of these fluxes indicates that we are overestimating one process, underestimating the other, or both. A resolution to this issue has been elusive, but is necessary for understanding carbon exchange relationships between surface and deep ocean ecosystems, as well as atmosphere-ocean CO₂ exchange. Estimates of riverine input of carbon to the ocean (~34 Tmol C a⁻¹) exceed that of net sedimentation (14 Tmol C a⁻¹), so the ocean overall can be regarded as net heterotrophic [Smith and Mackenzie, 1987]. This imbalance, however, is small when viewed against total ocean net primary production (NPP) (order 3,500 to 5,000 Tmol C a⁻¹) [del Giorgio and Williams, 2005; Westberry et al., 2008] and carbon export to depth (order 1000 Tmol C a⁻¹ [Williams et al., 2012]). This latter flux is linked to surface net community production (NCP = net primary production minus community respiration), and the magnitude of this excess production can be constrained (based on geochemical principles) using measurements of carbon export fluxes or estimates of mesopelagic and bathypelagic respiration. The former approach yields global NCP values ranging from 250 to 2,650 Tmol C a⁻¹ (average 1251 Tmol C a⁻¹) [del Giorgio and Duarte, 2002; Laws et al., 2000] (Table 1). The latter approach gives similar values of 630 to
2800 Tmol C a⁻¹ (average 1918 Tmol C a⁻¹) [Aristegui et al., 2003, 2005] (Table 1). These ‘indirect’ estimates of NCP indicate that a large fraction of NPP must be exportable, requiring global euphotic-zone ecosystems to be predominantly net autotrophic.

[3] Net community production and respiration can be assessed directly in the field by measuring changes in O₂ concentration following a 24 h incubation. In principle, these measurements should be the simplest and least ambiguous planktonic rate assessments to make. Nevertheless, a major issue surrounds these in vitro measurements: they generally indicate negative NCP in regions of low NPP (e.g., the central oligotrophic gyres). In other words, they suggest that community respiration often exceeds primary production. Early on, it was suggested that this apparent net heterotrophy arose in part from the form of analysis applied [Williams and Bowers, 1999], but this has since been disproven [Duarte and Regaudie-de-Gioux, 2009; Robinson and Williams, 2005].

[4] While a number of researchers [Canfield et al., 1989; Duarte and Agustí, 1998; Duarte et al., 1999, 2001] appear comfortable with the concept of net heterotrophy in remote marine ecosystems, others are not [Geider et al., 1998a, 1998b; Williams and Bowers, 1999]. Central oceanic gyres are oligotrophic precisely because of their isolation. Accordingly, it is difficult to see how the organic subsidy necessary to sustain net heterotrophy could arise from external sources [Williams and Bowers, 1999]. To illustrate the scale of the problem, applying the mean NCP deficit of 9 mol O₂ m⁻² a⁻¹ (8.2 mol C m⁻² a⁻¹ using a PQ of 1.1) observed at Station ALOHA in the North Pacific [Williams et al., 2004] to all open ocean gyres (taken to be one third of the surface open ocean) yields a total carbon deficit of c. 800 Tmol C a⁻¹ for oligotrophic systems. A similar finding was reported by Duarte and Agustí [1998] who calculated area NCP rates using a derived relationship between depth integrated photosynthesis and respiration applied to primary production rates calculated by Longhurst et al. [1995]. The authors found ~80% of the ocean to be areas of net heterotrophy, with the organic deficit being made up by the remaining 20% of the oceanic area. Such deficits would have to be fueled by what we would regard as an improbable import of organic carbon from elsewhere. The likelihood of this net heterotrophy is also called to question given that alternative, in situ geochemical measurements, consistently indicate net autotrophy in oligotrophic gyres, with typical NCP rates of 1–4 mol C m⁻² a⁻¹ [Luz and Barkan, 2009; Quay et al., 2010]. Further, the 13C of the dissolved inorganic carbon of the mixed layer of the tropical gyres requires net autotrophy and is not consistent with import of external biologically produced organic material as a means of making up the deficit [Williams et al., 2012].

[5] The objective of the present study is to examine the notion of widespread net heterotrophy from an alternative perspective. The present field data set of NCP and respiration measurements is paltry (~2,500–3,000 observations) compared to that of planktonic photosynthesis (~100,000 to 250,000 observations [Williams and del Giorgio, 2005]), and very unevenly distributed (Figure 1). However, relationships between photosynthesis and respiration can be derived from these data and then applied to satellite-based estimates of NPP to achieve global distributions of NCP. This sort of approach has been used for regional NCP assessments [Duarte et al., 2001; Serret et al., 2002], but never applied at the global scale. The question we pose is, can field-based parameterizations of PVR relationships give global NCP rates that comply with independent constraints from geochemical assessments? For this investigation, we employed the Carbon-based Production Model (CbPM) of Westberry et al. [2008], which accounts for photoaclimation throughout the water column and relief from nutrient stress at depth. Our results are compared globally to monthly resolved estimates of particulate export flux from the empirical model of Dunne et al. [2005] and from a synthesis of circulation models [Najjar et al., 2007], and locally to in situ estimates of NCP at four well-characterized sites.

2. Methods

2.1. Auditing the Productivity (P) and Respiration (R) Database

[6] A variety of field techniques exist for assessing photosynthesis (¹⁴C or ¹⁸O₂ assimilation, O₂ derived rates, ¹⁸O₂ disequilibria) and respiration (electron transport system rate measurement (ETS), dark bottle O₂ uptake). However, only the O₂-technique provides a common approach for both processes. Combining assessments from different techniques requires application of conversion factors that carry uncertainties and can be dependent on uncharacterized physiological variability. The current analysis was therefore based only on in vitro oxygen flux measurements with paired measurements of NCP and respiration. Many of these data were used in earlier analyses [Robinson, 2008; Robinson and Williams, 2005], but they have been supplemented here with additional data kindly provided by Drs. Susana Agustí, Javier Aristegui, Carlos Duarte, Dominique Lefèvre, Aurore Regaudie-de-Gioux and Pablo Serret. The compilation is publicly available at http://www.uea.ac.uk/env/people/facstaff/robinsonc.

[7] The full compilation of field data (~3000 observations) was first audited by removing all data not derived from chemically determined dark bottle respiration and light bottle NCP measurements. The main scientific loss here was that we were not able to incorporate data from the JGOFS EqPac study. We then removed data where either the
measured rate of respiration or calculated rate of photosynthesis was less than twice the standard error. Finally, in a few cases where standard errors were not reported, we removed data where photosynthesis or respiration rates were <0.3 mmol O₂ m⁻³ d⁻¹. This criterion was based on analysis of data distributions using Anderson-Darling and Kolmogorov-Smirnov plots, which showed a departure from normality below 0.3 mmol m⁻³ d⁻¹, at this point the measurement error becomes very significant. Combined, these auditing criteria roughly halved the useable data set to 1,637 paired measurements. While the spatial distribution of these data is far from uniform (Figure 1a), the range of values they encompass is representative of the full oceanic range (Figure 1b).

2.2. Statistical Analyses

[8] The filtered field data set (see above) was used to define global and regional relationships between photosynthesis and respiration. Model II regressions between log-transformed rates were performed using a reduced major axis procedure [Draper, 1998; Sokal and Rohlf, 1995]. Resulting fits were converted from the logarithm form (log(R) = b * log(P) + c) to an equivalent power relation (R = aPᵇ), where R and P are the rates of respiration and photosynthesis (units mmol O₂ m⁻³ d⁻¹), and b and c are the slope and intercept of the logarithmic fit, respectively. The coefficient ‘a’ in the power law equation is calculated as 10ᶜ.

[9] Uncertainties associated with each of the regressions were characterized by the 95% confidence interval estimated from the standard error of each regression [Haworth and Vincent, 1974]. This provides an upper and lower bound for respiration rate estimates which are carried through the subsequent NCP calculations. In addition, uncertainties in satellite NPP estimates (see next section) were derived from inter-model variability between annual NPP fields generated using 3 different models, the Vertically Generalized Productivity Model (VGPM) [Behrenfeld and Falkowski, 1997], a VGPM-variant with temperature dependence modeled after Eppley [1972], and the Carbon-based Productivity Model [Westberry et al., 2008]. These two sources of uncertainty were combined in a Monte Carlo-like framework to estimate the final uncertainties on the resulting NCP.

2.3. The Productivity Model, Respiration and NCP Rates

[10] Estimates of NPP were calculated globally using the spectral- and depth-resolved Carbon-based Productivity Model.
Model (CbPM) of Westberry et al. [2008]. To ensure that our overall results were insensitive to this choice of model, all analyses were also carried out using two alternative satellite NPP algorithms [Behrenfeld and Falkowski, 1997]. Results for these algorithms are presented in the auxiliary material and are not significantly different from those presented here. Calculations of NPP used monthly, ~9 km fields of physical and ocean color-based quantities (e.g., SST, Chlorophyll, Photosynthetically Available Radiation, etc.). For the present work, data for 2004 were taken as a representative year.

[11] Satellite-derived NPP fields (mmol C m⁻² d⁻¹) were converted to O₂ equivalents (mmol O₂ m⁻³ d⁻¹) using a photosynthetic quotient (PQ) of 1.4 or 1.1, dependent on the primary nitrogen source for a given phytoplankton community [Laws, 1991]. Nitrogen nutrition was evaluated at each monthly pixel using World Ocean Atlas 2009 nitrate (NO₃) concentrations [Garcia et al., 2010]. When nitrate concentration in the upper 100 m was less than 1 μM, ammonia was presumed to be the principal inorganic nitrogen source and a PQ of 1.1 was applied, while pixels having NO₃ > 1 μM were ascribed a PQ of 1.4. O₂-based NPP values were used to calculate daily respiration rates (mmol O₂ m⁻³ d⁻¹) based on coefficients (Table 2) derived from our analysis of field data (see above) and then respiration rates were converted back into carbon units using a respiratory quotient of 1.1. This conversion coefficient assumes that only organic respiration is governing oxygen consumption, and so tacitly implies that no nitrification is occurring in the incubations [Ward, 2008]. Field-based PvR relationships were applied to depth-resolved output from the CbPM and then vertically integrated to yield euphotic-zone areal rates of production, respiration, and NCP (mol C m⁻² d⁻¹). It is assumed here that satellite-based NPP can be used as a proxy for the incubation-based production, though in practice we know them to be slightly different. Accounting for this difference would be complex and inexact, therefore we make no attempt at this in the present analysis. However, a first order effort to quantify the error in this assumption is presented in the auxiliary material and we find this assumption not to be critical for interpreting the results presented here. In effect, the NCP values presented herein might be considered as conservative estimates.

2.4. Deriving the Export Production Rates

[12] Expressions relating the particulate export ratio (pe-ratio) to common ecosystem parameters (e.g., sea-surface temperature, chlorophyll, net primary productivity) exist and successfully capture the large scale variability observed in the ocean [Dunne et al., 2005; Eppley and Peterson, 1979; Laws et al., 2000]. Here, the model of Dunne et al. [2005] was used with monthly global fields of SST and NPP to estimate particulate export at the base of the euphotic zone (mg C m⁻² d⁻¹). This particular export model was chosen because of its simplicity and superior predictive capability in diverse ocean environments [see Dunne et al., 2005, Table 1] and was demonstrated to explain 61% of the observed variance in pe-ratios, the highest in the synthesis of Dunne et al. [2005]. The Dunne model requires input NPP in a nitrogen currency, so a Redfield value of 5.7 was used to convert satellite-based NPP (in units of carbon) to nitrogen. Export of organic material also occurs in dissolved phase. In a recent analysis, Carlson et al. [2010] measured export of DOC as a small, but not insignificant, fraction of total organic export (~9 to 20%). Thus, total carbon export was assessed here as the sum of particulate and dissolved phases, with estimates of DOC export rates kindly provided by John Dunne (J. Dunne, personal communication, 2011).

[13] A second, and wholly independent, estimate of total export flux was taken from Najjar et al. [2007] and represents a composite of twelve different Biogeochemical Ocean General Circulation Models, compiled as part of the Ocean Carbon-cycle Model Intercomparision Project Phase 2 (OCMIP-2). In this case, annual zonally integrated values were only available in coarse latitudinal bands, so the satellite based estimates were binned to match this resolution where needed.

3. Results

3.1. Determination of the Photosynthetic and Respiration Relationships

[14] Three sets of photosynthesis versus respiration (PvR) relationships were developed using the audited field data of paired measurements (N = 1637). First, a single relationship

---

[Table 2. Parameters Derived From Analysis of In Vitro Photosynthesis (P) and Respiration (R) Measurements]

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>r²</th>
<th>Slope</th>
<th>Intercept (mmol O₂ m⁻³ d⁻¹)</th>
<th>a</th>
<th>b</th>
<th>P = R (mmol O₂ m⁻³ d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duarte and Agustí [1998]</td>
<td>280</td>
<td>0.46</td>
<td>0.50</td>
<td>0.019</td>
<td>1.04</td>
<td>0.50</td>
<td>1.1</td>
</tr>
<tr>
<td>Robinson and Williams [2005]</td>
<td>957</td>
<td>0.44</td>
<td>0.62</td>
<td>0.040</td>
<td>1.10</td>
<td>0.62</td>
<td>1.3</td>
</tr>
<tr>
<td>All data</td>
<td>1,637</td>
<td>0.38</td>
<td>0.82 (0.02)</td>
<td>0.003 (0.010)</td>
<td>1.01</td>
<td>0.82</td>
<td>1.0</td>
</tr>
<tr>
<td>Open ocean (inc Med)</td>
<td>1,057</td>
<td>0.49</td>
<td>0.78 (0.02)</td>
<td>-0.033 (0.099)</td>
<td>0.93</td>
<td>0.78</td>
<td>0.7</td>
</tr>
<tr>
<td>High latitudes (&gt;60°)</td>
<td>208</td>
<td>0.38</td>
<td>0.90 (0.05)</td>
<td>-0.203 (0.036)</td>
<td>0.63</td>
<td>0.90</td>
<td>*</td>
</tr>
<tr>
<td>Mid latitudes (40°–60°)</td>
<td>322</td>
<td>0.46</td>
<td>0.81 (0.03)</td>
<td>-0.072 (0.021)</td>
<td>0.85</td>
<td>0.81</td>
<td>0.4</td>
</tr>
<tr>
<td>Low latitudes, inc Med (10°–40°)</td>
<td>419</td>
<td>0.60</td>
<td>0.77 (0.02)</td>
<td>0.047 (0.012)</td>
<td>1.11</td>
<td>0.77</td>
<td>1.6</td>
</tr>
<tr>
<td>Equatorial (0°–10°)</td>
<td>108</td>
<td>0.12</td>
<td>1.04 (0.09)</td>
<td>-0.096 (0.028)</td>
<td>0.80</td>
<td>1.04</td>
<td>*</td>
</tr>
<tr>
<td>Med</td>
<td>93</td>
<td>0.63</td>
<td>1.16 (0.07)</td>
<td>0.003 (0.028)</td>
<td>1.01</td>
<td>1.16</td>
<td>1.0</td>
</tr>
<tr>
<td>Coastal (inc Med)</td>
<td>580</td>
<td>0.18</td>
<td>0.84 (0.03)</td>
<td>0.063 (0.020)</td>
<td>1.16</td>
<td>0.84</td>
<td>2.5</td>
</tr>
<tr>
<td>All but 10°–40°</td>
<td>638</td>
<td>0.41</td>
<td>0.84 (0.03)</td>
<td>-0.110 (0.016)</td>
<td>0.78</td>
<td>0.84</td>
<td>0.2</td>
</tr>
</tbody>
</table>

*See methods for details. Slope and intercept refer to Model II regression coefficients for log-transformed P and R rates estimated using reduced major axis. Errors for each regression coefficient given in parentheses and were estimated following Sokal and Rohlf [1995]. Here “a” and “b” are their power law equivalents. Note that the parameter “a” has units (mmol O₂ m⁻³ d⁻¹)⁻¹. The asterisk means data considered unreliable.

---

A. All Oceanic data (n = 1057)

B. Oceanic data, excluding 10°-40° (n = 638)

C. High Latitudes, 60° & above (n = 202)

D. Mid-latitudes, 40°-60° (n = 322)

E. Low Latitudes, 10°-40° (n = 419)

F. Equatorial, 0°-10° (n = 108)

Figure 2. Scatterplots of in vitro determined photosynthesis and respiration rates (mmol O₂ m⁻³ d⁻¹) for (a) the whole data set and (b–f) various subsets. In each panel, the solid red line is a major reduced axis Model II regression fit and the two accompanying dashed lines are the 95% confidence limits (see Table 2 for fit parameters and statistics). The dashed black line is the 1:1 line.
was derived using all data (Figure 2a). In a second analysis, the data were partitioned by latitude into four zones (Figure 1, dashed black lines): high latitudes (60° and above), midlatitudes (40° to 60°), low latitudes (10° to 40°), and equatorial (0° to 10°) (Figures 2c–2f). These divisions coarsely reflect differing nutrient regimes: the >60° zone for regions where nutrient exhaustion is uncommon, the 40°–60° zone where seasonal nutrient depletion does occur, the 10°–40° zone comprising the subtropical gyres where nutrient recycling is very rapid (notably shorter than typical incubation times), and the 0°–10° zone encompassing regions of equatorial upwelling. Clearly, this separation is imperfect and could be refined using a wider diversity of biogeographic provinces [Longhurst, 2007]. However, while such an approach has been employed at local to regional scales [Duarte et al., 2001; Serret et al., 2002], it is obvious from Figure 1 that we are far from having sufficient data to achieve similar resolution at the global scale. Finally, our third approach was to develop a single PvR relationship using all the audited field data except those from the low latitude (10°–40°) zone (Figure 2b). Scatterplots and regression fits for our 3 different approaches are shown in Figure 2, with derived parameter values and statistics given in Table 2. We have also included in Table 2, the coefficients from two earlier analyses of global PvR data sets [Duarte and Agustí, 1998; Robinson and Williams, 2005] for comparison.

[15] In an earlier study, Duarte and Regaudie-de-Gioux [2009] conducted a PvR analysis somewhat similar to ours, but in their case, relationships were derived for each individual field data set. This approach led to generally higher correlation coefficients than in our analyses, presumably reflecting greater methodological consistency within a given study than when data are pooled from multiple studies.

### 3.2. Distribution of Net Community Production (NCP)

[16] A central objective of the current study was to compare global estimates of NCP based on PvR relationships derived from field O₂-based measurements with NCP requirements implied by the global distribution of annual carbon export, particularly in areas where field observations of NCP are reported to be persistently negative. Combining particulate and dissolved carbon fluxes, the Dunne et al. model yields a global NCP requirement of 700 ± 245 Tmol C a⁻¹ (Table 3, first and second columns) with significant regional differences in annual flux but positive net carbon export in all regions (Figure 3a). Export rates from Najjar et al. [2007] show a similar pattern, but with slightly higher values across all latitude bands (Table 3, third column) and a global annual export equal to 1302 ± 471 Tmol C a⁻¹. In contrast, application of mean parameters from two previously published PvR relationships [Duarte and Agustí, 1998; Robinson and Williams, 2005] to our satellite-based NPP data yielded a global NCP deficit of −782 Tmol C a⁻¹ (Table 3, fifth column). Clearly, this assessment is fundamentally at odds with our understanding of the ocean carbon budget. However, if we replace this earlier relationship with the single global PvR relationship derived from the current analysis.
Figure 3. Global distributions of modeled particle export and estimated NCP (mol C m\(^{-2}\) a\(^{-1}\)).
(a) Annual particle export fluxes derived from the model of Dunne et al. [2005], (b) NCP estimated using a single set of parameters from the whole open ocean data set, (c) NCP estimated from parameters determined for four latitudinal zones (see text for details), and (d) NCP estimated with PfR parameters drawn from data set with values from latitudes 10\(^{\circ}\)–40\(^{\circ}\) removed. In all cases, NCP values <0 mol C m\(^{-2}\) a\(^{-1}\) have been set to white.

(Figure 2a), estimated global NCP increases to +139 ± 325 Tmol C a\(^{-1}\) (Table 3, sixth column) and the distribution of NCP is in reasonable agreement with both the Dunne model based export at latitudes >40\(^{\circ}\)N (Figure 4a; see also Figures 3a and 3b). However, it is apparent that major issues remain with this global PfR relationship because it yields large regions of NCP deficit, particularly at low latitudes and in the Southern ocean (Figure 3b, white areas).

[17] An improved correspondence between export-based and O\(_2\)-based NCP estimates might be anticipated if zonal differences in PfR relationships are accounted for. However, while this expectation is realized for the Southern ocean (Figure 4b), applying our zonally defined PfR parameters to global NPP data did not alleviate the NCP deficit problem over the latitude range 10\(^{\circ}\)–40\(^{\circ}\) which includes the subtropical gyres (Figure 3c). In fact, these low latitude regions caused the zonal parameterization to give a global NCP of −106 ± 456 Tmol C a\(^{-1}\) (Table 3, seventh column), thus as one should expect worsens the discrepancy with the export-based estimate. This result, however, clearly highlights the problematic field data in this region.

[18] When a single ‘global’ PfR relationship is recalculated using all field data except those from the 10\(^{\circ}\)–40\(^{\circ}\) band, the resultant NCP estimates exhibit (1) a latitudinal distribution in close agreement with both the Dunne model and Najjar et al.’s analysis (Figures 4c and 4d), (2) a global distribution with apparent net heterotrophy only in the extreme south Pacific gyre and part of the Sargasso sea (Figure 3d), and (3) a global surplus production of 781 ± 393 Tmol C a\(^{-1}\) (Table 3, eighth column) that is similar to the export-based assessment of NCP. With respect to the ultraoligotrophic south Pacific, it should be noted that Claustre et al. [2008] reported NCP rates for this region that were not significantly different from zero (1.2 ± 6.1 mmol C m\(^{-2}\) d\(^{-1}\) and that we are beginning to project rates significantly beyond the spread of the data used to derive the parameters. Further, if the satellite NPP values are corrected to more closely approximate O\(_2\) equivalent production rates as calculated in bottle incubations, then the zones of negative heterotrophy are all but eliminated (see auxiliary material).

3.3. Comparison of NCP Estimates and In Situ Field Observations

[19] In the previous section, comparison of export-based NCP values with estimates from various O\(_2\)-based PfR relationships suggests that the latter measurements may be problematic in regions where low rates of primary production are coupled to roughly equivalent consumption rates and rapid nutrient recycling (i.e., the subtropical, 10\(^{\circ}\)–40\(^{\circ}\) band). This suggestion can be further evaluated at well-characterized sites where additional in situ data on NCP are available (Table 4).

[20] Hawaii Ocean Time series (HOT) site: In vitro NCP has been well characterized at the HOT site [Williams et al., 2004], with a mean of −8.2 ± 1.5 mol C m\(^{-2}\) a\(^{-1}\) (Figure 5a (top) and Table 4). This value is similar to monthly resolved NCP estimates from our low-latitude zone parameterization (Figure 5a, bottom). In contrast, a variety of in situ approaches for assessing NCP all indicate net autotrophy at HOT, with an average value of 2.3 mol C m\(^{-2}\) a\(^{-1}\) (Figure 5a (top)
and Table 4). These latter findings are consistent with monthly resolved NCP estimates from both the Dunne et al. export model and our satellite-based assessment of NCP using the PrR relationship with the data from the 10°–40° latitude band excluded (Figure 5a, bottom).

[21] Bermuda Atlantic Time Series (BATS) site: In situ measurements at the BATS site consistently indicate net autotrophy, with the most recent argon/oxygen-based assessment [Luz and Barkan, 2009] giving a value of 1.6 ± 0.4 mol C m⁻² a⁻¹ (Table 4). Our current assessment (parameterized with 10°–40° latitude field data excluded) suggests a similar value, albeit with larger degree of uncertainty (0.6 ± 1.1 mol C m⁻² a⁻¹). In stark contrast, our monthly NCP estimates based on the 10°–40° latitude parameterization suggest strongly net heterotrophic conditions at BATS (Figure 5b, red bars). Using data from Luz and Barkan [2009] provides another independent check against the predicted respiration rate used to calculate NCP. Subtracting their O₂/Ar-based NCP from their ¹⁷O₂-based estimate of gross oxygen production suggests respiration rates of 23, 40, 44, and 94 mmol O₂ m⁻² d⁻¹ during May, July, September and October, respectively. Our satellite-based respiration estimates for the same months are 24 ± 4, 24 ± 4, 24 ± 4, and 26 ± 4 mmol O₂ m⁻² d⁻¹.

[22] Equatorial Pacific: Bender et al. [1999] reported NCP values ranging from 65 to 205 mmol O₂ m⁻² d⁻¹ (mean = 120 mmol O₂ m⁻² d⁻¹ or 31 mol C m⁻² a⁻¹ assuming a PQ of 1.4) in the equatorial Pacific, based on classical in vitro oxygen measurements. These rates were 4–20 times greater than estimates based on nearby sediment trap data and in vitro isotope tracer measurements, which the authors interpreted as indicating the in vitro O₂ rates were erroneous. More recent measurements using non-incubation methods indicate much smaller NCP rates of 2.5 ± 2.3 and 1.5 ± 0.2 mol C m⁻² a⁻¹ for the eastern and western Equatorial Pacific, respectively [Hendricks et al., 2005; Stanley et al., 2010]. For these same regions, we calculate NCP values of ~5.7 ± 0.2 mol C m⁻² a⁻¹ and ~3.6 ± 2.7 mol C m⁻² a⁻¹ (Table 4), which agree well with the in situ data given the large year-to-year variability of the Equatorial region. In addition, Stanley et al. [2010] suggested their values may be low due to their assumption of zero upwelling in their calculation (which introduces oxygen deficient water) and also that their estimates are for the mixed layer only, not the entire euphotic zone.

[23] Subarctic Pacific Station P (50°N; 145°W): Based on 5 summer (May–August) cruises during two years, Emerson et al. [1991] estimated NCP from argon/oxygen and ²²⁲Rn measurements at Station P as ranging from 7 to 21 mmol O₂ m⁻² d⁻¹, with a mean of 13.4 mmol O₂ m⁻² d⁻¹ (or 5–15 mmol C m⁻² d⁻¹ with a mean of 9.6 mmol C m⁻² d⁻¹ using a PQ of 1.4). The span in their estimates reflects uncertainty in the oxygen flux across the halocline. For the same period of the year, we obtain a very similar NCP estimate of 2.7 mol C m⁻² a⁻¹ (or 9 mol C m⁻² d⁻¹ assuming a PQ of 1.4) in the equatorial Pacific, based on classical in vitro oxygen measurements. These rates were 4–20 times greater than estimates based on nearby sediment trap data and in vitro isotope tracer measurements, which the authors interpreted as indicating the in vitro O₂ rates were erroneous. More recent measurements using non-incubation methods indicate much smaller NCP rates of 2.5 ± 2.3 and 1.5 ± 0.2 mol C m⁻² a⁻¹ for the eastern and western Equatorial Pacific, respectively [Hendricks et al., 2005; Stanley et al., 2010]. For these same regions, we calculate NCP values of ~5.7 ± 0.2 mol C m⁻² a⁻¹ and ~3.6 ± 2.7 mol C m⁻² a⁻¹ (Table 4), which agree well with the in situ data given the large year-to-year variability of the Equatorial region. In addition, Stanley et al. [2010] suggested their values may be low due to their assumption of zero upwelling in their calculation (which introduces oxygen deficient water) and also that their estimates are for the mixed layer only, not the entire euphotic zone.

**Figure 4.** Comparison of annual rates of NCP and export production integrated through the euphotic zone. (a) Open histograms: NCP estimated from audited global ocean data set. Filled histograms: Particle export data from Dunne et al. [2005] plus estimated DOC export (J. P. Dunne, personal communication, 2011). Error bars are the 95% confidence limits. (b) Open histograms: NCP estimated from the audited global ocean data set, resolved into the latitude bands 0°–10°, 10°–40°, 40°–60°, 60° and above. Other details as Figure 4a. (c) Open histograms: NCP estimated from audited global ocean data set from which observations in the 10°–40° latitude zone have been excluded. Other details as in Figure 4a. (d) Open histograms: NCP estimated from audited global ocean data set from which observations in the 10°–40° latitude zone have been excluded, summed over the latitude zones reported by Najjar et al. [2007]. Dark gray histograms: Total organic carbon export from Najjar et al. [2007]. Light gray histograms: POC plus estimated DOC export from Dunne et al. [2005], see above; summed over the latitude zones reported by Najjar et al. [2007]. Other details as in Figure 4a.
Table 4. Estimates of NCP and Export Production From In Situ Observations at HOT, BATS, and in the Equatorial Pacific and Subarctic Northeast Pacific*

<table>
<thead>
<tr>
<th>Method</th>
<th>Location</th>
<th>Reported Rates (mol C m⁻² a⁻¹)</th>
<th>Rates From Present Study</th>
</tr>
</thead>
<tbody>
<tr>
<td>HOT/Station ALOHA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emerson et al. [1997]</td>
<td>Surface oxygen budgets</td>
<td>Station ALOHA</td>
<td>+2.0 ± 1.0</td>
</tr>
<tr>
<td>Bentzen-Nelson et al. [2001]</td>
<td>²³⁴Th analysis</td>
<td>Station ALOHA</td>
<td>+1.5 ± 0.8</td>
</tr>
<tr>
<td>Quay and Stutsman [2003]</td>
<td>DIC and d¹³ measurements</td>
<td>Station ALOHA</td>
<td>+2.7 ± 1.4</td>
</tr>
<tr>
<td>Hamme and Emerson [2006]</td>
<td>Ar/O₂ ratios</td>
<td>Station ALOHA</td>
<td>+1.1 ± 0.5</td>
</tr>
<tr>
<td>Emerson et al. [2008]</td>
<td>O₂ from moorings</td>
<td>Station ALOHA</td>
<td>+4.1 ± 1.9</td>
</tr>
<tr>
<td>Quay et al. [2010]</td>
<td>¹⁴C/O₂ disequilibria</td>
<td>Station ALOHA</td>
<td>+3.7 ± 1.0</td>
</tr>
<tr>
<td>Present study</td>
<td>Model</td>
<td>Station ALOHA</td>
<td>−8.2 ± 1.5</td>
</tr>
<tr>
<td>Williams et al. [2004]</td>
<td>In vitro determined of flux</td>
<td>Station ALOHA</td>
<td></td>
</tr>
<tr>
<td>BATS/Sargasso Sea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jenkins [1980]</td>
<td>Tritium/¹³He box model</td>
<td>Sargasso Sea</td>
<td>5.1*</td>
</tr>
<tr>
<td>Musgrave [1990]</td>
<td>Tritium/¹³He</td>
<td>Sargasso Sea; 32°N, 64°W</td>
<td>2–3*</td>
</tr>
<tr>
<td>Spitzer and Jenkins [1989]</td>
<td>Upper ocean O₂ balance</td>
<td>Sargasso Sea; 32°N, 64°W</td>
<td>4 ± 1.1*</td>
</tr>
<tr>
<td>Luz and Barkan [2009]</td>
<td>Ar/O₂ ratios</td>
<td>BATS</td>
<td>1.6 ± 0.4*</td>
</tr>
<tr>
<td>Present study</td>
<td>Model</td>
<td>BATS</td>
<td></td>
</tr>
<tr>
<td>Present study revised productivity for Nov–March (see text)</td>
<td></td>
<td>BATS</td>
<td>+1.1 ± 0.6</td>
</tr>
<tr>
<td>Equatorial Pacific</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hendricks et al. [2005]</td>
<td>Ar/O₂ ratios</td>
<td>Equatorial Pacific 95° to 110°W</td>
<td>+2.5 ± 2.3</td>
</tr>
<tr>
<td>Present study</td>
<td>Model</td>
<td>Equatorial Pacific 95° to 110°W</td>
<td>+5.7 ± 2.0</td>
</tr>
<tr>
<td>Stanley et al. [2010]</td>
<td>Ar/O₂ ratios</td>
<td>Equatorial Pacific 153°E to 180°</td>
<td>+1.5 ± 0.2</td>
</tr>
<tr>
<td>Present study</td>
<td>Model</td>
<td>Equatorial Pacific 153°E to 180°</td>
<td>+3.6 ± 2.7</td>
</tr>
<tr>
<td>Station Papa</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emerson et al. [1991]</td>
<td>Ar/O₂ ratios and ²²²Rn</td>
<td>Subarctic NE Pacific 50 N 145 W</td>
<td>+3.2 ± 3.2</td>
</tr>
<tr>
<td>Present Study</td>
<td>Model</td>
<td>Subarctic NE Pacific 50 N 145 W</td>
<td>+2.5 ± 1.1</td>
</tr>
</tbody>
</table>

* Sediment trap observations have been omitted as they may have been used to calibrate the Dunne et al. model. Data from the BATS site have been converted from oxygen to carbon rates using a PQ = 1.4 [see Luz and Barkan, 2009].

value of 12.4 ± 6.6 mmol C m⁻² d⁻¹, which is also in agreement with the Dunne et al. export-based estimate (Figure 5c and Table 4). Also, it is significant to note that at this location all three of the PvR relationships generally yield NCP values not significantly different from in situ observations. For example, NCP estimates using a single set of parameters derived from the full field data set (including those from 10°–40°) and those derived from latitude binned PvR relationships give NCP values of 6.3 ± 6.0 and 9.6 ± 7.5 mmol C m⁻² d⁻¹ respectively.

4. Discussion

[24] The limited spatial and temporal coverage of historical in vitro measurements of O₂-based plankton respiration and NCP prohibit their direct use for evaluating global distributions of these processes. However, these data do encompass a span of values representative of the full oceanic range, allowing development of photosynthesis-versus-respiration relationships that can be coupled with satellite data to generate global distributions of NCP. In the current study, this basic approach was followed using three different sets of PvR parameterizations. In the first two parameterizations where data from all latitudes were included, large areas of the global ocean emerged as net heterotrophic (Figures 3b and 3c, white areas). This finding is similar to that of Duarte and Agustí [1998] who found 25 of the 56 biogeochemical provinces described by Longhurst [2007] in organic deficit, and which occupied ~80% of the surface ocean. In that work, this deficit was proposed to be made up by surpluses in the remaining ecological provinces. However, these conspicuous regions of NCP deficit were near entirely eliminated by employing a single PvR relationship derived from in vitro data collected outside the 10°–40° latitude zone (Figure 3d). NCP values from this third parameterization gave a global annual rate (781 ± 393 Tmol C a⁻¹) and latitudinal distribution consistent with independent estimates based on modeled carbon export. Agreement was also found at the local scale with in situ measurements of NCP (Table 4). Additionally, this satellite-based global NCP estimate is broadly consistent with data on meso- and bathypelagic respiration, which suggest NCP ranging from 630 to 2,800 Tmol C a⁻¹ and having a mode of 1,500 Tmol C a⁻¹ (Table 1).

[25] The comparisons described above provide good reason to believe that a problem exists regarding in vitro measurements of NCP in low-productivity, rapidly recycling low latitude systems (i.e., the oligotrophic gyres). However, before discussing this issue further, it is worthwhile considering the implications of broad ocean regions of net heterotrophy. For example, our global PvR relationship yielded NCP deficits for 52% of the global ocean surface area (Table 2, second and third rows) result in 77% of the open ocean being net heterotrophic (not shown).

4.1. Implications of Large-Scale, Persistent Net Heterotrophy in Oligotrophic Gyres

[26] The oceans have a very low carrying capacity for particulate and dissolved organic carbon (POC and DOC) that, without supplementation, cannot support extended periods of net heterotrophy over broad scales. If the NCP deficits implied in Figures 3b and 3c were real, then these deficits must be fueled by imported organic material, transferred either in time or space. If we take 50 mmol C m⁻² d⁻¹ as the average carbon deficit for the surface ocean (median
A. HOT

Field Observations

Model Results

B. BATS

C. Station P

Figure 5. Field and model estimates of NCP at HOT, BATS, and Station P. (a) Average in situ, in vitro, and modeled NCP rates at the HOT site. Model NCP and particulate export are shown for each month. All rates are in mmol C m$^{-2}$ d$^{-1}$. (b) As in Figure 5a, but for the BATS site. In situ and in vitro data not shown. (c) As above, but for Station P in the subarctic Northeast Pacific.
value from the studies of Duarte et al. [2001], Gist et al. [2009], González et al. [2001], Robinson et al. [2002], Serret et al. [2001], Williams et al. [2004], and Aranguren-Gassis et al. [2011] and assume a mean mixed layer depth of 50 m (neither value is critical), the required replenishment rate for organic material is 1 mmol C m$^{-3}$ d$^{-1}$ ($\sim$350 mmol C m$^{-3}$ a$^{-1}$). Using these values and some simple assumptions, scaling analyses can be conducted to assess possible routes for the necessary organic subsidy.

[27] Transfer of organic material in time has been put forward as an explanation for observed net heterotrophy. In this scenario, oligotrophic systems are viewed as alternating between heterotrophic and autotrophic periods, or exhibiting infrequent bursts of intense autotrophy. This on-and-off switching of net autotrophy is a familiar feature of temperate regions with seasonality [Blight et al., 1995; Serret et al., 1999]. However, the subtropical oligotrophic oceanic lacks strong seasonal forcing to drive changes in nutrient stress. Despite the suggestion of Serret et al. [2006] that net heterotrophy is not always associated with nutrient stress, Gist et al. [2009] make a convincing case for changes in the balance between photosynthesis and respiration being associated with shifts in nutrient stress. They propose that such shifts arise from changes in the relative depths of the mixed layer and nitracline in the South Atlantic subtropical gyre, but a similar relationship is not observed at the HOT site in the Pacific [Williams et al., 2004]. However, temporary spikes in oxygen concentration are seen in the upper water column at HOT, lending support to the notion of intermittent bursts of net autotrophy [Karl et al., 2003]. This concept of intermittency is hard to sustain as a basis for the protracted column at HOT, lending support to the notion of intermittent spikes in oxygen concentration are seen in the upper water column, and the DOC concentration at that point $\sim$1,000 mmol m$^{-3}$ above that at the center of the gyre (see auxiliary material). Horizontal gradients and concentrations of DOC or POC of this magnitude are never approached in the oceans, and the gradients that do exist tend to have the reverse sense. That is, the DOC concentration tends to decrease as one moves from the center of oligotrophic gyres outward [Abell et al., 2000; Hansell et al., 2009].

[28] Gist et al. [2009] estimated that to sustain the inferred net heterotrophic period of the Atlantic Subtropical Gyres, $\sim$7.5 mol C m$^{-2}$ would need to be transferred from the autotrophic to heterotrophic phase. A similar value can be estimated from observations of Serret et al. [1999]. In neither case was the mechanism of transport discussed in detail, but if we assume the storage to be distributed through a water column of 100 m, then there would need to be an elevation of DOC + POC of 75 mmol C m$^{-3}$ as one enters the net heterotrophic period. Even though Gist et al. [2009] demonstrate sufficient excess production during periods of net autotrophy in some places, it is hard to see how the required quantities of organic material can be transferred over time as we simply do not observe elevations in the abiotic organic pool on this scale. Carlson et al. [1994] found seasonal fluctuations in DOC inventory at the BATS site to be $<10$ mmol C m$^{-3}$ in the upper water column and $<1$ mol C m$^{-2}$ when integrated over the upper 250 m.

[29] Input of new organic material to the gyres can occur from i) the sides (eddy diffusion), ii) below (by upward mixing of deep water DOM), or iii) above (aeolian deposition and diffusion from the atmosphere). We discuss each of these pathways in turn.

[30] Lateral transport has been suggested as a plausible mechanism by some investigators [Duarte et al., 1999, 2001; Serret et al., 2002], but the most detailed analysis was given by Hansell et al. [2004]. In that work, the authors analyzed the specific case of the North Atlantic subtropical gyre, where reported NCP deficits are 8–38 mol C m$^{-2}$ a$^{-1}$ [Duarte et al., 2001; González et al., 2001; Robinson et al., 2002; Serret et al., 2001]. Hansell et al. [2004] found that the combined import of allochthonous organic material is an order of magnitude or more lower (0.7 mol C m$^{-2}$ a$^{-1}$) than the required rate and that the region was in approximate metabolic balance.

[31] A more general argument can be made regarding lateral transport by calculating the concentration gradient required to make up the above estimated 1 mmol C m$^{-3}$ d$^{-1}$ deficit. If we consider diffusion through the circumference of a disk, then given a parameterization of horizontal diffusivity and the previously stated net consumption rate, the concentration gradient and concentrations at points along the radius can be calculated. Okubo’s [Okubo, 1971] analysis of horizontal diffusivity provides a length-scaled diffusion coefficient of $4.7 \times 10^{-5}$ r$^{4/3}$ m$^2$ s$^{-1}$, where $r$ is the radius of the patch (the gyre in this case) in meters. At 500 km from the center of the disk, the concentration gradient required to drive the inward diffusion would be $\sim$1 mmol m$^{-3}$ km$^{-1}$ and the DOC concentration at that point $\sim$1,000 mmol m$^{-3}$ above that at the center of the gyre (see auxiliary material). Horizontal gradients and concentrations of DOC or POC of this magnitude are never approached in the oceans, and the gradients that do exist tend to have the reverse sense. That is, the DOC concentration tends to decrease as one moves from the center of oligotrophic gyres outward [Abell et al., 2000; Hansell et al., 2009].

[32] Vertical gradients of bulk DOC and POC also have the opposite sense to that required for net import of organic material. However, there is evidence that a component of upwelling DOC is assimilated by bacteria in the epipelagic zone [Cherrier et al., 1999]. If we assume mean concentrations and radiocarbon-based ages of 35 mmol C m$^{-3}$ and 6,000 years for upwelling DOC and 65 mmol C m$^{-3}$ and 2,200 years for downwelling DOC, we derive a figure of 10 mmol C m$^{-3}$ for the quantity of upwelled deep-water DOC potentially available to the epipelagic population (auxiliary material). The above-estimated demand of 40 mmol C m$^{-2}$ d$^{-1}$ ($\sim$15,000 mmol m$^{-2}$ a$^{-1}$) would require an upwelling rate of $\sim$4 m per day (1,500 m a$^{-1}$). Estimates of global oceanic upwelling rates are only a small fraction of this value [Munk, 1966].

[33] Atmospheric input of organic carbon has also been proposed as a mechanism for meeting the NCP deficit [Dachs et al., 2005]. Organic material is supplied to the oceans from the atmosphere by three main mechanisms: dry deposition, wet deposition, and exchange diffusion. The first two processes are reasonably well constrained [Jurado et al., 2008], but their globally averaged rates ($\sim$0.1 mmol C m$^{-2}$ d$^{-1}$) are well below those required to make up the implied organic deficit in the oligotrophic oceans. By comparison, the diffusive input of organic material from the atmosphere has been measured to be many times greater, with rates of 20–30 mmol m$^{-2}$ d$^{-1}$ [Dachs et al., 2005; Jurado et al., 2008; Ruiz-Halpern et al., 2010] and approaching the 40 mmol m$^{-2}$ d$^{-1}$ deficit calculated above. However, it is seems unlikely that these rates are widespread and persistent enough to meet the organic demand at the global scale. Further, these high diffusive rates
reported in the literature come from unique physical settings
(e.g., coastal fjord) not representative of the global ocean.
In their extensive review of atmospheric fluxes to the global
ocean, Kanakidou et al. [2012] report values of less than 0.6 gC
m$^{-2}$ annum$^{-1}$ ($\sim$ 0.15 mmol C m$^{-2}$ d$^{-1}$) for soluble carbon
deposition in the oligotrophic gyres, far below the 50 mmol C
m$^{-2}$ d$^{-1}$ estimated above to meet the requirements of the
purported net heterotrophy. Two additional lines of evidence
further support the inability of atmospheric deposition to
support the purported heterotrophic deficit. First, it has been
noted that the $\delta^{13}$C of mixed layer dissolved inorganic carbon
(DIC) in the subtropical gyres requires net autotrophy and is
not consistent with import of external biologically produced
organic material [Williams et al., 2012]. Second, subtropical
oligotrophic gyres are characterized by seasonal decreases in
DIC [e.g., Michaels et al., 1994], whereas an external subsidy
would necessitate seasonal increases in DIC. Therefore, we are
ultimately unable to identify any mechanisms that might support
an organic subsidy to the central oligotrophic gyres.

[34] As discussed in section 1, the concept of persistent,
large-scale net heterotrophy is quantitatively difficult to
reconcile with our current understanding of ocean carbon
cycling. In the present analysis, we show that global
assessment of NCP based on field observations, outside the
problematic oligotrophic gyres, gives rise to distributions and
total annual budgets consistent with independent esti-
mates based on modeled carbon export and deep-water res-
spiration rates. We also note that in situ techniques for
assessing NCP, that do not require bottle incubations con-
sistently, indicate net autotrophy in the central ocean gyres.
Finally, we have evaluated potential sources for carbon
subsidies that could support broad regions of net heterotro-
phy and have failed to identify any candidate mechanisms.
Taken together, it therefore seems that the most likely
explanation for the ‘net heterotrophy paradox’ is that a
methodological error or bias exists in in vitro measurements
that is only detected in oligotrophic systems. Four immediate
questions follow from this conclusion. (1) Does the bias/
error arise from an underestimation of photosynthesis,
overestimation of respiration, or both? (2) What is the pri-
mary driver giving rise to the bias/error? (3) What is the
underlying physiological mechanism? (4) What are the
general consequences of this issue with respect to other rate
measurement techniques?

4.2. Bias in In Vitro Measurements Likely Underlies
Apparent Net Heterotrophy

[35] The ocean biogeochemical community has been
inclined to attribute the issue of a net heterotrophic bias in
the in vitro measurement to an artifactual enhancement of
respiration, rather than inhibition of photosynthesis [Morán
et al., 2007]. In some respects, this is counter-intuitive and
it can be argued that inhibition of photosynthesis is more
likely. Stimulation of respiration would require growth of
the heterotrophs or an increase in their substrate concentra-
tion. The growth rate of these organisms in the ocean is low
($<0.2$ d$^{-1}$ [Ducklow, 2000]) and it is questionable whether
they could increase their biomass sufficiently within the
timescale of incubation. Similarly, no mechanism has been
identified that could sustain increased substrate concentra-
tion. Substrates may be adsorbed onto surfaces (the walls of
containers), but the gradient required for diffusion to sustain
transport toward the adsorbing surface requires that con-
centrations near the surface be lower than in the bulk envi-
rnonment. Further, the timescales of incubation are too short
for extensive adsorption (see below). One potential pertur-
bation that could impact respiration is exclusion of large and
rare zooplankton that feed on microheterotrophs. Under-
representation of these larger predators could conceivably
enhance micrograzer respiration during an incubation by
decreasing their mortality. We are unable to quantify this so
it must be left open.

[36] On the other hand, suppression of photosynthesis
can be rapid or even instantaneous. Quay et al. [2010]
measured photosynthesis at the HOT site using both in
situ ($^{15}$O$_2$) and in vitro ($^{18}$O$_2$ tracer) methodologies and
reported that in situ rates exceeded in vitro rates by 25–
60% (Figure 6). Applying this error alone to in vitro
determined photosynthetic rates is sufficient to transform
the negative NCP values reported by Williams et al. [2004]
for HOT, into net autotrophic rates comparable to the in
situ data of Quay et al. [2010]. By comparison, if we take
Quay et al.’s value of 14 ± 4 mmol O$_2$ m$^{-2}$ d$^{-1}$ as an
average in situ argon/oxygen-determined NCP rate and their
mean $^{15}$O$_2$ in situ-determined gross photosynthetic rate of
103 mmol O$_2$ m$^{-2}$ d$^{-1}$, we obtain a mean in situ-determined
respiration rate of 89 mmol O$_2$ m$^{-2}$ d$^{-1}$ (Figure 6). Williams
et al. [2004] reported a mean in vitro dark bottle respiration
rate over a 13 month period of 86 mmol O$_2$ m$^{-2}$ d$^{-1}$ for the
same location. This consistency between independent mea-
surements strongly suggests that the bias/error associated
with in vitro measurements does not reside in the assessment of
respiration rates.

[37] Given the aforementioned consideration, it again
appears most likely that the problem with the in vitro tech-
nique lies in the accurate representation of photosynthesis.
This conclusion should not, in fact, be especially surprising.
The respiration rate measured in a ‘dark bottle’ during an in
vitro incubation is fueled by production that occurred in situ
(i.e., under natural conditions), and predominantly by produc-
tion that occurred in the very recent past for tightly coupled
ecosystems such as those of oligotrophic gyres. In contrast,
the photosynthetic rate derived from the ‘light bottle’ treatment
reflects production occurring on the day of the incubation in a
static environment very much different from in situ conditions.
It seems reasonable to think that some aspect of this artificial
environment is the root cause for suppression in photosynthesis,
but at this point we have yet to definitively identify precisely the
mechanism(s) involved. Nevertheless, a number of candidate
issues can be evaluated.

[38] One of the key issues for understanding the problem
of the in vitro technique is identifying whether the error/bias
is unique to measurements made in oligotrophic systems or
is a common problem to all areas that is simply over-
whelmed by much higher rates of net autotrophy in other
systems. While we cannot rule out this latter possibility, it
would mean that in vitro measurements of NCP are under-
estimated everywhere. Accordingly, a global correction to
in vitro-based NCP estimates would drive values at mid- and
high-latitudes well above the constraints imposed by the in
situ data and model estimates of carbon export, suggesting
that perhaps the problem is limited to oligotrophic waters.
We have no definitive proof of this, but this conclusion helps
narrow the range of possible explanations. For example,
fixed-depth incubation of samples collected from an active mixing layer creates an unnatural daily light regime that could significantly impact light-bottle photosynthesis (either through enhancing photoinhibition or causing light limitation, depending on incubation depth). However, it is not clear why such effects would be limited to in vitro measurements in oligotrophic systems. Similarly, high surface temperatures at low latitudes could impact both photosynthesis and bacterial respiration [Rivkin and Legendre, 2001], but we do not observe the apparent net heterotrophy in equatorial waters adjacent to the oligotrophic gyres. One interesting observation by Teira et al., 2001] was that net heterotrophy could be correlated to phytoplankton size and DOC release, but this observation provides no insight on why in vitro incubations yield a deficit while in situ measurements do not.

4.3. The Cause and Mechanism of False Heterotrophy

[39] It may be useful, in exploring the basis of false heterotrophy, to separate the ultimate cause and the immediate mechanism of the bias. If the biases seen in the in vitro measurements of NCP are restricted to the oligotrophic zones, then this should give insight to the primary cause as it would need to be a unique feature of these areas. Conversely, the mechanism that gives rise to the bias, i.e., the process it invokes can be general – such as some general feature of the in vitro procedure.

[40] A distinguishing feature of the gyres is that photosynthesis is largely supported by rapidly recycling nutrients. González et al., 2002] and Gist et al., 2009 both noted a relationship between measured net autotrophy and separation of the mixed layer and nitricline: the greater the separation between these horizons, the more negative NCP became. In a tightly coupled recycling system, ammonia turnover times are typically less than a day (i.e., notably shorter than typical incubation times). Data of Alwyn and Rees, 2007] for 6 h 15NH3 tracer incubations suggest an ammonia turnover time of 8.5 ± 10 h. Much shorter turnover times have also been observed (3.7 ± 3.1 h (D. Bronk, unpublished data, 2011)). True turnover rates may be even lower than those observed, as the incubation time is prone to control the calculated value. With such rapid recycling, there is clearly a potential for in vitro incubations impacting photosynthesis through disruption of the tight coupling between ammonia generation and utilization.

[41] If a perturbed nutrient environment is indeed the primary cause of the apparent net heterotrophy problem, then the specific mechanism(s) involved must be systemic in the in vitro approach, rather than due to sample collection and processing. In general, three things result when a sample is incubated in a bottle: 1) turbulence is quickly and almost completely extinguished, 2) a new surface is presented (the incubation bottle wall), and 3) the sample is isolated from the adjacent environment. Past discussion of so-called “bottle effects” has focused on the second of the three phenomena, although in many respects it is the least likely to give rise to adverse effects. In the following subsections we explore these three issues in greater detail.

[42] Extinguished turbulence: Once a sample is placed in a container with rigid walls, turbulent diffusion is extinguished within seconds. On the scale of a typical 125 cm3 incubation bottle in a well-mixed water column, the turbulent diffusion coefficient will have values of the order 10-6 to 10-7 m2 s-1 (derived from the analysis of Okubo, 1971]). These values can be compared to molecular diffusion coefficients for nutrients, which are of the order 10-9 m2 s-1 [Blackburn and Fenchel, 1999]. The loss of turbulence means that mixing rates within the bottle as a whole fall by ~100-fold or more (from a few minutes to hours to several days). The reduction in mixing means that, on scales >10 mm, homogenization will be incomplete, opening up the possibility for an uneven distribution of nutrients within the incubation bottle. One might envision zones of enhanced and depleted nutrient concentrations around point sources of production and consumption. Given NH3 cycling times of 3 h (see above), material produced (or consumed) by point sources greater than 3 mm apart will not be uniformly mixed between them. Heterotrophic
protists are major sources of recycled nitrogen and occur at 0.25 to 1 \times 10^6 \text{ cells m}^{-3} \ [\text{Beers et al., 1975; Jackson, 1980}] giving them a mean spacing of 10–15 mm. However, they are motile and the separation distance between the nutrient tails they leave behind is critical. Taking the above abundances and assuming swimming speeds of 0.2 to 1 mm s\(^{-1}\) \ [\text{Strom and Morello, 1998; Wang et al., 2008}], we obtain spatial separations between nutrient trails of 0.1 to 0.4 mm \ [\text{Jackson, 1980}] calculated similar separation distances), which would be mixed within a few minutes or less. Even in the case of the mesozooplankton, the separation distance of nutrient trails (3 mm) estimated by \text{Jackson, 1980} is within the diffusion time for a 3 h cycling time. Thus, on the size and time scales of \textit{in vitro} \text{O}_2 incubations and the environments we are considering, turbulence is not needed to maintain the regenerated nutrient supply to photosynthetic organisms. From purely theoretical studies \text{Munk and Riley, 1952} and \text{Lazier and Mann, 1989} came to a similar conclusion, that turbulence is not necessary to prevent the formation of microzones.

[43] \textit{A new surface}: Once turbulence is extinguished, the main non-biological motion is molecular diffusion. If we take 1 cm as half the distance between the center of the incubation bottle and its wall and assume a diffusion coefficient of \(10^{-9}\) and \(10^{-10}\) m\(^2\) s\(^{-1}\) for nutrients and DOM, respectively \ [\text{Blackburn and Fenchel, 1999}], then a characteristic timescale for diffusion may be calculated as L\(^2\) D\(^{-1}\) (where L is the length scale and D the molecular diffusion coefficient \ [\text{Lazier and Mann, 1989}]). This gives timescales of \(10^2\) to \(10^6\) seconds (i.e., \(>24\) h to several days), which is comparable to or much longer than an incubation. Thus, within the timescale of the incubation, the wall is a distant object and processes generated by the wall itself (adsorption or release of organic and inorganic nutrients, or toxic metals, etc.) will have insufficient time to significantly impact the bulk sample. Further the growth rate \((0.2\ \text{ day}^{-1}\ \text{[Ducklow, 2000]})\) of open ocean bacteria noted earlier is too low to give much effect over the period of incubation.

[44] Container walls have also been argued to be a site facilitating bacterial growth. However, the organisms must migrate to the surface before they can establish themselves and grow. Although bacteria swim quite rapidly (up to 100 \(\mu\)m s\(^{-1}\)), their progress is primarily random. Calculations \ [\text{Blackburn et al., 1997}] and observations \ [\text{Kiorboe et al., 2003}] suggest that net diffusion rates for motile bacteria are in the range of \(10^{-9}\) to \(10^{-10}\) m\(^2\) s\(^{-1}\), which is less than the molecular diffusion coefficient and far too slow to enable extensive colonization of the internal surface during a 24 h incubation. This conclusion is consistent with the observations of \text{Garcia-Martin et al., 2011} who found no evidence for a wall effects in 24 h \textit{in vitro} measurements of oxygen consumption rates.

[45] \textit{Isolation}: Enclosing a seawater sample in a bottle isolates it from external exchange and essentially excludes organisms that occur at low abundances. In oligotrophic areas, nitrate is continually or intermittently \ [\text{Johnson et al., 2010}] supplied within the mixed layer by turbulent diffusion from below the nitricline. Isolation of the sample will surely disrupt this process, but evaluating its effect requires careful consideration. First, while enclosing seawater in an incubation bottle reduces input of new nitrate, it also prevents any export of newly fixed organic matter. Assuming a steady state (relative to the timescale of incubation), this trapped material then becomes substrate for production during the incubation in proportion to the loss of nitrate due to enclosure. This thinking further assumes that the organic matter is fully labile and recycled near-instantaneously. However, even if this assumption is violated and the nitrogen contained in the export fraction is not recycled over the timescale of the incubation, then the consumers trapped in the bottle will be excreting ammonium from the production consumed 24 h earlier. Thus, it does not seem that cutting off supply of nitrate in a 24 h incubation will have a great effect.

[46] As noted earlier, another consequence of isolation is the exclusion of rare particles (e.g., large zooplankton). In the oligotrophic ocean, mesozooplankton (e.g., copepods) occur at abundances of 100 animals m\(^{-3}\) or less \ [\text{Beers et al., 1975; Jackson, 1980}]. Isolation of the sample will surely. This thinking further assumes that the organic matter is

4.4. Consequences of Our Interpretation for In Vitro Field Measurements in General?

[48] Our analysis leads us to the view that the negative NCP rates predicted for, and observed in, oligotrophic waters result primarily from partial inhibition of photosynthesis.
Although these effects have been demonstrated using oxygen flux measurements, the photosynthetic metabolisms of carbon and oxygen are tightly coupled over the period of \textit{in vitro} incubations, so the inhibition should also apply to \textit{in vitro} carbon-based measurements of photosynthesis (e.g., $^{14}$C) in oligotrophic regions. Quay \textit{et al.} [2010] found that the scale of inhibition during \textit{in vitro} incubations is of order 10% to 40%. P. Quay (personal communication, 2012) quantifies the underestimate in \textit{in vitro} observations for the $^{14}$C technique to be ~25%. We can derive an estimate of the inhibition from parameters in Table 4 (see auxiliary material, section S5), which yield somewhat higher errors of 40% to 60%. The difference may reflect, in major part, the different processes measured by the oxygen and $^{14}$C techniques in the light bottle.

[50] In conclusion, our analysis leads us to the view that \textit{in vitro} light bottle measurements of photosynthesis give systematically low values in oligotrophic areas. Outside these areas, we simply have no clear evidence that serious errors exist with the \textit{in vitro} technique. In addition, we have no evidence to suggest that \textit{in vitro} measurements of respiration give unreliable estimates of in situ rates either in oligotrophic areas or elsewhere. Williams and del Giorgio [2005] argued that, because of its time integrating properties, respiration was a better property than photosynthesis as a measure of carbon flux. The present study further suggests it may also be a more accurate measure.

5. Conclusions

[50] 1) Modeled NCP, based upon the Pvor relationship derived from \textit{in vitro} measurements taken from outside oligotrophic regions, predict NCP rates that are broadly consistent with geochemical constraints (particle export and in situ gas measurements).

[51] 2) Within oligotrophic waters, both \textit{in vitro} field observations and model NCP derived from them return rates that are significantly lower than both in situ gas-derived and other field measurements, as well as particle export rates. This finding suggests that \textit{in vitro} observations of NCP in oligotrophic areas are in error and we propose that this error stems from suppression of photosynthesis in \textit{in vitro} incubations, although the root cause of the problem is unresolved.

[52] 3) We find no grounds to conclude that stimulation of respiration contributes to the erroneous negative \textit{in vitro} NCP rates. Thus, unless evidence arises to the contrary, the present analysis gives no grounds to question the respiration rates given by \textit{in vitro} measurements in oligotrophic regions of the ocean or elsewhere.

[53] 4) NCP models using parameters derived from a global \textit{in vitro} data set, but with oligotrophic observations removed, give acceptable rates for the oligotrophic areas of the oceans.

[54] Acknowledgments. We wish to thank people who contributed to the compilation of field measurements (Susana Agustí, Javier Aristegui, Carlos Duarte, Dominique Lefèvre, Aurore Regaudie-de-Gioux, Pablo Serret, and Carol Robinson). Without their efforts, this work would not have been possible. Allen Milligan and Kim Halsey also contributed significantly with many helpful discussions throughout this work. We thank Paul Quay for drawing our attention to the significance of the DIC $^{13}$C observations and for other valuable input. Debbie Brock provided input on ammonia recycling times. John Dunne kindly provided guidance on the use of the export production model and also estimates of global dissolved export rates from his own calculations. We also thank Raymond Najjar for providing numerical data on surface ocean export production rates. This work supported by NASA grant NNX08AK70G. We are also indebted to two anonymous referees for insightful and constructive reviews.

References


