

# The Oligotrophic Ocean Is Autotrophic\*

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\*This review is part of a three-article series on the metabolic state of the oligotrophic subtropical gyres of the open ocean. For the introduction, see Ducklow & Doney (2013); for the case for net heterotrophy, see Duarte et al. (2013).

## Keywords

productivity, carbon balance, isotopic tracers, oxygen budgets, organic balance

## Abstract

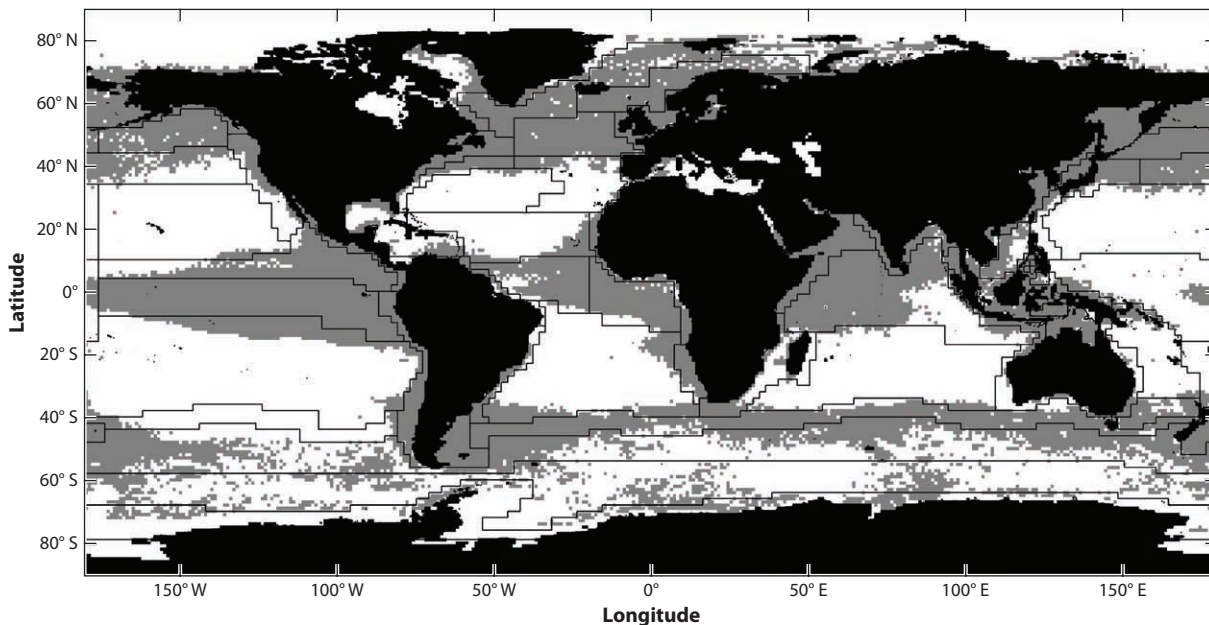
In vitro observations of net community production (NCP) imply that the oligotrophic subtropical gyres of the open ocean are net heterotrophic; in situ observations, in contrast, consistently imply that they are net autotrophic. At least one approach must be returning an incorrect answer. We find that (a) no bias in in situ oxygen-based production estimates would give false-positive (net autotrophy) rates, (b) observed <sup>13</sup>C enrichment of surface water dissolved inorganic carbon (DIC) can be explained only by positive NCP (net autotrophy), (c) lateral and vertical inputs of organic carbon are insufficient to sustain net heterotrophy, and (d) atmospheric input of organic material is too small to support in vitro rates of net heterotrophy and would yield  $\delta^{13}\text{C}$  depletion of surface DIC, quite the opposite of what is observed in the subtropical gyres. We conclude that the in vitro observations, implying net heterotrophy, must contain a bias that is due to an underestimate of photosynthetic rate and/or an overestimate of respiration rate.

## THE BASIS OF THE CONTROVERSY

Using *in vitro* estimates of bacterial respiration and algal photosynthesis, del Giorgio et al. (1997) suggested that respiration exceeds planktonic photosynthesis in areas of low production, causing these broad ocean regions to be net sources of CO<sub>2</sub>. Duarte & Agustí (1998) further proposed that 25 of the 56 biogeochemical provinces described by Longhurst (1998)—approximately 80% of the area of the global ocean—are net heterotrophic, based on an empirically determined relationship between photosynthesis and respiration and the global pattern of photosynthetic rates reported by Longhurst et al. (1995). **Figure 1** shows a characteristic map of the geographical distribution of net autotrophic and heterotrophic zones from an analysis made by Westberry et al. (2012) in which the heterotrophic regions amount to 57% of the ocean surface area.

Other workers (e.g., Geider 1997, Williams 1998) have been uncomfortable with the conclusion of sustained net autotrophy, and there is growing evidence (**Table 1**) from *in situ* studies that the upper mixed layers of oligotrophic areas are net sources, not sinks, of oxygen. Geider (1997) and Williams (1998) both suggested that methodological problems embedded in the earlier analyses were responsible for apparent net heterotrophy, but subsequent field measurements of *in vitro* oxygen flux in low-productivity areas continued to support del Giorgio et al.'s (1997) conclusions (see upper part of **Table 1**). *In situ* studies continue to suggest otherwise (lower part of **Table 1**).

The existence of substantial areas of net heterotrophy in the oceans would require an organic carbon (OC) source to fuel the associated respiration, yet the oceans generally have a very low OC



**Figure 1**

Calculated global distribution of net community production based on the production-versus-respiration relationship  $R = 0.93P^{0.78}$  (where  $R$  and  $P$  are, respectively, the respiration and photosynthetic rates in  $\text{mmol C m}^{-3} \text{ day}^{-1}$ ), derived from 1,057 pairs of observations taken, with additions, from a database compiled by Dr. Carol Robinson. All data where the rates were less than twice the standard error were omitted from the analysis. Calculation details are given in Westberry et al. (2012). The autotrophic zones are shown in gray; the heterotrophic zones are shown in white.

**Table 1** Reported rates of net community production (NCP) for oligotrophic subtropical gyres of the open ocean

Study	Method(s)	Location	Biogeochemical zone(s)	NCP ± SE (mmol O <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> )
<b>In vitro observations</b>				
Gist et al. 2009	In vitro O <sub>2</sub> flux	—	NAST-E (Sp)	-3
Serret et al. 2001	In vitro O <sub>2</sub> flux	—	NAST-E (Su)	-111 ± 17
Serret et al. 2002	In vitro O <sub>2</sub> flux	—	NAST-E (Au)	-33 ± 14
Gist et al. 2009	In vitro O <sub>2</sub> flux	—	NAST-E (Au)	-15
González et al. 2002	In vitro O <sub>2</sub> flux	—	NAST-E (Sp, Au)	-77 ± 162
Marañón et al. 2007	In vitro O <sub>2</sub> flux	—	NAST-E and NATR (Sp)	-26 ± 33
González et al. 2001	In vitro O <sub>2</sub> flux	—	NAST-E and NATR (Su)	-129 ± 18
Marañón et al. 2007	In vitro O <sub>2</sub> flux	—	NAST-E and NATR (Su)	-132 ± 28
Aranguren-Gassis et al. 2011	In vitro O <sub>2</sub> flux	—	NAST-E and NATR (Au) <sup>a</sup>	-19 ± 19
Aranguren-Gassis et al. 2011	In vitro O <sub>2</sub> flux	—	NAST-E and NATR (Au) <sup>b</sup>	58 ± 15
Marañón et al. 2007	In vitro O <sub>2</sub> flux	—	NAST-E and NATR (Au)	-44 ± 21
Duarte et al. 2001	In vitro O <sub>2</sub> flux	—	NAST-E and NATR (Sp, Au)	-38
González et al. 2002	In vitro O <sub>2</sub> flux	—	NATR (Sp)	11
González et al. 2002	In vitro O <sub>2</sub> flux	—	NATR (Au)	-102
González et al. 2002	In vitro O <sub>2</sub> flux	—	NATR and CNRY (Sp, Au)	15 ± 29
González et al. 2002	In vitro O <sub>2</sub> flux	—	ETRA (Sp, Au)	-119 ± 33
Serret et al. 2001	In vitro O <sub>2</sub> flux	—	ETRA (Sp)	-137 ± 18
Morán et al. 2004	In vitro O <sub>2</sub> flux	—	ETRA (Sp, Au)	-35 ± 27
Morán et al. 2004	In vitro O <sub>2</sub> flux	—	ETRA (Sp, Au)	-68 ± 16
González et al. 2002	In vitro O <sub>2</sub> flux	—	SATL (Sp)	69
Serret et al. 2002	In vitro O <sub>2</sub> flux	—	SATL (Sp)	20 ± 3
Gist et al. 2009	In vitro O <sub>2</sub> flux	—	SATL (Sp)	5
González et al. 2002	In vitro O <sub>2</sub> flux	—	SATL (Sp, Au)	-255 ± 167
Gist et al. 2009	In vitro O <sub>2</sub> flux	—	SATL (Au)	-14
Williams & Purdie 1991	In vitro O <sub>2</sub> flux	Station ALOHA	NPTG-E (Su, Au)	-0.9 ± 43
Williams et al. 2004	In vitro O <sub>2</sub> flux	Station ALOHA	NPTG-E (All)	-24 ± 5
<b>In situ observations</b>				
Emerson et al. 1997	Surface O <sub>2</sub> budgets	Station ALOHA	NPTG-E (All)	5.5 ± 2.7
Benitez-Nelson et al. 2001	<sup>234</sup> Th analysis	Station ALOHA	NPTG-E (All)	4.1 ± 2.2
Quay & Stutsman 2003	DIC and DIC δ <sup>13</sup>	Station ALOHA	NPTG-E (All)	7.4 ± 3.8
Hamme & Emerson 2006	Ar/O <sub>2</sub> ratios	Station ALOHA	NPTG-E (All)	3.0 ± 1.4
Emerson et al. 2008	O <sub>2</sub> from moorings	Station ALOHA	NPTG-E (All)	11 ± 5.2
Quay et al. 2010	<sup>17</sup> O <sub>2</sub> disequilibria	Station ALOHA	NPTG-E (All)	10 ± 2.7
Jenkins 1980	Tritium/ <sup>3</sup> He box model	Sargasso Sea	NAST-W	14
Musgrave 1990	Tritium/ <sup>3</sup> He box model	Sargasso Sea (32° N, 64° W)	NAST-W	6.8
Spitzer & Jenkins 1989	Upper-ocean O <sub>2</sub> balance	Sargasso Sea (32° N, 64° W)	NAST-W (All)	11 ± 3

(Continued)

**Table 1** (Continued)

Study	Method(s)	Location	Biogeochemical zone(s)	NCP ± SE (mmol O <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> )
Luz & Barkan 2009	Ar/O <sub>2</sub> ratios	Sargasso Sea (32° N, 64° W)	NAST-W (All)	4.4 ± 1.1

Abbreviations for biogeochemical zones [as given in Longhurst's (1998) classification]: CNRY, Canary Current Coastal; ETRA, Eastern Tropical Atlantic; NAST, North Atlantic Subtropical Gyre; NATR, North Atlantic Tropical Gyre; NPTG, North Pacific Tropical Gyre; SATL, South Atlantic Tropical Gyre. E and W refer to eastern and western regions of those zones, respectively. All refers to a full annual study; Sp, Su, and Au refer to spring, summer, and autumn sampling, respectively.

<sup>a</sup>Minimum value.

<sup>b</sup>Maximum value.

carrying capacity per unit volume. For example, if we take a figure of 50 mmol C m<sup>-2</sup> day<sup>-1</sup> as the average carbon deficit for the oligotrophic ocean (the median value from Aranguren-Gassis et al. 2011, Duarte et al. 2001, Gist et al. 2009, González et al. 2001, Robinson et al. 2002, Serret et al. 2001, and Williams et al. 2004) and assume a mean mixed-layer depth of 50 m (neither value is critical), then the required replenishment rate of organic material is ~1 mmol C m<sup>-3</sup> day<sup>-1</sup> (~350 mmol C m<sup>-3</sup> year<sup>-1</sup>). Applying this consumption rate to a representative value of 20 mmol C m<sup>-3</sup> for the labile/semilabile dissolved organic carbon (DOC) pool (Carlson et al. 2010, Ducklow et al. 1995) would exhaust this entire DOC stock within approximately a month. The other refractory component of the surface DOC pool is respired at a rate of only ~1 nmol C m<sup>-3</sup> day<sup>-1</sup> [calculated assuming a photochemically rendered labile component of 10 mmol C m<sup>-3</sup> (see Appendix A) and a residence time in the surface ocean of 30 years], which is negligible in the context of the metabolic balance debate.

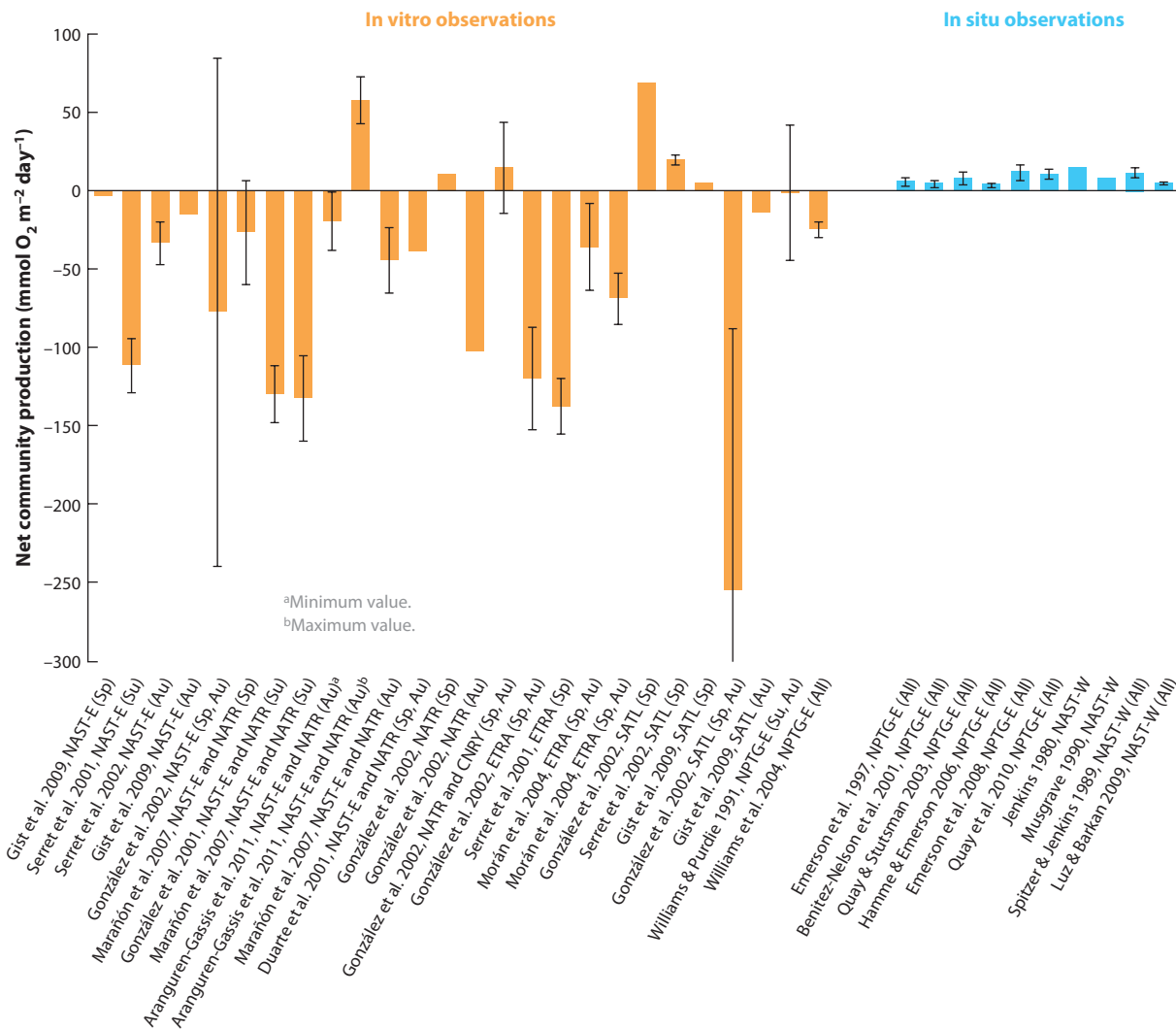
The preceding calculations clearly demonstrate that the apparent net heterotrophy suggested by in vitro measurements cannot be sustained for extended periods without external supplementation. This need for an organic subsidy was recognized by Duarte & Agustí (1998), who argued that excess production in net autotrophic zones is sufficient to meet the organic carbon (OC) deficit of oligotrophic regions; however, Williams & Bowers (1999) questioned whether physical mechanisms in the ocean could transport the required quantities of organic material. Nevertheless, if we accept the in vitro observations for the moment, then a number of questions arise:

- Is the difference between in vitro and in situ observations statistically significant and without biases from sampling strategies such that there is a problem to debate?
- Is there any evidence for biases in the in situ estimates of autotrophy in the subtropical gyres?
- Can we identify an OC supply to the subtropical gyres that makes up the OC deficit implied by net heterotrophy?

We address each of these questions below and find no evidence to refute the conclusion of in situ observations that the oligotrophic subtropical gyres are net autotrophic.

## IS THE DIFFERENCE BETWEEN THE IN VITRO AND IN SITU OBSERVATIONS STATISTICALLY SIGNIFICANT?

**Figure 2** shows published in vitro and in situ net community production (NCP) rates for the oligotrophic subtropical gyres in the Atlantic and Pacific [using biogeochemical zones in Longhurst's (1998) classification]. The disparity in NCP results for the two approaches is obvious, despite the relatively wide value range for the in vitro data.



**Figure 2**

Reported rates of net community production for oligotrophic subtropical gyres based on **Table 1**. Abbreviations for biogeochemical zones [as given in Longhurst's (1998) classification]: CNRY, Canary Current Coastal; ETRA, Eastern Tropical Atlantic; NAST, North Atlantic Subtropical Gyre; NATR, North Atlantic Tropical Gyre; NPTG, North Pacific Tropical Gyre; SATL, South Atlantic Tropical Gyre. E and W refer to eastern and western regions of those zones, respectively. All refers to a full annual study; Sp, Su, and Au refer to spring, summer, and autumn sampling, respectively.

We can investigate this difference more thoroughly using the extensive data sets available for Hawaii Ocean Time-Series (HOT) station ALOHA in the central North Pacific Subtropical Gyre. For this representative oligotrophic site, Williams et al. (2004) and subsequent workers calculated integrated NCP from in vitro observations and found that 26 of 28 integrated profiles yielded negative rates, whereas only 2 gave positive rates. In contrast, Quay et al. (2010) assembled a set of 20 in situ observations of mixed-layer net oxygen ( $\text{O}_2/\text{Ar}$ ) supersaturation and observed positive NCP on all occasions. If we use a conservative nonparametric signs test, then the probability of

all in vitro observations being negative by chance is  $0.5^{24}$ . Similarly, the probability of all in situ rates being positive by chance is  $0.5^{20}$ .

Thus, it may be concluded beyond reasonable doubt that the two approaches are systematically giving different NCP results for the same subtropical location. There is clearly a problem to debate. At least one of the measurement approaches must be returning a wrong answer, and we must look at the methodology for systematic errors.

## POSSIBLE BIASES IN THE IN SITU ESTIMATES OF AUTOTROPHY

Two very different lines of in situ study indicate net autotrophy at the HOT and Bermuda Atlantic Time-Series Study (BATS) sites: (a)  $O_2/Ar$ -derived estimates of oxygen flux in the upper mixed layer, and (b)  $^{13}C$  enrichment of the mixed-layer dissolved inorganic carbon (DIC) relative to the atmosphere. We review these approaches critically below.

### $O_2/Ar$ -Derived Estimates of Oxygen Flux

The in situ method that has often been used to estimate rates of NCP or OC export in the surface ocean is based on an  $O_2$  budget. As typically applied, this method includes two terms that represent net biological  $O_2$  production and net air-sea  $O_2$  gas exchange flux, and assumes steady-state conditions and negligible impacts from mixing. A net autotrophic condition exists if the surface layer is supersaturated in  $O_2$ ; conversely, a net heterotrophic condition exists if the surface layer is undersaturated in  $O_2$ . Possible biases in the in situ  $O_2$  budget method could result from (a) non-steady-state conditions, (b) insufficient sampling frequency, (c) the impact of warming/cooling, (d) incorrect assessment of the gas exchange coefficient, (e) bubble injection on  $O_2$  saturation, (f) input or loss of  $O_2$  by mixing, and/or (g) the shallower integration depth used in in situ studies compared with that of in vitro studies.

Emerson et al. (1997) modified the  $O_2$  budget approach by normalizing the  $O_2$  concentration to the Ar gas concentration ( $O_2/Ar$ ). This normalization has the advantage that the  $O_2/Ar$  saturation in the surface layer is effectively independent of warming/cooling and bubble injection because the solubility of Ar is very similar to that of  $O_2$ . Hamme & Emerson (2006) demonstrated this advantage by measuring several inert gases at the HOT site to constrain the impacts of bubble flux and warming effects on  $O_2$  saturation, concluding that “determining productivity from  $O_2/Ar$  ratios removes the need to quantify bubble processes” (p. 90). They also examined the impact of mixing at the base of the mixed layer on the  $O_2$  budget and concluded that any amount of vertical mixing below the mixed layer would cause an underestimation of NCP (by up to 70% for higher mixing rates) owing to loss of  $O_2$  from the mixed layer. The main source of error in NCP rates derived from the  $O_2/Ar$  method is uncertainty in the air-sea gas exchange rate ( $\pm \sim 30\%$ ) (Hamme & Emerson 2006), but this uncertainty affects only the magnitude of the derived rate and cannot change the sign of the  $O_2$  flux. In other words, this uncertainty does not compromise the method’s ability to unequivocally distinguish between net autotrophy and net heterotrophy, because this switch between system states changes the sign of the  $O_2$  flux (i.e., into or out of the surface layer). Thus, observation of  $O_2/Ar$  supersaturation using the in situ approach implies net autotrophic conditions.

The short residence time of dissolved  $O_2$  and Ar gases in the surface layer (1–2 weeks) suggests that steady-state conditions should be reached on a timescale shorter than the monthly sampling interval at the HOT site. Thus, the  $O_2/Ar$  saturation state measured every month at this site reflects primarily the strength of the  $O_2/Ar$  sources and sinks over the previous few weeks and is minimally affected by saturation-state conditions observed during the previous month. Emerson

et al.'s (2008) analysis of continuous mooring-based measurements of surface O<sub>2</sub> and N<sub>2</sub> gases at the HOT site clearly indicates that the magnitude of the rate-of-change term is minor (~10%) relative to the NCP term in the surface O<sub>2</sub> budget. Furthermore, Emerson et al.'s (2008) mooring-based O<sub>2</sub> and N<sub>2</sub> observations at the HOT site yielded a positive NCP over the annual cycle (for 2005) that was only slightly higher than previous NCP estimates based on monthly snapshots of O<sub>2</sub>/Ar saturation state at the HOT site.

Although interannual variability is a potential source of biases for any in situ measurements, O<sub>2</sub>/Ar (or O<sub>2</sub>/N<sub>2</sub>) data covering an annual cycle at the HOT site have been collected in four different years, and in all cases these data yield positive NCP rates of 4–11 mmol m<sup>-2</sup> day<sup>-1</sup> and autotrophic conditions (Emerson et al. 1997, 2008; Hamme & Emerson 2006; Quay et al. 2010). It is unlikely that such consistent results do not represent the climatological mean trophic condition in the subtropical North Pacific.

The in situ studies characteristically integrate over the mixed layer, whereas the in vitro studies tend to integrate over the photic depth; thus, if the zone below the base of the mixed layer were strongly heterotrophic, it might be argued that this is the basis for the difference between the findings of in vitro and in situ studies. However, the annual O<sub>2</sub> cycle measured using Argo float data from both the subtropical North and South Pacific indicates net autotrophy below the mixed layer to the base of the photic layer at ~150 m (Riser & Johnson 2008). In this study, the authors found a net autotrophy of ~1.9 and ~1.1 mmol C m<sup>-2</sup> day<sup>-1</sup> over the annual cycle in the depth region between the base of the mixed layer and the photic layer in the subtropical North and South Pacific, respectively. Thus, the shallower integration depth used in the in situ studies may, if anything, underestimate the local autotrophy. Hamme & Emerson (2006) had also reached this conclusion (see above).

### **<sup>13</sup>C Enrichment of the Mixed-Layer DIC**

A second in situ method that indicates a net autotrophic state in the subtropical surface oceans and corroborates the O<sub>2</sub>/Ar observations derives from the <sup>13</sup>C/<sup>12</sup>C of DIC (i.e., δ<sup>13</sup>C-DIC). The DIC pool of the mixed layer in the subtropical gyres has δ<sup>13</sup>C-DIC values generally around 1.5‰; for instance, surface δ<sup>13</sup>C-DIC at the HOT site ranges from 1.2‰ to 1.5‰ (Quay & Stutsman 2003, figures 1 and 3a; Quay et al. 2003). In contrast, equilibrium of the DIC pool with the atmosphere would give a substantially lower value for δ<sup>13</sup>C-DIC of around 0‰ (Quay & Stutsman 2003, figure 1).

The ~1.5‰ difference between the atmospheric equilibrium and observed δ<sup>13</sup>C-DIC in the subtropical gyres is highly significant (the error of the δ<sup>13</sup>C measurement is 0.027‰; Quay & Stutsman 2003). The observed positive <sup>13</sup>C anomaly is the result of a process that enriches the mixed-layer δ<sup>13</sup>C-DIC. Calcium carbonate production and export can be eliminated as a process that enriches the δ<sup>13</sup>C-DIC, as the calcium carbonate δ<sup>13</sup>C is similar (within 1‰) to that of the DIC (Emrich et al. 1970) and thus has little effect on the mixed-layer δ<sup>13</sup>C-DIC. Vertical mixing would decrease the surface-layer δ<sup>13</sup>C-DIC by bringing up <sup>13</sup>C-depleted DIC from below. The only process that can yield the positive difference between measured δ<sup>13</sup>C-DIC and the value set by equilibrium with the atmosphere is the net production of photosynthetic organic material. Photosynthetically produced marine organic material is depleted in <sup>13</sup>C, with a δ<sup>13</sup>C of approximately -21‰ (Fry et al. 1998, Goericke & Fry 1994), and thus the net production of organic material in the mixed layer leaves behind a DIC pool enriched in <sup>13</sup>C. Therefore, the δ<sup>13</sup>C enrichment of DIC relative to the atmospheric equilibrium in subtropical surface waters is a clear signature of net autotrophy within the mixed layer. A number of studies have used this δ<sup>13</sup>C-DIC enrichment to estimate NCP rates in the subtropical gyres. For example,

Gruber et al. (1998) derived an NCP rate of  $6.3 \pm 2.5 \text{ mmol C m}^{-2} \text{ day}^{-1}$  at the BATS site, and Emerson et al. (1997), Keeling et al. (2004), and Quay & Stutsman (2003) derived NCP rates of 4–7  $\text{mmol C m}^{-2} \text{ day}^{-1}$  at the HOT site.

The observed  $\delta^{13}\text{C}$ -DIC values in subtropical surface waters are higher than that expected in equilibrium with atmospheric  $\text{CO}_2$ , which demands that the subtropical gyres are net autotrophic and exporters of  $^{13}\text{C}$ -depleted organic material. Furthermore, this conclusion cannot be avoided by assuming that these oligotrophic gyres are instead net heterotrophic and sustained by imported photosynthetically produced organic material. OC imported from a distant source, whether marine or terrestrial, will be depleted in  $^{13}\text{C}$  (see further discussion below). Thus, if the purported net heterotrophy of  $\sim 50 \text{ mmol C m}^{-2} \text{ day}^{-1}$  (i.e., the median value calculated above) is supported by distant OC sources, then the respiration of this  $^{13}\text{C}$ -depleted organic material would reduce the  $\delta^{13}\text{C}$  of the mixed layer and require even greater local net autotrophy to account for the observed enriched  $\delta^{13}\text{C}$ -DIC. The in situ  $\delta^{13}\text{C}$  measurements in the mixed layer of the subtropical gyres are therefore wholly inconsistent with net heterotrophy.

### **CAN SUFFICIENT EXTERNAL ORGANIC MATERIAL BE SUPPLIED TO SUSTAIN THE PURPORTED NET HETEROTROPHY?**

The  $\text{O}_2/\text{Ar}$  and  $\delta^{13}\text{C}$  in situ methods discussed above both consistently indicate autotrophic conditions at the HOT site and, more generally, in the subtropical gyres. There is no evidence that any bias exists in these methods that is sufficient to alter this conclusion (e.g., bubble injection, gas exchange rate uncertainty, mixing, rate of change, interannual variability, sampling frequency, depth of integration, etc.). However, we can also investigate the issue by evaluating whether a sufficient source of OC can be identified that would satisfy the level of net heterotrophy implied by in vitro measurements.

#### **A Local Supply of Organic Material**

Transfer of organic material over time has been put forward as an explanation to support observed net heterotrophy. In this scenario, oligotrophic systems alternate between heterotrophic and autotrophic periods and exhibit infrequent bursts of intense autotrophy. Although seasonal on-and-off switching of net autotrophy is a familiar feature of temperate regions (Blight et al. 1995, Serret et al. 1999), its importance in subtropical regions is unclear.

Gist et al. (2009) estimated that  $\sim 7.5 \text{ mol C m}^{-2}$  would need to be transferred from the autotrophic phase to the heterotrophic phase to sustain the inferred net heterotrophic period of the Atlantic subtropical gyres. A similar value can be estimated from observations of Serret et al. (2009). In neither case was the vehicle or mechanism for transport in time discussed in detail, but if we assume the storage to be distributed through a 100-m-deep water column, then an elevation of DOC plus particulate organic carbon (POC) of  $75 \text{ mmol C m}^{-3}$  would be needed at the onset of the heterotrophic period. Carlson et al. (1994) found seasonal fluctuations in DOC inventory at the BATS site to be  $< 10 \text{ mmol C m}^{-3}$  in the upper water column (0–100 m) and  $< 1 \text{ mol C m}^{-2}$  when integrated over the upper 250 m. Thus, DOC inventory changes can, at most, supply  $< 15\%$  of the necessary OC supplement, with the actual contribution likely being significantly less because dissolved organic matter (DOM) is exported to deeper water (Carlson et al. 1994). Thus, although excess organic material from pulses of net autotrophy can potentially be transferred over time, there is no evidence that this flux occurs on a scale sufficient to support the extended periods of significant net heterotrophy indicated by the in vitro negative NCP estimates reported for the oligotrophic subtropical gyres.



## An External Supply of Organic Material

Inputs of external organic material into the oligotrophic gyres can occur from the sides (eddy diffusion, advection), from below (turbulent mixing), and from above (atmospheric contributions). Here, we evaluate the potential magnitude of these pathways for organic material subsidy.

**Lateral and vertical supplies of organic material.** Lateral transport has been suggested as an important mechanism supplying OC to oligotrophic regions (Duarte et al. 1999, 2001; Serret et al. 2002). A detailed analysis by Hansell et al. (2004), however, has cast doubt on the significance of this flux. In that study, the authors investigated the specific case of the North Atlantic Subtropical Gyre, where the reported NCP deficits are 8–38 mol C m<sup>-2</sup> year<sup>-1</sup> (Duarte et al. 2001, González et al. 2001, Robinson et al. 2002, Serret et al. 2001). They found that the combined import of allochthonous organic material (0.7 mol C m<sup>-2</sup> year<sup>-1</sup>) is at least an order of magnitude too small to support the alleged net heterotrophy, and concluded that the region is instead in approximate metabolic balance.

A more general argument can be made regarding lateral transport by calculating the OC concentration gradient required to support the 1.0 mmol C m<sup>-3</sup> day<sup>-1</sup> deficit estimated above. If we consider diffusion through the circumference of a disk as representing a gyre, then the concentration gradient and concentrations at points along the radius can be calculated, given a parameterization of horizontal diffusivity and the previously stated net consumption rate (see Appendix A). At 500 km from the center of the disk, the concentration gradient required to drive the inward diffusion would be ~1 mmol m<sup>-3</sup> km<sup>-1</sup>, and the DOC concentration at that point would need to be ~1,000 mmol m<sup>-3</sup> above that at the center of the gyre (see Appendix A). Horizontal gradients and concentrations of DOC or POC of this magnitude are not observed in the oceans. In fact, the DOC concentration tends to decrease as one moves outward from the center of oligotrophic gyres (Abell et al. 2000, Hansell et al. 2009), which is precisely the opposite gradient needed to support net heterotrophy.

Similarly, DOC and POC concentrations decrease with depth in the subtropical gyres, which is opposite the expected gradient for a significant deepwater supplement of organic material to the surface layer. Indeed, these vertical gradients are instead indicative of surface carbon export. Macronutrient concentrations, in contrast, increase with depth. Consequently, vertical exchange during episodic or seasonal mixed-layer deepening will tend to favor net autotrophy by diluting organic material levels for respiratory consumption and supplementing surface nutrient stocks for autotrophic production.

**Atmospheric supply of organic material.** Primary OC supplements to the surface ocean from the atmosphere occur through the dry deposition of aerosols, wet deposition of particles, and wet deposition of volatile gases. The combined global flux of the former two processes has been estimated at 56 Tg C year<sup>-1</sup> (Jurado et al. 2008); the latter flux of gas deposition is less well constrained but has been estimated at 187 Tg C year<sup>-1</sup> (Jurado et al. 2008), although this may be an underestimate. Making the conservative assumption that these fluxes are uniformly distributed across the oceans (in reality, they are considerably lower over the central ocean gyres than in more coastal waters), we estimate a potential range for the atmospheric organic material supplement of 0.04 (excluding volatiles) to 0.17 (including volatiles) mmol C m<sup>-2</sup> day<sup>-1</sup>. Comparison of these values with the average carbon deficit of 50 mmol C m<sup>-2</sup> day<sup>-1</sup> for the oligotrophic ocean (see above) demonstrates that atmospheric inputs fall far short of the necessary OC supplement required to support the proposed rates of net heterotrophy. To sustain the purported net heterotrophy, the 187 Tg C year<sup>-1</sup> of Jurado et al. (2008) would need to be underestimated by 200-fold or more—which seems highly improbable.

Although the preceding results indicate a meager atmospheric organic material contribution, the uncertainties in the modeled fluxes are large. However, field  $\delta^{13}\text{C}$ -DIC observations place a strong constraint on the potential significance of atmospheric carbon inputs. Atmospheric organic material will be depleted in  $^{13}\text{C}$  by  $\sim 20\%$  if it is derived from distant marine production (see above) and by  $\sim 27\%$  if it is derived from a terrestrial source. As discussed above, respiration of this material in the oligotrophic gyres will drive a reduction in  $\delta^{13}\text{C}$ -DIC. If the atmospheric OC input to oligotrophic regions is considerably larger than our above estimate, then the observed net enrichment of  $\delta^{13}\text{C}$ -DIC relative to equilibrium with atmospheric  $\text{CO}_2$  would imply even greater net autotrophy than is currently estimated from  $^{13}\text{C}/^{12}\text{C}$  data. In other words, apparent net heterotrophy cannot be accounted for by assuming a larger atmospheric carbon input because the  $\delta^{13}\text{C}$ -DIC constraint requires that export production changes in proportion to atmospheric inputs.

## CONCLUSIONS

The analyses described above lead to four central conclusions:

1. The reported negative and positive NCP rates in the oligotrophic subtropical gyres based on in vitro and in situ methods, respectively, are significantly different.
2. No systematic biases in the in situ  $\text{O}_2$ -based approaches exist that would yield net heterotrophy instead of net autotrophy.
3. Observed  $\delta^{13}\text{C}$ -DIC enrichment of surface water DIC in the subtropical gyres is wholly inconsistent with net heterotrophy.
4. There is no evidence for an external supply of organic material from either marine or terrestrial sources of sufficient quantity to support the rate of net heterotrophy in the subtropical gyres implied by in vitro estimates of NCP.

In summary, we find no oceanographic observation to indicate that the subtropical gyres can exist in a permanent heterotrophic state, and therefore conclude that the in vitro approach for estimating NCP must be significantly biased in these regions. The in situ field observations, however, are wholly consistent with net autotrophy.

## IMPLICATIONS AND UNRESOLVED ISSUES

There are two key implications of our conclusions. First, the general net autotrophy of the oligotrophic subtropical gyres eliminates the need to identify significant external carbon sources for respiration, but raises issues regarding sources of nutrients supporting the positive NCP. And second, a bias toward net heterotrophy in the in vitro  $\text{O}_2$ -based measurements calls into question whether the same issues exist for other in vitro measurements (i.e.,  $^{14}\text{C}$  and  $^{15}\text{N}$  measurements) and how such biases impact our understanding of oceanic organic production. Clearly, additional work is needed to resolve these issues and identify the basis for the in vitro artifacts.

What mechanisms supply the external nutrients needed to support net autotrophy? Based on nitrate and  $^3\text{He}$  observations at the BATS site, Jenkins & Doney (2003) made the case that the net supply of nutrients to the photic layer in the subtropical North Atlantic supporting autotrophic conditions cannot be explained by a one-dimensional vertical supply of nutrients from below, and instead likely involves a more convoluted path that includes large-scale gyre circulation, winter convection, and eddy mixing. Emerson et al. (2008) also rejected a one-dimensional vertical supply of nutrients to explain the  $\text{O}_2$  supersaturation in the subtropics because of the  $\text{O}_2$  deficit associated with the nutrient supply in a Redfield ocean; based on observations at the HOT site, they proposed that DOM production plays an important role because its longer turnover time allows air-sea gas

exchange to decouple O<sub>2</sub> deficiency from nutrient supply. However, Johnson et al. (2010) used mooring-based measurements of nitrate at the HOT site to demonstrate the importance of short episodic entrainment events that vertically transport nutrients from depth (up to 250 m) into the photic layer and support NCP. Although nitrogen fixation in the surface ocean may represent a significant source of new nutrients for phytoplankton, other physical sources are still needed to account for the phosphate supplement also required for net autotrophy. In short, although there is strong in situ evidence for an autotrophic subtropical ocean, we do not yet fully understand the link between external nutrient supply and net export of organic material.

Where does the problem lie with the in vitro measurements? Beyond very short timescales (less than seconds), photoautotrophic metabolisms of CO<sub>2</sub> and O<sub>2</sub> are closely coupled. Our analysis indicates that in vitro measurements of NCP contain an error in the measurement of photosynthesis or respiration (or both). Thus, an important question arises of whether these errors in O<sub>2</sub>-based measurements are equally relevant to CO<sub>2</sub> uptake rates measured by the <sup>14</sup>C technique. As this latter method is the foundation of many estimates of oceanic productivity and biological carbon flux, a potential bias is a serious matter.

Westberry et al. (2012) inferred that the in vitro O<sub>2</sub> error was most likely due to an underestimate of photosynthesis (rather than an overestimate of respiration), as bottle incubations should represent a greater perturbation to natural light conditions for mixed-layer phytoplankton than they do to respiratory conditions for heterotrophs. This suggestion is supported by comparison of in vitro and in situ data from the HOT site (Quay et al. 2010, Westberry et al. 2012), which shows general agreement between respiratory rates for the two approaches but significantly lower primary productivity for in vitro measurements. If this proposed underestimate of photosynthesis is correct, then we should anticipate similar biases for in vitro production rates assessed from <sup>14</sup>C uptake. However, specific mechanisms underlying in vitro perturbations to production are unresolved, and we should not disregard the possibility that there are problems associated with accurately representing respiration.

## APPENDICES

### Appendix A: Horizontal Transfer of DOC

**Required rate of transfer across circumference.** Assume a per-unit area deficit of 50 mmol C m<sup>-2</sup> day<sup>-1</sup> (the median value from Aranguren-Gassis et al. 2011, Duarte et al. 2001, Gist et al. 2009, González et al. 2001, Robinson et al. 2002, Serret et al. 2001, and Williams et al. 2004) and a mean mixed-layer depth of 50 m. This gives a mean volumetric demand of 1 mmol m<sup>-3</sup> day<sup>-1</sup>, or 10 × 10<sup>-6</sup> mmol m<sup>-3</sup> s<sup>-1</sup>. Approximating the gyre as a disk 1 m thick, the required inward flux would scale with the radius, giving a flux (dC/dt) of 10 × 10<sup>-6</sup> πr<sup>2</sup>/2πr = 5 × 10<sup>-6</sup> r (mmol m<sup>-2</sup> s<sup>-1</sup>).

**Horizontal diffusion coefficient.** Okubo (1971) gave a length-scaled horizontal advection/diffusion coefficient ( $Z_H$ ) of 4.7 × 10<sup>-5</sup> r<sup>4/3</sup> m<sup>2</sup> s<sup>-1</sup>, where  $r$  is the radius of the patch in meters.

**Required concentration gradient.** Fick's first law relates the diffusive flux to the concentration gradient at steady state as

$$dC/dt = Z_H \cdot (dC/dx),$$

where dC/dt is the mass flux per unit area [dC/dt = 5 × 10<sup>-6</sup> r (mmol m<sup>-2</sup> s<sup>-1</sup>)],  $Z_H$  is the horizontal diffusion coefficient [ $Z_H = 4.7 \times 10^{-5} r^{4/3} (m^2 s^{-1})$ ], and dC/dx is the concentration

gradient ( $\text{mmol m}^{-3} \text{ m}^{-1}$ ), all in SI units. The concentration gradient at a given  $r$  would be

$$dC/dx = (5 \times 10^{-6}r)/(4.7 \times 10^{-5}r^{4/3}) = 0.1(r^{-1/3}) \text{ mmol m}^{-3} \text{ m}^{-1}.$$

At  $r = 500 \text{ km}$ , for example,  $dC/dx = 1.25 \text{ mmol m}^{-3} \text{ km}^{-1}$ ; at  $r = 1,000 \text{ km}$ ,  $dC/dx = 1.0 \text{ mmol m}^{-3} \text{ km}^{-1}$ .

**Integration to give the concentration at  $r$ .** The concentration at a given  $r$  is then calculated as

$$C_r = 0.1(r^{2/3})/(2/3) + C_0 = 0.15(r^{2/3}) + C_0 \text{ mmol m}^{-3}.$$

Here,  $C_r$  at  $500 \text{ km} \approx 1,000 + C_0 \text{ mmol m}^{-3}$ , and  $C_r$  at  $1,000 \text{ km} \approx 1,500 + C_0 \text{ mmol m}^{-3}$ .

## Appendix B: Vertical Transfer of DOC from Deep Water

After Williams (2000) and Druffel et al. (1992),

upwelling DOC concentration =  $35 \text{ mmol m}^{-3}$ ,  $^{14}\text{C}$  age 6,000 years,

and

downwelling DOC concentration =  $65 \text{ mmol m}^{-3}$ ,  $^{14}\text{C}$  age 2,200 years.

Assuming no decomposition, the deep DOC will be diluted by  $65/35$ , giving a  $^{14}\text{C}$  age of  $6,000 \times 35/65$ , or 3,230 years. Thus, the fraction of the original that has been lost will be  $(3,230 - 2,200)/3,230$ , i.e., approximately 30% of the original  $35 \text{ mmol m}^{-3}$ , or  $\sim 10 \text{ mmol m}^{-3}$ . This is within Mopper et al.'s (1991) calculated range of 12%–48% of the deepwater DOC being rendered labile by photochemical processes.

Thus, we have  $10 \text{ mmol m}^{-3}$  of DOC available in upwelling water and a need for  $50 \text{ mmol m}^{-2} \text{ day}^{-1}$  of labile DOC. Accordingly, we would require an upwelling rate of  $5 \text{ m day}^{-1}$  or  $\sim 1,500 \text{ m year}^{-1}$ : half the deep water column. These rates are many times larger than calculated global upwelling rates (Munk 1966).

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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## LITERATURE CITED

Abell J, Emerson S, Renaud P. 2000. Distributions of TOP, TON and TOC in the North Pacific subtropical gyre: implications for nutrient supply in the surface ocean and remineralization in the upper thermocline. *J. Mar. Res.* 58:203–22

- Aranguren-Gassis M, Serret P, Fernández E, Herrera JL, Domínguez JF, et al. 2011. Production and respiration control the marine microbial metabolic balance in the eastern North Atlantic subtropical gyre. *Deep-Sea Res. I* 58:768–75
- Benitez-Nelson C, Buesseler KO, Karl DM, Andrews J. 2001. A time-series study of particulate matter export in the North Pacific Subtropical Gyre based on  $^{234}\text{Th}$  :  $^{238}\text{U}$  disequilibrium. *Deep-Sea Res. I* 48:2595–611
- Blight SP, Bentley TL, Lefevre D, Robinson C, Rodrigues R, et al. 1995. Phasing of autotrophic and heterotrophic plankton metabolism in a temperate coastal ecosystem. *Mar. Ecol. Prog. Ser.* 128:61–75
- Carlson CA, Ducklow HW, Michaels AF. 1994. Annual flux of dissolved organic carbon from the euphotic zone in the northwestern Sargasso Sea. *Nature* 371:405–8
- Carlson CA, Hansell DA, Nelson NB, Siegel DA, Smethie WM, et al. 2010. Dissolved organic carbon export and subsequent remineralization in the mesopelagic and bathypelagic realms of the North Atlantic basin. *Deep-Sea Res. II* 57:1433–45
- del Giorgio PA, Cole JJ, Cimleris A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. *Nature* 385:148–51
- Druffel ERM, Williams PM, Bauer JE, Ertel JR. 1992. Cycling of dissolved and particulate organic matter in the open ocean. *J. Geophys. Res.* 97:15639–59
- Duarte CM, Agustí S. 1998. The  $\text{CO}_2$  balance of unproductive aquatic ecosystems. *Science* 281:234–36
- Duarte CM, Agustí S, Aristegui J, González N, Anadón R. 2001. Evidence for a heterotrophic subtropical northeast Atlantic. *Limnol. Oceanogr.* 46:425–28
- Duarte CM, Agustí S, del Giorgio PA, Cole JJ. 1999. Regional carbon imbalances in the oceans. *Science* 284:1735
- Duarte CM, Regaudie-de-Gioux A, Arrieta JM, Delgado-Huertas A, Agustí S. 2013. The oligotrophic ocean is heterotrophic. *Annu. Rev. Mar. Sci.* 5:551–69
- Ducklow HW, Carlson CA, Bates NR, Knap AH, Michaels AF. 1995. Dissolved organic carbon as a component of the biological pump in the North Atlantic Ocean. *Philos. Trans. R. Soc. Lond. B* 348:161–67
- Ducklow HW, Doney SC. 2013. What is the metabolic state of the oligotrophic ocean? A debate. *Annu. Rev. Mar. Sci.* 5:525–33
- Emerson S, Quay P, Karl D, Winn C, Tupas L, Landry M. 1997. Experimental determination of the organic carbon flux from open-ocean surface waters. *Nature* 389:951–54
- Emerson S, Stump C, Nicholson D. 2008. Net biological oxygen production in the ocean: remote in situ measurements of  $\text{O}_2$  and  $\text{N}_2$  in surface waters. *Glob. Biogeochem. Cycles* 22:GB3023
- Emrich K, Ehhalt DH, Vogel JC. 1970. Carbon isotope fractionation during the precipitation of calcium carbonate. *Earth Planet. Sci. Lett.* 8:363–71
- Fry B, Hopkinson CS Jr, Nolin A, Wainright SC. 1998.  $^{13}\text{C}/^{12}\text{C}$  composition of marine dissolved organic carbon. *Chem. Geol.* 152:113–18
- Geider RJ. 1997. Photosynthesis or planktonic respiration? *Nature* 388:132
- Gist N, Serret P, Woodward EMS, Chamberlain K, Robinson C. 2009. Seasonal and spatial variability in plankton production and respiration in the subtropical gyres of the Atlantic Ocean. *Deep-Sea Res. II* 56:931–40
- Goericke R, Fry B. 1994. Variations of marine plankton  $\delta^{13}\text{C}$  with latitude, temperature, and dissolved  $\text{CO}_2$  in the world ocean. *Glob. Biogeochem. Cycles* 8:85–90
- González N, Anadón R, Marañón E. 2002. Large-scale variability of planktonic net community metabolism in the Atlantic Ocean: importance of temporal changes in oligotrophic subtropical waters. *Mar. Ecol. Prog. Ser.* 233:21–30
- González N, Anadón R, Mourino B, Fernández E, Sinha B, et al. 2001. The metabolic balance of the planktonic community in the North Atlantic Subtropical Gyre: the role of mesoscale instabilities. *Limnol. Oceanogr.* 46:946–52
- Gruber N, Keeling CD, Stocker TF. 1998. Carbon-13 constraints on the seasonal inorganic carbon budget at the BATS site in the northwestern Sargasso Sea. *Deep-Sea Res. I* 45:673–717
- Hamme RC, Emerson SR. 2006. Constraining bubble dynamics and mixing with dissolved gases: implications for productivity measurements by oxygen mass balance. *J. Mar. Res.* 64:73–95

- Hansell DA, Carlson CA, Repeta DJ, Schlitzer R. 2009. Dissolved organic matter in the ocean: a controversy stimulates new insights. *Oceanography* 22(4):202–11
- Hansell DA, Ducklow HW, Macdonald AM, Baringer MO. 2004. Metabolic poise in the North Atlantic Ocean diagnosed from organic matter transports. *Limnol. Oceanogr.* 49:1084–94
- Jenkins WJ. 1980. Tritium and  $^3\text{He}$  in the Sargasso Sea. *J. Mar. Res.* 38:533–69
- Jenkins WJ, Doney SC. 2003. The subtropical nutrient spiral. *Glob. Biogeochem. Cycles* 17:1110
- Johnson KS, Riser SC, Karl DM. 2010. Nitrate supply from deep to near-surface waters of the North Pacific subtropical gyre. *Nature* 465:1062–65
- Jurado E, Dachs J, Duarte CM, Simo R. 2008. Atmospheric deposition of organic and black carbon to the global oceans. *Atmos. Environ.* 42:7931–39
- Keeling CD, Brix H, Gruber N. 2004. Seasonal and long-term dynamics of the upper ocean carbon cycle at Station ALOHA near Hawaii. *Glob. Biogeochem. Cycles* 18:GB4006
- Longhurst A. 1998. *Ecological Geography of the Sea*. San Diego: Academic. 398 pp.
- Longhurst A, Sathyendranath S, Platt T, Caverhill C. 1995. An estimate of global primary production in the ocean from satellite radiometer data. *J. Plankton Res.* 17:1245–71
- Luz B, Barkan E. 2009. Net and gross oxygen production from  $\text{O}_2/\text{Ar}$ ,  $^{17}\text{O}/^{16}\text{O}$  and  $^{18}\text{O}/^{16}\text{O}$  ratios. *Aquat. Microb. Ecol.* 56:133–45
- Marañón E, Pére V, Fernández E, Anadón R, Bode A, et al. 2007. Planktonic carbon budget in the eastern subtropical North Atlantic. *Aquat. Microb. Ecol.* 48:261–75
- Mopper K, Zhou XL, Kieber RJ, Kieber DJ, Sikorski RJ, Jones RD. 1991. Photochemical degradation of dissolved organic carbon and its impact on the oceanic carbon cycle. *Nature* 353:60–62
- Morán XA, Fernández E, Pérez V. 2004. Size-fractionated primary production, bacterial production and net community production in subtropical and tropical domains of the oligotrophic NE Atlantic in autumn. *Mar. Ecol. Prog. Ser.* 274:17–29
- Munk WH. 1966. Abyssal recipes. *Deep-Sea Res.* 13:707–30
- Musgrave DL. 1990. Numerical studies of tritium and helium-3 in the thermocline. *J. Phys. Oceanogr.* 20:344–73
- Okubo A. 1971. Oceanic diffusion diagrams. *Deep-Sea Res.* 18:789–802
- Quay PD, Peacock C, Björkman K, Karl DM. 2010. Measuring primary production rates in the ocean: enigmatic results between incubation and non-incubation methods at Station ALOHA. *Glob. Biogeochem. Cycles* 24:GB3014
- Quay PD, Sonnerup R, Westby T, Stutsman J, McNichol A. 2003. Changes in the  $^{13}\text{C}/^{12}\text{C}$  of dissolved inorganic carbon in the ocean as a tracer of anthropogenic  $\text{CO}_2$  uptake. *Glob. Biogeochem. Cycles* 17:1004
- Quay PD, Stutsman J. 2003. Surface layer carbon budget for the subtropical N. Pacific:  $\delta^{13}\text{C}$  constraints at station ALOHA. *Deep-Sea Res. I* 50:1045–61
- Riser S, Johnson K. 2008. Net production of oxygen in the subtropical ocean. *Nature* 451:323–25
- Robinson C, Serret P, Tilstone G, Teira E, Zubkov MV, et al. 2002. Plankton respiration in the Eastern Atlantic Ocean. *Deep-Sea Res. I* 49:787–813
- Serret P, Fernández E, Robinson C. 2002. Biogeographic differences in the net ecosystem metabolism of the open ocean. *Ecology* 83:3225–34
- Serret P, Fernández E, Sostres JA, Anadón R. 1999. Seasonal compensation of microbial production and respiration in a temperate sea. *Mar. Ecol. Prog. Ser.* 187:43–57
- Serret P, Robinson C, Fernández E, Teira E, Tilstone G. 2001. Latitudinal variation of the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean. *Limnol. Oceanogr.* 46:1642–52
- Serret P, Robinson C, Fernández E, Teira E, Tilstone G, Perez V. 2009. Predicting plankton net community production in the Atlantic Ocean. *Deep-Sea Res. II* 56:941–53
- Spitzer WS, Jenkins WJ. 1989. Rates of vertical mixing, gas exchange and new production: estimates from seasonal gas cycles in the upper ocean near Bermuda. *J. Mar. Res.* 47:169–96
- Westberry TK, Williams PJLB, Behrenfeld MJ. 2012. Global net community production and the putative net heterotrophy of the oligotrophic oceans. *Glob. Biogeochem. Cycles*. In press
- Williams PJLB. 1998. The balance of plankton respiration and photosynthesis in the open oceans. *Nature* 394:55–57

- Williams PJLB. 2000. Heterotrophic bacteria and the dynamics of dissolved organic material. In *Microbial Ecology of the Oceans*, ed. DL Kirchman, pp. 153–200. New York: Wiley-Liss
- Williams PJLB, Bowers DG. 1999. Regional carbon imbalances in the oceans. *Science* 284:1735
- Williams PJLB, Morris PJ, Karl DM. 2004. Net community production and metabolic balance at the oligotrophic ocean site, station ALOHA. *Deep-Sea Res. I* 51:1563–78
- Williams PJLB, Purdie DA. 1991. *In vitro* and *in situ* derived rates of gross production, net community production and respiration of oxygen in the oligotrophic subtropical gyre of the North Pacific Ocean. *Deep-Sea Res. A* 38:891–910



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## Errata

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