

What is the Metabolic State of the Oligotrophic Ocean? – A Debate.

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ABSTRACT

For more than a decade there has been controversy in oceanography regarding the metabolic state of the oligotrophic gyres of the open sea. Here we review background on this controversy, commenting on several issues to set the context for a moderated debate between two groups of scientists. In a companion paper, Williams et al (2013) take the view that the oligotrophic subtropical gyres of the global ocean exhibit a state of net autotrophy, that is, the gross primary production (GPP) exceeds community respiration (R), when averaged over some suitably extensive region and over a long duration. Duarte et al (2013) take the opposite view, that the oligotrophic subtropical gyres are net heterotrophic, with R exceeding the GPP. This idea -- that large, remote areas of the upper ocean could be net heterotrophic raises a host of fundamental scientific questions about the metabolic processes of photosynthesis and respiration that underlie ocean ecology and global biogeochemistry. The question remains unresolved, in part, because the net state is finely balanced between large opposing fluxes and most current measurements have large uncertainties. This challenging question must be studied against the background of large, anthropogenically-driven changes in ocean ecology and biogeochemistry. Current trends of anthropogenic change make it an urgent problem to solve and also greatly complicate finding that solution.

INTRODUCTION

In this paper, we introduce a new feature for Annual Reviews of Marine Science: a moderated debate between two groups of scientists over a controversial topic in the marine sciences. In this instance, Peter J LeB Williams and Carlos Duarte and their coauthors exchange views on the topic of the metabolic balance of the oligotrophic oceans. Williams et al (2013) take the view that the oligotrophic subtropical gyres of the global ocean exhibit a state of net autotrophy, that is, the gross primary production (GPP) exceeds community respiration (R), when averaged over some suitably extensive region and over a long duration. Duarte et al (2013) take the opposite view, that the oligotrophic subtropical gyres are net heterotrophic, with R exceeding the GPP. We serve as moderators, having helped to frame the terms of the debate, and in this article, reviewing the background of the controversy, and commenting on several issues to set the context for the debate. We refrain from critically evaluating the respective claims of the debating parties. Reviewed drafts of all three articles were exchanged among the authors, and each had the opportunity to revise their papers following the exchange.

DEFINITIONS AND CONCEPTS

The concept of the metabolic balance of the ocean (or some part of it) is encapsulated in two different equations:



$$\text{GPP} = \text{NCP} + \text{R} \quad (2)$$

Equation 1 defines photosynthesis (proceeding to the right) or respiration (to the left).

Equation 2 specifies the balance between photosynthesis and respiration (Figure 1), with

NCP (Net Community Production) being the organic matter remaining after consumption of the GPP through respiration by plants (autotrophs), microbes and animals (heterotrophs). Precise definitions of GPP and NPP (net primary production) are reviewed by Williams (1993) and will not be discussed further here. The net metabolic state is set in Equation 1 by the balance between the rates of the forward versus back reactions. When (or where) the forward reaction predominates, there is a state of net autotrophy; if the back reaction is greater, there is net heterotrophy, or excess consumption of organic matter over the amount produced in situ by the autotrophs. A positive NCP reflects surplus organic matter production that is available for lateral or vertical export to fuel, for example, respiration in the mesopelagic and deep sea. The estimation of NCP is often closely tied with the concept of new production; that part of autotrophic productivity supported by external or “new” sources of nutrients to the euphotic zone usually cast in terms of nitrogen (Dugdale & Goering 1967).

The concept of metabolic balance in the sea has a long history. Sverdrup et al. (1942) had the concept of the metabolic balance between GPP and R in mind when they wrote:

“In nature, the oxygen accumulates in layers of organic production and thus its fluctuations in time and space give a measure of the intensity of phytoplankton outbursts. It can provide only minimal values because the exact quantity of oxygen produced is obscured by the respiratory activities of animals and bacteria, and in the case of surface supersaturation some oxygen is given off to the atmosphere.” (page 934).

In our debate, both papers evaluate estimates of the balance between GPP and R based on short-term incubation of captured water samples, and incubation-free approaches, whereby the net balance is derived from measurements of chemical tracers such as dissolved oxygen and the isotopic content of dissolved or particulate carbon. Sverdrup et al. already considered these two approaches, and Riley (1957) compared them in his famous debate with Steemann Nielsen (1954) over the magnitude of primary production in the sea (see Peterson (1980) and Mills (1989) for discussion of this debate and related issues).

In 1949 Sargent and Austin (1949) pioneered the flowing water method to measure the net productivity of a coral reef community by determining the net increase or decrease of oxygen and organic matter as ocean water flowed across the reef flat. H.T. and E.P. Odum (1955) employed the approach in their seminal paper on the trophic structure and metabolism of the Eniwetok (Enewetak) coral atoll. They found that the reef had high GPP but low NCP, a state that complicates detection of metabolic balance to this day. H. T. Odum (1956) formalized the approach with the equation:

$$Q = GPP - R + D_{in} + A \quad (3)$$

where Q is the time rate of change of dissolved oxygen (dO_2/dt), GPP and R are as defined above, D_{in} is the diffusive input (or loss) and A the advective input (or loss). Bottle incubations isolate a small water parcel from external fluxes, NCP is estimated from the change in O_2 , and $GPP-R = Q$. By contrast, the oxygen budget of the ocean mixed layer is strongly influenced by exchange with the atmosphere across the air-sea interface, and to first approximation Equation (3) reduces to a steady-state balance between NCP and the diffusive air to sea flux, $GPP-R \sim -D_{air-sea}$. (Jenkins 1985). The

seasonal thermocline below the mixed layer is more isolated from the atmosphere and acts like a long-duration bottle incubation; a positive NCP over the growing season would result in a build-up (supersaturation) in subsurface oxygen, $GPP - R \sim Q$.

If we consider other tracers besides oxygen such as organic matter (as did Odum and Odum, 1955), Equation 3 makes the important point that ecosystems are not isolated, but rather are open systems in which the input of nutrients and organic matter from adjacent systems may be critical in determining the metabolic balance. The relationships and balance among GPP, R and various inputs and exports from open terrestrial ecosystems have been critically reviewed and formulated (Chapin III et al 2006). Chapin III et al. distinguish between Net Ecosystem Production (NEP), the balance between GPP and R, as in Equation 2, and the Net Ecosystem Carbon Balance (NECB), a term that includes exchanges with neighboring systems as in Equation 3. These points are especially important for the problem of defining the metabolic balance of the oligotrophic subtropical gyres.

External inputs of organic matter could tip the balance between net autotrophy and heterotrophy for oligotrophic ocean regions, which are typically marked by microbial planktonic ecosystems, high biological recycling rates and relatively low rates of net community production. In contrast to oligotrophic enclosed basins like the Mediterranean Sea or other oligotrophic regions nearer to the continental margins, the subtropical gyres are remote from land and from more productive ocean systems that might serve as sources of organic matter via lateral advection and mixing. Another potential source is net atmospheric input of organic material from gas exchange, particulate/aerosol deposition, and/or rainfall (Duce et al 1983, Willey et al 2000). Atmosphere deposition of

organic matter to the sea surface is poorly characterized and includes components of terrestrial, fossil fuel and marine origin (Raymond 2005); the marine component would not constitute a net source to the upper ocean but rather reflects material recycled through the atmosphere. The relative importance of this marine component, and especially the volatile fraction is uncertain, but possibly large. A related argument concerns the possibility that the dissolved organic carbon (DOC) pool of the global ocean is changing with time. In particular, if it were found to be declining over the long term, it could serve as a subsidy fueling net bacterial heterotrophy in the central gyres. Williams and Duarte and their co-authors address the question of the relative magnitudes of external inputs and/or a non-steady state DOC pool as potential sources of net heterotrophy in the oligotrophic subtropical gyres. In a microcosm of the present debate, Fouilland and Moustajir (2010) assert that the oceanic bacterial carbon demand (a major component of community respiration) is not satisfied by local primary production. However this argument relies on assumptions about poorly-known conversion factors (Morán & Alonso-Sáez 2010), rather than direct measurements of elemental fluxes.

BIOLOGICAL PRODUCTION IN THE OLIGOTROPHIC GYRES

There are many tens of thousands of estimates of the rate of marine primary production using the ^{14}C incubation approach (Steemann Nielsen 1952); however they are not directly pertinent to the ocean metabolic balance, since the method yields an estimate that lies somewhere between GPP and NPP, depending on environmental (and incubation) conditions and the preceding history of the population being measured. Nonetheless, ^{14}C incubations are sensitive and easy to perform, and the size of the historical database

makes it invaluable for evaluating the magnitude of primary production, and therefore an important element in this debate.

The application of incubation-free, geochemical tracer estimates of new production in the early 1980s (Jenkins & Wallace 1992, Shulenberger & Reid 1981) triggered an overall reassessment of primary production estimates in the subtropical gyres, and a critical reexamination of the concepts of gross, net and new primary production (Eppley 1992). In part this assessment of primary production was motivated by realization that the new incubation-free tracer methods gave in some cases much greater productivity estimates than ^{14}C incubations; yet the tracer approaches really measured the *new* production (similar to NCP), itself a subcomponent of the total production! The seeds of a resolution were planted in 1982, when John Martin developed trace metal-clean techniques for sampling and incubating plankton samples without contaminating them with potentially toxic concentrations of copper and other metals (Fitzwater 1982). Open-ocean phytoplankton are exquisitely sensitive to trace metals, and incubation in glass bottles resulted in inhibition of ^{14}C labeled inorganic carbon uptake, yielding low estimates of the PP rates. Once new, clean sampling and incubation technology was implemented, the resulting new, higher ^{14}C -based PP rates enabled a more objective comparison of incubation-based and incubation-free approaches, as in this debate. Ironically, Riley's (1957) primary production estimates for the Sargasso Sea, once dismissed as being impossibly high, now seem much more in line with current understanding, and the original ^{14}C estimates of Steeman Nielson were probably contaminated.

While less common than ^{14}C -based productivity estimates, bottle incubation experiments for quantifying oxygen production and consumption rates have been conducted for a range of marine biogeographical regimes and seasons. The experiments often involve paired light and dark bottles where the rate of change in oxygen for the light bottle is equated with NCP and the dark bottle change with bacterial or community respiration R ; planktonic GPP can then be estimated from Equation 2. By the late 1990's sufficient O_2 bottle incubation data existed for cross-ecosystem analyses. del Giorgio et al. (1997) reported that O_2 -based bacterial respiration exceeds ^{14}C -based primary production in low-productivity subtropical gyres, reflecting a steeper decline in photosynthesis than respiration under low productivity conditions. Duarte and Agustí (1998) presented similar results by comparing trends of bottle O_2 -based NCP versus GPP rates. Other authors (e.g., Geider 1997; Williams 1998) countered that these findings were aliased by both methodological artifacts and the difficulty of interpreting the O_2 bottle incubation results. In contrast to ^{14}C -PP, O_2 bottle incubations attempt to measure the small difference between two large and opposing rates, GPP and R . The number of O_2 bottle incubation studies has grown substantially from the late 1990s but the basic story remains; many experiments indicate net heterotrophy ($\text{NCP} < 0$), often with large negative rates and with substantial variance both within and across studies (see Williams et al. 2013 and Duarte et al 2013 and references therein).

The spatial and seasonal coverage of tracer-based NCP estimates have expanded over the same time period. The most common technique involves measurements of O_2/Ar ratios for the mixed layer from water column sampling at time-series stations and along ship transects (e.g., Quay et al. 2010; Stanley et al. 2010; and Hamme et al. 2012). *In situ*

oxygen sensors on autonomous robotic profiling floats and gliders are greatly expanding capabilities to monitor seasonal upper ocean oxygen trends (Nicholson et al 2008, Riser & Johnson 2008). Recent glider surveys near Hawaii failed to detect periodic bursts of primary production (see Duarte et al. 2013) but Riser and Johnson (2008, Abstract) concluded that their observations were "...consistent with an ecosystem that is a net producer of fixed carbon (net autotrophic) throughout the year, with episodic events not required to sustain positive oxygen production." Argon has similar molecular diffusivity and solubility characteristics as O₂ and is used to correct the observed oxygen saturation for physical effects such as heating and bubble injection (Spitzer and Jenkins 1989; Luz and Barkan 2009). Mixed layer oxygen in oligotrophic regions is typically supersaturated with respect to the atmosphere (even after applying the argon adjustments). The oxygen supersaturation is interpreted as the remnants of net autotrophy (NCP > 0) producing excess O₂, most of which is lost by gas exchange to the atmosphere. Other tracer-based NCP approaches examine seasonal build up in subsurface oxygen, seasonal drawdown in mixed layer and subsurface dissolved inorganic carbon and nutrients, seasonal variations of inorganic carbon isotopes, and supply rates of new nutrients required to support NCP (Jenkins and Wallace 1992; Gruber et al. 1998). Measurement precision has improved such that *in situ* diurnal variations are resolvable for some situations. On the other end of the time-scale, observational and modeling studies have reconstructed the time-mean spatial patterns of net ocean-atmosphere O₂ and CO₂ fluxes; unfortunately the signal of local upper-ocean metabolism is often masked by large-scale circulation, surface warming and cooling, and inputs of subsurface waters with large metabolic CO₂ burdens and O₂ deficits (Gruber et al. 2001; Gruber et al. 2009; Takahashi et al. 2009).

BOTTLE INCUBATIONS VERSUS TRACER TECHNIQUES

Scientific lines of evidence supporting and refuting the conclusion that the oligotrophic open-ocean is net heterotrophic are presented in two columns in Table 1. At the heart of the on-going debate is the apparent inconsistency between the results of *in vitro* O₂ bottle incubations and *in situ* O₂ and other geochemical tracer techniques, which is fleshed out in more depth by Duarte et al. (2013) and Williams et al. (2013). Both approaches have their unique strengths and pitfalls, and much of the discussion centers on potential methodological biases. Some skepticism is probably warranted for any biological rate estimates that derive from direct manipulation of plankton samples, particularly for oligotrophic microbial systems where autotrophy and heterotrophy appear tightly coupled. Further, measurements of net property changes are often plagued by relatively small signal to noise ratios. On the other hand, tracer approaches are dependent on the often challenging task of resolving open-ocean physical transport rates (Equation 3) -- vertical mixing, gas exchange and lateral advective divergence; in fact the objective of the mixed layer O₂/Ar method is to equate NCP to air-sea O₂ exchange and is, therefore, sensitive to uncertainties in gas transfer velocity.

Perhaps equally important are the differences in the time and space scales captured by the two basic approaches. Bottle incubations inherently sample a small volume of water for a short period of time (hours to a day), and large numbers of samples are required to overcome ocean heterogeneity. The tracer-based techniques integrate over larger and longer scales: weeks for O₂/Ar-based mixed layer NCP and weeks to seasons for other methods. Particularly for underway transects, steady-state is assumed, though this may not always hold true (Hamme et al 2012). Further, the choice of depth

integration can strongly influence estimates of water-column integrated NCP because GPP tends to decrease sharply with depth, reflecting in part declining photosynthetically available radiation, while R tends to be more constant with depth. Based on an analysis of seasonal O₂ variations, Najjar and Keeling (1997) suggest that the switch between net community production and net community consumption, or oxygen compensation, falls at a depth of approximately 80-100 m in the subtropics. Few studies have combined incubation-based and tracer-based estimates for net ocean metabolism, and given the scale mismatches, well formulated studies would require paired high-frequency biogeochemical measurements over an extended time period and careful attention to ocean physics.

CONCLUSION

The idea that large parts of the most remote areas of the open sea could be net heterotrophic is a profoundly intriguing, if not disquieting proposition. This idea has been an active area in ocean biogeochemistry for over a decade, and has stimulated much research into the metabolic state of the oceanic gyres, including development of novel approaches to estimate net and gross oxygen and carbon fluxes. Current trends of anthropogenic change make it an urgent problem to solve and also greatly complicate finding that solution. The debate remains unresolved because the net state is finely balanced between large opposing fluxes and most current measurements have large uncertainties. Even so, the papers presented here suggest some clear research priorities including continued methods refinement, improvements in understanding of the relevant physical transport and mixing processes, and a better definition of autotrophic community production, encompassing oxygenic photosynthesis and anoxygenic production.

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Table 1 Arguments for and against the proposition that the oligotrophic subtropical gyres of the open ocean are heterotrophic, composed by the authors of the three debate articles

Arguments against net heterotrophy	Arguments for net heterotrophy
<ul style="list-style-type: none"> • In vitro methods suffer from errors deriving from confinement/bottle effects. • Estimates resulting from incubation-free, in situ oxygen and carbon dioxide fields consistently find oligotrophic zones to be autotrophic, and although some uncertainties remain in these assessments, none have the potential to change the sign of the results (i.e., from net autotrophic to net heterotrophic). • The euphotic zone has comparatively small reserves of labile organic carbon, and thus allochthonous inputs of organic carbon are needed to sustain heterotrophy. No transport system can be identified that operates on the required scale. Atmospheric inputs of organic carbon cannot represent a significant carbon subsidy to oligotrophic regions because they would give rise to $\delta^{13}\text{C}$ depletion of surface dissolved inorganic carbon (DIC), which is opposite the $\delta^{13}\text{C}$-DIC enrichment observed in the subtropical gyres. • The euphotic layer in the open ocean supports significant exports amounts of organic carbon and fishery yields, which is incompatible with sustained heterotrophy in these zones. • Heterotrophic metabolism is a transient phenomena balanced temporally by autotrophic periods, with communities being in near balance when integrated across adequate timescales not captured by discrete in vitro incubations. • The observed ^{13}C enrichment of subtropical surface DIC can be explained only by positive net autotrophy. 	<ul style="list-style-type: none"> • Available evidence consistently suggests that respiration exceeds primary production below a certain threshold of gross primary production, suggesting that less productive communities should be heterotrophic. • Estimates from incubation-free, in situ oxygen and carbon dioxide fields contain substantial errors that give rise to biased estimates and cannot reliably resolve metabolic rates. • The open ocean receives substantial allochthonous inputs of organic carbon. • Estimates of community respiration rates typically deliver underestimates. • Respiration rates below the mixed layer are much greater than the flux of organic carbon from the mixed layer. • Oxygen pools in the ocean are declining. • Nonoxygenic autotrophic processes may contribute to organic production in the open ocean, which would not be captured by the net oxygen flux and therefore would result in underestimates of net community production.

Figure 1. Cartoon illustrating metabolic exchanges, transformations and related processes in the surface ocean, influencing the balance between net autotrophy and heterotrophy. GPP and NPP are gross and net primary production, respectively. NCP is net community production. See text for equations and definitions of these terms. DOM includes dissolved organic matter produced by phytoplankton and consumers and utilized by heterotrophic bacteria (and some phytoplankton) in situ, and also that supplied from external sources. Vertical, horizontal and atmospheric sources of exogenous (new) nutrients (e.g., nitrogen, iron) support a varying fraction of the GPP, termed new production. This is quantitatively equivalent to the NCP over appropriate time and space scales. The new production and NCP are available for export from the system (only vertical exports shown). The air-sea exchange and lateral transport are possible sources and sinks for organic matter that can affect NCP. Other forms of metabolism (e.g., anoxygenic photosynthesis) not shown.

