What Is the Metabolic State of the Oligotrophic Ocean? A Debate

Hugh W. Ducklow[1] and Scott C. Doney[2]

[1]The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543; email: hducklow@mbl.edu

[2]Department of Marine Chemistry and Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543; email: sdoney@whoi.edu

Annu. Rev. Mar. Sci. 2013. 5:525–33

The *Annual Review of Marine Science* is online at marine.annualreviews.org

This article's doi:
10.1146/annurev-marine-121211-172331

Keywords

net autotrophy, net heterotrophy, net community production, oligotrophic gyres, oxygen

Abstract

For more than a decade there has been controversy in oceanography regarding the metabolic state of the oligotrophic subtropical gyres of the open ocean. Here we review the background of this controversy, commenting on several issues to set the context for a moderated debate between two groups of scientists. In one of the two companion articles, Williams et al. (2013) take the view that these gyres exhibit a state of net autotrophy—that is, their gross primary production (GPP) exceeds community respiration (R) when averaged over some suitably extensive region and over a long duration. In the other companion article, Duarte et al. (2013) take the opposite view, that these 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 article, we introduce a moderated debate between two groups of scientists over a controversial topic in the marine sciences: the metabolic state of the oligotrophic subtropical gyres of the global ocean. In the two companion articles, Peter J. le B. Williams and Carlos M. Duarte and their coauthors each make the case for their respective views. Williams et al. (2013) take the view that these gyres exhibit a state of net autotrophy—that is, their 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 these gyres are net heterotrophic, with R exceeding the GPP. We serve as moderators, initially having helped frame the terms of the debate and then, in this article, reviewing the background of the controversy and commenting on several issues to set the context. 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 group had the opportunity to revise their articles 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:

$$6CO_2 + 6H_2O \leftrightarrow C_6H_{12}O_6 + 6O_2 \tag{1}$$

and

$$\mathrm{GPP} = \mathrm{NCP} + \mathrm{R}. \tag{2}$$

Equation 1 defines photosynthesis (proceeding to the right) or respiration (proceeding 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 (either autotrophs or heterotrophs), and animals (heterotrophs). Precise definitions of GPP and net primary production (NPP) have been 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 and back reactions. When (or where) the forward reaction predominates, there is a state of net autotrophy, or excess production of organic matter; when (or where) the back reaction predominates, there is a state of 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 zone and deep sea. The estimation of NCP is often closely tied to the concept of new production, which is the 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. (p. 934)

In the present debate, both companion articles evaluate estimates of the balance between GPP and R based on short-term incubation of captured water samples as well as incubation-free approaches,

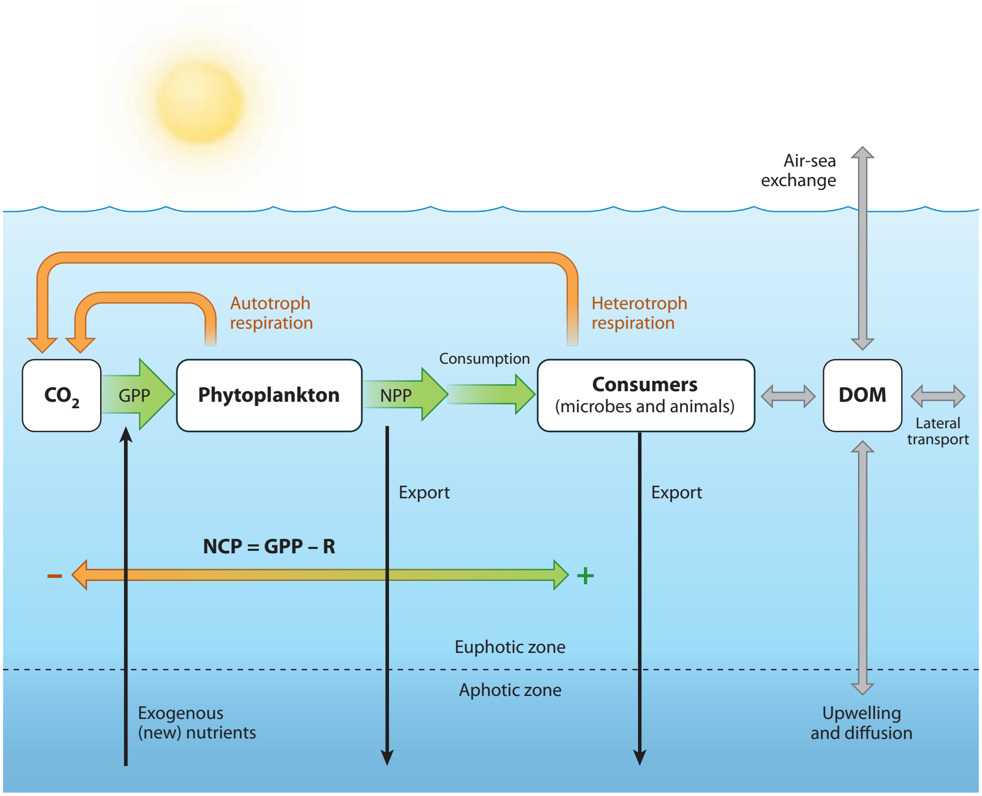

Figure 1

Metabolic exchanges, transformations, and related processes in the surface ocean, all of which influence the balance between net autotrophy and heterotrophy. GPP and NPP are gross and net primary production, respectively; NCP is net community production; and R is community respiration. Dissolved organic matter (DOM) includes that 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 and 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 are 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) are not shown.

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. (1942) had 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 (for discussion of this debate and related issues, see Peterson 1980 and Mills 1989).

Sargent & 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 flows across the reef flat. Odum & Odum (1955) employed this approach in their seminal paper on the trophic structure and metabolism of the Eniwetok (now spelled Enewetak) coral atoll. They found that the reef had high GPP but low NCP, a state that complicates the detection of metabolic balance to this day. Odum (1956) formalized the approach with the equation

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

where Q is the 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 is 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 ($GPP - R \sim -D_{\text{air-sea}}$) (Jenkins & Goldman 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 buildup (supersaturation) in subsurface oxygen ($GPP - R \sim Q$).

If we consider tracers other than oxygen, such as organic matter [as did Odum & 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. Chapin et al. (2006) critically reviewed and formulated the relationships and balance among GPP, R, and various inputs and exports from open terrestrial ecosystems. They distinguished between the 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 NCP rates. In contrast to oligotrophic enclosed basins (like the Mediterranean Sea) and 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 the 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 would reflect 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 this pool were found to be declining over the long term, it could serve as a subsidy fueling net bacterial heterotrophy in the central gyres. In the companion articles, Williams et al. (2013) and Duarte et al. (2013) 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 & Mostajir (2010) asserted that the oceanic bacterial carbon demand (a major component of R) is not satisfied by local primary production. However, this argument relies on assumptions about poorly known conversion factors (Morán & Alonso-Sáez 2010) rather than on 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 that use the ^{14}C incubation approach (Steemann Nielsen 1952); however, they are not directly pertinent to the ocean metabolic balance, because the method yields an estimate that lies somewhere between GPP and NPP, depending on environmental (and incubation) conditions and the history of the population being measured. Nonetheless, ^{14}C incubations are sensitive and easy to perform, and the size of the historical database makes this approach invaluable for evaluating the magnitude of primary production, which therefore also makes it an important element in this debate.

The application of incubation-free geochemical tracer estimates of new production starting in the early 1980s (Shulenberger & Reid 1981, Jenkins & Wallace 1992) triggered an overall reassessment of primary production estimates in the subtropical gyres as well as a critical reexamination of the concepts of gross, net, and new primary production (Eppley 1992). This assessment of primary production was partly motivated by the realization that in some cases the new incubation-free tracer methods gave much greater productivity estimates than ^{14}C incubations did—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 Martin and colleagues (Fitzwater et al. 1982) developed trace-metal-clean techniques for sampling and incubating plankton samples without contaminating them with potentially toxic concentrations of copper and other metals. 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 primary production rates. After new, clean sampling and incubation technologies were implemented, the resulting higher ^{14}C-based primary production rates enabled a more objective comparison of incubation-based and incubation-free approaches, as in the present 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 Steemann Nielsen were probably contaminated.

Although 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 O_2 for the light bottle is equated with NCP and the dark bottle change is equated with bacterial or community respiration (R); planktonic GPP can then be estimated from Equation 2. By the late 1990s, 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 in respiration under low-productivity conditions. Duarte & Agustí (1998) presented similar results by comparing trends of O_2 bottle–based NCP and 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-based techniques, 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 since the late 1990s, but the basic story remains: Many experiments indicate net heterotrophy (NCP < 0), often with large negative rates and with substantial variance both within and across studies (see Williams et al. 2013, Duarte et al. 2013, and references therein).

The spatial and seasonal coverage of tracer-based NCP estimates have expanded over the same 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, Hamme et al. 2012). In situ oxygen sensors on autonomous robotic profiling floats and gliders are greatly expanding capabilities for monitoring 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 & Johnson (2008) 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" (p. 323). Argon has molecular diffusivity and solubility characteristics similar to those of oxygen and is used to correct the observed oxygen saturation for physical effects such as heating and bubble injection (Spitzer & Jenkins 1989, Luz & 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 oxygen, most of which is lost by gas exchange to the atmosphere. Other tracer-based NCP approaches examine seasonal buildup 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 & 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 timescale, observational and modeling studies have reconstructed the time-mean spatial patterns of net sea-air oxygen and carbon dioxide 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 carbon dioxide burdens and oxygen deficits (Gruber et al. 2001, 2009; Takahashi et al. 2009).

BOTTLE INCUBATIONS VERSUS TRACER TECHNIQUES

Table 1 presents scientific lines of evidence for each side of the present debate about the metabolic state of the oligotrophic subtropical gyres of the open ocean. At the heart of this ongoing debate is the apparent inconsistency between the results of in vitro O_2 bottle incubations and in situ O_2 and other geochemical tracer techniques, which is fleshed out in more depth by Williams et al.

Table 1 Arguments for net autotrophy and net heterotrophy in the oligotrophic subtropical gyres of the open ocean, composed by the authors of the three debate articles

Arguments for net autotrophy	Arguments for net heterotrophy
• 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 $\delta^{13}C$ depletion of surface dissolved inorganic carbon (DIC), which is opposite the $\delta^{13}C$-DIC enrichment observed in the subtropical gyres. • The euphotic layer in the open ocean supports significant export 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.	• 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.

(2013) and Duarte et al. (2013). Each approach has its own unique strengths and weaknesses, 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 to be tightly coupled. Furthermore, measurements of net property changes are often plagued by relatively low signal-to-noise ratios. Tracer approaches, in comparison, are dependent on the often challenging task of resolving open-ocean physical transport rates (Equation 3) of vertical mixing, gas exchange, and lateral advective divergence; in fact, the objective of the mixed-layer O_2/Ar method is to equate NCP to air-sea oxygen exchange, and this method 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 longer scales: weeks for O_2/Ar-based mixed-layer NCP, and weeks to seasons for other methods. Particularly for underway transects, a steady state is assumed, though this may not always hold true (Hamme et al. 2012). Furthermore, the choice of depth integration can strongly influence estimates of water-column-integrated NCP because the GPP tends to decrease sharply with depth, reflecting in part declining photosynthetically available radiation, whereas R tends to be more constant with depth. Based on an analysis of seasonal oxygen variations, Najjar & Keeling (1997) suggested that the switch between NCP and net community consumption, or oxygen compensation, falls at a depth of approximately 80–100 m in the subtropics. Few studies have combined incubation- 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 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 in part because the net state is finely balanced between large opposing fluxes and most current measurements have large uncertainties. Even so, the articles presented here suggest some clear research priorities, including continued refinement of methods, improvements in understanding of the relevant physical transport and mixing processes, and a better definition of autotrophic community production, encompassing both oxygenic photosynthesis and anoxygenic production.

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.

ACKNOWLEDGMENTS

The authors acknowledge support from the US National Science Foundation (NSF) through the Center for Microbial Oceanography: Research and Education (C-MORE), an NSF Science and Technology Center (EF-0424599), and NSF award OPP 0823101 (Palmer LTER) from the Antarctic Organisms and Ecosystems Program.

LITERATURE CITED

Chapin FS III, Woodwell GM, Randerson JT, Rastetter EB, Lovett GM, et al. 2006. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9:1041–50

del Giorgio PA, Cole JJ, Cimberlis A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. *Nature* 385:148–51

Duarte CM, Agustí S. 1998. The CO_2 balance of unproductive aquatic ecosystems. *Science* 281:234–36

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

Duce RA, Mohnen VA, Zimmerman PR, Grosjean D, Cautreels W, et al. 1983. Organic material in the global troposphere. *Rev. Geophys.* 21:921–52

Dugdale RC, Goering JJ. 1967. Uptake of new and regenerated forms of nitrogen in primary production. *Limnol. Oceanogr.* 12:196–206

Eppley RW. 1992. Toward understanding the roles of phytoplankton in biogeochemical cycles: personal notes. In *Primary Productivity and Biogeochemical Cycles in the Sea*, ed. PG Falkowski, AD Woodhead, pp. 1–7. New York: Plenum

Fitzwater S, Knauer G, Martin JH. 1982. Metal contamination and its effect on primary production measurements. *Limnol. Oceanogr.* 27:544–51

Fouilland E, Mostajir B. 2010. Revisited phytoplanktonic carbon dependency of heterotrophic bacteria in freshwaters, transitional, coastal and oceanic waters. *FEMS Microbiol. Ecol.* 73:419–29

Geider RJ. 1997. Photosynthesis or planktonic respiration? *Nature* 388:132

Gruber N, Gloor M, Fan S, Sarmiento JL. 2001. Air-sea flux of oxygen estimated from bulk data: implications for the marine and atmospheric oxygen cycles. *Glob. Biogeochem. Cycles* 15:783–804

Gruber N, Gloor M, Mikaloff Fletcher SE, Doney SC, Dutkiewicz S, et al. 2009. Oceanic sources, sinks, and transport of atmospheric CO_2. *Glob. Biogeochem. Cycles* 23:GB1005

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* 145:673–717

Hamme RC, Cassar N, Lance VP, Vaillancourt RD, Bender ML, et al. 2012. Dissolved O_2/Ar and other methods reveal rapid changes in productivity during a Lagrangian experiment in the Southern Ocean. *J. Geophys. Res.* 117:C00F12

Jenkins WJ, Goldman JC. 1985. Seasonal oxygen cycling and primary production in the Sargasso Sea. *J. Mar. Res.* 43:465–91

Jenkins WJ, Wallace DWR. 1992. Tracer-based inferences of new primary production in the sea. In *Primary Productivity and Biogeochemical Cycles in the Sea*, ed. PG Falkowski, AD Woodhead, pp. 299–316. New York: Plenum

Luz B, Barkan E. 2009. Net and gross oxygen production from O_2/Ar, $^{17}O/^{16}O$ and $^{18}O/^{16}O$ ratios. *Aquat. Microb. Ecol.* 56:133–45

Mills EL. 1989. *Biological Oceanography: An Early History, 1870–1960*. Ithaca, NY: Cornell Univ. Press. 378 pp.

Morán XAG, Alonso-Sáez L. 2010. Independence of bacteria on phytoplankton? Insufficient support for Fouilland & Mostajir's (2010) suggested new concept. *FEMS Microbiol. Ecol.* 78:203–5

Najjar RG, Keeling RF. 1997. Analysis of the mean annual cycle of the dissolved oxygen anomaly in the World Ocean. *J. Mar. Res.* 55:117–51

Nicholson DS, Emerson S, Eriksen CC. 2008. Net community production in the deep euphotic zone of the subtropical North Pacific gyre from glider surveys. *Limnol. Oceanogr.* 53:2226–36

Odum HT. 1956. Primary production in flowing waters. *Limnol. Oceanogr.* 1:102–17

Odum HT, Odum EP. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.* 25:291–320

Peterson BJ. 1980. Aquatic primary productivity and the ^{14}C-CO_2 method: a history of the productivity problem. *Annu. Rev. Ecol. Syst.* 11:359–85

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

Raymond PA. 2005. The composition and transport of organic carbon in rainfall: insights from the natural (^{13}C and ^{14}C) isotopes of carbon. *Geophys. Res. Lett.* 32:L14402

Riley GA. 1957. Phytoplankton of the north central Sargasso Sea, 1950–52. *Limnol. Oceanogr.* 2:252–70

Riser SC, Johnson KS. 2008. Net production of oxygen in the subtropical ocean. *Nature* 451:323–25

Sargent MC, Austin TS. 1949. Organic productivity of an atoll. *Trans. Am. Geophys. Union* 30:245–49

Shulenberger E, Reid JL. 1981. The Pacific shallow oxygen maximum, deep chlorophyll maximum, and primary productivity, reconsidered. *Deep-Sea Res. A* 28:901–19

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

Stanley RHR, Kirkpatrick JB, Cassar N, Barnett BA, Bender ML. 2010. Net community production and gross primary production rates in the western equatorial Pacific. *Glob. Biogeochem. Cycles* 24:GB4001

Steemann Nielsen E. 1952. The use of radioactive carbon (C^{14}) for measuring organic production in the sea. *J. Cons. Int. Explor. Mer* 18:117–40

Steemann Nielsen E. 1954. On organic production in the ocean. *J. Cons. Int. Explor. Mer* 19:309–28

Sverdrup HU, Johnson MW, Fleming RH. 1942. *The Oceans: Their Physics, Chemistry and General Biology*. Englewood Cliffs, NJ: Prentice Hall. 1,087 pp.

Takahashi T, Sutherland SC, Wanninkhof R, Sweeney C, Feely RA, et al. 2009. Climatological mean and decadal change in surface ocean pCO_2, and net sea–air CO_2 flux over the global oceans. *Deep-Sea Res. II* 56:554–77

Willey JD, Kieber RJ, Eyman MS, Avery GB Jr. 2000. Rainwater dissolved organic carbon: concentrations and global flux. *Glob. Biogeochem. Cycles* 14:139–48

Williams PJLB. 1993. Chemical and tracer methods of measuring plankton production. *ICES Mar. Sci. Symp.* 197:20–36

Williams PJLB. 1998. The balance of plankton respiration and photosynthesis in the open oceans. *Nature* 394:55–57

Williams PJLB, Quay PD, Westberry TK, Behrenfeld MJ. 2013. The oligotrophic ocean is autotrophic. *Annu. Rev. Mar. Sci.* 5:535–49

Annual Review of
Marine Science

Volume 5, 2013

Contents

Reflections About Chance in My Career, and on the Top-Down Regulated World
Karl Banse 1

Causes for Contemporary Regional Sea Level Changes
Detlef Stammer, Anny Cazenave, Rui M. Ponte, and Mark E. Tamisiea 21

Gravity Flows Associated with Flood Events and Carbon Burial: Taiwan as Instructional Source Area
James T. Liu, Shuh-Ji Kao, Chih-An Huh, and Chin-Chang Hung 47

A Deep-Time Perspective of Land-Ocean Linkages in the Sedimentary Record
Brian W. Romans and Stephan A. Graham 69

Remote Sensing of the Nearshore
Rob Holman and Merrick C. Haller 95

High-Frequency Radar Observations of Ocean Surface Currents
Jeffrey D. Paduan and Libe Washburn 115

Lagrangian Motion, Coherent Structures, and Lines of Persistent Material Strain
R.M. Samelson 137

Deglacial Origin of Barrier Reefs Along Low-Latitude Mixed Siliciclastic and Carbonate Continental Shelf Edges
André W. Droxler and Stéphan J. Jorry 165

The Trace Metal Composition of Marine Phytoplankton
Benjamin S. Twining and Stephen B. Baines 191

Photophysiological Expressions of Iron Stress in Phytoplankton
Michael J. Behrenfeld and Allen J. Milligan 217

Evaluation of In Situ Phytoplankton Growth Rates: A Synthesis of Data from Varied Approaches
Edward A. Laws 247

Icebergs as Unique Lagrangian Ecosystems in Polar Seas
K.L. Smith Jr., A.D. Sherman, T.J. Shaw, and J. Sprintall 269

Ecosystem Transformations of the Laurentian Great Lake Michigan by Nonindigenous Biological Invaders
Russell L. Cuhel and Carmen Aguilar 289

Ocean Acidification and Coral Reefs: Effects on Breakdown, Dissolution, and Net Ecosystem Calcification
Andreas J. Andersson and Dwight Gledhill 321

Evolutionary Adaptation of Marine Zooplankton to Global Change
Hans G. Dam 349

Resilience to Climate Change in Coastal Marine Ecosystems
Joanna R. Bernhardt and Heather M. Leslie 371

Oceanographic and Biological Effects of Shoaling of the Oxygen Minimum Zone
William F. Gilly, J. Michael Beman, Steven Y. Litvin, and Bruce H. Robison 393

Recalcitrant Dissolved Organic Carbon Fractions
Dennis A. Hansell 421

The Global Distribution and Dynamics of Chromophoric Dissolved Organic Matter
Norman B. Nelson and David A. Siegel 447

The World Ocean Silica Cycle
Paul J. Tréguer and Christina L. De La Rocha 477

Using Triple Isotopes of Dissolved Oxygen to Evaluate Global Marine Productivity
L.W. Juranek and P.D. Quay 503

What Is the Metabolic State of the Oligotrophic Ocean? A Debate
Hugh W. Ducklow and Scott C. Doney 525

The Oligotrophic Ocean Is Autotrophic
Peter J. le B. Williams, Paul D. Quay, Toby K. Westberry, and Michael J. Behrenfeld 535

The Oligotrophic Ocean Is Heterotrophic
Carlos M. Duarte, Aurore Regaudie-de-Gioux, Jesús M. Arrieta, Antonio Delgado-Huertas, and Susana Agustí 551

Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at http://marine.annualreviews.org/errata.shtml