The Oligotrophic Ocean Is Heterotrophic*

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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 autotrophy, see Williams et al. (2013).

Keywords

production, respiration, metabolism, plankton, carbon inputs

Abstract

Incubation (in vitro) and incubation-free (in situ) methods, each with their own advantages and limitations, have been used to derive estimates of net community metabolism in the oligotrophic subtropical gyres of the open ocean. The hypothesis that heterotrophic communities are prevalent in most oligotrophic regions is consistent with the available evidence and supported by scaling relationships showing that heterotrophic communities prevail in areas of low gross primary production, low chlorophyll *a*, and warm water, conditions found in the oligotrophic ocean. Heterotrophic metabolism can prevail where heterotrophic activity is subsidized by organic carbon inputs from the continental shelf or the atmosphere and from nonphotosynthetic autotrophic regions is likely to be tilting the metabolic balance of the ocean toward a greater prevalence of heterotrophic communities.

THE PARADIGM OF THE OCEAN AS AN AUTOTROPHIC ECOSYSTEM

Despite supporting only 0.2% of the photosynthetic biomass in the biosphere, the global ocean is responsible for approximately half of the net primary production of the biosphere (Smith 1981, Falkowski et al. 2000), supporting annual fishery catches of 96 million tons (Duarte et al. 2009) and the functioning of the dark ocean ecosystem (Arístegui et al. 2009). The important role of marine autotrophs in the Earth system helped confirm the paradigm that plankton communities in the euphotic layer of the ocean are autotrophic (Ducklow & Doney 2013), an idea that was already present in Odum's first conceptualizations of ecosystem metabolism (see Odum 1956, figure 2).

Heterotrophy was, in Odum's (1956) conceptualization, a characteristic of dysfunctional ecosystems, such as those affected by high organic inputs; autotrophic ecosystems were represented as healthy. However, Smith & Hollibaugh (1993) proposed that the ocean as a whole is a heterotrophic system, on the basis that the riverine inputs of organic carbon (A_{input}) exceed the burial of carbon (B) in ocean sediments (i.e., $A_{input} - B > 0$). This rationale assumes that the pelagic organic carbon pool in the ocean is in a steady state and therefore that the only compartment of the ocean that accumulates organic carbon is the sediment, so that the rate of change in organic carbon stocks, $\frac{\partial C_{org}}{\partial r}$, equals B in the mass balance equation for organic carbon

$$\frac{\partial C_{\text{org}}}{\partial t} = \text{GPP} - \text{R} + f_{\text{air-sea}} + A_{\text{input}},\tag{1}$$

where GPP and R are the gross primary production and community respiration, respectively, and $f_{air-sea}$ is the air-sea exchange of organic carbon, which here equals 0. This rationale implies that net community production (NCP) < 0, because

$$NCP = GPP - R = B - A_{input}.$$
 (2)

Smith & Hollibaugh (1993) estimated the heterotrophy in the global ocean, supported by riverine inputs, to be approximately 0.2 Pg C year⁻¹. However, this estimate refers to the entire ocean, where the layer below the euphotic layer is, despite significant chemosynthetic contributions to organic matter production (Arístegui et al. 2009, Middelburg 2011), clearly heterotrophic (del Giorgio & Duarte 2002, Arístegui et al. 2009).

Yet del Giorgio et al. (1997) suggested that plankton communities in the euphotic layer of the oligotrophic ocean are heterotrophic because bacterial carbon use tends to exceed net primary production. The finding that planktonic R tends to exceed GPP in unproductive aquatic ecosystems further suggested that the oligotrophic ocean tends to support net heterotrophic communities (Duarte & Agustí 1998). A parallel paper argued that oceanic plankton communities were in approximate metabolic balance (Williams 1998). The ensuing argument (see Duarte et al. 1999, Williams & Bowers 1999, del Giorgio & Duarte 2002, Karl et al. 2003) has extended for approximately a decade, and the arguments supporting and challenging the prevalence of heterotrophic communities in the oligotrophic ocean led to the debate articles presented in this volume of the *Annual Review of Marine Science* (see also Ducklow & Doney 2013 and Williams et al. 2013). Controversies often stimulate new insights (Hansell et al. 2009), and so this controversy about the metabolic status of the ocean has provided the impetus for significant methodological and conceptual advances discussed here and in the companion articles.

Here, we present arguments supporting the conclusion that heterotrophic communities prevail in the oligotrophic ocean. We consider three sets of arguments, based respectively on (*a*) empirical evidence, (*b*) scaling, and (*c*) logical and theoretical considerations.

EMPIRICAL EVIDENCE FOR A PREVALENCE OF HETEROTROPHY IN THE OLIGOTROPHIC OCEAN

The currently available empirical basis for NCP values in ocean communities amounts to 4,799 estimates (A. Regaudie-de-Gioux & C.M. Duarte, manuscript submitted), with an uneven distribution across the ocean (**Figure 1**). One-third (33%) of the 1,265 depth-integrated NCP estimates correspond to heterotrophic communities (NCP < 0 mmol O₂ m⁻² day⁻¹), and 45% of the 3,534 volumetric NCP estimates correspond to heterotrophic communities (NCP < 0 mmol O₂ m⁻³ day⁻¹) (A. Regaudie-de-Gioux & C.M. Duarte, manuscript submitted). The stations in the data set assembled by A. Regaudie-de-Gioux & C.M. Duarte (manuscript submitted) were classified as located in the central oligotrophic gyres, following the delimitation of these areas provided by McClain et al. (2002), who used ocean color and dynamic height along with other ancillary data to delineate the oligotrophic gyres.

Of the 4,799 NCP estimates available, only 1,630 (34%) are estimates of net community metabolism for the oligotrophic ocean. Most of these estimates correspond to the eastern margin of the North Atlantic Subtropical Gyre, the Mediterranean Sea, the western margin of the South Atlantic Subtropical Gyre, and the North Pacific Subtropical Gyre, with very few estimates for the western sector of the North Atlantic Subtropical Gyre or any other subtropical gyres (**Figure 1**, **Table 1**). Of these 1,630 estimates, including those for the oligotrophic subtropical gyres and the Mediterranean Sea, 923 (57%) correspond to net heterotrophic communities.

The estimates also point to a prevalence of heterotrophic communities in the North Atlantic Subtropical Gyre and the Mediterranean Sea, the regions of the oligotrophic ocean most



Figure 1



 Table 1
 Number of estimates of net community production (NCP) and related results for plankton in the oligotrophic ocean and the Mediterranean Sea

| | Number of | Number of | Mean volumetric | Mean integrated | Median |
|--|-----------|-------------|-------------------|-------------------|-----------------|
| Region | estimates | communities | $m^{-3} day^{-1}$ | $m^{-2} day^{-1}$ | $GPP/R \pm SE$ |
| North Atlantic Subtropical Gyre | 215 | 144 (67%) | -0.37 ± 0.06 | -20.8 ± 8.8 | 0.62 ± 0.15 |
| South Atlantic Subtropical Gyre | 193 | 87 (45%) | 3.55 ± 1.09 | -18.6 ± 12.3 | 0.67 ± 0.28 |
| North Pacific Subtropical Gyre | 475 | 239 (50%) | 0.03 ± 0.11 | 142.7 ± 14.1 | 0.75 ± 0.23 |
| South Pacific Subtropical Gyre | 10 | 1 (10%) | 0.01 ± 0.34 | 16.7 ± 3.9 | 1.17 ± 0.53 |
| South Indian Ocean Subtropical Gyre | 32 | 7 (22%) | 1.70 ± 0.34 | 45.8 ± 13.8 | 2.12 ± 0.41 |
| Mediterranean Sea | 705 | 445 (63%) | -0.99 ± 0.23 | -9.2 ± 15.5 | 0.74 ± 0.22 |

Estimates derived from the data set compiled by A. Regaudie-de-Gioux & C.M. Duarte (manuscript submitted). Abbreviations: GPP, gross primary production; R, community respiration.

intensively sampled (Figure 1), for which NCP was estimated at significantly <0 and the median GPP/R ratio was estimated at <1 (Figure 1, Table 1). In the estimates for these two regions, 67% and 63% of the communities were heterotrophic, respectively (Table 1). The median GPP/R ratio of the South Atlantic Subtropical Gyre was also <1 (0.67), but the NCP was not significantly <0 (Table 1). The data for the North Pacific Subtropical Gyre point to a median GPP/R ratio of <1 (0.75), but 50% of communities were heterotrophic, and the NCP indicated an approximate metabolic balance (Table 1).

In the oligotrophic ocean, communities in shallow waters (<25 m) tend to be in metabolic balance or slightly autotrophic (**Figure 2**). Deeper waters, in contrast, have shown a prevalence of heterotrophic communities with negative average community production (**Figure 2**). Approximately 70% of the communities at 120 m—the average depth of the deep chlorophyll *a* maximum in the oligotrophic ocean—support autotrophic communities (**Figure 2**).

Hence, the empirical evidence indicates that heterotrophic communities are found more frequently than autotrophic communities in the oligotrophic ocean, as the median GPP/R ratio of the volumetric estimates of community metabolism are <1 for all oligotrophic regions for which estimates are available (>50 sites) (**Table 1**). Heterotrophic communities clearly prevail in the North Atlantic Subtropical Gyre and Mediterranean Sea, whereas the evidence indicates that communities in the South Atlantic and North Pacific Subtropical Gyres are in approximate metabolic balance (**Table 1**). Data on the metabolic balances of the Indian Ocean and South Pacific Subtropical Gyres are insufficient to venture any inference (**Table 1**). The limited empirical basis remains a major bottleneck to directly determining the metabolic balance of the oligotrophic ocean (e.g., Robinson & Williams 2005).

INCUBATION VERSUS INCUBATION-FREE ASSESSMENTS OF NET COMMUNITY PRODUCTION

The estimates discussed above were derived using a range of methods, including incubation (in vitro) and incubation-free (in situ) techniques, which contributed a total of 1,311 and 319 of



Figure 2

Depth distributions of the (*a*) average (\pm SE) percentage of heterotrophic communities and (*b*) average (\pm SE) net community production in the oligotrophic subtropical gyres of the open ocean. Depth values were derived from data assembled by A. Regaudie-de-Gioux & C.M. Duarte (manuscript submitted) and averaged by 10-m bins. The dashed line in panel *a* indicates equal proportions of autotrophic and heterotrophic communities; the dashed line in panel *b* separates autotrophic from heterotrophic communities.

the NCP estimates for the oligotrophic ocean, respectively. Incubation techniques allow the assessment of NCP at discrete depths and over the length of the incubations, typically 24 h. In contrast, incubation-free techniques resolve NCP integrated across a fixed depth range, typically the surface mixed layer, and deliver rates integrated over weeks to months (Robinson & Williams 2005).

Incubation techniques involve the confinement of the community and are therefore prone to artifacts. The dark-light incubation technique is known to underestimate R—and thus to overestimate GPP, which is calculated as NCP – R—because R is typically higher in the light than in the dark, contrary to assumptions of the method (Bender et al. 1987, Dickson & Orchardo 2001). However, this does not affect NCP estimates. Incubation techniques typically miss the contribution of larger zooplankton, which leads to an underestimation of R, typically by approximately 3% (Robinson & Williams 2005), and therefore to an overestimation of NCP by that same magnitude in absolute terms. This underestimation implies that, in the data set used here, the proportion of heterotrophic communities in the oligotrophic ocean was likely to be underestimated, although only slightly, by 1.5%.

The enclosure can also affect the light regime. Most NCP estimates obtained in vitro have been produced using borosilicate bottles, which remove the UVB component of the solar radiation spectrum (Godoy et al. 2012). Removal of UVB affects NCP, often leading to overestimation of NCP (Godoy et al. 2012). Accordingly, published estimates of NCP derived from incubation techniques have overestimated NCP and hence underestimated the extent of the heterotrophy of oceanic plankton communities because they do not include all of the heterotrophic community and because they exclude UVB radiation by borosilicate bottles.

The observation that the ratio of autotrophic to heterotrophic biomass declines during incubations led to suggestions that confinement could bias the estimates of plankton metabolism (Calvo-Díaz et al. 2011). However, high-frequency time-series studies in oligotrophic ocean waters have reported that autotrophs experience strong diel variability in situ (Llabrés et al. 2011, Loisel et al. 2011) resulting from high cell mortality rates at the beginning of the night as damaged cells fail to divide (Llabrés et al. 2011). Bacterial production has also been reported to display diel cycles in oligotrophic environments (Gasol et al. 1998). Changes observed during incubations are indeed consistent with in situ observations and therefore are not necessarily an artifact of enclosure in bottles.

Incubation-free techniques for estimating NCP comprise a range of approaches, including time series of O_2 and pCO_2 sensors mounted on Lagrangian buoys (Moore et al. 2011), Argo floats (e.g., Riser & Johnson 2008), and gliders (e.g., Nicholson et al. 2008) as well as methods of inferring rates that use anomalies in the O_2/N_2 ratio (e.g., Emerson et al. 2008) or O_2/Ar ratio (e.g., Kaiser et al. 2005). Techniques based on triple O_2 isotopes have also been applied (e.g., Luz & Barkan 2000, 2009), but these deliver estimates of GPP alone and do not allow NCP to be determined, and the assumptions and calculations involved are subject to considerable disagreement (e.g., Quay et al. 2010, Kaiser 2011, Nicholson 2011, Prokopenko et al. 2011, Marra 2012).

Incubation-free techniques avoid the problems derived from confinement, but suffer from several limitations because the estimates are critically dependent on assumptions about the mixing rate in the mixed layer and about exchanges with the underlying and neighboring waters and overlying atmosphere (Luz & Barkan 2009). The assumption that the mixed layer is actually mixing at the time of sampling, which is implicit in some of these methods, is probably correct in most cases. NOAA climatology data (NCEP_Marine, provided by the NOAA Office of Oceanic and Atmospheric Research, Earth System Research Laboratory, Physical Sciences Division, at http://www.esrl.noaa.gov/psd) point at average wind speeds of approximately 7 m s⁻¹ in the oligotrophic gyres, for which equations in Denman & Gargett (1983) predict mixing times of approximately 3 h (at 20° latitude and 200 m mixed depth). Estimates of the O_2 exchange with the atmosphere, typically a large flux (e.g., Sarma et al. 2005), depend on parameterizations of the gas transfer velocity from wind speed that can introduce uncertainties of up to 30%, or even larger (Calleja et al. 2009), in the resulting NCP estimates (Robinson & Williams 2005). The contribution of bubbles to transport and exchanges can also be important (Emerson et al. 2008), affecting the calculations derived from most O_2 -based incubation-free methods. The use of O_2/N_2 anomalies to extract biological signals also involves considerable uncertainty because of the different solubilities of O_2 and N_2 (Emerson et al. 2008), although this is a smaller problem when O₂/Ar ratios are used (Kaiser et al. 2005). Incubation-free techniques often assume atmospheric gases to be constant in terms of partial pressure, isotopic composition, and O_2/N_2 and O_2/Ar ratios, but variability in atmospheric O_2 and N_2 (e.g., Stephens et al. 2003, Bender et al. 2005) may also be a source of error, albeit a comparatively small one.

Incubation-free techniques also include examination of the carbon stable isotopic composition of dissolved inorganic carbon (DIC) in the euphotic layer (δ^{13} C-DIC) (Williams et al. 2013). However, NCP in the oligotrophic ocean is generally too small to affect δ^{13} C signatures above the level of detection. When in isolation, autotrophic and heterotrophic communities should lead to more positive and more negative δ^{13} C isotopic signatures of DIC, respectively, as argued by Williams et al. (2013). However, the production and removal of CO₂ associated with NCP are small relative to the DIC pool. For instance, considering an NCP of -5 mmol C m⁻² day⁻¹ accumulated over a year would lead to a δ^{13} C-DIC decline of approximately 0.18, close to the analytical error (\pm 0.1), ignoring all other factors that contribute to δ^{13} C-DIC variability such as calcification and carbonate dissolution and air-sea exchange. Whereas heterotrophic metabolism is clearly responsible for a decline in δ^{13} C-DIC below the mixed layer (Kroopnick 1985), biological effects in the mixed layer are more difficult to resolve owing to buffering effects associated with air-sea exchange of CO₂. Hence, arguments on the net metabolism of the oligotrophic ocean based on trends in δ^{13} C-DIC (Williams et al. 2013) appear unreliable. As a result, the uncertainty associated with NCP estimates based on incubation-free techniques is considerable, challenging the detection of the very low NCP rates characteristic of communities in oligotrophic gyres. For instance, Stanley et al. (2010) reported that the average NCP near Papua New Guinea was $4.8 \pm 0.6 \text{ mmol } \text{O}_2 \text{ m}^{-2} \text{ day}^{-1}$ with a standard deviation of $\pm 6.0 \text{ mmol } \text{O}_2 \text{ m}^{-2}$ day⁻¹, and Emerson et al. (2008) used error propagation techniques to calculate that net biological O₂ production was determined to $\pm 54\%$ from records of O₂ and N₂ at the Hawaii Ocean Time-Series (HOT) site. However, the integration of discrete in vitro estimates to derive euphotic layer rates also involves substantial error, as demonstrated using error propagation techniques, which yield a coefficient of variation for the integrated NCP of 19.5% for a subsample of the oligotrophic ocean stations in our data set.

Lastly, the euphotic zone often extends below the mixed layer in oligotrophic subtropical gyres. Because incubation-free methods typically integrate metabolism over the mixed layer, the resulting NCP estimates exclude the lower part of the euphotic layer, where a sizable fraction of production may occur (e.g., Luz & Barkan 2009) but also where (most importantly) R tends to be high relative to GPP (**Figure 2**) (e.g., Regaudie-de-Gioux & Duarte 2010). As a consequence, incubation-free methods involve considerable uncertainty and may overestimate NCP when communities within the fraction of the euphotic layer below the mixed layer are heterotrophic. Hence, comparisons of nonsynoptic NCP data derived in vitro and in situ (Williams et al. 2013) need to consider the different depths of integration, which may account for the tendency of in situ techniques to yield more positive NCP values (Williams et al. 2013). The argument that oligotrophic regions cannot support heterotrophic communities because this is not supported by incubation-free techniques (Williams et al. 2013) therefore ignores the limitations of these techniques and the limited data available based on these techniques.

Hence, both incubation and incubation-free estimates of NCP are affected by multiple sources of error and bias and have both advantages and limitations. Quay et al. (2010) questioned production estimates derived in vitro on the basis that triple O_2 isotope methods, which they assumed to be superior (e.g., Quay et al. 2010, Williams et al. 2013), derived much greater estimates of GPP, possibly suggesting that NCP is underestimated in vitro. Yet Marra (2012) calculated that, compared with chlorophyll *a* concentrations, production derived from triple O_2 isotope methods by Quay et al. (2010) exceeded the theoretical limits imposed by quantum yields, and questioned their reliability. Arguments for the superiority of one method over another are spurious and can be challenged unless the methods are compared directly through synoptic studies (Marra 2012), which has been reported only twice (Marra 2002, Robinson et al. 2009). Both of these studies concluded that in vitro and in situ estimates of NCP were in good agreement when averaged over days.

SCALING ARGUMENTS FOR A PREVALENCE OF HETEROTROPHY IN THE OLIGOTROPHIC OCEAN

An alternative approach to assessing whether heterotrophic metabolism prevails in specific regions of the ocean has been to derive scaling laws that allow inferences about the metabolic balance.

Scaling Gross Primary Production and Community Respiration

Examination of the relationship between GPP and R has shown that GPP does not scale proportionately to R in oceanic plankton communities (Duarte & Agustí 1998; Robinson & Williams 2005; A. Regaudie-de-Gioux & C.M. Duarte, manuscript submitted). The most comprehensive representation of the relationship between GPP and R (in units of mmol $O_2 m^{-3} day^{-1}$) is that of A. Regaudie-de-Gioux & C.M. Duarte (manuscript submitted),

$$R = 1.07 \text{GPP}^{0.78(\pm 0.01)}$$

$$(R^2 = 0.31, \ n = 3,061),$$
(3)

which confirms that R tends to be highest relative to GPP in unproductive waters and that the GPP/R ratio increases with increasing GPP. Indeed, GPP is significantly higher for autotrophic communities (5.2 \pm 0.5 mmol O₂ m⁻³ day⁻¹) than for heterotrophic ones (1.3 \pm 0.3 mmol O₂ m⁻³ day⁻¹) (A. Regaudie-de-Gioux & C.M. Duarte, manuscript submitted). Logistic regression shows that the GPP threshold separating autotrophic from heterotrophic communities is 1.41 mmol O₂ m⁻³ day⁻¹ (A. Regaudie-de-Gioux & C.M. Duarte, manuscript submitted). The existence of a GPP threshold at approximately 2 mmol O2 m⁻³ day⁻¹ below which plankton communities tend to be heterotrophic has been confirmed repeatedly through surveys of communities at regional and global levels, time series of plankton community metabolism, experimental manipulations in mesocosms, and theoretical models (Duarte & Regaudie-de-Gioux 2009) and is therefore a robust result. This threshold also suggests that the least productive regions within the oligotrophic ocean are likely to support heterotrophic communities. Indeed, the mean GPP in the oligotrophic ocean is 1.69 \pm 0.08 mmol O₂ m⁻³ day⁻¹ (A. Regaudie-de-Gioux & C.M. Duarte, manuscript submitted), which is very close to the threshold separating autotrophic from heterotrophic communities. Yet the limited and skewed geographic distribution of oceanic GPP estimates precludes delineation of the distribution of ocean regions where, on the basis of this threshold, heterotrophic communities would be expected to prevail.

Scaling Net Community Production to Temperature and Chlorophyll a

An alternative scaling approach involves the elucidation of thresholds separating autotrophic from heterotrophic communities on the basis of properties that can be derived from space, such as temperature and chlorophyll *a*, both of which affect plankton community metabolism. Metabolic theory predicts that respiration rates should rise more rapidly than GPP as temperature increases (Harris et al. 2006, López-Urrutia et al. 2006, Regaudie-de-Gioux & Duarte 2012). Indeed, a recent assessment indicated that the activation energy—a metric derived from the Arrhenius equation describing the temperature dependence of a process—for planktonic R is 0.66 \pm 0.05 eV, twice as high as that for GPP (0.32 \pm 0.04 eV) (Regaudie-de-Gioux & Duarte 2012). That R increases more rapidly with warming than GPP does implies that NCP should decline with warming. Regaudie-de-Gioux & Duarte (2012) reported a negative relationship between temperature and the GPP/R ratio of oceanic plankton communities, implying that communities in waters warmer than 21°C tend to be heterotrophic. The areas of the ocean with mean annual surface temperatures of >21°C, where heterotrophic communities would be expected to prevail, occupy 39.6% of the ocean surface, including the tropical and subtropical ocean and most of the Mediterranean Sea (**Figure 3**).

GPP (mmol O₂ m⁻³ day⁻¹) is also scaled to chlorophyll *a* concentration (mg m⁻³), a property available from remotely sensed products, as described by the fitted regression equation (A. Regaudie-de-Gioux & C.M. Duarte, manuscript submitted)

$$GPP = 3.38Chl a^{1.05(\pm 0.03)}$$

$$(R^2 = 0.26, \ p < 0.05),$$
(4)

where the power slope is close to 1.0, showing that GPP increases proportionally to chlorophyll *a*. Autotrophic communities support greater chlorophyll *a* concentrations than heterotrophic ones do $(1.65 \pm 0.10 \text{ mg m}^{-3} \text{ versus } 0.81 \pm 0.06 \text{ mg m}^{-3}, \text{ respectively; A. Regaudie-de-Gioux & }$





Figure 3

Areas of the ocean with (*a*) mean chlorophyll *a* concentrations of $<0.44 \text{ mg m}^{-3}$ in 2011 (*purple*) and (*b*) mean annual surface temperatures of $>21^{\circ}$ C (*purple*), indicative of waters likely to support heterotrophic plankton communities. White areas were not evaluated owing to ice cover or other factors. Images derived from NASA Aqua MODIS data (http://oceandata.sci.gsfc.nasa.gov/MODISA/Binned/Annual).

C.M. Duarte, manuscript submitted), and logistic regression indicates that a threshold of 0.44 mg Chl a m⁻³ separates autotrophic from heterotrophic communities (A. Regaudie-de-Gioux & C.M. Duarte, manuscript submitted). The waters with mean annual chlorophyll a values of <0.44 mg m⁻³, where heterotrophic communities should prevail, occupy most (72.4%) of the ocean surface (**Figure 3**). The delineation of putative heterotrophic areas shown in **Figure 3** applies to the surface ocean alone, which is well represented by satellite products.

OCEAN ECOSYSTEMS ARE OPEN, NON-STEADY-STATE SYSTEMS

The controversy around the claim that the oligotrophic ocean is heterotrophic does not come from the empirical evidence alone; it is also fueled by conceptual barriers to considering the possibility of a prevalence of heterotrophy in the oligotrophic ocean. These barriers ultimately depend on the assumption that the oligotrophic ocean is essentially a closed system that does not receive significant inputs of allochthonous organic carbon.

Open systems can be heterotrophic while exporting organic carbon vertically if allochthonous carbon inputs suffice to support both fluxes (Cole et al. 2007). The conditions required to sustain heterotrophic communities (GPP – R < 0) can be best understood by separating $\frac{\partial C_{\text{org}}}{\partial t}$ in Equation 1 into two terms: $\frac{\partial C_{\text{org stock}}}{\partial t}$, the rate of change in the size of the organic carbon stock in the euphotic layer, and EC_{org} , the export below the euphotic layer. The organic carbon balance for the euphotic layer is then represented as

$$\frac{\partial C_{\text{org stock}}}{\partial t} = \text{GPP} - \text{R} + A_{\text{input}} + f_{\text{air-sea}} - EC_{\text{org}}.$$
(5)

Heterotrophic communities can be sustained if (a) $A_{input} + NCP \ge 0$, (b) $f_{air-sea} + NCP \ge 0$, (c) NCP $-\frac{\partial C_{org \, stock}}{\partial t} \ge 0$, or (d) $A_{input} + f_{air-sea} - \frac{\partial C_{org \, stock}}{\partial t} > 0$, implying significant lateral or atmospheric inputs of organic carbon and/or a decline in the pool of organic carbon in the euphotic layer. Moreover, ocean ecosystems can be heterotrophic and yet support a vertical export of organic matter if $A_{input} + f_{air-sea} + NCP > 0$, where NCP < 0. In a steady-state situation (i.e., $\frac{\partial C_{org \, stock}}{\partial t} = 0$), this leads to an export flux of organic carbon ($EC_{org} = A_{input} + f_{air-sea} + NCP$) corresponding to a net biological removal of CO₂ in the euphotic layer. Heterotrophy is possible in the absence of significant allochthonous organic inputs only if organic stocks are decreasing over time (i.e., $\frac{\partial C_{org \, stock}}{\partial t} < 0$).

Hence, two questions need be addressed to help settle the debate on the metabolic balance of the oligotrophic ocean: Does the oligotrophic ocean receive significant inputs of organic matter? And is the organic stock of the euphotic layer declining?

Does the Oligotrophic Ocean Receive Significant Inputs of Organic Matter?

Inputs of land-derived organic carbon driving Mediterranean plankton communities toward net heterotrophy are derived from the watersheds discharging to the Mediterranean Sea, including a significant fraction of those in northern Africa and southern Europe (Regaudie-de-Gioux et al. 2009). However, the existence of significant inputs of allochthonous organic carbon fueling heterotrophic communities in the central oligotrophic gyres is not straightforward. Depictions of the ocean carbon budget, such as those in the Intergovernmental Panel on Climate Change reports (Intergov. Panel Clim. Change 2001, Denman et al. 2007), imply that the ocean exchanges only CO_2 with the atmosphere and that marine biota in the surface ocean are net autotrophic, with an NCP of 11 Gt C year⁻¹ supporting a global export of the same magnitude. Yet the ocean does receive significant atmospheric inputs (del Giorgio & Duarte 2002): Rainfall contains organic carbon, aerosol deposition delivers organic carbon to the ocean (Duarte et al. 2005, Jurado et al. 2008), and many semivolatile organic compounds in the atmosphere can be transferred to the ocean through diffusive fluxes (Dachs et al. 2005, Ruíz-Halpern et al. 2010, Dixon et al. 2011). Dachs et al. (2005) and Duarte et al. (2006) reported that organic carbon inputs from dry aerosol deposition average 1 mmol C m⁻² day⁻¹, and Jurado et al. (2008) estimated that organic carbon inputs from total aerosol deposition deliver 0.24 Pg C year⁻¹ to the ocean. Dachs et al. (2005) reported a large air-sea exchange of volatile organic carbon supplying 25–31 mmol C m⁻² day⁻¹ to the subtropical northeast Atlantic.

This high atmospheric organic carbon input is likely to represent an upper value for the ocean, as the subtropical northeast Atlantic is an area supporting particularly high atmospheric inputs (Jickells et al. 2005), but even input rates six times lower than those reported for the subtropical northeast Atlantic would suffice to support excess R over GPP in the least productive regions of the ocean. Research in a subarctic fjord showed an average input of atmospheric semivolatile organic material of 9.6 \pm 4 mmol C m⁻² day⁻¹, sufficient to affect the carbon budget of the ecosystem (Ruíz-Halpern et al. 2010). Methanol, an important component of atmospheric organic carbon, has been found to support between 4% and 17% (average 9.5%) of the bacterial carbon demand in oligotrophic waters of the North Atlantic Gyre and up to 54% in more productive waters (Dixon et al. 2011). Diffusive fluxes of semivolatile organic carbon are likely to dominate the input of organic atmospheric materials to the ocean (Jurado et al. 2008). Whereas the paucity of estimates precludes the assignment of a global flux of organic carbon deposition to the ocean, depictions of the ocean carbon budget should at least acknowledge this process (**Figure 4**).

Riverine input of carbon has been estimated at $0.8 \text{ Pg C year}^{-1}$ (Denman et al. 2007), half of which corresponds to organic carbon. Much of this input is believed to be respired within the coastal ocean (Borges 2005, Duarte et al. 2005). Yet vegetated coastal habitats formed by macrophytes, including seagrass meadows, salt marshes, and mangrove forests, are strongly autotrophic (Duarte & Cebrián 1996) and have the capacity to export substantial amounts of carbon to the open ocean (Duarte et al. 2005). Indeed, recent analyses of the organic carbon budget of the coastal ocean indicate that the coastal ocean exports up to 8.5 Pg C year⁻¹ to the open ocean (C. Barrón & C.M. Duarte, manuscript submitted). Regional estimates have indicated that the coastal ocean exports between 1.4 and 124.2 Gg C year⁻¹ per kilometer of shelf break, with a median export rate of 19.9 Gg C year⁻¹ per kilometer of shelf break, equivalent to approximately 5 Pg C year⁻¹ (C. Barrón & C.M. Duarte, manuscript submitted). The suggestion that a large flux of organic carbon exported from the coastal ocean could reach the open ocean, subsidizing heterotrophic metabolism therein (Duarte & Agustí 1998), was met with the criticism that this "would also require massive water transport-perhaps 50 to 1500 sverdrups, which is a flow comparable to or many times greater than the Gulf Stream" (Williams & Bowers 1999). This calculation turns out to be very reasonable, as an integration of the multiple mechanisms responsible for hydrological exchanges between the coastal and open ocean yield, as a rule of thumb, an average hydrological exchange rate of approximately 1 sverdrup (1 Sv = $10^6 \text{ m}^3 \text{ s}^{-1}$) per 1,000 km of shelf break (Huthnance 1995). With a global shelf-break length of 300,000 km, the resulting water exchange between the coastal and open ocean of 300 Sv is consistent with that required by Williams & Bowers (1999).

The ocean is, therefore, an open system receiving organic carbon inputs from the atmosphere and the coastal ocean, potentially able to support heterotrophic communities, particularly in the oligotrophic ocean, where allochthonous organic carbon inputs would be most important relative to GPP. The existence of a GPP threshold below which plankton communities tend to be heterotrophic (see above) is consistent with the existence of a low but significant background flux of allochthonous organic carbon (Duarte & Regaudie-de-Gioux 2009). This GPP threshold of approximately 2 mmol C m⁻² day⁻¹ has been argued to provide an indirect estimate of the



Figure 4

Modified representation of the organic carbon budget of the oligotrophic ocean, showing the additional net processes that must be resolved to assess the hypothesized prevalence of heterotrophy by solving the mass balance equation NCP = $\frac{\partial C_{\text{org stock}}}{\partial t} - fC_{\text{org}} - EC_{\text{org}} - AC_{\text{org}}$ (modified from Equation 1). NCP is net community production, $\frac{\partial C_{\text{org stock}}}{\partial t}$ is the rate of change in organic carbon stocks, fC_{org} is the input of organic carbon from the atmosphere, EC_{org} is the vertical export flux of organic carbon, and AC_{org} is the net input of organic carbon from the continental shelf. DOC is dissolved organic carbon.

magnitude of allochthonous organic inputs to the oligotrophic ocean (Duarte & Regaudie-de-Gioux 2009). The rationale above is implicitly adopted in depictions of the predisturbance carbon budget of the ocean, which indicates the ocean to be a weak source of CO_2 to the atmosphere at an amount equal to the size of the recognized allochthonous inputs of organic carbon of 0.6 Pg C year⁻¹ (Denman et al. 2007). If the ocean was heterotrophic throughout the Holocene and the biological pump has not been perturbed, then, as a corollary, marine biota should remain heterotrophic.

Is the Organic Stock of the Euphotic Layer Declining?

No area of the ocean is likely to be permanently autotrophic or heterotrophic, so the question debated here is which metabolic mode prevails over relevant temporal and spatial scales. At seasonal or shorter scales, pulses of autotrophy have been invoked to balance the prevalent heterotrophic metabolism off Hawaii (e.g., Karl et al. 2003). However, the evidence presented was based on changes in O_2/N_2 ratios, which could be explained equally by temperature anomalies affecting O_2 and N_2 differentially because of their different solubilities (see Karl et al. 2003, figure 1). Pulses of increased GPP and R can be produced, respectively, when the mixed layer shoals or deepens owing to the passage of eddies and Rossby waves (Nicholson et al. 2008). However, continuous monitoring of the region using gliders fitted with O_2 sensors has not produced evidence for the occurrence of pulses of primary production (Riser & Johnson 2008). Net community metabolism

also changes seasonally, and Agustí (2012) has reported a trend for the plankton community in surface waters of the tropical and subtropical central Atlantic to be more strongly heterotrophic in autumn than in spring owing to changes in respiration rates, possibly associated with shifts in the temperature regime.

Recent reports have provided evidence that the primary production of the ocean is declining (Gregg & Conkright 2002)—particularly in the unproductive oligotrophic gyres (Antoine et al. 2005), which seem to have recently expanded in size (Polovina et al. 2008)—and that the chlorophyll a concentration has declined globally at rates of approximately 1% per year, which is related to increasing sea surface temperature and vertical stratification (Boyce et al. 2010). Whether these trends represent long-term monotonous trends or climatic-driven decadal fluctuations is subject to debate, particularly where trends depend on aggregating data derived using different instruments and methods (e.g., Boyce et al. 2011, Mackas 2011, Rykaczewski & Dunne 2011). Reanalysis of SeaWiFS (Sea-Viewing Wide Field-of-View Sensor) records of chlorophyll a anomalies in warm, permanently stratified ocean waters (including the oligotrophic gyres) indicates a period of increase in 1997–1998 followed by a period of decline extending to 2009 (O'Malley et al. 2009), confirming previously reported negative relationships between temperature and primary production and chlorophyll a (Behrenfeld et al. 2006). Elucidating whether these changes represent long-term monotonous changes driven by anthropogenic climate change or rather reflect decadal climatic fluctuation will require a coherent record beyond that currently available. Hence, primary production in the euphotic layer of the oligotrophic ocean is not static but rather appears to be declining recently and/or to experience decadal oscillations. For NCP to remain unchanged while GPP and chlorophyll *a* decrease, R should show a parallel decline, which cannot be tested because similar long-term records are not available for R. Instead, R tends to increase relative to GPP as GPP decreases (Equation 2). Warming, argued to be responsible for the decline in GPP and chlorophyll *a* (Polovina et al. 2008, Boyce et al. 2010), is expected to increase R relative to GPP. increasing the likelihood of heterotrophic community metabolism (Regaudie-de-Gioux & Duarte 2012).

During periods when the oligotrophic ocean expands, GPP and chlorophyll *a* decline and the oceans warm, and a greater fraction of oligotrophic ocean communities would then lie below the 2 mmol C m⁻² day⁻¹ and 0.44 mg Chl *a* m⁻³ thresholds and above the 21°C threshold separating autotrophic from heterotrophic communities, further increasing the likelihood of communities in the oligotrophic ocean being heterotrophic. Hence, changes in NCP are likely to occur with ocean warming, possibly reverting the role of oceanic plankton in the global budget (Regaudie-de-Gioux & Duarte 2012).

Hence, representations of the ocean as a static system presenting two steady-state modes of carbon cycling—a predisturbance mode and a mode affected by anthropogenic disturbances— do not recognize the dynamic nature of ocean ecosystems in a context of rapid change. Since humans began exerting significant changes in the carbon cycles, the oceans have warmed, CO_2 concentrations have increased, pH and O_2 have declined, and GPP and chlorophyll *a* appear to be declining in the oligotrophic gyres. Continuing to assume, for the convenience of calculations, that the carbon budget of oceanic plankton communities is in a steady state is difficult to reconcile with the wealth of evidence pointing at change.

Is the Metabolic Budget of the Ocean Sufficiently Represented by Photosynthesis and Respiration?

An additional conceptual tenet in this debate is that the metabolic budget of oceanic plankton communities is sufficiently constrained through the balance between photosynthetic carbon fixation and respiration. Indeed, the classical model of the marine microbial food web is based on the idea that all the organic carbon and energy available to the marine microbial food web are generated by oxygenic photosynthesis, with all subsequent processes supported by the oxidation of photosynthetic-derived organic carbon using O_2 as the final electron acceptor. Although this holds true for most of the carbon and energy flowing through marine food webs, several alternative pathways exist that supply additional organic carbon and energy.

Aquatic heterotrophic prokaryotes incorporate 4%–6% of the new biomass production as inorganic carbon via the anaplerotic reactions of the tricarboxylic acid cycle (Jørgensen 2006). However, biomass production usually accounts for a small part (10%–20%) of the total prokaryotic carbon use. Thus, heterotrophic carbon fixation via anaplerotic reactions could only be responsible for a few percent of the carbon demands of heterotrophic prokaryotes, which shows that not all the organic carbon available to heterotrophs is produced by oxygenic photosynthesis. However small relative to GPP and R, heterotrophic carbon fixation via anaplerotic reactions may produce enough organic carbon to raise respiration significantly above the ceiling imposed by photosynthesis, significantly lowering NCP even in the absence of allochthonous inputs.

Dark fixation of DIC by chemoautotrophs, although most important in the dark ocean (Ingalls et al. 2006, Reinthaler et al. 2010), is not confined to the dark ocean. Crenarchaeota organisms have been shown to autotrophically incorporate bicarbonate into their lipids in surface waters of the North Sea (Wuchter et al. 2003). Despite uncertainties regarding the metabolic pathways and energy sources fueling chemoautotrophy (Reinthaler et al. 2010), this process supplies an estimated 0.28 Pg C year⁻¹ to the euphotic zone (Middelburg 2011). In addition, many heterotrophs have been found to subsidize their metabolism with extra energy by light-dependent mechanisms (mixotrophs). Proteorhodopsins are light-driven proton pumps that enhance the production of ATP and lower the oxidative carbon requirements of marine heterotrophs. Proteorhodopsin genes are commonly found in surface marine bacteria, and approximately 50% of the bacteria in the Sargasso Sea harbor them (Campbell et al. 2008). The ability of heterotrophs to obtain extra energy from light may not appear to be relevant for the autotrophy-versus-heterotrophy debate because it does not necessarily generate new organic carbon. However, genomic analysis of Polaribacter sp. MED152, a proteorhodopsin-containing marine bacterium, revealed a remarkably large number of genes related to anaplerotic metabolism (González et al. 2008). Although Polaribacter sp. MED152 is an obligate heterotroph, CO_2 fixation experiments revealed that it was able to fix CO_2 much faster in the light than in the dark (González et al. 2008), indicating that proteorhodopsins increase the relative importance of anaplerotic carbon fixation in marine microbes.

Aerobic anoxygenic photosynthetic bacteria (AAPBs) are also relatively abundant members of microbial assemblages, representing a significant fraction of the heterotrophic prokaryotes in surface waters of the oceans (Jiao et al. 2007). AAPBs are obligate aerobic heterotrophs containing bacteriochlorophyll *a* and are able to use both light and organic substrates to produce energy. Physiological evidence suggests that aerobic anoxygenic photosynthesis may be an adaptation to oligotrophic conditions (Yurkov & Gemerden 1993, Suyama et al. 2002), although these organisms are also found in eutrophic environments. AAPBs also show enhanced inorganic carbon fixation in the presence of light (Kolber 2001), probably by lowering their respiratory requirements and enhancing the flow of carbon through their biosynthetic routes, as has been deduced by the genomic interpretation (Swingley et al. 2007) and metabolic analysis (Tang et al. 2009) of the cultured AAPB *Roseobacter denitrificans* OCh114. The latter study showed that *R. denitrificans* can derive 10%–15% of its protein carbon directly from inorganic carbon.

Thus, chemoautotrophy and mixotrophy are widespread mechanisms that produce significant amounts of organic carbon in the surface ocean. None of these metabolic pathways produce O_2 , and they are therefore missed in both in vitro and in situ O_2 -based estimates of GPP and NCP;

however, they do produce organic carbon, which can be oxidized heterotrophically, contributing to R. Although the contribution of each of these metabolic process is relatively small, the accumulated contribution of all known pathways (and those yet to be discovered) may be substantial, particularly relative to NCP. Hence, rather than rejecting empirical evidence for imbalanced community metabolism as necessarily flawed, a search for potential explanations needs to consider an unaccounted role for anoxygenic production of organic carbon in raising respiration rates beyond the boundaries imposed by photosynthetic carbon production.

CONCLUSION

The available evidence supports a prevalence of heterotrophic communities in the North Atlantic Subtropical Gyre and Mediterranean Sea and suggests that heterotrophy may also prevail in the South Atlantic and North Pacific Subtropical Gyres. We remain skeptical that even sustained efforts to measure NCP in cruises with a combination of the best in vitro (quartz bottles including 18 O additions) and in situ (based on the O₂/Ar ratio) methods will provide the data required to conclusively resolve whether the oligotrophic ocean is heterotrophic, as more than a decade of sustained effort has failed to do so and the ocean has been shifting in the meantime. We predict that the trends toward reduced primary production, reduced chlorophyll a, and warming of the ocean should be conducive to a growing prevalence of heterotrophic communities, possibly reverting the role of oceanic plankton from a sink to a source of CO₂, consistent with feedbacks between the ocean and the carbon cycle in past phases of a warm Earth climate. Further pursuing the key questions outlined here regarding the magnitude and source of allochthonous organic carbon inputs to the oligotrophic ocean, the contribution of anoxygenic organic carbon production, and deviations of the ocean ecosystem from a metabolic steady state is likely to increase our understanding of the functioning of the open ocean beyond resolving whether the oligotrophic ocean is autotrophic or heterotrophic.

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LITERATURE CITED

- Agustí S. 2012. Seasonal and latitudinal patterns of pelagic community metabolism in surface waters of the Atlantic Ocean. *Biogeosci. Discuss.* 9:1–19
- Antoine D, Morel A, Gordon HR, Banzon VF, Evans RH. 2005. Bridging ocean color observations of the 1980s and 2000s in search of long-term trends. J. Geophys. Res. 110:C06009
- Arístegui J, Gasol JM, Duarte CM, Herndl GJ. 2009. Microbial oceanography of the dark ocean's pelagic realm. *Limnol. Oceanogr.* 54:1501–29

Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR, Sarmiento JL, et al. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444:752–55

Bender ML, Grande K, Johnson K, Marra J, Williams PJLB, et al. 1987. A comparison of four methods for determining planktonic community production. *Limnol. Oceanogr.* 32:1085–98

Bender ML, Ho DT, Hendricks MB, Mika R, Battle MO, et al. 2005. Atmospheric O₂/N₂ changes, 1993–2002: implications for the partitioning of fossil fuel CO₂ sequestration. *Glob. Biogeochem. Cycles* 19:GB4017

Borges AV. 2005. Do we have enough pieces of the jigsaw to integrate CO₂ fluxes in the coastal ocean? *Estuaries* 28:3–27

Boyce DG, Lewis MR, Worm B. 2010. Global phytoplankton decline over the past century. *Nature* 466:591–96 Boyce DG, Lewis MR, Worm B. 2011. Boyce et al. reply. *Nature* 472:E8–9

- Calleja ML, Duarte CM, Prairie Y, Agustí S, Herndl G. 2009. Evidence for surface organic matter modulation of air-sea CO₂ gas exchange. *Biogeosciences* 6:1105–14
- Calvo-Díaz A, Díaz-Pérez L, Suárez LA, Morán XAG, Teira E, Marañón E. 2011. Decrease in the autotrophicto-heterotrophic biomass ratio of picoplankton in oligotrophic marine waters due to bottle enclosure. *Appl. Environ. Microbiol.* 77:5739–46
- Campbell BJ, Waidner LA, Cottrell MT, Kirchman DL. 2008. Abundant proteorhodopsin genes in the North Atlantic Ocean. Environ. Microbiol. 10:99–109
- Cole J, Prairie Y, Caraco N, McDowell W, Tranvil L, et al. 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10:171–84
- Dachs J, Calleja ML, Duarte CM, del Vento S, Turpin B, et al. 2005. High atmosphere-ocean exchange of organic carbon in the NE subtropical Atlantic. *Geophys. Res. Lett.* 32:L21807
- del Giorgio PA, Cole JJ, Cimbleris A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. *Nature* 385:148–51
- del Giorgio PA, Duarte CM. 2002. Respiration in the open ocean. Nature 420:379-84
- Denman KL, Brasseur G, Chidthaisong A, Ciais P, Cox PM, et al. 2007. Couplings between changes in the climate system and biogeochemistry. In *Climate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. S Solomon, D Qin, M Manning, Z Chen, M Marquis, et al., pp. 499–587. Cambridge: Cambridge Univ. Press
- Denman KL, Gargett AE. 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. *Limnol. Oceanogr.* 28:801–15
- Dickson ML, Orchardo J. 2001. Oxygen production and respiration in the Antarctic Polar Front region during the austral spring and summer. *Deep-Sea Res. II* 48:4101–26
- Dixon JL, Beale R, Nightingale PD. 2011. Rapid biological oxidation of methanol in the tropical Atlantic: significance as a microbial carbon source. *Biogeosciences* 8:2707–16
- Duarte CM, Agustí S. 1998. The CO₂ balance of unproductive aquatic ecosystems. Science 281:234–36
- Duarte CM, Agustí S, Cole JJ, del Giorgio PA. 1999. Regional carbon imbalances in the oceans. Science 284:1735
- Duarte CM, Cebrián J. 1996. The fate of marine autotrophic production. Limnol. Oceanogr. 41:1758-66
- Duarte CM, Dachs J, Llabrés M, Alonso-Laita P, Gasol JM, et al. 2006. Aerosol inputs enhance new production in the subtropical northeast Atlantic. J. Geophys. Res. 111:G04006
- Duarte CM, Holmer M, Olsen Y, Soto D, Marbà N, et al. 2009. Will the oceans help feed humanity? *BioScience* 59:967–76
- Duarte CM, Middelburg JJ, Caraco N. 2005. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2:1–8
- Duarte CM, Regaudie-de-Gioux A. 2009. Thresholds of gross primary production for the metabolic balance of marine planktonic communities. *Limnol. Oceanogr.* 54:1015–22
- 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, Stump C, Nicholson D. 2008. Net biological oxygen production in the ocean: remote in situ measurements of O₂ and N₂ in surface waters. *Glob. Biogeochem. Cycles* 22:GB3023
- Falkowski P, Scholes RJ, Boyle E, Canadell J, Canfield D, et al. 2000. The global carbon cycle: a test of our knowledge of earth as a system. *Science* 290:291–96

- Gasol JM, Doval MD, Pinhassi J, Calderon-Paz JI, Guixa-Boixareu N, et al. 1998. Diel variations in bacterial heterotrophic activity and growth in the northwestern Mediterranean Sea. Mar. Ecol. Prog. Ser 164:107–24
- Godoy N, Canepa A, Lasternas S, Mayol E, Ruíz-Halpern S, et al. 2012. Experimental assessment of the effect of UVB radiation on plankton community metabolism along the Southeastern Pacific off Chile. *Biogeosciences* 9:1267–76
- González JM, Fernández-Gómez B, Fernàndez-Guerra A, Gómez-Consarnau L, Sánchez O, et al. 2008. Genome analysis of the proteorhodopsin-containing marine bacterium *Polaribacter* sp. MED152 (Flavobacteria). *Proc. Natl. Acad. Sci. USA* 105:8724–29

Gregg WW, Conkright ME. 2002. Decadal changes in global ocean chlorophyll. Geophys. Res. Lett. 29:1730

- 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
- Harris LA, Duarte CM, Nixon SW. 2006. Allometric laws and prediction in estuarine and coastal ecology. *Estuaries Coasts* 29:340–44
- Huthnance JM. 1995. Circulation, exchange and water masses at the ocean margin: the role of physical processes at the shelf edge. *Prog. Oceanogr.* 35:353–431
- Ingalls AE, Shah SR, Hansman RL, Aluwihare LI, Santos GM, et al. 2006. Quantifying archaeal community autotrophy in the mesopelagic ocean using natural radiocarbon. Proc. Natl. Acad. Sci. USA 103:6442–47
- Intergov. Panel Clim. Change. 2001. Climate Change 2001: The Scientific Basis: Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Ed. JT Houghton, Y Ding, DJ Griggs, M Noguer, PJ van der Linden, et al. Cambridge: Cambridge Univ. Press. 881 pp.

Jiao N, Zhang Y, Zeng Y, Hong N, Liu R, et al. 2007. Distinct distribution pattern of abundance and diversity of aerobic anoxygenic phototrophic bacteria in the global ocean. *Environ. Microbiol.* 9:3091–99

- Jickells TD, An ZS, Andersen KK, Baker AR, Bergametti G, et al. 2005. Global iron connections between desert dust, ocean biogeochemistry, and climate. Science 308:67–71
- Jørgensen BB. 2006. Bacteria and marine biogeochemistry. In *Marine Geochemistry*, ed. HD Schulz, M Zabel, pp. 169–206. Berlin: Springer-Verlag. 2nd ed.
- Jurado E, Dachs J, Duarte CM, Simó R. 2008. Atmospheric deposition of organic and black carbon to the global ocean. *Atmos. Environ.* 42:7931–39
- Kaiser J. 2011. Consistent calculation of aquatic gross production from oxygen triple isotope measurements. Biogeosciences 8:1793–811
- Kaiser J, Reuer MK, Barnett B, Bender ML. 2005. Marine productivity estimates from continuous O₂/Ar ratio measurements by membrane inlet mass spectrometry. *Geophys. Res. Lett.* 32:L19605
- Karl DM, Laws EA, Morris P, Williams PJLB, Emerson S. 2003. Metabolic balance of the open sea. *Nature* 426:32
- Kolber ZS. 2001. Contribution of aerobic photoheterotrophic bacteria to the carbon cycle in the ocean. *Science* 292:2492–95
- Kroopnick P. 1985. The distribution of ¹³C ΣCO₂ in the world oceans. Deep-Sea Res. A 32:57-84
- Llabrés M, Agustí S, Herndl GJ. 2011. Diel in situ picophytoplankton cell death cycle coupled with cell division. *J. Phycol.* 47:1247–57
- Loisel H, Vantrepotte V, Norkvist K, Mériaux X, Kheireddine N, et al. 2011. Characterization of the biooptical anomaly and diurnal variability of particulate matter, as seen from scattering and backscattering coefficients, in ultra-oligotrophic eddies of the Mediterranean Sea. *Biogeosciences* 8:3295–317
- López-Urrutia A, San Martin E, Harris RP, Irigoyen X. 2006. Scaling the metabolic balance of the oceans. *Proc. Natl. Acad. Sci. USA* 103:8739–44
- Luz B, Barkan E. 2000. Assessment of oceanic productivity with the triple-isotope composition of dissolved oxygen. Science 288:2028–31
- Luz B, Barkan E. 2009. Net and gross oxygen production from O₂/Ar, ¹⁷O/¹⁶O and ¹⁸O/¹⁶O ratios. *Aquat. Microb. Ecol.* 56:133–45
- Mackas DL. 2011. Does blending of chlorophyll data bias temporal trend? Nature 472:E4-5
- Marra J. 2002. Approaches to the measurement of plankton production. In *Phytoplankton Productivity: Carbon Assimilation in Marine and Freshwater Ecosystems*, ed. PJLB Williams, DN Thomas, CS Reynolds, pp. 78–108. Cambridge, UK: Blackwell

- Marra J. 2012. Comment on "Measuring primary production rates in the ocean: enigmatic results between incubation and non-incubation methods at Station ALOHA" by P. D. Quay et al. *Glob. Biogeochem. Cycles* 26:GB2031
- McClain CR, Signorini SR, Christian JR. 2002. Subtropical gyre variability observed by ocean color satellites. NASA/TM—2002-211616, NASA Goddard Space Cent., Greenbelt, MD. http://ntrs.nasa.gov/archive/ nasa/casi.ntrs.nasa.gov/20020080613_2002131986.pdf

Middelburg JJ. 2011. Chemoautotrophy in the ocean. Geophys. Res. Lett. 38:L24604

- Moore TS, DeGrandpre MD, Sabine CL, Zappa CJ, McGillis WR, et al. 2011. Sea surface pCO₂ and O₂ in the Southern Ocean during the austral fall, 2008. *J. Geophys. Res.* 116:C00F11
- Nicholson DP. 2011. Comment on "Consistent calculation of aquatic gross production from oxygen triple isotope measurements" by Kaiser (2011). *Biogeosci. Discuss.* 8:7127–39
- Nicholson DP, 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. 1:112-17
- O'Malley RT, Behrenfeld MJ, Siegel DA, Maritorena S. 2009. Global ocean phytoplankton. Bull. Amer. Meteor. Soc. 91(Suppl.):S75–78
- Polovina JJ, Howell EA, Abecassis M. 2008. Ocean's least productive waters are expanding. *Geophys. Res. Lett.* 35:L03618
- Prokopenko MG, Pauluis OM, Granger J, Yeung LY. 2011. Exact evaluation of gross photosynthetic production from the oxygen triple-isotope composition of O₂: implications for the net-to-gross primary production ratios. *Geophys. Res. Lett.* 38:L14603
- Quay PD, Peacock C, Björkman K, Karl D. 2010. Measuring primary production rates in the ocean: enigmatic results between incubation and non-incubation methods at Station ALOHA. *Glob. Biogeochem. Cycles* 24:GB3014
- Regaudie-de-Gioux A, Duarte CM. 2010. Compensation irradiance for planktonic community metabolism in the ocean. *Glob. Biogeochem. Cycles* 24:GB4013
- Regaudie-de-Gioux A, Duarte CM. 2012. Temperature dependence of planktonic metabolism in the ocean. Glob. Biogeochem. Cycles 26:GB1015
- Regaudie-de-Gioux A, Vaquer-Sunyer R, Duarte CM. 2009. Patterns in planktonic metabolism in the Mediterranean Sea. *Biogeosciences* 6:3081–89
- Reinthaler T, Van Aken HM, Herndl GJ. 2010. Major contribution of autotrophy to microbial carbon cycling in the deep North Atlantic's interior. *Deep-Sea Res. II* 57:1572–80
- Riser SC, Johnson KS. 2008. Net production of oxygen in the subtropical ocean. Nature 451:323–26
- Robinson C, Williams PJLB. 2005. Respiration and its measurement in surface marine waters. In *Respiration in Aquatic Ecosystems*, ed. P del Giorgio, PJLB Williams, pp. 148–81. Oxford, UK: Oxford Univ. Press
- Robinson R, Tilstone GH, Rees AP, Smyth TJ, Fishwick JR, et al. 2009. Comparison of in vitro and in situ plankton production determinations. *Aquat. Microb. Ecol.* 54:13–34
- Ruíz-Halpern S, Sejr MK, Duarte CM, Krause-Jensen D, Dalsgaard T, et al. 2010. Air-water exchange and vertical profiles of organic carbon in a subarctic fjord. *Limnol. Oceanogr.* 55:1733–40
- Rykaczewski RR, Dunne JP. 2011. A measured look at ocean chlorophyll trends. Nature 472:E5-6
- Sarma VS, Abe O, Hashimoto S, Hinuma A, Saino T. 2005. Seasonal variations in triple oxygen isotopes and gross oxygen production in the Sagami Bay, central Japan. *Limnol. Oceanogr.* 50:544–52
- Smith SV. 1981. Marine macrophytes as a global carbon sink. Science 211:838-40
- Smith SV, Hollibaugh JT. 1993. Coastal metabolism and the oceanic organic carbon balance. Rev. Geophys. 31:75–89
- 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
- Stephens BB, Keeling RF, Paplawsky WJ. 2003. Shipboard measurements of atmospheric oxygen using a vacuum-ultraviolet absorption technique. *Tellus B* 55:857–78
- Suyama T, Shigematsu T, Suzuki T, Tokiwa Y, Kanagawa T, et al. 2002. Photosynthetic apparatus in Roseateles depolymerans 61A is transcriptionally induced by carbon limitation. Appl. Environ. Microbiol. 68:1665–73

- Swingley WD, Sadekar S, Mastrian SD, Matthies HJ, Hao J, et al. 2007. The complete genome sequence of Roseobacter denitrificans reveals a mixotrophic rather than photosynthetic metabolism. J. Bacteriol. 189:683– 90
- Tang K-H, Feng X, Tang YJ, Blankenship RE. 2009. Carbohydrate metabolism and carbon fixation in *Roseobac*ter denitrificans OCh114. PLoS ONE 4:e7233
- Williams PJLB. 1998. The balance of plankton respiration and photosynthesis in the open oceans. *Nature* 394:55–57
- Williams PJLB, Bowers DG. 1999. Regional carbon imbalances in the oceans. Science 284:1735
- Williams PJLB, Quay PD, Westberry TK, Behrenfeld MJ. 2013. The oligotrophic ocean is autotrophic. Annu. Rev. Mar. Sci. 5:535–49
- Wuchter C, Schouten S, Boschker HYS, Sinninghe Damsté J. 2003. Bicarbonate uptake by marine Crenarchaeota. FEMS Microbiol. Lett. 219:203–7
- Yurkov VV, Gemerden H. 1993. Impact of light/dark regimen on growth rate, biomass formation and bacteriochlorophyll synthesis in *Erythromicrobium bydrolyticum*. Arch. Microbiol. 159:84–89

Annual Review of Marine Science

Volume 5, 2013

Contents

| Reflections About Chance in My Career, and on the Top-Down Regulated World <i>Karl Banse</i> |
|---|
| Causes for Contemporary Regional Sea Level Changes Detlef Stammer, Anny Cazenave, Rui M. Ponte, and Mark E. Tamisiea |
| Gravity Flows Associated with Flood Events and Carbon Burial: Taiwan as Instructional Source Area James T. Liu, Shuh-Ji Kao, Chih-An Hub, and Chin-Chang Hung |
| A Deep-Time Perspective of Land-Ocean Linkages in the Sedimentary Record <i>Brian W. Romans and Stephan A. Graham</i> |
| Remote Sensing of the Nearshore Rob Holman and Merrick C. Haller |
| High-Frequency Radar Observations of Ocean Surface CurrentsJeffrey D. Paduan and Libe Washburn115 |
| Lagrangian Motion, Coherent Structures, and Lines of Persistent Material Strain <i>R.M. Samelson</i> |
| Deglacial Origin of Barrier Reefs Along Low-Latitude Mixed Siliciclastic and Carbonate Continental Shelf Edges André W. Droxler and Stéphan J. Jorry |
| The Trace Metal Composition of Marine Phytoplankton Benjamin S. Twining and Stephen B. Baines |
| Photophysiological Expressions of Iron Stress in Phytoplankton Michael J. Behrenfeld and Allen J. Milligan |
| Evaluation of In Situ Phytoplankton Growth Rates: A Synthesis of Data from Varied Approaches <i>Edward A. Laws</i> |

| 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 <i>Russell L. Cuhel and Carmen Aguilar</i> | 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 <i>L.W. Juranek and P.D. Quay</i> | 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. Bebrenfeld | 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