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Regional Carbon Imbalances in the Oceans

Recent studies (*1, 2*) have suggested that respiration exceeds photosynthetic oxygen production in large areas of the oceans. If correct, the conclusion has profound implications for our understanding of the oceanic carbon cycle. C. M. Duarte and S. Augusti conclude that four-fifths of the ocean are net heterotrophic, with photosynthesis providing for only 75% of respiration (*2*). We estimate this shortfall as 0.5 petamole C year^{-1} (*3*), which is difficult to account for. Nonlocal sources such as river and aeolian input probably contribute no more than 0.015 petamole as a whole to the open oceans (*4*), that is, only 3% of the calculated shortfall. Major inputs from upwelling dissolved organic carbon (DOC) or from the net autotrophic areas are unlikely because they would be associated with concurrent input of nutrients and consequent eutrophication. Furthermore, they would also require massive water transport—perhaps 50 to 1500 sverdrups (*5*), which is a flow comparable to or many times greater than the Gulf Stream. Thus, there are major difficulties balancing the proposed regional deficits with nonlocal sources, even in combination. An alternative analysis based on depth integrations of individual productivity stations gave no evidence for major systematic imbalances (*6*). Because the data sets used in all three studies are similar (*6*), one comes to the conclusion that the discrepancy must lie in the form of analysis.

Duarte and Agusti (*2*) used an allometric equation in reaching their conclusion: $R = aP^{b}$, where R is the community respiration rate, a and b are operational constants, and P is the gross primary production rate. This equation is an unsatisfactory model when extrapolating across ecosystems of widely differing productivities because the term "a" is not a constant, but dependent on the scale of local photosynthesis [table 1 in the report (*2*)]. The $R = aP^{b}$ relationship attempts to fit a single curve to a series of curves (parallel lines in the case of a log-log plot). This ascribes a single value for respiration to each value of photosynthesis, which effectively treats oligotrophic areas as the lower part of the water column of more productive ones. The result is that the critical value where $R = P$ is wrongly evaluated. As an illustration, we have examined a simple situation and show the general relationship between P and R for a balanced water column to be $R = bP_0^{(1-b)}P^{b}$ (*7*). Even when all the water columns in the data set are in balance, if an intermediate relationship is used, there would be an overestimate of respiration for areas of low photosynthesis and the reverse at high photosynthesis, the degree of error depending on the distribution of photosynthetic observations in the data set (Fig. 1). Thus, the conclusion (*2*) that substantial areas of the ocean are in organic deficit is very likely to be a product of an oversimplistic analysis. We would conclude, rather, that there is (*6*, p. 57) "no evidence to suggest that the open oceans, either as a whole or regionally, are substantially out of organic balance." Our analysis does not preclude the possibility that major imbalances exist, but such a conclusion would need to come from detailed studies of the areas of the ocean concerned, and not from generalized relations obtained across different systems.

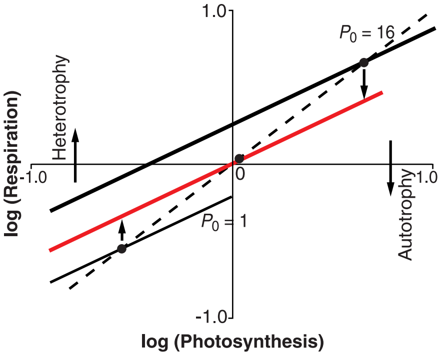

Fig. 1. Relation of photosynthesis and respiration based on the equation $R = bP_0^{(1-b)}P^{b}$ (*7*). Dashed line indicates $P = R$. Two solid black lines show P versus R relation for two values of P_0. Dots indicate the particular value where $P = R$. Red line is from the equation given by Duarti and Agusti (*2*). Arrows show the movement of the line consequent to the simplifying assumption of a single relationship. Units are μmoles dm^{-3} day^{-1}.

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2. C. M. Duarte and S. Agusti, *Science* **281**, 234 (1998).
3. Back calculated from table 1 in a study by A. R. Longhurst *et al*. [*J. Plankton Res*. **17**, 1245 (1995)] and the information in the report by Duarte and Agusti (*2*).
4. S. V. Smith and J. T. Hollibaugh, *Rev. Geophysics* **31**, 75 (1993); J. I. Hedges and R. G. Keil, *Marine Chem*. **49**, 81 (1995); P. Buat-Ménard, H. Cachier, R. Chesselet, in *Chemical Oceanography*, J. P. Riley and R. Chester, Eds. (Academic Press, London; 1989), vol. 10, pp. 251–279.
5. A sverdrup is a flow of ocean water of 10^{6} cubic meters per second. To calculate the transfer from net autotrophic areas, assume that one-fifth of the oceans supports 25% of the carbon demand of the remaining four-fifths; that is, it will require 25% of the productivity of the areas in positive balance. Assuming this area to be concentrated in the top 100-m column, then one would need to transfer 25% of the top 100 m of 20% of the oceanic area (~ 3 x 10^{14} m^2) annually equivalent to about 50 sverdrups. To calculate input from upwelling, assume that the deep-water DOC concentration is 0.050 mol C m^{-3}. and that 20% is labile [E. R. M. Druffel, P. M. Williams, J. E. Bauer, J. R. Ertel, *J. Geophys. Res*. **97**, 15,639 (1992)]. Thus, an input of 0.5 x 10^{15}/0.5 x 0.05 m^3 year^{-1} ≈ 1500 sverdrups would be required, whereas current estimates of upwelling are 10-fold smaller [F. P. Chave, and J. R. Toggweiler, in *Upwelling in the Oceans: Modern Processes and Ancient Records*, C. P. Summerhayes *et al*., Eds. (Wiley, New York, 1995), pp. 313–320].
6. P. J. le B. Williams, *Nature* **394**, 55 (1998). The integrated data presented in figure 2 in the report by Duarte and Agusti fall close to the 1:1 line, that is, no systematic imbalance. The significance of this result was not discussed by the authors (*2*).
7. The derivation is as follows. If the photosynthetic rate is proportional to irradiance, which may be assumed to decreases exponentially with depth (that is, $P_z = P_0\,e^{-kz}$, where P_z and P_0 are, respectively, the photosynthetic rates at depth and at the surface, and k is the extinction coefficient), then

$$\int_{z=0}^{\infty} P_z dz = \int_{0}^{\infty} P_0 e^{-kz} = \left[-\frac{1}{k}P_0 e^{-kz}\right]_0^{\infty} = \frac{P_0}{k}$$

assume respiration at a single site is determined by photosynthesis as $R_z = aP_z^{b}$, then

$$R_z = a(P_0 e^{-kz})^{b} = aP_0^{\,b}\,e^{-bkz}$$

$$\int_{z=0}^{\infty} R_z dz = \int_{0}^{\infty} aP_0^{\,b} e^{-bkz}\,dz =$$

$$aP_0^{\,b}\left(-\frac{1}{bk}\right)\left[e^{-bkz}\right]_0^{\infty} = \frac{aP_0^{\,b}}{bk}$$

If integrated respiration and photosynthesis are in balance, that is

$$\int_{z=0}^{\infty} R_z dz = \int_{z=0}^{\infty} P_z dz$$

then

$$\frac{P_0}{k} = \frac{aP_0^{\,b}}{bk}$$

thus,

$$a = bP_0^{(1-b)}$$

and thus,

$$R = bP_0^{(1-b)}P^{b}$$

8. We are indebted to S. Sathendraynath, S. Smith, and D. Kirchman for invaluable advice and guidance.

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Response: Is the open ocean heterotrophic? Taken as an entire ecosystem, and at long time scales, the world's oceans respire more organic C than they produce by primary production. That is, the importation of terrestrial organic C from rivers exceeds burial in the sediments by on the order of 25 Tmol year^{-1} (*1*). Most geochemists concur that this simple budget implies that biotic processes in the sea are supported, in part, by subsidy from land. Whether the pelagic surface waters exhibit the same net heterotrophic nature of the ocean as a whole remains controversial (*2–5*). This controversy may partially derive from different methods of analysis, although not in the way argued by Williams and Bowers (*6*). Rather, the conclusion that biological production (*P*) generally exceeds respiration (*R*) in the open ocean (*5*) appears to be a product of the choice of analysis (*7*). In addition, the data sets they use are not particularly well suited for examining the balance between *R* and *P* in the open ocean, which was not the main goal of some of the studies (*2, 3*). In particular, the data set Williams used to specifically address this question (*5*) was biased towards highly productive waters (*8*), because the mean depth-integrated value of *P* in the data set [122 mmol O_2 m^{-2} day^{-1} or 1500 mg C m^{-2} day^{-1}, calculated with the use of a photosynthetic quotient of 1.0 (*5*)] is more than fourfold greater than the average primary production of the open ocean [approximately 350 mg C m^{-2} day^{-1} (*9*)]. In Williams' data set (*5*), 97% of the data exceed this average oceanic value of *P*.

The conclusion that the surface waters of the open oceans are generally autotrophic and in metabolic balance (*5*) is, therefore, flawed by the extrapolation from unusually productive waters to the global open ocean with the underlying assumption that *P/R* does not vary systematically with *P*. The bias towards highly productive systems in the relation between *R* and *P* results because observations on the balance between production and respiration in the oligotrophic ocean are still few. Unbiased analyses should, therefore, be derived from studies of the balance between *R* and *P* in individual areas of the ocean, which are best summarized by the resulting *P/R* ratios (*3, 10*), to then test for systematic variations in this balance across systems. The data set assembled by Williams shows a decline in the ratio *P/R* with declining primary production across regions (Fig. 1). It is not possible, with the use of Williams' data, to further extend this pattern because there are no data below 350 mg C m^{-2} day^{-1}, but we combined the existing data sets (*3, 5*) to further compare the *P/R* ratios in unproductive (that is, below the average oceanic *P* of 350 mg C m^{-2} day^{-1}) and productive regions of the sea. The *P/R* ratio of the unproductive communities tended to be (Wilcoxon sign ranked test, $p < 0.05$, $z = -2.2$) below the value of 1.0, indicating respiration to exceed production, whereas the reverse holds for productive ocean regions (Wilcoxon sign ranked test, $p < 0.001$, $z = -6.4$) and demonstrates that the declining pattern in *P/R* extends to the most oligotrophic areas (Fig. 1), where the biota tend to be a net source of CO_2. This analysis confirms that the *P/R* ratio in the biogenic layer of the oligotrophic ocean tends to be below unity and that the biota is a net source of CO_2.

The annual organic carbon input needed to support the excess organic carbon consumption in the unproductive areas of the open ocean has been estimated at 0.5 Pmol C by Williams and Bowers. This estimate of deficit is only indicative, for it is extrapolated from a comparative analysis (*3*), but it suggests the utilization of large amounts of allochthonous organic matter in these oligotrophic areas. Yet, it does not imply that the overall *P/R* ratio, which is driven by the highly productive oceanic areas, is less than 1. The carbon deficit in oligotrophic areas may be met by carbon surpluses from the most productive areas, which export about 0.46 Pmol C annually (*11*). The production of this excess carbon is not homogeneously distributed over the autotrophic 20% of the ocean's surface, but is concentrated in an area comprising at most 5% of the ocean surface (*12*). That the excess carbon produced in the coastal zone is exported to the unproductive open ocean follows from the consideration that only about 0.012 Pmol C are buried annually in the coastal zone (*11*), and that there is no evidence of a long-term increase in the organic carbon concentration of coastal waters. That the export from the coastal zone is a significant source of carbon to the open ocean, where it fuels heterotrophic metabolism (*13*), appears to be well established (*14, 15*).

The conclusion that allocthonous inputs of organic carbon are essential for the functioning of the oligotrophic ocean should promote research aimed at quantifying these inputs and their sources, and to expand the presently meager empirical basis on pelagic *R* and *P* estimates there, because extrapolation from highly productive situations can lead to misleading perceptions of the functioning of the open oceans. To dismiss the pattern towards heterotrophy in the oligotrophic ocean as artifactual or conceptually impossible does not account for the bulk of the available empirical evidence.

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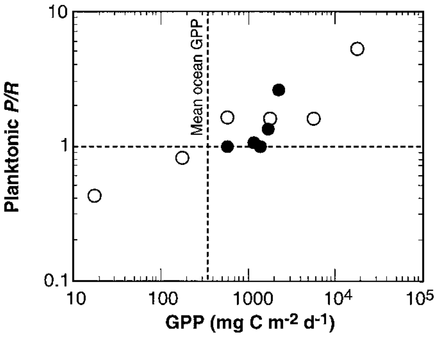

Fig. 1. Average depth-integrated planktonic *P/R* ratio in oceanic regions of different gross phytoplankton production (GPP). GPP and *P/R* values in the data set resulting from combining the data used by Duarte and Agustí (*3*) and Williams (*5*) were binned (*13*) for areas with comparable GPP's (< 30, 30 to 100, 100 to 300, 301 to 1000, 1001 to 3000, 3001 to 10,000, and > 10,000 mg C m^{-2} day^{-1}) and then averaged (open circles). Regional averages of GPP and *P/R* reported by Williams in table 1 of (*5*) (black circles) show the same pattern of declining *P/R* ratios with declining GPP within a narrower range of GPP. Trend towards declining *P/R* with decreasing GPP is highly statistically significant ($R^2 = 0.75$, $p < 0.001$). All data were converted to mg C m^{-2} day^{-1} and assume PQ = 1 (*5*).

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6. The constant "a" in the power equation $R = aP^b$ does not depend on local photosynthesis (*P*) (as suggested Williams and Bowers), but rather on differences in the respiration (*R*) that can be supported at a constant *P* of 1 g of O_2 m^{-3} d^{-1} among types of aquatic ecosystems (*3*). The statement by Williams and Bowers that the *R* versus *P* relation is a series of parallel lines assumes this relation to be linear, whereas it has been consistently found to be nonlinear, conforming to a two-thirds power law (*3, 5, 10*). Their derivation of the relationship between *R* and *P* in a balanced water column assumes photosynthesis to be proportional to irradiance (*I*), whereas photosynthesis-irradiance curves are inherently nonlinear and photosynthesis also depends on photosynthetic biomass, which may show a quasi-inverse distribution with incident irradiance in unproductive waters (*16, 17*). Their formulation also assumes photosynthesis at the surface and the light extinction coefficient to be independent, which is unlikely. Last, whether a power equation of the form $P = aP^{0.5}$ appropriately describes the scaling between *R* and *P* with depth at any one site, as they assume, is yet to be demonstrated.
7. The analysis of the relation between *R* and *P* using a linear regression on the arithmetic values, as used by Williams (*5*), assumes the ratio between *P* and *R* to be independent of *P*, and cannot, therefore, test the hypothesis that the *P/R* ratio increases with increasing *P* (*2, 3*). Further, the choice to fit the linear regression equation to the arithmetic *R* and *P* values violates the statistical assumptions of this analysis (*18*), for the variance in the residuals of the relationship derived by Williams increases significantly with increasing P($r = 0.32$, $p = 0.008$). The recommended procedure to avoid heteroscedasticity is to log-transform the variables prior to linear regression analysis (*18*), equivalent to fitting a power equation of the form $R = aP^b$, which also allows the test of the

hypothesis of independence of the *P/R* ratio on *P* (that is, H_0: b = 1) (*3*).
8. The anomalously high primary production in the data set used by Williams to investigate the metabolic balance in the open ocean partially results from the inclusion of studies in productive coastal areas, which represent 33% of the estimates from the Southern Ocean (*5, 19*), and 60% of those for the Mediterranean Sea, where 18 of the 47 stations studied were located in the dilution zone of the Rhone River (*5, 20*). In addition, the data for the North Atlantic corresponds to the spring bloom (*5*), the period of highest primary production in the year, which is not representative of the conditions prevailing during the rest of the year.
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12. The coastal zone, defined as the area of the ocean supporting benthic primary producers, is calculated to extend over 67,106 km^2 (*21*), or 2% of the area of the ocean, and is assumed to extend to 50 m depth (for example, LOICZ programme), although most plant biomass is confined to the area shallower than 20 to 30 m (*22*). The excess carbon produced by the macrophytes growing there, which export 20 to 40% of their production, represents about one-third of the estimated 0.5 Pmol C deficit of the unproductive open ocean (*11*). In addition, combination of the frequency distribution of the area and predicted net community production (*3*) in the coastal provinces of the ocean (*23*) predicts the net production of the planktonic communities developing in the most productive 4% of the area of the coastal ocean to be similar to the remaining 70% of the carbon deficit in the unproductive open sea. These areas include the upwelling zones that extend over 2.5% of the ocean's surface (*23*), most of which primary production is exported to the open ocean (*24*).
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