Respiration in the open ocean

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A key question when trying to understand the global carbon cycle is whether the oceans are net sources or sinks of carbon. This will depend on the production of organic matter relative to the decomposition due to biological respiration. Estimates of respiration are available for the top layers, the mesopelagic layer, and the abyssal waters and sediments of various ocean regions. Although the total open ocean respiration is uncertain, it is probably substantially greater than most current estimates of particulate organic matter production. Nevertheless, whether the biota act as a net source or sink of carbon remains an open question.

Oceanic primary production (P) represents about half of the planet's primary production[1], ranging from 35 to 65 gigatonnes of carbon per year ($Gt\,C\,yr^{-1}$) (refs 1–5) with open ocean production accounting for over 80% of the total[2]. Only a small fraction of this organic matter is buried in the ocean's sediments, the bulk of the organic matter produced being instead remineralized through respiration[3]. Planktonic microbes, particularly heterotrophic bacteria, are responsible for a large fraction of the respiration in the water column of the ocean, particularly in the least productive areas[6]. Although this microbial respiration is supported by dissolved organic carbon (DOC), researchers have traditionally focused on particulate carbon flux[7], which represents only a fraction of the total carbon flux in the ocean[8]. Approaches based on particle fluxes may therefore underestimate the global ocean carbon flux and specifically, the respiration term that is often derived from these models[9]. Planktonic respiration has been measured directly after changes in O_2 or CO_2 in enclosed water samples[6,10], but this approach is effective only in areas where metabolic rates are higher, such as in surface waters. As a result, respiration (R) remains the least constrained term in most models of metabolism, gas exchange and carbon mass balance in the ocean[4].

A major assumption in contemporary oceanography has been that, over a year and across large spatial scales, primary production must be nearly balanced by planktonic respiration. But direct estimates of microplankton oxygen consumption in oceanic surface waters have challenged this assumption[10–13] and several recent comparative studies have suggested that respiration may systematically exceed production in large areas of the oceans[14,15]. The ensuing debate[16,17] has focused on the processes that occur in the uppermost, illuminated layer only, which covers less than 6% of the ocean volume. Mass balance and carbon export studies generally suggest a modest contribution of intermediate waters to total R relative to that of surface waters[7]. However, direct metabolic measurements systematically suggest that a large fraction of the total carbon mineralization may occur in intermediate waters[18,19].

Here, we review the current information on the contribution of various biotic components and depth layers to respiration in the open ocean. We examine estimates of microplankton respiration in the ocean surface, which comprises the illuminated or photic zone (where primary production takes place), the mesopelagic layer, and the ocean interior (>1,000 m), which includes the respiration of benthic communities in the ocean floor. We also assess the possible contribution of metazoan zooplankton and larger metazoans to respiration in the water column. Finally, we evaluate the probable magnitude of total respiration, as well as the extent of the remaining uncertainties.

The photic layer

The photic layer extends roughly to the depth receiving 1% of the surface illumination, located at less than 200 m depth in most oceanic areas. The respiration rate in the surface layer is scaled to the primary production[11–14]. Some results[14,15] suggest a tendency for respiration to exceed production in the photic layer of oligotrophic oceans, whereas some others[16] suggest an overall balance between production and respiration in the photic layer of the different regions of the ocean. Although there is an overall positive relationship between respiration and the level of system productivity over large spatial scales, there is often a large degree of uncoupling between the two processes at smaller scales[10,20,21]. Rates of respiration in the surface layer of the ocean are typically high, with average values of about $1.2\,g\,C\,m^{-2}\,d^{-1}$ (refs 15, 16), which, if extrapolated over the $290 \times 10^6\,km^2$ of the open ocean, represent a global respiration of about $143\,Gt\,C\,yr^{-1}$. This estimate is about three to four times the accepted estimates of production ($35–65\,Gt\,C\,yr^{-1}$) (refs 1–5) because the available estimates of respiration in the photic layer are biased towards more-productive regions and periods of high metabolic activity[17].

Intermediate waters

The mesopelagic layer extends roughly from below the base of either the photic layer or the mixed surface layer, generally below 150–200 m, to a depth of approximately 1,000 m, and contains the thermocline where steep chemical and physical gradients occur. Although early studies[22] found measurable respiration rates below 200 m in the open Atlantic and Pacific, the mesopelagic and abyssal respiration was traditionally regarded as insignificant[23]. But the intermediate waters within the thermocline are now believed to be the main site for organic matter mineralization, which is necessary to re-supply the photic layer with inorganic nutrients[24].

The volumetric rates of respiration decrease sharply below the base of the photic layer, and often remain low throughout the thermocline, typically at 1–30% of the rates found in the overlying photic layer[18,22]. Yet, the depth-integrated microplankton respiration over the much thicker layer covered by the mesopelagic waters often reaches values comparable to those in the photic layer. Models predict[25,26] that the integrated respiration rate in the 200–1,000 m layer should range from 30 to 130% of the integrated respiration in the 0–200 m layer. These predictions are broadly in agreement with *in situ* determinations of respiration in the surface and mesopelagic layers of various oceanic regions[9,18,24,27–29].

In addition to relatively high integrated rates, discrete subsurface metabolic maxima, with rates comparable or even higher than those in surface waters, have often been reported within the ocean's thermocline[19,24,29,30]. In general terms, these deep layers of high metabolism are relatively thin and limited to tens of metres, but they can nevertheless contribute heavily to the total respiration in intermediate waters[30].

The ocean interior

The rates of water oxygen consumption below 1,000 m are often extremely low and difficult to measure[6,22] resulting in rather

few direct measurements of respiration in the ocean's interior. Fiadeiro and Craig[31] calculated a rate of respiration below 1,000 m of 2 μl O_2 l^{-1} yr^{-1}, similar to other estimates available for the ocean interior[19,32]. These estimates of deep water respiration agree with recent estimates of DOC consumption rates in the ocean interior[33]. The combination of estimates of deep-ocean benthic respiration together with estimates of organic matter flux in the water column[34] yielded an estimated total respiration in the ocean interior of 1.2×10^{14} mol O_2 yr^{-1}, of which benthic respiration represents 45%, in agreement with other independent estimates of deep-ocean respiration[31–33].

Metazooplankton and vertebrates

Estimates of the contribution of metazooplankton to respiration in the ocean are highly variable, varying from less than 1% to more than 50% of respiration depending on the oceanic region, productivity, depth, and method of estimation[22,28,35–38]. Estimates of the contribution of vertebrates to respiration in the open ocean are very few. But assuming that vertebrates occur at least three trophic levels above primary producers and assuming also an efficiency of 10% at each trophic level, vertebrate respiration must be, on average, ≤1% of the respiration in the open ocean.

Temporal and spatial variability in open-ocean respiration

The spatial and temporal variation in water-column respiration is still insufficiently characterized in oceanic systems, and this limitation adds further uncertainty to any global or regional estimate. Although there is an overall positive relationship between photic zone respiration and primary production over large spatial scales, respiration appears to be much less variable than other biological processes, including primary production[10,11,13–15,20,21,39]. One of the reasons ocean respiration is less variable than production is that heterotrophic microorganisms utilize a diversity of organic matter, and not just that derived from contemporary production. Much of the respiratory carbon demand in the open ocean is supported by DOC[8,9,40], but this does not necessarily imply exclusive use of recent primary production, because organic matter may persist for months, or hundreds or thousands of years in the dissolved form. The consumption of past primary production, stored in the form of the very large[30,41] (about 685 to 700 Gt C) oceanic DOC pool, potentially allows an uncoupling between primary production and respiration extending over millennia, the mean age of the ocean's DOC pool[42], resulting in a lack of steady-state at shorter timescales.

The oceanic *P*/*R* ratio may have varied considerably over geological times. For example, there is evidence that in the period between the Last Glacial Maximum and the Holocene epoch the oceans acted as a source of CO_2, of at least 170 Gt C, to up to 1,350 Gt C (ref. 43), although it is unclear whether this was the result of increased respiration or decreased primary production. Indeed, respiratory processes are closely dependent on temperature[44], so that variability in water temperature may account for spatial and temporal variability in open-ocean respiration beyond that induced by changes in primary production.

Total respiration in the open ocean

Estimating the total oceanic respiration is important for our understanding of the global carbon cycle. It should also help us to test the consistency of present estimates of global primary production and organic inputs to the different compartments of the open ocean. We have used the information available to provide a first, necessarily imprecise, approximation of the magnitude of the total respiration in the open ocean that may reduce the present uncertainty.

We do not as yet have a representative mean value of respiration for the surface layer of the ocean[17]. However, two equations scaling respiration and photosynthetic rates are available, a linear equation[16], and a nonlinear one, which suggests that the *P*/*R* ratio is lowest in oligotrophic regions of the ocean and increases with increasing primary production[15]. We used these two equations to derive a first-order estimate of the total respiration in the photic layer for the open ocean. We applied each of these two equations to the estimates of the average primary production of each of the biogeochemical provinces in the open ocean[2], and then scaled the calculated average rates of photic layer respiration to the area of each province. We then aggregated the respiration estimates for each province to yield estimates of the total respiration in the surface layer of the open ocean between 32 Gt C yr^{-1} (using the linear equation[16]) and 42 Gt C yr^{-1} (using the nonlinear equation[15]).

Table 1 **Open ocean respiration and organic matter inputs**

Component	Low estimate (Gt C yr^{-1})	High estimate (Gt C yr^{-1})	Central estimate (Gt C yr^{-1})
Respiration			
Photic zone*	32	42	37
Mesopelagic†	21	28	24.5
Ocean interior‡	1.3	1.6	1.5
Mesozooplankton§	1.5	4.5	3
Vertebrates			0.01
Total respiration	**55.8**	**76.1**	**66**
Organic matter inputs			
Measured primary production (^{14}C-based)	28	52	40
Unmeasured gross production‖	13.4	25	19.2
Total production	41.4	77	59.2
Import from coastal areas	6	6	6
Atmospheric inputs	3	3	3
Ancient organic matter	0.5	0.5	0.5
Total inputs	**50.9**	**86.5**	**68.7**
Export and new production			
Suess[7]			<6
Emerson *et al.*[65]			<11
Sambrotto *et al.*[66]			15
Falkwoski *et al.*[67]			16
This paper¶	**23**	**31.8**	**27.5**

*The range results from applying the two available equations (in refs 15 and 16) to scale *R* to *P*.
†Assumed to be two-thirds of photic layer *R* and a minimum error of 35%.
‡A minimum error of 10%.
§Assumed to be on average 10% of total *R* with a minimum error of 50% around central value.
‖Assuming 35% algal respiration and 10% DOC release of ^{14}C-based production.
¶Calculated as $R_{mesopelagic} + R_{interior} + (0.5 \times R_{zooplankton})$.

These estimates of photic layer respiration (R_{photic}) suggest a central value of about 37 Gt C yr^{-1} (Table 1) with an uncertainty of at least 15% (that is, ±5 Gt C yr^{-1}).

Most studies show that integrated respiration in the mesopelagic layer is at least of a similar magnitude to the integrated microplankton respiration in the photic layer of the open ocean, and often greater. Based on the published information reviewed above, the integrated respiration in the mesopelagic layer ($R_{mesopelagic}$) can be conservatively taken to amount to two-thirds of the average microplankton respiration in the photic layer (R_{photic}) of the open ocean. R_{photic} is estimated to be 32–42 Gt C yr^{-1}, so the total $R_{mesopelagic}$ for the open ocean is likely to be of the order of 21–28 Gt C yr^{-1}, with a probable central value of around 24.5 Gt C yr^{-1} (Table 1). The uncertainty about this best estimate is extremely large: it is affected by the 15% uncertainty about R_{photic}, and the variability about the ratio of $R_{mesopelagic}$ to R_{photic}. The latter is unknown, but it is unlikely to be less than 20%, thereby resulting in a minimum uncertainty of 35% about the best estimate of $R_{mesopelagic}$ derived with the information available.

Converted to carbon consumption assuming a respiratory quotient of 1, the estimate of respiration in open ocean waters below 1,000 m derived by Jahnke[34] yields an estimate of total microplankton $R_{interior}$ of around 1.5 Gt C yr^{-1} (Table 1). The calculated net rate of microbial utilization of DOC in the deep ocean[33] (0.5 μM C yr^{-1}) supports a respiration rate, if extrapolated to the ocean interior, of about 0.7 Gt C yr^{-1}, which is about half of the total respiration in the ocean interior calculated by Jahnke[34] and suggests once again that a large fraction of respiration is supported by DOC. The respiration rate within the ocean interior (water column + ocean floor) appears to be rather well constrained, with a 10% variability about the different estimates[34].

As with the respiration in the interior of the thermocline, it is difficult to estimate the contribution of metazooplankton to total plankton respiration, but a contribution of 5 to 10% seems most plausible from the information available. We will conservatively assume that $R_{zooplankton}$ represents 5% of the combined microplankton respiration in the photic and thermocline waters, with total $R_{zooplankton}$ representing, therefore, about 3 Gt C yr^{-1} (Table 1). A recent meta-analysis of published data[45] has concluded that approximately 5.5 Gt of phytoplankton carbon are consumed per year in the global ocean, with a respiratory loss of approximately 1.5 Gt C yr^{-1}, but this independent estimate of mesozooplankton respiration is conservative because it does not include the respiration of the non-phytoplankton carbon ingested, which may support a large portion of the zooplankton C demand in open-ocean systems[45].

The information on vertebrate respiration in the open ocean is even sparser, and only indirect calculations can be used to derive a global view of its importance. The total reported fisheries catches amount to approximately 0.3×10^{12} g C yr^{-1} for the oceanic gyre systems[46]. The total fish production can be approximated assuming that the catch represents 20% of the total fish production[46], which would then amount to 0.0015 Gt C yr^{-1}. Assuming fish respiration to be 9-fold greater than their production, an estimate of only 0.0135 Gt C yr^{-1} is derived, far below the estimated planktonic respiration in the open ocean and of little significance at a global scale.

The sum of the components discussed above results in a likely range for respiration in the open ocean of 56 Gt C yr^{-1} to 76 Gt C yr^{-1}, with a central value for total respiration of about 66 Gt C yr^{-1} (Table 1). This estimated range of open ocean respiration represents a crude first-order approximation, because in addition to the paucity of data, there are many problems associated with the direct measurement of respiration in open-ocean waters[6,10,40], and with the extrapolation of these measurements to larger scales[47]. But these estimates are also conservative, thereby defining a probable lower range of values, and offer a basis for comparison with other better understood aspects of ocean metabolism.

The metabolic balance

Current estimates of primary production in the oceans vary widely, but most estimates for the global ocean are in the range of 35 to over 65 Gt C yr^{-1} (refs 1–5). Open-ocean production accounts for at least 80% of the total[2], so most current estimates place open-ocean productivity in the range of 28–52 Gt C yr^{-1} (Table 1). The likely range in total open-ocean respiration of 56 Gt C yr^{-1} to 76 Gt C yr^{-1} is higher than the accepted range in global oceanic production, but this apparent imbalance does not imply that either range of estimates is wrong. The validity of global estimates of planktonic primary productivity obtained from satellite remote sensing depends greatly on the quality of calibration data, which are based on ^{14}C incorporation into particulate material[4,5]. There are two major problems associated with ^{14}C-based production estimates that may result in an underestimation of primary production and in the apparent discrepancy with oceanic respiration. First, ^{14}C-based production estimates do not necessarily represent gross primary production (GPP), because some algal respiration has already been accounted for in the estimate. The fraction of GPP lost to algal respiration varies widely but averages at about 35% (refs 48, 49).

Second, the incorporation of ^{14}C into particulate material does not capture the production of new dissolved organic matter by phytoplankton, which can be significant, particularly in unproductive regions[8,9,50]. The proportion of primary production that is directly excreted as DOC varies widely, and at least part of this variation may be due to uncertainties associated to the actual measurements[50]. Meta-analysis of published data has suggested that DOC production represents, on average, 13% of the ^{14}C incorporation[51] after respiratory losses, and we will use this conservative estimate to correct current productivity estimates for comparison with respiration.

The oceanic primary production estimates based on ^{14}C incorporation measurements can thus be incremented by about 48% to account for the average algal respiration and DOC production (Table 1). This correction yields a revised estimate of the oceanic GPP in the order of 41 to 77 Gt C yr^{-1} (Table 1), comparable to the estimated range of total respiration in the open ocean of 55 to 76 Gt C yr^{-1} derived above. This very rough correction of open-ocean production estimates narrows the gap between oceanic respiration and production, but some discrepancies in open-ocean metabolism still persist.

The surface waters of the vast, unproductive open-ocean gyres appear to be characterized by extremely high respiration relative to primary production, with P/R ratios often ≤1 (refs 14, 15). This pattern cannot be explained solely on the basis of underestimation of production by ^{14}C-based techniques, because the same results have been obtained using O_2-based measurements, which do not underestimate GPP[10–13,20,21]. The validity of the high values of respiration in the ocean is supported by consideration that bacterial production represents about 25 to 35% of primary production in the photic layer of the open ocean[3,52]. Given that bacterial carbon growth efficiency in the open ocean tends to be below 30% (ref. 40), bacterial respiration alone in the photic layer must be comparable to, if not greater than, primary production in the open ocean[40]. In addition, depth profiles show that integrated bacterial production in various open ocean regions often exceeds the estimated particulate carbon export from the photic zone[3,20]. Recent large-scale studies of bacterial metabolism and primary production in the southern Atlantic have shown that large areas in the oceanic gyres are indeed dominated by heterotrophic bacterial metabolism, whereas at higher latitudes the balance is autotrophic[53]. The apparent imbalance in the open oceans may be simply the result of temporal lags between P and R, or the lateral transport of recently

produced organic matter[14,16,20], but in some areas the imbalance is sufficiently persistent to suggest that alternative sources of organic matter must be used. The crucial question is then: what are the sources of organic matter that fuel these relatively high rates of respiration in the surface waters of oligotrophic oceans?

Allochthonus organic inputs to the open ocean

Coastal areas typically produce an excess organic carbon[54] that, together with organic inputs from land[55] can be exported to the open ocean and oxidized there by microorganisms. For example, inputs of particulate organic carbon (POC) and, particularly, DOC from ocean margins to the ocean interior may be an order of magnitude greater than inputs of recently produced organic matter from surface waters[55,56]. It is believed that only a small fraction of the primary production on land (<1%, calculated from the estimated riverine input of about 0.45 Gt C yr^{-1} and the terrestrial net primary production[1] of about 56.4 Gt C yr^{-1}) reaches the coastal ocean. A rough estimate of the organic carbon available to be transferred from the coastal to the open sea can be derived as the sum of the excess production by coastal ecosystems, estimated to range between 2.7 Gt C yr^{-1} (ref. 54) and 6 Gt C yr^{-1} (refs 16, 48), and the difference between the riverine input organic carbon, of about 0.45 Gt C yr^{-1} (ref. 57) and the 0.1 Gt C yr^{-1} buried in coastal sediments[41]. These approximations result in an estimated organic carbon transfer from the coastal to the open ocean of at most 6 Gt C yr^{-1}. Regrettably, present models of the organic carbon cycle ignore coastal inputs, because the boundary conditions of general circulation models are set at the shelf break, assuming, therefore, no exchange between open and coastal waters.

The total atmospheric organic carbon input to the open ocean is at present unknown, although there are some relatively high estimates[58]. A very rough, order-of-magnitude estimate of the atmospheric organic carbon input can be derived from consideration of the input of dissolved organic nitrogen (DON), estimated to be about (2–6) × 10^{12} mol N yr^{-1} (ref. 59), and a conservative atmospheric DOC/DON ratio of about 20, yielding an estimate of atmospheric DOC deposition of 0.48 to 1.44 Gt C yr^{-1}. The C:N ratio of atmospheric dissolved organic matter is likely to be higher, but even the assumption of a C:N ratio of 40 yields a total atmospheric DOC input of up to 3 Gt C yr^{-1}. These values represent minimum estimates, because they do not include POC deposition.

Organic carbon surplus from past episodes of enhanced ocean upwelling and productivity, such as that apparently occurring during the last glacial period[60] may have entered a long-term dissolved reservoir. A connection between ancient primary production and contemporary respiration could be a plausible mechanism to account for an excess respiration in the open ocean. But this would require a long-term trend for a net decline of the oceanic organic carbon inventory, for which there is no evidence, and the actual estimates of the net consumption of deep-ocean DOC[33] (0.5 μM C yr^{-1}) are low. Nevertheless, the slow but steady consumption of ancient, recalcitrant organic matter may be an important mechanism buffering fluctuations in open-ocean metabolism by uncoupling respiration from contemporary primary production. The DOC below the photic layer of the ocean is old, typically having originated thousands of years ago[42]. Even though ancient DOC is believed to be refractory, it may be photodegraded to forms more readily used by bacteria upon exposure to intense light when deep oceanic water is returned to the ocean's surface[61]. Indeed, radiocarbon evidence indicates that surface water bacteria consume significant amounts of ancient DOC in the open oceans, but less so in the more productive coastal areas[62]. The mobilization of the excess organic carbon buried in the continental margins due to erosion by rising sea level[63] during interglacial periods may be another significant source of ancient organic matter fueling present-day respiration in the open ocean that should be further investigated.

Balancing act

Terrestrial, coastal and atmospheric sources may thus account for organic matter inputs to the open ocean of approximately 9 Gt C yr^{-1}, with an additional 0.5 Gt C yr^{-1} from the use of ancient DOC. Assuming that most of these inputs are oxidized in the water column, they would be sufficient to sustain a small but systematic imbalance between P and R in the surface waters of the open oceans, particularly where P is low.

The total organic inputs to the open ocean can be estimated from the sum of the corrected open-ocean primary production (41 to 77 Gt C yr^{-1}), and the additional allochthonous organic matter inputs (9–10 Gt C yr^{-1}), and probably range from 51 to 86 Gt C yr^{-1} (Table 1). The total organic inputs to the ocean calculated in this way compare well with the estimated range in open-ocean respiration, which we hypothesize to vary around a probable central value of 66 Gt C yr^{-1} (Table 1)

Although there is a correspondence between the plausible organic matter inputs and respiration at a global scale, there are incongruities with specific aspects of this budget. The respiration in the dark layers of the ocean represents up to half of the total respiration in the upper layers, and requires, therefore, a significant input of organic matter. The estimates of export production from the photic zone, based on particle flux and mass balances, have systematically increased during the past decade[7,64–67]. But even the highest current estimates[67] would still represent approximately half of the apparent organic matter mineralization calculated from direct respiration measurements in intermediate and abyssal waters of the open oceans (Table 1). There is, therefore, a need to revise both the estimates of organic carbon export and mesopelagic respiration to reconcile these estimates.

We suggest that production and export estimates for the open ocean may have to be revised upwards by at least 50%. The traditional emphasis on the flux of POC has neglected the direct production of DOC by phytoplankton, and this component of oceanic productivity is still largely unconstrained. In fact, a significant portion of the carbon flux both within and out of the photic zone may be through carbon-rich DOC[9,24,50,66]. A priority in the future should be the accurate estimation of the production and export of oceanic DOC.

Oceanic respiration and the global C budget

Oceanic respiration is estimated here at about 55 to 76 Gt C yr^{-1}, but this estimate does not include the respiration in shallow coastal and continental shelf areas, which can be significant[54]. It is clear that oceanic respiration represents a major source of CO_2 in the biosphere, comparable to the estimated 70 to 80 Gt C yr^{-1} contributed by soil respiration[68]. Soil respiration has been generally regarded as the largest biological source of atmospheric CO_2 (ref. 43) and there are currently intense efforts to establish the links between increasing global temperature and CO_2 concentrations with soil respiration and terrestrial carbon storage[43,68]. Although there are indications that open-ocean R is at least as large as soil respiration, the uncertainty in the magnitude of the former is also much larger, and its importance as a source of CO_2 to the atmosphere is as yet unclear.

Current estimates of the magnitude of the oceanic sink of atmospheric CO_2 (approximately 2.2 Pg C yr^{-1}) based on net CO_2 uptake derived from global pCO_2 surveys[69], should not be affected by a reassessment of ocean R. However, consideration of oceanic respiration may help explain the distribution of CO_2 source regions in the ocean. In particular, the role of much of the subtropical ocean as a source of CO_2 to the atmosphere[69] is consistent with evidence that respiration in the photic layer exceeds primary production there[10,11,14,15,53]. Yet, the role of the subtropical ocean as a CO_2 source has been exclusively attributed to temperature effects[69,70]. Biological processes have been traditionally considered to act exclusively as

CO_2 sinks in the ocean[41,64,69,70], implicitly assuming that the oceanic P/R ratio consistently exceeds 1, an assumption that is unsupported by direct measurements of P and R (refs 10, 14, 15, 21). An increased awareness of the importance of oceanic R will probably lead to a better understanding of the drivers of this exchange, a key to eventually being able to predict how climate change will affect air–sea CO_2 flux. In the short-term, only planktonic respiration within the photic layer can influence air–sea CO_2 exchange directly, but the large amount of CO_2 released by planktonic respiration within the intermediate waters of the ocean certainly contributes to the CO_2 efflux to the atmosphere, as these waters ventilate within timescales of a few decades.

One of the main drivers of oceanic respiration is contemporary primary production, and climatic changes that affect patterns of ocean circulation and stratification, as well as increased atmospheric N inputs, may result in profound changes in global open-ocean productivity and in the balance between respiration and primary production[3,71]. But factors other than recent production also strongly influence oceanic respiration, because respiration integrates organic matter inputs on a much larger time and spatial scale. This integration in turn provides long-term stability to the system. Temperature plays a major direct role in the regulation of respiration in aquatic ecosystems, so that global warming should lead to increased carbon consumption[44], as well as fundamental changes in the patterns of organic matter use by oceanic bacteria[72]. Although the net effect of these various processes on oceanic respiration and their consequences in terms of changes in carbon storage in the oceans are not well understood, a likely scenario is that global warming may lead to increased oceanic respiration, perhaps comparable to the predicted increase in soil respiration by 3.3 Gt C yr^{-1} per °C increase[68].

In summary, we identify oceanic respiration as one of the major components of the carbon flux in the biosphere, and highlight the considerable uncertainty in its magnitude as well as in our capacity to predict its response to global change. The International Panel for Climate Change (IPCC) has recently concluded that "current ocean climate models are severely limited by the ability to parameterize important biological activities and to specify the temporal and spatial variations in these parameterizations". This is particularly true in the case of ocean respiration. Reducing the large present uncertainties as to the magnitude of open-ocean respiration will require the large-scale concerted effort of the international oceanographic community that led to our present knowledge of primary production in the oceans. After all, we cannot claim to grasp the global carbon cycle when we do not know whether the biota of the world's oceans is a net source or sink for carbon. □

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