

Respiration in the dark ocean

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Received 5 September 2002; accepted 28 October 2002; published 18 January 2003.

[1] The dark ocean, the waters below 200 m depth, comprises about 95% of the volume of the ocean, but its contribution to the metabolism of the ocean is poorly quantified. Here we show that the respiration rate of microplankton declines exponentially at a rate of 0.53 km^{-1} in the dark ocean, and is enhanced at the interface between the mesopelagic and the abyssal layers (1,000–2,000 m). The respiratory CO_2 production in the dark ocean, estimated at 20 to $33.3 \text{ Gt C yr}^{-1}$, renders it a major component of the carbon flux in the biosphere. **INDEX TERMS:** 4805 Oceanography: Biological and Chemical: Biogeochemical cycles (1615); 4806 Oceanography: Biological and Chemical: Carbon cycling; 4850 Oceanography: Biological and Chemical: Organic marine chemistry; 4855 Oceanography: Biological and Chemical: Plankton. **Citation:** Arístegui, J., S. Agustí, and C. M. Duarte, Respiration in the dark ocean, *Geophys. Res. Lett.*, 30(2), 1041, doi:10.1029/2002GL016227, 2003.

1. Introduction

[2] Recent revision of the respiratory activity of microplankton as a major source of CO_2 in the ocean has focussed on the mixed layer, comprising the top 200 m of the ocean [Duarte and Agustí, 1998; Williams, 1998; Duarte et al., 2001]. Although this layer supports intense metabolic processes it represent <5% of the volume of the ocean. The dark ocean, the waters below 200 m depth, represents the main reservoir of organic carbon [Field et al., 1998] and an important component of the carbon cycle, through the remineralisation of organic matter [Ducklow, 1995], in the ocean. Yet, the estimation of the respiratory activity in the dark ocean is cumbersome due to the low rates therein, about 10 to 100-fold lower than those in the photic layer [Packard et al., 1988; Biddanda and Benner, 1997], and has, therefore, received little attention. As a consequence, the total C flux involved has only been assessed indirectly, as the difference between the export of organic carbon from the mixed layer and the burial of organic carbon in the ocean floor. However, these estimates range by an order of magnitude [Sambrotto et al., 1993; Falkowski et al., 1998; Louanchi and Najjar, 2000], indicating that the magnitude of respiration in the dark ocean is poorly constrained by such indirect estimates. We, therefore, compiled available estimates of respiratory activity in the dark ocean (Table 1) to attempt a direct assessment of the global respiration rate there.

2. Methods

[3] Direct estimates of microplankton respiratory activity through oxygen consumption in the dark ocean are only available from the Gulf of México [Biddanda and Benner, 1997], a highly eutrophic region which does not represent open ocean conditions (Table 1). The bulk of the available estimates were derived from measurements of the respiratory electron transport system (ETS) activity. On the contrary to the oxygen method, the ETS approach allows the collection of large data sets during field cruises, facilitating the extension of our knowledge of oceanic respiration over large temporal and spatial scales. The ETS method estimates the maximum overall activity of the enzymes associated with the respiratory electron transport system under substrate saturation, in both eukaryotic and prokaryotic organisms. ETS activity measurements represent, therefore, potential respiration rates. These were converted to actual respiratory rates using a constant (0.086) derived from empirical relationships with oxygen consumption rates determined in vitro from monospecific cultures of bacteria [Christensen et al., 1980]. These estimates involve an error of $\pm 30\%$ [Packard et al., 1988]. In essence, the derivation assumes an average relationship between enzyme mass and respiratory activity applicable to bacterial communities, independently of depth, temperature, geographic location and other local conditions. Such an assumption introduces uncertainty on these estimates that can only be assessed through future validation. Hence, calculated respiration rates must be interpreted with some degree of caution.

3. Results and Discussion

[4] The available estimates of areal respiration in the dark ocean (200 m to ocean floor) indicate rates in the order of about $5 \text{ mol C m}^{-2} \text{ yr}^{-1}$, or about 20 Gt C yr^{-1} over the global dark ocean, being in close agreement with oxygen utilization rates inferred from large-scale tracer balances [Jenkins, 1982; Jenkins and Wallace, 1992] and other biogeochemical tracer techniques for determining the total new production [Carlson et al., 1994].

[5] Most profiles of respiration rates indicate an exponential decline in respiration rates with increasing depth, with rates averaging 0.56 km^{-1} for the different sites examined (Table 1). The estimation of the total respiration in the global dark ocean by up-scaling from the published areal rates is suboptimal, due to the differential integration depths used in the various studies (Table 1). Improved estimates can be derived from the depth-dependence of respiration rates, which decline exponentially with increas-

Table 1. Areal Estimates of Microplankton Respiration (R) in the Dark Ocean

Ocean	Depth range (m)	R ($\mu\text{mol C m}^{-2} \text{ yr}^{-1}$)	N stations	Method
Atlantic (Sargasso Sea) ^a	200–1000	3.3		AOU/tracers
Atlantic (Sargasso Sea) ^b	200–1000	1.5	8	ETS
"	1000–bottom	0.7	8	ETS
Atlantic (west Iberia/Morocco) ^c	200–1500	6.9	1	ETS
Atlantic (meddies) ^c	200–1500	6.1	2	ETS
Atlantic (Canary Islands) ^d	200–1000	2.4	11	ETS
Atlantic (Gulf of Mexico) ^e	100–500	118.1	7	Winkler
Mediterranean (west) ^c	200–1500	6.8	2	ETS
Mediterranean (west) ^f	200–3000	1.3	8	ETS
Mediterranean (west) ^g	200–800	2.2	24	ETS
Mediterranean (west) ^h	200–1000	1.2	10	ETS
Mediterranean (east) ⁱ	200–3000	4.3	>10	ETS
Indian Ocean (Arabian Sea) ^j	200–2400	5.2	6	ETS
Indian Ocean (Bay of Bengal) ^j	200–2400	2.2	6	ETS
Pacific Ocean (Guinea Dome) ^b	200–1000	3.9	>15	ETS
"	1000–bottom	2.6	>4	ETS
Southern Ocean (Indian sector) ^k	200–1000	1.5	7	ETS

ETS = Respiratory Electron Transport System activity; Winkler = Winkler oxygen determination; AOU/tracers = estimates from oxygen fields and water mass age.

^aJenkins and Wallace, 1992.

^bPackard et al., 1988.

^cSavenkoff et al., 1993a.

^dJ. Aristegui, unpublished data.

^eBiddanda and Benner, 1997.

^fChristensen et al., 1989.

^gSavenkoff et al., 1993b.

^hLefèvre et al., 1996.

ⁱLa Ferla and Azzaro, 2001.

^jNaqvi et al., 1996.

^kAristegui et al., 2002.

ing depth (Z , Figure 1a), as described by the fitted regression equation R ($\mu\text{mol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) = $18.0 e^{-0.53 Z (\text{Km})}$ ($R^2 = 0.760$, $F = 73.6$, $P < 0.00001$). Inspection of the residuals showed an enhanced respiratory activity at 1,000–2,000 m depth, corresponding to the base of the permanent thermocline separating the mesopelagic from the abyssal layers, relative to that expected from the general decline in respiratory activity with depth (Figure 1b). Examination of the individual profiles (Table 1) showed the enhanced respiratory activity to be a consistent feature in various seas and oceans, rather than an anomaly of a particular basin. The origin of these enhancements remains unclear, but may derive from mixing of water masses at the base of the

thermocline, or may be produced in situ by migrant zooplankton.

[6] These results indicate that 50% of the microplankton respiration within the dark ocean occurs between 200 and 700 m depth, and that 90% of the microplankton respiration within the dark ocean occurs between 200 and 4,500 m (Figure 2). The integration of the depth-averaged estimates of microplankton respiration in the dark ocean (Figure 1) using the percentage of the ocean surface comprised within the different depth zones [Menard and Smith, 1966], yielded an estimate of total respiration in the dark ocean of 33.3 Gt C yr^{-1} , pointing to microplankton respiration in the dark ocean as a major source of CO_2 . This estimate must be

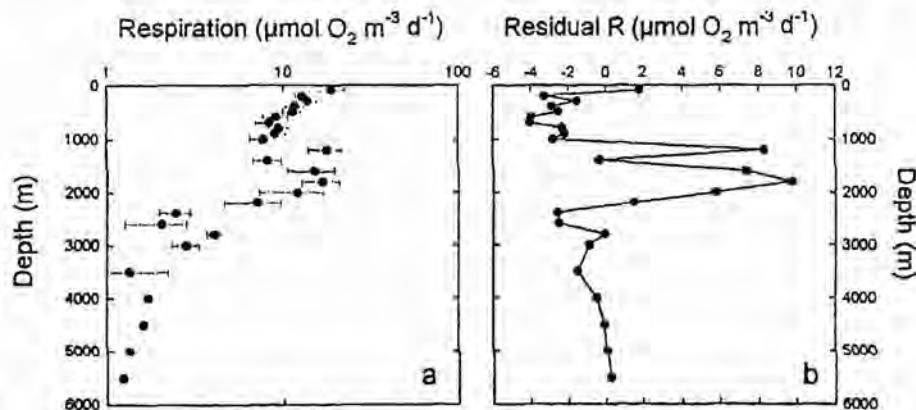


Figure 1. The depth distribution of the average (\pm SE) respiration rate in the dark ocean (a) and the depth distribution of the residuals from the fitted exponential equation (b). Rates compiled from references in Table 1.

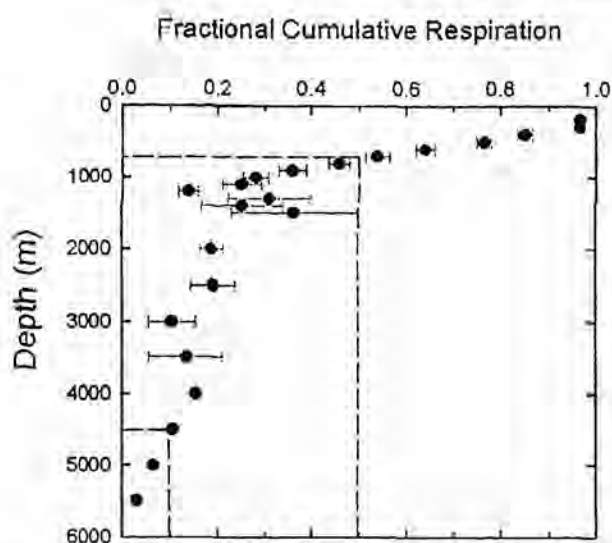


Figure 2. The depth distribution of the average (\pm SE) cumulative respiration rate in the dark ocean. Rates compiled from references in Table 1. Dotted lines indicate depths comprising 50% and 10% of the water column respiration in the dark ocean.

regarded as a first approximation, because the data set available (Table 1) is unbalanced in the depth and geographical distribution. Although the 200–2,000 m layer is covered by a significant ($N = 600$) empirical base, that between 2,000 and the ocean floor is still meager ($N = 25$). The geographical spread of the data is also dominated by estimates from the Atlantic and the Mediterranean Seas. However, the estimates available suggest limited geographical variability in the rates observed in the dark ocean (Table 1), particularly those in the abyssal waters (Figure 1a), so that the estimate of $33.3 \text{ Gt C yr}^{-1}$ is proposed to be indicative of the bulk figure contributed by microplankton respiration in the dark ocean.

[7] The estimates of respiration in the dark ocean derived here do not include respiration by metazoans, which may contribute a significant percentage of the total respiration in the dark ocean [Longhurst et al., 1990], nor benthic respiration, which is believed to add about 0.8 Gt C yr^{-1} [Jahnke, 1996]. Hence, although the estimates of respiration in the dark ocean, ranging between 20 Gt C yr^{-1} , derived from the areal rates, and $33.3 \text{ Gt C yr}^{-1}$, derived from the depth-distribution of the rates, may seem high, they should be considered to be conservative.

[8] The respiration in the dark ocean has been inferred indirectly in the past from the estimated organic carbon inputs to the dark ocean. The total organic carbon exported from the photic layer of the ocean is estimated at $15\text{--}16 \text{ Gt C yr}^{-1}$ [Sambrotto et al., 1993; Falkowski et al., 1998], but does not include active transport of organic matter by mesozooplankton, lateral inputs from the shelf, estimated at about 2 Gt C yr^{-1} [Liu et al., 2000], nor organic matter produced by chemosynthesis in the dark ocean, the magnitude of which remains unknown. However, the estimates of the organic carbon inputs to the dark ocean have been steadily increasing in the past, particularly since these

estimates, traditionally based on particulate export were expanded to include export of dissolved organic carbon as well [Carlson et al., 1994]. Indeed, it has recently been suggested that sediment traps may severely underestimate the sinking particle flux [Michaels et al., 1994]. This would partly explain the large discrepancies between particulate organic carbon flux and both benthic carbon remineralization in the deep ocean [Wenzhöfer and Glud, 2002] and export production inferred from geochemical tracers [Carlson et al., 1994; Michaels et al., 1994]. Hence, the size of the organic carbon input to the dark ocean is still under revision. The estimates derived by up-scaling from ETS-based measurements provided here are, however, consistent with those derived using geochemical tracers [Jenkins, 1982; Jenkins and Wallace, 1992; Carlson et al., 1994].

4. Conclusions

[9] In summary, the analysis presented here confirms respiration in the dark ocean to be a major component of the carbon cycle in the biosphere. The much lower volumetric rates compared to those in the photic layer are compensated by the vastly larger volume of the dark ocean. This results in an estimated respiratory CO_2 production in the dark ocean of 20 to 33 Gt C yr^{-1} , to which the enhanced microplankton respiration at the base of the permanent thermocline (1,000–2,000 m) has an important contribution. These estimates help constrain present estimates of the inputs of organic carbon to the dark ocean, which are critical to establish the role of the biological pump in the removal of atmospheric CO_2 . In particular, the results presented should promote an improved understanding of the oceanic carbon cycle able to accommodate the large respiration rates occurring in the dark ocean.

[10] **Acknowledgments.** We gratefully acknowledge Hugh Ducklow and one anonymous reviewer for valuable suggestions. Thanks also to Ted Packard for encouraging research on ETS. This work was supported by grants from the Spanish Plan Nacional de I+D to project COCA (REN2000-1471-CO2-02/MAR).

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