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Significance of non-sinking particulate organic carbon and dark CO_2 fixation to heterotrophic carbon demand in the mesopelagic northeast Atlantic

Federico Baltar,[1] Javier Arístegui,[1] Eva Sintes,[2,4] Josep M. Gasol,[3] Thomas Reinthaler,[2,4] and Gerhard J. Herndl[2,4]

[1] It is generally assumed that sinking particulate organic carbon (POC) constitutes the main source of organic carbon supply to the deep ocean's food webs. However, a major discrepancy between the rates of sinking POC supply (collected with sediment traps) and the prokaryotic organic carbon demand (the total amount of carbon required to sustain the heterotrophic metabolism of the prokaryotes; i.e., production plus respiration, PCD) of deep-water communities has been consistently reported for the dark realm of the global ocean. While the amount of sinking POC flux declines exponentially with depth, the concentration of suspended, buoyant non-sinking POC (nsPOC; obtained with oceanographic bottles) exhibits only small variations with depth in the (sub)tropical Northeast Atlantic. Based on available data for the North Atlantic we show here that the sinking POC flux would contribute only 4–12% of the PCD in the mesopelagic realm (depending on the primary production rate in surface waters). The amount of nsPOC potentially available to heterotrophic prokaryotes in the mesopelagic realm can be partly replenished by dark dissolved inorganic carbon fixation contributing between 12% to 72% to the PCD daily. Taken together, there is evidence that the mesopelagic microheterotrophic biota is more dependent on the nsPOC pool than on the sinking POC supply. Hence, the enigmatic major mismatch between the organic carbon demand of the deep-water heterotrophic microbiota and the POC supply rates might be substantially smaller by including the potentially available nsPOC and its autochthonous production in oceanic carbon cycling models. **Citation:** Baltar, F., J. Arístegui, E. Sintes, J. M. Gasol, T. Reinthaler, and G. J. Herndl (2010), Significance of non-sinking particulate organic carbon and dark CO_2 fixation to heterotrophic carbon demand in the mesopelagic northeast Atlantic, *Geophys. Res. Lett.*, *37*, L09602, doi:10.1029/2010GL043105.

1. Introduction

[2] It is generally accepted that the deep-water heterotrophic food web relies on the organic matter (OM) generated by primary production in the sun-lit surface waters. On a global average, about 30% of the surface water's primary production is exported into the dark ocean as sedimenting particles [*Arístegui et al.*, 2005b; *Buesseler and Boyd*, 2009]. Although the concentration of dissolved organic carbon (DOC) is generally about 10 times higher than that of particulate organic carbon (POC), the surface-exported DOC pool makes it greatest contribution to oxygen consumption in the upper ocean [*Hansell et al.*, 2009]) and it least at greater depths (about 10% of oxygen consumption [*Arístegui et al.*, 2002]). Hence, passively sinking particles originating from the euphotic zone have been considered as the principal source of organic carbon available for the heterotrophic food web in the ocean's interior [*Buesseler et al.*, 2007]. The majority of the POC exported from the euphotic zone is remineralized in the mesopelagic layer (between 100–1000 m depth), leading to a typical exponential attenuation of the sinking POC concentration with depth.

[3] Assuming mass balance, the supply rate of organic carbon (generally calculated from sinking POC collected by sediment traps) reaching the ocean's interior should match the carbon demand of the heterotrophic biota inhabiting the meso- and bathypelagic realm. The deep-water biota is vastly dominated by prokaryotes, in terms of abundance and biomass. However, the prokaryotic organic carbon demand (the total amount of organic carbon required to sustain the heterotrophic metabolism of prokaryotes, determined as respiration plus production, PCD) has been shown to continuously exceed the sinking POC flux into the dark ocean [*Burd et al.*, 2010]. Recent estimates report a mismatch between deep-water PCD and sinking POC flux by up to 2–3 orders of magnitude [*Reinthaler et al.*, 2006; *Steinberg et al.*, 2008; *Baltar et al.*, 2009]. Moreover, a global budgeting exercise indicated that even the highest estimate of sinking POC flux from surface waters would only explain about 50% of the measured oxygen consumption in the dark ocean [*del Giorgio and Duarte*, 2002]. This paradoxical imbalance has been shown to vary spatially. PCD was 3–4 times and around 10 times greater than the sinking POC flux in the subtropical and subarctic Pacific, respectively [*Steinberg et al.*, 2008]. This strong imbalance between POC supply and demand represents one of the great challenges in contemporary biological oceanography and marine biogeochemistry, and indicates major gaps in our understanding of the deep ocean carbon flux. It is apparent that some major components and aspects of organic carbon stocks and fluxes have not been taken into account adequately.

[4] One of the major POC pools in the ocean's interior not adequately taken into account in the oceanic carbon budgets

[1]Facultad de Ciencias del Mar, Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria, Spain.
[2]Faculty Center of Ecology, Department of Marine Biology, University of Vienna, Vienna, Austria.
[3]Departament de Biologia Marina i Oceanografia, Institut de Ciències del Mar, CSIC, Barcelona, Spain.
[4]Department of Biological Oceanography, Royal Netherlands Institute for Sea Research, Den Burg, Netherlands.

is slow-sinking, or almost suspended non-sinking POC (nsPOC) collected with oceanographic bottles but, due to their buoyant nature, not accumulating in sediment traps used to determine sinking POC flux [*Arístegui et al.*, 2009]. In a previous study, *Baltar et al.* [2009] found a significant correlation between nsPOC and potential respiration (the main parameter determining PCD) in the deep waters of the subtropical Northeast Atlantic, supporting the view that nsPOC plays a key role in dark ocean metabolism, and hence in supplying bioavailable substrates to support the PCD. Nevertheless, the quantitative origin of this nsPOC still remains largely enigmatic. The bulk meso- and bathy-pelagic nsPOC may come from different sources: i) from self-assembly of dissolved organic material yielding porous microgels that can be readily colonized by microorganisms [*Chin et al.*, 1998], ii) from sinking particles disaggregated by physical forces [*Burd and Jackson*, 2009] or the activity of microbes and zooplankton [*Sheridan et al.*, 2002], iii) from laterally advected nsPOC, or iv) from in situ production of organic material due to prokaryotic chemoautotrophs.

[5] Here we quantify the contribution of dark ocean chemosynthesis to PCD in the subtropical Northeast Atlantic and compare it with the contribution of the sinking POC flux. We use data collated from the meso- and bathypelagic North Atlantic on sedimenting particulate organic matter (POM) flux, POM standing stock (thus including the resident nsPOC) and PCD to re-evaluate the apparent discrepancy between prokaryotic organic matter demand and supply in the ocean's interior.

2. Methods

2.1. Study Site and Sampling

[6] More than 9000 km were covered during the AR-CHIMEDES-I (November–December 2005) cruise on board RV *Pelagia* to resolve the areal variability in organic matter and prokaryotic activity in the meso- and bathypelagic waters of the eastern North Atlantic (Figure S1 in Text S1 of the auxiliary material).[1] Samples were taken from seven depths: the surface mixed layer (average depth 50 m) for particulate organic matter (POM) and electron transport system (ETS) only, the base of the mixed layer (100 m layer), the mesopelagic (250, 500 and 900 m), the North East Atlantic Deep Water (NEADW; average depth 2750 m) and the Lower Deep Water (LDW; average depth 4000 m). Samples from the distinct water masses were collected with 12 L NOEX (no oxygen exchange) bottles mounted on a CTD (conductivity, temperature, depth) frame to determine total prokaryotic abundance, leucine incorporation, POM, ETS and dark DIC fixation as described below.

2.2. Prokaryotic Abundance, Heterotrophic Metabolism and Particulate Organic Matter Concentrations

[7] Prokaryotic abundance, leucine incorporation, particulate organic carbon and nitrogen, respiratory activity of the electron transport system (ETS) and non-sinking particulate organic carbon (nsPOC) and nitrogen (nsPON) were ana-

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[1]Auxiliary materials are available in the HTML. doi:10.1029/2010GL043105.

lyzed as explained in a previous study [*Baltar et al.*, 2009] (see also auxiliary material).

2.3. Dissolved Inorganic Carbon (DIC) Fixation

[8] DIC fixation was measured via the incorporation of [^{14}C]-bicarbonate (3.7×10^6 Bq, Amersham) in 50 ml seawater samples. Triplicate samples and formaldehyde-fixed blanks were incubated in the dark at in situ temperatures for 60–72 h. Incubations were terminated by the addition of formaldehyde (2% final concentration) to the samples, filtration onto 0.2-μm polycarbonate filters and rinsing with 10 ml of ultra-filtered seawater (<30 kDa). Afterward, the filters were exposed to a fume of concentrated HCl for 12 h, transferred into scintillation vials and after adding 8 ml scintillation cocktail (Canberra-Packard, Filter Count), counted in the scintillation counter for 10 min. The resulting mean disintegrations per minute (DPM) of the samples were corrected for the mean DPM of the blanks and converted into DIC fixed over time and corrected for the natural DIC concentrations as measured by continuous flow analysis [*Stoll et al.*, 2001].

3. Results and Discussion

[9] Unlike the general exponential decline in sinking POC with depth [*Martin et al.*, 1987], the average concentrations of nsPOC and nsPON remained fairly constant with depth down to bathypelagic waters (4000 m depth) of the (sub) tropical Northeast Atlantic (Figures 1a and 1b). This pattern contrasts with the reported decrease with depth of nsPOC at the Bermuda Atlantic Time-series (BATS) station, in the center of the North Atlantic subtropical Gyre, but is similar to the distribution observed by *Alonso-González et al.* [2009] in the Canary Current (CanC), at the northeastern side of our sampling region. Overall, our nsPOC values spans the range of the observed CanC and BATS concentrations (Figure S2 in Text S1 of the auxiliary material), suggesting a transitional continental shelf-open ocean gradient in nsPOM concentrations. Generally, the prokaryotic contribution to the nsPOC and nsPON decreased with depth (Figures 1c and 1d). Subtracting the prokaryotic contribution from the bulk nsPOC and nsPON pool, we obtain the amount potentially available for heterotrophic utilization of nsPOC (nsPOC_Av) and nsPON (nsPON_Av), which did not exhibit a general depth-related trend (Figures 1e and 1f). The ratio nsPOC_Av: nsPON_Av was also fairly constant throughout the water column suggesting that there are no major shifts in the C:N ratio of nsPOM in deep-waters (Figure 1g), in contrast to the reported increasing C:N ratios with depth of sedimenting POM and DOM [*Schneider et al.*, 2003; *Hopkinson and Vallino*, 2005]. This stability in the elemental composition of suspended POM, in combination with its fairly constant concentration throughout the water column of our region of study suggests that it is either not utilized biotically or that its utilization by the deep-sea biota is matched by in situ production or external import of nsPOM. *Alonso-González et al.* [2009] observed lower average C:N ratios in the CanC than in our study, although their ratios clearly increased in their western stations of the sampling box, according to the measured high respiration of nsPOC through its westward transport.

[10] Prokaryotic respiration (R) is the main parameter affecting the PCD in the deep Atlantic, as it is typically 1–
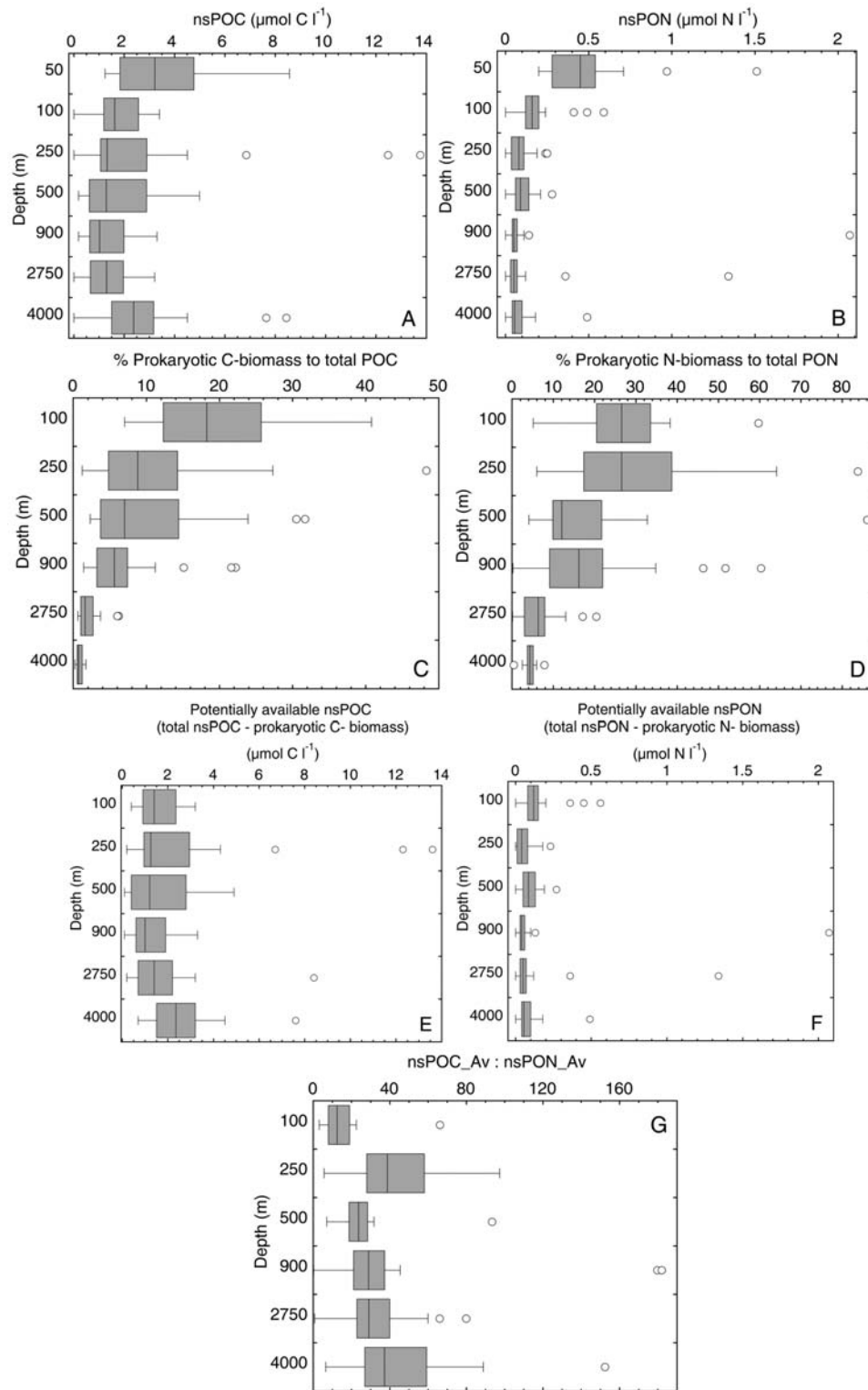
Figure 1. Box-Whisker plot of the vertical distribution of (a) bulk non-sinking particulate organic carbon (nsPOC) and (b) nitrogen (nsPON), contribution of the prokaryotic biomass to the bulk (c) nsPOC and (d) nsPON, potentially available (e) nsPOC and (f) nsPON after subtracting the prokaryotic C- and N-biomass, respectively, and (g) the ratio of potentially available nsPOC to nsPON. All organic matter concentrations are in μmol l^{-1}.

2 orders of magnitude higher than prokaryotic heterotrophic production [*Reinthaler et al.*, 2006; *Baltar et al.*, 2009]. Therefore, our PCD estimates greatly rely on the conversion of measurements of the electron transport system (ETS) to

R, i.e., the R:ETS ratio used (see auxiliary material). Our PCD estimates were bracketed based on an R:ETS ratio of 0.086, derived from bacterial cultures in senescent phase [*Christensen et al.*, 1980], and of 0.6, obtained from the

Table 1. Comparison of the Variation in the Different Depth Layers of the Prokaryotic Carbon Demand[a]

Depth (m)	PCD (R:ETS = 0.086)	PCD (R:ETS = 0.6)	OUR NAtl	OUR SAtl	AP
100	58.9	353.4			41.3
250	18.3	109.5	36.5	26.4	32.4
500	11.9	71.5	14.7	16.8	3.7
900	4.2	25.2	6.5	12.3	0.3
2750	3.3	19.9			0.2
4000	4.7	28.5			0.3

[a]PCD, prokaryotic carbon demand. Assuming an R:ETS ratio of 0.086 and 0.6, oxygen utilization rates (OUR) reported for the North Atlantic Subtropical Gyre (OUR NAtl) [*Jenkins*, 1982], and for the South Atlantic Subtropical Gyre (OUR SAtl) [*Brea*, 2008], and dark DIC fixation rates (AP, autotrophic production). Metabolic rates in μmol C m^{-3} d^{-1}.

same cultures in exponential growth phase [*Christensen et al.*, 1980] and *in situ* measurements of active mesopelagic prokaryotes in the CanC region [*Arístegui et al.*, 2005a]. The PCD decreased by one order of magnitude from the base of the euphotic zone towards the bathypelagic zone independent of the R:ETS ratio used (Table 1). The oxygen utilization rates (OUR) reported for the centers of the North and South Atlantic subtropical Gyres [*Jenkins*, 1982; *Jenkins and Wallace*, 1992; *Brea*, 2008] are within the range of our PCD estimates (Table 1). Assuming that these biogeochemical estimates represent average values from our region of study, the R:ETS ratio should be closer to 0.2. Nevertheless, it is more plausible to assume that the R:ETS ratio varies between 0.2 and 0.6, since our region of study spans a transition zone with more nsPOM than observed in the centers of the subtropical Gyres.

[11] Dissolved inorganic carbon (DIC) fixation by chemoautotrophic microbes occurs throughout the deep waters of the Atlantic [*Herndl et al.*, 2005], amounting on average 12 ± 5 μmol C m^{-3} d^{-1} in the mesopelagic realm of the (sub)tropical Northeast Atlantic (Table 1). This freshly produced

organic carbon represents an nsPOC source in the meso- and bathypelagic waters, as microbial cells are too small to sediment. The autochthonously produced nsPOC potentially accounts for $72 \pm 53\%$ to $12 \pm 9\%$ (considering an R:ETS of 0.086 and 0.6, respectively) of the daily heterotrophic prokaryotic carbon demand in the mesopelagic realm (Table 2).

[12] For comparison, the sinking POC flux based upon a model from a compilation of sediment trap data of the North Atlantic [*Antia et al.*, 2001] was used to estimate the potential contribution of the sinking POC to PCD. We calculated the sinking POC using the surface primary production (PP) estimates from the NE Atlantic gyre [*Longhurst et al.*, 1995] (28 mmol C m^{-2} d^{-1}), from the western gyre [*Steinberg et al.*, 2001] (35 mmol C m^{-2} d^{-1}) and as an upper limit 50 mmol C m^{-2} d^{-1} (for the entire North Atlantic [*Longhurst et al.*, 1995] including temperate regions where PP is higher). The potential contribution of the sinking POC amounts to 4–6% to the PCD per day when using a surface PP of 28 and 35 mmol C m^{-2} d^{-1}, respectively (Table 2). Only when using the unrealistically high surface PP of 50 mmol C m^{-2} d^{-1} for this (sub)tropical mid-oceanic region, the contribution of the sinking POC to the mesopelagic PCD equals the contribution (12%) of the dark CO$_2$ fixation (Table 2). Despite the rather low DIC fixation rates in the bathypelagic realm, even in this layer the contribution of the sinking POC to the PCD does not exceed the contribution derived from DIC fixation (Table 2). Thus, a significant fraction (at least similar to the sinking POC contribution) of the organic carbon required by the meso- and bathypelagic microbial community could be supplied by chemoautotrophic CO$_2$ fixation in the (sub)tropical Northeast Atlantic's interior.

[13] As shown previously, the major energy source for prokaryotic DIC fixation is likely derived from ammonia oxidation by *Crenarchaeota*, as archaeal *amo*A genes are by far more abundant than bacterial *amo*A genes in the mesopelagic realm of the North Atlantic [*Agogué et al.*, 2008].

Table 2. Potential Contribution (in %) of Dark CO$_2$ Fixation (AP) and of the Available Sinking POC to the PCD[a]

Depth	AP	Sinking POC (PP = 28)	Sinking POC (PP = 35)	Sinking POC (PP = 50)
		% Contribution to PCD Assuming R:ETS = 0.086		
100	70	55	82	154
250	177	38	57	106
500	31	18	27	51
900	7	19	29	54
2750	5	4	6	10
4000	7	1	2	4
mesop avg	72 ± 53	25 ± 6	37 ± 10	70 ± 18
bathy avg	6 ± 1	3 ± 1	4 ± 2	7 ± 3
Mesop AP: Sinking ratio		2.8	1.9	1.0
Bathyp AP: Sinking ratio		2.4	1.6	0.9
		% Contribution to PCD Assuming R:ETS = 0.6		
100	12	9	14	26
250	30	6	9	18
500	5	3	5	8
900	1	3	5	9
2750	1	1	1	2
4000	1	0	0	1
mesop avg	12 ± 9	4 ± 1	6 ± 1	12 ± 3
bathy avg	1	0	1	1
Mesop AP: Sinking ratio		2.8	1.9	1.0
Bathyp AP: Sinking ratio		2.4	1.6	0.9

[a]Assuming an R:ETS of 0.086 and 0.6. The contribution from the sinking POC was inferred from a POC flux model [*Antia et al.*, 2001] assuming a surface primary production (PP) of 28 mmol C m^{-2} d^{-1} (NE Atlantic gyre [*Longhurst et al.*, 1995]), 35 mmol C m^{-2} d^{-1} (western gyre [*Steinberg et al.*, 2001]) and of 50 mmol C m^{-2} d^{-1} (N Atlantic [*Longhurst et al.*, 1995]).

Based on the radiocarbon signature of archaeal lipids, it has been shown recently that 83% of the archaeal carbon is derived by autotrophy in the subtropical mesopelagic North Pacific (at 670 m depth) [*Ingalls et al.*, 2006]. The radiocarbon signature of DNA collected from mesopelagic Pacific waters (670–915 m) allowed to differentiate between the three major carbon pools that are potentially available to prokaryotes: fresh DOC released from POC (Δ^{14}C > +50‰), ambient DIC (Δ^{14}C ~ −200 to −100 ‰), and aged bulk DOC (Δ^{14}C = −525‰) [*Hansman et al.*, 2009]. These authors concluded that both DIC and fresh DOC (presumably released from sinking POC) are utilized substantially, while ambient DOC is not a major substrate for mesopelagic prokaryotes [*Hansman et al.*, 2009]. There is also evidence of considerable chemolithotrophic production on sinking POC collected by sediment traps deployed in the mesopelagic (100–750 m depth) North Pacific, where prokaryotes contributes between 7–90% of the total microbial production [*Karl et al.*, 1984].

[14] Taken together, the current perception on the dependence of the dark ocean's heterotrophic microbial activity on sedimenting POC, and the previously reported mismatch between organic carbon supply and demand need revision [*Reinthaler et al.*, 2006; *Steinberg et al.*, 2008; *Baltar et al.*, 2009; *Burd et al.*, 2010]. The large and fairly constant stock of buoyant, nsPOC needs to be considered as a potentially available dynamic pool of POC for heterotrophic deep-water microbes. We have shown that about 12 ± 9–72 ± 53% of the amount of PCD required by microheterotrophs in the mesopelagic ocean is potentially supplied by deep-water chemolithotrophs via DIC fixation. Therefore, the apparent gap between heterotrophic organic matter demand and supply in the mesopelagic realm might be substantially smaller than previously thought. Nevertheless, the external sources for this nsPOM still needs to be constrained. Figure S3 (in Text S1 of the auxiliary material) illustrates the overall contribution of autotrophic production (AP) and sinking POC to PCD assuming a PP of 28 mmol C m^{-2} d^{-1} and a R:ETS range of 0.4–0.2, which based on the above information probably represents realistic average values for our region of study. The view emerging from Figure S3 is that, in spite of the significant contribution of AP to PCD a considerable fraction of the PCD still needs to be accounted by other sources. According to our observations, we suggest that continuous lateral advection of nsPOM from the continental margins may represent an important fraction of the missing carbon respired in our region of study. Future research should focus on refining the nutritive quality of buoyant nsPOC versus sedimenting POC. The refined pathways of organic matter supply and demand in the dark ocean might allow us to arrive at a mechanistic understanding of deep ocean food web structure and activity and ultimately, should lead to improved models on the dark ocean's role in global carbon cycling.

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J. Arístegui and F. Baltar, Facultad de Ciencias del Mar, Universidad de Las Palmas de Gran Canaria, Campus Universitario de Tafira, E-35017 Las Palmas de Gran Canaria, Spain. (federico.baltar102@doctorandos.ulpgc.es)

J. M. Gasol, Departament de Biologia Marina i Oceanografia, Institut de Ciències del Mar, CSIC, Pg. Marítim de la Barceloneta 37-49, E-08003 Barcelona, Spain.

G. J. Herndl, Department of Biological Oceanography, Royal Netherlands Institute for Sea Research, NL-1790 AB Den Burg, Netherlands.

T. Reinthaler and E. Sintes, Faculty Center of Ecology, Department of Marine Biology, University of Vienna, Althanstr. 14, A-1090 Vienna, Austria.