

## Fueling Western Mediterranean deep metabolism by Deep Water formation and shelf-slope cascading : evidence from 1981

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### ABSTRACT

We focus here on microbial respiration and its potential enhancement by organic-carbon injection via Deep and Intermediate Water formation in the western Mediterranean Sea. Electron transport system (ETS) activities of the nanoplankton and microplankton in the intermediate and deep water from this area show unexpected enhancement. Since ETS is a proxy for respiration these measurements indicate elevated respiration in these waters. In addition, they suggest horizontal transport of organic-carbon rich water-masses. In the western Mediterranean Sea the metabolic rates below 1,500 m were greater than rates at the same depths in the Atlantic. When all the profiles were corrected to the same temperature and normalized by the metabolic rate at 200 m, the Western Mediterranean rates were greater than rates from the same depths in both the Atlantic and equatorial Pacific Oceans. They also exceeded rates predicted from sediment traps. Furthermore they were not consistent with organic matter being supplied via rapidly sinking particulate material. Instead, they may be supported by dissolved organic carbon (DOC) transported to depth by eddies (van Haren *et al.*, 2006), wintertime deepwater convection, or the type of wintertime cold-water cascading recently observed in the canyons on the Catalan-Occitan continental shelf and slope (Canals *et al.*, 2006; Font *et al.*, 2007).

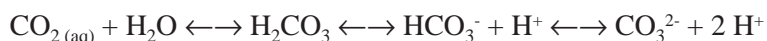
### BACKGROUND

Respiration in the deep-sea (deep metabolism, (Craig, 1971)) is an important factor in understanding the ocean's role as a sink for CO<sub>2</sub>, in determining the magnitude of the new production, and in understanding deep-sea ecology, food chains, and variations in fisheries yield. Deep-sea respiration helps to dampen the build-up of CO<sub>2</sub> in the atmosphere by converting DOC and POC originally produced in the surface waters to CO<sub>2</sub> and sequestering it in the deep water. Three types of mechanisms for transporting carbon from the sea-surface to the deep-sea are currently recognized: the soft-tissue pump (biological pump), the carbonate pump and the solubility pump. All involve vertical fluxes and normally do not include horizontal transport in the subsurface waters. Here, we consider horizontal carbon fluxes associated with the entrainment of dissolved organic carbon (DOC) and particulate organic carbon (POC) in sinking surface waters. These waters, after cooling, reach great depths by sinking in the open ocean or by cascading off shelves

and down canyons. At depth they spread along isopycnal surfaces increasing, temporarily, the volume of Deep and Intermediate Waters. Injection of CO<sub>2</sub> into the seawater occurs when the entrained POC and DOC are oxidized via respiration, i.e.,



The CO<sub>2</sub> is then distributed into the different species of the carbonate system, carbonic acid (H<sub>2</sub>CO<sub>3</sub>), bicarbonate, (HCO<sub>3</sub><sup>-</sup>), and carbonate (CO<sub>3</sub><sup>2-</sup>).



Since the residence time of the Mediterranean Deep Water is on the order of 22 years (Bethoux, 1980), this injected CO<sub>2</sub> is effectively removed from the atmosphere for this time period: the rate at which CO<sub>2</sub> is produced from POM in the deep sea is thought to balance the sinking rate of POM from the near-surface waters. This sinking rate, in turn, is thought to balance the rate of phytoplankton new production in the near-surface waters. So a measure of either one of these three rates serves as an estimate of the others as well as an estimate of the soft tissue pump. However, none of the three rates considers the horizontal flux of carbon. If the deep metabolism is enhanced by horizontal carbon inputs then both calculations of vertical carbon flux and new production will be exaggerated. Furthermore curvature of the depth functions of the metabolism, POC, and DOC will be decreased. In other words, the attenuation of these quantities with depth will be less than if the fuel source for deep metabolism was from vertical flux. Here we observe, in the measurements of ETS activity, evidence for attenuation in the vertical depth function of respiration in the Western Mediterranean and suggest that it is caused by horizontal injections of POC and DOC subsequent to deep water formation in the Gulf of Lions.

## DATA

The method for measuring ETS activity and its relationship to vertical carbon flux and new Production are given in Packard and Christensen (2004); Packard and Codispoti (2007); and references within these papers. The basic idea behind the ETS measurement is as follows. The biological breakdown of organic matter (C<sub>6</sub>H<sub>12</sub>O<sub>6</sub>) produces CO<sub>2</sub>, protons (H<sup>+</sup>), and electrons (e<sup>-</sup>). The ETS in biomembranes transports the protons and the electrons to oxygen while concurrently producing adenosine triphosphate (ATP, cellular energy currency). The ETS method uses a redox dye (INT), an electron acceptor, to quantitatively intercept the electrons moving along the membrane towards oxygen. Thus in the presence of INT, the cellular respiratory reactions, instead of reducing oxygen to water, reduce INT to a scarlet end product. The formation rate of this end product, a formazan, is easier to measure than is the consumption of oxygen and so it serves as a proxy for respiration. The biochemical meaning of ETS and ETS activity, the relationship of the ETS to metabolism and respiration, its oceanographic use in bacterioplankton, phytoplankton, zooplankton, the deep-sea, and the oceanic euphotic zone are discussed in Nelson and Cox (2005); Packard (1985a,b); Hernandez-Leon and Gomez (1996); del Giorgio and Williams (2005); Aristegui and Montero (1995). The ETS data used here are from Packard *et al.* (1988); Christensen *et al.* (1989); La Ferla *et al.* (2003).

## RESPIRATION PROFILES

Vertical profiles of ETS activity from the Mediterranean Sea and the Atlantic and Pacific Oceans were converted into respiration profiles and plotted as rates of CO<sub>2</sub> production (Figure 1) as in Packard *et al.* (1988) and Packard and Christensen (2004).

The vertical plots of respiration for the Atlantic (Sargasso Sea) and the Pacific (central Northern gyre) oceans have a much more pronounced curvature than those from the Mediterranean Sea. The western Mediterranean has the least curvature. If the Atlantic and Pacific respiration profiles are representative of systems where deep-sea metabolism is fueled by vertical carbon flux and the Mediterranean profiles display less curvature, the difference should yield information about the

extent of horizontal carbon flux at depth. To facilitate this comparison, the Mediterranean respiration profiles from Figure 1 were normalized to their 200 m value and compared to similarly normalized Atlantic and Pacific profiles (Figure 2).

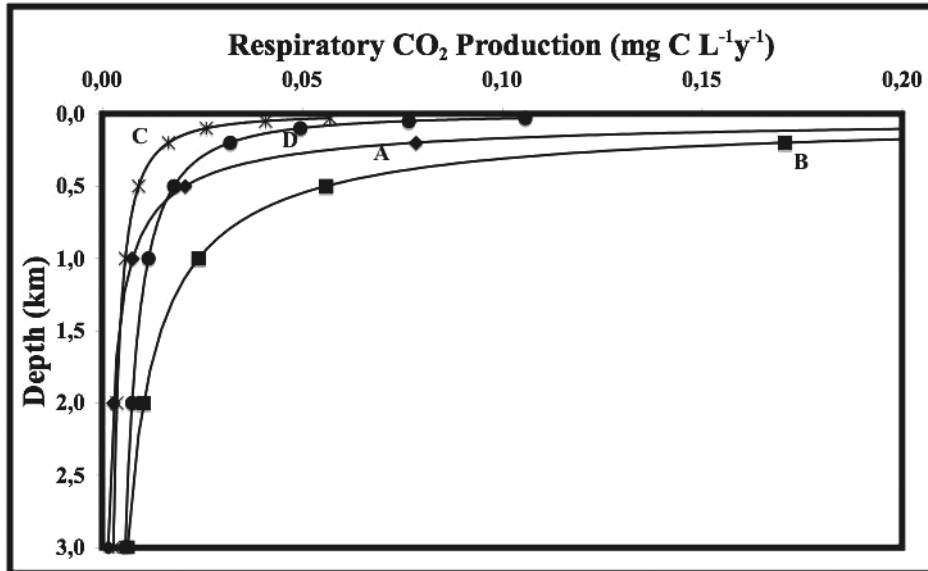


Figure 1. Vertical profiles of respiratory carbon production at *in situ* temperature in the: (A) Northern Sargasso Sea (Atlantic); (B) Central North Pacific Ocean; (C) W. Mediterranean Sea (MEDIPROD IV cruise); and (D) Central Mediterranean Sea. Units of respiration represent the mg C as CO<sub>2</sub> per liter that microorganisms and microzooplankton generate through their respiration in a year. This is stoichiometrically equal to the amount of organic carbon consumed by the same organisms in a year. Note the reduced curvature in the Mediterranean profiles.

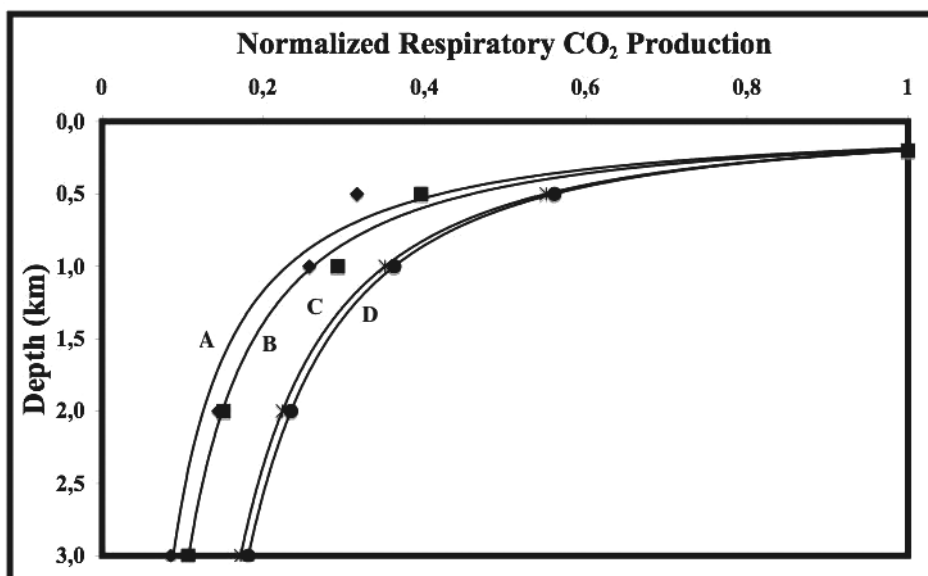


Figure 2. Vertical profiles from Figure 1 recalculated with the Arrhenius equation for Mediterranean temperatures at equivalent ocean depths. These profiles have been normalized by their respiratory carbon consumption at 200 m so they are unitless. (A) Northern Sargasso Sea (Atlantic); (B) Central North Pacific Ocean; (C) W. Mediterranean Sea (MEDIPROD IV cruise); and (D) Central Mediterranean Sea. Note the relatively high respiration at the deeper depths in the Mediterranean profiles.

To eliminate the effect on the respiration of the different temperatures in the samples from the different deep waters, the Atlantic and the Pacific respirations have been corrected by the Arrhenius equation to respirations at Mediterranean temperatures for equivalent depths. Mediterranean Deep Water is about 10° C warmer than Atlantic and Pacific Deep Water so this correction shifts the deep-sea respiration up by about a factor of 2. Nevertheless, the respiration rates in the deep parts of the two Mediterranean profiles are relatively higher and the curvature of the profiles is lower than their counterparts in the Atlantic and Pacific. These differences suggest horizontal organic carbon input. They were measured in 1981, but likely represent conditions of today.

From these profiles there is no way to determine the seasonal, annual, or regional variability in the deep respiration. Neither can one determine whether the enhanced metabolism is derived from the open sea deep-water formation, eddy circulation, or from shelf cascading events. Modeling, at this stage of knowledge, cannot resolve these questions. An important step in their resolution would require deep respiration time-course profiles in the Gulf of Lions as well as seasonal and annual deep-sea respiration sections along the axis of deep-water flowing out of the Gulf of Lions. Still, this would not differentiate the impact of concurrent events of cascading and deep convective overturning in the open sea. For this, the development of biochemical water mass tracers using techniques such as peptide mass fingerprinting of proteins isolated by SDS-PAGE (Suginta, 2007), lipid fingerprinting by a combination of mass spectrometry, gas chromatography and nuclear magnetic resonance (De Souza *et al.*, 2006) or molecular biological analysis would be helpful.

The impact of open sea deep water formation and shelf cascading on deep-sea biology depends on the magnitude and frequency of these events. They should both accelerate the delivery and improve the quality of organic carbon being made available to the deep-sea biota. Accordingly they should enhance growth, respiration and biomass of the deep-sea populations of microbes, zooplankton and nekton. Fisheries harvesting deep-sea populations of fish, squid and shell-fish should note positive responses to these events after a suitable lag time. In other parts of the Western Mediterranean similar enhanced mesopelagic respiration has been found. In the Levantine Sea LaFerla and Azzaro (2001) attribute it to carbon injection from the Aegean Sea. In the Liguro-Provençal front Savenkoff *et al.* (1993) attributed it to vertical organic carbon transport in anticyclonic eddies (Meddies, Richardson *et al.*, 2000). In the NE Atlantic Ocean near the Canary Island (Hernandez-Leon *et al.*, 2001; Hernandez-Guerra *et al.*, 2005) lateral transport of organic carbon has been shown to account for between 30 and 60 % of the mesopelagic (100-1,000 m) respiration (Alonso-González *et al.*, 2009). It remains to be seen if the response of the fishery is in this order of magnitude.

The impact of these events on the biology of the near-surface waters should also be significant because the mixing that always co-occurs with deep-water formation will enrich the near-surface waters with inorganic nutrient salts ( $\text{PO}_4^{3-}$ ,  $\text{NO}_3^-$ , and  $\text{Si}(\text{OH})_4$ ). Accordingly, as soon as the euphotic zone stabilizes, the phytoplankton will start to grow and a bloom will ensue. This will, in turn, enrich the epipelagic biota (microbes, zooplankton, and nekton) and fisheries dependent upon it.

## EPILOGUE

Lateral transport of organic material in the deep-sea and its impact on deep metabolism now seems certain after the work of Christensen *et al.* (1989); Savenkoff *et al.* (1993); La Ferla and Azzaro (2001); Alonso-González *et al.* (2009). Furthermore, from different evidence this horizontal input was inferred in the works of Walsh (1991); Falkowski *et al.* (1994); Barth *et al.* (2002). The directionality of this flux changes the conceptual model upon which the decade-long JGOFS program was based, namely that the deep-metabolism was fueled by vertical carbon flux (Doney and Ducklow, 2006). Yet, as when Christensen *et al.* (1989) first alerted the scientific community of its potential role, these horizontal carbon inputs to the deep-sea have not been incorporated into current thinking about mesopelagic biota, metabolism, and food chains. Perhaps now, after the description of new mechanisms for injecting organic carbon into the deep sea involving cascading (Palanques *et al.*, 2009) and gyres (van Haren *et al.*, 2006), horizontal carbon fluxes in the deep-sea will be factored into research on mesopelagic biotic processes.

**Acknowledgements:** we thank Mariona Segura, Jordi Font, Jordi Salat, Pere Puig, and Dolors Blasco for their comments, support, and encouragement. This contribution was funded by the University of Las Palmas de Gran Canaria (ULPGC), the Spanish Ministry of Education and Science, the Graduate Program in Oceanography at the ULPGC and the research grant EXOME (CTM 2008-01616). This is contribution #200907 from the Bigelow Laboratory for Ocean Sciences.