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Modeling vertical carbon flux from zooplankton respiration

Theodore T. Packard *, May Gómez

Plankton Ecophysiology Group, Instituto Universitario de Oceanografía y Cambio Global, Universidad de las Palmas de Gran Canaria, Canary Islands, Spain

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ABSTRACT

The transport of carbon from ocean surface waters to the deep sea is a critical factor in calculations of planetary carbon cycling and climate change. This vertical carbon flux is currently thought to support the respiration of all the organisms in the water column below the surface, the respiration of the organisms in the benthos, as well as the carbon lost to deep burial. Accordingly, for conditions where the benthic respiration and the carbon burial are small relative to the respiration in the water column, and where horizontal fluxes are known or negligible, the carbon flux can be calculated by integrating the vertical profile of the water-column plankton respiration rate. Here, this has been done for the zooplankton component of the vertical carbon flux from measurements of zooplankton ETS activity south of the Canary Island Archipelago. From zooplankton ETS activity depth profiles, zooplankton respiration depth profiles were calculated and using the equations for the profiles as models, the epipelagic (3.05 μmol CO_2 m^{-3} h^{-1}), mesopelagic (112.82 nmol CO_2 m^{-3} h^{-1}), and bathypelagic (27.89 nmol CO_2 m^{-3} h^{-1}) zooplankton respiration for these waters were calculated. Then, by integration of the depth-normalized respiration profiles, zooplankton-associated carbon flux profiles below 150 m were calculated. These had an uncertainty of ±40%. At the station level (local regional variation) the variability was ±114% ($n = 16$). At 150 m and 500 m the average passive carbon flux associated with the zooplankton was 36 (±114%) and 20 (±113%) μmol C m^{-2} h^{-1}. The carbon transfer efficiency (T_{eff}) from the 150 to the 500 m levels averaged 51 ± 21% and a new metric, the nutrient retention efficiency (NRE), averaged 49 ± 21%. This metric is an index of the efficiency with which nutrients are maintained in the epipelagic zone and is directly related to the respiration in the water column. The carbon flux equation describing the pooled data ($n = 16$) was $131.14Z^{-0.292}$. Using this as a model for zooplankton-associated carbon flux south of the Canary Islands one can calculate that carbon flux from epipelagic waters at 200 m is 27.91 μmol C m^{-2} h^{-1}, and the carbon flux from mesopelagic waters at 1000 m, is 17.45 μmol C m^{-2} h^{-1}.

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1. Introduction

Understanding and quantifying the mode and the rate of carbon flux to the deep ocean as well as understanding and quantifying the mechanisms of its attenuation has been the focus of intense oceanographic research in the last 25 years (McCave, 1975; Fasham, 2003; Buesseler and Lampitt, 2008). Carbon flux through the water column is needed to calculate the carbon sequestration rate in the deep ocean (Packard et al., 1988, Ridgwell et al., 2011), export production from the ocean's euphotic zone, and the carbonate compensation depth (Pälike et al., 2012). In addition, this flux is important in learning the limits of deep ocean metabolism (Arístegui et al., 2009), future CO_2 increases in the atmosphere, climate change (Doney et al., 2012), among other topical planetary questions (Riebesell et al., 2009, Bruhwiler et al., 2011). There are, at least, four facets of carbon flux in the ocean water column, the passive flux, the active flux, the dissolved organic carbon (DOC) flux, and the lateral flux. Zooplankton are thought to drive the active flux, but their metabolic needs impact the other three. The passive flux is the rain of particulate organic carbon (POC) that falls gravitationally through the ocean water column to depths below. The active flux is the carbon pumped between two different oceanic layers during the diel vertical migration of the zooplankton. The most common situation is where zooplankton eat phytoplankton and other microorganisms in epipelagic waters during the night, swim down to the mesopelagic layer, respire, and excrete part of this organic matter while resting during the day. The DOC flux refers to the dissolved organic carbon (DOC) flux that is transported by a variety of mixing mechanisms from the sea surface where it is produced, to subsurface ocean layers. And finally, the lateral carbon flux refers to the carbon that is transported horizontally along isopycnal surfaces from one oceanic province to another.

Each of these fluxes is important in sustaining deep-ocean pelagic and benthic populations and each of these fluxes needs to be considered and measured if accurate models of the ocean carbon cycling and climate change are to be constructed (Karl et al.,

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* Corresponding author. Address: Facultad de Ciencias del Mar, ULPGC, Campus Tafira, 35017 Las Palmas Gran Canaria, Spain. Tel.: +34 928452905; fax: +34 928452922.

E-mail address: tedpackard@dbio.ulpgc.es (T.T. Packard).

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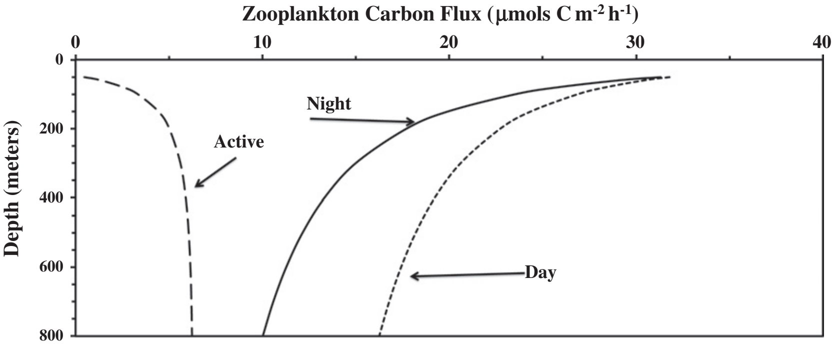

Fig. 1. Conceptual model of the vertical carbon flux associate with zooplankton respiration. The active F_c, rooted in diel vertical migration, is the difference (absolute value) between the day and night F_c profiles.

2012). The first of these fluxes, the passive or gravitational carbon flux of POC, was the focus of the large international research program, JGOFS (Joint Global Ocean Flux Study) in which sediment traps and the (^{234}Th/^{238}U) method were used to assess the rain of carbon falling down through the ocean water column. The second, the active flux (Fig. 1), was recognized long ago by Riley (1951) and Vinogradov (1955) and then popularized in the 1960s as Ketchum's yoyo (Ketchum, 1957) by Munk (1966). More recently it was defined by Longhurst and Harrison (1988) and Dam et al. (1995), and investigated extensively in the Canary Island region (Hernández-León et al., 2001, 2010; Putzeys and Hernández-León, 2005). Active flux, itself, has four sub-components. The gut flux (Angel, 1984) refers to the chlorophyll-containing organic matter derived from euphotic zone feeding that is transported to depth and released as faecal pellets. Then there is a second sub-component that fuels CO_2 production in the mesopelagic waters (Longhurst et al., 1990) produced from the digestion and metabolism of euphotic-zone derived organic matter. Then another in which the dissolved organic carbon (DOC), derived from the same diel migration and feeding processes, is excreted at depth (Steinberg et al., 2008). The final sub-component is the reverse active flux in which mesopelagic zooplankton migrate into the epipelagic each night, eat, defecate, and excrete ammonium into these surface waters (Dagg et al., 1989).

After the active flux, the DOC flux (No. 3), occurs where Intermediate and Deep Waters are formed at convergence zones. At these locations upper ocean waters are transferred to depth as dense waters slide downward along isopycnal surfaces. This happens during storms and during winter in places like the confluence of the Oyashio and Kuroshio Currents, Irminger Sea, Labrador Sea, Weddell Sea, Golf de Lyons, etc. Arístegui et al. (2002) have estimated this DOC flux to support 10% of mesopelagic ocean respiration.

Finally the lateral, the fourth carbon flux, has not been well quantified. Walsh (1991) predicted from sediment trap measurements that off-shelf DOC transport significantly impacts deep ocean metabolism. Christensen and Packard (1989) attributed DOC entrainment during deep-water formation in the Gulf of Lions to cause high microbial metabolism in the northwestern Mediterranean. Alonso-González et al. (2009, 2010), argue that lateral DOC transport from the upwelling zone off NW Africa supported 28–59% of the mesopelagic respiration as far west as 20°W in the subtropical NE Atlantic Ocean.

Regardless of the type of carbon flux, respiration, the transformation of POC into CO_2, was the principal biological process involved in its attenuation. Here this concept is employed in demonstrating how the zooplankton role in attenuating vertical carbon flux can be calculated from an enzymatic proxy for zooplankton respiration, the activity (sensu Michaelis-Menten, Nelson and Cox, 2008) of the respiratory electron transport system (ETS) (Packard et al., 1971).

The objective here was to demonstrate how zooplankton ETS activity could be used to calculate profiles of zooplankton respiration and the zooplankton contribution to the vertical POC flux in the ocean water column. The approach was to apply the conceptual model of Packard and Christensen (2004) that was used to calculate the microplankton (microbe size $\geqslant 0.7$ μm) contribution to the vertical POC flux in the Gulf of Maine. The rationale is that aside from advection and diffusion, biotic processes control the spatial and temporal distribution of the particulate and dissolved non-conservative elements in the deep-dark ocean. This rationale includes the rain of POC that falls through the ocean water column from the surface, where it is produced, to the seafloor where it supports benthic communities and finally, when too refractory to support metabolism, gets buried.

Here, previously published zooplankton ETS activities in water column profiles made in the NE Atlantic south of the Canary Islands (Hernández-León et al., 2001) were used to calculate zooplankton respiration depth profiles. Then these were integrated from the respiratory maximum to a deep-water minimum to calculate zooplankton carbon flux profiles for this region. In addition, from these fluxes, the biological pump transfer efficiency between 150 and 500 m in the ocean water column (Buesseler et al., 2007) and a new index, the nutrient retention efficiency (NRE) for the upper 150 m of the water column, were calculated. Finally, a heuristic calculation of the active transport from the epipelagic to the mesopelagic zone is made.

2. Methods

2.1. ETS activity and respiration

The zooplankton ETS samples from 16 stations of the R/V Hespérides MAST 9308 expedition to southern waters of the Canary Island Archipelago were taken obliquely using a Longhurst–Hardy Plankton Recorder (LHPR, Longhurst and Williams, 1976) with a mesh size of 200 μm Hernández-León et al., 2001. The stations were situated in the oceanic region outside the influence of filaments from the NW African upwelling system (Meunier et al., 2012). The samples were classified as day (8:00–18:00 h), night (20:00–6:00 h), dawn (6:01–7:59 h), or twilight (18:01–19:59 h) according to the hour at which they were taken (Table 1). Samples were taken while the LHPR was returning to the surface to minimize the animals' stress during capture. Only one, 2 h LHPR cast was made per station. Inspection on deck found most zooplankton healthy at the time they were frozen in liquid nitrogen for later analysis. One ETS activity measurement was made from each of four different size fractions. Here, the sum of these four different

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