Progress in Oceanography 149 (2016) 121–133

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Modeling downward particulate organic nitrogen flux from zooplankton ammonium regeneration in the northern Benguela

I. Fernández-Urruzola [a,*], N. Osma [a], M. Gómez [a], F. Pollehne [b], L. Postel [c], T.T. Packard [a]

[a] Marine Ecophysiology Group (EOMAR), Universidad de Las Palmas de Gran Canaria, 35017, Spain
[b] Bentho-pelagic Coupling Group, Baltic Sea Research Institute, D-18119 Rostock, Warnemünde, Germany
[c] Zooplankton Ecology Group, Baltic Sea Research Institute, D-18119 Rostock, Warnemünde, Germany

ARTICLE INFO

Article history:
Received 26 October 2015
Received in revised form 1 September 2016
Accepted 20 October 2016
Available online 2 November 2016

Keywords:
Zooplankton
Dissolved inorganic nitrogen (DIN)
Glutamate dehydrogenase (GDH)
Ammonium excretion
Benguela upwelling system

ABSTRACT

The vertical fluxes of particulate organic matter play a crucial role in the distribution of nutrients throughout the oceans. Although they have been the focus of intensive research, little effort has been made to explore alternative approaches that quantify the particle export at a high spatial resolution. In this study, we assess the minimum nitrogen flux (F_N) required to sustain the heterotrophic metabolism in the water column from ocean depth profiles of zooplankton NH_4^+ excretion ($R_{NH_4^+}$). The reduction of $R_{NH_4^+}$ as a function of depth was described by a power law fit, $R_{NH_4^+} = (R_{NH_4^+})_m\ (z/z_m)^b$, whereby the *b*-value determines the net particulate nitrogen loss with increasing depth. Integrating these excretory functions from the base of the euphotic zone to the ocean bottom, we calculated F_N at two stations located over the Namibian outer shelf. Estimates of F_N (ranging between 0.52 and 1.14 mmol N m^{-2} d^{-1}) were compared with the sinking fluxes of particles collected in sediment traps (0.15–1.01 mmol N m^{-2} d^{-1}) 50 m over the seafloor. We found a reasonable agreement between the two approaches when fast-sinking particles dominated the ecosystem, but the F_N was somewhat at odds with the measured gravitational flux during a low-sedimentation regime. Applying our conceptual model to the mesozooplankton $R_{NH_4^+}$ we further constructed a section of F_N along a cross-shelf transect at 20° S, and estimated the efficiency of the epipelagic ecosystem to retain nutrients. Finally, we address the impact of the active flux driven by the migrant mesozooplankton to the total nitrogen export. Depending on the sedimentation regime, the downward active flux (0.86 mmol N m^{-2} d^{-1} at 150 m) accounted for between 50 and 307% of the gravitational flux.

1. Introduction

Particulate organic matter (POM) export down to the deep ocean is a critical mechanism in understanding the carbon balance across the air-sea interface. Carbon and inorganic nutrient salts are converted in the epipelagic ocean into organic matter mainly by phytoplankton, and rapidly regenerated through heterotrophic processes. This fuels the biological production by direct feedback loops within the relatively thin sunlit layer. In productive ecosystems such as the Benguela upwelling system, the phytoplankton growth rates often exceed the grazing pressure and as a result, either advection or gravitational settling processes gain importance in the biogenic material loss. Indeed, some authors have demonstrated an export flux out of the euphotic zone as high as 25% in coastal upwellings (Martin et al., 1987; Buesseler, 1998; Osma et al., 2014). Most of these sinking particles undergo a suite of biologically-mediated chemical transformations while falling down through the ocean water column, which cause the speciation of carbon and associated elements (i.e., nitrogen and phosphorus) into their inorganic forms. Factors such as particle composition, community structure and ambient temperature will determine the decline of this downward POM flux with increasing depth. In addition to the rain of POM, the mixing of dissolved organic matter along isopycnals and the active downward transport by migrating zooplankton act as a complex network collectively known as the "biological pump" (Volk and Hoffert, 1985). All these processes together constrain the upper limit of the dark ocean metabolism (Arístegui et al., 2009) as well as the capacity to sequester elements in the ocean interior (Packard et al., 1988; Ridgwell et al., 2011).

Surface primary productivity, vertical flux and heterotrophic consumption below the photic layer have been traditionally related by means of direct measurements of trap-collected particles, despite the recognition that some biases affect the sediment

* Corresponding author.
E-mail address: ifernandez@becarios.ulpgc.es (I. Fernández-Urruzola).

http://dx.doi.org/10.1016/j.pocean.2016.10.010
0079-6611/

traps efficiency (Gardner, 2000). These methodological uncertainties may partially explain the apparent carbon budget imbalances (Burd et al., 2010), and foster efforts to explore complementary approaches to estimate global export fluxes. Oceanic depth profiles of both plankton respiration, as principal component involved in POM attenuation, and thorium-234 radionuclide have also been fruitfully applied to trace particle utilization through the ocean water columns (e.g., Packard et al., 1988; Buesseler, 1991; Steinberg et al., 2008; Maiti et al., 2010). In this line, Packard and Christensen (2004) employed enzyme activity measurements of electron transport system (ETS) to model vertical carbon flux by integrating plankton respiration from the bottom of the mixed layer to the seabed. Both processes are closely related, mathematically described by a power function, and therefore each can be calculated from the other. This approach based on enzymology was subsequently used to assess the carbon transference by zooplankton down to 3000 m in waters from Canary islands (Packard and Gómez, 2013), and compared with sediment-trap measurements in the mesopelagic zone from the northern Benguela (Osma et al., 2014). It was precisely on a plankton respiration basis that Packard et al. (2015) modeled a synoptic section of carbon flux in the Peru upwelling system, and demonstrated the utility of this approach to quantify the ability of an ocean layer to retain its nutrients. Here we extrapolate this concept into nitrogen metabolism in a first attempt to perform similar nitrogen flux calculations. In order to achieve this goal, we assayed glutamate dehydrogenase (GDH), a widespread enzyme in nature whose role in the oxidative deamination of glutamate argues for its control over a great proportion of ammonium (NH_4^+) production in marine ecosystems. The rationale behind this conceptual model is the assumption that the resident deep-sea zooplankton and smaller microheterotrophs consume sinking particulate organic nitrogen (PON), among other non-conservative elements, to satisfy their metabolic requirements. As a result, these organisms release NH_4^+ as part of the dissolved inorganic nitrogen (DIN) pool, as well as other organic nitrogenous compounds either in the dissolved (urea and amino acids) or particulate (fecal pellets) forms. Although these organic end-products may represent a significant budget in the nitrogen export (Steinberg et al., 2002), we focus on NH_4^+ excretion processes because they account for 60–100% of the total nitrogen excreted by marine zooplankton (Regnault, 1987). At the intracellular biochemical level, NAD^+-specific GDH activity is thought to be responsible for most of the NH_4^+ synthesis in heterotrophs and consequently, it should provide a good index of NH_4^+ regeneration in seawater. Furthermore, such an enzymatic technique would allow a high data acquisition rate and enough sensitivity to detect excretion processes even in the deep ocean, while obviating methodological artifacts associated with direct metabolic analyses involving bottle incubations (Bidigare, 1983).

In the present study we calculate downward particulate nitrogen flux from the integration of nano/micro- and mesozooplankton NH_4^+ excretion depth profiles, and compare our modeled flux with *in situ* measurements of nitrogen collected by two sediment traps moored in waters off Namibia. Previously, we investigated in that same region the carbon losses from the water column respiration and demonstrated the influence of particle composition on the carbon attenuation efficiency (Osma et al., 2014). Changes in the flux attenuation, i.e., in the curvature of either respiration or NH_4^+ excretion depth profiles, will ultimately affect the capacity of epipelagic ecosystems to retain their nutrients (Packard et al., 2015) and thereby, to maintain a high regenerated production. Further, we address the relevance of zooplankton diel migrations at 20° S as important drivers of active nitrogen flux relative to the vertical export of PON. The research was conducted in the northern Benguela current since these waters represent an interesting scenario for the vertical nutrient exchange, which should result in a balance between the downward transference of PON and the upwelling flux of DIN (Longhurst and Harrison, 1989). Nevertheless, the nitrogen transfer down to the seafloor will vary in the short-term according to the fluctuations in the upwelling pulses. In this context, we show how the different productivity regimes impact the vertical recycling of PON off the Namibian coast.

2. Material and methods

2.1. Zooplankton sampling

Sampling was carried out in waters off Terrace Bay (Namibia) onboard RV Maria S. Merian during the austral winter from August 24th to September 17th, 2011. Nano/microzooplankton (0.7–100 μm) and large zooplankton (>100 μm) GDH profiles were performed at those stations in which sediment-traps were placed. Accordingly, two traps were successively moored for 13 days at an inshore station (NAM006), and 10 days over the shelf-break at an offshore station (NAM011) (see Fig. 1). Both locations were, in any case, situated under the influence of mesoscale structures such as upwelling pulses and filaments emerging from the southern perennial cell. Water column samples for GDH activities were first taken as the shallower sediment-trap was recovered (NAM006r) and then, during the outer trap deployment (NAM011d) and subsequent recovery (NAM011r). In addition, mesozooplankton was collected in four consecutive surveys throughout a cross-shelf transect at 20°S, which covered 12 stations along 230 km from the shore (broadly described by Fernández-Urruzola et al., 2014). NAM011 was sampled for mesozooplankton during both day (07:06–18:54 h) and night (18:55–07:05 h) in order to quantify the magnitude of diel vertical migrations.

Hydrographic data (salinity, temperature and dissolved oxygen concentration) were recorded by casting a CTD SBE 911+ equipped with a WETlab FLRT-1754 fluorometer. Chlorophyll-a concentrations were likewise determined in water samples taken by 10-L Niskin bottles mounted on a rosette. Seawater from eight (NAM006r) to nine (NAM011d/r) discrete depths were collected for nano/microzooplankton (below 100 μm) GDH activities. After sieving through a 100 μm mesh size, 4–6 L of seawater (depending on organism densities at each depth) were filtered at room temperature by GF/F glass fiber filters. Phytoplankton would not interfere in our measurements as their NAD^+-specific GDH activity is negligible (King, 1984; Park et al., 1986). Furthermore, large zooplankton were sampled for vertical distribution using a Multinet (Hydrobios GmbH, Kiel, Germany), fitted with 100 and 500 μm meshed nets which ensured a quantitative zooplankton sampling between 0.1–0.5 mm and 0.5–10 mm sizes, respectively. Two flowmeters installed on the net-frame quantified the volume of water filtered during each haul. In this case, five (NAM006r) to six (NAM011d/r) depth layers were considered to calculate mesozooplankton GDH vertical profiles down to the seafloor, whereas three depth intervals were used to assess mesozooplankton NH_4^+ regeneration in the upper 200 m along the transect. Once on deck, the samples were immediately fractionated for the 100–200, 200–500, 500–1000 and >1000 μm size classes, frozen in liquid nitrogen and stored at −80 °C awaiting enzymatic analyses in the land based laboratory.

2.2. NH_4^+ excretion rates ($R_{NH_4^+}$) in terms of GDH activity

The enzyme GDH was assayed as a proxy for NH_4^+ excretion in zooplankton. In heterotrophs, this enzyme deaminates glutamate to produce NADH, NH_4^+ and α-ketoglutarate, thus feeding the tricarboxylic acid cycle. Samples were sonicated in Tris buffer