



Relative inputs of upwelled and atmospheric nitrogen to the eastern tropical North Atlantic food web: Spatial distribution of $\delta^{15}\text{N}$ in mesozooplankton and relation to dissolved nutrient dynamics

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ABSTRACT

The Eastern Tropical North Atlantic (ETNA) is characterised by a strong east to west gradient in the vertical upward flux of dissolved inorganic nitrogen to the photic zone. We measured the stable nitrogen isotope ($\delta^{15}\text{N}$) signatures of various zooplankton taxa covering twelve stations in the ETNA (04°–14°N, 016–030°W) in fall 2009, and observed significant differences in $\delta^{15}\text{N}$ values among stations. These spatial differences in $\delta^{15}\text{N}$ within zooplankton taxa exceeded those between trophic levels and revealed an increasing atmospheric input of nitrogen by N_2 fixation and Aeolian dust in the open ocean as opposed to remineralised NO_3^- close to the NW African upwelling. In order to investigate the spatial distribution of upwelling-fuelled versus atmospheric-derived nitrogen more closely, we examined the $\delta^{15}\text{N}$ signatures in size-fractionated zooplankton as well as in three widely distributed epipelagic copepod species on a second cruise in fall 2010 in the ETNA (02–17°35'N, 015–028°W). Copepods were sampled for $\delta^{15}\text{N}$ and RNA/DNA as a proxy for nutritional condition on 25 stations. At the same stations, vertical profiles of chlorophyll-*a* and dissolved nutrients were obtained. High standing stocks of chl-*a* were associated with shallow mixed layer depth and thickening of the nutricline. As the nitracline was generally deeper and less thick than the phosphocline, it appears that non-diazotroph primary production was limited by N rather than P throughout the study area, which is in line with enrichment experiments during these cruises. Estimated by the $\delta^{15}\text{N}$ in zooplankton, atmospheric sources of new N contributed less than 20% close to the African coast and in the Guinea Dome area and up to 60% at the offshore stations, depending on the depth of the nitracline. $\delta^{15}\text{N}$ of the three different copepod species investigated strongly correlated with each other, in spite of their distinct feeding ecology, which resulted in different spatial patterns of nutritional condition as indicated by RNA/DNA.

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1. Introduction

In the Eastern Tropical North Atlantic (ETNA), a marked east to west gradient exists in the dissolved inorganic nutrient load between surface waters affected by coastal upwelling and large oligotrophic areas in the highly stratified central basin. Remote sensing of ocean colour indicates high standing stocks of phytoplankton biomass within and close to the Mauritanian Upwelling off NW Africa, contrasting vast areas of lower productivity in the tropical North Atlantic (Longhurst et al., 1995; Hoepffner et al., 1999). Within the coastal upwelling zones, the export of organic nitrogen (N) from the photic zone exceeds the vertical supply of DIN (Agusti et al., 2001). At the same time, N-loss processes seem to occur at the shelf sediment (Jaeschke et al. 2010) that would further decrease the nitrogen to phosphorus (P) ratio in upwelled

waters, although average subsurface O_2 concentrations in the ETNA are generally too high to allow large-scale N loss processes. Low N/P values in upwelled waters result in overall N-limitation of non-diazotroph primary production at the surface. In turn, this supposedly leads to a competitive advantage of diazotrophic cyanobacteria that are ultimately P and Fe-colimited (Mills et al., 2004) and benefit from the DIP surplus as well as from the atmospheric iron input by Saharan dust deposition. Biogeochemical basin-scale estimates of N-fixation in the North Atlantic support this view (Hansell et al., 2004). These estimates are based on the observation of net “excess N” (N^* as a measure of deviation from the Redfield ratio) in the pool of inorganic nutrients at depth (~150–400 m) due to the remineralization of diazotroph-derived N-rich particulate organic matter (Gruber and Sarmiento, 1997). However, both the absolute rates and the relative importance of diazotrophs as opposed to non-diazotrophs to total production often remain somewhat unclear, especially in regions of strong spatial gradients in the vertical flux of nutrients to the photic zone. On a global scale, currently even the most conservative

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estimates of oceanic N losses exceed those of N input, which might partly be due to a gross underestimation of N-fixation rates (Mahaffey et al., 2005; Großkopf et al., 2012).

Nitrogen fixation by filamentous cyanobacteria of the genus *Trichodesmium* has been demonstrated to contribute significantly to the nitrogen pool of the oligotrophic tropical and subtropical Atlantic (Capone et al., 2005). While most observations emphasise its importance in the western part of the basin (Carpenter and Romans, 1991; Montoya et al., 2002; Capone et al., 2005; Goebel et al., 2010), direct measurements of cyanobacterial abundance and/or nitrogen fixation in the ETNA, and especially in the Guinea Dome area, are scarce and vary by orders of magnitude depending on the season and the methods used (Voss et al., 2004; Capone et al., 2005; Staal et al., 2007). Satellite imagery has revealed some seasonality in the formation of *Trichodesmium* blooms in the ETNA (Westberry and Siegel, 2006), with the largest areal expansion in the fall quarter (September–November). However, the authors point out that the seasonal development is less pronounced than in other ocean basins and may be changed due to single dust pulses. Still, this seasonality is consistent with point observations on Atlantic Meridional Transect (AMT) cruises in fall and spring (Tyrrell et al., 2003) and observations close to the NW African coast (16–22°N) by Margalef (1973) and Vallespinós (1985). Using a coupled biological–physical model, Hood et al. (2004) predicted high abundances of *Trichodesmium* and, consequently, high rates of N₂ fixation in the ETNA based upon ecological characteristics of this genus. Since *Trichodesmium* was the only diazotroph used in this model, Hood et al. (2004) likely underestimated N₂ fixation rates. Non-filamentous cyanobacteria and heterotrophic bacteria comprising *nifH*-genes have been found even at depth and under nitrate availability (Langlois et al., 2005), contrasting the optimal environmental conditions of *Trichodesmium* (warm, N-depleted surface waters). Moreover, the use of an improved N₂ fixation rate measurement technique (Mohr et al., 2010) recently demonstrated that especially non-filamentous cyanobacterial N₂ fixation is vastly underestimated with standard methods (Großkopf et al., 2012).

Mesozooplankton consumption in the oligotrophic open ocean is expected to rely relatively more on heterotrophic protozoan prey than on phytoplankton (Stoecker and Capuzzo, 1990; Sommer and Sommer, 2006). Since phagotrophic flagellates and ciliates directly ingest unicellular cyanobacteria, this contingent may quite efficiently enter the metazoan food web (Sommer et al., 2006). As a result of pulsed N₂ tracer incubations near Cape Verde, Wannicke et al. (2010) estimated that direct grazing accounts for approximately half of gross mesozooplanktonic N incorporation, while the rest was channelled through the microbial loop. Direct

foraging on *Trichodesmium* filaments has only been observed for few zooplankton species, especially harpacticoid copepods (O'Neil and Roman, 1994), but *Trichodesmium*-associated communities include diatoms, dinoflagellates and ciliates (Sheridan et al., 2002) that provide suitable prey items for a variety of zooplankton species. Furthermore, diatom–diazotroph associations (DDAs, e.g. *Rhizosolenia* and *Chaetoceros* associated with *Calothrix rhizosoleniae* and *Richelia intracellularis*, respectively) can provide a pathway of direct transfer of diazotroph N to consumers (Foster et al., 2009). In this context, the export efficiency of surface diazotroph-derived N also depends on the composition of the diazotroph community. The large and spiny diatom host cells of DDAs not only aggregate and sink fast, but are also readily consumed and repackaged into faecal pellets by mesozooplankton. Besides increasing sinking velocity by repackaging, mesozooplankton contribute significantly to export of matter from surface waters due to active diel vertical migration with night time feeding at the surface and daytime defecation and excretion at depth (Steinberg et al., 2002). However, a considerable fraction of zooplankton-ingested nitrogen is also directly recycled via excretion within the photic zone (e.g. Isla et al., 2004).

The pathways of nitrogen within the food web are difficult to assess. Stable nitrogen isotopes have been widely used to examine trophic interactions in aquatic systems, as well as characterising sources and sinks. Specifically, low $\delta^{15}\text{N}$ values of particulate organic matter are known to correspond to high rates of biological nitrogen fixation and/or dust input (Ryabenko et al., 2011). Montoya et al. (2002) found that the $\delta^{15}\text{N}$ values of size-fractionated mesozooplankton was decreasing from east to west in the western and central tropical North Atlantic (approximately 030° to 055°W), corresponding to increasing abundance of *Trichodesmium*. Using $\delta^{15}\text{N}$ of particulate matter and zooplankton, the contribution of fixed N₂ to the pelagic food web can be estimated (Montoya et al., 2002; Landrum et al., 2011) by attributing low $\delta^{15}\text{N}$ values entirely to phototrophic N₂ fixation. However, dust deposition is not only providing an iron source to surface waters, fuelling N₂-fixation, but also contains substantial amounts of inorganic dissolved nitrogen as NO_x and NH_x (Baker et al., 2003; Formenti et al., 2003; Baker et al. 2007) with an isotopic signature < 0 that is readily available to phytoplankton (Aberle et al., 2010).

In this study, we aimed to spatially resolve the differential impact of atmospheric and upwelled inorganic nitrogen to the food web via stable nitrogen isotopic signatures of zooplankton. An additional aim was to assess whether the choice of species influences the spatial distribution of zooplankton $\delta^{15}\text{N}$ values to differences in feeding ecology.

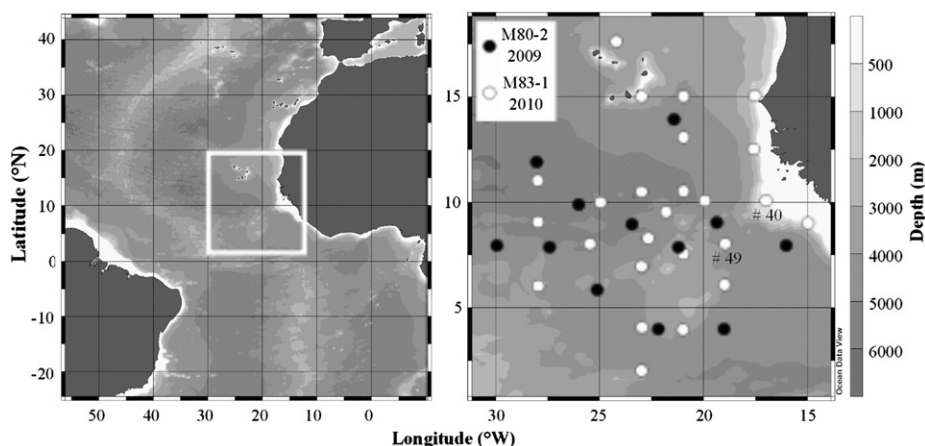


Fig. 1. Overview of sampling area (white rectangle) in the tropical eastern North Atlantic. Sampling stations are indicated by black (M80-2) and white (M83-1) circles. The two stations marked (profiles 40 and 49) are those represented in Fig. 4.

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