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Stable isotope patterns in micronekton from the Mozambique Channel

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ABSTRACT

We measured the stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic composition of tissues of micronektonic organisms (fishes, squids, crustaceans and gelatinous organisms) collected in the Mozambique Channel during two scientific cruises in 2008 and 2009. The oceanic circulation in the Mozambique Channel is dominated by mesoscale cyclonic and anticyclonic eddies which play a key role in biological processes of less-productive deep-sea ecosystems. We investigated the potential impact of mesoscale features on the $\delta^{13}C$ and $\delta^{15}N$ values of 32 taxa of micronekton. Fishes, squids, crustaceans and gelatinous organisms encompassed a wide range of isotopic niches, with large overlaps among species. Our results showed that mesoscale features did not really influence the isotopic signatures of the sampled organisms, although cyclonic eddies can occasionally impact the nitrogen signatures of micronekton. We show that $\delta^{13}C$ values were intermediate between standard offshore and nearshore signatures, suggesting that pelagic production in the Mozambique Channel could be partly supported by the transport and export of inorganic and organic particles from the Mozambican coast toward the offshore area. Trophic levels calculated from $\delta^{15}N$ values ranged from 2.6 to 4.2, showing that micronekton taxa can be tertiary consumers in the Mozambique Channel. Our findings evidenced clusters of micronektonic organisms according to their $\delta^{15}N$ or $\delta^{13}C$ isotopic signatures, but variations in stable isotope values reflect a complex set of embedded processes linked to physical mesoscale dynamics (rotational dynamics of eddies) and basic biology and ecology of micronektonic organisms (vertical habitat, migration pattern, dietary habits, body length) that are discussed with regard to the stable isotope method based on time-integrated assimilated food.

1. Introduction

The circulation in the Mozambique Channel (south-west Indian Ocean) is governed by important mesoscale activity (De Ruijter et al., 2002) where rotating eddies propagate southwards along the western edge of the channel (Schouten et al., 2003; Quartly and Srokosz, 2004). These mesoscale features contribute to ocean mixing processes and consequently impact the biological activity at different scales. Cyclonic eddies (clockwise rotating in the southern hemisphere) generate vertical pumping of nutrients in their centers (McGillicuddy Jr. et al., 1998; Bakun, 2006; Chelton et al., 2011), enhancing local primary production (Mizobata et al., 2002; Benitez-Nelson et al., 2007; Tew-Kai and Marsac, 2009). In contrast, anticyclonic eddies (counter-clockwise rotating) are usually associated with low chlorophyll levels (Bakun, 2006; Chelton et al., 2011). However, phytoplankton enrichment has also been associated with the upward movement of nutrient rich waters at the edges of either cyclonic or anticyclonic eddies (Mizobata et al., 2002; Quartly and Srokosz, 2004). In addition, coastal primary production produced on the western side of the channel can be horizontally advected by continuous contra-rotating eddy pairs, referred to as dipoles and propagating southwards (Roberts et al., 2014; Ternon et al., 2014). By influencing the horizontal and vertical distribution at the base of the food web (nutrients, phytoplankton and zooplankton), these features have been suggested to alter the distribution of intermediate trophic links such as micronekton, and thus the distribution of upper-trophic level organisms.

Biological responses to mesoscale eddies have been documented for mesozooplankton and fish larvae (Bakun, 2006; Muhling et al., 2007), for tunas and swordfish (Young et al., 2001; Seki et al., 2002; Potier et al., 2014), for turtles (Polovina et al., 2004; Lambardi et al., 2008), for seabirds (Nel et al., 2001; Weimerskirch et al., 2004; Hyrenbach et al., 2006), or for marine mammals (Bailleul et al., 2010). In spite of their importance, the impact of mesoscale features on micronektonic organisms remains

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fragmented and is still poorly quantified (see Potier et al., 2014). Recent investigations showed that eddies can shape the distribution and the aggregation patterns of micronekton through bottom-up processes (Sabarros et al., 2009; Drazen et al., 2011). Micronekton refers to small, but actively swimming, organisms (ca. from 1 to 20 cm), mainly crustaceans, fishes, and squids, that form the link between zooplankton and large fish predators in open-sea ecosystems (Brodeur and Yamamura, 2005; Potier et al., 2007). Most of the micronekton perform large diel vertical migrations during the crepuscular periods (dawn and dusk), from depths below 400 m during the day to the surface layers at night (Benoit-Bird et al., 2009).

In this study, we analyzed the ratios of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in the tissues of micronektonic organisms collected in the Mozambique Channel within the framework of the MESOBIO programme (Ternon et al., 2014). Carbon and nitrogen isotopes have often successfully been applied to investigate foraging ecology and trophic relationships in marine ecosystems (e.g., Ménard et al., 2007; Revill et al., 2009; Cherel et al., 2010; Olson et al., 2010; Fanelli et al., 2011; Stowasser et al., 2012). Stable isotope ratios of carbon and nitrogen in consumer tissues reflect those of their prey in a predictable manner, and depend on the isotopic signature at the base of the food web (Post, 2002; Fry, 2006). The $\delta^{15}N$ values mainly estimates the relative trophic position of an animal thanks to predictable enrichment of ^{15}N with increasing trophic level (Vanderklift and Ponsard, 2003). Thus, $\delta^{15}N$ has been used for quantifying and comparing trophic levels of consumers (e.g., Cherel et al., 2008). In contrast, $\delta^{13}C$ variations are used to determine the sources of primary production, inshore versus offshore, or pelagic versus benthic contribution to food intake (Rubenstein and Hobson, 2004). Different processes affect isotopic baselines of $\delta^{13}C$ and $\delta^{15}N$, including nutrient source, primary productivity, depth and ocean mixing processes (Fry, 2006). The present work aims to (1) investigate the potential impact of mesoscale features on the ratios of stable carbon and nitrogen isotopes of micronektonic organisms and (2) interpret the isotopic niches and the trophic levels of micronektonic species in the Mozambique Channel.

2. Material and methods

2.1. Sample collection

Micronekton samples were collected from two scientific cruises during December 2008 on board R.V. *Fridtjof Nansen* (2008 ASCLME survey, leg 4, called hereafter MC08A) and during November 2009 on board R.V. *ANTEA* (referred to as MC09B). A Young Gadoid Pelagic Trawl (YGPT) was used during MC09B with a cod-end lined with 5 mm knotless nylon delta mesh netting, while an Akrahamn pelagic trawl with cod-end 10 mm was used during MC08A. Trawls were conducted during the day on aggregations detected by acoustics, and during the night at the surface on sound scattering layers (0–200 m). Night trawl depth was selected according to the highest acoustic detections. Each trawl was towed for 30 min at a speed of 3 to 4 knots. A total of 16 and 18 trawls were performed during MC08A and MC09B, respectively (from which 2/3 were carried out at night). The whole catch was sorted and soft tissues of selected micronekton species were removed for further isotopic analyses: dorsal muscle for fishes, mantle for squids, abdomen for crustaceans and body wall for pelagic gastropod molluscs, siphonophorans, leptocephali larvae and salps. Body length of each individual was measured except for salps: standard length (SL) for fishes, dorsal mantle length (DML) for squids, cephalothorax length (CT) for crustaceans, and total length for the other taxa.

2.2. Stable isotope analysis

Samples were freeze-dried and ground to a fine homogeneous powder. Since lipids are depleted in ^{13}C, lipids were removed using dichloromethane on an accelerated solvent extraction system (ASE®, Dionex; Bodin et al., 2009). This method does not alter $\delta^{15}N$ signatures. The extent of lipid extraction was checked through the C/N mass ratio of the samples (Post et al., 2007). Lipid-free samples were dried at 50 °C before processing, and then 300 to 400 μg of homogenized powder were packed into 8×5 mm^2 tin containers. Isotopic ratios were determined by a continuous flow mass spectrometer coupled on line to an elemental analyzer. Replicate measurements of internal laboratory standards indicated measurement errors less than 0.15‰ and 0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Triplicate measurements performed on some samples confirmed that analytical reproducibility was very good (0.2‰ maximum variation). Isotopic ratios are expressed in the conventional δ notation as parts per thousand (‰) deviations from the international standards: atmospheric nitrogen (N_2) for $\delta^{15}N$ and VPDB Belemnite for $\delta^{13}C$.

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$.

2.3. Data analysis

Satellite altimetry allows identification of mesoscale features (Chelton et al., 2007). One mesoscale feature among five classes (anticyclone, A; cyclone, C; divergence, D; front, F; and shelf station, S) was assigned to each of the 34 trawling stations. The classification of each individual station was processed using three explanatory variables (sea level anomaly, geostrophic speed and bathymetry) and a discriminant function estimated from an extra training dataset (Lamont et al., 2014). Ocean bathymetry was extracted from ETOPO1 Global Topography (data access: http://www.ngdc.noaa.gov/mgg/global/global.html). Sea level anomaly and the corresponding geostrophic speed were extracted from AVISO products "DT-MSLA Ref" (Delayed Time, DT; Reference, "Ref") with $0.33 \times 0.33^{\circ}$ spatial resolution on a Mercator grid. The predictions from the linear discriminant analysis were estimated for each station using the values taken by the three explanatory variables at the corresponding temporal and spatial positions.

Links between isotope values ($\delta^{15}N$ and/or $\delta^{13}C$), and broad categories and mesoscale features were investigated using multivariate analysis of variance (MANOVA), Kruskal–Wallis (KW) non-parametric tests and univariate regression tree (URT). URT is a powerful statistical tool that explains the variation of a single response variable ($\delta^{15}N$ or $\delta^{13}C$) using several explanatory variables by growing a tree that partitions the data set into mutually exclusive groups (Venables and Ripley, 2002). The objective is to partition the response into homogeneous groups. All the data are represented by a single node at the top of the tree. Then the tree is built by repeatedly splitting the data. Each split is defined by a simple rule based on a single explanatory variable. Splits are chosen to maximize the homogeneity of the resulting two nodes. However, the splitting procedure grows an overlarge tree. To keep the tree reasonably small, a prune back procedure is applied. Each final group is characterized by mean values of $\delta^{15}N$ or $\delta^{13}C$.

As the content of ^{15}N in animal tissues is biomagnified along the length of a food chain (Post, 2002), trophic levels (TL) of micronekton taxa were calculated on the basis of isotopic measurements using the following equation:

$$\text{TL} = 2.0 + \frac{\delta^{15}N_i - \delta^{15}N_{\text{primary consumer}}}{3.2} \quad (2)$$