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Carbon and nitrogen stable isotope ratios of pelagic zooplankton elucidate ecohydrographic features in the oligotrophic Red Sea

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Disclosure

BK conceived and planned the study. BK and SK carried out fieldwork and analyzed zooplankton stable isotope samples. USt carried out POM SIA. USt and TH carried out additional zooplankton SIA. AA, ME, and RD identified zooplankton. RD identified phytoplankton. GB recorded ADCP data. NZ evaluated ADCP data. BK wrote the manuscript. NZ, BHJ, USt and US provided editorial advice. The authors declare that they have no conflict of interest.

Abstract

Although zooplankton occupy key roles in aquatic biogeochemical cycles, little is known about the pelagic food web and trophodynamics of zooplankton in the Red Sea. Natural abundance stable isotope analysis (SIA) of carbon ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) is one approach to elucidating pelagic food web structures and diet assimilation. Integrating the combined effects of ecological processes and hydrography, ecohydrographic features often translate into geographic patterns in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at the base of food webs. This is due, for example, to divergent ^{15}N abundances in source end-members (deep water sources: high $\delta^{15}\text{N}$, diazotrophs: low $\delta^{15}\text{N}$). Such patterns in the spatial distributions of stable isotope values were coined isoscapes. Empirical data of atmospheric, oceanographic, and biological processes, which drive the ecohydrographic gradients of the oligotrophic Red Sea, are under-explored and some rather anticipated than proven. Specifically, five processes underpin Red Sea gradients: a) monsoon-related intrusions of nutrient-rich Indian Ocean water; b) basin scale thermohaline circulation; c) mesoscale eddy activity that causes up-welling of deep water nutrients into the upper layer; d) the biological fixation of atmospheric nitrogen (N_2) by diazotrophs; and e) the deposition of aerosol-derived N. This study assessed relationships between environmental samples (nutrients, chlorophyll *a*), oceanographic data (temperature, salinity, current velocity [ADCP]), particulate organic matter (POM), and net-phytoplankton, with the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of zooplankton collected in spring 2012 from 16°28' to 26°57'N along the central axis of the Red Sea. The $\delta^{15}\text{N}$ of bulk POM and most zooplankton taxa increased from North (Duba) to South (Farasan). The potential contribution of deep water nutrient-fueled phytoplankton, POM, and diazotrophs varied among sites. Estimates suggested higher diazotroph contributions in the North, a greater contribution of POM in the South, and of small phytoplankton in the central Red Sea. Consistent variation across taxonomic and trophic groups at latitudinal scale, corresponding with patterns of nutrient stoichiometry and phytoplankton composition, indicates that the zooplankton ecology in the Red Sea is largely influenced by hydrographic features. It suggests that the primary ecohydrography of the Red Sea is driven not only by the thermohaline circulation, but also by mesoscale activities that transports nutrients to the upper

water layers and interact with the general circulation pattern. Ecohydrographic features of the Red Sea, therefore, aid in explaining the observed configurations of isoscapes at the macroecological scale.

Keywords

Food webs, macroecology, mesoscale eddies, Red Sea, stable isotope analysis, *Trichodesmium*, upwelling, zooplankton

1. Introduction

Plankton organisms in aquatic ecosystems play complex and fundamental roles in mediating the flux of macronutrients, such as carbon (C) and nitrogen (N), from primary producers toward consumers at higher trophic levels (Azam et al., 1983; Fenchel, 1988; Legendre and Rivkin, 2002; Stibor et al., 2004; Turner, 2004). Our understanding of the flow of energy from producers through zooplankton to edible fish is, however, limited (Azam, 1998; Falkowski et al., 1998; Turner, 2004). Parameterizations are often based on crude estimates of production and assumed subsequent trophic-dynamic relationships (Ryther, 1969; Fuchs and Franks, 2010). A detailed understanding of the pelagic ecosystem is key to effectively model the effects of climate change and anthropogenic stressors (Marine Zooplankton Colloquium 2, 2001; Buitenhuis et al., 2006).

Ecological stoichiometry provides an integrative conceptual explanation, demonstrating how the availability of macronutrients controls the composition of phytoplankton available to higher trophic levels (Elser et al., 2000; Sterner and Elser, 2002). Low nutrient concentrations generally preclude larger phytoplankton from proliferation in oligotrophic waters, as evident in the Red Sea where small pico- and nanophytoplankton account for up to 90% of total biomass (Raven, 1998; Li et al., 1998; Lindell and Post, 1995; Sommer, 2000; Dao, 2013). Ambient hydrodynamics (e.g. vertical mixing vs. stratification) and chemical properties (nutrient stoichiometry) typically determine the way nutrients are used by phytoplankton (allochthonous vs. autochthonous), the type of phytoplankton production (new vs. regenerated), and the size of organisms (large

cells [diatoms] vs. small cells [cyanobacteria, bacteria and microflagellates]). Ultimately, the configuration of food webs (herbivorous vs. microbial) is determined through these bottom-up processes (Legendre and Rassoulzadegan, 1995; Sommer, 2000; Sommer et al., 2002a; Sterner and Elser, 2002). Conversely, zooplankton exert top-down controls on primary producers and control the configuration of phytoplankton communities (Sommer and Stibor, 2002; Stibor et al., 2004; Ye et al., 2013). Sommer (2002) gauged the relative strengths of bottom-up versus top-down control mechanisms in a series of batch-experiments. Results indicated that microphytoplankton in the oligotrophic Gulf of Aqaba are mainly controlled by bottom-up and comparatively weaker top-down controls (e.g. grazing). Constraining the abiotic determinants and the hydrography of the Red Sea would improve the understanding of the pelagic food web of the Red Sea.

Global inputs and biogeochemical pathways of N in marine ecosystems are complex. Phytoplankton typically optimize uptake of a full spectrum of available nutrients (Legendre and Rassoulzadegan, 1995). With mesozooplankton, numerous interconnected food chains and respective pathways of N within the multivorous food webs (*sensu* Legendre and Rassoulzadegan, 1995) lead from primary producers towards higher trophic levels. The concept of the multivorous food web assumes that the strictly herbivorous and the microbial food chains coexist by means of a continuous trophodynamic transition (Legendre and Rassoulzadegan, 1995; Azam et al., 1998). The transition between markedly herbivorous and microbial zooplankton communities over time and space were acknowledged in the North Atlantic and the adjacent North Sea (de Laender et al., 2010; Kürten et al., 2013a). Size-selective feeding by zooplankton and subsequent cascading top-down control was identified among the important, strongly intertwined mechanisms that alter plankton communities and component biomass (Polis et al. 2000; Sommer, 2008; Zöllner et al., 2009; Fuchs and Franks, 2010; Trebilco et al., 2013). Although bacteria are the most numerous organisms in marine ecosystems and through them flow large fractions of primary production (Azam et al., 1983; Fenchel, 1984; Fenchel, 1988), most picoplankton taxa including *Synechococcus* and *Prochlorococcus* are too small to be selectively grazed by mesozooplankton. Instead, members of the microbial loop are usually preyed on by microphagous and detritivorous zooplankton as well as heterotrophic nanoflagellates, wherever bacteria colonize aggregates of

senescent plankton, detritus, and dissolved and particulate organic matter (Christiaki et al., 2001; Turner, 2004; Casanova et al., 2012; Kürten, 2010; Kürten et al., 2013a). By linking grazer dynamics and algal nutritional status, zooplankton, therefore, exert a significant impact on global biogeochemical pathways (Verity and Smetacek, 1996; Falkowski et al., 1998; Buitenhuis et al., 2006).

The Red Sea generally features little-explored nutrient gradients at several scales – none of them well explored and some rather assumed than proven. Theoretically, the Red Sea ecoregion offers a unique basin-wide study system of biogeography and biogeochemical processes at macroecological scale. Plankton biomass and biodiversity are closely governed by hydrography and wind systems (Sverdrup et al., 1942; Halim, 1984; Brown and Maurer 1989; Barton et al., 2013). The Red Sea, lying enclosed between the African continent and the Arabian Peninsula, has only one major hydrographic connection to the Indian Ocean through the narrow strait of Bab-al-Mandab toward the Gulf of Aden in the South. Passing the Tropic of Cancer, the Red Sea is surrounded by hot arid deserts, receives negligible precipitation and terrestrial runoff, and is subject to high evaporation and high salinity (Edwards, 1987; Sofianos and Johns, 2007; Bower and Farrar, 2015). The significant heat flux results in strong vertical stratification throughout most of the sea, contributing to its overall oligotrophy. Although anthropogenic point sources of nutrients alter the ecology of coral reef biota and the plankton biodiversity on the shelf of the Red Sea (Kürten et al., 2014b; Kürten et al., 2014a), nutrients become diluted and depleted to background concentrations within a few kilometers toward the open Red Sea (Peña-García et al., 2014). Hence, the mid-basin pelagic water body largely reflects the natural macronutrient dynamics attributable to the hydrography of the Red Sea, rather than being influenced by an array of complex land-based sources.

Thus, considering negligible land-based sources, we assume that spatial and seasonal variation in the availability of N in the open Red Sea can be attributed primarily to oceanographic, atmospheric and biological processes. Specific processes include the monsoon-related intrusion of nutrient and plankton-rich Indian Ocean water (Sofianos and Johns, 2007; Raitzos et al. 2015), the biological fixation of atmospheric N₂ by

diazotrophic Cyanobacteria (e.g. *Trichodesmium erythraeum*), the deposition of aerosols (Böttger-Schnack, 1995; Chen et al., 2007; Aberle et al., 2010; Wankel et al., 2010), and diazotroph-eukaryote symbiosis (Kimor et al., 1992; Kürten et al., 2014b). N₂ fixation and aerosol deposition may play significant roles in the N budget of the Red Sea considering the large net export of N toward the Arabian Sea (Aberle et al., 2010; Bange et al., 2000; Wankel et al., 2010). Supposition of vertical mixing and up-welling of deep water nutrients as a result of mesoscale eddies by Raitso et al. (2013), and their potential spatial association with bathymetric depressions (Quadfasel and Baudner, 1993), were only recently represented in modelling studies (Yao et al. 2014a, b), and *in situ* studies (Zarokanellos et al., 2014). Bower and Farrar (2015) advocated that the general horizontal circulation in the Red Sea is subject to complex flow fields dominated by persistent quasi-stationary eddies with associated transport an order larger than the general overturning basin-wide circulation and complex air-sea interaction. Evidence, however, for the oceanographic control on plankton communities of the Red Sea is scarce.

Stable isotope analysis (SIA) of ¹³C:¹²C ($\delta^{13}\text{C}$) and ¹⁵N:¹⁴N ($\delta^{15}\text{N}$) is one tool to describe food webs and macronutrient fluxes through pelagic and benthic animal communities (e.g. Hobson and Welch, 1992; Hobson, 1999; Kaehler et al., 2000; Polunin et al., 2001; Kürten et al., 2013a, b). Low $\delta^{15}\text{N}$ values have been attributed to primary producers including the cyanobacteria *Trichodesmium* spp. sourcing N from either N₂ fixation (Minagawa and Wada, 1984; Peterson and Fry, 1987; McClelland et al., 2003; LaRoche and Breitbarth, 2005; Lesser et al., 2007; Alamaru et al., 2009), or atmospheric deposition (Aberle et al., 2010; Wankel et al., 2010), whereas higher $\delta^{15}\text{N}$ values of ~5‰ are typically measured for remineralized N sources such as nitrate from the deep ocean upwelling (Brandes et al., 1998; Sigman et al., 2000; Ryabenko et al., 2012). Spatial patterns of $\delta^{15}\text{N}$ in zooplankton support inferences about the relative importance of N end-members from their $\delta^{15}\text{N}$ signatures, e.g. separating upwelled vs. diazotroph-fixed N at the macroecological scale (Fry and Quiñones, 1994; Koppelman et al., 2009; Wannicke et al., 2010; Hauss et al. 2013; McMahon et al., 2013a, b; Sandel et al. 2015). When combined, C and N SIA offers an opportune approach to studying ecosystem processes and ecological relationships, as trophodynamic information is translated into scalable, descriptive, and confined

units of food webs (*sensu* Cousins, 1987). The $\delta^{13}\text{C}$ values mainly offer clues about C sources utilized by primary producers and adjacent trophic levels, whereas $\delta^{15}\text{N}$ conveys both N source information and insight into the relative trophic position (RTP) of consumers due to the larger Δ along food chains (Vander Zanden et al., 1997; Post, 2002).

By integrating the effects of geography, hydrographic regime, biogeochemistry, biological responses, and ecosystem processes, an ecohydrography framework emerges (Kürten et al., 2014a). Advances in SIA and amalgamation of available isotopic data sets revealed isotopic geographic patterns, referred to as isoscapes, that are largely reflecting the underlying long-term stability in ecohydrographic conditions (Jennings and Warr, 2003; Bowen, 2010; Hauss et al., 2013; McMahon et al., 2013a; Vokhshoori and McCarthy, 2014). Since spatial variations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the biota at the base of food webs designate characteristic ecohydrographic features, for example, in the North Atlantic (McMahon et al., 2013a), it is assumed that major sources of N largely relate to divergent $\delta^{15}\text{N}$ signatures of the N sources in the Red Sea. As knowledge about zooplankton of the lower pelagic food web in the Red Sea is limited, and studies at a comparable macroecological scales are scarce (e.g. García-Comas et al., 2014; Sandel et al., 2015), we discuss three aspects pertaining to the Red Sea: i) oceanographic conditions; ii) stable isotope data of zooplankton; and iii) ecohydrographic features.

The oceanographic and environmental conditions are interpreted from thermohaline sections and Acoustic Doppler Current Profiler (ADCP) data disclosing water current direction and velocity, and oceanographic features. We hypothesized that the general oceanographic and biogeochemical parameters, such as salinity, temperature, nutrients, and phytoplankton biomass (proxy chlorophyll fluorescence), gradually change along the latitudinal gradient in agreement with patterns described in seminal *in situ* and remote sensing studies (Sofianos and Johns, 2007; Acker et al., 2008; Raitso et al., 2013). Next, we present an overview of site, taxon and trophic guild differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of POM and zooplankton. Finally, following the latitudinal pattern of primary productivity (Raitso et al., 2013) and potential influence of aerosols and

diazotrophs in the northern Red Sea (Aberle et al., 2010; Wankel et al., 2010), we supposed that the importance of atmospheric and diazotroph N end-members as indicated by low $\delta^{15}\text{N}$ gradually decreases towards the South, where the inflow of Indian Ocean water contributes N sources with higher $\delta^{15}\text{N}$ (Raitsos et al., 2015). We conclude that the observed ecohydrographic features underlying the Red Sea isoscape modify the trophodynamics of zooplankton.

2. Material and methods

2.1. Study area and cruise timing

The general thermohaline circulation pattern of the Red Sea can be described by an inflow of Gulf of Aden water through the Bab-al-Mandab strait in the South, a northward advection with corresponding increases in salinity due to evaporation and decreasing temperature, convection in the North creating down-welling, and backflow as bottom water (Patzert, 1974; Edwards, 1987; Quadfasel and Baudner, 1993; Eshel and Naik, 1997; Zhai and Bower, 2013). Moreover, surface currents converge with north-northwest monsoon winds in the southern Red Sea from October to May, whereas north of 18° – 19°N winds and currents are directed southeasterly throughout the year (Patzert, 1974; Halim, 1984). Remote sensing and modelling efforts indicated deep convection during the winter and the presence of a recurrent cyclonic gyre in the North. These mechanisms may transport small amounts of nutrients from coastal (reef-borne) sources and upwelling (Acker et al., 2008; Yao et al., 2014b). The Gulf of Aden Water, however, is the primary source of nutrients for the whole Red Sea.

In situ observations and samples were collected from 8-20 April 2012 aboard *RV Pelagia* (cruise 64PE351) following the axial trough of the Red Sea for approximately 1300 km from a site in the southern Red Sea, west of the Farasan Archipelago ($16^{\circ}28'\text{N}$, $40^{\circ}54'\text{E}$), toward the oligotrophic northern Red Sea, west off Duba ($26^{\circ}57'\text{N}$ $35^{\circ}05'\text{E}$). The seven sampling sites (**Fig. 1**) were spaced to capture the latitudinal gradient of primary production in spring (Acker et al., 2008; Raitsos et al., 2013). Some sampling sites matched the positions of geologically recognized deeps. An additional short, east-west transect toward the shallow reefs of

the Farasan Archipelago was included. Following the description of seasonal trends of phytoplankton biomass in the Red Sea by Raitzos et al. (2013), our sampling took place approximately 5-8 weeks after the winter bloom in the South (Farasan) and during the early-spring bloom in the North.

2.2 Collection of Acoustic Doppler Current Profiler (ADCP) data

The *RV Pelagia* was equipped with a hull-mounted 75 kHz Acoustic Doppler Current Profiler (ADCP; Teledyne RD Instruments). The ADCP collected profiles of current velocity during the cruise and provided a dynamic representation of the whole Red Sea. The ADCP data were continuously recorded during the ship transits between stations with single-ping measurements taken over the bottom. For consistency, all ADCP Profiles were interpolated to standard depth intervals (bins) of 10 m with the first bin at 18 m. All velocity profiles were averaged over five minute intervals. The velocities were calculated using the ship's onboard gyro compass and the onboard GPS.

2.2. Collection of seawater and particulate organic matter

A SBE 911 CTD/SBE 32 water sampler, equipped with a SBE 43 dissolved oxygen sensor (Sea-Bird Electronics, USA) and a Chelsea Aquatracka MKIII fluorometer (Chelsea Technologies Group, UK), were used to obtain vertical hydrographic profiles and to collect water samples from discrete depths. At solar noon, seawater was collected from 20-25 m (surface mixed layer), deep chlorophyll maximum (DCM), 120 m (below the DCM), oxygen minimum zone (OMZ; 300-350 m), 600 m, 900 m, and approximately 10 m above the bottom (ranging from 850-2532 m).

Prior to filtration, seawater samples were screened through 50 μm mesh to exclude larger organisms from suspended particulate organic matter (POM) collections, assuming that up to 98% of POM in the northern Red Sea is < 50 μm (Cornils et al., 2007). Six replicates of POM were filtered onto pre-combusted (4 h, 450 °C), pre-weighed, 25 mm GF/F (Whatman, UK) using a light vacuum. Known volumes of water (5-14 L) were added to the filtration units until clogging of the filters occurred. Filters were then oven-dried at 50 °C and

stored in desiccators. Likewise, POM was collected in triplicates on pre-combusted (4 h, 450 °C) 47 mm GF/F for determinations of chlorophyll *a* (hereafter chl *a*) and accessory pigment concentrations by high-performance liquid chromatography (HPLC; filtered volume: 17-40 L). Filters for pigment analysis were wrapped in aluminum foil and stored in liquid N₂ during the expedition and at -80 °C at the laboratory.

2.3. Nutrients

Seawater for total nitrogen (TN) and total phosphorous (TP) measurements were not screened and aliquots of 60 mL were filled in HDPE bottles and stored at -20 °C. Samples for the analysis of dissolved nitrate and nitrite (hereafter NO_x), phosphate, and silicate were filtered through 0.2 µm Nuclepore™ filter (Whatman). Aliquots of 20 mL were frozen in scintillation vials to -20 °C. Concentrations of TN, TP, and dissolved nutrients were determined in triplicates following Grasshoff et al. (1999), using a Skalar San Plus auto-analyzer system (Skalar Analytical B.V., NL). As growth of phytoplankton, grazing by zooplankton, and remineralization rates are very rapid in oligotrophic ecosystems, dissolved inorganic nutrients are maintained within a comparatively narrow range of low concentrations (Furnas et al., 2005). Thus, using TN and TP for assessing the nutrient inventory at large spatial scale was preferred for the open Red Sea (Vollenweider and Kerekes, 1982; Downing, 1997).

2.4. Collection of phytoplankton

Phytoplankton samples for light-microscopic enumeration were collected during the daytime using an Apstein net (Hydro-Bios; cowl opening diameter = 15 cm, 20 µm mesh size, non-filtering cod end). The net was towed vertically from 120 m depth to the surface at 0.5 m sec⁻¹. The phytoplankton samples were stored in amber glass bottles and preserved with Lugol's iodine solution (5-6 mL) and concentrated formalin (1-2 mL). Microscopic enumeration was performed using a Sedgewick-type counting chamber (1 mL capacity) on an inverted microscope (Meiji HWF) following Utermöhl (1958).

2.5. Collection of zooplankton

Zooplankton were collected from vertical tows (1000 m to surface) of an Indian Ocean Standard Net (IOS; 55 μ m mesh size, opening diameter 113 cm, non-filtering cod end; Hydro-Bios, FRG), and from vertical tows from 200 m to surface of a WP2 net (150 μ m mesh size, opening diameter 57 cm, non-filtering cod end; Hydro-Bios). The fresh zooplankton samples were split into two subsamples (Folsom-type plankton splitter, Hydro-Bios). One half of the samples was preserved with buffered formalin (4% final concentration). The remaining half was transferred into 5 L buckets filled with filtered seawater, and kept in a refrigerator for 1-3 h to allow time for gut evacuation. Using stereo microscopes (SMZ168, Motic, FRG), chilled zooplankton were sorted live to the species and genus level, or the next most resolved taxonomic level for those taxa that could not be described to species. From 10883 total specimens 557 zooplankton samples were prepared for stable isotope analysis (SIA) most at the genus level and mostly as triplicates. Where applicable, we selected predominantly adult females (e.g. of Calanoida, Cyclopoida, Harpacticoida, Poecilostomatoida). All specimens were briefly washed in ultrapure water. Depending on body mass and availability, 1-130 individuals were placed in pre-weighed *Sn*-capsules (HEKAtech, FRG), oven-dried (48-72 h, 50 °C), and stored in desiccators pending SIA. For larger-bodied taxa such as fish larvae, Penaeidae, and Euphausiacea, muscle tissue was prepared from the abdomen and homogenized to fine powder in glass tubes.

2.6. Pigment analysis

Prior to HPLC analysis, filters and cells were disrupted with glass pearls on a cooled bead beater and extracted using acetone as solvent. Supernatants were separated in a Varian Microsorb-MV column (100-3, C8, 100 x 4.6 mm), with 70% MeOH / 30% 1M NH_4 -acetate and 100% MeOH as eluents. Pigments were identified and quantified using both a fluorescence detector (Waters 474 Scanning Fluorescence Detector, Waters GmbH, FRG) and a photodiode array absorption detector (Waters 2996 Photodiode Array Detector) after calibration with commercially available standards. In this manuscript only chlorophyll *a* data are shown.

2.7. Stable isotope analysis

Removal of carbonates via routine acidification of tissue samples prior to SIA potentially biases $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of whole animals (e.g. Bunn et al., 1995; Carabel et al., 2006). Contrary to those of other crustaceans, the chitinous exoskeletons of copepods are not calcified (Kaestner, 1993; Veit-Koehler et al. 2013), and are therefore comparable among studies regardless of prior acidification (Bosley and Wainright, 1999; Soreide et al., 2006; Mateo et al., 2008; Kolasinski et al., 2008; De Lecea et al., 2011). Due to the lack of carbonates in this taxon and considering the small amount of specimens obtained in oligotrophic systems such as the Red Sea, we abstained from acidification. The $\delta^{13}\text{C}$ values of the calcareous shelled taxa (i.e. Atlantidae, Ostracoda, Pteropoda and of veliger larvae), were arithmetically corrected following Pomerleau et al. (2014). In addition, since zooplankton lipids are primarily dietary in origin, extracting lipids or normalizing $\delta^{13}\text{C}$ based on C:N ratios excludes major dietary sources and therefore may be inappropriate for taxa which do not accumulate larger lipid stores such as tropical zooplankton (Hagen and Auel, 2001; Matthews and Mazumder, 2005).

Provisional measurements of the elemental C and N content for each zooplankton taxon were carried out. In contrast to well-studied temperate species, no information was available on elemental C and N content for most of the Red Sea zooplankton species at the time of analysis. The *Sn* capsules containing zooplankton were re-weighed and samples assigned to three sets corresponding to the approximate lower precision thresholds for N of the three isotope ratio mass spectrometry (IRMS) systems used during the present study, and then randomly measured. Stable isotope ratios of C and N are expressed in conventional δ notation as a measure of heavy to light isotope using the equation: $\delta X (\text{‰}) = [(R_{\text{Sample}} : R_{\text{Standard}}) - 1] \times 1000$, where δX is ^{13}C or ^{15}N , and R is the $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ ratio. Stable isotope analysis for samples with a content $> 30 \mu\text{g N}$ were determined using an elemental analyzer (varioISOPE cube, Elementar, FRG) in CN mode, connected to a stable isotope ratio mass spectrometer (IRMS; IsoPrime100, IsoPrime, UK; King Abdulaziz University, KSA). Triplicates of an internal reference material (acetanilide #1; Merck, FRG) were analyzed after every 10th unknown sample. Calibration of acetanilide #1 was carried out against certified reference material (IAEA-N-1, IAEA-N-2 for $\delta^{15}\text{N}$; IAEA-CH-3, IAEA-CH-6, IAEA-CH-7 for $\delta^{13}\text{C}$). Zooplankton samples with an

approximate N content of 10-30 $\mu\text{g N}$, and POM filters were analyzed on a ThermoElectron Delta V IRMS (Leibniz Institute for Research on Evolution and Biodiversity, FRG). At the laboratory, POM filters were randomly assigned to two sets of filters. One set of filters was exposed to HCl fumes in a glass desiccator for 12 h to remove inorganic carbonates prior to C SIA and then re-dried again (24 h, 50 °C). All filters were re-weighed and packed for SIA. Filters for N SIA were not acidified. Peptone standards with known isotopic composition (N-content 11%; C-content 44%; $\delta^{15}\text{N}$ 7.6‰; $\delta^{13}\text{C}$ -14.3‰) were used after every 5th unknown sample and calibrated with IAEA-N-1 and IAEA-N-2 once a month. Stability of the instrumentation, analytical precision, drift correction and linearity performance were calculated from the repetitive analysis of the Peptone standard. The standard deviation for replicate Peptone samples was <0.2‰ for both isotopes. Zooplankton samples with an approximate N content of 2-10 $\mu\text{g N}$ were analyzed using a customized elemental analyzer (EA 1110, Fisons Instruments, Milan, Italy) connected to a ThermoElectron DeltaPlus Advantage IRMS (Hansen and Sommer, 2007; Geomar, FRG). Isotope measurements were calibrated against IAEA-N1, IAEA-N2, IAEA-N3 for $\delta^{15}\text{N}$ and IAEA-600 for $\delta^{13}\text{C}$ ($\delta^{13}\text{C}$ $-27.77 \pm 0.04\text{‰}$; $\delta^{15}\text{N}$ $1.0 \pm 0.2\text{‰}$). The internal laboratory standard acetanilide with $1.62 \pm 0.16\text{‰}$ and $\delta^{13}\text{C}$ $-27.75 \pm 0.09\text{‰}$ was measured after every 6th sample. Integrability of all analytical batches and across the three IRMS was verified by using a second internal reference material (acetanilide #2; Schimmelmann et al., 2009) measured as first and last ‘unknown’ sample in each analytical batch sequence. Acetanilide #2 was measured with a mean $\delta^{13}\text{C}$ value of $-29.53 \pm 0.2\text{‰}$ and $\delta^{15}\text{N}$ of $1.32 \pm 0.2\text{‰}$.

2.8. Data evaluation

Correlations between environmental data and SIA results were evaluated using Redundancy Analysis (RDA, in CANOCO 5) following Lepš and Šmilauer (2003), applying a multiple linear regression fitted to a combination of environmental variables accounting best for the variation in the stable isotope data. By using a forward selection procedure (Blanchet et al., 2008), RDA detected and visualized the relationships between the isotopic composition of zooplankton and environmental parameters. Individual Monte Carlo permutation

tests (999 permutations) ranked the significance of each available environmental variable in importance for predicting the response data. Pseudo- F statistic-values represent the test of the variation explained on the first constrained axis by the specified variable and represent a partial test of its unique contribution. Corresponding P values are Type I error estimates calculated from the results of the Monte Carlo permutation test. The remaining collinear variables were passively projected in the RDA plot, because adding unimportant variables to an already well-fitted model has practically no impact on the explained variance measured by the adjusted coefficient of a multiple determination (Blanchet et al., 2008).

TwoStep cluster analysis was performed using seawater TN:TP, TP:Si, TN:Si ratios, chl a concentration, as well as zooplankton $\delta^{15}\text{N}$ (SPSS v21.0). TwoStep cluster analysis is a model-based clustering assuming Gaussian relationships and uncertainty of the modeled distances between the clusters. In brief, the first step is a random computation of a large number of preclusters. Hierarchical procedures are subsequently used, combining the preclusters sequentially to form homogenous clusters using goodness-of-fit statistics (Bayes Information Criterion). The validity of the clustering solution was *a posteriori* verified using criteria introduced by Mooi and Sarstedt (2011). The clusters were: i) substantial – the size of clusters were large enough to serve; ii) differentiable - the cluster segmentation was distinguishable (here followed up by one-way ANOVA and Tukey's post-hoc test) and conceptually comprehensible; iii) relevant - segmentation was relevant to our hypotheses; and iv) compact – clusters exhibited a high degree of within-cluster homogeneity and between-cluster heterogeneity.

Zooplankton was categorized into taxonomic groups as well as trophic guilds (**Tab. 2**). Typically, taxonomic groups of zooplankton often differ in their ecological strategies and trait associations (Fanelli et al., 2009; Fanelli et al. 2011; Kürten et al., 2013a; Litchman et al., 2013). Differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of zooplankton between sites and trophic guilds were evaluated using non-parametric Kruskal-Wallis tests followed by individual comparisons using Mann-Whitney U tests. Due to the different total number of samples per site, we randomly selected a minimum of 66 samples for each site gaining equal loads in the

Mann-Whitney U tests. For trophic guild comparisons we applied a Monte Carlo procedure for the Mann-Whitney U tests (SPSS v22.0).

In order to quantitatively assess the trophodynamics of zooplankton, the source partitioning Bayesian mixing model SIAR has been developed (Parnell et al., 2010). The description of trophic relationships in food webs using SIA depends on knowledge about the isotopic baseline (Post, 2002). Particulate organic matter (POM) samples are frequently used to determine the isotopic phytoplankton baseline of the herbivorous food web on which zooplankton potentially prey, but the complex mixture of detrital organic matter and other living organisms including bacteria, protozoa, and other microzooplankton, of which the body sizes overlap, usually compromise its cogency. The mixing model constrains the isotopic source contributions by dietary end-members to the diet of consumers (Layman et al., 2012). SIAR incorporates variance in parameters such as trophic enrichment factors in an additional error term and propagates sources of uncertainty into posterior probability distributions (Parnell et al., 2010). Prior to running SIAR, three potential dietary macronutrient sources were defined: (i) phytoplankton; (ii) diazotrophs (hereafter *Trichodesmium*); and (iii) bulk POM, the latter without discriminating between its constituents. It was assumed that the isotopic composition ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of the mucus net-feeding *Thalia democratica* (Tunicata; Mullin, 1983; Vargas and Madin, 2004) represented the isotopic baseline of small 'autotrophic phytoplankton' and bacteria fueled by deep water nitrate. As a proxy for the diazotrophic food web based on biological N_2 fixation we estimated the isotopic baseline by cyanobacteria (*Trichodesmium*) from the copepod *Macrosetella gracilis* (Harpacticoida), a species known to feed extensively but not exclusively on *Trichodesmium* (Harpacticoida; O'Neill, 1998; Eberl and Carpenter, 2007; Mompeán et al., 2013). As a third potential macronutrient end-member for zooplankton, POM was used as a proxy for fresh and detrital organic matter within the 0.7 to 50 μm size range that is available through the microbial food web. Frequently a $\delta^{15}\text{N}$ trophic enrichment factor of 3.4‰ has been used, but smaller trophic enrichment factors have been described e.g. for ammonotelic invertebrates (McCutchan Jr. et al., 2003). The isotopic values of the sources were inferred from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary consumers with relatively well-known diets (*Thalia* and *Macrosetella*) by subtracting a trophic enrichment

factor of $2.4 \pm 1\%$ for $\delta^{15}\text{N}$ and $1.3 \pm 0.3\%$ for $\delta^{13}\text{C}$ (Fry and Quiñones, 1994; McCutchan Jr. et al., 2003; Vanderkift and Ponsard, 2003; Wyatt et al., 2010). No trophic enrichment factor was subtracted from POM. Careful interpretation is generally required regarding the interpretation of trophic enrichment across multiple trophic steps within the lower pelagic food web and in particular in association with the microbial loop and POM (McCarthy et al, 2007; Gutiérrez-Rodríguez et al., 2014). However, the choice of trophic enrichment factors will not affect the general conclusions of our analysis about zooplankton trophodynamics relative to each other. SIAR was used to estimate the relative contributions of dietary end-members (% , mean $\pm$ SD) for the zooplankton population for each site. Assuming relatively constant trophic fractionation factors across trophic levels, the isotopic baseline for a food chain within the food web can be estimated from the isotope values of primary consumers (Post, 2002). Producer species are assigned to trophic level 1. Consumer values range from 2 (primary consumers) to 5 or greater. Generating a continuous fractional measure of relative trophic position (RTP) population at each site, we calculated the weighted mean RTP from the $\delta^{15}\text{N}$ of trophic level one ($\lambda = 1$) for three primary producers (RTP_{Base}) following Post (2002), where $\text{RTP}_{\text{Consumer}} = \sum_i \{ \lambda + [(\delta^{15}\text{N of Base}_i - \delta^{15}\text{N}_{\text{Consumer}}) : 2.4] * \text{Contribution of Base}_i \}$, and used POM, Phytoplankton and *Trichodesmium* as prospective Base_i .

3. Results

3.1. Environmental setting

The overall hydrography of the Red Sea was characterized by a latitudinal gradient of decreasing temperatures and increasing salinity from South to North following the general thermohaline circulation (**Fig. 2a, b**). The low salinity water in the south appears to be Gulf of Aden surface water that is depleted in primary nutrients, well oxygenated (not shown), and has relatively low chlorophyll concentrations. This is consistent with the inflow of Gulf of Aden surface water during the winter described by Smeed (2004) and Yao et al. (2014b). Localized heating in the southern Red Sea creates the temperature maximum observed at 18°N latitude with general cooling of the surface sea toward higher latitudes. In the subsurface layer, nitrate concentrations

increased with depth, generally covarying inversely with dissolved oxygen. The deep chlorophyll maximum (DCM) was shallower than 50 m in the southern Red Sea, deepened to between 60 and 90 m in the central Red Sea, and shallowed in the north to between 20 and 50 m. The overall distribution of the DCM is similar to the top of the nutricline (**Fig. 2**). The overall trophic state during the spring bloom in the Red Sea was classified as oligotrophic, as chl *a* concentrations at the DCM nowhere exceeded 1000 ng L⁻¹. Temperature and salinity sections may suggest an incomplete transition from deep winter mixing to thermal stratification in summer at the northern sites, causing a shallow DCM at approx. 20-25 m North of 26°N with chl *a* concentration up to 947 ± 37 ng L⁻¹ (**Fig. 2, Fig. 3, Table 1**).

Velocity estimates derived from Acoustic Doppler Current Profiler (ADCP) measurements provided a glimpse of the upper layer circulation along the axis of the Red Sea. The South-North transect revealed several eddies (**Fig. 1**). Satellite altimetry images revealed that the northern Red Sea circulation was characterized by a cyclonic gyre offshore from Duba (data not shown, www.aviso.altimetry.fr/en/home.html). Adverse weather conditions resulted in poor quality ADCP data in this region so that the feature could not be validated from *in situ* measurements.

In between Duba and Mabahiss we observed a strong northbound current occurring in the first 70 m of the water column. Around 23°N, a northeast current occurred and the maximum surface current speed reached approximately 55-60 cm sec⁻¹. Between Nereus and Suakin, complex variations in the flow field suggest the presence of multiple eddies that are not fully characterized by the axial transect. The flow patterns suggest the possibility of a pair of eddies characterized by a clockwise circulation that penetrated vertically the first 200 m of the water column (vertical profiles not shown). The circulation created a region of apparent divergence near the Atlantis II deep (**Fig. 1, Fig. 10**). The vertical displacement of temperature and nitrate in this region (21.5°N; **Fig. 2**) penetrated to at least 200 m depth, consistent with this divergence. In the southern Red Sea, an anticyclonic circulation centered on Suakin and the hydrography reflected this circulation with deepening

of isotherms and nutrient isopleths to at least 200 m. Notable was the southbound velocity of surface water detected during the transit between the Farasan archipelago and the sampling site offshore.

The spatial pattern of nutrient concentrations and relative composition followed a unimodal pattern for TN:Si and TP:Si, with highest ratios in the central and lowest ratios in the southern Red Sea. TN:TP approached the Redfield ratio at the central sites (Redfield et al., 1963), but exhibited a high ratio (~18.8) at the Mabahiss deep and off Duba and low ratio (12.7) off Farasan (**Fig. 3b**).

Particulate organic carbon (POC) and nitrogen (PON) concentrations were strongly correlated (Pearsons $R = 0.943$, $p < 0.01$). Comparatively large concentrations of POC and PON were measured in the northern Red Sea off Duba with $121 \pm 3.1 \mu\text{g L}^{-1}$ and $14.8 \pm 1.1 \mu\text{g L}^{-1}$, respectively, whereas at the Suakin deep concentrations were lowest ($37.7 \pm 3.2 \mu\text{g L}^{-1}$ and $5.3 \pm 0.7 \mu\text{g L}^{-1}$; **Fig. 3c, Table 1**). POC:PON ratios were similar at the most northern and southern sites off Duba and Farasan (both ~8.4), and around 8.0 at the Atlantis II deep in the central Red Sea (**Fig. 3c, Table 1**). Lower POC:PON (6.9 - 7.4) were measured at the other sites.

The RDA axes 1 and 2 explained 61.6% of variability of isotopic values of zooplankton in relation to the environmental variables. The environmental variables included in the constrained RDA provided evidence for a latitudinal background gradient of temperature and salinity (**Fig. 4, Tab. 3**). Yet, isotopic values of zooplankton in the Southern Red Sea were significantly correlated with silicate, phosphate and NO_x . 16.1% of variability in the zooplankton isotopic composition was correlated with high PON (and POC) concentrations, parting the sites in the Northern Red Sea (Duba and Mabahiss).

3.2. Phytoplankton

Resembling the pattern described for POC:PON ratios, the abundance of net phytoplankton reached comparatively high cell counts at Farasan ($1307 \text{ cells L}^{-1}$), the Atlantis II deep ($1228 \text{ cells L}^{-1}$), and at Duba ($1274 \text{ cells L}^{-1}$; **Fig. 5**). At the latter two sites, diatoms contributed approximately 88% to the total phytoplankton community. Off Farasan, however, cyanobacteria (*Trichodesmium erythraeum*) contributed

39.7% and diatoms only 54.0% to the total cell counts. The lanceolate diatom *Ceratoneis closterium* (382 cells L^{-1}) and the chain-forming diatom *Dactyliosolen fragilissimus* (173 cells L^{-1}) were the most abundant diatom taxa at Duba, whereas the phytoplankton community at Atlantis II was dominated by *Nitzschia longissima* and *Pseudonitzschia delicatissima* (both 126 cells L^{-1}). *T. erythraeum* was present at all sites (~10 to 20 cells L^{-1}) but occurred in larger numbers only at Farasan (707 cells L^{-1}), whilst dinoflagellates showed higher abundances at the Red Sea Rift (26.7%), as well as at the Suakin (39.8%), the Nereus (29.1%) and at the Mabahiss deep (18.8%).

3.3. Zooplankton and POM SIA

Overall, the zooplankton community was highly diverse and dominated by Copepoda. Samples for SIA were from 30 diversified taxa: nine Calanoida (*Candacia* sp., *Eucalanus* sp., *Euchaeta* sp., *Macandrewella* sp., *Nannocalanus* sp., *Pleuromamma* sp., *Pontellina* sp., *Rhincalanus* sp., and *Undinula* sp.), four Poecilostomatoida (*Oncaea* sp., *Corycaeus* sp., *Sapphirina* sp., *Copilia* sp.), two Ostracoda (*Cypridina* sp., *Conchoecia* sp.), as well as Gastropoda (*Atlanta* sp.), Pteropoda (*Clio pyramidata*), Cyclopoida (*Oithona* sp.), Harpacticoida (*Macrosetella gracilis*), Amphipoda (Hyperiididae), Euphausiacea, Penaeidae, Zoea and Megalopa stages of Decapoda (Anomura and Caridea), Cnidaria (Siphonophora), Bivalvia, Polychaeta (Tomopteridae), Chaetognatha, Thaliacea (*Thalia democratica*) and small larvae of fish (Osteichthyes).

The correlation between $\delta^{13}C$ and $\delta^{15}N$ of the zooplankton community was significant but weak (Pearson $R = -0.085$, $p = 0.044$, $N = 564$). The $\delta^{13}C$ and $\delta^{15}N$ of zooplankton was significantly influenced by geographic location (one-way-ANOVA, $\delta^{13}C$: $F_{(6,563)} = 9.747$, $p < 0.0001$; $\delta^{15}N$: $F_{(6,563)} = 113.863$, $p < 0.0001$). Across sites, zooplankton occupied significantly discrete δ -spaces and four clusters of sites were identified (**Fig. 6a**). Zooplankton were considerably ^{15}N depleted and ^{13}C enriched were zooplankton at the northern sites Duba and Mabahiss ($\delta^{13}C = \sim -19.0\text{‰}$, $\delta^{15}N = \sim 4.1\text{‰}$; cluster I). Although zooplankton $\delta^{13}C$ and $\delta^{15}N$ values were not significantly different, those of Duba were slightly higher (**Tab. 4**). Cluster II comprised the Atlantis II and the Nereus deep, whereas somewhat more ^{15}N enriched zooplankton were collected at the Red Sea Rift and the

Suakin deep (Cluster III). Notable was the similarity between the low $\delta^{15}\text{N}$ values of zooplankton at the Nereus deep, Mabahiss, and Duba. The Nereus deep, situated in the oligotrophic NCRS, showed lowest POM $\delta^{15}\text{N}$ and much lower zooplankton $\delta^{13}\text{C}$ values.

However, there was no significant difference between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of zooplankton at the Atlantis II and at Suakin. The most ^{15}N enriched zooplankton samples were collected off Farasan in the South ($\delta^{13}\text{C} = \sim -19.5\text{‰}$, $\delta^{15}\text{N} = \sim 8.0\text{‰}$; cluster IV; **Fig. 6a**). Microphagous and herbivorous zooplankton displayed the lowest $\delta^{15}\text{N}$ values, whereas those of plankton predators and detritivores were highest (**Fig. 6b**, **Tab. 5**). The $\delta^{13}\text{C}$ values of several functional groups fell into a relatively narrow range with no significant differences from each other, suggesting similar C sources. Non-crustacean plankton predators such as fish larvae, Chaetognatha, Siphonophora, and the Tomopteridae also displayed high $\delta^{15}\text{N}$ values (6.3 – 6.7‰) and similar $\delta^{13}\text{C}$ values, showing large overlap with crustacean zooplankton in the bi-plot (**Fig. 6c**).

The most ^{13}C and ^{15}N depleted taxon were the *T. democratica*. The highest $\delta^{13}\text{C}$ values were observed in Pteropoda, Gastropoda (*Atlanta* sp.), and Bivalvia Veliger. The Harpacticoida species *M. gracilis* showed the lowest $\delta^{15}\text{N}$ signatures among the crustacean zooplankton (**Fig. 6d**). We note that some specimens of *M. gracilis* were found preying on chain-forming diatoms during microscopic observations of fresh samples (Al-Aidaros, pers. comm.), providing further evidence that similar-shaped phytoplankton taxa other than *Trichodesmium* sp. can be consumed by *M. gracilis*. The suspension-feeding *Undinula vulgaris* and detritivorous *Macandrewella chelipes* occupied the highest position in δ -space (**Fig. 6d**). Mean relative trophic positions (RTPs) of zooplankton ranged from 1.8 ± 0.4 for *M. gracilis* to 3.5 ± 0.4 for *M. chelipes* (**Tab. 2**). Maximal RTPs were observed for the plankton predators, such as Chaetognatha and fish larvae. The suspension-feeders *Oithona* sp. and *Saphirina* sp. attained relatively high RTPs with 4.4 at the Nereus deep and 4.3 at Duba. However, both taxa showed similar ^{13}C depleted values ($\sim -22.2\text{‰}$; **Fig. 6d**).

Pooled together, the $\delta^{15}\text{N}$ values of zooplankton tended to increase from North to South (**Fig. 7a**), and those of *Thalia* sp. and particulate organic matter (POM) followed the same latitudinal trend. POM $\delta^{15}\text{N}$ values were

lowest at the Nereus deep ($1.4 \pm 0.3\text{‰}$) and highest at Farasan ($6.3 \pm 0.8\text{‰}$). The copepod *M. gracilis*, however, had similar $\delta^{15}\text{N}$ values at all sites. The $\delta^{13}\text{C}$ values of POM were lower than those of bulk zooplankton, and *T. democratica* and *M. gracilis* throughout the Red Sea (**Fig. 7b, Table 2**). Zooplankton and POM $\delta^{13}\text{C}$ values also followed similar trends and increased over latitude as shown for $\delta^{15}\text{N}$. POM $\delta^{13}\text{C}$ values were most depleted in the South at the Red Sea Rift ($-24.7 \pm 0.1\text{‰}$) and most enriched off Duba ($-22.6 \pm 0.4\text{‰}$). There was a central peak in $\delta^{13}\text{C}$ values at the Atlantis II site along the latitudinal trend, also present in the zooplankton data although of smaller magnitude. There was little variation in the $\delta^{13}\text{C}$ values of *T. democratica*. The variation of *M. gracilis* tended to decrease from South to North (**Fig. 7b**).

The latitudinal gradient in $\delta^{15}\text{N}$ signatures was observed across most taxa (**Fig. 8**). SIA indicated that $\delta^{15}\text{N}$ values of zooplankton increased toward the south. Zooplankton at the three northern sites of Duba, Mabahiss, and Nereus showed similar $\delta^{15}\text{N}$ values and were significantly ^{15}N depleted compared to zooplankton in the central and southern Red Sea (one-way-ANOVA, $\delta^{15}\text{N}$: $F_{(1,563)} = 490.661$, $p < 0.0001$). Noticeable was a peak at the Atlantis II site for some taxa, including the herbivorous taxa *Rhincalanus* sp. and Euphausiacea, microphagous *T. democratica*, and the plankton predatory Tomopteridae. Although most taxa showed similar low $\delta^{15}\text{N}$ values at the three northern sites, some taxa such as Amphipoda, Conchoecia, Copilia, and Tomopteridae exhibited slightly higher $\delta^{15}\text{N}$ values at Duba compared to the other two sites (**Fig. 8**).

We have presented multiple evidences for ecohydrographic features and eddy-induced upwelling of the Red Sea using ADCP data (**Fig. 1**), environmental variables (**Fig. 2, Fig. 3**), phytoplankton counts (**Fig. 5**) and bulk $\delta^{15}\text{N}$ values of individual zooplankton taxa (**Fig. 8**). The complementary output from the mixing model provides an additional line of evidence, despite the uncertainties in sensitivity with Bayesian mixing models including potentially non-linear fractionation processes. The relative contribution of POM and diazotrophs (*Trichodesmium* sp.) discriminated the sites in the northern and southern Red Sea. In the northern Red Sea, at Duba, Mabahiss, and Nereus, the relative contribution of diazotrophs (*Trichodesmium* sp.) was estimated at 75.5 to 82.1%. In contrast, in the southern Red Sea POM was a relatively more important food source for

zooplankton at the Suakin deep ($66.6 \pm 19.1\%$), the Red Sea Rift ($83.3 \pm 12.8\%$), and off Farasan ($76.8 \pm 16.6\%$; **Fig. 9**). This pattern was interrupted by the contribution of phytoplankton. SIAR indicated that the contribution of deep water, nitrate-fueled phytoplankton to the diet of zooplankton followed a similar unimodal pattern as, for example, displayed for the TN:TP and TP:Si ratios (**Fig. 3**), and other ecohydrographic variables. The largest contribution of phytoplankton was seen at the Atlantis II deep ($64.5 \pm 28.6\%$) and the smallest contributions off Duba ($1.5 \pm 2.5\%$) and Farasan ($0.3 \pm 0.5\%$; **Fig. 9**).

4. Discussion

Our study suggests that the Red Sea is significantly influenced by physical, eddy-like features with considerable implications for biogeochemical processes. We began by discussing environmental and stoichiometric controls, how spatial features of the Red Sea translate to geographic patterns in isotopic composition of biota (isoscape) that determine the isotopic end-members, provide general ecological insights for the zooplankton in the Red Sea, and highlight diverging food web configurations. This led to a conceptualization of the ecohydrographic framework of the Red Sea (**Fig. 10**) to illustrate the complexity of the system.

4.1. Ecohydrographic framework of the Red Sea

The general circulation pattern and ecohydrography of the Red Sea are governed by strong thermohaline and wind forces (Patzert, 1974; Edwards, 1987; Quadfasel and Baudner, 1993; Eshel and Naik, 1997; Zhai and Bower, 2013; Yao et al., 2014 a,b). The Red Sea is influenced by the north-northwest monsoon winds occurring in the southern Red Sea from October to May. North of the convergence zone at 18° – 19° N, winds blow southeastward throughout the year (Patzert, 1974; Halim, 1984). Our study corroborates earlier modeling as well as *in situ* and satellite observations (Patzert, 1974; Edwards, 1987; Sofianos and Johns, 2007; Raitsos et al., 2013), which summarize the overall latitudinal thermohaline circulation as an upper layer northbound and reverse southbound flow (**Fig. 10**). The inflow of water from the Gulf of Aden typically introduces water with lower salinity and higher temperature, carrying typically high concentration of nutrients and plankton

into the southern Red Sea (Yao et al., 2015). Representing the southernmost end-member in this study, the site to the west of the Farasan archipelago was influenced by the inflow of water from the Gulf of Aden (Patzert, 1974; Sofianos and Johns, 2007; Bower and Farrar, 2015), as indicated by hydrographic sections. Further details are provided on the relationships between the thermohaline characteristics and the stoichiometric controls in section 4.2.

The upper-layer circulation is also controlled by quasi-permanent and/or recurrent eddies (Quadfasel and Baudner, 1993; Sofianos and Johns, 2007; Raitos et al., 2013; Zarokanellos et al., 2014). It has been suggested that the advection of Gulf of Aden water toward the North resembles a meandering pattern where both wind forces and eddies play a profound role (Bower and Farrar, 2015). What remains inconclusive is if and how far northward the Gulf of Aden water can be traced using temperature-salinity relationships. ADCP velocity data documents a series of anti-cyclonic eddy features south of 21°N. It appears, however, that two anti-cyclonic eddies to the north and south of the Atlantis II generate a diverging surface water displacement. This divergence gives rise to an upward transport of deep nutrient-rich water toward the upper layer (**Fig. 10**). Considering indications of persistent, quasi-permanent eddies in this region (Bower and Farrar, 2015), the observed separation appears as one plausible explanation for a frequently mentioned separation of the Red Sea into a NCRS and SCRS (*sensu* Raitos et al., 2013). Moreover, this study provides an explanation for an upwelling mechanism near the Atlantis II station, for which additional multiple and complementary evidence exists, including nutrient data, POM, phytoplankton count and modeled zooplankton food source data (see discussion below). In fact, modeling studies already indicate that the general Red Sea upper water flow is affected by a temporally and spatially variable and complex array of eddy systems (Zhan et al., 2014). We suggest, therefore, that eddies have the potential to interact with the general thermohaline circulation of the Red Sea, but with variable lifespan and positioning (**Fig. 10**; *sensu* Zhan et al., 2014).

A spatially constrained and quasi-persistent cyclonic eddy seems to characterize the NRS, most likely owing to the overall winter convection, generally less variable wind forcing from northwest, but also eastward

coastal currents (Acker et al., 2008; Sofianos and Johns, 2007; Raitso et al., 2013; Bower and Farrar, 2015). Sampling in the NRS took place in spring, demarking the transition period between deep mixing and stratification in winter. The observed elevation of the isopycnals toward the North (**Fig. 2**) suggests that this cyclonic eddy likely influences primary productivity by injecting nutrients from the deep water into the euphotic zone (McGillicuddy et al., 1998; Li and Hansell, 2008; Yao et al., 2014b). Further, the eddy transports water and concomitantly disperses nutrients from the coastal coral reefs toward the open sea off Duba (Eshel and Naik, 1997; Acker et al., 2008). After presenting the hydrographic setting of our study, we proceed with descriptions of how the observed hydrographic processes relate to the ecological stoichiometric criteria and finally mediate food web dynamics.

4.2. *Environmental and stoichiometric controls*

Hydrography, elemental composition of plankton organisms, and food web configuration are strongly intertwined and were summarized in the term ecohydrography (Sverdrup et al., 1942; Redfield et al., 1963; Sommer et al., 2002a; Sterner and Elser, 2002; Kürten et al., 2014a). Organic matter in marine environments is commonly characterized by its elemental composition, isotopic signatures and biochemical properties (e.g. Middelburg and Herman, 2007). Frequently, POC:PON ratios have been associated with POM quality in marine environments, separating fresh (~6.2) from detrital (~18) organic matter (Cifuentes et al., 1988), because POC:PON values of marine algae usually increase upon diagenesis (Hedges et al., 1997; Herman and Heip, 1999). Here, POM was composed mainly of fresh organic matter, as POC:PON ratios did not exceed a ratio of 8.4 and were rather uniform at most sites (~6.9-7.4; **Table 1**). Our reported C:N ratios were in the typical range of marine POM and approximated the Redfield ratio (Redfield et al., 1963; Geider and LaRoche, 2002). Judging by the POC:PON ratio, phytoplankton at most sites were neither C nor N depleted. POC:PON ratios off Duba, at the Atlantis II deep and off Farasan, were somewhat increased, coinciding with higher phytoplankton cell counts at these sites and potentially concomitant diagenetic processing of phytoplankton. However, considering the nutrients available to phytoplankton, TN:TP ratios showed that Duba and Mabahiss

were only slightly N deficient (<20) and the sites in the NCRS and SCRS approached the Redfield ratio (~ 16), whereas off Farasan TN:TP ratios suggest N limitation (Redfield et al., 1963; Downing, 1997; Guildford and Hecky, 2000). Therefore, somewhat increased POC:PON ratios of POM further corroborate our indication of N limitation at Farasan (Geider and LaRoche, 2002). In the NRS, salinity and TN:TP ratio data indicated relatively similar N and P availability at Duba and Mabahiss. The particulate organic matter (POM) composition mirrored this hydrographic separation (**Fig. 3**).

The bottom-up axiom food web theory predicts that supplies of C, total N (TN), total phosphorous (TP), and silicate (Si) – and their proportions relative to each other – are important bottom-up determinants of resource dynamics and food web configurations at the base of food webs for the oligotrophic northern Red Sea and the Gulf of Aqaba (Sommer, 2000; Sommer et al., 2002a). Sommer and Stibor (2002) proposed that if nutrients derive from deep water, TN:Si and TP:Si ratios would be low and cause diatoms to prosper. Both indicative criteria are supported by high chl *a* concentrations and diatom counts at Duba (**Fig. 3b**, **Fig. 5**). Furthermore, there was a compelling similarity in nutrient ratios and salinity between the Suakin and Nereus deeps (NCRS, SCRS) to the north and to the south of the Atlantis II deep. This similarity in nutrient rations and salinity provides support for the supposition that eddies have the potential to locally interact with the general latitudinal thermohaline circulation (**Fig. 10**). Given that diatoms dominated the phytoplankton at Duba and the Atlantis II site (**Fig. 5**), it seems plausible that the overturning circulation in the northern Red Sea – which, as described above, typically includes a cyclonic eddy and winter convection – sustains phytoplankton with deep water nutrients until stratification establishes in early summer. We observed a high chlorophyll concentration mid-April, which seems late in season given the climatology and phenology of primary production described before (c.f. Raitsos et al., 2013; Racault et al., 2015). Despite the importance of the supposed N_2 fixation in the North, the slight increase of $\delta^{15}N$ values seen for some taxa at the Duba site compared to Mabahiss and Nereus (**Fig. 8**), may be related to the deep mixing.

Conversely, although highest Si concentrations were measured off Farasan, TN and TP were depleted (**Table 1**). We suggest that the Farasan region was sampled during a transitional phase from the winter bloom toward a N-limited body of water, so that diatoms (39.7% of the phytoplankton community) were outnumbered by the diazotroph *Trichodesmium erythraeum* (54.0%). Previously, *Trichodesmium* has been documented to thrive in the N-depleted southern Red Sea (Kürten et al., 2014b). As *Trichodesmium* regularly supports pelagic food webs via organic matter release (Glibert and Bronk, 1994; Capone et al., 1997; McClelland et al., 2003), we suggest that the elevated POC:PON ratio at Farasan at least partly relates to the presence of *Trichodesmium* (**Fig. 3c**). The ratio of PON:chl *a* has been used as an index of the quantity of N that can be attributed to phytoplankton, approaching numerical unity under optimal growth conditions (McCarthy and Nevins, 1986). During our study, PON:chl *a* ($\mu\text{g L}^{-1}:\mu\text{g L}^{-1}$) ranged between 13.4 at Farasan to 15.3 at Duba (equivalent to 0.96 and 1.09 $\mu\text{mol kg}^{-1}:\mu\text{g L}^{-1}$), suggesting that POM contained detrital and heterotrophic materials at all sites. This leads to an unanswered question: why POM and zooplankton off Farasan were still ^{15}N enriched, despite abundant but typically ^{15}N depleted *Trichodesmium*?

4.3. Spatial features of the Red Sea isoscape

Provided that ecohydrographic features typically translate into isoscapes, we continue with discussing zooplankton stable isotope data, starting at the highest level of taxonomic aggregation. Mean zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data revealed significant variation at the macroecological scale. The Duba and Mabahiss cluster (low mean zooplankton $\delta^{15}\text{N} \approx 4.0\text{-}4.2\text{‰}$) in the NRS cyclonic eddy region (c.f. Raitso et al., 2013) denotes the northernmost latitudinal end-member along the studied transect, with an approximate difference of 4‰ to the southernmost site off Farasan (high mean zooplankton $\delta^{15}\text{N} \approx 8.0\text{‰}$; **Fig. 7**). The latitudinal trends in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values measured in POM and zooplankton samples of our study support that their isotopic compositions are governed by ecohydrographic controls that alter the isotopic baseline. A propagation of baseline $\delta^{15}\text{N}$ values from POM through zooplankton and contiguous food chains has been shown before (e.g. Minagawa and Wada, 1996; Jennings and Warr, 2003; Jennings et al., 2008; Kürten et al., 2013a, b), and summarized by

creating macroecological isoscapes of zooplankton (McMahon et al., 2013a). Assuming that ^{15}N -enriched nutrients (POM , NO_3^-) from the Arabian Sea enter the Red Sea during the winter monsoon (Brandes et al., 1998; Sigman et al., 2000; Sofianos and Johns, 2007), enriched $\delta^{15}\text{N}$ values of zooplankton may indicate that the ^{15}N enriched N from the Arabian Sea propagates through the pelagic food web in the SRS, and then follows a subsequent meandering flow northwards (Patzert, 1974; **Fig. 10**). The hydrographic influence of the Gulf of Aden water can be traced up to 21°N in the central Red Sea (pers. observation). Coupled with the consistent trend of northward decreasing $\delta^{15}\text{N}$ values of POM and zooplankton in our study, a dilution of the enriched $\delta^{15}\text{N}$ end-member with more ^{15}N depleted N in the isoscape of the Red Sea is plausible. This opens another question: which ecological processes actually manifest in the trend of ^{15}N depletion toward the North and in the NRS?

Lower $\delta^{15}\text{N}$ values of plankton often relate to the relative importance of diazotrophs over deep water N sources, and its isotopes elucidate differences of N cycling at oceanic scale attributable to the presence of the diazotroph *Trichodesmium* (e.g. Fry and Quiñones, 1994; Capone et al. 1998; Montoya et al., 2002; Dorado et al., 2012; Hauss et al., 2013). A recent study on coral reef biota and neritic zooplankton along the Saudi Arabian coast suggested that the larger relative importance of atmospheric nitrogen over deep-water nitrate as N source in the NRS, where mean zooplankton $\delta^{15}\text{N}$ values were low ($1.8 \pm 1.3\text{‰}$), and more ^{15}N enriched in the South ($4.6 \pm 1.6\text{‰}$; Kürten et al., 2014a). When compared to zooplankton in coral reefs and in the Gulf of Aqaba (Aberle et al., 2010; Kürten et al., 2014a), $\delta^{15}\text{N}$ values of offshore zooplankton in the NRS (Duba, Mabahiss and Nereus deep) showed 2‰ to 4‰ higher $\delta^{15}\text{N}$ values. This pattern contrasts, for example, with the ^{15}N depletion of offshore vs. neritic zooplankton in the Gulf of Mexico observed by Dorado et al. (2012). There, the observed ^{15}N depletion offshore reflected the presence of *Trichodesmium* as N end-member. Thus, despite open questions about the temporal scales underlying the differences between neritic and offshore zooplankton $\delta^{15}\text{N}$ values in the Red Sea, $\delta^{15}\text{N}$ values support either the presence of an inshore-offshore gradient in trophodynamics, and/or a change in isotopic baseline. Kürten et al. (2014a) recently confirmed observations of zooplankton with low $\delta^{15}\text{N}$ in the Gulf of Aqaba in the NRS, where herbivorous zooplankton

at times assimilates ^{15}N depleted food lowering their $\delta^{15}\text{N}$ values down to -0.7 to 1.8‰ (Aberle et al., 2010). Because abundances of *Trichodesmium* cells were scarce during their study, Aberle et al. (2010) inferred that new N with low $\delta^{15}\text{N}$ values was channeled into the food web through either deposition of aerosols (Chen et al., 2007) or other single-celled diazotrophic cyanobacteria such as *Cyanothece* (Zehr et al., 2001; Foster et al., 2009). As both processes introduce depleted N to the Gulf of Aqaba and the Red Sea in general, aerosol and dust inputs cannot easily be differentiated from N_2 fixation using N isotopes (Wankel et al., 2010), despite their importance as additional N source (**Fig. 10**).

There were divergences from the general latitudinal $\delta^{15}\text{N}$ trend peaking at the Atlantis II deep for a few zooplankton taxa that are consistent with environmental data. Predominantly herbivorous *Rhincalanus nasutus* (Calanoida, Schnack-Schiel et al., 2008) and Euphausiacea (Timonin, 1971; Schnetzer and Steinberg, 2002), predatory Tomopteridae (Polychaeta; Fauchald and Jumars, 1979), and microphagous *Thalia democratica* (Thaliacea; Vargas and Madin, 2004), exhibited more ^{15}N enrichment than approximated from the overall latitudinal trend (**Fig. 8**). This observation coincides with maxima of environmental parameters (e.g. high TN:Si, TP:Si, POC, PON, and POC:PON ratios), and with increased nitrate and diatom biomass in the area where ADCP data revealed surface water displacement due to two eddy systems (**Figs. 1, 2, 3, 5**).

Furthermore, the mesopelagic *R. nasutus* showed higher abundances at Duba and the Atlantis II deep (A.M. Al-Aidaros and B. Kürten, unpubl. data). This substantiates the importance of diatoms as important trophodynamic end-member at these sites, because *R. nasutus* typically grazes on large diatoms during upwelling-induced diatom blooms (Longhurst, 1967; Weikert, 1982; Beckmann, 1984; Sommer et al., 2002b; Schnack-Schiel et al., 2008). Our observations at the Atlantis II deep appear to relate to upwelling occurring at the edges of two mesoscale eddies in the central Red Sea, that were situated to the north and south of the Atlantis II deep (Raitsos et al., 2013; Zarakanellos et al., 2014). It is plausible that upwelling of deep-water nitrate fuels phytoplankton (diatom) growth at the Atlantis II deep, and therefore channels macronutrients with an enriched $\delta^{15}\text{N}$ through the grazing food chain toward higher trophic levels. As the larger contribution of phytoplankton-derived C and N over POM and *Trichodesmium* at the Atlantis II deep was consistent with the

environmental observations and highlighted in the SIAR model (**Fig. 9**), the zooplankton isotope data supports evidence for cascading, upward transport of ^{15}N -enriched nutrients across both members of the herbivorous and the detritivorous food web. Although systematic investigations of eddy-driven macronutrient fluxes in the Red Sea are requisite for a more comprehensive delineation of macronutrient fluxes, the regional relative persistence over time of the above mentioned mesoscale eddies advocates for the ecohydrographic singularity of the Atlantis II deep. The historical attention to the Atlantis II deep – often the focus and prominent location of past research – may have led to biased extrapolations regarding the ecology of the whole Red Sea.

4.4. *Zooplankton stable isotope analysis*

Despite some exceptions, $\delta^{15}\text{N}$ values of most taxonomic and functional groups demonstrated an inverse relationship to latitude consistent with the overall ecohydrographic patterns of the Red Sea. Following the latitudinal pattern of mean ($\pm\text{SE}$) zooplankton and POM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, herbivores ($4.4 \pm 0.2\text{‰}$) usually showed low and top-predator carnivores ($6.7 \pm 0.4\text{‰}$) high $\delta^{15}\text{N}$ values. The observed patterns in the environmental data support the notion that the configurations of pelagic food webs in the Red Sea are generally governed by physical oceanographic processes that manifest in the isotopic composition of zooplankton in the Red Sea. Most descriptions of Red Sea plankton were of a taxonomic nature and assessed the biodiversity of phytoplankton and/or zooplankton at variable spatial scales, most frequently at the Atlantis II deep (e.g. Weikert, 1982; Halim, 1984; Böttger-Schnack, 1990; Scheider et al., 1994; Böttger-Schnack, 1995; Seeberg-Elverfeldt et al., 2004; Claessens et al., 2010). There are few broad species-specific studies of pelagic zooplankton using SIA (e.g. Hannides et al., 2009; Koppelman et al., 2009; Aberle et al., 2010; Fanelli et al., 2011; Couturier et al., 2013; Kürten et al., 2013a). Though poorer in species than the Indian Ocean, the Red Sea planktonic population is diverse and subject to a pronounced north-south biogeographic gradients and seasonal variations (Halim, 1984; Böttger-Schnack, 1995). Copepods are the most numerous plankton group in the Red Sea, accounting for up to 83% of all metazoan organisms in the central region (Weikert, 1982; Böttger, 1987). The larger mesozooplankton fraction in the epipelagic zone is usually

dominated by Calanoida such as *Eucalanus* and *Pleuromamma*, whereas the Podoplea orders, Cyclopoida, Poecilostomatoida, and Harpacticoida, account for up 75% of the small-sized taxa (Weikert, 1982; Böttger-Schnack, 1990). Among the latter, the most conspicuous taxa are *Oncaea* sp., *Oithona* sp., *Corycaeus* sp., *Sapphirina* sp., and *Macrosetella* sp. (Weikert, 1982; Böttger-Schnack, 1994; Böttger-Schnack, 1995). Some inferences about trophodynamic information can be derived from taxonomic relationships and studies conducted in other tropical ecosystems, yet overall ecological knowledge about many zooplankton taxa in the Red Sea is scarce. Our study sought to provide the first isotope-derived information on the feeding ecology and trophodynamics of many zooplankton taxa in the Red Sea.

Microphagous pteropods and *Thalia*, the harpacticoid *Macrosetella*, and Poecilostomatoida (*Oncaea*, *Corycaeus*) exhibited lower $\delta^{15}\text{N}$ values than plankton predators such as Tomopteridae, Chaetognatha and fish larvae. This result provided clear evidence of their trophodynamic function. The largest difference between the $\delta^{15}\text{N}_{\text{POM}}$ and $\delta^{15}\text{N}_{\text{Zooplankton}}$ was calculated for plankton predators, which were on average enriched over POM by 2.1‰. Among the most ^{15}N depleted taxa was *Macrosetella*. *Macrosetella* is known for its association with and feeding on the filamentous cyanobacteria *Trichodesmium* spp. (O’Neil and Roman, 1994; O’Neil, 1998; Eberl and Carpenter, 2007). Here, it attained similar low mean $\delta^{15}\text{N}$ values at all sites ($2.7 \pm 0.2\text{‰}$), a typical $\delta^{15}\text{N}$ value of zooplankton grazing on *Trichodesmium* spp. (Wada and Hattori, 1976). Having evidence for the presence of *T. erythraeum* at all sites (**Fig. 3**), the feeding of *Macrosetella* seems plausible from the isotopic perspective, considering that *T. erythraeum* typically attains $\delta^{15}\text{N}$ values of -2.1 to 1.0‰, and considering a $\delta^{15}\text{N}$ TEF of 3.2‰. In addition, *Trichodesmium* not only exhibits low $\delta^{15}\text{N}$ but also enriched $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}$ -21 to -15‰; Tschernov and Lipschultz, 2008), which falls into the range of $\delta^{13}\text{C}$ values observed in the Red Sea (**Fig. 7**). Moreover, *Trichodesmium* not only influences the $\delta^{15}\text{N}$ value of *Macrosetella* through direct grazing, but also the isotopic composition of POM and other plankton components. This was evidenced, for example, by the deviation of the trend line in $\delta^{15}\text{N}_{\text{POM}}$ values at the Nereus deep to $1.4 \pm 0.3\text{‰}$ (**Fig. 7a**), coinciding with higher free *Trichodesmium* trichome counts (20 cells L^{-1}). *Trichodesmium* colonies in association with *Macrosetella* are known for releasing dissolved organic matter (DOM), subsequent

regeneration of NH_4^+ , and enhancing the production of primary producers that then typically carry a lower $\delta^{15}\text{N}$ signature (Glibert and Bronk, 1994; O'Neil et al., 1996; Mompeán et al., 2013). Hence, the *Trichodesmium-Macrosetella* association in oligotrophic oceans emerged as a strong and significant source of new N for – and link to – the microbial food webs. This is likely through NH_4^+ -regeneration via excretion and sloppy feeding (O'Neil et al., 1996; Montoya et al., 2002; Mompeán et al., 2013). This study concludes that the trophodynamic *Trichodesmium-Macrosetella* interaction may influence the cycling of N in the Red Sea akin to other oligotrophic oceans (e.g. Wada and Hattori, 1976; Minagawa and Wada, 1996; Carpenter et al., 1997; McClelland et al., 2003; Mompeán et al., 2013).

Overall, suspension feeders, detritivores and omnivores exhibited similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Laying in the C and N δ -space next to each other, the suspension feeders *Oithona* sp. and *Sapphirina metallina* apparently consumed similar food. *Sapphirina* typically associates with the DCM layer (Chae and Nishida, 1995), where, together with *Oithona*, it feeds on POM including small motile and sinking particles such as flagellates, ciliates, and fecal pellets (Paffenhöfer, 1993; González and Smetacek, 1994; Calbet and Landry, 1999). *Oncaea* sp. have been described as non-selective omnivores which tend to consume preferentially small (< 20 μm) diatoms. However, we observed *Oncaea* sp. attached to particles and larvacean houses preying on particle-laden mucus (Alldredge, 1972; Paffenhöfer, 1993; Wu et al., 2004). The lower $\delta^{15}\text{N}$ of the omnivores *Copilia quadrata* and *Oncaea* sp. – the latter being represented mainly by *Oncaea media*, *O. venusta*, and *O. mediterranea* in the present study – concurs with findings in the Gulf of Aqaba, where *Oncaea* and *Copilia* occupied a low position in the food web (Aberle et al., 2010). Since picoplankton and cyanobacteria contribute up to 80% of phytoplankton biomass in the Red Sea, we assume that autotrophic picoplankton including non-diazotrophic cyanobacteria, such as *Synechococcus*, produce an important C source for mesozooplankton in the central and southern Red Sea (Gradinger et al. 1992, Kürten et al., unpub. data). As these are generally too small to be grazed upon by larger zooplankton, heterotrophic nanoflagellates have been found to bridge the macronutrient flux in the Red Sea from dissolved organic matter, to bacteria of the microbial loop, and toward mixo-/heterotrophic dinoflagellates, whilst nanoflagellates are in turn preyed upon by mesozooplankton

(Weisse, 1989; Ohlndieck et al., 2000). Although the biogeography of most zooplankton taxa such as the *Oncaea* groups remains to be assessed in thorough taxonomic descriptions, the abundance of small copepods increases toward the SRS (Böttger-Schnack, 1995). Their larger abundance toward the Gulf of Aden may relate to the larger availability of POM through the microbial food web utilization. Since functionally these smaller genera play major roles in the degradation of marine snow aggregates (Kiørboe, 2000), a similar ecological role can be assumed for the Red Sea, as indicated by a larger utilization of POM by zooplankton in the SRS.

Although it could be sampled only from the SRS, the relatively high $\delta^{15}\text{N}$ of the calanoid copepod *Undinula vulgaris* is notable, because the fine suspension feeding *U. vulgaris* is known from other regions for its diverse but mainly herbivorous diet that includes diatoms, dinoflagellates and few microzooplankton (Timonin, 1971; Kleppel et al., 1996). As *U. vulgaris* constitutes an important component in the diet of whale sharks, manta rays, and midwater fish (Myctophidae; Kinzer and Schulz, 1985; Hacohe-Domené et al., 2006; Couturier et al., 2013), further investigation on its feeding ecology are needed. Likewise, notable was the high RTP occupied by *Macandrewella chelipes*, a common inhabitant in subtropical seas including the Red Sea, which has been described before as a hyperbenthic and detritivorous species (Ohtsuka et al., 2002). In contrast, unexpected was the RTP of *Pontellina plumata* (2.7 ± 0.2). The carnivore *Pontellina* sp. is typically present in all oligotrophic subtropical oceans (Fleminger and Hulsemann, 1974), but according to its position in δ -space we consider this species as an omnivore (Timonin, 1971), rather than as a raptorial ambush predator that preys on *Oncaea* sp. (Ohtsuka and Onbé, 1991). Thus, given that the important and abundant taxa are *Oncaea* sp., *Oithona* sp., *Corycaeus* sp., *Sapphirina* sp., and *Macrosetella* sp. (Weikert, 1982; Böttger-Schnack, 1994; Böttger-Schnack, 1995), of which many are omnivores, it is suggested that facultative omnivory plays a pivotal role in Red Sea zooplankton trophodynamics and therewith for C and N cycling in the pelagic realm of the Red Sea.

Overall, our findings emphasize that bulk POM constitutes a central macronutrient source for Red Sea zooplankton. Our finding is justifiable because POM-derived C and N are available through predation on organisms of the microbial loop food web including flagellates and microzooplankton (Azam et al., 1983; Angel, 1984). The $\delta^{15}\text{N}$ values of *Macrosetella*, however, were on average 2.2‰ lower compared to POM, suggesting that POM alone was not the only food source for zooplankton. Typically ^{13}C is conservatively fractionated as it moves through food webs (DeNiro and Epstein, 1978). Assuming a $\delta^{13}\text{C}$ frequently applied trophic enrichment factor (FATE) of 1‰, differences between POM and zooplankton $\delta^{13}\text{C}$ values in the present study would account for at least 3-4 trophic levels between POM and zooplankton. This illustrates that food sources other than POM contribute to the diet of zooplankton in the Red Sea.

Zooplankton $\delta^{15}\text{N}$ tended to be similar in the NRS, as no statistically significant differences in zooplankton $\delta^{15}\text{N}$ values were apparent between the sites Duba, Mabahiss deep and Nereus deep. South of the Nereus deep the $\delta^{15}\text{N}$ then increased gradually toward the SRS (**Fig. 8**). This deviance from the straight latitudinal pattern potentially demarks the extent of the average northward advection of water from the Gulf of Aden and provides additional evidence for the ecohydrographic separation of the NRS from the central and SRS. With due caution toward the generalization of the model output, estimates of the contribution to the diet of zooplankton indicates the relative larger importance of POM over phytoplankton and diazotrophs in the SRS compared to the NRS Red Sea where N of diazotrophic origin is of greater importance (**Fig. 9**).

One may ask why there was no tendency toward more ^{15}N depleted and ^{13}C enriched zooplankton and POM isotope values in the SRS where *Trichodesmium* was most abundant. It could be claimed that the comparatively low TN concentrations measured off Farasan caused ^{15}N enrichment because of preferential uptake of ^{15}N depleted nitrate which fractionates the remaining N pool. But, similar POM $\delta^{13}\text{C}$ values (-24 to -24.7‰) at the three southernmost sites contradict this argument. First, substantial contributions of *Trichodesmium*-derived C appears unlikely considering its typical $\delta^{13}\text{C}$ values (-21 to -15‰; Tschernov and Lipschultz, 2008). Secondly, if significant *Trichodesmium*-derived C input constituted the primary C source,

then several diagenetic steps within the microbial food web would be required and this would have led to additional significant ^{13}C enrichment. The microbial food web was potentially supplied with macronutrients of the diatom *Ceratoneis closterium* off Duba, because it not only colonizes aggregates of marine snow, but due to its own extracellular mucilage production promotes nutrient recycling through associated bacteria during N and P limitation (Corner et al., 1984; Glibert et al., 1988; Alcoverro et al., 2000). Hence, lower $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ support the idea that microbial loop-derived POM contributes an important fraction to the diet of zooplankton in the SRS, whereas more ^{13}C enriched POM in the NRS and at the Atlantis II deep suggest contributions from other diazotrophic C sources.

Unfortunately there are some obstacles to untangling ^{15}N fluxes in oligotrophic oceans and the importance of diazotrophic vs. regenerated production. Ammonotelic remineralization of NH_4^+ by zooplankton and ^{15}N loss from the euphotic zone due to grazing and sedimentation also result in ^{15}N depleted N sources that are preferentially retained through tight coupling within the multivorous food web (Checkley Jr. and Entzeroth, 1985; Checkley Jr. and Miller, 1989; Legendre and Rassoulzadegan, 1995; Koch, 2007). An additional, yet diffuse source of C and N in the NRS, relates to the collision of two coastal currents in the northwestern Red Sea. The currents generate a jet-like plume, transporting reef-borne nutrients – with also potentially low $\delta^{15}\text{N}$ – toward the east and fuels down-stream primary production in the offshore Red Sea (Eshel and Naik, 1997; Acker et al., 2008). Nevertheless, acknowledging the described uncertainties in source delineation using N isotopes, three main N end-members within the multivorous pelagic food web were put forward: diazotrophs (hereafter *Trichodesmium*) with low $\delta^{15}\text{N}$ that fuel the microbial web, autotrophic phytoplankton fueled by deep water nitrate (high $\delta^{15}\text{N}$) supporting the herbivorous food web, and bulk POM as important component of the microbial loop and detritivorous food web (c.f. Legendre and Rassoulzadegan, 1995).

4.5. Food web configurations in the Red Sea

Concurrent with recent empirical corroboration by mesocosm experiments (e.g. Díez et al., 2013), it was hypothesized that the proportional abundances of nutrients (TN:TP:Si) not only influences primary

productivity but also the configuration of pelagic food webs and the length of food chains therein (Sommer et al., 2002a; Sommer and Stibor, 2002; Stibor et al., 2004). In their conceptual appraisal of relationships between ecological stoichiometry and food web configurations, Sommer et al. (2002a) predicted that under nutrient-rich conditions with low TN:Si ratios (prevailent in the SRS and the NRS) a high share of diatoms emerges, fed upon directly by herbivorous copepods. These copepods then occupy trophic level 2 and place carnivorous zooplankton at trophic level 3. Conversely, low nutrient conditions lead to a dominance of phytoplankton too small for ingestion by copepods. Therefore, rotatoria (mainly ciliates and heterotrophic nanoflagellates) act as intermediate trophic level placing copepods at trophic level 3 and carnivorous zooplankton at trophic level 4 (Weisse, 1989; Ohlendieck et al., 2000; Sommer et al. 2002a). With these longer food chains, planktivorous fish will occupy trophic level 4 to 5, as corroborated by our study.

Although the ecological prediction of a higher share of diatoms in environments with low TN:Si seem confirmed, the present study suggested a high degree of omnivory and/or redundant trophodynamic roles due to the exploitation of similar food sources. This implies that because of the multifaceted feeding relationships, zooplankton cannot easily be assigned to one discrete trophic level. In fact, both omnivory and functional redundancy may explain why often rapid and short-lived changes in the isotope baseline signatures, attributable to the herbivorous and microbial loop food web, cause signal attenuation toward consecutive trophic levels that is not well-understood (Hoch et al., 1992; Vanderklift and Ponsard, 2003; Caut et al., 2009; Kürten et al., 2013a, b). There are several reasons for reduced discriminatory power of C and N isotopes as source and trophic level indicators in multivorous food webs. Possibly the homogenization of N isotope values by the microbial food web could make it impossible to distinguish between consumers feeding on a combination of auto- and heterotrophic protists and those feeding exclusively on phytoplankton (Hannides et al., 2009; Gutiérrez-Rodríguez et al., 2014). The blending of discrete trophic levels due to quick recycling and competition at the generally resource-poor 'Station ALOHA' in the North Pacific, keeps zooplankton RTPs within a small range (RTPs ~2-3; Hannides et al., 2009), as similarly observed in the Red Sea (**Tab. 2**).

A further complication relates to the preferential utilization of dissolved nutrients by phytoplankton in resource-poor environments with a large share of picophytoplankton. *Synechococcus*, for instance, almost completely relied on NH_4^+ uptake and its continuous regeneration through grazing and decomposition of organic matter during spring in the Gulf of Aqaba (Lindell and Post, 1995; Lindell et al., 2005). Isotopically, it is plausible that rapid recycling through the microbial loop food web (Azam and Ammermann, 1984) and excretion of lighter ^{14}N by zooplankton and concomitant depositional losses, maintains the residual organic matter in the NRS fractionated toward ^{15}N depletion (Checkley and Miller, 1989). It may be that higher conservation of N occurs in trophic transfers of the microbial loop, leading to less overall isotopic N isotope fractionation when compared to a frequently applied trophic enrichment factor (FATE; c.f. Fry and Quiñones, 1994). Rapid remineralization processes of the microbial loop, therefore, could be responsible for leveling the $\delta^{15}\text{N}$ values in the NRS. If the recycling within the microbial loop (*sensu* Landry and Kirchman, 2002) is rapid, then N isotopes may not reveal pronounced trophic fractionation (*sensu* Sommer et al., 2002a) with autotrophs, heterotrophic nanoflagellates and microzooplankton as consecutive trophic levels. Our findings imply that this could be the predominant case in resource-poor environments such as the Red Sea, where growth, grazing, and remineralization processes are rapid and tightly coupled.

5. Conclusions

Our study provides evidence from the Red Sea that spatial isotopic baseline variations propagate through pelagic food webs toward higher trophic levels and lay the foundation of isoscapes (Wada and Hattori, 1976; Jennings and Warr, 2003; Bowen, 2010; Kürten et al., 2013a, b; Hauss et al., 2013; McMahon et al., 2013a, b). Unlike coral reef zooplankton and other biota such as fish follow a generic N to S gradient (Kürten et al., 2014a), pelagic zooplankton isotopes are linked tighter to regional ecohydrographic features. Following the latitudinal pattern of primary productivity and potential influence of aerosols and diazotrophs in the northern Red Sea (Aberle et al., 2010; Wankel et al., 2010), we show that the importance of atmospheric and diazotroph N end-members, as indicated by low $\delta^{15}\text{N}$, gradually decreases towards the South, where the inflow of Indian

Ocean water contributes N sources with higher $\delta^{15}\text{N}$ (Raitsos et al., 2015; Bange et al., 2000). Considering the ecohydrographic framework of the Red Sea and its environmental and stoichiometric controls (summarized in **Fig. 10**), we suggest that the latitudinal gradient overlaid on the thermohaline circulation of the Red Sea translates into an overall isoscape of the Red Sea with higher and lower $\delta^{15}\text{N}$ values in the South and North, respectively. The latitudinal gradient, however, is not as static and uniform as suggested in earlier studies owing to spatial and temporal variability that mesoscale features such as eddies generate. Doubtless, eddies appear to play a significant role in the dynamics, cross-basin exchange, and the productivity of the Red Sea. The observed *in situ* velocity pattern, however, advocate to reconsider the generalized notion of only two anticyclonic eddies that are situated quasi-permanent in the North Central and South Central Red Sea (see Raitsos et al., 2013). Providing ample evidence from oceanographic, water chemistry, plankton taxonomy, and the stable isotope ecology perspective, the interdisciplinarity of this study has demonstrated the significance of diazotrophic and atmospheric sources and the inflow of nutrient- and plankton-rich water from the Gulf of Aden. Together, these processes constitute biogeochemical end-members in the Red Sea, but eddy-induced upwelling of deep water nutrients, where and whenever it occurs, supplies nutrients to the surface.

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Figure captions

- Figure 1 Map illustrating sampling sites and Acoustic Doppler Current Profiler (ADCP) data (current velocity and direction) in the surface mixed layer (surface to 18 m bin) following the cruise track.
- Figure 2 Hydrographic sections of the Red Sea from 08-20 of April 2012 following the central axis of the Red Sea. Plots show a) temperature, b) salinity, c) nitrate [NO_3^-], and chlorophyll *a* across the Red Sea.
- Figure 3 Latitudinal variations of biological-oceanographic parameters at the deep chlorophyll maximum (DCM). Data from a) CTD casts [temperature, salinity], and HPLC-derived chlorophyll *a* concentrations, b) stoichiometric ratios of total nitrogen (TN), total phosphorous (TP), and dissolved silicate (Si) concentrations (TN:TP, TN:Si, TP:Si), and c) concentrations of particulate organic carbon (POC) and nitrogen (PON), and POC:PON ratios (see Tab. 1 for depth details).
- Figure 4 Relationships with and among environmental variables and zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data with highest fit to shown Redundancy Analysis (RDA) ordination axes (vectors; blue = variables selected in forward selection procedure; black = additionally selected collinear variables).
- Figure 5 Net-phytoplankton compositions in the Red Sea. Contribution of major phytoplankton groups (diatoms, dinoflagellates, and cyanobacteria [*Trichodesmium erythraeum*]) to net-phytoplankton abundance (cells L^{-1}) as determined by light-microscopic enumeration (Others = unidentified phytoplankton).
- Figure 6 Bi-plots of zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the Red Sea. Isotopic composition of a) zooplankton at the seven sampling sites, b) zooplankton aggregated to trophic guilds, c) taxonomic grouping, and d) of crustacean zooplankton. The superimposed dashed circles (panel a) represent associations to clusters as indicated by 2-step cluster analysis. The symbol color of each crustacean taxon shown in panel d) corresponds to the respective group-associations shown in panel b).
- Figure 7 Mean ($\pm\text{SE}$) a) $\delta^{15}\text{N}$ and b) $\delta^{13}\text{C}$ values of zooplankton, particulate organic matter (POM), *Thalia democratica* (Tunicata), and *Macrosetella gracilis* (Harpacticoida).

- Figure 8 Natural abundance $\delta^{15}\text{N}$ values (mean $\pm$ SD) in Red Sea zooplankton at latitudinal scale.
- Figure 9 Tentative allocation of isotopic food sources to the diet of zooplankton at the whole assemblage level. Estimated isotopic contributions (%) of the three prospective macronutrient sources, phytoplankton, *Trichodesmium* sp., and particulate organic matter (POM), as determined by the Bayesian mixing model SIAR (mode $\pm$ SD).
- Figure 10 Conceptual model of the ecohydrography of the Red Sea.

Table 1 Characteristics of environmental variables and particulate organic matter (POM) collected in April 2012 at the sampling sites in the Red Sea. The sampling depths corresponded to the deep chlorophyll maximum (DCM) depth as indicated by *in situ* fluorescence measurements (Chelsea Aquatracka MKIII fluorometer).

Parameter	Site													
	Duba		Mabahiss		Nereus		Atlantis II		Suakin		Red Sea Rift		Farasan	
	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD
Sampling depth [m]	25		65		65		68		80		65		40	
Temperature [°C]	22.9		22.2		23.7		24.8		23.7		26.1		25.4	
Salinity [PSU]	40.4		40.4		40.0		39.2		40.0		38.9		37.7	
Chlorophyll <i>a</i> [ng L ⁻¹]	947	37	631	47	444	26	475	63	307	13	441	26	580	28
TN [μmol L ⁻¹]	18.9	0.4	18.8	0.1	19.7	1.9	20.8	0.3	21.0	1.2	20.5	1.2	8.9	1.1
TP [μmol L ⁻¹]	1.0	0.1	1.0	0.1	1.2	0.1	1.3	0.1	1.3	0.1	1.2	0.1	0.7	0.1
Si [μmol L ⁻¹]	0.9	0.1	1.2	0.1	1.0	0.1	0.7	0.1	1.2	0.1	1.7	0.1	1.6	0.1
TN:TP	18.9		18.8		16.4		16.0		16.2		17.1		12.7	
TN:Si	21.0		15.7		19.7		29.7		17.5		12.1		5.6	
TP:Si	1.1		0.8		1.2		1.9		1.1		0.7		0.4	
POC [μg L ⁻¹]	121.8	3.1	88.2	2.1	46.7	3.5	66.8	3.4	37.7	3.2	44.0	2.2	64.7	9.6
PON [μg L ⁻¹]	14.5	1.1	12.2	0.6	6.3	0.5	8.4	0.4	5.3	0.7	6.4	0.2	7.7	0.0
POC:PON	8.4		7.2		7.4		8.0		7.2		6.8		8.4	
δ ¹³ C _{POM} [‰]	-22.6	0.4	-22.9	0.1	-24.0	0.3	-22.9	0.1	-24.4	0.5	-24.7	0.1	-24.0	0.3
δ ¹⁵ N _{POM} [‰]	2.8	0.3	3.4	0.2	1.4	0.3	5.1	0.2	5.2	0.2	4.8	0.5	6.3	0.8

Table 2 Mass (mg Ind.⁻¹), elemental composition (C:N), results from carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope analysis (SIA), and relative trophic position (RTP, weighted by mean site-wide food contributions as indicated by SIAR), of zooplankton aggregated to trophic guilds (N = Number of SIA; Ind. = total number of analyzed specimens; SE = standard error, SD = standard deviation; Min. = lowest value, Max. = highest value).

Trophic guild	Taxon	N	Ind.	Mass [mg Ind. ⁻¹]	C:N	$\delta^{13}\text{C}$ [‰]				$\delta^{15}\text{N}$ [‰]				RTP				Reference(s)
				Mean	Mean	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.	Mean	SD	Min.	Max.	
Carnivore	Amphipoda	45	153	0.466	4.7	-18.5	0.2	-21.1	-16.3	5.3	0.3	3.1	9.6	2.7	0.5	2.0	3.7	1
	<i>Candacia</i>	13	123	0.078	3.9	-21.4	0.1	-22.1	-20.8	5.5	0.4	3.4	8.3	2.6	0.3	2.1	3.1	30, 20
	<i>Corycaeus</i>	20	1819	0.005	5.1	-20.9	0.1	-21.6	-20.3	5.0	0.4	2.7	9.3	2.4	0.4	2.1	3.5	30, 14
	<i>Eucalanus</i>	14	160	0.092	4.3	-20.6	0.1	-21.9	-20.2	6.6	0.3	4.3	8.2	2.9	0.3	2.3	3.6	13
	<i>Euchaeta</i>	13	132	0.115	4.1	-20.9	0.2	-21.4	-19.7	6.7	0.5	4.8	10.5	3.2	0.5	2.7	4.5	4, 11
	Megalopa	7	16	0.963	5.2	-19.7	0.3	-20.6	-18.2	4.6	0.6	3.1	7.7	2.5	0.2	2.2	2.8	15
	<i>Nannocalanus</i>	9	44	0.045	4.3	-20.6	0.2	-21.2	-19.9	5.8	0.6	3.1	8.5	2.6	0.4	2.0	3.2	16
	<i>Pleuromamma</i>	20	552	0.065	3.8	-20.9	0.1	-21.4	-19.8	5.6	0.4	3.3	8.5	2.8	0.3	2.1	3.2	11
	<i>Pontellina</i>	4	16	0.079	4.7	-20.5	0.2	-21.1	-20.2	3.9	0.2	3.5	4.2	2.7	0.2	2.5	2.8	21
Detritivore	Cypridina	14	272	0.062	4.7	-20.8	0.1	-21.9	-20.0	5.4	0.4	3.9	7.8	2.7	0.4	2.1	3.4	2
	<i>Macandrewella</i>	16	111	0.248	3.8	-19.9	0.1	-20.5	-19.4	7.3	0.5	4.9	10.2	3.5	0.4	2.7	4.0	22
Herbivore	Euphausiacea	13	49	0.632	3.8	-20.2	0.2	-21.3	-18.8	6.1	0.5	3.8	8.8	2.9	0.4	2.3	3.6	30, 25
	<i>Macrosetella</i>	11	1066	0.004	6.9	-20.1	0.2	-21.2	-19.1	2.7	0.2	2.0	4.4	1.8	0.4	0.8	2.0	19, 3
	<i>Rhincalanus</i>	8	63	0.147	8.1	-20.8	0.4	-22.5	-19.6	4.7	0.9	2.0	9.6	2.6	0.7	1.9	4.1	17, 27, 24
Mi-crophagous	Pteropoda	33	285	0.797	5.8	-15.3	0.5	-22.1	-10.0	4.4	0.3	1.6	7.8	2.3	0.5	1.4	3.5	9, 8
	Thaliacea	21	37	1.662	4.7	-21.8	0.1	-22.4	-20.9	4.1	0.3	0.8	5.7	2.0	0.3	1.4	2.7	18, 32
Omnivore	Conchoecia	16	578	0.037	4.9	-19.6	0.2	-20.6	-18.2	6.0	0.4	3.7	8.6	2.9	0.4	2.2	3.6	30
	<i>Copilia</i>	11	298	0.034	4.4	-21.3	0.1	-21.9	-20.6	4.6	0.4	2.7	6.5	2.3	0.3	1.9	2.7	1
	Penaeidae	18	29	0.519	3.9	-19.0	0.2	-19.8	-17.7	5.4	0.3	4.1	8.8	2.2	0.3	1.8	2.7	34
	Oncaeidae	17	1678	0.007	4.7	-21.8	0.1	-22.4	-21.1	4.7	0.4	2.5	7.3	3.0	0.3	2.6	3.8	23, 33
	Zoea	60	426	0.286	4.0	-19.9	0.2	-21.8	-17.1	6.2	0.3	3.1	9.6	3.0	0.5	1.9	3.7	16, 15
Plankton predator	<i>Atlanta</i>	6	18	1.078	6.1	-13.8	0.5	-15.0	-11.7	5.0	0.6	3.0	7.2	2.4	0.3	2.0	2.7	29
	Chaetognatha	31	514	0.335	3.7	-19.9	0.1	-22.0	-18.4	6.8	0.3	3.8	10.3	3.2	0.4	2.7	4.1	7, 12
	Fish larvae	43	125	0.558	3.7	-20.0	0.1	-21.3	-19.0	7.0	0.3	4.1	9.5	3.3	0.4	2.6	4.4	34
	Siphonophora	34	467	0.657	3.6	-20.0	0.2	-21.6	-16.8	5.9	0.3	1.7	9.4	2.9	0.4	1.4	4.0	1
	Tomopteridae	14	160	0.245	4.2	-20.9	0.2	-22.0	-19.6	7.3	0.5	3.9	10.0	3.2	0.4	2.5	3.8	6, 5
Suspension feeder	Bivalvia	7	727	0.024	6.5	-12.9	0.6	-14.4	-10.1	5.8	0.4	3.7	6.3	2.3	0.4	1.6	2.8	28
	<i>Oithona</i>	16	555	0.003	4.3	-22.1	0.2	-24.0	-20.9	5.9	0.5	3.0	9.6	2.8	0.7	1.9	4.4	23, 10
	<i>Sapphirina</i>	14	354	0.023	3.5	-22.2	0.2	-23.0	-20.6	5.8	0.4	3.0	8.1	2.7	0.5	2.0	4.3	34
	<i>Undinula</i>	9	56	0.136	3.8	-20.4	0.1	-21.0	-19.6	7.2	0.4	5.6	8.5	2.8	0.3	2.5	3.2	30, 31

References: 1) Aberle et al., 2010; 2) Cannon, 1934; 3) Eberl and Carpenter, 2007; 4) El-Sabaawi et al., 2009; 5) Fanelli et al., 2011; 6) Fauchald and Jumars, 1979; 7) Feigenbaum and Maris, 1984; 8) Gerber and Gerber, 1979; 9) Gilmer, 1972; 10) González and Smetacek, 1994; 11) Hannides et al., 2009; 12) Kehayias et al., 1996; 13) Kleppel et al., 1996; 14) Landry et al., 1985; 15) Le Vay et al., 2001; 16) Lebour, 1922; 17) Longhurst, 1967; 18) Mullin, 1983; 19) O'Neil and Roman, 1994; 20) Ohtsuka and Onbé, 1989; 21) Ohtsuka and Onbé, 1991; 22) Ohtsuka et al., 2002; 23) Paffenhöfer, 1993; 24) Schnack-Schiel et al., 2008; 25) Schnetzer and Steinberg, 2002; 26) Schukat et al., 2014; 27) Sommer et al., 2002; 28) Strathmann et al., 1972; 29) Thiriot-Quiévreux, 1973; 30) Timonin, 1971; 31) Turner, 1986; 32) Vargas and Madin, 2004; 33) Wu et al., 2004; 34) This study.

Table 3 Details of the redundancy analysis forward selection regression procedure (RDA 1 = 42.5%, RDA 2 = 19.1%, df = 6).

Explanatory variable	Contribution [%]	pseudo- <i>F</i>	<i>P</i>
Temperature	36.8	7	0.001
PON [$\mu\text{g L}^{-1}$]	16.1	3.8	0.002
PO ₄ [$\mu\text{mol L}^{-1}$]	14.8	4.6	0.003
NO _x [$\mu\text{mol L}^{-1}$]	10.8	4.5	0.005
Si [$\mu\text{mol L}^{-1}$]	11.4	9	0.003
TN:Si	10.1	2	0.001

Table 4 Results for pair-wise comparisons of sites using Mann-Whitney U test for $\delta^{13}\text{C}$ (upper diagonal; Kruskal-Wallis: df = 6, Chi-Square = 83.115), and $\delta^{15}\text{N}$ (lower diagonal; Kruskal-Wallis: df = 6, Chi-Square = 253.913), and attribution to the regional clusters indicated by TwoStep cluster analysis (see also **Fig. 4a** showing the superimposed clusters; n.s. = not significant at $P < 0.05$).

Site	Duba	Mabahiss	Nereus	Atlantis II	Suakin	Red Sea Rift	Farasan
TwoStep cluster	I	I	II	II	III	III	IV
Duba	1	0.248 (n.s.)	<0.001	<0.001	<0.001	<0.001	0.006
Mabahiss	0.498 (n.s.)	1	<0.001	<0.001	<0.001	0.002	<0.001
Nereus	0.434 (n.s.)	0.181	1	0.074 (n.s.)	0.321 (n.s.)	0.014	<0.001
Atlantis II	<0.001	<0.001	<0.001	1	0.431 (n.s.)	0.33 (n.s.)	0.009
Suakin	<0.001	<0.001	<0.001	0.321 (n.s.)	1	0.096 (n.s.)	0.001
Red Sea Rift	<0.001	<0.001	<0.001	0.003	0.052 (n.s.)	1	0.112
Farasan	<0.001	0.114	<0.001	<0.001	<0.001	<0.001	1

Table 5 Results for pair-wise comparisons of trophic guilds using Mann-Whitney U test for $\delta^{13}\text{C}$ (upper diagonal; Kruskal-Wallis: df = 6, Chi-Square = 83.115), and $\delta^{15}\text{N}$ (lower diagonal; Kruskal-Wallis: df = 6, Chi-Square = 253.913; n.s. = not significant at $P < 0.05$).

Trophic guild	Carnivore	Detritivore	Herbivore	Microphagous	Omnivore	Plankton predator	Suspension feeder
Carnivore	1	0.75 (n.s.)	0.819 (n.s.)	0.146 (n.s.)	0.098 (n.s.)	0.005	<0.001
Detritivore	0.028	1	0.833 (n.s.)	0.444 (n.s.)	0.384 (n.s.)	0.051 (n.s.)	<0.001
Herbivore	0.004	0.001	1	0.264 (n.s.)	0.429 (n.s.)	0.097 (n.s.)	0.001
Microphagous	<0.001	<0.001	0.872 (n.s.)	1	0.052 (n.s.)	0.609 (n.s.)	<0.001
Omnivore	0.494 (n.s.)	0.126 (n.s.)	0.002	<0.001	1	0.001	0.001
Plankton predator	<0.001	0.629 (n.s.)	<0.001	<0.001	0.001	1	<0.001
Suspension feeder	0.039	0.573 (n.s.)	0.002	<0.001	0.22 (n.s.)	0.138 (n.s.)	1

Figure 1

Figure 2

Figure 3

Figure 4

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Figure 5

Figure 6

Figure 8

Figure 9

Figure 10

Highlights

- Spatial isotopic baseline variations propagate through pelagic food webs toward higher trophic levels and lay the foundation of the Red Sea isoscape
- The latitudinal gradient overlaid on the thermohaline circulation of the Red Sea translates into an overall isoscape of the Red Sea with higher and lower zooplankton $\delta^{15}\text{N}$ values in the South and North, respectively
- Eddy-induced upwelling of deep water nutrients – where and whenever it occurs – supplies nutrients to the surface and thereby modifies C and N fluxes in the Red Sea