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ABSTRACT

Coral reef and atoll lagoons are among the most diversified marine ecosystems but also the most affected by the combined effects of climate change and human activities. The Iles Eparses (Scattered Islands) in the Western Indian Ocean have been little affected by human pressure and can be considered to be "pristine" ecosystems. Metazooplankton plays a major role in the functioning and productivity of aquatic ecosystems, and this study was undertaken: (i) to determine the spatial abundance, distribution and species composition of metazooplankton, (ii) to assess the effect of metazooplankton grazing on pico- and nanophytoplankton and (iii) to analyze the trophic positions of metazooplankton by using the stable isotope signatures of a wide variety of taxa and particulate organic matter from the Iles Eparses and Mayotte. Tromelin Island (which is not located in the Mozambique Channel) had the lowest metazooplankton abundance with no cyanobacteria *Trichodesmium* spp. or mollusks (pteropods) presence, and with $\delta^{15}N$ signatures of organisms that were higher than for the islands in the Mozambique Channel. *Trichodesmium* spp. was found in the Mozambique Channel and the plankton food web was probably based preferentially on these cyanobacteria with lower $\delta^{15}N$ signatures indicating direct or indirect trophic transfer of diazotrophic nitrogen to metazooplankton. Three of the islands were distinct: Europa had the highest proportion of copepods, with oithonids being dominant, which is typical of rich mangrove systems, while Juan de Nova and Mayotte seemed to be the sites most affected by human activity with a high abundance of appendicularians and distinct particulate organic matter $\partial^{13}C$ signatures. Grazing experiments showed that food could be a limiting factor for metazooplankton in the Iles Eparses. However, the effect of metazooplankton grazing on phytoplankton appeared to be very low (0.01–2.32% of the total phytoplankton per day).

1. Introduction

Metazooplankton (defined as metazoan planktonic organisms) plays a major role in the functioning and productivity of aquatic ecosystems through its effect on nutrient dynamics and its key position in food webs (Harris et al., 2000). Most of these organisms exert a strong grazing effect on phytoplankton and protozooplankton (Pont, 1995; Calbet et al., 2008). They are also considered to be prey for small pelagic fishes, shrimps and mysids (Viitasalo and Rautio, 1998; Pollack et al., 2008; Spinelli et al., 2012). Several studies have suggested that climate-mediated changes in metazooplankton abundance and composition may affect upper trophic levels and fisheries (Beaugrand, 2003). Metazooplankton can also be used as biological indicators for pollution, water quality and eutrophication (Attayde and Bozelli, 1998; Webber et al., 2005).

For a long time, copepods (which constitute the bulk of metazooplankton in the oceans; Kiørboe, 1998) were thought to be strictly herbivorous, consuming 10%–30% of primary production, particularly diatoms. Poulet (1983) suggested that copepods could potentially obtain food from any known stock of organic matter, in either dissolved or particulate form. The food web is, therefore,

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more complex than just diatoms to copepods to pelagic fishes, with the microbial food web having intermediate trophic levels (microzooplankton, nanoplankton) (Rassoulzadegan et al., 1988). A large number of laboratory studies have been undertaken into the ingestion and egg production rates of copepods feeding mainly on monospecific or mixed phytoplankton diets (Paffenhöfer et al., 1982; Kiørboe et al., 1985; Caparroy et al., 1998). Since the establishment of the trophic link between the microbial community and copepods (Stoecker and Sanders, 1985; Gifford and Dagg, 1988), many studies have confirmed copepod predation on microzooplankton (e.g. Stoecker and Egloff, 1987; Vargas and Gonzáles, 2004). In particular, the importance of ciliates as food for copepods is now well understood (Stoecker and Egloff, 1987; Tiselius, 1989). Copepods are able to discriminate between different foods on the basis of particle size and food quality (Irigoien et al., 2000).

The diet of metazooplankton has been studied in the laboratory using grazing experiments (Mauchline, 1998), in cinematographic studies (Paffenhöfer et al., 1982) and, in the field, through microscopic examination of fecal pellets (Turner, 1984). Food web studies have also been based on carbon and nitrogen isotopic ratios. For carbon, there appears to be, on average, a slight enrichment of ^{13}C in a consumer relative to its diet (0.5‰–1‰), and, for nitrogen, a more significant enrichment of ^{15}N (3‰–4‰; Michener and Kaufman, 2007). The lower isotopic fractionation for carbon can be useful in tracing two food sources with distinctly different $\partial^{13}C$ values, whereas nitrogen isotope ratios are usually used as trophic position indicators (Peterson and Fry, 1987). Stable isotope analysis is a powerful, complementary approach to traditional feeding studies and has proved invaluable for understanding the food web structure and energy flow in aquatic ecosystems.

Coral reef and atoll lagoons are among the most diversified marine ecosystems although they are the most affected by the combined effects of climate change and human activities. The Iles Eparses (Scattered Islands) located in the Western Indian Ocean (WIO) around Madagascar have been little affected by human action and can be considered to be “pristine” ecosystems (Bouvy et al., 2016). In these islands, which form the 5th district of the French Southern and Antarctic Lands (TAAF), the coral reef lagoons may, therefore, be considered as baseline sites for the general evaluation of the impact of anthropogenic forcing. In coral reef and atoll lagoon environments, metazooplankton are part of the benthic and pelagic food webs and play a fundamental role in sustaining biodiversity and productivity in these fragile ecosystems (Bozec et al., 2004; Alldredge and King, 2009). However, few studies have considered the metazooplankton community structure and trophic relationships in atoll lagoons (Gerber, 1981; Pagano et al., 2012) and there is no data on the lagoons of the Iles Eparses.

As part of the international program “Eparses 2011–2013”, a survey was carried out in April 2011 on board the R/V Marion Dufresne II, the TAAF supply vessel, to collect data from lagoon and ocean stations in each of the five Iles Eparses, with an additional station in Mayotte lagoon. This was the first time that microbial communities and their interactions with their environmental conditions had been studied at different types of site (lagoon and ocean) for each of the five Iles Eparses (Bouvy et al., 2016).

This study sets out (i) to determine the spatial abundance, distribution and species composition of metazooplankton, (ii) to assess the effect of metazooplankton grazing on pico- and nanophytoplankton through a series of experiments, and (iii) to analyze the trophic positions of metazooplankton by using the stable isotope signatures of a wide variety of taxa and particulate organic matter from the Iles Eparses and Mayotte.

2. Material and methods

2.1. Study site and sampling strategy

The Iles Eparses (Scattered Islands) are small coral reef islands located in the Indian Ocean close to Madagascar (from 22° 21′S to 12° 46′S and 39° 44′E to 54° 31′E, Fig. 1), and became the 5th district of the French Southern and Antarctic Lands (TAAF) in February 2007. Four of these islands lie in the Mozambique Channel, west of Madagascar (from south to north: Europa, Bassas da India, Juan de Nova and Glorieuses) and the fifth (Tromelin island) lies about 450 km east of Madagascar (Fig. 1). Lagoon areas are very variable according to the island, with 193, 165, 87 and 47 km^2 for Juan de Nova, Glorieuses, Bassas da India and Europa, respectively. Due to its geographical location, Mayotte lagoon, which suffers from anthropogenic impacts as the result of a population explosion (Gourbesville and Thomassin, 2000), has also been sampled during the survey. Geographical coordinates of each station were reported in Bouvy et al. (2016).

The survey was based on 16 stations (Table 1) with water and plankton samples taken from April 5 to April 23, 2011 for each island (Fig. 1). One ocean station outside the lagoon and a number of lagoon stations depending on the area of the lagoon were sampled by island except in Tromelin Island (without lagoon) (Table 1). To determine the chemical and microbial parameters, water was sampled at depths of 0.5 m and 10 m (when it is possible; Table 1) using a Niskin bottle. The samples from the two depths were pooled, transferred immediately to acid-washed polyethylene bottles and kept in the dark at *in situ* temperatures until processed in the laboratory on board within 2 h. At each sampling station, a CTD profiler (YSI 600 XM) was deployed to record the temperature, salinity, depth, dissolved oxygen and pH along a vertical profile. These results are presented elsewhere (Bouvy et al., 2016).

Metazooplankton was collected in 2 vertical hauls (bottom to surface) using a 80 μm mesh WP2 net equipped with a Hydrodata flowmeter. At each station, one haul was used for stable isotope analysis and grazing experiments and the second haul was fixed with formaldehyde at 4% final concentration and used for identification and enumeration of the taxa. At the lagoon station of Bassas da India (station BL), where samples were taken directly on the reef barrier at ebb tide (water depth ca 0.5–1 m), a smaller net (0.3 m diameter, 80 μm mesh size) was used, “towed” horizontally at mid depth, using the current.

For grazing experiments of metazooplankton, wild metazooplankton was collected by vertical haul using a 200 μm mesh WP2 net (see paragraph 2.4).

2.2. Autotrophic components

Pico- and nanophytoplankton samples were fixed with formaldehyde (2% final concentration), and counted using a Facs Aria Flow cytometer (Becton Dickinson, San Jose, CA, USA) equipped with an HeNe air-cooled laser (633 nm, 20 mW). Cells excited at 633 nm were detected and enumerated according to their forward-angle light scatter (FALS) and right angle light scatter (RALS) properties and their orange fluorescence (576/26 nm) and red fluorescence (>650 nm) from phycoerythrin and chlorophyll pigments, respectively. Fluorescent beads (1–2 μm for picophytoplankton and 2–6–10–20 μm for nanophytoplankton) were systematically added to each sample. List-mode files were analyzed using BD FACSDiva software. This method discriminates various autotrophic groups such as autotrophic picoeukaryotes, picocyanobacteria (for example, *Prochlorococcus* and *Synechococcus*) and nanophytoplankton using their phycoerythrin content and chlorophyll pigments (Bouvy et al., 2016).

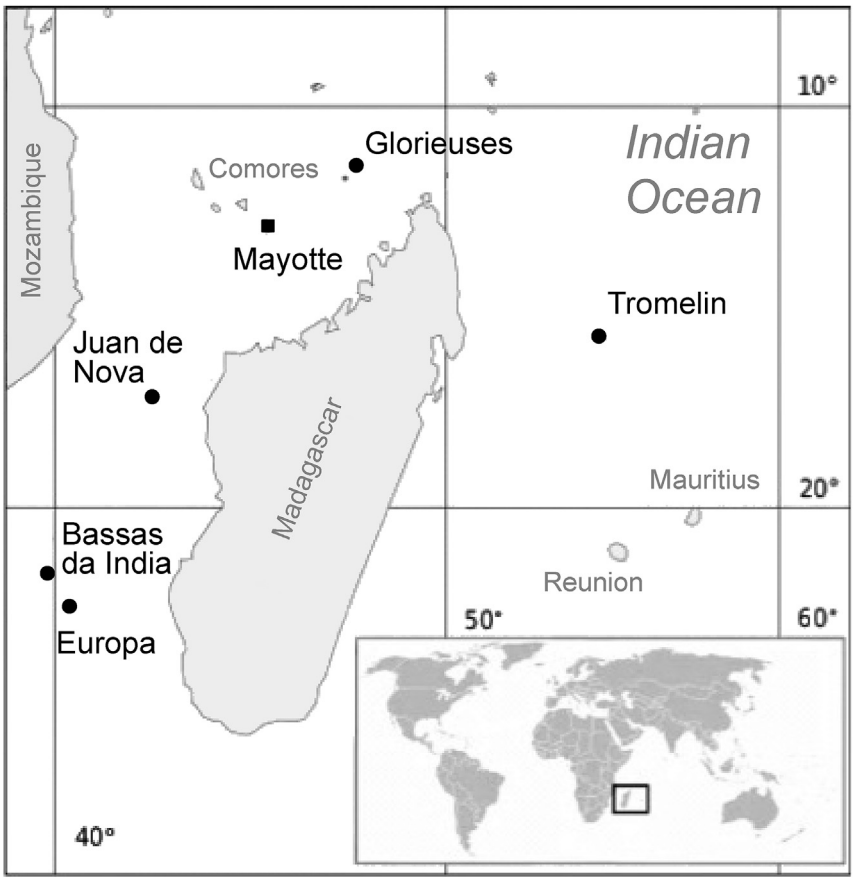

Fig. 1. Location of the Eparses Islands (Europa, Bassas da India, Juan de Nova, Glorieuses and Tromelin; black dots) and Mayotte island (black square) in the West Indian Ocean.

Table 1
List of stations studied in the five Iles Eparses and in Mayotte Island in West Indian Ocean in April 2011. Site code for each station and mean of some biological parameters of the 16 studied sites (lagoon and oceanic stations) are reported from the 0.5 m depth samplings. Maximum depth are reported for the lagoon stations. Picoeuk: picoeukaryotes; Picocya: picocyanobacteria; Nano: nanophytoplankton; Chloro: chlorophyll-a; nd: non determined.

Parameters Units	Code	Max depth m	Picoeuk 10^3 ml^{-1}	Picocya 10^3 ml^{-1}	Nano 10^2 ml^{-1}	Chloro µg l^{-1}
Europa						
Ocean	EO	nd	54.14	40.1	1.32	0.184
lagoon	E1	3	33.40	8.31	4.69	0.529
Lagoon	E2	4	57.59	4.95	4.48	0.522
Lagoon	E3	4	47.39	4.64	2.73	0.684
Bassas da India						
Ocean	BO	nd	47.11	34.6	1.06	0.340
Lagoon	BL	1	32.86	39.3	2.01	0.581
Juan de Nova						
Ocean	JO	nd	0.30	18.1	1.50	0.164
Lagoon	J1	7	33.18	24.4	1.25	0.265
Lagoon	J2	14	93.23	78.5	2.95	0.555
Lagoon	J3	18	87.94	72.5	3.26	0.759
Mayotte						
Lagoon	ML	19	78.27	2 26.9	2.69	0.429
Glorieuses						
Ocean	GO	nd	2.76	20.5	1.35	0.162
Lagoon	G1	8	57.44	54.1	1.84	0.625
Lagoon	G2	10	146.50	112.0	3.68	0.526
Lagoon	G3	13	25.35	8.71	0.55	0.152
Tromelin						
Ocean	TO	nd	1.26	1.92	0.07	0.054

Chlorophyll concentrations were determined by fluorometry after filtration onto Whatman GF/F fiberglass filters and direct extraction using methanol (Yentsch and Menzel, 1963).

The presence or absence of filamentous cyanobacteria (*Trichodesmium* spp.) was determined by observation (inverted microscope; Olympus IX70) of water samples (500 ml fixed with alcalin lugol iodine; 2% final concentration) with a Utermöhl settling chamber (Hydro-Bios combined plate chamber).

All these data are presented in detail in the companion paper (Bouvy et al., 2016). This study, however, focuses on the mean values per station to assess potential autotrophic components available as prey for metazooplankton.

2.3. Metazooplankton identification

The taxa were identified and enumerated using sub-samples taken using wide bore piston pipettes (0.5–5 ml). At least 100 individuals of the main taxa were counted in each sub-sample under a dissecting microscope (Olympus SZX200, magnification ×200 to ×500). The rarest taxa were estimated from the whole sample. Metazooplankton taxa were identified as described by Tregouboff and Rose (1957), Razouls et al. (2005, 2014) and Conway et al. (2003).

2.4. Grazing experiments of metazooplankton

Eight grazing experiments were performed during the survey (5 ocean stations and 3 lagoon stations; EO, BO, JO, GO, TO and E2, J2, ML; see Table 1). We used the >200 µm metazooplankton fraction (>90% of the biomass) to minimize the introduction of non-zooplankton items in the experimental sets. After collection and

sorting, homogeneous sets of total metazooplankton (25–50 individuals according to the sample abundance) were constituted volumetrically using a wide bore piston pipettes 5 ml and quickly checked under a dissecting microscope. Then, organisms were incubated in 500 ml flasks that had been filled with sea water sieved through 60 μm net. For each experiment, three experimental bottles (with metazooplankton) and three controls (without metazooplankton) were prepared. The metazooplankton density in the bottles (50–100 ind l^{-1}) was up to 10 times greater than the *in situ* density, which is within the range of values currently used for metazooplankton grazing experiments (Harris et al., 2000). The bottles were incubated in the dark for about 24 h in a deck incubator with circulating surface seawater. At the end of the experiment, 1.8 ml subsamples were taken from the bottles, fixed with prefiltered (0.2 μm) formaldehyde (2% final concentration) and stored in liquid nitrogen for subsequent analysis of autotrophic groups (picoeukaryotes, picocyanobacteria with the genus *Prochlorococcus* and *Synechococcus* and nanophytoplankton) as described above. Largest potential prey (as diatoms or large dinoflagellates) were not considered due to their very low concentrations in the field (Bouvy et al., 2016), leading to a possible underestimation of total ingestion rates. The following factors were used to convert the abundance into carbon biomass: cyanobacteria: 119 fgCcell^{-1} (mean value for *Prochlorococcus* and *Synechococcus*; Charpy and Blanchot, 1998); picoeukaryotes: 836 fgCcell^{-1} (Verity et al., 1992); nanophytoplankton: 3140 fgCcell^{-1} (Pelegri et al., 1999). The biovolumes of the cells were calculated by comparison with calibrated micro-beads.

At the end of the experiment, the metazooplankton from the bottles was transferred to a formalin solution (4% final concentration) for subsequent enumeration and measurements in order to calculate the metazooplankton abundance and biomass. The individual weight of each taxon was estimated from their size measured under a dissecting microscope (×500 magnification). The carbon weights of the organisms were then estimated using length–weight relationships given in the literature (Nassogne, 1972; Purcell, 1981; Uye, 1982; Chisholm and Roff, 1990; Mauchline, 1998).

The ingestion rates for each phytoplankton category and for total phytoplankton (I, expressed as μm^3 ind^{-1} d^{-1} or as μgC μgC^{-1} d^{-1}) were calculated from the difference in the cell concentration between the control (without zooplankton) and experimental bottles at the end of the experiment, assuming zero or negligible algal growth in the jar as the bottles had been kept in the dark (Pagano, 2008):

$$I = Cc - Ce/(V \times Z \times t);$$

where *Cc* and *Ce* are the cell concentrations (cell ml^{-1}) in the control and experimental bottles respectively, at the end of the incubation period, *V* is the bottle volume (ml), *Z* is the metazooplankton abundance (or carbon biomass) per bottle and *t* is the incubation time (day).

Selectivity coefficients (W_i) were calculated for each type of prey as described by Vanderploeg and Scavia (1979):

$$W_i = (r_i/p_i)/(r_i/p_i)max$$

where r_i is the percentage of the prey i in the food ingested, p_i is the percentage of the same prey in the available food and(ri/pi)max is the maximal (r_i/p_i) value ($0 < W_i < 1$).

The daily metazooplankton community grazing rate (cell ml^{-1} d^{-1}) was estimated by multiplying the ingestion rates by the *in situ* metazooplankton abundance. It was expressed as a percentage of the *in situ* phytoplankton concentration consumed daily by the metazooplankton (%d^{-1}).

2.5. Signature of stable isotopes of major plankton components

At each station, samples were taken at depths of 0.5 m and 10 m using a Niskin bottle, and the water from the two depths at each station was pooled; for lagoons with several sampling stations, the samples from all the stations were also pooled (e.g. for Europa, EL in Fig. 6 represents the pooled samples from E1, E2 and E3 stations). Seawater subsamples (500 ml–7 L depending on the station) were filtered onto a Whatman GF/F (47 mm in diameter). Filters were precombusted at 490 °C for 2 h to eliminate any organic carbon content. Each filter was oven-dried at 50 °C and kept dry in sealed plastic bags until it was returned to La Rochelle University. For each station, four discs (10 mm in diameter) were cut from each filter and packed into individual tin capsules for stable isotope analysis of particulate organic matter (POM). As suggested by Kennedy et al. (2002), POM samples were decarbonated using HCl fumes to get rid of carbonates (as aragonite, dolomite and calcite) in order to obtain $\delta^{13}C$ values of particulate organic carbon (POC). As the decarbonatation process alters $\delta^{15}N$ values we used $\delta^{15}N$ values from non-decarbonated subsamples of POM (Jacob et al., 2005).

For each station, the most abundant species, genera or taxa in the live samples were sorted on board. 20 to 300 individuals (depending on the size of the taxon) belonging to each taxon were fixed in 70% ethanol and sent to La Rochelle University for analysis. The samples were removed from the ethanol and washed carefully with distilled water to remove all the ethanol and/or dead organic matter and phytoplankton. When the organisms had been sorted and washed they were frozen (−80 °C, 48 h), freeze-dried (24 h) and then ground to a fine powder. A pool of individuals of each taxon was then packed into tin capsules for stable isotope analysis. The samples were not treated with acid to remove carbonates because previous studies did not find any significant changes in the relative abundance of ^{13}C and ^{15}N before or after treatment with acid (Bode et al., 2004; Chouvelon et al., 2014).

The natural abundance of carbon and nitrogen stable isotopes in the plankton was determined using a Thermo Scientific Delta V Advantage mass spectrometer coupled to a Thermo Scientific Flash EA1112 elemental analyzer. The results were expressed as isotope ratios δX (‰) relative to international standards (Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen), using the formula:

$$\delta X = \left[\left(R_{sample}/R_{standard}\right) - 1\right] * 10^3$$

where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Peterson and Fry, 1987).

Replicate measurements of internal laboratory standards (acetanilide) indicated a precision of approximately 0.2‰ for both$\delta^{13}C$ and $\delta^{15}N$ values.

The carbon and nitrogen stable isotopes metazooplankton and *Trichodesmium* spp. data were corrected in relation with the mode of sample preservation (70% ethanol) knowing their effect on the isotopic signatures (Chouvelon et al., 2014). This correction was applied according to Chouvelon et al. (2014):

- $\delta^{13}C$ preservation corrected = ($\delta^{13}C$ 70% ethanol preserved, analyzed by mass spectrometry − 8.18)/1.35
- $\delta^{15}N$ preservation corrected (B) = ($\delta^{15}N$ 70% ethanol preserved, analyzed by mass spectrometry − 1.23)/0.92.

The trophic positions (TPs) of each group (or genus or species) of metazooplankton were calculated according to Sommer and Sommer (2004) and Kürten et al. (2013). $\delta^{15}N$ of POM based TP

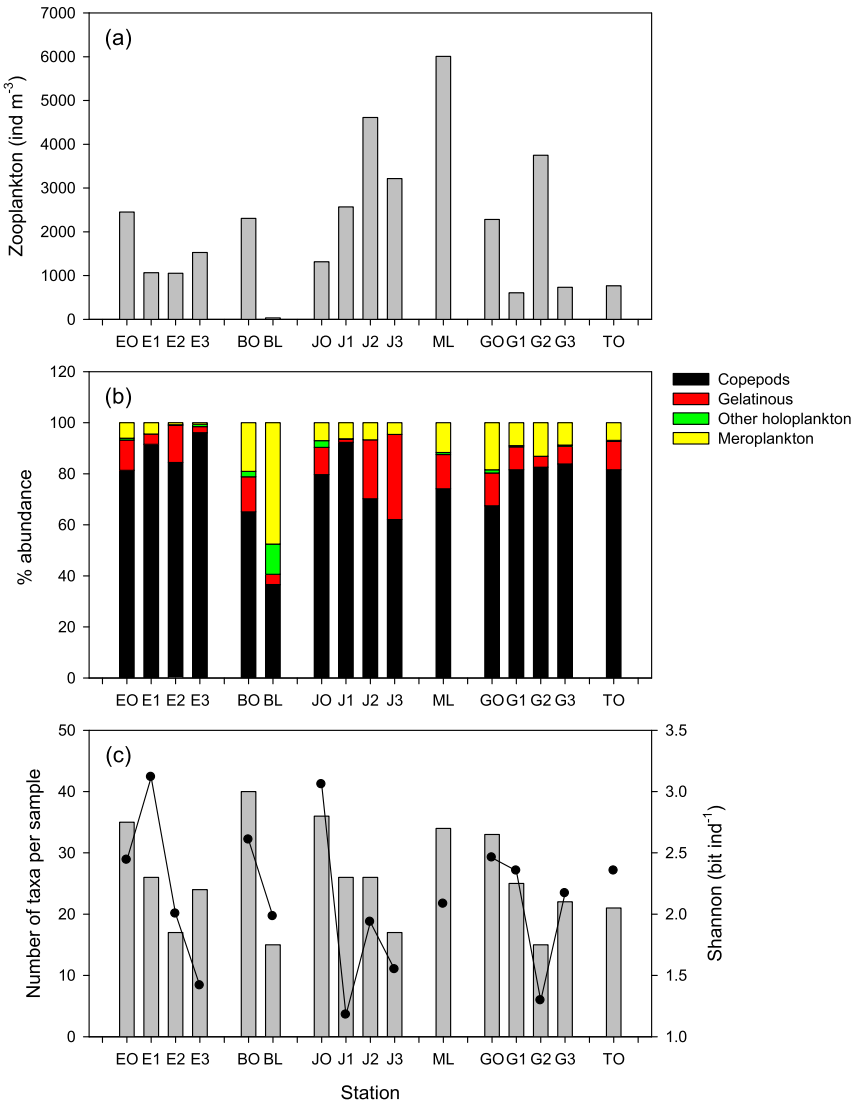

Fig. 2. Abundances (a) and abundance percentage of the main metazooplankton groups (b) and, taxonomic richness (number of taxa per sample) and Shannon diversity index (c) at the different stations (see abbreviations in Table 1).

estimates assumed that TP POM values of 1 represented the isotopic baseline, and that a trophic fractionation factor of 3.4‰ represented one trophic transfer (Minagawa and Wada, 1984):

$$TP = \left(\delta^{15}N \text{ metazooplankton} - \delta^{15}N \text{ POM}\right)/3.4 + 1$$

2.6. Data analysis

The spatial variation of the metazooplankton community composition was determined by Non-metric Multi-Dimensional Scaling (NMDS). A species/station matrix was created for abundance data. The abundance data were log x + 1 transformed before estimating station similarity using the Bray Curtis metric. The similarity matrix was then ordinated by NMDS. A SIMPER (similarity percentage) analysis was performed to determine which species contributed most to the similarity or dissimilarity between stations for the groups of stations identified by NMDS. Non-parametric rank Kruskal–Wallis ANOVA was performed to compare the mean values of environmental and metazooplankton variables between the various clusters. Multiple linear regression was then used to determine which environmental variables were most strongly related to the community composition, with the first two dimensions of the NMDS analysis being the independent variables and the environmental variables being considered the dependent variables (Hosie and Cochran, 1994). The environmental variables used were longitude, latitude, depth, salinity, temperature (data in Bouvy et al., 2016), pico- and nanophytoplankton, chlorophyll-*a*, and carbon isotope signature ($\partial^{13}C$) of the particulate organic matter (POM).

The spatial variation of the metazooplankton trophic positions was determined by hierarchical cluster analysis (HCA) using the Euclidean distance and complete linkage sorting.

3. Results

3.1. Potential autotrophic prey for metazooplankton

In a previous study, Bouvy et al. (2016) described the environmental conditions in terms of chemical and biological variables for all the ocean and lagoon stations sampled during the survey in

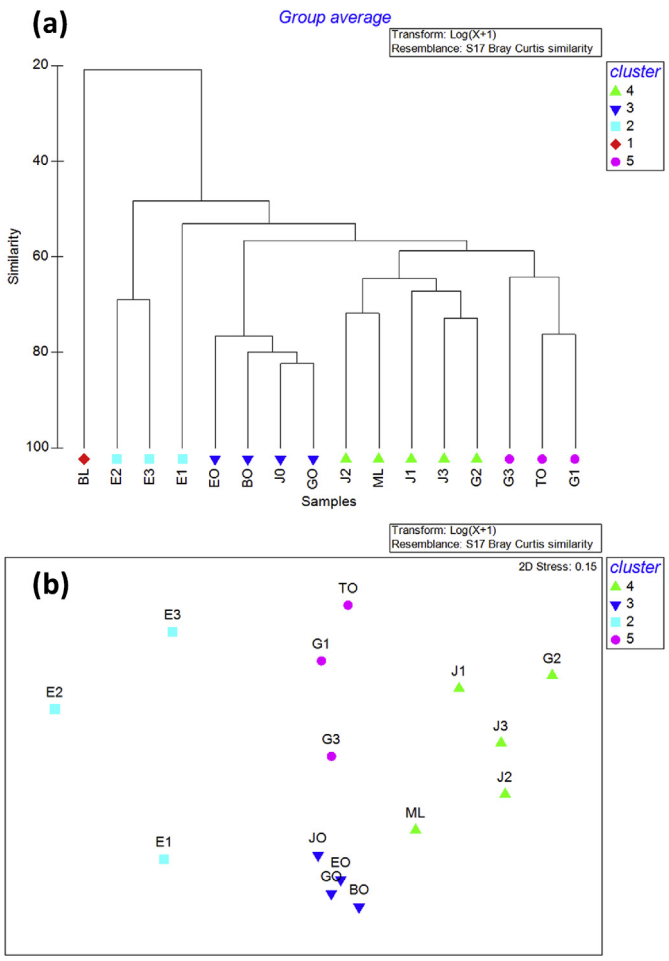

Fig. 3. Estimation of station similarity using the Bray Curtis metric based on the metazooplankton taxa abundance (square root transformed data): clusters spatial distribution and ordination (a) and Non-metric Multi-Dimensional Scaling (NMDS) (b). Station BL was considered as an outlier in the NDMS ordination.

April 2011. The mean values of environmental and trophic variables are shown in Table 1. The phytoplankton groups with the highest abundance were the picoeukaryotes (picoeuk) and the picocyanobacteria (picocya) mainly *Synechococcus* and *Prochlorococcus*. Picoeukaryotes and picocyanobacteria abundances were similar in the ocean and lagoon sites (mean of 21 × 10^3 ml^{-1} and 23 × 10^3 ml^{-1}, respectively) whereas picoeukaryotes abundances were significantly higher in the lagoon sites, especially in the Europa lagoon (t-test; $p < 0.05$). There were very few nanophytoplankton cells (Nano) especially in the ocean sites (mean of 1.06 × 10^2 ml^{-1}). The mean chlorophyll-*a* concentrations, considered here as a proxy of total phytoplankton biomass, were generally low and statistically different (t-test; $p < 0.05$) between the ocean and lagoon stations (0.181 μg l^{-1} in ocean and 0.507 μg l^{-1} in lagoon sites).

3.2. Metazooplankton abundance and species compositions

Sixty taxa were enumerated during the survey (Table 2). They included 35 copepods (including undetermined nauplii and harpacticoids), 5 gelatinous taxa, 6 undetermined holoplanktonic groups and 11 meroplankton taxa. The number of taxa per sample varied from 15 to 40, and the value was higher in the ocean station than in the adjacent lagoon stations for a given island.

Metazooplankton abundance varied from 33 to 6000 ind m^{-3}, with the highest value for Mayotte (station ML) and the lowest for the reef barrier of Bassas da India (station BL) (Fig. 2a). Copepods were dominant, accounting for more than 70% of total metazooplankton abundance, except at station BL (37%) where meroplankton was dominant (48%) (Fig. 2b).

NDMS ordination of the metazooplankton taxa abundance data (stress value of 0.13 indicating a strong ordination) discriminated five clusters (Fig. 3): cluster 1 comprised only station BL, cluster 2 comprised the lagoon stations at Europa (stations E1, E2 and E3), cluster 3 comprised four ocean stations in the Mozambique channel (stations EO, BO, JO and GO), cluster 4 comprised lagoon stations, in particular those at Juan de Nova (stations J1, J2, J3, ML and G2) and cluster 5 comprised stations TO, G1 and G3. Overall, similarity between stations within a cluster was high (>56%). Dissimilarity between clusters 2, 3, 4 and 5 ranged between 45 and 55% while dissimilarity between cluster 1 and the other clusters was always greater than 71%.

Cluster 1 was clearly distinct from the other four clusters. It was characterized by very low abundance of metazooplankton (33 ind m^{-3} *vs* > 700 ind m^{-3} in clusters 2, 3, 4, 5), by low taxa richness (15 taxa per sample *vs* > 22 in clusters 2, 3, 4, 5) and by the dominance of meroplankton (48% of abundance *vs* < 14% in clusters 2, 3, 4, 5). Copepod abundance in cluster 1 was only 37% (*vs* > 75% in clusters 2, 3, 4, 5) (Figs. 2b, c, and 3).In clusters 2, 4 and 5, *Oithona* spp. was the taxa contributing the most to the similarity between stations within each cluster (>12%) but the other major contributors depended on the cluster: *Macrosetella* spp. (11%) and *Oncaea* spp. (11%) for cluster 2, Appendicularian (10%) and Trochophore larva (9%) for cluster 4, (14%), *Corycaeus* spp. (9%) and *Macrosetella* spp. (9%), for cluster 5. In cluster 3, which included all the ocean stations located in the Mozambique Channel (EO, GO, JO and BO), *Paracalanus* spp. (6%), *Oithona* spp. (6%) and *Corycaeus* spp. (5.5%) were the taxa contributing the most to the similarity between stations. Interestingly, this "ocean" cluster (cluster 3) had the highest mean values for taxonomic richness (36 taxa per sample *vs* 15 for cluster 1 and between 22 and 24 for clusters 2, 4 and 5; no significant difference, Kruskal–Wallis ANOVA, $p > 0.1$). Furthermore, the mean Shannon diversity index (2.65 bit ind^{-1}) for cluster 3 was significantly higher ($p < 0.001$) than in the other clusters (<2.20 bit ind^{-1}) (Fig. 2c).

Multiple regression analysis showed that the carbon isotope signature ($\partial^{13}C$) of the particulate organic matter (POM) ($r^2 = 0.57$, $p = 0.006$), the biomass of nanophytoplankton ($r^2 = 0.53$, $p = 0.010$), the biomass of picoeukaryotes ($r^2 = 0.501$, $p = 0.015$) and the temperature ($r^2 = 0.49$, $p = 0.020$) were the main variables strongly correlated with the taxa abundance distribution (represented by the first two dimensions of the NMDS) (data not shown).

3.3. Metazooplankton grazing

The metazooplankton taxonomic composition in the grazing flask was strongly dominated by copepods (>79% abundance) except at JL where gelatinous organisms (60%) were dominant, and, to a lesser extent at GO, where meroplankton (19%) was also very dominant (Table 2).

The prey composition varied from station to station (Fig. 4a) with picophytoplankton being the dominant fraction in terms of biovolume, except for the Europa lagoon stations (EL = pooled E1, E2 and E3) where nanophytoplankton was dominant. For station GO, picocyanobacteria dominated. In most cases, nanophytoplankton was the preferred prey for metazooplankton (stations BO, J2, JO, TO and ML) while picocyanobacteria (*Prochlorococcus* and *Synechococcus*) were the preferred prey for

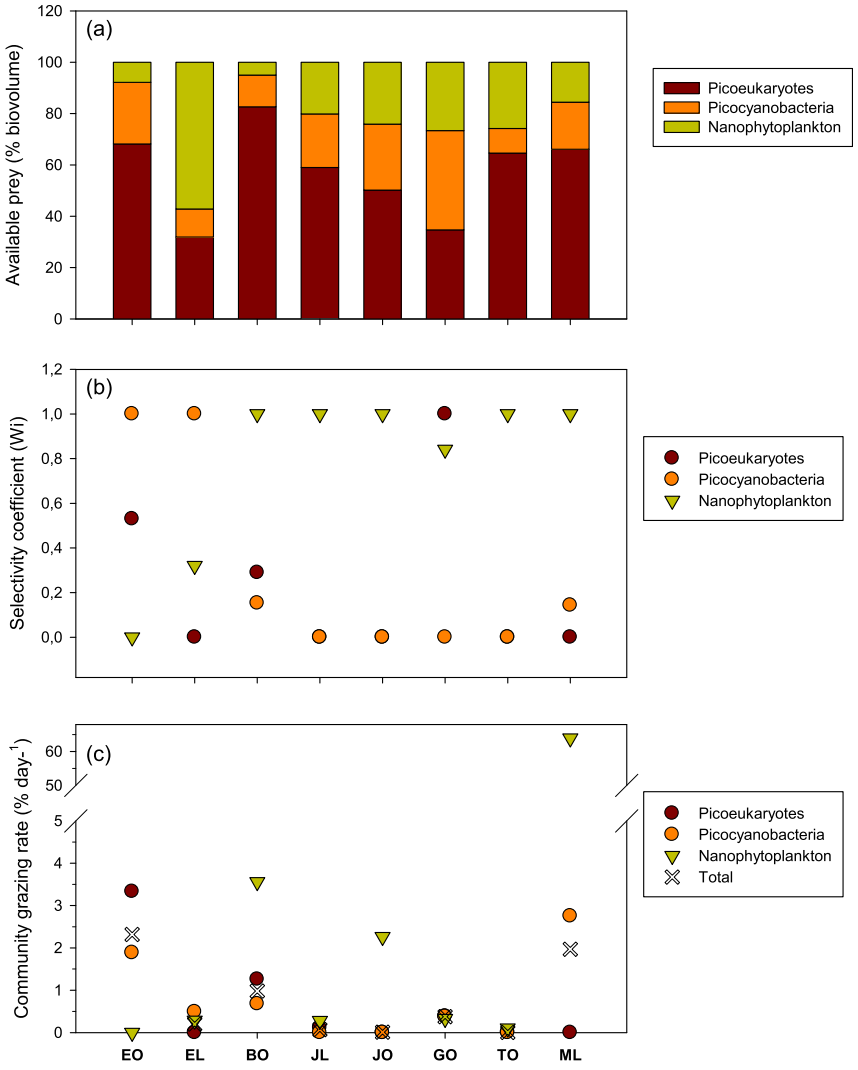

Fig. 4. Grazing experiments with metazooplankton: variation between stations of the percentages of available prey (a), of the selectivity coefficients (b) and of the community grazing rate (c) (expressed as % of the prey stock removed per day) for the three preys considered (picoeukaryotes, picocyanobacteria and nanophytoplankton). Data from the different lagoon stations at Europa and Juan de Nova (EL and JL) are averaged in order to have a mean value per lagoon (see M&M section).

Europa (stations EO and EL) (Fig. 4b). For station GO, picoeukaryotes and nanophytoplankton were equally preferred while picocyanobacteria were not preferred despite their dominance in the water.

There was a significant positive correlation ($p < 0.01$) between total individual or weight-specific ingestion rates and food concentration (Fig. 5), showing that food could be a limiting factor for metazooplankton in the ecosystems. The highest ingestion rates were found for BO and EO and the lowest for TO, GO, JO and E2 with intermediate values for J2 and ML.

The daily community grazing rate varied from 0.2 to 1750 cells ml^{-1} d^{-1} and represented only a low fraction of the stocks of potential prey (<4% in most cases) (Fig. 4c) except for Mayotte lagoon where grazing had a significant effect on nanophytoplankton (60% d^{-1}). This represented 0.01–2.32% of the total phytoplankton per day (Table 3).

3.4. Stable isotope analysis of the major plankton components

A wide variety of metazooplankton present in the stations was analyzed in order to cover a range of potential trophic positions (Table 4) and sources covered by the organisms (groups) that constitute the pelagic community (Fig. 6). As mentioned in the Material and methods section, the samples taken from various sampling stations in each lagoon for each island were pooled (EL, GL, JL). Typically, the lowest $\partial^{15}N$ were found for primary producers such as filamentous cyanobacteria *Trichodesmium* spp. ($\partial^{15}N = -0.988‰$) at all the stations in the Mozambique Channel. Copepods such as *Oncaea* spp., *Macrosetella* spp., *Temora* spp., *Eucalanus* spp., *Calanus* spp., *Paracalanus* spp., *Oithona* spp., Pontellidae, different larvae (undetermined fish, decapode, crab, shrimp, echinoderms) and salps and doliolids hava an average of $\partial^{15}N$ from 1.14 to 3.40‰. The highest values for $\partial^{15}N$ were recorded for chaetognaths (station TO; $\partial^{15}N = 10.18‰$) followed by siphonophores ($\partial^{15}N = 9.10‰$), *Acartia* sp. (station TO; $\partial^{15}N = 8.75‰$), *Eucheta* sp. (station TO; $\partial^{15}N = 8.42‰$), polychaete larvae ($\partial^{15}N = 7.94‰$), salps and doliolids (station TO; $\partial^{15}N = 7.81‰$), *Labidocera* spp. ($\partial^{15}N = 7.78‰$), *Clausocalanus* sp. and *Oithona* spp. (station TO; $\partial^{15}N = 7.40‰$) and the larvae of an undetermined fish (station E; $\partial^{15}N = 7.18‰$). Intermediate values of $\partial^{15}N$ (between 4 and 7‰) were found for the appendicularians, chaetognaths, megalope larva and copepods such as *Acartia* spp., *Clausocalanus* spp., *Corycaeus* spp., *Eucheta* spp., *Oncea* spp. (station GL), *Temora* spp. (station ML) and *Undinula* spp..

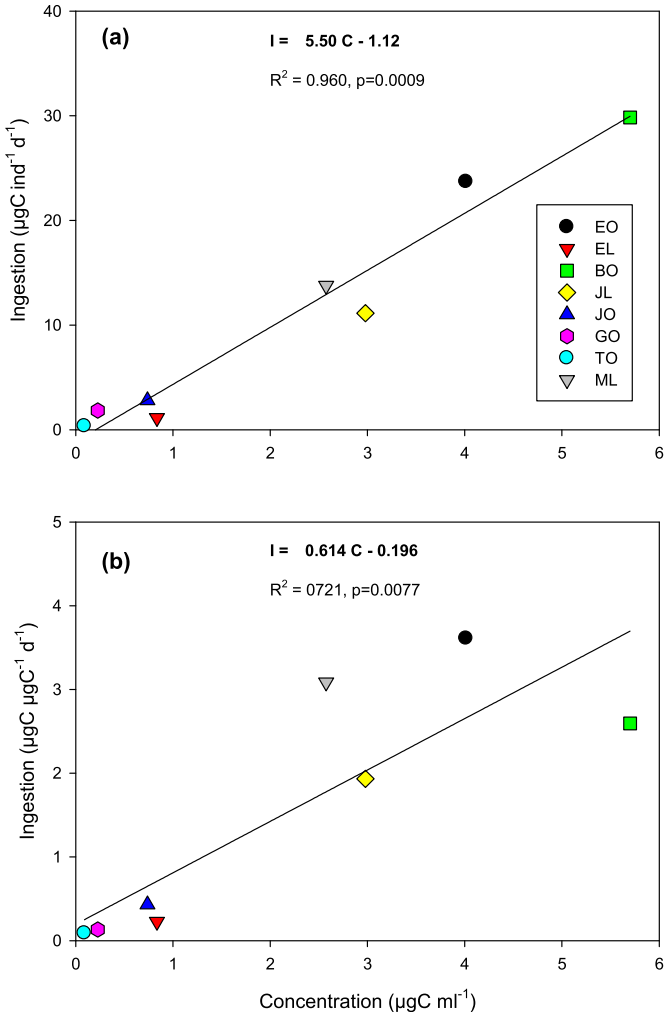

Fig. 5. Grazing experiments with metazooplankton: variations of the individual ingestion rate (a) and of the weight-specific (ie expressed per body carbon weigh) ingestion rate (b) with total food concentration expressed as carbon unit. Data from the different lagoon stations at Europa and Juan de Nova (EL and JL) are averaged in order to have a mean value per lagoon.

The trophic positions of metazooplankton taxa were calculated with $\delta^{15}N$ of metazooplankton and $\delta^{15}N$ POM (TP of POM = 1 represented the isotopic baseline) assuming that a trophic fractionation factor of 3.4‰ represented one trophic transfer (Minagawa and Wada, 1984). Based on the TPs and HCA analysis, 4 groups of signatures could be distinguished (Fig. 7): (1) the group of *Oithona* spp. from the islands in the Mozambique Channel with the lowest TPs, (2) the group where TPs were low, from 0 to 0.43, as *Oncaea* spp., *Macrosetella* spp., *Eucalanus* spp., *Temora* spp., Pontellidae and different types of meroplankton (larva), (3) the group where TPS were the highest, from 1.5 to 2.0, as *Acartia* spp. and *Eucheta* spp. from TO, *Labidocera* spp., chaetognaths from TO, siphonophora and fish larva from E, and finally, (4) the intermediary group where TPs were between 0.48 and 1.40 as appendicularia, chaetognaths and copepods such as *Undinula* spp. and *Corycaeus* spp..

The lowest average carbon isotope ratios for metazooplankton were found in *Macrosetella* spp. ($\partial^{13}C = -21.51‰$) followed by doliolids ($\partial^{13}C = -21.37‰$). The highest average carbon isotope ratios were found in shrimps from Juan de Nova lagoon (JL), *Oithona* spp. from Europa lagoon (EL) and decapod larvae from Glorieuses lagoon (GL) ($\partial^{13}C = -15.39$, -15.79 and $-17:00‰$; respectively).

POM isotope signatures were different from those of metazooplankton. The average POM $\partial^{13}C$ was $-23.96‰$ with values ranging from -25.95 to $-20.39‰$. POM $\partial^{13}C$ signatures for JL and ML were closed to the signatures of ocean stations, and significantly different from the other lagoon systems of Bassas da India (BL), Glorieuses (GL) and Europa (EL). $\partial^{15}N$ ranged from 4.20 to 8.01‰ with an average of 5.32‰.

4. Discussion

The first regional study conducted in the Western Indian Ocean (WIO), provided a preliminary insight into the spatial distribution of the plankton communities in the Iles Eparses (Bouvy et al., 2016). Although these results should be interpreted with caution since they were obtained during only one season (April) and on the basis of one sample per station, the distribution patterns of microbial and metazooplankton components are apparently related to the location of the island in the WIO. The phytoplankton was dominated by picoeukaryotes and picocyanobacteria, as generally reported in oceanic waters (Flombaum et al., 2013). On average, these groups were significantly less abundant in ocean waters than in the lagoons. However, their concentrations were lower in the Europa mangroves as they are believed to be outcompeted by other phytoplankton in high-nutrient waters (Partensky et al., 1999). Europa Island was characterized by highly productive bacterial communities associated with mangroves (Bouvy et al., 2016). The marine ecosystem of Tromelin Island had the lowest biological productivity, with the lowest nutrient concentrations and bacterial growth rates, and a high ratio of heterotrophic bacteria to picoautotrophic organisms suggesting a microbial metabolism based on CO_2 production. On the other hand, bacteria and nanoflagellate dynamics were closely linked at certain lagoon stations (J2, E2 and BL) suggesting a potentially active microbial network. However, it has been demonstrated that both herbivorous and microbial grazing pathways of metazooplankton may play an important role in the transfer of matter and energy towards the top predators in these types of lagoon systems (Pagano et al., 2006, 2012). One of the aims of this study was to assess the effect of metazooplankton grazing on pico- and nanophytoplankton and to determine the trophic positions within the plankton ecosystem by analyzing the stable isotope signatures of a wide variety of taxa from all the islands sampled.

4.1. Metazooplankton communities

Multivariate analyses showed a strong divergence of metazooplankton taxa, reflecting differences in communities between the various sites. The metazooplankton community sampled from the coral reef of Bassas da India (station BL) was clearly characterized by very low abundance and diversity and by the dominance of meroplankton, mostly bivalve and gastropod larvae, which accounted for > 45% of the total abundance. These features are typical of coral reefs where the dominance of meroplankton is associated with the proximity of coral benthic communities and where the low metazooplankton abundance is partly due to consumption by planktivorous fishes when the water crosses the reef during ebb and flood tides (Hamner et al., 2007).

On the other hand, the ocean community in the Mozambique Channel (stations BO, EO, GO and JO) was characterized by the highest taxonomic richness and diversity and dominated by small copepods (>70%), particularly Paracalanidae (12%), followed by appendicularians (5%) and chaetognaths (3%). These characteristics are consistent with the community described by Huggett (2014) for the same area in the Mozambique Channel (14–25°S and 36–43°E), including ocean stations close to Bassas da India and Juan de Nova.

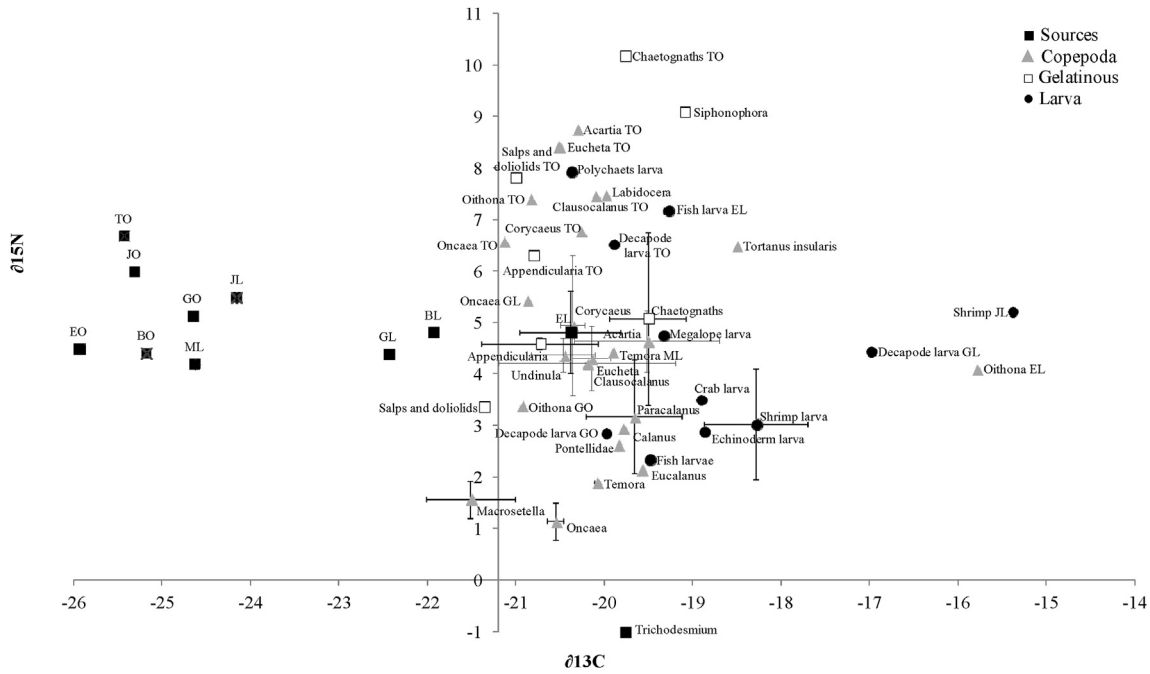

Fig. 6. Plots of average of carbon and nitrogen stable isotope values (‰ ± SD) of different planktonic groups (Copepoda, Gelatinous, Larva) in comparison to POM and *Trichodesmium* spp. (sources). No SD indicated one sample. For codes of stations, see Table 1. Data from the different lagoon stations at Europa and Juan de Nova (EL and JL) are averaged in order to have a mean value per lagoon.

The metazooplankton community sampled at the ocean station of Tromelin Island (TO), to the east of Madagascar Island, had lower abundance and diversity than those observed in the Mozambique Channel, mainly due to a higher relative contribution of copepods (abundance 81% *vs* 73 ± 4%), especially *Paracalanus* spp. (20.5% *vs* 11.6 ± 2%) and a lower contribution of meroplankton (6% *vs* 13 ± 3%), mollusca (absent for TO) and amphipods.

The difference between the Tromelin Island and Mozambique Channel ocean communities may arise from the particular hydrodynamic features in the Mozambique Channel, which have been shown to have a strong effect on phytoplankton and zooplankton distribution clearly associated with ocean fronts and mesoscale eddies (Lamont et al., 2014; Huggett, 2014). The lower metazooplankton abundance for Tromelin Island is also consistent with previous results for microbial components (Bouvy et al., 2016) showing that Tromelin Island had the lowest biological productivity, with the lowest nutrient concentrations and bacterial growth rates. The absence of molluscs for Tromelin Island, in particular pteropods (such as *Limacina* spp. and *Cavolinia* spp.) is also consistent with this finding because these microphagous organisms were found to be highly dependent on the bacterial food chain (Gaudy et al., 1996).

The distribution of the lagoon metazooplankton communities could be classified into two groups of sites. The first group comprised the Europa lagoon stations (E1, E2 and E3), which were in a rich mangrove system. It was characterized by the highest mean proportion of copepods (91%), and the dominance of oithonids (39% of copepod abundance) which are typical of mangrove ecosystems (McKinnon and Klumpp, 1998; Ara, 2004). The second group comprised the Juan de Nova (J1, J2, J3) and Mayotte (ML) lagoon stations which can be considered as the sites most affected by human activities. Mayotte lagoon is affected by the urban and industrial activities of Mamoudzou harbor and Juan de Nova has been an important bird area with strong phosphate deposits that were exploited from the start of the 20th century until 1970 (Le Corre and Safford, 2001). In these sites, the metazooplankton had the highest mean abundance value (4030 ± 597 ind m^{-3}, *vs* less than 1300 ind m^{-3} for the other lagoon sites), which may be due to higher primary production linked to fertilization by human activity (Mayotte) or bird guano (Juan de Nova). Furthermore, the POM $\partial^{13}C$ signatures for JL and ML were significantly different from the other lagoon systems of Bassas da India (BL), Glorieuses (GL) and Europa (EL) and close to the signatures of ocean stations. The values of POM $\partial^{13}C$ signatures at JL and ML can be affected by human activities cited above. In contrast, the lowest values of POM $\partial^{13}C$ signatures at ocean stations corresponded to a marine influence generally reported using natural stable isotope. Finally, Juan de Nova and Mayotte were also characterized by gelatinous plankton exclusively composed of appendicularians which are known to benefit from high phytoplankton productivity (Acuna et al., 2002; Lombard et al., 2009).

Relationships were found between several variables defining trophic conditions for metazooplankton (for example, biomass of nanophytoplankton and picoeukaryotes, POM $\partial^{13}C$). These suggest a possible link between the structure of the metazooplankton communities and the origin and composition of the organic particulate matter of their biotopes (Fig. 6 and Table 4). This is consistent with the stable isotope analyses (see discussion below) showing clear differences in trophic structure between areas, in particular between Tromelin Island and the other islands in the Mozambique Channel.

4.2. Trophic structure of metazooplankton

The trophic positions calculated from $\delta^{15}N$ stable isotope analysis from POM and metazooplankton agreed globally with diet and trophic position found in the literature. *Oncaea* spp., *Macrosetella* spp., *Temora* spp., *Eucalanus* spp., *Paracalanus* spp., *Calanus* spp., *Undinula* spp., salps and doliolids (inside the Mozambique Channel), and different types of meroplankton (larva), showed a low trophic position (<0.5) as reported by many studies (Madin and Kremer, 1995; Suzuki et al., 1999; Gibson and Paffenhöfer, 2000;

Table 2
Mean values of total metazooplankton abundance, number of taxa, Shannon diversity index and mean percentage abundance of the determined taxa in the five clusters defined by the NDMS analysis. Copepod taxa are expressed as the sum of copepodites and adult stages.

Taxa	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
Total abundance (ind m^{-3})	33.1	1215.3 ± 157.0	2084.5 ± 261.1	4031.3 ± 596.7	701.7 ± 48.4
Number of taxa	15.0	22.3 ± 2.7	36.0 ± 1.5	23.6 ± 3.4	22.7 ± 1.2
Shannon index (bits ind^{-1})	2.0	2.2 ± 0.5	2.6 ± 0.1	1.6 ± 0.2	2.3 ± 0.1
Copepoda %	**36.6**	**96.0 ± 3.4**	**75.8 ± 4.2**	**75.5 ± 5.2**	**85.8 ± 0.8**
Nauplii	12.9	47.1 ± 18.6	23.2 ± 6.6	38.2 ± 6.9	33.8 ± 2.1
Paracalanus spp.	3.0	6.0 ± 2.9	12.1 ± 2.7	7.2 ± 3.9	12.5 ± 6.5
Clausocalanus spp.	0.0	0.9 ± 0.9	0.0 ± 0.0	0.1 ± 0.1	1.5 ± 1.3
Acartia spp.	0.0	0.3 ± 0.2	1.7 ± 0.8	2.2 ± 0.8	1.4 ± 0.3
Centropages spp.	0.0	0.1 ± 0.1	1.5 ± 0.4	0.5 ± 0.4	1.7 ± 1.1
Candacia varicans	0.0	0.2 ± 0.1	0.2 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
Temora spp.	0.0	0.0 ± 0.0	0.3 ± 0.1	0.1 ± 0.1	0.0 ± 0.0
Mecynocera sp.	0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.2
Calanus spp.	0.0	1.4 ± 0.6	0.3 ± 0.0	0.1 ± 0.1	0.3 ± 0.3
Acrocalanus sp.	0.0	0.4 ± 0.0	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0
Nanocalanus sp.	0.0	0.2 ± 0.2	0.3 ± 0.3	0.0 ± 0.0	0.1 ± 0.1
Calocalanus sp.	0.0	0.0 ± 0.0	4.6 ± 1.2	0.1 ± 0.0	0.8 ± 0.4
Eucalanus sp.	0.0	0.0 ± 0.0	0.3 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Euchaeta sp.	0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Phaenna sp.	0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Tortanus insularis	0.0	0.0 ± 0.0	0.1 ± 0.1	1.5 ± 0.3	0.0 ± 0.0
Rhincalanus sp.	0.0	0.1 ± 0.1	0.9 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
Calanopia minor	0.0	0.1 ± 0.0	0.2 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Pseudodiaptomus sp.	0.0	0.0 ± 0.0	0.8 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Undinula vulgaris	0.0	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Lubockia sp.	0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Unidentified calanoid	0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.2
Oncaea spp.	0.0	6.9 ± 3.0	6.1 ± 1.8	0.6 ± 0.4	3.0 ± 0.2
Oithona spp.	4.0	19.0 ± 7.7	12.8 ± 3.5	20.8 ± 6.4	17.6 ± 3.6
Corycaeus spp.	1.0	0.7 ± 0.6	4.7 ± 0.3	0.6 ± 0.4	4.9 ± 0.9
Sapphirina sp.	0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Copilia sp.	0.0	0.1 ± 0.1	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Euterpina sp.	6.9	5.0 ± 4.7	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
Clytemnestra sp.	0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Tisbe sp.	0.0	0.6 ± 0.5	0.0 ± 0.0	1.6 ± 1.2	0.9 ± 0.7
Macrosetella sp.	0.0	4.9 ± 2.1	4.1 ± 0.3	1.4 ± 0.5	6.3 ± 2.6
Harpacticoid unidentified sp1	0.0	1.4 ± 1.3	0.7 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Harpacticoid unidentified sp2	7.9	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Harpacticoid unidentified sp3	1.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Harpacticoid unidentified sp4	0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Other holoplankton %	**15.8**	**0.5 ± 0.3**	**1.6 ± 0.4**	**0.3 ± 0.2**	**0.4 ± 0.0**
Ostracoda	5.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.0
Amphipoda	1.0	0.2 ± 0.1	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Isopoda	4.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Worms	2.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Mollusca (Pteropoda)	0.0	0.0 ± 0.0	1.4 ± 0.4	0.2 ± 0.2	0.0 ± 0.0
Water mites	4.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Gelatinous %	**0.0**	**1.6 ± 3.8**	**8.8 ± 0.7**	**15.2 ± 5.9**	**5.3 ± 1.2**
Salps and doliolids	0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Chaetognaths	0.0	1.4 ± 0.8	2.8 ± 0.6	0.4 ± 0.2	1.9 ± 0.7
Medusae	0.0	0.2 ± 0.2	0.8 ± 0.1	0.3 ± 0.1	0.6 ± 0.3
Appendicularia	0.0	0.0 ± 0.0	4.9 ± 1.0	14.5 ± 5.4	2.2 ± 0.3
Siphonophora	0.0	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.7 ± 0.2
Larva (meroplankton) %	**47.5**	**1.9 ± 1.2**	**13.7 ± 3.5**	**9.0 ± 1.7**	**8.5 ± 0.7**
Polychaetes	5.9	0.4 ± 0.1	0.4 ± 0.1	0.5 ± 0.2	0.5 ± 0.1
Actinotroch	0.0	0.1 ± 0.1	0.3 ± 0.2	0.5 ± 0.2	0.3 ± 0.3
Trochophores	0.0	0.0 ± 0.0	4.3 ± 1.6	3.7 ± 1.6	1.7 ± 1.7
Gastropod	9.9	0.2 ± 0.2	0.2 ± 0.1	3.3 ± 2.5	4.1 ± 2.0
Bivalve	31.7	0.3 ± 0.1	0.5 ± 0.2	0.6 ± 0.1	0.7 ± 0.3
Decapod	0.0	0.7 ± 0.6	6.7 ± 3.7	0.1 ± 0.1	0.5 ± 0.3
Euphausiid	0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
Cirriped	0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.4 ± 0.3
Fish eggs	0.0	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.1
Asteroid	0.0	0.0 ± 0.0	0.5 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Undetermined	0.0	0.0 ± 0.0	0.5 ± 0.4	0.0 ± 0.0	0.0 ± 0.0

Dam and Lopes, 2003; Chen et al., 2010; Hauss et al., 2013). However, some differences appeared for meroplankton larva, probably explained by the larval stage. In contrast, the highest trophic positions were found for *Labidocera* spp., *Eucheta* spp., *Acartia* spp., siphonophora and chaetognaths (Tromelin island, TO), as reported by many studies (Turner, 1984; Gifford and Dagg, 1988; Hauss et al., 2013).

For the same species found in different stations, inside or outside the Mozambique Channel, the calculated trophic positions of metazooplankton taxa showed similar values whereas $\partial^{15}N$ signatures were different between the sites. Thus, these species were probably characterized by the same diet (same TP) whatever

Table 3
Mean values of total metazooplankton abundance, and mean individual weight (Wi) and percentage abundance of the determined taxa in the grazing flasks during the eight grazing experiments. Copepod taxa are expressed as the sum of copepodites and adult stages. The mean individual weights were determined from the mean size according to length–weight relationships from Chisholm and Roff, 1990 ([1]), Nassogne 1972 ([2]), Purcell 1981 ([3]) and Uye 1991 ([4]). Data from the different lagoon stations at Europa and Juan de Nova (EL and JL) are averaged in order to have a mean value per lagoon.

	Wi μgC	EO	EL	BO	JL	JO	GO	TO	ML
Total number (ind 500 ml^{-1})		24.7	50.3	34.5	30.7	45.0	25.0	26.3	38.0
Copepoda %		**98.6**	**94.6**	**97.1**	**30.4**	**97.8**	**70.2**	**100.0**	**79.8**
Nauplii	0.3[4]	2.8	0.4	2.9	3.3	3.3	7.0	5.1	0.0
Paracalanus spp.	5.3[1]	28.2	16.6	29.0	8.7	43.3	19.3	6.3	42.1
Clausocalanus spp.	6.4[1]	1.4	0.0	0.0	0.0	2.2	0.0	0.0	0.0
Acartia spp.	3.9[1]	0.0	0.0	1.4	2.2	16.7	5.3	16.5	21.1
Centropages spp.	5.6[1]	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Candacia varicans	23.9[1]	1.4	0.9	1.4	1.1	0.0	0.0	0.0	0.0
Eucalanus sp.	113.2[1]	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0
Euchaeta sp.	172.7[1]	1.4	0.0	0.0	0.0	1.1	0.0	0.0	0.0
Calocalanus sp.	5.6[1]	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhincalanus sp.	113.2[1]	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0
Pseudodiaptomus sp.	16.9[1]	0.0	0.9	1.4	0.0	0.0	1.8	0.0	0.9
Pontellina sp.	16.9[1]	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ctenocalanus sp.	16.9[1]	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Lucicutia sp.	23.9[1]	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Unidentified calanoid	5.6[1]	2.8	1.3	0.0	3.3	2.2	0.0	2.5	1.8
Oncaea spp.	4.9[1]	7.0	34.1	23.2	3.3	6.7	1.8	2.5	4.4
Oithona spp.	3.0[1]	40.8	36.3	14.5	5.4	7.8	10.5	11.4	5.3
Corycaeus spp.	2.8[1]	5.6	0.4	13.0	2.2	12.2	12.3	40.5	0.0
Sapphirina sp.	37.3[1]	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Copilia sp.	16.9[1]	0.0	0.0	2.9	0.0	1.1	0.0	1.3	1.8
Euterpina sp.	1.1[1]	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Tisbe sp.	1.9[1]	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Macrosetella sp.	1.9[1]	4.2	1.3	1.4	1.1	1.1	12.3	10.1	2.6
Harpaticoïd unidentified spp.	1.9[1]	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Other holoplankton %		**0.0**	**0.4**	**0.0**	**5.4**	**0.0**	**1.8**	**0.0**	**0.0**
Amphipoda	19.8[3]	0.0	0.4	0.0	5.4	0.0	1.8	0.0	0.0
Gelatinous %		**1.4**	**1.3**	**0.0**	**59.8**	**1.1**	**8.8**	**0.0**	**19.3**
Salps and doliolids	48.0[2]	0.0	0.4	0.0	0.0	1.1	0.0	0.0	0.0
Chaetognaths	14.2[3]	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Appendicularia	2.6[2]	0.0	0.0	0.0	59.8	0.0	8.8	0.0	19.3
Siphonophora	9.9[2]	1.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Larva (meroplankton) %		**0.0**	**3.6**	**2.9**	**4.3**	**1.1**	**19.3**	**0.0**	**0.9**
Polychaetes	4.0[2]	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Decapod	55.6[3]	0.0	2.7	1.4	3.3	0.0	19.3	0.0	0.0
Fish larvae	11.8[2]	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.9
Undetermined	4.0[2]	0.0	0.0	0.0	1.1	1.1	0.0	0.0	0.0

the locations: for example *Oncea* spp., *Corycaeus* spp. and appendicularia. In contrast, the $\partial^{15}N$ signature and, thus trophic position, was very variable for *Oithona* spp., which presented a very low TP in the station for the islands in the Mozambique Channel compared to Tromelin (TO). The change in TP and $\partial^{15}N$ signature would be manifested in difference spatial diet of *Oithona* spp.. The POM and metazooplankton for Tromelin Island station had higher values of $\delta^{15}N$ than the POM and similar taxa at other stations in the Mozambique Channel. At this oceanic station outside the Mozambique Channel (TO), Bouvy et al. (2016) found the highest ratio between heterotrophic and autotrophic microorganisms suggesting largely a heterotrophic material available for metazooplankton. Therefore, previous studies have suggested that a substantial part of the standing stock of chlorophyll-*a* in oligotrophic tropical and subtropical oceans can be attributed to the diazotroph *Trichodesmium* spp. (e.g. Sellner, 1997; Capone et al., 1997). Stable isotopic analysis of N ($\delta^{15}N$) has shown that the N fixed by diazotrophs is isotopically 'light' because the origin is atmospheric nitrogen (whose $\delta^{15}N$ by definition is 0‰). Hence, pelagic food webs in which diazotrophic cyanobacteria proliferate have very different isotopic ratios from food webs without diazotrophs, where the $\delta^{15}N$ is normally higher (5–15‰; Owens, 1987). In our study, analysis of microphytoplankton indicated the presence of *Trichodesmium* spp. in the stations inside the Mozambique Channel and its total absence outside the channel (Tromelin Island station). However, the $\delta^{15}N$ signatures of POM at sites from the Mozambique Channel were not characterized by low $\delta^{15}N$ values even if *Trichodesmium* was present. Our sampling method (subsample of water from Niskin bottle) was certainly not enough appropriate as reported by Chang (2000), where subsampling from a Go-Flo bottle contributes 90%–94% of the total variance observed in abundance revealing a heterogeneous distribution of *Trichodesmium* trichomes in a sampling bottle. However, the $\delta^{15}N$ signature of some metazooplankton taxa as chaetognaths, *Acartia* spp., *Eucheta* spp., *Clausocalanus* spp., *Oithona* spp. and salps and doliolids presented lower TPs inside the Mozambique Channel compared to the outside Channel (Tromelin island). This observation indicated a different spatial diet for these organisms and probably a trophic transfer (direct or indirect) of diazotrophic nitrogen (from *Trichodesmium* spp.) to metazooplankton in the Mozambique Channel. It can, therefore, be concluded that a plankton food web was probably preferentially based on *Trichodesmium* spp. in marine systems in the Mozambique Channel but not for Tromelin Island. In the future studies, patterns in stable N isotope ratios of amino acids in metazooplankton and in *Trichodesmium*, as proposed by McClelland et al. (2003), will permit to definitively prove that diazotrophs are the source of the planktonic web in the

Table 4
Metazooplankton $\delta^{15}N$ POM-based trophic position (TPs): mean and SD. TO: Tromelin; EL: Europa lagoon; GO: Glorieuses ocean; GL: Glorieuses lagoon; ML: Mayotte; JL: Juan de Nova lagoon. Data from the different lagoon stations at Europa, Juan de Nova and Glorieuses (EL, JL and GL) are averaged in order to have a mean value per lagoon.

Copepoda	Mean TP	SD TP
Acartia	0.908	0.343
Acartia TO	1.608	
Corycaeus	1.051	0.554
Corycaeus TO	1.026	
Eucheta	0.919	0.186
Eucheta TO	1.510	
Oithona EL	−0.718	
Oithona GO	−1.751	
Oithona TO	0.715	
Oncaea	−0.114	0.313
Oncaea GL	1.305	
Oncaea TO	−0.113	
Clausocalanus	0.831	0.753
Clausocalanus TO	1.229	
Pontellidae	0.005	
Temora	0.199	0.082
Temora ML	1.067	
Tortanus insularis	1.289	
Undinula	0.820	0.029
Calanus	0.568	
Eucalanus	0.213	
Labidocera	1.908	
Macrosetella	0.042	0.240
Paracalanus	0.491	0.431
Gelatinous		
Appendicularia	0.922	0.303
Appendicularia TO	0.889	
Chaetognaths	1.189	0.496
Chaetognaths TO	2.027	
Salps and doliolids	0.483	
Salps and doliolids TO	1.330	
Siphonophora	1.707	
Larva (meroplankton)		
Crab larva	0.615	
Decapode larva GL	1.012	
Decapode larva GO	0.326	
Decapode larva TO	0.952	
Megalope larva	0.428	
Shrimp larva	0.401	0.280
Shrimp JL	0.914	
Echinoderm larva	0.339	
Fish larva	0.388	
Fish larva EL	1.697	
Polychaetes larva	1.368	

Mozambique Channel.

In this study, the trophic link with *Trichodesmium* spp. was particularly close for the copepods *Oncaea* spp. and *Macrosetella* sp. (see Fig. 6). So far as we are aware, a direct trophic link between *Trichodesmium* spp. and *Oncaea* spp. has never been established. However, *Oncaea* species were shown to have a predominantly omnivorous/detritivorous diet (Atkinson, 1998) being able to use their sharp maxillipeds to catch large prey, such as chaetognaths (Go et al., 1998) and appendicularian houses (Nishibe et al., 2015). Thus, the detritus and aggregates associated with *Trichodesmium* spp. and even the large trichomes should benefit this copepod. The association of *Macrosetella gracilis* with the colonial cyanobacterium *Trichodesmium* spp. has been shown in several studies. This pelagic harpacticoid copepod is known to use *Trichodesmium* spp. as a physical substrate for juvenile development and/or as a food source, being immune to cyanobacterial toxins harmful to other species of copepods (O'Neil and Roman, 1994; Eberl and Carpenter, 2007). Its association with a buoyant colonial cyanobacterium is interpreted as a successful way of living within the plankton, whereas most harpacticoids are benthic (O'Neil, 1998). In this study, when preparing the metazooplankton sets for grazing experiments or for isotopic analyses, a high abundance of *Macrosetella* sp., particularly ovigerous females, associated with *Trichodesmium* spp. trichomes was observed.

4.3. Grazing of metazooplankton on phytoplankton

In our experiment, the largest potential phytoplankton preys (as diatoms or large dinoflagellates) were not considered, leading to a possible underestimation of total ingestion rates. However the measured daily ratios reached very high values (up to 360% of carbon body weight per day) as compared to literature data (Mauchline, 1998) suggesting that this bias should be minor. The experiments showed a positive relationship between ingestion rate and natural food concentration (total autotrophic microorganisms), indicating that food could be a limiting factor for metazooplankton in the area. This is fairly standard in such oligotrophic environments (chlorophyll concentration $< 0.7\ \mu g\ l^{-1}$) characterized by the dominance of picoplanktonic cells not easily accessible for most filter feeders, and particularly for copepods (high abundance in the sites studied) known to feed mostly on nanoplankton (Mauchline, 1998). They clearly showed that metazooplankton tended not to prey on picophytoplankton, despite its dominance in the prey assemblages, and preferred nanophytoplankton. Furthermore, there were few typical picoplankton grazers. For example, salps and doliolids are known to feed efficiently on picoplankton (Madin and Kremer, 1995) but none were found in the samples except for the Glorieuses ocean station (GO). These features also suggest the potential role of micro-heterotrophs (ciliates and heterotrophic nanoflagellates, not considered in this study) as part of the metazooplankton diet, as this type of prey can be ingested in large quantities when stocks of phytoplankton are depleted (Loder et al., 2011; Pagano et al., 2012).

Grazing by metazooplankton on autotrophic microorganisms had very little effect, representing less than 3% of the phytoplankton stocks per day. Metazooplankton grazing has already been reported to have little effect on phytoplankton in low-chlorophyll zones within the inter-tropical zone, as for example in the equatorial Pacific Ocean (Champalbert et al., 2003). However, in these low-chlorophyll areas, grazing may have a strong effect on micro-heterotrophs, sometimes leading to increased biomass of nanoplankton (Schnetzer and Caron, 2005). Around the Iles Eparses, high grazing pressure on micro-heterotrophs cannot be excluded, but the low proportion of nanophytoplankton excludes the possibility of such cascading effects.

4.4. Conclusion

Overall, based on one single survey in April combined with several grazing experiments, these results showed that the hydrodynamics of the Mozambique Channel created particular conditions with a high abundance of *Trichodesmium* spp. and a direct or indirect trophic transfer of diazotrophic nitrogen to metazooplankton. On the other hand, the absence of *Trichodesmium* spp. and mollusks (Pteropods) in the ocean waters near Tromelin Island (outside the Mozambique Channel) created a particular trophic food web with the highest $\delta^{15}N$ signatures. Furthermore, Juan de Nova Island can be considered as being the most affected by human activities, with a trophic state resembling that of the anthropized Mayotte lagoon. Phytoplankton may be a limiting factor for metazooplankton throughout all the “Iles Eparses”.

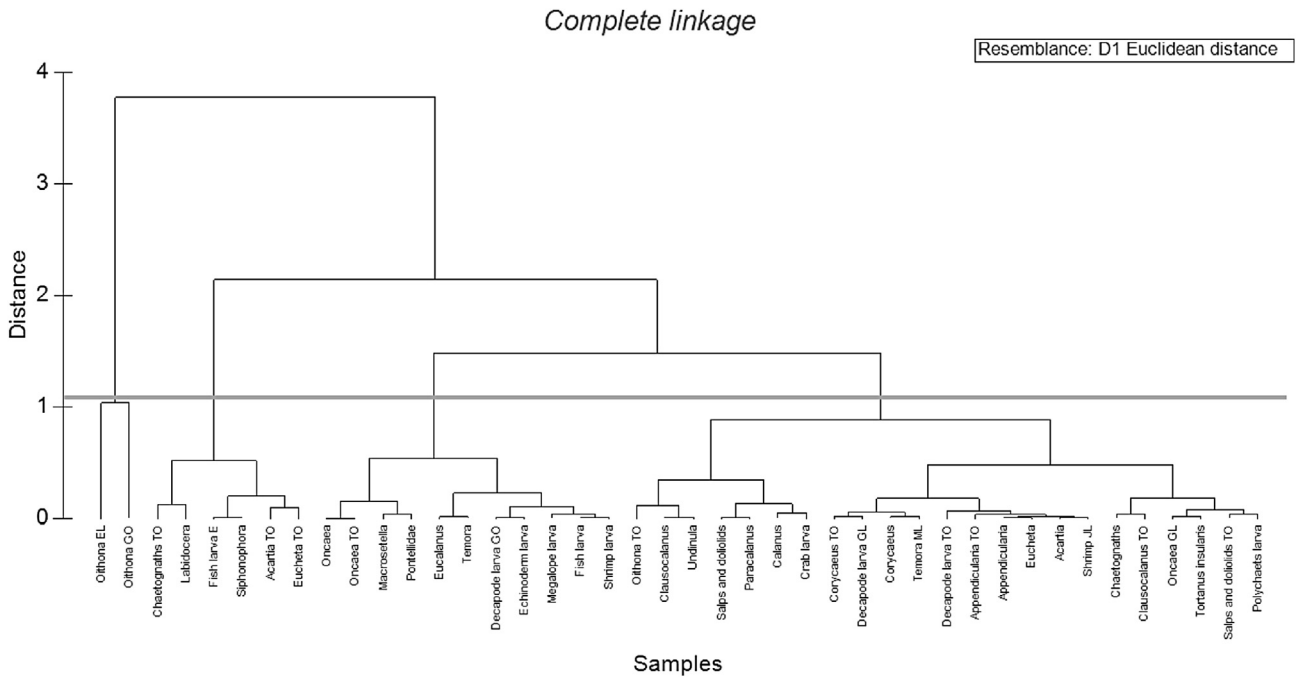

Fig. 7. Hierarchical Cluster Analysis (HCA) using Euclidian method and complete linkage sorting, based on trophic positions of metazooplankton taxa (Copepoda, Gelatinous, Larva). Data from the different lagoon stations at Europa and Juan de Nova: (EL and JL) are averaged in order to have a mean value per lagoon.

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