



Trophic relationships between metazooplankton communities and their plankton food sources in the Iles Eparses (Western Indian Ocean)



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ARTICLE INFO

Article history:

Received 18 November 2015

Received in revised form

21 February 2016

Accepted 23 February 2016

Available online 27 February 2016

Keywords:

Metazooplankton
Spatial distribution
Grazing effect
Feeding ecology
Iles Eparses
Mayotte

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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ 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).

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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 Gonzales, 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 $\delta^{13}\text{C}$ 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 km² 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).

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