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Plankton distribution within a young cyclonic eddy off south-western Madagascar

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ABSTRACT

Mesoscale eddies are major features in ocean dynamics that significantly influence ocean production depending on their polarity, life-stage, location and time of formation. Eddies in the south-west Indian Ocean have been the focus of many studies, especially in the Mozambique Channel where southward-moving cyclonic and anticyclonic eddies feed into the Agulhas Current. However, eddies formed south of Madagascar that move westwards towards the coast of South Africa have been much less studied, despite their significant contribution to the Agulhas Current. This study aims to understand how the plankton communities (i.e. pico-, nano-, phyto-, microzoo- and mesozooplankton) are distributed in a cyclonic eddy generated off southern Madagascar. We also investigate a possible link between the Madagascar shelf and the eddy. Temperature, salinity, fluorescence and plankton abundance were measured at 25 stations spaced at 18.5 km intervals across a young (~ 1 month old) cyclonic eddy, and at three locations on the Madagascar shelf, in July 2013. A patch of enhanced chlorophyll *a* concentration was found at four stations in the eddy, homogeneously distributed vertically in the upper mixed layer and characterised by a higher proportion of diatoms compared to the other stations. Abundances of picoplankton, nanoplankton, ciliates and dinoflagellates were very similar within and outside the eddy. Zooplankton followed a contrasting pattern with higher biomass at four stations just to the west of this high diatom patch. The mesozooplankton composition at these four stations revealed greater species similarities with the Madagascar shelf than with the other stations, suggesting a link between the shelf and the western side of the eddy. The periphery of the eddy seems to have been primarily influenced by a strong geostrophic current propagating from the southern shelf of Madagascar which then wrapped itself around the eddy. This filament may be the source of the high zooplankton biomass in the eddy periphery, which would account for the similarities in zooplankton community composition between the eddy periphery and the shelf.

1. Introduction

Mesoscale eddies are important oceanographic features in the world ocean, being more prominent at the ends of western boundary currents such as the Gulf Stream in the western Atlantic Ocean and the Agulhas Current in the South-West Indian Ocean. They are highly energetic phenomena which can stimulate local biological production via processes of enrichment, concentration and retention, thereby providing enhanced feeding conditions for higher trophic levels, as well as influencing distributions and densities of marine organisms through mixing and advection (Bakun, 2006; Godø et al., 2012).

The Mozambique basin is characterised by intense mesoscale activity, with interactions between eddies formed in the Mozambique Channel flowing southwards, and eddies originating on the southern shelf of Madagascar moving westwards (Beal et al., 2011; de Ruijter et al., 2004; Halo et al., 2014; Quartly and Srokosz, 2002). Although the Mozambique Channel eddies are now relatively well understood (Ternon et al., 2014), far fewer studies, especially biological studies, have been conducted on eddies formed south of Madagascar, despite both eddy pathways contributing significantly to the flow and the variability of the Agulhas Current (Beal et al., 2011; de Ruijter et al., 2004; Halo et al., 2014; Quartly et al., 2006; Quartly and Srokosz, 2004; Ridderinkhof et al., 2013). Gaube et al. (2014) highlighted three main physical mechanisms by which mesoscale eddies influence planktonic communities. The first is the horizontal advection of plankton either by the stirring of surface currents around the eddy peripheries, or the

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trapping of parcels of water with unique physical and biological properties within the eddy core and advecting them away from the region of formation. A second is the vertical flux of nutrients which subsequently influences the planktonic communities during the different life stages of the eddy (*i.e.* intensification and decay), primarily occurring along the isopycnal gradients. The third mechanism is the influence of eddies on stratification, where in some cases phytoplankton cells are maintained and concentrated within the euphotic layer (e.g. when the mixed layer is deeper than the euphotic zone), leading to increased primary production. During their early stages (intensification phase), cold core eddies are generally considered to upwell deep nutrient rich waters into the upper mixed laye (UML), enhancing primary and subsequently secondary production. As such, cold-core eddies are usually more productive than warm-core eddies (Goldthwait and Steinberg, 2008; Huggett, 2014; Landry et al., 2008; Quartly and Srokosz, 2004; Riandey et al., 2005) although the opposite has also been observed (Hernández-León et al., 2001; Lévy et al., 2001; Strzelecki et al., 2007). Several factors seem to influence the biological dynamics of eddies and how they vary over time, such as the origin of the eddy (*i.e.* the environment where it was generated), its polarity (*i.e.* cyclonic or anti-cyclonic), its status (*i.e.* intensification or decay phase), its age and its interaction with adjacent water masses which modifies its dynamics and thus the composition of its residents (Bakun, 2006).

In addition to the intrinsic mechanisms of production enhancement, eddies also have the capacity to entrain planktonic organisms over long distances, of the order of hundreds of kilometres (Heywood et al., 1996; Lobel and Robinson, 1986; Mackas et al., 2005a; Mackas and Galbraith, 2002; Quartly and Srokosz, 2004) which can have important consequences for the dispersal and recruitment of larval stages (Atwood et al., 2010; Hare et al., 2001; Holliday et al., 2012; Kasai et al., 2002; Mackas et al., 2005a). Hence eddies are also recognised as vectors of connectivity between populations separated by long distances (Mackas et al., 2005b). More specifically in the South West Indian Ocean, some similarities have been observed between fauna inhabiting the east coast of South Africa and the southern coast of Madagascar, and it has been hypothesised that eddies may be the transport mechanism for this possible biological connectivity between the two landmasses (Halo et al., 2014; Marsac et al., 2014; Ockhuis et al., 2017).

In this study, we sampled physical and biological parameters along a transect crossing an eddy which originated off the southwest coast of Madagascar. We investigated the planktonic communities at a high spatial resolution (18.5km between stations). Our primary objective was to understand how phytoplankton, microzooplankton and mesozooplankton were distributed within the eddy in terms of abundance and species composition. We also explore the possibility of entrapment of zooplankton by the eddy from its region of formation.

2. Material and methods

2.1. Sampling

Sampling was conducted between 16 and 22 July 2013 on-board the RV *Algoa*. Three stations were sampled on the south-west shelf of Madagascar (stations 26, 28 and 29; Fig. 1). These stations were selected as they were identified as the closest to the area of the eddy formation. Twenty five stations, 18.5km apart, were sampled along a transect located between 26°01'28.2"S − 42°30'30.599"E (station 30) and 27° 42'2.88"S, 38°33'28.799"E (station 54), crossing a cyclonic eddy (Fig. 1). Satellite sea surface height anomalies were downloaded from the Colorado Centre for Astrodynamics Research (CCAR) for eddy tracking prior to the cruise and on-board the vessel (http://eddy.colorado.edu/ccar/ssh/nrt_global_grid_viewer). For data interpretation requiring Sea Surface Height products, data were downloaded from the Copernicus website (http://www.copernicus.eu/). Gridded altimetry products were produced using multi-mission data and are the same products (no change in scientific content) as were previously distributed by AVISO. In addition, a mesoscale eddy tracking algorithm, as used by Halo et al. (2014), was employed to track the eddy from its formation on 16 June 2013 when a closed contour eddy was detected in the imagery, to 24 October 2013 where it last appeared as a closed contour eddy just east of the KwaZulu-Natal Bight. The eddy tracking algorithm uses a hybrid of two parameters – the closed contours of sea surface height (as used by Chelton et al., 2011) and a negative Obuko-Weiss parameter (*i.e.* regions where the normal and shear components of strain dominate over those of vorticity in terms of eddy formation as per Henson and Thomas, 2008) to determine the extent of a coherent geostrophic eddy (Halo et al., 2014). This method is considered more robust than using the closed contour or Okubo-Weiss methods individually (Halo et al., 2014). Within the eddy tracking scheme, the eddies are tracked with reference to their cores as per the method suggested by Penven et al. (2005).

At each station, a 12-bottle Niskin (5 L) rosette equipped with a Seabird 911 + CTD-F (conductivity, temperature, depth – fluorescence) system sampled the physical parameters of the water column to a depth of about 1000 m. The fluorescence profiles were calibrated against discrete chlorophyll *a* concentration (mg Chl *a* m^{-3}), measured by HPLC from samples collected at several depths at each station (see Barlow et al., 2017). Physical and chemical data profiles were plotted using Ocean Data View (Schlitzer, 2015). The mixed layer depth (MLD) was calculated as per de Boyer Montégut et al. (2004) using a fixed threshold criterion of 0.03 kg m^{-3} change from a depth of 10 m.

Due to a technical problem with the vessel's Acoustic Doppler Current Profiler (ADCP), current data were not available for this cruise. Given the lack of ADCP and the small-scale resolution of the sampling design, we were not able to use the criteria described by Lamont et al. (2014) to discriminate the zones of the eddy.

At each station, seawater samples were collected for flow cytometry analysis and microscopic taxonomic identification of auto- and heterotrophic organisms. A bongo net fitted with 200 µm mesh size, equipped with a flowmeter, was towed obliquely down to a depth of 200 m and back to sample the mesozooplankton community.

2.2. Phytoplankton and protozooplankton analysis

For microscopic identification of phytoplankton and small protozooplankton, surface seawater samples were collected with a Niskin bottle at approximately 2 m below the surface and were fixed in a Lugol's solution of 1% final concentration and stored in dark bottles. On return to the laboratory, sub-samples of 25–50 mL were settled in Utermöhl chambers for 48 h Phytoplankton and other protists were then identified and counted using an Olympus CKX41 inverted microscope. For this study, we used a degree of identification restricted to large taxa such as nanoflagellates, dinoflagellates, diatoms and ciliates. A volume of 4.5 mL of seawater was collected in a 5 mL cryovial for flow cytometry analysis, to which 0.5 mL of a glutaraldehyde solution (2% initial concentration) was added to yield a final concentration of 0.2%. Samples were then frozen at −80 °C. Once ashore, each sample was analysed for a counting time of 300s using a Beckman Coulter Cytomics FC 500, and a volume of 0.270 mL. The fluorescence mode was employed to trigger the count of particles, adapted from the method of Schapira et al. (2012), and as such only photosynthetic cells were counted. We can consider that most of the particles counted with this method are picoplanktonic organisms (< 2 µm).

2.3. Mesozooplankton analysis

The zooplankton samples, collected from the upper 200 m at each station with bongo nets were concentrated using a 200 µm mesh with filtered seawater and then preserved with formaldehyde (4% final solution). Samples were collected without regard to the diurnal cycle due to the restricted sampling time and cruise schedule. The diurnal cycle can influence zooplankton abundance as some species perform diel

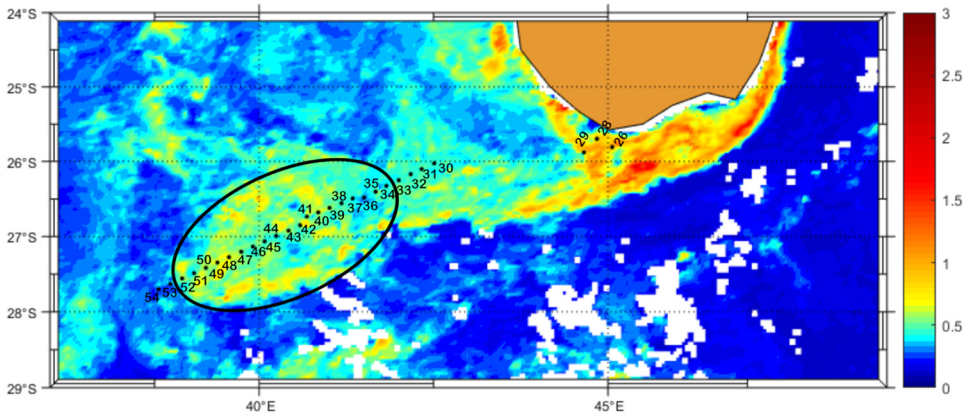

Fig. 1. Map of stations sampled on the southern Madagascar shelf and along a transect through a cyclonic eddy during July 2013 superimposed on a 7-day (13–20 July 2013) composite of Chlorophyll *a* concentration from MODIS. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

vertical migration (DVM), although Huggett (2014) showed that this phenomenon is limited in the area studied. We tested the possible influence of DVM on the zooplankton samples here by testing if there were significant differences between the stations sampled at night (*i.e.* 30, 31, 35, 36, 37, 41, 42, 43, 47, 48, 49, 53, 54) and during day time (*i.e.* 32, 33, 34, 38, 39, 40, 44, 45, 46, 50, 51, 52). Back in the laboratory, the samples were poured into an adequately sized graduated cylinder and settled for 24–48 h to measure the settled volume. The sample was then split into two halves using a Folsom splitter. The first half was filtered onto 200 µm mesh and dried at 60 °C for 24–48 h.The dry weight (DW) was then measured to obtain the integrated dry biomass of zooplankton over the upper 200 m of the water column. The other half of the sample was split further to reach a size suitable for counting under a dissecting stereo-microscope. We fixed the size of the sub-sample counted to a minimum of 100 adult calanoid copepods to ensure enough individuals were counted to properly represent the community. The adult calanoid copepods were identified to species for most of the larger copepods while the smaller copepods (approximately 1 mm total length), were identified to genus level (*e.g. Acrocalanus* spp., *Calocalanus* spp., *Clausocalanus* spp.). *Oithona* spp. and *Oncaea* spp. were also counted only to genus level and no differentiation between copepodites and adults was made. Finally, the other larger zooplankton were counted to a broad taxonomic level such as chaetognaths, appendicularians, salps. A Principal Correspondence Analysis (PCA) was performed on the species composition of the zooplankton to find similarities between stations and groupings of stations was confirmed with a cluster analysis based on a Bray Curtis similarity matrix. SIMPROF (PRIMER, Anderson et al., 2008) was performed to test whether the clusters were significantly different from each other. Three diversity indices - species richness, Shannon Index and Pielou's evenness index - were calculated using PRIMER (Anderson et al., 2008).

3. Results

3.1. Characterisation of the eddy structure

Sea surface height imagery and the mesoscale eddy tracking algorithm (as described above, Fig. 2) revealed the presence of two eddies southwest of Madagascar at the time of sampling (Fig. 2c): a strong asymmetrical cyclonic eddy, which we sampled from north-east towards the south-west, and a smaller cyclonic eddy, northeast of the first one. Also depicted was the apparent extension of the South-East Madagascan Current (SEMC) flowing off the southern shelf of Madagascar, as noted by Barlow et al. (2017), and along the southern peripheries of the cyclonic eddies. The MODIS composite image from 13 to 20 July (Fig. 1) shows the presence of elevated sea surface Chl *a* ($> 0.5\,mg\,m^{-3}$) over the shelf, with a possible filament extending in a south-westward direction and curving across the western part of the transect through the larger cyclonic eddy.

It is necessary to contextualise our sampling period within the lifetime of the eddy. A time series of sea surface height, partly shown in Fig. 2, indicates that this cyclonic feature was first detected as an enclosed, coherent eddy on 16 June 2013 (Fig. 2b), in the south-eastern Mozambique Channel, a zone identified previously as a region of cyclonic eddy formation (Halo et al., 2014; Quartly and Srokosz, 2004). The eddy subsequently travelled westwards while strengthening (Fig. 2c), and reached a peak in intensity on 15 August, mid-way in its propagation across the southern Mozambique Channel (Fig. 2d). Sea surface height was relatively constant as the eddy propagated across the remainder of the Mozambique Channel, only decreasing in intensity around 9 October, to finally disappear around 24 October 2013 offshore from the coast of South Africa (east of the KwaZulu-Natal Bight, Fig. 2e). The eddy thus lasted for approximately four months and was sampled about one month after it first emerged on the eddy detection scheme (Fig. 2c). The cyclonic eddy was part of a dipole structure with a strong anticyclonic eddy located to the south, as observed in previous studies in the region (de Ruijter et al., 2004).

At the time of sampling, the eddy was still intensifying, suggesting possible upwelling of deep cold and nutrient-rich waters into the eddy centre. However, the temperature profiles indicated only a weak doming of the isotherms, starting around station 35 on the eastern side of the transect and with a relatively steeper slope on the western side at stations 51–52 (Fig. 3). The boundaries of the cyclonic eddy were determined using satellite observations by Barlow et al. (2017) as stations 34 to the east and 52 to the west. On average, the MLD was between 90 and 100 m with a well-mixed layer above this depth (Fig. 3b). Note that the MLD did not vary significantly within the eddy itself.

3.2. Primary producers and small heterotrophs composition

The chlorophyll *a* concentration was relatively low, never exceeding $1.88\,mg\,m^{-3}$ along the transect, with an enhanced patch of Chl *a* at stations 44–47 (Fig. 4). The Chl *a* was homogeneously distributed vertically within the UML at all stations, without a distinct chlorophyll maximum. The enhanced patch was characterised by a higher concentration of diatoms compared to the other stations, reaching a maximum of 55 cells mL^{-1} at station 46 (Fig. 5). The most common genera of diatoms recorded were *Chaetoceros* and *Thalassiosira*. Dinoflagellate abundances averaged less than 1 cell mL^{-1} with *Ceratium* being the most common genus and the ciliate abundances were particularly low with only 0.32 cells mL^{-1}. Photosynthetic nanoflagellate and picoplankton abundances were also highly variable across the eddy with overall concentrations of 1341 ± 763 cells mL^{-1} and 20992 ± 8122 cells mL^{-1}, respectively. The only difference was found outside the eddy, at station 53 and 54, where the mean concentration of nanoflagellates was relatively high (3300 cells mL^{-1}) while that of picoplankton was relatively low (6684 cells mL^{-1}) compared to the rest of the transect. No other distinct differences were observed in the samples.

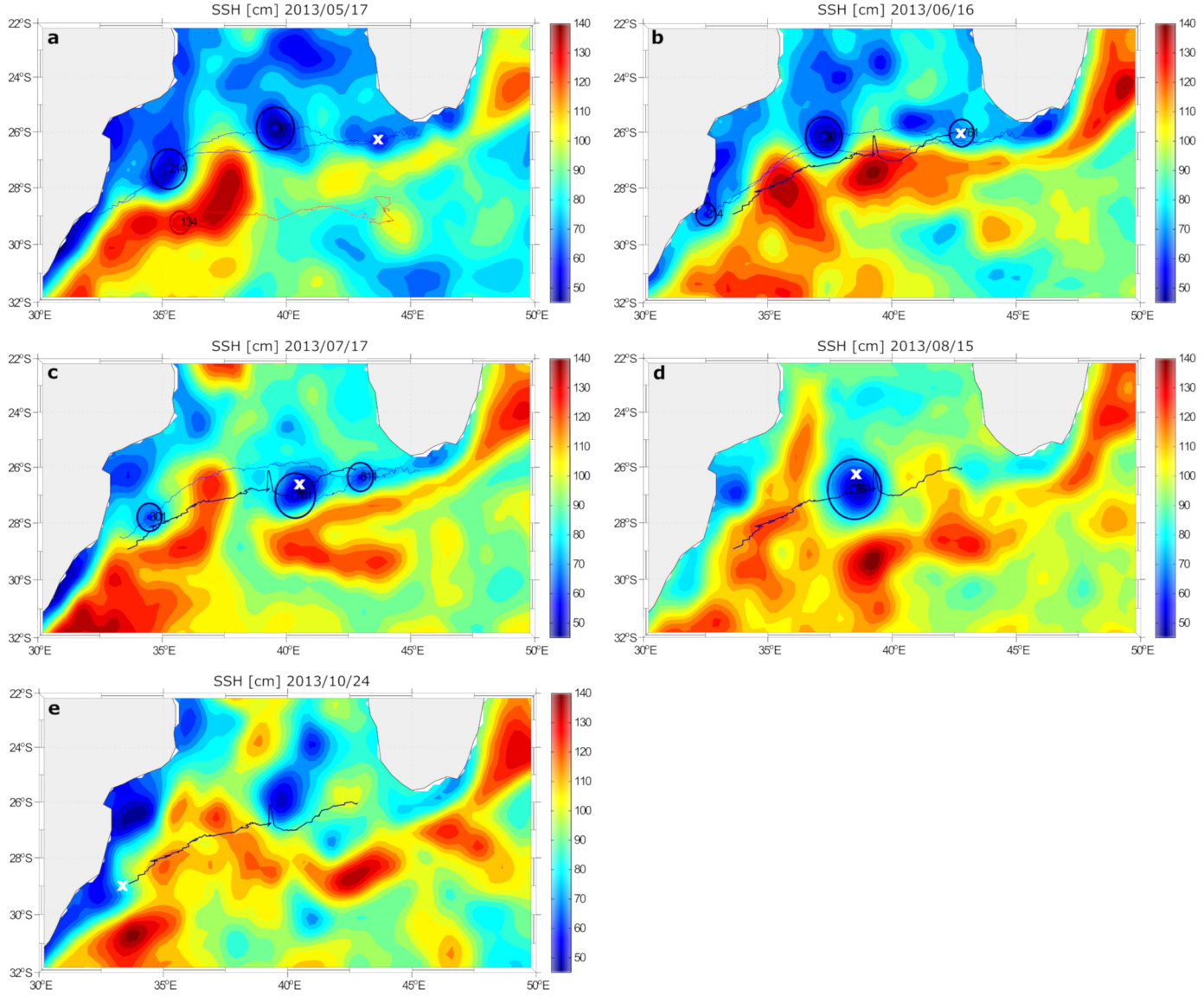

Fig. 2. Satellite images illustrating the life cycle of the cyclonic eddy studied. Sea surface height (SSH in cm) for (a) 17 May 2013 before the eddy was formed, (b) 16 June 2013 when the eddy appeared for the first time with closed contour line, (c) 17 July 2013 when the eddy was sampled, (d) 15 August 2013 when the eddy was at its maximum SSH, (e) 24 October 2013 when the eddy disappeared off the South African shelf edge. The white cross indicates the eddy sampled. The blue lines show the path of the eddies from the mesoscale eddy tracking algorithm from Halo et al. (2014). The thick blue line is the eddy sampled during this study. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

3.3. Mesozooplankton biomass and species composition

Along the transect, zooplankton settled volume ranged from 0.05 to 0.42 mL m^{-3} and dry biomass from 0.21 up to 14.84 mg m^{-3}, whereas the shelf contained zooplankton in much higher concentrations, as expected (0.8–2.7 mL m^{-3} and 20–40 mg m^{-3} for settled volume and biomass, respectively; Fig. 6a). A peak in biomass was distinguishable at stations 48–51 on the western side of the eddy, which did not coincide with the enhanced patch of Chl *a* (*i.e.* stations 44–47). No significant differences were observed between day and night biomass (ANOVA, $p > 0.05$). The most abundant zooplankton taxa found were mostly small copepods: *Oncaea* spp., *Oithona* spp., *Acrocalanus* spp., *Paracalanus* spp. and *Clausocalanus* spp. (Table 1). Copepod nauplii and copepodites of large and small calanoid copepods were also highly abundant together with appendicularians and chaetognaths.

The cluster analysis and the PCA, both performed on the zooplankton composition, highlighted four distinct groups amongst the stations sampled during this cruise ($p < 0.001$, SIMPROF test, Fig. 6b and d). First, the stations on the eastern and western side of the transect (30, 31, 32, 34, 36 and 52, 53, 54; Cluster 4) had a very similar composition and were the most different from all the other stations. Within the eddy, we found that station 50, which had a high zooplankton biomass (12 mg m^{-3}), was very similar to two stations on the shelf (26 and 28; Cluster 1). The second and third groups were slightly more similar to each other compared to the other stations, yet Cluster 2 grouped the western stations of the eddy, *i.e.* 48, 49 and 51, with the shelf station 29. When looking at the PCA only, which explains 77% of the total variability, we can see that Clusters 1 and 2 are on the negative side of PC1 and are opposed to Cluster 4, suggesting a stronger relationship between the shelf and the western side of the eddy than with the other stations outside the eddy. Cluster 3 is not well represented on the PC 1–2 plan. Cluster 1 was mostly influenced by small calanoid copepodites and *Paracalanus* spp., while Cluster 2 was influenced by *Oncaea* spp, copepod nauplii, *Oithona* spp., appendicularians and large calanoid copepodites (Fig. 6c). None of the following diversity indices showed differences throughout the transect: species richness

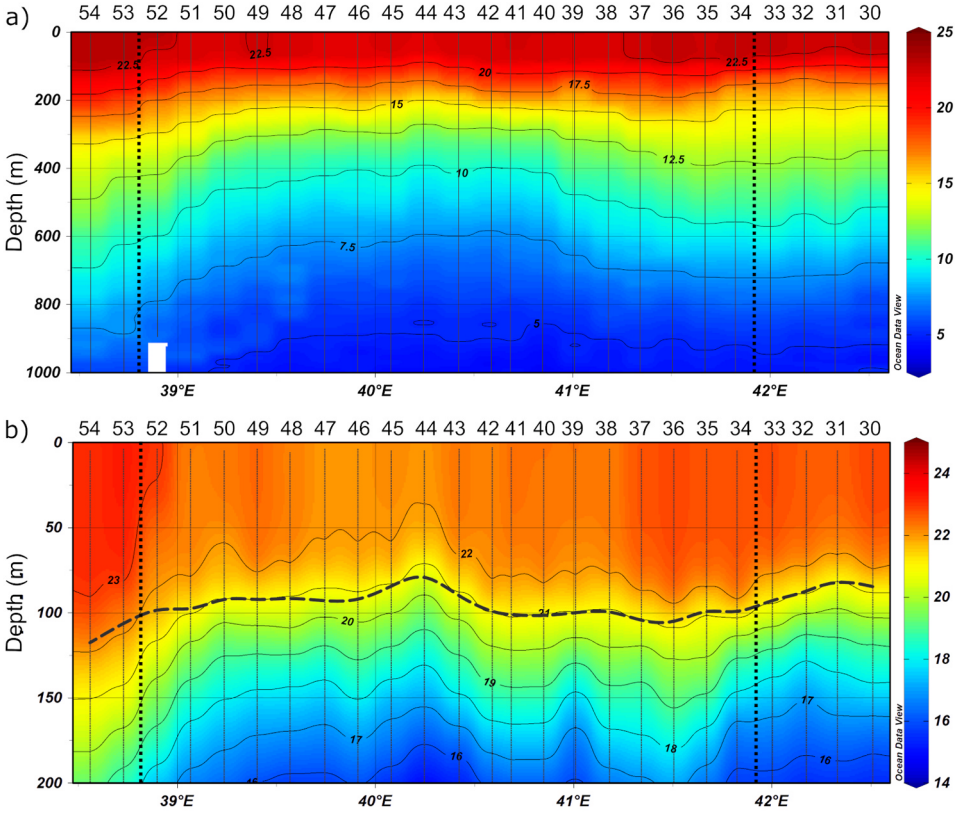

Fig. 3. Temperature (°C) profile along the transect across the eddy (stations 30–54) to a depth of 1000 m (a) and 200 m (b). The dashed line in the lower panel shows the mixed layer depth and the other lines correspond to the isotherms. The two vertical dotted lines indicate the eddy perimeter.

(30.5 ± 10, n = 28), Shannon Index (2.24 ± 0.49) and Pielou's evenness index (0.7 ± 0.06). The lack of differences in these diversity indices together with the similarities in the species composition observed during the study (Table 1 and Fig. 6c) suggests that the station groupings were due to differences in abundances of several species rather than the presence or absence of certain key species. No significant differences in abundance between day and night were observed for any of these specific taxa or species (ANOVA, $p > 0.05$).

4. Discussion

The productivity of mesoscale eddies is influenced by many factors, such as the eddy size, its age, the source of the water masses and/or the interaction with wind and land (e.g. Gaube et al., 2014; Huggett, 2014; Landry et al., 2008; Mackas et al., 2005b; Strzelecki et al., 2007). The cyclonic eddy which is the focus of this study was relatively young (approximately one month old), and was evidently associated with a strong geostrophic current (approximately 1 m s^{-1}; Barlow et al., 2017) flowing along its south-eastern periphery. This ultimately flowed into a region of positive sea surface height forming an anticyclonic eddy. This flow resembles the deep-reaching jet first described by de Ruijter et al. (2004) that was later interpreted as flow "pulses" originating from the discontinuous South East Madagascar Current (Quartly et al., 2006; Srokosz et al., 2015). The MODIS images reveal a surface filament of Chl *a* emanating from the Madagascar shelf which then streams into the cyclonic eddy, presumably coincident with the strong current, suggesting a link between the two areas at the time of sampling.

Chlorophyll *a* concentration was clearly enhanced at four stations along the transect with values close to 2 mg m^{-3}, while the region outside of the eddy was comparatively low, not exceeding 1 mg m^{-3}. The maximum Chl *a* concentration measured in this study is in the same range as earlier observations in the Mozambique Channel, as well as

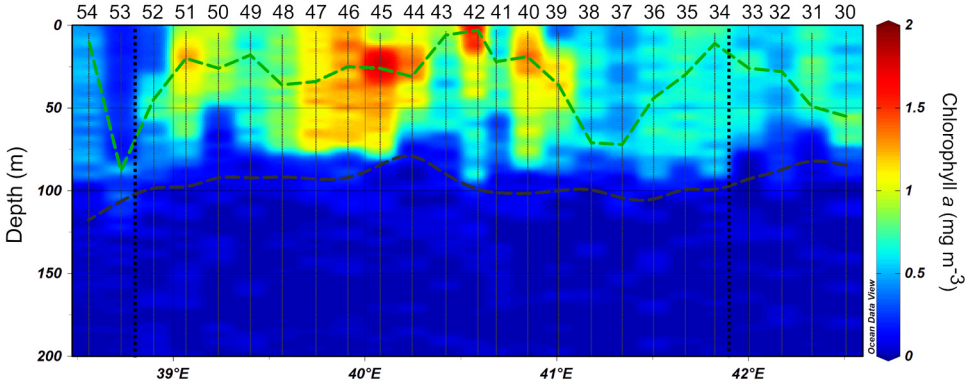

Fig. 4. Chlorophyll *a* concentration (mg m^{-3}) along the transect across the eddy. The dark dashed line corresponds to the depth of the mixed layer and the green dashed line to the maximum Chlorophyll *a*. The two vertical dotted lines indicate the eddy perimeter. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

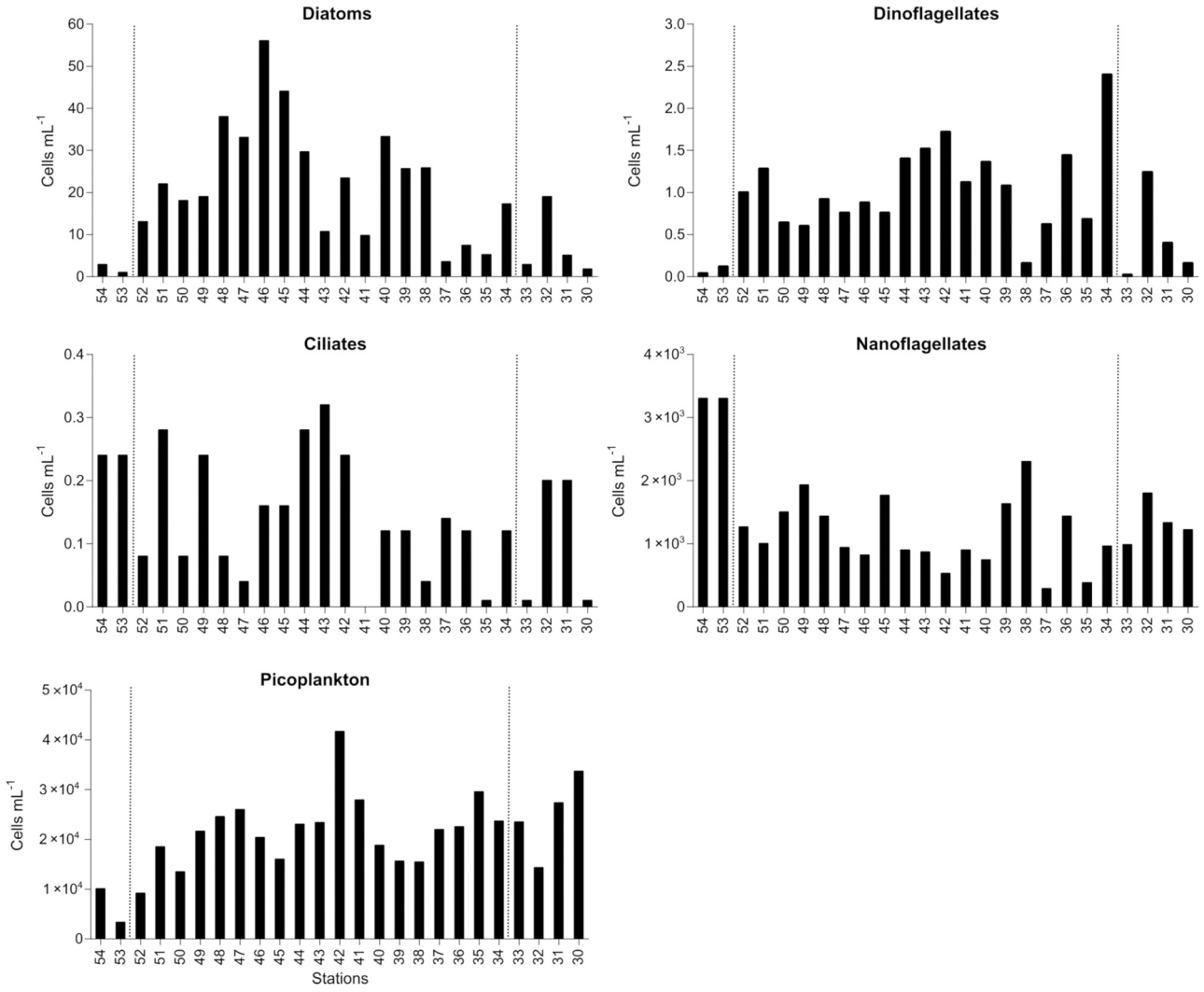

Fig. 5. Concentrations (cell mL^{-1}) of diatoms, dinoflagellates, ciliates, nanoflagellates and picoplankton from the surface for all the stations along the transect crossing the eddy. The eddy perimeter is indicated by dotted vertical lines.

those in other oligotrophic areas in response to an increase in nutrient availability (Barlow et al., 2014; Zubkov and Quartly, 2003; Brown et al., 2008). An unusual observation was the even vertical distribution of enhanced Chl *a* in the UML, which contrasts with other cyclonic eddies where a strong, thin and deep Chl *a* maximum layer is often measured, close to where the nutrients are upwelled (Bibby et al., 2008; Hanson et al., 2007; Huggett, 2014; McGillicuddy et al., 1999; Nencioli et al., 2008; Srokosz and Quartly, 2013). Such evenly distributed Chl *a* suggests high vertical mixing rates within the UML, perhaps induced by surface heat loss or surface wind stress (Feng et al., 2007). Photo-adaptation measurements of phytoplanktonic cells also suggested that the upper layer was well-mixed during the survey (Barlow et al., 2017).

The patch of enhanced Chl *a* was characterised by a higher proportion of diatoms compared to the other stations, while picoplankton, nanoplankton, dinoflagellates and ciliates were distributed homogenously along the transect. The abundances of these groups were in the same range of values found in other oligotrophic areas (Paterson et al., 2007; Quevedo et al., 2003; Sanders et al., 2000) although it seems that ciliate abundances were relatively low compared to the literature (Paterson et al., 2007 and reference therein). In oligotrophic environments, diatoms are often associated with sudden increases of nutrients as they respond rapidly to nutrient input compared to other smaller autotrophic cells (Barber and Hiscock, 2006; Brown et al., 2008; Nencioli et al., 2008; Rii et al., 2008). Barber and Hiscock (2006) stressed, however, that all phytoplankton taxa benefit from nutrient pulses. Diatoms, due to their fast growth rates, can "overprint" the other phytoplankton communities, but would not replace them. Other studies also seem to support this scenario of "overprinting" rather than "succession" (*e.g.* Brown et al., 2008; Hlaili et al., 2014; Linacre et al., 2010; Mahaffey et al., 2012, McAndrew et al., 2008). In this study however, it remains to be proven that nutrients were advected into the UML. Indeed, nutrient concentrations in the UML (data shown in Barlow et al., 2017) were low and only a slight doming of the isotherms was visible despite the eddy still spinning up. The low nutrient concentrations in the UML could be a consequence of nutrient uptake by autotrophs, being as rapid as the rate of supply (McGillicuddy and Robinson, 1997). It is also possible that the eddy core was highly influenced by the water entrapped during formation (Early et al., 2011; Greenwood et al., 2007; Thompson et al., 2007). In the Leeuwin current, diatoms entrapped on the shelf during eddy formation were found to grow in low nutrient concentrations and to occur even long after the eddy moved offshore (Thompson et al., 2007). In this eddy, the higher proportion of diatoms may be linked to the Madagascar shelf water, being either trapped during eddy formation or fed via the cross-shore filament as shown in the MODIS images. The higher abundance of Chl *a* and diatoms at stations 44–47 could also be related to higher phytoplankton growth rates, exceeding losses (Behrenfeld, 2010 and references therein). Losses could either be due to an increase in stratification

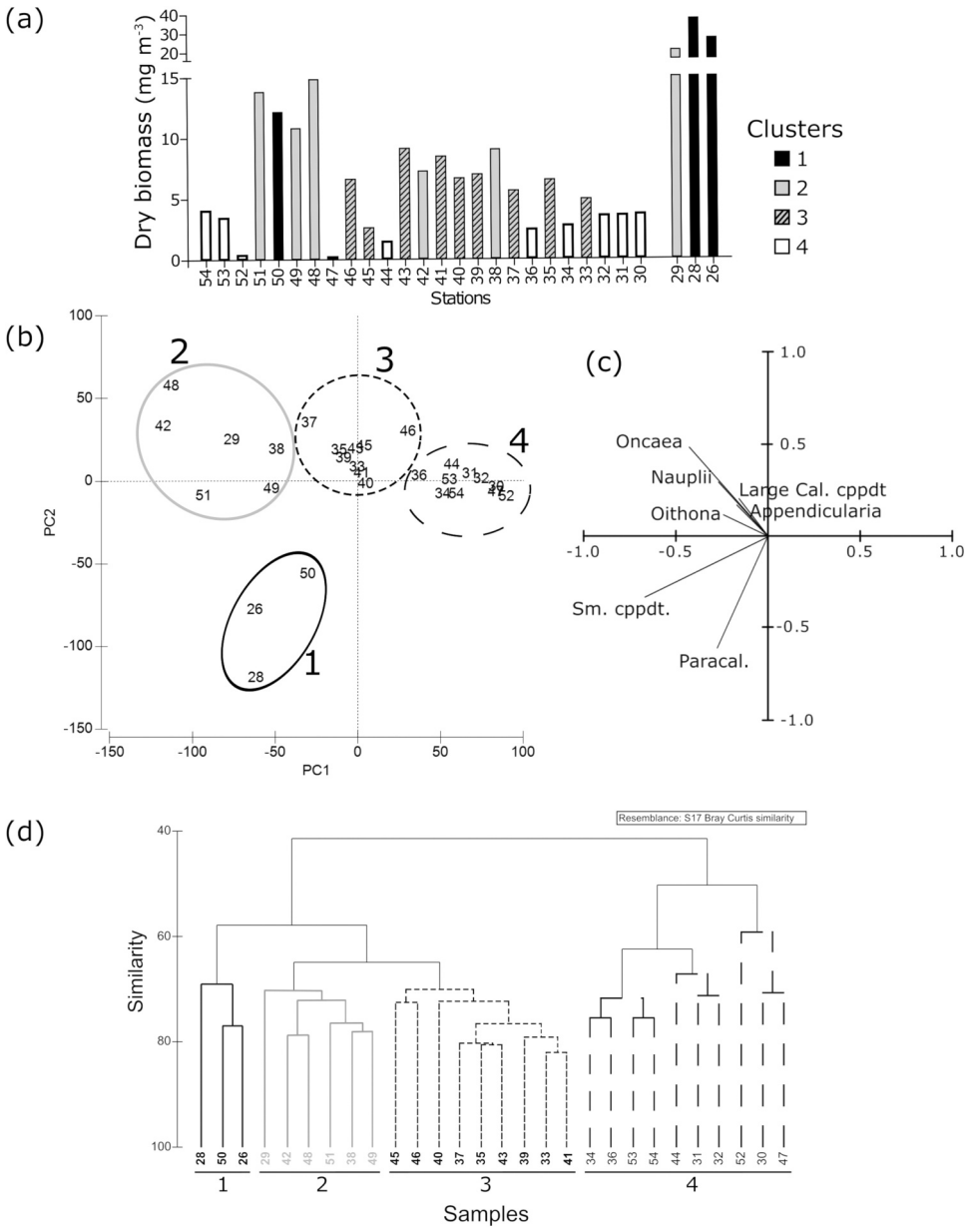

Fig. 6. (a) Zooplankton dry biomass (mg m^{-3}) for all the stations along the transect crossing the eddy and the three shelf stations (29, 28, 26). (b) Principal Correspondence Analysis (PCA) on the zooplankton species composition and (c) the vector plot showing only the taxa with a correlation coefficient higher than 0.2. (d) Dendrogram showing the cluster analysis on the zooplankton species composition for all the stations. The clusters (1 – 4) originated from the cluster analysis (d). (For (c) the abbreviations are as follows: Paracal.: *Paracalanus* spp; Sm. cppdt.: Small calanoid copepodites; Large Cal. cppdt: Large calanoid copepodites).

and/or to grazing. Considering the lower zooplankton abundance at these stations, low grazing pressure as well as higher growth rates could explain this higher abundance of diatoms.

Zooplankton biomass was highest on the shelf and on the western side of the eddy (stations 48–51). Zooplankton biovolume measured inside the eddy was in the same range as that found on average in cyclonic eddies in the Mozambique Channel (approx. 0.3 mL m^{-3}), but it never reached the highest values found previously in a well-developed cyclonic eddy (1.25 mL m^{-3}; Huggett, 2014).

Retention of zooplankton organisms in eddies has sometimes been associated with DVM behaviour. By remaining deeper within the eddy, organisms may avoid lateral mixing and advection associated with the highly turbulent upper layer and thus remain longer within the eddy (*e.g.* Mackas et al., 2005b). In this study, DVM did not seem to explain the similarity of zooplankton species composition and thus their retention within the eddy. It is worth noting that most of the zooplankton species caught do not have an enhanced vertical migratory behaviour. Only a few specimens of true vertical migrators such as euphausiids, amphipods and large copepods (*e.g. Euchaeta* or *Pleuromamma*) were caught. Some of these organisms, especially the larger ones, are strong swimmers and may have avoided the nets.

High zooplankton biomass has been observed previously in the core of cyclonic eddies and was assumed to be in response to the high primary production due to the upwelling (Landry et al., 2008). Other authors found higher zooplankton densities at the periphery of cyclonic eddies instead, as was observed in our study. Some have suggested this to be an accumulation resulting from high production in the core being pushed outwards by the natural divergent flow of (intensifying) cyclonic eddies (Goldthwait and Steinberg, 2008; Hernández-León et al., 2004). A similar scenario was drawn from studies focusing on micronekton and top-predators (Sabarros et al., 2009; Sánchez-Velasco et al., 2013; Tew-Kai and Marsac, 2009). Others have attributed the

Table 1
Mean abundances (ind m^{-3}) and relative abundances (% of total) of zooplankton species collected with a bongo net (200μm mesh size) during the cruise outside the eddy in the eddy and on the shelf.

Taxa	Outside Eddy		Eddy		Shelf	
	ind m^{-3}	%	ind m^{-3}	%	ind m^{-3}	%
Canthocalanus pauper	0.39	0.18	0.75	0.17	5.33	0.88
Undinula vulgaris	0.32	0.15	0.67	0.15	7.82	1.29
Subeucalanus spp	1.12	0.53	3.72	0.83	10.96	1.81
Acrocalanus spp	3.51	1.65	12.75	2.84	22.50	3.70
Calocalanus spp	2.02	0.95	4.59	1.02	3.15	0.52
Paracalanus spp	6.53	3.07	22.45	5.00	75.96	12.51
Clausocalanus spp	11.29	5.31	19.31	4.30	18.73	3.08
Acartia spp.	2.65	1.25	3.53	0.79	2.66	0.44
Oithona spp. (all stages incl.)	19.24	9.05	42.83	9.54	50.86	8.38
Oncaea spp (all stages incl.)	23.10	10.86	56.97	12.69	38.50	6.34
Corycaeus spp (all stages incl.)	9.44	4.44	12.76	2.84	26.80	4.41
Subeucalanus spp. copepodites	3.52	1.66	14.39	3.21	29.43	4.85
Euchaeta spp copepodites	4.46	2.10	8.22	1.83	15.89	2.62
Other large Calanoid copepodites	21.33	10.03	28.88	6.43	20.18	3.32
Small Calanoid copepodites	25.78	12.12	62.26	13.87	126.48	20.83
Copepod nauplii	4.85	2.28	23.69	5.28	38.62	6.36
Radiolaria	8.57	4.03	15.58	3.47	3.88	0.64
Foraminifera	3.18	1.50	8.34	1.86	2.26	0.37
Bivalve Larvae	2.92	1.37	3.75	0.84	0.48	0.08
Siphonophora	0.33	0.16	1.95	0.43	10.26	1.69
Heteropoda	1.82	0.86	5.77	1.29	3.07	0.51
Limacinidae	1.52	0.71	5.30	1.18	2.02	0.33
Ostracoda	7.28	3.42	14.48	3.23	4.28	0.70
Chaetognatha	11.52	5.42	12.69	2.83	10.97	1.81
Appendicularia	11.11	5.22	25.55	5.69	29.72	4.89
Others	24.86	11.69	37.62	8.38	46.40	7.64
Total	**212.66**	**100**	**448.77**	**100**	**607.22**	**100**

enrichment of micronekton and fish larvae at the periphery of cyclones to the entrainment of coastal waters as the eddy travelled parallel to the coast (Holliday et al., 2011; Sabarros et al., 2009; Sánchez-Velasco et al., 2013). This latter mechanism may explain the high zooplankton biomass and the similarities in species composition between the western side of the eddy and the Madagascan shelf found in our study. Indeed, the strong geostrophic current flowing on the south-eastern edge of the eddy could have entrained shelf waters with their associated zooplankton community into the eddy. Similar examples of cross-shelf entrapment of organisms have been identified in other oceanic regions (Atwood et al., 2010; Holliday et al., 2012, 2011; Mackas et al., 2005a; Waite et al., 2007). In the Leeuwin Current, similarities in plankton between warm-core eddies and the shelf were also attributed to the source water and the "jets", or filaments, feeding into these eddies (Muhling et al., 2007; Strzelecki et al., 2007; Thompson et al., 2007; Waite et al., 2007). The young age of the eddy (*i.e.* just one month old) may also help to explain the similarities in zooplankton assemblages between the shelf and eddy periphery (Holliday et al., 2012, 2011). A more mature eddy would probably have lost part of its shelf signature as it interacted with other water masses and moved away from the South East Madagascar current. The zooplankton assemblages at the stations outside of the eddy were also extremely similar to each other (Cluster 4 in PCA), suggesting that the influence of the shelf was restricted to the eddy only, and that the eddy was an enclosed feature which did not lose any biological material to the outside. This is also reinforced by the fact that the eddy was still intensifying.

The stations on the shelf were chosen in accordance with the preliminary hypothesis that the water masses within the core of a cyclonic eddy are more similar to the area of eddy formation. However, the satellite data show that the course of the current flowing towards the eddy does not seem to pass through the shelf stations we sampled. Unfortunately, we cannot clarify this point from the existing dataset. For our hypothesis to be valid, it would imply that the zooplankton community on the shelf is relatively homogeneous and/or that particles released on the whole of the south coast of Madagascar are entrapped by this current. In fact, another study conducted on the shelf at the same time showed that the copepod species composition was relatively homogeneous across the southern shelf of Madagascar (Z. Rasoloarijao pers. comm.). Srokosz et al. (2015), using a Lagrangian particle trajectory model, also considered the whole south coast as one single region from which to release particles, while de Ruijter et al. (2004) showed that cyclonic eddies seem to draw their waters from the inshore side of the South East Madagascar Current, without making a further distinction between the eastern and the western side of the Madagascar shelf. Although the stations were grouped distinctively according to their zooplankton species composition, the differences were only in term of abundance of several species rather than of a few indicator species. This was confirmed by the lack of differences in diversity indices along the transect and the absence of unique species at any of the stations. The main zooplankton species found were mostly small-sized omnivorous/herbivorous species which are typical of oligotrophic waters (Gallienne and Robins, 1998).

Generally, the functioning of eddies is characterised by the eddy type (cyclonic vs. anticyclonic), its status (intensifying or decaying) and its source and trajectory (oceanic vs. coastal) (Benitez-Nelson and McGillicuddy, 2008; Gaube et al., 2014; Owen, 1981). This study has reinforced the importance of these parameters and especially the influence of the cross-shore transport via a filament associated with the geostrophic current flowing on the south east of the eddy, entraining material from the Madagascan shelf into the eddy. The young age of the eddy at the time of sampling also likely impacted on the intensity of the processes discussed above.

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