Zooplankton size and distribution within mesoscale structures in the Mozambique Channel: a comparative approach using the TAPS acoustic profiler, a multiple net sampler and ZooScan image analysis

A. Lebourges-Dhaussy<sup>a,∗</sup>, J. Huggett<sup>b,c</sup>, S. Ockhuis<sup>b</sup>, G. Roudaut<sup>a</sup>, E. Josse<sup>a</sup>, H. Verheye<sup>b,c</sup>

<sup>a</sup>Institut de Recherche pour le Développement (IRD), UMR LEMAR 195 (UBO/CNRS/IRD/Ifremer), Campus Ifremer, BP 70, 29280 Plouzané, France
<sup>b</sup>Oceans and Coastal Research, Department of Environmental Affairs, Private Bag X2, Roggebaai 8012, Cape Town, South Africa
<sup>c</sup>Marine Research Institute, University of Cape Town, Private Bag, Rondebosch 8001, Cape Town, South Africa
<sup>d</sup>Institut de Recherche pour le Développement (IRD), UMR 212 EME (IRD/IFREMER/UM2), Avenue Jean Monnet, BP 171, 34203 Sète cedex, France

* Corresponding author:
Anne.Lebourges.Dhaussy@ird.fr,
Tel. +33 2 98 22 45 05
Fax. +33 2 98 22 45 14

<table>
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<tr>
<th>Author name</th>
<th>Email address</th>
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<tr>
<td>Anne Lebourges-Dhaussy</td>
<td><a href="mailto:anne.lebourges.dhaussy@ird.fr">anne.lebourges.dhaussy@ird.fr</a></td>
</tr>
<tr>
<td>Jenny Huggett</td>
<td><a href="mailto:jhuggett@environment.gov.za">jhuggett@environment.gov.za</a></td>
</tr>
<tr>
<td>Samantha Ockhuis</td>
<td><a href="mailto:sockhuis@environment.gov.za">sockhuis@environment.gov.za</a></td>
</tr>
<tr>
<td>GildasRoudaut</td>
<td><a href="mailto:gildas.roudaut@ird.fr">gildas.roudaut@ird.fr</a></td>
</tr>
<tr>
<td>Erwan Josse</td>
<td><a href="mailto:erwan.josse@ird.fr">erwan.josse@ird.fr</a></td>
</tr>
<tr>
<td>Hans M. Verheye</td>
<td><a href="mailto:hverheye@environment.gov.za">hverheye@environment.gov.za</a></td>
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ABSTRACT
Two surveys were conducted onboard the R/V ANTEA in the Mozambique Channel in 2009 (November) and 2010 (April/May), in order to study the impact of mesoscale eddies on the zooplanktonic compartment of the ecosystem; this was the first goal of this paper. Complementary approaches were used to sample zooplankton: (1) acoustics with a TAPS™ multifrequency zooplankton profiler, and (2) biological sampling using a multinet device, samples from which were processed by classical settled biovolume measurements, followed by (3) Zooscan imaging and analysis to obtain information on biovolume, size and taxonomic composition. The second goal of this paper is thus a comparison of these methods. There was a large overlap in the size range detected by all methods, but this study showed that each method was more favorable for a particular size fraction of the population: the microzooplankton (<0.1 mm ESR) for the TAPS, and the larger sizes (>3mm ESR) for the Multinet and ZooScan. In the case of the 2009 cruise, during which a well established cyclone/anticyclone dipole was studied, despite the methods’ specificities, all results were in good agreement, and showed a higher concentration of zooplankton in the cyclonic feature than in the anticyclonic one, and very stable distributions. The TAPS also detected high very surface [0-22m] concentrations of what was possibly microzooplankton in the cyclonic feature. In 2010, two types of cyclonic and anticyclonic features were sampled during the cruise, with different life histories and levels of stability. The results for this cruise varied depending on which size component of the population was addressed, with either the cyclonic or anticyclonic feature having higher planktonic biomass. Species composition did not clearly vary between mesoscale features, differences being mainly a matter of relative biovolume. High variability within the system thus results in an equivalent instability in the zooplankton distribution. 

Keywords: Mozambique Channel, Zooplankton, TAPS, Acoustics, Multinet, ZooScan, Eddies

1. Introduction
The Mozambique Channel is characterized by the southward circulation of a global flux, that cannot be seen as a steady current (Quartly and Srokosz, 2004) as it is dominated by a train of eddies, particularly large anticyclonic ones of diameters of more than 300 kms. They propagate each year at a frequency of four per year, and at speeds of 3 to 6 km per day (Backeberg and Reason, 2010) along the western edge of the channel (de Ruijter et al., 2002; Schouten et al. 2003), to reach the bottom of the channel and propagate southward, generating disturbances in the Agulhas Current (Backeberg and Reason, 2010).

Mesoscale physical features such as fronts or eddies are typically the flow type with the largest kinetic energy in the ocean (besides the tides) (Capet et al., 2008) and this mechanical energy may become accessible for augmenting trophic energy available to biological organisms (Bakun, 2006) creating attractive pelagic habitats for higher trophic level marine organisms (Godø et al., 2012). The upwelling which results from the divergence of the surface water in the cyclonic eddies, leading to negative sea level anomaly (SLA) at their centers, may transport nutrients into the euphotic zone and facilitate its enrichment (McGillicuddy et al., 1998, Oschlies and Garçon, 1998). The anticyclonic features that result in a local downwelling caused by a positive SLA in the center of the eddy (Bakun, 2006) may concentrate surface material (Yebra, 2005). Various works have shown the importance of eddies in oligotrophic areas for increasing the nutrients and primary productivity (Falkowski et al., 1991; McGillicuddy and Robinson, 1997; McGillicuddy et al., 1998; Oschlies and Garçon, 1998; Seki et al. 2001; Benitez-Nelson et al., 2007; Tew-Kai and Marsac, 2009; Kolasinski et al., 2012). The periphery of eddies may also be enriched by at least two possible phenomena: one is the advection of rich shelf waters when the cyclonic or the anticyclonic eddy passes close to the coast and is then driven offshore (Machu, 2001; Quartly et al., 2004), another is the accumulation of the upwelled deep material from the center of the cyclonic features.

The frontal areas between eddies have been observed to be interesting for top-predators like frigate birds in the Mozambique Channel, particularly around the cyclonic features albeit not exclusively (Weimerskirch et al., 2004; Tew-Kai and Marsac, 2010). The advection of coastal nutrient-rich waters has been observed in this case (Sabarros et al., 2009). Indeed high concentrations of micronekton are measured at the feature’s periphery, with by day a higher
probability to encounter large aggregations when the SLA gradient is high (Sabarros et al., 2009). An indication of high abundance of micronekton related with a cyclonic feature has been observed also in Hawaiian waters (Drazen et al., 2011). In the central Gulf of Mexico, a comparison of a biomass proxy from ADCP data, in a cold-core mesoscale feature separating two warm-core features, showed that the cold-core region was a zone of local aggregation of zooplankton and micronekton (Zimmerman and Biggs, 1999). However, the opposite observation has also been made in the Indian Ocean off Western Australia, with microzooplankton biomass clearly higher in a warm-core eddy than in a cold-core one (Paterson et al., 2007). Studies on zooplankton and micronekton in these areas are still few, the exact mechanisms of the eddy-induced effects are still controversial (Gruber et al., 2011) and there are also few papers on the vertical stratification of the organisms, such as the Mulhing et al. (2007) work showing a stronger vertical structure of the ichthyoplankton assemblages in a cold-core eddy than in a warm-core eddy. There is a real need to document the zooplankton at a fine scale, in relation to the mesoscale features, and more generally with the hydrologic parameters of the area.

This is one of the aims of this paper, which includes also a methodological component, as a Multinet plankton sampling system has been coupled for the first time in this area with an acoustic zooplankton profiler (TAPS™).

2. Material and methods

2.1 Equipment and survey protocol

The data considered here originate from two cruises performed onboard the R/V ANTEA in the Mozambique Channel. Cruise MC09B during November 2009 was concentrated in the southwest part of the channel (23.4°S-25.1°S/35.8°E-38°E), in order to study a previously characterized cyclone–anticyclone dipole. Cruise MC10A during April/May 2010 was more extensive spatially and located in the centre of the channel (15°S-22°S/39.2°E-43°E). This cruise had two parts with different scientific objectives: the first Leg was dedicated to the study of trophic relationships from the first level of the food chain (phytoplankton) to the intermediate level (micronekton) and to top predators (tuna and associated species). The second Leg was designed to investigate primary and secondary production processes. The strategy was to sample
along a transect at a high spatial resolution (15 nautical miles between stations) through a well-established dipole.

During these cruises, acoustic data were acquired from two types of equipment. The continuous data provided by the SIMRAD echosounder ER60 are the subject of another paper, Behagle et al. (accepted, this issue). The present paper focuses on the multi-frequency data provided by the TAPS-6™ (Tracor Acoustic Profiling System) profiler over a maximum depth of 200 meters. This equipment has been designed to detect micro- and mesozooplankton as it operates at 6 high frequencies (265, 420, 710, 1100, 1850, 3000 kHz) (Holliday and Pieper, 1980). During these cruises, the lowest frequency malfunctioned, thus processing was based on the other 5 frequencies. Unfortunately the 1850 kHz frequency also malfunctioned at some of the 2010 stations. A total of 14 profiles were acquired during the MC09B cruise and 35 profiles were acquired during the MC10A cruise, enabling sampling of the different types of mesoscale structures during both cruises.

Acoustic data were acquired in combination with physico-chemical measurements using a CTDO sensor (SBE 911) for temperature, salinity and oxygen data, while light information was acquired with a PAR sensor. Rosette sampling provided information on discrete chlorophyll a concentration as the data provided by the fluorescence profiler sensor were unfortunately not usable (Lamont et al., submitted, this issue). Zooplankton sampling was conducted using a Hydrobios Multinet type Midi (200-µm mesh; mouth area 0.25m²). The Multinet was towed obliquely at a speed of ~1 m s⁻¹, from a depth of 200 m to the surface, collecting zooplankton samples from 5 depth layers. The TAPS-6 was mounted on the Multinet. All zooplankton samples were fixed and preserved with 4% v/v formaldehyde buffered with CaCO₃ and stored in plastic jars for later taxonomic and dry weight analyses. Details of these analyses can be found in Huggett (submitted, this issue).

2.2 Data processing

In terms of acoustic data, only TAPS-6 data are considered here. As denoted in §2.1, the 265 kHz transducer malfunctioned, thus processing was based on the frequency range 420 kHz-3MHz for the majority of the stations and without the 1850 kHz for those presenting a problem on that
frequency. The size range explored in the inversion process was 0.05-3 mm. The basic algorithm to process the multi-frequency data is an inversion algorithm (Holliday, 1977a; Greenlaw and Johnson, 1983), with the non-negative least-squares (NNLS) method (Lawson and Hansen, 1974) most commonly used. An abundant literature shows that the method has been successfully applied to small zooplankton (Kleppel et al., 1988; Holliday et al., 1989; Pieper et al., 1990; Smith et al., 1992; Napp et al., 1993, Lebourges-Dhaussy et al., 2009), krill (Greenlaw, 1979), mesopelagic fishes (Kalish, 1986), and epipelagic fishes (Holliday, 1977b, 1985).

The TAPS-6 was used in “cast mode” for the MESOBIO program, i.e. with the TAPS-6 in a horizontal position while profiling the water column, at a descent speed of 0.5 m/s, sampling at each ping a small volume of about 5 l, thus focusing on small and abundant organisms such as copepods, with the larger and less abundant ones such as euphausiids having less chance to pass through this small volume (Pieper et al., 2001). The data acquisition window is centered at 1.30 m from the TAPS-6 transmitting face. Each ping results in an average of 5 sampling points around and at this central position. The acquisition configuration was set to an average of 4 pings per data sample at a given depth in 2009, but at 1 ping in 2010. Vertical binning of the data was used to obtain regularly spaced values for a final vertical resolution in the present case of 1 meter. This resulted in a new average of about 2 samples per binned data during 2009, and a new average of about 8 samples per binned data in 2010. Each Sv (volume backscattering strength) data point finally obtained is therefore the result of averages of about 40 samples. The inversion algorithm (Greenlaw and Johnson, 1979) requires input from a model for the acoustic backscattering of small zooplankton organisms such as copepods. For the “cast” mode used here, where the sampled volume is small (~5 l), leading to a focus on the small and abundant organisms, the truncated fluid sphere (TFS) model (Holliday, 1992) is appropriate. The settings for g (density contrast between the organism and its surrounding water) and h (sound velocity contrast between the organism and its surrounding water) were kept to the values determined by D.V. Holliday (g = 1.12, h = 1.09; Holliday, 1992). Comparisons of biovolumes with the biological Multinet sampling were in accordance with these parameter settings in a previous study on the South-African shelf, performed with 5 frequencies from 420 kHz to 3 MHz (Lebourges-Dhaussy et al., 2009). The vertical resolution of the zooplankton profiles is 1 meter, which is the same as for the physical parameters, and allows small-scale vertical studies. The data
analysis provides profiles of biovolume per class of equivalent spherical radius (ESR). The number of classes retained must be no higher than the number of available frequencies. As a result of the malfunction of the 265 kHz and sometimes of the 1850 kHz, as well as the global size distribution obtained, the following four classes of ESR were defined for both cruises, in order to highlight meaningful differences in vertical distribution: 0-0.2 mm, 0.2-0.5 mm, 0.5-1 mm, and 1-3 mm. To assess the effect of suppressing the 1850 kHz for some of the stations, the results obtained with inversions based on 5 and on 4 frequencies were compared. The biovolume profiles obtained were identical, and the mean biovolume over the profiles as well as the patterns provided by each inversion configuration for the profiles by size class were very close (Figure 1).

A discriminant functional analysis performed on Sea Level Anomalies (SLA), geostrophic velocities and high-resolution bathymetry was used to classify each station as cyclonic, anticyclonic, divergence, frontal or shelf, as described in Lamont et al. (submitted, this issue). The number of TAPS stations per mesoscale structure and time of day (day or night) for each cruise is shown in Table 1, and the relationship between geostrophic velocity and SLA for each station during both surveys is shown in Figure 2a. The mesoscale structures are clearly separate during 2009 because mainly cyclonic, anticyclonic and frontal classes were represented, which displayed more strongly contrasting characteristics. In 2010 there were very few frontal stations, with weaker geostrophic velocity compared with 2009, and many more divergence stations. This corresponded to weaker hydrographic phenomena, in particular low SLA (in absolute value) and low geostrophic velocity. The spatial distribution of the stations is shown in Figure 2b. The area sampled during MC09B was much farther south than during MC10A. Furthermore, there were no divergence stations sampled in 2009, and very few frontal stations sampled in 2010. The shelf stations were unique for both years thus patterns cannot really be discerned.

2.3 Image analysis of zooplankton
Zooplankton samples (or aliquots thereof) from the MultiNet were subjected to image analysis using the Hydroptic ZooScan. The overall approach, which includes sample preparation, scanning with ZooScan hardware and image processing with ZooProcess and Plankton Identifier software, is described in detail by Gorsky et al. (2010), who also discuss the building and validation of training sets, the selection of classification algorithms and the accuracy of body size
and biomass estimations that can be derived from the ZooScan system. In brief, after calibration of the ZooScan in respect of pixel size and range of grey level, a background blank scan using filtered seawater was obtained daily prior to the scanning of the samples. The large frame was used, and blanks and samples were scanned at a high resolution (2400 dpi). The fixative of each sample was first removed and replaced with freshwater at room temperature to avoid air bubble formation; water was added to the scanning cell to ensure that all organisms were on the bottom of the cell and on the same plane level. Prior to digitizing a sample, as many animals as possible were manually moved around in the scanning cell using a soft cactus needle to separate specimens overlapping and touching one another and to avoid specimens from touching the frame edges. Whenever dissatisfied with this manual separation, the separation tool provided in ZooProcess was used once the sample was scanned.

Each scanned raw 16-bit grey image recorded by ZooProcess was normalized and converted to an 8-bit source image from which the background blank image was subtracted. After automatic removal of objects touching the sides of the frame, this final image was used for object detection and the extraction of measurement variables from each detected object; by default, only objects having an equivalent spherical diameter (ESD) of >0.3 mm are detected and processed. All images were checked for background subtraction and correct object contours by viewing segmented black and white images.

A learning set of selected categories was then created, which each contained digital images of individual objects of similar visual appearance (i.e. vignettes). Each folder represented a taxonomic group of organisms (e.g. copepods, chaetognaths, ostracods, etc.) or abiotic objects (e.g. bubbles, fibres and detritus) that were visually ‘dragged-and-dropped’ into the relevant folder. Exactly 200 such vignettes were extracted from each scanned image. This learning set was then used for the automatic classification of objects by applying the Random Forest classifier within Plankton Identifier, interfaced with ZooProcess, across all scanned images. The vignettes were subsequently validated (using XnView) by checking the automatic sorting and making corrections when necessary (i.e. by manually dragging incorrectly classified objects to the correct folder). Measurements of major and minor axes (mm) of each object were used to calculate biovolume (mm$^3$) based on ESD, where ESD volume = $4/3\pi (\text{Area}/\pi)^{3/2}$.
3. Results

3.1 Hydrographic structure of mesoscale features

3.1.1. MC09B survey

It is evident that each mesoscale feature in 2009 corresponded to typical profiles as shown for temperature and oxygen in Figures 3 and 4. The depth of the mixed layer (MLD) differed considerably between features, as did the slope of the thermocline, but the surface temperatures were very similar (25°C to 26°C for all structures). Anticyclonic and frontal profiles were quite similar, but cyclonic profiles differed strongly from the others with a much shallower mixed layer (Figure 4). There was a highly significant positive correlation between the SLA and the MLD (R = 0.95, p=1.51e-07) (Figure 5). The depth of the chlorophyll maximum increased from cyclonic (40-50 m) to frontal (60-120 m) to anticyclonic profiles (105-120 m). The chlorophyll maxima were similar for cyclonic (0.62 mg m⁻³, mean value) and anticyclonic (0.67 mg m⁻³) stations, and higher than at frontal (0.51 mg m⁻³) ones. Surface chlorophyll as well as integrated chlorophyll concentrations were clearly higher at anticyclonic stations (0.28 mg m⁻³, 68 mg m⁻²), compared with cyclonic (0.15 mg m⁻³, 27 mg m⁻²) and frontal (0.1 mg m⁻³, 34 mg m⁻²) ones. Station 4 stands out from other frontal stations, in that it had a shallow mixed layer and a fairly shallow and strong fluorescence maximum (60 m, 0.73 mg m⁻³).

3.1.2. MC10A survey

Station classification procedure was the same as for 2009, but for 2010 the variability within each group of profiles was higher (Figure 3), and the larger number of stations was more spatially extensive (Figure 2b). The MLD varied within the mesoscale structures, as did surface temperature, although remaining between 27 and 30°C for all structures, i.e. much warmer than during the MC09B cruise. Although the MLD was shallower for the cyclonic structures, the difference in MLD between structures was less marked in 2010 than in 2009 (Figures 3 and 4), and all four structures in 2010 had some stations with a relatively shallow mixed layer (Figure 3). There was also a positive correlation between the SLA and the MLD but it was weaker and less significant (R=0.40, p=0.014) (Figure 5). In each structure two groups of stations were apparent, with surface temperatures around 30°C for one group, and 28°C for the other group,
corresponding globally to Leg 1 and Leg 2 of the cruise, respectively. As in 2009, the depth of the chlorophyll maximum in 2010 varied from shallow at cyclonic stations (25-60 m), to intermediate at frontal (60-80 m) and divergence stations (40-95 m), to deep at anticyclonic stations (75-120 m). On average, values of the chlorophyll maximum were highest in the cyclonic (0.61 mg m$^{-3}$) and frontal (0.60 mg m$^{-3}$) structures, decreasing at stations in the divergence (0.46 mg m$^{-3}$) and anticyclonic (0.38 mg m$^{-3}$) structures. Peak integrated chlorophyll concentrations were observed at the cyclonic stations (on average 50.9 mg m$^{-2}$), with lower but similar values found in the three other structures (on average 41.9 mg m$^{-2}$ in anticyclonic, 42.6 mg m$^{-2}$ in divergence and 42.9 mg m$^{-2}$ in frontal structures respectively). In contrast, there was a gradual decrease in the average surface chlorophyll concentrations from cyclonic (0.25 mg m$^{-3}$) to divergence (0.24) to anticyclonic (0.23) to frontal (0.20) structures.

3.2 Integrated biovolume and size composition

Considering the possible presence of surface bubbles and thus the lack of surface values for some of the stations, the common depth range for which all stations from both years have data available is the 22-200 m range. Global comparisons are thus based on this depth range. However, for stations where the mixed layer was shallow, this surface layer may in fact be a very rich and important layer to consider, thus the results of both calculations are given (keeping in mind that there is a varying number of samples in the surface layer [0-22m] for all stations). Linear mixed-effects models were used to test the effect of methods on biovolume for each year. Each biovolume observation was classified according to the year in which the cruise was carried out. The year effect was treated as random variation around a population mean, and the sampling device was assessed as a fixed covariate. Such a mixed model combines an experimental factor (the method) and a blocking factor (the year) for which we use random effects. Results show that the sampling device strongly influenced the zooplankton biovolume (p<0.001): Multinet > TAPS[0-200m] > ZooScan > TAPS[22-200m]. In addition, mean zooplankton biovolume was always higher in 2010 than in 2009, as reported by Huggett (submitted, this issue) with plankton nets (Figure 6).

Different biovolume patterns in relation to the mesoscale structures were observed for the two years (Figure 7). In 2009 there were significant correlations between Multinet and TAPS[22-
200m] (p<0.1, R=0.92), between the ZooScan and TAPS[22-200m] (p<0.5, R=0.95) and also between the Multinet and the ZooScan (p<0.1, R=0.94). The correlation coefficients between the Multinet as well as the ZooScan results with the TAPS[0-200m] results, although quite high (0.75 and 0.74 respectively), were not significant (p=0.25 and 0.26). In 2010, none of these correlations were significant. Thus, although a consistent trend between the methods was observed for 2009, this was not the case in 2010.

In 2009, cyclonic stations were clearly the richest compared to frontal stations (medium mean biovolume) and in particular to anticyclonic stations, which displayed relatively low biovolume (Figure 7). The mean TAPS-derived values (for both depth ranges) were consistent with the estimates provided by the nets (Multinet and ZooScan) (Figure 7). Student’s t-tests of differences between the TAPS mean values over 22-200m were significant for cyclonic versus anticyclonic stations, and for the 0-200m means for the cyclonic versus frontal comparison; anticyclonic versus frontal were significantly different only for the nets results (Table 2). There was high biovolume at the surface [0-22m] in the cyclonic structures, corresponding to the depth of the mixed layer, but low surface biovolume in the other structures. Taking into account the surface layer highlights the dominance of the cyclonic features in terms of biovolume compared to the other features.

In contrast to 2009, the TAPS results for 2010 indicate lowest mean biovolume for the cyclonic and divergence structures, with higher biovolume for the anticyclonic and frontal structures, although the latter was represented by only two stations compared to the better sampled other three structures (cyclonic, anticyclonic and divergence; Figure 7). High surface concentrations in the shallow mixed layer of both frontal stations result in a biovolume maximum in the frontal features if the 0-200m mean value is used, but in the anticyclonic feature if the 22-200m mean value is used. The pattern inferred from the TAPS data contrasts with that from the nets: even though the mean biovolumes obtained from the TAPS were consistent with the values obtained with the nets, for one or the other method (ZooScan or Multinet) the trends between the features are different: for TAPS the anticyclonic structures indicate higher mean biovolume than the cyclonic structures, while the nets show the opposite. However, none of the differences between
the structures were significant except for the acoustic anticyclonic versus cyclonic and divergence comparisons when the surface values were removed (Table 2).

There were marked differences in the size composition of the zooplankton populations between the two cruises (Figure 8). In 2009 the smallest size class (0-0.2 mm ESR) was dominant in terms of TAPS-measured biovolume within the upper 200m, mainly through the influence of the surface layer at the cyclonic stations. This was due to a few stations with very high biovolume near the surface, and was not the case for the other features (Figure 8a). From the results for the 22-200 m depth range, which apply to all stations, the largest size class (>1 mm ESR) dominated for all three mesoscale features (Figure 9), particularly at anticyclonic stations, with more balanced contributions for the other three size classes. The cyclonic stations had the lowest contribution from the largest size class and the highest contributions of the 0-0.2mm and 0.5-1mm size classes. Size composition at the frontal stations was intermediate to that of the cyclonic and anticyclonic stations (Figure 9).

During 2010, in contrast to 2009, whenever there was a high concentration of small organisms in the surface layer, this was common to all four features (except for the “shelf” with only one station) (Figure 8b). For the 22-200m depth range, the largest size class contributed least and the smallest size class contributed the most to size composition in the anticyclonic features for both Legs (Figure 9). The contribution of the largest size class increased for frontal, then divergence and cyclonic equivalently during Leg1, but increased from divergence to cyclonic during Leg2. The contribution of the smallest size class decreased for frontal, then divergence, then cyclonic features. The proportion of biovolume within these two classes (smallest and largest) declined from Leg1 to Leg2, i.e. from the sampling of stable structures to the sampling of unstable and splitting structures, in favour of the 0.5-1mm size class (Figure 9). The second size class (0.2-0.5mm) was consistently the least represented in all structures, in both 2009 (except at anticyclonic stations) and 2010.

These observations allowed us to investigate relationships between the richness of a station in terms of TAPS-measured biovolume, and environmental parameters such as SLA, geostrophic velocity, depth and concentration of the chlorophyll maximum, and integrated chlorophyll
biomass (Table 3). There was a strong negative correlation between biovolume (total biovolume as well as for 3 of the 4 size classes) and SLA in 2009, but not in 2010. There was no apparent link with geostrophic velocity or with any of the chlorophyll data (Table 3). There was a negative correlation between mixed layer depth and biovolume, which was highly significant in 2009 \( (p = 9.2e^{-4}) \), but only apparent in 2010 for the smaller size class with a relatively low significance \( (p = 0.047) \).

3.3 Zooplankton vertical structure

Vertical sections of TAPS biovolume in relation to environmental conditions over the entire cruise route are shown in Figure 10a (2009) and Figure 10b (2010). To keep the same station numbering for comparison with Figure 6C of Huggett (submitted, this issue), stations 6, 7 and 8 in 2009, for which there were no TAPS data, are shown as missing data, as well as for the last “cyclonic” station of the Huggett figure. Vertical distribution of biovolume within each size class, in relation to the depth of the chlorophyll maximum, is shown in Figure 11 for all cyclonic and anticyclonic stations.

Highest biovolume densities in 2009 were clearly associated with cyclonic stations. Vertical structure in terms of temperature, oxygen and salinity was similar at all these stations, and zooplankton biovolume also displayed similar vertical distribution patterns, with biovolume mainly restricted to the upper mixed layer. This was particularly evident for the smallest size class, which displayed very low biovolume at the anticyclonic stations. There was no discernible pattern in biovolume vertical distribution for the second size class, except for areas of highest biovolume where maximum chlorophyll values were observed in the cyclonic features (Figure 11). Vertical distribution of the third size class resembled that of the smallest size class, although biovolume was more deeply distributed. At cyclonic stations, the highest concentrations of the 0.5-1mm class occurred above the depth of the chlorophyll maximum, while at the anticyclonic stations, the chlorophyll maximum depth coincided with the areas of highest biovolume (Figure 11). The largest size class was distributed throughout the entire water column with no strong pattern; however at cyclonic stations the layer of peak biovolume was located at the bottom of the mixed layer (around 50 m deep), coincident with the depth of the chlorophyll maximum (Figure 11).
The relationship between biovolume density and mesoscale structure was less clear in 2010. High densities were not encountered exclusively at cyclonic stations, and more saline, well oxygenated and cooler surface waters were common to each structure from station 19 onward to the end of the cruise, reflecting a mixture of different water masses (second Leg of the cruise, Figure 10b). These conditions appear to have different impacts depending on the size of the organisms. The smallest size class, although still largely restricted to the upper water column, was distributed over a somewhat broader depth range compared with 2009, with low densities penetrating the deeper less saline, less oxygenated and warmer part of the water column for the first 18 stations. The second size class occupied a deeper depth range, with highest concentrations around 50 m, associated with peak chlorophyll levels at cyclonic stations (Figure 11). Low to moderate densities also extended deeper into the water column during the first half of the cruise. The vertical distribution of the third size class was similar to that of the smallest size class, but penetrated much deeper into the water column from station 19 onwards, into a more saline and well oxygenated water mass. It should be noted that the logarithmic scale used to represent biovolume in these plots tends to magnify differences that are weak on a linear scale. The largest size class was distributed over the entire water column throughout the cruise, with no clear association with any of the hydrological parameters examined. Highest densities were associated with the depth range of the chlorophyll maxima (Figure 11).

Correlations between the profiles of biovolume with salinity versus biovolume with temperature for all stations (Figure 12) indicate some separation between mesoscale features. In 2009 cyclonic and anticyclonic stations were clearly separated by their correlation coefficient with temperature (oxygen gave the same results as temperature) which was highly positive and significant for the cyclonic stations. Frontal stations could not be distinguished from either cyclonic or anticyclonic stations. In 2010, this separation was not apparent - all stations had a highly significant positive correlation with the corresponding temperature and oxygen profiles. However, separation between cyclonic and anticyclonic stations can be inferred from the negative correlations with salinity: apart from the values between -0.1 and 0.1, all correlations were significant, but were stronger for cyclonic stations than for anticyclonic stations. Frontal and divergence stations were mixed with the others.
Similar observations were found when the data were analyzed according to size class (Figure 13). In 2009, the cyclonic/anticyclonic separation is still noticeable for the first three size classes: the smallest and third size class had higher significant positive correlation of biovolume with temperature for cyclonic compared to anticyclonic stations, whereas the second class showed weak but significant correlations between biovolume and temperature profiles (positive correlation) and biovolume and salinity profiles (negative correlation) for anticyclonic stations, with correlations for the cyclonic stations not significant. The frontal stations were mixed with or intermediate to the cyclonic and anticyclonic stations. In 2010, despite a high correlation of all the smallest size class biovolume profiles with temperature, indicating a surface distribution of this size class whatever the mesoscale feature, a partial separation between cyclonic and anticyclonic stations can still be made on the basis of the correlation between the biovolume of the smallest size class and the salinity profiles, with a strongly negative coefficient for some of the cyclonic stations. For the other size classes, however, the plots do not indicate any separation between features.

Detailed vertical profiles of total biovolume are shown separately for all day-time and night-time stations during the MC09B cruise and for Leg1 and Leg2 of the MC10A cruise (Figures 14 and 15). These profiles indicate the important role of the MLD with respect to vertical structure of the organisms. For example in Figure 14, by day within the Frontal stations, there is one profile with high surface concentrations which corresponds to the temperature profile with the shallower MLD, a hydrological profile close to those of the cyclonic stations. For the latter, as well as for this particular frontal station, the very high surface concentrations in the mixed layer are mainly composed of the smallest size class. In Figure 15, the two cyclonic daytime stations of Leg 1 have particularly shallow mixed layers (around 20 m) and also particularly high surface concentrations of zooplankton, composed mainly of the 0-0.2mm size class. There is no clear evidence of diel vertical migration, and this aspect is difficult to investigate as the day- and night-time stations were not in the same locations.

3.4. Taxonomic composition of the size classes
Zooscan analysis and image processing of Multinet samples yielded a total of 42 taxonomic or abiotic groups. The most abundant and most commonly found organisms within the four TAPS size classes at representative cyclonic and anticyclonic stations for both cruises, as well as of the larger organisms (>3.0 mm ESR) not sampled by TAPS but collected with the Multinet, are shown in Figure 16. They are represented by 28 taxonomic groups, including one for ‘detritus’, a grouping of copepod-detritus matrices (copepods clustered together by detrital material that were inseparable) and one for ‘various meroplankton’, which includes bivalve, brachiopod, cyphonaute, cirripede, echinoderm and gastropod larvae, as well as crab zoeae. The smallest size class (0.0-0.2 mm ESR) comprised mostly small copepods (calanoids, poecilostomatoids and cyclopoids), detritus and ostracods at both cyclonic and anticyclonic stations during both cruises, as well as some dinoflagellates (likely Pyrocystis sp.) and foraminiferans (likely Globigerina sp.) at the cyclonic stations in 2009. The second size class (0.2-0.5 mm ESR) comprised mainly calanoid copepods and detritus, with low proportions of ostracods, small chaetognaths and appendicularians. The 0.5-1.0 mm ESR size class had a similar taxonomic composition as well as an increased proportion of chaetognaths at most stations. The fourth size class (1.0-3.0 mm ESR) comprised mainly large calanoid copepods and chaetognaths, considerably more detritus during 2010, gelatinous zooplankton (e.g. siphonophores, salps), and euphausiid furcilia. The largest size class (>3.0 mm ESR) comprised mainly large chaetognaths and gelatinous zooplankton (siphonophores, salps, hydromedusae, ctenophores), large calanoid copepods, detritus or copepod-detritus matrices, and larger crustaceans such as euphausiids (especially at night) and decapod larvae.

The taxonomic composition of the dominant zooplankton as determined by the ZooScan process, thus only to broad taxonomic groupings, did not vary greatly between cyclonic and anticyclonic stations, or at frontal and divergence stations (data not shown). There also does not appear to be strong clustering of functional groups amongst the four TAPS size classes, as all size classes were dominated by largely herbivorous or omnivorous calanoid copepods, with some carnivorous species in all size classes. The increased proportion of gelatinous zooplankton in the larger size classes included both herbivorous (salps, doliolids, appendicularians) and predatory (siphonophores, hydromedusae) species. The proportion of detritus was greater during 2010,
including a greater proportion of biovolume attributed to a copepod/detritus matrix, which was sticky and difficult to separate.

4. Discussion

4.1 Methods comparison

Mean Multinet-sampled biovolume was consistently greater than that estimated by both the ZooScan and TAPS. This is due to two main reasons. Firstly the Multinet biovolume measurements reflect settled biovolume, which overestimates true biovolume due to the water trapped in the interstitial spaces between organisms. Thus Multinet-derived settled biovolume will always exceed the more accurate biovolume measurements of the ZooScan, which are based on the dimensions of each scanned object. Secondly, although the 200-µm mesh size of the Multinet results in under sampling of the smallest size class reported on here compared to the TAPS (effectively 0.05-0.2 mm ESR, equivalent to 100-400µm ESD), it is also able to sample much larger organisms than the TAPS. As the largest size fraction sampled by the Multinet (>3mm ESR) consistently comprised the greatest proportion of total Multinet biovolume, and the largest size fraction sampled by TAPS (>1 mm ESR) consistently comprised the greatest proportion of total TAPS biovolume (Figure 9), one can deduce that the Multinet will consistently have sampled the most biovolume, even accounting for high concentrations of particles too small to be retained by the 200-µm mesh. In some situations with particularly high concentrations of the smallest sized organisms very close to the surface, the TAPS[0-200m] and Multinet results were similar, as in 2009 for the cyclonic feature and in 2010 for the anticyclonic one (Figures 7 and 8).

Another important consideration is that the ZooScan’s pixel resolution of 10.6 µm makes the ZooScan a suitable tool only for analysis of organisms >300 µm ESD (Gorsky et al., 2010). Despite this technical principle, there were generally minor differences between TAPS and ZooScan results, except for when the 0-0.2mm class dominated the composition (e.g. cyclonic stations in 2009, most features in 2010; Figures 7 and 8). Additionally, the processing mode of each method for determining its own equivalent spherical radius includes uncertainties: with acoustics the algorithm leads to the most probable population proving the data measured, with
optics the position and thus view angle of the organisms when scanned has an influence on the diameter determination. Some shifts may have happened between the 0-0.2/0.2-0.5mm size classes on one hand, and between the 0.2-0.5/0.5-1mm classes on the other (Figure 8).

The three methods were consistent according to the global comparisons between the two years (Figure 6) with higher biovolumes in 2010 than in 2009. The more detailed comparisons, according to mesoscale features (Figures 7 and 8) show that whereas there was good coherence with the trends between features in 2009, it was not the case in 2010. All three methods are expected to characterize mainly the mesozooplankton, but as noted previously, each method is more favorable for a particular size fraction of the population. Nonetheless, these methods are ultimately complementary.

Vertical profiling with the TAPS provides fine scale resolution of the vertical distribution of particles in different size classes that cannot be obtained with conventional net sampling. Conversely, both microscope and imaging analysis provide information on the taxonomic composition of organisms in the water column that cannot be inferred from the acoustic data, and are also able to assess larger sizes. Zooscan gets us one step closer to taxonomic identification of the community without detailed microscope identification, and the vertical fine resolution which is possible with the TAPS provides tighter relationships with environmental parameters. However, the results from this study indicate both similarities and differences between these methods when aggregating the data according to year, mesoscale feature and size class, and these are explored further below.

4.2 Year and mesoscale feature impacts on zooplankton distribution and composition

The apparent difference in ecosystem variability between the 2009 and 2010 cruises is substantiated by a closer examination of the eddy field in both years, as characterized by altimetry. A well-defined dipole (anticyclonic-cyclonic eddy pair) was sampled during 2009, which had formed approximately 2 months prior to the cruise, and remained stable during the cruise (Ternon et al., submitted, this issue). In contrast, the eddy field sampled in 2010 was more extensive and largely unstable. The most consistent feature was the well-developed cyclonic eddy in the narrows of the Mozambique Channel (15-18°S), which remained stable during both legs of
the cruise (see Lamont et al., submitted, this issue, their Figs 5a-d). The large anticyclonic eddy sampled during leg 1 of the cruise suddenly shifted westwards halfway through the cruise, then merged with a smaller anticyclonic eddy moving southwards beyond the Mozambique shelf (Ternon et al., submitted, this issue). Consequently, the “anticyclonic” stations sampled during leg 2 of the cruise were located in the rapidly retreating and dissipating eastern perimeter of the eddy. Finally, the cyclonic eddy situated farther south (20-21°S) that was sampled during leg 2, was newly formed and with a comparatively weak SLA (Lamont et al., submitted, this issue).

4.2.1 Global results

The results obtained in 2009 clearly indicate that the trends in biovolume between features are the same for all methods, showing in particular higher concentrations of zooplankton in the cyclonic features compared to the anticyclonic ones. This is consistent with the mechanism of locally upwelled cool and rich deep water in the core of the cyclonic feature that enriches the surface waters in oligotrophic environments (McGillicuddy et al., 1998; Oschlies and Garçon, 1998; Zimmerman and Biggs, 1999). The same observations have been made during this study with respect to total chlorophyll a concentration at the surface by Barlow et al. (submitted, this issue) and also for higher trophic levels, for the micronekton concentration by Behagle et al. (accepted, this issue). In 2010, the difference in concentrations obtained at cyclonic and anticyclonic features was smaller than in 2009, but more importantly, the relationship between these features varies depending on the method used to determine biovolume. We have seen above that each method is better suited for a particular size range of organisms, despite the high overlap in their sampling ranges. A model coupling the biogeochemical model PISCES and the regional oceanic model ROMS, has found results that are in contrast with previous studies in the open ocean, with relatively poor cyclonic eddies and rich anticyclonic eddies according to the chlorophyll concentration at their cores (José et al., submitted, this issue). It is also shown in Behagle et al. (accepted, this issue) that depending on the acoustic frequency considered, either the cyclonic or anticyclonic feature yields the higher mean concentration of organisms, according to the type and size of the organisms considered. These results demonstrate that the variability of the ecosystem functioning was high during 2010, resulting in high variability within the mesoscale features from one ecosystem compartment to another. The specific generation of the features in 2010 and a possible shelf effect and transport of coastal production, leads to results that are different to
those obtained in the open ocean (Ternon et al., submitted, this issue; José et al., submitted, this issue; Kolasinski et al., 2012).

The two cruises were conducted during different seasons, 2009 in austral summer and 2010 closer to austral winter. There was no relationship between zooplankton concentration and surface chlorophyll \(a\) concentration in the present study, but existing knowledge of phytoplankton dynamics in the region is consistent with the findings of this study. Several features are relevant: (1) Levy et al. (2007) found surface chlorophyll \(a\) to be maximal in winter (July) and minimal in summer (December); (2) it is usual to find higher concentrations of phytoplankton in cyclonic features than anticyclonic ones (Tew-Kai and Marsac, 2007), which was the case in 2009 but not in 2010, when both features had similar concentrations (Barlow et al., submitted, this issue); (3) surface phytoplankton in the central part of the channel is constrained more by mesoscale activity than seasonality (Tew-Kai and Marsac, 2007). For the zooplankton, there were rich stations for all mesoscale structures in 2010, thus global biovolume was higher than in 2009 where the enrichment was effective only for cyclonic, and to a lesser extent frontal, structures.

4.2.2 Relationships with environment

The influence of the SLA on the enrichment of an area is demonstrated in 2009 by the negative correlation with mean biovolume over a depth of 200m, as is the importance of the depth of the mixed layer: the shallower it is, the higher the zooplankton concentration. These observations are evident for all stations as there is good homogeneity of the hydrological structure within each group of stations. Note that one of the frontal daytime stations (station 4, green curve, Figure 15) has been classified as “Frontal”, and indeed the SLA value is lower than those of the cyclonic stations and comparable to one of the night-time frontal stations. However, the vertical hydrological structure, with a shallow mixed layer characteristic of the cyclonic stations, is probably a key parameter that has contributed to the high biovolume of zooplankton at that station compared with the other frontal stations. In all the other cases, the hydrological characteristics are very reproducible for each feature, indicating a well established and stable cyclonic/anticyclonic dipole. The zooplankton profiles are also reproducible for similar hydrological conditions.

In 2010 two different cyclonic structures were sampled, which had different generation histories (Ternon et al., this issue). During Leg1 the northern, stable cyclone (around 16°S; c1d and c1n...
on Figure 2b) was sampled, whilst the cyclone sampled during Leg 2 (around 21°S; c2d, c2n, Figure 2b) was newly established and in the process of splitting (Ternon et al., this issue). The SLA associated with the northern cyclone was deeper than that of the southern one. The very shallow mixed layer combined with the stability of the cyclonic feature during Leg 1 most likely provided favorable conditions for particle enrichment at the surface for the daytime cyclonic feature. In contrast, there were no clear enrichment phenomena in the newly established cyclonic feature sampled during Leg2. Also, the vertical distribution of the zooplankton appears to be strongly constrained by the hydrological structure of the water column (Figure 15), despite the MLD and the SLA not having been proven to be correlated with global enrichment for this 2010 cruise (Table 3). However, the characteristic of being a “cyclonic” or an “anticyclonic” feature may not be the determining factor in such a complex and unstable system, as noted by Godø et al., (2012), who mention the increase in marine life within mesoscale eddies in general, and also the need for more detailed sampling of the structures. The stations sampled during this study provide point-based information for relatively few locations subject to local variability. However the MESOBIO study provides a beam of convergent results in connection with the particular situation of the 2010 cruise.

4.2.3 Size composition

The nature of the particles that were too small to be sampled by the Multinet, but were “captured” by the TAPS, can only be speculated upon, as no water samples for the <200 µm size range were preserved. However, it is possible, if not likely, that these small particles were microzooplankton (protozooplankton), which could include tintinnids, ciliates and heterotrophic dinoflagellates, as well as metazoans such as juvenile stages of small copepods. Hopcroft et al. (2001) note that over half to one quarter of the copepod biomass in tropical waters is missed by sampling with a 200-µm net, the missed component comprising largely nauplii and small copepodites. There are no data available on microzooplankton abundance for the Southwest Indian Ocean (SWIO), but Edwards et al. (1999) report an average abundance of 3 200 cells l⁻¹ in oligotrophic conditions in the Arabian Sea, and up to 16 000 cells l⁻¹ in upwelling waters. The Arabian Sea microzooplankton was dominated by ciliated protozoa, mostly aloricate oligotrichs and choreotrichs, while the metazoan component comprised copepod nauplii and small appendicularians. Stelfox et al. (1999) found average standing stocks of microzooplankton (~100
mgC m$^{-2}$) to be similar to those of mesozooplankton in oligotrophic conditions, and a third of mesozooplankton standing stocks in more nutrient rich waters, indicating the potential importance of the microzooplankton component in this region. Furthermore, microzooplankton abundance is likely to be enhanced by higher nutrient concentrations, such as those resulting from cyclonic eddy-associated upwelling. The highest concentrations of small particles during this study were associated with the cyclonic eddy in 2009. In 2010, high concentrations of this possible microzooplankton component near the surface were observed, in particular for the two close cyclone 1 daytime stations (c1d on Figure 2b), but also for stations belonging to the other types of structures, perhaps as a result of the structures being less stable and with weaker hydrographic characteristics. Furthermore, sampling at the two “c1d” stations, although spatially very close, occurred one week apart, showing the high stability of this cyclonic structure in the narrows (16°S, Figure 15).

Differences in biovolume distribution according to mesoscale structure, size and depth were, for both years, mainly a result of greater or lower concentrations of the same community complex, with larger organisms tending to occupy greater depths as a result of their ability to migrate deeper on a diel basis. Similarity in species composition between warm- and cold-core eddies was observed for the Mozambique Channel during 2007 and 2008 (Huggett, submitted, this issue) as well as for other areas, including the Hawaiian islands (Landry et al., 2008) and Western Australia (Strzelecki et al., 2007). What is evident from the TAPS results for both years in the present study, specifically in the cyclonic features, is the concentration of organisms from size classes 0.2-0.5 mm and > 1 mm ESR around the depth of the chlorophyll maximum. This is difficult to interpret given the similarity in community composition between the features. The two smallest size classes were dominated by copepods of all feeding modes, but the smallest class was confined to the upper mixed layer. There were mainly herbivorous/omnivorous organisms (copepods, euphausiids, salps) in the largest TAPS size class but these were also mixed with some carnivorous taxa (chaetognaths, siphonophores). This suggests there may be two separate communities – one concentrated in the upper mixed layer, dominated by the smallest size fraction (0-0.2 mm ESR), comprising mainly microzooplankton and very small copepods feeding on small particles, but also comprising some larger organisms, and a separate, generally larger component of the community (>0.2 mm ESR) concentrated around the depth of
maximum chlorophyll $a$, the latter providing a favorable feeding environment for herbivorous zooplankton and their predators.

**Acknowledgements**

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**References**


Figure captions

Figure 1. Comparison of the results obtained from the inversion algorithm with four (420, 700, 1100, 3000 kHz) and five frequencies (420, 700, 1100, 1850, 3000 kHz) on one station of the MC10A cruise.

Figure 2a. Geostrophic velocity versus SLA for the TAPS stations in 2009 (top) and 2010 (bottom), with corresponding mesoscale classification.

Figure 2b. Location of the TAPS stations in 2009 (left panel) and 2010 (right panel) with their corresponding mesoscale classification (circle: cyclonic; triangle: shelf; cross: frontal; square: anticyclonic; diamond: divergence). c1d: “cyclone leg1 day”, c2d: “cyclone leg2 day”, c1n: “cyclone leg1 night”, c2n: “cyclone leg2 night”, a1: “anticyclone leg1”, 1 day and 1 night station on each side, the “anticyclone leg2” are the remaining ones.

Figure 3. Temperature profiles per mesoscale feature in 2009 (left panel) and 2010 (right panel)

Figure 4. Mean hydrographic profiles per mesoscale feature and per year

Figure 5. Relationships between the mixed layer depth and the Sea Level Anomaly, for both years, and configurations corresponding to the stations for each mesoscale feature.

Figure 6. Mean biovolume (± SE) for each year, from the three measurement methods (ml.100m$^{-3}$).

Figure 7. Mean biovolume (± SE) per mesoscale feature, for each year and for all three measurement methods (ml.100m$^{-3}$).

Figure 8. Mean biovolume (± SE) per size class as measured by the TAPS and by the ZooScan, per mesoscale feature and for each year (ml.100m$^{-3}$).

Figure 9. Proportions of each size class within the total mean biovolume from the TAPS[22-200m] results.

Figure 10. Vertical sections along the cruise track of the hydrological parameters (temperature, oxygen and salinity) and of zooplankton biovolume, total and by size class, in terms of log10(biovolume), for 2009 (a) and 2010 (b). Superimposed letters indicate the corresponding mesoscale feature at each station. Dots from white to black indicate the depth of the chlorophyll maximum, with darker dots indicating a higher chlorophyll concentration.
Figure 11. Profiles of zooplankton biovolume by size class, focusing on the cyclonic and anticyclonic stations. The depth of the chlorophyll maximum is superimposed as a diamond for each station.

Figure 12. Stations positioned on bi-correlation graphs: correlation between profiles of $X = $ Biovolume versus Temperature, $Y = $ Biovolume versus Salinity, for total biovolume.

Figure 13. Stations positioned on bi-correlation graphs: correlation between profiles of $X = $ Biovolume versus Temperature, $Y = $ Biovolume versus Salinity, for each size class.

Figure 14. Vertical profiles of total biovolume (mm$^3$.m$^{-3}$) and of temperature, provided per mesoscale feature and per diel period for 2009. Corresponding SLA for the stations presented are added. For daytime Front stations, the underlined SLA value corresponds to the green profile (station 4).

Figure 15. Vertical profiles of total biovolume (mm$^3$.m$^{-3}$) and of temperature, provided per mesoscale feature, per Leg of the cruise and per diel period for 2010. Corresponding SLA for the stations presented are added.

Figure 16. Composition of the zooplanktonic population (biovolume, mm$^3$.m$^{-2}$) in five different size classes (ESR, mm) for representative stations from cyclonic and anticyclonic features, for 2009 (top) and 2010 (middle and bottom), during both day and night. For 2010, the example of each feature is provided for both legs 1 and 2 of the cruise. Station numbering is equivalent to that used in Huggett (submitted, this issue, Figures 4, 5 and 6).

Tables

Table 1. Distribution of the stations for each mesoscale structure and time of day (*: transition period)

<table>
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<tr>
<th>Survey/Structure</th>
<th>Cyclone</th>
<th>Anticyclone</th>
<th>Front</th>
<th>Divergence</th>
<th>Shelf</th>
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<td>3</td>
<td>6</td>
<td>-</td>
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<tr>
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<td>1</td>
<td>2</td>
<td>-</td>
<td>1</td>
<td>7</td>
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<td>2</td>
<td>14</td>
<td>1*</td>
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<tr>
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<td>4</td>
<td>2</td>
<td>9</td>
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Table 2. Student t-test results for mean biovolume over a depth of 200 m (*: significant difference at p<0.05). TAPSa: 0-200m mean, TAPSb: 22-200m mean.

<table>
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<th></th>
<th>MC10A</th>
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<td>TAPSb</td>
<td>ZooScan</td>
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<td>TAPSb</td>
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<td>Anticyclone vs Divergence</td>
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<td>0.460</td>
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Table 3. Significant (p<0.05) correlation coefficients between mean biovolume (0-200m) and various environmental factors.

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<th>vs Geost. velocity</th>
<th>vs Surf Chl</th>
<th>vs Chl maximum</th>
<th>vs Integ Chl</th>
<th>vs Depth of Chl max</th>
<th>vs Depth of mixed layer</th>
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<tr>
<td>0.5-1</td>
<td>-0.67</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-0.74</td>
</tr>
<tr>
<td>&gt;1</td>
<td>-0.85</td>
<td>-</td>
<td>-0.65</td>
<td>-</td>
<td>-0.7</td>
<td>-</td>
<td>-0.77</td>
</tr>
</tbody>
</table>

| MC10A Total          | -      | -                  | -           | -              | -            | -                    | -                       |
| 0-0.2                | -      | -                  | -           | -              | -            | -                    | -0.34                   |
| 0.2-0.5              | -      | -                  | -           | -              | -            | -                    | -                       |
| 0.5-1                | -      | -                  | -           | -              | -            | -                    | -                       |
| >1                   | 0.41   | -                  | -           | -              | -0.7        | -                    | 0.59                    |
Figure 1
Figure 3
Figure 4

Figure 5
Figure 6

Figure 7
Figure 8
Figure 9
Figure 10
Log(Biovolume) and Depth of the Chlorophyll maximum

Figure 11
Stations localization per mesoscale feature on the bi-correlations plots

Figure 12

Figure 13
Figure 14
Figure 15