Mesoscale features and micronekton in the Mozambique Channel: an acoustic approach

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ABSTRACT

The oceanic circulation in the Mozambique Channel is dominated by mesoscale cyclonic and anticyclonic eddies which are known to play a key role in biological processes of less-productive deep-sea ecosystems by converting physical energy in trophic energy. In this study, acoustics was used to investigate the spatial distribution of micronekton according to four classes of mesoscale features and assess whether cyclonic, anticyclonic or eddy edges impact the biomass of micronekton. Acoustic data were collected continuously with a Simrad EK60 split-beam echosounder during three surveys carried out in the Mozambique Channel within the framework of the MESOBIO programme. Firstly, a difference was observed between day and night micronekton distributions, confirming diel vertical migration of micronekton organisms during crepuscular periods (dawn and dusk). For the three surveys, the acoustic responses were richest in the surface layer at night and the bottom layer during the day. Secondly, differences in the acoustic responses of micronekton by class of eddy were evidenced. During two of the three surveys, cyclonic eddies showed higher micronekton acoustic biomass than anticyclonic eddies for day and night. On the contrary, during the last survey, the highest micronekton biomass was observed in the anticyclonic eddies. To explain this dissimilarity, several hypotheses are proposed, including the seasonality and difference of wind-forcing between the southwest monsoon and the northeast monsoon, and the age of eddies.

KEY WORDS acoustics, mesoscale eddies, micronekton, Mozambique Channel, satellite altimetry.

1. INTRODUCTION
The Mozambique Channel is located in the southwestern Indian Ocean between the east coast of Africa and the west coast of Madagascar and is characterised by important mesoscale activity (De Ruijter et al., 2004). The circulation in this area is dominated by mesoscale cyclonic and anticyclonic eddies that propagate southwards along the western edge of the channel (Schouten et al., 2003; Quartly and Srokosz, 2004). Mesoscale eddies can be characterised using different but complementary attributes such as rotational sense, dimension, intensity (e.g., sea surface height, geostrophic and rotational velocities), lifetime, origin, trajectory, and propagation distance (Bakun, 2006; Chelton et al., 2011). In the Mozambique Channel these mesoscale features have an average diameter of 300 km and may have a physical effect extending 1000 to 2000 m below the surface, but impact mainly the top 400 m of the water column (De Ruijter et al., 2004; Schouten et al., 2003).

Eddies play a key role in biological processes of less-productive deep-sea ecosystems by converting physical energy into trophic energy (Bakun, 2006). Eddies can cause upwelling or downwelling in the centre and edges, depending on the rotational sense (clockwise and counter-clockwise respectively for cyclonic and anticyclonic eddies in the southern hemisphere). Cyclonic eddies are generally associated with divergent surface flows, leading to upwelling of nutrient-rich cold waters into the eddy centre (McGillicuddy et al., 1998; Bakun, 2006), causing an increase of local primary production (Mizobata et al., 2002; Benitez-Nelson et al., 2007; Tew-Kai and Marsac, 2009). Anticyclonic eddies are generally associated with convergent horizontal surface movements, from the edges towards the centre of the eddy, which allow downwelling of organisms towards deeper layers in the centre (Bakun, 2006). Moreover, phytoplankton enrichment has also been associated with the upward movement of nutrient rich waters at the edges of either anticyclonic or cyclonic eddies (Mizobata et al., 2002; Quartly and Srokosz, 2004). Such influence on the transport and distribution of nutrients can impact the spatial structure of biological activity. By
imparting the horizontal and vertical distribution at the base of the food web (nutrients and phytoplankton), these mesoscale features also affect the distribution of upper-trophic level organisms. Several studies have analysed the links between mesoscale eddies and mesozooplankton or fish larvae (Bakun, 2006; Muhling et al., 2007), tunas (Bertrand et al., 1999; Young et al., 2001; Tew-Kai and Marsac, 2010), swordfish (Seki et al., 2002), turtles (Polovina et al., 2004; Lambardi et al., 2008), seabirds (Nel et al., 2001; Weimerskirch et al., 2004; Hyrenbach et al., 2006), and marine mammals (Bailleul et al., 2010). However, few studies have investigated the effect of mesoscale features on intermediate trophic levels, i.e. the micronektonic organisms. Drazen et al. (2011) recently showed that eddies may aggregate micronekton, which probably feed on the enhanced secondary productivity associated with these eddies. Additionally, mesoscale features can shape the distribution and the aggregation patterns of micronekton through bottom-up processes (Sabarros et al., 2009).

In this study, acoustic data was collected during three surveys carried out in the Mozambique Channel in 2008, 2009 and 2010, within the framework of the MESOBIO programme (Ternon et al., this issue). Acoustics is a non-destructive and efficient method for simultaneously and continuously monitoring micronekton at large scales (Bertrand et al., 2003; Kloser et al., 2009). Acoustics is used in this study to investigate the spatial distribution of micronekton according to mesoscale features to assess whether cyclonic, anticyclonic or eddy edge impact the biomass of micronekton.

2. MATERIAL AND METHODS

2.1. Acoustic data collection

Three oceanographic surveys were carried out in the Mozambique Channel on board two research vessels: firstly, between 13-23°S and 35-43°E on the RV Dr Fridtjof Nansen (IMR, Norway) from the 28th of November to the 17th of December 2008 (referred to here as
MC08A); secondly, between 23-26°S and 35-39°E on the RV Antéa (IRD, France) from the
27th of October to the 23rd of November 2009 (MC09B); and finally, between 14-23°S and
39-43°E on the RV Antéa from the 12th of April to the 6th of May 2010 (MC10B).

*In situ* acoustic data were collected continuously (day and night) at four frequencies with a
Simrad EK60 split-beam echosounder. The depths of the hull-mounted acoustic transducers
on the RV Dr Fridtjof Nansen and RV Antéa were approximately 5 and 3 m below the water
surface, respectively. Consequently, acoustic data were processed with an offset of 10 m
below the surface. The transducers were calibrated following standard procedures (Foote et
al., 1987).

The water column was sampled vertically from the surface to a depth of 1000 m and 750 m
during the MC08A and MC09B-MC10A surveys, respectively. Data was recorded with the
ER60 software (Simrad, 2008) (*.raw* files) and converted into *.hac* format for post-
processing using ‘Movies+’ software (Weill et al., 1993). Settings used during data
acquisition were the same for the surveys, except for slight differences during the MC08A
survey (Table 1).

2.2. Data analysis

2.2.1. Acoustic data processing

Movies+ was used for visual data control prior to processing, to assess the data quality and
remove noisy pings and bubble dropouts. During this inspection a minimal number of shoals
and aggregations were observed, and therefore, echo-integration by layers (Simmonds and
MacLennan, 2005) was applied during this study. Echo-integration by layers allows the
quantification of the micronekton acoustic biomass of an area from the cumulative acoustic
energy reverberated by all the targets in the zone sampled (Lurton, 2002). The minimum
acquisition and echo-integration thresholds were set at -80 and -75 decibels (dB),
respectively. The elementary sampling unit (ESU) was fixed at 1 nautical mile (nmi, 1 nmi = 1852 m), and the water column was echo-integrated into 37 layers of 20 m depth, to a maximum depth of 740 m. The Nautical Area Scattering Coefficient (NASC, $s_A$ in square metre of reflection surface per square nautical mile, $m^2 \text{nmi}^{-2}$) (MacLennan et al., 2002) was used to determine the micronekton acoustic biomass (Bertrand et al., 1999). To standardise the comparison of acoustic data among the three surveys, a common frequency with a maximum vertical range was selected. Therefore, only the 38 kHz frequency was used to investigate the link between mesoscale eddies and the distribution of micronekton.

To take into account the diel variation, diurnal and nocturnal periods were processed separately, and the crepuscular periods (dawn and dusk) corresponding to micronekton ascents and descents (Lebourges-Dhaussy et al., 2000; Benoit-Bird et al., 2009) were excluded from the analyses. An initial analysis of the echograms showed that organisms are organised vertically into three main layers. Therefore, the water column was separated into three layers: 10-200 m (surface layer, $L_{200}$, corresponding NASC $s_{A1}$), 200-400 m (intermediate layer, $L_{400}$, $s_{A2}$) and 400-740 m (deep layer, $L_{740}$, $s_{A3}$). Given the separation of the data into day/night surveys and into three vertical layers, and the vertical range limits of the transducers, there were six possible outputs to analyse micronekton biomass.

The survey path of each survey was divided into several linear transects according to period of time (night versus day) and acoustic data quality. Transects close to the shelf were removed from the analyses because of a peculiar bias in acoustic responses in these regions.

### 2.2.2. Environmental data

Satellite altimetry allows identification of mesoscale features (e.g., Chelton et al., 2007). One mesoscale feature among four classes (anticyclone, A; cyclone, C; divergence, D; and fronts, F) was assigned to each ESU. The classification of each ESU was processed using three
explanatory variables (sea level anomaly, geostrophic speed and bathymetry) and a discriminant function estimated from an extra training dataset (Lamont et al., this issue). Ocean bathymetry was extracted from ETOPO1 Global Topography (data access: http://www.ngdc.noaa.gov/mgg/global/global.html). Sea level anomaly and the corresponding geostrophic speed were extracted from AVISO products “DT-MSLA Ref” (Delayed Time, DT; Reference, Ref) with 0.33 × 0.33° spatial resolution on a Mercator grid. The predictions from the linear discriminant analysis were estimated for each ESU using the values taken by the three explanatory variables at the corresponding temporal and spatial positions.

2.2.3. Statistical analysis

Links between acoustic biomass estimates ($s_A$) representing the vertical distribution of micronekton, period of the day, depth layers ($L_{200}$, $L_{400}$, and $L_{740}$), and mesoscale features, were investigated using multivariate analysis of variance (MANOVA), Kruskal-Wallis (KW) non-parametric tests and pairwise Wilcoxon rank sum tests. Moreover, multinomial models (from the Generalized Linear Model family) were applied to quantify the link between eddy classes and acoustic responses for each survey. The vector of predicted classes of eddy ($Y_i$, $i \in \{1, N\}$, with $N$ = total number of ESUs) was assumed to be a realisation of a random variable $Y$. $Y$ takes its values in the set $E = \{A, C, D, F\}$ of four categories. The model was designed in terms of the probability function of $Y$, conditional to the acoustic responses ($s_{A1}$), ($s_{A2}$), and ($s_{A3}$), which are continuous covariates. The logistic form was chosen. For $j \in E$, the probability distribution ($Pr$) is written:

$$Pr \left( Y_i = j \mid s_{A1_i} = x_1, s_{A2_i} = x_2, s_{A3_i} = x_3 \right) = f(\lambda_j + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3)$$

(1)

where $f$ is the logistic function and $\lambda$, $\beta_1$, $\beta_2$, $\beta_3$ are the unknown parameters to be estimated. Day and night datasets were investigated separately. The Akaike Information Criterion (AIC)
was used to select the covariates \( s_{A1}, s_{A2} \) and/or \( s_{A3} \) of the most parsimonious models.

Reference models including sea level anomaly and geostrophic speed as covariates were also fitted and matched to the selected model based on acoustic responses only. In addition, estimated probabilities from equation (1) permitted the prediction of the most likely eddy class from the acoustic responses. Predicted classes were then matched with original assigned eddy classes, and a global score of correct classification was computed for each model.

Statistical analyses were conducted with R (R Development Core Team, 2007) using the `multinom` function in the MASS package (Venables and Ripley 2002).

### 3. RESULTS

A total of 2669 ESUs combining data from the three surveys (Table 2) were processed following two steps. Firstly, a preliminary analysis investigated the difference in the vertical distribution of micronekton between day and night. Secondly, the effect of eddy classes on the micronekton biomass was investigated.

#### 3.1. Diel vertical distribution of micronekton

Data from the three surveys were combined to test differences in the acoustic responses between the three layers (\( L_{200}, L_{400}, L_{740} \)). KW tests performed on day and night data were highly significant (\( p < 0.001 \) each). Pairwise comparisons between layers (\( L_{200} \) vs. \( L_{400}, L_{200} \) vs. \( L_{740}, L_{400} \) vs. \( L_{740} \)) with corrections for multiple testing were significant too (pairwise Wilcoxon rank sum tests, \( p < 0.001 \) for day and night). Indeed, the vertical distribution of micronekton differed between day and night. During the day, more than 70% of the acoustic biomass estimates of micronekton was detected in the \( L_{740} \) layer, compared to the lower biomasses detected in the \( L_{200} \) (approximately 20%) and \( L_{400} \) (less than 10%) layers in all surveys (Fig. 2). Conversely, during the night, more than 60% of the acoustic biomass
estimates was detected in the L_{200} layer, compared to the lower biomasses detected in the L_{740} (approximately 30%) and L_{400} (less than 10%) layers in all surveys.

3.2. Link between eddies and acoustic biomass estimates

MANOVA tests performed by survey and by period of time (day and night) showed that the overall acoustic biomass estimates of the three depth layers differed significantly among eddy classes (Table 3). KW tests allowed for the testing of differences layer by layer (Table 3). During daytime periods of the MC08A survey, eddy classes impacted the acoustic biomass estimates of the intermediate layer (L_{400}) only. During the MC09B and MC10A surveys, the daytime differences in the acoustic biomass estimates were significant between the three layers, except for the intermediate layer (L_{400}) of MC10A. In contrast, during the night, the differences in the acoustic biomass estimates for the three surveys were significant between the three layers, except for the intermediate layer (L_{400}) of MC08A (Table 3).

However, as previously shown, the acoustic responses recorded in the intermediate layers did not contribute substantially to the overall recorded acoustic signal during the day and night (Fig. 2). Therefore, only the critical layers were considered henceforward, i.e. the deep layer (L_{740}) during the day and the surface layer (L_{200}) during the night.

During the day, cyclonic eddies sampled during the MC08A and MC09B surveys exhibited larger acoustic biomass averages in the deep layer (L_{740}) than anticyclones (2252 versus 1933 m^2 nmi^-2 for MC08A; 1823 versus 1382 m^2 nmi^-2 for MC09B). However, the acoustic biomasses of the MC08A survey were not significantly different during the day, while for MC09B, the acoustic biomasses were significantly different between cyclonic and anticyclonic eddies. Moreover, for MC09B, anticyclones did not differ from fronts, and cyclones did not differ from divergences (Fig. 3a). The MC10A survey exhibited a different pattern, with anticyclones not significantly different from divergences, and both classes
exhibiting the highest acoustic biomass averages (1614 and 1520 m² nmi⁻², respectively) compared to cyclones and fronts (1141 and 1066 m² nmi⁻², respectively).

During the night, the same trend was observed in the surface layer (L₀₀0) during the MC08A and MC09B surveys, with anticyclones exhibiting the lowest averages (1702 and 1264 m² nmi⁻², respectively) compared to cyclones (2541 and 1983 m² nmi⁻², respectively), divergences and fronts, which did not differ significantly from each other (Fig 3b). MC10A exhibited a different pattern again, with anticyclone averages larger than cyclones (1741 versus 1273 m² nmi⁻²), while the highest acoustic average was recorded in divergences (2059 m² nmi⁻²).

All multinomial model configurations selected the three acoustic responses s_A1, s_A2 and s_A3 as covariates of the final models. Results are given in terms of AIC and scores of correct classification of eddy classes (Table 4). Reference models showed considerably lower AIC than models based on acoustic responses, and reference models logically obtained outstanding classification scores. Conversely, models with acoustic responses displayed varying scores. MC09B exhibited scores of 69% based mainly on correct classifications of anticyclones and cyclones. For MC08A, the day dataset gave a poor score (18%), whereas the high score (67%) of the night dataset was based on divergences only. Half of the eddies of MC10A were misclassified.

4. DISCUSSION

This study demonstrated that the spatial distribution of micronekton is impacted by the circadian rhythm and shaped by mesoscale dynamics (Fig. 2 and 3). However, the links between mesoscale features (anticyclones, cyclones, divergences and fronts) and acoustic responses of micronekton, measured as Nautical Area Scattering Coefficient (s_A in m² nmi⁻²), were not consistent from one survey to another. Acoustics allowed for the identification of
differences in micronekton acoustic biomass estimates at mesoscale, but additional data would be needed to provide information on the underlying ecological processes that could determine these patterns. Hypotheses are proposed below to support the results, taking into account the sampling methods and the special nature of the data used in this study.

Acoustic transducer settings were different during the MC08A survey compared to MC09B and MC10A, however, Korneliussen et al. (2008) indicate that such differences do not impact the results. During the acquisition and processing of acoustic data, thresholds were applied to obtain the best signal/noise ratio, and transects were selected for processing according to several criteria, i.e. the optimal vessel speed, the nature of eddy crossed, the distance from the shore and the linearity of these transects. Although, the latter means that the survey tracks were not completely used, the data processing and analyses were standardised across all three surveys.

Most of the acoustic responses come from migratory micronekton that typically occur in the surface layer during the night and migrate below 400 m depth during the day (Figure 2). Micronekton ascents and descents during the crepuscular periods (dawn and dusk) characterise this process of diel vertical migration (e.g., Lebourges-Dhaussy et al., 2000; Benoit-Bird et al., 2009). For each survey, the acoustic biomass estimates in the surface layer during the night and in the deep layer during the day were similar. However, acoustic biomass estimates recorded in the deep layer during the night remained relatively high (half that recorded in the surface layer). This suggests that organisms either migrate from layers deeper than 740 m (beyond the range of the 38 kHz transducer) to occupy the 400-740 m layer, or that some organisms do not ascend during dusk but reside in the same habitat during the night. Indeed, partial diel vertical migration has been reported in the literature: resident and migrant strategies can co-exist in some populations and the factors affecting migration can be a multifaceted and plastic response (Olsson et al. 2009; Mehner and Kasprzak, 2011).
Multi-frequency acoustic analyses based on several transducers could provide information on these complex patterns, especially for investigating the migration processes during the crepuscular periods.

Eddy classes were assigned to acoustic elementary sampling units (ESU) using data extracted from satellite altimetry and a discriminant function analysis (Lamont et al., this issue). The ESU was fixed at 1 nmi, while the satellite data (sea level anomaly and the corresponding geostrophic speed) were complex products from merged datasets and model outputs produced by AVISO, with a larger spatial resolution of about 0.33°, corresponding to approximately 40 km (Chelton et al., 2011). Sea surface height fields from satellite altimetry reveal mesoscale features in the field, but they are probably not sufficient for the accurate tracking of the processes recorded by acoustics at small spatial scales. The eddy classification approach was used to discriminate between anticyclone, cyclone, divergence and frontal areas. As described by Lamont et al. (this issue), divergences and fronts were characterized by negative sea level anomalies and by low and high geostrophic speeds, respectively. The separation between divergence and frontal areas can be blurred, and additional information would allow for further investigation. However, this approach was a suitable compromise permitting an objective assignment of eddy class using an efficient way of identifying mesoscale features in the field.

The nature of eddies, especially cyclonic and/or anticyclonic eddies, have been suggested to impact the distribution of marine organisms through bottom-up effects (e.g., Seki et al., 2002; Muhling et al., 2007; Domokos et al., 2007; Domokos 2009; Sabarros et al., 2009; Bailleul et al., 2010). During MC08A and MC09B, cyclonic eddies showed higher micronekton acoustic biomass estimates than anticyclonic eddies during the day and night. All tests were significant except for the day dataset of MC08A (Fig. 3). On the contrary, micronekton acoustic biomass estimates were higher in anticyclonic than cyclonic eddies during the
MC10A survey. Cyclonic eddies are generally characterised by divergent surface flows from their centre. Consequently, the upwelling of deep, cold, nutrient-rich water into the euphotic zone triggers primary production (McGillicuddy and Robinson, 1997; Bakun, 2006; Muhling et al., 2007). Anticyclones have nutrient-depleted surface waters within the eddy centre (convergent flow and downwelling of warm surface water), but enrichments have been reported around the periphery of these eddies (Franks et al., 1986; Mizobata et al., 2002). Anticyclonic eddies have a counter-clockwise rotational sense in the Mozambique Channel, and therefore, as they propagate southwards they can play an important role in the transport and export of particles from the African coast toward offshore area (McGillicuddy and Robinson, 1997; McGillicuddy Jr. et al., 1998; Roberts et al., this issue; Ternon et al., this issue). In addition, contra-rotating eddy pairs, referred to as dipoles, generate important energetic fronts, causing the accumulation of biological material with the formation of filaments (Tew Kai and Marsac, 2009).

These contrasting biological responses between cyclones and anticyclones occur under specific environmental conditions, and therefore, may vary with changes in environmental conditions. Siegel et al. (2011) detected “mode-water eddies which have an anticyclonic circulation but a biological response similar to a cyclone”. Similar biological responses to anticyclonic eddies were also observed by Dongseon et al. (2011) in the Japan Sea. Wind-forcing has been shown to possibly lead to anomalously higher chlorophyll inside anticyclonic eddies compared to those expected from classic eddy pumping (Siegel et al., 2011). Moreover, eddy/wind interaction can amplify the phytoplankton biomass in mode-water eddies and reduce the eddy-induced upwelling in cyclonic eddies (McGillicuddy et al., 2007). Exploring these mechanisms propagating along the food chain up to micronekton is beyond the scope of this study. However, it is possible that the acoustic biomass estimate differences between cyclones and anticyclones during the MC08A and MC09B surveys.
compared to the MC10A survey were mainly due to the wind-forcing according to the seasonal wind monsoon regime in the western Indian Ocean (Schott and McCreary 2001). During austral winter, the southwest monsoon (from April to early November) is associated with strong winds and high transport flows through the Mozambique Channel (Biastoch and Krauss, 1999). In contrast, during the austral summer the northeast monsoon (from November to March) is associated with low winds and low or null transport flows through the Mozambique Channel. MC10A was the only survey occurring during the winter period, with the other two (MC08A and MC09B) carried out during austral summer. In winter, increases in wind-forcing could lead to a stronger transport than during summer, and to an increase in primary production in anticyclonic eddies and a decrease of the upwelling efficiency in cyclonic eddies. In contrast, the low wind-forcing regime in austral summer might not disturb the eddy pumping mechanisms in cyclonic eddies. Furthermore, the age of eddies may impact the biological responses up to micronekton by changing the flows in an eddy, such as when the eddies rotate very rapidly or when they are very small (Bakun, 2006; Chelton et al., 2011). The three surveys did not sample the same patterns of eddies and/or dipoles. In 2009 (MC09B), mesoscale features were very stable and well established compared to 2008 (MC08A) and 2010 (MC10A), where eddies were in their early stages and unstable, respectively (Ternon et al., this issue). In summary, biogeochemical and biological responses along the food chain up to mid-trophic levels such as micronekton may be variable and the underlying mechanisms are complex to disentangle. Despite these complex interactions, this study improves the understanding of the impact of mesoscale eddies on the distribution of this important mid-trophic level group, and illustrates that investigating the bottom-up factors that shape the distribution of micronekton is an important step towards understanding the relationship between physical oceanography and biological compartments in pelagic ecosystems.
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Table 1: Acoustic settings used with the Simrad EK60 split-beam echosounder during the three acoustics surveys (MC08A, MC09B and MC10A).

Table 2: Number of elementary sampling units (ESUs, 1 nautical mile) for the three surveys (MC08A, MC09B and MC10A), the time period (day and night) and the mesoscale features (A, anticyclonic; C, cyclonic; D, divergence; and F, front).

Table 3: MANOVA and Kruskal-Wallis (KW) comparison tests of the acoustic biomass estimates ($s_A$, m$^2$ nmi$^{-2}$) between the eddy classes, by depth layers ($L_{200}$, surface layer, 10-200 m; $L_{400}$, the intermediate layer, 200-400 m; $L_{740}$, the deep layer, 400-740 m), by time period (day and night), and for the three surveys (MC08A, MC09B and MC10A). Results of the tests are given as p-values.

Table 4: Multinomial models with (i) sea level anomaly (sla) and geostrophic speed (speed) and (ii) acoustic biomass estimates (Nautical Area Scattering Coefficient, m$^2$ nmi$^{-2}$) for the surface layer (10-200 m depth, $s_{A1}$), intermediate layer (200-400 m depth, $s_{A2}$) and deep layer (400-740 m depth, $s_{A3}$) as covariates. Results are given in terms of Akaike Information Criterion (AIC) and scores of correct classification of eddy classes (%).
**Figure 1:** Survey tracks (lines of dots) of surveys MC08A, MC09B and MC10A in the Mozambique Channel, with one dot per elementary sampling unit (ESU): 1130 ESUs for the MC08A, 491 ESUs for the MC09B and 1048 ESUs for the MC10A survey. Dot colours indicate classes of mesoscale features.

**Figure 2:** Contribution of the micronekton acoustic biomass estimates (based on the Nautical Area Scattering Coefficient $s_A$ in $m^2 \text{nmi}^{-2}$; echosounder frequency 38 kHz) per depth layer ($L_{200}$, the surface layer, 10-200 m; $L_{400}$, the intermediate layer, 200-400 m; and $L_{740}$, the deep layer, 400-740 m), during the day and night, for the three surveys (MC08A, MC09B and MC10A).

**Figure 3:** Boxplots and variations (values are means and standard deviations) of acoustic biomass estimates of micronekton (based on the Nautical Area Scattering Coefficient $s_A$ in $m^2 \text{nmi}^{-2}$; echosounder frequency 38 kHz) according to eddy class (A, anticyclone; C, cyclone; D, divergence; and F, fronts): (a) in the deep layer $L_{740}$ (400-740 m depth, $s_{A3}$) for day data, and (b) in the surface layer $L_{200}$ (10-200 m depth, $s_{A1}$) for night data of the three surveys (MC08A, MC09B and MC10A).
### Table 1

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<th>Pulse length (s)</th>
<th>Power (kW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MC08A</td>
<td>18</td>
<td>3 to 5</td>
<td>1.024 x 10⁻³</td>
<td>2.00</td>
</tr>
<tr>
<td></td>
<td>38</td>
<td>3 to 5</td>
<td>1.024 x 10⁻³</td>
<td>2.00</td>
</tr>
<tr>
<td></td>
<td>120</td>
<td>3 to 5</td>
<td>1.024 x 10⁻³</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>3 to 5</td>
<td>1.024 x 10⁻³</td>
<td>0.12</td>
</tr>
<tr>
<td>MC09B</td>
<td>38</td>
<td>1</td>
<td>5.120 x 10⁻⁴</td>
<td>1.00</td>
</tr>
<tr>
<td>and MC09A</td>
<td>70</td>
<td>1</td>
<td>5.120 x 10⁻⁴</td>
<td>0.70</td>
</tr>
<tr>
<td>MC10A</td>
<td>120</td>
<td>1</td>
<td>5.120 x 10⁻⁴</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>1</td>
<td>5.120 x 10⁻⁴</td>
<td>0.09</td>
</tr>
</tbody>
</table>

### Table 2

<table>
<thead>
<tr>
<th>Time period</th>
<th>Total</th>
<th>Day</th>
<th>Night</th>
<th>A</th>
<th>C</th>
<th>D</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>MC08A</td>
<td>1130</td>
<td>541</td>
<td>589</td>
<td>240</td>
<td>45</td>
<td>610</td>
<td>235</td>
</tr>
<tr>
<td>MC09B</td>
<td>491</td>
<td>292</td>
<td>199</td>
<td>154</td>
<td>179</td>
<td>56</td>
<td>102</td>
</tr>
<tr>
<td>MC10A</td>
<td>1048</td>
<td>509</td>
<td>539</td>
<td>260</td>
<td>274</td>
<td>449</td>
<td>65</td>
</tr>
<tr>
<td>Total</td>
<td>2669</td>
<td>1342</td>
<td>1327</td>
<td>654</td>
<td>498</td>
<td>1115</td>
<td>402</td>
</tr>
</tbody>
</table>

### Table 3

<table>
<thead>
<tr>
<th>Time period</th>
<th>Covariates</th>
<th>MC08A</th>
<th>MC09B</th>
<th>MC10A</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day</td>
<td>sla, speed</td>
<td>204 (95%)</td>
<td>70 (93%)</td>
<td>30 (99%)</td>
</tr>
<tr>
<td></td>
<td>sA₁, sA₂, sA₃</td>
<td>934 (67%)</td>
<td>390 (69%)</td>
<td>1148 (52%)</td>
</tr>
<tr>
<td>Night</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>158 (96%)</td>
<td>34 (99%)</td>
<td>18 (100%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1196 (18%)</td>
<td>508 (69%)</td>
<td>1010 (50%)</td>
</tr>
</tbody>
</table>
Figure 1
Figure 2
Figure 3