
Influence of mesoscale eddies on biological production in the Mozambique Channel: Several contrasted examples from a coupled ocean-biogeochemistry model

Y.S. José^{a,*}, O. Aumont^b, E. Machu^b, P. Penven^{a,b}, C.L. Moloney^c, O. Maury^{a,d}

^a Department of Oceanography, Marine Research Institute, University of Cape Town, South Africa

^b Laboratoire de Physique des Océans (UMR 6523 CNRS, Ifremer, IRD,UBO), LMI ICEMASA, France

^c Department of Zoology, Marine Research Institute, University of Cape Town, South Africa

^d Institut de Recherche pour le Développement - UMR 212 EME, France

*: Corresponding author : Y. S. José, email address : yonss.jose@gmail.com

Abstract:

The impact of mesoscale activity on phytoplankton and nutrient distribution in the Mozambique Channel was simulated by coupling a biogeochemical model (PISCES) with a regional oceanic model (ROMS). Examples of the effects of eddies on the biogeochemistry of the Mozambique Channel are presented to illustrate the complexity of the system. In the model, several cyclonic eddies were found with low concentrations of chlorophyll at their cores, which contrasts with previous studies in the open ocean. In addition, several anticyclonic eddies were simulated with high concentrations of chlorophyll at their cores. Phytoplankton growth within these mesoscale features (both cyclonic and anticyclonic eddies) occurred in response to nutrient injection into the euphotic zone by advection, and subsequent retention of surrounding nutrient-rich waters within eddies. Offshore nutrient distributions depended strongly on lateral advection of nutrient-rich water from the coastal regions, induced by eddy interaction with the shelf. The environmental conditions at the locations where eddies were generated had an important effect on nutrient concentrations within these structures.

Keywords : Ocean physical-biogeochemical coupling ; Cyclonic and anticyclonic eddies ; Chlorophyll; Nutrients ; Mozambique Channel

1. Introduction

Phytoplankton is a major component of ocean biogeochemical cycling (Broecker et al., 1982 and Sarmiento and Gruber, 2006). By maintaining primary production, phytoplankton organisms

36 represent the first level of the marine food web and exert the major control on its structure and
37 richness (Legendre and Rassoulzadegan, 1995). Primary production in the oceans is driven by the
38 availability of nutrients in the euphotic zone where light is available for photosynthesis (Valiela,
39 1995), while mortality, egestion and excretion of planktonic organisms determine the fate of organic
40 matter produced in the upper layers. This matter is exported through sedimentation and hence
41 depletes nutrients in surface waters. Nutrients can be replenished by lateral transport from high
42 nutrient regions and/or by vertical input from nutrient-rich intermediate waters, through the
43 seasonal variability of the thermocline or by Ekman pumping (Sarmiento and Gruber, 2006).

44

45 In the Mozambique Channel (MC), circulation is dominated by strong mesoscale activity (de
46 Ruijter et al., 2002) and large anticyclonic eddies have been observed to move in a southerly
47 direction (de Ruijter et al., 2002; Schouten et al., 2003). These eddies are responsible for an average
48 southward transport of about 15 Sv in the MC (de Ruijter et al., 2002). According to Schouten et al.
49 (2003) and de Ruijter et al. (2002, 2005), they appear at a frequency of about 4-5 per year, with a
50 diameter of up to 300 km and can extend to the bottom at $\sim 17^{\circ}\text{S}$ (Schouten et al., 2003). In recent
51 years, many studies have tried to relate marine ecosystem components to mesoscale features,
52 notably top predators, due to the recent development of miniaturized position devices (Haney
53 (1986); Nel et al. (2001); Weimerskirch et al. (2004); Weimerskirch (2007); Cotté et al. (2007);
54 Tew-Kai and Marsac (2010); Scheffer et al. (2010); Cottin et al. (2012)). For example,
55 Weimerskirch et al. (2004) found that the preferred foraging areas for frigatebirds in the MC is in
56 the western sector of the Channel and they suggested that this preference is related to the presence
57 of eddies. Tew-Kai and Marsac (2010) found higher chlorophyll concentrations and purse-seine
58 tuna catches associated with mesoscale structures. At lower trophic levels, Lebourges-Dhaussy et al.
59 (2013) investigated the impact of mesoscale eddies on zooplankton in the MC ecosystem. Based on
60 2 surveys conducted over 2 different years and seasons, they concluded that species composition
61 was not significantly different between the mesoscale features that were investigated. These authors
62 suggested that differences are mainly related to relative biovolume which seems to vary according
63 to the life history and stability of the mesoscale structure. Huggett et al. (2013) found that
64 biovolume was on average twice as high in cyclonic eddies compared to anticyclonic eddies,
65 although significant variability was apparent from one year to the next.

66

67 In the open ocean, primary production can be sustained by the vertical flux of nutrients induced by
68 the dynamics of mesoscale eddies, particularly the uplift of isopycnal surfaces in the core of
69 cyclonic eddies that upwells nutrient-rich subsurface water into the euphotic zone (McGillicuddy

70 and Robinson (1997); Oschlies and Garçon (1998); Longhurst (2001)). In an anticyclonic eddy,
71 downwelling entrains nutrients from the euphotic zone into the aphotic zone through the deepening
72 of isopycnal surfaces at its core (Yentsch and Phinney, 1985; Franks et al., 1986; McGillicuddy and
73 Robinson, 1997; Longhurst, 2001). Kishi (1994) showed that only the light intensity and the
74 balance between uptake and vertical diffusion of dissolved nutrients are important in maintaining
75 subsurface chlorophyll maxima in anticyclonic eddies, and suggested that upwelling could occur
76 between two anticyclonic structures. In addition, Williams and Follows (1998) suggested that eddies
77 might enhance the lateral transport of nutrients from nutrient-rich regions to oligotrophic gyres.
78 Along the southwestern coast of Madagascar, Quartly and Srokosz (2003) observed cyclonic eddies
79 with low chlorophyll concentrations ($<0.1 \text{ mg m}^{-3}$) in their cores and enhanced chlorophyll at their
80 periphery (0.2 mg m^{-3}) that was derived from coastal water that had been advected offshore from
81 coastal upwelling regions. In the Australian Leeuwin Current system, Waite et al. (2007) observed
82 anticyclonic eddies trapping productive coastal waters in their cores. In the California and Canary
83 Current systems, Gruber et al. (2011) demonstrated that mesoscale processes could induce lateral
84 transport of nutrients from the nearshore region to the open ocean, reducing biological production in
85 the coastal upwelling domain. Mesoscale eddies induced a subduction of near surface nutrients at
86 100-300 km offshore and the authors related this subduction to the weakening of the lateral eddy
87 transport. Other processes responsible for the injection of nutrients into the surface layer are the
88 sub-mesoscale frontal dynamics associated with mesoscale structures (Abraham, 1998; Levy et al.,
89 2012). Lévy et al. (2001) estimated that more than 1/3 of the large scale new production and
90 phytoplankton subduction is induced by these sub-mesoscale physical processes.

91

92 The objective of this work was to analyse the life history of eddies that presented contrasting
93 surface biological signatures. The study investigated whether the production within eddies was
94 stimulated by vertical injection of nutrients in the eddy cores, or by offshore advection and retention
95 of productive coastal waters. Five typical mesoscale features (2 cyclonic and 3 anticyclonic eddies),
96 differing from one another in terms of chlorophyll content, were selected and analyzed. For this
97 purpose, we used the ROMS ocean model (Regional Oceanic Modeling System; Shchepetkin and
98 McWilliams, 2005) coupled with the PISCES biogeochemical model (Pelagic Interaction Scheme
99 for Carbon and Ecosystem Studies; Aumont and Bopp, 2006). Both observed and simulated eddies
100 were investigated and the processes relating to phytoplankton growth were assessed. This assisted
101 in evaluating the contributions of vertical supply mechanisms and advection from coastal waters to
102 sustaining primary production in the MC.

103

104 **2. Methods**

105

106 *2.1. Model description*

107

108 ROMS is an explicit free surface ocean model based on terrain-following vertical coordinates
109 (Shchepetkin and McWilliams, 2005). It solves the primitive equations in a rotating frame following
110 the Boussinesq and hydrostatic approximations and using third-order precision advection schemes
111 in space and time. The unresolved vertical mixing processes are parameterized according to a non-
112 local K-Profile Parameterization - KPP (Large et al., 1994).

113

114 PISCES is a biogeochemical model designed to represent the first trophic levels of the marine
115 ecosystem and the main biogeochemical cycles (Aumont et al., 2003, Aumont and Bopp, 2006).
116 The model simulates 24 compartments. It is composed of two phytoplankton size classes
117 (nanophytoplankton and diatoms) and two zooplankton size classes (microzooplankton and
118 mesozooplankton). Phytoplankton growth can be limited by the availability of five different
119 nutrients: nitrate, ammonium, phosphate, iron and silicate. Diatoms differ from nanophytoplankton
120 by their dependence on silicate as well as by their higher half-saturation constants. The small
121 phytoplankton size-class includes an implicit parameterization of calcite production and nitrogen
122 fixation. PISCES also presents three non-living compartments: semi-labile dissolved organic matter
123 (with a lifetime typically comprised of between a month and several years), small slow-sinking
124 particles and big fast-sinking particles. The model includes the supply of nutrients to the ocean from
125 three different sources: atmospheric deposition, river discharge and sediment mobilization (only for
126 iron). The atmospheric dust deposition used was estimated from the monthly climatological maps
127 simulated by Fung and Tegen (1995), assuming constant values for iron content and solubility
128 (Tagliabue et al., 2008). The river discharges were derived from the dissolved inorganic and organic
129 carbon discharges simulated by Ludwig et al. (1996). Carbon discharges were derived from an
130 empirical model and were calculated as a function of a drainage intensity, basin slope and amount
131 of carbon stored in soils. An iron flux from the continental shelf was added, with the concentrations
132 on the shelf set to 1 nM.

133

134 As the MC is a region of high eddy activity (de Ruijter et al., 2002), it requires an eddy-resolving
135 ocean model to capture the potential impacts of this energetic mesoscale activity on marine
136 ecosystems. Because of the high order accuracy of ROMS numerics (allowing for enhanced
137 effective resolution) (Shchepetkin and McWilliams, 2005), and taking into account the first

138 baroclinic Rossby radius of deformation of the MC (which varies from 40-100 km from South
139 towards the equator) (Chelton et al., 1998), a model with a horizontal resolution of $1/6^\circ$ (19 km on
140 average for the MC) should be sufficient to accurately simulate most of the spectrum of mesoscale
141 eddy variability (Halo et al., 2013). To keep computational costs reasonable, while preserving large
142 scale influences, a high resolution regional model (called the child model) was nested into a larger
143 scale model at $1/2^\circ$ resolution (called the parent model). We employed the ROMS AGRIF two-way
144 embedding procedure, in which the parent grid provides the boundary conditions for the child grid,
145 and where the solution of the child grid is used to improve the large scale parent grid solution
146 (Debreu et al., 2008, 2012). Conservation of oceanic properties is enforced at the parent/child
147 interface, allowing for long term integration (Debreu et al., 2012). The parent domain extended
148 from 40°S - 4.5°N and from 25.1° - 80°E . An important point for regional ecosystem modelling is the
149 requirement for consistency between physical and biogeochemical variables at the open boundaries.
150 To solve this key issue, the parent model was connected for all its prognostic variables (i.e. both for
151 the physics and for the biogeochemistry) at its lateral open boundaries to a monthly climatology,
152 derived from a single global biogeochemical simulation based on the models NEMO and PISCES
153 (Koné et al., 2009). The open boundary scheme is an adaptive radiation condition used in
154 conjunction with nudging and sponge layers in the vicinity of the boundaries (Marchesiello et al.,
155 2001). The child domain extended from 32° - 1.5°S and from 28° - 61°E . Both model grids had 45
156 vertical levels, using the following values for vertical stretching parameters: $\theta_s=5.5$, $\theta_b=0.0$
157 and $h_c=10$ m (Haidvogel and Beckmann, 1999). The resulting vertical resolution ranged from
158 0.226-5.75 m for the surface layer and 1.3-594.2 m for the bottom layer, allowing for a proper
159 representation of the upper ocean processes. The model topographies were derived from the 1°
160 gridded GEBCO dataset (General Bathymetric Chart of the Oceans: www.gebco.net). To prevent
161 model errors associated with excessive slopes in iso- σ layers, the topography (h) was smoothed in
162 order to keep the parameter $(h_{i+1/2}-h_{i-1/2})/(h_{i+1/2}+h_{i-1/2}) < 0.2$ (Haidvogel and Beckmann, 1999).

163

164 The surface forcing fields of the models were derived from monthly climatologies following
165 ROMSTOOLS methodology (Penven et al., 2008): Atlas of Surface Marine Data (Da Silva et al.,
166 1994) for the heat and freshwater fluxes, QuikSCAT scatterometer observations (Liu et al., 1998)
167 for the wind stress components, and Pathfinder sea surface temperature (SST) (Casey and
168 Cornillon, 1994) for the correction term accounting for the SST feedback on surface heat fluxes. In
169 addition, atmospheric dust deposition (Fung and Tegen, 1995) and dissolved inorganic and organic
170 carbon discharges from rivers (Ludwig et al., 1996) were used for the biogeochemical model. Both
171 model grids were initialized for January from a monthly climatology derived from the global ocean

172 simulation (Koné et al., 2009). The simulation was run for 10 years and the outputs averaged every
173 2 days. Integrated properties showed that both physical and biogeochemical models reached
174 statistical equilibrium (determined by the volume-integrated properties converging toward an
175 equilibrium value) after 5 years (not shown). The solution was analyzed from year 6 to year 10.

176

177 *2.2. Eddy diagnostics*

178

179 To follow variations of biogeochemical properties inside eddies during their propagation, each eddy
180 was tracked back to its generation site. The eddy core position was identified as a local extreme in
181 SSH (sea surface height). The eddy shape was determined using a combination of closed contours
182 of SSH and of the Okubo-Weiss parameter as described by Halo et al. (2013). The modelled
183 chlorophyll and nitrate concentrations were averaged over the top 10 m of the ocean to be consistent
184 with SeaWiFS observations. The nitracline depth was defined at the depth of the $1 \mu\text{mol} \cdot \text{L}^{-1}$
185 isoline. To follow variability of the nitrate supply within an eddy, new production and nitrate
186 transport were averaged over a volume delimited on the horizontal plane by the detected eddy shape
187 and on the vertical plane by the mixed layer. Because nitrate is the only limiting nutrient in this
188 region (Koné et al., 2009), we have restricted our analysis to the nitrate concentrations inside eddies
189 and the nitrate fluxes across the eddy boundaries. The nitrate fluxes were calculated from the
190 velocity fields and the nitrate concentration and new production according to O'Niell et al. (1989).

191

192 *2.3. Data products*

193

194 Different data products were used to evaluate model performance and to define the contrasting eddy
195 cases the model was able to simulate. They included ocean colour from SeaWiFS, altimetry from
196 AVISO and in situ hydrological and biogeochemical observations from the CSIRO Atlas of
197 Regional Seas (CARS). SeaWiFS weekly surface chlorophyll concentrations for the period 1998-
198 2009 were used in this study. These data were produced by the NASA Goddard Space Flight Center
199 (McClain et al., 1998). AVISO Sea Surface Height (SSH) was obtained by combining sea level
200 anomalies derived from satellite altimetry with mean dynamic topography (Ducet and Le Traon,
201 2000; Le Traon et al., 2003). For temperature, salinity and nitrate data, we used annual mean fields
202 from the CARS climatology at a spatial resolution of $1/2^\circ$, obtained from CSIRO (Commonwealth
203 Scientific and Industrial Research Organization). CARS is an atlas derived from two major datasets
204 interpolated onto standard depths (Dunn and Ridgway, 2002; Ridgway et al., 2002): the NODC
205 World Ocean Atlas 1998 hydrographic data (www.nodc.noaa.gov) and the CSIRO archive of

206 Australian hydrographic data.

207

208 **3. Results**

209

210 *3.1. Model behaviour*

211

212 We compared the annual mean SSH from the child domain ($1/6^\circ$ resolution) of our modelling
213 experiment to the AVISO SSH data (Fig. 1a, b). In both the model and observed data, a broad South
214 Equatorial Current (SEC) flowed westward towards Madagascar between 12°S and 18°S . The SEC
215 split into two branches when it reached the coast at 17°S . The southern branch formed the East
216 Madagascar Current (EMC), which flows southward to become a source of the Agulhas Current
217 (AC) after passing the southern tip of Madagascar (Schott and McCreary, 2001, DiMarco et al.,
218 2002). The northern branch formed the Northern Madagascar Current which sweeps the northern tip
219 of Madagascar to flow towards the African continent. It splits at the African coast at 11°S to form
220 the East African Current which flows northward, and a southward branch which flows into the MC,
221 becoming another source of the AC (Schott and McCreary, 2001, DiMarco et al., 2002). Southeast
222 of Madagascar, the recently discovered South Indian Ocean Counter current (Palastanga et al.,
223 2007) flowed eastward towards the centre of the Indian Ocean. The locations of these major
224 patterns in the mean surface oceanic circulation, and mirrored in the isolines of mean SSH, are
225 similar in the model outputs and the observed data. However, the simulated SEC is faster than the
226 observation, with typical velocities of the order of $35 \text{ cm}\cdot\text{s}^{-1}$ compared with $30 \text{ cm}\cdot\text{s}^{-1}$. This could
227 be caused by a bias in the inflow provided by the global ocean model at the eastern open boundary.

228

229 In Fig. 1c, d, surface Eddy Kinetic Energy (EKE) calculated from the simulated currents was
230 compared with EKE derived from AVISO altimetry data. EKE is the energy associated with
231 fluctuations in the currents (after filtering out the seasonal cycle), and is a direct measure of the
232 variability associated with eddies. The values of EKE in the central part of the MC are among the
233 largest in the world's oceans. This is principally associated with the southward propagation of large
234 anticyclones, in addition to oceanic turbulence at the scale of the Rossby radius of deformation
235 (Halo et al., 2013). South of Madagascar, a secondary maximum was related to the generation of
236 eddies and dipoles at the detachment of the EMC from the coast. In general, modeled EKE was
237 comparable with observations (Fig. 1c, d) allowing the use of this simulation to test the effects of
238 mesoscale turbulence on the biogeochemistry of the MC. Nevertheless, simulated levels of EKE in
239 the northern and central MC were larger than observed. This could be related to the amplified
240 strength of the SEC in the model, which generated larger than observed eddies with large

241 amplitudes in the MC (Halo et al., 2013). However, this bias might also be related to the sea state
242 bias in ocean altimetry (Tran et al., 2010) or the methodologies used in the estimation of the mean
243 dynamic topography maps (Vossepoel, 2007, Maximenko et al., 2009).

244

245 The surface chlorophyll distributions (Fig. 2) showed characteristically low concentrations in the
246 Western Indian Ocean subtropical gyre east of Madagascar (Machu et al., 2005), high concentrations
247 in the upwelling regions on the Sofala Bank and off Somalia (Koné et al., 2009), south of
248 Madagascar (Machu et al., 2002), and along the western equatorial region, with important seasonal
249 fluctuations for the latter two. Chlorophyll a concentrations were generally lower in summer (Fig.
250 2a, c) than in winter (Fig. 2b, d). However, there was some discrepancy between the simulated and
251 observed chlorophyll concentrations. In summer, the simulated chlorophyll levels were lower than
252 the observed. The patch of high chlorophyll concentration, observed moving eastward from the
253 south of Madagascar in the summer months (Longhurst, 2001), was absent in the simulated
254 chlorophyll concentrations. In winter, the extent of the high chlorophyll patch in the Somalian
255 upwelling region was smaller than in the observed data. Chlorophyll concentrations in the
256 subtropical gyre were lower in the model compared to these observations, while in the upwelling
257 region south of Madagascar, the high levels extended further offshore than in the observed SeaWiFS
258 data. The higher values observed in the coastal zone were also absent from the simulated
259 chlorophyll concentrations. The strong simulated SEC observed at the northern tip of Madagascar
260 induced a branch of enhanced chlorophyll to the west, a feature that was absent from the
261 observations. The high chlorophyll concentrations observed in the south of the MC were
262 exaggerated in winter in the modelling experiment.

263

264 In order to evaluate the ability of the model to represent the vertical structure of principal oceanic
265 properties, a zonal vertical section at 24°S of simulated temperature, salinity and nitrate was
266 compared to CARS data (Fig. 3). Simulated temperature indicated a thermocline between 100 m
267 and 300 m, in agreement with observations (Fig. 3a, d). Although model surface temperatures were
268 about 2°C warmer than observed, the model was able to reproduce the sharp thermocline and water
269 temperature at intermediate levels. Salinity in surface waters was 35.1-35.3 (Fig. 3b, e) and
270 characterized by the presence of Tropical Surface Water (DiMarco et al., 2002). Higher salinities
271 typical of Subtropical Surface Water were present below this layer between 100 m and 400 m
272 (DiMarco et al., 2002, New et al., 2007). Fresher water was located below a sharp halocline at ~
273 500 m, with characteristics of the intrusion of Antarctic Intermediate Water (AAIW). AAIW is
274 characterized by salinity lower than 34.7, and is observed between 600 m and 1500 m (DiMarco et

275 al., 2002, New et al., 2007). The model was able to simulate the presence of these water masses and
276 a strong halocline, but it underestimated the salinity maximum by 0.15 for Subtropical Surface
277 Water and the salinity minimum by 0.125 for AAIW. This bias could be induced by diapycnal
278 mixing or by the remote influence of global circulation which might be inaccurately reproduced at
279 the open boundary conditions of our domain. Vertical nitrate distribution displayed a more intense
280 gradient in our modelling experiment than in the CARS data (Fig. 3c, f respectively). However,
281 surface layers were depleted in nitrate in the CARS observations as well as in the simulation, the
282 nitracline being slightly shallower for the latter (~ 60-70 m). Many reasons could explain the
283 discrepancies that have been mentioned, but the model was nevertheless able to simulate the large
284 scale patterns of regional circulation and associated biogeochemical responses, and could be used to
285 investigate the history of mesoscale features and define their enrichment processes.

286

287 *3.2. Mesoscale eddies and biogeochemical responses*

288

289 As described above, the initial biogeochemical response to mesoscale eddy activity is chlorophyll
290 enrichment in the core of cyclonic eddies in response to the upliftment of isopycnal surfaces
291 bringing nutrient-rich water into the euphotic zone, and chlorophyll depletion in the centre of
292 anticyclones resulting from the convergence and downwelling of isopycnal surfaces. However, one
293 could easily imagine that reality is far more complex and that the observed biogeochemistry of an
294 eddy depends on its life history (including its origin) and its interaction with other mesoscale
295 features or with shelf regions during its lifetime. Fig. 4 presents different case studies that were
296 investigated. In each case, the chlorophyll enrichment relative to the kind of eddy (cyclonic or
297 anticyclonic) has been depicted as snapshots of both satellite observations and model outputs.
298 Various contrasting case studies were specifically selected.

299

300 Two situations of surface chlorophyll concentrations associated with cyclonic eddies (C1, C2 and
301 C1_{obs}, C2_{obs}) are described, one where enrichment occurs in the centre and another without
302 noticeable enrichment. Three different signatures of surface chlorophyll enrichment associated with
303 anticyclonic eddies are then presented. A1 and A1_{obs} were anticyclones close to the coast that seemed
304 to entrain enriched coastal waters by rotational activity. A2 and A2_{obs} were anticyclones showing
305 enrichment across the eddy, while A3 and A3_{obs} were eddies located in the middle of the MC
306 containing higher chlorophyll at their periphery. The advantage of the model is that it allows a
307 backward investigation of eddy structure as well as a study of its three-dimensional evolution. We
308 present the life history of the eddies in these snapshots and explain why they exhibit particular

309 characteristics.

310

311 3.3. High production in a cyclonic eddy and low production in an anticyclonic eddy

312

313 Fig. 4a, b illustrates a cyclonic eddy that is chlorophyll-enriched at its core, a case that can be
314 explained by the eddy upwelling mechanism proposed by McGillicuddy and Robinson (1997).
315 Cyclonic eddy C1_{obs} observed in the southern part of the MC exhibited elevated chlorophyll
316 concentrations at its core, with values of $\sim 0.35 \text{ mg m}^{-3}$ (Fig. 4a). In a similar feature simulated by
317 the model (Fig. 4b), surface chlorophyll concentrations varied from 0.05-0.15 mg m^{-3} . A vertical
318 section of nitrate concentration across C1 (Fig. 5a) showed higher values in the eddy core than at
319 the periphery in the upper 70 m, which is the depth of the nitracline. Below the nitracline, the nitrate
320 isolines shoaled between 39.5°E and 41°E, around the core of C1. The vertical nitrate flux (Fig. 5b)
321 revealed downwelling in the eddy core, with a maximum loss of nitrate of more than $0.04 \mu\text{mol m}^{-2}$
322 d^{-1} , and upwelling at the periphery that was more intense on the western side. This result appears
323 inconsistent with the shoaling of the isolines observed in the nitrate vertical distribution. We
324 therefore tracked the eddy back in time in order to follow the evolution of its biogeochemical
325 characteristics prior to the snapshot shown in Fig. 4. C1 was generated south of Madagascar and
326 propagated towards west-south-west (Fig. 5c). During the first two months, nitrate concentrations
327 decreased steadily over time, with the core of C1 generally having higher levels than the
328 surrounding waters (Fig. 5d). These nutrients sustained new production rates of $0.03 \mu\text{mol N L}^{-1} \text{d}^{-1}$
329 during the first phase of the eddy's life (Fig. 5f). After this initial phase of two months, the decrease
330 in surface nitrate concentrations accelerated, resulting in a significant decline in new production and
331 in surface chlorophyll concentrations (Fig. 5d). The decrease in surface chlorophyll commenced at
332 the periphery of the eddy and then became noticeable within its core about two weeks later. The
333 temporal evolution of the C1 amplitude showed a linear increase during the first two months after
334 its generation (Fig. 5e). After this period the eddy appeared stable, with no significant increase in its
335 amplitude, which then decayed a few days later. Nitrate flux through C1 (Fig. 5f) indicated that
336 nitrate was predominantly supplied to the eddy across the vertical boundary. Maximum injection of
337 $1 \mu\text{mol N L}^{-1} \text{d}^{-1}$ was observed when the eddy was near its generation site south of Madagascar.
338 Offshore, the nitrate transport was weaker and decreased with time and location towards the site of
339 observation that was further south at $\sim 27^\circ\text{S}$.

340

341 Anticyclone A1 (Fig. 4c, d) was observed in the central part of the MC. The eddy was depleted in
342 chlorophyll at its centre, being $<0.1 \text{ mg m}^{-3}$ in the SeaWiFS image and $<0.05 \text{ mg m}^{-3}$ in the model

343 simulation, but was enriched at its periphery. The zonal transect across A1 showed the impact of A1
344 on nitrate concentrations (Fig. 6a). The convergence at the centre of the eddy depressed the nitrate
345 isolines (deeper than 80 m) and caused them to be shallower at the periphery (50 m). Vertical nitrate
346 fluxes (Fig. 6b) indicated weak downward fluxes in the centre and upwelling at the periphery.
347 Greater upward fluxes of nitrate were associated with the eastern edge of A1, which interacted with
348 cyclonic eddy C2 (Fig. 4d).

349

350 During its formation, A1 entrained coastal waters from the north of Madagascar (Fig. 6c). These
351 waters were nutrient-enriched and supported new production of $\sim 0.01 \mu\text{mol N L}^{-1} \text{d}^{-1}$ (Fig. 6e). At
352 the initial back-tracked locations in late October, a maximum in new production (Fig. 6e) was
353 associated with elevated surface nitrate and chlorophyll (Fig. 6d), while the mixed layer was deeper
354 (not shown). This initial nutrient input was taken up by phytoplankton as the anticyclonic eddy
355 propagated towards the MC, without any new nutrient injection. This explained the low chlorophyll
356 content of the eddy in February (Fig. 6d). In mid-December and mid-January, a small nitrate input
357 produced a small peak in new production and a weak chlorophyll increase. These peaks occurred
358 when the eddy was closest to the coast ($\sim 14^\circ\text{S}$ and 20°S), suggesting an entrainment of surface
359 coastal waters. Nitrate flux into eddy A1 is shown in Fig. 6e, demonstrating the dominance of
360 vertical transport during A1's lifetime. Maximum injection of nitrate was observed in mid-
361 December, with an injection of $0.4 \mu\text{mol N L}^{-1} \text{d}^{-1}$, resulting in a peak in new production and
362 surface chlorophyll concentration.

363

364 *3.4. Low production in a cyclonic eddy and high production in an anticyclonic eddy*

365

366 A cyclonic eddy with low chlorophyll concentration at its core was simulated by the model (C2,
367 Fig. 4d) and a similar situation was indicated by satellite observation (C2_{obs}, Fig. 4c). The predicted
368 nitrate distribution across C2 (Fig. 7a) showed lower concentrations at the surface everywhere
369 within the eddy, with no significant variations between its core and its periphery. Below the surface,
370 the nitracline was shallow at the core of the eddy at a depth of ~ 45 m, and deepened slightly by ~ 5
371 m at the periphery. This doming of the nitrate isolines was more pronounced deeper in the water
372 column, with an upward incline of ~ 20 m at 100 m depth. Unexpectedly, because of the doming,
373 vertical nitrate fluxes indicated a weak downwelling in the core of the eddy. This downwelling is at
374 its maximum at about 41.5°E and may explain the simulated deepening of the nitracline there. On
375 both boundaries of C2, the model simulated upwelling of subsurface nitrate, being significantly
376 stronger on the western boundary, but the nitracline gave no indication of this upwelling.

377

378 The back-tracking of C2, from its location in Fig. 4d to where it was generated, is shown in Fig. 7c.
379 This eddy was generated in the mid-MC and travelled in a westerly direction. The mean chlorophyll
380 concentration in the eddy remained very low at 0.035 mg m^{-3} and showed no significant variation
381 between its core and its boundaries over its tracked course (note the small values of the order of \sim
382 $10^{-4} \text{ mg m}^{-3}$ in Fig. 7d). Similarly, nitrate concentrations and new production were also extremely
383 low at $<5.5 \times 10^{-7} \text{ } \mu\text{mol N L}^{-1}$ and $7 \times 10^{-7} \text{ } \mu\text{mol N L}^{-1} \text{ d}^{-1}$ respectively (Fig. 7d, e). The depths of the
384 nitracline and chlorophyll maximum displayed similar temporal behaviour, especially for their
385 mean values, with the chlorophyll maximum located 5-10 m below the nitracline, similar to the
386 results for C1 (not shown). A comparison between the horizontal and vertical nitrate fluxes
387 indicated a dominance of vertical injection into eddy C2 (Fig. 7e), with the maximum being
388 observed from mid to late January at rates $>0.08 \text{ } \mu\text{mol N L}^{-1} \text{ d}^{-1}$. Subsequently, vertical injection
389 declined though to the end of the tracking period on 6 February 2010. The temporal evolution of
390 new production within C2 displayed a slight increase with time (Fig. 7e).

391

392 SeaWiFS data indicated a productive anticyclonic eddy ($A2_{\text{obs}}$) in the MC where chlorophyll
393 concentrations were 0.25 mg m^{-3} at the core (Fig. 4e). The model simulation was consistent with
394 the observations, producing a similar productive anticyclonic eddy (A2, Fig. 4f). A vertical section
395 across A2 revealed high nitrate concentrations at its core and decreasing towards the periphery (Fig.
396 8a). Instead of a deepening of the nitrate isolines at the core, and thus of the nitracline as observed
397 in eddy A1, eddy A2 exhibited the opposite trend with relatively more elevated nitrate
398 concentrations at the surface. The nitracline was located at $\sim 70 \text{ m}$ and vertical nitrate fluxes
399 indicated upward transport in the core and downward transport towards the boundaries of A2 (Fig.
400 8b).

401

402 A2 was generated in the eastern MC close to Madagascar in the vicinity of 20°S (Fig. 8c). From
403 early February to mid-March, surface nitrate and chlorophyll concentrations were low (Fig. 8d). At
404 the beginning of April, during its southwestly propagation, A2 merged with another anticyclonic
405 eddy generated further south ($A2^*$, Fig. 8c). The merging of the two eddies seems to have had an
406 impact on chlorophyll and nitrate distributions (Fig. 8d) because this period was associated with a
407 decline in surface nitrate and chlorophyll concentrations. Chlorophyll concentrations in A2 began to
408 increase in early May from 0.05 mg m^{-3} to reach 0.2 mg m^{-3} in the eddy core by the end of May
409 (Fig. 8d). This corresponded to a change in the trajectory of A2 (Fig. 8c). The temporal evolution of
410 new production closely followed the evolution of surface nitrate and chlorophyll distributions (Fig.

411 8e), confirming an injection of nutrients during the last month of the lifetime of eddy A2. The
412 vertical and horizontal components of the nitrate fluxes within A2 (Fig. 8e) indicated the dominance
413 of lateral nitrate transport during this month and a resulting increase in production.

414

415 *3.5. High production at the boundary of an anticyclonic eddy*

416

417 Anticyclonic eddies A3_{obs} and A3 (Fig. 4g, h) were characterized by positive sea surface height
418 anomalies, with high chlorophyll concentrations at the boundary and decreasing towards the core.
419 The vertical distribution of nitrate indicated higher concentrations at the core than at the periphery
420 (Fig. 9a) and nitrate isolines were depressed at 38°E, reflecting downward nitrate fluxes between
421 37°E and 38°E (Fig. 9b). Vertical nitrate fluxes on either side of the core indicated upwelling of
422 nutrients towards the periphery of this anticyclonic eddy (Fig. 9b). Surprisingly, chlorophyll
423 concentrations did not match the nitrate distribution, i.e. chlorophyll was not maximum at the core
424 of the eddy where nitrate levels were highest. In this particular case, the flux core of the eddy was
425 iron-depleted (Fig. 9f) limiting phytoplankton growth, unlike the periphery where iron
426 concentrations were higher. This case was the only model that simulated significant iron limitation
427 in the MC.

428

429 Similar to A1, A3 was generated near the northeastern tip of Madagascar (Fig. 9c). The initial
430 concentrations, as well as the supply of nitrate and iron to the surface layers, were sufficient to
431 support new production of $\sim 0.01 \mu\text{mol N L}^{-1} \text{d}^{-1}$ and maintain chlorophyll levels at $0.25\text{-}0.3 \text{ mg}$
432 m^{-3} (Fig. 9d, e). During the second half of August, new production increased rapidly and the
433 concentration of chlorophyll averaged over the whole eddy was twice that at the core. This scenario
434 was maintained until mid-September and indicated that production occurred mainly towards the
435 boundary of the eddy. The peak in production coincided with a depletion in surface iron
436 concentrations (Fig. 9f), ultimately resulting in chlorophyll decreasing as well (Fig. 9d). After mid-
437 September, the chlorophyll maximum and the nitracline deepened significantly, especially at the
438 core of A3 (not shown). Nitrate flux over the mixed layer was characterized by a dominance of
439 vertical injection during the early life of A3 when the eddy was near its initial location, with a
440 maximum of about $0.4 \mu\text{mol N L}^{-1} \text{d}^{-1}$ (Fig. 9e). From late July to mid-August, nitrate flux was
441 mainly lateral, but the maximum lateral transport was 50 % less than the vertical transport observed
442 earlier in the eddy lifetime. From mid-August to the end of the simulation on 14 October 2010,
443 maximum nitrate transport occurred across the vertical boundary at a rate of $0.3 \mu\text{mol N L}^{-1} \text{d}^{-1}$.
444 Weak positive lateral transport was also simulated, however, and this coincided with an increase in

445 iron concentration at the periphery of the eddy.

446

447 *3.6. Eddy-shelf interaction*

448

449 Model simulations of an anticyclonic eddy (A4) and a cyclonic eddy (C3) moving south and
450 interacting with the Mozambique shelf are presented in Fig. 10a. A4 was characterized by reduced
451 chlorophyll concentrations at its core ($<0.1 \text{ mg m}^{-3}$) and increasing levels towards the boundary,
452 reaching 0.15 mg m^{-3} (Fig. 10b). On the northwestern side of this eddy, a patch of higher
453 chlorophyll was depicted, which decreased during its southward advection. South of A4, a cyclonic
454 eddy C3, located closer to the coast, was clearly identifiable by maximum chlorophyll
455 concentrations at its core, exceeding 0.3 mg m^{-3} (Fig. 10b). The elevated chlorophyll of C3 merged
456 with the chlorophyll plume on the southern extension of A4 (37° - 38° E).

457

458 The passage of eddies moving past 24° S are shown as time and longitude Hovmoller plots in Fig.
459 10c-e. Nitrate concentrations were reduced in the core of anticyclones during late February and late
460 April, with concentrations $<0.5 \text{ } \mu\text{mol N L}^{-1}$ (Fig. 10d) and resulting in low chlorophyll levels (Fig.
461 10e). In contrast, nitrate and chlorophyll concentrations were elevated on the southern boundaries of
462 the anticyclones (Fig. 10c, d) and entrainment of nitrate and chlorophyll from the shelf could have
463 contributed to these increased levels. The passage of cyclonic eddies appeared to induce an increase
464 in nitrate up to levels $>3 \text{ } \mu\text{mol N L}^{-1}$. This suggested a shoaling of the nitracline depth to less than
465 50 m at the core of these eddies, resulting in an upliftment of nitrate into the euphotic zone.
466 Enhanced nutrients would have induced phytoplankton growth, leading to elevated chlorophyll
467 levels at 24° S as the cyclones passed by (Fig. 10e).

468

469 **4. Discussion**

470

471 The complex biophysical dynamics of the oceanic waters of the MC have been simulated using a
472 biogeochemical model (PISCES) coupled to a hydrodynamic model (ROMS). The evaluation of
473 model outputs indicated that the main circulation and hydrological aspects (temperature and
474 salinity) were fairly well represented by the models, as were the distributions of nitrate and
475 chlorophyll. The model overestimated the intensity of the SEC and winter chlorophyll
476 concentrations, however, and also underestimated phytoplankton pigment for the summer. The
477 discrepancy in the SEC circulation could be related to the eastern boundary conditions, while the
478 winter overestimation of chlorophyll may be related to the non-seasonal properties of the river

479 discharge of nutrients used in the simulation. A potential explanation of the underestimated
480 chlorophyll levels during summer is the relatively coarse resolution of the model which cannot
481 properly resolve submesoscale dynamics. In previous modelling studies, submesoscale dynamics
482 has been shown to significantly increase primary productivity and nutrient supply in oligotrophic
483 conditions (Lévy et al., 2001).

484

485 The model was used to study the history of eddies in the MC that displayed contrasting physical and
486 biogeochemical characteristics, as seen in the snapshots of model outputs. We have shown that the
487 characteristics of an eddy observed as a snapshot can be misleading, because eddies integrate
488 several months of life history. Therefore, eddies were tracked for periods of one (C2) to four (A1,
489 A2) months back in time, allowing identification of the processes responsible for enrichment in
490 these eddies along their migratory routes.

491

492 *4.1 Importance of the origin on eddy characteristics*

493

494 Anticyclonic eddies A1, A2 and A3 that were observed in the MC showed different surface
495 characteristics (Figs 6, 8 and 9). Intensity differed considerably between A1 and A3, both formed at
496 the entrance of the MC (12°S), and A2, which originated to the west of Madagascar. Eddies A1 and
497 A3 were more barotropic and energetic than eddy A2, which is consistent with their generation sites
498 as described by Halo et al. (2013). The enrichment mechanisms varied among the eddies, with
499 nitrate and chlorophyll concentrations in the surface layers varying by two orders of magnitude and
500 the nitracline depth ranged from a few meters to 70 m. Both A1 and A3 exhibited their highest
501 nitrate concentrations in the surface layers at the location of their origin north of Madagascar,
502 relatively close to the shelf. Despite their high energy, no additional nutrients were injected into the
503 surface layers during their three-month passage through the MC from north to south.

504

505 For eddy A2, enrichment occurred at the end of its trajectory, when it moved closer to the shelf.
506 This suggests that primary production in anticyclonic eddies is enhanced mainly when they interact
507 with the coastal domain, where nutrient loading occurs as a result of river runoff, local upwelling
508 and mixing, sediment mobilization and erosion. Such an observation supports a previous study by
509 Whitney and Robert (2002) that indicated the role of anticyclonic eddies in the offshore transport of
510 coastal nutrients and enhanced productivity. In all cases, the phytoplankton was sensitive to the
511 availability of nitrate and any input to the surface layers was immediately taken up to enhance new
512 production, as occurs in any oligotrophic area where nitrate availability limits production.

513 Therefore, the correlation between nitracline depth, surface nitrate concentrations and net primary
514 production was strong. Among eddies we tracked, the depth of the chlorophyll maximum was often
515 located about 10 m below the depth of the nitracline.

516

517 Cyclonic eddies C1 and C2 also showed contrasting and different characteristics (Figs 5 and 7), that
518 could be explained by their different origins. C2 was formed in the central MC where oligotrophic
519 conditions prevailed at the time, with a sharp, deep nitracline and low surface nitrate concentrations.
520 During its propagation that was tracked for about one month, nothing unusual was recorded for this
521 eddy. C1 was generated at the southern tip of Madagascar, where nutrients were high because of
522 coastal upwelling. This eddy retained water properties from where it originated and displayed the
523 largest surface concentration of nitrate and the highest levels of new production of all the eddies
524 that were investigated. The initial input of nutrients maintained new production for about two
525 months, before the nitracline deepened and the nutrient supply and new production decreased in the
526 mid-MC. Such a decrease in new production, while the amplitude of the eddy was increasing, was
527 not consistent with the conceptual model that proposes upwelling processes in the core of cyclonic
528 eddies (McGillicuddy and Robinson (1997). The interaction of eddies with the shelf (Fig. 10)
529 illustrated the role of anticyclones in the offshore transport of nutrients and phytoplankton biomass
530 from the shelf, thus enhancing open ocean productivity and corroborating previous studies by
531 Whitney and Robert (2002) and Gruber et al. (2011).

532

533 In summary, this study established that the conceptual model described by McGillicuddy and
534 Robinson (1997) for explaining the enrichment of eddies in subtropical regions was valid for the
535 Mozambique Channel from a dynamical point of view. It was also demonstrated that examining the
536 life history of an eddy is necessary for understanding the biological pattern observed in a snapshot
537 image. The history of these structures can therefore provide valuable information for investigating
538 the relationship between evolving eddy characteristics and the various trophic levels of the marine
539 food web. The examples selected illustrated the complexity of the ecosystem and the importance of
540 models for assessing details of the mechanisms responsible for primary production within eddies.
541 The next step is to implement a study of the higher trophic levels utilising an End to End ecosystem
542 model.

543

544 **Acknowledgments**

545

546 This research was supported by the AIRD (Agence Inter-établissements de Recherche pour le
547 Développement) through its capacity building program and the LMI ICEMASA (International

548 Centre for Education, Marine and Atmospheric Sciences over Africa). The MDT CNES-CLS09 data
 549 used in this work was produced by CLS Space Oceanography Division and distributed by AVISO,
 550 with support from CNES (<http://www.aviso.oceanobs.com/>). The topography used in the simulation
 551 of the Mozambique Channel dynamics was provided by GEBCO Digital Atlas, published on CD-
 552 ROM by the British Oceanographic Data Centre on behalf of the Intergovernmental Oceanographic
 553 Commission and the International Hydrographic Organization 2003. We also thank the anonymous
 554 reviewers for their valuable comments.

555

556 **References**

557

558 Abraham, E.R., 1998. The generation of plankton patchiness by turbulent stirring. *Nature*, 391,
 559 577–580.

560

561 Aumont, O., Bopp, L., 2006. Globalizing results from Ocean in situ iron fertilization studies. *Global*
 562 *Biogeochem. Cycles* 20, GB2017. doi:10.1029/2005GB002591.

563

564 Aumont, O., Maier-Reimer, E., Blain, S., Monfray, P., 2003. An ecosystem model of the global
 565 Ocean including Fe, Si, P colimitations. *Global Biogeochem. Cycles* 17.
 566 doi:10.1029/2001GB001745.

567

568 Broecker, W.S., Peng, T.H., Beng, Z., 1982. Tracers in the sea. Lamont-Doherty Geological
 569 Observatory, Palisades, New York.

570

571 Casey, K.S., Cornillon, P., 1994. A comparison of satellite and in situ based sea surface temperature
 572 climatologies. *J. Climate* 12, 1848–1863.

573

574 Chelton, D.B., DeSzoeke, R.A., Schlax, M.G., Naggar, K.E., Siwertz, N., 1998. Geographical
 575 variability of the first baroclinic rossby radius of deformation. *J. Phys. Oceanogr.* 28, 433–460.

576

577 Cotté, C., Park, Y.H., Guinet, C., Bost, C.A., 2007. Movements of foraging king penguins through
 578 marine mesoscale eddies. *Proc. R. Soc. B* 274, 2385–2391.

579

580 Cottin, M., Raymond, B., Kato, A., Amelieau, F., Maho, Y. L., Raclot, T., Galton-Fenzi, B.,
 581 Meijers, A., Ropert-Coudert, Y., 2012. Foraging strategies of male adelic penguins during their first
 582 incubation trip in relation to environmental conditions. *Mar. Biol.* 159, 1843–1852.

583

584 Da Silva, A.M., Young, C.C., Levitus, S., 1994. Atlas of Surface Marine data 1994, vol. 1.
 585 Algorithms and Procedures, NOAA Atlas NESDIS 6, NOAA. Silver Spring.

586

587 de Ruijter, W.P.M., Ridderinkhof, H., Lutjeharms, J.R.E., Schouten, M.W., Veth, C., 2002.
 588 Observations of the flow in the Mozambique Channel. *Geophys. Res. Lett.* 29, 1401–1403.

589

590 de Ruijter, W.P.M., Ridderinkhof, H., Schouten, M.W., 2005. Variability of the southwest Indian
 591 Ocean. *Phil. Trans. R. Soc. A* 363, 63–76.

592

593 Debreu, L., Marchesiello, P., Penven, P., Cambon, G., 2012. Two-way nesting in split-explicit ocean
 594 models: algorithms, implementation and validation. *Ocean Model.* 49-50, 1-21.

595

596 Debreu, L., Vouland, C., Blayo, E., 2008. AGRIF: Adaptive grid refinement in Fortran. *Comput.*
 597 *Geosci.* 34, 8–13.

- 598
599 DiMarco, S.F., Chapman, P., Jr., W.D., Hacker, P., Donohue, K., Luther, M., Johnson, G.C., Toole,
600 J., 2002. Volume transport and property distributions of the Mozambique Channel. *Deep-Sea Res. II*
601 49, 1481–1511.
602
603 Ducet, N., Le Traon, P.Y., 2000. Global high-resolution mapping of ocean circulation from
604 TOPEX/Poseidon and ERS1 and 2. *J. Geophys. Res.* 105, 19477–19498.
605
606 Dunn, J.R., Ridgway, K.R., 2002. Mapping ocean properties in regions of complex topography.
607 *Deep-Sea Res. I*, 49, 591–604.
608
609 Franks, P.J.S., Wroblewski, J.S., Flierl, G.R., 1986. Prediction of phytoplankton growth in response
610 to the frictional decay of a warm-core ring. *J. Geophys. Res.* 91, 7603–7610.
611
612 Fung, I., Tegen, I., 1995. Contribution to the atmospheric mineral aerosol load from land surface
613 modification. *J. Geophys. Res.* 18, 707–726.
614
615 Gruber, N., Lachkar, Z., Frenzel, H., Marchesiello, P., Munnich, M., McWilliams, L.C., Nagai, T.,
616 Plattner, G.K., 2011. Eddy-induced reduction of biological production in eastern boundary
617 upwelling systems. *Nat. Geosci.* 4, 787–792.
618
619 Haidvogel, D.B., Beckmann, A., 1999. *Numerical Ocean Circulation Modeling*. Vol. 2 of *Environ.*
620 *Sci. Manage.* 2. Imperial College Press. London.
621
622 Halo, I., Backeberg, B., Penven, P., Ansorge, C. R. I., Ulgren, J., 2013. Eddy properties in the
623 Mozambique Channel: A comparison between satellite altimetry and Ocean Circulation models.
624 *Deep-Sea Res. II*
625
626 Haney, J.C., 1986. Seabird Patchiness in Tropical Oceanic Waters: The influence of Sargassum
627 “Reefs”. *The Aku* 103, 141–151.
628
629 Huggett, J.A., 2013. Mesoscale distribution and community composition of zooplankton in the
630 Mozambique Channel. *Deep-Sea Res. II*
631
632 Kishi, M., 1994. Prediction of Phytoplankton Growth in a Warm-Core Ring Using Three
633 Dimensional Ecosystem Model. *J. Oceanogr.* 50, 489–498.
634
635 Koné, V., Aumont, O., Levy, M., Resplandy, L., 2009. Physical and biogeochemical controls of the
636 phytoplankton seasonal cycle in the Indian Ocean: A modelling study. *Geophys. Monogr. Ser.* 185,
637 147–166.
638
639 Large, W.G., McWilliams, J.C., Doney, S.C., 1994. Oceanic vertical mixing: A review and a model
640 with a nonlocal boundary layer parameterization. *J. Geophys. Res.* 32, 363–403.
641
642 Le Traon, P.Y., Faugere, Y., Hernandez, F., Dorandeu, J., Mertz, F., Ablain, M., 2003. Can We
643 Merge GEOSAT Follow-On with TOPEX/Poseidon and ERS-2 for an Improved Description of the
644 Ocean Circulation? *J. Atmos. Oceanic Technol.* 20, 889–895.
645
646 Lebourges-Dhaussy, A., Huggett, J., Ockhuis, S., Roudaut, G., Josse, E., Verheye, H., 2013.
647 Zooplankton size and distribution within mesoscale structures in the Mozambique Channel: a

- 648 comparative approach using the TAPS acoustic profiler, a multiple net sampler and ZooScan image
 649 analysis. *Deep-Sea Res. II*
 650
- 651 Legendre, L., Rassoulzadegan, F., 1995. Plankton and nutrient dynamics in marine waters. *Ophelia*
 652 41, 153-172.
 653
- 654 Lévy, M., Ferrari, R., Franks, P.J.S., Martin, A.P., Rivière, P., 2012. Bringing physics to life at the
 655 submesoscale. *Deep-Sea Res. I* 39, 1–13.
 656
- 657 Lévy, M., Klein, P., Treguier, A.M., 2001. Impact of sub-mesoscale physics on production and
 658 subduction of phytoplankton in an oligotrophic regime. *J. Mar. Res.* 59, 535–565.
 659
- 660 Liu, W.T., Tang, W., Polito, P.S., 1998. NASA scatterometer provides global ocean-surface wind
 661 fields with more structures than numerical weather prediction. *Geophys. Res. Lett.* 25, 761–764.
 662
- 663 Longhurst, A., 2001. A major seasonal phytoplankton bloom in the Madagascar Basin. *Deep-Sea*
 664 *Res. I* 48, 2413–2422.
 665
- 666 Ludwig, W., Probst, J., Kempe, S., 1996. Predicting the oceanic input of organic carbon by
 667 continental erosion. *Global Biogeochem. Cycles* 10, 23–41.
 668
- 669 Machu, E., Biastoch, A., Oschlies, A., Kawamiya, M., Lutjeharms, J.R.E., Garon, V., 2005.
 670 Phytoplankton distribution in the Agulhas system from a coupled physical biological model. *Deep-*
 671 *Sea Res. I* 52, 1300–1318.
 672
- 673 Machu, E., Lutjeharms, J.R.E., Webb, A.M., Aken, H. M. V., 2002. First hydrographic evidence of
 674 the southeast Madagascar upwelling cell. *Geophys. Res. Lett.* 29, 1–5.
 675
- 676 Marchesiello, P., McWilliams, J.C., Shchepetkin, A., 2001. Open boundary conditions for long-term
 677 integration of regional oceanic models. *Ocean Model.* 3, 1–20.
 678
- 679 Maximenko, N., Niiler, P., Melnichenko, M.H.R.O., Centurioni, L., Chambers, D., Zlotnicki, V.,
 680 Galperin, B., 2009. Mean dynamic topography of the ocean derived from satellite and drifting buoy
 681 data using three different techniques. *J. Atmos. Oceanic Technol.* 26, 1911–1919.
 682
- 683 McClain, C.R., Cleave, M.L., Feldman, G.C., Gregg, W.W., Hooker, S.B., Kuring, N., 1998.
 684 Science Quality SeaWiFS Data for Global Biosphere Research. *Sea Technol.* 10–16.
 685
- 686 McGillicuddy, D.J., Robinson, A.R., 1997. Eddy-induced nutrient supply and new production in the
 687 Sargasso Sea. *Deep-Sea Res. I* 44, 1427–1450.
 688
- 689 Nel, D.C., Lutjeharms, J.R.E., Pakhomov, E.A., Anson, I.J., Ryan, P.G., Klages, N.T.W., 2001.
 690 Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche*
 691 *chrysostoma* in the southern Indian Ocean. *Mar. Ecol. Prog. Ser.* 217, 15–26.
 692
- 693 New, A.L., Alderson, S.G., Smeed, D.A., Stansfield, K.L., 2007. On the circulation of water masses
 694 across the Mascarene Plateau in the South Indian Ocean. *Deep-Sea Res. I* 54, 42–74.
 695
- 696 O’Niell, R.V., DeAngelis, D.L., Pastor, J.J., Jackson, B.J., Post W.M., 1989. Multiple nutrient
 697 limitations in ecological models. *Ecol. Model.* 46. 147-163.

- 698
699 Oschlies, A., Garcon, V., 1998. Eddy-induced enhancement of primary production in a model of the
700 North Atlantic Ocean. *Nature* 394, 266–269.
701
- 702 Palastanga, V., van Leeuwen, P.J., Schouten, M.W., de Ruijter, W.P.M., 2007. Flow structure and
703 variability in the Subtropical Indian Ocean: Instability of the South Indian Ocean Countercurrent.
704 *J. Geophys. Res.* 112, 1–11.
705
- 706 Penven, P., Marchesiello, P., Debreu, L., Lefevre, L., 2008. Software tools for pre and
707 postprocessing of oceanic regional simulations. *Environ. Model. Softw.* 23, 660–662.
708
- 709 Quartly, G.D., Srokosz, M.A., 2003. A plankton guide to ocean physics: colouring in the currents
710 around South Africa and Madagascar. *Ocean Challenge* 12, 19–23.
711
- 712 Ridgway, K.R., Dunn, J.R., Wilkin, J.L., 2002. Ocean interpolation by four dimensional weighted
713 least Squares-Application to the waters around Australasia. *J. Atmos. Oceanic Technol.* 19, 1357–
714 1375.
715
- 716 Sarmiento, J.L., Gruber, N., 2006. *Ocean Biogeochemical Dynamics*. Princeton University Press.
717 Princeton.
718
- 719 Scheffer, A., Trathan, P. N., Collins, M., 2010. Foraging behaviour of King Penguins (*Aptenodytes*
720 *patagonicus*) in relation to predictable mesoscale oceanographic features in the Polar Front Zone to
721 the north of South Georgia. *Prog. Oceanogr.* 86, 232–245.
722
- 723 Schott, F.A., McCreary, J.P., 2001. The monsoon circulation of the Indian Ocean. *Prog. Oceanogr.*
724 51, 1–123.
725
- 726 Schouten, M.W., de Ruijter, A.P.M., van Leeuwen, P.J., Ridderinkhof, H., 2003. Eddies and
727 variability in the Mozambique Channel. *Deep-Sea Res. II* 50, 1987–2003.
728
- 729 Shchepetkin, A.F., McWilliams, J.C., 2005. The regional oceanic modeling system (ROMS): a split-
730 explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model.* 9, 347–404.
731
- 732 Tagliabue, A., Bopp, L., Aumont, O., 2008. Ocean biogeochemistry exhibits contrasting responses
733 to a large scale reduction in dust deposition. *Biogeosci.* 5, 11–24.
734
- 735 Tew-Kai, E., Marsac, F., 2010. Influence of mesoscale eddies on spatial structuring of top predators’
736 communities in the Mozambique Channel. *Prog. Oceanogr.* 86, 214–223.
737
- 738 Tran, N., Vandemark, D., Labroue, S., Feng, H., Chapron, B., Tolman, H.L., Lambin, J., Picot, N.,
739 2010. Sea state bias in altimeter sea level estimates determined by combining wave model and
740 satellite data. *J. Geophys. Res.* 115, 1–7.
741
- 742 Valiela, I., 1995. *Marine Ecological Processes*. Springer Verlag, New York.
743
- 744 Vossepoel, F.C., 2007. Uncertainties in the mean ocean dynamic topography before the launch of
745 the gravity field and steady-state ocean circulation explorer (GOCE). *J. Geophys. Res.* 112, 1–20.
746
- 747 Waite, A., Thompson, P., Pesant, S., Feng, M., Beckley, L., Domingues, C., Gaughan, D., Hanson,

748 C., Holl, C., Koslow, T., Meuleners, M., Montoya, J., Moore, T., Muhling, B., Paterson, H., Rennie,
749 S., Strzelecki, J., Twomey, L., 2007. The Leeuwin Current and its eddies: An introductory overview.
750 *Deep-Sea Res. II* 54, 789–796.

751

752 Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? *Deep-Sea Res. II* 54,
753 211–223.

754

755 Weimerskirch, H., Corre, M. L., Jaquemet, S., Potier, M., Marsac, F., 2004. Foraging strategy of a
756 top predator in tropical waters: great frigatebirds in the Mozambique Channel. *Mar. Ecol.* 275, 297–
757 308.

758

759 Whitney, F., Robert, M., 2002. Structure of Haida eddies and their transport of nutrient from coastal
760 margins into the NE Pacific Ocean. *J. Oceanogr.* 58, 715–723.

761

762 Williams, R.G., Follows, M.J., 1998. The Ekman transfer of nutrients and maintenance of new
763 production over the North Atlantic. *Deep-Sea Res. I* 45, 461–489.

764

765 Yentsch, C.S., Phinney, D.A., 1985. Rotary motions and convection as a means of regulating
766 primary production in warm core rings. *J. Geophys. Res.* 90, 3237–3248.

767

768 **Figure legends**

769

770 Fig. 1. Annual mean SSH (10 cm) for (a) ROMS and (b) AVISO altimetry, and annual mean EKE
771 ($10^2 \text{ cm}^2 \text{ s}^{-2}$) for (c) ROMS and (d) AVISO altimetry.

772

773 Fig. 2. Sea surface chlorophyll concentration (mg Chl m^{-3}) in (a, c) summer (January, February,
774 March) and in (b, d) winter (July, August, September) for (a, b) model simulation and (c, d)
775 SeaWiFS observations.

776

777 Fig. 3. Vertical distribution of (a, d) annual mean temperature ($^{\circ}\text{C}$), (b, e) salinity, and (c, f) nitrate
778 concentration ($\mu\text{mol N L}^{-1}$) at 24°S for (a-c) model simulation and (d-f) CARS climatology.

779

780 Fig. 4. Surface chlorophyll concentration (Chla , in colour, mg m^{-3}) and superimposed sea surface
781 height anomaly (SLA, contours, cm) for various mesoscale eddies in the Mozambique Channel.
782 Left panels are SeaWiFS and AVISO observations (obs) and right panels are model outputs. Bold
783 lines indicate positive anomalies and thin lines are negative anomalies. C1_{obs}: 15 and 16 July 2003
784 for SLA and Chla respectively; C1: average for 6-12 November, year 8; A1_{obs}: 16 and 17 April 2008
785 for SLA and Chla respectively; A1: average for 4-6 February, year 10; C2_{obs}: 16 and 17 April 2008
786 for SLA and Chla respectively; C2: average for 4-6 February, year 10); A2_{obs}: 27 and 28 May 2009
787 for SLA and Chla respectively; A2: average for 20-26 May, year 9; A3_{obs}: 28 January 2004 for both
788 SLA and Chla; A3: average for 12-14 October, year 10.

789

790 Fig. 5. Vertical sections across C1 (Fig. 4b) for (a) nitrate concentrations ($\mu\text{mol N L}^{-1}$), (b) vertical
791 nitrate flux ($\mu\text{mol N m}^{-2} \text{ s}^{-1}$), (c) evolution of the centre of C1 tracked back in time, (d) chlorophyll
792 and nitrate concentrations averaged over the upper 10 m, (e) C1 amplitude along the time track, and
793 (f) nitrate fluxes and new production averaged over the mixed layer. Shading and negative values in
794 (b) indicates downward fluxes. Bold and dashed lines in (f) indicate horizontal and vertical nitrate
795 fluxes.

796

797 Fig. 6. Vertical sections across A1 (Fig. 4d) for (a) nitrate concentrations ($\mu\text{mol N L}^{-1}$), (b) vertical

798 nitrate flux ($\mu\text{mol N m}^{-2} \text{s}^{-1}$), (c) evolution of the centre of A1 tracked back in time, (d) chlorophyll
799 and nitrate concentrations averaged over the upper 10 m, and (e) nitrate fluxes and new production
800 averaged over the mixed layer. Shading and negative values in (b) indicates downward fluxes. Bold
801 and dashed lines in (e) indicate horizontal and vertical nitrate fluxes.

802

803 Fig. 7. Vertical sections across C2 (Fig. 4d) for (a) nitrate concentrations ($\mu\text{mol N L}^{-1}$), (b) vertical
804 nitrate flux ($\mu\text{mol N m}^{-2} \text{s}^{-1}$), (c) evolution of the centre of C2 tracked back in time, (d) chlorophyll
805 and nitrate concentrations averaged over the upper 10 m, and (e) nitrate fluxes and new production
806 averaged over the mixed layer. Shading and negative values in (b) indicates downward fluxes. Bold
807 and dashed lines in (e) indicate horizontal and vertical nitrate fluxes.

808

809 Fig. 8. Vertical sections across A2 (Fig. 4f) for (a) nitrate concentrations ($\mu\text{mol N L}^{-1}$), (b) vertical
810 nitrate flux ($\mu\text{mol N m}^{-2} \text{s}^{-1}$), (c) evolution of the centre of A2 tracked back in time, (d) chlorophyll
811 and nitrate concentrations averaged over the upper 10 m, and (e) nitrate fluxes and new production
812 averaged over the mixed layer. Shading and negative values in (b) indicates downward fluxes. Bold
813 and dashed lines in (e) indicate horizontal and vertical nitrate fluxes.

814

815 Fig. 9. Vertical sections across A3 (Fig. 4h) for (a) nitrate concentrations ($\mu\text{mol N L}^{-1}$), (b) vertical
816 nitrate flux ($\mu\text{mol N m}^{-2} \text{s}^{-1}$), (c) evolution of the centre of A3 tracked back in time, (d) chlorophyll
817 and nitrate concentrations averaged over the upper 10 m, (e) nitrate fluxes and new production
818 averaged over the mixed layer, and (f) iron concentrations. Shading and negative values in (b)
819 indicates downward fluxes. Bold and dashed lines in (e) indicate horizontal and vertical nitrate
820 fluxes.

821

822 Fig. 10. Model simulations of an anticyclonic eddy (A4) and a cyclonic eddy (C3) interacting with
823 the shelf for (a) sea surface height anomalies (cm) (8 April, year 10) and (b) chlorophyll
824 concentrations (mg m^{-3}) averaged over the upper 10 m. The passage of eddies moving past 24°S are
825 shown as time and longitude Hovmoller plots for (c) sea surface height anomalies (cm), (d) nitrate
826 concentrations ($\mu\text{mol N L}^{-1}$) at 50 m, and (e) chlorophyll concentrations (mg m^{-3}) at 50 m. Shading
827 in (c) indicates negative anomalies.

828

829



















