We wish to thank referee #1 for his/her detailed analysis and his/her thoughtful comments, which will improve the quality of this manuscript. Here, you will find a detailed reply to each comments :

Response to Referee#1's Comments

Major Comments

1) Verbose "Results" Section

The paper by Auger et al. has the great merit of analyzing in depth the results of the model and of using cross-analysis of several different quantities to validate the hypothesis of the Authors. However, I have found the Results section pretty heavy to read, especially due to the amount of numbers listed within the text. This has a peak in sections 3.1.3 and section 3.2.3. I strongly suggest to summarize the results sections since the plots already contain much of the information that is explained in words in these chapters. The many many numbers listed in sections 3.1.3 and section 3.2.3 could instead be included directly in the pictures, for example above the bars, or in a table. As a general comment, I suggest to summarize/reorganize the Results section and use it to highlight general features and important trends in the Figures, rather than describing them element by element. This way the readers can really grasp the major highlights and findings without getting lost in too much information, while they can still look at the plots/tables for more details.

We agree that some parts (in particular section 3.1.3 and 3.2.3) of the « Results » Section is dense, and that our major findings are perhaps lost in too much numbers listed in the text. According to the referee's suggestion (shared with referee #3), numbers in sections 3.1.3 and 3.2.3 have been removed from the text. The Results Section has also been clarified to higlight the major features of the study region shown in the figures.

2) Why Spring

It was not clear to me until the Discussion section 4.3 the reason why some of the analysis in the paper was focusing on spring and I am still not sure that I have comprehended all the rational behind it. I suggest to motivate this choice more in depth before to present the results to the reader, stressing on the motivations that lie behind the choice of presenting a detailed analysis of the fluxes in this specific season only, despite all the known subregional variability of upwelling and seasonality in the system.

Indeed, the three referees noted that the justification of why we partly focus on spring should be done earlier than in section 4.3. The main justification is that observed offshore extension of Chl-a do present a marked seasonal variability with a peak in boreal spring. Therefore, focusing only on annual averages would have raised questions about the significance of our results during the time period that sees most of the offshore export. Choice has thus been made to show annual average but also the spring period.

According to shared referees' comments on this point, the choice of the spring season for the analysis of offshore boxes is now clearly motivated in the introduction by modifying the sentence p.3/l.8 from :

« The following section is focused on the description of the meridional variability of annual wind forcings, ocean response and primary productivity as simulated by the model in the different coastal boxes (Section 3.1) and offshore boxes (Section 3.2). »

to

« Then, we describe the meridional variability of wind forcing, ocean response and primary productivity as simulated by the model in the different coastal (Section 3.1) and offshore boxes (Section 3.2), on annual average and also during spring (seasonal maximum of the chlorophyll offshore extension as shown in Lathuilière et al, 2008). »

At the beginning of the Results Section 3.2.1 we also modified p.10/l.9 from :

« The offshore extension of chlorophyll has been shown to display a marked seasonal variability with a maximum in spring (Lathuilière et al., 2008; see Fig.1). In the offshore region, the chlorophyll variability depends on the export of coastal productivity. Additionally, the wind stress can be responsible for vertical mixing that enhances the exchanges of inorganic and organic matter between the euphotic and aphotic layers. The vertical nutrient supply to the enlightened surface layer and the phytoplankton export below the euphotic layer may also be enhanced by positive/negative Ekman pumping, respectively linked to positive/negative wind stress curl. In order to explicit the offshore extension in spring of the rich phytoplankton pattern, mean wind forcings from March to

May (i.e. wind intensity and wind curl) are first presented in Fig. 8 (a & b). During these months, the wind intensity increases from the northern Saharan Bank to Cape Blanc (where it peaks) and then decreases southward (Fig. 8a). »

to

« Off NW Africa, the offshore extension of coastal chlorophyll has been shown to display a marked seasonal variability with a maximum in spring (Lathuilière et al., 2008). Thus, spring averages from March to May were considered to investigate the factors driving primary productivity in offshore boxes. Mean spring wind forcing (i.e. wind intensity and wind curl) are first presented in Fig. 8 (a & b). During spring, the wind intensity increases from the northern Saharan Bank to Cape Blanc (where it peaks) and then decreases southward (Fig. 8a). »

3) Model Evaluation: Nitrate

Most of the discussion in the paper by Auger et al. is focusing on Nitrate, however there is no model evaluation of the nitrate distribution in the model. I suggest to include this in the paper.

We added, in Figure 1, white contours of nitrate concentrations at 100m depth (the depth of the boxes defined for our analysis) both in the model and the WOA2013 global atlas product. This permits us to show the sharp change in nutrient concentrations which occurs off Cape Blanc between nutrient-poor North-Atlantic Central Water north of Cape Blanc, and nutrient-rich South-Atlantic Central Water south of Cape Blanc. This is now mentioned in the text p.5/l.12 :

« Noticeably, the flow of the undercurrent over the slope is always poleward (not shown) in agreement with observations (Mittelstaedt, 1983).

Besides the model represents, at latitudes around Cape Blanc, the sharp gradient of nutrient concentrations in upwelling source waters between nutrient-poor North Atlantic Central Water (NACW) and nutrient-rich South-Atlantic Central Water (SACW), respectively north and south of Cape Blanc; observed from the World Ocean Atlas 2013 (Garcia et al., 2014; see the contours of nitrate concentration at 100m depth in Fig. 1). This actually results from the deepening of the poleward undercurrent transporting SACW, and its intensive mixing with NACW north of Cape Blanc (Mittelstaedt, 1983). The seasonal variability is reproduced except a negative bias in nitrate concentration off Cape Blanc in summer. Yet, NACW has already been encountered south of the Cape

Verde Frontal Zone as far as Senegal (Verstraete, 1985) and in situ observations off NW Africa are scarce. Moreover, this bias between model and observations may be due to an overestimation of the southward NACW transport by the Canary Current in the model (Fig. 1) and/or a deepening of the SACW flowing northward that occurs too early. »

4) Box analysis Figures

The paper by Auger et al. presents most of the results in the form of fluxes analysis. However, some of the Figures are confusing. Figure 7, Figure 13: Why are there 2 arrows of different color and size for each one of the lateral fluxes between the boxes? Eg, in Figure 7 the meridional flux between SS and SM in the nearshore is represented by both a large red arrow and a not so large orange arrow, so there are 2 arrows of different size for a single flux. What does this mean? Isn't the size of the arrows proportional to the intensity of the fluxes? Is the size of the arrows of one box comparable with the size of the arrows in the other boxes or do each box have a different scale?

As mentioned in their captions, Figures 7 and 13 present the « contribution of the different source and sink terms of nitrate and phytoplankton concentration within each box defined in this study. <u>Each color corresponds to a box</u> ». The size of the arrows of one box is then comparable with the size of the arrows of other boxes in terms of their contribution to the nitrate or phytoplankton concentration in each box. As this was only mentioned in the figure captions, we now mention it in the text when these figures 7 and 13 are presented at the end of Section 3.1.3 and 3.2.3, respectively.

Minor Comments

1) page 3: title "Material and Methods" maybe should be "Materials and Meth-
ods"? (missing s)

We agree and took into account this suggestion.

2) page 3, lines 24-25: What is the output frequency of the model? Monthly means?

Model outputs are saved as 5-day averages. This information will be added in the caption of Figure 1 by replacing the sentence :

« Same for ROMS-PISCES in (c) winter and (d) summer. »

by « Same seasonal climatology computed with the 5-days outputs of ROMS-PISCES in (c) winter and (d) summer. »

3) page 4, lines 30-31: The large cyclonic recirculation introduced here and fed by the NECC is generally referred to as Mauritanian Current [J. Arístegui et al./Progress in Oceanography 83 (2009) 33–48] in its northward alongshore component. This current is referred to again in page 5 lines 7-12

We agree and took into account this suggestion by modifying the text p4/l.30 from : « South of 19° N, a large cyclonic recirculation is found between the south-westward flowing Canary Current and the coast, especially in summer when trade winds extend farther north (see Barton et al., 1998; Mittelstaedt, 1983, 1991). »

to

« South of 19° N, a large cyclonic recirculation is found between the south-westward flowing Canary Current and the coast, especially in summer when trade winds extend farther north (see Barton et al., 1998; Mittelstaedt, 1983, 1991). It generates a poleward alongshore flow at its eastern flank generally referred as Mauritanian Current (Aristegui et al., 2009). »

The text p.5/l.7 has been modified from : « Alternatively, a moderate poleward current (which can be seen as an extension of the NECC, see Fig. 1) lays south of Cape Blanc both in the model and in the data during summer when upwelling-favourable winds are weak. »

to

« Alternatively, a moderate expression of the poleward Mauritanian Current lays south of Cape Blanc both in the model and in the data during summer when upwelling-favourable winds are weak. »

4) page 5 lines 1-2: “Maximum velocity is found equatorward in the coastal upwelling jet”: this sentence is a bit odd as regard to English syntax, it may be reformulated in a clearer way

This has been reformulated.

5) page 5 line 3: (and all the next occurrences) Cape Boujdour (FR) in English is called Cape Bojador

We agree and took into account this suggestion.

6) page 6 lines 9-18: this block of lines sounds more like a “Model Results” paragraph and it seems out of place; if moved somewhere else the Box Analysis section actually sounds much more coherent; maybe it can be located in a more adequate position

The structuration of the manuscript and the way our results are presented relies on the definition of spatial boxes which represent homogeneous subregions in terms of physical-biogeochemical characteristics. Consequently, this is a key element of methodology that needs to appear in the dedicated Subsection « Box analysis » of the Section « Materials and Methods ».

We thus preferred to keep subsection as it was.

7) page 10 line 12: I don’t think that “enlightened” is the right word here (eg, enlightened = Having or showing a rational, modern, and well-informed outlook; spiritually aware)

« enligthened » has been replaced by « euphotic ».

8) page 10 line 28: at the bottom of the offshore boxes (missing “the” before "offshore boxes")

We agree and took into account this suggestion.

9) page 10 lines 31-32: the sentence about vertical velocities and nitrate supply is not clear to me, this finding may be better explained

This sentence has been modified as follows : « The vertical nitrate supply by advection off the northern and southern Saharan Bank is particularly weak (inward nitrate fluxes despite averaged outward velocities due to episodic inward events) with respect to vertical diffusion. »

10) page 11 line 10 page 12 line 2: Annual Mean? Or Spring Mean? In general,suggest always to remark throughout the discussion and conclusions section whether your sentences are referring to the annual mean or spring mean analysis

We agree and took into account this suggestion.

11) Figure 14: Why are the lines in subplot c and d dashed?

The lines in (c) have been set solid and the caption of Figure 14 has been modified as follows to give the signification of solid and dashed lines : « Seasonal climatology of (a) wind intensity (negative is upwelling-favourable, m s-1), (b) bottom vertical velocity (m s-1), (c) zonal velocities (m s-1) and (d) meridional velocities (m s-1) averaged within and over each edge of the coastal boxes (i.e. north, south, west and bottom ; defined positive inward, so vertically upward), respectively. In (d), a solid (dashed) line represents a velocity at a northern (southern) edge of a box, respectively. Each colour corresponds to a box (see legends in Fig. 2 for coastal and Fig. 8 for offshore boxes): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS). »

We wish to thank referee #2 for his/her detailed analysis and his/her thoughtful comments, which will improve the quality of this manuscript. Here, you will find a detailed reply to each comments :

Response to Referee#2's Comments

Major and specific comments

1) Figure 1: Why not add a figure comparing model and measured data for nitrate in, for example, surface waters? Besides chlorophyll and surface currents, there is not much comparison with observations, which would add robustness to the model results.

In response to referee #1 and #2, we added, in Figure 1, white contours of nitrate concentrations at 100m depth (the depth of the boxes defined for our analysis) both in the model and the CARS 2009 global atlas product. This permits us to show the sharp change in nutrient concentrations which occurs off Cape Blanc between nutrient-poor North-Atlantic Central Water north of Cape Blanc, and nutrient-rich South-Atlantic Central Water south of Cape Blanc. This is now mentioned in the text p.5/l.12 :

« Noticeably, the flow of the undercurrent over the slope is always poleward (not shown) in agreement with observations (Mittelstaedt, 1983).

Besides the model represents, at latitudes around Cape Blanc, the sharp gradient of nutrient concentrations in upwelling source waters between nutrient-poor North Atlantic Central Water (NACW) and nutrient-rich South-Atlantic Central Water (SACW), respectively north and south of Cape Blanc; observed from the World Ocean Atlas 2013 (Garcia et al., 2014; see the contours of nitrate concentration at 100m depth in Fig. 1). This actually results from the deepening of the poleward undercurrent transporting SACW, and its intensive mixing with NACW north of Cape Blanc (Mittelstaedt, 1983). The seasonal variability is reproduced except a negative bias in nitrate concentration off Cape Blanc in summer. Yet, NACW has already been encountered south of the Cape Verde Frontal Zone as far as Senegal (Verstraete, 1985) and in situ observations off NW Africa are scarce. Moreover, this bias between model and observations may be due to an overestimation of the southward NACW transport by the Canary Current in the model (Fig. 1) and/or a deepening of the SACW flowing northward that occurs too early. »

2) Section 3.1.1, lines 15-16: The sentences "Offshore transport of nitrate… cross-shore velocities" do not really fit this paragraph because they describe the nutrient behavior while the paragraph is about ocean circulation. They should be moved to line 23, before "Vertical (upwelling-induced) nitrate supply...". Then, remove "(see above)" and add (Fig. 3d) at the end of "cross-shore velocities".

We agree and took into account this suggestion.

3) I think it will be nice to indicate somewhere (for example in section 3.1.1, end of line 6) that negative velocities indicate outside transport (out of the box) while positive values indicate inward transport (inside the box). Am I correct? If this is the case, what does negative advection mean in bottom waters?

Indeed, it is mentioned in the figure captions, velocities and tracer fluxes are « defined positive inward, so vertically upward » the boxes, but this clarification has been added in the text at the beggining of Section 3.1.1.

Moreover, « Bottom velocity » has been replaced by « bottom vertical velocity » as suggested by the referee in Minor Comment 10b.

4) Section 3.1.2 (page 7 and 8): This section is a bit difficult to follow due to its structure. Why not start this paragraph with the description of Figures 3e-h and then introduce Figures 4 and 5? So mainly move "Off Cape Blanc, phytoplankton biomass....(Fig. 3d)." to the beginning of the paragraph. Then continue with "Phytoplankton biomass, averaged over ... (Fig. 3a)." and then focus on PP. In this case, I would plot figure 4c (phyto) in position 4a, figure 4a (PP) in position 4b and figure 4b (f-ratio) in position 4c. For consistency, I would also rename the title of the section as: "Phytoplankton biomass, primary production and phytoplankton fluxes". Perhaps. the paragraph will then need some rephrasing.

We do not agree with the reorganization proposed by the referee because we find more logical to go from primary production to phytoplankton biomass, than the contrary.

5) Figures 7 and 13 are very similar and it takes some time to understand their main differences, as well as why both are relevant. It will be good to stress out more the differences and mention

why both are relevant to this work. It is also not very clear why the spring average is now more relevant than the annual average, and why spring more than other seasons (i.e. besides being the most productive, what are the advantages to show spring processes?). Is there a way to combine these 2 figures and their respective descriptions in a summary section?

This comment is related to comments of the 2 other referees who asked for introducing the choice of the spring period earlier in the paper.

The main justification is that observed offshore extension of Chl-a do present a marked seasonal variability with a peak in boreal spring. Therefore, focusing only on annual averages would have raised questions about the significance of our results during the time period that sees most of the offshore export. Choice has thus been made to show annual average but also the spring period.

Interestingly, there is very little change in the repartition of the fluxes driving nitrate and phytoplankton concentrations in spring compared to annual average, as shown by the little difference between Figures 7 and 13. We feel that this finding is a result on its own and would not appear as evident to a new reader. Even if *a posteriori*, Figures 7 and 13 appears as redondant, we feel that, *a priori,* a new reader would ask to see the seasonality of the fluxes we are discussing, particularly during the peak period. Therefore we feel that it was justified to keep those 2 figures unchanged.

However, we stressed the little difference between both figures and what it means in the Discussion Section 4.3, p.16/l.18 : « Note that our conclusions will be also valid on annual average since the drivers of nitrate and phytoplankton biomass in offshore boxes are similar on spring and annual average (see Fig. 7 and 13). »

6) Section 3.2.1, line 32: What does "vertical velocities are pointing downward" mean in this context?

This sentence has been modified as follows : « The vertical nitrate supply by advection off the northern and southern Saharan Bank is particularly weak (inward nitrate fluxes despite averaged outward velocities due to episodic inward events) with respect to vertical diffusion. »

7) Section 3.2.2, lines 20-25: Is there any other model or measurement data also showing the strong diffusion in this region? It would be nice to compare these results to published data or at least mention how reliable these results are.

Indeed, the strong vertical mixing in this region is found in the global climatology of mixed-layer depth (MLD) of de Boyer Montégut et al. (2004), as mentioned in the Discussion Section 4.3.

8) Section 4.1, lines 10-16 (page 14): Same as comment 7. Is there any model or measurement data to compare these results to?

To the authors knowledge, no data or model results are available to validate our findings. These are actually innovative model results that would require further observational studies, as it is now stressed at the end of this Discussion Section 4.1., p.14/l.14 : « In the NW African region, coastal topography effects and alongshore geostrophic flow (related to large scale circulation patterns) may noticeably influence the convergence/divergence of coastal water masses. They would modulate the coastal divergence driven by the Ekman transport, i.e. the response of coastal upwelling to the wind forcing. Our modelling approach stresses processes that are yet difficult to study with observations due to their scarcity. Therefore, this work strongly advocates for dedicated observational studies. »

9) Section 4.3, line 18 (page 17): Are the results of intrusion of nutrient-rich waters in the Senegalo-Mauritanian region in agreement with Lazaro et al., 2005 and Mittelstaedt, 1991? If so, it will be good to specify it: "originating from the Guinean upwelling. This is in agreement with previous finding of Lazaro et al., 2005 and Mittelstaedt, 1991." How do the results of Lazaro et al., 2005 and Mittelstaedt, 1991 compare to those of this paper?

This sentence has been clarified as follows : « Nevertheless, our model results indicate that the nutrient input is not only from the coastal region. Indeed, we identified a significant impact of transient southern intrusions of nutrient-rich waters in the Senegalo-Mauritanian region originating from the Guinean upwelling due to the presence of the Guinea Dome, a large scale cyclonic feature centred south of the Cape Verde archipelago (Lázaro et al., 2005; Mittelstaedt, 1991). »

10) Figure 14: Could these model parameters be compared to measurements, other model results or a theoretical average?

The strength and seasonality of surface horizontal currents is validated against a global drifter-derived climatology of surface currents (see Fig. 1). Concerning vertical velocities which we mainly attribute to the coastal upwelling, they fall in the range of observed (Benitez-Barrios et al., 2011) or modeled values (Mason et al., 2011) off Morocco (so north of our study region). To the authors knowledge, observational data are missing in the study region to validate our estimations. This is now mentioned in the Results Section, p.7/l.11 : « Observational data are known to be scarce in our study region. However vertical velocities fall in the range of the few studies that have been published with observed (Benítez-Barrios et al., 2011) or modelled values (Mason et al., 2012) focusing on northern Morocco. »

11) Section 3.2.2 starts with "Annual mean PP", but it should be "Spring average PP...", I think.

Indeed, this has been modified.

12) Section "Discussion", line 11: This comment relates to point 5). Because it is not really mentioned before, I would shortly indicate, at the end of this paragraph, why spring processes are analyzed.

See response to comment #5.

13) Section 4.1, line 22 (page 13): "Therefore it gives us confidence…" how much confidence? Some, good, very good...? I would indicate it here.

No data for quantitative validation is available but we can infer qualitatively that the model represents well the surface circulation of water masses in the study domain. This sentence has been modified as follows : « Our simulated spatial and temporal variability of surface circulation is in good agreement with the satellite-tracked drifters (see Section 2.2), so the model can be used to infer the factors responsible for the sensitivity of coastal upwelling to the wind forcing. »

14) Section 4.1, line 23 (page 13): "For this latter purpose, we further ..." This sentence does not really explain in what way the analysis of seasonal cycles at the edge of the coastal boxes will add

confidence to the model. Especially because these sensitivity results are not compared to observations or theoretical behavior. Please be more specific about the importance of this analysis.

We think that the correction made on the previous sentence (see previous comment) made clear that the analysis presented in Figure 14 allows to « infer the factors responsible for the sensitivity of coastal upwelling to the wind forcing. » (i.e. « this latter purpose »).

15) Section 4.2, lines 33 (Page 14) and line 1 (page 15): Are these new results or do they include those of Barton et al., 2004, García-Muñoz et al., 2004 and Karakas et al., 2006? Please specify which part of these results are new or used to confirm previous ones.

To clarify this point, we modified the sentence from :

« The combined effect of this local growth and the high filament activity around Cape Boujdour (Barton et al., 2004; García-Muñoz et al., 2004; Karakaş et al., 2006) results in an offshore transport of phytoplankton-rich and nitrate-depleted water masses. »

to :

« The combined effect of this local growth and the high filament activity around Cape Boujdour (the latter point being documented in Barton et al., 2004; García-Muñoz et al., 2004; Karakaş et al., 2006) results in an offshore transport of phytoplankton-rich and nitrate-depleted water masses. »

16) Section 4.2, line 15 (page 15): "Zooplankton excretion..." What is the explanation of the zooplankton excretion being more important for regenerated production in areas with lateral transport?

We actually mean that the zooplankton excretion « participates to enhance regenerated production in areas where the lateral input of plankton biomass is elevated » because zooplankton biomass, and then zooplankton excretion, is in this case high where the

phytoplankton biomass is high. Accordingly, we modified the end of the paragraph from p.15/l.9 :

« In general the regenerated production relies on high residence time favourable to efficient recycling (Fig. 15a). However, in our results, the water masses residence time in the southern Saharan Bank and off Cape Blanc is low and can not explain the high level of regenerated production. In this region the regenerated production is rather due to the remineralization of organic matter supply and zooplankton excretion (Fig. 5a). Note that the meridional variability of secondary production (grazing rate) follows that of PP (not shown) suggesting a bottom-up control of the phytoplankton biomass rather than a top-down control by zooplankton grazers. Zooplankton biomass and excretion activity are then enhanced when the plankton biomass is elevated, which is especially the case in the southern Saharan Bank and off Cape Blanc. »

17) Section 4.3, lines 17-19 (page 15): "This supports the idea that, ..." Is this sentence in agreement or in opposition to the previous hypothesis? What do other authors say about lateral transport of organic matter in this area?

This sentence is in agreement with the previous hypothesis which is that regenerated production is controlled by lateral inputs of organic matter (either living or dead) rather than by residence times. Indeed, in this area, the regenerated production is precisely low in spite of high residence times. Accordingly, we modified the first sentences of the paragraph from p.15/l.16 :

« In the Senegalo-Mauritanian region, only moderate regenerated production is found year round although residence time is relatively high with respect to the southern Saharan Bank and Cape Blanc areas. This supports the idea that, in the southern Saharan Bank, Cape Blanc and Senegalo-Mauritanian regions, regenerated production is rather driven by the amounts of organic matter supplies through lateral boundaries than by high residence time. »

18) Section 4.3, lines 14-19 (page 16): "For this purpose, we focus...", this sentence should be briefly mentioned before as mentioned in comment 12, and here, it should be improve. Please clarify why this specific setting (maximal coastal upwelling at the Saharan Bank and maximum phytoplankton extension off Cape Blanc) is a good scenario to be tested with the model.

As indicated to answer to comment 12, the choice of the spring season for the analysis of offshore boxes is now motivated in the introduction, and at the beginning of the Results Section 3.2.1. Moreover, the sentence concerned by this comment has been improved : « For this purpose, we focused on the offshore region in the spring period when the maximum chlorophyll extension is found (Lathuilière et al., 2008). At this season, maximum coastal upwelling is found off the Saharan Bank (Fig. 2c). Following the hypothesis of Lathuilière et al. (2008), this should traduce in a maximum of phytoplankton biomass extension at the Saharan Bank latitudes. Instead, maximum extension is found off Cape Blanc and in the Senegalo-Mauritanian region as attested by the meridional variation of phytoplankton biomass in the offshore region (Fig. 10). »

<u>*Minor comments/Technical corrections*</u>

We agree with most of the minor comments made by the referee, and we wish to thank his/her for his/her great effort. We only answer to a few comments either to justify a disagreement, precise our thinking, or indicate an important correction that has been made to the manuscript.

1) Section"Abstract" line 29: Did you mean "lateral advection transports coastal nutrients..."? **OK**

2) Section "Introduction" line 2: "... and seasonally variable one...". I would remove "one". **OK**

3) Section "Introduction" line 29: There is a missing comma, "Here, we ...", **OK**

4) Subsection "Model validation" line 22: Are AVHRR initials? If so, they probably should be written in full, here.

We think that AVHRR initials are very well known, so we made to choice to avoid the entire signification of the acronym.

5) Subsection "Model validation" line 25: To ease the understanding of Figure 1, I would replace the titles "SeaWiFS/Drifters SVP" and "ROMS" by "Observations" and "Model", respectively. I could

not figure it out what SVP means. Then, add in caption "from observation given by SeaWiFS satellite data... Same for ROM-PISCES model in…"
We prefered to mention the name of the datasets shown on the validation Figure 1 as it does not requires more space and provide more informations to the reader. Nonetheless, we changed the titles to « SeaWiFS/Drifters GDP observations » and « ROMS-PISCES model ». The GDP (Global Drifter Program) acronym has been added in the figure caption.

6) Subsection "Model validation" line 6 and 7 (page 5): I would remove "see" from both "see Fig. 1" in this paragraph. I would also move the second fig. reference, line 7, to the end of the sentence: "both in the model and in the data during summer (Fig. 1)". This is, because the NECC is not entirely shown in the figure and creates some confusion if the figure reference is placed after mentioning the NECC. **OK**

7a) Subsection "Model validation" line 14 and Figure 1: If maximum values of chlorophyll in both satellite and model data go up to 10 mgChl m^{-3}, why stop at 5 mgChl m^{-3} in the color bar of Fig. 1?
We chose to stop at 5 mgChl m^{-3} the color bar of Fig. 1 because there is increased overestimation of the satellite data with increasing chlorophyll concentrations (Gregg and Casey, 2004).

7b) Figure 1: At first I could not see the 5 coastal areas. Maybe by coloring the lines in white, instead of black, the boxes will be more visible. In the caption of Figure 1, "The ten boxes" could also be replaced by "The 5 coastal and 5 offshore boxes", so it is even more clear that the 5 coastal boxes are shown in the figure. **OK**

7c) Missing figure: Please remove the sentences "Main surface currents and deep water masses over ... South Atlantic Central Water" or add the missing plot and describe it in the main text, but only if it adds relevant information to the article. **OK**

8a) Section 3.1, title: To simplify, why not just call it "Meridional variability in the coastal region"? **OK**

8b) Section 3.1, title: Maybe add “Annual average of the meridional variability in the coastal region"

We changed the title of Section 3.1 to « Meridional variability in the coastal region »

9) Section 3.1.1, line 7: “on the edge of coastal boxes" gives a vague description of what we are actually looking at in the figure. Maybe replace by “on each edge of the coastal boxes (i.e. North, South, West and bottom)". **OK**

10a) Figure 2: Are the “BOX" and the black lines needed for figure 2a and 2b? I think they do not add much information, unlike for Fig. 2c, 2d, 2e, and 2f. These plots (Fig. 2a and 2b) alone clearly represent the entire box.

We chose to modify the figure to make easier the lecture and understanding of the figures 2 and 8.

10b)Figures 2-3: These figures are good, but they are a bit difficult to get at first (especially Fig. 2, since it is the first one of the series). To make Fig. 2 easier to understand, I would separate the main title “Wind and currents" to “Wind (m s^{-1})" and “Velocities (m s^{-1})". This will make it clear that this figure is showing 2 different things. I would write “Wind (m s^{-1})" on top of Figure 2a and 2b and “Velocities (m s^{-1})" on top of Figures 2b, 2c, 2d, 2e and 2f, as done for Fig. 3. Please use velocities instead of currents, because the word current is not as often used as velocity in the main text. Please also change the title of figure 2c to “c-Bottom (upwelling)" or “c-Bottom (vertical velocities)". The chosen title, “c-Bottom velocity" is misleading, as it suggests horizontal bottom velocities. **OK**

10c) Please check the sub-numbering of the figures, some do not follow a logic order. **OK**

11) Section 3.1.2, line 30: Please rephrase “... of PP in the boxes north and south of Cape Blanc are simulated, respectively." **OK**

12) Section 3.1.3, lines 26-30: This sentence is difficult to follow, maybe rephrase to "... the total rate of change of nitrate concentration and phytoplankton biomass in each coastal box are presented..." **OK**

13) Section 3.1.3, line 8: replace "is not anymore" by "is no longer" **OK**

14) Section 3.1.3, line 13: rephrase "from the northern Saharan Bank and the Senegal-Mauritanian region, respectively." **OK**

15) Section 3.1.3, line 31 (page 9): remove "tentative" **OK**

16a) Section 3.2, title: Same as comment 8: To simplify, change it to "Meridional variability in the offshore region". **OK**

16b) I think, here, the title of section 3.2 should also mention that the results are now only for spring: "Spring meridional variability in the offshore region". For me this was not clear until the discussion.

We agree and changed the title of Section 3.2 to « Spring meridional variability in the offshore region ».

17) Section 3.2.2, line 27: I would remove "finally". **OK**

18) Section 4, line 10: Please replace "we will seek to explicit" by "we explain" **OK**

19a) Section 4.3, line 10 (page 17): Space missing, please correct "that filaments" **OK**

19b) Section 4.3, line 14(page 17): Please replace "hypothesis" by "processes". The points mentioned before are not hypotheses. **OK**

20) Figure 8: Same comment as 10a for Figure 2 regarding the black lines and the BOX. **OK**

21) Figure 11a and 11b are missing.

This should be « a- Bottom advection » and « b- Bottom diffusion », so this has been modified.

22) Figure 14: Why Fig 14c is suddenly represented with dashed lines? What do the plain and dashed lines represent in Fig. 14d? **OK**

23) Please check the usage of acronyms, especially in the legend of the figures. I would always use the full subregion names or always the acronyms. Personally, I would avoid the acronyms (also in the text).
We agree and now always use the full subregion names.

24) Section 4.3, line 8: Please correct "2ZOLTLathuiliere2008" **OK**

25) I would replace most "see Fig." by "Fig.", except maybe the one in line 24, page 4. **OK**

Further suggestions

We agree with all these further suggestions made by the referee, and we wish to thank her again for his/her great effort.

1) Section 4.1, line 15-16 (page 13): Rephrase "It appears that coastal upwelling" by "However, coastal upwelling". This makes it more clear that this information comes from the literature and not the model results. **OK**

2) Section 4.1, line 20 (page 13): Replace "The simulated" by "Our simulated" **OK**

3) Section 4.2, line 4: "for 50 % of new production", please indicate if it is a model result or a general statement. Can this be seen in one of the figures? If yes, please indicate in which one.
This is shown in figure 6.

4) Section 4.2, lines 6-8: Would it be possible to compare this with observations of mixed layer depth (MLD) off Cape Blanc? If the MLD is large there, it will give some extra validation for this result.

At the coast off Cape Blanc, there is phytoplankton subduction by advection and not by diffusion, so this feature is not related to the vertical mixing.

5) Section 4.2, lines 9-10: I would replace "Usually" by "In general", and in the following sentence, I would add "However, in our results, the water ...." **OK**

6) Section 4.2, line 35 (page 15): The word "provide" is maybe not the best word, here. I suggest "lead to", instead. **OK**

7) Section 4.2, lines 1-2 (page 16): To ease the reading, I would briefly remention why this is the case, instead of referring to the previous section.
Section 4.1 mentions several points and it is not exactly clear to which one this sentence refers to. I would also remove "(see above)", it is not clear to what it is referring to. **OK**

8) Section 4.3, line 27: Please add "In our results, the vertical mixing..." and replace "Indeed" by "This is even more visible in the results for spring, where the mixed layer...". **OK**

9) Section 4.3, lines 33-34: To better differentiate between the new results and published data, please rephrase the sentence as follows: " In fact, the vertical mixing, as previously suggested by Huntsman and Barber 1977, is also responsible for …" **OK**

10) Section 4.3, line 1: Maybe replace "participate to" by "partly". **OK**

11) Section 4.3, line 7: To help the reader, it would be nice to briefly mention what is the hypothesis of Lathuilère et al., 2008. **OK**

12) Section 4.3, lines 8-9: To better differentiate between the new results and published data, please add " In our results, the advection by ..." and "...off Cape Blanc, in agreement with Kostianoy and Zatspein, 1996. **OK**

13) Section 4.3, line 10: To better differentiate between the new results and published data, please add “may enhanced cross shelf transport, as also shown by satellite data in Lathuilère et al., 2008". **OK**

We wish to thank referee #3 for his/her detailed analysis and his/her thoughtful comments, which will improve the quality of this manuscript. Here, you will find a detailed reply to each comments :

Response to Referee#3's Comments

General comments

Title could be shortened to: What drives the spatial variability of primary productivity and matter fluxes in the North-West African upwelling system? A modelling approach.

We agree and shortened the title as suggested by the referee.

Throughout the manuscript ’explicit’ is used as a verb. It is not a verb, it can be used as a noun (eg. The explicitness of the data allow us to draw some very solid conclusions) but usually an adverb (The data allow us to explicitly show that...) or adjectve (e.g. The data is explicit, it shows that...).

The term « explicit » has been replaced by an adequate verb each time it was badly used in the manuscript.

It seems a bit unclear as to why the spring means are used for the offshore domains and annual means for the coastal domains. It is mentioned only later in the discussion, but it should be clearer sooner. Why not show the spring mean for coastal and offshore domains (surely using the annual mean for the coastal domain masks the seasonal signal and is therefore unrealistic?). Does it make sense to link the coastal and offshore domains in terms of the offshore fluxes for example if you are looking at averages for different periods?

This comment is related to comments of the 2 other referees who asked for introducing the choice of the spring period earlier in the paper.

The main justification is that observed offshore extension of Chl-a do present a marked seasonal variability with a peak in boreal spring. Therefore, focusing only on annual averages would have raised questions about the significance of our results during the time period that sees most of the offshore export. Choice has thus been made to show annual average but also the spring period.

Interestingly, there is very little change in the repartition of the fluxes driving nitrate and phytoplankton concentrations in spring compared to annual average, as shown by the little difference between Figures 7 and 13. We feel that this finding is a result on its own and would not appear as "evident" to a new reader. Even if *a posteriori*, Figures 7 and 13 appears as redundant, we feel that, *a priori,* a new reader would ask to see the seasonality of the fluxes we are discussing, particularly during the peak period. Therefore we feel that it was justified to keep those 2 figures unchanged.
However, we stressed the little difference between both figures and what it means in the Discussion Section 4.3, p.16/l.18 : « Note that our conclusions will be also valid on annual average since the drivers of nitrate and phytoplankton biomass in offshore boxes are similar on spring and annual average (see Fig. 7 and 13). »

The results section is very laborious and therefore difficult to read, especially sections 3.1.3 and 3.2.3 (the percentages in paretheses are not necessary), and could be shortened.
According to the referee's suggestion (shared with referee #1), numbers in sections 3.1.3 and 3.2.3 have been removed from the text. The Results Section has also been clarified to higlight the major features of the study region shown in the figures.

We agree with most of the minor comments made by the referee, and we wish to thank him/her for his/her great effort. We only answer to a few comments either to answer a question or indicate an important correction that has been made to the manuscript.

<u>*Specific comments*</u>
page 2, line 4: 'of coastal topography are' should be 'of coastal topography is' **OK**

page 2, line 5: '...and then the response of nutrient upwelling to wind forcings'. This is unclear. Are you saying that the large scale circulation pattern impacts the wind driven upwelling of nutrients?
Large scale circulation patterns actually affect the response to the wind forcing of the vertical velocities at 100m depth (which we attribute to coastal upwelling), and so the vertical nutrient inputs in the euphotic layer.

Introduction

Page 3, line 17: ’in regards of environmental forcings’ should be ’with regard to environmental forcings’ **OK**

Page 4, line 2: ’To this end, comparative box analysis...’ should be ’To this end, a comparative box analysis...’ or ’To this end, comparative box analyses......have been conducted’. **OK**

Page 4, line 3, ’Those subregions’ should be ’The subregions’ **OK**

Page 4, line 4,’ in regards of’ should be ’with regard to’ **OK**

Page 4, Line 14: ’explicit’ cannot be used as a verb, try ’identify’, **OK**

Last two paragraphs of Introduction are laborious and could be more succinctly summarised.
According to the referee's comment, the last two paragraphs have been modified as follows :

« First, we present the model configuration and a validation of near-surface circulation and surface chlorophyll biomass using in-situ and satellite data (Section 2.1 and 2.2, respectively). Then, we describe the meridional variability of wind forcing, ocean response and primary productivity as simulated by the model in the different coastal (Section 3.1) and offshore boxes (Section 3.2), on annual average and also during spring (seasonal maximum of the chlorophyll offshore extension as shown in Lathuilière et al, 2008). Each section is split in three parts which describe the meridional variability of (i) the wind forcing, current velocity and nitrate fluxes, (ii) the primary production (PP), phytoplankton biomass and phytoplankton fluxes, and (iii) the sources and sinks of nitrate concentration and phytoplankton biomass in each box. Finally, we discuss in Section 4 (i) the sensitivity of coastal upwelling to the wind forcing along the NW African coast, (ii) the meridional variability of coastal phytoplankton biomass and PP (new and regenerated production) in relation to matter transfers and (iii) the meridional variability of the offshore extension of coastal chlorophyll off NW Africa. »

Last two sentences of Introduction seem out of place.

Indeed, these two sentences have been removed.

Methods

Page 4,line 26: unbalanced parenthesis **OK**

Page 5, line 23: ’thinner’ is ambiguous in this context, ’narrower’ is clearer **OK**

Page 6, line 3: ’The upwelling filaments off Cape Ghir and Cape Boujdour are responsible for strong seaward deflections of the coastal current.’ I wouldn’t necessarily say that the filaments are responsible for the seaward deflection – they are ’connected’, both associated with the same initial mechanism (perhaps wind/topography) and then they probably enhance one another. **OK**

Page 6, Line 2: ’explicit’ cannot be used as a verb, try ’identify’ **OK**

Page 6, line 2-4: ’.........the meridional variability of primary productivity off the NW African coast, we carried out a box analysis focusing on nitrate (the main limiting nutrient) and phytoplankton carbon budgets (12–27°N, see Fig. 1)’, rather say:’.........the meridional variability of primary productivity off the NW African coast between 12–27°N, we carried out a box analysis focusing on nitrate (the main limiting nutrient) and phytoplankton carbon budgets’ **OK**

Page 6, line 7: ’...was split ito five latitudinal bands.’ rather: ’...was split into five latitudinal bands (see Fig. 1).’ **OK**

Page 6, line 12: remove ’On the opposite,’, start with ’In the southernmost...’ **OK**

Page 6, line 17: what do you mean by ’globally’? It usually refers to something involving the whole globe/world.

The term 'globally' has been removed since it is not essential.

Page 6, line 20: ’In like manner...’ rather ’Similarly..’ **OK**

Results

Page 8, line 6: ’Wind curl shows a clear maximum off Cape Blanc but a weak meridional variability’. This sentence is not clear. Do you mean that the meridional variability in wind stress curl is weak or do you mean that the alongshore variability of meridional wind stress is weak?

We mean that the meridional variability in wind stress curl is weak. This has been clarified (see General Comment #4).

Figure 2 c : this is labelled as upwelling intensity (vertical velocity at the bottom). For upwelling intensity, it would be better to use vertical velocity at the base of the Ekman layer (your 100 m depth of the boxes is probably too deep?).

In this paper, we are interested in the primary productivity. In consequence, we designed boxes extending vertically from the free surface down to 100m depth to encompass the euphotic layer where light is available for phytoplankton photosynthesis and primary production. We then consider the upwelling-induced nutrient flux at the base of the boxes (100m depth) since the nutrients that enter this layer are susceptible to be consumed for primary production.

Page 8, line 24: remove ’inversely’ **OK**

Page 8, line 32: ’...associated to...’ should be ’...associated with...’ **OK**

Page 9, line 11: ’does not translate in...’ should be ’does not translate into....’ **OK**

Page 9, line 14: ’Noteworthy, the phytoplankton biomass is found maximum off Cape Blanc and the South Saharan Bank contrasting with minimum upwelling-induced nitrate supplies (Fig. 3a).

rather:

’It is noteworthy that maximum phytoplankton biomass is found off Cape Blanc and the South Saharan Bank despite the fact that upwellling-induced nitrate supplies are at a minimum at those locations (Fig. 3a).’ **OK**

Section 3.1.3: laborious

According to the referee's suggestion (shared with referee #1), numbers in Sections 3.1.3 have been removed from the text. The Results Section has been generally clarified to higlight the major features of the study region shown in the figures.

page 10, line 6: ’sinks’ should be ’sink’ **OK**

page 11, line 12: ’enlightened’ is very archaic in this context. Replacing it with ’euphotic zone’ would be better. **OK**

Page 11, line 14: ’explicit’ cannot be used as a verb and whole sentence is unclear. **OK**

Page 11, line 17: ’Alternatively’ since you’re not offering an alternative to a previous statement, something like ’On the other hand’ works better. **OK**

Page 11, line 22: ’Noteworthy, at the western...’, change to ’It is noteworthy that at western boundaries velocities are...’ **OK**

Page 11, line 23: replace ’happen to be’ with ’are’ **OK**

Page 11, line 29: replace ’..falls in the same order of magnitude than diffusion...’ with ’..is the same order of magnitude as diffusion...’ **OK**

Page 11, line 31: replace ’Noteworthy...’ with ’It is noteworthy that vertical nitrate supply...’ **OK**

Page 12, line 10: In the text it states that Fig. 10 is annual mean, but the figure caption says Spring mean. **OK**

Page 12, line 18: replace ’......, in less manner,....’ with ’..., less so,...’ **OK**

Page 13, line 2: In the text it states that fig 12 shows the annual mean source and sink terms but the figure caption says it is the spring mean. **OK**

Discussion

Page 14, line 9: 'in relation with the...', should be 'in relation to the...' **OK**

Page 14, line 10: 'Finally, we will seek to explicit...' should be 'Finally, we will seek to identify...' **OK**

Page 14, line 13: 'In our simulation, the meridional variability of coastal upwelling is not correlated to the local variability of wind-driven Ekman transport and Ekman pumping. This result questions the estimation of vertical velocities based on local wind forcing that were commonly used in EBUS'. **OK**

- two points on this statement: 'were' should be 'are' **OK**

The estimation of upwelling using alongshore wind stress is for vertical velcoities at the base of the Ekman layer. Your level of 100m, or the bottom in places shallower than 100 m, may be too deep. **We agree and the sentence has been modified as follows : « In our simulation, the meridional variability of vertical velocities at 100m depth (which roughly corresponds to the euphotic layer) is not correlated to that of upwelling-favourable winds and Ekman pumping on annual average. This result questions the estimation of upwelling-induced nutrient inputs in the euphotic layer based on the wind-driven Ekman transport and the nutrient concentrations in upwelling source waters, a method commonly used in EBUS (Bakun, 1990; Lathuilière et al., 2008; Messié et al., 2009; Messié and Chavez, 2014). »**

Page 14, line 16: You state that the large scale transport could be a factor explaining the mismatch in upwelling intensity and Ekman transport. With the model output you can calculate it directly to verify your statement.

The mismatch between Ekman transport and upwelling intensity off Cape Blanc implies that other mechanisms than the Ekman transport play against coastal upwelling to create downward vertical velocities. These can be internal waves, mesoscale processes (like fronts and eddies) or the convergence of water masses. We clearly show that downward vertical velocities in the coastal box off Cape Blanc from May to July co-occur with alongshore velocities at both the northerm and southern boundaries directed

inward, which demonstrates that the convergence of water masses is the most plausible explanation for this mismatch.

Page 14,line 22: ’...explicit...’, can’t be used as a verb. You could use ’identify’ **OK**

Page 14, line 23 and figure 14: you use the bottom velocity to assess the sensitivity of coastal upwelling to wind forcing. You should rather use vertical velocity at the base of the Ekman layer. **The point here is to investigate the sensitivity to wind forcing of the vertical velocities at 100m depth (attributed to the coastal upwelling) that participate to the vertical nutrient fluxes in the euphotic layer where nutrients are consumed for primary production (see our response to the comment in Section Results « Figure 2 c »).**

Page 14, line 26: ’lead’ should be ’leads’ **OK**

Page 15, line 18: instead of ’Albeit’ use ’Although’. **OK**

Page 16, line 31: sentence starting with ’This points a gap...’ is confusing **OK**

Page 17, line 13: ’the coast, the wind stress curl...’ should be ’the coast, (ii) the wind stress curl...’ **OK**

Page 17, line 14: ’hypothesis’ should be hypotheses’ **OK**

Page 17, line 15: ’explicit’ should be ’identify’ **OK**

Page 17, line 20: ’associated to’ should be ’associated with’ **OK**

Page 17, line 22: ’Our results indicate downward and upward wind-induced Ekman pumping of respectively north and south of Cape Blanc’ should be ’Our results indicate downward and upward wind-induced Ekman pumping north and south of Cape Blanc respectively’ **OK**

Page 18, line 1: ’participate’ should be ’help’ **OK**

Page 18, line 8: ’2ZOTLathuliere2008’ – a latex referencing bug? **OK**

Page 18, line 10: ’thatfilaments’ should be ’filaments’ **OK**

Conclusion

Page 18, line 21: ’of the primary production spatial distribution in’ should be ’of the spatial distribution of primary production’ **OK**

Page 18, line 25: ’ production in’ should be ’production with’ **OK**

Page 18, line 31: ’excepted’ should be ’except’ **OK**

Figures

Figure 1: include the box labels that you use in the text and in other figures **OK**

Figures 1-4: in some you include just the abbreviations of the box areas, in others you have the full name. When you don’t have the full names in the legend, you could include them in the caption **OK**

Figure 6: label x-axis with latitude as well, or at least show where north is **OK**

Figure 10 and 12: the captions dont agree with the text (Annual vs. Spring mean) **OK**

Figure 14: it is not clear how these averages are calculated (in the caption or in the text). In the caption you state: ’within and at the boundaries of coastal boxes’. Is it an average of meridional wind, bottom velocity, cross-shore velocity and alongshore velocity within the entire coastal strip? If so, does this make sense, given that your interest is the meridinal variability of primary productivity

In the text, it was modified as : « For this latter purpose, we further analyze the seasonal cycles of meridional wind versus vertical and horizontal velocities averaged within and over each edge of the coastal boxes (Fig. 14). »

The caption has also been modified as follows : « Figure 14: Seasonal climatology of (a) wind intensity (negative is upwelling-favourable, m s-1), (b) bottom vertical velocity (m s-1), (c) zonal velocities (m s-1) and (d) meridional velocities (m s-1) averaged within and over each edge of the coastal boxes (i.e. north, south, west and bottom ; defined positive inward, so vertically upward), respectively. In (d), a solid (dashed) line represents a velocity at a northern (southern) edge of a box, respectively. Each colour corresponds to a box (see legends in Fig. 2 for coastal and Fig. 8 for offshore boxes): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS). »

What drives the spatial variability of primary productivity and matter fluxes in the North-West African upwelling system ? A modelling approach

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Abstract. A comparative box analysis based on a multi-decadal physical-biogeochemical hindcast simulation (1980–2009) was conducted to characterize the drivers of the spatial distribution of phytoplankton biomass and production in the North-West (NW) African upwelling system. Alongshore geostrophic flow related to large scale circulation patterns associated with the influence of coastal topography is suggested to modulate the coastal divergence, and then the response of nutrient upwelling to wind forcing. In our simulation, this translates into a coastal upwelling of nitrate being significant in all regions but the Cape Blanc (CB) area. However, upwelling is found to be the dominant supplier of nitrate only in the northern Saharan Bank (NSB) and the Senegalo-Mauritanian (SM) regions. Elsewhere, nitrate supply is dominated by meridional advection, especially off Cape Blanc. Phytoplankton displays a similar behaviour with a supply by lateral advection which equals the net coastal phytoplankton growth in all coastal regions except the Senegalo-Mauritanian area. Noticeably, in the Cape Blanc area, the net coastal phytoplankton growth is mostly sustained by high levels of regenerated production exceeding new production by more than two fold which is in agreement with the locally weak input of nitrate by coastal upwelling. Further offshore, the distribution of nutrients and phytoplankton is explained by the coastal circulation. Indeed, in the northern part of our domain (i.e. Saharan Bank), the coastal circulation is mainly alongshore resulting in low offshore lateral advection of nutrients and phytoplankton. On the contrary, lateral advection transports coastal nutrients and phytoplankton towards offshore areas in the latitudinal band off the Senegalo-Mauritanian region. Moreover, this latter offshore region benefits from transient southern intrusions of nutrient-rich waters from the Guinean upwelling.

1 Introduction

Among the four major eastern boundary upwelling systems (EBUS), the North-West (NW) African upwelling region is the most spatially and seasonally variable in terms of primary productivity (Carr and Kearns, 2003). This variability may impact the distribution and abundance of fish populations, and their associated fisheries, on a large range of time scales (Arístegui et al., 2009). It also constrains the dynamics of nutrient and organic carbon export from the coastal margin (Helmke et al., 2005; Muller-Karger et al., 2005). Various studies have established that upwelling-driven nutrient supply is the key factor regulating chlorophyll concentration and primary production off NW Africa (Lathuilière et al., 2008; Messié and Chavez, 2014; Ohde and Siegel, 2010; Pradhan et al., 2006). However, the mechanisms that control the spatio-temporal variability of primary productivity are still poorly understood.

In EBUS, primary production and phytoplankton biomass are first enhanced by the wind-driven coastal upwelling of nutrient-rich waters into the euphotic zone (Allen, 1973). Upwelled waters are redistributed by advection processes, while turbulent mixing accounts for their dilution into surrounding waters. Mixing naturally acts against the build-up of plankton biomass. Indeed, the nutrient utilization can only be optimized by retentive physical mechanisms in the coastal area which enhance microbial remineralization of particulate organic matter and zooplankton excretion, and then regenerated production through ammonium consumption.

During the last decade, several studies focused on the characterization of the variability of satellite-derived surface chlorophyll in the NW African region which they interpreted with regard to environmental forcing (Lathuilière et al., 2008; Pradhan et al., 2006; Thomas et al., 2001). One of their main findings was that the seasonal variability of wind-forcing is the main driver of the surface chlorophyll seasonal variability. If this main result is expected, it does not give the full account of the latitudinal discrepancies of the seasonal variability of the surface chlorophyll and the related underlying processes within the NW African upwelling system. Indeed, the region between 24° N and 33° N (most of the Moroccan sub-region including the northern Saharan Bank) is characterized by a weak seasonality and chlorophyll confined to the coast. The Cape Blanc area (19–24° N, including the southern Saharan Bank) also presents a weak seasonality but is the site of a persistent offshore extension of the coastal chlorophyll pattern. In the Senegalo-Mauritanian region (10–19° N), chlorophyll is enhanced together with a large offshore extension during winter/spring, followed by an abrupt drop during summer. Lathuilière et al. (2008) suggest that nutrient limitation is the key factor that explains the weak offshore extension of chlorophyll in the north. In the south, they partly attribute the drop of chlorophyll to the seasonal intrusion of nutrient-depleted waters from the North Equatorial Counter Current (NECC).

Here, we propose a modelling approach to gain the first mechanistic understanding of the underlying processes controlling the spatial variability of primary productivity and to test the satellite-based hypothesis proposed by Lathuilière et al. (2008). In our study, outputs of a multi-decadal physical-biogeochemical hindcast simulation (1980–2009; see Auger et al., 2015) were used to characterize spatially the drivers of phytoplankton biomass and production in the NW African upwelling system with a particular focus on the mechanisms that control the sensitivity of primary productivity to the wind forcing and the coastal upwelling. To this end, a comparative box analysis representing homogeneous sub-regions in the NW African upwelling system has been conducted. The sub-regions have been defined using the near-surface horizontal circulation patterns. In each box, we analysed the dynamics of primary productivity and nutrients with regard to advective and diffusive matter fluxes at the boundaries and local biological production/uptake. The nature and variability of the matter exported from the coastal margin to the adjacent open ocean were also subsequently depicted.

First, we present the model configuration and a validation of near-surface circulation and surface chlorophyll biomass using in-situ and satellite data (Section 2.1 and 2.2, respectively). Then, we describe the meridional variability of wind forcing, ocean response and primary productivity as simulated by the model in the different coastal (Section 3.1) and offshore boxes (Section 3.2), on annual average and also during spring (seasonal maximum of the chlorophyll offshore extension as shown in Lathuilière et al, 2008). Each section is split in three parts which describe the meridional variability of (i) the wind forcing, current velocity and nitrate fluxes, (ii) the primary production (PP), phytoplankton biomass and phytoplankton fluxes, and (iii) the sources and sinks of nitrate concentration and phytoplankton biomass in each box. Finally, we discuss in Section 4 (i) the sensitivity of coastal upwelling to the wind forcing along the NW African coast, (ii) the meridional variability of coastal phytoplankton biomass and PP (new and regenerated production) in relation to matter transfers and (iii) the meridional variability of the offshore extension of coastal chlorophyll off NW Africa.

2 Materials and methods

A multi-decadal hindcast simulation of the physical-biogeochemical dynamics in the NW African upwelling system was run over the period 1980–2009. We used the three-dimensional (3D) primitive equations, sigma-coordinates, free surface Regional Oceanic Modeling System (ROMS – Shchepetkin and McWilliams, 2005) configured for the NW African upwelling system (Machu et al., 2009; Marchesiello and Estrade, 2009). Model parameterizations, including a parameterization of the Mediterranean outflow, are described by Marchesiello and Estrade (2009). The physical model was coupled to a biogeochemical model (PISCES – Aumont et al., 2003; Aumont and Bopp, 2006) which simulates plankton productivity and carbon biomass based upon the main nutrients (nitrate, ammonium, phosphate, silicate and iron). This model includes two size classes of phytoplankton (nanoflagellates and diatoms), zooplankton (ciliates and copepods) and two classes of detritus (the latter differ by their sinking velocity: 5/30 m day^{-1} for small/large particulate material, respectively). Phytoplankton growth depends on light, temperature and the external availability in nutrients. Diatoms differ from nanoflagellates by their silicate requirement, higher requirement in iron (Sunda and Huntsman, 1997) and higher half-saturation constant due to larger size. Microzooplankton differs from mesozooplankton by food diet (related to the prey/predator size ratio), grazing rates and mortality parameterization. PISCES has previously been used in global (e.g.

Aumont et al., 2003; Aumont and Bopp, 2006; Gorgues et al., 2010), basin-scale (e.g. Gorgues et al., 2005; José et al., 2014) and regional upwelling studies (e.g. Albert et al., 2010; Auger et al., 2015; Echevin et al., 2008).

Heat, solar and water fluxes from the CFSR atmospheric reanalysis (1/3° resolution, NCEP Climate Forecast System Reanalysis, Saha et al., 2010) were used to force our interannual simulation at a 6-hour time scale. Lateral open boundary conditions of both physical and biogeochemical fields were provided by a 5 days archived NEMO-PISCES simulation of the North-Atlantic basin (1/4° resolution, T. Gorgues, pers. comm.). Surface nutrient fertilization were solely provided by iron dust deposition, parameterized using a modelled climatology of the atmospheric dust deposition (for details, see Aumont et al., 2008).

The topography was based on GEBCO 1' resolution (General Bathymetric Chart of the Oceans, http://www.gebco.net). A ”child” grid focused on the NW African upwelling (10–35° N / 9–23° W, 1/12° resolution, eddy-resolving) was embedded in a lower resolution ”parent” grid (5–40° N / 5–30° W, 1/4° resolution) through a two-way coupling (AGRIF – Debreu et al., 2012). The use of this technique limits the influence of discontinuities emerging from low spatio-temporal resolution of open boundary conditions on the “child” solution, and also produces upscaling effects on the “parent” solution. More details on the simulation can be found in Auger et al. (2015).

2.1 Physical-biogeochemical model

2.2 Model validation

As previously described by Auger et al. (2015), the general distribution of sea surface temperature (SST) agrees well with AVHRR satellite data although a warm/cold bias of about 1°C exists in offshore/nearshore SST, respectively. The coastal region of cold surface waters is notably narrower in the model particularly off Cape Blanc and, during the upwelling winter season, off Mauritania (see Fig. 2 in Auger et al., 2015). However, the general circulation and its seasonal variability are well reproduced by the model (Fig. 1, winter and summer averages) as attested by climatology of near-surface currents from the model (15m) and derived from satellite-tracked near-surface drifting buoy (1979–present, 1/2° resolution, Lumpkin and Johnson, 2013).

As part of the eastern branch of the North-Atlantic subtropical gyre, the Canary Current flows equatorward along the NW African coast and separates from the coast around Cape Blanc (19–21° N) where it feeds the North Equatorial Current (Fig. 1e). South of 19° N, a large cyclonic recirculation is found between the south-westward flowing Canary Current and the coast, especially in summer when trade winds extend farther north (see Barton et al., 1998; Mittelstaedt, 1983, 1991). It generates a poleward alongshore flow at its eastern flank generally referred as Mauritanian Current (Aristegui et al., 2009). The southern branch of the recirculation gyre is fed by the eastward flowing North Equatorial Counter Current (NECC) which is located near 10° N in summer and 5° N in winter (Mittelstaedt, 1991; Stramma et al., 2005). A particularly intense coastal upwelling jet flowing equatorward (Canary Upwelling Current) is present all year round north of Cape Blanc due to strong and constant upwelling-favourable winds (Benazzouz et al., 2014). The upwelling filaments off Cape Ghir and Cape Bojador are related to strong seaward deflections of the coastal current. As a matter of fact, strong westward velocities off Cape Bojador most likely limits the drifter sampling over the Saharan Bank (Fig. 1). Surface currents then turn west in the inter-gyre region off Cape Blanc feeding the North Equatorial Current (Fig. 1e). In the Senegalo-Mauritanian region, surface currents are directed south-westward during the winter upwelling season. Alternatively, a moderate expression of the poleward Mauritanian Current lays south of Cape Blanc both in the model and in the data during summer when upwelling-favourable winds are weak. However, this poleward current does not persist during winter in our simulation as well as in the drifter climatology offshore of Mauritania. The seasonality of the coastal current in the same latitudinal band, a crucial feature, is nevertheless well simulated with strong equatorward advection in winter and moderate poleward advection in summer. Noticeably, the flow of the undercurrent over the slope is always poleward (not shown) in agreement with observations (Mittelstaedt, 1983).

Besides the model represents, at latitudes around Cape Blanc, the sharp gradient of nutrient concentrations in upwelling source waters between nutrient-poor North Atlantic Central Water (NACW) and nutrient-rich South-Atlantic Central Water (SACW), respectively north and south of Cape Blanc; observed from the World Ocean Atlas 2013 (Garcia et al., 2014; see the contours of nitrate concentration at 100m depth in Fig. 1). This actually results from the deepening of the poleward undercurrent transporting SACW, and its intensive mixing with NACW north of Cape Blanc (Mittelstaedt, 1983). The seasonal variability is reproduced except a negative bias in nitrate concentration off Cape Blanc in summer. Yet, NACW has already been encountered south of the Cape Verde Frontal Zone as far as Senegal (Verstraete, 1985) and in situ observations off NW Africa are scarce. Moreover, this bias between model and observations may be due to an overestimation of the southward NACW transport by the Canary Current in the model (Fig. 1) and/or a deepening of the SACW flowing northward that occurs too early.

The spatial and seasonal variability of surface chlorophyll is consistent with SeaWiFS satellite data (Fig. 1). In both model and satellite data, chlorophyll concentrations are globally maximum in the coastal upwelling (5–10 mgChl m^{-3}) and decrease offshore toward the subtropical gyre (0.1–0.2 mgChl m^{-3}). However, nearshore chlorophyll concentrations and values of PP (see Auger et al., 2015) are lower than satellite-based estimates (Carr, 2001; Gregg et al., 2003). Thus, the cross-shore gradient is not as sharp in the model as in satellite observations. However, SeaWiFS may actually overestimate in situ data in the Mauritanian upwelling. Gregg and Casey (2004) attributed this over-estimation to unmasked Saharan dust in the atmospheric correction algorithm (Moulin et al., 2001). Increased overestimation with increasing chlorophyll concentrations were also evidenced (Gregg and Casey, 2004). Moreover, model results fall in the range of in situ measurements in the Mauritanian upwelling (Atlantic Meridional Transect, AMT; Aiken et al., 2009; Gibb et al., 2000; Marañon et al., 2000; Pradhan et al., 2006) which reveal lower chlorophyll concentrations than SeaWiFS data. Large phytoplankton cells (diatoms) are generally dominant in the coastal upwelling region (not shown) in agreement with AMT measurements (Aiken et al., 2009). It shows an increasing contribution of smaller cells toward the open ocean. Our model is also able to reproduce this observed shift in phytoplankton community structure from nearshore to offshore (Gutiérrez-Rodríguez et al., 2011).

The seasonal variability, both in the model and in the data (Fig. 1), is maximum in the Senegalo-Mauritanian region, and minimum off Cape Blanc. Over the Saharan Bank, peaks of plankton productivity occur in spring/summer whereas a relaxation of Trade winds globally induces a lower production in fall. In contrast, plankton productivity peaks in winter/spring in the Senegalo-Mauritanian region. As described from satellite observations (Lathuilière et al., 2008), the surface chlorophyll maximum is confined to the coast north of Cape Bojador. The offshore extension of chlorophyll then increases equatorward from the Saharan Bank to Cape Blanc in summer, and to the Senegalo-Mauritanian region in winter. Noticeably, maximum offshore extension is found year round off Cape Blanc (21° N). South of Cape Blanc, maximum offshore extension occurs when nearshore chlorophyll concentrations are maximum in winter, whereas the contrary is found north of Cape Blanc.

2.3 Box analysis

In order to identify the factors controlling the meridional variability of primary productivity off the NW African coast between 12-27°N, we carried out a box analysis focusing on nitrate (the main limiting nutrient) and phytoplankton carbon budgets based on a climatology of model outputs over our simulation period (1980–2009). First, we distinguished between the coastal region (from the coast to 0.5° offshore) and the offshore region (covering 4° of longitude further offshore). Second, based on near-surface horizontal circulation patterns in the coastal region, offshore export and bathymetric considerations, the study domain was split into five latitudinal bands (see Fig. 1). The vertical extension of the five coastal and five offshore boxes was chosen from the free surface down to 100m (or the bottom in areas shallower than 100m) to encompass the euphotic layer.

Starting from the northern part of our simulated domain, the circulation off the **Saharan Bank (21–27° N)** is generally characterized by year round equatorward velocities. Moreover, strong offshore velocities differentiate the **northern Saharan Bank (NSB, 24–27° N)** from the **southern Saharan Bank (SSB, 21–24° N)**.

In the southernmost part of our domain, the **Senegalo-Mauritanian region (12–19° N)** is characterized by a seasonal reversal of meridional velocities with southward/northward direction in winter/summer, respectively, and by enhanced westward velocities in winter. Noticeably, we separated the **southern Senegal region (SS, 12–15° N)** from the rest of the **Senegalo-Mauritanian region (SM, 15–19° N)** because the circulation patterns differ significantly and the continental shelf is wider south of Cape Verde implying different coastal dynamics.

At the frontier of the two previous main zones, the **Cape Blanc area (CB, 19–21° N)** including the Arguin Bank is the place of a meridional convergence of surface water masses and strong offshore velocities.

In these boxes, meridional wind speed and wind curl were averaged to respectively compare upwelling-favourable forcings and Ekman pumping between boxes. Similarly, the horizontal and vertical velocities and advective/diffusive fluxes of nitrate and phytoplankton biomass (mol m^{-2} s^{-1}) were averaged over the edge of each box and the phytoplankton biomass and PP (new and regenerated) were averaged and compared between boxes. Net biological rates (biological source minus sink) in each box were also computed to offer an integrated view of the source and sink terms of phytoplankton biomass and nitrate in each box (mol s^{-1})(i.e. the respective contribution of the advective/diffusive transport at the box boundaries and the net biological rate). Additionally, the mean residence time of upwelled water masses in each box was derived from a lagrangian tracking of passive particles based on 3D current fields from the physical model (see full description in Auger et al., 2015). The meridional variability of the ecosystem functioning then could be fully characterized.

3 Results

3.1 Meridional variability in the coastal region

3.1.1 Wind forcing, current velocity and nitrate fluxes

Mean annual coastal wind forcing imposed in our simulation, i.e. meridional wind intensity (negative equatorward) and wind curl, are presented in Fig. 2 (a & b). Equatorward upwelling-favourable wind is maximum in the southern Saharan Bank and off Cape Blanc (Fig. 2a). Wind curl is everywhere positive implying upward Ekman pumping, and shows weak meridional variability except a clear maximum off Cape Blanc (Fig. 2b).
Mean annual current velocities (vertical and horizontal) over each edge of the coastal boxes (defined positive inward, so vertically upward) are presented in Fig. 2 (c & d-e-f). Coastal upwelling shows a strong latitudinal variability with a clear weakening southward (Fig. 2c). Maximum upwelling intensity is by far found over the northern Saharan Bank which is under the influence of particularly active upwelling cells found in Cape Bojador and Cape Juby areas (Arístegui et al., 2004; Barton et al., 2004). Minimum upwelling intensity is found off Cape Blanc. Observational data are known to be scarce in our study region. However vertical velocities fall in the range of the few studies that have been published with observed (Benítez-Barrios et al., 2011) or modelled values (Mason et al., 2012) focusing on northern Morocco.

Cross-shore velocities are everywhere directed offshore with maxima off the northern Saharan Bank and Cape Blanc (Fig. 2f) where advection by filaments is the most active (Barton et al., 2004; García-Muñoz et al., 2005; Karakaş et al., 2006).
Southward circulation is found over the Saharan Bank as the signature of a strong upwelling-induced coastal jet (Fig. 2d-e). On the contrary, the northward circulation found in the Senegalo-Mauritanian region represents the eastern branch of the large scale cyclonic circulation characterizing the region of the recirculation gyre (Mittelstaedt, 1991). The Cape Blanc area is thus characterized by the average meridional convergence of water masses from the Saharan Bank and Mauritania, and this occurs together with minimum coastal upwelling intensity (Fig. 2c).

Mean annual nitrate fluxes (vertical and horizontal) over each edge of the coastal boxes are presented in Fig. 3 (a & b-c-d). Vertical (upwelling-induced) nitrate supply is maximum in the northern Saharan Bank and the Senegalo-Mauritanian region (Fig. 3a), and minimum off Cape Blanc according to minimum upwelling intensity (see above). However, the southward weakening of upwelling intensity is not reflected in upwelling-induced nitrate supply. Indeed, the vertical nitrate supply is higher south of Cape Blanc than in the southern Saharan Bank, contrasting with upwelling-favourable wind intensity, owing to higher nitrate concentration in upwelling source waters south of Cape Blanc (Fig. 1). Offshore fluxes of nitrate are found maximum in the Cape Blanc and Senegalo-Mauritanian regions. Noticeably, they are significantly higher off Cape Blanc than in the northern Saharan Bank despite equivalent cross-shore velocities (Fig. 3d).

3.1.2 Primary production, phytoplankton biomass and phytoplankton fluxes

The meridional coastal distribution of the annual Primary Production (PP) shows a well-marked maximum off Cape Blanc (Fig. 4a), while similar levels of PP are simulated in the boxes north and south of Cape Blanc, respectively.

The annual mean new production follows the upwelling-induced nitrate supply (Fig. 3a and 4a), except off Cape Blanc where maximum new production is associated with minimum vertical nitrate supply. On the contrary, regenerated production (ammonium consumption, Fig. 4a) shows a meridional structure opposed to the one seen in upwelling-induced nitrate supplies (Fig. 3a) with higher levels in the southern Saharan Bank, off Cape Blanc (although showing the minimum f-ratio; Fig. 4b), as well as in the southern Senegal coastal box (Fig. 4a). This agrees with the meridional variability of the ammonium production by microbial remineralization (Fig. 5a) which brings 60–70 % of the ammonium (not shown). Microbial remineralization depends on detritus concentration, and then potentially on lateral inputs of organic matter. Zooplankton excretion is also minimum in the northern Saharan Bank with a significant overall contribution of mesozooplankton (20–30 %, not shown) and to a lesser extent microzooplankton (5–15 %, not shown). Noticeably, in all coastal boxes except the northern Saharan Bank, PP is mostly related to regenerated production (Fig. 4b; f-ratio$<$0.5).

Phytoplankton biomass, averaged over the 100 meters depth of the boxes, mirrors that of PP with a maximum off Cape Blanc (Fig. 4c). However, phytoplankton exhibits higher biomass north of Cape Blanc than south which does not translate into higher PP in the northern boxes (i.e. North Saharan Bank & South Saharan Bank). Phytoplankton biomass in the Senegalo-Mauritanian region and the North Saharan Bank are similar while PP is different. It is noteworthy that maximum phytoplankton biomass is found off Cape Blanc and the southern Saharan Bank despite the fact that upwelling-induced nitrate supplies are at a minimum at those locations (Fig. 3a).

The vertical export of phytoplankton biomass is maximum off Cape Blanc (Fig. 3e). Otherwise, there is weak meridional variation of vertical phytoplankton export. The meridional variability of horizontal phytoplankton fluxes (Fig. 3f-g-h) is nearly the same as current velocities (Fig. 2d-e-f), which contrasts with nitrate. Maximum fluxes of phytoplankton are directed southward and occur in coastal boxes north of Cape Blanc. In particular, the southern Saharan Bank and Cape Blanc boxes are characterized by strong horizontal inputs of phytoplankton through their northern boundaries. In the Senegalo-Mauritanian region, the southward fluxes of phytoplankton biomass are interestingly opposed to the northward flux of nitrate. Zonal fluxes of phytoplankton are directed offshore with a maximum off Cape Blanc and in the northern Saharan Bank and show maxima off Cape Blanc and in the northern Saharan Bank (Fig. 3h). This latter feature contrasts with nitrate fluxes (Fig. 3d).

3.1.3 Meridional distribution of the processes controlling the coastal nitrate concentration and phytoplankton biomass

The annual mean contribution of each source and sink terms (i.e. advective/diffusive tracer fluxes and net biological rate) to the total rate of change of nitrate concentration and phytoplankton biomass in each coastal box are presented in Fig. 6 (a & b). From northern to southern boxes, the functioning in each box is described. Note that the contribution of diffusion, i.e. horizontal and vertical mixing, is negligible compared to advection.

In the northern Saharan Bank, the nitrate supply seems to be dominated by coastal upwelling, which exceeds nitrate advection from the north. The major sink is found to be horizontal advection, shared between southward and westward (offshore) advection, actually exceeding biological uptake. The net phytoplankton growth exceeds the transport of phytoplankton by advection through the northern boundary of the northern Saharan Bank box. Phytoplankton is then equally exported offshore and southward, and to a much lesser extent through sedimentation below 100m.

In the southern Saharan Bank, the nitrate supply is shared between advection through the northern boundary from the northern Saharan Bank and coastal upwelling. Southward advection to the Cape Blanc area is then the main nitrate sink while both contributions from the biological sink and offshore export are reduced compared to their role in the northern Saharan Bank. In the southern Saharan Bank, the net local phytoplankton growth is no longer the main source of phytoplankton since the transport of phytoplankton from the northern Saharan Bank is more important. Phytoplankton biomass is then exported southward and offshore, the vertical export below 100m depth still being low.

Off Cape Blanc, as in the southern Saharan Bank, the nitrate budget is mostly driven by horizontal advective fluxes. The nitrate supply is mostly due to transport through the southern and northern boundaries from the Senegalo-Mauritanian region and the southern Saharan Bank, respectively. Most of the nitrate is then exported offshore. The respective contributions of the coastal upwelling source and the biological sink are of minor importance. As in the southern Saharan Bank, phytoplankton biomass is mostly enhanced by southward advection through the northern boundary exceeding net biological production. Noticeably, this region displays the highest offshore export of phytoplankton. Contributions of southward and vertical transport are weak.

In the Senegalo-Mauritanian region, the nitrate supply is shared between coastal upwelling and northward advection from southern Senegal. Nitrate sinks are almost equally distributed between offshore export, northward advection to Cape Blanc and biological activity. In this region, phytoplankton increases mostly because of net local growth. Phytoplankton transport from the north and toward the south are of minor importance. Phytoplankton is then primarily exported offshore.

Finally, in southern Senegal, nitrate is mostly supplied by advection from the southernmost boundary of our boxes and disappears due to northward advection toward the Senegalo-Mauritanian region. Contributions of the coastal upwelling source and the biological sink are weaker while the offshore export is even less important. Phytoplankton fluxes are very similar to those found in the Senegalo-Mauritanian region with a main source related to net local growth and a main sink through offshore export. Phytoplankton transport from the north and toward the south are of minor importance.

A schematic representing the main fluxes for nitrate and phytoplankton in each box is given in Fig. 7 (each colour corresponds to a box). It shows that coastal upwelling of nitrate, despite being significant in all regions but the Cape Blanc area, is the dominant supplier only in the northern Saharan Bank and the Senegalo-Mauritanian region. In all other regions, nitrate supply is dominated by meridional advection. Indeed, the southern Saharan Bank is mostly fuelled by nitrate advected southward from the northern Saharan Bank while the Cape Blanc area gets nitrate inputs from the southern Saharan Bank and the Senegalo-Mauritanian region. South of this frontal zone in our 2 southernmost boxes (i.e. the Senegalo-Mauritanian and southern Senegal regions), northward nitrate transport becomes a key player in the nitrate budget. Net local phytoplankton growth is the most important source of phytoplankton in 3 of our 5 boxes (i.e. the northern Saharan Bank, Senegalo-Mauritanian and southern Senegal regions) but this prevalence is mostly marked only in our 2 southernmost boxes. The 3 north boxes display close contributions of the phytoplankton supply from northward advection and the net local growth with the latter only dominating in the northernmost box (i.e. the northern Saharan Bank).

3.2 Spring meridional variability in the offshore region

3.2.1 Wind forcing, current velocity and nitrate fluxes

In the offshore region, the chlorophyll seasonal variability may depend on the export of coastal productivity. Additionally, the wind stress can be responsible for vertical mixing that enhances the exchanges of inorganic and organic matter between the euphotic and aphotic layers. The vertical nutrient supply to the euphotic surface layer and the phytoplankton export below the euphotic layer may also be enhanced by positive/negative Ekman pumping, respectively linked to positive/negative wind stress curl.

Off NW Africa, the offshore extension of coastal chlorophyll has been shown to display a marked seasonal variability with a maximum in spring (Lathuilière et al., 2008). Thus, spring averages from March to May were considered to investigate the factors driving primary productivity in offshore boxes. Mean spring wind forcing (i.e. wind intensity and wind curl) are first presented in Fig. 8 (a & b). During spring, the wind intensity increases from the northern Saharan Bank to Cape Blanc (where it peaks) and then decreases southward (Fig. 8a). On the other hand, wind stress curl shows a monotonous southward increase (Fig. 8b) from the northern Saharan Bank to southern Senegal with negative values from the northern Saharan Bank to the Cape Blanc region.

During spring, the vertical velocities at the bottom of the offshore boxes display the same meridional structure (Fig. 8c) as the wind curl. As a proxy of offshore export from the coastal band, inward velocities at the eastern boundary are found maximum off the northern Saharan Bank and off Cape Blanc (Fig. 8g), and minimum off the southern Saharan Bank. It is noteworthy that at the western boundaries, velocities are directed offshore except off the northern Saharan Bank where shoreward intrusions from the subtropical gyre are detected (Fig. 8f). Maximum offshore velocities are found at the latitude of the Cape Blanc region. Southward velocities are found off the southern Saharan Bank and off Cape Blanc (Fig. 8e) while northward velocities are found off southern Senegal (Fig. 8d). Off the Senegalo-Mauritanian region, inward velocities at both north and southern boundaries indicate the presence of a convergence zone in this latitudinal range during spring (Fig. 8d-e).

Mean spring vertical nitrate fluxes (advection and diffusion) at the bottom of the offshore boxes are presented in Fig. 9 (a & b). A striking result is that vertical advection fluxes are of the same order of magnitude as diffusion fluxes with an opposite meridional variability. On the one hand, vertical nitrate supply by advection is found in all offshore boxes (but weak for the northern Saharan Bank) except in the latitudinal band of the southern Saharan Bank region (Fig. 9a). The vertical nitrate supply by advection off the northern and southern Saharan Bank is particularly weak (inward nitrate fluxes despite averaged outward velocities due to episodic inward events) with respect to vertical diffusion. On the other hand, the vertical nitrate supply due to turbulent diffusion shows a clear southward decrease (Fig. 9b). It is actually stronger off the Saharan Bank (North and South) and Cape Blanc than off Mauritania and Senegal.

The patterns of lateral nitrate fluxes during spring (Fig. 9c-d-e-f) mainly follow current velocities but with significant deviations (Fig. 8d-e-f-g). Maximum alongshore fluxes are found south of Cape Blanc and are directed northward (Fig. 9c-d). Nitrate inputs from the coastal band (eastern boundary) increase southward compared to cross-shore currents, especially off the Senegalo-Mauritanian region (Fig. 9f), which is attributed to a southward increase of nitrate concentrations in upwelling source waters (Fig. 1). The maximum off Cape Blanc is smoothed compared to current velocities (Fig. 8g) indicating a relative nutrient depletion of coastal waters off Cape Blanc.

3.2.2 Primary production, phytoplankton biomass and phytoplankton fluxes in spring

Spring mean PP (new and regenerated production), f-ratio and phytoplankton biomass are presented in Fig. 10. According to the meridional pattern of offshore extension of chlorophyll in spring (Lathuilière et al., 2008), offshore PP and phytoplankton biomass are found maximum off Cape Blanc and significantly higher in the Senegalo-Mauritanian region than off the Saharan Bank. Both new and regenerated production display the same meridional variability. Nevertheless, regenerated production is generally more intense (except off the northern Saharan Bank) and also more variable in space compared to new production. This corresponds to the meridional variability of ammonium production by both microbial remineralization and zooplankton excretion (Fig. 5b) which respectively contribute to 75 % and 30–40 % (15–20 % for both micro- and mesozooplankton, not shown). The meridional variability of PP is then controlled first by organic matter inputs from the coastal band which stimulate regenerated production and, less so, by local zooplankton excretion; second by nutrient inputs from the coastal band responsible for new production.

Mean spring vertical phytoplankton fluxes (advection and diffusion) at the bottom of the offshore boxes are presented in Fig. 11 (a & b). A striking result is that diffusion fluxes exceed advection fluxes by one order of magnitude. Turbulent diffusion is overall responsible for vertical export off the Saharan Bank, and to a lesser extent off Cape Blanc (Fig. 11b). Moreover, the offshore vertical export of phytoplankton biomass due to advection exclusively occurs off the Saharan Bank and off Cape Blanc (Fig. 11a). The meridional variability of vertical advection is indeed driven by wind curl (Fig. 8). As a result, the total offshore vertical export is clearly maximum off the Saharan Bank which is also a sign of maximum dilution of phytoplankton biomass over the water column in this region.

Mean spring phytoplankton horizontal advective fluxes at the boundaries of offshore boxes are presented in Fig. 11c-d-e-f. The meridional variability of lateral phytoplankton fluxes is nearly the same as current velocities (Fig. 8d-e-f-g). Nevertheless, the westward fluxes through the eastern boundary are more important than expected from lateral velocities from Cape Blanc to Senegal.

3.2.3 Which processes control the offshore nitrate concentration and phytoplankton biomass?

Spring mean contribution of each source and sink terms of nitrate concentration and phytoplankton biomass in offshore boxes, i.e. advective/diffusive tracer fluxes and net biological rate, are presented in Fig. 12 (a & b). From northern to southern boxes, the functioning in each box is described. Note that the contribution of horizontal diffusion is negligible compared to vertical diffusion and advection.

In the northern Saharan Bank, the nitrate supply is equally due to coastal inputs and vertical mixing, the contribution of nitrate advection from the north and offshore upwelling remaining insignificant. At the same time, the major sink is found to be the biological activity, clearly exceeding southward advection. Alternatively, in the southern Saharan Bank, the nitrate supply is shared between vertical mixing and northerly advection from the northern Saharan Bank, exceeding southerly advection. Nitrate then mostly disappears due to biological activity. Off Cape Blanc, the nitrate supply is mostly due to coastal inputs, and then removed by biological activity and offshore export. In the Senegalo-Mauritanian region, the nitrate supply is dominated by coastal inputs, and then northerly advection from southern Senegal and offshore upwelling. In like manner, the nitrate sink is more or less equally distributed between biological activity and westward advection. Finally, in southern Senegal, nitrate is mostly supplied by southerly advection and disappears due to lateral advection (equally distributed between westward and northward advection), more than biological activity.

The source of phytoplankton biomass off the northern Saharan Bank is equally distributed between net phytoplankton growth and coastal inputs. Phytoplankton biomass is then mostly removed by vertical export through vertical mixing and, less so, by southward transport. Alternatively, in the southern Saharan Bank, phytoplankton biomass is mostly due to lateral advection, equally originating from the north and from the coast, and less so, to net phytoplankton growth. Phytoplankton biomass is still mostly exported vertically through vertical mixing Off Cape Blanc, the phytoplankton biomass mainly results from coastal inputs and removed through lateral advection, i.e. offshore and southward, which exceeds the sinks due to vertical mixing and biological activity. Finally, in the Senegalo-Mauritanian and southern Senegal regions, phytoplankton biomass is mostly enhanced by coastal inputs and disappears through biological activity. Southward inputs have also a noticeable contribution off southern Senegal.

To summarize (Fig. 13, each colour corresponds to a box), off the Saharan Bank, nitrate is equally supplied by vertical mixing and lateral advection whether from the coast in the northern Saharan Bank or from the north in the southern Saharan Bank. As a consequence, phytoplankton biomass results from net biological production and lateral advection. Phytoplankton biomass almost exclusively disappears through vertical mixing. Alternatively, south of the Saharan Bank, the nitrate supply is dominated by lateral advection whether from the coast off Cape Blanc, from the coast and the south off the Senegalo-Mauritanian region, and from the south off southern Senegal. In these regions, the phytoplankton biomass is mostly enhanced by zonal advection and disappears through a negative net biological rate. Indeed, the corresponding boxes were defined in the transition zone between eutrophic coastal waters and oligotrophic waters of the subtropical gyre where phytoplankton communities collapse through mortality and grazing. Off Cape Blanc, zonal advection however dominates due to stronger nutrient and phytoplankton inputs. Thus, the collapse of phytoplankton communities is expected further offshore.

4 Discussion

In this study, we investigated the processes driving the meridional variability of phytoplankton biomass and PP in coastal and offshore regions. We will first discuss the sensitivity of coastal upwelling to the wind forcing, which is a key player for the vertical nutrient supply in the coastal region. Then we will focus on the meridional variability of coastal phytoplankton biomass and PP (new and regenerated production) in relation to the transport of matter along the coastal band and to the open ocean. Finally, we will seek to identify the processes driving the meridional variability of the offshore extension of the coastal chlorophyll pattern which peaks during the spring upwelling season.

4.1 Sensitivity of coastal upwelling to the wind forcing

In our simulation, the meridional variability of vertical velocities at 100m depth (which roughly corresponds to the euphotic layer) is not correlated to that of upwelling-favourable winds and Ekman pumping on annual average. This result questions the estimation of upwelling-induced nutrient inputs in the euphotic layer based on the wind-driven Ekman transport and the nutrient concentrations in upwelling source waters, a method commonly used in EBUS (Bakun, 1990; Lathuilière et al., 2008; Messié et al., 2009; Messié and Chavez, 2014). However, coastal upwelling depends on many other factors including the large scale dynamical state of the ocean and the coastal geomorphology (Benazzouz et al., 2014; Mason et al., 2012). As an example, the upwelling limitation by onshore geostrophic flow have been shown to play a key role in driving some coastal upwellings (Marchesiello and Estrade, 2010; Messié and Chavez, 2014). Local and large scale processes, while not entirely decoupled (e.g. NECC intensity and the seasonal weakening of trade winds are coupled; Mittelstaedt, 1991), act at different time scale and impact in different ways the coastal upwelling. Our simulated spatial and temporal variability of surface circulation is in good agreement with the satellite-tracked drifters (see Section 2.2), so the model can be used to infer the factors responsible for the sensitivity of coastal upwelling to the wind forcing. For this latter purpose, we further analyze the seasonal cycles of meridional wind versus vertical and horizontal velocities averaged within and over each edge of the coastal boxes (Fig. 14).

In the northern part of our domain, the presence of the Cape Bojador Filament (Barton et al., 2004; García-Muñoz et al., 2004; Karakaş et al., 2006) leads to a year round strong offshore export (associated with a strong cross-shore divergence) in the northern Saharan Bank (Fig. 14c). In the southern Saharan Bank and off Cape Blanc, upwelling-favourable wind increases during spring and/or early fall (Fig. 14a). This induces an acceleration of the equatorward jet from the northern Saharan Bank to the Cape Blanc area (Fig. 14d) which tends to create a meridional divergence promoting coastal upwelling over the northern Saharan Bank.

Southward, during the spring/summer and fall/winter transitions, the poleward geostrophic circulation which establishes from southern Senegal to Cape Blanc (Fig. 14d; Lázaro et al., 2005; Mittelstaedt, 1991; Stramma et al., 2005; Wooster et al., 1976) limits the southward extension of the equatorward jet found over the Saharan Bank. It creates a meridional convergence of coastal water masses Saharan Bank in the Cape Blanc area (Fig. 14d) which limits significantly the intensity of the coastal upwelling (Fig. 2c). Indeed, a downwelling period is paradoxically found in summer off Cape Blanc when upwelling-favourable wind is maximum (Fig. 14a-b). Downwelling occurs as the cold and dense upwelling water from the Saharan Bank encounters the warm and stratified equatorial water from the NECC (Mittelstaedt, 1991). Noticeably, the response of the Cape Blanc filament (spring and fall peaks of cross-shore velocities) is delayed by one month compared to the alongshore jet peaks. This suggests that the local downwelling (driven by meridional convergence) and the inertia of the upwelling jet over the Saharan Bank (as described by Benazzouz et al., 2014) are the primary drivers of the response of the Cape Blanc filament to the wind forcing. In the southernmost part of our domain, the Senegalo-Mauritanian region, the seasonal cycle of the coastal upwelling is likewise partly driven by the equatorward wind intensity and a downwelling which is detected in late spring while the equatorward wind is weakening (but is not yet minimum).

In the NW African region, coastal topography effects and alongshore geostrophic flow (related to large scale circulation patterns) may noticeably influence the convergence/divergence of coastal water masses. They would modulate the coastal divergence driven by the Ekman transport, i.e. the response of coastal upwelling to the wind forcing. Our modelling approach stresses processes that are yet difficult to study with observations due to their scarcity. Therefore, this work strongly advocates for dedicated observational studies.

4.2 Meridional variability of coastal phytoplankton biomass, primary production and matter transfers

Although PP is mainly regulated by new production and the amount of nitrate supply by wind-driven upwelling (Ohde and Siegel, 2010), the meridional variability of PP and phytoplankton biomass is noticeably influenced by regenerated production (fuelled by the uptake of ammonium) on annual average. High regenerated production is a sign that upwelled nitrate is efficiently used (Lachkar and Gruber, 2011; Messié and Chavez, 2014) as a result of high residence time in the NW African upwelling system (Lachkar and Gruber, 2011). We show that the meridional variability of regenerated production actually deviates from the variability of new production as a result of (1) the lateral advection of ammonium, particulate detritus and dissolved organic matter that are remineralized, and (2) retention patterns increasing the residence times of water masses.

In the northern Saharan Bank, new production and phytoplankton biomass remain relatively low. Low nitrate concentration in upwelling source waters (North Atlantic Central Water; Arístegui et al., 2009) and short residence time (due to high horizontal advection by the coastal upwelling jet, Fig. 15a) limit the phytoplankton growth. Phytoplankton indeed requires time to complete nutrient uptake (Dugdale et al., 1990; Zimmerman et al., 1987) and low residence times also limit regenerated production leading to minimum PP (Checkley and Barth, 2009; Messié et al., 2009). Upwelled water masses are then exported southward and offshore. Nitrate is mainly exported southward (coastal water masses) while there is relatively more phytoplankton exported offshore. During synoptic events of coastal upwelling, the coastal jet exports nitrate-rich and phytoplankton-poor water masses to the south. Inversely, the relaxation of the coastal jet enhances residence time and promotes the local building of phytoplankton biomass. The combined effect of this local growth and the high filament activity around Cape Bojador (the latter point being documented in Barton et al., 2004; García-Muñoz et al., 2004; Karakaş et al., 2006) results in an offshore transport of phytoplankton-rich and nitrate-depleted water masses.

New production, fuelled by nitrate upwelled in the north Saharan Bank, happens partly further downstream in the southern Saharan Bank where such remote influence accounts for 50 % of new production (Fig. 6). This phenomenon has also been observed downstream of major other upwelling cells as in the Benguela region for example (Hardman-Mountford et al., 2003).

Off Cape Blanc, the meridional convergence of water masses results in subduction events which enhances the vertical extension of the plankton-rich pattern and lead to high levels of phytoplankton biomass when integrated over the 0-100m surface layer. The phytoplankton biomass is maintained by maximum levels of regenerated production, actually exceeding new production by more than two fold. In general the regenerated production relies on high residence time favourable to efficient recycling (Fig. 15a). However, in our results, the water masses residence time in the southern Saharan Bank and off Cape Blanc is low and can not explain the high level of regenerated production. In this region the regenerated production is rather due to the remineralization of organic matter supply and zooplankton excretion (Fig. 5a). Note that the meridional variability of secondary production (grazing rate) follows that of PP (not shown) suggesting a bottom-up control of the phytoplankton biomass rather than a top-down control by zooplankton grazers. Zooplankton biomass and excretion activity are then enhanced when the plankton biomass is elevated, which is especially the case in the southern Saharan Bank and off Cape Blanc.

In the Senegalo-Mauritanian region, only moderate regenerated production is found year round although residence time is relatively high with respect to the southern Saharan Bank and Cape Blanc areas. This supports the idea that, in the southern Saharan Bank, Cape Blanc and Senegalo-Mauritanian regions, regenerated production is rather driven by the amounts of organic matter supplies through lateral boundaries than by high residence time. In the Senegalo-Mauritanian region, new production is enhanced by vertical nitrate supply during the winter/spring upwelling period (South Atlantic Central Water; Arístegui et al., 2009), and by southerly inputs of equatorial nutrient-rich water masses from the Gulf of Guinea in late spring and late fall (Lázaro et al., 2005; Mittelstaedt, 1991). Some authors have also reported the potential impact on primary productivity of horizontal advection of warm, nutrient- and chlorophyll-poor waters by the NECC (Lathuilière et al., 2008) when the trade winds weaken in summer and early fall (Mittelstaedt, 1991; Stramma et al., 2005). Indeed, the weakening of the trade winds and the advection by the NECC are actually coupled but the transition period might enable transient intrusions of nutrient-rich coastal waters from the Gulf of Guinea. Let us also mention that nutrient loads by rivers, which are not accounted for in our model configuration, may significantly sustain marine productivity during the monsoon summer period as high coastal concentrations of nutrients have been recently observed at the end of the rainy season in southern Senegal (E. Machu, pers. comm.).

At the coast, the meridional variability of new production follows the pattern of vertical nitrate supply, except off Cape Blanc where maximum new production and phytoplankton biomass is mostly related to lateral nitrate injection. This points a gap of the first estimates of nitrate supply by coastal upwelling based on the wind-driven Ekman transport and nitrate concentrations in upwelling source waters (Gruber et al., 2011; Messié et al., 2009; Messié and Chavez, 2014) which were used to explore the link between nutrient supply and primary productivity in EBUS. Off NW Africa, this method may actually lead to misleading vertical nitrate supply in the northern Saharan Bank (underestimation) and off Cape Blanc (overestimation) since the coastal upwelling does not only depend on the wind intensity (see Section 4.1). In particular, horizontal convergence and subduction of nutrients in late spring/early summer seem to limit the annual vertical nitrate supply by the upwelling off Cape Blanc in our simulation. Interestingly, satellite-derived diagnostics of low residence time off Cape Blanc (Messié and Chavez, 2014), confirmed by our model results (Fig. 15), also suggest that subduction may play a key role in regulating PP off Cape Blanc. Based on the results of Messié and Chavez (2014), the potential overestimation of vertical nitrate supply identified in this study may also concern other EBUS.

4.3 Extension of the coastal-rich phytoplankton pattern in spring/summer

The offshore extension of the coastal surface chlorophyll pattern is highly variable in space and time off NW Africa. As described from SeaWiFS data (Lathuilière et al., 2008), the chlorophyll extension is narrow over the Saharan Bank (less than 100 km), wide off Cape Blanc (approximately 200 km) and can reach 400 km at the end of the spring upwelling season in the Senegalo-Mauritanian region. Focusing on the meridional variations, Lathuilière et al. (2008) investigated the potential impact of several physical and biological processes on this offshore extension: (i) the distance of the upwelling front from the coast, (ii) the wind stress curl, (iii) the impact of mesoscale and submesoscale dynamics on the cross shelf transport, and (iv) the limitation of phytoplankton growth by nutrients. Our modelling approach was designed to test some of their hypotheses and to better explain the mechanisms driving the offshore extension of surface chlorophyll off NW Africa. For this purpose, we focused on the offshore region in the spring period when the maximum chlorophyll extension is found (Lathuilière et al., 2008). At this season, maximum coastal upwelling is found off the Saharan Bank (Fig. 2c). Following the hypothesis of Lathuilière et al. (2008), this should traduce in a maximum of phytoplankton biomass extension at the Saharan Bank latitudes. Instead, maximum extension is found off Cape Blanc and in the Senegalo-Mauritanian region as attested by the meridional variation of phytoplankton biomass in the offshore region (Fig. 10). Note that our conclusions will be also valid on annual average since the drivers of nitrate and phytoplankton biomass in offshore boxes are similar on spring and annual average (see Fig. 7 and 13).

Upward Ekman pumping due to positive wind curl has been reported to contribute significantly to the vertical mass flux associated with coastal upwelling in a band extending 200 km from the coast (Castelao and Barth, 2006; Enriquez and Friehe, 1995). Off NW Africa, Ekman pumping has been suggested to contribute to half of the surface chlorophyll variability on interannual timescale (Pradhan et al., 2006). Our results indicate downward and upward wind-induced Ekman pumping in spring north and south of Cape Blanc, respectively (Figs. 8b & 9a). However, the contribution of vertical advection to the nitrate input in the surface layer is negligible compared to lateral advection and vertical mixing (Fig. 12a). Thus, the offshore extension of the phytoplankton biomass is not primarily driven by the nutrient supply due to Ekman pumping, as already suggested by Lathuilière et al. (2008).

In our results, the vertical mixing contributes significantly to nitrate supply off the Saharan Bank (especially in the southern Saharan Bank, Fig. 12a). This is even more visible in spring when the mixed layer depth can reach more than 100 m off the Saharan Bank as a result of winter convection, while remaining generally less than 60 m in the Senegalo-Mauritanian region (not shown). This is consistent with the global climatology of the mixed layer depth from de Boyer Montégut et al. (2004). However, such nitrate supply does not translate into high phytoplankton biomass. In fact, the vertical mixing, as previously suggested by Huntsman and Barber (1977), is also responsible for a significant vertical export of phytoplankton biomass below 100 m which may limit the phytoplankton biomass off the Saharan Bank. The redistribution of phytoplankton biomass within the mixed layer most likely decreases the surface phytoplankton biomass detected by satellite (dilution effect) which may partly explain the weak offshore extension of surface chlorophyll north of Cape Blanc (Lathuilière et al., 2008).

Overall, our study shows that the lateral advection of nutrients and phytoplankton biomass is mostly directed alongshore (southward) off the Saharan Bank and cross-shore south of Cape Blanc all year round. Thus, inputs of nutrients and phytoplankton biomass from the coast are mainly found south of Cape Blanc (Fig. 9f & 11f). This is consistent with the high regenerated production (Fig. 10) found together with low residence times south of Cape Blanc (Fig. 15b). Nutrient limitation might then play a minor role in the weak offshore extension of chlorophyll north of Cape Blanc questioning the contradictory hypothesis of Lathuilière et al. (2008). In our results, the advection by filaments is found to be a major process enhancing cross shelf transport off Cape Blanc, in agreement with Kostianoy and Zatsepin (1996). Likewise, high kinetic energy in the Senegalo-Mauritanian region suggests that filaments and mesoscale eddies may enhance cross shelf transport, as shown from satellite data by Lathuilière et al. (2008). In this region, the coastal upwelling jet develops inshore of a large scale northward circulation, and the resulting current shear may help the development of baroclinic instabilities mostly responsible for eddy generation in upwelling systems (Capet et al., 2008). In contrast, off the Saharan Bank, the coastal upwelling jet flows southward together with the Canary Current which may limit the development of such mesoscale activity. The greater offshore extension of the coastal phytoplankton biomass in the Senegalo-Mauritanian region may then be primarily explained by the lateral advection of nutrients and phytoplankton biomass, as already suggested by Lathuilière et al. (2008). Nevertheless, our model results indicate that the nutrient input is not only from the coastal region. Indeed, we identified a significant impact of transient southern intrusions of nutrient-rich waters in the Senegalo-Mauritanian region originating from the Guinean upwelling due to the presence of the Guinea Dome, a large scale cyclonic feature centred south of the Cape Verde archipelago (Lázaro et al., 2005; Mittelstaedt, 1991).

5 Conclusion

In the present study, a physical-biogeochemical modelling approach seeks to provide a first mechanistic understanding of the drivers of the seasonal variability of the spatial distribution of primary productivity in the NW African upwelling system. To this aim, a comparative box analysis representing homogeneous sub-regions in terms of near-surface horizontal circulation was conducted. Our physical-biogeochemical simulation reproduced accurately observed patterns of surface ocean circulation and chlorophyll in our region of interest. We then analysed the distribution (and its variability) of phytoplankton biomass and production with regard to advective and diffusive fluxes of nutrients and phytoplankton at the box boundaries.
Our results suggest that coastal topography effects and alongshore geostrophic flow related to large scale circulation patterns modulate the coastal divergence driven by the Ekman transport. The effect of wind is amplified off Cape Bojador and dampened off Cape Blanc. Coastal upwelling of nitrate, despite being significant in all regions but the Cape Blanc area, is the dominant supplier only in the northern Saharan Bank and the Senegalo-Mauritanian region. Elsewhere, nitrate supply is dominated by meridional advection. Thus, the meridional variability of new production follows that of vertical nitrate supply, except off Cape Blanc where maximum new production is mostly related to lateral nitrate injection from the northern or southern part of our domain depending on seasonality. Net local phytoplankton growth is the exclusive driver of phytoplankton biomass only in the Senegalo-Mauritanian region. North of Cape Blanc, the phytoplankton supply from northward advection becomes as important as the net local phytoplankton growth with the latter only dominating off Cape Bojador. The phytoplankton biomass is also maintained by high levels of regenerated production exceeding new production by more than two fold off Cape Blanc in particular. While the regenerated production relies on high residence time

favourable to efficient recycling in the southern Saharan Bank, regenerated production is more impacted by the amounts of organic matter supplies through lateral boundaries than by residence time in the Cape Blanc and Senegalo-Mauritanian regions.

As previously suggested by Lathuilière et al. (2008), the offshore extension of the phytoplankton biomass in spring, more pronounced south of Cape Blanc, is not driven by the nutrient supply due to Ekman pumping. We additionally show that, off the Saharan Bank, the vertical mixing is responsible for a significant vertical export of phytoplankton biomass below 100 m which is not the case south of Cape Blanc. Besides, the redistribution of phytoplankton biomass within the mixed layer may artificially decrease the surface phytoplankton biomass detected by satellite north of Cape Blanc (dilution effect). Overall, the lateral advection of nutrients and phytoplankton biomass is mostly directed alongshore (southward) off the Saharan Bank and cross-shore south off Cape Blanc. Nutrient limitation due to low nutrient concentrations in upwelling source waters might then only play a minor role in the weak offshore extension of surface chlorophyll north of Cape Blanc. The greater offshore extension of phytoplankton biomass in the Senegalo-Mauritanian region then effectively results from a lateral advection of coastal nutrients and phytoplankton biomass. Nevertheless, the nutrient input is not only from the coast as transient southern intrusions of nutrient-rich waters from the Guinean upwelling may significantly fertilize the Senegalo-Mauritanian region.

Future studies should investigate the response in primary productivity to the intra-seasonal and event-scale variability of wind-induced coastal upwelling and nutrient inputs at the box boundaries, and its impact on interannual variability. The year-to-year evolution of fish stocks and migrations may greatly depend on changes in the physical and biogeochemical conditions. This could be tested using our modelling approach by comparing our model inter-annual variability with estimations of fish abundance in the NW African region. Understanding the processes which drive seasonal and inter-annual variability of the upwelling region also represents a first step towards a robust projection of the effect of climate change on the biogeochemistry of the region and therefore on the fisheries resources.

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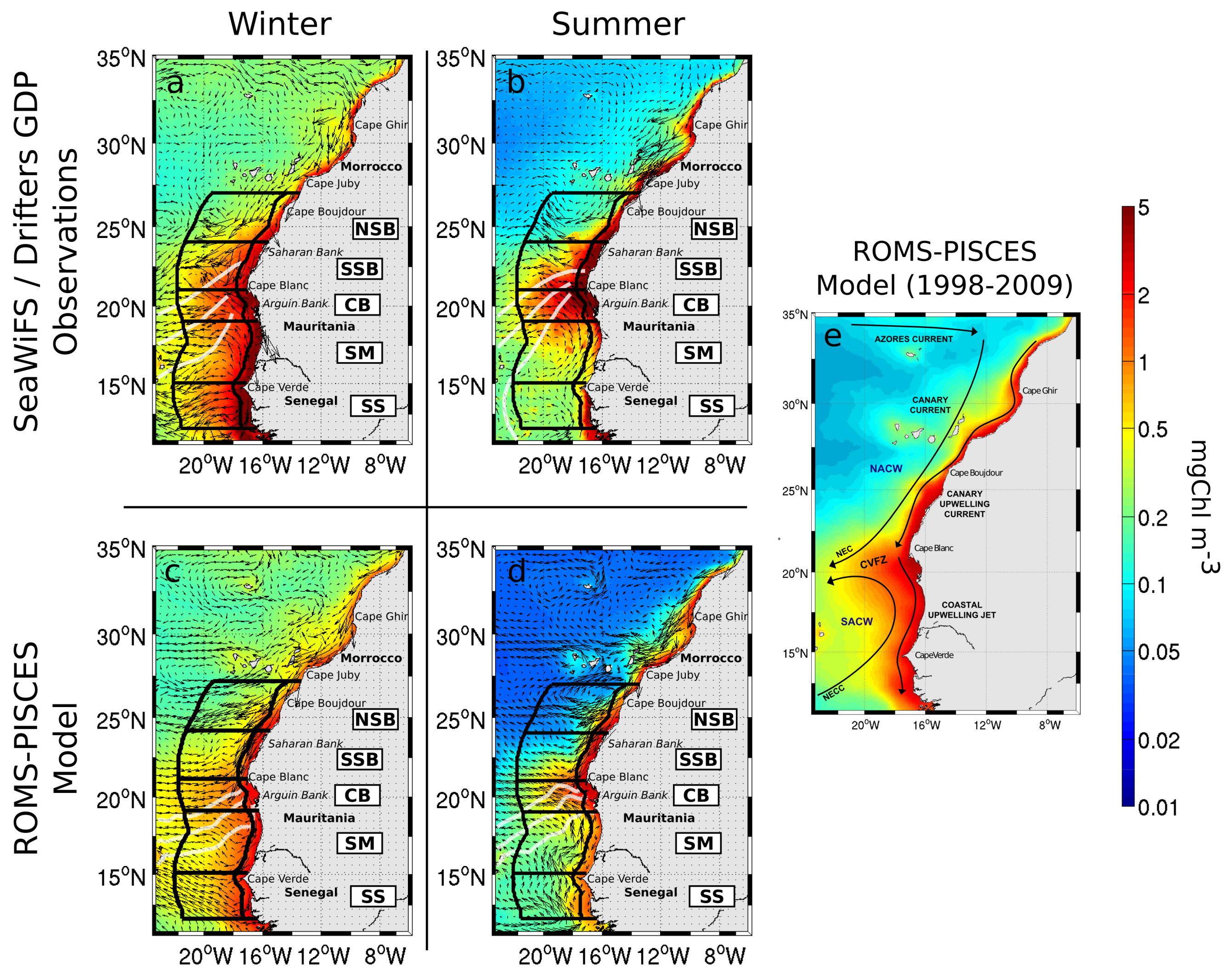

Figure 1: Seasonal climatology of sea surface chlorophyll concentrations (background) from SeaWiFS satellite data (1998–2009), near-surface currents (vectors) from the Global Drifter Program (1979–present, Lumpkin and Johnson, 2013) and nitrate concentration at 100m depth (white contours of 10, 15 and 20 mmolN m^{-3} from north to south) from the World Ocean Atlas 2013 (Garcia et al., 2014) in (a) winter (January–March) and (b) summer (July–September). Same seasonal climatology computed with the 5-days outputs of ROMS-PISCES in (c) winter and (d) summer. Main surface currents and deep water masses over the study area are presented over a map of simulated surface chlorophyll averaged over the SeaWIFS period (e). NEC: North Equatorial Current; NECC: North Equatorial Counter current; CVFZ: Cape Verde Frontal Zone; NACW: North Atlantic Central Water; SACW: South Atlantic Central Water. The 5 coastal and 5 offshore boxes used in this study are superimposed (black boxes): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

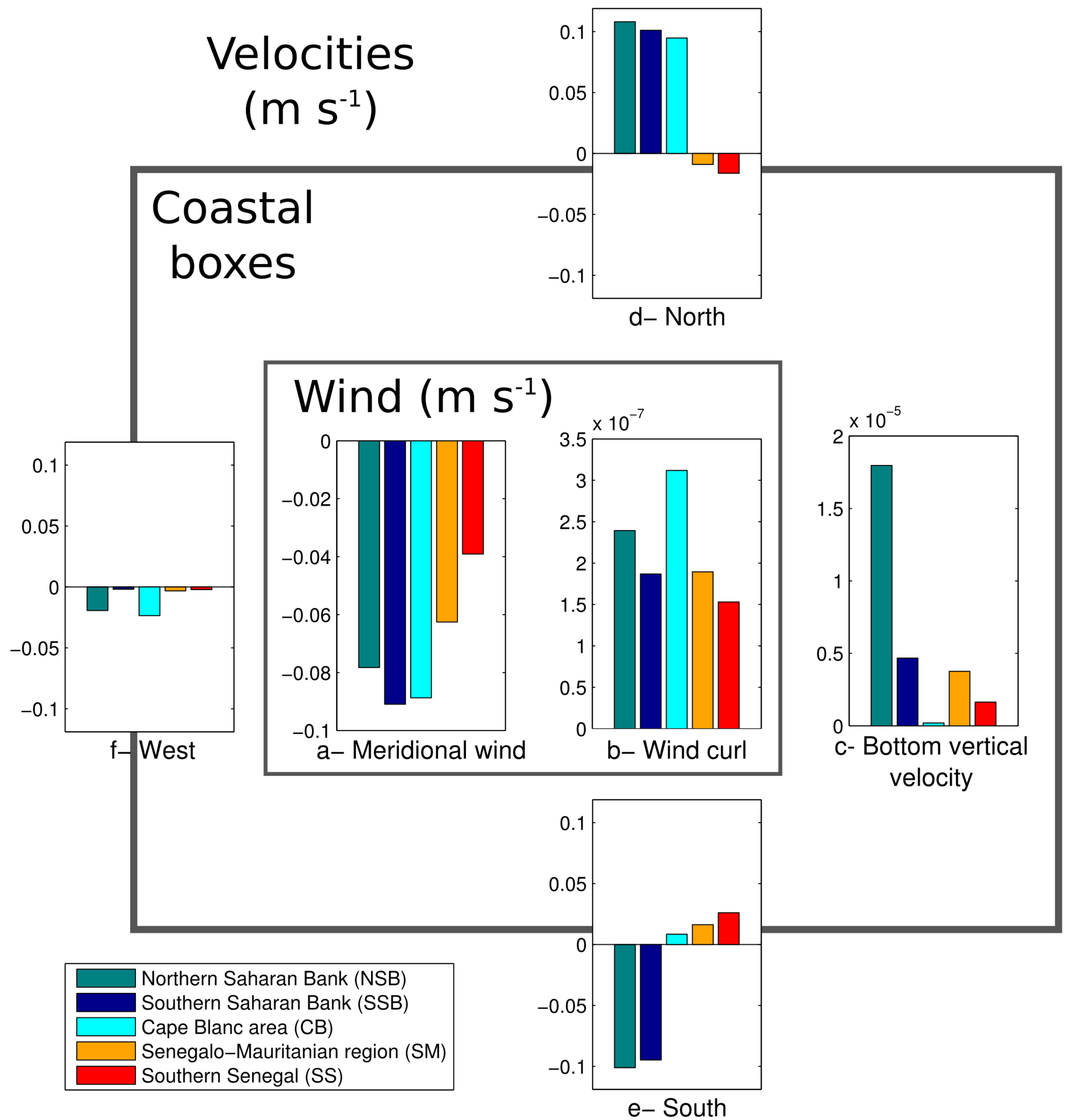

Figure 2: Annual mean of (a) wind intensity (m s^{-1}) and (b) wind curl (s^{-1}) at the surface of the coastal boxes, (c) upwelling intensity (bottom vertical velocity, in m s^{-1}) within the coastal boxes and lateral velocities at the (d) northern, (e) southern and (f) western boundaries (m s^{-1}). Vertical and lateral velocities are defined positive inward (so vertically upward). Each colour corresponds to a box (see legend).

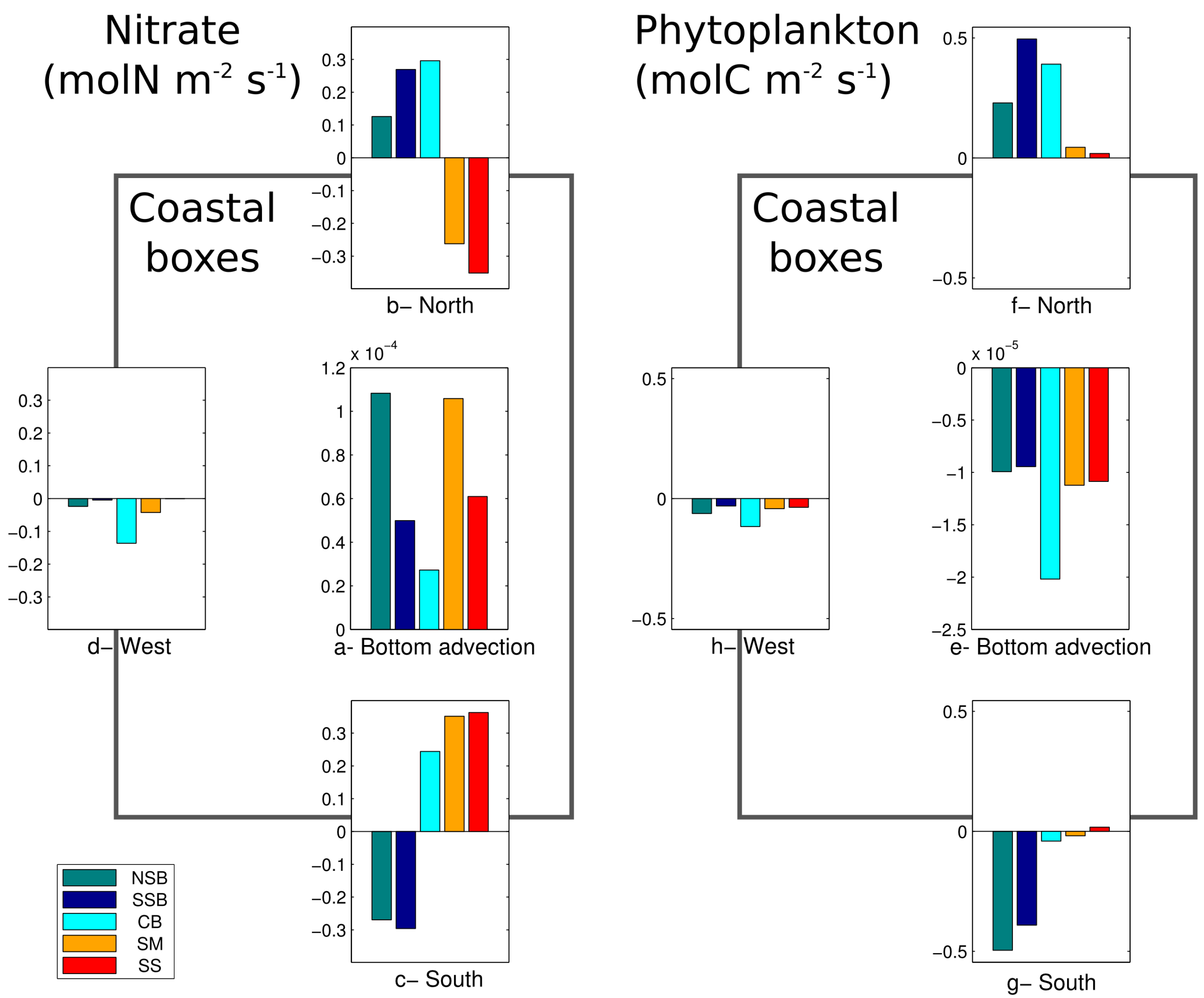

Figure 3: Annual mean of (a) vertical nitrate fluxes at the bottom of the coastal boxes and (b-c-d) lateral fluxes at the (b) northern, (c) southern and (d) western boundaries (molN m^{-2} s^{-1}); annual mean of (e) vertical phytoplankton fluxes at the bottom of the coastal boxes and (f-g-h) lateral fluxes at the (f) northern, (g) southern and (h) western boundaries (molC m^{-2} s^{-1}). Vertical and lateral fluxes are defined positive inward (so vertically upward). Note that the fluxes due to vertical diffusion are one order of magnitude lower compared to advection in the coastal boxes. Each colour corresponds to a box (see legend): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

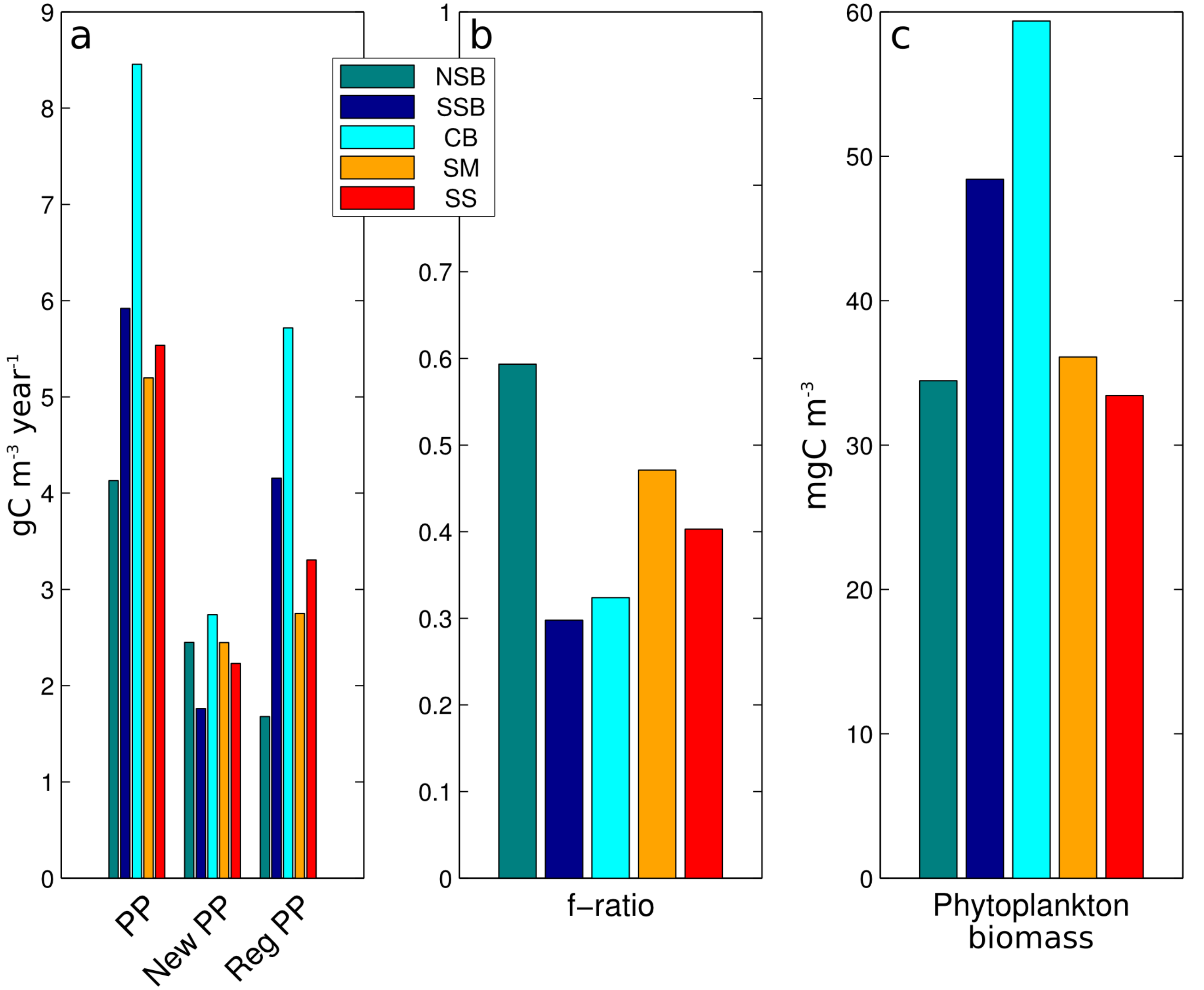

Figure 4: Annual mean of (a) primary production (PP, gC m^{-3} year^{-1}), new production (gC m^{-3} year^{-1}) and regenerated production (gC m^{-3} year^{-1}), (b) f-ratio (new/regenerated production) and (c) phytoplankton biomass (mgC m^{-3}) in the coastal boxes. Each colour corresponds to a box (see legend): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

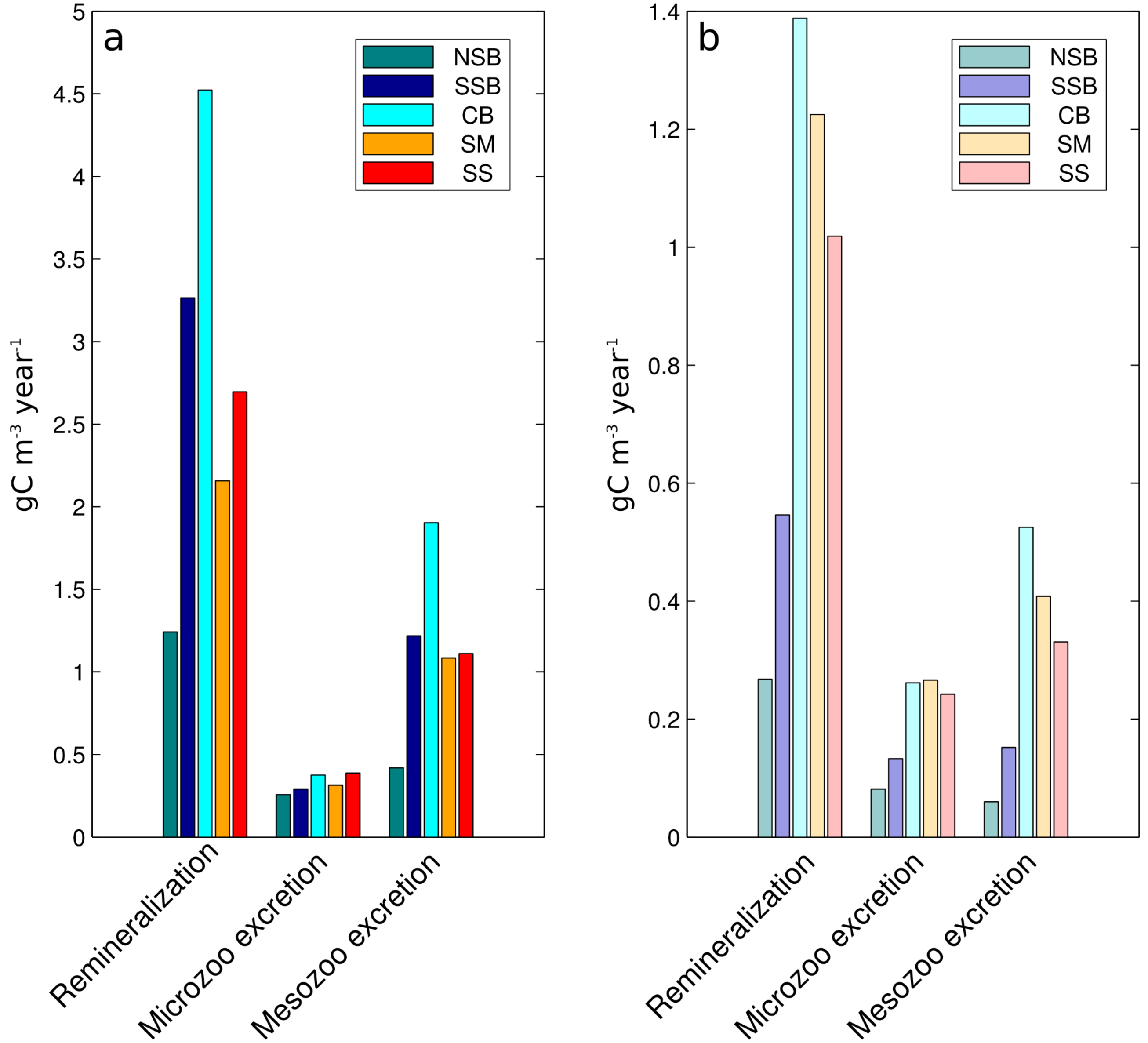

Figure 5: Remineralization rate of organic carbon (gC m^{-3} year^{-1}) through microbial activity and zooplankton excretion (micro- and mesozooplankton) (a) averaged annually in the coastal boxes and (b) over the spring period (March–May) in the offshore boxes. Each colour corresponds to a box (see legend): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

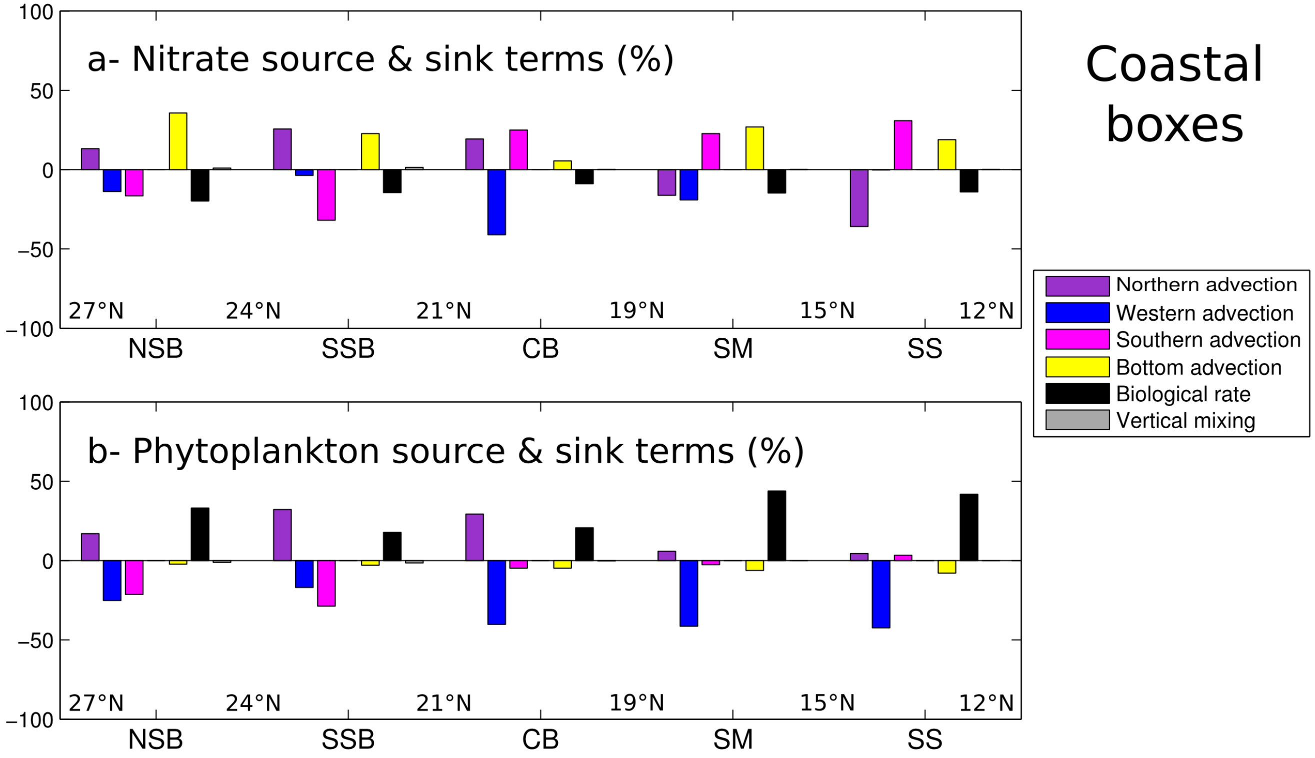

Figure 6: Annual mean contribution of the different source and sink terms of (a) nitrate and (b) phytoplankton biomass in the coastal boxes (%, positive inward): northern, western and southern horizontal advection, vertical advection and diffusion (vertical mixing) at the bottom and net local biological rate of change. From north to south: northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

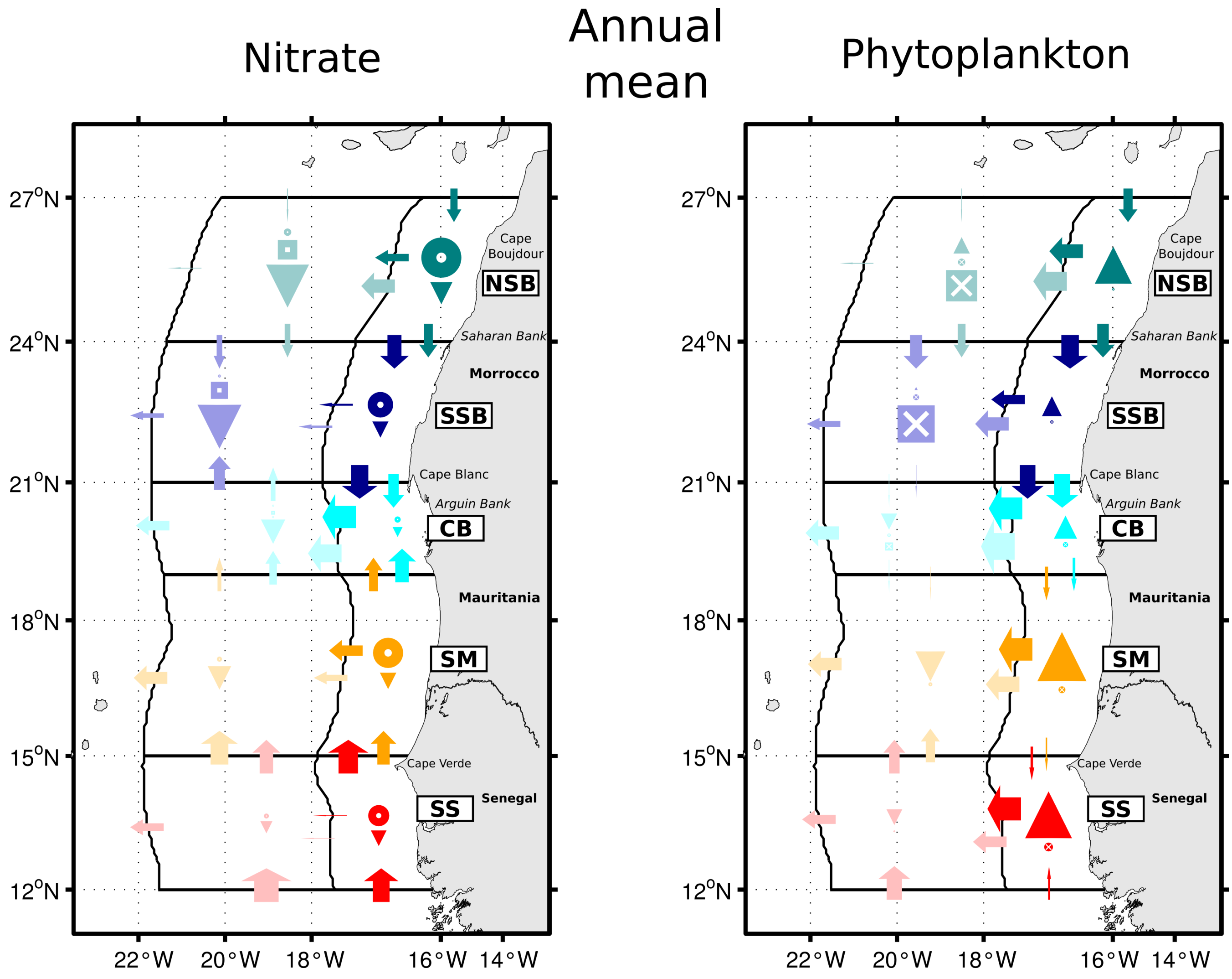

Figure 7: Schematic of the annual mean contribution of the different source and sink terms of nitrate and phytoplankton concentration within each box defined in this study. Each colour corresponds to a box (see legends in Fig. 2 for coastal and Fig. 8 for offshore boxes): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS). Arrows indicate horizontal advection, circles indicate vertical advection, squares indicate vertical mixing and triangles indicate biological processes. Within a circle or square, a white point indicates a source while a white cross indicates a sink; biological processes are a source/sink if a triangle heads upward/downward, respectively. The size of arrows, circles, squares and triangles indicates the magnitude of the contribution of each source/sink term. For coastal boxes, the information is equivalent to that given in Fig. 6.

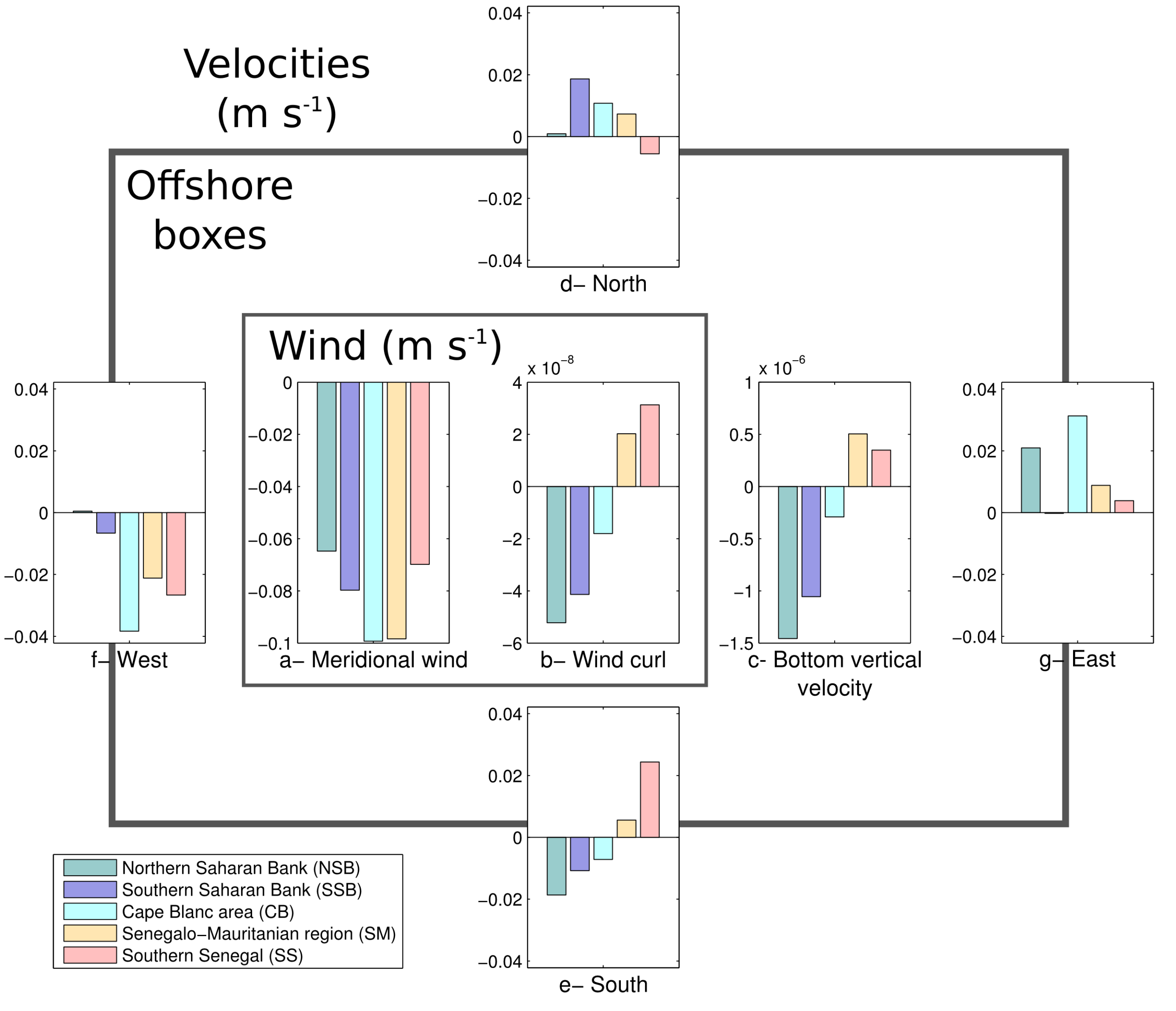

Figure 8: Spring mean (March–May) of (a) wind intensity (m s^{-1}) and (b) wind curl (s^{-1}) at the surface of the offshore boxes and (c) upwelling intensity (bottom vertical velocity, in m s^{-1}) within the offshore boxes and lateral velocities at the (d) northern, (e) southern, (f) western and (g) eastern boundaries (m s^{-1}). Vertical and lateral velocities are defined positive inward (so vertically upward). Each colour corresponds to a box (see legend).

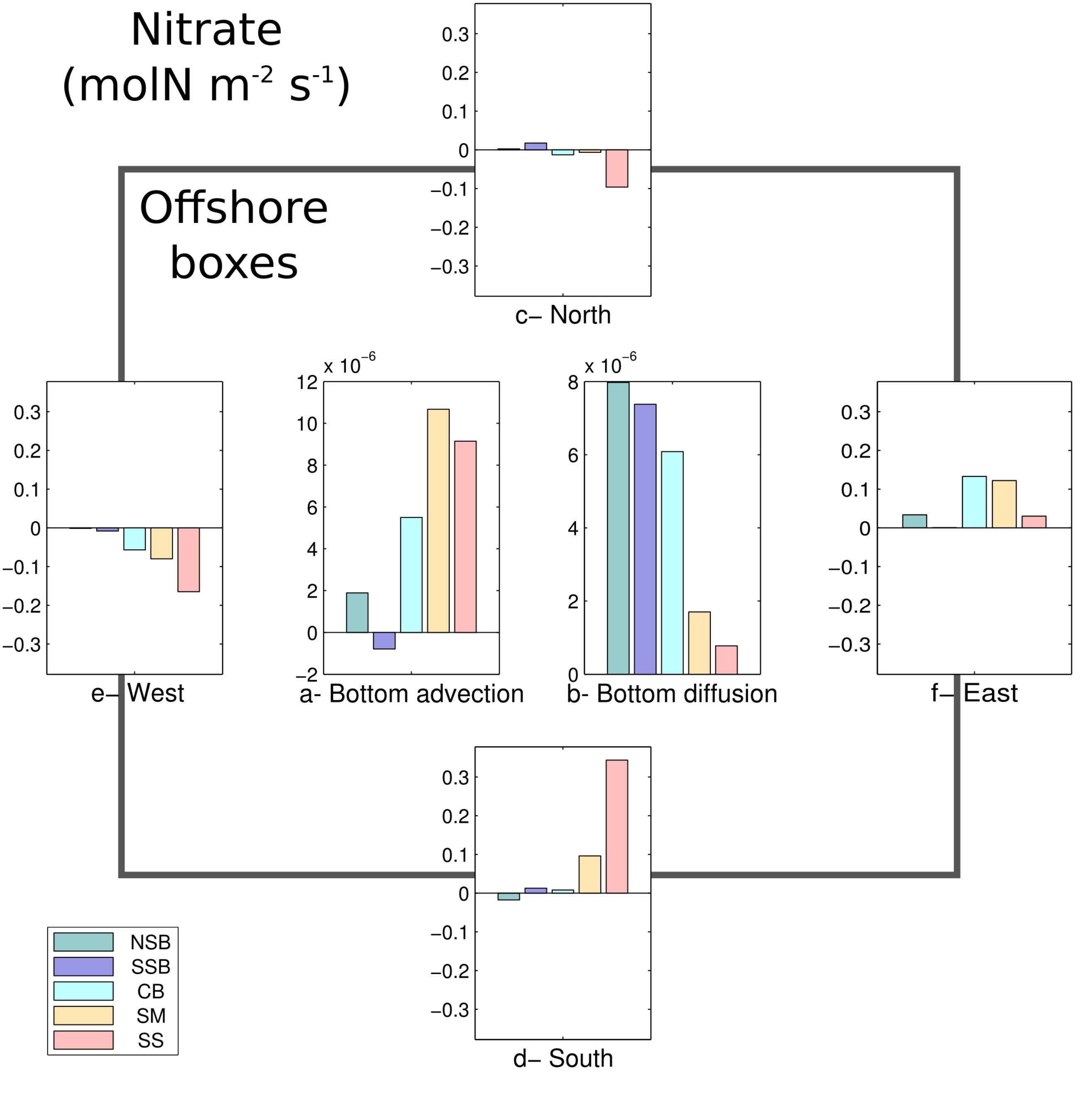

Figure 9: Spring mean (March–May) of vertical nitrate fluxes at the bottom of the offshore boxes by (a) advection and (b) diffusion (vertical mixing) and (c-d-e-f) lateral fluxes at the (c) northern, (d) southern, (e) western and (f) eastern boundaries (defined positive inward, so vertically upward) (molN m^{-2} s^{-1}). Each colour corresponds to a box (see legend): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

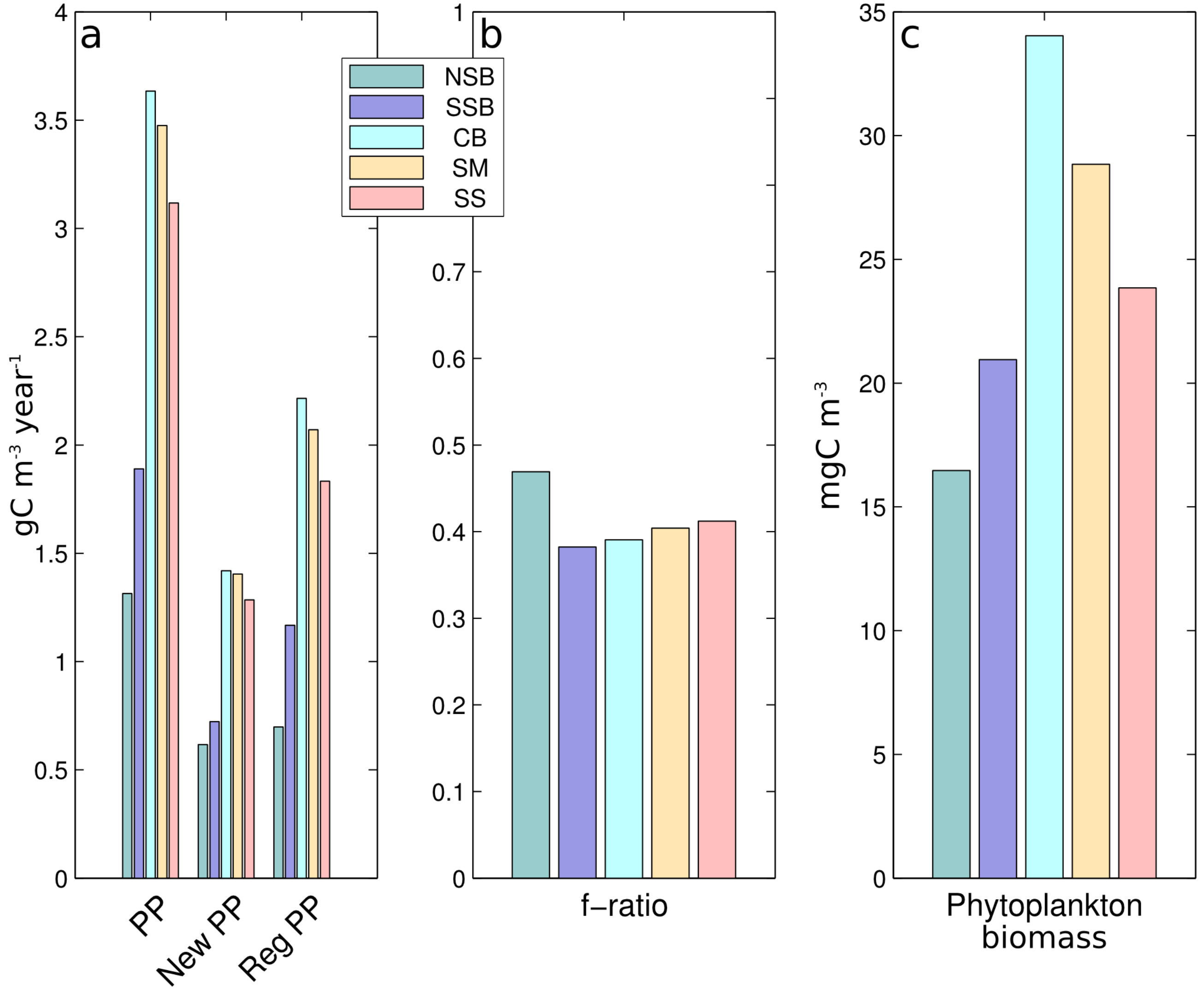

Figure 10: Spring mean (March–May) of (a) primary production (PP, gC m^{-3} year^{-1}), new production (gC m^{-3} year^{-1}) and regenerated production (gC m^{-3} year^{-1}), (b) f-ratio (new/regenerated production) and (c) phytoplankton biomass (mgC m^{-3}) in the offshore boxes. Each colour corresponds to a box (see legend): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

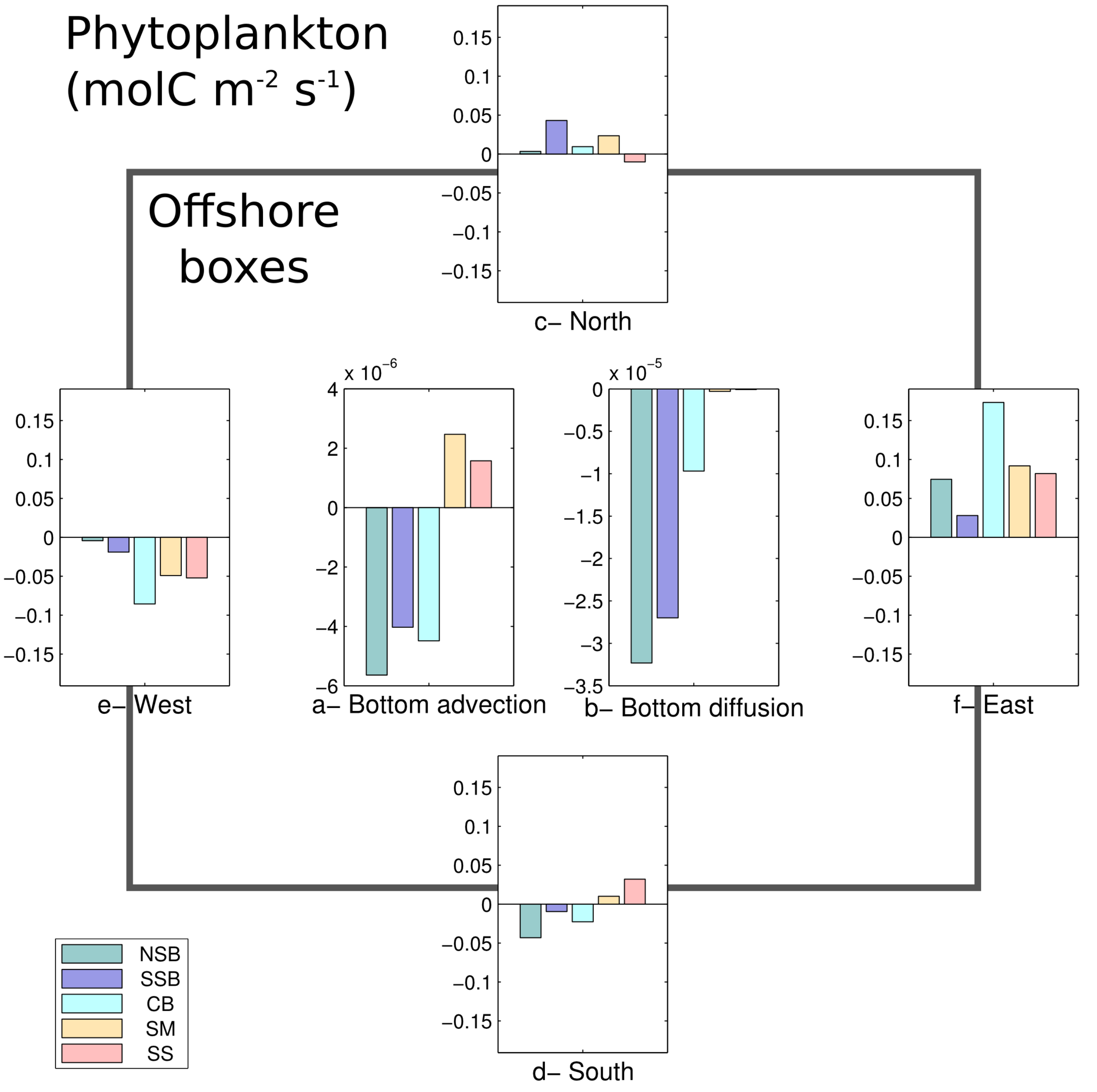

Figure 11: Spring mean (March–May) of vertical phytoplankton fluxes at the bottom of the offshore boxes by (a) advection and (b) diffusion (vertical mixing) and (c-d-e-f) lateral fluxes at the (c) northern, (d) southern, (e) western and (f) eastern boundaries (defined positive inward, so vertically upward) (molC m^{-2} s^{-1}). Each colour corresponds to a box (see legend): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

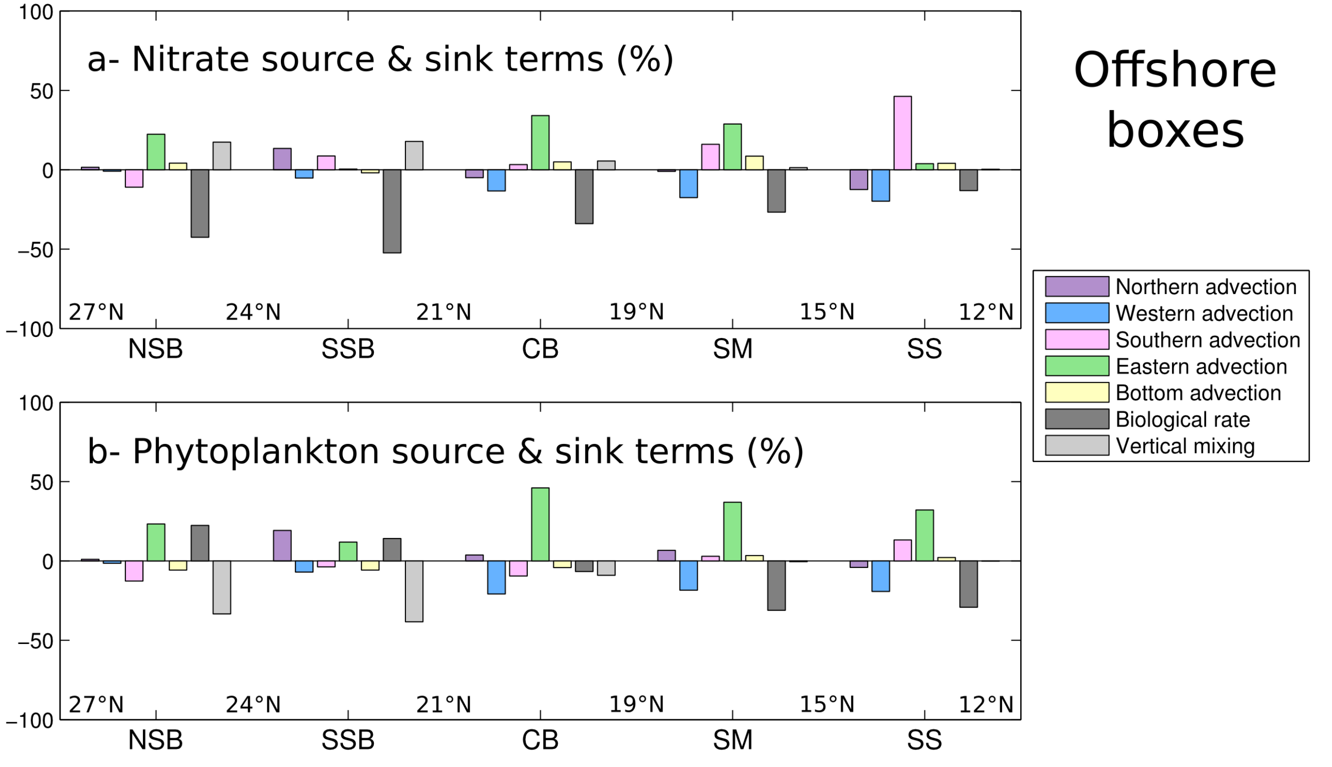

Figure 12: Spring mean (March–May) contribution of the different source and sink terms of (a) nitrate and (b) phytoplankton biomass in the offshore boxes (%, positive inward): northern, western, southern and eastern horizontal advection, vertical advection and diffusion (vertical mixing) at the bottom and the net local biological rate of change. From north to south: northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

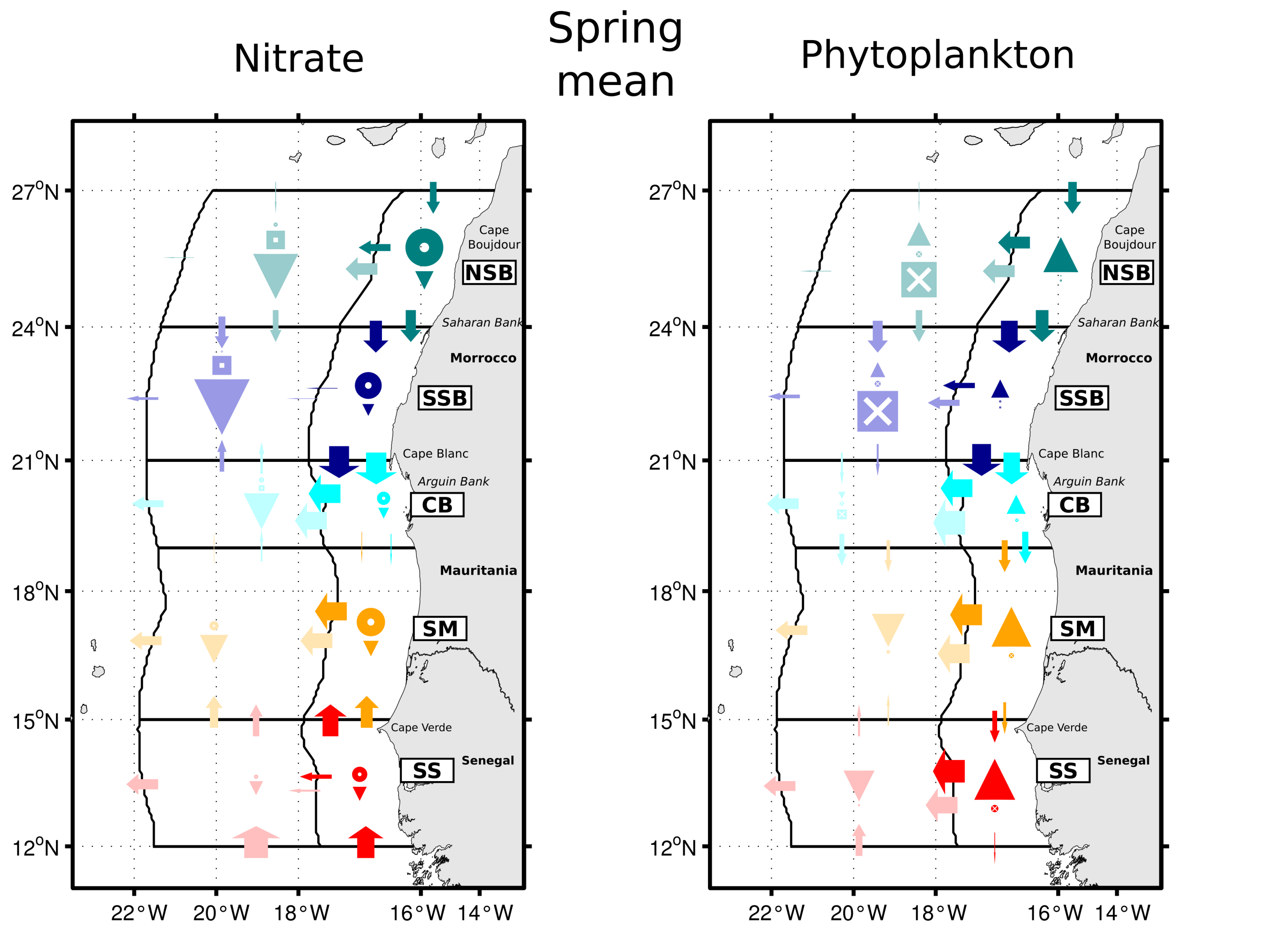

Figure 13: Schematic of the spring mean contribution of the different source and sink terms of nitrate and phytoplankton concentration within each box defined in this study. Each colour corresponds to a box (see legends in Fig. 2 for coastal and Fig. 8 for offshore boxes): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS). Arrows indicate horizontal advection, circles indicate vertical advection, squares indicate vertical mixing and triangles indicate biological processes. Within a circle or square, a white point indicates a source while a white cross indicates a sink; biological processes are a source/sink if a triangle heads upward/downward, respectively. The size of arrows, circles, squares and triangles indicates the magnitude of the contribution of each source/sink term. For offshore boxes, the information is equivalent to that given in Fig. 12.

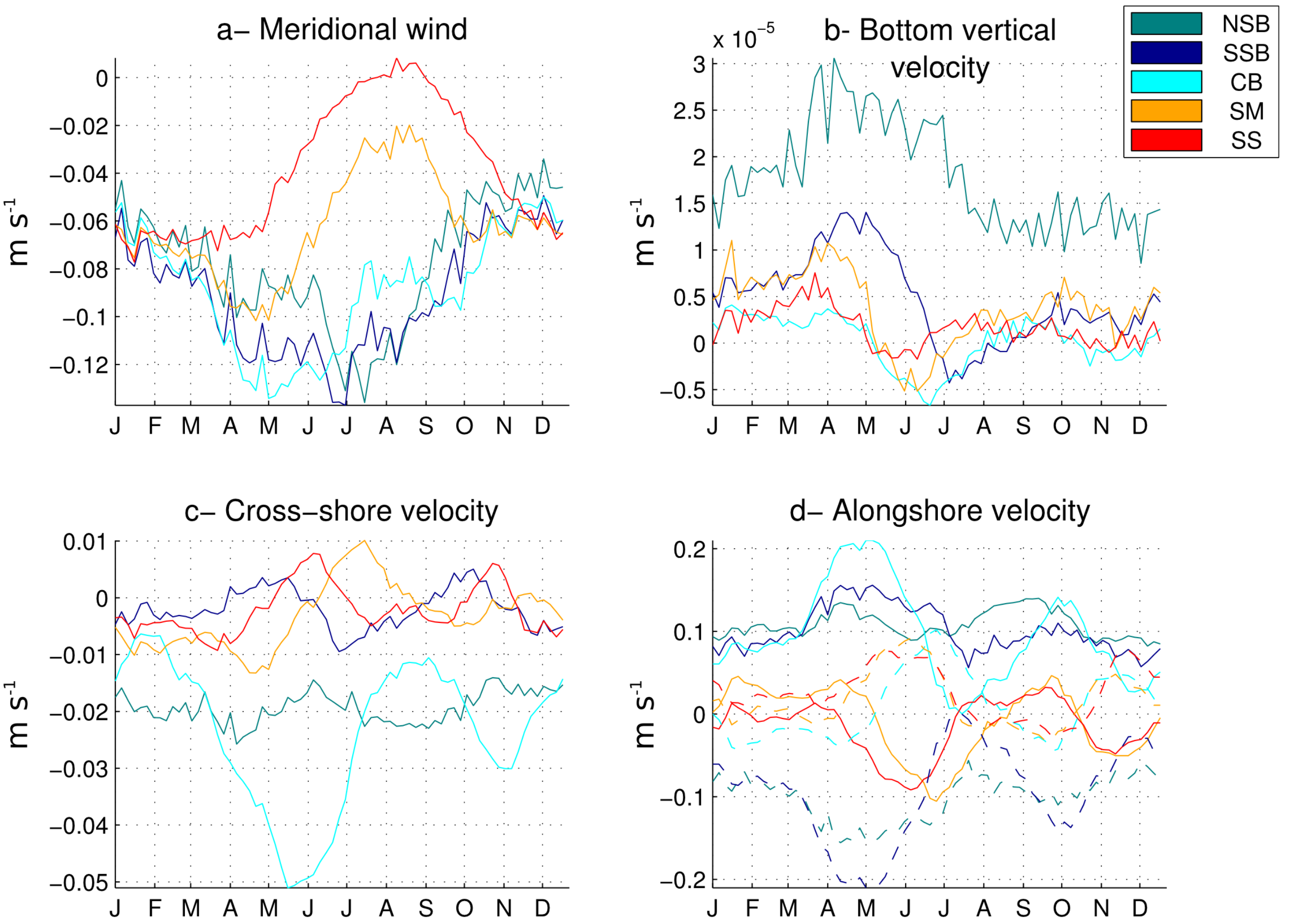

Figure 14: Seasonal climatology of (a) wind intensity (negative is upwelling-favourable, m s^{-1}), (b) bottom vertical velocity (m s^{-1}), (c) zonal velocities (m s^{-1}) and (d) meridional velocities (m s^{-1}) averaged within and over each edge of the coastal boxes (i.e. north, south, west and bottom ; defined positive inward, so vertically upward), respectively. In (d), a solid (dashed) line represents a velocity at a northern (southern) edge of a box, respectively. Each colour corresponds to a box (see legends in Fig. 2 for coastal and Fig. 8 for offshore boxes): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).

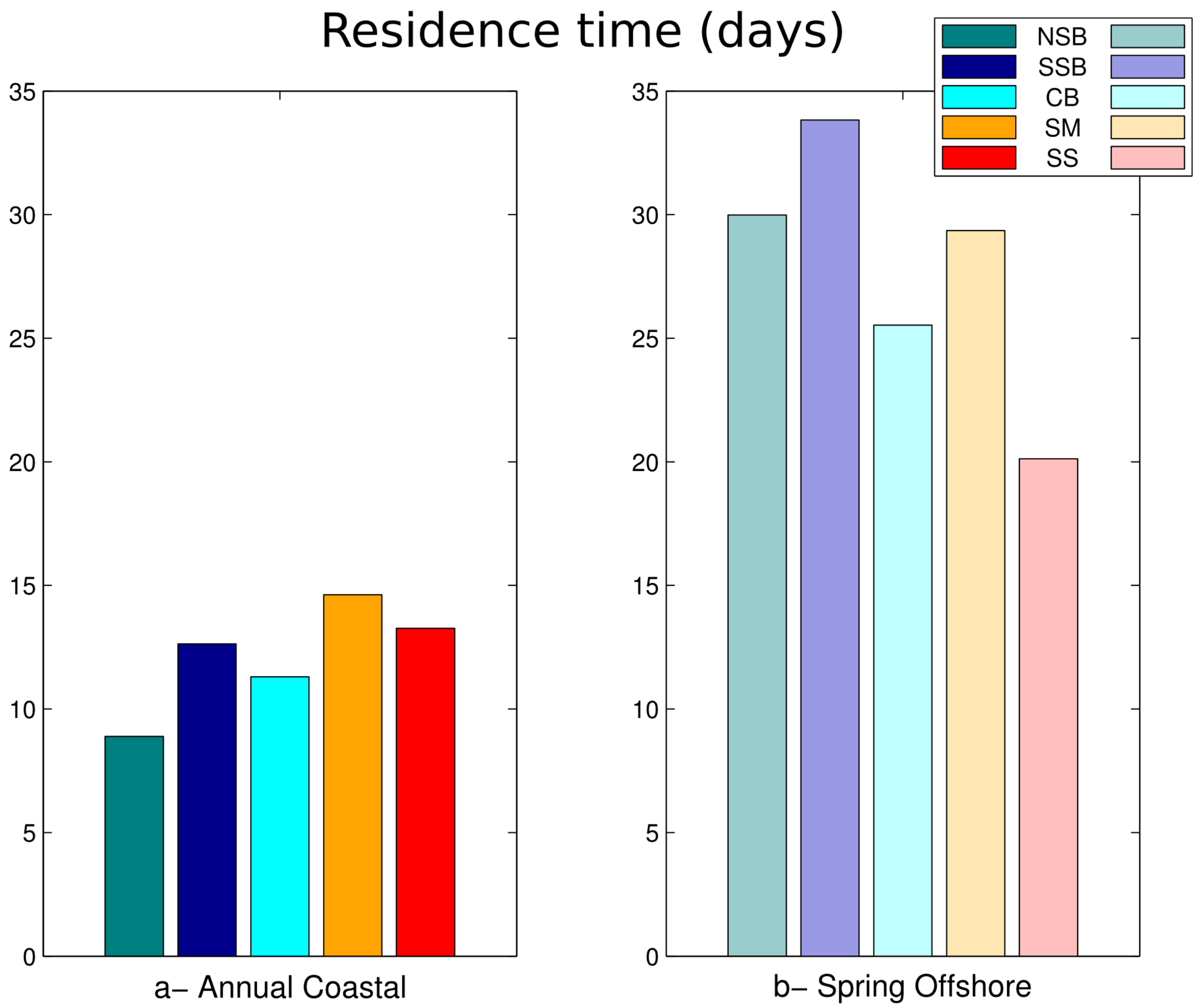

Figure 15: (a) Annual mean residence time (in days) of upwelled water masses in the coastal boxes and (b) spring average (March–May) residence time (in days) of upwelled water masses in the offshore boxes. Each colour corresponds to a box (see legends in Fig. 2 for coastal and Fig. 8 for offshore boxes): northern Saharan Bank (NSB), southern Saharan Bank (SSB), Cape Blanc area (CB), Senegalo-Mauritanian region (SM) and southern Senegal region (SS).