
MINOR REVISION

Thank you for your letter of response to the reviewers and for submitting a revised manuscript. The changes you have introduced solve some of the interpretation problems highlighted by the reviewers. While the information available is not sufficient to determine unequivocally the mechanism responsible for the lack of seasonality in integrated chla concentration, your comprehensive dataset is valuable and contributes to advance our understanding of the biological oceanography of subtropical pelagic ecosystems. I am therefore recommending publication of your manuscript in Biogeosciences, subject to minor revisions. Please take into account the editorial comments below when preparing the final version of the article.

(Authors' response) We thank the editor for his comments and for recommending the publication of the manuscript in Biogeosciences. All editorial comments have been taken into account and are presented below in a point-by-point manner. We would also like to draw your attention to the fact that Dr. Victor F. Camacho-Ibar is now in the list of authors of the paper. All former authors consider his contribution to be important and merits his inclusion as a co-author of the paper. We hope there is no problem in doing that. The acknowledgments section was changed accordingly.

(Editor) p. 2 line 3 Phrase 'the GOM, as a whole, is a contrasted trophic environment' is vague. What is a 'trophic environment'? Please re-write; if what is meant is that, overall, the region is oligotrophic, just say so.

(Authors' response) The sentence p. 2 line 3 was rewritten "*From a biogeochemical point of view, the deep waters of the GOM are considered oligotrophic (...)*" instead of **"***From a biogeochemical point of view, the GOM, as a whole, is a contrasted trophic environment. The deep basin and the continental shelf are considered oligotrophic (...)*".

(Editor) p.2 line 19: There are more recent studies highlighting the importance of changes in phytoplankton chlorophyll content: Behrenfeld et al. 2016 Nature Climate Change 6 323, Jakobsen and Markager (2016) Limnol. Oceanogr., 61: 1853–1868. Also the review by Halsey and Jones 2015 (Ann Rev Mar Sci) is relevant here. Note also that phytoplankton chla content changes not only in response to light, but is also sensitive to nutrient availability and temperature.

(Authors' response) We thank the reviewer for his suggestions. The references mentioned above were added in the manuscript, p.2 line 19.

(Editor) p.3 lines 4-5 What is measured here is fluorescence. Correct phrase is 'chlorophyll fluorescence', not 'fluorescence chlorophyll'

(Authors' response) "*fluorescence chlorophyll*" was replaced by "*chlorophyll fluorescence*".

(Editor) page 3, lines 12. Here authors should state which are those mechanisms.

(Authors' response) The sentence p.3 line 12 has been rewritten following editor's suggestions. *"(...) would be associated with a vertical redistribution of subsurface chlorophyll and/or photoacclimation processes."* instead of *"(...) would be associated with other mechanisms described and analyzed in the following sections."*.

(Editor) page 3 End of Introduction: remove ‘This is the most important result of our study’ (not informative).

(Authors’ response) The sentence was removed.

(Editor) page 4, lines 15-16. Confusing description of method. What is ‘above 0.9 times the mixed layer’? The MLD is a depth, say 50 m. Then 0.9 x 50 = 45 m. Would this mean that the value of CHL at 45 m is extrapolated to the surface? Please clarify, bearing in mind that ‘mixed layer’ is not the same as ‘mixed layer depth’.

(Authors’ response) We agree with the editor that the sentence is unclear. What we wrote in the manuscript meant to be “mixed layer depth”, not “mixed layer” and we thank the editor for noticing this confusion. Thus, p. 4, line 15-16, the sentence was rewritten: *“The method consists in finding, within the layer between the surface and 0.9 times the mixed layer depth (MLD), the highest FLUO value (FLUO$_{max}$) and its depth (FLUO$_{z,max}$). FLUO$_{max}$ is then extrapolated from FLUO$_{z,max}$ (considered as a proxy of the thickness of the layer potentially affected by the NPQ) up to the surface.”* Instead of *“The method consists of extrapolating the highest FLUO value, encountered above 0.9 15 times the mixed layer, up to the surface.”*.

(Editor) page 4 line 29 ‘timeS’

(Authors’ response) Done.

MAJOR REVISION

Dear Editor,

Please find below our responses to the questions and comments of the reviewers. To respond, some part of the paper were rewritten and additional methodological information, discussion and references, as well as a new figure, were added, hoping they will answer both reviewers concerns and provide a better interpretation of our results. Although the results we obtained are not fully conclusive, we are convinced that they provide a significant step forward with respect to previous knowledge of the chlorophyll variability in the Gulf of Mexico (GOM). We do emphasize that our conclusions apply to basin-scale climatological averages, and they are meant to explain what is seen in a typical year in the GOM as a whole. In the following, responses to the reviewers and related changes in the manuscript are presented (the numbering of lines or pages refers to the new version of the manuscript). We do note that most of the material presented here was already sent to the open discussion.

Reviewer #1

(Reviewer) This manuscript examines estimates of the temporal and spatial distribution of chlorophyll concentration estimates in the Gulf of Mexico derived from eight profiling floats. These floats provided chlorophyll estimates by in vivo fluorescence. The authors have therefore collected a novel dataset. The primary objective result of the paper is that the spatial and temporal patterns of surface chlorophyll concentrations derived from the profiling buoys confirms the temporal and spatial chlorophyll estimates observed by ocean color satellites since the late 1970's, and published on extensively. They confirm the seasonal deepening of the surface mixed layer depth in northern winter, in the interior of the Gulf of Mexico, and shoaling in summer. This has also been published on extensively. The causes for the seasonal surface increase and decrease in chlorophyll, and the spatial patterns defined by circulation have been also explained extensively in the literature over the past 20+ years. So, in general, the paper finds similar temporal and spatial patterns (i.e., associated with circulation features) in the Gulf of Mexico as have many other people in the past. The paper is well written in the sense that it flows well, has good prose, and is written in good English. Yet there are several problems with the paper, which may be serious enough to warrant a very deep revision and withholding publication.

(Authors' response) We thank Referee #1 for his/her review and comments. Our intention in this manuscript was to address the basin-wide seasonal average of chlorophyll concentration in the water column (not only at the surface), which is, to our knowledge, not well documented in the GOM. We agree that this data set confirms some of the main aspects of what is known about the seasonal variability of surface chlorophyll. However, this study yield the first (and to our knowledge the only one) description of the seasonal dynamics of the vertical distribution of the chlorophyll concentration ([CHL]) in the GOM, at a basin scale.

The reviewer suggests there are some serious problems in our paper. We address all the reviewer comments and criticisms in detail below, hoping they will answer the reviewer concerns and provide a better interpretation of our results.

For example, I don't understand what the authors did to compute near-surface chlorophyll concentration from the float data. They say that they took the fluorescence profile, found the highest FLUO value found above 0.9 times the mixed layer depth (MLD) and extrapolated this to the surface (as per Xing et al., 2012). They calibrate this against an ocean color satellite-derived estimate of chlorophyll concentration multiplied times 1.5 the estimated euphotic depth.

(Authors' response) Indeed, the first step of the procedure is to correct profiles for non-photochemical quenching (NPQ). We applied the method of Xing et al. (2012) which is actually implemented in the international BGC-Argo program and consists of extrapolating the highest fluorescence value encountered within the mixed layer up to the surface. Once the fluorescence profile is corrected from the NPQ, we determine instrumental gain and offset using ocean color satellite-derived estimates of chlorophyll concentration. For the comparison against satellite-derived estimate of chlorophyll concentration, the whole 1.5 euphotic layer is used instead of only surface records to minimize the error that would be induced by a wrong NPQ parameterization. Note that the whole procedure is described in detail in Lavigne et al., (2012) paper. So, our near-surface chlorophyll concentration estimates are based on currently accepted international standard procedures (see answer below too).

To make these points clearer, the methodological section was rewritten in page 4, from L.14 to L.19.

In addition, page 4, L.31-32, the sentence *"For the comparison, the whole 1.5 euphotic layer was used instead of only surface records to minimize the error that would be induced by a wrong NPQ parameterization."* was added.

(Reviewer) One problem with this approach is that they make the same assumption of Xing et al (who did a study in the Southern Ocean) that the vertical profile of chlorophyll observed is largely due to quenching of fluorescence, and that the deep chlorophyll maximum (DCM) is therefore not ’real’. The authors probably know that there are data collected and published since the 1960’s-1970’s to show that the DCM in the Gulf of Mexico is real and seasonal. I wonder if the XIXIMI-2 (July 2011) and XIXIMI-3 (February-March 2013) cruises used by the authors to obtain more than 900 water samples from 74 profiles also had some chlorophyll data? There are DNA profiles, bacterial profiles, and actual spectrophotometric and HPLC observations that show that the DCA is real and not simply an in vivo chlorophyll fluorescence quenching artifact, as the authors observed.

(Authors’ response) We are aware that the calibration/interpretation of fluorescence measurements is critical, and this is why we paid a great deal of attention to the calibration of the data in the manuscript (section 2.2). The Xing et al. (2012) procedure has been validated and applied in various regions (e.g. BATS, HOT, DYFAMED) where a DCM is present. The relevance of the NPQ correction in these conditions/regions was specifically assessed in Lavigne et al (2012) which shows it has a positive and significant impact on the estimates of chlorophyll. That is the reason why we chose the Xing et al (2012) method for our study.

We would like to point out that we do not say that the DCM is not real or does not exist in the Gulf of Mexico. Quite the opposite, the manuscript shows how this DCM varies in concentration and depth both for the entire time series (Fig. 3) as well as seasonally in the climatological averages shown in Table 2. In fact, the NPQ correction only concerns the mixed layer and as a consequence, the impact of the correction on the fluorescence profile is generally limited to the surface and does not impact the observed DCM (except on the occasions when the mixed layer is deep enough to reach the DCM. Note that during XIXIMI cruises no HPLC observations were made.

To clarify this point, the next sentence was added, in section 2.2, page 4, L.19-20: *“The relevance of this NPQ correction in oligotrophic areas was specifically addressed in Lavigne et al., (2012) which showed it has a positive and significant impact on the estimates of chlorophyll.”.*

(Reviewer) It is not clear to me whether the constant CHLtot seasonal cycle that they find is an artifact of the way they computed the vertical profile with the quenching correction.

(Authors’ response) The vertically integrated chlorophyll ($[CHL]_{tot}$) depends largely on the chlorophyll content at the DCM. Hence, the contribution of the NPQ correction (which is limited to the mixed layer) is small. This can be verified in Fig. 1 below, which shows times-series from one float (float number 02 in the submitted manuscript) with and without the NPQ correction. One can see the constant [CHL]tot seasonal cycle is not an artifact of the NPQ correction.

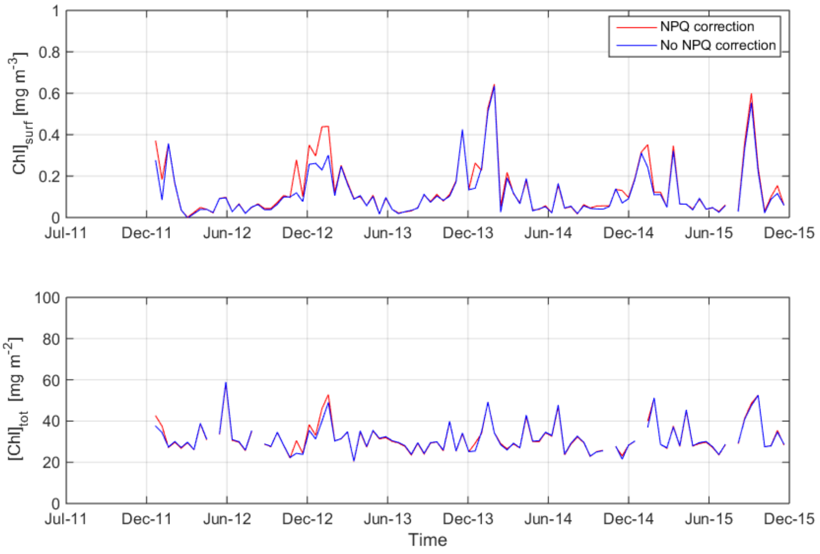

Figure 1. Float 02 time-series of the (top) mean surface chlorophyll concentration and (bottom) integrated content of chlorophyll over the 0-350 m layer.

(Reviewer) It seems a major flaw in this paper is the conclusion that: "the present dataset reveals a vertically integrated content of chlorophyll which remains constant throughout the year, suggesting that the surface increase results from a vertical redistribution of subsurface chlorophyll or photoacclimation processes, rather than a net increase of primary productivity."

(Authors' response) The reviewer is absolutely right. The sentence in the abstract "... *the present dataset reveals a vertically integrated content of chlorophyll which remains constant throughout the year, suggesting that the surface increase results from a vertical redistribution of subsurface chlorophyll or photoacclimation processes, rather than a net increase of primary productivity*" is wrong. We thank the reviewer for noticing that, and the term primary production was changed to biomass, which is what we actually meant and missed to correct before submitting. Note that this was correctly stated in our conclusion number 3.

The sentence in the abstract, page 1, L.17-19, is now: *"... the present dataset suggests that the basin scale climatological surface increase in chlorophyll content results from a vertical redistribution of subsurface chlorophyll and/or photoacclimation processes, rather than a net increase of biomass."*

(Reviewer) The problem is that the integrated water column productivity of a water column with a DCM is not the same as that same water column under a "spring bloom" condition, when phytoplankton biomass is high throughout the mixed layer. The literature is replete with actual measurements of primary productivity that show this. In my opinion, the ecological and biogeochemical interpretation that biomass is the same as productivity is a fatal flaws for this paper. The authors need to go back and fully investigate what mixing can do to phytoplankton blooming in the ocean. They need to review what chlorophyll represents (a crude index of biomass), what productivity is (a rate), and what other factors may play a role in changing these over time and space.

(Authors' response) We fully agree with the reviewer that chlorophyll is only an index of biomass which is not the same as productivity and regret some confusions made in the manuscript. In the revised version, we are careful to describe fluorescence measurements as a proxy of chlorophyll concentrations, and then to discuss these data (with respect to backscattering measurements) solely in terms of biomass. Primary production (and more precisely new primary production), is now evoked only when nutrients fluxes are estimated (section 3.3), with the aim to discuss it as a hypothesis and/or a possible mechanism (not as a direct result of chlorophyll measurements).

In order to make these points clearer, substantial changes were made in the new version of the manuscript:

The section 3.1 was deeply rewritten from page 7, L.28 to page 8, L.28, and, in particular, the next sentences were added (from page 7, L.32-33 to page 8, L.1-2) to stress what chlorophyll represents *"… one may wonder how much of the phytoplankton chlorophyll variability is reflective of true changes in total biomass in the entire water column. Indeed, it is well known that the [CHL] is not a sole function of phytoplankton biomass and depends on several other factors, such as photoacclimation processes (e.g. Geider, 1987).".*

Section 3.3.2 page 11, L.9, *"… does not necessarily reflect a real increase …"* Instead of *"… does not reflect a real increase …".*

Section 3.3.2, sentences *"This is in full agreement with results obtained from [CHL]. Thus, the idea that winter production in the GOM is enhanced in winter by new nutrients availability may be a misconception."* were removed.

Section 3.3.3, page 12, L. 3 "*…a higher chlorophyll concentration was measured…* " instead of *"… a higher biomass concentration was measured…".*

Section 3.3.3 page 12, L.18 "… *the observed enhanced [CHL] and biomass* …" instead of "… *the observed enhanced biomass* …".

Given that it implies of lot of suppositions and that it does not add significant information in Section 3.3.3. the sentence *"Nevertheless, we can note that the estimated NPP in CG is higher than in AG by a factor 1.13 ± 0.02, on average, which is surprisingly close to the mean [CHL]tot ratio between CG and AG (1.15 ± 0.08)."* was removed.

Conclusion number 4, the sentence *"This result stands in contradiction with the current paradigm of an enhanced primary production in winter, triggered by nutrient input through vertical mixing …."* was removed.

Conclusion number 8 page 13, L.27, "*the mechanisms controlling biomass variability and primary production in the GOM.*" instead of *"…the mechanisms controlling primary production in the GOM.*"

(Reviewer) What is amazing is that the authors consider past biological oceanographic studies and conclusions of observations in the Gulf of Mexico to be 'beliefs', and proceed to completely misinterpret the chlorophyll signal they observe.

(Authors' response) We agree the term is not appropriate. We were trying to emphasize the fact that, in the GOM, the seasonal cycle of chlorophyll, at a basin scale, has been almost exclusively addressed using satellite measurements, which only provide surface information.

Sentences in questions were rewritten to make clear we are just comparing our results and hypothesis with others studies, not disregard them.

In the abstract, page 1, L.16-17 "*a possible interpretation*" instead of "*current belief*".

In the introduction, page 2, L.13 "*it has been suggested*" instead of "*it is currently thought*".

In the introduction, page 3, L.10-12 "*Our analysis indicates that at a basin scale, the winter surface [CHL] maximum in the GOM may not necessarily be produced by a biomass increase, but would be associated with other mechanisms …*" instead of "*In contrast to common belief, our analysis indicates the winter surface [CHL] maximum in the GOM is not produced by a biomass increase, but by other mechanisms …*".

(Reviewer) They interpret their observations to mean that there are no water-column integrated changes in chlorophyll AND in primary productivity in the Gulf of Mexico. This is clearly a gross misinterpretation of the crude biomass index data they collected. The authors did not exploit the data to make inferences on primary productivity (e.g. perhaps by looking at hour-to-hour and day-to-day changes in biomass). The authors should note that estimates of primary productivity and of chlorophyll concentration are also out of phase in time in the Gulf of Mexico. This has also been reviewed in the literature.

(Authors' response) As we answered above, we agree that we can only address biomass with chlorophyll data, and modifications have been done to make it clearer in the manuscript (see comment above). We indeed observed that the integrated content of chlorophyll does not show a clear seasonal variability, which we interpret as total biomass remaining constant throughout the year at monthly timescales (which is consistent with the analysis of the bbp data shown in the supplementary material). In addition, the temporal resolution of our floats measurements (14 days) prevented us to infer hour-to-hour and day-to-day changes in biomass to estimate in an appropriate manner primary production.

(Reviewer) Another problem is the interpretation of nutrient data. The authors have a rich nutrient dataset with the density data computed from the buoy profiles and the nutrient data from the XIXIMI-2 (July 2011) and XIXIMI-3 (February-March 2013) cruises. The analysis of the density vs. nutrient data is very nice. The problem starts when the authors interpret the nutrient profiles in a biogeochemical and ecological manner. They assume that simply because we see a winter-time increase in chlorophyll concentration in the mixed layer, there also needs to be a clear, measureable signal in nutrient concentrations. Since they don't see this, they conclude that "there are no significant inputs of nutrients by vertical mixing to sustain significant winter new primary production (NPP)". This is incorrect. Nutrients will not be measurable as they are taken up by the phytoplankton. This has been published over and over in the course of the past half century or longer.

(Authors' response) We agree with the reviewer's comment that "Nutrients will not be measurable as they are taken up by the phytoplankton" (see e.g. page 11, L.19-20 in the manuscript). To make this point clearer, we made the following modifications:

Section 3.1 page 8, L.26-28, "*the mixed layer in winter, although sufficiently deep to reach the DCM, would be, nonetheless, insufficient for bringing up large quantities of nutrients and support a significant net increase in phytoplankton biomass*" Instead of "*the mixed layer in* *winter is sufficiently deep to reach the DCM but nonetheless insufficient for bringing up nutrients*".

Section 3.3.2, page 11, L.11-15, was rewritten "*... Z_N is always found at depth and does not show a clear seasonal pattern (regardless of the group). In addition, the climatological winter mixed layer is generally shallower than the nitracline (Fig. 5). Hence if we assume that large inputs of nutrients can only be expected when the MLD reaches below the average nitracline depth (Z_N), it is likely that nutrients injections to the photic layer by vertical mixing are low on average, even in winter*." instead of "*... Z_N is always found at depth (regardless of the group) and never approaches the surface, even in winter. This result means that there is no NN accumulation in surface waters and that the deep nutrient reservoir is always isolated from the surface layer ...".*

Section 3.3.2, page 11, L.21-23, "*Thus, apart from sporadic and rather localized events, it seems likely that large supplies of nutrients to the surface layer are not that common in winter in the GOM as a whole, since the basin scale, monthly climatological basin-scale averages of the MLD are shallower than the estimated depth of the nitracline"* Instead of *"it is likely that on average, there are no significant inputs of nutrients by vertical mixing to sustain significant winter new primary production (NPP)."*

Section 3.3.2, sentences *"This is in full agreement with results obtained from [CHL]. Thus, the idea that winter production in the GOM is enhanced in winter by new nutrients availability may be a misconception."* are removed.

Conclusion number 4, page 13, L5-11 was rewritten: "*In addition, our observations show that the winter mixed layer is generally not deep enough to reach the nitracline. The sampling, however, only allows to reach conclusions in a broad sense. Therefore, we suggest that, on a climatological basin-scale average, a relatively small amount of nutrients are potentially injected to the surface layer through vertical mixing. This does not discard the fact that at short time-scales (days to weeks), events may result in high nutrient inputs to the photic layer which translate in a local phytoplankton bloom, particularly during winter storms. Our interpretation is that the net effect of those blooms is not big enough to determine the basin scale averages of surface chlorophyll content, hence nutrient supply by winter mixing is not necessarily the main cause of the seasonal, basin-scale variability of surface chlorophyll content.*".

(Reviewer) The authors seem to somehow dismiss biological oceanography theory in general, including historical knowledge of patterns of vertical distribution of chlorophyll concentration, how these vary in time, and how all this and oceanographic conditions (both biotic and abiotic) affect primary productivity.

We have not found literature which addresses the seasonal variability of the vertical distribution of chlorophyll in the Gulf of Mexico. Indeed, in the 90s Muller- Karger et al., (1991) stated: *"(. . .) in situ oceanographic data set for the Gulf of Mexico is still insufficient to address questions and processes affecting the distribution of biological and chemical properties.*" and recently (Muller-Karger et al., 2015): "*The waters of the interior of the Gulf of Mexico seaward of the continental margin continue to be seriously undersampled. (...). We were not able to derive a good chlorophyll concentration dataset from historical field observations archived at the NOAA NODC to compare with either CZCS, SeaWiFS, or MODIS chlorophyll estimates. Most samples in the Gulf of Mexico available at the NODC are from the northern and eastern shelf regions, with relatively few samples available from offshore waters. Thus, information derived* *from remote sensing is essential for characterization of the deep water areas of the Gulf*." Moreover, we are not aware of studies showing mixed layer depth climatologies based on direct measurements for the Gulf of Mexico either, since the ones available are indirect estimates based on models or parametrizations (Mandoza et al., 2005; Muller-Karger et al., 2015; Zavala-Hidalgo et al., 2014).

In this paper we specifically focused on the measured MLD and considered the ecosystem from a bottom-up perspective. We agree that biomass is regulated by a wider range of processes (e.g. biotic processes) which are not directly addressed in our manuscript since to answer these questions would require other measurements that were not at our disposal. This is a limitation to our work which we were careful to mention in the manuscript (section 3.3.3 page 12 lines 20-23, and conclusion 7 page 13, L.9-13). Hence, we consider that the new measurements of water column chlorophyll and bpp seasonal variability invite to new hypotheses that are worth exploring.

To clarify, a conceptual diagram has been added in the revised manuscript (Fig. 8) to outline the processes we are addressing (MLD and mesoscale) and their impact on the vertical distribution of the [CHL] in the GOM.

(Reviewer) The reference: Heileman, S., and Rabalais, 2009, cited to provide a reference on the productivity of the Gulf of Mexico is not a reference for the characterization of productivity in the Gulf. It does not provide summary data. The authors should cite where the actual productivity data comes from that they use to characterize productivity in the Gulf of Mexico.

(Authors' response) In the new version of the manuscript, the reference Heilman and Rabalais (2009) is not used anymore to characterize primary production in the GoM.

The paragraph in the introduction, page 2 L.3-8 was partially rewritten and two references (with the corresponding estimates of primary production) were added: "*From a biogeochemical point of view, the GOM, as a whole, is a contrasted trophic environment. The deep basin and the continental shelf are considered oligotrophic and nutrient-limited being relatively isolated from coastal and eutrophic waters (Heileman and Rabalais, 2009). In deepwater GOM, historical in situ measurements indicate low biological productivity* (< 150 mgC m^{-2} d^{-1}) *and low surface chlorophyll concentration (hereafter* $[CHL]_{surf}$) *with values ranging from 0.06 to 0.32 mg* m^{-3}, *and being 2-3 times higher in subsurface waters (Biggs and Ressler, 2001; El-Sayed, 1972; Koblenz-Mishke et al., 1970).*" Instead of "*From a biogeochemical point of view, the GOM, as a whole, is a moderately high productivity ecosystem* (< 300 gC m^{-2} yr^{-1}) *with a contrasting trophic environment (Heileman and Rabalais, 2009). The deep basin and the continental shelf are considered oligotrophic and nutrient-limited being relatively isolated from coastal and eutrophic waters (Heileman and Rabalais, 2009). In situ measurements indicate surface chlorophyll concentration (hereafter* $[CHL]_{surf}$) *ranging from 0.06 to 0.32 mg* m^{-3}, *with [CHL] 2-3 times higher in subsurface waters (Biggs and Ressler, 2001).*"

(Reviewer) The authors do this often– they cite relatively recent references (in the decade of the 2000's). When they cite earlier literature, they do this in passing and in a dismissive manner, not fully acknowledging that many of the points treated in this paper has already been discussed and explained previously. The problem is that, in doing this, they miss important background knowledge about the oceanography of the Gulf of Mexico.

(Authors' response) A total of 9 references were added in the introduction (see response above) and in section 2.5 and 3.2.

(Reviewer) Also, the authors cite studies by Behrenfeld et al (2005), Mignot et al (2014), etc. as suggesting that all temporal changes in chlorophyll observed by satellite are due to changes in pigment concentration in phytoplankton cells. This may be part of what happens, but it is not an accurate characterization of the changes that occur in the Gulf that they measured.

(Authors' response) We agree with the reviewer that the observed changes may not only be due to photoaclimation, and we do not state that this is the only relevant processes involved (see our discussion in section 3.1, page 8, L9-25, and our conclusion number 7). However, this new dataset suggests that photoacclimation may be relevant and worth exploring. The above references of Behrenfeld et al., (2005), Mignot et al., (2014) are in the discussion to support this hypothesis.

To make it clearer, following changes were made:

Section 3.1 page 8, the section was deeply rewritten (see our response above). In particular the discussion about the relevance of the different mechanisms that could lead to a winter $[CHL]_{surf}$ increase without a similar trend in $[CHL]_{tot}$, was developed (page 8, from L.9 to L.28).

Reviewer #2

(Reviewer) The manuscript Temporal variability of chlorophyll distribution in the Gulf of Mexico: bio-optical data from profiling floats by Pasqueron De Fommervault et al. attempts to evaluate the temporal and spatial variability of chlorophyll concentration in the Gulf of Mexico. The study utilises data from eight bio-optical profiling floats. The paper addresses the winter increase in sea surface chlorophyll concentration and the impact of mesoscale eddies on phytoplankton biomass in the Gulf of Mexico. This is done by applying already published methods to a rather new dataset. The problem is that, most of the time, the methods cannot be applied or are not applied correctly. Consequently, most of the results presented in the manuscript are flawed. Additionally, the manuscript is poorly written, the arguments are hard to follow, and often not justified by the appropriate references. The amount of work needed for publication in Biogeosciences is considerably more than for a major revision.

(Authors' response) We thank Referee #2 for his/her review and comments. The major criticisms are related to methodological issues that prevent, according to the reviewer, an accurate analysis of our dataset. Below, we address and discuss all the comments hoping they will clarify our work and answer the reviewers' concerns. Additional references and figures are also presented. The comment that the manuscript is poorly written and the arguments hard to follow is difficult to address since no specifics are provided. We however added a conceptual diagram in the revised manuscript (Fig. 8) hoping it will make the arguments easier to follow.

One of the conclusion of the manuscript is that the winter increase in sea surface chlorophyll concentration is due a photoacclimation process or a reentrainment of phytoplankton cells at depths. I felt like the authors have chosen to copout on testing one hypothesis over another. The authors have all the data necessary to investigate what causes the winter increase in sea surface chlorophyll concentration Gulf of Mexico. They need to do more than just commenting on the float observations.

(Authors' response) In the manuscript it is suggested that the winter surface chlorophyll increase could result from (i) photoacclimation within the mixed layer (ML) due to a reduction in average light availability, and/or (ii) from mixing of the deep chlorophyll maximum (DCM) into the ML. Processes involved in (i) are considered on a seasonal basis. The hypothesis is that during the winter mixing period, the average light intensity for phytoplankton is reduced in the ML with respect to summer conditions leading to an increase of intracellular chlorophyll content. Since, on average, a low bbp/[chl] ratio at the surface is persistent in winter, this hypothesis seems reasonable to explain the variability observed in surface. Hypothesis (ii) supposes that low-light acclimated cells from the DCM are transported to the surface by mixing process, thus increasing the bbp/[chl] ratio at the surface. Considering only (ii) assumes that phytoplankton cells do not have time to re-acclimate to their new light environment (hours to days processes). So it is not warranted to test (ii), given the temporal resolution of our floats (two profiles per month from each float. We do not think the data have enough temporal resolution to determine what causes the winter increase in surface chlorophyll. That is the reason why we are cautious and suggest that is difficult to attribute the observed changes in chlorophyll to only one mechanism and suggest/speculate possible mechanisms. However we fully agree with the reviewer that this point would require a deeper discussion.

Accordingly, all the section 3.1 was rewritten and, in particular, the discussion about the relevance of both mechanisms (page 8, L.9-28) was detailed.

In addition in the abstract, page 1, L. 19 "… *a vertical redistribution of subsurface chlorophyll <u>and/or</u> photoacclimation processes."* Instead of *"… a vertical redistribution of subsurface chlorophyll <u>or</u> photoacclimation processes.".*

In the conclusion number 3, page 13, L. 4 *"…a vertical redistribution of chlorophyll <u>and/or</u> photoacclimation processes, rather than a true biomass increase*." Instead of *"…a vertical redistribution of chlorophyll <u>or</u> photoacclimation processes.*".

(Reviewer) The authors use the depth of the 6C isotherm to classify the eddies in the Gulf of Mexico. They argued that this isotherm has a mean depth of 795 m and that Bunge et al (2002) found that this isotherm separates the deep stable water from the eddy-influenced surface water. Finally, it is said that Hamilton et al. 2017 found a strong correlation between the isotherm and upper layer eddies. First, Bunge et al. (2002) did not identify eddies with this isotherm. It was used to delineate the depth of the Loop Current in the Yucatan channel. Consequently, the use of the 6C isotherm to identify mesoscale eddies cannot be justify by this reference. Second, the vertical extent of eddies core is comprised, in average, between 300 and 400 m. What is the rationale of using such a deep isotherm to detect eddies that impact the first 400m of the water column? Third, the authors claimed that Hamilton et al. (2017) found a correlation between mesoscale eddies and the 6C isotherm. However, this reference seems to be an oral presentation and again it cannot be used to justify the utilization of the 6C isotherm.

(Authors' response) First, note that the analysis is meant to detect mesoscale structures (*i.e* nearly geostrophic flow structures that can be identified from sea surface height anomalies / thermocline depth anomalies) but also structures that are part of the mean circulation. In the Gulf of Mexico (GOM), besides transient eddies such as the anticyclones detached from the Loop Current (LC), the cyclones that often accompany the detachment process and other eddies present inside the GOM, there are semi-permanent structures that, for example, can be seen in the figure below (Figure 2) which shows the mean dynamic topography of the GOM (Rio and

Hernandez, 2004, and mean-dynamic topography https://www.aviso.altimetry.fr/en/applications/ocean/large-scale-circulation/mean-dynamic-topography.html). One can see that the LC itself (anticyclonic), the cyclonic gyre of the Bay of Campeche and the (anticyclonic) eddy/gyre straddling the central GOM (produced in part by the path of LC eddies inside the GOM) are features of the mean circulation.

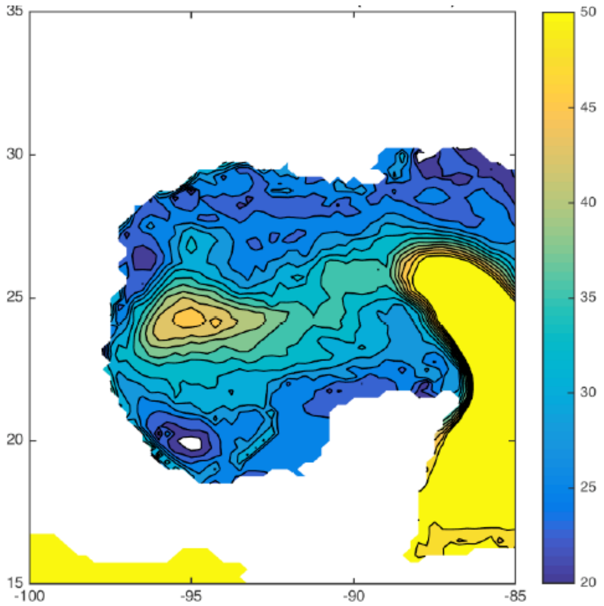

Figure 2. Mean Dynamics topography in the Gulf of Mexico (RIO-AVISO).

Hence, to avoid misunderstanding and to make sure it is clear we are referring to mesoscale structures and not only "eddies" which are generally understood as transient and closed circulation features, we have made the following changes:

Section 2.5, from page 5, L.31 to page 6, L. 1 "*The classification of the mesoscale structures (which, in the GOM, encompass eddies but also structures that are part of the mean circulation such as LC and LC eddies), was carried out using the depth of the 6°C-isotherm…*"instead of "*The classification of the eddy structures was carried out using the depth of the 6°C isotherm…*".

Section 2.5, page 6, L.23 the term *eddy* is now replaced by *mesoscale*.

Section 2.5 the sentence "*One should note that our determination of mesoscale anticyclonic structures encompasses both the eddies and the Loop Current*" was removed.

Section 3.3.1, page 10, L.12 "*the two groups*" instead of "*the two eddy groups*".

Second, in several references (e.g. Donohue et al., 2007; Hamilton 2007; Sheinbaum et al., 2007; Donohue et al., 2008; Hamilton et al., 2016) it is shown that the vertical displacement of the 6 to 10◦C isotherms (located at the base of the LC and LC eddies) is anti-correlated with sea-surface height displacements, highlighting the importance of first baroclinic mode dynamics in the GOM. 6-7◦C isotherms are at 450-500 m depth within some cyclonic eddies. Donohue et al., (2008), Cox et al., (2010) and Hamilton et al., (2016) suggest the 6◦C isotherm is a better choice for a two-layer analysis, and Kolodziejczyk et al., (2012) find the zero crossing of the first baroclinic mode near 1000 m depth.

We agree with the reviewer that not enough references or explanations for using the 6°C isotherm depth (T6) variability used to identify mesoscale structures were given in the submitted manuscript. Thus, to make a stronger case for the use of T6 to identify mesoscale structures, 5 references were added (Section 2.5, page6, L.6, 7, 10 and 11) and list items of pages 6 (L.4-12) were rewritten:

- *The GOM can be studied as a two-layer baroclinic system, with vertical displacements of the 6 to 10°C isotherms (located at the base of the LC and LC eddies and at 400-600 m depth in cyclonic eddies) being anti-correlated with sea-surface height (Donohue et al., 2007 and 2008; Hamilton 2007b, 2016a and 2016b; Sheinbaum et al., 2007).*

- *T6 is in the lower thermocline and has been used as the interface for a two layer system, separating deep waters from the more energetic upper layer containing mesoscale structures and the LC (Bunge et al., 2002; Donohue et al., 2008; Hamilton et al. 2016a and 2016b).*

- *T6 is directly measured by the profiling floats.*

Third, the depth of T6 is directly measured by the floats. Hence we decided to use this parameter to track mesoscale structures instead of sea surface height (SSH) measured by satellites, which have limited spatial resolution so the required interpolation to the locations of our profiles would add additional errors. This is discussed in the manuscript (page 6, Line 26-33) and the figure S1 (supplementary material of the manuscript), show that using SSH instead of T6 leads to essentially the same results.

Finally, note that the baroclinic signal of the mesoscale structures reaches down below 600m (or more) in the GOM (e.g. Lewis et al., 1989; Donohue 2016a and b, Sheinbaum et al., 2007, Hamilton et al., 2016a), even if the eddies' core is shallower. Additionally, Hamilton et al., (2016a) reference given in the manuscript is not an oral presentation (it is a BOEM-MMS technical report which is available online (https://www.boem.gov/ESPIS/5/5583.pdf). The link is now included in the reference list.

Given the above, we decided to leave the analysis as is, using the T6 criteria to obtain the anticyclonic/cyclonic subsets.

(Reviewer) The section on the impact of mesoscale eddies on phytoplankton biomass is largely inspired by the study of Dufois et al. 2014. The authors compared the float observations when the floats were profiling in a cyclonic structure with the observations when the floats were profiling in an anticyclonic structure. By averaging observations that were collected at different times of the year and locations in the Gulf of Mexico, you are looking at signals that are both influenced by the seasonal and large scale variability and the mesoscale activity; this is not correct. To properly assess the impact of eddy signal on a given variable, one needs to look at the departure from the seasonal mean (see Cushman-Rosin, 1994). All sections about the role of mesoscale structures need to be changed.

(Authors' response) We did not "average observations that were collected at different times of the year and locations in the Gulf of Mexico" as the referee writes, since we did not average different times of the year. We clustered the data in different groups based on identifying whether the profiles were taken in anticyclonic, cyclonic or neutral vorticity anomalies, following the criteria explained in the text (see also comment above), and then simply computed monthly climatologies for the anticyclonic and cyclonic subsets, gathering all profiles corresponding to each month regardless of the year and the geographic position, and looked for differences between these two clusters. Data are evenly distributed so each month of the year has a similar number of profiles (figure 1, right panel in the manuscript). One may question the representativeness of this climatology given the amount of data (two vertical profiles per month during 5 years from seven APEX floats distributed unevenly in the GOM), but it is what is available now and sufficient, in our view, to make this computation worthwhile.

It is well known that the seasonal cycle of geophysical and biogeochemical variables is not monochromatic and has time scales that overlap those of mesoscale turbulence. Both processes are thus impossible to separate properly, "even by defining running variances over 6-month windows or by subtracting a mean seasonal cycle from the time series before variance computations" (Penduff et al., 2004). So a decomposition of a variable as a time-mean+seasonal+"eddy" is not necessarily warranted as a means to separate seasonal and mesoscale eddy signals. Besides, depending on how calculations are made, the "eddy" part will include lower frequency variations too. Although there is certainly seasonal variability in the GOM related to atmospheric forcing (air-sea interaction river run-off), spectra (e.g. SSH) shows comparable or more energetic variations related to the mesoscale, in a band of frequencies that overlaps with seasonal variations (3-4 months, Jouanno et al, 2016; Hamilton and Lee, 2005).

Having said that, we followed the suggestion of the reviewer to first remove the seasonal signal to try to separate it from the mesoscale variability. We first calculate the climatology for the variable in question using all profiles, and then substract the monthly mean value from each profile to compute the anomalies. These anomalies have now mesoscale as well as lower frequency (interannual) signals. The profiles are then separated in the two clusters (cyclonic and anticyclonic), and a monhtly climatology of the anomalies is obtained. Figures below (Figures 3 and 4), same as figure 5 and figure 7 in the manuscript but for anomalies, show the same results as those obtained from the original calculation. Namely that anticyclones tend to show a deeper mixed layer depth (MLD) than cyclones in winter, that cyclones have slighlty larger integrated chlorophyll content than anticyclones, and that the nitracline depth and steepness is larger for cyclones throughout the year.

We decided not to use the anomalies, given that they are only useful to show relative differences between the two groups (anticyclonic vs cyclonic) of a given parameter, but it becomes complicated when two parameters are to be compared (e.g. the depth of the ML with that of the DCM). We think the discussion is clearer if we stick to the absolute values, and given the results above, we hope that the reviewer agrees with us.

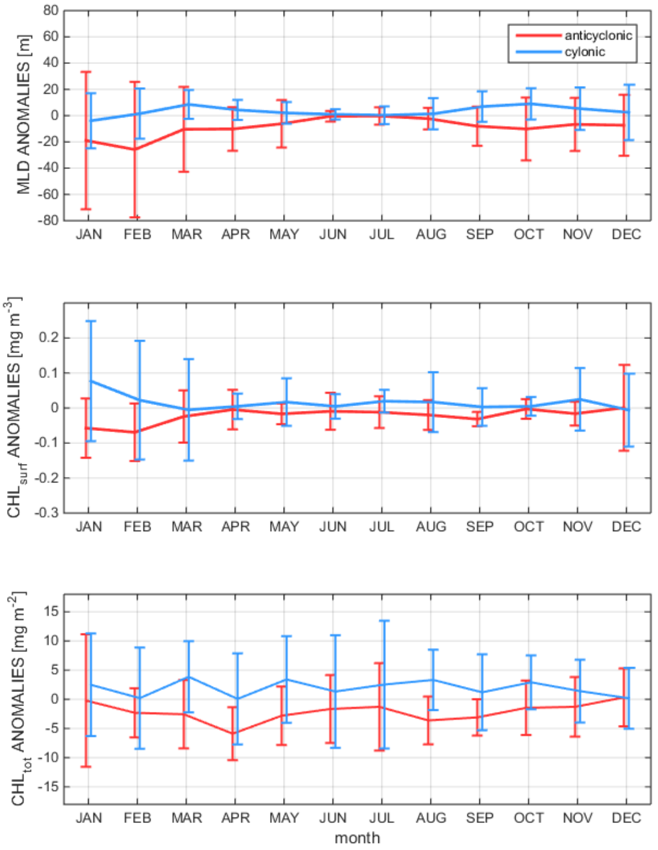

Figure 3. Same as fig. 5 in the submitted manuscript but for anomalies: (top) the mixed layer depth, (middle) surface chlorophyll and (bottom) integrated chlorophyll over the first 350m.

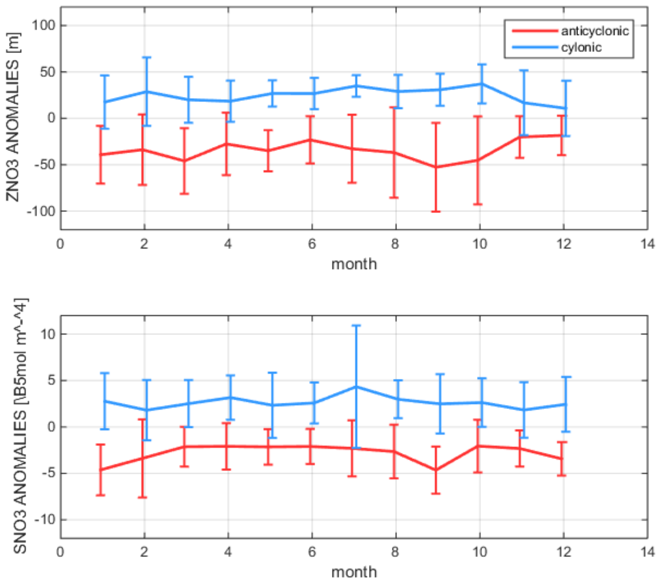

Figure 4. Same as fig. 7 in the submitted manuscript but for anomalies: (top) the mixed layer depth, (middle) surface chlorophyll and (bottom) integrated chlorophyll over the first 350m.

Given the above, we made the following changes in the section 3.2:

Page 9, L.1 the title was changed: "*Impact of mesoscale structures on the annual cycle*" instead of "*Role of mesoscale structures in shaping the annual cycle*".

Page 9, L.12-19, The next paragraph was added: "*It is well known that the seasonal cycle of geophysical and biogeochemical variables is not monochromatic and has time scales that overlap those of mesoscale turbulence (e.g. Penduff et al., 2004) thus, it is not possible to separate them properly. Although there is certainly seasonal variability in the GOM related to atmospheric forcing (air-sea fluxes and river run-off), spectra shows comparable or more energetic variations related to the mesoscale in a band of frequencies that overlaps with seasonal variations (3-4 months for sea surface height, e.g., Hamilton and Lee, 2005; Jouanno et al, 2016). Hence, it could be expected that the variability observed at a given period of the year also depends on the presence of mesoscale structures. We therefore analysed the seasonal cycle gathering data on a monthly-basis and considering separately profiles acquired in cyclonic and anticylonic structures, to assess MLD and [CHL] ([CHL]$_{surf}$ and [CHL]$_{tot}$) differences between the two groups.*".

Page 9, L.20, "*climatological basin-scale averaged MLD*" instead of "*MLD*".

Page 9, L.29, "*The monthly climatological mean [CHL]$_{tot}$*" instead of "*Monthly mean [CHL]tot*".

Legend of figure 5 and 7 were also modified:

Figure 5: "*Basin-scale, monthly climatological mean and standard deviation of: (top) the mixed layer depth, (middle) surface chlorophyll and (bottom) integrated chlorophyll over the first 350m. Red (blue) shows statistics for all profiles in anticyclonic (cyclonic) structures*." Instead of "*Monthly mean and standard deviation of: (top) the mixed layer depth, (middle) surface chlorophyll and (bottom) integrated chlorophyll over the first 350m.*".

Figure 5: "*Basin-scale, monthly climatological mean and standard deviation of: (top) the nitracline depth, (bottom) the nitracline steepness. Red (blue) shows statistics for all profiles in anticyclonic (cyclonic) structures. Red (blue) shows statistics for all profiles in anticyclonic (cyclonic) structures.*" Instead of "*Monthly mean and standard deviation of: (top) (top) the nitracline depth, (bottom) the nitracline steepness.*".

(Reviewer) The depth of an isopycnal surface cannot be used to determine a nitracline depth. In the open ocean, nutrient concentrations are controlled by both physical processes such as vertical/horizontal advection and diffusion, convection, and biological processes such as phytoplankton growth, remineralization, etc: : : At a pinch, Eq. (2) can be used to give a crude estimation of the nitracline depth for a quasi-1D steady state system with a surface layer depleted in nutrients, with no change in solar radiation and MLD. In your case, these assumptions do not hold. Sections 3.3.3 and 3.3.3 need to be removed and the conclusion need to be changed accordingly.

(Authors' response) We fully agree that the nitracline depth is controlled by both physical and biological (i.e. depth-dependent) processes. However, actual XIXIMI bottle measurements (obtained both in summer and winter) indicate that, overall, nutrient and density vertical distribution are highly correlated (figure 6 in the submitted manuscript). This is not something we hypothesize or suggest, nor is it new, it is what the observations indicate. Such a co-orientation of nitrate with density is not surprising, because dynamical processes that vertically displace water masses with their properties are generally strong, compared to the biological pump (Ascani et al., 2013; Omand et al., 2013 and 2015; While et al., 2010). Thus, we considered that, for the time scales addressed in our analysis (*i.e.* seasonal), the methodology provides relevant information in the absence of direct nutrient measurements.

This methodology was applied to profiling float data by Omand et al., (2015) near the station BATS, a region characterized by the passage of mesoscale eddies and winter storms. They showed that the overall nitrate-density relationship varied relatively little throughout the year, and that the "*Fluctuation in the nitracline depth due to deep mixing and mesoscale eddies (. . .) though apparent in depth coordinates (. . .) are not distinguishable in density coordinates*". Note that a similar approach using an isotherm was also previously applied in the GOM to interpret the seasonal variability of surface chlorophyll (Jolliff et al., 2008). Additionally, if we look at the data at the monthly climatological scale (i.e. not profile-to-profile), the summer nitracline is generally found deeper than the winter MLD, which supports the hypothesis that large input of nutrients to the photic layer by winter mixing are likely limited at these time scales. For the above-mentioned reasons we do not consider that sections 3.3.2 and 3.3.3 need to be removed. However and as also suggested by reviewer #1 changes in sections 3.3 were realized to make the arguments easier to follow (see our response to reviewer 1), and conclusion 4 rewritten.

In particular:

Section 3.3.2, page 11, L.11-15, was rewritten "*... Z_N is always found at depth and does not show a clear seasonal pattern (regardless of the group). In addition, the climatological winter mixed layer is generally shallower than the nitracline (Fig. 5). Hence if we assume that large inputs of nutrients can only be expected when the MLD reaches below the average nitracline depth (Z_N), it is likely that nutrients injections to the photic layer by vertical mixing are low on average, even in winter*." instead of "*... Z_N is always found at depth (regardless of the group) and never approaches the surface, even in winter. This result means that there is no NN accumulation in surface waters and that the deep nutrient reservoir is always isolated from the surface layer ...*".

Section 3.3.2, page 11, L.21-23, the sentence "*Thus, apart from sporadic and rather localized events, it seems likely that large supplies of nutrients to the surface layer are not that common in winter in the GOM as a whole, since the basin scale, monthly climatological basin-scale averages of the MLD are shallower than the estimated depth of the nitracline." was added.*

Conclusion number 4, page 13, L5-11 was rewritten: "In addition, our observations show that the winter mixed layer is generally not deep enough to reach the nitracline. The sampling, however, only allows to reach conclusions in a broad sense. Therefore, we suggest that, on a climatological basin-scale average, a relatively small amount of nutrients are potentially injected to the surface layer through vertical mixing. This does not discard the fact that at short time-scales (days to weeks), events may result in high nutrient inputs to the photic layer which translate in a local phytoplankton bloom, particularly during winter storms. Our interpretation is that the net effect of those blooms is not big enough to determine the basin scale averages of surface chlorophyll content, hence nutrient supply by winter mixing is not necessarily the main cause of the seasonal, basin-scale variability of surface chlorophyll content.".

We would like to mention that the biogeochemical model study by Damien *et al.*, (submitted to Journal of Geophysical Research- Ocean) confirms that a winter MLD deeper than the nitracline (and a subsequent input of nutrients to the surface layer), is not a common feature in the Gulf of Mexico. This reference was added in the revised manuscript and the next sentence added in the conclusion number 9 (page 13, L. 23-27): *"The model results are consistent with the hypothesis stated in this work, but also highlights that the BOEM floats' sampling scheme is unable to resolve all the scales of temporal and spatial variability."*

LIST OF RELEVANT CHANGES

- Dr. Victor F. Camacho-Ibar was added in the list of authors of the paper.
- 14 references were added.
- 1 figure was added (Figure 8).
- Methodological section was rewritten p. 4 L. 12-20 "Calibration of fluorescence profiles" and p.6 L. 4-12 "Detection of mesoscale structures".
- Section 3.1 "Seasonal cycle" was entirely rewritten and a discussion was added.
- Section 3.2 "Impact of mesoscale structures on the annual cycle". A discussion was added p.9 L. 9-16.
- Section 3.3.2 "3.3.2 Winter mixing" was rewritten p.11 L.7-12 and p.11 L.16-19.
- Conclusion number 4 was rewritten.

MARKED-UP MANUSCRIPT VERSION

Temporal variability of chlorophyll distribution in the Gulf of Mexico: bio-optical data from profiling floats

Orens Pasqueron de Fommervault[1], Paula Perez-Brunius[1], Pierre Damien[1], Victor F. Camacho-Ibar[2], Julio Sheinbaum[1]

[1] Departamento de Oceanografìa Fisica, Centro de Investigacion Cientìfica y de Educacion Superior de Ensenada, Ensenada, 22860, Mexico
[2] Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, PO Box 453, Ensenada, Baja California, Mexico 22830

Correspondence to: Orens Pasqueron de Fommervault (orens@cicese.mx)

Abstract. Chlorophyll concentration is a key oceanic biogeochemical variable. In the Gulf of Mexico (GOM), its distribution, which is mainly obtained from satellite surface observations and scarce *in situ* experiments, is still poorly understood. In 2011-2012, eight profiling floats equipped with biogeochemical sensors were deployed for the first time in the GOM and generated an unprecedented dataset that significantly increased the number of chlorophyll vertical distribution measurements in the region. The analysis of these data, once calibrated, permits us to reconsider the spatial and temporal variability of the chlorophyll concentration in the water column. At a seasonal scale, results confirm the surface signal seen by satellites, presenting maximum concentrations in winter and low values in summer. It is shown that the deepening of the mixed layer depth is the primary factor triggering the chlorophyll surface increase in winter. In the GOM, a possible interpretation is that this surface increase corresponds to a biomass increase. However, the present dataset suggests that the basin scale climatological surface increase in chlorophyll content results from a vertical redistribution of subsurface chlorophyll and/or photoacclimation processes, rather than a net increase of biomass. One plausible explanation for this is the decoupling between the mixed layer depth and the deep nutrient reservoir since mixed layer depth only reaches the nitracline in sporadic events in the observations. Float measurements also provide evidence that the depth and the magnitude of the deep chlorophyll maximum is strongly controlled by the mesoscale variability, with higher chlorophyll biomass generally observed in cyclones rather than anticyclones.

1 Introduction

The Gulf of Mexico (GOM) is a semi-enclosed sea linked to the Caribbean Sea through the Yucatan Channel and to the Atlantic Ocean through the Florida Straits. It is characterized by a complex circulation dominated by the Loop Current (LC) that regularly forms large anticyclonic eddies (~ 200-300 km diameter) that propagate westwards (e.g. Sturges and Leben, 2000). LC and LC eddies can be identified by Caribbean subtropical underwater (*i.e.* high salinity in the upper layer), and are clearly distinguishable from Gulf of Mexico common water which is formed by vertical convective mixing within the gulf's uppermost 200 m in winter or by mixing induced by the collision of LC rings against the western gulf boundary (Elliott, 1982; Nowlin and McClellan, 1967; Vidal et al., 1992). Another important feature of the circulation in the GOM is the presence of relatively smaller cyclonic and anticyclonic eddies in many parts of the basin (e.g. Hamilton et al., 2002; Hamilton, 2007a; Schmitz, 2005).

From a biogeochemical point of view, the deep waters of the GOM are considered oligotrophic and nutrient-limited being relatively isolated from coastal eutrophic waters (Heileman and Rabalais, 2009). In deepwater GOM, historical *in situ* measurements indicate low biological productivity (< 150 mgC m^{-2} d^{-1}) and low surface chlorophyll concentration (hereafter $[CHL]_{surf}$) with values ranging from 0.06 to 0.32 mg m^{-3}, and being 2-3 times higher in subsurface waters (Biggs and Ressler, 2001; El-Sayed, 1972; Koblenz-Mishke et al., 1970).

Other studies, mostly based on satellite surface chlorophyll measurements (Müller-Karger et al., 1991; Salmerón-García et al., 2011), or numerical simulations (Fennel et al., 2011; Walsh et al., 1989; Xue et al., 2013), suggest important seasonal variations. Lower $[CHL]_{surf}$ values are observed from May to July and maximum values are found in winter from December to February. This cycle is considered to be primarily triggered by annual changes in ocean-atmosphere fluxes (Virmani and Weisberg, 2003), resulting in the deepening of the mixed layer in winter. In the GOM, it has been suggested that a higher $[CHL]_{surf}$ in winter occurs concomitantly with a biomass increase, as a consequence of nutrient entrainment to the surface (Jolliff et al., 2008; Melo Gonzalez et al., 2000; Müller-Karger et al., 1991; Müller-Karger et al., 2015; Salmerón-García et al., 2011). However, this has never been truly demonstrated due to the absence of sufficient data at the proper spatio-temporal scales in the water column. Furthermore, recent studies conducted in various oligotrophic environments, also suggest that [CHL] variability in the surface layer may primarily reflect changes in intracellular pigment concentration, rather than biomass variability (Behrenfeld et al. 2016; Halsey and Jones, 2015; Jakobsen and Markage, 2016; Siegel et al., 2013). Hence, the main processes involved in the seasonal variability of surface chlorophyll in the GOM have not yet been resolved.

Superimposed on the seasonal variability, several sporadic processes, such as mesoscale and sub-mesoscale activity (Belabbassi et al., 2005; Biggs and Ressler 2001; Linacre et al., 2015; Toner et al., 2003) or river run-off (Lohrenz et al., 1997; Nababan et al., 2011) may alter the [CHL] distribution in the deep GOM. These structures are hardly detectable from traditional *in situ* measurements (ship-based data rarely achieve the required spatio-temporal resolution), and their impact on the phytoplankton distribution and dynamics in the GOM remains to be established. The overall lack of data in the deepwater GOM has, so far, produced a very limited picture of the [CHL] distribution, with low time and spatial resolution contributing to this uncertainty.

The development of autonomous Lagrangian platforms equipped with miniaturized bio-optical sensors now provides high-frequency and multiannual time series of physical and biogeochemical observations (Johnson et al., 2009). In the GOM, the pioneer work of Green et al., (2014) demonstrated the great potential of using profiling floats with bio-optical sensors and showed the complex [CHL] variability present in the deep GOM. Following this first successful attempt, and with the aim to monitor the water column of the entire GOM, seven other floats with bio-optical sensors (chlorophyll and CDOM fluorimeter, Backscatterometer) and CTD were deployed in 2011 and 2012, as part of a project funded by the Bureau of Ocean Energy Management (BOEM, see Hamilton et al., 2016a). Each float obtained bi-monthly profiles over a total period of nearly 5 years inside the GOM.

In this study, we focus specifically on chlorophyll fluorescence (FLUO) measurements. For the first time in the GOM, we present high-frequency calibrated chlorophyll fluorescence time-series using profiling floats, simultaneously acquired in different parts of the basin. The objective is to study the influence of physical forcing on the variability of the [CHL] vertical distribution. Of particular interest is its annual cycle, since it is the first time enough *in situ* measurements are available to resolve this temporal scale at depth, and explore to what extent the surface dynamics, as seen by satellite, is representative of the variability within the water column. We also investigate the [CHL] variability at shorter time-scales and evaluate the role of mesoscale structures/water masses in shaping the annual cycle. This work provides a better understanding of the mechanisms controlling the distribution and the dynamics of phytoplankton in the deep GOM. Our analysis indicates that at a basin scale, the winter surface [CHL] maximum in the GOM may not necessarily be produced by a biomass increase, but would be associated with a vertical redistribution of subsurface chlorophyll and/or photoacclimation processes.

2 Data and methods

2.1 APEX float database

The float database is composed of eight Apex profiling floats (Teledyne-Webb Research, Inc.) deployed in the deep GOM. Two of them experienced technical issues (floats “05” and “08”) and were discarded from the dataset. The profiling floats had a rest depth of 1500 m and profiles were made every 14 days for most of the study. Data were transmitted in real-time using Iridium communication each time the float surfaced.

In addition to the standard conductivity-temperature-depth (CTD) sensors mounted on typical Argo profiling floats (Roemmich et al., 2003), BOEM floats were also equipped with an ECO FLbbCD-AP2 sensor (WET Labs, Inc.). This sensor allowed the measurement of [CHL] and colored dissolved organic matter (CDOM) fluorescence, as well as the optical backscattering (bbp) at 700 nm (see Green et al., (2014) for more details). Bio-optical estimations were performed from 0 to 1500 m-depth (about 5 m resolution in the 0–200 m layer, 10 m resolution in the 200-500 m layer, 20 m resolution in the remaining range).

Data were collected over a time period of approximately five years (2011 through 2015), and a total of 537 profiles of both physical and bio-optical parameters were acquired in the whole GOM basin (Table 1). The resulting dataset has good spatial coverage (fig. 1, left panel), and, on a monthly basis, all periods were sampled in an equivalent manner (Fig. 1, right panel). Hereafter, we focus our discussion on the [CHL] time-series.

2.2 Fluorescence profiles calibration

The measurement of *in vivo* FLUO is widely used as a proxy for [CHL] (Lorenzen, 1966) which is, in turn, the main proxy for phytoplankton biomass (Cullen, 1982; Strickland, 1965). However, the conversion of FLUO into [CHL] must be done with great care. FLUO and [CHL] are generally considered proportional, which can be formalized as:

$$[CHL] = \alpha \, . (FLUO - \beta) \qquad (1)$$

where the α and β coefficients (respectively instrumental gain and offset) are provided by the manufacturer. However, the values of these coefficients are rarely satisfactory and require post-processing evaluation (Boss et al., 2008; Guinet et al., 2013; Mignot et al., 2011; Xing et al., 2012). In addition, other biogeochemical processes, such as taxonomic composition and physiological acclimation mechanisms, are known to modulate the proportionality of FLUO and [CHL] (Cunningham et al.,1996; Falkowski and Kiefer, 1985; Kiefer, 1973), and must be taken into account for calibration purposes.

Among the physiological acclimation mechanisms affecting the FLUO-[CHL] relationship, the most serious issue is the non-photochemical quenching (NPQ) related to the decrease of the FLUO signal at the surface, in conditions of high light intensity (Cullen and Lewis, 1995). The first step of the calibration procedure is to provide a systematic correction of the NPQ. We applied the method of Xing et al., (2012) which is actually implemented in the international biogeochemical-Argo program (Schmechtig et al., 2014). The method consists in finding, within the layer between the surface and 0.9 times the mixed layer depth (MLD), the highest FLUO value ($FLUO_{max}$) and its depth ($FLUO_{z,max}$). $FLUO_{max}$ is then extrapolated from $FLUO_{z,max}$ (considered as a proxy of the thickness of the layer potentially affected by the NPQ) up to the surface.For this specific purpose, FLUO profiles were smoothed, using a 5-point moving median filter, and the MLD was calculated from density profiles, using a 0.03 kg m^{-3} density criterion (de Boyer Montegut et al., 2004). The relevance of this NPQ correction in oligotrophic areas was specifically addressed in Lavigne et al., (2012) which showed it has a positive and significant impact on the estimates of chlorophyll.

The second step of the procedure is to correct FLUO profiles from instrumental offset. For each profile, the mean value at depth (*i.e.* deeper than 500 m), was then computed ($FLUO_{deep}$). Assuming [CHL] is zero below 500 m, β (which indicates the response of the instrument in the absence of signal), was then determined as the median value of $FLUO_{deep}$ (Table 1).

The third step of the procedure is to evaluate the α parameter. This was performed following the method of Lavigne et al., (2012) and using ocean color satellite measurements (8-day composite images at 4 km spatial resolution from the Aqua MODIS satellite ocean color sensor, OCx Algorithm, available on http://oceancolor.gsfc.nasa.gov/). Float and satellite data were matched-up considering 8-day time intervals and ± 0.25° spatial windows centered on the geographical position of the float profile. Corresponding satellite [CHL] values were extracted and averaged. The match-up was taken into account in the calibration procedure if at least 30% of satellite values were available. The number of valid match-ups was 60, 74, 67, 75, 82 and 74% for floats “00”, “01”, “02”, ”03”, ”04”, and ”06”, respectively. The integrated chlorophyll content over 1.5 times the euphotic depth was then estimated from satellite [CHL] using empirical relationships (Uitz et al., 2006) and compared to the corresponding FLUO value (previously corrected for offset and NPQ). For the comparison, the whole 1.5 euphotic layer was used instead of only surface records to minimize the error that would be induced by a wrong NPQ parameterization. Finally, for a given float, α was calculated as the median value of the multiplicative coefficients obtained by the match-up (Table 1).

Although this method was not directly validated in the GOM, a comparison between satellite calibrated profiles and *in situ* HPLC [CHL] data was performed by Lavigne et al., (2012) at the station BATS (32°N and 64°W, in the Sargasso Sea). It was shown that calibrated profiles were unbiased with an associated median error of 29%, which is reduced to 16% when climatological averages are compared. These values may be reasonably applied to the GOM, considering the vertical distribution of the [CHL] at BATS is relatively close to what is observed in the GOM (Michaels and Knap, 1996).

2.3 Particle backscattering profiles

Profiles of particulate backscattering coefficient at 700 nm (bbp, in m^{-1}) were obtained following Green et al., (2014) protocol, and using the laboratory calibrations. High-frequency spikes were further removed from the bbp data applying successively a 5-point running median filter and a 7-point mean filter spikes (Briggs et al., 2011).

In our study, the bbp that is to first order correlated to the chlorophyll concentration (Huot et al., 2008; Loisel and Morel, 1998; Morel and Maritorena, 2001), was used as an alternative measure of the phytoplankton carbon biomass (e.g. Behrenfeld et al., 2005; Westberry et al., 2010). The [CHL]-bbp relationship is however known to be altered by physiological variations (Antoine et al., 2011; Behrenfeld and Boss, 2003) in particular because the CHL signal is strongly impacted by changes in intracellular pigment concentration resulting from photoacclimation (Fennel and Boss, 2003; Kitchen and Zaneveld, 1990; Mitchell and Kiefer, 1988). Hence, in this work, we also considered the ratio bbp/[CHL] as a proxy of phytoplankton carbon biomass to CHL and used it to track changes in phytoplankton photoacclimation processes (Behrenfeld and Boss, 2003; Behrenfeld and Boss, 2006; Mignot et al., 2014). It is worth noting that in the absence of published empirical conversion factors in the GOM, bbp data were not converted to a carbon equivalent. We therefore considered qualitatively bbp, and used them primarily to assist in the interpretation of [CHL] profiles.

2.4 Nutrient data

In the present study we also used nutrients (more precisely nitrate + nitrite concentrations, hereafter [NN]) from bottle measurements acquired during the XIXIMI-2 (July 2011) and XIXIMI-3 (February-March 2013) cruises. More than 900 water samples were acquired from 74 profiles in the deep water region of the southern GOM (25°N to 20°N and 87°W to 95°W; Fig. 1, left panel). Nutrient analyses were performed with a Skalar SANplus segmented-flow nutrient analyzer according to the protocols described in Gordon et al., (1993), and [NN] were determined according to a modification of the Armstrong et al., (1967) procedure.

2.5 Detection of mesoscale structures

In the present study, mesoscale structures, were characterized according to the vertical distribution of temperature, considering that isotherms are generally displaced downward (upward) in anticyclonic (cyclonic) structures in comparison with the background field (McGillicuddy and Robinson, 1997). The objective was to see if biological patterns could be identified in response to different physical situations. The classification of the mesoscale structures (which, in the GOM, encompass eddies but also structures that are part of the mean circulation such as LC and LC eddies), was carried out using the depth of the 6°C-isotherm (hereafter T6) for the following reasons:

- The GOM can be studied as a two-layer baroclinic system, with vertical displacements of the 6 to 10˚C isotherms (located at the base of the LC and LC eddies and at 400-600 m depth in cyclonic eddies) being anti-correlated with sea-surface height (Donohue et al., 2007 and 2008; Hamilton 2007b, 2016a and 2016b; Sheinbaum et al., 2007).

- T6 is in the lower thermocline and has been used as the interface for a two layer system, separating deep waters from the more energetic upper layer containing mesoscale structures and the LC (Bunge et al., 2002; Donohue et al., 2008; Hamilton et al. 2016a and 2016b).

- T6 is directly measured by the profiling floats.

BOEM float profiles were thus gathered in different clusters according to the depth of T6, and, for statistical reasons, criteria were chosen symmetrical to the mean T6 depth to obtain groups of equivalent size. From here on, the cyclonic group (CG) will correspond to profiles with shallowest T6 (< 770 m) and the anticyclonic group (AG) to profiles of deepest T6 (> 820 m), with the remaining profiles (*i.e.* 770 m > T6 > 820 m) considered undefined or neutral. Even though T6 is not very sensitive to seasonal variability, profiles are homogeneously distributed within each group. *i.e.*, all seasons are equally sampled on average, with 14 profiles available per group and per month (Fig. 1, right panel). The spatial distribution of cyclones and anticyclones resulting from the T6 depth analysis are given in Fig. 2 (top panel).

A T-S diagram using all the profiles (Fig. 2, bottom right panel) shows that most cyclones have Gulf of Mexico common water (uniform salinity of ~ 36.5 between the 1024.5 and 1025.6 kg m^{-3} isopycnal levels) while the anticyclones are more mixed. Eastern structures have a clear Caribbean subtropical underwater signal (warm and salty water at the structure's core, red diamonds on Fig. 2) whereas western structures tend towards Gulf of Mexico common water (red squares). In that sense, this classification also characterizes profiles in terms of water mass properties.

The relationship between T6 and sea surface height (SSH) obtained from altimetry, which is more conventionally used for the identification of eddies in the GOM (e.g. Leben and Born, 1993), was examined in our dataset. T6 was plotted against SSH at the location and time of the profile (left bottom panel on fig. 2, see legend for SSH calculation details). Results reveal a good and positive correlation between T6 and SSH values ($R^2 = 0.58$) and confirms the results of Hamilton et al., (2016a), obtained from a larger dataset (*i.e.* maximum SSH values in anticyclones and minimum values in cyclones). This also suggests that the depth of T6 is a good proxy to classify profiles from a mesoscale perspective in the GOM. The ability of the method to identify mesoscale features was verified comparing results with those obtained using an SSH criterion which yield only a minor difference (supporting information S1).

3 Results and discussion

3.1 Seasonal cycle

During the five years of observation the BOEM floats provided a repeated coverage of the deep GOM. The mixed layer depth (MLD, generally considered to be the main physical factor influencing upper layer phytoplankton dynamics and chlorophyll concentration ([CHL], e.g. Mann and Lazier, 2006), show consistent seasonal patterns (Fig. 3 and Fig. 4).

Regarding the MLD, in summer (*i.e.* from June to August) shallow values are measured (mean value = 18±8 m) as an indication of a well-stratified water column. In autumn (September-October) a deepening of the mixed layer is observed, with a mean value of 37±19 m. Relative maximum values are reached in winter from December to February (mean value of 50±30 m), and this period is also characterized by a strong scattering of the values in which MLD deeper than 80 m are not uncommon. Maximum MLD are present in the float "01" time-series in winter 2012/2013 and float "06" time-series in winter 2013/2014 (Fig. 3 and Fig. 4). During these periods, maximum MLD can reach more than 150 m. In spring (from March to May), there is a gradual increase of surface density, leading to a progressive stratification of the water column and the mixed layer becomes thinner (Fig. 3 and Fig. 4).

Concerning [CHL], large variability is observed above 200 m in all time-series. Overall, a deep chlorophyll maximum (DCM), characteristic of an oligotrophic environment, is detected at around 70-100 m depth throughout the year, although this feature tends to disappear in winter

(Fig. 3, Table 2). At a seasonal scale, $[CHL]_{surf}$ here calculated as the mean [CHL] in the 0-30 m layer, exhibits a clear pattern despite the strong spatial and inter-annual variability produced by mixed layer dynamics (Fig. 4). In summer, when the MLD is minimum, $[CHL]_{surf}$ is very low and generally under 0.1 mg m^{-3} (Fig. 4). During this season the MLD is occasionally found deeper than the top of the DCM (defined as the first depth were $[CHL]_{surf}$ exceeds 0.1 mg m^{-3}, *i.e.* 4 times the detection limit of the sensor), but such events are very rare (11% of the profiles). In autumn, the mean $[CHL]_{surf}$ remains low (0.09 mg m^{-3}) although slightly higher than the concentration measured in summer. The MLD reaches the top of the DCM in around 40% of the autumn profiles. Maximum values of $[CHL]_{surf}$ are observed in winter (mean value of 0.22 mg m^{-3}) when the MLD is generally the deepest. During this season, the MLD shows large variability and generally reaches the DCM (~ 80 % of the winter profiles), which results in large dispersion of the measured $[CHL]_{surf}$ values (Fig. 4). In spring, $[CHL]_{surf}$ decreases (mean values of 0.09 mg m^{-3}), and a MLD deeper than the top of the DCM is only observed in 26% of the profiles. The seasonal cycle of the $[CHL]_{surf}$ obtained from the float profiles is consistent with that reported using satellite measurements (Müller-Karger et al., 1991; Salmerón-García et al., 2011).

If the integrated content of CHL over the 0-350 m layer ($[CHL]_{tot}$) is now examined, interestingly, no clear seasonal variability is observed, or at least, its spatial and/or inter-annual variability is higher. $[CHL]_{tot}$ remains almost constant all along the seasons, with a mean value around 30 mg m^{-2} (Fig. 4). In other words, the winter increase in $[CHL]_{surf}$ is not mirrored by the $[CHL]_{tot}$. This is a noteworthy result, given that the seasonal cycle of the [CHL] in the GOM, at a basin scale, has been almost exclusively addressed using satellite observations, which only provide surface information. Having said that, one may wonder how much of the phytoplankton chlorophyll variability is reflective of true changes in total biomass in the entire water column. Indeed, it is well known that the [CHL] is not a sole function of phytoplankton biomass and depends on several other factors, such as photoacclimation processes (e.g. Geider, 1987). In our study, this question was addressed considering particulate backscattering measurements (bbp) performed by the floats, that could be viewed as an alternative and independent estimate of phytoplankton carbon biomass (Behrenfeld and Boss, 2003). Results presented in supporting information (S2) show no increase of bbp in winter in either surface mean or vertically integrated values. This seems to confirm that, at a seasonal scale, the total phytoplankton biomass (*i.e.* integrated over the 0-350 m layer) would remain relatively stable in deepwater GOM, and that the surface increase in $[CHL]_{surf}$ might not reflect an increase in phytoplankton biomass.

Having said that, different mechanisms could explain this result. In a two-layer approach, *i.e.* considering separately the upper part of the photic layer (*a priori* nutrient limited and light limited only in winter) and the lower part (*a priori* light limited but less nutrient starved), the $[CHL]_{surf}$ increase, without a similar trend in the bbp signal, (figure S2) would be the result of photoacclimation processes (Mignot et al., 2014). The underlying assumption is that during the winter period, the average light intensity for phytoplankton is reduced in the mixed layer with respect to summer conditions leading to an increase in intracellular chlorophyll content. This scenario seems reasonable to explain the winter $[CHL]_{surf}$ increase but becomes alone questionable if we take into account that $[CHL]_{tot}$ remains constant at a seasonal scale. Another mechanism to explain the distribution of the [CHL] in winter would be a vertical redistribution of the phytoplankton over the water column (Mayot et al., 2017). Low-light acclimated cells from the DCM would be transported to the surface by mixing process, and *vice versa*. This could be the case in the GOM, given that the mixed layer is generally deep enough to reach the DCM in winter (~ 80 % of the profiles), thus connecting the upper and the lower part of the euphotic zone. Considering only the pure stirring of the DCM into the mixed layer assumes that phytoplankton cells do not have time to re-acclimate to their new light environment (hours to days processes). So it is not warranted to test this hypothesis, given the temporal resolution of our floats (two profiles per month from each float). *In situ* observations by Qian et al., (2003) also suggested shifts in the surface phytoplankton community that could also account for changes in $[CHL]_{surf}$.

All these mechanisms are not necessarily exclusive and could even act together to explain the observed [CHL] seasonal cycle. In any case, relatively stable vertically integrated chlorophyll (and bbp) values indicate a constant phytoplankton biomass in the water column throughout the year. This would also imply that the mixed layer in winter, although sufficiently deep to reach the DCM, would be, nonetheless, insufficient for bringing up large quantities of nutrients and support a significant net increase in phytoplankton biomass. This contrasts with conclusions from previous studies conducted in the GOM that suggest an increase of biomass in winter based on surface information from chlorophyll satellite observations (Jolliff et al., 2008; Melo Gonzalez et al., 2000; Müller-Karger et al., 1991; Müller-Karger et al., 2015; Salmerón-García et al., 2011) and will be further discussed in section 3.3.

3.2 Impact of mesoscale structures on the annual cycle

Superimposed to a seasonal signal, float profiles also show chlorophyll variability that occurs at shorter time-scales. Subsurface temporal changes in [CHL] are closely related to isopycnals (black lines, Fig. 3), and the vertical displacement of the DCM is highly coherent with density. When profiles for which the MLD reaches the DCM are excluded (*i.e.* when the DCM structure is eroded), depth variations of the subsurface DCM are correlated with the vertical displacement of the nearby 1025.5 kg m^{-3}-isopycnal ($R^2 = 0.57$). Since the 1025.5 kg m^{-3}-isopycnal is also correlated with T6 ($R^2 = 0.48$), we observed that DCM is, on average, deeper in the anticyclonic group (AG) than in the cyclonic group (CG), whatever the time period (Table 2). Besides, a student-t test confirms that the difference in DCM mean depth observed between the two groups is statistically significant independent of season (level of significance $p = 0.05$). This variability overlaps with the seasonal deepening and shallowing of the DCM, characterized by deepest values in summer (82±18 m in CG and 105±17 m in AG) and shallowest values in winter (68±19 m in CG and 75±11 m in AG).

It is well known that the seasonal cycle of geophysical and biogeochemical variables is not monochromatic and has time scales that overlap those of mesoscale turbulence (e.g. Penduff et al., 2004) thus, it is not possible to separate them properly. Although there is certainly seasonal variability in the GOM related to atmospheric forcing (air-sea fluxes and river run-off), spectra shows comparable or more energetic variations related to the mesoscale in a band of frequencies that overlaps with seasonal variations (3-4 months for sea surface height, e.g., Hamilton and Lee, 2005; Jouanno et al, 2016). Hence, it could be expected that the variability observed at a given period of the year also depends on the presence of mesoscale structures. We therefore analysed the seasonal cycle gathering data on a monthly-basis and considering separately profiles acquired in cyclonic and anticylonic structures, to assess MLD and [CHL] ($[CHL]_{surf}$ and $[CHL]_{tot}$) differences between the two groups. Fig. 5 shows that the climatological basin-scale averaged MLD is generally deeper in AG than in CG, as expected (Dufois et al., 2014; Kouketsu et al., 2012), although this difference is most often not significant ($p < 0.05$, except in April, September and October) due to the strong dispersion in MLD measurements. The maximum difference is observed in January and February, with mean values around 70m in AG and 50 m in CG (Fig. 5). In both groups, maximum climatological monthly values of $[CHL]_{surf}$ are also observed in January and February (Fig. 5). A higher increase in $[CHL]_{surf}$ is however observed in CG (only statistically significant in February), even though the mean MLD is shallower than in AG (mean $[CHL]_{surf}$ for those months range around 0.2-0.1 mg m^{-3} for AG and 0.3-0.2 mg m^{-3} for CG).

Consistent with the results of section 3.1, $[CHL]_{tot}$, shows no clear winter increase on either group (Fig. 5). By contrast, statistically significant differences ($p < 0.05$) between CG and AG are found from March to October, when the MLD is shallower. The monthly climatological mean $[CHL]_{tot}$ is higher, on average, in CG (~ 32 mg m^{-2}) than in AG (~ 28 mg m^{-2}) which is most likely related to an intensification of the DCM in CG (level of significance $p = 0.05$, Table 2). Since the DCM is found significantly deeper in AG than in CG, one might expect that differences in $[CHL]_{tot}$ may not be reflective of changes in phytoplankton biomass, but may result from changes in environmental conditions (e.g. light) and a consequent modification of the ratio of CHL to phytoplankton carbon biomass. However, bbp vertical profiles suggest that the increase of $[CHL]_{tot}$ in CG is also related to carbon biomass enhancement. Indeed, a higher bbp signal is observed in CG compared to AG (supporting information S3). In addition, in the DCM, the ratio bbp/CHL (proxy of phytoplankton carbon biomass to CHL), which tracks changes in phytoplankton physiology (Behrenfeld and Boss, 2003; Behrenfeld and Boss 2006; Mignot et al., 2014), is very similar between the two groups (supporting information S3). Thus, it can be reasonably assumed that the CHL difference between CG and AG in the lower euphotic zone results from biomass variations and not from photoacclimation processes. As a consequence, in the GOM, the phytoplankton biomass may be more enhanced in cyclones than in anticyclones. The results agree with the negative correlation between SSH and $[CHL]_{surf}$ anomaly found by Gaube et al., (2014) within the GOM suggesting higher [CHL] concentrations in cyclones.

3.3 Underlying processes: nutrient supply to the surface layer

3.3.1 Estimations of nutrient concentrations

To better understand the possible mechanisms that explain the differences observed in the [CHL] field within the seasons and the two groups, we address here the role of nutrients (here nitrate + nitrite, [NN]). In the absence of direct measurements, the vertical distribution of [NN] along float trajectories was estimated using XIXIMI-2 and XIXIMI-3 data. The objective was to infer the [NN] from float density profiles. Indeed, when [NN] are plotted against density (Fig. 6), three different layers can be distinguished: the surface layer where [NN] are exhausted; the intermediate layer where [NN] almost linearly increases with density, and the deep layer within which [NN] are decreasing. In the intermediate layer, which corresponds roughly to the pycnocline and the nitracline (black points on Fig. 6), we estimated the nitracline depth (Z_N) and the nitracline steepness (S_N) from linear regression ($R^2 = 0.91$). Upper and lower limits of the intermediate layer (respectively 1025.5 kg m^{-3} and 1027.4 kg m^{-3}) were chosen according to density criteria (since our goal was to infer the [NN] from float density profiles), and in order to minimize the error of the linear regression of [NN] versus density. In this way, the intermediate layer extends from the [NN] depleted layer to the [NN] maximum.

The linear fit to the [NN] versus density data (red line in fig. 6) is:

$$[NN] = 16.58(\pm 0.59)\ \sigma_\theta - 422.93(\pm 15.69) \qquad (2)$$

where σ_θ is the potential density anomaly (the numbers in parenthesis are the 95% confident intervals). According to Omand and Mahadevan (2015), we can then find the [NN] depletion density $\sigma_\theta(0)$, where [NN] goes to zero as: $\sigma_\theta(0) = 422.93/16.58 = 25.5$ kg m^{-3}. $\sigma_\theta(0)$ represents the deepest isopycnal at which nitrate + nitrite is depleted (named also the nitrate depletion density, Kamykowski and Zentara, 1986). As a comparison, Z_N was compared to the nitracline depth estimated by Jolliff et al., (2008) using the 23.2°C-isotherm with good agreement between the two methods ($R^2 = 0.96$). S_N was also estimated, and can be deduced from Eq. 2:

$$S_N = \frac{\Delta[NO_3]}{\Delta Z} = \frac{16.58.(\sigma_{Z2} - \sigma_{Z1})}{Z2 - Z1} \qquad (3)$$

Thus by choosing σ_{Z2} and σ_{Z1} as the lower and upper limits of the intermediate layer (*i.e.* 1025.5 kg m^{-3} and 1027.4 kg m^{-3}), S_N can be determined from float density profiles (Fig. 7).

3.3.2 Winter mixing

In the deepwater GOM, the deepening of the mixed layer in winter is assumed to carry cold and nutrient-rich subsurface water into the euphotic zone, in agreement with the annual cycle of the satellite surface chlorophyll (Jolliff et al., 2008; Müller-Karger et al., 1991). However, our analysis of the [CHL] over the whole water column suggests that the winter [CHL]$_{surf}$ increase does not necessarily reflect a real increase in phytoplankton biomass resulting from new nutrient availability. This hypothesis is now tested by considering [NN] estimated from the float observations.

Fig. 7, which represents the monthly climatological basin-scale mean and standard deviation of the nitracline depth and the nitracline steepness, shows that Z_N is always found at depth and does not show a clear seasonal pattern (regardless of the group). In addition, the climatological winter mixed layer is generally shallower than the nitracline (Fig. 5). Hence if we assume that large inputs of nutrients can only be expected when the MLD reaches below the average nitracline depth (Z_N), it is likely that nutrients injections to the photic layer by vertical mixing are low on average, even in winter. A profile-to-profile comparison shows that, in our dataset, a MLD much deeper than the inferred Z_N was observed only once (in an AG structure), on January 23th, 2014. During this event, the MLD reached 171 m (Fig. 4, the maximum value measured by the floats), and the [CHL]tot reached more than 60 mg m^{-3}, *i.e.* twice the mean winter [CHL]$_{tot}$ value (i.e. 0.22 mg m^{-3}). Nutrient may not be measured in surface as they are taken up by phytoplankton. However, the fact that we do not observe NN accumulation in surface means that nutrient refuelling is relatively small or, in some ways, slower than its uptake by biota. Thus, apart from sporadic and rather localized events, it seems likely that large supplies of nutrients to the surface layer are not that common in winter in the GOM as a whole, since the basin scale, monthly climatological basin-scale averages of the MLD are shallower than the estimated depth of the nitracline. Note however that our results are limited by the temporal resolution of the floats' profiles (*i.e.* 14 days), as well as their uneven spatial distribution. This is particularly critical in winter, when the question of the biomass response to MLD deepening events is addressed. The variability in MLD and [CHL]$_{tot}$ (and also in Z_N) deduced from bi-monthly profiles is likely underestimated, because mixing events are shorter than the temporal interval of the measurements. Our dataset only demonstrates that a [CHL]$_{tot}$ increase in winter could be exclusively observed in specific areas and/or episodically (*i.e.* when the MLD is very deep and reaches the nitracline), and that such events do not contribute noticeably to the basin-scale monthly climatological averages.

3.3.3 Nutrient vertical distribution in cyclones and anticyclones

Float data also showed that the mesoscale activity is a main source of variability for the [CHL] field in the deepwater GOM. In particular, a higher chlorophyll concentration was measured in cyclones with respect to anticyclones (Fig. 5). Fig. 7 indicates that the [NN] distribution is also potentially modulated by the presence of mesoscale structures. Thus, Z_N is significantly shallower in cyclonic than in anticyclonic structures ($p < 0.05$), around 80 m in CG and 140 m in AG. This result is consistent with a shallower and intensified DCM in CG than in AG, and in agreement with the conventional view, namely an upward doming of isopycnal surfaces accompanied by a shallowing of the nutricline and an elevated biomass in cyclones (McGillicuddy and Robinson, 1997; McGillicuddy et al., 1998; Oschlies and Garcon, 1998). However, understanding the factors that favor and maintain an enhanced biomass in cyclones is still debated, and the literature addresses a range of processes (see McGillicuddy (2016) for a review). Our approach allows us to explore at least one mechanism: the role of the vertical flux of [NN] from below, *via* vertical diffusion. This flux is generally considered proportional to the nitrate vertical gradient (S_N) through the relationship $F_N = K_z . S_N$ (with Kz the diffusion coefficient, Okubo, 1971). The latest estimate of K_z for the interior Gulf of Mexico is 0.15 10^{-4} $m^2 s^{-1}$ (Ledwell et al., 2016), which is similar to what is observed in the open ocean (e.g. Ledwell et al., 1998). Thus considering K_z constant, a steeper nitracline in CG ($p < 0.05$, Fig. 7) suggests a higher upward diffusive flux in cyclones with respect to anticyclones. Mean F_N in CG and AG were estimated to be around 26 and 23 mmol m^{-2} yr^{-1}, respectively. As a consequence, the NPP (based on the vertical diffusive flux of NN through the pycnocline) would also be higher in CG than in the AG. This higher NPP could thus be a factor contributing to the observed enhanced [CHL] and biomass in cyclones, as already suggested by previous studies (Biggs et al., 1988; Biggs, 1992; Biggs and Müller-Karger, 1994; Yoder and Mahood, 1983; Zimmerman and Biggs, 1999), although it is difficult to assess with our database. Regenerated production, local regeneration (Belabbassi et al., 2005) and grazing (Banse, 1995) may also have a fundamental influence, but the answer to this question requires other measurements that are not at our disposal (e.g. oxygen).

4 Summary and conclusions

The use of profiling floats equipped with biogeochemical sensors provide continuous vertical profile data over wide areas that cannot be obtained otherwise at reasonable cost. The recent deployment of such platforms in the Gulf of Mexico (GOM) generated a remarkable and unique dataset which covers a five-year period. It allowed us to study the variability in phytoplankton biomass using *in situ* bio-optical data across the region, at a spatio-temporal resolution not reported before. Measurements provided information about the seasonal cycle at the surface and at depth, allowing to study the influence of physical processes on the deep chlorophyll maximum (DCM), and the identification of the Gulf of Mexico (GOM) as an oligotrophic system (see Fig. 8 for a conceptual view).

(1) The surface chlorophyll ($[CHL]_{surf}$) annual pattern viewed by satellite is confirmed, and mixed layer depth (MLD) dynamics appears to be the main factor controlling this cycle.

(2) When considering the integral content of chlorophyll ($[CHL]_{tot}$), no seasonal variability is observed.

(3) $[CHL]_{tot}$ combined with the analysis of backscattering (bbp) data suggest that the total phytoplankton biomass is relatively constant at an annual scale, and that the winter increase in $[CHL]_{surf}$ is primarily associated with a vertical redistribution of chlorophyll and/or photoacclimation processes, rather than a true biomass increase (Fig. 8).

(4) In addition, our observations show that the winter mixed layer is generally not deep enough to reach the nitracline. The sampling, however, only allows to reach conclusions in a broad sense. Therefore, we suggest that, on a climatological basin-scale average, a relatively small amount of nutrients are potentially injected to the surface layer through vertical mixing. This does not discard the fact that at short time-scales (days to weeks), events may result in high nutrient inputs to the photic layer which translate in a local phytoplankton bloom, particularly during winter storms. Our interpretation is that the net effect of those blooms is not big enough to determine the basin scale averages of surface chlorophyll content, hence nutrient supply by winter mixing is not necessarily the main cause of the seasonal, basin-scale variability of surface chlorophyll content.

(5) Float profiles also reveal the subsurface CHL dynamics which cannot be determined by satellite observations. The temporal variability of the deep chlorophyll maximum (DCM) appears coherent with isopycnal vertical excursions, and a shallower and intensified DCM is found in cyclonic-like structures (Fig. 8), *i.e.* when isopycnals are uplifted.

(6) The subsurface [CHL] increase in cyclones is also accompanied by a noticeable bbp increase, supporting that phytoplankton biomass is higher than in anticyclones. A potential but not conclusive explanation is a higher nutrient diffusive flux in cyclones that could contribute to strengthen the new primary production. This suggests that, at the annual scale, the impact of mesoscale features on the phytoplankton biomass may be more important than seasonal processes.

(7) This analysis mainly considered the ecosystem from a “bottom-up” perspective, and we focus mostly on resources regulating phytoplankton growth (light and nutrients) rather than factors influencing losses (grazing, mortality). Other processes, such as submesoscale features (Klein and Lapeyre, 2009) or river run-off (Lohrenz et al. 1997) were not addressed in this study, although they could potentially impact the [CHL] distribution, particularly at shorter spatio-timescales than the ones analyzed in this study (Johens and DiMarco, 2008).

(8) Further deployments of bio-optical profiling floats in the GOM equipped with other biogeochemical sensors, such as nitrate (Johnson and Coletti, 2002; Pasqueron de Fommervault et al., 2015) or oxygen (Körtzinger et al., 2004; Riser and Johnson, 2008), and an increase in the temporal resolution of the profiles would significantly improve our understanding of the mechanisms controlling biomass variability and primary production in the GOM.

(9) Another realistic alternative lies on the use of coupled biochemical/physical models to take advantage of the comprehensive 4D vision they provides in terms of physics, nutrient dynamics and simulated biological processes. However, at this time, the realism of numerical tools still needed to be improved in the GOM. The major barrier to this was the lack of *in situ* observations over the water column (specifically in deep waters) which remain essential for model validation (Walsh et al., 1989). This valuable dataset has recently been used to calibrate a coupled biochemical/physical model (NEMO-PISCES) and to evaluate its performances in the GOM (Damien et al., submitted). The model results are consistent with the hypothesis stated in this work, but also highlights that the BOEM floats’ sampling scheme is unable to resolve all the scales of temporal and spatial variability.

Acknowledgements

The APEX floats were part of the ‘‘Lagrangian Study of the Deep Circulation in the Gulf of Mexico’’, funded by the Bureau of Ocean and Energy Management, USA. Data acquisition and preprocessing thanks to H. Furey, T McKee, and A. Ramsey (Woods Hole Oceanographic Institution). Nutrient data were measured during the XIXIMI-2 and XIXIMI-3 cruises, funded by INECC-SEMARNAT, FOINS-CONACYT, Mexico. O. Pasqueron de Fommervault acknowledges a postdoctoral scholarship from CICESE, funded via a grant of the National Council of Science and Technology of Mexico - Secretariat of Energy -Hidrocarbons Trust, project 201441. This is a contribution of the Gulf of Mexico Research Consortium (CIGoM).

References

Antoine, D., Siegel, D. A., Kostadinov, T., Maritorena, S., Nelson, N. B., Gentili, B., Vellucci, V., and Guillocheau, N.: Variability in optical particle backscattering in contrasting bio-optical oceanic regimes, Limnol. Oceanogr., 56, 955–973, 2011.

Armstrong, F. A. J., Stearns, C. R., and Strickland, J. D. H.: The measurement of upwelling and subsequent biological process by means of the Technicon Autoanalyzer® and associated equipment, Deep-Sea Res. Oceanogr. Abstr., 14, 3, 381-389, 1967.

Banse, K.: Zooplankton: Pivotal role in the control of ocean production I. Biomass and production, ICES J. Mar. Sci., 52, 3-4, 265-277, 1995.

Behrenfeld, M. J., and Boss, E.: The beam attenuation to chlorophyll ratio: an optical index of phytoplankton physiology in the surface ocean? Deep-Sea Res. Pt. I, 50, 12, 1537-1549, 2003.

Behrenfeld, M. J., and Boss, E.: Beam attenuation and chlorophyll concentration as alternative optical indices of phytoplankton biomass, J. Mar. Res., 64, 3, 431-451, 2006.

Behrenfeld, M. J., Boss, E., Siegel, D.A., and Shea, D.M.: Carbon-based ocean productivity and phytoplankton physiology from space, Global Biogeochem. Cy., 19, 1006, doi:10.1029/2004GB00229, 2005.

Behrenfeld, M. J., O'Malley, R. T., Boss, E. S., Westberry, T. K., Graff, J. R., Halsey, K. H., A.J., Milligan, D. A., Siegel and Brown, M. B.: Revaluating ocean warming impacts on global phytoplankton. Nat. Clim. Change, 6(3), 323-330, 2016.

Belabbassi, L., Chapman, P., Nowlin, W. D., Jochens, A. E., and Biggs, D. C.: Summertime nutrient supply to near-surface waters of the northeastern Gulf of Mexico: 1998, 1999, and 2000, Gulf of Mexico Science, 23, 2, 137, 2005.

Biggs, D. C.: Nutrients, plankton, and productivity in a warm-core ring in the western Gulf of Mexico, J. Geophys. Res., 97, C2, 2143-2154, 1992.

Biggs, D. C., and Müller-Karger, F. E.: Ship and satellite observations of chlorophyll stocks in interacting cyclone-anticyclone eddy pairs in the western Gulf of Mexico, J. Geophys. Res., 99, C4, 7371-7384, 1994.

Biggs, D. C., and Ressler, P. H.: Distribution and abundance of phytoplankton, zooplankton, ichthyoplankton, and micronekton in the deepwater Gulf of Mexico, Gulf of Mexico Science, 19, 1, 7-29, 2001.

Biggs, D., Wourmut, J., Mc Eachran, J., Brooks, D., and Kelly, F.: Multi-disciplinary study of Marn-and Cold core rings in the Gulf of Mexico, Congreso Iberoamericano y del Caribe, Punta de Piedras, Nueva Esparta, Venezuela. 8-15, 1988.

Boss, E., Swift, D., Taylor, L., Brickley, P., Zaneveld, R., Riser, S., Perry, M.J., and Strutton, P. G.: Observations of pigment and particle distributions in the western North Atlantic from an autonomous float and ocean color satellite, Limnol. Oceanogr., 53, 5, 2112, 2008.

Briggs, N., Perry, M. J., Cetinić, I., Lee, C., D'Asaro, E., Gray, A. M., and Rehm, E.: High-resolution observations of aggregate flux during a sub-polar North Atlantic spring bloom, Deep-Sea Res. Pt. I, 58, 10, 1031-1039, 2011.

Bunge, L., Ochoa, J., Badan, A., Candela, J., and Sheinbaum, J.: Deep flows in the Yucatan Channel and their relation to changes in the Loop Current extension, J. Geophys. Res., 107, C12, 2002.

Cullen, J. J.: The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a, Can. J. Fish. Aquat. Sci., 39, 5, 791-803, 1982.

Cullen, J. J., and Lewis, M. R.: Biological processes and optical measurements near the sea surface: Some issues relevant to remote sensing, J. Geophys. Res., 100, C7, 13255-13266, 1995.

Cunningham, A., Cid, A., and Buma, A. G. J.: Variability of in-vivo chlorophyll fluorescence and its implication for instrument development in bio-optical oceanography, Sci. Mar., 60, 309–315, 1996.

Damien, P., Pasqueron de Fommervault, O., Sheinbaum, J., Jouanno, J., and Duteil O.: Partitioning of the Gulf of Mexico based on the seasonal and interannual variability of chlorophyll concentration. J. Geophys. Res., submitted.

de Boyer Montégut, C., Madec, G., Fischer, A. S., Lazar, A., and Iudicone, D.: Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology, J. Geophys. Res., 109, C12, 2004.

Donohue, K., Hamilton, P., Leaman, K. Leben, R., Prater, M., Waddell, E. and Watts. R.: Exploratory Study of Deepwater Currents in the Gulf of Mexico, Vol. I: Executive Summary and Vol. II: Technical Report. OCS Study MMS 2006-073, 2006-074, 2007.

Donohue, K., Hamilton, P., Leben, R., Watts R., and Waddell, E.: Study of Deepwater Currents in the Northwestern Gulf of Mexico,Vol. I: Executive Summary and Vol II: Technical Report. OCS Study MMS 2008-030 and 2008-031 Volume I - 73 pgs and Volume II - 375 p, 2008.

Dufois, F., Hardman-Mountford, N. J., Greenwood, J., Richardson, A. J., Feng, M., Herbette, S., J. and Matear, R.: Impact of eddies on surface chlorophyll in the South Indian Ocean, J. Geophys. Res., 119, 8061–8077, 2014.

Elliott, B. A.: Anticyclonic rings in the Gulf of Mexico, J. Phys. Oceanogr., 12, 11, 1292-1309, 1982.

El-Sayed, S.Z.: Primary productivity and standing crop of phytoplankton, pp. 8-13. In: Chemistry, primary productivity, and benthic algae of the Gulf of Mexico. V.C. Bushnell (e.d.). Americain Geographical Society, New York, 1972.

Falkowski, P., and Kiefer, D. A.: Chlorophyll a fluorescence in phytoplankton: relationship to photosynthesis and biomass. J. Plankton Res., 7, 5, 715-731, 1985.

Fennel, K., and Boss, E.: Subsurface maxima of phytoplankton and chlorophyll: steady state solutions from a simple model. Limnol. Oceanogr, 48, 1521–1534, 2003.

Fennel, K., Hetland, R., Feng, Y., and DiMarco, S.: A coupled physical-biological model of the Northern Gulf of Mexico shelf: model description, validation and analysis of phytoplankton variability, Biogeosciences, 8, 7, 1881-1899, 2011.

Gaube, P., McGillicuddy, D. J., Chelton, D. B., Behrenfeld, M. J., and Strutton, P. G.: Regional variations in the influence of mesoscale eddies on near- surface chlorophyll, J. Geophys. Res., 119, 12, 8195-8220, 2014.

Geider, R. J.: Light and temperature dependence of the carbon to chlorophyll a ratio in microalgae and cyanobacteria: implications for physiology and growth of phytoplankton. New Phytologist, 106, 1, 1-34, 1987.

Gordon, L. I., Jennings Jr, J. C., Ross, A. A., and Krest, J. M.: A suggested protocol for continuous flow automated analysis of seawater nutrients (phosphate, nitrate, nitrite and silicic acid) in the WOCE Hydrographic Program and the Joint Global Ocean Fluxes Study, WOCE Operations Manual, Part, 3, 3, 91-1, 1993.

Green, R. E., Bower, A. S., and Lugo-Fernández, A.: First autonomous bio-optical profiling float in the Gulf of Mexico reveals dynamic biogeochemistry in deep waters, PloS one, 9, 7, e101658, doi: 10.1371/journal.pone.0101658, 2014.

Guinet, C., Xing, X., Walker, E., Monestiez, P., Marchand, S., Picard, B., Jaud, T., Authier, M., Cotte, C., Diamond, E., Diamond, E., Antoine, D., Lovell, P., Blain, S., D'Ortenzio, F., and Claustre, H.: Calibration procedures and first dataset of Southern Ocean chlorophyll a profiles collected by elephant seals equipped with a newly developed CTD-fluorescence tags, Earth Syst. Sci. Data, 5, 1, 15-29, 2013.

Halsey, K. H., and Jones, B. M.: Phytoplankton strategies for photosynthetic energy allocation. Annu. Rev. Mar. Sci 7, 265-297, 2015.

Hamilton, P.: Eddy statistics from Lagrangian drifters and hydrography for the northern Gulf of Mexico slope, J. Geophys. Res., 112, C9, 2007a.

Hamilton, P. and Lee, T. N.: Eddies and Jets Over the Slope of the Northeast Gulf of Mexico, in Circulation in the Gulf of Mexico: Observations and Models, eds W. Sturges and A. Lugo-Fernandez, American Geophysical Union, Washington, D. C., doi:10.1029/161GM010, 2005.

Hamilton, P.: Deep-Current Variability near the Sigsbee Escarpment in the Gulf of Mexico, J. Phys. Oceanogr, 37(3), 2007b.

Hamilton, P., Berger, T. J., and Johnson, W.: On the structure and motions of cyclones in the northern Gulf of Mexico, J. Geophys. Res., 107, C12, 2002.

Hamilton, P., Bower, A., Furey, H., Leben, R.R., and Pérez-Brunius P.: Deep Circulation in the Gulf of Mexico: A Lagrangian Study, U.S. Dept. of the Interior, Bureau of Ocean Energy Management, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study BOEM 20166081, 289 pp., 2016a. (Available online at https://www.boem.gov/ESPIS/5/5583.pdf).

Hamilton, P., Lugo-Fernández, A. and Sheinbaum, J.: A Loop Current experiment: Field and remote measurements, Dyn. Atmos. Oceans., 76 , pp.156-173, 2016b.

Heileman, S., and Rabalais, N.: XV-50 Gulf of Mexico: LME# 5. The UNEP Large Marine Ecosystem Report. A perspective on the changing condition in LMEs of the world's Regional Seas, United Nations Environment Programme, Nairobi, Kenya, UNEP Regional Seas Report and Studies, 182, 637-688, 2009.

Huot, Y., Morel, A., Twardowski, M. S., Stramski, D., and Reynolds, R. A.: Particle optical backscattering along a chlorophyll gradient in the upper layer of the eastern south Pacific Ocean, Biogeoscience, 5, 495–507, 2008.

Jakobsen, H. H., and Markager, S.: Carbon-to-chlorophyll ratio for phytoplankton in temperate coastal waters: Seasonal patterns and relationship to nutrients. Limnol. Oceanogr, 61(5), 1853-1868, 2016.

Jochens, A. E., and DiMarco, S. F.: Physical oceanographic conditions in the deepwater Gulf of Mexico in summer 2000–2002. Deep-Sea Res. Pt. II, 55, 24, 2541-2554, 2008.

Johnson, K. S., and Coletti, L. J.: In situ ultraviolet spectrophotometry for high resolution and long-term monitoring of nitrate, bromide and bisulfide in the ocean, Deep-Sea Res. Pt. I, 49, 7, 1291-1305, 2002.

Johnson, K. S., Berelson, W. M., Boss, E., Chase, Z., Claustre, H., Emerson, S. R., Gruber, N., Körtzinger, A., Perry, M.J., and Riser, S. C.: Observing biogeochemical cycles at global scales with profiling floats and gliders prospects for a global array, Oceanography, 22, 3, 216-225, 2009.

Jolliff, J. K., Kindle, J. C., Penta, B., Helber, R., Lee, Z., Shulman, I., Arnone, R., and Rowley, C. D.: On the relationship between satellite-estimated bio-optical and thermal properties in the Gulf of Mexico, J. Geophys. Res., 113, G1, 2008.

Jouanno, J., Ochoa, J., Pallàs-Sanz, E., Sheinbaum, J., Andrade-Canto, F., Candela, J., and Molines, J.-M.: Loop Current Frontal Eddies: Formation along the Campeche Bank and Impact of Coastally Trapped Waves. J. Phys. Oceanogr., 46(11), 3339–3363, doi.org/10.1175/JPO-D-16-0052.1, 2016.

Kamykowski, D., and Zentara, S. J.: Predicting plant nutrient concentrations from temperature and sigma-t in the upper kilometer of the world ocean, Deep-Sea Res. Pt. I, 33, 1, 89-105, 1986.

Kiefer, D. A.: Chlorophyll a fluorescence in marine centric diatoms: responses of chloroplasts to light and nutrient stress, Mar. Biol., 23, 1, 39-46, 1973.

Kitchen, J., and Zaneveld, J.R.: On the noncorrelation of the vertical structure of light scattering and chlorophyll-a in case I waters, J. Geophys. Res., 95, 20237–20246, 1990.

Klein, P., and Lapeyre, G.: The oceanic vertical pump induced by mesoscale and submesoscale turbulence. Annual review of marine science, 1, 351-375, 2009.

Körtzinger, A., Schimanski, J., Send, U., and Wallace, D.: The ocean takes a deep breath, Science, 306, 5700, 1337-1337, 2004.

Koblenz-Mishke, O. J., Volkovinsky, V. K., and Kabanova, J. C.: Plankton primary production of the world ocean, pp. 183-193. In: Scientific Exploration of the south pacific. W.W. Wooster (e.d.). National Academy of Science, Washington, DC., 1970.

Kouketsu, S., Tomita, H., Oka, E., Hosoda, S., Kobayashi, T., and Sato, K.: The role of meso-scale eddies in mixed layer deepening and mode water formation in the western North Pacific, Journal of Oceanography, 68, 63–77, 2012.

Lavigne, H., D'Ortenzio, F., Claustre, H., and Poteau, A.: Towards a merged satellite and in situ fluorescence ocean chlorophyll product, Biogeosciences, 9, 6, 2111-2125, 2012.

Leben, R. R., and Born, G. H.: Tracking Loop Current eddies with satellite altimetry, Adv. Space Res., 13,11, 325-333, 1993.

Ledwell, J. R., He, R., Xue, Z., DiMarco, S. F., Spencer, L. J., and Chapman, P.: Dispersion of a tracer in the deep Gulf of Mexico, J. Geophys. Res., 121, 1110-1132, doi:10.1002/2015JC011405, 2016.

Ledwell, J. R., Watson, A. J., and Law, C. S.: Mixing of a tracer in the pycnocline, J. Geophys. Res., 103, C10, 21499-21529, 1998.

Linacre, L., Lara-Lara, R., Camacho-Ibar, V., Herguera, J. C., Bazán-Guzmán, C., and Ferreira-Bartrina, V.: Distribution pattern of picoplankton carbon biomass linked to mesoscale dynamics in the southern Gulf of Mexico during winter conditions, Deep-Sea Res. Pt. I, 106, 55-67, 2015.

Lohrenz, S. E., Fahnenstiel, G. L., Redalje, D. G., Lang, G. A., Chen, X., and Dagg, M. J.: Variations in primary production of northern Gulf of Mexico continental shelf waters linked to nutrient inputs from the Mississippi River. Mar. Ecol. Prog. Se., 155, 45-54, 1997.

Loisel, H. and Morel, A.: Light scattering and chlorophyll concentration in case 1 waters: A reexamination. Limnol. Oceanogr. 43, 847–858, 1998.

Lorenzen, C. J.: A method for the continuous measurement of in vivo chlorophyll concentration. Deep-Sea Res. Oceanogr. Abstr., 13, 2, 223-227, 1966.

Mann, K. H., and Lazier, J. R. N.: Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans, Wiley-Blackwell, Malden, Mass, 2006.

Mayot, N., D'Ortenzio, F., Taillandier, V., Prieur, L., Pasqueron de Fommervault, O., Claustre, H., Bosse, A., Testor, P., and Conan, P.: Physical and biogeochemical controls of the phytoplankton blooms in North- Western Mediterranean Sea: A multiplatform approach over a complete annual cycle (2012–2013 DEWEX experiment), J. Geophys. Res., doi: 10.1002/2016JC012052, 2017.

McGillicuddy, D.J.: Mechanisms of physical-biological-biogeochemical interaction at the oceanic mesoscale, Annual Review of Marine Science 8, 125–159, 2016.

McGillicuddy, D. J., and Robinson, A. R.: Eddy-induced nutrient supply and new production in the Sargasso Sea. Deep-Sea Res. Pt. I, 44, 8, 1427-1450, 1997.

McGillicuddy, D.J., Robinson, A., Siegel, D., Jannasch, H., Johnson R., Dickey, T., McNeil, J., Michaels, A., and Knap, A.: Influence of mesoscale eddies on new production in the Sargasso Sea, Nature, 394, 6690, 263–266, 1998.

McGillicuddy, D. J., Anderson, L. A., Bates, N. R., Bibby, T., Buesseler, K. O., Carlson, C. A., Davis, C. S., Ewart, C., Falkowski, P. G., Goldthwait, S. A., Hansell, D. A., Jenkins, W. J., Johnson, R., Kosnyrev, V. K., Ledwell, J. R., Li, Q. P., Siegel, D. A., and Steinberg, D. K.: Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms, Science, 316, 1021–1026, 2007.

Melo González, N. M., Müller-Karger, F. E., Estrada, S. C., De Los Reyes, R. P., Del Rio, I. V., Pérez, P. C., and Arenal, I. M.: Near-surface phytoplankton distribution in the western Intra-Americas Sea: The influence of El Nino and weather events, J. Geophys. Res., 105, C6, 14029, 2000.

Michaels, A. F. and Knap, A. H.: Overview of the U.S. JGOFS Bermuda Atlantic Time-series Study and the Hydrostation S program, Deep-Sea Res. Pt. II, 43, 157–198, doi:16/0967-0645(96)00004-5, 1996.

Mignot, A., Claustre, H., D'Ortenzio, F., Xing, X., Poteau, A., and Ras, J.: From the shape of the vertical profile of in vivo fluorescence to Chlorophyll-a concentration, Biogeosciences, 8, 8, 2391, 2011.

Mignot, A., Claustre, H., Uitz, J., Poteau, A., D'Ortenzio, F., and Xing, X.: Understanding the seasonal dynamics of phytoplankton biomass and the deep chlorophyll maximum in oligotrophic environments: A Bio-Argo float investigation, Global Biogeochem. Cy., 28, 8, 856-876, 2014.

Mitchell, B.G., and Kiefer, D.A.: Variability in pigment specific particulate fluorescence and absorption spectra in the northeastern Pacific Ocean, Deep-Sea Res. Pt. I, 35, 665–689, 1988.

Morel, A and Maritorena, S.: Bio-optical properties of oceanic waters: a reappraisal, J. Geophys. Res., 106, 7163–7180, 2001.

Müller-Karger, F. E., Walsh, J. J., Evans, R. H., and Meyers, M. B.: On the seasonal phytoplankton concentration and sea surface temperature cycles of the Gulf of Mexico as determined by satellites, J. Geophys. Res., 96 C7, 12645-12665, 1991.

Müller-Karger, F. E., Smith, J. P., Werner, S., Chen, R., Roffer, M., Liu, Y., Muhling, B., Lindo-Atichati, D., Lamkin J., Cerdeira-Estrada, S. and Enfield, D. B.: Natural variability of surface oceanographic conditions in the offshore Gulf of Mexico, Prog Oceanogr., 134, 54-76, 2015.

Nababan, B., Müller-Karger, F. E., Hu, C., and Biggs, D. C.: Chlorophyll variability in the northeastern gulf of mexico, Int. J. Remote Sens., 32, 23, 8373-8391, 2011.

Nowlin, W. D., and McLellan, H. J.: A characterization of Gulf of Mexico waters in winter, J. Mar. Res., 25,1, 29, 1967.

Okubo, A.: Oceanic diffusion diagrams, Deep-Sea Res. Oceanogr. Abstr., 18, 8, 789-802, 1971.

Omand, M. M., and Mahadevan, A.: The shape of the oceanic nitracline, Biogeosciences, 12, 11, 3273, 2015.

Oschlies, A., and Garcon, V.: Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean, Nature, 394, 6690, 266–269, 1998.

Pasqueron de Fommervault, O., D'Ortenzio, F., Mangin, A., Serra, R., Migon, C., Claustre, H., Lavigne, H., Ribera d'Alcala, M., Prieur, L., Taillandier, V., Schmechtig, C., Poteau, A., Leymarie, E., Dufour, A., Besson, F., and Obolensky, G.: Seasonal variability of nutrient

concentrations in the Mediterranean Sea: Contribution of Bio-Argo floats, J. Geophys. Res., 120, 8528–
8550, doi:10.1002/2015JC011103, 2015.

Penduff, T., Barnier, B., Dewar, W.K. and O'Brien, J.J.: Dynamical Response of the Oceanic Eddy Field to the North Atlantic Oscillation: A Model–Data Comparison. J. Phys. Oceanogr., 34, 2615–2629, doi.org/10.1175/JPO2618.1, 2004.

Qian, Y., Jochens, A. E., Kennicutt II, M. C., and Biggs, D. C.: Spatial and temporal variability of phytoplankton biomass and community structure over the continental margin of the northeast Gulf of Mexico based on pigment analysis, Cont. Shelf Res., 23, 1-17, 2003.

Riser, S. C., and Johnson, K. S.: Net production of oxygen in the subtropical ocean, Nature, 451, 7176, 323-325, 2008.

Roemmich, D. H., Davis, R. E., Riser, S. C., Owens, W. B., Molinari, R. L., Garzoli, S. L., and Johnson, G. C.: The argo project. global ocean observations for understanding and prediction of climate variability, Scripps institution of oceanography, La Jolla, C.A, 2003.

Salmerón-García, O., Zavala-Hidalgo, J., Mateos-Jasso, A., and Romero-Centeno, R.: Regionalization of the Gulf of Mexico from space-time chlorophyll-a concentration variability, Ocean Dyn., 61, 4, 439-448, 2011.

Schmechtig, C., Claustre, H., Poteau, A., and D'Ortenzio, F.: Bio-Argo quality control manual for the Chlorophyll-A concentration, doi.org/10.13155/35385, 2014.

Schmitz, W. J.: Cyclones and Westward Propagation in the Shedding of Anticyclonic Rings from the Loop Current, in Circulation in the Gulf of Mexico: Observations and Models, eds. Sturges and Lugo-Fernandez, American Geophysical Union, Washington, D. C., doi: 10.1029/161GM18, 2005.

Sheinbaum, J., Badan, A., Ochoa. J., Candela, J., Rivas, D. and Gonzalez, J. I.: Full-Water Column Current Observations in the Central Gulf of Mexico, Final Report. OCS Study MMS 2007-022, 2007.

Siegel, D. A., Behrenfeld, M.J., Maritorena, S., McClain, C.R., Antoine, D., Bailey, S.W., Bontempi P.S., Boss, E.S., Dierssen, H.M., Doney, S.C., Eplee Jr, R.E., Evans, R.H., Feldman, G.C., Fields, E., Franz, B.A., Kuring, N.A., Mengelt, C., Nelson, N.B., Patt, F.S., Robinson, W.D., Sarmiento, J.L., Swan, C.M., Werdell, P.J., Westberry, T.K., Wilding, J.G., and Yoder, J.A.: Regional to global assessments of phytoplankton dynamics from the SeaWiFS mission, Remote Sens. Environ., 135, 77-91, doi:10.1016/j.rse.2013.03.025, 2013.

Strickland, J. D. H.: Production of organic matter in the primary stages of the marine food chain, Chem. oceanogr., 1, 477-610, 1965.

Sturges, W., and Leben, R.: Frequency of ring separations from the Loop Current in the Gulf of Mexico: A revised estimate, J. Phys. Oceanogr., 30, 7, 1814-1819, 2000.

Toner, M., Kirwan, A. D., Poje, A. C., Kantha, L. H., Müller-Karger, F. E., and Jones, C. K. R. T.: Chlorophyll dispersal by eddy-eddy interactions in the Gulf of Mexico, J. Geophys. Res., 108, C4, 2003.

Uitz, J., Claustre, H., Morel, A., and Hooker, S. B.: Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll, J. Geophys. Res., 111, C8, 2006.

Vidal, V., Vidal, F. V., and Pérez-Molero, J. M.: Collision of a Loop Current anticyclonic ring against the continental shelf slope of the western Gulf of Mexico, J. Geophys. Res., 97, C2, 2155-2172, 1998.

Virmani, J. I., and Weisberg, R. H.: Features of the observed annual ocean-atmosphere flux variability on the west Florida shelf, J. climate, 16, 4, 734-745, 2003.

Walsh, J. J., Dieterle, D. A., Meyers, M. B., and Müller-Karger, F. E.: Nitrogen exchange at the continental margin: A numerical study of the Gulf of Mexico, Prog Oceanogr., 23, 4, 245-301, 1989.

Westberry, T. K., Dall'Olmo, G., Boss, E., Behrenfeld, M. J., and Moutin, T.: Coherence of particulate beam attenuation and backscattering coefficients in diverse open ocean environments, Opt. Express, 18, 15419–15425, 2010.

Xing, X., Claustre, H., Blain, S., D’Ortenzio, F., Antoine, D., Ras, J., and Guinet, C.: Quenching correction for in vivo chlorophyll fluorescence acquired by autonomous platforms: A case study with instrumented elephant seals in the Kerguelen region (Southern Ocean), Limnol. Oceanogr. -Meth., 10, 483-495, 2012.

Xue, Z., He, R., Fennel, K., Cai, W. J., Lohrenz, S., and Hopkinson, C.: Modeling ocean circulation and biogeochemical variability in the Gulf of Mexico, Biogeosciences, 10, 11, 7219-7234, 2013.

Yoder, J., and Mahood, A.: Primary production in Loop Current upwelling, Woodward-Clyde Consultants/Skidaway Institute of Oceanography, Southwest Florida Shelf Ecosystems Study-Year, 2, 1983.

Zimmerman, R.A. and Biggs, D.C.: Patterns of distribution of sound-scattering zooplankton in warm- and cold-core eddies in the Gulf of Mexico, from a narrowband acoustic Doppler current profiler survey, J. Geophys. Res., 104:5251-5262, 1999.

Table 2: Practical information about float Mission and α and β coefficients values used for the calibration of fluorescence profiles measured by apex floats.

Float	4902284_ G4901600	4902285_ G4901601	4902286_ G4901602	4902289_ G4901603	4902287_ G4901604	4902290_ G4901606
start date	20 Jul 2011	12 Jan 2012	16 Jan 2012	24 Jun 2012	11 Jul 2012	25 Sep 2012
end date	18 Aug 2013	11 Nov 2015	18 Nov 2015	19 Nov 2015	21 Nov 2015	12 Nov 2015
number of profiles	83	99	99	88	87	81
$\boldsymbol{\alpha}$	0.63	0.63	0.66	0.59	0.60	0.66
$\boldsymbol{\beta}$	0.030	0.050	0.039	0.026	0.031	0.028

Table 2: Seasonal mean and standard deviation of the phytoplankton maximum (DCM_{max}, in mg m^{-3}) and the depth of the phytoplankton maximum (DCM_{Z}, in m). Values were obtained by considering only profiles for which the MLD is shallower than the DCM.

		Dec-Feb	Mar-May	Jun-Aug	Sep-Nov
All	DCM_{max}	0.54±0.13	0.74±0.23	0.64±0.25	0.62±0.27
	DCM_{Z}	69±17	75±19	91±21	82±24
Cyclonic	DCM_{max}	0.53±0.14	0.80±0.23	0.73±0.28	0.70±0.29
	DCM_{Z}	68±19	69±17	82±19	74±20
Anticyclonic	DCM_{max}	0.55±0.08	0.60±0.18	0.53±0.14	0.45±0.12
	DCM_{Z}	75±11	91±15	105±17	100±22

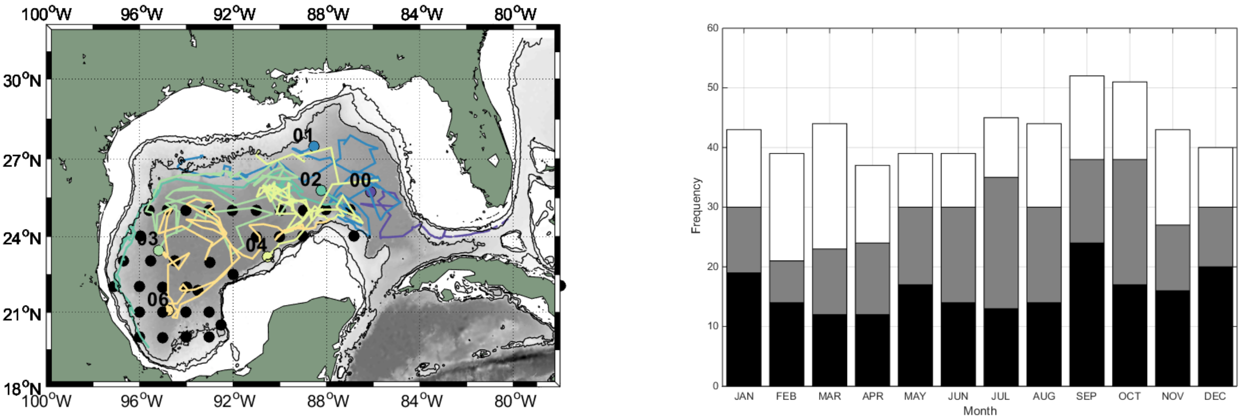

Figure 1: left) Map of the study area, with tracks of BOEM floats (colored lines), and XIXIMI-2 and XIXIMI -3 sampling stations (black circles). Floats position at deployment are indicated by colored circle and numbers. right) Temporal distribution of the profiles acquired by the BOEM (in black cyclonic group profiles, in grey anticyclonic group profiles and in white remaining profiles).

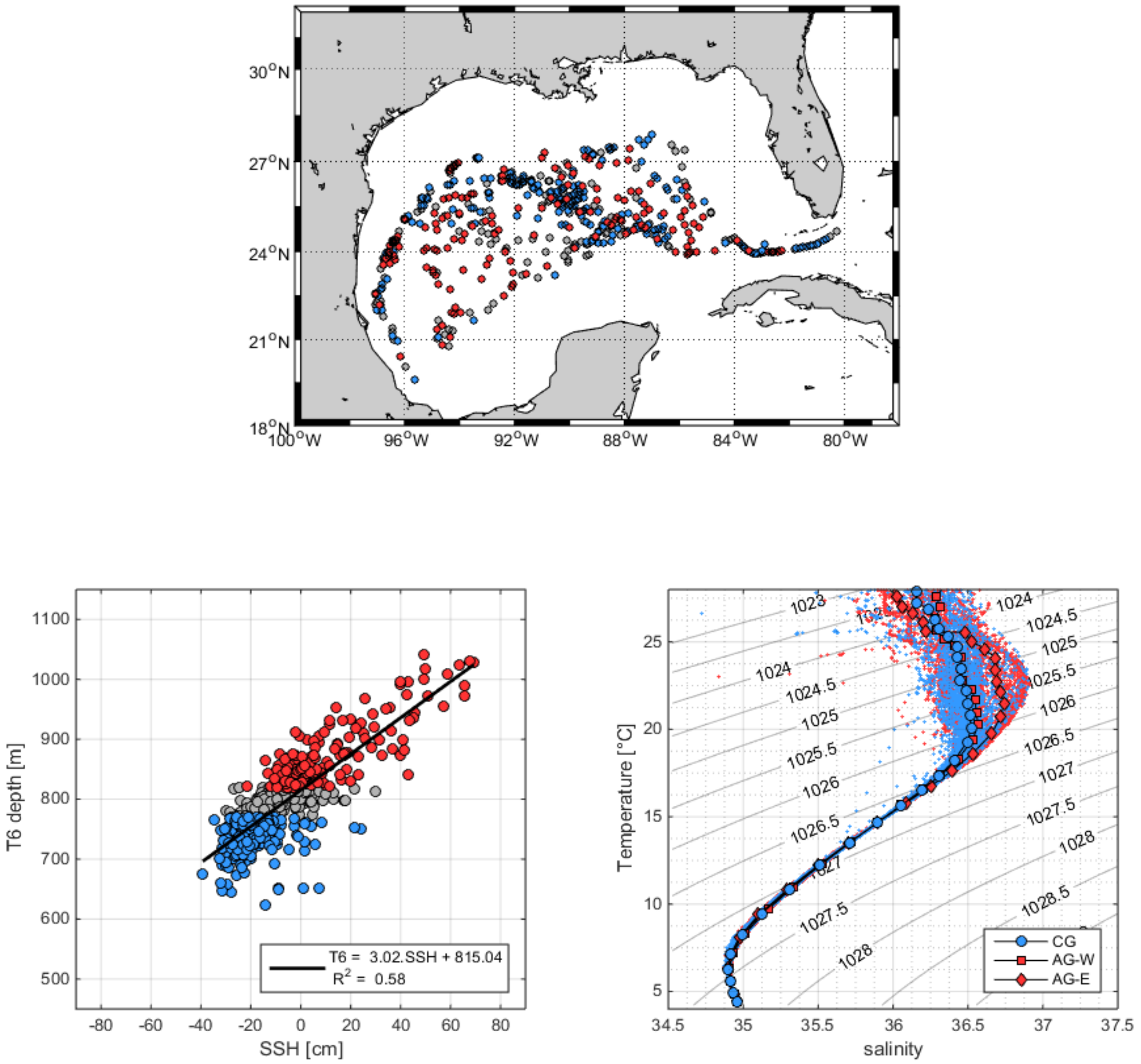

Figure 2: Top) Position of float profiles. Depth of the 6°C-isotherm derived cyclones and anticyclones are given by blue and red circles. Bottom left) Depth of the 6°C-isotherm versus SSH (gridded data with a spatial resolution of 1/8°, produced by Ssalto/Duacs and distributed by AVISO, with support from CNES (http://www.aviso.altimetry.fr/duacs). To remove seasonal steric effects of large-scale heating and cooling of the upper water column, daily mean SSH calculated in the Gulf of Mexico were systematically subtracted from SSH values. Blue points correspond to the cyclonic group, and red points to the anticyclonic group. Bottom right) T/S diagram. Cyclones are identified in blue (blue circles are mean values) and anticyclones in red (red square are profiles acquired at a latitude west of -88° (west GOM) and red diamond are profiles acquired at a latitude east of -88° (east GOM).

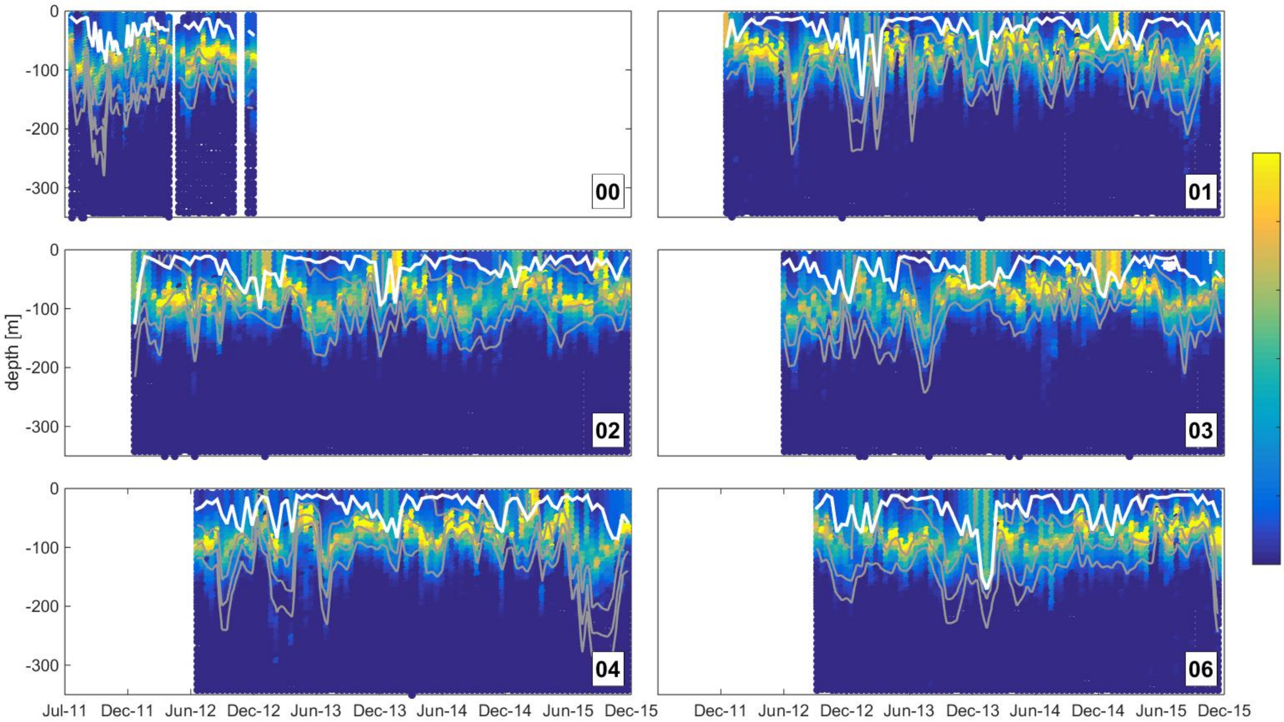

Figure 3: Calibrated [CHL] float transects in mg m-3. Contour plots of density (1024.5 1025.5 1026 kg m-3, grey lines), and mixed layer depth calculated as the depth where the difference of density from the surface reference, fixed at 10 m-depth, is 0.03 kg m-3 (solid white line), are superimposed.

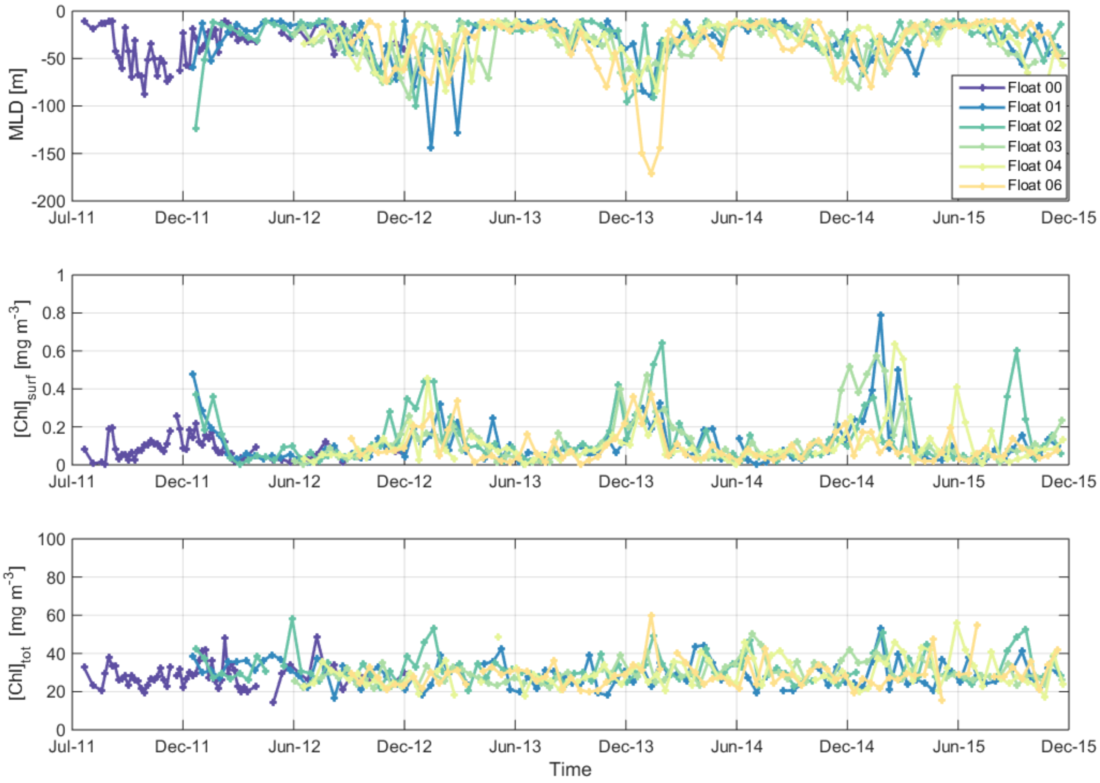

Figure 4: Float time-series of the (top) mixed layer depth, (middle) mean surface chlorophyll concentration and (bottom) integrated content of chlorophyll over the 0-350 m layer.

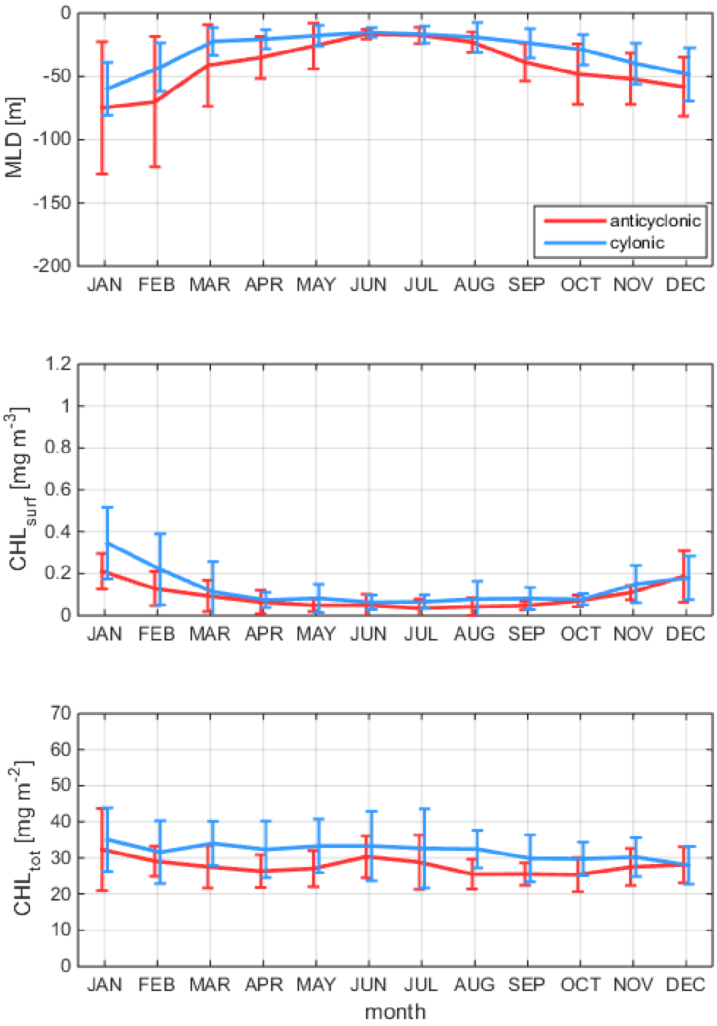

Figure 5: Basin-scale, monthly climatological mean and standard deviation of: (top) the mixed layer depth, (middle) surface chlorophyll and (bottom) integrated chlorophyll over the first 350m. Red (blue) shows statistics for all profiles in anticyclonic (cyclonic) structures.

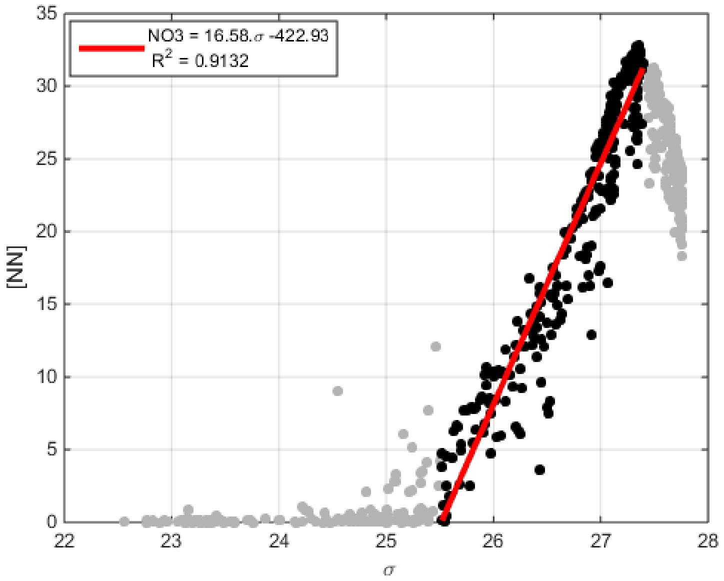

Figure 6: Nitrate + nitrite concentrations versus potential density anomaly data from XIXIMI-2 and XIXIMI-3 survey cruises. Measurements corresponding to the intermediate layer are plotted in black and were used for the determination of the linear fit (see text).

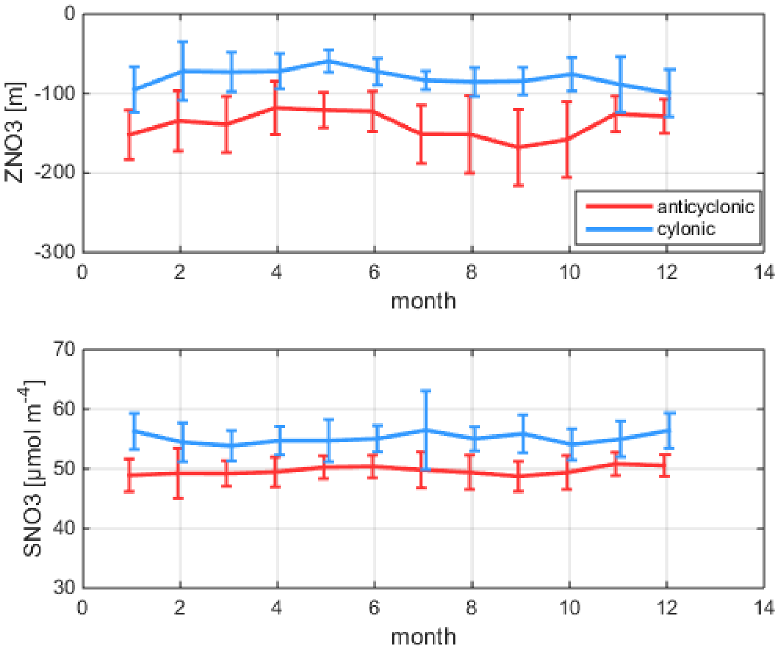

Figure 7: Basin-scale, monthly climatological mean and standard deviation of: (top) the nitracline depth, (bottom) the nitracline steepness. Red (blue) shows statistics for all profiles in anticyclonic (cyclonic) structures. **Red (blue) shows statistics for all profiles in anticyclonic (cyclonic) structures.**

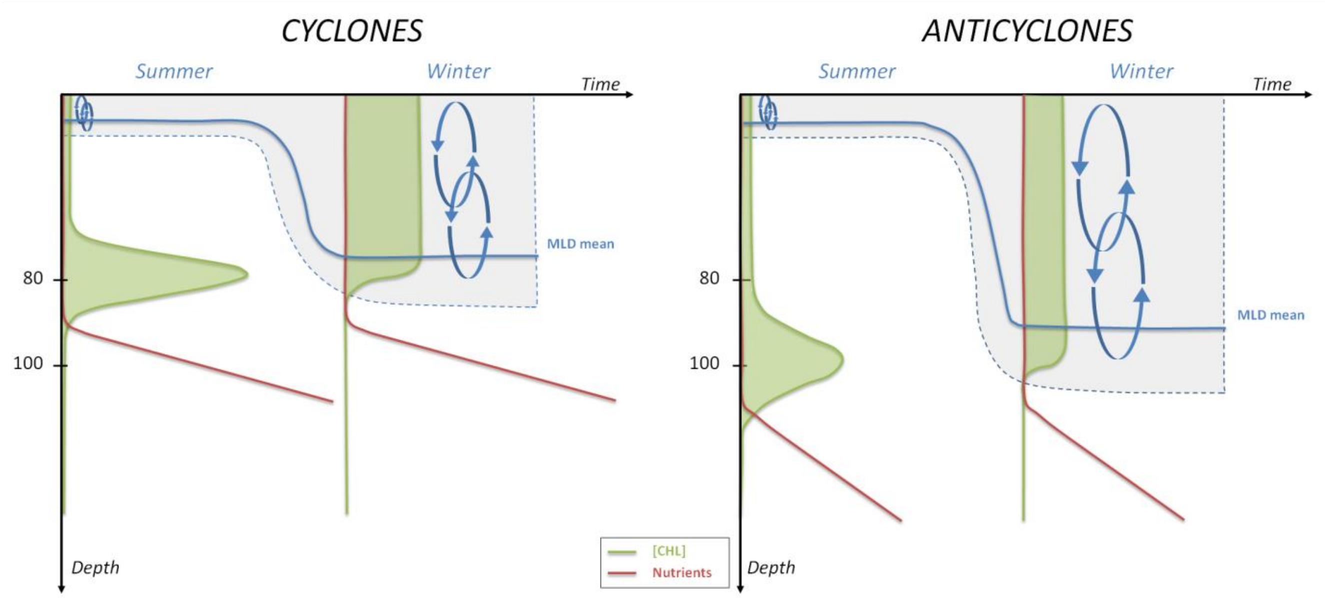

Figure 8: Conceptual view summarizing the basin-scale seasonal changes in the vertical distribution of chlorophyll (green), nutrients (red), mixed layer (shaded gray area) and mean mixed layer depth (blue), in cyclones and anticyclones. The total chlorophyll content is represented by the green area, which is approximately the same in summer than winter for either cyclones or anticyclones. By contrast, the chlorophyll content in cyclones is larger than in anticyclones for either season, showing that cyclones have slightly higher biomass. This may be the result of slightly higher nutrient supply in cyclones due to a steeper nutricline, and hence a higher diffusive flux. Finally, note that the mixed layer does not on average reach the nutricline in winter, but it does reach the deep chlorophyll maximum, resulting in the vertical redistribution of chlorophyll via vertical mixing and/or photoacclimation processes.