

Review of Gonzalez-Gil et al.

**C1:** As the authors state, the manuscript is a resubmission of a manuscript rejected from L&O letters. I was the more critical reviewer and I assure them I did not approach the review with ill will. I am very disappointed by the fact that the authors have resubmitted an at best marginally revised manuscript. While the authors may not agree with reviewer feedback, it does reflect likely reader responses and should be taken seriously. It is in the author's best interest to address reviewer feedback so they can get their point across, even to those of us who are misguided and don't follow the argument they are making. A reviewer's take on a paper is possibly wrong, but those misconceptions need to be addressed for the work to have impact. The review process is entirely voluntary and I have taken considerable time out to provide constructive feedback to help the authors get their message across. The representation of the manuscripts history and reviewer feedback is disingenuous. The 'positive' review was a 263 word summary of some aspects of the paper. That review had no substance. Maybe I am wrong and the DRH has amply been demonstrated, but just listing a bunch of papers that include review papers and restatements of the same points, largely from people working with Behrenfeld who originated the idea, doesn't make a substantive case. This is not to suggest those works aren't good. I find the DRH intriguing and likely applicable in some circumstances, as the authors state, but it will find greater support when critically evaluated. There were many other concerns stated in the prior review that were not disclosed in the manuscripts history or addressed in the revised manuscript. It's up to the authors to reflect upon those points and engage in the review process. I was genuinely excited to see a revision of this manuscript, thus I accepted the review invite. On another note, I am concerned that junior co-authors are being trained to ignore reviewer feedback. The senior authors may also consider the serious burden they put on the review process as outlined by Fenchel et al. <http://www.int-res.com/abstracts/meps/v258/p297-309/>

*AR: We really appreciate the time and effort invested in our manuscript by the reviewer. As reviewers ourselves of many papers, we perfectly understand what this represents and the importance of this voluntary labor, and we always take reviewers' comments seriously. When our paper got rejected in L&O letters, we could not discuss and respond to the reviewer's comments, and we are glad we have a new chance to address them in more depth. We think that, thanks to this, the paper has definitely improved.*

*We believe a key issue in our apparent disagreement with the reviewer is a difference in what we mean by "the DRH," which we will try to clarify in this response and also in the revised manuscript. In our context, "testing the DRH" does not mean evaluating any proposition about large-scale averages in the open North Atlantic. We use "the DRH" to mean a disequilibrium-based view of spring phytoplankton dynamics and, as we indicate in our response to comment C4, other works have addressed the ideas in this view before the formalization of the DRH. This view is not tied to specific methods or scales from Behrenfeld et al.'s own line of work. It is a hypothesis that could be correct or incorrect at Stonehaven, whether it is a good descriptor of the open North Atlantic or not. This is why we decided, after careful consideration, to resubmit the paper in substantially the same form, instead of discarding it.*

*When disclosing the previous history in other journals, we focused on what we thought were the main reasons for its rejection, and copied those comments we considered summarized best these reasons (in particular comments C3, C4 and C7). We have copied an edited part of our previous response to these comments. Our only intention was avoiding a lengthy text, excluding also*

*favorable comments from both reviewers. Nevertheless, we have learnt the lesson and to avoid any misunderstanding in future occasions, we will do better and disclose all the comments.*

**C2:** Gonzalez-Gil et al present an analysis of a 20 year time series of hydrographic data and water column properties from a single station a few miles offshore of Scotland. They use these data to support their hypothesis that this is the first documentation of a hypothesized spring bloom formation mechanism (DRH) for a coastal site.

The manuscript is competently prepared, the presentation is clear, the writing easy to follow. The figures could be improved and the methods are too sparse to judge the manuscript. To my reading, the authors have fundamentally misinterpreted the DRH and instead have a demonstration of classic spring bloom formation in response to relieve from light limitation. The authors have a fine data set that could support a multivariate analysis and descriptive manuscript – if those topics have not been covered in prior publications of this time series, of which there are several citations in the text. Overall, the paper reads to be stretching their data and trying to fit in the focused format of L&O letters. Below I outline my reasoning.

*AR: We thank again the reviewer for all the comments on our manuscript. We address below all the suggestions and concerns one by one, including why we believe the dynamics we find at Stonehaven are not the same as a classic spring bloom but rather fit the core concept of the DRH.*

**C3:** Empirical documentation of the DRH is nearly impossible and has not been accomplished. The disturbance recovery hypothesis was generated using satellite data collected for over a decade across the North Atlantic in regions covering hundreds of kms. The phenomenon of a slight excess in net phytoplankton growth rate ( $r$ ) – on the order of  $0.01 \text{ d}^{-1}$  – emerges from the analysis of this massive, time and space averaged data set. The emergence of a positive  $r$  relies on averaging across a dynamic and heterogeneous ocean. It's a statistical phenomenon that has not been empirically demonstrated by concurrent measurements of  $\mu$  and  $I$  (using author terminology). It has been inferred from subsequent observations. Measurements of  $r$  at the magnitude of  $0.01 \text{ d}^{-1}$  is at least one order of magnitude higher resolution than the dilution method supports (e.g. Chen 2015, Morrison et al. 2017 L&O Methods). The result is a statistical phenomenon that is not currently measurable in situ. This also applies to the assertion that there is a relationship between  $r$  and  $d\mu/dt$ . As an aside, the claim that the DRH has amply been demonstrated is false, to my knowledge and is not supported in the introduction, other than citations of summary/review style papers by the proponents of the DRH. Moreover, other spring bloom formation hypotheses, such as the role of mixing and turbulence do not find evaluation.

*AR: There are two issues here: whether the DRH has been amply demonstrated in the literature on other scales in other places using other methods (like the large-scale spatial statistics the reviewer refers to), and whether that prior demonstration is necessary as a basis for our study. We agree that our summary of the literature papered over a lot of legitimate disagreement, and we have softened our language about the existing DRH literature in the Introduction. However, we do not feel it changes our study either in aims or method: even if the DRH were only a concept and had never been established or tested in the open ocean, one could still examine the relationship among  $r$ ,  $\mu$ , and  $d\mu/dt$  in a well-resolved coastal time series and (locally) test it.*

*We agree that an average  $r$  of  $0.01\text{ d}^{-1}$  must be statistically reconstructed, not measured in situ instantaneously, as we have done by smoothing  $r$  and biomass variability in time to focus on a seasonal scale (see for instance Mignot et al., 2018; Arteaga et al., 2020). However, our argument does not hinge on this value at one instant in time but rather the shape of the seasonal cycle of  $r$  from autumn through late spring, as we explain further under C4.*

*About evaluating the role of mixing and turbulence, we mentioned in the manuscript that the strong winds and tidal currents that occur in the study coastal location (48-m deep) in winter, together with the observations of a vertical homogeneous environment (we observed in general no difference between surface and bottom temperatures and salinities), indicate a well-mixed water column. We address this point in comment C19.*

**C4:** Let's assume the mechanism proposed in the DRH is correct, does it apply to the data on hand? The DRH suggests that  $r$  turns positive not because resources return, but because losses are reduced. That is, the onset of the spring bloom occurs in the depth of the light limitation, in November and December. Figure 4 in Behrenfeld 2010 clearly shows  $r$  turning positive when MLD still increases. Modifications of the original hypothesis stated in 2010 by including light and other factors does not alter this fundamental argument. The increase in MLD is both a proxy for increasing dilution (=decreasing predator prey encounter rates) and continued and increasing light limitation. The data presented in this ms is a beautiful demonstration of the opposite phenomenon: once light limitation is relieved, a positive  $r$  is observed. The timing after the winter solstice is classic for northern temperate waters. Figure 2 in the manuscript clearly shows that the initiation of the bloom occurs when PAR turns from decreasing to increasing. T zero is firmly when  $d\text{PAR}/dt$  is zero.

*AR: The Disturbance Recovery Hypothesis (DRH) claims that the phytoplankton biomass accumulates due to the disequilibrium between phytoplankton growth and loss rates caused by different types of environmental "disturbances" (Behrenfeld and Boss, 2018). This is a broader view than its initial formulation, called the Dilution Recoupling Hypothesis (Behrenfeld, 2010), where the focus was the dilution effect of winter mixing, one of the mechanism that can generate this disequilibrium. As stated in our reply to comment C1, we consider that this view is not tied to any specific scale or methodology, including those in Behrenfeld et al.'s own research line. The importance of this imbalance for phytoplankton blooms has been previously addressed by studies such as Evans and Parslow (1985) and Banse (1994). This imbalance can be due to a reduction in loss rates, as indicated by the reviewer, but also due to an acceleration in the growth rate, if the losses cannot keep pace during that acceleration. This family of disequilibrium-based bloom-formation mechanisms is what we mean by "the DRH", as we now clarify in the text.*

*This family of mechanisms (which we cannot choose among using the data available at Stonehaven) is fundamentally different from what the reviewer calls "a classic spring bloom formation" where "once light limitation is relieved, a positive  $r$  (phytoplankton biomass accumulation rate) is observed". Light limitation is a function of light, not rate of change of light, and so in that classic spring bloom scenario, we would expect  $r$  to become positive after light reached a critical level sometime in spring. However, we observed that 1)  $r$  becomes positive very soon after the winter solstice, when light is **most** limiting in the year, and 2) negative and positive  $r$  occurs respectively before and after the winter solstice at similar light levels (and thus presumably at similar phytoplankton specific growth rates). These observations cannot be*

*explained as the “classic bloom formation” driven by light-limited growth per se, as opposed to the imbalance between light-limited growth and other losses.*

**C5:** While some data are indeed available for 20 years, a lot of the key data are actually only available for a couple years (counts, flow cytometry). I am sensitive to how much work it is to generate these that but given the considerable intra-annual variability in species composition data, the data are really too sparse to support a time series analysis. I was disappointed to realize the sparsity of the data, expecting a 20 year time series based on the abstract and introduction.

*AR: We now clearly indicate in the abstract and at the end of the introduction the type of data that was available for the 21-year time series. All the key data are available for these 21 years: the physicochemical environmental variables, the meteorological information, and the Chl a concentrations (note that almost identical  $r$  values can be estimated using Chl instead of biomass,  $R^2 = 0.99$  in Fig. S5). Those are the ones that allowed us to reach our main conclusions (see Figs. 1, 2, and 4).*

*The cell count data allowed us to estimate a C:Chl seasonality (see Supplementary Notes 4 and 5) and to describe the variability of the phytoplankton biomass composition for 3 years (Fig. 3). We think both analyses complement well our major results, but are not fundamental to reach our main conclusions.*

**C6:** What are the lag phases relating nutrient availability or light availability to phytoplankton growth? Did you do a correlation analysis?

*AR: This is a good suggestion. In fact, during the initial data exploration, we performed regression analyses between net phytoplankton growth rate (i.e. the biomass accumulation rate,  $r$ ) and all the other environmental variables (including light availability, nutrient concentration, salinity, temperature and the difference between surface and bottom salinities and temperatures) around the onset of phytoplankton biomass accumulation (approximately November-February, Fig. 4). Different lag phases were explored, from 0 to approximately 2 months, and we also inspected these relationships for Chl a or phytoplankton biomass. After reviewing our previous regression analyses, we only found two other potential other drivers for  $r$ , surface Total Oxidized Nitrogen concentrations (TOxN) and surface temperature.*

*-In the first case, positive correlations were found between  $r$  and TOxN at different lags. At a 0 lag, we do not think that TOxN is a driver of  $r$  for November-February. At this moment of the year, phytoplankton growth is no nutrient-limited (TOxN is rarely below  $4 \text{ mmol m}^{-3}$ ), but light-limited instead (Cloern, 1999; Harrison and Li, 2008; Regaudie-De-Gioux et al., 2015). We also think that TOxN from several weeks ago can be discarded as a driver, as we consider that it is actually the phytoplankton consumption at lag 0 what largely controls the measured nutrient concentrations (there is a negative relationship between TOxN and phytoplankton biomass). For instance, the very low TOxN concentration observed in summer might largely respond to a large phytoplankton uptake, as occurs in other coastal areas of the North Sea (Moneta et al., 2014)*

*-In the second case, negative correlations were found between  $r$  and temperature. We included now this in the Discussion: “In addition to light variations, other factors might contribute to the observed seasonal pattern in biomass accumulation around the spring bloom onset. For instance, Rose and Caron (2007) showed that decreasing temperatures impact more negatively*

*microzooplankton than phytoplankton maximal growth rates (i.e., measured under resource-saturated conditions, Caron and Rose, 2008; Marañón et al., 2014), which could favor the bloom initiation. In fact, Figure 2 suggests a negative relationship between  $r$  and temperature, as confirmed through previous exploratory analyses. However, considering that phytoplankton community growth rates are temperature-insensitive under strong light limitation (Marañón et al., 2014; Edwards et al., 2016) and that very low chlorophyll concentrations might even reverse the expected relationship between the proportion of phytoplankton production grazed by microzooplankton and temperature (Chen et al., 2012), we hypothesize a lesser role of temperature than light variations. Nevertheless, the contribution of temperature to the observed seasonality around the onset of biomass accumulation has to be further investigated.”*

**C7:** How could observations at a single station reflect the large scale patterns proposed in the DRH? Morison et al. 2020 L&O letters show some semblance of a mechanistic documentation of the DRH by showing phytoplankton grow more rapidly in response to increasing light availability than predator grazing. However, the processes occur much more rapidly, and less linearly than proposed in the DRH, accumulation of biomass occurs on the order of 2-3 days with a significant fraction lost on subsequent days, resulting in a slight net accumulation over a week.

*AR: As mentioned in comments C1, C3 and C4, according to our understanding, the DRH focuses on the mechanisms behind the accumulation of phytoplankton biomass in the spring bloom, but not on a particular spatial scale. We do not make any claims regarding large-scale patterns in the manuscript.*

*As for timescale, this may also be a matter of definitions, and in the introduction, we now better explain what is our understanding of the spring bloom and its initiation. We consider that the spring bloom is usually a much longer event than a net biomass accumulation over a week; it is a period in which positive accumulation rates of phytoplankton biomass ( $r$ ) dominate, allowing the increase in biomass from a seasonal minimum to a seasonal peak. This process of accumulation is not constant. In our study, negative and positive  $r$  probably alternate during several spring bloom days due, for instance, to fast changes in light intensity (Morison et al., 2020). However, a positive  $r$  has to prevail because our weekly samples show an overall seasonal accumulation trend in biomass, starting every year close to the winter solstice (Figs. 1a and 1b). At the seasonal scale (the focus of our study),  $r$  values smoothed in time change from zero to a maximum (Figs. 1c and 2a), implying a non-linear process. Whether we see the spring peak in biomass as a short-term event that begins and ends in spring, or as the culmination of a seasonal process that begins at the winter solstice, is one of the conceptual questions at stake in testing the DRH and distinguishing it from the classic spring bloom concept (see C4 above).*

**C8:** The assumption that the spring bloom is a ‘large accumulation’ is wrong. It’s a lot of biomass but it only represents an accumulation of 2-3 divisions.

*AR: We have modified the sentence by “an accumulation of large phytoplankton biomass”. This is what we meant with “large accumulation of phytoplankton biomass”. However, we consider that a spring phytoplankton bloom can represent more than 2-3 division, especially as 2-3 divisions imply different time spans depending on the dominant phytoplankton species and environmental conditions. Even if this time span is over a week, as stated in comment C7, we still consider that a spring bloom is frequently not so explosive, spanning a longer amount of time.*

**C9:** The testing of the DRH on a single time series is likely to fail, as the DRH is based on averaging over spatial and temporal variability over kms and weeks to arrive at a very small signal.

*AR: We have addressed the concerns about the large spatial scales in our response to comments C1, C3 and C4. To reiterate, we do not use “the DRH” to mean any claim about a large spatial average.*

**C10:** Why were data collected after Dec 2017 not included? Particularly since those would presumably include more of the species composition data.

*AR: The length of this time series analyzed keeps growing every year, and we decided to stop including new information in our analysis in 2019. At that moment, only data until 2017 for all the variables analyzed were processed, verified, and quality controlled in the laboratory.*

*However, we think that 21 years of a very similar seasonal pattern for the onset of phytoplankton biomass accumulation shows enough consistency. The analysis of the species composition data for the whole community (i.e., including flowcytometry data) is an interesting complement to our main conclusions but, as stated in our response to comment C5, these are not the key data and results.*

**C11:** The methods are verbose (e.g. lines 59-64) yet are unclear and too sparse. E.g. what exactly is the Chl a signal? Extracted or some fluorescence?

*AR: We have modified the methods section, including more details and information. About the Chl a signal, we now include in the main text: “For Chl analysis, depending on time of year, a subsample of 1 or 2 L (rarely 500 mL) was filtered through a GF/F filter and stored at -80 °C until it was extracted in acetone and analyzed fluorometrically following the method of Arar and Collins (1992)”*

**C12:** What’s the reference for the kd calculation approach?

*AR: In the Supplementary Note 1 of the submitted version, Devlin et al. (2008), Heath et al. (2017) and Bresnan et al. (2016) were included as references for the Kd calculation approach. We give now more methodological details in both the main text and Supplementary Note 1, including also Heath et al. (2015) as reference and clearly stating that we followed Devlin et al. (2008) to calculate a relationship between Secchi disk depths and Kd for the Stonehaven site.*

**C13:** Why is the analysis based on a C, using an averaged C:Chl a ratio rather than Chla, since the metric of interest are rates of change? The reasoning here needs to be spelled out. I am very surprised at the suitability of this approach, as outlined in the supplemental. Why does it work at all, as there should be many shifts in C: Chl a over seasons, taxa, communities, shifts in abundance etc.

*AR: We transformed Chl a into C biomass for the whole phytoplankton community because “organic carbon is the relevant “currency” with respect to trophic exchange” (Behrenfeld and Boss, 2018). We consider that our estimation of C biomass concentration is a better*

*approximation of the phytoplankton standing stock than Chl a concentration. Calculating rates of change using Chl alone would imply an even starker assumption, that C:chl was completely constant and irrelevant. Nevertheless, we show in Fig. S5 of the supplementary that the  $r$  based on Chl a and the one based on our estimated C biomass are almost identical ( $R^2 = 0.99$ ) and thus, this does not affect our conclusions (see lines 99-100 in Material and Methods).*

**C14:** The sampling is not done in a Lagrangian fashion, how are samples from different dates connected? To what degree are water masses coherent? Could this simply be different water masses?

*AR: We thank the reviewer for this interesting comment. As discussed in the main text, a southward current flows parallel to the coast at a regional scale (Holt and Proctor, 2008; León et al., 2018). We think it is difficult to imagine how this transport could be the main factor explaining the observed seasonal pattern at Stonehaven: one would need to hypothesize mechanisms to maintain a spatial gradient as well as hypothesizing the temporal evolution along that gradient. However, advection might influence the seasonal shape of the biomass accumulation pattern by, for instance, delaying the onset of biomass accumulation as it might bring waters with lower phytoplankton concentration.*

*In light of the reviewer's question we now give further context and reasoning in the Discussion: "Additionally, our study location belongs to an area where strong winds and tidal currents mix and homogenize the environment, allowing only intermittent stratification in summer (Pingree and Griffiths, 1978; Van Leeuwen et al., 2015). The Stonehaven site is often taken to be representative of this area of the Scottish coastal North Sea, identified as a distinct hydrodynamic region (Van Leeuwen et al., 2015). Nevertheless, advective processes such as the mentioned southward coastal flow (Holt and Proctor, 2008; León et al., 2018) could still create some heterogeneity in the region."*

**C15:** What about other potential drivers of  $r$ ? The GAM would allow interpretation of other important factors. Did they all fall short to reveal any patterns, if so, that should be discussed? The description of the statistical methods doesn't allow assessment of what was done.

*AR: As we mentioned in our response to comment C6, during the exploration phase of the data we analyzed and inspected other potential drivers of  $r$ , using linear models and GAMs that included different explanatory variables and exploring their effects at different lags. We now have expanded the statistical methods to mention that we performed previous exploratory analyses to discard some potential environmental drivers.*

**C16:** Figures: the figures are not overwhelming. Simple formatting issues, like using presumably y-axis labels as titles, but more importantly, asking readers to eyeball goodness of fit for two time series presented E.g. S5.

*AR: We have created a new version of Fig. 2 with the y-axis labels placed to the left of the y-axis. Although this is more standard, now the figure is less compact and the label titles are smaller. We leave to the reviewer and editor the decision of which figure version should be kept. About*

*Fig. S5, we have enlarged the  $R^2$  of the linear relationship between the two series ( $R^2 = 0.99$ ) that was already embedded in the figure.*

**C17:** Line [124]: the dominance of small taxa is actually unusual for coastal sites.

*AR: We discuss this in lines 202-204 of the Discussion. We observed this dominance of small taxa in winter, when Chl a and phytoplankton biomass concentrations were low and phytoplankton growth was expected to be very limited due to low light availability. This observation agrees with the results found by Marañón et al. (2012), who through a meta-analysis of a wide range of environmental conditions (including productive coastal environments) showed that the resource availability (for both nutrients and light) is the main driver of the phytoplankton size structure (see also Marañón, 2015; Marañón et al., 2015). In particular, they claim that when resources become more limiting, the dominance of small phytoplankton taxa increases and vice versa. The authors discuss that the advantage of small cells when light is limiting (as in winter in temperate and polar areas) could be due to their smaller package effect. We now write “This observation agrees with the expected dominance of smaller phytoplankton species when resources such as light availability are limiting, even in coastal productive environments (Marañón et al., 2012, 2015).”*

**C18:** Line [175]: classic Sverdrup.

*AR: We have already addressed this comment in our response to comments C3 and C4. We think this result clearly differs from Sverdrup’s expectations, as the onset of the biomass accumulation occurs when phytoplankton growth is still strongly limited by light availability.*

**C19:** Mixed layer depth, a key variable in the DRH could not be measured for this study. Weakening the ‘test’ of the hypothesis.

*AR: We added already a comment about MLD to the submitted version in light of the reviewer’s original review (lines 80-83).*

*Nevertheless, we note that in our study area—in contrast to the open North Atlantic, which we are not concerned with—at the time of the onset of spring phytoplankton biomass accumulation (around the winter solstice), the water column was in general fully homogenized due to the strong tidal and wind stirring (see our response to comment C3). Thus, during this time of the year, there is no signal of incipient seasonal stratification that could lead to a marked improvement in light conditions (Sverdrup, 1953). Additionally, the constant stirring due to the harsh environmental conditions probably hinders the relaxation of turbulent mixing for a period long enough (Huisman et al., 1999).*

#### *References:*

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