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On the relationship between stratification and primary productivity in the North Atlantic

M. Susan Lozier,[1] Apurva C. Dave,[1] Jaime B. Palter,[2] Lisa M. Gerber,[1] and Richard T. Barber[1]

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[1] Recent observational studies linking variability in global ocean productivity with upper ocean warming are based on the paradigm that warming produces a more stable water column which, in turn, inhibits primary productivity for a large fraction of the global ocean, namely the tropics and subtropics. Though seemingly straightforward, this paradigm relies on the assumption that an increase in the stratification of the upper ocean water column decreases the vertical mixing or overturning of the surface waters such that the supply of nutrients to the euphotic zone is reduced, and so too the primary productivity. Here we show, using observational data in the North Atlantic subtropical gyre, that while upper ocean stratification and primary productivity are strongly linked on seasonal time scales, they have at most a weak correlative relationship on interannual time scales over the modern observational record. We suggest that interannual variability in ocean biomass and primary productivity depends on a host of variables that are not easily predicted from the expected temperature response to climate variability and change. These variables include the strength of local and remote wind and buoyancy forcing and the surface or subsurface advective supply of nutrients. **Citation:** Lozier, M. S., A. C. Dave, J. B. Palter, L. M. Gerber, and R. T. Barber (2011), On the relationship between stratification and primary productivity in the North Atlantic, *Geophys. Res. Lett.*, *38*, L18609, doi:10.1029/2011GL049414.

1. Introduction

[2] The photosynthetic production of organic matter in the ocean's surface waters sustains nearly all marine life and transports carbon from the surface to the deep ocean. This production is critically dependent upon the supply of nutrients from the subsurface ocean to the euphotic zone [*Falkowski et al.*, 1998; *Gruber et al.*, 2002]. Traditionally, this nutrient supply has been attributed primarily to vertical processes and, as such, is believed to hinge on upper ocean density stratification for the simple reason that it takes more energy to overturn or mix a more stratified water. Thus, as suggested by a series of recent climate modeling studies, variability in upper ocean stratification is expected to translate into primary productivity variability for the tropical and subtropical ocean where productivity is not light limited [*Bopp et al.*, 2002; *Boyd and Doney*, 2002; *Sarmiento et al.*, 2004]. Increasing stratification is expected to inhibit productivity, whereas decreasing stratification would promote productivity.

[3] Recent assessments of the ocean density and color field have seemingly confirmed this expectation: *Behrenfeld et al.* [2006] used re-analyzed temperature and salinity fields to show that an increase in the globally-averaged tropical and subtropical upper ocean stratification occurring in the aftermath of the 1997–1998 El Nino was accompanied by a decline in globally-averaged chlorophyll and net primary productivity. Likewise, an expansion of the global ocean's nutrient-limited, low-chlorophyll oligotrophic regions has been attributed to the increasing stratification of the mid-latitude surface ocean [*Polovina et al.*, 2008]. Both impacts - large scale decreases in low- and mid-latitude ocean productivity and oligotrophic expansion – are suggested to presage the likely marine ecosystem response to a warming climate [*Behrenfeld et al.*, 2006; *Doney*, 2006; *Polovina et al.*, 2008]. Warming, however, may impact other factors that influence the nutrient supply to the euphotic zone that are as important as the background stratification of the surface waters. Although vertical stratification provides the resistance of the water column to overturning, variability in stratification in and of itself should not predetermine productivity variability. Factors that destroy the stratification and factors that affect nutrient concentrations must also be considered. Indeed, the sensitivity of the spring chlorophyll bloom in the subtropical North Atlantic to wind and buoyancy forcing that provide the energy for vertical mixing has been established [*Follows and Dutkiewicz*, 2001], as has the importance of surface and subsurface horizontal advection to the supply of nutrients to the sunlit waters [*Palter et al.*, 2005; *Williams and Follows*, 1998]. Thus, a closer examination of the impact of vertical stratification on ocean primary productivity is warranted. Such an examination is also timely since a recent study [*Boyce et al.*, 2010] has documented a decline in phytoplankton concentration over the past century in eight of ten ocean regions and because thousands of temperature profiles from Argo floats over the past decade have significantly expanded the number of observed stratification measures that are contemporaneous with satellite color fields.

2. Comparing In Situ Measures of Stratification and Productivity

[4] This study focuses on the subtropical North Atlantic, a well-sampled oligotrophic basin (Figure 1) surrounded by more productive coastal and subpolar waters. Annual cycles in primary productivity in this basin have been shown to be

[1]Division of Earth and Ocean Sciences, Nicholas School of the Environment, Duke University, Durham, NC 27708 USA.

[2]Department of Atmospheric and Oceanic Science, McGill University, Montreal, Quebec, Canada.

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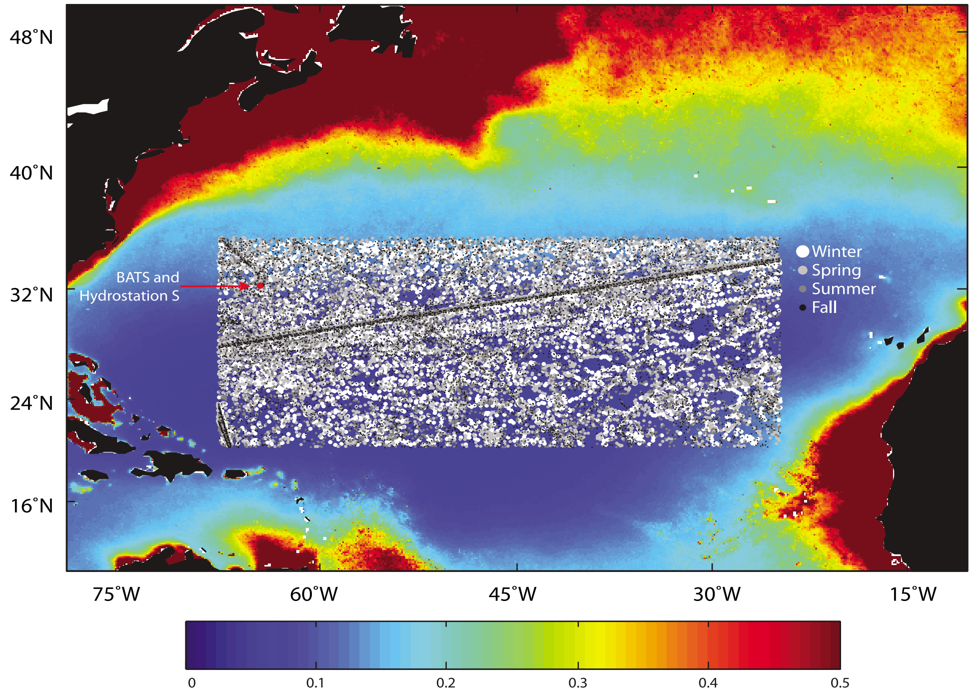

Figure 1. Annual mean SeaWiFS chlorophyll *a* concentration (mg/m^3) superposed with the locations of the 35,831 hydrographic profiles contained within the spatial and temporal domain (20–35°N, 25–67.5°W, 1997–2009) of this study. The seasonal distribution of these profiles is: 8623 in winter (JFM), 8622 in spring (AMJ), 8659 in summer (JAS) and 9927 in fall (OND).

controlled by stratification. *Wilson and Coles* [2005], for example, report strong, positive correlations in this region between seasonal changes in mixed layer depth and satellite-derived surface ocean chlorophyll-*a* (chl-*a*) concentration, the latter of which has long been used to estimate phytoplankton biomass and net primary productivity [*Eppley et al.*, 1985]. Time series from BATS (Bermuda Atlantic Time-Series Study), with a nearly continuous record of biological and physical variables since 1988, allow for a direct comparison between *in situ* measures of productivity and upper ocean stratification. This comparison (Figure 2a) reveals a pronounced seasonal cycle of stratification that strongly co-varies with productivity (r = −0.79) and with surface chl-*a* (r = −0.80). This correlative relationship is assumed causal: strongly stratified surface waters in the summer are believed to inhibit the overturning necessary to bring nutrient-rich waters into the euphotic zone. Likewise, relatively productive waters during winter are attributed to a weakly stratified upper ocean water column that is easily overturned to provide the nutrients needed to sustain surface productivity. Additionally, deeper mixing in winter is thought to dilute grazers over a greater depth, thus allowing for enhanced net primary productivity via the decoupling of phytoplankton growth and losses [*Evans and Parslow*, 1985; *Marra and Barber*, 2005; *Behrenfeld*, 2010]. Finally, we note that the seasonal change in surface productivity is mirrored by the seasonal change in surface chl-*a* (r = +0.91).

[5] An extension of this investigation to interannual time scales (Figure 2b) shows the expected relationship: higher concentrations of chl-*a* are associated with weaker stratification and lower concentrations with stronger stratification. However, this relationship, clearly driven by seasonal variability, does not hold at the limits of weak and strong stratification: a wide range of surface chl-*a* values are associated with a weakly stratified water column, and there is little to no appreciable decrease in surface chl-*a* for $\rho_{200} - \rho_0 > 2$ kg/m^3. The relationship between integrated primary productivity and stratification (Figure 2b) shows a similar pattern.

[6] Removing monthly means from all variables in Figure 2b reveals that there is little association between interannual changes in stratification and surface chl-*a* or between stratification and integrated primary productivity (Figure 2c). Only 9% of the variance in surface chl-*a* can be attributed to varying stratification, and less than 1% of the integrated primary productivity. Repeating this analysis using other measures of stratification yields similar results, as does the use of surface primary productivity data in place of integrated values. Likewise, a substitution of the local mixed layer depth for stratification shows no relationship with chl-*a* or productivity on interannual scales (Figure 2d). Though winter mixing is clearly associated with phytoplankton blooms, a large range of surface chl-*a* and integrated primary productivity values accompany any given mixed layer depth. This insensitivity is particularly true for the large wintertime mixed layer depths (>100 m), where the entire annual range of observed surface chl-*a* and integrated primary productivity is observed.

3. Comparing Basin-Wide Measures of In Situ Stratification and Satellite Productivity

[7] Though this investigation with BATS data is advantaged by contemporaneous measures of temperature,

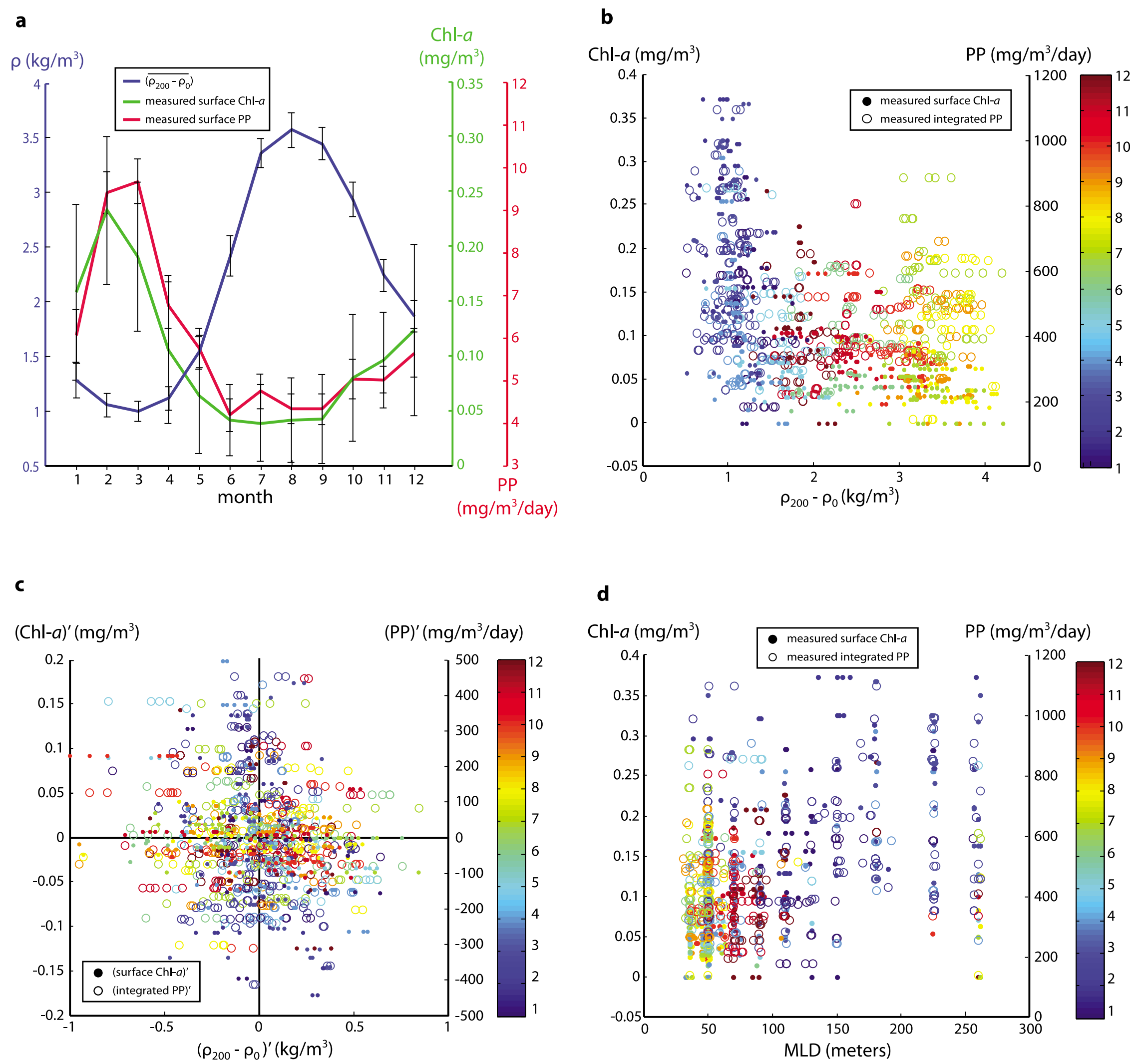

Figure 2. Data from Hydrostation S and BATS. (a) Monthly means over 1988–2006 of $\rho_{200} - \rho_0$ (blue line), surface chl-*a* (green line) and surface primary productivity (red line), with standard error bars. $\rho_{200} - \rho_0$ is calculated from each profile prior to the monthly averaging. (b) Surface chl-*a* (solid circles) and integrated primary productivity (open circles) plotted as a function of stratification, $\rho_{200} - \rho_0$, with no temporal averaging. Dot color indicates month of observation. (c) As in Figure 2b, but with monthly mean removed. (d) Surface chl-*a* (solid circles) and integrated primary productivity (open circles) as a function of mixed layer depth with data points colored by month. Mixed layer depths are computed using a method outlined by *Rappold et al.* [2007].

salinity, surface chl-*a* and primary productivity at scales sufficient to resolve intra- and interannual variability, it represents variability at one fixed locale in the North Atlantic subtropical gyre. Exploring the representativeness of these results for a broad swath of the subtropical gyre necessitates the use of SeaWiFS ocean color as a measure of ocean biomass. Over this same domain, measures of stratification (now measured as $T_0 - T_{200}$) are determined from individual hydrographic stations and Argo profiles, numbering over 35,000 for the time period that overlaps the SeaWiFS data (September, 1997 – December, 2009).

[8] To link contemporaneous measures of stratification and chl-*a* and to accommodate concerns about ocean color patchiness, we match each hydrographic profile with values from the corresponding monthly SeaWiFS chl-*a* field averaged over a 'capture-radius' that defines the spatial domain for which the hydrographic measurement is representative (see Supporting Materials). The profiles and associated satellite ocean color data provide 12+ years of contemporaneous measurements that adequately capture seasonal and interannual variability in our study domain (see Figures S1–S2 of the auxiliary material).[1] After subtracting local monthly means from each variable and then averaging the resultant anomalies for each month and each year over the spatial domain, time series depicting the interannual variability of basin-averaged chl-*a* and stratification can be compared (Figure 3a). The comparison is not favorable: though both time series show considerable variability over the temporal domain, stratification and chl-*a* are not correlated on interannual scales, a confirmation of the results using BATS data.

[1]Auxiliary materials are available in the HTML. doi:10.1029/2011GL049414.

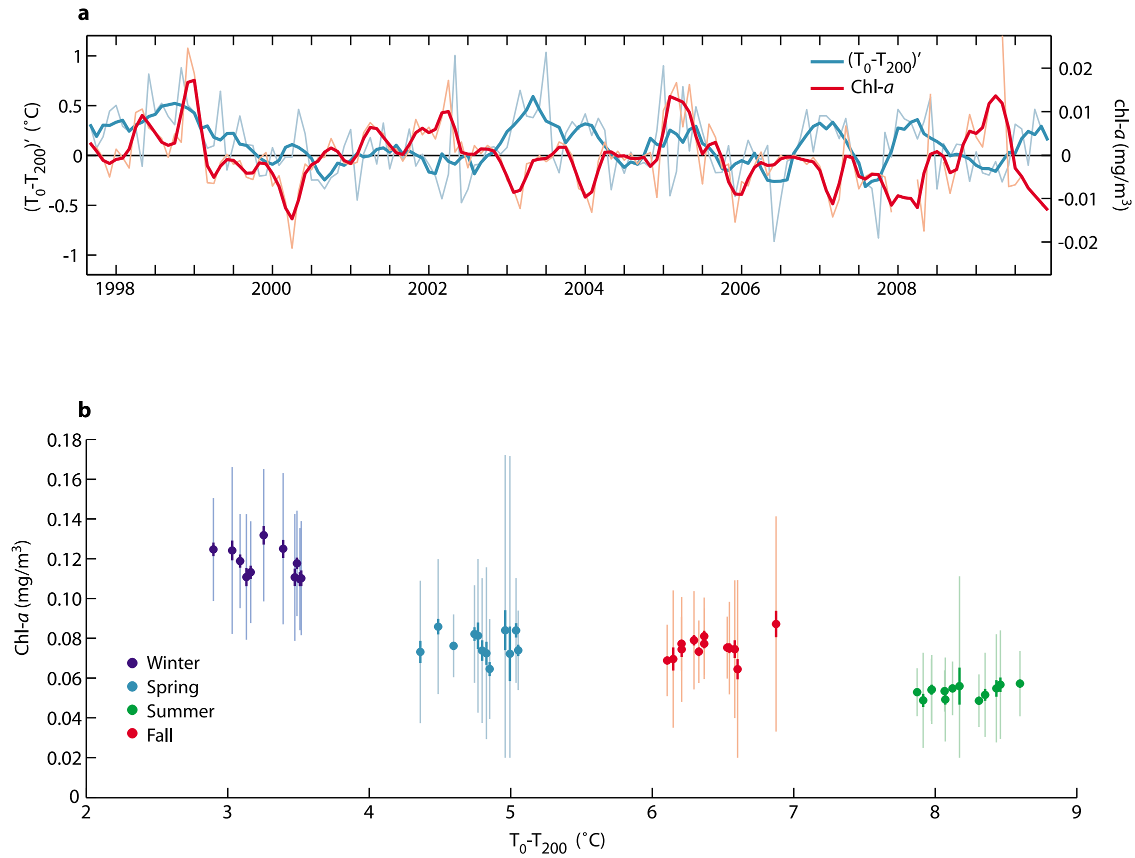

Figure 3. A comparison of stratification and surface chl-*a* variability over the study domain from Sep 1997 to Dec 2009. (a) Time series comparison of $T_0 - T_{200}$ (blue) anomalies, as measured by hydrographic profiles, and chl-*a* (red) anomalies, as measured by the 'profile-captured' SeaWiFS data. Each time series consists of the average of all local anomalies in the subtropical North Atlantic domain for each month of each year (see Supporting Materials for details). Thin (bold) lines show monthly (5-month running) averages. Neither the unsmoothed nor smoothed time series exhibits a statistically significant correlation ($p < 0.05$). (b) Scatter comparison showing the seasonally averaged anomalies in stratification and contemporaneous, profile-captured chl-*a* from winter of 1997 to winter of 2009. The shaded vertical bars indicate the standard deviations for chl-*a*, while the solid bars show ±2 standard errors. Each seasonal value shown is produced by averaging the monthly anomalies shown in the upper panel and then adding the corresponding seasonal mean for the whole domain. The resulting points are colored to indicate the seasons, as defined in Figure 1. None of the seasonal groupings reveal a statistically significant correlation from year to year ($p < 0.05$). The correlative relationships for the time series and scatter comparisons are quantified in Table S1 of the auxiliary material.

[9] A scatter comparison (Figure 3b) further demonstrates that, although stratification and chl-*a* are strongly correlated seasonally (as noted by the intergroup comparison), there is no discernable association from year to year within a given season (as noted by the intragroup comparison). In other words, for all seasons, there is no significant correlation among the year-to-year stratification and chl-*a* measures. Similar results are obtained if daily SeaWiFS chl-*a* fields are used, if chl-*a* fields are lagged relative to stratification and if chl-*a* tendency is used rather than the value itself. Finally, similar results are obtained when data are simply averaged over the spatial domain at each monthly time step (Figure S3a of the auxiliary material) and also when satellite-derived productivity fields are used in place of the chl-*a* field (Figure S3b of the auxiliary material). Thus, this comparison of contemporaneous and co-located measures of stratification, chl-*a* and productivity in the subtropical North Atlantic shows no significant linkage between local stratification and productivity; a result that stands in contrast to *Behrenfeld et al.* [2006], who show a strong correlation between globally-averaged stratification and chl-*a* measures. To allay concerns that methodological or dataset differences account for the different study results, we have reproduced the analysis of *Behrenfeld et al.* [2006] using the same re-analyzed hydrographic data and satellite-derived productivity estimates for the subtropical North Atlantic. With this analysis, interannual changes in stratification show no significant correlation with the productivity fields (Figure S3c of the auxiliary material), in sharp contrast to the variance (73%) reported by *Behrenfeld et al.* [2006] for the global domain. Thus, we suggest the possibility that the global correlations reported previously do not apply everywhere and are likely dominated by strong associations in a particular region.

4. Considering the Influence of Wind Variability on Vertical Mixing

[10] Why would interannual changes in subtropical upper ocean stratification be so weakly linked with changes in

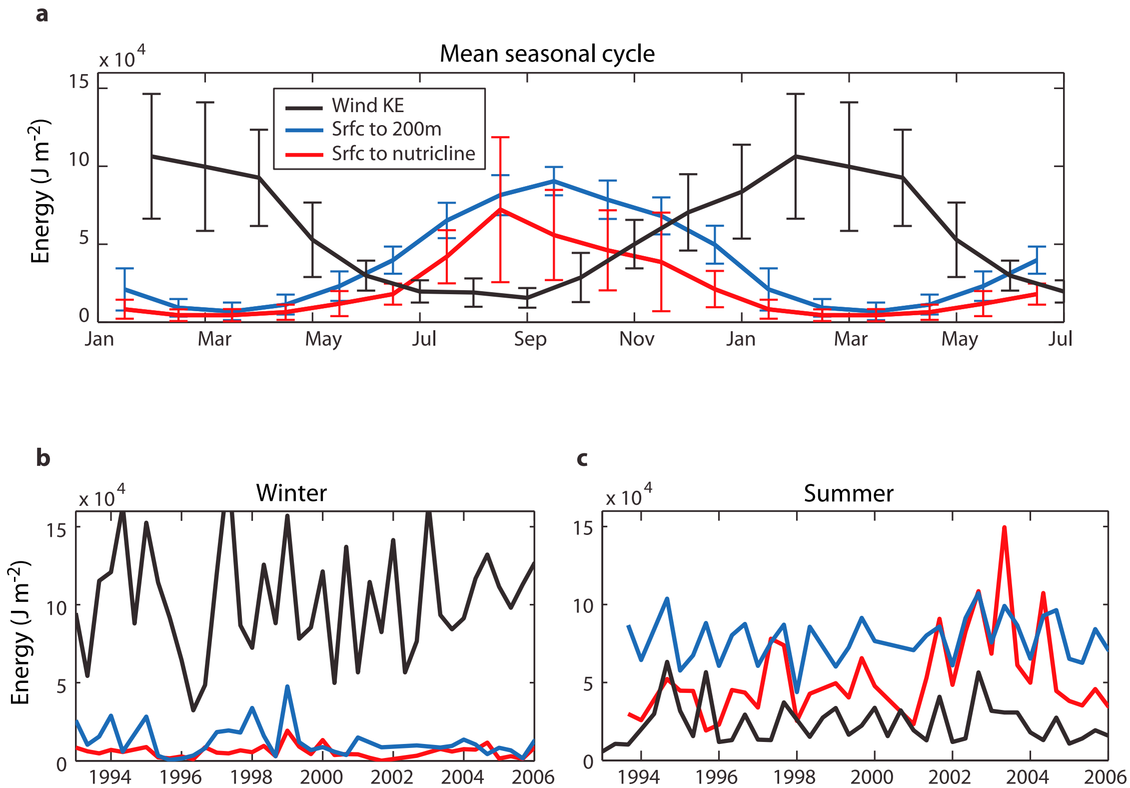

Figure 4. A comparison of the energy required to overturn the water column to the energy available in the winds at BATS. (a) Annual time series of the energy available for mixing from the local winds (black), and the energy required to overturn the water column at BATS from 200 m to the surface (blue) and from the nutricline to the surface (red). All variables are calculated as monthly means over 1993–2006. Error bars are one standard deviation constructed using the monthly mean values. (b) As for Figure 4a, but averaged over the winter months (January - April) for each year. (c) As for Figure 4a, but averaged over the summer months (June - September) for each year.

ocean chlorophyll or productivity? One explanation, suggested by a recent analysis of observational data from the subtropical North Pacific, is that interannual stratification variability in large parts of the subtropical ocean may not be large enough to drive a significant or coherent productivity response [*Dave and Lozier*, 2010]. A comparison of the amplitude of interannual stratification changes to those of seasonal changes (Figure 3b) lends credence to that possibility. Another possible explanation is that shifts in intracellular chlorophyll concentrations in response to photoacclimation decouple changes in chlorophyll and productivity [e.g., *Geider et al.*, 1997] (although this explanation should only complicate the stratification-chlorophyll relationship and not the relationship between stratification and primary productivity). However, our most favored explanation is that stratification, with fairly weak interannual variability, is only one of many factors that control the vertical mixing of nutrients into the euphotic zone. Upper ocean density gradients provide a measure of the water column resistance to overturning, but whether the water column does indeed overturn also depends upon local wind and buoyancy forcing. Furthermore, the amount of nutrients delivered to the sunlit surface waters also depends upon the concentration of nutrients at the base of the mixed layer. Thus, the expectation that interannual variability in background stratification determines interannual variability in surface biomass is undermined by studies documenting strong interannual variability in the winds, air-sea fluxes, and formation of water masses over the North Atlantic subtropical gyre [*Marshall et al.*, 2001].

[11] To illustrate the need to consider the variability of other factors, we compare the energy required for overturning the upper water column to the energy available for overturning from the local winds (Figure 4, also auxiliary material). In winter, energy available in the local winds at BATS is consistently an order of magnitude greater than that required to completely overturn the top 200 m of the water (Figure 4a). Such an imbalance is manifest at the end of winter when the mixed layer almost always exceeds 200 m. Furthermore, the average wind energy also exceeds the energy required to overturn the water column from the surface to the top of the nutricline. Conversely, strong upper ocean stratification in summer translates to an energy requirement for overturning that is more than double the available wind energy (Figure 4a), minimizing the possibility for fully mixing the upper water column. Thus, on average, there is more than enough wind energy in the winter to mine the top of the nutricline, whereas in summer there is never enough. Under such conditions, interannual variability of stratification (calculated between the surface and a fixed depth horizon) within each season would not be a predictive factor for surface productivity.

[12] An examination of the interannual variability of these energy measures for the winter and summer months (Figures 4b and 4c, respectively) reveals that the energy required for overturning is consistently mismatched with the

energy available to do so during the 14 years of this study, particularly in the winter. The energy required for overturning the upper 200 m in the summer exhibits weak interannual variability compared to the energy required to overturn the water column to the depth of the nutricline. Thus, at least for this location and for this time period, variability in nutricline depth is seemingly a more likely candidate for summertime variability in vertical nutrient fluxes than the little-varying stability of the summertime water column.

[13] As suggested by the seasonal cycle of the energy required for accessing nutrients at depth (Figure 4a), the impact that upper ocean stratification has on primary productivity may lie with its timing rather than with its magnitude. The winds gain strength in the fall just as the stratification is weakening, allowing for a convergence of these energy measures that can lead to an increase in productivity (Figure 2a). Likewise, decreasing wind strength and increasing stratification in the spring effectively dampen winter productivity. Thus, though we might expect the onset and conclusion of the winter bloom to be timed to the erosion and re-establishment of upper ocean stratification [*Henson et al.*, 2009], it is not obvious why the magnitude of the nutrient entrainment flux or the magnitude of surface chl-*a* should be linked to the strength of density stratification throughout the year.

5. Concluding Remarks

[14] This investigation has focused on how the consideration of wind forcing complicates the assumed causal relationship between ocean stratification and productivity on interannual time scales, yet it is surmised that changes in buoyancy forcing, the horizontal supply of nutrients via surface currents and the varying concentration of nutrients at depth, also complicate this paradigm. Though continued ocean warming will likely produce increasingly stratified surface waters in some regions, it is suggested here that the impact on ocean productivity will be limited until the energy required for seasonally overturning the water column to the nutricline exceeds the available energy from winds or buoyancy forcing. At present, observations suggest we have not reached that point in the subtropical North Atlantic.

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R. T. Barber, A. C. Dave, L. M. Gerber, and M. S. Lozier, Division of Earth and Ocean Sciences, Nicholas School of the Environment, Duke University, Durham, NC 27708, USA. (mslozier@eduke.edu)

J. B. Palter, Department of Atmospheric and Oceanic Science, McGill University, Montreal, QC H2X 1C4, Canada.