# Phenology of phytoplankton blooms in the Nova Scotian Shelf–Gulf of Maine region: remote sensing and modeling analysis

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Remotely sensed ocean color data and numerical modeling have been used to study the phenology of both spring and fall phytoplankton blooms (FPBs) in the Nova Scotian Shelf (NSS)-Gulf of Maine (GoM) region. The ocean color data reveal a general pattern of westward progression of the spring phytoplankton bloom (SPB), and an eastward progression of the FPB in the NSS-GoM region. The spatial pattern of mean chlorophyll concentration in spring is similar to that in fall, with a lower concentration in the NSS and higher in the GoM. Interannually, there is a weak but significant tendency for years with earlier (delayed) SPBs to be followed by delayed (earlier) FPBs, but the mean chlorophyll concentrations during SPBs are not correlated with those during FPBs. The interannual variability of SPB timing is significantly correlated with sea surface salinity (SSS), but the FPB timing is correlated with both SSS and sea surface temperature. The process-oriented numerical modeling experiments suggest that (i) salinity is the main factor influencing the bloom timing and magnitude in the NSS-GoM region, especially for the timing of SPBs; (ii) compared to buoyancy forcing induced by vertical salinity gradients, the impact of surface heating and surface wind stress on the blooms variability is much weaker; and (iii) the nutrient level controls the bloom magnitude, but only has a minor effect on bloom timing. This study provides a quantitative estimation of relationship between changes in local/ remote environmental forcing and phytoplankton phenological shifts, thus improving our understanding on the possible impact of climate change on coastal/shelf ecosystems.

KEYWORDS: Phytoplankton bloom; Phenology; Remote sensing; Environmental conditions; Nova Scotian Shelf; Gulf of Maine

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Phenology, the study of annually recurring biological phenomena in relation to climate conditions, can provide particularly sensitive indicators of system responses to major external disturbances. Such studies have been conducted extensively in terrestrial and freshwater systems, and have begun to receive attention in marine systems (see a review in Ji et al., 2010), including coastal (e.g. Oviatt, 2004; Mackas et al., 2007) and open ocean systems (e.g. Hughes, 2000; Edwards and Richardson, 2004; Henson et al., 2009; Platt et al., 2009; Vargas et al., 2009). Phytoplankton blooms certainly encompass one of the most important biological processes in coastal oceans. Changes in the timing and magnitude of blooms can affect the coupling of phenological relationships in pelagic food-webs, and can thus have important ramifications for trophic interactions and overall system productivity, as suggested by the classical Hjort-Cushing match/mismatch theory (Hjort, 1914; Cushing, 1975; Townsend and Cammen, 1988; Cushing, 1990). Therefore, it is of fundamental importance to identify regional and temporal variations in phenology and understand the underlying forcings that drive phenological shifts, i.e. the inter-annual variability of phytoplankton blooms.

Climate change is expected to affect environmental conditions in the ocean (e.g. temperature, salinity and wind stress) and thus influence the timing and magnitude of phytoplankton blooms and primary production with important consequences for aquatic life and the ocean carbon cycle (e.g. Stenseth and Mysterud, 2002; Edwards and Richardson, 2004; Hays et al., 2005; Vargas et al., 2009). The vertical structures of temperature and salinity influence the water column stability and light and nutrient conditions in the upper ocean and, consequently, exert controls on phytoplankton bloom dynamics. For example, Sarmiento et al. (Sarmiento et al., 2004) suggested that warmer ocean temperatures increase stratification of the surface mixed layer, inhibiting the entrainment of nutrients from below that support primary production. In the Nova Scotian Shelf (NSS) to Gulf of Maine (GoM) region, changes in the intensity of low-salinity Scotian Shelf Water (SSW) inflow can significantly influence the spring phytoplankton dynamics as suggested from the satellite data analyses (Ji et al., 2007) and modeling experiments (Ji et al., 2008). Other environmental factors, such as surface wind, can influence the phytoplankton bloom dynamics by changing the strength and depth of vertical mixing. For example, Ueyama and Monger (Uevama and Monger, 2005) showed that wind-induced mixing during the bloom period

appeared to be the key forcing agent contributing to interannual variability of spring bloom intensity in the North Atlantic. Greenan *et al.* (Greenan *et al.*, 2004) found that wind-driven vertical mixing and coastal upwelling also could affect bloom dynamics significantly on the Scotian Shelf.

On the Northwest Atlantic Shelf, pronounced seasonal changes in surface heat fluxes that produce large differences in sea surface temperatures (SSTs) and thermal stratification (Umoh and Thompson, 1994; Mountain et al., 1996) exert a strong influence on the evolution of the planktonic ecosystem, including phytoplankton blooms. However, inflows of relatively cold, low salinity SSW flow from the NSS to GoM region in the surface layers, and their seasonal and interannual variability can alter the water properties and stratification patterns significantly. Decadal-scale variability of the sea surface salinity (SSS) in the NSS-GoM region has been observed, with a general freshening in the late 1990s compared with the 1980s (Smith et al., 2001; Mountain, 2003; Belkin, 2004). The change in surface salinity can affect water column stability and mixed layer depth (e.g. Ji et al., 2007; Taylor and Mountain, 2009) and likely cause phytoplankton phenological shifts in this region.

Phytoplankton blooms in the shelf region from NSS to GoM are highly seasonal, and typically exhibit a major spring bloom in late winter/early spring and a lesser and broader fall bloom. The spring phytoplankton bloom (SPB) in this region has been studied for many decades (e.g. Bigelow, 1926; Riley, 1942; O'Reilly et al., 1987; Townsend et al., 1992; Thomas et al., 2003; Ji et al., 2007). The dynamics of the fall phytoplankton bloom (FPB), in contrast, are much less studied despite growing recognition of the importance of the FPB to the ecosystem (Greene and Pershing, 2007; Friedland et al., 2008). The interannual variability of SPBs in the NSS-GoM region has been documented and the influence of freshening on the SPB was hypothesized (Durbin et al., 2003; Thomas et al., 2003; Townsend et al., 2006; Greene and Pershing, 2007; Ji et al., 2007), but there has been almost no study making quantitative examination of relationships between the environmental conditions and the FPBs.

In this study, we further expand the previous studies (Ji *et al.*, 2007, 2008) and examine both SPB and FPB dynamics in the NSS–GoM region. First, we analyze the remotely sensed ocean color data to understand: (i) the general spatial pattern and interannual variability of both SPBs and FPBs with respect to both timing and magnitude of blooms; (ii) the link between SPBs and FPBs; and (iii) the relationships between bloom dynamics and climate-change-related environmental

conditions. Then, a 1-D ecosystem model is used to identify the impact of individual environmental factors on the phytoplankton blooms through sensitivity analysis of the targeted numerical experiments.

### METHOD

Daily chlorophyll concentrations from 1 January 1998 to 31 December 2008 over the NSS-GoM region were obtained from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Level-3 mapped data with 9-km resolution, retrieved from the National Aeronautics and Space Administration (NASA) ocean-color website (http ://seadas.gsfc.nasa.gov/). The climatology of the chlorophyll concentration was computed by averaging over the 11 years (1998-2008) in a  $0.5^{\circ} \times 0.5^{\circ}$  mesh and used for the spatial distribution analysis. Seven representative zones are selected for the interannual variability study (Fig. 1). The zones were selected from the deep regions in the NSS-GoM (excluding regions shallower than 60 m while maintaining data availability). SST data were from the Advanced Very High Resolution Radiometer (AVHRR) Pathfinder SST version 5 (http://www.jpl.nasa.gov/) and salinity profile data (including SSS) were retrieved from Canadian Ocean Science Hydrographic Climate Database (http:// www.mar.dfo-mpo.gc.ca/). Surface wind data were derived from SeaWinds on Quick Scatterometer (QuikSCAT) L2B Level data, through the Centre de Recherche et d'Exploitation Satellitaire (CERSAT) at Institut Français pour l'Exploitation de la Mer (IFREMER), Plouzané (France).

Peak timing and magnitude were chosen as key quantities of blooms dynamics. The peak timing of SPB and FPB was estimated from a shifted-Gaussian model fit (e.g. Yamada and Ishizaka, 2006; Platt *et al.*, 2009). The mean chlorophyll concentration during the bloom period was used to represent bloom magnitude. Since the SPB duration is usually from March to June and the FPB from September to December in most of the NSS–GoM region, we defined the mean chlorophyll concentration from 1 March to 30 June as the SPB magnitude, and the mean from 1 September to 31 December as the FPB magnitude.

We use the ecosystem model of Stock and Dunne (Stock and Dunne, 2010) implemented into a 1-D mixed-layer model as described in Song et al. (Song et al., 2010). The ecosystem model is an NPZD-type functional group model (e.g. Fasham et al., 1990) with coarsely resolved size classes within the phytoplankton, zooplankton and detritus groups. Details of this model can be found in Stock and Dunne (Stock and Dunne, 2010) or at http://www.whoi.edu/sites/ji\_bloom (click on "1-D Modeling" on the left panel). The ecosystem model has been shown to capture global crossecosystem patterns in key ecosystem properties including primary production, mesozooplankton production and export production (Stock and Dunne, 2010). It also reproduces observed regional differences in the timing and magnitude of the spring and FPBs within the NSS-GoM region and observed inter-annual differences in SPB timing over the past decade (Song et al., 2010). Four individual factors (i.e. salinity, temperature, wind-speed and nutrients) were included in the process-oriented modeling experiments. To examine their individual influences, only one of these factors was adjusted to have high, medium and low levels within the observed range from both the central Gulf of Maine (cGoM) and Eastern Scotian Shelf (ESS) zones (two specific zones with distinct environmental features in terms of water column properties), while the other three



Fig. 1. Map of the study area and seven zones selected for data analysis.

were kept the same. The baseline of the surface forcing for the model is derived from cGoM in 1999.

### RESULTS

### Spatial and interannual variability of blooms from satellite data

The general spatial patterns of the peak timing and mean chlorophyll of the SPB and the FPB are presented in Fig. 2. The peak timing of SPB is generally earlier in the NSS region (in mid-March at earliest) and later in the GoM region (in mid-to-late May at latest). A distinct pattern exists in near shore regions: the SPB peak timing is delayed in the northern margin of GoM while it is relatively early on Georges Bank (GB) and near the New England coast (Fig. 2, top left). The mean surface chlorophyll during SPB is lower on the NSS (~0.85 mg m<sup>-3</sup>) than that in the GoM (~1.25 mg m<sup>-3</sup>), but much higher on the GB and in the nearshore waters (~2.5 mg m<sup>-3</sup>)

(Fig. 2, top right). The peak timing of the FPB is generally opposite to that of the SPB. It is later on the NSS (where blooms can occur as late as December), earlier in the GoM (around October) and much earlier in some nearshore waters and on GB (as early as September, Fig. 2, bottom left). The spatial distribution of the mean chlorophyll during the FPB has a similar pattern to that of SPB, with a slightly lower mean chlorophyll concentration in FPB than that in SPB in the entire domain (Fig. 2, bottom right). The results demonstrated the substantial spatial variability of both the timing and magnitude of the SPBs and FPBs in the NSS-GoM region: a general pattern of westward progression exists at the peak timing of SPB, agreeing with the results from a coarse resolution analysis by Ji et al. (Ji et al., 2007); whereas an eastward progression pattern can be found for the FPB peak timing, contrary to the SPB.

The regional variability of chlorophyll seasonality (from a climatological point of view) for the seven zones in Fig. 1 is shown in Fig. 3. In the Wilkinson Basin (WBa), the peak timing of the SPB and the FPB is in



Fig. 2. Spatial distribution of bloom peak timing and mean chlorophyll concentration during blooms. SeaWiFS-derived climatological chlorophyll data were used, and the black dots are the actual data points.



Fig. 3. Time series of climatological daily chlorophyll concentration in the seven zones as specified in Fig. 1. The black dots represent the zonal mean chlorophyll from SeaWiFS, and the lines show the Gaussian fit.

late-April and the end of October, respectively. The SPB timing in cGoM is similar to that in WBa, but the FPB timing is ~15 days earlier than that of WBa. In the Jordan Basin (JBa), the SPB occurs from early-April to late-May with a relatively longer duration than other zones, while the FPB reaches the peak earlier (about 1 October) with the strongest magnitude among the seven zones. On the Northeast Peak of Georges Bank, there is a major SPB but no distinctive FPB due to elevated summertime chlorophyll concentration fueled by continuous nutrient supply from the deep GoM through tidal pumping (Loder and Platt, 1985; Hu *et al.*, 2008). The SPB on the West Scotian Shelf (WSS) is early, strong and short-lived, while the FPB is late and

weak. The SPB (FPB) on the ESS has the earliest (latest) peak timing and the weakest magnitude for both blooms among the seven zones. In general, the west-ward progression of SPB timing and eastward progression of FPB timing between ESS and JBa match the results from the spatial analysis (Fig. 2).

The interannual variation of the bloom peak timing is shown in Fig. 4A. For the WBa, cGoM and JBa zones, the peak timings of the SPB covary and show sharp interannual changes: relatively early blooms in 1998, 2001 and 2006, and later in 2000 and 2002. For the Georges Basin (GBa) and GB, the SPB timing after 2002 is consistent with that in WBa, cGoM and JBa, but different in years 1998-2001. The SPBs in the ESS and WSS occur early relative to the other zones in all years and have a weaker interannual variability. The peak timing of FPB (Fig. 4A, bottom) is generally opposite to that of SPB both spatially (i.e. across zones) and interannually: areas with early SPBs usually have late FPBs, and years with early SPBs are associated with delayed FPBs within the same area. The bloom magnitude covaries across all seven zones in both spring and fall (Fig. 4B), except for SPB in the GB zone in some years (e.g. 2003 and 2005). Moreover, the variation of the chlorophyll concentration during SPB appears to be consistent with that of FPB during 1998-2001 and 2005-2008, but has an opposite pattern during 2002-2004 between the chlorophyll concentration of SPB and FPB.

The correlation analysis of the peak timing and mean chlorophyll concentration between SPBs and FPBs reveals a significant negative correlation between the peak timing of SPBs and FPBs in each zone (r = -0.446, P < 0.01,Fig. 5, top left), suggesting that zones with a late/early SPB also have an early/late FPB. If we pool the seven zones together, a weak but significant negative correlation exists between the peak timing of SPBs and FPBs interannually (r = -0.235, P < 0.05, Fig. 5, bottom left),suggesting that the late/early FPBs may occur in the years with the early/late SPBs. For the mean chlorophyll concentration, there is a significant positive correlation between SPBs and FPBs spatially (r = 0.939, P < 0.01, Fig. 5, top right), but no correlation in terms of interannual variability (P > 0.05, Fig. 5, bottom right). This is probably due to the fact that spatial variability of the nutrient levels (the main control factor of the chlorophyll magnitude, see below) is stronger than the interannual variability (see following for details).

## Impact of environmental factors on blooms dynamics

The impact of climate-change-related environmental factors on bloom dynamics was examined using the



Fig. 4. Interannual variability of bloom peak timing (A) and mean chlorophyll concentration during blooms (B) in the seven zones (specified in Fig. 1) from 1998 to 2008.

available SSS, SST and surface wind stress data. For the peak timing of SPBs, there is a significant positive correlation with the interannual anomaly of April mean SSS in all of the seven zones (r = 0.415, P < 0.01, Fig. 6, top left), but no correlation exists between the SPB peak timing and the April mean SST or surface wind-speed (P > 0.05, Fig. 6, middle and bottom left). On the other hand, for the FPB, both SSS and SST (October mean) have a weak but statistically significant negative correlation with the peak timing (P < 0.05, Fig. 6, top and middle right). Similar to the SPB case, the surface wind-speed is not correlated with FPB timing (Fig. 6, bottom right).

The process-oriented 1-D model was used here to examine how sensitive the bloom dynamics are to individual environmental factors including salinity, temperature, wind-speed and nutrients. The model results further support that, in the NSS-GoM region, the salinity structure is the main factor that affects the bloom magnitude and timing, especially the SPB timing (Fig. 7). First, high springtime surface salinity (S1 and S4 in Fig. 7) is associated with late SPB, and low springtime surface salinity (S3 and S6 in Fig. 7) with an early SPB. Second, the chlorophyll concentration in different seasons is also linked to the SPB timing. For example, in the high salinity S1 case, the SPB is significantly delayed due to high salinity at the surface layer in spring (represented as SSS, Fig. 7, bottom panel), which is associated with a weaker water column stratification. However, the weakened water column stratification associated with high SSS also results in strong exchanges between surface and deep waters and enhanced replenishment of surface nutrients in the winter. This leads to relatively high chlorophyll concentration from summer to early fall. On the contrary, the early SPB and associated low summer chlorophyll concentration occurs in a low salinity case (e.g. S6 case).

The changes in temperature (resulting from different surface heating in different years) have almost no effect on the bloom dynamics in the NSS–GoM region (Fig. 8). The SPB timing is almost the same with very small differences in chlorophyll concentration in all the six temperature cases, in which SST varies significantly during the SPB period. Lastly, the model suggests that the impact of wind speed on blooms is also very weak (Fig. 9), consistent with the analysis of the observational data.

Compared to SPBs, FPBs usually have less distinct peak but with longer duration. Therefore, the change in FPB timing is much more subtle and difficult to quantify. To magnify subtle changes in FBP timing, the cumulative percentile approach was used (Greve et al., 2005) and the day with 50% of cumulative chlorophyll from September to December is defined as the FPB peak timing. The results show that FPB is delayed by  $\sim 2$  weeks in the low SSS case relative to the high SSS case (Fig. 10, left). This pattern is consistent with the analysis of observational data (Fig. 6, top right). However, the model result shows almost no change in the FPB timing between the low SST case and the high SST case (Fig. 10, middle). This suggests that the significant negative correlation apparent in the observations (Fig. 6, middle right) may reflect covariation of SST with another factor that is truly driving



Fig. 5. Correlation of bloom peak timing and mean chlorophyll concentration between SPB and FPB. The locations of spatial data points are shown as black dots in Fig. 2. Normalized anomaly is obtained by computing anomaly first and then normalized by the standard deviation.

changes in bloom timing (e.g. salinity, see Discussion). Strong wind can make the FPB slightly stronger and occur earlier (Fig. 10, right).

The impact of nutrient concentration on bloom dynamics is difficult to assess from observation alone, mainly due to the limited availability of nutrient data and the dynamic coupling between nutrients and phytoplankton. Our model results suggest that, under the condition of no horizontal advection, a change in the initial nutrient concentration leads to different nutrient conditions over the entire year (Fig. 11, bottom panel), but the chlorophyll concentration before SPB and after FPB remains similar (Fig. 11, top panel). Consequently, changes in nutrient concentration have almost no effect on the timing of SPB initiation and FPB termination, but it can enhance the peak chlorophyll concentration and extend the bloom duration of both SPB and FPB. During the summer, the chlorophyll concentrations are positively correlated with the initial nutrient concentrations. This result is consistent with the conceptual model: nutrients are not a limiting factor between later fall and early spring, so changing the nutrient concentration will not significantly affect primary production and phytoplankton biomass; whereas surface nutrient is much limited between later spring and fall, and higher initial nutrient concentration will allow more nutrient availability for phytoplankton and thus enhance production and elevate phytoplankton biomass.

### DISCUSSION

Regulated by the depth of the mixed layer relative to the critical depth (Sverdrup, 1953), the spring diatom bloom is thought to result from the formation of stratification in spring, at a time when nutrient concentrations



Fig. 6. Correlation of SSS, SST and wind speed to the peak timing of SPB and FPB.

are high throughout the water column following strong winter mixing, and irradiance is increasing. The bloom abruptly ends once nutrients are depleted in the surface

waters, and may be further influenced by weather events, self-shading and zooplankton grazing pressure (Ji *et al.*, 2008). The fall bloom is mainly formed by



Fig. 7. Time series of modeled surface chlorophyll and salinity under different salinity forcing. The heat flux and wind forcing observed in cGoM in 1999 were used for all model case runs, whereas the salinity forcing is year- and zone-specific. S1, cGoM in 2000; S2, cGoM in 1999; S3, cGoM in 1998; S4, ESS in 2001; S5, ESS in 2003; S6, ESS in 1998.



Fig. 8. Time series of modeled surface chlorophyll and temperature under different heat flux forcing. The SST differences in the model runs were represented as anomalies (daily data minus mean value of six cases). The salinity and wind forcing were the same for all the cases. T1, cGoM in 2007; T2, cGoM in 2002; T3, cGoM in 2000; T4, ESS in 2005; T5, ESS in 2007; T6, ESS in 2000.



Fig. 9. Time series of modeled surface chlorophyll and wind speed under different wind forcing. The wind speed data were just shown the mean of April and October from the wind input data. The heat flux and salinity forcing were the same for all the cases. W1, cGoM in 2007; W2, cGoM in 1998; W3, cGoM in 2004; W4, ESS in 2000; W5, ESS in 1998; W6, ESS in 2003.



Fig. 10. The differences of accumulated chlorophyll during FPB between the high and low cases of SSS, SST and wind speed. Every chlorophyll concentration was deducted 0.25 mg m<sup>-3</sup>. SSS cases are the subcases of S2 (high) and S6 (low) in Fig. 7, SST cases are the subcases of T4 (high) and T1 (low) in Fig. 8 and wind-speed cases are the subcases of W5 (High) and W1 (Low) in Fig. 9.

mixing (convective cooling and winds) results in a compromise between increased nutrient flux from depth

small phytoplankton and occurs as increased vertical to the ocean surface and enough vertical stratification and light to maintain photosynthesis (Findlay et al., 2006).



Fig. 11. Time series of modeled surface chlorophyll and nutrient concentration with different initial nutrient profiles. All the heat flux, salinity and wind forcing were kept the same and just initial nutrient profiles were changed. The initial nutrient of N2 and N5 are the base profiles for the cGoM and ESS model runs, respectively. The nutrient concentration of N1 (N4) is 2  $\mu$ M higher than that of N2 (N5) throughout the profiles, whereas N3 (N6) is 2  $\mu$ M lower than N2 (N5).

Our results demonstrate that the substantial spatial and interannual variability in the timing and magnitude of SPB and FPB occurs in the NSS–GoM region in response to variability of the climate-change-related environmental conditions. For the spatial progression of the bloom timing, Ji *et al.* (Ji *et al.*, 2007) pointed out that the timing difference of the SPB is associated with the spatial gradient of SSS from the NSS to the GoM. This is further supported by the high-resolution analysis in this study. Here we further suggest that FPBs show an opposite pattern, progressing from the GoM to the NSS.

Our data analysis suggests that the interannual variability of SPB timing is negatively correlated with that of FPB timing. We have shown that the SPB timing is correlated with the SSS, and the FPB timing is correlated with both SSS and SST. Following the correlation between the SSS and water stability, freshening in the NSS-GoM region is known to form a more stable water column in spring and cause earlier SPBs (e.g. Ji *et al.*, 2007, 2008; Taylor and Mountain, 2009); the stable stratification could also mean the column is more difficult to break down in the fall, and therefore the freshening can delay the FPBs. However, the negative correlation between SST and FPB timing is less intuitive. In the spring, variations in sea surface density (SSD) are dominated by the SSS ( $R^2 = 0.87, P < 0.01$ ), while variation in SSD in the fall is correlated with both SSS (positive,  $R^2 = 0.41$ , P < 0.01) and SST (negative,  $R^2 = 0.23$ , P < 0.01) in the fall (Fig. 12). This means that the temperature could potentially be one of the key factors affecting the water column stability in the fall, but not in the spring (possibly due to the temperature being at or near seasonal minimum during SPB). Theoretically, high SST in fall is capable of inhibiting vertical mixing (low SSD and low surface nutrient) and delaying the FPB. The FPB is indeed slightly delayed in model simulations with uncharacteristically high SST (Fig. 10, middle). However, the changes are relatively weak and the observations (Fig. 6, middle right) suggest an association of high temperatures with early FPB timing that is contrary to this mechanism. In reality, high (low) SST anomalies are often associated with high (low) SSS anomalies in this region (Fig. 12, bottom two). This is mainly due to variations in the advection of cold, fresh waters flowing onto the Scotian Shelf (Smith, 1989; Mountain and Manning, 1994). Consequently, there are two covarying drivers, temperature and salinity, of FPB dynamics in the NSS-GoM region which have opposite effects. If the effect of



Fig. 12. Correlation among the observed SSS, SST and sea surface density (SSD) of April and October in the seven zones during 1998–2008. SSS and SST data are averaged for the surface 30 m, and SSD are calculated by the mean values of SSS and SST.

salinity is stronger than that of temperature (as suggested by the modeling experiments conducted herein), a negative correlation between SST and FPB timing such as that shown in Fig. 6 will arise.

Nutrient concentration may affect the magnitude of both SPB and FPB. Observations show that the surface nitrogen concentration during winter-spring in the NSS region is  $\sim 5 \ \mu M$  and increases to  $\sim 10 \ \mu M$  in the

GoM region (Ji *et al.*, 2007). The differences in nutrient concentration between these two regions are probably related to the different water masses entering the systems at depth: compared to the NSS, the GoM is influenced more by Warm Slope Water (WSW, higher nutrient concentration) than that of Labrador Slope Water (LSW, lower nutrient concentration) (Townsend *et al.*, 2006). Moreover, the surface perennial inflow of SSW (low salinity) can stabilize the water column and thus impede the nutrient supply from deep water and this effect is stronger in the NSS than that in the GoM.

The modeling test on the nutrient effect suggests that the nutrient concentrations only affect the chlorophyll concentration between spring and fall. High nutrient concentration can induce a stronger bloom with a higher peak concentration and a longer lasting bloom, but the SPB initial timing and the FPB end timing appear to be the same as in a low nutrient level case. It is thus concluded that nutrient concentrations mainly affect bloom magnitude, but have a secondary impact on bloom timing. Moreover, from the analysis above, we see that the distinct spatial distribution of nutrients in the NSS-GoM region can cause a significant positive correlation between the mean chlorophyll of SPB and FPB spatially: areas with strong SPBs usually have a strong FPB (Fig. 5, top right). Interannually, however, nutrients may vary much from spring to fall in the same year, possibly due to the change of the deep slope water inflow (in terms of the contribution of LSW and WSW) within a year and the extent of mixing from bottom to surface with different water column stability. Therefore, no significant correlation can be found in terms of the interannual variability of the mean chlorophyll between SPB and FPB (Fig. 5, bottom right).

It is worth noting that the year day when the chlorophyll reaches a peak was chosen as the index of bloom timing in this study. The Gaussian fitting approach we used here can identify the peak timing reasonably well even for the satellite-derived data, which can be noisy and have a lot of temporal gaps on days with high cloud coverage. We recognize that this is probably not the best index and many other timing indices were have been used in previous studies. For example, Yamada and Ishizaka (Yamada and Ishizaka, 2006) and Platt et al. (Platt et al., 2009) defined the time when the chlorophyll concentration reaches some proportion of the amplitude of the Gaussian fitted curve; Siegel et al. (Siegel et al., 2002) used the year/day where chlorophyll levels first rise a small threshold above median values; Sharples et al. (Sharples et al., 2006) used the timing of maximum daily rate of change of surface biomass. These methods appear to focus on timing of the bloom onset/initiation, thus avoiding the complexity involved in determining the decline of the bloom (which could be caused by nutrient depletion, top-down control from grazers or other factors). However, these methods require continuous time series data without much noise and are probably more suitable for analyzing model results (no gap in time series) or spatially/temporally averaged (less noisy) observation data set.

experiments presented herein is subject to some methodological limitations. First, there are uncertainties in the estimates of remotely derived chlorophyll, especially in the nearshore area due to the influences of colored dissolved organic matter (CDOM) and suspended sediments (Balch et al., 2004). The influences of CDOM and sediments are the strongest in the bays and estuaries of the GoM. The primary regions analyzed in this study were outside bays and estuaries and in depths >60 m to minimize the impact of CDOM and sediments, but the exclusion of CDOM and suspended sediments from the calculations is a notable caveat of the analysis herein. A more comprehensive model that combines river and sediment dynamics, carbon chemistry and planktonic ecosystem dynamics is required to analyze the impacts of CDOM and suspended sediments. Second, the NSS-GoM region has strong coastal currents and cross-shelf flows (e.g. Brooks, 1985; Lynch et al., 1997) that are not resolved by the 1-D approach used herein. However, past studies of the seasonal evolution of the water column in the region suggest that a local 1-D balance can explain the majority of observed changes in water column temperatures and thermal stratification (e.g. Umoh and Thompson, 1994; Mountain et al., 1996). Also, the advection of salinity between regions considered in this analysis has been accounted for by relaxing salinity profiles at each site towards monthly observations. A full multi-year 3-D modeling is left for future studies.

The analysis of remote sensing data and 1-D modeling

### SUMMARY

Remotely sensed ocean color data and process-oriented modeling have been used to understand the spatial and interannual variability of the timing and magnitude of SPB and FPB in the NSS-GoM region, as well as their relationships to the SSS, SST, surface wind stress and nutrient level. The results show that there is a substantial spatial and interannual variability in both the timing and magnitude of the SPB and FPB in the NSS-GoM region. Salinity is the main factor influencing the bloom dynamics in the NSS-GoM region, especially for the timing of SPBs. SST anomalies may weakly affect the FPB timing, but are generally counteracted by covarying SSS anomalies. The nutrient level is the main factor that affects bloom magnitude, but has almost no effect on bloom timing. This study provides a quantitative estimation of relationship between changes in local/remote environmental forcing and phytoplankton phenological shifts, thus improving our understanding of the possible impact of climate change on coastal/shelf ecosystems.

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