Modeling the influence of low-salinity water inflow on winter-spring phytoplankton dynamics in the Nova Scotian Shelf–Gulf of Maine region

RUBAO JI^{1,6}*, CABELL S. DAVIS¹, CHANGSHENG CHEN^{2,6}, DAVID W. TOWNSEND³, DAVID G. MOUNTAIN⁴ AND ROBERT C. BEARDSLEY⁵

¹DEPARTMENT OF BIOLOGY, WOODS HOLE OCEANOGRAPHIC INSTITUTION, WOODS HOLE, MA 02543, USA, ²THE SCHOOL FOR MARINE SCIENCE AND TECHNOLOGY, UNIVERSITY OF MASSACHUSETTS DARTMOUTH, NEW BEDFORD, MA 02744, USA, ³SCHOOL OF MARINE SCIENCES, UNIVERSITY OF MAINE, ORONO, ME 04469, USA, ⁴NATIONAL MARINE FISHERIES SERVICE, WOODS HOLE, MA 02543, USA, ⁵DEPARTMENT OF PHYSICAL OCEANOGRAPHY, WOODS HOLE OCEANOGRAPHIC INSTITUTION, WOODS HOLE, MA 02543, USA AND ⁶MARINE ECOSYSTEM AND ENVIRONMENT LABORATORY, SHANGHAI OCEAN UNIVERSITY, CHINA

*CORRESPONDING AUTHOR: rji@whoi.edu

Received July 9, 2008; accepted in principle August 28, 2008; accepted for publication September 2, 2008; published online September 9, 2008

Corresponding editor: Roger Harris

Previous analyses of SeaWiFS ocean color and hydrographic data [Ji, R., Davis, C. S., Chen, C. et al. (2007) Influence of ocean freshening on shelf phytoplankton dynamics. Geophys. Res. Lett., 34, L24607. doi: 10.1029/2007GL032010] have suggested that changes in the intensity of low-salinity Scotian Shelf Water (SSW) inflow can significantly influence the winterspring phytoplankton dynamics in the Scotian Shelf and Gulf of Maine region. In the present study, a 3-D coupled biological-physical model was applied to examine underlying mechanisms through a quantitative comparison of circulation pattern, water column stability, nutrient/ phytoplankton concentrations and net primary productivity between low and high freshening scenarios. The model results revealed that observed levels of surface freshening can significantly change water column stability and therefore control the winter-spring phytoplankton bloom dynamics in different regions. Freshening caused earlier blooms both on the Scotian Shelf and in the eastern Gulf of Maine, agreeing with inferences drawn from prior empirical analyses. Earlier phytoplankton blooms in the low surface salinity case were followed by earlier depletion of nutrients at the surface along with earlier decline of blooms compared with the high surface salinity case. The model results also suggested that surface water freshening can impede vertical nutrient exchange between surface and deep waters, thus reducing the overall spring primary productivity throughout the region. The coupled model described in this study provides a unique tool to quantify the response of lower trophic level production to climate-scale environmental disturbances in a complex but ecologically important shelf ecosystem that has a history of such alternations in surface salinity.

INTRODUCTION

The dynamics of phytoplankton populations lie at the heart of ecosystem structure and function and can affect productivity at higher tropic levels in the Nova Scotian Shelf–Gulf of Maine region possibly through bottom-up processes (e.g. Durbin *et al.*, 2003; Platt *et al.*,

2003; Frank *et al.*, 2007; Greene and Pershing, 2007). Due to their importance, phytoplankton dynamics, including blooms, have enjoyed a long history of research in this region since the early 20th century (e.g. Bigelow, 1926; Riley, 1942; Townsend and Spinard, 1986; O'Reilly *et al.*, 1987; Townsend *et al.*, 1992;

doi:10.1093/plankt/fbn091, available online at www.plankt.oxfordjournals.org

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Townsend *et al.*, 1994; Thomas *et al.*, 2003; Ji *et al.*, 2006), and continue to be an important research topic with recent focus expanded to examine the variability at multiple spatial and temporal scales (e.g. Ji *et al.*, 2007).

Similar to many temperate coastal ecosystems (Sverdrup, 1953; Cushing, 1959; Colebrook, 1979; Harris, 1986), phytoplankton in the Gulf of Maine exhibits a major bloom in late winter/early spring (e.g. Townsend *et al.*, 1994; Townsend *et al.*, 2006). The bloom usually results from the formation of the seasonal thermocline during the winter-spring transition period, at a time when nutrient concentrations are high throughout the water column following strong winter mixing and irradiance is increasing. The bloom abruptly ends once nutrients are depleted in surface waters, and may be further shortened by weather events, self-shading and zooplankton grazing pressure. For convenience purposes, we refer to winter-spring phytoplankton blooms as spring blooms.

Local or remote forcings that affect light and nutrient conditions may vary from year to year, and therefore one would expect to see an interannual variation of phytoplankton dynamics, including changes in the timing and magnitude of blooms and seasonal cycle of primary productivity. Indeed, significant interannual variations of spring blooms in the Gulf of Maine have been detected from remote sensing and field observation data. For example, Thomas et al. (Thomas et al., 2003) examined SeaWiFS ocean color data from September 1997 to August 2001 and found delayed and reduced spring blooms in 1998 and 2000, and relatively early development of blooms in 1999. From winter cruises across the central Gulf of Maine in late February of both 1999 and 2000, Durbin et al. (Durbin et al., 2003) also observed a significant difference in the timing of blooms in these 2 years, matching well with the SeaWiFS data presented by Thomas et al. (Thomas et al., 2003). A detailed analysis of SeaWiFS and hydrographic data (Townsend et al., 2006; Ji et al., 2007) revealed that changes in the low-salinity water inflow from the Scotian Shelf can significantly affect the general pattern of the westward propagation of spring blooms from the Nova Scotian Shelf to the western Gulf of Maine.

While much of our understanding stems from earlier empirical results, this study uses a dynamic biological– physical coupled model we recently developed to better understand the underlying mechanisms linking the freshening and spring bloom dynamics in the Nova Scotian Shelf–Gulf of Maine region. The coupled model is particularly useful in this regard since it allows us to examine the effect of individual environmental forcing in a complex system, where the variability of phytoplankton dynamics may involve multiple biological and physical interactions, and is possibly influenced by the interplay of both external and local forcings. For instance, the timing of onset, intensity and spatial progression of blooms could be influenced by the balance of major external forcings including surface SSW and deep Warm Slope Water (WSW) inflows and by temporally/spatially variable local forcings (tides, surface winds, insolation, heat flux and freshwater runoff). It is difficult to identify the influence of freshening from so many factors by observation alone due to insufficient spatial and temporal resolution and data coverage.

In this communication, we develop a conceptual model that describes the system dynamics and hypotheses to be tested (Conceptual Model section), followed by a brief introduction of the numerical model and the design of process-oriented numerical modeling experiments (Numerical Model section). The model results and discussion are then presented in following sections, respectively.

CONCEPTUAL MODEL

The waters in the Gulf of Maine and the Nova Scotian Shelf are connected (Fig. 1). Relatively cold, low salinity SSW enters the Gulf of Maine in the surface layers around Cape Sable and meets warmer and more saline slope water (called WSW) that enters at depth through the Northeast Channel. The primary source of SSW is the West Greenland/Labrador Current system, with additional input from the St Lawrence system (Houghton and Fairbanks, 2001; Fratantoni and Pickart, 2007). These two waters progressively mix as they move in a general counter-clockwise pattern around the Gulf of Maine, and then turn clockwise around Georges Bank with the major portion of the flow continuing westward into the Mid-Atlantic Bight (Beardsley et al., 1997; Wiebe et al., 2002). The general circulation pattern in the upper and lower layers of the Gulf of Maine has been described in detail based on hydrographic survey data (e.g. Bigelow, 1927; Brooks, 1985; Pettigrew et al., 1998), and analyzed by various modeling studies (e.g. Lynch et al., 1996; Xue et al., 2000; Chen et al., 2001). These studies seem to reach a consensus that the circulation in the Gulf of Maine is characterized by a seasonally varying (intensified in summer-fall but weak in winter-spring) general counter-clockwise gyre around the entire Gulf, along with smaller counter-clockwise surface gyres around deep basins. The variation of SSW inflow from the northeast of the domain (termed as "upstream" hereafter), influenced by large-scale freshening, may alter water properties and stratification patterns as illustrated in Fig. 1. Enhanced inflow of low salinity SSW at the surface can stabilize the

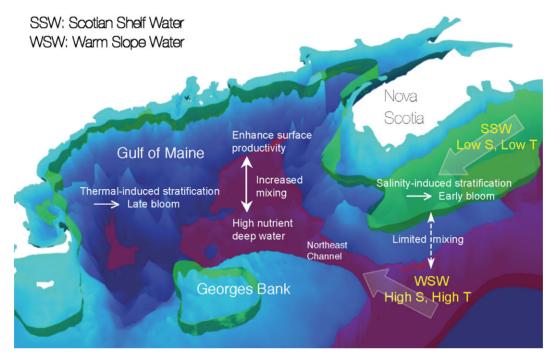


Fig. 1. A conceptual model describing the potential impact of Scotian Shelf Water (SSW) and Warm Slope Water (WSW) on the phytoplankton blooms and primary productivities in the Scotian Shelf and the Gulf of Maine region. The West Greenland/Labrador Current system and the St Lawrence system mentioned in the text are located further north (outside of the domain shown in this figure).

water column in the Nova Scotian Shelf region, and facilitate earlier spring blooms than in the Gulf of Maine region (where thermal stratification induced by surface heating usually occurs in April), causing an apparent westward propagation of blooms. On the other hand, enhanced SSW inflow might reduce the overall productivity in the Gulf of Maine, since decreased surface salinity can impede winter convection and result in a weak exchange between surface and deep waters (Taylor and Mountain, 2008), lowering nutrient concentrations available for phytoplankton growth in surface water during springtime. As a result, the duration of spring blooms may be shortened and the post-bloom productivity decreased. The influence of freshening is expected to be more prominent in the Nova Scotian Shelf and the eastern Gulf of Maine region than that in the western Gulf of Maine, since the intensity of freshening can be significantly attenuated westward by increased mixing of surface water with high-salinity deep water in the Gulf. The following numerical experiments were designed to examine the above conceptual model.

NUMERICAL MODEL

We used a 3-D high-resolution biological-physical coupled model system in this study. The system includes

a hydrodynamics model—the finite volume coastal ocean model (FVCOM) and a four-compartment [nitrogen—phytoplankton—zooplankton—detritus (NPZD)] biological model. The general modeling framework is shown in Fig. 2 and the FVCOM model grid is shown in Fig. 3. A detailed description of the model coupling and configuration is given in Ji *et al.* (Ji *et al.*, 2008), and only a brief summary is presented here.

The modeling system consists of (i) a nested regional community atmospheric mesoscale model (MM5) that provides surface wind stress and heat flux for the ocean model, (ii) an ocean model (FVCOM) driven by realistic surface and boundary forcings and with assimilation of satellite/buoy data and (iii) a simple NPZD model. The integrated model system can run with idealized forcing and boundary conditions to investigate specific processes. As the central component of the modeling system, FVCOM is a prognostic, unstructured-grid, finite-volume, free-surface, 3D primitive equation coastal ocean circulation model (Chen et al., 2003; Chen et al., 2007). The model is solved numerically by a second-order accurate discrete flux calculation of the integral form of the governing equations over an unstructured triangular grid. The NPZD model coupled with FVCOM contains key aspects of lower trophic-level food web dynamics, and the model is proven capable of capturing major seasonal nutrient

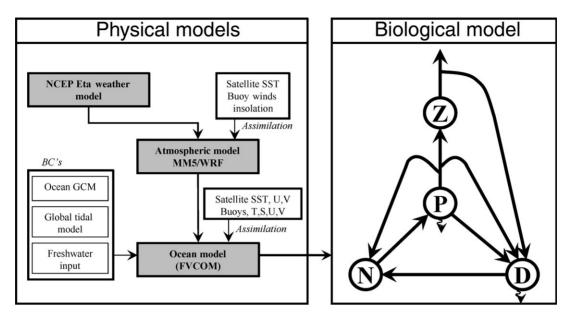


Fig. 2. The framework of the biological-physical-coupled model system, with the physical model (FVCOM) providing temperature, diffusivity and flow fields for the biological model (NPZD model).

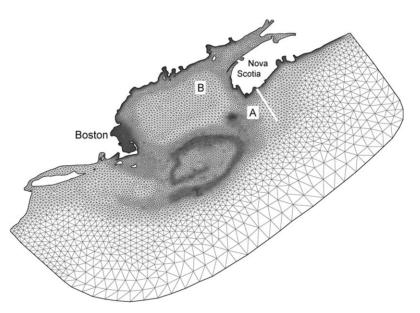


Fig. 3. FVCOM model grids with a total of 13 504 node points horizontally and 30 σ -layers vertically. (A) and (B) represent locations for the profiles plotted in Figs 11 and 12. The white line across the Nova Scotian Shelf represents the transect plotted in Fig. 10.

and phytoplankton dynamics across the Gulf of Maine and Georges Bank regions as a function of local and remote forcings (Ji *et al.*, 2008). Specifically, the model is nitrogen-based and has features such as (i) Michaelis– Menten kinetics in nutrient uptake, (ii) Holling type III functional response of zooplankton grazing on phytoplankton, (iii) temperature/light-dependent growth for phytoplankton and temperature-dependent grazing and respiration for zooplankton, (iv) self-shading of phytoplankton growth and (v) sinking of phytoplankton and detritus. For all biological source and sink terms, the temperature effect is incorporated using a simple Q10 relationship with a Q10 value of 2. Additionally, a constant N (mmols):Chl *a* (mg) of 0.5 is used to convert between nitrogen and Chl *a*, assuming a C:Chl *a* weight ratio of 40 and the Redfield ratio (C:N = 5.67 by weight) in phytoplankton cells. The simplicity of the biological model allows us to examine the response of

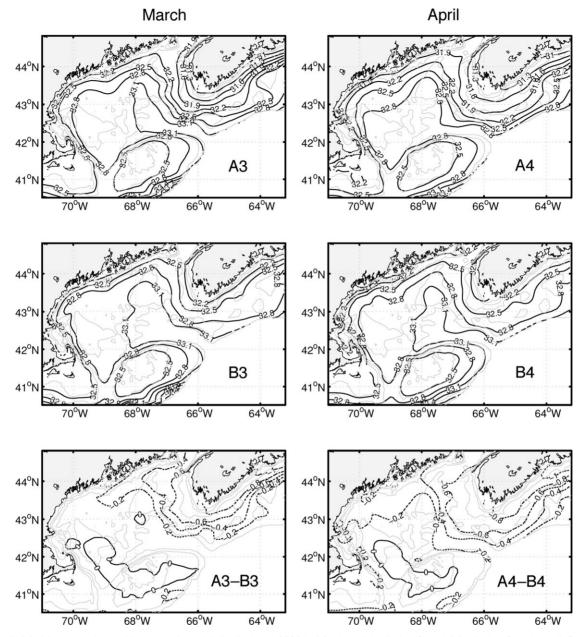


Fig. 4. Model-computed, monthly averaged, spatial distributions of SSS in March and April. A3, Case A March; A4, Case A April; B3, Case B March; B4, Case B April; A3–B3, difference between Cases A and B in March; A4–B4, difference between Cases A and B in April.

the food web to forcings while avoiding large uncertainties in the parameterization of biological transformation processes within the food web.

For the purpose of scenario testing, neither the hydrodynamic model nor the biological model was designed for the realistic simulation of specific years. Instead, we used a process-oriented modeling approach, in which climatological, realistic and idealized forcings and initial/boundary conditions were used jointly in the following two targeted numerical experiments: *Case A*: Low surface salinity (LSS)—for the hydrodynamic model, December monthly averaged climatological temperature and salinity fields (retrieved from NODC Ocean Climatology database) were used as initial conditions, and the model was integrated over a year using surface (heat and wind) and boundary forcings in 1999, a year known to be relatively fresh in the Nova Scotian Shelf–Gulf of Maine region (Mountain, 2003; Drinkwater and Gilbert, 2004; Mountain, 2004; Ji *et al.*, 2007). Case B: High surface salinity (HSS)—same as Case A, except that the salinity of incoming water was set to be not lower than 31.5 PSU in the upstream boundary (the first 13 grid points along the open boundary across the Nova Scotian Shelf counting from the coast, representing ~ 150 km). As shown in the following section, this treatment elevated the sea surface salinity (SSS) in the model domain, and provides a controlled "experimental condition" for examining the response of nutrient and phytoplankton to different degree of freshenings.

In both cases, the same climatological initial condition for hydrography is used; the only difference is the salinity of incoming waters from the upstream boundary. The cut-off salinity of 31.5 PSU in Case B is to produce a perturbation in the system such that the resulting SSS distribution represents a typical high salinity scenario. Given that the minimum salinity pulse arrives at the southwestern tip of Nova Scotia between February and March (Smith, 1989) and that it takes 1-2 months for the low salinity water to arrive there from the upstream boundary, the change of salinity at the upstream boundary at the beginning of the year is justifiable. The purpose of this treatment is to facilitate a clear comparison of biological responses to freshening from upstream without considering the local forcings and initial conditions. One of the major concerns for this treatment is that the salinity difference at the upstream can only start to affect the Gulf of Maine water several months later (as shown in the model results). Indeed, the modeled salinity signal does not fully penetrate through the western Gulf of Maine and onto Georges Bank by March, such that the memory of the initial conditions could affect the modeled SPB dynamics in those regions. Therefore, the analysis of model results will focus on the Nova Scotian Shelf and the eastern Gulf of Maine regions. The same climatological initial condition for the NPZD model (as specified in Ji et al., 2008) was used in both cases, along with a no-gradient open boundary condition (no net advective and diffusive flux across the open boundary). This treatment ensures that any biological responses in the model were mainly caused by the differences in salinity and subsequent changes in stratification and circulation patterns.

MODEL RESULTS

The gradient of increasing SSS from the Nova Scotian Shelf in the east to the western Gulf of Maine can be seen clearly in the monthly averaged distribution of SSS from selected winter-spring months, as shown in Fig. 4. This pattern agrees well with the general circulation pattern outlined in the Conceptual Model section (discussed earlier). In both LSS and HSS cases, low salinity waters were mostly trapped along the coastal regions, with significantly lower salinity in Case A (<30 PSU) than that in Case B in both March and April. The pattern of decreasing salinity shoreward can be seen clearly from transect survey data collected for AZMP (Atlantic Zone Monitoring Programme: http://www.meds-sdmm.dfompo.gc.ca/zmp/main_zmp_e.html). Lower salinity water inflow from upstream produced a lower SSS in the Nova Scotian Shelf and the eastern Gulf of Maine, as shown in the differences between Cases A and B in March (A3–B3) and April (A4-B4) (Fig. 4 bottom two panels). The influence of SSW influx on the salinity distribution in the inner Gulf of Maine became more noticeable as the model progressed from March to April. This model-computed SSS distributional pattern provided a necessary "experimental setting" for the subsequent analyses regarding the influence of freshening on nutrient-phytoplankton dynamics.

The model also showed that the circulation patterns have been altered as a result of the salinity changes at the upstream boundary (Fig. 5). In both March and April, the near-shore residual currents in the Nova Scotian Shelf and Gulf of Maine were significantly higher (up to 8 cm/s) in the LSS case than that in the HSS case, suggesting that freshening-induced enhancement of the cross-shelf baroclinic pressure gradient contributed to the strengthening of the southwestward flow on the shelf. This is consistent with earlier modeling studies in this region by Han *et al.* (Han *et al.*, 1997) and Hannah *et al.* (Hannah *et al.*, 2001), in which they showed that the baroclinic pressure field is the primary forcing for the overall southwestward flow on the shelf.

Lower SSS in Case A was associated with a relatively more vertically stable water column in the Nova Scotian Shelf and the eastern Gulf of Maine than that in Case B, as shown in Fig. 6, in which the spatial distribution of mixed layer depth (MLD) is plotted for March (left panels) and April (right panels) in both cases. Excluding the shallow well-mixed regions near shore and on Georges Bank, the MLD did not extend to the bottom (varying from 40-60 m in the Nova Scotian Shelf region to >100 m in deep basins inside the Gulf of Maine), indicating that the water column was not completely mixed even in winter. The MLDs became shallower in April than those in March, especially in the Nova Scotian Shelf and areas surrounding the central Gulf of Maine, suggesting that the water became more stable as more low-salinity water from the Nova Scotian Shelf arrived in the system, along with increased surface heating in April. Previous analysis of the climatological hydrographic data in this region (Ji et al., 2007)

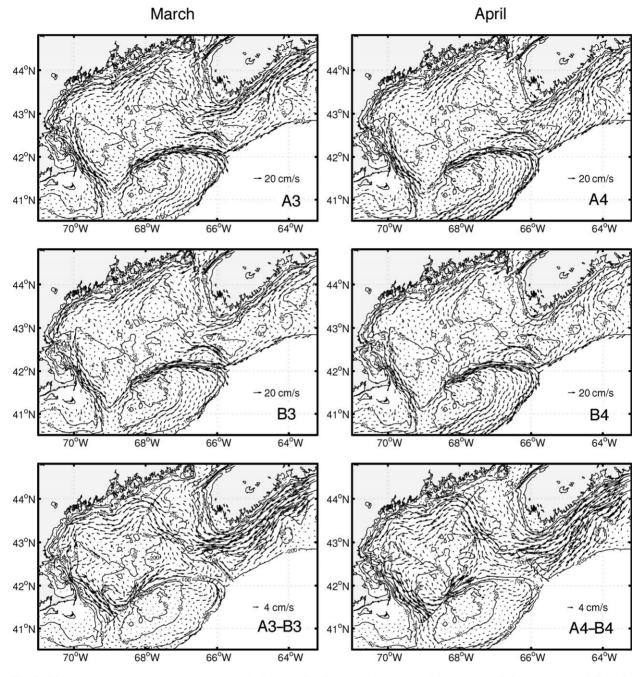


Fig. 5. Model-computed, monthly averaged, spatial distributions of surface residual currents in March and April. See the caption of Fig. 4 for label details.

demonstrated that, in general, the variability of SSS can explain nearly all ($\sim 97\%$) the variability of surface water density and about 40–60% of the variability of MLD in this region during the winter-spring period. Lower SSS in Case A resulted in shallower MLD in both March (A3–B3) and April (A4–B4) (Fig. 6 bottom two panels). The spatial distribution of negative MLD differences appears to mirror the surface circulation

pathways described above, showing low-salinity water flowing along the inner Nova Scotian Shelf and around the Gulf of Maine with across-shelf meandering on the Nova Scotian Shelf and bifurcation in the central Gulf of Maine.

Ji et al. (Ji et al., 2007) suggested that lighter surface water in the Nova Scotian Shelf formed a relatively shallow surface mixed layer (40-60 m), providing

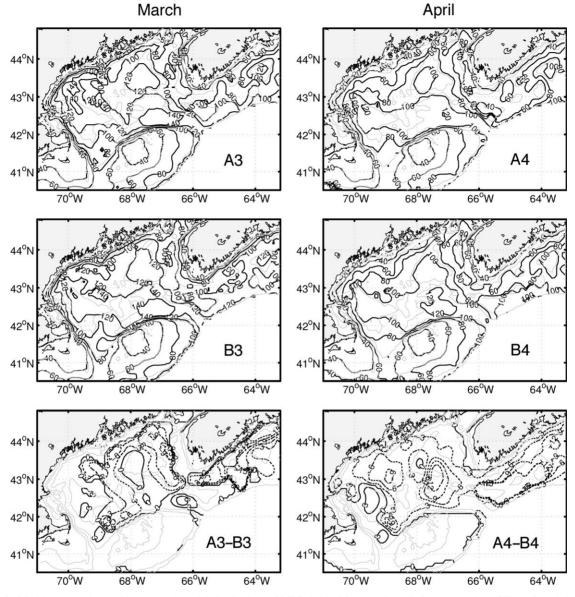


Fig. 6. Model-computed, monthly averaged, spatial distributions of MLD (m) in March and April. See the caption of Fig. 4 for label details. An integral depth-scale (also called trapping depth) method developed by Price *et al.*, 1986) was used to compute MLD.

a more favorable condition for early phytoplankton blooms in Case A than that in Case B. The model results from these numerical experiments support this argument. The model-computed Chl *a* distribution for Case A in March (Fig. 7, A3) has higher Chl *a* concentrations than that in Case B (Fig. 7, B3) in the Nova Scotian Shelf and eastern/central Gulf of Maine. The regional difference is clearly demonstrated in the contour plot of the difference between Cases A and B in March (A3–B3) (Fig. 7, bottom left panel). The depth-integrated net primary productivity (NPP) (Fig. 8, left panels) has a similar spatial distribution pattern as that of Chl *a*. These results support the argument that the low-salinity-induced stratification could trigger earlier blooms in the domain, especially in the upstream regions. Consequently, the nutrient concentration in March (Fig. 9, left panels) was significantly lower where chlorophyll and NPP were higher, with much lower nutrient concentration in the LSS case. In April, the model showed higher Chl *a* concentrations (compared with March) throughout the region in both LSS and HSS cases (Fig. 7, right panels). That is, the bloom was developing in both cases. The difference between LSS and HSS in April (A4–B4) showed that the monthly averaged Chl *a* concentration was lower in the Nova Scotian Shelf and a large portion of the Gulf of Maine.

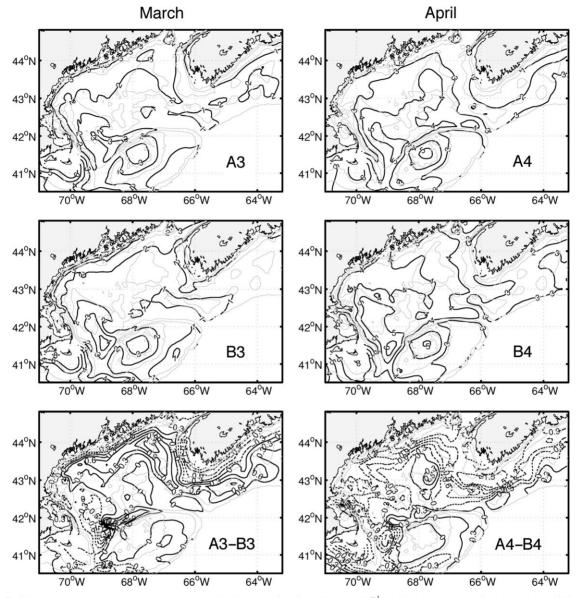


Fig. 7. Model-computed, monthly averaged, spatial distributions of surface Chl $a (\mu g L^{-1})$ in March and April. See the caption of Fig. 4 for label details.

This situation is opposite to that in March, suggesting that the freshening-induced early blooms might have drawn down the surface nutrient concentration significantly (Fig. 9, right panels) and subsequently the primary productivity has been reduced in the later spring throughout the region for the LSS case. Again, the distributional pattern and difference between Cases A and B for depth-integrated NPP had similar patterns to those for Chl *a*.

Although the focus of this study is the off-shore regions, the model results also revealed some patterns in the near-coastal regions that are contrary to the off-shore patterns. Both Chl a and NPP in March are

lower in the coastal Nova Scotian Shelf–Gulf of Maine in Case A than that in Case B (Figs 7 and 8, A3–B3). A transect view across the southwest Nova Scotian Shelf (Fig. 10) shows that the lateral gradients in salinity appear to prevent high nutrient water from reaching the coast and cause slower phytoplankton growth in the LSS case (given the near-shore MLDs are governed by topography and tidal mixing, a process less influenced by salinity change).

The monthly averaged surface distributions of NO_3 , Chl *a* and NPP described above reflect general patterns of the influence of freshening on areal phytoplankton productivity, but yield little or no information on

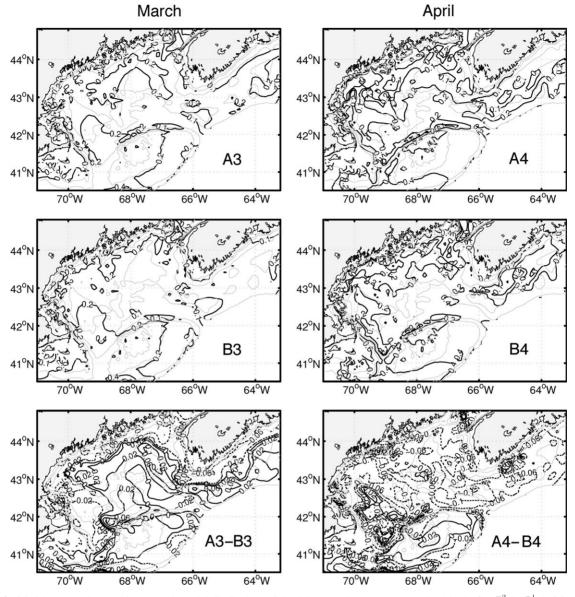


Fig. 8. Model-computed, monthly averaged, spatial distributions of depth-integrated net primary productivity (g C $m^{-2} day^{-1}$) in March and April. See the caption of Fig. 4 for label details.

temporal (e.g. daily) evolution and vertical distribution of these biological quantities. Contour plots for individual stations are shown in Figs 11 and 12, in which the changes of vertical Chl *a* and N profiles in time are illustrated for stations A and B in Fig. 3, respectively. Model results revealed relatively weaker, but earlier, blooms at the surface of Nova Scotian Shelf and Jordan Basin sites in Case A, with the difference of Chl *a* concentration (A–B) ranging from ~0.5 to 1.5 µg/L in March (year day <90) and ~ -1.5 µg/L throughout April (Fig. 11). The Chl *a* pattern is mirrored by the earlier reduction of nutrients at the surface in both regions (Fig. 12 left and right panels). The Chl *a* concentration (before year day 90) below the surface 30-40 m was higher in Case B, possibly due to the deeper mixed layer (induced by high SSS) that allowed phytoplankton to exploit nutrients at the deeper pycnocline depth. In both regions, after year day ~110, the differences of surface N concentration between the two cases became undetectable, and both Chl *a* concentration and NPP (not shown) were significantly higher in Case B, indicating that increased vertical fluxes of nitrogen (supply rate rather than standing stock) was probably controlling the productivity and eventually the biomass of phytoplankton at the surface.

With higher Chl *a* and NPP in March but lower in April in Case A, a logical follow-on question is how

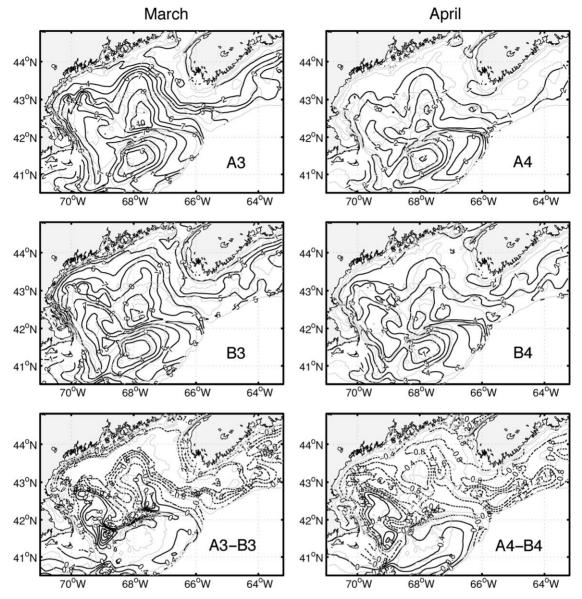


Fig. 9. Model-computed, monthly averaged, spatial distributions of surface N (μM) in March and April. See the caption of Fig. 4 for label details.

does freshening affect the overall productivity considering both months? We would expect that the weakened vertical mixing will reduce the flux of nutrient-rich deep water upward for photosynthesis, and therefore reduce the overall productivity (integrated from pre- to postbloom periods) even though the bloom may occur earlier. This idea is supported by the modeling results (Fig. 13), where average depth-integrated NPP for March and April combined was much lower (up to $0.08 \text{ g C m}^{-2} \text{ day}^{-1}$) in Case A than that in Case B. The model results also suggest that a delay in bloom timing can contribute to the apparent higher overall productivity in March and April in Case B, given the fact that there is a time lag for the bloom being completely grazed down by zooplankton after April. If we integrate the NPP over a longer time period, the influence of freshening on overall NPP should be weakened.

DISCUSSION

Our numerical experiments explicitly demonstrate a pronounced role of salinity by showing significant changes in bloom dynamics when all the other environmental factors were held constant. The model-derived general response pattern of nutrient-phytoplankton

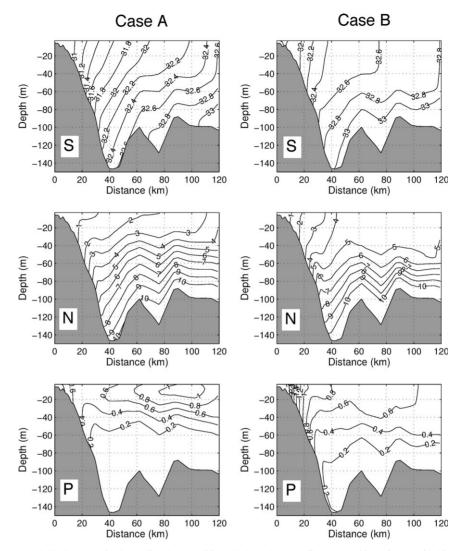


Fig. 10. Model-computed distribution of salinity (S), nitrogen (N) and phytoplankton (P) across a Nova Scotian Shelf transect (white line on Fig. 3). Case A, left panel; Case B, right panel.

dynamics to the freshening matches well with the conceptual model. The blooms in the Nova Scotian Shelf and eastern Gulf of Maine occurred earlier when the surface salinity of Nova Scotian Shelf inflow was lower, in association with a shallower MLD and more stable water column (as described by Ji et al., 2007). Most of the above-mentioned changes in surface phytoplankton dynamics can be detected from satellitederived ocean color data. However, only very few water column profile datasets exist to establish a direct linkage between freshening and winter-spring nutrient and phytoplankton dynamics and therefore validate our model results. One such example is from surveys across the eastern Gulf of Maine in late February/early March of 1999 and 2000 by Durbin et al. (Durbin et al., 2003). From the vertical profiles of temperature, salinity, size-fractioned Chl *a* and nutrients at multiple sites, their study showed that blooms occurred earlier in 1999 when the surface water was colder but fresher than that in 2000. Most of the Chl *a* in the bloom waters in 1999 was in the $>5 \,\mu$ m size-fraction, whereas most of the Chl *a* was in the $<5 \,\mu$ m size-fraction in the 2000 samples (indicative of pre-bloom conditions in 2000). Relatively lower concentrations of nitrate in the 1999 samples were likely associated with enhanced nitrogen uptake by phytoplankton, a process that is supported by our numerical model results.

The numerical model results also suggest that earlier blooms drew down nutrients at the surface and caused earlier termination of the bloom, as the nutrient supply from deeper waters was impeded by the enhanced water column stability. Profiles collected at AZMP

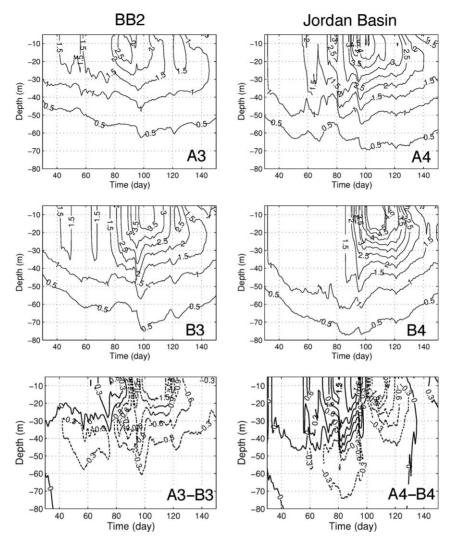


Fig. 11. Model-computed vertical profile of Chl *a* from year day 30 to 150 in BB2 (Station A in Fig. 3, left panel) and Jordan Basin (Station B in Fig. 3, right panel). Case A, first row; Case B, middle row; Difference between Case A and B, bottom row.

Browns Bank transect (BB2) in early April, 1999 and 2000 (Fig. 14) support this model-based result. The vertical profile of σ_t at BB2 showed clearly that the MLD was much shallower in April 1999 than that in 2000, mainly due to the lower salinity in 1999. The concentration of nitrate+nitrite was lower in 1999 with values near the detection limit near the surface (water depth <20 m), associated with a low surface Chl *a* concentration.

It is worth emphasizing that the numerical experiments in this study were designed with a perturbation of SSS at the upstream boundary occurring at the beginning of the year. This configuration determines that the bloom dynamics in the western Gulf of Maine is less likely to be impacted due to the advection time scale, and therefore confines our analysis within the Nova Scotian Shelf and the eastern Gulf of Maine regions only. It is well recognized that changes in the timing of freshening would likely affect the bloom dynamics. For instance, if the peak of low-salinity water enters the system in the previous year (i.e. before January), not only will the winter-spring blooms be affected, but also the fall phytoplankton blooms (e.g. Greene and Pershing, 2007). In addition, the spatial coverage of influence would be much wider. From our modeling analysis, it is reasonable to say that freshening shifts the timing of the bloom earlier throughout the region, but more comprehensive numerical experiments are needed to fully address the spatial gradient issue raised in the conceptual model.

Influences of local forcings (e.g. surface winds, surface irradiance and freshwater discharge from surrounding rivers) on the inter-annual variability of nutrientphytoplankton dynamics in the Gulf of Maine have

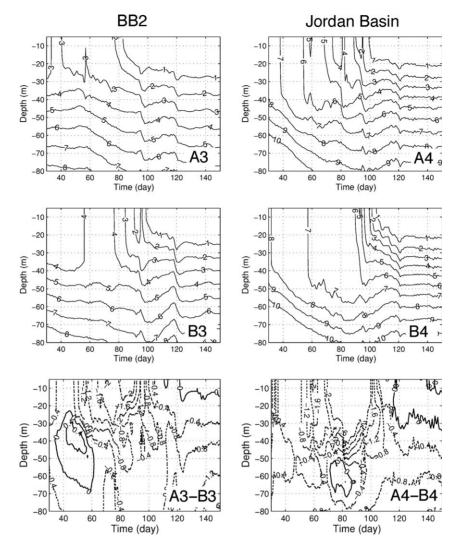


Fig. 12. Model-computed vertical profile of N from year day 30 to 150 in BB2 (Station A in Fig. 3, left panel) and Jordan Basin (Station B in Fig. 3, right panel). Case A, top row; Case B, middle row; Difference between Case A and B, bottom row.

been examined for many years, which have led to conflicting conclusions. For example, by computing the anomalies of 8-day averaged wind mixing strength, Thomas et al. (Thomas et al., 2003) found no clear relationship between local wind forcing and bloom initiation/duration and overall phytoplankton biomass. Durbin et al. (Durbin et al., 2003) showed that although the bloom was much earlier in 1999 than in 2000, the computed critical depths in February of both years were not significantly different, and they suggested that the change in surface irradiance between years may not be responsible for the interannual variability of bloom initiation. Townsend and Cammen (Townsend and Cammen, 1988) drew the opposite conclusion, however, with respect to smaller scale, near-shore regions of the coastal Gulf of Maine. These different conclusions likely

are scale-dependent; for example, our examination of International Satellite Cloud Climatology Project (ISCCP) data suggests that the interannual variability of surface insolation is insignificant when integrated over the entire Gulf of Maine, while the surface winds and sensible and latent heat fluxes produced by a regional meteorological model (GoM-MM5, Chen et al., 2005) exhibit significant interannual variability on a gulf-wide scale. Finally, comparison of seasonal river discharge rates (USGS river discharge data) with long-term Gulf of Maine salinity data suggests that the surrounding rivers do not exert a significant contribution to the interannual variability in the salinity structure in the Gulf of Maine, especially in the deeper areas away from the coast. However, this does not exclude the potential impact of river discharge on areas such as Wilkinson

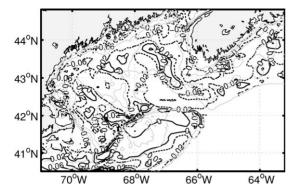


Fig. 13. Model-computed spatial distributions of depth-integrated net primary productivity (g C $m^{-2}~day^{-1}$) integrated throughout March and April.

Basin, which the river plumes are known to reach when local river discharge is high (Chen *et al.*, 1995; C. Manning, personal communication).

Although our model results have demonstrated that freshening is a major forcing that influences the interannual variability of nutrient and phytoplankton dynamics in the Nova Scotian Shelf-Gulf of Maine region, earlier studies have suggested that other large-scale forcings, such as slope water inflows, may also play a role. For instance, Townsend and Spinard (Townsend and Spinard, 1986) argued that spring phytoplankton blooms can occur earlier and be stronger when the WSW inflow is more dominant than the Labrador Slope Water (LSW) inflow into the Gulf of Maine. Since WSW is warmer, more saline and nutrient-rich than LSW, it enhances the upward doming of dense slope water to isolate an upper mixed layer that could promote early blooms. On the other hand, the spring bloom will be weaker or even less likely to occur when a significant LSW inflow occurs, partially due to the decreased doming effect, but more importantly, because LSW has much lower nutrient concentrations than WSW (Thomas et al., 2003). This hypothesis was used to explain the occurrence of an early spring bloom in Jordan Basin in February 1984 and was later used to explain the disappearance of the spring bloom in 1998 and a strong and early bloom in 1999 (Thomas et al., 2003). However, from the bottom temperature and salinity anomaly data collected in the deep basins of the Gulf of Maine (NOAA Northeast Fisheries Science Center oceanography survey data, http://nefsc.noaa.gov/epd/ocean/MainPage/ioos.html), it appears that the bottom water was cooler and fresher during 1999, which argues against this hypothesis. While our modeling work reported here did not address the influence of slope waters directly, we suggest that the different types of slope waters probably play a secondary role in controlling phytoplankton bloom dynamics (Ji *et al.*, 2008), mainly because the variability of water column stability is significantly correlated to the variability of SSS during winter-spring period (Ji *et al.*, 2007; Taylor and Mountain, 2008).

One important effect of climate change on plankton dynamics is that it might influence the timing and magnitude of these annually recurring phytoplankton blooms and resulting decoupling of phenological relationships within a pelagic food-web, which would have important implications for trophic interactions, as suggested by the Hjort-Cushing match/mismatch theory (Hjort, 1914; Cushing, 1975; Cushing, 1990). For example, earlier spring blooms may provide critical food supply for copepod prey of larval fish, although overall spring primary production may be lower. Previous studies have been focused on the changes in temperature (warming) in various ecosystem, including lakes (e.g. Winder and Schindler, 2004), open oceans (Hughes, 2000; Edwards and Richardson, 2004) and coastal oceans (Oviatt, 2004). From our simple numerical experiments in this study, we showed that climate-induced changes in surface salinity can be a major factor driving ecosystem changes. More studies to better understand ecosystem response to freshening are warranted since increasing evidence has suggested that climate-induced freshening occurs more and more frequently in higher-latitude oceans, including the North Atlantic (e.g. Häkkinen, 2002; Belkin, 2004; Curry and Mauritzen, 2005; Josey and Marsh, 2005), the North Pacific (e.g. Freeland et al., 1997; Lucas, 2001) and the Southern Ocean (Jacobs et al., 2002). Given that the salinity anomaly across the Gulf of Maine has already exceeded 1 PSU during some freshening years (Mountain, 2004), it would not be a surprise to see even more enhanced freshening in the future caused by increased glacial melting and enhanced precipitation and river runoff at high latitude (Curry and Mauritzen, 2005; Peterson et al., 2006). As a result, the bloom occurrence could be further advanced towards early winter in the upstream areas along the Nova Scotia Shelf, and draw-down surface water nutrient concentration before the water enters the Gulf of Maine. The consequence could be significant for many aspects of the ecosystem dynamics in the region due to the changes of timing and productivity at lower trophic levels. The coupled model used in this study is simple when compared with the real ocean, yet it serves well as a first-order approximation of the magnitude of the phytoplankton response to changes in salinity and associated circulation and water column properties in a complex coastal/shelf system. More importantly, the results from simple numerical experiments allow us to

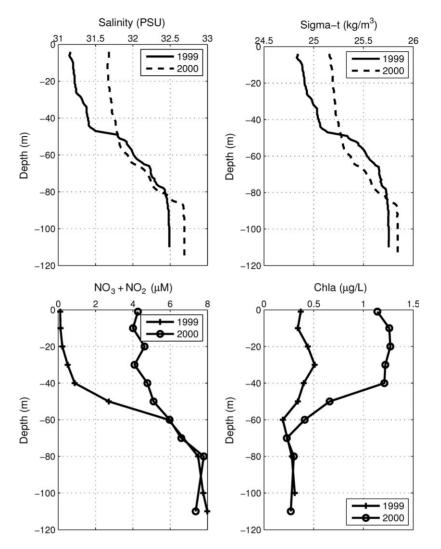


Fig. 14. Observation data collected at AZMP BB2 showing the difference of salinity, σ_t , NO₃ + NO₂ and Chl *a* profiles in April, 1999 and 2000. AZMP data source: Fisheries and Oceans Canada.

ask more refined ecological questions and therefore promote more targeted observation strategies and improve future modeling studies.

SUMMARY

Numerical experiments have been conducted to examine the influence of surface freshening on water column stability and associated winter-spring phytoplankton bloom dynamics in the Nova Scotian Shelf– Gulf of Maine region. The model results support the conceptual model that freshening caused earlier blooms both on the Nova Scotian Shelf and in the eastern Gulf of Maine. Earlier phytoplankton blooms in the LSS case were followed by earlier depletion of nutrients at the surface along with earlier decline of blooms compared with the HSS case. Freshening can impede vertical nutrient exchange between surface and deep waters, thus reducing the overall spring primary productivity throughout the region. The model results suggest that climate-related surface freshening has a significant influence on regional nutrient-plankton dynamics, and therefore have significant ramifications for ecosystem dynamics from lower to higher trophic levels.

FUNDING

We thank NSF grant OCE-0727033 and NOAA grant NA17RJ1223 to R.J., C.S.D. and R.C.B., NSF grants OCE-0606612 and OCE-0726577 to D.W.T., and NSF grants OCE-0606928 and OCE-0726851 to C.C.

ACKNOWLEDGEMENTS

M. Taylor at NOAA NMFS provided MARMAP and ECOMON data. We would like to thank Q. Xu for his help on setting up the physical model run; R. Tian for providing initial biological conditions (with original data from Pierre Clement at Bedford Institute of Oceanography); G. Cowles for his help on FVCOM parallel running and post-processing; and S. Hu for providing MM5 model output. We also want to thank two anonymous reviewers for their constructive comments that have improved the manuscript significantly. The US GLOBEC contribution number is 603.

REFERENCES

- Beardsley, R. C., Butman, B., Geyer, W. R. et al. (1997) Physical oceanography of the Gulf of Maine: an update. Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop. Report 97-1. Regional Association for Research in the Gulf of Maine, Hanover, NH, USA, 39–52.
- Belkin, I. M. (2004) Propagation of the "Great Salinity Anomaly" of the 1990s around the Northern North Atlantic. *Geophys. Res. Lett.*, **31**, L08306. doi: 10.1029/2003GL019334.
- Bigelow, H. B. (1926) Plankton of the offshore waters of the Gulf of Maine. Bull. US Bur. Fish., 40, 1–509.
- Bigelow, H. B. (1927) Physical oceanography of the Gulf of Maine. Bull. US Bur. Fish., 40, 511-1027.
- Brooks, D. A. (1985) Vernal circulation in the Gulf of Maine. *J. Geophys. Res.*, **90**, 4687–4705.
- Chen, C., Beardsley, R. C. and Limeburner, R. (1995) Variability of water properties in late spring in the northern Great South Channel. *Cont. Shelf Res.*, 15, 415–431.
- Chen, C., Beardsley, R. and Franks, P. J. S. (2001) A 3-D prognostic numerical model study of the Georges Bank ecosystem. Part I: physical model. *Deep-Sea Res. II*, 48, 419–456.
- Chen, C. S., Liu, H. D. and Beardsley, R. C. (2003) An unstructured grid, finite-volume, three-dimensional, primitive equations ocean model: application to coastal ocean and estuaries. *J. Atmos. Oceanic Technol.*, **20**, 159–186.
- Chen, C., Beardsley, R., Hu, S. et al. (2005) Using MM5 to hindcast the ocean surface forcing fields over the Gulf of Maine and Georges Bank region. J. Atmos. Oceanic Technol., 22, 131–145.
- Chen, C., Huang, H., Beardsley, R. et al. (2007) A finite volume numerical approach for coastal ocean circulation studies: comparisons with finite difference models. *J. Geophys. Res.*, **112**, C03018. doi: 10.0129/2006JC003485.
- Colebrook, J. M. (1979) Continuous plankton records: seasonal variation in the distribution and abundance of plankton in the North Atlantic and the North Sea. *J. Plankton Res.*, 4, 435–462.
- Curry, R. and Mauritzen, C. (2005) Dilution of the northern North Atlantic Ocean in recent decades. *Science*, **308**, 1772–1774.
- Cushing, D. H. (1959) The seasonal variation in oceanic production as a problem in population dynamics. J. Cons. Int. Explor. Mer., 24, 455–464.
- Cushing, D. H. (1975) Marine Ecology and Fisheries. Cambridge University Press.

- Cushing, D. H. (1990) Plankton production and year-class strength in fish populations—an update of the match mismatch hypothesis. Adv. Mar. Biol., 26, 249–293.
- Drinkwater, K. F. and Gilbert, D. (2004) Hydrographic variability in the Waters of the Gulf of St. Lawrence, the Scotian Shelf and the Eastern Gulf of Maine (NAFO Subarea 4) During 1991–2000. *J. Northu. Atl. Fish. Sci.*, **34**, 85–101. doi:110.2960/J.v2934.m2545.
- Durbin, E. G., Campbell, R. G., Casas, M. C. *et al.* (2003) Interannual variation in phytoplankton blooms and zooplankton productivity and abundance in the Gulf of Maine during winter. *Mar. Ecol. Prog. Ser.*, 254, 81–100.
- Edwards, M. and Richardson, A. J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881–884.
- Frank, K. T., Petrie, B. and Shackell, N. L. (2007) The ups and downs of trophic control in continental shelf ecosystems. *Trends Ecol. Evol.*, 22, 236–242.
- Fratantoni, P. S. and Pickart, R. S. (2007) The western North Atlantic shelfbreak current system in summer. *J. Phys. Oceangr.*, 37, 2509–2533.
- Freeland, H., Denman, K., Wong, C. S. et al. (1997) Evidence of change in the winter mixed layer in the Northeast Pacific Ocean. *Deep-Sea Res. I*, 44, 2117–2129.
- Greene, C. H. and Pershing, A. J. (2007) Climate drives sea change. *Science*, **315**, doi:10.1126/science.1136495.
- Häkkinen, S. (2002) Freshening of the Labrador Sea surface waters in the 1990s: another great salinity anomaly? *Geophys. Res. Lett.*, 29, 2232. doi: 10.1029/2002GL015243.
- Han, G., Hannah, C., Loder, J. W. et al. (1997) Seasonal variation of the three-dimensional mean circulation over the Scotian Shelf. *J. Geophys. Res.*, **102**, 1011–1025.
- Hannah, C., Shore, J. A. and Loder, J. W. (2001) Seasonal circulation on the western and central Scotian Shelf. J. Phys. Oceangr. 31, 591–615.
- Harris, G. P. (1986) Phytoplankton Ecology: Structure, Function and Fluctuation. Cambridge University Press.
- Hjort, J. (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P-V Reun. Cons. Int. Explor. Mer.*, 1, 5–38.
- Houghton, R. W. and Fairbanks, R. G. (2001) Water sources for Georges Bank. Deep-Sea Res. II, 48, 95–114.
- Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.*, **15**, 56–61.
- Jacobs, S. S., Giulivi, C. F. and Mele, P. A. (2002) Freshening of the Ross Sea during the late 20th century. *Science*, **297**. doi: 10.1126/ science.1069574.
- Ji, R., Chen, C., Franks, P. J. S. et al. (2006) Spring bloom and associated lower trophic level food web dynamics on Georges Bank: 1-D and 2-D model studies. *Deep-Sea Res. II*, 53, 2656–2683.
- Ji, R., Davis, C. S., Chen, C. et al. (2007) Influence of ocean freshening on shelf phytoplankton dynamics. Geophys. Res. Lett., 34, L24607. doi: 10.1029/2007GL032010.
- Ji, R., Davis, C. S., Chen, C. *et al.* (2008) Influence of local and external processes on the annual nitrogen cycle and primary productivity on Georges Bank: a 3-D biological-physical modeling study. *J. Mar. Syst.*, **73**, 31–47.
- Josey, S. A. and Marsh, R. (2005) Surface freshwater flux variability and recent freshening of the North Atlantic in the eastern subpolar gyre. *J. Geophy. Res.*, **110**. doi:10.1029/2004JC002521.

- Lucas, R. (2001) Freshening of the upper thermocline in the North Pacific subtropical gyre associated with decadal changes of rainfall. *Geophys. Res. Lett.*, 28, 3485–3488.
- Lynch, D. R., Ip, J. T C., Naimie, C. E. *et al.* (1996) Comprehensive coastal circulation model with application to the Gulf of Maine. *Cont. Shelf Res.*, **12**, 37–64.
- Mountain, D. G. (2003) Variability in the properties of Shelf Water in the Middle Atlantic Bight, 1977–1999. *J. Geophys. Res.*, **108**, 3014. doi: 10.1029/2001JC001044.
- Mountain, D. G. (2004) Variability of the Water Properties in NAFO Subareas 5 and 6 During the 1990s. *J. Northus Atl. Fish. Sci.*, 34, 103–112. doi: 10.2960/J.v34.m475.
- O'Reilly, J. E., Evans-Zetlin, C. E., Busch, D. A. et al. (1987) Primary production. Georges Bank. MIT Press, Cambridge, MA, pp. 220–233.
- Oviatt, C. A. (2004) The changing ecology of temperate coastal waters during a warming trend. *Estuaries*, 27, 895–904.
- Peterson, B. J., McClelland, J., Curry, R. *et al.* (2006) Trajectory shifts in the Arctic and Subarctic freshwater cycle. *Science*, **313**. doi: 10.1126/science.1122593.
- Pettigrew, N. R., Townsend, D., Xue, H. et al. (1998) Observations of the Eastern Maine Coastal Current and its offshore extensions. *7. Geophys. Res.*, **103**, 30623–30640.
- Platt, T., Fuentes-Yaco, C. and Frank, K. T. (2003) Marine ecology: spring algal bloom and larval fish survival. *Nature*, **423**, 398–399.
- Price, J. F., Weller, R. A. and Pinkel, R. (1986) Diurnal cycling: observations and models of the upper ocean response to diurnal heating, colling, and wind mixing. *J. Geophys. Res.*, **91**, 8411–8427.
- Riley, G. A. (1942) The relationship of vertical turbulence and spring diatom flowering. *J. Mar. Res.*, 5, 67–87.
- Smith, P. C. (1989) Seasonal and interannual variability of current temperature and salinity off southwest Nova Scotia. *Can. J. Fish. Aquat. Sci.*, **46**, 4–20.

- Sverdrup, H. U. (1953) On conditions for the vernal blooming of phytoplankton. J. Cons. Int. Explor. Mer., 18, 287–295.
- Taylor, M. H. and Mountain, D. G. (2008) The influence of surface layer salinity on wintertime convection in Wilkinson Basin, Gulf of Maine. *Cont. Shelf Res.*, in press.
- Thomas, A. C., Townsend, D. W. and Weatherbee, R. (2003) Satellite-measured phytoplankton variability in the Gulf of Maine. *Cont. Shelf Res.*, **23**, 971–989.
- Townsend, D. W. and Cammen, L. M. (1988) Potential importance of the timing of spring plankton blooms to benthic pelagic coupling and recruitment of juvenile demersal fishes. *Biol. Oceanogr.*, 5, 215–229.
- Townsend, D. W. and Spinard, R. W. (1986) Early phytoplankton blooms in the Gulf of Maine. *Cont. Shelf Res.*, **6**, 515–529.
- Townsend, D. W., Keller, M. D., Sierachi, M. E. et al. (1992) Spring phytoplankton blooms in the absence of vertical water column stratification. *Nature*, **360**, 59–62.
- Townsend, D. W., Cammen, L. M., Holligan, P. M. et al. (1994) Causes and consequences of variability in the timing of spring phytoplankton blooms. *Deep-Sea Res. I*, 41, 747–765.
- Townsend, D. W., Thomas, A. C., Mayer, L. M. et al. (2006) Oceanography of the Northwest Atlantic Continental Shelf. In Robinson, A. R. and Brink, K. H. (eds), *The Sea*. Vol. 14. Harvard University Press, pp. 119–168.
- Wiebe, P., Beardsley, R., Mountain, D. et al. (2002) U.S. GLOBEC Northwest Atlantic/Georges Bank Program. Oceanography, 15, 13–29.
- Winder, M. and Schindler, D. E. (2004) Climatic effects on the phenology of lake processes. *Global Change Biol.*, **10**, 1844–1856.
- Xue, H., Chai, F. and Pettigrew, N. R. (2000) A model study of the seasonal circulation in the Gulf of Maine. *J. Phys. Oceangr.*, **30**, 1111–1135.