Historic 2005 toxic bloom of *Alexandrium fundyense* in the west Gulf of Maine:

1. In situ observations of coastal hydrography and circulation

Ruoying He¹ and Dennis J. McGillicuddy Jr.²

Received 21 October 2007; revised 28 March 2008; accepted 29 May 2008; published 26 July 2008.

[1] An extensive *Alexandrium fundyense* bloom occurred along the coast of the Gulf of Maine in late spring and early summer 2005. To understand the physical aspects of bloom’s initiation and development, in situ observations from both a coast-wide ship survey and the coastal observing network were used to characterize coastal circulation and hydrography during that time period. Comparisons between these in situ observations and their respective long-term means revealed anomalous ocean conditions during May 2005: waters were warmer and fresher coast-wide owing to more surface heating and river runoff; coastal currents were at least 2 times stronger than their climatological means. Surface winds were also anomalous in the form of both episodic bursts of northeast winds and a downwelling-favorable mean condition. These factors may have favored more vigorous along-shore transport and nearshore aggregation of toxic *A. fundyense* cells (a red tide) in 2005.


1. Introduction

[2] Blooms of the toxic dinoflagellate *Alexandrium fundyense* are a common feature during the late spring and summer months in the Gulf of Maine (GOM). These blooms pose a serious human health threat due to the accumulation of neurotoxins in shellfish that feed on the algal cells, resulting in a potentially fatal illness known as paralytic shellfish poisoning (PSP). Earlier studies have shown that *A. fundyense* blooms are regulated by a suite of complex biological and physical processes, and the timing and distributions of the bloom are closely related to the GOM coastal circulation (see for example, Anderson et al. [2005a], DSR II Special Volume).

[3] The general circulation of the GOM (Figure 1) is cyclonic [e.g., Bigelow, 1927; Brooks, 1985; Brown and Irish, 1993; Lynch et al., 1997; Pettigrew et al., 1998; Pettigrew et al., 2005]. The eastern segment of the circulation comprises the Eastern Maine Coastal Current (EMCC), and inflow from the Scotian shelf. The EMCC is a turbulent, cold coastal current. It often veers offshore south of Penobscot Bay. Some EMCC waters continue moving offshore, and some return shoreward to form the western Maine Coastal Current (WMCC). Downstream, the WMCC waters can separate into two branches near Cape Ann, one entering Massachusetts Bay, and the other traveling along the eastern flank of Stellwagen Bank. Further downstream, the Stellwagen Bank segment undergoes another bifurcation, one leaving the GOM through the Great South Channel, and the other turning east toward Georges Bank. Another element in the coastal current system is the so-called Gulf of Maine Coastal Plume (GOMCP) [Keafer et al., 2005]. This transport pathway is shoreward of both EMCC and WMCC. It carries fresh river water emanating from riverine sources along the coast all the way to the western GOM, making direct connection between eastern and western gulf, especially during the spring/early summer when river runoff is large. These “mean” circulation features mentioned above are in fact very dynamic. Depending upon the local and remote forcing conditions, the structure of the coastal current system may vary dramatically, and in turn significantly affect the transport and distribution of *A. fundyense* populations and other material properties.

[4] The extensive *A. fundyense* bloom that occurred in 2005 was considered to be the worst in at least 33 years [Anderson et al., 2005b]. The entire coastline from eastern Maine to Massachusetts, as well as 40,000 km² of federal waters offshore, were closed to shellfish harvesting. A fundamental question of both scientific and societal interest is why did this extensive bloom occur in 2005? Anderson et al. [2005b] presented some initial observations and suggested several biological and physical factors may have contributed to the bloom. Pettigrew and Xue [2006] described the anomalous GOM coastal current system response to the late spring northeasterly wind-forcing. Our objective here is to explore physical factors pertinent to this bloom event in detail. We utilize in situ observations...
collected by a coast-wide ship survey and the regional coastal ocean observing network. Coastal hydrography, circulation, and its associated forcing conditions during this bloom event are further characterized via comparison with their long-term mean conditions.

2. Data

2.1. Ship Observations

The coast-wide ship survey was executed on the R/V *Oceanus* (Voyage OC412) between 9 and 18 May 2005, a period coinciding with the initial phase of bloom development. During the 10-day field survey, a total of 133 hydrographic stations between Massachusetts Bay and the Bay of Fundy were occupied (Figure 2). CTD casts were conducted at each station, providing 1-m-resolution vertical profiles of hydrographic properties including temperature, salinity, in situ fluorescence, and light transmission. Water samples were also collected from Niskin bottles on the CTD rosette for nutrient analysis and *A. fundyense* cell counts. In addition, shipboard Acoustic Doppler Current Profiler (ADCP) measurements were made underway, providing depth profiles of current speed and direction throughout the survey.

2.2. Observations From Coastal Observing Network

Time series measurements of surface wind, sea level, and river runoff were obtained from National Oceanic and Atmospheric Administration (NOAA), National Ocean Service (NOS) coastal tidal gauges and United States Geological Survey (USGS) river gauges. Meteorological and hydrographic data measured by buoys of the Gulf of Maine Ocean Observing System (GoMOOS, http://www.gomoos.org/) were also collected throughout this bloom event. Earlier studies have suggested that surface wind fields in the GOM are spatially heterogeneous [e.g., *He et al.*, 2005]. As such, we also utilized NOAA NCEP surface flux
reanalysis data (http://www.ncep.noaa.gov) to examine the temporal and spatial variability of wind fields in 2005.

3. Results

3.1. Ship Data

3.1.1. Hydrography

[7] Temperature and salinity data from CTD casts provide a coast-wide, synoptic view of the hydrographic conditions in May 2005 (Figure 3). Sea surface temperatures (SST) in the western GOM were several degrees warmer than in the eastern gulf, a common characteristic of SST in the GOM. This contrast is primarily due to stronger tidal mixing in the eastern gulf, which brings cold deep water up to the surface. The salinity field indicates an alongshore band of fresh water with salinity less than 31.5 psu. Comparing these observations with climatological temperature and salinity fields for Gulf of Maine provides a useful context to describe the hydrographic conditions observed in summer 2005. The climatology used here [Loder et al., 1997; Lynch et al., 1996, 1997] consists of historical hydrographic data comprising about 54,000 stations with coincident temperature and salinity measurements. Gulf-wide temperature and salinity climatological values were then optimally interpolated in four-dimensional space (two horizontal coordinates, depth and time). Interested readers are referred to Loder et al. [1997] for additional detail about this climatology.

[8] Several unique features stand out when comparing May climatological surface temperature and salinity fields with our CTD data. First, surface water temperatures in May 2005 (Figure 3, top left) were generally warmer than the climatological mean condition (Figure 3, top right). A northeast-to-southwest temperature gradient of \( \sim 4^\circ C \) to \( 6^\circ C \) is apparent in the climatology off midcoast Maine. This gradient appears to have been shifted from east of Casco Bay in the climatology to east of Penobscot Bay in the observed field, indicating that relatively warm water occupied the western GOM in May 2005. Second, coastal waters in May 2005 were fresher than the climatological mean salinity field by up to 4 psu along the coast and 1 psu in the gulf interior. Anderson et al. [2005b] indicated that the major rivers of midcoast Maine (i.e., the Kennebec, Androscoggin, and Penobscot; see Figure 2) in the GOM had discharges 50% higher than their respective 80-year averages due to heavy snowmelt and excessive precipitation in spring and summer 2005. Contrast between the observed salinity field (Figure 3, bottom left) and its climatological counterpart (Figure 3, bottom right) therefore reflect a consequence of excessive fresh water input. The salinity comparison further shows the freshening was actually coast-wide, including the coastal region south of Nova Scotia. Given the connectivity between coastal waters in this region and waters on the Scotian shelf and further upstream, the freshening must have been influenced by remote sources as well.

[9] To explore subsurface water property differences, observed temperature and salinity fields were compared with their climatological counterparts across 5 transects in

Figure 2. Locations of CTD stations of May 2005 Oceanus survey in the GOM. Also shown are the locations of five sections where across-shelf temperature and salinity data are examined in Figure 4, and the geographic locations (indicated by triangles) of GoMOOS moorings A and B.
the gulf (Figure 4). This was achieved by interpolating May climatological temperature and salinity data to the same sampling grid and depth bins of our ship CTD data. Except transect 1 (the southernmost transect), observed across-shelf temperatures were all about 1–2°C warmer than the climatology in the upper 100 m. The middepth temperature minimum usually observed at 30–40 m was much less prominent and the thermal stratification significantly reduced in 2005. Associated with the weakened thermal stratification was strengthened haline stratification. Nearshore salinity in 2005 was 2–4 psu fresher than its climatology owing to excessive river runoff and the resultant larger river plumes. As indicated by the salinity transects, the river plumes extended to more than 50 m at depth. Both temperature and salinity determine the density field. The mean GOM coastal buoyancy frequency $N^2 = \frac{\partial^2 p}{\partial z^2}$ computed from all CTD stations in 2005 is $5.6 \times 10^{-5}$ s$^{-2}$, substantially higher than the mean climatological value $4.1 \times 10^{-5}$ s$^{-2}$, which was computed in the same way on the same grid and depth bins as the CTD stations. Thus, the coastal waters of the GOM in May 2005 were over all more buoyant than the average condition.

These coastal temperature and salinity observations in May 2005 also document substantial departures from climatological water mass characteristics. On the basis of the definitions of Brown and Irish [1993], the Maine Intermediate Water (MIW) is classified as the water having 31.75 to 33.25 psu in salinity range and 1.5 to 6°C in temperature range; while the Maine Surface Water (MSW) is referred to waters fresher than 31.75 psu. Comparison of T-S diagrams between our observations and those extracted from the climatology at the same locations (Figure 5) indicates that much more MSW resided in the GOM in May 2005. We recognize that part of the reason for such apparent increase in MSW may be because the nearshore regions, especially estuaries and freshwater plumes, are not well represented in the climatology [Lynch et al., 1997].

3.1.2. Geostrophic Currents

Temperature, salinity and depth data measured by CTD were used to compute the synoptic dynamic height (DH) field (Figure 6a) and associated geostrophic circulation. DH is obtained by integrating relative to the offshore starting point of each section, and a baroclinic velocity is computed to balance the local depth-varying pressure gradient that gives zero pressure gradient (and hence no motion) at the seafloor [Csanady, 1979; Loder et al., 1997]. Because the gulf waters were relatively warmer and fresher near the coast in 2005, the computed DH is larger nearshore than it is further offshore. Some local DH maxima are associated with large fresh water runoff, and are clearly seen in the vicinity of major rivers (i.e., St. Johns, Kennebec and Androscoggin, and Merrimack).

Despite the imperfect assumption of no motion at the seafloor, the resulting geostrophic currents (GC) successfully capture many known GOM circulation features, including the inflow from Scotia shelf, the EMCC, its offshore turning off Penobscot Bay, and the WMCC. Differences are evident when comparing DH and GC in May 2005 with their climatological counterparts (Figure 6b). The DH near the coast is more than 0.10 m higher in 2005 than the mean condition. The resulting stronger than normal across-shelf pressure gradient consequently produces a GC
that is 2 times larger in 2005 than the climatological GC (note the change of vector scale in Figure 6b).

3.1.3. Shipboard ADCP Currents

Shipboard Acoustic Doppler Current Profiler (ADCP) data provide more complete measurements of coastal current in that both baroclinic and barotropic components of velocity are captured. Depth-averaged along-track ADCP currents are complex in this region (Figure 7a) owing to the presence of strong, time-dependent tidal currents, particularly in the eastern GOM. To recover the subtidal circulation that dominates material property transport, we first constructed the barotropic tidal current at each time and location where the ADCP current was sampled in the survey. For such purpose, we utilized the harmonic tidal prediction method of Pawlowicz et al. [2002] in conjunction with a North Atlantic tidal harmonic constant database generated by the ADCIRC model [Luetich et al., 1992]. The resulting barotropic tidal currents were then subtracted from the depth-averaged ADCP measurements to produce the depth-averaged synoptic subtidal circulation field (Figure 7b). While some tidal residuals are still present owing to inaccurate tidal solutions in a few areas, the spatial structure of ADCP measured subtidal current field is consistent with the GC calculation shown in Figure 6a.

3.2. Mooring Data

To put these synoptic observations in a longer temporal context, we next examine meteorological and oceanic data collected by moorings of the Gulf of Maine Ocean Observing System (GoMOOS) (http://gomoos.org). Most of GoMOOS coastal moorings cover the period from July 2001 to present, thereby providing highly valuable data set for evaluating the variability of GOM coastal circulation and hydrography on timescales from hours to years.
3.2.1. Surface Current

[15] Surface currents (2-m) were examined at GoMOOS mooring A (at 65 m isobath), B (at 62 m isobath), C (at 46 m isobath), E (at 100 m isobath), and I (at 100 m isobath). At each mooring location (see Figure 2), hourly u and v components of the surface velocity data were 36-h low-pass filtered to remove tides, and then averaged to form a monthly mean velocity vector for May 2005 (Figure 8). To reveal how these surface velocity vectors vary with respect to the May “long-term mean” condition, surface velocity observations in May 2002, 2003, and 2004 were processed in the same manner, and then averaged into long-term mean surface vectors. In addition, the long-term mean velocity hodograph ellipses were also computed to provide principal variances information for each station.

[16] Comparisons of surface velocity vectors between May 2005 and the “mean” May conditions highlight dramatic interannual differences in circulation. Consistent with the geostrophic calculation and shipboard ADCP data shown above, the speed of the surface circulation in May 2005 was at least 2 times larger than the long-term mean and...

Figure 5. Comparison of (top) climatological T-S diagram and (bottom) its observed counterpart. Shaded areas indicate the range where the Maine Surface water resides, based on work by Brown and Irish [1993].

Figure 6. (a) Surface dynamic height and its associated geostrophic current field computed with CTD data collected in Oceanus survey and (b) their climatological counterparts. Note the change of vector scale.

Figure 7. (top) Depth-averaged shipboard ADCP current field and (bottom) its detided (subtidal) rendition.
significantly exceeded the normal range of principal variance. This implies that transport of material properties in the western GOM from Penobscot Bay to Massachusetts Bay would take only 1–2 weeks versus 2–4 weeks in average conditions. Moreover, mean velocity vectors in May 2005 also had more onshore components than average, which implies enhanced shoreward transport of *A. fundyense* population and other material properties.

### 3.2.2. Surface Salinity

[17] Given the importance of salinity in determining dynamic height and the associated geostrophic pressure field in the GOM (Figure 6a), we now examine the temporal evolution of surface salinity with 5-year time series collected by conductivity sensors on GoMOOS moorings A and B. For each time series, seasonal cycle was first constructed by least squares fitting the raw salinity observations to a mean and two annual harmonics:

\[ S_{\text{seasonal}} = \text{const} + a \sin(\omega t) + b \cos(\omega t), \]

where \( t \) is time in days, \( \omega = 2\pi / 365 \text{ d}^{-1} \), and \( a \) and \( b \) are coefficients of the harmonic fit. The resulting \( S_{\text{seasonal}} \) was then subtracted from the original salinity time series to form salinity anomaly at each station, i.e., \( S_{\text{anomaly}} = S_{\text{raw}} - S_{\text{seasonal}} \). A 30-day low-pass filter was then applied to \( S_{\text{anomaly}} \) to remove high-frequency variability. The resulting salinity anomaly time series are thus suitable for studying the underlying interannual variability (Figure 9).

[18] At Mooring B, the low-pass filtered salinity anomaly from July 2001 to December 2004 had rather small (<1 psu) departures from the seasonal cycle, implying the balance between fresh water input from local and upstream river runoff, plus evaporation-precipitation (E-P). The salt content of the ambient coastal water was within its typical range during this 3-year time period. The following period from January 2005 to March 2006 was rather different, showing a 15-month-long negative salinity anomaly. This freshening trend reached its peak (–3 psu) in April-May 2005 and continued with reduced magnitude until the following March.

[19] Similar conditions are also observed at Mooring A. At this site, the confluence of fresh water originated from both local and upstream river sources produced even larger salinity anomaly. Two peaks are evident, one in April-May 2005 (as at mooring B), and the other in October 2005, which reached –8 psu. The former freshening peak was caused by large river runoff due to snowmelt and spring precipitation, as documented by Anderson et al. [2005b]. The latter event was related to another strong river runoff event in the western GOM, which was due to the record rainfall in October-November 2005. In fact, the USGS record shows October 2005 is the wettest October and the
second wettest month on record for the western GOM. As an example, Figure 10 shows the discharge time series of Kennebec River (see Figure 1 for its location) between March and December of 2004 and 2005 with respect to its long-term mean (1978–2007). Runoff of the Kennebec River in 2004 was similar to the long-term mean condition, whereas runoff in 2005 was about threefold more than that in 2004 and the long-term mean. Such anomalously large riverine input is the subject of a model sensitivity experiment by He et al. [2008].

3.2.3. Surface Wind

As most of GoMOOS coastal buoys are equipped with meteorological sensors that measure wind speed and direction, it is possible to examine surface wind time series and its interannual variability as well. Using GoMOOS mooring B in the western GOM as an example, comparison of surface wind time series between May 2004 (a “typical” year, see 3.3 below) and May 2005 show completely different wind characteristics (Figure 11): May 2004 was characterized with more southerly to southwesterly winds, whereas winds in May 2005 were more northeasterly owing to successive northeaster storms.

To obtain a first-order estimate of differences in transport induced by such interannual variations in surface wind field, we followed the approach of Fong et al. [1997], which computes the rate of water parcel displacement simply as the Ekman transport divided by the Ekman layer depth $h$ (assumed to be comparable with the local water depth at mooring B). The corresponding displacement is

$$\Delta s = \frac{\tau^r}{\rho h},$$

where $\tau^r$ is the surface wind stress computed using bulk formula of Large and Pond [1981], $\rho$ is water density, and $f$ is Coriolis parameter. We used the GoMOOS mooring B surface wind time series in May 2004 and May 2005 to estimate the corresponding water parcel net displacement during these month-long periods (i.e., progressive vector diagram (PVD) calculation). We found the upwelling favorable winds in May 2004 would cause 35 km net offshore displacement, whereas downwelling favorable winds in May 2005 would result in 80 km net onshore displacement. Although the simplicity of Ekman model and spatial heterogeneity in current field preclude strict interpretation of the PVD net displacement calculation, these results suggest the winds in May 2005 would cause much stronger onshore transport of an offshore bloom, enhancing coastal exposure to the A. fundyense population.
3.3. Surface Wind and Heat Flux Reanalysis

[22] To put the aforementioned surface wind characteristics into a broader spatial context, temporally and spatially continuous wind fields were obtained from NOAA NCEP reanalysis. We constructed the GOM wind climatology for May by averaging wind fields over 58 years (from 1948 to 2005). Similarly, monthly mean wind fields for May 2004 and May 2005 were also produced by averaging wind fields over each of those two month-long periods (Figure 12). Comparisons of these means reveal the southwesterly flow in 2004 was typical with respect to the climatology. In contrast, the mean wind field in May 2005 was predominantly from the northeast, causing downwelling-favorable conditions over the entire gulf.

[23] A similar analysis was applied to NCEP net surface heat flux reanalysis and its four constituents: shortwave radiation, longwave radiation, sensible heat, and latent heat. Because the ocean responds to surface heat flux variability more slowly (on the order of months) than it does to surface wind variability (on the order of a pendulum day), we also included heat flux data in the proceeding month (i.e., April) in the comparison. That is, for each surface heat flux component, we computed the difference between its April-May mean in 2005 and its climatological April-May mean obtained by averaging over 58 years from 1948 to 2005 (Figure 13). We found the shortwave radiation in April-May 2005 was less than its climatological counterpart by 5–10 w/m² in the western GOM and by 15–20 w/m² in the eastern gulf. In contrast, the longwave radiation, sensible heat and latent heat in 2005 all exceeded their climatological counterparts by 10–15 w/m² over almost the entire gulf. Consequently, the net heat flux in April-May 2005 was ~5–10 w/m² larger than the climatological net heat flux. The largest difference is located in the coast region between Casco Bay and Grand Manan Island (see Figure 1), coinciding with the south-to-north position shift of the surface temperature front (see Figure 3).

Figure 10. Time series of Kennebec River discharge during March to November in 2004 (solid gray line) and 2005 (solid thin line), and 30-year mean (1978–2007, dashed gray line).

Figure 11. Surface wind time series measured by GoMOOS mooring B in (top) May 2004 and (bottom) May 2005. The shaded area in the bottom panel indicates the time period when the Oceanus survey was performed.
water density, \( \rho \) water depth, \( \rho C_p H \) where \( Q \) is net surface heat flux, \( \rho C_p H \) the water specific heat, and \( H \) and local water depth, 1–10 w/m² more heat flux would increase temperature of 50m water column approximately by \( \sim 1 \) degree over one month period. This estimation is consistent with hydrographic observations that show surface water temperatures in May 2005 were generally warmer than the climatological condition by 1°C (i.e., Figure 3), suggesting anomalous heating was at least part of the reason for warmer water temperatures in 2005.

4. Discussion

The anomalous hydrographic conditions in May 2005 may have contributed to the historic \( A. \) fundyense bloom in several ways. First, coastal water temperatures were warmer than the average owing to enhanced surface heating. At the same time, coastal waters were fresher, owing to excessive river runoff and precipitation in 2005. The freshening trend started in January 2005, and reached a minimum in salinity during April-May (at Mooring A, another low-salinity peak was observed in October 2005). Hydrographic survey data indicated this freshening event was in fact coast-wide, suggesting inflow waters from the Scotian shelf were also fresher. The anomalous temperature and salinity conditions were advantageous for \( A. \) fundyense, as the organism’s growth processes depend on both of these variables [McGillicuddy et al., 2005; Stock et al., 2005]. Taking the \( A. \) fundyense growth model of Stock et al. [2005],

\[
G(T, S) = \mu \times f(T) \times g(S),
\]

\[
f(T) = -0.000513T^3 + 0.0160T^2 - 0.0867T + 0.382,
\]

\[
g(S) = 0.0000882S^3 - 0.00808S^2 + 0.2205 - 0.872,
\]

where \( G(T, S) \) is the \( A. \) fundyense growth rate, \( T \) and \( S \) are ambient temperature and salinity, and \( \mu \) is the light and nutrient saturation coefficient. In this model, which has been calibrated extensively with laboratory observations, a 1 degree increase in temperature and 5 psu decrease in salinity would cause approximate 30% increase in the growth term \( G \) under the same light and nutrient conditions.

In addition, warmer and fresher coastal waters supported a larger than average dynamic pressure gradient along the coast, and consequently stronger than average coastal current, which enhanced along-coast transport of \( A. \) fundyense [e.g., Franks and Anderson, 1992]. Both geostrophic current calculations and shipboard ADCP current measurements indicated the coastal current in summer 2005 were at least 2 times stronger than the mean current. These observations were further confirmed by GoMOOS mooring data with respect to the long-term mean current records. Stronger alongshore transport could allow material properties to be delivered from the eastern GOM to western GOM much more quickly, therefore may have affected the timing of \( A. \) fundyense bloom in 2005.

Surface wind fields were also anomalous in May 2005. In contrast to the typical upwelling-favorable mean condition, winds in May 2005 were downwelling-favorable as a result of successive northeaster storms. Such anomalous wind-forcing enhanced alongshore and onshore transport of the \( A. \) fundyense population. One possible wind-forcing scenario is that upstream and offshore cell populations were steered into Massachusetts Bay rather than flowing along the eastern flank of Stellwagen bank. This could explain why Massachusetts Bay received such an extensive exposure to the \( A. \) fundyense bloom in 2005.

5. Conclusions

The combined effect of coastal hydrography, circulation and forcing conditions favored the \( A. \) fundyense bloom in spring-summer 2005. In situ observations, long-term time series of GoMOOS mooring data, and NCEP reanalysis fields all quantify significant anomalies in the GOM coastal ocean environment during this time period. Many details of the bloom dynamics still remain unanswered with only physical oceanographic data. For instance, what is the relative importance of the physical factors enumerated above in controlling and regulating the bloom? How do biological and physical factors interplay to determine the timing and ultimate distribution of the bloom? Answering these questions necessitates the use of a coupled hydrodynamic and \( A. \) fundyense population dynamic model that can fill the temporal and spatial gaps of in situ
observations. Model realizations of the physical and biological states can also be valuable to reveal detailed mechanisms controlling this complex coupled system. We refer interested readers to He et al. [2008] of this study, in which we report our coupled model simulations and associated diagnostics.

Acknowledgments. The authors thank technical and logistical support provided by B. Keafer, K. Norton, A. Molitor, O. Kosnyreva, V. Kosnyreva, and L. Anderson. Thanks go to the captain, crews and support personnel of the R/V Oceanus. We are grateful to NOAA NOS, NOAA NCEP, and GoMOOS for providing data product online. Research support was provided through the Woods Hole Center for Oceans and Human Health, National Science Foundation (NSF) grant OCE-0430723 and National Institute of Environmental Health Science (NIEHS) grant 1-P50-ES012742-01, ECOHAB program through NSF grant OCE-9808173 and NOAA grant NA06OAR4720245. This is ECOHAB contribution 268.

References


R. He, Department of Marine, Earth and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695, USA. (rhe@ncsu.edu)

D. J. McGillicuddy Jr., Department of Applied Ocean Physics and Engineering, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.