Suppression of the 2010 *Alexandrium fundyense* bloom by changes in physical, biological, and chemical properties of the Gulf of Maine

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Abstract

For the period 2005–2009, the abundance of resting cysts in bottom sediments from the preceding autumn was a first-order predictor of the overall severity of spring–summer blooms of *Alexandrium fundyense* in the western Gulf of Maine and southern New England. Cyst abundance off mid-coast Maine was significantly higher in autumn 2009 than it was preceding a major regional bloom in 2005. A seasonal ensemble forecast was computed using a range of forcing conditions for the period 2004–2009, suggesting that a large bloom was likely in the western Gulf of Maine in 2010. This did not materialize, perhaps because environmental conditions in spring–summer 2010 were not favorable for growth of *A. fundyense.* Water mass anomalies indicate a regional-scale change in circulation with direct influence on *A. fundyense*'s niche. Specifically, near-surface waters were warmer, fresher, more stratified, and had lower nutrients than during the period of observations used to construct the ensemble forecast. Moreover, a weaker-than-normal coastal current lessened *A. fundyense* transport into the western Gulf of Maine and Massachusetts Bay. Satellite ocean color observations indicate the 2010 spring phytoplankton bloom was more intense than usual. Early season nutrient depletion may have caused a temporal mismatch with *A. fundyense*'s endogenous clock that regulates the timing of cyst germination. These findings highlight the difficulties of ecological forecasting in a changing oceanographic environment, and underscore the need for a sustained observational network to drive such forecasts.

Blooms of the toxic dinoflagellate *Alexandrium fundyense* occur annually in the Gulf of Maine, leading to accumulation of toxins in shellfish that can cause a threat to human health through paralytic shellfish poisoning (PSP). There is considerable seasonal-to-interannual variability in the magnitude of the blooms and the severity of the associated shellfish toxicity, posing difficult challenges for resource management (Shumway et al. 1988). Although some isolated *A. fundyense* populations persist in certain estuaries and embayments, the phenomenon is regional in character, intimately connected to the oceanography of the Gulf of Maine and surrounding areas (Anderson 1997; Townsend et al. 2001). Blooms are initiated by germination from resting cysts, the timing of which is controlled by an endogenous clock (Anderson et al. 2005c). Excystment from the two primary cyst beds (one at the mouth of the Bay of Fundy and the other offshore of mid-coast Maine) inoculates the coastal current system (Fig. 1) with vegetative cells that grow and divide at rates that depend on temperature, light, nutrient availability, and other environmental conditions (McGillicuddy et al. 2005a; Stock et al. 2005). *A. fundyense* populations are typically advected from the northeast toward the southwest in the coastal current system. Driven by both buoyancy and wind-forcing, the coastal current is prone to variation on a variety of time

scales from synoptic to seasonal to interannual (Brooks and Townsend 1989; Lynch et al. 1997; Pettigrew et al. 2005). The distribution and abundance of *A. fundyense* is, thus, governed by a complex combination of physical and biological factors. These aspects of *A. fundyense* population dynamics have been incorporated into a suite of hydrodynamic models, facilitating process-oriented studies using climatological mean conditions (McGillicuddy et al. 2005a) as well as hindcasting studies (He et al. 2008; Li et al. 2009).

The New England coast was affected by a particularly severe occurrence of shellfish toxicity in 2005, perhaps the worst the region had experienced in the last 30 yr (Anderson et al. 2005a). Hindcasts of the event suggested that, although wind and buoyancy forcing played an important role in bloom transport, the primary cause of the large regional bloom was a tenfold increase in the abundance of resting cysts off mid-coast Maine (He et al. 2008). This led to the hypothesis that autumn cyst abundance was a first-order predictor of the overall magnitude of the bloom the subsequent spring. Cyst abundance off mid-coast Maine dropped by ~ 50% in autumn 2005, and predictions for the 2006 bloom to be about half as bad as 2005 proved to be correct (Li et al. 2009).

Herein we provide observations demonstrating that this correlation between the abundance of resting cysts and the extent of toxicity in the western Gulf of Maine and

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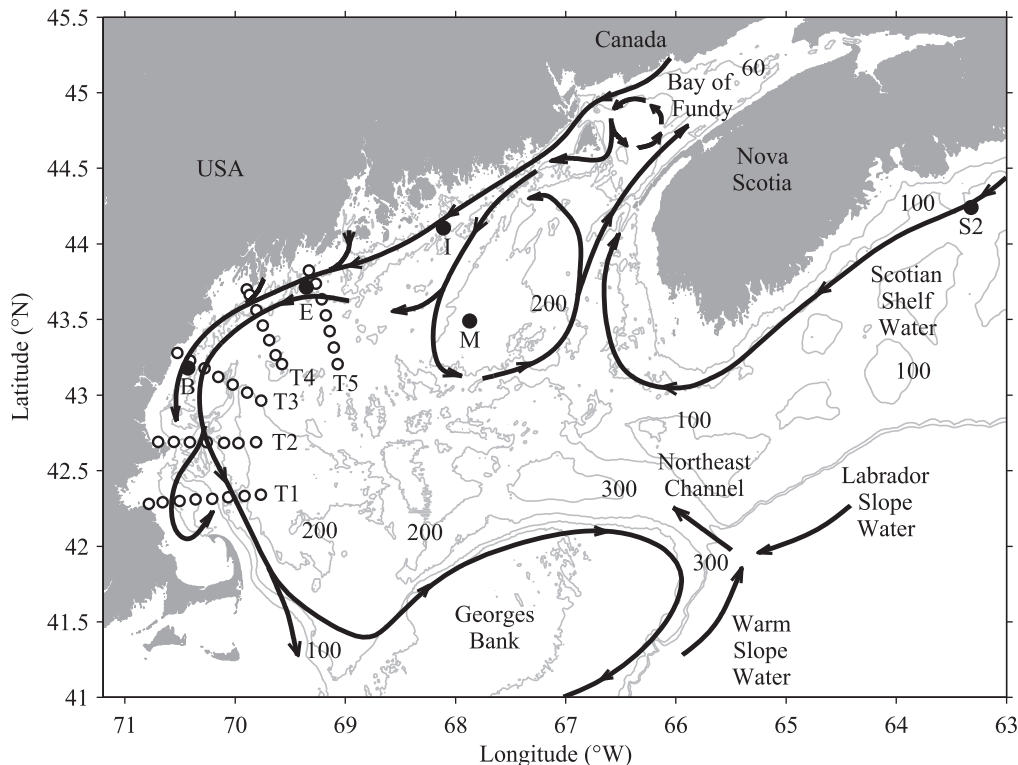* Corresponding author: dmcgillicuddy@whoi.edu

Fig. 1. Regional domain of the *A. fundyense* bloom in the Gulf of Maine. Features of the near-surface circulation relevant to the results described herein are shown as solid black lines with arrows. This schematic of the circulation has been adapted from earlier depictions in Beardsley et al. (1997), Lynch et al. (1997), Keafer et al. (2005), and Pettigrew et al. (2005). Open circles along transects T1–T5 indicate the hydrographic sampling grid from which water mass properties are reported in Figs. 6–10. Note that additional stations are utilized in cell-count maps presented in Fig. 5. Locations of NERACOOS moorings B, E, I, M, and AZMP time-series sta. 2 are shown as black dots.

southern New England persisted for the period 2005–2009. The autumn 2009 cyst survey revealed that cyst abundance offshore of mid-coast Maine was higher than in all prior measurements, including those that preceded the severe blooms of 2005 and 2008. A seasonal forecast was computed based on the range of forcing conditions for the period 2004–2009, suggesting a large bloom was likely in the western Gulf of Maine. Real-time forecasts of *A. fundyense* abundance made during the bloom season (http://omglnx3.meas.ncsu.edu/GOMTOX/2010forecast/) were generally within the range of variation predicted by the seasonal ensemble. Model predictions of a larger than usual bloom in the western Gulf of Maine did not materialize in May and June, and the correlation between cyst abundance and extent of toxicity ceased.

What factors prevented a large *A. fundyense* bloom from occurring in 2010? Observations from a series of four hydrographic cruises reveal the presence of water mass anomalies at the times and locations of the expected *A. fundyense* blooms. Origins of these anomalies are inferred from temperature–salinity characteristics, and evidence of their onset is discernable from time-series data provided by coastal ocean observing systems. Satellite ocean-color data also reveal a regional-scale phytoplankton response to the environmental perturbation, which appears to have contributed to suppression of the 2010 *A. fundyense* bloom in the Gulf of Maine.

Methods

Hydrographic profiles and water samples were collected with a standard Conductivity, Temperature, Depth–rosette system with Niskin bottles (*see* Fig. 1 for station positions). Nutrient samples were filtered through Millipore HA filters, placed immediately in a seawater ice bath for 5–10 min, and frozen at $-18°C$. Concentrations of $NO_3 + NO_2$, NH_4, $Si(OH)_4$, and PO_4 were measured with a Bran Luebbe AA3 AutoAnalyzer using standard techniques.

A. fundyense cells were enumerated from water samples using an oligonucleotide probe and methods described in Anderson et al. (2005b). Both *A. tamarense* and *A. fundyense* occur in the Gulf of Maine, and these are considered to be varieties of the same species. Available molecular probes cannot distinguish between them, and only detailed analysis of the thecal plates on individual cells can provide this resolution, which is not practical for large numbers of field samples. Accordingly, for the purpose of this study, the name *A. fundyense* is used to refer to both forms.

Cysts of *A. fundyense* were collected and enumerated from sediment samples using methods described in Anderson et al. (2005c). Samples were obtained with a Craib corer in coast-wide surveys typically consisting of 12–15 cross-shore transects with ~ 100 stations. *A. fundyense* cysts from the upper 1 cm of sediment are viable for
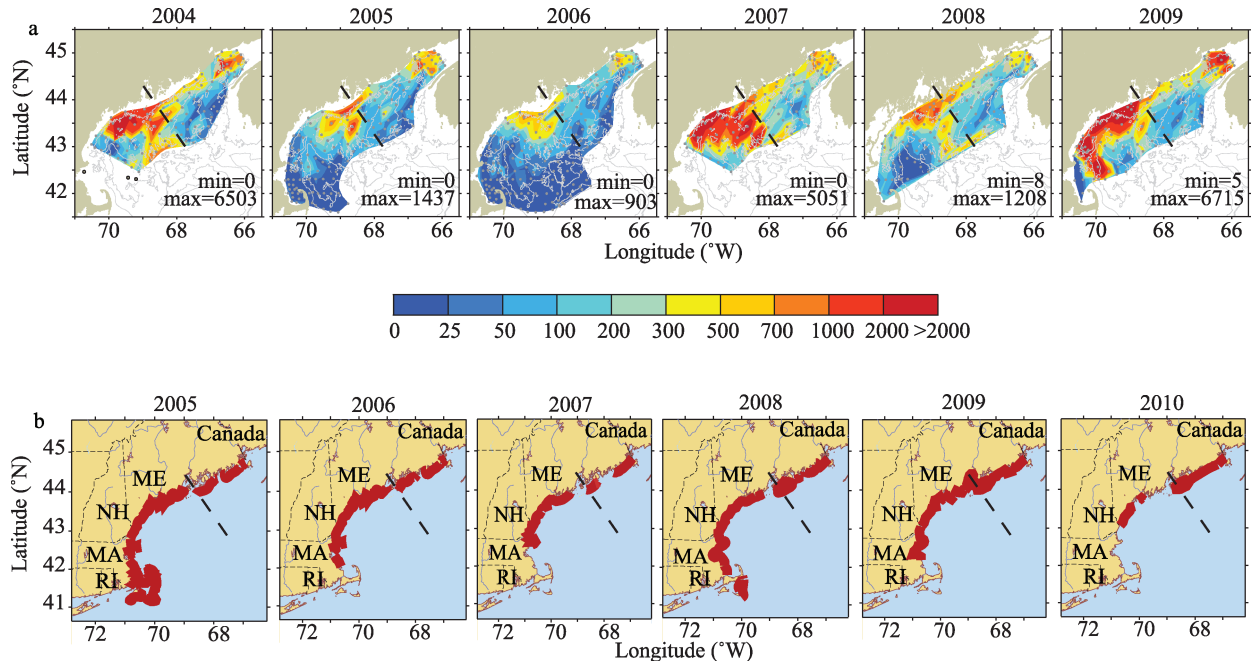
Fig. 2. (a) Cyst abundance 2004–2009. Minimum and maximum values are indicated in each panel. Open circles denote the locations of sediment samples used to construct the maps. (b) Spatial extent of PSP closures 2005–2010. The calculations for the western Gulf of Maine and southern New England presented in Fig. 3 pertain to the area south and west of the dashed line.

germination (Anderson et al. 2005c) and, thus, only that vertical fraction of the sediment samples is included in the computations presented herein.

PSP toxin measurements were based on the blue mussel *Mytilus edulis*, using the standard mouse bioassay. These data were kindly provided by the Maine Department of Maine Resources, the New Hampshire Department of Environmental Services, and the Massachusetts Division of Marine Fisheries. A set of coastal locations are monitored on a weekly basis, and shellfish beds are closed when the mouse bioassay reaches the quarantine level of 80 μg saxitoxin equivalents per 100 g of shellfish tissue.

Simulations of *A. fundyense* were conducted with a coupled physical–biological model based on the Regional Ocean Modeling System (ROMS; http://www.myroms.org/). The coupled model is run on a high-resolution mesh (1–3 km in the horizontal, 36 vertical layers) spanning the Gulf of Maine (He et al. 2008). The biological component is posed as a one-tracer advection–diffusion–reaction equation that includes parameterizations of *A. fundyense* germination, growth, and mortality (McGillicuddy et al. 2005a; Stock et al. 2005). The coupled model is nested within a shelf-scale ROMS model that encompasses the Mid-Atlantic Bight and the Gulf of Maine (R. He and K. Chen unpubl.), which is, in turn, nested within an operational data-assimilative model run globally at 10-km resolution (Hybrid Coordinate Ocean Model [HYCOM] plus Navy Coupled Ocean Data Assimilation [NCODA]; http://hycom.org/). This multiply nested configuration provides the spatial resolution necessary for coastal applications, making direct use of an operational model to provide the open boundary conditions needed for regional domains. *See* He et al. (2008) and Li et al. (2009) for more complete descriptions of the coupled model system.

Results

The time-series of cyst maps documents persistence of two major cyst deposits in the system: one in the Bay of Fundy, and the other offshore of mid-coast Maine (Fig. 2a). Whereas cyst abundance is relatively stable over time in the Bay of Fundy, the mid-coast Maine cyst bed fluctuates by more than an order of magnitude. Cyst abundance in the western Gulf of Maine deposit is a surprisingly good predictor of the extent of downstream toxicity closures for 2005–2009 (Figs. 2b, 3).

The observed correlation between cyst abundance and toxicity provides a conceptual basis on which to compute seasonal forecasts of bloom severity. In a sense, this approach is analogous to techniques used for fisheries management—'recruitment' is measured in the autumn via quantifying the abundance of resting cysts, thereby facilitating an estimate of the 'stock' of *A. fundyense* in the subsequent bloom season. With analysis of cyst samples from the autumn 2009 survey completed in winter 2010, an ensemble forecast was carried out and made public in the form of a press release (http://www.noaanews.noaa.gov/stories2010/20100224_redtide.html) and also published on the web (http://omglnx3.meas.ncsu.edu/yli/10ensemble_2d/dino_10ensemble.htm). The six-member ensemble was based on hydrodynamic hindcasts for each year during the period 2004–2009. Varying conditions during this time period affect the abundance and distribution of *A. fundyense* cells through environmental influences on germination, growth, mortality, and transport. Although the hindcasts for 2004–2009 did not span the range of all possible outcomes, they provided contrasting conditions, including one with strong downwelling-favorable winds
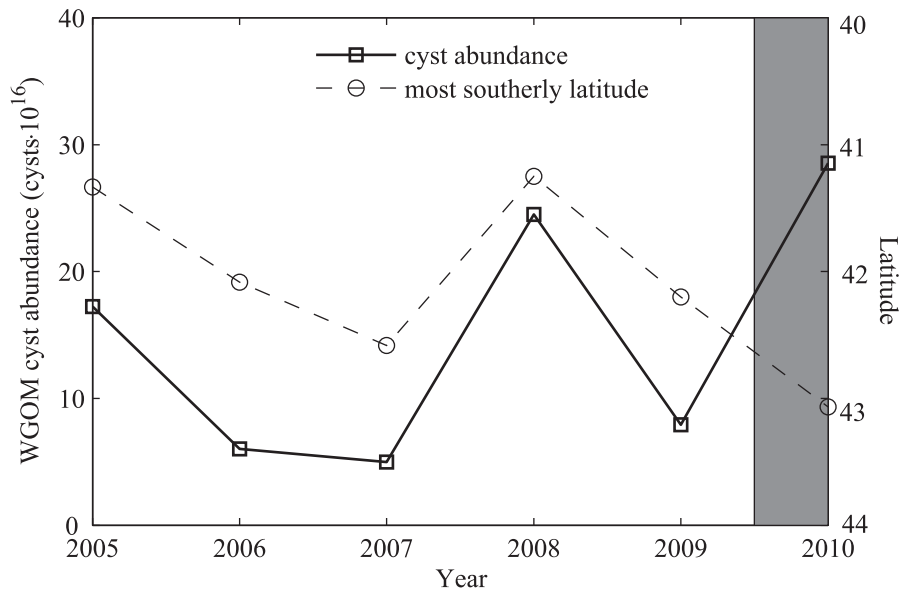
Fig. 3. Time-series of cyst abundance in the western Gulf of Maine (WGOM) and the most southerly latitude of coastal shellfish toxicity closures (note axis reversal). These calculations pertain to the area south and west of the line running southeast from Penobscot Bay (Fig. 2). Time-series of various metrics of length of coastline closed are similar in pattern to the most southerly latitude of closure. For visual compatibility and correlation analysis, the cyst abundance time-series has been shifted by 1 yr, such that the autumn of 2004 is reported as 2005, etc. During the period 2005–2009, the correlation coefficient for the time-series of cyst abundance and most southerly latitude of closure is -0.93 ($p = 0.02$).

and anomalously high river discharge in May (2005) and one with near climatological conditions (2004). They also spanned the range from major toxicity outbreaks (2005, 2008) to moderate (2006, 2007) to low (2004) levels of toxicity (Figs. 2, 3). All members of the ensemble forecast indicated a severe bloom in the western Gulf of Maine, on par with the historic bloom of 2005 (Fig. 4).

The same coupled physical–biological model was also used to make real-time forecasts of *A. fundyense* on a weekly cycle during the bloom season (http://omglnx3.meas.ncsu.edu/GOMTOX/2010forecast/). Model runs utilized the most up-to-date HYCOM plus NCODA ocean forecast, atmospheric forecasts from the National Center for Environmental Prediction, and stream gauge data from the U.S. Geological Survey. As in the seasonal ensemble forecast, the nutrient fields were specified from a climatological database (Petrie and Yeats 2000) updated with recent observations (Rebuck 2011). Real-time forecasts of *A. fundyense* abundance generally fell within the envelope of the seasonal ensemble forecast (Fig. 5a). However, the larger than usual bloom in the western Gulf of Maine predicted by the model did not materialize in May and June (Fig. 5b), and the prior correlation between cyst abundance and extent of toxicity ceased (Fig. 3).

Discussion

Correlation between cyst abundance and toxicity extent— The correlation between resting cyst abundance and the extent of coastal shellfish toxicity observed during 2004–

2009 is surprising for a number of reasons. To begin with, growth dynamics are typically considered to be more important than the size of the excystment inoculum in determining bloom magnitude (Anderson et al. 1983). Secondly, offshore blooms of *A. fundyense* lead to toxicity closures only to the extent that nearshore shellfish beds are exposed to the algae. In that sense, shoreward transport by wind-driven surface currents can be a key regulator of the effect of these blooms on shellfish toxicity along the coast (Thomas et al. 2010). Indeed, analysis of 6 yr of *A. fundyense* vegetative cell abundance and coastal shellfish toxicity revealed no significant statistical relationship between the two (McGillicuddy et al. 2005b). This suggested that, at least for the years examined (1993, 1994, 1998, 2000, 2001, 2002), interannual variations in toxicity may have been regulated more by transport and delivery of offshore cell populations than the absolute abundance of the populations themselves. However, that analysis was based on a period in which *A. fundyense* concentrations and shellfish toxicity in the western Gulf of Maine were relatively low. Unfortunately, the only measurements available to assess the cyst distribution during that time come from a single survey in the autumn of 1997, from which the abundance in the western Gulf of Maine was estimated to be 2.7×10^{16} cysts. The most southerly latitude of toxicity for the corresponding bloom season (1998) was 42.88°. Comparing these values with the time-series presented in Fig. 3, cyst abundance and toxicity extent were lower than any year during the period 2004–2009. Thus, the present findings are not necessarily at odds with the earlier analysis of McGillicuddy et al. (2005b).
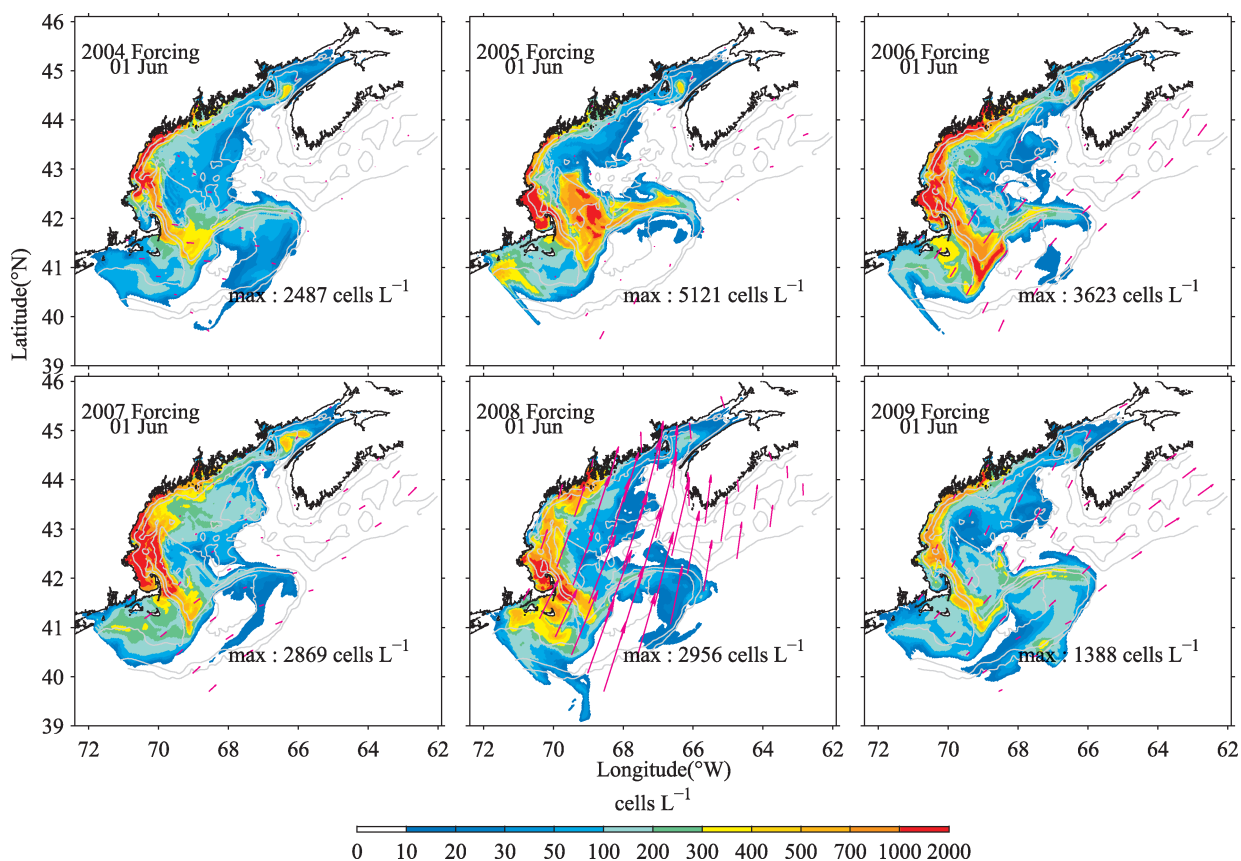
Fig. 4.   Ensemble *A. fundyense* forecast for 01 June, based on the autumn 2009 cyst map together with hydrodynamic and atmospheric forcing from 2004 to 2009. Pink arrows depict the instantaneous wind-forcing. Maximum (max) cell concentrations in each panel are indicated at the lower right. For animated presentation of the runs, *see* http://omglnx3.meas.ncsu.edu/yli/10ensemble_2d/dino_10ensemble.htm.

Specifically, the significant correlation between cyst abundance and toxicity observed during the period 2004–2009 ($r = -0.93$, $p = 0.02$; Fig. 3) suggests the effect of the source population overshadowed wind-forcing in control of interannual variations in toxicity during that time. This may reflect a new regime of *A. fundyense* dynamics in the western Gulf of Maine: the post-2004 abundance of cysts in the mid-coast Maine seedbed is substantially larger than the last time it was mapped systematically (1997; *see* Anderson et al. [2005c] for map), and overall toxicity in the western Gulf of Maine is higher than the prior decade (D.M. Anderson and D. Couture unpubl.).

Of course it is possible that the correlation between cyst abundance and toxicity extent observed during 2004–2009 is spurious, resulting from random fluctuations that happened to co-vary in this relatively short time-series. We assessed the robustness of the correlation using two different statistical methods. First, the result was 'cross-validated' (Francis 2006) by systematically leaving 1 yr out of the time-series, fitting a linear relationship between cyst abundance and toxicity extent in the remaining years, and then using that relationship to predict toxicity extent from cyst abundance in the year that was left out of the time-series. The correlation between predicted and observed toxicity extent in the cross-validation experiments ($r = 0.81$) is somewhat lower in magnitude than the raw

correlation between cyst abundance and toxicity extent in the original time-series, yet it is still statistically significant ($p = 0.09$). Notwithstanding the result of the cross-validation experiments, another potential caveat to the observed correlation relates the issue of autocorrelation in the original time-series. Specifically, serial correlation of the time-series being compared can effectively decrease the degrees of freedom and, thereby, affect the significance level of the inferred correlation (Myers 1998). We computed the autocorrelation from the two time-series and found neither to be statistically significant (cyst abundance: $r = -0.48$, $p = 0.53$; toxicity extent: $r = -0.53$, $p = 0.47$), although power of the significance test is low for such a small sample size. We examined the issue of autocorrelation more fully by modeling time-series of cyst abundance and toxicity extent as autoregressive 1 processes $f_{t+1} = \lambda f_t + g_t$, where g is a standard Gaussian random variable and the parameter λ defines the autocorrelation (Box and Jenkins 1970). For the purposes of this illustration, we considered a case in which the autocorrelations in two independent time-series are much higher than we observed here, namely $\lambda = 0.9$. The two models were then used to construct 100,000 simulated time-series of each. In only 4% of the cases did the magnitude of the correlation between simulated cyst abundance and toxicity extent meet or exceed that of the observed time-series. The
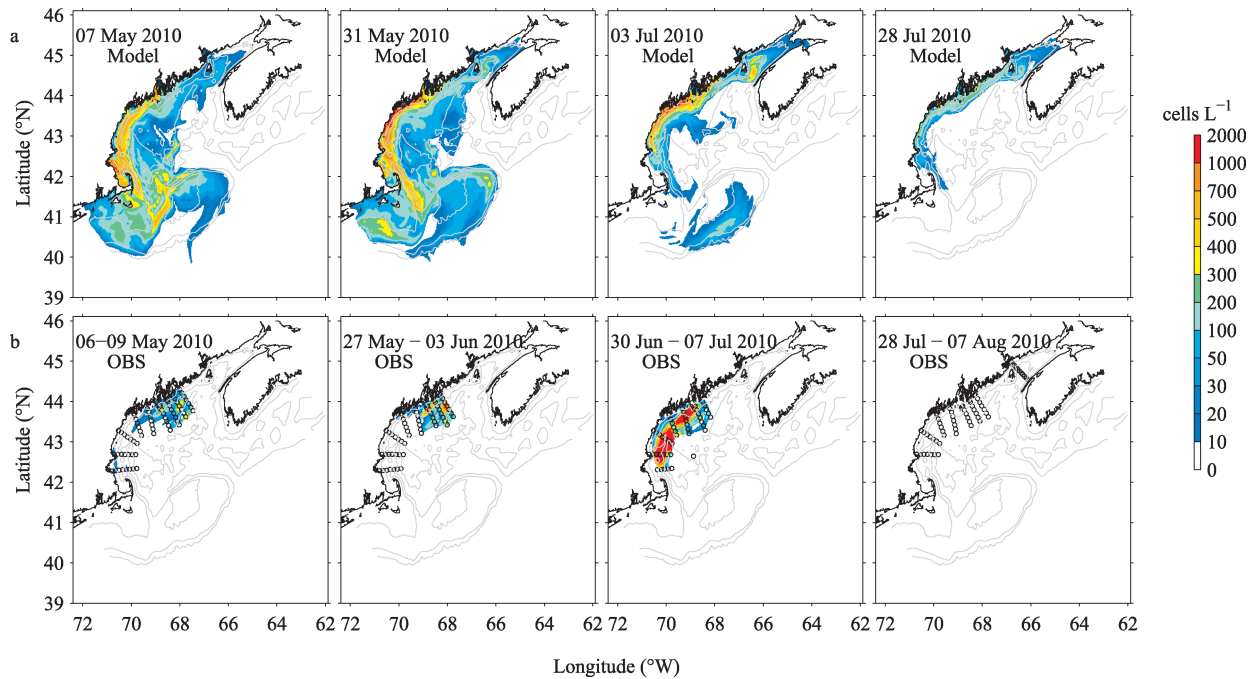
Fig. 5.   (a) *A. fundyense* model predictions for 2010. For a complete description of the forecast system and 2010 results, *see* http://omglnx3.meas.ncsu.edu/GOMTOX/2010forecast/. (b) Observations for early May, late May–early June, late June–early July, and late July–early August. Note that the cell-count maps include all available stations (open circles), whereas the hydrographic comparisons in Figs. 6–10 only include those stations in common with all (transects T1–T5 in Fig. 1).

equivalent *p*-value of 0.04 for the simulated time-series with high autocorrelation suggests that the possibility of spurious correlation in the observations is remote. Nevertheless, caution is of course prudent in interpreting such short time-series.

Factors that may have prevented a large A. fundyense *bloom from occurring in 2010*—There was a distinct water mass anomaly in the Gulf of Maine in 2010 (Fig. 6) that was outside the envelope of variability in the 'training set' used in development of coupled physical–biological model
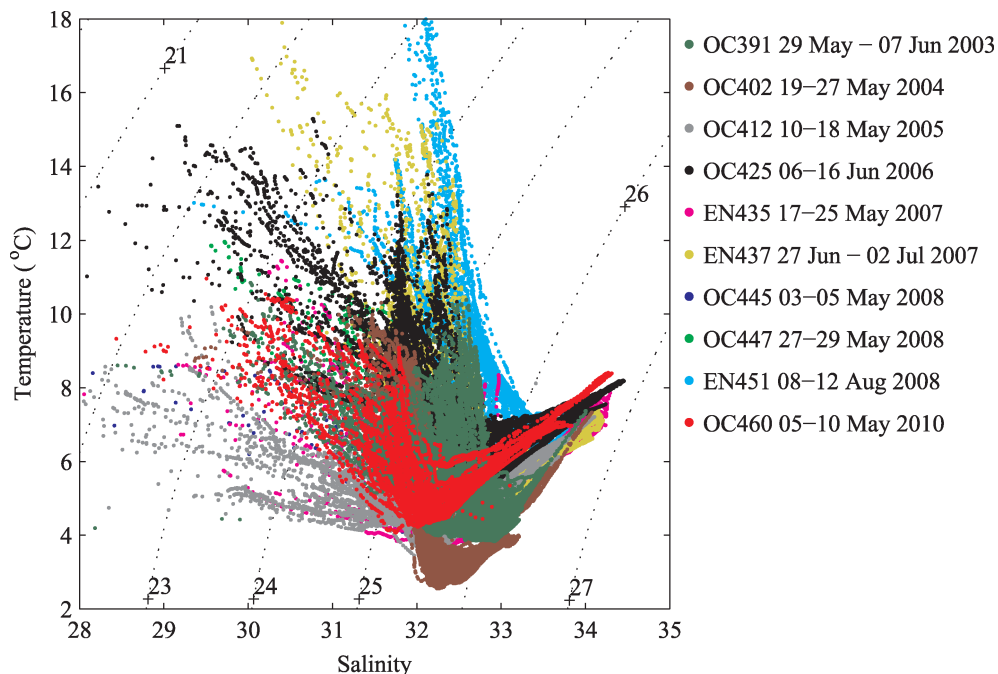
Fig. 6.   Temperature–salinity characteristics from *A. fundyense* surveys in the Gulf of Maine, spring–summer 2003–2010. Dotted lines are contours of sigma-T density anomaly.

Early May
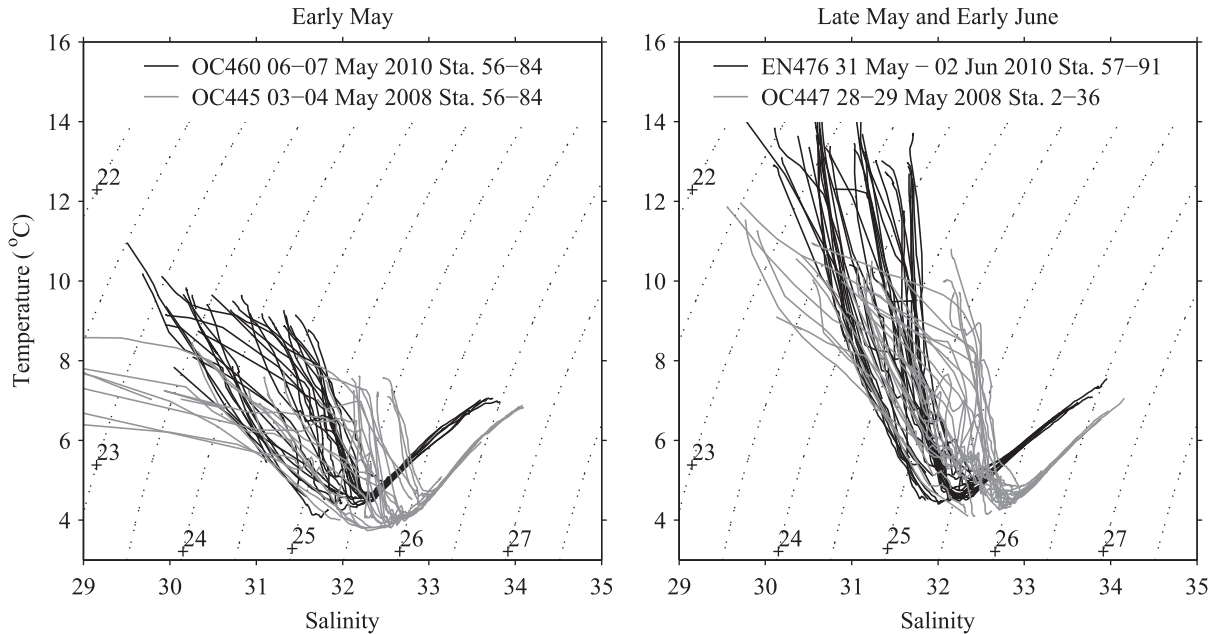
Late May and Early June

Fig. 7. Interannual variability in water mass characteristics in the western Gulf of Maine, 2008 (gray) vs. 2010 (black): early May (left) and late May–early June (right). Locations of the stations used in this comparison are denoted by open circles in Fig. 1. These stations are a subset of the stations occupied on each cruise, restricted to include only the stations sampled in all cruises. Dotted lines are contours of sigma-T density anomaly.

and forcing of the ensemble forecast (Fig. 4). The deep-water end-member was warmer than prior observations 2003–2009. Maine Intermediate Water (MIW) was fresher than all prior years except for 2005, when MIW was colder. Local freshwater discharge into the Gulf of Maine was average in 2010 (Y. Li and R. He unpubl.), which indicates the salinity anomaly had an advective origin. This anomaly was not well-represented in the real-time forecast model for 2010, suggesting data assimilation is needed to accurately capture such events.

Comparisons between 2010 and the most recent year a major bloom took place (2008) facilitate detailed assessment of the water mass anomalies (Fig. 7). In early May, deep waters were warmer and fresher in 2010 compared with 2008; MIW was a few tenths of a degree warmer and a few tenths fresher. Near-surface waters in early May 2010 were several degrees warmer than they were in early May 2008. The deep and intermediate water-mass anomalies persisted into late May–early June, and surface temperatures were 2–4°C warmer in 2010 than they were in 2008.

Although T–S characteristics of deep waters remained relatively constant during spring–summer 2010, water mass anomalies lessened over time in intermediate and surface waters (Fig. 8). Specifically, salinity increased in these layers, particularly in July and August. This transition was accompanied by a temporary increase in the western Gulf of Maine *A. fundyense* population in July (Fig. 5). Note that the low concentrations observed in transect T4 (Fig. 1) might have been due to temporal aliasing. The survey began with transect T3 and proceeded south. Microscopic counts of *A. fundyense* conducted on board contained a significant fraction of planozygotes, suggesting the bloom

was beginning to terminate. It is possible that by the time R/V *Oceanus* returned to transect T4 after sampling transects T2 and T1, the cells may have already vacated surface waters.

The early season water-mass anomaly was accompanied by anomalies in the nutrient environment in the western Gulf of Maine. In early May, nitrate, phosphate, silicate, and ammonium were systematically lower in 2010 than in 2008, although the differences tended to be less in the near-surface region where most nutrients are depleted (Fig. 9). By late May–early June, the contrast in the nutrient environment lessened, such that there was no significant difference in nitrate, phosphate, and silicate profiles for 2010 vs. 2008 (Fig. 10). However, this appears to have been driven largely by a decrease in deep nutrient concentrations over time in 2008 rather than an increase over time in 2010 (cf. Figs. 9, 10). In any case, given the depletion of nitrate in near-surface waters during this time period, the lower ammonium concentrations in the upper 50 m in late May–early June 2010 (Fig. 10) may have negatively affected the growing conditions for *A. fundyense*.

Ocean color data from the Moderate Resolution Imaging Spectroradiometer (MODIS) provide some clue as to why near-surface nutrient concentrations in May–June 2010 were so low. The spring phytoplankton bloom in this region began earlier than usual, and its peak was the highest observed in the entire record (Fig. 11), which spans the time period from which the members of the ensemble forecast were generated. Satellite-derived chlorophyll subsequently decreased to the lowest postbloom condition in June. This negative anomaly in chlorophyll was confirmed by in situ measurements (D.W. Townsend and M.A. Thomas unpubl.).
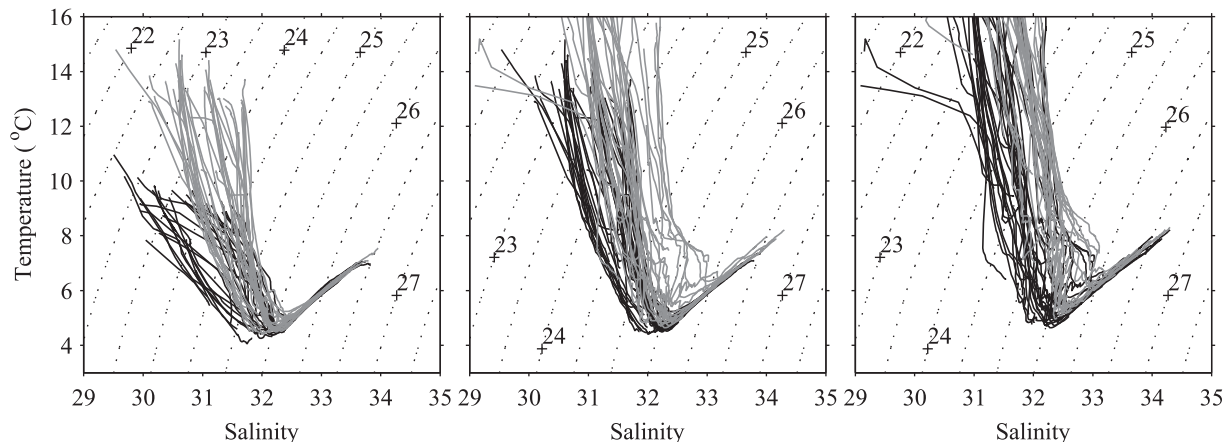
Fig. 8.   Seasonal variability in water mass characteristics in the western Gulf of Maine during spring–summer 2010. Four time intervals are documented: 06–07 May, 31 May–02 June, 05–07 July, and 02–03 August. In each panel, the earlier cruise is shown in black and the later cruise in gray. Dotted lines are contours of sigma-T density anomaly.

This unusual spring bloom may have been related to the water mass anomaly, insofar as warm and fresh intermediate and surface waters would tend to foster increased stratification. A more stratified water column would favor an earlier and more intense bloom. Indeed, time-series at mooring B of the Northeastern Regional Association of Coastal Ocean Observing Systems (NERACOOS) array indicates monthly mean stratification in the upper 20 m of the western Gulf of Maine was higher in April 2010 than in all other Aprils from 2003 to 2009 (Fig. 12a). The springtime stratification anomaly is most evident in the western Gulf of Maine, but also present further north and east (NERACOOS mooring E and I; not shown). These findings are consistent with the analysis of Song et al. (2010), which documents correlation between salinity anomaly and timing of the spring bloom in this region, such that fresher waters favor an earlier bloom. In the postbloom period, higher stratification combined with lower nitrate and ammonium concentrations below the euphotic zone would both favor decreased nitrogenous nutrient supply, perhaps contributing to the anomalously low chlorophyll (Fig. 11) and poor growing conditions for *A. fundyense*.

It also appears that conditions were unfavorable for hydrodynamic transport of *A. fundyense* along the coast. Moored time-series at NERACOOS mooring B indicate that mean alongshore currents in the western Gulf of Maine in May were moderately low in 2010 as compared with prior years (Fig. 12b). In June 2010, mean alongshore current was the weakest of the last nine Junes. Surface drifters released from a cross-shore transect off Casco Bay also document anomalous patterns in the coastal current (Fig. 13). Trajectories for the first 12 d after deployment show the current to be very sluggish overall in May and July, as drifters transited only a fraction of the distance transited by numerical drifters inserted into the climatological average flow described by Manning et al. (2009). In

June, the two offshore-most drifters indicated the flow was directed offshore, in contrast to the along-shore flow characteristic of the mean conditions. Sensitivity analysis of the modeled drifter trajectories suggests the primary driver of the anomalous currents was the density field, with wind-forcing playing a relatively minor role in the anomaly (J.P. Manning unpubl.).

Reduced alongshore transport in the western Gulf of Maine is consistent with the presence of anomalously warm and freshwater offshore, leading to a reduced cross-shore pressure gradient. Geostrophic calculations indicate a weaker-than-normal coastal current in the western Gulf of Maine in May–June (R. He unpubl.). Again, this was not well-predicted by the forecast model, as the observed water-mass anomalies are not adequately simulated without hydrographic data assimilation in the regional domain.

It is noteworthy that the alongshore current at NERACOOS mooring B accelerated in July (Fig. 12b), suggesting the apparent increase in *A. fundyense* observed during that period (Fig. 5) may have resulted from advection. Increased along-shore flow is also evident in geostrophic calculations based on hydrographic observations from transects T1 to T5 in July (not shown), although surface drifters deployed in July do not indicate this acceleration (Fig. 13).

Processes that might have driven the unusual conditions in the Gulf of Maine in 2010—Townsend et al. (2010) describe three major transport pathways for deep (> 100 m) water into the Gulf of Maine: warm slope water (WSW; warm, salty, high nitrate) and Labrador slope water (LSW; cold, fresh, low nitrate) flowing in through the Northeast Channel, and Scotian shelf water (SSW; cold, fresh, low nitrate) flowing in through the sill between Nova Scotia and Browns Bank (Fig. 1). A time-series from NERACOOS mooring M in Jordan Basin (Fig. 1) indicates that water mass characteristics in July 2009 were 'normal,'
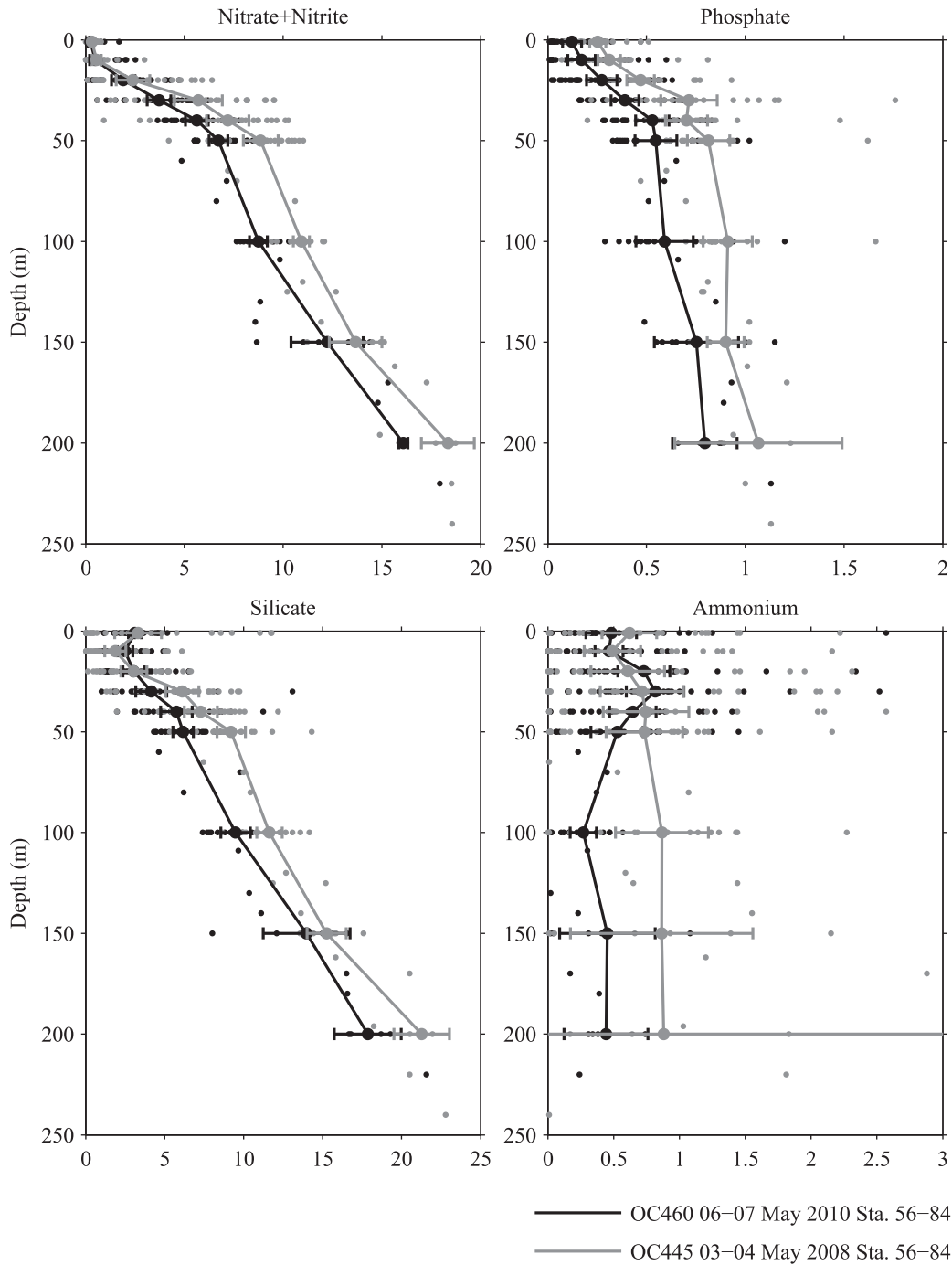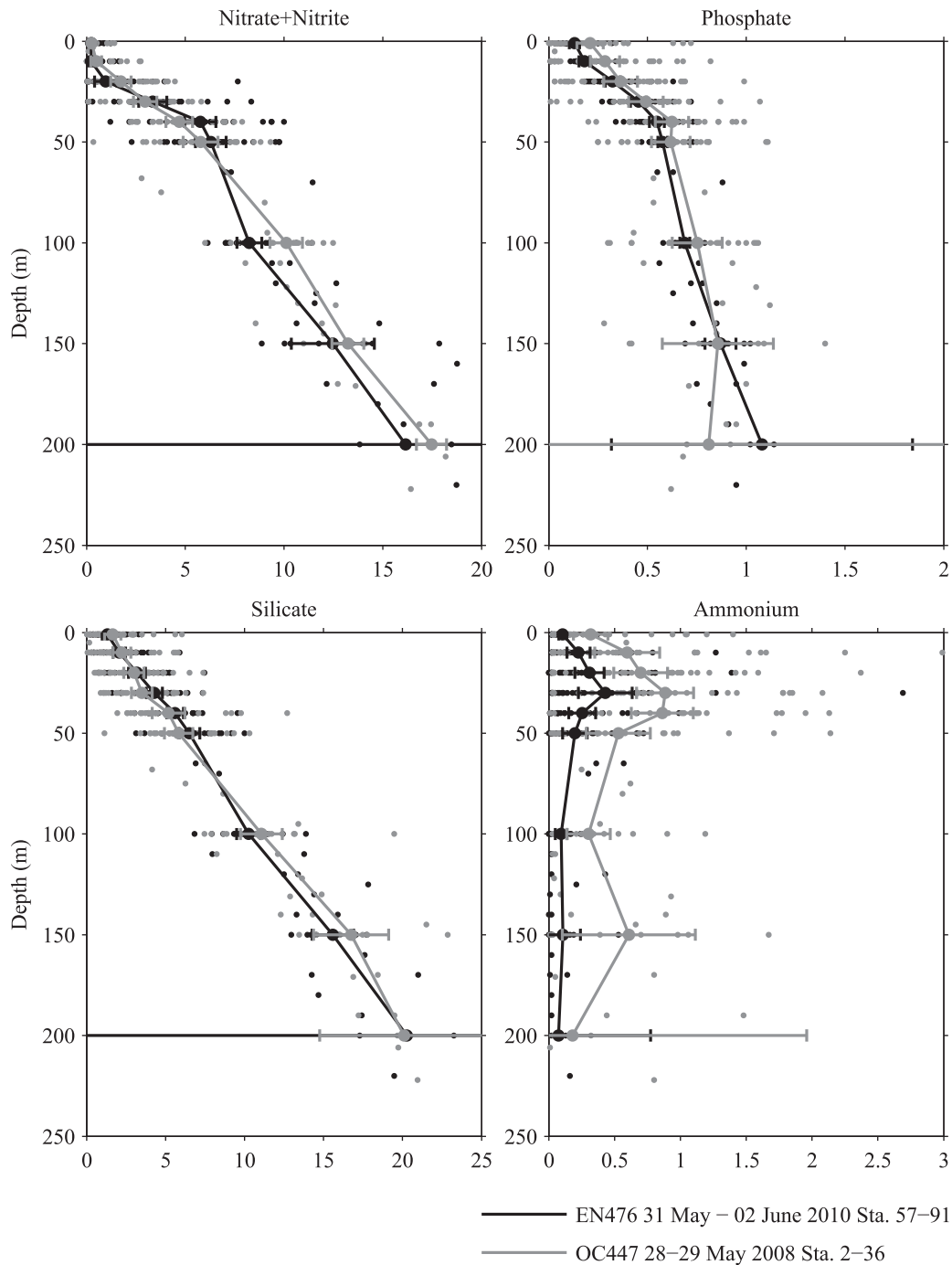
Fig. 9. Profiles of nitrate + nitrite, phosphate, silicate, and ammonium in the western Gulf of Maine for early May 2008 (gray) and 2010 (black). Individual data points are indicated by small dots. These comparisons are based on stations in transects T1–T4 in Fig. 1. Solid lines depict mean profiles with 95% CIs.

similar to that observed in May 2008 (Fig. 14). The first hint of a WSW anomaly appeared the following month, and by September the deep-water mass anomaly was about 50% of the way toward conditions observed in shipboard hydrographic measurements in May 2010. By March 2010, the deep-water anomaly had reached full strength, and T–S properties observed at the mooring fall along a mixing line between WSW and an anomalously

warm and fresh SSW end-member. Warming of the upper layers from March to April 2010 formed the elbow in T–S characteristic of MIW, albeit warmer and fresher than normal. Comparison of the measurements from the mooring with the cruise data in May 2010 confirms their compatibility, thus justifying use of the moored time-series to make inference about regional-scale hydrographic variability.

Fig. 10.   Profiles of nitrate + nitrite, phosphate, silicate, and ammonium in the western Gulf of Maine for late May 2008 (gray) and late May–early June 2010 (black). Individual data points are indicated by small dots. These comparisons are based on stations in transects T1–T5 in Fig. 1. Solid lines depict mean profiles with 95% CIs.

Both WSW and SSW water-mass anomalies present in the interior Gulf of Maine during spring–summer 2010 (Fig. 14) were detected in advance within their source regions farther upstream. Warm and salty slope waters were clearly evident in the Northeast Channel in February 2010 (Fig. 15; cf. Feb 2008). The anomalous SSW water mass can be traced to its origins using time-series data from

the Scotian Shelf collected by Fisheries and Oceans Canada's Atlantic Zone Monitoring Program (AZMP; Therriault et al. 1998) at Sta. 2 (Fig. 1). Near-surface water-mass characteristics in January–February 2010 (Fig. 16) were at the edge of the envelope of all measurements 1999–2010. In particular, near-surface and near-bottom salinities were amongst the lowest measured at
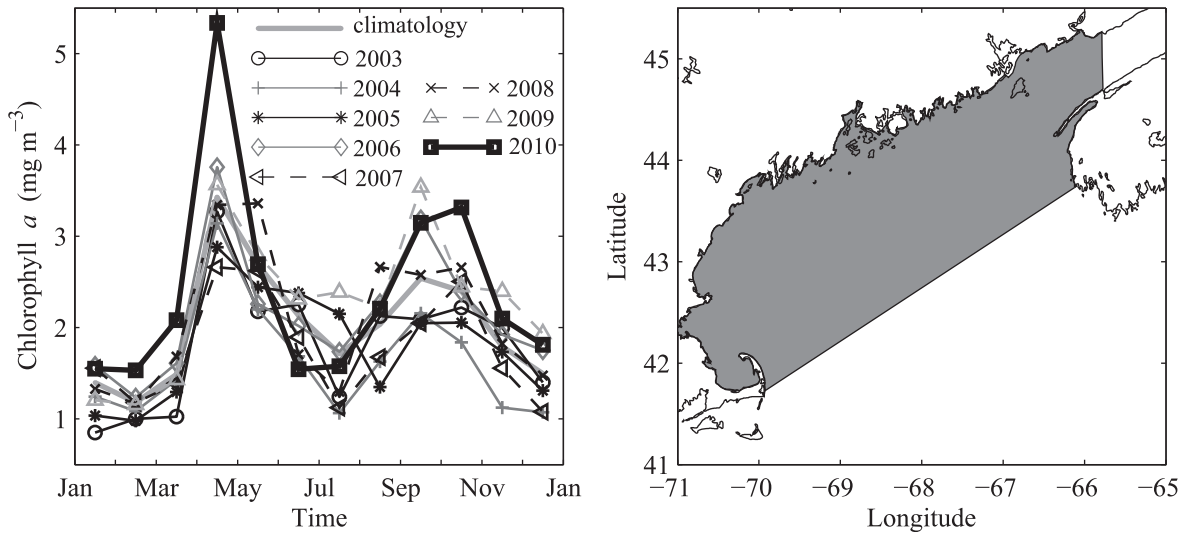
Fig. 11.   Time-series of monthly averaged chlorophyll *a* from MODIS-Aqua (reprocessing 2010.0) in the coastal Gulf of Maine (shaded area in right panel).
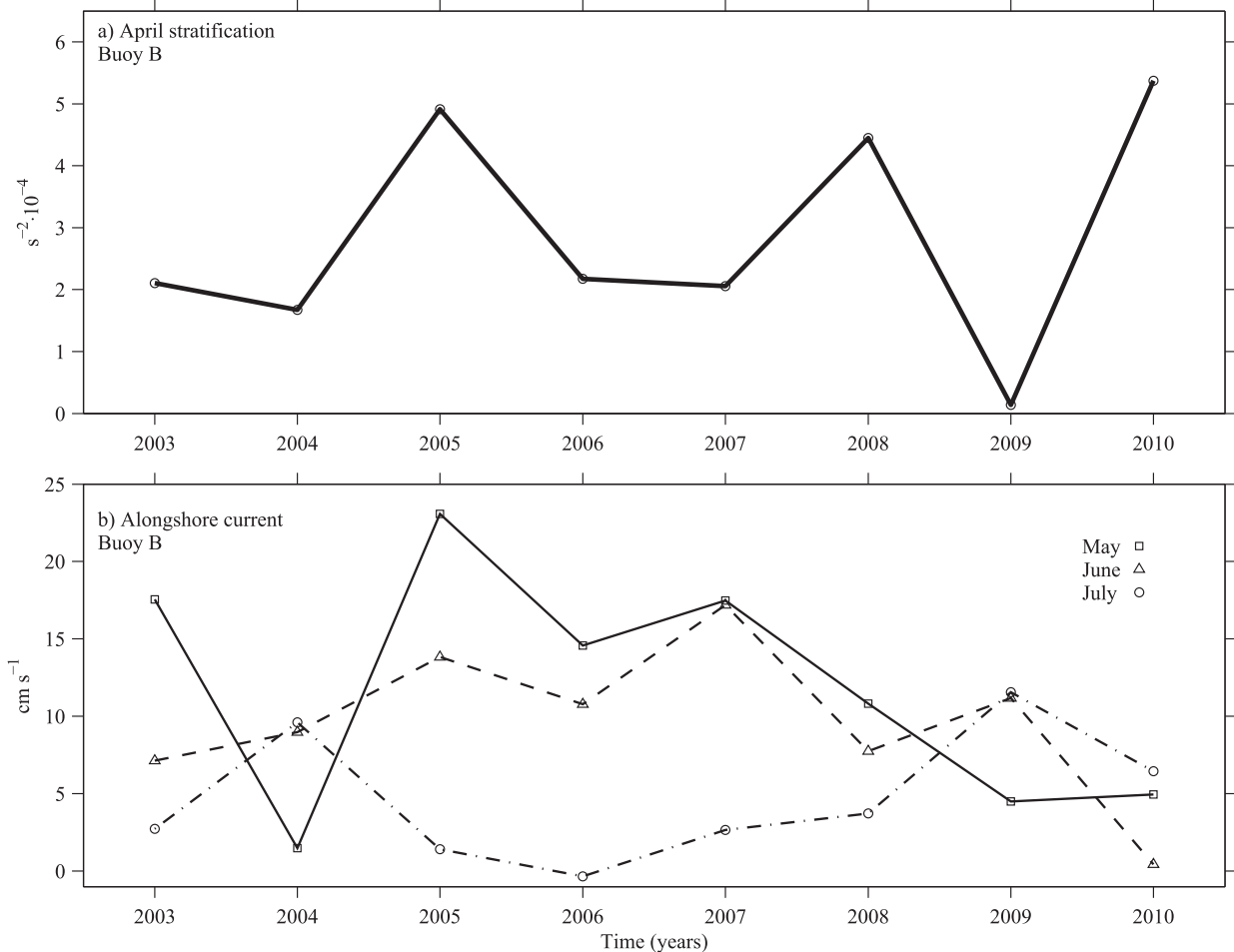
Fig. 12.   (a) Brunt–Väisälä frequency at NERACOOS buoy B, based on density time-series at 2 m and 20 m for April 2003–2010. (b) Time-series of alongshore current (positive southwestward) at 2 m for NERACOOS buoy B, May–July 2003–2010.
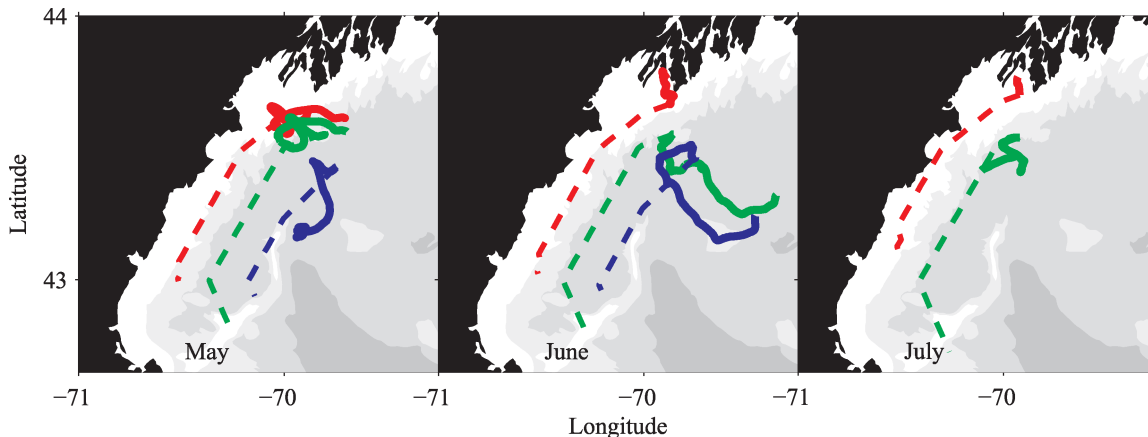
Fig. 13.   Trajectories of surface drifters released from a cross-shore transect off Casco Bay on 07 May, 01 June, and 06 July, 2010. The first 12 d of drifter tracks are depicted by solid lines. Dashed lines indicate trajectories computed from the climatological flow described in Manning et al. (2009).
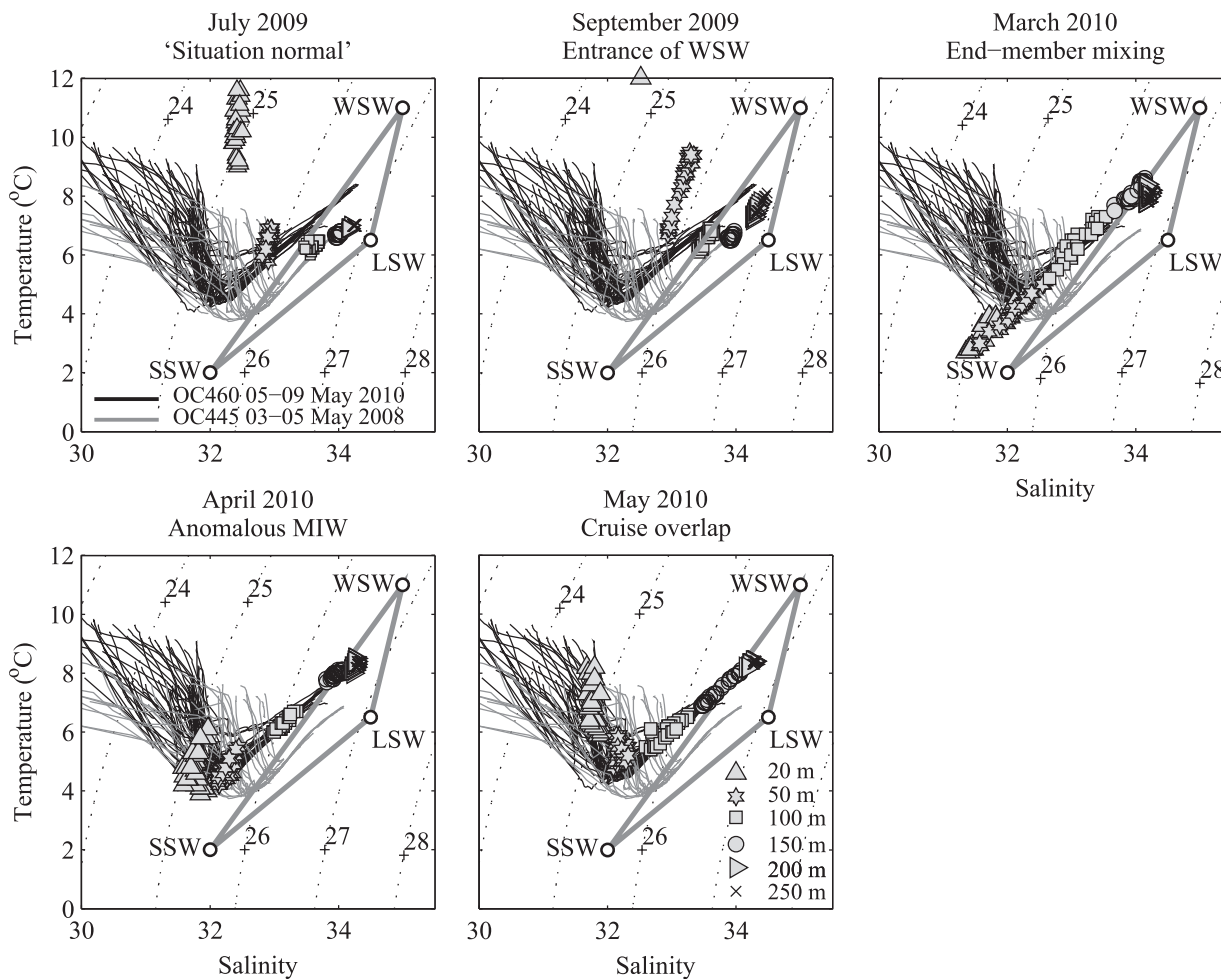
Fig. 14.   Time-series of temperature–salinity diagrams from NERACOOS mooring M in Jordan Basin. Daily values are plotted in each month. Dotted lines are contours of sigma-T density anomaly. Vertices of the mixing triangle consist of the canonical water-mass characteristics for Warm Slope Water (WSW), Labrador Slope Water (LSW), and Scotian Shelf Water (SSW) described in Smith et al. (2001).
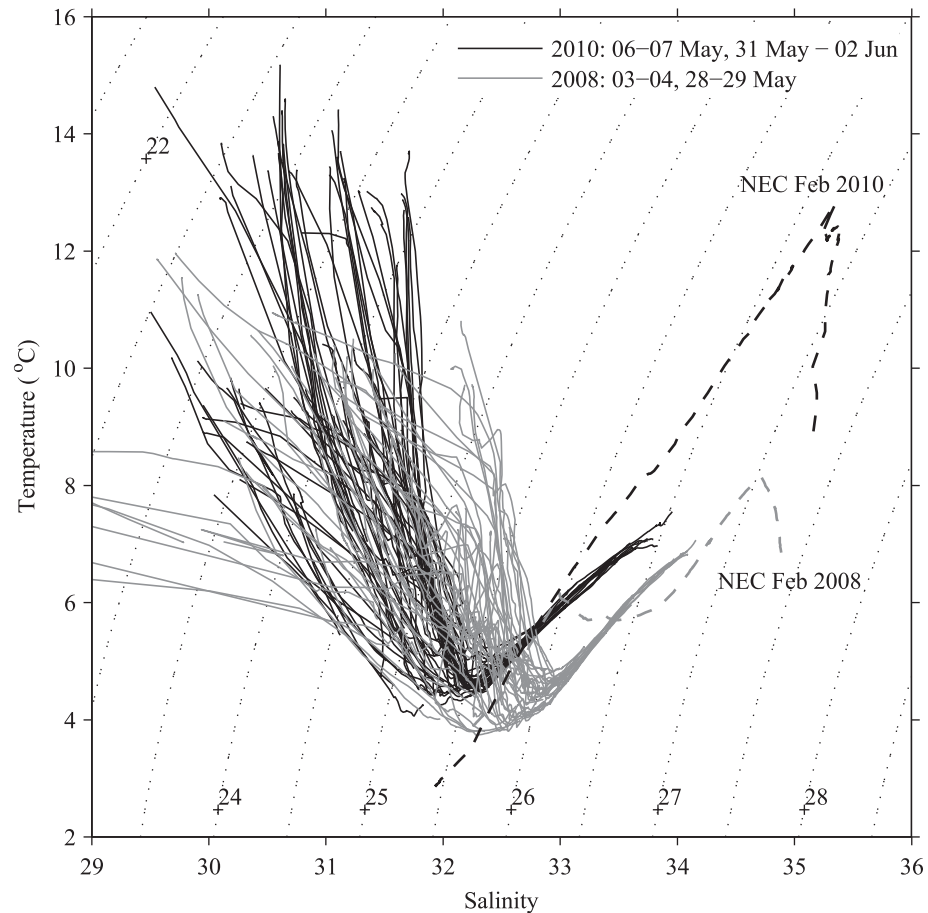
Fig. 15. Interannual variability in water mass characteristics in the Northeast Channel (NEC) observed in the National Oceanic and Atmospheric Administration's Northeast Fisheries Science Center's surveys in February 2008 (gray-dashed) and February 2010 (black-dashed). For reference, the western Gulf of Maine profiles from Fig. 7 are also plotted. Dotted lines are contours of sigma-T density anomaly.

those temperatures. The closest antecedent profile is August 2009, in which the salinity anomaly is not present. Thus the precise timing of the onset is not known, only that it must have taken place sometime between August 2009 and January 2010. In any case, the timing of water mass anomalies observed in the source regions relative to their appearance in the interior of the Gulf of Maine is consistent with an advective time scale of several months, which is characteristic of this region (Petrie and Drinkwater 1993; Loder et al. 1998; Smith et al. 2001). It is possible that the observed changes are related to a longer term trend of increased inflow from the Scotian Shelf and reduced inflow from the Northeast Channel (Smith et al. in press), both of which would favor fresher waters in the interior of the Gulf of Maine.

Bloom dynamics and the prospects for ecological forecasting—Despite the presence of an unusually large source population of resting cysts, a major regional bloom of *A. fundyense* did not occur in the western Gulf of Maine in 2010. In situ measurements revealed water mass variations reflecting changes in inflow characteristics into the Gulf of Maine from the Northeast Channel and Scotian shelf.

Admixture of these two anomalies had a direct influence on the niche of *A. fundyense*, causing the upper ocean to be warmer, fresher, and lower in nutrients than in recent years. Increased stratification likely played a role in the unusually intense spring phytoplankton bloom, which may have also contributed to nutrient impoverishment of near-surface waters. It appears that this earlier than normal nutrient depletion led to unfavorable growing conditions for *A. fundyense* at precisely the same time as germination from resting cysts reached its full potential in late spring. As such, this regional change in the environment appears to have caused a mismatch with *A. fundyense*'s endogenous clock for germination. Moreover, the water mass anomalies resulted in a weaker than normal coastal current, which lessened transport of *A. fundyense* into the western Gulf of Maine.

The 2010 bloom illustrates one of the many challenges involved in making ecological predictions in a changing ocean environment. Failure of the forecast was a direct consequence of the fact that conditions were outside the envelope of prior observations used to construct the ensemble. Specifically, the late-springtime nutrient conditions associated with the water mass anomaly were unfavorable for growth of the *A. fundyense* population,
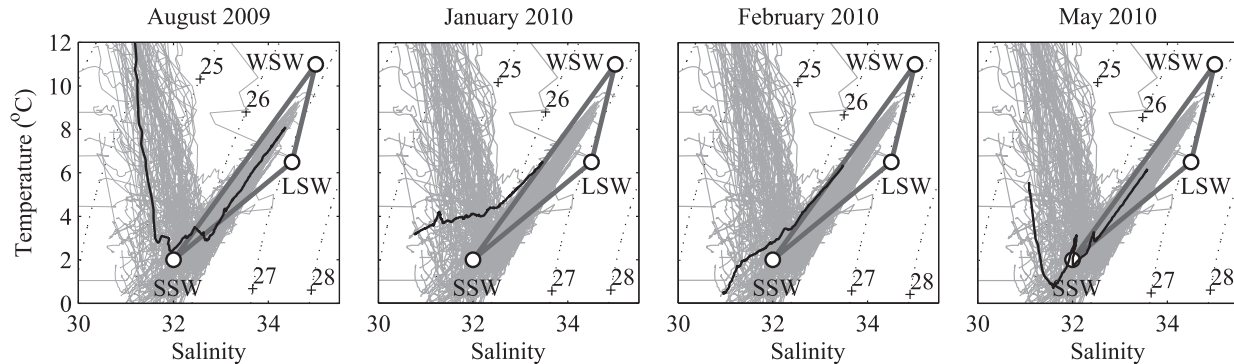
Fig. 16.   Time-series of temperature–salinity diagrams from Sta. 2 of the Atlantic Zone Monitoring Program (AZMP), located on the Scotian Shelf in 155 m of water offshore of Halifax, N44.27, W63.32 (Fig. 1). Solid lines indicate the sequence of profiles from August 2009, January 2010, February 2010, and May 2010, with the remainder of the time-series 1999–2010 plotted in light gray. The salinity anomaly present in January–February 2010 is bracketed in time by profiles in August 2009 and May 2010. Dotted lines are contours of sigma-T density anomaly. Vertices of the mixing triangle consist of the canonical water-mass characteristics for Warm Slope Water (WSW), Labrador Slope Water (LSW), and Scotian Shelf Water (SSW) described in Smith et al. (2001).

quite different from the climatological values used in both the ensemble forecast and real-time predictions. Moreover, because the forecast model did not accurately depict the water mass anomaly and its slowing effect on the coastal current, along-coast transport of the simulated *A. fundyense* population was overestimated. Fortunately, the water mass anomaly was detectable months in advance by the existing coastal ocean observing system, and this knowledge can be used to improve future forecasts. As a start, something akin to a 'traffic light' approach (Koeller et al. 2000; Caddy and Defeo 2003) could provide a caveat to interpretation of the forecast when anomalous conditions are detected. Nevertheless, ongoing monitoring is necessary because conditions can change during the forecast period itself.

Lessons learned here are, in some ways, reminiscent of the development of El Niño–Southern Oscillation (ENSO) phenomena. The introduction of dynamical forecast models in the 1980s (Cane et al. 1986) led to several years of remarkably skillful predictions (Latif et al. 1998). In the 1990s, there was a significant drop in forecast skill when ENSO entered a distinctly different mode of variability (Ji et al. 1996), which ushered in a new wave of model improvement (Chen et al. 1995). Indeed, long-term hindcasting studies suggest interdecadal variations in ENSO predictability that reflect temporal changes in the underlying dynamics of the system (Chen et al. 2004). It can be argued that ecological forecasting will be even more prone to fluctuations in predictability than the physical climate system, owing to even stronger nonlinearities in biological dynamics (Frank et al. 1994). As such, assimilation of data will be essential to keep predictive ecological models on track. Although data assimilation into coupled physical–biological models is still in its infancy (Hofmann and Friedrichs 2002), there are some promising inroads being made (Gregg et al. 2009). In any case, the 2010 *A. fundyense* bloom in the Gulf of Maine highlights the need for intimate connection between observational networks and forecast systems, and how these aspects must evolve together to meet the grand challenge of ecological forecasting in the ocean.

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