



Nutrients and water masses in the Gulf of Maine–Georges Bank region: Variability and importance to blooms of the toxic dinoflagellate *Alexandrium fundyense*



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ABSTRACT

We report here the results of ten oceanographic survey cruises carried out in the Gulf of Maine–Georges Bank region of the Northwest Atlantic during the late spring to summer period in 2007, 2008 and 2010, for which we examine and characterize relationships among dissolved inorganic nutrient fields, water mass dynamics and cell densities of the toxic dinoflagellate *Alexandrium fundyense*. Nutrients are supplied to continental shelf waters of the Gulf of Maine–Georges Bank region by inflows of deep offshore water masses; once in the Gulf they are transported with the residual circulation and mix with surface waters, both in the Gulf and on the Bank. Those fluxes of offshore water masses and their nutrient loads are the major source of nutrients for phytoplankton production in the region, including annual blooms of *A. fundyense* in the Gulf and on Georges Bank. This much is already known. We suggest here that the locations and magnitude of *A. fundyense* blooms are controlled in part by variable nutrient fluxes to the interior Gulf of Maine from offshore, and, those interior Gulf of Maine waters are, in turn, the main nutrient source to Georges Bank, which are brought onto the Bank by tidal pumping on the Northern Flank. We present evidence that nitrate is the initial form of nitrogenous nutrient for *A. fundyense* blooms, but it is quickly depleted to limiting concentrations of less than 0.5 μM , at which time continued growth and maintenance of the population is likely fueled by recycled ammonium. We also show that phosphate may be the limiting nutrient over much of Georges Bank in summer, allowing recycled ammonium concentrations to increase. Our temperature–salinity analyses reveal spatial and temporal (seasonal and interannual) variability in the relative proportions of two deep source waters that enter the Gulf of Maine at depth through the Northeast Channel: Warm Slope Water (WSW) and Labrador Slope Water (LSW). Those two source waters are known to vary in their nutrient loads, with nitrate concentrations about 50% higher in WSW than LSW, for example, and as such the proportions of these two water masses to one another are important determinants of the overall nutrient loads in the interior Gulf. In addition to these deep slope water fluxes, we show evidence here of episodic fluxes of relatively fresh and low-nutrient shelf waters from the Nova Scotian Shelf, which enter the Gulf in pulses at depths between the surface and approximately 150 m, displacing deep slope waters, and consequently they significantly dilute the Gulf's interior waters, reducing nutrient concentrations and, in turn, affect the magnitude of *A. fundyense* blooms.

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1. Introduction

1.1. *Alexandrium fundyense* blooms

Studies of the oceanography and population dynamics of the toxic dinoflagellate *A. fundyense*, blooms of which are responsible for outbreaks of Paralytic Shellfish Poisoning in the Gulf of Maine region

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(Fig. 1) and shelf waters throughout much of the world ocean (Wyatt and Jenkinson, 1997), have intensified in recent years (e.g., see Anderson, 1997; Anderson et al., 2005a; and papers in this issue). Those studies have led to a number of important refinements in our understanding of the basic physical and biological factors that control bloom dynamics, and have begun to highlight the importance of variable water mass dynamics in the Gulf region and the resulting variability in dissolved inorganic nutrient fluxes.

Blooms of *A. fundyense* occur annually in the Gulf of Maine and on Georges Bank but they vary among years in their cell densities and areal coverage (McGillicuddy et al., 2005a, 2014; Anderson et al., 2014a). Seasonal blooms in the coastal Gulf of Maine commence when

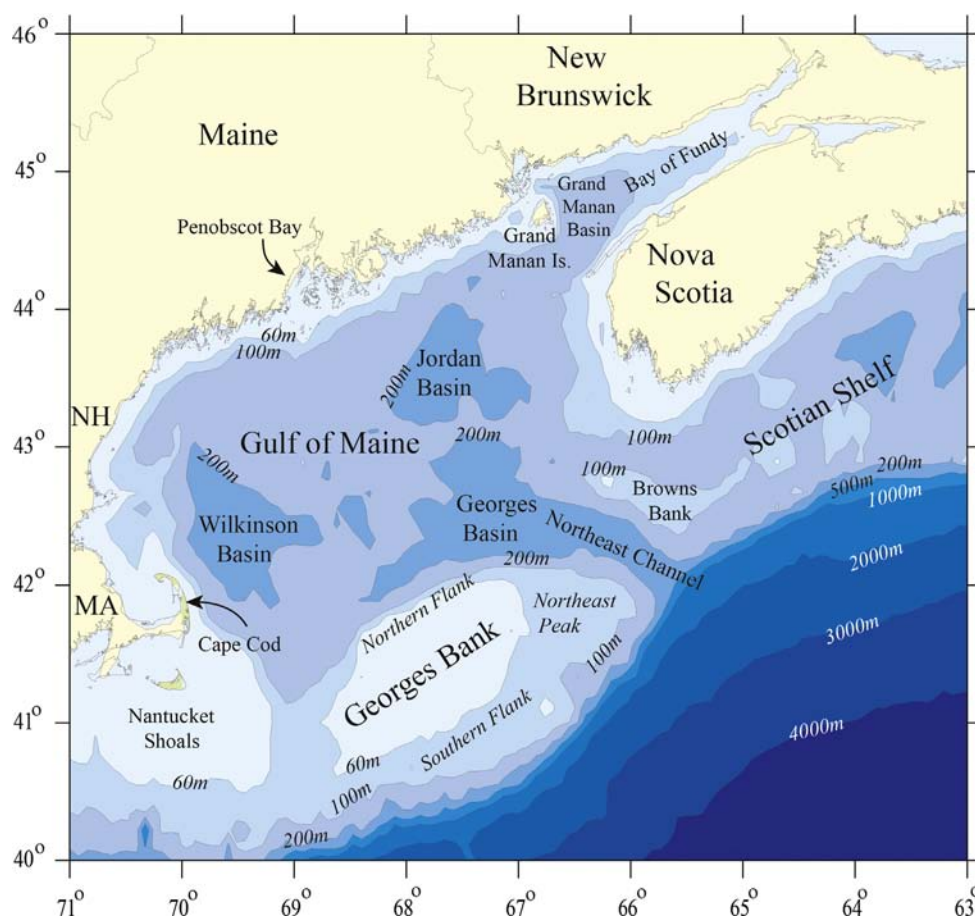


Fig. 1. Map of the Gulf of Maine and Georges Bank with key bathymetric features identified, and specific geographic areas identified. Bottom depths are given in meters.

overwintering benthic resting cysts germinate in the spring and inoculate surface waters with vegetative cells (Anderson et al., 2005b; Matrai et al., 2005), although suspended cysts may also play a role (Kirn et al., 2005; Pilskaln et al., 2014). The initial appearance of these *A. fundyense* cells generally follows the annual spring phytoplankton bloom, which is dominated by diatoms (Bigelow, 1926; Bigelow et al., 1940). The *A. fundyense* growth season may begin as early as March in near shore waters, and in some years it can last into October, especially in offshore waters on Georges Bank and in the Bay of Fundy (e.g., Anderson et al., 2014a; McGillicuddy et al., 2014). As the *A. fundyense* cells multiply they are transported throughout the region in the residual near-surface circulation. Of course, being autotrophic phytoplankton, their rates of photosynthesis and population growth are potentially limited by a number of factors, including light and nutrients (Townsend et al., 2001; McGillicuddy et al., 2005b), zooplankton grazing (Turner and Borkman, 2005), and possibly by competitive interactions with other phytoplankton taxa, particularly diatoms (Townsend et al., 2005; Gettings, 2010; Gettings et al., 2014).

In addition to bloom dependence on the initial stock size of benthic resting cysts each year (Anderson et al., 2014b; McGillicuddy et al., 2011), interannual variability in the distributions and cell densities of *A. fundyense* blooms may be controlled by the availability of dissolved inorganic nutrients (Townsend et al., 2001, 2005), concentrations and proportions of which (e.g., proportions of nitrate and silicate) may in turn be undergoing climate change-related alterations in the Gulf of Maine region (Townsend et al., 2010; Rebeck, 2011).

Dependence of *A. fundyense* bloom initiation and population maintenance on the availability of dissolved inorganic nitrogen, in

the form of nitrate, explains the occurrence of three fairly distinct population centers in the region where cells reach their highest densities; those population centers are the western Bay of Fundy, the northern Gulf of Maine, and Georges Bank (Anderson, 1997; Townsend et al., 2005; McGillicuddy et al., 2014). Each of these areas is characterized by vigorous vertical mixing by tides and associated tidal pumping of deep water nutrients into surface waters, which are subsequently entrained in the residual surface circulation; those areas of energetic tidal mixing are easily seen as cooler surface waters in satellite images of sea surface temperature (e.g., Townsend et al., 2006; Fig. 2). The first of these three *A. fundyense* population centers, the western Bay of Fundy, is believed to be a site of significant retention of plankton populations in the Minas Basin cyclonic gyre, in warmer, vertically stratified surface waters surrounded by tidally well mixed waters where new nutrients are injected which stimulate and sustain the blooms. The gyre itself is leaky (e.g., see Aretxabaleta et al., 2008, 2009) and as a result, some cells escape the Bay of Fundy and seed the northern Gulf of Maine population where cells continue to grow in the Eastern Maine Coastal Current (EMCC), waters that are also enriched with nutrients as a result of tidal mixing (Townsend et al., 1987; Brooks and Townsend, 1989). Perhaps more important than cells leaking from the Bay of Fundy in seeding the Gulf of Maine population is the additional input of cells into the EMCC from an extensive benthic cyst bed off the Maine coast (Anderson et al., 2005b). The trajectory and volume transport of the EMCC that carries cells and nutrients to the west is variable, with a branch turning offshore in the eastern Gulf of Maine (Pettigrew et al., 2005), and an inner coastal limb (the Western Maine Coastal Current) that can at times extend much farther to the west along

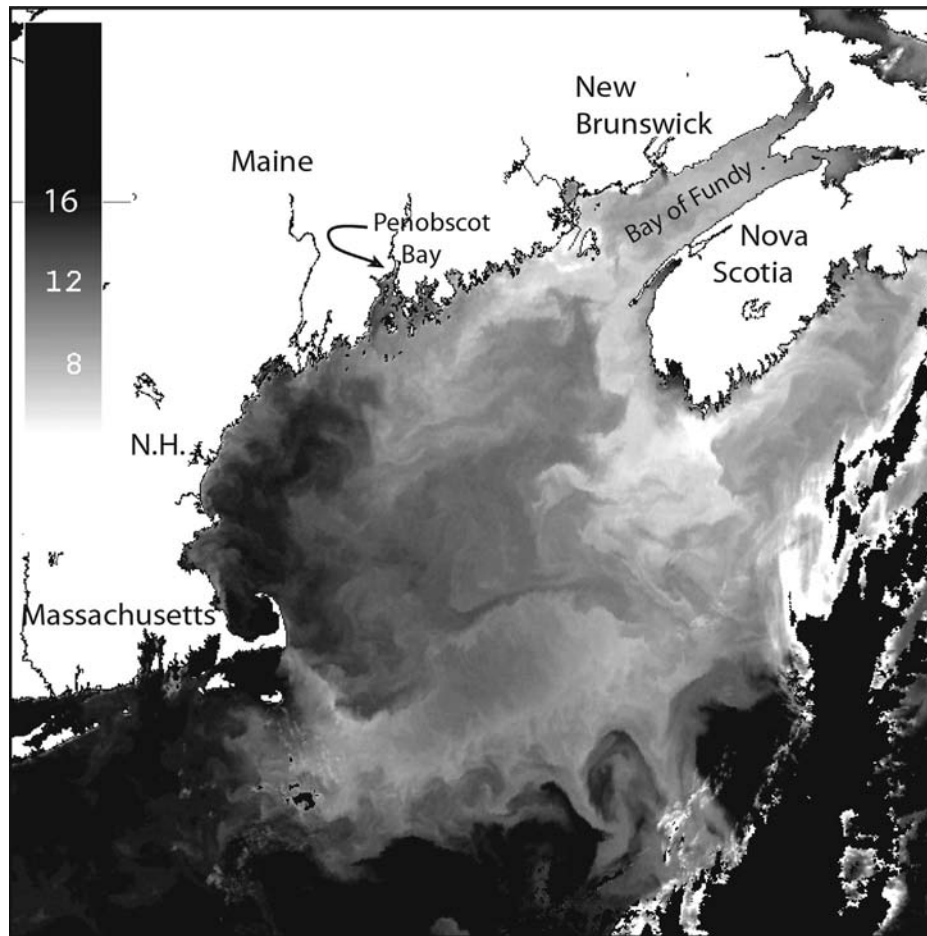


Fig. 2. AVHRR satellite image of sea surface temperature in the Gulf of Maine region in June 1998 (year day 153); temperature scale ($^{\circ}\text{C}$) is given (after Townsend et al., 2006).

the coasts of Maine, New Hampshire and Massachusetts and well into the western Gulf of Maine, carrying with it a growing population of *A. fundyense* cells as far as Cape Cod, Massachusetts, and beyond (Anderson et al., 2005c).

The third *A. fundyense* population center, on Georges Bank, has only recently been described (McGillicuddy et al., 2014). This population is analogous in its dynamics to the northern Gulf of Maine (EMCC) *A. fundyense* population in that also appears to be fueled by new nutrient injections that result from intense tidal mixing along the Northern Flank of the Bank (e.g., see Hu et al., 2008) that population of cells and nutrient-rich waters are advected in the clockwise circulation around the Bank. The Georges Bank population is anomalous, however, in that the inoculum, or source of cells to the Bank, remains speculative; cells may originate from resuspended benthic cysts in the western Gulf of Maine that upwell onto the Bank, from small numbers of cysts in Georges Bank sediments (Anderson et al., 2014a, 2014b, 2014c), or from advection to the Bank of surface waters and vegetative cells from the northern Gulf of Maine (McGillicuddy et al., 2014). Once on the Bank, where the initial injection of new nitrogen (nitrate) along the northern edge becomes depleted by populations of *A. fundyense* and, especially, other phytoplankton, as they drift with the residual currents, continued maintenance and further growth of the populations in the western Gulf of Maine as well as on Georges Bank would appear to be supported less by new nitrate injections, and more on recycled ammonium, as suggested by McGillicuddy et al. (2014), further evidence of which is given in this communication.

The importance of the nutrient field to annual *A. fundyense* blooms in the western portions of the northern Gulf of Maine was

shown by McGillicuddy et al. (2011) in their comparison of blooms in 2008 and 2010. They showed that despite a significant stock of pre-growth season benthic resting cysts in the Gulf of Maine, which have been a good predictor in numerical models of subsequent *A. fundyense* bloom magnitudes (He et al., 2008; Li et al., 2009; McGillicuddy et al., 2011; Anderson et al., 2014a, 2014b, 2014c), the bloom in 2010 did not materialize as predicted. Instead, the 2010 bloom was significantly reduced, both in areal extent and cell densities. The bloom appeared to have been suppressed as a result of intrusions of anomalous water masses into the western Gulf early in the season, waters that were characterized by lower salinities and reduced inorganic nutrient concentrations (nitrate, phosphate and silicate) at all depths as compared with 2008. The nutrient field in 2010 may also have been depleted by an unusually strong spring phytoplankton bloom earlier that same spring. Peak surface chlorophyll concentrations in the spring of 2010 reached ca. $5.5 \mu\text{g L}^{-1}$ which were approximately $1.5 \mu\text{g L}^{-1}$ greater than any of the five previous years, and were about $2 \mu\text{g L}^{-1}$ greater than the climatological spring bloom average (McGillicuddy et al., 2011).

1.2. Nutrients and water masses in the Gulf of Maine–Georges Bank region

While an important determinant of annual *A. fundyense* blooms in the Gulf of Maine–Georges Bank region (with the possible exception of blooms on Georges Bank) is the magnitude of the inoculum – the initial supply of cells from benthic resting cysts – we hypothesize here that the extent of subsequent population growth is largely set by fluxes of new nitrate, and by the degree of

subsequent recycling of ammonium. Further, we hypothesize that the nutrient fields are controlled by flows of deep and intermediate-depth water masses into and out of the Gulf of Maine region and their associated nutrient loads, processes that are highly variable in space and time.

Changes over the past several decades in dissolved inorganic nutrient concentrations and their proportions to one another, as well as changes in water mass properties, have been reported for the Gulf of Maine (Townsend et al., 2010; Rebeck, 2011), and have been attributed in part to changes in the relative proportions of Warm Slope Water (WSW) and Labrador Slope Water (LSW; e.g., Houghton and Fairbanks, 2001; Mountain, 2012) in the Gulf. Those changes are at least partly under the influence of the North Atlantic Oscillation (NAO; e.g., Mountain, 2012), which appears to determine which of the two deep slope water masses resides at the mouth of the Northeast Channel and subsequently dominates deepwater flows into the Gulf. These deepwater intrusions of both WSW and LSW through the Northeast Channel from off the continental shelf are the principal sources of dissolved inorganic nutrients that sustain primary production in the interior Gulf of Maine and on Georges Bank (Townsend, 1991, 1998; Townsend and Pettigrew, 1997; Hu et al., 2008). However, the two slope water masses differ significantly in their nutrient loads: nitrate concentrations are much higher in WSW than LSW, by about 50%, and silicate concentrations are higher in WSW by about 10% (Townsend et al., 2006; Townsend and Ellis, 2010).

In their analysis of historical nutrient and hydrographic data, Townsend et al. (2010) showed significant variations in decade-averaged, deep (> 100 m) water properties (temperature and salinity) and concentrations of nitrate and silicate in the Gulf of Maine, which were not correlated with NAO. Dating from the 1960s, those data revealed variable fluxes into the Gulf of Maine of both slope water sources, LSW and WSW that initially correlated well with NAO in the 1960s and 1970s, but not in later decades. That study showed that deep water layers in the Gulf (> 100 m) have become slightly fresher and cooler since the 1970s, with lower nitrate (by ca. 2–4 μM) but higher silicate (also by ca. 2–4 μM), changes that were opposite to that expected based on cycles in the North Atlantic Oscillation, but which were commensurate with the recent, rapid melting in the Arctic (e.g., Perovich and Richter-Menge, 2009). The altered nutrient regime in the Gulf of Maine in recent decades is interpreted as the result of a greater proportion of a mixture of shelf and slope water influxes of Labrador Sea origin, as compared with the two deep slope water sources, LSW and WSW. Greater fluxes of fresh water produced by Arctic rivers and increases in melting of the Arctic ice cap since the 1970s would appear to have intensified the southward baroclinic flow of shelf and slope waters in the Labrador Sea and along the coasts of Maritime Canada and the Northeast U.S. As those shelf and slope waters mix off Labrador and Newfoundland and flow along the continental shelf at all depths from the Grand Banks of Newfoundland to the Gulf of Maine, the nutrient loads become altered by both benthic denitrification, which depletes nitrate concentrations, and accumulations of terrestrially derived silicate in river run off (Townsend et al., 2010).

In addition to the recent changes in nutrients and water properties of the Gulf of Maine, there is also evidence of altered currents flowing into and out of the Gulf. Changes in fluxes of deep slope waters through the Northeast Channel in the last decade have been documented by Pettigrew et al. (2008) and Smith et al. (2012) based on the moored current meter records. Water mass flows through the Northeast Channel have traditionally been thought to be directed into the Gulf of Maine at all depths on the eastern side of the channel, and out of the Gulf at all depths on the western side, with periodic reversals at depth (> 150 m). Below 150 m, the net flow is, or has been assumed to be, generally directed into the Gulf. However, evidence has shown that in the

early and mid 2000s, during which time current meter records are available that flow pattern changed to one that in recent years is characterized by episodes of greater outflow of deep waters (Smith et al., 2012). Smith et al. show that the deep water outflow is a mass balance response to a greater volume transport of shelf water from the Scotian Shelf into the Gulf of Maine; in keeping with the hypothesis put forth by Townsend et al. (2010), this results in a greater influx to the Gulf of lower-nutrient shelf waters and an outflow from the Gulf of high-nutrient deep and bottom waters. Furthermore, Smith et al. (2012) showed that these influxes of shelf water are reflected in large (± 10 cm) short-term (interannual) variations in coastal sea level in Nova Scotia.

Water mass dynamics in the Gulf of Maine region are variable, and may be undergoing a decadal-scale change that has been altering the proportions and total loads of new dissolved inorganic nutrients brought to the Gulf. Those changes can be expected to affect dynamics of phytoplankton, both diatoms during the spring bloom, and subsequent populations of non-diatom phytoplankton, such as *A. fundyense*. It is against this backdrop that we present the results of extensive nutrient and hydrographic measurements made during a series of research cruises in the Gulf of Maine and Georges Bank region during the spring and summer of 2007, 2008 and 2010, which show variable proportions of different water masses, with variable nutrient loads that affect patterns of *A. fundyense* blooms. We use those data to examine the hypotheses discussed above that nutrient fields are controlled by flows of deep and intermediate-depth water masses into and out of the Gulf of Maine region that such flows are highly variable in space and time, and that the resulting nutrient fluxes influence locations and magnitudes of annual *A. fundyense* blooms. We also present a hypothesis that the unique morphology and hydrographic processes on Georges Bank may lead to summertime periods of phosphate limitation, which allows for ammonium concentrations to increase, and which may favor *A. fundyense* population growth.

2. Materials and methods

Ten oceanographic survey cruises were conducted in the Gulf of Maine and on Georges Bank as part of the GOMTOX Program during 2007, 2008 and 2010 (Table 1). Station locations for each cruise are given in Fig. 3. At each station a standard CTD cast was made within 5 m of the bottom with a SeaBird 911 CTD and carousel water sampler equipped with Niskin bottles. *A. fundyense* cells in two-liter water samples were concentrated by sieving through a 20 μm mesh sieve prior to preserving in formalin for later processing (details in Anderson et al., 2005d). Quantitative cell counts were determined in Dr. D.M. Anderson's laboratory at Woods Hole Oceanographic Institution using epifluorescence microscopy and an oligonucleotide probe that identifies both *Alexandrium tamarensis* and *A. fundyense*, which

Table 1
Cruise dates, ship and cruise numbers for the ten oceanographic surveys in 2007, 2008 and 2010.

Year	Cruise dates	Ship/cruise number
2007	17–31–31 May	R/V Endeavor/EN435
	20–5–5 July	R/V Endeavor/EN437
2008	28 April–5 May	R/V Oceanus/OC445
	27 May–4 June	R/V Oceanus/OC447
	27 June–3 July	R/V Endeavor/EN448
	7–13–13 August	R/V Endeavor/EN451
2010	1–10–10 May	R/V Oceanus/OC460
	26 May–4 June	R/V Endeavor/EN476
	30 June–8 July	R/V Oceanus/OC465
	29 July–6 August	R/V Oceanus/OC467

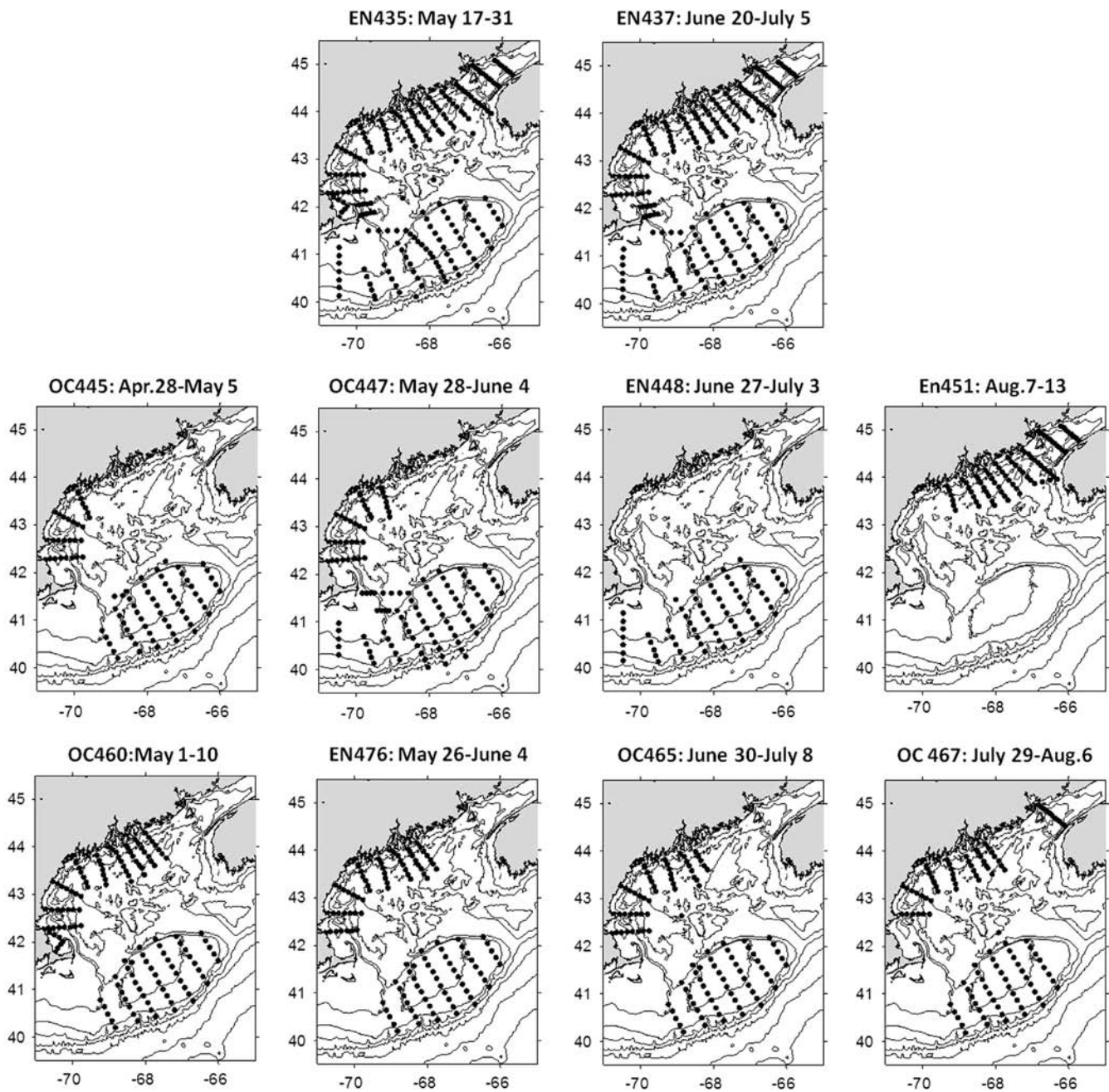


Fig. 3. Station locations for each of the ten survey cruises listed in Table 1. These maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

are considered to be varieties of the same species (Anderson et al., 2005d). We use *A. fundyense* to refer to both forms. Water samples for analyses of dissolved inorganic nutrients were taken at all stations from standard depths of 1, 10, 20, 30, 40, 50, 100, 150, 200 and 250 m, within depth constraints; in each case the deepest water sample was collected from within a few meters of the bottom. Water samples (20 ml) from each bottle depth were filtered through 0.45 μm Millipore cellulose acetate filters, immediately placed in a sea water ice bath for 5–10 min, and then frozen at $-18\text{ }^{\circ}\text{C}$ for subsequent analyses on shore for concentrations of nitrate plus nitrite ($\text{NO}_3^- + \text{NO}_2^-$), silicate ($\text{Si}(\text{OH})_4$), phosphate (PO_4^{3-}), and ammonium (NH_4^+), using a Bran Luebbe AA3 Autoanalyzer and standard techniques. Because nitrite concentrations are typically less than 0.2 μM , far less than that of nitrate in these waters, and because the two nutrients can be measured together in a single run on our autoanalyzer, we present here only the sum of nitrate plus nitrite ($\text{NO}_3^- + \text{NO}_2^-$); hereafter we refer

to the two simply as nitrate. Phytoplankton chlorophyll concentrations were measured fluorometrically on discrete water samples collected at depths of 1, 10, 20, 30 and 40 m (Parsons et al., 1984). Water samples (100 mls) were filtered onto GF/F filters, extracted in 90% acetone in a freezer ($-18\text{ }^{\circ}\text{C}$) for 12–24 h, and then analyzed at sea using a Turner Model 10 fluorometer. Plots of results were prepared using MATLAB software.

3. Results and discussion

3.1. Hydrographic fields

A total of 1186 stations were sampled over the course of ten survey cruises in the Gulf of Maine and on Georges Bank in 2007, 2008 and 2010. A complete distillation and analysis of this

extensive data set, which includes more than 8500 nutrient samples will be ongoing for some time; in this communication we focus on characterizing the main features of the nutrient fields in relation to water masses, and show how phytoplankton distributions (inferred from phytoplankton chlorophyll distributions) and cell densities of *A. fundyense* may be influenced.

A principal conclusion that quickly reveals itself in this 10-cruise data set is that there is significant spatial and temporal (seasonal and interannual) variability in water properties, phytoplankton biomass (chlorophyll) and *A. fundyense* cell densities. Spatial variability throughout the region is best revealed in sea surface temperatures (e.g., Fig. 2), which are given in Fig. 4, and which show that the coldest surface waters are in the northeastern Gulf (best seen for the period from June 20 to July 5 in 2007), in an area well known for its intense tidal mixing. Those temperature data also show both seasonal and interannual variability. Waters in the northern Gulf of Maine at the end of May and beginning of

June varied from relatively cold surface temperatures in 2007 to progressively warmer temperatures at the same time of year in 2008 and 2010. Fewer stations were sampled in the Gulf of Maine in 2008 and 2010 than in 2007, and they were limited to the western portions of the northern Gulf; nonetheless, the temperature differences among years are clear. A similar, but less pronounced, warming of surface waters from 2007 to 2008 to 2010 can also be seen on Georges Bank for the same May–June period. Those interannual differences in surface temperature on the Bank are more evident in mid-summer, during the June–July cruises in those years, when surface water temperatures ranged from about 10 to 11 °C in 2007 to greater than 16 °C over parts of the Bank in 2010.

Surface salinities for the ten cruises are given in Fig. 5, and illustrate the freshening influence of Maine rivers along the coast of the northern Gulf in 2007, with evidence of freshening extending farther offshore between the two survey cruises (May and June–July of 2007). Salinities in the western Gulf of Maine in 2010

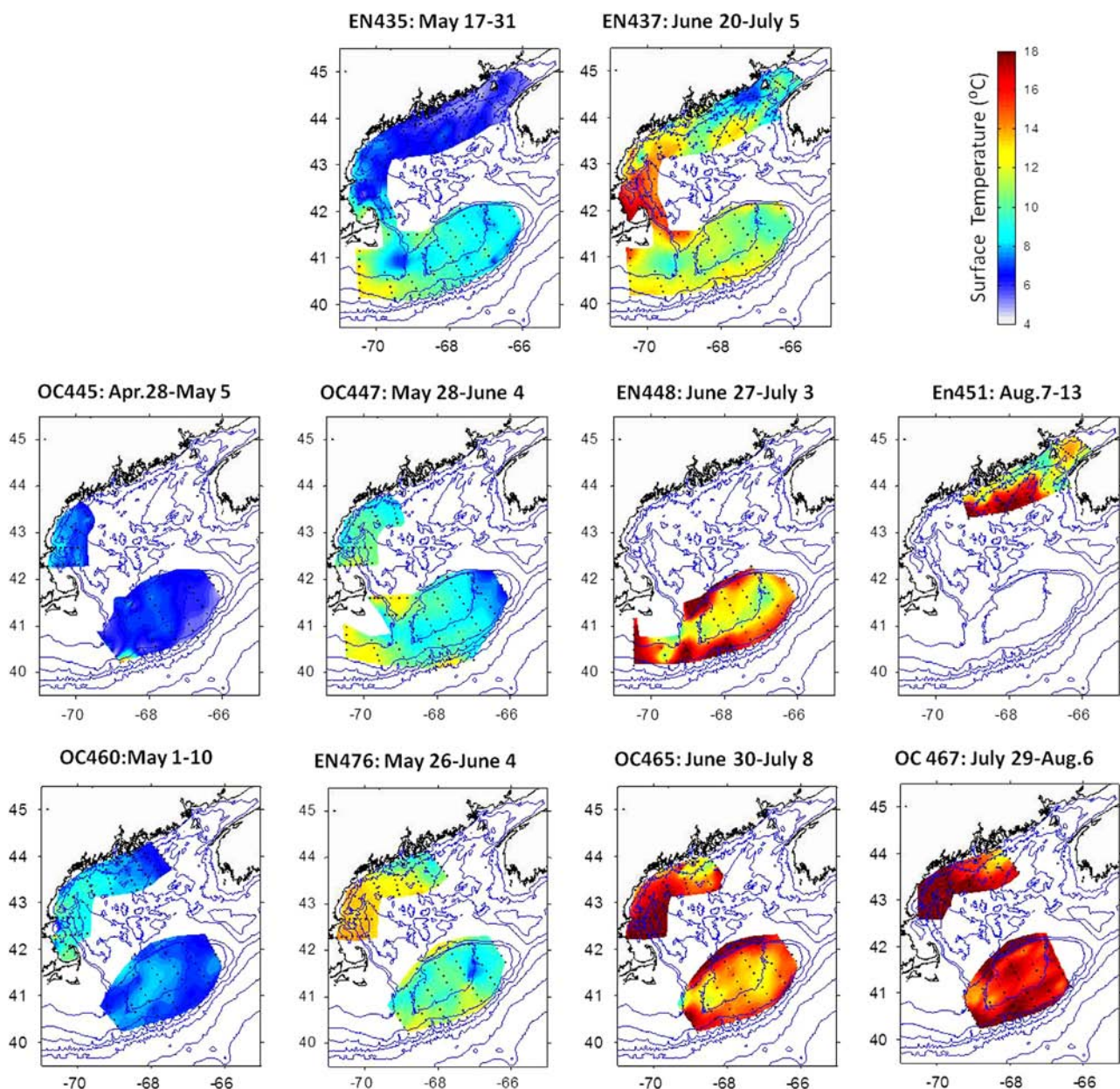


Fig. 4. Areal contour plots of surface water temperature (°C) for each of the ten cruises. Contour maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

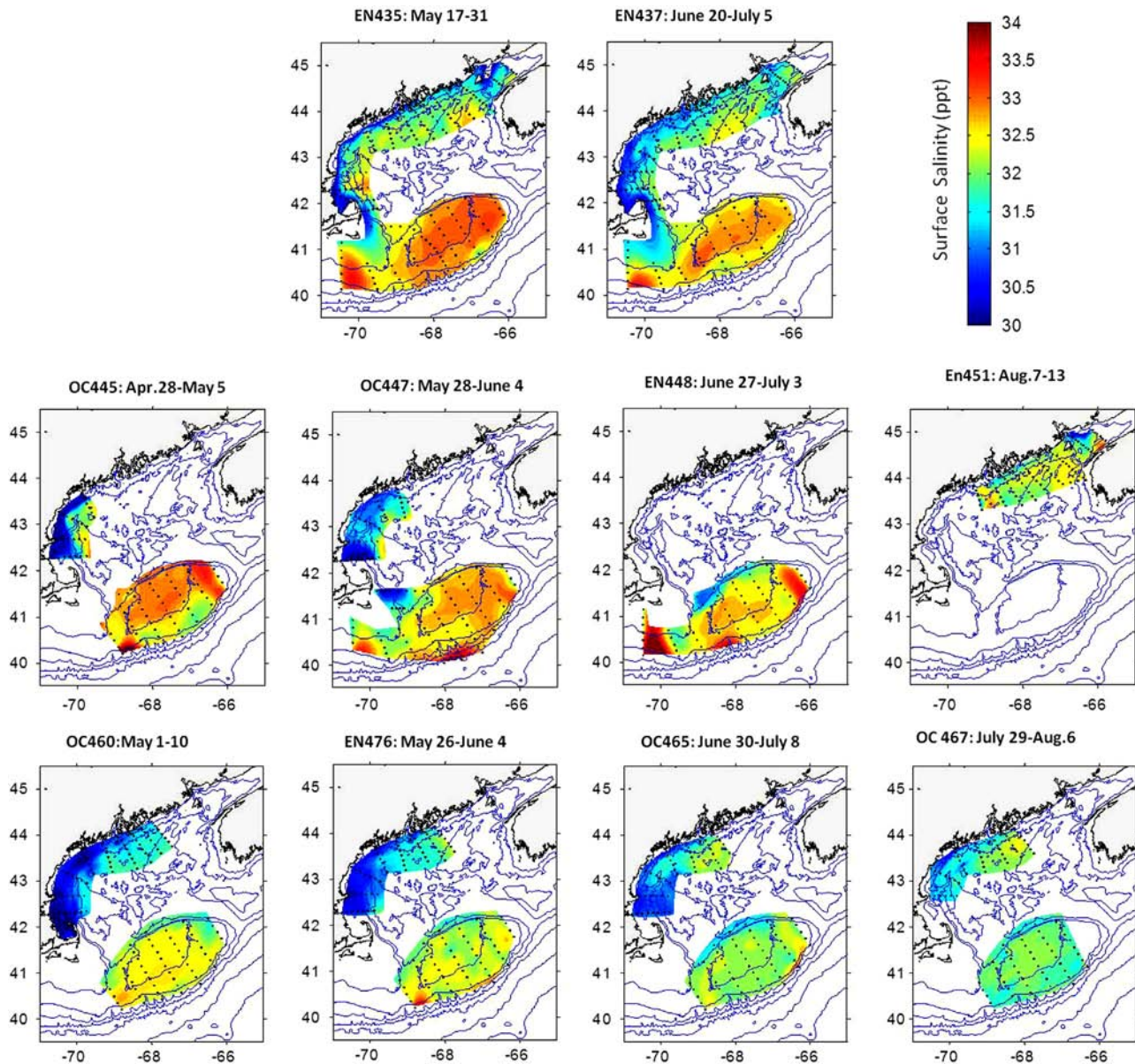


Fig. 5. Areal contour plots of surface water salinity (ppt) for each of the ten cruises. Contour maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

(a year in which western Gulf of Maine stations were sampled four times) were fresher than in 2007 or 2008 but became progressively saltier with time over the summer. On the other hand, surface salinities farther offshore, on Georges Bank, for the same four cruises in 2010 became progressively fresher with time, as did the salinities during the three cruises in 2008, no doubt reflecting the advection of the spring freshet from local rivers to the offshore Bank in early summer, but also advection of fresh waters from the St. Lawrence River by way of the Gulf of St. Lawrence and the Nova Scotian Shelf. More than half the freshwater flux to the Gulf of Maine is from this source outside the Gulf (Bigelow, 1927; reviewed in Townsend et al., 2006). The edges of Georges Bank also show evidence of tidal pumping or upwelling of higher salinity water onto the Bank, especially along the Northern Flank. In general, salinities of surface waters in the offshore eastern Gulf were higher than in the western Gulf, which is downstream of coastal freshwater outflows from the major rivers in the region, and is farther removed from the point of entry of deep, high salinity slope waters; Jordan Basin in the east typically

has a greater volume of these slope waters than Wilkinson Basin in the west (Townsend, 1991).

3.2. Phytoplankton chlorophyll and *A. fundyense* distributions and abundances

The concentrations of surface chlorophyll, assumed here to be a proxy for phytoplankton biomass, for the ten cruises are given in Fig. 6, and are similar to results reported earlier for the Gulf of Maine and Georges Bank following the spring phytoplankton bloom (e.g., Townsend et al., 2006). Chlorophyll concentrations are generally highest in the vicinity of the nutrient-rich EMCC (Eastern Maine Coastal Current) in the northern Gulf, as described by Townsend et al. (1987), and in patches over the central portions and Northeast Peak on Georges Bank. In each case, the patches of phytoplankton are likely produced, initially, in response to injections of new nutrients as a result of tidal pumping and subsequent advection and spreading of those waters on the Bank (Hu et al., 2008). Across the central portions of the Bank, however, phytoplankton are more

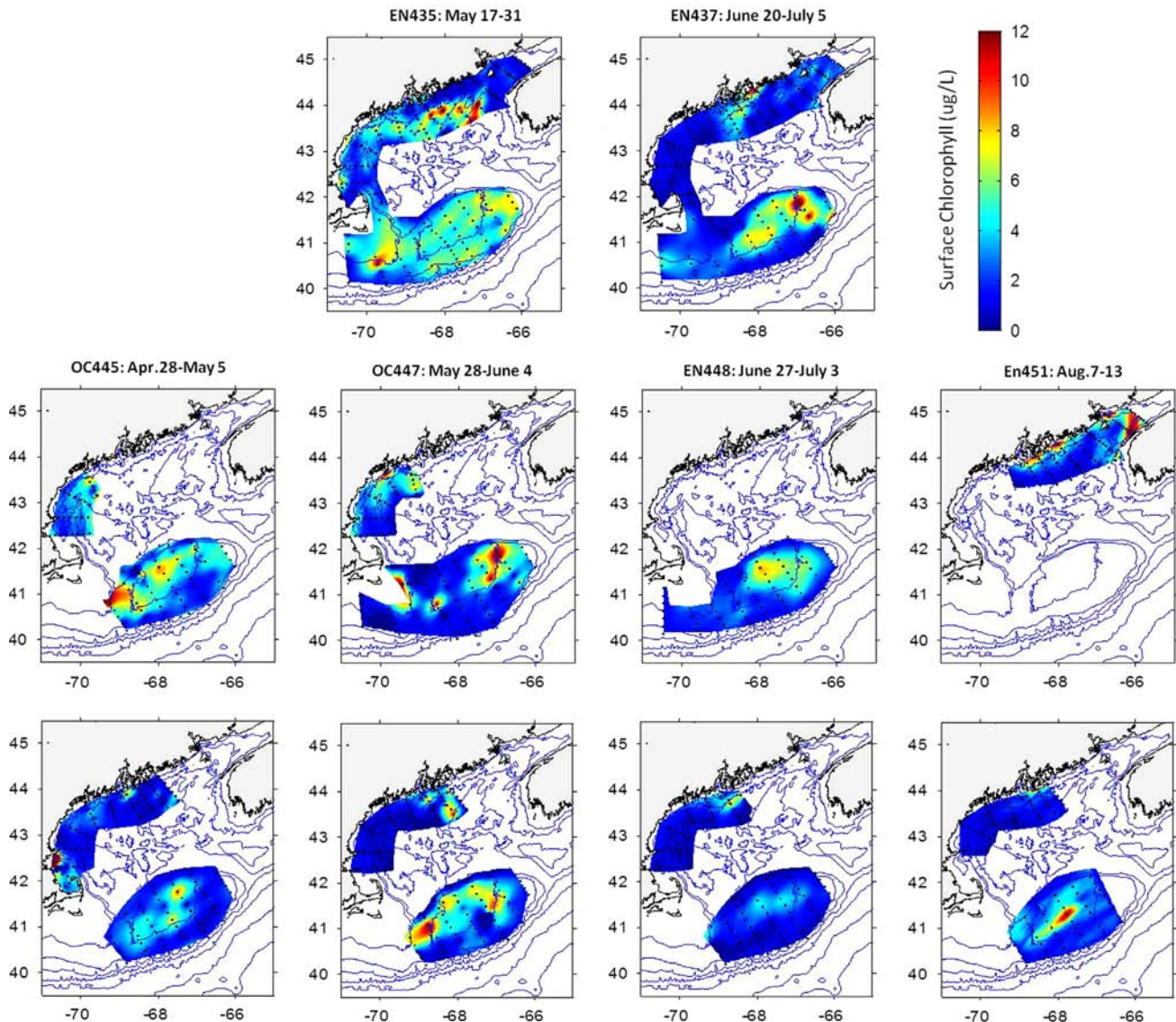


Fig. 6. Areal contour plots of surface phytoplankton chlorophyll ($\mu\text{g/L}$) for each of the ten cruises. Contour maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

likely fueled by recycled ammonium in that there is limited exchange of nutrient-rich waters across isobaths from beyond the Bank's edges (Townsend and Pettigrew, 1997; Hu et al., 2008).

Cell densities of *A. fundyense* at the surface are presented in Fig. 7 for each of the ten cruises; a more complete analysis of *A. fundyense* distributions that includes their vertical distributions is reported elsewhere (McGillicuddy et al., 2014). In both 2007 and 2008 we observed a large bloom of *A. fundyense* on Georges Bank, reaching cell densities greater than several thousand cells $\cdot\text{l}^{-1}$ across a broad portion of the Bank. The *A. fundyense* bloom was well underway upon our arrival on Georges Bank in mid to late May of 2007, with highest cell densities of more than 7000 cells $\cdot\text{l}^{-1}$ on western portions of the central Bank and across the Southern Flank; the bloom was still present some four weeks later during the June–July cruise that year. Highest cell densities in June–July were similar to those in May, but the areal distribution of the bloom was not as broad and was more confined to the Southern Flank. The next year, in 2008, we were able to schedule cruises to bracket better the initiation and demise of the Georges Bank bloom, which reached maximum cell densities of more than 5000 cells $\cdot\text{l}^{-1}$ during the second cruise, in May–June, but its areal

extent was more limited than the 2007 bloom, and was distributed more downstream, on the western portions of the Southern Flank. By the third survey cruise, in June–July of 2008, the maximum cell densities were generally less than 100 cells $\cdot\text{l}^{-1}$, and were distributed primarily across the Northeast Peak and the Southern Flank. A brief survey from 29 August to 3 July 3, 2008, with the R/V Tioga covering two transects (not shown) verified that the Georges Bank bloom was over. Consequently, we did not return to that area during our fourth cruise in July–August of 2008 but instead sampled the northeastern Gulf of Maine, where there were relatively few cells, on the order of 100 cells $\cdot\text{l}^{-1}$. It is probable that we missed the Gulf of Maine *A. fundyense* bloom which may have peaked earlier in the year (e.g., Townsend et al., 2001, 2005).

Unlike Georges Bank, the *A. fundyense* bloom in the Gulf of Maine was not yet underway in May of 2007; there were only a few tens of cells $\cdot\text{l}^{-1}$ along the Maine coast, but as many as 50 cells $\cdot\text{l}^{-1}$ in the western Bay of Fundy, where a bloom may have been starting to develop. Later that same year, in June–July 2007, as the Georges Bank bloom was winding down, blooms in the northeastern Gulf in the vicinity of the EMCC and in the Bay of Fundy were apparently getting underway; cell densities were on the order

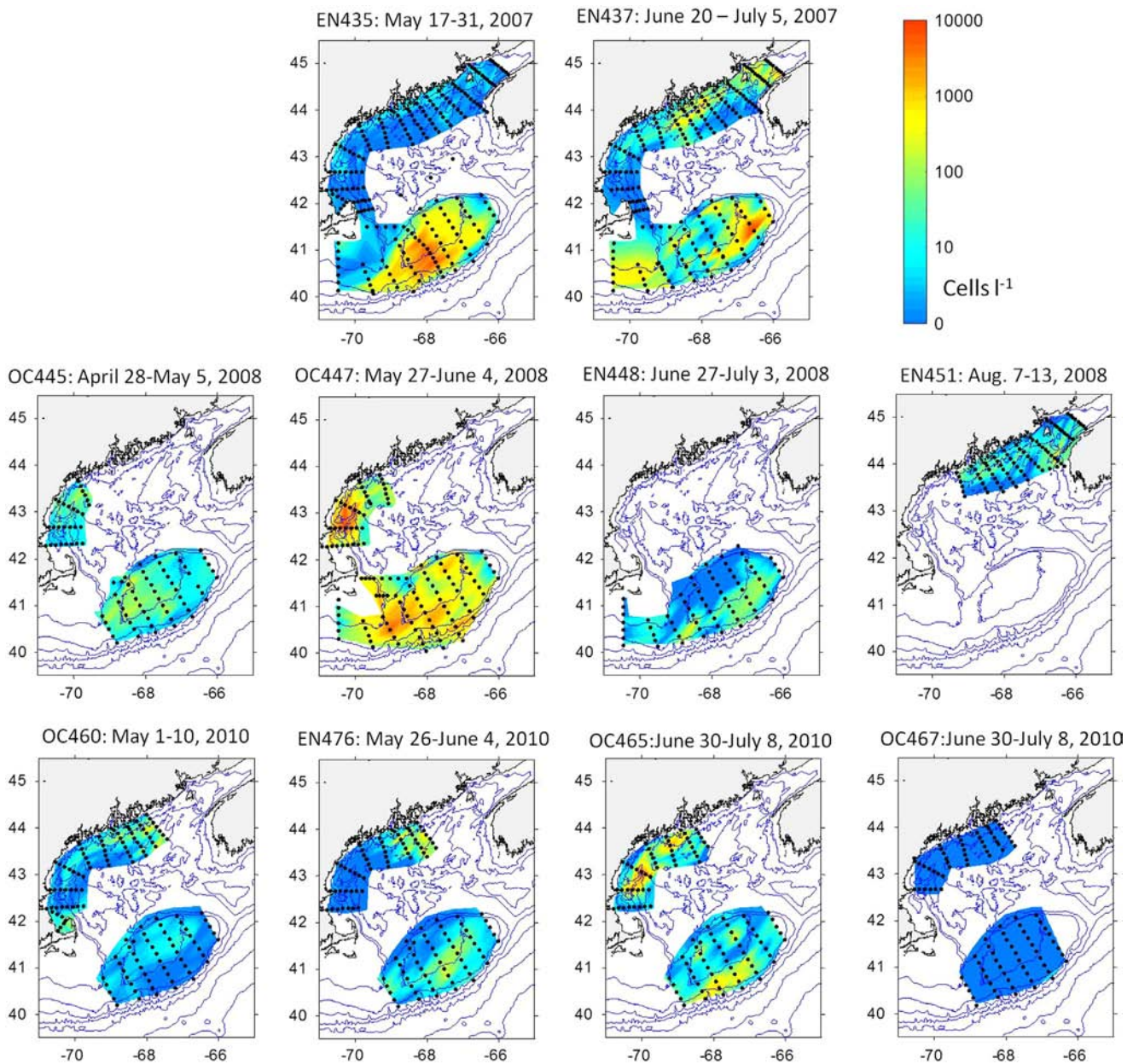


Fig. 7. Areal contour plots of surface *Alexandrium fundyense* cell densities (cells per liter) for each of the ten cruises (after McGillicuddy et al., 2013). Contour maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

of a few hundred cells \cdot l $^{-1}$. The western Gulf of Maine, however, was nearly devoid of cells during both our cruises in 2007.

In 2008, *A. fundyense* cells were present in the western Gulf early in the season, during the April–May cruise, with cell densities generally less than 100 cells \cdot l $^{-1}$. During the May–June cruise cell densities were significantly greater, with several hundred cells \cdot l $^{-1}$ common, and some stations with several thousand cells \cdot l $^{-1}$; maximum cell densities were greater than 7500 cells \cdot l $^{-1}$. These were the only cruises to sample the western Gulf in 2008; our fourth cruise that year was focused on the northeastern Gulf where cell densities were generally less than 150 cells \cdot l $^{-1}$ (one station off Nova Scotia, had ca. 400 cells \cdot l $^{-1}$).

In 2010, *A. fundyense* cell densities were generally low, both on Georges Bank and in the western Gulf of Maine. Cell densities were especially low during the first two cruises, in May and May–June; by August of 2010, during the fourth cruise, there were virtually no cells in either the Gulf, on Georges Bank, nor in the Bay of Fundy, where a single transect of stations was sampled (not contoured in

Fig. 7). On our first cruise, in May 2010, *A. fundyense* cells in the Gulf of Maine were present only at the easternmost stations of our sampling domain, east of Penobscot Bay, where several stations had more than 100 cells \cdot l $^{-1}$; the maximum was just under 500 cells \cdot l $^{-1}$. Farther to the west, there were either no cells detected, or only some 10 s of cells \cdot l $^{-1}$ at a few stations. On the next cruise, in May–June 2010, *A. fundyense* cells in the Gulf of Maine were again limited to the easternmost stations, off Penobscot Bay, where they reached as many as 1300 cells \cdot l $^{-1}$ at one station. Farther to the west, cells were absent altogether. It was not until the third cruise, in June–July of 2010, when cells were detected in the western Gulf, in two patches, supported by what appeared to be refreshed nitrate in the upper 40 m (see Fig. 9; this 2010 mid-summer increase in nutrients is also discussed below). There were a few stations in the westernmost patch that had more than 2800 cells \cdot l $^{-1}$; the second patch farther east had several stations with several hundred cells \cdot l $^{-1}$ and one station with more than 2300 cells \cdot l $^{-1}$. The differences in *A. fundyense* cell densities during the first two cruises in the

western Gulf of Maine between 2008 and 2010 are discussed more fully in [McGillicuddy et al. \(2011\)](#).

On Georges Bank in May of 2010 there was a patch of *A. fundyense* cells that extended along the Northern Flank, with densities of only a few 10 s of cells \cdot l $^{-1}$. That patch appears to have advected around the Bank by the time of our May–June cruise, when there was swath of cells extending from the Northeast Peak to the Southern Flank; cell densities reached several hundred cells l $^{-1}$ (maximum was only about 250 cells l $^{-1}$ in the far western edge of the Bank). By June–July, cell densities on the Bank had continued to increase, with one station reaching > 1300 cells l $^{-1}$. On the fourth cruise in August 2010, we found virtually no *A. fundyense* cells at all on Georges Bank; a trace was found at only one station.

3.3. Nutrient fields

Seasonal and interannual differences in *A. fundyense* blooms are likely related to differences in the nutrient fields. Following the late winter to early spring period, surface water concentrations of nitrate and silicate are usually depleted to near detection limits (less than 0.1–0.2 μ M) throughout much of the Gulf of Maine–Georges Bank region ([Townsend and Thomas, 2001](#); [Townsend et al., 2006](#)). An example of this surface water nutrient depletion is illustrated in [Fig. 8](#) for a Gulf of Maine station sampled during our July 2007 cruise. It reveals an upper mixed layer that extends to about 20 m, below which is the seasonal pycnocline, defined by decreasing temperatures and increasing salinities with depth. Concentrations of nitrate, silicate and phosphate are all depleted to low levels in the surface mixed layer, and each increases in concentration at greater depths; an exception is ammonium,

which has its highest concentrations in the near surface waters. We return to a discussion of ammonium below. Because of this seasonal depletion of surface water nutrients, we have presented in [Figs. 9–12](#) the average concentrations of each nutrient, nitrate, silicate, ammonium and phosphate, from the surface to 40 m depth (the average of five sample depths: 1, 10, 20, 30 and 40 m) for each of the ten cruises. These near surface averages better characterize areal and interannual differences in upper water column nutrient loads than just presenting surface values, and also helps to identify regions of ongoing or recent vertical nutrient fluxes.

The distributions of nitrate in the Gulf and on Georges Bank ([Fig. 9](#)) reinforce the generalities just discussed. In May of 2007 nitrate is depleted to near zero throughout the top 40 m on Georges Bank, having been taken up much earlier by the winter–spring phytoplankton bloom, whereas there are significant nitrate concentrations in the northeastern Gulf, associated with the EMCC, and in the Bay of Fundy. Those nitrate concentrations are the result of new nutrient injections around the periphery of Minas Basin in the Bay of Fundy, and into surface waters at the upstream end of the EMCC that result from tidal mixing and pumping of deep waters, especially along the coast of eastern Maine and around Grand Manan Island at the mouth of the Bay of Fundy ([Townsend et al., 2006](#); [Aretxabaleta et al., 2008, 2009](#); see [Fig. 1](#)). Similarly elevated nitrate concentrations can be seen in August of 2008 as well. [Fig. 9](#) also shows an area of relatively high nitrate concentrations in the top 40 m of the Gulf of Maine in May of 2007 that is well offshore of the EMMC, over Jordan Basin; those high nitrate values reflect a shallow nutricline there. The depth of the halocline and pycnocline (and nutricline) all shoal from relatively deep depths inshore, adjacent to the tidally mixed eastern Maine coast, to offshore stratified waters, where the surface mixed

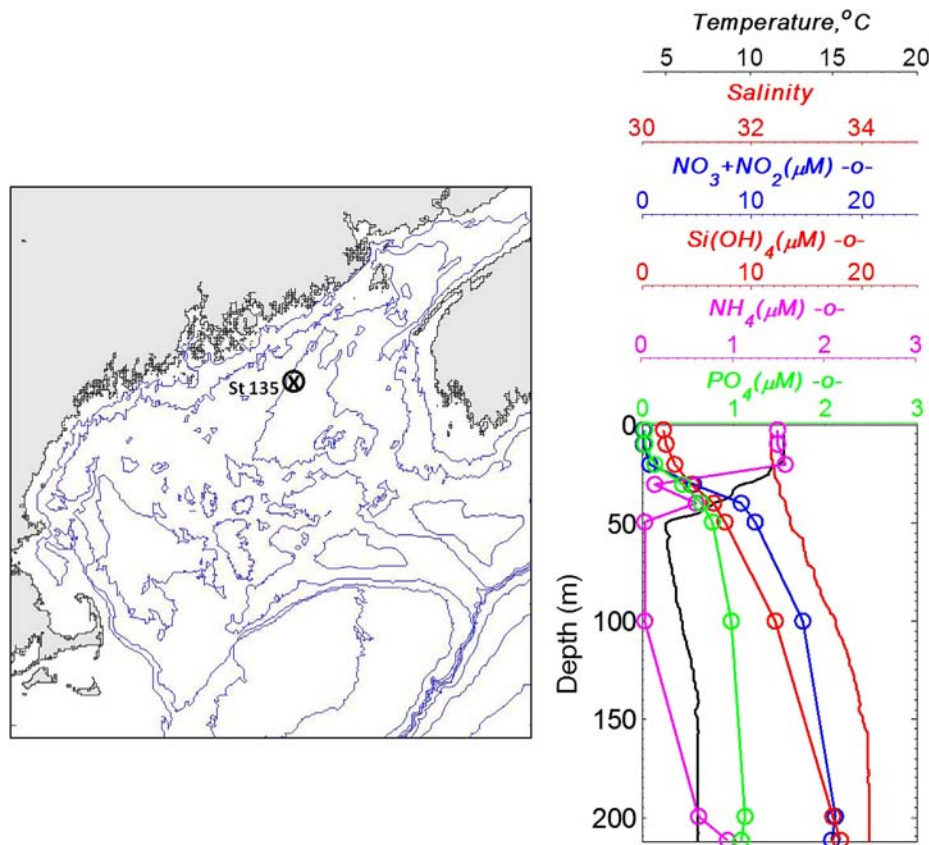


Fig. 8. Vertical profiles of temperature, salinity, nitrate plus nitrite (NO₃⁻ + NO₂⁻), silicate (Si(OH)₄), ammonium (NH₄⁺) and phosphate (PO₄³⁻) in the Gulf of Maine at the station shown in July 2007.

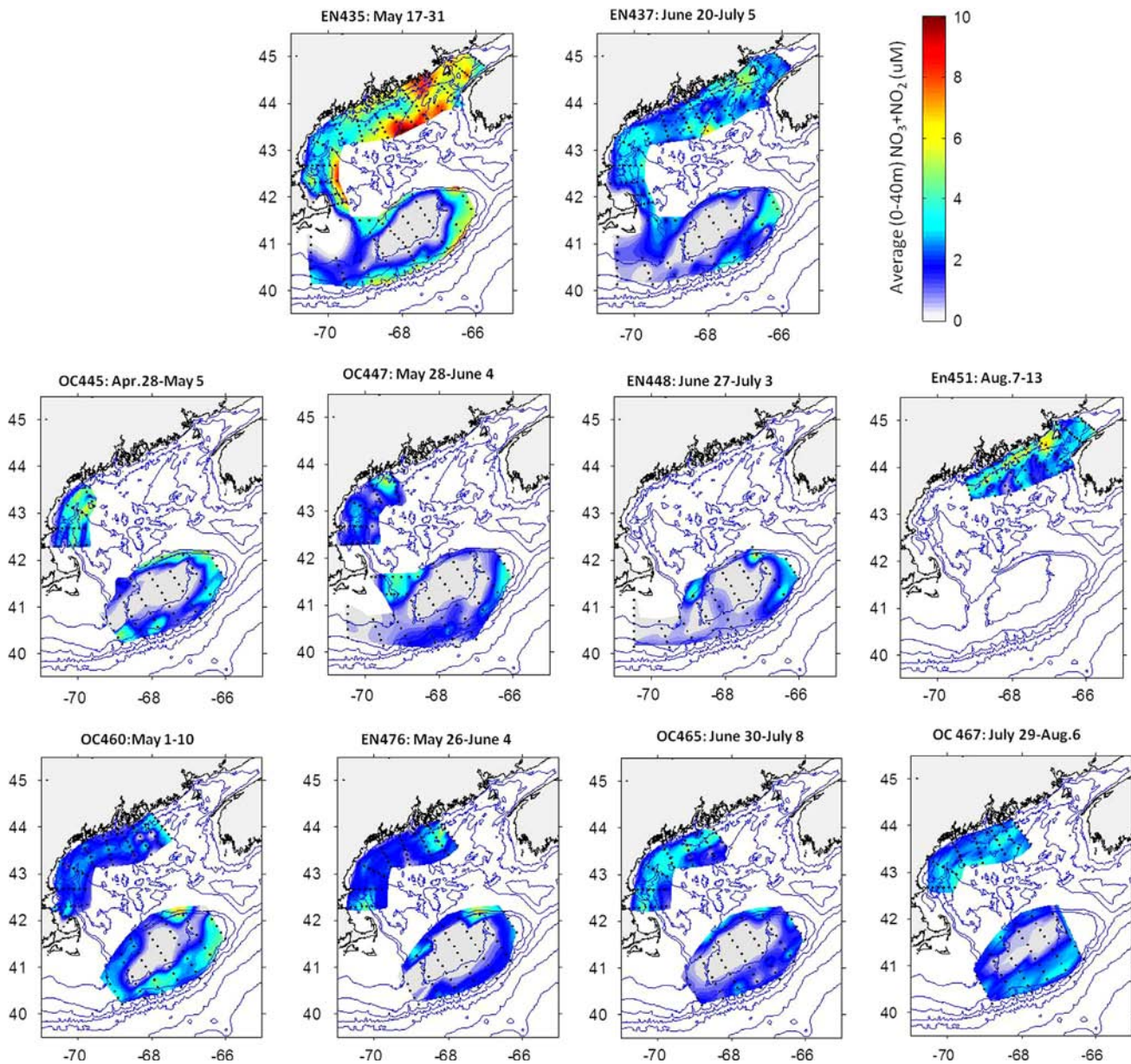


Fig. 9. Areal contour plots of concentrations of nitrate plus nitrite ($\text{NO}_3^- + \text{NO}_2^-$) in micromoles per liter averaged over the top 40 m for each of the ten cruises. Contour maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

layer is quite shallow, and therefore our 0–40 m average includes sub-pycnocline, sub-nutricline waters over Jordan Basin. A similar offshore phenomenon of relatively high nitrate concentrations in the top 40 m can also be seen in the western Gulf.

The EMCC carries nutrient-rich, tidally mixed waters downstream along the coast where they stimulate phytoplankton growth, especially at frontal edges of that cold-water current, as seen in the surface chlorophyll distributions in Fig. 6. In April–May of 2008, elevated nitrate concentrations persist quite far to the west in the northern Gulf, but they have been further depleted by the next cruise, in May–June, presumably the result of significantly higher light levels later in the season and greater phytoplankton production. Earlier in 2010 (May) the nitrate concentrations in the upper 40 m of the northern Gulf are noticeably lower than the same time of year in 2007 (although station coverage in 2010 extends eastward only to mid-Maine); likewise, nitrate is lower in the western Gulf in 2010 than in 2008. In general, Gulf of Maine nitrate concentrations early in the year are least in 2010, although, as alluded to above and discussed in more

detail below, there is evidence of a recharge of nutrients into the upper 40 m during the two latter survey cruises that year. Those new nutrients apparently stimulated the growth of the two patches of *A. fundyense* in the western Gulf during the June–July cruise that year (see Fig. 7).

On Georges Bank, nitrate concentrations are depleted across most of its area in all nine of our cruises in which those waters were sampled (Fig. 9), but elevated nitrate concentrations can be seen ringing the Bank at times (the earlier cruises each year) and there is evidence of injections of nitrate from deeper waters onto the Bank along the Northern Flank and Northeast Peak. This phenomenon of nutrient depletion on the central portions of Georges Bank has been described earlier as the ‘donut’ phenomenon (Townsend and Pettigrew, 1997; Hu et al., 2008), whereby deeper waters and their nutrient loads are tidally pumped onto the Northern Flank and Northeast Peak where they are advected clockwise around the periphery, with relatively little cross-isobath exchange occurring across the Bank to the central portions.

In general, the distributions of silicate are similar to those of nitrate throughout most of the Gulf of Maine and on Georges Bank, with a couple exceptions. First, the coastal waters are clearly enriched in silicate, the result of silicate-rich river run off, and concentrations exceed those of nitrate. Second, the distributions are more patchily distributed than nitrate, with areas of relatively high silicate concentrations offshore. There is evidence of regeneration of significant concentrations of silicate on Georges Bank, with 0–40 m average concentrations greater than $4 \mu\text{M}$ later in the summer in both 2008 and 2010, a phenomenon that has been described earlier (Townsend and Thomas, 2002). Localized patches of relatively high silicate concentrations on the Bank are most likely the result of regeneration of silicate from diatom frustules produced in during previous winter–spring diatom bloom, as rising water temperatures in spring and summer increase their dissolution rate. This is especially evident in the 2010 data, where silicate concentrations on Georges Bank are on the order of $2\text{--}4 \mu\text{M}$, with higher concentrations in localized patches. Concentrations of $2\text{--}4 \mu\text{M}$ are at or below

the half-saturation constants for diatom growth (Paasche, 1973; Egge and Aksnes, 1992).

Ammonium, the regenerated form of dissolved inorganic nitrogen, is notoriously patchy in its distribution in the oceans, and indeed, such is the case in these survey results. Ammonium is produced by metabolic activity of heterotrophic bacteria and other planktonic and nonplanktonic heterotrophs, which convert particulate organic nitrogen (plankton, their food) into dissolved form. Once formed, ammonium is taken up quickly by phytoplankton; being the chemically reduced form, ammonium is the often-preferred species of dissolved inorganic nitrogen (Mulholland and Lomas, 2008). When the uptake rate by phytoplankton matches or exceeds the ammonium regeneration rate, concentrations will remain low. Only when these processes are decoupled can significant accumulations of ammonium occur. This decoupling can be either temporal (net heterotrophy following a period of net autotrophy) or spatial (net heterotrophy downstream of an area of net autotrophy).

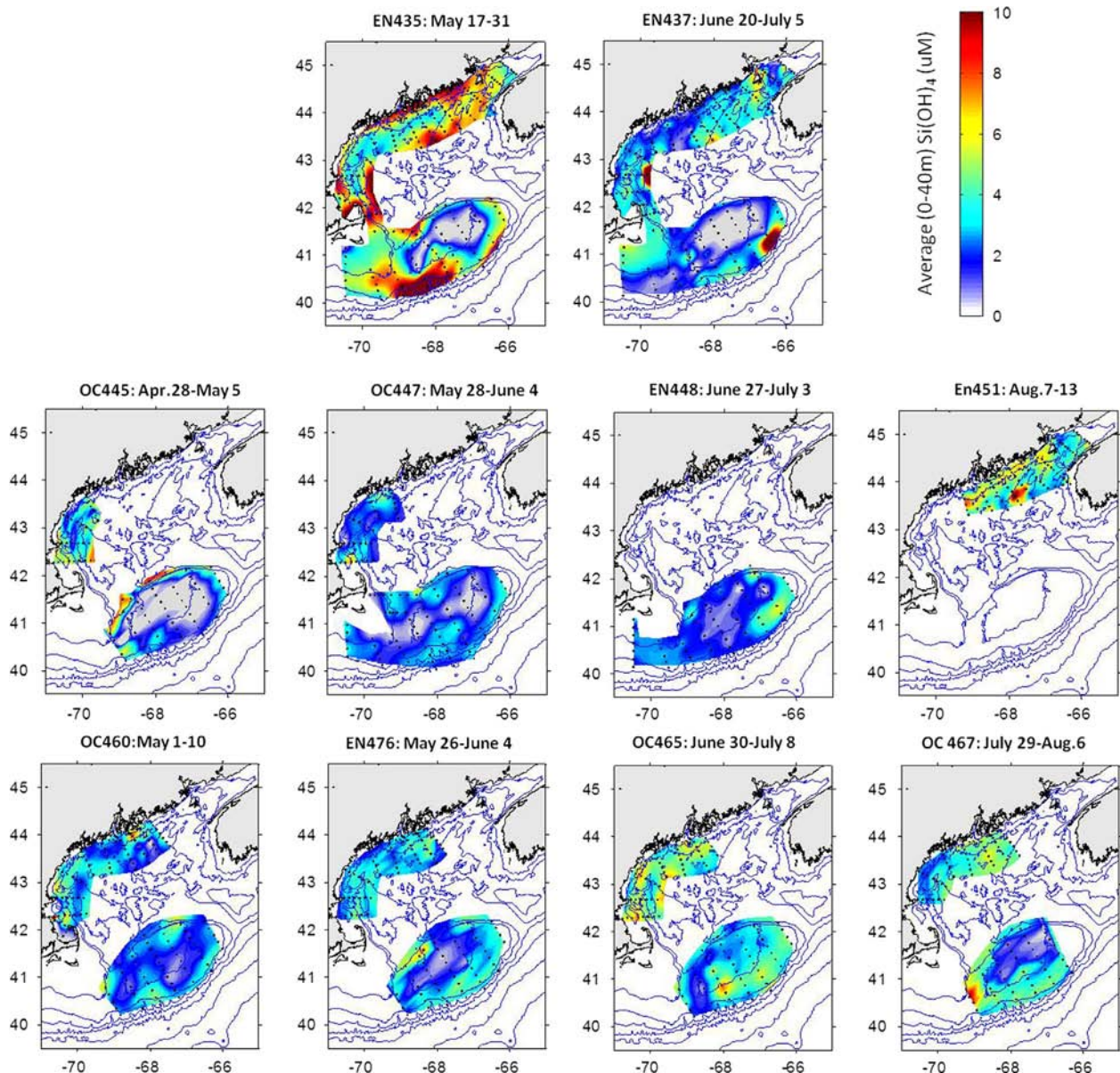


Fig. 10. Areal contour plots of concentrations of silicate ($\text{Si}(\text{OH})_4$) in micromoles per liter averaged over the top 40 m for each of the ten cruises. Contour maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

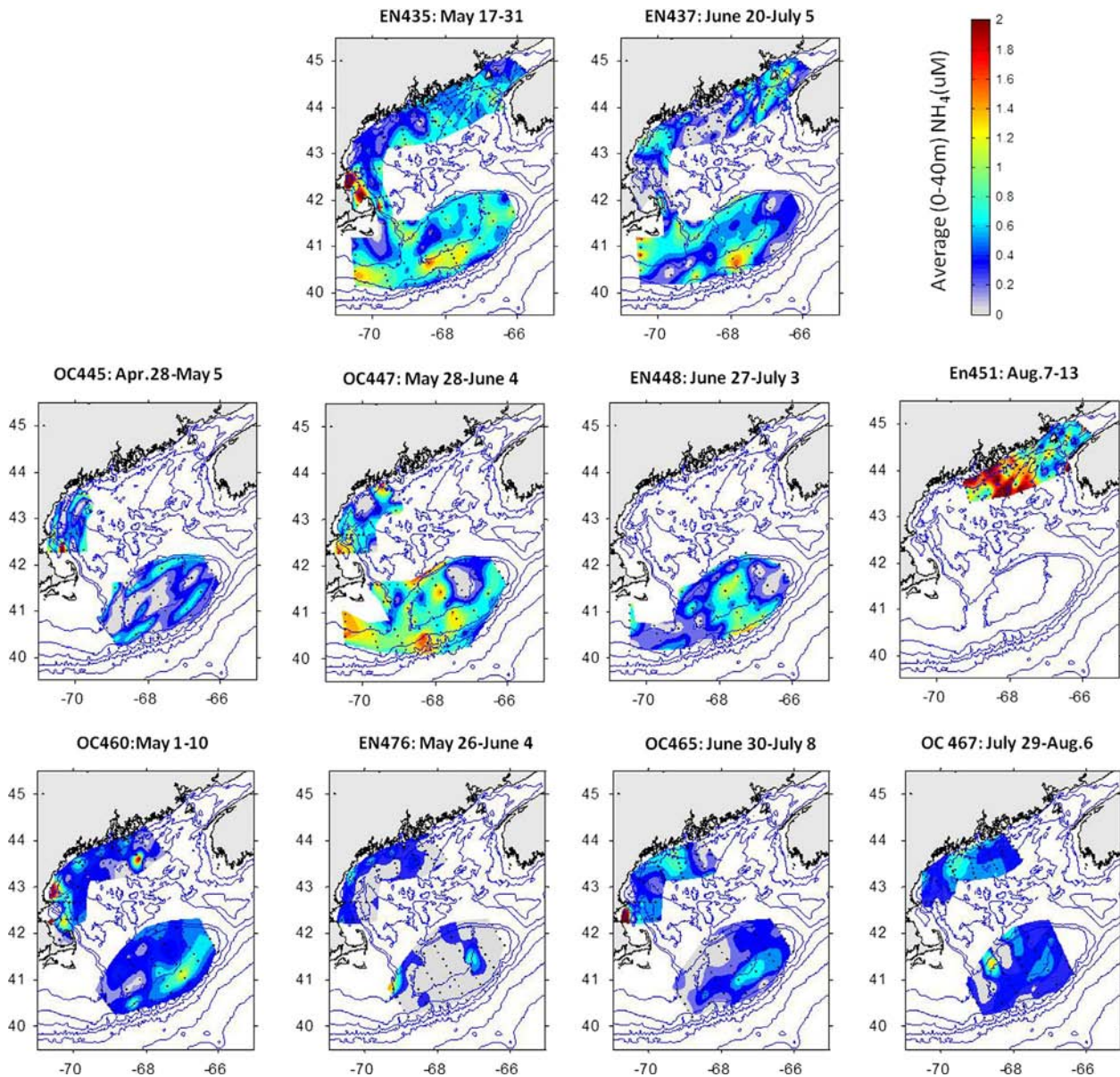


Fig. 11. Areal contour plots of concentrations of ammonium (NH_4^+) in micromoles per liter averaged over the top 40 m for each of the ten cruises. Contour maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

In May of 2007 the highest concentrations of ammonium, on the order of $2 \mu\text{M}$ averaged over the top 40 m, are in Massachusetts Bay in the far western portions of the Gulf, with patches of lower concentrations throughout much of the northern Gulf (Fig. 11). A particularly large patch, with concentrations also on the order of $2 \mu\text{M}$, can be seen in the eastern and central portions of the northern Gulf during August of 2008 at the downstream end of the EMCC, where the current splits into two branches as discussed above, and downstream of the high chlorophyll concentrations. Smaller patches of ammonium are observed in April–May and May–June of 2008 in the western Gulf, and in two of the cruises in 2010, May–June and June–July. On Georges Bank, we see several patches of ammonium in 2007 and 2008, over the central portions and especially along the Southern Flank during the May–June and June–July cruise periods. With the exception of one or two patches of moderately elevated ammonium concentrations, 2010 was a year of very low ammonium on the Bank. Low nutrient concentrations in the interior Gulf of Maine in general were the rule at the start of the growth season in 2010, and because those waters

are the source of nutrients to Georges Bank (as we discuss in more detail in the next section) this led to reduced overall plankton production in the Gulf and on the Bank, which means there was little dissolved or particulate organic nitrogen available with which to regenerate ammonium.

Surface concentrations of phosphate are given in Fig. 12 for the ten cruises, and as can be seen, there are instances when it drops to very low concentrations, especially on the central portions of Georges Bank. Phosphate is not usually considered to be the limiting nutrient in the Gulf of Maine nor on Georges Bank; instead, it is dissolved inorganic nitrogen (nitrate, nitrite and ammonium) that has been shown to become limiting to phytoplankton production first (e.g., Townsend and Thomas, 2002). Nonetheless, there are portions of the central crest of Georges Bank that in 2008, for example, have average phosphate concentrations over the top 40 m that are below our detection limits (e.g., below about $0.1 \mu\text{M}$), and ammonium concentrations at and exceeding $2.0 \mu\text{M}$. Phosphate may be limiting in such locations on the Bank.

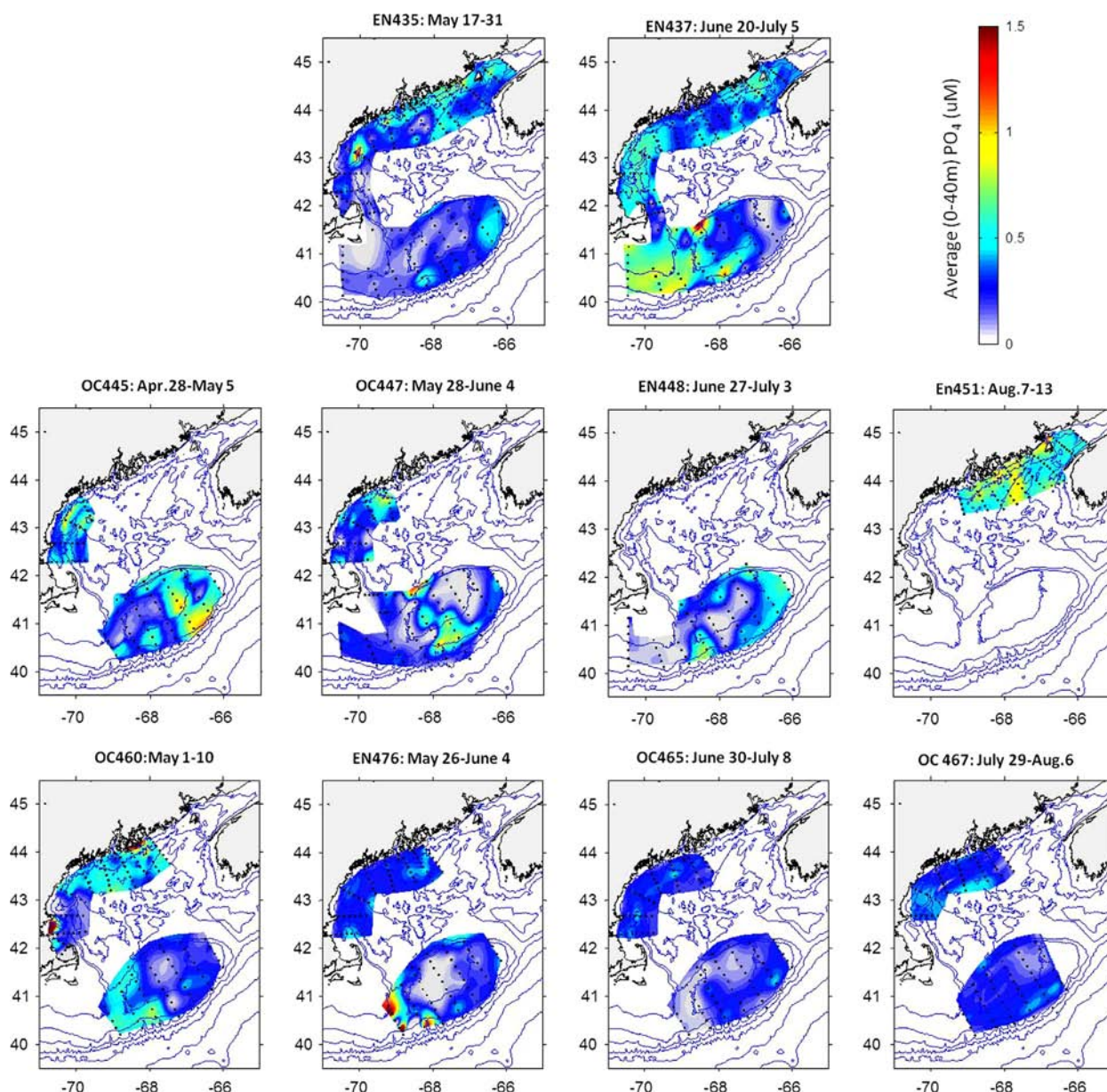


Fig. 12. Areal contour plots of concentrations of dissolved inorganic phosphate (PO_4^{3-}) in micromoles per liter averaged over the top 40 m for each of the ten cruises. Contour maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

In well oxygenated sediments, such as those on the shallow, tidally well-mixed central regions of Georges Bank, iron oxides may form, which in turn are known to strongly adsorb dissolved phosphate in sediment pore waters (Huettel et al., 1998), thus contributing to the removal of phosphate from the water column. It is interesting to speculate that it is in these central regions on Georges Bank, where phosphate can become limiting that ammonium concentrations can accumulate, providing what amounts to a surplus of dissolved inorganic nitrogen relative to phosphorus which cannot otherwise be taken up by phytoplankton. In such cases, *A. fundyense* may have a competitive advantage over other phytoplankton taxa. Some species of *Alexandrium* (e.g., *Alexandrium catanella*) are known to thrive in phosphate-poor waters (Jauzin et al., 2010) by utilizing dissolved organic phosphorus (e.g., Perry, 1972). Such would account for the maintenance and growth of what is otherwise, in the absence of detectable nitrate concentrations, anomalously high *A. fundyense* cell densities on Georges Bank. We assume that *A. fundyense*, like most other phytoplankton taxa, assimilates regenerated ammonium and utilizes dissolved

organic phosphorus (Dyhrman and Ruttenberg, 2006), the capability for which has been shown for this genus (Gonzalez-Gil et al., 1998; Oh et al., 2002).

In addition to instances when phosphate may become limiting to net phytoplankton production on Georges Bank, the assumption that nitrogen is the limiting nutrient element for these waters does not always hold up. As already discussed, the major source of nutrients to the Gulf of Maine is the influx of deep slope waters from beyond the edge of the continental shelf, of which the two kinds differ in their nutrient loads: Warm Slope Water (WSW), of North Atlantic and Gulf Stream origin, has nitrate concentrations $> 23 \mu\text{M}$; Labrador Slope Water (LSW) from the Labrador Sea has 16–17 μM nitrate. Silicate concentrations in both water masses, on the other hand, are on the order of 10–14 μM , with WSW having about 10% more silicate than LSW (Townsend and Ellis, 2010). These high nutrient waters are mixed with one another and with interior waters upon entering the Gulf and are therefore significantly diluted, reducing the nutrient concentrations; nonetheless, both slope water masses initially carry significantly more nitrate

than silicate. This excess of nitrate over silicate becomes important in determining the species composition of the phytoplankton. Because diatoms, which overwhelmingly dominate the spring bloom in the Gulf of Maine and on Georges Bank, take up nitrate and silicate in roughly equal proportions, silicate, not nitrate, would limit the spring bloom, as has been shown for the winter–spring bloom on Georges Bank (Townsend and Thomas, 2001, 2002). This means that as diatoms become silicate-limited, excess nitrate over silicate in the source waters will result in a residual nitrate level remaining in surface waters, which non-diatom species can utilize, thus leading to a species succession in the phytoplankton community. On the other hand, nearer the coast and the influence of riverine sources of silicate (river waters can exceed 200 μM silicate; Anderson et al., 2008), the waters are enriched in silicate and the bloom would be limited first by nitrate.

As already discussed, the Gulf of Maine appears to be receiving, on average, a greater volume of shelf water influxes relative to deep slope water influxes than it did in decades past (Smith et al., 2012), and those shelf waters carry concentrations of, and proportions of, nitrate and silicate that are markedly different from the deep slope water masses. Shelf waters have lower concentrations of nitrate and somewhat elevated concentrations of silicate, giving them a lower nitrate residual than that of deep slope waters. This has resulted in changes in the decade-averaged nitrate and silicate concentrations in the deep waters of the interior Gulf since the 1970s, such that nitrate is no longer necessarily present in higher concentrations than silicate in newly upwelled surface waters (Townsend et al., 2010). The nitrate residual (nitrate minus silicate) is approaching zero, which means there should be less nitrate remaining after faster-growing diatoms become silicate-limited than was once the case.

While influxes of shelf waters appear to be increasing on average, their volume fluxes relative to deep slope waters (which include both Labrador Slope Water and Warm Slope Water) are variable from year to year, which means that the nitrate residuals of deep source waters that are available for mixing with surface

waters are variable in time and space as alternating high nitrate residual waters (shelf waters) and low nitrate residual waters (slope waters) enter and mix with interior Gulf waters. Examples of this variability in deep slope and shelf water nitrate and silicate concentrations are given in Fig. 13, which presents hydrographic profiles of temperature, salinity, in situ chlorophyll fluorescence, nitrate+nitrite (nitrate) and silicate at adjacent stations on the eastern portion of the Southern Flank of Georges Bank. Those stations were selected to demonstrate how nitrate and silicate vary spatially within a year, apparently in relation to salinity, and how the same two stations, with similar salinities, vary between years. The first three stations in Fig. 13 were sampled in May 2007 and are located adjacent to one another (spaced ca. 10 km between stations) on a transect running from shallower to deeper water (> 250 m) across the edge of the Bank. A station sampled a year later on the May–June cruise in 2008 at the same, or very nearly the same off-Bank location is shown in the fourth panel. zSub-pycnocline nutrients vary with salinities in 2007, independent of biological uptake, as evidenced by the shallower chlorophyll maximum, with nitrate concentrations increasing with salinity, but silicate does not change in proportion to nitrate. At the deeper offshore station in 2007, nitrate and silicate concentrations at depth are nearly the same. The next year, in 2008, that same station had different water masses, in which the nitrate concentrations are greater than silicate. Such changes in concentrations and proportions of nitrate and silicate with changes in salinity cannot be explained solely by variable fluxes of the two deep slope water types. Only by influxes of shelf waters, which have been influenced by biological activity (denitrification, regeneration, etc.) and near shore additions (e.g., silicate in river waters) can such dramatic changes be explained.

The near-surface nitrate residuals, averaged over the top 40 m, are given in Fig. 14 for the ten cruises. Spatial patterns in these data are difficult to discern and no doubt reflect variations in source waters, mixing and phytoplankton uptake in surface

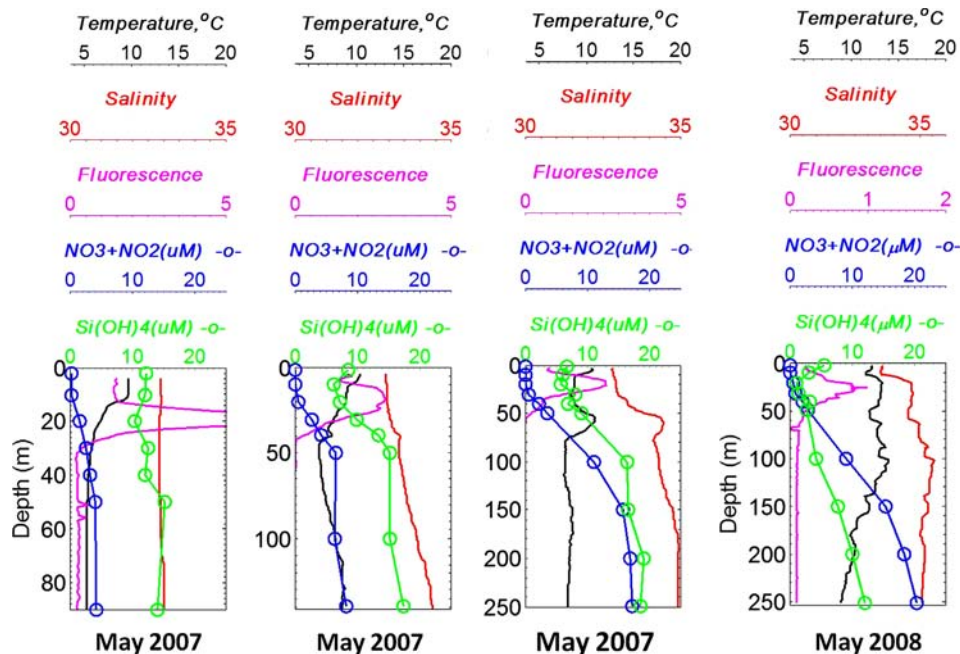


Fig. 13. Hydrographic profiles of temperature, salinity, in situ chlorophyll fluorescence (relative units), nitrate+nitrite (nitrate) and silicate at four stations on the southeastern Flank of Georges Bank selected to represent a range in salinities and different nitrate residuals. The first three were sampled in May 2007 at adjacent stations on a transect from shallower to deeper water > 250 m off the edge of the Bank. The same off-Bank station, sampled on the May–June cruise in 2008, is shown in the fourth panel. Sub-pycnocline nutrients vary with salinities in 2007, independent of biological uptake, as evidenced by the shallower chlorophyll maximum, with nitrate concentrations increasing with salinity. The change in salinity is independent of like changes in silicate. At the deeper offshore station, nitrate and silicate concentrations are nearly equal. In 2008, in a different water mass, the deep nitrate concentrations are greater than silicate.

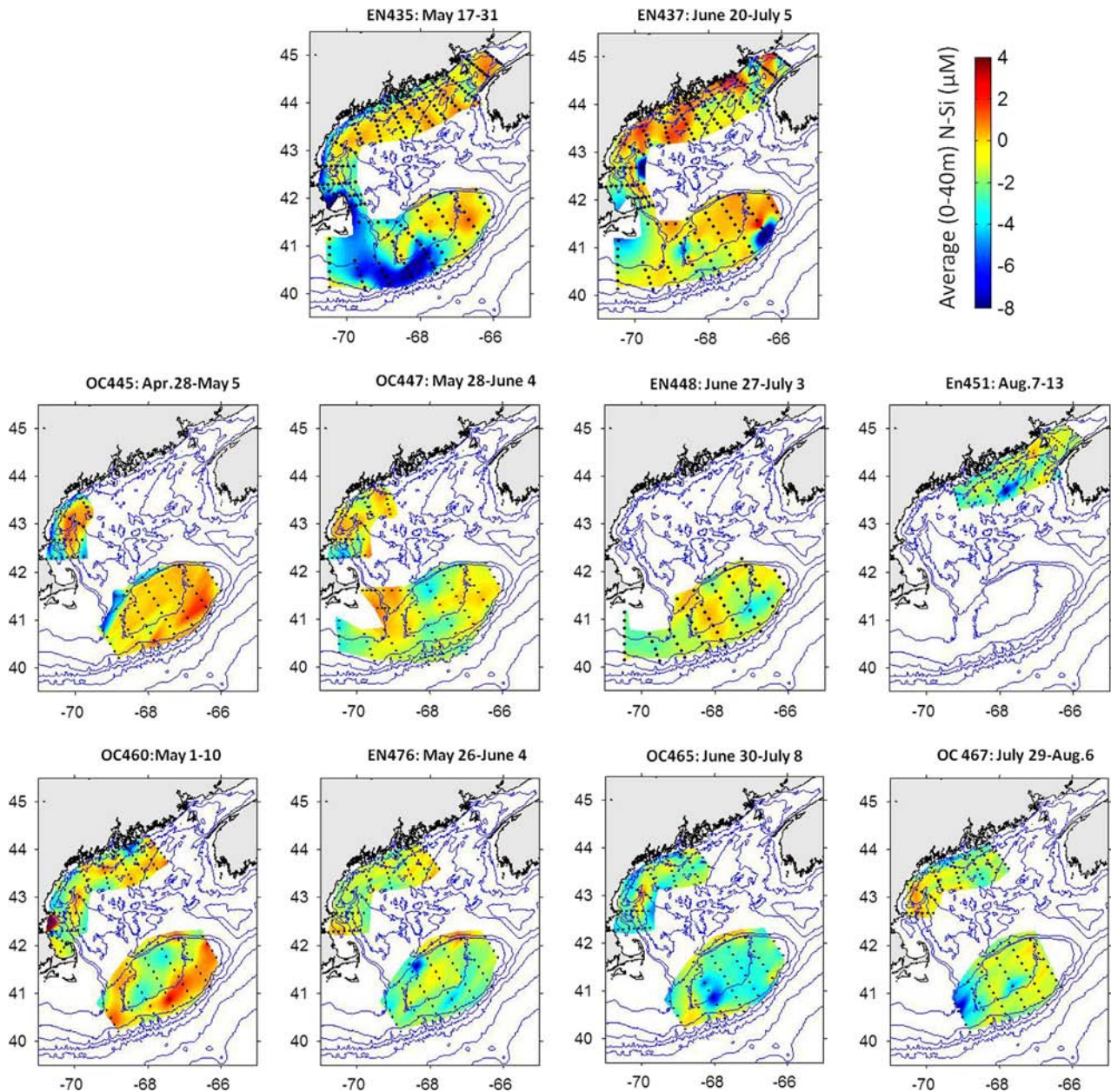


Fig. 14. Areal contour plots of average nitrate residual (equals [nitrate] minus [silicate]) averaged over the top 40 m, given in micromoles per liter, for each of the ten cruises. Contour maps are presented by cruise year from top to bottom (top row 2007; center row 2008 and bottom row 2010) and by the time of year from left to right.

waters. On Georges Bank, the highest residuals tend to be on the central portions of the Bank, while patterns in the Gulf of Maine show highest values in the tidally mixed upwelling areas in the northeastern Gulf, but with higher values also extending into the western Gulf. On the whole nitrate residuals in the top 40 m are, with few exceptions, near zero; however, there do appear to be very general differences that we can identify among the three years. Nitrate residuals in the western Gulf of Maine are relatively high in 2007 and 2008, and show an increase between the May 2007 cruise and the May–June 2008 cruise; the western Gulf of Maine values are lowest among years for all four cruises in 2010. Likewise, the Georges Bank values are also generally lower in 2010 than either 2007 or 2008, with the exception of a patch with a nitrate residual of 1–2 μM on the Southern Flank in May of 2010. These interannual variations likely reflect not only biological uptake but also the variability in source water residuals, and in

general areas of higher nitrate residuals are consistent with locations where *A. fundyense* reached higher cell densities.

One would expect that *A. fundyense* and other non-diatoms would proliferate more in nutrient environments with a positive nitrate residual. Following winter convective mixing and nutrient recharge of the surface waters with a nitrate residual of near zero, and after the spring diatom bloom draws down nitrate and silicate equally, eventually becoming silicate-limited at concentrations of 2–4 μM silicate, there would be little nitrate remaining for subsequent growth of non-diatom phytoplankton. Not only do post spring-bloom phytoplankton populations depend on the residual nitrate in deep source waters, but a similar species succession also occurs where deep waters are mixed to the surface year round. In the case of tidal pumping of deep waters in eastern Maine, which supplies nutrients to the EMCC, and the Northern Flank of Georges Bank, it is diatoms that thrive first. Diatoms outcompete other

phytoplankton groups in both systems, the EMCC and Georges Bank, forming diatom blooms some distance downstream. Farther downstream, low nitrate concentrations would limit growth of non-diatom species, such as *A. fundyense*. However, should *A. fundyense* populations gain a foothold and establish a growing population, it is likely that they maintain that population size by utilizing ammonium regenerated from the phytoplankton populations that were produced by the initial nitrate injections farther upstream.

3.4. Water mass fluxes and nutrient loads

Both the nitrate residual and overall nutrient concentrations in source waters to the Gulf of Maine and Georges Bank are determined by the nature and history of those waters, their relative proportions of Labrador Slope Water and Warm Slope Water, and the degree to which they are both diluted by shelf waters, the nutrient loads of which reflect biological processes and coastal fresh water additions. We refer here to shelf water as Scotian Shelf Water, the relatively fresh and cold water mass that, during the colder months, extends from the surface to the bottom on the Nova Scotian continental shelf; it generally flows south-westward with a portion of its volume turning around Nova Scotia

and into the Gulf (at times, a portion may cross over the Northeast Channel to Georges Bank, Bisagni et al., 1996; Williams et al., 2001; Ji et al., 2006). Much or most of that flow entering the Gulf occurs between the coast and Browns Bank and includes a mixture of shelf and slope waters emanating from the Labrador Sea (e.g., Chapman and Beardsley, 1989) and a mixture of those waters with fresh waters from the St. Lawrence River, inside the Gulf of St. Lawrence. The identification and tracking of these various water masses are facilitated by the use of temperature–salinity (T – S) diagrams.

Temperature–salinity diagrams for 2007 are given for stations in the western Gulf as well as for all stations sampled in the northern Gulf for the two cruises that year, in May and in May–June (Fig. 15). Such diagrams for the Gulf of Maine typically exhibit the classical “V” like pattern that illustrates the centers of mass of the three prominent water masses in the Gulf as described by Hopkins and Garfield (1979); they are (1) Gulf of Maine Bottom Water, relatively warm and salty waters (the highest salinity waters in the Gulf) comprising the deep and bottom layer, which are of deep slope water origin (as distinguished from surface slope waters that occasionally mix across the shelf-slope front); these bottom waters include those T – S pairs that fall on a line stretching to the upper right from the base of the “V”; (2) Gulf of

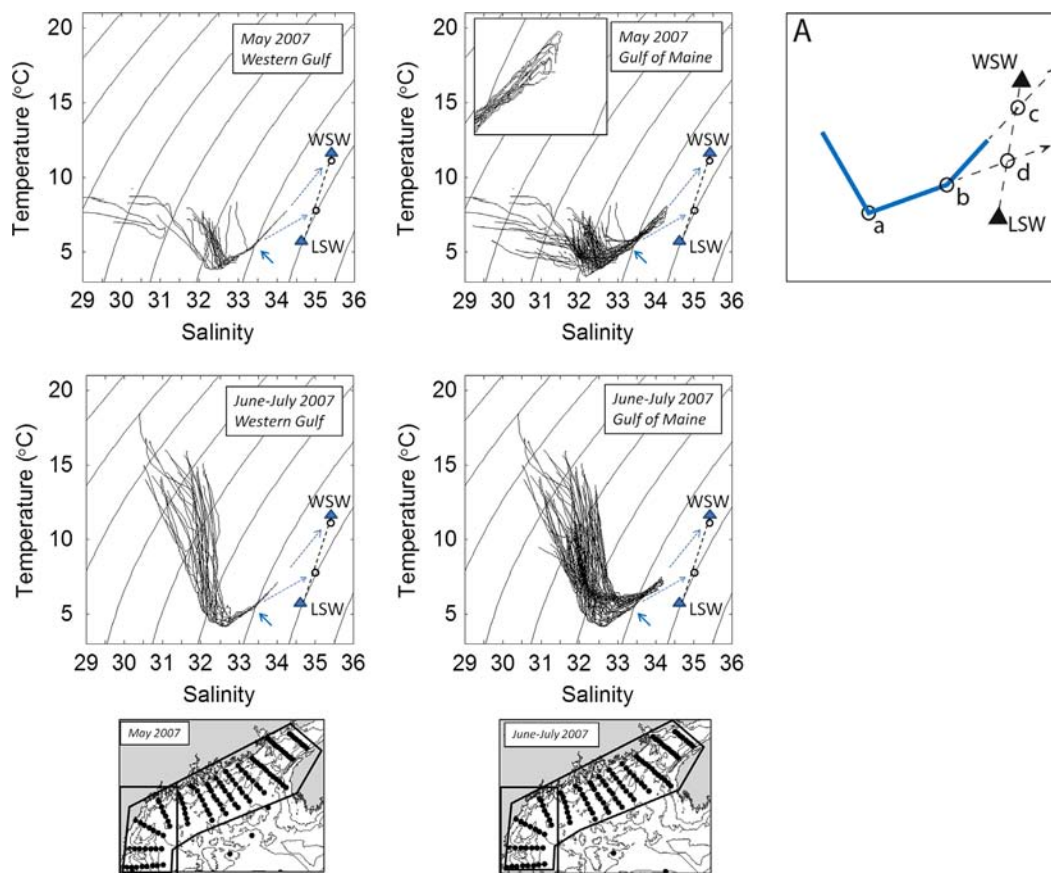


Fig. 15. Temperature–salinity diagrams for stations sampled in the northern Gulf of Maine on both cruises in 2007: 17–31 May and from 20 June to 5 July. The plots are presented for just western Gulf of Maine stations (labeled Western Gulf) and for the entire set of Gulf of Maine stations (labeled Gulf of Maine) as shown in the accompanying maps. The curved lines are contours of constant density, with density increasing toward the bottom right and decreasing toward the top left. Characteristic T – S values for Warm Slope Water (WSW; 11°, 35‰) and Labrador Slope water (LSW; 6.5°, 34.5‰) are given, as well as a mixing line between them. The solid blue arrows indicate a change in slope in the T – S plot of the bottom water layers, indicating a change in bottom mixing end members, as indicated by the dashed arrows and circles (see text). The insert in the top right panel is an enlargement, showing the downward trending terminus of several stations, indicating a deep mixture with Labrador Slope Water. Panel A is a schematic interpretation of different mixing scenarios of bottom and intermediate water layers. Circle b represents the position of the change in slope of the bottom water mixing line, as indicated by the solid blue arrows on the T – S diagrams. Circle d represents the core of the cold intermediate water layer; circles c and d represent positions on a mixing line between LSW and WSW. The arrows in Panel A indicate the trajectory of the mixing lines between points b and points c and d, on the LSW–WSW mixing line.

Maine Intermediate Water (MIW), of which the center of mass is indicated by the base of the “V”, and which is the coldest water in the Gulf (outside of winter), having been formed by convective sinking of surface waters the previous winter; (3) Gulf of Maine Surface Water, which includes all those points to the left of the base of the “V”, and includes the warmer, lower salinity waters residing above the Intermediate Water, which are influenced most by seasonal warming and also by runoff from local rivers and other freshwater sources farther upstream. Fig. 15 shows continued warming of the surface waters between the two cruise periods in 2007 that warming also extends to subsurface depths and causes the temperatures of MIW to rise, with temperatures of shallower depths rising more than, and faster than, deeper layers, which over time produces a displacement of the temperature minimum in the T - S diagram to progressively higher salinities.

The division of these data into the western Gulf, as well as showing them for the entire northern Gulf, illustrates the warmer (and, based on the previous argument, therefore saltier) character of MIW in the eastern Gulf. The intermediate waters in the western Gulf are better defined and persist longer into the summer, whereas intermediate waters in the eastern Gulf are eroded more quickly by persistent tidal mixing together with heating during the warmer months of the year (Hopkins and Garfield, 1979). East–west differences also may be the result of less surface heat loss and winter convective sinking in the eastern Gulf because of its being farther removed from dry, cold air outbreaks that come across the continental U.S. Also obvious in the T - S diagrams in Fig. 15 are the overall higher salinities of surface waters in the eastern Gulf, which we discussed earlier (Fig. 5).

Looking only at the bottom water portions of each diagram in Fig. 15 (to the right of the temperature minimum that defines the core of the intermediate water layer), we can identify a line of data points – a mixing line – with a characteristic slope extending from lower left, which is the cold intermediate water, to the upper right. An extension of that line effectively points to the temperature and salinity of deep source waters with which the intermediate waters have mixed, and are mixing. The source waters that make up the bottom waters inside the Gulf include both deep Labrador Slope Water (LSW), with characteristic, or average, temperature and salinity properties of 6.0 °C and 34.6‰, and Warm Slope Water (WSW), with average properties of 12.0 °C and 35.4‰ (as defined by Mountain, 2012), which are identified in each panel of Fig. 15.² A mixing line between the average values of the two source waters is indicated, as are the probable end members on that line toward which an extension of the deep water portion of the T - S plot is directed, shown by the upper dashed arrow; this phenomenon is clearest in the western Gulf plots, but it is also evident in the plot for all the northern Gulf. In general that projection (the upper dashed arrow) intersects the LSW–WSW mixing line at a point that is closer to WSW, indicating that more of that warmer and saltier (and more nutrient-rich) water than

LSW is mixing with the intermediate layer waters. But, notice that those bottom waters, represented by the line of data from the intermediate water temperature minimum to the end point on the right, exhibit a change in slope about halfway. That is, the line of points has a bend, an elbow, at about 5 °C and 33.4‰, as indicated by the solid blue arrow in Fig. 15. Because mixing lines are straight lines, there are actually two mixing lines between the intermediate and bottom waters. Fundamentally, there are two ways this can happen. First, some time earlier in its history, this deep and bottom water mass may have been mixing with waters that had more LSW than WSW, as indicated by the lower dashed arrow in Fig. 15, which is directed toward an end member closer to LSW. Second, it is also possible to create a bend in the deep and bottom water mixing line by the introduction of a different intermediate water end member, to the left of the bend (versus, or in addition to, the introduction of a different bottom slope water mass). Notice that the intermediate waters represented by the temperature minima in Fig. 15 are quite variable in their T - S properties, possibly reflecting the introduction of variable water masses at a depth shallower than either LSW or WSW slope waters, which is affected by winter convective mixing. That is, mixing of deep and bottom waters with a warmer and/or fresher intermediate water mass could also produce the bend. These deep water T - S characteristics, exhibiting a bend, thus representing two mixing lines, are virtually the same for the northern Gulf as a whole, for both cruises that year. The key point here is that, in the case of our first explanation, the deep Gulf of Maine waters can be a mixture of both deep slope waters, often comprising more of one than the other. As such, nutrient concentrations in surface and intermediate waters in 2007, then, would reflect the lower nutrient concentrations characteristic of LSW, whereas the deepest waters would reflect more the higher nutrient concentrations of WSW. We return to this general discussion of variability of intermediate (shelf) and bottom (slope) waters below.

The T - S diagram that includes stations in both the eastern and western Gulf waters, on the right in Fig. 15, show evidence of an influx of LSW that has not yet completely mixed with the waters of WSW origin; the two water masses have retained their identities following their entry into the Gulf, with warmer and less dense WSW riding over fresher, but colder and denser LSW that has entered the Gulf beneath WSW. Remnants of the two deep water masses can be identified by the downward-directed ends of the T - S plots (representing the deepest waters sampled at those stations) as shown in the enlarged insert in Fig. 15. Once those waters mix, the resulting T - S plot will have a slope that is nearer to that of the lower dashed line, reflecting a greater proportion of LSW, similar to an earlier time before the deflection, or bend, in the bottom water line was created, as just discussed. Thus, these T - S diagrams would indicate a recent history of water mass influxes into the Gulf, where at one point the deep and bottom waters were receiving influxes of a greater proportion of LSW than WSW. Sometime later, the proportion of WSW became more important, followed by yet another phase, the most recent phase, when LSW again increased in importance. The differences between the two T - S diagrams, for the western Gulf versus the entire northern Gulf, show that the waters in the eastern Gulf are younger in the sense that they comprise more recently entered deep and bottom waters that have yet to completely mix with intermediate waters, and that they are somewhat isolated from the western Gulf with which they have not yet mixed. We assume that eventually, much or most of those waters will enter the residual circulation that will bring them to the western Gulf, although some may recirculate inside Georges Basin and exit back out of the Gulf through the Northeast Channel (e.g., Pettigrew et al., 2008; Smith et al., 2012).

² These are average values. Various values of temperature and salinity characterizing LSW and WSW have been reported in the literature, and in addition, the T - S properties of both LSW and WSW will change some with season, and between and among years. Generally, WSW is warmer, saltier and less dense than LSW. We have further analyzed archived CTD data (from the World Ocean Database [<http://www.nodc.noaa.gov>]) along two on-shelf to off-shelf transects, one to the east off Labrador (June 1997) and the other to the south off Georges Bank (August 1997), presented in Appendix Fig. A1. These data show still higher salinities than those selected by Mountain or other authors in their definitions of LSW and WSW (e.g., ca. 34.8‰ at 200 m depth in the Labrador Sea, and 36.5‰ at 200 m for WSW off Georges Bank) and colder LSW temperatures (e.g., ≤ 3.0 °C at 200 m). These source water properties become modified in transit across the shelf to the Gulf of Maine and Georges Bank.

Our analysis of water masses on Georges Bank in 2007 is given in Fig. 16 for the entire Bank, and for just those stations on the Northern Flank. The T - S properties of the Northern Flank are similar to those of the western Gulf of Maine in Fig. 15, indicating that western Gulf of Maine water is the proximal source of waters to the Bank as has been shown by numerical models (Lynch et al., 1996; Hu et al., 2008). While similar to Gulf of Maine waters, the T - S properties of waters on the Northern Flank of Georges Bank, however, are nonetheless significantly different in that the intermediate water–bottom water mixing line does not exhibit a change in slope producing an upward bend, as is the case in the Gulf of Maine; rather, it dips slightly, and is directed more toward LSW as the bottom source waters. We therefore hypothesize that the deep and bottom waters in the Gulf of Maine, characterized during these cruises by the change in slope of the mixing line, have not yet been advected to Georges Bank, and as a result the Northern Flank was still under the influence of the earlier water mass mixture in the Gulf that had more LSW as its deep and bottom water source.

The individual dots visible in the T - S diagrams in the center panels in Fig. 16 are stations on the shallow, tidally well mixed crest of Georges Bank, which exhibit very nearly the same temperatures and salinities top to bottom, and hence plot together in a tight cluster, almost as a single point. The T - S diagram for the Bank as a whole shows that it is a mixture of waters of a warmer

and saltier origin, in addition to waters from the Gulf of Maine. The whole Bank plot for June–July 2007 shows clearly two stations that exhibit all four water masses we are discussing: Gulf of Maine Surface Water and Intermediate Water, plus, rather than a mixture of the two deep slope waters WSW and LSW forming a single Bottom Water mass, both slope water masses are identifiable. In addition, there is evidence of a fifth water mass, Gulf Stream Water, with characteristic properties of 16° and 36‰ , which probably represents the remains of a Warm Core Gulf Stream Ring that impinged onto the Southern Flank.

Stations on the Northeast Peak of Georges Bank are plotted in Fig. 17 for all cruises. Many of those stations exhibit the two deep slope water masses, WSW and LSW, at the deeper stations on and near the 200 m isobath (identified as those T - S lines that extend farthest to the lower right in the plot, indicating denser bottom waters). Also given in Fig. 17 is an example profile for one of those stations (Sta. 43; May–June 2010). It shows the four main water masses: a surface water mass of relatively warm and fresh waters overlying an intermediate water layer of relatively cold temperatures (ca. 7°C), which are the coldest waters in the profile, and which are centered at about 40 m. Beneath the coldest intermediate water layer, temperatures increase with depth, as does salinity, reaching highest salinities (ca. 35.7‰) and warmest temperatures (ca. 13.8°C) between 100 m and 120 m, representing remnants of WSW source waters. Below the WSW layer and all the

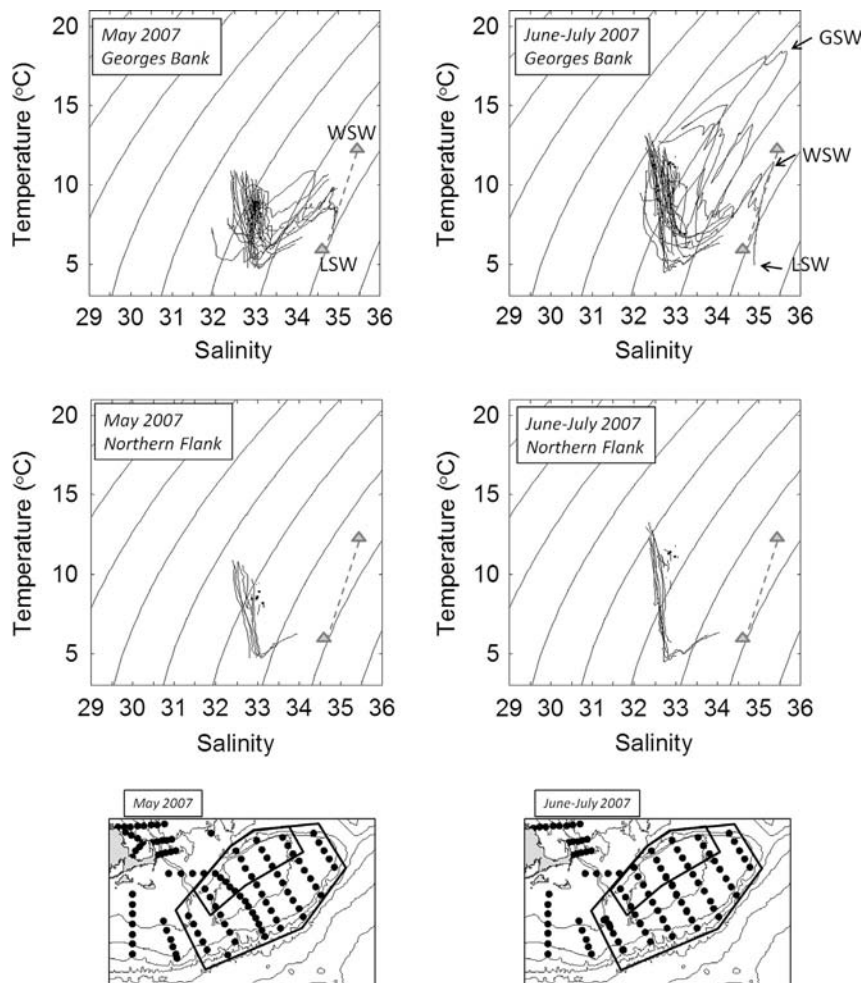


Fig. 16. Temperature–salinity diagrams for stations sampled on Georges Bank on both cruises in 2007, with characteristic properties of Warm Slope Water (WSW) and Labrador Slope Water (LSW) given as gray triangles with a dashed mixing line between them. The top panels include all stations on the bank, whereas the middle panels include only stations on the Northern Flank, as shown on the station maps in the bottom two panels. The evidence for three source water masses, Gulf Stream Water (GSW), WSW and LSW on the Bank is indicated in the top right panel.

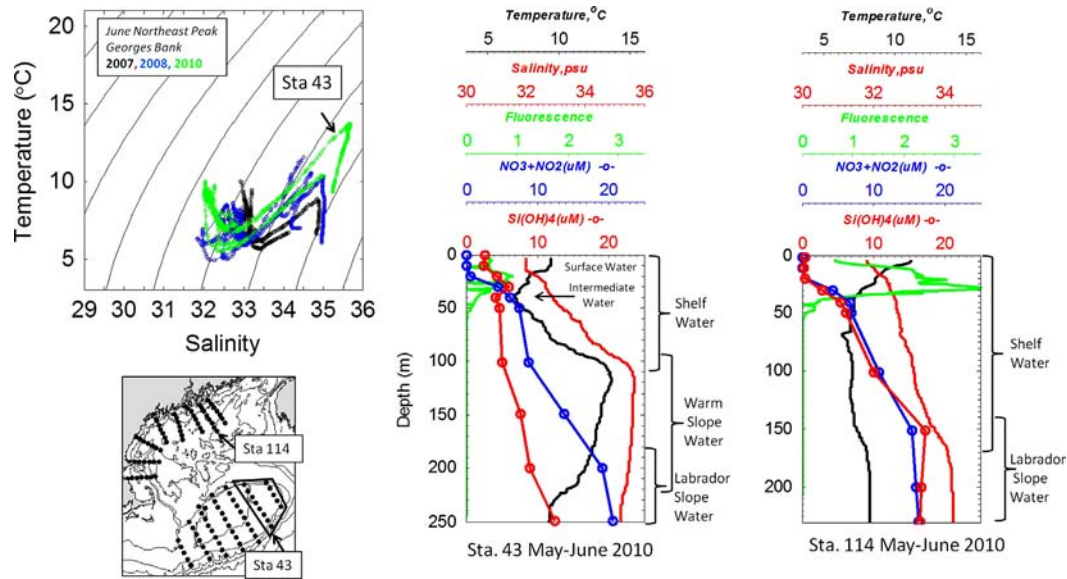


Fig. 17. Top left: Temperature–salinity diagram for stations on the Northeast Peak of Georges Bank during the June–July cruises in 2007, 2008 and 2010; WSW and LSW characteristic properties are given as gray triangles with a dashed mixing line between them. Station No. 43 sampled during the May–June 2010 cruise is identified in the T–S diagram (green). Stations 43 and Station 114, in the Gulf of Maine (see map in lower left), are plotted as profiles of temperature, salinity, nitrate, silicate and in situ chlorophyll fluorescence (relative units). Notice that the salinity scales are different. The different water masses identifiable in the profiles are indicated, with overlapping vertical distributions indicating mixing with one another.

way to the bottom, temperatures drop as do salinities; at about 200 m a volume of modified Labrador Slope Water is more clearly evident, with bottom temperatures about 9.5 °C and salinities about 35.3‰. Modified remnants of the two deep water masses, of WSW and LSW origins, are identifiable and have not yet completely mixed with one another. Similar stations, exhibiting the four water mass layers, are evident in the T–S diagram, with shapes analogous to a backward “N”, versus the more traditional “V” shape T–S signature characteristic of inner Gulf of Maine water masses in summer.

The nutrient profiles in Fig. 17 for the May–June cruise in 2010, in Jordan Basin and on the Southern Flank of Georges Bank, both show a curious “bite”, or removal that appears to have been taken out of the nitrate and silicate profiles between depths of 50 m and 100 or 150 m, giving what would appear to be anomalously lower concentrations at intermediate depths. For example, at Station 43 on Georges Bank the profiles of nitrate and silicate show relatively low concentrations at 100 m of ca. 5–6 µM silicate and 7–8 µM nitrate; not only are these relatively low concentrations, but the difference between them, the nitrate residual, is less than at the deeper depths; those deeper depths, on the other hand, reflect the higher nitrate residual of both slope water types, LSW and WSW. These low nutrient concentrations at intermediate depths likely reflect an influx of, and mixing with, cold, low salinity shelf waters that extend from the surface to deeper than 100 m.

Similar deep-water nutrient profiles with low nutrient concentrations at intermediate depths corresponding to low salinity shelf waters, were also observed at the deeper Gulf of Maine stations during the May 2010 cruise, as well as during the subsequent May–June cruise, which we discuss below, but they were less obvious during the latter two cruises. An example is given for a station sampled in Jordan Basin (Sta. 114; Fig. 17), which, like Station 43 on Georges Bank, also exhibits the apparent “bite” feature in the profiles that characterizes cold, low-salinity, low-nutrient shelf waters, which in this case extend to 150 m. Below 150 m the temperature and salinity both increase, indicating the presence of slope waters on the bottom; however, the temperature of the bottom waters is quite cold, about 8.5 °C and the salinities

quite fresh, about 34.2‰, indicating a bottom water mixture dominated by Labrador Slope Water. The nitrate and silicate concentrations in these bottom waters are about equal to one another; we suggest that at this station, and in much of the deeper waters of the eastern Gulf during this cruise, these water properties are the result of shelf waters having mixed with bottom waters to depths well below 150 m. The presence of cold, low salinity shelf waters in the Jordan Basin area of the Gulf of Maine is also revealed in mooring data collected in Jordan Basin (see: www.gyre.umeoce.edu; N.R. Pettigrew, unpublished) as presented by Li et al. (2014) in their Figs. 8 and 9, showing colder temperatures and low salinities from the surface to deeper than 100 m for the first half of 2010 and extending to deeper than 150 m in June.

The T–S diagrams for the 2008 cruises are similar to those in 2007 for the northern Gulf of Maine stations and stations on Georges Bank (not shown), with the exception that the warmer surface temperatures noted in 2008 (e.g., Fig. 4) are reflected in the slightly warmer, and therefore slightly more saline, intermediate water temperature minima.

The T–S diagrams for the four 2010 cruises (Fig. 18) are generally similar to those of 2007 for both the Gulf of Maine and Georges Bank, with their characteristic “V” shapes. The top row of T–S diagrams for the northern Gulf in 2010 show the seasonal warming of the upper water column, but also a clearer separation of waters into two sets, or groupings, of water masses, each with different surface salinities, intermediate water temperature minima, and slopes of bottom water–intermediate water mixing lines, which reflect differences between the eastern and western Gulf waters, as just discussed for 2007. Erosion of the MIW layer with time from the second to the fourth cruises is evident, with the temperature minimum defining the core of MIW all but absent during the last cruise. For example, by May–June of 2010, there are clearly visible two, and perhaps three, separate sets of water masses that can be identified based on a clustering of lines. On the next two cruises, in June–July and August of 2010, only two remain prominent. Both sets of water masses appear to have been mixed with the same deep slope water mixture, however, in that the slopes of the bottom water–intermediate water mixing lines

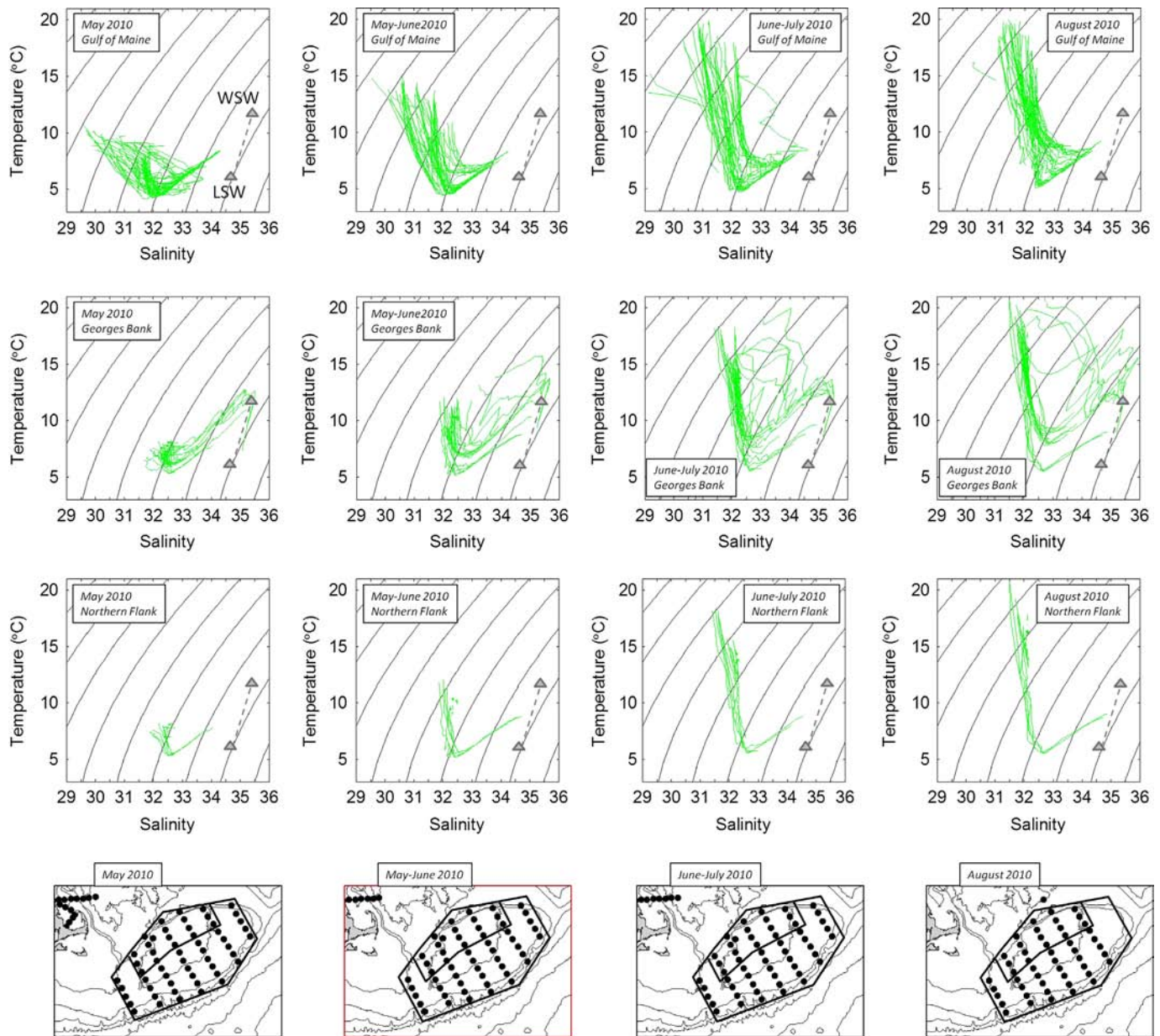


Fig. 18. Temperature–salinity diagrams for stations sampled in the Gulf of Maine and on Georges Bank on each of the four cruises in 2010; WSW and LSW characteristic properties are given as gray triangles with a dashed mixing line between them. The top panels include all stations sampled in the Northern Gulf, as shown in the station map in Fig. 3. The second row of panels includes all stations sampled on Georges Bank, and the third row includes only stations sampled on the Northern Flank, as shown in the station maps at the bottom.

intersect, or converge, at a common point at the upper right. Two sets of water masses – two “V” like patterns – are apparent on Georges Bank as well, but only on the Bank as a whole, and are clearly identifiable only after the first cruise; Northern Flank waters show only western Gulf of Maine waters. The mixing lines for the two sets of deep water masses on the Bank do not converge on a common point at the deepest depths, however, which indicates different bottom source waters for each – more WSW for the warmer set, and more LSW for cooler set. In addition, there are significant volumes of warm and salty Gulf Stream Water and perhaps surface slope waters on the Bank on all four of these 2010 cruises.

While the overall character of water masses in the Gulf of Maine in 2010 were similar to earlier years, there were important differences evident when compared with 2007 and 2008 (Figs. 19 and 20); moreover, the northern Gulf exhibited a water

mass change during the summer of 2010, evidence of which we captured in our four cruises that year (Fig. 21).

As shown by McGillicuddy et al. (2011) the water masses in the Gulf of Maine in late spring–early summer of 2010 were warmer, saltier, lower in nutrients and supported a reduced population of *A. fundyense* compared with 2008. As can be seen in Fig. 19, where we overlay and compare the *T–S* diagrams of northern Gulf of Maine stations (eastern and western Gulf) sampled on our May–June cruises in 2007, 2008 and 2010, the 2010 water properties stand out as quite different. The minimum temperature of the intermediate water layer in 2010 was warmer than that in either 2007 or 2008 (about 4.5 °C versus about 3.6 °C in 2007 and 4 °C in 2008); the salinity of the core of the intermediate water in 2010 was 32.2‰, the same as 2007, but fresher than 2008, which was > 32.5‰. Also evident are the differences in surface water temperatures among the three years, with 2010

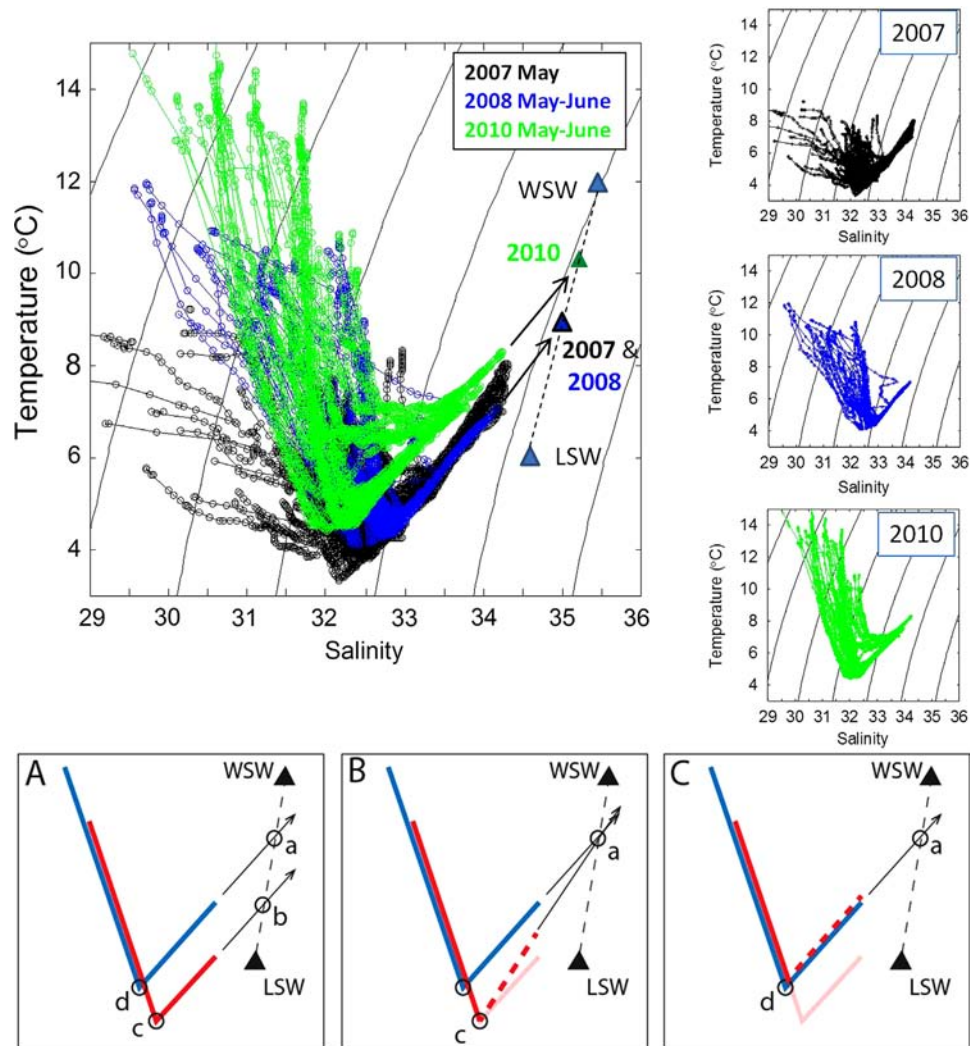


Fig. 19. Temperature–salinity diagrams for all Gulf of Maine stations sampled for the cruises indicated in 2007, 2008 and 2010, plotted together on the left, and individually on the right. Characteristic T – S values for Warm Slope Water (WSW; 11° , 35‰) and Labrador Slope water (LSW; 6.5° , 34.5‰) are given, as well as a mixing line between them, and the positions of mixing end members for 2010, and for both 2007 and 2008. The bottom panels illustrate the probable mixing that produced the 2010 deep water masses, as explained in the text.

being the warmest, as we discussed earlier. But, most significant is the difference in the intermediate water–bottom water mixing line in 2010 as compared with 2007 and 2008. That mixing line has an extrapolated intercept with bottom source water T – S properties that reflect a greater importance of WSW than is the case for 2008; the 2008 mixing line shows evidence of more LSW than WSW. The T – S plot for the mid to late May cruise of 2007 showed evidence of earlier mixing (earlier in the spring) of LSW with intermediate waters in the western Gulf, as indicated by the break in slope of that mixing line (as discussed earlier, but which is obscured in these plots; see Fig. 15). Based solely on these apparent deep source water end members, we might conclude that nutrient concentrations should be higher in May–June of 2010 than the corresponding cruise in 2008, but they are actually quite similar to one another. During the first cruises in 2008 (28 April–5 May) and 2010 (1–10 May), the nitrate concentrations were lower in 2010, as discussed in McGillicuddy et al. (2011). A month later, on the May–June 2010 cruises, nitrate concentrations are nearly equal to those for the same period in 2008, as shown in Fig. 20 for all depths sampled in May–June each year. The lowest deep-water nitrate concentrations for the late May early June period were in 2007, which likely reflect the influence of earlier mixing with a

greater proportion of low-nutrient LSW, as shown in the T – S diagrams in Fig. 15. If there were more nutrient-rich WSW source waters mixing with intermediate waters in May–June of 2010 (followed by mixing with surface waters) as appears in the T – S diagram in Fig. 19, then there would be higher overall nutrient concentrations throughout the water column, but that is not the case, which means that the situation is more complicated. The similar nutrient concentrations in May–June 2010 and May–June 2008, despite deep water source end members that were so different from one another, can only be explained by an influx of low-nutrient shelf waters at shallow and intermediate water depths, as diagrammed schematically in Fig. 19. Therefore, the deep water mass in 2010 was not just the result of mixing with WSW, which would have changed the slope of the intermediate water–bottom water mixing line, as shown in Panel B of Fig. 19. Rather, an additional mixture of shelf water that extends to the depths of the cold intermediate water layer (between 50 and 150 m) is required to explain the resulting position of the deep mixing line, which has lower salinities but the same slope as 2008, as shown in panel C.

This flux of shelf water from the Nova Scotian Shelf was also evident in the profile shown in Fig. 17. The deeper stations over Jordan Basin in the eastern Gulf of Maine in 2010 showed clear

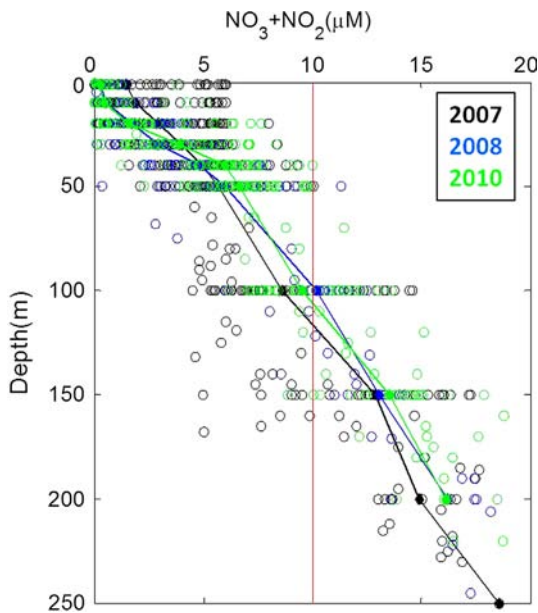


Fig. 20. Vertical profile of nitrate (nitrate plus nitrite) concentrations for all northern Gulf of Maine stations (eastern and western Gulf) for the mid to late May 2007 cruise (17–31 May), the 28 May–4 June 2008 cruise and the 26 May–4 June cruise in 2010. Averages were computed at each standard depth (1, 10, 20, 30, 40, 50, 100, 150, 200 and 250 m) and lines drawn connecting them.

evidence of relatively cold, low-salinity and low-nutrient water from the surface to about 150 m.

As just explained, it is clear that the makeup of water masses in the Gulf of Maine was different early in the season in 2010, with more shelf waters present early in the year, as compared with 2007 and 2008. But that difference was relatively short lived, as there was an influx into the Gulf of Maine of higher salinity, nutrient rich water during the last two cruises in 2010 (Fig. 21).

The T - S diagram in Fig. 21 includes all the northern Gulf of Maine stations sampled on the four cruises in 2010. Those plots illustrate nicely a couple points brought out earlier: first, the warming over time of surface waters, those waters shallower than, but also including, the intermediate water (MIW) depths, is clearly evident. Second, the salinity of the temperature minimum, the core of the intermediate water layer, shifts accordingly to higher salinities, as summer progresses and those subsurface waters warm over time. Also apparent in that plot are much fresher surface waters sampled on the first cruise, in May of 2010, which are gone by the second and third cruises; no doubt those fresher waters are from the spring freshet. Their disappearance is due to those coastal waters being advected out of the sampling domain in the northern Gulf as part of the residual clockwise circulation which brings those waters to the southwest, with some leaving the Gulf around Cape Cod, and some making it to Georges Bank. Somewhat hidden in those data, however, is the increase over time in the relative proportion of relatively warm, high salinity and nutrient-rich waters, as the intermediate water–bottom water mixing line can be seen extending further to the upper right in the T - S diagram with each successive cruise date, reflecting larger contributions of source waters that are closer to WSW. Thus, these T - S diagrams indicate progressively more warm, salty and nutrient-rich waters are entering and mixing with intermediate waters, and eventually with surface water. That interpretation is consistent with the seasonal increase in both nitrate concentrations and salinity in the northern Gulf

as shown for profiles taken at the same stations as in the T - S diagram (Fig. 21).

The above interpretation of water mass fluxes in 2010 is consistent with our observations of the hydrographic and nutrient fields. As can be seen in Fig. 21, the deep and intermediate depth salinities increased by more than 0.5‰ over the period of the four cruises (early May to early August), and nitrate concentrations increased by about 4 μM between the first two and last two cruises. That increase in salinity is also evident in the surface salinity plots in Fig. 5 and the 0–40 m average nitrate concentrations in Fig. 9. Also, the greater proportion of shelf waters early in 2010 and their lower nutrient concentrations are consistent with vertical profiles of T , S and nutrients in the eastern Gulf, an example of which is given in Fig. 17. They are also consistent with the lower concentrations of nitrate and phosphate observed in the upper water column, the top 40 m, of the northern Gulf and Georges Bank (Figs. 9 and 11), and perhaps also with elevated silicate in the latter half of 2010 in both areas (silicate recycling complicated this interpretation, however). The reduced nutrient loads early in 2010 led to lower phytoplankton production in the Gulf and on Georges Bank that year, as indicated by chlorophyll concentrations, and a reduced *A. fundyense* bloom in both areas. The greater shelf water flux in 2010 would also result in lower nitrate residuals, thus impeding the initiation of *A. fundyense* growth, and would result in lower rates of subsequent ammonium recycling, because of the overall reduction in production plankton biomass to be recycled. Later in 2010, when the deep and bottom water mass changed to one with a greater volume of nutrient-rich WSW, we observed a short-lived pulse in *A. fundyense* numbers (Fig. 7).

4. Conclusions

The observations reported here allow the interpretation of how variability in nutrient fields influence *A. fundyense* blooms in these waters, in particular: how the nutrient field limits, or determines, the areal distributions of annual *A. fundyense* blooms in the Gulf of Maine and on Georges Bank; how nutrients fields influence the timing of seasonal bloom initiation and decline in both regions; and how nutrients as modified by water mass dynamics may be at the heart of interannual variability in the overall size and duration of blooms. We present evidence of both temporal (interannual and within seasons) and spatial variability of water properties in the Gulf of Maine and on Georges Bank, which directly influence the nutrient fields, and indirectly influence distributions and abundances of *A. fundyense*, and phytoplankton in general. Nutrient loads differ among three deep and intermediate water mass types (LSW, WSW and shelf water), and spatial and temporal changes and variability in the relative proportions of those water masses, inferred from their characteristic water properties (temperature–salinity relationships), help interpret distributions and abundances of *A. fundyense*. Deep water mixing lines, between intermediate-depth waters and bottom slope waters, showed within-year and interannual variability in the relative importance of the three water mass types. Nutrient loads and abundances of *A. fundyense* were lowest in early 2010, as compared with 2007 and 2008, most likely the result of a greater proportion of low-nutrient shelf waters in the Gulf region in May and early June. Later in the summer of 2010, an influx of deep waters into the Gulf of WSW origin produced an increase in the nutrient concentrations, and may have stimulated a later growth response of *A. fundyense*. In general, we conclude that following initial fluxes of nitrate into surface waters, which vary in their nitrate residuals depending on source water proportions, and which may be important in the initiation of *A. fundyense* blooms, the populations are later

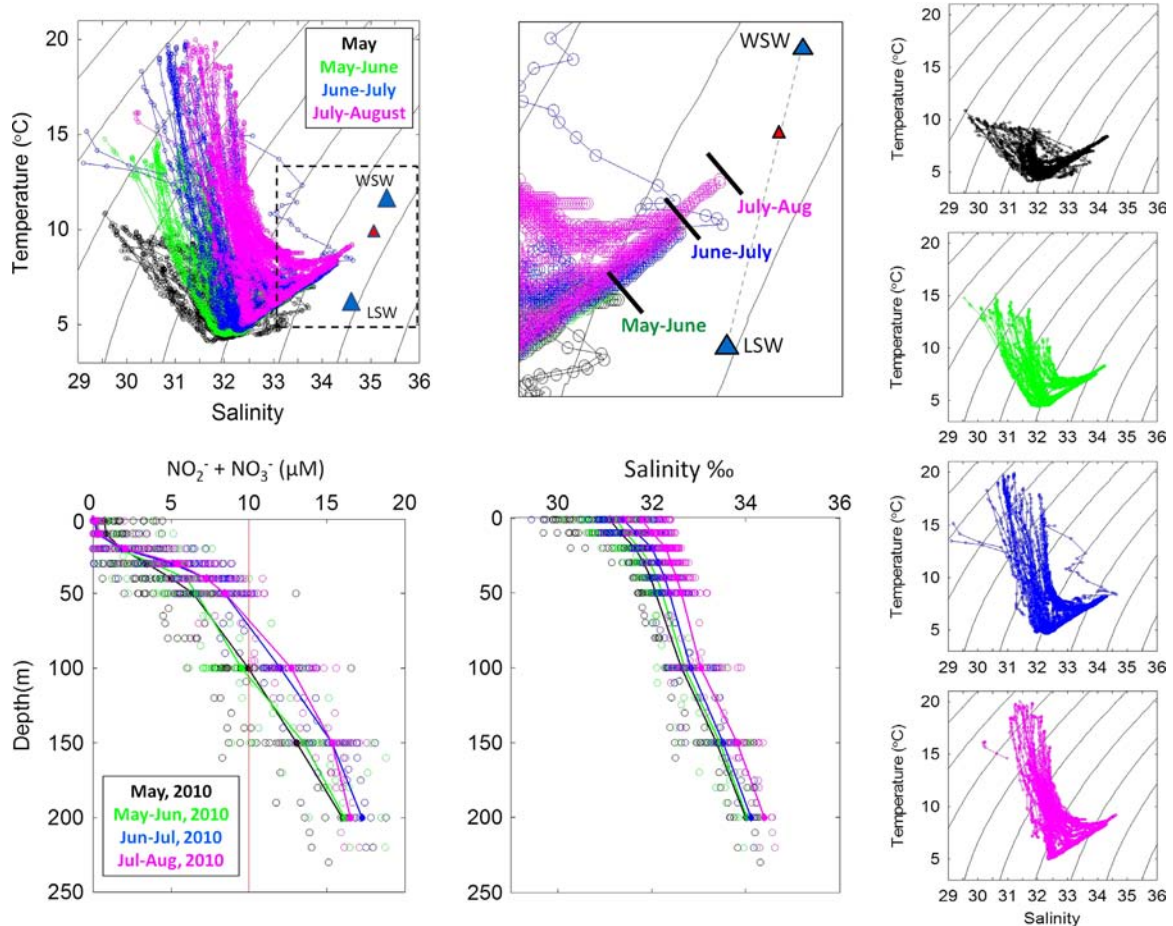


Fig. 21. Temperature–salinity diagram of all Gulf of Maine stations sampled on the four cruises in 2010, as shown in the station maps in Fig. 3 (August Bay of Fundy stations excluded), given together (top left and center panels) and individually (right panels), illustrating the seasonal evolution of water properties. Characteristic T – S values for Warm Slope Water (WSW; 11° , 35‰) and Labrador Slope water (LSW; 6.5° , 34.5‰) are given, as well as a mixing line between them. The red triangle indicates the probable T – S source of the bottom mixing end member. An enlargement of the dashed box in the upper left panel is given, showing the end points of the intermediate water–bottom water mixing line. Solid black lines are drawn approximating the end points for the May–June, June–July and July–August cruises in 2010. Bottom panels are vertical profiles of nitrate (nitrate plus nitrite) concentrations and salinities; sample data are color coded as are lines drawn connecting the average values at each standard depth (1, 10, 20, 30, 40, 50, 100, 150, and 200 m).

sustained by recycled ammonium. We also observed phosphate concentrations of less than $0.1 \mu\text{M}$ on Georges Bank suggests phosphate limitation of phytoplankton production, which may allow for patches of recycled ammonium to accumulate. We suggest that *A. fundyense* may have a low phosphate requirement, allowing populations on the Bank to be sustained by ammonium, or that *A. fundyense* relies on dissolved organic phosphorus; the importance of dissolved organic phosphorus in the initiation and maintenance of *A. fundyense* blooms in the GOM and Georges Bank is an area for further research.

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Appendix A

See Fig. A1.

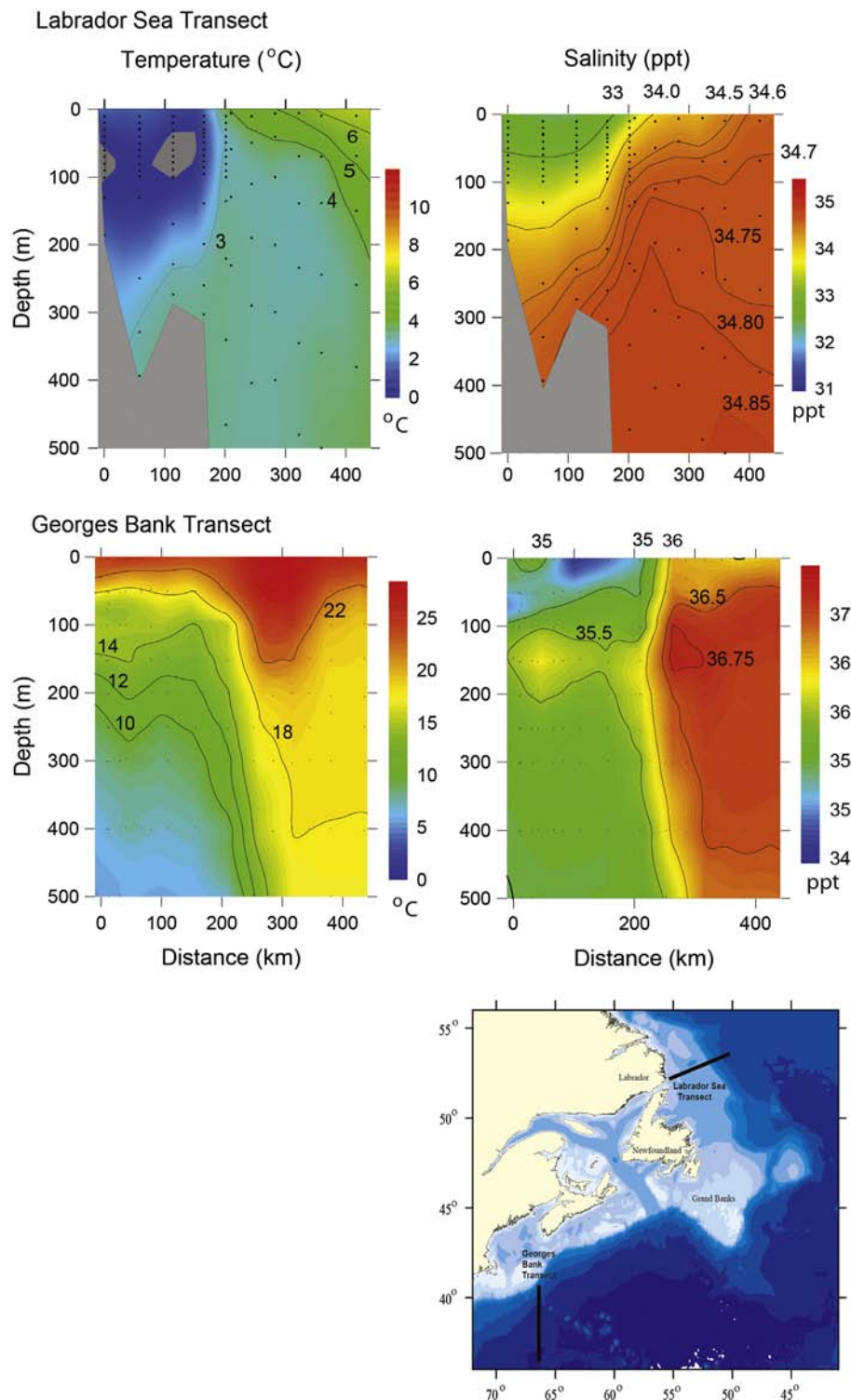


Fig. A1. Vertical cross sections of temperature and salinity for the top 500 m, in the Labrador Sea and south of Georges Bank; approximate transect locations are shown in the map. The Labrador Sea transect was sampled in June, 1997; the Georges Bank transect was sampled in August, 1997. Distances along the transects are given in km. Data are from the World Ocean Database; <http://www.nodc.noaa.gov>.

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