Summer 8-20-2020

Distributions and Abundances of the Red Tide Dinoflagellate Alexandrium catenella in the Eastern Gulf of Maine and Bay of Fundy in Relation to Diatoms in June, July and August of 2019

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DISTRIBUTIONS AND ABUNDANCES OF THE RED TIDE DINOFLAGELLATE *ALEXANDRIUM CATENELLA* IN THE EASTERN GULF OF MAINE AND BAY OF FUNDY IN RELATION TO DIATOMS IN JUNE, JULY AND AUGUST OF 2019

By

Kimberly D'Adamo

B.S., Sacred Heart University, 2017

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Marine Biology)

The Graduate School

The University of Maine

August 2020

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Thesis Advisor: Dr. David W. Townsend

An Abstract of the Thesis Presented
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A series of three oceanographic survey cruises were conducted in June, July, and August of 2019 in the northeastern Gulf of Maine and Bay of Fundy. Surface water samples were collected and analyzed for enumerations of cell densities of the dinoflagellate *Alexandrium catenella* in relation to cell densities of diatoms. Hydrographic profiles of temperature, salinity, and nutrients (silicate and nitrate) were also made at each station. Data were analyzed to determine if there was any statistically significant evidence of allelopathic interference imparted by diatoms that impede *A. catenella*. *A. catenella* cells were most abundant in June, reaching 6,195 cells per liter at the surface (1 m), with the highest densities occurring at offshore stations. Diatoms were also most abundant in June (681,667 cells/L), reaching highest cell densities at inshore stations, spatially separated from *A. catenella* maximal densities, which suggested an allelopathic inhibition of *A. catenella* by diatoms, as had been suggested by earlier workers; however, there was no statistically significant inverse relationship

(according to Pearson correlation analysis; r=-0.42, P=0.131). Distributions of *A. catenella* and diatoms were similar to one another in July, with the highest densities occurring at shallower inshore stations (3,378 *A. catenella* cells/L and 108,333 diatom cells/L). The August survey cruise was limited in coverage and occupied fewer stations. *A. catenella* cell densities were highest in the interior Bay of Fundy in August (867 cells/L) while diatoms were more abundant in shallower, coastal waters off of Maine, and Nova Scotia (66,111 cells/L). The highest surface cell densities of both *A. catenella* and diatoms occurred in waters low in both nitrate and silicate in all three months, which is consistent with previous observations.

The dominant diatom genera included (in order): a) in June: *Thalassiosira, Chaetoceros, Cylindrotheca, Pseudonitzschia, Thalassionema,* and *Rhizosolenia;* b) in July: *Chaetoceros, Thalassiosira, Cylindrotheca, Pseudonitzschia, Rhizosolenia, Guinardia, Thalassionema;* and c) in August: *Skeletonema, Chaetoceros, Thalassiosira, Cylindrotheca, Pseudonitzschia, Guinardia***,** *Cylindrotheca,* and *Achnanthes.*

Pearson correlation analyses also showed that there were no statistically significant correlations between either *A. catenella* or diatom cell densities and surface concentrations of the nutrient silicate; however, in June, *A. catenella* did show a statistically significant inverse correlation with nitrate (P=0.0187).

Overall there was a seasonal decline from June to August, which contrasts with earlier reports that showed seasonal increases from June to August in the NE Gulf of Maine and Bay of Fundy. In June, there was a positive correlation between A. catenella

and salinity, which corresponded with the time of greatest A. catenella densities offshore ($r=0.44$; $p= 0.003$). In July, A. catenella were significantly inversely correlated with temperature where cells are usually most abundant in the colder waters of the Eastern Maine Coastal Current ($r=0.32$; $p=0.036$). August had fewer stations making it difficult to draw conclusions. Overall the data did not support the original hypothesis of allelopathy, as there was no statistically significant Pearson correlation between diatoms and A. catenella for any of the three summer surveys.

ACKNOWLEDGEMENTS

I want to thank Dr. David Townsend for choosing me to work under his wing and funding my efforts in pursuing a Master's Degree. He believed in me when I did not believe in myself and always encouraged me to do my best. Not only does he have extensive knowledge in numerous areas, but he is always willing to share what he knows. He also has an inspiring passion and hunger to learn and discover continuously. I am thankful for the opportunity he presented me to learn about topics I never heard of and experience new things along the way.

I would also like to give a special thanks to Maura Thomas. She taught me how to conduct lab work, use MATLAB, be efficient, and be confident in doing things on my own. She always had time to help me and always checked on me. I would also like to thank Hsiao-Yun Chang for all the statistics advice and assistance; she always went above and beyond to help, even remotely. Thank you to my committee members: Dr. Lee Karp-Boss, for offering your knowledge, especially with identifying species and Dr. Jeffrey Runge for your insightful comments and thoughts.

I want to give a special thanks to Drajad Seto for always offering wisdom, knowledge, advice and friendship along with Faith Hoyle, who would always cheerfully offer information on microscope identification or phytoplankton species. I would also like to thank Kyle Capistrant-Fossa, who would always lend a helping hand whenever he could and never stopped trying to keep me motivated.

Thank you to Bruce Keafer, the cruise chief scientist, and the captain and crew of the *R/V Connecticut* for all their hard work and support at sea, especially when I needed them most.

Very special thanks to my friends, Brian, Dr. Mark Beekey and my family, for supporting me during my pursuit of a Master's Degree.

I dedicate this work to my parents, who always encouraged my expansion of knowledge through education and encouraged me to always give it my best.

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I. INTRODUCTION

I. 1. Background

The dinoflagellate *Alexandrium catenella,* formerly known as *Alexandrium fundyense,* is responsible for annually recurrent outbreaks of Paralytic Shellfish Poisoning (PSP) in coastal waters of the Gulf of Maine (e.g., reviewed in Anderson et al., 2014, Anderson et al. 2012). The genus *Alexandrium* is thought to have as many as ten toxic species along with ten others whose toxicity is less well known (Balech, 1995). Species of *Alexandrium* are present throughout the world oceans, including sub-Artic, temperate, and tropical waters (Reyes-Vasquez et al. 1995; Wyatt and Jenkenson, 1997). Three toxic species have been identified from the Gulf of Maine: *A. tamarense, A. catenella, and A. ostenfeldii* (Anderson, 1997; Gribble et al., 2005). *A. ostenfeldii* is a larger cell than either *A. tamarense or A. catenella* (Tomas, 1997), and both *A. ostenfeldii* and *A. tamarense* are significantly less abundant than *A. catenella* (Anderson et al., 2005; Townsend et al., 2005).

Blooms of *A. catenella* in the Gulf of Maine usually occur between April and August, but have been reported to occur as late as October (e.g., Anderson et al. 2014a; McGillicuddy et al. 2014b). Bloom commencement is dependent on a supply of over-wintering benthic resting cysts and sufficient concentrations and/or flux rates of dissolved inorganic nitrogen, usually in the form of nitrate (Anderson 1997, Anderson et al. 2014b). Highest cell densities are often observed in summertime blooms in offshore waters away from coastal shellfish beds in surface waters with low or undetectable nitrate concentrations (Love et al. 2005, Poulton et al. 2005, McGillicuddy et al. 2014b, Townsend et al. 2001, 2005, 2014). Incidences of PSP in shellfish beds along the coasts

are thought to be the result of wind-driven transport of cells residing in more offshore waters (more below).

I. 2. Life Cycle

Dinoflagellates, in general, are larger than most other flagellate groups, ranging in size approximately from 20 to 50 μm; they may be thecate (armored) or athecate (unarmored), but all possess a pair of flagella enabling limited swimming ability and allowing for slight control over their vertical distributions in the water column. Not all dinoflagellates are strictly autotrophic; some species are heterotrophs, while others may be mixotrophs.

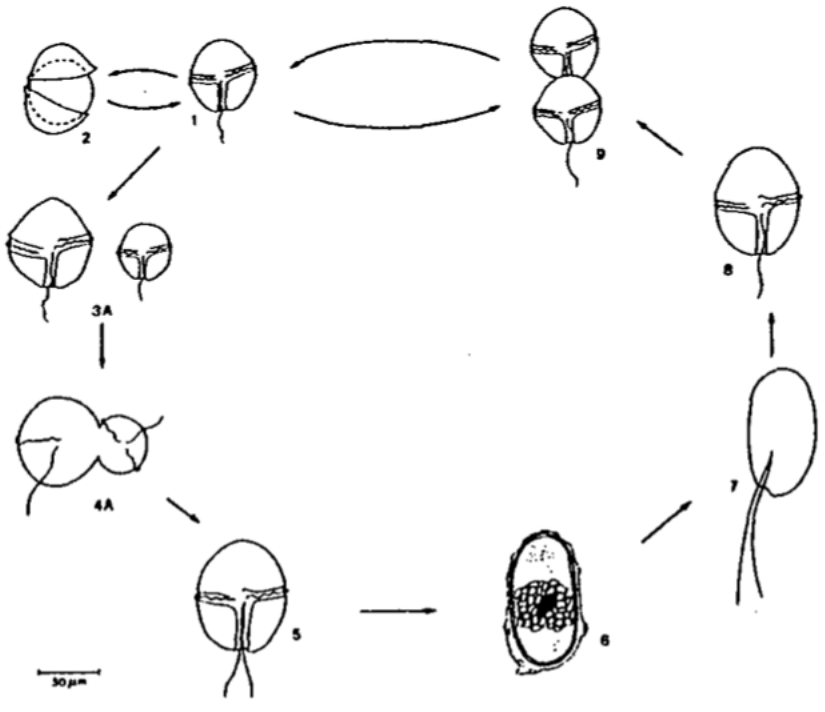

Figure 1. Life cycle diagram of *Alexandrium tamarense*. Staged are identified as follows (1) vegetative, motile cell;(2) temporary or pellicle cyst; (3) anisogamous "female' and "male" gametes; (4) fusing gametes; (5) swimming zygote or planozygote; (6). Resting cyst or hypnozygote; (7&8) motile, germinated cell or planomeiocyte; and (9) pair of vegetative cells following division. Adapted from Anderson et al. 1996.

The life cycle of *A. catenella* is complex and includes both vegetative and sexual phases of reproduction and a benthic resting stage (Fig. 1; Anderson et al. 1995). Laboratory culture experiments have suggested that sexual reproduction commences when nutrients (principally nitrate) become limiting to the vegetative cells that can create blooms. It has also been thought that sexual reproduction and gamete formation is stimulated when internal cellular nutrient pools become exhausted or are controlled by an endogenous clock (Anderson and Keafer 1987, Anderson 1998).

In sexual reproduction, gametes produced by vegetative cells, fuse to form planozygotes, which in turn divide to produce dormant resting cysts, or hypnozygotes, that settle to the bottom (Ishikawa et al. 2014). Here they may remain dormant for several years before beginning excystment to become vegetative cells, which are haploid, starting the cycle anew (Anderson 1998; Figueroa 2005 ; Figueroa et al., 2007). The planozygote stage is diploid, produced by gamete conjugation, or the fusing of gametes. Vegetative cell division occurs through desmoschisis, where each daughter cell maintains half the mother cell thecal plates.

Factors that initiate cyst germination are not well understood (Anderson, 1995). Temperature changes associated with seasonal warming in spring may trigger germination; however, it has also been found that germination can occur without temperature changes (Huber and Nipkow, 1922, 1923; Anderson and Wall, 1978; Anderson and Morel, 1979; von Stosch, 1973; Pfiester, 1975, 1977; Binder and Anderson, 1987; Anderson, 1980). Several laboratory studies have shown that cysts stored at cold temperatures may remain quiescent until exposed to warming temperatures

(Huber and Nipkow, 1922, 1923; Anderson and Wall, 1978; Anderson and Morel, 1979; von Stosch, 1973; Pfiester, 1975, 1977; Binder and Anderson, 1987; Anderson, 1980).

In the Gulf of Maine, *A. catenella* benthic resting cysts appear to excyst in late winter and early spring under conditions that are not fully understood (Anderson et al., 1998, 2014). Because these dinoflagellates possess a pair of flagella and are motile upon emergence from bottom sediments, the new vegetative cells swim to the surface layers. Under favorable conditions of light and nutrients, asexual reproduction, or simple cell division, may lead to blooms of high cell densities. After some period of asexual cell division, or upon exposure to some environmental cue, the cells form gametes that fuse to form planozygotes, which in turn produces resting cysts (Anderson et al. 1998).

Some dinoflagellate species experience a different resting stage involving vegetative cells turning into temporary, or pellicle, cysts during unfavorable conditions such as abrupt changes in temperature or salinity or mechanical shock. When favorable conditions resume, the temporary cysts return to the vegetative motile stage. Temporary cysts are commonly observed in the laboratory (Townsend, unpublished) but are also known to occur in nature (Anderson 1995). Blooms of *A. catenella* are not uniformly distributed throughout the region, however, but tend to be associated with regions of vertical mixing and vertical nutrient fluxes (Townsend et al., 2001; 2005). *A. catenella* blooms are seasonally recurrent. There is usually an absence of cells and PSP toxins during the winter months (Anderson 1997).

I. 3. Annual Blooms of *A. catenella* in the Gulf of Maine

While it is thought that increases in the frequency and severity of harmful algal blooms (including *A. catenella* blooms and resulting PSP events) may be a result of rising ocean temperatures and increasing coastal eutrophication (McCarthy et al. 2015), this scenario is less clear for Gulf of Maine waters. Following a dramatic "red tide" in the Gulf of Maine in 1972, after which monitoring programs for PSP in shellfish commenced, episodes of PSP and presumably *A. catenella* blooms, have occurred to some extent every year along the coasts of Maine, New Hampshire, and Massachusetts, from spring through late summer (Anderson 1997; Fig. 2). The timing of appearance of *A. catenella* (with interannually variable cell densities) tends to follow the spring diatom bloom, after silicate becomes limiting to diatoms, at which time species succession leads to a non-diatom phytoplankton assemblage dominated by flagellates and dinoflagellates, including *A. catenella* (Townsend et al., 2005; 2014; Gettings et al., 2014).

Blooms of *A. catenella* in the Gulf of Maine region are thought to be dependent on the availability and/or flux rates of nitrate, one of the dissolved inorganic forms of the limiting nutrient element nitrogen. However, Shankar et al. (2014) demonstrated with laboratory culture experiments that *A. catenella* grows well on ammonium and that they initially preferred ammonium over nitrate, in keeping with earlier studies, showing a phytoplankton preference for reduced nitrogenous nutrient ammonium over nitrate. While the initiation of *A. catenella* blooms in the Gulf of Maine is thought to be dependent on any remaining post-diatom bloom nitrate concentrations, especially deep-water nitrate injections into surface waters, which occur via tidal mixing, recycled ammonium may be

essential to sustained cell growth (McGillicuddy et al. 2014b, Townsend et al. 2014), as was shown for Georges Bank (Gettings et al., 2010; Shankar et al., 2014).

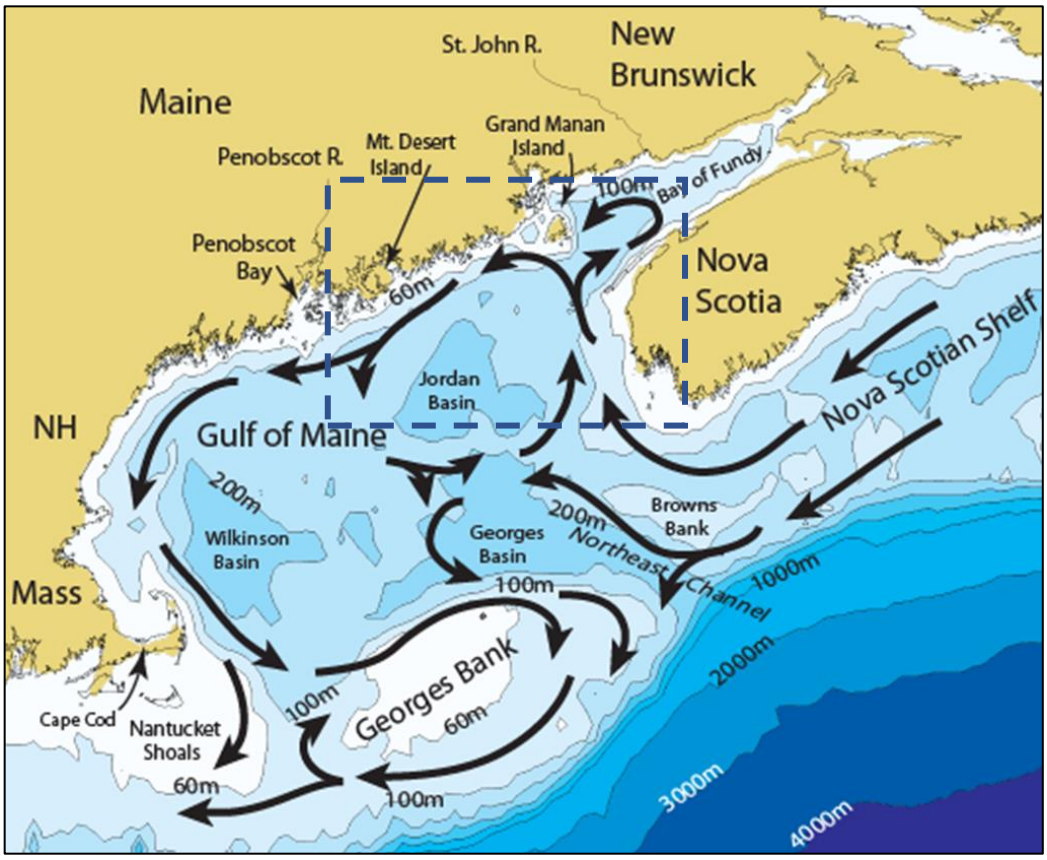

Figure 2. Near surface circulation in the Gulf of Maine, with bottom depths and features referred to in the text (after Pettigrew et al., 2005). Study region for this thesis is shown by the dashed box.

A series of focused field studies of *A. catenella* bloom dynamics in relation to the oceanography of the Gulf of Maine commenced in the late 1990s (see: Anderson et al., 2005 DSR II Special Volume). Results of these studies suggest that blooms occur naturally offshore (Townsend et al., 2001) in nutrient-rich waters of the Eastern Maine Coastal Current (EMCC; Townsend et al., 2006).

Benthic cyst beds in the Bay of Fundy, as well as cysts that remain suspended in the water column over the winter (Kirn et al., 2005), provide a source of cells that feed

the EMCC and produce a developing bloom that reaches high cell densities some distance downstream in waters offshore of Mt. Desert Island and beyond (Fig. 2). Depending on the highly variable path of the EMCC (Pettigrew et al., 2005), cells may be brought to the nearshore waters creating shellfish toxicity (PSP).

Blooms are not restricted to the eastern Gulf of Maine and Bay of Fundy, however. The infamous 1972 *A. catenella* bloom and widespread PSP event may have been initiated as just described, but its influence extended down the coast, causing shellfish toxicity in New Hampshire and Massachusetts (Shumway et al. 1988). Since the 1972 event, there have been shellfish harvesting closures because of PSP each year all along the northern New England-Gulf of Maine coastline, especially during the spring and summer months (reviewed in Anderson, 1997; Townsend et al., 2001; Anderson et al., 2005a, Keafer et al. 2005).

The circulation features of the Gulf of Maine and their variability are critical to the dynamics of annual *A. catenella* blooms; a generalized description of those circulations is given in Townsend et al. (2006). Surface currents in the Gulf of Maine can be viewed as beginning with a flow of shelf waters from the Nova Scotian shelf that enters the Gulf of Maine from the southern tip of Nova Scotia (Fig. 2). Responding to the earth's rotation (Coriolis Effect) that flow hugs the coast of SW Nova Scotia and is directed into the NE Gulf and Bay of Fundy, where tidal mixing and other physical processes create the Eastern Maine Coastal Current (EMCC), a current of tidally well-mixed and nutrient-rich water that flows down the Maine coast. The EMCC extends from the Bay of Fundy, centered approximately on the 100 m isobath, to off the mouth of Penobscot Bay, where it may be partially directed offshore and join a cyclonic flow

around the Jordan Basin. The vertically well-mixed waters of the EMCC tend to become more vertically stratified as they flow away from the more tidally energetic NE Gulf, which leads some distance downstream to a developing population of phytoplankton, including *A. catenella* (Townsend et al., 2001; 2005; 2014). A portion of that flow may continue down the Maine coast, transporting *A. catenella* cells to coastal areas of the western Gulf (Keafer et al., 2005).

Aretxabaleta et al. (2014) hypothesized that interannual variability in the magnitude of *A. catenella* blooms in the NE Gulf of Maine may be related to the degree of retention of Bay of Fundy blooms (fed by cyst beds in the Bay of Fundy; Martin and White, 1988; Anderson, 1996) located upstream of, and which feed, the EMCC. Depending on the hydrodynamics operating in the Bay of Fundy, which in turn are dependent on interannual variations in deep water intrusions into the Bay of Fundy, the gyre circulation in the mouth of the Bay may vary in its intensity. Aretxabaleta et al. (2014) posed what has become known as their "Leaky Gyre" hypothesis, where in some years, a well-developed gyre circulation will retain *A. catenella* cells in the Bay, whereas in other years the gyre is less well developed, *A. catenella* cells will leak from the Bay of Fundy into the EMCC, potentially leading to more intense *A. catenella* bloom in the Gulf of Maine.

This thesis is a result of survey work done in the Bay of Fundy and NE Gulf of Maine in the summer of 2019 aimed at testing aspects of the "Leaky Gyre" hypothesis, which provided an opportunity to examine more closely the development of the *A. catenella* bloom in those waters and its relationship to nutrient fields and diatom populations.

I. 4. Goals and Hypothesis

The overall goal of this research was to examine spatial and temporal patterns of major diatom taxa in relation to abundances and distributions of *A. catenella* in the northeastern Gulf of Maine and Bay of Fundy during the summer of 2019 and to relate each to the nutrient and hydrographic fields. The overall hypothesis was that diatoms and *A. catenella* would show an inverse relationship with one another, indicating an allelopathic interference imparted by diatoms, which impedes the growth of *A. catenella.* Results of studies conducted by Townsend et al. (2005; 2014) suggested that coastal waters high in silicate from freshwater sources tended to support post-spring diatom populations, which may inhibit the development of high cell densities of *Alexandrium* cells, constituting an allelopathic inhibition of *Alexandrium* by diatoms. Laboratory studies by Gettings (2010) support that phenomenon.

Specific goals were to investigate the following:

- Possible evidence of allelopathic interference between diatoms and *A. catenella*, as suggested by Townsend et al. (2005), whereby high cell densities of diatoms interfere with and impede the presence of *A. catenella*.
- Possible correlations among cell densities of diatoms and *A. catenella* in surface waters with chlorophyll fluorescence, temperature, salinity, and concentrations of the dissolved inorganic nutrients nitrate (NO_3^-) and silicate (silicic acid, or silicate, $Si(OH)_4$).

- The relative proportions of *A. catenella* life-history stages (planozygotes, vegetative cells, doublets, and gametes) at times and locations of high cell densities.
- The species composition (dominant genera) of diatoms at stations with high diatom cell densities.

II. MATERIALS AND METHODS

II. 1 Oceanographic Surveys

A series of three oceanographic survey cruises in the northeastern Gulf of Maine and Bay of Fundy was conducted in the summer of 2019 aboard the *R/V Connecticut*: 12-19 June, 9-11 July, and 10-12 August. The sampling stations for each cruise area are provided in Figure 3.

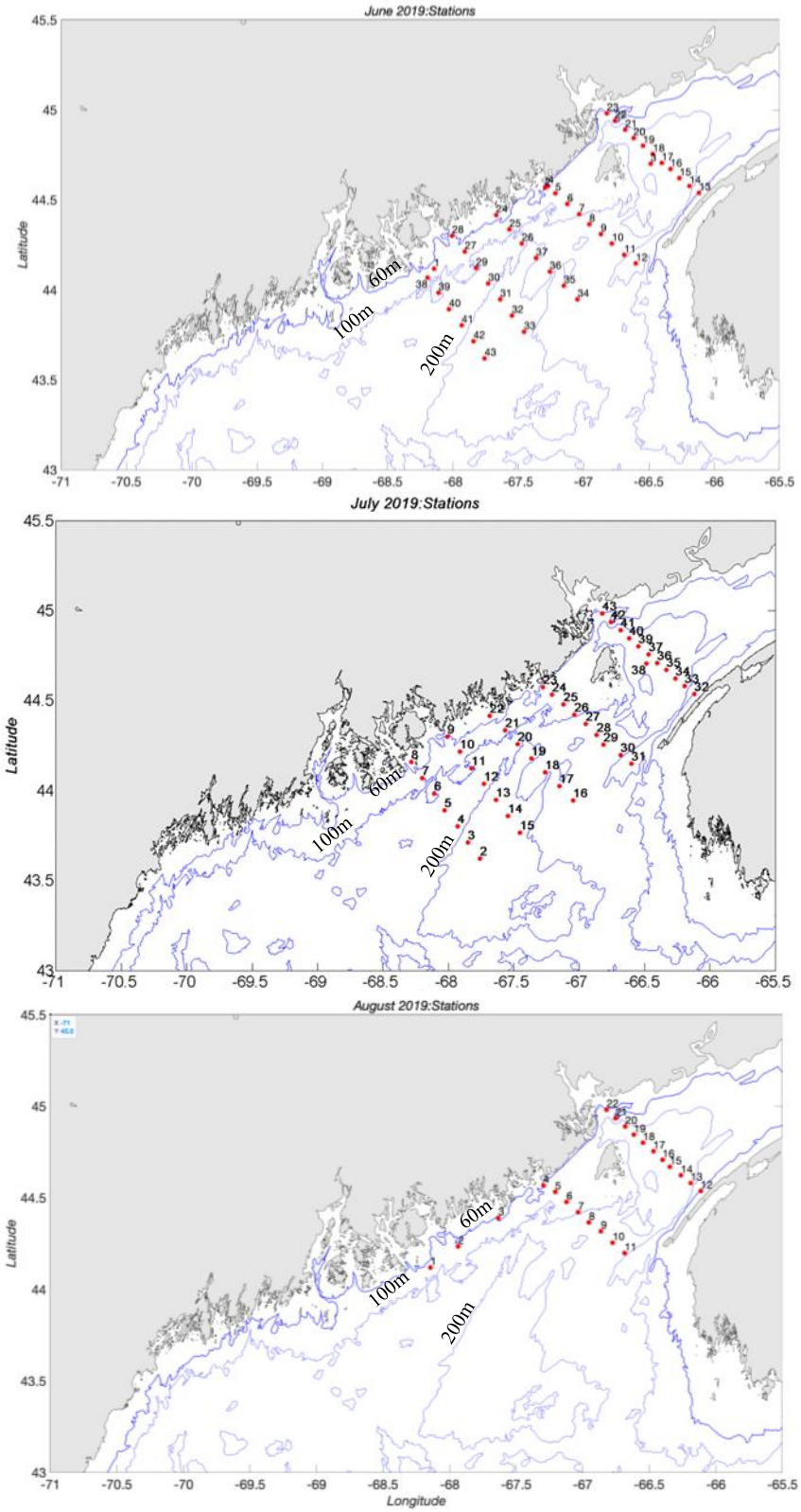

Figure 3. Station locations for the three survey cruises aboard the *R/V Connecticut* in summer, 2019: Top: 12-17 June; Middle: 9-11 July; Bottom: 10-12 August.

During each cruise, standard hydrocasts were made at each station using a SeaBird 911 CTD with a Wet Labs *in situ* fluorometer and SeaBird carousel water sampler equipped with 5-liter Niskin bottles. The CTD package was lowered to be within 5 meters of the bottom at all stations and water was collected during the up-cast. Water samples were collected for dissolved inorganic nutrient analyses at various depths between the surface and near-bottom, filtered through Millipore HA filters, and frozen at -18 °C to be analyzed for nitrate, analyzed here as the sum of nitrate (NO_3) and nitrite (NO_2), and silicate ($Si(OH)_4$) using an autoanalyzer and standard techniques as reported in Townsend et al. (2014).

Determinations of *A. catenella* cell densities in surface waters (1 m) for the same cruises were conducted by colleagues at Woods Hole Oceanographic Institution using a DNA probe.

II.2 Diatom Cell Densities

Water samples for the determination of total diatom cell densities were collected at the surface (1 m) using a 6-L Van Dorn bottle. The entire contents (6 L) were sieved through a 20 μm mesh sieve; the concentrate was transferred to 15 ml vials and preserved in a 5% formaldehyde seawater solution, bringing the final volume to approximately 10 ml. A total of 94 stations were sampled for the three cruises.

For microscopic enumerations, each sample vial was inverted several times to mix the sample thoroughly, and a 1 ml sub-sample was placed on a 1-ml gridded Sedgwick-Rafter counting cell and examined under a compound microscope at 100X magnification. The Sedgwick-Rafter cell was divided into 1000 grids (20 by 50). At least 100 diatom

cells were counted for each sample; usually, this total was met by counting a single row across the slide. Total diatom cell densities at the surface were computed for each sample (each station) and presented as cells/L.

II. 3 Diatom Genera

In addition to total diatom cell densities (at all stations), the dominant diatom genera were determined for select stations (the top nine stations for June and July and the top two stations for August with the highest total diatom cell densities) based on the previously described diatom cell counts. Identifications were based upon descriptions and keys in, Smith (1977), Gowen and Mulligan (1978), Tomas (1997), Horner (2002), Gladu et al. (2003), Kraberg et al. (2010) Westheide (2011). For each selected station, 1ml of a sample was placed in the gridded Sedgwick-Rafter cell. A random number generator was used to select random grids on the slide, and the genera of diatoms determined for at least 100 cells. If 100 cells were obtained within the first random grid, a second grid was also counted.

II. 4 Alexandrium Life History Stages

The top nine stations for June and July and the top two stations for August with the highest cell densities of *A. catenella* (based on counts using a DNA probe performed at Woods Hole Oceanographic Institution) were examined as described above, and apparent *A. catenella* cells were staged as either vegetative cells, doublets, gametes or planozygotes. Locations on the gridded Sedgwick-Rafter cell were randomly selected using a random number generator. Cells that were 40 um or larger were considered

planozygotes (Figueroa et al. 2005). Cells 20 um or smaller were assumed to be gametes, and anything in between was considered vegetative cells (Figueroa et al. 2005). Cells that looked like two adjoined cells were conjoined considered doublets. Because these identifications of *A. catenella* cells were not verified as with the DNA probe, identification to species is uncertain, and cells are referred to as presumably *Alexandrium* spp.

All data analyses and plots were performed using R Studio, MATLAB, and Excel. Surface contour plots were constructed using MATLAB for temperature, salinity, total diatom cell densities, *A. catenella* cell densities, chlorophyll fluorescence, and surface nitrate and silicate concentrations (μm). Pearson correlation coefficient analyses were performed using R Studio among surface variables (T, S, fluorescence) and cell densities of diatoms and *A. catenella*.

III. RESULTS AND DISCUSSION

III. 1. June Cruise

The surface distributions and cell densities of *A. catenella* and diatoms in June are provided in Figure 4. June was when *A. catenella* was observed to be the most abundant of the three cruise periods, reaching a maximum of 6,195 cells per liter in the offshore stations (Station 36; see Appendix I), with significantly lower cell densities nearer the shorelines of Maine and Nova Scotia. The highest cell densities of diatoms were also observed during this cruise, reaching 681,667 cells/L (Station 38); however, their maximum distribution was more inshore than that of *A. catenella*. While there appears to be an inverse relationship between *A. catenella* and diatoms, the correlation, while negative, is weak and not statistically significant ($R = -0.11$, $p = 0.498$; Table 2); the lack of statistical significance is likely the result of the spatial overlap between highest densities of diatoms inshore and highest densities of *A. catenella* offshore (Fig. 4). The densities of *A. catenella* cells during the June cruise are generally greater than has been observed in the Gulf of Maine (e.g., Anderson et al., 2005; 2014 [DSR II special issues]) with the exception of Martin and White (1988), who observed densities greater than 1 million cells/L in the same region of the Gulf of Maine.

Table 1 summarizes the species composition (genera) of diatoms at the ten highest-density stations for total diatoms in June. The highest diatom densities were at Station 38, which was dominated by *Thalassiosira* spp. followed by *Chaetoceros* spp.. *Cylindrotheca* spp. was also present at this station along with other unidentified diatoms species.

Other less abundant diatom genera in June included *Pseudonitzschia* spp., *Thalassionema* spp, and *Rhizosolenia* spp.. There were various dinoflagellate species, including *Ceratium* spp., *Protoperidinium* spp., and *Dinophysis* spp. in addition to *A. catenella*. Other plankton groups included the silicoflagellate *Dictyocha* spp., invertebrate larvae, copepods, and *Tintinids.*

With respect to the *Alexandrium* life history stages for June 2019, all stations were dominated by vegetative cells (82%). Planozygotes were second in abundance (14%) for the majority of the stations and gametes were least abundant; however, there were stations where gamete densities were equal to greater than that of planozygotes (Stations 34, 35, 36, 37).

Aerial contour plots of surface temperature, salinity, and chlorophyll fluorescence for June are given in Figure 5. The surface temperatures where the highest *A. catenella* cell densities were observed ranged from about 8 to 12 °C, indicating no particular temperature preference within this range. Maximum diatom cell densities were observed in waters with surface temperatures spanning a similar temperature range. However, the highest *A. catenella* densities did correspond with higher surface salinities ($R = 0.44$; $p = 0.003$; Table 2), which occurred farther offshore. Diatoms appeared to be more inshore and not completely occurring in the offshore higher salinity waters with A. catenella, making them seem unrelated to surface salinity. However, there was a significant negative Pearson correlation with diatoms and salinity ($r = -0.042$; $p=0.008$). Both *A. catenella* and diatoms were clearly associated with surface waters depleted in both nitrate and silicate, with negative correlations (Table 2); however, only *A. catenella* was significantly negatively correlated with nitrate. Figure 7 is a plot of cell

densities of *A. catenella* and diatoms across the ranges of temperature and salinity where they were collected, which further indicates no apparent temperature preference by either group. However, a narrow salinity range, clustered around salinity 32, over which *A. catenella* was observed. Temperatures of occurrences for both diatoms and *A. catenella* were between 7 and 12 °C, with the highest abundances occurring between 8 and 10 °C.

In situ chlorophyll fluorescence in the surface waters were more closely related to, and significantly positively correlated with, diatom distributions ($R = 0.66$; $p < 0.001$) than was the case for *A. catenella*, *w*hich is in keeping with the significantly greater biomass (cell densities) of diatoms (maxima of 681,667 cells per liter diatoms, versus 6,195 cells per liter *A. catenella*).

The complete Pearson correlation analysis for the June cruise is given in Table 2, with significant correlations provided in bold font. Significant negative correlations are seen between *A. catenella* and nitrate, diatoms and salinity, silicate and temperature, nitrate and temperature, and salinity, and chlorophyll fluorescence. Significant positive correlations are seen for *A. catenella* and salinity, diatoms and fluorescence, and nitrate and silicate.

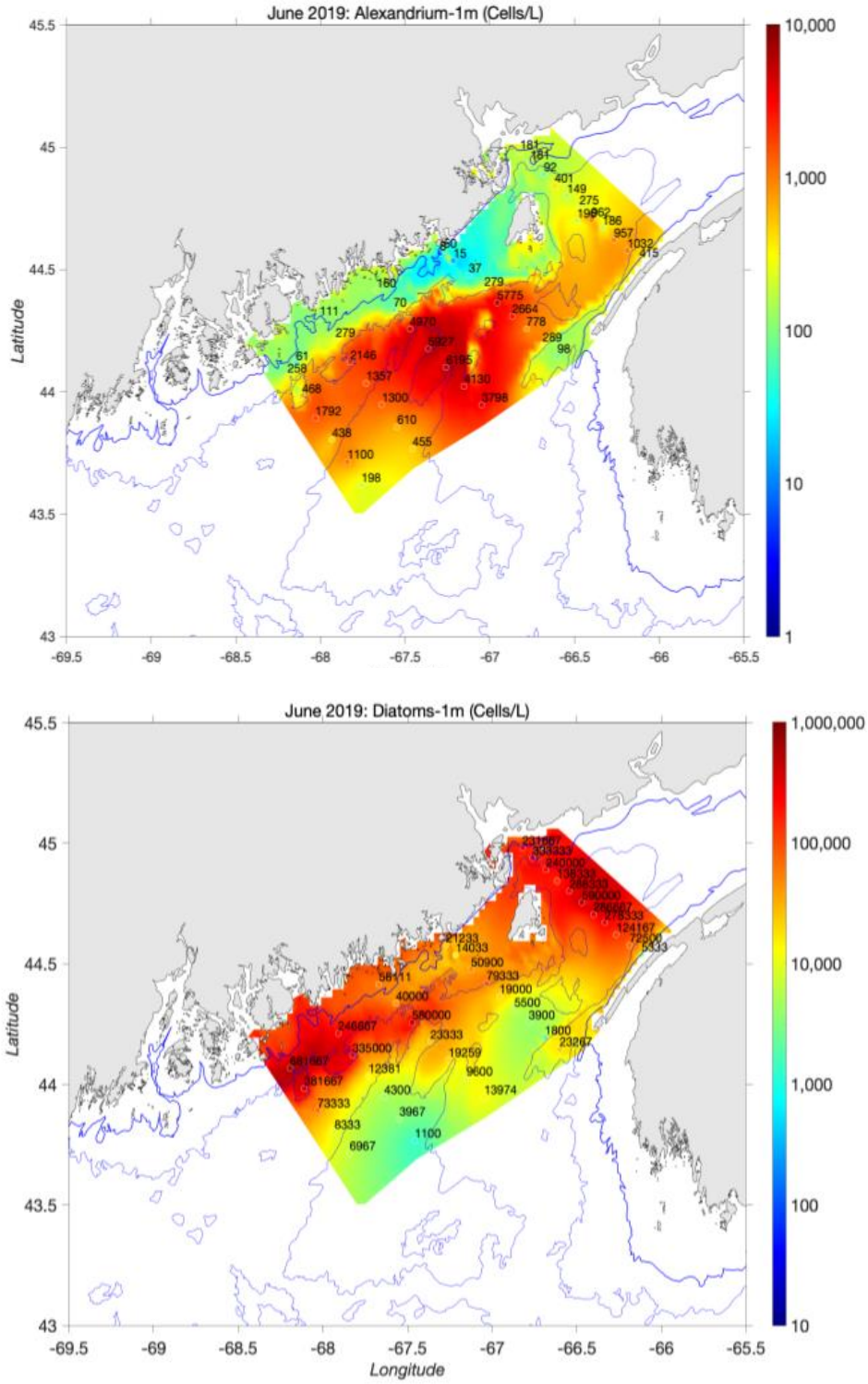

Figure 4. Contours of surface cell densities (No. Cells/L) of *Alexandrium catenella* (Top Panel) and total diatoms (Bottom Panel) for the June 2019 survey.

Table 1. Major genera of diatoms at stations with the highest total densities of diatoms for the June 2019 cruise. Both percent of total, and density (cells/L) are given.

	Station 38		Station 18		Station 26		Station 39		Station 29		Station 22		Station 19		Station 17		Station 16		Station 6	
Taxon	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*
Thalassiosira spp.	84%	553,333	80%	444,167	83%	455,000	67%	213,333	76%	160,833	75%	269,167	67%	174,167	65%	180,833	67%	195,833	89%	46,250
Chaetoceros spp.	15%	99,167	17%	95,833	15%	83,333	30%	94,167	18%	39,167	22%	77,500	31%	81,667	32%	87,500	27%	79,167	3%	1,667
Guinardia spp.																				
Pseudonitzschia spp.			1%	3,333					2%	4,167					0%	833				
Thalassionema spp.					1%	3,333														
Cylindrotheca spp.	0%	833	0%	2,500	0%	833	1%	2,500	1%	2,500	0%	833	1%	1,667	0%	833	1%	1,667	2%	833
Leptocylindrus spp.																				
Rhizosolenia spp.									0%	833										
Achnanthes spp.																				
Ditylum spp.																				
Cosinodiscus spp.																				
Unknown	1%	9,167	2%	11,667	1%	5,000	2%	7,500	2%	5,000	3%	11,667	1%	3,333	2%	6,667	6%	16,667	6%	3,333
Surface Nitrate (uM)	0.47		0.11		0.85		0.51		1.60		1.42		1.68		0.56		0.47		5.99	
Surface Silicate (uM)	0.82		0.63		2.27		1.32		2.00		2.61		1.96		1.45		0.52		5.76	

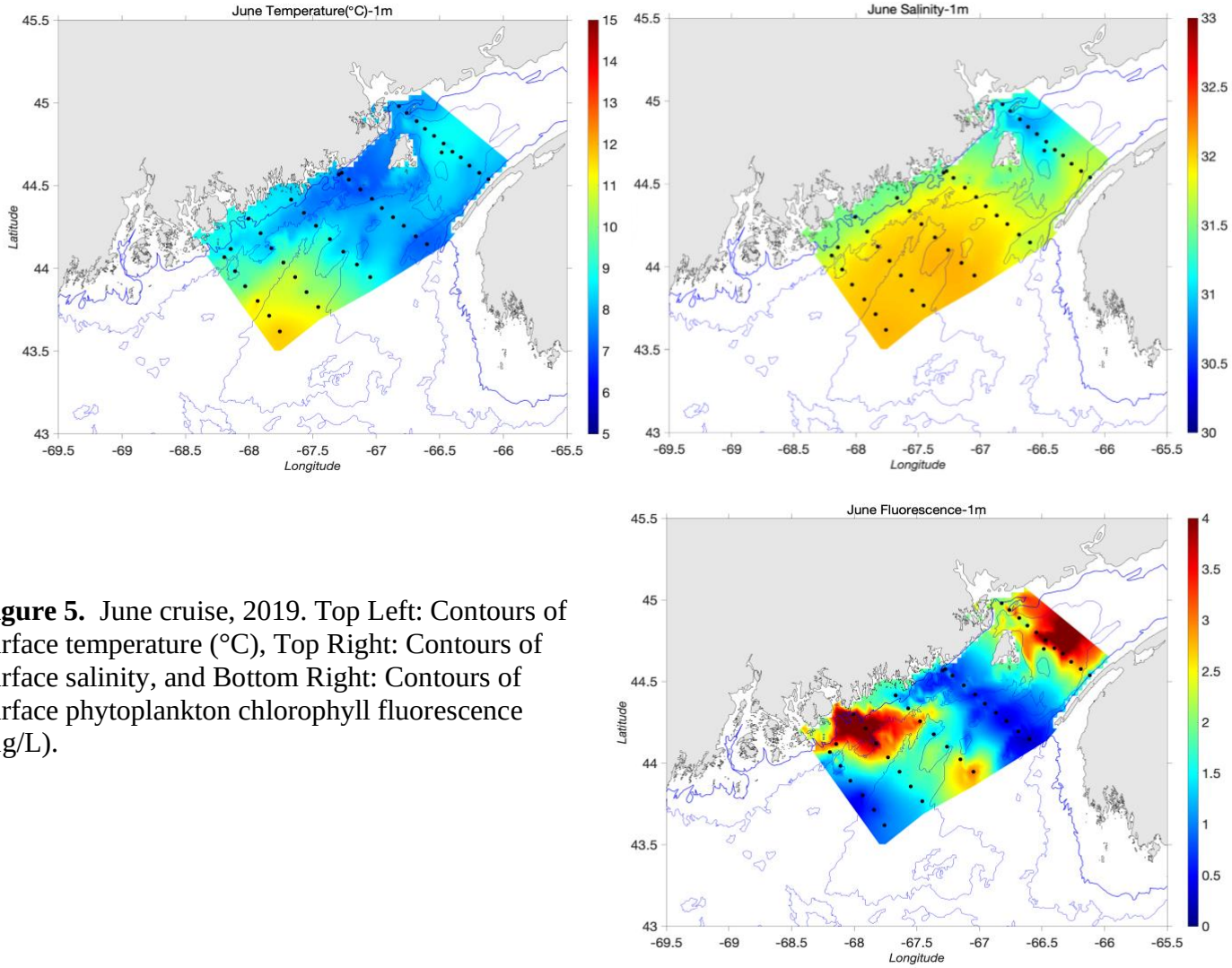

Figure 5. June cruise, 2019. Top Left: Contours of surface temperature (°C), Top Right: Contours of surface salinity, and Bottom Right: Contours of surface phytoplankton chlorophyll fluorescence (µg/L).

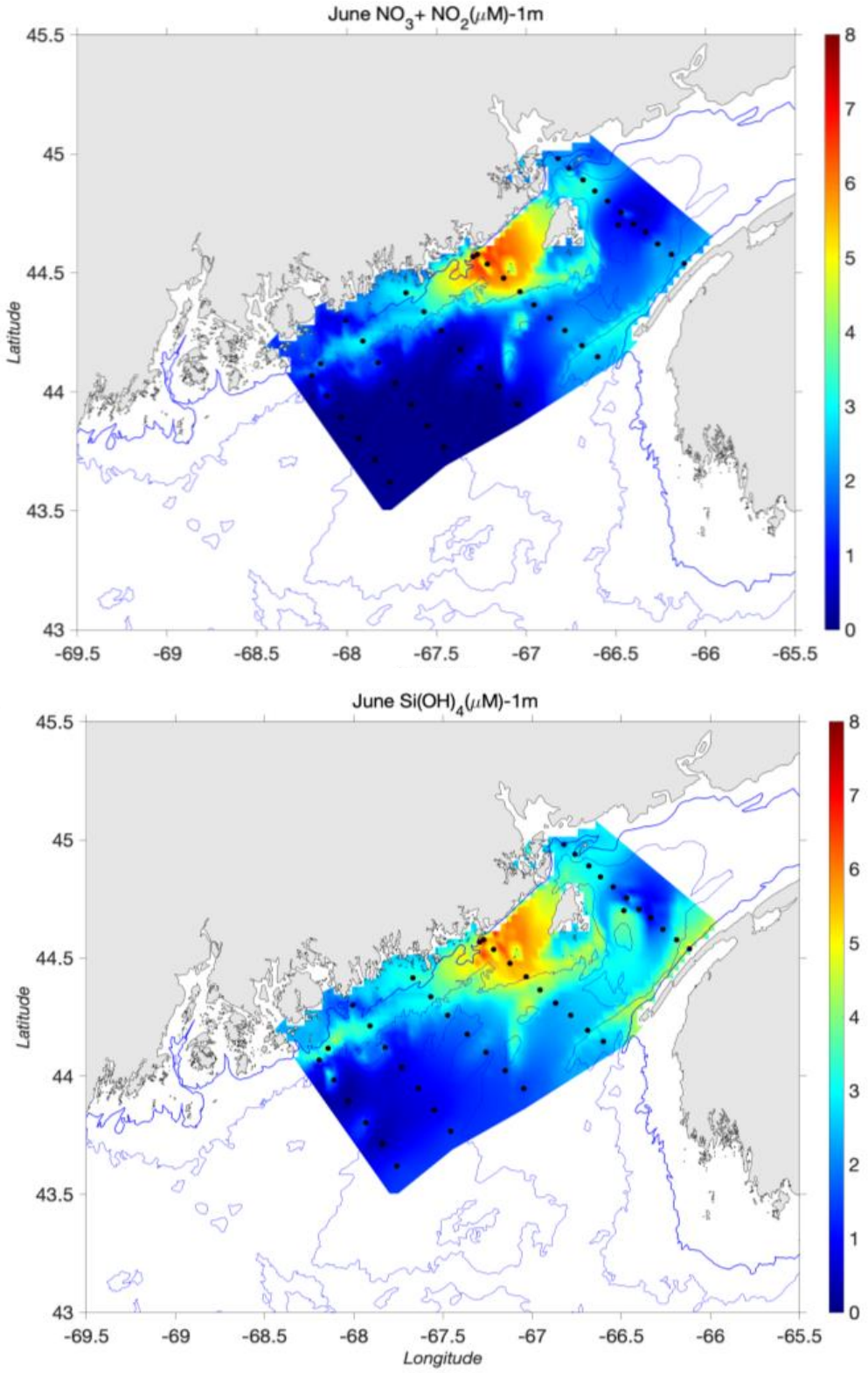

Figure 6. June cruise, 2019. Contours of surface nitrate (µM) and silicate (µM).

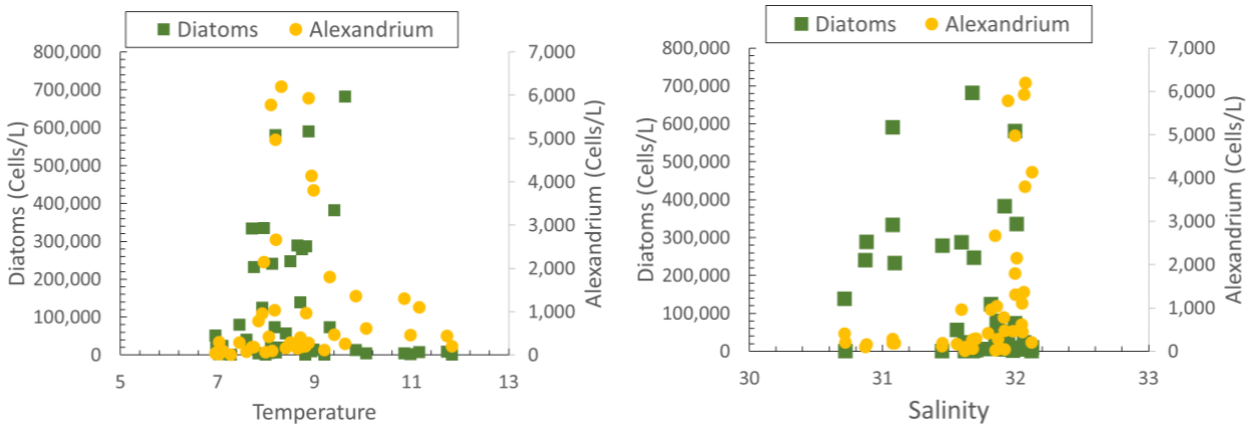

Figure 7. June cruise, 2019: Densities of *A. catenella* and total diatoms plotted against surface temperatures (left panel) and surface salinity (right panel) for the June cruise.

Table 2. June cruise, 2019: Pearson correlation analysis of *A. catenella* (cells/L), total diatoms (cells/L), surface nitrate and silicate (µM), surface temperature (°C), salinity, and *in situ* chlorophyll fluorescence (µg chlorophyll *a* per liter). Values are given for the correlation coefficient, r, the p value, and sample size (n). Statistically significant correlation coefficients (<0.05) are in bold font.

	Alexandrium	Diatoms	Silicate	Nitrate	Temperature	Salinity	Fluorescence
Alexandrium		r=-0.11 p=0.498 n=38	r=-0.19 p=0.212 n=43	r=-0.36 **p=0.0187** n=43	r=0.032 p=0.836 n=43	r=0.44 **p=0.00304** n=43	r=-0.0069 p=0.965 n=43
Diatoms			r=-0.25 p=0.134 n=38	r=-0.20 p=0.239 n=38	r=-0.014 p=0.932 n=38	r=-0.42 **p=.00880** n=38	r=0.61 **p=4.381e-05** n=38
Silicate				r=0.88 **p=1.082e-14** n=43	r=-0.64 **p=3.644e-06** n=43	r=-0.15 p=0.323 n=43	r=-0.29 p=0.0587 n=43
Nitrate					r=-0.72 **p=6.811e-08** n=43	r=-0.18 p=0.239 n=43	r=-0.31 **p=0.0429** n=43
Temperature						r=0.27 p=0.0834 n=43	r=0.03 p=0.848 n=43
Salinity							r=-0.34 **p=0.0267** n=43
Fluorescence							

III. 2. July Cruise

The surface distributions of *A. catenella* and diatoms in July are given in Figure 8. Cell densities of both *A. catenella* and diatoms were lower than in June, reaching maxima of 3,378 cells/L *A. catenella* and 108,333 cells/L diatoms (Station 9; Appendix II).

Table 3 provides the species composition (genera) of the most common diatoms at stations where the total diatom cell densities were highest for the July cruise. The highest diatom density observed in the July counts was 108,333 cells/L at Station 9. *Chaetoceros spp.* was the most abundant diatom at this station (68,333 cells/L), followed by *Thalassiosira spp.* (10833 cells/L). There were also *Cylindrotheca spp.* present (5,000 cells/ Liter) along with unknown species (30,000 cells/L). Station 37 had the lowest diatom abundance (200 Cells/L).

Surface temperature, salinity, and chlorophyll fluorescence in July are given in Figure 9. The surface temperatures where the highest *A. catenella* cell densities were observed were similar to the case in June, ranging from about 8 to 12.5 °C; however, there was a significant negative correlation between *A. catenella* and temperature (Table 4), indicating their more common occurrence in colder waters of the Eastern Maine Coastal Current. The highest densities for diatoms occurred between 9 and 12 °C. There was no clear indication of a salinity preference as *A. catenella*, and diatoms' highest densities occurred between 31 and 32.5. Diatoms in July appeared to occur over a wider range of salinities as compared with June.

Figure 9 displays cell densities of *A. catenella* and diatoms across the ranges of temperature and salinity. Maximum cell densities of *A. catenella* were observed across a range of temperatures that were slightly warmer than in June; diatoms occurred over a

similar range of temperatures. Unlike June, *A. catenella* was observed over a relatively wide range of salinities and did not show a peak at 32. Diatoms showed a similar salinity distribution. Like in June, *A. catenella* and diatoms did not have a clear association with surface nutrient concentrations (nitrate and silicate), as shown in Figure 10.

For the *Alexandrium* life-history stages in July 2019, vegetative cells again dominated (87%). However, gametes tended to dominate more over planozygotes at more stations on this cruise (8%, 5%, respectively). Doublets were present in July (in trace amounts) but not in June.

Table 3 gives the species composition (genera) of diatoms at the ten highest diatom density stations in July. In the initial density counts, highest diatom densities were at Station 9 (108,333 cells/L); however, when recounted for identification of genera, Station 30 (82,222 cells/L) displayed the highest densities. Diatoms were dominated by *Chaetoceros* spp. (68,333 cells/L) followed by unidentified diatom taxa (30,000 cells/L), Thalassiosira *spp.* (10,833 cells/L) and *Cylindrotheca* spp. (5,000 cells/L). The pennate diatom *Pseudonitzschia* spp. was also present at this station (833 cells/L). Other diatom genera for the July cruise included *Thalassionema* spp., *Guinardia spp. Rhizosolenia spp.* along with several unidentified taxa. There were various dinoflagellate species, including *Ceratium* spp., *Protoperidinium* spp. and *Dinophysis* spp., in addition to *A. catenella*. Other plankton groups included the silicoflagellate *Dictyocha* spp., invertebrate larvae, copepods, *Tintinids*, microflagellates, and other unidentified cells.

Highest densities of diatoms correlated with high chlorophyll fluorescence, whereas the highest A. *catenella* cell densities occurred in areas of lower fluorescence.

Results of the Pearson correlation analysis for the July cruise are given in Table 4. Significant negative correlations were observed between *A. catenella* and temperature (as discussed above), silicate and temperature, and between nitrate and temperature. Significant positive correlations were observed between *A. catenella* and both silicate and nitrate (although r values were weak, at ca. 0.3), diatoms and fluorescence, and between silicate and nitrate.

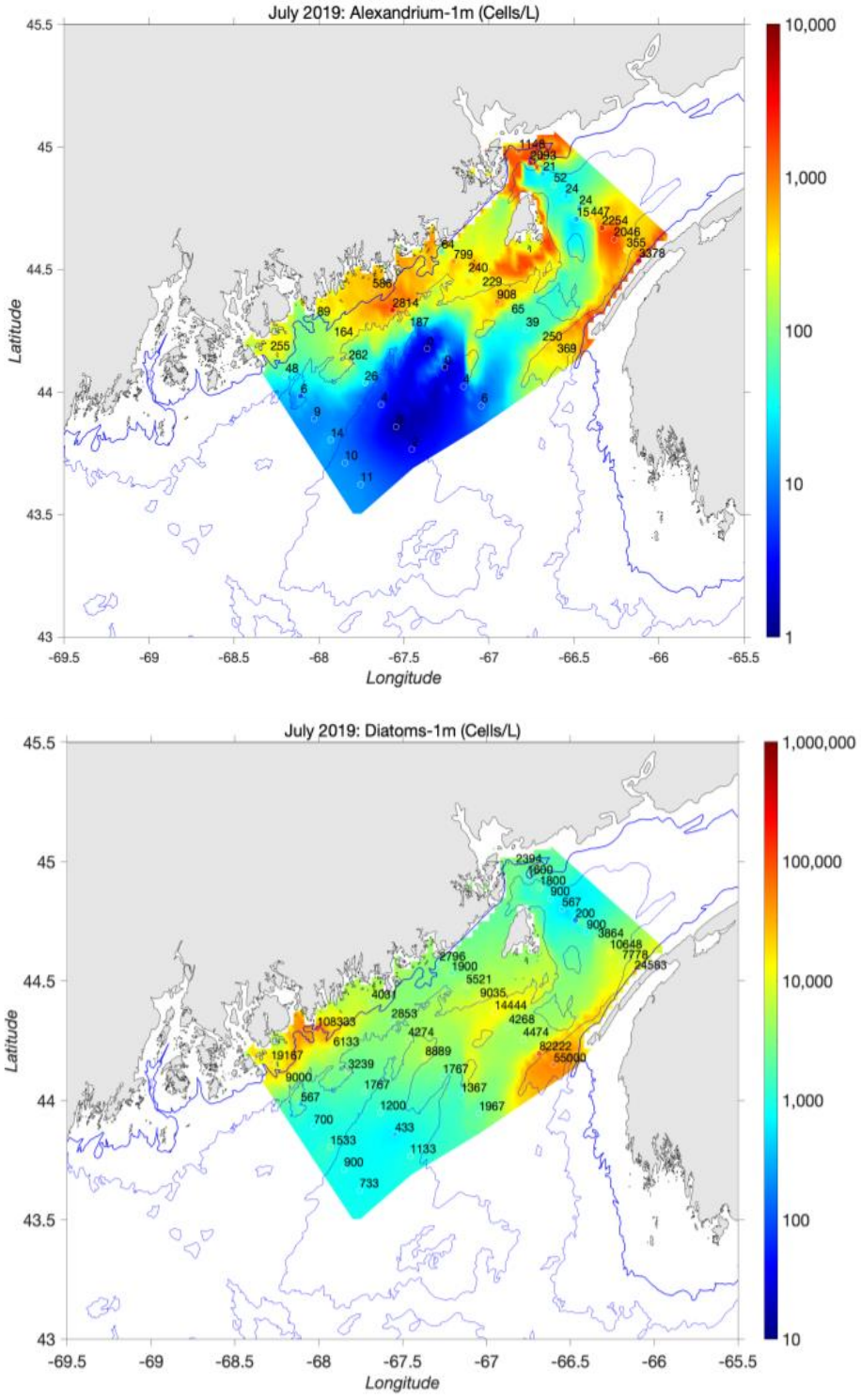

Figure 8. Contours of surface cell densities (No. Cells/L) of *Alexandrium catenella* (Top Panel) and total diatoms (Bottom Panel) for the July 2019 survey.

Table 3. Major genera of diatoms at stations with the highest total densities of diatoms for the July 2019 cruise. Both percent of total, and density (cells/L) are given.

	Station 9		Station 30		Station 31		Station 32		Station 8		Station 27		Station 34		Station 26		Station 7		Station 21	
Taxon	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*	%	*No. Cells/L*
Thalassiosira spp.	9%	10,833	3%	3,333	5%	3,889	9%	3,333	7%	5,000	8%	2,222	3%	833	20%	1,600	11%	1,222	11%	333
Chaetoceros spp.	59%	68,333	71%	69,167	82%	63,889	47%	17,667	83%	58,889	46%	13,333	32%	7,917	33%	2,667	35%	4,000	47%	1,500
Guinardia spp.									2%	1,111					1%	67				
Pseudonitzschia spp.	1%	833	1%	833					2%	1,667	7%	1,944	3%	833	1%	67	8%	889	11%	333
Thalassionema spp.			2%	1,667																
Cylindrotheca spp.	4%	5,000	2%	1,667	2%	1,667	3%	1,000	1%	556	4%	1,111	5%	1,250	4%	333	3%	333	13%	417
Leptocylindrus spp.																				
Rhizosolenia spp.			1%	833	1%	556	1%	333					2%	417						
Achnanthes spp.																				
Ditylum spp.																				
Cosinodiscus spp.																				
Unknown	26%	30,000	21%	20,000	11%	8,333	41%	15,333	5%	3,889	36%	10,556	54%	13,333	41%	3,267	44%	5,111	18%	583
Surface Nitrate (uM)	0.33		2.52		2.7		2.59		0.03		2.01		2.93		1.91		0.84		5.94	
Surface Silicate (uM)	1.44		2.24		2.46		2.89		1.01		2.36		2.89		2.37		1.55		4.08	

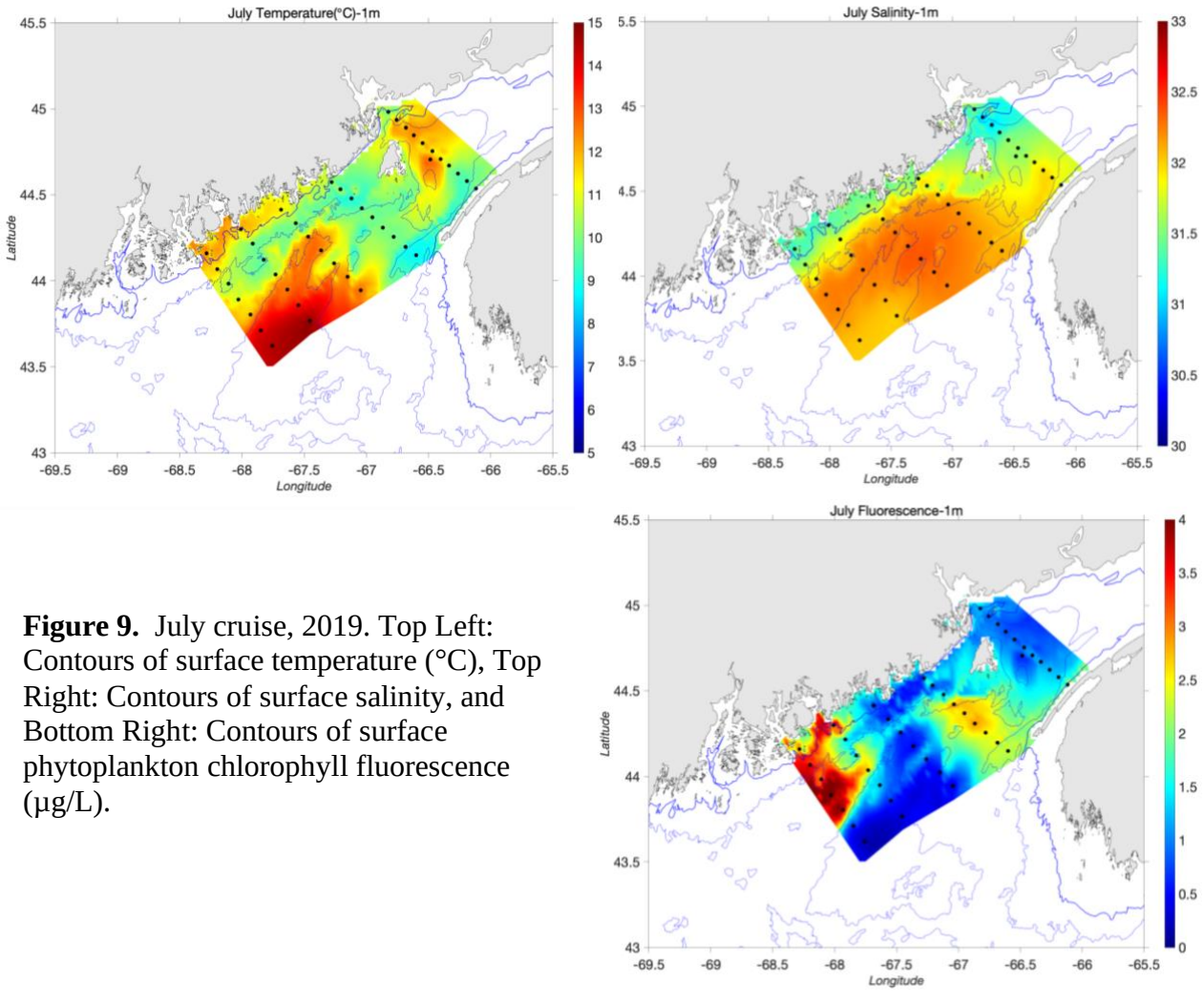

Figure 9. July cruise, 2019. Top Left: Contours of surface temperature (°C), Top Right: Contours of surface salinity, and Bottom Right: Contours of surface phytoplankton chlorophyll fluorescence (µg/L).

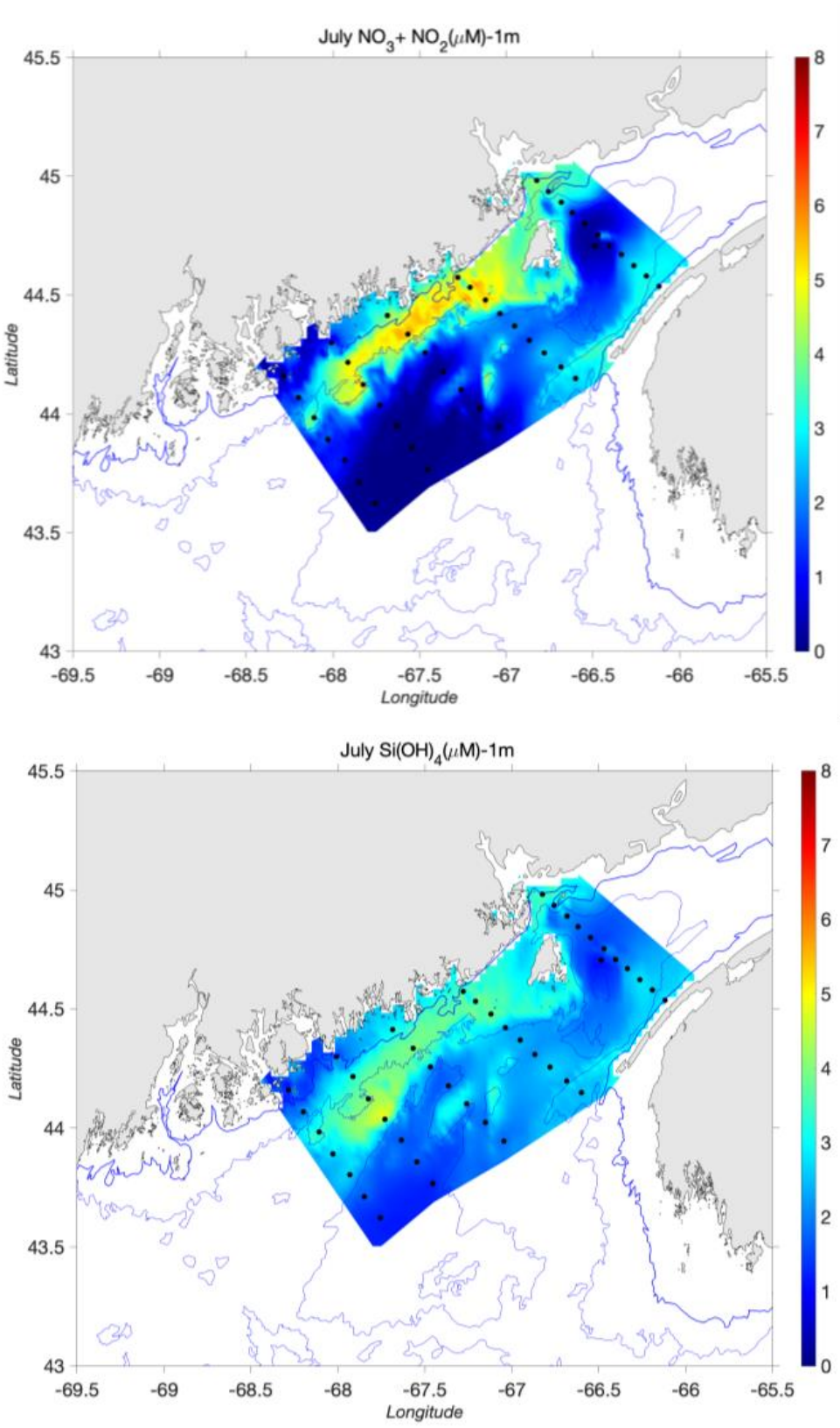

Figure 10. July cruise, 2019. Contours of surface nitrate (µM) and silicate (µM).

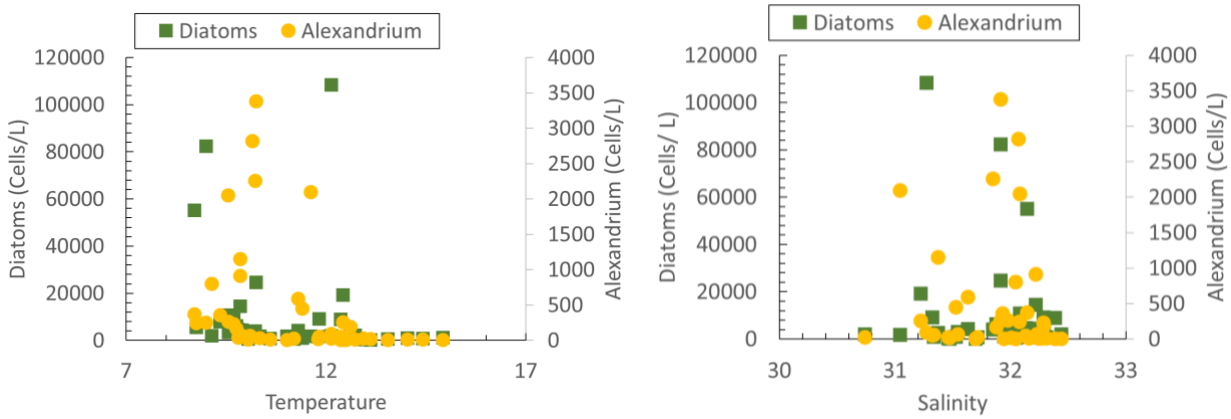

Figure 11. July cruise, 2019: Densities of *A. catenella* and total diatoms plotted against surface temperatures (left panel) and surface salinity (right panel) for the July cruise.

Table 4. July cruise, 2019: Pearson correlation analysis of *A. catenella* (cells/L), total diatoms (cells/L), surface nitrate and silicate (µM), surface temperature (°C), salinity, and *in situ* chlorophyll fluorescence (µg chlorophyll *a* per liter). Values are given for the correlation coefficient, r, the p value, and sample size (n).

	Alexandrium	Diatoms	Silicate	Nitrate	Temperature	Salinity	Fluorescence
Alexandrium		r=0.021 p=0.897 n=41	r=0.32 **p=0.0382** n=42	r=0.32 **p=0.0382** n=42	r=-0.32 **p=0.0368** n=42	r=-0.099 p=0.534 n=42	r=-0.07 p=0.659 n=42
Diatoms			r=-0.16 p=0.313 n=41	r=-0.16 p=0.313 n=41	r=-0.19 p=0.231 n=41	r=-0.15 p=0.334 n=41	r=0.42 **p=0.00595** n=41
Silicate				r=1.00 **p=0.000** n=43	r=-0.41 **p=0.00627** n=43	r=0.22 p=0.158 n=43	r=0.089 p=0.571 n=43
Nitrate					r=-0.41 **p=0.00627** n=43	r=0.22 p=0.158 n=43	r=0.089 p=0.571 n=43
Temperature						r=-0.19 p=0.223 n=43	r=-0.37 **p=0.0132** n=43
Salinity							r=0.085 p=0.589 n=43
Fluorescence							

III. 3. August Cruise

The surface distributions and cell densities of *A. catenella* and diatoms in August are given in Figure 12. Fewer stations were sampled in August, so little can be concluded about their spatial distributions. Nonetheless, the maximum cell densities of *A. catenella* and diatoms appear to be inversely correlated, with the highest densities of *A. catenella* found in the Bay of Fundy (867cells/L at Station13, Appendix III)), and the maximum diatom densities in the Gulf of Maine (66,111 cells/L at Station 9). The correlation was not statistically significant, however (Table 6).

The corresponding surface temperature, salinity, and chlorophyll fluorescence for August are given in Figure 13. The surface temperatures where *A. catenella* cell densities were observed ranged from 10 to 13 °C, which is higher than in either June or July, reflecting the seasonal warming of surface waters (Figure 15). The maximum *A. catenella* densities were observed between about 12 to 14 °C.

Diatoms were observed in waters with surface temperatures between 10 and 14 °C. The highest densities for both diatoms and *A. catenella* occurred in waters with surface salinities between about 31.5 and 32.5 (Figure 15).

The spatial distributions of *A. catenella* in August did not display a clear association with silicate or nitrate, except that, like the case in June and July, they occurred in nutrient-depleted surface waters. However, there was a significant inverse correlation between *A. catenella* and nitrate (Table 6) that is not apparent in the surface contour plots in Figures 12 and 13. Higher densities of diatoms appeared to be associated

with higher silicate surface waters, but there was no significant correlation (Table 6). There was a positive and statistically significant correlation between *A. catenella* and surface temperature (Table 6), but no apparent relationships between diatoms and either temperature or salinity. Interestingly, there was no correlation between *A. catenella* cell densities and surface temperatures in June, followed in July by a statistically inverse correlation, and a statistically positive correlation in August, which leads to the conclusion that it is not the temperature that controls their distributions. There were no correlations between diatom cell densities and temperature in June, July, or August.

Figure 11 shows the cell densities of *A. catenella* and diatoms plotted across the ranges of temperature and salinity, which further supports the conclusion that there is no apparent temperature preference by either group in August; however, *A. catenella* can be seen to cluster about the salinity of 32 to 32.5. The surface temperatures where the highest *A. catenella* cell densities were observed ranged from 10 to 12.5 °C. Likewise, the maximum diatom cell densities were observed in waters with surface temperatures between 13 and 14.5 °C. Highest *A. catenella* densities lay between 32 and 32.5 salinity, while diatoms lay between 31.5 and 32.

When considering the life cycle stages from August compared to June and July, there were fewer life cycle counts completed because August had significantly fewer stations. However, vegetative cells again dominated in August (83%), followed by gametes (12%). This station also had trace numbers of doublets.

In situ chlorophyll fluorescence in the surface, waters were closely related to the diatom distributions, as can be seen in Figures 12 and 13; diatoms were strongly and

statistically correlated with fluorescence (r = 0.6; Table 12); there was no apparent association between the relatively low cell densities of *A. catenella* and fluorescence.

Table 5 gives the species composition (genera) of diatoms at the ten stations where the total diatom cell densities were highest for the August cruise. The highest diatom densities were at Station 9 (66,111 cells/L; Appendix III), which was dominated by *Chaetoceros* spp. (39,444 cells/L) followed by *Skeletonema* spp. (28,333 cells/L). *Guinardia* spp., *Pseudonitzscha* spp., *Thalassiorira* spp., *Cylindrotheca* spp., *Ac hnanthes* spp, and unidentified diatoms, were also present at this station (at densities of 1,667, 1,667, 1,111,556, 556, 10,556 cells/L respectively). There were various dinoflagellate species, including *Ceratium* spp. *Protoperidinium* spp. and *Dinophysis* spp., in addition to *A. catenella*. Other groups included the silicoflagellate, *Dictyocha* spp., unidentified invertebrate larvae, copepods, tintinnids, and microflagellates.

The results of Pearson correlation analyses for the August cruise are given in Table 6. Significant negative correlations were observed between *A. catenella* and nitrate, diatoms and silicate, temperature and salinity, and between temperature and fluorescence. There were significant positive correlations between *A. catenella* and temperature (as already mentioned), diatoms and fluorescence, silicate and nitrate, silicate and salinity, and between nitrate and salinity.

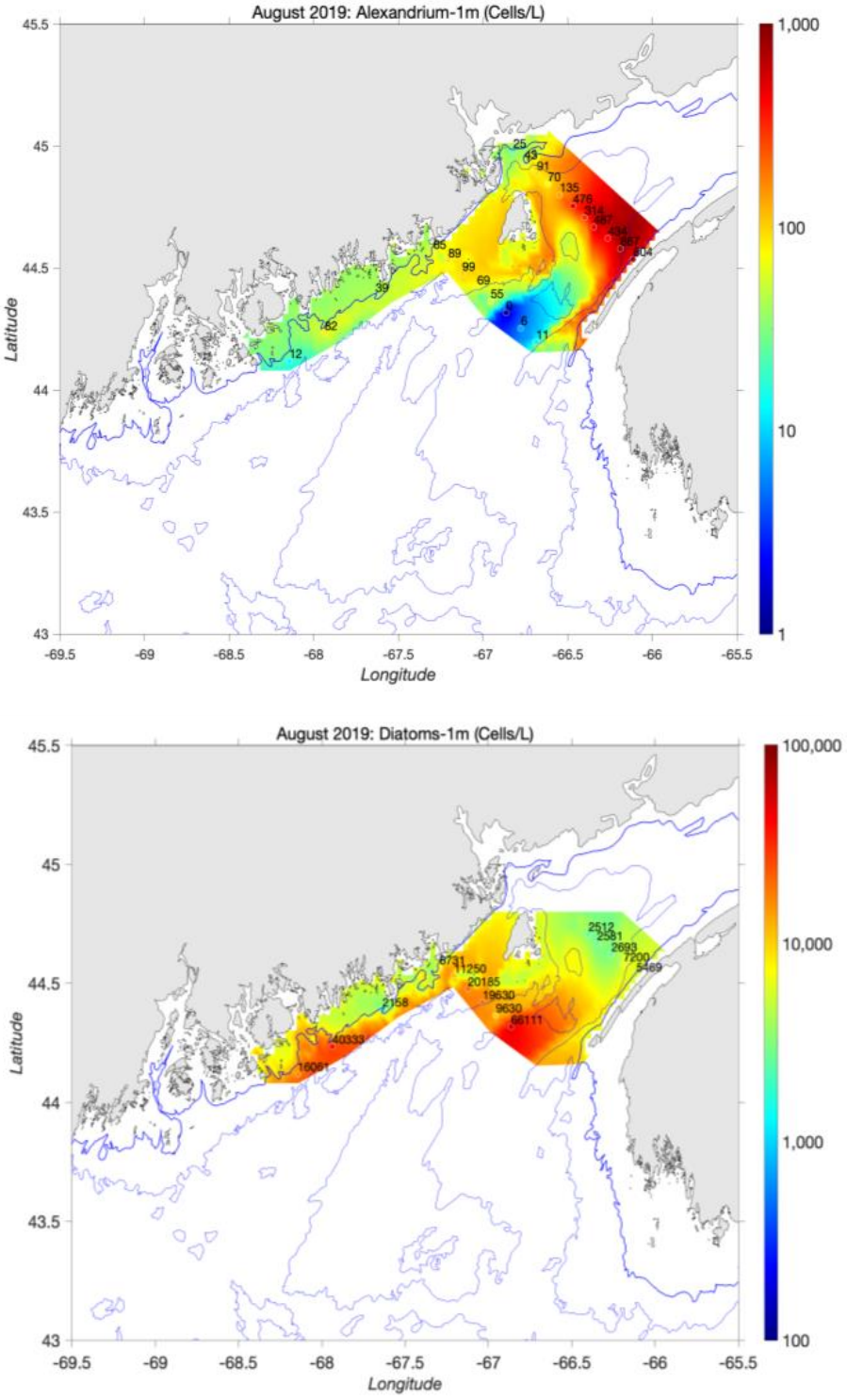

Figure 12. Contours of surface cell densities (No. Cells/L) of *Alexandrium catenella* (Top Panel) and total diatoms (Bottom Panel) for the August 2019 survey.

Table 5. Major genera of diatoms at stations with the highest total densities of diatoms for the August 2019 cruise. Both percent of total, and density (cells/L) are given.

	Station 9		Station 2	
Taxon	%	*No. Cells/L*	%	*No. Cells/L*
Thalassiosira spp.	1%	1,111	4%	7,500
Chaetoceros spp.	47%	39,444	1%	2,500
Guinardia spp.	2%	1,667		
Pseudonitzschia spp.	2%	1,667		
Thalassionema spp.				
Cylindrotheca spp.	1%	556		
Leptocylindrus spp.				
Rhizosolenia spp.				
Achnanthes spp.	1%	556		
Ditylum spp.				
Cosinodiscus spp.				
Skelotonemia spp.	34%	28,333	78%	147,500
Unknown	13%	10,556	21%	40,000
Surface Nitrate (uM)	0.89		1.42	
Surface Silicate (uM)	1.74		3.58	

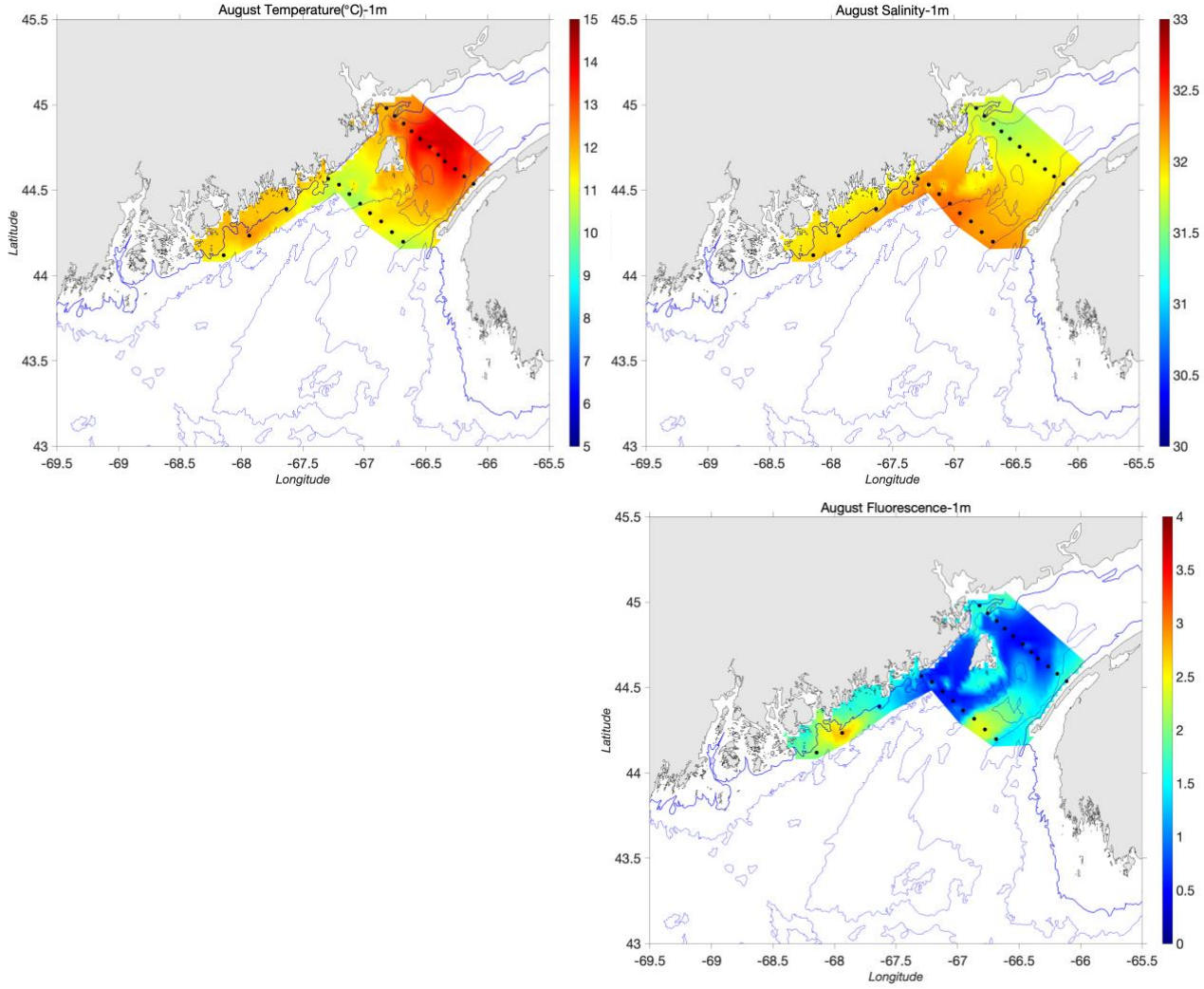

Figure 13. August cruise, 2019. Contours of surface temperature (°C), salinity, phytoplankton chlorophyll fluorescence (µg/L).

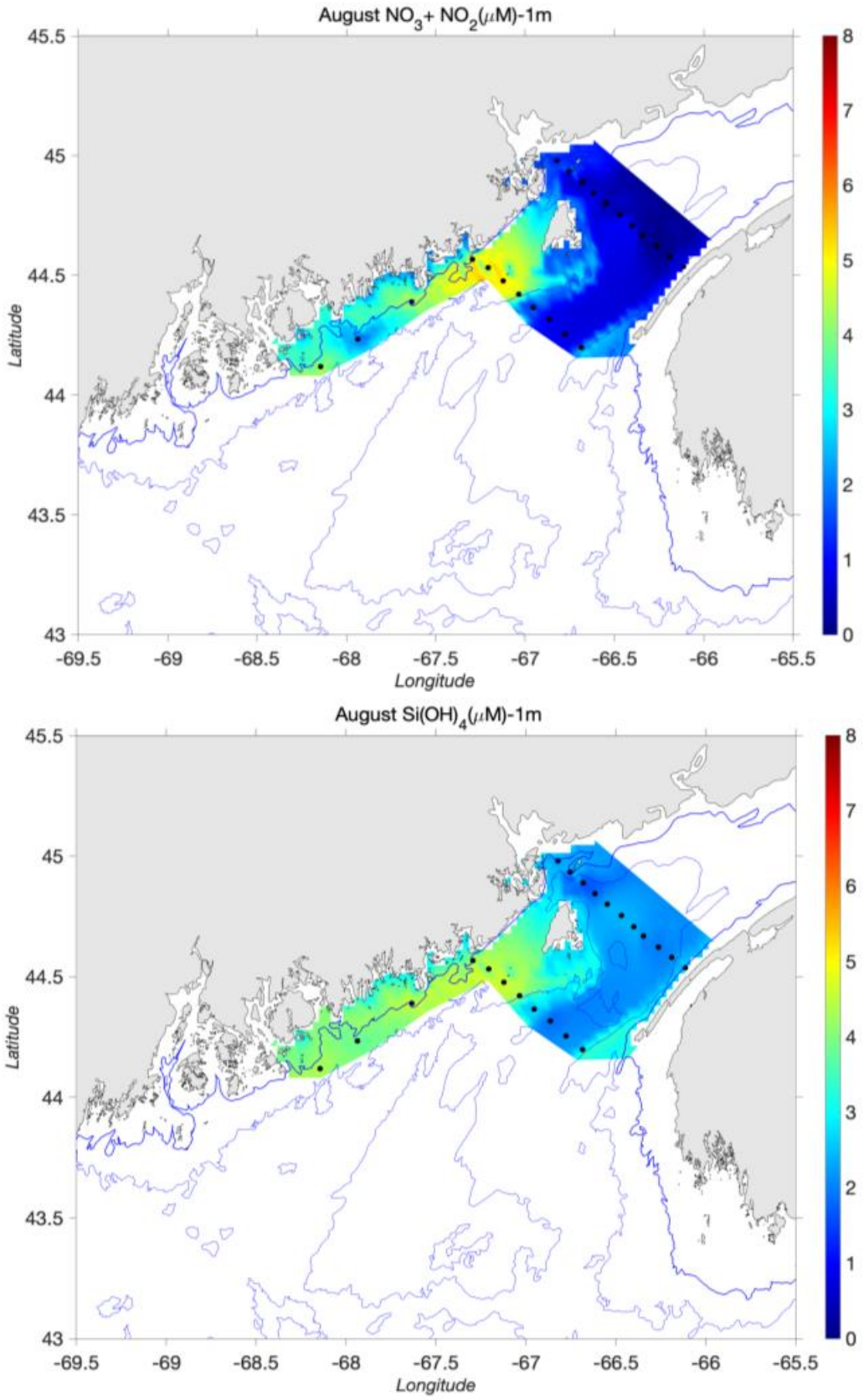

Figure 14. August cruise, 2019. Contours of surface nitrate (µM) and silicate (µM).

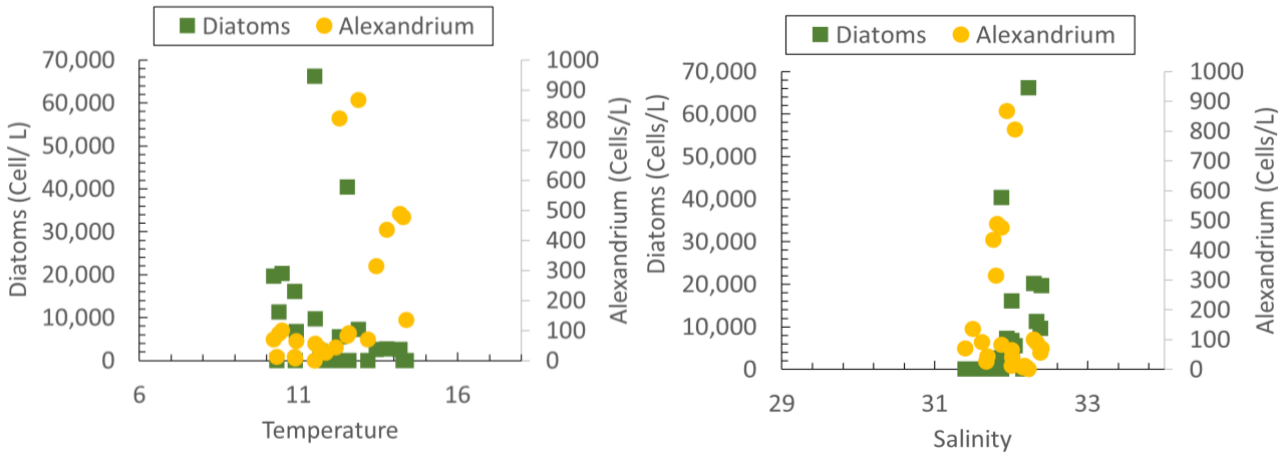

Figure 15. August cruise, 2019: Densities of *A. catenella* and total diatoms plotted against surface temperatures (left panel) and surface salinity (right panel) for the August cruise.

Table 6. August cruise, 2019: Pearson correlation analysis of *A. catenella* (cells/L), total diatoms (cells/L), surface nitrate and silicate (µM), surface temperature (°C), salinity, and *in situ* chlorophyll fluorescence (µg chlorophyll *a* per liter). Values are given for the correlation coefficient, r, the p value, and sample size (n).

	Alexandrium	Diatoms	Silicate	Nitrate	Temperature	Salinity	Fluorescence
Alexandrium		r=-0.42 p=0.131 n=14	r=-0.28 p=0.200 n=22	r=-0.44 **p=0.0409** n=22	r=0.52 **p=0.0123** n=22	r=-0.12 p=0.580 n=22	r=-0.088 p=0.697 n=22
Diatoms			r=-0.097 p=0.740 n=14	r=-0.041 p=0.889 n=14	r=-0.27 p=0.342 n=14	r=0.30 p=0.300 n=14	r=0.60 **p=0.0225** n=14
Silicate				r=0.94 **p=1.133e-10** n=22	r=-0.62 **p=0.00209** n=22	r=0.55 **p=0.00780** n=22	r=-0.068 p=0.762 n=22
Nitrate					r=-0.74 **p=7.598e-05** n=22	r=0.55 **p=0.00746** n=22	r=-0.14 p=0.525 n=22
Temperature						r=-0.74 **p=7.826e-05** n=22	r=-0.23 p=0.304 n=22
Salinity							r=0.07 p=0.756 n=22
Fluorescence							

IV. CONCLUSIONS

A few key findings of this study are summarized here. First, the results from the three survey cruises in 2019 in the northeastern Gulf of Maine and Bay of Fundy demonstrate a seasonal decline in cell densities of both *A. catenella* and diatoms over the summer, from June to July to August. The highest diatom and *A. catenella* densities were in June 2019 (681,667 cells/L and 6,195 cells/L respectively), the lowest densities were in August 2019 (66,111 cells/L and 867 cells/L, respectively). This result contrasts reports by Townsend et al. (2001) for surveys in 1998, which showed an increase in cell densities in the Bay of Fundy, from June to July to August, and a less pronounced increase in the NE Gulf.

The highest cell densities of *A. catenella* in June of 2019 were well offshore, versus that of diatoms, which were more inshore. However, there were no statistical correlations between *A. catenella* and diatoms for any of the three surveys, presumably because of the confounding effect of overlapping distributions, as can be seen in Figures 4 and 8). There was no similarly suggestive, but statistically inconclusive, evidence of allelopathic interference by diatoms in July or August.

Aerial distributions of *A. catenella* and diatoms in surface waters did not show a preference for any particular temperature. While *A. catenella* was not correlated with temperature in June, when the highest cell densities were offshore, they were significantly inversely correlated with temperature in July, meaning that cells were most abundant in colder waters, characteristic of the Eastern Maine Coastal Current (Figure 8). In August, *A. catenella* was statistically positively correlated with surface temperature

when their maximum abundances were in the Bay of Fundy. Their presence in high numbers is likely the result of processes independent of or unrelated to surface temperatures.

In laboratory culture experiments with *Alexandrium fundyense,* Etheridge and Roesler (2005) found a strong relationship between temperature and P max, where P max increased at increasing temperatures, but at higher temperatures, the growth rate decreased. Seto et al. (2019) showed that in *A. catenella* cultures maintained under uniform temperature (15°C) and pH conditions, the growth rate decreased when temperature increased to 20°C, consistent with findings from Etheridge and Roesler (2005). In their laboratory, culture experiments with *Alexandrium fundyense*, Etheridge and Roesler found that growth rates increased with increasing temperature until 15°C but decreased at higher temperatures of 20°C and 25°C. Townsend et al. (2005) noted that *A. fundyense* were typically found at surface water temperatures between 8 and 11°C; growth rates at these temperatures would be half of that measured by Etheridge and Roesler (2005) at 15°C. The highest cell densities observed in this study were between 9 and 10 °C in June and July, but at about 13 °C in August, leaving one to speculate that factors other than water temperatures, such as nutrient fluxes, were controlling growth and therefore cell distributions.

Cell densities of *A. catenella* were significantly correlated with salinity in June, the time of the greatest cell densities offshore, showing an apparent preference for 32 salinity. Townsend (2020) interpreted the salinity correlation and offshore maximum cell densities of *A. catenella* to unusual vertical fluxes of nutrients offshore in June of 2019,

and possibly less allelopathic inhibition there versus more inshore waters, rich in silicate, and where diatoms were most abundant.

These results on distributions of *A. catenella* in the northeastern Gulf of Maine are consistent with reports by Townsend et al. (2001, 2005, 2014), which showed the highest densities of cells closely associated with the Eastern Maine Coastal Current. In July, but not in June (which appears to be an unusual phenomenon, as just discussed (Townsend, 2020) or in August, *A. catenella* surface distributions were greatest in cold surface waters that are also associated with the Eastern Maine Coastal Current system (Townsend et al. 2001). In a study conducted by Townsend et al. (2010), the highest *A. catenella* cell densities were associated with the inshore frontal edge of the cold, high nutrient waters of the southwestward also following the EMCC. However, this study showed fewer cells along the outer edge of the EMCC. Highest cell densities were confined to waters inshore of the 31.4 isohaline. Within that patch, *A. catenella's* highest densities did not abut the shoreline; instead, they were seaward and not coincident with the lowest salinity waters immediately adjacent to the coast.

Waters of the EMCC are known to have the highest surface concentrations of inorganic nutrients of any area of the Gulf of Maine region (Townsend et al., 1987; Townsend, 1998), and dinoflagellates, in general, have high affinities for both light and nutrients (Eppley and Thomas, 1969; Eppley et al., 1969; Langdon, 1987; Chang and McClean, 1997). The association between high *A. catenella* cell densities and the EMCC is, therefore, the result of favorable growth conditions of high nutrient concentrations and longer daylengths in June (Townsend et al. 2001; Townsend et al., 1987; Brooks and

Townsend, 1989; Pettigrew et al., 1998) and, as shown by Townsend et al. 2001), it is during the time of maximal solar insolation was maximal in June that the highest *A. catenella* densities occurred. Like the findings in 1998 (Townsend et al., 2001), as the summer progressed, cell densities decreased in the Gulf of Maine surface waters.

In addition to nutrient limitation, and the possibility of allelopathic interactions, zooplankton grazing may also play a role in defining the temporal and areal distributions and abundances of both diatoms and *Alexandrium* (Smayda, 1972; Teegarden and Cembella, 1996; Turner and Borkman, 2005, Campbell et al. 2005, Turner 2010). Unfortunately, we did not sample zooplankton and cannot speculate on their role in the summer of 2019 in the NE Gulf of Maine and Bay of Fundy.

The EMCC receives some of its *A. catenella* cells from the "Leaky Gyre" in the Minas Basin, as some cells escape the Bay of Fundy and seed the northern Gulf of Maine where cells continue to grow in the EMCC waters which are enriched with nutrients as a result of tidal mixing (Townsend et al., 1987; Brooks and Townsend, 1989). Tidal pumping of deep waters in eastern Maine supplies nutrients to the EMCC, where diatoms usually thrive first and outcompete other phytoplankton groups (Townsend et al. 2014). The EMCC carries nutrient-rich tidally mixed waters downstream along the coast, stimulating phytoplankton growth, especially frontal edges of the cold-water current (Townsend et al. 2014). It was observed in this study that *A. catenella* cell densities increase with distance "downstream" within the EMCC, in increasingly vertically stratified surface waters.

Other findings of interest from this study include:

Throughout the summer months of 2019, diatoms had much higher cell densities (*i.e.,* biomass) when compared to A. *catenella.* Diatoms were also found to be significantly correlated with *in situ* chlorophyll fluorescence, while *A. catenella* was not correlated.

In July, diatoms and *A. catenella* did not display temperature preferences; however, both diatoms and *A. catenella* occurred about a salinity between 31 and 32.5.

Also, a noteworthy point for July, *A. catenella* resumed its "normal distribution" within the EMCC and was negatively correlated with temperature. High densities of *A. catenella* cells were distributed in large surface patches of greater than 1000 cells L^{-1} and one smaller patch with surface densities greater than 10,000 cells L^{-1}. The pattern of cells appeared to be positioned about the cooler EMCC waters off the mid-Maine coast.

For the three cruises, there was no clear association between *A. catenella* and surface nutrients; however, higher densities of diatoms seemed to be in areas of higher silicate for June and August, while July did not.

Overall there is not enough evidence to support that diatoms have an allelopathic interference on A. catenella. There may be some sort of indication in June; however, there is no statistically significant evidence to support the hypothesis. A combination of

factors lies behind the dynamics of Alexandrium in the Gulf of Maine and Bay of Fundy, as suggested by these results.

The timing of Alexandrium population growth, the degree to which they reach bloom densities, the areal extent of those blooms, and the population crash ending the blooms, all depend on a number of environmental factors that hold the potential for fruitful lines of research in the future.

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APPENDIX

APPENDEX I: RV Connecticut June July and August 2019 sampling locations, bottom depth, salinity, sigma t, temperature, fluorescence, nutrient concentrations, and cell densities

Table 7. June 2019 sampling locations, bottom depth, salinity, sigma t, temperature, fluorescence, nutrient concentrations, and cell densities

RV Connecticut June 12-17, 2019

Station	Latitude	Longitude	Bottom	Salinity	Sigma t	Temperature	Fluorescence	NO3+NO2	Si(OH)4	Diatoms	Alexandrium
	Decimal	Decimal	depth(m)	Sal00	Sigma-é00	°C	µg/L	(µM)	(µM)	(Cells/L)	(Cells/L)
1	44.118	-68.144	64	31.68	24.67	7.99	3.30	2.71	4.93	NaN	61
2	44.567	-67.296	64	31.62	24.72	7.28	0.60	6.48	5.48	NaN	8
3	44.701	-66.485	175	30.72	23.80	8.81	2.23	1.02	4.15	NaN	196
4	44.578	-67.272	70	31.62	24.76	6.98	0.58	7.1	8.52	21,233	50
5	44.536	-67.216	80	31.85	24.94	7.04	0.49	6.73	5.1	14,033	15
6	44.477	-67.125	65	31.92	25.00	6.96	1.11	5.99	5.76	50,900	37
7	44.421	-67.034	100	31.87	24.89	7.46	0.41	4.81	5.66	79,333	279
8	44.365	-66.956	126	31.94	24.86	8.11	0.63	1.86	4.15	19,000	5,775
9	44.309	-66.868	180	31.85	24.77	8.21	0.51	1.3	2.19	5,500	2,664
10	44.257	-66.783	183	31.91	24.87	7.85	0.26	2.58	2.49	3,900	778
11	44.194	-66.689	146	31.70	24.82	7.04	0.25	2.91	2.54	1,800	289
12	44.147	-66.600	95	31.63	24.75	7.11	0.19	2.39	2.4	23,267	98
13	44.539	-66.117	93	31.79	24.75	8.06	1.00	2.98	5.44	5,333	415
14	44.577	-66.189	118	31.86	24.78	8.18	2.77	2.25	4.18	72,500	1,032
15	44.621	-66.267	142	31.82	24.79	7.93	2.63	2.34	1.94	124,167	957
16	44.671	-66.335	136	31.45	24.38	8.75	4.09	0.47	0.52	278,333	186
17	44.705	-66.401	166	31.59	24.48	8.83	3.28	0.56	1.45	286,667	962
18	44.755	-66.470	166	31.08	24.07	8.88	5.77	0.11	0.63	590,000	275
19	44.801	-66.545	127	30.88	23.95	8.65	3.33	1.68	1.96	288,333	149
20	44.844	-66.617	125	30.72	23.81	8.71	1.88	3.06	3.23	138,333	401
21	44.890	-66.682	103	30.87	24.02	8.13	2.36	3.37	2.85	240,000	92
22	44.939	-66.760	73	31.08	24.24	7.72	3.41	1.42	2.61	333,333	181
23	44.981	-66.822	68	31.09	24.24	7.75	2.19	2.26	2.38	231,667	181
24	44.416	-67.669	40	31.56	24.51	8.41	1.05	3.36	3.51	56,111	160
25	44.336	-67.569	66	31.88	24.88	7.60	0.92	2.26	2.62	40,000	70
26	44.257	-67.473	183	32.00	24.89	8.20	3.60	0.85	2.27	580,000	4,970
27	44.213	-67.909	74.5	31.69	24.60	8.50	4.82	3.23	3.27	246,667	279
28	44.301	-68.006	62	31.45	24.31	9.21	4.42	0.25	1.03	NaN	111
29	44.121	-67.824	98	32.01	24.93	7.96	4.34	1.6	2	335,000	2,146
30	44.035	-67.730	138	32.06	24.68	9.85	2.82	0.11	0.57	12,381	1,357
31	43.947	-67.638	200	32.00	24.47	10.85	1.54	0.09	0.9	4,300	1,300
32	43.857	-67.548	204	32.05	24.64	10.07	1.71	0.09	0.67	3,967	610
33	43.767	-67.456	215	31.98	24.43	10.98	1.33	0.09	1.36	1,100	455
34	43.947	-67.047	165	32.07	24.83	8.98	3.18	0.09	1.44	13,974	3,798
35	44.023	-67.152	125	32.13	24.88	8.94	2.67	0.15	1.57	9,600	4,130
36	44.101	-67.259	162	32.07	24.93	8.32	1.24	0.53	1.74	19,259	6,195
37	44.177	-67.365	208	32.07	24.84	8.88	1.14	0.09	1.79	23,333	5,927
38	44.068	-68.195	94	31.68	24.42	9.63	1.61	0.47	0.82	681,667	258
39	43.983	-68.111	84	31.92	24.64	9.41	0.75	0.51	1.32	381,667	468
40	43.892	-68.031	164.7	32.00	24.72	9.31	1.18	0.07	0.18	73,333	1,792
41	43.803	-67.933	153.6	32.05	24.35	11.73	0.41	0.05	1.68	8,333	438
42	43.714	-67.842	215	32.05	24.45	11.16	0.61	0.09	0.2	6,967	1,100
43	43.619	-67.758	228	32.12	24.39	11.83	0.99	0.1	1.31	NaN	198

Table 8. July 2019 sampling locations, bottom depth, salinity, sigma t, temperature, fluorescence, nutrient concentrations, and cell densities

RV Connecticut July 9-11, 2019

Station	Latitude	Longitude	Bottom	Salinity	Sigma t	Temperature	Fluorescence	NO3+NO2	Si(OH)4	Diatoms	Alexandrium
	Decimal	Decimal	depth(m)	Sal00	Sigma-é00	°C	µg/L	(µM)	(µM)	(Cells/L)	(Cells/L)
1	42.599	-69.560	178	31.70	22.55	18.81	0.49	0.09	4.03	NaN	
2	43.622	-67.756	231	32.01	23.79	14.43	0.19	0.09	1.2	733	11
3	43.711	-67.849	221	32.16	23.99	14.04	0.53	0.07	1.7	900	10
4	43.804	-67.932	157	32.23	24.47	11.81	3.96	0.98	2.6	1,533	14
5	43.891	-68.029	168	32.31	24.75	10.61	4.54	1.7	2.8	700	9
6	43.983	-68.108	113	32.27	24.81	10.05	3.04	4.71	4.07	567	6
7	44.068	-68.198	98	31.33	23.77	11.84	3.74	0.84	1.55	9,000	48
8	44.160	-68.284	35	31.22	23.58	12.43	2.97	0.03	1.01	19,167	255
9	44.300	-68.009	60	31.28	23.67	12.14	4.07	0.33	1.44	108,333	89
10	44.216	-67.913	75	31.88	24.55	9.77	1.34	5.02	3.37	6,133	164
11	44.122	-67.825	91	31.98	24.66	9.57	1.37	5.33	3.96	3,239	262
12	44.037	-67.730	142	32.29	24.78	10.35	2.77	1.2	5.19	1,767	26
13	43.949	-67.635	201	32.25	24.36	12.50	1.33	0.03	1.57	1,200	4
14	43.857	-67.546	207	32.05	24.00	13.55	0.66	0.06	1.84	433	0
15	43.766	-67.454	228	31.95	23.63	14.93	0.35	0.03	1.15	1,133	2
16	43.945	-67.045	173	32.25	24.31	12.74	0.33	0.03	1.82	1,967	6
17	44.023	-67.151	127	32.27	24.39	12.39	0.47	0.04	1.79	1,367	4
18	44.102	-67.260	158	32.44	24.78	11.02	0.73	1.36	2.54	1,767	0
19	44.177	-67.364	207	32.39	24.49	12.37	0.46	0.09	1.85	8,889	0
20	44.257	-67.468	180	32.29	24.37	12.62	0.53	1.48	2.19	4,274	187
21	44.335	-67.567	61	32.07	24.64	10.16	0.33	5.94	4.08	2,853	2,814
22	44.414	-67.686	48	31.63	24.10	11.30	0.46	4.12	3.19	4,031	586
23	44.574	-67.279	68	31.54	24.24	10.10	0.83	4.7	3.49	2,796	64
24	44.532	-67.209	70	32.05	24.78	9.15	0.83	6.07	4.09	1,900	799
25	44.479	-67.120	90	32.08	24.87	8.76	1.51	5.4	3.77	5,521	240
26	44.422	-67.037	120	32.29	24.88	9.70	3.00	1.91	2.37	9,035	229
27	44.369	-66.952	124	32.22	24.81	9.86	2.67	2.01	2.36	14,444	908
28	44.309	-66.868	175	32.23	24.80	9.91	3.09	1.49	2.13	4,268	65
29	44.256	-66.781	181	32.13	24.74	9.82	2.53	2.78	2.78	4,474	39
30	44.197	-66.685	154	31.92	24.70	9.00	2.66	2.52	2.24	82,222	250
31	44.149	-66.599	94	32.15	24.93	8.72	2.24	2.7	2.46	55,000	369
32	44.537	-66.118	93	31.92	24.50	10.25	2.70	2.59	2.89	24,583	3,378
33	44.580	-66.191	118	31.94	24.66	9.36	1.29	3.23	2.69	7,778	355
34	44.623	-66.264	140	32.08	24.75	9.55	1.22	2.93	2.89	10,648	2,046
35	44.670	-66.335	133	31.85	24.45	10.23	1.10	2.09	2.46	3,864	2,254
36	44.708	-66.403	165	31.53	24.00	11.42	1.28	0.36	1.73	900	447
37	44.754	-66.469	164	31.46	23.67	12.94	0.42	0.09	0.8	200	24
38	44.706	-66.486	170	31.47	23.64	13.12	0.38	0.02	0.86	NaN	15
39	44.801	-66.548	124	31.72	24.19	11.20	1.02	0.12	1.66	567	24
40	44.846	-66.619	122	31.34	23.68	12.37	0.80	1.13	1.86	900	52
41	44.890	-66.682	102	30.74	23.26	12.14	0.91	3.47	2.15	1,800	21
42	44.936	-66.757	67.9	31.05	23.59	11.62	0.89	3.52	2.96	1,600	2,093
43	44.982	-66.824	67	31.37	24.15	9.86	1.15	4.17	3.62	2,394	1,148

Table 9.. August 2019 sampling locations, bottom depth, salinity, sigma t, temperature, fluorescence, nutrient concentrations, and cell densities

RV Connecticut August 10-12, 2019

Station	Latitude	Longitude	Bottom	Salinity	Sigma t	Temperature	Fluorescence	NO3+NO2	Si(OH)4	Diatoms	Alexandrium
	Decimal	Decimal	depth(m)	Sal00	Sigma-é00	°C	µg/L	(µM)	(µM)	(Cells/L)	(Cells/L)
1	44.119	-68.145	66	32.01	24.47	10.88	1.87	4.73	4.52	16,061	12
2	44.234	-67.937	73	31.87	24.06	12.54	3.18	1.42	3.58	40,333	82
3	44.390	-67.635	50	32.02	24.33	11.69	1.47	4.46	4.60	2,158	39
4	44.567	-67.295	65	32.01	24.46	10.94	0.86	5.11	4.35	6,731	65
5	44.532	-67.207	76	32.33	24.80	10.40	0.40	5.71	4.78	11,250	89
6	44.477	-67.122	79	32.30	24.76	10.49	0.51	5.02	4.57	20,185	99
7	44.421	-67.035	139	32.40	24.88	10.23	0.54	4.97	4.56	19,630	69
8	44.365	-66.955	123	32.38	24.64	11.54	0.62	1.24	2.45	9,630	55
9	44.317	-66.864	177	32.23	24.52	11.52	2.41	0.89	1.74	66,111	0
10	44.254	-66.777	182	32.16	24.58	10.90	2.39	0.75	2.14	NaN	6
11	44.198	-66.686	159	32.18	24.69	10.33	1.52	2.14	3.02	NaN	11
12	44.537	-66.113	88	32.05	24.25	12.29	2.03	0.61	2.78	5,469	804
13	44.580	-66.189	116	31.95	24.05	12.88	1.68	0.20	2.05	7,200	867
14	44.623	-66.263	138	31.77	23.74	13.78	0.66	0.03	1.96	2,693	434
15	44.669	-66.346	123	31.82	23.69	14.19	0.45	0.18	1.94	2,581	487
16	44.707	-66.400	161	31.80	23.83	13.46	0.58	1.05	2.52	2,512	314
17	44.754	-66.469	162	31.87	23.71	14.30	0.38	0.49	2.64	NaN	476
18	44.801	-66.547	122	31.50	23.41	14.39	0.50	0.25	2.41	NaN	135
19	44.845	-66.617	123	31.40	23.57	13.19	0.71	0.93	1.68	NaN	70
20	44.890	-66.681	102	31.62	23.85	12.60	0.79	0.13	1.54	NaN	91
21	44.934	-66.754	71	31.69	23.99	12.17	1.92	1.58	2.35	NaN	43
22	44.981	-66.821	68	31.68	24.04	11.87	1.47	1.19	2.18	NaN	25

BIOGRAPHY OF THE AUTHOR

Kimberly Lina D'Adamo was born in the Bronx, New York, in 1995, where she graduated from Preston High school in 2013. She graduated with Magna Cum Laude when receiving a Bachelor of Science degree in Biology: Ecology and Conservation and also minored in psychology at Sacred Heart University, Fairfield, Connecticut, in 2017. She was on the Women's Division 1 Rowing team. She was on the Dean's List and the Metro Atlantic Athletic Conference (MACC) Academic Honor Roll. At Sacred Heart, she was an Academic Enrichment Specialist and Classroom Learning Assistant. She was also a member of Nu Phi Chapter of Beta Beta Beta Biological Honor Society and the Sacred Heart Biology Club. She was a research assistant for a few years, which included studying abroad in Ireland, and it was her professors that she conducted research for that sparked her motivation to continue her education. She is a candidate for the Master of Science degree in Marine Biology from the University of Maine in August 2020.