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The physical and biological mechanisms controlling the winter-spring phytoplankton bloom in Long Island Sound

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Abstract of the Thesis

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The spring phytoplankton bloom is an annual event that occurs at middle and high latitudes, in the world's oceans, is an important source of organic matter for marine food webs, and can influence global carbon cycles. The spring bloom is controlled by many physical and biological factors. This study examined the biological and physical mechanisms controlling the onset and demise of the spring phytoplankton bloom in Long Island Sound (LIS) during 2010 and 2011 with a focus on zooplankton grazing, phytoplankton growth, and the effects of increased seawater temperature on these factors. During 2010 and 2011, the spring bloom initiated when there was no stratification of the water column (ΔT from surface to bottom = -0.02 °C and -0.28 °C, respectively), and peaked in early February when temperatures were at the annual minimum (1.0 °C and 0.8 °C). The bloom magnitude and duration were a function of phytoplankton growth and zooplankton grazing, with bloom initiation occurring when cellular growth exceeded grazing (net growth rates were 0.34 d^{-1} and 0.35 d^{-1}), and the bloom demise

occurring when grazing exceeded growth (>100% of primary productivity grazed per day). During the bloom collapse, nutrients were drawn down and the phytoplankton community was nitrogen-limited, suggesting the bloom demise was due to both top-down and bottom-up effects. Over the entire study, measured percentages of primary production consumed daily by microzooplankton were capable of accurately forecasting the occurrence of the spring bloom during both study years. Mesocosm experiments demonstrated that experimentally increased seawater temperature (+3C^{o}) increased zooplankton grazing and decreased phytoplankton biomass. This study demonstrates that the winter-spring bloom in LIS is controlled by the interaction of phytoplankton growth and zooplankton grazing but not water column stratification, and that phytoplankton growth and zooplankton grazing are, in turn, controlled by temperature and nutrient availability.

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INTRODUCTION

The spring phytoplankton bloom is an annual event that occurs at middle and high latitudes in the world's oceans and is characterized by a significant accumulation of phytoplankton biomass in the upper water column (Sverdrup 1953; Riley 1967; Behrenfeld 2010). The spring bloom results in a significant net uptake of carbon dioxide and as bloom-associated plankton sink, this event can transport large amounts of organic carbon to the deep ocean and coastal benthos (Sommer and Lengfellner 2008; Bagniewski et al. 2011). As the spring phytoplankton bloom is grazed by zooplankton, energy is transferred and consequently made accessible to higher trophic levels (Mousseau et al. 1998; Daniels et al. 2006). Additionally, sinking plankton aggregates and zooplankton fecal pellets provide organic matter (POC) to benthic communities (Miller 2004). Thus, the spring phytoplankton bloom plays a key role in global carbon cycles and the functioning of marine food webs.

The physical and biological interactions responsible for the occurrence of the spring bloom have been studied for decades (Sverdrup 1953; Riley 1959; Townsend et al. 1994; Behrenfeld 2010). The magnitude and duration of the spring phytoplankton bloom are controlled by a variety of factors including temperature, stratification of the water column, availability of light and nutrients, and losses due to zooplankton grazing and respiration (Lucas et al. 1999; Mann et al. 2006). During the winter, low light levels and rapid, deep mixing of the surface ocean prevents net phytoplankton growth despite high nutrient levels. During the spring, temperature and light levels increase leading to stratification of the nutrient-rich, upper water column, facilitating rapid cellular growth of phytoplankton and consequently, a phytoplankton bloom. In late spring, nutrients in the surface layer become depleted resulting in slowed cellular

growth of phytoplankton as zooplankton stocks increase and contribute to bloom collapse (Sieracki et al. 1993; Miller 2004).

The spring phytoplankton bloom has been traditionally explained by the Critical Depth Hypothesis (Sverdrup 1953; Riley 1967; Smetacek and Passow 1990) that states that bloom initiation begins when the surface mixed layer shoals to a depth less than the critical depth that provides light levels sufficient for intrinsic phytoplankton growth rates to exceed cellular respiration rates thus permitting positive cellular growth (Sverdrup 1953; Platt et al. 1991; van Haren et al. 1998). Since Sverdrup's Critical Depth Hypothesis postulates that the bloom is a result of stratification above a certain depth, the most important factors controlling the initiation of the bloom are light and temperature. In the Critical Depth Hypothesis, Sverdrup (1953) assumed phytoplankton loss rates, including zooplankton grazing, to be constant over time leading to the idea that the spring bloom initiation results from increased phytoplankton cell division rates. Recently, however, Behrenfeld (Behrenfeld 2010; Boss and Behrenfeld 2010) has reconsidered the biological and physical mechanisms that control the North Atlantic spring bloom and has developed a new hypothesis, known as the Dilution-Recoupling Hypothesis as a replacement for the Critical Depth Hypothesis. The Dilution-Recoupling Hypothesis states that stratification of the water column is not required for the spring phytoplankton bloom to begin (Behrenfeld 2010). Rather, a deep winter mixed layer is a requisite for bloom formation since it dilutes the encounter of phytoplankton and zooplankton and thus allows net phytoplankton growth and phytoplankton biomass to accumulate (Behrenfeld 2010).

The Dilution-Recoupling Hypothesis is consistent with prior studies that have found that relaxed grazing pressure by zooplankton during cold months may contribute toward the initiation of the spring bloom (Martin 1970; Backhaus et al. 1999). In addition, during the past decade,

some studies have noted that during warm winters, there is a weak or absent spring phytoplankton bloom despite high nutrient levels, and it has been hypothesized this could be due to higher zooplankton grazing rates (Keller et al. 1999, 2001; Oviatt et al. 2002, 2004). Rose and Caron (2007) established that growth rates of herbivorous protists decline more rapidly with decreasing temperature than do those of phototrophic protists, and at very low temperatures, the maximal growth rates of herbivorous protists are less than half the maximal growth rates of phototrophic protists. They hypothesized that annual algal blooms are due, in part, to differences in the relationship between growth and temperature for phototrophic protists and their grazers (Rose and Caron 2007).

Although microzooplankton and mesozooplankton are both important grazers of phytoplankton, their different reproduction rates affect their role in controlling phytoplankton blooms (Calbet et al. 2003; Stoecker and Gustafson 2002). Microzooplankton have rapid growth and grazing rates (Olson and Strom 2002; Calbet and Landry 2004) and therefore often play a key role in the consumption of phytoplankton biomass (Stoecker et al. 2008) particularly during the North Atlantic spring phytoplankton bloom (Banse 1992; Verity et al. 1993; Gifford et al. 1995). These high grazing rates may be further enhanced by warm water temperatures through increased growth and reproduction rates of microzooplankton (Rose and Caron 2007).

This study examined the biological and physical mechanisms controlling the onset and demise of the spring phytoplankton bloom in Long Island Sound (NY-CT, USA) during 2010 and 2011. The temporal dynamics of the physical environment, nutrients, phytoplankton and zooplankton densities, and zooplankton grazing rates were investigated to determine the impacts of each factor on the initiation of the spring phytoplankton bloom. In addition, the effects of seawater temperatures on the spring bloom and zooplankton abundance and grazing rates were

examined experimentally through mesocosm experiments performed during the peak of the spring bloom each year.

METHODS

Field sampling

Seawater samples were collected from the upper mixed layer (~ 3 m) of central Long Island Sound (41˚ 3.572 N, 73˚ 8.674 W) weekly to bimonthly during the months of December through April in 2010 and 2011. Seawater was collected in the mornings between 9 am and 12 pm from the *RV Pritchard* and the *RV Privateer* of Stony Brook University. In 2011, two additional sites westward of the central LIS sampling site were studied; Execution Rock (40˚ 52.320N, 73˚ 44.040W) and a site between the central station and Execution Rock (40˚ 59.085N, 73˚ 27.038W). These additional sites were visited bimonthly on the SoMAS vessel, the *RV Seawolf*.

Water Properties

On station, the water column was characterized for temperature, salinity and photosynthetically-active radiation (PAR) using a Seabird CTD. In addition, a handheld YSI 85 probe was used to record surface temperature, salinity and dissolved oxygen. Seawater samples were filtered through a combusted (2h at 450ºC) glass-fiber filter (GF/F) and analyzed for dissolved nutrient concentrations, including silicate, nitrate, nitrite, ammonium, and inorganic phosphate using standard wet chemistry and colorimetric methods (Parsons et al. 1984) adapted to a 96-well plate reader. Total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) were analyzed in triplicate by persulfate oxidation techniques (Valderrama 1981) and dissolved organic nitrogen (DON) and dissolved organic phosphate (DOP) were calculated by subtracting

levels of inorganic nitrogen and phosphorus pools from concentrations of TDN and TDP. Particulate organic carbon and nitrogen (POC, PON) samples were collected on combusted glass-fiber filters (GF/F, 0.7µm nominal pore size) and stored frozen. POC and PON samples were then dried at 60˚C before analysis on a Carlo Erba NA 1500 NCS system (Cutter et al. 1991).

Phytoplankton community characterization

The total phytoplankton community was characterized using size-fractionated chlorophyll *a*, flow cytometric analysis of small phytoplankton (< 2 µm), and microscopic analysis of larger nano- and microphytoplankton (> 2 µm). Together, these analyses provided a comprehensive assessment of the phytoplankton communities in Long Island Sound (LIS). All plankton community characterizations for this project focused on the upper mixed layer in LIS, which is typically highly similar in composition to populations found at depth, with the latter being lower in biomass (Capriulo et al. 2002).

Size-fractionated phytoplankton biomass was estimated by quantifying concentrations of chlorophyll *a* retained on 0.2 µm, 2 µm, and 20 µm polycarbonate filters to determine biomasses of picoplankton (0.2 – 2 µm), nanoplankton (2 – 20 µm), and microplankton (> 20 µm), respectively. Chlorophyll *a* analysis was performed using the non-acidification method using a Turner Designs Trilogy fluorometer (Welschmeyer 1994). Whole seawater was also preserved in 5% Lugol's iodine solution for enumeration of plankton (>5 μm) under an inverted microscope. The total number of microphytoplankton and microzooplankton were characterized and quantified using inverted light microscopy on Lugol's iodine stained cells. Whole seawater samples were collected from the surface mixed layer and preserved immediately in acidic Lugol's iodine (5% final concentration) and stored in the dark (Stoecker et al. 1994). Samples

were analyzed using standard settling techniques and inverted light microscopy (Hasle 1978) and the abundances of autotrophic flagellates, dinoflagellates, diatoms, non-loricate ciliates and tintinnids were quantified. A minimum of 200 organisms or 100 grids were counted per sample (Omori and Ikeda 1984).

Whole seawater samples were preserved with 10% buffered formalin (0.5% v/v final) and analyzed flow cytometrically to assess picoplankton densities (Olson et al. 1991). Abundances of heterotrophic bacteria (stained with SYBR Green I; Jochem 2001), phycoerythrin-containing picocyanobacteria, and photosynthetic picoeukaryotes were quantified using a FACSCalibur (BD®) flow cytometer using fluorescence patterns and particle size from side angle light scatter (Olson et al. 1991). Flow cytometric images were analyzed using Cyflogic version 1.2.1 (©Perttu Terho & ©CyFlo Ltd).

Zooplankton communities

The composition of preserved plankton samples in DAPI-stained microscope slides, Lugol's iodine solution, and 10% buffered formalin was determined to major taxonomic/trophic groups at a minimum and to the species level when possible to characterize the zooplankton communities in LIS. The total number of nanophytoplankton and nanozooplankton were characterized and quantified using epifluorescence microscopy on DAPI-stained material. Whole seawater samples (20-50 ml) were preserved with 1% gluteraldehyde, DAPI-stained, filtered through 0.8 µm polycarbonate filters, and mounted on microscope slides (Porter and Feig 1980, Gifford and Caron 2000), and stored frozen until processing. Samples were enumerated using a Zeiss Axioskop HBO 50 epifluorescence trinocular microscope (Porter and Feig 1980, Gifford and Caron 2000). DAPI-stained samples were analyzed for heterotrophic and autotrophic flagellates, heterotrophic and autotrophic dinoflagellates, and ciliates.

The mesozooplankton community was characterized and quantified using light microscopy on formalin-preserved organisms. Oblique net tows with a 64-µm and a 202-µm net fitted with a flowmeter were performed off the back of the boat. Net tow samples were filtered through a 64-µm sieve for both nets and preserved in 10% buffered formalin (final concentration 5%). Samples were identified and enumerated to the lowest taxonomic level using an Olympus SZX12 dissecting microscope. Samples were analyzed for nauplii, copepods, and non-copepod mesozooplankton.

Experimental Incubations

Experiments were conducted at Stony Brook University's Flax Pond Marine Laboratory in the greenhouse, located on the shoreline of LIS using tanks (2 m^3) filled with LIS seawater and equipped with dual-control heaters and chillers and circulation pumps. The temperature of the tanks was adjusted to match levels found in the upper water column of LIS during seawater collection and were adjusted for all incubations. Light and temperature in tanks were monitored every minute for the duration of the experiments with Onset© HOBO loggers. Maintenance of tanks in a greenhouse with semi-transparent screening ensured exposure of experimental bottles to 13% of natural, incoming irradiance at the surface of the tanks and 2% at the bottom, mimicking a depth of 1 - 4 m in LIS during winter months (Capriulo et al 2002). Placement of all experimental incubation bottles in these tanks permitted experiments to be performed at light and temperature levels that matched those of the upper water column of LIS when seawater was collected. Incubation experiments were specifically conducted to determine primary production, microzooplankton grazing, and intrinsic phytoplankton growth rates, and the effects of nutrients on intrinsic phytoplankton growth rates in LIS.

Primary production

Whole seawater samples for primary productivity studies were obtained from the upper mixed layer in LIS. Seawater was transferred into the light and dark bottles (n = 6 for each) with minimal aeration to minimize artificial increases in oxygen concentrations, and incubated for 24 hours (Parsons et al. 1984). Measurements of initial and final dissolved oxygen concentrations were determined using a Clark-style oxygen electrode (YSI 5100) according to Koch and Gobler (2009). Primary productivity measurements were obtained by converting dissolved oxygen concentrations to daily carbon production using the Redfield ratio of oxygen to carbon (138:106).

Phytoplankton grazing mortality and growth rates

The dilution technique is a method used for estimating *in situ* microzooplankton grazing (Landry et al. 1995). Seawater collected from the upper mixed layer in LIS was used to create a dilution series consisting of whole seawater (100%) and three dilutions (70%, 40%, 15%; n = 3 for each), all with nutrient enrichment (N, P, Si). An additional treatment of whole seawater without nutrient enrichment (n = 3) was included as the control (Landry et al. 1995). The series was diluted using 0.2 µm filtered seawater from the same sampling station. Experimental bottles (1.1-L, polycarbonate, acid-washed) were incubated for 48 hours. After incubation, changes in levels of whole chlorophyll *a* (using GF/F filters, 0.7 µm nominal pore size) and size-fractionated chlorophyll *a* (using 0.2 µm, 2 µm, and 20 µm polycarbonate filters) were determined and net growth rates were calculated. In addition, flow cytometric characterization of the phytoplankton community was performed to evaluate changes in plankton community composition.

Microzooplankton grazing coefficients (g; d^{-1}) and phytoplankton cellular growth coefficients (k; d^{-1}) were estimated by measuring the net rate of change of chlorophyll *a* (d^{-1})

(Landry et al. 1995). Grazing mortality was calculated from the regression between net phytoplankton growth rate (with nutrients) and fraction of whole seawater. This mortality estimate was then compared with the adjusted estimate of phytoplankton intrinsic growth without nutrients to assess the percentage of primary production consumed day^{-1} (Landry et al. 1995; Calbet and Landry 2004).

Phytoplankton nutrient limitation

Experiments were performed to determine if nutrients influenced the net growth rates of phytoplankton in LIS. Triplicate sets of bottles containing 100% whole seawater amended with nitrate (20 µM), silicate (20 µM), or phosphate (1.25 µM), a combination of all three (N+P+Si), or unamended whole seawater were prepared. These nutrient concentrations were similar to previously observed increases of these nutrients in the water column of LIS (Gobler et al. 2006), and ratios were consistent with Redfield stoichiometry. The bottles (1.1-L, polycarbonate, acid-washed) were incubated in the tanks describe above for 48 h after which changes in levels of chlorophyll *a* (using GF/F filters, 0.7 µm nominal pore size) were determined and net growth rates were calculated.

Mesocosm experiments

To evaluate the effects of temperature on the spring bloom plankton community, mesocosm experiments were conducted during the peak of the spring bloom each year at ambient and experimentally-altered temperature regimes. The mesocosms were 300-L cylindrical, translucent polyethylene tanks which have been used successfully in the past to assess the impacts of a sundry of environmental variables on the structure of coastal planktonic communities (Cerrato et al. 2004, Wall et al. 2008, 2011). There were four mesocosm replicates for two temperature treatments (ambient, +3º C) for a total of eight mesocosms. The mesocosms

were kept at a desired temperature by being placed in 2 m^3 tanks (described above), each set to a specific temperature level. At the beginning of each experiment, ambient temperature was measured and the two temperature levels (ambient, +3º C) were set accordingly. Temperatures in tanks were monitored every minute for the duration of the experiments with Onset© HOBO loggers.

Seawater was transferred from the surface mixed layer at the entrance of Stony Brook Harbor, located along the southern shores of LIS < 10 km from the primary sampling site, an hour before high tide when the water flow was strongest into a 5,000-L tank. Initial plankton communities, nutrient levels, temperature, and salinity of the seawater used for mesocosm experiments were not significantly different from what was found for the primary sampling site in LIS. Mesocosms were simultaneously filled by pumping approximately 250 L of seawater from the holding tank into each mesocosm. An additional replicate mesocosm was filled in tandem to characterize the plankton community, nutrients, and initial zooplankton grazing rates. Seawater was specifically collected at the initiation of the spring bloom each year and the mesocosms were maintained under experimental conditions for two - three weeks allowing phytoplankton and heterotrophic protists to respond to the altered temperatures (Graneli and Turner 2002). Nutrients (N, P, Si) were added daily in ratios consistent with the Redfield stoichiometry.

Plankton samples and incubations

Whole chlorophyll *a* (using GF/F filters, 0.7 µm nominal pore size) was measured daily and size-fractionated chlorophyll *a* (0.2 µm, 2 µm, and 20 µm) was measured every other day to assess the impacts of temperatures on changes in pico-, nano- and microphytoplankton biomass. Physical and chemical parameters (temperature, salinity, dissolved nutrients and POC/PON),

characterization of the plankton community (chlorophyll *a*, flow cytometry, DAPI-stained nanoplankton samples, and Lugol's samples), primary productivity measurements, and microzooplankton grazing experiments were performed at the beginning, and thereafter each week at each experimental temperature. All sample processing and experimental incubations were performed as described above for the field component of this project.

Statistical analyses

Over the course of the study, central LIS was sampled on 22 occasions. Relationships between measured parameters were evaluated by means of a Spearman's rank order correlation matrix. *P*-values <0.05 were deemed to be significantly correlated and the correlation coefficient reported as r. For nutrient amendment experiments, differences in phytoplankton net growth rates among treatments for each size class of plankton pigments were statistically evaluated using analyses of variance (ANOVA). During mesocosm experiments, comparison of parameters among temperature treatments were statistically assessed by means of Student T-tests.

RESULTS

Winter/Spring bloom dynamics

2010 winter/spring bloom

In 2010, the Long Island Sound (LIS) spring phytoplankton bloom occurred in early February, with chlorophyll *a* concentrations reaching 11 µg L^{-1} and primary production rates of 0.51 ± 0.08 mg C L^{-1} d^{-1} during the bloom peak (Fig. 2; Table 2,3). Chlorophyll *a* concentrations averaged 3 µg L^{-1} prior to the bloom in late January and dropped to less than 2 µg L^{-1} after the bloom demise in late February (Fig. 2; Table 2). The bloom community was comprised of a mix

of picophytoplankton (0.2–2 µm; 36%), nanophytoplankton (2–20µm; 30%) and microphytoplankton (35%; >20µm; Table 2). Diatoms dominated the autotrophs during bloom, with densities increasing from approximately 100 cells mL^{-1} before the bloom to ~7,000 cells mL^{-1} during the bloom peak (Fig. 4; Table 3). The dominant diatom genera during the bloom were *Leptocylindrus*, *Skeletonema*, and *Guinardia*. Other autotrophs such as dinoflagellates, picoeukaryotes, and picocyanobacteria were less abundant (63 ± 58 cells mL^{-1}, 1,310 ± 226 cells mL^{-1} and 159 ± 5 cells mL^{-1}, respectively; Fig. 4; Table 3) whereas heterotrophic bacteria densities averaged 3.68 ± 0.46 x 10^5 cells mL^{-1} and increased after the bloom (Table 3).

The zooplankton population during the 2010 bloom was numerically dominated by heterotrophic nanoflagellates (HNAN), which increased from concentrations of 400 cells mL^{-1} before the bloom, to more than 5,000 cells mL^{-1} at the peak of the bloom, and decreased to 3,000 cells mL^{-1} at the end of the bloom (Table 3). In contrast, heterotrophic dinoflagellate abundances (0 – 413 cells mL^{-1}; Table 3) were low during January and early February but peaked in late February and March whereas ciliate densities remained constant throughout the bloom but decreased after the bloom collapse (concentrations ranged from 5 – 9 cells mL^{-1}; Table 3). Copepods comprised 86% of the mesoplankton community in 2010 and were dominated by the genus *Acartia* (Table 3). Mesozooplankton densities were 3 ± 1 individuals L^{-1} during January and early February but increased to 8 ±2 cells L^{-1} in late February and March during the bloom demise (Table 3).

The spring phytoplankton bloom had a strong effect on nutrient concentrations in LIS as dissolved inorganic nitrogen, orthophosphate, and silicate were reduced by 100%, 84%, and 96%, respectively, and all three were drawn down to less than 1.5 µM (25 Feb; Fig. 2). At this time, the experimental addition of nitrate significantly increased the concentration of

phytoplankton biomass relative to the control and all other treatments ($p<0.05$; Tukey test). On all other dates, nutrient levels were higher and the addition of nutrients did not alter the net growth rates of phytoplankton. The 2010 bloom coincided with the lowest surface seawater temperatures of the year, with the peak of the bloom occurring around 1 ºC (Fig. 1). The difference in temperature from the surface to the bottom of LIS (= ΔT) averaged -0.11 ºC during the bloom (ΔT = -0.02 ºC during bloom initiation), indicating it was warmer at depth and suggesting minimal stratification during the bloom (Fig. 1). Surface salinity ranged from 25.9 – 26.7 during the bloom, with a mean value of 26.4 ± 0.2 from January to March (Table 1); differences between surface and bottom salinities (= ΔS) were always less than -1.19 (mean ΔS = -0.49 ± 0.48 during the bloom).

Phytoplankton growth and microzooplankton grazing

Significant rates of microzooplankton grazing and phytoplankton intrinsic growth were detected throughout this project, even when surface temperatures were 1ºC (Table 4). Intrinsic growth rates of phytoplankton averaged 0.40 ± 0.11 d^{-1} during the initiation and peak of the bloom, but declined significantly during the bloom collapse (Fig. 3). Microzooplankton grazing rates were low during the bloom initiation period (0.15 ± 0.03 d^{-1}), but rose sharply during the peak and demise of the bloom (0.62 ± 0.11 d^{-1}; Fig. 4) when these rates exceeded phytoplankton intrinsic growth rates and resulted in 100 – 400% of primary production being consumed d^{-1} (9 and 25 February; Table 4). Microzooplankton grazing of picoplankton (heterotrophic bacteria, picoeukaryotes, and picocyanobacteria) was similar to those of chlorophyll *a* in pattern (peaking during the bloom demise) and magnitude (0.27 ± 0.13 d^{-1}, 0.39 ± 0.33 d^{-1}, 0.40 ± 0.24 d^{-1} respectively; Table 5).

2011 winter/spring bloom

The 2011 LIS spring phytoplankton bloom occurred in early February, similar to 2010, but was about 40% more intense with chlorophyll *a* concentrations reaching 15 µg L^{-1} and primary production rates reaching 0.74 ± 0.05 mg C L^{-1} d^{-1} during the peak of the bloom (Fig. 5; Table 4). Chlorophyll *a* concentrations (2 - 4 µg L^{-1}) and productivity rates (0.05 – 0.09 mg C L^{-1} d^{-1}) were low before and after the bloom occurred (Fig. 5; Table 2,4). The 2011 bloom community was comprised of 12%, 28%, and 60%, pico-, nano- and microphytoplankton, respectively (Table 2). Diatoms dominated the microplankton community of the bloom, with densities increasing from approximately 100 cells mL^{-1} before the bloom to approximately 9,000 cells mL^{-1} during the bloom peak and decreasing to 2,000 cells mL^{-1} during the bloom demise (Fig. 7). The dominant genera during the 2011 bloom were *Skeletonema*, *Thalassiosira*, and *Thalassionema*. Picoeukaryotes, picocyanobacteria, and autotrophic dinoflagellates were minor components of the bloom (2.67 ± 2.57 x 10^3, 131 ± 114, and 19 ± 22 cells mL^{-1}, respectively (Table 3). Heterotrophic bacteria densities averaged 3.00 ± 0.32 x 10^5 cells mL^{-1}, and generally increased during the bloom demise (Table 3).

The grazing population during the 2011 bloom was numerically dominated by heterotrophic nanoflagellates (HNAN), which increased from concentrations of 800 cells mL^{-1} before the bloom to over 3,200 cell mL^{-1} at the peak of the bloom (Table 3). On the other hand, heterotrophic dinoflagellate and ciliate concentrations remained low throughout the bloom, increasing slightly during the bloom collapse (ranging from 0 – 210 cells mL^{-1} and 2 – 25 cells mL^{-1} respectively; Figure 7; Table 3). Copepods comprised 76% of the mesoplankton community between January and March, and were dominated by the genus *Acartia* (Table 3). Mesozooplankton densities were 2 ± 1 individuals L^{-1} during January and early February, and increased to 4 ± 1 cells L^{-1} in late February and March during the bloom demise (Table 3).

The spring phytoplankton bloom had a strong effect on the nutrients in LIS (Fig. 5). During the bloom concentrations of dissolved inorganic nitrogen, orthophosphate, and silicate were reduced by 92%, 64%, and 86% respectively and all three were drawn down to less than 2.6 µM during the bloom peak (24 Feb; Fig. 5). At this time, experimental nitrate enrichment significantly increased the concentration of phytoplankton biomass relative to the control and all other treatments ($p<0.05$; Tukey test). Nutrients did not alter the net growth rates of phytoplankton on any other date in 2011. The spring bloom coincided with the lowest surface seawater temperatures of the year and remained $\leq$1 ºC throughout the bloom (Fig. 5). Difference in temperature between the surface to the bottom of LIS (= ΔT) averaged 0.14 ºC during the bloom, however ΔT was -0.28 ºC during bloom initiation, suggesting colder surface temperatures during bloom initiation and warming of the upper mixed layer during the bloom demise (Fig. 5). In 2011, surface salinity measurements ranged from 27.4 – 28.1 during the bloom, with a mean value of 27.7 ± 0.2 (Table 1); differences between surface and bottom salinities (= ΔS) were always less than -1.34 (mean ΔS = -0.15 ± 0.24 during the bloom).

Phytoplankton growth and microzooplankton grazing

Cellular growth rates of phytoplankton were low prior to the spring bloom (0.21 ± 0.04 d^{-1}; 6 Jan), increased three-fold during bloom initiation (0.60 ± 0.02 d^{-1}; 30 Jan), and then decreased down to pre-bloom levels during the peak and demise of the bloom (0.23 ± 0.08 d^{-1}; 7-24 Feb; Fig. 6). Microzooplankton grazing rates followed a pattern similar to those displayed by phytoplankton intrinsic growth rates, but were offset by ~ two weeks. The highest grazing rate occurred during the bloom peak (10 - 24 February; mean grazing value of 0.35 ± 0.04 d^{-1}; Fig. 6) which resulted in 100 - 340% of primary production being consumed per day (Fig. 6; Table 4). Size-fractionated chlorophyll *a* grazing rates revealed significantly higher grazing on

microphytoplankton (0.54 ± 0.06 d^{-1} on cells > 20 µm) during the bloom compared to pico- and nanophytoplankton ($p<0.05$; Tukey test). Microzooplankton grazing rates on heterotrophic bacteria remained constant throughout the bloom, while grazing on picocyanobacteria increased during the peak and collapse of the bloom, and grazing on picoeukaryotes increased at the end of the bloom (Table 5). Mean grazing rates of microzooplankton on heterotrophic bacteria, picocyanobacteria, and picoeukaryotes were 0.32 ± 0.14 d^{-1}, 0.39 ± 0.26 d^{-1}, and 0.13 ± 0.08 d^{-1}, respectively (Table 5).

For the entire study (2010 and 2011), the percent primary production consumed by the microzooplankton measured during a given sampling was significantly correlated with *in situ* changes of phytoplankton biomass in LIS between that sampling date and the following sampling date ($p = 0.01$; Fig 8A). Changes in chlorophyll *a* concentrations in LIS were predicted using the equation of the regression of net phytoplankton growth rates and percent primary productivity grazed and the levels of chlorophyll measured on the first sampling date each year (Fig 8B,C). While these predicted chlorophyll *a* concentrations were, on average, 31% lower than the observed chlorophyll *a* in LIS during the peak of the bloom, the general bloom pattern was successfully predicted for both years, with higher temporal accuracy in 2011 (Fig. 8).

Cross-LIS sampling

During 2011, two additional sites, western Long Island Sound (WLIS) and the Narrows, were sampled in addition to the central LIS (CLIS) sampling site (Fig. 1), allowing for cross-LIS examination of phytoplankton intrinsic growth and zooplankton grazing. Chlorophyll *a* concentrations increased westward along the Sound, showing significantly lower chlorophyll *a* levels at the regularly sampled CLIS site (15.34 ± 0.77 µg L^{-1}) compared to the Narrows (27.52 ±0.76 µg L^{-1}; $p<0.05$) during the bloom peak (Fig. 9). Microzooplankton grazing of

phytoplankton increased westward across LIS as well, with sites hosting higher chlorophyll *a* concentrations having higher grazing. Mean grazing coefficients at CLIS, western Long Island Sound (WLIS), and the Narrows were 0.22 ± 0.12 d^{-1}, 0.28 ± 0.16 d^{-1}, and 0.51 ± 0.19 d^{-1}, respectively (Fig. 9).

Mesocosm experiments

2010 Mesocosm experiment

The 2010 mesocosm experiment was conducted from February 18 – March 4, at two temperature treatments; 1 ºC and 4 ºC (Fig. 10). During this experiment chlorophyll *a* levels averaged 9.5 µg L^{-1} during the first week, and showed a separation between the two temperature treatments by the end of the experiment, with the 1 ºC mesocosm harboring significantly higher levels of chlorophyll *a* ($p<0.05$; t-test). The 1 ºC mesocosm also had significantly higher levels of diatoms and significantly lower levels of ciliates compared to the 4 ºC mesocosm (1 ºC and 4 ºC diatoms levels = 6,710 ± 361 and 3,505 ± 497 cells mL^{-1} respectively; $p< 0.01$; t-test); 1 ºC and 4 ºC ciliate levels = 13 ± 3 and 30 ± 5 cell mL^{-1} respectively; $p<0.05$; t-test; Fig. 10). Microzooplankton grazing and phytoplankton cellular growth rates were lower in the 1 ºC mesocosm compared to the 4 ºC mesocosm (mean grazing rates of 0.17 ± 0.03 and 0.26 ± 0.07 d^{-1} respectively; and mean growth rates of 0.19 ± 0.13 and 0.30 ± 0.20 d^{-1} respectively; Fig. 9; Table 6). Heterotrophic nanoflagellates abundances increased slightly by the end of the experiment, and were similar for both temperature treatments (4.51 ± 0.61 x 10^3 and 4.80 ± 0.23 x 10^3 cells mL^{-1} for 1 ºC and 4 ºC; Table 6). The addition of inorganic nutrients (nitrate, phosphate, and silicate) yielded higher total chlorophyll *a* growth rates relative to unamended samples for both temperature treatments (Table 6).

2011 Mesocosm experiment

The 2011 mesocosm experiment was conducted from February 8 – 28 again at 1 ºC and 4 ºC (Fig. 10). During this experiment chlorophyll *a* levels decreased during the first week, and then remained constant during the second week and displayed separation between treatments during the third week, with the 1 ºC mesocosm showing significantly higher levels of chlorophyll *a* (1 ºC and 4 ºC chlorophyll *a* levels = 5.66 ± 0.20 and 4.47 ± 0.25 µg L^{-1} respectively; $p<0.01$; t-test). The 1 ºC mesocosm also had significantly higher levels of diatoms compared to the 4 ºC mesocosm (1 ºC and 4 ºC diatom levels = 3,122 ± 791 and 1,108 ± 222 cells mL^{-1} respectively; $p<0.01$; t-test; Fig. 11). Unlike 2010, ciliate densities were similar between the 1 ºC and 4 ºC temperature treatment (ciliate densities were 74 ± 16 and 78 ± 11 cells mL^{-1} respectively; Fig. 11). Heterotrophic nanoflagellates abundances increased slightly by the end of the experiment, and were similar for both temperature treatments ($3.64 \pm 0.29 \times 10^3$ and $3.83 \pm 0.59 \times 10^3$ cells mL^{-1} for 1 ºC and 4 ºC; Table 6). Microzooplankton grazing rates and phytoplankton intrinsic growth rates were similar in the 1 ºC and 4 ºC temperature treatment (mean grazing rates of 0.35 ± 0.04 and 0.33 ± 0.04 d^{-1} respectively; mean growth rates of 0.32 ± 0.02 and 0.26 ± 0.11 d^{-1} respectively; Fig. 11; Table 6). Despite this, a comparison of percent primary production grazed showed a difference between the two temperature treatments, with lower levels of consumption in the 1 ºC mesocosm (106% compared to 133%; Table 6). The addition of inorganic nutrients (nitrate, phosphate, and silicate) yielded higher total chlorophyll *a* growth rates relative to unamended samples for all temperature treatments (Table 6).

DISCUSSION

The spring phytoplankton bloom is an annual event that occurs in temperate ecosystems (Sverdrup 1953; Robinson 1970; Miller 2004), and is an important source of organic matter for

marine food webs and can influence global carbon cycles (Tian et al. 2000; Sommer and Lengfellner 2008; Bagniewski et al. 2011). The spring bloom can be controlled by both top-down and bottom-up processes, including grazing, nutrients, light, temperature, and mixing (Riley 1967; Miller 2004), and has most commonly been explained by the Critical Depth Hypothesis (Sverdrup 1953; Riley 1967). However, our understanding of plankton dynamics and the mechanisms that control the spring bloom continue to evolve (Behrenfeld 2010; Taylor and Ferrari 2011; Chiswell 2011). During 2010 and 2011, the winter-spring bloom in Long Island Sound (LIS) initiated when there was minimal stratification of the water column and the bloom peaked in early February during the coldest temperatures of each year. The bloom magnitude and duration was a function of phytoplankton intrinsic growth rates and microzooplankton grazing rates with bloom initiation occurring when growth exceeded grazing, and the bloom demise occurred when grazing exceeded growth. In mesocosm experiments, increased temperature led to increased microzooplankton grazing and a reduction in phytoplankton biomass and the warmer of the two study years had a less intense spring bloom. Collectively, these results provide insight on the physical and biological factors that regulate the initiation and collapse of the winter-spring bloom, and provide support for an alternative hypothesis on the mechanisms controlling the North Atlantic spring bloom. Furthermore, these findings demonstrate how climatic warming may interact to affect the intensity of the spring bloom and thus collectively bring new insight to this phenomenon.

Initiation of the spring bloom in temperate ecosystems has been traditionally explained by the Critical Depth Hypothesis, which states that the spring bloom initiates when the mixed layer shoals above the critical depth (Sverdrup 1953). However, this hypothesis has recently been called into question by several researchers, most notably Behrenfeld (2010), Taylor and

Ferrari (2011), and Chiswell (2011), who also proposed alternative hypotheses for the North Atlantic spring bloom initiation. Behrenfeld's (2010) Dilution Recoupling Hypothesis challenged the belief that stratification is necessary for initiation of the spring bloom, and instead proposed that deep winter-mixing actually facilitates bloom formation. On the other hand, Taylor and Farrari (2011) and Chiswell (2011) demonstrated that stratification is necessary for spring bloom formation, but proposed alternative mechanisms and assumptions from Sverdrup's hypothesis in their air-sea flux reduction model and stratification-onset model, respectively (Taylor and Ferrari 2011; Chiswell 2011). While each alternative hypothesis is compelling, for the purposes of this discussion I will be focusing on the comparison between Behrenfeld and Sverdrups' hypotheses for the North Atlantic spring bloom.

Behrenfeld's Dilution-Recoupling Hypothesis postulates that the deep winter mixed layer creates a dilution of phytoplankton and zooplankton, allowing intrinsic phytoplankton growth to exceed grazing because of density-dependent grazing thresholds, and consequent initiation of the winter-spring bloom (Behrenfeld 2010). This hypothesis was developed using a nine-year satellite record of phytoplankton biomass, photosynthetically active radiation (PAR), and mixed layer depth in the North Atlantic (Behrenfeld 2010) and was confirmed by *in situ* physical and optical measurements using a profiling float in the North Atlantic by Boss and Behrenfeld (2010). Neither study, however, examined phytoplankton intrinsic growth rates in parallel with zooplankton grazing rates.

The physical and biological interactions observed during the 2010 and 2011 winter-spring bloom initiation in LIS generally support the findings in Behrenfeld (2010) and Boss and Behrenfeld (2010). During 2010 and 2011, the LIS winter-spring phytoplankton bloom initiation occurred during late-January when surface water temperatures were low (2.6 °C and 1.8 °C) and

there was minimal stratification in the water column (ΔT = -0.02 °C and -0.28 °C, respectively). These observations are clearly contrary to Sverdrup's hypothesis that stratification and shoaling of the mixed layer above a critical depth are necessary for the initiation of the spring bloom, but are consistent with Behrenfeld (2010) who showed that bloom initiation occurs in the winter when there is a deep mixed layer. Nevertheless, to verify this further, change in density (σ_T or σ_Θ) should also be looked at to assess differences in density in the water column during the onset of the LIS spring bloom for both years. In late-January during 2010 and 2011, phytoplankton cellular growth rates (0.34 ± 0.03 and 0.35 ± 0.24 d^{-1}, respectively) exceeded zooplankton grazing rates (0.15 ± 0.02 and 0.22 ± 0.14 d^{-1}, respectively) accounting for the accumulation of phytoplankton biomass during the spring bloom. Prior to the onset of the bloom and during the bloom initiation, dissolved inorganic nitrogen, silicate, and orthophosphate concentrations were high (6.4 ± 1.5, 34.9 ± 5.2, 1.6 ± 0.1 μM for 2010 and 11.6 ± 0.6, 39.1 ± 3.5, 2.4 ± 0.1 μM for 2011) and irradiance (PAR) was increasing. These conditions collectively indicate that the phytoplankton biomass increase during the LIS winter-spring bloom was driven by predator-prey interactions rather than simply phytoplankton specific growth rates or the onset of stratification (Banse 1992; Sverdrup 1953). The ability of measurements of the percentage of primary production grazed by zooplankton to predict the timing and approximate magnitude of the spring bloom in LIS each year further affirms this conclusion.

The winter-spring phytoplankton bloom in LIS was similar in 2010 and 2011 with regards to phytoplankton intrinsic growth rates and zooplankton grazing, but also displayed differences with regard to the intensity and phytoplankton taxa dominating the blooms. The 2010 and 2011 blooms had almost identical chlorophyll *a* patterns, with bloom initiation occurring in late-January, the peak occurring in early February, and bloom demise occurring in late February.

However, the two events differed in dominant phytoplankton groups, with the 2010 bloom equally dominated by pico-, nano-, and microphytoplankton (36%, 30%, and 35%) and the 2011 bloom largely dominated by microphytoplankton (60%). Diatoms numerically dominated the bloom both years, peaking at 6,500 and 9,000 cells mL^{-1} during 2010 and 2011. Consistent with prior studies (Stelfox-Widdicombe et al. 2000; Karayanni et al. 2005), the grazing population was numerically dominated by HNAN in both years, peaking at 5,000 and 3,200 cells mL^{-1} in unison with the spring bloom peak. Ciliate and copepod densities remained low during the bloom, and peaked during the bloom demise in late February and March for both years. Trends regarding diatoms and HNAN are consistent with my mesocosm experiments suggesting that lower temperatures during the spring bloom (as occurred in 2011) are likely to yield more diatoms and fewer grazers and lower community grazing rates.

The collapse of the North Atlantic spring phytoplankton bloom is traditionally considered to be the result of top-down (high grazing) and bottom-up (low nutrient) effects (Landry and Calbet 2004; Strom et al 2001; Johansson et al 2004; Banse 2002). During 2010 and 2011, the LIS winter-spring phytoplankton bloom demise was observed in late-February and in both years the bloom had a strong effect on dissolved nutrients (inorganic nitrogen, silicate, orthophosphate) in LIS, reducing nutrient levels by an average of 93% and 81% during the bloom demise in late February. Once these nutrients were depleted, intrinsic growth rates of phytoplankton decreased from 0.41 ± 0.04 and 0.34 ± 0.19 d^{-1} during the bloom initiation and peak to 0.17 ± 0.02 and 0.19 ± 0.06 d^{-1} during the bloom collapse for 2010 and 2011. These findings suggest a decrease in nutrient availability played a large role in decreasing phytoplankton cellular growth rates (Banse 2002) in late-February. This hypothesis was affirmed by nutrient amendment experiments that demonstrated that nutrient enrichment enhanced intrinsic growth rates of phytoplankton only

during the peak of the bloom in both years, when the addition of nitrate significantly increased the concentration of phytoplankton biomass relative to the control and all other treatments. Collectively, these data demonstrate that nitrogen limitation of phytoplankton cellular growth rates was partly responsible for the collapse of the spring blooms in 2010 and 2011.

In contrast to decreasing intrinsic growth rates of phytoplankton, microzooplankton grazing rates increased (two-fold and four-fold respectively) during the spring bloom collapse in late-February in 2010 and 2011. Furthermore, the percent of primary productivity grazed by zooplankton exceeded 100% both years only during the bloom demise. These findings demonstrate that the collapse of the winter-spring bloom was due to microzooplankton grazing rates exceeding the cellular growth rates of phytoplankton which were low due to nutrient limitation (Banse 1992; Behrenfeld 2010; Boss and Behrenfeld 2010). In addition, physical processes could have enhanced predator-prey interaction and microzooplankton grazing as the first signs of stratification were observed during the bloom collapse (2010 $\Delta T = 0.17$ °C; 2011 $\Delta T = 0.90$ °C). This lends support to the hypothesis that the phytoplankton bloom demise is caused by a recoupling of grazers to phytoplankton due to stratification of the water column and shoaling of the upper mixed layer (Behrenfeld 2010; Boss and Behrenfeld 2010).

Microzooplankton are important components of marine food webs and have been found to have an important role in the consumption of the North Atlantic spring phytoplankton bloom (Gifford et al. 1995; Stelfox-Widdicombe et al. 2000; Strom et al. 2001; Landry and Calbet 2004; Johansson et al 2004; Aberle 2007). Moreover, it has been hypothesized that warmer winters may lead to enhanced microzooplankton grazing pressure, resulting in a reduced or absent spring phytoplankton bloom (Martin 1965; Oviatt 1994; Li and Smayda 1998; Oviatt et al. 2004; Rose and Caron 2007). The LIS winter-spring bloom results from a balance between

growth and grazing, therefore it is important to understand how increased temperature will affect microzooplankton grazers in LIS and as a result, the phytoplankton bloom.

Mesocosm experiments conducted at 1 °C and 4 °C during the 2010 and 2011 spring blooms showed that higher temperatures yielded significantly lower phytoplankton biomass. In addition higher temperatures were related to higher microzooplankton grazing rates, more grazers, and/or more primary production consumed, all findings consistent with results from previous studies showing warmer temperature mesocosms had increased microzooplankton biomass, growth, and grazing (Aberle et al 2007). Also consistent with this pattern, ciliate and heterotrophic nanoflagellate densities increased in the 4 °C temperature mesocosm compared to the 1 °C mesocosm, confirming ciliates ability for fast reproduction and a shift in community towards increased ciliate abundance with warmer temperature (Aberle et al. 2007). In contrast, diatom densities and chlorophyll *a* levels showed the opposite trend, with diatom abundances decreasing two-to-three fold in the 4 °C mesocosm compared to the 1 °C mesocosm. These findings are consistent with studies reporting enhanced grazing (Aberle et al. 2007; Montagnes and Lessard 1999; Martin 1965) and a less intense phytoplankton bloom (Oviatt et al. 2002, 2004) with increased temperature. In addition, these findings are consistent with the implications of the Dilution-Recoupling Hypothesis (Behrenfeld 2010); increased winter water temperatures will lead to earlier stratification of the upper water column thereby leading to a recoupling of phytoplankton and grazers, resulting in increased grazing rates and lower phytoplankton biomass (Behrenfeld 2010; Boss and Behrenfeld 2010). Importantly, however, these mesocosm experiments demonstrate that higher temperatures can minimize the intensity of the spring bloom through enhanced grazing in the absence of any 'recoupling' since all mesocosms were well-mixed and not stratified. As such, Behrenfeld's (2010) observation that the spring bloom occurs

when temperatures are minimal may be due to lowered zooplankton grazing resulting from physiological responses (Rose and Caron 2009) or community structure effects (Aberle et al. 2007) rather than physical dilution. Regardless, this and previous studies (Evans and Parslow 1985; Marra and Barber 2005; Behrenfeld 2010) are contrary to the Critical Depth Hypothesis that increased temperature promotes the spring bloom through stratification and enhanced intrinsic growth rates of phytoplankton (Sverdrup 1953).

The North Atlantic spring phytoplankton bloom is controlled by biological and physical mechanisms with the accumulation of biomass dependent on a balance between phytoplankton growth and zooplankton grazing. Consistent with the Dilution-Recoupling Hypothesis presented in Behrenfeld (2010), I found that stratification of the water column was not needed for the winter-spring bloom initiation to occur, and phytoplankton biomass accumulation was a result of increasing net population growth rate rather than the traditionally considered phytoplankton specific growth rate (Sverdrup 1953). The phytoplankton bloom collapse occurred due to a shift in phytoplankton cellular growth rates and zooplankton grazing balance brought about by nitrogen limitation and a larger grazing impact by the zooplankton community. Results from the mesocosm experiments suggest the spring bloom collapse can be accelerated by increases in winter water temperatures due to increased microzooplankton grazing rather than a recoupling of grazers and phytoplankton. Given the expected 4ºC increase in global temperatures this century (I.P.C.C. 2007), the spring bloom may be significantly less intense in the future, an occurrence that could reduce the productivity of marine food webs and ocean carbon sequestration.

REFERENCES

Aberle N., Lengfellner K., Sommer U. (2007) Spring bloom succession, grazing impact and herbivore selectivity of ciliate communities in response to winter warming. Oecologia 150:668-681.

Alcaraz M., Saiz E., Calbet A., Trepat I., Broglio E. (2003) Estimating zooplankton biomass ugh image analysis. Marine Biology 143:307-315.

Backhaus J.O., Hegseth E.N., Wehde H., Irigoien X., Hatten K., Logemann K. (2003) Convection and primary production in winter. Marine Ecology-Progress Series 251:1-14.

Backhaus J.O., Wehde H., Hegseth E.N., Kampf J. (1999) 'Phyto-convection': the role of oceanic convection in primary production. Marine Ecology-Progress Series 189:77-92.

Bagniewski W., Fennel K., Perry M.J., D'Asaro E.A. (2011) Optimizing models of the North Atlantic spring bloom using physical, chemical and bio-optical observations from a Lagrangian float. Biogeosciences 8:1291-1307.

Banse K. (1992) Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. Primary productivity and biogeochemical cycles in the sea. Plenum Press, New York, NY Pg 409-440.

Banse K. (1994) Grazing and zooplankton production as key controls of phytoplankton production in the open ocean. Oceanography 7:13-20.

Banse K. (2002) Steeman Bielsen and the zooplankton. Hydrobiology 480:15-28.

Behrenfeld M.J. (2010) Abandoning Sverdrup's Critical Depth Hypothesis on phytoplankton blooms. Ecology 91:977-989.

Boss E., Behrenfeld M. (2010) In situ evaluation of the initiation of the North Atlantic phytoplankton bloom. Geophysical Research Letters 37.

Calbet A., Landry M.R. (2004) Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnology and Oceanography 49:51-57.

Capriulo G.M., Smith G., Troy R., Wikfors G.H., Pellet J., Yarish C. (2002) The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication. Hydrobiologia 475:263-333.

Cerrato R.M., Caron D.A., Lonsdale D.J., Rose J.M., Schaffner R.A. (2004) Effect of the northern quahog *Mercenaria mercenaria* on the development of blooms of the brown tide alga *Aureococcus anophagefferens*. Marine Ecology-Progress Series 281:93-108.

Chiswell S.M. (2011) Annual cycles and spring blooms in phytoplankton: don't abandon Sverdrup completely. Marine Ecology-Progress Series 443:39-50.

Conover, S.A.M (1956) Oceanography of Long Island Sound, 1952-54. IV. Phytoplankton Bulletin of the Bingham Oceanographic Collection 15:62-112.

Cutter L.S., Cutter G.A., Sandiegomcglone M.L.C. (1991) Simultaneous determination of inorganic arsenic and antimony species in natural-waters using selective hydride generation with gas-chromatography photoionization detection. Analytical Chemistry 63:1138-1142.

Dale T., Bagoien E., Melle W., Kaartvedt S. (1999) Can predator avoidance explain varying overwintering depth of Calanus in different oceanic water masses? Marine Ecology-Progress Series 179:113-121.

Daniels R.M., Richardson T.L., Ducklow H.W. (2006) Food web structure and biogeochemical processes during oceanic phytoplankton blooms: An inverse model analysis. Deep-Sea Research Part Ii-Topical Studies in Oceanography 53:532-554.

Evans G.T., Parslow J.S. (1985) A model of annual plankton cycles. Biological Oceanography 3:327-347.

Fry B., Wainright S.C. (1991) Diatom sources of C-13-rich carbon in marine food webs. Marine Ecology-Progress Series 76:149-157.

Gifford D.J., Fessenden L.M., Garrahan P.R., Martin E. (1995) Grazing by microzooplankton an mesozooplankton in the high-latitude North Atlantic Ocean – spring versus summer dynamics. Journal of Geophysical Research-Oceans 100:6665-6675.

Gifford D.J., Caron D.A. (2002) Sampling, preservation, enumeration and biomass of protozooplankton. ICES Zooplankton Methodology Manual, Academic Press, London Pg 193-221.

Gobler C.J., Buck N.J., Sieracki M.E., Sanudo-Wilhelmy S.A. (2006) Nitrogen and silicon limitation of phytoplankton communities across an urban estuary: The East River-Long Island Sound system. Estuarine Coastal and Shelf Science 68:127-138.

Gran, H.H., Braarud, T. (1935) A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine. Journal of the Biological Board of Canada 1:279-467.

Graneli E., Turner J.T. (2002) Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study. Marine Ecology-Progress Series 239:57-68.

Hasle G.R. (1978) Some *Thalassiosira* species with one central process (*Bacillariophyceae*). Norwegian Journal of Botany 25:77-110.

Hayward, T.L, Venrick, E.L. (1982) Relation between surface chlorophyll, integrated \ chlorophyll and integrated primary production. Marine Biology 69:247-252.

Henson S.A., Dunne J.P., Sarmiento J.L. (2009) Decadal variability in North Atlantic phytoplankton blooms. Journal of Geophysical Research-Oceans 114.

Intergovernmental panel on climate change (I.P.C.C). (2007)

Jochem F.J. (2001) Morphology and DNA content of bacterioplankton in the northern Gulf of Mexico: analysis by epifluorescence microscopy and flow cytometry. Aquatic Microbial Ecology 25:179-194.

Johansson M., Gorokhova E., Larsson U. (2004) Annual variability in ciliate community structure, potential prey and predators in the open northern Baltic Sea proper. Journal of Plankton Research 26:67-80.

Karayanni H., Christaki U., Van Wambeke F., Denis M., Moutin T. (2005) Influence of ciliated protozoa and heterotrophic nanoflagellates on the fate of primary production in the northeast Atlantic Ocean. Journal of Geophysical Research-Oceans 110.

Keller A.A., Klein-MacPhee G., Burns J.S. (1999) Abundance and distribution of ichthyoplankton in Narragansett Bay, Rhode Island, 1989-1990. Estuaries 22:149-163.

Koch F., Gobler C.J. (2009) The Effects of Tidal Export from Salt Marsh Ditches on Estuarine Water Quality and Plankton Communities. Estuaries and Coasts 32:261-275.

Kortzinger A., Send U., Lampitt R.S., Hartman S., Wallace D.W.R., Karstensen J., Villagarcia M.G., Llinas O., DeGrandpre M.D. (2008) The seasonal pCO(2) cycle at 49 degrees N/16.5 degrees W in the northeastern Atlantic Ocean and what it tells us about biological productivity. Journal of Geophysical Research-Oceans 113.

Landry M.R., Calbet A. (2004) Microzooplankton production in the oceans. Ices Journal of Marine Science 61:501-507.

Landry M.R., Kirshtein J., Constantinou J. (1995) A refined dilution technique for measuring the community grazing impact of microzooplankton, with experimental tests in the central equatorial Pacific. Marine Ecology-Progress Series 120:53-63.

Lochte K., Ducklow, H.W., Fasham, M.J.R., Stienen, C. (1993) Plankton succession and carbon cycling at 47N, 20W during the JGOFS North Atlantic Bloom Experiment. Deep-Sea Research II 40:91-114.

Li Y.Q., Smayda T.J. (1998) Temporal variability of chlorophyll in Narragansett Bay, 1973-1990. Ices Journal of Marine Science 55:661-667.

Lucas L.V., Koseff J.R., Cloern J.E., Monismith S.G., Thompson J.K. (1999) Processes governing phytoplankton blooms in estuaries. I: The local production-loss balance. Marine Ecology-Progress Series 187:1-15.

Mann K.H., Lazier R.N. (2006) Dynamics of marine ecosystems. Biological-Physical Interactions in the Oceans, Blackwell, Boston, MA

Marra J., Barber R.T. (2005) Primary productivity in the Arabian Sea: A synthesis of JGOFS data. Progress in Oceanography 65:159-175.

Martin J.H. (1965) Phytoplankton-zooplankton relationship in Narragansett Bay. Limnology and Oceanography 10:185-191.

Miller C.B. (2004) Biological Oceanography. Blackwell, Boston, MA

Montagnes D.J.S., Lessard E.J. (1999) Population dynamics of the marine planktonic ciliate *Strombidinopsis multiauris*: its potential to control phytoplankton blooms. Aquatic Microbial Ecology 20:167-181.

Mousseau L., Fortier L., Legendre L. (1998) Annual production of fish larvae and their prey in relation to size-fractionated primary production (Scotian Shelf, NW Atlantic). Ices Journal of Marine Science 55:44-57.

Olson M.B., Strom S.L. (2002) Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an Emiliania huxleyi bloom Deep-Sea Research Part Ii-Topical Studies in Oceanography 49:5969-5990.

Olson, R.J., Zettler, E.R., DuRand, M.D. (1991) Phytoplankton analysis using flow cytometry. Handbook of Methods in Aquatic Microbial Ecology 22:175-186.

Omori M., Ikeda T. (1984) Methods in marine zooplankton ecology. Sons Inc. USA Pg 332.

Oviatt C., Keller A., Reed L. (2002) Annual primary production in Narragansett Bay with no bay-wide winter-spring phytoplankton bloom. Estuarine Coastal and Shelf Science 54:1013-1026.

Oviatt C.A. (2004) The changing ecology of temperate coastal waters during a warming trend. Estuaries 27:895-904.

Parsons T.R., Harrison P.J., Acreman J.C., Dovey H.M., Thompson P.A., Lalli C.M., Lee K., Li G.G., Chen X.L. (1984) An experimental marine ecosystem response to crude-oil and corexit-9527. Marine Environmental Research 13:265-275.

Platt, T., Bird, D.F., Sathyendranath, S. (1991) Critical depth and marine primary productivity. Proceedings of the Royal Society of London B 246:205-217.

Porter K.G., Feig Y.S. (1980) The use of DAPI for identifying and counting aquatic microflora. Limnology and Oceanography 25:943-948.

Riley G. A. (1959) Oceanography of Long Island Sound, 1954 – 1955. Bulletin of the Bingham Oceanographic Collection 17:1.

Riley G.A. (1967) Transport and mixing processes in Long Island Sound. Bulletin of the Bingham Oceanographic Collection 19:35.

Robinson, G.A. (1970) Continuous plankton records: variation in the seasonal cycle of phytoplankton in the North Atlantic. Bulletin of Marine Ecology 6:333-345.

Rose J.M., Caron D.A. (2007) Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. Limnology and Oceanography 52:886-895.

Siegel D.A., Maritorena S., Nelson N.B., Hansell D.A., Lorenzi-Kayser M. (2002) Global distribution and dynamics of colored dissolved and detrital organic materials. Journal of Geophysical Research-Oceans 107.

Sieracki, M.E., Verity, P.G., Stoecker, D.K. (1993) Plankton community response to sequential silicate and nitrate depletion during the 1989 North Atlantic spring bloom. Deep-Sea Research II 40:213-225.

Smetacek V. (1985) Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Marine Biology 84:239-251.

Smetacek V., Passow U. (1990) Spring bloom initiation and Sverdrup critical-depth model. Limnology and Oceanography 35:228-234.

Sommer U., Lengfellner K. (2008) Climate change and the timing, magnitude, and composition of the phytoplankton spring bloom. Global Change Biology 14:1199-1208.

Stelfox-Widdicombe C.E., Edwards E.S., Burkill P.H., Sleigh M.A. (2000) Microzooplankton grazing activity in the temperate and sub-tropical NE Atlantic: summer 1996. Marine Ecology-Progress Series 208:1-12.

Stoecker D.K., Gifford D.J., Putt M. (1994) Preservation of marine planktonic ciliates – losses and cell shrinkage during fixation. Marine Ecology-Progress Series 110:293-299.

Stoecker D.K., Gustafson D.E. (2002) Predicting grazing mortality of an estuarine dinoflagellate, *Pfiesteria piscicida*. Marine Ecology-Progress Series 233:31-38.

Stoecker D.K., Thessen A.E., Gustafson D.E. (2008) "Windows of opportunity" for

dinoflagellate blooms: Reduced microzooplankton net growth coupled to eutrophication. Harmful Algae 8:158-166.

Strom S.L., Brainard M.A., Holmes J.L., Olson M.B. (2001) Phytoplankton blooms are strongly impacted by microzooplankton grazing in coastal North Pacific waters. Marine Biology 138:355-368.

Sverdrup H.U. (1953) On conditions for the vernal blooming of phytoplankton. Journal du Conseil International pour I'Exploration de la Mer 18:287-295.

Tian R.C., Vezina A.F., Legendre L., Ingram R.G., Klein B., Packard T., Roy S., Savenkoff C., Silverberg N., Therriault J.C., Tremblay J.E. (2000) Effects of pelagic food-web interactions and nutrient remineralization on the biogeochemical cycling of carbon: a modeling approach. Deep-Sea Research Part Ii-Topical Studies in Oceanography 47:637-662.

Townsend, D.W., Cammen, L.M., Holligan, P.M., Campbell, D.E., Pettigrew, N.R. (1994) Causes and consequences of variability in the timing of spring phytoplankton blooms. Deep-Sea Research 41:747-765.

Townsend D.W., Mayer L.M., Dortch Q., Spinrad R.W. (1992) Vertical structure and biological-activity in the bottom nepheloid layer of the Gulf of Maine. Continental Shelf Research 12:367-387.

Van Haren, H., Mills, D.K., Wetsteyn, L.P.M.J. (1998) Detailed observations of the phytoplankton spring bloom in the stratifying central North Sea. Journal of Marine Research 56:655-680.

Valderrama J.C. (1981) The simultaneous analysis of total nitrogen and total phosphorus in natural-waters. Marine Chemistry 10:109-122.

Verity P.G., Stoecker D.K., Sieracki M.E., Nelson J.R. (1993) Grazing, growth and mortality of microzooplankton during the 1989 North-Atlantic spring bloom at 47-degrees-W. Deep-Sea Research Part I-Oceanographic Research Papers 40:1793-1814.

Wall C.C., Peterson B.J., Gobler C.J. (2008) Facilitation of seagrass Zostera marina productivity by suspension-feeding bivalves. Marine Ecology-Progress Series 357:165-174.

Wall C.C., Peterson B.J., Gobler C.J. (2011) The Growth of Estuarine Resources (*Zostera marina, Mercenaria mercenaria, Crassostrea virginica, Argopecten irradians, Cyprinodon variegatus*) in Response to Nutrient Loading and Enhanced Suspension Feeding by Adult Shellfish. Estuaries and Coasts 34:1262-1277.

Welschmeyer N.A. (1994) Fluorometric analysis of chlorophyll-*a* in the presence of chlorophyll-*b* and pheopigments. Limnology and Oceanography 39:1985-1992.

FIGURES

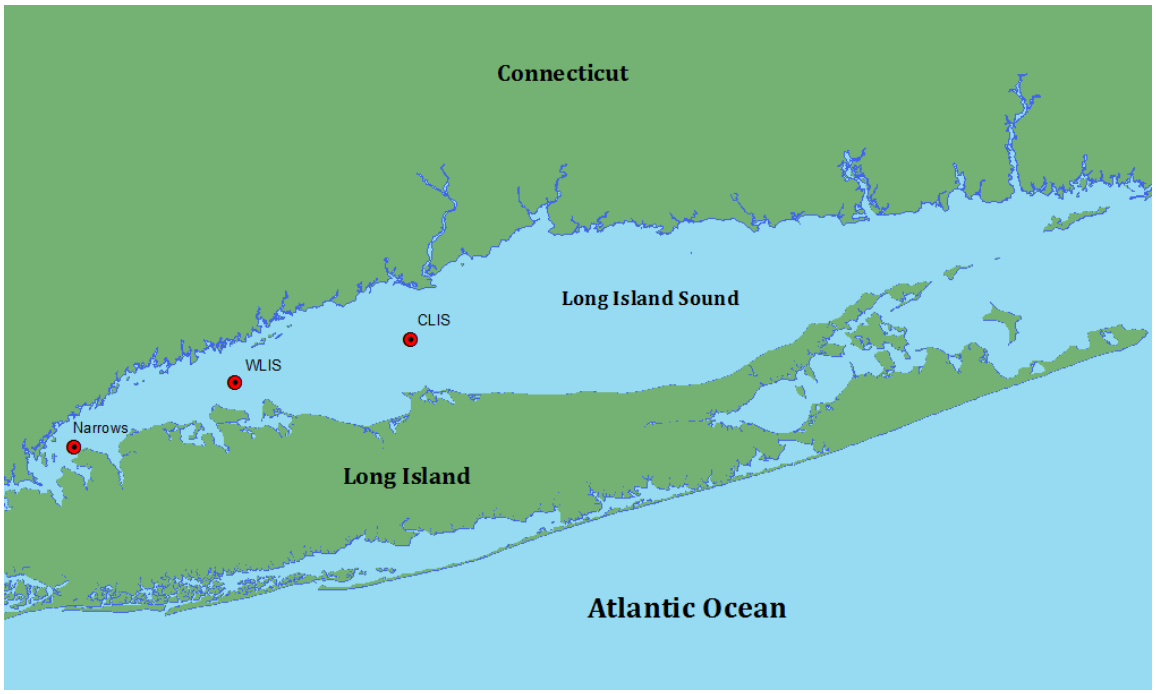

Figure 1. Field sampling sites in Long Island Sound. Central LIS (CLIS) was sampled regularly during 2010 and 2011. Western LIS (WLIS) and the Narrows were sampled in tandem with CLIS on four dates throughout January – March (pre-bloom, during bloom, post-bloom) in 2011.

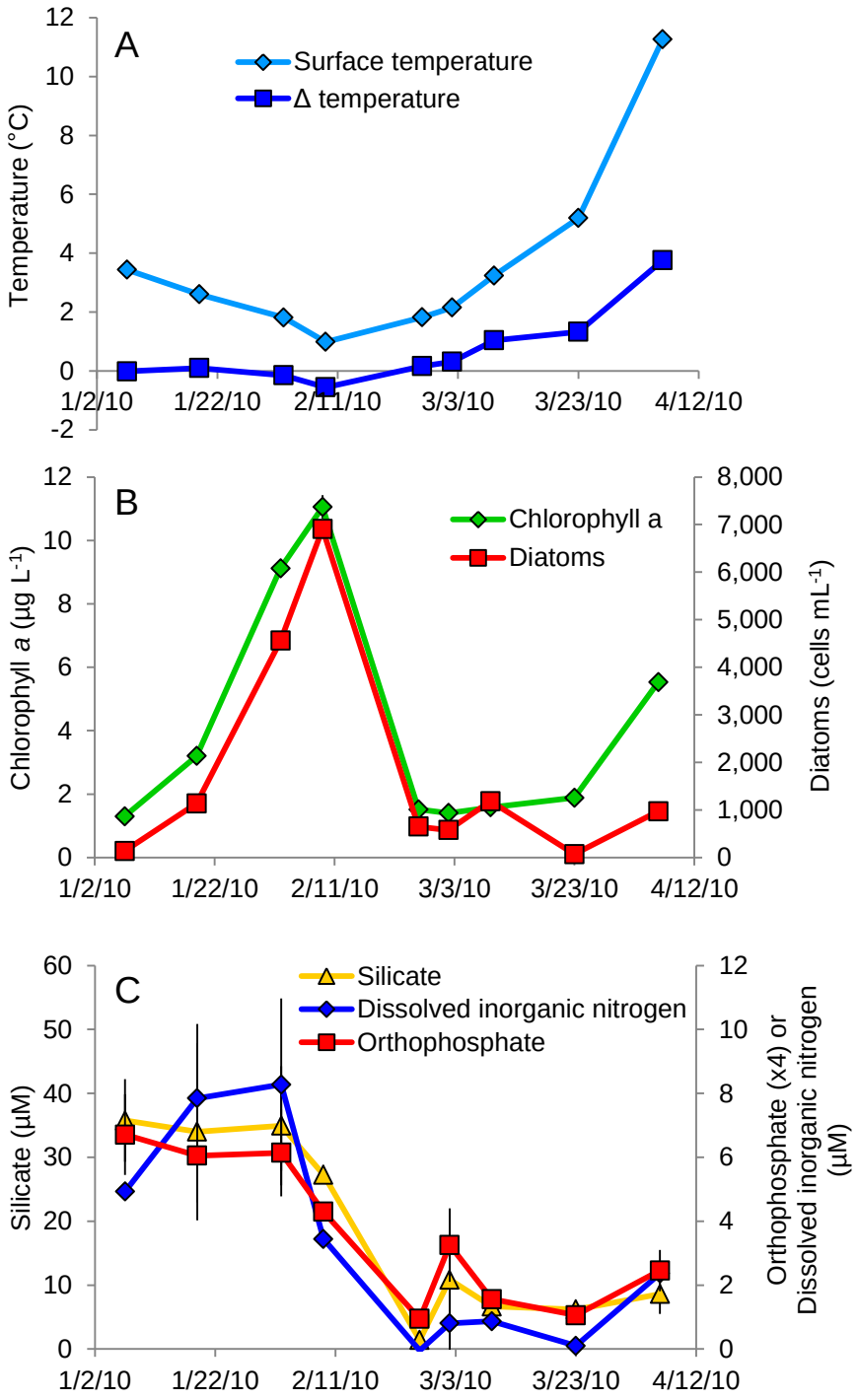

Figure 2. Dynamics of A) surface temperature and change in temperature from surface to bottom of LIS, ΔT, B) chlorophyll *a* concentrations and diatom abundance, and C) dissolved nutrient concentrations in Long Island Sound during January to April 2010.

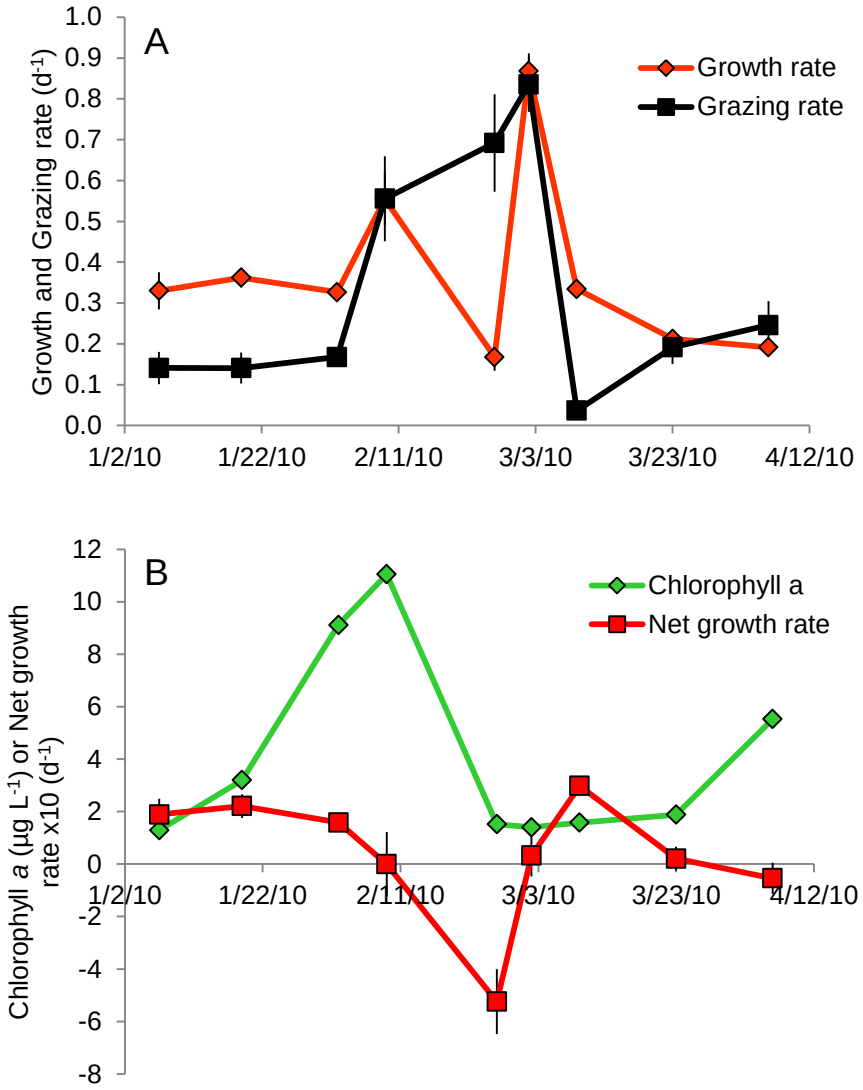

Figure 3. Dynamics of A) intrinsic phytoplankton growth rate and microzooplankton grazing rate and B) chlorophyll *a* concentrations and net phytoplankton growth rate in Long Island Sound during January to April 2010.

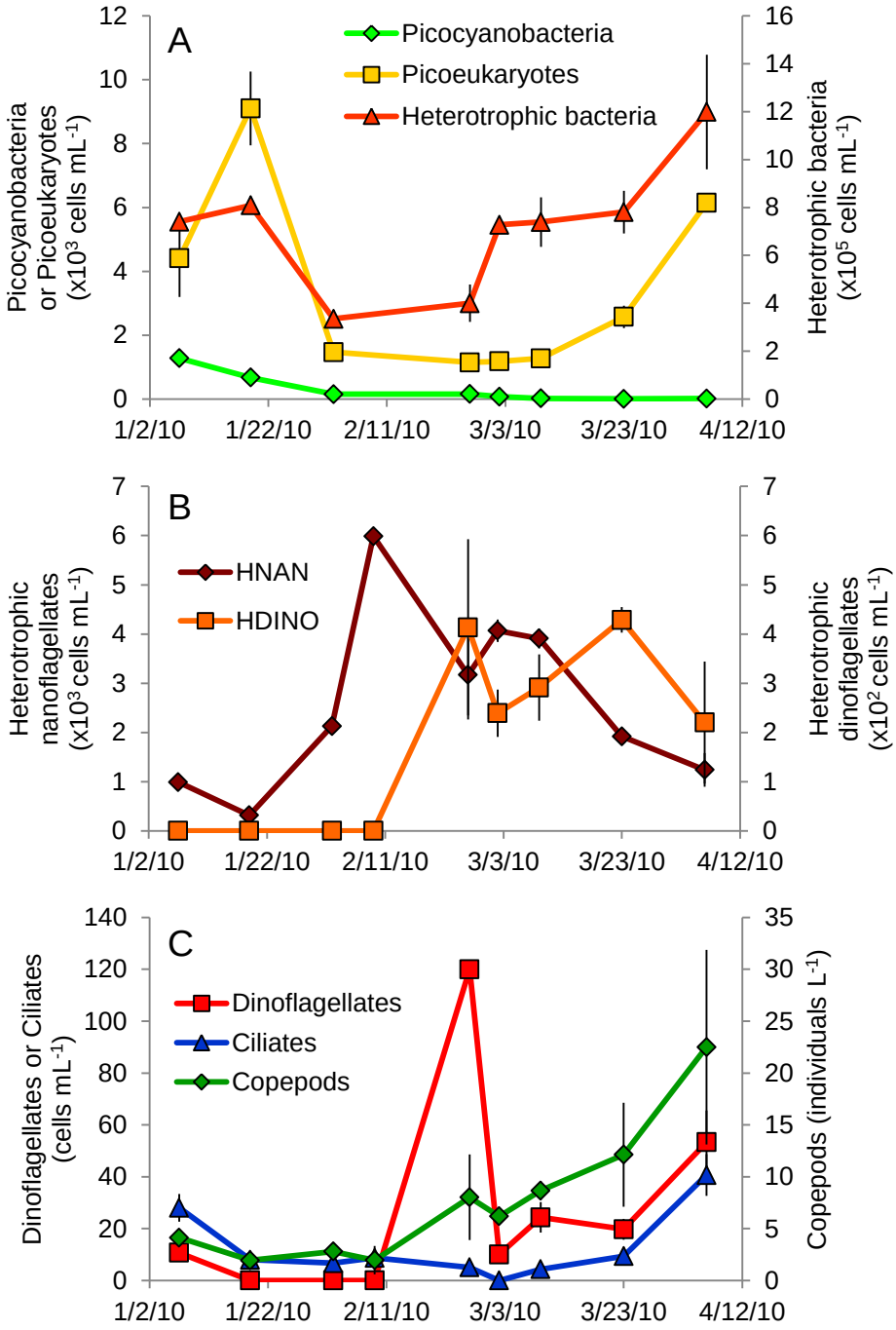

Figure 4. Dynamics of A) picoplankton abundance: picocyanobacteria, picoeukaryotes, and heterotrophic bacteria, B) nanoplankton abundance: heterotrophic nanoflagellates (HNAN), heterotrophic dinoflagellates (HDINO), and ciliates, and C) microplankton and mesoplankton abundance: dinoflagellates and ciliates and copepods in Long Island Sound during January to April 2010.

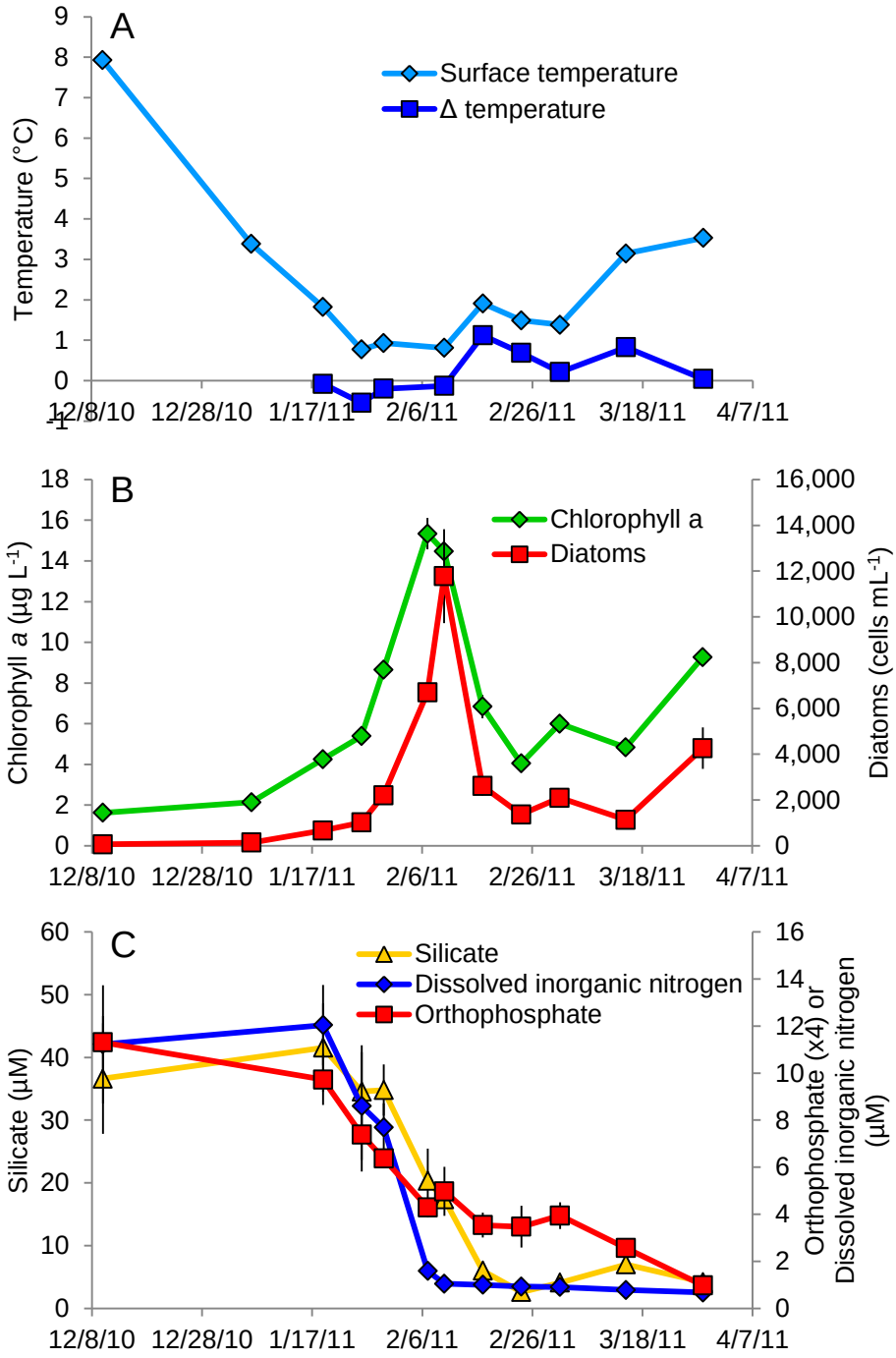

Figure 5. Dynamics of A) surface temperature and change in temperature from surface to bottom of LIS, ΔT, B) chlorophyll *a* concentrations and diatom abundances, and C) dissolved nutrient concentrations in Long Island Sound during December to April 2011.

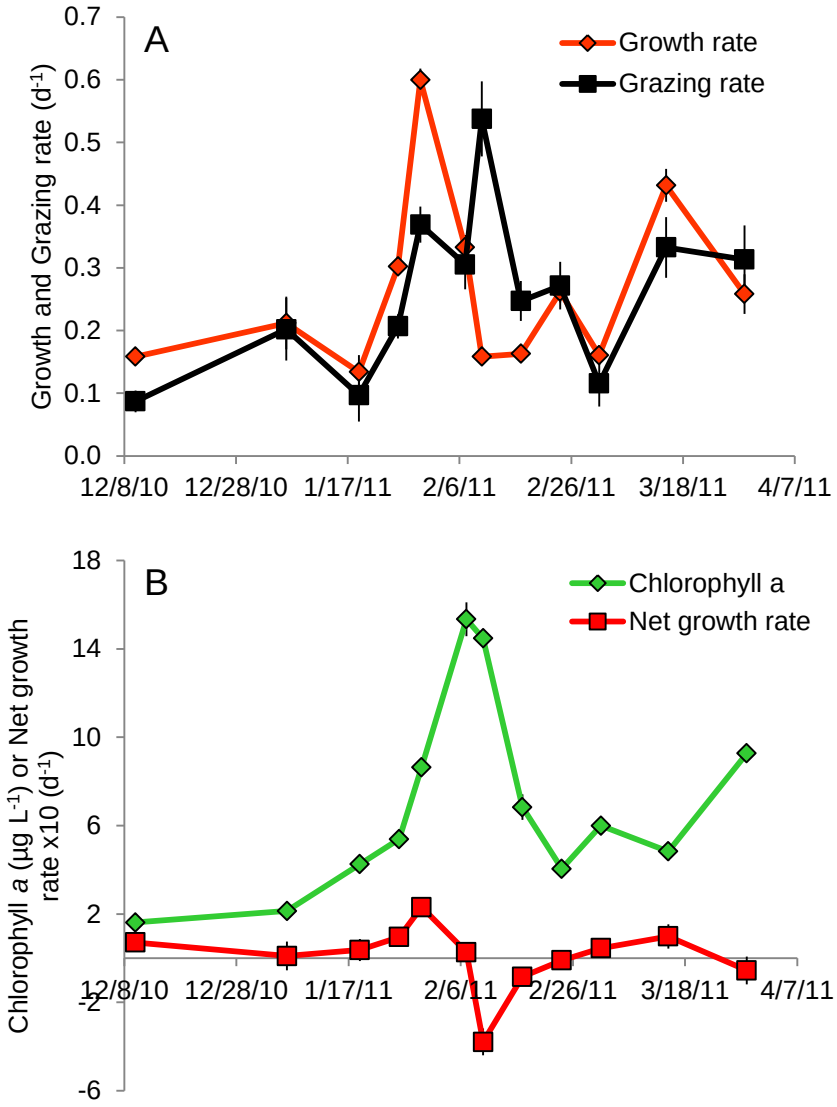

Figure 6. Dynamics of A) intrinsic phytoplankton growth rate and microzooplankton grazing rate and B) chlorophyll *a* concentrations and net phytoplankton growth rate in Long Island Sound during December to April 2011.

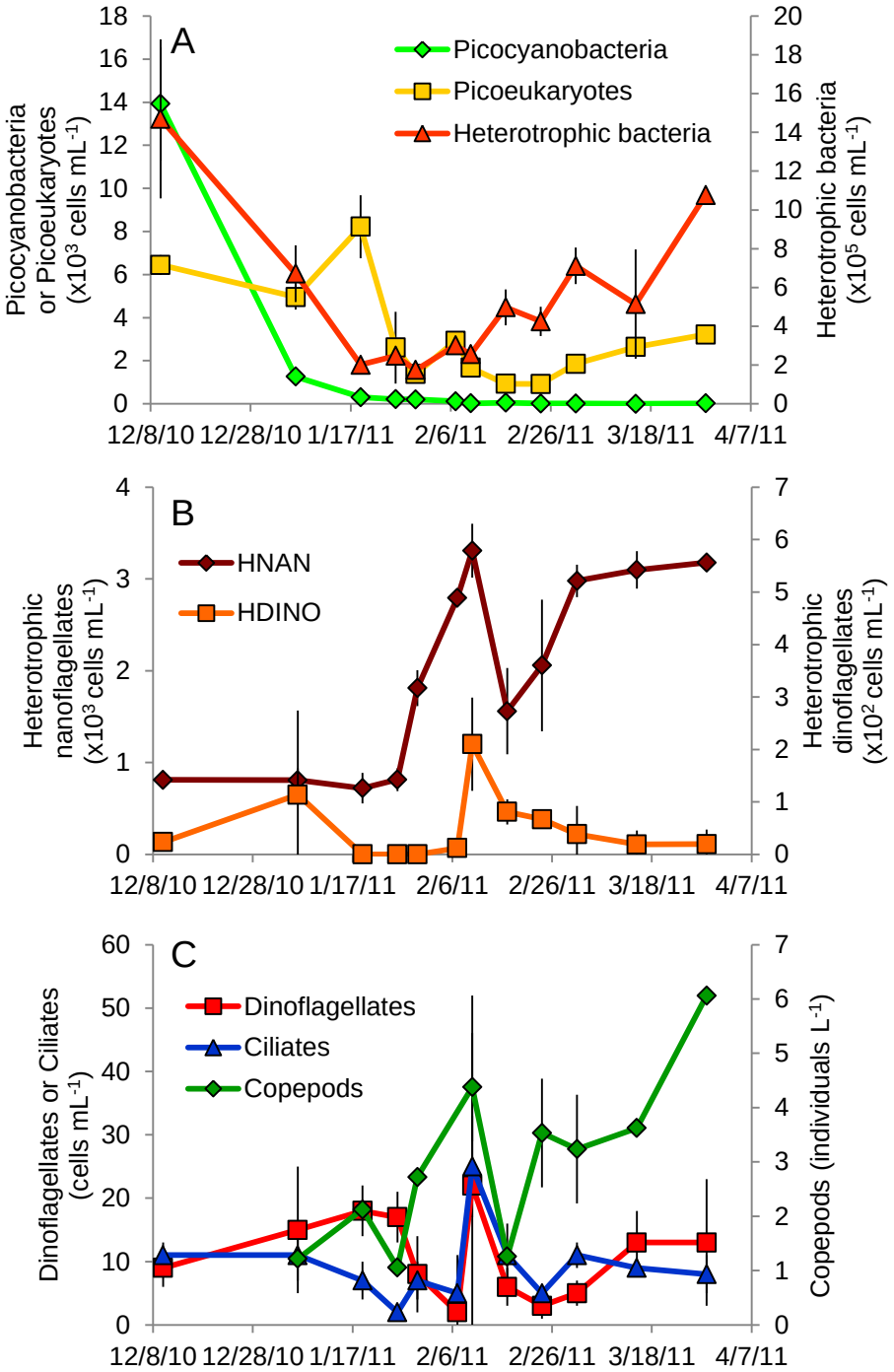

Figure 7. Dynamics of A) picoplankton abundance: picocyanobacteria, picoeukaryotes, and heterotrophic bacteria, B) nanoplankton abundance: heterotrophic nanoflagellates (HNAN), heterotrophic dinoflagellates (HDINO), and ciliates, and C) microplankton and mesoplankton abundance: dinoflagellates and ciliates and copepods in Long Island Sound during December to April 2011.

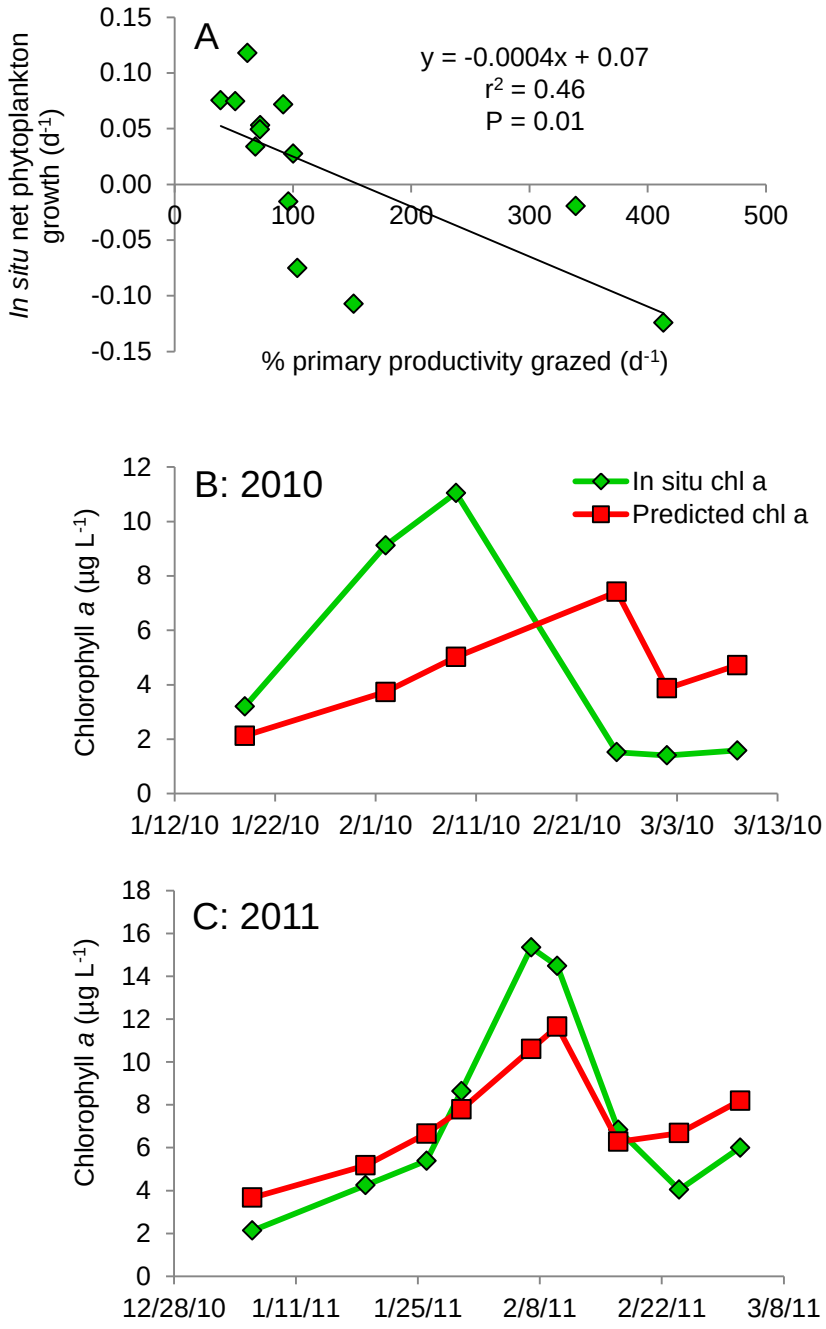

Figure 8. A) Percent primary production consumed by microzooplankton is significantly correlated with *in situ* changes in LIS phytoplankton biomass for both 2010 and 2011, B) and C) predicted chlorophyll *a* concentrations calculated from net phytoplankton growth rates using the regression equation and percent primary productivity grazed, for 2010 and 2011 respectively.

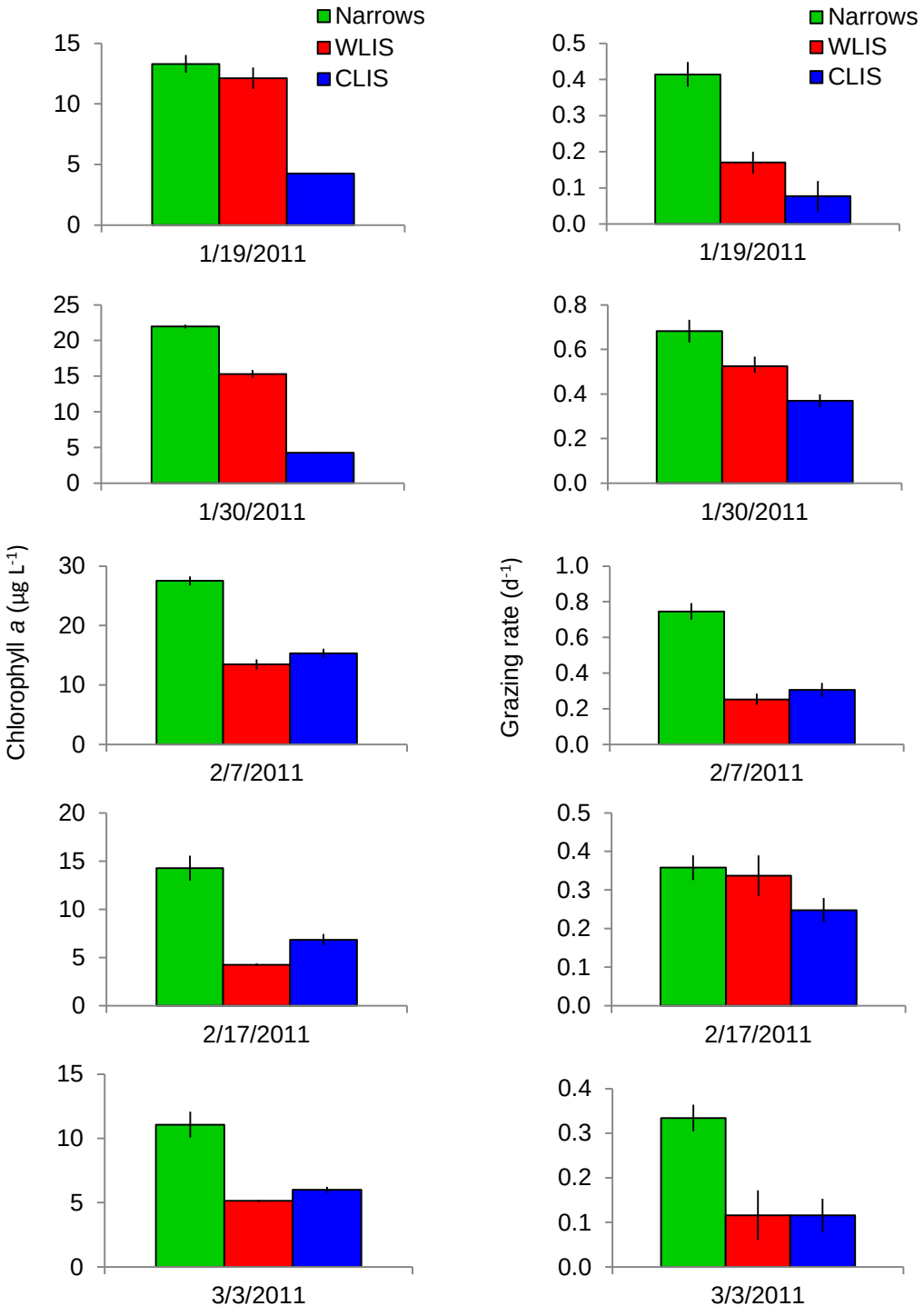

Figure 9. Chlorophyll *a* concentrations and microzooplankton grazing rates at three sampling stations (CLIS, WLIS, Narrows) across Long Island Sound from January – March 2011. Narrows stations (site furthest West) consistently had the highest chlorophyll *a* concentrations and grazing rates.

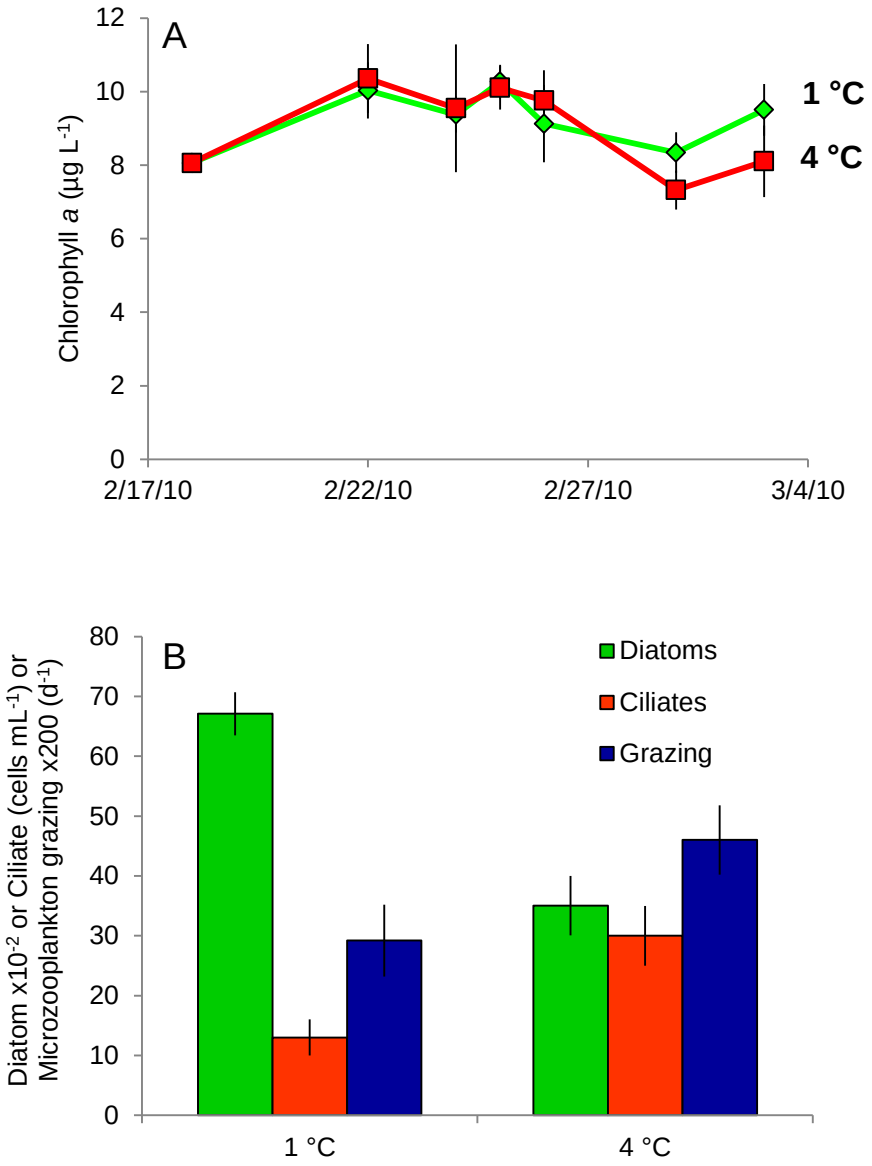

Figure 10. A) Dynamics of chlorophyll *a* at 1 °C and 4 °C in a two-week mesocosm experiment during the 2010 spring phytoplankton bloom, 1 °C has significantly higher levels of chlorophyll *a* at the end of the experiment ($p<0.05$; t-test) and B) diatom and ciliate abundances and microzooplankton grazing rates at 1 °C and 4 °C at the end of the two-week mesocosm experiment, 1 °C has significantly higher levels of diatoms and significantly lower levels of ciliates ($p<0.01$ and $p<0.05$; t-test; respectively). At the time of the experiment, ambient LIS waters were 1 °C.

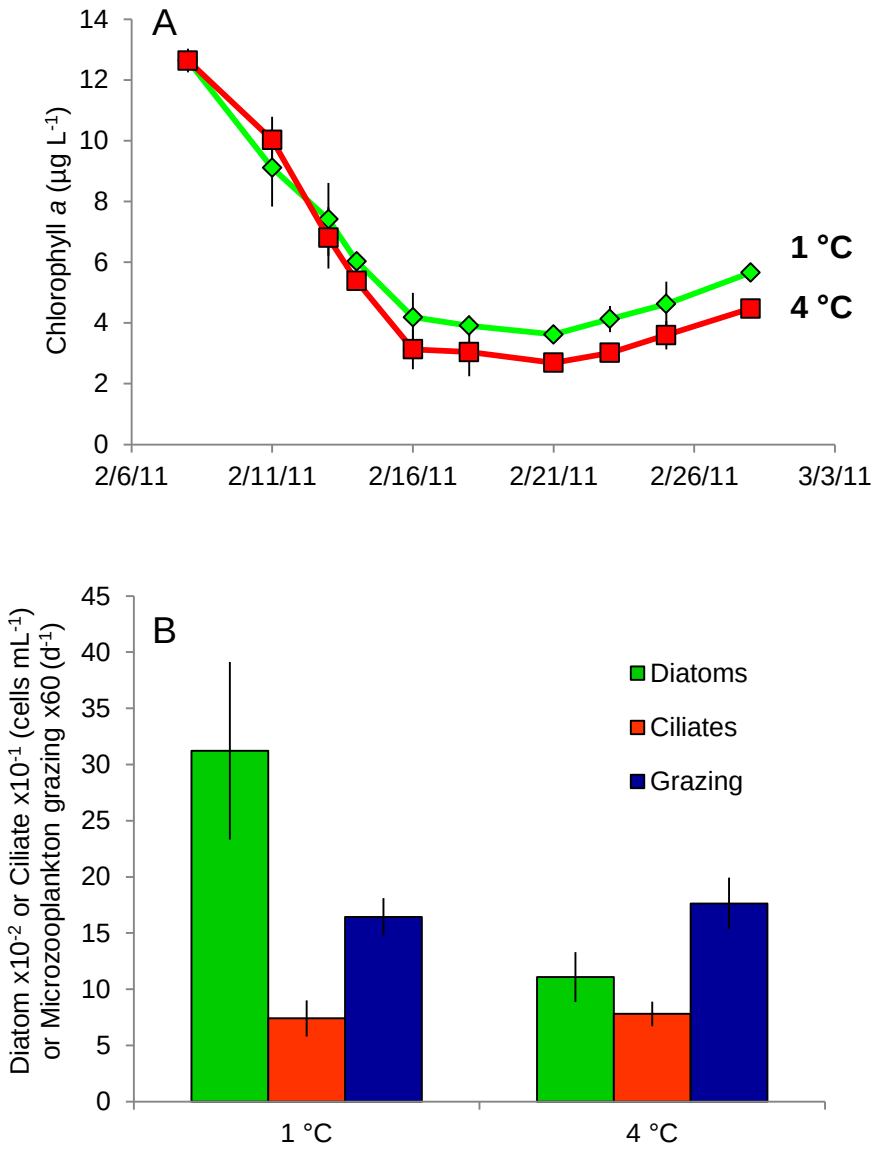

Figure 11. A) Dynamics of chlorophyll *a* at 1 °C and 4 °C in a three-week mesocosm experiment during the 2011 spring phytoplankton bloom, 1 °C has significantly higher levels of chlorophyll *a* at the end of the experiment ($p<0.01$; t-test) and B) diatom and ciliate abundances and microzooplankton grazing rates at 1 °C and 4 °C at the end of the two-week mesocosm experiment 1 °C has significantly higher levels of diatoms ($p<0.01$; t-test). At the time of the experiment, ambient LIS waters were 1 °C.

TABLES

Table 1. Levels of salinity, temperature (°C), and dissolved oxygen (mg L^{-1}) at the Central LIS (CLIS) sampling station in Long Island Sound during December to April of 2010 and 2011.

Date	Surface Salinity	Bottom Salinity	Surface Temperature	Δ Temperature	Dissolved Oxygen
1/7/10	26.54	26.85	3.44	-0.02	10.80
1/19/10	26.70	26.81	2.61	0.10	11.10
2/2/10	26.59	26.84	1.82	-0.15	12.27
2/9/10	25.91	27.10	0.99	-0.56	11.83
2/25/10	26.58	26.99	1.83	0.17	14.30
3/2/10	25.91	26.68	2.16	0.32	15.31
3/9/10	26.01	27.14	3.24	1.04	13.81
3/23/10	25.65	26.37	5.20	1.33	13.81
4/6/10	NA	NA	11.27	3.76	12.03
4/20/10	NA	NA	NA	NA	NA
12/10/10	NA	NA	7.93	NA	11.00
1/6/11	NA	NA	3.38	NA	10.75
1/19/11	27.58	27.82	1.82	-0.08	11.60
1/26/11	27.60	27.83	0.77	-0.55	16.26
1/30/11	27.42	27.81	0.93	-0.20	13.22
2/7/11	NA	NA	NA	NA	NA
2/10/11	27.66	27.98	0.81	-0.13	13.57
2/17/11	26.85	27.83	1.91	1.12	13.30
2/24/11	28.09	27.83	1.49	0.69	13.49
3/3/11	27.13	26.92	1.38	0.21	14.20
3/15/11	26.00	27.33	3.15	0.83	13.55
3/29/11	25.74	26.71	3.53	0.04	15.79

Table 2. Phytoplankton size fractionation for December – April 2010 and 2011 determined from chlorophyll *a* concentration (μg L^{-1}) at CLIS. Standard deviations of duplicate measurements are in parentheses (SD).

Date	Total	0.2-2 μm	2-20 μm	> 20 μm
1/7/10	1.30 90.05)	1.21 (0.19)	0.28 (0.07)	0.27 (0.00)
1/19/10	3.20 (0.12)	0.56 (0.18)	1.99 (0.10)	1.37 (0.16)
2/2/10	9.12 (0.21)	7.17 (0.28)	2.10 (0.11)	3.95 (0.22)
2/9/10	11.05 (0.37)	6.65 (1.51)	2.00 (0.94)	4.38 (0.08)
2/25/10	1.52 (0.13)	0.54 (0.17)	0.84 (0.07)	0.90 (0.02)
3/2/10	1.40 (0.05)	0.22 (0.03)	0.69 (0.08)	0.73 (0.05)
3/9/10	1.58 (0.03)	0.28 (0.34)	1.20 (0.35)	0.49 (0.05)
3/23/10	1.89 (0.02)	0.56 (0.13)	1.20 (0.06)	0.24 (0.03)
4/6/10	5.53 (0.03)	3.11 (0.96)	3.47 (0.11)	1.26 (0.24)
4/20/10	1.24 (0.06)	0.55 (0.17)	0.55 (0.11)	0.43 (0.04)
12/10/10	1.62 90.07)	0.14 (0.27)	0.73 (0.18)	0.50 (0.05)
1/6/11	2.14 (0.25)	0.85 (0.75)	0.75 (0.85)	0.60 (0.03)
1/19/11	4.25 (0.08)	0.06 (0.30)	1.46 (0.23)	2.71 (0.14)
1/26/11	5.39 (0.13)	1.53 (0.47)	1.65 (0.14)	4.00 (0.11)
1/30/11	8.64 (0.40)	0.06 (0.30)	1.46 (0.23)	2.71 (0.14)
2/7/11	15.34 (0.77)	4.36 (0.84)	4.36 (1.56)	11.38 (1.30)
2/10/11	14.48 (0.41)	4.21 (0.79)	5.10 (1.10)	10.73 (0.43)
2/17/11	6.84 (0.58)	1.30 (1.24)	1.87 (0.47)	5.03 (0.20)
2/24/11	4.04 (0.23)	0.06 (0.21)	1.52 (0.28)	2.77 (0.12)
3/3/11	6.00 (0.23)	1.96 (1.23)	2.78 (1.02)	4.78 (0.10)
3/15/11	4.83 (0.42)	0.11 (0.46)	2.58 (0.33)	1.92 (0.09)
3/29/11	9.27 (0.14)	0.55 (0.51)	2.93 (0.77)	4.89 (0.40)

Table 3. Plankton community composition and abundances for December – April 2010 and 2011. Picophytoplankton community includes picocyanobacteria, picoeukaryotes, and heterotrophic bacteria. Nanoplankton community includes autotrophic nanoflagellates, autotrophic dinoflagellates, heterotrophic nanoflagellates, heterotrophic dinoflagellates, and ciliates (< 20µm). Microplankton community includes diatoms, dinoflagellates, and ciliates. Mesoplankton community includes (adult) copepods and other non-copepod mesoplankton. Standard deviations of duplicate measurements are in parentheses (SD). Dates without samples are denoted as NA.

	Picoplankton			Nanoplankton					Microplankton			Mesoplankton	
Date	Cyanobacteria	Eukaryotes	H. bacteria	ANAN	ADINO	HNAN	HDINO	Ciliates	Diatoms	Dinoflagellates	Ciliates	Copepods	Other
1/7/10	1,281 (141)	4,411 (1210)	740,468 (1,865)	852 (105)	68 (24)	980 (129)	0 (0)	10 (13)	136 (8)	11 (3)	28 (5)	4 (0)	0 (0)
1/19/10	679 (99)	9,101 (1159)	808,690 (27,572)	1,368 (177)	237 (37)	316 (76)	0 (0)	0 (0)	1136 (38)	0 (0)	8 (2)	2 (1)	0 (0)
2/2/10	155 (33)	1,470 (143)	335,161 (23,989)	368 (66)	76 (50)	2,129 (11)	0 (0)	0 (0)	4,560 (83)	0 (0)	7 (1)	3 (0)	1 (0)
2/9/10	NA NA	NA NA	NA NA	698 (307)	0 (0)	5,990 (14)	0 (0)	0 (0)	6,909 (112)	0 (0)	9 (1)	2 (1)	0 (0)
2/25/10	162 (39)	1,150 (141)	400,313 (7,8141)	1,753 (498)	114 (6)	2,994 (906)	413 (179)	176 (35)	651 (26)	120 (3)	5 (1)	8 (4)	1 (1)
3/2/10	78 (29)	1,181 (96)	727,585 (26,626)	1,023 (272)	32 (15)	3,880 (228)	239 (48)	190 (22)	578 (20)	10 (2)	0 (0)	6 (0)	1 (1)
3/9/10	26 (36)	1,278 (181)	739,105 (102,994)	1,455 (290)	43 (53)	3,733 (202)	291 (67)	178 (33)	1,184 (31)	24 (6)	4 (2)	9 (1)	1 (0)
3/23/10	11 (11)	2,575 (347)	780,678 (88,984)	2,183 (677)	1,299 (221)	1,560 (98)	429 (26)	360 (123)	69 (5)	20 (4)	9 (2)	12 (5)	0 (0)
4/6/10	18 (23)	6,148 (103)	1,198,678 (239,375)	2,421 (393)	3,153 (571)	1,239 (342)	220 (124)	0 (0)	971 (38)	53 (12)	41 (8)	23 (9)	1 (0)
4/20/10	NA NA	NA NA	NA NA	2,213 (210)	86 (97)	4,422 (667)	88 (16)	0 (0)	1,259 (65)	31 (7)	31 (6)	29 NA	0 NA
12/10/10	13,925 (2635)	6,448 (461)	1,469,969 (410,575)	483 (107)	0 (0)	810 (91)	23 (1)	0 (0)	57 (27)	9 (3)	11 (2)	1 (0)	0 (0)
1/6/11	1,263 (344)	4,953 (582)	671,661 (146,291)	2,853 (570)	0 (0)	808 (126)	114 (161)	0 (0)	138 (59)	15 (10)	11 (4)	1 (0)	0 (0)
1/19/11	307 (16)	8,219 (1460)	201,089 (36,719)	2,002 (1,079)	0 (0)	721 (167)	0 (0)	0 (0)	667 (39)	18 (4)	7 (3)	2 (0)	0 (0)
1/26/11	214 (39)	2,605 (1673)	247,216 (21,205)	2,389 (211)	0 (0)	814 (125)	0 (0)	0 (0)	1,013 (166)	17 (4)	2 (1)	1 (0)	0 (0)
1/30/11	204 (16)	1,386 (292)	174,220 (13,371)	1,595 (3)	0 (0)	1,811 (197)	0 (0)	0 (0)	2,201 (170)	8 (6)	7 (3)	3 (0)	1 (0)
2/7/11	117 (24)	2,923 (38)	301,088 (30,443)	910 (184)	16 (23)	2,795 (92)	12 (0)	0 (0)	6,700 (232)	2 (0)	5 (6)	NA NA	NA NA
2/10/11	17 (8)	1,672 (39)	255,516 (10,422)	979 (281)	56 (24)	3,250 (295)	210 (89)	59 (83)	11,772 (2,052)	22 (30)	25 (8)	4 (1)	2 (0)
2/17/11	48 (17)	931 (8)	497,622 (92,420)	19 (27)	19 (27)	1,521 (470)	81 (24)	38 (1)	2,609 (414)	6 (3)	11 (5)	1 (0)	1 (0)
2/24/11	11 (0)	917 (105)	425,470 (75,140)	2,925 (1,048)	39 (55)	1,989 (717)	67 (11)	70 (0)	1,364 (306)	3 (2)	5 (1)	4 (1)	2 (0)
3/3/11	17 (8)	1,855 (194)	711,646 (94,617)	1,896 (518)	0 (0)	2,955 (178)	38 (54)	24 (0)	2,090 (4)	5 (2)	11 (2)	3 (1)	2 (0)
3/15/11	0 (0)	2,635 (470)	514,343 (281,316)	2,238 (220)	95 (26)	3,098 (205)	19 (27)	0 (0)	1,132 (74)	13 (5)	9 (1)	4 (0)	3 (0)
3/29/11	22 (0)	3,212 (81)	1,076,757 (49,313)	2,516 (193)	0 (0)	3,179 (83)	20 (28)	0 (0)	4,263 (904)	13 (10)	8 (3)	6 (0)	5 (0)

Table 4. Plankton growth and grazing rates in LIS for 2010 and 2011. Primary production rate (d^{-1}), intrinsic phytoplankton growth rate (d^{-1}), net phytoplankton growth rate (d^{-1}), and microzooplankton grazing rate (d^{-1}) of phytoplankton, and percent primary productivity grazed (d^{-1}) by microzooplankton. All rates were determined using water sampled from CLIS. Standard error of duplicate measurements is in parentheses (SE). Dates without samples are denoted as NA.

Date	1° Production		Growth		Net growth		Grazing		% grazed
1/7/10	NA	NA	0.33	(0.05)	0.19	(0.06)	0.14	(0.04)	43
1/19/10	NA	NA	0.36	(0.02)	0.22	(0.04)	0.14	(0.04)	39
2/2/10	0.18	(0.04)	0.33	(0.01)	0.16	(0.03)	0.17	(0.02)	51
2/9/10	0.51	(0.08)	0.55	(0.06)	0.00	(0.12)	0.56	(0.10)	100
2/25/10	0.06	(0.07)	0.17	(0.03)	-0.52	(0.12)	0.69	(0.12)	413
3/2/10	-0.05	(0.05)	0.87	(0.04)	0.03	(0.08)	0.84	(0.07)	96
3/9/10	0.11	(0.01)	0.33	(0.01)	0.30	(0.01)	0.04	(0.01)	11
3/23/10	0.07	(0.02)	0.21	(0.02)	0.02	(0.05)	0.19	(0.04)	90
4/6/10	0.22	(0.03)	0.19	(0.01)	-0.05	(0.06)	0.25	(0.06)	128
4/20/10	NA	NA	NA	NA	NA	NA	NA	NA	NA
12/10/10	-0.03	(0.02)	0.16	(0.00)	0.07	(0.02)	0.09	(0.02)	55
1/6/11	0.05	(0.06)	0.21	(0.04)	0.01	(0.07)	0.20	(0.05)	95
1/19/11	0.41	(0.03)	0.13	(0.03)	0.04	(0.05)	0.10	(0.04)	72
1/26/11	NA	NA	0.30	(0.01)	0.10	(0.02)	0.21	(0.02)	68
1/30/11	0.59	(0.02)	0.60	(0.02)	0.23	(0.03)	0.37	(0.03)	61
2/7/11	0.66	(0.03)	0.33	(0.02)	0.03	(0.04)	0.31	(0.04)	92
2/10/11	0.83	(0.06)	0.16	(0.01)	-0.38	(0.06)	0.54	(0.06)	339
2/17/11	0.30	(0.01)	0.16	(0.01)	-0.08	(0.03)	0.25	(0.03)	151
2/24/11	0.09	(0.03)	0.26	(0.02)	-0.01	(0.04)	0.27	(0.04)	104
3/3/11	0.41	(0.03)	0.16	(0.02)	0.05	(0.04)	0.12	(0.04)	72
3/15/11	0.11	(0.06)	0.43	(0.03)	0.10	(0.06)	0.33	(0.05)	77
3/29/11	0.18	(0.03)	0.26	(0.03)	-0.06	(0.06)	0.31	(0.05)	121

Table 5. Picoplankton growth and grazing rates in LIS for 2010 and 2011. Intrinsic growth rate (d^{-1}), microzooplankton grazing rate (d^{-1}), and percent productivity grazed (d^{-1}) by microzooplankton for picocyanobacteria, picoeukaryotes, and heterotrophic bacteria. All rates were determined using water sampled from CLIS. Standard error of duplicate measurements is in parentheses (SE). Dates without samples are denoted as NA.

	Picocyanobacteria			Picoeukaryotes			Heterotrophic bacteria		
Date	**Growth**	**Grazing**	**% grazed**	**Growth**	**Grazing**	**% grazed**	**Growth**	**Grazing**	**% grazed**
1/7/10	0.03	0.08 (0.12)	264	0.66	0.31 (0.09)	47	0.34	0.21 (0.03)	61
1/19/10	0.15	0.19 (0.09)	127	0.23	0.23 (0.05)	99	0.42	0.12 (0.07)	29
2/2/10	0.05	0.36 (0.08)	671	0.55	0.17 (0.10)	30	0.22	0.34 (0.04)	157
2/9/10	NA	NA NA	NA	NA	NA NA	NA	NA	NA NA	NA
2/25/10	0.49	0.66 (0.22)	136	0.72	0.77 (0.16)	107	0.52	0.36 (0.05)	69
3/2/10	0.17	0.56 (0.25)	328	0.37	0.56 (0.14)	151	0.60	0.76 (0.14)	126
3/9/10	1.21	1.08 (0.26)	89	0.35	0.16 (0.07)	46	0.44	0.26 (0.07)	60
3/23/10	1.29	1.34 (0.22)	104	0.01	0.19 (0.01)	1,703	0.42	0.13 (0.06)	30
4/6/10	0.90	0.76 (0.22)	84	0.00	0.23 (0.06)	6,806	0.53	0.73 (0.05)	137
4/20/10	NA	NA NA	NA	NA	NA NA	NA	NA	NA NA	NA
12/10/10	0.81	0.18 (0.12)	22	0.97	0.04 (0.08)	4	0.41	0.42 (0.08)	103
1/6/11	1.33	0.29 (0.08)	21	1.39	0.22 (0.10)	16	0.50	0.40 (0.05)	81
1/19/11	0.88	0.15 (0.08)	17	1.04	0.05 (0.11)	5	0.92	0.36 (0.15)	39
1/26/11	1.56	0.01 (0.08)	0	2.13	0.13 (0.15)	6	0.73	0.21 (0.06)	29
1/30/11	0.89	0.44 (0.21)	50	0.94	0.11 (0.08)	11	0.96	0.35 (0.05)	36
2/7/11	0.38	0.35 (0.15)	92	0.52	0.02 (0.16)	3	0.66	0.22 (0.07)	34
2/10/11	0.75	0.71 (0.45)	95	0.47	0.14 (0.19)	30	0.40	0.41 (0.11)	104
2/17/11	0.08	0.34 (0.23)	411	0.74	0.21 (0.11)	29	0.89	0.54 (0.07)	61
2/24/11	0.51	0.70 (0.50)	138	0.15	0.25 (0.32)	166	0.42	0.13 (0.09)	30
3/3/11	0.43	0.48 (0.22)	111	-0.10	0.36 (0.17)	-353	0.40	0.05 (0.04)	13
3/15/11	NA	NA NA	NA	0.28	0.27 (0.21)	99	0.53	0.23 (0.14)	44
3/29/11	0.05	0.00 (0.01)	9	0.42	0.44 (0.10)	103	0.52	0.18 (0.06)	34

Table 6. 2010 and 2011 mesocosm experiments at 1 °C and 4 °C (T=temperature treatment); ambient LIS water = 1 °C. Dynamics of chlorophyll *a* concentrations (µg L^{-1}), heterotrophic nanoflagellate (HNAN) abundance (cells mL^{-1}), intrinsic phytoplankton growth rate (d^{-1}), nutrient enriched intrinsic phytoplankton growth rate (d^{-1}), microzooplankton grazing rate of phytoplankton (d^{-1}), and percent primary productivity grazed (d^{-1}) by microzooplankton. Significantly higher levels of chlorophyll *a* were observed in the 1 °C treatment compared to the 4 °C treatment for both years ($p<0.05$ and $p<0.01$; t-test; respectively). Standard error of duplicate measurements is in parentheses (SE).

Date	T	Chlorophyll a	HNAN	Growth	Enriched Growth	Grazing	% grazed
2/18/10	1 °C	6.98 (1.09)	4,261 (1,264)	0.35 (0.02)	0.38 (0.03)	0.20 (0.04)	57
2/25/10		7.84 (0.17)	4,035 (442)	0.12 (0.01)	0.25 (0.02)	0.17 (0.03)	140
3/4/10		7.13 (0.26)	4,509 (608)	0.10 (0.00)	0.27 (0.02)	0.15 (0.03)	140
2/18/10	4 °C	6.98 (1.09)	4,261 (1,264)	0.51 (0.02)	0.60 (0.03)	0.34 (0.04)	67
2/25/10		7.90 (0.68)	4,448 (786)	0.12 (0.01)	0.36 (0.03)	0.20 (0.05)	175
3/4/10		6.30 (0.17)	4,801 (229)	0.28 (0.00)	0.64 (0.02)	0.23 (0.03)	83

Date	T	Chlorophyll a	HNAN	Growth	Enriched Growth	Grazing	% grazed
2/8/11	1 °C	12.64 (0.05)	3,125 (801)	0.34 (0.03)	0.43 (0.03)	0.32 (0.05)	94
2/14/11		6.03 (0.15)	3,472 (394)	0.32 (0.02)	0.52 (0.03)	0.41 (0.04)	127
2/21/11		3.62 (0.05)	3,509 (267)	0.30 (0.02)	0.54 (0.03)	0.36 (0.05)	119
2/28/11		5.66 (0.20)	3,638 (291)	0.33 (0.01)	0.53 (0.02)	0.27 (0.03)	83
2/8/11	4 °C	12.64 (0.05)	3,125 (801)	0.43 (0.02)	0.59 (0.02)	0.48 (0.03)	112
2/14/11		5.39 (0.07)	3,501 (636)	0.20 (0.01)	0.46 (0.03)	0.34 (0.04)	170
2/21/11		2.69 (0.06)	3,692 (510)	0.18 (0.01)	0.47 (0.04)	0.22 (0.05)	120
2/28/11		4.47 (0.25)	3,833 (592)	0.23 (0.01)	0.44 (0.02)	0.29 (0.04)	128