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Factors controlling and promoting blooms of microalgae (*Thalassiosira* spp.) and macroalgae (*Ulva* sp.) in a hypereutrophic, urban estuary, Jamaica Bay, NY, USA

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Ryan B. Wallace

We, the thesis committee for the above candidate for the

Master of Science degree, hereby recommend

acceptance of this thesis.

Dr. Christopher J. Gobler, Professor - Thesis Advisor

School of Marine and Atmospheric Sciences

Dr. Robert Swanson, Professor – Second Reader

School of Marine and Atmospheric Sciences

Dr. James Ammerman, Professor – Third Reader

School of Marine and Atmospheric Sciences

This thesis is accepted by the Graduate School

Charles S. Taber

Interim Dean of the Graduate School

Abstract of the Thesis

Factors controlling and promoting blooms of microalgae (*Thalassiosira* spp.) and macroalgae (*Ulva* sp.) in a hypereutrophic, urban estuary, Jamaica Bay, NY, USA

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Hypereutrophic estuaries are increasingly common features along global coastlines and are typically prone to micro- and macroalgal blooms, yet studies concurrently assessing the factors controlling these distinct algal populations in a single system have been rare. Jamaica Bay is an urban estuary that is hypereutrophic and experiences algal blooms that have been poorly characterized. During 2010 - 2012, the temporal and spatial dynamics of macro- and microalgal communities in Jamaica Bay were investigated in parallel with the factors that control the growth of these algal populations. Phytoplankton communities within the poorly flushed regions of Jamaica Bay (i.e. North Channel and Grassy Bay) reached extremely high densities during the spring and summer (> 135 μg L^{-1} chlorophyll *a*; > 55,000 algal cells mL^{-1}) and were dominated by centric diatoms of the genera *Thalassiosira* spp.. The differences in the absolute magnitude of phytoplankton biomass across Jamaica Bay could be largely predicted from the residence time of water. Dissolved nitrogen (N) and phosphorus (P) concentrations were high throughout the

year in Jamaica Bay while silicate (Si) concentrations were sometimes reduced to < 1µM and limited the growth of the dominant diatoms (*Thalassiosira* spp.) during the late spring and early summer. Such limitation facilitated a transition within the phytoplankton community toward autotrophic nanoflagellates. While often associated with excessive nutrient loading and poorly flushed water, dinoflagellates never dominated the algal community in Jamaica Bay. The macroalgal community in Jamaica Bay was dominated by the green alga, *Ulva* sp., with the densest populations (> 98% bottom coverage) present in the shallow, central portion of the bay and significantly lower coverage within deeper regions. The $\delta^{15}N$ signature of *Ulva* tissue samples across most of the bay (13 - 17 ‰) indicated that waste water was the primary source of N for this alga and the N content of their tissues revealed that this alga was generally N replete. Accordingly, while nutrients almost never restricted the growth of *Ulva*, multiple lines of evidence indicated these populations were light limited within the deeper regions of Jamaica Bay. Finally, experimental incubations of phytoplankton and *Ulva* populations in Jamaica Bay indicated that phytoplankton can inhibit the growth of *Ulva*, likely via shading. Collectively, this study demonstrates that while phytoplankton communities in Jamaica Bay were largely controlled by flushing and Si, *Ulva* populations are controlled by light availability, which was largely controlled by phytoplankton communities.

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INTRODUCTION

Many coastal watersheds have become increasingly populated by humans and this coastal urbanization has led to an accelerated delivery of nutrients to surface waters (Savage et al. 2010). Such accelerated nutrient loading increases the production of organic matter leading to eutrophication (Nixon 1995). Nutrient loading in coastal and estuarine waters can lead to decreases in dissolved oxygen concentrations (Valiela et al. 1992; de Jonge et al. 2002), loss of seagrasses (Valiela et al. 1997; Orth et al. 2006), declines in shellfish and finfish populations (Valiela et al. 1992; Lotze et al. 2006), and degradation of the structure and function of aquatic ecosystems (Valiela et al. 1992; Breitburg et al. 2009). Since many of these negative consequences can stem from the overgrowth of micro- and macroalgae (Valiela et al. 1992; Nixon 1995; Anderson et al. 2002; Phlips et al. 2011), understanding the precise factors controlling these populations in eutrophic estuaries is needed to resolve these problems. While studies investigating the factors promoting microalgal or macroalgal blooms in estuaries are common, studies investigating factors concurrently controlling both populations are rare.

There are strong links between nutrients and algal blooms in many estuaries (Anderson et al. 2008; Heisler et al. 2008) and, given the negative consequences of algal blooms, determining the nutrient that limits the growth of algae is often a primary objective of estuarine management agencies. In many coastal ecosystems, N loading controls the accumulation of phytoplankton biomass and thus primary producers are N-limited (Ryther and Dunstan 1971; Howarth 1988; Fisher et al. 1992), due to high denitrification rates, slow N fixation rates, and substantial releases of P from sediments (Boynton and Kemp 1985; Howarth 1988). There are strong links between nutrients and harmful dinoflagellate blooms in many estuaries (Margalef 1978; Smayda 1997; Heisler et al. 2008). In some cases, there are direct correlations between nutrient loading

rates and dinoflagellate bloom intensity (Heil et al. 2005; Brand and Compton 2007). In other cases, the links between dinoflagellate blooms and nutrients may be indirect, as blooms may be promoted by high levels of organic nitrogen (Gobler et al. 2012) or high levels of algal prey (Adolf et al. 2008), both of which are ultimately a consequence of an elevated N load (Gobler et al. 2005; Sunda et al. 2006; Adolf et al. 2008).

Another group of autotrophs that is often promoted by nutrient loading in shallow coastal waters are macroalgae (Valiela et al. 1997; Conley et al. 2009). The overgrowth of macroalgae is a common symptom of eutrophication as many species are capable of rapid growth in the presence of high nutrient concentrations and have a high assimilative capacity for nutrients (Valiela et al. 1997; Neori et al. 2004; Zertuche-Gonzalez et al. 2009). Despite the great diversity of macroalgae, eutrophic conditions in temperate estuaries often lead to dominance by opportunistic Ulvalean species (Valiela et al. 1997). In some cases, blooms of Ulvalean macroalgae can be considered harmful, as they can replace critical benthic habitats, promote diel hypoxia, and inhibit the growth of larval bivalves (Valiela et al. 1997; Nelson et al. 2003; Bricker et al. 2008; Howarth 2008; Thornber et al. 2008). The relative dominance of primary producers in estuaries can often be predicted by nutrient loading rates and water residence times (Valiela et al. 1997). Specifically, as nutrient loading rates increase, the dominant primary producers shift from seagrasses to macroalgae and eventually to exclusively phytoplankton at the highest loading rates (Valiela et al. 1997). Macroalgae generally dominate estuaries with high nutrient loads and short residence times due to their ability to attach and grow on the benthos (Valiela et al. 1997). In addition to residence times and nutrient loadings, recent studies suggest allelopathy may also strongly affect the interactions between macroalgae and phytoplankton (Gross et al. 2007; Tang and Gobler 2011; Wang et al. 2012).

Study Site

Jamaica Bay is an urban, eutrophic estuary located along the southwest corner of Long Island, NY, USA, and encompasses an area of ~ 50 km^2 (NYCDEP 2007). Jamaica Bay connects with the Atlantic Ocean to the west through a single inlet (Rockaway Inlet) and receives the discharge of almost 300 million gallons of treated effluent per day from four major sewage treatment plants that service more than one million New York City residences. This sewage load is approximately 1000 kg N ha^{-1} yr^{-1} (Benotti et al. 2007) and represents the largest sources of N and fresh water into the Bay (NYCDEP 2007). While Jamaica Bay once hosted one of the largest Eastern oyster (*Crassostrea virginica*) fisheries in the US, excessive loading of sewage and associated pathogens has resulted in a 90-year ban on shellfishing in Jamaica Bay (since 1921; NYCDEP 2007). Jamaica Bay also experiences summer bottom water hypoxia (NYCDEP 2007). While high biomass blooms of phytoplankton and macroalgae ultimately contribute to hypoxia and ecological disruption in Jamaica Bay (NYCDEP 2007), little is known regarding the composition of, or controls on, micro- and macroalgal communities in this system.

The goal of this study was to establish the temporal and spatial dynamics of nutrients, phytoplankton communities, and macroalgae in Jamaica Bay and assess factors that limit the growth of phytoplankton and macroalgae across this estuary. Surveys of both micro- and macroalgal species abundance and distribution were conducted at multiple stations across Jamaica Bay from 2010 – 2012. Nutrient amendment experiments were conducted to determine which nutrient limited the growth of both micro- and macroalgae. Separate and tandem incubations of these populations were used to assess competition between these populations. *In situ* incubations of *Ulva* were used to assess how the growth of these populations changes vertically and horizontally across the estuary.

METHODS

Field sampling and water quality analyses

I collected samples from nine locations across Jamaica Bay from 2010 - 2012. Specific sampling locations were consistent with New York City Department of Environmental Protection (NYCDEP) sampling locations (Fig. 1). The stations close to, and further away from, known sewage discharge locations and Rockaway Inlet permitted an evaluation of the relative impact of sewage effluent and this inlet on multiple water quality parameters. Samples were collected on a biweekly basis from March through November. Seawater was collected in the morning aboard the NYCDEP's *HSV Osprey* or a small craft provided by the National Park Service (NPS). Stations in Grassy Bay (J7 & J12) and station J1, closest to Rockaway Inlet, represented extremes in distance and general water quality and thus were sampled more frequently than the other six locations to better assess the impact of sewage treatment plant effluent on water quality in Jamaica Bay.

At each station, a CTD cast was made to determine the vertical structure of temperature (T), salinity (S), and dissolved oxygen (DO) in the water column. Surface water was collected at each station using a CTD rosette or a single Niskin bottle (depending on the vessel). Secchi disc measurements were made at each station and the percent of light at the benthos was determined according to Cole 1975 and light levels at the benthos were estimated from mean light levels common to the south shore of Long Island as described in Mulholland et al 2002. Particulate organic carbon and N (POC, PON) samples were collected on pre-combusted (2h at 450°C) glass fiber filters (GF/F with nominal pore size of 0.7 μm) and were analyzed using an a CE Instruments Flash 1112 elemental analyzer (Cutter and Radford-Knoery 1991). Whole water was filtered for nutrient analysis using pre-combusted (2h at 450°C) GF/F. Filtrate was

colorimetrically analyzed for dissolved nutrient concentrations, including silicate, nitrate, nitrite, ammonium, and orthophosphate, using standard wet chemistry and spectrophotometer methods (Parsons 1984) adapted to a 96-well plate reader.

Phytoplankton community composition

The community composition was firstly assessed by the analysis of size fractionated chlorophyll *a* (0.2 μm, 2 μm, and 20 μm) using polycarbonate filters and standard fluorometric techniques (Parsons 1984). Whole water Lugol's iodine preserved plankton samples were settled in counting chambers and enumerated on a light microscope (Hasle 1978). Microphytoplankton (> 10 μm) were identified to the genus or species level and grouped as diatoms, dinoflagellates, autotrophic nanoflagellates, and ciliates. To assess the effects of residence times on phytoplankton populations in Jamaica Bay, the mean biomass of phytoplankton populations were compared to the age of water parcels in different regions of the Bay as determined by Benotti et al (2007). A Spearman's rank order correlation matrix was performed in SigmaStat 4.0 to assess associations between differing environmental variables and algal groups.

Photosynthesis and respiration of plankton communities

To establish the rates of photosynthesis and respiration of the plankton community, clear and dark 300 mL borosilicate glass bottles were washed with 10% HCl, liberally rinsed with deionized water, and filled in triplicate with seawater from sampling locations without bubbling. An initial DO measurement of each bottle was made using a high precision, Clark-type electrode (YSI 5100) as described in Koch and Gobler 2009. Bottles were incubated for ~ 24 h at a depth of 0.5 m in eastern Shinnecock Bay, at the Stony Brook Southampton Marine Science Center

Southampton, NY, mimicking the light and temperature regime found in the surface waters of Jamaica Bay. After this incubation period, final DO concentrations were measured. Pelagic respiration rates determined from changes in oxygen levels in dark bottles whereas changes in oxygen levels in light bottles, corrected for respiration rates, were considered rates of gross photosynthesis. Rates were converted from O_2 to C using the Redfield ratio of 138:106 according to Laws (1991).

Mapping macroalgal populations and their $\delta^{15}N$ signature

Temporal and spatial dynamics of macroalgae were established from seasonal (fall and late spring) bottom surveys of their relative abundance. Random sampling was conducted at 40 sites across the Bay. At each site, percent cover of macroalgae was determined using Ocean Systems, Inc. Deep Blue underwater camera, attached to a 0.25 m^2 gridded quadrat, interfaced to a Garmin Ltd. GPS-100 overlay unit. Four random deployments at each of the 40 sites ensured accurate coverage estimates. Still, color images were uploaded into the image analysis software SigmaScan® Pro 5 and percent coverage of macroalgae was determined based on the percent of pixels covered with macroalgae within the gridded quadrat. At each site with macroalgae, samples of the fresh thalli were collected and stored frozen. The dominant genera of macroalgae in all samples was *Ulva* sp. Recently, four species of *Ulva* that are morphologically indistinguishable have been identified in the Northeast United States: *Ulva lactuca*, *U. rigida*, *U. compressa*, and *U. pertusa* (Hofmann et al. 2010). For the purposes of this study I will refer to these macroalgae as *Ulva* spp. Samples were dried at 55°C and then homogenized with a mortar and pestle. The ^{15}N signature and N content of the homogenized macroalgae were analyzed using an elemental analyzer interfaced to a continuous flow isotope ratio mass spectrometer on a

Europa 20/20 isotope ratio mass spectrometer equipped with an automated nitrogen and carbon analyzer at the UC Davis Stable Isotope Facility. Stable nitrogen isotope ($\delta^{15}N$) ratios can be used to identify anthropogenic nitrogen sources in many organisms including macroalgae (Cole et al. 2004). Primary producers generally possess $\delta^{15}N$ signatures that matches their dominant nitrogen source (Valiela et al. 1992). The primary source of nitrogen to urban estuaries is often waste water, this anthropogenic N is usually in the form of nitrate or ammonium with a heavy $\delta^{15}N$ signature (Valiela et al. 1992). In contrast, systems impacted by agriculture are often enriched in fertilizer-based N which is often depleted of ^{15}N (McClelland et al. 1997). Point data of the percent cover and $\delta^{15}N$ signatures of macroalgae were used to produce spatial distribution maps for Jamaica Bay using ESRI® ArcGIS® 10 and using the Geostatistical Analyst extension, an ordinary Kriging algorithm was used to interpolate between the random point data. $\delta^{15}N$ values were ranked into five categories, ranging from < 6‰, 6 - 8‰, 8 - 11‰, 11 - 14‰, and > 14‰.

Experimental incubations

To establish the effects of nutrient enrichment on both phytoplankton and *Ulva* sp. in Jamaica Bay, nutrient amendment experiments were performed using 1.1 L polycarbonate bottles. Bottles were washed with 10% HCl and liberally rinsed with deionized water prior to use. For phytoplankton, triplicate sets of bottles filled with Bay water from northern and eastern stations (J7, J12, J8, & J9A) were enriched with nitrate (50 μM), silicate (50 μM), phosphate (3 μM), or were left unamended as a control treatment. These nutrient ratios are consistent with the Redfield stoichiometry while concentrations were within the range of levels found in Jamaica Bay during this study. For *Ulva*, both triplicate sets of filtered seawater (0.2 μm) and whole

seawater were enriched with nitrate (50 μM), phosphate (3 μM), nitrate (50 μM) & phosphate (3 μM), or were left unamended as a control treatment. Performing these incubations in filtered and whole seawater allowed potential competition between *Ulva* and phytoplankton populations to be assessed. *Ulva* discs of uniform size (3.5 cm in diameter) punched from fresh specimens obtained in Jamaica Bay with a sharpened Perspex tube (Geertzhansen and Sandjensen 1992) were washed free of epiphytes using filtered (0.2 μm) seawater and added to each bottle. Phytoplankton experimental bottles were incubated for ~ 24 h at a depth of 0.5 m in eastern Shinnecock Bay. At the completion of the incubation period, aliquots from experimental bottles were preserved in 2% Lugol's iodine solution and filtered for size fractionated (0.2 μm, 2 μm, and 20 μm) chlorophyll *a* analysis as described above. Growth rates for different size fractions and phytoplankton groups were calculated as ln(Bf / Bi) where Bf is final biomass and Bi is the initial biomass. Experimental bottles containing *Ulva* discs were incubated for ~7 days at a depth of 0.5 m in eastern Shinnecock Bay. Upon the completion of the incubation period, aerial growth rates of *Ulva* (cm^2 d^{-1}) were calculated based on differences in the *Ulva* discs before and after incubations as determined by scanned images of discs analyzed on SigmaScan® Pro 5. Significant differences in growth rates of algal populations were assessed using a one-way (phytoplankton) or two-way (macroalgae) ANOVA and post-hoc multiple comparisons tests within SigmaStat® 4.0 where nutrients were the main treatment effects (nitrogen and phosphorus only for the macroalgae). Competition between phytoplankton populations and *Ulva* was assessed by comparing the growth rates of each population incubated alone (whole seawater for phytoplankton, filtered seawater for *Ulva*) and together using a two-way ANOVA and post-hoc multiple comparisons tests within SigmaStat® 4.0 where the presence of a competitor and nutrients levels (added or not) were the main treatment effects.

In situ *Ulva* growth experiments were performed at multiple locations across the Bay (stations J1, J2, J7, & JMS; Fig 1). Triplicate, in situ 10 cm^2 incubation cages constructed of 1 cm^2 mesh were deployed at both 1 m and 3 m depths for ~ 7 days. Growth rates of *Ulva* in cages were calculated as described above. Significant differences in growth rates of algal populations were assessed using a two-way ANOVA and post-hoc multiple comparisons tests within SigmaStat® 4.0 where location and depth were the main treatment effects.

RESULTS

During 2010 and 2011, chlorophyll *a* levels generally increased in the eastern regions of Jamaica Bay (Stations J7 & J12) during the late spring and summer months to concentrations exceeding 100 µg L^{-1}, but then declined during fall months (Fig 2; Table 1). There was a consistent spatial gradient of phytoplankton communities across Jamaica Bay, with the highest chlorophyll *a* levels occurring in the eastern and northern regions (stations J7, J12, J8 & J9A) and the lowest chlorophyll *a* concentrations occurred closer to Rockaway Inlet in the western and southern regions of the bay (station J1; Fig 2; Table 1). These high density blooms (chlorophyll *a* concentrations >100 µg L^{-1}) in the late spring and early summer were dominated by nanoplankton, cells between 2 and 20 µm, as this group accounted for 60-80% of total chlorophyll *a*. Gross photosynthetic rates followed a similar trend and peaked during the summer months in the northern and eastern regions of Jamaica Bay (> 3.8 ± 0.81 mg C L^{-1} d^{-1}; stations J7 & J12; Table 2), but were lower in the inlet (2.31 ± 0.52 mg C L^{-1} d^{-1}; station J1; Table 2).

Phytoplankton blooms in Jamaica Bay were initially dominated by diatoms of the *Thalassiosira* genera that were succeeded by blooms of autotrophic nanoflagellates (Figs 3, 4). For example, in the early summer of 2010, both stations in the eastern regions of Jamaica Bay (J7 & J12) experienced a dense *Thalassiosira* sp. bloom (> 5 x 10^4 cells mL^{-1}; Fig 4) during which the phytoplankton community was nearly devoid of any other class or species of nano- or microphytoplankton (Fig 3, 4). By July, the phytoplankton community in eastern Jamaica Bay became dominated by autotrophic nanoflagellates with cell densities exceeding 3.5 x 10^4 cells mL^{-1} at station J7 and 2 x 10^4 cells mL^{-1} at station J12, while diatom densities were < 3 x 10^3 cells mL^{-1} at both stations (Fig. 3a & b). In early August, *Thalassiosira* sp. again dominated the phytoplankton in eastern Jamaica Bay, reaching cell densities of 4 x 10^4 cells mL^{-1} (Fig 4). In late August, nanoflagellates dominated the phytoplankton community, with cell densities at station J12 reaching 7.5 x 10^4 cells mL^{-1}, while diatom densities declined to < 400 cells mL^{-1} (Fig 3b). The following year a similar pattern of succession was observed with *Thalassiosira* sp. dominating the phytoplankton community in eastern Jamaica Bay in early April (Figs 3, 4) and nanoflagellates dominating in late May and early June (Fig 3a & b). Nanoflagellate cell densities decreased by early August (Fig 3a & b) when there was another high density *Thalassiosira* sp. bloom (> 5 x 10^4 cells mL^{-1}; Fig 4). *Thalassiosira* blooms were primarily dominated by smaller species, including *T. weissflogii* and *T. pseudonana,* particularly during warmer months and by the larger species, *T. aestivalis,* during cooler months. During the study, temperatures ranged from 7°C in the early spring to 27°C during the summer. Salinities ranged from 19 to 26 PSU in the northeast region of the bay and 22 to 30 PSU at the inlet.

The concentrations of nitrate, ammonium and phosphate in eastern Jamaica Bay were high throughout this study while concentrations of silicate during spring and early summer were

more dynamic and occasionally low (Table 3). For example, during the spring and early summer, average nitrate, ammonium, and phosphate, concentrations in northern and eastern Jamaica Bay were 23.21 ± 2.16 μM, 28.53 ± 5.84 μM and 4.96 ± 0.64 μM, respectively while silicate levels were concurrently 3.21 ± 1.19 μM (Table 3). By the late summer months, silicate concentrations in northern and eastern Jamaica Bay increased by an order of magnitude, to 51.8 ± 7.39 μM while concentrations of nitrate, ammonium and phosphate remained high (32.52 ± 2.75 μM, 47.41 ± 6.93 μM and 7.82 ± 0.47 μM, respectively; Table 3). Dissolved inorganic nitrogen to phosphate ratios (DIN:DIP) were generally near the Redfield ratio (16:1) during this study (13.25 ± 1.00; Table 3). DIN to silicate ratios (DIN:DSi) were high in the spring and early summer (17.40 ± 4.02; Table 3), but were lower later in the season (3.40 ± 1.15).

The supply of silicon limited the growth of phytoplankton during experiments performed in the spring and early summer months. Specifically, on 5/18/2010, 6/15/2010, 6/29/2010 and 7/28/2011 at station J7 and on 3/15/2011 at stations J12, J8 and J9A (Table 4) and on 4/5/2011 at station J8, experimental bottles enriched with silicon produced significantly higher growth rates of phytoplankton compared to the control, nitrate and phosphate treatments ($p < 0.05$ for all experiments; Table 4). The >20μm size class was most frequently limited by silicon (5 experiments) followed by the 0.2 – 2μm size class (4 experiments). Furthermore, nutrient enrichment experiments showed significantly faster growth rates of the diatom *Thalassiosira* spp. in silicate treatments when compared to the control (Fig 5a-f) with final experimental cell densities in silicate treatments sometimes exceeding 160,000 cells mL^{-1} compared with < 30,000 cells mL^{-1} in control bottles. Nitrogen increased the growth of phytoplankton in Jamaica Bay during one experiment (8/3/10; $p<0.05$) while phosphorus never did so (Table 4).

***Ulva* populations in Jamaica Bay**

The macroalgal community was dominated by green alga of the *Ulva* spp. with the densest populations (> 98% bottom coverage) found in the central portion of the bay within close proximity of station JMS (Figs 1 & 6). While present, other macroalgae were far less abundant in Jamaica Bay and always covered < 20% of the bottom (data not shown). During the fall in central areas, *Ulva* bottom coverage ranged from 20-40% and some southern sites had bottom coverage of up to 60% (Fig 6a). Shallow areas in the west had bottom coverage ranging from 10-15% while most other sites had bottom coverage < 10% (Fig 6a). In the late spring of 2012, *Ulva* spp. had expanded significantly throughout the shallow central portion of Jamaica Bay to 50-100% coverage (Fig 6b). *Ulva* sp. bottom coverage in shallower regions north of stations J9A and J8 ranged from 60-90% coverage while *Ulva* coverage in the deeper northern, eastern, and southern channels had almost no *Ulva* at that time (< 2%; Fig 6b). $\delta^{15}N$ signatures of *Ulva* sp. ranged from 5-17 ‰, with lower values generally in the western areas of the Bay and values exceeding 10‰ in the central areas sampled (Figs 7 & 8). Two stations in the northeastern area of the bay had lower $\delta^{15}N$ signatures. The N content of *Ulva* tissues ranged from 35 to 50 mg N g^{-1} dry weight throughout the year (Fig 8). During two years of experimental incubations, *Ulva* growth was limited by N in one experiment (11/10/10; $p < 0.05$; Table 5) while no experiment revealed phosphorus limitation.

The growth of *Ulva* differed vertically ($p < 0.001$) and horizontally ($p = 0.001$) across Jamaica Bay. In situ *Ulva* experiments conducted at station J1 (inlet, lowest DIN), station JMS (central, intermediate DIN) and station J7 (northeastern, high DIN) showed that *Ulva* growth rates decreased from east to west (stations J7 > JMS > J1) from 0.199, to 0.135, to 0.002 d^{-1},

respectively (Fig 9a). *Ulva* growth rates at 1 meter depth were significantly higher than the *Ulva* incubated at 3 meters depth ($p < 0.001$; Fig 9b).

Microalgal – macroalgal competition experiments

In all microalgae - *Ulva* competition experiments, growth rates of *Ulva* were significantly higher in the filtered seawater without phytoplankton than in the whole seawater. The growth of *Ulva* sp. in the presence of the whole phytoplankton community was depressed by 37 – 58% compared to incubations in whole seawater ($p<0.05$ for all; Fig 10). This trend did not change when incubations were performed with the addition of nutrients ($p>0.5$ for all; Fig 10). In contrast, phytoplankton growth rates were not significantly altered by the presence of macroalgae (data not shown).

DISCUSSION

As human populations have expanded along coastlines during the past century, eutrophic estuaries have become increasingly common. For example, a recent survey has found that the large majority of US estuaries are eutrophic (Scavia and Bricker 2006; Bricker et al. 2008). One of the most common environmental problems in eutrophic estuaries is blooms of micro- and macroalgae (Valiela et al. 1992; Valiela et al. 1997; Valiela 2006). Yet, a comprehensive understanding of the factors that concurrently control these two different algal populations is lacking, in part, because the studies that concurrently consider both populations are rare. This study of the hypereutrophic, urban estuary, Jamaica Bay found that phytoplankton blooms dominated by *Thalassiosira* spp. were controlled by silicate supply and residence times and

restricted the proliferation of *Ulva* populations through light limitation. Collectively, these findings provide new insight into the factors controlling algal populations in eutrophic estuaries.

While phytoplankton blooms in Jamaica Bay reached extremely high densities (>100 μg *chla* L^{-1}, >5 x 10^4 cells mL^{-1}), the intensity of phytoplankton blooms lessened from the northeast to the southwest (Stations J7 & J12 > J8 & J9A > J1), with Rockaway Inlet (station J1) consistently having the lowest algal biomass (Fig 2). According to Benotti et al. 2007, the oldest water (40 days) or longest residence times in Jamaica Bay exist in the easternmost portions of the estuary (Stations J7 & J12) and the youngest water (0-5 days) or shortest residence times are present within the Inlet (Station J1). The age of water in Jamaica Bay was strongly correlated with chlorophyll *a* concentrations in Jamaica Bay measured during this study (R^2= 0.7; Fig 11) suggesting that accumulation of phytoplankton biomass in this estuary is largely controlled by physical flushing. However, dissolved silicon seems to play a key role in influencing phytoplankton community composition.

Chronically high levels of DIP and DIN (> 3 and 25 μM; respectively; Table 2) present at values close to the Redfield ratio and the nearly chronic inability of N or P to significantly enhance phytoplankton growth rates in Jamaica Bay during experiments (Table 4) suggests N and P rarely limits the production of phytoplankton biomass in Jamaica Bay. This contrasts with some other temperate estuaries, where N-limitation is common (Fong et al. 1993; Doering et al. 1995; Hartzell and Jordan 2012) and P-limitation is sometimes observed during spring months (Malone et al. 1996; Mallin et al. 1999). These differences are likely due, to excessive anthropogenic N and P loading associated with sewage discharge in Jamaica Bay (NYCDEP 2007). Since anoxic sediments overlain by hypoxic waters are a rich source of P to estuaries (Ingall and Jahnke 1994) and since bottom dissolved oxygen and orthophosphate in this system

were inversely correlated ($p<0.00001$; $R=-0.67$), it is likely that benthic fluxes are an additional source of P to this system.

Nutrient ratios are often used to assess the extent to which nutrients may limit the growth of various phytoplankton populations. On average, diatoms require one mole of Si for every mole of N (Brzezinski 1985) and ratios of DIN:DSi exceeding one can limit the growth of diatoms (Smayda 1990; Turner et al. 1998; Graneli et al. 1999; Gobler and Boneillo 2003; Gobler et al. 2006). DIN:DSi were high in the spring and early summer (17.40 ± 4.02; Table 3) when silicate concentrations were often < 4 μM, the half-saturation constant for silicate for diatoms (Egge and Aksnes 1992) further suggesting silicate could have limited the growth of diatoms. Accordingly, there was a strong inverse correlation between Si and diatoms in eastern Jamaica Bay ($p<0.00001$; $R=-0.64$). Low levels of silicate likely contributed toward the seasonal silicon limitation of *Thalassiosira* sp. observed during experiments and succession of phytoplankton communities in Jamaica Bay (Fig 12). Specifically, when high density *Thalassiosira* sp. blooms occurred in eastern Jamaica Bay, silicate concentrations were drawn down to low levels (< 4 μM; Fig 12) that limited the growth of these diatoms. Once *Thalassiosira* sp. was limited by the Si supply, this population was succeeded by autotrophic nanoflagellates (Fig 12) and silicate concentrations increased, suggesting these were likely not silicoflagellates. Once silicate concentrations increased, *Thalassiosira* sp. would again grow to dominate the phytoplankton community (Fig 12). During summer, silicate levels were generally higher than the rest of the year and diatoms consistently dominated the phytoplankton community, likely due in part to benthic fluxes of Si during warm temperatures. The dissolution of benthic Si is temperature dependent (Kamatani 1982; Conley and Malone 1992) and silicate concentrations were significantly correlated with bottom temperature in Jamaica Bay ($p<0.005$;

R=-0.32). The alternating dominance of diatoms and nanoflagellates continued until the fall months, when both groups decreased in abundance. While non-selective grazing may have also contributed toward this trend (Strom and Fredrickson 2008), zooplankton grazing rates were not quantified during this study.

In most temperate marine ecosystems, phytoplankton undergo a seasonal succession with diatoms dominating during cooler months with low light but high nutrients, and flagellates and dinoflagellates dominating summer months (Sverdrup 1953; Barlow et al. 1993; Behrenfeld 2010). While there was a succession of diatoms and autotrophic flagellates in Jamaica Bay, these patterns were not linked to seasons, but rather linked to silicate availability. Jamaica Bay is a hypereutrophic estuary and receives a surplus amount of both N and P throughout the year that seemingly enabled the phytoplankton with the fastest growth rates, specifically, diatoms (Smayda 1997) to dominate the communities until the silicate pool was depleted. The ability of diatoms to maintain rapid growth rates under low light conditions may have also contributed to their proliferation during high density blooms when light attenuation was high (MacIntyre et al. 2002; Allen and Polimene 2011). Diatom abundances were highly correlated with concentrations of chlorophyll *a*, POC, and PON ($p<0.000001$ for all; R=0.81, 0.63, and 0.82, respectively) while other groups of plankton were not, demonstrating this group dominated algal biomass during most of this study. While dinoflagellates are known to be promoted by eutrophication (Anderson et al. 2008; Heisler et al. 2008) they generally possess slow growth rates (Smayda 1997) and thus, often bloom when inorganic nutrient levels in surface waters are low since they exploit organic compounds and diel vertically migrate to form blooms (Anderson et al. 2008; Burkholder et al. 2008). Hence, the chronically high levels of inorganic nutrients in Jamaica Bay that promote rapid, nutrient replete growth of diatoms and autotrophic

nanoflagellates do not allow dinoflagellates to realize their ecological niche. Therefore, while some degree of excessive nutrient loading may promote harmful algal blooms caused by dinoflagellates (Margalef 1978; Heisler et al. 2008), the extreme levels of nutrient loading and chronically high levels of N and P in hypereutrophic estuaries such as Jamaica Bay may prohibit the dominance of dinoflagellates. Finally, since *Ulva* sp. is known to allelopathically inhibit the growth of many dinoflagellates (Jin et al. 2005; Nan et al. 2008; Tang and Gobler 2011), its role in restricting the proliferation of this algal group in Jamaica Bay cannot be discounted.

Nutrients rarely limited the growth of *Ulva* sp. in Jamaica Bay (Table 5). Lyngby et al. (1999) defined a critical tissue concentration of N needed for maximum growth as 18-23 mg N g^{-1} dry tissue and *Ulva* populations in Jamaica Bay consistently had tissue N concentrations significantly higher than this. In one of our two in situ *Ulva* experiments, this alga showed decreased growth rates from east to west across Jamaica Bay (J7 > JMS > J1), as ambient DIN concentrations during experiments declined from 164, to 62, to 51 μM, respectively (Fig 9a) suggesting that higher concentrations of DIN supported more rapid net growth rates of *Ulva* in Jamaica Bay. *Ulva*, however, is known to harbor large stores of nutrients which may buffer their response to nutrients over short time scales (Steffensen 1976; Bjornsater and Wheeler 1990; Viaroli et al. 1996) perhaps accounting for the lack of response in other experiments.

$\delta^{15}N$ signatures can be used to identify anthropogenic nitrogen sources in many organisms including macroalgae (Cole et al. 2004). The primary source of nitrogen within Jamaica Bay is waste water (Benotti et al. 2007). *Ulva* sp. populations collected across Jamaica Bay showed a spatial gradient regarding $\delta^{15}N$ signatures with heavier values generally found in populations collected in closer proximity to sewage outfalls (Fig 7). Samples collected from western areas in the Bay where there is less discharge from wastewater treatment plants and

more flushing with Atlantic Ocean water (Benotti et al. 2007) generally had lighter $\delta^{15}N$ signatures (Fig 7). Tissue samples collected in close proximity to the Rockaway and 26th Ward outfalls in the central, northern, and eastern regions had heavier $\delta^{15}N$ signatures demonstrating that sewage effluent is the dominant N source to *Ulva* in this region (Valiela et al. 1992; Cole et al. 2004). Interestingly, there was a region (two stations) near the Jamaica wastewater plant (northeast) that had unusually light $\delta^{15}N$ signatures (< 9‰). This area of the bay is heavily influenced by wastewater N (Table 2) and has extended residence times but also experiences the greatest frequency of combined sewer overflow (CSO) outfalls (Benotti et al. 2007). Since higher levels of sewage treatment may result in heavier $\delta^{15}N$ signatures due to increased microbial processing (Costanzo et al. 2005), we hypothesize that *Ulva* with lighter $\delta^{15}N$ signatures in the northeast of the Bay are utilizing N from CSO's that has not been treated.

It has been proposed that the relative dominance of primary producers in estuaries can be predicted by N loading rates and water residence times in estuaries (Valiela et al. 1997). While estuaries that experience intermediate N loading (300 – 500 kg ha^{-1} yr^{-1}) are usually co-dominated by macroalgae and phytoplankton, N loading to rates > 500 kg ha^{-1} yr^{-1} generally cause a shift in primary production toward dominance by phytoplankton (Valiela et al. 1997). This shift is expected to be complete and to occur at even lower N loading rates in estuaries with extended residence time (Valiela et al. 1997). Given the long residence time (> 45 d) and massive sewage N loading rate for Jamaica Bay (~1000 kg ha^{-1} yr^{-1}; Benotti et al. 2007), phytoplankton there would be expected to competitively exclude all benthic primary producers (Valiela et al. 1997). Since *Ulva* covered up to 90% of the shallower regions of Jamaica Bay (< 3m; Fig 6), it would seem a third factor that must be considered regarding the dominance of

primary producers in estuaries, specifically depth which influenced the light *Ulva* populations received and seemed to play a central role in controlling these populations in this system.

There were five lines of evidence indicating that *Ulva* populations in Jamaica Bay were limited by light and that light levels were, in turn, controlled by phytoplankton populations. Firstly, deployment of *Ulva* across Jamaica Bay at 3m yielded significantly lower growth rates compared to individuals deployed at 1m ($p < 0.001$; Fig 9b). Second, bottle experiments with *Ulva* sp. co-incubated with phytoplankton growth yielded significantly reduced *Ulva* growth rates compared to incubations without phytoplankton (Fig 10). Since this outcome was nearly identical with or without added nutrients this growth inhibition of *Ulva* populations was likely due to shading by phytoplankton (Fig 10). Third, for all of Jamaica Bay, light penetration was inversely correlated with total chlorophyll ($p<0.000001$; $R=0.68$; Fig 13) indicating that phytoplankton controlled light penetration in this estuary. Next, *Ulva* populations are known to require 1% of surface irradiance to survive (Sand-Jensen 1988) and in the deeper regions of Jamaica Bay such as stations J7 and J12 (8 – 12 m), the 1% light depth was always above the bay bottom whereas in the shallower center region of the Bay (e.g. JMS) the bottom was always exposed to >1% of incoming irradiance (Table 6). Accordingly, dense coverage of *Ulva* (> 60%; Fig 6) was limited to the central area of Jamaica Bay (Fig 6) where it is shallow and light can penetrate to the bottom and permit *Ulva* to proliferate during much of the year (Sfriso and Marcomini 1996; Nelson et al. 2008). Finally, greater abundance of *Ulva* sp. during May compared to November (Fig 6) was likely due to the increased daylight hours in May (increased light intensity) and the fact that the fall survey was conducted after months of light attenuating algal blooms. While a number of recent studies have cited the ability of *Ulva* sp. to inhibit the growth of many dinoflagellates (Nan et al. 2008; Wang et al. 2009; Tang and Gobler 2011;

Wang et al. 2012), phytoplankton densities were unaffected by co-incubation with *Ulva* during this study. Given that the dominant phytoplankton in Jamaica Bay were diatoms, it may be that this class of algae is more resistant to *Ulva* than dinoflagellates. Moreover, coastal diatoms in the genus *Thalassiosira* such as those found in Jamaica Bay are known to be well-adapted to low light (Sakshaug et al. 1987) accounting for their dominance in the Bay and in co-incubations with *Ulva*.

In conclusion, the discharge of two large wastewater treatment plant outfalls into the region with the longest extended residence times (northeast Jamaica Bay; Benotti et al. 2007) promotes the proliferation and persistence of high density phytoplankton blooms during the spring, summer, and fall. The enormous input of nutrients from these plants prevents N or P from limiting the growth of phytoplankton or macroalgae. Phytoplankton biomass in Jamaica Bay is largely is controlled by flushing whereas phytoplankton diversity is seasonally controlled by the availability of Si. High density phytoplankton blooms increase turbidity in Jamaica Bay and restrict the growth of macroalgae to the shallowest, central regions of the bay (< 4 m). Collectively, the dynamics of primary producers in Jamaica Bay is, thus, a function of nutrient loading, silicate concentrations, light attenuation within the water column, and residence time.

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APPENDIX

Figures

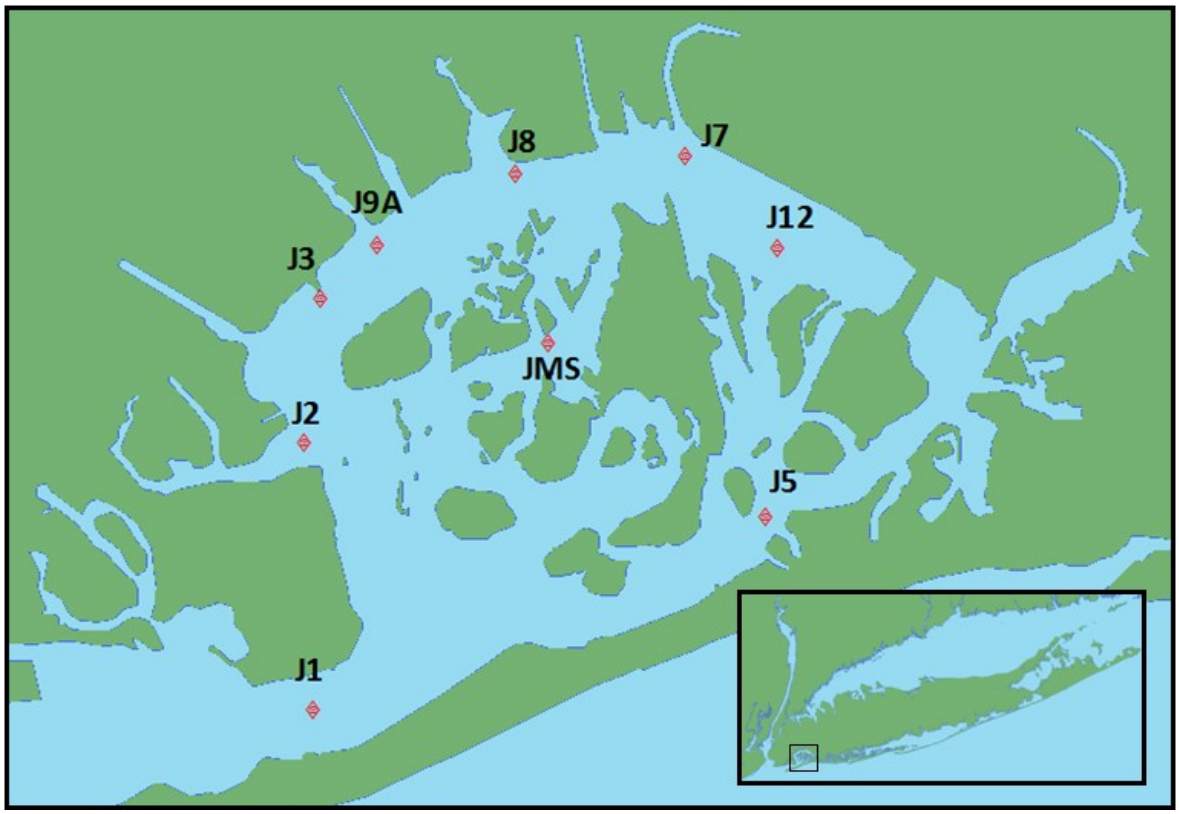

Figure 1. Sampling stations in Jamaica Bay 2010 – 2011.

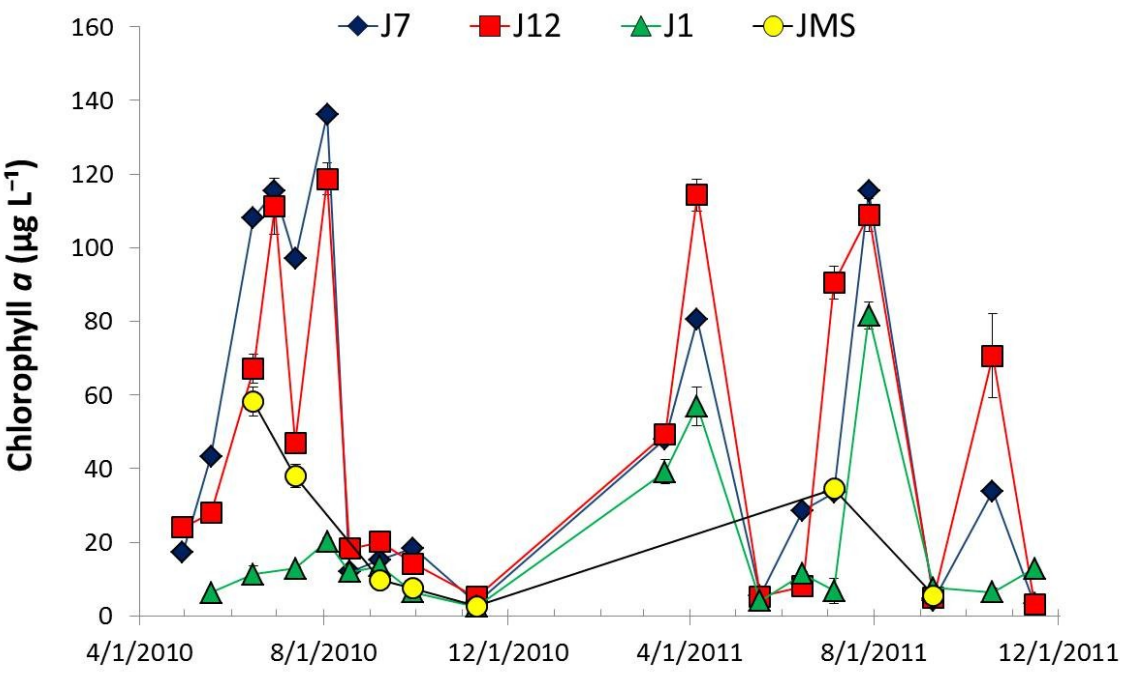

Figure 2. Dynamics of total phytoplankton biomass as indicated by chlorophyll a at four stations in Jamaica Bay.

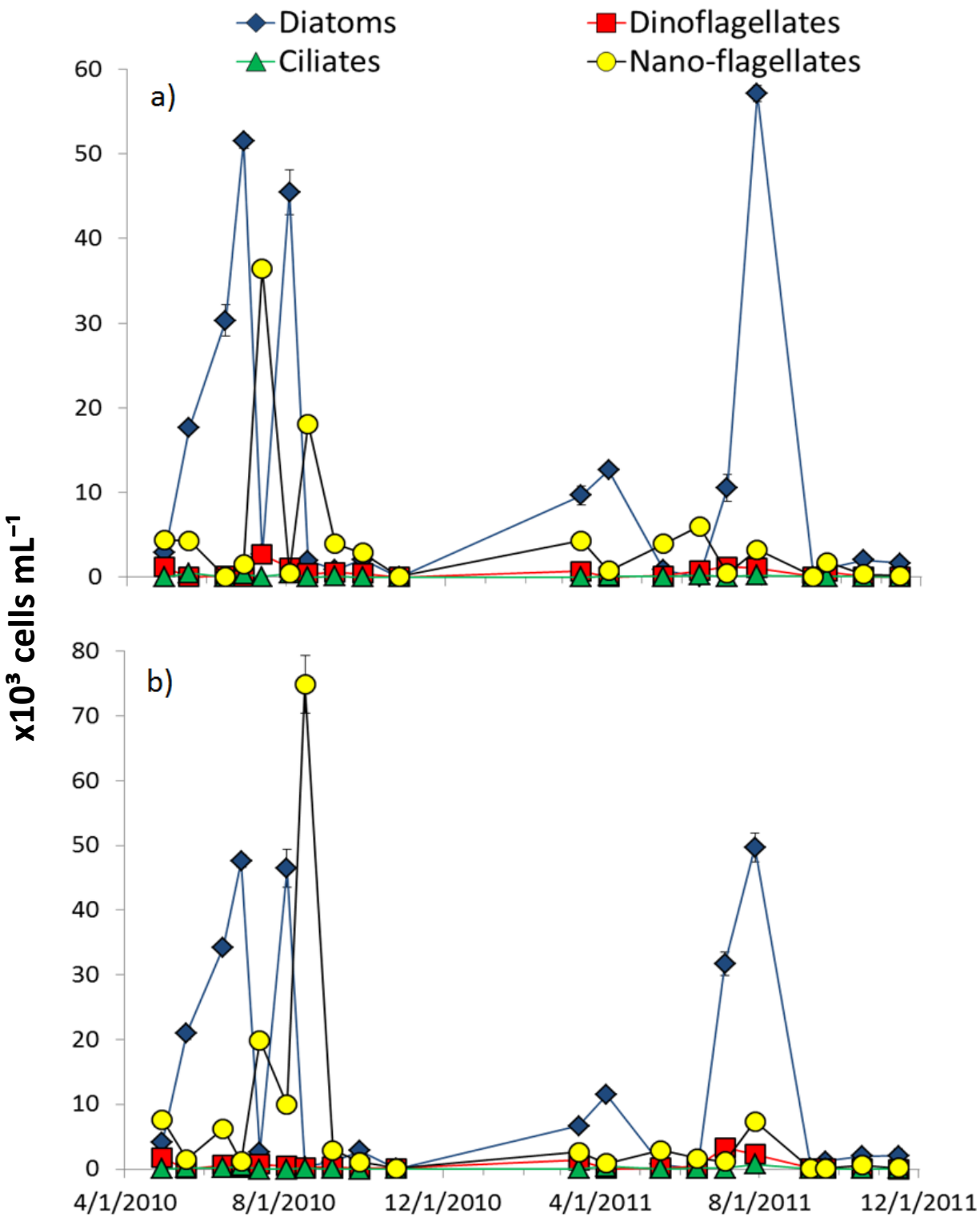

Figure 3a & b. Dynamics of the densities of four classes of plankton at **a)** station J7 **b)** station J12

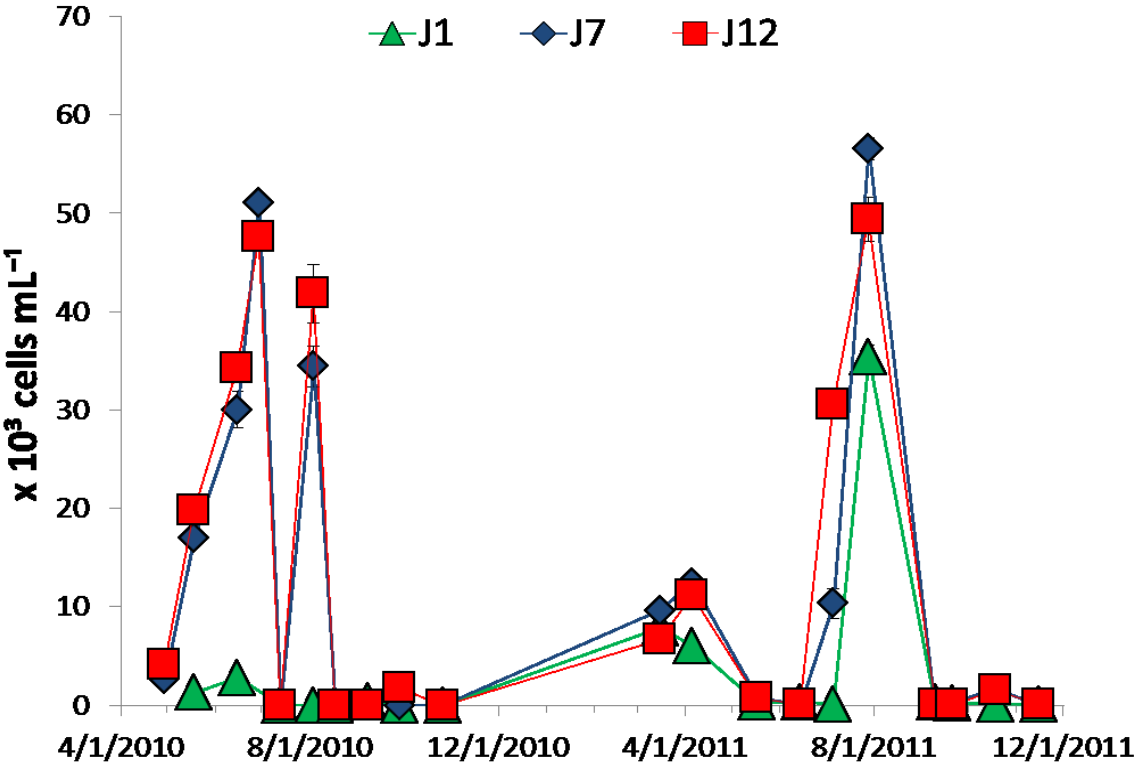

Figure 4. Dynamics of the diatom *Thalassiosira* sp. at three stations in Jamaica Bay

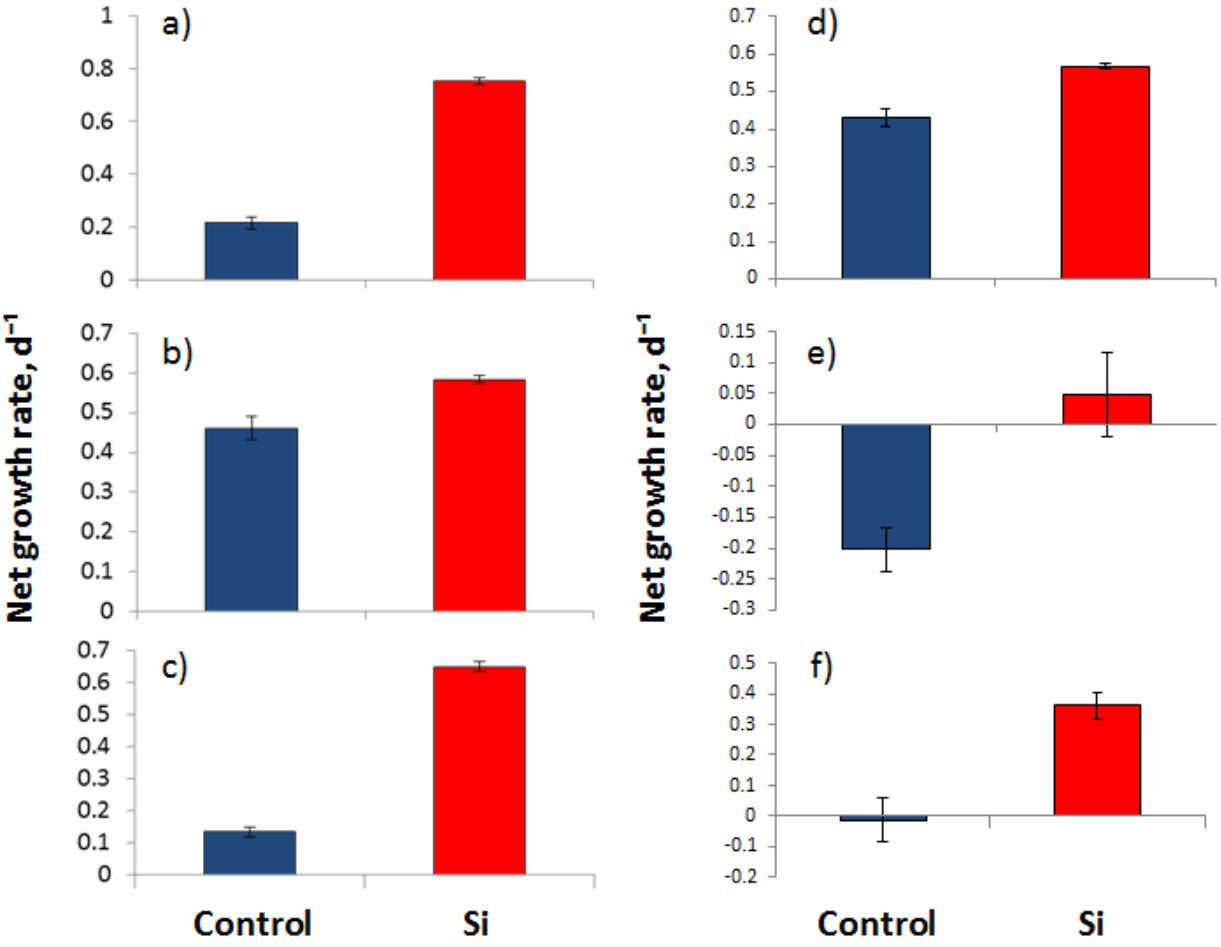

Figure 5a-f. Response of *Thalassiosira* spp. to silicate enrichment at **a)** station J7 in May of 2010 **b)** station J7 in mid-June of 2010 **c)** station J7 in late June of 2010 **d)** station J9A in March of 2011 **e)** station J12 in July of 2011 **f)** station J7 in July of 2011.

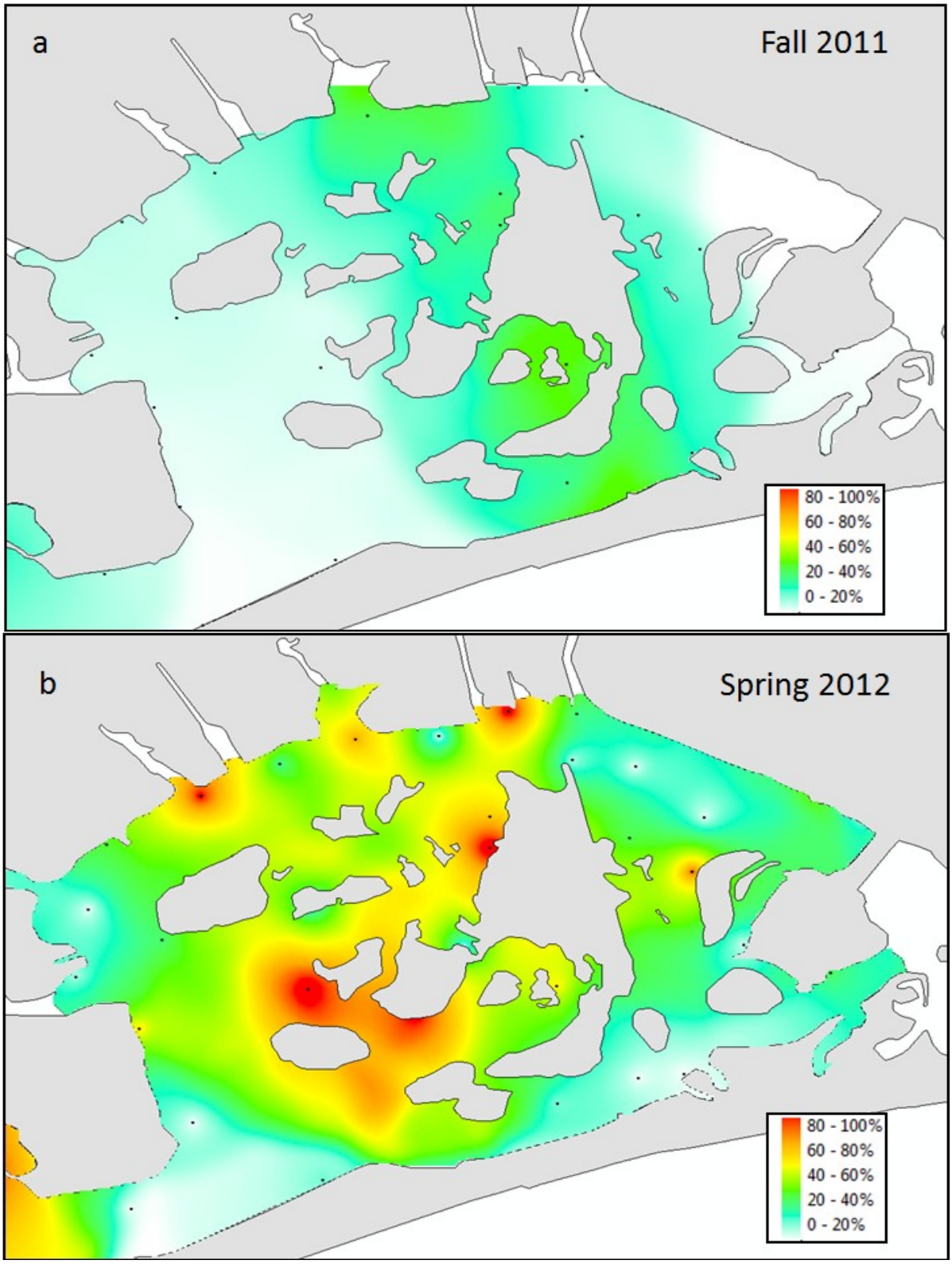

Figure 6. Percent bottom coverage of *Ulva* sp. in Jamaica Bay during a.) Fall 2011 and b.) spring 2012

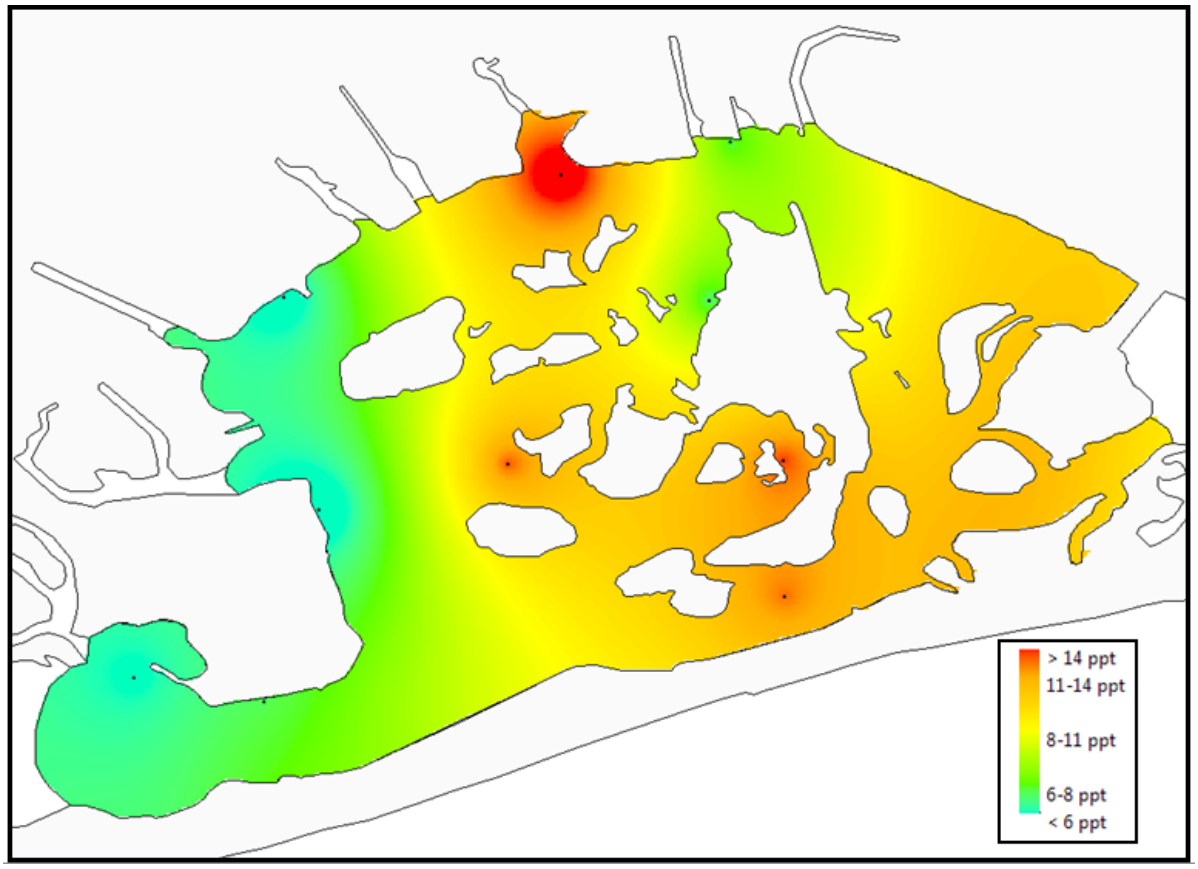

Figure 7. $\delta^{15}N$ signatures of *Ulva* sp. in Jamaica Bay

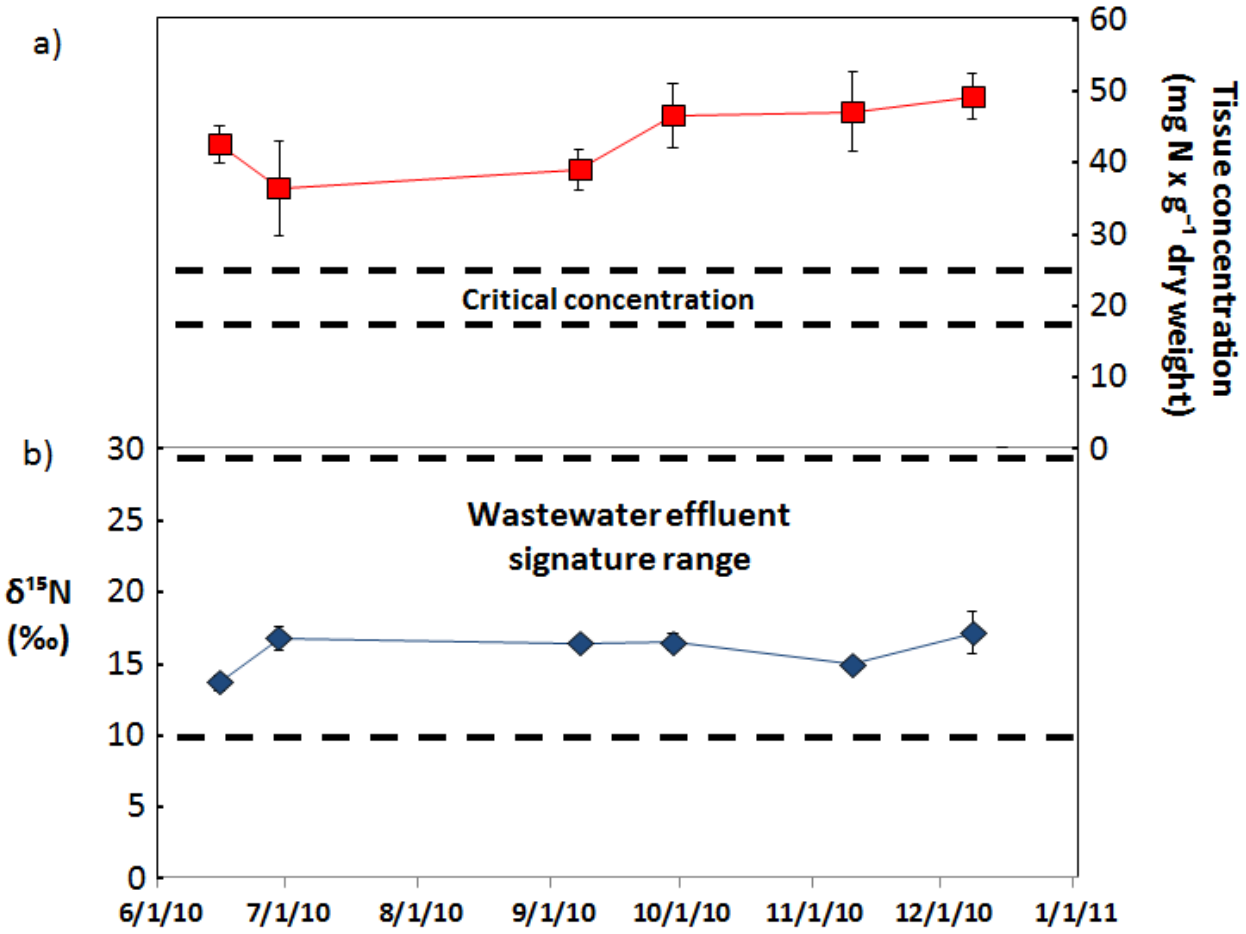

Figure 8a & b. a) Total nitrogen tissue concentration. Dashed lines represent minimum tissue concentration needed for maximum growth (18 – 23 mg N x g^{-1} dry weight) as defined by Lyngby et al. (1999). **b)** $\delta^{15}N$ signature of Ulva sp. collected from central Jamaica Bay. Dashed lines indicate the wastewater signature range (10 -30‰ Bannon & Roman 2008; McClelland et al. 1997).

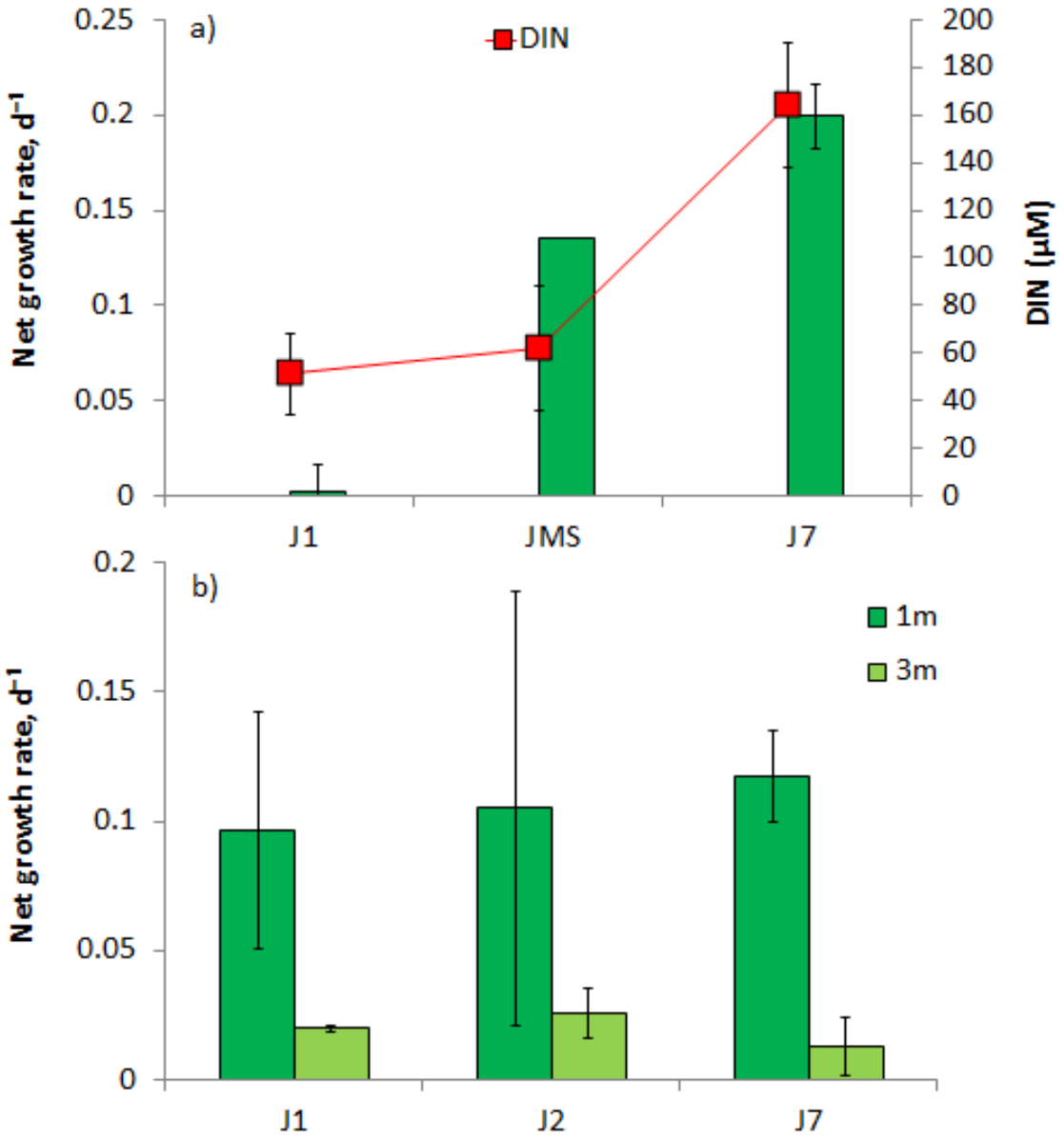

Figure 9a & b. In situ growth rates of *Ulva* sp. at **a)** 1m depth & mean DIN in September of 2011 **b)** 1m & 3m depths in October of 2011.

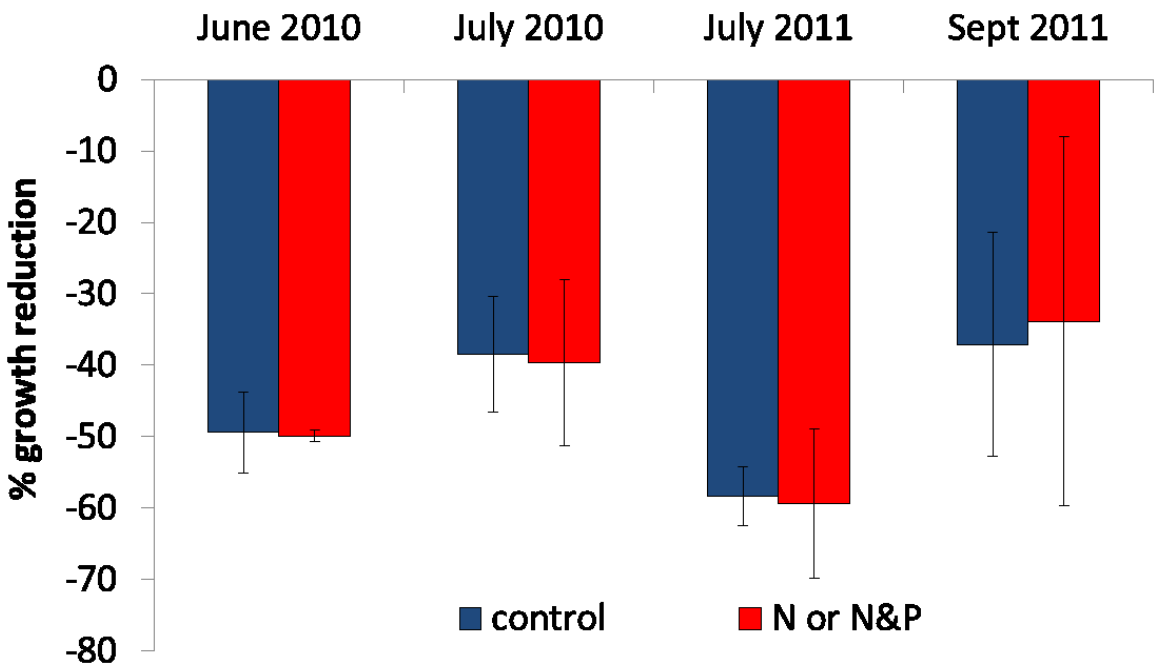

Figure 10. Percent reduction in growth of *Ulva* sp. when incubated with whole phytoplankton community compared to incubations in filtered seawater, with and without nutrient additions. In 2010, only nitrate was added. In 2011, both nitrate and phosphate were added.

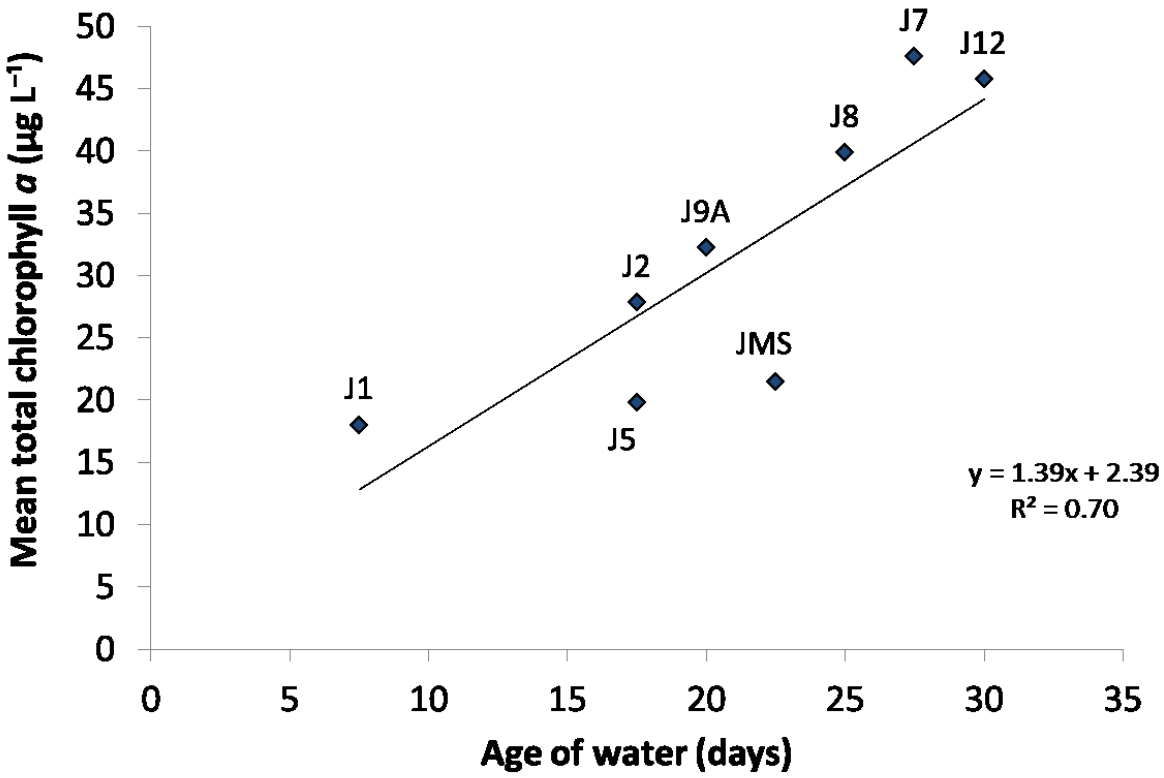

Figure 11. Comparison of mean chlorophyll *a* concentrations and age of water at eight stations across Jamaica Bay

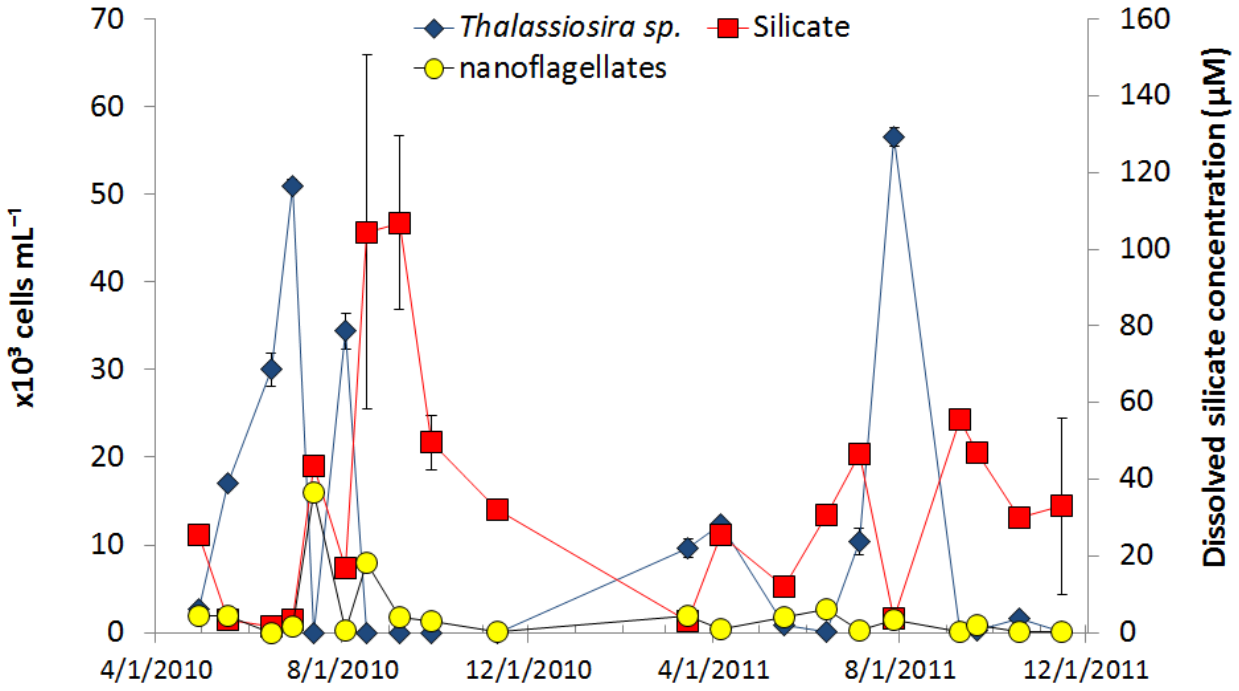

Figure 12. Dynamics of the diatom *Thalassiosira* sp., autotrophic nanoflagellates, and dissolved silicate concentrations at station J7.

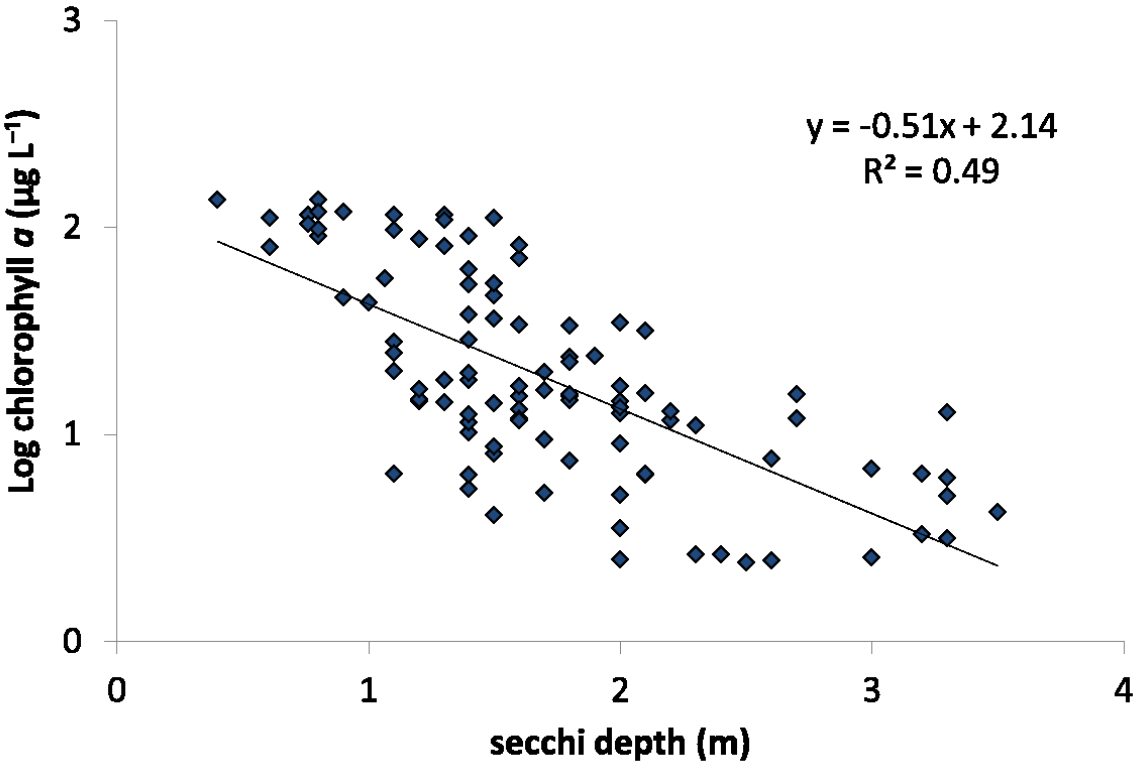

Figure 13. Log chlorophyll *a* concentrations and secchi depth at all stations sampled in Jamaica Bay from 2010-2011.

Tables

	J8		J7		J12		J1		J9A		J2		JMS		J5	
date	chla	stdev	chla	stdev	chla	stdev	chla	stdev	chla	stdev	chla	stdev	chla	stdev	chla	stdev
4/29/2010	14.52	1.13	17.18	2.76	24.05	0.84			11.73	0.88						
5/18/2010	14.49	0.93	43.33	1.77	27.97	2.35	6.37	0.53	19.87	1.11	14.80	0.82			24.87	2.43
6/15/2010	45.45	3.54	108.16	11.06	67.04	3.93	11.34	2.38	30.71	1.41	43.79	1.24	58.13	3.90	38.10	4.28
6/29/2010	81.59	4.38	115.38	21.28	111.16	7.61			62.39	1.59						
7/13/2010	52.86	0.65	97.03	28.50	47.02	1.73	12.92	0.49	53.67	4.62	36.32	1.42	37.91	3.18	22.33	0.95
8/3/2010	119.07	5.89	136.27	2.95	118.69	4.31	20.16	0.99	87.71	1.06	90.44	2.55			45.74	2.79
8/18/2010	13.20	0.69	11.92	0.37	18.32	1.13	11.96	0.71	17.15	0.32	11.72	1.24			15.64	1.23
9/7/2010	12.65	2.11	15.20	2.73	20.05	0.78	13.53	1.47	16.28	1.83	23.73	0.54	9.68	0.96	11.02	1.46
9/29/2010	15.36	2.95	18.37	1.04	14.22	0.53	6.44	0.43	9.44	1.48	14.57	0.41	7.45	0.42	8.98	0.61
11/10/2010	2.53	0.08	3.54	0.41	5.09	0.12	2.48	0.21	2.45	0.13	2.40	0.01	2.64	0.19	2.64	0.19
3/15/2011	54.20	2.12	48.11	1.95	49.32	2.04	39.18	3.23	62.20	4.37						
4/5/2011	111.45	4.82	80.45	0.58	114.27	4.43	56.94	5.33	103.29	5.23						
5/17/2011	6.45	0.66	5.46	2.08	5.20	2.22	4.07	0.45	6.41	2.04						
6/14/2011	14.09	2.84	28.57	4.04	8.03	0.96	11.41	0.55	10.18	0.44	12.52	1.13			8.69	0.71
7/5/2011			33.42	1.12	90.49	4.41	6.81	3.50					34.50	2.55		
7/28/2011			115.39	3.07	108.92	4.46	81.56	3.77								
9/9/2011			4.21	0.43	5.02	0.28	7.65	0.64					5.51	1.05		
9/20/2011			31.71	6.07	6.42	0.68	11.99	1.55					15.87	0.45		
10/18/2011			33.93	2.38	70.58	11.42	6.42	1.23	15.66	3.52						
11/15/2011			3.29	0.74	3.14	0.20	12.84	0.44	6.17	0.75						

Table 1. Total chlorophyll *a* (± SD) at eight stations across Jamaica Bay

date	J7		J12		J8		J9A		J1	
	mean	stdev	mean	stdev	mean	stdev	mean	stdev	mean	stdev
4/29/2010	2.46	0.10								
5/18/2010	5.86	0.09								
6/15/2010	5.67	0.66	7.26	0.22	6.04	0.17	5.51	0.09	1.24	0.02
7/13/2010	8.98	0.62	4.30	0.22	4.40	0.26	3.61	0.17	1.01	0.08
4/5/2011	1.85	0.20	1.82	0.02	1.97	0.56	2.11	0.04	1.50	0.12
5/17/2011	0.29	0.06	0.36	0.03	0.49	0.10	0.32	0.02	0.35	0.02
6/14/2011	1.36	0.12	0.75	0.05	0.94	0.09	1.11	0.32	2.02	0.05
7/28/2011	4.07	1.25	3.38	1.62					2.88	0.73
9/9/2011	2.80	0.10	2.35	0.15					3.39	0.56
9/20/2011	3.39	0.54	1.33	0.13					1.98	0.02
10/18/2011	2.43	0.07	2.48	0.19			2.51	0.11	0.74	0.02
11/15/2011	0.21	0.07	0.18	0.03			0.14	0.02	0.17	0.02
Mean (±SE)	3.28	0.73	2.42	0.68	2.77	1.06	2.19	0.72	1.53	0.33

Table 2. Mean gross primary production rates (mg C L^{-1} d^{-1}) at five stations across Jamaica Bay

date	Station J7													
	Nitrate		Ammonium		Phosphate		Silicate		DIN		DIN:DIP		DIN:DSi	
	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev
4/29/2010	34.93	2.16	50.18	1.70	4.33	0.49	25.42	0.92	85.10	2.33	19.81	2.16	3.35	0.12
5/18/2010	33.42	1.42	84.38	2.03	5.94	0.21	3.20	0.17	117.80	3.28	19.85	1.06	36.91	1.63
6/15/2010	17.46	0.71	34.78	0.70	8.66	0.61	1.73	0.52	52.24	0.52	6.05	0.39	31.86	8.01
6/29/2010	17.30	4.48	31.90	6.98	9.75	2.00	3.22	0.53	49.20	11.46	5.03	0.39	16.03	6.14
7/13/2010	16.46	1.79	80.26	1.60	13.33	0.54	43.62	2.78	96.71	2.88	7.26	0.22	2.22	0.17
8/3/2010	23.37	2.39	8.69	0.07	5.78	0.05	16.97	2.45	32.06	2.35	5.55	0.37	1.93	0.35
8/18/2010	31.43	4.78	69.76	12.86	8.31	1.08	104.52	46.14	127.10	16.93	15.29	0.59	1.36	0.44
9/7/2010	56.65	13.09	76.28	26.25	11.23	1.99	106.91	22.62	145.93	28.35	13.00	1.05	1.37	0.09
9/29/2010	32.44	1.79	77.60	0.83	9.35	0.57	49.58	6.98	110.04	2.36	11.80	0.83	2.25	0.33
11/10/2010	45.33	0.60	40.35	4.73	5.33	0.25	32.07	2.28	85.68	4.66	16.07	0.18	2.67	0.07
3/15/2011	21.32	1.64	43.09	0.56	3.41	0.49	2.88	0.50	64.41	1.91	19.17	2.85	22.65	3.98
4/5/2011	11.24	0.22	89.83	5.75	4.76	0.26	25.63	1.87	101.07	5.59	21.24	1.11	3.95	0.08
5/17/2011	22.09	3.60	50.96	0.58	4.79	0.09	11.98	0.18	73.05	3.36	15.25	0.81	6.10	0.27
6/14/2011	14.58	1.13	57.21	4.92	9.24	0.42	30.80	0.47	71.79	5.44	7.78	0.69	2.33	0.20
7/5/2011	22.32	0.38	67.34	1.36	11.12	0.34	46.75	0.35	89.66	1.48	8.07	0.37	1.92	0.02
7/28/2011	26.43	2.88	62.01	2.29	10.54	0.28	3.78	0.10	88.44	3.13	8.40	0.49	23.62	1.28
9/9/2011	45.15	1.76	100.46	2.22	8.99	0.32	55.58	0.97	145.61	3.68	16.20	0.57	2.62	0.11
9/20/2011	57.57	1.93	124.86	27.48	9.15	0.11	47.09	0.37	182.42	27.76	19.93	2.91	3.87	0.59
10/18/2011	43.54	3.19	89.97	4.98	6.55	0.21	30.09	2.47	133.51	7.21	20.36	0.66	4.45	0.16
11/15/2011	32.03	21.94	55.53	33.10	4.15	0.97	33.00	23.05	87.56	55.01	16.12	8.66	2.84	0.53

Table 3a. Dissolved nutrient concentrations & ratios at station J7

date	Station J12													
	Nitrate		Ammonium		Phosphate		Silicate		DIN		DIN:DIP		DIN:DSi	
	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev
29-Apr-10	23.27	7.36	38.96	9.68	2.75	0.52	21.08	7.53	62.23	17.04	22.38	2.11	3.03	0.28
18-May-10	40.17	0.79	68.52	0.83	5.06	0.29	2.36	0.14	108.69	1.38	21.53	1.28	46.22	2.78
15-Jun-10	11.54	2.00	21.61	1.01	7.91	0.37	1.12	0.11	33.15	2.85	4.20	0.42	29.85	4.72
29-Jun-10	23.02	0.98	45.46	1.60	10.19	1.04	2.55	0.49	68.48	2.49	6.78	0.87	27.84	6.73
13-Jul-10	14.43	1.61	59.94	6.96	12.78	0.31	43.99	1.33	74.37	6.27	5.82	0.52	1.69	0.10
3-Aug-10	18.09	2.23	7.51	0.38	6.20	0.17	27.43	1.64	25.60	1.86	4.13	0.29	0.94	0.12
18-Aug-10	23.99	1.26	36.82	4.16	7.27	1.21	76.47	7.03	80.44	8.09	11.27	1.86	1.09	0.20
7-Sep-10	49.79	2.16	49.67	2.05	9.08	1.86	106.69	3.02	94.87	2.36	10.74	1.94	0.89	0.04
29-Sep-10	41.47	3.96	55.48	4.56	8.00	1.44	26.84	2.98	123.86	5.24	15.98	3.70	4.64	0.34
10-Nov-10	26.68	4.15	41.24	2.29	5.32	0.27	31.62	1.95	61.26	13.15	11.53	2.56	1.94	0.43
15-Mar-11	23.61	2.21	18.04	0.32	2.35	0.06	0.93	0.38	41.65	2.26	17.70	0.63	51.68	22.57
5-Apr-11	33.89	4.14	2.23	0.28	0.89	0.03	0.75	0.16	36.12	4.40	40.96	6.26	49.30	17.28
17-May-11	20.60	3.76	43.33	0.59	4.25	0.09	8.83	0.39	63.93	4.10	15.07	1.17	7.25	0.50
14-Jun-11	14.42	0.59	37.57	0.81	7.51	0.20	28.11	0.84	51.99	1.33	6.93	0.11	1.85	0.05
5-Jul-11	25.11	3.08	30.57	6.51	8.72	0.37	27.53	0.37	55.68	9.25	6.39	1.07	2.02	0.35
28-Jul-11	10.15	1.05	9.20	0.25	6.80	0.29	1.56	0.74	19.34	0.81	2.85	0.14	14.56	6.46
9-Sep-11	32.59	1.46	70.34	3.70	8.07	0.22	46.86	1.13	102.93	4.71	12.77	0.89	2.20	0.09
20-Sep-11	34.95	1.79	58.36	3.38	6.56	0.04	41.17	3.00	93.32	4.15	14.23	0.70	2.27	0.17
18-Oct-11	23.77	15.35	31.76	13.43	1.43	0.31	6.87	4.85	55.53	28.76	48.54	27.46	9.39	2.50
15-Nov-11	49.72	2.83	91.05	7.42	8.00	0.17	52.48	1.76	140.77	9.82	17.60	1.07	2.69	0.22

Table 3b. Dissolved nutrient concentrations & ratios at station J12

date	Station J8													
	Nitrate		Ammonium		Phosphate		Silicate		DIN		DIN:DIP		DIN:DSi	
	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev
29-Apr-10	32.95	1.60	41.93	3.51	3.30	0.33	26.48	1.48	74.88	2.17	22.87	2.76	2.83	0.13
18-May-10	27.35	3.23	28.86	1.72	4.04	0.35	2.06	0.17	56.21	1.79	14.01	1.48	27.46	3.16
15-Jun-10	11.45	0.83	15.82	0.75	6.58	1.08	1.46	0.06	27.27	1.41	4.26	0.89	18.75	1.58
29-Jun-10	19.72	0.35	13.10	0.78	7.07	0.57	3.57	2.75	32.82	1.12	4.67	0.50	16.73	13.12
13-Jul-10	15.27	1.11	22.96	0.26	9.80	0.34	40.48	1.18	38.23	1.08	3.91	0.24	0.94	0.02
3-Aug-10	20.30	0.37	1.45	2.48	4.77	1.17	19.82	0.43	20.26	0.70	4.42	1.02	1.02	0.02
18-Aug-10	25.54	5.11	57.28	10.15	9.17	0.50	92.54	20.21	99.44	13.12	10.87	1.58	1.10	0.20
7-Sep-10	34.44	15.72	32.61	7.57	9.02	1.88	64.66	11.93	73.93	26.43	8.01	1.44	0.99	0.18
29-Sep-10	32.90	1.77	39.69	1.89	4.51	0.40	25.63	2.53	72.59	1.99	16.19	1.53	2.85	0.29
10-Nov-10	34.80	0.88	17.71	0.16	3.77	0.60	23.22	0.22	52.52	0.97	14.13	1.75	2.26	0.04
15-Mar-11	31.99	3.68	17.11	1.57	2.24	0.18	1.74	0.20	49.11	4.48	22.08	2.95	29.37	5.67
5-Apr-11	26.02	3.37	5.57	0.91	0.99	0.14	0.83	0.17	31.59	4.22	31.93	9.86	38.27	14.15
17-May-11	39.53	2.43	54.73	0.81	5.63	0.15	15.15	0.61	94.26	1.69	16.76	0.64	6.23	0.34
14-Jun-11	15.71	4.84	38.18	6.47	6.35	1.18	23.83	5.79	53.89	11.30	7.60	0.48	2.28	0.11

Table 3c. Dissolved nutrient concentrations & ratios at station J8

date	Station J9A													
	Nitrate		Ammonium		Phosphate		Silicate		DIN		DIN:DIP		DIN:DSi	
	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev	µM	stdev
29-Apr-10	19.49	0.74	29.18	4.82	2.54	0.51	20.06	3.87	48.67	5.29	19.42	2.10	2.46	0.22
18-May-10	23.25	1.13	21.41	2.15	3.16	0.87	2.07	0.65	44.66	1.58	14.76	3.04	23.19	7.10
15-Jun-10	17.27	2.28	17.64	1.94	6.84	0.70	2.25	0.69	34.91	0.63	5.14	0.50	16.45	4.66
29-Jun-10	10.06	0.87	4.89	0.57	5.61	0.49	2.46	0.33	14.95	1.44	2.66	0.08	6.15	0.88
13-Jul-10	15.16	1.46	15.40	1.16	9.50	0.33	37.14	1.44	30.57	1.11	3.22	0.13	0.82	0.04
3-Aug-10	12.19	0.37	0.60	0.74	4.09	0.47	25.00	3.71	12.84	0.85	3.17	0.40	0.53	0.11
18-Aug-10	27.70	3.52	51.23	4.19	8.69	1.28	101.01	8.57	80.69	4.93	9.48	1.83	0.80	0.06
7-Sep-10	46.18	19.15	27.13	6.25	11.80	2.76	78.64	40.95	69.45	22.09	5.80	0.52	0.97	0.23
29-Sep-10	32.19	1.11	25.96	0.60	4.60	0.05	20.88	4.43	58.16	1.59	12.65	0.25	2.89	0.65
10-Nov-10	34.27	6.86	17.83	1.53	3.32	0.30	22.07	1.64	52.10	8.37	15.68	1.85	2.35	0.21
15-Mar-11	20.01	1.43	2.52	0.23	1.38	0.12	1.09	0.56	22.52	1.31	16.40	0.98	25.29	12.59
5-Apr-11	44.19	0.73	3.83	0.26	2.45	1.03	2.26	0.35	48.02	0.92	21.63	6.51	21.53	2.75
17-May-11	40.46	4.94	41.66	2.72	6.00	0.25	12.11	0.53	82.12	4.03	13.71	1.12	6.79	0.41
14-Jun-11	16.85	0.71	33.04	0.55	7.18	0.17	27.33	0.33	49.88	0.90	6.95	0.19	1.83	0.04
18-Oct-11	31.01	6.48	13.46	0.60	3.73	0.67	14.14	3.41	44.48	5.95	12.01	0.60	3.21	0.38
15-Nov-11	40.05	1.94	36.22	0.31	5.53	0.14	39.51	0.52	76.28	1.98	13.78	0.32	1.93	0.06

Table 3d. Dissolved nutrient concentrations & ratios at station J9A

date	Grassy Bay		North Channel	
	J7	J12	J8	J9A
4/29/2010	NL	n/a	n/a	n/a
5/18/2010	Si***	n/a	n/a	n/a
6/15/2010	Si***	n/a	n/a	n/a
6/29/2010	Si*	n/a	n/a	n/a
7/13/2010	NL	NL	NL	NL
8/3/2010	NL	N**	N***	N*
8/18/2010	NL	NL	NL	NL
9/7/2010	NL	Si**	NL	NL
9/29/2010	NL	NL	NL	NL
11/10/2010	NL	NL	NL	NL
3/15/2011	NL	Si***	Si**	Si**
4/5/2011	NL	NL	Si*	NL
5/17/2011	NL	NL	NL	NL
6/14/2011	NL	NL	NL	NL
7/5/2011	NL	n/a	n/a	n/a
7/28/2011	Si***	NL	n/a	n/a
9/9/2011	NL	NL	n/a	n/a
9/20/2011	NL	NL	n/a	n/a
10/18/2011	NL	NL	n/a	NL

Table 4. Limiting nutrient determined by significant increases in the net growth rate of phytoplankton compared to control treatments during nutrient enrichment experiments. NL= no limitation. n/a = data not available / experiment not performed. $p < 0.05$* $p < 0.01$** $p < 0.001$***

Date	Limiting Nutrient
6/15/2010	NL
6/29/2010	NL
9/7/2010	NL
9/29/2010	NL
11/10/2010	Nitrogen*
12/8/2010	NL
7/5/2011	NL
9/9/2011	NL
9/20/2011	NL
10/18/2011	NL

Table 5. Limiting nutrient determined by growth rate of *Ulva* sp. during nutrient enrichment experiments. NL= no limitation. $p < 0.05$*

date	J9A	J8	J7	J12	J1	J2	J5	JMS	J3
4/29/2010	5.72	14.14	0.12	0.25					
5/18/2010	0.01	0.00	0.00	0.00	0.01	0.00	0.01		0.00
6/29/2010	0.00	0.04	0.00	0.00					
7/13/2010	1.64	0.04	0.00	0.00	0.01	0.00	0.31	5.17	
8/3/2010	0.03	0.00	0.00	0.00	0.00	0.00	0.00		0.00
8/18/2010	0.16	0.01	0.03	0.00	0.00	0.01	0.37		
9/7/2010	1.03	0.97	0.03	0.00	0.03	0.00	0.96		
9/29/2010	0.03	0.01	0.00	0.00	0.01	0.00	0.21	10.88	
10/26/2010					0.11				
11/10/2010	0.20	0.21	0.01	0.00	0.00	0.14	0.48	3.64	
4/5/2011	0.00	0.00	0.00	0.00	0.00	0.00	0.01		0.00
5/17/2011	0.00	0.14	0.06	0.01	0.00	0.00	1.77		0.00
6/14/2011	0.18	0.10	0.01	0.00	0.00	0.00	0.20		0.00
7/5/2011			0.01	0.00	0.16			13.59	
7/28/2011			0.00	0.00	0.00				
9/9/2011			1.75	0.28	0.06				
9/20/2011			0.06		0.10			17.76	
10/18/2011	0.52		0.01	0.00	0.21				
11/15/2011	0.19		0.52	0.15	0.19				
mean	0.69	1.30	0.15	0.04	0.05	0.02	0.43	10.21	0.00
± SE	0.41	1.17	0.10	0.02	0.02	0.01	0.17	2.62	0.00

Table 6a. Percent surface irradiance at bottom at nine stations across Jamaica Bay.

date	J9A	J8	J7	J12	J1	J2	J5	JMS	J3
4/29/2010	85.83	212.08	1.81	3.72					
5/18/2010	0.13	0.00	0.00	0.00	0.13	0.00	0.12		0.00
6/29/2010	0.00	0.63	0.01	0.00					
7/13/2010	24.53	0.61	0.00	0.00	0.11	0.00	4.72	77.51	
8/3/2010	0.41	0.00	0.00	0.00	0.00	0.00	0.01		0.00
8/18/2010	2.45	0.14	0.49	0.00	0.04	0.20	5.61		
9/7/2010	15.46	14.48	0.41	0.02	0.38	0.04	14.43		
9/29/2010	0.40	0.13	0.02	0.00	0.17	0.02	3.14	163.24	
10/26/2010					1.65				
11/10/2010	3.04	3.19	0.11	0.02	0.04	2.09	7.22	54.57	
4/5/2011	0.00	0.00	0.00	0.00	0.00	0.00	0.18		0.00
5/17/2011	0.02	2.04	0.91	0.12	0.05	0.01	26.59		0.01
6/14/2011	2.77	1.49	0.14	0.01	0.01	0.00	2.98		0.05
7/5/2011			0.22	0.00	2.46			203.78	
7/28/2011			0.00	0.00	0.00				
9/9/2011			26.29	4.27	0.85				
9/20/2011			0.89		1.49			266.38	
10/18/2011	7.78		0.10	0.00	3.18				
11/15/2011	2.80		7.87	2.32	2.89				
mean	**10.40**	**19.57**	**2.18**	**0.62**	**0.79**	**0.24**	**6.50**	**153.10**	**0.01**
± SE	**6.11**	**17.54**	**1.48**	**0.34**	**0.27**	**0.21**	**2.62**	**39.32**	**0.01**

Table 6b. Light at the bottom (µmol m^{-2} s^{-1}) at nine stations across Jamaica Bay.