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Spatial and temporal variability in macroalgal blooms in a eutrophied coastal estuary

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Abstract

All three macroalgal clades (Chlorophyta, Rhodophyta, and Phaeophyceae) contain bloom-forming species. Macroalgal blooms occur worldwide and have negative consequences for coastal habitats and economies. Narragansett Bay (NB), Rhode Island, USA, is a medium sized estuary that is heavily influenced by anthropogenic activities and has been plagued by macroalgal blooms for over a century. Over the past decade, significant investment has upgraded wastewater treatment from secondary treatment to water-quality based limits (i.e. tertiary treatment) in an effort to control coastal eutrophication in this system. The goal of this study was to improve the understanding of multi-year macroalgal bloom dynamics through intensive aerial and ground surveys conducted monthly to bi-monthly during low tides in May-October 2006-2012 in NB. Aerial surveys provided a rapid characterization of macroalgal densities across a large area, while ground surveys provided high resolution measurements of macroalgal identity, percent cover, and biomass.

Macroalgal blooms in NB are dominated by *Ulva* and *Gracilaria* spp. regardless of year or month, although all three clades of macroalgae were documented. Chlorophyta cover and nutrient concentrations were highest in the middle and upper bay. Rhodophyta cover was highest in the middle and lower bay, while drifting Phaeophyceae cover was patchy. Macroalgal blooms of >1,000 grams fresh mass (gfm)/m^2 (max = 3,510 gfm/m^2) in the intertidal zone and > 3,000 gfm/m^3 (max = 8,555 gfm/m^3) in the subtidal zone were observed within a heavily impacted embayment (Greenwich Bay). Macroalgal percent cover (intertidal), biomass (subtidal), and diversity varied significantly between year, month-group, site, and even within sites, with the highest species diversity at sites outside of Greenwich Bay. Total intertidal macroalgal percent cover, as well as subtidal *Ulva* biomass, were positively correlated with temperature. Dissolved inorganic nitrogen concentrations were correlated with the total biomass of macroalgae and the subtidal biomass of *Gracilaria* spp. but not the biomass of *Ulva* spp. Despite seasonal reductions in the nutrient output of wastewater treatment facilities emptying into upper Narragansett Bay in recent years, macroalgal blooms still persist. Continued long-term monitoring of water quality, macroalgal blooms, and ecological indicators is essential to understand the changes in macroalgal bloom dynamics that occur after nutrient reductions from management efforts.

Key Words: Eutrophication, green tide, macroalgal bloom, *Ulva*, long-term monitoring

1. Introduction

Macroalgal blooms are a worldwide hazard that damage coastal habitats and economies by outcompeting perennial macrophytes and phytoplankton for light and nutrients (McGlathery et al., 1997, 2001; Valiela et al., 1997; Hauxwell et al., 1998), creating hypoxic or anoxic conditions through nightly respiration and eventual decomposition (Valiela et al., 1992; Diaz, 2001), producing toxic chemicals (Nelson et al., 2003a; Eklund et al., 2005), and interfering with boat traffic, fishing, and tourism by clogging waterways and fouling beaches (Lee and Olsen, 1985; Thomsen and McGlathery, 2006; Leliaert et al., 2009). Through their environmental impacts, blooms can result in reduced macrophyte, invertebrate, and vertebrate diversity and abundance (Valiela et al., 1992; Hauxwell et al., 2001; Thomsen and McGlathery, 2006; Berezina et al., 2007; Tyler, 2007; Wennhage and Pihl, 2007; Schein et al., 2012). Consequent herbivore reductions can exacerbate bloom conditions by initiating a feedback loop where reduced herbivory leads to increased macroalgal biomass, which further reduces herbivore abundance (Engelsen et al., 2010).

Laboratory culturing, mesocosm studies, and field studies have demonstrated a strong positive relationship between macroalgal bloom formation and nutrient enrichment, particularly when algae are grown at optimal temperatures and light conditions (Valiela et al., 1992, 1997; Taylor et al., 2001; Bintz et al., 2003; Nelson et al., 2003b; Cohen and Fong, 2004; Sousa et al., 2007; Teichberg et al., 2010). Field observations support these findings and highlight the additional importance of the complex physical characteristics of a local geographic site, including geographic orientation in relation to prevailing winds, currents, tidal dynamics, and bathymetric features (Aldridge and Trimmer, 2009; Lyons et al., 2009; Lee et al., 2011; Liu et al., 2013; Hu et al., 2014). Herbivory can also limit bloom biomass (Geertz-Hansen et al., 1993; Williams and Ruckelshaus, 1993; Korpinen et al., 2007), though this influence varies by bloom species, herbivore species, and abiotic conditions and is often insufficient to prevent bloom formation in highly eutrophic areas (Horne et al., 1994; Hauxwell et al., 1998; Morgan et al., 2003; Worm and Lotze, 2006; Fox et al., 2012; Guidone et al., 2015).

All three macroalgal clades (Chlorophyta, Rhodophyta, and Phaeophyceae) contain bloom-forming species. The largest and most frequently occurring macroalgal bloom type is the 'green tide', which is composed of one or more Chlorophyta species (Fletcher, 1996; Valiela et al., 1997; Morand and Merceron, 2005). Recurring *Ulva* blooms have been reported from around the world, including off the coast of Qingdao, China (Leliaert et al., 2009), Brittany, France (Merceron and Morand, 2004), Venice, Italy (Sfriso et al., 1992), Washington, USA (Nelson et al., 2003b), California, USA (Kamer et al., 2001), and throughout the New England region of the United States from Maine through Long Island Sound (Conover, 1958; Nixon and Oviatt, 1973; Granger et al., 2000; Vadas et al., 2004; McAvoy and Klug, 2005; Lyons et al., 2009; Guidone and Thornber, 2013; this study).

Despite the global occurrence of macroalgal blooms and extensive knowledge of how abiotic factors impact bloom species, there is a limited understanding of the long-term patterns in bloom formation, persistence, and severity, particularly within the context of management efforts and climate change. For those systems where long-term data does exist, there is evidence that management policies resulting in reduced nutrient inputs do lead to improved water quality (Deacutis, 2008; Greening et al., 2014), though whether a reduction in macroalgal biomass occurs appears to vary by algal species (Leston et al., 2008). These studies demonstrate the importance of long-term monitoring and the necessity of collecting data prior to, during, and following shifts in nutrient inputs. Moreover, because of the linkage of macroalgal growth to local nutrient levels, the thorough understanding of bloom dynamics that is gained through these monitoring programs can facilitate future management of anthropogenic nutrient loads through the development of ecological indices, as exemplified by work done in relation to the European Water Framework Directive (Scanlan et al., 2007; Sfriso et al., 2007, 2009; Wells et al., 2007; Wilkinson et al., 2007; Sfriso and Facca, 2012).

The goal of this study was to improve understanding of multi-year macroalgal bloom dynamics through intensive aerial and ground surveys of Narragansett Bay (NB), Rhode Island, USA. This estuarine system is particularly well suited to long-term study of macroalgal blooms because it is annually impacted by blooms of *Ulva* spp. and also experiences periodic blooms of *Gracilaria* spp. (Granger et al., 2000; Guidone and Thornber, 2013; this study). In addition, Narragansett Bay presents the opportunity to monitor the impacts of regulatory nutrient permit limit revisions that required wastewater treatment facilities (WWTFs) to decrease their inputs to the Bay. These regulations were implemented in stages from 2006 to 2014 and, as of 2015, they have resulted in more than a 50% decrease in nitrogen loads from WWTFs (A. Liberti, personal communication). In response to this phased decrease, it was predicted that a corresponding decrease in the observed abundance of macroalgae in the lower Providence River and Upper Narragansett Bay would occur, as these areas are closest to the sewage point sources (Deacutis, 2008). Results of these surveys provide large- and small-scale documentation of macroalgal distribution patterns in a eutrophic estuary as well as a long-term data set that can aid in distinguishing between interannual variability and management-linked decreases in bloom biomass and/or alterations in macroalgal diversity.

2. Methods

2.1 Abiotic Influences in Narragansett Bay

Narragansett Bay is a medium-sized estuary (370 km^2, Ries, 1990) on the southern coast of New England, USA (Fig. 1). It has large anthropogenic nutrient loads, with the majority of nutrients coming from WWTFs (Nixon et al., 1995, 2008; Pryor et al., 2007). Low freshwater inflows (Ries, 1990), along with extensive damming of the rivers in the 1800's (Nixon et al., 1995), resulted in the majority of the estuary having polyhaline waters. A small mesohaline zone is present in the upper estuary (Providence and Seekonk tidal rivers), although the extent of this zone is dependent on river flows. Water residence time varies seasonally and among years, linked directly to river flows. Maximum residence time (~35 days) occurs during the summer months (July-September), while the minimum residence time (~20 days) occurs in spring when river flows peak (February-April; Pilson, 1985). In extremely dry summers, or with sustained winds that counteract estuarine flushing, the residence time may be up to 100 days (C. Kinkaid and W. Prell, personal communication).

Narragansett Bay has recently undergone a significant change in nitrogen loading due to management efforts that required major WWTFs to reduce their total nitrogen output by 50% in comparison to 1995-1996 levels. This target was achieved in 2015, reducing May through October baywide WWTF nitrogen inputs from 5462.6 kg/day in 2004 to 1885.6 kg/day in 2015 (A. Liberti, unpublished data). Climate change is another transformative force in NB; mean sea surface water temperature in the Bay has increased 1.4-1.6°C since 1960 (Fulweiler et al., 2015), while precipitation has increased an average of 3.05 mm per year since 1905 (Pilson, 2008). To account for these factors, survey data were examined within the context of sampling year, region of the Bay (aerial surveys only), and available temperature, nutrient, and salinity measurements (ground surveys only).

2.2 Aerial Survey

2.2.1 Data Collection

Aerial oblique digital photographs of macroalgal presence were collected along the western shore of NB once a month within ± 2 hours of spring low tide from May through October 2007 to 2012. Narragansett Bay experiences semi diurnal tides with a tidal range of 1.0-1.5 m (https://tidesandcurrents.noaa.gov/). A helicopter was flown along the lower intertidal-subtidal zone at a distance of 160 ± 73 m from shore and an altitude of 113 ± 28 m at a horizontal speed of 60-90 km/h. Photographs were taken using a Kodak DCS Pro 14N high-resolution (14 MP) digital camera with a Nikkor 14 mm rectilinear wide angle lens. The camera was handheld at an oblique downward angle to capture images encompassing the area below the helicopter to the shoreline; images were recorded automatically every 10 seconds. A wide area augmentation system (WAAS) enabled Garmin GPS Map 76 device was connected to the camera to record GPS locations with each image.

Within 3 days of each aerial survey, ground-truthing surveys were conducted during low tide at up to 17 sites (median of 8 sites/survey) spread across the aerial trackline (Fig. 1). At each site, the dominant macroalgal species were photographed and recorded. For species of questionable identity, whole thalli were collected and returned to the lab for a thorough morphological examination. Due to the cryptic morphology of *Ulva* species in this area (Guidone et al., 2013), the morphological characteristics observed (blade or tubular; attached or unattached) were recorded rather than identifying *Ulva* thalli to the species level.

2.2.2 Image Analysis

Each photograph represented one sample point along the estuarine shoreline. Where the same macroalgal beds could be observed in sequential images, the image analyzer recorded the observable bed density across images, typically combining two images as a single data / density value for each taxa. All digital photographs with adequate image quality (clear edges to objects; minimal glare; adequate coverage of the intertidal and subtidal zones) were mapped using Arc GIS 9.2. Photographs were rendered from Kodak Raw format into GPS-stamped tiff files using Kodak DCS Photodesk software. All tiffs were then identically enhanced in Adobe Photoshop CS with automatic histogram equalization and saturation increases. Photographs were then analyzed visually for ordinal density classification of the Chlorophyta, Rhodophyta, and Phaeophyceae present; visual classification was confirmed via comparison to ground-truthing results. Macroalgal densities were categorized into five ordinal density classes ranging from none (0) to very dense (4) based on the Paine (1981) classification scheme (Table S1). The minimum size of objects that could be satisfactorily recognized was estimated at 2 m^2 (15 x 25 pixels).

2.2.3 Statistical Analysis

For statistical analysis, the western shoreline of NB was divided into three regional segments: upper, middle, and lower Bay, each of which was further subdivided into finer subregions for a total of three major Bay regions and ten subregions (Fig. 1). Sampled months were grouped together into two-month units to account for missing data from months when aerial surveys could not be conducted due to inclement weather (n = 0-1 month/year, except 2010 where n = 2). Month-groups were defined as May-June, July-August, and September-October. Ordinal logistic regression was used to identify significant differences among Chlorophyta, Rhodophyta, and Phaeophyceae algal density classes among survey years, month-groups, regions, and subregions nested within region (JMP v. 12). To ensure a fully factorial analysis, data from 2010 were excluded from these regression models, as aerial surveys could not be conducted in September and October 2010. Relationships among the survey variables and algal density classes were further explored using multiple correspondence analysis (JMP v. 12).

2.3 Ground Survey

2.3.1 Site Descriptions and Data Collection

Nine permanent field sites were established during 2005-2006; seven were distributed around the shoreline of Greenwich Bay, a subestuary located on the western side of NB (Oakland Beach, Oakland Beach Cove, Warwick City Park, Budlong Farm, Sylvia Drive, Chepiwanoxet Point, and Goddard State Park). Additional sites were located to the south of Greenwich Bay at Sandy Point and to the north of this Bay at Conimicut Point (Fig. 2; see Table S2 for GPS coordinates). All sites have a sand and/or mud substrata except Chepiwanoxet Point, which is a man-made boulder field. Monthly data were analyzed starting in 2006 for intertidal surveys at all sites except Oakland Beach Cove (subtidal only site). Similarly, monthly subtidal survey data analysis began with 2007 at all sites except Chepiwanoxet Point and Conimicut Point, (intertidal only sites). Surveys were conducted during low tides with a predicted low less than or equal to 0.15 m above mean low water and every effort was made to place the transects in the exact same location during each visit.

For intertidal surveys, two 10 m transects were sampled per site. These were placed parallel to the shoreline and located at least 30 m apart from each other. At every meter along each transect, a 0.25 m^2 quadrat was used to assess the percent cover of each algal species as well as of bare space. The identity and abundance of each invertebrate species present within the quadrats was also recorded. All living algal material was removed from each quadrat, placed into labeled plastic bags, and returned to the laboratory. In the laboratory, algae were rinsed in seawater to remove all sand and debris, spun in a salad spinner to remove excess water, and weighed to determine the total algal wet mass (grams fresh mass, gfm). Intertidal algal biomass per unit area was calculated by taking the gfm in a quadrat (0.25 m^2) and multiplying it by a factor of 4 to obtain gfm/m^2.

For subtidal surveys, one 30 m transect was sampled per site; this transect was placed perpendicular to the shore. At every third meter, all living material was removed from a 0.4 m by 0.5 m area using a dip net with a 6 mm mesh pore diameter. The water depth was also recorded in order to calculate the volume of water sampled. All algae were placed in labeled plastic bags, transported to the lab, rinsed, spun in a salad spinner, and sorted to the species level. In some instances, species identification was not possible because multiple species in the same genera have significant overlap in morphological characteristics, which require molecular sequencing (e.g. *Ulva*, Guidone et al., 2013; *Gracilaria,* Nettleton, 2012) or cross-section analysis (e.g. *Polysiphonia*). There have been reports of five species of blade-forming *Ulva* (hereafter referred to as *Ulva* blade, Guidone et al., 2013, Green *unpub. data*), six species of tubular *Ulva* (hereafter referred to as *Ulva* tube, Guidone et al., 2013), and two species of *Gracilaria* (Nettleton, 2012) in Narragansett Bay. In these cases, species were identified to the genus level. The wet mass of each individual species and the abundance of each invertebrate species were recorded. Subtidal algal biomass per unit volume was determined and standardized to obtain gfm/m^3.

2.3.2 Data Analysis

Differences in macroalgal community composition for both the intertidal and subtidal surveys were assessed by calculating a Bray-Curtis similarity matrix on square-root transformed data, followed by an analysis of similarity (ANOSIM) to assess differences in year and month-group. Month-groups were defined as in Section 2.2.3, with added month-groups January-February, March-April, and November-December. Similarity percentage analysis (SIMPER) was used to assess the relative contributions of species to the macroalgal community observed (Primer v.6.0).

Based on results from the SIMPER analysis (see Section 3.2.1), during the typical summer bloom-forming season (May through October), intertidal spatial and temporal patterns of total macroalgal biomass and the percent cover of *Ulva* blades, *Ulva* tubes, and *Gracilaria* spp. were analyzed via four-way ANOVAs using year, month-group, site, and transect nested within site, as fixed factors. Subtidal patterns of total macroalgal biomass and the biomass of *Ulva* blades, *Ulva* tubes, and *Gracilaria* spp. were analyzed by three-way ANOVAs with year, month-group, and site as factors in a fully factorial design. Data could not be transformed to meet the assumption of normality or heteroscedasticity; however ANOVA is robust to deviations from these assumptions, in balanced experiments with reasonable sample sizes (Underwood, 1997). Due to local conditions, Budlong Farm could not be sampled during July-August of 2010. Therefore, data imputation was used to represent the uncertainty around the missing data points, after which fully-factorial analyses were re-run using each possible outcome. Multiple data imputations to replace missing data points resulted in similar conclusions (G. Puggioni, personal communication; Frimpong and Angermeier, 2009). All ANOVA analyses were conducted using JMP (v. 12). To further assess differences among years and month-groups for the bloom-forming season, total macroalgal biomass for both intertidal and subtidal transects were also analyzed using multi-dimensional scaling plots on square root transformed data (Primer v.6.0, Primer-E Ltd, Plymouth, UK). Additionally, the Shannon-Wiener species diversity index was calculated for each intertidal quadrat (using percent cover) and subtidal net sweep (using biomass) to assess diversity differences in year, month-group, and site in a three-way ANOVA with Tukey post-hoc analyses using a fully-factorial design for the bloom period month-groups and imputation analysis to confirm ANOVA results (as described above).

Potential correlations between invertebrate density and macroalgal abundance were assessed using Spearman Rho correlations (JMP v. 12). Mud snail (*Ilyanassa obsoleta*) and total invertebrate density excluding mud snails were examined against the subtidal biomass of *Ulva* blades, *Ulva* tubes, *Gracilaria* spp., and total macroalgae for all subtidal sites.

Correlations between monthly abiotic conditions and macroalgal biomass were examined using Spearman Rho correlations (JMP v. 12). Correlation analyses compared sea surface temperature, surface salinity, precipitation (24 hours, 48 hours, and 30 days before ground surveys), and dissolved inorganic nitrogen with *Ulva* blade, *Ulva* tube, *Gracilaria* spp., other macroalgae, and total macroalgae percent cover (intertidal) or biomass (intertidal total macroalgae and subtidal data) for each Greenwich Bay site. Sea surface temperature and salinity data were obtained from the Rhode Island Department of Environmental Management Greenwich Bay Buoy (except 2012 when data from the Sally Rock Buoy was used; http://www.dem.ri.gov/bart/netdata.htm). Precipitation data were obtained from the National Climatic Data Center as recorded at T. F. Green Airport (approximately 3.2 km from Greenwich Bay). Dissolved inorganic nitrogen (DIN) data were provided by the Marine Ecosystems Research Laboratory at the Graduate School of Oceanography at the University of Rhode Island. Measurements were made at Greenwich Bay Marina (Warwick, RI) monthly from 2006-2011. Total DIN was determined by adding NH_3, NO_2, and NO_3 (μM) measurements together.

3. Results

3.1 Aerial Survey

In total 6,515 photographs from 25 aerial surveys conducted from 2007 to 2012 were analyzed. Ground-truthing surveys confirmed that, due to the resolution limitation of 2 m^2, observable patches of Chlorophyta and Rhodophyta tended to be large drift ephemeral patches. *Fucus* spp. and *Ascophyllum nodosum* (Phaeophyceae), when present, were attached to rocky substrata and difficult to distinguish in the photographs. On rare occasions, drift

Punctaria/*Petalonia* spp. (Phaeophyceae) aggregated into mats that were large enough to be clearly observable in the photographs.

Ordinal logistic regression analysis demonstrated significant density class differences among years, month-groups, regions, and subregions, as well as significant interactions among all factors, for the Chlorophyta and Rhodophyta (Table S3). For Phaeophyceae density classes, only the four-way interaction term was significant in the whole model analysis (Table S3). Subsequent ordinal logistic regression analysis by year indicates that in four of the five analyzed survey years Phaeophyceae density classes varied significantly by subregion (Table S4).

Across all aerial surveys, Chlorophyta densities were higher in the middle and upper bay than in the lower bay (Fig. 3), though variation existed among the subregions within each larger region. (For detailed maps see http://nbep.org/publications/NBEP-17-179.pdf.) Multiple correspondence analysis showed Chlorophyta density classes 3 and 4 most associated with the Middle Bay subregion Wickford and the upper bay subregions Upper Providence River, Bullock Reach, and Conimicut (Fig. S1A). Density class 4 was also most closely associated with the survey year 2008, which is the year that the densest mats of Chlorophyta were observed across the middle and upper bay. In contrast, Rhodophyta densities were greater in the middle and lower bay, where a greater frequency of density classes 2 and 3 occurred (Fig. 3); multiple correspondence analysis showed a close association between density class 3 and the middle bay subregion Wickford and the lower bay subregions Lower West Passage 1 and Lower West Passage 2 (Fig. S1B). A close association between Rhodophyta density class 0 and upper bay subregions Upper Providence River and Bullock Reach (Fig. S1B) was also observed. The majority of observations for Phaeophyceae were in the 0 density class for all three Bay regions, although the lower bay had the greatest frequency of the class 1 Phaeophyceae (Fig. 3; Fig. S1C). Phaeophyceae in the middle and upper bay regions that did exceed 10% cover were observed during ground-truthing to consist of drift *Punctaria*/*Petalonia* spp. Phaeophyceae density never reached a class 4 density (> 70% cover).

3.2 Ground Survey

3.2.1. Full-year community analyses

Three major species groups, *Ulva* blade (Fig. 4A), *Ulva* tube (Fig. 4B), and *Gracilaria* spp. (Fig. 4C-D), were major contributors to the macroalgal community across both years and month-groups. While species abundance and composition significantly varied across month-groups and years in both the intertidal and subtidal, Global R values were low, suggesting little differences among years and month-groups (Table S5-S7). In the intertidal habitats, *Ulva* blades, *Ulva* tubes, *Gracilaria* spp., as well as *Ceramium* spp. were consistently abundant each year, cumulatively contributing 68.91% to 92.92% of the relative similarities among study years (Table S8-S10). These species were also present throughout each year, although the actual abundance varied seasonally, consistently contributing 63.47% to 94.00% of the relative similarities for each month-group. *Petalonia*/*Punctaria* spp. was observed in relatively high abundances only from January to April (Table S10). Subtidally, across all years *Gracilaria* spp. tended to be the most abundant macroalgae, contributing between 47.65% and 58.61% of the relative similarity, although *Ulva* blades and *Ulva* tubes were also major contributors. Similarly, within each year (across all month-groups), these three groups were the most abundant species present (Table S11-S14; Fig. 4E-F)).

3.2.2 Macroalgal abundance during the bloom-forming season

Consistent yearly, bimonthly, and site patterns were not detected within the ground survey data. Three of the measured intertidal bloom features – mean total algal biomass, mean total algal percent cover, and the mean percent cover of *Ulva* blades – were significantly affected by survey year, month-group, site, and transect within site, with significant interactions observed for all factors (Table S15). The mean percent cover of *Ulva* tubes significantly differed with all examined factors except month-group, while the mean percent cover of *Gracilaria* significantly differed with all factors except transect; both *Ulva* tubes and *Gracilaria* mean percent cover demonstrated significant interactions among all variables (Table S15). Multivariate analysis via

MDS did not reveal any additional relationships with respect to macroalgal abundance among the intertidal survey month-groups (Fig. S2) or years (Fig. S3).

Among the intertidal samples, the highest mean total algal biomass was 3,510 ± 946 gfm/m^2, observed in July-August of 2006 at Sylvia Drive (Fig 5A); additional peaks greater than 1,000 gfm/m^2 were observed at Sandy Point during July-August 2011, September-October 2012, and May-June 2013. Mean total % cover of all macroalgae ranged from 0-90%, with a maximum observed in September-October of 2007 at Conimicut Point Park (Fig. 5B). Maximum values for mean % cover of *Ulva* blades, *Ulva* tubes, and *Gracilaria* were below 10% for most survey periods and sites (Figs. S4-S6). Peaks above 10% for these species varied by site and did not consistently occur in the same months or years among the species. *Ulva* blade % cover peaked at Conimicut Point Park and Sandy Point (Fig. S4), *Ulva* tubes % cover peaked at Sandy Point, Sylvia Drive, Budlong Farm, and Oakland Beach (Fig. S5), and *Gracilaria* % cover peaked at Oakland Beach and Goddard State Park (Fig. S6).

Species diversity (H_s) varied among years ($F_{7,5123}$=2.21, p=0.03) and sites ($F_{7,5123}$=13.61, p<0.01) in the intertidal, with significant interactions for all factors. Across all years and month-groups, diversity was nearly twice as high in sites outside Greenwich Bay (Conimicut Point Park and Sandy Point) than in all inner bay sites combined (Fig. 6A). Intertidal diversity remained consistent within the bloom season each year, with no significant differences observed for month-group (Table S16; Fig. 6B). Diversity differed among years, with peak diversity observed in 2010 (Fig. 6C). In general, *Scytosiphon lomentaria* and *Punctaria/Petalonia* were observed from May-June, *Agardhiella* subulata from June-October, and *Ceramium virgatum, Gracilaria* spp., *Ulva* blade, and *Ulva* tube from May-October (Figs. S7-S14).

Within the subtidal surveys, mean *Ulva* blade and *Ulva* tube biomasses were significantly affected by all factors, with significant interactions (year, month-groups, and site; Table S17). Mean total subtidal algal biomass was significantly affected by all factors except month-group, though all interactions were significant (Table S17). In contrast, mean *Gracilaria* spp. biomass only differed significantly when the interactions of month-group and/or site were considered with year (Table S17). The highest mean subtidal total macroalgal wet biomass was 8,555 ± 4,263 gfm/m^3 in July-August 2011 at Sandy Point (Fig. 7), an event that was dominated by *Ulva* blades (Fig. S15). Additional substantial (mean > 3,000 gfm/m^3) total subtidal biomass events were observed at Sandy Point, Budlong Farm, and Warwick City Park (Fig. 7). *Ulva* blades consistently dominated at Sandy Point, while *Gracilaria* spp. dominated the September-October 2012 event at Warwick City Park; in contrast, the two largest events at Budlong Farm consisted of a mix of *Ulva* blades, *Ulva* tubes, and *Gracilaria* spp. (Figs. S15-S17). Of the three bloom species complexes, *Ulva* tubes had the smallest maximum subtidal biomass, with biomasses most often < 200 gfm/m^3 at all sites (Fig. S16). Consistent with the intertidal analysis, MDS did not reveal any significant relationships with respect to total macroalgal biomass among the subtidal years (Fig. S18) or month-groups (Fig. S19).

Species diversity also varied significantly across year ($F_{6,2130}$=5.12, p<0.01), month-group ($F_{2,2130}$=63.00, p<0.01), and sites ($F_{6,2130}$=21.64, p<0.01) for the subtidal surveys with significant interactions among all factors (Table S16; Fig. 8A-C). Diversity tended to decline slightly from the early to late bloom season (May-October) across all years and sites, however, no consistent patterns were seen with respect to H_s throughout the course of the surveys (Fig. 8C).

The peaks in observed biomass between the intertidal and subtidal maximums varied spatially. For example, within the intertidal, the greatest mean total algal biomass was observed at Sylvia Drive during July-August 2006 (Fig. 5A); however the corresponding mean subtidal biomass for that time period was comparable to the other survey sites (Fig. 7). In contrast, biomass peaks at Sandy Point occurred within the same months for both the intertidal and subtidal.

3.2.3 Invertebrate Densities at Bloom Sites

The mud snail *Ilyanassa obsoleta* was the most common invertebrate in the intertidal and subtidal macroalgal surveys (Tables S18-S24). Other commonly collected invertebrates included crabs and shrimp. Mussels, limpets, fish, polychaetes, oysters, ctenophores, amphipods, isopods, and clams were collected infrequently.

The density of *Ilyanassa obsoleta* (per m^3) and the density of all invertebrates excluding *I. obsoleta* were positively correlated with the total subtidal biomass of macroalgae as well as the subtidal biomasses of *Ulva* blade, *Ulva* tube, and *Gracilaria* spp. (Table S25).

3.2.4 Macroalgal Correlations with Abiotic Parameters

Mean total macroalgal intertidal % cover (Spearman's ρ = 0.3462, p = 0.0138; Fig. 9) and subtidal biomass (Spearman's ρ = 0.3164, p = 0.0364; Fig. 10) of blade-forming *Ulva* in Greenwich Bay were positively correlated with sea surface temperature (Fig. 11A). No bay-wide relationship was found between *Ulva* blade % cover or biomass with surface salinity, precipitation, or dissolved inorganic nitrogen. Subtidal biomass of *Ulva* tube was correlated with surface salinity (Spearman's ρ = -0.4058, p = 0.0063). Dissolved inorganic nitrogen (DIN) was positively correlated with *Gracilaria* spp. subtidal biomass (Spearman's ρ = 0.4982, p = 0.0299) and total subtidal macroalgal biomass Spearman's ρ = 0.5509, p = 0.0145; Fig. 11B). The average DIN was highest in June (8.94 ±2.76 uM) and monthly averages ranged from 3.29 to 8.94 uM. No relationship was detected between any of the examined abiotic variables and *Ulva* tube or *Gracilaria* spp. intertidal percent cover.

Two additional taxa – *Scytosiphon lomentaria* and the *Petalonia/Punctaria* spp. complex – were also examined, as they were often abundant during May surveys. Both intertidal *Scytosiphon lomentaria* and *Petalonia/Punctaria* percent cover were negatively correlated with surface temperature (Spearman's ρ = -0.4574, p = 0.0008; Spearman's ρ = -0.3083, p = 0.0294) and surface salinity (Spearman's ρ = -0.2815, p = 0.0477; Spearman's ρ = -0.3135, p = 0.0266). Site-specific correlations are described in Figs. S20-S26.

Discussion

The bay-wide aerial surveys demonstrated a north to south trend of increasing Rhodophyta and Phaeophyceae cover and decreasing Chlorophyta cover in Narragansett Bay (Fig. 3), similar to Harlin et al. (1992), Guidone and Thornber (2013) and Villard-Bohnsack and Harlin (1992). Many Chlorophyta genera (e.g. *Ulva*) are ephemeral, opportunistic species that have high growth rates and wide environmental tolerances (Raffaeli et al., 1998), which allow them to thrive in areas with high anthropogenic impacts (Ye et al., 2011), such as the upper Bay. Villalard-Bohnsack and Harlin (1992) reported that Phaeophyceae accounted for approximately 22% of the macroalgal species, while Chlorophyta represented only 23%. In the present study, Phaeophyceae cover rarely reached >10% and displayed a patchy distribution. Contrastingly, Harlin and Rines (1993) found that when Phaeophyceae were present, they often represented significant coverage (e.g. *Fucus* spp. 72%, *Ascophyllum nodosum* 25%). While not visible in the aerial surveys, the ground-truthing surveys did detect fucoids in *Spartina* marshes in the northern Bay, which concurs with findings by Harlin et al. (1992) and Newton and Thornber (2012).

The macroalgal bloom composition and biomass results were consistent with previous studies within Narragansett Bay, Rhode Island and the New England region, although the present data represent a much more complete bay-wide coverage than prior efforts, due to repeated aerial and shore-based surveys. In NB, *Ulva* and/or *Gracilaria* spp. most often dominated the macroalgal communities within the central regions of the western Bay, consistent with previous work that identified Greenwich Bay (Granger et al., 2000; Guidone and Thornber, 2013) and Bissel Cove (Nixon and Oviatt, 1973) as areas regularly impacted by *Ulva* spp. blooms or mixed *Ulva*-*Gracilaria* blooms. Throughout New England, *Ulva* spp. have been previously reported to form dense mats with similar biomasses in Maine (Vadas and Beal, 1987), New Hampshire (Hofmann et al. 2010; Nettleton, 2012), Massachusetts (Conover, 1958; Lyons et al., 2009; Shaw, 2013), and Connecticut (McAvoy and Klug, 2005; Guidone, personal observation), while dense mats of *Gracilaria* spp. have been reported from New Hampshire (Nettleton, 2012) and

Massachusetts (Conover, 1958; Shaw, 2013). Macroalgal blooms are a global phenomenon and blooms of *Ulva* spp. and *Gracilaria* spp. have been documented from Asia (*Ulva:* Leliaert et al., 2009), Europe (*Ulva:* Merceron and Morand, 2004; *Gracilaria:* Viaroli et al., 2008; Cacabelos et al., 2012), and Australia (*Ulva:* McComb and Humphries, 1992). The largest *Ulva* blooms on record occurred in the Yellow Sea and resulted in an accumulation of over one million tons of algae (Liu et al., 2013).

Nutrient loading is considered one of the primary causes of macroalgal blooms (Raffaelli et al., 1998; Bricker et al., 2008; Teichberg et al., 2010; Smetacek and Zingone, 2013), and nitrogen is the primary nutrient limiting macroalgal growth during the summer months in the northeast United States (Taylor et al., 1995). Total nitrogen concentrations are highest in the northern regions of NB (≥ 30 uM TN; Oviatt et al. 2002), where *Ulva* densities were typically greatest, with maximum densities from May-July annually. Ulvoids have been associated with high N concentrations in other systems (e.g. Teichberg et al. 2010, Martínez et al. 2012) when light and temperature conditions are optimal. DIN concentrations were correlated with the total biomass of macroalgae in Greenwich Bay and the subtidal biomass of *Gracilaria* spp., but not the biomass of *Ulva* blades or *Ulva* tubes. This may be due to the difference in timing between nutrient sampling and macroalgal surveys.

Total intertidal macroalgal % cover, as well as subtidal *Ulva* biomass, were both positively correlated with mean temperature. Other studies have shown that ulvoid macroalgae respond favorably to warming temperatures (Lotze and Worm, 2002; Green, unpublished data) and that herbivory of ulvoids increases with temperature (Best et al., 2015). The waters of Narragansett Bay have warmed by 1.4°-2.2°C since 1960 (Nixon et al., 2009; Fulweiler et al., 2015) and are predicted to warm an additional 1°- 4°C by the end of the 21st century (IPCC 2014). As a result of this warming, there have been documented shifts in phenology of phytoplankton (Nixon et al., 2009), ctenophores, and copepods (Sullivan et al., 2007) in NB.

Therefore, although *Ulva* and macroalgal abundance tend to increase with increasing temperatures, further warming may result in a shift in bloom phenology.

There was significant variation in bloom composition within subregion (aerial surveys), between sites, and even within the same site (ground surveys). Intertidal drift biomass is linked to local hydrodynamics as well as biological interactions (Biber, 2007; Lyons et al., 2009; Qiao et al., 2011; Smetacek and Zingone, 2013). Small-scale local factors, such as wind direction, water currents, and nutrient loading, can differ spatially and temporally (Martins et al., 2001). Based on aerial surveys, the greatest accumulation of drift algae occurred in areas of restricted flushing (e.g. Wickford and western Greenwich Bay) or in shallow, crescent-shaped coves facing NE or SW (e.g. Conimicut Point, see http://nbep.org/publications/NBEP-17-179.pdf), most likely due to longshore drift and predominant wind directions.

While *Ulva* blooms can have many deleterious impacts on the ecology of benthic environments, blooms also form complex habitats that can provide shelter and food to associated invertebrates (Lyons et al., 2014). We found that the mud snail *Ilyanassa obsoleta* was the most abundant invertebrate in macroalgal blooms in Greenwich Bay and the density of *I. obsoleta* was positively correlated with *Ulva* biomass. In addition to *I. obsoleta,* we documented a range of invertebrates in bloom material including ctenophores, crabs, shrimp, and amphipods. While Green et al. (2014) reported that a mat of *Ulva* with 840-930 g of algae decreased the species abundance and diversity of benthic invertebrates by 67% and 19%, respectively, within two weeks, Green and Fong (2014) showed that *Ulva* mats < 1.5 cm thick actually increased the abundance of subsurface deposit feeders. In systems dominated by *Ulva,* algal biomass and its persistence are critical for the benthic and mobile invertebrate community.

Macroalgal blooms have a significant ecological impact on coastal systems (Lyons et al., 2014). Long-term studies are needed to determine the drivers and causes of complex phenomenon such as macroalgal blooms. New technologies for monitoring macroalgal blooms, including synthetic aperture radar (SAR; Shen et al., 2014) and aerial tracking techniques (S. Licht, unpublished data), will enable researchers to monitor larger geographical areas more efficiently. These monitoring efforts should include frequent sampling of abiotic factors, including nutrient concentrations, salinity, and precipitation, in order to determine the relationship between macroalgal abundance and environmental conditions. This study documented high variability in macroalgal abundance and diversity across month-groups, years, sites, and even within individual sites in a eutrophic estuary. These findings highlight the importance of long-term monitoring to improve the understanding of persistent multi-year macroalgal blooms.

Management efforts, including the reduction of nitrogen pollution released from WWTFs are necessary to decrease eutrophication in coastal systems. Rhode Island has invested in significant WWTF upgrades in recent years; however, these treatment plants service a limited amount of the watershed. For example, Warwick, RI (Greenwich Bay watershed) offers sewer service to only 65% of its residents, and 3,000 residents that have the ability to connect to the sewer system have not to date (City of Warwick, 2013). Further management efforts are required to decrease nutrient inputs from point sources (e.g. WWTFs) and non-point sources throughout coastal watersheds. Even with point source reductions, ecosystem recovery will take several years to decades and may not return to pre-eutrophication status due to shifting baselines and altered trophic interactions (Duarte et al., 2009; Greening et al., 2014). At present, annual macroalgal blooms still occur in Greenwich Bay (L. Green, personal observation). Eutrophication management efforts should be coupled with continued long-term monitoring of water quality, macroalgal blooms, and other ecological indicators to conclusively determine the short- and long-term impacts of nutrient reduction on coastal ecosystems.

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Figure Captions

Fig. 1. Regions and subregions of Narragansett Bay included in aerial surveys.

Fig. 2. Sampling sites located in and around Greenwich Bay, RI. CP: Conimicut Point, OB: Oakland Beach and Oakland Beach Cove, WC: Warwick City Park, BF: Budlong Farm, SD: Sylvia Drive, CH: Chepiwanoxet Point, GS: Goddard State Park, and SP: Sandy Point.

Fig. 3. Percent of Chlorophyta, Rhodophyta, and Phaeophyceae observed in each density class during aerial surveys conducted from 2006-2012. The areas of Narragansett Bay have been divided into Lower, Middle, and Upper Bay sections.

Fig. 4. Photo plate showing the typical morphology of *Ulva* blade (A), *Ulva* tube (B), *Gracilaria* spp. (C-D), as well as a typical intertidal (E) and subtidal (F) macroalgal bloom in Greenwich Bay.

Fig. 5. A) Mean total algal biomass (grams fresh weight, gfm) and B) percent cover observed during intertidal surveys.

Fig. 6. Species diversity (H_S) ± 1SE across sites (A), month-groups (B), and years (C) for intertidal surveys (mean ±1 SE). Letters indicate significant differences among bars following post-hoc analyses. CP: Conimicut Point, OB: Oakland Beach, WC: Warwick City Park, BF: Budlong Farm, SD: Sylvia Drive, CH: Chepiwanoxet Point, GS: Goddard State Park, and SP: Sandy Point.

Fig. 7. Mean total algal biomass (grams fresh weight, gfm) observed during subtidal surveys.

Fig. 8. Species diversity (H_S) ± 1SE across sites (A), month-groups (B), and years (C) for subtidal surveys. Sites are listed from outer Greenwich Bay to inner Greenwich Bay. Letters indicate significant differences among bars following post-hoc analyses. OB: Oakland Beach, OBC: Oakland Beach Cove, WC: Warwick City Park, BF: Budlong Farm, SD: Sylvia Drive, GS: Goddard State Park, and SP: Sandy Point.

Fig. 9. Mean macroalgal percent cover of the most commonly observed species in the intertidal zone of Greenwich Bay during May-September plotted with sea surface temperature and salinity.

Fig. 10. Mean macroalgal biomass (grams fresh weight, gfm/m^3) of the most commonly observed species in the subtidal zone of Greenwich Bay during May-September plotted with sea surface temperature and salinity.

Fig. 11. A) Mean subtidal biomass of *Ulva* (gfm/m^3) plotted with sea surface temperature during the bloom-forming season in 2009, 2010, and 2011. There was a significant positive correlation between *Ulva* biomass and sea surface temperature. B) Mean subtidal biomass of *Gracilaria* spp. and total macroalgae (gfm/m^3) plotted with dissolved inorganic nitrogen (DIN) from May-September in 2008 and 2009. Both *Gracilaria* spp. and total macroalgal biomass were significantly positively correlated with DIN.

Fig. 1

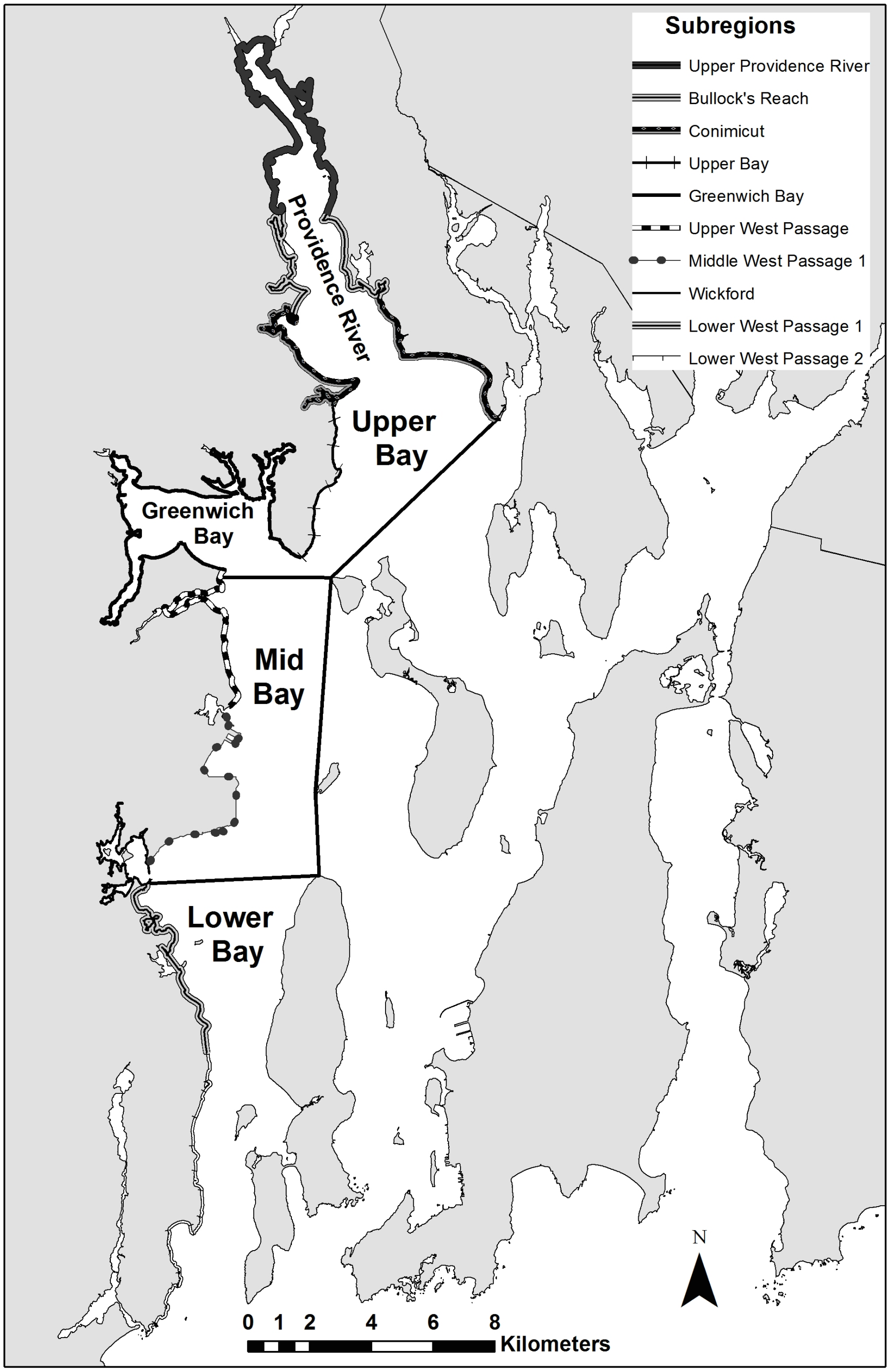

Subregions
Upper Providence River
Bullock's Reach
Conimicut
Upper Bay
Greenwich Bay
Upper West Passage
Middle West Passage 1
Wickford
Lower West Passage 1
Lower West Passage 2
Providence River
Upper Bay
Greenwich Bay
Mid Bay
Lower Bay
N
0 1 2 4 6 8
Kilometers

Fig. 2

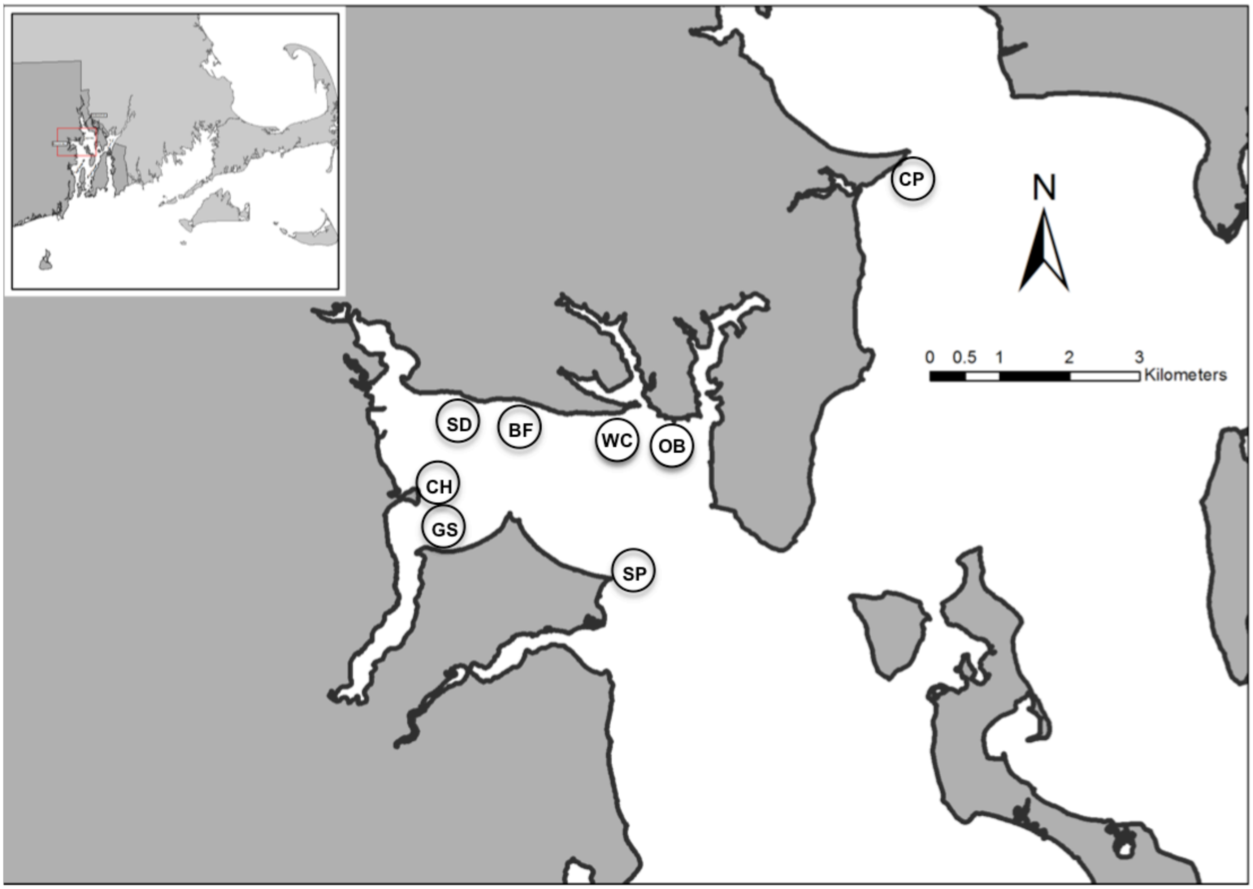


Fig. 3

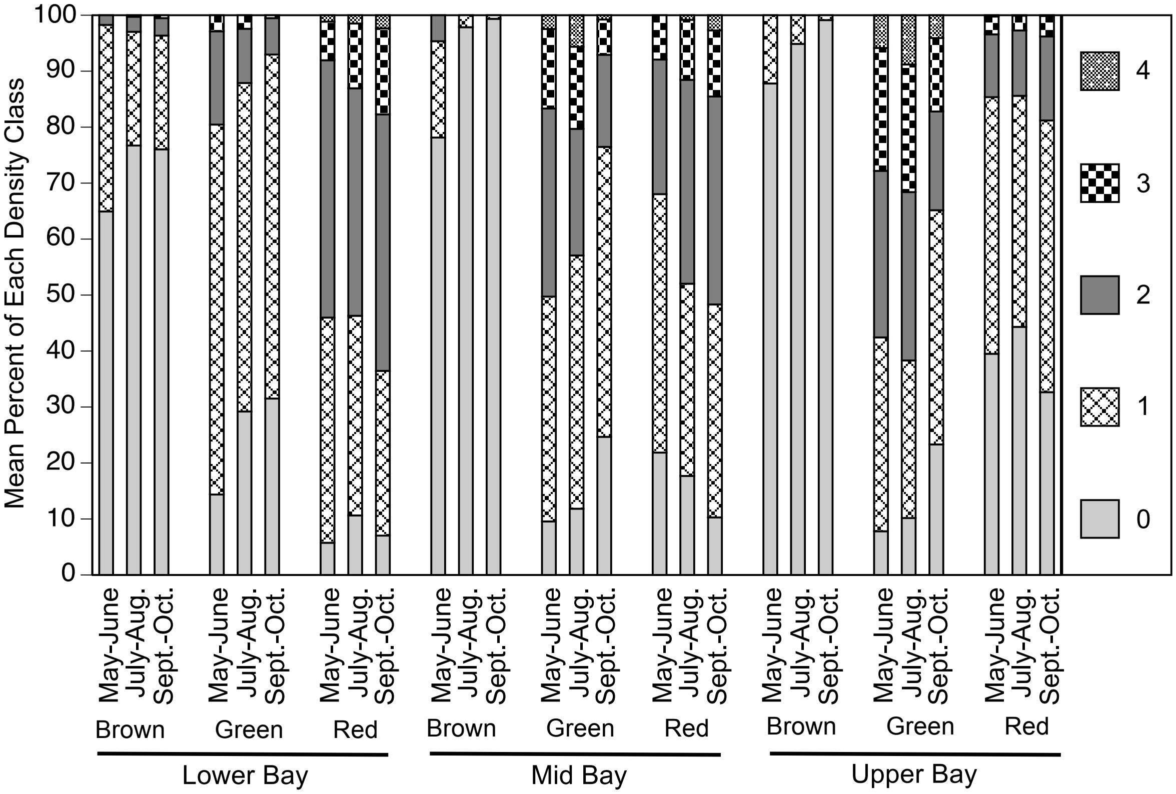

Mean Percent of Each Density Class
100
90
80
70
60
50
40
30
20
10
0
4
3
2
1
0
May-June
July-Aug.
Sept.-Oct.
Brown
Green
Red
Lower Bay
Mid Bay
Upper Bay

Fig. 4

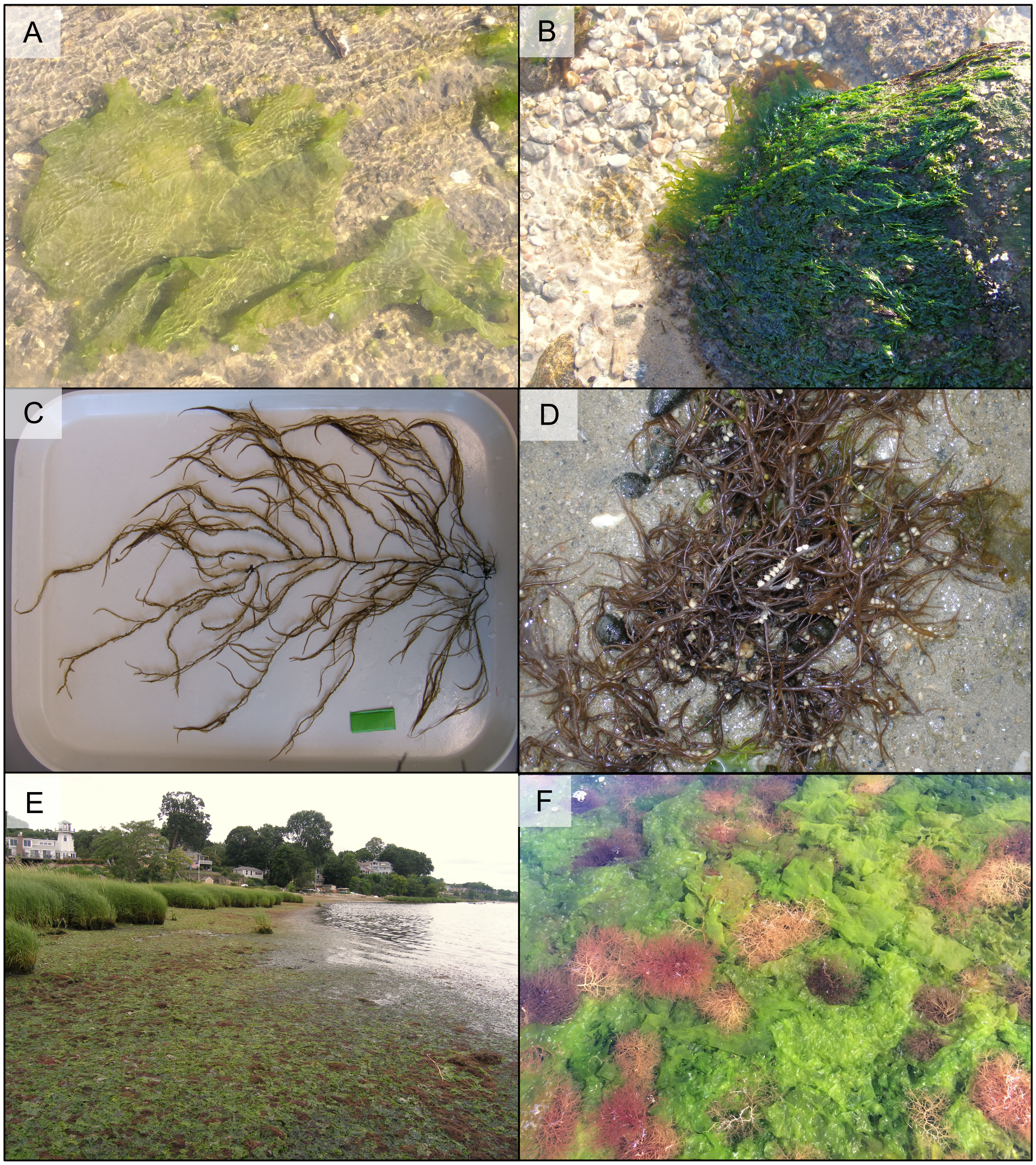


Fig. 5

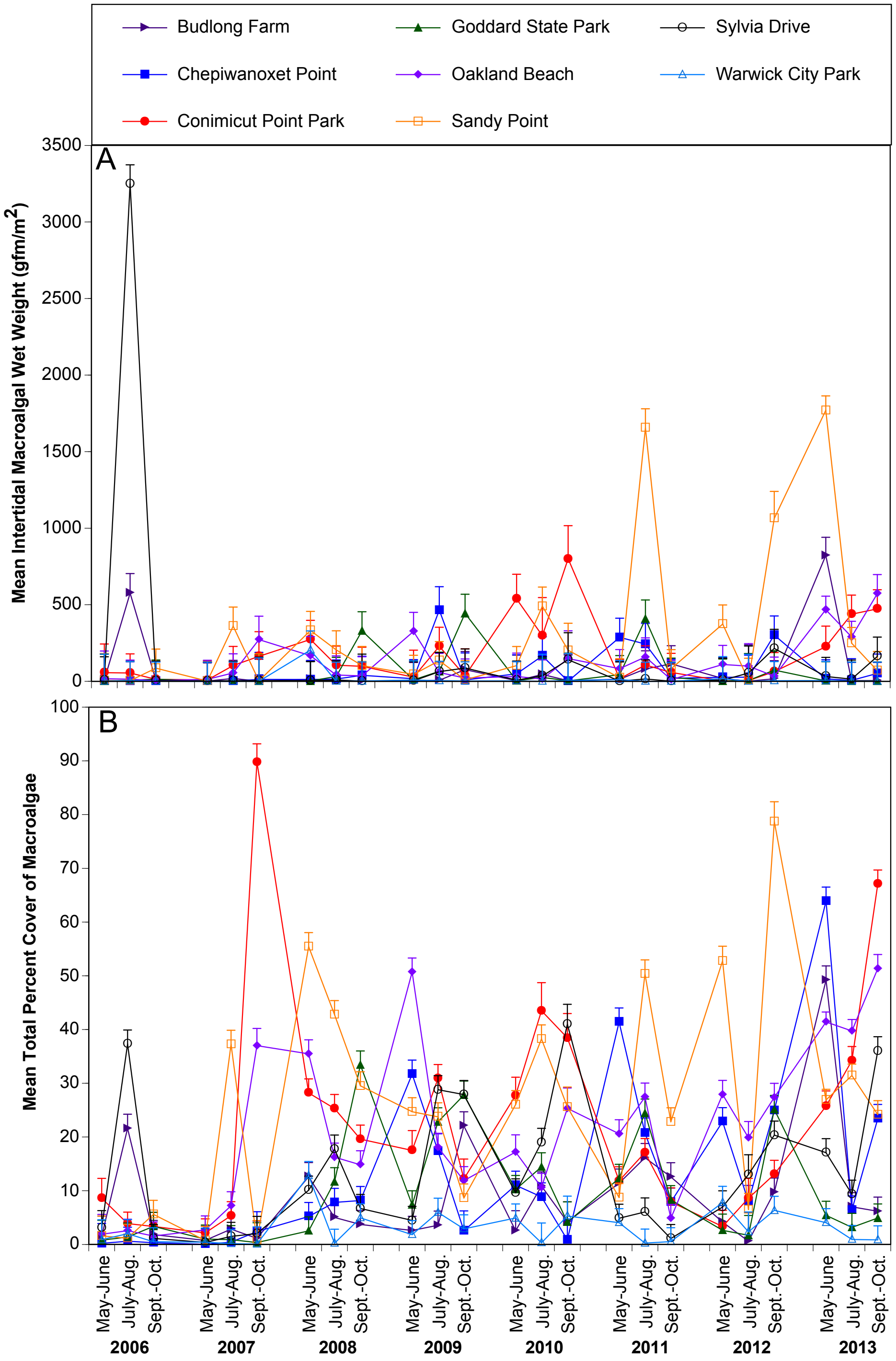

Budlong Farm
Goddard State Park
Sylvia Drive
Chepiwanoxet Point
Oakland Beach
Warwick City Park
Conimicut Point Park
Sandy Point
A
Mean Intertidal Macroalgal Wet Weight (gfm/m^2)
0
500
1000
1500
2000
2500
3000
3500
B
Mean Total Percent Cover of Macroalgae
0
10
20
30
40
50
60
70
80
90
100
May-June
July-Aug.
Sept.-Oct.
2006
2007
2008
2009
2010
2011
2012
2013

Fig. 6

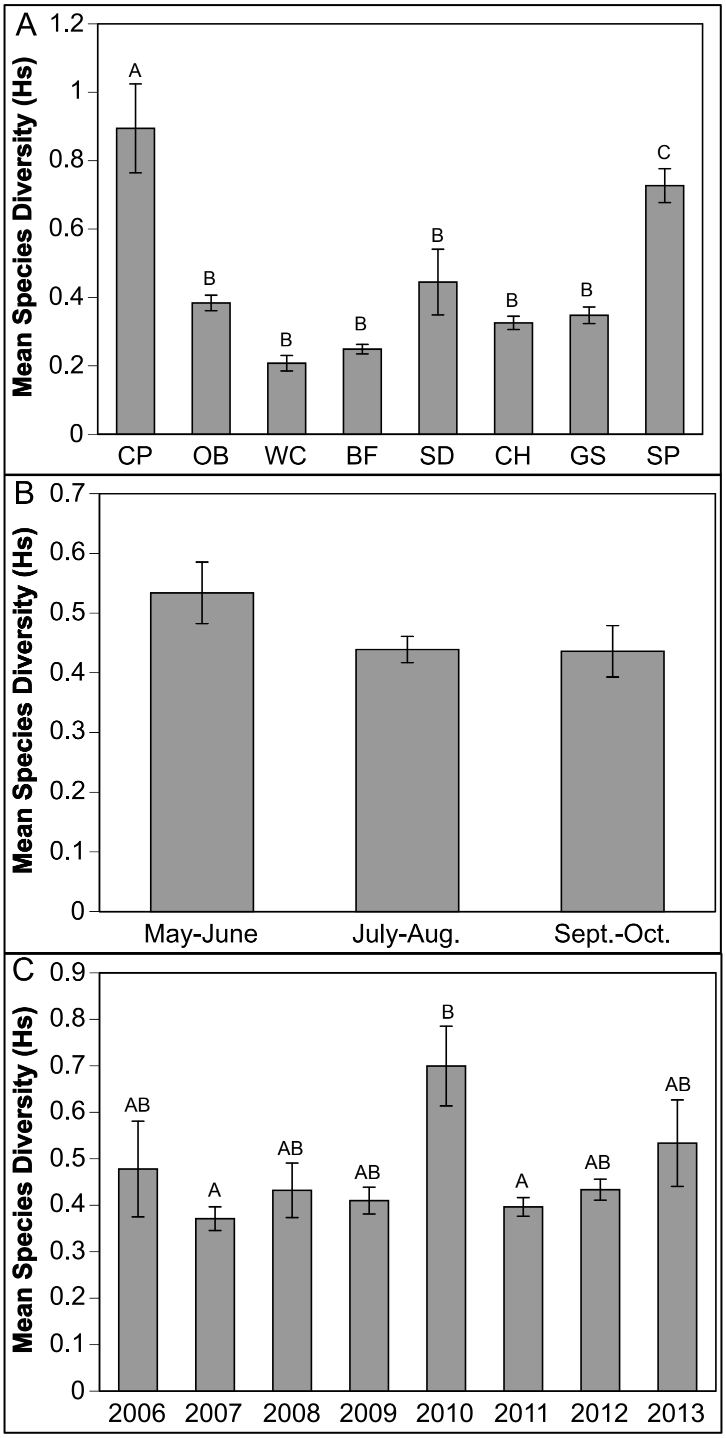
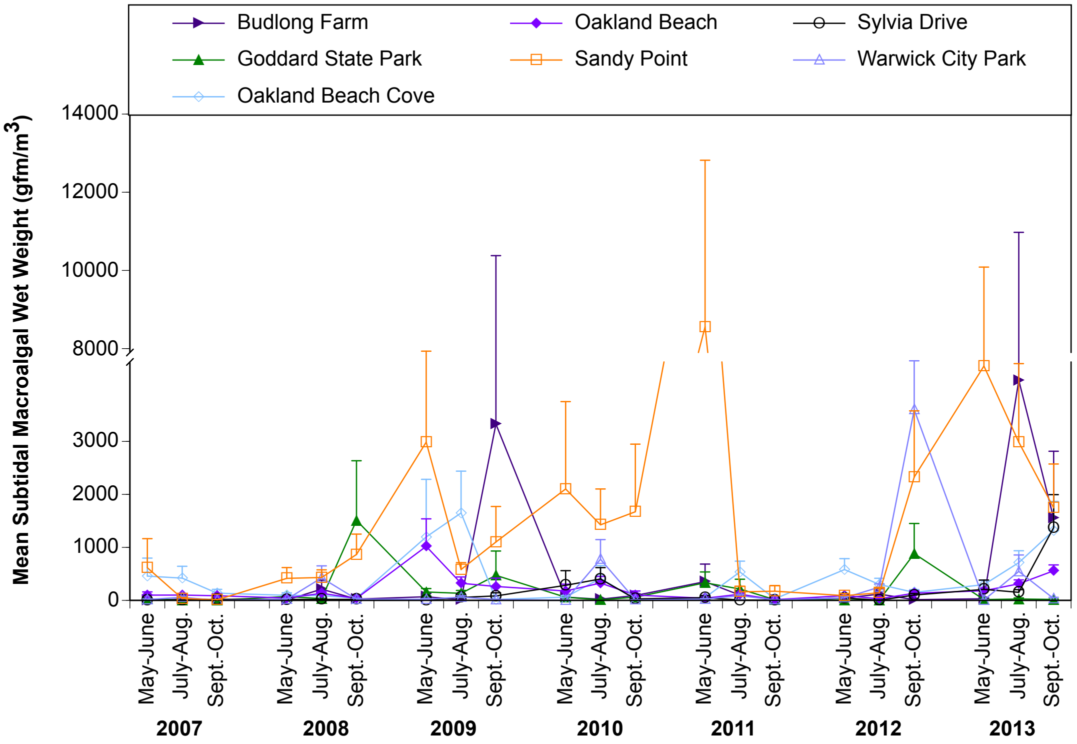

A
Mean Species Diversity (Hs)
1.2
1
0.8
0.6
0.4
0.2
0
A
B
B
B
B
B
B
C
CP
OB
WC
BF
SD
CH
GS
SP
B
Mean Species Diversity (Hs)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
May-June
July-Aug.
Sept.-Oct.
C
Mean Species Diversity (Hs)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
AB
A
AB
AB
B
A
AB
AB
2006
2007
2008
2009
2010
2011
2012
2013

Fig. 7



Budlong Farm
Oakland Beach
Sylvia Drive
Goddard State Park
Sandy Point
Warwick City Park
Oakland Beach Cove
Mean Subtidal Macroalgal Wet Weight (gfm/m^3)
14000
12000
10000
8000
3000
2000
1000
0
May-June
July-Aug.
Sept.-Oct.
2007
2008
2009
2010
2011
2012
2013

Fig. 8

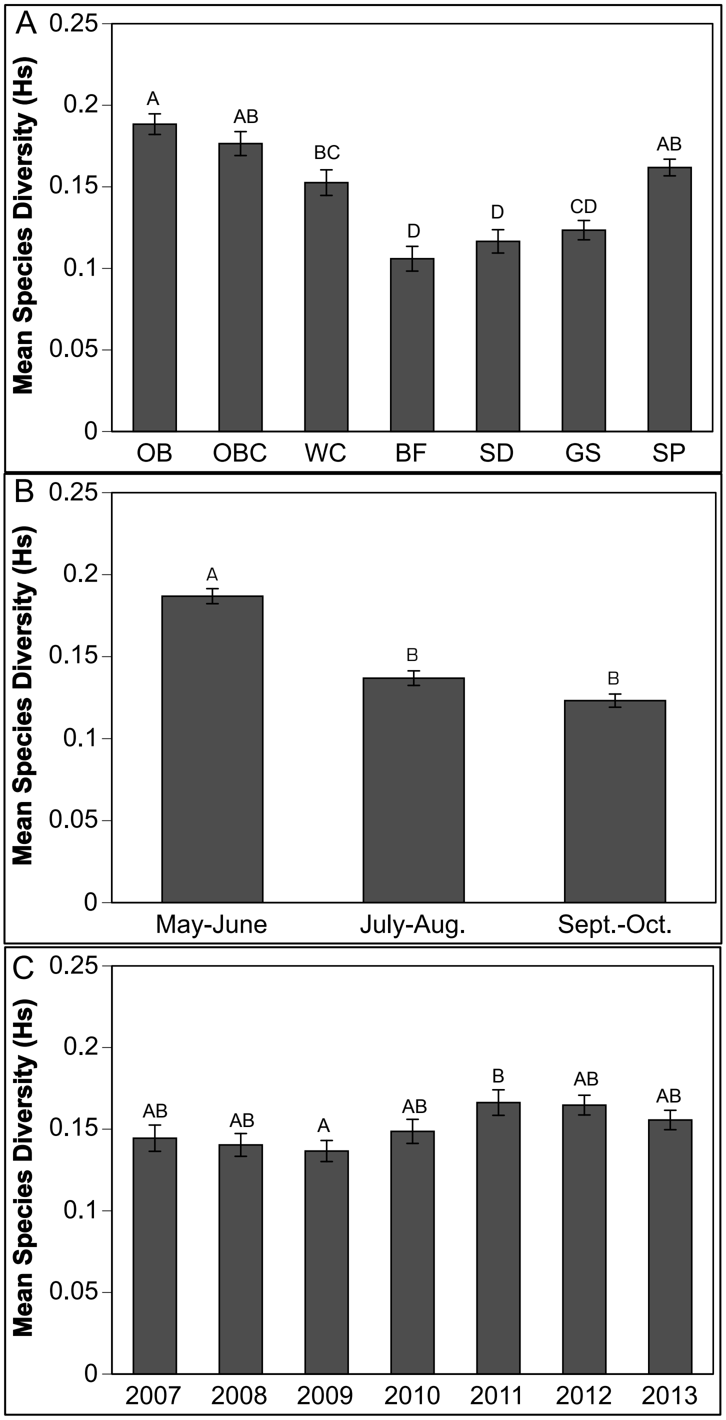

A
Mean Species Diversity (Hs)
0.25
0.2
0.15
0.1
0.05
0
A
AB
BC
D
D
CD
AB
OB
OBC
WC
BF
SD
GS
SP
B
Mean Species Diversity (Hs)
0.25
0.2
0.15
0.1
0.05
0
A
B
B
May-June
July-Aug.
Sept.-Oct.
C
Mean Species Diversity (Hs)
0.25
0.2
0.15
0.1
0.05
0
AB
AB
A
AB
B
AB
AB
2007
2008
2009
2010
2011
2012
2013

Fig. 9

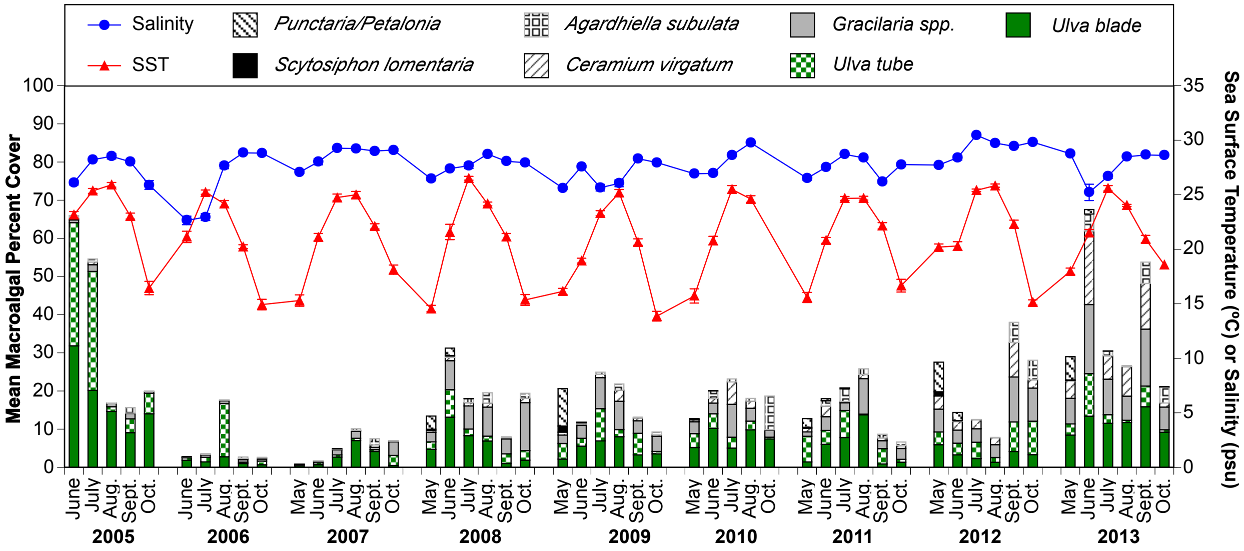

Salinity
SST
Punctaria/Petalonia
Scytosiphon lomentaria
Agardhiella subulata
Ceramium virgatum
Gracilaria spp.
Ulva tube
Ulva blade
Mean Macroalgal Percent Cover
Sea Surface Temperature (°C) or Salinity (psu)
0
10
20
30
40
50
60
70
80
90
100
0
5
10
15
20
25
30
35
June July Aug. Sept. Oct.
2005
June July Aug. Sept. Oct.
2006
May June July Aug. Sept. Oct.
2007
May June July Aug. Sept. Oct.
2008
May June July Aug. Sept. Oct.
2009
May June July Aug. Oct.
2010
May June July Aug. Sept. Oct.
2011
May June July Aug. Sept. Oct.
2012
May June July Aug. Sept. Oct.
2013

Fig. 10

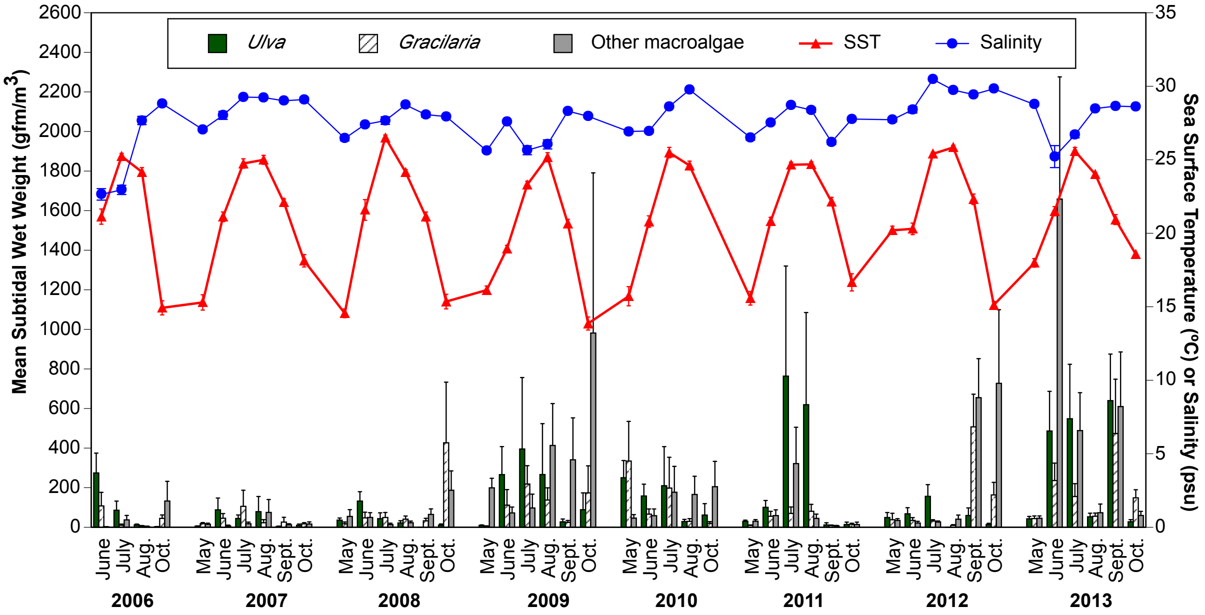
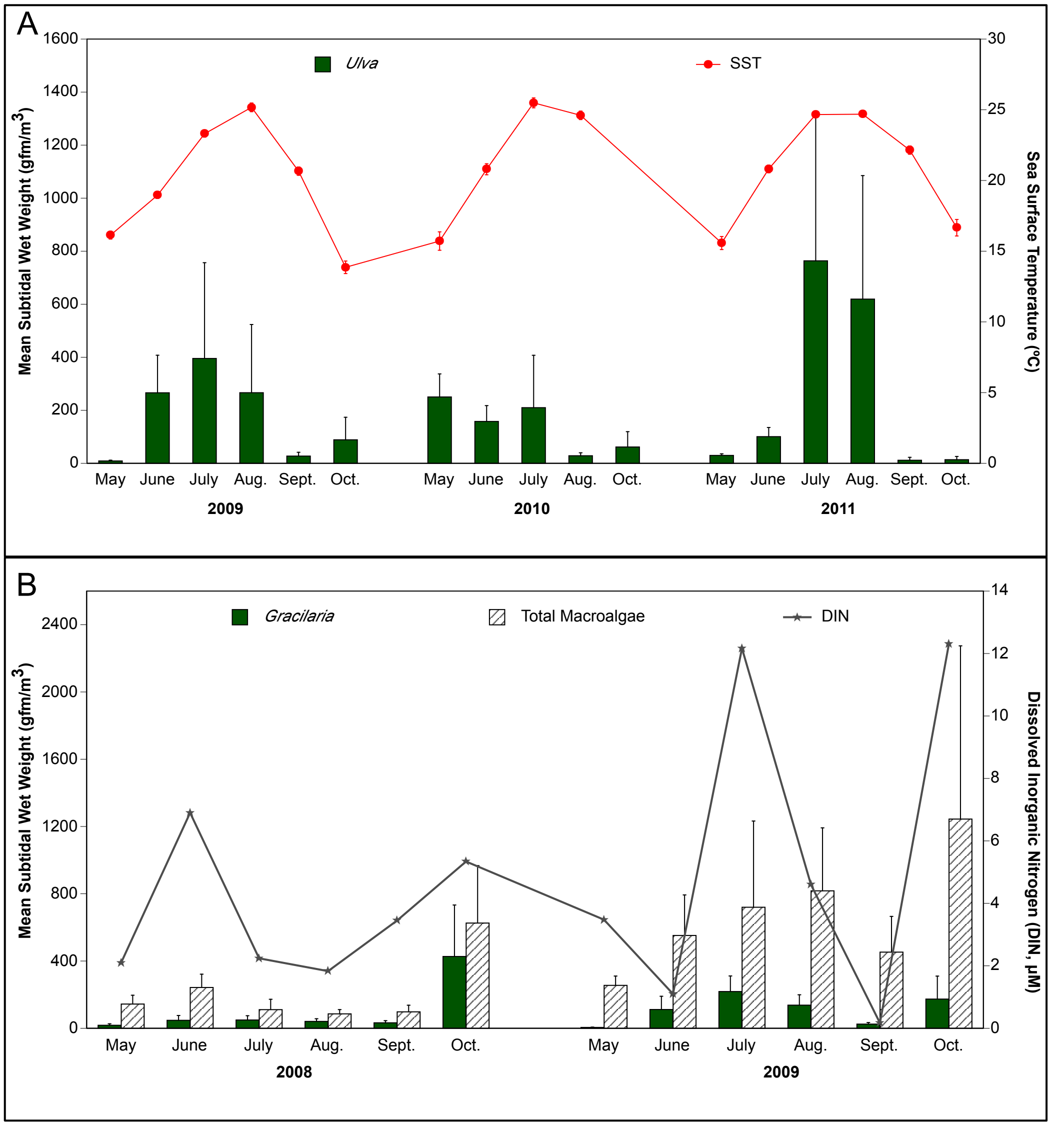

Ulva
Gracilaria
Other macroalgae
SST
Salinity
Mean Subtidal Wet Weight (gfm/m^3)
Sea Surface Temperature (°C) or Salinity (psu)
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
35
30
25
20
15
10
5
0
June
July
Aug.
Oct.
May
Sept.
2006
2007
2008
2009
2010
2011
2012
2013

Fig. 11


A
Ulva
SST
Mean Subtidal Wet Weight (gfm/m^3)
Sea Surface Temperature (°C)
0
200
400
600
800
1000
1200
1400
1600
0
5
10
15
20
25
30
May
June
July
Aug.
Sept.
Oct.
2009
2010
2011
B
Gracilaria
Total Macroalgae
DIN
Mean Subtidal Wet Weight (gfm/m^3)
Dissolved Inorganic Nitrogen (DIN, µM)
0
400
800
1200
1600
2000
2400
0
2
4
6
8
10
12
14
May
June
July
Aug.
Sept.
Oct.
2008
2009