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Examination of *Ulva* bloom species richness and relative abundance reveals two cryptically co-occurring bloom species in Narragansett Bay, Rhode Island

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Abstract

Blooms caused by the green macroalga *Ulva* pose a serious threat to coastal ecosystems around the world. Despite numerous studies of the causes and consequences of these blooms, we still have a limited understanding of *Ulva* bloom species richness and abundance due to difficulties in identifying *Ulva* species using morphological features. Along the northeastern U.S. coastline, all blooms of distromatic *Ulva* blades were previously identified as *U. lactuca*. Recent molecular sequencing, however, discovered the presence of additional distromatic *Ulva* species. Therefore, in order to determine the relative abundance of *Ulva* species within blooms, we conducted monthly surveys at four Narragansett Bay, RI, sites representing a gradient of bloom severity. We found that the biomass of *Ulva* within blooms was a mix of *U. compressa* and *U. rigida*, not *U. lactuca* as previously reported. In contrast, sites not impacted by blooms that were located near the mouth of Narragansett Bay were dominated by *U. lactuca*. We also observed spatial and temporal differences in *Ulva* and total macroalgal diversity between bloom-impacted sites, indicating that *Ulva* bloom composition can be radically different between similar sites within close proximity. We discuss our results in the context of *Ulva* blooms worldwide, highlighting the need to definitively determine bloom species composition in order to fully understand bloom dynamics.

Key words: biomass, diversity, eutrophication, macroalgal bloom, survey, *Ulva*

1. Introduction

The formation of blooms of filamentous and/or thin foliose macroalgae are frequently a consequence of coastal eutrophication (Fletcher, 1996; Valiela et al., 1997; Morand and

Merceron, 2005; Ye et al., 2011). Macroalgae with these morphologies have a high surface area to volume ratio that enables them to rapidly uptake nutrients for greatly increased growth (Littler and Littler, 1980; Hein et al., 1995; Pedersen and Borum, 1996), provided favorable bathymetric, temperature, and light conditions exist (Rivers and Peckol, 1995; Taylor et al., 2001; Cohen and Fong, 2004; Sousa et al., 2007; Liu et al., 2010).

Bloom macroalgae often form large floating mats in the water column, in which individual thalli grow, fragment, and asexually reproduce via zoospores (Gao et al., 2010; Ye et al., 2011). These floating mats of algae alter coastal light, nutrient, and water flow conditions, causing decreases in perennial algae, seagrasses, and benthic invertebrates (Valiela et al., 1997; Hauxwell et al., 1998, 2001; Thomsen and McGlathery, 2006; Worm and Lotze, 2006). Nightly respiration and decomposition of bloom macroalgae contribute to hypoxic events (Valiela et al., 1997; Raffaelli et al., 1998) that can result in substantial mortality of invertebrates and fishes (Deacutis et al., 2006; Berezina et al., 2007). In addition, several species produce toxins that negatively impact co-occurring organisms (Nelson et al., 2003a; Eklund et al., 2005; Van Alstyne et al., 2006). Moreover, blooms interfere with coastal commercial and recreational activities (Lee and Olsen, 1985; Thomsen and McGlathery, 2006; Deacutis, 2008; Leliaert et al., 2009).

Bloom-forming macroalgal species can be found within the phyla Chlorophyta, Heterokontophyta, and Rhodophyta, but most macroalgal blooms, including the largest ever recorded, are caused by Chlorophyta species, such as those within the genus *Ulva* Linnaeus (Fletcher, 1996; Valiela et al., 1997; Morand and Merceron, 2005). For example, the 2008 bloom of *Ulva prolifera* offshore of Qingdao, China contained an estimated 20 million wet tons of algae spanning approximately 13,000 km^2 in the Yellow Sea. This bloom required the removal of more than 1 million tons of *U. prolifera* from the shoreline, at a cost of over $100 million US dollars (Leliaert et al., 2009; Gao et al., 2010).

Ulva species are notoriously difficult to identify due to a lack of distinguishing morphological features among species and a tremendous degree of phenotypic plasticity within species (Blomster et al., 1999; Blomster et al., 2002; Leskinen et al., 2004). Until recently, this morphological uncertainty hindered our ability to accurately assess species richness within *Ulva* blooms. In the last decade, however, numerous molecular studies from bloom and non-bloom impacted habitats around the world have greatly increased our understanding of *Ulva* richness (e.g. Hayden et al., 2003; Leliaert et al., 2009; Kraft et al., 2010; Liu et al., 2010). However, detailed surveys of the relative abundance of different *Ulva* species, as well as physiological and ecological studies utilizing molecularly confirmed *Ulva* species, remain lacking (but see Liu et al., 2010; Yokoyama and Ishihi, 2010; Kim et al., 2011). These knowledge gaps pose a serious barrier in our ability to understand *Ulva* bloom dynamics, and consequently hinder the development of macroalgal bloom risk assessments and well-informed coastal management practices.

We conducted extensive surveys at four Narragansett Bay, Rhode Island sites (Figure 1), to determine: 1) which *Ulva* species is (are) the main contributor(s) to *Ulva* blooms in Narragansett Bay; 2) if bloom-forming *Ulva* species are found throughout Narragansett Bay or only in bloom-impacted areas; and 3) how the species richness and relative abundance of all macroalgal species varies amongst bloom and non-bloom sites. We discuss our results in the context of previously studied *Ulva* bloom systems and highlight the importance of determining their species composition for understanding bloom dynamics.

2. Methods

2.1. Study locale and species

Narragansett Bay is a well-studied estuary in which annual blooms of distromatic *Ulva* blades and, less often, monostromatic tubular *Ulva* spp. (formerly *Enteromorpha*, Hayden et al., 2003) and *Gracilaria* spp. occur in the anthropogenically impacted northern portions of the bay (Granger et al., 2000; Calabretta and Oviatt, 2008; Deacutis, 2008; Oczkowski et al., 2008; Thornber and Guidone, unpublished data). While tubular *Ulva* species in Rhode Island cannot be identified to the species level based on morphological features alone, significant progress has been made in distinguishing between *Ulva* blades in this region. Originally identified as monospecific blooms of *U. lactuca*, molecular sequencing of *Ulva* blades within Narragansett Bay and along the outer Rhode Island coast detected three species of *Ulva* blades: *U. compressa* Linnaeus, *U. lactuca* Linnaeus, and *U. rigida* C. Agardh (Guidone et al., unpublished data). Similar results were found in molecular assessments of *Ulva* in the Great Bay Estuarine System in New Hampshire and Maine (Hofmann et al. 2010). These blade-forming species can be reliably distinguished based on a suite of cellular features including cell size, shape, and arrangement, chloroplast position, and pyrenoid number (Guidone et al., unpublished data; Hofmann et al., 2010).

2.2. Survey methodology

We first assessed the biomass of *Ulva compressa*, *U. lactuca*, and *U. rigida,* and the percent cover of all algal species throughout Narragansett Bay by conducting monthly surveys from May-September 2009 at four field sites: Brushneck Cove and Chepiwanoxet, Warwick, RI and The Graduate School of Oceanography (GSO) and Pier 5, Narragansett, RI (Figure 1).

Brushneck Cove and Chepiwanoxet are located in Greenwich Bay, a subestuary of Narragansett Bay that experiences annual *Ulva* blooms (Granger et al., 2000; Thornber and Guidone, unpublished data). Both Brushneck Cove and Chepiwanoxet are intertidal mud flats bordered by fringing salt marshes; however, Chepiwanoxet has a longer water residence time (1.5 days versus 0.3 days), a greater mean depth, and experiences lower temperatures and a greater incidence of hypoxic events (Granger et al., 2000; Thornber and Guidone, unpublished data). These sites were contrasted to GSO and Pier 5 (Figure 1), which are near the mouth of Narragansett Bay and are not impacted by annual *Ulva* blooms. GSO is a narrow beach of mixed sand and cobblestone, while Pier 5 is a boulder field.

For comparison across seasons, additional surveys were conducted in February and May 2010 at all four sites. Monthly surveys were subsequently continued at the two bloom-impacted sites from June 2010 to November 2011.

We conducted all surveys during spring low tides. For each survey, at each site, we placed two 10 m transects parallel to the shore; transects were at least 30 m apart and placed at the same tidal height. Transect positioning corresponded to the tidal height where *Ulva* wrack was most commonly observed at low tide; this was directly below the fringing marsh at Brushneck Cove and Chepiwanoxet, and directly above the waterline at GSO and Pier 5. For our initial May-September surveys, we used a 0.25 m^2 quadrat to calculate the percent cover of all algal taxa at one meter intervals along each transect, for a total of twenty replicate samples per site and sampling month. Subsequent surveys assessed percent cover at two-meter intervals, for a total of ten replicate samples per site and sampling month. Due to the overlap of macroalgal thalli within drift mats, the total percent cover of all species often totaled more than 100%. Algae were identified to the lowest taxonomic unit possible in the field. The *Ulva* blades within each quadrat were collected and returned to the laboratory. Additionally, beginning in February 2010 we collected *Ulva* tubes from the bloom-impacted sites for biomass comparison to *Ulva* blades. In the laboratory, we identified each blade to species using distinguishing cellular features determined from molecularly confirmed voucher specimens (Guidone et al., unpublished data). Following identification, blades were spun to a constant weight using a salad spinner and then weighed.

2.3 Statistical analyses

We analyzed *Ulva* bloom biomass data for our 2009-2010 survey and our bloom-impacted sties (2010-2011) using fully factorial nested ANOVAs with fixed factors for month-year, site, species, and transect nested within site (JMP, version 8, SAS Institute Inc., North Carolina, USA). We were unable to normalize our data via transformation, however the analysis of variance test is robust to departures from normality and homogeneity of variances when datasets are large. In this instance, our datasets were sufficiently large to ensure that our results were not impacted by violating these assumptions (Underwood, 1997).

Percent cover data for our 2009-2010 and 2010-2011 surveys were used to calculate the average Shannon-diversity index (H') and Pielou's evenness (J') for each site. Additionally, algal percent cover was assessed for differences in taxa among sites and sampling months using a two-way crossed analysis of similarity (ANOSIM). The contribution of each taxon to the average similarity and dissimilarity among sites and months was determined using a similarity of percentages analysis (SIMPER). Prior to ANOSIM and SIMPER analysis, data were fourth-root transformed to increase the importance of rare species; all analyses were conducted on Bray-

Curtis similarities. Non-parametric analyses were conducted using Primer-E (version 6, Primer-E Ltd., Plymouth UK).

3. Results

3.1. Ulva species richness and relative abundance

Ulva lactuca was the dominant blade forming *Ulva* species at non-bloom sites, while *U. compressa* and *U. rigida* dominated at bloom sites. Overall, *Ulva* species biomass varied significantly amongst sites and months (Table 1). In 2009-2010, *U. lactuca* was the only blade species found at the non-bloom impacted Pier 5, with peak mean wet biomass of 75.48 g/m^2 in May 2010 (Figure 2a). *Ulva lactuca* also dominated at GSO, where we only found small fragments (< 0.4 g per piece) of *U. compressa* and *U. rigida* during three of the seven survey months (Figure 2b).

In contrast, over the entire course of this study (2009-2011), *U. lactuca* was rarely found at either of our bloom-impacted sites, while *U. compressa* and *U. rigida* were consistently present at both sites (Figure 3). The mean *Ulva* biomass was significantly greater at Brushneck Cove than the other three sites during 2009-2010 (Tukey post-hoc test, $p < 0.05$); there was no significant difference in biomass between Brushneck Cove and Chepiwanoxet in 2010-2011 (Table 1b). Additionally, while we observed no impact of transect placement during our 2009-2010 surveys, transect did have a significant impact on biomass at our bloom sites during 2010-2011 (Table 1).

At both bloom-impacted sites, biomass consistently peaked during June-July with subsequent crashes in August (Figure 3). One exception to this pattern occurred during 2009 at Brushneck Cove, which saw continued high biomass through September 2009 (Figure 3b). Total mean wet biomass was greatest during June 2009 (882.80 g/m^2; maximum observation 1,662.24 g/m^2) at Brushneck Cove and July 2010 (665.88 g/m^2; maximum observation 1,804.60 g/m^2) at Chepiwanoxet.

Throughout our surveys from 2009-2011, *U. compressa* was nearly always the largest component of *Ulva* mats at Chepiwanoxet, except during April 2011, May of each year, and Sept. 2009, when *Ulva* tubes dominated (Figures 3-5). By contrast, *U. rigida* biomass was greater than *U. compressa* during 2009 and 2010 at Brushneck Cove, while summer peaks in June and July 2011 were dominated by *U. compressa*. Low densities of tubular *Ulva* species were only present at Brushneck Cove during May of each year and April 2011 (Figures 3-5).

Despite having reliable morphological descriptions for our three targeted *Ulva* species, we were occasionally (< 12% of samples) unable to identify *Ulva* blades to species level. Unidentifiable blades were more frequently encountered at Brushneck Cove and were more abundant during the spring months (Figure 3).

3.2. Total macroalgal species richness and abundance

3.2.1. 2009-2010 survey

A total of 34 taxonomic groups were observed throughout our 2009-2010 surveys (Figure 4, Table 2). Species diversity (Shannon H') was highest at non-bloom Pier 5 and lowest at bloom-impacted Brushneck Cove (Table 3; one-way ANOVA $F_{3, 456} = 91.40$, $p < 0.0001$, Tukey post-hoc $p < 0.05$). However, no clear correlation between bloom-impacted and non-impacted sites was evident, as diversity was higher at bloom-impacted Chepiwanoxet than at GSO. In addition, evenness (Pielou's J') was highest at Chepiwanoxet. Of the 34 taxa recorded, 22 were found at only one or both of the lower-bay sites (Table 2). No individual taxa were unique to the two bloom-impacted sites; however, Chepiwanoxet was the only site that contained mats of intertwined *Agardhiella subulata, Ceramium virgatum, Gracilaria* spp., and *Polysiphonia* spp. (hereafter ACGP mats). While these mats could reach greater than 50% cover, the thalli within them were often small fragments, making separation of the component species impracticable. Therefore, we considered these mats as a unique entity for this study.

Taxon assemblages were significantly different amongst all sites and sampling months (ANOSIM, $p = 0.001$; Table 4). In concurrence with the Shannon diversity index, the largest difference in algal composition was observed between bloom-impacted Brushneck Cove and non-bloom Pier 5 (Table 4a), while the smallest difference was between bloom-impacted Chepiwanoxet and non-bloom GSO. However, the high R-value and significance ($p = 0.001$) of all pairwise tests between sites indicates strong separation of algal communities among all sites (Table 4a). Differences in algal composition between the bloom and non-bloom impacted sites were largely due to the greater percent cover of *Ulva* blades at the bloom impacted sites and the presence of *Chondrus crispus* at the non-bloom sites (Figure 4, Table 5). In addition, while *Ulva* tubes were found at all four sites, their occurrence and percent cover varied temporally (Figure 4, Table 5).

Amongst months, the largest differences in flora were between February and August; the smallest differences were between July and August (Table 4b). Seasonal shifts in algal composition were apparent from June to July, August to September, and September to February (Figure 4, Table 4b).

3.2.2. 2010-2011 survey of bloom-impacted sites

As in the 2009-2010 survey, algal composition from June 2010-November 2011 differed significantly between the two bloom-impacted sites (ANOSIM global $R = 0.272$, $p = 0.001$), with a greater diversity at Chepiwanoxet than at Brushneck Cove (Table 3). The dominant taxa at both sites were also similar to 2009-2010, with *Ulva* blades dominating the algal community at Brushneck Cove during all months except January-May 2011; *Ulva* blades, *Ulva* tubes, and ACGP mats dominated at Chepiwanoxet (Figures 4, 5, Table 2). Taxa observed in 2010-2011 that were not previously observed during 2009-2010 included *Ectocarpus* spp., *Porphyra* spp., *Cladophora* spp., and *Scytosiphon lomentaria* (Table 2).

4. Discussion

4.1. Ulva in Narragansett Bay

4.1.1. Species distribution

Our results demonstrate that *U. compressa* and *U. rigida* are responsible for the blooms of *Ulva* blades in the northern portions of Narragansett Bay, RI. Neither of these bloom-forming species was found at Pier 5, our field site closest to the open coast. In contrast, *U. lactuca* was regularly observed at the two non-bloom sites near the mouth of Narragansett Bay and rarely found at the bloom-impacted sites.

In a molecular assessment of *Ulva* species within the Great Bay Estuarine System of New Hampshire and Maine, USA, Hofmann et al. (2010) found a similar distributional pattern for these three species, with *U. compressa* and *U. rigida* typically occurring together at inner estuarine sites and *U. lactuca*, along with *U. pertusa,* occurring at higher salinity sites closer to the open coast. Their results, in conjunction with our own, suggest that *U. compressa* and *U. rigida* are more physiologically and/or ecologically similar to each other than either is to *U.*

lactuca. Based on the distributional pattern of these species in Narragansett Bay and the Great Bay Estuarine System, we hypothesize that *U. lactuca* is rarely found in northern Narragansett Bay bloom-impacted sites due to a lower tolerance of high water temperatures, salinity fluctuations, and/or hypoxia or other factors. Likewise, if *U. compressa* and *U. rigida* are adapted to the abiotic conditions found in shallow, low-flow eutrophic estuaries, they might be absent from open coastal areas due to nutrient limitations or intolerance to higher salinities or wave exposure.

One alternate explanation exists for the distributional pattern of *U. compressa*. Tan et al. (1999) observed that distromatic blades of *U. compressa* were concentrated in low salinity areas of an estuary in Aberdeenshire, Scotland, while *U. compressa* with a tubular morphology was found at higher salinity sites near the North Sea. Taking this into consideration, it is possible that *U. compressa* in Narragansett Bay persists in lower salinity eutrophic areas as a distromatic blade and is present at lower bay and outer coast sites as a monostromatic tube. Although we did not identify tubular *Ulva* to species in this survey, prior molecular analysis of outer coast samples supports this hypothesis (Guidone et al., unpublished data).

In addition to abiotic factors, *Ulva* species distribution may be restricted by differences in *Ulva* palatability and/or herbivore communities amongst the study sites. Nelson et al. (2008) found that *Ulva* and *Ulvaria* (both in the family Ulvaceae) differed in abiotic tolerances and palatability, causing the more palatable but stress tolerant *Ulva* to dominate intertidally while the unpalatable *Ulvaria* thrived in the herbivore populated subtidal. Similarly, blooms in the Baltic Sea were dominated by the unpalatable *Pilayella littoralis* when herbivores were abundant and the palatable *Ulva intestinalis* when herbivores were absent or nutrient levels were enriched (Lotze et al., 2000; Lotze and Worm, 2000). Although not directly quantified in this study, based on previous studies and our own field observations, herbivore communities between our bloom and non-bloom sites can be substantially different (Guidone et al., unpublished data).

4.1.2. Bloom species relative abundance

While similar densities of *Ulva* were found at both bloom-impacted sites during the summers of 2010 and 2011, the relative abundance of each *Ulva* blade species, as well as the proportion of tubular *Ulva* species present, differed significantly. These spatial and temporal fluctuations indicate that even between eutrophic sites within close proximity (only 3.5 km apart), small abiotic or biotic differences, or stochasticity, may lead to markedly different *Ulva* bloom compositions. Nelson et al. (2003b) observed similar patterns amongst *Ulva* blades, *Ulva* tubes, and *Ulvaria*, on a slightly larger scale in the Pacific Northwest. Our observation that *Ulva* biomass differed amongst transects during 2010-2011 indicates that temporal changes in water flow and/or wind patterns may play an important role in *Ulva* bloom deposition patterns in the intertidal.

4.2. Total macroalgal diversity at bloom and non-bloom sites

As we had expected, Pier 5 had the highest diversity of the four sites sampled in 2009-2010. This site is closest to the open coast and likely receives drift from a large area of the lower Narragansett Bay and open ocean sites. Pier 5 also has an abundance of hard substrata available for algal attachment, unlike the other three field sites.

Contrary to our expectations, we did not find a strict pattern of high diversity (H') at non-bloom sites vs. low diversity at bloom-impacted sites, as Chepiwanoxet had the second highest diversity of the four sites. This is particularly perplexing in light of environmental measurements (dissolved oxygen, water residence time; Granger et al., 2000) that indicate Chepiwanoxet is the most eutrophic of the four sites. Since the algae sampled at all sites was largely drift, it is unclear whether the diversity observed at Chepiwanoxet is representative of the site itself, or if circulation patterns deposit a wide diversity of species from adjacent areas. However, all areas within close proximity to Chepiwanoxet are also bloom-impacted, suggesting that the diversity observed at this site is truly representative of the bloom-impacted community. Furthermore, Chepiwanoxet had the highest evenness of the four sites sampled from 2009-2010, which differs from general patterns that indicate eutrophication has a larger negative impact on evenness than species richness (Hillebrand et al., 2007). Similar results were found in subestuaries of Waquoit Bay, Massachusetts, USA, where macroalgal bloom biomass (*Cladophora vagabunda* and *Gracilaria tikvahiae*) was linked to nutrient enrichment, while species richness was not (Fox et al., 2008).

4.3. Narragansett Bay blooms compared to Ulva blooms around the world

To our knowledge, this is the first report of *Ulva* bloom biomass that has extensively examined the relative contribution of cryptically co-occurring distromatic blade species following molecular confirmation of the *Ulva* species present within an area (Guidone et al., unpublished data). We are unaware of any previous estimates of *U. compressa* bloom biomass, but reports of *Ulva* bloom biomass based solely on morphology have identified *U. rigida* as the causative species of blooms in Europe (Sfriso et al., 1992; Coat et al., 1998; Balducci et al., 2001; Merceron and Morand, 2004 as *U. armoricana*) and the Philippines (Largo et al., 2004 as *U. armoricana*). *Ulva lactuca* has been reported to bloom in North America (Lyons et al., 2009), New Zealand (Park, 1992), and South Africa (Anderson et al., 1996). The density of

Narragansett Bay blooms fall within the range of densities reported for most blooms of *U. rigida* and *U. lactuca* (150-3,000 g/m^2 wet mass). One notable exception to this range is the bloom of *U. rigida* in the Venice Lagoon, Italy, reported to have a biomass range of 5-20 kg/m^2 wet mass (Schramm, 1999).

Given the difficulty in identifying *Ulva* species using morphology alone, and based on our observation that *U. rigida* and *U. compressa* often bloom simultaneously, it is likely that some prior reports of *Ulva* blooms have either misidentified the *Ulva* species involved or underestimated the number of species present within the bloom. For example, a recent molecular survey of *Ulva* in New Zealand found *U. lactuca* to be present at only 3 out of 195 sampled sites (Heesch et al., 2009), indicating that New Zealand blooms are likely formed by another, more abundant *Ulva* species. Additionally, based on a small sampling of *Ulva* blades within blooms in Brittany, France, Merceron and Morand (2004) tentatively identified three co-occurring ulvoid species (*U. rigida* as *U. armoricana*, *U. rotundata*, and *Umbraulva olivascens* as *U. olivascens*). Unfortunately, even when armed with molecularly verified species descriptions, if morphological features cannot be found to separate co-occurring species, detailed surveys of *Ulva* bloom diversity such as we conducted will be challenging.

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Figure 1 Map of Rhode Island, USA, showing the location of our four study sites.

Figure 2 *Ulva* biomass during the May-September 2009 and February and May 2010 surveys at A) Pier 5 and B) GSO. Error bars are ± 1 SE.

Figure 3 *Ulva* biomass at the two bloom-impacted sites A) Chepiwanoxet and B) Brushneck Cove. Error bars are ± 1 SE.

Figure 4 Algal percent cover at all sites during 2009-2010. Species comprising less than 10% cover in all months are not shown. Site abbreviations follow Table 2. ACGP refers to mixed mats of *Agardhiella subulata*, *Ceramium virgatum*, *Gracilaria* spp., and *Polysiphonia* spp. * indicates no sampling due to ice cover.

Figure 5 Algal percent cover at bloom-impacted sites during 2010-2011. Species comprising less than 4% cover in all months are not shown. Site abbreviations follow Table 2. ACGP refers to mixed mats of *Agardhiella subulata*, *Ceramium virgatum*, *Gracilaria* spp., and *Polysiphonia* spp. * indicates no sampling due to storm surge.

Table 1. Results of a nested ANOVA on *Ulva* biomass among month-year, site, transect nested within site, and species for a) all study sites from 2009-2010, and b) Brushneck Cove and Chepiwanoxet from 2010-2011.

(a)

Source	df	MS	F	P
Month-Year	6	6,267.02	19.19	< 0.0001
Site	3	24,238.75	74.21	< 0.0001
Transect[Site]	4	109.38	0.33	0.85
Species	3	8,006.74	24.51	< 0.0001
Month-Year*Site	18	4,348.83	13.31	< 0.0001
Month-Year*Transect[Site]	24	2,202.50	6.74	< 0.0001
Month-Year*Species	18	3,645.81	11.16	< 0.0001
Site*Species	9	5,645.93	17.28	< 0.0001
Transect[Site]*Species	12	650.59	1.99	0.0217
Month-Year*Site*Species	54	3,210.02	9.83	< 0.0001
Month-Year*Transect[Site]*Species	72	1,107.17	3.39	< 0.0001
Error	1,624	326.65		

(b)

Source	df	MS	F	p
Month-Year	15	12,946.93	30.22	< 0.0001
Site	1	6.79	0.016	0.90
Transect[Site]	2	6,889.20	16.08	< 0.0001
Species	3	44,216.10	103.20	< 0.0001
Month-Year*Site	15	721.90	1.68	0.048
Month-Year*Transect[Site]	30	5,333.94	12.45	< 0.0001
Month-Year*Species	45	8,984.53	20.97	< 0.0001
Site*Species	3	8,087.41	18.88	< 0.0001
Transect[Site]*Species	6	4,578.26	10.69	0.0013
Month-Year*Site*Species	45	2,230.41	5.21	< 0.0001
Month-Year*Transect[Site]*Species	90	4,134.88	9.65	< 0.0001
Error	1227	428.47		

Table 2. Taxa observed during our 2009-2010 field surveys. Site abbreviations are: P Pier 5, G GSO, C Chepiwanoxet, and B Brushneck Cove. Genera marked with an asterisk require microscopic examination for species determinations.

	2009																				2010							
	May				June				July				August				September				February				May			
	P	G	C	B	P	G	C	B	P	G	C	B	P	G	C	B	P	G	C	B	P	G	C	B	P	G	C	B
Ulva blades	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X			X	X		X	X		X	X	X	X
Ulva tubes	X	X	X	X	X		X	X	X	X	X		X	X	X				X				X			X	X	X
Agardhiella subulata											X				X				X			X	X				X	
Ahnfeltia plicata																						X						
Ascophyllum nodosum	X				X				X				X				X				X				X			
Bonnemaisonia hamifera					X				X	X															X			
Bryopsis plumosa										X				X														
Ceramium virgatum	X	X	X	X	X		X		X	X				X		X			X	X		X			X	X	X	X
Chaetomorpha spp.*									X	X			X															
Champia parvula									X	X																		
Chondrus crispus	X	X			X				X	X			X	X			X				X	X			X	X		
Codium fragile ssp. *fragile*	X								X		X		X		X				X			X	X				X	
Corallina officinalis																					X							

Cystoclonium purpureum	X	X			X																				X			
Desmarestia viridis	X				X				X																X			
Dumontia contorta																									X	X		
Ectocarpus spp.		X													X													
Fucus distichus					X				X				X				X				X				X			
Fucus vesiculosus								X																				
Gracilaria tikvahiae & G. vermiculophylla		X	X	X			X	X			X	X				X			X	X		X					X	X
Grateloupia turuturu	X	X							X				X	X								X						
Heterosiphonia japonica																										X		
Hypnea musciformis	X																											
Leathesia marina	X																											
Mastocarpus stellatus	X				X								X												X			
Palmaria palmata	X				X				X				X				X				X				X			
Petalonia & *Punctaria* spp.*		X	X	X				X														X	X			X		
Phyllophora membranifolia													X									X						
Polyides rotundus	X				X																X				X			

Polysiphonia & *Neosiphonia* spp.*	X		X	X	X	X	X		X	X		X	X			X	X
Porphyra spp.*	X			X										X	X		
Saccharina latissima	X	X		X	X		X	X						X			
Scytosiphon lomentaria	X																
Ulothrix flacca											X						
Vertebrata lanosa	X			X										X			

Table 3. Average species richness (S), Pielou's evenness (J'), and Shannon diversity index (H') for our 2009-2010 and 2010-2011 field surveys.

Survey	Site	S	J'	H'
2009-2010	Brushneck Cove	1.56	0.34	0.12
	Chepiwanoxet	2.92	0.76	0.76
	GSO	1.45	0.72	0.33
	Pier 5	4.45	0.68	0.92
2010-2011	Brushneck Cove	1.81	0.67	0.33
	Chepiwanoxet	2.38	0.60	0.52

Table 4. Results from a two-way crossed ANOSIM for differences amongst sites and months in our 2009-2010 survey. R-values close to 1.00 indicate complete separation between groups while R-values close to 0 indicate little separation between groups. All pairwise tests were significant (p = 0.001). (a) Tests for differences between site groups across all month groups. (b) Tests for differences between month groups across all site groups.

(a)

Global R: 0.760	Brushneck Cove	Chepiwanoxet	GSO	Pier 5
Brushneck Cove				
Chepiwanoxet	0.736			
GSO	0.787	0.703		
Pier 5	0.908	0.830	0.766	

(b)

Global R: 0.470	May 2009	June	July	August	September	February 2010	May
May 2009							
June	0.179						
July	0.481	0.518					
August	0.413	0.515	0.162				
September	0.468	0.444	0.689	0.681			
February	0.460	0.690	0.683	0.755	0.702		
May 2010	0.215	0.379	0.560	0.565	0.558	0.256	

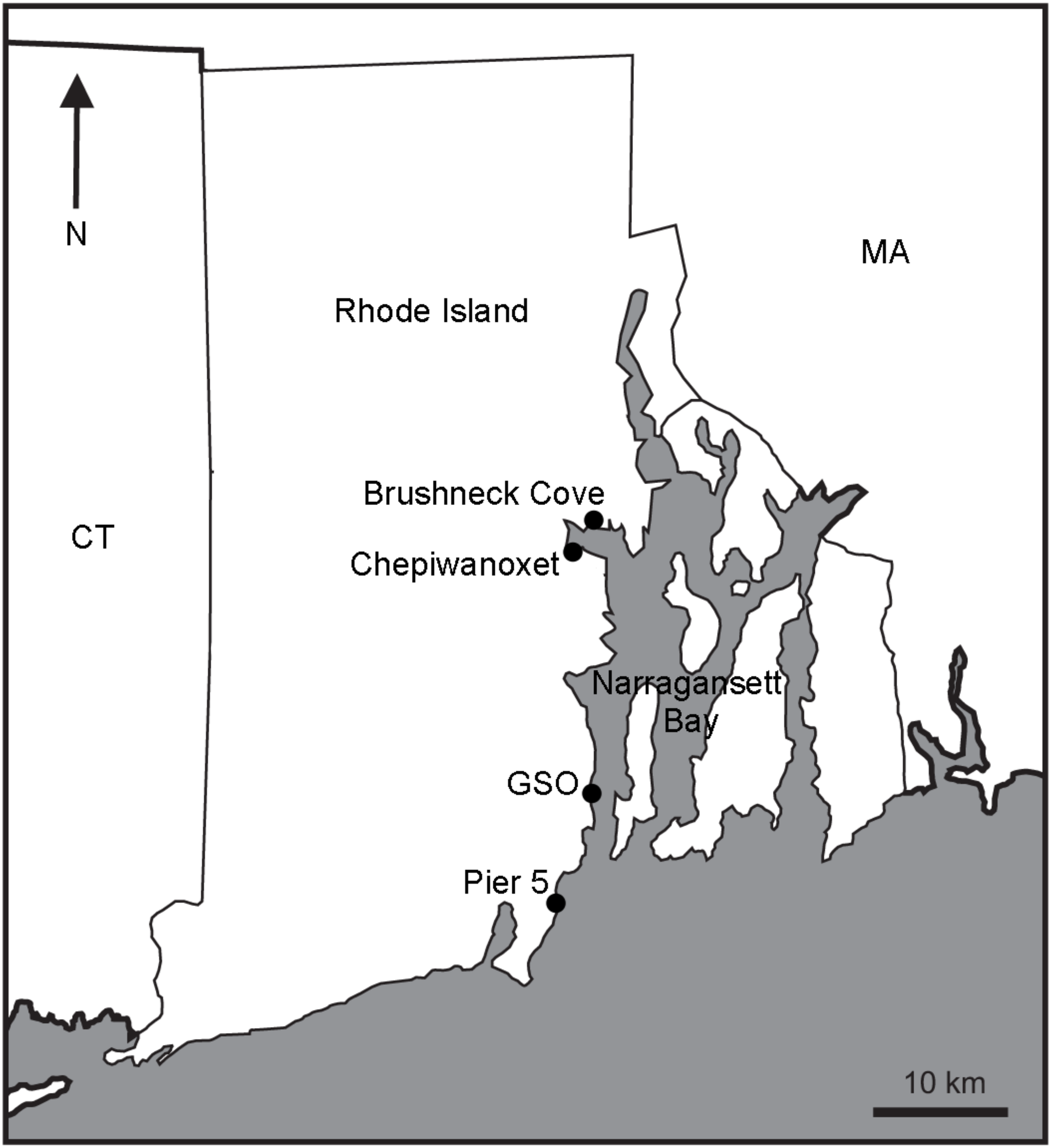
Table 5. Results from a two-way crossed SIMPER analysis for average similarity and dissimilarity amongst sites across all months in our 2009-2010 survey. ACGP refers to mats of intertwined *Agardhiella subulata, Ceramium virgatum, Gracilaria* spp., and *Polysiphonia* spp. Site abbreviations follow Table 2.

	Percent contribution	Cumulative percent
Within site similarity		
Brushneck Cove– Average similarity: 77.69		
Ulva blades	95.74	95.74
Chepiwanoxet – Average similarity: 65.76		
Ulva tubes	34.73	34.73
Ulva blades	33.30	68.03
ACGP	20.71	88.74
Gracilaria spp.	5.47	94.21
GSO – Average similarity: 45.89		
Ulva tubes	58.22	58.22
Polysiphonia spp.	13.72	71.95
Ceramium virgatum	11.53	83.48
Chondrus crispus	7.68	91.16
Pier 5 – Average similarity: 54.19		
Chondrus crispus	43.58	43.58
Saccharina latissima	17.87	61.45
Ulva blades	9.77	71.22
Palmaria palmata	9.33	80.55
Ulva tubes	6.21	86.76
Desmarestia viridis	3.45	90.21

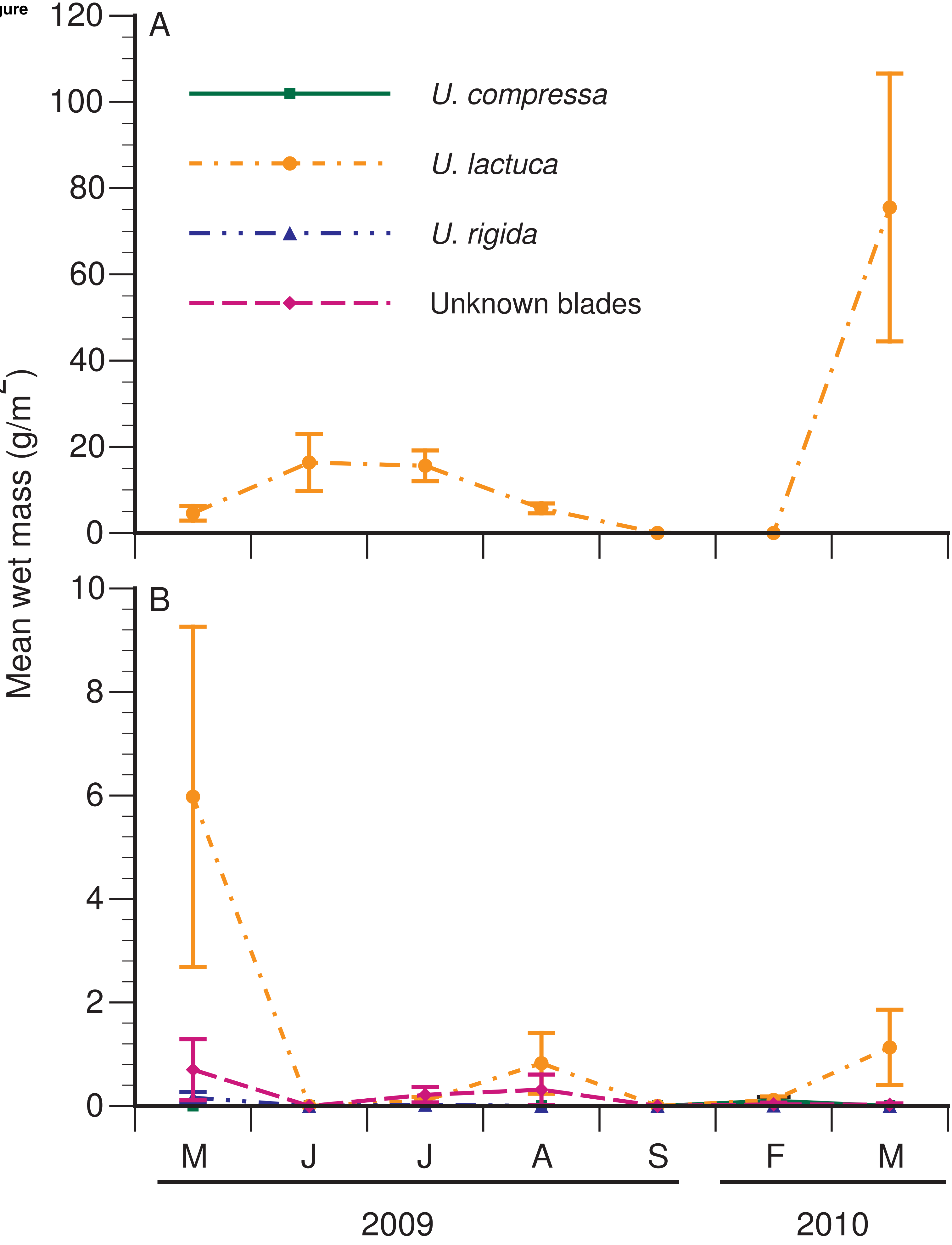
Between site dissimilarity	Percentage contribution to average dissimilarity between sites					
Taxon	B-C	B-G	B-P	C-G	C-P	G-P
Ulva blades	21.87	60.42	24.08	29.66	12.58	8.43
Ulva tubes	32.11	15.82	9.57	22.95	14.15	8.62
ACGP	24.52	-	-	14.94	10.24	-
Ascophyllum nodosum	-	-	-	-	-	2.48
Ceramium virgatum	6.10	5.39	-	8.15	2.80	3.63
Chondrus crispus	-	-	20.65	4.33	17.73	30.73
Codium fragile ssp. *fragile*	-	-	-	-	1.86	-
Desmarestia viridis	-	-	2.86	-	3.17	4.20
Fucus spp.	-	-	5.21	-	4.30	5.91
Gracilaria spp.	9.72	8.01	4.31	7.86	4.89	-
Grateloupia turuturu	-	-	-	-	-	1.50
Palmaria palmata	-	-	8.31	-	5.58	7.63

Polysiphonia spp.	-	5.14	4.53	4.62	3.65	2.49
Porphyra spp.	-	-	-	-	-	2.20
Saccharina latissima	-	-	10.81	-	7.84	15.75
Ulothrix flacca	-	-	-	-	2.68	-
Total contribution of species	94.32	94.77	90.33	92.51	91.47	91.35
Average between site dissimilarity	57.16	92.68	85.55	82.62	83.83	87.21

Figure 1

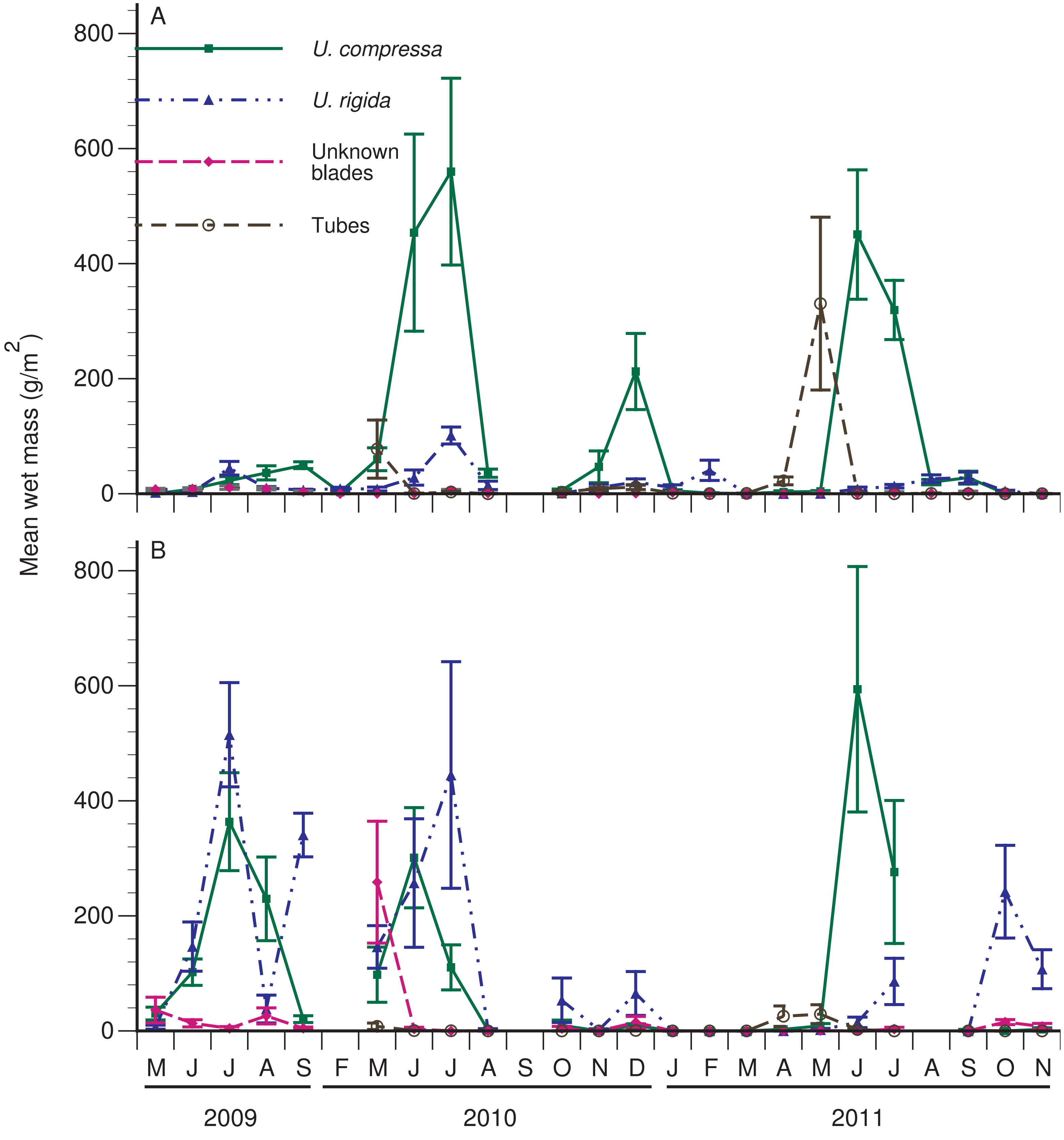

N
MA
Rhode Island
CT
Brushneck Cove
Chepiwanoxet
Narragansett Bay
GSO
Pier 5
10 km

Figure

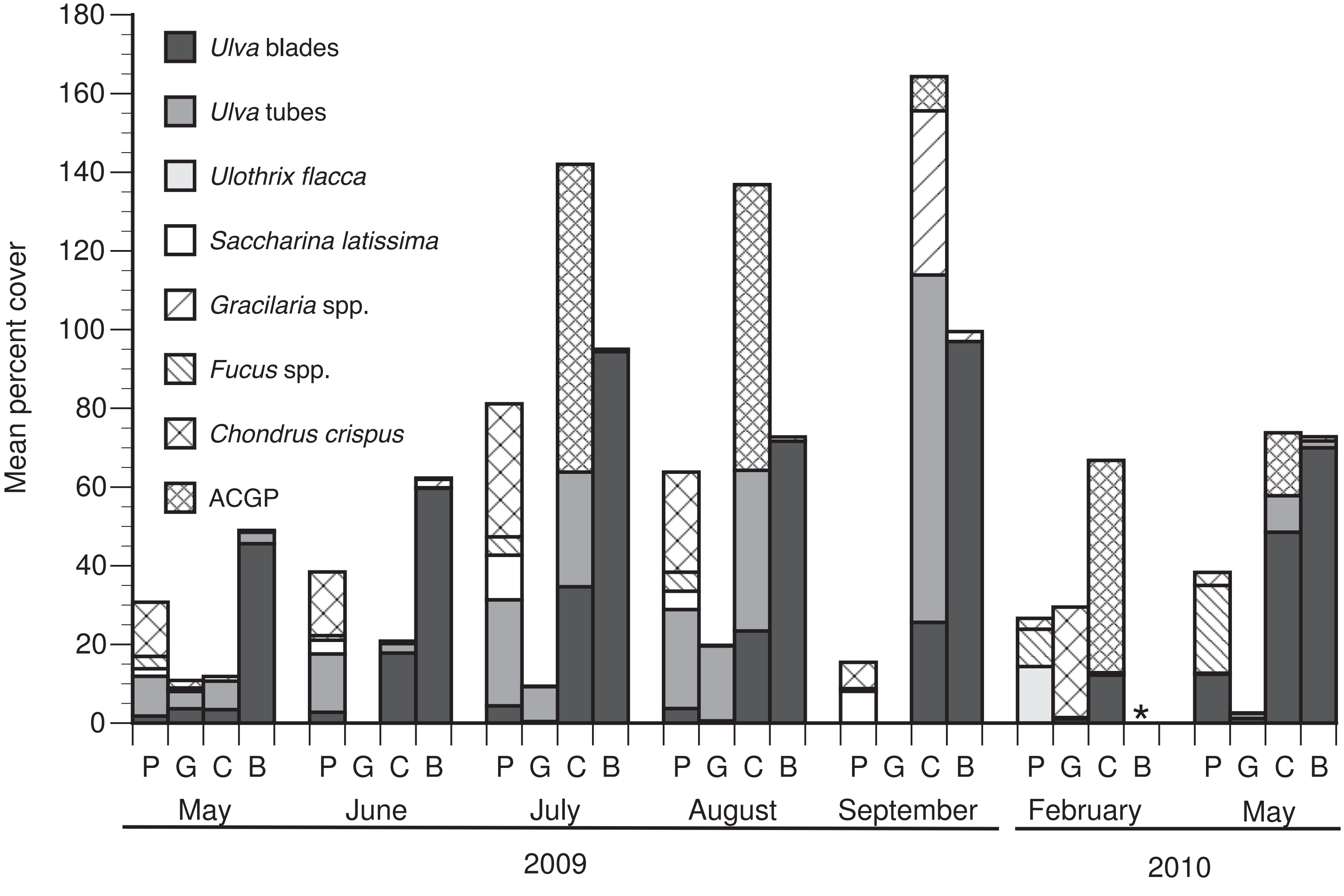


A
B
120
100
80
60
40
20
0
10
8
6
4
2
0
Mean wet mass (g/m^2)
U. compressa
U. lactuca
U. rigida
Unknown blades
M
J
J
A
S
F
M
2009
2010

Figure

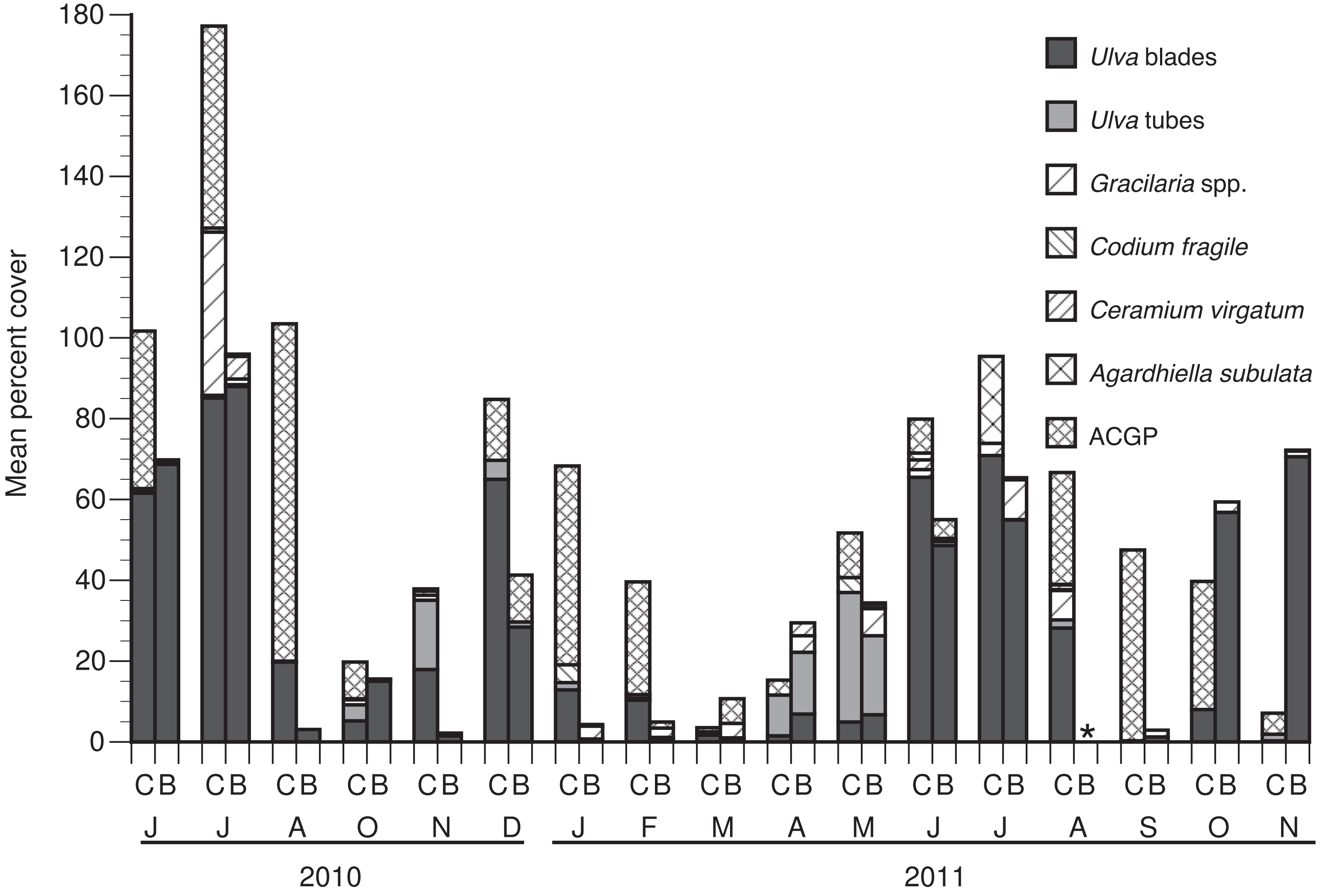

A
B
U. compressa
U. rigida
Unknown blades
Tubes
Mean wet mass (g/m^2)
0
200
400
600
800
M
J
J
A
S
F
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
2009
2010
2011

Figure



180
160
140
120
100
80
60
40
20
0
Mean percent cover
Ulva blades
Ulva tubes
Ulothrix flacca
Saccharina latissima
Gracilaria spp.
Fucus spp.
Chondrus crispus
ACGP
*
P G C B
May
June
July
August
September
February
2009
2010

Figure



Mean percent cover
0
20
40
60
80
100
120
140
160
180
Ulva blades
Ulva tubes
Gracilaria spp.
Codium fragile
Ceramium virgatum
Agardhiella subulata
ACGP
*
C B
J
J
A
O
N
D
J
F
M
A
M
J
J
A
S
O
N
2010
2011