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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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18 **Abstract**

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

35

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

37

38 **1. Introduction**

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

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

46 Bloom macroalgae often form large floating mats in the water column, in which
47 individual thalli grow, fragment, and asexually reproduce via zoospores (Gao et al., 2010; Ye et
48 al., 2011). These floating mats of algae alter coastal light, nutrient, and water flow conditions,
49 causing decreases in perennial algae, seagrasses, and benthic invertebrates (Valiela et al., 1997;
50 Hauxwell et al., 1998, 2001; Thomsen and McGlathery, 2006; Worm and Lotze, 2006). Nightly
51 respiration and decomposition of bloom macroalgae contribute to hypoxic events (Valiela et al.,
52 1997; Raffaelli et al., 1998) that can result in substantial mortality of invertebrates and fishes
53 (Deacutis et al., 2006; Berezina et al., 2007). In addition, several species produce toxins that
54 negatively impact co-occurring organisms (Nelson et al., 2003a; Eklund et al., 2005; Van
55 Alstyne et al., 2006). Moreover, blooms interfere with coastal commercial and recreational
56 activities (Lee and Olsen, 1985; Thomsen and McGlathery, 2006; Deacutis, 2008; Leliaert et al.,
57 2009).

58 Bloom-forming macroalgal species can be found within the phyla Chlorophyta,
59 Heterokontophyta, and Rhodophyta, but most macroalgal blooms, including the largest ever
60 recorded, are caused by Chlorophyta species, such as those within the genus *Ulva* Linnaeus
61 (Fletcher, 1996; Valiela et al., 1997; Morand and Merceron, 2005). For example, the 2008 bloom
62 of *Ulva prolifera* offshore of Qingdao, China contained an estimated 20 million wet tons of algae
63 spanning approximately 13,000 km² in the Yellow Sea. This bloom required the removal of more

64 than 1 million tons of *U. prolifera* from the shoreline, at a cost of over \$100 million US dollars
65 (Leliaert et al., 2009; Gao et al., 2010).

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

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

86

87 2. Methods

88 2.1. Study locale and species

89 Narragansett Bay is a well-studied estuary in which annual blooms of distromatic *Ulva*
90 blades and, less often, monostromatic tubular *Ulva* spp. (formerly *Enteromorpha*, Hayden et al.,
91 2003) and *Gracilaria* spp. occur in the anthropogenically impacted northern portions of the bay
92 (Granger et al., 2000; Calabretta and Oviatt, 2008; Deacutis, 2008; Oczkowski et al., 2008;
93 Thornber and Guidone, unpublished data). While tubular *Ulva* species in Rhode Island cannot be
94 identified to the species level based on morphological features alone, significant progress has
95 been made in distinguishing between *Ulva* blades in this region. Originally identified as
96 monospecific blooms of *U. lactuca*, molecular sequencing of *Ulva* blades within Narragansett
97 Bay and along the outer Rhode Island coast detected three species of *Ulva* blades: *U. compressa*
98 Linnaeus, *U. lactuca* Linnaeus, and *U. rigida* C. Agardh (Guidone et al., unpublished data).
99 Similar results were found in molecular assessments of *Ulva* in the Great Bay Estuarine System
100 in New Hampshire and Maine (Hofmann et al. 2010). These blade-forming species can be
101 reliably distinguished based on a suite of cellular features including cell size, shape, and
102 arrangement, chloroplast position, and pyrenoid number (Guidone et al., unpublished data;
103 Hofmann et al., 2010).

104

105 2.2. Survey methodology

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

110 Brushneck Cove and Chepiwanoxet are located in Greenwich Bay, a subestuary of Narragansett
111 Bay that experiences annual *Ulva* blooms (Granger et al., 2000; Thornber and Guidone,
112 unpublished data). Both Brushneck Cove and Chepiwanoxet are intertidal mud flats bordered by
113 fringing salt marshes; however, Chepiwanoxet has a longer water residence time (1.5 days versus
114 0.3 days), a greater mean depth, and experiences lower temperatures and a greater incidence of
115 hypoxic events (Granger et al., 2000; Thornber and Guidone, unpublished data). These sites were
116 contrasted to GSO and Pier 5 (Figure 1), which are near the mouth of Narragansett Bay and are
117 not impacted by annual *Ulva* blooms. GSO is a narrow beach of mixed sand and cobblestone,
118 while Pier 5 is a boulder field.

119 For comparison across seasons, additional surveys were conducted in February and May
120 2010 at all four sites. Monthly surveys were subsequently continued at the two bloom-impacted
121 sites from June 2010 to November 2011.

122 We conducted all surveys during spring low tides. For each survey, at each site, we
123 placed two 10 m transects parallel to the shore; transects were at least 30 m apart and placed at
124 the same tidal height. Transect positioning corresponded to the tidal height where *Ulva* wrack
125 was most commonly observed at low tide; this was directly below the fringing marsh at
126 Brushneck Cove and Chepiwanoxet, and directly above the waterline at GSO and Pier 5. For our
127 initial May-September surveys, we used a 0.25 m² quadrat to calculate the percent cover of all
128 algal taxa at one meter intervals along each transect, for a total of twenty replicate samples per
129 site and sampling month. Subsequent surveys assessed percent cover at two-meter intervals, for a
130 total of ten replicate samples per site and sampling month. Due to the overlap of macroalgal
131 thalli within drift mats, the total percent cover of all species often totaled more than 100%. Algae
132 were identified to the lowest taxonomic unit possible in the field. The *Ulva* blades within each

133 quadrat were collected and returned to the laboratory. Additionally, beginning in February 2010
134 we collected *Ulva* tubes from the bloom-impacted sites for biomass comparison to *Ulva* blades.
135 In the laboratory, we identified each blade to species using distinguishing cellular features
136 determined from molecularly confirmed voucher specimens (Guidone et al., unpublished data).
137 Following identification, blades were spun to a constant weight using a salad spinner and then
138 weighed.

139

140 *2.3 Statistical analyses*

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

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

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

157

158 **3. Results**

159 *3.1. Ulva species richness and relative abundance*

160 *Ulva lactuca* was the dominant blade forming *Ulva* species at non-bloom sites, while *U.*
161 *compressa* and *U. rigida* dominated at bloom sites. Overall, *Ulva* species biomass varied
162 significantly amongst sites and months (Table 1). In 2009-2010, *U. lactuca* was the only blade
163 species found at the non-bloom impacted Pier 5, with peak mean wet biomass of 75.48 g/m² in
164 May 2010 (Figure 2a). *Ulva lactuca* also dominated at GSO, where we only found small
165 fragments (< 0.4 g per piece) of *U. compressa* and *U. rigida* during three of the seven survey
166 months (Figure 2b).

167 In contrast, over the entire course of this study (2009-2011), *U. lactuca* was rarely found
168 at either of our bloom-impacted sites, while *U. compressa* and *U. rigida* were consistently
169 present at both sites (Figure 3). The mean *Ulva* biomass was significantly greater at Brushneck
170 Cove than the other three sites during 2009-2010 (Tukey post-hoc test, $p < 0.05$); there was no
171 significant difference in biomass between Brushneck Cove and Chepiwanoxet in 2010-2011
172 (Table 1b). Additionally, while we observed no impact of transect placement during our 2009-
173 2010 surveys, transect did have a significant impact on biomass at our bloom sites during 2010-
174 2011 (Table 1).

175 At both bloom-impacted sites, biomass consistently peaked during June-July with
176 subsequent crashes in August (Figure 3). One exception to this pattern occurred during 2009 at
177 Brushneck Cove, which saw continued high biomass through September 2009 (Figure 3b). Total

178 mean wet biomass was greatest during June 2009 (882.80 g/m²; maximum observation 1,662.24
179 g/m²) at Brushneck Cove and July 2010 (665.88 g/m²; maximum observation 1,804.60 g/m²) at
180 Chepiwanoxet.

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

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

191

192 3.2. Total macroalgal species richness and abundance

193 3.2.1. 2009-2010 survey

194 A total of 34 taxonomic groups were observed throughout our 2009-2010 surveys (Figure
195 4, Table 2). Species diversity (Shannon H') was highest at non-bloom Pier 5 and lowest at
196 bloom-impacted Brushneck Cove (Table 3; one-way ANOVA $F_{3, 456} = 91.40$, $p < 0.0001$, Tukey
197 post-hoc $p < 0.05$). However, no clear correlation between bloom-impacted and non-impacted
198 sites was evident, as diversity was higher at bloom-impacted Chepiwanoxet than at GSO. In
199 addition, evenness (Pielou's J') was highest at Chepiwanoxet. Of the 34 taxa recorded, 22 were
200 found at only one or both of the lower-bay sites (Table 2). No individual taxa were unique to the

201 two bloom-impacted sites; however, Chepiwanoxet was the only site that contained mats of
202 intertwined *Agardhiella subulata*, *Ceramium virgatum*, *Gracilaria* spp., and *Polysiphonia* spp.
203 (hereafter ACGP mats). While these mats could reach greater than 50% cover, the thalli within
204 them were often small fragments, making separation of the component species impracticable.
205 Therefore, we considered these mats as a unique entity for this study.

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

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

221

222 3.2.2. 2010-2011 survey of bloom-impacted sites

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

231

232 **4. Discussion**

233 *4.1. Ulva in Narragansett Bay*

234 *4.1.1. Species distribution*

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

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

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

253 One alternate explanation exists for the distributional pattern of *U. compressa*. Tan et al.
254 (1999) observed that distromatic blades of *U. compressa* were concentrated in low salinity areas
255 of an estuary in Aberdeenshire, Scotland, while *U. compressa* with a tubular morphology was
256 found at higher salinity sites near the North Sea. Taking this into consideration, it is possible that
257 *U. compressa* in Narragansett Bay persists in lower salinity eutrophic areas as a distromatic
258 blade and is present at lower bay and outer coast sites as a monostromatic tube. Although we did
259 not identify tubular *Ulva* to species in this survey, prior molecular analysis of outer coast
260 samples supports this hypothesis (Guidone et al., unpublished data).

261 In addition to abiotic factors, *Ulva* species distribution may be restricted by differences in
262 *Ulva* palatability and/or herbivore communities amongst the study sites. Nelson et al. (2008)
263 found that *Ulva* and *Ulvaria* (both in the family Ulvaceae) differed in abiotic tolerances and
264 palatability, causing the more palatable but stress tolerant *Ulva* to dominate intertidally while the
265 unpalatable *Ulvaria* thrived in the herbivore populated subtidal. Similarly, blooms in the Baltic
266 Sea were dominated by the unpalatable *Pilayella littoralis* when herbivores were abundant and
267 the palatable *Ulva intestinalis* when herbivores were absent or nutrient levels were enriched
268 (Lotze et al., 2000; Lotze and Worm, 2000). Although not directly quantified in this study, based

269 on previous studies and our own field observations, herbivore communities between our bloom
270 and non-bloom sites can be substantially different (Guidone et al., unpublished data).

271

272 *4.1.2. Bloom species relative abundance*

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

283

284 *4.2. Total macroalgal diversity at bloom and non-bloom sites*

285 As we had expected, Pier 5 had the highest diversity of the four sites sampled in 2009-
286 2010. This site is closest to the open coast and likely receives drift from a large area of the lower
287 Narragansett Bay and open ocean sites. Pier 5 also has an abundance of hard substrata available
288 for algal attachment, unlike the other three field sites.

289 Contrary to our expectations, we did not find a strict pattern of high diversity (H') at non-
290 bloom sites vs. low diversity at bloom-impacted sites, as Chepiwanoxet had the second highest
291 diversity of the four sites. This is particularly perplexing in light of environmental measurements

292 (dissolved oxygen, water residence time; Granger et al., 2000) that indicate Chepiwanoxet is the
293 most eutrophic of the four sites. Since the algae sampled at all sites was largely drift, it is unclear
294 whether the diversity observed at Chepiwanoxet is representative of the site itself, or if
295 circulation patterns deposit a wide diversity of species from adjacent areas. However, all areas
296 within close proximity to Chepiwanoxet are also bloom-impacted, suggesting that the diversity
297 observed at this site is truly representative of the bloom-impacted community. Furthermore,
298 Chepiwanoxet had the highest evenness of the four sites sampled from 2009-2010, which differs
299 from general patterns that indicate eutrophication has a larger negative impact on evenness than
300 species richness (Hillebrand et al., 2007). Similar results were found in subestuaries of Waquoit
301 Bay, Massachusetts, USA, where macroalgal bloom biomass (*Cladophora vagabunda* and
302 *Gracilaria tikvahiae*) was linked to nutrient enrichment, while species richness was not (Fox et
303 al., 2008).

304

305 4.3. Narragansett Bay blooms compared to *Ulva* blooms around the world

306 To our knowledge, this is the first report of *Ulva* bloom biomass that has extensively
307 examined the relative contribution of cryptically co-occurring distromatic blade species
308 following molecular confirmation of the *Ulva* species present within an area (Guidone et al.,
309 unpublished data). We are unaware of any previous estimates of *U. compressa* bloom biomass,
310 but reports of *Ulva* bloom biomass based solely on morphology have identified *U. rigida* as the
311 causative species of blooms in Europe (Sfriso et al., 1992; Coat et al., 1998; Balducci et al.,
312 2001; Merceron and Morand, 2004 as *U. armoricana*) and the Philippines (Largo et al., 2004 as
313 *U. armoricana*). *Ulva lactuca* has been reported to bloom in North America (Lyons et al., 2009),
314 New Zealand (Park, 1992), and South Africa (Anderson et al., 1996). The density of

315 Narragansett Bay blooms fall within the range of densities reported for most blooms of *U. rigida*
316 and *U. lactuca* (150-3,000 g/m² wet mass). One notable exception to this range is the bloom of
317 *U. rigida* in the Venice Lagoon, Italy, reported to have a biomass range of 5-20 kg/m² wet mass
318 (Schramm, 1999).

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

331

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342

343 **6. References**

- 344 Anderson, R.J., Monteiro, P.M.S., Levitt, G.J., 1996. The effect of localised
345 eutrophication on competition between *Ulva lactuca* (Ulvaceae, Chlorophyta) and a
346 commercial resource of *Gracilaria verrucosa* (Gracilariaceae, Rhodophyta).
347 *Hydrobiologia* 326/327, 291-296.
- 348 Balducci, C., Sfriso, A., Pavoni, B., 2001. Macrofauna impact on *Ulva rigida* C. Ag.
349 production and the relationship with environmental variables in the lagoon of Venice.
350 *Mar. Environ. Res.* 52, 27-49.
- 351 Berezina, N.A., Tsiplenkina, I.G., Pankova, E.S, Gubelit, J.I., 2007. Dynamics of
352 invertebrate communities on the stony littoral of the Neva Estuary (Baltic Sea) under
353 macroalgal blooms and bioinvasions. *Transitional Waters Bulletin* 1, 65-76.
- 354 Blomster, J., Bäck, S., Fewer, D.P., Kiirikki, M., Lehvo, A., Maggs, C.A., Stanhope,
355 M.J., 2002. Novel morphology in *Enteromorpha* (Ulvophyceae) forming green tides. *J.*
356 *Bot.* 89, 1756-1763.
- 357 Blomster, J., Maggs, C.A., Stanhope, M.J., 1999. Extensive intraspecific
358 morphological variation in *Enteromorpha muscoides* (Chlorophyta) revealed by
359 molecular analysis. *J. Phycol.* 35, 575-586.
- 360 Calabretta, C.J., Oviatt, C.A., 2008. The response of benthic macrofauna to

- 361 anthropogenic stress in Narragansett Bay, Rhode Island: a review of human stressors and
362 assessment of community conditions. *Mar. Pollut. Bull.* 56, 1680-1695.
- 363 Coat, G., Dion, P., Noailles, M.-C., de Reviers, B., Fontaine, J.-M., Berger-Perrot, Y.,
364 Loiseaux-de Goér, S., 1998. *Ulva armoricana* (Ulvales, Chlorophyta) from the coasts of
365 Brittany (France). II. Nuclear rDNA ITS sequence analysis. *Eur. J. Phycol.* 33, 81-86.
- 366 Cohen, R.A., Fong, P., 2004. Physiological responses of a bloom-forming green
367 macroalga to short-term change in salinity, nutrients, and light help explain its ecological
368 success. *Estuaries* 27, 209-216.
- 369 Deacutis, C., 2008. Evidence of ecological impacts from excess nutrients in upper
370 Narragansett Bay, In: Desbonnet, A., Costa-Pierce, B.A. (Eds.), *Science for Ecosystem-*
371 *Based Management*. Springer, New York, pp. 349-381.
- 372 Deacutis, C., Murray, D., Prell, W., Saarman, E., Korhun, L., 2006. Hypoxia in the
373 upper half of Narragansett Bay, RI, during August 2001 and 2002. *Northeast. Nat.* 13,
374 173-198.
- 375 Eklund, B., Svensson, A.P., Jonsson, C., Malm, T., 2005. Toxic effects of
376 decomposing red algae on littoral organisms. *Estuar. Coast. Shelf S.* 62, 621-626.
- 377 Fletcher, R.L., 1996. The occurrence of green tides -- a review, In: Schramm, W.,
378 Niehuis, P.K. (Eds.), *Marine benthic vegetation: recent changes and the effects of*
379 *eutrophication*. Springer, Berlin, pp. 7-43.
- 380 Fox, S.E., Stieve, E., Valiela, I., Hauxwell, J., McClelland, J., 2008. Macrophyte
381 abundance in Waquoit Bay: effects of land-derived nitrogen loads on seasonal and multi-
382 year biomass patterns. *Estuar. Coast.* 31, 532-541.
- 383 Gao, S., Chen, X., Yi, Q., Wang, G., Pan, G., Lin, A., Peng, G., 2010. A strategy for

- 384 the proliferation of *Ulva prolifera*, main causative species of green tides, with formation
385 of sporangia by fragmentation. PLoS ONE 5, e8571.
- 386 Granger, S.L., Mark, J., Buckley, B.A., Schwartz, M., 2000. An assessment of
387 eutrophication in Greenwich Bay. Rhode Island Sea Grant, Narragansett.
- 388 Hauxwell, J., Cebrián, J., Furlong, C., Valiela, I., 2001. Macroalgal canopies
389 contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems.
390 Ecology 82, 1007-1022.
- 391 Hauxwell, J., McClelland, J., Behr, P.J., Valiela, I., 1998. Relative importance of
392 grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries.
393 Estuaries 21, 347-360.
- 394 Hayden, H.S., Blomster, J., Maggs, C.A., Silva, P.C., Stanhope, M.J., Waaland, J.R.,
395 2003. Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera. Eur.
396 J. Phycol. 38, 277-294.
- 397 Heesch, S., Broom, J.E.S., Neill, K.F., Farr, T.J., Dalen, J.L., Nelson, W.A., 2009.
398 *Ulva*, *Umbraulva*, and *Gemina*: genetic survey of New Zealand taxa reveals diversity and
399 introduced species. Eur. J. Phycol. 44, 143-154.
- 400 Hein, M., Pedersen, M.F., Sand-Jensen, K., 1995. Size dependent nitrogen uptake in
401 micro- and macroalgae. Mar. Ecol. Prog. Ser. 118, 247-253.
- 402 Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E.S., Cleland, E.E., Elser, J.J.,
403 Harpole, W.S., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Consumer
404 versus resource control of producer diversity depends on ecosystem type and producer
405 community structure. P. Natl. Acad. Sci. 104, 10904-10909.
- 406 Hofmann, L.C., Nettleton, J.C., Neefus, C.D., Mathieson, A.C., 2010. Cryptic

- 407 diversity of *Ulva* (Ulvales, Chlorophyta) in the Great Bay Estuarine System (Atlantic
408 USA): introduced and indigenous distromatic species. *Eur. J. Phycol.* 45, 230-239.
- 409 Kim, J.-H., Kang, E.J., Park, M.G., Lee, B.-G., Kim, K.Y., 2011. Effects of
410 temperature and irradiance on photosynthesis and growth of a green-tide-forming species
411 (*Ulva linza*) in the Yellow Sea. *J. App. Phycol.* 23, 421-432.
- 412 Kraft, L.G.K., Kraft, G.T., Waller, R.F., 2010. Investigations in southern Australian
413 *Ulva* (Ulvophyceae, Chlorophyta) taxonomy and molecular phylogeny indicate both
414 cosmopolitanism and endemic cryptic species. *J. Phycol.* 46, 1257-1277.
- 415 Largo, D.B., Sembrano, J., Hiraoka, M., Ohno, M., 2004. Taxonomic and ecological
416 profile of 'green tide' species of *Ulva* (Ulvales, Chlorophyta) in central Philippines.
417 *Hydrobiologia* 512, 247-253.
- 418 Lee, V., Olsen, S., 1985. Eutrophication and management initiatives for the control of
419 nutrient inputs to Rhode Island coastal lagoons. *Estuaries* 8, 191-202.
- 420 Leliaert, F., Zhang, X., Ye, N., Malta, E., Engelen, A., Mineur, F., Verbruggen, H., De
421 Clerck, O., 2009. Research note: Identity of the Qingdao algal bloom. *Phycol. Res.* 57,
422 147-151.
- 423 Leskinen, E., Alström-Rapaport, C., Pamilo, P., 2004. Phylogeographical structure,
424 distribution and genetic variation of the green algae *Ulva intestinalis* and *U. compressa*
425 (Chlorophyta) in the Baltic Sea area. *Mol. Ecol.* 13, 2257-2265.
- 426 Littler, M.M., Littler, D.S., 1980. The evolution of thallus form and survival strategies
427 in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am.*
428 *Nat.* 116, 25-44.
- 429 Liu, D., Keesing, J.K., Dong, Z., Zhen, Y., Di, B., Shi, Y., Fearn, P., Shi, P., 2010.

- 430 Recurrence of the world's largest green-tide in 2009 in Yellow Sea, China: *Porphyra*
431 *yezoensis* aquaculture rafts confirmed as nursery for macroalgal blooms. Mar. Pollut.
432 Bull. 60, 1423-1432.
- 433 Lotze, H., Worm, B., Sommer, U., 2000. Propagule banks, herbivory and nutrient
434 supply control population development and dominance patterns in macroalgal blooms.
435 Oikos 89, 46-58.
- 436 Lotze, H.K., Worm, B., 2000. Variable and complementary effects of herbivores on
437 different life stages of bloom-forming macroalgae. Mar. Ecol. Prog. Ser. 200, 167-175.
- 438 Lyons, P., Thornber, C., Portnoy, J., Gwilliam, E., 2009. Dynamics of macroalgal
439 blooms along the Cape Cod National Seashore. Northeast. Nat. 16, 53-66.
- 440 Merceron, M., Morand, P., 2004. Existence of a deep subtidal stock of drifting *Ulva* in
441 relation to intertidal algal mat developments. J. Sea Res. 52, 269-280.
- 442 Morand, P., Merceron, M., 2005. Macroalgal population and sustainability. J. Coast.
443 Res. 21, 1009-1020.
- 444 Nelson, T.A., Haberlin, K., Nelson, A.V., Ribarich, H., Hotchkiss, R., Van Alstyne,
445 K.L., Buckingham, L., Simunds, D.J., Fredrickson, K., 2008. Ecological and
446 physiological controls of species composition in green macroalgal blooms. Ecology 89,
447 1287-1298.
- 448 Nelson, T.A., Lee, D.J., Smith, B.C., 2003a. Are "green tides" harmful algal blooms?
449 Toxic properties of water-soluble extracts from two bloom-forming macroalgae, *Ulva*
450 *fenestrata* and *Ulvaria obscura* (Ulvophyceae). J. Phycol. 39, 874-879.
- 451 Nelson, T.A., Nelson, A.V., Tjoelker, M., 2003b. Seasonal and spatial patterns of "green tides"

- 452 (ulvoid algal blooms) and related water quality parameters in the coastal waters of
453 Washington State, USA. *Bot. Mar.* 46, 263-275.
- 454 Oczkowski, A., Nixon, S., Henry, K., DiMilla, P., Pilson, M., Granger, S., Buckley, B.,
455 Thornber, C., McKinney R., Chaves, J., 2008. Distribution and trophic importance of
456 anthropogenic nitrogen in Narragansett Bay: an assessment using stable isotopes. *Estuar.*
457 *Coast.* 31, 53-69.
- 458 Park, S., 1992. *Ulva lactuca* monitoring programme. Bay of Plenty Regional Council,
459 Tech. Rep. 32.
- 460 Pedersen, M.F., Borum, J., 1996. Nutrient control of algal growth in estuarine waters.
461 Nutrient limitation and the importance of nitrogen requirements and nitrogen storage
462 among phytoplankton and species of macroalgae. *Mar. Ecol. Prog. Ser.* 142, 261-272.
- 463 Raffaelli, D., Raven, J.A., Poole, L.A., 1998. Ecological impact of green macroalgal
464 blooms. *Oceanogr. Mar. Biol.* 36, 97-125.
- 465 Rivers, J.S., Peckol, P., 1995. Summer decline of *Ulva lactuca* (Chlorophyta) in a
466 eutrophic embayment: interactive effects of temperature and nitrogen availability? *J.*
467 *Phycol.* 31, 223-228.
- 468 Schramm, W., 1999. Factors influencing seaweed responses to eutrophication: some
469 results from EU-project EUMAC. *J. App. Phycol.* 11, 69-78.
- 470 Sfriso, A., Pavoni, B., Marcomini, A., Orio, A.A., 1992. Macroalgae, nutrient cycles,
471 and pollutants in the Lagoon of Venice. *Estuar. Coast.* 15(4), 517-528.
- 472 Sousa, A.I., Martins, I., Lillebø, A.I., Flindt, M.R., Pardal, M.A., 2007. Influence of
473 salinity, nutrients and light on the germination and growth of *Enteromorpha* sp. spores. *J.*
474 *Exp. Mar. Biol. Ecol.* 341, 142-150.

- 475 Tan, I.H., Blomster, J., Hansen, G., Leskinen, E., Maggs, C.A., Mann, D.G., Sluiman,
476 H.J., Stanhope, M.J., 1999. Molecular phylogenetic evidence for a reversible
477 morphogenetic switch controlling the gross morphology of two common genera of green
478 seaweeds, *Ulva* and *Enteromorpha*. *Mol. Biol. Evol.* 16, 1011-1018.
- 479 Taylor, R., Fletcher, R.L., Raven, J.A., 2001. Preliminary studies on the growth of
480 selected 'green tide' algae in laboratory culture: effects of irradiance, temperature, salinity
481 and nutrients on growth rate. *Bot. Mar.* 44, 327-336.
- 482 Thomsen, M., McGlathery, K., 2006. Effects of accumulations of sediments and drift
483 algae on recruitment of sessile organisms associated with oyster reefs. *J. Exp. Mar. Biol.*
484 *Ecol.* 328, 22-34.
- 485 Underwood, A.J., 1997. *Experiments in ecology*. Cambridge University Press, Cambridge.
- 486 Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K., 1997.
487 Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem
488 consequences. *Limnol. Oceanogr.* 42, 1105-1118.
- 489 Van Alstyne, K.L., Nelson, A.V., Vyvyan, J.R., Cancilla, D.A., 2006. Dopamine
490 functions as an antiherbivore defense in the temperate green alga *Ulvaria obscura*.
491 *Oecologia* 148, 304-311.
- 492 Worm, B., Lotze, H.K., 2006. Effects of eutrophication, grazing, and algal blooms on
493 rocky shores. *Limnol. Oceanogr.* 51, 569-579.
- 494 Ye, N.-H., Zhang, X.-W., Mao, Y.-Z., Liang, C.-W., Xu, D., Zou, J., Zhuang, Z.-M.,
495 Wang, Q.-Y., 2011. 'Green tides' are overwhelming the coastline of our blue planet:
496 taking the world's largest example. *Ecol. Res.* 26, 477-485.
- 497 Yokoyama, H., Ishihi, Y., 2010. Bioindicator and biofilter function of *Ulva* spp.

498 (Chlorophyta) for dissolved inorganic nitrogen discharged from a coastal fish farm —
499 potential role in integrated multi-trophic aquaculture. *Aquaculture* 310, 74-83.
500
501
502

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

504

505 **Figure 2** *Ulva* biomass during the May-September 2009 and February and May 2010 surveys at

506 A) Pier 5 and B) GSO. Error bars are ± 1 SE.

507

508 **Figure 3** *Ulva* biomass at the two bloom-impacted sites A) Chepiwanoxet and B) Brushneck

509 Cove. Error bars are ± 1 SE.

510

511 **Figure 4** Algal percent cover at all sites during 2009-2010. Species comprising less than 10%

512 cover in all months are not shown. Site abbreviations follow Table 2. ACGP refers to mixed mats

513 of *Agardhiella subulata*, *Ceramium virgatum*, *Gracilaria* spp., and *Polysiphonia* spp. * indicates

514 no sampling due to ice cover.

515

516 **Figure 5** Algal percent cover at bloom-impacted sites during 2010-2011. Species comprising

517 less than 4% cover in all months are not shown. Site abbreviations follow Table 2. ACGP refers

518 to mixed mats of *Agardhiella subulata*, *Ceramium virgatum*, *Gracilaria* spp., and *Polysiphonia*

519 spp. * indicates no sampling due to storm surge.

520

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

524

525 (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		

526 **Table 2.** Taxa observed during our 2009-2010 field surveys. Site abbreviations are: P Pier 5, G GSO, C Chepiwanoxet, and B

527 Brushneck Cove. Genera marked with an asterisk require microscopic examination for species determinations.

528

	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
<i>Ulva</i> blades	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X		X	X		X	X			X	X	X	X
<i>Ulva</i> tubes	X	X	X	X	X	X	X		X	X	X		X	X	X		X				X				X	X	X	X
<i>Agardhiella</i> <i>subulata</i>									X				X				X				X	X			X			
<i>Ahnfeltia</i> <i>plicata</i>																					X							
<i>Ascophyllum</i> <i>nodosum</i>	X				X				X				X				X				X				X			
<i>Bonnemaisonia</i> <i>hamifera</i>					X				X	X															X			
<i>Bryopsis</i> <i>plumosa</i>									X				X															
<i>Ceramium</i> <i>virgatum</i>	X	X	X	X	X	X			X	X			X	X				X	X		X				X	X	X	X
<i>Chaetomorpha</i> spp.*									X	X			X															
<i>Champia</i> <i>parvula</i>									X	X																		
<i>Chondrus</i> <i>crispus</i>	X	X			X				X	X			X	X			X				X	X			X	X		
<i>Codium fragile</i> ssp. <i>fragile</i>	X								X	X			X	X			X				X	X						X
<i>Corallina</i> <i>officinalis</i>																					X							

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

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

530 **Table 3.** Average species richness (S), Pielou's evenness (J'), and Shannon diversity index (H')

531 for our 2009-2010 and 2010-2011 field surveys.

532

533

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

534

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

540

541 (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	

542

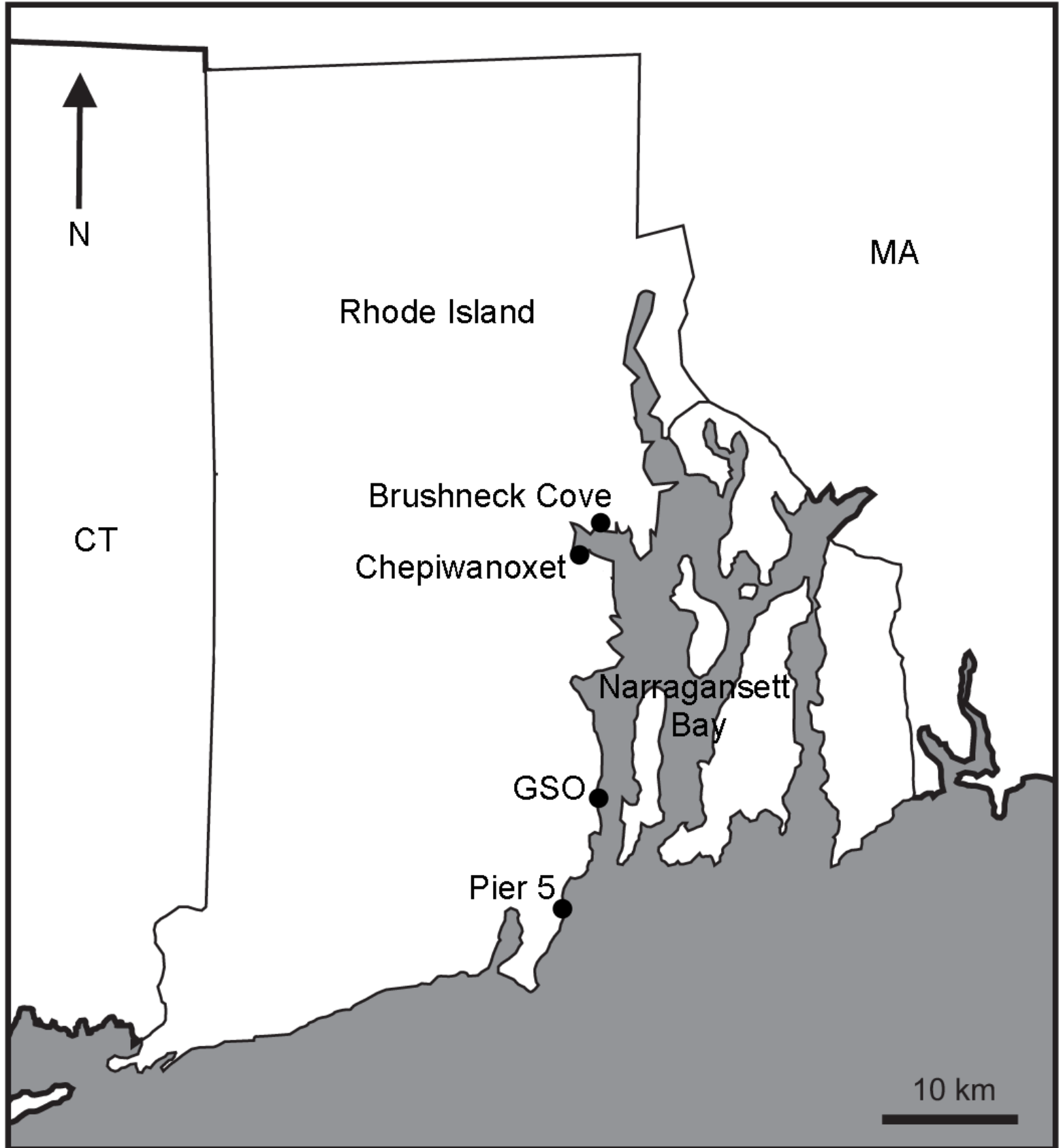
543 **Table 5.** Results from a two-way crossed SIMPER analysis for average similarity and
 544 dissimilarity amongst sites across all months in our 2009-2010 survey. ACGP refers to mats of
 545 intertwined *Agardhiella subulata*, *Ceramium virgatum*, *Gracilaria* spp., and *Polysiphonia* spp.
 546 Site abbreviations follow Table 2.
 547

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

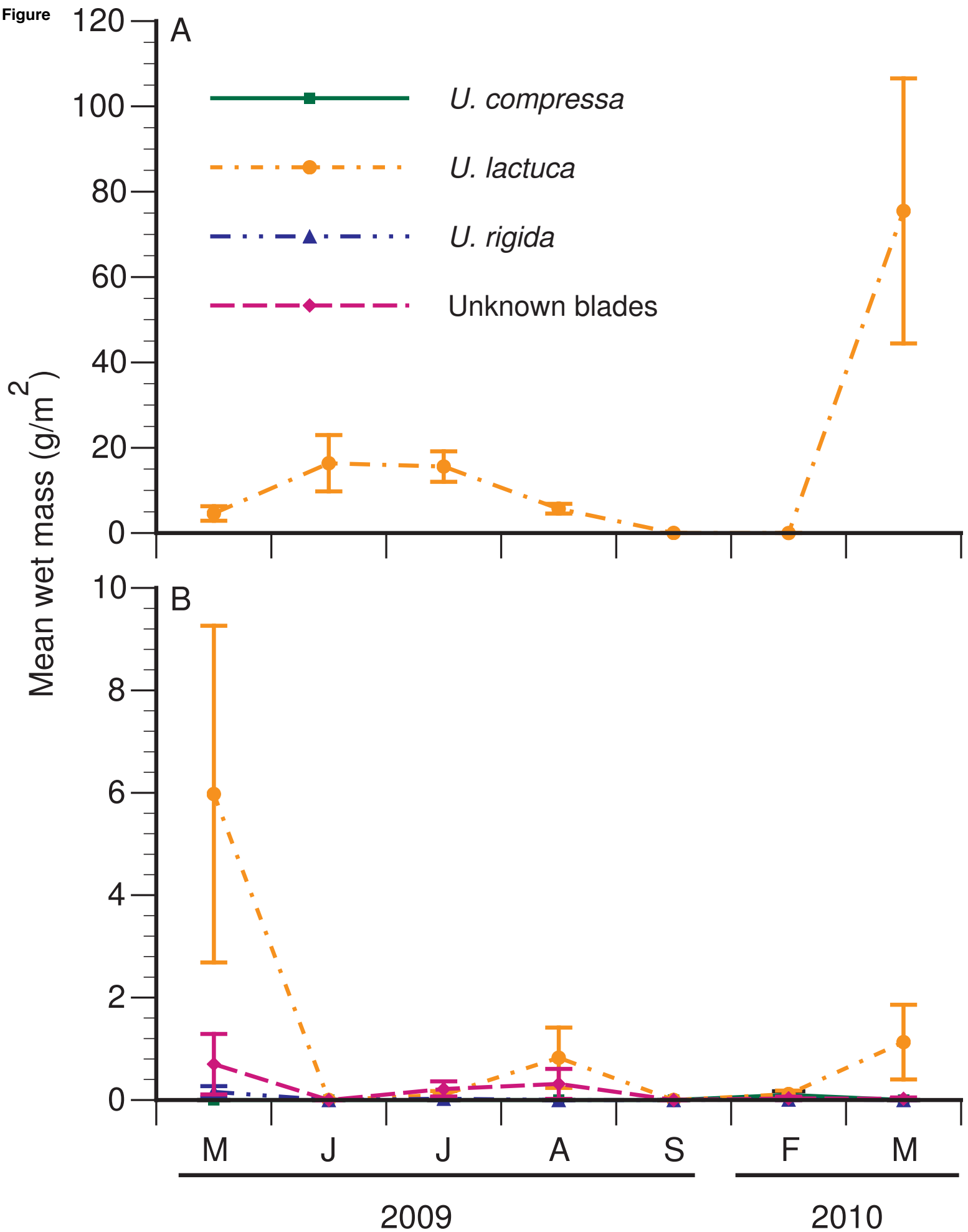
<i>Between site dissimilarity</i> Taxon	Percentage contribution to average dissimilarity between sites					
	B-C	B-G	B-P	C-G	C-P	G-P
<i>Ulva</i> blades	21.87	60.42	24.08	29.66	12.58	8.43
<i>Ulva</i> tubes	32.11	15.82	9.57	22.95	14.15	8.62
ACGP	24.52	-	-	14.94	10.24	-
<i>Ascophyllum nodosum</i>	-	-	-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

<i>Polysiphonia</i> spp.	-	5.14	4.53	4.62	3.65	2.49
<i>Porphyra</i> spp.	-	-	-	-	-	2.20
<i>Saccharina latissima</i>	-	-	10.81	-	7.84	15.75
<i>Ulothrix flacca</i>	-	-	-	-	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

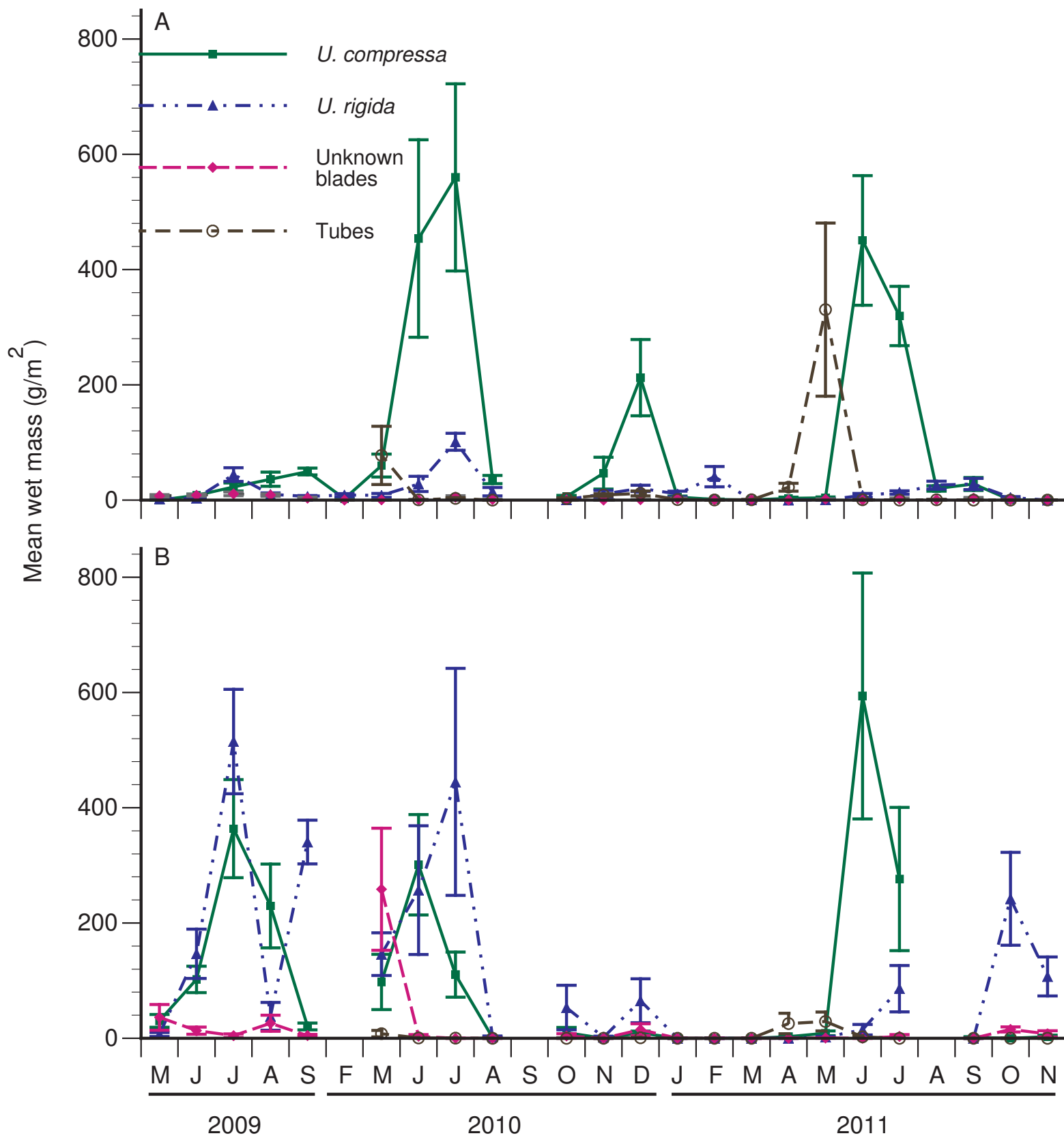
Figure 1



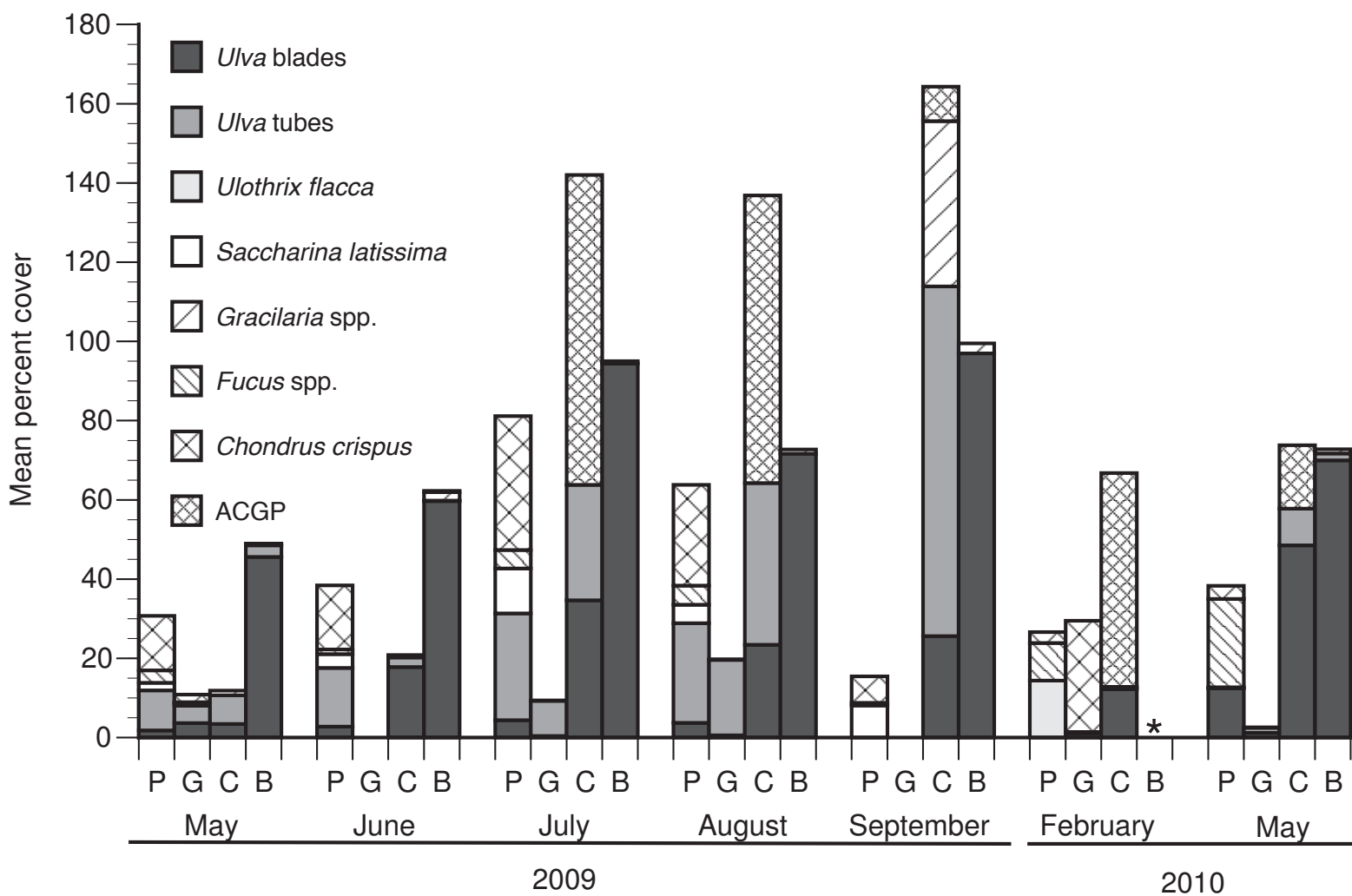
Figure



Figure



Figure



Figure

