

Macroalgal biodiversity of the Indian River Lagoon: updating the puzzle*

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Abstract Given the Indian River Lagoon (IRL)'s abundance of macroalgae and its rapidly changing environments, the establishment of a macroalgal biodiversity inventory and baseline is essential. Knowledge of IRL macroalgal biodiversity has grown considerably since 1994, when the initial IRL Biodiversity Conference was held, largely due to the 2008 publication of *Submersed Plants of the Indian River Lagoon* by Littler et al. 2008. A current list of macroalgal taxa is provided to encompass the taxonomic changes that have occurred since 2008. The number of macroalgal taxa has increased from 142 in 1994 to 207 in 2020 (an increase of 45.8%); rhodophytes increased from 74 to 110 (48.6%), chlorophytes from 45 to 61 (35.6%), and phaeophyceans from 23 to 36 (56.5%). Spatial and temporal trends in the IRL macroalgal community were analyzed from a data set collected contemporaneously (1994 – 1996; n = 1,042 samples) with the Biodiversity Conference. The macroalgal community was primarily composed of unattached, “drift” algae, with the rhodophyte *Gracilaria tikvahiae* the most abundant species (59% of biomass). Macroalgal abundance increased, with evidence of shifts in species composition, from north to south and no consistent temporal patterns. This study provides baseline data to determine long-term changes in community structure of IRL macroalgae and a call to address important research questions.

Keywords biodiversity, *Gracilaria tikvahiae*, Indian River Lagoon, macroalgae, seaweed

Introduction

The global significance and ecological importance of macrophytes, often called Submerged Aquatic Vegetation (SAV), in coastal and estuarine areas throughout the world is well-established (Dennison et al. 1993, Barbier et al. 2011, Fourqurean et al. 2012). Globally, macroalgae are the most productive marine macrophytes (Smith 1981, Duarte and Cebrián 1996). Macroalgal biomass provides significant food to herbivores and detritivores (Kang et al. 2008) and habitat for invertebrates, fishes, and marine mammals (Anderson 1994, Lippert et al. 2001, Rigby et al. 2007). Macroalgae are important in the carbon cycle (Smith 1981, Krause-Jensen and Duarte 2016) and have important roles in cycling nitrogen and phosphorus (McGlathery et al. 2004), serving as both nutrient sources and sinks (Hanisak 1993).

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* This paper is dedicated to the memory of Sherry Reed, who loved working on the macroalgae of the Indian River Lagoon.

The Indian River Lagoon (IRL), located along 251 km of the east-central coast of Florida, is an estuarine system known for its high biodiversity (e.g., Gilmore et al. 1983, Bulletin of Marine Science 1995). This richness is attributed to the IRL's geographical location, where warm temperate and tropical biota overlap, and to its diverse and complex macrophyte-defined habitats, which include seagrass beds, salt marshes, mangrove forests, and macroalgal communities. Scientists and resource managers recognize that macrophytes are a critical component of the Lagoon, playing an important role in biological productivity and species diversity. A macrophyte-based ecosystem was first identified as a high priority for the management of the IRL in the original goals of the IRL Surface Water Improvement and Management (SWIM) Plan (Steward et al. 1989):

- “Goal 1: To attain and maintain water and sediment of sufficient quality to support a healthy, macrophyte-based estuarine lagoon ecosystem
- Goal 2: To attain and maintain a functioning, macrophyte-based ecosystem which supports endangered and threatened species, fisheries, and recreation
- Goal 3: To achieve heightened public awareness and coordinated interagency management of the Indian River Lagoon ecosystem that results in the accomplishment of the two aforementioned goals”

This high priority has been recognized by agencies managing the Lagoon, including the Indian River Lagoon National Estuary Program (IRLNEP 1993, Steward et al. 1994, IRLNEP 2019).

While macrophyte research in the IRL has focused on seagrasses (e.g., Dawes et al. 1995, Steward et al. 1995, Vaslet et al. 2012), there are remarkably few studies on the marine algae of the central east coast of Florida. The earliest scientific macroalgal collections from this region were described by several distant phycologists based on materials from local collectors (Harvey 1852, 1853, 1858; Ashmead 1857a, b, 1858; Melville 1875, Farlow 1876; Howe 1903, 1904, 1905). William Randolph Taylor included collections from this area in his monographs (Taylor 1928, 1960), followed by Humm (1952), Stevenson and Stevenson (1952), and Jewett et al. (1976). The first inventories characterizing the diverse macroalgal flora of the IRL occurred 40 – 60 years ago, with a handful of collections mainly focused near the Fort Pierce and St. Lucie Inlets (Phillips and Ingle 1960, Phillips 1961, Eiseman and Benz 1975, Eiseman et al. 1978, Benz et al. 1979). The IRL macroalgal community consists primarily of unattached “drift algae” (macroalgae that are not attached to the substrate and are readily aggregated or dispersed by currents and winds) dominated by red algae, especially *Gracilaria* spp. (Benz et al. 1979, Eiseman and Gallaher 1979, Hall and Eiseman 1981, Virnstein and Carbonara 1985). Abgrall and Walters (2003) conducted monthly sampling of the abundance and diversity of drift macrophytes (macroalgae and seagrasses) in central Mosquito Lagoon for a two-year period and recorded 26 species; those authors found no consistent temporal patterns of macrophyte abundances. Breithaupt et al. (2019), also working in central Mosquito Lagoon, included macroalgae in their analysis of vegetative wrack accumulating on the shoreline;

those authors reported that red and green algae were most abundant in winter and spring, but negligible in the summer and fall.

At the 1994 Conference on the Biodiversity of the Indian River Lagoon (Bulletin of Marine Science 1995), there were no presentations on macroalgae, but later that year the author was asked by Dr. Hilary Swain to help assemble a macroalgal checklist as part of the initial IRL Species Inventory (now at irlspecies.org). That checklist was based on the literature above and other collections at the author's lab. A total of 142 species were included: 74 Rhodophyta (red algae), 45 Chlorophyta (green algae), and 23 Phaeophyceae (brown algae). It was evident that this checklist was just a start: "I hope you can appreciate the magnitude of the biodiversity problem, even for 'simple' species lists, for the algae ... what I have are pieces to the IRL macroalgal puzzle ..." (pers. comm. from M Dennis Hanisak to Hilary Swain, October 14, 1994). In 2008, after 8 years of collections and analyses, the book *Submersed Plants of the Indian River Lagoon* (Littler et al. 2008) was published, which provided a much more complete picture of IRL macroalgal biodiversity and demonstrated how little we knew about the flora. A total of 212 species of marine macroalgae were included and contained 130 new records for the IRL, of which 47 were new records for Florida and three were new records for the Western Atlantic.

This communication presents a current list of macroalgal taxa, updated with taxonomic revisions since Littler et al. (2008). In addition, spatial and temporal trends in the IRL macroalgal community were analyzed from a previously unpublished data set collected contemporaneously (1994 – 1996) with the initiation of the Species Inventory and the 1994 IRL Biodiversity Conference. That data set was collected as a small portion of a study to determine relationships of light attenuation, water quality, and SAV at stations representing a range of water quality conditions in the IRL (Hanisak 2001). The goal of this communication is to provide current insights into the "macroalgal puzzle" of the Lagoon, which can facilitate future research into this important, biodiverse group of organisms.

Materials and Methods

IRL Macroalgae: Current Taxonomic Checklist. Macroalgal biodiversity was assessed to address the focus of the Indian River Lagoon Symposium 2020, *Reassessing IRL Biodiversity*, specifically changes in the IRL's biodiversity since the 1994 Conference on the Biodiversity of the Indian River Lagoon. For the current compilation of macroalgal species, "macroalgae" were considered members of the three major, traditional taxonomic groups of macroscopically visible algae [Phylum Rhodophyta ("red algae"), Phylum Chlorophyta ("green algae"), and Class Phaeophyceae ("brown algae"), which is in Phylum Ochrophyta]. The initial source for the compilation was derived from Littler et al. (2008). Current nomenclature and distributions were determined by reviewing AlgaeBase (<https://www.algaebase.org/>), a global database of information on algae, and WoRMS (<http://www.marinespecies.org/>), a world register of marine species. To assess what more is known now about IRL macroalgal biodiversity since 1994, this checklist was compared to the one provided by the author to the initial IRL Species Inventory (pers. com. M Dennis Hanisak to Hilary Swain, October 14, 1994).

IRL Macroalgae: Spatial and Temporal Patterns. Spatial and temporal trends in the IRL macroalgal community were assessed and analyzed from a data set collected contemporaneously with the 1994 initiation of the Species Inventory and the 1994 IRL Biodiversity Conference (Hanisak 2001). Quarterly samples of the macroalgal community were collected over two years (1994 – 1996) at seven

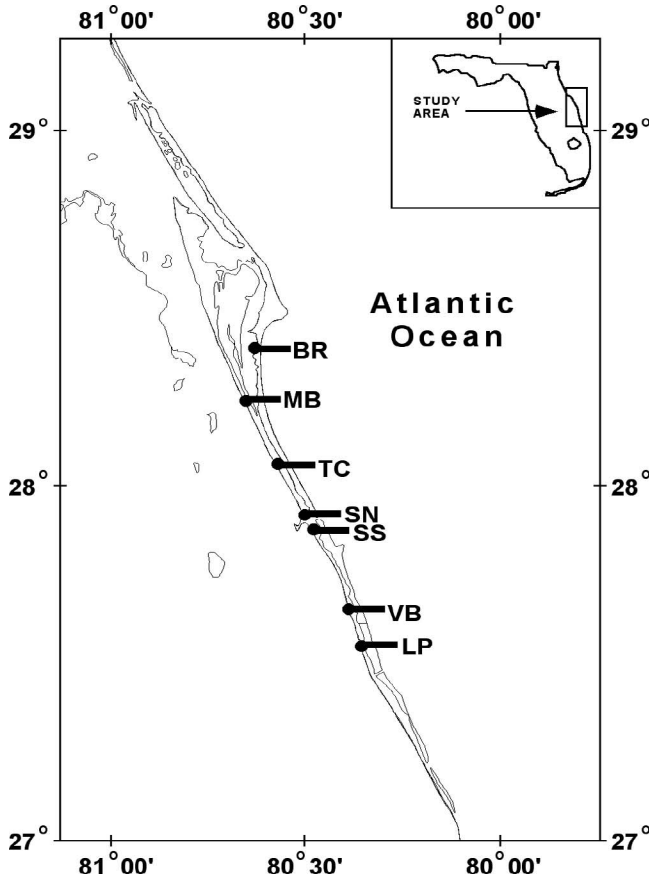


Figure 1. Location of Indian River Lagoon stations sampled in this study.

sites (Figure 1, Table 1). One station (VB) sampled in Year 1 was replaced in Year 2 by another station (TC) due to a change in the overall monitoring plan (Hanisak 2001). Thus, five stations were continuously monitored for 2 years, and two stations were monitored for 1 year each. The seven stations (Figure 1) were:

- BR (“Banana River”; 28° 30.34’ N, 80° 35.30’ W) was located in the northern Banana River, which, at the time, along with the northern region of the IRL proper and the southern Mosquito Lagoon, were generally considered to be the least impacted, most natural areas of the IRL system. This station had a well-developed, multi-species seagrass bed (primarily consisting of *Halodule wrightii* and *Syringodium filiforme*, with small quantities of *Halophila engelmannii*).
- MB (“Melbourne”; 28° 09.00’ N, 80° 38.11’ W) was located north of Eau Gallie Causeway on the western shore of the IRL in Melbourne, Brevard County. This station was selected to represent an area of stunted, sparse monospecific beds of *H. wrightii* and poor water quality.
- TC (“Turkey Creek”; 28° 01.89’ N, 80° 34.55’ W), monitored only during Year 2, was located south of Melbourne and south of Turkey Creek. Like MB, TC was in an area of sparse monospecific beds of *H. wrightii* and poor water quality.

Table 1. Dates of quarterly macroalgal samplings. VB was sampled only during 1994 and February 1995 and TC was sampled only during 1995 and February 1996. The total number of samples for the entire study was n = 1,042.

Sampling Event	Sampling Dates	Number of Samples per Station							
		BR	MB	TC	SN	SS	VB	LP	
February 1994	February 8 – 12, 1994	22	10	—	22	22	22	22	
April 1994	April 25 – 29, 1994	22	10	—	22	22	22	22	
August 1994	August 5 – 9, 1994	22	10	—	22	22	22	22	
November 1994	October 28 – November 3, 1994	22	10	—	22	22	22	22	
February 1995	January 30 – February 3, 1995	22	10	10	22	22	22	22	
May 1995	May 8 – 10, 1995	22	10	10	22	22	—	22	
August 1995	August 14 – 16, 1995	22	10	10	22	22	—	22	
November 1995	November 27 – 29, 1995	22	10	10	22	22	—	22	
February 1996	February 8 – 13, 1996	22	10	10	22	22	—	22	
	Station Totals	198	90	50	198	198	110	198	

- SN (“Sebastian-North”; 27° 51.81’ N, 80° 29.53’ W) and SS (“Sebastian-South”; 27° 50.98’ N, 80° 29.21’ W) were located on the western shore of the IRL, near the mouth of the Sebastian River, a tannic, nutrient-rich, freshwater system. Seagrasses at these stations consisted of nearly monospecific beds of *H. wrightii*, with traces of *S. filiforme* and *Halophila* spp.
- VB (“Vero Beach”; 27° 34.52’ N, 80° 21.51’ W), located near the southern end of Vero Beach on the western shore of the IRL, was sampled only during Year 1. This site, along with the next station (LP), were selected because they both were in lush, multi-species seagrass beds consisting of *H. wrightii*, *S. filiforme*, and *Thalassia testudinum*.
- LP (“Link Port”; 27° 32.10’ N, 80° 20.86’ W) was located at a site that probably has the greatest history of sampling anywhere in the IRL because of its proximity to Harbor Branch Oceanographic Institute.

Collectively, these stations encompassed considerable variability in SAV and water quality parameters within the IRL. BR was representative of conditions in the northern IRL; VB and LP were more representative of conditions in the southern IRL. Those three stations all had high-biomass seagrass beds. MB and, to a lesser extent, TC had small, low-density seagrass populations. The two Sebastian stations (SN, SS) facilitated the monitoring of the immediate impacts of freshwater inputs. Four stations (MB, TC, SN, SS) had monospecific (*H. wrightii*) beds; three stations (BR, VB, LP) had multiple seagrass species. *H. wrightii* was present at all stations.

There were nine quarterly samplings made over the two-year period (Table 1) along three permanently located transects. At each station, a permanent transect (Transect 1) was established perpendicular to the shoreline as a “Whole-bed Transect” and extended to just beyond the “deep edge” of the seagrass bed. Two additional transects, both 20-m long and perpendicular to Transect 1, were established at all stations but MB and TC. The rationale for these short transects was that one (“Transect 2”) was a “Mid-bed Transect” and the other (“Transect 3”) was at the “deep-edge” of the seagrass bed. At MB and TC, sampling by HBOI was limited to Transect 2 because of the small seagrass population, a minimal depth gradient along Transect 1, and no identifiable “deep edge”.

Sampling locations along transect lines were determined randomly by the generation of random numbers for each transect. For each station except MB and TC, 10 macroalgal samples were taken along Transect 1, and 6 each along Transects 2 and 3; more samples were taken along Transect 1 because of its greater length and depth gradient relative to the other transects (Table 1). At MB and TC, 10 samples were taken along Transect 2. Thus, for most stations, a total of 22 samples were taken, and at MB and TC, 10 samples were taken, for a total of 120 samples quarterly in Year 1 and 108 samples quarterly in Year 2. A total of 1,042 samples (Table 1) were collected and analyzed.

Macroalgal samples were collected with PVC corers (15.4 cm in diameter, 186 cm² in area, pushed deep enough to capture all seagrass rhizomes and roots), sieved on a 1-mm mesh sieve to remove sediment, placed in individual, labeled plastic bags on ice, and frozen at -20°C until processed. Total macroalgal biomass from the cores was sorted by species, dried at 80°C to constant weight, and weighed.

Data are presented as means \pm standard errors (SE). Statistical analyses were performed with SAS statistical software (SAS Institute 1988). Statistical significance among means was tested with analyses of variance (ANOVA, $\alpha = 0.05$). Data were transformed with the logarithmic (for biomass) or the arcsine transformation (for percent cover) (Sokal and Rohlf 1981) to meet the required assumptions of normality and homogeneity of variance prior to performing the ANOVAs. When ANOVA results were significant, the Tukey-Kramer post-hoc test (T-K) was used to identify pairwise differences among means.

Results

IRL Macroalgae: Current Taxonomic Checklist. The current compilation of Indian River Lagoon macroalgae (Table 2) is comprised of 207 species. Macroalgal biodiversity is dominated by rhodophytes (110 taxa, 53.1%) followed by chlorophytes (61 taxa, 29.5%) and phaeophyceans (38 taxa; 17.4%). Most of these taxa are warm-water cosmopolitan species, e.g., 88.9% of IRL macroalgal taxa reported in the Caribbean, 86.0% in the Gulf of Mexico, 81.6% in South America, 69.6% in Africa, and 70.0% in the Pacific Ocean. Some taxa appear to be quite capable of living in cooler waters: 55.1% of the IRL macroalgal taxa have been reported in North Carolina, 30.4% in New England, and 10.1% in the Arctic Ocean; future work with molecular tools may determine some of the latter records are indeed different species.

Largely due to the work of Littler et al. (2008), knowledge of IRL macroalgal biodiversity has grown considerably since 1994, when the initial IRL Biodiversity Conference (Bulletin of Marine Science 1995) occurred. The overall number of macroalgal taxa has increased from 142 taxa in 1994 to 207 in 2020 (an increase of 45.8%); rhodophytes increased from 74 to 110 (48.6%), chlorophytes from 45 to 61 (35.6%), and phaeophyceans from 23 to 36 (56.5%). Since Littler et al. (2008), there have been considerable systematic revisions to taxa that occur in the IRL. Due to synonymies, there are now three fewer taxa. The names of 24 taxa (17 rhodophytes, 5 chlorophytes, and 2 phaeophyceans) have changed (see dates listed for taxa in Table 2). There has been considerable revision in higher taxonomic ranks, too, with changes in families for 30 rhodophytes, 4 chlorophytes, and 2 phaeophyceans, and changes in orders for 4 rhodophytes, 1 chlorophyte, and 1 phaeophycean.

IRL Macroalgae: Spatial and Temporal Patterns. The grand mean macroalgal cover for all stations sampled from 1994 – 1996 (Figure 2) was $15 \pm 1\%$, with the lowest mean at BR ($1 \pm 1\%$) and the highest mean at VB ($41 \pm 4\%$). The grand mean macroalgal biomass was 17.0 ± 2.0 g dry weight/m², almost all of which was composed of unattached, “drift” algae; 65% (11.0 ± 1.3 g dry weight/m²) of the total belonged to the red algal genus *Gracilaria*.

Macroalgal abundance increased along the north-south gradient of stations, ranging from 0.7 ± 0.2 g dry weight/m² at BR to 35.6 ± 6.4 and 41.5 ± 11.5 g dry weight/m² at LP and VB, respectively. There was evidence of shifts in species

Table 2. Updated compilation of Indian River Lagoon macroalgae (2020).

Phylum	Class	Order	Family	Species	Authors
Rhodophyta	Stylonematophyceae	Stylonematales	Stylonemataceae	<i>Sylozomena alsidii</i>	(Zanardini) K.M. Drew 1956
	Compsopogonophyceae	Erythropeletales	Erythrotrichiaceae	<i>Erythrotrichia carnea</i> <i>Porphyrostromium ciliare</i>	(Dillwyn) J. Agardh 1883 (Carmichael) M.J. Wynne 1986
	Bangiophyceae	Bangiales	Bangiaceae	<i>Bangia fuscopurpurea</i>	(Dillwyn) Lyngbye 1819
	Florideophyceae	Hildenbrandiales	Hildenbrandiaceae	<i>Hildenbrandia rubra</i>	(Sommerfelt) Meneghini 1841
		Colaconematales	Colaconemataceae	<i>Colaconema hypneae</i> <i>Colaconema saviatum</i>	(Børgesen) A.A. Santos & C.W.N. Moura 2010 (Meneghini) R. Nielsen 1994
		Corallinales	Corallinaceae	<i>Colaconema gracile</i> <i>Jania pedunculata</i> var. <i>adhaerens</i>	(Børgesen) Ateweberhan & Prud'homme 2005 (J.V. Lamouroux) A.S. Harvey, Woelkerling & Reviers 2020
			Lithophyllaceae	<i>Jania capillacea</i> <i>Amphiroa brasiliiana</i>	Harvey 1853 Decaisne 1842
			Mastoporaceae	<i>Titanoderma pustulatum</i>	(J.V. Lamouroux) Nägeli 1858
		Nemaliales	Liagoraceae	<i>Pneophyllum fragile</i> <i>Liagora ceranoides</i>	Kützting 1843 J.V. Lamouroux 1816
		Ceramiales	Callithamniaceae	<i>Aglaohammion cordatum</i> <i>Aglaohammion flexibile</i> <i>Aglaohammion halliae</i>	(Børgesen) Feldmann-Mazoyer 1941 N.E. Aponte & D.L. Ballantine 1995 (Collins) Aponte, D.L. Ballantine & J.N. Norris 1997
			Ceramiaceae	<i>Aglaohammion uruguayense</i> <i>Centroceras gasparrinii</i> <i>Centroceras minutum</i> <i>Centroceras</i> sp. <i>Ceramium cimbriticum</i> <i>Ceramium cimbriticum</i> f. <i>flaccidum</i> <i>Ceramium codii</i> <i>Ceramium diaphanum</i>	(W.R. Taylor) N.E. Aponte, D.L. Ballantine & J.N. Norris, 1994 (Meneghini) Kützting 1849 Yamada 1944 — H.E. Petersen 1924 (H.E. Petersen) G. Furnari & Serio 1996 (H. Richards) Mazoyer 1938 (Lightfoot) Roth 1806

Table 2. Continued.

Phylum	Class	Order	Family	Species	Authors
				<i>Gayliella flaccida</i>	(Harvey ex Kützing) T.O. Cho & L.J. Melvor 2008
				<i>Ceramium floridanum</i>	J. Agardh 1894
				<i>Ceramium leptozonum</i>	M. Howe 1918
				<i>Ceramium nitens</i>	(C. Agardh) J. Agardh 1851
				<i>Ceramium subtile</i>	J. Agardh 1851
				<i>Ceramium</i> sp.	—
	Callithamniaceae			<i>Crouania attenuata</i>	(C. Agardh) J. Agardh 1842
				<i>Spyridia clavata</i>	Kützing 1841
				<i>Spyridia filamentosa</i>	(Wulfen) Harvey 1833
				<i>Spyridia hypnoides</i>	(Bory de Saint-Vincent) Papenfuss 1968
				<i>Spyridia hypnoides</i> subsp. <i>complanata</i>	(J. Agardh) M.J. Wynne 1998
				<i>Caloglossa lepricuri</i>	(Montagne) G. Martens 1869
	Delesseriaceae			<i>Dasya abbotiana</i>	D.L. Ballantine & N.E. Aponte 2004
				<i>Dasya baillouviana</i>	(S.G. Gmelin) Montagne 1841
				<i>Dasya caribica</i>	Børgesen 1919
				<i>Dasya crouaniana</i>	J. Agardh 1890
				<i>Dasya harveyi</i>	Ashmead 1858
				<i>Dasya</i> sp.	—
				<i>Hypoglossum hypoglossoides</i>	(Stackhouse) Collins & Hervey 1917
				<i>Myriogramme prostrata</i>	(E. Y. Dawson, Neushul & Wildman) M.J. Wynne 1990
				<i>Anotrichium tenue</i>	(C. Agardh) Nägeli 1862
	Wrangeliaceae			<i>Composothamnion thuyoides</i>	(Smith) Nägeli 1862
				<i>Pleonosporium boergesenii</i>	(A.B. Joly) R.E. Norris 1985
				<i>Tiffaniella gorgonea</i>	(Montagne) Doty & Meñez 1960
				<i>Wrangelia argus</i>	(Montagne) Montagne 1856
				<i>Acanthophora muscoides</i>	(Linnaeus) Bory 1828
	Rhodomelaceae			<i>Acanthophora spicifera</i>	(M. Vahl) Børgesen 1910

Table 2. Continued.

Phylum	Class	Order	Family	Species	Authors
				<i>Acanthosiphonia echinata</i>	(Harvey) Savoie & G.W. Saunders 2018
				<i>Alsidium seaforthii</i>	(Turner) J. Agardh 1841
				<i>Alsidium triquetrum</i>	(S.G. Gmelin) Trevisan 1845
				<i>Bostrychia moritziana</i>	(Sonder ex Kützing) J. Agardh 1863
				<i>Bostrychia radicans</i>	(Montagne) Montagne 1842
				<i>Bostrychia tenella</i>	(J.V. Lamouroux) J. Agardh 1863
				<i>Bryocladia cuspidata</i>	(J. Agardh) De Toni 1903
				<i>Carradoriella demodata</i>	(Dillwyn) Savoie & G.W. Saunders 2019
				<i>Chondria atropurpurea</i>	Harvey 1853
				<i>Chondria baileyana</i>	(Montagne) Harvey 1853
				<i>Chondria capillaris</i>	(Hudson) M.J. Wynne 1991
				<i>Chondria collinsiana</i>	M. Howe 1920
				<i>Chondria dasyphylla</i>	(Woodward) C. Agardh 1817
				<i>Chondria littoralis</i>	Harvey 1853
				<i>Digenea simplex</i>	(Wulfen) C. Agardh 1822
				<i>Herposiphonia delicatula</i>	Hollenberg 1968
				<i>Herposiphonia parca</i>	Setchell 1926
				<i>Herposiphonia secunda</i>	(C. Agardh) Ambrom 1880
				<i>Laurencia filiformis</i>	(C. Agardh) Montagne 1845
				<i>Laurencia obtusa</i>	(Hudson) J.V. Lamouroux 1813
				<i>Laurencia</i> sp.	—
				<i>Melanohammus harveyi</i>	(Bailey) Diaz-Tapia & Maggs 2017
				<i>Polysiphonia atlantica</i>	Kapraun & J.N. Norris 1982
				<i>Polysiphonia binneyi</i>	Harvey 1853
				<i>Polysiphonia scopulorum</i>	Harvey 1855
				<i>Polysiphonia subtilissima</i>	Montagne 1840
				<i>Wilsonosiphonia howei</i>	(Hollenberg) D. Bustamante, Won & T.O. Cho 2017
				<i>Yuzurua poiteaui</i>	(J. V. Lamouroux) Martin-Lescambe 2010

Table 2. Continued.

Phylum	Class	Order	Family	Species	Authors
Gelidiales			Gelidiaceae	<i>Gelidium crinale</i>	(Hare ex Turner) Gaillon 1828
				<i>Gelidium floridanum</i>	W.R. Taylor 1943
				<i>Parviphyucus setaceus</i>	(Feldmann) J. Alfonso-Carrillo, M. Sanson, C. Sangil & T. Diaz-Villa 2007
			Pterocladaceae	<i>Pterocladiaella capillacea</i>	S.G. Gmelin) Santelices & Hommersand 1997
				<i>Hypnea cornuta</i>	(Kützing) J. Agardh 1851
				<i>Hypnea musciformis</i>	(Wulfen) J.V. Lamouroux 1813
				<i>Hypnea spinella</i>	(C. Agardh) Kützing 1847
			Cystocloniaceae	<i>Hypnea valentiae</i>	(Turner) Montagne 1841
				<i>Chondracanthus saundersii</i>	C.W. Schneider & C.E. Lane 2005
			Gigartineae	<i>Agardhiella subulata</i>	(C. Agardh) Kraft & M.J. Wynne 1979
<i>Meristotheca gelidium</i>	(J. Agardh) E.J. Faye & M. Masuda 2004				
Solieriaceae	<i>Solieria filiformis</i>	(Kützing) Gabrielson 1985			
	<i>Crassiphycus caudatus</i>	(J. Agardh) Gurgel, J.N. Norris & Fredericq 2018			
Gracilariales			<i>Crassiphycus secundus</i>	(Gurgel & Fredericq) Gurgel, J.N. Norris & Fredericq 2018	
			<i>Crassiphycus usneoides</i>	(C. Agardh) Gurgel, J.N. Norris & Fredericq 2018	
			<i>Gracilaria cervicornis</i>	(Turner) J. Agardh 1852	
			<i>Gracilaria damicornis</i>	J. Agardh 1852	
			<i>Gracilaria flabelliformis</i>	(P. Crouan & H. Crouan) Fredericq & Gurgel 2004	
			<i>Gracilaria hayi</i>	Gurgel, Fredericq & J.N. Norris 2004	
			<i>Gracilaria tikvahiae</i>	McLachlan 1979	
			<i>Gracilariopsis carolinensis</i>	L.M. Liao & Hommersand 2003	
			<i>Grateloupia filicina</i>	(J.V. Lamouroux) C. Agardh 1822	
			<i>Grateloupia gibbesii</i>	Harvey 1853	
Halymeniales			<i>Halymenia elongata</i>	C. Agardh 1822	
			<i>Halymenia floresii</i>	(Clemente) C. Agardh 1817	
			<i>Halymenia floridana</i>	J. Agardh 1892	

Table 2. Continued.

Phylum	Class	Order	Family	Species	Authors
Ochrophyta	Phacophyceae	Dictyotales	Rhodymeniaceae	<i>Botryocladia occidentalis</i>	(Borgesen) Kylin 1931
			Champiaceae	<i>Champia parvula</i>	(C. Agardh) Harvey 1853
			Lomentariaceae	<i>Champia parvula</i> var. <i>prostrata</i>	L.G. Williams 1951
				<i>Hooperia divaricata</i>	(Durant) M.J. Wynne, C.W. Schneider & G.W. Saunders 2019
			Dictyotaceae	<i>Canistrocarpus cervicornis</i>	(Kützing) De Paula & De Clerck 2006
				<i>Diczyopteris delicatula</i>	J.V. Lamouroux 1809
				<i>Diczyota caribaea</i>	Hörnig & Schmitter 1992
				<i>Diczyota humifusa</i>	Hörnig, Schmitter & Coppejans 1992
				<i>Diczyota menstrualis</i>	(Hoyt) Schmitter, Hörning & Weber-Peukert 1987
				<i>Diczyota pulchella</i>	Hörnig & Schmitter 1988
Sphacelariales	Sphacelariaceae	<i>Padina gymnospora</i>	(Kützing) Sonder 1871		
		<i>Padina pavonica</i>	(Linnaeus) Thivy 1960		
		<i>Spatoglossum schroederi</i>	(C. Agardh) Kützing 1859		
		<i>Stypodium zonale</i>	(J.V. Lamouroux) Papenfuss 1940		
		<i>Sphacelaria novae-hollandiae</i>	Sonder 1845		
		<i>Sphacelaria rigidula</i>	Kützing 1843		
		<i>Acinetospora crinita</i>	(Carmichael) Sauvageau 1899		
		<i>Acinetospora</i> sp.	—		
		<i>Feldmannia mitchelliae</i>	(Harvey) H.-S. Kim 2010		
		<i>Hincksia granulosa</i>	(Smith) P.C. Silva 1987		
Ectocarpales	Actinetosporaceae	<i>Hincksia onstowensis</i>	(Amsler & Kapraun) P.C. Silva 1987		
		<i>Hincksia ovata</i>	(Kjellman) P.C. Silva 1987		
		<i>Hincksia sandriana</i>	(Zanardini) P.C. Silva 1987		
		<i>Cladosiphon occidentalis</i>	Kylin 1940		
		<i>Hummia onusta</i>	(Kützing) J. Fiore 1975		
		<i>Kuetzingiella elachistaeformis</i>	(Heydrich) M. Balakrishnan & Kinkar 1981		
		<i>Ectocarpus siliculosus</i>	(Kuckuck) Gallardo 1992		
		var. <i>dasyacarpus</i>			
		<i>Ectocarpus siliculosus</i>	(Dillwyn) Lyngbye 1819		

Table 2. Continued.

Phylum	Class	Order	Family	Species	Authors			
Chlorophyta	Ulvoephyceae	Ulotrichales	Seytosiphonaceae	<i>Colpomenia simuosa</i>	(Mertens ex Roth) Derbès & Solier 1851			
				<i>Rosenvingea intricata</i>	(J. Agardh) Børgesen 1914			
				Scytothamiales	Fucales	Bachelotiaceae	<i>Rosenvingea sanctae-crucis</i>	Børgesen 1914
							<i>Bachelotia antillarum</i>	(Grunow) Gerloff 1959
				Sargassaceae	<i>Sargassum acinarium</i>	(Linnaeus) Setchell, 1933		
					<i>Sargassum bermudense</i>	Grunow 1916		
					<i>Sargassum cymosum</i>	C. Agardh 1820		
					<i>Sargassum filipendula</i>	C. Agardh 1824		
					<i>Sargassum fluitans</i>	(Børgesen) Børgesen 1914		
					<i>Sargassum natans</i>	(Linnaeus) Gaillon 1828		
					<i>Sargassum vulgare</i> var. <i>foliosissimum</i>	(J.V. Lamouroux) C. Agardh 1820		
					<i>Turbinaria turbinata</i>	(Linnaeus) Kuntze 1898		
					<i>Gayralia oxysperma</i>	(Kützing) K.L. Vinogradova ex Scagel & al. 1989		
					<i>Ulothrix flacca</i>	(Dillwyn) Thuret 1863		
					<i>Blidingia marginata</i>	(J. Agardh) P.J.L. Dangeard ex Bliding 1963		
					<i>Blidingia marginata</i>	(Nägeli ex Kützing) Kylin 1947		
				<i>Ulva chaetomorphaoides</i>	(Børgesen) H.S. Hayden, Blomster, Maggs, P.C. Silva, Stanhope & Waaland 2003			
				Ulvoaceae	<i>Ulva clathrata</i>	(Roth) C. Agardh 1811		
					<i>Ulva compressa</i>	Linnaeus 1753		
					<i>Ulva flexuosa</i>	Wulfen 1803		
<i>Ulva intestinalis</i>	Linnaeus 1753							
<i>Ulva lactuca</i>	Linnaeus 1753							
<i>Ulva linza</i>	Linnaeus 1753							
<i>Ulva paradoxa</i>	C. Agardh 1817							
<i>Ulva prolifera</i>	O.F. Müller 1778							
<i>Ulva pseudorotundata</i>	Cormaci, G. Furnari & Alongi 2014							
<i>Ulva rigida</i>	C. Agardh 1823							
<i>Ulvella lens</i>	P. Crouan & H. Crouan 1859							

Table 2. Continued.

Phylum	Class	Order	Family	Species	Authors
		Cladophorales	Anadyomenaceae	<i>Anadyomene stellata</i>	(Wulfen) C. Agardh 1823
			Cladophoraceae	<i>Chaetomorpha brachygona</i>	Harvey 1858
				<i>Chaetomorpha gracilis</i>	Kützing 1845
				<i>Chaetomorpha linum</i>	(O. F. Müller) Kützing 1845
				<i>Chaetomorpha minima</i>	Collins & Hervey 1917
				<i>Cladophora albida</i>	(Nees) Kützing 1843
				<i>Cladophora laetevirens</i>	(Dillwyn) Kützing 1843
				<i>Cladophora liniformis</i>	Kützing 1849
				<i>Cladophora prolifera</i>	(Roth) Kützing 1843
				<i>Cladophora vadorum</i>	(Areschoug) Kützing 1849
				<i>Cladophora vagabunda</i>	(Linnaeus) Hoek 1963
				<i>Lychaete pseudobainesii</i>	(C. Hoek & Searles) M.J. Wynne 2017
				<i>Rhizoclonium riparium</i>	(Roth) Harvey 1849
				<i>Bryopsis hypnoides</i>	J.V. Lamouroux 1809
				<i>Bryopsis pennata</i>	J.V. Lamouroux 1809
				<i>Bryopsis rhizophora</i>	M. Howe 1914
				<i>Trichosolen duchassaingii</i>	(J. Agardh) W.R. Taylor 1962
				<i>Caulerpa brachypus</i>	Harvey 1860
				<i>Caulerpa chemnitzia</i> var. <i>laetevirens</i>	(Montagne) Fernández-García & Riosmena-Rodriguez 2017
				<i>Caulerpa cupressoides</i>	(Vahl) C. Agardh 1817
	<i>Caulerpa fastigiata</i>	Montagne 1837			
	<i>Caulerpa mexicana</i>	Sonder ex Kützing 1849			
	<i>Caulerpa microphyta</i>	(Weber Bosse) Feldmann 1955			
	<i>Caulerpa prolifera</i>	(Forsskål) J.V. Lamouroux 1809			
	<i>Caulerpa sertularioides</i>	(S.G. Gmelin) M. Howe 1905			
	<i>Caulerpa verticillata</i>	J. Agardh 1847			
	Codiaceae		<i>Codium corticatum</i>	(Woodward) M. Howe 1911	
			<i>Codium intertextum</i>	Collins & Hervey 1917	
			<i>Codium ishmocladum</i>	Vickers 1905	
			<i>Codium taylorii</i>	P.C. Silva 1960	

Table 2. Continued.

Phylum	Class	Order	Family	Species	Authors
			Derbesiaceae	<i>Derbesia marina</i>	(Lyngbye) Solier 1846
				<i>Derbesia vaucheritiformis</i>	(Harvey) J. Agardh 1887
			Halimedaceae	<i>Halimeda discoidea</i>	Decaisne 1842
				<i>Halimeda incrassata</i>	(J. Ellis) J.V. Lamouroux 1816
				<i>Halimeda scabra</i>	M. Howe 1905
			Udoteaceae	<i>Batophora oerstedii</i>	J. Agardh 1854
				<i>Cladocephalus luteofuscus</i>	(P. Crouan & H. Crouan) Borgesen 1909
				<i>Penicillus capitatus</i>	Lamarck 1813
				<i>Udotea dixonii</i>	D.S. Littler & Littler 1990
				<i>Udotea flabellum</i>	(J. Ellis & Solander) M. Howe 1904
				<i>Udotea luna</i>	D.S. Littler & Littler 1990
			Polyphysaceae	<i>Acetabularia calyculus</i>	J.V. Lamouroux 1824
				<i>Acetabularia crenulata</i>	J.V. Lamouroux 1816
				<i>Acetabularia farlowii</i>	Solms-Laubach 1895
				<i>Acetabularia schenckii</i>	Möbius 1889

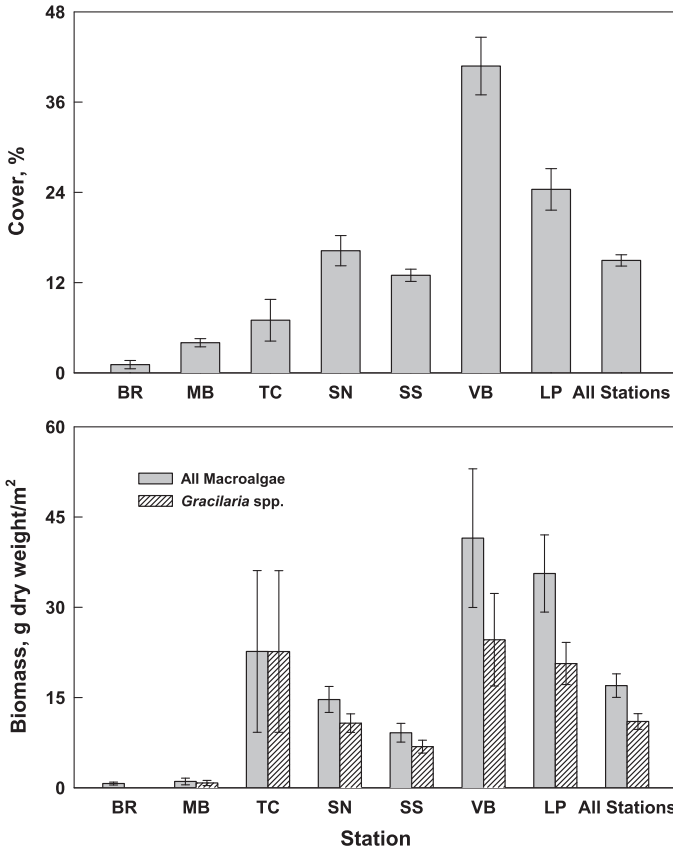


Figure 2. Station means (\pm SE) for cover and biomass of all macroalgae and biomass of *Gracilaria* spp.

composition along the north-south gradient, which was particularly noticeable for *Gracilaria*. No *Gracilaria* was collected at the northernmost station (BR), it was the only alga collected in measurable quantities at TC, and was higher at intermediate stations (MB, SN, SS; 73-76%) than at the southernmost stations (VB, LP; 58-59%).

Macroalgal cover, total macroalgal biomass, and *Gracilaria* biomass (Figure 3) increased along the north-south gradient of stations: lowest at BR and MB, highest at VB and LP, and intermediate at the other stations (ANOVA: $p = 0.0001$, T-K: $p < 0.05$). The only significant interannual differences occurred at LP (Figure 3), where macroalgal cover, total macroalgal biomass, and *Gracilaria* biomass were all higher in 1994 than in 1995 (ANOVA: $p = 0.0001$, 0.0004 , 0.0005 , respectively).

Despite strong seasonal patterns at individual stations, there was no consistent temporal pattern in macroalgal cover and biomass (Figure 4). At each station, the patterns of *Gracilaria* biomass and total macroalgal biomass were similar. Seasonal patterns at each station included:

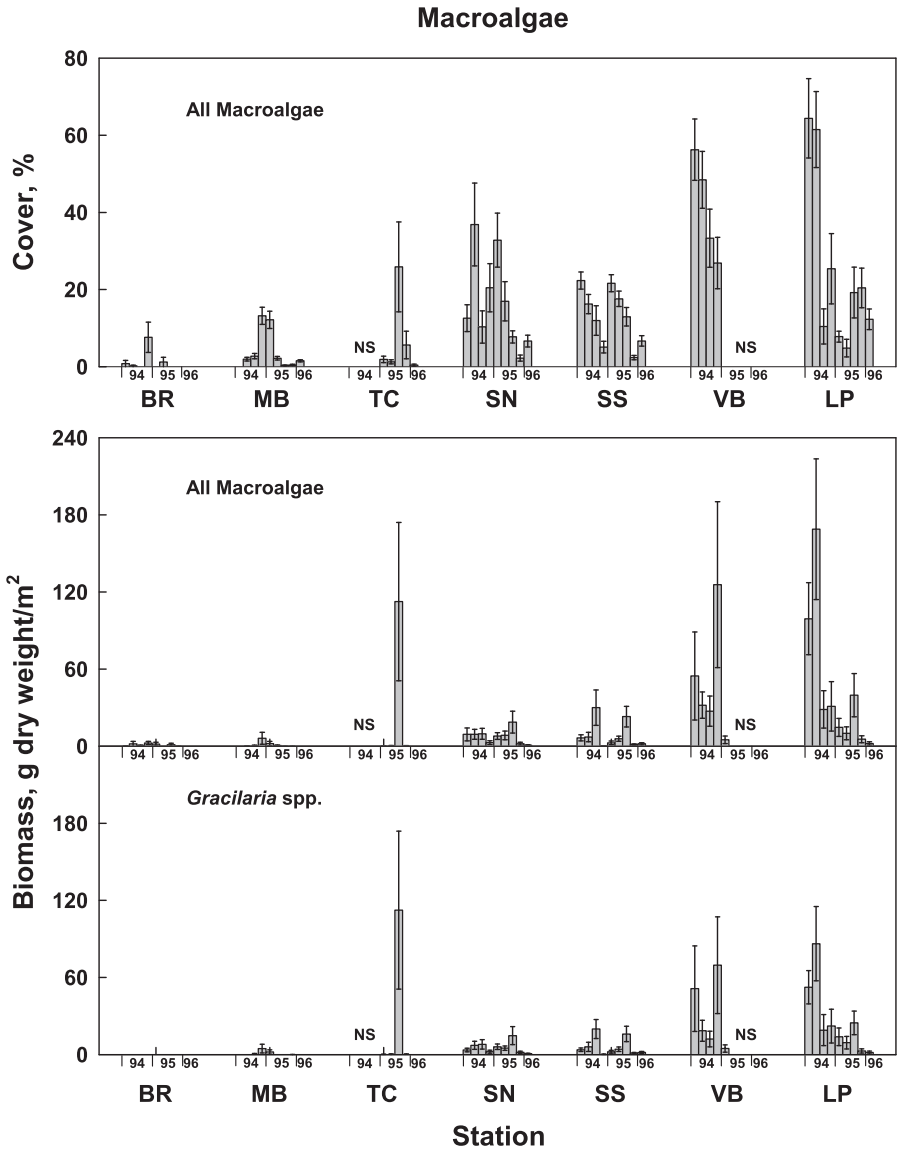


Figure 3. Cover and biomass of all macroalgae and biomass of *Gracilaria* spp. by station and season. Data are means (\pm SE); NS = not sampled (VB was sampled only during Year 1, TC only during Year 2).

- At BR, macroalgal cover was higher in November 1994 than in other months (ANOVA: $p = 0.01$; T-K: $p < 0.05$). Biomass was higher in November 1994 than in May 1995, November 1995, and February 1996 (ANOVA: $p = 0.02$; T-K: $p < 0.05$)
- At MB, macroalgal cover was highest in November 1994 and February 1995 (ANOVA: $p = 0.0001$; T-K: $p < 0.05$). Biomass was higher in November 1994

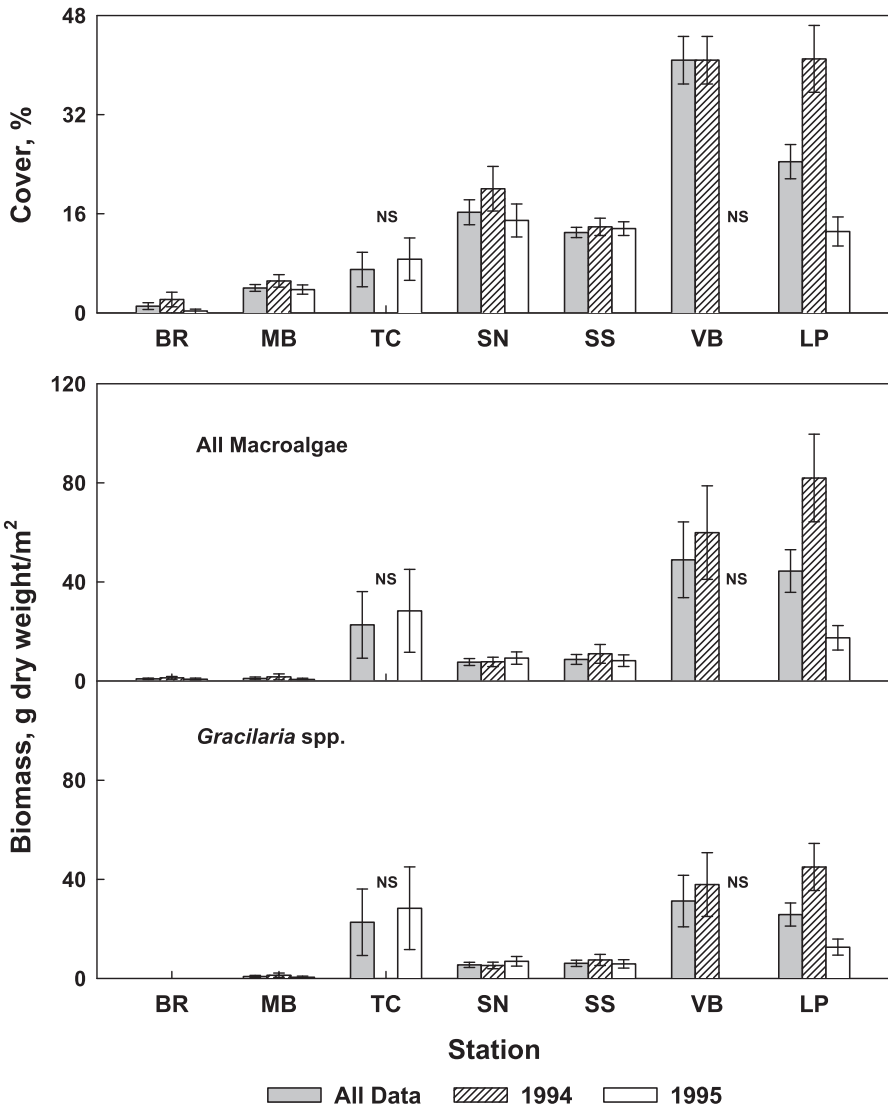


Figure 4. Interannual variation in cover and biomass of all macroalgae and biomass of *Gracilaria* spp., based on station means (\pm SE); NS = not sampled (VB was sampled only during Year 1, TC only during Year 2).

than February 1994, August 1995, November 1995, and February 1996 (ANOVA: $p = 0.02$; T-K: $p < 0.05$).

- At TC, macroalgal cover and biomass were higher in August 1995 than in all other months (ANOVA: $p = 0.001$; T-K: $p < 0.05$).
- At SS, macroalgal cover was highest in February 1994 and 1995 and lowest in August 1994, November 1994 and 1995, and February 1996 (ANOVA: $p =$

0.0001; T-K: $p < 0.05$). Biomass was higher in August 1994 and August 1995 than in November 1994 (ANOVA: $p = 0.0001$; T-K: $p < 0.05$).

- At VB, macroalgal cover was maximal in February 1994 and minimal in November 1994 (ANOVA: $p = 0.02$; T-K: $p < 0.05$). Biomass did not vary significantly among months (ANOVA: $p > 0.05$).
- At LP, macroalgal cover was higher in February 1994 and April 1994 than in all other months (ANOVA: $p = 0.0001$; T-K: $p < 0.05$). Biomass was higher in February 1994 and April 1994 than in February 1996 (ANOVA: $p = 0.0001$; T-K: $p < 0.05$).

The rhodophyte *Gracilaria tikvahiae* was the most abundant species of macroalgae (59% of the biomass). Five species were each responsible for 5-6% of total macroalgal biomass (in order from highest to lowest): *Hypnea spinella*, *Spyridia filamentosa*, *Crassiphycus secundus* (until 2018 = *Hydropuntia secunda*), *Spyridia hypnoides*, and *Cladophora prolifera*. Two species were each responsible for 1-2% of total macroalgal biomass (in order from highest to lowest): *Acanthophora spicifera* and *Yuzurua poiteaui* (until 2010 = *Chondrophycus poiteaui*). Finally, four species were each responsible for 0.3-0.6% of total macroalgal biomass (in order from highest to lowest): *Bryothamnion seaforthii*, *Agardhiella subulata*, *Caulerpa prolifera*, and *Hypnea musciformis*.

Among the abundant species, there were conspicuous spatial patterns along the north-south gradient of the IRL, but less consistent temporal (seasonal) patterns (Figure 5). *G. tikvahiae*, the most abundant species, was widespread at the stations, with little temporal variation (Figure 5A). In contrast, *H. spinella* was more abundant at northern stations, and quite variable temporally (Figure 5B). *Spyridia filamentosa* and *S. hypnoides* exhibited a third spatial pattern of distribution (Figure 5C), being more abundant at BR and the two southernmost stations (VB and LP) and usually absent in between; *S. filamentosa* was more abundant than *S. hypnoides* at BR. Lastly, a fourth pattern (Figure 5D) was observed for the most common chlorophyte, *Cladophora prolifera*, which was most abundant at the Sebastian stations (SN and SS), to a lesser extent at the southern stations (VB and LP), and absent at the northern stations (BR, MB, and TC).

Discussion

This study provides a baseline to determine long-term changes in biodiversity and community composition of IRL macroalgae. The current checklist is a revision based on Littler et al. (2008), which was a major contribution to the assessment of IRL macroalgal biodiversity. Prior to that field guide, identification of IRL macroalgae was difficult, largely requiring the use of outdated and user-unfriendly monographs, without adequate keys and with limited collections from the IRL. With the information synthesized since the last IRL Biodiversity Conference (Bulletin of Marine Science 1995), it appears that in the IRL only the biodiversity of fish has been as well-documented (Gilmore et al. 1983) as the macroalgae. Although the status of macroalgal biodiversity is now better known, it is certainly still understated. For example, Littler et al. (2008) omitted a number of taxa due to

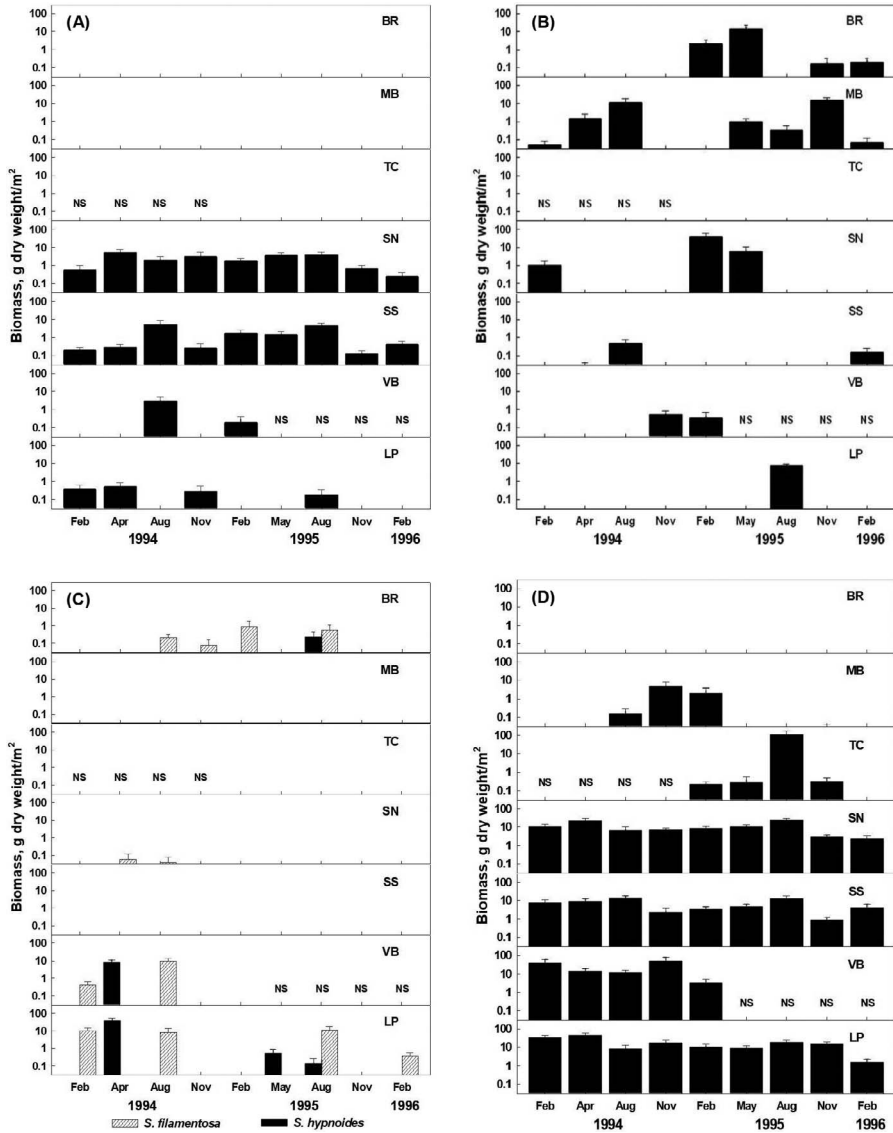


Figure 5. Seasonal variation in cover and biomass of selected abundant algae, (A) *Gracilaria tikvahiae*, (B) *Hypnea spinella*, (C) *Spyridia filamentosa* and *S. hypnoides*, and (D) *Cladophora prolifera*, based on station means (\pm SE); NS = not sampled (VB was sampled only during Year 1, TC only during Year 2).

the lack of quality photographs and illustrations, which are important features of that field guide, or lack of access to specimens of previously reported species that were not collected more recently. These are criteria also followed in the current communication. Moreover, new species and other systematic changes in the IRL flora will occur as more species that are cryptic are scrutinized with molecular

approaches, such as an analysis of the widespread phaeophycean *Lobophora variegata* that resulted in the identification of at least five cryptic new species in the Western Tropical and Subtropical Atlantic (Schultz et al. 2015).

Although it is clear that IRL macroalgae communities are highly variable in time and space, very few other studies have carefully dissected the IRL macroalgal community composition and measured biomass or productivities. Maximal biomass values reported in this study (123.0 ± 42.7 g dry weight/m², at LP in April 1994) were considerably higher than those reported from seagrass beds near the Fort Pierce Inlet (Benz et al. 1979), and are about 2.5 times higher than maximal bed-wise values reported previously at Link Port (Virnstein and Carbonara 1985). However, the seasonality of macroalgae at LP, with a winter maximum and summer minimum, agrees well with the previous study at this site (Virnstein and Carbonara 1985). The inverse pattern occurred in the northern Lagoon, but given the large amount of interannual variability that can occur at a single site (e.g., Virnstein and Carbonara (1985) observed a 25-fold increase between April maxima in successive years), the north-south gradient in macroalgal abundance and other perceived patterns should be confirmed with additional studies. Recent acoustic measurements in the northern IRL have demonstrated considerable spatial and temporal variability in seagrass and macroalgal biomass (Riegl et al. 2005, Foster et al. 2018), but no studies have been made at fine scales like the 1994 – 1996 data set in this communication.

Invasive species are a concern in IRL management (IRLNEP 2019); indeed, introductions of non-indigenous species to new ecosystems are considered one of the greatest threats to native marine biodiversity (Norse 1993, Carlton 2000). Marine macroalgae comprise a globally significant component of such introductions (Schaffelke 2006). Fortunately, this is not a major issue for IRL macroalgae to date. There is one invasive species, *Caulerpa brachypus*, a native of the Pacific Ocean likely introduced by the aquarium trade, that was discovered invading reef communities off Palm Beach County in 2001 (Jacoby et al. 2004, Lapointe et al. 2005). As *C. brachypus* spread northward, there were concerns that it would invade and spread throughout the Lagoon. However, after 20 years, it has only been occasionally found near the southern inlets of the IRL (Littler et al. 2008), and it does not seem able to live in the IRL itself, perhaps due to the lower salinity.

Macroalgae, such as members of the genus *Gracilaria*, have served as food for many coastal cultures since pre-history and are commercially valuable for a range of modern industrial uses. There has been a considerable amount of research conducted on IRL macroalgae for aquaculture applications that range from phycocolloid production to biofuels to human food, often with a bioremediation component, usually nutrient reduction (Hanisak 1987, 1990; Wills et al 2012, Laramore et al. 2016, Bianchine et al. 2019). The applications of this research that has demonstrated rapid growth rates and short generation times of macroalgae could readily be extended to IRL management issues. In short, IRL macroalgae are excellent indicators of environmental health and probes for experimental studies of ecosystems.

Although the species richness of marine macroalgae is high and their biochemical/physiological diversity is immense, macroalgae are quite underappreciated by researchers and managers. In the IRL, macroalgae are often overlooked because they are hard to sample and quantify given their “drift” nature. Research on IRL macroalgae has increasingly demonstrated their ecological importance and applications to management. For example, macroalgae are important in nutrient cycles, alternately acting as nutrient sources or sinks. Macroalgae assimilate and store large quantities of nutrients when ambient supplies are higher than what is required for growth (Hanisak 1983, Lavery and McComb 1991). When external nutrient levels are low, these internal reserves can sustain growth. Thus, macroalgae are nutrient sinks in the system. When seaweeds decompose, they become sources of nutrients to the system; if seaweeds are abundant, the timing and magnitude of their nutrient releases during decomposition are likely to be ecologically significant. Hanisak (1993) determined the release rates of nitrogen accumulated in *Gracilaria* and *Ulva* during decomposition, as well as the effects of temperature on those rates. That publication recommended that the release of stored nutrients from decaying macroalgae should be included in nutrient budgets and models. Such source-sink relationships are important ecologically and can be applied toward efforts to use macroalgae as environmental monitors of anthropogenic eutrophication and to cultivate macroalgae for the improvement of water quality.

These experiments from 25 years ago are readily applicable to the harmful algal blooms that have plagued the northern IRL for the last decade, leading to devastation of seagrass resources and triggering catastrophic fish kills and reductions in shellfish success (Gobler et al. 2013, Philips 2014). Curiously, the drift macroalgae community declined precipitously in summer-fall 2010, prior to the first major bloom in 2011 and subsequent seagrass decline, events that followed a period of extreme environmental variability. Hanisak (2016) conducted a series of single-factor and multi-factor experiments on the effects of extreme salinity, temperature, and low light levels on drift macroalgae in laboratory-controlled tanks. Results indicated that the most likely cause for this macroalgal die-off was low light availability. That macroalgae declined before seagrass reflects their much lower capacity for storing food reserves compared to seagrasses. Furthermore, nitrogen (N) and phosphorus (P) flux measurements demonstrated the ability of these macroalgae to act as important nutrient sinks and sources in the IRL system. When the macroalgae declined, they contributed significant amounts of N and P to the environment, which were then available to bloom-forming phytoplankton. Thus, disruption of the nutrient source-sink relationships of macroalgae have contributed to the development and persistence of the severe phytoplankton blooms in 2011.

While much attention has appropriately been paid to the importance of seagrass in estuarine waters, including the IRL, more work is needed to describe the spatial and temporal variability of macroalgae, to understand the causes of these variation, and to determine the consequences of such variability to other tropic levels and to biogeochemical cycles in these systems. A short list of needs that appear deceptively simple, but which will require much careful research to address includes:

- Better understanding of patterns of productivity and relationships to nutrients (nitrogen, phosphorus) – While we know a fair amount about growth responses for some of the major IRL macroalgae, that is largely based on measurements from closed systems. Can we do a better job of conducting *in situ* experiments that focus on how environmental factors determine macroalgal growth and productivity, especially with regard to the complexities of nitrogen and phosphorous cycling that is widely variable from season to season, year to year, place to place, due to the incredible temporal variability of conditions in the IRL?
- Better understanding of habitat value – While it is clear that macroalgae do have important habitat value in the IRL (e.g., Kulczycki et al. 1981, Virnstein and Carbonara 1985, Virnstein and Howard 1987, White and Snodgrass 1988), there is a persistent reluctance to consider it equally valuable to seagrass habitat, largely because macroalgae populations are more ephemeral than seagrasses. But with the near extinction of seagrass in a large part of the Lagoon (Morris et al. 2021, this issue), can other macrobenthic primary producers such as attached *Caulerpa*, serve at least as a temporary alternative to seagrasses until the latter can recover to their former preeminent role? Also important is to explore how different algal morphologies act as habitat for different fishes and invertebrates. If we lose one macroalgal taxon (or growth form), what co-occurring taxa would be affected?
- Better understanding of the “drift” of “drift” algae – Well documented by Kingsford (1995) in California, drifting macroalgae have been poorly studied but constitute important structures and increase habitat complexity in coastal waters. For example, in the IRL, we do not know to what extent aggregations of drift algae are due to localized growth versus accumulation from a much larger area. Can we better sample “drift algae” on appropriate spatial and temporal scales? Can we tag small clumps of macroalgae to see where they go?
- Better understanding of the interaction of macroalgae with seagrass – The relationships of macroalgae (be they drift or attached species) and seagrasses in the IRL are not well understood, but appear complex (Virnstein and Carbonara 1985, Taplin et al. 2005). Generally, macroalgae and seagrasses are considered to be competitors in the IRL. For example, when macroalgae are abundant, they can shade out seagrasses. However, seagrasses may actually facilitate drift algal growth by snagging small clumps and allowing them a foothold in a more productive location for growth. The apparent alternation of seasonal peaks in abundance between macroalgae and seagrasses, at least at some sites, is intriguing (Virnstein and Carbonara 1985; this communication); it is suggestive that the two major benthic autotrophic components of the IRL are able to optimize temporally for available resources to take advantage of different environmental conditions during the year. Is there an optimal level of macroalgae in a seagrass bed? Are there other positive synergies between macroalgae and seagrasses? Can the negative impacts of excessive macroalgae on seagrass be better quantified?
- Better understanding of the role of macroalgae in nutrient cycling – In addition to a better understanding of the source-sink relationships discussed above, more

work is needed to understand the differential responses (i.e., uptake, assimilation, growth) of individual species to different sources of nitrogen and phosphorus. How do specific human activities lead to different impacts on IRL macroalgae? One approach to address this question is the use of stable isotopes for tracking sewage nitrogen contamination of the IRL (Lapointe et al. 2015). Can we utilize what we know about the aquaculture of macroalgae from the IRL (Hanisak 1987, 1990) to reduce eutrophication?

What have we learned about macroalgal diversity in the IRL over the last quarter of a century? We know much more about macroalgal species composition. We are beginning to understand better that macroalgae play an important role in the Lagoon's ecology, with important management implications. However, much of the "macroalgal puzzle" remains to be solved. Hopefully, over the next 25 years, that puzzle will be much closer to solution. That will not be easy, given the challenges described above and the likely accelerating changes in the IRL environment. In addition to the current threats from the human population (e.g., eutrophication, habitat destruction, invasive species), the impacts of climate change that are now inevitable (e.g., sea level rise, coastal acidification, warmer winters) will fundamentally change the IRL as we knew it in 1994, and as we know it in 2020. Given the large reservoir of biodiversity in IRL macroalgae, it is likely that some species will increase in distribution and abundance while others will contract. Some species may disappear from the Lagoon due to changing conditions, while other species, including more exotic ones, may join the IRL flora. Will the puzzle actually be more complicated in 25 years than it is today?

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