Macroalgae at Gray's Reef National Marine Sanctuary, Georgia

Nisse A. Goldberg[1,*] and John N. Heine[1]

Abstract - Macroalgal assemblages were described from Gray's Reef National Marine Sanctuary (GRNMS), GA and compared to records from 25 years ago. For quantitative comparisons in species richness and biomass, divers collected algae from Searle's four northern sites and another four southern sites (*n* = six 400-cm^2 quadrats per site). To compare species richness among sites, algae were also collected across limestone reefs at each site, and any new species were added to those recorded from the quadrat samples. Of the 55 species identified, 8 were new GRNMS records, 4 were new records to Georgia, and 36 had been recorded previously. Nine species were present at all of the 8 sites. Although species richness per site was significantly greater in southern GRNMS, biomass and species richness per 400 cm^2 were similar between northern and southern sites. Sediment movement likely contributed to variability in species composition across the reefs.

Introduction

Gray's Reef National Marine Sanctuary (GRNMS), GA, is located 27 km offshore between the inner and middle continental shelf (Fig. 1). Due to its distance from the mainland, GRNMS is relatively undisturbed with respect to coastal anthropogenic influences. The sanctuary is valued by the public for its sand and reef habitats in depths of approximately 17–22 m. Of the 58-km^2 area in GRNMS, approximately 25% of the seafloor consists of rocky limestone reefs with ledges and low-lying platforms, and approximately 75% consists of unconsolidated sediment (Kendall et al. 2007). The reefs provide hard substrata for algae to colonize, although a layer of shell and sand of variable thickness is typically present (Kendall et al. 2007, Schneider and Searles 1991).

The macroalgae of GRNMS belong to the warm-temperate flora of the North Atlantic, extending from Cape Hatteras, NC to Cape Canaveral, FL (Searles 1984). In an effort to describe species richness, Searles (1987) conducted seasonal surveys of the macroalgae in GRNMS from 1983 to 1986, identifying 64 species from limestone ledges and adjacent platforms. Species richness and abundance were greatest in July through early August. Over winter months, a smaller number of perennial species are present (Searles 1988). Differences in algal diversity were likely related to temporal changes in water temperature and clarity, nutrient concentrations, seasonal storm events, and exposure to tropical and temperate water masses (Kendall et al. 2007).

The objectives of this study were to describe species richness of subtidal macroalgae in GRNMS and to compare present-day patterns to those of the 1980s collections (Searles 1987).

[1]Department of Biology and Marine Science, Jacksonville University, 2800 University Boulevard North, Jacksonville, FL 32211. [*]Corresponding author - ngoldbe@ju.edu.

Methods

Site description

To describe macroalgal species richness, surveys were conducted at four sites nearest to where Searles (1987) had sampled in the northern region and another four sites in the southern region of GRNMS (Fig. 1, Table 1). The collection sites were characterized by limestone reefs approximately 15 cm in height above the sandy bottom. Collections in 2011 were made in the summer months of June and July, when species richness is typically greatest (Searles 1987). Water temperatures in those months were 25.7–29.0 °C, with a mean of 27.3 °C (NOAA 2011). On the days that were sampled, water temperatures were 25.6 –26.0 °C.

Sampling

To estimate algal diversity as a function of biomass, 6 quadrats were placed haphazardly on limestone reefs at each of the eight sites. Given the small sizes of the algae (on average 2 cm tall, with an occasional alga approx. 10 cm tall) and low algal cover on the reef, a 400-cm^2 quadrat was considered appropriate to estimate relative abundance. All macroalgae were collected by hand and knife and then placed into 6 separate collecting bags. In an effort to collect species that may not

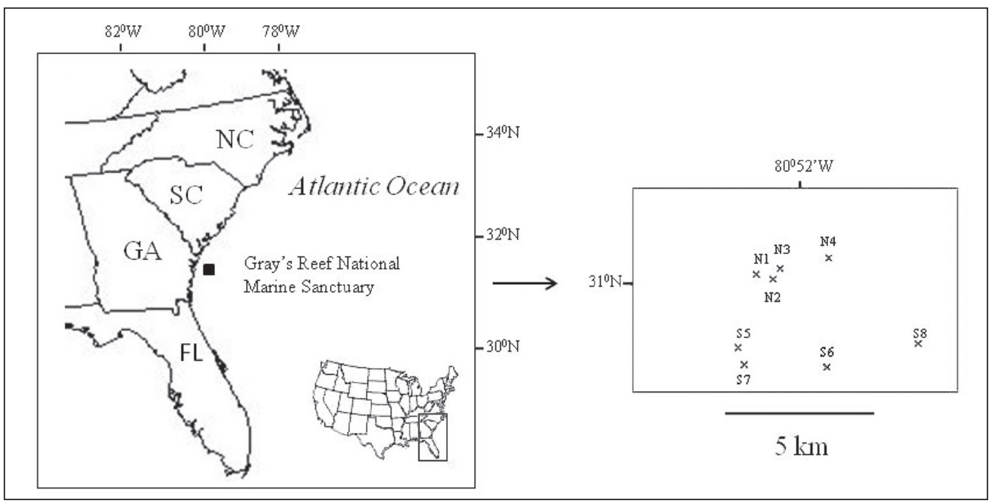

Figure 1. Gray's Reef National Marine Sanctuary off the coast of Georgia, showing the 4 northern and 4 southern study sites.

Table 1. Sites sampled at Gray's Reef National Marine Sanctuary, GA, in June and July 2011. North 1 through North 4 were sites that had been sampled by Searles (1987).

Site	Location	Sampling date	Depth (m)
North 1	31°23.773'N, 80°53.153'W	June 13	18.6
North 2	31°23.721'N, 80°52.832'W	June 13	19.5
North 3	31°23.882'N, 80°52.742'W	July 1	20.4
North 4	31°24.052'N, 80°51.900'W	July 1	19.5
South 5	31°22.517'N, 80°53.461'W	July 20	19.8
South 6	31°22.197'N, 80°51.937'W	July 20	20.1
South 7	31°22.240'N, 80°53.355'W	July 21	19.5
South 8	31°22.588'N, 80°50.372'W	July 21	20.7

have been present in the quadrat collections, divers randomly collected algae from an area of approximately 100 m^2 at each of the 8 sites. These qualitative samples were placed in a single bag and kept separate from the quadrat-level samples. Algae from both collections were kept frozen until processed. Thawed specimens provide sufficient detail for species identifications (Abbott and Hollenberg 1992).

Algae were sorted, and then each species was wet-weighed to the nearest 0.1 g. Trace amounts of a species (i.e., <0.1 g) were not included in biomass estimates. Macroalgae were identified to lowest taxonomic level, using the keys of Searles (1988) and Schneider and Searles (1991). Currently accepted species names and distributions were taken from the Web site Algaebase.com (Guiry and Guiry 2011) and Wynne (2011).

Two sets of data were used for analyses: 1. species richness and biomass per 400 cm^2 (n = 6 samples per site), and 2. species richness per site from the combined quadrat and reef collections. Summary data were reported as mean values ± 1 SE. To describe species frequency of occurrence across the GRNMS study sites, categories were based on the number of quadrats that each species was recorded: common (present in ≥50% of the 48 quadrats collected), occasional (<50% of the quadrats), and rare (present only from the diver survey collections). Searles (1987) reported three similarly named categories, but had not included definitions. Nested analysis of variance was used to compare species richness and biomass per 400 cm^2 between northern and southern locations. Sites were nested within location. Comparison in species richness per site was tested with a t-test, and the main factor was location. Assumptions of normality and heterogeneity of variances were met.

Results

Comparison of present-day species diversity with Searles (1987)

Fifty-five benthic algal species were recorded from the 8 sampling sites (Table 2). Thirty-six of the species were recorded from the areas sampled in the 1980s (Searles 1987). Eight species were new records for GRNMS, of which 4 were also new records for Georgia (denoted by *): **Agardhiella subulata*, **Agardhinula browneae*, **Erythrocladia endophloea*, *Bryopsis plumosa*, *Ceramium cimbricum*, *Chondria dasyphylla*, *Gracilariopsis hummi*, and **Lithothamnion occidentale* (Table 2; Guiry and Guiry 2011, Schneider and Searles 1991). *Callithamniella silvae*, an endemic to the sanctuary (Schneider and Searles 1991), was listed in Searles (1987) and collected in our surveys. *Sebdenia flabellata* was reported as common in Searles (1987), but was rare in the current study (Table 3). Eleven of the seventeen species that were not found in the present study were listed as rare in Searles (1987) (Table 3).

Comparisons in species richness and biomass per 400 cm²

No differences in species richness per 400 cm^2 were observed between the northern and southern locations. Instead, species richness per 400 cm^2 was significantly different among sites (Nested ANOVA: $F_{\text{site(location) } 6,40} = 8.05$, $P < 0.001$; $F_{\text{location}1,6} = 2.57$, $P = 0.160$; Fig. 2). Nine species were found at all 8 sites. *Champia parvula* var. *prostrata*, *Ceramium cimbricum* f. *flaccidum*, *Griffithsia globulifera*, and *Dictyota menstrualis* were the most common species in the

Table 2. Algal species present in GRNMS from Searles (1987) and 2011. New records to GRNMS are in bold and * denotes report of a new record for Georgia. Species frequency of occurrence (FOC) reported in Searles (1987) and from the 8 sites is listed with the following classifications: rare (R, only collected from reef surveys), occasional (O, collected from 1–23 quadrats across all sites), common (C, collected from 24–48 quadrats). ^{R} denotes reproductive and/or ^{E} epiphytic specimens were observed. The number in superscript designates the number of sites that each species was observed.

Species	Former species name in Searles (1987)	FOC (1987)	FOC (2011)
Acrochaetium bisporum (Børgesen) Børgesen	*Audouinella bispora* (Børgesen) Garbary	O	$O^{RE,4}$
Acrochaetium hoytii Collins	*Audouinella hoytii* (Collins) C.W. Schneid.	O	$O^{RE,4}$
***Agardhiella subulata* (C. Agardh) Kraft & M.J. Wynne**			**O^{1}**
***Agardhinula browneae* (J. Agardh) De Toni**			**$O^{R,3}$**
Aglaothamnion halliae (Collins) Aponte, D.L. Ballant.	*Aglaothamnion pseudobyssoides* (P. Crouan et H. Crouan) Halos	O	$O^{RE,7}$
Antithamnionella breviramosa (BertholdE.Y.Dawson) E.M.Woll.	*Antithamnionella spirographidis* (Schiffn.) E.M.Woll.	R	$O^{E,2}$
Asparagopsis taxiformis (Delile) Trev.	*Falkenbergia hillebrandii* (Bornet) Falkenb.	R	O^{1}
Boodleopsis pusilla (Collins) W.R. Taylor, A.B. Joly et Bernatowicz		C	O^{3}
Botryocladia occidentalis (Børgesen) Kylin		C	O^{6}
Botryocladia wynnei D.L. Ballant.		R	$O^{R,3}$
Branchioglossum minutum C.W. Schneid.		O	$O^{RE,3}$
***Bryopsis plumosa* (Huds.) C. Agardh**			**O^{4}**
Callithamniella silvae Searles	*Callithamnionella* sp.	R	$O^{E,6}$
Caulerpa mexicana Sond. ex Kütz.		R	O^{8}
***Ceramium cimbricum* H.E. Petersen**			**$O^{E,1}$**
Ceramium cimbricum f. *flaccidum* (H.E. Petersen) G. Furnari et Serio	*Ceramium fastigiatum* f. *flaccidum* H.E. Peterson	C	$C^{RE,8}$
Champia parvula var. *prostrata* L.G. Williams		C	$C^{R,8}$
***Chondria dasyphylla* (Woodw.) C. Agardh**			**$O^{R,2}$**
Cladophora dalmatica Kütz.		R	$O^{E,5}$
Cladophora laetevirens (Dillwyn) Kütz.		R	$O^{E,2}$
Cladophora pellucidoidea C. Hoek		O	$O^{E,5}$
Codium isthmocladum Vickers		C	O^{8}
Colpomenia sinuosa (Mert. ex Roth) Derbès et Solier		O	$O^{E,3}$
Dasya baillouviana (S.G. Gmel.) Mont.		R	$R^{R,1}$
Dictyopteris hoytii W.R. Taylor		O	$O^{R,4}$
Dictyota menstrualis (Hoyt) Schnetter, Hörnig., et Weber-Peukert	*Dictyota dichotoma* var. *menstrualis* Hoyt	C	$C^{R,8}$

Table 2, continued.

Species	Former species name in Searles (1987)	FOC (1987)	FOC (2011)
Dudresnaya crassa M. Howe		O	O^{2}
***Erythrocladia endophloea* M. Howe**			$\mathbf{O^{E,1}}$
Erythrotrichia carnea (Dillwyn) J.Agardh		R	$O^{E,6}$
Gracilaria blodgettii Harv.		R	O^{3}
***Gracilaria mammillaris* (Mont.) M. Howe**		**R**	$\mathbf{O^{R,4}}$
Gracilariopsis hummi Freshwater et Hommers.	*Gracilaria verrucosa* (Huds.) Papenf.		$O^{R,1}$
Griffithsia globulifera Harvey ex Kütz.		C	$C^{E,8}$
Griffithsia sp.			$O^{E,4}$
Grinnellia americana (C.Agardh) Harv.		O	R^{1}
Halymenia elongata C.Agardh	*Halymenia agardhii* De Toni	C	O^{7}
Halymenia brasiliensis S.M. Guim. et M.T. Fujii	*Halymenia floridana* J. Agardh	C	O^{7}
Halymenia hancockii W.R. Taylor		R	$O^{R,6}$
Hydrolithon farinosum (J.V.Lamour.) Penrose et Y.M.Chamb.	*Fosliella farinosa* (J.V. Lamour.) M. Howe	R	$O^{E,3}$
Hypoglossum hypglossoides (Stackh.) Collins et Herv.		C	$O^{R,6}$
Lejolisia exposita C.W. Schneid. et Searles	*Lejolisia* sp.	R	$O^{E,6}$
***Lithothamnion occidentale* (Foslie) Foslie**			$\mathbf{R^{3}}$
Lomentaria baileyana (Harv.) Farl.		C	$O^{R,8}$
Pneophyllum fragile Kütz.	*Pneophyllum lejolisii* (Rosanov) Y.M. Chamb.	R	$O^{R,2}$
Polysiphonia atlantica Kapraun et J.N.Norris		C	$O^{E,5}$
Polysiphonia schneideri Stuercke et Freshwater	*Polysiphonia denudata* (Dillwyn) Grev. ex Harv.	R	$O^{R,8}$
Rhodymenia pseudopalmata (J.V. Lamour.) P.C. Silva		O	O^{5}
Rosenvingea intricata (J. Agardh) Børgesen		R	O^{3}
Sahlingia subintegra (Rosenv.) Kormann	*Erythrocladia irregularis* f. *subintegra* (Rosenv.) Garbary, G.I. Hansen et Scagel	R	$O^{E,1}$
Sargassum filipendula C. Agardh		C	$O^{R,8}$
Scinaia complanata (Collins) Cotton		C	O^{4}
Sebdenia flabellata (J. Agardh) P.G. Parkinson	*Sebdenia polydactyla* (Børgesen.) M.S. Balakr.	C	R^{3}
Solieria filiformis (Kütz.) P.W. Gabrielson		R	$O^{R,4}$
Spatoglossum schroederi (C. Agardh) Kütz.		O	$O^{R,5}$
Stylonema alsidii (Zanardini) K.M.Drew		O	$O^{E,4}$

collections, being present in 47, 36, 30 and 26 of the 48 quadrats sampled, respectively (Table 2). The remaining five species—*Caulerpa mexicana*., *Codium*

Table 3. Species present in Searles (1987) but not collected in 2011.

Species	Former name in Searles (1987)	Abundance (Searles 1987)	Month of collection
Anotrichium tenue (C. Agardh) Näg.		R	July, Aug
Bryopsis pennata J.V. Lamour.		O	July, Aug
Chondria polyrhiza Collins et Herv.		C	June, Aug
Colaconema ophioglossum (C.W. Schneid.) Afonso-Carrillo, Sansón et Sangil	*Audouinella ophioglossa* C.W. Schneid.	C	July, Aug
Derbesia marina (Lyngb.) Solier		R	Aug
Derbesia turbinata M. Howe et Hoyt		R	Aug
Dipterosiphonia reversa C.W. Schneid.		R	July, Aug
Dudresnaya georgiana Searles		O	June, July, Aug
Dudresnaya puertoricensis Searles et D.L. Ballant.		C	July, Aug
Hincksia mitchelliae (Harv.) P.C. Silva	*Giffordia mitchelliae* (Harv.) Hamel	R	July
Hincksia onslowensis (Amsler et Kapraun)	*Giffordia onslowensis* Amsler et Kapraun	R	July
Leptophytum sp.		R	Aug
Onslowia endophytica Searles		C	July, Aug
Pleonosporium boergesenii (A.B. Joly) R.E. Norris		R	Aug, Sept
Predaea feldmannii Børgesen		R	July, Aug
Ptilothamnion occidentale Searles	*Ptilothamnion* sp.	R	July
Spyridia hypnoides (Bory) Papenf.		R	July, Aug

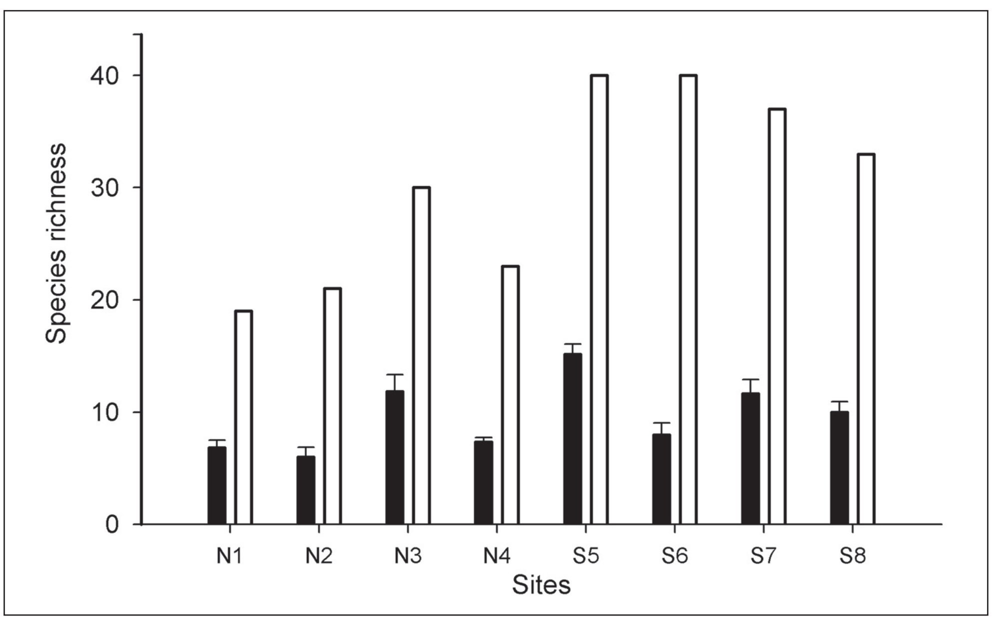

Figure 2. Comparison in species richness among northern and southern sites sampled in Gray's Reef National Marine Sanctuary, GA. Black column: mean species richness (+ 1 SE) per 400 cm^2 (n = 6 samples per site). White column: total species richness.

isthmocladum, *Lomentaria baileyana, Polysiphonia schneideri*, *Sargassum filipendula*—were present in fewer than 24 samples. The majority (69%) of species recorded were present in 10 or fewer quadrats (Table 2).

Biomass per 400 cm^2 was not significantly different between locations or among sites (Fig. 3) (Nested ANOVA: $F_{location1,6} = 3.45$, $P = 0.113$; $F_{site(location)\ 6,40} = 1.96$, $P = 0.095$). The North 1 site had the greatest biomass of 38.5 ± 8.6 g per 400 cm^2 due to *Champia parvula* var. *prostrata, D. menstrualis* and *Halymenia brasiliensis*. The North 4 site was more similar to the southern sites with lower mean biomass.

No species was consistently dominant with respect to mean biomass per 400 cm^2 across the 8 sites. Of the 9 species found at all 8 sites, only 2 species contributed a mean biomass ≥10.0 g per 400 cm^2 per site (Table 2). *Dictyota menstrualis* contributed a mean biomass of 10.5 ± 5.1 g and 12.8 ± 6.5 g per 400 cm^2 at North 2 and 3, respectively. *Sargassum filipendula* contributed a mean biomass of 10.9 ± 10.9 g per 400 cm^2 at North 1. At the same site, *C. parvula* var. *prostrata* had the greatest mean biomass of 9.5 ± 4.4 g per 400 cm^2. These 3 species each contributed <5.0 g per 400 cm^2 at the remaining sites. The other 6 common species contributed a mean biomass <1.0 g per 400 cm^2 per site. Of the occasional species that did contribute ≥10.0 g per 400 cm^2 in at least one site, *Botryocladia occidentalis* was present at 7 sites and contributed a mean biomass of 14.2 ± 7.0 g per 400 cm^2 at South 8. *Halymenia brasiliensis* was present at 7 sites and contributed a mean biomass of 12.2 ± 8.9 g at North 1 (Table 2). All other species contributed a mean biomass of <10 g per 400 cm^2 per site.

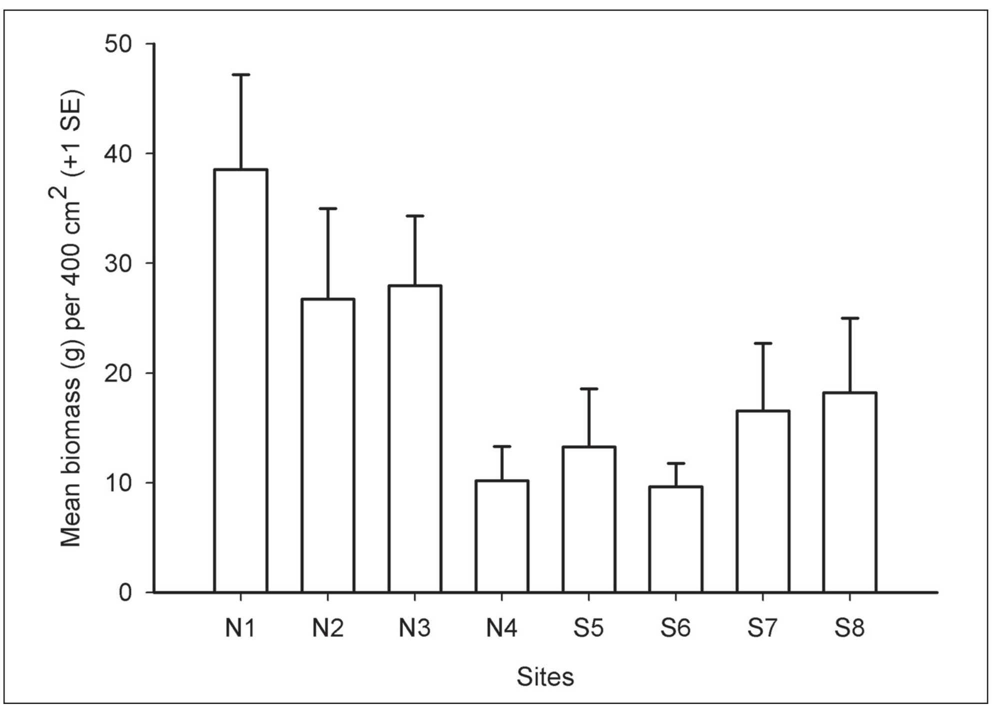

Figure 3. Comparison in mean biomass (+1 SE) per 400 cm^2 among northern and southern sites sampled in Gray's Reef National Marine Sanctuary, GA. *n* = 6 samples per site.

Comparisons in total species richness per site

Total species richness per site differed between the northern and southern locations of GRNMS (Fig. 2). Total species richness was based on the combined species lists from the 6 quadrat samples and reef collections per site. The southern sites had significantly greater numbers of species (35.2 ± 2.2 species) than the northern sites (20.7 ± 1.9 species; t-value = -4.99, $P = 0.004$, df = 5). Twelve species were found only at the southern sites, including 5 of the 8 new species records to GRNMS: *Botryocladia wynnei*, *Ceramium cimbricum*, *Colpomenia sinuosa*, *Erythrocladia endophloea*, *Hydrolithon farinosum*, *Gracilaria blodgettii*, *Gracilaria mammillaris*, *Gracilariopsis hummi*, *Grinnellia americana*, *Pneophyllum lejolisii*, *Rosenvingea intricata,* and *Sebdenia flabellata*. Three species were found only at the northern sites: *Chondria dasyphylla*, *Dudresnaya crassa*, and *Asparagopsis taxiformis*.

Discussion

Similarity in species recorded in the sanctuary to those from the 1980s collections (Searles 1987) provides support of a flora that is temporally persistent and spatially patchy in GRNMS. In addition, these algae are representative of the warm-temperate flora described by Searles (1984). No dominant alga was observed. Only 9 species were present at all 8 sites, and 50 species contributed less than 10.0 g per 400 cm^2. Peckol and Searles (1983) observed that on North Carolina reefs exposed to storm surge, no dominant alga was observed, and instead diversity was likely influenced by seasonal variability in propagule availability, colonization success, and ability to survive physical disturbances. Species that can grow above the sand layer (e.g., *Sargassum filipendula*), on other organisms as epiphytes (e.g., *Polysiphonia* spp., *Ceramium* spp., *Champia parvula*), or along the substratum with buried rhizomes and with upright fronds (e.g., *Caulerpa mexicana*) were representative of the algae at GRNMS. These growth strategies would help promote a resilient flora growing in an environment subjected to periodic scour and burial events.

Differences in species richness between Searles (1987) and the current study are due, in part, to changes in taxonomy and differences in collecting effort. Freeman et al. (2007) attributed changes in sponge taxonomy and collecting techniques to explain the significant differences between GRNMS collections from the early 1980s to those 25 years later. Of the species listed by Searles (1987), 20 algal taxa were revised or have been recently recognized (Wynne 2011). Eleven of the 17 species reported by Searles (1987) that were not found in the current study were reported as rare, although he used this measure qualitatively, and four were only recorded in August and September. Searles had surveyed repeatedly in the northern portion, sampling 3–7 times per site (Searles 1987). Although each site was sampled once in this study, 5 species that were new records to GRNMS were collected from the southern region. Increased survey efforts would produce a more comprehensive species list.

Disturbance from shifting sediments likely contributed to the low species occurrences on the low-lying reefs (Kendall et al. 2007, Searles 1987). Renaud et al. (1997) suggest that sediment movement in association with storm events may be responsible for temporal changes in algal diversity at Onslow Bay, NC. Intra-annual variability in the thickness of the sand layer ranged from 0 cm to a maximum of 10 cm at one site located in depths of 24.0–25.5 m (Renaud et al. 1997). Sediment movement remains to be studied at GRNMS.

Despite the persistent sand layer, the algae of GRNMS can respond with considerable growth that varies within and among years. Kendall et al. (2007) had observed significant differences in algal cover between August 2004 (mean cover of 0.6%) and 2005 (mean cover of 11.6%) surveys at GRNMS. Although temperatures have remained relatively consistent at the GRNMS oceanographic buoy (annual mean ± 1 SE = 21.5 ± 0.2 °C; NOAA 2011) during the years of 1988–1991 and 2000–2009, variability in water clarity may have contributed to differences in diversity. Algal biomass has been correlated with periods when the relatively clear water of the Gulf Stream was near GRNMS (Schneider and Searles 1991). At a broader scale, the estimated algal biomass at GRNMS (mean ± 1 SE = 500 ± 61 g/m^2) was comparable and similarly variable to that estimated along the continental shelf of North Carolina (June estimates: 372 ± 56 g/m^2; Schneider and Searles 1979).

The low species occurrences within and among sites, the greater species richness in the southern sites, and the considerable interannual differences in algal biomass (Kendall et al. 2007) highlight the need for more algal research at GRNMS. Although not addressed in this study, biological factors such as grazing by fishes, urchins, and other invertebrates may also impact species diversity, as reported from studies in Onslow Bay (Peckol and Searles 1983, Thomas and Cahoon 1993). If models that predict increases in the frequencies or relative intensities of storm and hurricane events as a function of climate change are correct (e.g., Bender et al. 2010), shifting sediments, variability in the thickness of the sand layer, and changes in water clarity will likely affect algal species diversity and also community dynamics (Renaud et al. 1996) even more in the years ahead. Future studies designed to monitor the same sites and correlate patterns in diversity to sediment movement, water quality, and biological factors would help elucidate the factors controlling algal diversity across GRNMS.

Acknowledgments

We thank the staff of the Gray's Reef National Marine Sanctuary and NOAA for providing vessel and diving assistance to support our work. We especially thank Greg McFall, Todd Recicar, Chris Briand, Sarah Fangman and Randy Rudd. Funding was provided by the PADI Foundation (award #5048) and Jacksonville University. We also thank the reviewers for their helpful comments.

Literature Cited

Abbott, I.A., and Hollenberg, G.J. 1992. Marine Algae of California. Stanford University Press, Stanford, CA.

Bender, M.A., T.R. Knutson, R.E. Tuleya, J.J. Sirutis, G.A. Vecchi, S.T. Garner, and I.M. Held. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science 22:454-458.

Freeman, C.J., D.F. Gleason, R. Ruzicka, R.W.M. van Soest, A.W. Harvey, and G. McFall. 2007. A biogeographic comparison of sponge fauna from Gray's Reef National Marine Sanctuary and other hard-bottom reefs of coastal Georgia, USA. Pp. 319–325, *In* M.R. Custódio, G. Lôbo-Hajdu, E. Hajdu, and G. Muricy (Eds.). Porifera Research: Biodiversity, Innovation and Sustainability. Série Livros 28, Museu Nacional, Rio de Janeiro, Argentina.

Guiry, M.D., and G.M. Guiry. 2011. AlgaeBase. Available online at http://www.algaebase.org. Accessed 17 August 2011.

Kendall, M.S., L.J. Bauer, and C.F.G. Jeffrey. 2007. Characterization of the benthos, marine debris, and bottom fish at Gray's Reef National Marine Sanctuary. NOAA Technical Memorandum NOS-NCCOS. No. 50. NOAA/National Centers for Coastal Ocean Science, Silver Spring, MD.

National Oceanic and Atmospheric Administration (NOAA). 2011. Station 41008 (LLNR 833) - GRAYS REEF - 40 NM Southeast of Savannah, GA. Available online at http://www.ndbc.noaa.gov/station_history.php?station=41008. Accessed 17 August 2011.

Peckol, P., and R.B. Searles. 1983. Effects of Seasonality and Disturbance on Population Development in a Carolina Continental Shelf Community. Bulletin of Marine Science 33:67–86.

Renaud, P.E., W.G. Ambrose, Jr., S.R. Riggs, and D.A. Syster. 1996. Multi-level effects of severe storms on an offshore temperate reef system: Benthic sediments, macroalgae, and implications for fisheries. Marine Ecology 17:383–398.

Renaud, P.E., S.R. Riggs, W.G. Ambrose, Jr., K. Schmid, and S.S. Snyder. 1997. Biological-geological interactions: Storm effects on macroalgal communities mediated by sediment characteristics and distribution. Continental Shelf Research 17:37–56.

Schneider, C.W., and R.B. Searles. 1979. Standing crop of benthic seaweeds on the Carolina continental shelf. Proceedings of the International Seaweed Symposium 9: 293–301.

Schneider, C.W., and R.B. Searles. 1991. Seaweeds of the Southeastern United States. Duke University Press, Durham, NC.

Searles, R.B. 1984. Seaweed biogeography of the mid-Atlantic coast of the United States. Helgoländer Meeresuntersuchungen 38:259–271.

Searles, R.B. 1987. Phenology and floristics of seaweeds from the offshore waters of Georgia. Northeast Gulf Science 9:99–108.

Searles, R.B. 1988. An illustrated field and laboratory guide to the seaweeds of Gray's Reef National Marine Sanctuary. NOAA Technical Mememo NOS MEMD, Vol. 22. US Department of Commerce, NOAA National Ocean Service, Office of Ocean and Coastal Resource Management, Washington, DC.

Thomas, C.J., and L.B. Cahoon. 1993. Stable isotope analyses differentiate between different trophic pathways supporting rocky reef fishes. Marine Ecology Progress Series 95:19–24.

Wynne, M.J. 2011. A checklist of benthic marine algae of the tropical and subtropical western Atlantic: Third revision. Nova Hedwigia, Beiheft 140:1–166.