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Seasonal and Spatial Variation in Algal Composition and Biomass on the Central Florida Gulf Coast Shelf

JANESSA COBB AND JOHN M. LAWRENCE

Information on primary producers is fundamental to the understanding of communities. Little is known about the primary producers of marine communities at intermediate depths on the Florida Gulf Coast shelf. The diversity and biomass of algae and seagrass were studied seasonally at three offshore sites (12- to 18-m depth) and one nearshore site (6-m depth) on the central Florida Gulf Coast shelf. Thirty-eight species of attached and drift macroalgae and one drifting seagrass, *Thalassia testudinum*, were found. The deepest collection site was the most productive in terms of standing biomass and had much more flora on limestone rubble than on sand. All other sites had relatively low floral biomass. Algal diversity varied considerably with season at 6- and 12-m depths, whereas a more stable diversity was observed at 18 m. Plant and algal communities in the Gulf of Mexico vary greatly between sites of different depths even when in close proximity. Intermediate depths contained lower algal biomass with more variable species composition over time than the deeper offshore sites.

Information on primary producers is fundamental to understanding energy transfer within communities. Data on subtidal flora at intermediate depths of the Florida Gulf Coast shelf are limited primarily to species lists (Dawes et al., 1967; Dawes and van Breedveld, 1969; Cheney and Dyer, 1974; Mathieson and Dawes, 1975). Although the species lists suggests seasonal variability, Dawes and Lawrence's study (1990) is the only report of seasonal variation in algal composition and biomass on the shelf. In their 2-yr study, biomass at a depth of 20 m was greater in the summer and could be completely absent in the winter as a result of hydrodynamics from storms. Variability over space and time is characteristic of environments such as the central Florida Gulf Coast shelf where considerable seasonal and annual variation in temperature and hydrodynamics occur. It is essential to know how much variation occurs in diversity and abundance of subtidal flora, including both macroalgae and seagrasses. Consequently, we provide data on the composition of the subtidal flora and its biomass near the same site studied by Dawes and Lawrence (1990) and at additional sites on the central Florida Gulf Coast shelf to document the variation that occurs between seasons, years, and locations.

MATERIALS AND METHODS

Field observations and collection.—Three offshore sites and one nearshore site along the central west coast of Florida were selected (Fig. 1). Observations were made and specimens collected at all sites using SCUBA.

Site 1 (28°8.56′N 83°8.82′W, depth 18 m): Site 1 was located approximately 35.7 km offshore of Clearwater, FL, and 3.6 km west of the sampling site used by Dawes and Lawrence (1990). The substratum consisted primarily of flat, rubble outcroppings of limestone with sparse patches of sand. Macroalgae were evenly distributed and included large stands of *Sargassum*, several meters in length, and several species of red and green macroalgae. Invertebrate species included primarily sponges, gorgonians, ascidians, the sea urchin *Arbacia punctulata*, and the sea stars *Oreaster reticulatus, Luidia clathrata, L. alternata,* and *Echinaster spinulosis.* Site 1 was 15.1 km west of sites 2 and 3.

Site 2 (28°7.56′N 82°59.70′W, depth 12 m): Large vertical limestone outcroppings were moderately scattered over swaths of sand. Sponges, ascidians, and some macroalgae were attached to rubble outcroppings. Bivalves such as *Atrina* spp., *Macrocalista nimbosa,* and *M. maculata* were commonly found on sand flats. *Arbacia punctulata* was often attached to limestone outcroppings whereas *Lytechinus variegatus* was abundant on sand, often with shells and algae heaped over its test. Occasionally *L. clathrata* was found on sand. Site 2 was 193 m from site 3.

Site 3 (28°7.45′N 82°59.70′W, depth 12 m): The few outcroppings were sparsely distributed and smaller in size than those at site 2. This

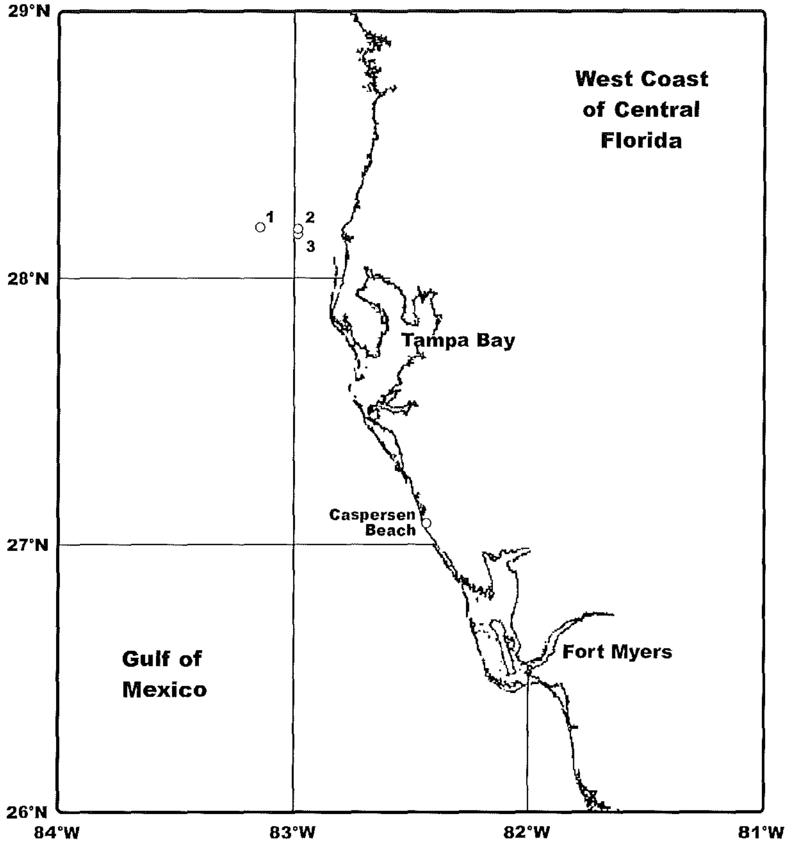

Fig. 1. Locations of offshore (1–3) and nearshore (Caspersen Beach) sites on the central Florida Gulf Coast shelf.

site was primarily composed of barren sand and shell hash. A few concrete bricks acted as artificial reef substratum for some ascidians and other sessile invertebrates. Bivalves as well as predatory gastropods were found commonly buried and exposed on sand flats. Shell hash and tubular sheaths from polychaetes were often heaped on the tests of *L. variegates,* which was found in abundance.

Caspersen beach (27°4′N 82°27′W, depth 6 m): Large rubble outcroppings were abundant on sand flats at approximately 6-m depth. Caspersen closely resembles site 2 although rubble outcroppings at Caspersen appear to merge into sand patches, whereas microhabitats at site 2 are discrete. Rubble outcroppings supported a number of ascidians, sponges, hydroids, and gorgonians. Many predatory gastropods and crustaceans were frequently observed. *Echinaster spinulosus* and holothuroids were found on occasion among the rubble. *Arbacia punctulata* was found only on rubble outcroppings, whereas *L. variegatus* was found on both substrata with shell fragments and drift algae heaped over the test. Macroalgae were distributed sparsely over rubble at sampling depths. However, drift algae were common over sand at most depths, and large stands of red macroalgae and *Caulerpa* spp. were noted in areas of high hydrodynamics at approximately 4-m depth.

Samples of macroalgae and plants (collectively referred to as flora) were collected to document the species present within each habitat and to estimate available biomass at each site. Five 0.25-m^2 quadrats were placed haphazardly over rubble and sand substrata for a total of 10 quadrats per collection. All erect, attached or drifting, flora in each quadrat were collected and preserved in a 4% formalin and seawater solution. Flora was primarily composed of macroalgae and occasionally of drifting seagrass.

Samples were collected from all offshore sites in the fall of 1999 and in the spring and fall of 2000. During the spring of 2000, an algal bloom prevented divers from locating rubble

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TABLE 1. Frequency of algae and plants collected in quadrats over rubble (R) and sand (S) at each site. Collection dates: 1 = 2 Oct. 1999, 2 = 8 April 2000, 3 = 12 Nov. 2000, 4 = 29 Sep. 1999, 5 = 17 Jan. 2000, 6 = 15 June 2000, and 7 = 23 Aug. 2000.

	Site 1						Site 2						Site 3						Caspersen							
	1		2		3		1		2		3		1		2		3		4		5		6		7	
	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S
Angiospermophyta																										
Thalassia testudinum Koenig *et* Sims	0	0	1	0	0	0	1	0	0	0	0	0	1	0	—	0	0	0	0	0	0	0	0	0	0	0
Chlorophyta																										
Batophora oerstedii J. Agardh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	1	0	0	0
Bryopsis pennata Lamouroux	0	0	0	0	0	0	0	0	0	0	0	0	1	0	—	0	0	0	0	0	1	0	0	0	0	0
Caulerpa ashmeadii Harvey	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	1	0	0	0	0	0	0	0	0	0	0
C. mexicana Sonder ex Kützing	0	0	1	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
C. prolifera (Frosskål) Lamouroux	0	1	0	2	0	0	0	0	0	0	0	1	0	0	—	0	0	1	0	0	0	0	0	0	0	0
C. racemosa var. *peltata* (Lamouroux) Eubank	2	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
C. sertularioides (S.G. Gmelin) Howe	1	1	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Cladophora spp. Kützing	0	0	5	5	0	0	0	0	5	4	0	0	0	0	—	4	0	0	0	0	0	0	0	0	0	0
Codium isthmocladum Vickers	0	0	0	0	2	1	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Halimeda discoidea Decaisne	3	0	2	1	1	0	0	1	1	0	1	0	0	0	—	0	1	0	0	0	0	0	0	0	0	0
Udotea conglutinata (Ellis & Solander) Lamouroux	4	1	1	0	3	4	0	0	0	0	0	0	1	0	—	0	0	0	0	0	0	0	0	0	0	0
Phaeophyta																										
Cladosiphon occidentalis Kylin	0	0	5	4	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Dictyota pulchella Hörnig & Schnetter	5	1	0	0	0	0	5	4	0	0	0	0	3	0	—	0	0	0	0	0	0	0	1	0	0	0
D. menstrualis (Hoyt) Schnetter, Hörnig & Weber-Peukert	0	0	1	0	4	1	0	0	0	0	1	0	0	0	—	0	1	0	0	0	0	0	0	0	5	2
Sargassum filipendula C. Agardh	3	1	4	2	5	1	0	0	0	0	0	0	1	0	—	0	4	0	5	0	0	0	0	0	1	0
Rhodophyta																										
Agardhiella subulata (C. Agardh) Kraft & Wynne	0	0	0	1	1	0	0	0	1	0	0	0	0	0	—	0	0	0	0	0	1	0	0	0	0	0
Amphiroa fragilissima (Linnaeus) Lamouroux	0	0	2	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Botryocladia occidentalis (J. Agardh) Kylin	3	0	3	0	2	1	0	0	0	0	3	0	2	0	—	0	0	0	1	0	0	0	0	0	2	1

TABLE 1. Continued.

	Site 1						Site 2						Site 3						Caspersen							
	1		2		3		1		2		3		1		2		3		4		5		6		7	
	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S
Ceramium flaccidum (Kützing) Ardissone	0	0	2	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Champia parvula (C. Agardh) Harvey	0	0	0	0	1	1	0	0	0	0	1	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Chondria littoralis Harvey	0	0	1	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	2	0	0	0	0	0
C. sedifolia Harvey	0	0	1	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	4	3
C. tenussima (Goodenough & Woodward) C. Agardh	0	0	2	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Chrsymenia halymeniodes Harvey	0	0	5	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Dasya baillouviana (S.G. Gmelin) Montagne	0	0	3	0	2	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Eucheuma isiforme var. *denudatum* (C. Agardh) J. Agardh	0	0	0	0	0	0	0	0	0	0	0	0	2	0	—	0	0	0	0	0	0	0	0	0	0	0
Gracilaria bursa-pastoris (S.G. Gmelin) Silva	3	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
G. caudata J. Agardh	1	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	1	0	1
G. damaecornis J. Agardh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	3	0	0	0	0	0	0	0
G. mammillaris (Montagne) Howe	5	1	3	2	3	1	0	0	0	0	0	0	1	0	—	0	0	0	1	0	0	0	0	0	0	0
G. tikvahiae McLachlan	0	0	0	0	0	0	0	0	0	0	0	0	2	0	—	0	0	0	0	0	0	0	0	0	0	0
Grinnellia americana (C. Agardh) Harvey	0	0	0	0	1	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Halymenia floresia (Clemente) C. Agardh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	1
Helminthocladia sp. J. Agardh	0	0	0	0	0	0	0	0	1	2	0	0	0	0	—	1	0	0	0	0	0	0	0	0	0	0
Hypnea spinella (C. Agardh) Kützing	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	5	1	5	2
Jania pumila Lamouroux	0	0	5	0	1	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Laurencia potteaui (L.V. Lamouroux) M.A. Howe	5	1	5	3	5	4	0	0	0	0	1	0	2	0	—	0	0	0	0	0	0	0	0	0	0	0
Polysiphonia subtilissima Montagne	0	0	5	3	0	0	0	0	0	1	0	0	0	0	—	0	0	0	0	0	0	0	2	0	0	0
Unknown red algae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0

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TABLE 2. Biomass and percent abundance by dry weight of dominant macroflora at offshore and nearshore sites. All attached and drift macroflora were collected in five quadrats over rubble and sand substrate. At site 3 in April 2000, no rubble outcroppings could be found because of low visibility. Values in parenthesis represent the number of species within that category.

	Rubble		Sand	
	Biomass (g dry m^{-2})	Abundance (%)	Biomass (g dry m^{-2})	Abundance (%)
Site 1				
2 Oct. 1999				
Caulerpa prolifera	0	0	0.15 ± 0.29	16
C. sertularioides	0.08 ± 0.17	0	0.32 ± 0.64	34
Halimeda discoidea	2.28 ± 2.51	10	0	0
Laurencia poiteaui	12.77 ± 8.03	56	0.18 ± 0.36	19
Udotea conglutinata	1.94 ± 2.30	9	0.23 ± 0.46	24
Other (7)	5.77 ± 1.79	25	0.07 ± 0.08	7
8 April 2000				
H. discoidea	0.50 ± 0.86	2	2.79 ± 5.58	67
L. poiteaui	14.60 ± 3.18	61	0.81 ± 1.37	19
Other (21)	8.68 ± 3.58	37	0.60 ± 0.51	14
12 Nov. 2000				
L. poiteaui	6.60 ± 6.65	81	1.34 ± 1.63	57
Sargassum filipendula	0.19 ± 0.15	2	0.57 ± 1.27	24
Other (11)	1.37 ± 0.84	17	0.46 ± 0.54	20
Site 2				
2 Oct. 1999				
Dictyota pulchella	0.08 ± 0.06	88	0.02 ± 0.02	88
H. discoidea	0	0	0.00 ± 0.01	12
Thalassia testudinum	0.01 ± 0.02	12	0	0
8 April 2000				
Agardhiella subulata	2.45 ± 4.25	56	0	0
H. discoidea	1.65 ± 2.85	38	0	0
Helminthocladia sp.	0.04 ± 0.06	1	0.34 ± 0.46	99
Other (2)	0.21 ± 0.28	5	0.00 ± 0.01	1
12 Nov. 2000				
Botryocladia occidentalis	10.88 ± 19.68	83	0	0
C. prolifera	0	0	0.00 ± 0.00	100
H. discoidea	2.17 ± 4.35	17	0	0
Other (3)	0.04 ± 0.05	0	0	0
Site 3				
2 Oct. 1999				
B. occidentalis	0.80 ± 0.92	30	0	0
Gracilaria tikvahiae	0.45 ± 0.67	17	0	0
L. poiteaui	0.32 ± 0.37	12	0	0
U. conglutinata	0.64 ± 1.28	24	0	0
Other (6)	0.42 ± 0.51	16	0	0
8 April 2000				
C. ashmeadii	—	—	2.04 ± 4.56	72
Cladophora spp.	—	—	0.77 ± 1.66	27
Helminthocladia sp.	—	—	0.01 ± 0.03	0
12 Nov. 2000				
C. prolifera	0	0	0.05 ± 0.11	100
D. menstrualis	0.01 ± 0.01	1	0	0
H. discoidea	0.56 ± 1.12	54	0	0
S. filipendula	0.48 ± 0.41	46	0	0

TABLE 2. Continued.

	Rubble		Sand	
	Biomass (g dry m^{-2})	Abundance (%)	Biomass (g dry m^{-2})	Abundance (%)
Caspersen				
29 Sep. 1999				
G. damaecornis	0.57 ± 1.00	35	0	0
S. filipendula	1.01 ± 0.89	62	0	0
Other (2)	0.05 ± 0.08	3	0	0
17 Jan. 2000				
A. subulata	0.00 ± 0.01	36	0	0
Bryopsis pennata	0.00 ± 0.00	10	0	0
Chondria littoralis	0.00 ± 0.01	54	0	0
15 June 2000				
G. caudata	0	0	0.01 ± 0.00	26
Hypnea spinella	0.42 ± 0.69	99	0.03 ± 0.00	74
Other (3)	0.00 ± 0.00	1	0	0
23 Aug. 2000				
Chondria sedifolia	0.50 ± 0.61	38	0.33 ± 0.41	25
D. menstrualis	0.37 ± 0.17	28	0.04 ± 0.06	3
G. caudata	0	0	0.64 ± 1.44	48
Halymenia floresia	0	0	0.14 ± 0.32	11
H. spinella	0.35 ± 0.29	27	0.18 ± 0.29	13
Other (2)	0.10 ± 0.12	8	0.01 ± 0.02	1

outcroppings to collect samples over hard substratum at one offshore site. Nearshore collections at Caspersen Beach were made in fall of 1999 and in winter, spring, and summer of 2000.

Analysis of habitat biomass.—All algal and plant specimens were carefully separated and then identified by external morphology and examination of cross sections according to Dawes (1974) with taxonomic names corrected using Wynne (1998). Algae growing epiphytically were removed from host plants and treated in the same manner as other macroalgae. Animals such as tunicates growing epiphytically on algae and sand attached to holdfasts of algae were discarded. All specimens were weighed separately before and after drying in an oven at 75 C for at least 24 hr.

Dry weight was used to determine relative percent biomass of each species of seagrass or algae by dividing the dry weight for each species by the total dry weight of all flora within a quadrat. Data from all quadrats were averaged to calculate biomass and relative abundance of flora over sand, rubble, and combined sand and rubble microhabitats. Total biomass from all quadrats was averaged to estimate floral biomass for each collection date. Two-factor analysis of variance (ANOVA) was used to compare differences in biomass between dates within each site, over different substrata. Available biomass was compared between sites using a single-factor ANOVA and Tukey's multiple comparison test.

The index of proportional similarity (Sc) of Czekanowski (as used in Verlaque and Nédelec 1983) was used to compare the diversity of macroflora between sites on the basis of the percent abundance of each species:

$$Sc = \sum \mathrm{MIN}(P_i, Q_i)/100$$

Variables P_i and Q_i represent the percent abundance of species i from collection sites P and Q. The index of similarity is the sum of the minimum (the lower of the two values P_i and Q_i) percent abundance of all species present at either site, divided by 100. Comparisons were made between all sites and dates over both rubble and sand.

RESULTS

Very few species of algae were collected consistently on all collection dates at offshore sites 2 and 3 and at Caspersen Beach (Table 1). Most were distributed sporadically within sites as indicated by frequency (the number of

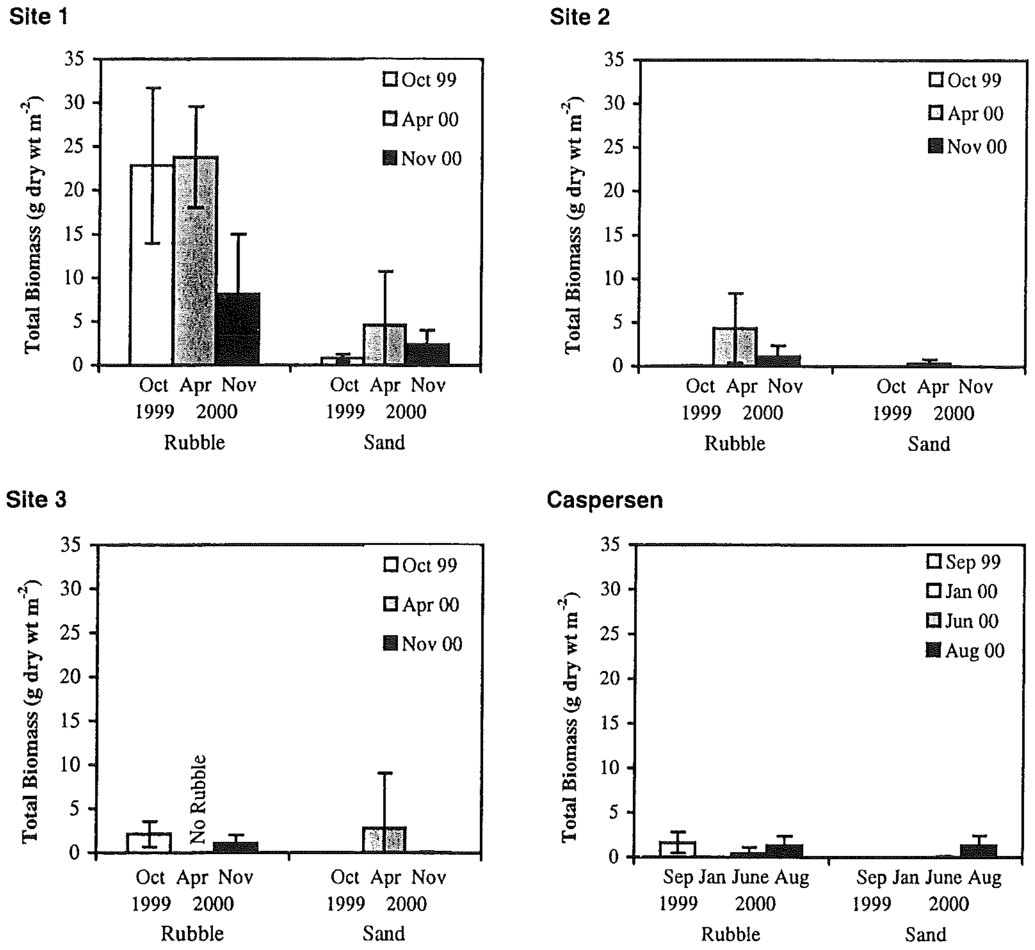

Fig. 2. Average biomass (mean ± SD) of algae and seagrass collected over rubble and sand substrata at different seasons (n = 5). An outlier was removed for the total biomass average during the Nov. 2000 collection at site 2 over rubble (n = 4). No samples were collected over rubble at site 3 during April 2000.

quadrats within which each species was present divided by the number of quadrats sampled) in Table 1. At site 1, *Halimeda discoidea, Udotea conglutinata, Sargassum filipendula, Botryocladia occidentalis, Gracilaria mammillaris* and *Laurencia poiteaui* were collected regularly during fall and spring. These were found more frequently in quadrats placed over rubble than those placed over sand.

Between 12 and 22 species of macroalgae and drifting turtle grass, *Thalassia testudinum,* were found on different collection dates at site 1. Biomass and percent abundance by dry weight of dominant floral species (>10% of total flora by dry weight on sand or rubble) for each site are listed in Table 2. *Laurencia poiteaui* was by far the dominant species in terms of dry weight over rubble on all collection dates at site 1 and was often present in sand collections as well. Calcareous green algae such as *H. discoidea* and *U. conglutinata* were also abundant over rubble and even more so over sand on certain dates. Coenocytic green algae such as *Caulerpa* spp. were abundant over sand only in Oct. 1999. Large stands of *Sargassum,* several meters high, were also present at this site. However, because of limitations of collecting by hand, large individuals of *Sargassum* could not be collected resulting in lower biomass estimates than actually present.

In terms of number of species, site 2 was less diverse than site 1, supporting only two macroalgal species and *T. testudinum* in Oct. 1999, and six macroalgal species on other sampling dates. The red algae *Agardhiella subulata* and *B. occidentalis* contributed the most biomass over rubble in April and Nov. 2000, respectively. However, very little flora was present over rubble in Oct. 1999 or over sand on any sampling date. Flora collected over sand was limited to small specimens of *Dictyota pulchella* and *Helminthocladia* sp. attached to shell fragments and *Caulerpa prolifera* planted in sand.

Diversity at nearby site 3 was also extremely low in comparison with site 1, supporting a maximum of nine species of macroalgae and *T. testudinum* in Oct. 1999. Macroalgal diversity on the few pieces of hard substratum present varied considerably with season. Attached *Caulerpa* spp. and drifting *Cladophora* spp. were the only species collected over sand in the year 2000. No algae were found over sand in Oct. 1999.

Although *Cladophora* spp. did not constitute a large proportion of the biomass at any offshore site, they were the most frequently sampled algae in April 2000 at all offshore sites. During this collection, drifting filamentous *Cladophora* spp. covered all substrata and were entangled with other algal species in almost every quadrat because of a prolific bloom that saturated the water column.

The greatest algal diversity at Caspersen Beach was observed in Aug. 2000, when seven species of macroalgae were collected. The most common attached species over rubble were small epiphytes such as *Chondria* spp. or *D. menstraulis,* growing on larger algae. Drifting red algae such as *Hypnea spinella* and *G. caudata* were common over both rubble and sand on various collection dates.

Overall, site 1 had the highest floral biomass, although this was primarily because of large amounts of algae collected in Oct. 1999 and April 2000 (Fig. 2). The average total biomass was significantly greater over rubble on these dates than on sand. No difference in total biomass between different substrata could be detected at any other offshore site. Combined attached and drifting floral biomass did not vary significantly among site 2, site 3, or Caspersen beach. One quadrat over rubble had an unusually large quantity of *B. occidentalis* in Nov. 2000, resulting in an extremely high standard deviation for that collection date. Data collected from that quadrat were deemed an outlier and not included in the total biomass estimate. No flora was present at site 3 over sand in Oct. 1999. Caspersen Beach also was devoid of flora over sand during Sep. 1999 and Jan. 2000. However, there was significantly more floral material collected over rubble in Sep. 1999 than in Jan. 2000 at Caspersen Beach.

Czekanowski's index of diversity, which considers abundance of each species, indicates very little similarity in macroflora communities between sites over sand or rubble outcroppings (Table 3). However, similarity values (65–74%) were moderately high among collection dates at site 1 over rubble.

DISCUSSION

With the exception of offshore site 1, both the inshore and offshore sites on the central Florida Gulf Coast shelf exhibited low diversity and a high degree of variability between seasons. Macroalgae found along the entire shelf consists of both tropical and subtropical species, including 96 species of Chlorophyta, 44 species of Phaeophyta, and 137 species of Rhodophyta (Dawes, 1974). We found 11 species of Chlorophyta (including five species of *Caulerpa*), four of Phaeophyta, and 23 of Rhodophyta (three species of *Chondria* and five species of *Gracilaria*). The proportions are similar to those found by Dawes and Lawrence (1990): nine species of Chlorophyta (six species of *Caulerpa*), one species of Phaeophyta (*S. filipendula*), and 16 species of Rhodophyta (no *Chondria* spp., four species of *Gracilaria*).

Although sites 2 and 3 (12-m depth) were less than 200 m apart and site 1 (18-m depth) was only 15.1 km west of them, community composition based on Czekanowski's index varied greatly among sites, suggesting patchy species distribution even within short distances. In addition, only offshore site 1, the deepest collection site, had similar community compositions between sampling dates and seasons. These data further support the hypothesis that community diversity at intermediate and shallow depths along the central Gulf shelf is often unstable whereas community composition may be stable at deeper locations throughout the year (Dawes and van Breedveld, 1969; Dawes and Lawrence, 1990). The data also indicate the necessity of multiple site and season sampling because of high variability in over time and short distances in community composition.

Dawes and Lawrence (1990) suggested the low diversity in macroalgae found on the central shelf was in part because of the limited number of sampling times and the collection of only the larger species. However, despite including the smaller epiphytic and drift species in the present study, measurements of available biomass and low diversity are surprising similar to those found by Dawes and Lawrence (1990). The similarity in the results of the two studies, two decades apart, suggests sampling is not the cause. Abiotic disturbances such as hydrodynamics and low winter temperatures may limit

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TABLE 3. Comparison of macroflora diversity over different substrates using Czekanowski's index of proportional similarity. Possible values range from 0.00 (dissimilar) to 1.00 (identical proportions of algae at both sites). Collection dates: 1 = 2 Oct. 1999, 2 = 8 April 2000, 3 = 12 Nov. 2000, 4 = 29 Sep. 1999, 5 = 17 Jan 2000, 6 = 15 June 2000, and 7 = 23 Aug. 2000. No comparison could be made at Site 3 on 8 April 2000 over rubble, because limestone outcropping could not be located.

		Site 1			Site 2			Site 3			Caspersen Beach			
		1	2	3	1	2	3	1	2	3	4	5	6	7
Rubble														
Site 1	1	1.00	0.74	0.65	0.03	0.10	0.18	0.44	—	0.12	0.14	0.00	0.00	0.11
	2	—	1.00	0.71	0.00	0.07	0.08	0.28	—	0.03	0.08	0.00	0.01	0.07
	3	—	—	1.00	0.01	0.01	0.01	0.22	—	0.03	0.05	0.00	0.00	0.03
Site 2	1	—	—	—	1.00	0.00	0.00	0.08	—	0.01	0.00	0.00	0.00	0.28
	2	—	—	—	—	1.00	0.17	0.00	—	0.38	0.00	0.36	0.00	0.00
	3	—	—	—	—	—	1.00	0.31	—	0.17	0.02	0.00	0.00	0.06
Site 3	1	—	—	—	—	—	—	1.00	—	0.04	0.23	0.01	0.00	0.11
	2	—	—	—	—	—	—	—	—	—	—	—	—	—
	3	—	—	—	—	—	—	—	—	1.00	0.46	0.00	0.00	0.02
Caspersen	4	—	—	—	—	—	—	—	—	—	1.00	0.00	0.00	0.04
	5	—	—	—	—	—	—	—	—	—	—	1.00	0.00	0.38
	6	—	—	—	—	—	—	—	—	—	—	—	1.00	0.27
	7	—	—	—	—	—	—	—	—	—	—	—	—	1.00
Sand														
Site 1	1	1.00	0.26	0.32	0.01	0.00	0.49	0.00	0.49	0.23	0.00	0.00	0.03	0.04
	2	—	1.00	0.22	0.12	0.01	0.03	0.00	0.07	0.47	0.00	0.00	0.05	0.05
	3	—	—	1.00	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.02	0.03
Site 2	1	—	—	—	1.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.04
	2	—	—	—	—	1.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
	3	—	—	—	—	—	1.00	0.00	0.72	0.19	0.00	0.00	0.00	0.00
Site 3	1	—	—	—	—	—	—	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	2	—	—	—	—	—	—	—	1.00	0.19	0.00	0.00	0.00	0.00
	3	—	—	—	—	—	—	—	—	1.00	0.00	0.00	0.00	0.01
Caspersen	4	—	—	—	—	—	—	—	—	—	0.00	0.00	0.00	0.00
	5	—	—	—	—	—	—	—	—	—	—	0.00	0.00	0.00
	6	—	—	—	—	—	—	—	—	—	—	—	1.00	0.44
	7	—	—	—	—	—	—	—	—	—	—	—	—	1.00

algal diversity and primary production (Dawes and Lawrence, 1990). However, the only significant decrease in temperature during the present collections occurred during Jan. 2000 at Caspersen Beach. Abiotic factors would have a greater effect on communities at intermediate depths such as Caspersen Beach and offshore sites 2 and 3.

Herbivory could also have a strong effect on flora diversity, particularly at sites of low production. The most prominent benthic herbivore noted at sites 2, 3, and Caspersen Beach was the sea urchin *L. variegatus.* Many large *L. variegatus* were observed primarily on sand flats at these sites and occasionally on small rubble. In shallow seagrass beds, *L. variegatus* occurs occasionally in large numbers that graze heavily on seagrass and algae resulting in barrens (Camp et al., 1973; Macia and Lirman, 1999). In addition to *L. variegatus,* the sea urchin *A. punctulata* occurred on rubble at offshore sites 1 and 2 and Caspersen Beach. Given the low amounts of available food, the large number of herbivores at these locations may be more dependant on drifting floral species or animals than suggested previously.

High productivity in the spring, maturation during late summer, and dying out by winter have been reported in the area (Dawes and van Breedveld, 1969; Dawes and Lawrence, 1990). Samples were not collected frequently enough to establish seasonal patterns, but site 1 appears to maintain higher biomass in spring and late fall than in early winter. Biomass values for site 1 are an underestimate because the larger individuals of *Sargassum* could not be collected. Biomass was usually low (< 1 g dry weight m^{-2}) on both sand and limestone substrata. High biomass of some species did occur on limestone bottoms, with 6 to nearly 15 g dry weight m^{-2} of *L. poiteaui* in Oct., Nov., and April and nearly 11 g dry weight m^{-2} of *B. occidentalis* in Nov. The highest biomass reported by Dawes and Lawrence (1990) was 8.8 g dry weight m^{-2} for *L. poiteaui* in Jan. and 6.8 g dry weight m^{-2} for *B. occidentalis* in Aug. However, total biomass at all sites was considerably less than shallow-water seagrass communities that have up to 815 g dry weight m^{-2} (Dawes et al., 1985). The results suggest that the central Florida Gulf Coast shelf is an area of low macroalgal availablity with considerable variability in species composition between relatively close locations and over time. This has significant implications for secondary production by herbivores.

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