

Seasonal Biomass and Energy Content in Seagrass Communities on the West Coast of Florida¹

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ABSTRACT

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Seasonal collections were made over a 16 month period in seven seagrass communities on the west coast of Florida. The seagrass component accounted for at least 45% of the total biomass and *Thalassia testudinum* was the dominant species. The 15 month mean of total biomass at six sites that were dominated year around by *T. testudinum* from Tampa Bay to Cedar Key, Florida was 385 g dry wt⁻¹ m⁻² or 1.42 tons dry wt⁻¹ acre⁻². The drift and attached seaweed components showed seasonal fluctuations in terms of species and biomass. Of the six open water sites, only one site, characterized by depressed salinity, showed significant differences in seasonal biomass for *T. testudinum* using a nested ANOVA and Student-Newman-Keul's test for variance. Available kilocalories ranged from a 16 month low of 344 to a high of 1837 kcal⁻¹ m⁻² with the highest biomass and caloric values occurring in the late spring and summer.

ADDITIONAL INDEX WORDS: Caloric levels, macrophytes, seagrass communities, seasonal biomass, subtidal region, *Thalassia*

INTRODUCTION

Seagrass beds are the most common subtidal communities in shallow water (0.5 to 3.0 m) along the west coast of Florida from Tampa Bay northward to Apalachicola Bay (PHILLIPS, 1960; BAUERSFELD *et al.*, 1969; HUMM, 1973; DAWES, 1974). These marine angiosperm communities serve as sediment traps, major primary producers, direct food sources, substrates for smaller algae and animals, and habitats, nurseries, and shelters (HUMM, 1973; DAWES, 1981). The beds contain a wide variety of attached and drift benthic seaweeds with *Thalassia testudinum* Koenig *ex* Banks (turtle grass) usually dominating open water sites. *Syringodium filiforme* Kutzing (manatee grass) and *Halodule wrightii* Ascherson (shoal grass) are also common (HUMM, 1973; DAWES, 1974).

Except for studies in seagrass beds near Anclote Key (DAWES *et al.*, 1979) and Apalachicola Bay (BAUERSFELD *et al.*, 1969), little information is available regarding seagrass and associated seaweed

biomass and available calories. The present study was designed to sample a number of discrete seagrass communities along the west coast of Tampa Bay to Cedar Key to determine uniformity and seasonal changes in biomass and calories. The study included all macrophytes in the seagrass community (seagrass species, attached and drift algal species) on a seasonal (15 month) basis.

MATERIALS AND METHODS

Three seagrass sites were sampled triweekly from 17 May 1982 to 8 July 1983 in the vicinity of Tampa Bay. The sites were located at the mouth of Cockroach Bay (27°41.5'N Lat. 82°31.5'W Long.), in the northern region of Anna Maria Island Sound (27°30.0'N Lat. 82°42.5'W Long.) and off Indian Bluff Island (28°06.0'N Lat. 82°47.5'W Long.). Four west coast seagrass sites were sampled bi-monthly from 30 July 1982 to 29 July 1983. These sites were located in the Anclote River anchorage (28°11.0'N Lat. 82°48.0'W Long.), Weeki Wachee

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River Bay (28°32.0'N Lat. 82°39.0'W Long.), Homosassa River Bay (28°45.0'N Lat. 82°44.0'W Long.), and off Seahorse Key channel at Cedar Key (29°05.1'N Lat. 83°04.0'W Long.). Depths ranged from 1 to 3 m (mean low tide) at all sites.

Salinity was measured using a refractometer and temperature with a hand-held thermometer, in the field. Samplings were made using a square meter quadrat with 10 cm² subdivisions. Five random square meter samples were taken at each site on a line transect run through the seagrass meadow. One-fourth of each meter was allotted for drift seaweed collection and three 10 cm² subunits were used in each quadrat for seagrass and attached seaweed collection. All samples were kept separate, and in the laboratory the species of each sample

were separated, identified and weighed. Subsamples of all algae and blades of seagrass species from all sites were dried and analyzed for ash, protein, soluble carbohydrate, and lipid (DAWES and LAWRENCE, 1983). Kilocalories were calculated from the organic constituents as described by BRODY (1964).

RESULTS

Temperature and Salinity

Seasonal fluctuations are shown in Figure 1A and 1B. The temperature for all seven sites had an overall range of 14 to 32 C (Figure 1A). Five sites had similar open water salinity ranges (Cockroach Bay = CRB, 20-30 ppt; Anna Marie Island Sound =

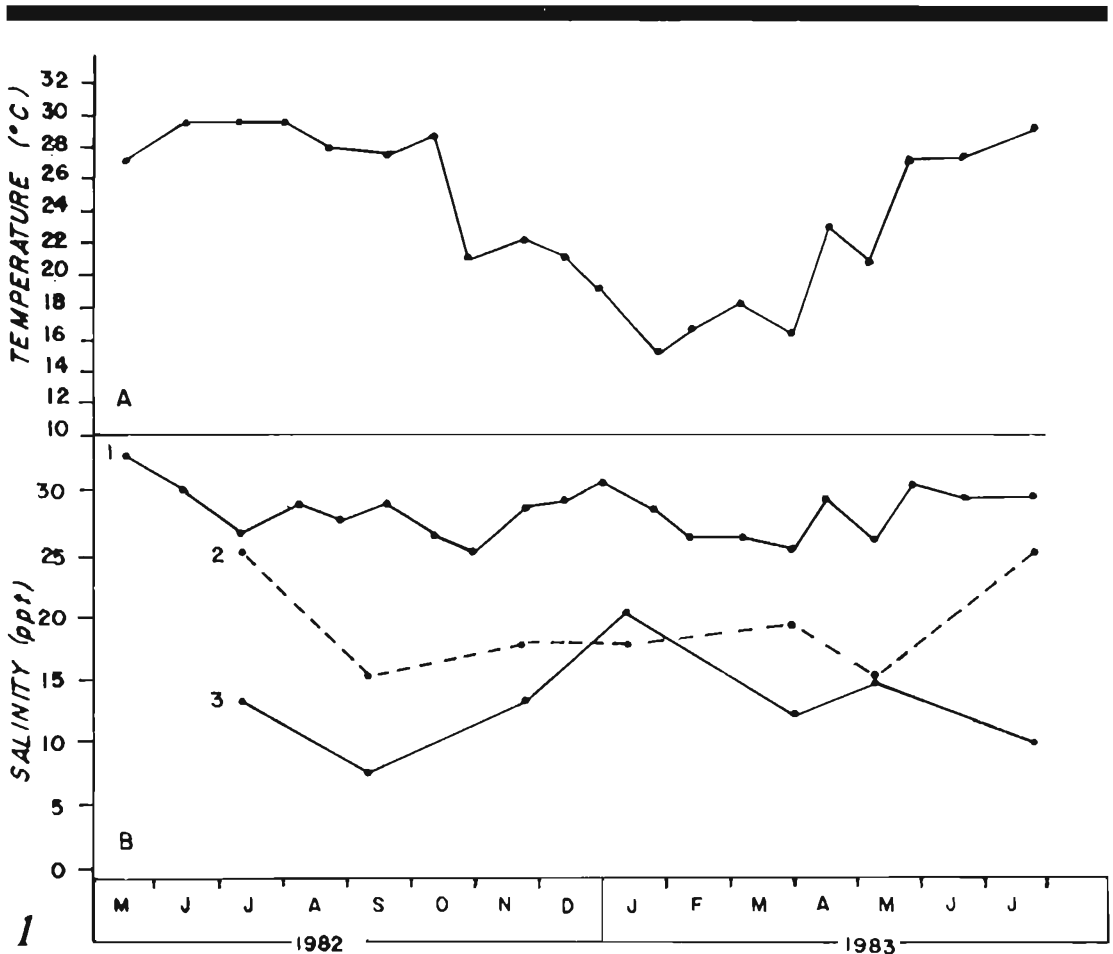


Figure 1. Mean water temperature (Figure 1A) for all seven seagrass communities and the mean of salinity (Figure 1B) for five sites with similar measurements (line 1; Cockroach Bay, Anna Marie Island Sound, Indian Bluff Island, Anclote River anchorage, Cedar Key) as well as the seasonal salinities recorded at Homosassa River Bay (line 2) and Weeki Wachee River Bay (line 3).

AMI, 29-36 ppt; Anclote Key anchorage = ANR, 25-32 ppt; Indian Bluff Island = IBI, 25-33 ppt; Cedar Key = CDK, 23-30 ppt), and the mean is shown in Figure 1B (line 1). Weeki Wachee River Bay (WWR, 7-21 ppt) and Homosassa River Bay (HSR, 16-26 ppt) had consistently lower salinities and are shown separately in Figure 1B (WWR = line 2, HSR = line 3).

Seagrasses

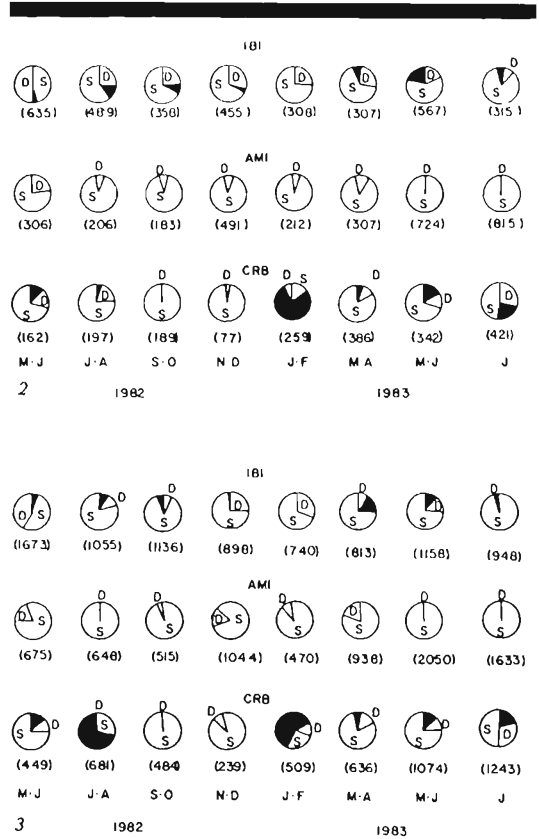
Based on triweekly collections at the three local sites (Figures 2 and 3), the seagrass bed at the mouth of Cockroach Bay (CRB), in Tampa Bay has the lowest biomass and caloric levels (Figure 2) with the highest biomass occurring on 25 March 1983 (seagrass 402 g dry wt.⁻¹m⁻²).

Thalassia testudinum at Anna Maria Island Sound (AMI) also showed variations in biomass and calories with patches of *Syringodium filiforme* and *T. testudinum*. A fall regrowth of turtle grass blades was evident in Nov.-Dec., 1982. Biomass peaked similar to that observed at CRB in the spring of 1983 (M-J = 724 g⁻¹m⁻², Figure 2) following a warm winter (low = 15C), although the highest biomass occurred on 27 May (838 g dry wt⁻¹m⁻²). Calories (Figure 3) closely paralleled the biomass when expressed on a m⁻² basis.

The highest caloric and biomass levels for the three sites was found at the open coast site off Indian Bluff Island (IBI, Figure 1, 2). *Thalassia testudinum* usually accounted for over 50% of the seagrasses in the mixed bed except from late June through early October. Highest biomass occurred in the spring and early summer months with moderate winter dieback of the blades evident during the period of low temperatures (Figure 1).

Thalassia testudinum dominated all four seagrass beds sampled bimonthly on the west coast of Florida (Figures 4 and 5). A seasonal cycle in biomass and similar to IBI was present at the southern-most of the four sites sampled bimonthly (Figures 4 and 5). Anclote River anchorage (ANR), and at the northern-most site in the study Seahorse Key channel of Cedar Key (CDK, Figures 4 and 5). A winter dieback occurred at all four sites on the west coast of Florida (Figure 4).

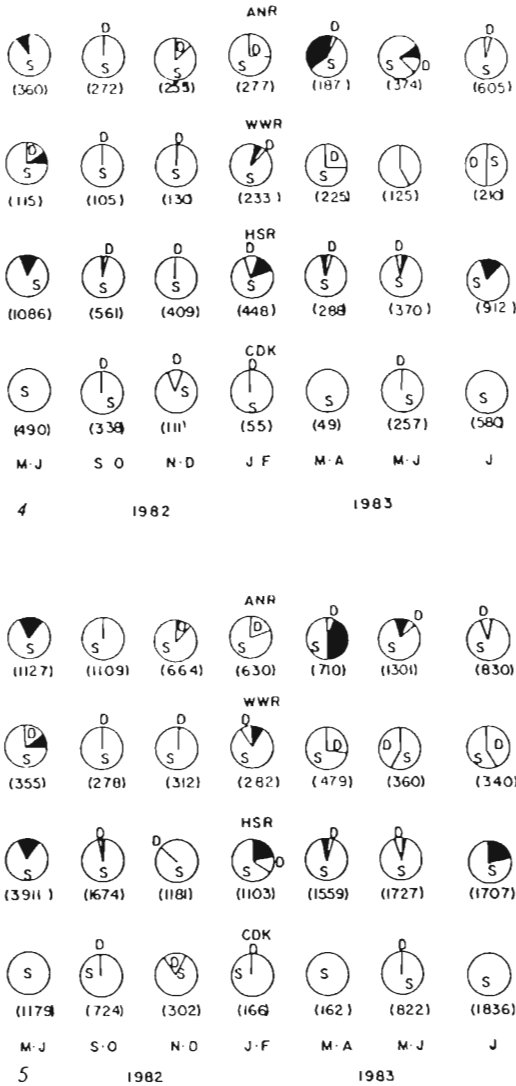
The seagrass biomass was lower at CDK (max. 580 g dry wt⁻¹m⁻²), while at ANR (max. 605 g dry wt⁻¹m⁻²) it was similar to that found at IBI (compare Figure 2 and 4). Patches of *Syringodium filiforme* at CDK were evident during the fall and spring samplings, and this species accounted for 40% of the



Figures 2 and 3. Mean biomass (Figure 2, g dry wt⁻¹m⁻²) and kilocalories (Figure 3, kcal⁻¹m⁻²) of all macrophytic components for the three seagrass communities near Tampa Bay, Florida based on means of triweekly collections (Indian Bluff Island = IBI, Anna Maria Island = AMI, Cockroach Bay = CRB). Seagrass (S), drift seaweeds (D), and attached algae (dark portion of circle) are represented as percent of the circle with mean total biomass (Figure 2) and kilocalories (Figure 3) given in parentheses below each mean.

biomass at ANR in the spring and early summer of 1983 (Figure 4).

The seagrass biomass at Weeki Wachee River Bay (WWR, Figure 4), and Homosassa River Bay (HSR, Figure 4) did not show typical seasonal cycling. A narrow bladed form of *Thalassia testudinum* was the only seagrass present in the low salinity waters of WWR, and the overall biomass was the lowest of the seven sites, although the lowest biomass occurred at CDK in March. Over 60% of the attached seagrass biomass during the winter months was composed of dead blades, thus a dip in energetics is evident but not in biomass for Jan.-Feb. (Figure 5).



Figures 4 and 5. Mean biomass (Figure 4, g dry wt⁻¹ m⁻²) and kilocalories (Figure 5, kcal⁻¹ m⁻²) of all macrophytic components for four seagrass beds on the west coast of Florida (Anclote River anchorage = ANR, Weeki Wachee River Bay = WWR, Homosassa River Bay = HSR, Cedar Key = CDK). See Figures 2 and 3 for code to circles.

A consistently high biomass was found at HSR (max. 1086 g dry wt⁻¹ m⁻², 29 June) and only a moderate winter dieback occurred (321 g dry wt⁻¹ m⁻², 28 Jan.). Patches of *Syringodium filiforme* dominated the seagrass component at HSR during the spring and fall months and in March 1982 accounted for %

of the biomass. Caloric and biomass levels were the highest of all seven sites including winter months.

Drift Seaweeds

The seasonal biomass and calories of the dominant drift seaweeds was most pronounced for the drift alga *Laurencia poitei* at IBI with the species accounting for half of the overall biomass in the bimonthly mean in May-June 1982 (Figures 2 and 4). A mixture of drift seaweeds (*Spyridia filamentosa*, *Hypnea musciformis*, *Polysiphonia denudata*, *Gracilaria mammillaris*) occurred at the two sites in and near Tampa Bay (CRB, AMI), with this seaweed mixture being the largest component in May, 1982 (38%) at CRB. Drift seaweeds only infrequently formed an important part of the biomass at HSR and ANR (Jan. 1983), and WWR (May, June 1983). Drift algae accounted for 59% in May and 49% in July 1983 at WWR when *Thalassia testudinum* blades showed little growth. Because of low biomass, the drift seaweeds did not constitute a large portion of the kilocalories available in the various seagrass communities except at IBI (Figures 3 and 5). The only site where drift seaweeds showed a clear seasonal cycle was at CRB where drift accumulated due to low currents and wave action so that populations remained entangled with the bases of seagrasses.

Attached Algae

Biomass of the attached algae was low and varied widely in the seven seagrass communities (Figures 2 and 4). The largest biomass occurred in CRB where the coenocytic green alga, *Caulerpa prolifera*, reached 83% of the overall dry weight in August (247 g dry wt⁻¹ m⁻²) and 45% in May 1983 (133 g dry wt⁻¹ m⁻²) and where *Enteromorpha intestinalis* also accounted for 94% (372 g dry wt⁻¹ m⁻²) in January 1983 (Figure 2). A number of attached algae also occurred at IBI but only in March did a species (*Halimeda incrassata*) account for more than 15% of the total biomass. Because of the low seagrass biomass in April at ANR, *Caulerpa prolifera* accounted for 45% of the total biomass and 38% of available calories (Figure 4).

Mean Biomass and Caloric Values

Except for winter collections at CRB, the seagrass component accounted for the largest fraction (at least 45%) of the biomass and resultant

calories and the attached algae the least (Figure 2). Drift algae were the most significant component at IBI (up to 50%) in the spring of 1982 but usually drift seaweed biomass was variable, constituting 25% or less. the highest mean biomass and caloric levels in the three seagrass beds around Tampa Bay for all 21 collections occurred at the open coast site at IBI (429 \pm 127 g dry wt¹m²; 1052 \pm 291 kcal¹m⁻²) with AMI intermediate (405 \pm 246 g dry wt¹m²; 997 \pm 568 kcal¹m⁻²) and CRB the lowest (254 \pm 120 g dry wt¹m²; 664 \pm 336 kcal¹m⁻²). Seasonally the highest total biomass occurred in the spring and summer at IBI and AMI and in the winter and spring at CRB (Figures 2 and 3).

Thalassia testudinum accounted for the largest portion of the biomass and calories in the four seagrass beds on the west coast of Florida sampled bimonthly (Figures 4 and 5). The mean biomass for all collections at CDK (269 \pm 212 g dry wt¹m²) and ANR (333 \pm 136 g dry wt¹m²) were lower than that at IBI and AMI. The largest mean biomass for all seven sites was at HSR (582 \pm 301 g dry wt¹m²), possibly due to a continuous shore (southerly current and protected conditions). The site with the lowest mean biomass was WWR (163 \pm 57 g dry wt¹m²). Drift seaweeds contributed a significant portion of the total biomass only at ANR and WWR in the winter and spring months which were the periods of lowest seagrass biomass (Figure 4). The southernmost site, ANR, had a lower drop in biomass in the winter than any of the other four west coast sites showing a similar seasonal cycle with IBI (Figures 2 and 3).

Large fluctuations were evident for total kilocalories at all four west coast sites (Figure 5) with the largest 16 month mean at HSR (1837 \pm 949 kcal¹m⁻²) and smallest at WWR (344 \pm 68 kcal¹m⁻²). No major differences occurred when biomass (Figure 4) and calories (Figure 5) are compared, although attached algae accounted for a greater amount of kilocalories at HSR and drift algae at WWR than the biomass levels would have suggested.

Available standing stock in the seagrass beds varied considerably with regard to site and season (Table 1). The seagrass bed at Indian Bluff Island had the highest mean biomass (477 g dry wt¹m² or 1.76 tons dry wt¹acre⁻¹, Table 1), with the highest level in the spring and early summer (635 g dry wt¹m² or 2.41 tons dry wt¹acre⁻¹) with the highest biomass also occurring in the spring (1202 g dry wt¹m² or 4.45 tons dry wt¹acre⁻¹, Table 1).

The 15 month mean standing stock of *Thalassia*

testudinum at the six sites accounted for about 59% of total standing stock (TSS) and was 229 g dry wt¹m⁻² (Table 1). Using a nested ANOVA and the Student-Newman-Keul's test for variables, the only site of the six dominated by turtle grass biomass was the Homosassa River Bay site.

DISCUSSION

The findings of the present study on the biomass and kilocalories of the macroalgal and seagrass beds along the west coast of Florida can be summed up with regard to three points: (1) The total biomass is similar to previous reports and the caloric values are primarily due to the seagrass component. (2) There was a high degree of uniformity between populations of *Thalassia testudinum* in all the sites regarding biomass and caloric values, although seasonal fluctuations were evident. (3) Seaweeds (attached and drift) showed a larger standing stock variation than the seagrasses and contributed about 18% of the total biomass at most sites.

The mean biomass of turtle grass for the six sites (Table 1) is similar to that reported in previous studies (Table 2) in Texas (ODUM, 1963), Biscayne Bay at Miami, Florida (JONES, 1968; ZIEMAN, 1975), sheltered sites in Cuba (BUESA, 1972, 1974), and the north coast of Jamaica (GREENWAY, 1976). None of the west coast sites had mean biomass levels (830 g dry wt¹m⁻²) reported for the same region by BAUERSFELD *et al.* (1969, Table 2), although such levels were found at AMI, IBI, and HSR for specific collection dates (see ranges, Table 1).

The seaweed component (drift and attached macroalgae) was lower than that reported by DAWES *et al.* (1979) at a site near ANR and IBI, but overall did account for about 18% of the total standing stock (Table 1). The highest mean drift and attached algal standing stock occurred at IBI (143 g dry wt¹m⁻²), and this accounted for 30% of the mean standing stock. Seaweeds accounted for 39% at CBR and 26% standing stock at WWR, both sites where seagrass biomass was low. Much lower standing stock (max. 42 g dry wt¹m⁻²) of *Gracilaria* were reported for *Syringodium filiforme* beds in the Indian River on the east coast of Florida (GILBERT and CLARK, 1981).

The extensive nature of the seagrass beds along the west coast of Florida is apparent if the size of the shallow subtidal region is considered. Seagrass beds occur at least 10 km offshore from Anclote Key to Cedar Key, Florida, an area of about 900 km² (900,000 ha). Based on aerial survey, it appears that

Table 1 The mean standing stock ± 1 standard deviation ($SS \pm S.E.$) expressed as grams dry weight m^{-2} , percent of the total standing stock ($\% TSS$) and seasonal ranges (SR, highest and lowest dry wt m^{-2}) of *Thalassia testudinum*, all seagrasses, all seaweeds (drift and attached algae), total biomass over the 15 month study (May, 1982 to July 1983) of seven seagrass beds on the west coast of Florida.

Site	<i>Thalassia testudinum</i>			All Seagrasses			All Seaweeds			Total Standing Stock					
	SS \pm SE	$\% TSS$	SR	SS \pm SE	$\% TSS$	SR	SS \pm SE	$\% TSS$	SR	TSS \pm SE	SR	SR			
CRB	47	75	20	156	124	67	401-0	89	12	39	396-0	231	174	712-17	
AMI†	302	297	78	838-0	357	296	92	1069-121	37	50	9	110-0	386	297	1078-122
IBI†	266	112	56	576-135	321	123	67	411-62	143	135	30	596-23	477	178	873-202
ANR†	194	125	53	342-29	311	155	85	571-87	69	65	19	201-31	365	136	605-191
WWR†	118	47	74	187-51	119	47	76	187-51	41	38	26	102-0	159	52	223-103
HSR†	315	170	48	632-147	535	242	82	905-321	95	102	14	297-3	656	294	1202-409
CDK†	180	168	67	409-0	264	212	98	580-490	6	9	2	20-0	270	210	580-49
TSS‡	229	77	59	320	136	83			69	46	18		389	171	

The seven west coast sites were Cockroach Bay (CRB) in Tampa Bay, Anna Maria Island Sound (AMI) at the mouth of Tampa Bay and 5 open coast sites: Indian Bluff Island (IBI), Anclote River anchorage (ANR), Weeki Wachee River Bay (WWR), Homosassa River Bay (HSR), and at Seahorse Key of Cedar Key (CDK).

† *Thalassia*-dominated sites.

‡ Mean of *Thalassia*-dominated sites.

Table 2. Means and seasonal range of standing stock (SS g dry wt⁻¹m⁻²) of *Thalassia testudinum* as reported in previous studies.

	Mean SS	Seasonal Range	Reference
Texas	373	(summer only)	Odum, 1963
Florida			
west coast	700	(summer only)	Bauersfeld <i>et al.</i> 1969
Boca Ciega Bay	81		Pomeroy, 1960
Boca Ciega Bay	80	1198-320 (Aug)	Taylor and Saloman, 1969
Tarpon Springs		820-601	Dawes <i>et al.</i> , 1979
Bear Cut, Miami	830	1800-700	Jones, 1968
Biscayne Bay, Miami	126 (inshore)	230-30	Zieman, 1975
Biscayne Bay, Miami	280 (offshore)	650-80	Zieman, 1975
Cuba			
	340 (sheltered)	517-240 (Aug)	Buesa, 1972; 1974
	80 (exposed)	80-76 (Aug)	Buesa, 1972; 1974
St. Croix	77		Zieman <i>et al.</i> , 1979
Jamaica	249	330-170	Greenway, 1976
Puerto Rico	80		Burkholder <i>et al.</i> , 1959

about 594,000 hectares (240,468 acres). If the mean overall standing stock (seagrasses and seaweeds) for the five west coast sites from Indian Bluff Island to Cedar Key is used (385 g dry wt⁻¹m⁻² or 1.42 tons dry wt⁻¹acre⁻²), then approximately 2.28 x 10⁹ metric tonnes or 3.4 x 10⁶ U.S. tons are present.

There was a seasonal shift in total biomass and resultant kilocalories in the seven seagrass communities sampled along the west coast of Florida. Biomass was highest in the spring and summer, a period of rapid growth and storage of food reserves (DAWES and LAWRENCE, 1980). This was also evident for the macroalgal component (DAWES *et al.*, 1979). Although lowest in the mid-winter months, kilocaloric values remained high at most sites throughout the year in spite of winter die-back. This suggests that the macroalgal component can influence this available kilocalories as seen for Cockroach Bay in January-February (Figure 2). This study found that although winter die-back does not result in lower biomass, the kilocaloric values do not drop as low as expected and thus these communities offer a significant source of nutrition even in the periods of little to no growth.

LITERATURE CITED

- BAUERSFELD, P.; KIFER, R.R.; DURRANT, N.W., and SYKES, J.E., 1969. Nutrient content of turtle grass (*Thalassia testudinum*). *Proceedings 6th International Seaweed Symposium, Santiago*, 6, 637-635.
- BRODY, S., 1964. *Biogenesis and Growth*. New York: Hafner, 1023p.
- BUESA, R.J., 1972. Produccion primaria de las praderas de *Thalassia testudinum* de la plataforma noroccidental de Cuba, INP, Cuba. *Cent. Invest. Pesqueras, Reun. Bal. Trab. CIP*, 3, 101-143.
- BUESA, R.J., 1974. Population and biological data on turtle grass (*Thalassia testudinum* Konig, 1805) on the northwestern Cuban shelf. *Aquaculture*, 4, 207-226.
- DAWES, C.J., 1974. *Marine Algae on the West Coast of Florida*. Coral Gables, Florida: University of Miami Press, 201p.
- DAWES, C.J., 1981. *Marine Botany*. New York: Wiley, 628p.
- DAWES, C.J.; BIRD, K.; DURAKO, M.; GODDARD, R.; HOFFMAN, W., and McINTOSH, R., 1979. Chemical fluctuations due to seasonal and cropping effects on an algal-seagrass community. *Aquatic Botany*, 6, 79-86.
- DAWES, C.J. and LAWRENCE, J.M., 1979. Effects of blade removal on the proximate composition of the rhizome of the seagrass *Thalassia testudinum* Banks ex Konig. *Aquatic Botany*, 7, 255-266.
- DAWES, C.J. and LAWRENCE, J.M., 1980. Seasonal changes in the proximate constituents of the seagrass *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme*. *Aquatic Botany*, 8, 371-380.
- DAWES, C.J. and LAWRENCE, J.M., 1983. Proximate composition and caloric content of seagrasses. *Marine Technical Society Journal*, 17(2), 53-58.
- GILBERT, S. and CLARK, K.B., 1981. Seasonal variations in standing crop of the seagrass *Syringodium filiforme* and associated macrophytes in the northern Indian River, Florida. *Estuaries*, 4, 223-225.
- GREENWAY, M., 1976. The grazing of *Thalassia testudinum* in Kingston Harbour, Jamaica. *Aquatic Botany*, 2, 292-297.

- HUMM, H.J., 1973. Seagrasses. In: J.I. Jones, R.E. King, M.O. Rinkel, and R.E. Petersburg (eds.), *A Summary of Knowledge of the Eastern Gulf of Mexico*. St. Petersburg, Florida: State University System Florida Institute Oceanography, pp. IIC 1-7.
- JONES, J.A., 1968. Primary production by the tropical marine turtle grass, *Thalassia testudinum* Konig, and its epiphytes. Unpublished Doctoral dissertation, University of Miami, Miami, Florida, 196p.
- ODUM, H.T., 1963. Productivity measurements in Texas turtle grass and the effects of dredging on intracoastal channel. *Publication Institute Marine Science University Texas*, 9, 48-58.
- PHILLIPS, R.C., 1960. *Observations on the Ecology and Distribution of the Florida Seagrasses*. Prof. Pap. 2, Florida State Board Conservation Marine Laboratory, St. Petersburg, Florida, 72p.
- POMEROY, L.R., 1960. Primary productivity of Boca Ciega Bay, Florida. *Bulletin Marine Science Gulf and Caribbean*, 10, 1-10.
- TAYLOR, J.L. and SALOMAN, C.H., 1969. Some effects of hydraulic dredging and coastal development in Boca Ciega Bay, Florida. *Fisheries Bulletin*, 67, 213-241.
- ZIEMAN, J.C., 1975. Quantitative and dynamic aspects of the ecology of turtle grass, *Thalassia testudinum*. In: L.E. Cronin (ed.), *Estuarine Research, Vol. 1, Chemistry, Biology, and the Estuarine System*. New York: Academic Press, 541-562.
- ZIEMAN, J.D.; THAYER, G.W.; ROBBLEE, M.B., and ZIEMAN, R.T., 1979. Production and export of seagrasses from a tropical bay. In: R.J. Livingston (ed.), *Ecological Processes in Coastal and Marine Systems*. New York: Plenum, 21-34.

