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Spatial and temporal pattern in seagrass community composition and productivity in south Florida

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Abstract We document the distribution and abundance of seagrasses, as well as the intra-annual temporal patterns in the abundance of seagrasses and the productivity of the nearshore dominant seagrass (*Thalassia testudinum*) in the south Florida region. At least one species of seagrass was present at 80.8% of 874 randomly chosen mapping sites, delimiting 12,800 km^2 of seagrass beds in the 17,000-km^2 survey area. *Halophila decipiens* had the greatest range in the study area; it was found to occur over 7,500 km^2. The range of *T. testudinum* was almost as extensive (6,400 km^2), followed by *Syringodium filiforme* (4,400 km^2), *Halodule wrightii* (3,000 km^2) and *Halophila engelmanni* (50 km^2). The seasonal maxima of standing crop was about 32% higher than the yearly mean. The productivity of *T. testudinum* was both temporally and spatially variable. Yearly mean areal productivity averaged 0.70 g m^{-2}day^{-1}, with a range of 0.05–3.29 g m^{-2} day^{-1}. Specific productivity ranged between 3.2 and 34.2 mg g^{-1} day^{-1}, with a mean of 18.3 mg g^{-1} day^{-1}. Annual peaks in specific productivity occurred in August, and minima in February. Integrating the standing crop for the study area gives an estimate of 1.4 × 1011 g *T. testudinum* and 3.6×10^{10} g *S. filiforme*, which translate to a yearly production of 9.4×10^{11} g *T. testudinum* leaves and 2.4×10^{11} g *S. filiforme* leaves. We assessed the efficacy of rapid visual surveys for estimating abundance of seagrasses in south Florida by comparing these results to measures of leaf biomass for *T. testudinum* and *S. filiforme*. Our rapid visual surveys proved useful for quantifying seagrass abundance, and the data presented in this paper serve as a benchmark against which future change in the system can be quantified.

Introduction

Seagrasses have not fared well worldwide in the last century because of human alteration of the coastal zone. In general, human activities have decreased the clarity of the water column, either because of increased turbidity or eutrophication; this has led to a concomitant decrease in seagrasses (see Duarte 1995; Short and Wyllie-Echeverria 1996 for review). Seagrass beds are often cited as some of the most productive ecosystems on earth, rivaling cultivated crops in annual net primary production (Zieman and Wetzel 1980). Despite the recognized importance of seagrasses (Costanza et al. 1997), continued human population growth, and the susceptibility of seagrass communities to anthropogenic disturbance, there have been few detailed spatially extensive monitoring programs designed to examine the status and trends of the seagrass beds at the regional scale (Duarte 1999). Before assessments of trends in such systems can be accomplished, it is imperative that spatial and intra-annual patterns in the seagrass beds be understood.

There are few areas where seagrasses are as widespread and conspicuous as the shallow marine waters surrounding the southern tip of the Florida peninsula (ca. 24.5°N, 80.5°W). Seagrass beds are the most common benthic community type in the region, they cover at least 14,000 km^2 (Fourqurean et al. in press). A lack of significant river discharge and vigorous mixing of coastal water bodies with oceanic water results in generally clear waters in south Florida; this water clarity allows sufficient light to penetrate to the sandy and muddy bottoms of the region to support seagrass growth. Seagrass beds, along with mangrove forests and the only barrier coral reef in the continental United States, provide the habitats that support commercial fishing and recreational use of the nearshore marine habitat.

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The litany of recent, perceived environmental problems in the nearshore marine environment in south Florida is long. Particular concern has been raised over the bleaching of reef corals (Jaap 1985; Williams et al. 1987; Fitt et al. 1993), loss of coral cover on the reef tract (Dustan and Halas 1987; Porter and Meier 1992), and increasing occurrence and types of coral diseases (Richardson 1998; Richardson et al. 1998). A poorly understood seagrass dieoff event in the late 1980s in adjacent Florida Bay (Robblee et al. 1991; Thayer et al. 1994; Hall et al. 1999) had ramifications that cascaded through the ecosystem, causing phytoplankton blooms and sponge dieoffs that in turn affected large mobile fish and invertebrates (Butler et al. 1995; Philips and Badylak 1996; Matheson et al. 1999; Thayer et al. 1999). Changing water quality has been implicated, as either a cause or an effect, of many of these environmental problems (e.g., Lapointe and Clark 1992; Porter et al. 1999). Direct physical damage to seagrass beds is also occurring in south Florida, mostly in the form of "prop scarring" caused by inadvertent or negligent operation of boats in shallow seagrass beds (Sargent et al. 1995). Human recognition of the value of the nearshore marine habitats, coupled with perceptions of degraded habitat quality that were partially supported by strong scientific data, were largely responsible for the creation of the Florida Keys National Marine Sanctuary (FKNMS) in 1990. The goal of the FKNMS is to "preserve and protect the physical and biological components on the south Florida estuarine and marine ecosystem to ensure its viability for the use and enjoyment of present and future generations" (NOAA 1996).

In this study, we describe the spatial pattern in the present-day distribution of seagrass communities in south Florida and describe the seasonal patterns in the biomass and productivity of *Thalassia testudinum*, a dominant seagrass, as a baseline against which future change in the ecosystem can be measured. The spatial scale and temporal resolution of the monitoring network described herein are without precedent in seagrass ecosystems; only through such large-scale studies can generalizable and reliable patterns and trends be detected. It is possible that relatively local phenomena may be missed in a monitoring program of such scope, but proper management of the FKNMS, as well as other seagrass ecosystems worldwide, depends on understanding general, regional-scale trends in the ecosystem (Duarte 1999).

Materials and methods

We surveyed the seagrass distribution and abundance throughout a 17,000-km^2 area in south Florida (Fig. 1). The FKNMS is a 9,600-km^2 region within this larger area. A stratified-random approach, with distance offshore as the strata, was used to locate 30 perma-

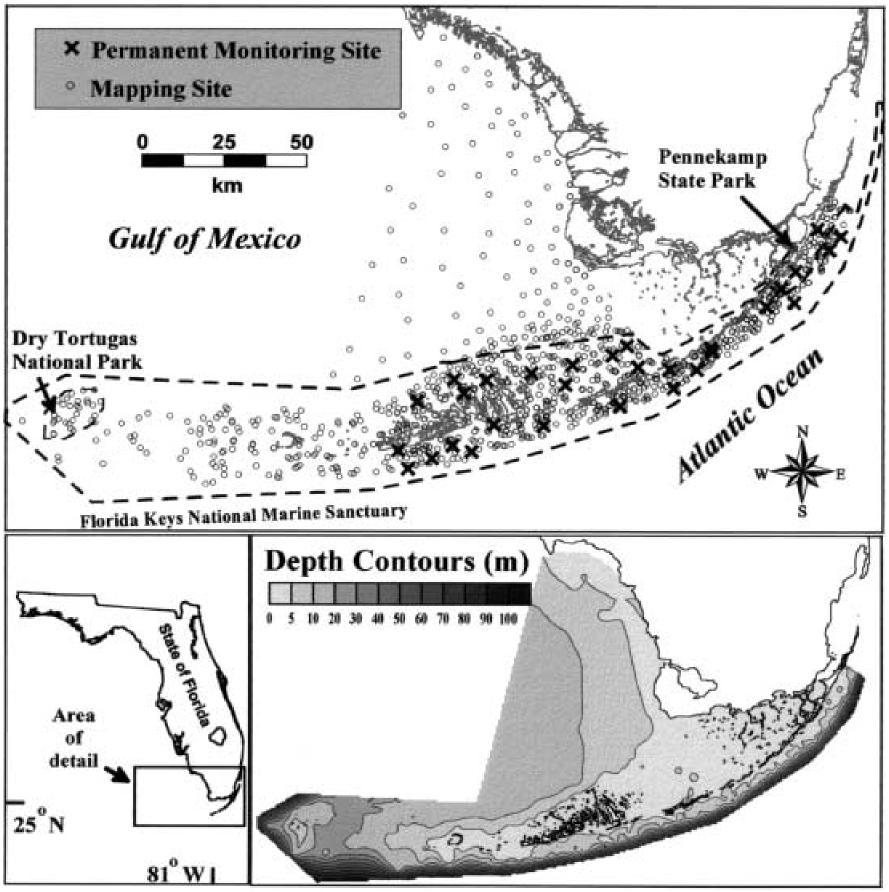


Fig. 1 Map of study area showing boundaries of management areas within the study area and the location of the 30 permanent monitoring sites and the 874 mapping sites

nent seagrass monitoring sites within the FKNMS (Fig. 1). Sites were sampled every 3 months from December 1995 through December 1998. In addition to these permanent sites, an additional 874 mapping sites were randomly selected across the FKNMS and the shallow portion of the Southwest Florida Shelf to the north of the FKNMS (Fig. 1); these sites were visited once during the summer months of 1996–1998 in order to rapidly estimate spatial extent and cover of benthic macrophytes in the FKNMS and adjacent shallow water marine environments.

A rapid, visual assessment technique developed early in the 20th century by the plant sociologist Braun-Blanquet (Braun-Blanquet 1972) was used to assess the abundance of seagrass and macroalgae. This method is very quick, requiring only minutes at each sampling site; yet it is robust and highly repeatable, thereby minimizing among-observer differences, and has recently been applied to seagrass research (Kenworthy et al. 1993; Rose et al. 1999). At each permanent seagrass monitoring site, a 50-m-long transect was established at the beginning of the study period by driving steel rods into the substratum at both ends of the transect. At each mapping site, a 50-m transect was set up by extending a meter tape along the bottom in an up-current direction. Ten quadrats ($0.25\ \mathrm{m}^2$) were placed along each transect at pre-determined random distances from one of the marker rods. A new set of random sampling positions were chosen before each visit to a site. Each quadrat was examined using SCUBA. All seagrass species occurring in the quadrat were listed, and a score based on the cover of the species in that quadrat was assigned (Table 1). Cover, as defined for this study, is the fraction of the total quadrat area that is obscured by a particular species when viewed from directly above.

From the observations of cover in each quadrat at a site, three statistics were computed for each species: density, abundance and frequency. Density (*D*) was calculated as:

$$D_i = \frac{\sum_{j=1}^{n} S_{ij}}{n} \tag{1}$$

where D_i = density of species *i*; *j* = quadrat number from 1 to *n*, the total number of quadrats sampled at a site, and S_{ij} = the Braun-Blanquet score for species *i* in quadrat *j*. For any species, *D* can range between 0 and 5, the maximum Braun-Blanquet score. At a site, however, the sum of all taxa *D* values can be >5, because of the relatively broad cover ranges for each Braun-Blanquet value and the fact that seagrass canopies are three dimensional. It should also be noted that a species may be observed at a site by the sample collector, but unless the species falls within one of the randomly-placed observation quadrats, the species receives a $D = 0$. Abundance (*A*) was calculated as:

$$A_i = \frac{\sum_{j=1}^{n} S_{ij}}{N_i} \tag{2}$$

where N_i is the number of quadrats at a site in which species *i* was present. For any species, *A* can range between 0 and 5, the maximum Braun-Blanquet score (note $D_i \leq A_i$). Frequency (*F*) was calculated as:

$$F_i = \frac{N_i}{n} \tag{3}$$

such that $0 \leq F_i \leq 1$. In addition to species-specific measures, seagrass species richness *S* was calculated for each site by summing the number of seagrass species for which $D > 0$.

Table 1 Braun-Blanquet abundance scores (*S*). Each seagrass species was scored in each quadrat according to this scale

S	Interpretation
0	Species absent from quadrat
0.1	Species represented by a solitary short shoot, < 5% cover
0.5	Species represented by a few (< 5) short shoots, < 5% cover
1	Species represented by many (> 5) short shoots, < 5% cover
2	Species represented by many (> 5) short shoots, 5%–25% cover
3	Species represented by many (> 5) short shoots, 25%–50% cover
4	Species represented by many (> 5) short shoots, 50%–75% cover
5	Species represented by many (> 5) short shoots, 75%–100% cover

Net aboveground productivity of *Thalassia testudinum* was measured on a quarterly basis at each permanent site using a modified leaf marking technique (Zieman 1974; Zieman et al. 1999). Six 10 × 20-cm quadrats were haphazardly distributed within 10 m of a permanent steel rod that marked the site. Within each quadrat, all short shoots (SS) of the seagrass *T. testudinum* were marked near the base of the leaves by driving an 18-gauge hypodermic needle through all of the leaves on a short shoot. Care was taken not to disturb other plant and animal taxa in the quadrats. The marked SS were allowed to grow for 10–14 days; after which all above-ground seagrass material in the quadrats was harvested. The number of SS of each seagrass species was counted. Plant material was separated by seagrass species; and *T. testudinum* leaves were separated further into newly produced (below the marks) and older leaf material. All leaves of all species were counted, measured (length and width to nearest millimeter), cleaned of epiphytes by gentle scraping, and dried to constant mass at 70°C. We quantified standing crop (SC) as the dry weight of green leaves per meter squared; short shoot density as the number of SS per meter squared; SS size as the dry weight of green leaves per SS; areal leaf production as the dry weight of green leaves produced per meter squared per day; and specific leaf production as dry weight of green leaves produced per gram of dry weight of green leaves per day.

Replicate measurements of seagrass parameters at each permanent site were reduced to a single mean for each site visit. Seasonal patterns in seagrass parameters were assessed by least-squares fitting of a sine function to the data:

$$\hat{Y} = \mathrm{mean} + A \times \sin(\mathrm{DOY} + \Phi) \tag{4}$$

where $\hat{Y}$ is the estimated value of the time series as a function of a yearly mean and a time-varying sine function with amplitude A, day of year (DOY) in radians, and a phase angle Φ. A similar model was used to describe seasonal patterns in biomass, productivity and nutrient content of *Syringodium filiforme* in the Indian River Lagoon, Florida (Short et al. 1993). Yearly values of some parameters, like areal leaf production and leaf emergence rate, were calculated by integrating the best-fit sine function over a period of 1 year.

At the permanent sites, the relationships between the Braun-Blanquet abundance score (A_i) and seagrass SC (defined as the dry weight of green leaves per meter squared) for the two most commonly encountered seagrass species (*T. testudinum* and *S. filiforme*) were determined using least-squares regression. These relationships were used to estimate SC of *T. testudinum* and *S. filiforme* across the region, by calculating SC from the A_i, then scaling this value by the Braun-Blanquet frequency score (F_i). Data from the random mapping sites and the permanent sites were used to generate continuous surfaces using a kriging algorithm (point kriging, isotropic linear variogram model, no drift, no nugget). We interpolated the existing data to a regular 1-km grid from mapping site data; this spatial resolution was the maximum that could be supported by the data. Spatial analysis software (Surfer; Golden Software, Golden, Colo.) was used to calculate areal extent of seagrass abundance, density and SC classes, as well as to integrate the surfaces of *T. testudinum* and *S. filiforme* SC to estimate the total biomass of green leaves of these two species in the area.

Results

Seagrass distribution

Seagrasses were found at 80.8% of the 874 randomly chosen mapping sites (Fig. 1, Table 2). *Thalassia testudinum* was the most commonly encountered species, occurring at 67.2% of all sites. *Syringodium filiforme* was also commonly encountered (38.9% of all sites); *Halodule wrightii* and *Halophila decipiens* were each found at about 15% of all sites, and *Halophila engelmanni* was rarely encountered (1.5% of sites). Most commonly, individual species had <25% cover ($D_i < 2$), but the most common cumulative density for all seagrasses at sites where seagrasses occurred was 50–75% cover ($3 < D < 4$).

We used our randomly located mapping sites to estimate the areal extent of each seagrass species within the study area. While any one mapping site may have been unrepresentative of the surrounding sea bed due to small-scale patchiness in seagrass distribution, we assumed that errors in predicting distribution caused by this patchiness were small when averaged over 874 observations. Using the criterion of $D_i \geq 0.1$ at a site for defining the presence of seagrass, seagrasses occurred over 12,800 km^2 of the 17,000 km^2 surveyed (Fig. 2). *Halophila decipiens* had the greatest range in the study area; it was found to occur over 7,500 km^2 of the study area (Fig. 3D). The range of *T. testudinum* was almost as extensive; it was found to occupy 6,400 km^2 (Fig. 3A). *S. filiforme* occupied 4,400 km^2 (Fig. 3B) and *Halodule wrightii* occupied 3,000 km^2 (Fig. 3C). The range of *Halophila engelmanni* was restricted to only 50 km^2. Note that these distribution maps do not imply continuous dense beds of seagrass over the entire area; rather they indicate where, on the scale of a 50-m transect, one would be likely to find each species.

Seagrass productivity, SC and short shoot density at permanent sites

The purpose of choosing the permanent sites was to monitor productivity of *T. testudinum*, the dominant seagrass species in most of south Florida. These permanent sites always contained *T. testudinum* and were thus not representative of seagrass occurrence or density in the survey area. This is evident from the frequency distribution of the mean short shoot density, SC, and A_i observed at the 30 permanent monitoring sites (cf. Fig. 4 and Table 2). Most commonly, the permanent sites had *T. testudinum* SC in the range of 40–50 g m^{-2}; at 17 of the 30 sites *S. filiforme* was also present. The only other seagrass species recorded from the permanent sites was *Halodule wrightii*; it was found as a minor and highly variable component of the seagrass beds at five of the 30 sites. At no point did *H. wrightii* comprise >5% of the seagrass SC. The mean short shoot densities of *T. testudinum* and *S. filiforme* were 395 and 377 SS m^{-2}, respectively; but since *S. filiforme* generally is much less massive than *T. testudinum* (means of 13 mg green leaves SS^{-1} for *S. filiforme* versus 110 mg SS^{-1} for *T. testudinum*), the seagrass SC at the sites was generally dominated by *T. testudinum* (mean = 38, compared to 9 g m^{-2} for *S. filiforme*). At a few sites, however, *S. filiforme* SC was greater than *T. testudinum*; *S. filiforme* SC approached 100 g m^{-2} on the Gulf of Mexico side of the middle Florida Keys. The difference in the spatial scale of the Braun Blanquet A_i data from the quadrat-collected data lead to a discrepancy in the frequency of occurrence of *S. filiforme* at the permanent sites (Fig. 4): *S. filiforme* was absent from only six of the 30 permanent sites at the scale of a 50-m transect compared to 13 of the 30 permanent sites at the scale of the quadrat estimates, which were collected from within 10 m of each permanent site.

Averaging across all sites, SC and A_i exhibited seasonal variation for both *T. testudinum* and *S. filiforme* (Fig. 5). Assessing seasonality as the amplitude of the sine wave fit through the data divided by the mean (Eq. 4), seagrass SC was more seasonal than A_i. Seasonalities of SC for *T. testudinum* and *S. filiforme* were 32.9% and 31.2%, respectively; while seasonalities of A_i for the two species were 16.9% and 15.6%. Seasonal peaks in SC and A_i of *T. testudinum* occurred in June, while peaks in these parameters for *S. filiforme* occurred in July–August. The degree of seasonality in SC and A_i

Table 2 Braun-Blanquet assessment of seagrass density (D) at 874 mapping sites

Species	Density class (D)								
0	0	$0<D\leq 0.1$	$0.1<D\leq 0.5$	$0.5<D\leq 1$	$1<D\leq 2$	$2<D\leq 3$	$3<D\leq 4$	$4<D\leq 5$	$D>5$
Fraction of all sites sampled (%)									
Thalassia testudinum	32.8	3.5	9.5	10.9	16.1	14.5	10.3	2.3	0.0
Syringodium filiforme	61.1	3.9	4.9	7.0	11.0	4.5	3.4	4.2	0.0
Halodule wrightii	83.2	3.8	6.4	2.5	2.7	1.1	0.1	0.1	0.0
Halophila decipiens	85.8	2.6	3.8	2.6	2.4	1.7	0.9	0.1	0.0
Halophila engelmanni	98.5	0.9	0.3	0.1	0.1	0.0	0.0	0.0	0.0
ΣD for all seagrasses	19.2	3.9	6.9	8.4	12.6	13.8	16.1	12.9	6.2
Fraction of sites where species occurs (%)									
T. testudinum		5.3	14.1	16.2	24.0	21.6	15.3	3.4	0.0
S. filiforme		10.0	12.6	17.9	28.2	11.5	8.8	10.9	0.0
H. wrightii		22.4	38.1	15.0	16.3	6.8	0.7	0.7	0.0
H. decipiens		18.5	26.6	18.5	16.9	12.1	6.5	0.8	0.0
H. engelmanni		61.5	23.1	7.7	7.7	0.0	0.0	0.0	0.0
ΣD for all seagrasses		4.8	8.5	10.3	15.6	17.1	20.0	16.0	7.6

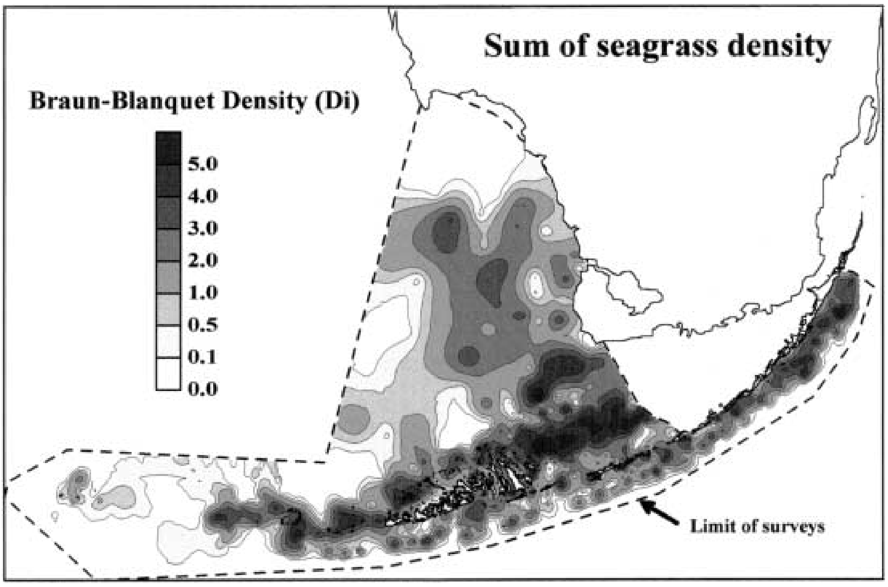


Fig. 2 Seagrass distribution across the study area. Data from the 874 mapping sites (Fig. 1) were interpolated using a kriging algorithm to generate contours of the sum of the Braun Blanquet density (D_i) for the five seagrass species. The total surveyed area was 17,000 km^2, of which 12,800 km^2 supported seagrasses

was variable among sites. Site-specific seasonality of *T. testudinum* SC ranged from a minimum of 11% to a maximum of 77%; while seasonality of *T. testudinum* A_i ranged from 4% to 67%. Seasonality of *S. filiforme* showed a similar variability, with seasonality in SC ranging between 5% and 87% and seasonality in A_i between 6% and 66%. There was no striking spatial pattern to the degree of seasonality of the abundance of *T. testudinum* and *S. filiforme*; and seasonality was not significantly correlated with water depth (linear regression, $r^2 < 0.03$ and $P > 0.45$ for all comparisons).

Productivity of *T. testudinum* was both temporally and spatially variable. Owing to weather and delays in setting up some of the permanent sites, we made 329 (out of a possible 360–30 sites × 12 sampling periods) determinations of *T. testudinum* productivity. The lowest areal productivity rate measured was 0.05 g m^{-2} day^{-1}, the highest was 3.29 g m^{-2} day^{-1}, and the mean was 0.70 g m^{-2} day^{-1}. Specific productivity ranged between 3.2 and 34.2 mg g^{-1}day^{-1}, with a mean of 18.3 mg g^{-1} day^{-1}. This large range in productivity was driven by both variation in SC among stations and by strong seasonality in productivity.

A strong seasonal pattern in productivity of *T. testudinum* was evident when results from all sites were averaged (Fig. 6). The yearly mean specific productivity for all sites, as indicated by the constant in the sine model (Eq. 4), was 18.2 ± 0.85 mg g^{-1} day^{-1}. The amplitude of the model was 5.6 ± 1.2 mg g^{-1} day^{-1}; hence the all-site average seasonality was 30.8%. Annual peaks in specific productivity occurred in August, and minima in February. On an areal basis, mean productivity of *T. testudinum* was 0.69 ± 0.06 g m^{-2} day^{-1} and the amplitude of the sine model was 0.42 ± 0.08 g m^{-2} day^{-1}. Seasonal maxima and minima were 60.9% above and below the mean productivity. Areal productivity peaked in July, because the areal productivity rate is a function of both specific productivity, which peaked in August (Fig. 6), and SC, which peaked in June (Fig. 5).

There was a strong spatial pattern to both the mean and the seasonality of specific productivity of *T. testudinum* at the sites. Mean productivity was generally higher on the south side of the Florida Keys and increased offshore (Fig. 7A). On the Gulf of Mexico side of the Florida Keys, the northernmost stations had a yearly mean specific productivity of 15–16 mg g^{-1} day^{-1}, while the sites furthest offshore on the Atlantic side of the Florida Keys had yearly means as high as 22 mg g^{-1} day^{-1}. In contrast to the yearly mean, seasonality of productivity was much lower on the Atlantic side of the Florida Keys (20–30% of the mean) than on the Gulf of Mexico side of the Keys (30–50% of the mean; Fig. 7B).

Both the mean and seasonality of specific productivity were related to water depth (Fig. 8). Mean annual specific productivity increased with water depth, at a rate of 0.60 ± 0.02 mg g^{-1} day^{-1} m^{-1}. Conversely, the seasonality of specific productivity decreased with water depth at a rate of 2.0 ± 0.6% m^{-1}. In shallow water, the amplitude in specific productivity was 50% of the mean annual value, while at our deepest sites (ca. 11.5 m) the amplitude was only 20% of the mean. In contrast to the relationships with water depth, there was no relationship between specific productivity and SC of *T. testudinum*, as would be expected if self-shading were an important control on productivity (linear regression, $r^2 = 0.03$, $P = 0.351$).

Relationships between rapid visual assessments and seagrass SC

The rapid visual assessments of seagrass abundance were correlated with measured seagrass SC for *T. testudinum* and *S. filiforme* (Fig. 9). A simple linear relationship

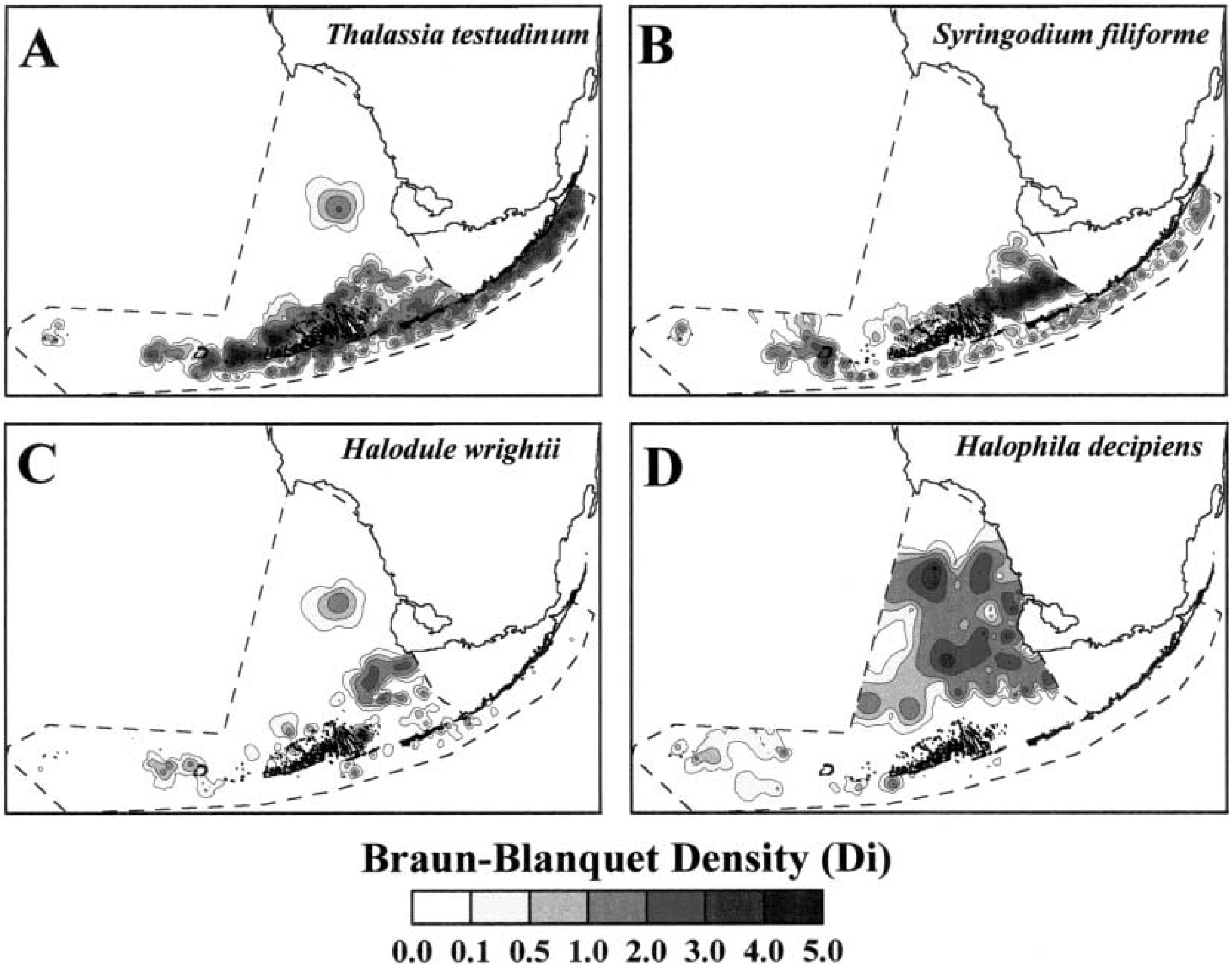


Fig. 3A–D Distribution of the four most common seagrass species across the study area. Data from the 874 mapping sites (Fig. 1) were interpolated using a kriging algorithm to generate contours of D_i. **A** *Thalassia testudinum* covered 6,400 km^2; **B** *Syringodium filiforme* covered 4,400 km^2; **C** *Halodule wrightii* covered 3,000 km^2; **D** *Halophila decipiens* covered 7,500 km^2

through the origin described 80% of the variation in *T. testudinum* SC, and 73% of the variation in *S. filiforme* SC, but the slope of the *T. testudinum* SC-A_i relationship [16.9 ± 0.5 (± 1 SE), $n = 314$] was twice as high as the slope of the same relationship for *S. filiforme* (8.9 ± 0.3, $n = 289$). Fitting an exponential model ($SC = e^{bA}$, where $b = 0.9$, $r^2 = 0.63$) to the relationship for *S. filiforme* did not improve the predictive power of the model. Using the linear regression relationships between SC and A_i for *T. testudinum* and *S. filiforme*, it is possible to plot contours of the SC of both species across the study area (Fig. 10). Integrating the SC for the study area gives an estimate of 1.4×10^{11} g *T. testudinum* and 3.6×10^{10} g *S. filiforme* in the study area. Using the areal extent of each species, this gives an average SC of 21.9 g m^{-2} for *T. testudinum* and 8.2 g m^{-2} for *S. filiforme* at sites where these species are found. Using the site-averaged mean specific productivity of 18.3 mg g^{-1} day^{-1} for *T. testudinum* and the total SC of *T. testudinum* in the study area, an order-of-magnitude prediction of the yearly production of new *T. testudinum* leaves is 9.4×10^{11} g year^{-1}.

Discussion

Seagrass beds were the most common benthic habitat encountered in our mapping surveys in southern Florida: 80.8% of the 874 mapping sites supported some seagrass (Table 2). The remaining 19.2% of the visited sites were a combination of living coral reef, hardbottom habitat, or unconsolidated sediments that did not support seagrasses. The seagrass beds surveyed in this study are only part of a larger, semi-continuous distribution of seagrasses along the southern tip of the Florida peninsula that runs from Biscayne Bay, through Florida Bay (Zieman et al. 1989; Fourqurean et al. in press), the Florida Keys, and north to Cape Romano; the western extent of the seagrasses on the southwest Florida Shelf has not been well-delineated but extends to at least the

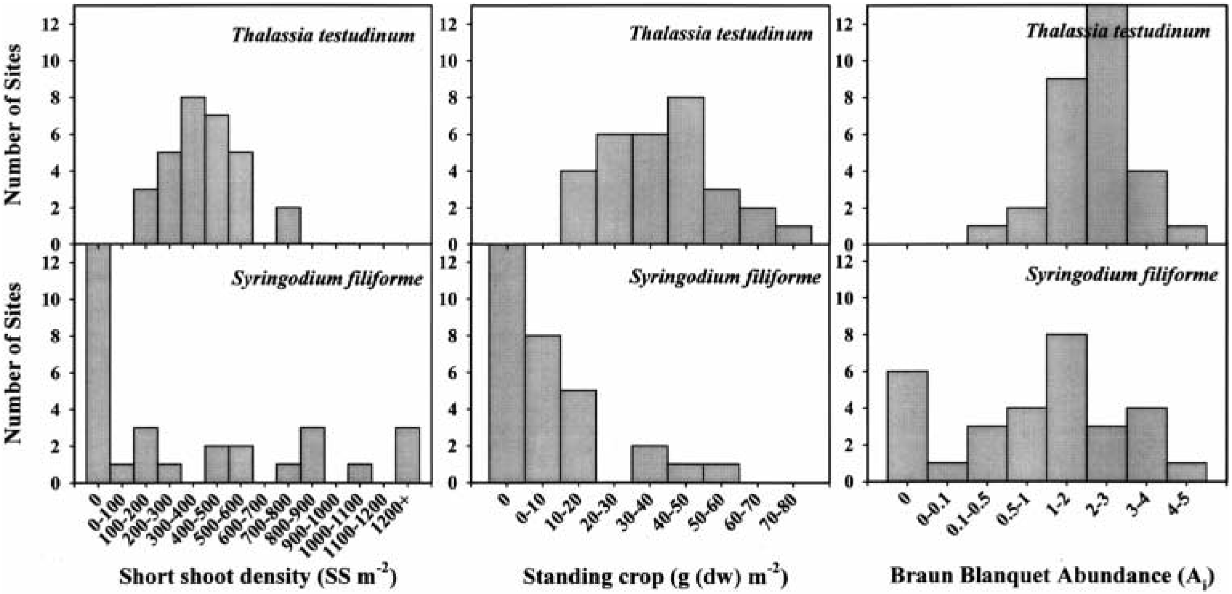


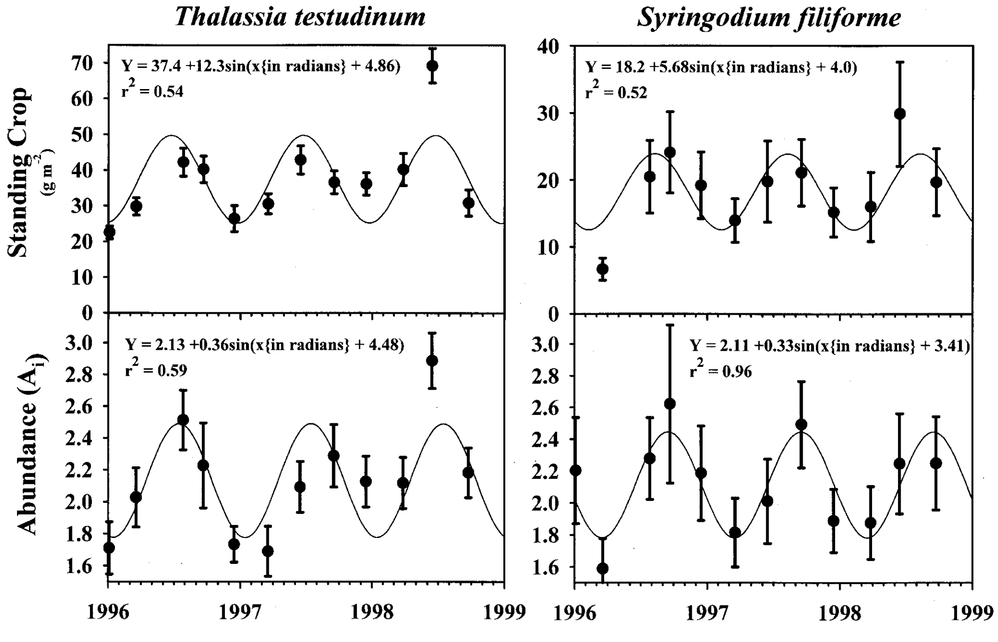
Fig. 4 Characteristics of seagrass communities at the permanent marking sites. The permanent sites were dominated by *T. testudinum*, with *S. filiforme* of secondary importance. The difference in the frequency of the 0 category between standing crop and Braun Blanquet abundance (A_i) for *S. filiforme* is caused by the different sampling scale employed. Short shoot densities were counted in 10 × 20-cm quadrats close to a central marker, while A_i data were collected along a 50-m transect

35-m isobath (Iverson and Bittaker 1986; Continental Shelf Associates 1991). While the extent of seagrass beds worldwide is not well described, the semi-continuous area supporting seagrasses in south Florida is the largest documented seagrass community in the world. This seagrass community is an important habitat for many of the commercially and recreationally important animal species in the region (e.g., pink shrimp, *Farfantepenaeus duorarum*; spiny lobster, *Panulirus argus*; queen conch, *Strombus gigas*; spotted seatrout, *Cynoscion nebulosus*) as well as the feeding grounds for many coral reef-associated fishes (Starck and Davis 1966).

Seagrass distribution and abundance

The rapid visual assessment techniques used in this study allowed us to conduct wide in situ surveys of seagrass distribution. In general, the densest seagrass beds in the study area were located on the Gulf of Mexico side of the middle Florida Keys (Fig. 2); these very dense areas were dominated by *Syringodium filiforme* (Fig. 3B). The ramet-level demographics and growth form of this unusually dense seagrass bed indicate that intense intra-

Fig. 5 Seasonality of standing crop and abundance of *T. testudinum* and *S. filiforme* at the 30 permanent sites. *Each point* is the mean of the 30 site means at each sampling period; *error bars* indicate ± 1 SE. *Lines* are the results of fitting the sine model (Eq. 4) to the data using an iterative least-squares routine. The estimates of all three model parameters (mean, amplitude and Φ, Eq. 4) were all significantly different from 0 at $P = 0.05$ for all four regressions



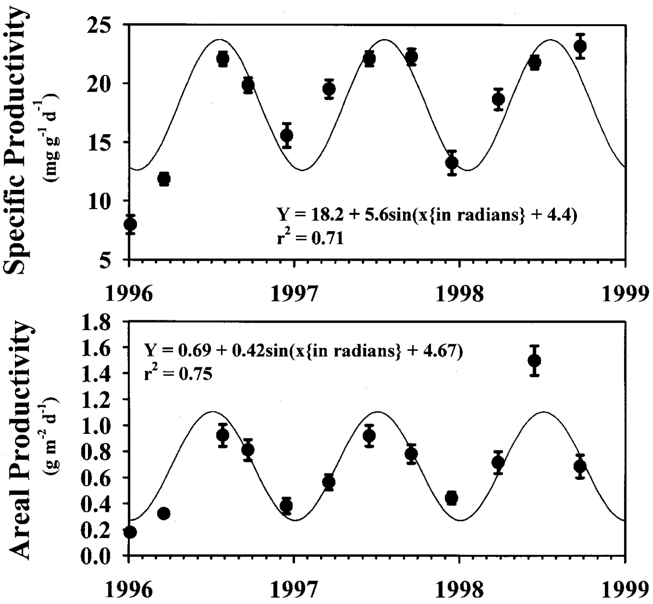


Fig. 6 Seasonality of productivity of *T. testudinum* at the 30 permanent sites. *Each point* is the mean of the 30 site means at each sampling period; *error bars* indicate ±1 SE. *Lines* are the results of fitting the sine model (Eq. 4) to the data using an iterative least-squares routine

specific competition in this seagrass bed is an important factor structuring the seagrass community (Kenworthy and Schwarzschild 1998). In order to escape low light conditions caused by self-shading, *S. filiforme* in this dense bed forms rhizome branches in the plant canopy; the resultant multi-layered canopy extends up to 1 m from the bottom. This very dense seagrass bed has also been experiencing very intense herbivory from an unusually large and dense population of sea urchins, and was being denuded at a rate of over 3000 m^{-2} day^{-1} in 1998 (Rose et al. 1999).

The seagrass species had quite different distribution patterns, leading to zones of dominance by different species (Fig. 3). Zonation of the seagrass bed at this large scale is likely a result of the differing habitat requirements of the species (Fourqurean et al. in press). *Thalassia testudinum* was the dominant seagrass species in the nearshore habitats of the surveyed area (Fig. 3A). One interesting *T. testudinum*-dominated site that was encountered west of Cape Sable on the southwest Florida Shelf was an exception to this pattern. If large solution holes occur in the carbonate bedrock of this area, it is possible that this isolated *T. testudinum* bed is associated with such a feature in much the same way that smaller circular *T. testudinum* beds are associated with solution holes in Biscayne Bay, Florida (Zieman 1972).

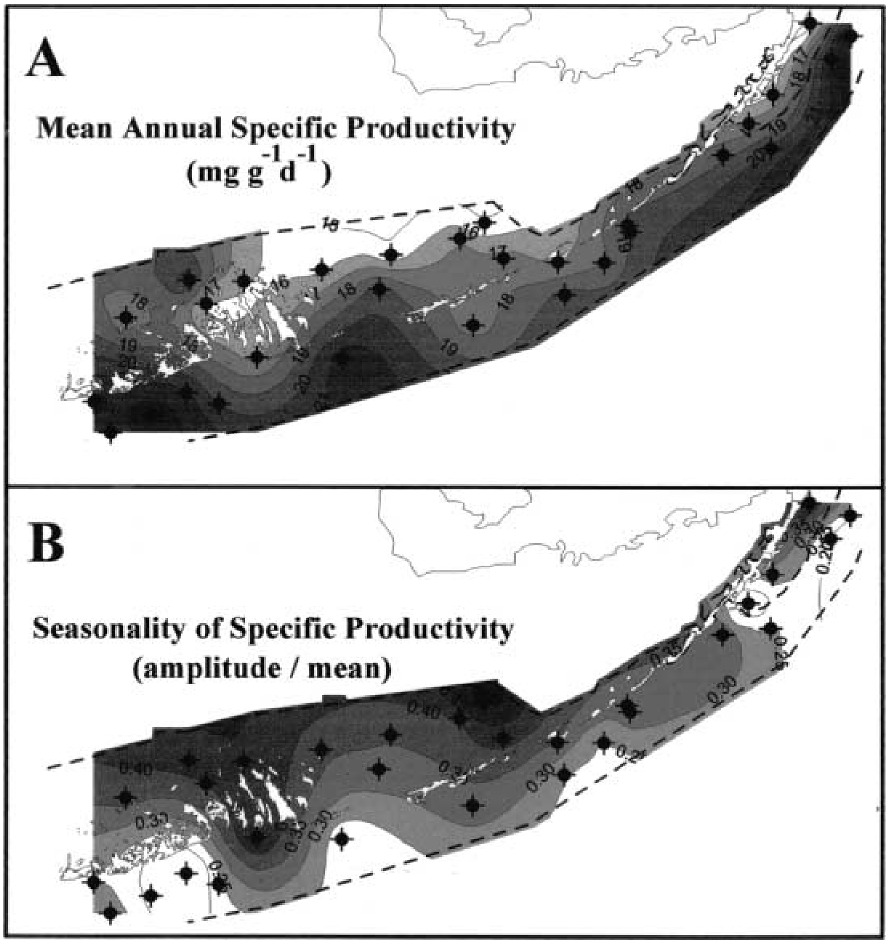


Fig. 7A, B Patterns in productivity of *T. testudinum* across the study area. *Contours* are based on data collected at the permanent monitoring sites, indicated by *closed symbols*, and were created using a kriging algorithm. **A** Contours of mean annual specific productivity; **B** Contours of seasonality in specific productivity, defined as the ratio of the amplitude divided by the constant of the sine model (Eq. 4)

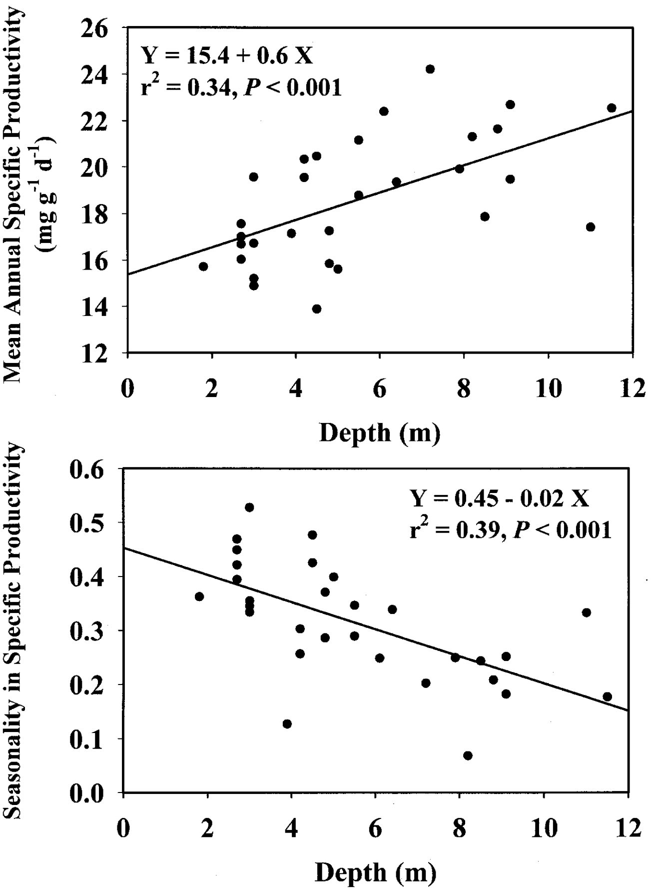


Fig. 8 Relationships between both mean annual specific productivity (*top*) and seasonality in specific productivity (*bottom*) and water depth at the site. *Lines* are statistically significant linear regressions through the data, $n = 30$

On the Atlantic Ocean side of the Florida Keys, the density of *S. filiforme* increased offshore. *Halodule wrigthii*, which is very common in Florida (Zieman et al. 1989; Durako et al. in press), was rarely found on the oceanside of the Keys but was quite common and dense to the north of the large *S. filiforme* bed (Fig. 3C). Further to the northwest there was a large area dominated by the seagrass *Halophila decipiens* (Fig. 3D). This largely undescribed, deep-water *H. decipiens* bed constitutes a large part of the total extent of seagrass beds in the region. In Australia, large areas of deep *Halophila* spp.-dominated seagrass beds support far fewer animals than shallow-water seagrass beds (Lee Long et al. 1996), but the productivity of these deep-water beds is relatively high despite their low biomass (Erftmeijer and Stapel 1999). Even at low biomass, seagrass beds are important habitats for resident epibenthic fauna in Florida (Fonseca et al. 1996). The opportunistic life history of *Halophila* species leads to a dynamic nature of such deep water seagrass beds, with large variations in cover and abundance (Lee Long et al. 1996). Deep water seagrass communities may be at enhanced risk of loss because of chronic anthropogenic water quality degradation.

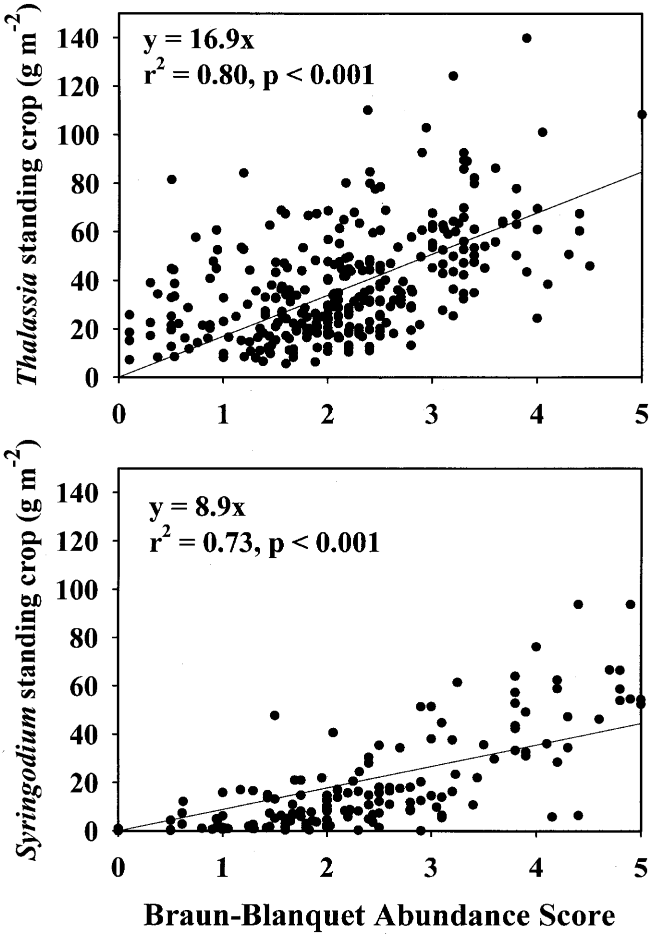


Fig. 9 Relationships between Braun Blanquet abundance (A_i), measured along a 50-m transect, and standing crop, measured in six 10 × 10-cm quadrats, of *T. testudinum* (*top*) and *S. filiforme* (*bottom*). *Each point* represents the mean standing crop value from the six quadrats measured at a site each sampling period; $n = 329$ for *T. testudinum* and $n = 289$ for *S. filiforme*. *Lines* are linear regression, forcing the relationship through the intercept

Converting the rapid visual assessments to SC values was only possible for the two species that were common at our 30 permanent monitoring sites. Simple linear regression provided statistically significant, albeit imperfect, conversion factors for *T. testudinum* and *S. filiforme* (Fig. 9). The scatter about the regression relationships was due to two factors: the different spatial scale and quadrat location of collection for the Braun-Blanquet data (ten randomly placed 0.25-m^2 quadrats placed along a 50-m transect) versus the SC data (six 200-cm^2 quadrats haphazardly placed over *T. testudinum* shoots), and the inherent non-linearity of the Braun-Blanquet scale at low cover values (Table 1). Nevertheless, these linear relationships allowed for a first-order conversion of the cover data to leaf biomass. The limits of the *T. testudinum* and *S. filiforme* beds as represented by SC (Fig. 10) are more restrictive of the limits of the beds as defined by the Braun-Blanquet data (Fig. 8A, B) because the SC maps are drawn with a minimum limit for bed definition of 10 g m^{-2}. This boundary is arbi-

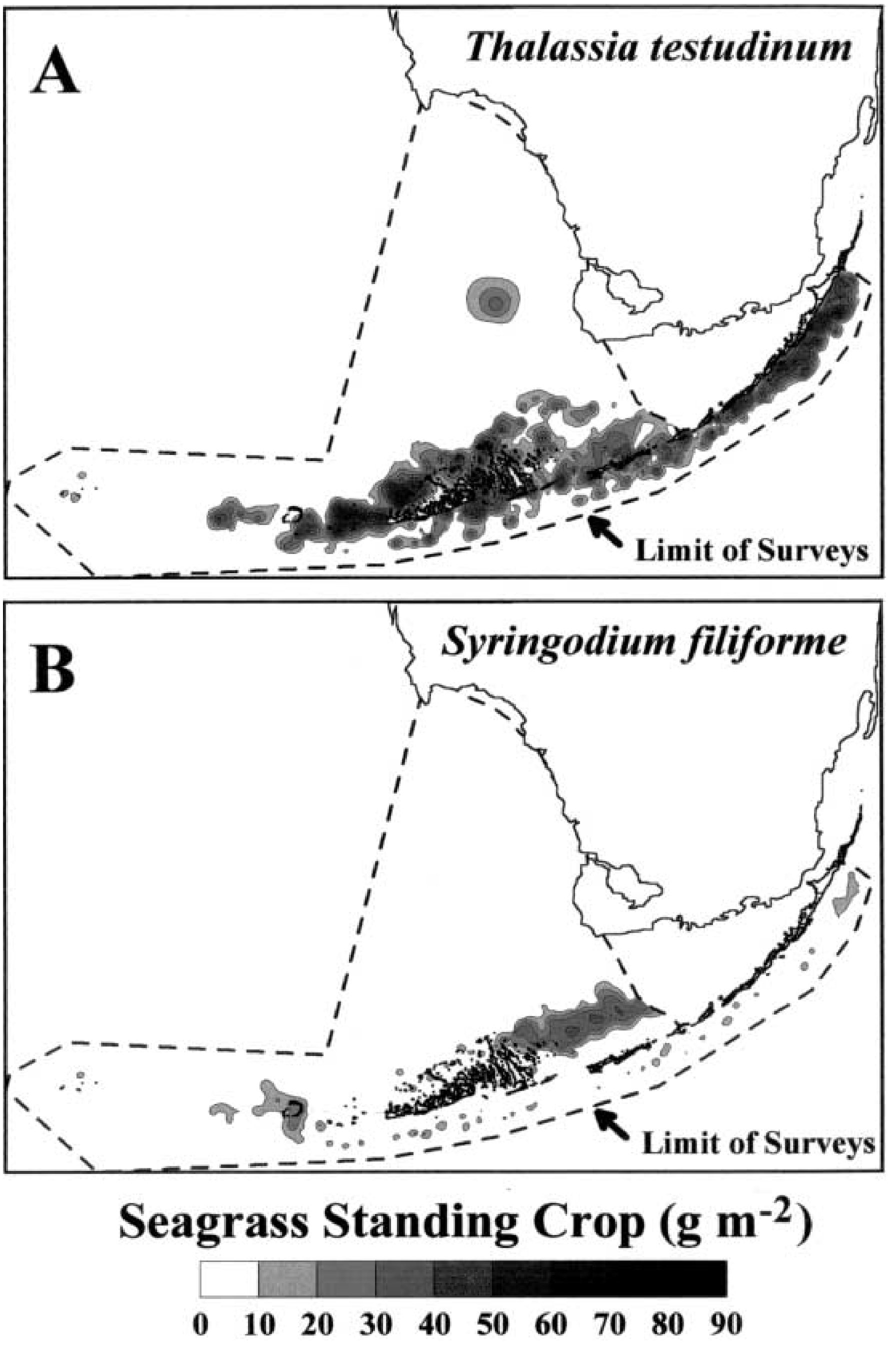


Fig. 10 Seagrass standing crop across the study area. Values for A_i at each of the 874 mapping sites were converted to standing crop using the linear relationships from Fig. 9, and *contours* were drawn by interpolating these values using a kriging algorithm

trary, but it roughly corresponds to a Braun-Blanquet abundance of 1%, or 5% cover. Integrating species-specific SC over the survey area yields estimates of 1.4×10^{11} g *T. testudinum* and 3.6×10^{10} g *S. filiforme*. Because our mapping sites were all censused in summer, and SC peaks in summer months (Fig. 5), these are estimates of maximum SC; winter lows may be as much as 50% lower. Because leaves make up on average only about 10% of the biomass *of T. testudinum* (Fourqurean and Zieman 1991) and *S. filiforme* (Kenworthy and Schwarzschild 1998) in south Florida, total seagrass biomass is an order of magnitude greater than the integrated SC values.

There was substantial interannual variability in the SC and A_i of *T. testudinum* during the study period. During the summer of 1998, mean SC was nearly double the values measured in the previous 2 years (Fig. 5). Similarly, A_i was 50% higher in 1998 than in the previous years. Such interannual variability makes it necessary to sample seagrass beds for more than 2 years in a monitoring program before making conclusions about trends.

The magnitude of the seasonal cycle in *T. testudinum* SC in south Florida was within the range of other published data sets (Table 2). We searched the literature for data on seasonality of *T. testudinum* SC and productivity, and analyzed this published data by fitting Eq. 4 to the time series (Table 3). Seasonality of SC, defined as the ratio of the amplitude of the sine model to the mean, did not follow the latitudinal gradient we expected to find for this tropical plant across the subtropical span of the Gulf of Mexico. With the exception of very high (94%) seasonality of SC in two north Florida embayments where leaf productivity virtually stops in winter (Iverson and Bittaker 1986), there was no increase in seasonality with latitude in the eight data sets compared over 7° of latitude. This is likely because SC is a function of both production and loss of leaves, and many factors control loss of seagrass leaves, like herbivory (Heck and Valentine 1995), storm energy (Thomas et al. 1961), and epiphyte loads (Littler and Littler 1999).

Thalassia testudinum productivity

The extensive occurrence of seagrasses in the region, coupled with an historically clear, oligotrophic water column overlying the seagrass beds, make seagrasses a very important contributor to primary productivity in the coastal zone in south Florida. *T. testudinum* produces, on an annual basis, 6.7 g new leaves g^{-1} SC. For the region surveyed, this results in an annual leaf production of 9.4×10^{11} g. If we assume that *S. filiforme* has a similar specific productivity (Barber and Behrens 1985), *S. filiforme* contributes another 2.4×10^{11} g leaves year^{-1}.

Mean leaf productivity of *T. testudinum* on an areal basis in this study was towards the low end of the range reported in the literature (Zieman and Wetzel 1980; Zieman 1982 and Table 2), most likely for two reasons: previous measurements of *T. testudinum* productivity were generally made during summer months, when productivity peaks; and most other reports of *T. testudinum* productivity were made in the densest areas of seagrass in the local area. In our work, sites were chosen without regard for seagrass density, hence many of our monitoring locations were in quite sparse seagrass beds. Therefore, our estimates of areal production are representative of the south Florida seagrass ecosystem as a whole, not just areas of dense seagrass. It should be noted that our (and generally other) estimates of areal productivity of seagrasses include only "aboveground" productivity of leaf blades; areal productivity rates for belowground roots and rhizomes of *T. testudinum* are about 50% of the areal leaf productivity estimates (Patriquin 1973; Kaldy and Dunton 2000).

Areal production of seagrass is the product of the density of seagrass and the specific productivity. Specific productivity of *T. testudinum* in this study, an annual average of 18.2 mg g^{-1} day^{-1}, was within the range reported in the literature. It was slightly less than the 21.5 mg g^{-1} day^{-1} reported for Biscayne Bay, Florida in 1969–1970 (Zieman 1975), yet higher than the 14.8 mg g^{-1} day^{-1} reported for Florida Bay for the period 1989–1996 (Zieman et al. 1999). Florida Bay was experiencing a drastic decline in seagrass abundance and light availability during the period 1989–1996, however, so Zieman et al.'s (1999) estimate of specific productivity may be aberrantly low (Robblee et al. 1991; Thayer et al. 1994; Hall et al. 1999).

In our review of the literature, there was a pronounced latitudinal trend in the seasonality of specific productivity of *T. testudinum*: the most tropical location [Puerto Morales, Mexico; latitude 20°51′N; (van Tussenbroek 1995)] had seasonality of only 6% while the northernmost location had a seasonality of 58% [Anclote Estuary, Fla.; latitude 28°10′N; (Barber and Behrens 1985)]. There was no latitudinal trend in areal productivity rates of *T. testudinum*, however. It is pos-

Table 3 Yearly means and seasonality of standing crop and productivity of *Thalassia testudinum* along a latitudinal gradient. Values from the literature were obtained by digitizing published figures and fitting the sine model (Eq. 4) to the data; mean values are the mean from the model fit and the seasonality (values in parentheses, expressed as %) is the ratio of the amplitude of the model to the mean

Location	Latitude	Longitude	Number of stations	Period of observation	Standing crop (g m^{-2})	Specific productivity (mg g^{-1} day^{-1})	Areal productivity (g m^{-2} day^{-1})
North Florida[a]	29°48′N	85°00′W	2	1970s	43.5 (94%)	–	–
Anclote Estuary, Florida[b]	28°10′N	82°45′W	2	1980–1981	–	13.9 (58%)	–
Sarasota Bay, Florida[c]	27°20′N	82°30′W	4	1992–1993	59.2 (37%)	25.3 (38%)	1.7 (59%)
Charlotte Harbor, Florida[d]	26°50′N	82°06′W	8	1995–1996	20.7 (108%)	19.0 (49%)	0.4 (138%)
Lower Laguna Madre, Texas[e]	26°10′N	97°14′W	2	1994–1997	102.8 (26%)	9.0 (38%)	1.4 (57%)
Biscayne Bay, Florida[f]	25°30′N	81°15′W	3	1969–1970	102.4 (25%)	21.5 (41%)	1.7 (46%)
Florida Bay, Florida[g]	25°00′N	80°45′W	8	1989–1996	83.0 (14%)	14.8 (23%)	1.1 (33%)
South Florida (this study)	24°30′N	81°30′W	30	1995–1998	38.0 (33%)	18.2 (31%)	0.7 (61%)
Chelem Lagoon, Mexico[h]	21°17′N	89°45′W	2	1997–1998			6.7 (37%)
Puerto Morelos, Mexico[i]	20°51′N	86°55′W	3	1990–1992	41.0 (28%)	41.7 (6%)	1.2 (28%)

[a] Iverson and Bittaker 1986
[b] Barber and Behrens 1985
[c] Tomasko et al. 1996
[d] Tomasko and Hall 1999
[e] Kaldy and Dunton 2000
[f] Zieman 1975
[g] Zieman et al. 1999
[h] Herrera-Silveira et al. 1999
[i] van Tussenbroek 1995

sible that had complete data been available for the northernmost studies in our compilation that areal productivity would have shown a latitudinal trend.

The spatial extent of the study area described in this paper allowed us to examine regional variability in both the mean and seasonality of seagrass productivity. Mean annual specific productivity of *T. testudinum* decreased from our back-reef sites closest to the Atlantic Ocean boundary of the FKNMS towards the Florida Keys, and this trend continued on the Gulf of Mexico side of the Florida Keys (Fig. 7A). Conversely, the trend in seasonality of specific productivity ran in the opposite direction: back-reef sites exhibited the lowest seasonality, and Gulf of Mexico sites the highest (Fig. 7B). We believe that this pattern was a consequence of water depth: deeper water sites were less seasonal and had higher mean annual specific productivity (Fig. 8). Shallow marine waters heat and cool rapidly in the Florida Keys, such that cold fronts during winter in this subtropical environment can lower water temperatures to as low as 8°C during winter in Florida Bay and quiescent periods during summer can raise the water temperature above 35°C (J.W. Fourqurean, unpublished data; Boyer et al. 1999). Both of these extremes are outside the thermal window for optimal productivity of *T. testudinum* (Zieman 1975). Deeper water and the influence of the Florida Current buffer back reef sites from such temperature extremes (Roberts et al. 1982), leading to less depression of seagrass productivity at these sites during summer and winter. There was no correlation between water depth and latitude for the 30 permanent stations (Fig. 1), indicating that our depth-productivity relationship was not merely an expression of the larger latitudinal gradient in productivity.

Increasing *T. testudinum* productivity with depth (Fig. 8) is in contrast to the often observed pattern of decreasing seagrass productivity with depth (e.g., Dennison and Alberte 1982; IIzumi 1996; Kaldy and Dunton 2000) that is a consequence of the general light-limited state of seagrass beds (see Dennison 1987; Duarte 1991 for review). In south Florida, productivity of *T. testudinum* increases with depth for two reasons: first, deeper waters are buffered against extremes in temperature; and second, water depth is not a good predictor of light availability on the regional scale. Nearshore, shallower waters in the study area are more turbid than the deeper, back-reef waters further offshore (Boyer and Jones in press).

The data presented in this paper quantifies the spatial extent, species composition, and net aboveground productivity of *T. testudinum* in the seagrass beds of southern Florida. The regional scale of this study is rare in the seagrass literature (Duarte 1999). These data serve as a benchmark against which future change in the system can be quantified. Marked spatial and temporal patterns exist in distribution, productivity and seasonality of seagrasses. It must also be emphasized that the shallow marine environment of south Florida is not a pristine environment; humans have substantially altered water flow patterns, harvested great quantities of animals, changed nutrient inputs to the marine waters, and dredged and filled previously existing seagrass beds. So, although seagrasses in south Florida are widespread and apparently healthy, the state of the seagrasses in the region has already been influenced by humans.

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