FLORIDA KEYS NATIONAL MARINE SANCTUARY

WATER QUALITY PROTECTION PROGRAM

SEAGRASS STATUS AND TRENDS MONITORING

ANNUAL REPORT
FISCAL YEAR 1999

Volume I

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Seagrass Monitoring in the Florida Keys National Marine Sanctuary

Executive Summary, Annual Report - FY 1999

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PROJECT OVERVIEW

The general objective of seagrass monitoring in the Florida Keys National Marine Sanctuary (FKNMS) is to measure the status and trends of seagrass communities to evaluate progress toward protecting and restoring the living marine resources of the Sanctuary. The scope and depth of this monitoring effort are without precedent or peer for seagrass ecosystems throughout the world. Specific objectives are: 1) To provide data needed to make unbiased, statistically rigorous statements about the status and temporal trends of seagrass communities in the Sanctuary as a whole and within defined strata; 2) To help define reference conditions in order to develop resource-based water quality standards; and 3) To provide a framework for testing hypothesized pollutant fate/effect relationships through process-oriented research and monitoring. In order to meet these objectives, we have developed these goals for the project:

- Define the present distribution of seagrasses within the FKNMS
- Provide high-quality, quantitative data on the status of the seagrasses within the FKNMS
- Quantify the importance of seagrass primary production in the FKNMS
- Define the baseline conditions for the seagrass communities
- Determine relationships between water quality and seagrass status
- Detect trends in the distribution and status of the seagrass communities

To reach these goals, four kinds of data are being collected in seagrass beds in the FKNMS:

- Distribution and abundance of seagrasses using rapid assessment Braun-Blanquet surveys
- Demographics of the seagrass communities using leaf-scar counting and population demographics techniques
- Seagrass productivity of the dominant species of seagrass in the FKNMS (*Thalassia testudinum*) using the leaf-mark and harvest method
- Seagrass nutrient availability using tissue concentration assays

These data are being collected at three different types of sites within the FKNMS:

- **Level 1 Stations**: Sampled quarterly for seagrass abundance, demographics, productivity and nutrient availability. These stations are all co-located with the water quality monitoring project's stations (Figure 1)
- **Level 2 Stations**: Randomly selected locations within the FKNMS, sampled annually for seagrass abundance, demographics and nutrient availability. Each year, new locations for Level 2 stations are chosen.
- **Level 3 Stations**: Randomly selected locations within the FKNMS, sampled annually for seagrass abundance. Each year, new locations for Level 3 stations are chosen.

We are assessing both inter-annual and intra-annual trends in seagrass communities. The mix of site types is intended to monitor trends through quarterly sampling at a few permanent locations (Level 1 sites) and to annually characterize the broader seagrass population through less intensive, one-time sampling at more locations (Level 2 and 3 sites).

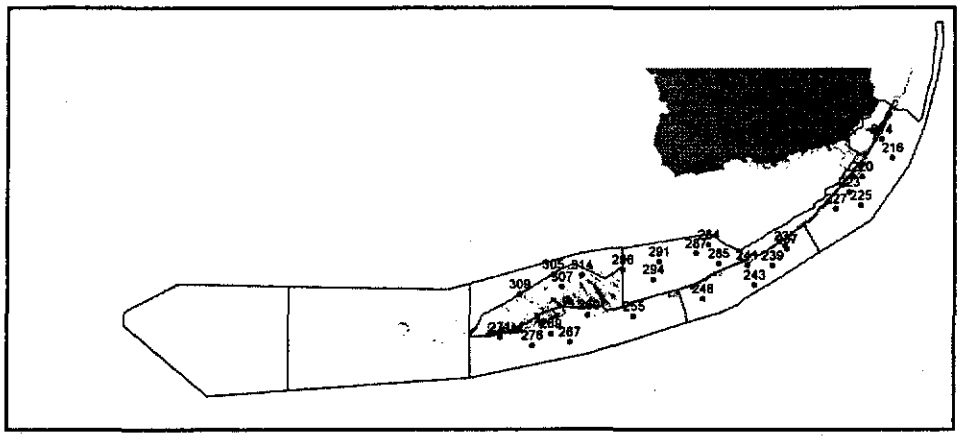

Figure 1. Location of Level 1 seagrass status and trends monitoring sites in the Florida Keys National Marine Sanctuary. Site numbers correspond to water quality monitoring locations.

PROJECT ACCOMPLISHMENTS FY 1999

In 1997, we reported data from quarterly collections from 28 permanent (Level I) stations. In cooperation with the FKNMS Special Permitting Areas monitoring program, two additional permanent Level I stations were established in the Western Sambos and Carysfort Ecological Reserves, bringing the total number of permanent monitoring stations to 30. During FY 1996 through FY 1999 summer sampling of Level 2 and Level 3 stations was conducted in May - August, and the number of sites visited each year is listed below (Figure 2):

	1996	1997	1998	1999
No. Level 2 Stations	65	87	82	78
No. Level 3 Stations	141	187	191	258
Total No. Stations	206	274	273	336

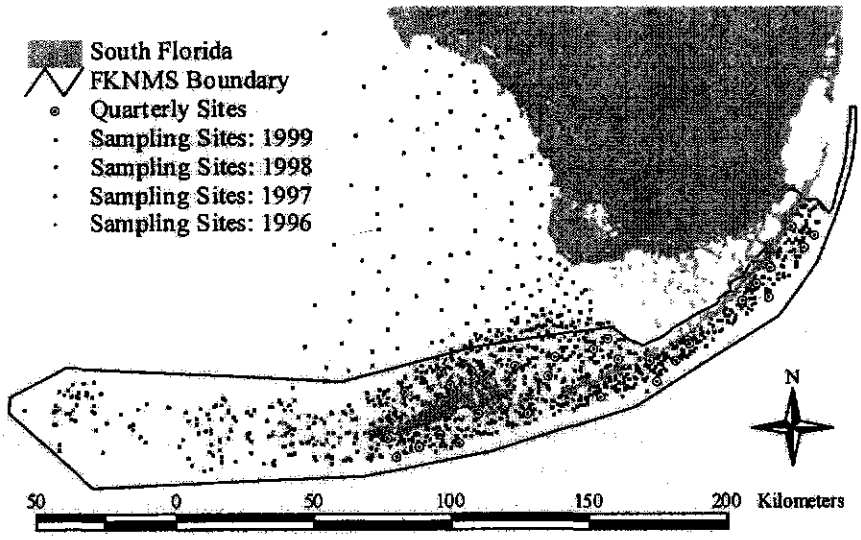

Figure 2. Level 2 and Level 3 sites sampled 1996 - 1999.

Spatial and temporal patterns in seagrass productivity

We assessed the efficacy of rapid visual surveys for estimating abundance of seagrasses in south Florida by comparing these results to more traditional analyses. 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 *Thalassia 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 engelmannii* (50 km^2). Abundance of seagrasses was seasonal, with seasonal maxima of standing crop about 32 % higher than the yearly mean. Productivity of *T. testudinum,* the dominant seagrass near-shore in the area, was both temporally and spatially variable (Figure 3). Yearly mean areal productivity averaged 0.70 g $m^{-2}d^{-1}$, with a range of 0.05 g m^{-2} d^{-1} to 3.29 g m^{-2} d^{-1}. Specific productivity ranged between 3.2 and 34.2 mg $g^{-1}d^{-1}$, with a mean of 18.3 mg $g^{-1}d^{-1}$. 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 x 10^{11} g of *T. testudinum* and 3.6 x 10^{10} g of *S. filiforme*, which translate to yearly production of 9.4 x 10^{11} g of *T. testudinum* leaves and 2.4 x 10^{11}g of *S. filiforme* leaves. 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.

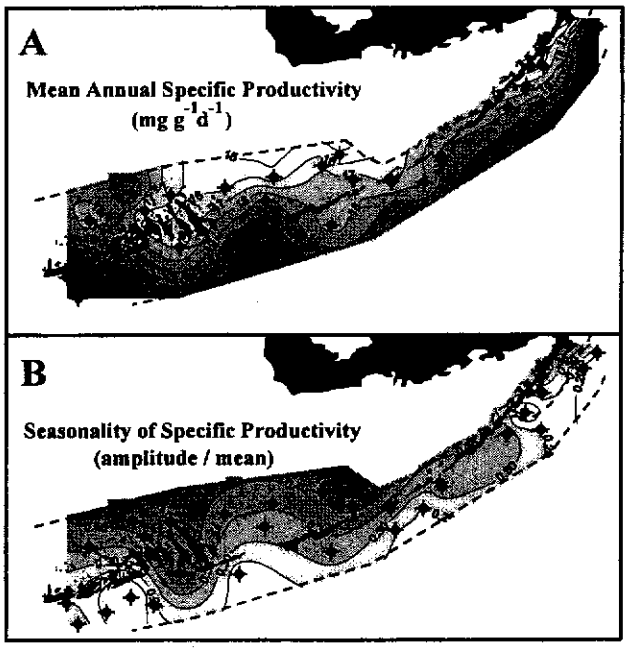

Figure 3. Spatial pattern in the mean and seasonality of productivity of the seagrass *Thalassia testudinum* in the FKNMS

Seagrass Demographic Analysis

An examination of the population age structure of 130 spatially separated sub-populations of *Thalassia testudinum* over the extent of the Florida Keys National Marine Sanctuary (FKNMS) during a two year period revealed significant spatial variation in short shoot demographic characteristics and population dynamics. Shoot age was determined for 13,544 short shoots. The number of leaf scars on individual shoots was converted to shoot ages using observed seasonally-variable leaf emergence rates. The yearly mean leaf emergence rate was 0.0295 ± 0.0128 leaves $SS^{-1}d^{-1}$ (± 1 SD), and the median age of censussed shoots was approximately 5 years. A significant relationship between asexual reproductive output and gross recruitment of short shoots into the populations ($r^2 = 0.15$, $p = 0.001$) and between mortality of short shoots and gross recruitment ($r^2 = 0.72$, $p < 0.001$) existed. Thus, the greatest risk of mortality occurred in

areas where gross recruitment was highest. The net population growth for *T. testudinum* within the boundaries of FKNMS was stable (mean = - 0.007 ± 0.092 y^{-1}). However, areas within FKNMS fluctuated between positive and negative net growth rates (-0.20 y^{-1} to 0.50 y^{-1}, Figure 3). The power of such large scale observations is the ability to identify areas of management concern and to frame questions that address the controlling mechanisms influencing these regions of fluctuating population growth.

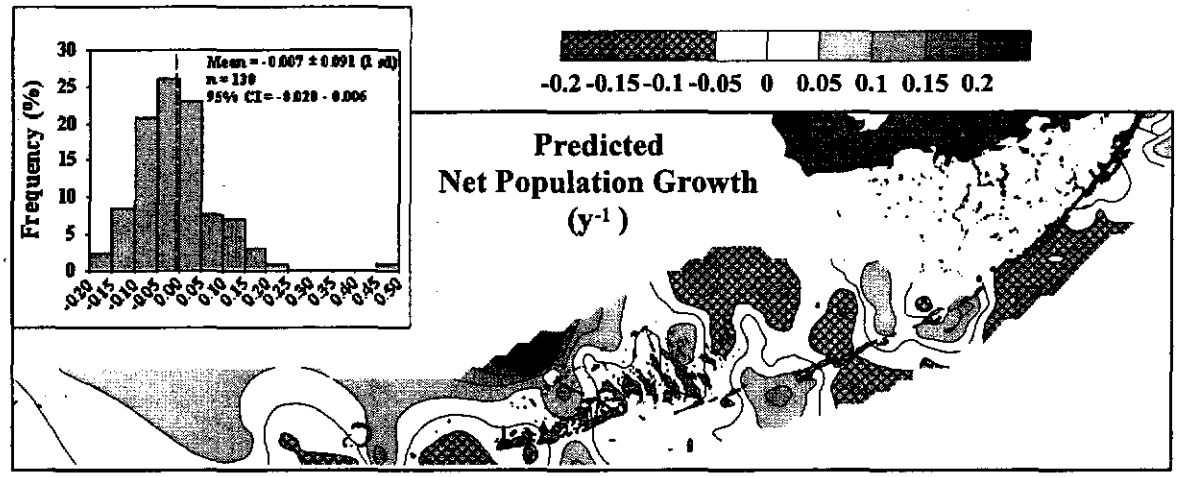

Figure 4. Spatial pattern in predicted *Thalassia testudinum* population growth rates

Key West Harbor Benthic Survey

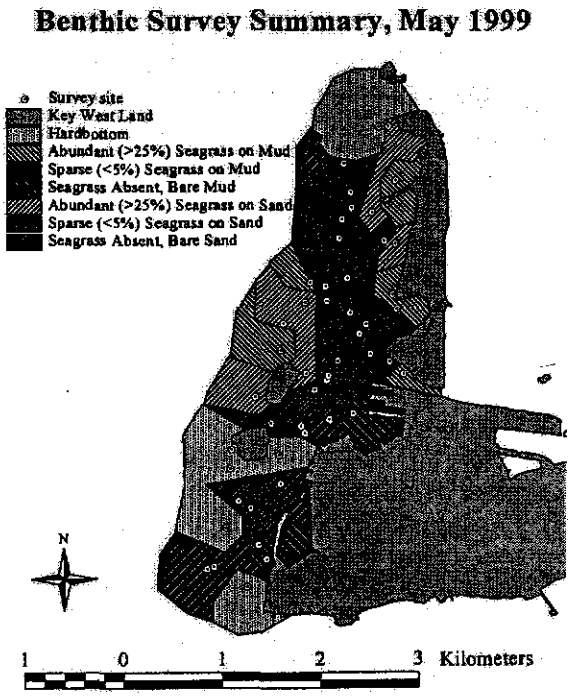

Figure 5. Benthic habitats of Key West Harbor.

In cooperation with commercial interests in the Key West Harbor area, we conducted a bottom survey of the harbor in May 1999 (Figure 4). We treated the 50 survey locations as regular synoptic survey stations in our program. We followed the standard project protocols in collecting the data. The data collected allowed for a mapping of sensitive benthic communities in the Harbor.

Data compilation in CD ROM format

We have compiled time series data and spatial maps from the monitoring effort for the period 1996 - 1999 on a CD. This CD allows for easy navigation through the data using internet browsing software; either by site for time series graphs or by taxa for distribution data. Limited numbers of the CD are available; please make a request for a copy to Jim Fourqurean at fourqure@fiu.edu.

Status and trends in seagrass communities in the FKNMS

Our surveys have provided clear documentation of the distribution and importance of seagrasses in the FKNMS. The seagrass bed that carpets 80% of the FKNMS is part of the largest documented contiguous seagrass bed on earth. These extensive meadows are vital for the ecological health of the FKNMS and the marine ecosystems of all of south Florida.

Synoptic surveys completed to date clearly describe the spatial extent of the seagrass beds, but these surveys were not designed to elucidate trends at this point, because sites were chosen randomly each year. Rather, the original EMAP protocols call for revisiting the exact sites in a second round of sampling. We propose that this second round of sampling be postponed until FY 2003, because the changes in the seagrass communities are expected to occur over this longer time scale. Second round data will allow for the direct comparison of the status of the seagrass communities at over 1000 sampling points.

Our permanent monitoring sites have provided valuable data on the inter- and intra-annual variability of seagrass cover and abundance. These 30 sites should continue to be monitored on a quarterly basis. There have been some striking trends in the seagrass communities at these permanent sites: seagrasses were lost completely at 3 of the 30 sites during hurricanes over the last 3 years. At the present time, human impacts have not been the apparent cause of any changes, but we do not understand completely the interaction man has with the natural dynamics of these systems.

Acknowledgments

This data report represents the dedicated work of many people. Craig Rose, Alan Willsie, Brad Peterson and Leanne Rutten led the field collection efforts and spearheaded the compilation of the data report; Cassandra Furst, Carlos Barrosso, Sean Meehan and Kevin Cunniff collectively put in the thousands of hours in the field and laboratory that went into the collection of these data. The field work was conducted under permits FKNMS-109-98 from the FKNMS, FDEP permit number 97S-774, FDEP Parks and Recreation Permit number 5-98-47, and a permit from the National Park Service.

SECTION 1

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

(Fourqurean, J.F., Willsie, A., Rose, C.D., Rutten, L.M.).

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

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Abstract

We assessed the efficacy of rapid visual surveys for estimating abundance of seagrasses in south Florida by comparing these results to more traditional analyses. 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 *Thalassia 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 engelmannii* (50 km^2). Abundance of seagrasses was seasonal, with seasonal maxima of standing crop about 32 % higher than the yearly mean. Productivity of *T. testudinum*, the dominant seagrass near-shore in the area, was both temporally and spatially variable. Yearly

mean areal productivity averaged 0.70 g $m^{-2}d^{-1}$, with a range of 0.05 g m^{-2} d^{-1} to 3.29 g m^{-2} d^{-1}. Specific productivity ranged between 3.2 and 34.2 mg $g^{-1}d^{-1}$, with a mean of 18.3 mg $g^{-1}d^{-1}$. 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 x 10^{11} g of *T. testudinum* and 3.6 x 10^{10} g of *S. filiforme*, which translate to yearly production of 9.4 x 10^{11} g of *T. testudinum* leaves and 2.4 x 10^{11}g of *S. filiforme* leaves. 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 man's 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). 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 landscape or 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.

The Florida Keys, a chain of islands extending southwest off of the southern tip of the Florida peninsula (ca. 24.5° N, 80.5° W), are surrounded by marine habitats typical of the tropical Atlantic and Caribbean - mangrove forests, seagrass beds, and the only barrier coral reef in the continental United States. These habitats provide support for commercial fishing and

recreational use of the nearshore marine habitat. Human perceptions of degraded habitat quality, in part supported by strong scientific data, coupled with continued human population growth in southern Florida, 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, 1995).

The litany of recent perceived environmental problems in the FKNMS is long. Particular concern has been raised over 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 1980's in adjacent Florida Bay (Robblee et al. 1991; 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; Phlips 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)).

Seagrass beds are the most common benthic community type in the FKNMS, they cover at least 14,000 km^2 in south Florida (Fourqurean et al. in press). 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). There are few areas where seagrasses are as widespread and conspicuous as south Florida. 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.

Water quality impact on seagrass beds have been documented in south Florida. Changes in water clarity following the seagrass dieoff in Florida Bay have been implicated in continuing changes in seagrass beds in Florida Bay (Thayer et al. 1994; Hall et al. 1999). Cultural eutrophication has also been suggested as a cause of loss of seagrasses in south Florida (Lapointe and Clark 1992; Lapointe et al. 1994; Tomasko et al. 1996), as well as a potential cause of deterioration of coral reefs (Lapointe 1997). 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).

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. Proper management of seagrass ecosystems worldwide depends on understanding general, landscape-scale trends (Duarte 1999).

Materials and Methods

The FKNMS is a 9600 km^2 region of shallow, tropical marine habitats on both the Gulf of Mexico and Atlantic sides of the Florida Keys (Figure 1). Though renown for its barrier coral reef, most of the area of the FKNMS is carpeted by seagrasses. The FKNMS encompasses only part of the over 14,000 km^2 of seagrass beds in south Florida (Fourqurean et al. in press). A stratified-random approach, with distance offshore as the strata, was used to locate 30 permanent seagrass monitoring sites within the FKNMS (Figure 1). Sites were sampled every three 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 Southwest Florida Shelf to the north of the FKNMS (Figure 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. The total area covered by these surveys was 17,000 km^2.

A rapid, visual assessment technique developed early in the 20th century by the plant sociologist Braun-Blanquet (Braun-Blanquet 1972) was used to assess 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. 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 m^2) were placed along each transect at pre-determined random distances from one of the marker rods. A new set of random numbers were chosen before each visit to a site. Each quadrat was examined by divers 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 purpose, is the fraction of the total quadrat area that is obscured by a particular species when viewed from directly above.

From the raw observations of cover in each quadrat at a site, three statistics were computed for each species: density, abundance and frequency. Density was calculated as $D_i = \Sigma S_{ij}/n$; 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 greater than 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 was calculated as $A_i = \Sigma S_{ij}/N_i$, 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 was calculated as $F_i = N_i/n$; $0 \leq F_i \leq 1$. In addition to species-specific measures, seagrass species richness S was calculated for each site by summing the number of seagrass species for which $D > 0$.

Primary 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 cm X 20 cm quadrats were haphazardly distributed within 10 m of a permanent steel rod that marked the site. Within each quadrat, all short shoots 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 short shoots were allowed to grow for 10 - 14 days; after which all above-ground seagrass material in the quadrats was harvested. The number of short shoots of each seagrass species was counted. Plant material was separated by seagrass species; and *T. testudinum* leaves were separated further into leaf newly produced and older leaf material. All leaves of all species were counted, measured (length and width to nearest mm), cleaned of epiphytes by gentle scraping, and dried to constant mass at 70°C. From these analyses, many descriptive quantities were calculated (Table 2).

Time series of seagrass parameters were generated for all permanent sites by reducing replicate measurements at each visit to a site to a single mean. Time series were assessed for a seasonal signal by least-squares fitting of a sine function to the data:

$$\hat{Y} = Mean + A \cdot \sin(DOY + \Phi) \qquad \text{Equation (1)}$$

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 has been successfully used to describe seasonal patterns in biomass, productivity and nutrient content of *Syringodium filiforme* in the Indian River Lagoon, FL, USA (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 one year.

At the permanent sites, the relationships between the Braun-Blanquet abundance score (A_i) and seagrass standing crop (SC, defined as the dry weight of green leaves m^{-2}) for the two most commonly encountered seagrass species (*Thalassia testudinum* and *Syringodium 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); spatial analysis software (Surfer, Golden Software, Golden, Co., USA) 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- At least one species of seagrass was present at 80.8 % of the 874 randomly-chosen mapping sites (Figure 1, Table 3). *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 engelmannii* was rarely encountered (1.5 % of sites). Most commonly, individual species had less than 25% cover ($D_i < 2$), but the most common cumulative density for all seagrasses at sites where seagrasses occurred was 50-75 % cover ($3<D<4$).

Using the criterion of $D_i \geq 0.1$ at a site for defining the presence of seagrass, it was possible to compute areal coverage of seagrass taxa in the study area. Of the 17,000 km^2 surveyed, seagrasses occurred over 12,800 km^2 (Figure 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 (Figure 3D). The range of *Thalassia testudinum* was almost as extensive; it was found to occupy 6,400 km^2 (Figure 3A). *Syringodium filiforme* occupied 4,400 km^2 (Figure 3B) and *Halodule wrightii* occupied 3,000 km^2 (Figure 3C). The range of *Halophila engelmannii* was restricted to only 50 km^2.

Seagrass productivity and standing crop at permanent sites- The purpose of choosing the permanent sites was to monitor productivity of *Thalassia testudinum*, the dominant seagrass species in most of south Florida; because of this these permanent sites always contained *T. testudinum* and were not a representative sampling 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 (compare Figure 4 and Table 1). These

sites were predominantly moderately dense *T. testudinum* beds; at 17 of the 30 sites *Syringodium 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 5 of the 30 sites. Never did *H. wrightii* comprise more than 5% of the seagrass SC. The mean short shoot density 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 of green leaves SS^{-1} for *S. filiforme* vs. 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 (Figure 4): *S. filiforme* was absent from only 6 of the sites at the scale of a 50 m transect compared to 13 sites at the scale of the quadrat estimates.

Averaging across all sites, SC and A_i were seasonal for both *Thalassia testudinum* and *Syringodium filiforme* (Figure 5). Assessing seasonality as the amplitude of the sine wave fit through the data divided by the mean (Equation 1), seagrass SC was more seasonal than A_i. Seasonality of SC for *T. testudinum* and *S. filiforme* were 32.9% and 31.2%, respectively; while seasonality of A_i for the two species was 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 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 *Thalassia 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 x 12 sampling periods) determinations of *T. testudinum* productivity. The lowest areal productivity rate measured was 0.05 g $m^{-2}d^{-1}$, the highest was 3.29 g m^{-2} d^{-1}, and the mean was 0.70 g m^{-2} d^{-1}. Specific productivity ranged between 3.2 and 34.2 mg $g^{-1}d^{-1}$, with a mean of 18.3 mg $g^{-1}d^{-1}$. 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 *Thalassia testudinum* was evident when results from all sites were averaged (Figure 6). The yearly mean specific productivity for all sites, as indicated by the constant in the sine model (equation 1), was 18.2 $\pm$ 0.85 mg $g^{-1}d^{-1}$. The amplitude of the model was 5.6 $\pm$ 1.2 mg $g^{-1}d^{-1}$; 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 $\pm$ 0.06 g m^{-2} and the amplitude of the sine model was 0.42 $\pm$ 0.08 g m^{-2}. 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 (Figure 6), and SC, which peaked in June (Figure 5).

There was a strong spatial pattern to both the mean and the seasonality of specific productivity of *Thalassia testudinum* at the sites. Mean productivity was generally higher on the south side of the Florida Keys and increased offshore (Figure 7A). On the Gulf of Mexico side of the Florida Keys, the northernmost stations had a yearly mean specific productivity of 15 - 16

mg $g^{-1}d^{-1}$, while the sites furthest offshore on the Atlantic side of the Florida Keys had yearly means as high as 22 mg $g^{-1}d^{-1}$. 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; Figure 7B).

Both the mean and seasonality of specific productivity were related to water depth (Figure 8). Mean annual specific productivity increased with water depth, at a rate of 0.60 ± 0.02 mg $g^{-1}d^{-1}m^{-1}$. Conversely, the seasonality of specific productivity decreased with water depth at a rate of 2.0% ± 0.6 % per meter. 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 *Thalassia 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 standing crop- The rapid visual assessments of seagrass abundance were correlated with measured seagrass SC for *Thalassia testudinum* and *Syringodium filiforme* (Figure 9). A simple linear relationship through the origin described 80% of the variation in *T. testudinum* SC, and 69% of the variation in *S. filiforme* SC, but the slope of the *T. testudinum* SC-A_i relationship (16.9 ± 0.5 (± 1 S.E), n=314) was twice as high as the slope of the same relationship for *S. filiforme* (8.4 ± 0.3, n = 289). Using the 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 (Figure 10). Integrating the SC for the study area gives an estimate of 1.4×10^{11} g of *T. testudinum* and 3.6×10^{10} g of *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 $g^{-1}d^{-1}$ 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 y^{-1}.

Discussion

Seagrass beds were the most common benthic habitat encountered in our mapping surveys of the Florida Keys National Marine Sanctuary and the southwest Florida shelf: 80.8% of the 874 mapping sites supported some seagrass (Table 3). The remaining 18.2% of the visited sites were a combination of living coral reef, hardbottom habitat, or unvegetated sediments. 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 35m 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- Our rapid visual assessment techniques allowed us to conduct wide *in-situ* surveys of seagrass distribution. Seagrass density was patchily

distributed across the survey area. In general, the densest seagrass beds in the study area were located on the Gulf of Mexico side of the middle Florida Keys (Figure 2); these very dense areas were dominated by *Syringodium filiforme* (Figure 3B). The ramet-level demographics and growth form of this unusually dense seagrass bed indicate that intense intraspecific competition in this seagrass bed is an important factor structuring the seagrass community (Kenworthy and Schwarzschild 1998). In order to escape competition for light, *S. filiforme* in this dense bed forms rhizome branches in the plant canopy; the resultant multi-layered canopy extends up to 1 m off of 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 $m^{-2}d^{-1}$ in 1998 (Rose et al. 1999).

The seagrass species had quite different distribution patterns, leading to zones of dominance by different species (Figure 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 (Figure 3A). One interesting *T. testudinum*-dominated site was encountered west of Cape Sable on the southwest Florida Shelf was an exception to this pattern. Large solution holes, which may be a conduit for terrestrial groundwater, are rumored to occur in this area. It is possible that this seemingly anomalous *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, FL (Zieman 1972). On the Atlantic Ocean side of the Florida Keys, the density of *Syringodium filiforme* increased in an offshore direction. *Halodule wrigthii*, which is very common in Florida Bay adjacent to our study area (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 (Figure 3C). Further to the north and west there was a large area

dominated by the seagrass *Halophila decipiens* (Figure 3D). This largely undescribed, deep water *H. decipiens* bed requires further study, since it constitutes such 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). 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. Deep water seagrass communities may be at enhanced risk of loss because of chronic anthropogenic water quality degradation, but rapid growth rates and relatively high rates of sexual reproduction would enable *Halophila* to recover quickly from acute disturbances.

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 *Thalassia testudinum* and *Syringodium filiforme* (Figure 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 (10 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 (Figure 10) are more restrictive of the limits of the beds as defined by the Braun-Blanquet data (Figures 8A and 8B) because the SC maps are drawn with a minimum limit for bed definition of 10 g m^{-2}. This boundary is arbitrary, but it roughly corresponds to a Braun-Blanquet abundance of 1, or 5% cover. We suspect that seagrass beds of very low density have less habitat value than those of moderate to dense cover,

as there have been numerous studies documenting the positive relationship between seagrass density and faunal density in tropical Atlantic seagrass meadows, e.g. (Sogard et al. 1987; Sogard et al. 1989; Fonseca et al. 1996). Integrating species-specific SC over the survey area yields estimates of 1.4×10^{11} g of *T. testudinum* and 3.6×10^{10} g of *S. filiforme*. Because our mapping sites were all censussed in summer, and SC peaks in summer months (Figure 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 *Thalassia testudinum* during the study period. During the summer of 1998, mean SC was nearly double the values measured in the previous two years (Figure 5). Similarly, A_i was 50% higher in 1998 than in the previous years. This interannual variability was likely due to year-to-year differences in climate, but we have not examined data records to ascertain what factors led to greater *T. testudinum* abundance in 1998. 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 *Thalassia testudinum* SC in south Florida was within the range of other published data sets (Table 4). We searched the literature for data on seasonality of *T. testudinum* SC and productivity, and analyzed this published data by fitting Equation 1 to the time series. 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 8

data sets collected 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 potentially epiphyte loads (Littler and Littler 1999).

Thalassia testudinum productivity- The expansive 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. *Thalassia testudinum* produces, on an annual basis, 6.7 g of new leaves per g of SC. For the region surveyed, this results in an annual leaf production of 9.4×10^{11} g. If we assume that *Syringodium filiforme* has a similar specific productivity (Barber and Behrens 1985), *S. filiforme* contributes another 2.4×10^{11}g of leaves y^{-1}.

Mean leaf productivity of *Thalassia 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 4), 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, our 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 in press).

Areal production of seagrass is the product of the density of seagrass and the specific productivity. Specific productivity of *Thalassia testudinum* in this study, an annual average of 18.2 mg $g^{-1}d^{-1}$, was within the range reported in the literature. It was slightly less than the 21.5 mg $g^{-1}d^{-1}$ reported for Biscayne Bay, Florida in 1969-1970 (Zieman 1975), yet higher than the 14.8 mg $g^{-1}d^{-1}$ reported for Florida Bay for the period 1989-1996 (Zieman et al. 1999). It should be noted that Florida Bay was experiencing a drastic decline in seagrass abundance and light availability during the period 1989-1996, however, so this estimate of specific productivity may be aberrantly low (Robblee et al. 1991; Thayer et al. 1994; Hall et al. 1999; Zieman et al. 1999).

In our review of the literature, there was a pronounced latitudinal trend in the seasonality of specific productivity of *Thalassia testudinum*: the most tropical location (Puerto Morales, Mexico; lat 20°51' N; (van Tussenbroek 1995) had seasonality of only 6% while the northernmost location had a seasonality of 58% (Anclote Estuary, FL; lat 28° 10'N; (Barber and Behrens 1985). There was no latitudinal trend in areal productivity rates of *T. testudinum*, however, since the areal productivity rate is the product of the SC, which displayed no latitudinal pattern, and the specific productivity. It is possible 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 *Thalassia 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 (Figure 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 (Figure 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 (Figure 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 water temperature above 35 °C (J.W. Fourqurean, unpublished data). 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.

Increasing *Thalassia testudinum* productivity with depth (Figure 8) is in contrast to the often-observed pattern of decreasing seagrass productivity with depth (e.g. (Dennison and Alberte 1982; Ilzumi 1996; Kaldy and Dunton in press), among many others) 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 primary productivity of *Thalassia testudinum* in the seagrass beds of southern Florida. The landscape-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 pattern exists in distribution, productivity and seasonality of seagrasses. The degree of seasonality in both biomass and productivity of seagrasses in the region is influenced by the depth and openness of the overlying ocean: seasonality was reduced offshore, where the

influence of the Florida Current buffers seasonality, and seasonality was pronounced in the shallower, more isolated waters of the Gulf of Mexico and Florida Bay that track more closely the subtropical climate of the region. It must also be emphasized that the FKNMS is not a pristine environment; man has 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 in south Florida. So, although seagrasses in south Florida are widespread and apparently healthy, the state of the seagrasses of the FKNMS has already been influenced by man.

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

Braun Blanquet Score, 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

Table 2. Descriptions of all of the things we calculated from the leaf marking measurements

	Units	Description
Standing crop (SC)	$g\ m^{-2}$	Dry weight of green leaves per square meter
Short shoot density	$SS\ m^{-2}$	Number of short shoots per square meter
Short shoot size	$g\ SS^{-1}$	Dry weight of green leaves per short shoot
Areal leaf production	$g\ m^{-2}d^{-1}$	Dry weight of green leaves produced per square meter per day
Specific leaf production	$mg\ g^{-1}d^{-1}$	Dry weight of new leaves produced per gram of green leaves per day

Table 3. Braun-Blanquet assessment of seagrass density (D) at 874 mapping sites.

Species	Density class (D)								
	0	0<D≤0.1	0.1<D≤0.5	0.5<D≤1	1<D≤2	2<D≤3	3<D≤4	4<D≤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 engelmannii	98.5	0.9	0.3	0.1	0.1	0.0	0.0	0.0	0.0
∑ D 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 (%)									
Thalassia testudinum		5.3	14.1	16.2	24.0	21.6	15.3	3.4	0.0
Syringodium filiforme		10.0	12.6	17.9	28.2	11.5	8.8	10.9	0.0
Halodule wrightii		22.4	38.1	15.0	16.3	6.8	0.7	0.7	0.0
Halophila decipiens		18.5	26.6	18.5	16.9	12.1	6.5	0.8	0.0
Halophila engelmannii		61.5	23.1	7.7	7.7	0.0	0.0	0.0	0.0
∑ D for all seagrasses		4.8	8.5	10.3	15.6	17.1	20.0	16.0	7.6

Table 4. 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 (Equation 1) 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. Superscripts by the location indicate data source: 1 = (Iverson and Bittaker 1986); 2 = (Barber and Behrens 1985); 3 = (Tomasko et al. 1996); 4 = (Tomasko and Hall 1999); 5 = (Kaldy and Dunton in press); 6 = (Zieman 1975); 7 = (Zieman et al. 1999); 8 = (Herrera-Silveira et al. 1999);9 = (van Tussenbroek 1995).

Location	Latitude	Longitude	Number of Stations	Period of observation	Standing Crop $g\ m^{-2}$	Specific Productivity $mg\ g^{-1}d^{-1}$	Areal Productivity $g\ m^{-2}\ d^{-1}$
North Florida[1]	29°48' N	85° 00' W	2	1970's	43.5 (94%)	–	–
Anclote Estuary, FL[2]	28°10' N	82° 45' W	2	1980-1981	–	13.9 (58%)	–
Sarasota Bay, FL[3]	27°20' N	82° 30' W	4	1992-1993	59.2 (37%)	25.3 (38%)	1.7 (59%)
Charlotte Harbor, FL[4]	26°50' N	82° 06' W	8	1995-1996	20.7 (108%)	19.0 (49%)	0.4 (138%)
Lower Laguna Madre, TX[5]	26°10' N	97° 14' W	2	1994-1997	102.8 (26%)	9.0 (38%)	1.4 (57%)
Biscayne Bay, FL[6]	25°30' N	81° 15' W	3	1969-1970	102.4 (25%)	21.5 (41%)	1.7 (46%)
Florida Bay, FL[7]	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[8]	21°17' N	89° 45' W	2	1997-1998			6.7 (37%)
Puerto Morelos, Mexico[9]	20°51' N	86° 55' W	3	1990-1992	41.0 (28%)	41.7 (6%)	1.2 (28%)

List of Figures

Figure 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.

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

Figure 3. Distribution of the four most common seagrass species across the study area. Data from the 874 mapping sites (Figure 1) were interpolated using a kriging algorithm to generate contours of the Braun Blanquet density (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.

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

Figure 5. Seasonality of standing crop and abundance of *Thalassia testudinum* and *Syringodium filiforme* at the 30 permanent sites. Each point is the mean of the 30 site means at each sampling period; error bars indicate ± 1 standard error. Lines are the results of fitting the sine model (Equation 1) to the data using an iterative least-squares routine.

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

Figure 7. Patterns in productivity of *Thalassia 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 (Equation 1).

Figure 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.

Figure 9. Relationships between Braun Blanquet abundance, measured along a 50 m transect, and standing crop, measured in six 10 cm X 10 cm quadrats, of *Thalassia testudinum* (top) and *Syringodium 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.

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

Fig 1

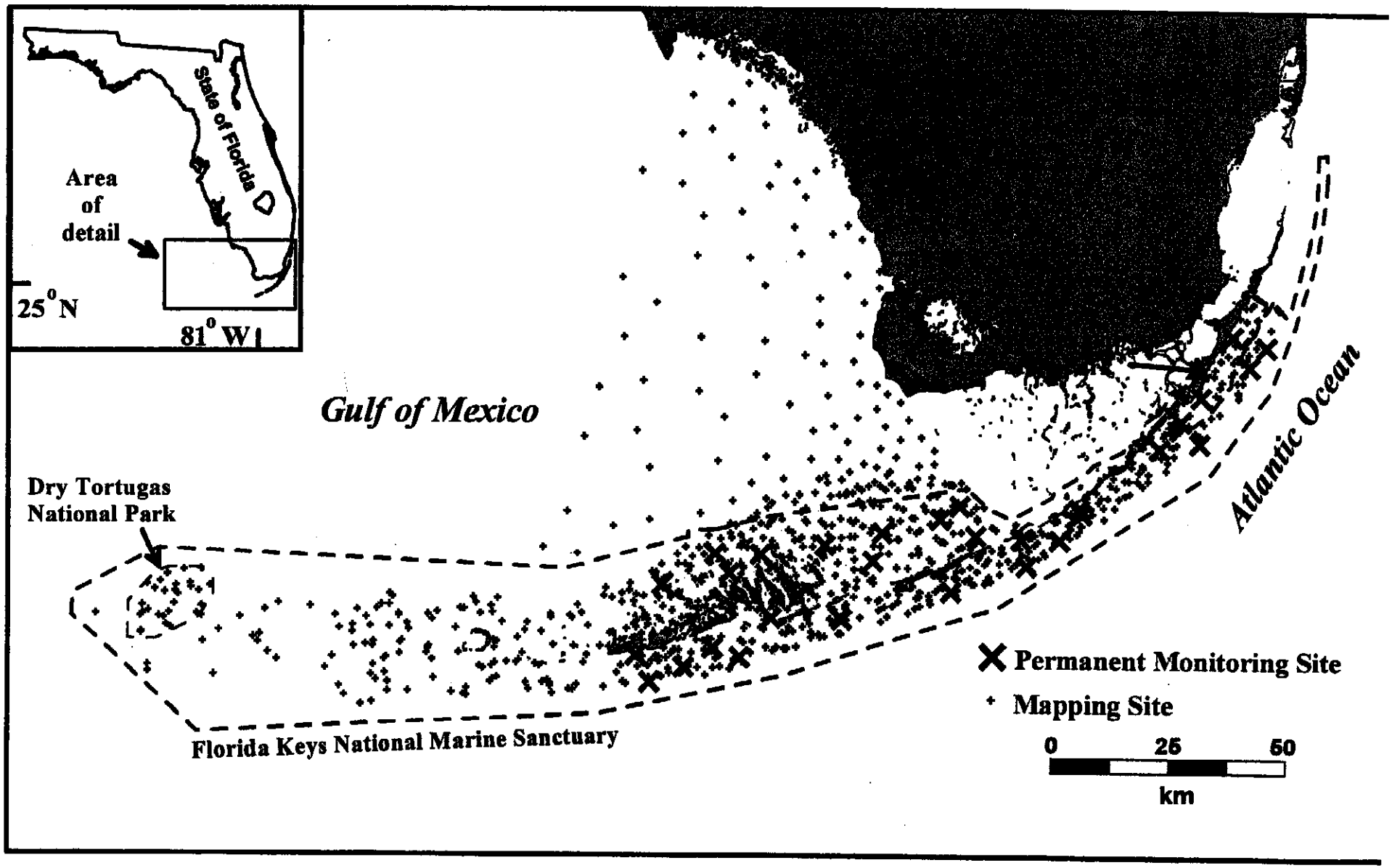
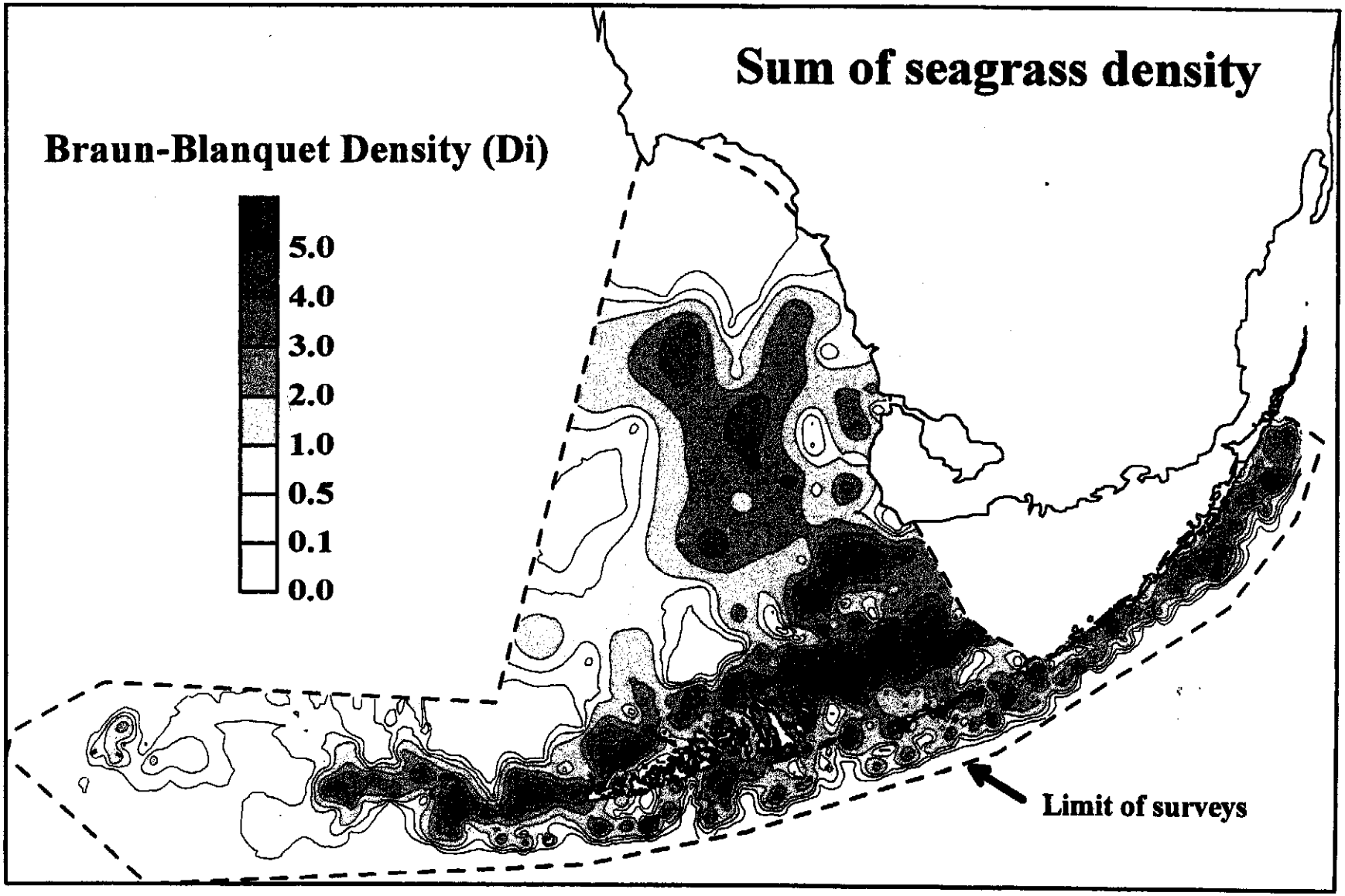
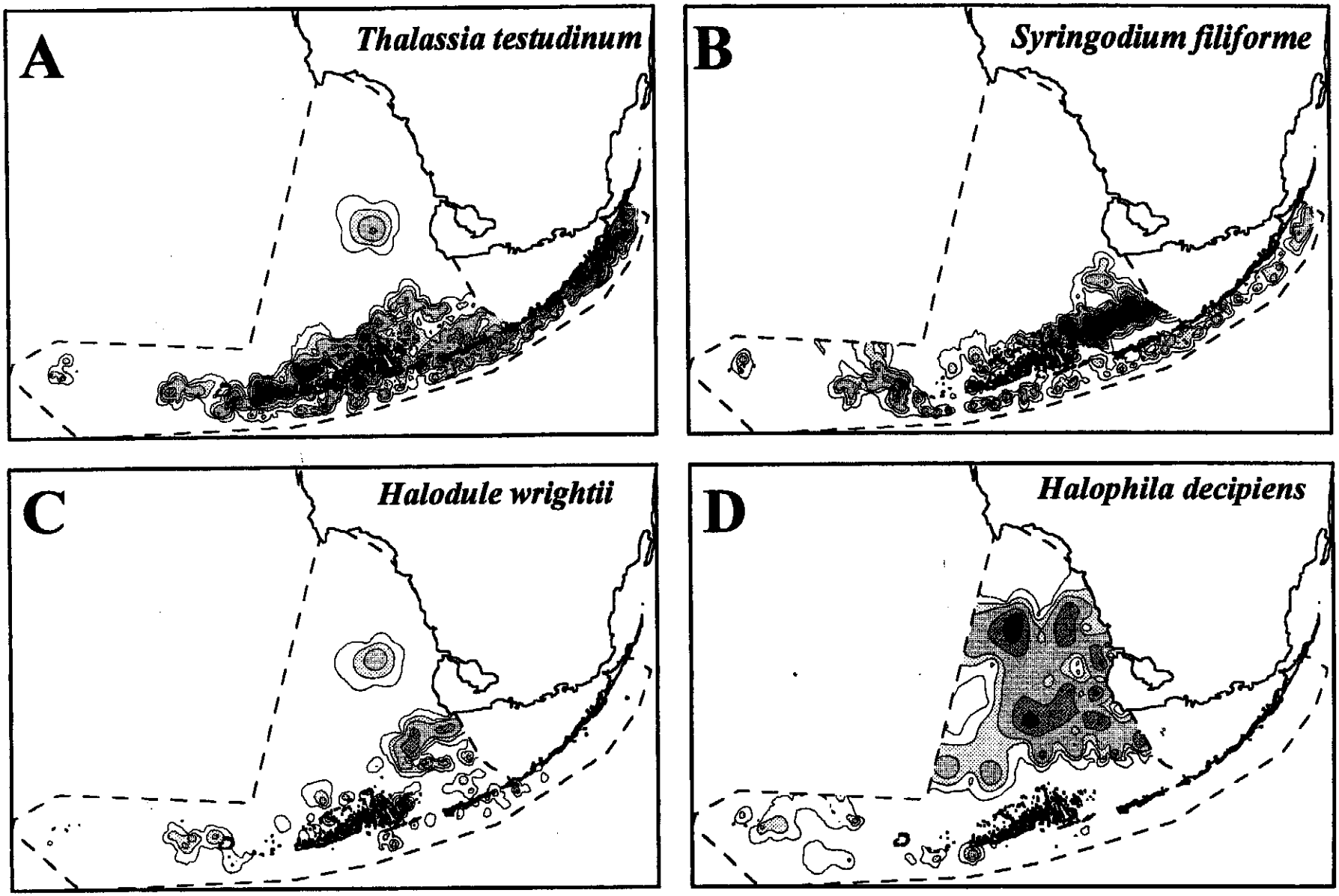
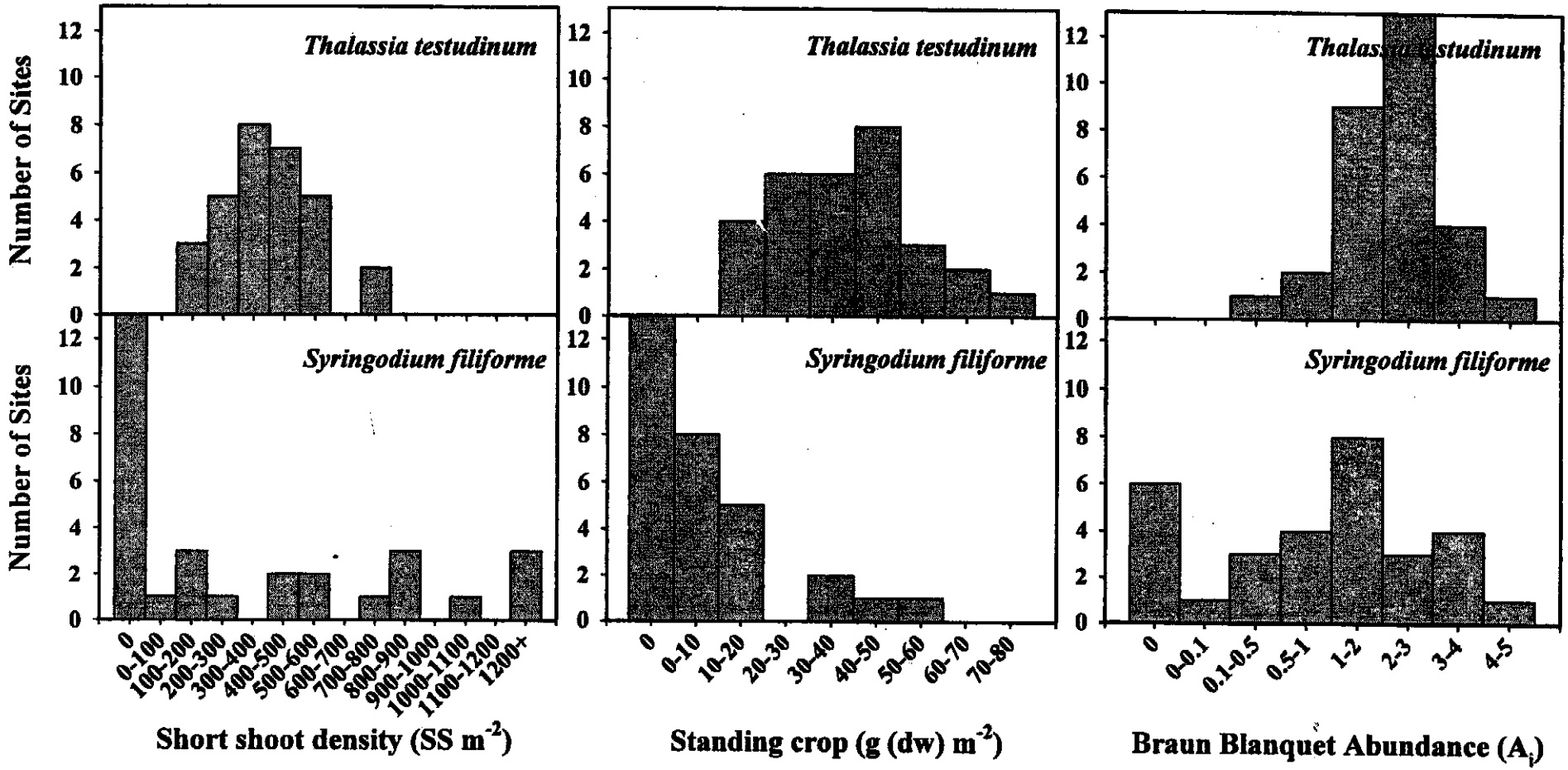

State of Florida
Area of detail
25° N
81° W
Gulf of Mexico
Atlantic Ocean
Dry Tortugas National Park
Florida Keys National Marine Sanctuary
Permanent Monitoring Site
Mapping Site
0
25
50
km

Fig 2

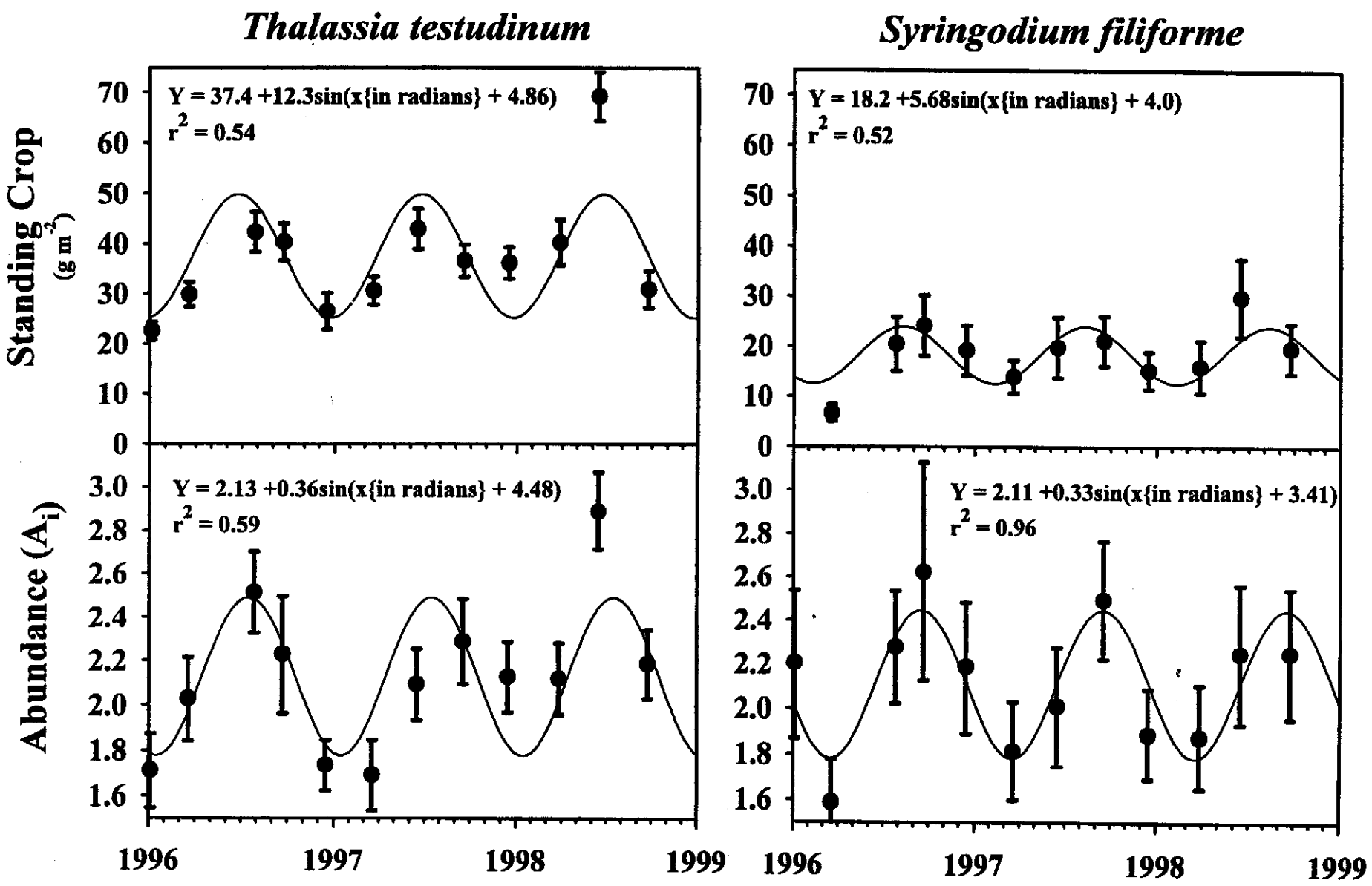

Sum of seagrass density
Braun-Blanquet Density (Di)
5.0
4.0
3.0
2.0
1.0
0.5
0.1
0.0
Limit of surveys


A
Thalassia testudinum
B
Syringodium filiforme
C
Halodule wrightii
D
Halophila decipiens
Braun-Blanquet Density (Di)
0.0 0.1 0.5 1.0 2.0 3.0 4.0 5.0

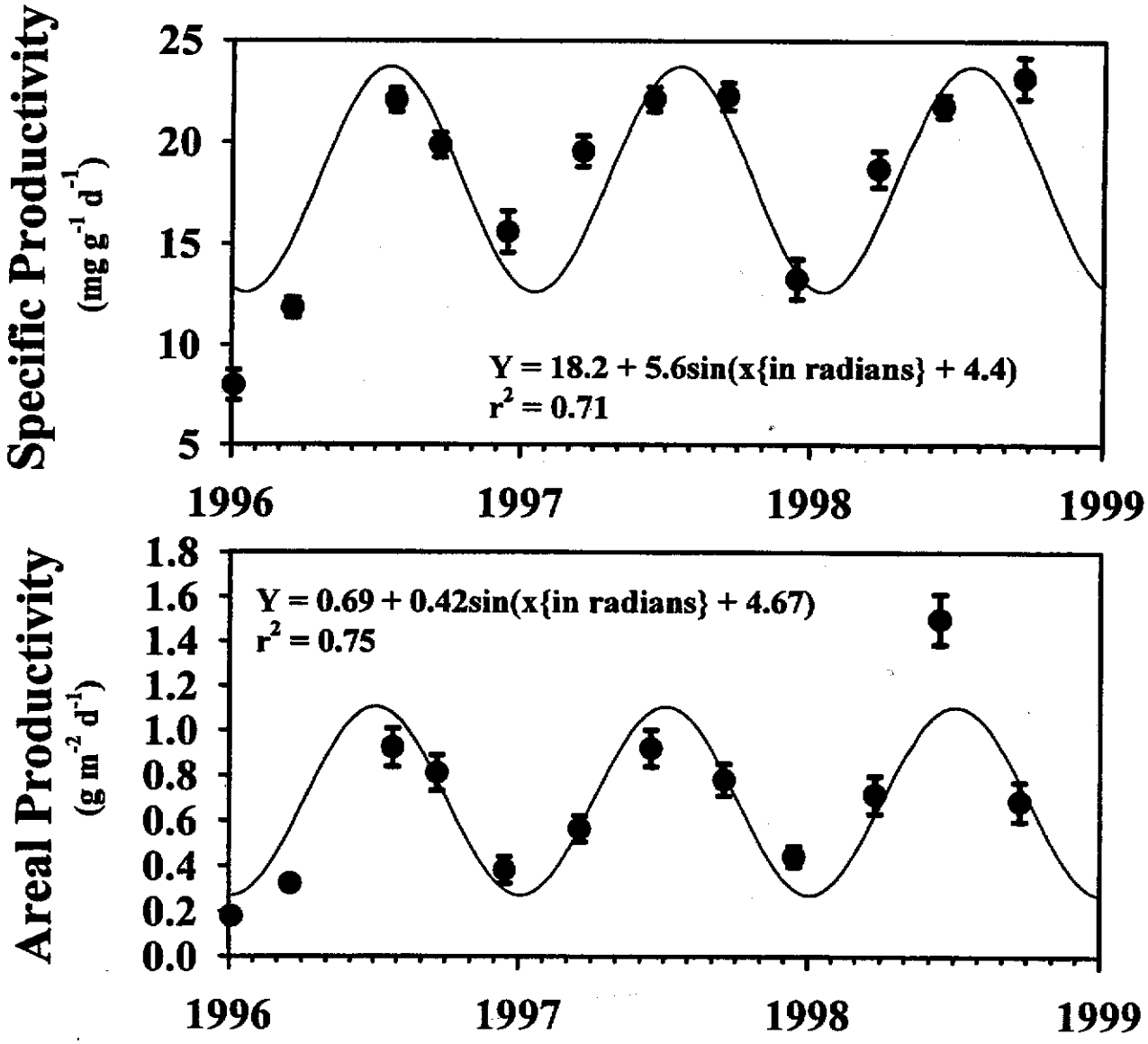
Fourqurean et al Figure 4

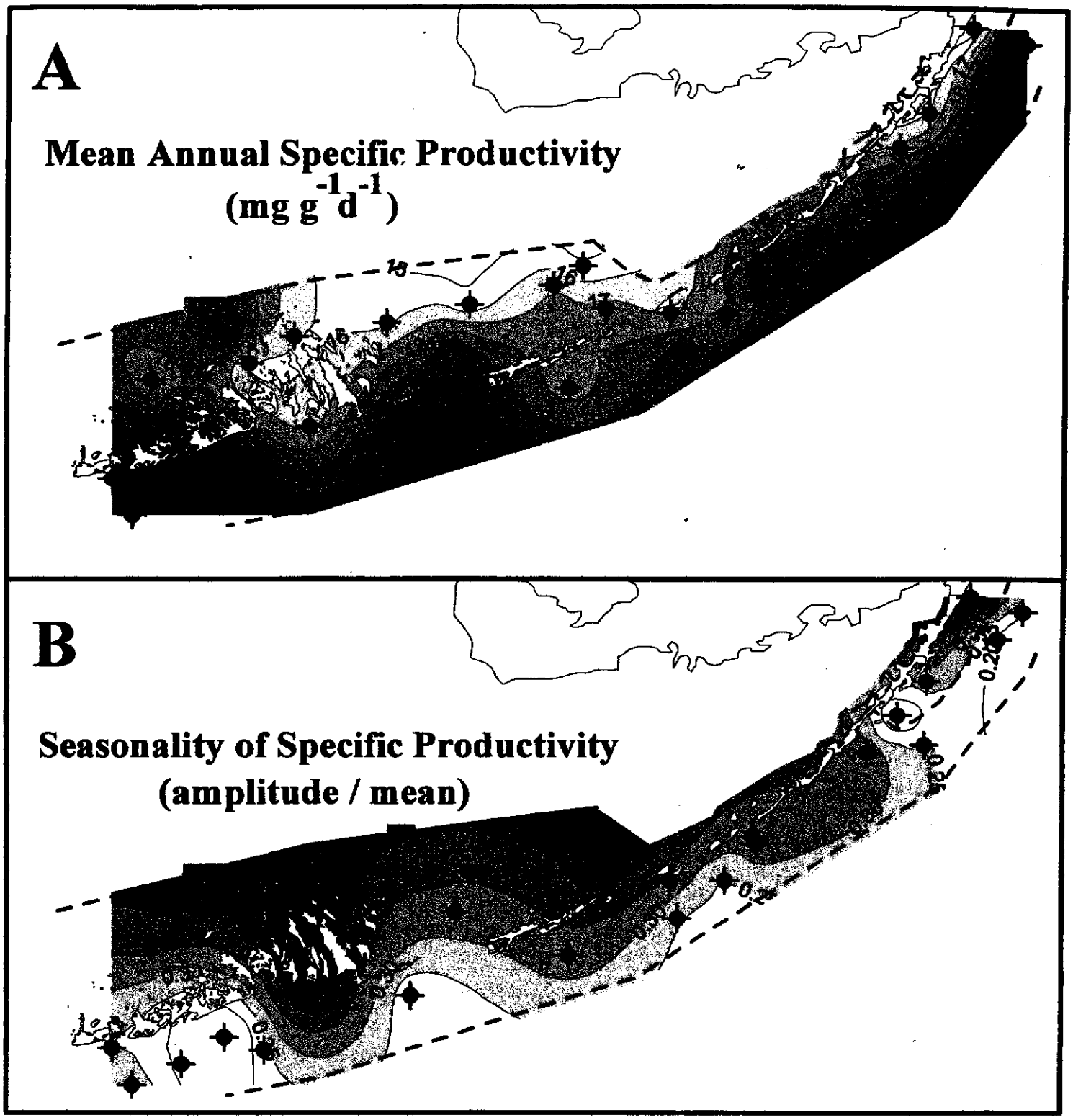


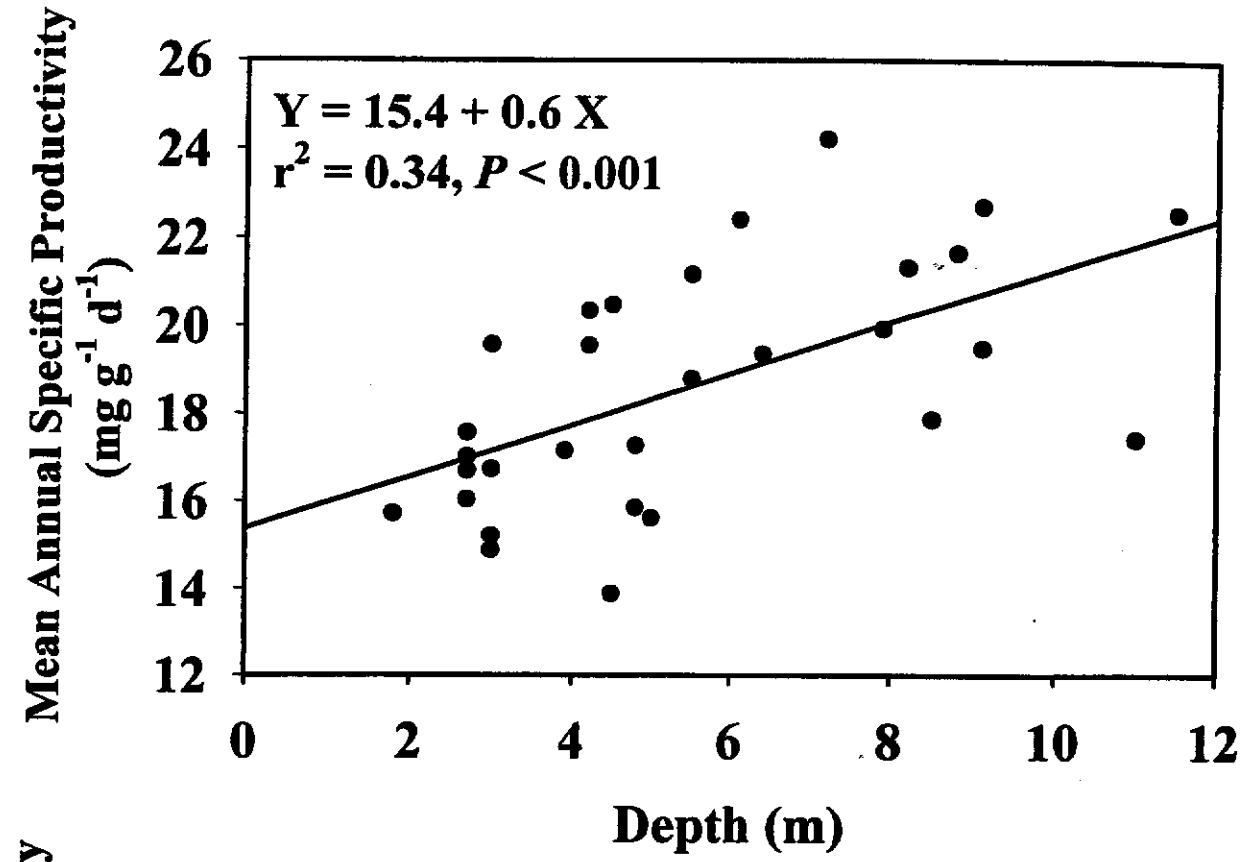
Fourqurean et al Figure 5

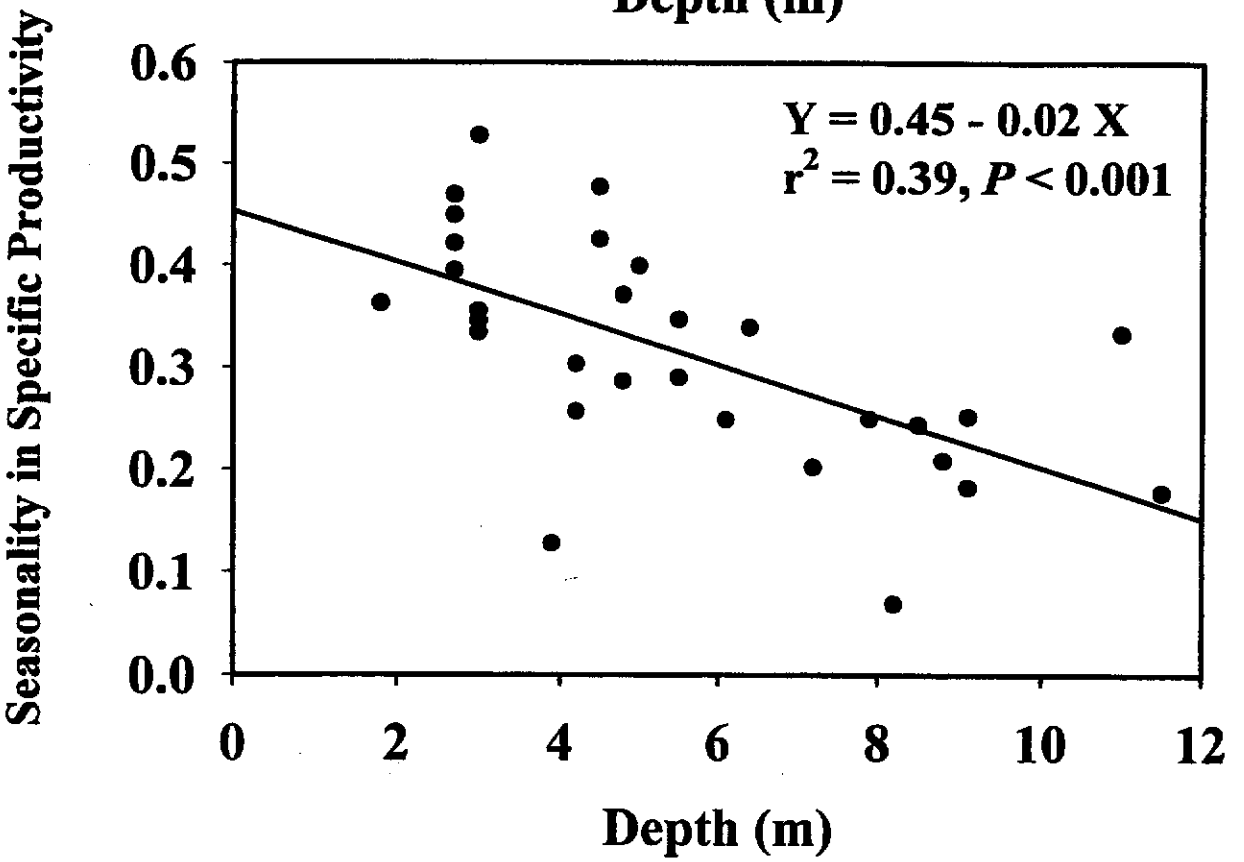


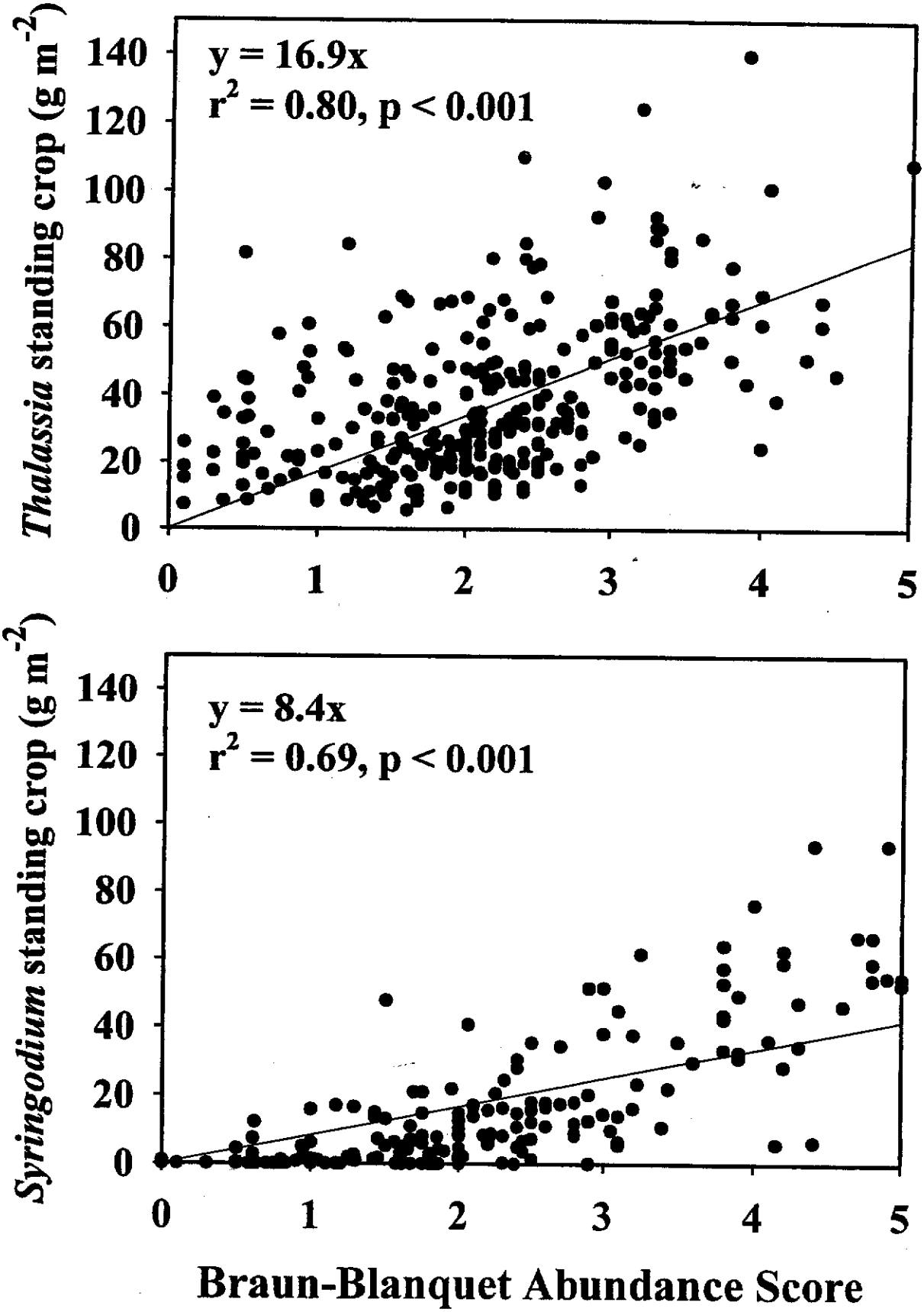
Fourqurean et al Figure 6

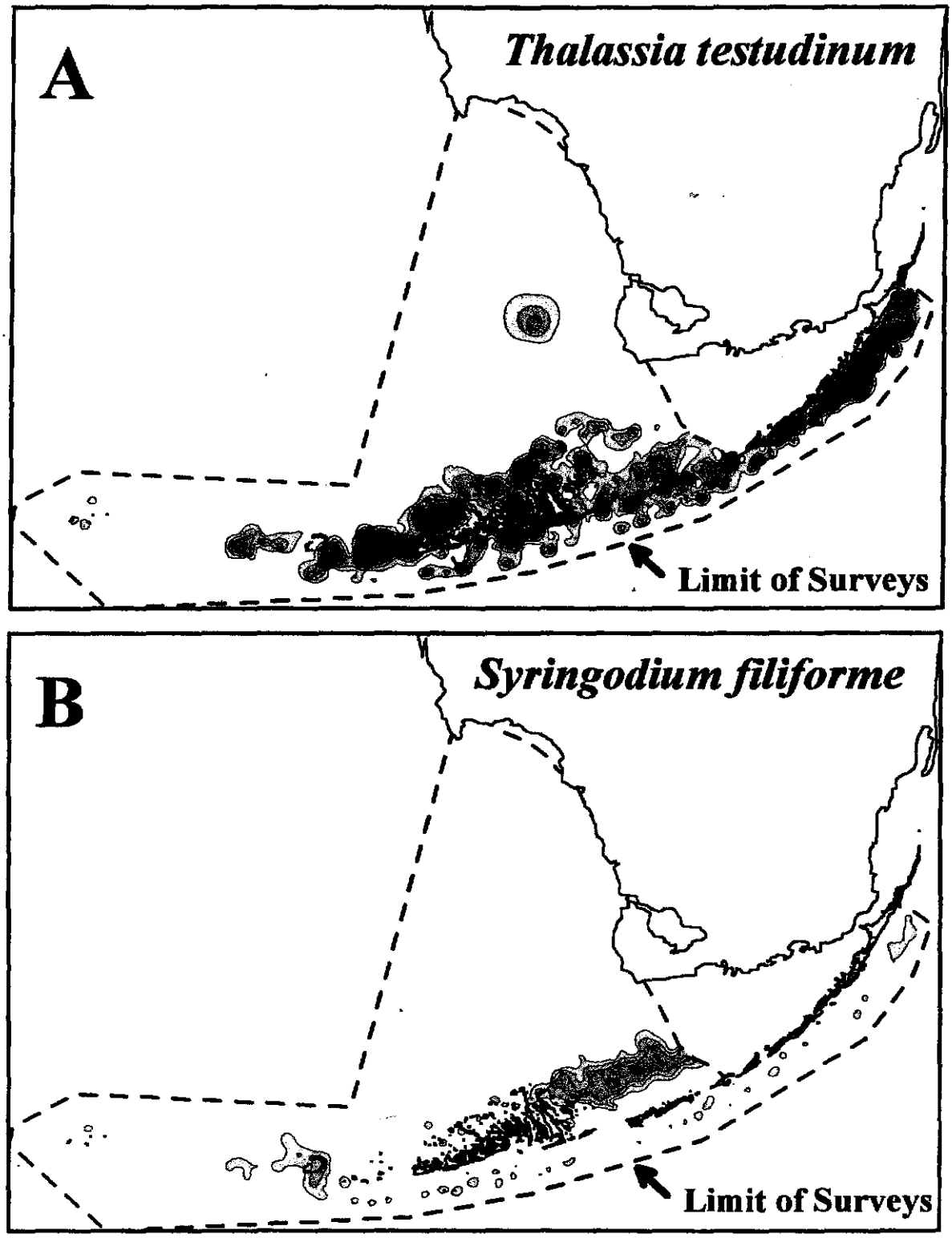



A
Mean Annual Specific Productivity
(mg g-1 d-1)
15
16
17
A5
B
Seasonality of Specific Productivity
(amplitude / mean)
0.20
0.25
0.30


Y = 15.4 + 0.6 X
r² = 0.34, P < 0.001
Mean Annual Specific Productivity (mg g⁻¹ d⁻¹)
26
24
22
20
18
16
14
12
0
2
4
6
8
10
12
Depth (m)


Y = 0.45 - 0.02 X
r² = 0.39, P < 0.001
Seasonality in Specific Productivity
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10
12
Depth (m)


y = 16.9x
r² = 0.80, p < 0.001
Thalassia standing crop (g m⁻²)
140
120
100
80
60
40
20
0
0
1
2
3
4
5
y = 8.4x
r² = 0.69, p < 0.001
Syringodium standing crop (g m⁻²)
140
120
100
80
60
40
20
0
0
1
2
3
4
5
Braun-Blanquet Abundance Score


A
Thalassia testudinum
Limit of Surveys
B
Syringodium filiforme
Limit of Surveys
Seagrass Standing Crop (g m-2)
0 10 20 30 40 50 60 70 80 90