

**Competing goals of spatial and temporal resolution: monitoring seagrass
communities on the regional scale**

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Introduction

Situated on the southern tip of the Florida peninsula, the Florida Keys are the downstream terminus of the wetland-dominated south Florida ecosystem that starts at the Kissimmee River, and includes Lake Okeechobee and the Florida Everglades (see (Trexler et al. in press for a description of a regional monitoring program in these wetland ecosystems). Water flows and levels have been extensively engineered in this ecosystem to allow for agriculture and urban development, but a monumental effort is now underway to reevaluate and redesign the management of freshwater flows in the south Florida ecosystem (Ogden et al. in press). This effort has as one of its major goals preventing irretrievable loss of components of the ecosystem as a consequence of altered supply and quality of freshwater as a result of satisfying competing human water-related needs in the region (USACE 1999; Redfield 2000; Kiker et al. 2001). While most of the engineering of natural water flows has taken place in the rivers, lakes and marshes of the ecosystem (Light and Dineen 1994), it is widely recognized that water management practices have also had effects on the estuarine and marine water bodies that receive these flows. Alterations in quantity, timing and/or quality of freshwater discharge have been implicated in changing the structure of benthic and planktonic communities in the Caloosahatchee estuary (Kraemer et al. 1999), the St. Lucie estuary (Chamberlain and Hayward 1996; Havens and Aumen 2000) and Florida Bay (reviewed in Fourqurean and Robblee 1999). It has also been suggested that these alterations may be causing general eutrophication of the marine environment in south Florida, possibly impacting seagrass

beds surrounding the Florida Keys (Lapointe et al. 1994) and the Florida Keys barrier coral reef (Porter et al. 1999). The impacts, both proven and perceived, of human alteration of water flow in south Florida on the estuarine and marine environment underscore the high interdependency of the various components of the south Florida ecosystem. Partially in response to concerns about upstream water management effects on the marine end of the south Florida ecosystem, the US Congress established the Florida Keys National Marine Sanctuary in 1990, with the aim 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)

The impacts of regional water management on the marine ecological communities of south Florida are compounded by local anthropogenic influences. The net annual budget of rainfall and evapotranspiration is near zero in Florida Bay and the Florida Keys (Nuttle et al. 2000), hence any human transport of water can significantly influence local water budgets. Almost all of the potable water used by the ca. 100,000 residents of the Florida Keys is piped in from groundwater wells on mainland Florida. Wastewater generated by the population of the Keys is, for the most part, disposed of in on-site sewage disposal systems (OSDS; septic tanks and cesspits) which release freshwater and nutrients into the shallow groundwater and eventually to the marine surface waters (Lapointe et al. 1990; Paul et al. 1997; Dillon et al. 1999).

Despite the widely-held opinion that human alterations of water and nutrient budgets on both regional and local scales are having deleterious effects on the estuarine and marine ecosystems of south Florida, direct causal links have mostly eluded detection. One major reason for this is the high degree of ecosystem variability in both time and space (Fourqurean and Robblee 1999). Water quality varies not only across the ecosystem, but also seasonally as a consequence of natural processes (Boyer et al. 1999; Boyer and Jones 2002). Interannual variability in climate can override the effects of human water management on the water budget of coastal bays (Nuttle et al. 2000). Standing stock and productivity of primary producers is highly seasonal, even in tropical-subtropical south Florida (Fourqurean et al. 2001). Extreme meteorological events like hurricanes and winter freezes can have impacts that last for years (Tilmant et al. 1994). Poorly understood outbreaks (e.g. Rose et al. 1999) or dieoffs (e.g. Lessios et al. 1984; Robblee et al. 1991; Butler et al. 1995) of organisms can have consequences that cascade through the ecosystem. Finally, long-term modification of predator and grazer populations by human activities also may be responsible for long-term gradual changes in the structure of marine ecosystems (Jackson 2001; Jackson et al. 2001). So, to determine the effects of water management practices on estuarine and marine resources of south Florida requires a monitoring program that is spatially expansive, temporally-intense, long-lived, and multidisciplinary.

There are few places on earth where seagrass beds are as expansive as the near-shore marine ecosystem of south Florida, where there are at least 14,000 km² of seagrass

beds (Fourqurean et al. 2002). In the shallow water nearest shore, seagrasses are especially prevalent; over 90% of the area in water less than 10m deep supports seagrass. Seagrass beds are recognized as among the most productive (Zieman and Wetzel 1980) and economically valuable (Costanza et al. 1997) of ecosystems, and the economy of the Florida Keys is inextricably tied to seagrass beds. Fisheries landings in the Florida Keys total over $12 \cdot 10^6$ kg annually of mostly seagrass-associated organisms (Bohnsack et al. 1994), and over half of all employment in the Florida Keys is dependent on outdoor recreation (NOAA 1996). But, the growing human population is placing visible strain on the marine communities surrounding south Florida, leading some to question the sustainability of the very ecological resources at the base of this portion of the regional economy.

Despite their recognized importance, worldwide loss of seagrass beds continues at an alarming rate (Short and Wyllie-Echeverria 1996). This loss largely has been attributed to anthropogenic inputs of sediment and nutrients. The difficulty of monitoring seagrass beds has led to obfuscation of the real extent of seagrass loss, as our best estimates of even the current global extent of this important habitat are at best within an order of magnitude (Duarte in press). In Florida alone, anthropogenic seagrass losses have been reported in Pensicola Bay, St Joseph Bay, Tampa Bay, Charlotte Harbor, the Florida Keys, Biscayne Bay and the Indian River Lagoon (see Sargent et al. 1995; Short and Wyllie-Echeverria 1996 for reviews), but accurate estimates of the current areal extent of

seagrasses even in a populated, first-world location like Florida are only recently available.

Design of the monitoring scheme for seagrass communities in south Florida

The monitoring plan for the seagrass-dominated marine communities of south Florida had to address two competing goals. First, the program had to define the spatial extent and present condition of the resource. Second, the monitoring program had to produce information that could be used to detect trends in the condition of the resource through time and be able to ascertain the causes of these trends. The reasons these goals were competing are quite simple: monitoring is an expensive, time consuming process, the area to be monitored is vast (ca. 18,000 km²) and heterogenous, and the financial resources to accomplish the goals were limited.

Choosing what to measure

The decision about what parameters to measure in a monitoring program is influenced by both conscious decision and subconscious bias. It is important that the measured parameters be:

1. Unambiguously related to the conceptual model guiding the monitoring plan.
2. Relatively easy to assess, for both economic reasons and because monitoring programs often outlast the investigators who originally designed the programs, making it a necessity that the techniques can be easily passed on to successive project personnel.

3. Precise enough to allow for exact characterization and change detection.
4. Robust enough so that slight differences among observers do not influence the interpretation of the data.

Research and technology advances constantly make possible new potential monitoring methods. These new methods should be incorporated and tested by comparison to more established methods as part of large monitoring programs, but using untried or unproven methods necessitates periodic assessment of the efficacy of such methods and a willingness to modify the monitoring program if the new methods do not prove effective.

Conceptual models used to guide monitoring the seagrass communities of south Florida

A successful monitoring program must be based on a solid understanding of the processes responsible for driving environmental. Without such an understanding, it is not possible to allocate monitoring resources in the appropriate temporal and spatial scale. The temporal scale is important, because sampling intensity must match the time course of ecological responses in the environment. Further, this understanding is important to manage the expectations of managers: ecosystem responses to changes in stressors can often play out over decades, which is much longer than the fiscal cycles normally used to fund monitoring programs. The spatial scale is important, because monitoring programs often are asked to be as spatially-extensive and regionally-representative as possible, requiring a broad spacing of monitoring sites. This regional representation can lead to the

failure to detect important localized ecological responses if the response varies at a smaller scale than the average spacing between monitoring sites.

The pattern of anthropogenically-driven loss of seagrass beds across the globe leads to a generalized model of the effects of eutrophication on seagrass beds (Duarte 1995). In general, eutrophication in aquatic environments shifts the competitive balance to faster-growing primary producers. The consequences of this generality in seagrass-dominated environments is that seagrasses are the dominant primary producers in oligotrophic conditions. As nutrient availability increases, there is an increase in the importance of macroalgae, both free-living and epiphytic, with a concomitant decrease in seagrasses because of competition for light. Macroalgae lose out to even faster-growing microalgae as nutrient availability continues to increase: first, epiphytic microalgae replace epiphytic macroalgae on seagrasses; then planktonic microalgae bloom and deprive all benthic plants of light under the most eutrophic conditions.

Using knowledge of the life history characteristics of local species and experimental and distributional evidence, this general model can be adapted to seagrass beds of south Florida. The south Florida case is more complicated than the general case described above because there are 6 common seagrass species in south Florida, and these species have different nutrient and light requirements, hence they have differing responses to eutrophication. Large expanses of the shallow marine environments in south Florida are so oligotrophic that biomass and growth of even the slowest-growing local seagrass species, *Thalassia testudinum*, are nutrient-limited (Fourqurean et al. 1992a;

Fourqurean et al. 1992b); at this very oligotrophic end of the spectrum, increases in nutrient availability actually cause increases in seagrass biomass and growth rate (Powell et al. 1989). As nutrient availability increases beyond what is required by a dense stand of *T. testudinum*, there are other seagrass species that will out-compete it. At locations with more constant marine conditions, there is evidence that *Syringodium filiforme* may be a superior competitor to *T. testudinum* in areas of enhanced nutrient availability (Williams 1987). In estuarine areas of south Florida, nutrient addition experiments show that *Halodule wrightii* will prevail over *T. testudinum* under fertilized conditions (Fourqurean et al. 1995). Evidence from the distribution of primary producers around point-sources of nutrient input show that in estuarine areas, there are zones of dominance of different species with respect to nutrient availability, from *T. testudinum* at lowest nutrient availability, to *H. wrightii* at higher availability, to *Ruppia maritima* at higher availability, followed by a microalgae dominated zone at highest nutrient availabilities (Powell et al. 1991). The abundance of macroalgal epiphytes also increases along the same gradient, up until the point that microalgae become dominant (Frankovich and Fourqurean 1997). The relative importance of the various primary producers, then, can be used to assess the trophic state of the community (Figure 1). Spatial pattern in the distribution of trophic states potentially can be used to assess nutrient sources in an ecosystem, and temporal changes in trophic state can be used as an indicator of trends in nutrient availability at a site.

Each species in the species dominance-eutrophication gradient model (Figure 1) can potentially dominate over a range of nutrient availability and the model predicts a change in species dominance as nutrient availability changes. These changes are not instantaneous, however. Field evidence suggests that species replacements may take place on a time scale of a decade or more (Fourqurean et al. 1995). It is desirable that we be able to predict the tendency of the system to undergo these changes in species dominance before they occur, so that management actions can be taken. Tissue nutrient concentrations can be monitored to assess the relative availability of nutrients to the plants. For phytoplankton communities, this idea is captured in the interpretation of elemental ratios compared to the familiar “Redfield ratio” of 106C:16N:P (Redfield 1958). Similar analyses can be made with data from seagrasses and macroalgae with the recognition that the taxon-specific “Redfield ratio” may be different from the phytoplankton ratio (Gerloff and Krombholz 1966; Atkinson and Smith 1983; Duarte 1992). For the seagrass *T. testudinum*, the critical ratio of N:P in green leaves that indicates a balance in the availability of N and P is ca. 30:1, and monitoring deviations from this ratio can be used to infer whether N or P availabilities are limiting this species’ growth (Fourqurean and Zieman in press). Hence, *T. testudinum* is likely to be replaced by faster-growing competitors if nutrient availability is such that the N:P of its leaves is ca. 30:1. A change in the N:P in time to a value closer to 30:1 is indicative of eutrophication (Figure 2). Spatial pattern in the N:P can be used to infer sources of

nutrients for supporting primary production in the ecosystem (Fourqurean et al. 1992a; Fourqurean et al. 1997; Fourqurean and Zieman in press).

These models lead directly to a definition of trends likely to be encountered in the seagrass communities of south Florida if humans are causing regional changes in nutrient available because of alterations to quantity and quality of freshwater inputs to the marine ecosystem:

1) regional eutrophication will cause N:P ratios of seagrasses to approach 30:1 from higher or lower values indicative of oligotrophic conditions; and

2) regional eutrophication will cause a shift in species dominance in south Florida seagrass beds. The first responses to eutrophication will be evidenced by an increase in the relative abundance of fast-growing seagrass species (*H. wrightii* and *S. filiforme*) at the expense of the now-dominant, slow-growing *T. testudinum*. At later stages of eutrophication, macroalgae and microalgae will become the dominant primary producers.

Parameters measured in this program

Benthic plant community structure was measured using the rapid, visual assessment technique developed early in the 20th century by the plant sociologist Braun-Blanquet (Braun-Blanquet 1972). This method is very quick, requiring only minutes at each sampling site; yet it is robust and highly repeatable, thereby minimizing among-observer differences. In this method, a series of quadrats are randomly placed on the bottom at a given location. All taxa occurring in the quadrat are listed, and a ranking based on abundance of the species in that quadrat is assigned for each species. We have

adopted a modified Braun-Blanquet scale for our work in south Florida (Table 1, (Fourqurean et al. 2002)). Ten randomly-placed replicate 0.25 m² quadrat observations were made at each survey point.

Three metrics were computed for each taxon at a site: abundance, frequency and density. Abundance was calculated as:

$$A_i = \frac{\sum_{j=1}^n S_{ij}}{N_i} \quad \text{Equation (1)}$$

where N_i is the number of quadrats at a site in which taxon i was present. For any taxon, A can range between 0 and 5, the maximum Braun-Blanquet score. Frequency was calculated as:

$$F_i = \frac{N_i}{n} \quad \text{Equation (2)}$$

where n is the total number of quadrats observed at a site, such that $0 \leq F_i \leq 1$. Density (D_i) was calculated as the product $A_i \times F_i$. It should also be noted that a taxon may be observed at a site by the sample collector, but unless the taxon falls within one of the randomly-placed observation quadrats, the taxon receives A_i , F_i and D_i scores of 0. In addition to taxon-specific measures, seagrass taxon richness S was calculated for each site by summing the number of seagrass taxon for which $D > 0$.

Elemental content (carbon, nitrogen and phosphorus) of green leaves was determined for all seagrasses (Fourqurean et al. 1992a). Elemental content was calculated on a dry weight basis; elemental ratios were calculated on a mole:mole basis. Net aboveground productivity and short shoot morphology of *T. testudinum* were measured on a quarterly basis at each permanent site using a leaf marking technique (Fourqurean et al. 2001).

One experimental monitoring approach was included in the monitoring program. Detecting change in ecological communities through repeated mapping takes many years, and at best can only illuminate changes that have occurred. It is desirable to monitor parameters that could predict the future trajectory of a resource before drastic changes occur. To this end, it has been proposed that estimates of future seagrass population size can be generated from the analysis of the age structure of seagrass shoots (Duarte et al. 1994). This method relies on the ability to age individual shoots of seagrasses by counting leaf scars and applying a plastochron interval (Erickson and Michelini 1957). The age-frequency distribution of shoots is a reflection of recruitment and mortality of individual shoots to the seagrass population. A potential advantage of this approach is that estimates of recruitment and mortality can be obtained from a single sampling event. Populations of shoots were collected from each site by excavating a sod, approximately 1 m², that contained > 100 shoots. The number of leaves produced over the lifespan of each shoot in a sample was determined by counting leaf scars and extant green leaves. Shoot age was estimated by the number of leaves produced by a shoot, scaled by the site-specific annual

leaf production rates. Instantaneous mortality and gross recruitment rates for each population were calculated from the age distribution at each site following the methods given in (Peterson and Fourqurean 2001); projected net population growth was calculated as the difference between gross recruitment and mortality.

Choosing where to measure

In order to describe the spatial extent and pattern in the benthic communities, monitoring sites must be selected across the extent of the monitoring area. This monitoring program was designed to assess status and trends in seagrass communities across the entire extent of the Florida Keys National Marine Sanctuary, a 9,000 km² area of ocean surrounding the Florida Keys (see Figure 5, Ogden et al, this volume). As if monitoring such a vast extent were not task enough, it was recognized early in the monitoring program that the expansive shallow marine habitats immediately to the north of the sanctuary on the southwest Florida Shelf also were important for determining the status of seagrass communities within the Sanctuary itself, so the monitoring program was extended to cover these additional 8,000 km² as well. It was a goal of the program to describe spatial pattern in the indicators of interest, hence it was important to sample the entire region. However, without data on the underlying variance in the indicators to be measured, it was not possible to determine *a priori* how many sites would be needed to assess mean state of any indicator. The number of sites needed to generate a synoptic map of the condition of any measured indicator was therefore determined in a very *ad hoc* way: the maximum number of sites that could be sampled by the manpower provided for

in the budget were selected. The locations for each of this number (n) of sites were chosen by laying a probability-based grid with n cells over the area of interest, and then randomly choosing a location within each grid cell (Figure 3). This method allowed sampling locations to be spaced quasi-evenly across the landscape while still maintaining the assumptions required for a random sample, i.e. all locations had an equal probability of being sampled. In each of the first 5 years of the monitoring program (1996-2000), the same arrangement of grid cells was employed, but new random points were selected within each cell each year. This allowed for the development of synoptic maps of measured indicators during each monitoring year, as well as a combined data set of quasi-evenly spaced random points collected over 5 years. The monitoring plan calls for revisiting the first year's sites during the sixth year, the second year's site during the seventh year, etc - so that trends in the resource over a 5 year interval can be tested with n pair-wise comparisons for 5 years in a row.

More detailed time series of data describing the state of the benthic communities than could be generated by the synoptic mapping efforts were required to evaluate the intra- and interannual patterns in indicators. To this end, 30 permanent monitoring sites were established in regions that could be routinely visited given the budget of the project. To allow for analyses of the relationships of indicators and trends in the benthic communities with overlying environmental variables, these permanent sites were located at a subset of sites used for a related water quality monitoring program (Boyer and Jones 2002); that program's sites were originally located using the same probability-based

design as described above for the synoptic stations. Further constraints were placed on the selection of permanent sites. In each of the segments of the FKNMS (Klein and Orlando 1994), two inshore, two offshore, and two intermediate sites were chosen. And, because many of the indicators are specific to *T. testudinum* (see above), permanent monitoring sites were required to be located where this species occurred. Permanent monitoring sites were visited 8 times a year, with 2 visits separated by 7-10 days every 3 months.

Visualizing monitoring data

Data by themselves are not generally useful to environmental managers, but instead they require synthesis and interpretation before they yield useful management information. This synthesis is a daunting task that can take years after the data are collected: data reports need to be digested, hypotheses about relationships and driving variables need to be tested, and finally peer-reviewed analyses of these data must be published in scientific journals for scientists running the monitoring program to feel as if they have produced a defensible product. But, intermediate results are often desperately needed by resource managers. How, then, to present a mass of monitoring data to resource managers in a way that will allow them to make their own interpretations of the data while the scientists continue to refine their analyses? New computer tools, from spatial analysis and mapping programs to internet access of hyperlinked data reports provide effective means to allow managers to make their own data analyses by representing spatial pattern at an instant in time or by generating time series at fixed points from their own desks. In this seagrass monitoring program, we accomplish this by

making the data freely available on the web site

(<http://serc.fiu.edu/seagrass/!CDreport/DataHome.htm>) as quickly as possible.

Synoptic views of the data are generated by interpolation between sample points using a kriging algorithm (Watson 1992) and then mapping these data using commercially-available software. Such maps allow clear presentation of spatial pattern in a form that is most useful to resource managers. Although it would be tempting to use such synoptic maps generated in successive years for a change analysis, there are problems with this approach if 1) the spatial points are not identical in the two years so that small-scale spatial variability creates apparent changes, or 2) differences in timing in the collection of the data lead to apparent changes that are caused by seasonality.

Seasonality in the data from the permanent stations was assessed by fitting a sine model to the data:

$$\hat{Y} = Mean + A \cdot \sin(DOY + \Phi) \quad \text{Equation (3)}$$

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) that determines the timing of the seasonal peak of the time series. This model assumes no long-term monotonic trend in the time series, as none have been yet detected in our monitoring program, but this model could also be easily applied to data with such a trend with the addition of a trend slope parameter. Once the seasonality was understood,

it became possible to do change analyses on data from these permanent sites by using data collected in the same phase of the seasonal cycle in successive years.

Some monitoring examples

Data from the synoptic sampling sites allowed for the creation of maps of the densities of benthic plants in the region (Figure 4). While the general nature of the mapped distribution was similar from year to year, there were differences in maps produced in different years. We detected no consistent patterns in direction or rate of change in seagrass populations through time at our permanent monitoring sites; this made it possible to combine data from all of the years of the synoptic study to produce a more detailed view of the distribution of seagrasses. The species distribution maps produced by this monitoring program are the first detailed inventory of benthic plants in south Florida, despite the recognized importance of seagrasses for the ecological continuity and economic health of the region.

Analyses of the spatial extent of seagrasses in the study region indicate that seagrass species respond differently to environmental conditions, so that densities of different species are not correlated (Fourqurean et al. 2002). These analyses support the conceptual model of the response of seagrass beds in south Florida to eutrophication (Figure 1). Each species has a separate ecological niche, one axis of which is the relative nutrient availability of the environment as outlined in Figure 1. Of course, there are many other axes of these niches. For example, seagrass species are capable of tolerating

different levels of salinity and salinity variability (McMillan and Moseley 1967). They also have different light requirements, so that some species can grow in deeper water than others (Wiginton and McMillan 1979).

The Braun Blanquet survey techniques provided three separate measures of the distribution of benthic plants at each survey site. Frequency (F_i) data provide information on the homogeneity of the distribution of the taxa; F_i values approaching 1.0 indicate that the taxa of interest is rather evenly distributed, and that the patches in the landscape are larger than the spatial extent of the sampling at a site. Abundance (A_i) data provide an indication of the potential maximum cover attainable by a taxa given the environmental conditions. For example, in the area immediately behind the barrier coral reef, *Thalassia testudinum* often had quite high abundance ($A > 3$), but relatively low frequency - because in this environment, *T. testudinum* meadows can be quite lush, but physical disturbance causes patchiness of this otherwise dense canopy, expressed by low values of F . The product $F \times A$ at a site yields the density (D_i). Hence, D can be low if A is consistently low at all quadrats at a site, or if especially lush patches are isolated in otherwise barren habitat. The independence of the measures F and A is underscored by the lack of any correlation between D and A for *T. testudinum* from 1500 sites visited over the 5 years of this study.

Analysis of the age structure of populations of *T. testudinum* short shoots produced estimates of mortality and gross recruitment that varied considerably across the spatial domain of our monitoring program. Both mortality and gross recruitment

estimates ranged from 0.01 to 1.30 y^{-1} at 118 sampling locations; mortality and gross recruitment at a site were highly correlated (Peterson and Fourqurean 2001). Variability in these population parameters led to a spatial pattern in predicted net population growth rates, which ranged from -0.2 to 0.5 y^{-1} , with a mean of ca. 0.0 y^{-1} (Figure 5). While these predictions of future population trajectory from the age structure of the population are as yet untested, the promise of this type of predictive monitoring is that it may be possible to detect change in a resource before the changes would be detected in a repetitive-mapping change analysis. There are still problems with applying these techniques to management, as some of the assumptions necessary for applying demographic models to field data can not necessarily be met (Jensen et al. 1996; Kaldy et al. 1999). The robustness of the estimates to violations of these assumptions must be understood before these tools can be routinely applied.

Spatial pattern in the elemental content of seagrass leaves indicated strong patterns in nutrient availability, and therefore trophic state, in *Thalassia testudinum* meadows in the study area. Elemental content did not vary randomly; rather there was a strong spatial pattern in the relative amounts of N and P in the samples (Figure 6). The spatial pattern suggested two main trends. The first trend was a decrease in the availability of P from the Gulf of Mexico eastward into Florida Bay, and the second pattern was an increase in relative P availability as distance from shore increases on the Atlantic Ocean side of the Florida Keys (Fourqurean and Zieman in press). While a similar onshore-offshore pattern has been documented for sediment nutrients (Szmant and

Forrester 1996), the seagrass leaf element content data adds to this previously established trend by documenting that changes in ratios of sediment nutrients are reflected in primary producers, and analysis of the seagrass leaf N:P data suggest that there is a qualitative shift from P-limitation to N-limitation of the seagrasses in different regions of our study area.

Time series data from the permanent monitoring stations underscore the importance of understanding seasonal cycles for monitoring programs. We have summarized data from the period of record from an example monitoring station (Figure 7). Because of this site is a relatively deep (3.5 m), nearshore location, it displays average seasonal amplitude compared to the rest of the sites in the program. Water temperature at this site varies in a predictable seasonal pattern, with wintertime lows of ca. 22 C and summertime highs of ca. 32 C (Figure 7A). The mean temperature from the sine model (Equation 3) was 26.5 C, with an amplitude of 4.9 C. Seasonality can be expressed as the amplitude/mean: seasonal peaks were 18.5% higher than the mean, while seasonal minima were 18.5% lower. The maximum temperature occurs on June 14 for an average year. Many of the measured seagrass parameters exhibited seasonal patterns very similar to temperature. The abundance (Figure 7B), productivity (Figure 7C), and C:P (Figure 7D) of *Thalassia testudinum* all had peaks roughly coincident with the temperature peak. Note that the abundance of *T. testudinum* had a seasonality (amplitude/mean) of 25%; hence abundance was highly dependent on the timing of sampling. Seasonality in productivity was even greater (50%), while seasonality in nutrient content was somewhat

less (19%). It is important to note that seasonality in these parameters is spatially variable across the monitoring region (Fourqurean et al. 2001).

Understanding how biological communities behave through time is one of the goals of any ecological monitoring program, but collecting and analyzing these biological data is an expensive and labor-intensive task. Because our understanding that the mechanisms leading to changes in biological communities in this environment are related to nutrient availability in the water column (Figure 1), it is imperative that we relate the biological responses we monitor to nutrient availability in the water column. Were these relationships fully understood, it may prove practical to only monitor the driving variables (water quality) and use mathematical models to predict change in the ecosystem. For this reason, linking the seagrass monitoring effort to a water quality monitoring effort was vital. The analysis of data needed to relate all of the factors monitored in this program to water quality is now underway, with the hopes of parameterizing a predictive model. For example, because of the concurrent water quality monitoring program, we know that seagrass leaf tissue elemental content is reflective of the relative concentration of N and P in the water column (median N:P of *Thalassia testudinum* leaves was related to the median N:P in the water column measured during 6 years of quarterly monitoring (1995-2000) of seagrasses and water quality (J.N. Boyer, Florida International University, unpublished data); $N:P \text{ of } T. \text{ testudinum} = 9.8 + 0.4[N:P \text{ of the water column}], r^2 = 0.38, p < 0.01$). Also, involvement of researchers in the monitoring effort to perform

manipulative experiments can elucidate the mechanisms relating environmental change to biological change.

Seagrass bed responses to changing water quality often occur over long time frames, but acute events can also be important in structuring these communities. Hurricanes are easily the most intense acute events to influence shallow water marine communities of south Florida. Fortunately for the residents of south Florida, few hurricanes have passed over the study area during the monitoring period, and these hurricanes (Georges and Mitch in 1998, Irene in 1999) were relatively mild. Hurricane Georges was the most intense storm during this period; it was a category 2 storm when it passed over Key West on September 25, 1998. The hurricane force winds were restricted to a relatively narrow band in the lower and middle Florida Keys. Such relatively small hurricanes had very substantial, but localized, effects. Over the network of 30 stations, the seagrass beds were completely destroyed by Georges at three stations. During the storm, two stations on the Atlantic Ocean side of the Florida Keys just behind the barrier reef experienced large waves coming from offshore that eroded sediments and the rhizome mat of *T. testudinum* was washed away. In contrast, one site on the Gulf of Mexico side of the Florida Keys experienced strong easterly winds that caused sediment deposition so that *T. testudinum* community was buried by 30 cm of sediment (Figure 8). Following the storm, early successional species (calcareous green algae and *Halodule wrightii*) quickly became established at the buried site, and after 2 years there was evidence of recovery of

the original *T. testudinum* dominated community. Hurricane impacts were very patchy in distribution - stations close to the affected stations were often unaffected by the storm.

Moving from determining status to detecting trends

This monitoring program has been very successful in defining the spatial extent and present condition of the seagrass beds in south Florida. The synoptic monitoring effort has provided a description of the distribution and species composition of seagrass beds whose detail and spatial extent are without precedent in marine benthic community monitoring. Spatial patterns in elemental content of one of the dominant seagrasses, *T. testudinum*, has led to the better understanding of the pattern of relative nutrient availability across the monitoring area. Analysis of the population age-structure has allowed for predictions of population density trends for this species. Further, monitoring at fixed stations has led to a description of the intra-annual pattern of species densities, growth rates and nutrient contents of seagrasses, as well as allowed for the detection of longer term trends in these parameters.

The spatial extent and species composition data comprise an important benchmark against which future changes may be gauged. The program is now poised to begin revisiting the thousands of synoptic monitoring points (Figure 4) in order to assess change in these parameters. It is tempting to apply change analysis techniques to data that was collected in separate years - for example, compare the surfaces generated from 2000 data to the surfaces generated with 1996 data - but such analyses are not to be trusted because

of spatial variability smaller in scale than the hexagons originally used to select the random sampling points. The consequences of small-scale spatial variability are that it is not possible to detect small changes in the status of indicators until two rotations of sampling the exact synoptic mapping points - or in this case, until 10 years of data collection.

The spatial sampling intensity of the synoptic mapping stations was sufficient for describing the gross features of the distribution of benthic habitats across the study area, but it has proven to be too coarse to detect already extant anthropogenic influences to these communities. Casual observation and some published accounts (e.g. Tomasko and Lapointe 1991; Lapointe and Clark 1992) document increases in epiphytism and some loss of seagrasses in the Florida Keys in the immediate nearshore environment - i.e. the first 0-100 m from shore. Further, natural point sources (like bird rookeries, Powell et al. 1991) of nutrients in the Florida Keys have effects that are confined to ca. 100 m offshore. These observations indicate that the natural oligotrophic nature of the nearshore environment is both strongly affected by nutrient releases and an efficient attenuator of nutrient effects because of rapid and efficient uptake. It is now obvious that the spatial sampling intensity must be increased in areas adjacent to human activity if such acute, localized effects are to be characterized and monitored. Hence, sampling site density was increased within the first kilometer of shoreline in 2000, the 5th year of the monitoring program. This new intensity of sampling is allowing for definitions of fine-scale, near-shore features that were not detected in the original monitoring plan (Figure 9), but the

effort required to monitor these smaller-scale phenomena necessarily diverts resources from the original, regional scope of the program.

The elemental composition of seagrass leaves was related to concentrations of nitrogen and phosphorus in the water column. This relationship is a useful one, because water quality is often variable in time at a single location - so that multiple determinations of concentrations of nutrients often are required to describe water quality at a site. Because seagrass nutrient content is a function of the average conditions at that site, a single sampling of seagrass leaves can be used as an integrative indicator of relative nutrient availability at that site. Some caution must be used with this approach, however, because elemental content of seagrass leaves is seasonal (Fourqurean et al. 1997 and Figure 7); but the use of tissue content as a proxy for water quality data can potentially save much time and effort in a monitoring program. The spatial pattern of N:P in seagrass tissues shows a clear pattern in relative availability of N and P in the study area (Figure 6), and indicates that nearshore seagrasses may be P-limited while offshore seagrasses are potentially N-limited. The conceptual models that form the basis for the monitoring program predict that as nutrient-limited *T. testudinum*-dominated sites receive anthropogenic nutrients, the N:P of *T. testudinum* leaves will move towards 30:1 (Figure 2); then biomass of *T. testudinum* will increase, followed by replacement of this species by faster-growing species (Figure 1). A further prediction of the conceptual models is that *T. testudinum*-dominated sites with leaf N:P ca. 30 are the most likely to experience a change in species dominance as a result of nutrient loading.

Changes in species dominance were caused by factors other than anthropogenic nutrient loading at one permanent monitoring station: a *T. testudinum* dominated community was replaced by a *H. wrightii* -calcareous green algae community at station 309 as a consequence of the passage of Hurricane Georges (Figure 8). Were it not for the time series of quarterly observations, this change could have been attributed to the consequences of anthropogenic nutrient loading. This explanation would have been particularly attractive because of the proximity of station 309 to the city of Key West. But, the time series data point to a clear explanation of the change: the healthy *T. testudinum* seagrass bed was destroyed by the acute event of the storm, and the reestablishment of the seagrass community through the process of ecological succession produced 2 years after the storm a community dominated by the same fast-growing species that are favored by increases in nutrient loading rates. Without the fine-scale temporal resolution, it would not be possible to positively ascribe a cause to the dynamics observed at site 309.

Three of the 30 permanent stations experienced the catastrophic loss of their seagrass communities as a result of hurricane damage during the study period, but this does not mean that storms are causing a 10% loss of seagrass habitat over each 5 year period. Physical disturbance creates a patchwork of disturbance in this community, and disturbed areas are slowly recolonized by early successional seagrass species (Patriquin 1975). Since the permanent stations were purposefully located at locations supporting seagrass beds, it was only possible at the beginning of this monitoring effort to observe

loss of seagrasses caused by storms and not recolonization of disturbed areas. We hope that monitoring these permanent stations will continue long enough so that it becomes possible to record the time course of recovery from such disturbances at many sites. Our experience with hurricanes underscores the importance of designing ecosystem monitoring programs to accommodate the natural pattern of disturbance.

One of the benefits of operating a monitoring program out of an academic or research institution is that experimental approaches to monitoring can be evaluated during the course of the monitoring program. In this program, we have been evaluating the use of the age structure of seagrass population to make predictions about the trajectory of the populations (Figure 5). While this is a common practice in fisheries management, it has only recently been reintroduced to seagrass ecologists (Duarte et al. 1994). It is a topic of ongoing debate whether the violations of the assumptions of the models necessary for making such population trajectory predictions will render these techniques invalid (Jensen et al. 1996; Durako and Duarte 1997; Kaldy et al. 1999), but this monitoring program is providing the structure for a long-term test of the applicability of the techniques by allowing a comparison of population trajectory predictions with more conventional long-term monitoring data. After the appropriate assessment, age structure analysis may prove to be a valuable, time-saving, predictive tool that can be used to assess the status of the community before changes in density or species composition are evident. Like age frequency analyses, new measures of the physiological status of seagrasses are now being proposed as potential new monitoring tools; we are currently

evaluating the utility of in-situ measures of the fluorescence characteristics of plants as a monitoring tool (Beer et al. 1998; Ralph et al. 1998; Beer and Björk 2000). Such new techniques have the potential to revolutionize monitoring programs, but properly assessing the utility of new techniques requires the involvement of research scientists in monitoring programs.

No monitoring program can practically encompass an entire ecosystem. This results from many factors, including the motivation for the monitoring program, the spatial extent of ecosystems, and jurisdictional boundaries that delineate responsibility for monitoring programs. Careful coordination between management agencies and research groups is necessary to ensure that data collected by different monitoring programs, for different goals funded by different agencies, can be pooled and analyzed as a whole for a more holistic view of regional ecosystem. Such careful coordination has been achieved in south Florida, where many different monitoring programs funded by federal, state and local agencies have agreed to use comparable monitoring techniques, thereby providing a unique opportunity to paint a truly regional view of the status of seagrass ecosystems in south Florida (Fourqurean et al. 2002). From this coordination, it is possible to expand the spatial scale of our understanding of the patterns in variation of these communities beyond the considerable spatial extent of the monitoring program described in this paper. For example, patterns in species diversity can be depicted from suburban Biscayne Bay, through Florida Bay and Everglades National Park, across the Florida Keys and out to the Dry Tortugas (Figure 10); this entire area is connected by water flows and is likely to

respond to anthropogenic changes in water delivery. This type of cooperation should serve as a model to other groups embarking on the assessment of resources over large geographic ranges.

Remote sensing has been used successfully to monitor some aspects of seagrass beds. Remotely sensed data has been successfully used to map seagrass distributions in many environments (e.g. Orth and Moore 1983; Lusczkovich et al. 1993; Ferguson and Korfmacher 1997). Large changes in seagrass cover have been documented by analysis of remotely-sensed data (e.g. Orth and Moore 1983; Robbins 1997; Ward et al. 1997). The large spatial scale, relatively small cost, and historic archive of aerial photographs and satellite images make the use of these data very appealing, but there are some serious limitations to the application of remotely-sensed data to seagrass monitoring programs. In general, it is not possible to distinguish seagrass beds from other dark areas on the bottom - so macroalgal beds and seagrass beds can not reliably be differentiated. Seagrass species are also not generally distinguishable from remotely-sensed data (Moore et al. 2000). As a consequence, remotely-sensed data at this time are not adequate to evaluate the trophic status of the benthic habitats in south Florida, since species composition is a key indicator of this status (Figure 1). Further, both satellite images and aerial photographs require an optically-clear water column and dense stands of macrophytes if they are to be useful for monitoring seagrasses, and it is common in south Florida for there to be very sparse seagrass communities overlain by an optically-dense water column. With continuing advances in active remote sensing techniques and multispectral imaging, these limitations

of remote sensing may be overcome in the future, but it is still necessary to send divers into the environment to collect the data needed for monitoring benthic communities in south Florida.

It is quite obvious that this monitoring program has led to a better understanding of the biology of seagrass beds in south Florida, but has the program been successful in terms of providing data useful to managers assessing impacts of human alteration of water and nutrient cycles in the region? At the present time, the program has yet to detect any common trends in seagrass nutrient content or community composition at the permanent monitoring locations. This can be interpreted to mean that there are no regional trends in the status of seagrass beds, but such an interpretation may be short-sighted. The lack of detectable trends poses a difficult challenge both to the monitoring team and to the management agencies responsible for funding monitoring programs. In such an instance, the monitoring team must reevaluate its monitoring scheme for proper spatial and temporal resolution, and the management agency must decide whether the potential for change in the monitored ecosystem is great enough to continue the program despite finding no trends in the ecosystems. In south Florida, the case can easily be made to continue the monitoring effort. Not only has natural disturbance (hurricanes) caused changes at the monitoring stations, but manipulative experiments in seagrass beds of south Florida demonstrate that the time course of the response of seagrass beds to eutrophication is on the order of decades, and we do not understand completely the interaction man has with the natural dynamics of these systems.

Lessons learned about ecological monitoring from this program

The major lessons learned from this monitoring program that should be heeded by others designing regional ecosystem monitoring plans are:

- Ensure that there is a strong conceptual model underlying the monitoring strategy.
- No one monitoring design is adequate for all questions asked within a monitoring plan. In particular, trade-offs between allocating resources to broad spatial coverage or fine-scale temporal coverage need to be addressed at the outset of the program. The split design we employed was an attempt to allocate resources to both of these goals.
- Not every monitoring technique ends up being adequate to answer the questions addressed by the monitoring program. Often these inadequacies are not apparent until years worth of data has been collected and analyzed. All monitoring programs should be required to reevaluate all of their techniques on a periodic basis, and make changes as appropriate. Research scientists involved with monitoring projects should be given this responsibility; peer-reviewed publication of results is one sure way to encourage such analyses.
- Keep methods as simple and universally used as possible. Often, seemingly small methodological differences between groups of investigators and monitoring programs make intercomparison of results

difficult or impossible. Further, careful consideration should be given to any change in techniques during the monitoring program, since small technique changes may render trend detection impossible.

- Disturbances are a natural structuring force in most ecosystems, so their impact should be taken into account when designing the monitoring program. Redundancy of sampling locations will lessen the impact of a natural disaster (such as a hurricane or fire) on the monitoring program, and it will also provide interesting research opportunities.

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Literature Cited

Atkinson, M.J., and S.V. Smith. 1983. C:N:P ratios of benthic marine plants. *Limnology and Oceanography* 28: 568-574.

Beer, S., and M. Björk. 2000. Measuring rates of photosynthesis of two tropical seagrasses by pulse amplitude modulated (PAM) fluorometry. *Aquatic Botany* 66: 69-76.

Beer, S., B. Vilenkin, A. Weil, M. Veste, L. Susel, and A. Eshel. 1998. Measuring photosynthetic rates in seagrasses by pulse amplitude modulated (PAM) fluorometry. *Marine Ecology Progress Series* 174: 293-300.

Bohnsack, J.A., D.E. Harper, and D.B. McClellan. 1994. Fisheries trends from Monroe County, FL. *Bulletin of Marine Science* 54: 982-1018.

Boyer, J.N., and R.D. Jones. 2002. View from the bridge: external and internal forces affecting the ambient water quality of the Florida Keys National Marine Sanctuary. Pp. 609-628. In: The Everglades, Florida Bay, and the coral reefs of the Florida Keys, edited by J. W. Porter and K. G. Porter, . CRC Press, Boca Raton.

Boyer, J.N., P. Sterling, and R.D. Jones. 1999. Maximizing information from a water quality monitoring network through visualization techniques. *Estuarine, Coastal and Shelf Science* 50: xxx-xxx.

Braun-Blanquet, J. 1972. *Plant sociology: the study of plant communities*. Hafner Publishing Company. New York.

Butler, M.J., IV, J.H. Hunt, W.F. Herrnkind, M.J. Childress, R. Bertelsen, W. Sharp, T. Matthews, J.M. Field, and H.G. Marshall. 1995. Cascading disturbances in Florida Bay, USA: cyanobacterial blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. *Marine Ecology Progress Series* 129: 119-125.

Chamberlain, R., and D. Hayward. 1996. Evaluation of water quality and monitoring in the St. Lucie estuary, Florida. *Water Resources Bulletin* 32: 681-696.

Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253-260.

Dillon, K.S., D.R. Corbett, J.P. Chanton, W.C. Burnett, and D.J. Furbish. 1999. The use of sulfur hexafluoride (SF₆) as a tracer of septic tank effluent in the Florida Keys. *Journal of Hydrology* 220: 129-140.

Duarte, C.M. 1992. Nutrient concentrations of aquatic plants: patterns across species. *Limnology and Oceanography* 37: 882-889.

Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87-112.

Duarte, C.M. in press. The future of seagrass meadows. *Environmental Conservation*.

Duarte, C.M., N. Marba, N. Agawin, J. Cebrian, S. Enriquez, M.D. Fortes, M.E.

Gallegos, M. Merino, B. Olesen, K. Sand-Jensen, J. Uri, and J. Vermaat. 1994.

Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Marine Ecology Progress Series* 107: 195-209.

Durako, M.J., and C.M. Duarte. 1997. On the use of reconstructive aging techniques for assessing seagrass demography: a critique of the model test of Jensen et al. (1996).

Marine Ecology Progress Series 146: 297-303.

Erickson, R.O., and F.J. Michelini. 1957. The plastochron index. American Journal of Botany 44: 297-305.

Ferguson, R.L., and K. Korfmacher. 1997. Remote sensing and GIS analysis of seagrass meadows in North Carolina, USA. Aquatic Botany 58: 241-258.

Fourqurean, J.W., M.J. Durako, M.O. Hall, and L.N. Hefty. 2002. Seagrass distribution in south Florida: a multi-agency coordinated monitoring program. Pp. 497-522. In: The Everglades, Florida Bay, and the coral reefs of the Florida Keys, edited by J. W. Porter and K. G. Porter, . CRC Press, Boca Raton.

Fourqurean, J.W., T.O. Moore, B. Fry, and J.T. Hollibaugh. 1997. Spatial and temporal variation in C:N:P ratios, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. Marine Ecology Progress Series 157: 147-157.

Fourqurean, J.W., G.V.N. Powell, W.J. Kenworthy, and J.C. Zieman. 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos* 72: 349-358.

Fourqurean, J.W., and M.B. Robblee. 1999. Florida Bay: a history of recent ecological changes. *Estuaries* 22: 345-357.

Fourqurean, J.W., A.W. Willsie, C.D. Rose, and L.M. Rutten. 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology* 138: 341-354.

Fourqurean, J.W., and J.C. Zieman. in press. Seagrass nutrient content reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida Keys, USA. *Biogeochemistry*.

Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell. 1992a. Phosphorus limitation of primary production in Florida Bay: Evidence from the C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* 37: 162-171.

Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell. 1992b. Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. *Marine Biology* 114: 57-65.

Frankovich, T.A., and J.W. Fourqurean. 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Marine Ecology Progress Series* 159: 37-50.

Gerloff, G.C., and P.H. Krombholz. 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. *Limnology and Oceanography* 11: 529-537.

Havens, K.E., and N.G. Aumen. 2000. Hypothesis-driven experimental research is necessary for natural resources management. *Environmental Management* 25: 1-7.

Jackson, J.B.C. 2001. What was natural in the coastal ocean? *Proceedings of the National Academy of Sciences USA* 98: 5411-5418.

Jackson, J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndahl, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J.M. Pandolfi, C.H. Peterson, R.S. Steneck, M.J. Tegner, and R.R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629-638.

Jensen, S.L., B.D. Robbins, and S.S. Bell. 1996. Predicting population decline: seagrass demographics and the reconstructive technique. *Marine Ecology Progress Series* 136: 267-276.

Kaldy, J.E., N. Fowler, and K.H. Dunton. 1999. Critical assessment of *Thalassia testudinum* (turtle grass) aging techniques: implications for demographic inferences. *Marine Ecology Progress Series* 181: 279-288.

Kiker, C.F., J.W. Milon, and A.W. Hodges. 2001. Adaptive learning for science-based policy: the Everglades restoration. *Ecological Economics* 37: 403-416.

Klein, C.J.I., and S.P.J. Orlando. 1994. A spatial framework for water-quality management in the Florida Keys National Marine Sanctuary. *Bulletin of Marine Science* 54: 1036-1044.

Kraemer, G.P., R.H. Chamberlain, A.D. Steinman, and M.D. Hanisak. 1999. Physiological responses of transplants of the freshwater angiosperm *Valisneria americana* along a salinity gradient in the Caloosahatchee estuary (southwestern Florida). *Estuaries* 22: 138-148.

Lapointe, B.E., and M.W. Clark. 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. *Estuaries* 15: 465-476.

Lapointe, B.E., J.D. O'Connell, and G.S. Garrett. 1990. Nutrient couplings between on-site sewage disposal systems, groundwaters, and nearshore surface waters of the Florida Keys. *Biogeochemistry* 10: 289-307.

Lapointe, B.E., D.A. Tomasko, and W.R. Matzie. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. *Bulletin of Marine Science* 54: 696-717.

Lessios, H.A., J.D. Cubit, D.R. Robertson, M.J. Shulman, M.R. Parker, S.D. Garrity, and S.C. Levings. 1984. Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. *Coral Reefs* 3: 173-182.

Light, S.S., and J.W. Dineen. 1994. Water control in the Everglades: a historical perspective. In: *Everglades: the ecosystem and its restoration*, edited by S. M. Davis and J. C. Ogden, 47-84. St. Lucie Press, Delray Beach, FL.

Luszkovich, J.J., T.W. Wagner, J.L. Michelak, and R.W. Stoffle. 1993. Discrimination of coral reefs, seagrass meadows, and sand bottoms from space: a Dominican Republic case study. *Photogrammetric engineering and remote sensing* 59: 385-389.

McMillan, C., and F.N. Moseley. 1967. Salinity tolerances of five marine spermatophytes of Redfish Bay, Texas. *Ecology* 48: 503-506.

Moore, K.A., D.J. Wilcox, and R.J. Orth. 2000. Analysis of the abundance of submersed aquatic vegetation communities in the Chesapeake Bay. *Estuaries* 23: 115-127.

NOAA. 1996 Florida Keys National Marine Sanctuary final management plan/environmental impact statement, volume 1: Management Plan. National Oceanographic and Atmospheric Administration, U.S. Department of Commerce, Washington, DC.

Nuttle, W.K., J.W. Fourqurean, B.J. Cosby, J.C. Zieman, and M.B. Robblee. 2000. Influence of net freshwater supply on salinity in Florida Bay. *Water Resources Research* 36: 1805-1822.

Ogden, J.C., S.M. Davis, and L.A. Brandt. in press. A strategy for the scientific support of a regional ecosystem monitoring and assessment program: the Florida Everglades example. In: *Ecological Monitoring of Ecosystem Initiatives*, edited by D. E. Busch and J. C. Trexler, . Island Press.

Orth, R.J., and K.A. Moore. 1983. Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. *Science* 222: 51-53.

Patriquin, D.G. 1975. "Migration" of blowouts in seagrass beds at Barbados and Carricou, West Indies, and its ecological and geological implications. *Aquatic Botany* 1: 163-189.

Paul, J.H., J.B. Rose, S.C. Jiang, X.T. Zhou, P. Cochran, C. Kellog, J.B. Kang, D. Griffin, S. Farrah, and J. Lukasik. 1997. Evidence of groundwater and surface marine water contamination by waste disposal wells in the Florida Keys. *Water Research* 31: 1448-1454.

Peterson, B.J., and J.W. Fourqurean. 2001. Large-scale patterns in seagrass (*Thalassia testudinum*) demographics in south Florida. *Limnology and Oceanography* 46: 1077-1090.

Porter, J.W., S.K. Lewis, and K.G. Porter. 1999. The effects of multiple stressors on the Florida Keys coral reef ecosystem: a landscape hypothesis and a physiological test. *Limnology and Oceanography* 44: 941-949.

Powell, G.V.N., J.W. Fourqurean, W.J. Kenworthy, and J.C. Zieman. 1991. Bird colonies cause seagrass enrichment in a subtropical estuary: observational and experimental evidence. *Estuarine, Coastal and Shelf Science* 32: 567-579.

Powell, G.V.N., W.J. Kenworthy, and J.W. Fourqurean. 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bulletin of Marine Science* 44: 324-340.

Ralph, P.J., R. Gademann, and W.C. Dennison. 1998. In situ seagrass photosynthesis measured using a submersible, pulse-amplitude modulated fluorometer. *Marine Biology* 132: 367-373.

Redfield, A.C. 1958. The biological control of chemical factors in the environment. *American Scientist* 46: 205-221.

Redfield, G.W. 2000. Ecological research for aquatic science and environmental restoration in south Florida. *Ecological Applications* 10: 990-1005.

Robbins, B.D. 1997. Quantifying temporal change in seagrass areal coverage: the use of GIS and low-resolution aerial photography. *Aquatic Botany* 58: 259-267.

Robblee, M.B., T.R. Barber, P.R. Carlson, M.J. Durako, J.W. Fourqurean, L.K.

Muehlstein, D. Porter, L.A. Yarbrow, R.T. Zieman, and J.C. Zieman. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress Series* 71: 297-299.

Rose, C.D., W.C. Sharp, W.J. Kenworthy, J.H. Hunt, W.G. Lyons, E.J. Prager, J.F.

Valentine, M.O. Hall, P.E. Whitfield, and J.W. Fourqurean. 1999. Overgrazing of a large seagrass bed by sea urchins in outer Florida Bay. *Marine Ecology Progress Series* 190: 211-222.

Sargent, F.J., T.J. Leary, D.W. Crews, and C.R. Kruer. 1995 Scarring of Florida's seagrasses: assessment and management options. FMRI Technical Report TR-1. Florida Marine Research Institute, St. Petersburg, FL.

Short, F.T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23: 17-27.

Szmant, A.M., and A. Forrester. 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. *Coral Reefs* 15: 21-41.

Tilmant, J.T., R.W. Curry, R.D. Jones, A. Szmant, J.C. Zieman, M. Flora, M.B. Robblee, D. Smith, R.W. Snow, and H. Wanless. 1994. Hurricane Andrew's effect on marine resources. *BioScience* 44: 230-237.

Tomasko, D.A., and B.E. Lapointe. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. *Marine Ecology Progress Series* 75: 9-17.

Trexler, J.C., W.F. Loftus, J.H. Chick, and S.A. Perry. in press. Setting and monitoring restoration goals in the absence of historical data: monitoring fishes in the Florida Everglades. In: *Monitoring of Ecosystem Initiatives*, edited by D.E. Busch and C. Trexler, . Island Press.

USACE. 1999 Central and southern Florida comprehensive review study: final integrated feasibility report and programmatic environmental impact statement. U.S. Army corps of Engineers, Jacksonville district, Jacksonville, FL, USA.

Ward, D.H., C.H. Markon, and D.C. Douglas. 1997. Distribution and stability of eelgrass beds at Izembek Lagoon, Alaska. *Aquatic Botany* 58: 229-240.

Watson, D.F. 1992. Contouring: a guide to the analysis and display of spatial data, vol. 10. Pergammon Press. New York.

Wiginton, J.R., and C. McMillan. 1979. Chlorophyll composition under controlled light conditions as related to the distribution of seagrasses in Texas and the U.S Virgin Islands. *Aquatic Botany* 6: 171-184.

Williams, S.L. 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. *Marine Ecology Progress Series* 35: 91-98.

Zieman, J.C., and R.G. Wetzel. 1980. Productivity in seagrasses: methods and rates. In: *Handbook of seagrass biology, an ecosystem prospective*, edited by R. C. Phillips and C. P. McRoy, 87-116. Garland STPM Press, New York.

Table 1. Braun-Blanquet abundance scale used to assess seagrass density. Cover is defined as the fraction of the bottom that is obscured by the species when viewed by a diver from directly above.

Cover Class	Description
0	Absent
0.1	Solitary individual ramet, less than 5 % cover
0.5	Few individual ramets, less than 5% cover
1	Many individual ramets, less than 5% cover
2	5% - 25 % cover
3	25 % - 50 % cover
4	50 % - 75 % cover
5	75 % - 100 % cover

Figure Captions

- Figure 1. A conceptual model relating nutrient availability (trophic state) to relative abundances of primary producers in near-shore marine waters of South Florida.
- Figure 2. A conceptual model of the relationship between seagrass leaf nutrient content and nutrient availability in south Florida.
- Figure 3. An illustration of the method used to distribute random samples quasi-evenly across the landscape. A number of hexagonal cells matching the desired number of sampling locations are packed into the sample area, and one random point is sampled from each cell for each year's sampling. Different symbols indicate a different year's sampling location within a hexagon.
- Figure 4. Synoptic maps of the density (D_t) of the seagrass *Thalassia testudinum* based on data collected in the years 1996 - 2000.
- Figure 5. Net population change predictions from analysis of the age structure of populations of short shoots of *Thalassia testudinum* (redrawn from Peterson and Fourqurean 2001).
- Figure 6. Spatial pattern in elemental content of green leaves of *Thalassia testudinum* in the eastern half of the study area (redrawn from Fourqurean and Zieman in press).

Figure 7. Time series data from an example permanent monitoring site. A. Temperature record. The line represents the fit of the sine model (Equation 7) to the data; $Y = 26.5 + 4.9\sin(\text{date in radians} + 4.4)$, $r^2 = 0.82$. B. Abundance of three conspicuous taxa of benthic plants: *Thalassia testudinum* (●; $Y = 3.2 + 0.8\sin(\text{date in radians} + 4.2)$, $r^2 = 0.71$), *Syringodium filiforme* (○; $Y = 0.5 + 0.4\sin(\text{date in radians} + 2.9)$, $r^2 = 0.31$); and calcareous green algae (▲; $Y = 0.4 + 0.1\sin(\text{date in radians} + 3.0)$, $r^2 = 0.77$). C. Productivity of green leaves of *Thalassia testudinum*, $Y = 1.0 + 0.5\sin(\text{date in radians} + 4.9)$, $r^2 = 0.63$. D. Elemental content (C:P) of green leaves of *Thalassia testudinum*, $Y = 1021 + 196\sin(\text{date in radians} + 4.0)$, $r^2 = 0.53$.

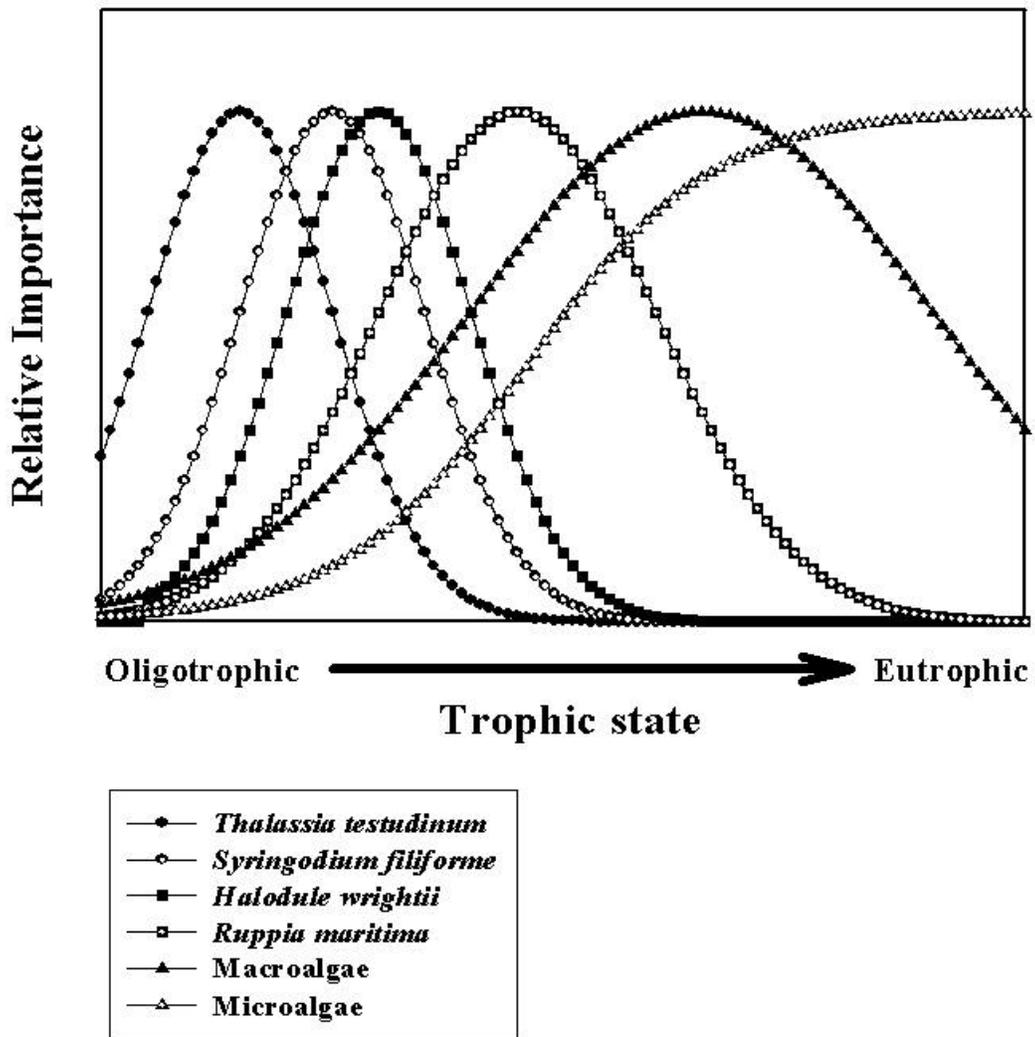
Figure 8. Time series of the abundance (A_i) of *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii* and calcareous green algal illustrating the impact of Hurricane Georges on the benthic plant communities at one site that was buried by 50 cm of sediment during the storm.

Figure 9. Comparison of contour maps of the density (D_i) of *Thalassia testudinum* generated using data from only the coarse-scale synoptic stations (top) and generated using data from the coarse-scale stations as well as additional near-shore station on a finer spatial scale.

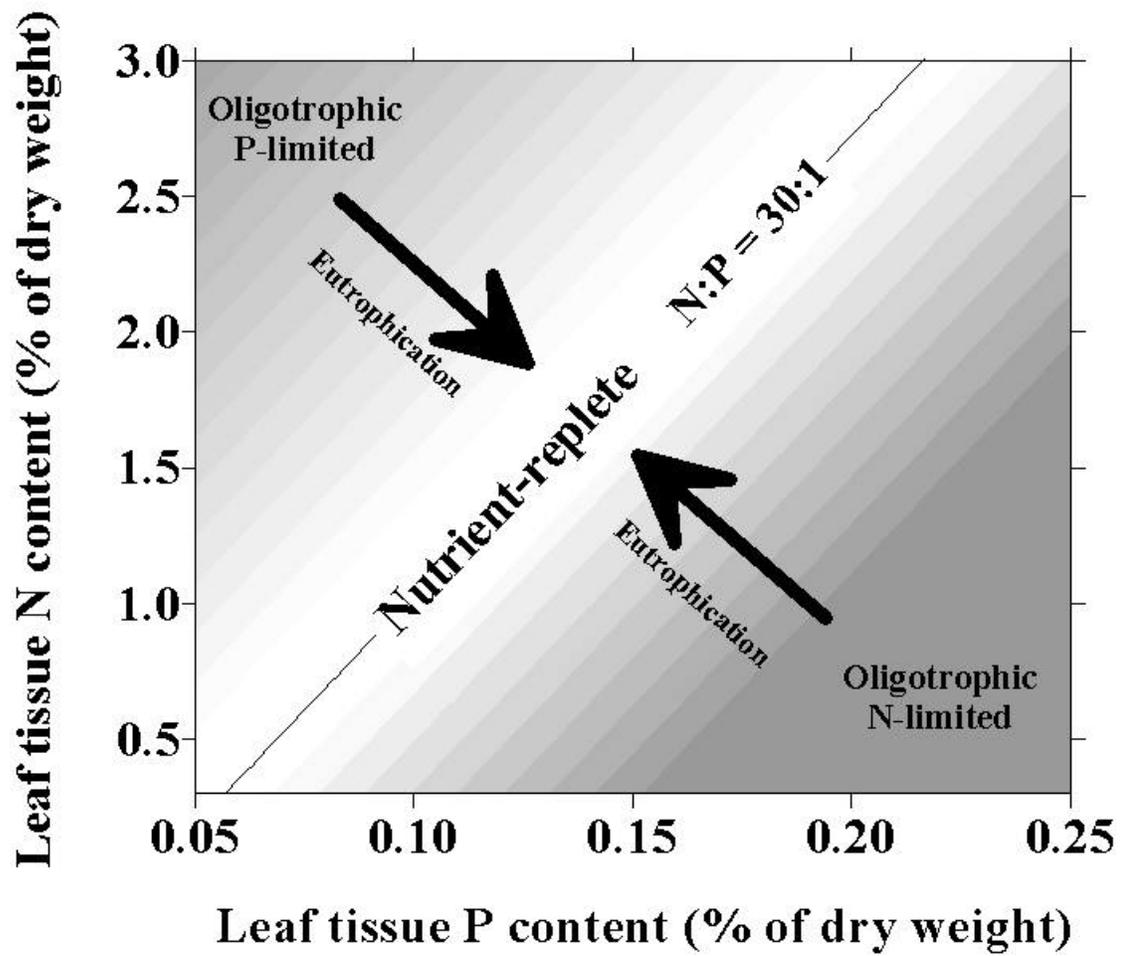
Figure 10. Species Richness on the regional scale. If monitoring programs ensure that their methods are easily comparable to other monitoring groups working in

similar systems, it is possible to elucidate patterns that occur on a larger scale than the original monitoring program.

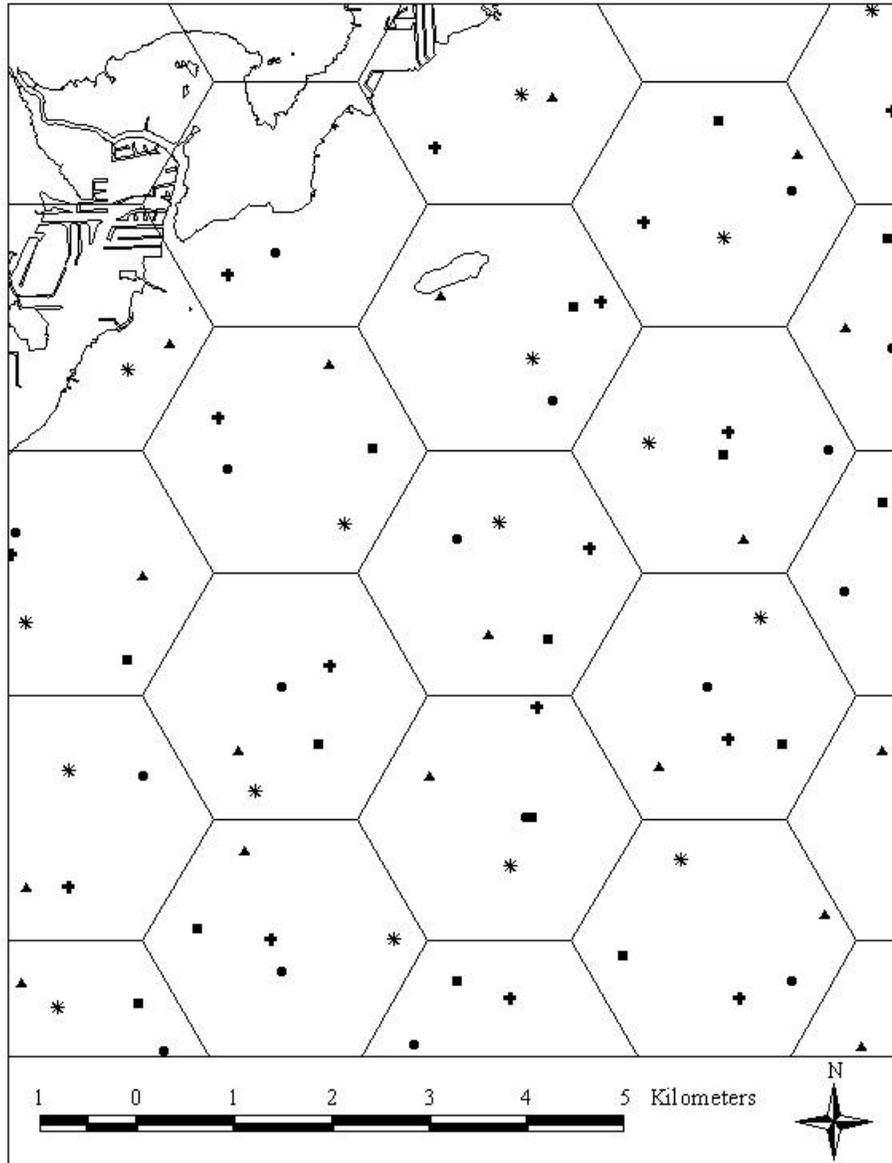
Eutrophication model



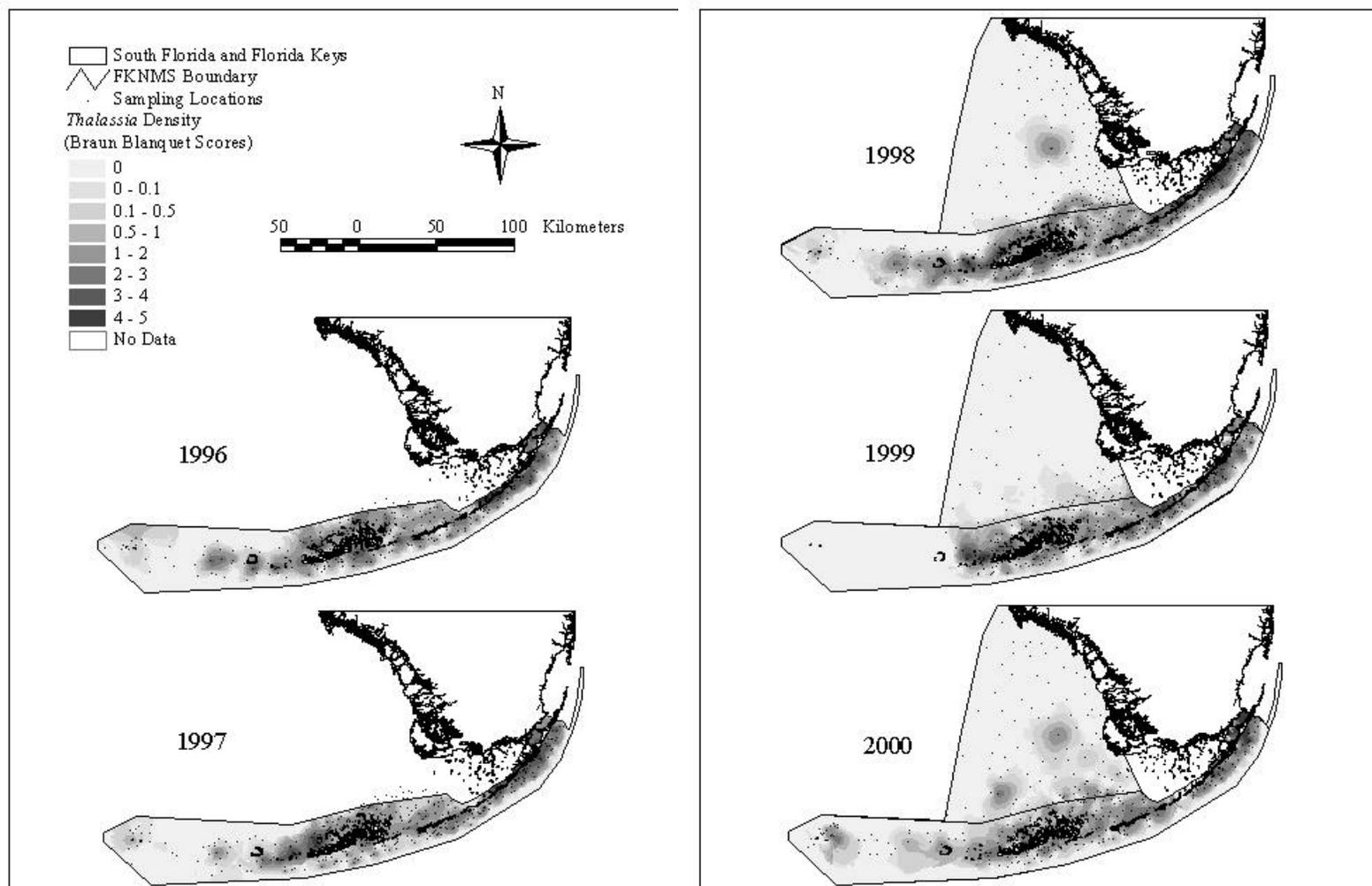
Fourqrean and Ruttan Figure 2



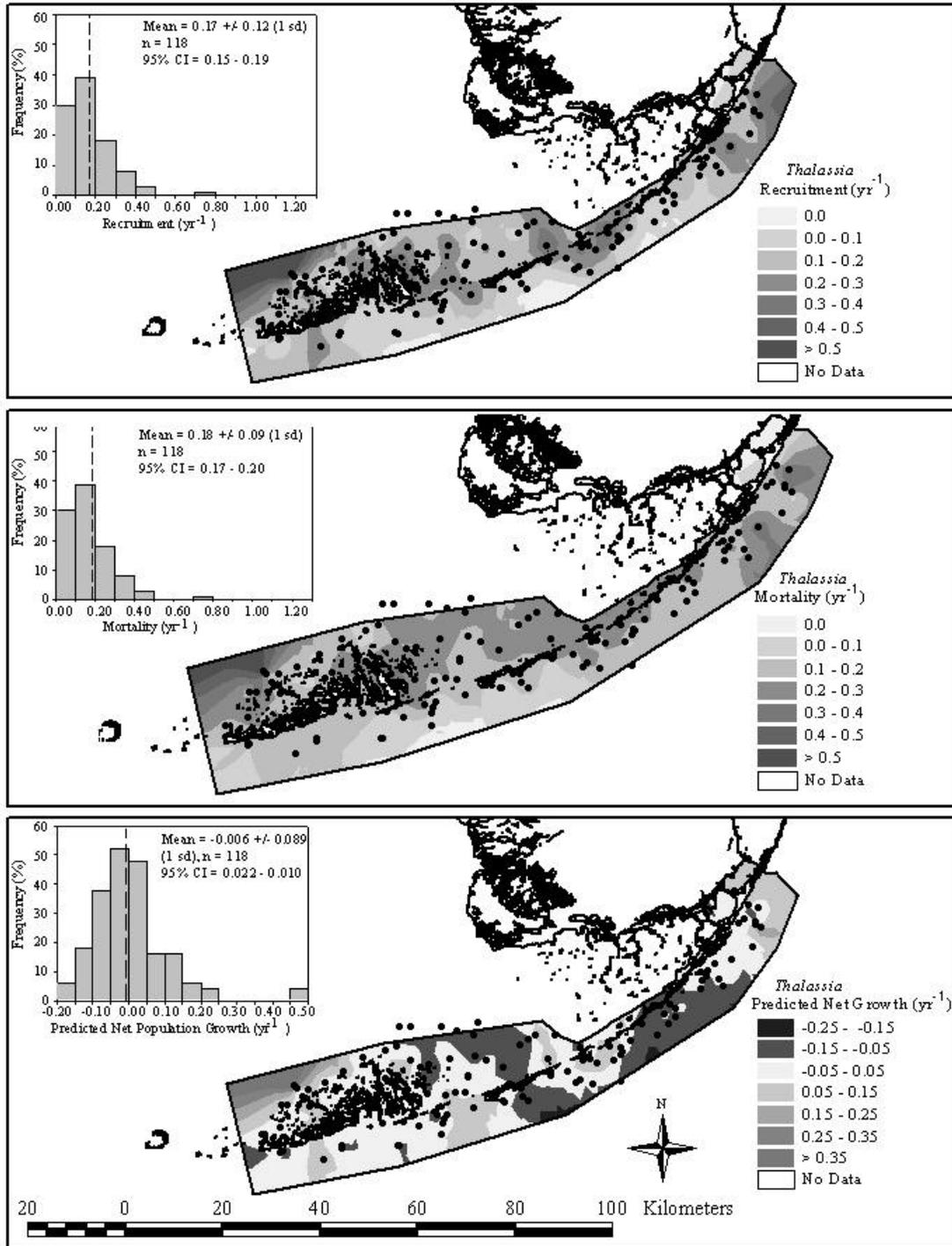
Fourqorean and Rutten Figure 3



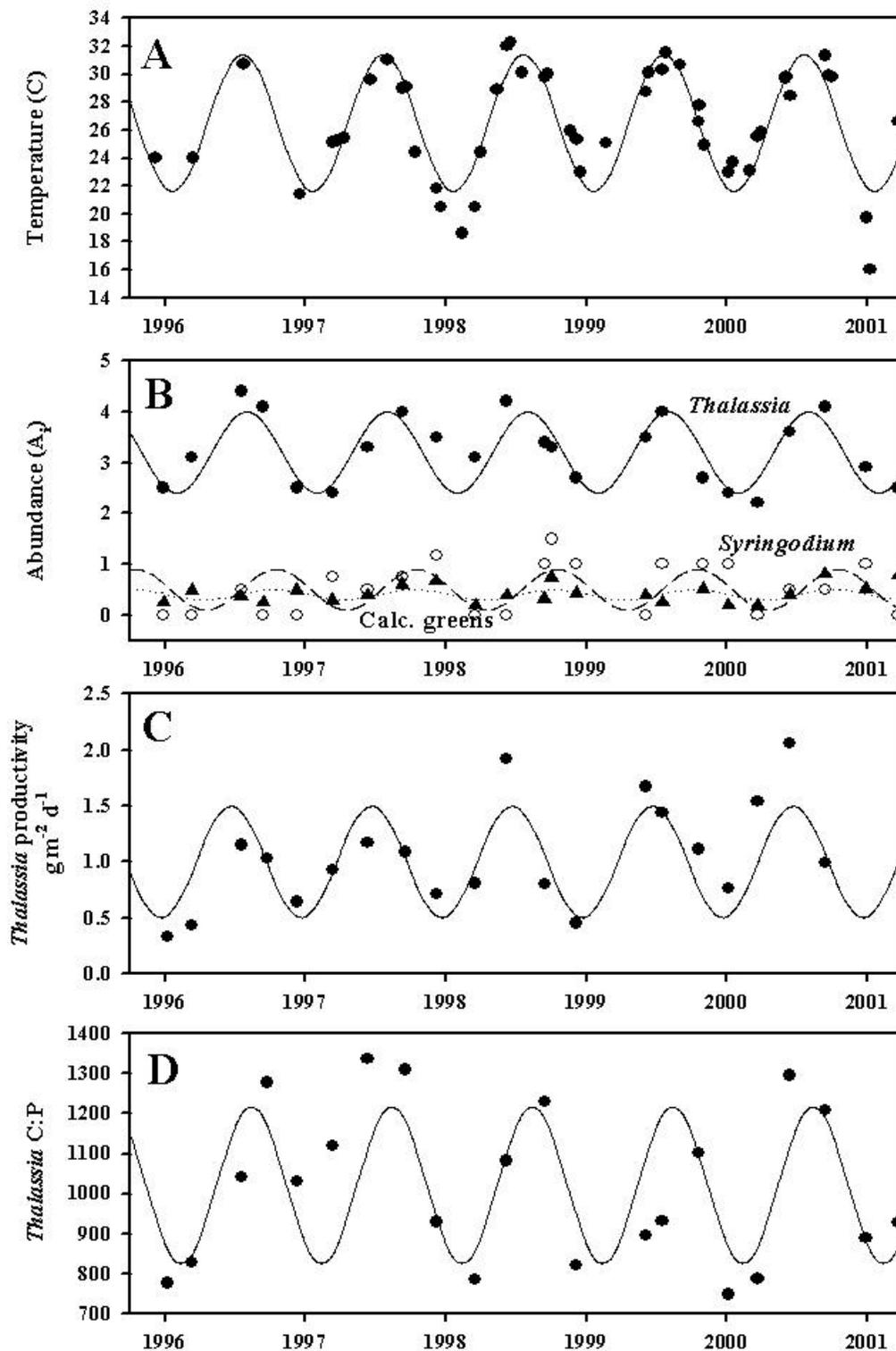
Fourqurean and Rutten Figure 4



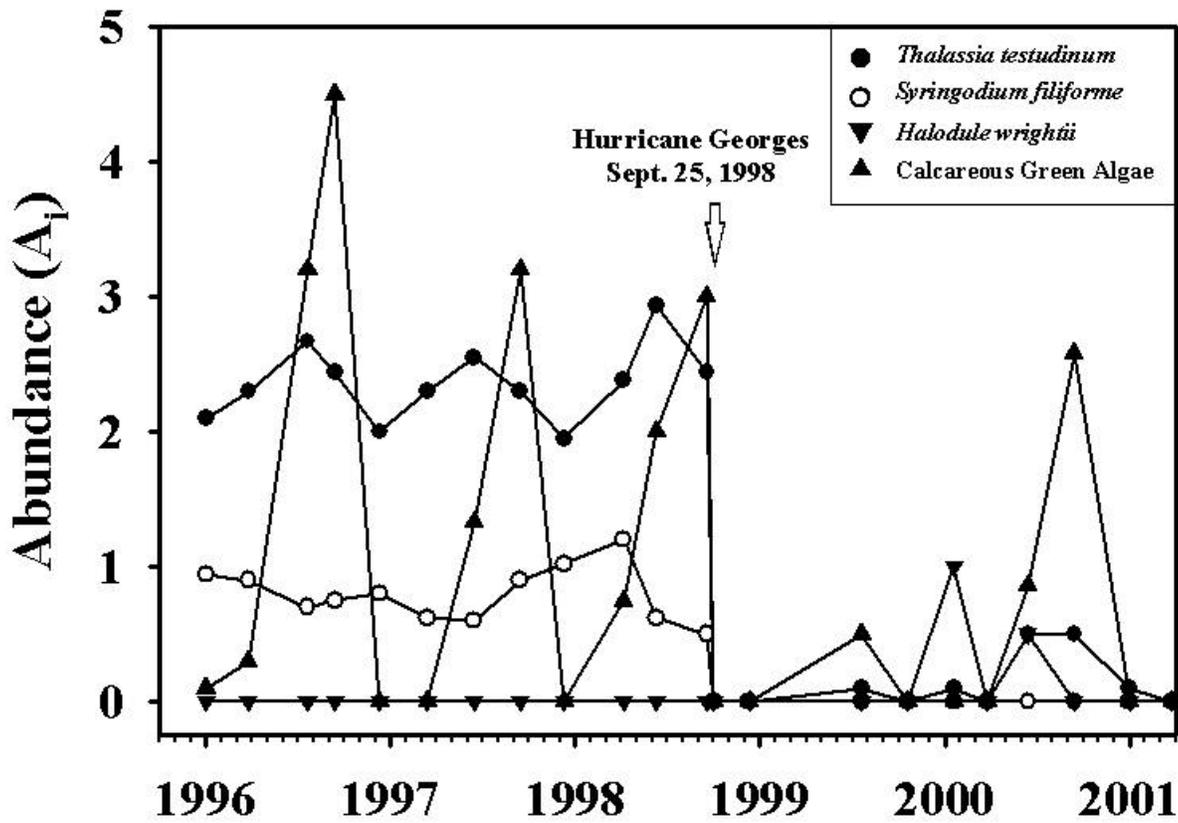
Fourqurean and Rutten Figure 5



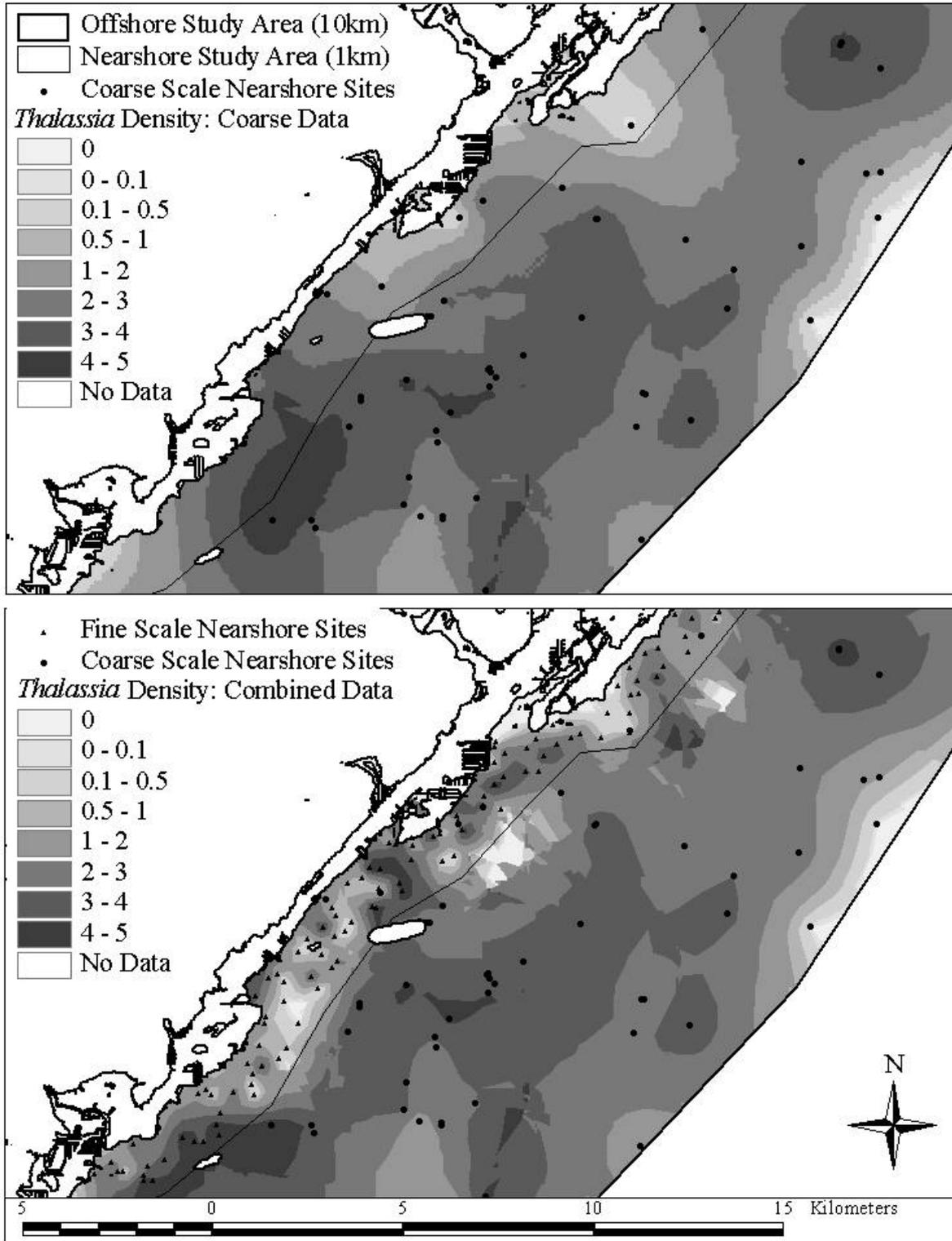
Fourqurean and Rutten Figure 7



Fourqurean and Rutten Figure 8



Fourqurean and Rutten Figure 9



Fourqurean and Rutten Figure 10.

