

SPATIOTEMPORAL VARIATION OF THE ABUNDANCE OF CALCAREOUS GREEN MACROALGAE IN THE FLORIDA KEYS: A STUDY OF SYNCHRONY WITHIN A MACROALGAL FUNCTIONAL-FORM GROUP¹

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The abundance of calcareous green algae was recorded quarterly at 28 sites within the Florida Keys National Marine Sanctuary (FKNMS) for a period of 7 years as part of a sea grass monitoring program. To evaluate the validity of using the functional-form group approach, we designed a sampling method that included the functional-form group and the component genera. This strategy enabled us to analyze the spatiotemporal patterns in the abundance of calcareous green algae as a group and to describe synchronous behavior among its genera through the application of a nonlinear regression model to both categories of data. Spatial analyses revealed that, in general, all genera displayed long-term trends of increasing abundance at most sites; however, at some sites the long-term trends for genera opposed one another. Strong synchrony in the timing of seasonal changes was found among all genera, possibly reflecting similar reproductive and seasonal growth pattern, but the variability in the magnitude of seasonal changes was very high among genera and sites. No spatial patterns were found in long-term or seasonal changes; the only significant relation detected was for slope, with sites closer to land showing higher values, suggesting that some factors associated with land proximity are affecting this increase. We conclude that the abundances of genera behaved differently from the functional-form group, indicating that the use of the functional-form group approach may be unsuitable to detect changes in sea grass community structure in the

FKNMS at the existing temporal and spatial scale of the monitoring program.

Key index words: algal assemblages; calcareous green algae; distribution; Florida Keys National Marine Sanctuary; functional-form group; long-term monitoring; macroalgae; macroalgal abundance; macroalgal communities; monitoring; spatiotemporal variation; synchrony

Abbreviation: FKNMS, Florida Keys National Marine Sanctuary

To detect any change within a community or ecosystem in the face of human alteration of the coastal zone, we first need to understand the spatiotemporal patterns that provide the benchmarks or context where changes may be occurring (Underwood et al. 2000, Fourqurean et al. 2003). To accomplish this task, we need to understand the structure and components of the community or ecosystem of interest well enough to determine the appropriate scales and units of measurement necessary to describe these patterns and changes. The spatial and temporal patterns of vegetated communities have been described either at the species level or using assemblages of species based on different systems or models for plant classification. Plant classifications may group species based on taxonomic level or on other approaches like life cycles, growth forms, or life form attributes and their correlations with environmental characteristics (Holdridge et al. 1971). Other models have been proposed based on adaptive characteristics (Grime 1981), where plants are classified as a result of a trade-off between adaptation to different levels of disturbance and stress, linked

¹Received 30 March 2004. Accepted 18 April 2005.

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with models based on reproductive strategies, such as the r-K selection model (MacArthur and Wilson 1967).

In the marine realm, classification of marine macroalgae based on morphology or life forms was initially proposed by several authors (Feldman 1937, Boudouresque 1971, Chapman and Chapman 1976). More recently, models of functional-form groups were proposed by Littler and Littler (1980), Steneck and Watling (1982), and Steneck and Dethier (1994). The usefulness of these functional-form group models is to reduce the high diversity of algal species to a few generally recognized groups (Steneck and Dethier 1994). Unfortunately, in these models, grouping is based on growth form or morphology; the inference of function is only deduced from a minimal amount of empirical data about correlations in adaptive strategies (Phillips et al. 1997, Padilla and Allen 2000).

In coastal marine ecosystems there is a need for monitoring programs specifically designed to understand and evaluate the declines in live corals and sea grass beds, which are often associated with shifts to macroalgal-dominated communities (Short and Wyllie-Echeverria 1996, Hughes et al. 1999, McManus and Polsenberg 2004). A general approach for these monitoring programs is to use functional-form groups (Steneck and Dethier 1994). Orfanidis et al. (2001) used the Littler and Littler (1980) model to evaluate shifts in coastal lagoons under different anthropogenic stress; however, they found that differences were mainly between late successional species and opportunistic species rather than between functional groups. A combination of size, functional-form categories, and life history patterns was used in the evaluation of long-term vegetation changes associated with sedimentation in the inner Gullmar fjord, and shifts between groups of species were better described by combinations of characteristics more diverse than those included in functional-form group models (Eriksson et al. 2002).

In a number of marine monitoring programs dealing with long-term ecosystem trends, the main groups of macroalgae are based on the functional-form group model; however, the categories are often modified to suit each program. For example, the Caribbean Coastal Marine Productivity Program (CARICOMP, http://www.ccdc.org.jm/caricomp_main.html) and the Atlantic and Gulf Rapid Reef Assessment (AGRRA, <http://www.coral.noaa.gov/agrra/>) both recognize the functional-form group of calcareous crust algae as one of its categories; however, other categories (e.g. turf algae) include species belonging to different functional-form groups.

The main objective of many monitoring programs is to detect changes in the spatiotemporal patterns within a given community or ecosystem with respect to environmental changes. Using groups of species as the unit of measurement assumes that the grouped species will respond similarly to environmental changes. Although responses to large-scale infrequent environmental changes (e.g. hurricane passage, oil spill) can affect the abundance of groups of species similarly, small-

scale, seasonal, or long-term environmental changes (e.g. localized nutrient loading or salinity fluctuations) may elicit differential responses at the species level. However, we still do not know whether the functional-form group model provides the correct resolution to detect temporal and spatial changes in populations and community structure. One way to evaluate the efficacy of using the functional-form group model, or any grouping system, is to determine whether all members of a group act similarly in space over time. Spatiotemporal covariation, also known as synchrony, has been shown to provide helpful information on population dynamics that facilitate detection of common trends in variation at different time and spatial scales (Bjørnstad et al. 1999, Driskell et al. 2001).

We used the calcareous green algae functional-form group used by the Florida Keys National Marine Sanctuary (FKNMS) sea grass monitoring program to evaluate the potential use of functional-form groups in monitoring programs. This selection was based on the fact that this is the only group with information at the group level as well as the genus level of its components. The abundance of calcareous green algae is recorded for both the functional-form group as a whole and at the genus level (*Halimeda*, *Udotea*, *Penicillus*, and *Rhipocephalus*). This unique set of data enabled us to analyze the long-term and seasonal spatiotemporal patterns of a functional-form group, calcareous green algae, and describe synchronous behavior among its components at the genus level. Our rationale was that if we detected synchrony among the components of a functional-form group, we can assume they share similar patterns in seasonal and long-term population dynamics resulting from similar growth, reproductive, and recruitment strategies in addition to their morphological similarities. The presence of synchrony among the components of a functional-form group could help support the functional-form group model and support the use of this grouping approach in monitoring programs. On the other hand, the absence of synchrony among the components of a functional-form group may indicate that this grouping approach should not be used in such monitoring programs.

MATERIALS AND METHODS

We analyzed data from the FKNMS sea grass ecosystem assessment and monitoring program conducted by the Seagrass Ecosystem Research Laboratory at Florida International University, Miami, Florida, USA (Fourqurean and Rutten 2003). The general objective of this program was to measure the status and trends of sea grass communities to evaluate progress toward protecting and restoring the living marine resources of the FKNMS. Measurement of the abundance of macroalgae was included, because they are an important component of the sea grass and other benthic communities within the FKNMS. We focused on the analysis of the trends of calcareous green algae as a functional-form group as well as trends of the separate genera.

Study area. The FKNMS encompasses about 9000 km² of subtropical marine communities surrounding the islands of the Florida Keys in southern Florida, USA (Fig. 1). The

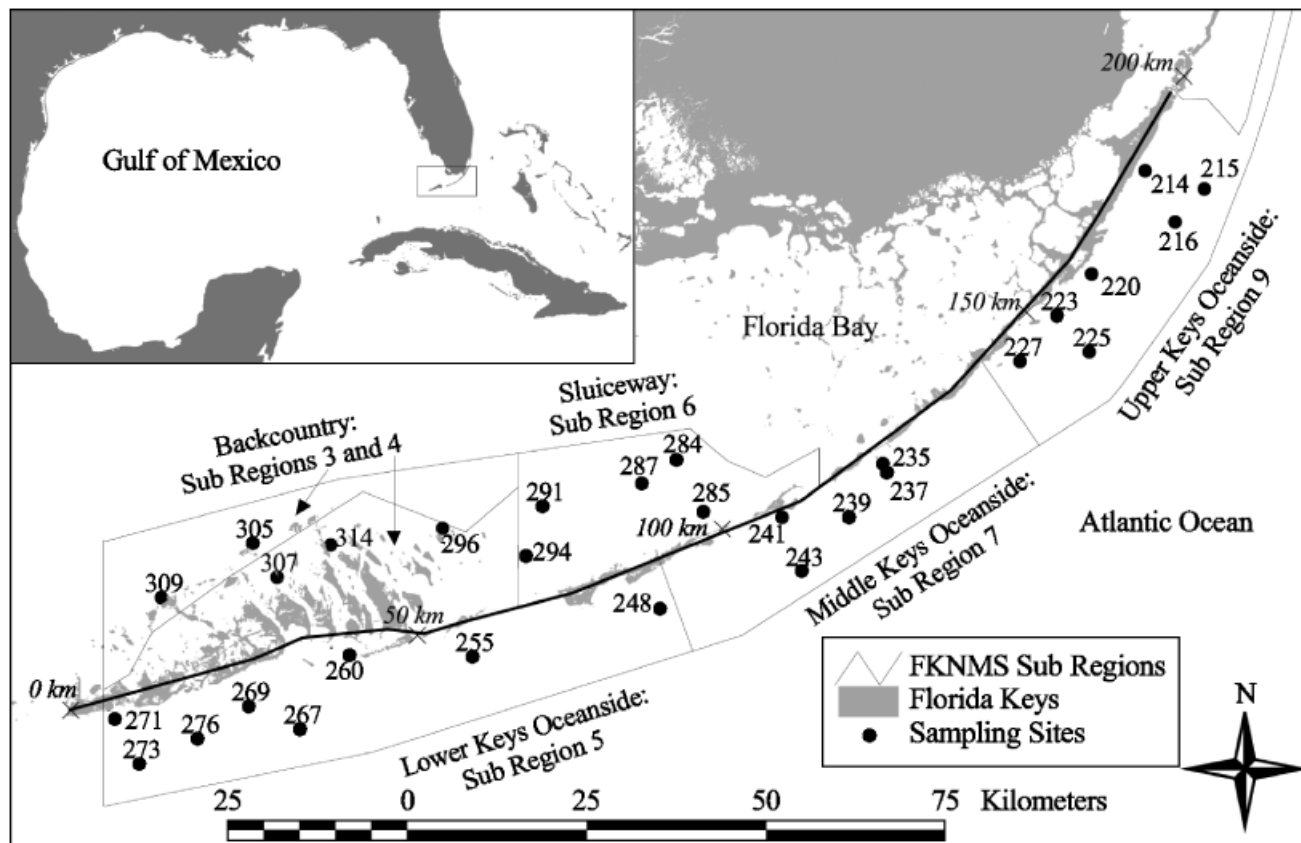


FIG. 1. Study area showing sample sites and geographic regions.

Florida Keys themselves are a line of islands nearly 300 km in length that extend in a southwesterly direction from the southern tip of Florida. These islands are generally divided into upper keys (Northern Key Largo to Upper Matecumbe), middle keys (from Upper Matecumbe to Pigeon Key), and lower keys (from Big Pine Key westward). The coastal marine ecosystems of the Florida Keys are composed of three dominant habitats: mangroves, sea grasses, and coral reefs. Sea grasses are found to cover more than 90% of subtidal areas less than 10 m in depth (Fourqurean et al. 2002).

The complex interaction of land and ocean and irregular topography results in a diverse set of subregions with particular characteristics. Local inhabitants of the Keys have described subregions of the region, which include a near-shore and reef-tract region on the Atlantic Ocean side of the Keys. A region of deeper water between the Keys and the reef tract is locally known as Hawk Channel, which runs parallel to the coast all along the Keys. The back-country region is associated with many small islands on the Gulf of Mexico side of the Keys, and the Sluiceway is a region with strong interchange currents between the Gulf of Mexico and the Atlantic Ocean. Based on currents and water influence, the Keys have also been segmented in different regions. For example, the northern side of the Florida Keys, locally referred to as "bay side," has a benthic habitat characterized by shallow water frequently affected by local wind-forcing currents and sediment disturbance; it is under the influence of Gulf of Mexico water. In contrast, to the south and east of the Florida Keys, locally referred to as "ocean side," is characterized by benthic habitats overlain by clearer water of a more oceanic character because this area is dominated by meanders of the Florida current (Lee et al. 2002). A more detailed segmentation of the FKNMS has been done to

provide a framework for the analysis of water quality behavior (Klein and Orlando 1994). Based on currents, topography, and winds, the Klein and Orlando (1994) suggested nine subareas. There is also reason to infer that benthic macroalgal communities would behave differently as a function of distance offshore from the Florida Keys, as the spatial pattern of N:P suggests a P-limited region of sea grass beds near shore and N-limited region of sea grass beds offshore (Fourqurean and Zieman 2002).

Monitoring techniques. The abundance of sea grasses and macroalgae was sampled quarterly from 1996 to 2002 at 28 permanent sites. The abundances of sea grass and algal taxa were recorded using a modified Braun-Blanquet method (Fourqurean and Rutten 2003). At each site, the abundance of taxa was recorded in 10 randomly located 0.25-m² quadrats along a 50-m permanent transect. The abundance of each taxa observed in each quadrat was assigned a score between 0 and 5. A score of 0 indicates that the genus or functional group was absent, 0.1 indicates the presence of a solitary individual covering <5%, 0.5 indicates few individuals covering <5%, 1 indicates numerous individuals covering <5%, 2 indicates 5%–25% cover, 3 indicates 25%–50% cover, 4 indicates 50%–75% cover, and 5 indicates 75%–100% cover. Abundance of each taxon (A_i) was calculated as

$$\text{Abundance } A_i = \left(\sum_{j=1}^n S_{ij} \right) / N_i$$

where N_i is the number of quadrats at a site in which taxon i occurred, n is the total number of quadrats observed, and S_{ij} is the Braun-Blanquet score for taxon i in quadrat j . Note $0 < A_i < 5$.

Data exploration. The recorded abundances of calcareous green algae were interpolated throughout the study area with a kriging interpolation routine (point kriging using linear variogram and no nugget) using the Surfer v. 7 program (Golden Software Inc., Golden, CO, USA). Maps displaying interpolated mean abundance were created for each calcareous green macroalgae genus and for calcareous green algae as a functional-form group; the mean abundance values across all 7 years (1996–2002) at a site were used as a proxy for overall group and genera abundance at each site.

Statistical analysis. To analyze the temporal patterns in abundance (e.g. long-term trends, seasonal cycles) at each site, a time series analysis was conducted in SPSS (SPSS Inc., Chicago, IL, USA, 1988–1999) using the following nonlinear regression model:

$$A_i = \text{intercept} + \text{slope} \times \text{time} + \text{amplitude} \times \sin(\text{time} + \phi)$$

where A_i is the abundance of species i , intercept represents the initial abundance, slope represents the long-term linear trend in abundance, amplitude represents the magnitude of seasonal changes in abundance, and ϕ (phase angle in radians) represents the timing of seasonal changes in abundance. Time was transformed into radians, where 1 year = 2π radians. This model was chosen for our analyses because a similar approach was successful in describing the temporal patterns of other aspects of the sea grass communities in the region (Fourqurean et al. 2001). The model was applied for each time series (7 years, four sampling events per year) for each taxon (e.g. individual genera or calcareous green algae as a group). Model results included estimated abundance curves and values for the three parameters of the estimated curve: slope, amplitude, and ϕ .

We applied a Bray-Curtis analysis of similarity to the slope, amplitude, and phase values to evaluate which components of the calcareous green algae group were characterized by similar temporal trends, or synchronous behavior. To this similarity matrix we applied a hierarchical agglomerative cluster analysis, with group-average linkage procedure to identify similarities in trends and behavior between genera within the group. Similarity and clustering analyses were done with Primer 5 (Plymouth Marine Laboratory, West Hoe, Plymouth, UK). We looked for similar behavior among calcareous green algal genera with respect to all three parameters, which would indicate a high level of synchrony in the long-term trend of abundance, with similar magnitude and timing of seasonal changes in abundance. The same method was applied to all calcareous green algal groups and genera abundance data to detect similarities between the 28 sites and to explore any potential site-specific anomalies in synchronous behavior within the study area.

To evaluate any relationship between temporal patterns in population abundance and geographic location at different spatial scales, we analyzed the three nonlinear regression model parameters as a function of different geographic segmentations and gradient suggested for the FKNMS: 1) along-shore distance representing the geographic extent of the FKNMS, at a spatial scale of 0 to 200 km; 2) offshore distance representing the proximity to land and potentially the nutrient gradient suggested by Fourqurean and Zieman (2002), at a spatial scale of 0 to 12 km; 3) bay-side or ocean-side location representing the environmental characteristics on either side of the Florida Keys, including the influence of Gulf of Mexico versus Atlantic Ocean waters as suggested by Lee et al. (2002); 4) the division of the FKNMS in nine segments following the proposed framework by Klein and Orlando (1994); and 5) a division by regions corresponding to local use and description such as near shore, reef track, back country, Hawk Channel, and Sluiceway.

The along-shore distance was calculated in ArcView 3.2 (Environmental Systems Research Institute Inc., Redlands,

CA, USA), using highway US1 (a highway running the length of the Florida Keys) as a general reference. The 0-km distance value coincided with the beginning of the highway US1 in Key West, which was to the west of our westernmost site, and the values increased heading north through the Florida Keys toward Miami. The along-shore distances were classified into four categories: 0–50, 50–100, 100–150, and 150–200 km. The offshore distance was also calculated in ArcView, with the distance from each site to the nearest point of land representing the offshore distance. The offshore distances were classified into three categories: 0–5, 5–9, and 9–12 km. For the bay-side and ocean-side comparison, we eliminated sites located in the upper keys because there are no bay-side sites in this region, and the analysis was done with the middle and lower keys only. From the nine segments proposed by Klein and Orlando (1994), we have sites in only five segments, and those were the only segments used. Because data were not normally distributed, significant differences were assessed with the Kruskal-Wallis nonparametric test. Site was the grouping variable in each different geographic analysis, and slope, amplitude, and phase values were the testing variables.

RESULTS

In the sea grass meadows of the FKNMS, the principal species of calcareous green algae we encountered were *Halimeda incrasata* (Ellis) Lamoroux, *H. monile* (Ellis & Solander) Lamoroux, *H. tuna* (Ellis & Solander) Lamoroux, *H. opuntia* (Linnaeus) Lamoroux, *Penicillus capitatus* Lamarck, *P. dumetosus* (Lamoroux) Blainville, *P. pyriformis* Gepp & Gepp, *Rhipocephalus phoenix* (Ellis & Solander) Kützing, *Udotea cyathiformis* Decaisne, and *U. flabellum* (Ellis & Solander) Howe.

The calcareous green algae total functional-form group was present in relatively high abundance throughout the FKNMS study area (Fig. 2a). Each calcareous green genus had a unique distribution. *Halimeda* (Fig. 2b) was characterized by the highest abundance and widest distribution. *Udotea* (Fig. 2c) was characterized by low abundances and very patchy distribution, *Penicillus* (Fig. 2d) had an intermediate level of abundance and a distribution similar to that of *Halimeda*, and *Rhipocephalus* (Fig. 2e) was the least-often encountered of all the genera. A marked seasonal pattern was detected for the functional-form group as a whole (Fig. 3), with lower values of abundance in winter and higher values in summer. Nonlinear regression fits of our model to the abundance time series generally described the time series data well, with a range of values of r^2 from 0.1060 to 0.8244 (Fig. 3). We used the estimated values of the model parameters (slope, phase, and amplitude) for further analysis. The long-term trends (i.e. the slope parameter) were generally positive for the functional-form group (representing long-term increases in abundance, Fig. 4). Individual calcareous green algal genera displayed a positive slope at almost all sites; however, the magnitude of the slope values differed among genera and sites. *Halimeda* had an order of magnitude higher slope than the other genera (Fig. 4).

Some differences in the slope values among individual genera are noteworthy, for example, the abun-

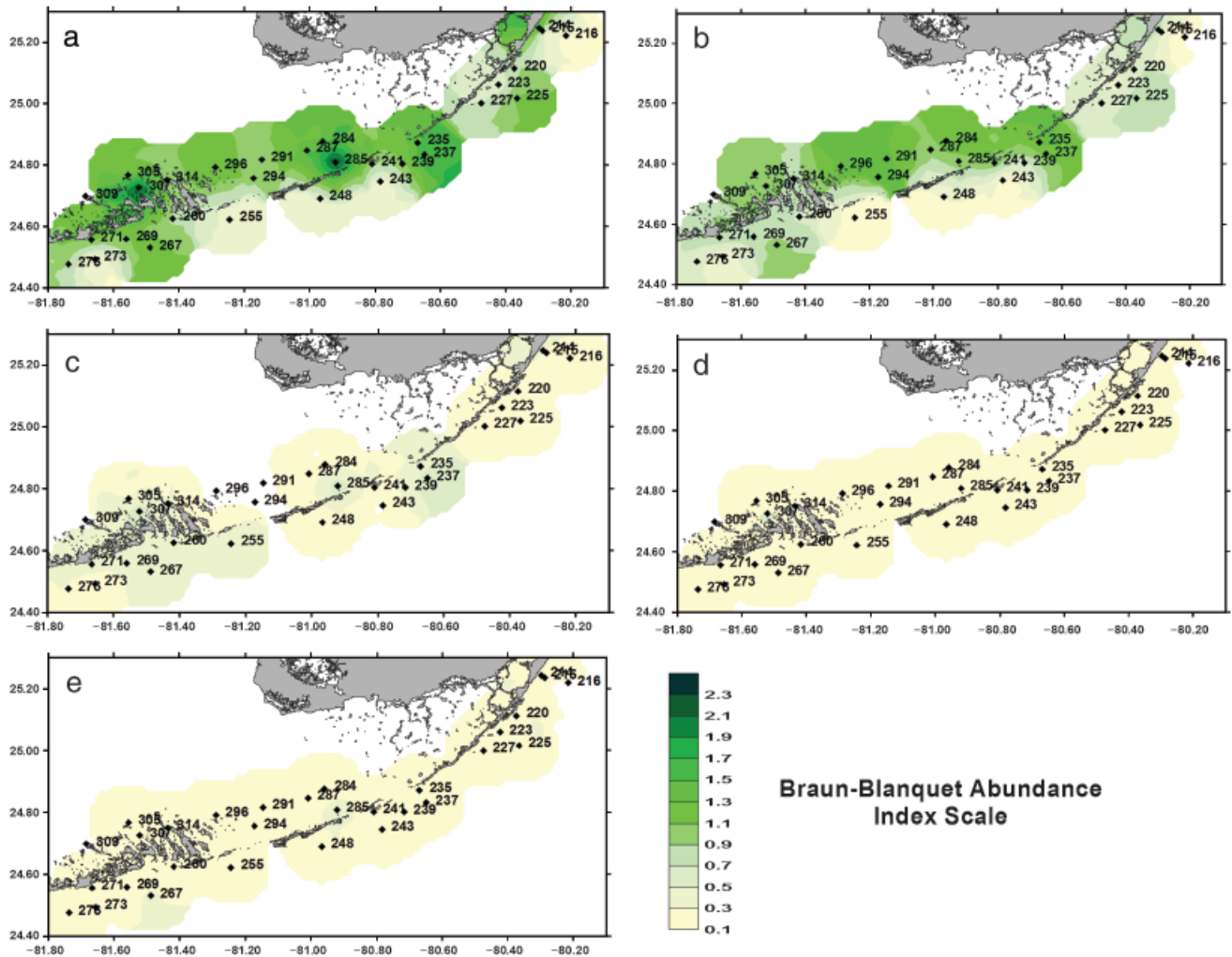


FIG. 2. Maps displaying interpolated mean abundance for each genus and for the functional-form group. (a) Calcareous green algae form-functional group, (b) *Halimeda*, (c) *Udotea*, (d) *Penicillus*, and (e) *Rhipocephalus*. Numbers inside the map show the sampling sites. Axes y and x show latitude and longitude coordinates. Color scale shows the abundance for each genus or group based on the Braun-Blanquet index.

dance of *Halimeda* increased at sites 235 and 241 (Fig. 5), whereas the abundances of other calcareous green genera remained stable. Sometimes the long-term

trends in the abundance of the functional-form group and all component genera were similar, for example, at site 255 (Fig. 5), stable abundance was observed for all

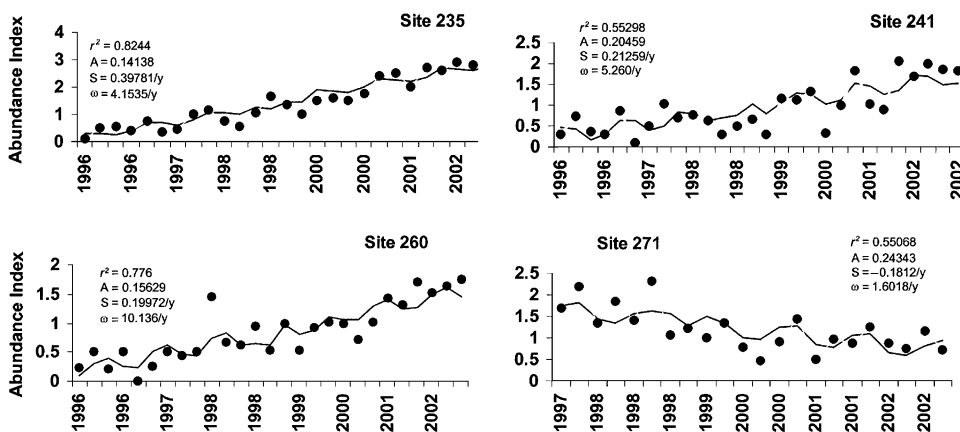


FIG. 3. Time series showing some examples of calcareous green algae functional-form group model results: observed (•) data and estimated curves. Time, x axis; abundance values, y axis.

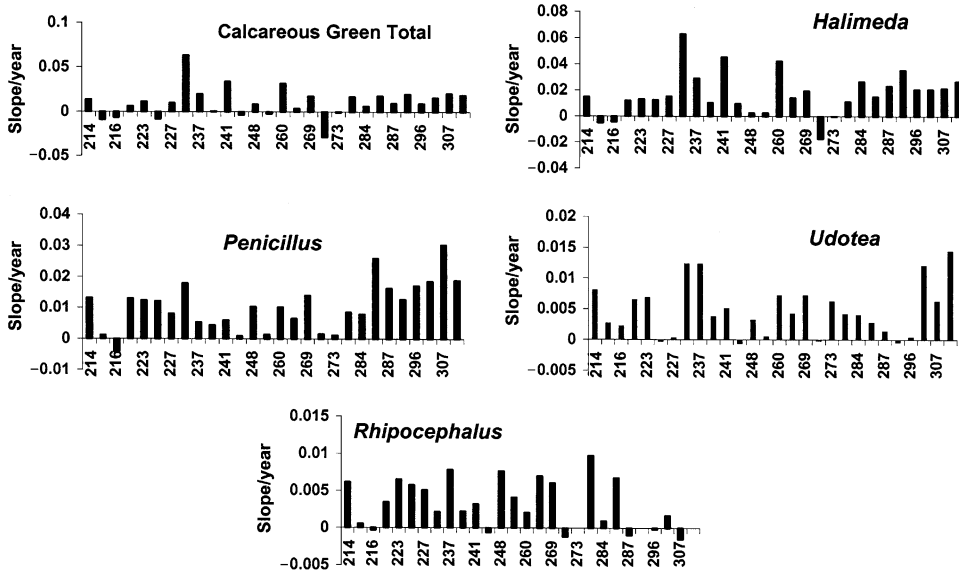


FIG. 4. Histograms showing slope/year values for each genus at each site. Sites, x axis; slopes, y axis.

genera as well as for calcareous green algae as a group. A variation of this situation was found at site 260 (Fig. 5), where *Halimeda* and *Penicillus* showed increases in abundance, each differing in magnitude, but other genera (*Udoatea*, *Rhipocephalus*) remained almost stable. At site 271 (Fig. 5), there was a decrease in the abundance of *Halimeda* while all other genera remained stable, whereas at site 276 (Fig. 5) all genera and the functional-form group calcareous green total (CGT) were clearly increasing in abundance. At sites where only one or two calcareous green genera were increasing while the others were decreasing or stable, the functional-form group trend normally followed the

trend of the most abundant genus, which may differ from the trends of other genera within the functional group (Fig. 5). These were just a few examples showing how the long-term abundances of genera belonging to the same functional-form group may behave differently within and among sites.

Bray-Curtis similarity analyses were conducted using the nonlinear regression model parameter values (slope, phase, and amplitude values) for all calcareous green algae genera. The analysis applied to the genera show that the slope, or long-term trend in abundance, of each genus was essentially different, with the four calcareous green genera clustered at only 40% similarity.

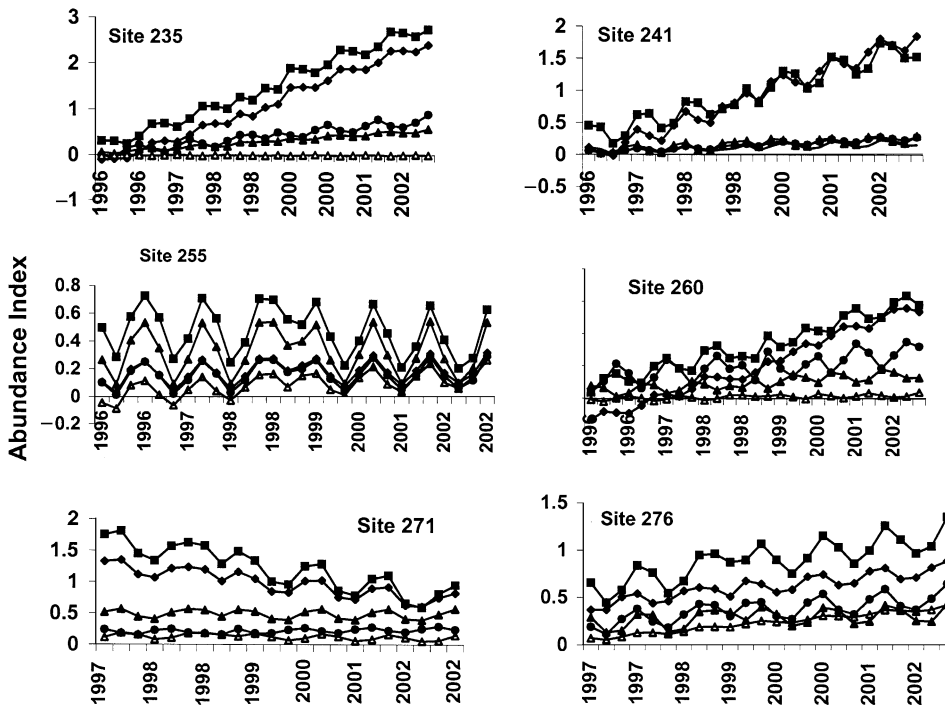


FIG. 5. Time series showing temporal estimated trend of the functional-form group and of each genus for all 7 years for selected sites. ■, Calcareous green total; ◇, *Halimeda*; ▲, *Udoatea*; ●, *Penicillus*; △, *Rhipocephalus*. Time, x axis; abundance values, y axis.

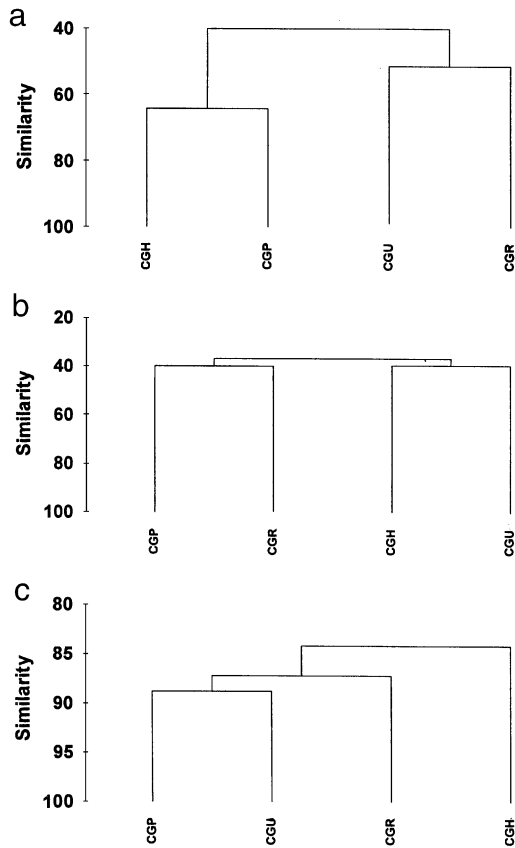


FIG. 6. Cluster showing results from the Bray-Curtis similarity matrix applied to genera, based on different parameters from the time series model. (a) Slope, (b) amplitude, and (c) phase. Categories are as follows: CGH, *Halimeda*; CGU, *Udotea*; CGP, *Penicillus*; CGR, *Rhipocephalus*.

Halimeda and *Penicillus* were clustered at >60% similarity, and *Udotea* and *Rhipocephalus* were clustered at 50% similarity (Fig. 6a). A similar analysis also revealed that the four genera differed greatly with respect to their amplitude, or the magnitude of variations in seasonal abundance; they were clustered at <40% similarity (Fig. 6b). In contrast, the analysis of phase values or the timing of seasonal variations in abundance showed that the four genera within the calcareous green algal group exhibited a very similar behavior at >80% similarity, which means the timing of their seasonal cycles of abundance was highly synchronized. In this case, *Penicillus* was clustered with *Udotea* at almost 90% similarity followed closely by *Rhipocephalus* clustered at <90% similarity and *Halimeda* clustered at 85% similarity (Fig. 6c).

Comparable Bray-Curtis similarity analyses were conducted for all 28 sites (using slope, phase, and amplitude values for all genera). The analysis of slope values showed that sites were grouped at <20% similarity; however, four clusters, including a total of 18 sites, were grouped separately at >75% similarity. Twenty sites, generally characterized by stable calcareous green algal abundance values, and including all 8 sites located on the bay side of the Florida Keys, were

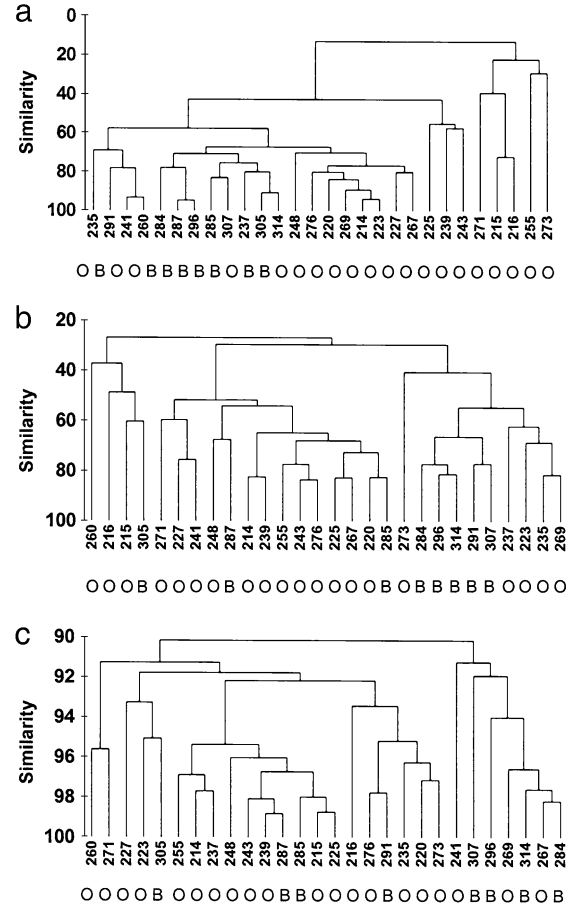


FIG. 7. Cluster showing results from the Bray-Curtis similarity matrix applied to sites, based on different parameters from the time series model. (a) Slope, (b) amplitude, and (c) phase. Sites categories are B, bay side, and O, ocean side.

clustered together in one group at >60% similarity. The remaining eight sites, all located on the ocean side of the Florida Keys, were characterized by increasing or decreasing abundance values (positive or negative slopes) (Fig. 7a). The analysis of amplitude values revealed a great deal of variability between sites, with <25% similarity across all sites; very few sites were clustered at a level above 75% similarity. Clusters grouped at above 75% similarity contain only two or three sites per cluster, and many of the bay-side sites were clustered together at that level (Fig. 7b). The sites that cluster together based on the slope values were different from those that cluster based on amplitude values. In contrast with the results of the slope and amplitude analyses, the analysis based on phase values showed all sites clustered at a level of similarity >90%, meaning all sites within the study area were synchronized in terms of the timing of seasonal variation in abundance of calcareous green algae (Fig. 7c). This suggests that environmental influences on calcareous green algae abundances may fluctuate on a similar seasonal schedule throughout the entire study area. It is interesting that in this case the sites located on the

TABLE 1. Kruskal-Wallis test comparing variables (testing variables) among different sites (grouping variables) under different geographic arrangements: along shore, offshore, bay side or ocean side, segments, and region. Bold numbers are statistically significant.

	Chi square	df	<i>P</i>
Along shore			
Slope	4.454	3	0.216
Amplitude	3.108	3	0.375
Phase	0.604	3	0.895
Offshore			
Slope	9.501	2	0.008
Amplitude	0.651	2	0.722
Phase	2.230	2	0.327
Bay or ocean side			
Slope	1.776	1	0.183
Amplitude	0.639	1	0.242
Phase	0.505	1	0.477
Segments			
Slope	5.626	4	0.229
Amplitude	4.267	4	0.371
Phase	3.947	4	0.413
Region			
Slope	10.499	4	0.033
Amplitude	5.826	4	0.212
Phase	3.726	4	0.444

bay side and the ocean side were not segregated by the clustering algorithm.

In general, no pattern was found in the estimates of model parameters as a function of the different geographic segmentations. We found that the values of amplitude and phase did not differ with respect to any proposed scheme of subdividing the study area (Table 1). Slope was the only parameter that showed significant difference in some cases. Offshore distance did show a significant difference for slope (Fig. 8, Table 1), higher values closer to land were detected, and significant difference was also found in the regional classification with higher values near shore and lower at the reef-track regions (Fig. 9, Table 1).

DISCUSSION

Calcareous green macroalgae are important components of sea grass meadows in the Florida Keys (Davis and Fourqurean 2001), where they play a significant role in primary production and sediment production and stabilization (Bosnce 1987). For example, in Card Sound, *Halimeda incrassata* (Ellis) Lamoroux accounted for more than half of the total sediment production estimated for the four major calcareous green genus (*Udotea*, *Penicillus*, *Rhipocephalus*, and *Halimeda*) (Bach 1979). In the FKNMS area these four genera are present with different numbers of species and abundances.

To our knowledge, this is the first study that investigated both long-term and seasonal patterns of calcareous green algal abundance at the genus and functional-form group levels. All four genera studied displayed highly synchronized seasonal patterns of

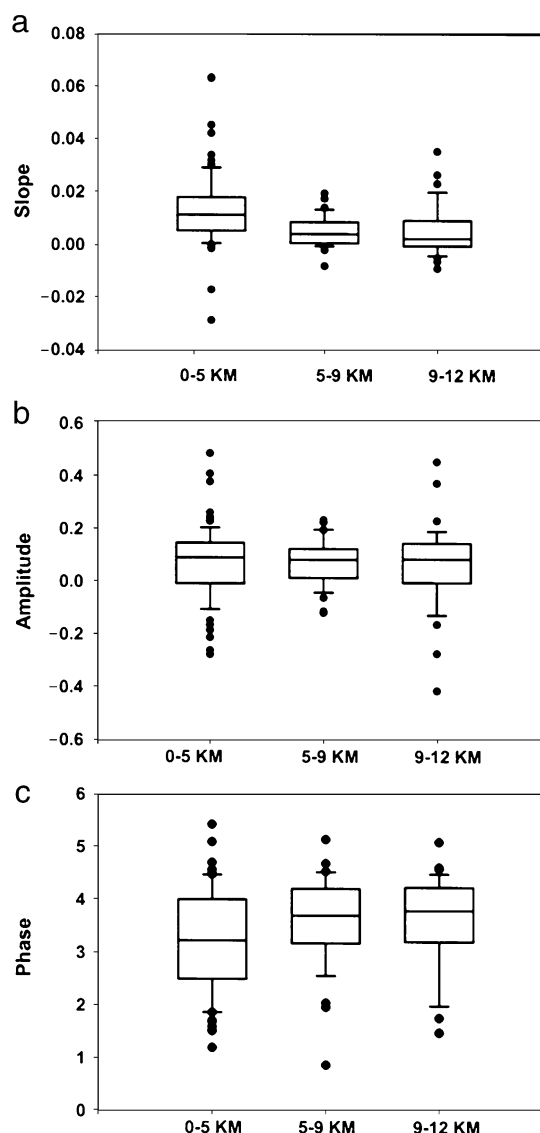


FIG. 8. Whisker box graph showing the values of the time series parameters as a function of along-shore distance. (a) Slope, (b) amplitude, and (c) phase. Boxes show the upper 75% and lower 25% percentiles, middle line shows the median, and whiskers show upper 90% and lower 10% percentiles.

abundance, with higher abundances during summer and lower abundances during winter. This observed seasonal trend corroborates the findings of two studies (Lirman and Biber 2000, Vroom et al. 2003) conducted on the Florida Keys reef, which described a clear pattern of increasing abundance in all *Halimeda* species during spring–summer and a subsequent decay in fall–winter. Also, seasonality in growth rates has been observed in several *Halimeda* populations all around the world (Drew 1983, Multer 1988, Payri 1988, Ballasteros 1991, Garrigue 1991). South Florida is a subtropical location and hence some seasonality was expected. However, seasonality has also been found in calcareous green algae in tropical waters (Drew

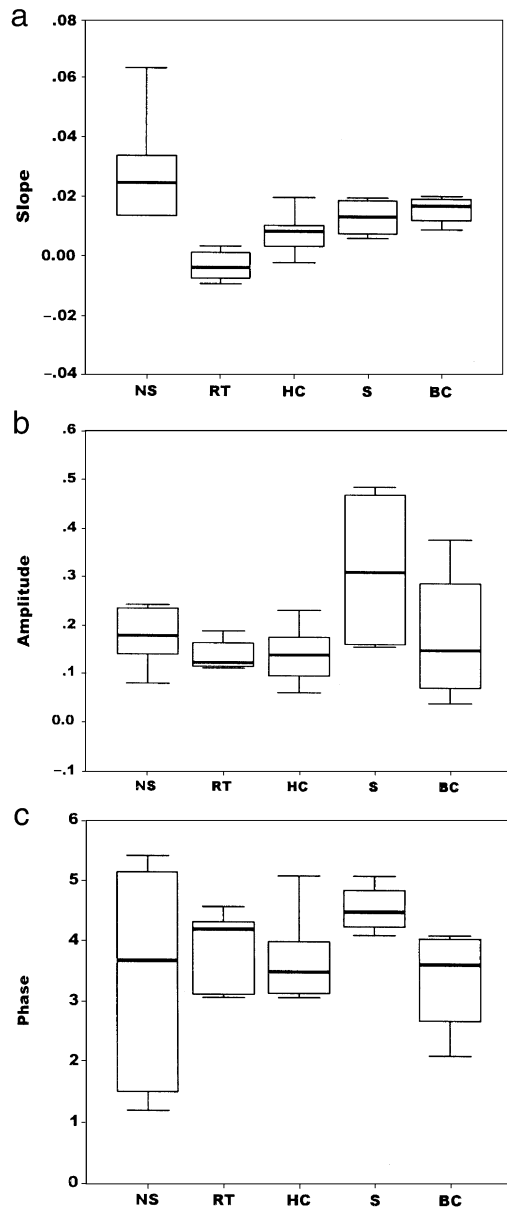


FIG. 9. Whisker box graph showing the values of the time series parameters as a function of offshore distance. (a) Slope, (b) amplitude, and (c) phase. Boxes show the upper 75% and lower 25% percentiles, middle line shows the median, and whiskers show upper 90% and lower 10% percentiles.

1983, Multer 1988, Payri 1988, Garrigue 1991), perhaps because of the reproductive strategies described by Clifton and Clifton (1999) for *Halimeda* spp., *Udotea* spp., *Rhipocephalus* spp., and *Penicillus* spp. among other members of the coenocytic green algae belonging to the Bryopsidales. Hillis-Colinvaux (1973) showed that species of these genera have a holocarpic life cycle (the whole content of the vegetative plant divides up into reproductive cells), and Clifton and Clifton (1999) showed that sexual reproduction is concentrated in a 3-month period coincident with the annual shift from dry season to wet season in Panama (March–June).

This mode of sexual reproduction may partially explain the strong synchrony of the timing of the seasonal cycle (phase parameter) of calcareous green algal abundance in FKNMS. However, the consequences of reproduction-derived variations in abundance on species interactions and community organization remain largely unexplored (Airoldi and Virgilio 1998, Lotze et al. 2000, Collado-Vides 2001, Santelices 2002). Besides the sexual reproduction, this group of genera also has the ability of clonal reproduction via ramets produced by rhizoidal extension (van den Hoek 1998). Of the four genera included in this study, only *Halimeda* has the ability to use fragmentation as a mode of asexual vegetative propagation besides the rhizoidal extension (Walters and Smith 1994, Walters et al. 2002, Vroom et al. 2003). This may explain, among other factors, the high abundance of *Halimeda* spp. compared with the other genera (*Udotea*, *Rhipocephalus*, and *Penicillus*), which are limited to sexual reproduction or clonal reproduction by rhizoidal extension. Similarities in the life cycle of these four genera may explain the synchrony in phase values and, in addition to morphological convergence, support the calcareous green algal group as a functional-form group.

The long-term trends in calcareous green algal abundance represent syntheses of reproduction, recruitment, growth, survival, and life strategies of these macroalgae and their interaction with the environment. The amplitudes, which reflect the magnitudes of seasonal changes in abundance, are largely influenced by population reproduction, recruitment, growth, and mortality rates each season. Our results show that the four genera in this study display positive slope values at most sites sampled, which means that over 7 years the abundance of calcareous green algae increased at almost all sites. However, it is important to note that not all genera behaved similarly at all sites, yet all genera did exhibit high synchrony of phase values, even if they did not share similar seasonal amplitudes or long-term trend magnitudes. Genera that are present in the same site (experiencing identical environmental conditions) performed differently in some cases and similarly in other cases; these differences were not possible to detect when all genera were analyzed as a functional-form group.

Among-site differences in calcareous green algal abundances found in this study showed no coherent spatial variation with respect to almost all different geographic patterns suggested for the Florida Keys. For example, the long-term increases in the abundance of *Halimeda* spp. exhibit patchy site-specific behavior rather than following predictable patterns within the FKNMS. This lack of coherent spatial variation implies that regional-scale gradients in environmental conditions (e.g. water temperature and salinity) did not play a major role in influencing the abundance of calcareous green algae in the FKNMS, although it may play a role in the strong synchrony found in phase. It is possible, however, that the small-scale environmental patchiness observed in the FKNMS may obscure the

potential effects of such regional-scale gradients. The only significant relation with any gradient detected was for slope as a function of distance from land, in two different systems of classifications, following the regional system and the offshore system. In both cases, sites closer to land did show higher values of long-term trend, suggesting that some factors associated with land proximity are affecting this increase, for example, nutrient influx from major agricultural areas or human population centers. As Fourqurean and Ziemann (2002) showed, near-shore sea grass beds are P limited and offshore sea grass beds are N limited. Davis and Fourqurean (2001) studied the competitive interaction between *Thalassia testudinum* Banks ex Koenig and *Halimeda incrassata*, and their findings suggest that competition for nutrients was the mechanism of interaction. An increase in nutrients closer to land might relieve the competition between *T. testudinum* and *Halimeda* spp., explaining the increase of the slope of the algae in this areas. It is also possible that the 7-year trend of increasing abundance of calcareous green algal density may be a response to some unidentified region-wide disturbance in the past. Fourqurean and Rutten (2004) showed that calcareous macroalgae were much more susceptible to disturbance from Hurricane Georges than the sea grasses in the region. However, that same study showed that prestorm abundance of calcareous green macroalgae were reached within 3 years of the disturbance. Consequently, if the 7-year increases in macroalgae are the result of the reestablishment after a disturbance, that disturbance must have been of significantly greater magnitude than Hurricane Georges.

The study of calcareous green algal abundance at 28 sites in the FKNMS allowed us to detect spatiotemporal covariation, or synchrony, among genera and sites over a 7-year period. Our results do support the grouping of *Halimeda*, *Penicillus*, *Udotea*, and *Rhipocephalus* in the same functional-form group for the purposes of describing the timing of seasonal changes in abundance (phase parameter) of calcareous green algae in the FKNMS. However, the use of the functional-form group as a sampling unit is not an appropriate way to detect the magnitude of long-term trends or seasonal changes (slope or amplitude parameters, respectively) in calcareous green algal abundance, which would be indicative of shifts in community structure. Spatiotemporal trends within each genus may be important indicators of shifts in community structure that would not be recognized if we combine all the component genera into a functional-form group. Based on the observed synchrony among calcareous green algal genera, we conclude that genus or species level may be needed to detect shifts in community structure resulting from small-scale or long-term environmental changes in the FKNMS. Comparative demographic and ecophysiological studies of the component genera of calcareous green algal functional-form group are needed to assist in the interpretation of the differential responses of each genera to the small-scale environ-

mental variability and regional environmental gradients in the FKNMS.

This study was conducted with the support of the Water Quality Protection Program of the Florida Keys National Marine Sanctuary, funded by the U.S. Environmental Protection Agency (contract X97468102-0) and the National Oceanographic and Atmospheric Administration (contract NA16OP2553). This 7-year monitoring program was possible to conduct thanks to the field work of many students and technicians, including C. D. Rose, A. Willsie, C. Furst, M. Ferdie, D. Byron, V. C. Cornett, and K. Cunniff. We thank Captain Dave Ward of the *R/V Magic* and Captain Mick O'Connor of the *R/V Expedition II* for vessel and logistical support. We thank two anonymous reviewers whose suggestions and comments helped improve the manuscript. This is contribution no. 264 of the Southeast Environmental Research Center at FIU.

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