2007

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Recommended Citation
Collado-Vides, L., V.G. Caccia, J.N. Boyer, J.W. Fourqurean. 2007. Tropical seagrass-associated macroalgae distributions and trends relative to water quality. Estuarine Coastal and Shelf Science 73: 680-694.

This material is based upon work supported by the National Science Foundation through the Florida Coastal Everglades Long-Term Ecological Research program under Cooperative Agreements #DBI-0620409 and #DEB-9910514. Any opinions, findings, conclusions, or recommendations expressed in the material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

Tropical Seagrass-associated Macroalgae Distributions and Trends relative to Water Quality

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ABSTRACT

Tropical coastal marine ecosystems including mangroves, seagrass beds and coral reef communities are undergoing intense degradation in response to natural and human disturbances, therefore, understanding the causes and mechanisms present challenges for scientist and managers. In order to protect our marine resources, determining the effects of nutrient loads on these coastal systems has become a key management goal. Data from monitoring programs were used to detect trends of macroalgae abundances and develop correlations with nutrient availability, as well as forecast potential responses of the communities monitored. Using eight years of data (1996 to 2003) from complementary but independent monitoring programs in seagrass beds and water quality of the Florida Keys National Marine Sanctuary (FKNMS), we 1) described the distribution and abundance of macroalgal groups, 2) analyzed the status and spatiotemporal trends of macroalgal groups, and 3) explored the connection between water quality and the macroalgal distribution in the FKNMS. In the seagrass beds of the FKNMS calcareous green algae were the dominant macroalgae group followed by the red group; brown and calcareous red algae were present but in lower abundance. Spatiotemporal patterns of the macroalgae groups were analyzed with a non-linear regression model of the abundance data. For the period of record, all macroalgal groups increased in abundance (Ab_i) at most sites, with calcareous green algae increasing the most. Calcareous green algae and red algae exhibited seasonal pattern with peak abundances (Φ_i) mainly in summer for calcareous green and mainly in winter for red. Macroalgae Ab_i and long-term trend (m_i) were correlated in a distinctive way with water quality parameters. Both the Ab_i and m_i of calcareous green algae had positive correlations with NO_3^-, NO_2^-, total nitrogen (TN) and total organic carbon (TOC). Red algae Ab_i had a positive correlation with NO_2^-, TN, total phosphorus and TOC, and the m_i in red algae was positively correlated with N:P. In contrast brown and calcareous red algae Ab_i had negative correlations with N:P. These results suggest that calcareous green algae and red algae are responding mainly to increases in N availability, a process that is happening in inshore sites. A combination of spatially variable factors such as local current patterns, nutrient sources, and habitat characteristics result in a complex array of the macroalgae community in the seagrass beds of the FKNMS.

Key words: Macroalgae, Florida Keys National Marine Sanctuary, monitoring, nutrients, seaweeds, spatiotemporal distribution, synchrony, water quality.

Abbreviations: FKNMS Florida Keys National Marine Sanctuary, CGT Calcareous Green Total, GO Green Other, BA Batophora-Acetabularia, RO Red Other, CR Calcareous Red, BO Brown Other.

1. Introduction

Tropical coastal marine ecosystems including mangroves, seagrass beds, and coral reef communities are undergoing intense degradation in response to natural and human disturbances (Jackson et al. 2001, McManus and Polsenberg 2004, Orth et al. 2006). Since 1987, several ecosystem-scale disturbances in Florida Bay and the Florida Keys have occurred, such as seagrass die-off (Robblee et al. 1991), cyanobacterial blooms (Phlips and Badylak 1996), sponge mortality (Buttler et al. 1995), and a decline in fisheries (Tabb and Roessler 1989, Tilmant 1989). These alterations, combined with growing human population pressure and an economy based on ocean-related tourism provided the impetus to protect and study this marine ecosystem. In 1990 Congress designated the Florida Keys a National Marine Sanctuary (FKNMS). The FKNMS contains diverse assemblages of terrestrial, estuarine, and marine fauna and flora, encompassing over 9500 km^2. In order to protect the FKNMS, understanding the effects of nutrient loads on this coastal system has become a key management goal.

A basic ruling premise in plant communities is that nutrient addition shifts the competitive balance from slow-growing primary producers to faster-growing species. In seagrass beds, a gradual shift is expected to occur as nutrient loads are increased (Duarte 1995; Valiela et al. 1997; Hauxwell et al. 2001; McGlathery 2001, Fourqurean and Rutten 2003), where macroalgae proliferations might overgrow and displace seagrasses. Nitrogen (N) is frequently a limiting nutrient in coastal systems, but increasing evidence for phosphorus (P) limitation suggests that both N and P enrichment are of concern in nearshore habitats (Howarth 1988). Under short term experimental conditions it has been shown that in P- (Lapointe 1989) and N-limited (Larned 1998) environments, tropical macroalgal response to nutrient enrichment varies among regions and is highly species-specific, suggesting that tropical macroalgae exhibit interspecific variation in responses to nutrient enrichment along gradients corresponding to background nutrient influence (Fong et al. 2003). This suite of short term experiments suggests a close interaction between nutrients and macroalgae; and that results are determined by the initial conditions (Ferdie and Fourqurean 2004), as well as by biotic or abiotic factors, such as grazing pressure, space, or level of disturbance (Artmitage et al 2005).

Long term trends in seagrasses and macroalgae abundance may be reliable indicators of changes in nutrient availability in coastal ecosystems, but the application of such long-term data requires a consistent monitoring of these organisms at multiple sites with different nutrient conditions. In 1995, such a long-term monitoring program was established in the FKNMS. In this study, we used data from the long term seagrass monitoring program (Fourqurean et al. 2001, Fourqurean et al. 2003), and the water quality monitoring program (Boyer and Jones, 2002) to detect the long term abundance trends of macroalgal groups and their correlations with median nutrient concentrations for a period of eight years in 30 different sites of the FKNMS. Our objectives were to 1) describe the distribution of the abundance of macroalgal groups and water quality parameters, 2) analyze the status and spatiotemporal trends of macroalgal groups, and 3) explore the connection between water quality and macroalgal distribution and trends in the FKNMS.

2. Materials and methods

2.1 Study area

The Florida Keys are an archipelago of sub-tropical islands of Pleistocene origin extending over 354 km in length in a southwesterly direction from the southern tip of Florida (Fig.1). The area includes mangrove-fringed shorelines, mangrove islands, seagrass meadows, hard bottom habitats, thousands of patch reefs, and the third largest coral reef system in the world (http://www.fknms.nos.noaa.gov/). The FKNMS is generally divided into three main geographical regions: Upper Keys, Middle Keys, and Lower Keys (Fig. 1). The Lower Keys are most influenced by cyclonic gyres that spin off the Florida Current, the Middle Keys by exchange with Florida Bay, while the Upper Keys are influenced by Florida Current frontal eddies and to a certain extent by exchange with Biscayne Bay (Klein and Orlando 1994). All three regions are also divided into ocean- or bay-side. Ocean-side regions are influenced by wind and tidally driven lateral Hawk Channel transport (Pitts, 1997). The two bay-side regions of the Lower and Middle Keys are distinguished as the Backcountry and Sluiceway (Fig. 1). The Backcountry region is a shallow water area associated with many small islands on the Lower Keys, and is influenced by water moving south along the SW Shelf. The Sluiceway may be considered part of western Florida Bay as it is strongly influenced by water transport from Florida Bay, the SW Florida Shelf, and Shark River Slough (Smith, 1994). Many of the Key channels that exchange water between the Gulf of Mexico and the Atlantic Ocean are located in this region, making for large currents and tides.

Regional currents may influence water quality over large areas by the advection of external surface water masses into and through the FKNMS (Lee et al. 1994, Lee et al. 2002) and by the intrusion of deep offshore ocean waters onto the reef tract as internal tidal bores (Leichter et al. 1996, Leichter et al. 2003). Local currents become more important in the mixing and transport of freshwater and nutrients from terrestrial sources (Smith 1994; Pitts 1997). As a result of this complex set of currents, water quality of the FKNMS may be directly affected both by external nutrient transport and internal nutrient loading sources.

The subtidal benthic marine habitats of the FKNMS are well-described. Most of the benthos of the FKNMS is carpeted by seagrass communities of varying density and species composition (Fourqurean et al. 2002). A smaller, but vitally important, portion of the FKNMS supports coral communities (Porter, 2002). Macroalgae are important components of both the seagrass and coral communities, but for this study we focused on the data from the seagrass monitoring sites. The most common seagrass in the part of the FKNMS that contains long-term seagrass monitoring sites is *Thalassia testudinum*, which is found from the shoreline across Hawk's Channel to the back-reef area. *Syringodium filiforme* is commonly encountered as well especially at the more off-shore monitoring sites. *Halodule wrightii* is occasionally present at the monitoring sites. The density and species composition of the seagrasses in south Florida is strongly controlled by nutrient availability (Fourqurean et al 1995, Ferdie and Fourqurean 2004)

2.2 *Methods*

2.2.1 Water quality

Eight years of data were analyzed from the Water Quality Monitoring and Protection Project of the FKNMS, conducted by Southeast Environmental Research Center at Florida International University Water Quality Monitoring Network (Boyer 2005). This project is based on quarterly sampling events (1995 to present) and includes 154 sites within the FKNMS. For this study we used data from March 1996 to May 2003 including 29 quarterly sampling events at 30 sites (Fig. 1). We selected the years and sites to correspond with the macroalgae data available. Field sampling and laboratory analyses are extensively described in Boyer and Jones (2002) and are the same used to analyze the present data. All analyses were completed within 1 month after collection in accordance to SERC laboratory QA/QC guidelines. All concentrations are reported as µM. All elemental ratios discussed were calculated on a molar basis, and salinity was measured using the Practical Salinity Scale.

Data from the 30 selected sites were processed to obtain the medians of the 8 year record (1996-2003) for selected water quality parameters, as well as the minimum and maximum value for each nutrient. Contour maps of nutrient distributions were produced (Surfer 8, Golden Software), using a kriging algorithm for the medians of Total Nitrogen (TN), Nitrate (NO_3^-), Nitrite (NO_2^-) Ammonium (NH_4^+), Total Phosphorous (TP), and Total Organic Carbon (TOC). A holistic analysis of all 154 sampling sites and 8 years of the nutrient trends can be found in Boyer (2005).

2.2.2 *Macroalgae*

Macroalgae abundance was measured quarterly from 1996 to 2003 at 30 permanent sites (Fig. 1). Fine scale taxonomic identification of the macroalgae was not always possible in the field, so macroalgae were grouped into easily identifiable groups: Calcareous Green Total (CGT), Batophora-Acetabularia (BA), Green Other (GO), Calcareous Red (CR), Red Other (RO), and Brown Other (BO). Abundance of these groups was scored using a modified Braun-Blanquet method (Fourqurean and Rutten 2003). At each site, the abundance of taxa was recorded in ten randomly located 0.25 m^2 quadrats along a 50 m permanent transect. The abundance of each group observed in each quadrat was assigned a score between 0 and 5. A score of 0 indicated that the genus or functional group was absent, 0.1 indicated the presence of a solitary individual covering < 5% of the quadrat area, 0.5 indicated few individuals covering < 5%, 1 indicated numerous individuals covering <5%, 2 indicated 5-25% cover, 3 indicated 25-50% cover, 4 indicated 50-75% cover, and 5 indicated 75-100% cover. Site-specific abundance of each taxon (Ab_i) was calculated as:

$$Ab_i = (\Sigma^n{}_{j=1}\, S_{ij}) / N_i$$

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 that the range of possible taxon-specific abundance scores was $0 < Ab_i < 5$. The spatial distribution of the eight year (1996-2003) mean Ab_i of each macroalgal group was obtained by interpolating mean values throughout the study area with a kriging interpolation routine (point kriging using linear variogram and no nugget, Surfer 8, Golden Software).

In order to analyze the temporal patterns in abundance (e.g. long-term trends, seasonal cycles) for each group at each monitoring site we applied a non-linear regression model (using the statistical package SPSS) with parameters to incorporate both long-term changes as well as seasonal fluctuations. Time series analyses were conducted using the following model:

$$Ab_i = \beta_i + m_i t + \alpha_i \cdot \sin (t+\Phi_i)$$

where Ab_i was the abundance of group *i*, β_i represented the initial abundance of group *i*, m_i represented the long-term linear trend in abundance of group *i*, *t* was time since the beginning of the time series (time in radians, 1 year = 2 π radians),

α_i represented the magnitude of seasonal changes in abundance of group *i*, and Φ_i (phase angle in radians) represented the timing of seasonal changes in abundance of group *i*. This particular model was chosen for our analyses because a similar approach has been successful in describing the temporal patterns of other aspects of the seagrass and algal communities in the region (Fourqurean et al 2001, Collado-Vides et al. 2005). The model was applied to the time series of abundances for the two most common groups, CGT and RO, for all sites. Because of the patchy distributions of other macroalgal groups (i.e. GO, BA, CR and BO), only the time series from sites with consistent abundance during all studied period were selected.

In order to detect seasonality of macroalgal groups abundance, we evaluated if the α_i parameter estimate was significantly different from zero. Once we detected seasonality, we applied a t-test to compare Φ mean between CGT and RO, the only groups with a clear seasonal pattern.

To evaluate any relationships between temporal patterns in population abundance and geographic location at different spatial scales, a Kruskal-Wallis test was used to test group-specific differences in Ab_i, m_i, α_i and Φ_i as a function of different geographic divisions of the FKNMS based on three different criteria. We tested for differences among the FKNMS segments proposed by Klein and Orlando (1994): Upper Keys (UK), Middle Keys (MK), Lower Keys (LK) on the ocean side of the Florida Keys; and Sluiceway, Hawk Channel and Backcountry (BC) with two sub-segments BC3 and BC4 on the bay side (Fig. 1). We also tested for differences among strata of offshore distances because of the spatial pattern in nutrient limitation along this gradient (Fourqurean and Zieman 2002). The final classification was based on alongshore distance representing the longitudinal distance from the highly urban area of Miami.

To detect any relationship between macroalgal group abundance Ab_i, long term trends m_i, and water column nutrient concentrations, a non-parametric correlation analysis (Kendall's τ-b) was applied to the site specific data.

3. Results

3.1 Water quality

For the period studied, the Florida Keys had a median surface water temperature of 27.7℃, with maximum values during summer (35.4℃) and minimum during winter (16.0℃). Salinity median was 36.3 with maximum values during summer (39.7) and minimum during winter (27.9) with low variability spatially.

In general, the FKNMS exhibited oligotrophic water quality condition with median NO_3^-, NO_2^- and NH_4^+ concentrations of 0.09 µM, 0.05 µM and 0.29 µM, respectively. NH_4^+ was the dominant DIN species in almost all of the samples (~70 %). However, DIN (NO_3^-, NO_2^- and NH_4^+) comprised a small fraction (4 %) of the TN pool with TON making up the bulk (median 10.78 µM) and TP median was 0.20 µM. Molar ratios of TN:TP suggested a general P limitation of the water column (median = 58). TOC median was 189.4 µM; a value higher than open-ocean levels but consistent with coastal areas.

DIN concentrations were highest in the Backcountry and Sluiceway sub-regions of the Lower and Middle Keys. NO_3^- was highest at site 260 (0.34 µM) the ocean side of the Lower Keys region; site 285 (0.24 µM) in the Sluiceway subregion of the Middle Keys, and site 235 (0.24 µM) the ocean side of the Middle Keys. NO_2^- exhibited the same behavior. NH_4^+ showed several sites of high concentration (>0.5 µM): site 314 in the Backcountry sub-region of the Lower Keys, site 260 in ocean side of the Lower Keys, site 235 and 241 in the ocean side of the Middle Keys. The distribution of TN and TON were very similar, exhibiting their highest concentrations (14-18 µM) in the Bay side of the Lower and Middle Keys, Backcountry subregion in sites 296, 307 and 314, Sluiceway subregion sites 284, 285 and 287, and in the ocean side in sites 260 in the Lower Keys and 235 in the Middle Keys (Fig. 2).

The highest concentrations of TP (>0.26 µM) were found in all five Backcountry sites. The TN:TP ratio showed a similar distribution pattern than the inorganic nutrients. TOC was higher in Sluiceway and the Backcountry (>230 µM), and was also distributed as a gradient from inshore to offshore (Fig. 2).

In general, the Upper Keys showed very low concentrations of all water quality parameters, except site 214 (the nearest to the coast) that had medium-high concentrations of NO_3^-, NH_4^+, TN:TP (Fig. 2).

Depth ranged from 2.7 m in site 296 to 10.6 m in site 216. In general the only region characterized by shallow sites was Sluiceway (2-4 m), the rest of the regions had sites with various depths.

3.2 Macroalgae

The Florida Keys had mainly tropical macroalgal species as their characteristic aquatic non-vascular flora. In the seagrass beds of the FKNMS, green algae were mainly represented by calcareous algae such as species of the genera *Halimeda, Penicillus, Rhipocephallus, Udotea*, or non calcareous green algae such as species of the genera *Avrainvillea*, *Caulerpa, Acetabularia, Batophora*, *Anadyomene* among others. Red algae were represented by species of the genera *Laurencia*, *Chondria*, *Acanthophora, Gracilaria* among others. Brown algae were mainly represented by species of the genera *Sargasum*, and *Dictyota*. Many other species were epiphytic on seagrass blades but were not included in this study.

Results of the monitoring program show that all algal groups were present and encountered year-round and throughout the eight-year span of our data, but there were large differences in the frequency of encounter and mean abundances of the algal groups. The consistently most abundant group of algae during the 8 year period was the CGT, followed by the RO. The rest of groups were present, but in an order of magnitude lower mean abundance (Fig. 3). Each group had a unique distribution. CGT was characterized by the highest abundance and widest distribution, with some high abundance spots in Backcountry (site 307) and Sluiceway (site 285); lower abundance was found at the ocean side of the Keys at sites 243, 255, and 273 (Fig. 3). RO had an intermediate level of abundance and a distribution more or less similar to that of the CGT; high abundance levels for RO were found mainly at sites 285 and 294 both in Sluiceway (Fig. 3). GO, CR and BO were characterized by low abundance and very patchy distribution.

The fits of our non-linear regression model to the abundance time series varied between the algae groups, the model generally described the time series data reasonably well for CGT and RO (Fig. 4), but the efficacy of the model varied among sites for the rarer groups (BO, BA, GO and CR). For this reason, we have only analyzed the spatial patterns in the model parameters m_i, α_i and Φ_i for CGT and RO.

Seasonality in the time series of macroalgal group abundance was assessed using model estimates of the α_i parameter; if the parameter estimate was significantly different from zero at the 0.05 confidence level (i.e., if the asymptotic 95% confidence interval for the value of the parameter did not contain zero) we concluded that there was a significant seasonal pattern in the time series. Using this criterion, only the time series of the two most abundant groups, CGT and RO, displayed significant seasonality for most sites. The Φ_i or timing of peaks in abundance between these macroalgal groups was significantly different (T-test, $p< 0.04$). Both groups showed variability with peaks in different seasons for different sites. For CGT 13 sites out of 30 peaked in summer, 8 in fall, 5 in spring, and only 4 in winter. In contrast, for RO 11 sites peaked in winter, 9 in fall, 6 in spring, and only 4 in summer.

The long-term trends (i.e., m_i) were significantly positive for the majority of sites for all groups, indicating that there were widespread increases in macroalgal abundance across the FKNMS, and that the increases were occurring in all monitored algal groups (Fig. 5). However, each group had a unique spatial behavior with highest slopes at different sites. CGT had the highest slopes in the ocean side at sites 235 ($m_i = 0.42/\mathrm{y}^{-1}$, 95% confidence interval $0.38 \leq m_i \leq 0.47$) and 241 ($m_i = 0.23/\mathrm{y}^{-1}$ 95% confidence interval $0.17 \leq 0.23 \leq 0.29$) in the Middle Keys, and site 260 ($m_i = 0.20/\mathrm{y}^{-1}$, $0.15 \leq m_i \leq 0.25$) Lower Keys. RO had the highest values at sites 294 at Sluiceway in the bay side of the Lower Keys ($m_i= 0.20/\mathrm{y}^{-1}$, $-0.036 \leq m_i \leq 0.43$), and in the ocean side RO had high values in the

Upper Keys, site 214 ($m_i = 0.13y^{-1}$, $0.048 \leq m_i \leq 0.21$) Middle Keys site 237 ($0.17/y^{-1}$, $0.027 \leq m_i \leq 0.31$) and Lower Keys 273 ($m_i = 0.14/y^{-1}$, $0.002 \leq m_i \leq 0.28$) (Figs. 1 and 5).

Abundance and trends in abundance of macroalgal groups exhibited complicated relations with geographic patterns. Only CGT average Ab_i and m_i showed significant mean differences among offshore strata, (Kruskall Wallis Ab_i $p< 0.01$, m_i $p< 0.02$), with higher values closer to land indicating that CGT was more abundant and Ab_i increased faster closer to land (Fig. 6). Long-term trends for RO had significant mean Ab_i and m_i differences among segment (Kruskall Wallis Ab_i $p< 0.04$, m_i $p< 0.05$) and significant mean Ab_i differences among alongshore (Kruskall Wallis Ab_i $p< 0.04$) strata, with lower values in Backcountry subregion 3 compared with Sluiceway which had low to medium values (Fig. 7). The intra-annual variability α_i and abundance peak Φ_i did not showed any significant differences among the three different geographic categories tested.

3.3 Macroalgae and water quality

Significant positive correlations were found between CGT Ab_i and m_i with different forms of N (NO_3^-, NO_2^-, TN, TON) and TOC in the water column (Table 1, Fig. 8). RO Ab_i had a significant positive correlation with NO_2^-, TN, TP and TOC; and the long-term trend of RO m_i with N:P (Table 1, Fig. 9). CR Ab_i had a significant negative correlation with TN:TP, and BO Ab_i had significant negative correlation with TN:TP (Table 1). BA Ab_i did not have any significant correlation with any water quality parameters (Table 1).

4. Discussion

This study show general trends and patterns and simple relationships between the spatiotemporal patterns of macroalgae abundance and median values of nutrients. The trends in abundance were trends only detectable by such a long-term monitoring program. Our analyses suggest that both the abundance and long-term increases in abundance of major macroalgal groups in the FKNMS were highest in the parts of our study areas with the highest availability of N in the water column.

Several physical factors such as light, salinity, and nutrients are known to affect the physiology and abundance of macroalgae (Lobban and Harrison 1997). At the physical level the region studied showed a clear seasonal pattern in its temperature and salinity, as the Florida Keys are located in a subtropical region. However at the spatial level differences in salinity and temperature were probably not the factor causing regional patterns in algal abundance. The sites sampled are all located out of the influence of the freshwater entering Florida Bay (Boyer and Jones 2002), unlike the adjacent Florida Bay, where salinity changes are strong and have influence on the abundance and distribution of macroalgae (Biber and Irlandi 2006). However, nutrient concentrations were found to differ spatially across the FKNMS (Fig. 2); it is likely that the spatial patterns in macroalagal abundance were functions of the pattern in nutrient availability.

The phycological flora found in the Florida Keys is very similar to the rest of the Caribbean (Taylor 1960, Littler and Littler 2000, Dawes and Mathieson 2002). The dominant group in the seagrass beds was the CGT, dominated by species of the genus *Halimeda* (Collado-Vides et al. 2005) followed by the RO, dominated by *Laurencia*. These results in general are similar to the reported flora by Biber and Irlandi (2006) for Florida Bay however the distribution might differ in particular cases such as *Batophora* that was found dominant by Zieman et al. (1989) in Florida Bay. *Batophora* was found in high abundance in Backcountry, which is similar to the general features of Florida Bay, and was present but inconspicuous in the rest of the FKNMS. The physical characteristics of each region and the inherent limitation of macroalgae to find the right substrate results in the patchy distribution found in this study. BA (*Batophora* and *Acetabularia*) are species characterized by small forms (up to 10 cm), usually found on hard substrata, i.e. small shells or hard rock, limiting its distribution from general sandy seagrass bottoms.

Spatiotemporal covariation, also known as synchrony, has been shown to provide helpful information on population dynamics by facilitating detection of common trends in variation at different time and spatial scales (Bjørnstad et al. 1999, Driskell et al. 2001). In this study synchrony is represented by Φ_i value of the regression model. CGT displayed highly synchronized seasonal patterns of abundance; with higher abundances during summer and fall when temperatures are high, and lower during winter when temperatures are low reflecting the fact that the Florida Keys are in a subtropical region with a marked seasonal behavior of its populations and they behave synchronically (Lunning 1993, Makarov et al 1999). The red algae also had a seasonal pattern but with high abundance during late fall/winter. This seasonal trend corroborates the findings of other studies conducted on marine coastal lagoons and coral reef environments which described a clear pattern of increasing abundance in green algal species during summer-fall and a subsequent decay in winter-spring, and an increase of red algae during the winter-spring and decay in summer-fall (Collado-Vides et al. 1994, Lirman and Biber 2000, Vroom et al. 2003, Artmitage et al 2005, Biber and Irlandi 2006).

Shifts from seagrass to macroalgal communities have been associated with nutrient increases in subtropical to temperate zones (Deegan et al 2002, McClanahan 1999, McClanahan et al. 2002, McClanahan et al. 2003, McClanahan et al. 2005). Similar mechanisms may influence shifts from corals or seagrass bed to algal dominated communities in the Caribbean and elsewhere too (Lapointe 1999, Duarte 1995; Valiela et al. 1997; Hughes et al. 1999, Hauxwell et al. 2001; McGlathery 2001).

Our results indicate that the abundance of almost all macroalgal groups was increasing in the FKNMS over the course of our study; particularly at sites with high N concentrations suggesting a limitation of N in general for at least CGT and RO. Eutrophication has been blamed for macroalgal bloom in the Florida Keys (Lapointe et al., 1994); and macroalgal increases, as a response of short-term nutrient enrichment, have been characterized by rapid increase of non corticated filaments (Lapointe et al. 2004, Karez et al. 2004). However, we found a slow and steady increase of slow growing calcareous green algae, that can not be defined as a macroalgal bloom, but steady increase of its abundance over 8 years of monitoring.

As a long term trend, red algae had a positive correlation with N, similar to experimental results in which enrichment with NH_4^+ resulted in increased photosynthesis and growth during summer of the red algae *Gracilaria tikvahiae* and of *Laurencia intricata* and *Digenia simplex* in the Bahamas (Lapointe et al 2004), and *Laurencia papillosa* and *Gracilaria coonopifolia* in Taiwan reefs (Tsai et al. 2004). It has also been reported, for some temperate red algae, that nutrient uptake is biphasic allowing these algae to exploit transient pulses of high nutrients (Lobban and Harrison 1997). Red algae might be exploiting the transient pulses of high nutrients reported for the FKNMS as upwelling episodic events (Leichter et al. 2003), affecting the offshore sites of the Keys, as well as other sources of nutrients coming from land use such as the high nutrient concentrations found close to land (Boyer and Jones 2002).

In contrast, a negative significant correlation between BO abundance and TN, was found; brown algae growth can be inhibited by high N concentrations (McClanahan et al. 2005), which is consistent with the negative correlation of BO found in our data, however no explanation is found still for this response.

The N limitation of CGT, has been demonstrated experimentally in this region. Davis and Fourqurean (2001) studied the competitive interaction between the seagrass *Thalassia testudinum* and the calcareous macroalga *Halimeda incrassate*; 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 these areas. These results are consistent with our results in which the higher slopes were found significant correlated to offshore distance, having higher values closer to land. However, Ferdie and Fourqurean (2004) showed that the response to increasing nutrients in seagrass beds might vary as a function of the initial status of nutrient limitation; in their study, enrichment resulted in an increase on the seagrass biomass at offshore sites, and in contrast in the inshore sites the enrichment leaded to an increase in algal biomass including *Halimeda*. This suggests that a continuous nutrient enrichment could lead to a shift from *Thalassia testudinum* to *Syringodium filiforme* in offshore sites, and to algal communities at inside shore (closer to land) sites. Also, Armitage et al. (2005) found, in their experimental nutrient enrichment in Florida Bay, that in general nutrient enrichment did not stimulated algal growth to the level to overgrow the seagrass beds, however some increases in calcareous green and ephemeral filamentous red were detected. This suite of results can be interpreted to suggest that in the Florida Keys and Florida Bay seagrass beds, calcareous green algae can be the first group of macroalgae to increase as nutrients loads are increased as well as some ephemeral red filamentous algae as epiphytes on seagrass blades.

Short term field studies in tropical regions suggest that it is difficult to find a significant correlation between N or P concentration and abundance of macroalgae (McCook et al. 1997, McCook 1999), and has been explained by the fact that physical and chemical processes controlling the availability of nutrients are very complex (Fong et al. 2001). However, in this long term, large scale region sampling program, we have been able to integrate the seasonal and yearly variability of macroalgal abundance and detect significant correlations between median water quality concentrations and macroalgae patterns in the FKNMS. These findings suggest that in areas with high nutrient concentration CGT and RO had higher slope values. Water quality parameters were higher in the Lower and Middle Keys than in the Upper Keys, and generally decreased from inshore to offshore consistent with a previous transect survey from these areas (Szmant and

Forrester, 1996); high N concentrations were found in the Middle Keys at the sites nearest to the shore (285, 241 and 235 sites with high CGT slope), these sites might be influenced by local anthropogenic inputs and the transport of the high N concentrations found in the western of Florida Bay, Shark River and Florida Shelf.

Nutrients are important for the algal communities as shown in this study; however we do not disregard other factors that might be playing a role in the long-term trends in the FKNMS macroalgal communities. It is possible that the distribution patterns and trends found 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. If the increase we found is the result of the reestablishment after a disturbance, that disturbance must have been of significantly greater magnitude than Hurricane Georges.

It is well recognized that decrease in herbivore activities is an import factor for observed coastal ecosystems changes including shift of coral dominated communities into macroalgal dominated communities (Jackson et al. 2001, MacManus and Polsenberg 2004, McClanahan et al. 2003, 2005). The Florida Keys is a heavily fished area (Bohnsack et al. 1994), and macroalgal communities in the reef as well as in the seagrass beds might be having a lower pressure, allowing some groups to increase, however not all macroalgal groups respond rapidly to herbivore exclusion in reef environments (McClanahan 1997).

The patchy and complex distribution of nutrients, as well as currents and sedimentation pattern play a role in the macroalgal distribution patterns found in this long term study, within a context of disturbance history, particularities of those sites, and history of herbivore activity.

5. Conclusions

The monitoring of the macroalgae at the group level was very useful to give us a general idea of the main trends with a good level of accuracy. A base line or status of the macrolagae and their trends is given with an analysis of their correlations with nutrients availability. The main results show a relationship between the CGT and N having an increasing trend of CGT closer to land sites.

The multifactorial processes that determines the nutrient availability, as well as multi-species component of each algal group make difficult to achieve a cause-effect interaction between the abundance of macroalgae and water quality results, however, with this type of monitoring programs we have been able to detect trends and set a base line of the status of the macroalgae in the FKNMS that are explained by results of experimental studies. The combination of complex water circulation patterns, diverse sources of nutrients, initial conditions and competitive interactions between benthic vegetation, can determine the increase of macroalgae detected, and these processes can vary at very local scale.

6. Acknowledgments

Data were provided by the SERC-FIU Water Quality Monitoring Network which is supported by EPA Agreement #X994621-94-0 and SFWMD/SERC Cooperative

Agreements #C-13178. The macroalgal sampling was conducted with the support of the Water Quality Protection Program of the Florida Keys National Marine Sanctuary, funded by the USEPA (contract X97468102-0) and the National Oceanographic and Atmospheric Administration (contract NA16OP2553). This eight year monitoring program was possible to conduct thanks to the field work of many students and technicians, including L. Rutten, C. D. Rose, A. Willsie, C. Furst, M. Ferdie, D. Byron, V. C. Cornett and K. Cunniff. We also 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. Anna Armitage and two anonymous reviewers made useful comments that helped improve the manuscript. This is contribution #x of the Southeast Environmental Research Center at FIU.

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Table 1. Kendall τ-b correlations of median values of nutrients and average abundance and slope values of macroalgal groups. Bold numbers are statistical significant correlations ($p < 0.05$). Ab= Abundance Index, S= Slope.

	CG		**BA**		**RO**		**CR**		**BO**	
	Ab	**S**	**Ab**	**S**	**Ab**	**S**	**Ab**	**S**	**Ab**	**S**
NO3	**0.30**	**0.32**	0.02	-0.17	0.15	0.02	0.04	0.01	0.01	-0.18
P	**0.01**	**0.01**	0.44	0.09	0.12	0.43	0.40	0.48	0.46	0.08
NO2	**0.26**	**0.25**	-0.07	-0.12	**0.28**	0.12	0.00	0.02	0.00	-0.01
P	**0.02**	**0.03**	0.31	0.18	**0.01**	0.18	0.49	0.45	0.49	0.46
NH4	0.09	0.15	-0.04	-0.07	0.12	0.03	-0.08	-0.08	-0.04	-0.10
P	0.24	0.12	0.39	0.29	0.17	0.42	0.27	0.27	0.39	0.23
TN	**0.33**	**0.32**	-0.10	0.00	**0.23**	0.08	-0.06	-0.16	-0.05	-0.07
p	**0.00**	**0.01**	0.24	0.49	**0.04**	0.28	0.32	0.11	0.35	0.28
TON	**0.30**	**0.32**	-0.11	-0.01	0.20	0.08	-0.07	-0.20	-0.07	-0.10
p	**0.01**	**0.01**	0.22	0.46	0.06	0.27	0.29	0.06	0.31	0.23
TP	0.08	0.14	0.04	-0.10	**0.27**	0.01	-0.01	-0.19	0.17	0.02
p	0.28	0.14	0.40	0.23	**0.02**	0.46	0.48	0.08	0.10	0.44
TOC	**0.30**	**0.23**	-0.06	0.07	**0.28**	0.05	0.01	-0.13	0.05	-0.04
p	**0.01**	**0.04**	0.33	0.30	**0.01**	0.35	0.48	0.17	0.35	0.39
TN:TP	0.09	0.15	-0.19	-0.14	-0.07	0.15	**-0.24**	-0.14	**-0.36**	-0.19
p	0.23	0.12	0.09	0.14	0.30	0.12	**0.04**	0.15	**0.00**	0.07
N:P	0.03	0.13	-0.06	-0.09	0.08	**0.30**	-0.07	0.13	-0.12	0.12
p	0.41	0.15	0.34	0.25	0.27	**0.01**	0.29	0.16	0.18	0.18

Legend of Figures

Figure 1. Study Area

Figure 2. Maps displaying interpolated median values for nutrients. Y and X axes show latitude and longitude coordinates. Color scale shows the median concentration of each nutrient.

Figure 3. Maps displaying interpolated mean abundance for the macroalgal groups: CG Calcareous green, GO Green other, RO Red Other, BA Batophora-Acetabularia, CR Crustose Red and BO Brown Other. Y and X axes show latitude and longitude coordinates. Color scales show the Braun-Blanquet abundance index.

Figure 4. Time series showing some examples of sites and algal groups model results: Dots = observed data, solid line= non-linear regression curve.

Figure 5. Histogram showing slope/year values for each group in each site. CG Calcareous green, GO Green other, RO Red Other, BA Batophora-Acetabularia, CR Crustose Red and BO Brown Other.

Figure 6. Box-plots showing significant differences of CG Ab_i, and m_i as a function of distance from shore category.

Figure 7. Box-plots showing significant differences of RO Ab_i, m_i as a function of segment and alongshore categories.

Figure 8. Scatter-plots showing correlation between CG and nutrients.

Figure 9. Scatter-plots showing correlation between RO and nutrients.

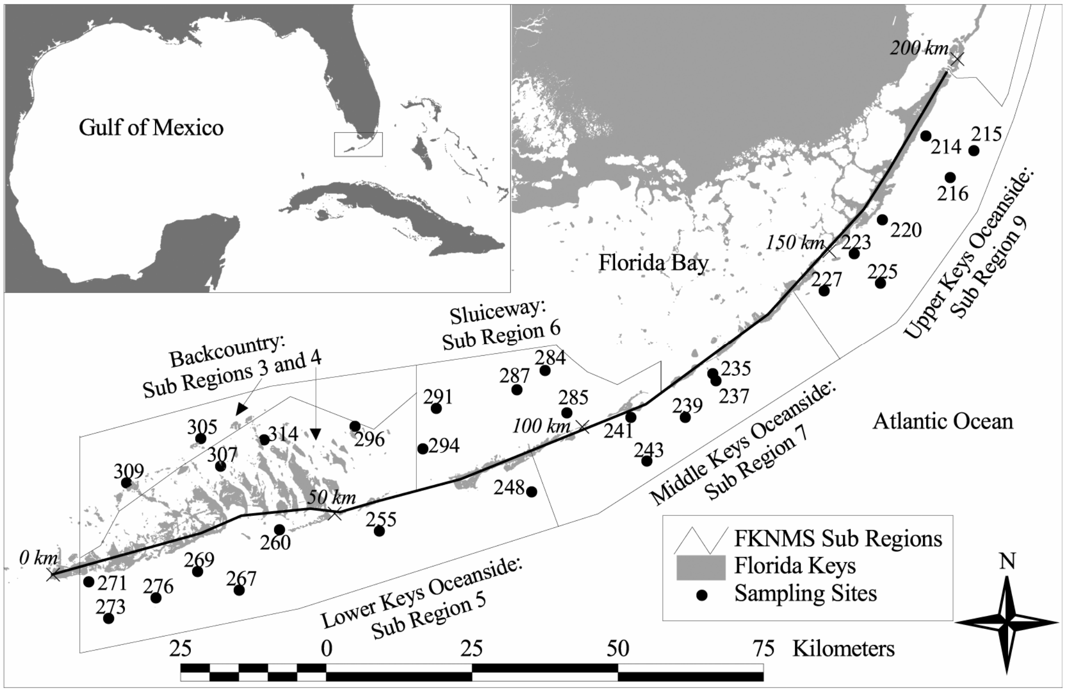
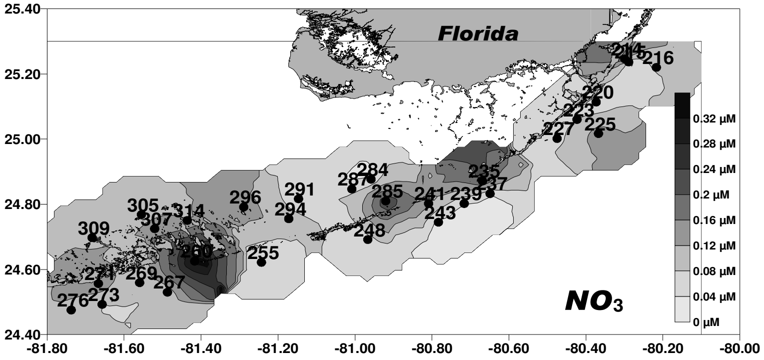
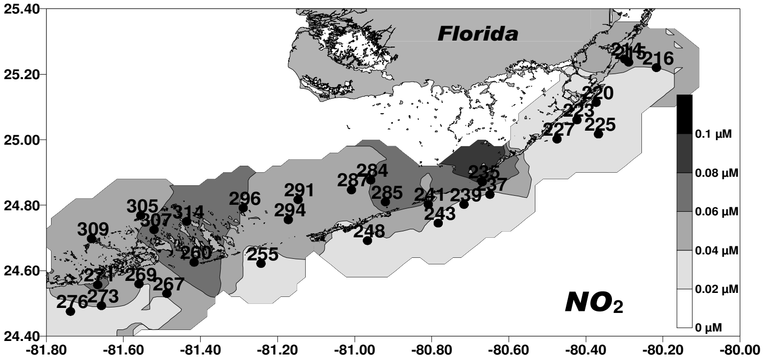
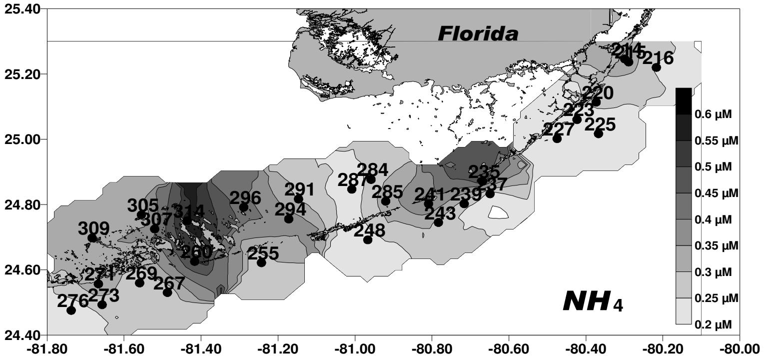


Figure 1. Study area showing regions and study sites


Florida
NO$_3$
0.32 µM
0.28 µM
0.24 µM
0.2 µM
0.16 µM
0.12 µM
0.08 µM
0.04 µM
0 µM
214
216
220
223
225
227
235
237
239
241
243
248
284
285
287
291
294
296
305
307
309
314
250
255
267
269
271
273
276
25.40
25.20
25.00
24.80
24.60
24.40
-81.80
-81.60
-81.40
-81.20
-81.00
-80.80
-80.60
-80.40
-80.20
-80.00


Florida
NO$_2$
0.1 µM
0.08 µM
0.06 µM
0.04 µM
0.02 µM
0 µM
214
216
220
223
225
227
235
237
239
241
243
248
284
285
287
291
294
296
305
307
309
314
260
255
267
269
271
273
276
25.40
25.20
25.00
24.80
24.60
24.40
-81.80
-81.60
-81.40
-81.20
-81.00
-80.80
-80.60
-80.40
-80.20
-80.00


Florida
NH$_4$
0.6 µM
0.55 µM
0.5 µM
0.45 µM
0.4 µM
0.35 µM
0.3 µM
0.25 µM
0.2 µM
214
216
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260
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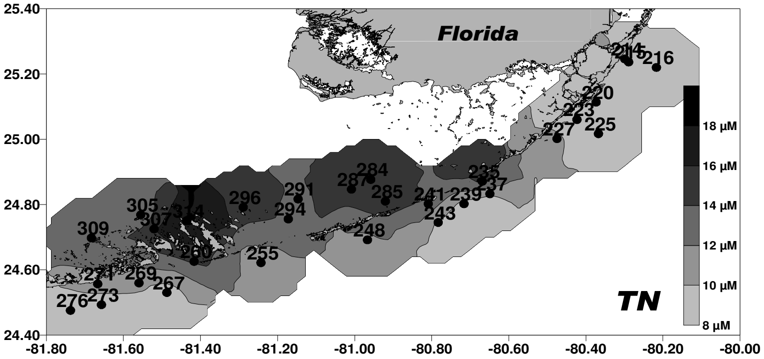
267
269
271
273
276
25.40
25.20
25.00
24.80
24.60
24.40
-81.80
-81.60
-81.40
-81.20
-81.00
-80.80
-80.60
-80.40
-80.20
-80.00


Florida
TN
18 µM
16 µM
14 µM
12 µM
10 µM
8 µM
214
216
220
223
225
227
235
237
239
241
243
248
284
285
287
291
294
296
305
307
309
314
260
255
267
269
271
273
276
25.40
25.20
25.00
24.80
24.60
24.40
-81.80
-81.60
-81.40
-81.20
-81.00
-80.80
-80.60
-80.40
-80.20
-80.00

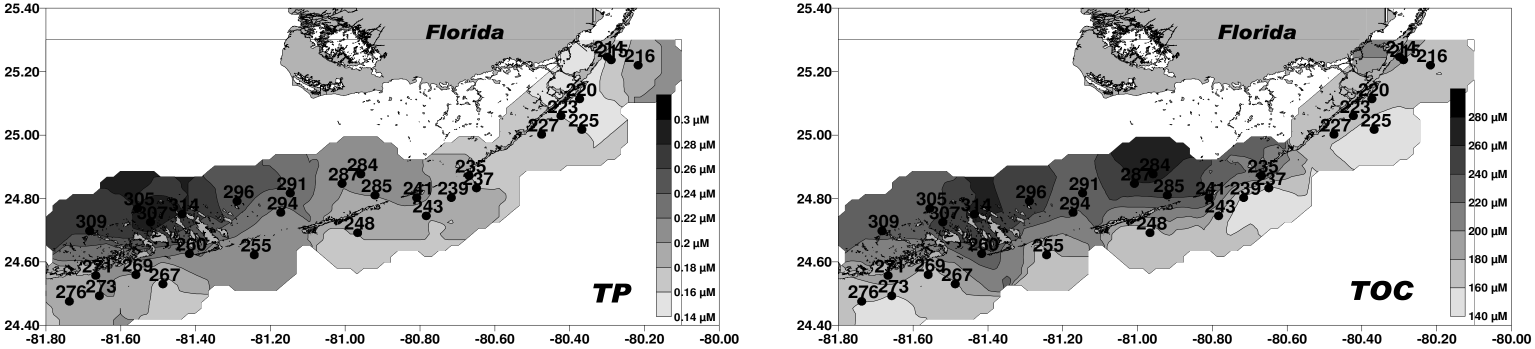
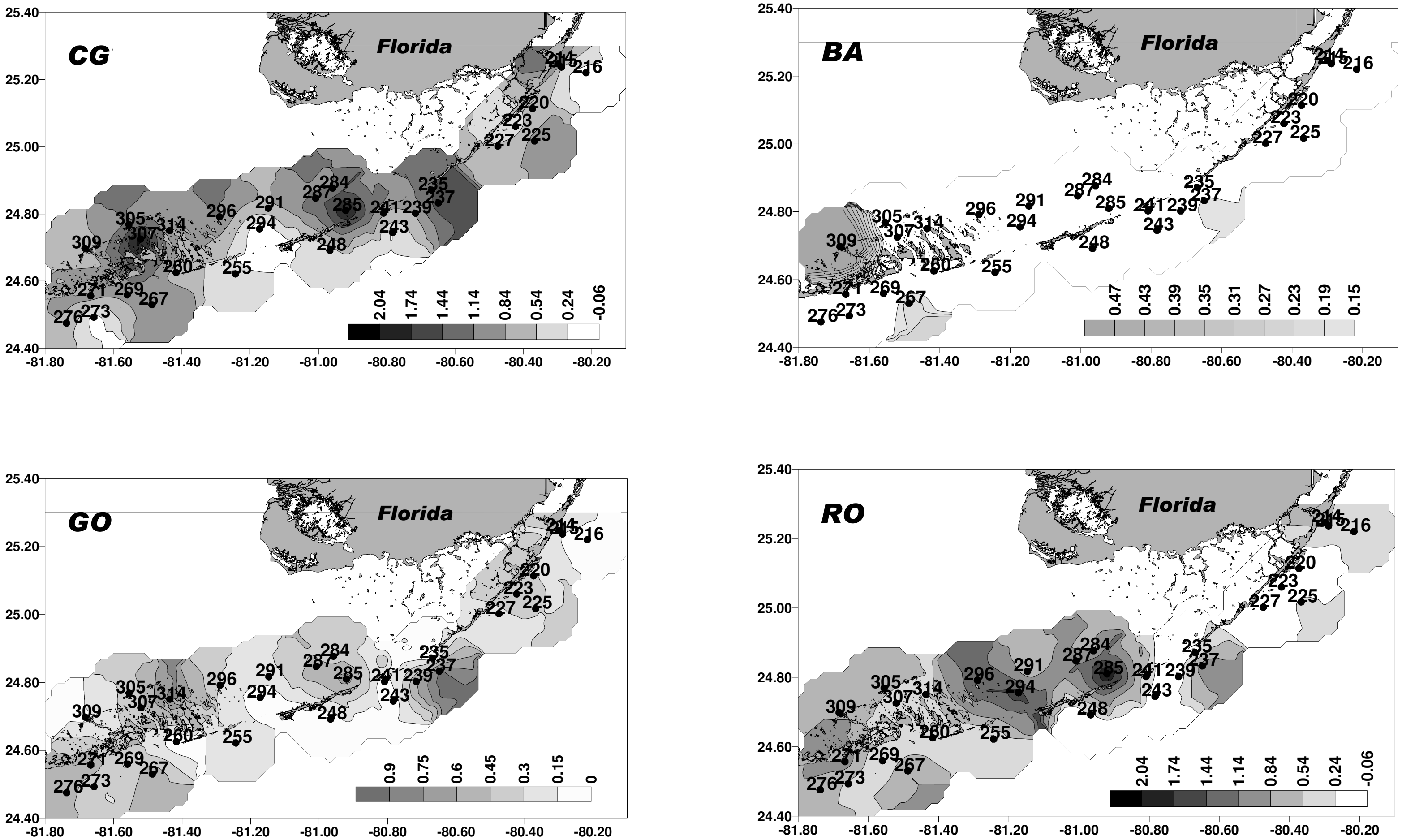


Figure 2. Maps displaying interpolated median values for nutrients. Y and X axes show latitude and longitude coordinates. Color scale shows the median concentration of each nutrient.


CG
BA
GO
RO
Florida
25.40
25.20
25.00
24.80
24.60
24.40
-81.80
-81.60
-81.40
-81.20
-81.00
-80.80
-80.60
-80.40
-80.20
2.04
1.74
1.44
1.14
0.84
0.54
0.24
-0.06
0.47
0.43
0.39
0.35
0.31
0.27
0.23
0.19
0.15
0.9
0.75
0.6
0.45
0.3
0.15
0
214
216
220
223
225
227
235
237
239
241
243
248
255
260
267
269
271
273
276
284
285
287
291
294
296
305
307
309
314

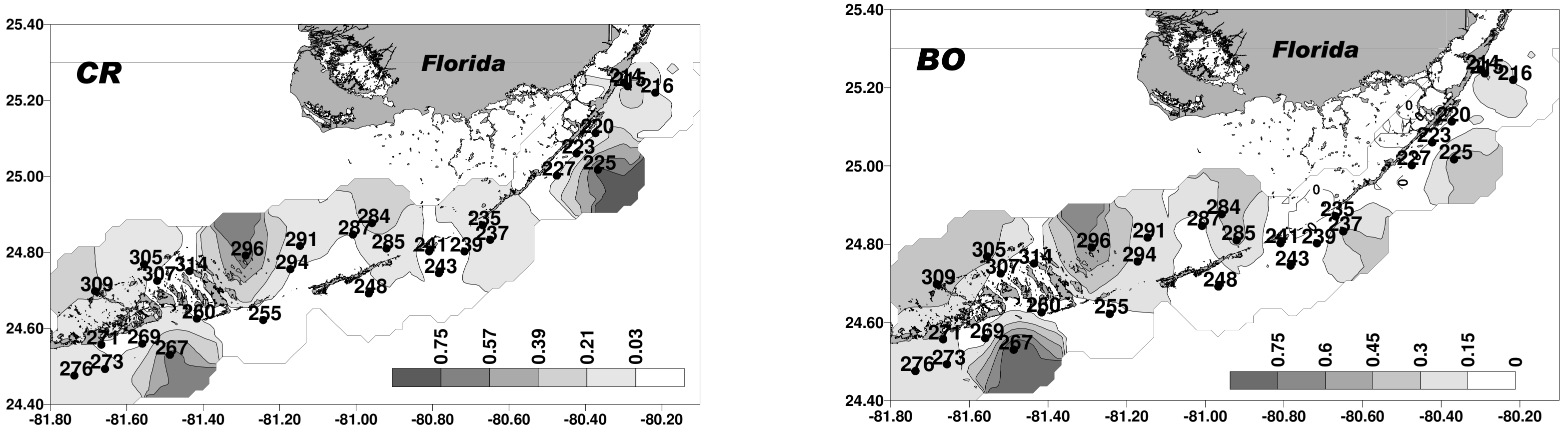


Figure 3. Maps displaying interpolated mean abundance for the macroalgal groups: CG Calcareous green, GO Green other, RO Red Other, BA Batophora-Acetabularia, CR Crustose Red and BO Brown Other. Y and X axes show latitude and longitude coordinates. Gray scale shows the Braun-Blanquet abundance index.

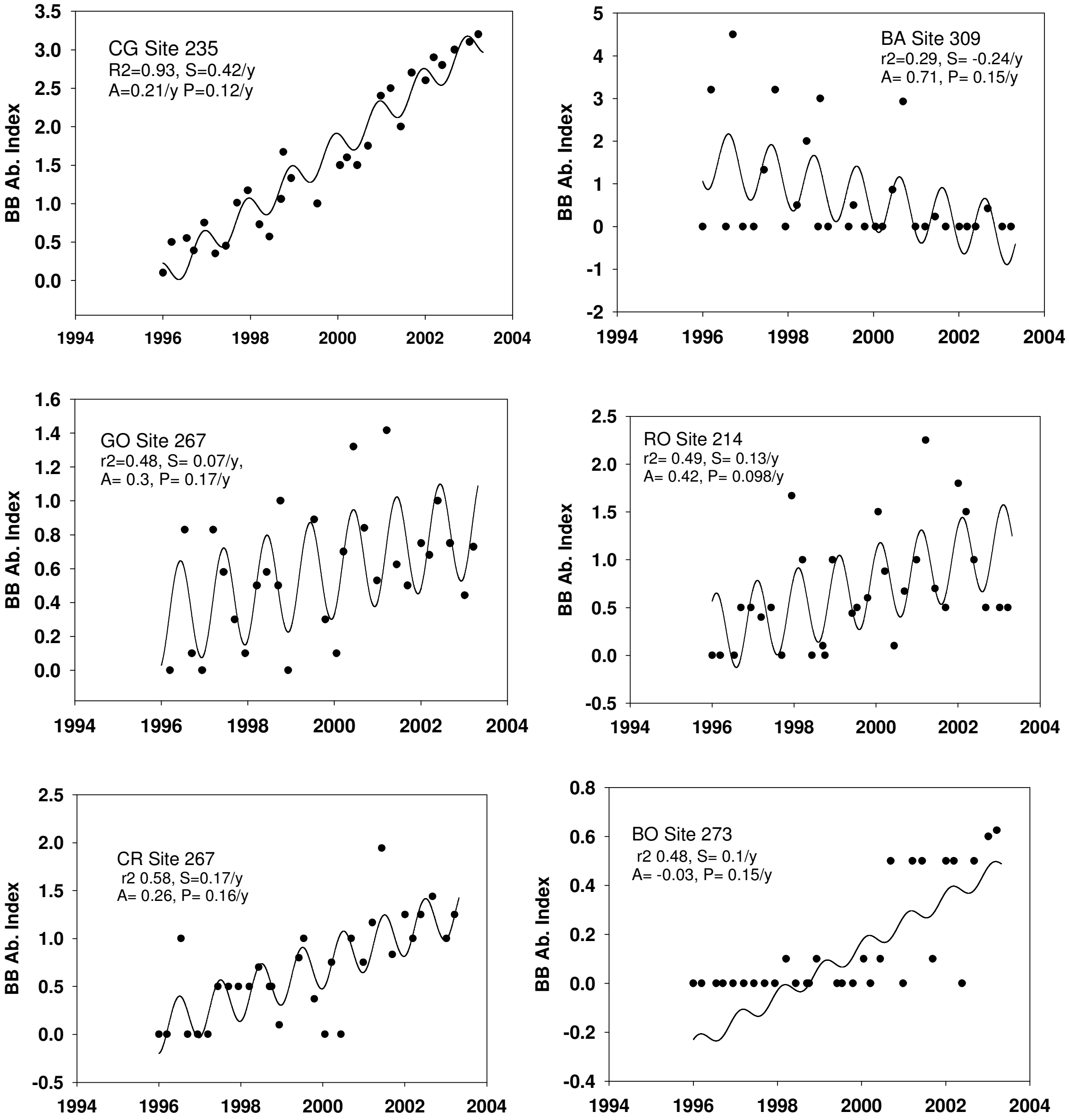


Figure 4. Time series showing some examples of sites and algal groups model results: Dots = observed data, solid line= non-linear regression curve.

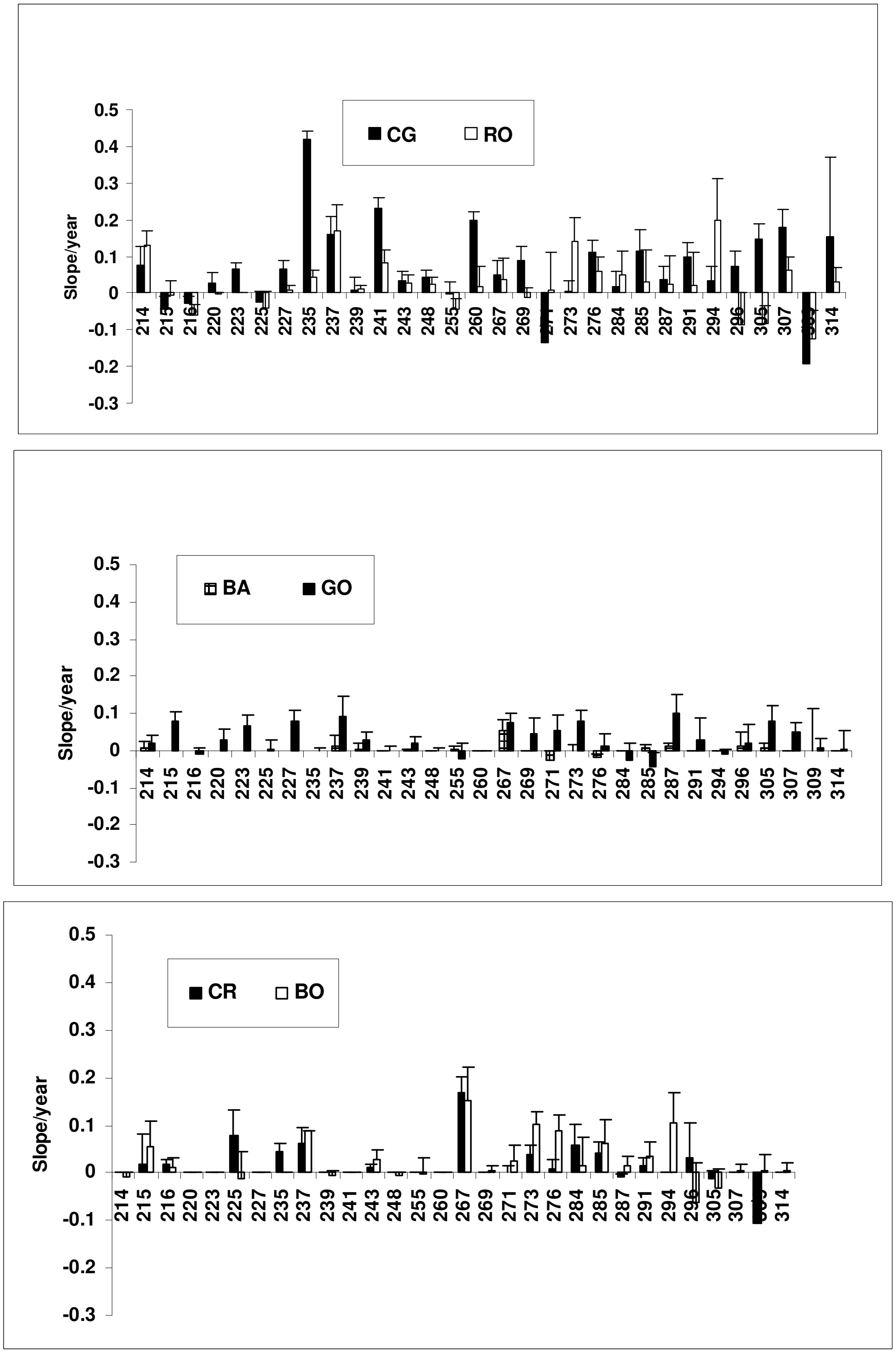


Figure 5. Histogram showing slope/year values for each group in each site. CG Calcareous green, GO Green other, RO Red Other, BA Batophora-Acetabularia, CR Crustose Red and BO Brown Other

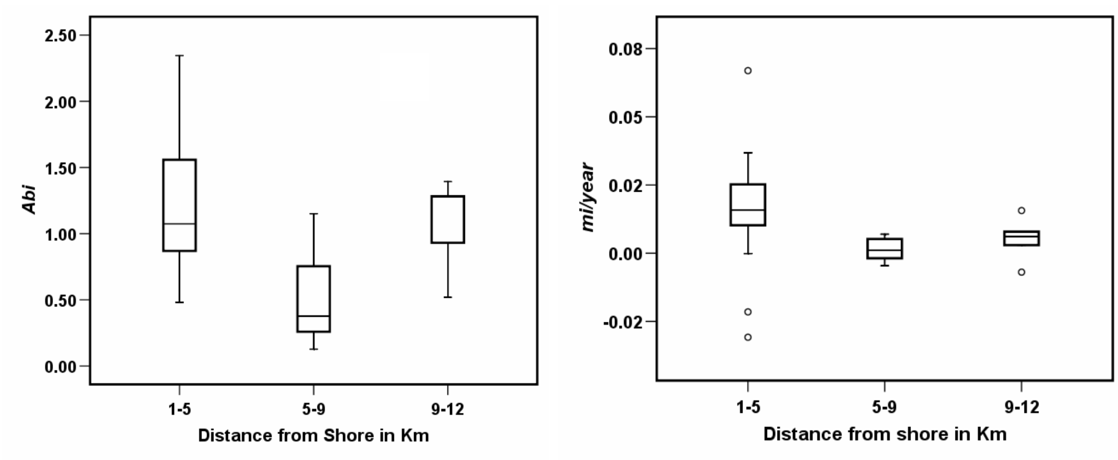


Figure 6. Box-plots showing CG Ab_i, and m_i as a function of distance to shore category.

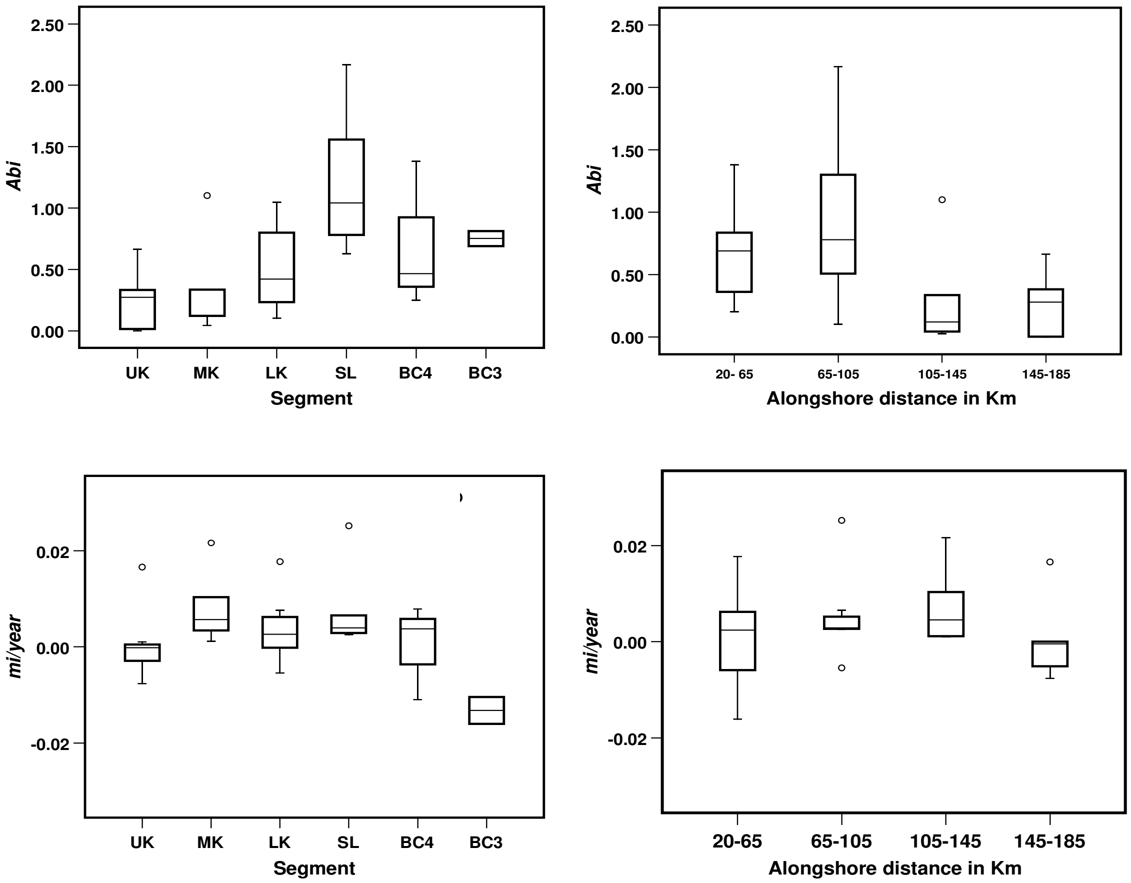


Figure 7. Boxplot showing differences of RO Ab_i and m_i as a function of Segment and Alongshore categories.

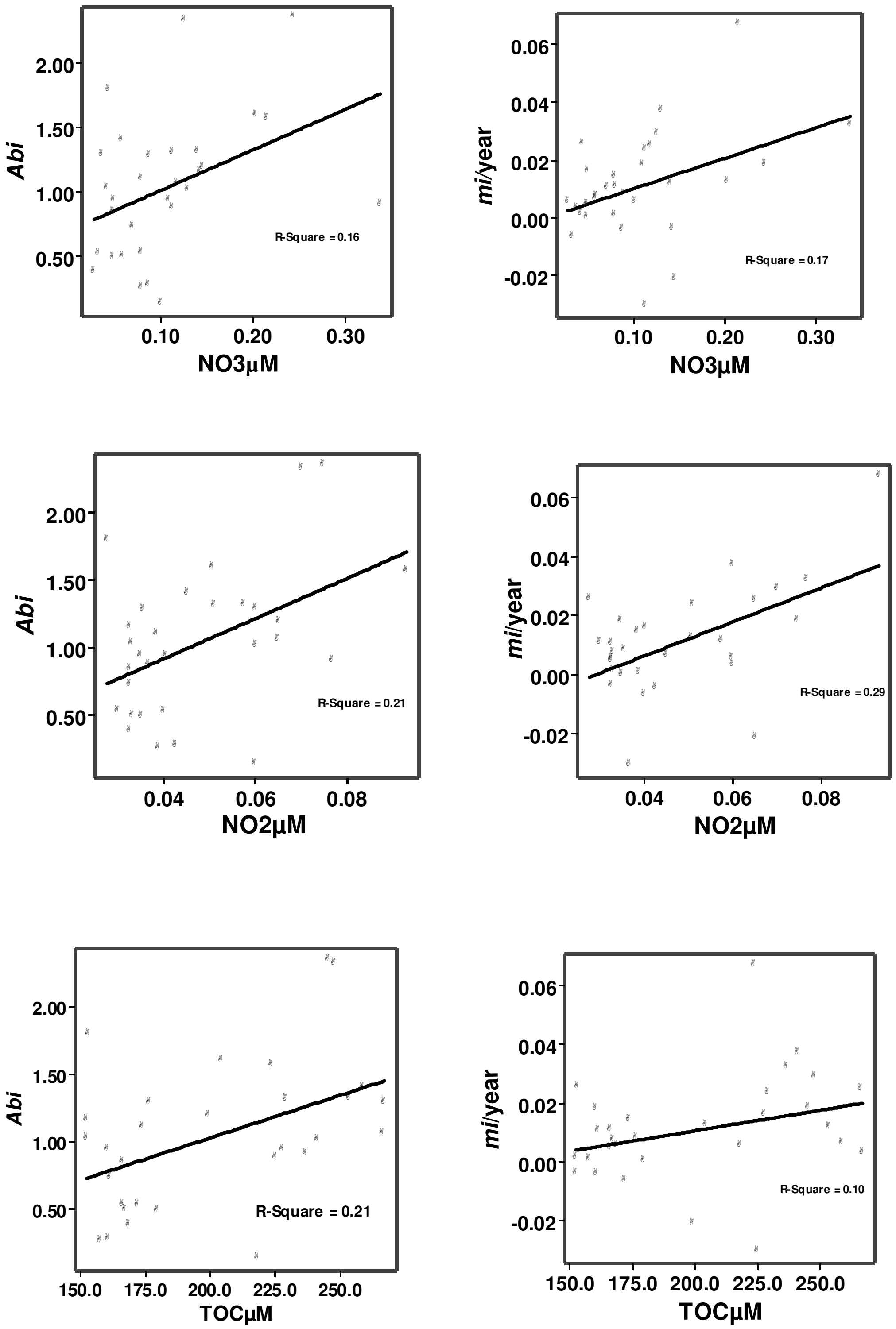


Figure 8. Scatter-plots showing correlation between CG Ab_i and m_i and nutrients

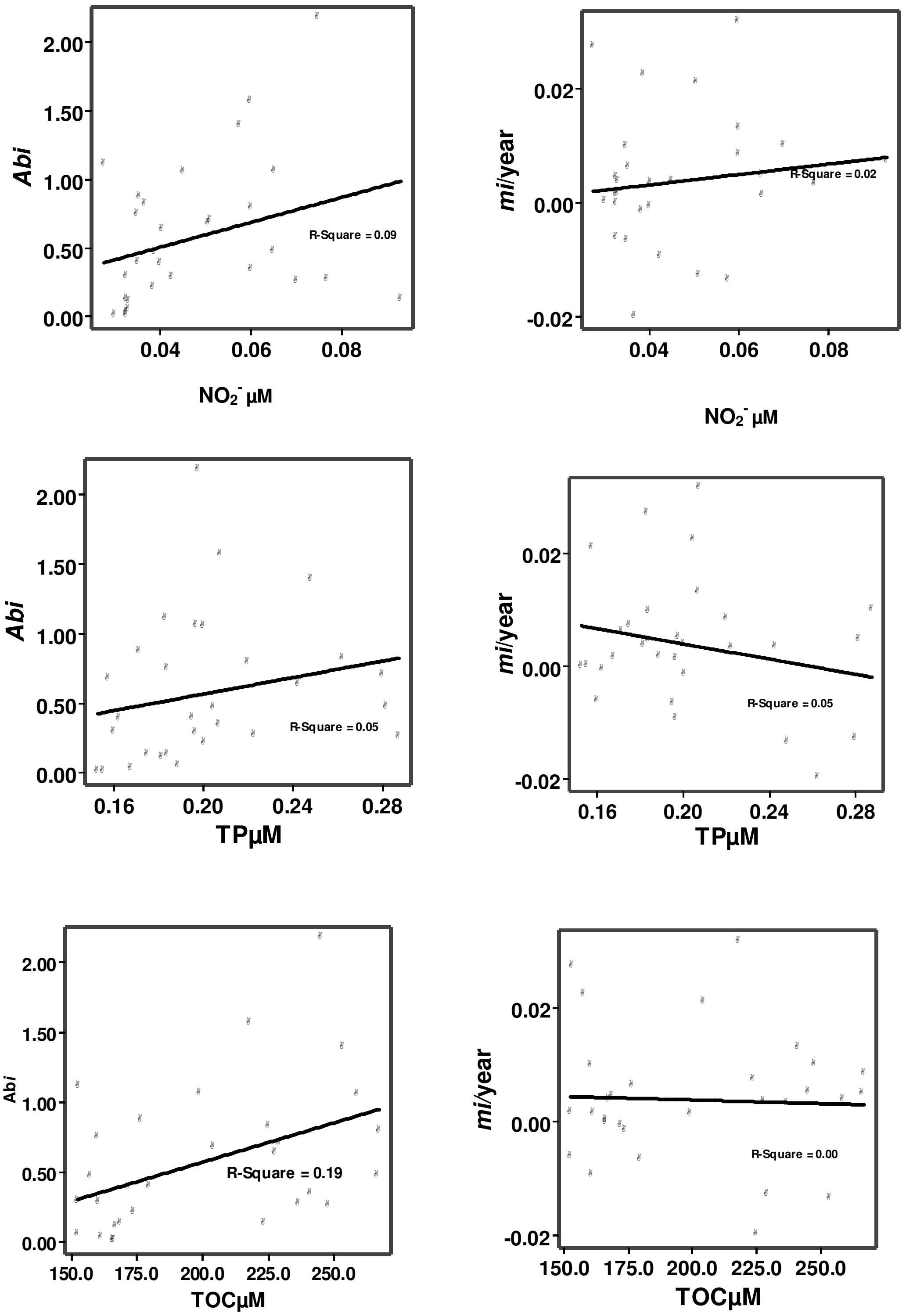


Figure 9. Scatter-plots showing correlation between RO *Ab_i* and *m_i* and nutrients