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The Ecology and Economics of Seagrass Community Structure

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

THE ECOLOGY AND ECONOMICS OF SEAGRASS COMMUNITY STRUCTURE

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Bryan M. Dewsbury

2014

To: Dean Kenneth G. Furton
College of Arts and Sciences

This dissertation, written by Bryan M. Dewsbury, and entitled The Ecology and Economics of Seagrass Community Structure, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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This dissertation document is a culmination of over a decade of intellectual discovery at Florida International University. Having received my Masters from the Department of Biological Sciences here at FIU, and then spending a subsequent year working as a technician; I view my dissertation as having built on the foundations I laid for myself in those early years. For all the trials and learning curves I have been through in order to complete this work I owe a debt of gratitude to many people. If I were to list every single individual who made a meaningful contribution to this work, this section will run multiple pages. So, to those who are not heretofore mentioned, please note that I am eternally grateful for all the contributions received including field help, manuscript comments, analysis advice, and general support over the years.

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Lastly, I would like to dedicate this dissertation in its entirety to my parents Reverend Sheldon and Angela Dewsbury, whose eternal sacrifice has made the few contributions that I have made to science and the common good possible.

ABSTRACT OF THE DISSERTATION

THE ECOLOGY AND ECONOMICS OF SEAGRASS COMMUNITY STRUCTURE

by

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Florida International University, 2014

Miami, Florida

Professor James W. Fourqurean, Major Professor

Coastline communities have experienced a marked increase in human populations over the last few decades. This increase in population places disproportionate pressure on coastal ecosystems to provide economic services to support local economies. At the same time, overuse of these services can aid in the destruction of the ecosystems responsible for them. Seagrass ecosystems are mainly found near coastlines, and are typically a chief provider of some of these economic goods and services. Many previous studies have documented the ecological functions of this seagrasses. Unfortunately, our increasing knowledge of seagrass structure and function has not been fully incorporated into economic models estimating their value. In this dissertation, I focus on the seagrass ecosystem in southern Biscayne Bay, and simultaneously study the ecological dynamics of the seagrass beds, and estimate its economic value. This value is based on recent ecological models in the literature as well as data I collected from the system. I focused on Biscayne Bay due to, 1) the relevance that this question had to the relationship between Biscayne Bay and the Miami metropolis, and 2) the lack of existing reliable models that explore this relationship in this area. More specifically, I became very interested in this question while working for Biscayne National Park, where such a model would have improved seagrass restoration work taking place there.

I found that southern Biscayne Bay is dominated by *Thalassia testudinum*, with other seagrasses following a spatial pattern primarily determined by salinity and water column nutrient distribution. *Syringodium filiforme* was mostly found east of the islands, *Halodule wrightii* was mostly found near the shoreline, and *Halophila engelmenii* was spotted at only two of the 190 sites visited. *T. testudinum* distribution was largely unaffected by nutrient enrichment at all sites, but it appeared to induce severe herbivory further from the coastline. For the calendar year 2004, we deduced using a Total Ecosystems Valuation (TEV) model that seagrass ecosystems potentially contributed over $198 million US dollars to the local economy. We argue that a simultaneous understanding and use of both ecological and economic models is important for future conservation efforts of seagrass ecosystems.

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Introduction

In the 1930s and 1940s J. William Kapp and Karl Polanyi were forming the first intellectual schools of thought on economics as a subsystem of natural capital (Ropke, 2004). Ecological Economics (later to be distinguished from Environmental Economics) provided the conceptual framework around which social policies could be made that fully considered the sustainability of ecosystem processes (Ropke, 2004). As global population rose in the coming decades, the need to understand the economic value of ecosystems rose. The demands that a burgeoning human population was placing on the environment in some cases led to irreversible negative impact. In response to this, some ecological economists attempted to estimate the economic value of various ecosystems. One of the more notable of these valuations was done by Robert Costanza and his colleagues (Costanza et al., 1997). This estimate put the world's natural capital at a value of 54 trillion US dollars (Costanza et al., 1997). While this estimate was often criticized for its emphasis on nutrient cycling functions, and lack of mentioning of other important processes, it did highlight the importance to continue to investigate the link between ecosystem function and economic value (Pearce, 1998).

Since the original thinkers on economics and sustainability in the 1940s, the movement for greater environmental conservation has substantially matured. Research into ecosystem structure and function has led to the creation of preserves and park systems that help maintain food web structures and fragile ecosystems. Simultaneously, ecosystem valuation approaches have better identified the various ways in which ecological processes contribute to local economies. As more human populations flock to cities and to coastlines however, the need to better establish the economic and ecological relationships has also increased greatly.

My own experience in this area stems from working at Biscayne National Park as a SCUBA diving technician in the Department of Environmental Resource Management. My main responsibilities there were to assist in the restoration of seagrass beds damaged by vessel groundings. Offenders who were caught damaging beds were charged based on the cost to the Park service to restore the damaged site. This replacement cost approach in my estimation severely undervalued the potential worth of damaged beds as it did not consider the services provided by the system. A more ecologically sound valuation would involve quantifying the ecosystem goods and services in the area as a function of the seagrass beds. In this scenario, services provided by seagrasses would be a function of their abundance and physiology. This would be in turn be affected by abiotic and biotic factors that affect the above parameters over different spatial and temporal scales. This approach would require a comprehensive assessment of the current seagrass distribution as well as more specific manipulations that assess how the seagrass community changes over time. Ultimately, once the ecological nature of the services is quantified, those values can be used to assess economic contribution.

In this dissertation, I use this approach to assess the ecology and economics of southern Biscayne Bay, an ecosystem in a state of transition. The restoration of historic freshwater flows from the Florida Everglades system means that in the near future Biscayne Bay will have more freshwater, especially near the coastline (Lirman & Cropper

Jr., 2003). This freshwater may bring with it nutrient runoff from farmlands and urbanized areas (Caccia & Boyer, 2007). As development continues in the greater Miami area, altered coastlines, and dredging for pipeline and waterway construction can affect the ecology of the estuary (Bhat & Stamatiades, 2003). In addition to the above, south Florida's continued reliance on tourism as a major income generator, means that heavy boat traffic and water-based tourism will be the norm for some time to come (Bush, 1999). These activities can have negative impacts on different aspects of the ecosystem.

I aim to use this ecological-economics model to 1) determine the structure and abundance of seagrass beds in southern Biscayne Bay 2) determine how ecological function varies over spatial and temporal scales and 3) use a Total Ecosystem Valuation approach to determine the economic value that those services provide for south Florida. This dissertation is broken down into four chapters. Chapter 1 is a comprehensive assessment of primary producer dynamics in Biscayne Bay in relation to multiple abiotic factors. Here I use my own benthic sampling regime together with long-term data sets from the Water Quality Monitoring program to establish relationships between nutrient distribution and different primary producer community types. I also create hypothetical scenarios that predict how these communities might change if some of the abiotic parameters shifted in the future. After determining ambient conditions in the Bay in chapter 1, I was then interested in determining how changes in some of those conditions might affect primary producer abundance and structure. In chapter 2 therefore, I describe a nutrient enrichment experiment set up at 3 sites across the Bay. These sites were chosen based on chapter one's determination of the background nutrient regime. The aim here was to determine how ecological function might change in the face of changing biotic and abiotic factors. In chapter 3 I review the valuation of seagrass ecosystems, and suggest a model by which can be used to approach valuations of this ecosystem in the future. I use this approach in chapter 4 to valuate the ecosystem services of southern Biscayne Bay. In this chapter I combine data from my own sampling efforts with data from independent estimates to determine the economic contribution of seagrass beds to the south Florida economy.

This dissertation uses an interdisciplinary approach to address an environmental concern. It establishes the importance of using sound ecological data to construct economic models that are useful to local stakeholders, and emphasizes the need to understand the ecosystem dynamics so we can better predict and anticipate change.

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CHAPTER I

Spatial patterns and abiotic drivers of primary producers in a subtropical estuary

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Abstract

In this paper we describe the results of a field sampling and data mining effort where we sought to shed light on the ecological dynamics of southern Biscayne Bay. Specifically, we were interested in the relationship between the water quality in the Bay and the abundance and distribution of primary producers. We show here that salinity and nitrogen gradients in the water column strongly influence primary producer structure especially in the southwestern, nearshore region of the Bay. Submerged aquatic vegetation is largely dominated by seagrasses of which *Thalassia testudinum* is the most abundant. The foliar tissue of this species also reflects the spatial gradient of nitrogen concentration found in the sediment and the water column. Ratios of total nitrogen to total phosphorus were mostly above 35:1 suggesting possible phosphorus limitation, a phenomenon consistent with other carbonate-based estuaries. A Hierarchical Discriminant Function model correctly classified 37% of previously identified communities. Modifications to this model to reflect hypothetical future scenarios in the estuary predicted distribution and abundance changes in both seagrass and macroalgal communities. Our work here can help managers and stakeholders of Biscayne Bay to better understand the ecological patterns of the system, but more importantly to predict the possible effects of future impacts to the community.

Introduction

The distribution, species composition and abundance of primary producers can determine the energy available to support heterotrophs and the structure of food webs (Posey et al. 1995; Scheu and Schaefer 1998). Because of this, factors affecting abundance and distribution of primary producers can have far-reaching effects on overall community structure (Alpine and Cloern 1992). In estuarine systems this effect has been extensively documented (Boyer et al. 2004; Armitage et al. 2005; Gil et al. 2006). Estuarine communities for example that are dominated by macroalgae and seagrasses are very different functionally than those dominated by microalgae (Deegan et al. 2002). Seagrass beds are dependent on relatively high light availability to the benthos (Peralta et al. 2002), and their extensive rhizome structure hold sediment in place reducing turbidity in the water column (Moore 2004). The morphology of seagrass beds also create a physical space that some juvenile marine species use as habitat until their adult stages (Heck and Thoman 1984; Orth et al. 1984; Nagelkerken et al. 2002; Heck et al. 2003; Heck and Valentine 2006). Microalgal blooms can cloud water columns in some estuaries however and prevent light from reaching the benthos (Valiela et al. 1997; McGlathery 2001). These estuaries are characterized by smaller populations of seagrasses and subsequentially a severe reduction in the ecosystem services they can provide (McGlathery 2001). While there is some evidence that herbivore pressure can moderate the effects of these blooms (Lotze and Worm 2000; Lotze et al. 2003), for nearshore systems, biogeochemical regime shifts remain the primary drivers of these phase shifts (Armitage et al. 2005).

Changes in water column and benthos biogeochemistry can be greatly affected by the presence of human development on and around the coastline (Smith et al. 2003; Gorgula and Connell 2004; Syvitski et al. 2005). Pulsed nutrient runoff from sewage effluent and agricultural systems can result in large additions of nitrogen and phosphorous which can then result in phase shifts from seagrass-dominated to microalgal-dominated communities (Syvitski et al. 2005). Given the complex array of ecosystem services provided by seagrasses (Barbier et al. 2011,Dewsbury et al., unpubl. data), the resulting loss in ecosystem services can have severe negative economic consequences for local communities (Hoagland et al. 2002; Dodds et al. 2009). For this reason, it is important for managers of local systems to understand the various nutrient fluxes that affect their estuaries.

Biogeochemical fluxes within estuaries often have complex relationships with primary producers. Water column nutrients and sediment nutrients may affect phytoplankton concentrations, macroalgae and seagrasses differently. When measured separately, it is important for managers to choose models that appropriately describe and predict the effect of any changes to existing conditions. For example, foliar nitrogen:phosphorus ratios can be used to determine relative nutrient limitation within seagrasses (Fourqurean et al. 1992). This in turn can assist managers to predict the possible effects of nutrient increases based on background values. Statistical models created for estuaries similar to Biscayne Bay have combined nutrient and primary producer dynamics from both the water column and the benthos to examine the relationship between each entity (Fourqurean et al. 2003; Lirman and Cropper Jr. 2003; Caccia and Boyer 2005; Herbert et al. 2011).

Biscayne Bay is a semi-enclosed estuary located to the southeast of the state of Florida (Figure 1). It extends from Haulover Beach to the north to Turkey Point to the south. The eastern boundary is dotted by numerous islands that separate the Bay from the coral reef tract to the east. To the west is a mostly developed shoreline that is part of the eastern border of Miami-Dade County. In the southern portion of Biscayne Bay lies the federally managed Biscayne National Park (BNP). Established in 1968, BNP was set up to address concerns concerning the protection of natural resources in light of the exploding human population in Miami-Dade County (Leynes and Cullison 1998). Biscayne Bay as a whole historically supported a number of activities including commercial fisheries, recreational fisheries and tourism-related activities (Leynes and Cullison 1998). Many of these activities are extremely important to the tourism-based economy of south Florida. Unfortunately, the prevalence of these activities exposes this estuary to much higher human impact. In addition to this, Biscayne Bay is the destination for a number of canals that deliver freshwater from the Everglades system. The South Florida Water Management District controls the timing and delivery of some of these canals. As part of a multi-billion-dollar restoration program to restore the Everglades ecosystem (McLean et al. 2002) the delivery of this freshwater has been increasing. Increases in the delivery of freshwater can create new pulses of nutrient supply into the estuary. As the delivery of freshwater increases, it is important for managers to determine the possible ecological effects of this significant change in freshwater supply.

Managers of the Bay have a number of legal mechanisms and public awareness campaigns whose aim is to help protect the natural assets of Biscayne Bay (Kirsch et al. 2005). Additionally, different institutions have established a number of independent projects and monitoring programs to better understand the ecological dynamics of the system. Data from some of these programs have helped establish rules pertaining to recreational fisheries, no-take zones and vessel use within the Biscayne Bay area (Ault et al. 2005).

There are many different agencies conducting various monitoring programs in Biscayne Bay. Efforts to conceptually draw linkages between the different aspects of the estuary have not kept up with the amount of available data from these programs. In this paper we use similar techniques to Fourqurean et al (2003), Caccia and Boyer (2005) and Herbert et al (2011) to analyze independently collected data sets in Biscayne Bay. The monitoring program largely responsible for generating the water quality data sets from those publications also collected data in our area of interest and thus we used their raw data used for our analysis. We also extensively sampled the benthic habitats in Biscayne Bay and foliar and sediment biogeochemistry to determine the relationships between biotic and abiotic aspects of the system. Our approach relies on similar assumptions made by previous publications (Brand et al. 1991; Fourqurean, Powell, et al. 1992; Boyer and Meeder 2001; Fourqurean et al. 2001; Fourqurean et al. 2003; Lirman and Cropper Jr. 2003; Caccia and Boyer 2005; Herbert et al. 2011; Burkholder et al. 2013) about the relationship between nutrient distribution in the benthos and water column and primary producer distribution.

While there are many similarities between Biscayne Bay and Florida Bay in terms of influential factors, there are also a number of important differences. Both systems are influenced somewhat by a managed freshwater supply, an increase in which can have consequences for primary producer communities near the shoreline (Fourqurean et al. 2003; Lirman and Cropper Jr. 2003). This freshwater supply can bring with it nutrients from terrestrial runoff (Caccia and Boyer 2007). The volume of freshwater entering Biscayne Bay however is substantially lower however since it is mostly delivered through a few canals in the southwestern part of the Bay versus the large sloughs that serve Florida Bay. Near Black Point on the southwestern coast of Biscayne Bay, there is a landfill that is responsible for large nitrogen fluxes in that area and into the Bay (Caccia and Boyer 2007).

In this manuscript, we were interested in understanding how different primary producers assembled across spatial scales in Biscayne Bay, and how those assemblages may be related to nutrient distribution in the water column, and sediment. We describe here in detail the primary producer distribution, its relationship to foliar nutrient concentration and discuss its implications for the ecosystem services that they can provide. We build on previous models that established relationships between nutrient fluxes and primary production in coastal ecosystems, and assume that continued delivery of freshwater to Biscayne might produce similar effects. To determine the potential nature of these effects, we use a combination of both data sets to discuss ecological patterns and predict habitat types in Biscayne Bay that can have implications for future conservation and restoration efforts.

Methods

Location

Our study does not cover the entire Biscayne Bay area for logistical reasons. We focused both our sampling and analysis on southern Biscayne Bay (study area henceforth will be referred to as Biscayne Bay) which is the area between the Port of Miami and Turkey Point (Figure 1). To the west of the Port of Miami is the downtown area of Miami, Florida. Along the shoreline south of downtown is high-rise condominiums, private residences and hotels with a few mangrove communities interspersed. The shoreline is less developed the further south one travels from downtown Miami. Just north of the Biscayne National Park headquarters lies a landfill in which non-recyclable waste from Miami-Dade County is placed. This landfill is located about 500 meters from the shoreline and previous studies have identified this location as a possible point source of organic nutrients into the Biscayne Bay estuary. Southern Biscayne Bay is a seagrass-dominated system with mostly saline conditions (Lirman and Cropper Jr. 2003). Federal regulations prohibit fisheries of any kind within Southern Biscayne Bay, but the Bay supports a number of recreational activities including SCUBA diving, kayaking, snorkeling and beach activities (Stynes and Sun 2003).

Distribution of benthic habitat types

We used a randomization tool in ArcGIS® to choose 190 sampling sites across our study area. Southern Biscayne Bay was divided into 'banks' and 'open water' sites. Banks were considered the shallower sites (<1 m deep) and all of the other sites were labeled open water. Using existing bathymetric surveys, we calculated the percentage of the Bay that fell under each category and randomly chose our sampling sites based on that ratio. In addition, we added 10 sites that were part of an existing long-term monitoring program through the Miami-Dade County Department of Environmental Resource Management (DERM). At each site two divers on SCUBA swam a 50m transect north of the GPS coordinate associated with the particular site. Using a free randomizing program (www.randomizer.org), we chose 10 locations along each transect to survey for primary producer species composition and abundance. At each location on the transect we placed a ¼ meter-squared quadrat immediately to the right of the transect tape and used a modified Braun Blanquet technique (Fourqurean et al. 2001;Fourqurean et al. 2002) to determine abundance of each identifiable primary producer species found within the quadrat. In this technique a score from 0 to 5 is used as a categorical variable representing a percentage range of coverage. A score of 0 = absent, 0.5 = sparse, 1 = 0-5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75% and 5 = 75-100%. We used these scores to determine average abundance for each species at the different sites. At each site we removed a small number of shoots of the available seagrasses for lab processing of nitrogen and phosphorus. The number of shoots removed for each species was determined by the amount of biomass needed to detect the nutrient content (3 *T. testudinum*, 20 *S. filiforme*, and 40 *H. wrightii*). We also used 1 cm diameter core tubes made out of modified 10mL syringes to remove 3 cubic centimeters of surface sediment also for processing of nitrogen and phosphorus. A kriging function (spherical variogram with no nugget) in ArcGIS® was used to visualize species distribution and abundance for the entire southern Biscayne Bay region.

Nutrient analysis

We used dried samples of seagrass tissue and sediment to determine total nitrogen and phosphorus content. Phosphorus content was determined using an acid hydrolysis technique followed by a colorometric reaction (Fourqurean et al. 1992). Total nitrogen was determined using a CHN analyzer (FISONS 1500) which determines nitrogen and carbon content via a combustion technique.

Water Quality

We used data from a water quality monitoring program run by the Southeast Environmental Research Center (SERC) at FIU (Caccia and Boyer 2005) that collected data between 1993 and 2009. Sampling of the seagrass community and the sediment took place in the summer of 2010. The water quality program measured dissolved oxygen (DO), nitrate (NO_3^-), nitrite (NO_2^-), ammonia (NH_4^+), turbidity, total organic nitrogen (TON), total phosphorus (TP), chlorophyll – *a* concentration (Chl–*a*), salinity, temperature, soluble reactive phosphorus (SRP), alkaline phosphatase activity (APA) and total organic carbon (TOC). A description of the collection and analysis techniques of these variables can be found in Boyer et al. (1999). We calculated Z scores with the long-term dataset for each variable to standardize the mean and the range of each of the parameters. Since water quality samples were taken from sites that were different to the sites from which seagrasses and sediments were sampled, we determined fields of means using kriging in ArcGIS® for each parameter across the sampling area. We then used a point extraction procedure (also in ArcGIS®) to estimate the values for our sites.

Statistical procedures

A k-means clustering algorithm was used to group the sites according to vegetation similarity. The number of clusters chosen was somewhat arbitrary, but further divisions led to extremely small groups with extremely low numbers or the combination of ecologically distinct groups. In the clustering process, each site represented an individual replicate of a particular vegetation subgroup. Our approach follows similar procedures used to classify primary producer groups within estuarine habitats based on abundances (Moore et al. 2000; Fourqurean et al. 2003). Principal components analysis (PCA) was used to identify groups of variables from the water quality dataset that correlated with one another. Like Caccia and Boyer (2005), we used this approach to identify groups of correlating water quality variables. Our PCA analysis here utilizes the same approach on the same dataset, except our analysis incorporates 4 years of data collected after Caccia and Boyer's (2005) analysis. We used a Hierarchical Discriminant Function Analysis (HDFA) to predict benthic habitat type (according to our cluster analysis) using water quality variables. We added variables into our HDFA in an order that in our estimation represented management concerns in this area. First, we entered the means and coefficients of variation (CV) for salinity, followed by light saturation percentage. We then followed this by adding variables from the PCA that was highly correlated with each component. The choice of the proxy variable was also guided by the management concerns. Each step was cross-validated using a jackknifed approach and the value of adding subsequent predictors was assessed using Wilk's lambda. We then attempted to predict the potential change in habitat type by adding half mean salinity, double CV and the proxy variables from the PCA to the final discriminant model. Using these variables was meant to simulate the potential changes that might occur if the magnitude of freshwater entering Biscayne Bay substantially increases.

Results

Primary producer abundance

Southern Biscayne Bay was dominated by the seagrass *Thalassia testudinum* (Figure 2). Most of the sampled sites contained dense patches (coverage greater than 50%) of this species. Other than *T. testudinum* we found three other species of seagrasses. *Halodule wrightii* was mostly prevalent nearer the shoreline to the center of the Bay (Figure 3).

Syringodium filiforme was found on sites east of the islands (Virginia Key, Key Biscayne, Boca Chita and Elliott Key) and in the northern sites near downtown Miami (Figure 2). Two of our sites also contained the rare *Halophila engelmanii*. Both sites were characterized by low water column visibility and high turbidity. Macroalgae abundance was mostly sparse and varied. The macroalgal groups that were most abundant were calcareous green *Halimeda* sp., *Penicillus* sp., and *Udotea* sp. *Laurencia* sp. and *Batophora oerstedii* were also fairly ubiquitous throughout the Bay, but sparse in their coverage. Our cluster analysis revealed 8 distinct communities of primary producers (Table 3). These communities were named based on the primary producer species that was abundant in the cluster according to its Braun Blanquet average score. The most prevalent were monospecific beds of *T.testudinum* found at 47 of our sites. These sites had coverage of *T. testudinum* between 50 and 75% and were located mostly to the northern and north-central areas of our study area (Figure 3). Sparse mixed species beds (36 sites) were the second most prevalent. Most of these sites were located in the south central and southeastern areas of the Bay (Figure 3). Sparse mixed species sites were characterized by low coverages of *T. testudinum*, *S. filiforme* and *H. wrightii* and macroalgal groups *Halimeda* sp., *Penicillus* sp., *Udotea* sp., *Laurencia* sp. and *Batophera* sp. The southwestern portion of the Bay contained a number of *T. testudinum* and *B. oerstdata* sites (Figure 3). In these sites both species had about 25-50% coverage on average. Relatively dense beds of *T. testudinum* and *S. filiforme* (24) were mostly found to the east of the Keys nearer the coral reef tract (Figure 5). No sites containing *S. filiforme* were found to the west of the islands south of Virginia Key. The fifth primary producer group was *T. testudinum* with sparse algae (21 sites). These sites were spread out throughout the sampling area and showed no coherent spatial pattern (Figure 3). These sites were characterized by *T. testudinum* abundance of about 25% with sparse abundance (BB score = 0.5) of the macroalgal species. There were 16 sites that were dense *T. testudinum* and *Laurencia* sp. beds. These beds had *T. testudinum* and *Laurencia* sp. BB scores around 4. A few beds were categorized based on a sparse mixture of only calcareous green algal species (*Halimeda* sp., *Udotea* sp., *Penicillus* sp.). Only 6 sites fell under this classification. Lastly, a few sites were densely populated with (25-50%) *H. wrightii*. Most of these sites were near the shoreline to the southwestern part of the Bay (Figure 3).

Seagrasses and nutrients

Concentrations of nitrogen and phosphorus followed different patterns in the sediment compared to the seagrass tissue (Figure 4 and 5). Due to its ubiquitous nature, we only used *T. testudinum* to investigate foliar nutrient concentrations throughout Biscayne Bay. Total nitrogen concentration was highest nearer the shoreline especially near the Black Point area. The concentration of nitrogen appeared to decrease eastward. Phosphorus concentration followed an opposite pattern (Figure 4 and 5). Higher concentrations of phosphorus in both the sediment and *T. testudinum* tissue were higher to the northern part of our sampling area and to the east of the keys.

The distribution of *Thalassia testudinum* (the dominant primary producer in the Bay) correlated strongly with water quality variables but not sediment nutrients. Neither sediment percent nitrogen (Pearson r = 0.083, p>0.05) nor sediment phosphorus (Pearson r = 0.053, p>0.05) correlated with *T. testudinum* distribution. *T. testudinum* distribution increased as salinity increased (Pearson r = 0.186, p<0.05) but decreased as water column ammonia (Pearson r = -0.307, p<0.05 and Pearson r = -0.18, p<0.05) and nitrate concentrations increased. *Thalassia testudinum* distribution also was greater in areas where its foliar tissue had higher concentrations of total percent phosphorus (Pearson r = 0.304, p<0.05) and nitrogen (Pearson r = 0.248, p<0.05). *Halodule wrightii* population was also more abundant where water column ammonia was more concentrated.

Water Quality

Water quality parameters ranged in value due the large spatiotemporal scales of the dataset. Some of the mean values we report (Table 1) are very similar to those reported in the previous publication on the first 14 years of this dataset (Caccia and Boyer 2005). Average water temperature was 26.0°C. Average salinity was 27.6. Average dissolved oxygen percentage was 6.2% and turbidity overall was fair at 4.4 nephelometric turbidity units. DIN occupied a slightly larger fraction of the TN pool (9.8%) than was reported 8 years ago (Caccia and Boyer 2005). As in the earlier anlaysis, DIN concentrations were driven mainly by nitrate (32.6%) and ammonia (61.8%). Chl-*a* concentrations averaged 2.5 µg/l. SRP comprised about 17.1% of the TP pool (Table 1).

The correlational structure among water quality variables allowed us to simplify the dimensionality of the dataset by defining 5 composite variables with eigenvalues greater than 1 that described 90% of the variation in the original data set (Table 2). The first component explained 24.8% of the variation and was strongly positively correlated with NO_2^-, NH_4^+, turbidity, Chl-*a*, temperature and TN:TP ratios. We believe that this correlation speaks to the strong role that DIN and temperature plays in driving phytoplankton blooms. PC_I also strongly negatively correlated with TP, salinity and SRP. This relationship probably represents the coastal area's tendency toward nitrogen limitation and the role that freshwater plays in the structure of the nearshore primary producer communities. PC_{II} was strongly correlated to NO_3^-, TON, temperature, DO, percent saturation of light and APA and overall explained 19.7% of the total variation. In our analysis, this component was also negatively correlated to NH_4^+. PC_{III} explained 16.8% of the total variation was mostly associated seemingly with the role that NO_3^- and SRP play in driving Chl-*a* concentrations. The correlations in this component were not as strong as in the first two components. PC_{IV} (15.5%) was considered to be the 'organic carbon' component owing to the strong negative relationship this component had with only organic carbon. PC_{IV} also had a positive correlation with temperature. This relationship may speak to the abundance of labile organic matter in the system (unpublished results), and the role that temperature may play in liberating it. PC_V

(13.6%) was correlated with DIN:TP ratios owing to the probability that the southwestern parts of the system are nitrogen-limited.

Discriminant Function Analysis

When entered by itself, mean salinity correctly classified 19.3% of all cases (Table 4, Wilk's lambda = 0.853, $p<0.001$). Adding salinity CV resulted in a significant increase in correct case classification to 29.9% (Table 4, Wilk's lambda = 0.814, $p<0.001$). When the remaining proxy variables were entered, case classification significantly improved to 37% (Table 4, Wilk's lambda = 0.491), better than the 12.5% classification that would have occurred by chance. The addition of NO_3^-, DO and TOC variability did not increase the predictive power of our model. The strength of classification of different clusters was inconsistent within our HDFA model (Table 5). Our HDFA was particularly good at predicting *T. testudinum* and *B. oerstdata* (Cluster 1) communities (72.4%) but was very poor at classifying *T. testudinum* and sparse mixed algal species (Cluster 7) communities. Most of the other communities had a classification accuracy of between 33 and 40%. Cluster 1 was primarily restricted to the southwestern edge of the bay (Figure 8). Beds containing sparse distributions of all seagrass and macroalgal species (Cluster 2) as well as *H. wrightii* beds (Cluster 4) were mainly found in the northern and northeastern edges of the sampling area (Figure 8 and 10). Monotypic dense *T. testudinum* stands (Cluster 3) as well as *T. testudinum* with *Laurencia* sp. stands (Cluster 8) were mostly located in the central portions of the Bay. *Syringodium filiforme* with *T. testudinum* (Cluster 6) were restricted mostly to the areas east of the islands which is consistent with the salinity range for *S. filiforme*. Reducing mean salinity by half, doubling salinity CV and doubling NO_3^- resulted in slight changes to habitat distribution. *Thalassia testudinum* and *S. filiforme* beds (Cluster 6) moved slightly eastward and dense patches of *T. testudinum* beds (Cluster 3) moved slightly northward (Figure 11). Both changes are due to the hypothetical consequences associated with a more freshwater system. Our model also predicted a reduction in the sparse, mixed species bed (Cluster 2) beds that were located near downtown Miami (Figure 12).

Discussion

Our surveys show that the benthic community in southern Biscayne Bay is largely seagrass-dominated. *Thalassia testudinum* is overall the most dominant seagrass species with ranges that span from the coral reef tract outside the Bay to the coastal areas. At some coastal sites *H. wrightii* are more dominant. This seems to be largely driven by the reduced salinity due to the freshwater input from the canals (Lirman and Cropper Jr. 2003), and also possibly due to the high concentrations of nitrogen found in the water column and sediment on the southwestern shoreline (Figure 4 and 7).*Thalassia testudinum* correlated significantly only with nitrogen concentrations in the water column and not with the distribution of total nitrogen in the sediment. Phosphorus concentrations were higher in the sediment in the northern portion of our study area and east of the Keys (Figure 8). Seagrass TN:TP ratios within the Bay (Figure 6) suggested that, like other carbonate-based estuaries, Biscayne Bay might overall be phosphorus-limited (Powell et al. 1989; Fourqurean et al. 1992). Other studies documenting the relative abundance of refractory nitrogen suggest that not all of this nitrogen is available for primary producers (Boyer et al. 2003).

Chemical analysis of the *T. testudinum* leaves show a variable pattern of nutrient limitation (Fourqurean et al. 1992; Ferdie and Fourqurean 2004) in Biscayne Bay. *Thalassia testudinum* N:P ratios indicate potential phosphorus limitation in the northwest, central and southern parts of the Bay (Figure 6). To the southwest and northeast regions of the Bay N:P ratios of this seagrass suggest light or nitrogen limitation. Macroalgae show varied abundance patterns throughout the study area. This may be an indication that there are other variables affecting the distribution of this group.

Our PCA identified relationships similar to those found in Caccia and Boyer (2005). Our analysis identified positive correlations between Chl-*a* abundance and total nitrogen probably due to the role these nutrients play in phytoplankton blooms (Gilbert et al. 2004). Strong correlations between TOC and temperature are also probably emblematic of the increased organic matter production that typically takes place during the summer time (Roman et al. 1983). Our analyses also suggest that it is the water column nutrients, and not the sediment nutrients, that drive *T. testudinum* distribution in the Bay. The correlations of water quality variables and primary producer community distribution were strong enough to suggest that these variables can fairly accurately predict habitat type. We did not measure sediment depth or sediment type however, two very important factors that affect the ability of seagrasses to take root and proliferate (Fourqurean et al. 1992). This omission may have affected the accuracy of our prediction model. In areas with little to no sediment, macroalgal species can dominate the primary producer community due to their ability to attach to hard substrates (Taylor and Wilson 2003). This may partially explain the difference in the predictive power between our model (37%) and the model from Fourqurean (2003) (56.7%). Despite this difference however, our model did fairly well at predicting the presence of various primary producer communities. The model performed more poorly with communities that had significant macroalgal abundances. This corroborates our findings from our seagrass-nutrient correlation analysis, and is indicative that there may be other factors affecting the distribution of macroalgal groups not captured in our model.

Previous studies have identified numerous point sources of nitrogen in this area that can have consequences for primary production along the coastline (Caccia and Boyer 2007). These nutrient inputs, along with increased freshwater flows and temperature also probably determine the availability and abundance of organic matter. The freshwater input into the Bay causes a pronounced drop in salinity in the nearshore area (Lirman and Cropper Jr. 2003; Caccia and Boyer 2005), but this effect disappears within a few hundred meters of the shoreline. Some areas nearer the coastline though have some of the densest *H. wrightii* beds, a reality that is consistent with its greater tolerance for these low saline levels (Lirman and Cropper Jr. 2003).

Southern Biscayne Bay has many ecological similarities to its subtropical neighbor Florida Bay. The proximity of these two systems to each other as well as their relatively important roles in the south Florida economy makes an ecological comparison relevant here. Both systems are affected in various ways by the Comprehensive Everglades Restoration Plan (CERP) that seeks to alter the delivery and timing of freshwater to the system (McLean et al. 2002). Increased delivery can result in changes to the primary producer community in the nearshore area. Seagrass beds are the dominant primary producer community and *T. testudinum* is the main seagrass species present. The distribution of *S. filiforme* and *H. wrightii* follows a spatial pattern that seems tied to the salinity gradients within both systems. Studies have shown Florida Bay to be a phosphorus-limited system (Powell et al. 1989; Fourqurean et al. 1992). This limitation has a spatial component, and is more pronounced in the interior portions of the Bay. One study has shown a similar effect in Biscayne Bay (Irlandi et al. 2004), on a small scale. Our data set here indicates that large parts of Biscayne Bay are phosphorus-limited, with pockets of nitrogen limitation to the southwest and northeast. This result adds to a body of literature demonstrating phosphorus limitation in similar estuaries (Fourqureanet al. 1992; Ferdie and Fourqurean 2004).

Biscayne Bay is of variable salinity (Table 1), and one can infer that this is largely due to the semi-enclosed nature of Florida Bay. Blocked only by 5 islands to the east, Biscayne Bay enjoys a fairly open exchange of water with the Atlantic Ocean, but also receives significant freshwater input from SFWMD canals. The salinity gradient certainly has influence on the primary producer communities within the Bay (Lirman and Cropper Jr. 2003).

While our study highlights the importance of understanding nutrient dynamics to predict primary producer ecosystem effects, we note that a full understanding is incomplete without considering top-down effects (Heck and Valentine 2007). A few recent studies have begun to highlight the role of herbivory in shaping community structure in this area (Bourque and Fourqurean 2013). It is unclear the role that herbivores may play in mitigating the effects of nutrient enrichment in different parts of the Bay. Also lacking are long-term datasets on primary producer abundance in Biscayne Bay. Our sampling took place over a single summer, and as a result we were unable to capture some of the temporal effects on these communities brought on by season.

Long-term ecological monitoring programs provide data that, when interpreted appropriately can help scientists and managers understand and predict ecological patterns in large ecosystems (Fourqurean et al. 2003). This ability can then assist managers in framing proper responses to sudden changes in ecological inputs. Ecosystems like Biscayne Bay are especially prone to these types of changes due to its proximity to the metropolis of the city of Miami. Exacerbating this relationship even further, is the fact that the economy of the greater Miami area is strongly dependent on the ecosystem services that Biscayne Bay provides (Leynes and Cullison 1998; Hazen and Sawyers Environmental Engineers and Scientists 2005). For this reason, it is very important that local managers understand how the nature of these services might change if there is substantive change in the primary producer community. There are many simultaneous efforts toward this end. Biscayne National Park, commissioned in 1978, has an active law enforcement arm that prosecutes vessel grounders and levies fines which is then used toward seagrass restoration. The Department of Environmental Resource Management (DERM), Water Quality Monitoring Network (no longer in operation) both had decadal programs monitoring various aspects of Biscayne Bay. What is missing from these efforts are analyses that draw meaningful conclusions about ecosystem behavior based on all of the data collected. Our analysis here, to the best of our knowledge, is the first to establish a direct connection between water quality dynamics and the distribution of seagrasses at the species level in this system.

Our work here also has more immediate practical relevance as well. Currently, seagrass restoration projects (funded primarily by fines levied on vessel grounders) are implemented using a combination of seagrass transplants and nutrient addition (either through manual application of fertilizer, or by the inducing of fecal matter addition from piscivorous birds using bird stakes). These approaches have had mixed results, partly due to a lack of information about the existing biogeochemistry of the benthos. The spatial component of nutrient limitation (nitrogen and/or phosphorus) in the Bay means that the choice of transplant species and nutrients added matters. Still unknown and relevant to this process is the role that top-down pressures play in shaping the primary producer community. We are currently analyzing a factorial manipulation experiment in Biscayne Bay specifically set up to answer that question.

As local managers continue to deliver on the specific objectives of CERP, and as Biscayne Bay continues to play a major role in the tourism economy of South Florida, the need for greater understanding of this estuary will grow. Recently, extensive documentation of seasonal *Anadyomene* sp. blooms have indicated that ecological phase shifts may already be taking place (Collado-Vides et al. 2013). These blooms have been documented in the same near coastline areas of high nitrogen concentration (Collado-Vides et al. 2013). The delivery of freshwater to the Bay has also increased recently as managers continue to slowly remove man-made impediments to the southward flow of freshwater over the Everglades (Smith 2013). We argue here that an understanding of the effects of the above processes, and any other inputs into the Bay is only possible if we can explain the ecological dynamics as they stand today. This is important not only for stakeholders of Biscayne Bay to gain an appreciation of its complex nature, but to enable managers to predict effects of existing and future impacts.

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Table 1. Average of Water Quality variables sampled between 1993 and 2007.

	Mean	**Median**	**Min**	**Max**	**1 SD**
Nitrate	1.04	0.38	BD	83.80	2.54
Nitrite	0.17	0.11	BD	9.94	0.26
Ammonia	1.97	0.93	BD	120.04	3.75
Turbidity	4.44	2.73	0.00	178.55	6.99
Total Organic Nitrogen	29.17	23.43	BD	311.04	20.49
Total Phosphorus	0.70	0.50	BD	8.80	0.61
Chlorophyll - *a*	2.48	1.47	BD	105.00	3.01
Salinity	27.61	32.00	0.00	63.00	11.30
Temperature	26.03	26.52	10.20	38.40	4.10
Dissolved Oxygen	6.24	6.28	0.30	24.40	1.37
Soluble Reactive Phosphorus	0.12	0.05	BD	5.32	0.23
Alkaline Phosphatase Activity	0.39	0.13	0.00	12.02	0.71
Total Organic Carbon	617.55	497.30	0.00	8712.50	437.03
Dissolved Inorganic Nitrogen	3.19	1.59	BD	120.47	5.08
Total Nitrogen	32.41	26.51	BD	314.88	21.71

Table 2. Principle Components Analysis of Water Quality Variables. Variables that vary significantly with components in bold for viewing ease.

	Component				
	1	2	3	4	5
Nitrate	-.306	**.516**	**.601**	-.033	.386
Nitrite	**.857**	.031	.328	.334	-.046
Ammonia	**.571**	**-.539**	.444	.287	.154
Turbidity	**.716**	-.092	**.586**	-.105	-.232
Total Organic Nitrogen	.451	**.822**	-.240	.030	-.088
Total Phosphorus	**-.816**	.061	.466	.131	-.107
Chlorophyll-*a*	**.609**	.378	**.503**	-.040	-.354
Salinity	**-.845**	-.191	.069	.436	-.069
Temperature	**.516**	**.539**	.009	**.526**	-.288
Dissolved Oxygen	.208	**.906**	.019	-.005	.259
Soluble Reactive Phosphorus	**-.567**	.237	**.503**	.400	.066
Alkaline Phosphatase Activity	-.330	**.776**	.268	-.174	.300
Total Organic Carbon	.405	.242	.202	**-.809**	.133
Total Nitrogen : Total Phosphorus	**.713**	.153	-.445	.278	.307
Dissolved Inorganic Nitrogen : Total Phosphorus	.437	-.261	.002	.385	**.596**

Table 3. We divided Biscayne Bay into 8 different clusters of primary producer communities. Tt=*T. testudinum*, Sf=*S. filiforme*, Hw=*H. wrightii*, CGH=Calcareous Green *Halimeda* sp., CGU=Calcareous Green *Udotea* sp., CGP=Calcareous Green *Penicillus* sp., Bato=*B. oersdata*, Lau=*Larencia* sp.

Cluster	**Group**	**# of sites**	**Tt**	**Sf**	**Hw**	**CGH**	**CGU**	**CGP**	**Bato**	**Lau**
1	*Thalassia* and *Batophora*	29	2.11	0.00	0.08	0.31	0.12	0.48	1.97	0.68
2	Sparse mixed-species bed	36	0.22	0.17	0.11	0.29	0.28	0.14	0.33	0.19
3	Dense *Thalassia*	47	4.34	0.14	0.12	0.59	0.05	0.35	0.22	0.34
4	*Halodule* bed	5	0.36	0.54	2.54	0.59	0.08	0.15	0.12	0.06
5	Calcareous green algae mixed bed	6	0.64	0.18	0.35	1.86	0.56	1.84	0.00	0.18
6	*Thalassia* and *Syringodium*	24	2.79	3.03	0.25	0.62	0.14	0.13	0.00	0.11
7	*Thalassia* and sparse algae	21	2.00	0.35	0.15	0.49	0.22	0.36	0.17	0.40
8	*Thalassia* and *Laurencia*	16	3.95	0.00	0.15	0.27	0.06	0.55	0.37	3.41

Table 4. Hierarchical Discriminant Function Analysis using different salinity metrics, mean light saturation and proxy variables from the PCA.

Step	**Variables entered**	**Cases classified correctly (%)**	**Wilk's lambda**	**p**
1	Mean salinity	19.3	0.853	<0.001
2	Salinity variability	29.3	0.814	<0.001
3	Mean Light saturation	37.0	0.491	<0.001
4	Mean NO_3^- Mean DO Mean TOC			
5	NO_3^- variability DO variability TOC variability	26.3	0.310	>0.05

Table 5. Percent classification accuracy of the discriminant function model. Cells indicate the percentage of the community type that will be supported given the habitat indicated in the column headers. Community types correspond to the communities identified by the cluster analysis explained in more detail in *Table 3.*

Actual benthic habitat	**Predicted benthic habitat type (%)**							
	Thalassia and *Batophora*	Sparse, mixed species bed	Dense *Thalassia*	*Halodule* bed	Calcareous green algae mixed bed	*Thalassia* and *Syringodium* bed	*Thalassia* and sparse mixed species bed	*Thalassia* and *Laurencia*
Thalassia* and *Batophora	72.4	0.0	0.0	0.0	3.4	0.0	3.4	20.7
Sparse, mixed species bed	16.7	36.1	8.3	11.1	2.8	22.2	0.0	2.8
Dense *Thalassia*	10.6	4.3	34.0	0.0	4.3	23.4	2.1	21.3
***Halodule* bed**	20.0	40.0	0.0	40.0	0.0	0.0	0	0.0
Calcareous green algae mixed bed	16.7	16.7	16.7	0.0	16.7	0.0	0	33.3
***Thalassia* and *Syringodium* bed**	0.0	16.7	25.0	8.3	16.7	33.3	0	0.0
***Thalassia* and sparse mixed algal bed**	33.3	9.5	9.5	0.0	4.8	14.3	4.8	23.8
Thalassia* and *Laurencia	25.0	0.0	31.3	0.0	0.0	6.3	0	37.5

Figure 1. Sampling area.

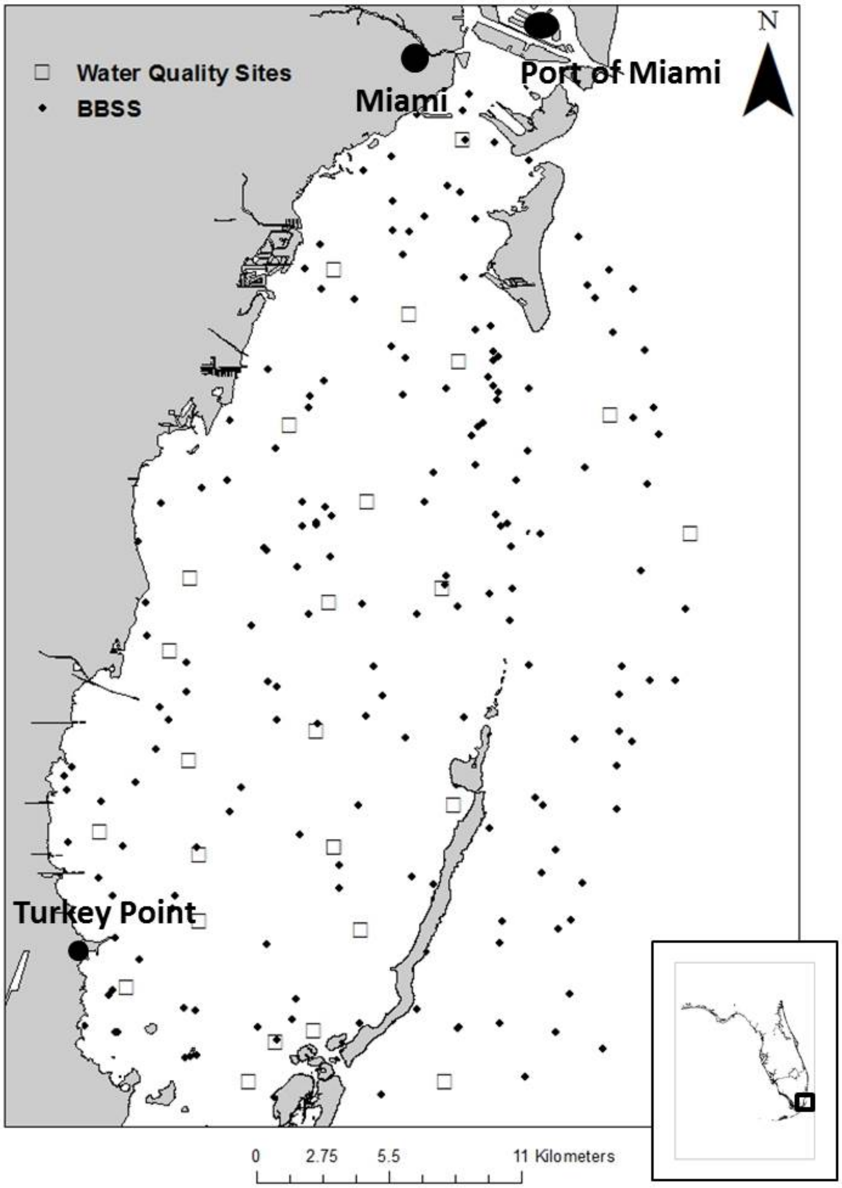


Figure 2. Species density of the three most common seagrasses in southern Biscayne Bay.

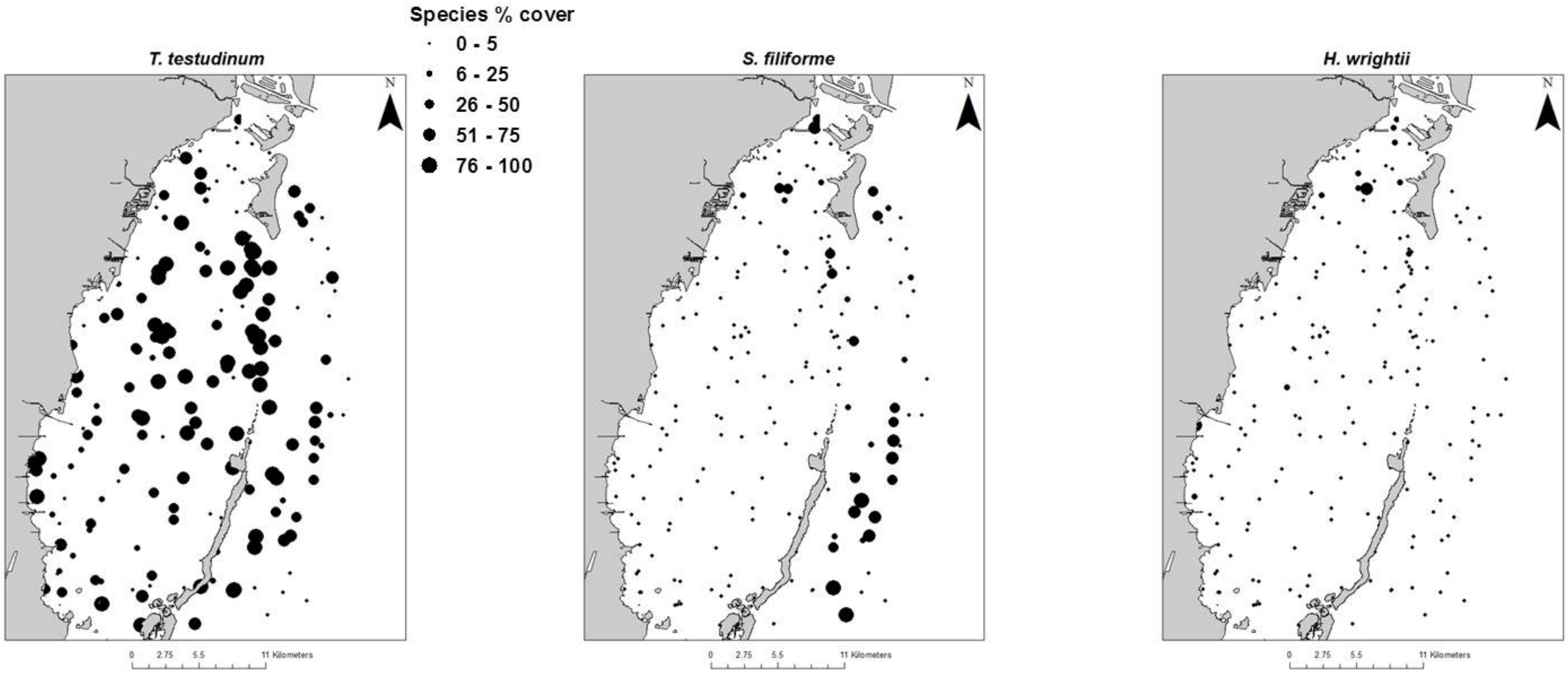


Figure 3. Location of different Clusters of primary producer communities. 1=*T. testudinum* and *B. oersdata*, 2=Sparse bed, 3=Dense *T. testudinum*, 4 = *H. wrightii*, 5=Calcareous green mixed bed, 6=*T. testudinum* and *S. filiforme*, 7=*T. testudinum* and sparse algae, 8=*T. testudinum* and *Laurencia* sp.

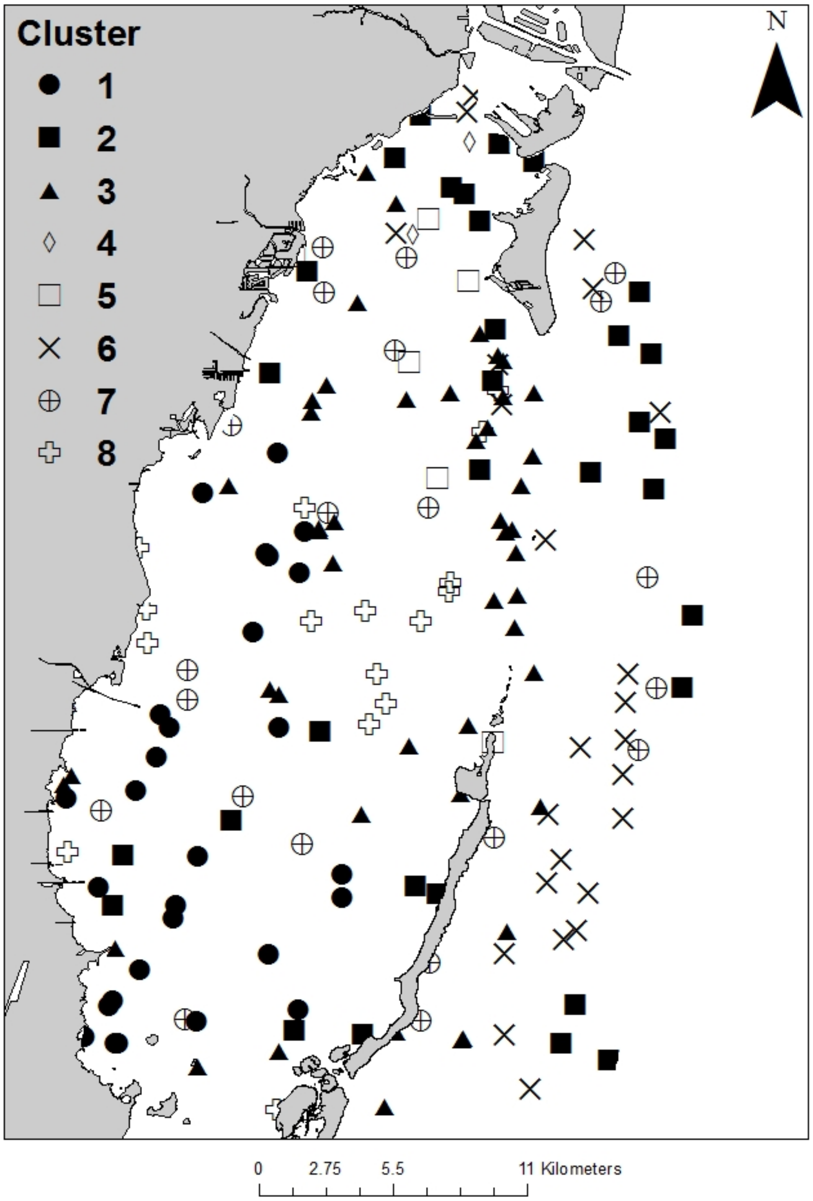
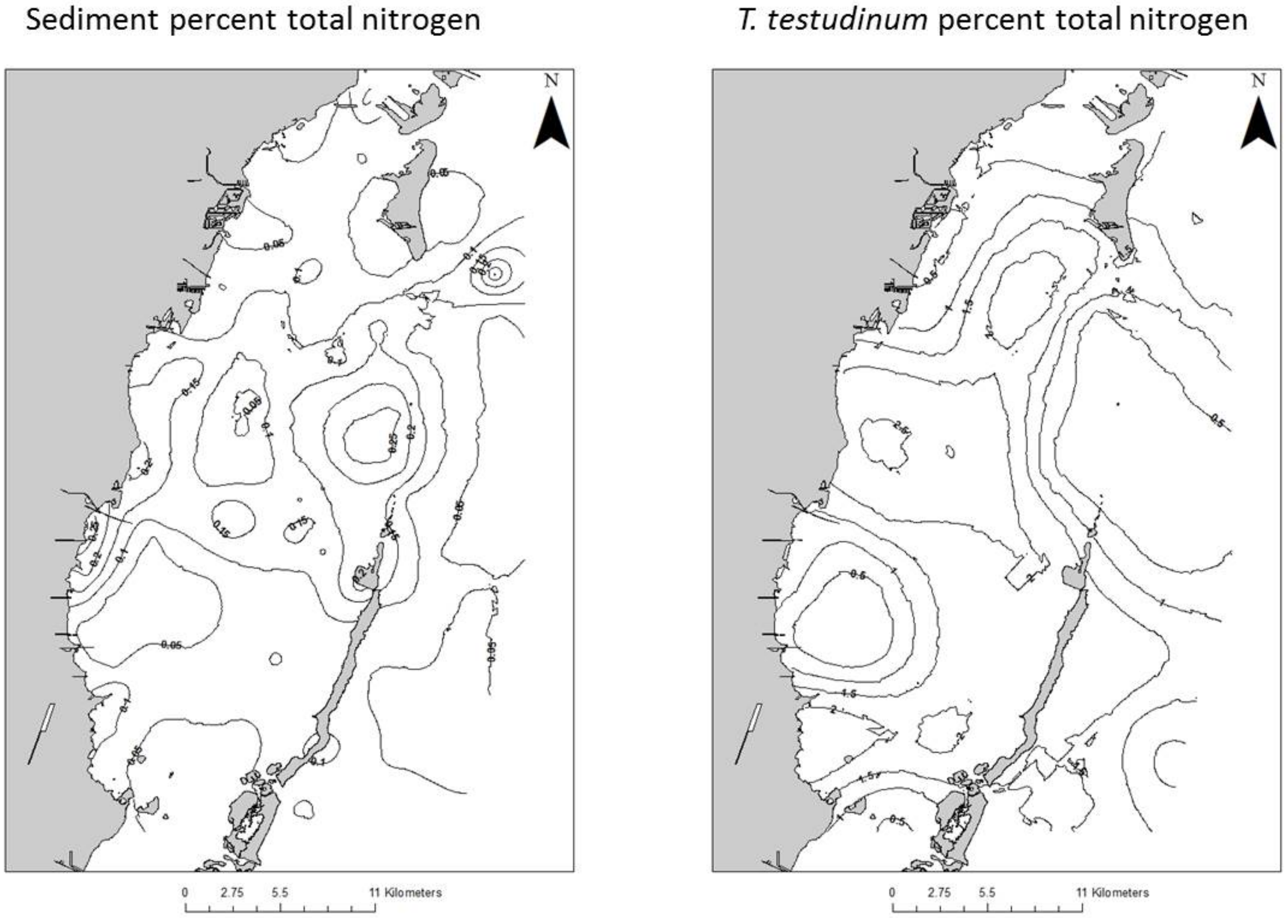


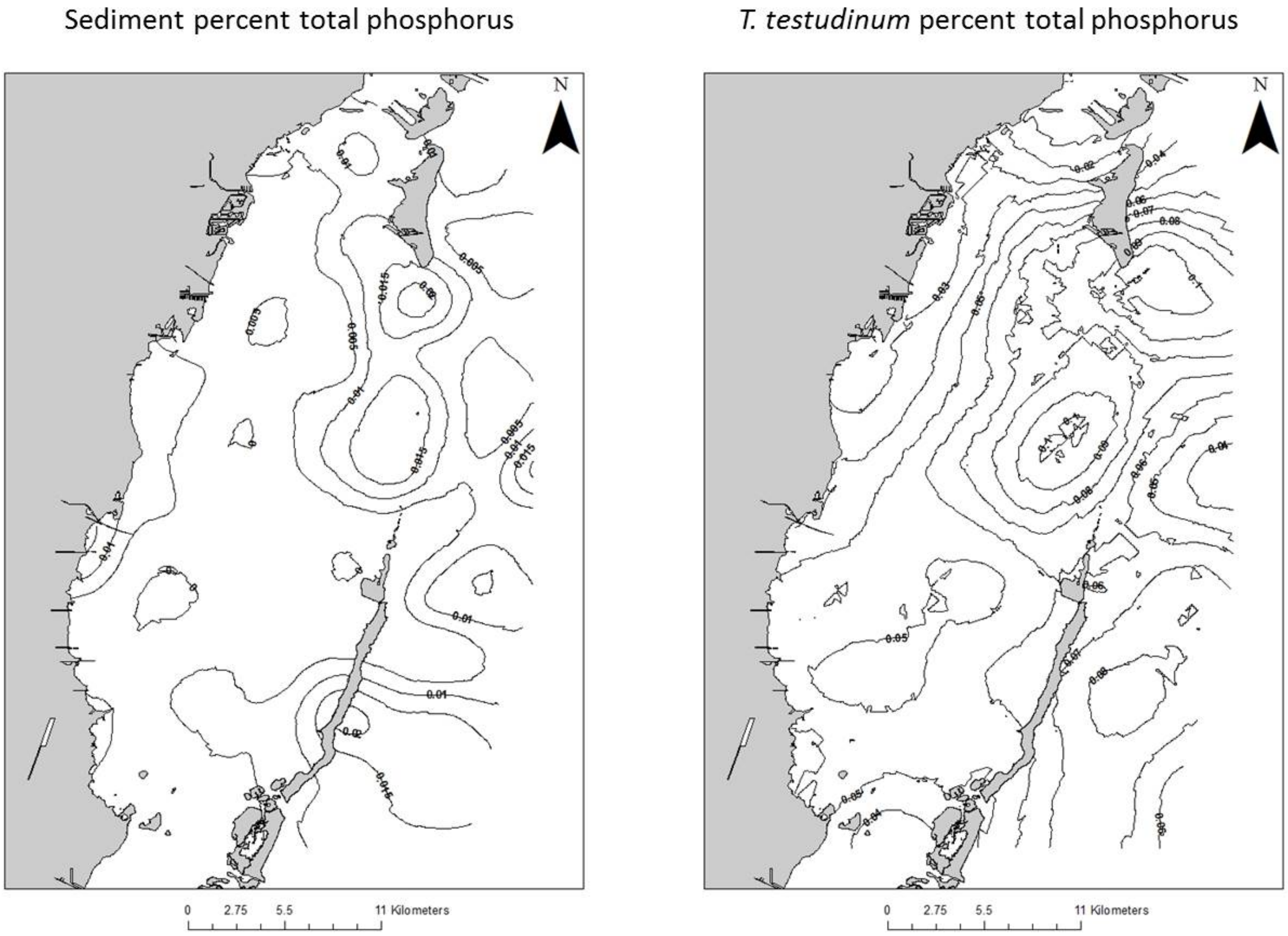
Figure 4. Total nitrogen in sediment and foliar tissue of *T. testudinum*.



Sediment percent total nitrogen

T. testudinum percent total nitrogen

Figure 5. Total percent phosphorus in sediment and the foliar tissue of *T. testudinum*


Sediment percent total phosphorus

T. testudinum percent total phosphorus

Figure 6. N:P ratios in the foliar tissue of *T. testudinum*

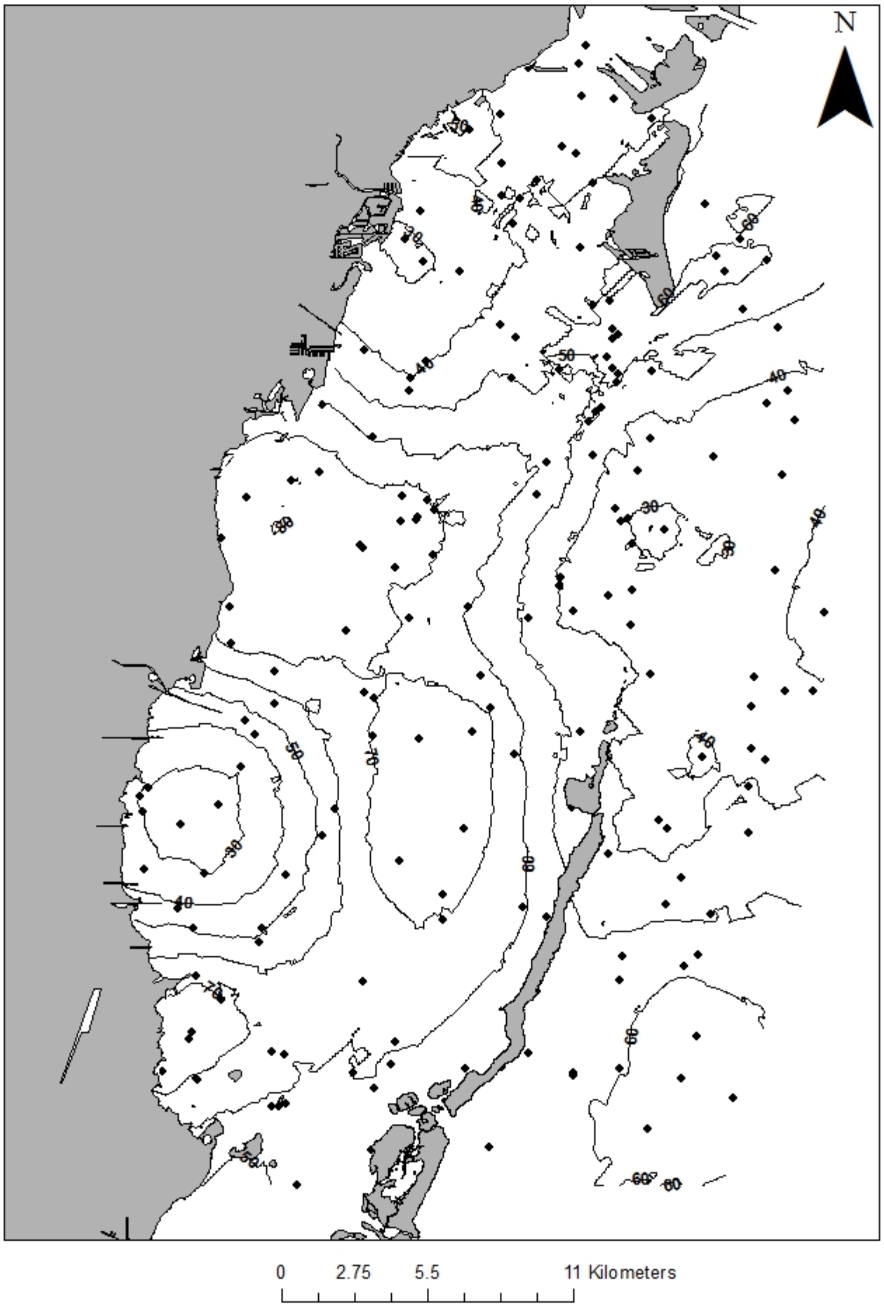


Figure 7. Spatial distribution of ammonia, nitrate and salinity in the water column of southern Biscayne Bay.

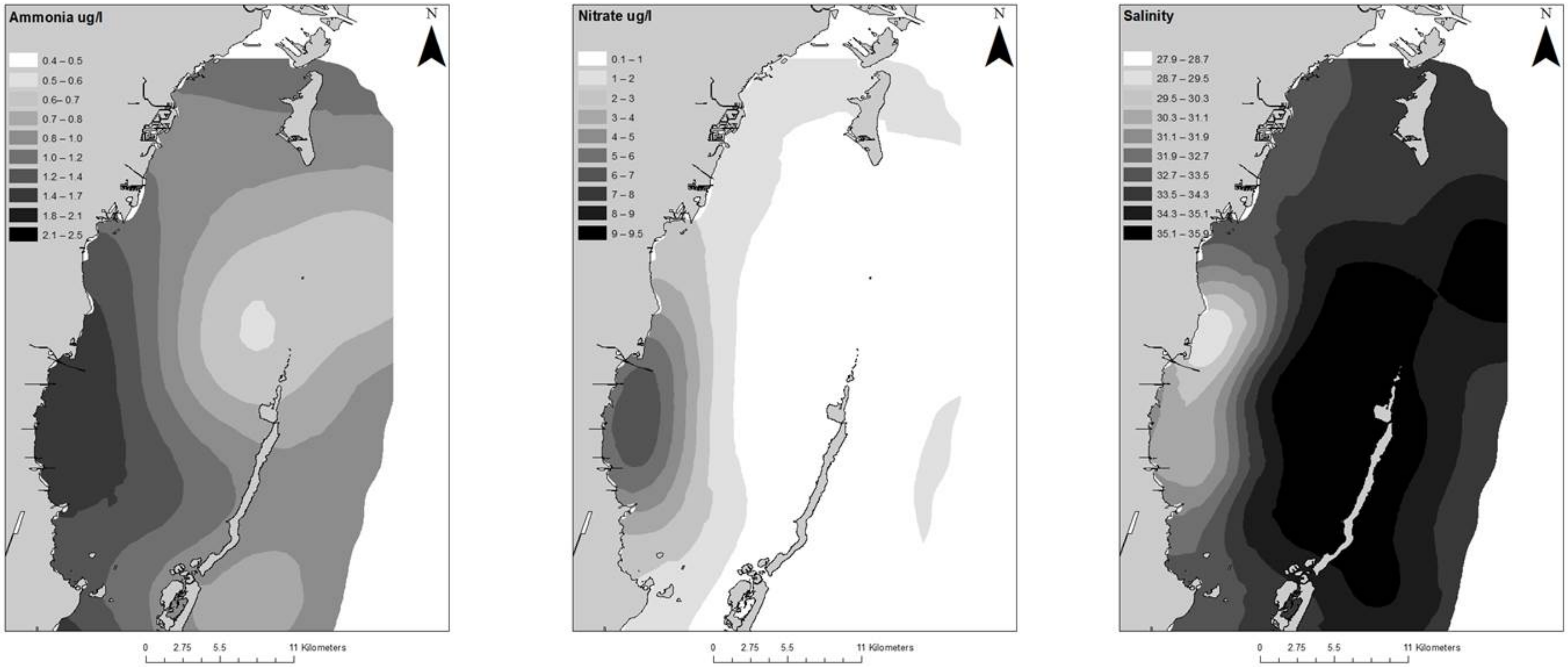
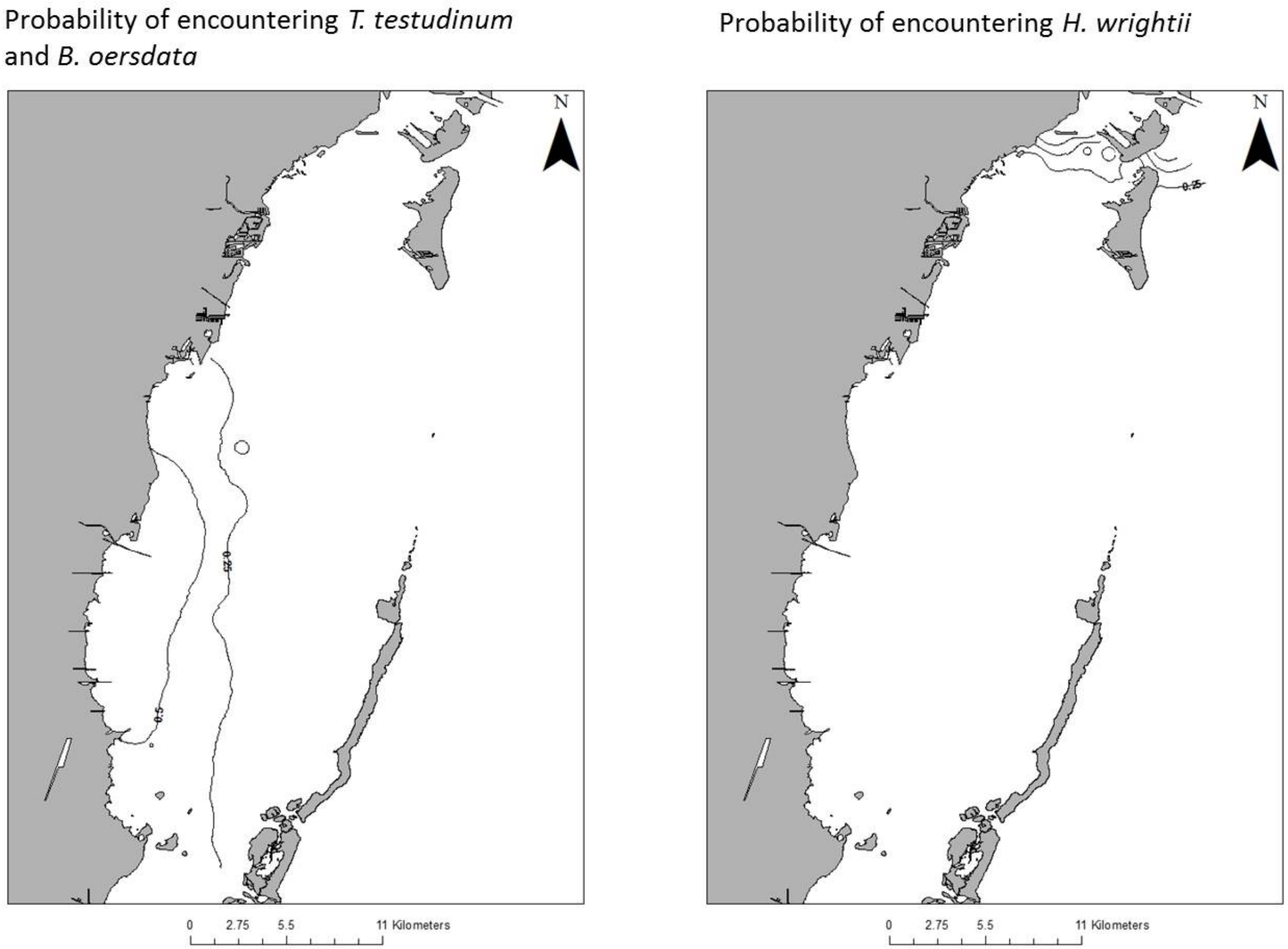
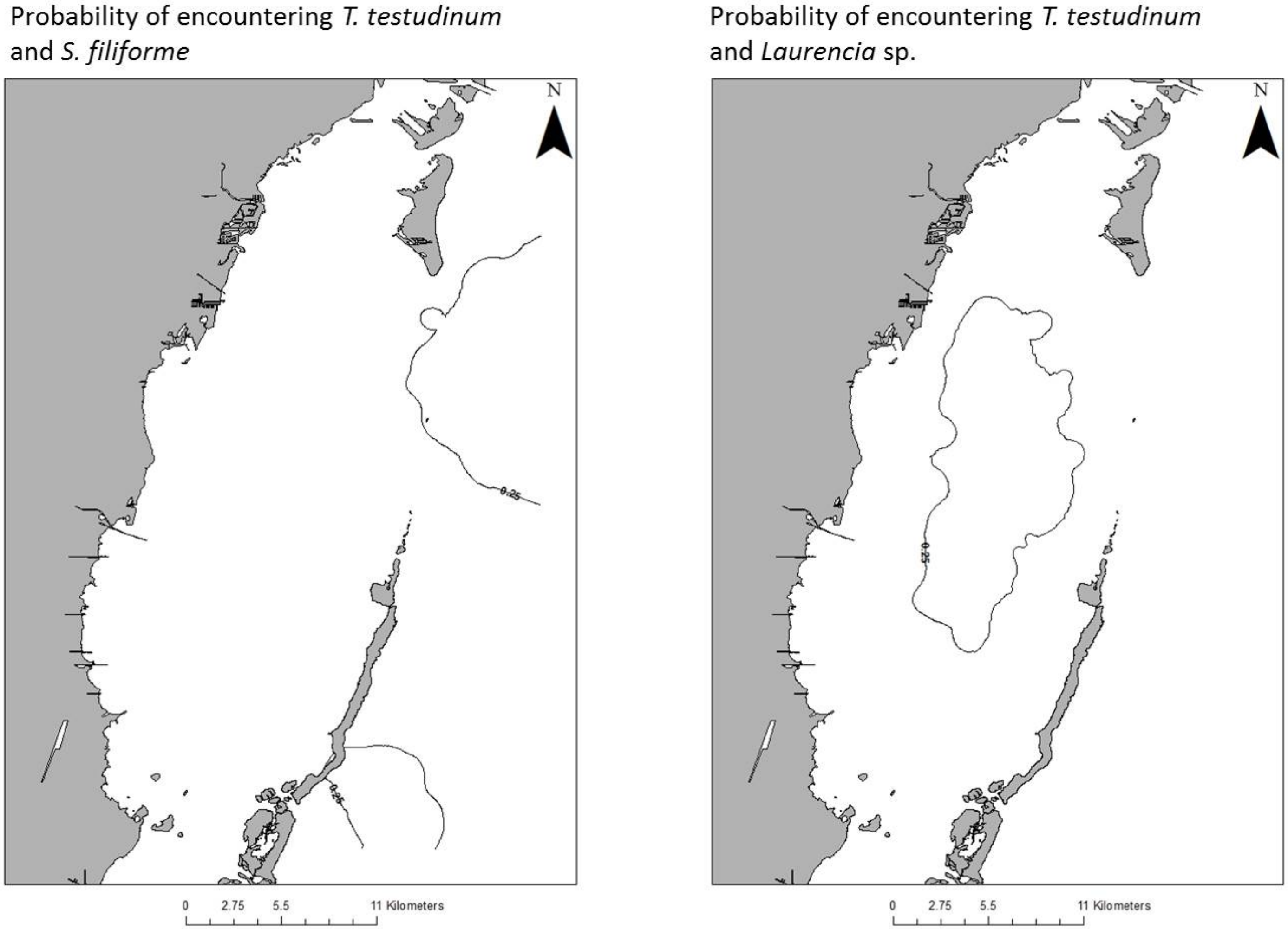


Figure 8. Probability of encountering species in Clusters 1 and 4.


Probability of encountering *T. testudinum* and *B. oersdata*

Probability of encountering *H. wrightii*

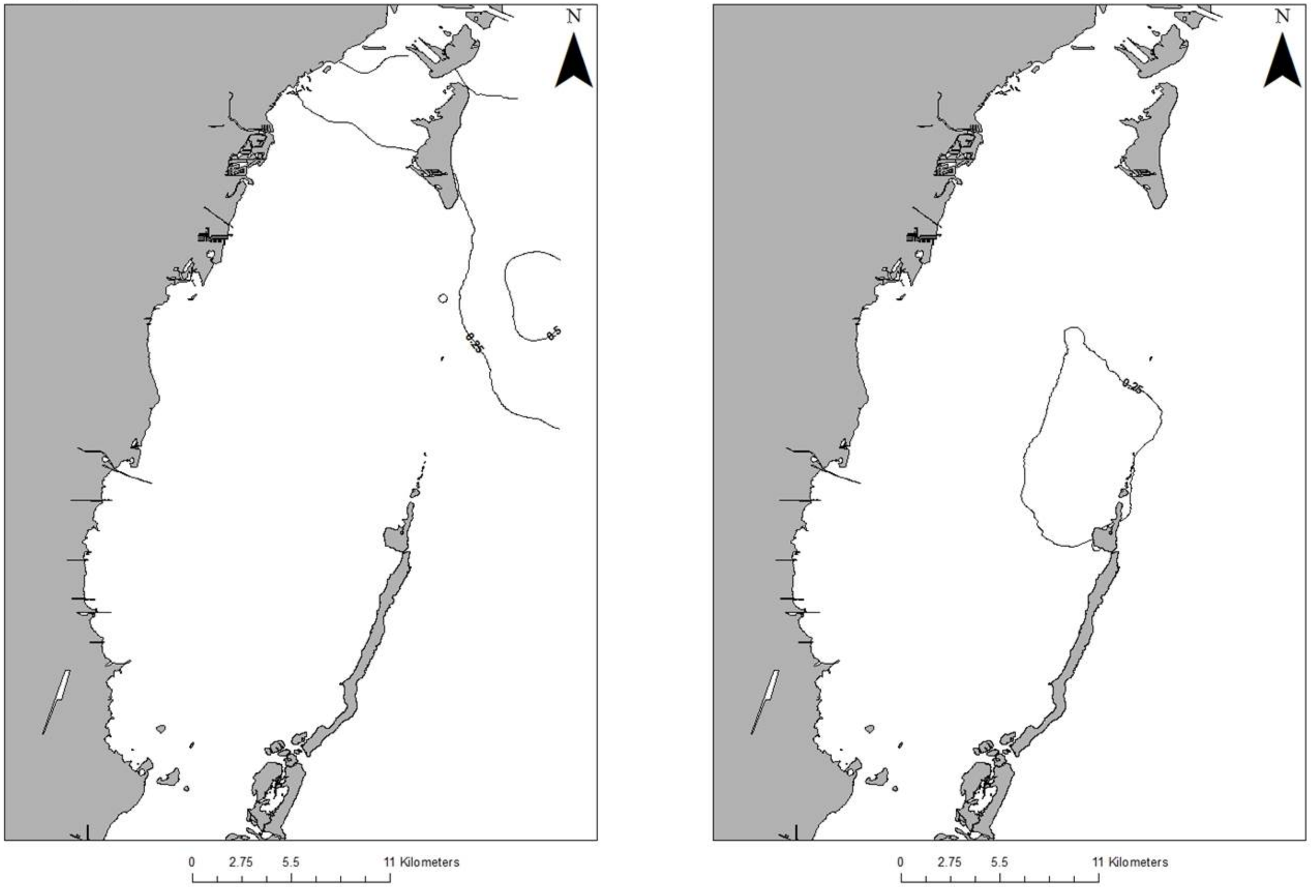
Figure 9. Probability of encountering Clusters 6 and 8.



Probability of encountering *T. testudinum* and *S. filiforme*

Probability of encountering *T. testudinum* and *Laurencia* sp.

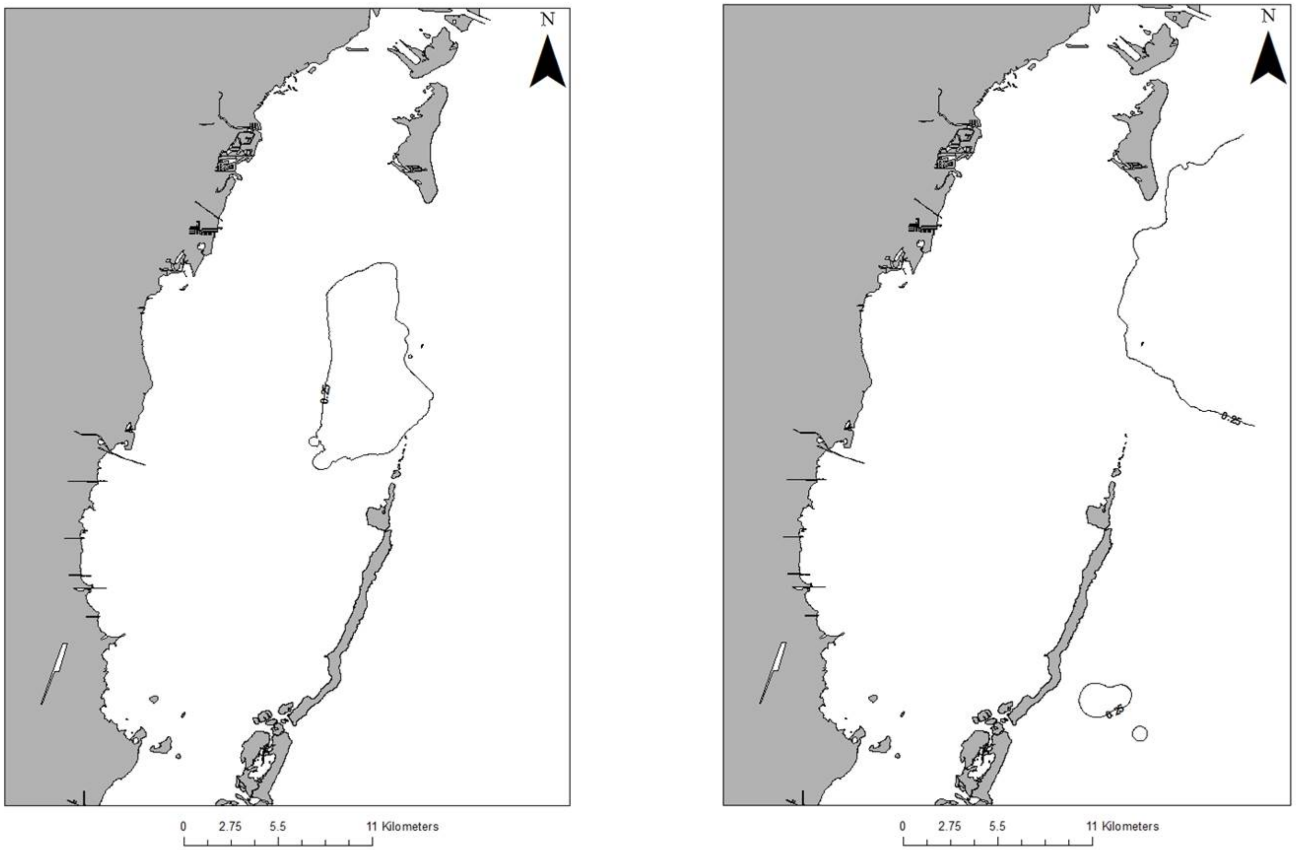
Figure 10. Probability of encountering Clusters 2 and 3



Probability of encountering sparse and mixed species bed

Probability of encountering dense *T. testudinum*

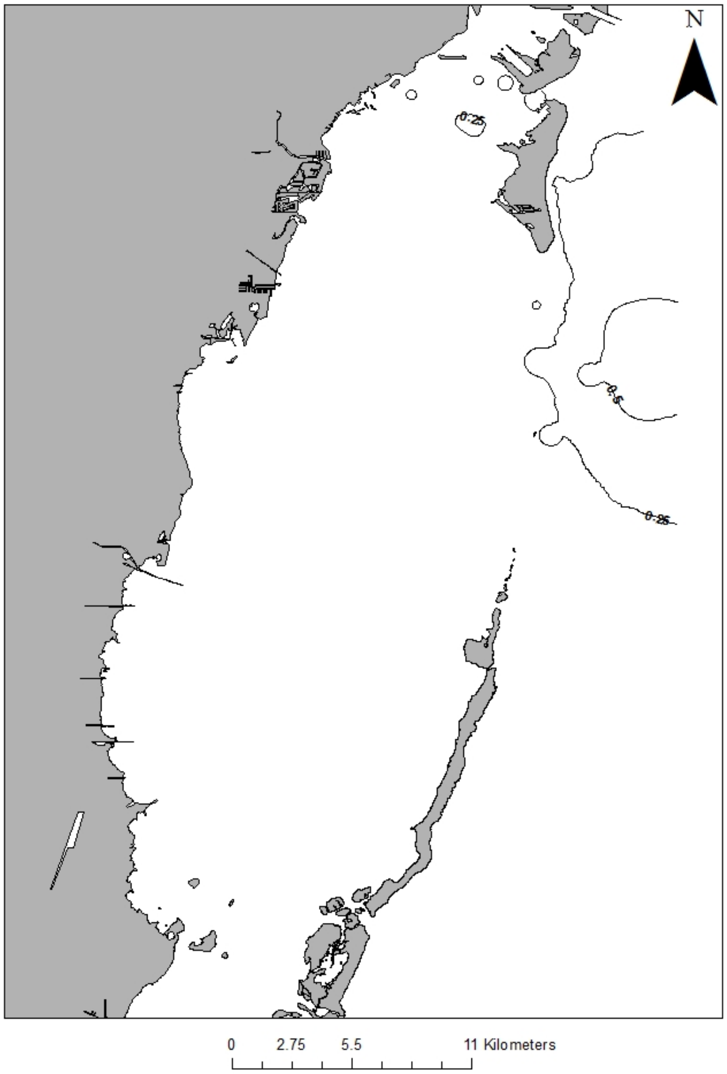
Figure 11. Predicted distributions of Clusters 3 and 6.



Predicted distribution of Cluster 3 reducing salinity by half, doubling salinity CV and doubling nitrate concentrations.

Predicted distribution of Cluster 6 reducing salinity by half, doubling salinity CV and doubling nitrate concentrations

Figure 12. Predicted distribution of Cluster 2.



CHAPTER II

Mixed effects of a nutrient enrichment experiment in a subtropical estuary

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Abstract

Biscayne Bay is semi-enclosed estuary located on the southeastern coastline of the state of Florida. Seagrass beds are the dominant primary producer community in this estuary. However, the Bay is located next to a large urbanized area, exposing the primary producer community to potentially very negative impacts from human activity. Some of these impacts include possibly increased nutrient inputs into the estuary. We conducted a nutrient enrichment experiment in the southern portion of the Bay within Biscayne National Park to determine how an increase in nitrogen and phosphorus might affect primary producer community structure at different locations of the estuary. We found that in a 7-month period, neither nitrogen nor phosphorus enrichment appeared to significantly affect nutrient ratios or abundance of the large primary producers at our sites. While nitrogen addition specifically appeared to affect the height of *Thalassia testudinum* at our N-limited site, changes in foliar N:P ratios indicated that nutrient limitation was no alleviated by our enrichment program. Field observations also suggested the mitigating presence of herbivores, which, at some sites may have augmented the effects of nutrient enrichment. Our results here can help managers frame responses to potential increased nutrient fluxes that can affect the system. However, a manipulation over a larger temporal scale would be necessary to determine the possibility of more enduring nutrient-induced phase shifts.

Introduction

Seagrass beds are often the dominant primary producers in many estuarine and marine communities (Duarte and Cebrian, 1996; Hillman et al., 1995; Moncreiff et al., 1992; Perez and Romero, 2008). Seagrasses act as a trophic base supporting complex food webs in many different climates. There are a number of ecological services that seagrass beds provide. Seagrass beds serve as a habitat for a number of benthic animals and provide a nursery for juvenile animals (Heck and Thoman, 1984; Heck et al., 2003; Nagelkerken et al., 2002). Some of the animals that use seagrass beds as nurseries reside primarily in deeper ocean waters in their adult stages, but spawn in seagrass beds (Jackson et al., 2001; Olney and Boehlert, 1988). Seagrass blades provide shelter for these organisms during their juvenile stages. The extensive root and rhizome network of seagrasses also holds sediment in place reducing turbidity in the water column (Madsen et al., 2001), allowing for a high incidence of light to reach seagrass beds as well as coral reef ecosystems that are sometimes adjacent to seagrass beds. Seagrasses also remove nutrients from the water column and use them for primary productivity, and in so doing reduce their availability for water column microalgae (Erftemeijer and Middelburg, 1995; Flindt et al., 1999).

The ecological services that seagrasses provide can have positive economic effects for local communities (De la Torre-Castro and Ronnback, 2004). Some of the fish species that utilize seagrass beds as habitat for protection can end up in commercial and recreational catches (Davis and Dodrill, 1989; Jackson et al., 2001; Watson et al., 1993).

Other species living in seagrass beds are permanent or transient residents of coral reef systems (Nagelkerken et al., 2002). These reefs often support tourist activities such as SCUBA diving and snorkeling (Barker and Roberts, 2004). Some studies have shown that the nutrient cycling function of seagrasses can also be considered economically value, especially if one considers the cost of creating a similar process manually (Costanza et al., 1997).

Like other primary producers, seagrass primary productivity is affected by a number of different factors. Firstly, the availability of light and nutrients influence the basic processes of photosynthesis and respiration. Secondly, herbivores can remove enough biomass to reduce overall growth rate (Heck and Valentine, 2006). And thirdly, competition within and among seagrass species as well as other primary producers can have a negative effect on growth rates (Fourqurean et al., 1995). These factors can act on seagrasses simultaneously, and there are a number of human activities that can enhance or reduce the role these factors play in determining seagrass community structure. For example, overfishing of top predators can remove the top-down pressure on herbivores thus releasing them to feed unimpeded on seagrass beds (Heck and Valentine, 2007). In severe cases this can result in a large amount of biomass removal. In even-numbered (Oksanen and Oksanen, 2000) food chains however, this overfishing can, via trophic cascades, remove the herbivores of epiphytes on seagrass blades. This increases the competition that seagrasses undergo for water column nutrients and light (Goecker et al., 2005). Biogeochemical changes can also affect seagrass community structure. Changes in nutrient availability to seagrasses can cause changes in seagrass growth rate, and community structure (Armitage et al., 2005). Increased nutrient availability may not only affect primary producers. It may also result in increased biomass of benthic epifauna (Baggett et al., 2013) or cause a shift in the community composition of the associated herbivore community (Gil et al., 2006).

The roles that top-down and bottom-up forces play in affecting seagrass distribution typically have a spatio-temporal component. Estuarine and marine sediments have varying concentrations of nitrogen and phosphorus, and their relative availability to primary producers can depend on number of factors including rate of nutrient uptake (Duarte, 1995) and the chemical forms of the nutrients (Boyer et al., 2003). Studies have demonstrated that primary producers in many carbonate-based estuaries are phosphorus limited (Short, 1987). This may be partly due to the strong adsorption of phosphorus by this type of sediment (Koch et al., 2001). This pattern does not always hold. Different factors affect distribution of nitrogen and phosphorus and as a result nutrient budgets in primary producers also varies widely. The effects of nutrient enrichment therefore are strongly dependent on the existing ratios of nitrogen to phosphorus, even in carbonate environments (Armitage et al., 2005; Ferdie and Fourqurean, 2004; Fourqurean et al., 1992; Powell et al., 1989). If seagrasses are limited by either nutrient, the addition of the limiting nutrient can result in an increase in primary productivity of that species.

Herbivores generally have specific ranges, feeding patterns and physiological traits that mediate their disposition to feeding in certain beds (Carr and Adams, 1973). Herbivores sometimes make feeding choices based on nutrient contents of the seagrass tissue (Burkholder et al., 2012). This selective feeding can shape seagrass communities by favoring one species over another (Armitage and Fourqurean, 2006). In some cases, where fidelity to particular species is extremely high, herbivory can result in the complete denudation of seagrass meadows (Fourqurean et al., 2010). Herbivore patterns can also be altered by external forces. In places where there is strong predation by top carnivores, hunting patterns by these carnivores can force herbivores away from preferred seagrass beds (Burkholder et al., 2013). This behavior-mediated trophic cascade can have positive consequences for primary productivity in seagrass beds.

Together, herbivory and nutrient availability shape seagrass beds in different ways at different locations at different points in time. Understanding the variation of these top-down bottom-up processes can help shape the way we understand and protect seagrass ecosystems.

We were interested in exploring this relationship in Biscayne Bay, a local estuary with a large seagrass population. Biscayne Bay is subtropical estuary located to the southeast of the state of Florida. The Bay extends from the city of North Miami Beach, Florida to the city of Homestead Florida. Between the northern and southern edges of the Bay along the shoreline lie well-developed urban areas including the city of Miami. All of the communities that make up these areas are characterized by dense human population, extensively developed waterfront property of different uses, periodically interrupted by mangroves and sand beaches. The southern portion of Biscayne Bay is part of the largest federal marine park in the continental United States. Biscayne National Park was formed in 1978 (Burrus Jr., 1984), and together with the Biscayne Aquatic Preserve supports a number of economic activities that are part of the lifeblood of the economy of South Florida.

Seagrasses are the dominant primary producer community in Biscayne Bay (Lirman and Cropper Jr., 2003). Previous studies have shown that the distribution of seagrasses and macroalgae changes with salinity as well as some nutrients (Lirman and Cropper Jr., 2003). Much of these nutrients emanate through the groundwater supply in the Black Point area, where a landfill leaks nitrates and ammonia into the porous limestone rock (Boyer and Meeder, 2001; Caccia and Boyer, 2007, 2005). Another potential source of nutrient influx is the canals that flow into Biscayne Bay from the Everglades (Brand et al., 1991; Caccia and Boyer, 2007, 2005). These canals are controlled by the South Florida Water Management District, and their role in restoring the Everglades to its historic delivery and timing of water is part of a Comprehensive Everglades Restoration Plan (CERP) (McLean et al., 2002). An increase in freshwater delivery can mean an increase in delivery of effluent nutrients to the estuary.

The long-term consequences of greater nutrient input into the Bay are currently unclear. Some studies have extensively documented a recent *Anadyomene* sp. bloom that occupies the northwestern edge of the Bay during the summer months near the canals, but disappears in the middle of the fall (Collado-Vides et al., 2013). These studies are however unclear on the definitive causative factors for the bloom (Collado-Vides et al., 2012).

Herbivory in Biscayne Bay also has a spatial component (Bourque and Fourqurean, 2013). Experiments using artificial seagrass planting units have shown that herbivory is strongest near the large tidal cuts in the eastern parts of the Bay. Herbivores also appeared to prefer *Syringodium filiforme* and *Halodule wrightii* over *Thalassia testudinum* (Bourque and Fourqurean, 2013). What is unknown however is how nutrient enrichment might affect the nature and strength of this herbivory pressure.

In this manuscript we describe an experiment set up in the southern portion of Biscayne Bay, to investigate the role that two nutrients (nitrogen and phosphorus) might play in primary producer community structure. Our experiment is based on previous studies that demonstrate estuarine primary producers showing variable responses to nitrogen and phosphorus, especially in carbonate estuarine systems (Armitage et al., 2005; Fourqurean et al., 1995; Powell et al., 1989). Where nutrients were limiting, the addition of the limiting nutrient resulted in morphological changes in the seagrasses (Armitage et al., 2005; Bourque and Fourqurean, 2013; Ferdie and Fourqurean, 2004; Fourqurean et al., 1992; Powell et al., 1991). Previous studies in Biscayne Bay also show spatial variation in nitrogen and phosphorus concentrations both in the sediment and water column (Dewsbury and Fourqurean unpubl., Collado-Vides et al. *in* press, Lirman and Cropper Jr., 2003). N:P ratios of *Thalassia testudinum* foliar tissue in Biscayne Bay suggest that this species, like neighboring Florida Bay, is primarily phosphorus limited. These ratios indicate that this limitation is strongest just north of Black Point along the coast and toward the central areas of the Bay. These ratios also indicate light and nitrogen limitation to the southwest areas of the Bay and to the east of the islands in the park (Dewsbury unpubl.). We hypothesized then that nutrient enrichment of nitrogen and phosphorus would result in an alleviation of mostly phosphorus limitation in *T. testudinum* and result in greater biomass and abundance of the primary producers present.

METHODS

Location

Our study was located in Biscayne National Park which is located in the southern portion of Biscayne Bay (Figure 13). Each site was chosen based on previously collected data of the nitrogen to phosphorus ratios within the park that established that a spatial component does exist with respect to nitrogen and phosphorus limitation. The northernmost site (called Key Biscayne because of its proximity to that island; 25.65952268570°N, 80.21165043°W) was nearest to the ocean. This site was characterized by a fairly low coverage of *T. testudinum* (but fairly high N:P ratios (55.7) indicating moderate phosphorus limitation. *Thalassia testudinum* leaves contained on average 2.5±0.02 percent N and 0.1±0.01 percent P (of total dry weight). Macroalgae was virtually non-existent at this site (Dewsbury and Fourqurean unpubl). The central site was called Central Biscayne (25.56359653830°N, 80.22246748°W). *Thalassia testudinum* leaf N:P ratios indicated more severe phosphorus limitation with percent N (3.0±0.06) and P (0.1±0.005) values yielding an N:P ratio of 71.2. *Thalassia testudinum* coverage was fairly dense with sparse populations of calcareous green *Halimeda* sp., *Udotea* sp. and *Penicillus* sp. Our southernmost site was called Turkey Point (25.47268809°N, 80.28447548°W) as it was a couple miles from the similarly named nuclear power plant operated by Florida Power and Light. This site was sparsely populated with *T. testudinum* as well as the same genus of calcareous green algae found at Central Biscayne. Foliar percent N was 0.7±0.003 and percent P was 0.05±0.001 yielding a N:P ratio of 31.4 (Dewsbury and Fourqurean unpubl).

Field methods

Our experiment had a 2X2 design where nitrogen (N) and phosphorus (P) were both factors. Each nutrient had two levels (+ and -). The resulting factorial design had 8 replications of nitrogen and phosphorus treatments with 4 of each treatment also receiving doses of the second treatment. The 16 ½ X ½ meter-squared plots were randomized according to a Latin Square design to block for possible within-site gradients. Phosphorus was added using ground calcium phosphate rock at a rate of 0.18 g P m^{-2} d^{-1} and nitrogen was added using slow-release fertilizer (Polyon, Pursell Technologies Inc., 88-0-0, 94% N as urea) at a rate of 1.43 g N m^{-2} d^{-1}. Both fertilizers were gently massaged into the sediment on a monthly basis. These rates were chosen partly based on previous studies using nutrient enrichment techniques in seagrass beds in this area, because they represent potential sewage loading rates in the south Florida area (Ferdie and Fourqurean 2004). Each site was sampled on SCUBA by two technicians for a number of response variables.

Sediment nutrients

At the beginning and at the end of the experiment sediment cores were taken for lab nutrient processing. We only sampled at the beginning and end because continuous sampling would have created too much disturbance over the sampling period. Three cubic centimeters of sediment were removed using modified syringe cores in each plot. We used two separate processes to determine if nitrogen and phosphorus were successfully enriching the sediment. Total nitrogen content of sediments was determined using a CHN analyzer (FISONS 1500) from the dried sediment sample. Phosphorus content was determined using an acid hydrolysis technique followed by a colorimetric analysis (Fourqurean et al., 1992).

Thalassia testudinum nutrients

Three shoots of *T. testudinum* were removed from each plot at the beginning and at the end of the experiment. We subsampled at the beginning and end so as not negatively affect our time series abundance estimates. Seagrass blades were scraped free of epiphytic algae, dried and ground into a fine powder. Chemical analysis of seagrass tissue followed the same procedures as the sediment. Nitrogen and phosphorus content are reported here as a percentage of total dry weight. Nitrogen:phosphorus ratios were calculated on a mol/mol basis.

Thalassia testudinum morphology

Seagrass blades were measured for height, width and number of leaves for each plot to determine if nutrient enrichment positively affected biomass increase. Height and width were measured in millimeters. Both of these variables were measured from harvested shoots. Total length was measured from the tip of the tallest leaf to the beginning of the meristematic area of the seagrass shoot.

Primary producer abundance

Primary producer coverage was estimated using a modified Braun Blanquet technique (Fourqurean et al., 2001). In this method, coverage was estimated using 6 categories. Sparse was recorded as 0.5, 1 = 0-5%, 2=5-25%, 3=25-50%, 4=50-75%, and 5=75-100%. Each seagrass species in each plot was assigned a score based on the above categories. Coverage of functional algal groups (calcareous green *Halimeda* sp., *Udotea* sp., and *Penicillus* sp.) was also determined in this way. Sites were visited once per month for 7 months to record change in community composition over that period of time.

Statistical Methods

To determine if there was any significant change in *T. testudinum* coverage we used a repeated measures one-way ANOVA with two nutrient addition factors (N = nitrogen, P

= phosphorus). Each nutrient factor had two levels (+ and -). We also had a time (month) factor with 7 levels corresponding to the consecutive months (March – September) when coverage estimation took place. We were particular interested in whether our nutrient treatments resulted in different primary producer community responses over time. For all other response variables (*T. testudinum* width and height, *T. testudinum* nutrient content, and sediment nutrient content) we used a similar repeated measures approach with the exception that month had two levels, since these variables were only sampled at the beginning and end of the experiment. All statistical analyses were run in SPSS® version 11.

RESULTS

Sediment nutrients

At the Key Biscayne site sediment total percent nitrogen increased significantly in the treatments where nitrogen fertilizer was added (Table 13, month x nitrogen, $p<0.001$). Sediment treatments enriched with phosphorus fertilizer were the only treatments that showed significant increases in phosphorus content during the sampling period (Table 15, month x phosphorus, $p=0.002$). At Central Biscayne sediment nitrogen also only increased significantly at the sites where the benthos was enriched with nitrogen (Table 13, month x nitrogen, $p<0.001$, Figure 18). While there was a time effect on sediment phosphorus, this effect was not significantly different between other treatments. Sediment nitrogen increased significantly on average at all of the treatments at Turkey

Point (Table 13, time, p<0.001, Figure 21). The N treatment's increase was most pronounced with percent nitrogen over five times higher than at the beginning of the experiment. There was a significant effect of time on sediment phosphorus concentrations. Overall, there was no significant change in sediment phosphorus concentrations between treatments.

Thalassia testudinum nutrients

There was no evidence that *T. testudinum* absorbed enriched nitrogen at Central Biscayne (Table 12, p=0.224, Figure 17). There was a significant effect of time in our experiment on *T. testudinum* percent phosphorus (Table 12, time, p<0.001, Figure 17) but phosphorus percent was not affected by nutrient addition type. At Turkey Point there was a significant increase in *T. testudinum* nitrogen content across all treatments (Table 13, time, p<0.001, Figure 19) thus it was unclear if any leaf nitrogen content increase was due to our artificial enrichment. Phosphorus concentration decreased significantly in the foliar tissue across all treatments at Turkey Point (Table 13, time, p<0.001).

Thalassia testudinum N:P ratios

There was a significant effect of time on foliar N:P ratios at Central Biscayne (Table 16, time, p=0.027, Figure 20). N:P ratios were nearer light limitation ratios at the beginning of the experiment and foliar tissue indicated severe phosphorus limitation at the end. At Turkey point a similar effect occurred. At Turkey point, N:P ratios increased significantly in all tissues (Table 16 time, p=0.012, Figure 20), owing primarily to the significant increase in leaf nitrogen content and decrease in leaf phosphorus content across all treatments. Initially, seagrass tissues were nitrogen limited (<N:P 25-30, (Fourqurean et al., 1992) and became phosphorus limited by the end of the experiment.

Thalassia testudinum coverage

Thalassia testudinum response varied between sites. At Key Biscayne, our site initially contained sparse patches of *T. testudinum* beds, but within one month of sampling this site attracted large schools of fish, including a number of herbivores. All visible benthic primary producers disappeared from this site by the third sampling event. Because of this we were unable to detect any trends that correlate with our different nutrient enrichment treatments. There was an effect of time on seagrass coverage at Central Biscayne (Table 6, time p<0.001, Figure 14). Changes in *T. testudinum* abundance however were not affected by additions of nitrogen and phosphorus. . There were no significant differences in *T. testudinum* abundance due to nutrient enrichment or time at the Turkey Point site (Table 6, time, p>0.515, Figure 15). All treatments at this site maintained *T. testudinum* coverage between 50 and 75% during the sampling period.

Calcareous Greens coverage

Three calcareous green genera were most prevalent in our plots. These were *Halimeda* sp., *Udotea* sp. and *Penicillus* sp. There was a significant effect of time on *Halimeda* populations at Central Biscayne (Table 7, time, p=0.011, Figure 14). Nutrient enrichment did not affect these abundances. Neither time nor nutrient enrichment affected the abundances of *Udotea* sp. but there was a significant interaction between time and phosphorus concentration on *Penicillus* abundance (Table 8, time x phosphorus, p=0.004). At Turkey Point, *Halimeda* varied significantly over the sampling period in response to nitrogen (Table 7, time x nitrogen, p=0.001, Figure 15). In nitrogen plots, *Halimeda* on average started and ended between 25% and 30%. There was much greater variation of *Halimeda* abundance in other treatments during the sampling period. *Udotea* abundance was affected by neither time nor enrichment. There was a significant effect of time on *Penicillus* abundance (Table 8, time, p<0.001). Nitrogen or phosphorus addition did not significantly affect abundance.

Thalassia testudinum morphology

There was a significant effect of time on *T. testudinum* height at the Central Biscayne site (Table 10, time, p=0.027, Figure 22). All treatments except for the nitrogen enrichment decreased from their original average length. There was also a significant effect of time on width since all of *T. testudinum* leaves were significantly narrower compared to the beginning of the experiment (Table 11, time, p<0.001, Figure 22). At Turkey Point time had a significant effect on *T. testudinum* height (Table 10, time, p<0.001, Figure 23,). All of the *T. testudinum* shoots at this treatment were longer on average when compared to the start of the experiment. Treatments enriched with nitrogen also showed significant increases in height (Table 10, time x nitrogen, p=0.041,

Figure 23). The nitrogen enrichment treatments however did not significantly affect leaf width.

DISCUSSION

Nutrient limitation of *T. testudinum* appears to vary spatially and temporally in Biscayne Bay. Contrary to our original hypothesis, we were not able to alleviate nutrient limitation in *T.testudinum.* Phosphorus also did not play a major role in shaping primary producer community structure over the seven-month duration of our experiment. Nearer to the coastline, though initial *T. testudinum* N:P ratios suggested nitrogen limitation, nutrient enrichment did not appear to significantly affect the abundance of the seagrass nor the macroalgae. It did however seem to be responsible for a significant increase in *T. testudinum* height. In the central part of Biscayne Bay ambient N:P ratios of *T. testudinum* indicate moderate phosphorus limitation and over the course of the experiment, the entire site became severely phosphorus limited. Over the course of the experiment nutrient enrichment with phosphorus caused a significant increase in abundance of *Penicillus* sp.

Previous studies on seagrass ecosystems in subtropical estuaries have established a range of N:P ratios that indicate relative nitrogen, light and phosphorus limitation (25-30:1 being light limited, below that value is nitrogen limitation and above that value is phosphorus limitation) (Fourqurean et al., 1992; Powell et al., 1989). Using these values we can infer the nutrient status of seagrasses in estuaries by analyzing their foliar tissue.

Based on this reasoning our Central Biscayne site was moderately phosphorus-limited at the beginning of our experiment and Turkey Point was nitrogen limited. Previous studies on nutrient limitation in seagrasses suggest that if a nutrient is limiting, the limiting nutrient will be detected in the foliar tissue of seagrasses when enrichment with that nutrient takes place (Atkinson and Smith, 1983; Barko and Smart, 1986; Gerloff and Krombholz, 1966). The increased nutrient supply over sufficient time scales should also increase primary productivity. We were not able to definitely detect any change in our primary producers due specifically to nutrient enrichment. The overall increase at all treatments in nitrogen at Turkey Point may be reflective of increased microbial activity that fixes nitrogen. The literature suggests that this fixation peaks in the summer time (McGlathery et al., 1998), which made up the bulk of our experimental period.

We were surprised at the lack of response in our study as the background N:P ratio gradients suggested that nutrient uptake would take place. Positive responses were observed when a similar nutrient enrichment protocol was implemented in neighboring systems (Ferdie and Fourqurean 2004 and Armitage et al. 2005). One important difference however was the reduced time scale of our nutrient addition regime. While our experiment lasted 7 months during the period where seagrasses in the subtropics tend to be most productive (Zieman, 1975), results from other nutrient enrichment manipulations suggest that a full understanding of the effects would require constant enrichment for multiple seasons (Ferdie and Fourqurean 2004, Armitage et al., 2005).

With only 3 sites, our spatial scale also probably did not span the entire range of nutrient limitation possibilities within the Bay. In fact, a recent comprehensive assessment of foliar tissue of *T. testudinum* along the shoreline of the Bay indicates that in that area, seagrasses are extremely phosphorus limited (Lirman et al. in press). This study reports N:P value ranges of 60 to 90 for this region. The upper limit of this range is significantly higher than the original N:P ratios of the seagrass tissue at of our sites.

Initial nutrient distribution values in this experiment seemed to corroborate previously reported values of nutrient variation in the sediment (Dewsbury unpubl). N:P ratios are much higher in the central areas of the Bay, lower to the northeast, and even lower to the southwest.. Previous studies have shown nutrients distributed similarly in the water column in this area (Caccia and Boyer, 2005). In estuarine systems these values would be indicative of potential phosphorus limitation (Fourqurean et al., 1992), but other studies in Biscayne Bay note however, that these ratios may not represent the actual nitrogen available to the primary producer (Caccia and Boyer, 2005). Though we did not see significant changes in the macroalgal community over the experimental time frame, other studies in Biscayne Bay on *Anadyomene* sp. blooms nearer to the shoreline, indicate that increased N inputs can be the driving force of this sudden growth (Collado-Vides et al., 2013).

While our experiment was not explicitly set up to quantify the effects of herbivory, evidence of top-down pressure was very evident at two of our sites. At Central Biscayne, technicians observed bite mark shapes on denuded seagrass blades that were consistent with those reported for green turtles (*Chelonia mydas*). In addition, this same species could be seen scampering away when divers approached for monthly sampling events. It was difficult to ascertain if the alleged herbivores had a strong preference for any particular plot. Repeated visits to particular plots were emblematic of the high site fidelity that *C. mydas* are known for (Broderick et al., 2007), but the denuded plots were from various treatments. At Key Biscayne, the site area was densely populated with large schools of parrotfish, snappers, grunts and numerous other species typically found on coral reefs. The site was also located near to a large channel through which tidal exchanges generate strong currents. A spatial analysis of herbivory in Biscayne Bay has shown this area to be one of the strongest locations for top-down pressure (Bourque and Fourqurean, 2013). Our enrichment, like other experiments in seagrass beds with strong herbivory (Armitage and Fourqurean, 2006), may have simply provided an enhanced meal for consumers. Because of the complete removal of all large primary producers from all plots, we are unclear as to the specific role of nutrient enrichment and herbivory (if at all) in driving the trends we observed at the Key Biscayne site. Anecdotal evidence of herbivory here as a potential community shaping factor in Biscayne Bay with changing biogeochemical regimes was consistent with other experiments in similar systems (McGlathery, 1995).

The nutrient response here contrasts seagrass response to nitrogen and phosphorus enrichment in Florida Bay (Armitage et al., 2005; Gil et al., 2006), and may speak to the role that other factors play in nutrient availability to seagrasses as well as to the time scale of our experiment. Understanding the potential role of nutrient enrichment in shaping primary producer communities dynamic is especially important in Biscayne Bay because of the numerous human-impact challenges that managers here deal with. Increased freshwater flow into Biscayne Bay may bring with it an increased nutrient supply which may have far-reaching effects on nearshore primary producer communities. Being able to predict the response of the primary producer community may help managers shape appropriate responses to potential impact.

Like other estuaries in this area, Biscayne Bay is also subject to frequent use by motorized vessels. In shallower areas of the Bay these vessels sometimes run aground or destroy seagrass beds with propeller scars (Zieman, 1976). Seagrass restoration programs in this area typically transplant seedlings of different seagrass species and enrich the restored beds with manually added fertilizer or naturally with bird stakes. The use of the bird stakes cause fertilization due to the defecation of piscivorous birds that temporarily reside on the stake. Previous experiments using this method have shown that the fecal matter can significantly augment biogeochemical regimes and subsequently community structure in nutrient limited areas (Powell et al., 1991). Our experiment demonstrates here that the success of this method is dependent on ambient nutrient conditions, the ratio of the nutrients being added, and the timeframe allowed for the response of the enriched area. In addition, if herbivory does in fact play a greater role in shaping communities away from the shoreline in enriched scenarios, then current methods of restoring denuded beds may simply be providing an enhanced food source for transient herbivores.

Our anecdotal observations at Central Biscayne and Key Biscayne suggest that future experiments should strongly consider the role that top-down forces play in shaping seagrass beds in deeper parts of the Bay. Such a manipulation might contain exclosures to examine more closely the response of these beds in a situation where they are not at risk of biomass removal. In nearshore sites where there is seemingly an absence of large top-down pressures, seagrasses may primarily respond to increases in nitrogen. We did not conduct tissue analysis on other primary producers in the system, so it is possible that in smaller temporal scales, faster growing species might respond better to nutrient addition (Kinney and Roman, 1998). A similar experiment to our manipulation over a larger time scale should help determine if in fact nutrient enrichment only causes short-term morphological changes in seagrasses, or if it can eventually engineer an entire phase shift to a new primary producer community structure.

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Table 6. Repeated measures analysis of *T. testudinum* abundance at Central Biscayne and Turkey Point. Abundance was measured using a modified Braun Blanquet.

Site	**Treatment**	**df**	**MS**	**F**	**Sig**
Central Biscayne	Month	6	2.093	5.63	**p<0.001**
	Month *Nitrogen	6	0.656	1.763	p=0.119
	Month*Phosphorus	6	0.489	1.315	p=0.262
	Month* Nitrogen*Phosphorus	6	0.099	0.266	p=0.951
Turkey Point	Month	6	0.238	0.879	p=0.515
	Month*Nitrogen	6	0.244	0.901	p=0.499
	Month*Phosphorus	6	0.119	0.440	p=0.850
	Month* Nitrogen*Phosphorus	6	0.244	0.901	p=0.499

Table 7. Repeated measures analysis of calcareous green *Halimeda* sp. abundance at Central Biscayne and Turkey Point. Abundance was measured using a modified Braun Blanquet.

Site	**Treatment**	**df**	**MS**	**F**	**Sig**
Central Biscayne	Month	6	0.927	3.005	**p=0.011**
	Month *Nitrogen	6	0.187	0.608	p=0.723
	Month*Phosphorus	6	0.167	0.540	p=0.776
	Month* Nitrogen*Phosphorus	6	0.634	2.054	p=0.069
Turkey Point	Month	6	0.974	2.851	**p=0.015**
	Month*Nitrogen	6	1.449	4.240	**p=0.001**
	Month*Phosphorus	6	0.332	0.972	p=0.451
	Month* Nitrogen*Phosphorus	6	0.308	0.900	p=0.500

Table 8. Repeated measures analysis of calcareous green Udotea sp. abundance at Central Biscayne and Turkey Point. Abundance was measured using a modified Braun Blanquet.

Site	**Treatment**	**df**	**MS**	**F**	**Sig**
Central Biscayne	Month	6	0.221	1.617	p=0.155
	Month *Nitrogen	6	0.093	0.683	p=0.664
	Month*Phosphorus	6	0.133	0.975	p=0.449
	Month* Nitrogen*Phosphorus	6	0.051	0.375	p=0.892
Turkey Point	Month	6	0.540	1.804	p=0.110
	Month*Nitrogen	6	0.351	1.873	p=0.330
	Month*Phosphorus	6	0.082	0.273	p=0.948
	Month* Nitrogen*Phosphorus	6	0.208	0.696	p=0.654

Table 9. Repeated measures analysis of calcareous green Penicillus sp. abundance at Central Biscayne and Turkey Point. Abundance was measured using a modified Braun Blanquet.

Site	**Treatment**	**df**	**MS**	**F**	**Sig**
Central Biscayne	Month	6	0.476	1.879	p=0.096
	Month *Nitrogen	6	0.108	0.428	p=0.858
	Month*Phosphorus	6	0.888	3.505	**p=0.004**
	Month* Nitrogen*Phosphorus	6	0.267	1.056	p=0.397
Turkey Point	Month	6	7.282	13.216	**p<0.001**
	Month*Nitrogen	6	0.347	0.629	p=0.706
	Month*Phosphorus	6	0.217	0.394	p=0.881
	Month* Nitrogen*Phosphorus	6	1.051	1.907	p=0.091

Table 10. Repeated measures analysis of *T. testudinum* height at Central Biscayne and Turkey Point.

Site	Treatment	df	MS	F	Sig
Central Biscayne	Month	1	3240.125	6.336	**p=0.027**
	Month *Nitrogen	1	98	0.192	p=0.669
	Month*Phosphorus	1	1922	3.758	p=0.076
	Month* Nitrogen*Phosphorus	1	406.125	0.794	p=0.390
Turkey Point	Month	1	12600.781	24.245	**p<0.001**
	Month*Nitrogen	1	2719.531	5.233	**p=0.041**
	Month*Phosphorus	1	1023.781	1.970	p=0.186
	Month* Nitrogen*Phosphorus	1	3633.781	6.992	**p=0.021**

Table 11. Repeated measures analysis of *T. testudinum* blade width at Central Biscayne and Turkey Point.

Site	Treatment	df	MS	F	Sig
Central Biscayne	Month	1	78.125	65.789	**p<0.001**
	Month *Nitrogen	1	0	0	p=1
	Month*Phosphorus	1	0.500	0.421	p=0.529
	Month* Nitrogen*Phosphorus	1	0.125	0.105	p=0.751
Turkey Point	Month	1	2	2.462	p=0.143
	Month*Nitrogen	1	0.125	0.154	p=0.702
	Month*Phosphorus	1	1.125	1.385	p=0.262
	Month* Nitrogen*Phosphorus	1	2	2.462	p=0.143

Table 12. Repeated measures analysis of *T. testudinum* leaf total nitrogen content at Central Biscayne and Turkey Point.

Site	Treatment	df	MS	F	Sig
Central Biscayne	Month	1	0.586	1.640	p=0.224
	Month *Nitrogen	1	0.024	0.066	p=0.801
	Month*Phosphorus	1	0.006	0.018	p=0.896
	Month* Nitrogen*Phosphorus	1	0.528	1.478	p=0.247
Turkey Point	Month	1	16.367	45.469	**p<0.001**
	Month*Nitrogen	1	0.750	2.082	p=0.175
	Month*Phosphorus	1	0.192	0.532	p=0.480
	Month* Nitrogen*Phosphorus	1	0.053	0.146	p=0.709

Table 13. Repeated measures analysis of sediment nitrogen content at Central Biscayne and Turkey Point.

Site	Treatment	df	MS	F	Sig
Central Biscayne	Month	1	0.458	22.265	**p<0.001**
	Month *Nitrogen	1	0.431	20.937	**p=0.001**
	Month*Phosphorus	1	0.001	0.937	p=0.847
	Month* Nitrogen*Phosphorus	1	0.005	0.219	p=0.648
Turkey Point	Month	1	0.474	37.886	**p<0.001**
	Month*Nitrogen	1	0.080	6.406	**p=0.026**
	Month*Phosphorus	1	0.081	6.465	**p=0.026**
	Month* Nitrogen*Phosphorus	1	0.012	0.928	p=0.354
Key Biscayne	Month	1	0.484	21.099	**p<0.001**
	Month*Nitrogen	1	0.411	19.273	**p<0.001**
	Month*Phosphorus	1	0.023	0.877	p=0.213
	Month* Nitrogen*Phosphorus	1	0.581	30.013	**p=0.019**

Table 14. Repeated measures analysis of *T. testudinum* phosphorus content at Central Biscayne and Turkey Point.

Site	Treatment	df	MS	F	Sig
Central Biscayne	Month	1	0.001	9.313	**p=0.010**
	Month *Nitrogen	1	$1.065*10^{-6}$	0.008	p=0.928
	Month*Phosphorus	1	$2.275*10^{-5}$	0.181	p=0.678
	Month* Nitrogen*Phosphorus	1	$4.014*10^{-5}$	0.319	p=0.583
Turkey Point	Month	1	0.034	215.925	**p<0.001**
	Month*Nitrogen	1	$4.517*10^{-7}$	0.003	p=0.958
	Month*Phosphorus	1	$1.149*10^{-5}$	0.073	p=0.791
	Month* Nitrogen*Phosphorus	1	0	1.020	p=0.332

Table 15. Repeated measures analysis of sediment phosphorus content at Central Biscayne and Turkey Point.

Site	Treatment	df	MS	F	Sig
Central Biscayne	Month	1	$1.281*10^{-10}$	0	p=0.998
	Month *Nitrogen	1	$7.803*10^{-5}$	4.873	**p=0.048**
	Month*Phosphorus	1	$7.863*10^{-7}$	0.049	p=0.828
	Month* Nitrogen*Phosphorus	1	$4.714*10^{-7}$	0.029	p=0.867
Turkey Point	Month	1	40593.661	101.152	**p<0.001**
	Month*Nitrogen	1	244.544	0.609	p=0.450
	Month*Phosphorus	1	545.138	1.358	p=0.266
	Month* Nitrogen*Phosphorus	1	6.038	0.015	p=0.954
Key Biscayne	Month	1	1.008	12.011	p=0.619
	Month*Nitrogen	1	201.01	0.981	p=0.129
	Month*Phosphorus	1	950.121	75.209	**p=0.002**
	Month* Nitrogen*Phosphorus	1	0.109	20.181	**p=0.001**

Table 16. Repeated measures analysis of *T. testudinum* N:P ratios at Central Biscayne and Turkey Point.

Site	Treatment	df	MS	F	Sig
Central Biscayne	Month	1	2148.188	6.347	**p=0.027**
	Month *Nitrogen	1	68.679	0.203	p=0.660
	Month*Phosphorus	1	99.578	0.294	p=0.597
	Month* Nitrogen*Phosphorus	1	431.051	1.274	p=0.281
Turkey Point	Month	1	0	8.865	**p=0.012**
	Month*Nitrogen	1	$2.181*10^{-5}$	0.702	p=0.419
	Month*Phosphorus	1	$2.135*10^{-5}$	0.687	p=0.423
	Month* Nitrogen*Phosphorus	1	$1.496*10^{-7}$	0.005	p=0.946

Figure 13. Location of field sites in Biscayne Bay. Larger map indicates the area of detail from the inset.

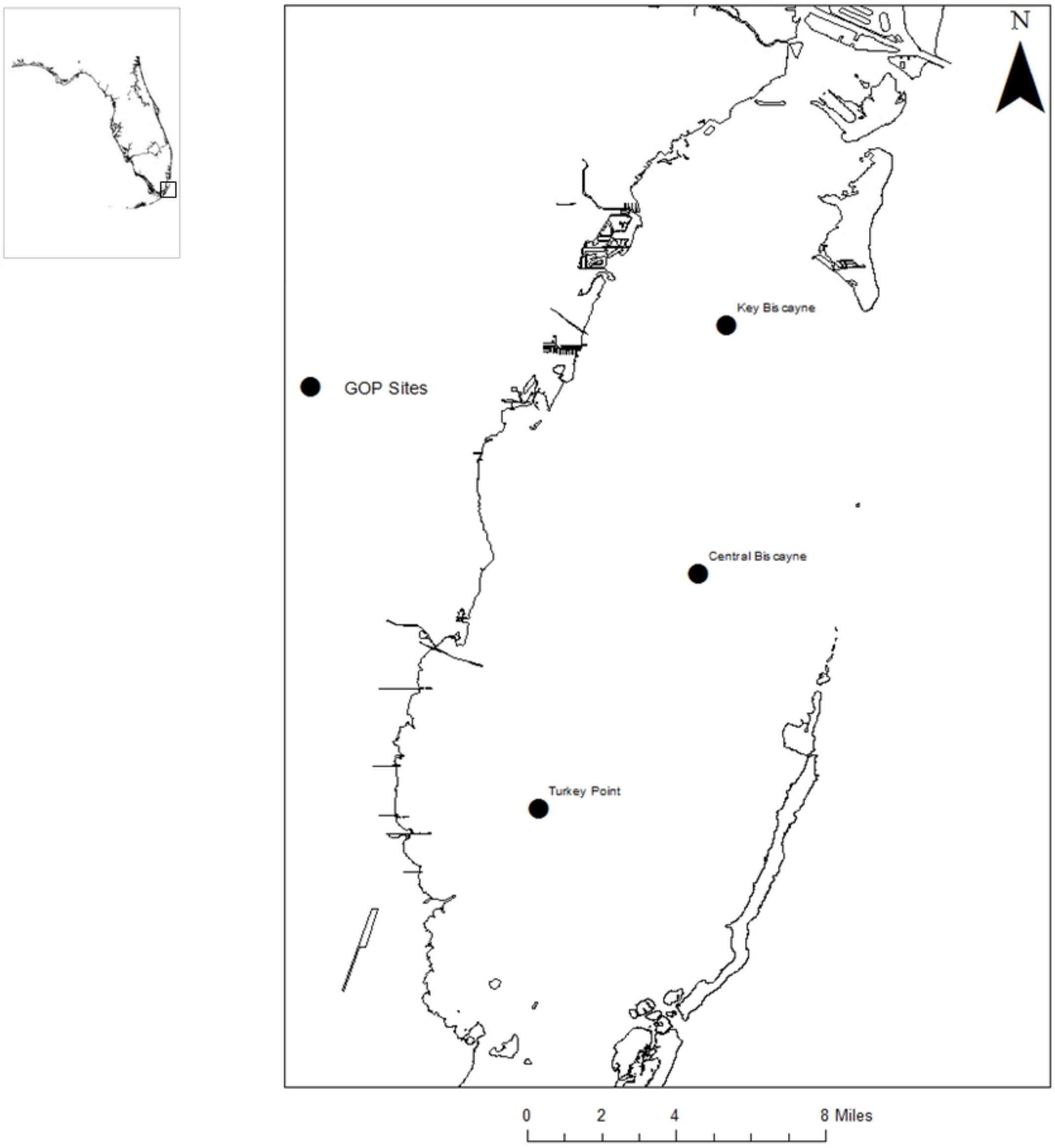


Figure 14. Change in *T. testudinum*, and calcareous green algae abundance over 7 months at Central Biscayne. Error bars represent standard error of the mean.

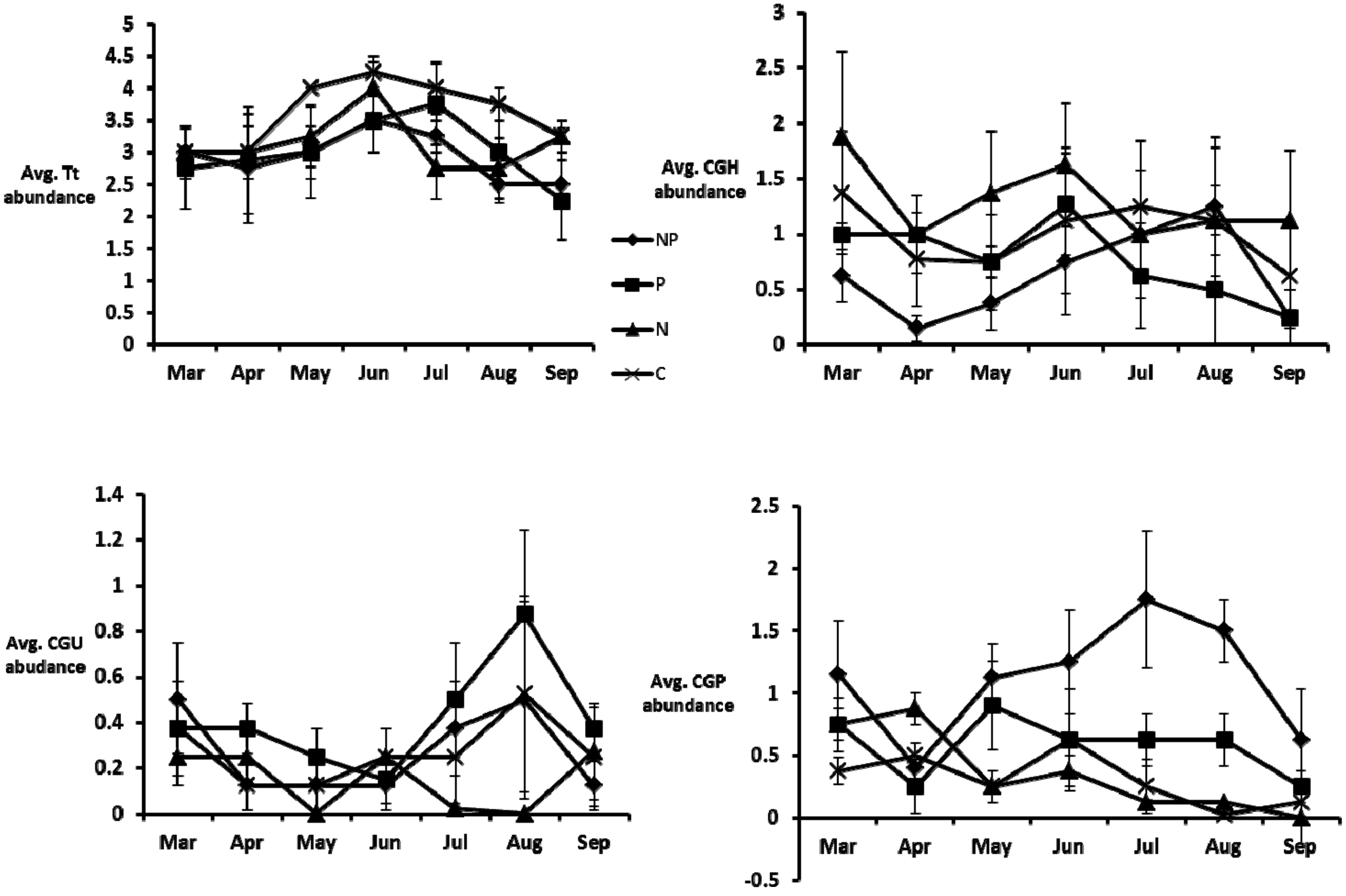


Figure 15. Change in *T. testudinum* and calcareous green algae abundance over 7 months at Turkey Point. Error bars represent standard error of the mean.

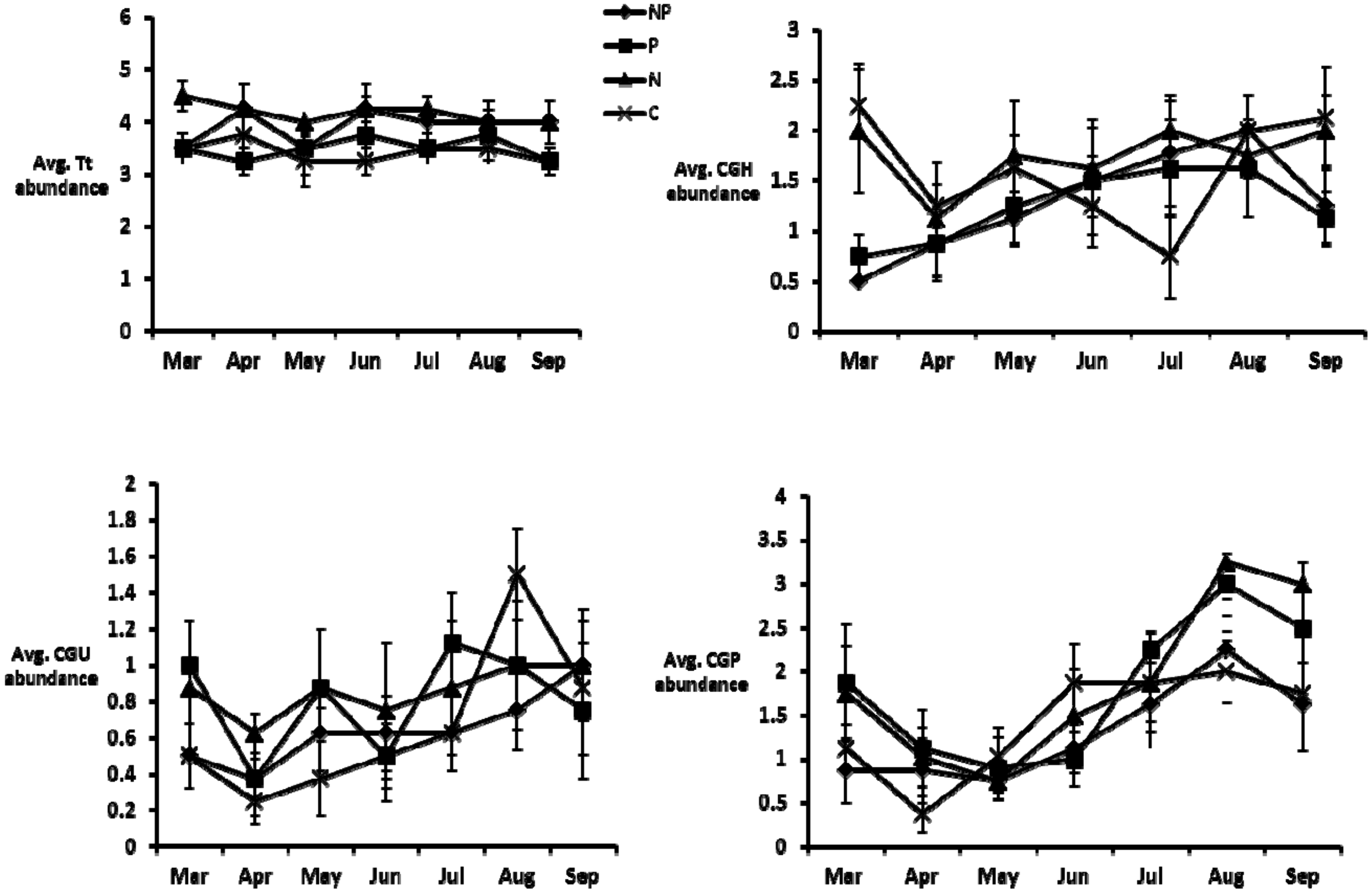


Figure 16. Sediment nutrients before and after seven months at Key Biscayne. Error bars represent standard error of the mean.

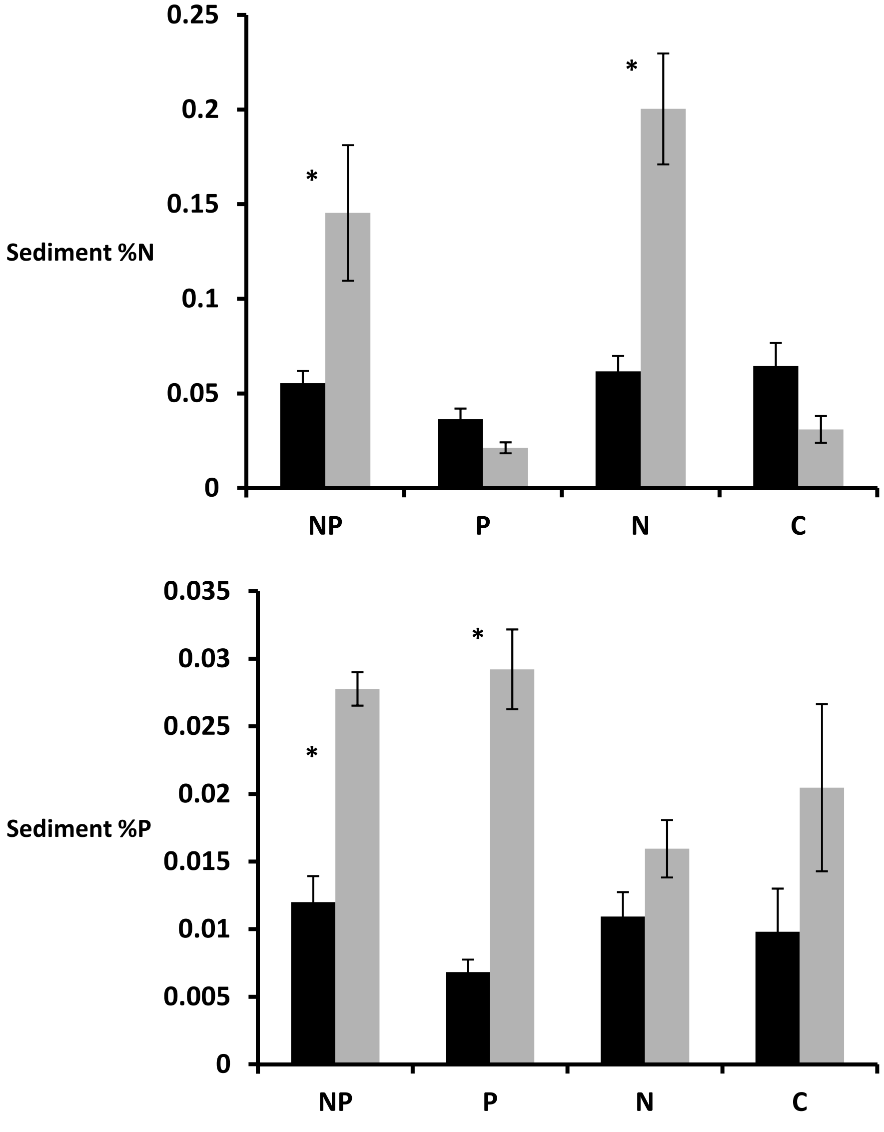
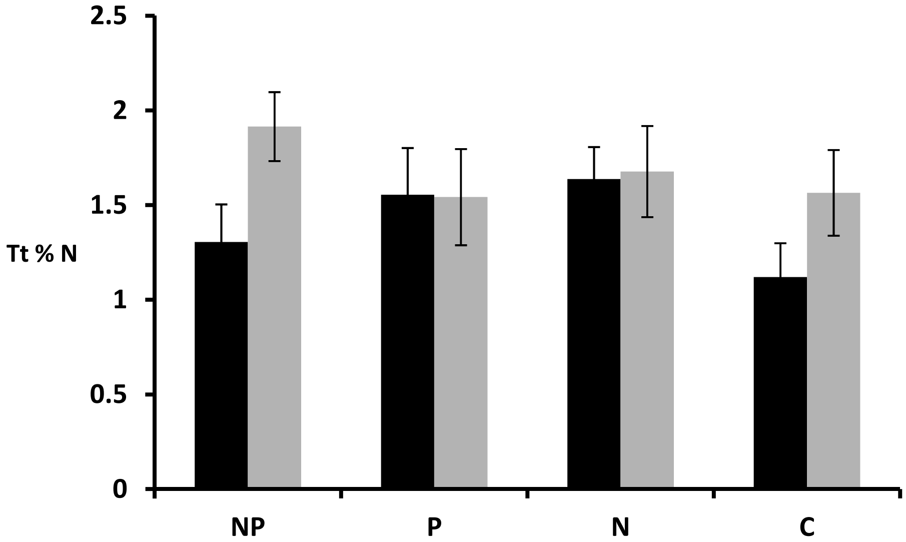


Figure 17. *T. testudinum* foliar nutrients at Central Biscayne before and after sampling period. Error bars represent standard error of the mean.



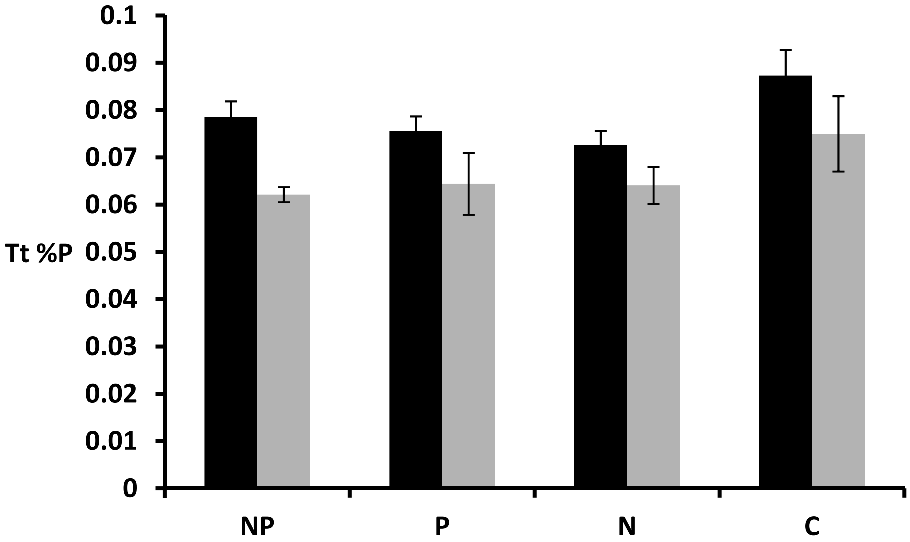


Figure 18. Sediment nutrients at Central Biscayne before and after 7-month period. Error bars represent standard error of the mean.

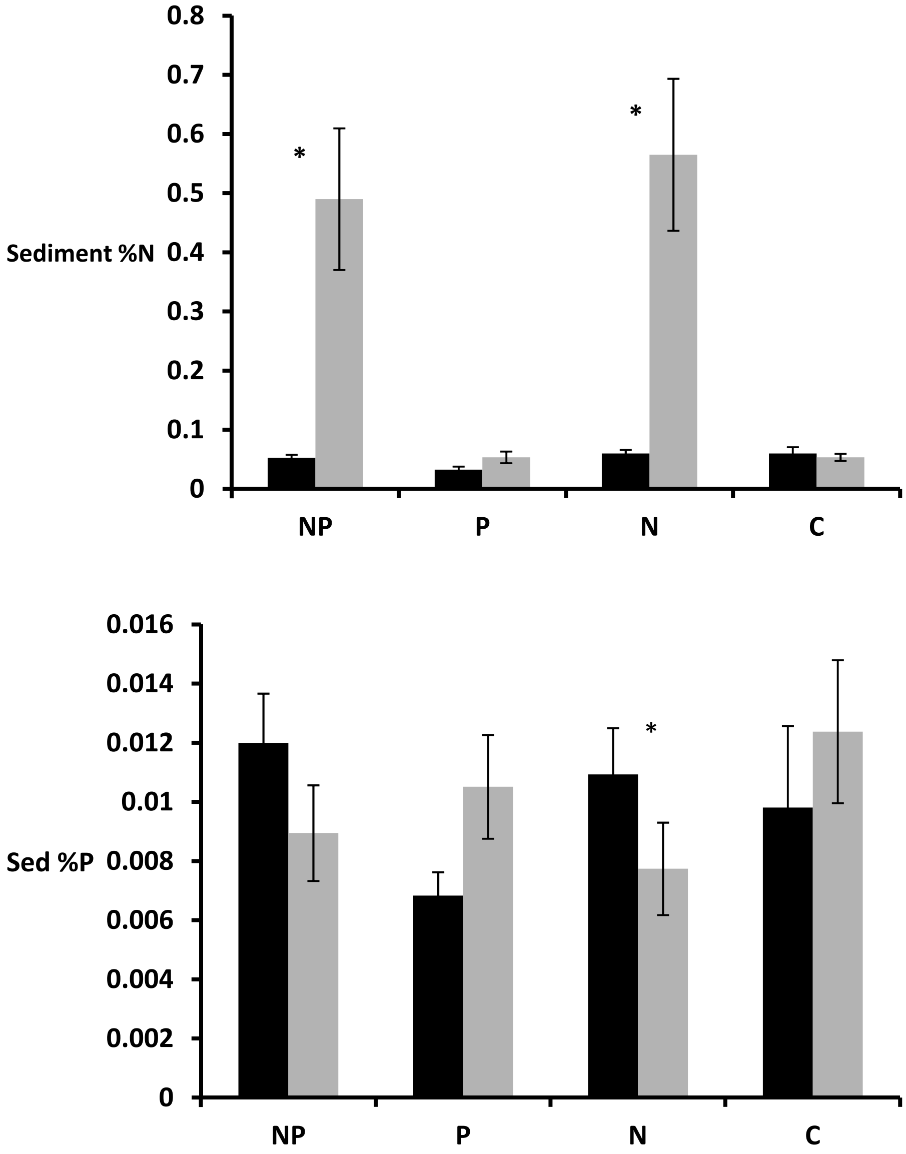
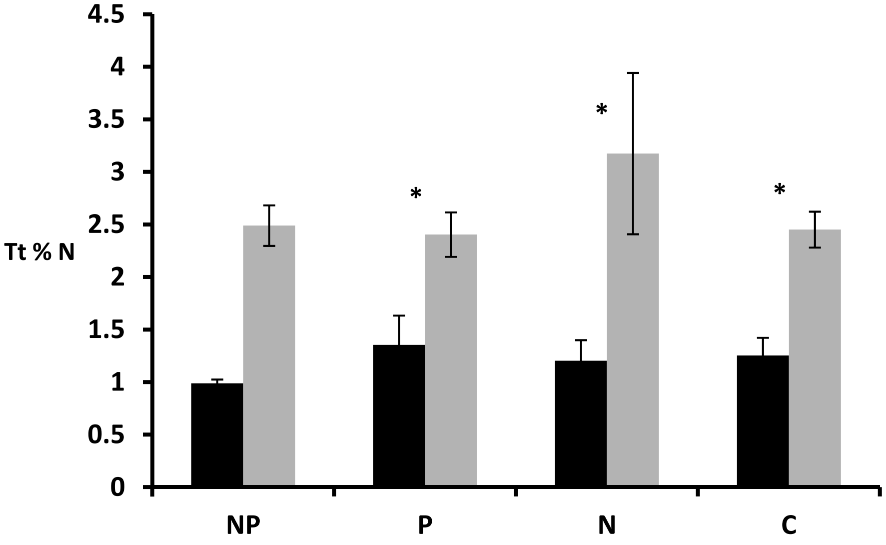


Figure 19. *T. testudinum* foliar nutrients before and after the 7-month sampling period at Turkey Point. Error bars represent standard error of the mean.



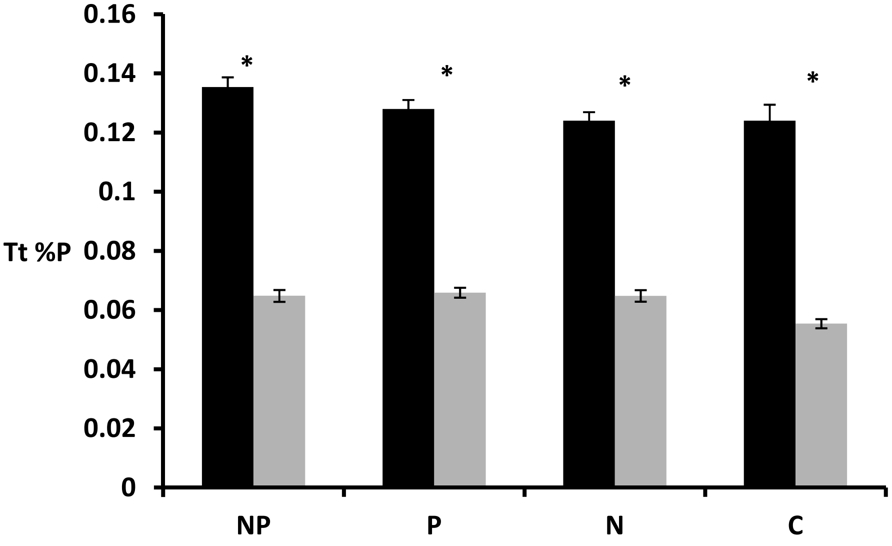


Figure 20. N:P ratios in *T. testudinum* leaves at Central Biscayne and Turkey Point.

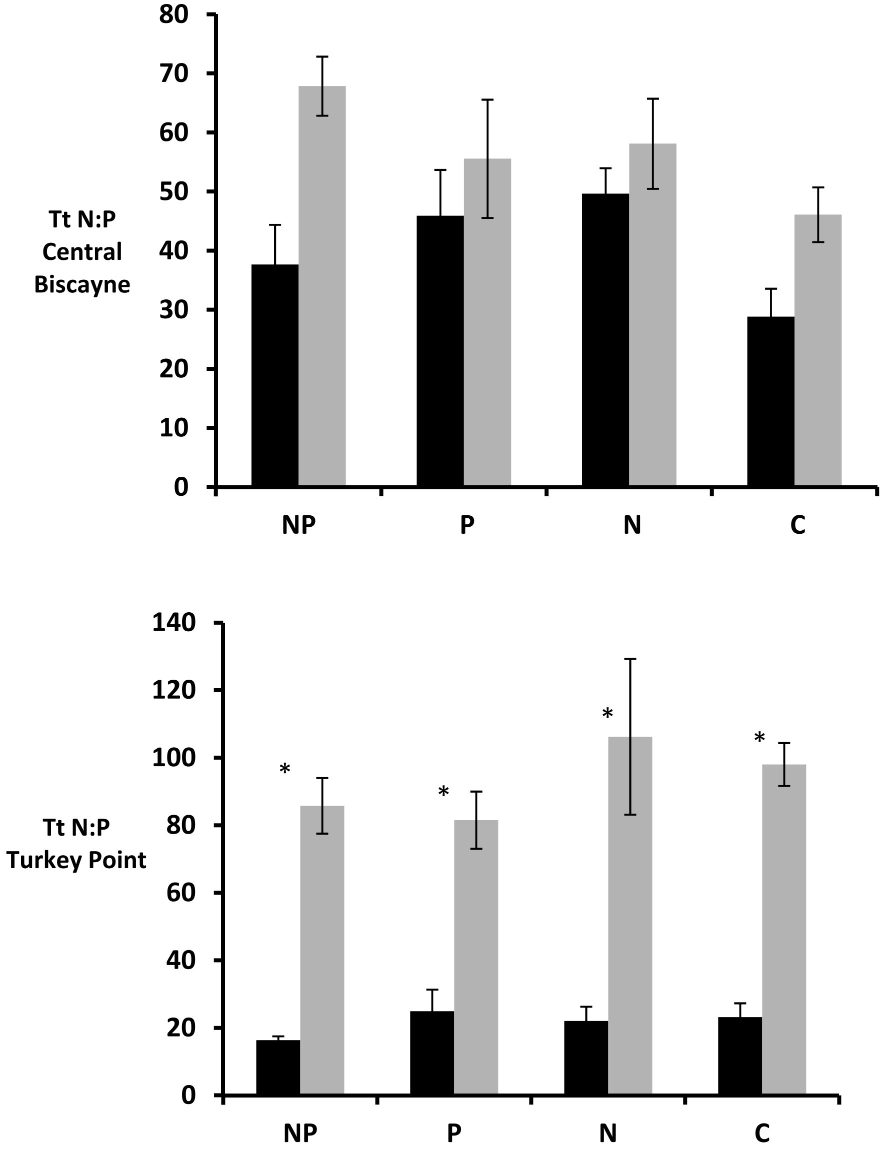
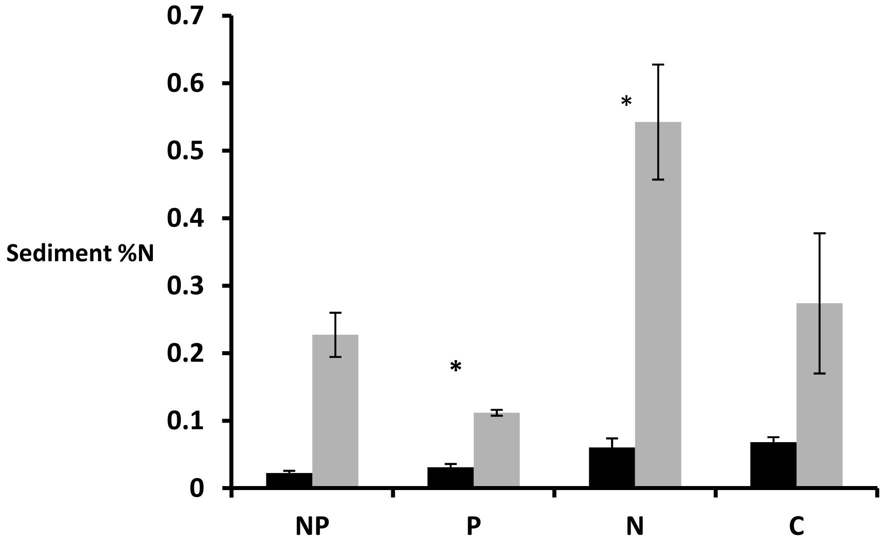


Figure 21. Sediment nutrients before and after the 7-month sampling period at Turkey Point. Error bars represent standard error of the mean.



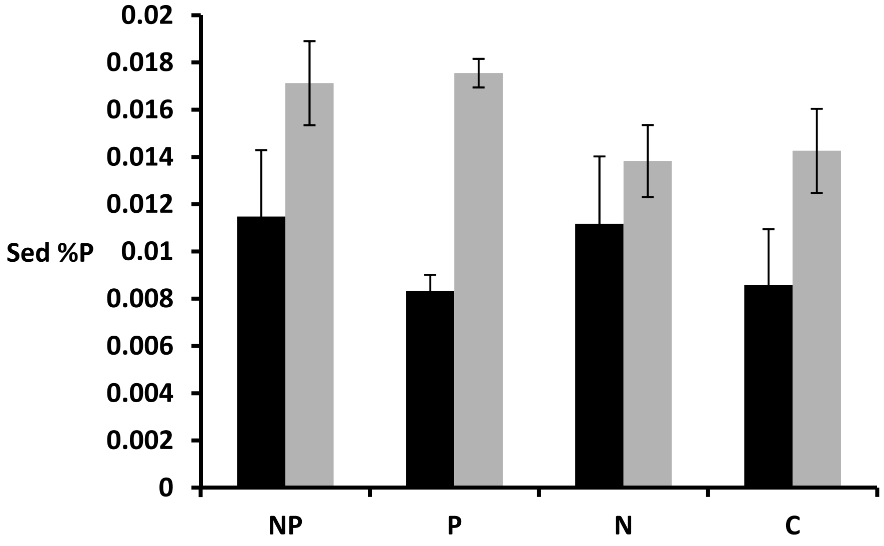
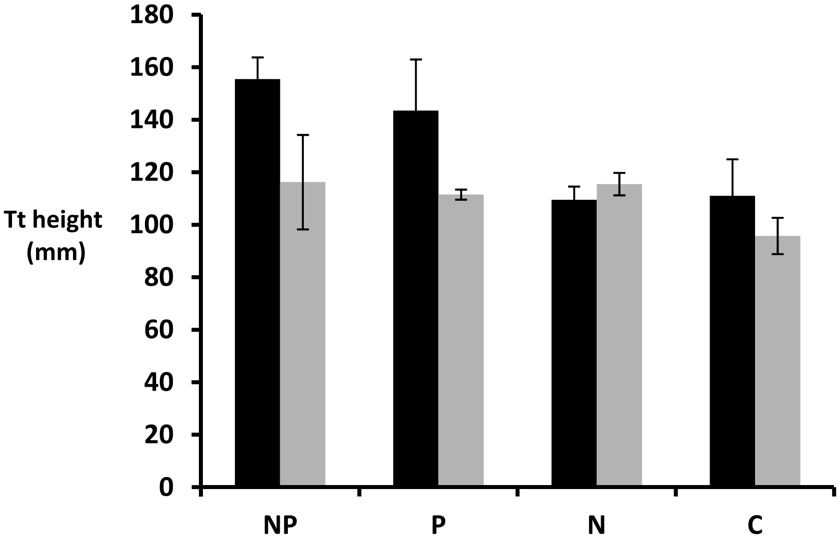


Figure 22. Seagrass morphometrics at Central Biscayne before and after 7-month sampling period. Error bars represent standard error of the mean.



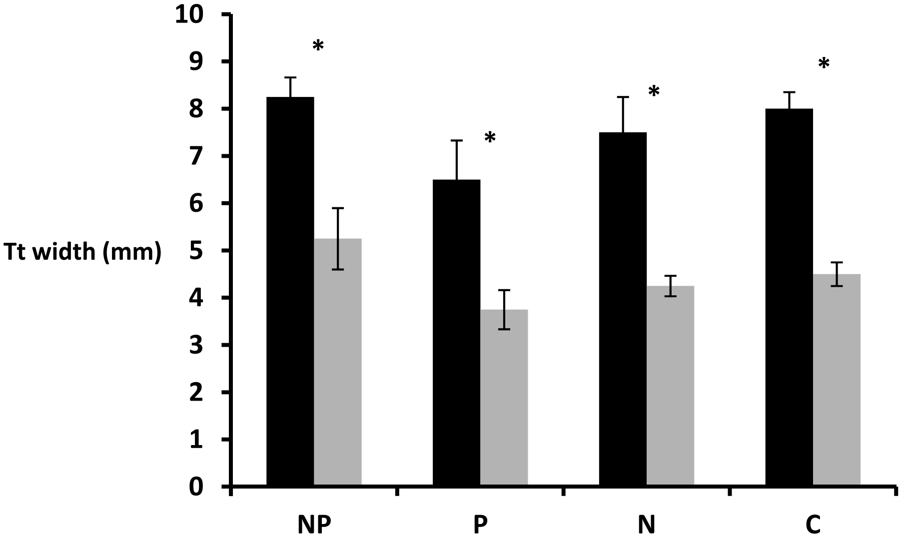
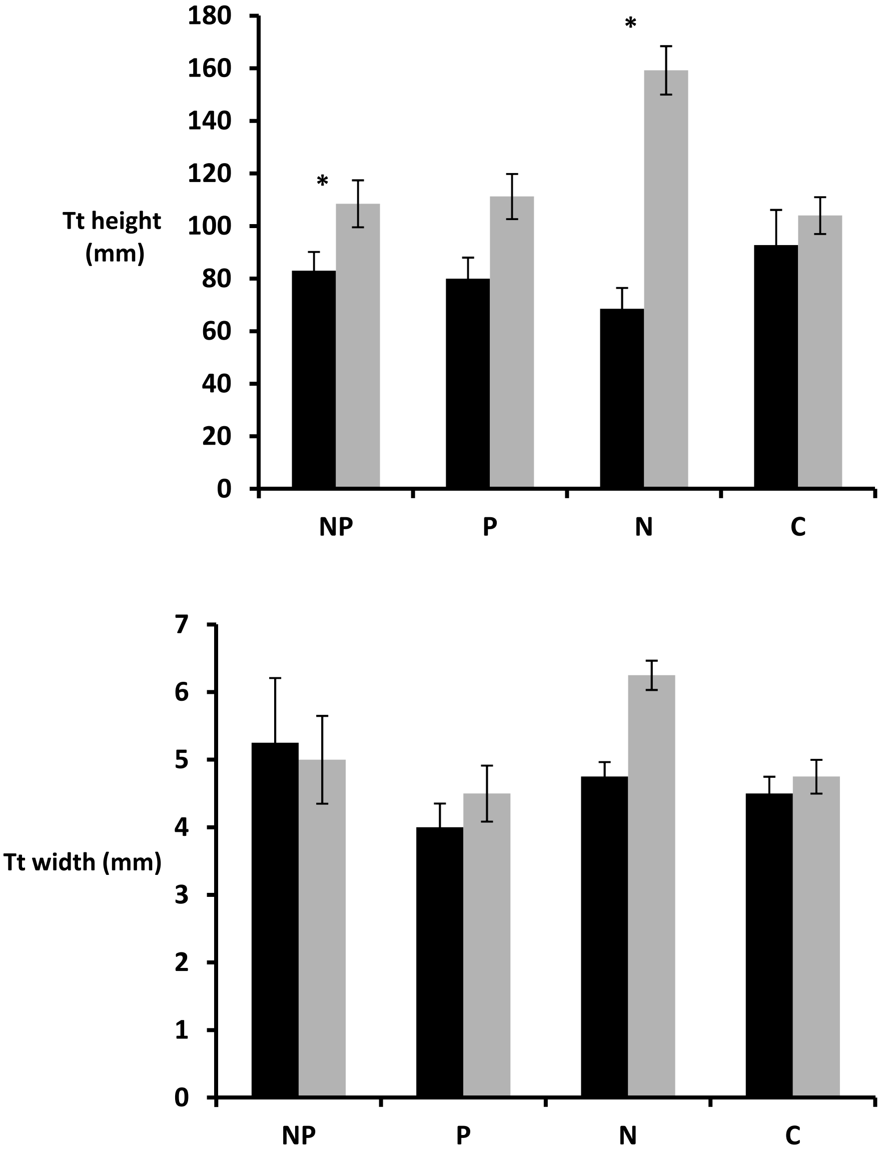


Figure 23. Seagrass morphometrics at Turkey Point before and after 7-month sampling period. Error bars represent standard error of the mean.



CHAPTER III

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A review of economic valuations of seagrass ecosystems

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Abstract

1. Abstract

Multiple studies have documented the ecologically important role that seagrasses play in estuarine and marine ecosystems. Unfortunately, economic valuations of these systems have not been as widespread. To date, most techniques rely on mechanisms that do not incorporate the actual ecological drivers behind the economic service, but rather rely on proxy measures to derive values. In this manuscript we review the many *use* values that seagrasses have that result in economic services, and the valuation techniques used to estimate their monetary value. We present a conceptual framework linking seagrass ecosystems to the economic services they provide, showing the areas where novel valuation approaches are most lacking. We conclude that indirect methods used to valuate seagrass ecosystems underestimate the economic value of their services, and that more derivative-based models linking ecological structure and function to all associated economic services are essential for accurate estimations of their dollar value.

Keywords – *seagrass, TEV, ecological services, ecosystem, valuation*

2. INTRODUCTION

Seagrasses are marine angiosperms that inhabit coastal ecosystems worldwide. While the taxonomic diversity of seagrass is low, its acreage typically extends to thousands of kilometers of the coastline (1, 2). Seagrasses provide many ecosystem services (3, 4). Many of these services have economic benefit for local human communities (5-7). Unlike other primary producers in the marine environment, seagrasses have a broad latitudinal range, inhabiting all but polar ecosystems (2). This means that the economic services provided by seagrass ecosystems occur at multiple spatial scales. The nature of some of these services and the proximity of seagrass ecosystems to densely populated areas however, exposes them to a wide variety of activities that negatively impact it (2, 8).

Recent studies have reported a perpetual worldwide decline in seagrass abundance (2). The causes of these declines vary spatially and temporally. Heavy dredging from marine construction is a well-documented negative impact activity on seagrass beds (reviewed in (9)) Shallow seagrass beds are especially prone to scouring from vessel grounding and scarring from the propellers of motorized boats (10). These injuries not only remove the aboveground biomass, but excavate the rhizomes and sediment sometimes creating blowholes. Marine fauna can then create further damage by excoriating the adjacent rhizome thus causing neighboring beds to collapse (11). Near shore seagrass beds are also vulnerable to allocthonous nutrient inputs as effluent from human activities (12) or from groundwater (13). These nutrient increases can result in a shift to faster growing micro and macroalgae both of which outcompete seagrasses for light, and are physiologically better equipped to proliferate in a high nutrient environment (14-16). Overfishing can also spur cascading effects that have negative effects on seagrasses in a couple of ways. Firstly, the removal of large predators releases the consumer pressure on smaller predators who feed on epibenthic fauna in seagrass ecosystems. Epibenthic fauna feed on epiphytic algae that accumulate on the blades of seagrasses. When epibenthic fauna is removed from the system, the accumulation of epiphytes on seagrass leaves can prevent seagrasses from accessing much needed light for photosynthetic activity (17). Secondly, the removal of large predators allows herbivores to feed unimpeded on seagrass beds (18).

Most of the negative impacts on seagrass beds arise from the reality that coastal ecosystems are by-and-large common use areas. High volumes of commercial, recreational and tourist activities mean that there is a large amount of boat and human traffic within a few miles from the shoreline resulting in direct impact on seagrass beds. In addition, 40% of the world's population live within 60km of the coastline (19), meaning that coastal communities may suffer from negative externalities associated with this population increase.

There have been many calls for stricter management policies to aid in the preservation and restoration of existing seagrass beds (20). While many of these requests cite the economic value of seagrass ecosystems, there have been only a few studies that provide dollar estimates of the value of these systems. A main reason for this is that seagrass itself does not have much direct market value, therefore, economic assessments of their worth rely on indirect values derived from the services these systems provide. Since some of these services result in social benefit, traditional market methods may be insufficient for deducing actual economic value. In addition, the specific ecological relationship between seagrasses and some of its benefits have only been relatively recently documented, and therefore efforts to translate certain ecosystem functions into economic terms are still in its infancy.

There is a clear need for greater progress to be made on seagrass valuation. As humans increasingly populate coastal cities, greater pressure is being applied to coastal ecosystems to satisfy local demands for space, food, and other resources. In order to create greater awareness among policymakers and the general public of the need to protect seagrasses, and to convince politicians to commit resources to do so, a clearer economic argument for seagrass ecosystem preservation needs to be made.

Commercial stakeholders tend to have an easier time demonstrating the economic value of their projects. Income from property taxes, corporate taxes and tourist revenue has visible and tangible benefits for the local economy. These linear economic relationships make it easier for these stakeholders to enlist the support of managers and politicians, even if the enactment of these projects produces long-term harm to coastal ecosystems. Environmental managers however have a more difficult time demonstrating the economic contribution of non-commercial ecosystem uses.

In this paper, we review the different use values of seagrass ecosystems and the valuation techniques used to estimate seagrass value around the world. We indicate here the strengths and weaknesses of each approach, and discuss the areas where the field can be advanced. We believe that recent literature on seagrass ecology has uncovered new ecosystem services, and therefore, the existing economic valuation studies may be incomplete.

We firstly discuss the economic valuation theoretical framework that guides our review of this issue. Secondly, we highlight the list the current attempts at valuation of seagrass ecosystems, pointing out the gaps in their approaches. Finally we create a conceptual model (Seagrass Ecosystem Valuation [SEV] model) that provides a framework to valuate and aggregate the multiple ecosystem services of seagrass ecosystems, discussing ways in which it can be used by managers and future stakeholders in local systems.

3. SEAGRASS VALUE

Total Economic Value (TEV) is an aggregate estimation of the function-based value that an ecosystem provides a local community. This value is a summation of *use* and *non-use* values. Use values refer to goods and services that are derived either directly or indirectly from the physical attributes of the system being evaluated. Direct services refer to goods that are physically extracted from the system (eg. fisheries) while indirect services refer to the secondary functions attributable to the system that also have economic value, but do not necessitate the physical removal of a good. Non-use value is the economic value derived not from any use of the system but the value placed simply on the existence of the system, or the potential to use the system in the future. The quantification of the different value types often requires different valuation approaches. We use the TEV framework here to discuss both past valuation attempts and areas where new approaches are needed.

3.1 Use Value

3.1.1 *Direct Use*

There is some history of direct human use of seagrass biomass. Its high silica content, slowness to rot, and the air pockets formed in dead seagrass mats made it ideal insulation material (21, 22). This was used for things ranging from thatching roofs to making sound proof recording studios. The dead material has also been historically used for the formation of dykes to help prevent beach erosion(21). Since current conservation policies in most parts of the world prevent direct harvesting of live seagrass material, contemporary direct use of seagrasses is therefore mostly restricted to dead or decaying material. These activities are somewhat localized to specific regions since some of the historical benefits of seagrass (like insulation) are now satisfied with more practical, efficient and readily available materials. In addition, different species of seagrasses have different fates after death. Species that are negatively buoyant remain submerged after death locking decaying organic matter within the local system (23). Other species can float over long distances and may be washed up on beaches in large quantities. In these situations, the dead material can have a number of uses including embroidery, erosion prevention, and mulch-use for home gardening. Some companies have been able to use seagrass material to develop a specific nutrient mix for horticultural use, but there have been only a few reported examples of this (24).

3.1.2 *Indirect Use*

Indirectly, seagrasses provide a number of valuable services to human communities. The juveniles of some commercial and recreationally caught fish species make their home in seagrass beds. There is also direct harvest of marine species from seagrass beds. These beds act as a nursery, providing protection from larger predators and reduce intra-species competition for resources (reviewed in (25)). Seagrasses also reduce the impact of wave action on coastlines thereby reducing erosion. Studies using wave tanks have shown that seagrass beds can cause wave attenuation up to 40%, making their effect comparable to those of salt marsh ecosystems (26). Their extensive rhizome structure also plays a very important role in keeping sediments bound thus reducing sedimentation (27). This water clarity is very important for the seagrasses themselves who are light dependent, but is also important for sometimes adjacent coral reef ecosystems, that depend on high light incidence to survive. A seagrass die-off in Florida Bay in 1990 was theorized to have caused the partial death of coral in the Florida Keys reef tract, exemplifying the importance of this relationship (28).

3.2 Non-use Value

There have been very few studies done on the non-use value of seagrass ecosystems. Reviews that we’ve found on ecosystem valuations of coastal ecosystems contain no data on non-use valuation. A possible reason for this might be the lack of public awareness of the presence of seagrass ecosystems (2) and their importance to the ecosystem goods and services coastal communities enjoy. In places where awareness is present (29), survey respondents demonstrate an understanding of the role that seagrasses play in the sustenance of the local fisheries and coral reef communities.

4. Seagrass Valuations

Attempts at seagrass ecosystem valuation have used a variety of approaches (Table 17). One common approach is willingness-to-pay (WTP). This is a choice modeling method where individuals indicate via a survey the amount of money they are willing to pay to ensure the continued existence of a good or service. The survey in essence measures the goods and services as a utility function. The value of the utility is often constrained by the individual's wealth (disposable income) and/or their knowledge of the service. Public awareness of the function and value of seagrass ecosystems is still limited. A recent purview of the scientific literature showed that peer-reviewed work on seagrasses still lag behind (in total volume) by orders of magnitude mangrove ecosystems and coral reefs (2). Recent studies highlighting the decline of seagrasses and their contribution as a possible carbon sink have however helped to increase awareness (30).

The replacement model is one of the more common valuation methods of seagrass ecosystems. This approach uses the cost of restoration of a seagrass bed or the function provided by that bed, including, labor, equipment and other associated materials as a proxy for the value of the seagrass bed itself. This approach is common in calculating costs incurred by vessels that inadvertently or otherwise run aground or inflict damage onto seagrass beds. The willful or accidental damage of seagrass beds or coral reef habitat is a misdemeanor offense in the state of Florida (31). While the replacement model serves as a convenient mechanism to ensure accountability by individuals who value the ecosystem services seagrasses provide, it is in reality an estimate of time and effort of seagrass restoration, and may grossly underestimate the value of the full complement of services seagrasses provide. This approach has also been used to calculate Habitat Equivalency Analyses (HEA), a technique devised to compensate the public for habitat loss by performing restoration work on a habitat of equal ecological value (32). The amount of restoration work and the costs associated are determined partially on a plot by plot comparison of community structure, as well as a summation of the time and effort required to conduct the damage assessment and carry out the interim and long-term restoration.

Some studies simply cite valuations used in similar ecosystems and apply the calculated value to seagrass ecosystems (33). This benefits-transfer approach is convenient since these calculations have sometimes already become part of policy, but it relies on the assumption that the ecosystem services provided by both systems are similar enough allow for the seamless use of the same analysis. Using valuations from mangrove ecosystems (34) for example ignores the vast differences between the two systems in terms of their nursery function and their respective roles in water quality improvement. The productivity method is the only method which actually links seagrass ecosystem structure and function to an ecosystem service that has market value. Some studies report location-specific values of seagrass beds based on catch-per-unit-efforts (CPUE), by extrapolating yearly estimates multiplied by the market price of the fish species in question (35). MacArthur and Boland (2006) used this approach to estimate the overall contribution of seagrass habitats to the economy in Australia to be US103.74 million per year. While this method might be the strongest approach linking primary productivity to the free market, the approach comes with a few noted assumptions. Firstly, the relationship between a commercial fish species and its seagrass habitat may not be necessarily linear. Complicated food web structures in some areas mean that the presence (or absence) of other non-commercial marine fauna can affect the abundance of commercial fish species. This reality is not always captured by the productivity approach. Productivity models will therefore have to be refined to incorporate more of the factors that affect both primary productivity (as a proxy for habitat quality) and secondary productivity (the market species of interest).

5. MISSING VALUATION METHODS

The most glaring gap in the seagrass valuation literature is the need to better link indirect use values to market goods and services (Table 17). This productivity approach would emphasize the relative contribution that a seagrass bed makes to the delivery of a particular ecosystem good or service. For example, Fonseca et al (3, 26, 27) determined the relative effects that various seagrass species had on the relative velocity of waves. This reduction in velocity has implications for the amount of erosion that may take place in the presence or absence of these seagrass species. Currently, some studies use hedonic pricing (a valuation technique that estimates a good based on its contributing characteristics) to estimate the value of coastal properties with or without erosion (36). The effect of seagrasses on reducing erosion of the coastline can be a contributing estimator toward the total value of the coastline area.

The term ‘water quality’ may have different meanings to different stakeholders in the marine/estuarine environment (37). To casual observers, water quality may simply be a measure of the ‘clarity’ of the water, i.e., an ability to see deep into the water column from the surface. This clarity is important for seagrasses as they require a high incidence of light to carry out its photosynthetic activities (38, 39). High turbidity in the water column or changes in depth can impede the ability of seagrasses to capture enough light for photosynthesis, and thus may become limiting factors for seagrass productivity (38). In this model, seagrasses improve water quality but are also themselves limited by this factor. Any estimation of the value of seagrass with respect to water quality will have to consider the contribution water quality makes to economic activities that depend on water clarity. In addition, water quality itself would have value in that it can be a determinant of seagrass abundance, whose overall economic value would be the total of its calculated economic contributions. Other estimators of water quality focus on its nutrient composition and its subsequent capability to support different types of primary producer communities (40-43). High values of nitrogen and phosphorus can result in stable state changes that favor faster growing macro and micro algae (43). The presence of seagrass beds can result in the incorporation of macronutrients from the water column into biomass, thus making it unavailable for microalgae (44). A primary producer community that comprises mostly algae is structurally very different to larger macrophytes and has broad implications for the types of secondary consumers they support (45). Higher microalgae concentrations can also severely reduce the attenuation of light to the benthos causing a collapse of the seagrass community (43). The rhizomes of seagrasses hold the sediment in place and thus reduce the flux of nutrients from the benthos into the water column. This lessens the probability of algal blooms taking place that can cause permanent seagrass loss.

Seagrasses act as a nursery habitat for various species of fish. This nursery hypothesis has been used as a primary reason to enact conservation policies of seagrass systems worldwide. Some of these species have commercial importance when they become adults. Other species are the prey for species that are commercially important (crustaceans are eaten by red snapper for example). There is a spatial component to seagrass' function as a nursery however. A meta-analysis of 'nursery' studies seems to indicate that this hypothesis holds truer for seagrass beds in the northern hemisphere versus the southern hemisphere (25). Ultimately, the quality of seagrass beds as a nursery depends largely on the structure of the blades of the seagrass species as opposed to its overall abundance (25). Clear relationships between seagrass beds and commercially caught species however have been established for different locations in the world, and this allows for better economic estimates to be made as far as seagrass' actual value. The seagrass nursery also provides habitat (and sometimes feeding grounds) for marine species that inhabit coral reefs in their adult stages, or make diurnal treks between reefs and surrounding seagrass beds (46). Current studies linking seagrass bed structure to secondary productivity are still mostly limited to comparative estimates of consumer biomass within and outside of seagrass beds. Our knowledge of seagrass beds as a nursery as a function of their morphology has improved such that new models should incorporate both this reality, and the contribution that primary productivity plays in creating this structure. Consumer biomass can then be calculated as a derivative of primary productivity and morphology.

The contributions of coral reef systems to local economies have been well documented across multiple spatial scales (47). Recreational SCUBA diving and snorkeling, concession boats and private boating all proliferate in regions where there are vibrant, intact coral reefs. The relationship between seagrass beds and coral reefs has also been fairly well studied. Seagrasses service coral reef ecosystems in a number of ways. Seagrass root structure keep water column transparent allowing corals to benefit from high light incidence, necessary for its survival (48). Seagrasses also house meiofauna that act as a food source for some reef fish species that leave the reef tract to feed in the seagrass beds at night (46). The relative contribution that seagrasses make to the overall survivability of a coral reef is not well quantified, and as a result, an economic valuation using this model might be a challenge. Until there is an empirical determination of the level of ecosystem function of coral reefs with and without a symbiotic relationship with seagrass beds, economic valuations using this relationship will have to rely on extrapolated estimates based on secondary productivity.

Until very recently, the role of seagrass ecosystems in carbon sequestration was not documented on a global scale. In the wake of concerns over the climate change effects that may come about in the face of increased carbon dioxide emissions, multiple stakeholders are seeking ways to reduce the global carbon footprint by reducing emissions, as well as increasing the number of sinks available. A recent compilation of the carbon sequestration potential of the global seagrass stock has documented exactly this effect (30). These estimates purport that globally, seagrasses can possibly store up to 19.9 Pg of organic carbon in their meadows. The economic implications of these calculations are made more apparent by the reality that many of these meadows are disappearing at a substantial rate. The loss of these meadows means that the resulting carbon release increases the atmospheric carbon pool. The economic loss caused by the amount of carbon lost to the atmosphere by seagrass meadow destruction can thus be used as an estimator of seagrass value.

6. SEAGRASS ECOSYSTEM VALUATION MODEL

Current valuation models typically address only partial functions of seagrass ecosystems. Most of the valuation estimates in the literature (Table 18) report seagrass value with respect to commercial fish production. The abundance of this particular estimate may be due to the reality that in the literature, this is the most documented ecological relationship between seagrasses and an economic good. In addition, fisheries as an economic good have a clear, tangible, market-related mechanism by which its value is measured. A few studies have also valued the economic contribution of seagrasses due to its nutrient cycling capability. This ‘replacement’ approach supposes the economic contribution to be tantamount to the cost of establishing a physical plant to perform a similar function. Another valuation approach ‘transfers’ the benefits deduced by other authors from a wetland ecosystem, with the assumption that the seagrass bed in that study had similar nutrient cycling capabilities. We were not able to find valuation studies for direct uses of seagrass beds as strong government protection for these ecosystems prevents direct harvesting.

Sorely lacking from the literature are studies that valuate seagrasses for their economic contribution to non-consumptive activities. These activities (snorkeling, SCUBA diving, boating etc.) are varied, and the ability to do them often relies on multiple attributes of the ecosystem above and beyond seagrasses. Valuation studies often calculate economic value (49) based on total ecosystem capacity and often fail to isolate the seagrass contribution to this figure. Carbon sequestration (another non-consumptive value) also doesn’t appear in many valuations partly because seagrasses as a major carbon sink (with global warming and economic ramifications) is a relatively recent discovery.

The bias in the type of valuations currently done on seagrass ecosystems is probably due to the paucity of research that significantly quantifies the relationship between seagrasses and economic goods and services. Economists have an easier time therefore valuing goods that have a clear market-based system in their analyses. Some of these relationships are only just being figured out. For instance, while it was been documented seagrasses can act as a significant carbon sink (30), we are yet to understand the rate by which this carbon might be returned to the atmospheric pool. The next stage of seagrass valuations need to incorporate more recent understandings ecological function and how those ecological functions can be economically quantified. A stepwise approach to this would involve conceptually laying out the ecological functions of a particular system and determining the best valuation approach for each service.

The seagrass ecosystem valuation model (Figure 24) is a framework that links an ecological model of a seagrass ecosystem with economic models that valuate its goods and services. The model in essence teases apart the different services that are derived from this system so that they can be delineated individually. This approach is important both for ecological and economic reasons. Ecologically speaking, it recognizes the fact that seagrass beds occupy a complex niche in estuarine and marine environments, and the dimensions of this niche are shaped by biotic and abiotic factors. By quantifying these factors for a given system, one can conceivably predictively model how a seagrass patch might function under a variety of scenarios. These scenarios will vary spatially and temporally. For instance, patch growth rate of a monospecific bed of *Thalassia testudinum* in Biscayne Bay, Florida will be very different to the patch growth rate of *Zostera marina* in Tomales Bay, California. The morphology of these beds (as well as patch diversity) will determine its relative ability to affect wave velocity, to act as suitable habitat, and to prevent sediment from being stirred into the water column. The rate of conversion of atmospheric carbon dioxide into organic matter will also vary with the rate of primary productivity of the species, and the fauna that inhabit these seagrass beds will vary widely spatially in terms of their economic importance (50). Economically, the model allows for the application of different valuation methods to quantify overall value. This differential use of valuation methods is based on the fact that goods and services provided by seagrass beds are qualitatively different, and should therefore be assessed using different approaches. For instance, an ecological understanding of the relationship between seagrass beds as habitat for commercial fish, can allow for the use of a ‘productivity method’ model to make a valuation estimate. However, estimating the economic contribution of tourism to the local economy will probably involve a travel-cost method that estimates the distance tourists are willing to cover to experience the pleasure of coral reefs and other seagrass-related pleasures. Coastal properties are also affected by hedonic pricing schemes, and a valuation model in this case would have to incorporate the role that an intact seagrass bed might play in the quality and ultimately the pricing of the adjacent real estate.

The total economic value of a seagrass ecosystem for a particular location will therefore be the sum of the value of the goods and services provided by the seagrass beds as determined by the multiple valuation metrics. Each connector (both ecological and economic) is a vector that represents processes that vary in the amount in contributes to its subsequent product. In systems where commercial fishing is the primary service provided by seagrass beds, the vector that represents this valuation will be the largest. In many seagrass systems, tourism services from coral reefs would not be a secondary service provided by seagrasses. The dynamic properties of this model allow it to have multiple applications for managers and local stakeholders.

7. MANAGEMENT APPLICATIONS OF THE SEV MODEL

7.1 *Costs-Benefit Analysis (CBA)*

By providing location-specific economic estimates of seagrass value, managers can implement CBAs that are better reflections of the actual cost of ecosystem destruction. This is important because in local situations where human development needs and ecosystem service provision clash, developers generally have an easier time demonstrating the economic benefit of brick and mortar structures through the property taxes generated and jobs created. The SEV model tailors the ecosystem services to the local community, such that if the needs of the local community and the environment clash, there is an available framework within which one can estimate which (and how much of it) service is being affected. The CBA approach can also be used by environmental managers interested in estimating the costs of protecting endangered ecosystems. The costs associated with staffing, concessions, monitoring, and infrastructure can be weighed against the services that these ecosystems provide the local community.

7.2 *Regulatory Impact Analysis (RIA)*

RIA is a widely used technique in developed and developing countries to ensure that regulations associated with a certain program or project do not result in a cost increase that negates the benefits of the project. CBAs are typically used to assess this. In a CBA used to determine the effect of regulations, the analysis can be built specifically to the services that the local ecosystem provides, with quantifiable estimates of each service as well as the regulations that are in place to ensure that the service is appropriately delivered.

7.3 *Damage assessment*

There are a number of damage assessment statutes implemented by the federal government to protect natural resources (51). These statutes provide certain federal institutions the power to pursue claims with respect to damage to natural resources, and mandate these institutions and guilty parties to make the injured areas whole, as well as provide the public compensation for the ecosystem services not received while recovery is taking place. Estimates of claims and compensation (using Habitat Equivalency Analyses (HEA)) are typically based on a combination of replacement costs and sometimes benefits transferred from other systems where valuations have already taken place. While some of the adjudicated damages can total fairly large amounts, damage assessments are still a reflection of proxy estimates of repair costs and are not derivatives of the actual services provided by the seagrass beds. Using the SEV model not only provides greater jurisprudence in determining economic costs of environmental damage, but gives spatial relevance to this estimate. For instance, all services provided by seagrass beds may not be occurring in the same magnitude at the site of the injury. By understanding the ecological dynamics of the local seagrass community and their relationship with the services they provide, damage assessments can be better tailored to the specific ecosystem that was damaged. In cases where HEAs are used to determine intermediate public compensation, the SEV model can be particularly useful. The HEA, uses simple ecosystem metrics as a proxy for function. The presence or absence of certain keystone species protected by a primary producer habitat will be used for example to determine if a particular system is functioning at or away from its ‘baseline’. While this is an ecologically valid approach it does not capture the full breadth of services that the area can provide. These relationships can be extracted from the SEV, and thus provide a more accurate estimate of what the societal compensation should be while the injury recovers.

8. FUTURE DIRECTIONS

Multiple studies have documented the services that seagrass ecosystems provide to local communities. Unfortunately, the economic valuations of these systems have not kept pace with the widening breadth of ecological knowledge. As coastal communities continue to develop disproportionately to their inland counterparts, better models need to be created to quantify both the economic value of coastal ecosystems as well as the monetary loss incurred when they become damaged. The SEV model provides a framework within which both the ecological and the economic relationships of seagrass ecosystems and the goods and services they provide can be delineated. By having the processes parsed out in this way, the model can be adapted across multiple spatial scales to address local variations. The robustness and reliability of the model will depend on the empirical determination of the variables that drive both the ecological and economic processes. For example, long-term monitoring can capture the temporal scales of patch growth dynamics within the context of the herbivory and nutrient pressure in a local system. Long-term monitoring can also capture fluxes in water column nutrients that are important both for the seagrass community, as well as the pelagic microalgae. Elucidating each vector that connects seagrass beds to an ecosystem function can provide an indication of how a basic understanding of ecological processes has large ramifications on local economies. As our understanding of these relationships improve, our conceptual framework of the seagrass ecology-economics relationship will simultaneously become more reliable.

Similarly, valuations of seagrass ecosystems should focus on specific relationships, as each relationship may require a different valuation approach. The total ecosystem value of seagrass beds can then be a summation of these different services.

CONCLUSION

The modeling of natural systems for the purposes of economic valuation is a field still in its developing stages, but a lot of progress has been made especially with respect to terrestrial systems. The Natural Capital project (52) for example, offers models that assist stakeholders in determining ecosystem service value of their managed system with a certain amount of spatial resolution. While these efforts as well as the model presented in this paper focus on the productivity model of ecosystem valuation, the contribution of WTP models should not be discounted. The existence value of seagrass ecosystems should be added to the other calculated use values. It is possible that with improved education and outreach, public understanding of seagrass systems will increase resulting in a corresponding increase in WTP.

With yearly declines in acreage, the need to valuate seagrass systems is urgent. Failure to completely grasp the full range of local ecosystem services that these systems provide means that the corresponding local economic loss is not known. As humans continue to populate coastlines, coastal ecosystems will continue to be exposed to increased anthropogenic pressure that may accelerate this loss. The absences of models that appropriately connect the ecological to the economic systems have resulted in valuations that are based on proxy variables that may unintentionally grossly undervalue seagrass beds. The SEV model provides a conceptual framework to use both existing ecological and economic models to address this need.

Table 17. Ecological contributions of seagrasses to local ecosystems and associated economic values. Vector labels correspond to the arrow labels in the SEV model. Ecology papers indicate various models used to quantify the ecological functions of seagrass beds. Economic papers indicate current publications that describe methods used to quantify these values. Vector labels correspond to arrows in the SEV conceptual model.

System	**Vector**	**Model**	**Reference**
Ecological	a	*Nutrient cycling* Root uptake = [(mineralization – diff.flux)/incorporation] X 100% Leaf uptake = [(diff.flux + (flushing x conc.))/incorporation] X 100%	Erftemeijer and Middelburg 1995 (53)
	b	*Water quality* Principle Components Analysis (PCA) of location-specific relevant water quality parameters	Fourqurean et al. 2003 (54)
	c	*Water quality effects on seagrass* 1. Discriminant Function Analysis (DFA) using PCA values and seagrass Cluster Analysis 2. K_d (PAR) = $(1/z_r)$ X $\ln(PAR_z/PAR_0)$ where PAR = photosynthetically active radiation	1. Fourqurean et al. 2003 (54) 2. Gallegos and Kenworthy 1996 (55)
	d	*Seagrass loss from herbivory* Location-specific biomass loss rates from the northern Florida Keys	Kirsch et al. 2002 (56)
	e	*Seagrass bed morphology* PCA of seagrass morphometrics with abiotic factors	Hackney 2003 (57)
	f	*Carbon sequestration*	Fourqurean et al. 2012 (30)
	g	*Wave energy reduction* $F = \rho C_d U^2$ where F is force per volume, ρ is density, C_d is the bulk drag coefficient for waves and steady currents, and U is the steady current speed at a particular height	Fonseca and Calahan 1992 (26)
	h	*Sediment stabilization* Ft = $a^* e^{-b^*H}$ *where FT = downward sediment flux in g DWm*$^{-2}$ *day*	Gacia et al. 1999 (58)
	i	*Sediment stabilization and water quality* Shields diagram $u_*^2 = \tau/\rho$ where u is friction velocity, τ is shear stress	Madsen et al. 2001 (59)

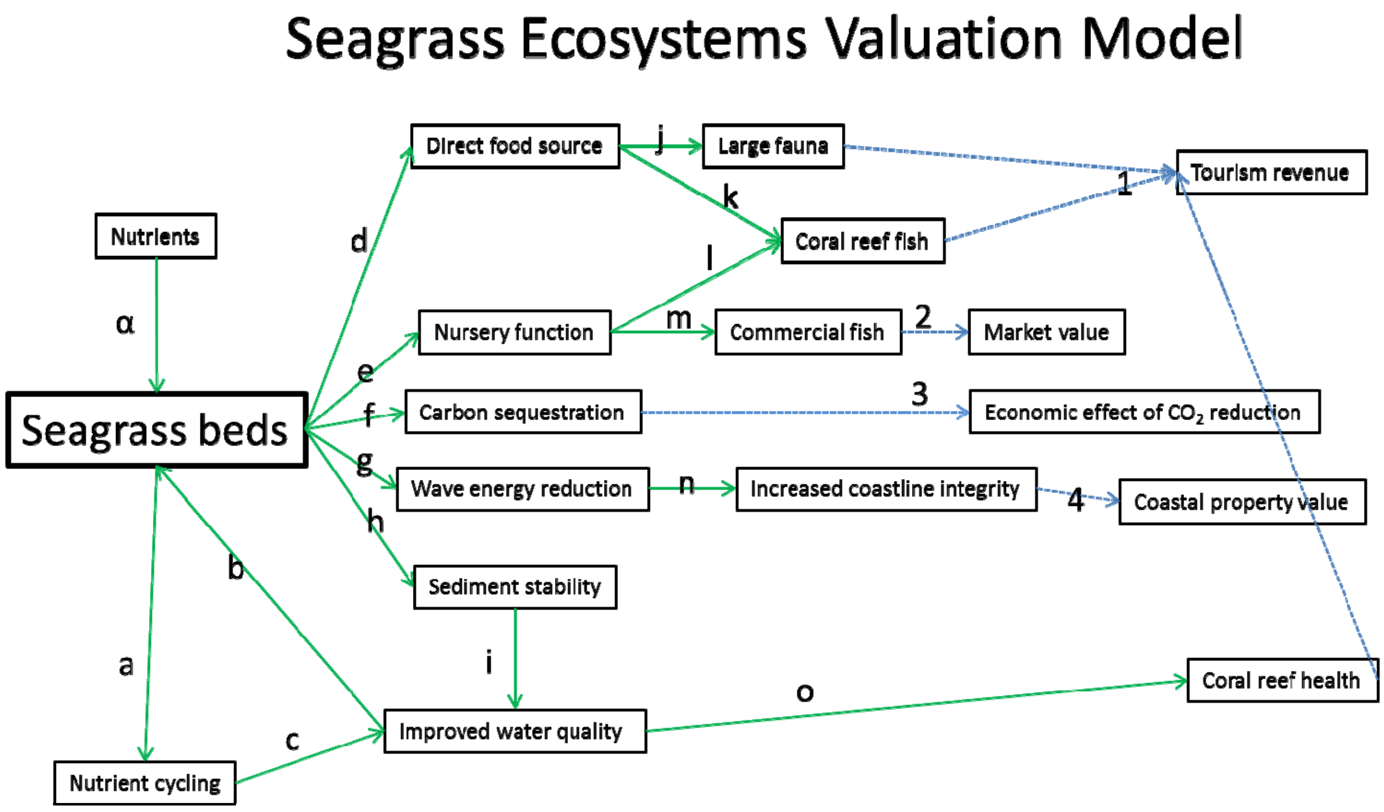
		on particles and ρ = water density	
	j,k	*Direct herbivory* Mixed-effects model for manatee feeding Feeding Cycle Length = $B_0 + B_1 X \ln(\text{body length} - 231.5\text{cm})$	Marshall et al. 2000 (60)
	l,m	*Nursery function* Seagrass Residency Index (SRI) – $S_i = ax_i + by_i + cz_i$	Scott et al. 2000 (61)
	n	*Wave energy and coastline integrity* $dX/dT \equiv F$ where dX/dT is the erosion rate and F is the force of the waves	Sunamara 1977 (62)
	o	*Water quality and coral reef health* Conceptual model	Haynes et al. 2007 (63)
System	Vector	Previous Valuation Approaches	Example Reference
Economic	1	Travel cost method, WTP	Spurgeon 1992 (64), Pendleton 1995 (65)
	2	Productivity method	MacArthur and Boland 2006(35)
	3	Cost-benefit analysis	Nordhaus 1991 (66)
	4	Hedonic pricing method	Feenberg and Mills 1980 (67), Joan Poor et al. 2007 (68)
	5	WTP	Vithayaveroj 2003 (29)

Table 18. Published seagrass ecosystem economic valuations.

Value	MEA Service	Ecology Studies	Economic Valuations	Valuation method	Value
Use (direct)					
Mulch	Fiber	Orquin et al. 1999 (69)			
Insulation	Fiber	Wyllie-Echeverria and Cox 1999 (21)			
Embroidery	Ornamental resources	Huong et al. 2003 (70)			
Use (indirect)					
Nursery	Food/Recreation	Heck et al. 2003 (25)	Anderson 1989 (5)	Productivity method (commercial fisheries)	US1.8million/yr
			Watson et al. 1993(56)	Productivity method (prawn commercial value)	US1150/ha/yr
			NOAA 1997(58),	Replacement	US28,000-684,000/ha
			Vithayaveroj 2003(59),	Productivity method	US203,200/yr
			McArthur and Boland 2006	Productivity method (fish commercial value)	US103.74 million/yr
			Paulsen 2007	CVM	US960,000/yr

			Samonte-Tan et al. 2007(62)	Productivity	US 204/ha/yr
			Guerrey et al. 2012(64)	Productivity method (multiple services)	US4585/ha
Tourism	Recreation	Daby 2003 (71)			
Carbon sequestration	Primary Production	Fourqurean et al. 2012 (30)			
Wave attenuation	Erosion regulation	Fonseca and Cahalan 1992 (26)			
Sediment stabilization	Erosion regulation	Terrados and Duarte 2000 (72)	Guerrey et al. 2012(64)	Productivity method (multiple services)	US4585/ha
Nutrient cycling	Nutrient cycling	Short 1987 (73)	Costanza et al. 1997(74)	WTP	US19,004/ha/yr
			Brenner et al. 2004(60)	Meta-analysis	US24,228/ha/yr
			Engeman et al. 2008(30)	Transfer method (original WTP, King 1998)	US140,752.23/ha
			Han et al. 2008(63)	CVM, Benefits-transfer, WTP	US100,640/ha
			Guerrey et al. 2012(64)	Productivity method (multiple services)	US4585/ha
Non-Use					
Existence			Vithayaveroj 2003(29)	WTP	US10.43million/yr

Figure 24. SEV model. Green arrows represent ecological function, blue arrows represent economic contribution.



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CHAPTER IV

The Total Ecosystem Valuation (TEV) of a seagrass ecosystem in a subtropical estuary

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1. Abstract

Understanding the true economic values of ecosystem services has gained interest among scientists, resource managers and policy makers. We conducted a Total Ecosystem Valuation (TEV) on a subtropical estuary in South Florida. We particularly considered certain ecological functions which hitherto have been unknown to the scientific community and were absent from existing seagrass valuations. Some of these values came from an extensive literature search, some from mining of existing datasets, and some from our own ecological research that quantifies some services. We concluded that the total economic value of the seagrass beds of Biscayne Bay in 2004 dollars was $198 million or $1,740.81 per hectare. These values are lower than some other estimates, but we believe are a more accurate representation of actual ecology services previous valuations. We believe our numbers to be very conservative as we only included values for which we could definitively quantify. We also separately analyzed some of the more recent findings of seagrasses as a sink for organic carbon, and the potential economic stock value that this storage can represent. Overall, our valuation indicates that we may have been significantly underestimating the value of seagrass beds. It also highlights the aspects of the ecosystem function-ecosystem services relationship that needs further investigation. We also suggest how our data can be used to make long-term policy for enhancing seagrass protection and conservation.

2. Introduction

Seagrass meadows provide a number of ecological services that make many of the aforementioned revenue-generating activities possible. Seagrasses are the dominant primary producers in many of the world's coastal estuarine/marine ecosystems (Kaldy et al., 2002). Seagrasses act as a nursery for juveniles of marine species that are present in both recreational and commercial catch (Heck and Thoman, 1984; Heck et al., 2003). Many of these species have different spatial life cycles. The young of some species grow up in the seagrass beds gaining biomass while being sheltered from larger predators that typically live in the open ocean (Heck et al., 2003). The extensive rhizomatous root system of seagrasses also holds the sediment in place thus reducing water column turbidity (Fonseca and Fisher , 1986). This allows sunlight to penetrate deep into the water column, necessary both for the coral reef system as well as the continued proliferation of the seagrass beds (Rogers, 1990). Seagrasses also remove nutrients from the water column and in so doing act as a protective buffer for the coral reefs from pulse nutrient additions (Flindt et al., 1999) that can produce ecological phase shifts on the coral reefs (Hughes, 1994). Recent studies have also documented the volume of organic matter that seagrass beds produce. This highly productive sequestration of carbon is among the world's largest stores of organic carbon (Fourqurean et al., 2012), and the ability of seagrass meadows to act as a sink for carbon has both ecological and economic relevance with respect to global climate change (Lavery et al., 2013).

Because of its proximity to a heavily populated urban zone, and the relative shallowness of the coastal zone, seagrass meadows are prone to heavy impact from human activities (Grech et al., 2011). This decline of seagrass meadows around the world have been extensively documented (Orth et al., 2006), the drivers of which include eutrophication (Cardoso et al., 2004), the overharvesting of top predators (releasing herbivores to feed unimpeded) (Heck Jr. and Valentine, 2007, 2006), and direct impact from mostly motorized vessels (Bell et al., 2002; Dunton and Schonberg, 2002).

Biscayne Bay is a large estuary located along the southeastern tip of the Florida coast in the United States. Biscayne Bay's boundaries encompass an estuary, a few uninhabited and habited keys, a coral reef tract, and a seagrass meadow. Over the years, an increasing number of boaters traveling in shallow areas of the meadow have left propeller scars that leave deep trailing indentations into the sediment. This not only inflicts immediate damage onto the bed, but also create a space for burrowing crustaceans to get under the rhizome bed and extend the damage by excavating the sediment beneath the beds (Patriquin, 1975). The unaided recovery time for these damaged beds has been estimated to be at minimum ten years (Zieman, 1976). In response to this, Biscayne National Park alongside several local agencies have been involved in both restoration projects aimed at rehabilitating these beds, and aggressive law enforcement where substantial fines are administered to caught perpetrators.

The enforcement of the fine is supported by state law regarding damage to natural resources, and is primarily based on a replacement cost (i.e. the cost to the park service in terms of man hours and equipment to rehabilitate the damaged meadow)(Heal, 2000). While the calculated figure may serve as a minor deterrent, it does not represent the true value in ecological and economic terms of the damaged bed. Attempts at valuation of seagrass beds in general have been fairly scarce, when compared to the valuation of other ecosystems. Most economic studies we found of Biscayne National Park do deduce the value of different revenue-generating activities, but treat each activity as a result of the entire ecosystem instead of just the seagrass ecosystem. Other activities isolate one ecological service provided by seagrass beds and assign that value it total to overall seagrass economic contribution. We were not able to find studies that focused on the role of only seagrasses and its role in some of these activities. A major reason for this might be because it is difficult to separate some of seagrass' ecological functions from other parts of the ecosystem.

In this manuscript we present a Total Ecosystem Valuation (TEV) of the seagrass ecosystem in Biscayne National Park. We combine studies on different economic activities related to seagrass beds or that are 100% a result of seagrass primary productivity. We show explicitly how the seagrass meadows in this subtropical estuary make an economic contribution to the local Miami economy using a value derived solely derived from the ecological services of seagrass. The use of the TEV and our approach in aggregating the values is relevant not only to provide an updated valuation for Biscayne Bay, but can also be used as a valuation model for other managed seagrass ecosystems where the primary producer ecological dynamics are well-documented.

2. Methods

2.1 Location

Biscayne Bay officially extends as far north as Haulover Bay, located to the northern end of North Miami Beach. Our study however focused on the area of Biscayne Bay between Turkey Point and the Port of Miami (Figure 26). Biscayne Bay is an estuary that is very saline (Lirman and Cropper Jr., 2003). The Bay is densely covered with primary producers (Thorhaug and Roessler, 1977). Among the seagrasses *Thalassia testudinum* is the dominant species, but there are also intermittently dense patches of *Halodule wrightii* along the shoreline, while dense stands of *Syringodium filiforme* are mostly located around the reef tract (Dewsbury et al. unpublished). The Bay is also home to a number of macroalgal species that are sparsely distributed both within the Bay and near the reef tract. While macroalgae contribute to the overall complexity of the primary producer structure, we consider only seagrasses for this TEV mostly because previous studies have established their structural dominance (Lewis III, 1987), and also because the services we discuss have been more clearly tied in the literature to seagrasses.

The Bay is bordered by the expanding sprawl of the city of Miami and North Miami, Florida to the west- northwest. Since before the development of the city of Miami, Biscayne Bay has been an important resource for food resources and transport, first for the Tequesta Indians that inhabited the environs, and then for the developing city of Miami (Harndon, 1975). The growing environmental movement in the early sixties spawned from a concern about the destruction of the Everglades forced the local and federal governments to pay greater attention to all of Florida's dwindling natural resources. This led to the southern part of Biscayne Bay being designated as a national park in 1968 (Burrus Jr., 1984).

After the park was appropriated, the rapidly growing local Miami community continued to use the bay and environs for fisheries and transportation. In fact, Biscayne Bay supported both commercial and recreational fisheries well into the 1990s (Berkeley et al., 1985; Davis, 1981). Greater protection for the area however also supported an expanding tourism industry that was to become a major contributor to the economy of south Florida (Mescon and Vozikis, 1985). For the past few decades, SCUBA diving trips, recreational boating, coastal leisure (a general term used here to encompass beach going, pleasure watching, birding, and near shore water sports) and 'glamour' activities to name a few have generated significant economic activity in the region (Bush, 1999). While the park boundaries do not cover the entire extent of the bay, a number of the aforementioned activities take place within park boundaries. This is partly due to the physical and logistical structure the park has in place to support these activities, but also because many of the natural resources that attract users are concentrated within the park boundaries.

2.2 Data collection

We used scientific paper databases such as ‘web of science’ and ‘ISI’ using search terms related to the individual services we were trying to valuate. For example, for tourism we entered ‘tourism seagrass economics Biscayne Bay’ into the search engine. Our literature searches yielded some peer-reviewed literature on these services in the context of Biscayne Bay, but it also produced numerous reports produced by both private and public entities on the economics of the entire Biscayne area. We conducted separate searches for economic studies on the Biscayne Bay area and the ecological processes that were the underlying drivers of these services. We searched extensively through the ecology and economics literature for valuations of goods and services from seagrass ecosystems and found little, especially in terms of valuations specific to seagrass beds. Most valuations were done on whole ecosystems (bays, lakes etc.), and similarly, the studies we found on Biscayne Bay treated seagrass beds as a contiguous part of a system that produced economically quantifiable services. For this reason we separated the economical services that seagrasses provided, and searched for valuation approaches for them individually. Where valuations were not found, we conducted valuations using our own datasets and/or knowledge of the ecological relationships between seagrass productivity and the service they provided. Due to the constraints of the available data and for simplicity, our valuation was done only on the calendar year 2004.

2.3 Components of TEV

There are many different ecosystem services that are provided or enhanced due to the presence of seagrasses. We restricted our analysis to services that were ecologically and economically quantifiable, and for which there were peer-reviewed studies. For instance, while seagrass beds have been shown to improve water quality and by extension contribute to real estate value on coastlines, we opted to exclude such benefits of seagrass, as the percent contribution of seagrasses to such value was unverifiable.

2.3.1 Tourism

We compiled a list of tourism activities that take place within Biscayne National Park. Items on this list were derived from published reports of economic activity within the park as a whole (Table 20). The tourism activities typically center on natural resources that are positively affected by the presence of a healthy seagrass bed. Using the travel cost model, Bhat (2003) estimated the value of traveler’s experience for a day’s trip to partake in tourism-related activities. We combined this value with Bak's (1978) documentation of the decreased calcification rates of coral reefs due to sedimentation. This study showed that sedimentation caused a 33% decrease in calcification rates in coral reefs. We assumed that the presence of an intact seagrass bed would prevent the negative effects on the coral community. We assumed then that the value of the traveler’s expedience associated with coral reefs (Bhat, 2003) similarly would be reduced by 33%. Finally, we estimated that the utility experiences by the tourist depend on equal contributions from seagrasses, coral reef and good water quality. For this reason the calculated value was divided by 3 to determine the final seagrass contribution.

2.3.2 Recreational fishing

Recreational fishing is a fairly restricted activity within Biscayne National Park. Removal of most reef-dwelling species is strictly prohibited. However, licenses are available for limited fishing of a few species. Many of these species rely on seagrass beds for habitat, especially in their juvenile stages. We made the assumption that the economic value of recreational fishing was fully dependent on the ability of intact seagrass beds to provide habitat. As a result we used a 2004 estimate of the economic value of recreational fisheries (Hazen and Sawyers Environmental Engineers and Scientists, 2005) in our analysis.

2.3.3 Commercial fishing

To calculate the contribution of seagrass beds to the revenue generated by commercial fishing, we considered the life cycles of one of the species caught and the market value this species held for the year in question. Not all commercial species rely on seagrass beds at any point in their life cycle. Those that do, typically do so during their juvenile years (Watson et al., 1993). The complexity of the seagrass meadow provides protection from predation and in some cases houses other microorganisms that serve as a food source for these juveniles (Orth et al., 1984). We assumed then that biomass gained over time of these juveniles is mainly due to the services they receive from the seagrasses. As adults in the open ocean, these species may or may not rely on seagrasses and we therefore did not consider this stage in our calculation. We assumed that once in the open ocean these species had a 100% probability of potentially being part of the commercial catch. The value of the seagrass beds was therefore calculated as the specific change in biomass during the time spent within the seagrass community multiplied by the market price of that particular species for 2004. For this analysis we focused on pink shrimp (*Panaeus duorarum*).

Pink shrimp typically migrate into the estuary as larvae during the summer months and leave in the late winter after maturing (Ewald, 1965; Fry et al., 1999). We used Robblee's (unpubl.) long-term shrimp monitoring program data to determine that larvae enter Biscayne Bay with an approximate carapace length (CL) of 2.6mm and leave as juveniles with an approximate CL of 10mm. CL of pink shrimp was shown to correlate with weight (lbs) of the shrimp using the formula $W=0.000731 \times CL^{(3.024)}$ (Diaz et al., 2001). We estimated stock abundance of pink shrimp using the long term data sets of Robblee (unpubl.) and multiplied these numbers by the calculated weight to determine stock weight for Biscayne Bay. We then used the market price for pink shrimp of that year (FWC 2004) to estimate the market value of the biomass of the entire stock of pink shrimp that could be attributed to Biscayne Bay.

2.3.4 Carbon sequestration

Seagrass beds are highly productive ecosystems that convert inorganic carbon to organic carbon most of which is stored in the sediment (Beer et al., 2002). To determine the average organic carbon concentration in Biscayne Bay, we sampled 190 randomly chosen sites for sediment using 10cc cores. Three cubic centimeters of sediment were destructively sampled at each site by technicians on SCUBA. The sediment samples were ground into a fine powder in the laboratory. We used 'loss on ignition' to determine organic carbon content. First the samples were analyzed for total carbon using a CHN analyzer (FISONS 1500). Afterward, a subsample of the original stock was combusted at 400°C for 4 hours to remove all organic carbon. The combusted sample was analyzed in the CHN analyzer (FISONS 1500) with the assumption that the remaining carbon was inorganic carbon. Organic carbon was calculated by subtracting the inorganic carbon abundance from the total carbon abundance determined in the un-ashed sample. Using these techniques we estimated carbon storage in Biscayne Bay sediments in Mg/ha. We multiplied total carbon storage in Biscayne Bay by a central estimate of the social cost of carbon published by Environmental Protection Agency (EPA; (*United States Government (USG) (2010) Technical support document: Social cost of carbon for regulatory impact analysis under executive order 12866*, 2010) at $41 per ton (Table 21). This central estimate represents the increased social cost of carbon due to the negative effects of climate change caused by carbon increase in the atmosphere. We considered carbon storage in this system is a fixed commodity as estimates of carbon emissions from these systems were highly variable.

3. Results

3.1 Tourism

Biscayne Bay is a popular destination for tourism related activities. Mild temperatures year round attract visitors from around the world, especially during the winter months of more temperate areas. Water-based recreational activities are also supported by locals, who contribute economically through boat-ownership (individual), and the development of small tourism-related businesses. The Biscayne Bay Economic Study for 2004 (Hazen and Sawyers Environmental Engineers and Scientists, 2005) identified a number of revenue producing activities in the Biscayne Bay area (Table 20). Of these activities, we isolated activities that we felt would not occur if not for the health and integrity of seagrass beds. These activities were mostly associated with coral reef visits and included snorkeling, SCUBA diving and visits to the reefs via glass-bottom boats. Bhat et al (2003) calculated that a day trip (traveler's expedience) to visit coral reefs in South Florida would be approximately $122 per day. Bak (1978) calculated that calcification in coral reefs is reduced by 33% in the presence of strong sedimentation. Sediment stabilization is a primary function of seagrass beds, so we assumed that in the absence of seagrass beds, the value of the coral reef experience should also decrease by 33%, resulting in a traveler's experience value of $81.74. Considering the number of visitors for each activity and the ‘equal’ contributions of seagrass, coral reefs and water quality to the experience of the visitor, we calculated a total economic value for seagrass-related tourism to be $108,114,773.

3.2 Recreational fisheries

The fish species that are most associated with the recreational fishing industry depend on seagrass beds for habitat. We estimated however that high quality water, an intact coral reef and a functioning seagrass bed are all important to sustain recreational fish populations. Seagrass beds then contributed approximately 33% to the total economic value of recreational fishing. We used the valuation of this industry by Hazen and Sawyers (2005) to represent total economic output that can be directly attributed to recreational fishing. We then estimated the seagrass contribution to that output to be 33% of $3,789,000. Seagrass contribution to recreational fisheries was $1,263,000.

3.3 Commercial fisheries

We estimated a total shrimp stock of Biscayne Bay to be 46,632,739.97 pounds, which, at a market price of $1.91 per pound brought $88,552,833 to the south Florida economy. In this calculation, we assumed that any adult shrimp leaving the bay had a 100% chance of being part of the commercial catch.

3.4 Carbon sequestration

Using 10cc sediment cores from 190 sites, we determined that organic carbon in the benthos of Biscayne Bay is 50.22523346 Mg/ha (Table 21). The sample area in this study is 113700.478 hectares. Using a central estimate of the social cost of new atmospheric carbon ($41 per ton) (Lavery et al., 2013), we determined the economic value of carbon sequestration in seagrass beds in Biscayne Bay to be $217,585,164.

4.1 Discussion

We estimate that the TEV of Biscayne Bay for the calendar year 2004 is $198 million US dollars (Table 19). This value is based on the economic goods and services from which we were able to quantify using an extensive literature search and our own ecological sampling. Though this figure is lower than other estimates provided for seagrass ecosystems, we believe that unlike other approaches, this estimate is a truer representation of the actual ecological services seagrasses provide than previous reports. We also estimate that 'blue carbon' represents a potentially valuable economic stock value that is approximately $217,585,164, based on our organic matter sampling. Furthermore, our valuation is an extremely conservation one as it did not address other notable services that seagrass ecosystems provide such as nutrient cycling (Erftemeijer and Middelburg, 1995) and non-use values of seagrasses due to lack of economic data. Our valuation of the relationship between seagrass beds and commercial fisheries only used one species. There are a number of other species that rely on seagrass beds for habitat for themselves, or for the organisms on which they feed. Some of these species become part of commercial catch, and others are part of the varied fauna that attract visitors to coral reefs each year (Nagelkerken et al., 2002). Even more complicated is the role that non-commercial organisms play in maintaining the marine food web. While some predators or primary consumers in Biscayne Bay might not be charismatic or become part of commercial catch, they may still play important roles in regulating the population (top-down or bottom-up) of other species that are easier to valuate (Armitage et al., 2005). Not including these species in our analysis results in an underestimation of seagrass value. We used a central estimate of the social cost of climate change due to increased carbon in the atmosphere. The estimated range of the social cost is from $7-$81 per ton of carbon increase (*United States Government (USG) (2010) Technical support document: Social cost of carbon for regulatory impact analysis under executive order 12866*, 2010). If social costs end up being closer to the higher end of this estimate, the value of carbon sequestration by seagrass beds will be much higher than we have estimated here. Our blue carbon estimate here is also conservative because we only subsampled 3 cubic centimeters of surficial sediment. We did not consider carbon stored within the living material of the primary producers (Duarte and Cebrian, 1996; Gattuso et al., 1998) as well as organic carbon that can be found up to 6 meters deep in some beds. A significant omission from this study also is the multiplier effects (Archer, 1982) that in some may owe their magnitude to the vitality of the seagrass beds. Small tourist businesses in the area, for example, may depend on an intact coral reef and seagrass system to be profitable. While it is possible to estimate those services, we did not think that it was necessary for this stage of the valuation. Seagrasses in Biscayne Bay are worth $1,740.81 per hectare for the year 2004. This estimate of the economic value of seagrass beds adds to the body of work regarding valuations done on seagrass systems (Barbier et al., 2011; Costanza et al., 1997; McArthur and Boland, 2006). While the numbers we report here might be lower than other estimates, we use an approach that more explicitly incorporates all of the different services of seagrass beds, and is conservative since a lack of data precluded a more precise estimation. To the best of our knowledge, this is the only valuation of seagrass beds that utilizes this approach.

Biscayne Bay is a highly managed marine park that supports a number of human activities. Attempts to increase public awareness about the importance of seagrass ecosystems to support these activities are still in its beginning stages. Economic valuations are necessary to heighten the awareness among the relevant stakeholders in this system of their *actual* value. For instance, in situations where managers have to make decisions about coastal development or marine engineering, an underestimation of the economic value of seagrasses can lead to decisions made in favor of developers (Bingham et al., 1995). This typically happens because developers can more easily demonstrate the economic value of construction to the local economy through taxes. A better understanding of the full economic contribution of seagrasses will allow those invested in its protection to make a more reasoned argument for policy geared toward protection of seagrasses. In South Florida, tourism is one of the main drivers of the local economy (Mescon and Vozikis, 1985). The critical role that seagrasses play in sustaining many of the tourism-related activities means that it is even more important to make its economic value known to all stakeholders.

In addition to awareness campaigns, there are other attempts to protect and conserve seagrass beds and other marine resources in South Florida. Biscayne National Park has an active program that supervises the restoration of impacted seagrass beds. This program also has a monitoring component that assesses the progress of restored beds. The enforcement arm of the park service prosecutes vessel owners who are caught damaging seagrass beds. The resulting fines and penalties are primarily used toward restoration efforts. The amount charged to the individual is derived largely from a calculation of the cost of replacement of the damaged bed, the response to the injury and assessment of its extent. The prosecution of vessel grounders is protected by the Park Service Resource Protection Act, but the cost of the damage is calculated on a case by case basis. Mild offenders may be given a fine of $50 (Howard, 2009) for small damages, but there have been cases where damage was calculated to be upwards of $30,000 (Nolin, 2006). At almost 2 thousand dollars per hectare, our valuation estimate is higher than the current fine levels. We are not necessarily arguing that fines should increase to 2 thousand dollars per hectare, but our analysis clearly shows that perpetrators of seagrass damage may have been undercharged for their offenses.

Our TEV approach to Biscayne Bay can be applied to other estuaries provided that information is available about the ecological components of those systems and the economic services they provide. Such an approach would need to appropriately identify the boundaries of the relationship between the ecosystem functions and human community being served. For example, Florida Bay, a neighboring estuary to Biscayne Bay, also has a dense population of seagrass beds (Fourqurean et al., 2002), but the borders of this estuary are not as densely populated. Florida Bay also does not host as much of the tourism related activities as Biscayne Bay. A TEV of this seagrass system would have a lower value for tourism-related activities, but possibly a larger value for Blue Carbon since it is larger in acreage than our study area. The use of this model requires both systematic and long-term approaches to understanding the ecological dynamics of local ecosystems, the specific services that those dynamics provide to the local community and a method by which those services can be economically quantified. By teasing apart the different components of ecological functions and ecosystem services, the TEV approach highlight the aspects of this relationship that still need quantifying. For example, our valuation would be more accurate if we had a better understanding of the ecological relationship between commercially caught juvenile snappers and the seagrass beds they sometimes use to feed or reside. We also don’t have a good handle on how to quantify (other than using a substitution method (Costanza et al., 1997) the nutrient cycling activity of seagrass. Blue carbon as an economic entity is recently described phenomenon (McLeod et al., 2011), and the economic values reported rely on the assumption that 100% of the organic carbon in the sediment can be returned to the atmospheric pool of carbon.

Our economic valuation does not capture all of the economic contributions that seagrasses make, but we believe it’s most comprehensive attempt made thus far. By aggregating the different services seagrass provide, we have shown the economic value of seagrasses in more explicit ecological terms. This new valuation can be used as a new metric to assess culpability when seagrass beds are negatively impacted, but more importantly should reinforce why it is critically important to conserve and protect them.

5. Conclusion

Seagrass ecosystems have been shown to be ecologically and economically valuable. Ecologically they support ecosystem structure by acting as a juvenile nursery and cycling nutrients from the water column. These ecological functions often translate into services that have economic value for communities that live along the coastline. The negative impact that these ecosystems receive however from growing human populations has made quantifying the economic contributions of seagrasses a necessary exercise.

We establish here that the Total Economic Value of seagrasses for the year 2004 was \$198 million dollars through, tourism, recreational fishing, and commercial fishing. We also establish that seagrasses potentially hold another \$217 million dollars in stock value in the form of ‘blue carbon’. Our estimates are lower than some previously reported values, but we believe them to be fairly conservative, as they did not incorporate a number of other known economic services that seagrasses provide. We argue that our

TEV approach is an appropriate way to identify separate ecosystem functions and establish total economic value where data are available. Such a framework can provide managers and policymakers the tools they need for seagrass protection and conservation.

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Table 19. Total Ecosystem Valuation of Biscayne Bay for 2004 in US dollars.

Good/Service	Ecological Relationship	Valuation method	References	Value (US$)
Tourism	Seagrass improves water quality making activities possible	Productivity	Biscayne Bay Economic Study 2005	**108,114,773.30**
Recreational fisheries	Seagrass provides nursery and habitat	Productivity	Johns 2004	**1,263,000.00**
Commercial fisheries	Seagrass provides nursery at critical life stages	Productivity	FWC 2004, Robblee unpubl., Ault et al. 2001, Kanciruk and Herrnkind 1976	**88,552,833.34**
Annual flows Total				**197,930,606.6**
Stock values				
Blue Carbon	Seagrasses acts as a sink for atmospheric carbon	Productivity	Fourqurean et al. 2013	**217,585,164.82**

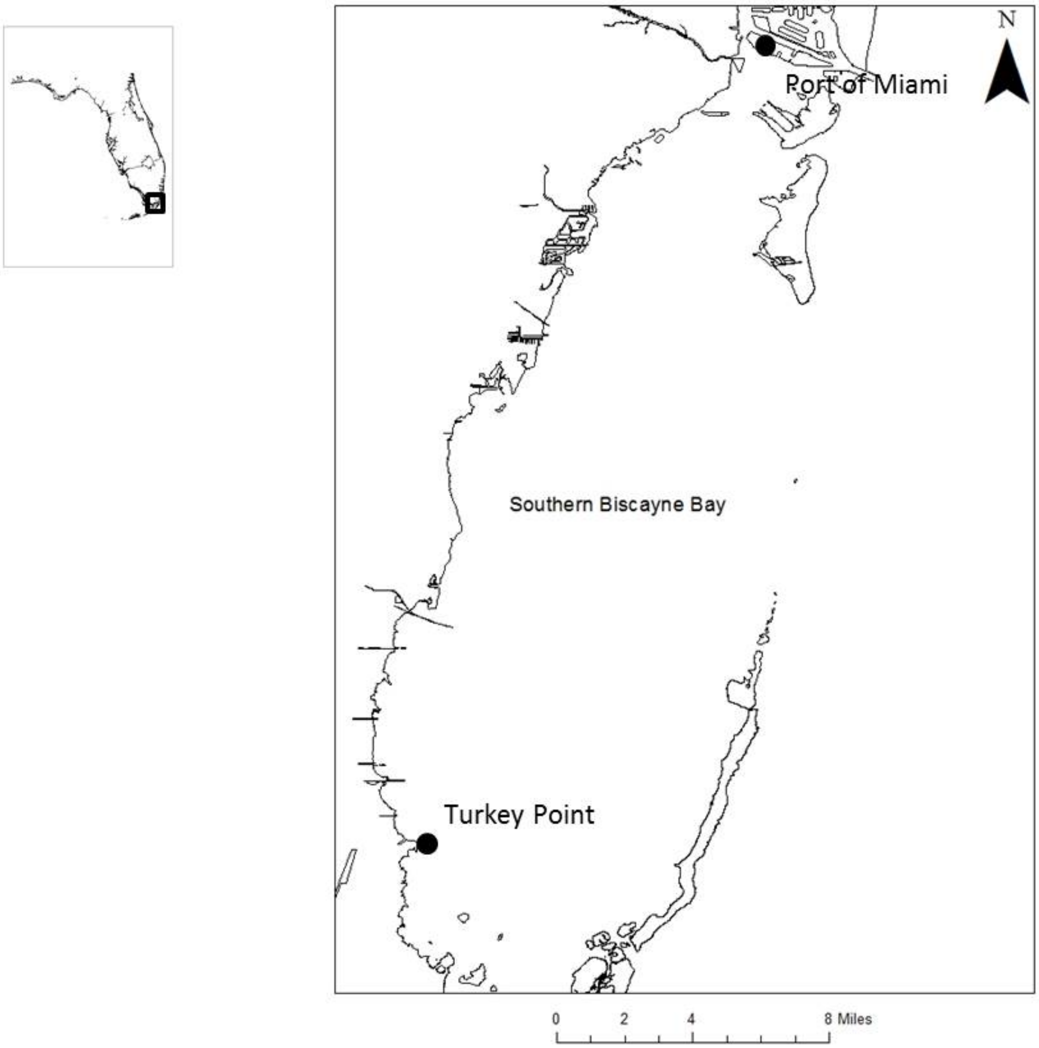
Table 20. Seagrass economic value due to tourism in US dollars. Value per day was determined using traveler’s expedience. Seagrass contribution estimated as 1/3 towards total value

Activity	Visitation (person days)	Value ($/day)	Total (US$)
Snorkeling	2,726,000	81.74	222,823,240.00
SCUBA	1,236,000	81.74	101,030,640.00
Glass bottom boat tours	6,000	81.74	490,440.00
Total			**324,344,320.00**
Total seagrass contribution			**108,114,773.30**

Table 21. Total potential value of organic carbon locked in Biscayne Bay sediments. Value is based on a low estimate of carbon market price.

Total Organic Carbon Biscayne Bay (Mg)	**5,710,633.0541**
Average Organic Carbon per hectare (Mg/ha)	50.22523346
Market price of carbon ([low estimate] $/Mg)	41
Total Value of Organic Carbon Biscayne Bay ($)	**217,585,164.82**

Figure 25. Southern Biscayne Bay. Our area of study focused on the area of Biscayne Bay between Turkey Point and the Port of Miami.



Conclusion

Southern Biscayne Bay contains a dense population of seagrasses that had an annual value of 198 million US dollars in 2004. This does not include potential stock value of 217 million US dollars due to blue carbon storage. The distribution of these seagrass beds are largely affected by abiotic factors in the water column. Anecdotal evidence and previous studies suggest however that further from shore, herbivory may play a stronger role in determining community structure. Increased nutrient concentrations and increased variations in salinity can result in community structure changes near the coastline, especially in the areas near downtown Miami.

I determined that southern Biscayne Bay is primarily a phosphorus-limited system that is densely populated by mostly *Thalassia testudinum*. *Syringodium filiforme* and *Halodule wrightii* are sparsely located to the east of estuary and in intermittent pockets respectively (Chapter 1). Water column nitrogen and salinity primarily determine *T. testudinum* distribution and changes in these variables can cause changes in the way in which primary producer communities are distributed (Chapter 1). Nutrient enrichment over a 7-month period did not significantly alleviate nutrient limitation in either the phosphorus-limited or nitrogen-limited sites (Chapter 2). Observational evidence at the two sites further from shore suggests a mitigating top-down role that could be a factor in community structure at enriched sites (Chapter 2).

A review of seagrass ecosystem valuation indicates that many valuations to this point rely on replacement estimates or substitutions costs as a proxy for the value of seagrass function. A few recent studies have begun to use productivity estimates of seagrass beds with respect of fishery production (Chapter 3). A Seagrass Ecosystems Valuation (SEV) model can effectively connect ecological function to ecosystem service, and thus provide a framework around which future seagrass valuations can be conducted. A conservative valuation of seagrass economic value in southern Biscayne Bay for the year 2004 showed seagrasses to be worth approximately 198 million US dollars (Chapter 4). This valuation is an estimate of ‘flow’ services, and does not include our estimation of blue carbon storage within the benthos of Biscayne Bay. This ‘stock’ value of blue carbon is possibly worth 217 million US dollars (Chapter 4). Our valuation here was limited somewhat by lack of ecological data on some of the commercially important fish species (eg. spiny lobster and blue crab), and appropriate mechanisms to quantify some of the ecological functions of seagrass beds (such as nutrient cycling).

Our ecological-economics model suggests that in South Florida, seagrass beds contribute strongly to supporting tourist activity, recreational and commercial fishing and carbon storage and that changes to the primary producer composition brought about by direct impact or salinity and nutrient changes can severely impact the services these beds provide. There is precedent for these negative cascading effects in similar estuaries. Multiple stressors resulted in a seagrass dieoff in Florida Bay in the early 1990s. The following year saw a steep drop in the commercial fisheries of pink shrimp

(*Panaeus duorarum*), presumably as a result of the loss of habitat for the juveniles of that species. This makes the argument that in addition to the water quality monitoring programs, Biscayne Bay probably could also benefit from a long-term seagrass monitoring program. Such a program would better identify spatio-temporal dynamics in seagrass ecosystem on a scale our work here could not provide, and may provide the kind of data to substantially enhance future valuations. Such an effort is especially important for southern Biscayne Bay. With its proximity to the growing Miami-Dade metro area, this estuary will likely experience greater impact associated with growing human populations.

In this dissertation I have attempted to address my own interpretation of how natural capital can inform stakeholders about the economic limits inherent in ecosystem services. I suggest here that as we seek ways to manage natural resources with an ecosystem-based management approach, it is important that we understand the dynamics of the ecosystem first, and then use those dynamics to quantify the economic value of goods and services. This can become valuable where estimates are used for punitive reasons (vessel groundings etc.), or in general to create awareness about the importance of preserving these systems. Most importantly, if managers are to both create contingency plans for possible impact, and argue to legislators for the financial support to do so, an understanding of both the ecology and economics of this relationship is absolutely essential.

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