CHANGES IN THE DISTRIBUTION AND DENSITY OF FLORIDA BAY MACROPHYTES: 1995 – 2004

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ABSTRACT

Benthic macrophyte cover and distribution data have been collected in ten basins within Florida Bay since 1995 as part of the Florida Bay Fisheries Habitat Assessment Program (FHAP). A weighted average for the most prevalent macrophytes during each sampling event since spring 1995 was calculated. Results indicate that the three most common seagrasses observed in Florida Bay, *Thalassia testudinum, Halodule wrightii,* and *Syringodium filiforme*, have increased in distribution since 1995. *Halodule wrightii* and *Syringodium filiforme* exhibited an increase in both frequency and cover at the bay-scale, an occurrence driven by their dramatic increases in the western-most FHAP study basins: Johnson and Rabbit Key Basins. *Acetabularia*, *Batophora*, *Halimeda*, and *Penicillus* also exhibited increases in both frequency and cover since spring 1995. The drift Rhodophytes increased in density and distribution between spring 1995 and spring 1998, but did not increase further after that time. *Batophora* proved to be the most ubiquitous macroalgae throughout Florida Bay and *Acetabularia* and the drift Rhodophytes showed the strongest seasonal fluctuations, as they were both much more abundant and widespread during spring samplings.

Spearman rank order correlation analysis of the Braun-Blanquet cover data showed that *Thalassia* was generally negatively correlated to all other macrophytes, while *Halodule*, *Halophila*, and *Syringodium* were positively correlated to one another on most occasions. These seagrasses fluctuated between positive and negative correlations with the macroalgae, and as a group, the macroalgae were positively correlated with one another on most occasions, although exceptions did apply.

Non-metric multidimensional scaling was used to create ordination plots of the ~ 315 sample stations. Density overlays were used in conjunction with these ordination plots, and together these showed that total seagrass cover and total macroalgal cover were generally mutually exclusive. Spearman rank order correlation analysis was further used to determine if this spatial separation of the two macrophyte groups was statistically significant at the bay-scale, and it was found that 11 of the 18 bi-annual sampling events yielded a statistically significant negative correlation between total seagrass cover and total macroalgae cover.

Canonical Correspondence Analysis (CCA) was used to determine which, if any, of the environmental/physical variables, collected as part of the FHAP data set, had a significant effect on macrophyte distribution within Florida Bay. Significance of these effects was determined using Monte Carlo Permutation Tests. CCA showed that depth and visibility were the initial driving forces in macrophyte distribution. During fall 2000, however, a spike in salinity was observed and by spring 2001 this became the most significant variable affecting macrophyte distribution, and it remained so, along with depth, throughout the duration of FHAP.

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CHAPTER 1

BASIN-SCALE CHANGES IN THE DISTRIBUTION AND DENSITY OF FLORIDA BAY MACROPHYTES: 1995- 2004

INTRODUCTION

Florida Bay is a unique marine ecosystem comprised of forty-nine shallow basins largely separated by a reticulating network of carbonate mudbanks and mangroves (Fourqurean and Robblee 1999). It is triangular in shape, with the Everglades occupying much of southern Florida to the north of the bay, and the Florida Keys, a ridge of Pleistocene coralline limestone, making up its southern and eastern boundaries. The Gulf of Mexico borders the bay along its western perimeter (FIG. 1).

Geologic formation of Florida Bay began approximately 4,500 years ago, when the southwestern portion of the bay began to flood as a result of the Holocene rise in sea level. A slope in the bedrock, deepening from northeastern to southwestern Florida Bay (Perkins 1977, Wanless and Tagett 1989), prevented the entire bay from flooding at once and the northeastern parts of the bay remained terrestrial until about 1,500 years ago (Enos and Perkins 1979).

This slope in bedrock, as well as age of formation, are cause for an increase in sediment and water column depth along a northeast to southwest diagonal gradient across the bay (Zieman et al. 1989). Unconsolidated carbonate mud sediments are deeper in the southwest than in the more northeastern parts of the bay where shelly bottoms and bedrock outcrops are not uncommon. Other than a shallow layer over the bedrock, accumulation of sediment in the northeast is primarily limited to the mudbanks that divide the relatively large and shallow basins. Basins in the southwest are smaller and

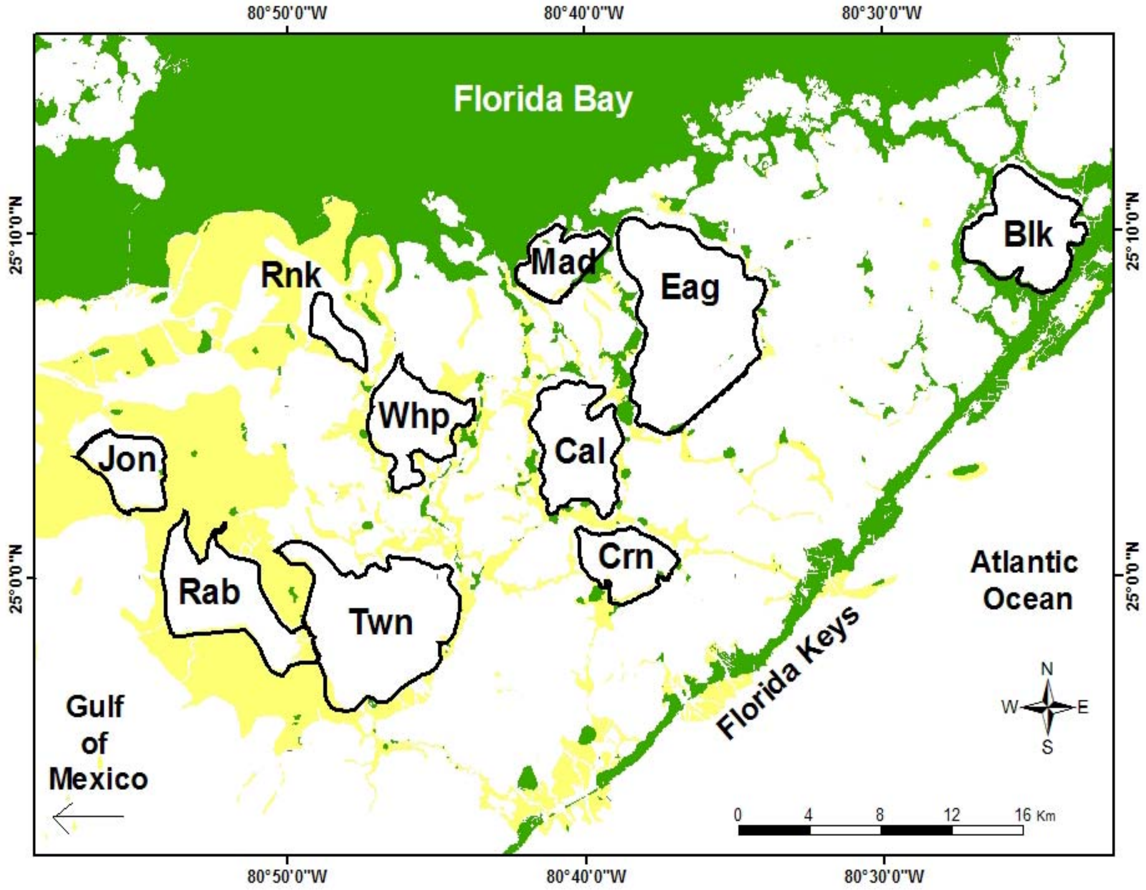


FIG. 1. Florida Bay map showing the ten FHAP study basins. The south Florida mainland, the Florida Keys, mangroves, and other islands are shown in green. Mudbanks are shown in yellow.

deeper than those in the northeast.

The western perimeter of Florida Bay that borders the Gulf of Mexico is subject to the most tidal fluctuations in depth, but the mudbanks towards the central and northeastern parts of the bay attenuate tidal influences to the extent that tides are virtually absent in the rest of the bay (Turney and Perkins 1972; Holmquist et al. 1989). Input from Taylor Slough and the C-111 canal, as well as rainfall, are therefore the major mechanisms of water addition throughout the eastern portion of the bay.

Annual precipitation over Florida Bay is about 1.2 meters per year and the majority of rain falls between May and October (Schomer and Drew 1982). The wet season coincides with intense summer heat in this subtropical climate and extensive heating in such shallow basins results in high evaporation rates that lead to water loss as great as that which is gained from rainfall (Fourqurean and Robblee 1999).

Historically, the Everglades ecosystem, a shallow, slow moving river that began at the Kissimmee watershed and Lake Okeechobee to the north, and extended south to Florida Bay (Davis et al. 1994, Lodge 1994), provided enough freshwater input to prevent hypersaline conditions caused by evaporative loss. Development in Florida, however, has been rapid over the past century and as a result, a great deal of the Everglades has either been lost to agriculture and residential development or has been otherwise modified (Solecki et al. 1999). Much of the water that originally entered Florida Bay through Taylor and Shark River Sloughs was redirected away from the bay through a system of control structures that regulate water levels for agricultural and urban flood protection and use (Davis et al. 1994). As a result, delivery of freshwater into Florida Bay has been reduced in its quantity, duration, and quality (Fennema et al. 1994, Light and Dineen 1994, Solecki et al. 1999, Smith et al. 1989). Because Florida Bay is composed of many shallow and relatively isolated interior basins with restricted circulation, it is susceptible to high temperatures, and fluctuating-to-hyper-salinities that are exacerbated by this lack of natural freshwater input (Lee et al. 2002, McIvor et al. 1994).

A decline in the health of the Everglades ecosystem over the past decades lead to the creation of the Comprehensive Everglades Restoration Plan (CERP) (http://www.evergladesplan.org), which is currently underway. CERP is an extensive and multi-million dollar restoration project aimed at gradually re-establishing historic hydrologic characteristics and water flow through the Everglades to the greatest extent currently possible (only 50% of the historic Everglades remain, while the rest have been irreversibly lost to agriculture and development). As Florida Bay is directly downstream from the Everglades, this restoration effort will affect the bay by increasing its freshwater input (Rudnick et al. 1999), potentially alleviating frequent hypersaline conditions.

In addition to anthropogenic stresses, such as this one typically caused by coastal development, natural stresses also occur in the bay. While most ecosystems are able to withstand some degree of stress, the synergistic effects of both natural and anthropogenic stressors may ultimately lead to a decline in ecological resilience, or the ability to adapt to changing conditions (Gunderson 2001). Florida Bay reached its threshold of resilience during summer 1987 when a massive seagrass die-off began in the western part of the bay (Robblee et al. 1991). It was first observed in Rankin Lake and then extended through approximately 30% of the dense seagrass beds of western Florida Bay by summer 1989. The die-off was most prevalent in shallow areas of protected lagoons with dense seagrass beds, and occurred most rapidly in fall and spring. Mortality occurred in patches and by 1991, an estimated 40 km^2 of *Thalassia* were lost and 230 km^2 were affected to a lesser extent in the west and central bay (Robblee et al. 1991).

Although causative agents for the die-off are not completely understood (Hall et al. 1999), several were implicated and include the following: a loss of the estuarine nature of the bay over many years (Zieman et al. 1988), high water temperatures, prolonged high salinities, build-up of seagrass biomass resulting from a lack of severe storms, hypoxia (Hall et al. 1999), sulfide toxicity, eutrophication (Lapointe and Clark 1992), and pathogens/disease (Durako and Kuss 1994). Two similar conceptual models of the die-off were developed and are presented below. The first was developed by Carlson et al. (1990) (FIG. 2). The second was developed by Zieman and although not pictured is discussed in Zieman et al. (1999) (FIG. 3).

Despite subtle differences in the models with regards to the weighted effects of different agents, both stress the importance of the combined effects of many years of stress and the cyclical nature of the resulting event. Following the initial die-off, and as portrayed in the models, further environmental change took place. Due to its extensive underground network of rhizomes that help to stabilize the sediment, *Thalassia* plays a major role in shaping the bay's physical characteristics. When the seagrasses died, the loss of rhizomes resulted in resuspension of sediments and the bay became turbid in many areas (Zieman et al. 1999). Light attenuation consequently increased. This acted to slow the recovery of *Thalassia* as well as cause a secondary thinning of seagrasses in some areas due to a decrease in available photosynthetically active radiation (Phillips et

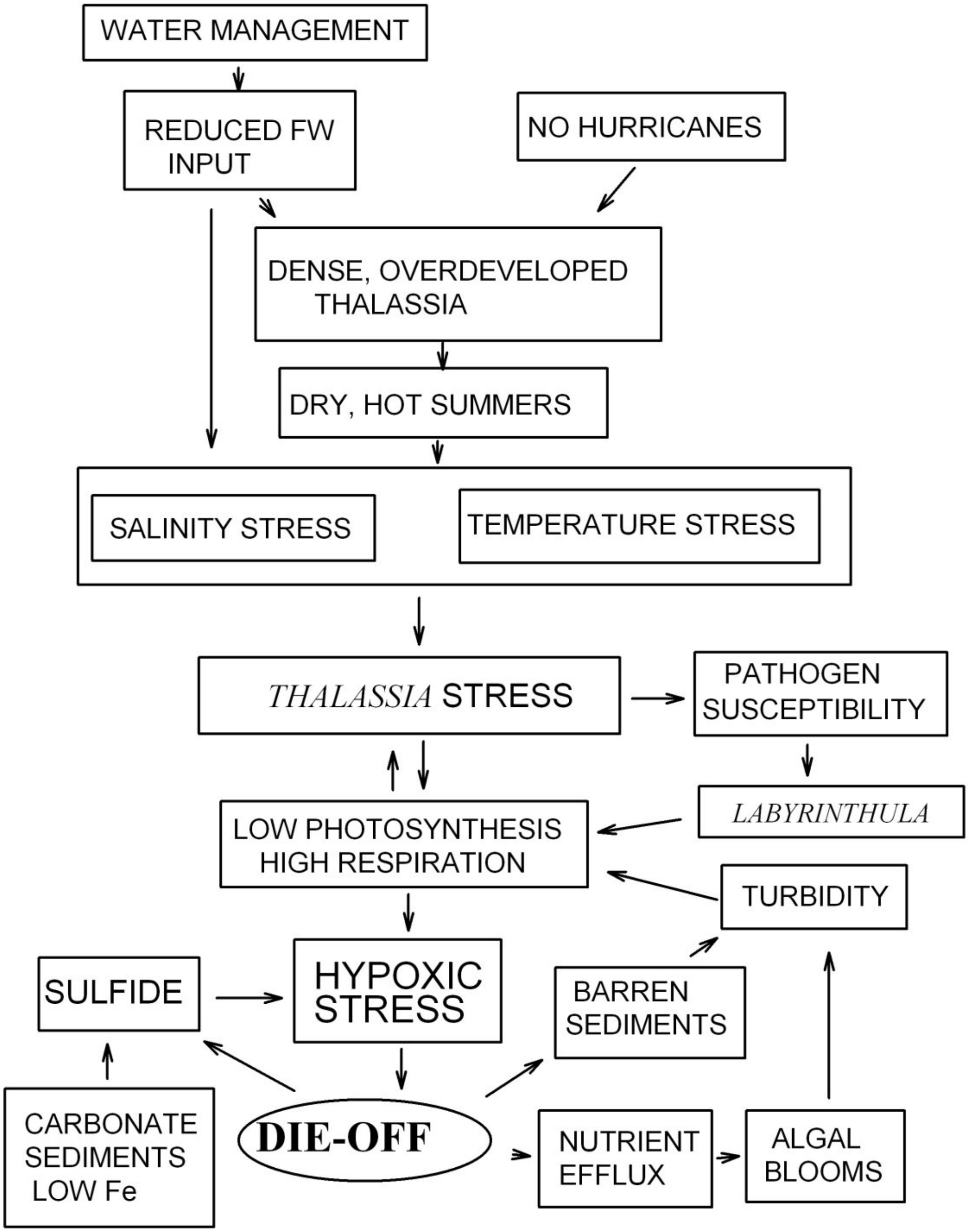


FIG. 2. Conceptual model of Florida Bay seagrass die-off by Carlson et al. (1990)

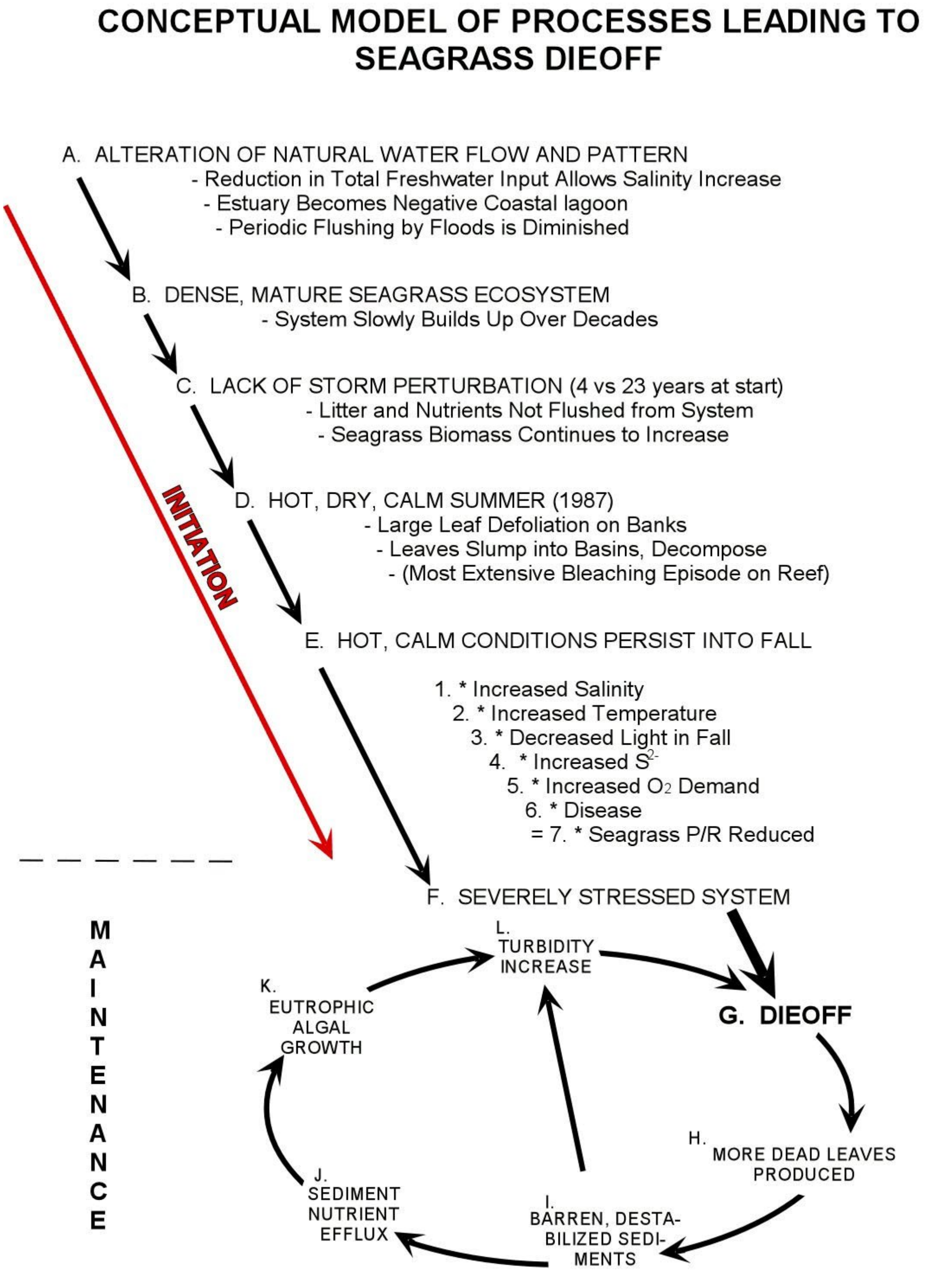


FIG. 3. Conceptual model of Florida Bay seagrass die-off by Zieman et al. (1999).

al. 1995). Phytoplankton blooms simultaneously became common as a result of the increase in available nutrients released from the decaying seagrass. These blooms were implicated in the mortality of sponges (Butler et al. 1995), which provide habitat for invertebrates such as the economically valuable (Hunt 1994) juvenile spiny lobster (Herrnkind et al. 1994).

Besides important habitat provided by sponges for the spiny lobster, ninety-five percent of the bay's bottom is dominated by seagrasses which play an important ecological role as nursery grounds for the Tortugas pink shrimp fishery (Allen et al. 1980, Kilma et al. 1986, Fourqurean and Robblee 1999), which is important to the south Florida economy. Other commercially important fish that depend on Florida Bay include the gray snapper, snook, red drum, and spotted seatrout (Chester and Thayer 1990). A number of birds, such as a variety of long-legged wading birds, brown pelicans, double-crested cormorants, herons, ospreys, roseate spoonbills, egrets, and bald eagles also rely in some part on Florida Bay (Zieman et al. 1989), as do threatened or endangered animals such as the green sea turtle and the Florida manatee, as well as the American alligator and crocodile (Fourqurean and Robblee 1999).

Due to the physical as well as ecological importance of seagrasses (Major and Dunton 2002), their loss and subsequent degradation of Florida Bay caused serious concern among scientists and managers that led to the creation of several research and assessment projects including the Florida Bay Fisheries Habitat Assessment Program (FHAP), which began in the spring of 1995 (Durako et al. 2002).

The objectives of FHAP are: 1) to identify and assess the spatial and temporal changes in species composition, distribution and density of Florida Bay's dominant benthic macrophytes, including both seagrasses and macroalgae; 2) to determine which morphometric, physiological, biochemical and dynamic characteristics are most useful as indicators of macrophyte physiological status (i.e. healthy, stressed or dying); and 3) to assess the population dynamics, reproductive potential and vigor of the dominant seagrass, *Thalassia testudinum*.

Seagrasses have been used as eco-indicators (Durako 1995, Hackney and Durako 2004, 2005, Durako and Kunzelman 2002, Kenworthy and Schwarzchild 1998) but because of their relatively slow growth rates, a response to changing ecological conditions may occur only after it is too late to intervene. Macroalgae have also been suggested and tested as potential eco-indicators (Panayotidis et al. 2004, Biber et al. 2004) and may be more useful as such because of their relatively rapid growth rates, their natural presence at moderate levels in seagrass beds, and their documented correlation to increases in nutrient availability and other ecosystem perturbations (Valiela et al. 1997).

Before a particular macrophyte species can be used as an eco-indicator, a baseline of knowledge is required regarding community structure and its seasonal and spatial dynamics in relation to other benthic macrophytes in a given ecosystem (Biber et al. 2004). Through a series of eighteen seasonal sampling events, FHAP has collected distribution and abundance data on all species of seagrasses and all conspicuous genera of macroalgae observed in the bay. Using FHAP data collected since 1995 when the project began, this study focused on the spatial and temporal changes in density and distribution of the major genera of both seagrasses and macroalgae observed in the bay from the spring of 1995 to the spring 2004.

Explicitly, the objectives of this study were to document macrophyte distribution and density change since 1995 in each of the ten FHAP study basins; to determine the extent of intra-annual versus inter-annual variation in distribution and density of each macrophyte within the ten FHAP study basins; and to determine if any observed macroalgal dynamics were correlated with seagrass dynamics within the ten FHAP study basins.

Twelve macrophytes were assessed in this study, including five species of seagrasses, six genera of macroalgae, and one group of Rhodophyte macroalgae categorized as “Drift Reds”. The seagrasses found in Florida Bay are *Thalassia testudinum* Banks ex König (Turtle grass), *Halodule wrightii* Ascherson (Shoal grass), *Syringodium filiforme* Kützig (Manatee grass), *Halophila engelmanii* Ascherson (Star grass), and *Ruppia maritima* L. (Widgeon grass). Macroalgal genera included in this study are *Acetabularia*, *Batophora*, *Caulerpa*, the Drift Reds, *Halimeda*, *Penicillus*, and *Sargassum*. See Table 1 for a list of macrophyte abbreviations. Other macroalgal genera were observed in the bay over the course of the decade but were not included in this study because of their infrequence and tendency to skew the results of statistical analysis. Data regarding these genera are, however, available for subsequent studies should they become more dominant in the bay in the future.

METHODS

Study Area and Data Collection

Florida Bay (ca. 25°05'N, 81°45'W) is located just south of the Florida mainland. It is bordered to the east and south by the Florida Keys but is open to the Gulf of Mexico on the west. Its 2200 km^2 area includes shallow lagoonal basins that have an average depth of only one meter, though actual depths range from less than one meter to a maximum of approximately four meters (Smith 2002). Ten of these were selected to serve as the FHAP study basins and they represent a range of the conditions and gradients found within Florida Bay. From East to West, the sampled basins are Blackwater Sound (Blk), Eagle Key Basin (Eag), Madeira Bay (Mad), Calusa Key Basin (Cal), Crane Key Basin (Crn), Whipray Basin (Whp), Rankin Lake (Rnk), Twin Key Basin (Twn), Rabbit Key Basin (Rab), and Johnson Key Basin (Jon) (FIG. 1). Analyses described below were performed on data from each individual basin and results are presented at the basin level, from east to west.

Each basin was partitioned into approximately 30-35 tesselated hexagonal grid cells. During each bi-annual sample period, sampling station locations were randomly chosen from within each cell, for a total generally ranging from 300-315 stations. This type of sampling design results in systematic random sampling, it scales the sampling effort to the size of the basin, and it is well-suited for interpolation and mapping of the data.

At each station, latitude, longitude, salinity, temperature, depth, secchi depth, and light attenuation (profiles at every other station) were determined. Depth and secchi depth were used to calculate water clarity (or percent visibility) using the following formula:

$$\% \text{ Visibility} = (\text{secchi depth} / \text{depth}) \times 100$$

Table 1. Macrophyte abbreviations used at times throughout text.

Macrophyte	Abbreviation
Thalassia	Tt
Halodule	Hw
Syringodium	Sf
Halophila	He
Ruppia	Rm
Acetabularia	Ace
Batophora	Bat
Caulerpa	Cau
Drift Reds	Drd
Halimeda	Hal
Penicillus	Pen
Sargassum	Sar

Both seagrass and macroalgal cover were visually quantified for each macrophyte present within four 0.25m^2 quadrats, by diving. Quadrats were haphazardly placed around the boat in a N, E, S, W orientation, always at least 3m apart. Cover/density values were assigned based on a modified Braun-Blanquet scale (Table 2) (Mueller-Dombois and Ellenberg 1974).

Frequency of occurrence and density for each species or plant group at each sample station was calculated using the following formulas:

Frequency = # of stations where observed /total # of stations

Density = sum of B-B scale values/ total # of quads.

Sampling began in the spring of 1995 and took place twice a year until 2004, when the project was extended to include sixteen more basins and became the South Florida Fish Habitat Assessment Program. Spring sampling took place in late May/early June, and fall sampling took place in mid-October, exact dates depending on housing and boat availability. Due to interruptions in funding, bi-annual sampling was cancelled twice. Fall sampling did not take place during the fall of 2001 or during the fall of 2004. Consequently, within this text, the results from eighteen sampling periods are reported.

Statistical Methods

To fulfill the objectives of this project the following null hypotheses were constructed and tested using the statistical methods given below.

Table 2. Modified Braun-Blanquet scale in which cover is the percent of the bottom that is obscured by the macrophyte when viewed by a diver from directly above.

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

H_o1: Intra-annual variability in the distribution and density of each macrophyte is not different than inter-annual variability, nor have these two parameters changed since 1995 within each of the ten FHAP study basins.

In order to express trends in the difference between inter- and intra-annual variability of each macrophyte, average densities as well as frequency of occurrence were computed for each basin and each sampling event. Graphs containing both histograms of density over time and line/scatter plots of frequency of occurrence over time were created for each macrophyte. Similar figures were constructed to show trends in the physical data collected as part of FHAP. Average salinity, depth, temperature, and visibility were calculated for each basin for each sampling event. Relative visibility was calculated as secchi depth divided by water column depth, multiplied by 100, and is given as a percent. These data are described as part of the physical characteristics for each basin in the results section.

A derivation of the Kruskall-Wallis test, the Dwass Steele Critchlow-Fligner method, which is a large sample approximation multiple comparison procedure based upon pairwise rankings (Hollander and Wolfe 1999), was performed on the Braun-Blanquet data to determine the number of times each macrophyte exhibited significant change between seasons and between years. Significance was determined at $\alpha \leq 0.05$. Spring to spring, both consecutive and non-consecutive, fall to fall, both consecutive and non-consecutive, and within year spring to fall changes were tested. Tables 3,5,7,9,11,13,15,17,19, and 21 give the number of times each macrophyte observed in a particular basin between 1995 and 2004 changed significantly. The two columns titled 'Spring' and 'Fall' have one number with parentheses and one without. The number without parentheses is the number of consecutive years in which each macrophyte increased or decreased significantly from one spring to the next, or one fall to the next (ie. spring 1996 – spring 1997, or fall 1995 – fall 1996). The number with parentheses is the number of non-consecutive times changes in density were found to be significant (ie. spring 1996 – spring 2004). The column titled 'S-F' includes within-year spring to fall changes. Finally, the column titled 'S'95 – S'04' indicates whether each macrophyte increased or decreased significantly between those two sample events (beginning and end of FHAP); it does not take into account interim changes. A dash (-) indicates that no significant change was found, whereas a Yes (+) or Yes (-) indicates that either a significant positive (+) or significant negative (-) change occurred.

To further show trends in the distribution and density of each macrophyte, and to more fully elucidate to what extent seagrass and macroalgal communities are co-occurring or becoming mutually exclusive, distribution and density maps were created. Shapefiles for each sampling event were created in ArcGIS ArcMap 8.3, and from these, grid surfaces were interpolated for each macrophyte from the Braun-Blanquet point data using the Inverse Distance Weighted technique in the Spatial Analyst Extension. This method was used instead of krigging because it is better suited for patchy environments, it is not a smooth interpolation method, meaning that it does not ignore true values, and it does not interpolate beyond the maximum or minimum values observed.

The Spatial Analyst IDW default settings in ArcMAP 8.3 were used. ArcMAP assigns a power of two to determine how much weight to assign to distant data points. It also automatically uses a variable search radius in which twelve points were used to interpolate areas without data. Instead of the default cell size, a smaller cell size of 25 was assigned to increase boundary smoothness. An outline of the basins was also used as an analysis mask, so that only interpolated surfaces within the basin boundaries were shown. Surface covers were classified and color-coded according to Braun-Blanquet values, which range from none present to 100% cover.

To compliment the surface grids of the ten FHAP study basins, basemaps outlining Florida Bay shorelines, mangroves, mudbanks, and basin outlines were used. Some representative maps are included within the text of this document. Refer to the CD-based appendix at the end of this document for a complete set of maps including surface cover grids for each macrophyte for each sampling event.

H_o2: The distribution and density of macroalgae are independent of those of the seagrasses.

Spearman Rank Order Correlation Analyses were applied to the Braun-Blanquet densities of all macrophytes within each basin to examine the relationships among them. Correlations were considered significant at $\alpha \leq 0.05$. This analysis was completed for each season and year to determine if relationships changed seasonally and annually, or remained consistent over time. Spearman Rank Order Correlation tables show both spring and fall correlations. To show differences and trends in seasonal correlations, the rectangular tables are divided diagonally by macrophyte abbreviations and correlations occurring during spring sampling are located in the upper right triangle, whereas correlations occurring during fall sampling are located in the lower left triangle. The year the correlation occurred is represented by the last digit of that year (ie. 1995 = 5). If the relationship was consistently positive, the cell is not shaded. If the relationship was consistently negative, the cell is shaded light gray. If the relationship changed from year to year, a plus or minus sign in front of the year indicates whether it was a positive (+) or negative (-) correlation, and the cell is left unshaded. Only years in which correlations were found are included in the cells. Empty cells mean no correlations were ever found between those macrophytes.

To further extract trends in macrophyte relationships and gain insight into community structure within each basin, multivariate analyses were applied to the Braun-Blanquet data. Bray-Curtis dissimilarity matrices were generated and when comparing samples, the Braun-Blanquet data were square-root transformed to account for macrophytes that occurred at both high and low densities (Clark and Warwick 2001). Stations that were devoid of plants were not included in the creation of the matrices, although rare or absent macrophytes were included.

Bray-Curtis dissimilarity matrices were then used for non-metric multi-dimensional scaling (nMDS), which is a method of ordination that positions sample units according to associations among species (McCune and Grace 2002). Specifically, nMDS is a method of indirect gradient analysis which uses an iterative procedure to successively refine positions of points within a chosen number of dimensions until they satisfy the dissimilarity relations between samples (Clark and Warwick 2001). The nMDS procedure was used to plot two-dimensional ordinations of the samples.

If two sample stations are similar in their species composition and density for each macrophyte present, they will be located near one another on the plot. If they do not have any macrophytes in common, they will be located farther apart. Likewise, when plotting all samples from a basin, a plot resulting in a tightly clustered ordination indicates a high degree of uniformity within that basin. If there is a large amount of spread across an ordination plot, there is a small degree of uniformity (McCune and

Grace 2002). By using graphic overlays of “Total Seagrass” (sum of all seagrass Braun-Blanquet values at each station) and “Total Macroalgae” (sum of all macroalgae Braun-Blanquet values at each station) densities in conjunction with the sample ordination plots, clear trends regarding spatial relationships and abundance patterns between the two groups were easily identifiable. All multivariate analyses were done using PRIMER 5 software (Plymouth Marine Laboratory).

RESULTS

The results of this study are presented separately for each of the ten FHAP study basins, in order from east to west. However, to clearly express trends across Florida Bay, many of the figures and maps display results for all of the basins simultaneously. For this reason, and to maximize the flow of the text, all of the graphs, maps, and ordination plots are placed at the end of the results section. Figures 4-7 show depth, visibility, temperature, and salinity means for each basin and sampling event. Figures 8-19 show macrophyte density means and frequencies for each sampling event. Figures 20-31 display spatially interpolated cover grids for each macrophyte within each basin during springs 1995, 1999, and 2004. Figures 32-61 are nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays for springs 1995, 1999, and 2004. Refer to the CD appendix accompanying this text for a complete set of maps and nMDS plots.

Blackwater Sound

Maps, Means, Frequency and Change

Blackwater Sound is a roughly diamond-shaped, 28.57 km^2 basin located in the northeastern tip of Florida Bay. It is surrounded by land with an opening to the Atlantic Ocean in the east. Depth ranges from less than 1 meter to more than 3 meters, but averages at approximately 2.3 meters, making it one of the deeper basins studied as part of FHAP. With the exception of spring 1995, mean visibility was always greater than 94%, and on most occasions 100% visibility was recorded at all sampling stations. Mean temperature ranged from 25.6°C to 31.1°C. Mean salinity varied widely over the years, ranging from 13.9 in fall 1995 to 42.5 in fall 2002. See Figures 4-7.

The average density of *Thalassia* remained fairly constant in Blackwater Sound over the past decade, and it never showed any significant intra- or inter-annual change, nor did it increase or decrease significantly since spring 1995 (TABLE 3). Its mean Braun-Blanquet average oscillated between 1.1 and 2.1. Since 1995, *Thalassia* has generally become more widespread, though it did drop to just over 60% frequency of occurrence in fall 1996. In the spring of 2002, *Thalassia* was observed at all stations. 100% frequency did not, however, coincide with the maximum mean density, which was recorded for both fall 1995 and spring 2000, each with an average Braun-Blanquet value of 2.1 (FIG. 8). Spatial interpolation shows that greatest *Thalassia* densities generally occur along a northeast–southwest diagonal across the sound (FIG. 20), whereas *Halodule* has maintained a presence primarily in the southeastern region: an area where *Thalassia* was consistently less dense (FIG. 21). The trend in *Halodule* frequency generally mirrors its density, though with a small time lag from increasing frequency to increasing density (FIG. 9). Maximum frequency was recorded for fall 1997 at 61%, closely followed by spring 2000 at 60%. Though *Halodule* has not exceeded an average Braun-Blanquet

Table 3. Number of times in which intra- and inter-annual, and decadal changes in macrophyte density were found to be statistically significant within Blackwater Sound.

	Spring	Fall	S to F	S'95-S'04
Thalassia	0(0)	0(0)	0	-
Halodule	0(0)	0(0)	0	-
Syringodium	0(0)	0(0)	0	-
Halophila	0(0)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	1(8)	0(10)	4	-
Batophora	1(13)	0(3)	1	-
Caulerpa	0(0)	0(0)	0	-
Drift Reds	1(4)	2(6)	5	-
Halimeda	0(0)	2(9)	1	-
Penicillus	0(7)	2(5)	1	-
Sargassum	0(0)	0(0)	0	-

value of more than 0.7, it still appears in greater abundance and more frequently than *Syringodium* (FIG. 10)*, Halophila* (FIG. 11)*,* and *Ruppia* (FIG. 12), which only occur rarely and as one or few individuals. Although average Braun-Blanquet values for *Halodule* fluctuated from season to season, and year to year, none of these changes were significant, nor was any significant overall increase or decrease in cover found within this basin since spring 1995 (TABLE 3).

As with density, *Syringodium, Halophila*, and *Ruppia* frequencies were usually near 0% (FIGS. 10-12). *Syringodium* did occur in 15% of the stations in fall 1995, though only a few ramets were recorded at each station where it was present. It appeared again in lower frequency but higher density in spring 2004 in the eastern parts of the sound (FIG. 22). Although these three seagrasses were occasionally observed in this basin, they did not show any inter- or intra-annual change in density, nor did they change significantly since spring 1995 (TABLE 3).

All of the macroalgae studied within the context of this project are represented in Blackwater Sound. *Acetabularia* exhibited an increasing trend in frequency and density, with highest densities observed in the northwestern region of the sound (FIG. 25). It was both more widespread and dense during spring sampling and was present in 88% of stations by spring 2004, when it also reached its highest mean density (Braun-Blanquet = 0.8) (FIG. 13). *Acetabularia* exhibited a high degree of significant intra-annual (seasonal) variability as well as annual variability, although significant annual change did not usually take place during consecutive years. While an increase in density was exhibited by *Acetabularia* within this basin, this increase was not significant when only comparing1995 to spring 2004 (TABLE 3).

Batophora exhibited an increase in both frequency and density during the period of study. Contrary to *Acetabularia*, *Batophora* was generally observed in higher densities during fall sampling. It reached its highest mean density in fall 2003 (Braun-Blanquet = 1.8) and highest frequency the following spring 2004, when it was observed in 85% of stations (FIG. 14). *Batophora* exhibited repeated significant spring to spring increases in density, but like *Acetabularia*, it did not significantly increase between spring 1995 and spring 2004 (TABLE 3) despite its generally-increasing trend. Spatial interpolation showed that *Batophora* was distributed throughout the Sound, but higher densities generally occurred in the northwest, like *Acetabularia*, and western regions (FIG. 26).

With the exception of the two most recent sampling events, *Caulerpa* density, which was usually higher in the spring than fall, declined. It did, however, maintain a near-constant frequency of occurrence around 20% (FIG. 15), and was usually observed in higher densities in the eastern region of the Sound (FIG. 27). Although it was found in higher densities during spring sampling, no statistically significant intra-annual changes occurred, nor did it exhibit any significant inter-annual, or decadal changes (TABLE 3).

Halimeda was also generally higher in density in the eastern region, although it was observed in all areas of Blackwater Sound to some extent (FIG. 28). In 1995 and 1996, *Halimeda* was only observed in the spring. In subsequent years while frequency, though variable, showed an increasing trend, density decreased. It then stabilized and was found in nearly equal densities during both seasons, with the exception of fall 2003, which had both higher frequency and density than the previous spring (FIG. 16). Significant seasonal change only occurred during one year, whereas significant inter-annual changes were observed between two consecutive falls and nine non-consecutive falls. It did not increase or decrease significantly between spring 1995 and spring 2004 (TABLE 3).

Penicillus densities were higher in the fall than spring, with the exception of 2003. Frequency of occurrence for this macrophyte generally increased, although its mean densities have remained fairly stable, oscillating between 0.0 and 0.6 (FIG. 17). Like the other rhizophytics, *Penicillus* is found throughout the sound, but higher densities are generally observed in the east (FIG. 29). Although *Penicillus* density did not change significantly between spring 1995 and spring 2004, significant changes were observed between seven non-consecutive springs and between seven falls, two of which were consecutive (TABLE 3).

Sargassum was observed in very low densities and frequencies, and distributed sporadically throughout Blackwater Sound (FIG. 30). Maximum frequency was recorded in spring 2000, when it was observed at 10% of the stations (FIG. 18). It did not show any significant intra- or inter-annual changes in density (TABLE 3).

The drift reds were spatially variable but occurred throughout Blackwater Sound (FIG. 31). They generally peaked in both frequency and density in the spring, although fall 1996 showed much higher frequency and density than spring 1996 (FIG. 19). These macroalgae did not show a significant overall increase or decrease over the years, but significant changes in density were observed a number of times both intra-and inter-annually (TABLE 3).

Overall, the macroalgae exhibited much more variability than the seagrasses, none of which exhibited any significant change within this particular basin since 1995. *Acetabularia* and the drift reds showed the most significant variation intra-annually, as well as a relatively high degree of inter-annual change, although it was seldom that the change occurred between consecutive years. *Batophora*, *Halimeda* and *Penicillus* all exhibited significant seasonal change on one occasion, but they exhibited inter-annual change many times (TABLE 3).

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of Blackwater Sound Braun-Blanquet data (TABLE 4) showed that *Thalassia* and *Halodule* densities were negatively correlated to one another during many sampling events, more often during fall than spring. *Thalassia* was also negatively correlated to *Acetabularia* repeatedly, during both spring and fall sampling events, but positively correlated to *Caulerpa* during four spring sampling events. *Halodule* was more often negatively correlated with *Batophora*. *Acetabularia* and *Batophora* were, likewise, positively correlated to one another during all springs except the first, but only positively correlated during two fall events. *Halimeda* and *Penicillus* were positively correlated often during spring sampling events as well. *Penicillus* was negatively correlated to both *Batophora* and *Acetabularia* three times each, as was *Caulerpa*. *Halimeda* was the only macroalgae to repeatedly change from positive to negative correlations. *Halimeda* was negatively correlated to *Thalassia* during the springs of 1995, 1996, and 1997, and then in 1998 switched to being positively correlated. It was not correlated at all again until spring 2004, when it was positive. Conversely, *Halimeda* was positively correlated with *Halodule* during spring 1995, and again in spring 1998. It showed similar behavior with *Acetabularia* and *Batophora*,

Table 4. Spearman Rank Order Correlations observed between macrophytes in Blackwater Sound. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein 1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive (+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	723				56804	4	5680		-5-6-7 +8+4	5	
Hw	56790	***Hw***			8	14	91234		50	+5 -8	0	
He			***He***		8							
Sf	5	5		***Sf***				24				
Rm					***Rm***							
Ace	9023					***Ace***	678901234	584	01	+5+6 -2-3-4	524	
Bat	53	67902				23	***Bat***	024	0	+5+6 -8-4	234	
Cau	8						0	***Cau***			8	
Drd	6	-6 +3		3			6		***Drd***			1
Hal	9						3	83		***Hal***	9024	
Pen		7					72	3		80	***Pen***	
Sar						5		3			3	***Sar***

which again were positively correlated with one another but negatively correlated to the two dominant seagrasses, *Thalassia* and *Halodule*. *Halimeda* was positively correlated with *Acetabularia* and *Batophora* during springs 1995 and 1996, but became negatively correlated with them during more recent sample years. See Table 4 for a complete set of correlations.

Non-Metric Multidimensional Scaling

nMDS was employed in this study to graphically express spatial trends in “Total Seagrass” cover and “Total Macroalgae” cover within each of the basins. Density overlay bubbles represent the totaled Braun-Blanquet values of all seagrasses and all macroalgae present at each station. Bubble size increases as cover increases, therefore large bubbles indicate dense macrophyte cover, and smaller bubbles represent sparse macrophyte cover at each station. Because stations which were totally devoid of vegetation were removed from the data set prior to the construction of the Bray-Curtis dissimilarity matrices from which these ordinations were derived, all stations in the plots must have a non-zero value of either total seagrass or total macroaglae or both. Figure 32 below is the ordination for Blackwater Sound in spring 1995. Total seagrass is given in the top pane, and total macroalgae in the bottom pane. This layout is used consistently throughout this text. While all sampling events were ordinated and are available for viewing in the CD appendix, only figures representing springs 1995, 1999, and 2004 samples will be given and discussed within the main text of this study.

Based on the principles of nMDS ordination, the fairly dispersed nature of the spring 1995 ordination plot is indicative of a lack of uniformity throughout the basin. It is also clear that seagrasses and macroalgae overlapped in spatial arrangement to a certain extent, although stations with higher seagrass cover generally contained lower values of total macroalgae cover. Higher macroalgae cover values were seen in areas where there was little or no seagrass. This implies that during spring 1995, a certain degree of exclusiveness is taking place with regard to macrophyte distribution in Blackwater Sound.

Ordination of spring 1999 Blackwater Sound samples is given in FIG. 33, and shows that again the seagrasses and macroalgae co-existed to some extent but higher values of each were observed where there was reduced presence of the other. It appears also that the basin became somewhat more uniform in its community assemblages over time, because the samples were more tightly clustered than what was seen in FIG. 32 for spring 1995.

Again in spring 2004 (FIG. 34), there was a spatial separation of macroalgae and seagrasses, with some degree of overlap in areas where both cover/densities were lower. The community assemblages continued to become more uniform over time as seen by the higher degree of clustering within the basin.

Eagle Key Basin

Maps, Means, Frequencies, and Change

Eagle Key Basin is the largest basin studied as part of FHAP and totals 62.27 km^2. It is located in the northeastern region of central Florida Bay and averages 1.8 meters in depth. Because of its position near the mainland, it is more affected by freshwater inflow from Taylor Slough and the C-111 canal and consequently is generally lower in salinity than other areas of the Bay. Its minimum average salinity recorded was 11.9 and maximum average was 35.3, a value similar to the overall averages of other basins. Visibility in this basin was very low at times, generally in the earlier years of FHAP sampling. During spring 1995, mean visibility was recorded at only 26%. Although secchi data for this basin are missing for falls 1995 and 1996, the water column showed a steady increase in visibility, with the exception of fall 1998, until it reached 100% in spring 1999. Fall 1999 to fall 2002 were highly variable with regard to visibility, but the more recent sampling events in 2003 and 2004 recorded 100% visibility at almost every station. Mean temperature in Eagle Key Basin ranged from 25.0°C to 30.8°C. See Figures 4-7.

In Eagle Key Basin, *Thalassia* frequency of occurrence has been over 92%, consistently since 1995, with half of the sampling events yielding 100% frequency. Such high frequency suggests a fairly homogenous *Thalassia* cover within this basin, but its mean density was only around a .5–1.5 Braun-Blanquet value (FIG. 8). This shows that it has a widespread, but sparse, distribution. Although density has not changed significantly since spring 1995, there were several occasions when both spring to spring and fall to fall changes were found to be statistically significant, suggesting that although *Thalassia* density has fluctuated between the years, it has remained relatively stable (TABLE 5). Spatial interpolation of the data shows that higher *Thalassia* cover was generally found within the western or southern portions of the basin, with both higher and lower values interspersed throughout the rest of the basin (FIG. 20).

Halodule is not nearly as ubiquitous or as dense as *Thalassia*, with a highly variable frequency of occurrence ranging from a low of 6% in fall 1996 to a high of 68%

in fall 2000 (FIG. 9). Density never exceeded a few individual ramets and interpolation showed that these ramets were both interspersed within the *Thalassia* beds and separated, yielding higher densities where *Thalassia* was absent or more sparse (FIG. 21). Even though *Halodule* was observed at low densities, inter-annual change in density was significant several times, usually between fall sampling events. No significant intra-annual change was observed (TABLE 5).

Neither *Halophila* (FIG. 11) nor *Ruppia* (FIG. 12) were ever observed in Eagle. *Syringodium* (FIG. 10) was only seen once, in spring 1997, at which time a solitary individual ramet was observed in one of four quadrats at one station. As such, no statistically significant change was observed (TABLE 5).

Similar to Blackwater, *Acetabularia, Batophora*, and the drift reds are the most commonly observed macroalgae in this basin. Mean density never exceeded Braun-Blanquet values of 0.7 for any of these algae, but frequencies as high as 82%, 88%, and 71% were found for *Acetabularia, Batophora,* and the drift reds, respectively. *Acetabularia* and the drift reds showed higher mean densities during the spring, while *Batophora* was found in greater density during the fall, but with less seasonal variability than *Acetabularia* and the drift reds (FIGS. 13, 14, and 19). Both *Acetabularia* and the drift reds yielded statistically significant intra-annual density changes during four and three of the sampling years, respectively, as well as several non-consecutive spring-to-spring density changes. *Acetabularia* increased significantly between spring 1995 and spring 2004, but the drift reds did not. *Batophora* also increased significantly between spring 1995 and spring 2004, and displayed significant inter-annual change many times as well (TABLE 5). Spatial interpolation did not yield any discernable pattern in spatial

Table 5. Number of times in which intra- and inter-annual, and decadal changes in macrophyte density were found to be statistically significant within Eagle Key Basin.

	Spring	Fall	S to F	S'95-S'04
Thalassia	1(4)	2(4)	0	-
Halodule	0(2)	1(7)	0	-
Syringodium	0(0)	0(0)	0	-
Halophila	0(0)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	2(13)	1(2)	4	Yes (+)
Batophora	3(15)	1(12)	0	Yes (+)
Caulerpa	0(0)	0(0)	0	-
Drift Reds	2(14)	0(0)	3	-
Halimeda	0(0)	0(0)	0	-
Penicillus	0(3)	0(5)	0	Yes (+)
Sargassum	0(0)	0(0)	0	-

distribution for either *Acetabularia* or *Batophora*. During some sampling events they were observed primarily in the west, sometimes in the east, and sometimes they were uniformly distributed throughout the basin (FIGS. 25 and 26). The drift reds, however, did show some trends of being primarily present in the northwest, west, and southwestern area of the basin in the early years of FHAP, but then became more variable in spatial distribution in the later years (FIGS. 31).

Sargassum was often present in this basin, but at very low frequencies and densities. Some seasonal variation was observed in the frequency, with spring values generally higher, but basin-averaged densities were generally so low as to be lost as a result of rounding. Spring 2004 was the only sampling event with a mean density high enough not to be rounded down to 0. This high density was concurrent with the highest frequency observed for *Sargassum*, 23% (FIG. 18). No significant temporal changes were therefore found for this macrophyte (TABLE 5).

Two of the three rhizophytic macroalgae common in the bay were observed in this basin, but *Caulerpa* was never observed during any sample events (FIG. 15). *Halimeda* was only observed during four of the eighteen sampling events, and at very low frequencies and densities (FIGS. 16). Like *Sargassum*, *Halimeda* was observed at such low densities that all but the standard deviations were lost due to rounding. Likewise, *Penicillus* was usually found as a solitary individual in one of four quadrats, and was consequently often rounded out. *Penicillus* frequency though was generally much higher than *Halimeda*. It was only observed once before spring 1998, when it appeared interspersed through the central and northern region of the basin in 28% of the sample stations. It has been present as one or few individuals in all samplings since then at frequencies ranging from 6% to 34% (FIG. 17). Based on such low densities, neither *Caulerpa* nor *Halimeda* showed any significant intra- or inter-annual change. *Penicillus*, on the other hand, showed a significant increase in density despite its low values, as well as significant inter-annual change many times also (TABLE 5).

To summarize variability, the two seagrasses observed in Eagle Key Basin, *Thalassia* and *Halodule*, showed some inter-annual variation, but not as often as some of the macroalgae. *Acetabularia*, *Batophora*, and *Penicillus* all increased significantly since 1995, and all showed a high degree of inter-annual variability. The drift reds also showed a great deal of inter-annual variability as well as intra-annual variability, but did not increase in density significantly since spring 1995.

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of Eagle Key Basin Braun-Blanquet data did not reveal as many macrophyte correlations as were found in Blackwater Sound. *Thalassia* was negatively correlated to *Halodule* only once during spring 1995. It was, however, negatively correlated with *Acetabularia* twice during fall sampling events, and *Batophora* a total of five times, three times in the fall, and twice in the spring. As would be suspected, *Acetabularia* was repeatedly correlated with *Batophora*, always positively. They were correlated during six of the spring sampling events and three fall events. *Acetabularia* was also positively correlated with the drift reds during three fall sampling events. Aside from these, only a few other associations were seen using Spearman correlation analysis in this basin, and those only occurred once. See Table 6 for details.

Non-Metric Multidimensional Scaling

The use of nMDS in Eagle Key Basin sample data showed that, relative to seagrass cover, there was fairly low macroalgal density in this basin during the springs of 1995, 1999, and 2004. The seagrasses that were present in spring 1995 (FIG. 35) were not uniformly distributed throughout the basin. There were some more densely packed stations, but as a whole, based on this plot and overlay, the cover values were not consistent across the basin and were somewhat low. The ordination also shows that the stations within this basin did not show a particularly high degree of uniformity with regards to their vegetative assemblages, as the samples are ordinated across the plot and do not show much clustering. Areas of higher seagrass cover co-occur with areas of lower macroalgal cover, and visa versa, with the exception of two stations 55 and 51 which have a high density of both seagrass and macroalgae. These stations are located in the more southern portion of Eagle Key Basin, but are not adjacent to one another (55 in the east and 51 in the west, approximately 4.6 km apart).

By spring 1999 (FIG. 36), there appears to have been an increase in seagrass density in about half of the basin that coincided with a decrease in total macroalgae. Only two stations, 21 and 23, appear to have a somewhat high density of macroalgae, and there was no seagrass observed in either. These two stations are located in the northeastern region of the basin, approximately 2.4 km apart.

Ordination of spring 2004 sample data (FIG. 37) showed an increase in macroalgal cover. It also appears that the macroalgae and seagrasses are co-occurring more than in spring 1995 and 1999. Cover values of both seagrass and macroalgae are generally similar in areas where both were observed.

Table 6. Spearman Rank Order Correlations observed between macrophytes in Eagle Key Basin. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein 1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive (+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	5					60		4			9
Hw		***Hw***					8					4
He			***He***									
Sf				***Sf***		7						
Rm					***Rm***							
Ace	58					***Ace***	901234				0	
Bat	690					780	***Bat***		0			9
Cau								***Cau***				
Drd	5	5				580			***Drd***			
Hal										***Hal***	7	
Pen						2					***Pen***	
Sar										0		***Sar***

Madeira Bay

Maps, Means, Frequencies, and Change

Madeira Bay is a small basin located in the north-central region of Florida Bay, surrounded by the Everglades on its western, northern, and eastern perimeter. Its 12.4 km^2 area has an average depth of 1 meter. Recorded mean salinities ranged from 13.4 to 48.6. With the exception of two years, 2000 and 2002, salinity was always much higher in the spring than fall. As in most of the other basins, visibility was lower during the early years of FHAP sampling and has since increased to at or near 100%. Temperature means range from 25.0°C to 30.7°C. See Figures 4-7.

Thalassia is ubiquitous throughout Madeira Bay. Frequency of occurrence was 100% during 11 of the 18 sample events, and did not go below 94% for any sampling. Density ranged between Braun-Blanquet values of 1.0 and 3.4, with mean density peaking in fall 2000 (FIG. 8). Despite the fall 2000 peak in density, there was still a significant increase in density between spring 1995 and spring 2004. *Thalassia* also exhibited significant inter- and intra-annual change on many occasions (TABLE 7). Spatial interpolation of the data showed that higher *Thalassia* cover was generally seen in the southern and western portions of the bay (FIG. 20), whereas *Halodule* was generally more abundant in the northern and eastern region of the bay (FIG. 21).

Halodule showed a steep decline in frequency after the first sampling event in spring 1995, when frequency was at its highest at 71%. During subsequent sampling events, *Halodule* fluctuated between approximately 20% and 30% frequency, and remained at low average densities with means ranging from 0.1 to 0.4 (FIG. 9). Inter-annual change in density was found to be significant five times, and although frequency declined a great deal for *Halodule*, its density did not change significantly between spring 1995 and spring 2004 (TABLE 7).

After fall 1995, when *Syringodium* was observed in 24% of the sampling stations at low densities, it became virtually absent in Madeira Bay (FIG. 10). *Halophila* was never observed in Madeira (FIG. 11), and *Ruppia* only once in fall 2000 (FIG. 12). Consequently, no significant changes were found for these three seagrasses (TABLE 7).

Both *Acetabularia* and *Batophora* became more widespread but not more dense in Madeira Bay. *Acetabularia* showed a strong seasonal signal, and was only observed in measurable densities during the spring. Frequency mirrored density patterns and both peaked in spring 2002 (FIG. 13). Although *Acetabularia* density did not increase significantly between spring 1995 and spring 2004, spring to spring density changes were significant eight times, although seven were during non-consecutive years. Intra-annual variability was only significant twice, most likely due to its extremely low spring densities (TABLE 7). When observed, *Acetabularia* generally occurred in higher densities in the southern portion of this basin (FIG. 25).

Batophora was also often observed at high densities in the southern portion of Madeira Bay, but on several occasions was observed in equally high densities throughout the rest of the basin (FIG. 26). *Batophora* frequency fluctuated greatly until spring 2002 when it leveled off at around 68%. As seen in Figure 14, there was clearly more *Batophora* in Madeira Bay during the recent sampling events, but that increase in density was not significant. However, several significant inter-annual fluctuations were found between springs (TABLE 7).

Table 7. Number of times in which intra- and inter-annual, and decadal changes in macrophyte density were found to be statistically significant within Madeira Bay.

	Spring	Fall	S to F	S'95-S'04
Thalassia	5(22)	2(13)	3	Yes (+)
Halodule	0(4)	0(1)	0	-
Syringodium	0(0)	0(0)	0	-
Halophila	0(0)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	1(7)	0(0)	2	-
Batophora	2(12)	0(10)	1	-
Caulerpa	0(0)	0(0)	0	-
Drift Reds	3(21)	0(0)	4	Yes (+)
Halimeda	0(0)	0(0)	0	-
Penicillus	0(0)	0(3)	0	-
Sargassum	0(4)	0(0)	0	-

The drift reds showed a statistically significant increase in density since spring 1995, and were the most seasonally variable macroalgae observed in Madeira Bay (TABLE 7). They were also spatially variable (FIG. 31) and were both more abundant and frequent during spring sampling events. Seasonal variability was extremely exaggerated in the more recent FHAP years, during which time it peaked in spring 2002 at 100% frequency and mean Braun-Blanquet value of 1.1 (FIG. 19).

Sargassum frequency and density both showed a decreasing trend over the past decade. *Sargassum* frequency peaked at 39% in spring 1996 and it has become less widely distributed in Madeira Bay since that time. During most sampling events, density was extremely low, with a high mean Braun-Blanquet value of only 0.2, which coincided with the peak in frequency (FIG. 18). Although significant inter-annual change was observed four times, the decrease in density between spring 1995 and spring 2004 was not statistically significant (TABLE 7).

Penicillus was not observed regularly in Madeira Bay until fall 1999, when it was observed in 12% of the sample stations (FIG. 17). It was initially observed in the western and central regions of the basin, but over time became more widespread in the eastern region (FIGS. 29). Over time, it increased in frequency, and in doing so showed some degree of seasonal variability, but it has changed little in density. It generally occurred as solitary individuals or in small clumps, maintaining a relatively low mean density. Change between years was only significant three times from fall to fall, and its increase in density between spring 1995 and spring 2004 was not significant (TABLE 7).

Halimeda was observed in Madeira Bay sporadically since spring 1995 and was always found at very low densities (FIG. 16). *Caulerpa* was only observed twice, once in fall 1999 and once in spring 2004, both times as solitary individuals (FIG. 15). As such, no significant variability in density was found for either of these macroalgae (TABLE 7).

In summary, there was significantly more *Thalassia* in Madeira Bay in spring 2004 than in spring 1995, whereas *Halodule* showed some loss. The drift reds again showed the most seasonal variation, followed by *Acetabularia*, and they were the only macroalgae to increase significantly since 1995. The other macroalgae present in Madeira Bay showed some degree of inter-annual variability as well, mostly during non-consecutive springs.

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of Madeira Bay Braun-Blanquet data yielded few correlations. *Thalassia* and *Halodule* were negatively correlated to one another, repeatedly, during both springs and falls from the beginning to the end of FHAP sampling. *Thalassia* was also negatively correlated to both *Acetabularia* and *Batophora* during several springs and a few falls. During the falls of 1996 and 1999, *Batophora* was negatively correlated to *Thalassia*, but positively correlated to *Halodule*. The same situation was observed in fall 2003 with *Acetabularia*: it was negatively correlated to *Thalassia* but positively correlated to *Halodule*. *Acetabularia* and *Batophora* were only positively correlated to each other twice though, once in spring 1995, and again in fall 2003. The drift reds were positively correlated to *Thalassia* twice, in springs 1996 and 1998, whereas they were negatively correlated with *Halodule* during springs 1996 and 1999. The drift reds altered their correlation with *Halodule* in spring 2001, at which time their correlation became positive. *Halimeda* followed suit, and was negatively correlated with *Thalassia* in spring 1998, but was positively correlated with *Halodule* at that time. *Halimeda* was again positively correlated with *Halodule* in spring 2002. See Table 8 for a complete set of correlations.

Non-Metric Multidimensional Scaling

Density overlays, in conjunction with nMDS ordination, of Madeira Bay sample data indicate seagrass densities in this basin were quite low at the initiation of FHAP sampling and then increased basin wide by spring 1999. In spring 1995 (FIG. 38), seagrasses occupied approximately half of the sample stations and were observed at relatively low densities. These stations are clustered together on the ordination plot. Low seagrass cover in this case clearly did not coincide with high macroalgal cover, as there were only a few stations in which macroalgae were observed at high densities. These stations were separate from the stations in which seagrass was observed.

By spring 1999 (FIG. 39), seagrasses were observed in much higher densities throughout the basin. Notice that the bubbles are all of similar size, indicating that a relatively uniform seagrass bed was observed at this time. Macroalgae were observed overlapping with seagrasses in some of the stations, and were even found in higher densities at some stations. Distribution increased relative to 1995, but many stations still lacked macroalgae, so although the two groups did co-exist, seagrass was clearly the more dominant macrophyte group in the basin at this time.

The spring 2004 ordination (FIG. 40) shows little change from the spring 1999 plot. The seagrasses remained evenly distributed throughout the basin at a fairly constant density. Macroalgae density and distribution increased but again, due to the fact that there

Table 8. Spearman Rank Order Correlations observed between macrophytes in Madeira Bay. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein 1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive (+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	567802				5781	892		68	8		6
Hw	579023	***Hw***					92		-6-9 +1	82		
He			***He***									
Sf				***Sf***					1			
Rm					***Rm***							
Ace	3	3				***Ace***	5					
Bat	69	69		5		3	***Bat***					
Cau								***Cau***				
Drd					0	0			***Drd***			
Hal		0							6	***Hal***		3
Pen	0								0		***Pen***	
Sar						8						***Sar***

was seagrass essentially everywhere, the two groups were not mutually exclusive.

Calusa Key

Maps, Means, Frequencies, and Change

Calusa Key Basin is a 26.44 km^2 basin located in central Florida Bay, just southwest of Eagle Key Basin. Its average depth is approximately 2 meters. Visibility has not always been as good as in the last several sampling trips, as it was only at 68% in spring 1995. It dropped to 34% visibility in spring 1996, and then became less and less turbid until fall 1999 when it again declined to 51%. Since spring 2000, visibility has been much better, usually averaging near 100%. Salinity in this basin ranged from 21 to 44.4 over the course of the study years. Only three of the ten sampling years yielded mean fall salinities higher than mean spring salinities. These years included 1997, 2000, and 2002. Of these, two sampling events showed particularly high mean salinities: fall 1997 at 43.2 and fall 2002 at 44.4. Mean temperature ranged from 26.1°C to 31.1°C. See Figures 4-7.

Thalassia is the dominant seagrass in Calusa Key Basin, with a mean Braun-Blanquet cover consistently between 1 and 2 (FIG. 8). Cover was greatest in fall 2000, a time when many other FHAP basins also exhibited increased *Thalassia* cover. Its distribution is extensive throughout the basin, with a frequency of occurrence always greater than 87% (FIG. 8). Statistically significant inter-annual change in density was discernible three times, but density did not increase significantly between spring 1995 and spring 2004 (TABLE 9). Spatial interpolation of the Braun-Blanquet data shows that higher densities of *Thalassia* usually occurred in the southern portion of Calusa (FIG. 20), while higher *Halodule* densities are generally in the northern portion of Calusa (FIG. 21).

Table 9. Number of times in which intra- and inter-annual, and decadal changes in macrophyte density were found to be statistically significant within Calusa Key Basin.

	Spring	Fall	S to F	S'95-S'04
Thalassia	0(0)	0(3)	0	-
Halodule	0(0)	0(0)	0	-
Syringodium	0(0)	0(0)	0	-
Halophila	0(0)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	0(7)	0(0)	0	Yes (+)
Batophora	1(21)	1(15)	1	Yes (+)
Caulerpa	0(0)	0(0)	0	-
Drift Reds	2(13)	1(5)	1	-
Halimeda	0(0)	0(0)	0	-
Penicillus	0(0)	0(2)	0	-
Sargassum	0(0)	0(0)	0	-

Halodule has been consistently sparse, with greatest densities occurring during the more recent sample events (FIG. 9), though it has not shown any significant change in density within or between any sample years (TABLE 9).

Halophila and *Ruppia* have never been observed during sampling in this basin, and *Syringodium* was found only once in spring 1999. Consequently, no significant change occurred in any of these seagrasses (TABLE 9).

The psammophytic macroalgae were not observed in particularly high densities here, but *Acetabularia* and *Batophora* both increased significantly in density since 1995. With the exception of spring 2001, *Batophora* frequency increased dramatically since 1995, and it exhibited significant inter-annual variability as well. *Acetabularia* again showed seasonality and was much more prevalent during spring (FIG. 13), but its variability was not as great as that of *Batophora* (TABLE 9). Spatial interpolation of *Acetabularia* cover data suggests that it pulses in frequency. Spring 1999 maps show *Acetabularia* restricted to the northwestern area of the basin. In spring 2000, this macroalgae spread throughout the basin, and then retreated to the northwest again in spring 2001. During spring 2002 sampling, it was again observed throughout the basin, and then retreated again in spring 2003, although its extent is much greater in spring 2003 than spring 2001. Spring 2004 again shows widespread distribution of *Acetabularia* with higher densities in the northwest (FIG. 25). Spatial interpolation of *Batophora* data, on the other hand, does not reveal any noteworthy trends. Its distribution and density varies from year to year and it does not occupy any particular areas more than others (FIG. 26).

The drift reds also showed a general increase in density and frequency, both peaking in spring 2002 when frequency reached 93% (FIGS. 19). Despite many years of significant inter-annual change, the increase in density was not statistically significant between spring 1995 and spring 2004 (TABLE 9). Drift red distribution was also variable, but high frequencies and densities in the northern portion of the basin were observed during several sampling events (FIG. 31).

Penicillus was the most prolific of the rhizophytic macroalgae in Calusa Key Basin, though it was generally observed as individuals or clumps of sparse individuals. Frequency increased since 1995, but never exceeded 39% (FIG. 17). Density varied inter-annually, but only significantly between two sampling periods, and it did not increase significantly since spring 1995 (TABLE 9). Spatially, this macroalgae did not tend to occupy any particular area, but instead was observed in different areas at different times (FIGS. 29).

Halimeda frequency was greatest in fall 2003, yet it was only observed in two sampling stations (FIG. 16). *Caulerpa* was only observed twice, during the springs of 2001 and 2002, when it was seen in one quadrat during each sampling event (FIG. 15). *Sargassum* was only observed in Calusa Key Basin during seven of the eighteen sampling events, and always at low frequencies and densities (FIG. 18). None of these macroalgae showed any significant variability (TABLE 9).

Overall, the seagrasses in Calusa Key Basin were fairly consistent over the ten-year sample period and did not increase or decrease significantly. *Acetabularia*, *Batophora*, and the drift reds were the only macroalgae to show any degree of variability, and it was primarily inter-annual increases in density. *Acetabularia* and *Batophora* were the only macrophytes to change (increase) significantly between spring 1995 and spring 2004.

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of Calusa Key Basin Braun-Blanquet data found only a few correlations between macrophytes. *Thalassia* was negatively correlated to both *Halodule* and *Acetabularia* only once during spring 2003, at which time *Acetabularia* and *Halodule* were positively correlated. *Syringodium* was positively correlated to both *Acetabularia* and *Batophora* in spring 1999, which became positively correlated to one another that spring, and remained so for the remainder of spring sampling events (1999-2004). *Thalassia* was positively correlated to *Batophora* during fall 1997, but became negatively correlated with it the following fall 1998. *Halimeda* and *Penicillus* were only correlated once, positively, in spring 2004, at which time they were also both positively correlated with *Halodule*. *Sargassum* and the drift reds were positively correlated twice, during springs 1999 and 2002. For a complete set of correlations, see Table 10.

Non-Metric Multidimensional Scaling

nMDS of Calusa Key Basin spring 1995 sample data shows that neither seagrass nor macroalgae were particularly dense throughout the basin. In the upper left corner of the spring 1995 plots (FIG. 41), there is a small cluster of stations. Based on this clustering, these stations were similar in their vegetative assemblages. This is reinforced by the density overlays, which indicate similar densities of seagrass, probably all of which is the same species, and no or little macroalgae. A spatial distinction between macroalgae and seagrass is quite visible in this plot, although some overlap does exist. The relatively clustered appearance of the rest of the plot indicates some

Table 10. Spearman Rank Order Correlations observed between macrophytes in Calusa Key Basin. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein 1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive (+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	3				3					5	
Hw		***Hw***				83				4	4	
He			***He***									
Sf				***Sf***		9	9					
Rm					***Rm***							
Ace						***Ace***	901234					
Bat	+7 -8					23	***Bat***				8	
Cau								***Cau***				
Drd							5		***Drd***			92
Hal							5			***Hal***	4	
Pen	9						8				***Pen***	
Sar												***Sar***

degree of uniformity throughout the basin, not just within those few stations in the upper left corner, but this clustering is exaggerated by the outlier formed by station 4. Clustering is not so extensive as to have warranted removal of this outlier from analysis.

Spring 1999 also contained an outlier sample which pushed the rest of the ordination to the left, but again it did not warrant removal from analysis as long as its influence is recognized. Seagrass density and distribution increased by spring 1999 (FIG. 42), and it appears that total macroalgae cover, with the exception of a few stations, decreased. Stations at which macroalgae cover was high were ones in which seagrass cover was low, and in a few locations, moderate densities of both were observed.

By spring 2004, seagrass cover, as well as uniformity within the basin (not attributed to outliers) decreased and macroalgae cover increased in some areas. This plot (FIG. 43) shows a distinction in the spatial arrangement between seagrasses and macroalgae. Based on the spread observed between the stations, this plot also shows a lack of uniformity throughout the basin, at the least a lack of outlier stations which skewed the results in earlier years.

Crane Key Basin

Maps, Means, Frequencies, and Change

Crane Key Basin is located just south of Calusa Key Basin in central Florida Bay and it is a relatively small basin with an area of only 15.3 km^2. Average depth is just less than 2 meters, and mean salinities have ranged from 26.1 to 48.2 over the FHAP study period. Crane has been one of the consistently less turbid basins. Every sampling trip, with the exception of one in fall 1999, has had visibilities over 88%. Mean temperatures have ranged from 24.8 to 31.2. Salinities here are usually higher in the spring, with the exception of 1997 and 2002, which also exhibited very high salinities in several of the other basins studied. See Figures 4-7.

Though proximal to Calusa Key Basin, Crane Key Basin has a slightly more dense *Thalassia* cover, with Braun-Blanquet means ranging from 1.1 to 2.6. The high density of 2.6 was observed twice, in falls 1996 and 2000 (FIGS. 8). Greater densities were generally observed on the banks of the basin and in the northeastern area, though *Thalassia* was almost always observed at every sample station (FIGS. 20). While *Thalassia* exhibited a relatively high degree of inter-annual variability, spring 2004 was not significantly different in density than spring 1995 (TABLE 11).

Halodule, on the other hand, was generally more dense in the center of the basin where *Thalassia* was less dense, with some fluctuation in distribution over the years (FIG. 19). *Halodule* frequency ranged from 3% to 29% and was usually higher in the spring than fall, as was *Halodule* density (FIG. 9). Neither *Halophila* nor *Ruppia* were ever observed in Crane Key Basin, but *Syringodium* was observed once as a solitary ramet at three stations in fall 1996 (FIG. 10). *Thalassia* was the only seagrass to show any significant temporal variability (TABLE 11).

Crane Key Basin generally had a great deal of *Batophora*, which was usually more dense during the fall sampling events than the spring. No *Batophora* was observed in spring 1996, and as with *Thalassia*, it peaked in fall 2000. After spring 1997, it was always found in more than 85% of the sample stations until spring 2004, when it was only observed in 71% (FIG. 14). There was significantly more *Batophora* in spring 2004 then there was in spring 1995, though *Batophora* showed a great deal of significant inter-

Table 11. Number of times in which intra- and inter-annual, and decadal changes in macrophyte density were found to be statistically significant within Crane Key Basin.

	Spring	Fall	S to F	S'95-S'04
Thalassia	2(5)	3(8)	1	-
Halodule	0(0)	0(0)	0	-
Syringodium	0(0)	0(0)	0	-
Halophila	0(0)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	0(0)	0(0)	0	-
Batophora	3(22)	2(11)	2	Yes (+)
Caulerpa	0(0)	0(0)	0	-
Drift Reds	0(1)	0(0)	0	-
Halimeda	0(0)	0(0)	0	-
Penicillus	2(9)	0(0)	0	-
Sargassum	0(0)	0(0)	0	-

annual changes (TABLE 11). Spatial interpolation showed that higher densities of *Batophora* were usually observed in the northwestern corner of the basin where seagrasses were not as dense (FIG. 26).

Acetabularia occurred in the northwest and southwestern areas of the basin at very low densities and relatively low frequencies, though the frequencies were high enough to show seasonal trends consistent with *Acetabularia* patterns in other basins (FIG. 25 and 13). There was not enough of it, however, to show any significant temporal variability (TABLE 11).

The drift reds also fluctuated seasonally, and were both more frequent and dense during spring sampling events, but never reached frequencies higher than 31% (FIG. 19), and only once expressed any significant temporal change (TABLE 11). Like *Batophora* and *Acetabularia*, the drift reds were observed more often in the western areas of the basin (FIG. 31).

As in Calusa, *Penicillus* was the most commonly observed rhizophytic macroalgae, and besides *Batophora*, was the only macroalgae to express any degree of temporal change (TABLE 11), although there were sampling events when it was not found at all. When it was observed, spatial distribution within the basin seemed somewhat random, as it was found in many different areas from year to year (FIG. 29). *Penicillus* frequencies reached almost 60% (FIG. 17), which is a great deal higher than both *Caulerpa* and *Halimeda* frequency maximums, which were 23% and 6% respectively (FIGS. 15 and 16). Though *Caulerpa* was sparsely observed during the first sampling event in spring 1995, it was not found again during subsequent trips. *Sargassum* was also only observed occasionally in this basin and always in very low densities (FIG. 18).

Neither *Caulerpa*, *Halimeda*, or *Sargassum* exhibited any significant temporal changes during FHAP sampling in this basin (TABLE 11).

In summary, *Thalassia* showed some variation over the years but its density was not significantly different in spring 2004compared to spring 1995. *Penicillus* also showed a relatively high degree of variability, but *Batophora* was the only macrophyte to change (increase) significantly between spring 1995 and spring 2004 in this basin. Other macrophytes included in this study either were not observed in this basin or did not significantly change.

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of Crane Key Basin Braun-Blanquet data showed that *Thalassia* and *Halodule* were negatively correlated during three spring sampling events and two fall events. *Thalassia* was also negatively correlated to both *Acetabularia* and *Batophora* a number of times. It was negatively correlated to *Acetabularia* during spring 1997, 1999, 2000, and 2002, but not during any falls because *Acetabularia* generally wasn't observed in this basin during fall sampling. In contrast, *Thalassia* was negatively correlated with *Batophora* during three falls, which were 1996, 1999, and 2003. This association also occurred during the springs of 1999 and 2003.

Acetabularia was positively correlated to *Halodule* twice, but not during the same years in which it was negatively correlated to *Thalassia*. *Acetabularia* and *Batophora* were only positively correlated once, in spring 2004, but *Acetabularia* was positively correlated to the drift reds during six of the ten spring sampling events. *Acetabularia* was also positively correlated with *Halimeda* in springs 2003 and 2004, at which times

Table 12. Spearman Rank Order Correlations observed between macrophytes in Crane Key Basin. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein 1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive (+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	724				7902	93				0	
Hw	57	***Hw***				81			50	04		
He			***He***									
Sf				***Sf***								
Rm					***Rm***							
Ace						***Ace***	4		790234	34		
Bat	693	8					***Bat***	5			8	
Cau								***Cau***				
Drd		8							***Drd***	34	9	
Hal										***Hal***		
Pen	5	58					+5 -2				***Pen***	
Sar												***Sar***

Halimeda was positively correlated with the drift reds on two occasions. For a complete set of correlations, see Table 12.

Non-Metric Multidimensional Scaling

nMDS of Crane Key Basin sample data produced ordination plots that, used in conjunction with density overlays, make clear that in spring 1995, there was a fairly dense seagrass bed occupying much of the basin. There was also a fair amount of macroalgae in Crane Key Basin at this time (FIG. 44). The two groups of macrophytes occupied the same areas at moderate densities, but the higher the seagrass cover in an area, the lower the macroalgae cover. The opposite was also true and this trend was seen repeatedly in other basins. There was some uniformity found within the basin, and these stations are clustered together on the plot.

Figure 45 represents spring 1999 and illustrates how spatially exclusive total seagrass and total macroalgae were at that time. Overlays of total seagrass show high densities at stations different than those where high densities of macroalgae were observed.

This trend is again very evident in the ordination of spring 2004 data (FIG. 46). Although there is some spatial overlap between stations high in seagrass and stations high in macroalgae cover, it is clear that this basin is one in which these two macrophyte groups are distributed in a more-or-less mutually exclusive manner. By 2004, most of the stations in this basin were more tightly clustered, which indicates some degree of homogeneity, but this may be a result of outlier stations.

Whipray Bay

Maps, Means, Frequencies, and Change

Whipray Bay is a relatively shallow basin in central Florida Bay. Its 21.79 km^2 area has a mean depth of approximately 1.6 meters. Although secchi data are missing from the first two fall sampling trips in 1995 and 1996, visibility in this basin initially decreased to a low of 45% in fall 1997. It then increased to 95% in spring 1998, after which time visibility remained relatively high for the duration of FHAP sampling and on many occasions reached 100%. Mean temperature, as in the other basins, had a very small range of 25.4°C to 30.3°C. Mean salinities varied widely, ranging from 21.2 to 55.2. See Figures 4-7.

Both *Thalassia* and *Halodule* had significantly higher densities in spring 2004 than in spring 1995, and both also showed some degree of inter-annual change, though no significant intra-annual change (TABLE 15). *Thalassia* density showed an increasing trend, whereas *Halodule* density peaked in spring 1999, and then generally declined (FIGS. 8 and 9).

Spatial interpolation shows that higher *Thalassia* densities were consistently observed in the southern and eastern portions of this basin (FIG. 20), whereas *Halodule* densities were always higher in the northern and western portions (FIG. 21).

Syringodium and *Ruppia* have never been observed in Whipray Bay during a sampling event, and *Halophila* has only been seen twice as individual ramets, in the spring and fall of 1999. Consequently, no significant temporal changes occurred for these seagrasses (TABLE 13).

Table 13. Number of times in which intra- and inter-annual, and decadal changes in macrophyte density were found to be statistically significant within Whipray Basin.

	Spring	Fall	S to F	S'95-S'04
Thalassia	0(4)	1(2)	0	Yes (+)
Halodule	0(12)	1(4)	0	Yes (+)
Syringodium	0(0)	0(0)	0	-
Halophila	0(0)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	0(1)	0(0)	0	-
Batophora	0(23)	1(13)	1	Yes (+)
Caulerpa	0(0)	0(0)	0	-
Drift Reds	2(13)	0(1)	1	-
Halimeda	0(0)	0(0)	0	-
Penicillus	0(10)	0(8)	0	Yes (+)
Sargassum	0(0)	0(0)	0	-

Acetabularia was not observed in Whipray until spring 2000, when it was found in one quadrat at low density. It was observed again in the springs of 2002, 2003, and 2004 at low frequencies and densities, spring 2004 being the highest for both (FIG. 13). Its distribution varied each time it was observed, moving from the southern portion of the basin to the northern portion, and finally occurring throughout the basin in spring 2004 (FIG. 25). It was never observed during fall sampling trips, and was always found at densities so low as to not show any significant inter- or intra-annual changes (TABLE 13).

Batophora, on the other hand, has become relatively abundant in Whipray, showing a dramatic increase in frequency since fall 1998, and a significant increase in density since spring 1995 (TABLE 13). It peaked in fall 2000 with a Braun-Blanquet value of 1.3, but frequency did not peak until spring 2003, when it was observed in 84% of the sampling stations (FIG. 14). *Batophora* was initially observed in the southern portion of the basin. It spread north and east over time, and was eventually observed throughout the basin but with higher densities always in the south and east (FIG. 26).

Drift red macroalgae were often found distributed throughout Whipray Bay or in small patches. They were fairly common and have shown an overall increase in density and frequency since spring 1995, but with some seasonal fluctuation. Many of the annual fluctuations were significant, but the spring 2004 densities were not significantly different than spring 1995 densities, regardless of the increasing trend (TABLE 13). The drift reds peaked in spring 2002 in both mean density and frequency values, equal to 1.0 and 81%, respectively (FIG. 19).

Penicillus has been the most successful rhizophytic in this area, reaching a maximum frequency of occurrence of 55% in spring 2004, when it also had significantly higher densities than in spring 1995 (TABLE 13). It was initially observed in sparse patches in the south-central area of the basin, but has spread north and to the perimeter over the course of the study period (FIG. 29).

Caulerpa was not often observed during sampling trips in Whipray Bay, and has only been seen on three occasions in very low frequencies and densities (FIG. 15). *Halimeda* has also only been observed at low frequencies and densities in the northern and central-western area of the basin (FIG. 28). *Sargassum* is not always observed here, having only been found during six of the eighteen sampling trips at random locations throughout the basin. Frequency peaked in spring 2002 at 32%, yet density was still quite low with a mean Braun-Blanquet value of 0.1 (FIG. 18). As such, none of these macroalgae have increased or decreased significantly from spring 1995 (TABLE 13).

Overall trends in Whipray Bay show both *Halodule* and *Thalassia* with significantly more cover in spring 2004 than spring 1995, and both showed a high degree of inter-annual variability. *Batophora* and *Penicillus* also showed a high degree of inter-annual variability, and had significantly more cover in spring 2004 than in spring 1995. The only other macrophytes to show any significant variability were the drift reds, but they were found at such low relative densities that they did not exhibit the typical basin-level intra-annual variability pattern often observed in other basins.

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of Whipray Bay Braun-Blanquet data found negative correlations between *Thalassia* and *Halodule* during two spring sampling

Table 14. Spearman Rank Order Correlations observed between macrophytes in Whipray Bay. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein 1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive (+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	93					5023		8			
Hw	5903	***Hw***				4					234	52
He			***He***								9	
Sf				***Sf***								
Rm					***Rm***							
Ace						***Ace***		2				
Bat	902	9					***Bat***				3	
Cau			9					***Cau***				
Drd	78						3		***Drd***		9	2
Hal										***Hal***	9	
Pen	0	02	9				2	9			***Pen***	
Sar												***Sar***

events and four fall events. During 1999 and 2003, this negative relationship was found during both seasons. *Thalassia* was correlated to *Batophora* on a number of occasions also, but this association was always positive, and occurred during four springs and three falls. It was also positively correlated to the drift reds during one spring and two falls. Besides *Halodule*, *Thalassia* was only negatively correlated to one other macrophyte, *Penicillus*, and only on one occasion, fall 2000. At this time, *Penicillus* was positively correlated to *Halodule*. Positive correlations were also observed between *Halodule* and *Penicillus* during fall 2002, and springs 2002, 2003, and 2004. For additional correlations, see Table 14.

Non-Metric Multidimensional Scaling

Ordination plots of Whipray Bay sample stations yielded somewhat unique results. Spring 1995, as seen in Figure 47, had very low densities of both seagrasses and macroalgae, and in fact, more stations were observed with higher macroalgae cover than seagrass cover. By spring 1999 (FIG. 48), total seagrass cover increased substantially and had much more extensive cover than macroalgae, which showed highest densities at stations where lower seagrass covers were observed. While the distribution of seagrass had spread throughout the basin by this time, the actual densities were still relatively low and uniform. During spring 2004 (FIG. 49), however, seagrass densities were higher at several stations, as were macroalgae densities. As expected, many of the stations with high values of either seagrass cover or macroalgal cover had lower values in the other, but a great deal of overlap also took place, wherein many stations had very high densities of both seagrasses and macroalgae.

Rankin Lake

Maps, Means, Frequencies, and Change

Rankin Lake is by far the smallest basin sampled as part of FHAP. It is only 5.83 km^2 and has an average depth of only 1.2 meters. Located in the northwestern area of Florida Bay, it is situated near the Everglades and is subject to freshwater run-off from Taylor Slough. This basin is the only one studied as part of FHAP that has clearly defined seasonal trends in salinity, depth, and visibility. With the exception of 2000 and 2002, salinity was always higher in the spring and lower during the fall wet season. Measured salinity means ranged from 20.1 to 55.5. Depth was always measurably greater in the fall, also due to increased freshwater input and higher seasonal sea level. Presumably due to this increase in freshwater and decrease in salinity, turbidity always increased in the fall and yielded poor visibility measurements during these time periods. During spring sampling after 1997, however, visibility was generally very high. Mean temperature ranged from 25.3°C to 32.5°C. See Figures 4-7.

Thalassia underwent a steep decline in frequency of occurrence from spring 1995 to fall 1996 in Rankin Lake, when it went from 81% to 29%. The decline in frequency did not coincide with a decline in mean density, however (FIG. 8). Spatial interpolation of the Braun-Blanquet data showed that *Thalassia* was initially not present or very sparse in the northwestern portion of Rankin, but relatively dense in the southeastern portion, a phenomenon that explains low frequency but high mean density. Following the frequency decline, both density and frequency rebounded, as *Thalassia* distribution spread to the northwestern region of Rankin, though it maintained a higher density in the south (FIG. 20). Mean density peaked in spring 2003 with a mean Braun-Blanquet value of 1.8, and frequency peaked the following fall at 97% (FIG. 8). Significance tests showed that *Thalassia* was highly inter-annually variable, and that there was significantly more *Thalassia* in spring 2004 than there was in spring 1995 (TABLE 15).

Spatial interpolation of *Halodule* Braun-Blanquet values showed that it was generally more dense in the north and eastern portions of Rankin, where *Thalassia* eventually colonized but remained less dense than in the south (FIG. 21). Besides three particularly low years, *Halodule* frequency was at least 81% during all sampling events and showed an overall increase (FIG. 9). *Halodule* densities were generally higher than *Thalassia* densities until spring 2002 when *Thalassia* densities surpassed *Halodule*. Mean density peaked at 2.6 in fall 1999, and although there were significant inter-annual changes between several springs and several falls, there was no significant difference between the *Halodule* densities in spring 2004 and spring 1995 (TABLE 15).

Syringodium increased in both frequency and density, achieving 39% frequency of occurrence in spring 2003. Mean densities remained low, not going over 0.1 (FIG. 10). Spatial interpolation showed that *Syringodium* occurred primarily in the northwestern area of Rankin, where *Halodule*, rather than *Thalassia*, dominates (FIG. 22). *Halophila* did not colonize Rankin Lake until spring 1999 and was frequently observed thereafter at sparse densities in the northwestern area, co-occurring with *Halodule* and *Syringodium* (FIG. 23). It peaked in frequency in spring 2002 at 43% occurrence (FIG. 11). *Syringodium* and *Halophila* expressed some significant inter-annual change (TABLE 15), but because *Ruppia* was never observed during sampling in this basin (FIG. 12), it did not.

Acetabularia was observed in Rankin Lake during spring sampling events only. Frequencies were generally high and densities low, both showing an overall increasing

Table 15. Number of times in which intra- and inter-annual changes in macrophyte density were found to be statistically significant within Rankin Lake.

	Spring	Fall	S to F	S'95-S'04
Thalassia	0(8)	0(5)	0	Yes (+)
Halodule	1(16)	0(13)	2	-
Syringodium	0(4)	0(0)	0	-
Halophila	0(4)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	2(17)	0(0)	2	Yes (+)
Batophora	0(13)	0(6)	0	Yes (+)
Caulerpa	3(8)	0(0)	1	Yes (+)
Drift Reds	0(4)	0(3)	0	-
Halimeda	2(19)	1(9)	1	Yes (+)
Penicillus	1(21)	1(14)	0	Yes (+)
Sargassum	2(0)	0(0)	1	-

trend and a significant difference in densities from spring 1995 to spring 2004. During Spring 2004, *Acetabularia* frequency peaked at 79% occurrence, and mean density peaked with a Braun-Blanquet value of 0.4 (FIG. 13). Along with showing significant intra-annual change twice, *Acetabularia* exhibited significant inter-annual change in density several times (TABLE 15). Distribution throughout Rankin Lake was highly variable over the years (FIG. 25).

Batophora was first observed in spring 1999 and subsequently showed the same trends as *Acetabularia*, increasing in both frequency and density, but with very low densities nonetheless. It peaked in density in fall 2003 with a 0.2 Braun-Blanquet value, and frequency in spring 2004 at 48% occurrence (FIG. 14). It never showed significant intra-annual change, but did exhibit significant inter-annual change many times, and also was found to have significantly higher densities in spring 2004 than in spring 1995 (TABLE 15). *Batophora* was commonly observed along the western perimeter and into the southern area of the lake, where *Thalassia* was more dense (FIG. 26).

Drift red macroalgae have been prevalent in Rankin Lake since spring 1995. Mean densities have been consistently within the 0.1-0.3 Braun-Blanquet value range, with little seasonal variation, which was not the case in several other basins. Frequency showed an overall increase, peaking at over 40% occurrence in spring 2002 (FIG. 19), but density did not change significantly between spring 1995 and spring 2004, and compared to the other macroalgae, the drift reds exhibited relatively little inter-annual change (TABLE 15). Spatial interpolation showed that drift reds were initially observed along the western edge of the lake possibly due to SE winds, and later in the southeastern portion as well, where *Thalassia* is more dense (FIG. 31). This could be attributed to the "Velcro effect" of *Thalassia*.

There was significantly more *Penicillus* and *Halimeda* in Rankin Lake in spring 2004 than there was in spring 1995, and both have increased in frequency as well, with *Penicillus* frequency reaching 97% in spring 2003 (FIG. 17). *Halimeda* frequency also peaked in spring 2003 at 82% (FIG. 16). Both *Penicillus* (FIG. 29) and *Halimeda* (FIG. 28) distributions were initially patchy and spatially variable, but became fairly ubiquitous over time. Both showed significant inter-annual variation (TABLE 15).

Caulerpa, on the other hand, was only found in the spring and was generally only observed in the northwestern area of the basin (FIG. 27). It was found in low densities but relatively high frequencies, which peaked at 61% in spring 2002 (FIG. 15). Significant inter-annual and intra-annual variation was observed, and it was found to be significantly more dense in the spring of 2004 than spring 1995 (TABLE 15).

Sargassum was only observed during spring sampling events and was variably distributed throughout the basin when present (FIG. 30). Frequency peaked in spring 1997 at 42%, but densities remained very low (FIG. 18). Significant change was seldom observed between or within sample years (TABLE 15).

To summarize the variability and change that occurred in Rankin Lake during FHAP sample years, all seagrasses observed showed some degree of inter-annual variability, particularly *Thalassia* and *Halodule*. *Thalassia* showed a significant overall increase in density and *Halodule* showed a significant seasonal change twice. All but two of the macroalgae, the drift reds and *Sargassum*, were found in significantly higher densities in spring 2004 than in spring 1995, inter-annual change much more evident than intra-annual in all macroalgae. *Acetabularia* was again the most intra-annually variable, but was only found to be significantly so twice.

Spearman Rank Order Correlations

Spearman Rank Order Correlation Analysis of Rankin Lake Braun-Blanquet data showed several repeated correlations. *Thalassia* and *Halodule* were negatively correlated during seven of the ten spring sampling events, and during four of the eight fall events. *Thalassia* was also negatively correlated to *Halophila* four times, *Syringodium* twice, *Caulerpa* three times, *Halimeda* three times, *Penicillus* once and *Sargassum* once. It was only positively correlated to *Syringodium* twice, during fall 1995 and spring 1996 (although this correlation later became negative in spring 2003), to *Acetabularia* once, and to the drift reds during falls 1997, 1998, 2002, and 2003, and spring 1997 and 1998. As might be expected, many of the macroalgae that exhibited one type of association with *Thalassia* exhibited an opposite association with *Halodule* during the same time. In spring 1998 and 1999, *Halimeda* was negatively correlated to *Thalassia* but positively correlated to *Halodule*, just as the drift reds were positively correlated to *Thalassia* in 1997 and 1998, but negatively correlated to *Halodule* during the same times.

Many correlations occurred between macroalgae, but often only once or twice. A positive correlation was only observed between *Acetabularia* and *Batophora* during two springs, and between *Batophora* and the drift reds during two springs. The drift reds were positively correlated with *Sargassum* on four occasions though, spring 1995, 2997, 2001, and 2003. *Sargassum* was also positively correlated to *Penicillus* twice, *Halimeda* once, and *Caulerpa* once, as well as to *Syringodium* and *Halophila* twice each. See Table 16

Table 16. Spearman Rank Order Correlations observed between macrophytes in Rankin Lake. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive (+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	7890134	034	+6 -3		0		724	78	89	5	4
Hw	6893	***Hw***	3	3		7	2	0	781	89	9	
He	2		***He***	3			4	14		02	9	94
Sf	5		3	***Sf***		2	1		4		0	02
Rm					***Rm***							
Ace						***Ace***	92		9	4		
Bat		3		3			***Bat***	4	94			
Cau								***Cau***			8	4
Drd	7823	89							***Drd***		4	5713
Hal	7						3			***Hal***	9	9
Pen	3	3									***Pen***	90
Sar			2									***Sar***

for other correlations.

Non-Metric Multidimensional Scaling

Macrophytes in general have increased in density in Rankin Lake since spring 1995. Figure 50, an nMDS ordination plot representing spring 1995 samples, shows a relatively high degree of clustering in the central area of the plot, indicating that at least some of the stations were similar in their vegetative community. Not a great deal of macroalgae was present in the basin in spring 1995, nor was there a great deal of seagrass. By spring 1999, however, there was a marked increase in both seagrasses and macroalgae, and also a decrease in uniformity, as the spring 1999 ordination plot (FIG. 51) indicates. Ordination of spring 2004 data (FIG. 52) showed an even more substantial increase in seagrass as well as macroalgae. There is a great deal of spread through the ordination, so sample uniformity must have been low at that time. Highest macroalgae cover values were at stations where seagrass cover was lower, but macroalgae and seagrasses co-existed at relatively high densities each at many of the stations.

Twin Key Basin

Maps, Means, Frequencies, and Change

Twin Key Basin is the second largest FHAP study basin, with an area of 54.13 km^2. Its average depth is approximately 2 meters, making it one of the deeper basins in Florida Bay. With the exception of fall 1997 when it averaged 56%, visibility was very high during the seasons for which data is available, and was usually 100%. Mean salinity values ranged from 29.2 to 53.0 and temperature means ranged from 25.6°C to 31.5°C. See Figures 4-7.

While there are several sandy patches inhabited by corals and macroalgae, Twin Key Basin has one of the more dense and evenly distributed *Thalassia* beds. *Thalassia* density peaked here in spring 2000 with a mean density of 3.2. The lowest mean density observed was a 2.0 in spring 2004. While there was large deviation from the mean, the actual *Thalassia* mean varied minimally over the years though it did show an overall slight decline by spring 2004. This decline was not statistically different from the spring 1995 densities, however, nor were any other changes in density significant (TABLE 17). Frequency of occurrence was always very high and reached 100% in eight of the eighteen sampling events. The lowest frequency was observed at 90% in spring 2004 (FIG. 8). Spatial interpolation shows that *Thalassia* was generally more dense around the perimeter and in the western area of the basin (FIGS. 20).

Halodule was also more heavily concentrated in the western region and into the central part of the basin, but never in the east (FIGS. 21). *Halodule* frequency and density were low throughout the years, and each also showed a slight decline, although there was no significant change in the density (TABLE 17). Maximum frequency was observed in spring 1997 at 42% (FIG. 9).

Syringodium (FIG. 10) and *Ruppia* (FIG. 12) were each only observed once, both during the fall of 1996, and each in only one quadrat. *Halophila* was never seen during sampling in this basin. No significant change was observed for these three seagrasses (TABLE 17).

Table 17. Number of times in which intra- and inter-annual, and decadal changes in macrophyte density were found to be statistically significant within Twin Key Basin.

	Spring	Fall	S to F	S'95-S'04
Thalassia	0(0)	0(0)	0	-
Halodule	0(0)	0(0)	0	-
Syringodium	0(0)	0(0)	0	-
Halophila	0(0)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	1(15)	1(2)	2	Yes (+)
Batophora	4(17)	0(1)	2	Yes (+)
Caulerpa	0(0)	0(0)	0	-
Drift Reds	1(4)	0(3)	1	-
Halimeda	0(10)	0(2)	0	Yes (+)
Penicillus	3(11)	2(2)	0	-
Sargassum	0(0)	0(0)	0	-

Acetabularia was fairly prolific in Twin, with frequencies showing a great deal of seasonality and a general increase over the years. It was observed in as many as 74% of the stations in spring 1998 (FIG. 13). Density remained relatively low, but showed a high degree of inter-annual variability as well as intra-annual difference during two sample years (TABLE 17). Although the high mean density of 0.7 was observed in spring 1998, there was also significantly more *Acetabularia* in spring 2004 than in spring 1995 (TABLE 17).

Batophora was observed in higher frequencies and densities than *Acetabularia*, but as with *Acetabularia*, both peaked in spring 1998, with values of 90% and 1.0, respectively (FIG. 14). It also showed a significant increase between spring 1995 and spring 2004 as well as a great deal of inter-annual variability, usually from spring to spring (TABLE 17). *Batophora* and *Acetabularia* both became more widespread over time, but not necessarily more dense. Both were spatially variable and did not appear to favor one area of the basin over another, as spatial interpolation did not yield any clear spatial trends (FIGS. 25 and 26).

Drift red macroalgae showed similar patterns to *Batophora* and *Acetabularia* but peaked in both frequency and density in spring 2000, rather than spring 1998 (FIGS. 19). Drift red algae were not, however, found in significantly greater density in spring 2004 than spring 1995, as most of their variability occurred during the mid-years of the study (TABLE 17).

Penicillus was generally observed in greater densities in the central and southern portion of the basin (FIG. 29) and was observed during every sampling event except for spring 1996. Other than that year, *Penicillus* frequency was usually high, peaking in fall

1999 at 84%. Density also peaked during that sampling trip with a mean Braun-Blanquet value of 0.5 (FIG. 17). Although it did exhibit some significant inter-annual variability a few times during consecutive years, there was no significant difference between spring 1995 and spring 2004 (TABLE 17).

Halimeda was not observed during the spring 1995, 1996 or the fall 1997 samples, but increased in frequency in subsequent years, until spring 1999, when it peaked at 77% occurrence (FIG. 16). It did not show a particularly strong seasonal signal in density or frequency variation, but did exhibit some inter-annual variability. With the exception of a few sampling events, *Halimeda* was generally observed with *Penicillus* in the central and southern portion of the basin (FIG. 28). Densities in spring 2004 statistically different than those observed in spring 1995, when no *Halimeda* was observed in this basin (TABLE 17).

Caulerpa was often present in the southeastern area of the basin at very low frequencies and densities (FIGS. 27 and 15), it was usually only found in one or two quadrats per trip, and no significant temporal variability was detected (TABLE 17).

Sargassum was not observed in Twin until spring 2001, when if was found at both low density and frequency (FIG. 18). It was only observed three more times in Twin, during fall 2002, spring 2003, and spring 2004, always in only one quadrat, never eliciting any significant variability (TABLE 17).

Overall, *Acetabularia*, *Batophora*, and *Halimeda* were the only macrophytes to be significantly more dense at the end of FHAP sampling than at the beginning. Similar to other basins, *Acetabularia*, *Batophora*, and the drift reds were the only macrophytes to exhibit any significant intra-annual variability. *Thalassia* remained stable over the years, as did *Halodule*.

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of Twin Key Basin Braun-Blanquet data revealed a pattern between the two dominant seagrasses and the macroalgae. This pattern was seen in other basins, but not as exclusively as it has occurred here. As usual, *Thalassia* and *Halodule* were negatively correlated to one another during several sampling events. *Thalassia* was also negatively correlated to every macroalgae except *Caulerpa* and *Sargassum*, with neither of which it held any correlation at all. It was negatively correlated to *Acetabularia* during four springs and four falls, although only during the same years in 1997 and 1999. It was also negatively correlated to *Batophora* during four springs and four falls, and many of these correlations overlapped with *Acetabularia* correlation years and seasons. Negative correlation with the drift reds occurred twice, with *Halimeda* five times, and with *Penicillus* during seven of the eight fall sampling events and five of the ten spring events. Concurrently, *Halodule* had positive correlations with all of the macroalgae except *Sargassum*, each only during one fall sampling. It was positively correlated with *Acetabularia* during three springs though, and the drift reds and *Halimeda* during spring 1999.

Acetabularia was positively correlated to every other macroalgae except *Sargassum* during at least one fall sampling, and to all except *Caulerpa* and *Sargassum* during at least one spring sampling. It was positively associated with the drift reds in spring 1999 and then switched to a negative association in spring 2000, and back to

Table 18. Spearman Rank Order Correlations observed between macrophytes in Twin Key Basin. Top triangle gives Spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive(+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	6783				5794	5724		3	80	57892	
Hw	589	***Hw***				589			9	9		
He			***He***									
Sf				***Sf***								
Rm					***Rm***							
Ace	7902	9				***Ace***	5014		+9 -0 +4	94	724	
Bat	5902	3				2	***Bat***		-8 +4	24	523	
Cau		3				3		***Cau***		83		
Drd	8	9				7	70		***Drd***		1	
Hal	783	8				79				***Hal***	8924	3
Pen	5678902	8				90				890	***Pen***	
Sar												***Sar***

positive in spring 2004. *Batophora* exhibited correlation reversal with the drift reds also, as it was positively correlated with them in fall 1997, negatively correlated in spring1998, positively correlated by fall 2000 and then positively correlated again in spring 2004. *Batophora* was also repeatedly and positively correlated to *Halimeda* and *Penicillus*, which were also positively correlated to one another several times during both spring and fall sampling. See Table 18 for more information.

Non-Metric Multidimensional Scaling

nMDS ordination resulted in plots that show some clustering but a general lack of uniformity in Twin Key Basin during the first season of FHAP sampling (FIG. 53). Clustering occurred based on similarities in seagrass makeup, as indicated by total seagrass overlays. Overlays show that macroalgae was dense in only a few areas and most dense where seagrass was less dense. Seagrass and macroalgae both increased in density by spring 1999, and again, although there was overlap, overlays show that high densities of each are somewhat spatially exclusive (FIG. 54). Clustering also decreased from the spring 1995 ordination plots, suggesting that the increase in macroalgae led to a less uniform community in the basin. Spring 2004 ordination (FIG. 55) was much more tightly clustered and exhibits an extensive separation of the two macrophyte groups, indicating that over time the basin again became more uniform in its species distribution.

Rabbit Key Basin

Maps, Means, Frequencies, and Change

Rabbit Key Basin is 31.8 km^2 and has an average depth of about 1.9 meters. It is in the western region of Florida Bay and thus more exposed to the Gulf of Mexico waters. Though it is proximal to ocean waters, it is still enclosed by mudbanks and is fairly shallow, and consequently, mean salinities ranged from 28.2 to 53.6. Mean temperature ranged from 24.2°C to 31.1°C. After spring 1998, visibility in this basin was usually very high, with the exception of fall 2002, when it averaged 72%. See Figures 4-7.

Thalassia frequency in Rabbit Key basin remained relatively constant over the past ten years, always reaching 93% or higher, and on many occasions sampling yielded 100% frequency of occurrence. *Thalassia* density was not so constant, however, and it displayed significant inter-annual change on a number of occasions (TABLE 19). From spring 1995 to fall 1998, mean density dropped from a Braun-Blanquet value of 3.9 to one of 2.0. Following that decrease in cover, *Thalassia* density rebounded and then leveled off with a mean around 3.0 for the last several sampling trips (FIG. 8). The difference in densities between spring 1995 and spring 2004 was not significant. While *Thalassia* makes up a large portion of the benthic flora in Rabbit Key Basin, spatial interpolation shows that it is much denser in the eastern region of the basin than in the west (FIG. 20).

Halodule on the other hand occupies the north and western portion of Rabbit Key Basin (FIG. 21), with fairly high frequencies and moderate mean densities. *Halodule* frequency showed an increasing trend over the years, as did density, although it peaked early on in spring 1999 with a mean Braun-Blanquet of 1.6 (FIG. 9). *Halodule* exhibited

Table 19. Number of times in which intra- and inter-annual, and decadal changes in macrophyte density were found to be statistically significant within Rabbit Key Basin.

	Spring	Fall	S to F	S'95-S'04
Thalassia	1(5)	0(1)	0	-
Halodule	0(16)	0(0)	0	Yes (+)
Syringodium	0(7)	0(3)	0	Yes (+)
Halophila	0(0)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	0(0)	0(0)	0	-
Batophora	0(0)	0(0)	0	-
Caulerpa	0(0)	0(0)	0	-
Drift Reds	1(12)	0(0)	2	-
Halimeda	0(12)	0(5)	0	Yes (+)
Penicillus	0(5)	0(4)	0	-
Sargassum	0(0)	0(0)	0	-

significant inter-annual change several times, and was also significantly greater in density in spring 2004 than in spring 1995 (TABLE 19).

Syringodium became fairly prevalent in the same area as *Halodule* (FIG. 22) and showed a steep increase in frequency in the past decade. Density also steadily increased until spring 2002 when it leveled off and remained fairly constant with Braun-Blanquet values around 1.0 (FIG. 10). There was significantly more *Syringodium* in Rabbit Key Basin in spring 2004 than in spring 1995 (TABLE 19).

Halophila was observed during the more recent sampling trips, but at very low densities and frequencies, generally only in one or two quadrats per sampling event (FIG. 11). *Ruppia* was never observed in this basin during a sampling trip (FIG. 12). No significant temporal variability was found for these seagrasses (TABLE 19).

Although *Acetabularia* and *Batophora* were generally the most prevalent macroalgae observed in Florida Bay, in this particular basin they are not as frequently observed and are much less dense than the rhizophytic algae and the drift reds. *Acetabularia* frequency peaked at 30% and mean density never exceeded a Braun-Blanquet value of 0.1 (FIG. 13). Likewise, *Batophora* frequency peaked at 26%, also with mean densities never exceeding 0.1 (FIG. 14). *Acetabularia* and *Batophora* were usually observed in the southern leg of Rabbit and *Acetabularia* occasionally on the western rim (FIGS. 23 and 24). Neither showed any variability in density (TABLE 19).

Drift reds were often also found in the southern leg, but their distribution often extended into the northern areas of the basin as well (FIG. 31). The drift reds peaked in frequency and density in spring 1998 and spring 1999, respectively, but then leveled out in the 5% to 20% frequency range and with mean densities not again exceeding 0.2 (FIG.

19). They were the only macroalgae in this basin to show significant seasonal variation, as well as inter-annual variation, but their densities were not significantly different between spring 1995 and spring 2004 (TABLE 19).

Halimeda and *Penicillus* have both become increasingly widespread since spring 1995, and both showed a high degree of inter-annual variability, but *Halimeda* alone was more dense in spring 2004 than in spring 1995 (TABLE 19). *Halimeda* frequency of occurrence peaked in spring 2004 at 59% with a corresponding mean density of 0.3 (FIG. 16). *Penicillus* peaked much earlier in fall 1999 at 61%, with a corresponding mean density of 0.2 (FIG. 17). *Halimeda* was almost exclusively observed in the northern knob of the basin, though its distribution did extend into the southern leg on more than one occasion (FIG. 28). Spatial interpolation showed that *Penicillus* distribution was similar to that of *Halimeda*. It was also normally present in the northwestern knob, although it occasionally reached into the southern leg of the basin or was present throughout the entire basin (FIG. 29).

Caulerpa, on the other hand, showed little overall change in frequency or density. It reached a maximum frequency in spring 1999 at 30%, but never exceeded a mean density of 0.2 (FIG. 15). It was normally observed in the northern knob of the basin, with the higher densities occurring along the western edge (FIGS. 27). *Sargassum* was only observed once in Rabbit Key Basin, during spring 2003, and at that time was only found in one quadrat (FIG. 18). Neither of these relatively rare macroalgae showed any significant variability (TABLE 19).

Although *Thalassia* mean densities were very high, it decreased steadily for several of the initial sampling events. It eventually rebounded and was not significantly less dense spring 2004 than in spring 1995. *Halodule* and *Syringodium* were significantly more dense in spring 2004 than in spring 1995, and all three displayed inter-annual variability, but no intra-annual variability. Only three other macrophytes exhibited any variability, and those were the drift reds, which showed intra-annual change twice, *Halimeda*, which also significantly increased since spring 1995, and *Penicillus*, which increased but did not do so significantly.

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of Rabbit Key Basin Braun-Blanquet data showed trends as clear as those found in Twin Key Basin. *Thalassia* once again had all negative correlations, but in this basin *Thalassia* was also negatively correlated to all other seagrasses present as well as to the macroalgae. It was negatively correlated to *Halodule* during every fall sampling and during seven of the spring sampling events. Likewise, *Thalassia* was negatively correlated to *Halophila* during one fall and one spring, and also to *Syringodium* during six of the fall trips as well as six of the spring trips. *Thalassia*-macroalgal negative correlations were repetitive, particularly with *Acetabularia*, *Halimeda*, and *Penicillus* during spring sampling. *Halodule*, on the other hand, had all positive correlations with other macrophytes, with the exception of a negative correlation with the drift reds in spring 2000. It was also positively correlated on one occasion to *Syringodium*, which was repeatedly and positively correlated with many of the macroalgae. Correlations between macroalgae were always positive, but they were not overly repetitive, with the exception of the *Halimeda/Penicillus* correlations which were found during three springs and falls. See Table 20 for further details of correlations.

Table 20. Spearman Rank Order Correlations observed between macrophytes in Rabbit Key Basin. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive (+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	7901234	4	901234		9034	4	79		0234	94	
Hw	56789023	***Hw***		4		0		9	0	8024	54	
He	3		***He***			0			4	0		
Sf	579023			***Sf***		90134			89	91234	924	
Rm					***Rm***							
Ace						***Ace***	4	3		90	9034	
Bat	3			0		2	***Bat***					
Cau	53	56	3	573				***Cau***				
Drd	7			7		2	2		***Drd***	8	8	
Hal	83	3		903				80	8	***Hal***	894	
Pen		3				2	2	8		803	***Pen***	
Sar												***Sar***

Non-Metric Multidimensional Scaling

Ordination plots created from spring 1995 sample data show that there was a great deal of uniformity in the benthic macrophyte community in Rabbit Key Basin at that time (FIG. 56). Only one station had a substantial amount of macroalgae and this same station, 57, had one of the lower total seagrass covers, which were generally high throughout the rest of the basin. nMDS of spring 1999 data resulted in an ordination plot (FIG. 57) exhibiting less clustering and therefore indicating less uniformity throughout the basin. There remained a great deal of seagrass at this time, but macroalgae cover had increased in many areas, which could be the reason for a decrease in uniformity. By spring 2004, seagrass was still widespread and abundant. Macroalgae was becoming much more widespread also, but compared to seagrass cover, it was still relatively sparse (FIG. 58). Stations with high seagrass densities corresponded to those with lower macroalgae densities, and the only station without seagrass had the highest cover value for macroalgae observed during this sampling.

Johnson Key Basin

Maps, Means, Frequencies, and Change

Johnson Key Basin is just northwest of Rabbit Key Basin and is the westernmost basin studied as part of FHAP. The perimeter of its relatively small area (14.23 km^2) is almost completely surrounded by mudbanks and mangroves, separating it, to a certain degree, from the waters of the nearby Gulf of Mexico. Average depth in this basin is about 1.4 meters and mean salinity ranged from 26.4 to 54.1 during the study. As was the case in many of the other FHAP basins, salinities were highest in falls 2000 and 2002.

Temperatures were fairly constant, ranging only from a mean of 25.0°C to 30.3°C. Visibility increased dramatically after fall 1995, when it averaged only 38.5%. Until spring 2000, when mean visibilities reached 100% and remained constant thereafter, spring visibilities were consistently higher than fall visibilities of the same year. See Figures 4-7.

Besides fall 1996, when there was a marked decrease in *Thalassia* frequency, this plant was relatively widespread in Johnson Key Basin. It underwent a fairly dramatic increase in mean cover, reaching a peak of 3.4 in spring 2004 (FIG. 8). This peak was significantly different than spring 1995 (TABLE 21), when Braun-Blanquet densities were much lower. Spatial interpolation indicates that initially *Thalassia* mean cover values were higher in the eastern area of the basin but then became generally higher in the northern area (FIG. 20).

Conversely, higher *Halodule* cover was initially seen in the north and then became greater in the east and south (FIG. 21). Both *Halodule* frequency and density showed an increasing trend until density peaked in fall 2000, after which time it declined to a Braun-Blanquet value of 1.0 (FIG. 9). There was, however, a significantly higher cover in spring 2004 than in spring 1995 (TABLE 21).

Syringodium perhaps showed the most dramatic increase in both frequency and density (statistically significant between spring 1995 and spring 2004) of any other macrophyte in any of the FHAP basins. A fair amount of seasonality was also detected, although none of the intra-annual variability was found to be significant (TABLE 21). As both frequency and density values climbed, spring values were almost always higher than the previous fall. Frequency reached 96% and density reached a high mean of 1.9, both

Table 21. Number of times in which intra- and inter-annual, and decadal changes in macrophyte density were found to be statistically significant within Johnson Key Basin.

	Spring	Fall	S to F	S'95-S'04
Thalassia	0(21)	0(12)	1	Yes (+)
Halodule	1(14)	0(14)	0	Yes (+)
Syringodium	0(21)	0(9)	0	Yes (+)
Halophila	1(3)	0(0)	0	-
Ruppia	0(0)	0(0)	0	-
Acetabularia	0(0)	0(0)	0	-
Batophora	0(0)	0(0)	0	-
Caulerpa	1(3)	0(0)	0	-
Drift Reds	1(7)	0(0)	2	-
Halimeda	0(4)	0(4)	0	Yes (+)
Penicillus	0(0)	0(2)	0	-
Sargassum	0(0)	0(0)	0	-

in spring 2004 (FIG. 10). Spatial interpolation shows that *Syringodium* spread from west to east, but maintained much higher densities in the west where *Thalassia* was generally less dense (FIG. 22).

Halophila was often observed in the central area of this basin, but at low densities not exceeding 0.2 (FIG. 11). *Ruppia* was only observed here during three of the sampling trips, and on each of those occasions was only found in one quadrat (FIG. 12). Although *Halophila* varied annually, there was no significant difference between beginning and ending densities, nor was any significant change ever detected in *Ruppia* (TABLE 21).

Acetabularia was not at all widespread or dense in this basin, only occurring with any regularity from spring 1997 to spring 1999 (FIG. 13), at which times it was observed in several different areas of the basin (FIG. 25). After that time, it was rarely observed, if at all, and no significant change was ever found (TABLE 21).

Batophora was not found in any more than one quadrat until spring 2002, at which time it was found at 18% of the sampling stations (FIG. 14), mostly in the eastern area of the basin. At these stations, it was found only as one or a few individuals (FIG. 26) and it did not exhibit any significant variability (TABLE 21).

The drift reds and the rhizophytics were more successful here than the psammophytics, in that they were observed with much more regularity and in higher densities. Drift red densities were generally higher in the spring, and peaked in spring 1998 at 0.4. Distribution fluctuated throughout the basin, and frequency ranged from 0% to 59% frequency of occurrence (FIG. 19). Besides *Thalassia*, they were the only macrophytes to show any significant intra-annual variability, although that only occurred during one year. They also showed some degree of inter-annual change, though not much (TABLE 21).

Halimeda showed an overall increase in frequency and density, but the increase in frequency was much more pronounced, indicating that while it was becoming a much more widespread plant, it was not becoming particularly more dense, never exceeding a Braun-Blanquet mean density of 0.2 (FIG. 16). By spring 2004, however, there was significantly more *Halimeda* in Johnson Key Basin than in spring 1995 (TABLE 21). Spatial interpolation shows that until spring 2002, *Halimeda* distribution was limited to the western and southern portions of the basin, but after this time it was spread throughout the entire basin (FIG. 28).

Penicillus was not observed until spring 1997, after which time its frequency increased to 35% in fall 1999 and then declined to 4% in spring 2004. Mean density never exceeded 0.2 (FIG. 17), and spatial interpolations showed that distribution was fairly random and changed from year to year (FIGS. 29). *Caulerpa*, likewise, never exceeded a mean density of 0.2 either, but did reach a high frequency of 46% in spring 2002 (FIG. 15). *Caulerpa* distribution was more concentrated on the western side of the basin during most sampling trips (FIG. 27). Although both of these macroalgae showed some significant inter-annual change, neither had significantly different densities in spring 2004 than in spring 1995 (TABLE 21).

Sargassum peaked at 23% frequency in spring 2000 (FIG. 18), when its greatest densities were observed in the central part of the basin (FIG. 30). It was only observed in small densities occasionally thereafter, and never showed any significant variability in density (TABLE 21).

To summarize significant change that took place in Johnson Key Basin during FHAP sampling, the three dominant seagrasses, *Thalassia*, *Halodule*, and *Syringodium*, all increased in density significantly, and in doing so exhibited significant inter-annual change on a number of occasions. The drift reds again showed the most intra-annual variability, and also some inter-annual variability. *Caulerpa*, *Halimeda*, and *Penicillus* also showed some inter-annual variability, but *Halimeda* was the only macroalgae to be observed at significantly higher densities in spring 2004 than in the beginning of FHAP sampling. *Acetabularia*, *Batophora*, and *Sargassum* didn't show any significant temporal change.

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of Johnson Key Basin Braun-Blanquet data exhibited trends similar to most other FHAP basins. *Thalassia* was negatively correlated to several other seagrasses as well as to macroalgae, although the correlations were not generally repetitive. *Halodule* was negatively correlated to *Syringodium* during five springs and one fall, but only otherwise negatively correlated to *Penicillus*, and only during one sampling event. Any correlation that occurred between macroalgae was positive, and many took place either in spring or fall 1997. *Acetabularia* was correlated to every other macroalgae, with the exception of *Caulerpa*, during at least one sampling event in 1997. The drift reds, *Halimeda*, and *Penicillus* were also all correlated to one another in fall 1997. Both spring and fall 2000 were also full of macroalgae correlations. For a complete set of correlations, see Table 22.

Table 22. Spearman Rank Order Correlations observed between macrophytes in Johnson Key Basin. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein1995 = 5, 1996 = 6, 2003 = 3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or - before the number indicates where that correlation was positive (+)or (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	2	4	3		80		8		0	8	
Hw	523	***Hw***		90234							8	
He	3		***He***			94	14	4	9	4		
Sf	3	9		***Sf***								8
Rm					***Rm***							
Ace						***Ace***	74	4	71	7		
Bat							***Bat***	4	0		23	
Cau	0					0		***Cau***	2	012	901	0
Drd						7			***Drd***	7		
Hal			02			70			7	***Hal***	01	03
Pen	23		3			70		0	7	70	***Pen***	0
Sar	2				9	7			79	702	7	***Sar***

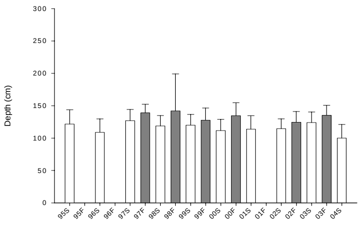
Non-Metric Multidimensional Scaling

Ordination of Johnson Key Basin sample data showed an increasing trend in seagrass density over time. During spring 1995 sampling, seagrass densities were fairly low at most sample stations, as were macroalgal densities (FIG. 59). By spring 1999, however, seagrass was observed in relatively high densities at almost every station. Macroalgae were also observed more often, but they contributed far less to bottom cover than seagrasses (FIG. 60), and higher densities were observed where seagrass densities remained low. An increased degree of clustering is also evident in the spring 1999 ordination, as seagrass densities given by the overlays look fairly similar throughout the basin. By spring 2004, there were relatively high densities of seagrass observed at every station and high densities of macroalgae at only a few (FIG. 61). Ordination suggests some degree of clustering to the left of the plot, but not extensive.

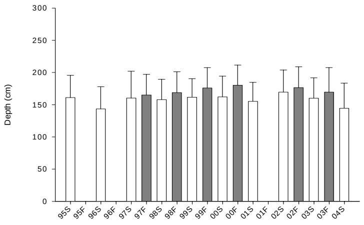
FIG. 4. Florida Bay Depth by Basin: Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Florida Bay Depth by Basin

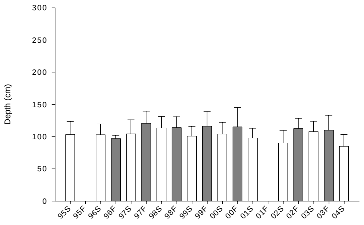
Rankin



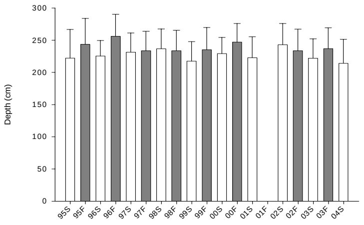
Whipray



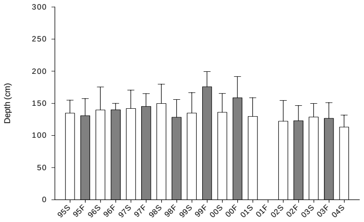
Madeira

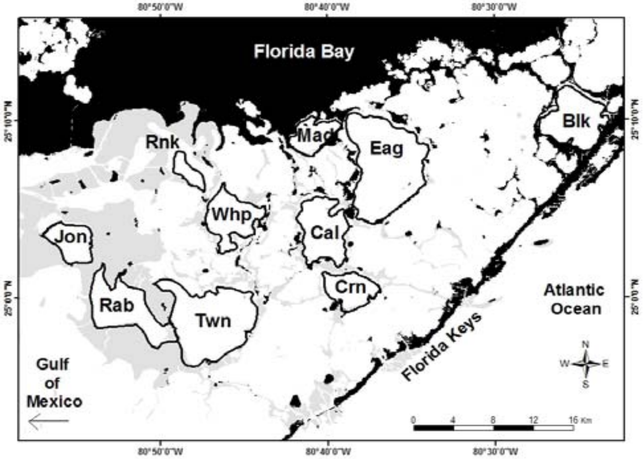


Blackwater

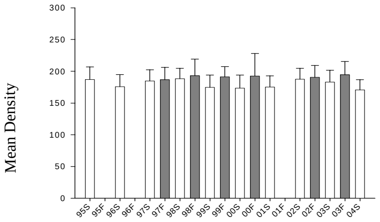


Johnson

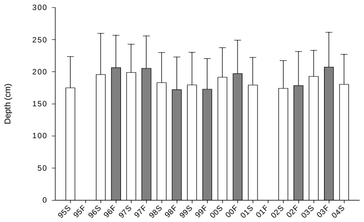




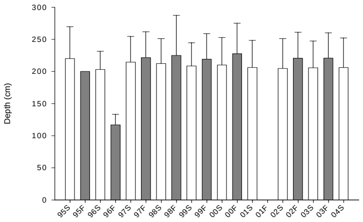
Eagle



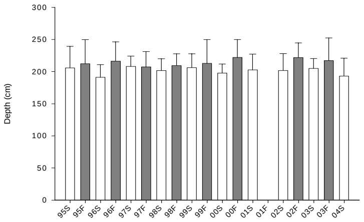
Rabbit



Twin



Calusa



Crane

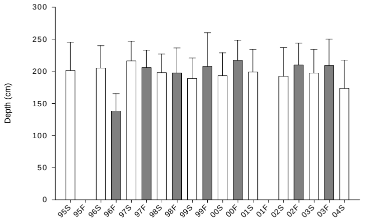


FIG. 5. Florida Bay Visibility by Basin: Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Florida Bay Visibility by Basin

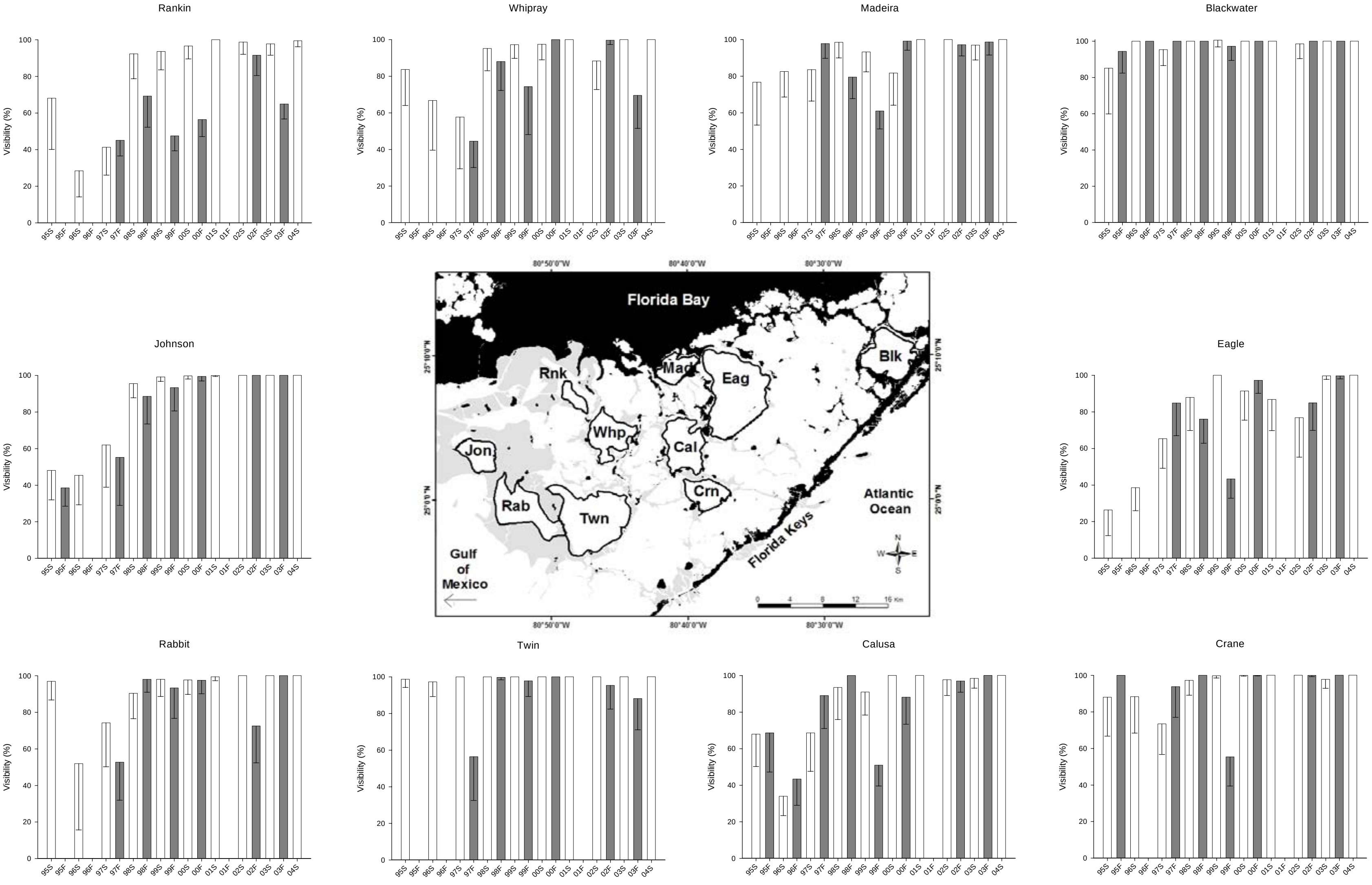


FIG. 6. Florida Bay Temperature by Basin: Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Florida Bay Temperature by Basin

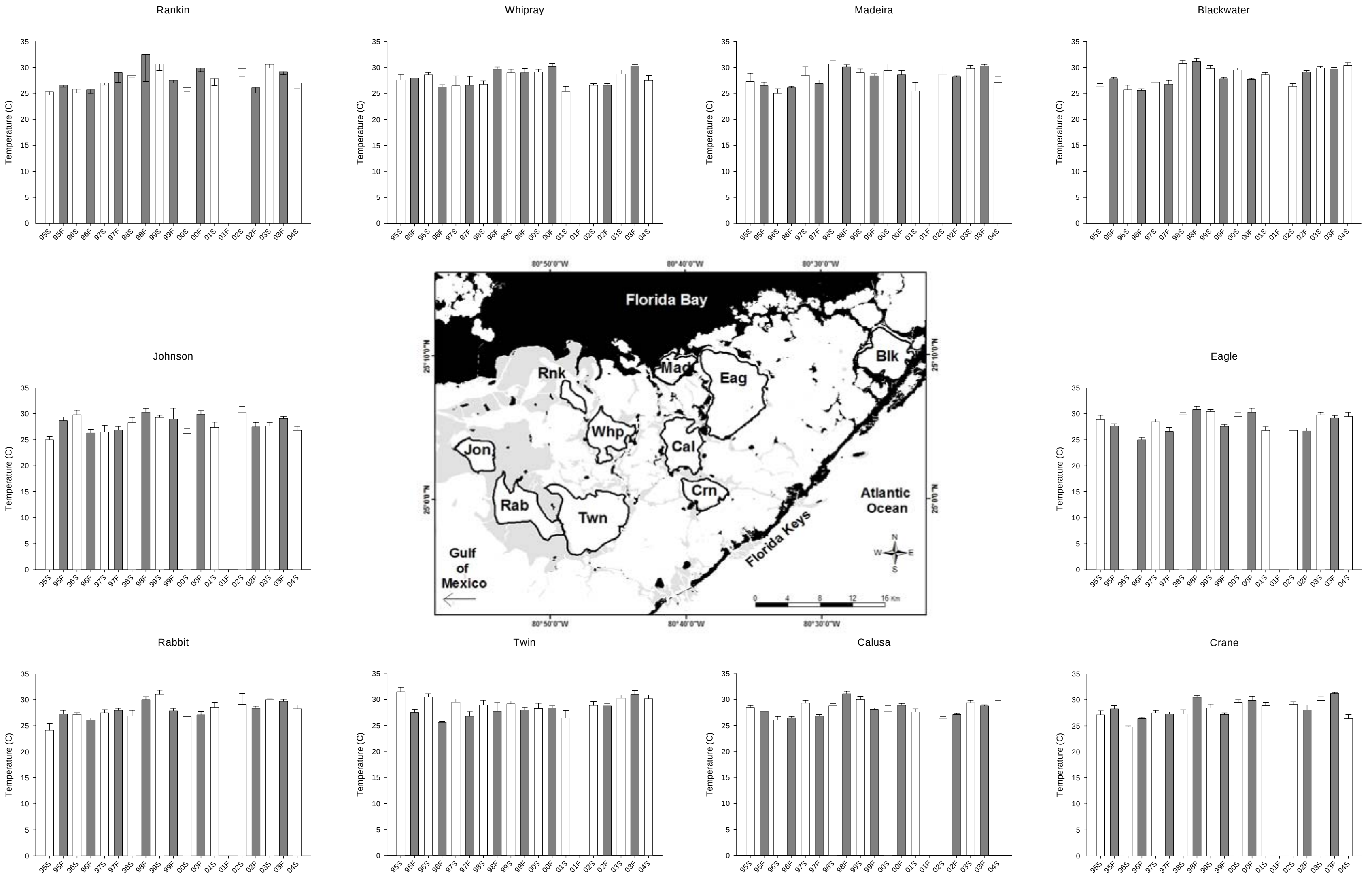


FIG. 7. Florida Bay Salinity by Basin: Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Florida Bay Salinity by Basin

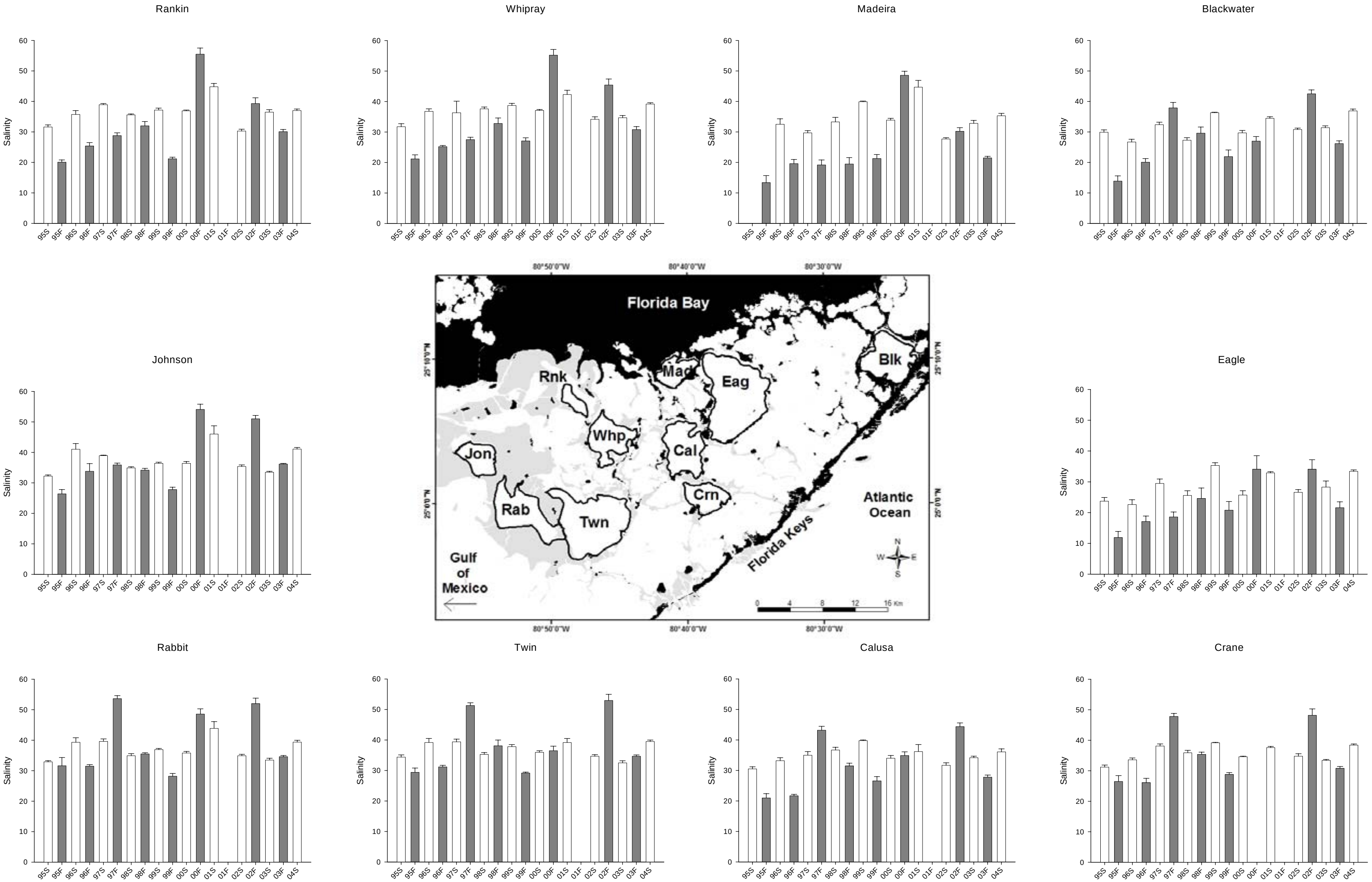


FIG. 8. *Thalassia* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Thalassia Density and Frequency

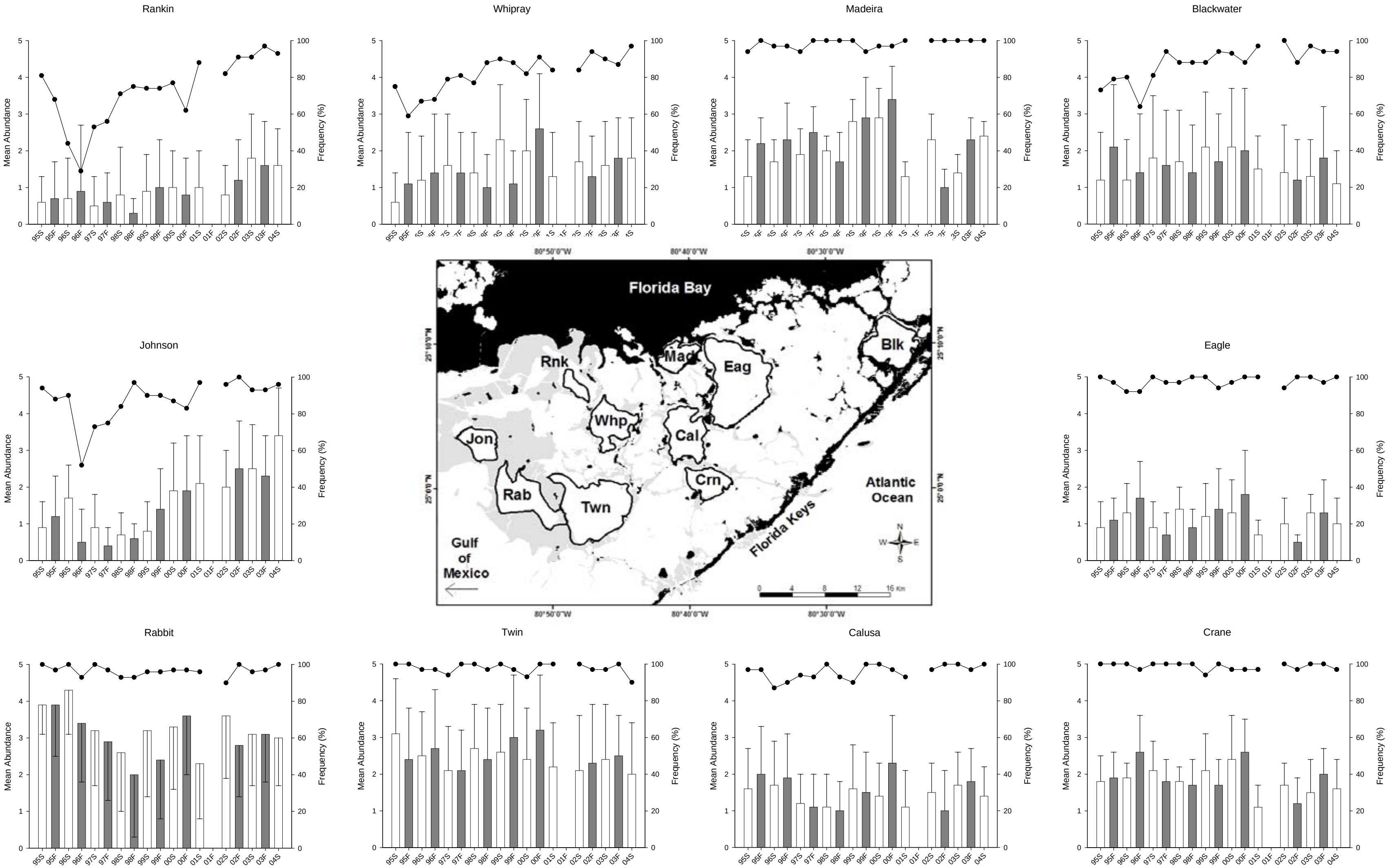


FIG. 9. *Halodule* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Halodule Density and Frequency

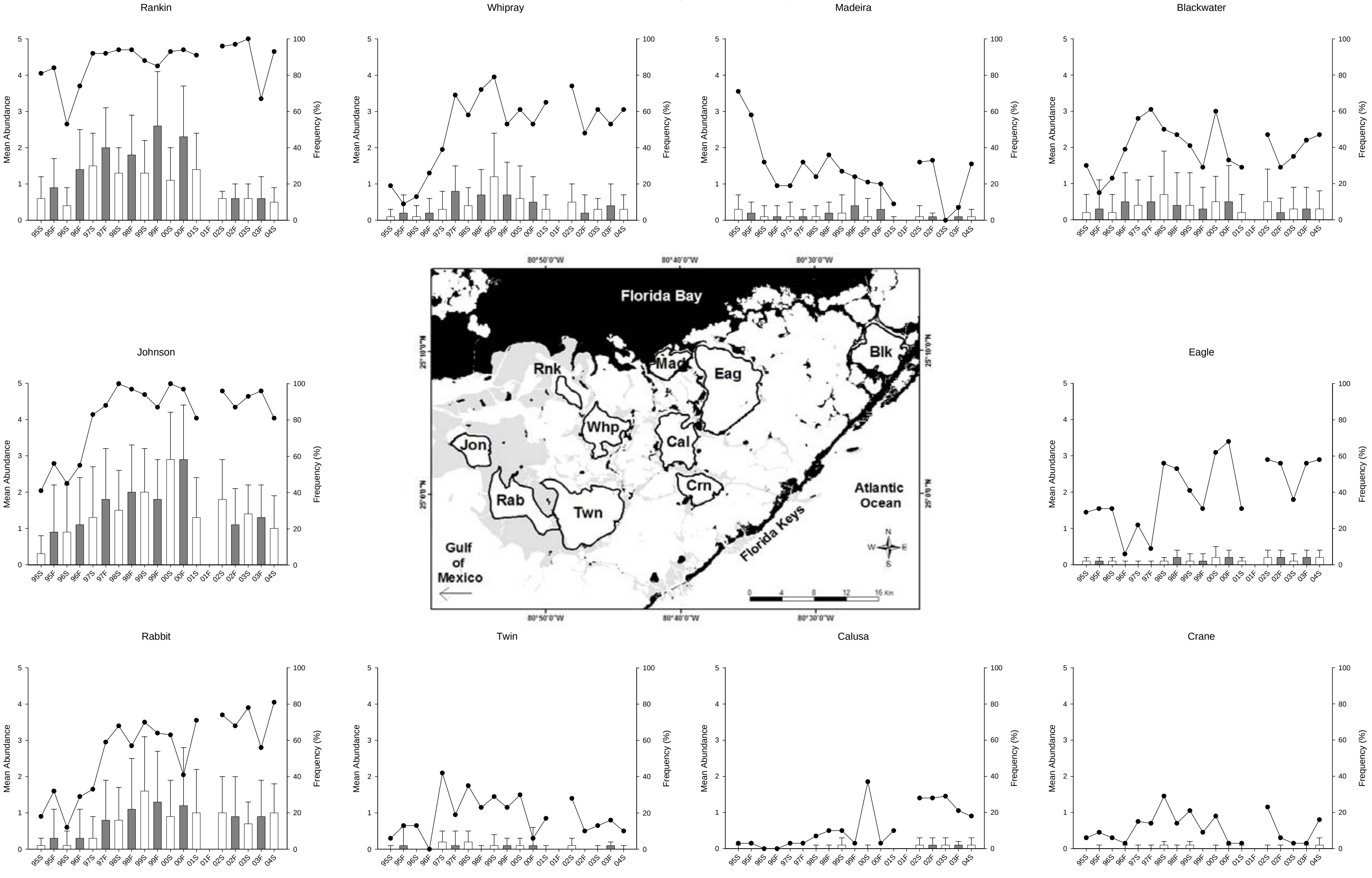


FIG. 10. *Syringodium* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Syringodium Density and Frequency

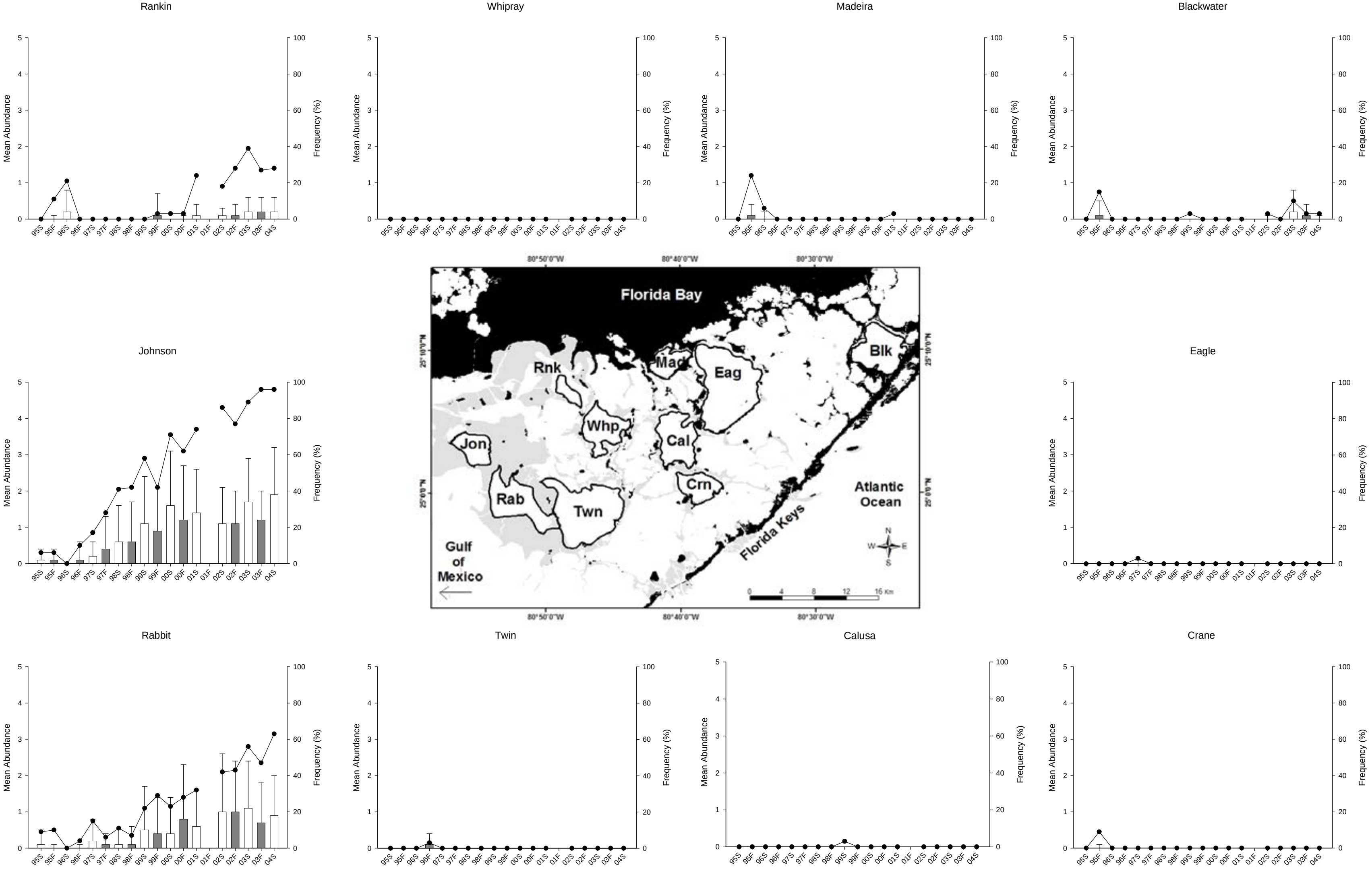


FIG. 11. *Halophila* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Halophila Density and Frequency

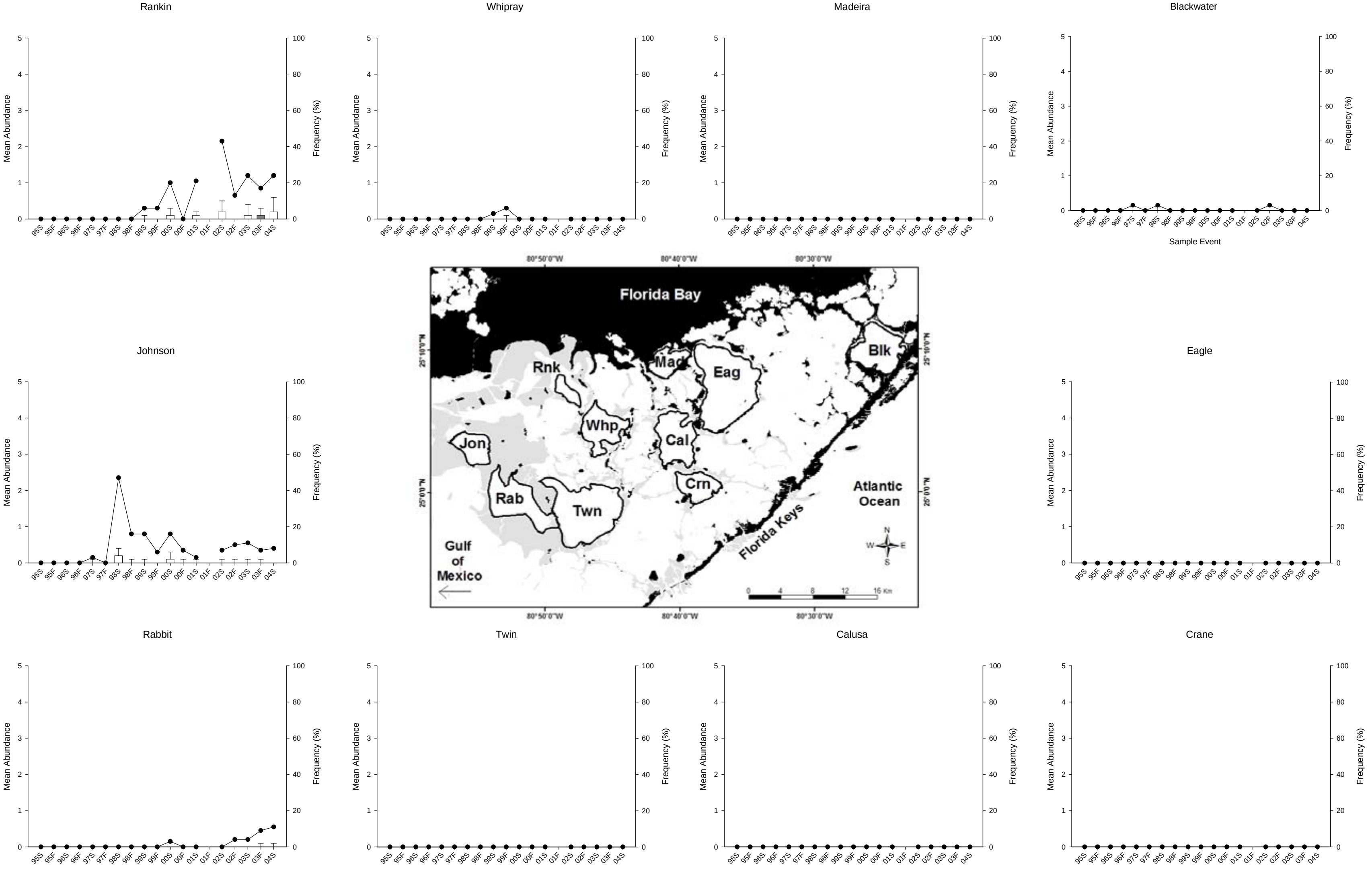
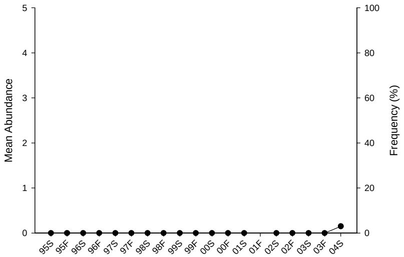


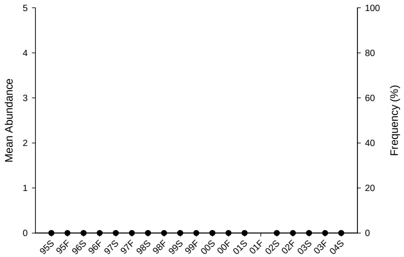
FIG. 12. *Ruppia* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Ruppia Density and Frequency

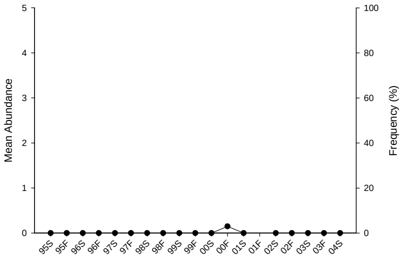
Rankin



Whipray

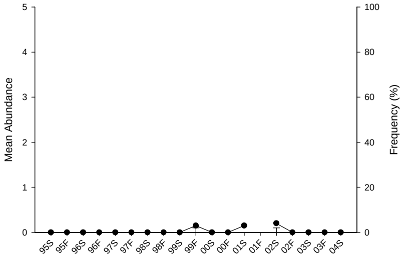


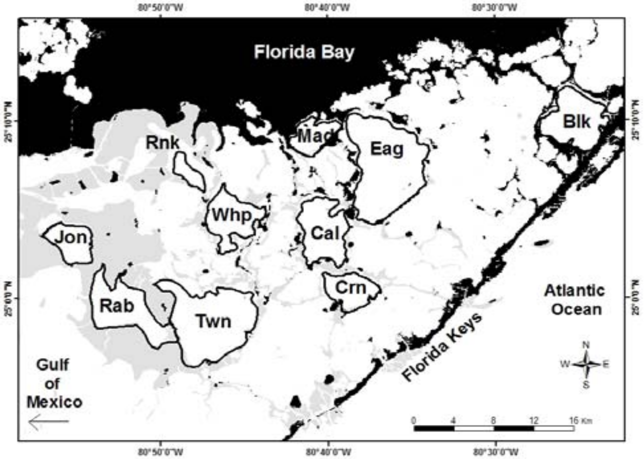
Madeira



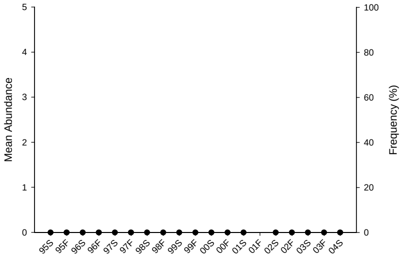
Blackwater

Johnson

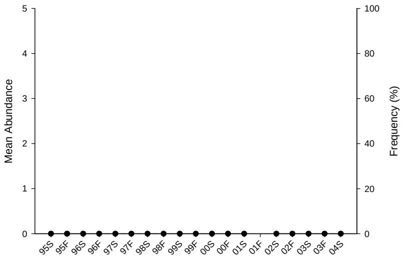




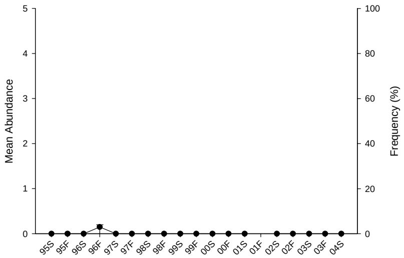
Eagle



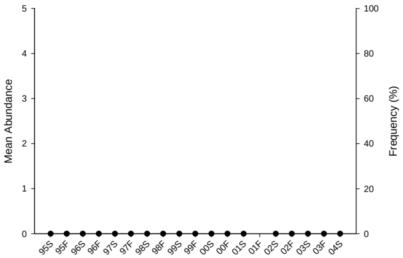
Rabbit



Twin



Calusa



Crane

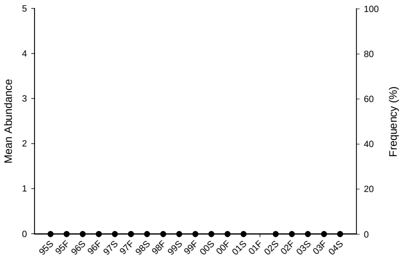


FIG. 13. *Acetabularia* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Acetabularia **Density and Frequency**

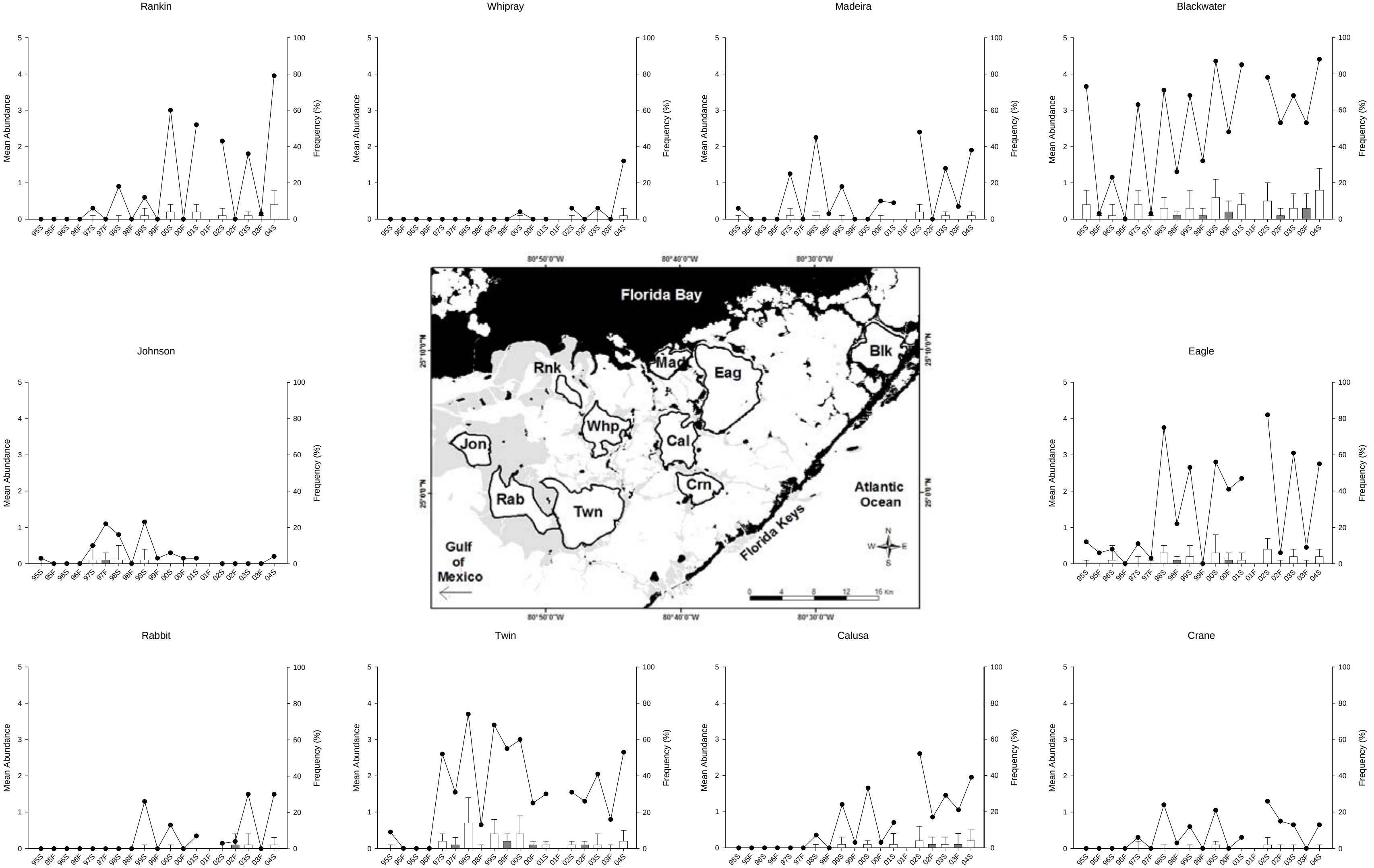
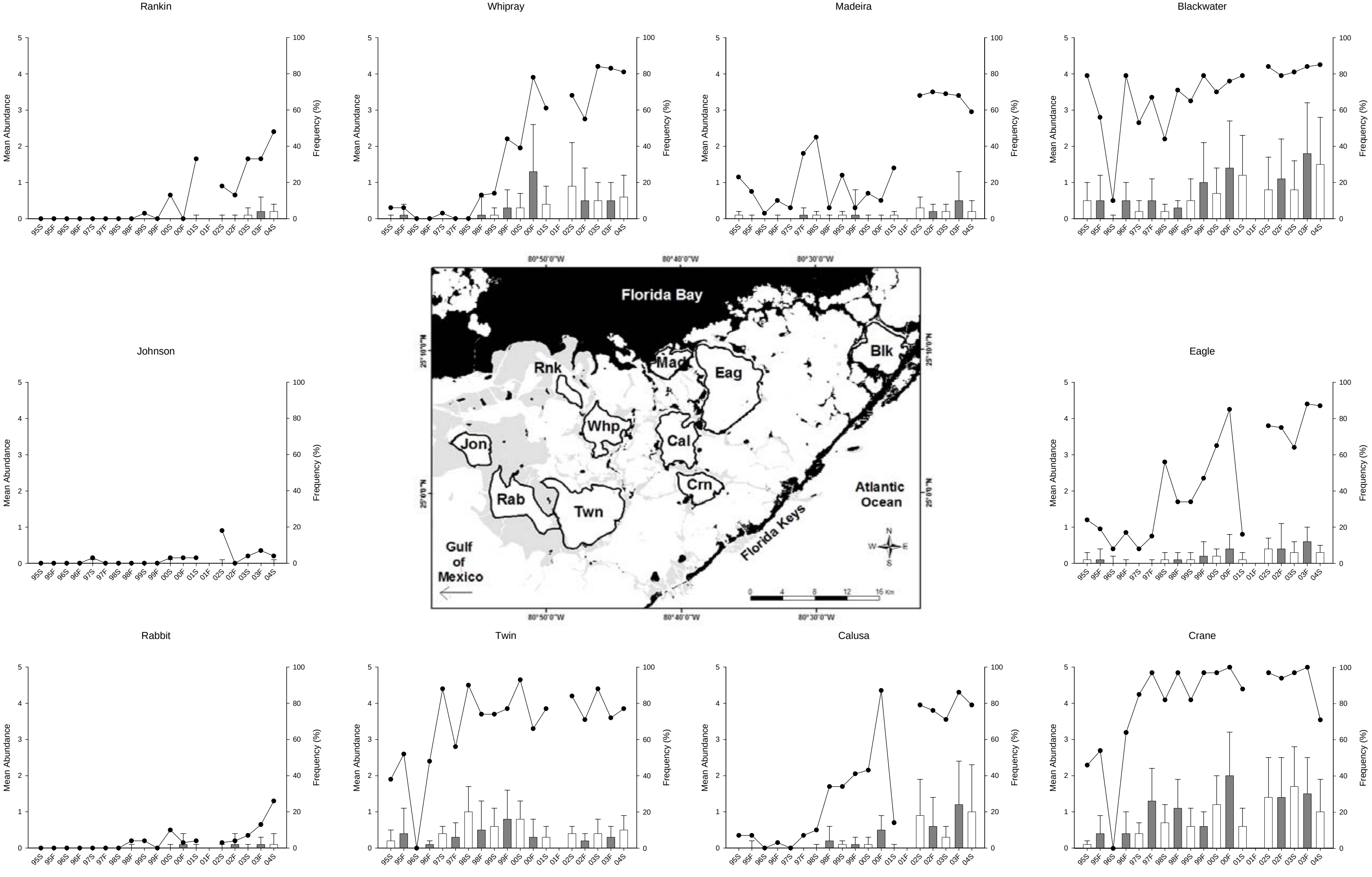


FIG. 14. *Batophora* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Batophora Density and Frequency



Rankin

Whipray

Madeira

Blackwater

Johnson

Eagle

Rabbit

Twin

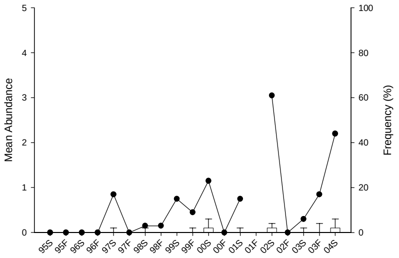
Calusa

Crane

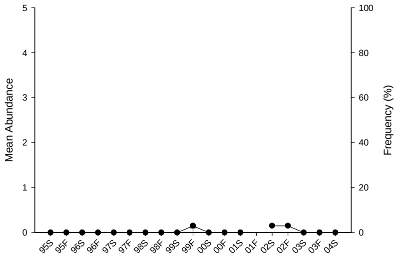
FIG. 15. *Caulerpa* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Caulerpa Density and Frequency

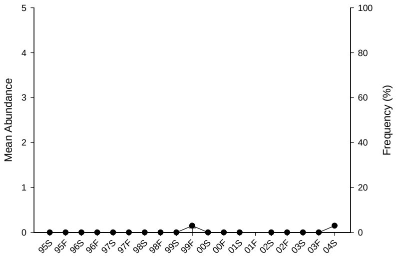
Rankin



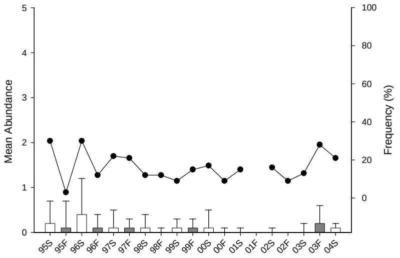
Whipray



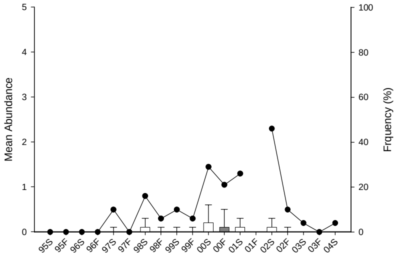
Madeira

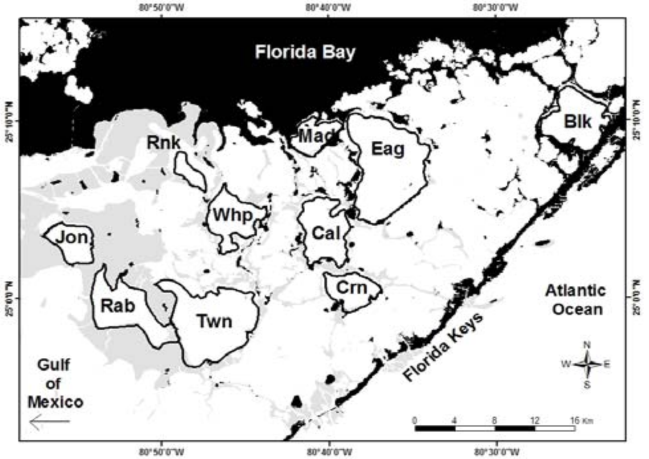


Blackwater

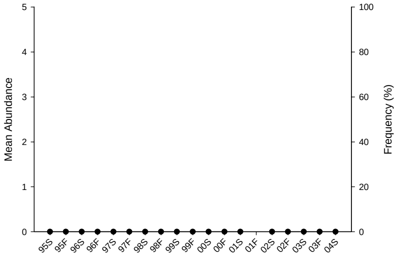


Johnson

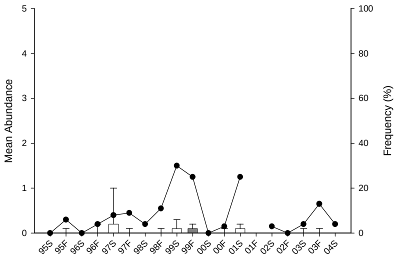




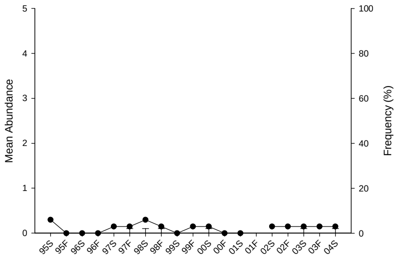
Eagle



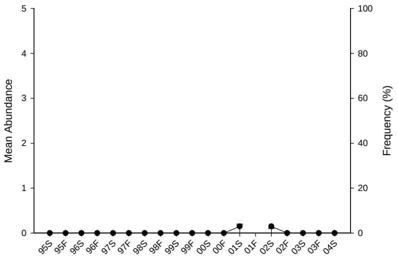
Rabbit



Twin



Calusa



Crane

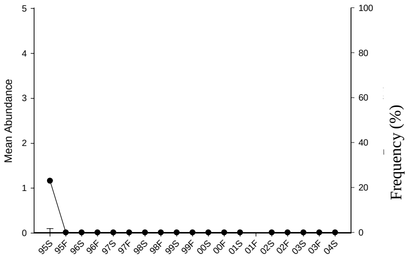


FIG. 16. *Halimeda* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Halimeda Density and Frequency

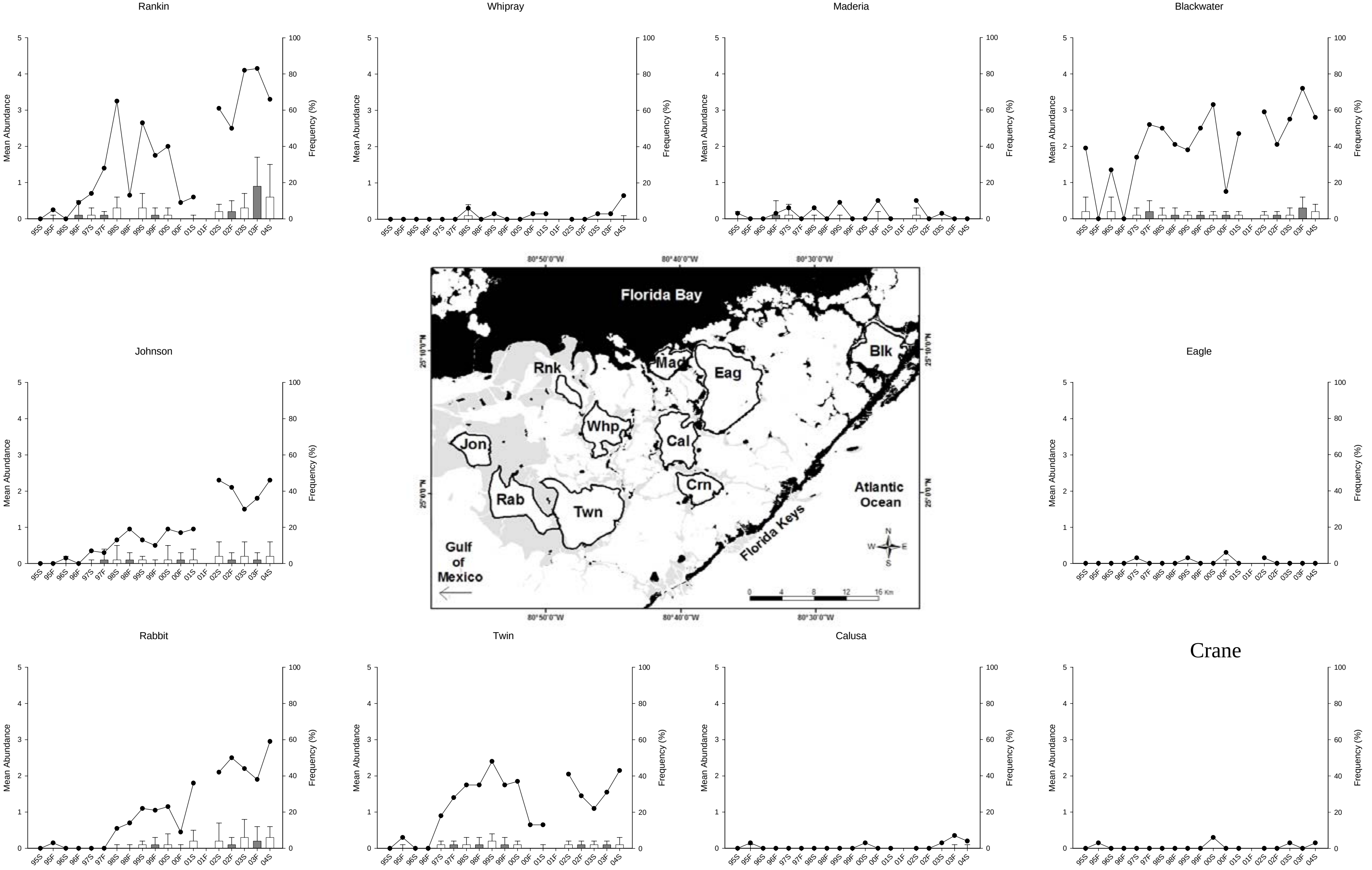


FIG. 17. *Penicillus* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Penicillus Density and Frequency

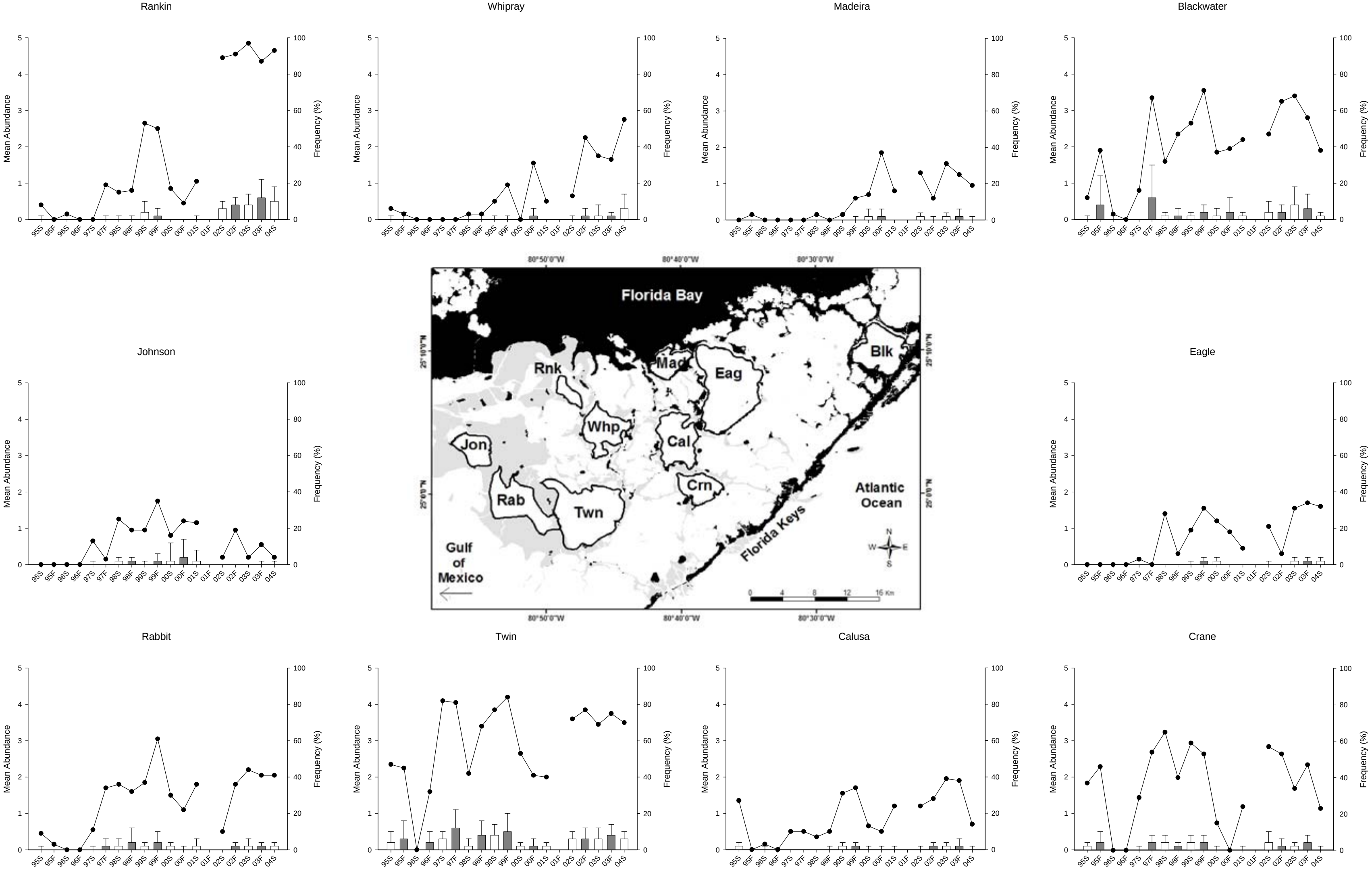


FIG. 18. *Sargassum* mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Sargassum Density and Frequency

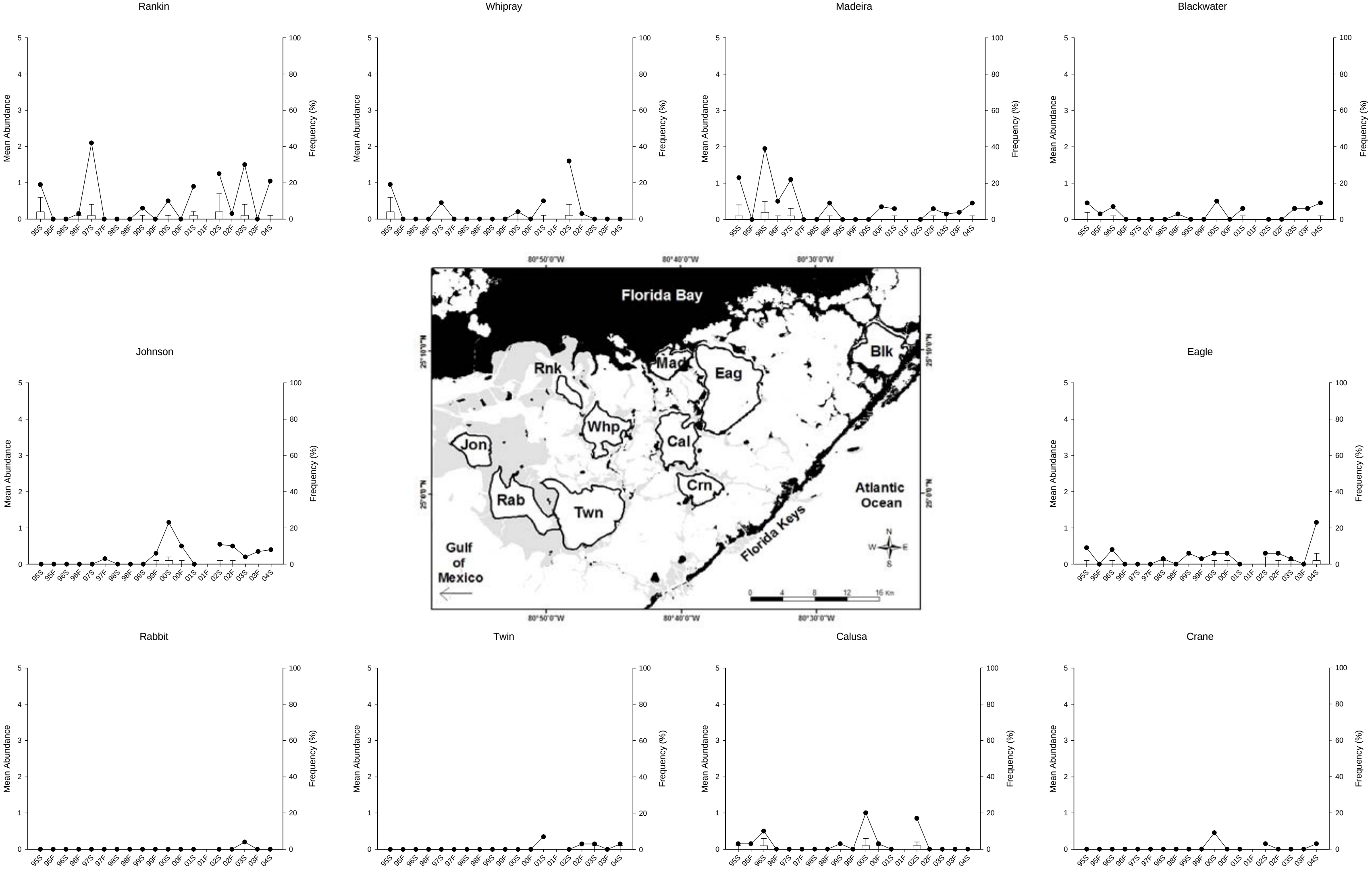
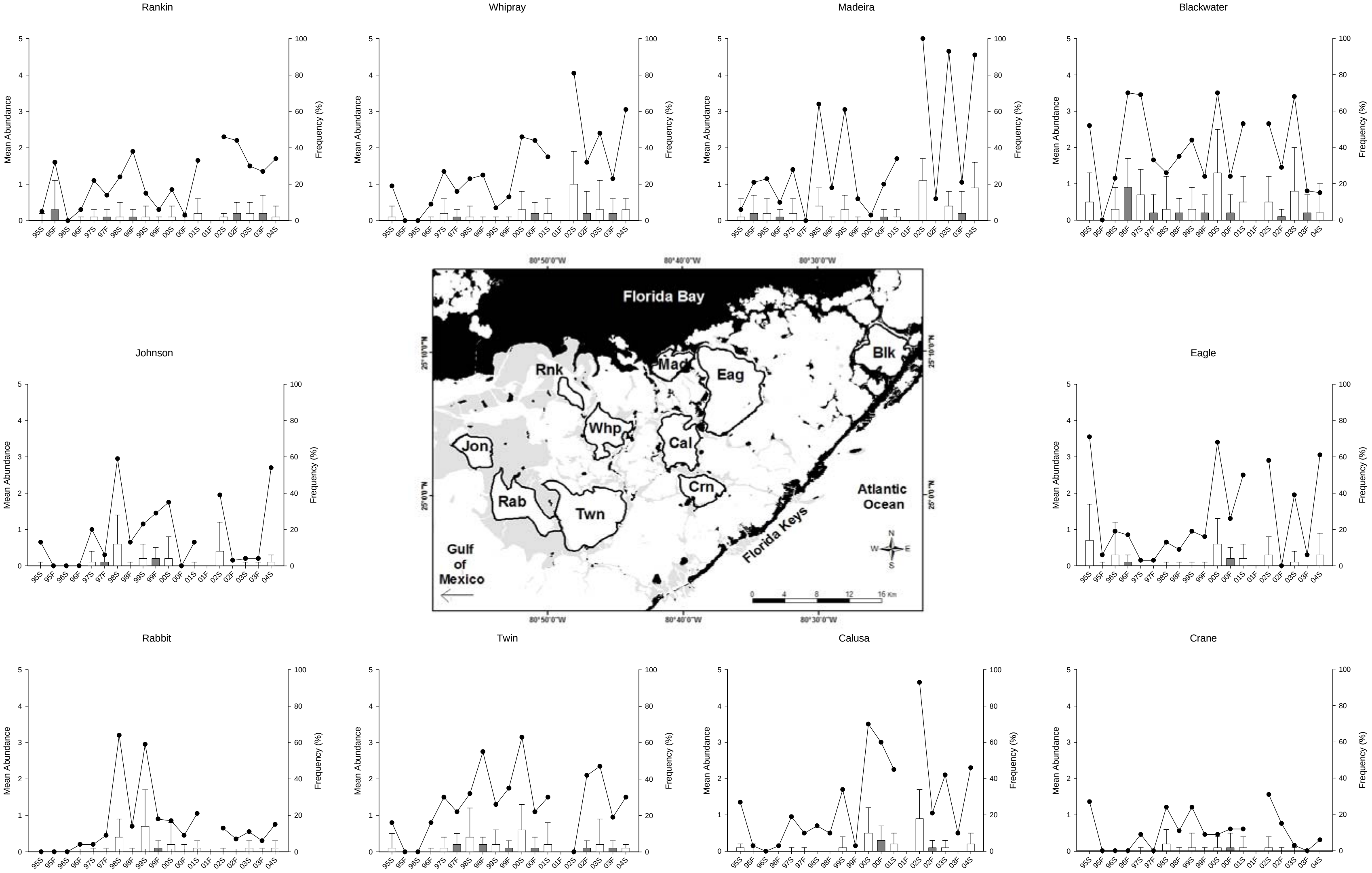


FIG. 19. Drift Red mean density and frequency of occurrence by basin. Mean Braun-Blanquet density/cover value on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring and fall sampling event means and standard deviation. Shaded columns give fall means and unshaded columns give spring means. Basin graphs are arranged logistically around central map for reference and to emphasize spatial trends.

Drift Red Density and Frequency



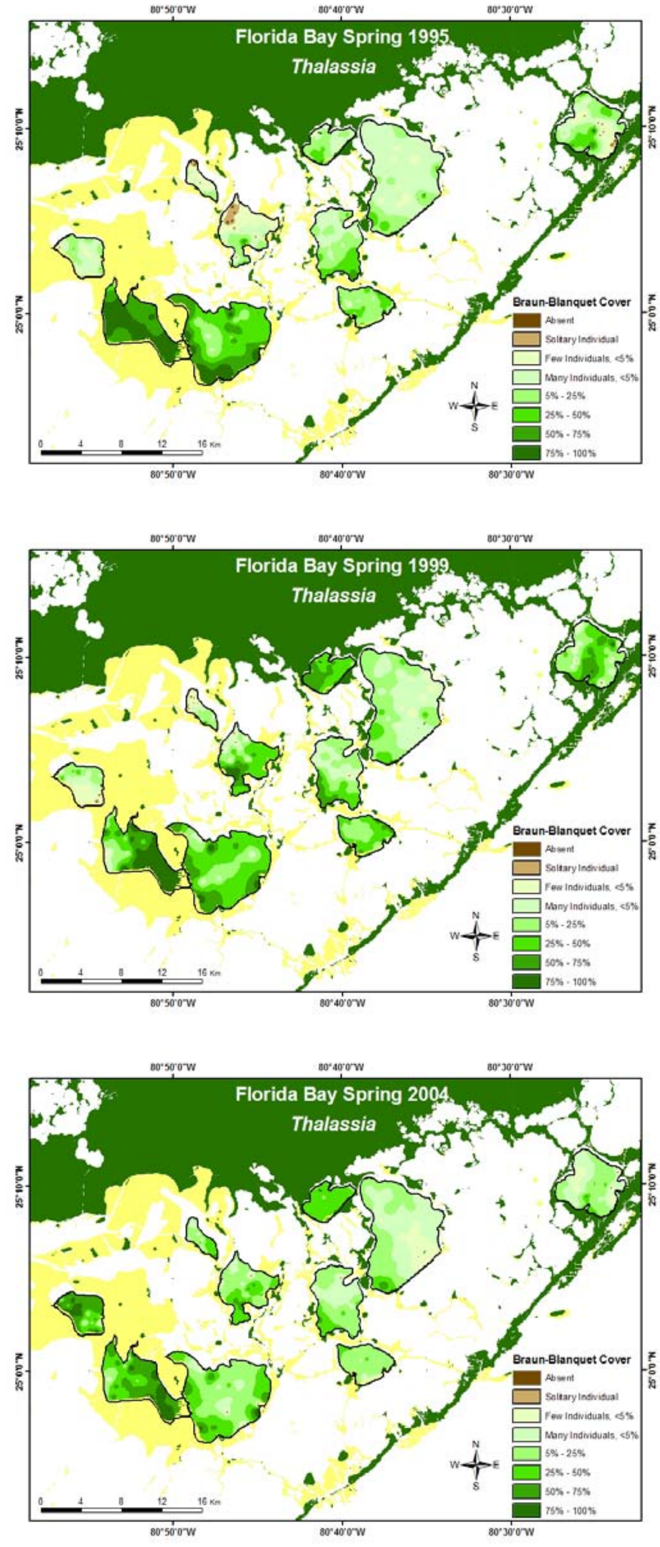


FIG. 20. Florida Bay *Thalassia* distribution during springs 1995, 1999, and 2004.

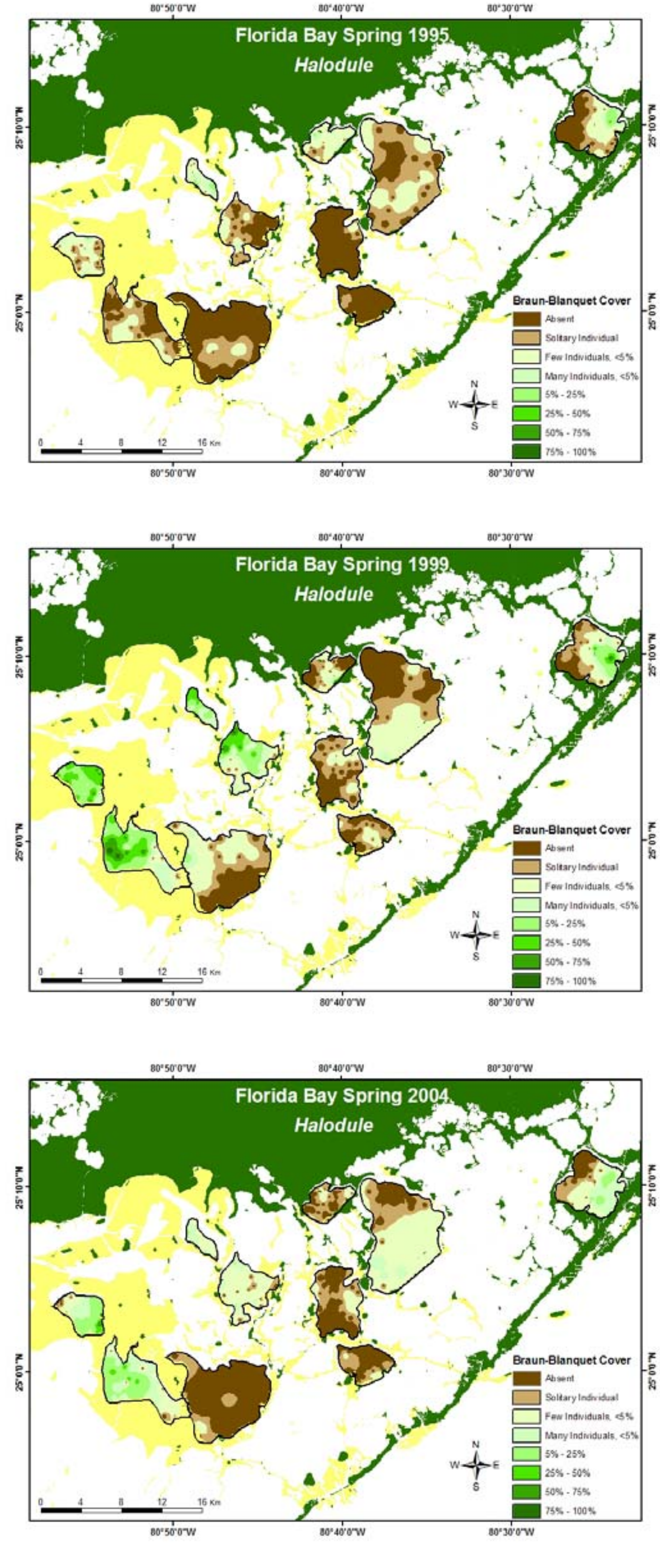


FIG. 21. Florida Bay *Halodule* distribution during springs 1995, 1999, and 2004.

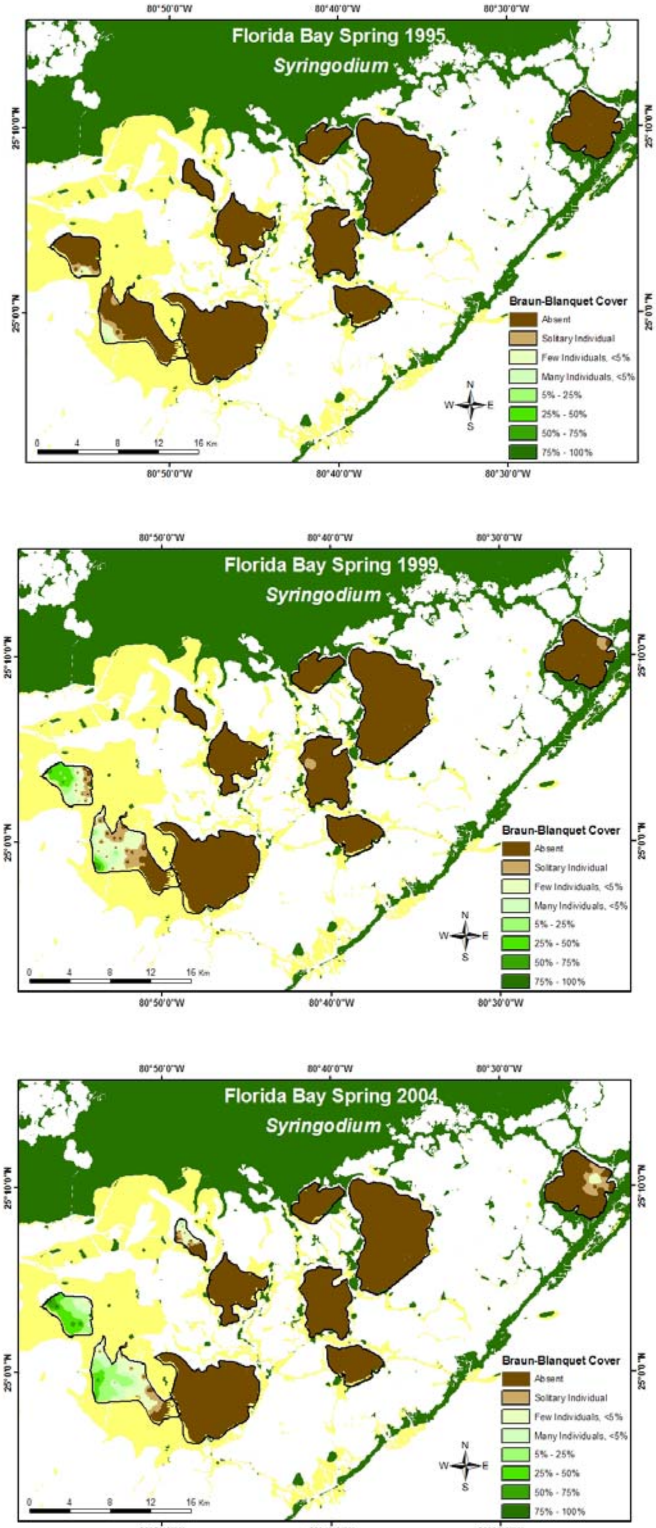


FIG. 22. Florida Bay *Syringodium* distribution during springs 1995, 1999, and 2004.

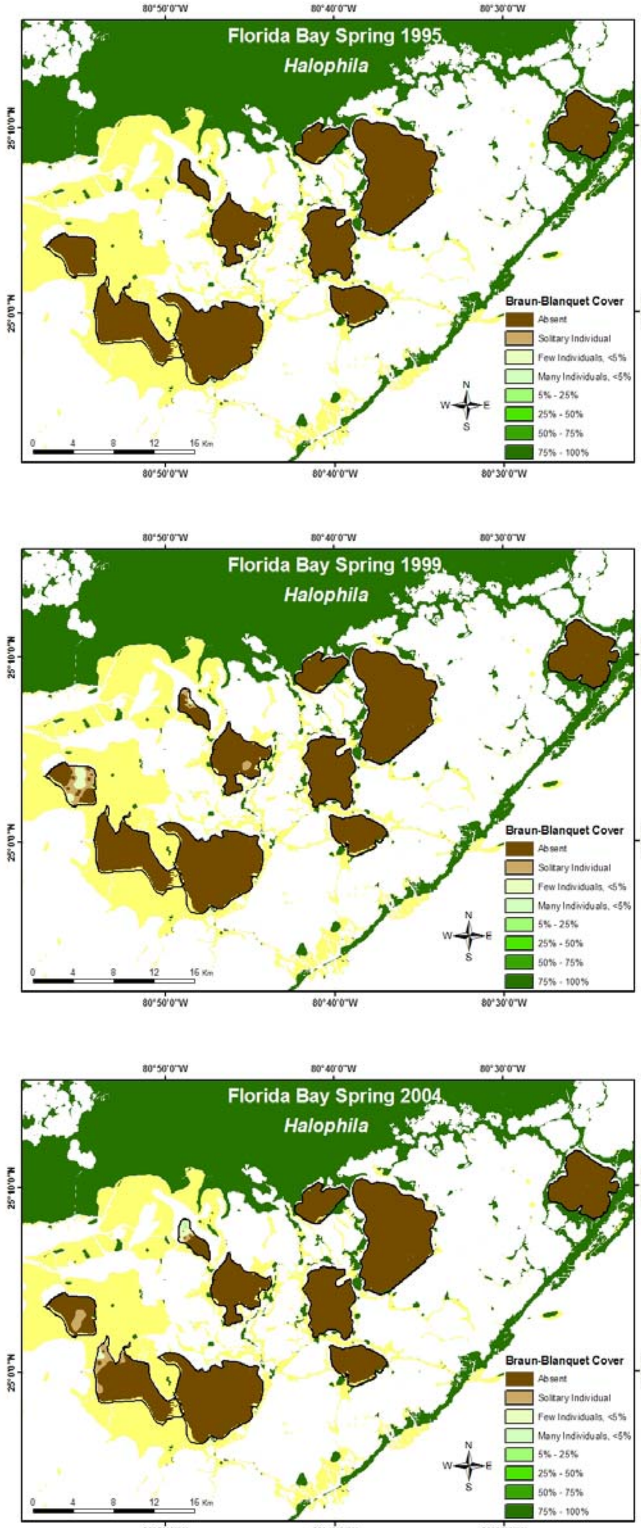


FIG. 23. Florida Bay *Halophila* distribution during springs 1995, 1999, and 2004.

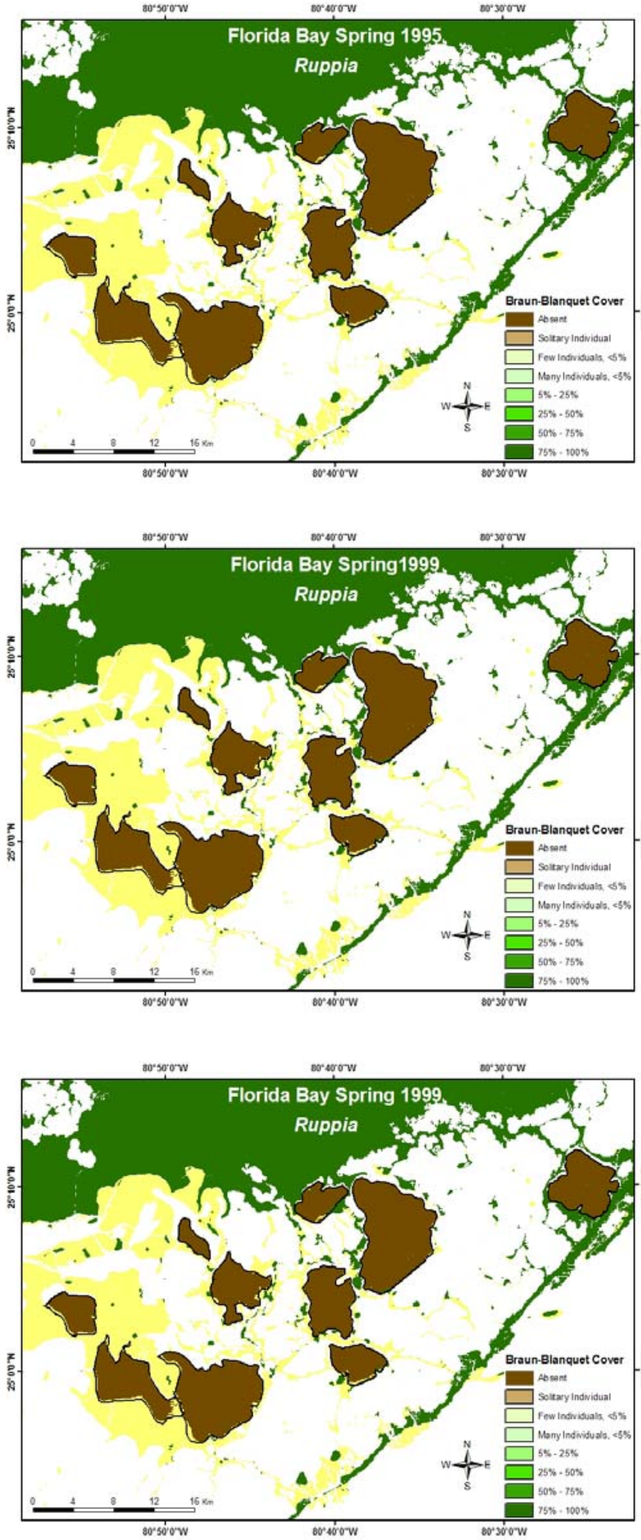


FIG. 24. Florida Bay *Ruppia* distribution during springs 1995, 1999, and 2004.

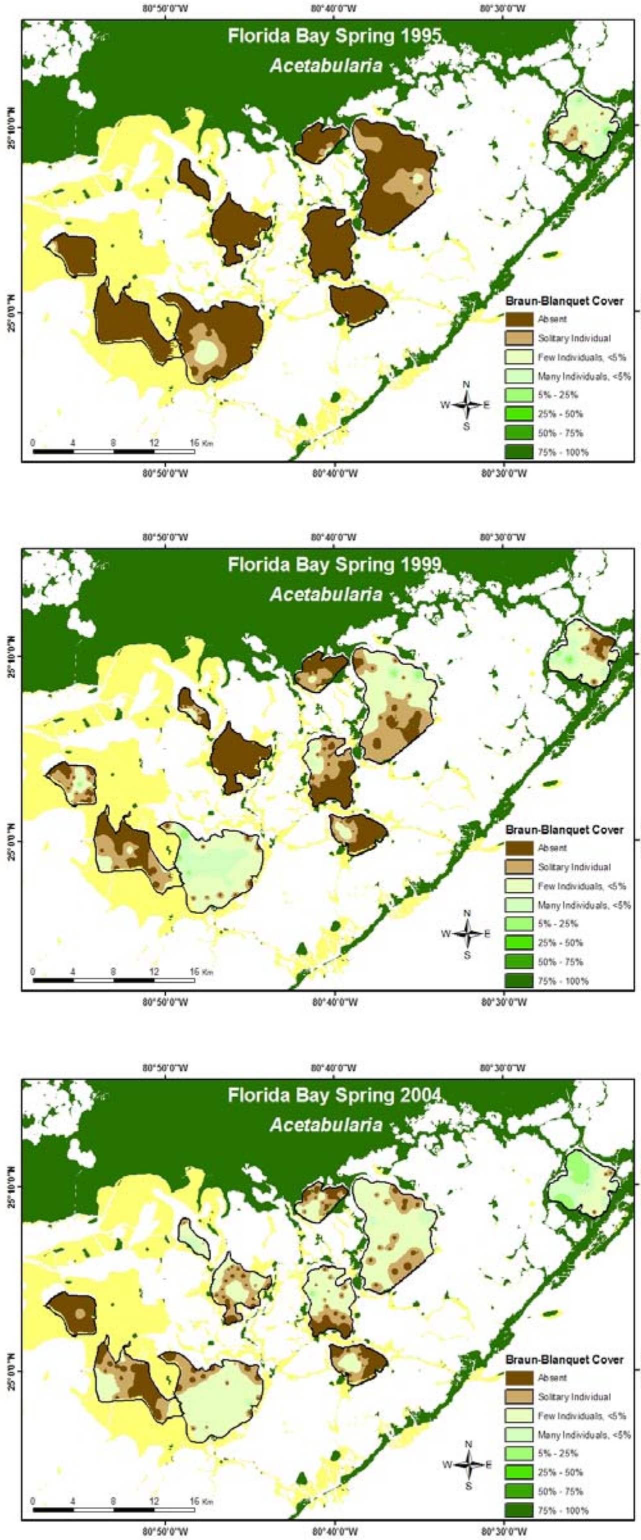


FIG. 25. Florida Bay *Acetabularia* distribution during springs 1995, 1999, and 2004.

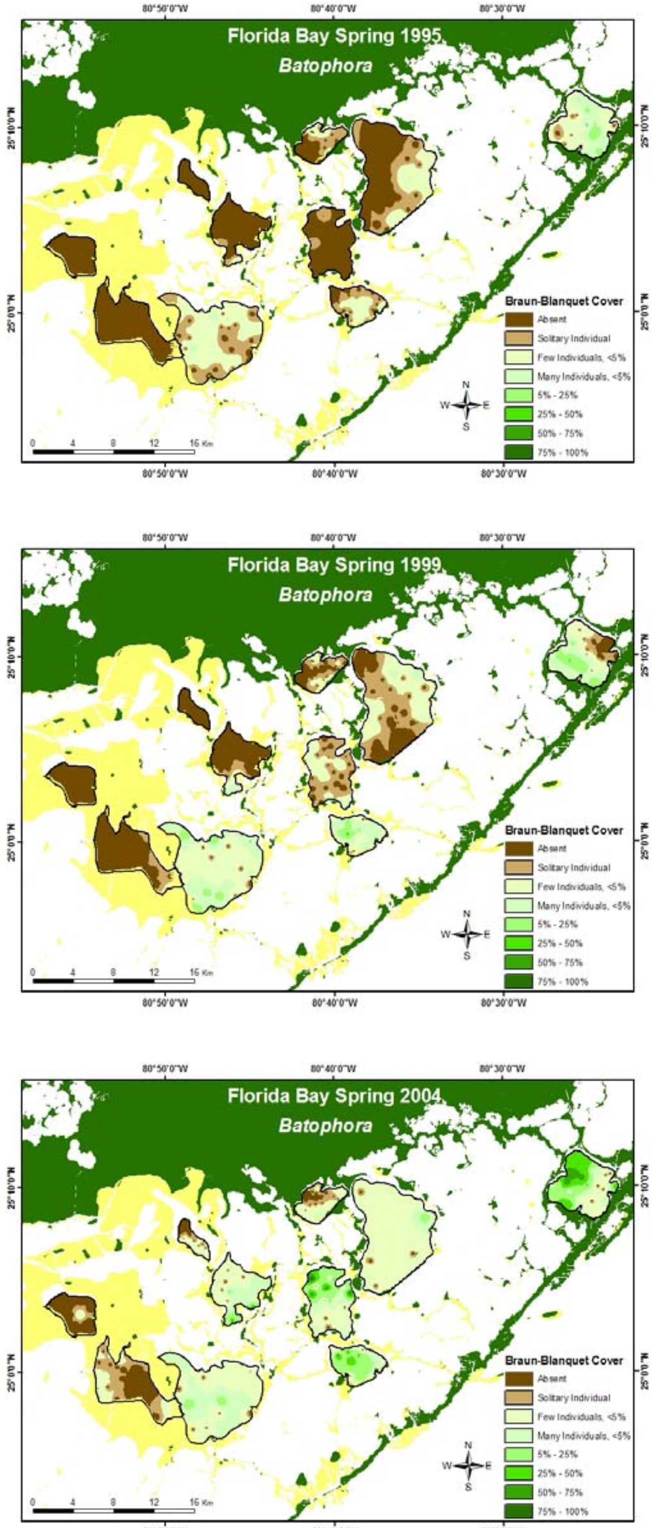


FIG. 26. Florida Bay *Batophora* distribution during springs 1995, 1999, and 2004.

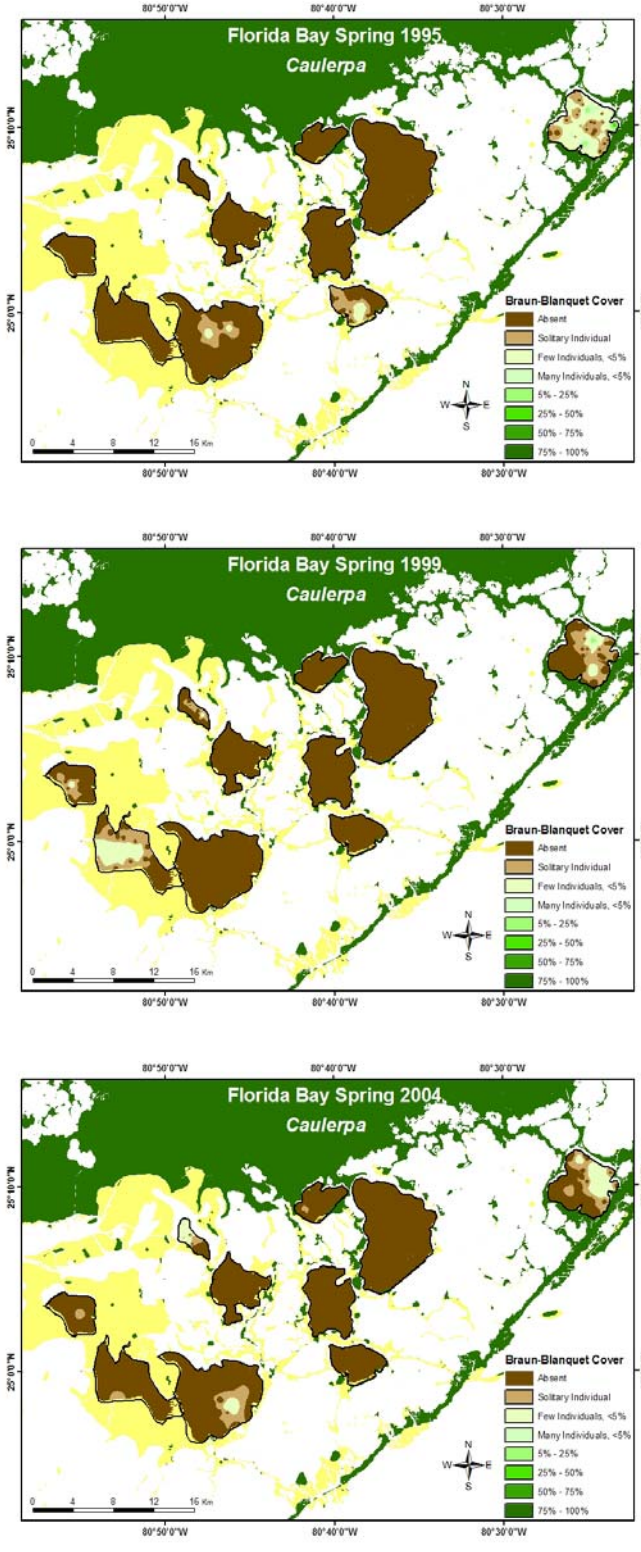


FIG. 27. Florida Bay *Caulerpa* distribution during springs 1995, 1999, and 2004.

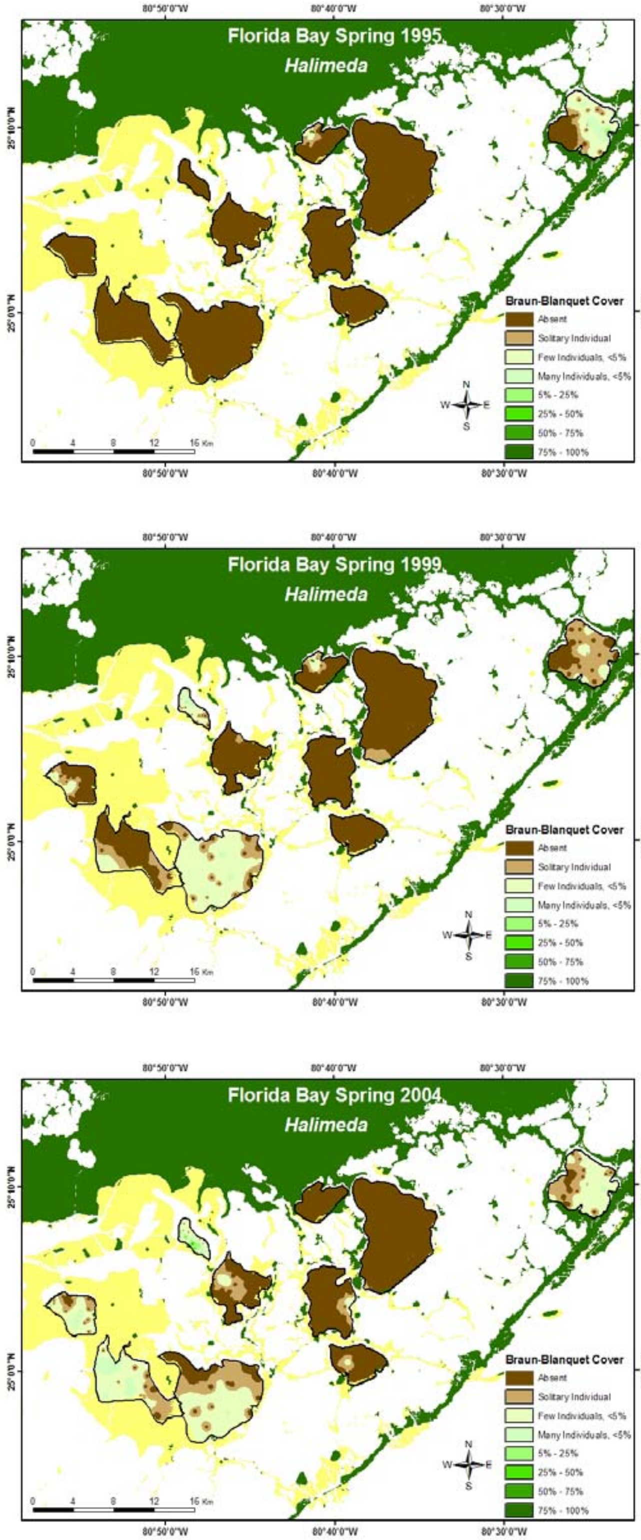


FIG. 28. Florida Bay *Halimeda* distribution during springs 1995, 1999, and 2004.

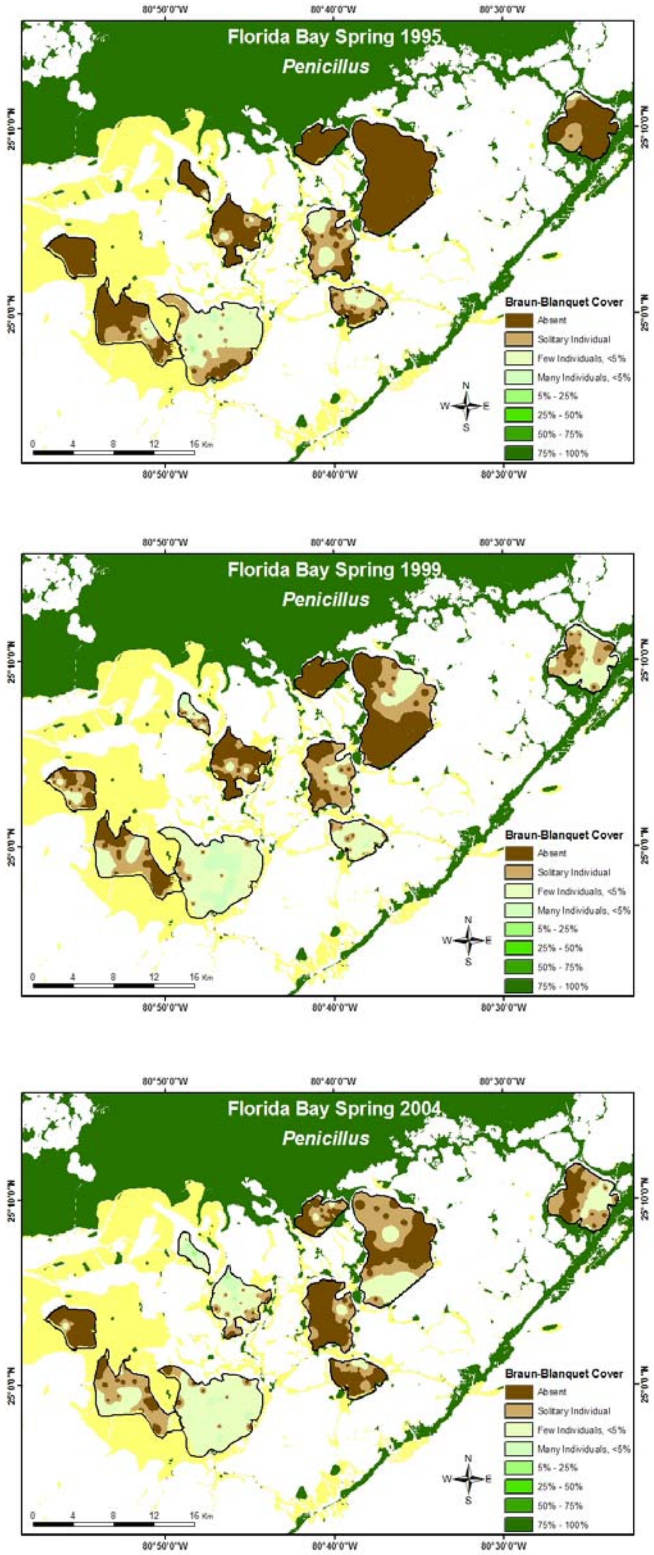


FIG. 29. Florida Bay *Penicillus* distribution during springs 1995, 1999, and 2004.

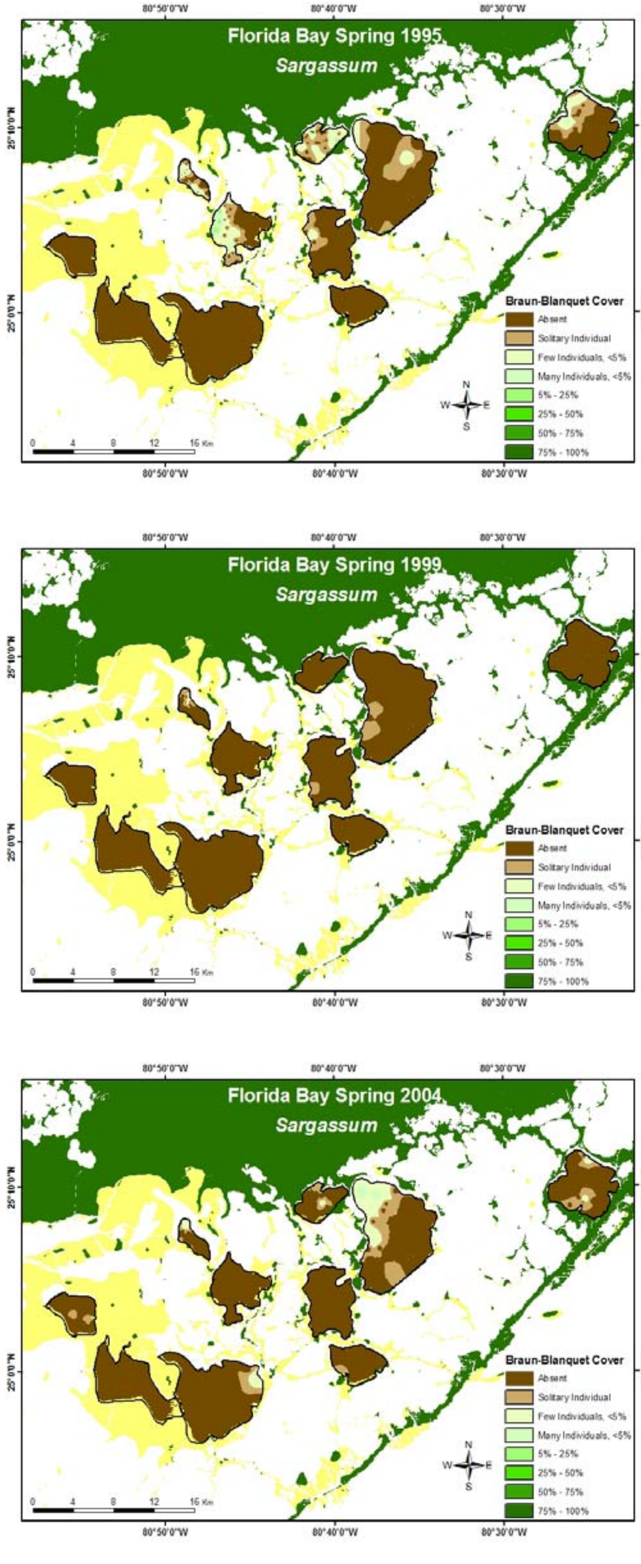


FIG. 30. Florida Bay *Sargassum* distribution during springs 1995, 1999, and 2004.

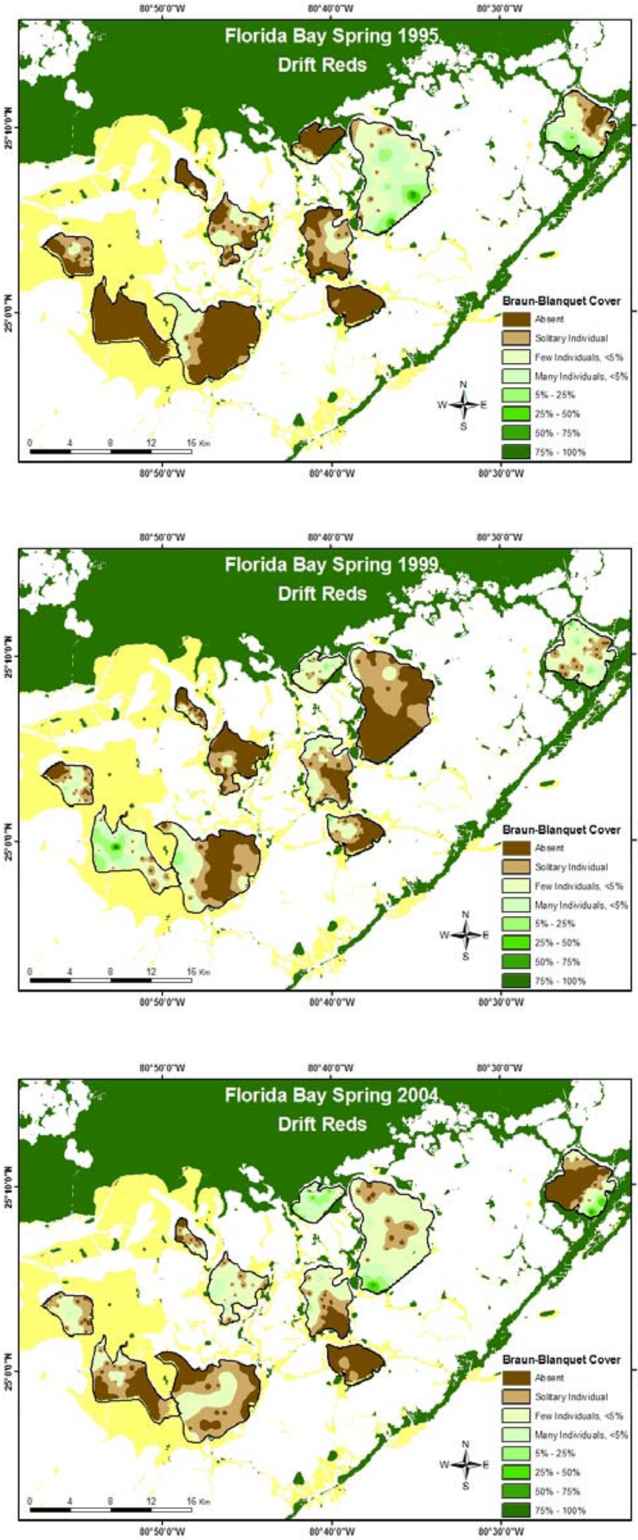
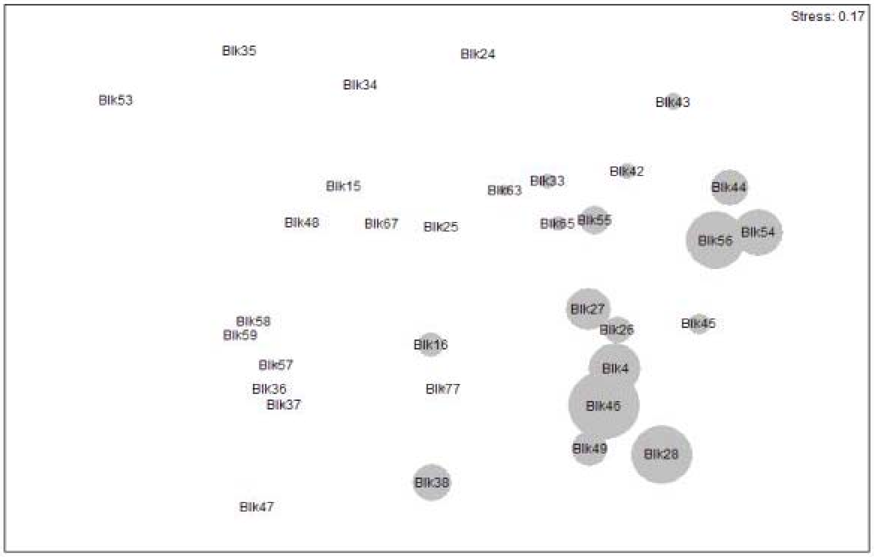


FIG. 31. Florida Bay Drift Red distribution during springs 1995, 1999, and 2004.

BlkS95: Total Seagrass



BlkS95: Total Macroalgae

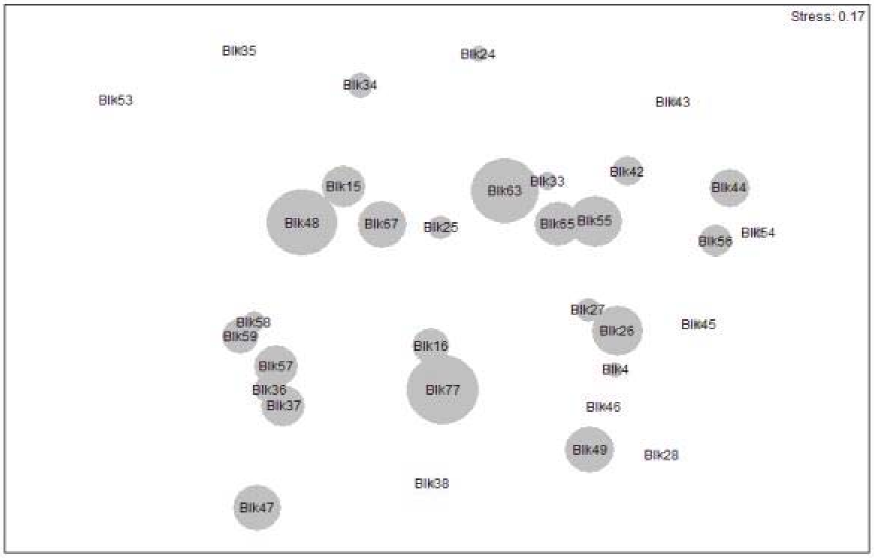
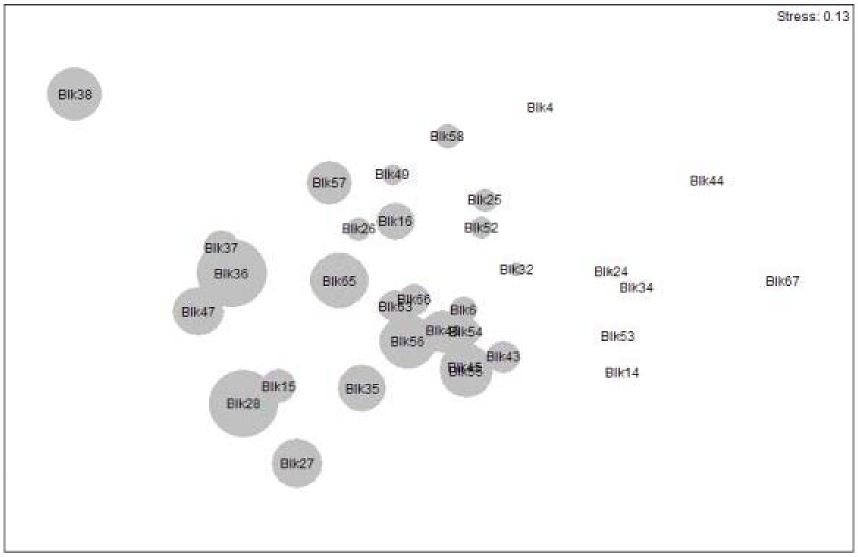


FIG. 32. nMDS ordination plot of spring 1995 Blackwater Sound sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

BlkS99: Total Seagrass



BlkS99: Total Macroalgae

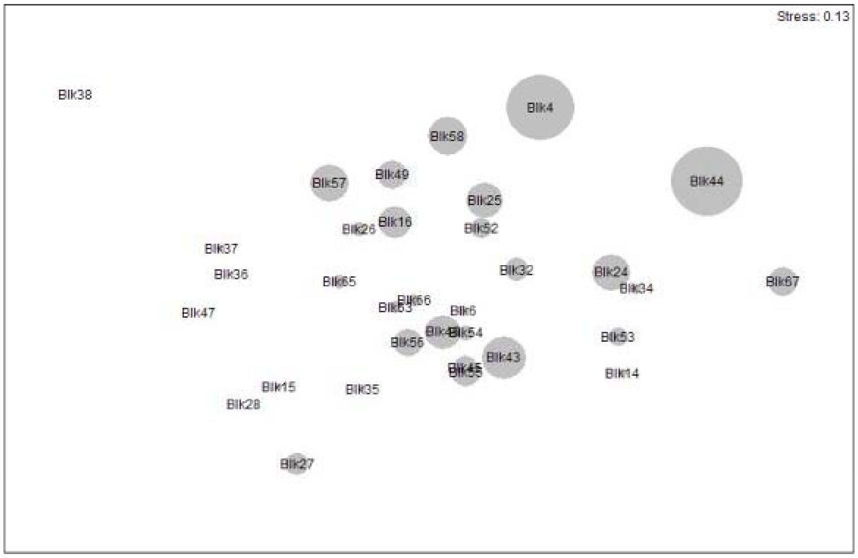
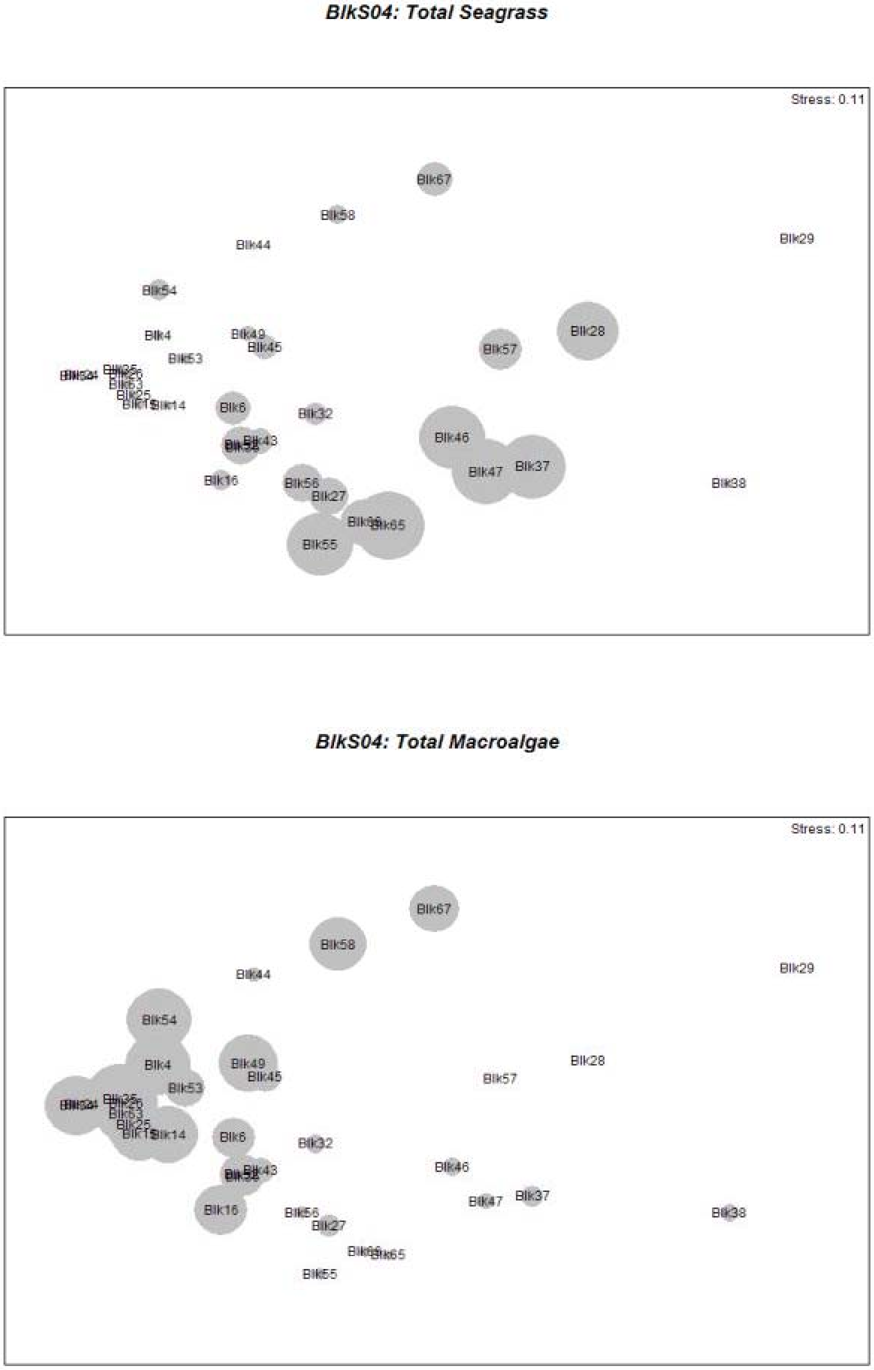


FIG. 33. nMDS ordination plot of spring 1999 Blackwater Sound sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

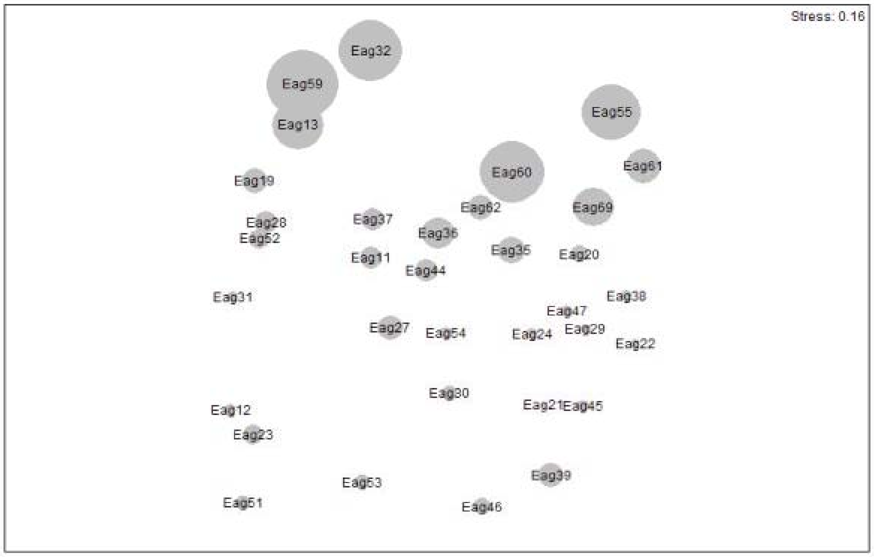


BlkS04: Total Seagrass

BlkS04: Total Macroalgae

FIG. 34. nMDS ordination plot of spring 2004 Blackwater Sound sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

EagS95: Total Seagrass



EagS95: Total Macroalgae

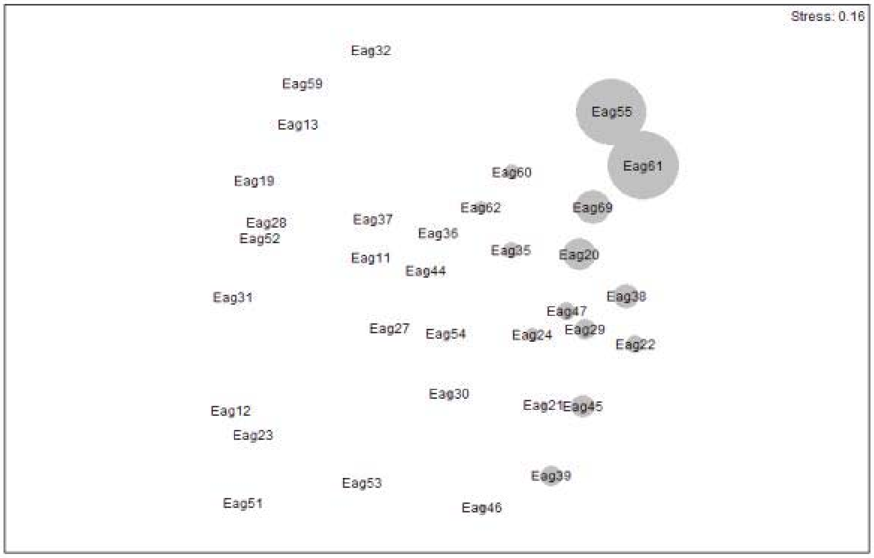
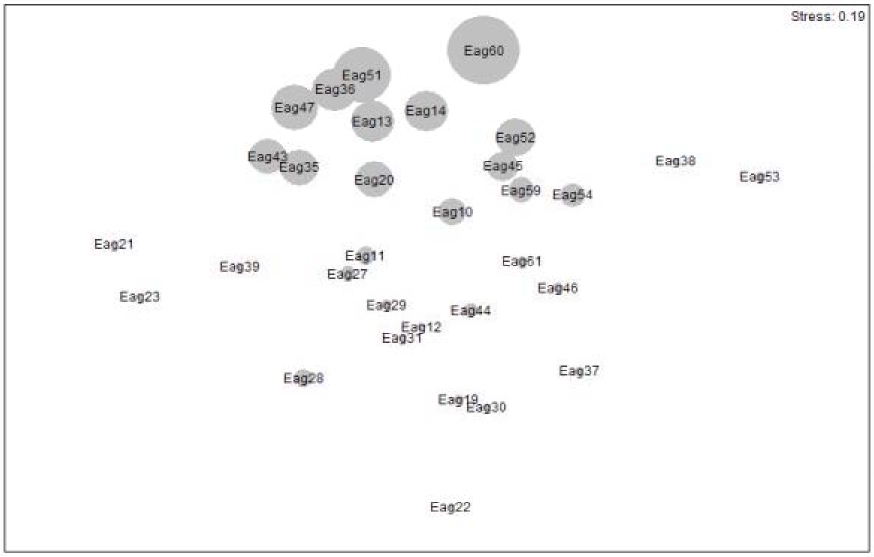


FIG. 35. nMDS ordination plot of spring 1995 Eagle Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

EagS99: Total Seagrass



EagS99: Total Macroalgae

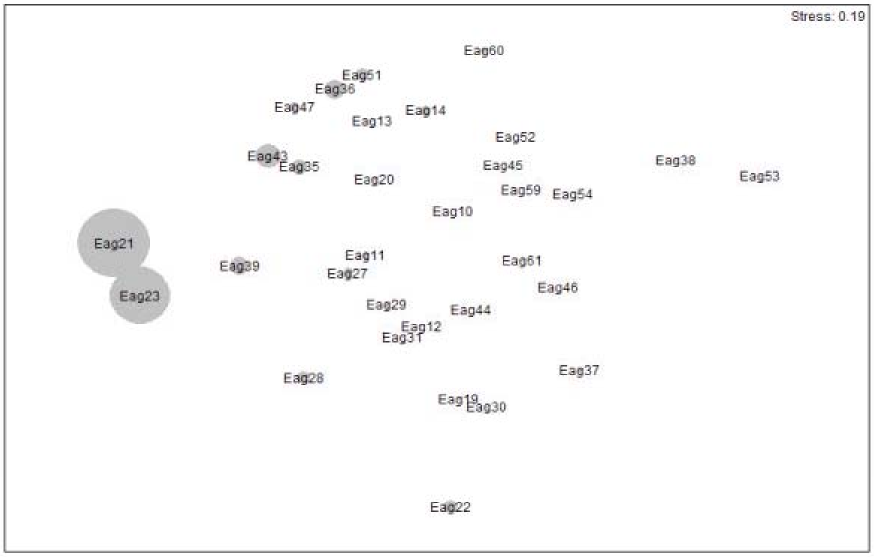
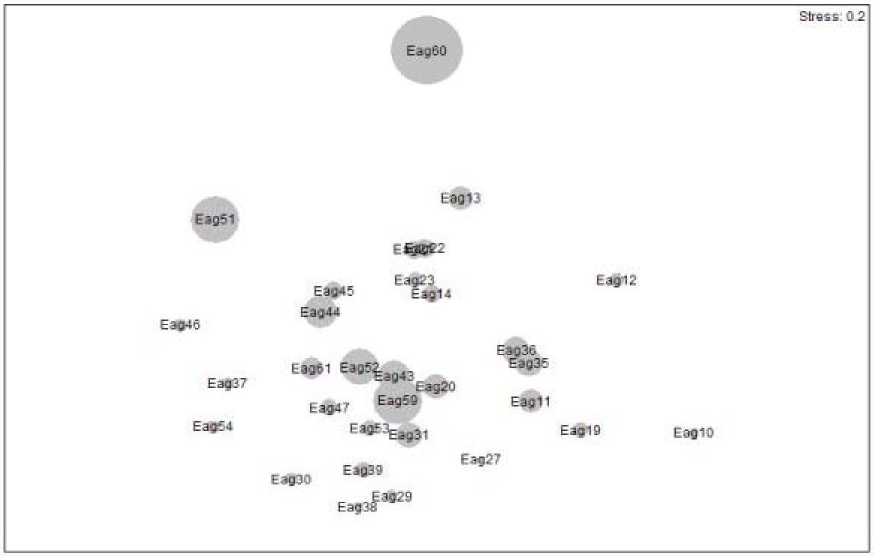


FIG. 36. nMDS ordination plot of spring 1999 Eagle Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

EagS04: Total Seagrass



EagS04: Total Macroalgae

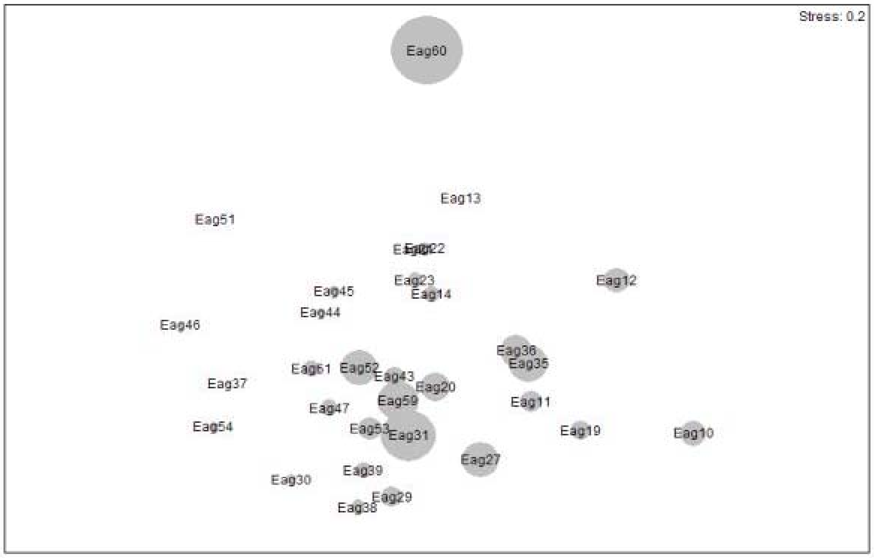
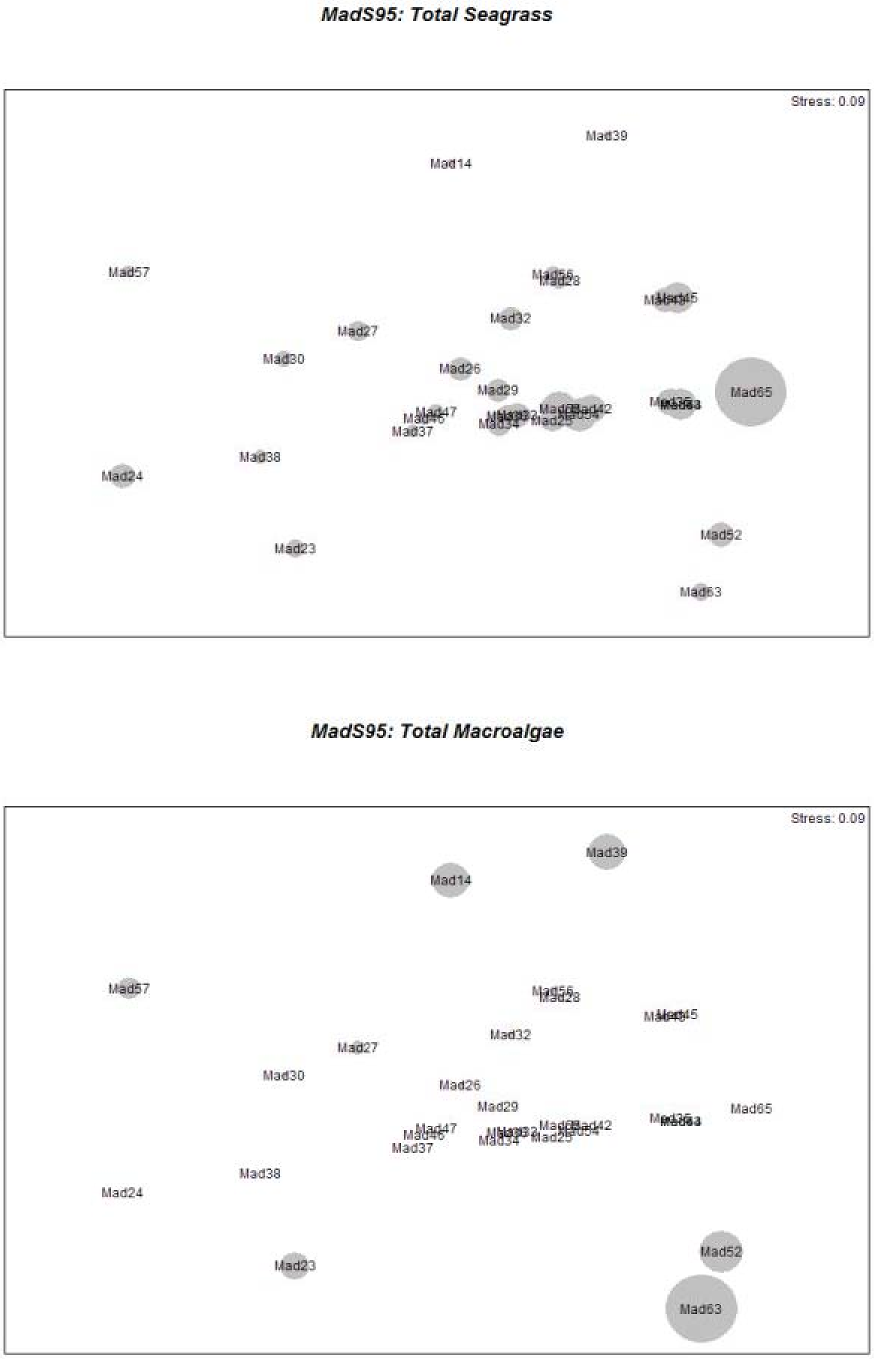


FIG. 37. nMDS ordination plot of spring 2004 Eagle Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

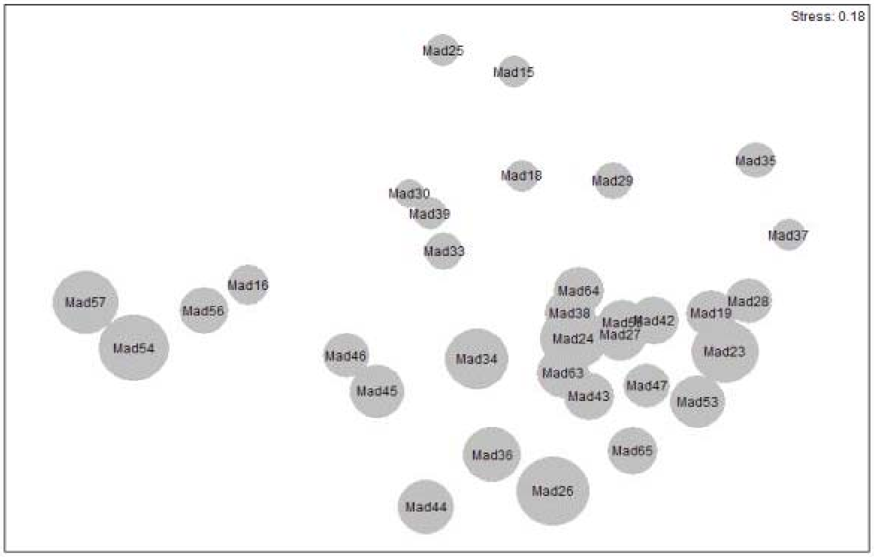


MadS95: Total Seagrass

MadS95: Total Macroalgae

FIG. 38. nMDS ordination plot of spring 1995 Madeira Bay sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

MadS99: Total Seagrass



MadS99: Total Macroalgae

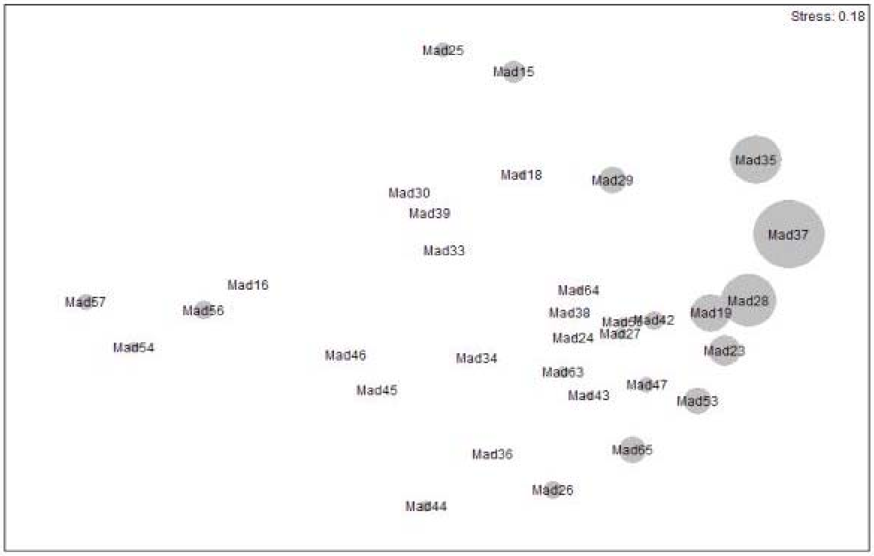


FIG. 39. nMDS ordination plot of spring 1999 Madeira Bay sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

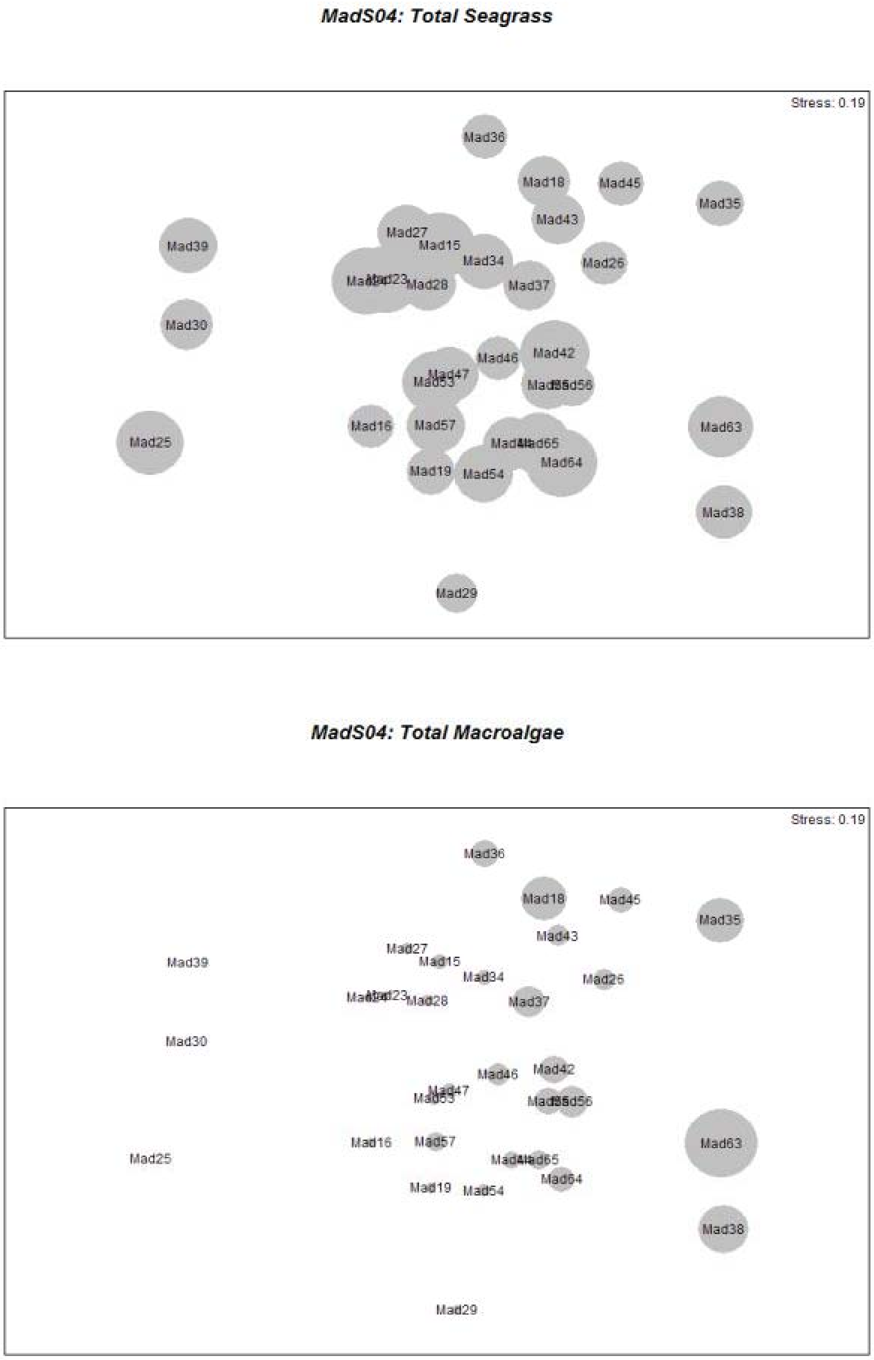


FIG. 40. nMDS ordination plot of spring 2004 Madeira Bay sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

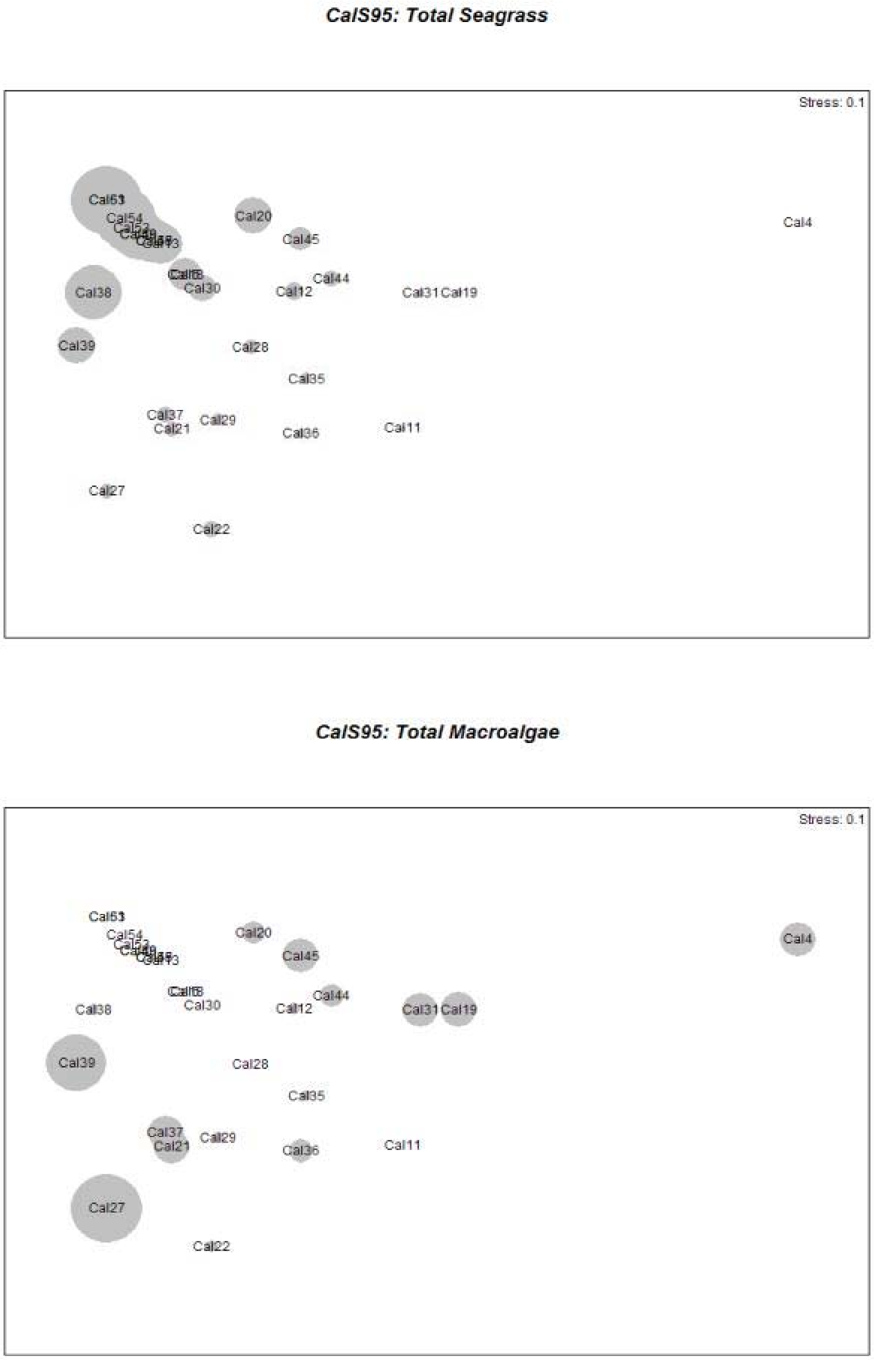
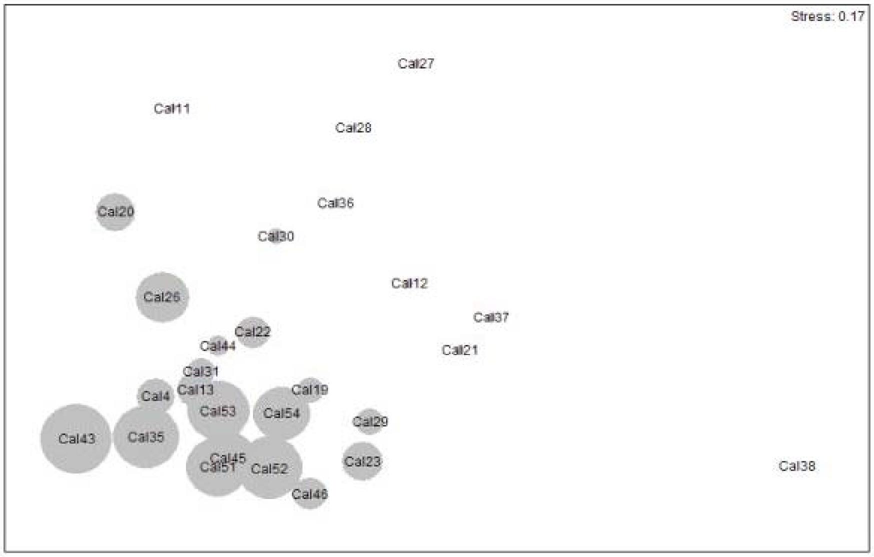


FIG. 41. nMDS ordination plot of spring 1995 Calusa Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

CalS99: Total Seagrass



CalS99: Total Macroalgae

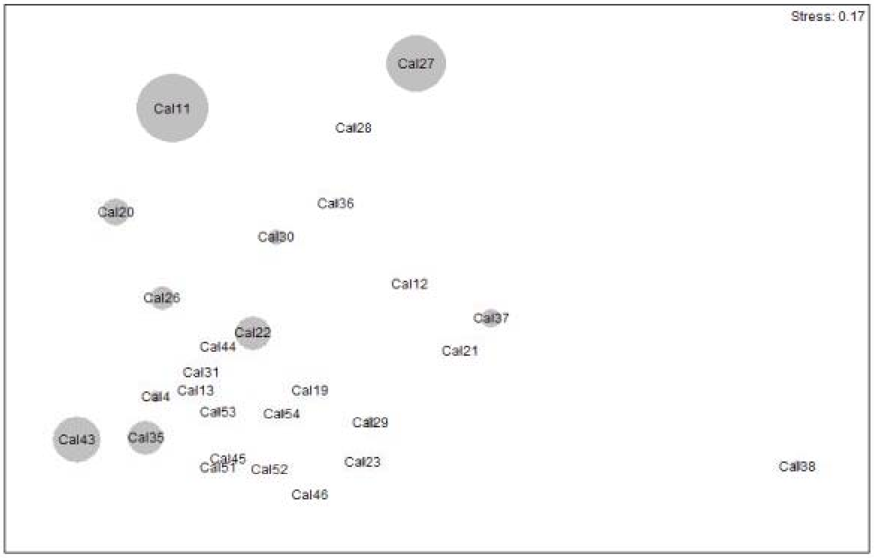
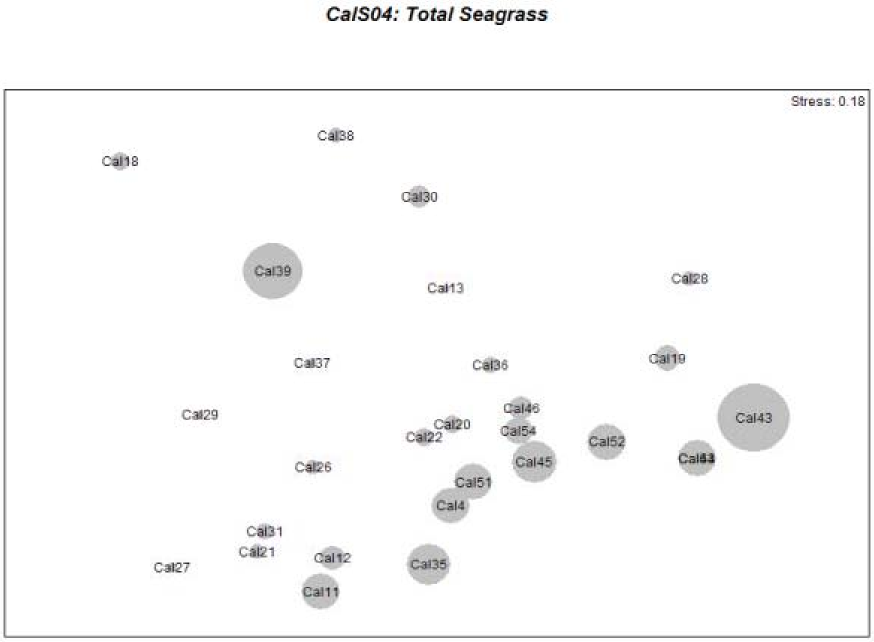


FIG. 42. nMDS ordination plot of spring 1999 Calusa Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.



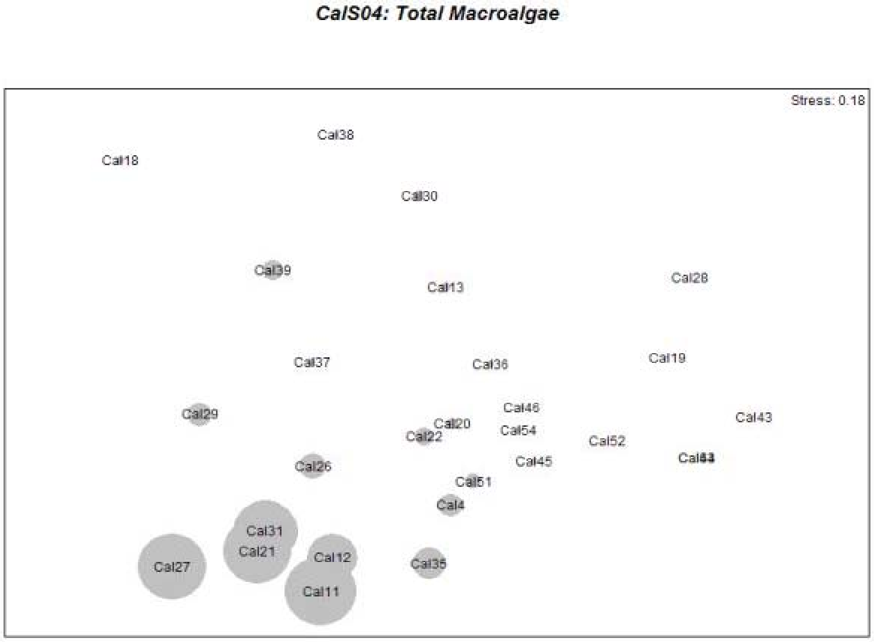
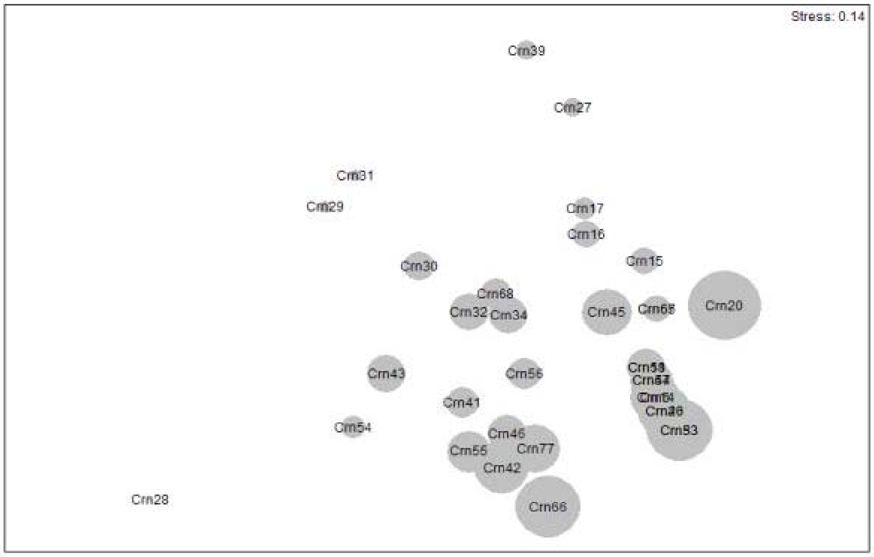


FIG. 43. nMDS ordination plot of spring 2004 Calusa Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively

CrnS95: Total Seagrass



CrnS95: Total Macroalgae

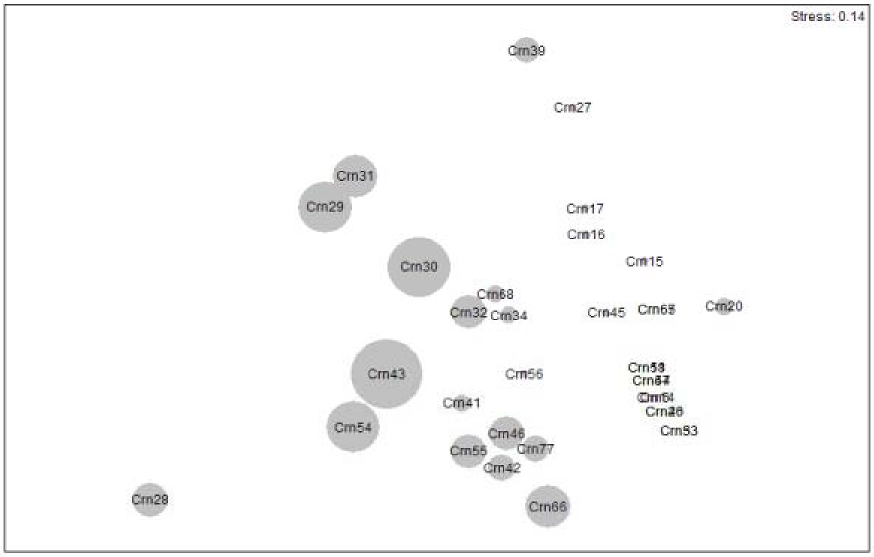
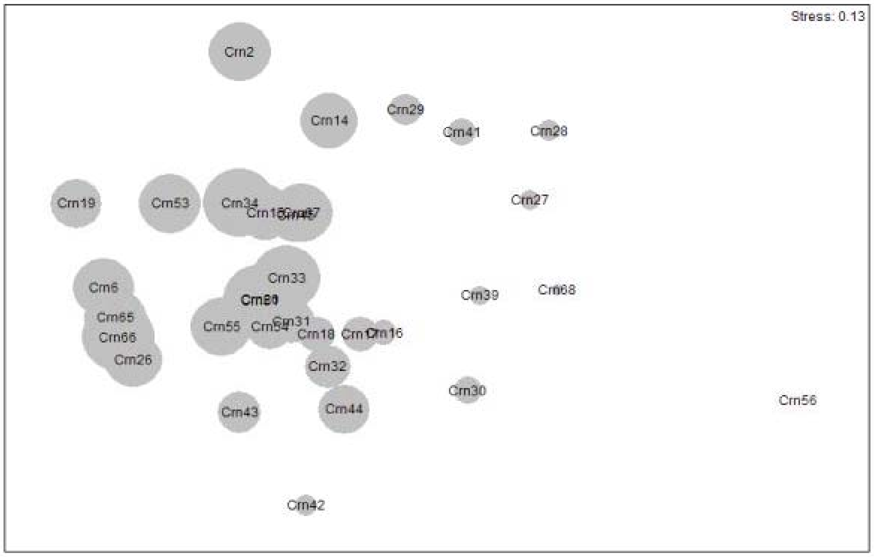


FIG. 44. nMDS ordination plot of spring 1995 Crane Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

CrnS99: Total Seagrass



CrnS99: Total Macroalgae

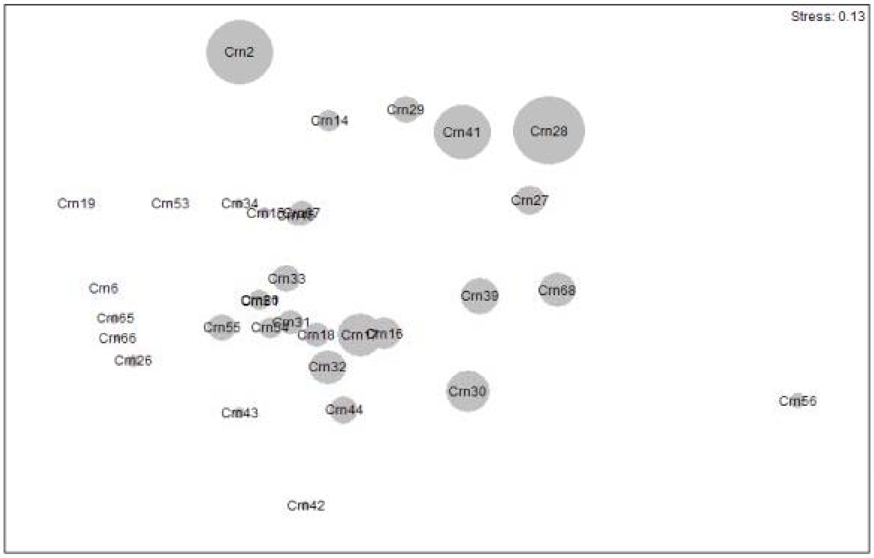
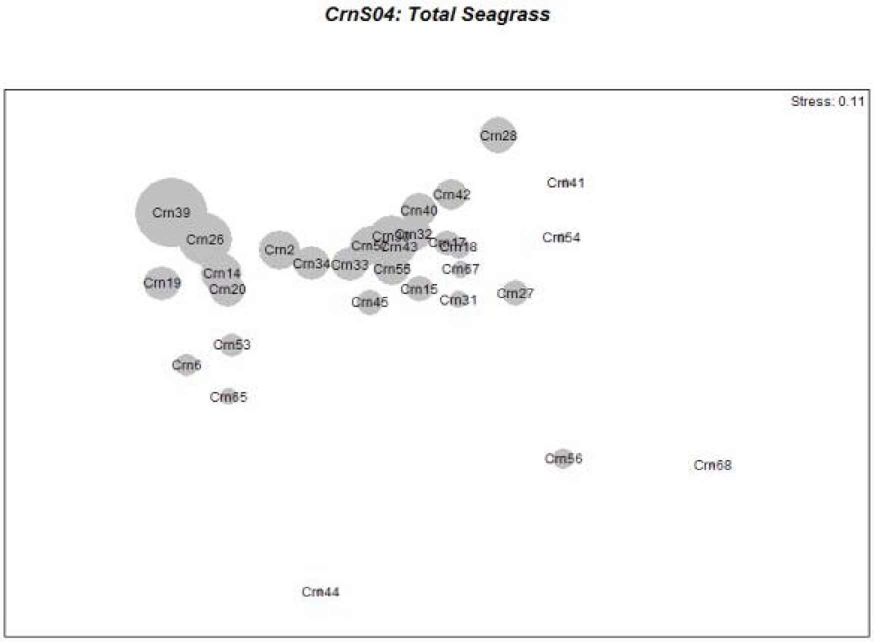


FIG. 45. nMDS ordination plot of spring 1999 Crane Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.



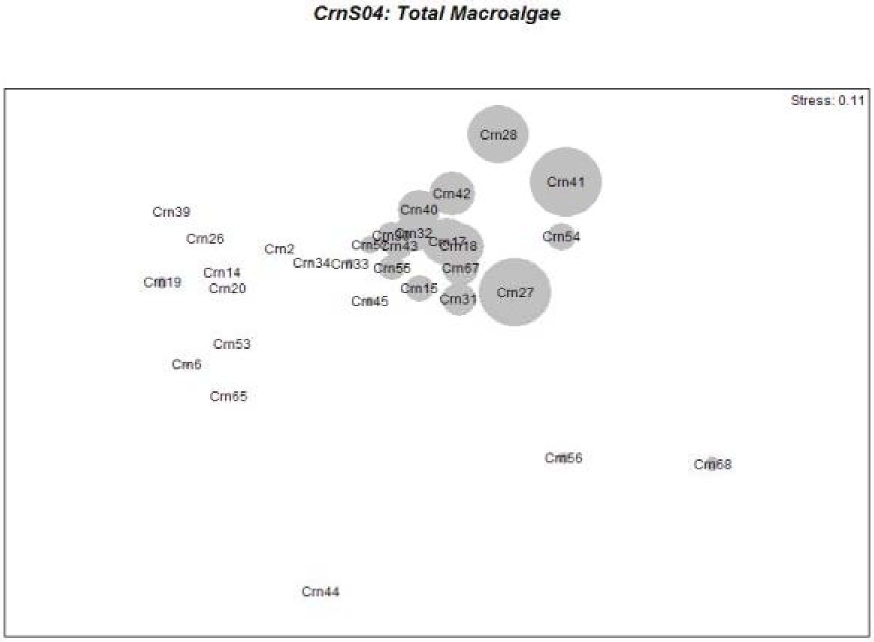
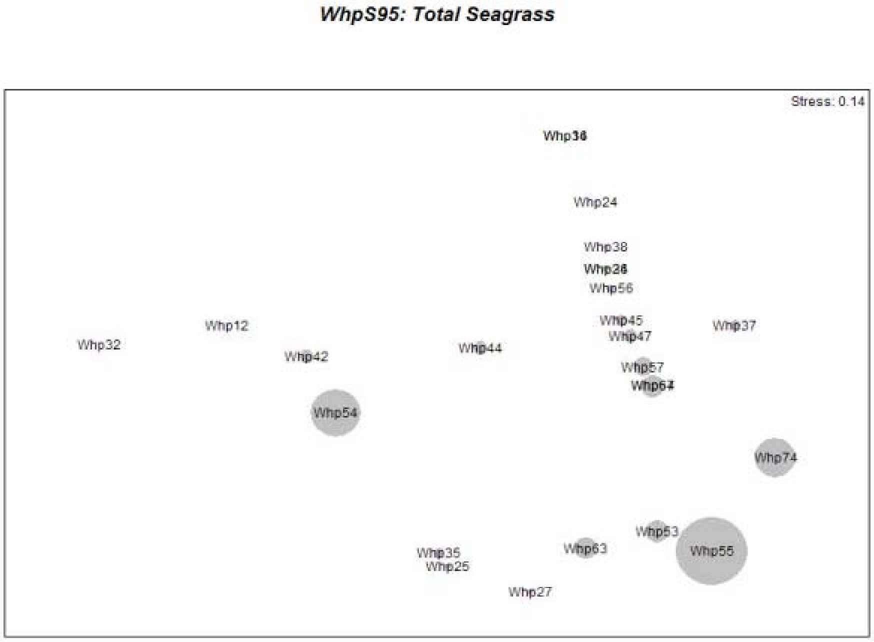


FIG. 46. nMDS ordination plot of spring 2004 Crane Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.


WhpS95: Total Seagrass

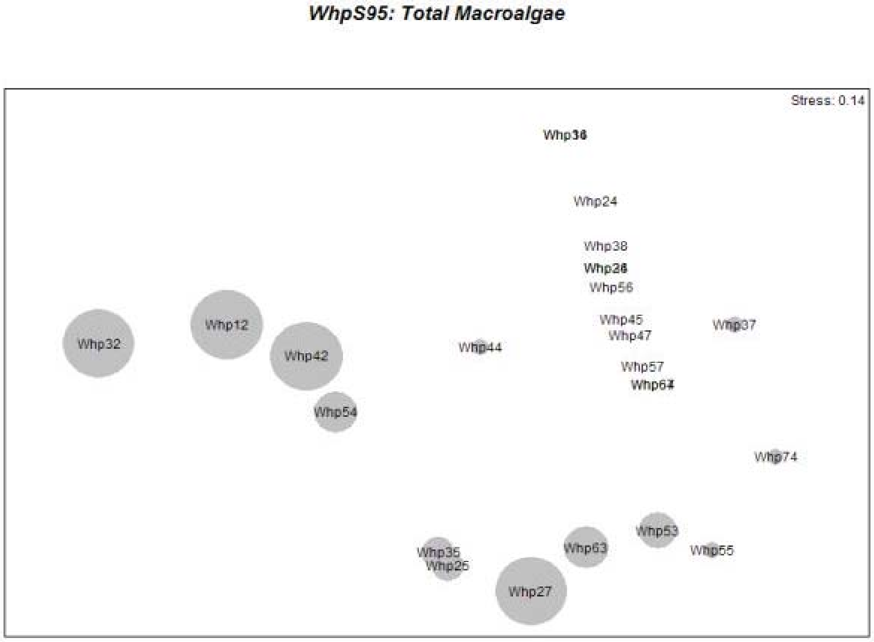
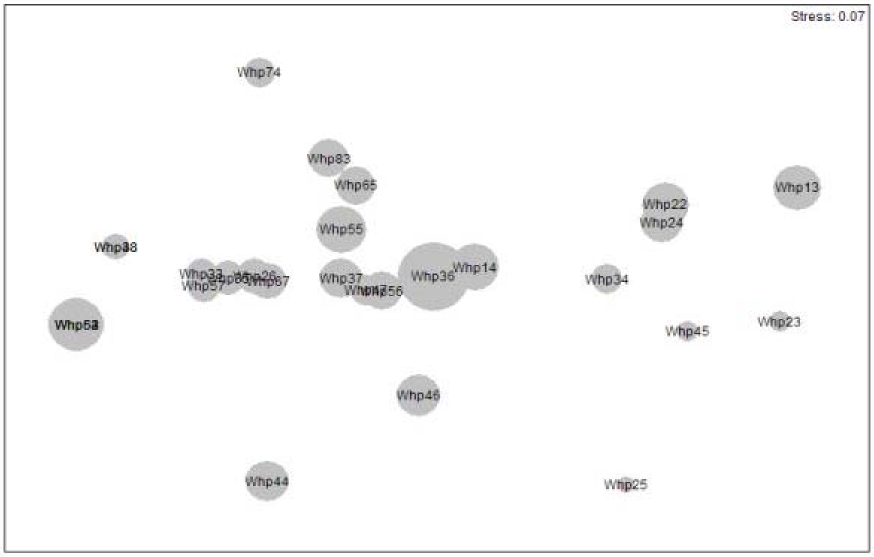

WhpS95: Total Macroalgae

FIG. 47. nMDS ordination plot of spring 1995 Whipray Bay sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

WhpS99: Total Seagrass



WhpS99: Total Macroalgae

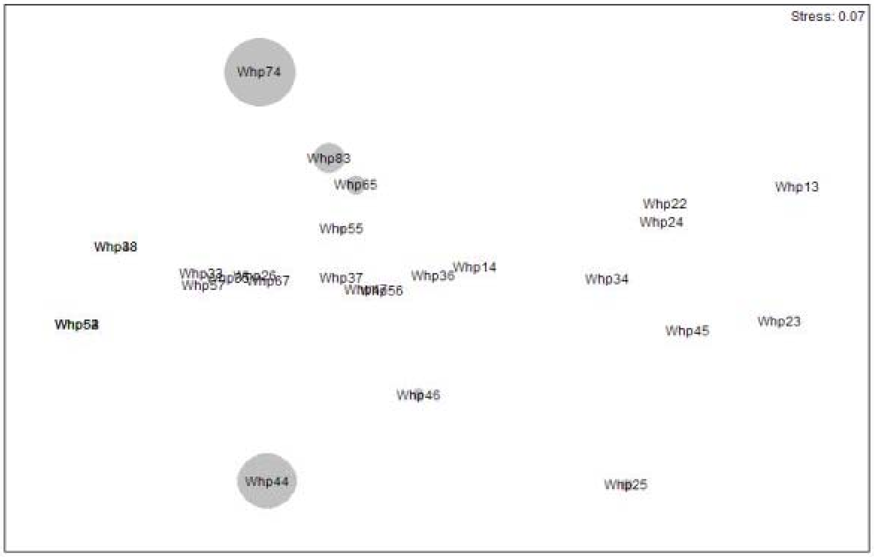
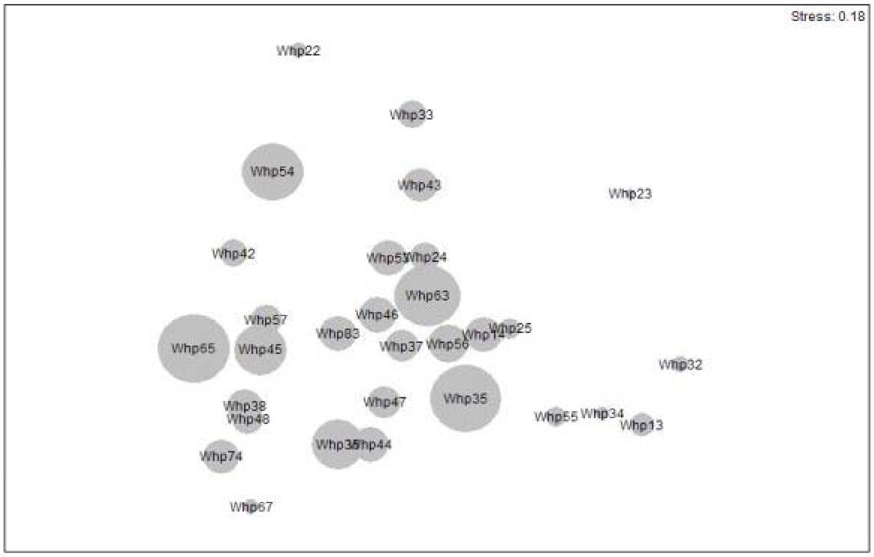


FIG. 48. nMDS ordination plot of spring 1999 Whipray Bay sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

WhpS04: Total Seagrass



WhpS04: Total Macroalgae

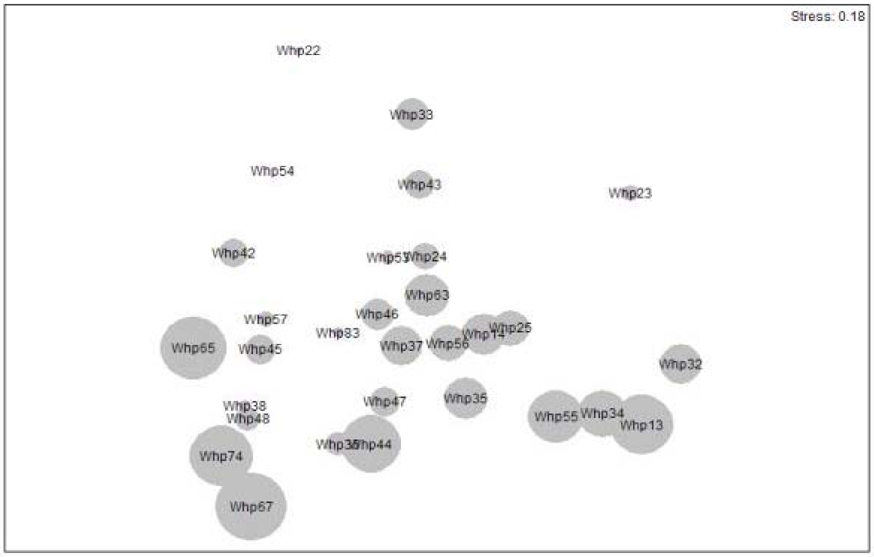
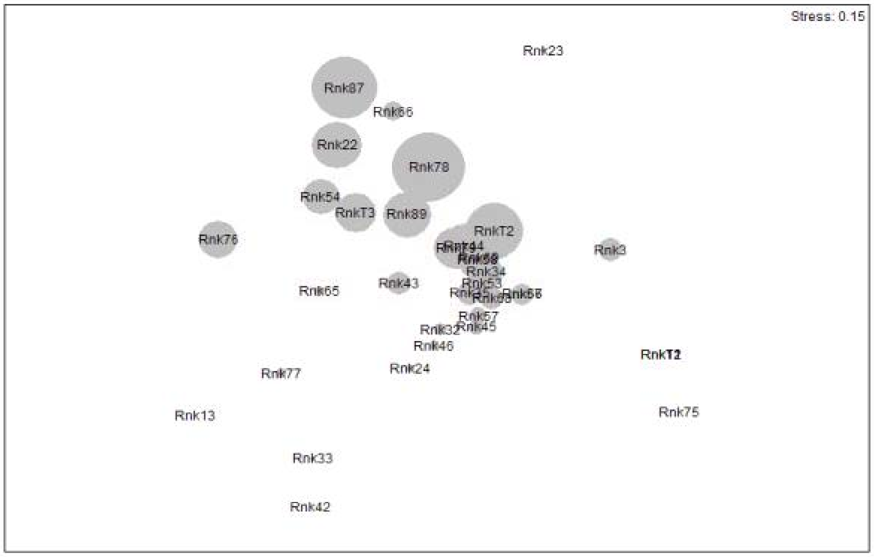


FIG. 49. nMDS ordination plot of spring 2004 Whipray Bay sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

RnkS95: Total Seagrass



RnkS95: Total Macroalgae

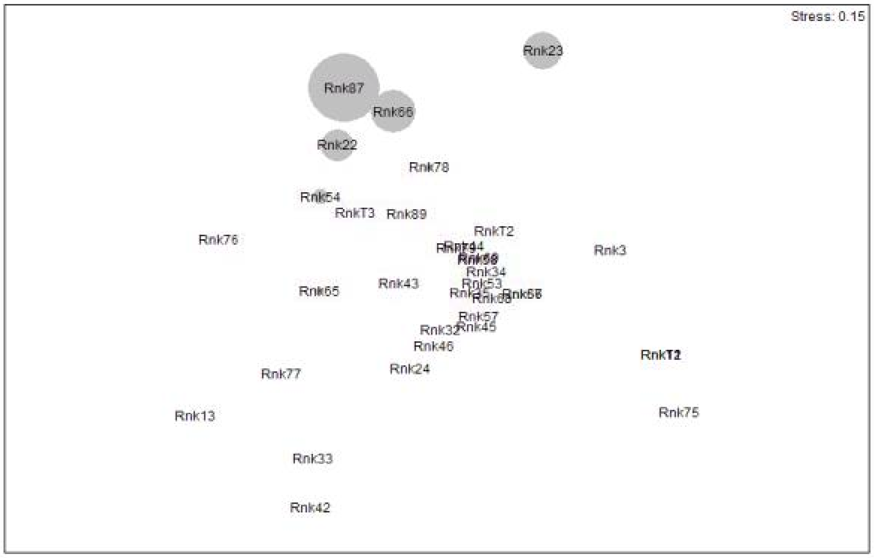
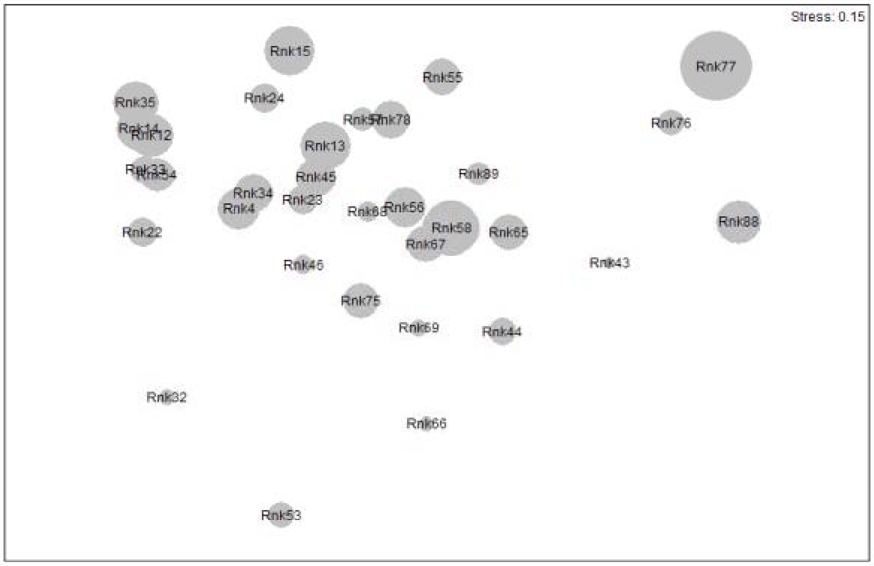


FIG. 50. nMDS ordination plot of spring 1995 Rankin Lake sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

RnkS99: Total Seagrass



RnkS99: Total Macroalgae

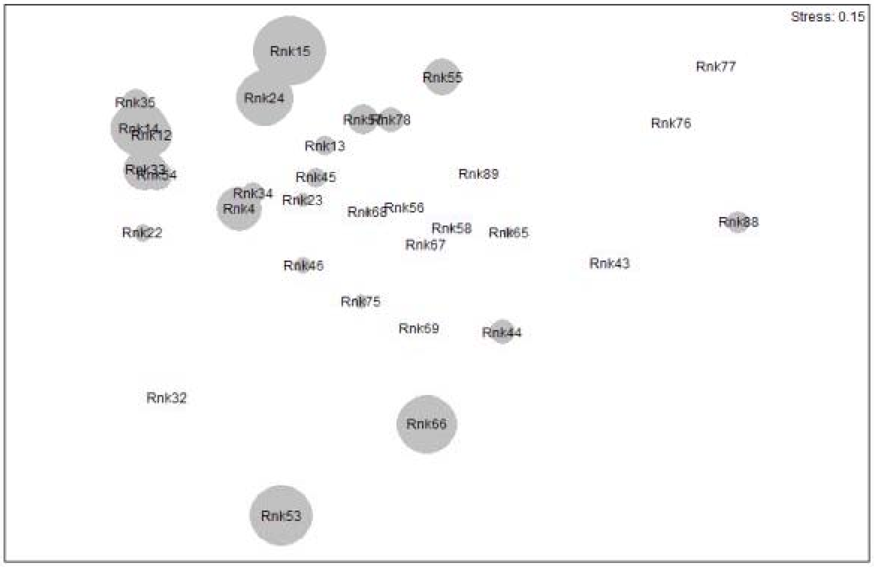


FIG. 51. nMDS ordination plot of spring 1999 Rankin Lake sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

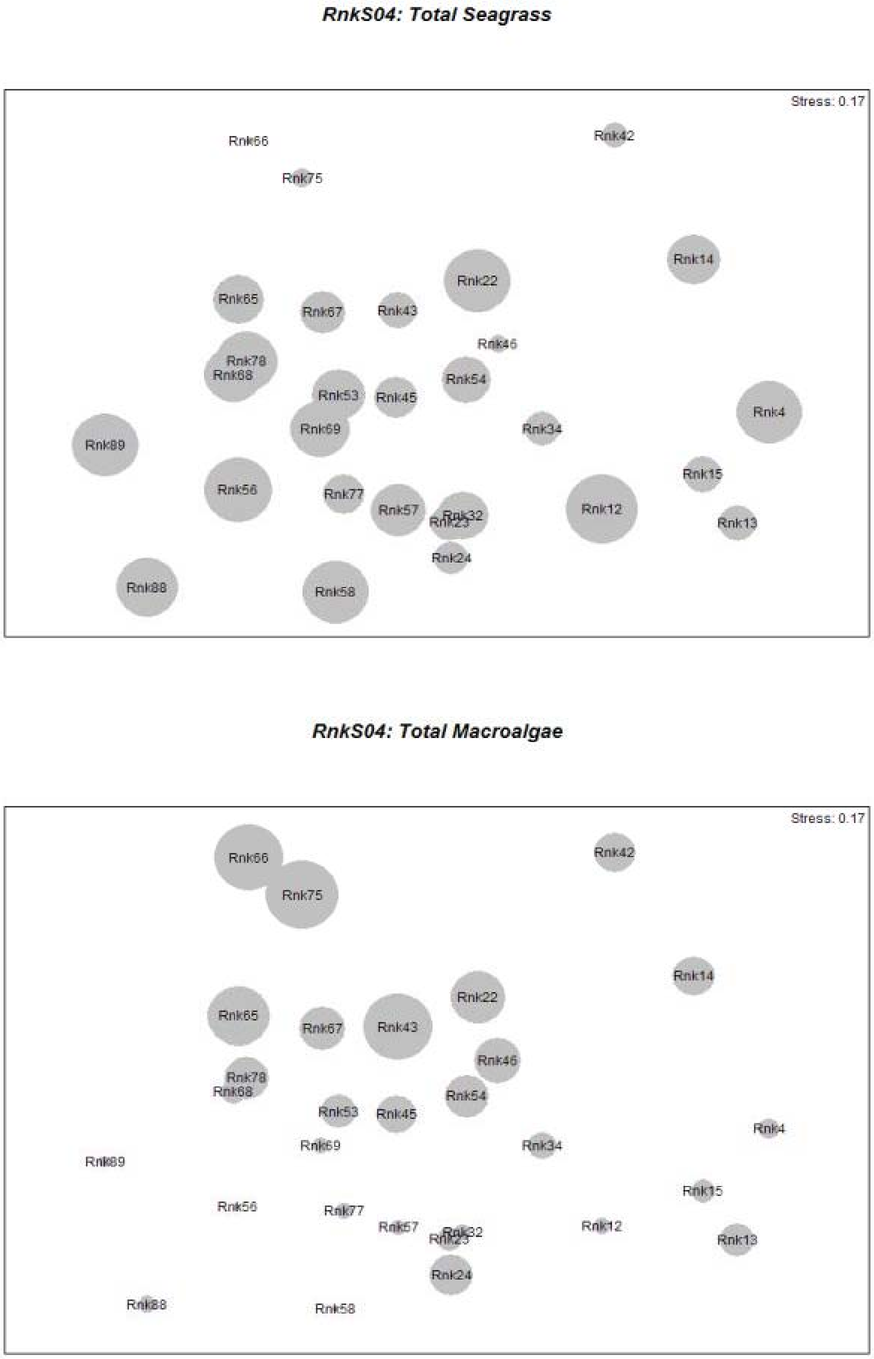
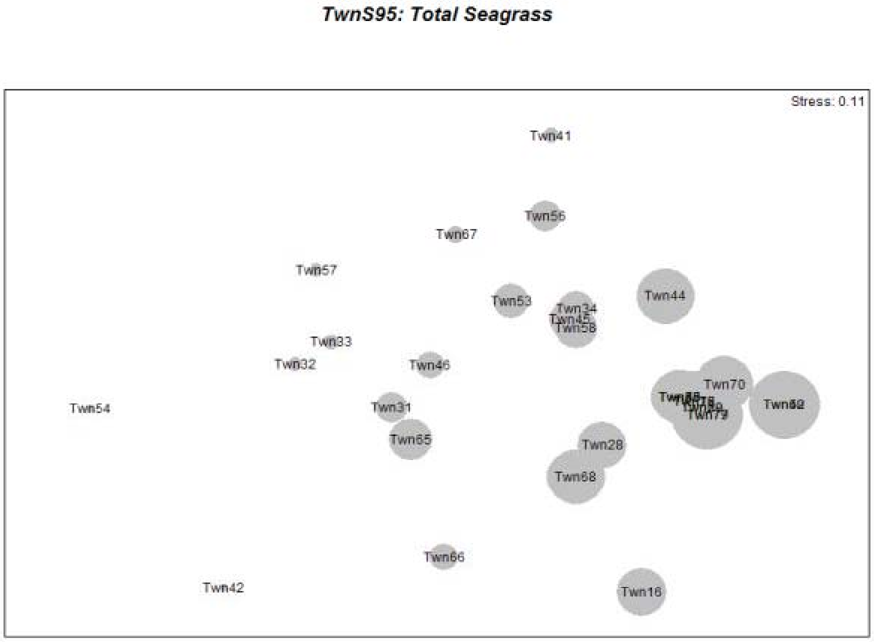


FIG. 52. nMDS ordination plot of spring 2004 Rankin Lake sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.


TwnS95: Total Seagrass

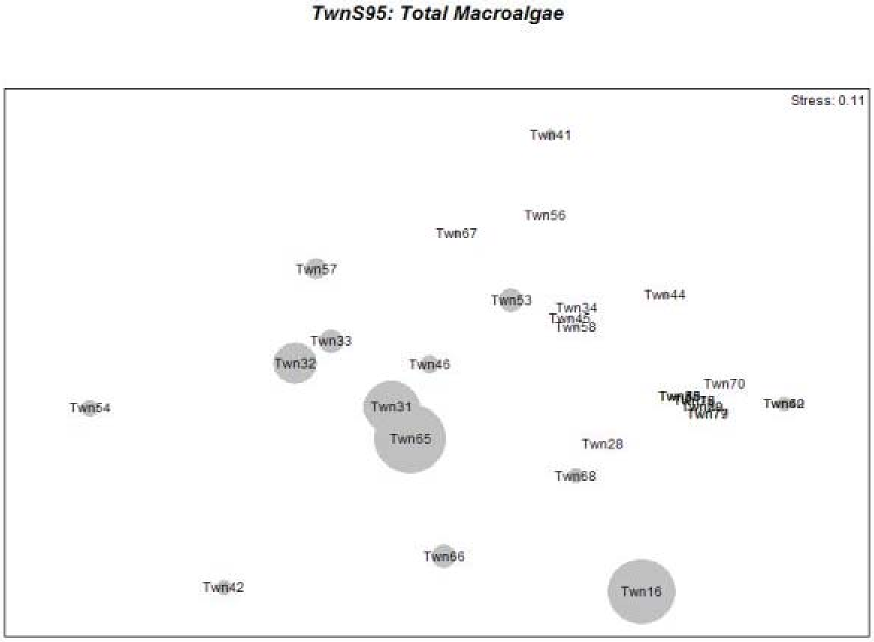
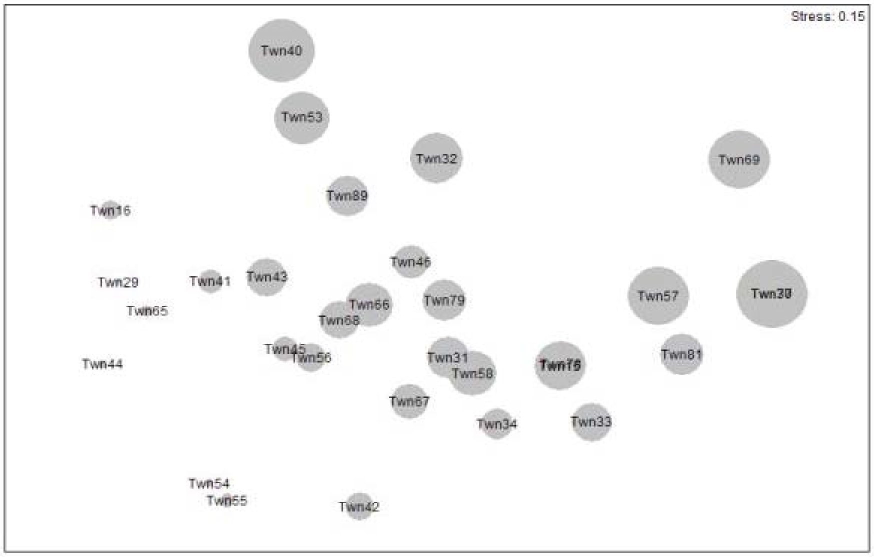
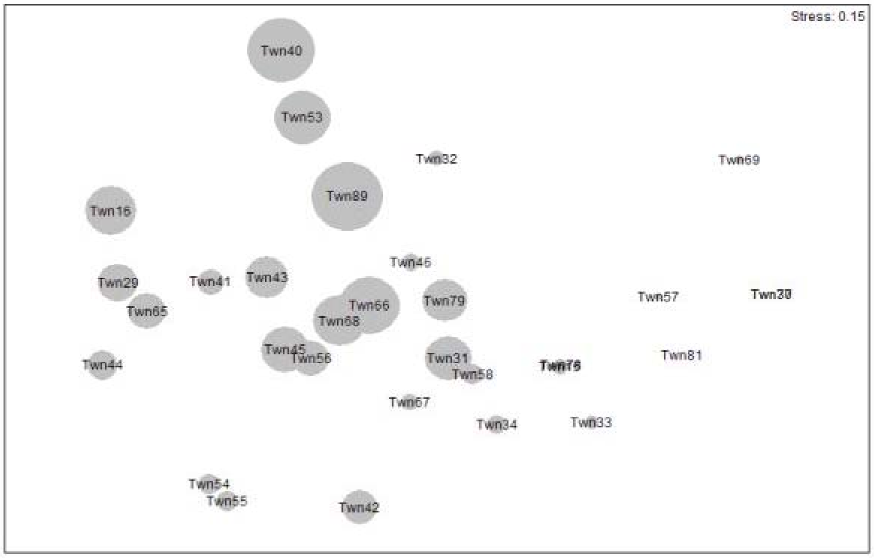

TwnS95: Total Macroalgae

FIG. 53. nMDS ordination plot of spring 1995 Twin Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

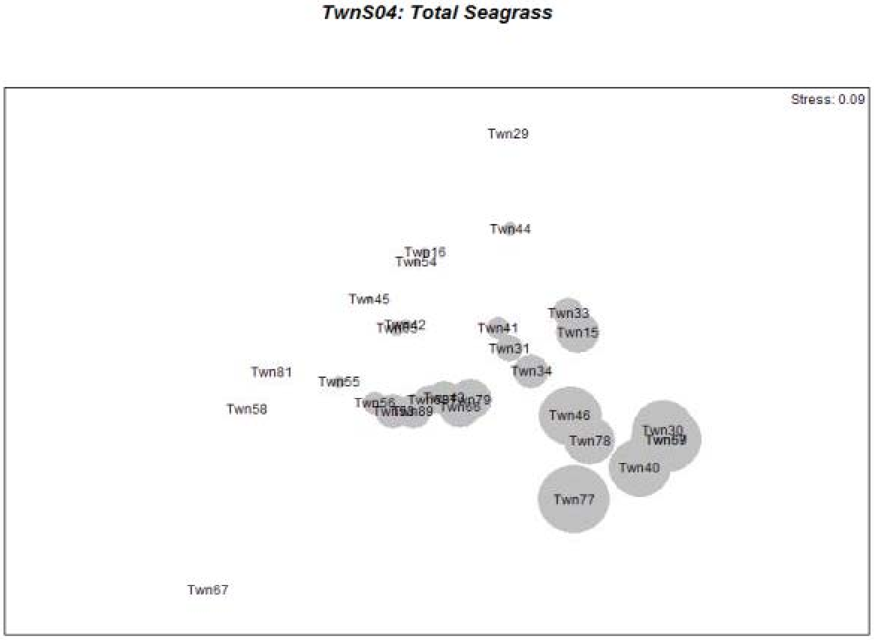


TwnS99: Total Seagrass



TwnS99: Total Macroalgae

FIG. 54. nMDS ordination plot of spring 1999 Twin Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.


TwnS04: Total Seagrass

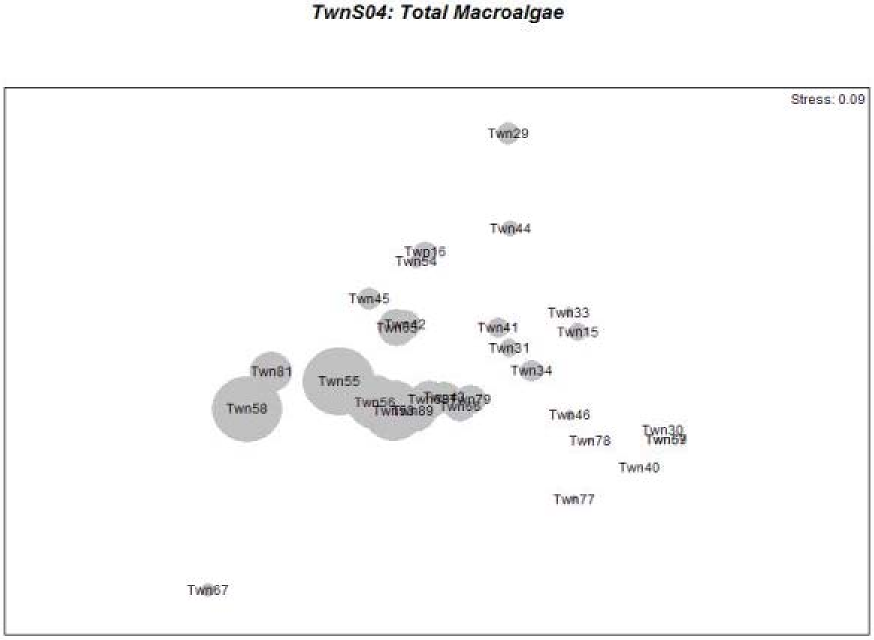
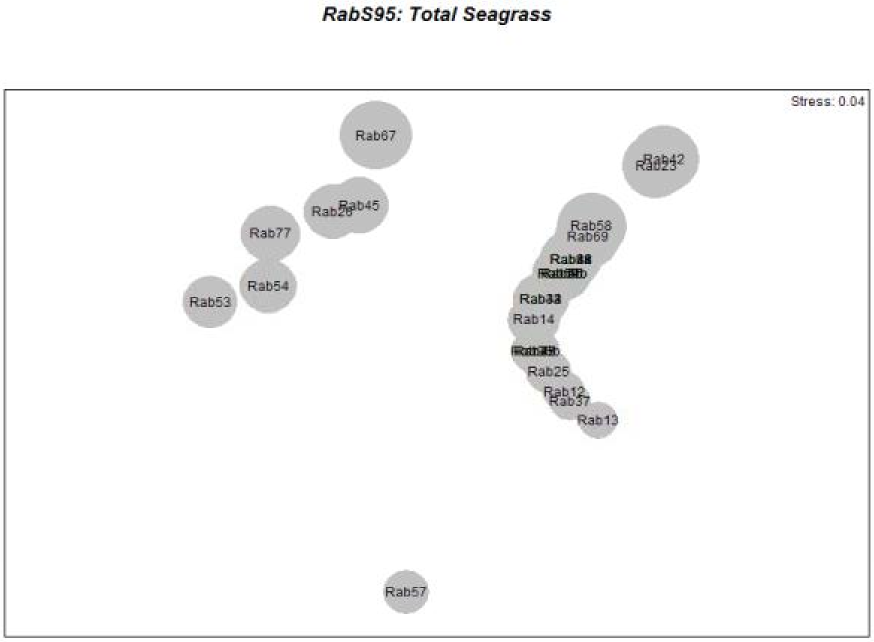
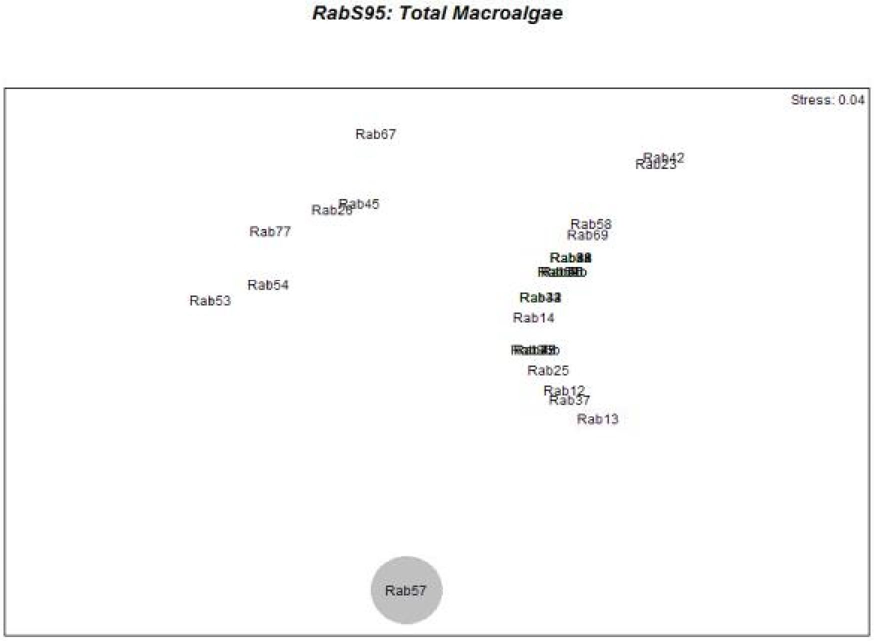

TwnS04: Total Macroalgae

FIG. 55. nMDS ordination plot of spring 2004 Twin Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.



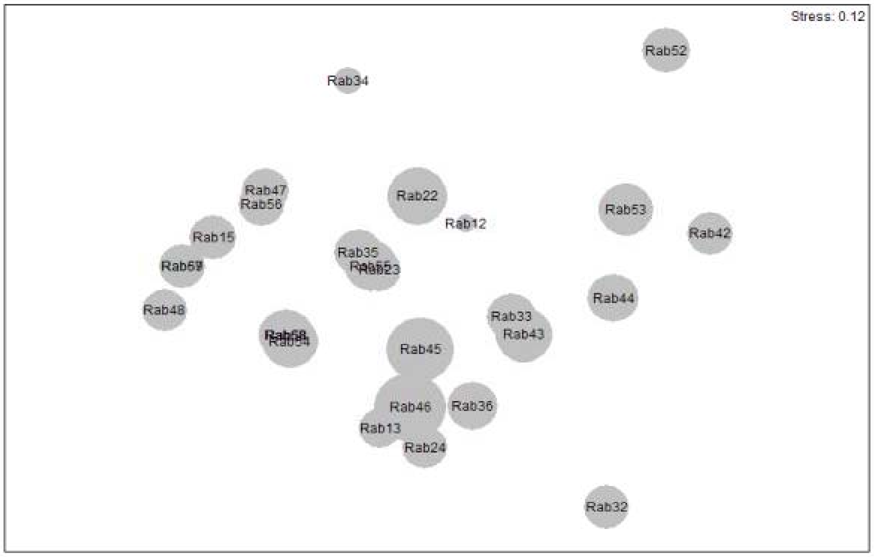
RabS95: Total Seagrass



RabS95: Total Macroalgae

FIG. 56. nMDS ordination plot of spring 1995 Rabbit Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

RabS99: Total Seagrass



RabS99: Total Macroalgae

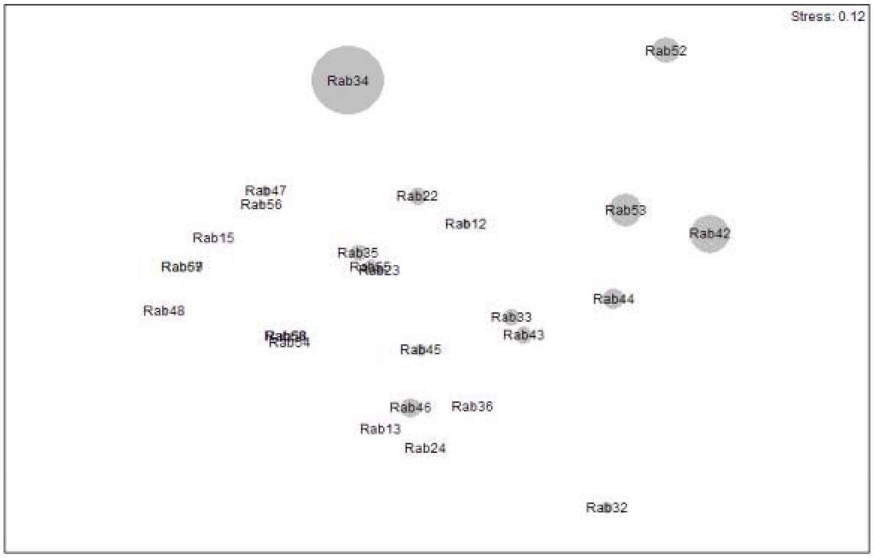
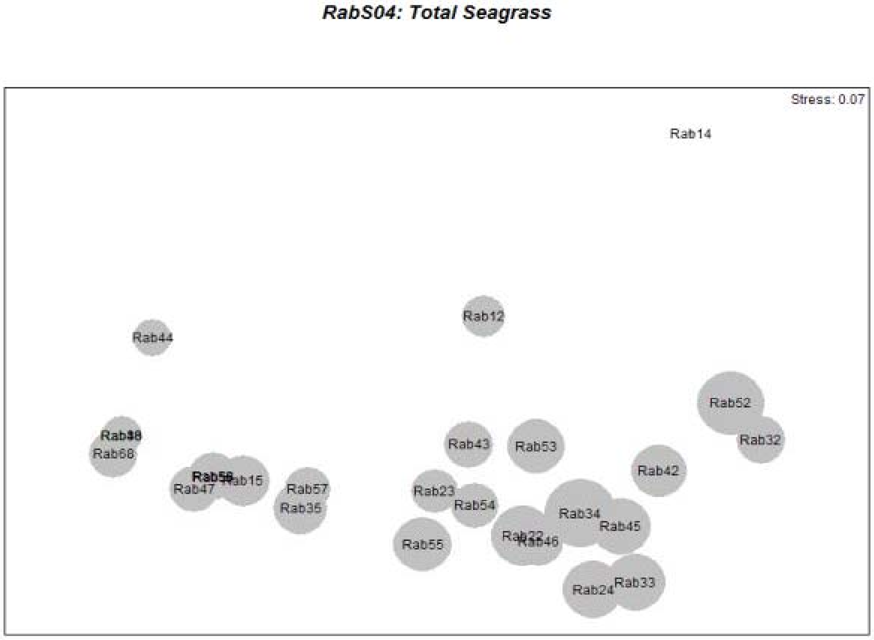


FIG. 57. nMDS ordination plot of spring 1999 Rabbit Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.



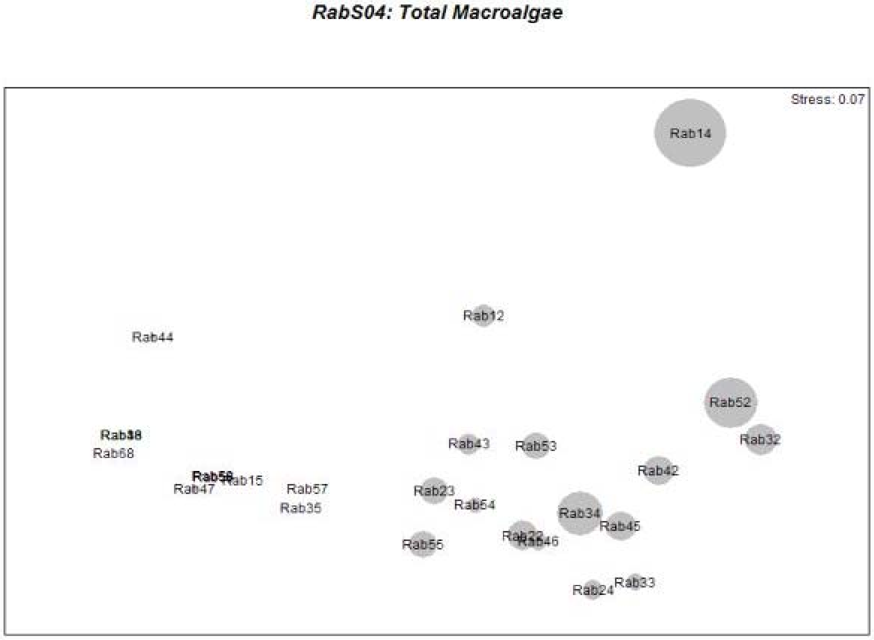
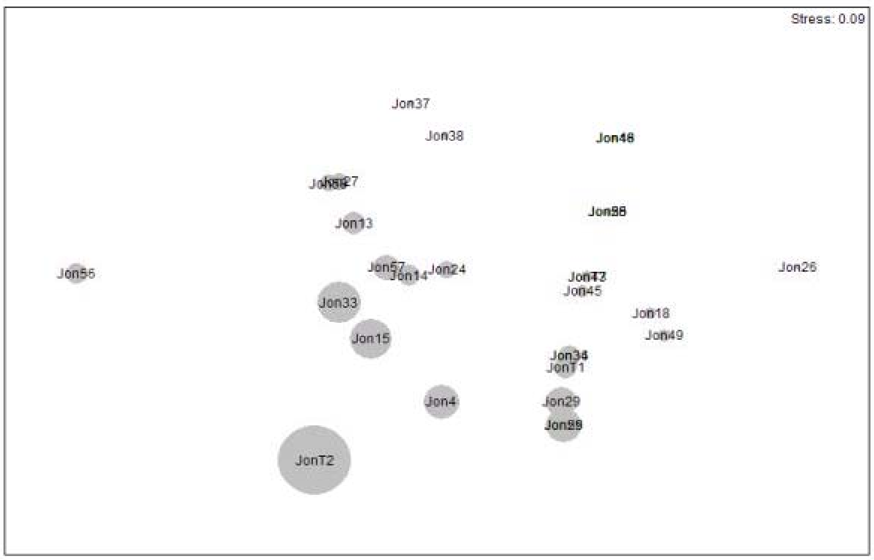


FIG. 58. nMDS ordination plot of spring 2004 Rabbit Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

JonS95: Total Seagrass



JonS95: Total Macroalgae

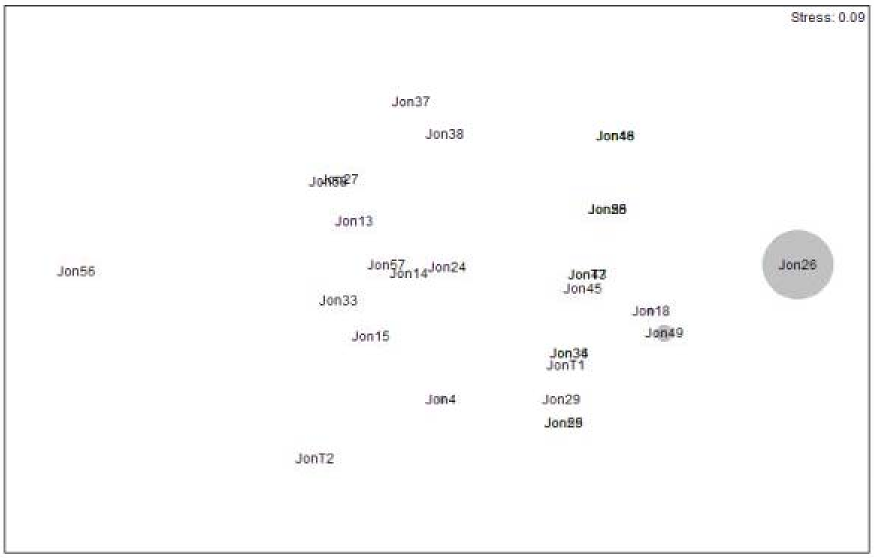
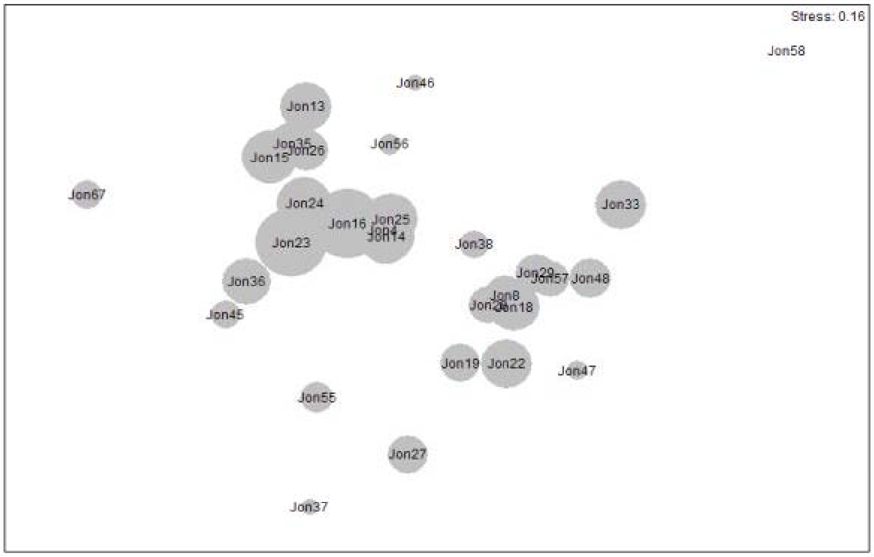


FIG. 59. nMDS ordination plot of spring 1995 Johnson Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

JonS99: Total Seagrass



JonS99: Total Macroalgae

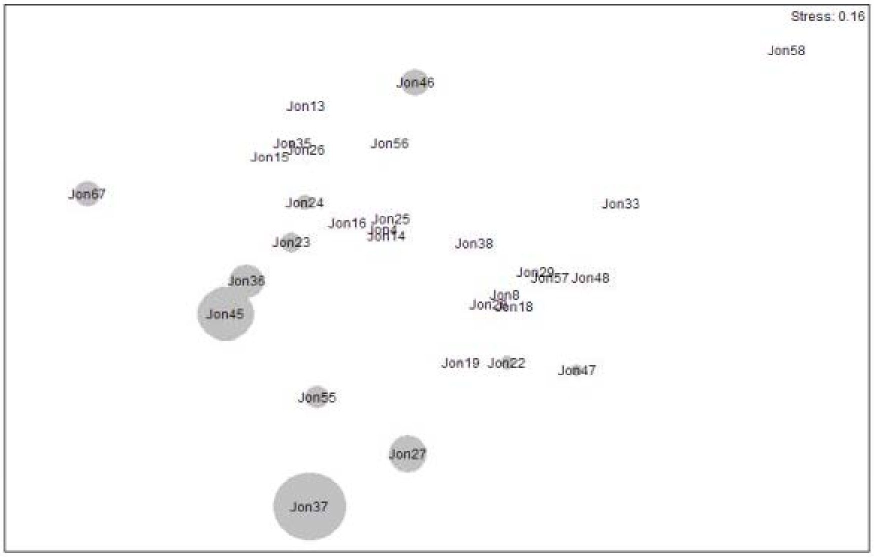
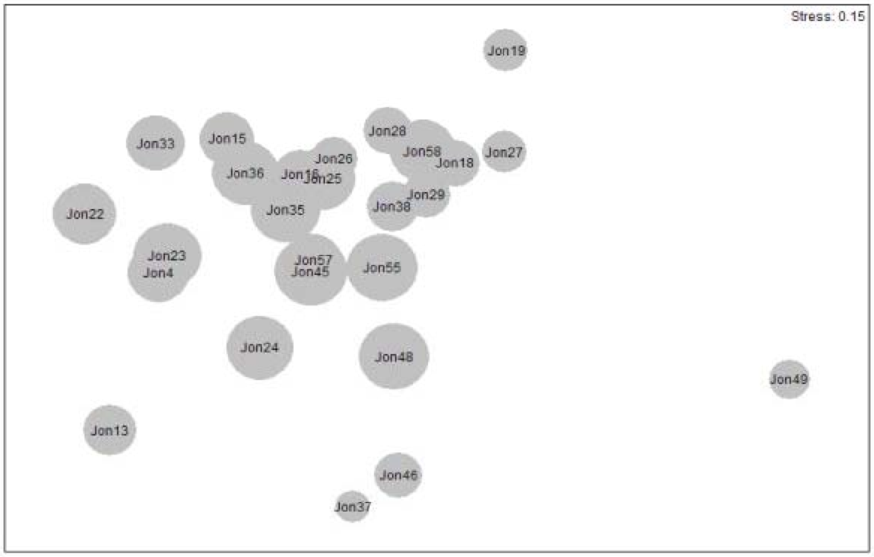


FIG. 60. nMDS ordination plot of spring 1999 Johnson Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

JonS04: Total Seagrass



JonS04: Total Macroalgae

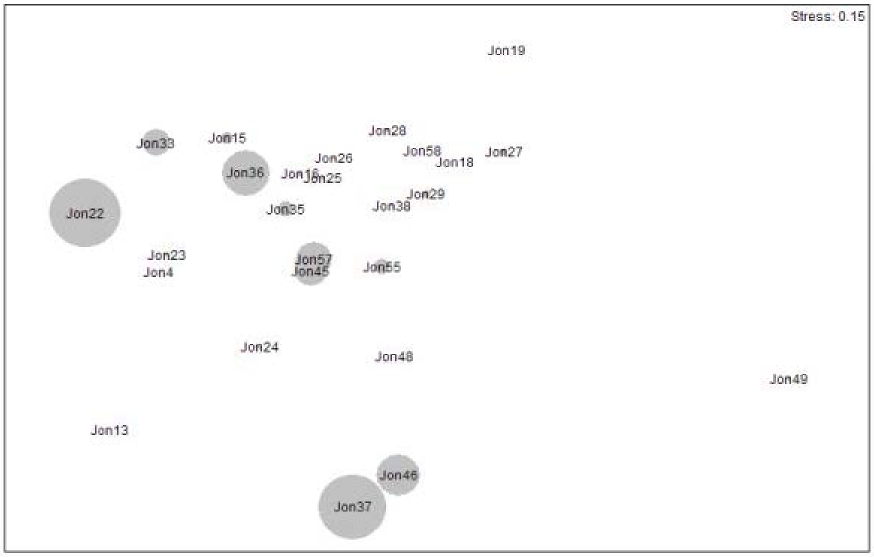


FIG. 61. nMDS ordination plot of spring 2004 Johnson Key Basin sample data. Total Seagrass cover and Total Macroalgae cover are represented by gray bubbles in the top and bottom panes, respectively.

DISCUSSION

Zieman et al. (1989) reported that sediment depth as well as water column depth increased along a northeast to southwest transect that ran through Eagle, Calusa, and Twin Key Basins. FHAP water depth data shows that moving perpendicular to that transect in either direction yields progressively shallower basins so that basins closer to land in either direction (mainland and the Florida Keys) have lower mean water column depths. Consequently, all western basins are not deeper than all eastern basins. For example, Calusa and Eagle are both on average deeper than the more western Johnson, and Johnson and Rabbit are both more shallow than the more eastern Twin.

Prior to this study, Zieman et al. (1989) and Fourqurean et al. (1993) reported the occurrence of chronic hypersaline conditions in the bay with salinities exceeding 50 psu. The bay was chronically hypersaline from 1987 – 1990 with the core of the bay exhibiting salinities greater than 50 psu for a 14-month period in 1989-1990 (Fourqurean 1993). Because *Thalassia* is a stenohaline plant (McMillan and Moseley 1967) with decreased productivity occurring when salinity conditions are extreme, salinity was implicated as a stressor to *Thalassia* and included as a potential causative agent for the die-off. After 1991, however, chronic hypersaline conditions in the bay were alleviated by a lessening of the regional drought that affected salinity before this time (Fourqurean and Robblee 1999). Between 1995 and 2004, FHAP data indicate that salinity values were mostly influenced by seasonal rainfall as higher average salinities were routinely recorded during spring sampling, which took place before the summer rainy season (FIG. 7). Johnson, Twin, and Rabbit Key Basins typically exhibited salinities closer to average seawater, while the central and northern basins exhibited slightly lower salinities because of their position to receive freshwater input from the Everglades, particularly after the summer rainy season.

Noteworthy exceptions occurred with high fall salinities in 1997 in Rabbit, Twin, Calusa, and Crane: all relatively southern basins with the exception of Calusa Key Basin, which is almost immediately in the center of the bay. These average salinities ranged from approximately 45 to 55. In fall 2000, high salinities, up to approximately 55, were recorded in Rankin, Whipray, Madeira, Johnson, and Eagle, all more northerly and shallow basins. Fall 2002 also produced abnormally high salinities (high ~ 52) in Whipray, Johnson, Rabbit, Twin, Calusa, Crane, and Blackwater. Rankin, Madeira, and Eagle also had mean salinities higher than their previous spring values, but they were not well beyond the normal range. Because FHAP data only reflect a single day per basin twice a year, these spikes in salinity were compared to water quality data obtained from the Southeast Environmental Research Center Water Quality Monitoring Program website (http://serc.fiu.edu/wqmnetwork/). This site has monthly salinity data since 1989 and shows the period of chronic hypersalinity lasting from 1989 until 1991 when the regional drought ended. After this time, each basin exhibited characteristic salinities (higher in western basins, lower in central and eastern basins) which oscillated seasonally. Highest values were recorded during the summer months and lowest salinity values were recorded during winter months. Intermediate values were recorded during spring and fall, with fall values lower than spring, as with FHAP data. Based on monthly salinity trends available at this site, it appears that the episodes of hypersalinity observed during FHAP sampling were isolated events and did not persist, although trends from the SERC website do show slightly elevated salinities from 2000 till 2002 in several basins.

Shallow water columns are more susceptible to rapid heating and cooling. Mean water column temperatures (FIG. 6) in this shallow sub-tropical system ranged from about 24^{o}C to 32^{o}C and showed some but minor seasonal oscillations as air temperatures remained high during both seasonal sampling events. Monthly trend data obtained from the Southeast Environmental Research Center Water Quality Monitoring Program website were compared to FHAP data and show typical seasonal fluctuations in water temperature, with spring and fall comparable but both slightly less than summer values and higher than winter values.

Blackwater Sound, which is relatively isolated from the other FHAP basins in Florida Bay, was the only basin to have almost consistently high percentages of water column clarity (FIG. 5), most likely attributable to protection from wind and currents. All other FHAP basins, particularly those located in western and central Florida Bay, were prone to reduced water clarity, primarily during the earlier years of sampling. With a few exceptions, after 2000, water column clarity throughout the bay was much higher. Eagle Key Basin was particularly prone to high turbidity, most likely due to the sparse vegetation cover, fine sediments and relatively large fetch in this particular basin. The bottom of Eagle Key Basin is composed of a very fine white carbonate mud and the water column rapidly becomes turbid during windy conditions. During calm conditions, sediments were observed to settle out of the water column, resulting in increased water clarity. While low water clarity was recorded in all of the basins at one time or another, Rankin, Johnson, Whipray, and Rabbit were particularly affected. These basins are all located in the western bay where the greatest seagrass die-off occurred beginning in 1987 (Robblee et al. 1991). Although data are anecdotal, water clarity prior to the die off was reportedly excellent in this portion of the bay. The die-off was followed by a period characterized by frequent resuspended sediments and persistent phytoplankton blooms that began only after its initiation (Stumpf et al. 1999). Although FHAP sampling began several years subsequent to the die-off, our results suggest that resuspended sediments and phytoplankton blooms were still a problem during initial sampling events, but that conditions improved steadily until near-100% clarity in all FHAP basins became more common after spring 1998.

Seagrasses

Florida Bay macrophytes have been the subject of several studies both before and after the 1987 *Thalassia* die-off that predominated in the western basins. Trends in macrophyte distribution outlined by Zieman et al. (1989) and Hall et al. (1999) were similar to those found by FHAP. *Thalassia* was the dominant seagrass in Florida Bay in 1984 (Zieman et al. 1989), 1994 (Hall et al. 1999), and now FHAP data indicates that it has remained the dominant seagrass over the ten-year period from 1995 to 2004.

Two basins are included in the FHAP sampling regime that were not included in either of the prior studies: Blackwater Sound and Calusa Key Basin. Since FHAP began in 1995, *Thalassia* density did not increase or decrease significantly by 2004 in Blackwater Sound, Eagle Key Basin, Calusa Key Basin, Crane Key Basin, Twin Key Basin, or Rabbit Key Basin. It did however exhibit oscillating densities over the time period in all basins. Oscillations occurred in which approximately two years would exhibit high densities, then the following two exhibited low densities, and then high densities again, and so on over the course of the decade. *Thalassia* in Johnson Key Basin, Rankin Lake, Whipray Bay, and Madeira Bay exhibited oscillating patterns but did increase significantly in density by 2004. While densities were increasing at the onset of sampling in 1995 in Rankin and Johnson, frequency of occurrence continued to decrease to a low in fall 1996, after which time distribution increased again. This may suggest that *Thalassia* beds were still being affected by die-off at the initiation of FHAP sampling, and may reflect *Thalassia's* ability to allocate resources (Tomasko and Dawes 1989). Resources may be shunted away from stressed areas and towards healthy areas, becoming more dense where beds still existed. After fall 1996, *Thalassia* distribution increased, possibly reflecting recovery from die-off and the subsequent chronic turbidity and phytoplankton blooms in these basins, and recolonization by *Thalassia* in areas previously denuded.

Thalassia did not show significant decreases in density between 1995 and 2004 in any of the FHAP basins, although *Thalassia* density in Rabbit Key Basin declined from about 75% -100% cover on average to about 50% cover during that time period. Frequency of occurrence however, remained at or near 100% (FIG. 8). This decrease took place steadily until spring 1999 and then rebounded and leveled off at about 50% cover by fall 2002. Spring 1999 in fact yielded high *Thalassia* densities in all basins. In some basins such as Johnson and Rankin, *Thalassia* continued to increase in density after that time, but in most others it peaked and then leveled off.

FHAP data indicates that *Halodule* density did not change significantly in Blackwater, Eagle, Madeira, Calusa, Crane, Rankin, or Twin from 1995 to 2004. It did however exhibit a dramatic increase in Rankin Lake followed by an equally dramatic decrease, so that while 1995 and 2004 were not significantly different, *Halodule* was very dynamic in this basin. Similar to results reported by Hall et al. (1999), highest *Halodule* densities were observed in the northwestern and western basins, particularly in Rankin, Johnson, Rabbit, and Whipray. Contrary to observations by Hall et al. (1999) which reported a decline in *Halodule* between 1984 and 1994, analysis of Johnson, Rabbit, and Whipray *Halodule* density data all yielded significantly higher densities in 2004 than were observed in 1995. Although *Halodule* was reportedly not affected by the 1987 die-off (Robblee et al. 1991), poor water quality was implicated in its later decline (Hall et al. 1999). FHAP data for the basins in which it increased significantly, as well as in Rankin Lake, showed that *Halodule* density steadily increased until about 1999/2000, at which time in all four basins it leveled off and then it decreased in density again (FIG. 9). Because water clarity continued to increase in these basins and salinities were stable during those years, this subsequent decline might be due to competition with *Thalassia* and to a lesser extent *Syringodium*. *Halodule* is a "pioneer" species, able to rapidly colonize disturbed areas because of higher rhizome elongation and growth rates; but it consequently has high nutrient requirements (Gallegos et al. 1994). *Halodule* has a short leaf and shoot lifespan, which makes it less able to store nutrients. *Thalassia* is a climax species that grows much slower, is able to store excess nutrients, and lives longer and can therefore outcompete *Halodule* under stable environmental conditions (Gallegos et al. 1994). *Halodule* may have colonized areas of *Thalassia* die-off in these central and western basins between 1995 and 2000. As *Thalassia* recovered, *Halodule* was not able to maintain these high densities, but it was not completely excluded as frequencies of occurrence continued to rise or remained stable through 2004.

Like *Thalassia*, *Halodule* exhibited a decreased frequency of occurrence in Rankin Lake (from 84% to 53%) as well as in Rabbit (from 32% to 12%), and to a certain extent in Johnson (from 56% to 45%), but this decrease took place in spring 1996 – prior to the fall 1996 *Thalassia* drop (FIG. 9). This may indicate that at the initiation of FHAP sampling, turbid conditions in the western bay were still inhibiting the recovery of *Thalassia* and *Halodule*, with *Thalassia* responding to turbid conditions slower than *Halodule* because of its larger belowground storage reserves.

This trend was also exhibited by *Syringodium*, another “pioneer” species. *Syringodium* is the only seagrass genus with cylindrical blades (Durako 1999). It is more typical of clear water with heavy tidal action. *Syringodium* was only present in significant amounts in Johnson, Rabbit, and Rankin Lake (FIG. 10) during FHAP sampling. Although Hall et al. (1999) found that it decreased in distribution and density between 1984 and 1994, it increased in both from 1995 to 2004. In Rankin Lake this increase in density was not significant, but both Johnson and Rabbit exhibited significant increases in density. Frequency of occurrence reached almost 100% in Johnson Key Basin in spring 2004 and while distribution and density were not as great in Rabbit, a steady increase was clearly discernible. With frequency continuing to increase but density leveling off, it appears that *Syringodium* started to compete with *Thalassia* during these later sampling events. Though physically dissimilar to *Halodule*, *Syringodium* does have a similar growth habit (Gallegos et al. 1994) and like *Halodule*, high densities are not maintainable when competing with *Thalassia*. Both *Halodule* and *Syringodium* can maintain a presence in *Thalassia* beds at lower densities but peak before and decline after *Thalassia* becomes more dense (Williams 1987). Gallegos et al. (1994) attributed *Halodule* and *Syringodium*'s lack of competitive advantage over *Thalassia* for space to higher growth rates, higher nutrient requirements, and higher mortality rates. Williams (1987) attributed *Syringodium*'s lack of competitive advantage to exploitative competition for sediment nutrients as well but also found that light is a significant influence on *Syringodium* survival in *Thalassia* beds due to shading. Once *Thalassia* beds become too dense for adequate light to reach *Syringodium*, the *Syringodium* density will level off or decline, as seen in our results.

Neither Zieman et al. (1989) or Hall et al. (1999) reported *Halophila engelmannii* in Florida Bay. *Halophila engelmannii* is common in lower light environments or may be found in the understory of larger seagrass beds (Durako 1999). It was not detected by FHAP sampling until fall 1996, when it was first observed in Johnson Key Basin at one station as a single ramet. It may have been transported in from deeper waters in outer Florida Bay at that time and was able to maintain a presence because of space availability and low-light conditions (high turbidity associated with die-off and subsequent resuspension of sediments and phytoplankton blooms), as it is a low-light-adapted plant (Durako 1995, 1999). By fall 1998 it was observed in Rankin Lake, and by spring 2000 it was reported in Rabbit Key Basin (FIG. 11). It was very sparse and at low densities every time it was found and was never found to significantly increase or decrease in density. Its spread from Johnson to Rankin may be attributed to uprooting and transport by high winds associated with Hurricanes Georges and Irene. The hurricanes will be discussed in more detail below.

Although Zieman et al. (1989) reported *Ruppia* along the mangrove fringes in the mainland area of Florida Bay, Hall et al. (1999) did not report any *Ruppia* in 1994. Likewise, FHAP data indicates *Ruppia* was only observed on eight occasions and then as solitary ramets (FIG. 12). *Ruppia* is most likely excluded from more-central and southerly Florida Bay benthic communities because it only grows in low-energy waters with salinities less than those in typical marine environments (Verhoeven 1975). This explains it’s occasional presence in Madeira, Rankin, Johnson, and Blackwater: all have more influence from terrestrial Everglades run-off than the other, more southerly, FHAP basins.

While *Ruppia* seems a small contribution to the FHAP-basin seagrass community now, as CERP progresses and an increased quantity of freshwater is delivered to Florida Bay, it is expected that more *Ruppia* will be observed in the future in response to lower and more widely fluctuating salinities (Fourqurean and Rutten 2003).

Upon examining south Florida hurricane data located on the National Hurricane Center website (http://www.nhc.noaa.gov/pastall.shtml), two major storms passed over the bay during the actual study period: Hurricane Georges in late September 1998 and Hurricane Irene in mid-October 1999. Both moved from southwest to northeast over the outer western portion of Florida Bay. While Georges didn’t appear to affect fall 1998 mean salinities or visibilities, it appears that Irene may have affected the bay moreso in fall 1999: fall 1999 salinities are lower than spring 1999 mean salinities (but still above 20) and water clarity in many of the basins was considerably reduced (down to about 40% in many basins).

Hurricanes are capable of causing severe damage to seagrass beds by mechanical thinning of the canopy (leaf removal by wave action), by burial of part of or the entire community, or by removal of the seagrass due to erosion of sediment in which it is anchored (Ballantine 1984, Fourqurean and Rutten 2004, Cruz-Palacios and van Tussenbroek 2005). Hurricanes may also be beneficial to seagrass meadows by flushing of potentially stagnant waters and by removal of leaf litter, highly organic sediment, and biomass build-up. A lack of major storm events over an extended period of time (>20years) was implicated as a potential contributing factor to the seagrass die-off in 1987 (Zieman et al. 1988). While the increase in seagrass distribution and abundance was slow initially and spatially variable, Hurricanes Georges and Irene may have prompted further recovery, particularly in Rabbit Key Basin, which was continuing to lose *Thalassia* density until these hurricanes passed over. The increase in *Thalassia* density in many of the basins beginning in 1999 (FIG. 8) supports this possibility.

The Dwass Steele Critchlow-Fligner method, a large sample approximation multiple comparison procedure based upon pairwise rankings, was used and found that the western basins were the most dynamic in terms of seagrass change since 1995. All significant changes in density were positive. This increase in density appears to represent a recovery of the system after the die-off in that area. Basins in which seagrass cover did not increase (basins where no die-off was reported) remained stable over the decade of study, despite oscillations. Any decreases in seagrass were not statistically significant.

Florida Bay macroalgae, however, were much more dynamic across the entire bay. Although Zieman et al. (1989) reported some trends in macroalgal distribution and density, descriptions were not as extensive as for the seagrasses, nor are there a great number of other studies concerning macroalgae in Florida Bay. The FHAP dataset is therefore the most comprehensive long-term monitoring of macroalgae available.

Psammophytic Macroalgae

Acetabularia and *Batophora* are both psammophytic algae found throughout Florida Bay. They are benthic, tropical macroalgae (Morrison 1984) that grow attached to shells, coral fragments, other algae, as well as on dead seagrass sheaths or rhizomes. *Acetabularia* and *Batophora* are often found together in the bay and provide an addition to the overall primary production. They do not have the physical stature to compete with seagrasses for habitat, but will often colonize shelly areas lacking seagrass or die-off areas where dead short-shoots or exposed rhizomes are present.

Batophora is the most ubiquitous macroalgae in Florida Bay and it exhibited a significant increase in density between 1995 and 2004 in several basins (Eagle, Calusa, Crane, Whipray, Rankin, and Twin Key Basins). While it was not statistically significant, an increasing trend in density was apparent and distribution increased from approximately 20% frequency to over 60% in Madeira Bay (FIG. 14). It also increased in density and frequency in Blackwater Sound, but this change was not significant. Zieman et al. (1989) noted the importance of *Batophora* in many of these basins. It was not however particularly prevalent in the western basins: Johnson and Rabbit. And although it increased significantly in density in Rankin, it was very sparse and did not appear until several years after sampling began, as was also noted in Johnson and Rabbit. Sediment type and substrate availability probably played a large role in *Batophora's* spatial distribution. The central and eastern basins where it occurred in highest frequencies and densities have more rocky outcrops and hard substrate on which to attach. These basins also have lower overall densities of seagrass than the western basins.

Its density and frequency patterns suggest a certain degree of seasonality and indeed intra-annual changes were significant on a number of occasions throughout the bay. Significant changes were more often recorded for inter-annual variations in density. Morrison (1984) studied *Batophora* seasonality and found summer and early fall abundances to exceed winter abundances at his study site off Key Largo. The abundance patterns corresponded to photosynthetic activity. This seasonal variability was also observed by FHAP sampling as Braun-Blanquet cover was usually somewhat higher during fall sampling than spring. Spring densities were also relatively high and they increased annually in most basins in part due to this species' reproductive strategy. *Batophora* is reproductive all year, but reproductive activity is most intense in late fall – cued by drops in temperature (Morrison 1984). This type of reproductive behavior is advantageous for annuals so that the population can continuously replenish itself as well as rapidly colonize space (Morrison 1984). Post-reproduction, the plant dies, explaining lower densities the following spring. Lower photosynthesis in the remaining plants observed during winter months does not allow biomass to increase until summer when temperatures increase again.

The euryhaline and eurythermal nature of *Batophora* combined with this very successful reproductive strategy (able to reproduce at 4 months old) has led to its great extent throughout the Caribbean (Morrison 1984). It may occur at very high densities because smaller algae are able to more rapidly remove nutrients from the water column (Hein et al. 1995) before they can be taken up by larger and more slow growing algae. It did however exhibit the same dramatic drop in frequency in spring 1996 that *Halodule* did, and in many of the same basins.

Of all of the macroalgae studied, *Acetabularia* exhibited the most dramatic seasonal oscillations in both distribution and density (FIG. 13). While it is known to be psammophytic and reproductive throughout the year (Morrison 1984), little else can be found in the literature regarding the ecology of this macrophyte. FHAP data suggests that a greater majority of the population than that of *Batophora* becomes reproductive simultaneously because frequency and density differences between seasons are much more dramatic than those of *Batophora*. Highest density and frequency values were recorded in spring rather than fall, suggesting that timing of most intense reproduction does not coincide with that of *Batophora*. Density and frequency patterns suggest that it must become reproductive sometime during the summer between June and September, as it is observed in higher densities when sampling takes place in the spring, but then is much more sparse when sampling is conducted again in the fall.

Spatial distribution patterns were similar to those found for *Batophora* as both use similar substrates. They both require solid substrates on which to attach their very small holdfasts. *Acetabularia* densities increased significantly from 1995 to 2004 in all but two of the same basins as *Batophora* (Eagle, Calusa, Rankin, and Twin). It did not increase in Whipray Bay or Crane Key, nor did it reach densities as high as *Batophora* in the other basins. While they are both small and consequently able to efficiently remove nutrients from the water column, *Acetabularia* is calcified, and calcification requires an increased amount of energy; energy therefore not available for the rapid growth and colonization rates seen in *Batophora*. Limited distributional patterns seen in the FHAP data may also been an artifact of the difficulty of sampling this genera. *Acetabularia* plants are small and at times inconspicuous – therefore not detected by divers. Furthermore, when its characteristic gametangial rays are not present, the plant is virtually invisible and may remain undetected during sampling – particularly in areas where other macrophytes are found in high densities.

Rhizophytic Macroalgae

Rhizophytic macroalgae of the order Bryopsidales are composed of one large cell (Vroom and Smith 2001) with lifespans ranging from one to four months (Williams 1990). They may be calcified (*Halimeda* and *Penicillus*) or uncalcified (*Caulerpa*) (Biber 2002). Calcified rhizophytic algae are highly productive and important contributors to the carbonate sediments of Florida Bay (Wefer 1980). They are also important in stabilizing the sediments, adding organic matter to sediments and creating more ideal situations for seagrass succession (Williams 1990, Thayer et al. 1994). They are not tolerant to low temperatures and display optimal growth up to 34^{o}C (O'Neal and Prince 1988). Optimal salinity ranges from 20-35 (Biber et al. 2004), although Back (1979) found highest growth rates for *Halimeda* at 37-38 ppt in Card Sound, Florida Bay. These plants also have the advantage of modified rhizoidal holdfasts (*Halimeda* and *Penicillus*, or seagrass like rhizomes as in *Caulerpa*), and are consequently able to access sediment nutrients as well as water column nutrients (Biber et al. 2004, Williams 1984, Vroom and Smith 2001).

Both frequency and density of *Halimeda* were generally higher during spring sampling, although there were exceptions. *Halimeda* may bear clusters of beadlike reproductive structures on branched stalks arising from the surface of the calcified segments, which are separated by lesser-calcified nodes (Lee 1989). Vroom and Smith (2001) reported that when fragmented (by herbivory, wave action, etc.), the broken pieces grow new attachment rhizoids within hours and may add up to 25 new segments within a week. After Hurricane Irene passed over the Keys in 1999, Vroom and Smith (2001) learned that *Halimeda* sections could remain buried for months and remain viable, waiting for conditions to improve. While propagation through vegetative fragmentation is apparently important for these plants, they also reproduce sexually. Vroom and Smith (2001) reported that approximately five percent of a population simultaneously develops reproductive structures and these individuals release gametes within minutes of one another right before dawn. The process begins with the development of gametangia along the upper margins of segments. The entire cellular contents of the plant go into these gametangia, turning them bright green and the rest of the plant white. Once gametes are released, the plants die and disintegrate (holocarpic), removing those adult plants from the population.

It appears that *Halimeda* exhibits highest reproductive effort sometime during the summer. Bach (1979) reported highest growth rates for *Halimeda incrassata* to take place in the summer due to elevated light and temperatures, and Lirman and Biber (2000) reported an increasing trend in cover for *Halimeda* from January to July. Most likely then, *Halimeda* sexual reproduction takes place in late summer to early fall, sometime before FHAP sampling in mid-October, when densities and frequencies are lower.

Halimeda exhibited an increase in frequency as well as a significant increase in density in Rankin Lake, Twin Key Basin, Rabbit Key Basin, and Johnson – all western basins. It was also present at low cover values but relatively high frequencies in Blackwater Sound, but with the exception of some seasonal fluctuations, did not change in density (FIG. 16). Density in Blackwater was similar to that observed in Johnson and Rabbit, but these two basins, along with Twin and Rankin Lake did not have any *Halimeda* during the first sampling trip whereas Blackwater did. It was very sparse in the remainder of the basins throughout the study period. Success in the western basins may be attributed to its ability colonize benthic habitats where ambient light intensities are significantly less than at the surface (Lee 1989), a characteristic that may give *Halimeda* an advantage in turbid waters (Davis and Fourqurean 2001).

Halimeda, along with other calcareous rhizophytics, have also been shown to play an important role in the successional sequence of Caribbean seagrass beds (Williams 1990). After a disturbance, rhizophytics such as *Halimeda* are often the first to recolonize an area, followed by pioneer species of seagrass, including *Halodule* and *Syringodium*, and then finally by *Thalassia*, the climax species. At the conclusion of this sequence, *Thalassia* dominates but the others remain present at reduced densities. The increased density and frequency observed for *Halimeda* in the western basins after the die-off reflects its role in the recovery of those basins, as well as its adaptation to environmental variables found in the western basins.

Bach (1979) found that *Halimeda incrassata* is more acclimated to shallow water (less than one meter), deep sediments (more than one meter), higher current velocities, and areas of dense *Thalassia* in Card Sound, northeast of Blackwater Sound. These conditions are similar to those in western Florida Bay where *Halimeda* was most prevalent. Although the basins average more than a meter depth, shallow mudbanks, deep sediments, and dense *Thalassia* characterize many areas. This area is also much more affected by tidal flow from the Gulf of Mexico. More shallow sediments and hard substrate may have prevented *Halimeda* from successfully colonizing the central and eastern basins. Although Blackwater Sound is in the east, it has areas of very deep sediment conducive to *Halimeda* rhizoids.

Penicillus was widespread throughout the bay, although mean cover never exceeded 5% (FIG. 17). Many basins exhibited overall increasing trends in frequency of occurrence, reaching nearly 100% in Rankin Lake during the most recent sampling events. Significant increases in density between 1995 and 2004 were only observed in Eagle Key Basin, Whipray Bay, and Rankin Lake – all more northerly basins. While frequency increased in Eagle, the significant increase in density is probably attributable to the fact that it was not recorded in that basin until spring 1997. Its distribution overlapped somewhat with *Halimeda*, but the highest and least variable densities were observed in Twin Key Basin and Blackwater Sound. Bach (1979) found higher growth rates for *Penicillus capitatus* in deeper (more than 3 meters) water, shallow sediment depths (from 5-20 cm), low currents and areas of sparse *Thalassia*. These conditions are similar to those in Twin and Blackwater: they are the two deepest FHAP basins, shallow sediments are common in both although both also have areas of deep sediments, and they both have limited tidal influence and sparse stands of *Thalassia*.

There are several species of *Caulerpa* found in the bay, all of which have extensive rhizomes connecting individual erect, frond-like shoots that have internal wallgrowths called trebeculae. Together with turgor pressure, these trebeculae support the plants' sometimes impressive size (Lee 1989). When fragmented, loss of cellular contents is rapidly abated by the formation of wound plugs and whole new plants are able to form from the fragmented pieces (Vroom and Smith 2001). Regardless of this seemingly impressive advantage which allows these plants to spread in non-traditional methods as well as through rhizome extension, *Caulerpa* was only consistently seen in three western FHAP basins (Rankin, Johnson, and Rabbit), and one eastern one (Blackwater Sound), and at relatively low densities in those. The only significant increase in density was in Rankin, where it was not observed during the first sampling event. Seasonal fluctuations are somewhat evident in frequency patterns despite the very low densities (FIG. 15). Frequency oscillated marginally around 20% in Blackwater Sound for the duration of the study period and frequencies were generally higher in the spring. O'Neal and Prince (1988) found that *C. paspaloides* grows most in spring and fall and that it is more photosynthetically efficient at low light levels. This perhaps explains its consistence in Blackwater Sound. Although the water in Blackwater is almost always very clear, it contains a great deal of colored dissolved organic matter (CDOM) due to being surrounded by mangrove-fringed shoreline along its western boundary and its proximity to Key Largo. Consequently, though the water is not turbid, spectral light attenuation is relatively high in Blackwater Sound. Collado-Vides and Robledo (1999) found similar results in a study testing the photosynthetic efficiency of different growth forms of *Caulerpa*. Species were found to be either sun-tolerant or shade-tolerant, with the shade-tolerant species performing best in mangrove-fringed lagoons and growing in the understory of seagrasses. This would likewise explain the presence of *Caulerpa* in the westernmost basins with the most lush seagrass meadows. The seagrass is providing the shade necessary for photosynthetic efficiency.

Caulerpa has become a pest species in many areas around the world; it's invasive ability leading to the decline of native plants as it takes over the benthic habitat (Vroom and Smith 2001). Although it has demonstrated its ability for rapid colonization, it remains in low to moderate densities in Florida Bay. Vroom and Smith (2001) pointed out this phenomenon in the Hawaiian Islands as well but also could not offer an explanation for what keeps *Caulerpa* in check in its native habitats while it grows rampantly in others.

Drift Macroalgae

Sargassum contributed very little to the overall macroalgal biomass in Florida Bay. Although relatively rare, it was most commonly observed in the more northern basins including Rankin, Whipray, Madeira, Eagle, and Blackwater (FIG. 18). No significant change in density was recorded in any of the basins. Frequency patterns however indicated an increased presence during spring sampling periods.

Drift reds, on the other hand, are common in Florida Bay. They are composed of several genera but *Laurencia* is the most commonly observed. Virnstein and Carbonara (1985) reported peak densities during spring months in the Indian River Lagoon, FL, with decreased abundance during the summer. Drift red algae have been observed within every FHAP basin at relatively high densities. They have also exhibited very distinct seasonal density and frequency patterns, both higher in the spring (FIG. 19). The only basin in which a significant increase in density occurred was Madeira Bay. Otherwise, densities appear to have oscillated around varying means within each basin. Consistently high densities were observed in Blackwater Sound and Madeira Bay. Frequencies of occurrence at or near 100% were recorded in Madeira and Calusa, and frequencies above 50% were recorded often in other basins. The general lack of spatial pattern is most likely attributed to their drifting habit and the fact that they may either originate in seagrass beds as epiphytes before they become too large and break off, thereby being reported often tangled in seagrass, or they may originate outside of seagrass beds and consequently be observed elsewhere (Bell and Hall 1997). Their impressive biomass causes them to break free of whatever substrate they are attached to and subsequently move with wind and currents. They were often observed in areas with deep prop scars, filling in the disturbed areas.

Although mean Braun-Blanquet values may be similar for two different macroalgae, such as *Batophora* and drift reds, it is important to note that similar values of cover do not indicate similar values for actual biomass. 100% cover of *Batophora* and 100% cover of *Laurencia* would yield vastly different dry weights if removed and dried. The oscillating cover values for the drift reds represent a great deal of biomass in the system. While nutrient limitation, particularly phosphorus, generally limits macrophyte biomass in oligotrophic waters typical of tropical to subtropical carbonate systems due to adsorption of phosphorus to calcium carbonate (Hines and Lyons 1982, Short et al. 1985), Lapointe (1989) reported the unique ability of some species of drift algae to access this nutrient. *Laurencia poitei* has a high activity of the enzyme alkaline phosphatase. High alkaline phosphatase activity allows *Laurencia* to utilize alternative phosphorus sources such as dissolved organic phosphorus compounds characteristic of fish and invertebrate excretions. This gives *Laurencia* a competitive advantage over other macrophytes in Florida Bay and may help explain the very high spring values and frequencies observed. This may also explain its increase in Madeira Bay. Madeira is located in northern Florida Bay and is directly affected by Everglades run-off. Although the Everglades are known to strip available phosphorus from the water before it enters Florida Bay (Brand 2002, Fourqurean and Zieman 1992, Rudnick et al. 1999), this area is also characterized by mangroves fringing the basin. Mangroves provide cover and refuge for many fish as well as hunting and nesting grounds for birds. It is possible that this area may have high nutrient availability in the form of nitrogen and organic phosphates from these two sources. Indeed, water quality data obtained from the SERC website for Terrapin Bay, just west of Madeira Bay in the northern fringe along the Everglades, does show low N:P trends and relatively high concentrations of total phosphorus (~0.035 ppm).

An increased nutrient regime in Florida Bay is an area of concern (Lapointe et al. 1994, Robblee et al. 1991, Fourqurean and Robblee 1999, Boyer et al. 1999) not only because of its impact on seagrass ecology (Fourqurean and Rutten 2003, 2004) but also because of its association with increased epiphyte loads and increased production of large drift algal mats (Irlandi et al. 2004). Large mats of drift algae contribute to the primary production in the bay and provide food and habitat for a number of invertebrates (Holmquist 1994). Positive and negative aspects of their presence within seagrass beds have been reported and appear to be a function of residence time. Irlandi et al. (2004) found that temporary and moderate cover of seagrass by drift algae is not harmful. Aboveground biomass of seagrass in Biscayne Bay (southeast Florida), decreased by about 25% after three months of consecutive macroalgal cover but belowground biomass was not affected: possibly reflecting the resource partitioning capabilities of *Thalassia*.

No further decline in aboveground biomass was detected after six months of macroalgal cover. In fact, Irlandi et al. (2004) also found that drift algae may benefit the underlying seagrass by scouring seagrass blades leading to a decrease in epiphytes. Epiphytes not only shade seagrass blades, they decrease the exchange of nutrients and gases across the leaf surface and are consequently detrimental to seagrass growth (Gacia et al. 1999). Epiphytes increase when nutrient supply increases although this may be moderated by the presence of grazers (Gacia et al. 1999). In this sense, drift macroalgae may also prove to be beneficial under certain conditions.

Moderation in time of drift algae cover is most likely key to the survival of underlying seagrasses. Holmquist (1997) found decreased seagrass biomass under drift algae after prolonged periods of exposure: generally greater than six months. The seasonal fluctuations in density and distribution observed by FHAP and the inherent fact that drift algae drift may prevent them from persisting in a single area for that long.

Norkko and Bonsdorff (1996) reported more detrimental affects associated with drifting macroalgae. Zoobenthic community structure under drift algal mats deteriorated rapidly and they found a 10-fold increase in phosphorus in the water due to nutrient fluxes during hypoxia, leading to localized enhanced eutrophication. This study took place in the northern Baltic Sea; not a subtropical calcium carbonate system with a high affinity for phosphorus ions, and therefore the results may not be applicable to Florida Bay.

The first objective of this study was to determine the extent of macrophyte change in the bay since 1995 and to determine the extent of intra- versus inter-annual variation. To summarize, *Thalassia* increased in density in the western and central basins with coincident increases in water clarity in that region. *Halodule* and *Syringodium* increased also, although densities of *Halodule* seem to have reached a plateau by the time this portion of the study ended. These increases reflect a continued recovery from die-off and the subsequent chronic turbidity, from 1991-1995, in these basins. *Batophora* and *Acetabularia* both showed a general increase in the central and eastern basins in both density and frequency. *Acetabularia* exhibited a great deal of seasonal variation. As both are psammophytic and need a hard substrate to attach to, their distribution may be attributed to sediment type. *Halimeda* increased in the westernmost basins and may have played a role in the successional sequence of the redevelopment of those beds. *Penicillus* increased in northern basins but maintained higher densities in Twin and Blackwater. Otherwise their densities didn't exhibit a great deal of change and they were found in highest densities in areas with conditions to which they were most adapted. *Caulerpa* did not increase significantly in any of the basins but did maintain a consistent presence in Blackwater Sound as well as in the western basins – areas where decreased light intensity from either CDOM (Blackwater) or canopy shading (western basin seagrass beds) allowed for higher photosynthetic efficiency. *Sargassum* was of minimal significance in the bay and did not exhibit any significant change. The drift reds were most abundant in the spring and exhibited a great deal of seasonal variability and only increased in density in Madeira Bay. Their high biomass may be attributed to their ability to utilize DOP not readily available to other macroalgae.

Overall macrophyte density and frequency increased in the bay. The seagrasses increased in the western and central bay, and macroalgae either didn't change or increased. The increase in seagrasses and *Halimeda* in the western basins suggests that those basins are recovering or have fully recovered from the late 1980's die-off and subsequent turbid conditions. Seagrasses oscillated but did not increase or decrease overall in density in the more eastern basins which were not heavily affected by the die-off. Macroalgae, however, did increase in these basins and trends suggest that this increase has not yet plateaued. Because there was no change in substrate availability, as there was due to the die-off in the western basins, this increase in macroalgae may be attributed to an increase in nutrient availability. Water quality data from the SERC website for the basins included in FHAP show an overall decreasing trend in Total Organic Nitrogen and Total Phosphorus since 1991 when data collection was initiated. More substantial decreases are noted in the western basins. The decrease in water column nutrients over time, concurrent with an increase in macrophytes, possibly suggests that the nutrients are being removed by the macrophytes and may not necessarily imply that nutrient input is actually decreasing.

Another point to consider is the global trend in overfishing and the reduction of herbivores on marine macrophytes. Overfishing and the decline of keystone species have been implicated as the cause for several major ecosystem shifts (Jackson et al. 2001). Removal of herbivorous fish and the 1983/84 mass mortality of the sea urchin *Diadema antillarium* (Hughes et al. 1985) have been linked to increases in macroalgal cover on Caribbean coral reefs (Hughes et al. 1999, Williams and Polunin 2001, Knowlton 2001), an affect independent of changes in nutrient availability. The importance of top-down (herbivores) as opposed to bottom-up (nutrients) control on macrophyte abundance (Thayer et al. 1984, Silliman and Zieman 2001, Silliman and Bertness 2002, Heck and Valentine 1995, Valentine and Heck 2001) has been emphasized in several studies. From salt marshes to seagrass meadows to coral reefs, it has been well documented that herbivores play an important role in controlling community structure. The disturbed condition of Florida Bay following the seagrass die-off in 1987 was implicated in a direct decline in fisheries as well as decreased viability as nursery habitat. Recreational and sport fishing also remove 700,000 – 80,000 fish from the bay per year and until the early 1980s, commercial fisherman were also allowed access to the bay, although this was limited after 1950 when the bay was added to Everglades National Park (Tilmant 1989). Large grazers are also significantly reduced in number in the bay (Thayer et al. 1984, Jackson et al. 2001). The lack of herbivores in Florida Bay, as opposed to increased nutrients, may therefore have contributed to the increase in macroalgal abundance that has been detected. It should also be considered that these two factors may be having a synergistic affect on macroalgal abundance.

Another major objective of this study was to gain an insight into community structure and in doing so to determine if seagrass dynamics are correlated with macroalgal dynamics. Spearman Rank Order Correlation Analysis as well as non-Metric Multidimensional Scaling were used for this purpose. These analyses indicated that *Thalassia* abundance was generally negatively correlated to all other macrophytes, although several exceptions did occur. Macroalgae, as a group, were generally positively correlated with one another, although like *Thalassia*, exceptions did occur. Correlations that weren’t repeated over time may just be an artifact of the extensiveness of the data set and be due to chance from repeated statistical testing and may not reflect actual biological correlations.

In most basins, *Thalassia* was repeatedly negatively correlated with *Halodule*, *Batophora,* and *Acetabularia*, and *Batophora* was repeatedly negatively correlated with *Halodule*. This may reflect the competition between *Thalassia* and *Halodule* and also suggests that *Batophora* is competing with *Halodule*. Perhaps *Batophora* is rivaling *Halodule* in its ability to rapidly colonize an area without *Thalassia*. *Acetabularia* and *Batophora* were almost always positively correlated – a reflection of their use of similar substrates, as were *Penicillus* and *Halimeda*. *Caulerpa* on the other hand was often positively correlated with *Thalassia*, which, as previously discussed, is most likely due to its affinity for shade provided by *Thalassia*.

The negative correlation between *Thalassia* and *Halodule* was seen in all basins on many occasions and most often in the western basins in which the greatest increases in seagrass abundance were observed. *Thalassia* was also negatively correlated to *Syringodium* in the western basins, repeatedly so in Rabbit and Johnson where densities increased dramatically over the years. Negative correlations also indicate that *Halodule* and *Syringodium* were competing as pioneers in these basins.

The drift reds were the most dynamic of the macroalgal groups observed in Florida Bay. Both their densities and frequencies fluctuated greatly in all of the FHAP study basins and there was really no clear determination of whether their presence was positively or negatively associated with seagrass density. Correlation analysis yielded alternating positive and negative correlations as they have the capacity to either become entangled in thick seagrass beds, or they may become trapped in depressions where seagrass die-off has occurred. In either case, whether the correlation was positive or negative had more to do with the basin or season in question. The only basin in which drift reds and seagrasses were consistently correlated was Rankin Lake, and here the relationship was a positive one.

The use of nMDS in conjunction with density overlays was perhaps the most effective way to express the overall trend in the associations observed between total seagrass and total macroalgae cover. Based on these analyses, it is apparent that despite some overlap in spatial extent, the distributions of the two plant groups are generally mutually exclusive. Where there is a dense cover of seagrass, there is generally less macroalgae, and where there is a dense cover of total macroalgae, there is generally less seagrass. This further supports the Spearman correlation analysis as *Thalassia* was generally negatively correlated to most macroalgae. This negative association does not appear to be having a negative impact on the ecosystem however. The increase in macroalgae did not prevent a seagrass recovery in the western and central basins, nor did it result in a decline in seagrass density in any of the other basins.

In terms of fisheries habitat assessment, FHAP has yielded a long-term comprehensive picture of the dynamics in Florida Bay over the past decade. The results presented here show that the western basins have been more highly variable with respect to both physical variables and macrophyte change, and that in very general terms, all macrophytes have either remained constant over time (though *Thalassia* oscillated up and down in density every few years), or increased over time. The only overall decline that took place over the period of study was that of *Thalassia* in Rabbit Key Basin, and despite this decrease, Rabbit Key Basin was the basin with the most lush and continuous seagrass bed in any of the FHAP study basins. This decline may also represent an artifact resulting from the near 100% cover of this species at the onset of FHAP sampling. With this type of cover the only type of change possible is a reduction.

While *Batophora* was perhaps the ‘dominant’ macroalgae observed in Florida Bay in terms of general ubiquity, the drift reds were the most variable and may be the best indicator of ecosystem health. Several studies have already been conducted linking them to a number of fluctuating variables (Josselyn 1977; Valiela et al. 1997; Biber 2002), and they are highly recognizable in the field, so would make convenient sample targets. Their density as well as frequency showed significant variations. They also perhaps have more ecological impacts, both positive and negative, on seagrass beds. And they have the ability to be more similar to seagrasses in terms of basic biomass than the other macroalgal groups commonly observed in Florida Bay.

In conclusion, although distribution and density of some of the macroalgal groups have increased in some of the FHAP study basins since spring 1995, the data suggest the macroalgal increase is not of bloom proportions or consequence. Some plants are increasing in density and distribution, but negative impacts on the ecosystem as a result of these increases (such as a decline in seagrass cover resulting from an increase in macroalgae cover) were not observed. While variables such as salinity, depth, temperature, and water clarity varied from basin to basin, within each basin they were relatively constant, with the exception of water clarity. Increased water clarity over the course of the study, especially in the western basins, may have influenced macrophyte dynamics in those basins, but the lack of experimental or mechanistic data reduces the possibility of elucidating a specific cause and effect scenario. Most likely, the increases in abundance observed in the western basins reflected recovery following the dramatic losses from both the seagrass die-off of 1987-1990 and the persistent turbidity over the period from 1991-1995.

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CHAPTER 2

BAY-SCALE CHANGES IN THE DISTRIBUTION AND DENSITY OF FLORIDA BAY MACROPHYTES: 1995- 2004

INTRODUCTION

Florida Bay is an ecologically and economically valuable resource located between the southern tip of Florida and the Florida Keys. A rapid and extensive die-off of the climax seagrass species, *Thalassia testudinum*, in western and central Florida Bay in the summer of 1987, and the subsequent decline in ecosystem health, lead to concern among the public, scientists, and managers of south Florida. The Fisheries Habitat Assessment Program (FHAP), a spatially and temporally expansive monitoring effort, was initiated in response to this concern (Durako et al. 2002). The goals and purpose of the assessment program are to establish temporal and spatial baselines and to document changes over time regarding the distribution and abundance of the bay's seagrasses and macroalgae.

Eighteen bi-annual FHAP sampling events were conducted between 1995 and 2004 and resulted in a long-term and robust dataset of density and cover information for five species of seagrasses, six genera of macroalgae, and one group of macroalgae defined as "drift reds." The twelve groups of macrophytes examined constitute all of the seagrasses, as well as the majority of macroalgal groups observed within Florida Bay. The drift reds are composed primarily of *Laurencia* spp., but the group also encompasses other Rhodophytes with the ability to become unattached and move about freely with the currents. The five seagrasses are *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*, *Halophila engelmanii*, and *Ruppia maritima*. The macroalgae include:

Acetabularia, *Batophora* (which may also include *Dasycladus*), *Caulerpa*, *Halimeda*, *Penicillus*, and *Sargassum*, as well as the previously mentioned drift reds.

Chapter One of this text reports results of analysis performed at the basin-scale. These results showed that, between 1995 and 2004, seagrasses recovered in the previously denuded western basins. The seagrass recovery followed a successional sequence in which calcareous green algae (primarily *Halimeda* and *Penicillus*), as well as the pioneering seagrasses *Halodule wrightii* and *Syringodium filiforme*, increased in distribution and abundance until *Thalassia* re-established dominance. Once *Thalassia* became more dominant, *Halodule* declined in density, but *Syringodium* and the calcareous greens appeared to still be increasing at the conclusion of this portion of the monitoring program. This sequence has been documented in other seagrass beds subjected to disturbance events (Zieman 1982, Fourqurean and Rutten 2003). Data also showed that macroalgae were highly variable in abundance but generally increased throughout the east-central and northeastern bay where the die-off did not take place. Seagrasses in these basins showed no significant change over the time course of study. The increase in macroalgae may be attributed to both bottom up (increased nutrients) and top down forces (loss of grazers), although neither possibility was conclusively accepted due to lack of experimental evidence.

Seagrasses and macroalgae were, in general, negatively correlated and exhibited spatially exclusive distribution patterns when analyzed using Spearman Rank Order Correlation Analysis and non-Metric Multidimensional Scaling. Because all seagrasses showed either static, oscillating, or increasing density trends, it was not concluded that the increase in macroalgae was having a negative effect on seagrasses, regardless of negative correlations and exclusive spatial patterns.

This chapter takes a broader approach and assesses the variability in distribution and abundance of Florida Bay macrophytes from a bay-scale perspective. Only by pooling data across the bay, and weighting data based on the area of each basin, is it truly discernible whether a particular macrophyte is increasing or decreasing in density within Florida Bay as a whole.

The specific objectives of this portion of the study were to determine to what extent macrophyte distribution and density have changed at the bay scale since 1995, to determine the extent of intra-annual versus inter-annual variation in distribution and density of each macrophyte at the bay scale, to gain insight into macrophyte community dynamics between macroalgae and seagrasses, and to determine if any correlations exist among macrophyte density and distribution and the following abiotic factors: depth, water clarity (termed visibility here), temperature, and salinity.

METHODS

Florida Bay is approximately 2200 km^2 in area and shows trends in physical characteristics from east to west as well as from north to south. Because Florida Bay is open to the Gulf of Mexico along its western perimeter, the western basins are more well mixed by tidal flushing and consistently exhibit more marine characteristics. They also generally have greater water depths and deeper sediments (Zieman et al. 1989). Central and eastern basins, however, have restricted circulation, are less affected by tidal flushing and are therefore less well mixed. They are typically shallower and are more likely to exhibit periods of hypersalinity (Lee et al. 2002, McIvor et al. 1994). Central and eastern basins are also directly down-stream from Taylor Slough and the C-111 canal basin and routinely receive varying amounts of freshwater from these sources, making them more likely to exhibit periods of lowered salinity. Sediment depth decreases on a west to east gradient (Zieman et al. 1989).

Data Collection

Ten basins in Florida Bay were selected for this long-term monitoring project. From East to West, the sampled basins are Blackwater Sound (Blk), Eagle Key Basin (Eag), Madeira Bay (Mad), Calusa Key Basin (Cal), Crane Key Basin (Crn), Whipray Basin (Whp), Rankin Lake (Rnk), Twin Key Basin (Twn), Rabbit Key Basin (Rab), and Johnson Key Basin (Jon) (Chapter One, FIG. 1).

Each basin was partitioned into approximately 30-35 tesselated hexagonal grid cells from which sampling station locations were randomly chosen. This allowed for sampling to take place quasi-evenly over the entire area of interest but still meet assumptions required for randomness – and resulted in a total number of sampling stations generally ranging from 300-315 per sampling event. It also scaled the sampling effort to the size of each basin, and was well-suited for interpolation and mapping of the data. At each station, latitude, longitude, salinity, temperature, depth, secchi depth, and light attenuation (profiles at every other station) were determined. Depth and secchi depth were used to calculate water clarity (or percent visibility) using the following formula:

$$\% \text{ Visibility} = (\text{secchi depth} / \text{depth}) \times 100$$

Both seagrass and macroalgal cover were visually quantified at each station within four $0.25m^2$ quadrats, by diving from a small vessel. Quadrats were haphazardly placed around the boat in a N, E, S, W orientation, always at least 3m apart. Cover/density values were assigned to each macrophyte present based on a modified Braun-Blanquet scale (Chapter One, Table 2) (Mueller-Dombois and Ellenberg 1974).

Frequency of occurrence and density for each species or plant group at each sample station was calculated using the following formulas:

Frequency = # of stations where observed/total # of stations

Density = sum of B-B scale values/ total # of quads

Sampling began in the spring of 1995 and took place twice a year until 2004, when the project was extended to include sixteen more basins and became the South Florida Fish Habitat Assessment Program. Spring sampling took place in late May/early June, and fall sampling took place in mid-October, exact dates depending on housing and boat availability within Everglades National Park. Due to interruptions in funding, sampling did not take place during the fall of 2001 nor during the fall of 2004. Consequently, within this text, the results from eighteen sampling periods are reported.

The twelve groups of macrophytes examined constitute all of the seagrasses, as well as the majority of macroalgal groups observed within Florida Bay. Other macroalgae have been observed with some regularity, such as *Anadyomene* and *Udotea*, but they comprise a very small proportion of the dataset and were found to skew the results of statistical analysis. Data, however, remain available for future analysis should any of these taxa become more abundant and widespread within Florida Bay.

Statistical Methods

To fulfill the objectives of this study the following null hypotheses were constructed and tested using the statistical methods given below.

H_o1: Intra-annual variability in the distribution and density of each macrophyte is not greater than inter-annual variability at the bay scale, nor have these two parameters changed since 1995.

In order to express trends in the inter- and intra-annual variability of each macrophyte at the bay scale, data from the ten FHAP study basins were pooled and bay-scale average densities, as well as frequencies of occurrence, were computed for each sampling event.

Bay-scale averages were computed for a given macrophyte by taking the average Braun-Blanquet value for each basin and multiplying it by the area of the basin (see Table 23 for basin sizes) and adding the product of each basin together for one overall bay mean. This was done to normalize data based on size differences among basins. Graphs containing both histograms of density over time and line/scatter plots of frequency of occurrence over time were created for each macrophyte to visualize the results of these analyses.

H_o2: The distribution and density of macroalgae are independent of those of the seagrasses at the bay scale.

Table 23. Area in square kilometers of each FHAP basin.

Basin	km^2
Blackwater Sound	28.57
Calusa Key	26.44
Crane Key	15.3
Eagle Key	62.27
Johnson Key	14.23
Madeira Bay	12.39
Rabbit Key	31.8
Rankin Lake	5.83
Twin Key	54.13
Whipray Bay	21.79

Spearman Rank Order Correlation analysis was applied to the pooled Braun-Blanquet densities of all macrophytes from each basin to examine potential bay-scale relationships. Correlations were considered significant at α # 0.05. This analysis was completed for each season and year to determine if relationships changed seasonally and annually, or remained consistent over time. To show differences and trends in seasonal correlations, a matrix was created to show both spring and fall correlations simultaneously. The matrix is divided diagonally by macrophyte abbreviations. Correlations that occurred during spring sampling are located in the upper right triangle, whereas correlations that occurred during fall sampling are located in the lower left triangle. The years in which the correlation occurred are represented by the last digit of that year (ie. 1995 = 5). If the relationship was found to be positive, the cell is not shaded. If the relationship was found to be negative, the cell is shaded light gray. If the relationship changed from year to year, a plus or minus sign in front of the year indicates whether it was a positive (+) or negative (-) correlation, and the cell is left unshaded. Only years in which significant correlations were found are included in the cells. All correlation analyses were done using SAS statistical software (Cary, NC).

Multivariate techniques were used to create Bray-Curtis dissimilarity matrices for each sampling event. When comparing samples, the Braun-Blanquet data were square-root transformed to account for macrophytes that occurred at both high and low densities. Stations that were devoid of plants were not included in the creation of the matrices, although rare or absent macrophytes were included.

These matrices were then used for non-metric multidimensional scaling (nMDS), which is a method of ordination that positions sample units according to associations among species (McCune and Grace, 2002). Specifically, nMDS is a method of indirect gradient analysis that uses an iterative procedure to successively refine positions of points within a chosen number of dimensions until they satisfy the dissimilarity relations between samples (Clark and Warwick, 2001).

Sample ordination plots were created to allow for the grouping of basins based on community assemblages and to determine the extent of uniformity across the bay. In essence, if two sample stations were similar in their species composition and density of each macrophyte present, they were located near one another on the plot. If they did not have any macrophytes in common, they will be located farther apart. Likewise, a plot resulting in a tightly clustered ordination indicates a high degree of uniformity among basins. If there is a large amount of spread across an ordination plot, there is a small degree of uniformity.

Density overlays were used in conjunction with the ordination plots. Total seagrass (sum of Braun-Blanquet values for each seagrass) and total macroalgae (sum of Braun-Blanquet values for each macroalgae) were shown for each station using gray bubbles, wherein the size of the bubble was relative to the total density value. Spearman Rank Order Correlation analysis was used again to determine if the total seagrass and total macroalgae values for each sampling event were correlated, either positively or negatively, or not at all. Spearman Correlation Coefficients and P-values are shown as an inset in the “Total Seagrass” plot of each set of ordinations. Multivariate analyses (nMDS) were done using PRIMER 5 software (Plymouth Marine Laboratory) and the SAS statistical package was again used for Spearman Rank Order Correlation Analysis (Cary, NC).

H_o3: Changes in macrophyte density are independent of depth, visibility, salinity and temperature.

Along with macrophyte distribution and density data, depth, secchi depth, temperature, and salinity values were also collected at each sampling location. Water column depth and secchi depth were used to calculate percent water visibility, wherein if the secchi depth was visible until half way to the bottom, percent visibility equaled 50%. In order to identify any potential abiotic factors that influenced macroalgal communities, variability in four parameters (depth, visibility, salinity, and temperature) were examined in relation to variations in macrophyte density and distribution using Canonical Correspondence Analysis (CCA). CCA, as opposed to nMDS, is a method of direct gradient analysis. Using direct gradient analysis, sample stations were ordinated according to measurements of environmental factors at those sample stations in order to learn how species were distributed with respect to environmental/physical variables (McCune and Grace, 2002).

CCA constrains an ordination of one matrix by a multiple linear regression on variables in a second matrix. The two matrices form a CCA ordination plot. In this case, one is a station by macrophyte matrix and the other is a station by physical variable matrix. The CCA ignores community structure that is not related to the physical variables and instead, performs an ordination on just the community data. Secondarily, that ordination is related back to the physical variables, allowing an expression of just community gradients followed by an independent assessment of the physical variables and their relative importance (McCune and Grace, 2002).

CCA was applied to the pooled data, once per sampling event. Because samples were from ten different basins within the bay and the values of their response variables were similar within each basin due to spatial proximity, they were treated as covariables. The use of the basins as covariables allowed for this influence to be accounted for in the data and consequently removed from the model (Leps and Smilauer, 2003).

Monte Carlo permutation tests were used to test the statistical significance of the CCA ordinations with respect to the null hypothesis that the species composition is independent from the physical variables. The physical variables were randomly assigned to the individual samples of species composition, ordination analysis was done with the reshuffled data set, and the value of the test statistic was calculated. The significance level of this test was then calculated as:

$$P= (n_x+1)/(N+1)$$

where n_x is the number of permutations where the test statistic was not lower in the random permutation than in the analysis of original data, and N is the total number of permutations (Leps and Smilauer, 2003). All canonical correspondence analyses were done using CANOCO 4.5 software.

RESULTS

Means, Frequencies, and Change

Thalassia is the dominant macrophyte in Florida Bay and it exhibited an oscillating bay-scale trend similar to those seen at the basin scale. The oscillations exhibited two to three year periodicities, increasing and decreasing in mean density in a sinusoidal fashion. There was very little difference in overall *Thalassia* density, however, between 1995 and 2004. Basin scale analysis showed that the majority of dense *Thalassia* beds were observed in the westernmost basins. It was, however, ubiquitous throughout the bay during the study, being observed in 80% to 100% of the approximately 300 to 330 stations sampled during each of the eighteen sampling events (FIG. 62). With the exception of the western basins where *Thalassia* was most dynamic, bay-scale *Thalassia* means showed trends similar to those found in the individual FHAP basins. This indicates that although the western basins were dynamic, those trends were not sufficient to affect overall bay-scale trends.

Thalassia exhibited a high mean density in fall 2000, at which time *Halodule* began to exhibit an overall decline (FIG. 63). While *Halodule* is the second most prominent seagrass within Florida Bay, its bay-scale mean densities were considerably lower than those of *Thalassia*. Note that figure 62 below is on a different scale than the previous graph depicting *Thalassia*, as are the remainder of the seagrass and macroalgae graphs. Following a decline from fall 1995 to spring 1996, *Halodule* density climbed steadily until fall 2000, after which time, it showed a generally decreasing trend. Like *Thalassia*, it was more dense in the western and northern basins, as well as in Blackwater Sound in the east, but was only observed at 20-60% of the sampling stations. Its bay-scale trend resembles the unimodal trend in density over time observed in the western basins (Johnson, Whipray, Rankin, and Rabbit) at the basin-scale, indicating that these basins are driving the bay-scale patterns.

While *Thalassia* varied little in overall density over the years, and *Halodule* increased in density and then subsequently decreased, *Syringodium* was the only seagrass to increase steadily throughout the duration of this study (FIG. 64). It peaked in mean density in spring 2003, but it never exceeded about 20% frequency of occurrence. This increase in density took place in the western basins, particularly in Johnson Key and Rabbit Key Basins, and to a lesser extent, Rankin Lake (Chapter One) and these western basins are responsible for driving the bay-scale trend because *Syringodium* is virtually absent in the other basins. Figure 64 shows that this particular macrophyte, like the other seagrasses, exhibited little seasonal variation in density.

Although the previously mentioned seagrasses were all relatively prominent in Florida Bay, *Halophila* (FIG. 65) and *Ruppia* (FIG. 66) were not. They occurred very rarely and at low densities throughout this study, *Ruppia* even moreso than *Halophila*. When observed, *Halophila* was generally found in the western basins and it was first observed in spring 1997.

The macroalgae exhibited much greater bay-scale variation in density and frequency than the seagrasses. *Acetabularia* showed a high degree of intra-annual change and was seen much more frequently and in higher densities during spring sampling events (FIG. 67). It was relatively sparse until spring 1998, after which time it remained at a somewhat constant densities within both spring and fall sampling events, although these seasonal mean densities were much different from one another. Frequency of occurrence peaked during the most recent sampling event, spring 2004, at nearly 50%. It became much more widespread over the course of the study.

Acetabularia was most frequently seen in Blackwater Sound and Twin Key Basin, where it was also generally more dense. Its bay-scale pattern resembles that seen at the basin scale in Blackwater Sound (Chapter One), although wherever it was seen in

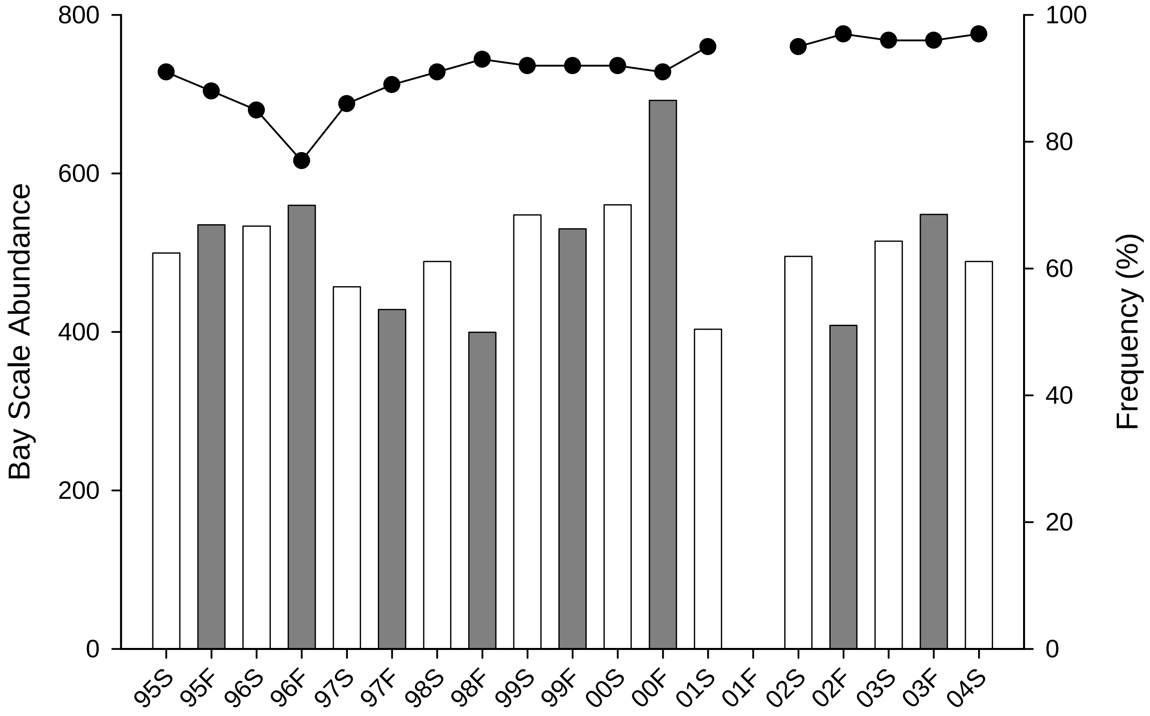


FIG. 62. *Thalassia* bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

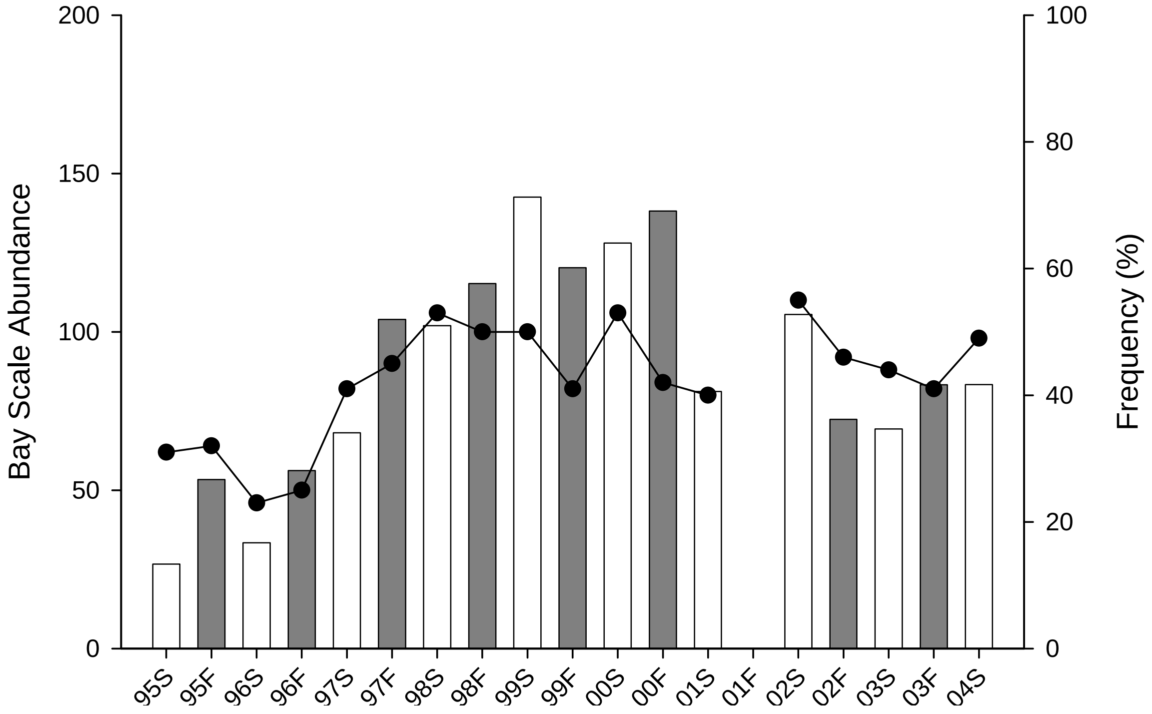


FIG. 63. *Halodule* bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

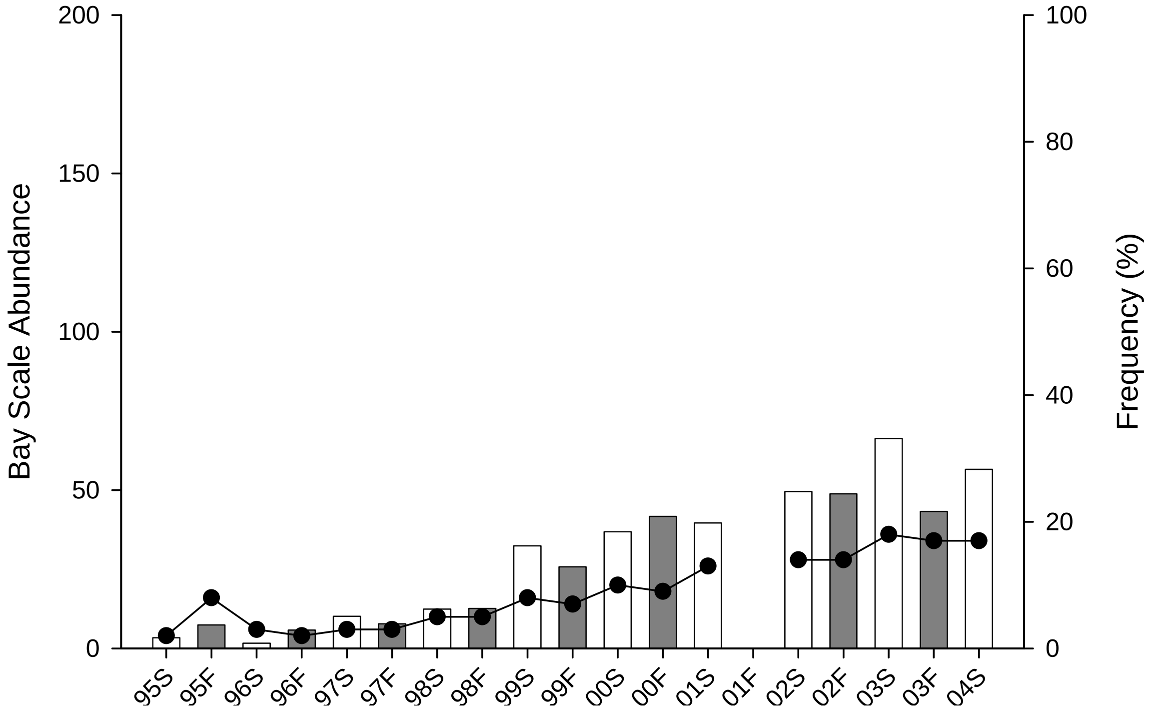


FIG. 64. *Syringodium* bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

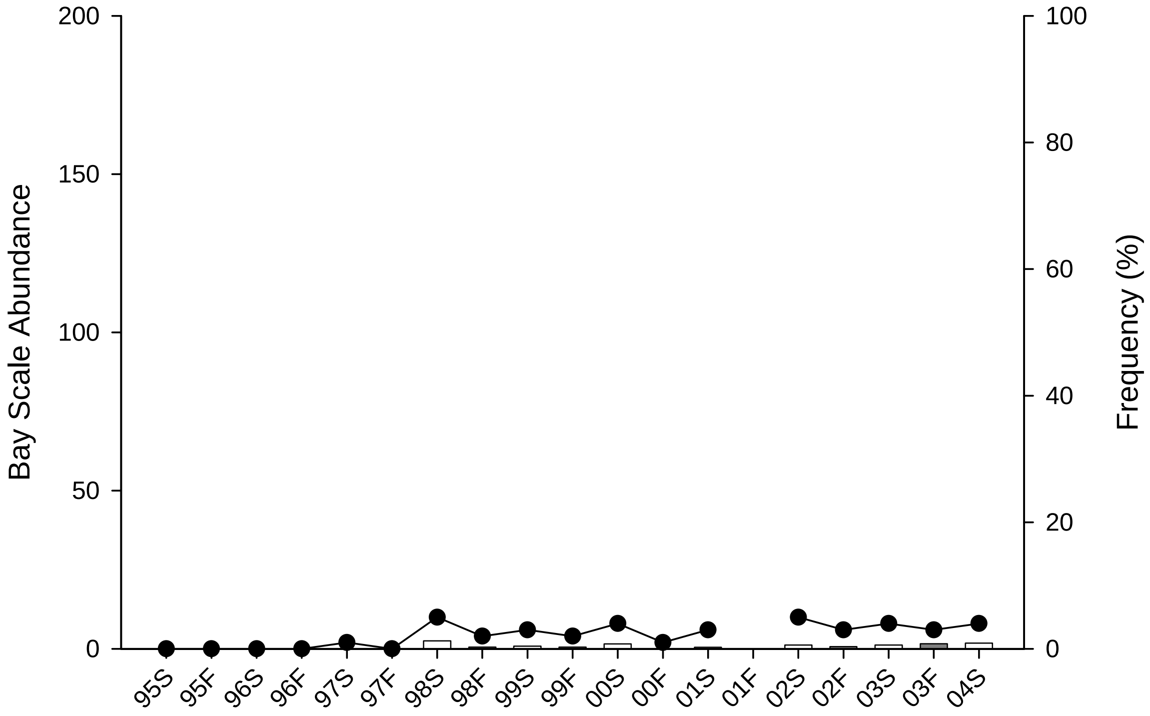


FIG. 65. *Halophila* bay-scale mean densities and frequency of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

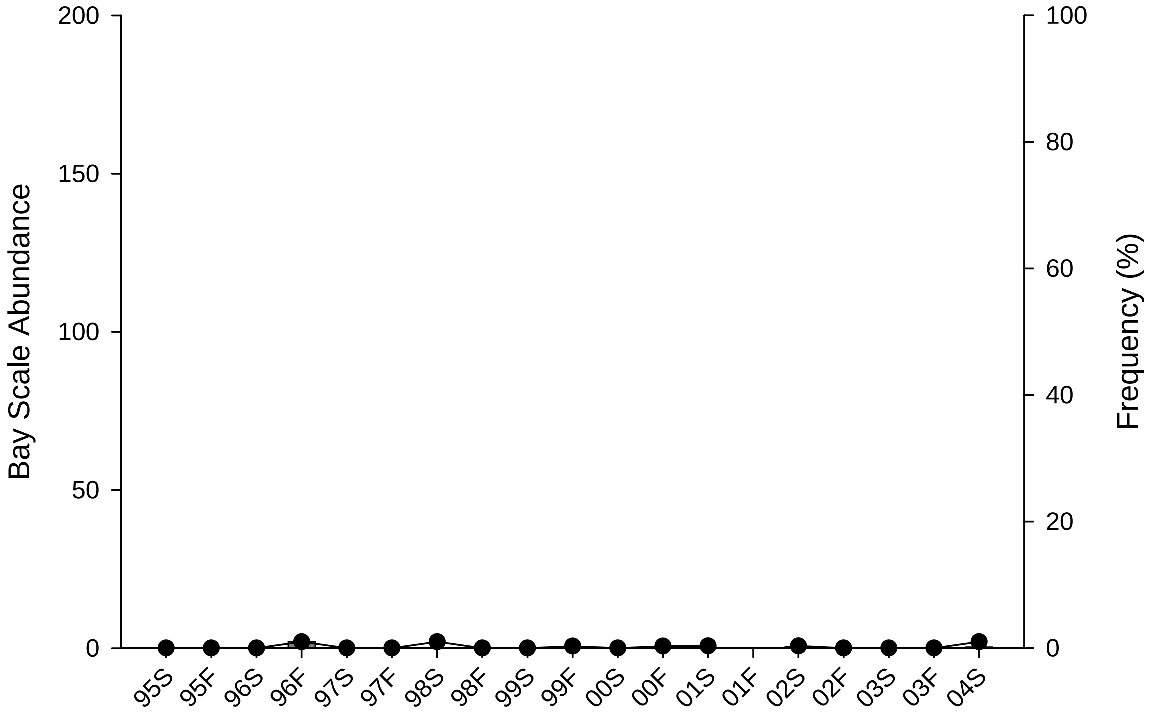


FIG. 66. *Ruppia* bay-scale mean densities and frequency of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

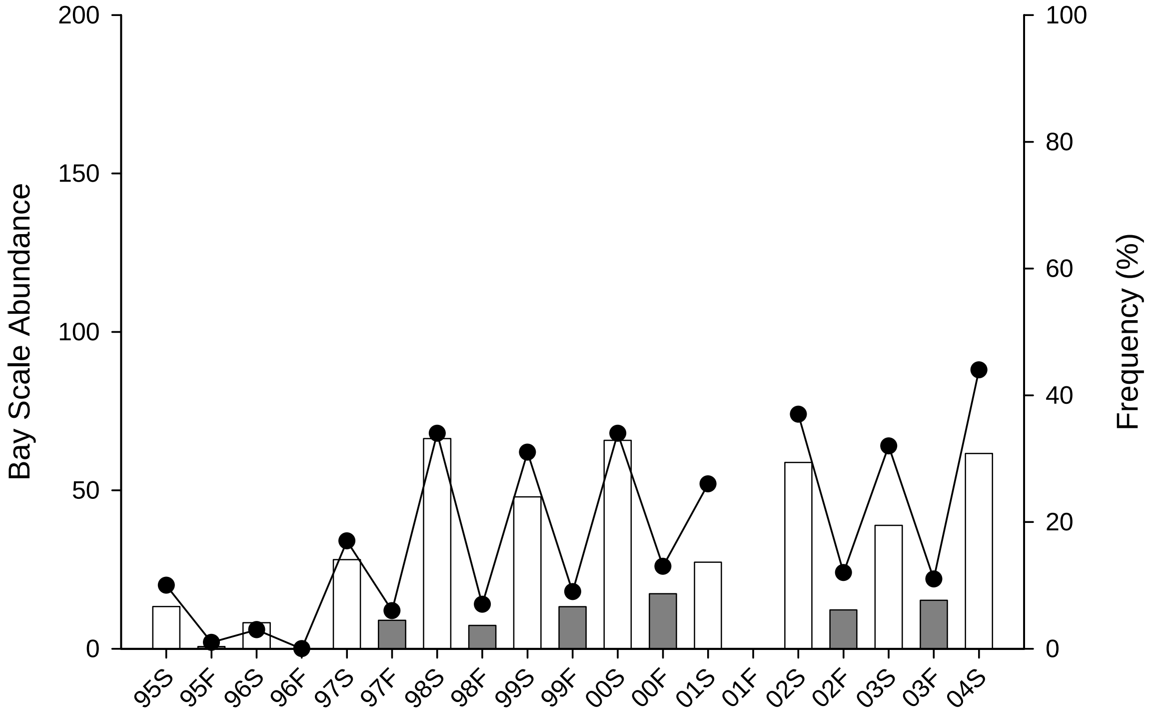


FIG. 67. *Acetabularia* bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

densities and frequencies great enough to register discernable patterns, intra-annual variability, particularly in frequency, was unmistakable.

Batophora showed a dramatic increase in density throughout Florida Bay, following an initial decline from spring 1995 to spring 1996, and was the most prominent macroalgae observed. Unlike *Acetabularia*, it exhibited little intra-annual variation (FIG. 68). By spring 2004, it was observed in over 60% of the sampling stations throughout the bay and was very prominent in Blackwater Sound and Twin Key Basin, though it was also observed at high densities in Eagle, Calusa, and Crane Key Basins, as well as in Whipray Bay. It was observed with some degree of frequency in the western basins, particularly Rabbit Key Basin, but was much more sparse there. Compared to basin scale trends, this bay-scale trend in increasing density and frequency most closely resembles the phenomenon that took place in Blackwater Sound. *Batophora* increased in Eagle, Calusa, and Madeira as well, but not to the great extent seen in Blackwater. Twin and Whipray increased in *Batophora* until about 2000, and then density declined in each.

Caulerpa densities and frequencies changed very little over the course of the study (FIG. 69). It was never observed in more than 15% of the sampling stations, and these were usually located in Blackwater Sound, the only basin in which *Caulerpa* was consistently seen. *Caulerpa* was also observed in Johnson Key, Rabbit Key, and Twin Key Basins and in Rankin Lake, but not consistently (Chapter One).

Halimeda, a calcareous macroalgae, was much more abundant in spring 2004 than in spring 1995 (FIG. 70). It was often recorded in the western basins, as well as in Blackwater Sound, but not often seen in the more central basins, such as Eagle, Calusa, and Crane Key Basins, or in Madeira Bay in the north (Chapter One). From spring 1998 to spring 2001, some intra-annual variation in frequency and density was detectable, although this trend was not discernable before or after this time period. Frequencies tended to be higher during spring sampling and initially declined from spring 1995 to fall 1996. This bay-scale density and frequency pattern most closely resembles that of Johnson Key Basin on the basin-scale, but it is not obviously driven by any one particular basin or group of basins, although Madeira frequency patterns do exhibit some of the intra-annual variability seen at the bay-scale.

Penicillus proved to be quite variable in frequency and density over time at the bay scale, and a general increasing trend was detected in both (FIG. 71). Because of its dynamic behavior at the basin scale as well, and because of its general ubiquity, it does not appear that any one basin or group of basins is driving this bay-scale trend. It is clear from Figure 71 that there was considerably more *Penicillus* in Florida Bay in spring 2004 than in spring 1995 and that it was least abundant during the spring 1996 sampling.

Sargassum fluctuated in both frequency and density over time, and there is some amount of seasonal variability detectable at the bay scale but it did not increase in overall density or distribution over the course of the study (FIG. 72). Seasonal patterns were also seen at the basin scale, particularly in Madeira Bay and Rankin Lake, the only two basins in which it was relatively abundant.

Finally, Figure 73 shows bay-scale density and frequency of occurrence of the drift reds, which based on their high frequencies and densities, were the most dynamic of the macroalgae. The drift reds exhibited a considerable amount of seasonal variability in both frequency and density. Following a decline from spring 1995 to spring 1996, bay-scale density peaked in spring 2000, but frequency of occurrence did not peak until spring 2002, when drift reds were observed in nearly 60% of the sampling stations throughout the bay. Following the peak, drift red density declined. Basin scale trends given in Chapter One are also highly variable both intra- and inter-annually, and no one basin or group of basins seems to have driven this bay-scale variability. Although frequency of occurrence has increased since spring 1995, the density observed in spring 2004 was slightly less than that in spring 1995. Overall, however, it appears that, as of spring 2004, the drift reds have not exhibited an overall change in density compared to the initiation of FHAP.

Overall, most macrophytes increased in density and frequency since the time period of 1995-1996. *Thalassia* exhibited little overall change; *Halodule* and S*yringodium* were both more abundant at the end than at the initiation of FHAP. *Acetabularia* and the drift reds showed the most seasonal variation and *Acetabularia* was much more dense by 2004 than in 1995. *Batophora* showed the most dramatic increase in both density and distribution, followed by *Penicillus*. *Halimeda* exhibited some increase, but not as extensively as *Penicillus*. Neither *Caulerpa* or *Sargassum*, or *Ruppia* or *Halophila* proved to be particularly dynamic macrophytes and have changed very little or not at all since 1995.

Spearman Rank Order Correlations

Spearman Rank Order Correlation analysis of the FHAP Braun-Blanquet cover/density data resulted in many correlations that were seen at the individual basin scale as well as many additional correlations. Only the trends or patterns that were

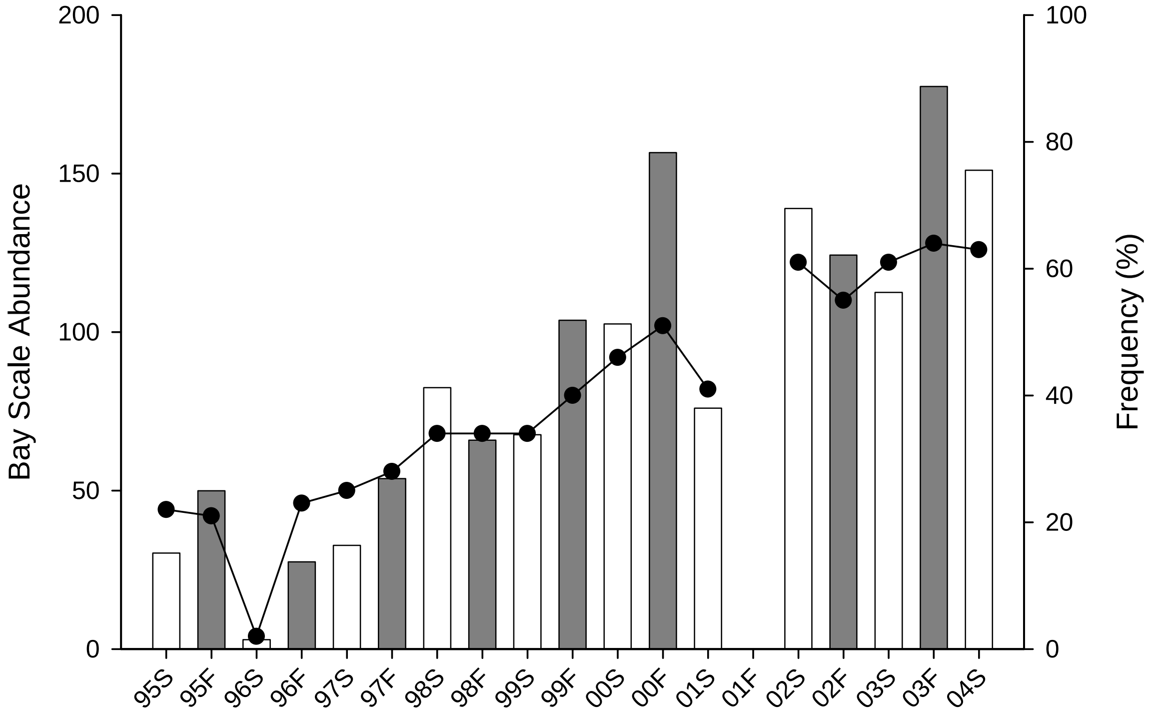


FIG. 68. *Batophora* bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

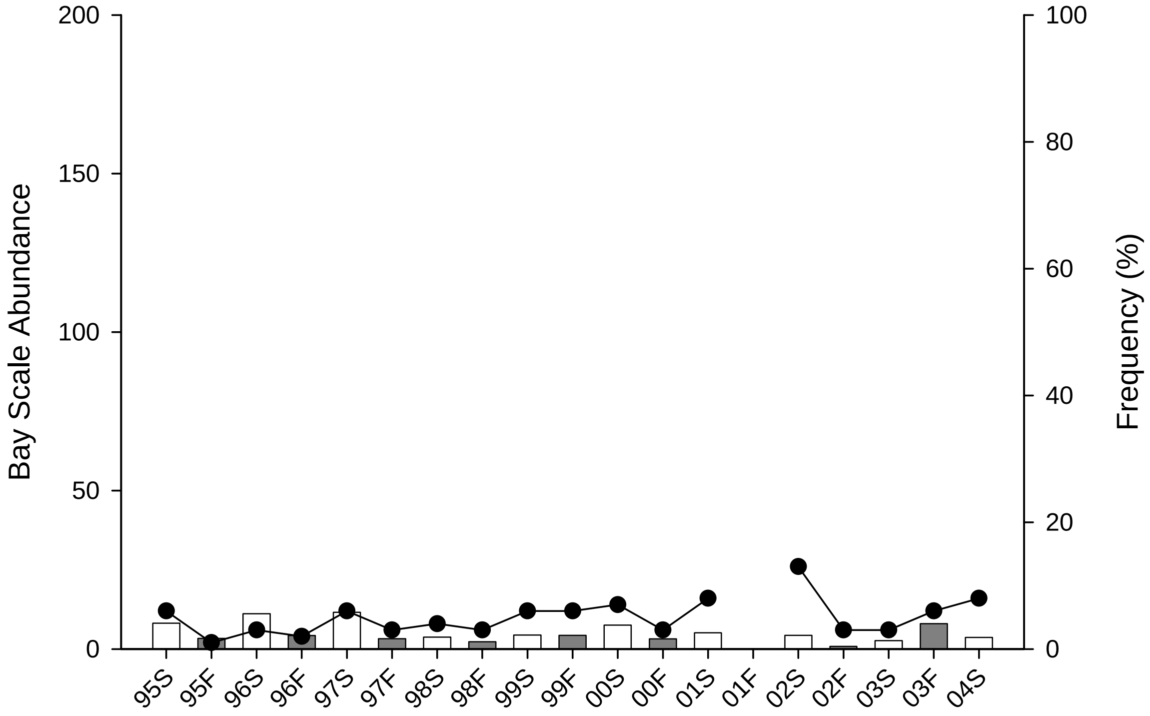


FIG. 69. *Caulerpa* bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

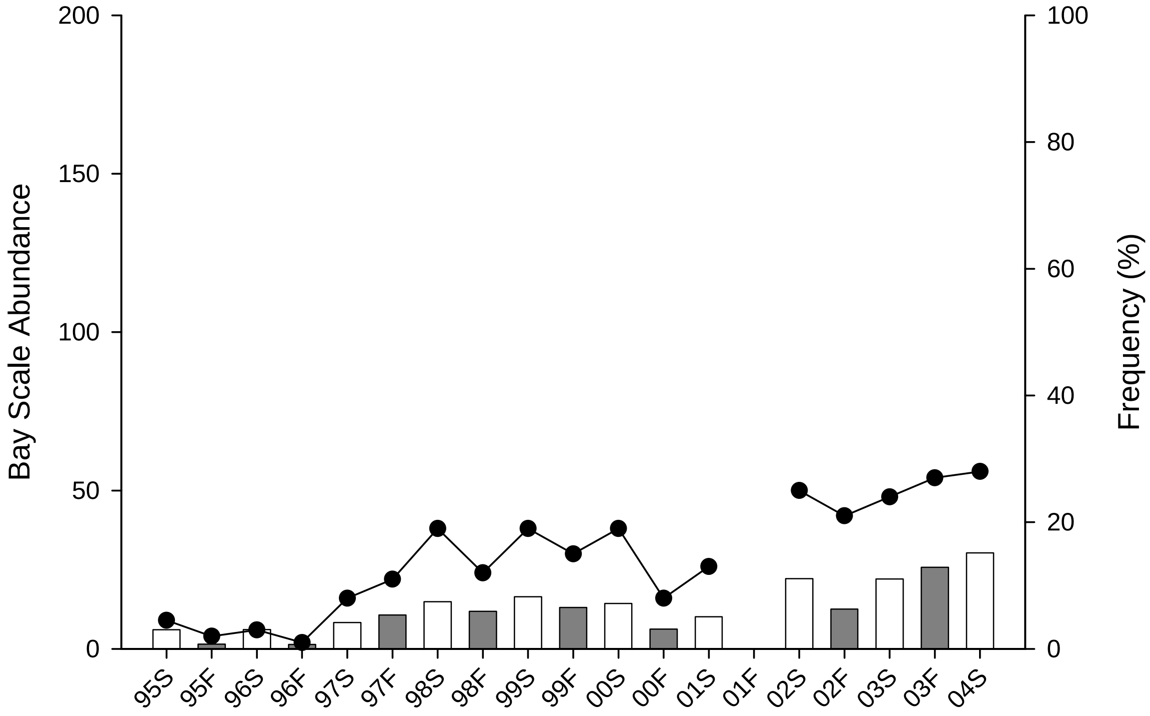


FIG. 70. *Halimeda* bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

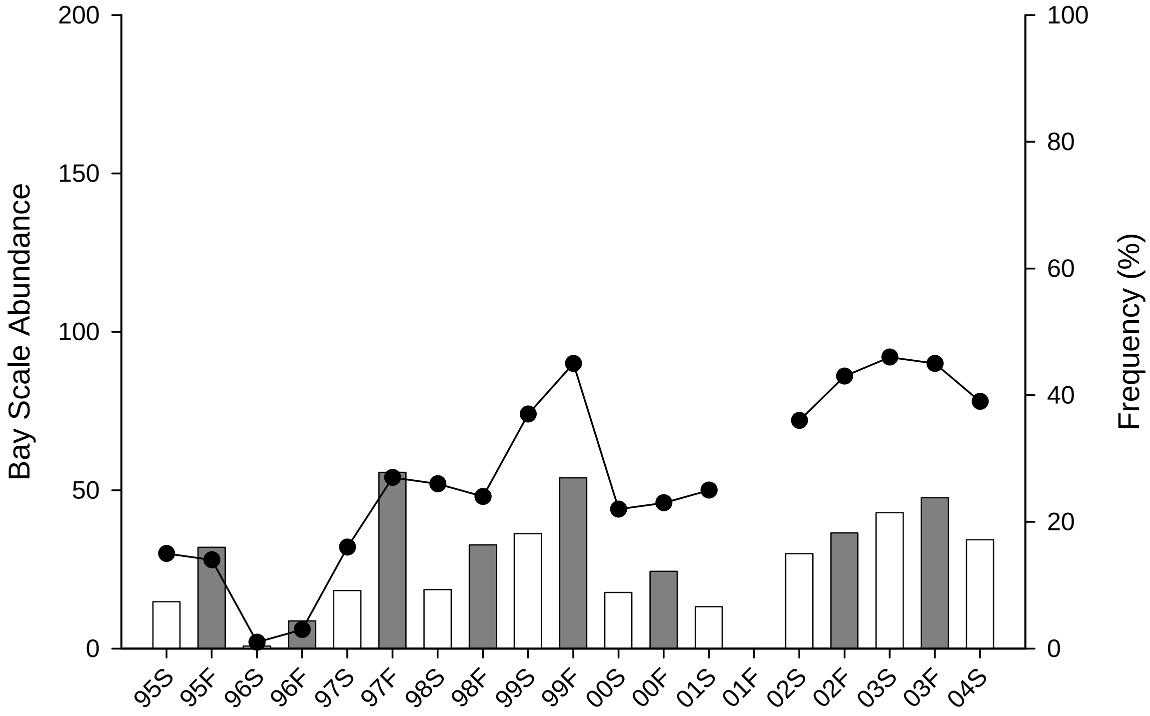


FIG. 71. *Penicillus* bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

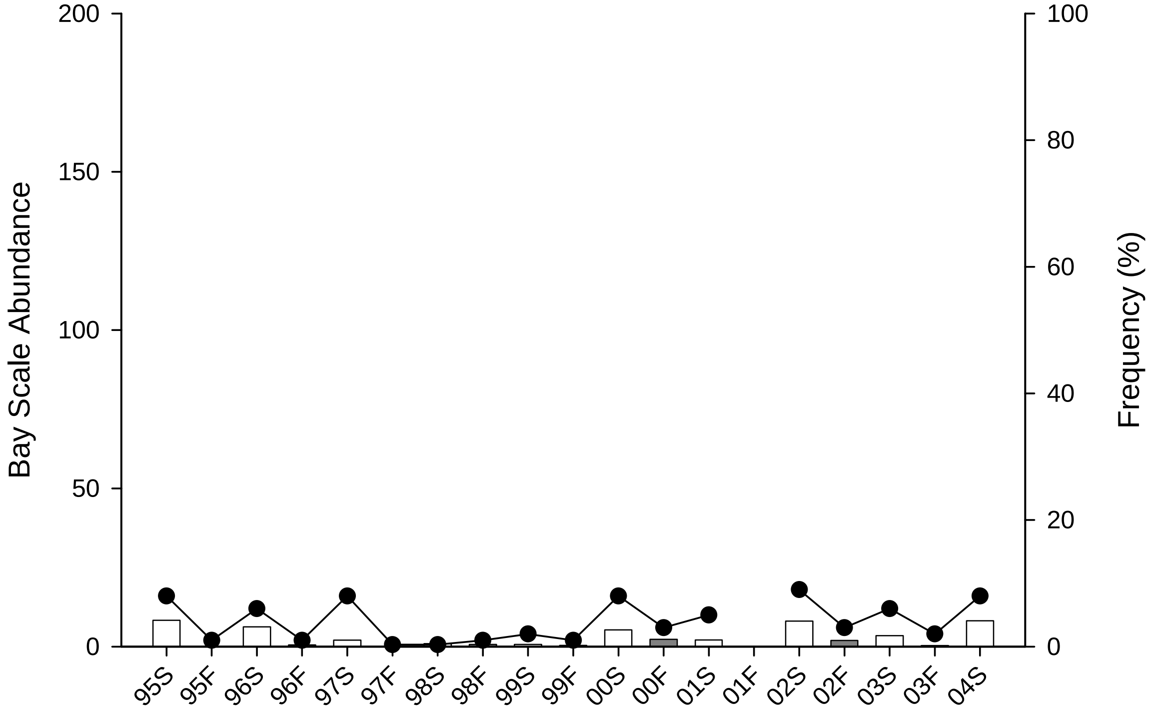


FIG. 72. *Sargassum* bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

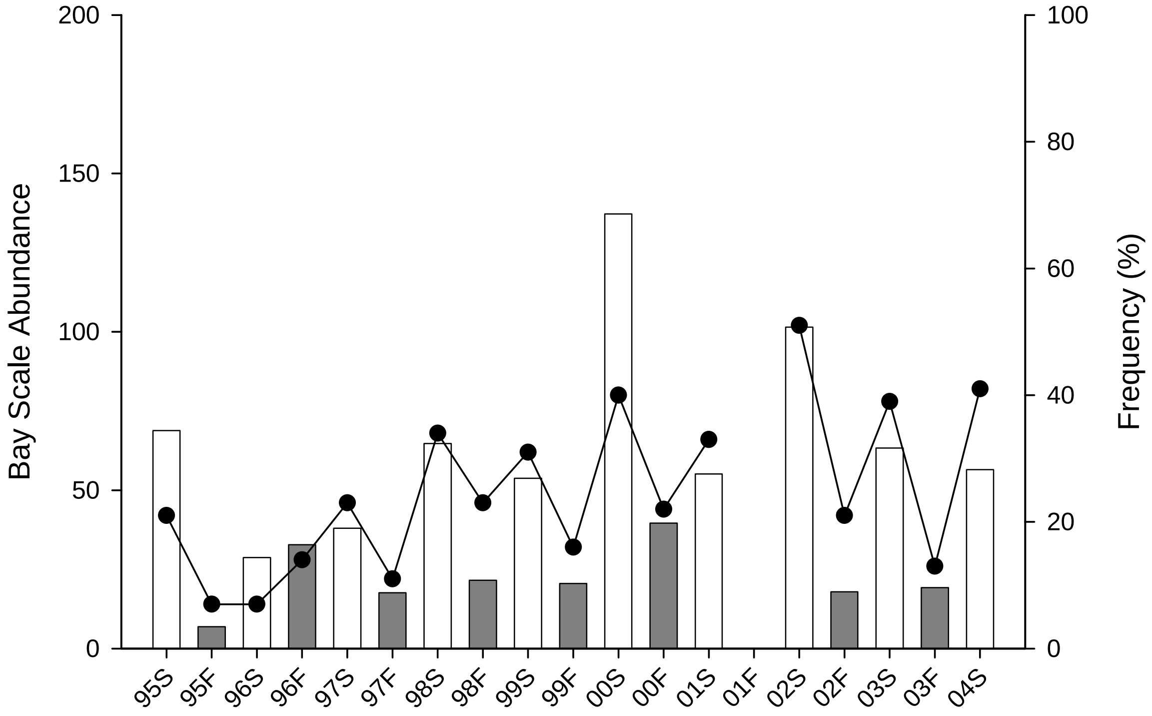


FIG. 73. Drift Red bay-scale mean densities and frequencies of occurrence. Mean Braun-Blanquet density/cover value is on left axis and frequency of occurrence is on right axis. Columns represent consecutive spring (unshaded) and fall (shaded) sampling event means. Points and line represent frequencies of occurrence.

observed repeatedly are considered in the following text, but all correlations are given in Table 24 below.

As was often seen at the basin-scale, *Thalassia* was repeatedly negatively correlated with most of the other macrophytes. It was negatively correlated with *Halodule* during most of the sampling events, as well as with *Halophila* during many spring sampling events. It was shown in Chapter One that *Thalassia* and *Halodule* seem to exhibit a certain degree of resource competition. That they are negatively correlated at the bay-scale as well as the basin-scale indicates that this competition is not limited to certain basins, but is occurring across Florida Bay.

Thalassia abundance was also correlated with *Syringodium* abundance on a few occasions, and this correlation changed from being negative during the earlier FHAP sampling events to being positive during some of the later sampling events. *Thalassia* was also correlated to each of the macroalgae at least once, and as with *Syringodium*, the direction of the correlation changed with both *Batophora* and *Penicillus*.

Thalassia was initially negatively correlated to *Batophora* in spring 1996, but it became a positive correlation by spring 1997. It remained so through spring and fall 1998, and then the two macrophytes were not correlated again until spring 2002, at which time the association had become negative once more and remained negatively correlated throughout the remainder of the study. This pattern between *Thalassia* and *Batophora* was similar to that observed between *Thalassia* and *Penicillus*, with the exception of the initial negative correlation. In the case of *Penicillus*, the two macrophytes were positively correlated during the earlier FHAP sampling events and then became and remained negatively correlated during the later sampling events.

Table 24. Spearman Rank Order Correlations observed between macrophytes in Florida Bay. Top triangle gives spring correlations and bottom triangle gives fall correlations. Years are represented by their last digit, wherein 1995=5, 1996 =6, 2003=3, etc. Shaded cells contain negative correlations and unshaded cells with numbers contain positive correlations. If correlations change, a + or – before the number indicates when that correlation was pos. (+) or neg. (-).

	Tt	*Hw*	*He*	*Sf*	*Rm*	*Ace*	*Bat*	*Cau*	*Drd*	*Hal*	*Pen*	*Sar*
Tt	***Tt***	5678902	890234	-8-9 +4	4	5601234	-6 +7+8 -2-3-4	724	03	56780	+5+7 -2-3-4	24
Hw	5678903	***Hw***	8901234	8901234	8	-2	78901234	790124	503	678901234	4	5723
He	3	89023	***He***	8034	4	1	890234	0124	+9 -0-2-3	70234	24	9034
Sf	-7-0 +2	5789023	8023	***Sf***	12	0124	8901234	901234	+8 -0-2-3	1234	2	
Rm					***Rm***	4		14				4
Ace	023	2		23		***Ace***	5678901234	5634	56790123	56789014	789034	
Bat	+7+8 -2-3	5789023	23	789023		589023	***Bat***	+5 -9-0-1-2-4	5702	+5+6+7 -2-3-4	5789	73
Cau	53	903	03	5903			0	***Cau***	+9 -4	6801234	81234	0124
Drd		+5 -0		+5 -0	9	789023	6780		***Drd***	+6+7 -2	2	6712
Hal	673	6789023	023	023		7893	+7 -0-2-3	789023	789	***Hal***	7901234	3
Pen	+7 -0-3	-5 +9+0		7		7890	5789	78903	82	789023	***Pen***	-5-7 +3
Sar			02	2	9	578		3	7	703		***Sar***

Thalassia exhibited consistent negative associations with *Acetabularia*, *Caulerpa*, the drift reds, *Halimeda*, and *Sargassum* during spring sampling events. These associations were not as consistent, however, or were not observed at all, during fall sampling events.

Unlike *Thalassia*, *Halodule* was positively correlated with the other seagrasses during many samplings. It was positively correlated with *Halophila* and *Syringodium* repeatedly, which were also repeatedly positively correlated with one another.

While *Halodule* was positively associated with *Halophila* and *Syringodium*, it was negatively associated with *Batophora* on many occasions, as were *Halophila* and *Syringodium* during both spring and fall sampling trips. On the other hand, these three seagrasses were very often positively correlated with both *Caulerpa* and *Halimeda* and these relationships were seen during both spring and fall sampling events. *Halodule* was only positively correlated to the drift reds once, during fall 1995 sampling, after which time all correlations between the two macrophytes were negative. *Halophila* and *Syringodium* were often correlated to the drift reds, but the association changed from positive during the early sampling trips to negative during the more recent sampling events.

Ruppia was only occasionally correlated to any of the other macrophytes and with the exception of one year in which it was negatively associated with *Thalassia*, these correlations were always positive.

In general, as was seen at the basin-scale, the macroalgae were positively correlated to one another. A few exceptions were observed. Besides one positive correlation with *Caulerpa* during spring 1995, *Batophora* and *Caulerpa* were often negatively correlated. *Batophora* was also correlated to *Halimeda* on many occasions, and these correlations switched from being positive early in the course of the study to being negative later in the study.

Acetabularia was positively correlated with all other macroalgae on several occasions, although only during spring sampling events with *Caulerpa* and only during fall sampling events with *Sargassum*. *Batophora* was likewise repeatedly and positively correlated with the drift reds and with *Penicillus*, but it was also negatively correlated to *Sargassum* twice. *Caulerpa* was positively correlated to both *Halimeda* and *Penicillus*, which were very often positively correlated to one another. *Caulerpa* and the drift reds were also often both positively correlated to *Sargassum*.

As was seen at the basin scale, the overall results of Spearman Rank Order Correlation Analysis indicate a negative association between *Thalassia* and most other macrophytes, as well as general positive correlations among the macroalgae.

Non-Metric Multidimensional Scaling

Non-metric multidimensional scaling (nMDS) applied to data pooled for the entire bay, in conjunction with “Total Seagrass” and “Total Macroalgae” density overlays, showed much the same basic results as were given at the basin scale in Chapter One. Ordination plots for each sampling event are seen in Figures 74 (Spring 1995) through 91 (Spring 2004) below, and show, in general and with some amount of overlap, that where there is a great deal of seagrass, there are limited amounts of macroalgae, and visa versa. In this chapter Spearman Rank Order Correlation Analysis was applied to

Total Seagrass and Total Macroalgae densities to determine if this separation was statistically significant.

nMDS of spring 1995 data (FIG. 74) showed that most of the stations were somewhat uniform at the bay scale, although it must be taken into account that there is some clustering taking place that is not discernible based on the large number of samples included in the ordination. Some stations are clearly separated from the overall cluster, and these include many stations from Blackwater Sound, some from Whipray Bay and Rankin Lake, and a few from Crane Key Basin and Madeira Bay. Total Seagrass and Total Macroalgae overlays indicate that there is some degree of spatial separation between the two groups, and this separation was significant and negatively correlated, as shown by the Spearman Correlation Coefficient (-0.19436) and P-value (0.0004) given in the lower right hand corner of the top ordination plot. In addition, the Total Macroalgae ordination plot shows greatest abundance at the Blackwater Sound stations.

During the following fall 1995 (FIG. 75), while there was much more seagrass than macroalgae observed in the bay, a difference in the spatial distribution was not as evident. Macroalgae were generally observed in the same areas as seagrass, only at lower densities. High abundances of macroalgae were observed at several Rankin Lake and Twin Key stations, in addition to Blackwater Sound. Although the Spearman correlation coefficient was negative (-0.06670), the two groups were not found to be significantly correlated (P-value = 0.2283). There is more spread between the samples, suggesting that the bay was less uniform than it was the previous spring. More distinct station clusters are visible, as are the stations which are separated from the large central cluster. Also visible is an artifact of the ordination procedure itself: the arch effect. The arch effect only affected a few of the samples and is a result of the algorithm's attempt to compress the ordination along a given axis into the confines of the two-dimensional space available. Arch effects were seen in several of the ordinations, but because they are statistically insignificant and do have any biological significance, they will not be discussed further.

Spring 1996 analysis did yield a significant and negative correlation between total seagrass and total macroalgae wherein the Spearman C.C. = -0.13099 and the P-value = 0.0193 (FIG. 76). As with spring 1995, there is a great deal of clustering with some stations separated from the main group, most of which are from Blackwater Sound, Rankin Lake and Eagle Key Basin. High macroalgae abundances were observed at several Eagle Key stations.

Fall 1996 ordination (FIG. 77) was more clustered than the previous fall, but once again did not yield a significant correlation between the two macrophyte groups, although the Spearman C.C. was negative (C.C. = -0.09232 and P-value = 0.0998). Several central basin stations in addition to Blackwater Sound stations were outliers.

Spring 1997 (FIG. 78) did not yield an even marginally significant correlation between total seagrass and total macroalgae (C.C. = 0.04929 and P-value = 0.3758). The ordination plot and overlays show that there was a great deal of overlap in the density and distribution of the two groups of macrophytes.

Inspection of the ordination plot for fall 1997 (FIG. 79) shows that there are distinct basin clusters – groups of stations from the same basins, separating out. The groups are relatively close to one another in sample space, but the clustering does indicate similarity among stations within basins and dissimilarity between within-basin stations and stations located farther away in sample space. While it would appear that the fall 1997 ordination and density overlays would yield a negative Spearman C.C. and significant P-value, the two groups of macrophytes were once again not found to be significantly correlated (C.C. = 0.02258 and P-value = 0.6856), although from the overlays it is still discernible that where there is a great deal of seagrass, there is little macroalgae, and where there is more macroalgae, there is less seagrass although moderate densities of both groups are evident at several stations within Blackwater, Johnson and Twin Key Basins.

Total seagrass and total macroalgae overlays show that the two groups are generally mutually exclusive in their spatial distribution for the next several sampling events, but they were not significantly negatively correlated again until spring 1999 when the Spearman C.C. = -0.11497 and the P-value = 0.0418 (FIG. 82). During the sampling events leading up to that time (spring 1998, FIG. 80; fall 1998, FIG. 81), the basins clustered together relatively closely, with several stations from Blackwater Sound, Eagle Key Basin, and Whipray Bay often seen as outliers on the plots. By spring 1999 (FIG. 83), the basins were still relatively clustered, but the overlays show a very definite distinction between the two groups, and they continue to do so for the next several sampling events. Fall 1999 (FIG. 83), spring 2000 (FIG. 84), and fall 2000 (FIG. 85) all yielded a significantly negative correlations between the seagrasses and macroalgae.

Data from the spring 2001 (FIG. 86) sampling event, however, yielded an extremely tight ordination plot with only a few stations from Whipray Bay, Calusa, Eagle, and Johnson Key Basins on the perimeter of the cluster. Total seagrass and total macroalgae overlapped a great deal and consequently a significant correlation was not observed. This tightly clustered ordination indicates that there was a great deal of uniformity in the distribution and density of macrophytes during this sampling period, which was still intact the following spring 2002, but to a lesser extent (FIG. 87). Total seagrass and total macroalgae densities correlated negatively at that time (C.C. =-0.34594 and P-value <.0001) and did so for each of the remaining sampling events during fall 2002 (FIG. 88), spring 2003 (FIG. 89), fall 2003 (FIG. 90) and spring 2004 (FIG. 91).

Table 25 summarizes the results of the total seagrass and total macroalgae Spearman Correlations. Although the two macrophyte groups were only negatively correlated during two of the earlier FHAP sampling trips, the density overlays often indicate some degree of spatial separation between them, whether it was significant or not. During the more recent years, however, the mutually exclusive nature of the spatial distributions of the two groups became regularly statistically significant. Overall, this spatial separation was significant during eleven of the eighteen sampling events.

Canonical Correspondence Analysis

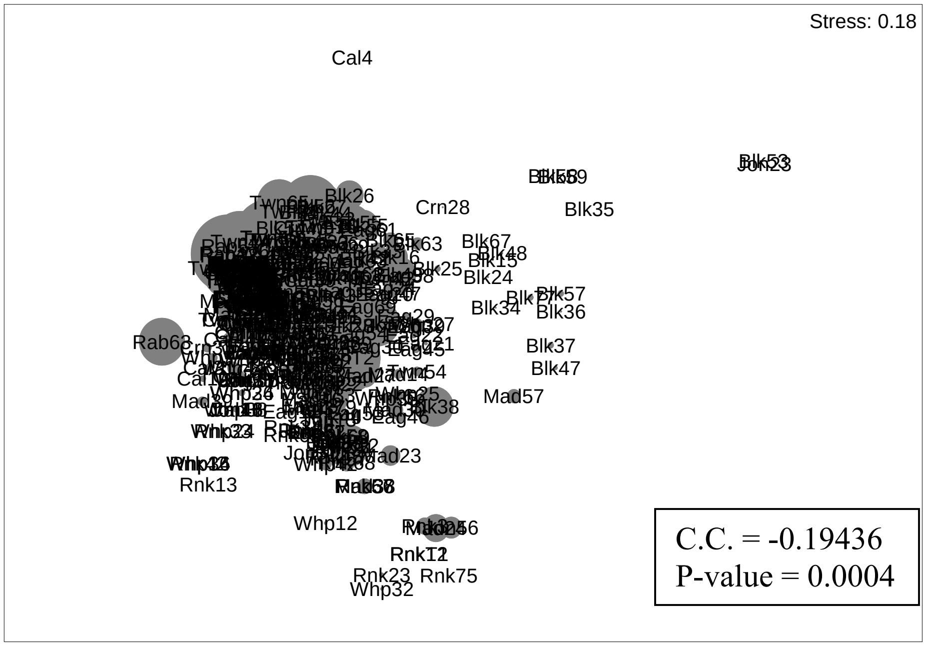
Canonical Correspondence Analysis (CCA) was used to determine which, if any, of the environmental/physical variables, collected as part of the FHAP data set, had a significant effect on the distribution of macrophytes within Florida Bay. Significance was determined by Monte Carlo Permutation tests. Results of these tests are summarized in Table 26 below. Figures 92 through 101 are the CCA plots for each year of FHAP sampling. CCA plots resulting from analysis of spring sampling are on top, and results of fall sampling are on bottom, with the exception of the years 2001 and 2004 when only spring sampling took place. The length of the vectors shown on each plot is relative to the

TABLE 25. Significance of Spearman Correlation between Total Seagrass and Total Macroalgae during each FHAP sampling event.

Sampling Event	Spearman C.C.	P-value
Spring 1995	-0.19436	0.0004*
Fall 1995	-0.0667	0.2283
Spring 1996	-0.13099	0.0193*
Fall 1996	-0.09232	0.0998
Spring 1997	0.04929	0.3758
Fall 1997	0.02258	0.6856
Spring 1998	0.08305	0.1395
Fall 1998	-0.10339	0.066
Spring 1999	-0.11497	0.0418*
Fall 1999	-0.24478	<.0001*
Spring 2000	-0.25638	<.0001*
Fall 2000	-0.41969	<.0001*
Spring 2001	-0.08508	0.1325
Spring 2002	-0.34594	<.0001*
Fall 2002	-0.22411	<.0001*
Spring 2003	-0.24614	<.0001*
Fall 2003	-0.43026	<.0001*
Spring 2004	-0.33065	<.0001*

indicates statistical significance at $\alpha \leq 0.05$

Spring 1995: Total Seagrass



Spring 1995: Total Macroalgae

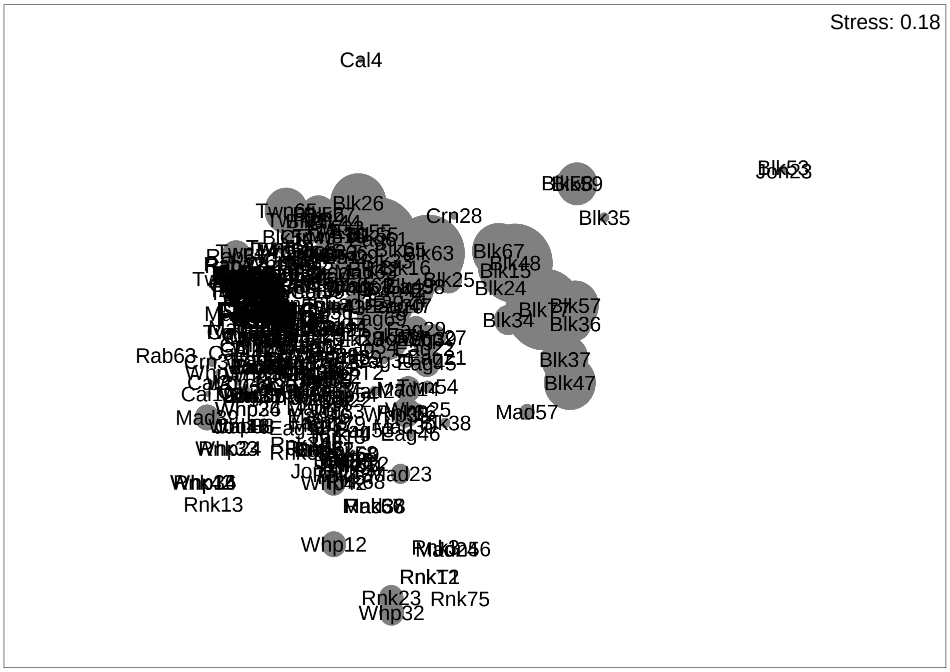
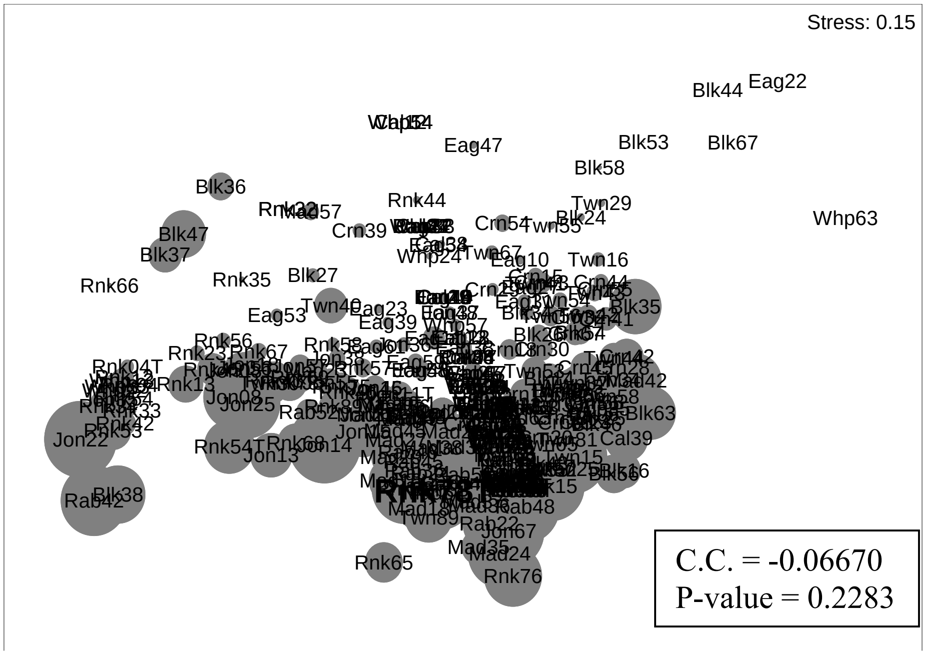


FIG. 74. Florida Bay Spring 1995 nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Fall 1995: Total Seagrass



Fall 1995: Total Macroalgae

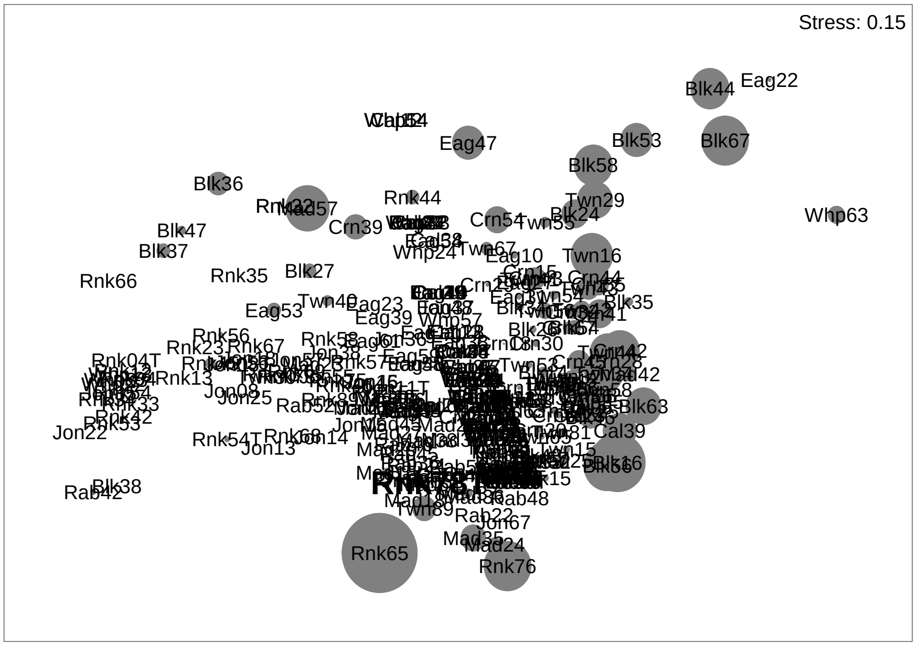
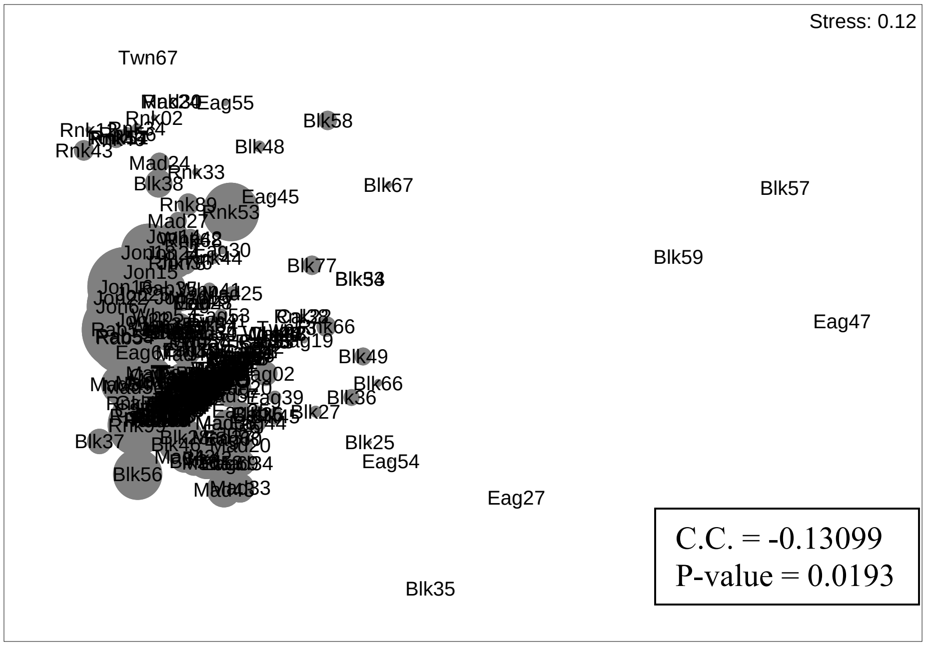


FIG. 75. Florida Bay Fall 1995 nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Spring 1996: Total Seagrass



Spring 1996: Total Macroalgae

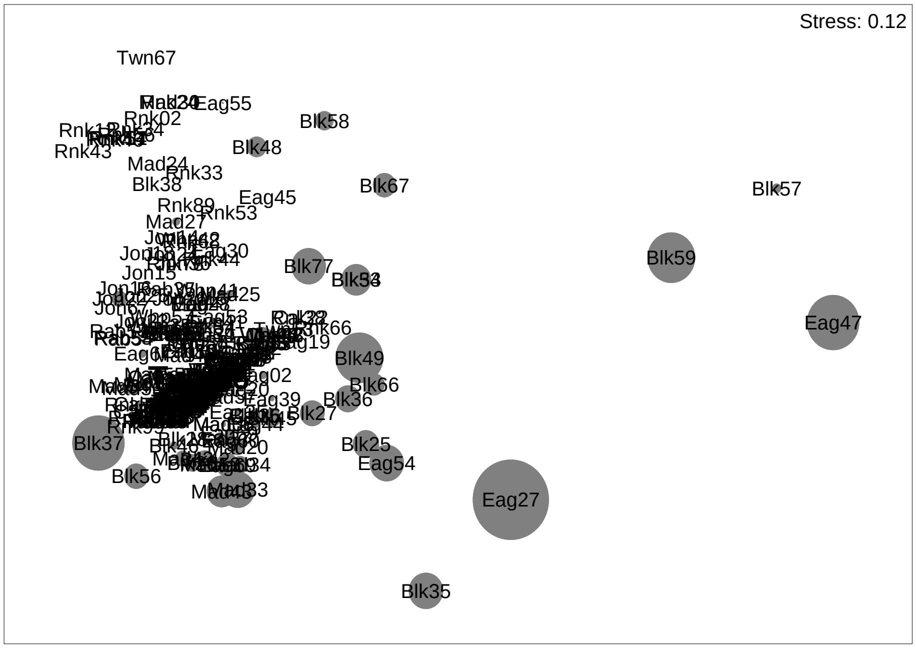
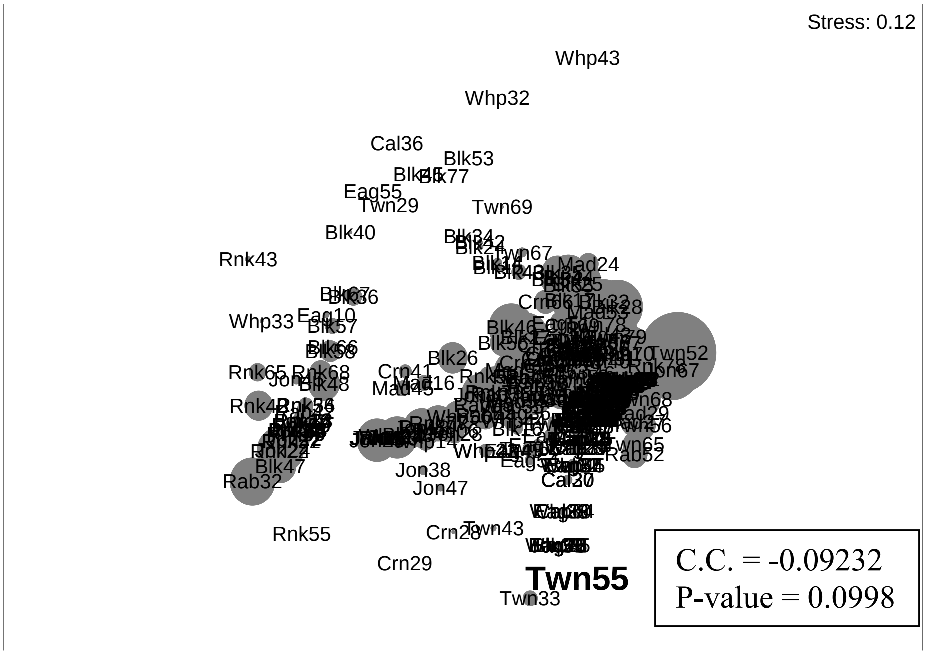


FIG. 76. Florida Bay Spring 1996 nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Fall 1996: Total Seagrass



Fall 1996: Total Macroalgae

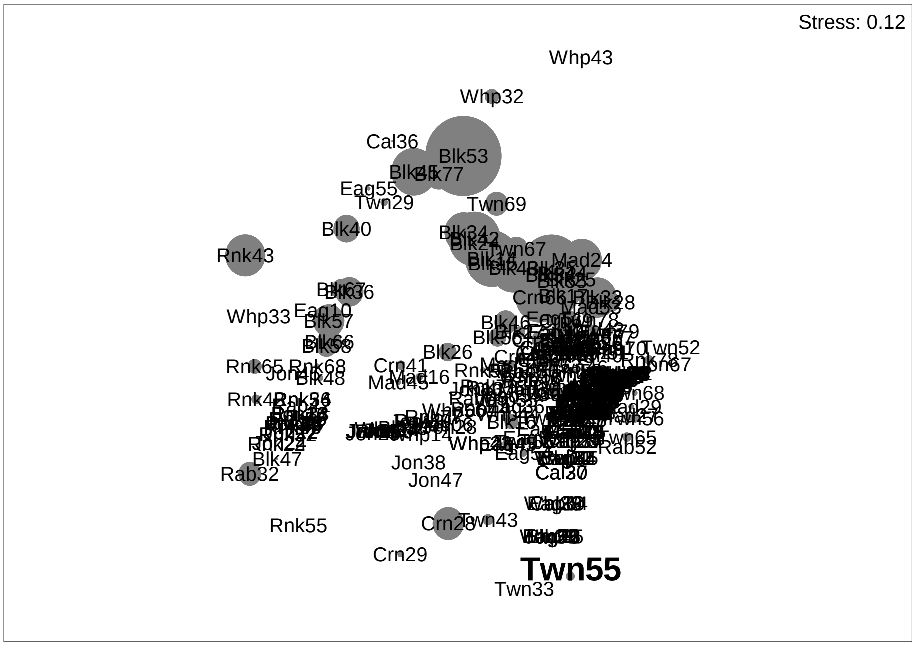
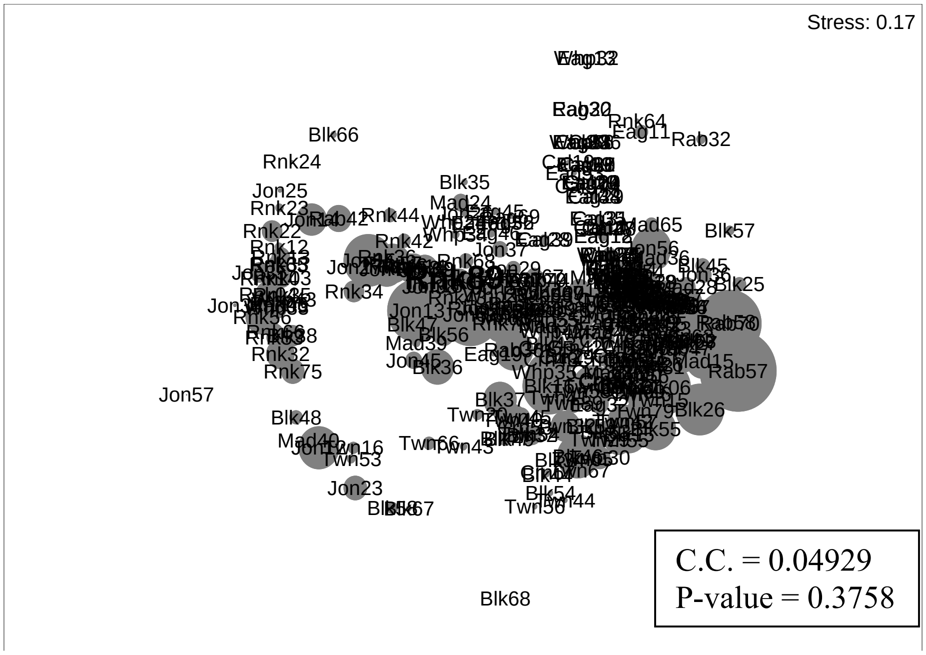


FIG. 77. Florida Bay Fall 1996 nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Spring 1997: Total Seagrass



Spring 1997: Total Macroalgae

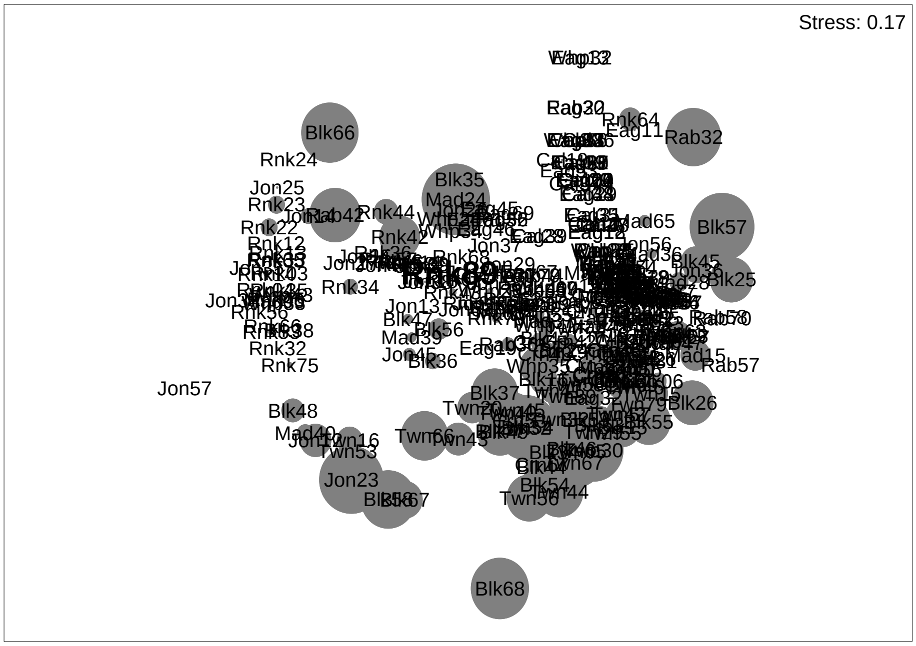
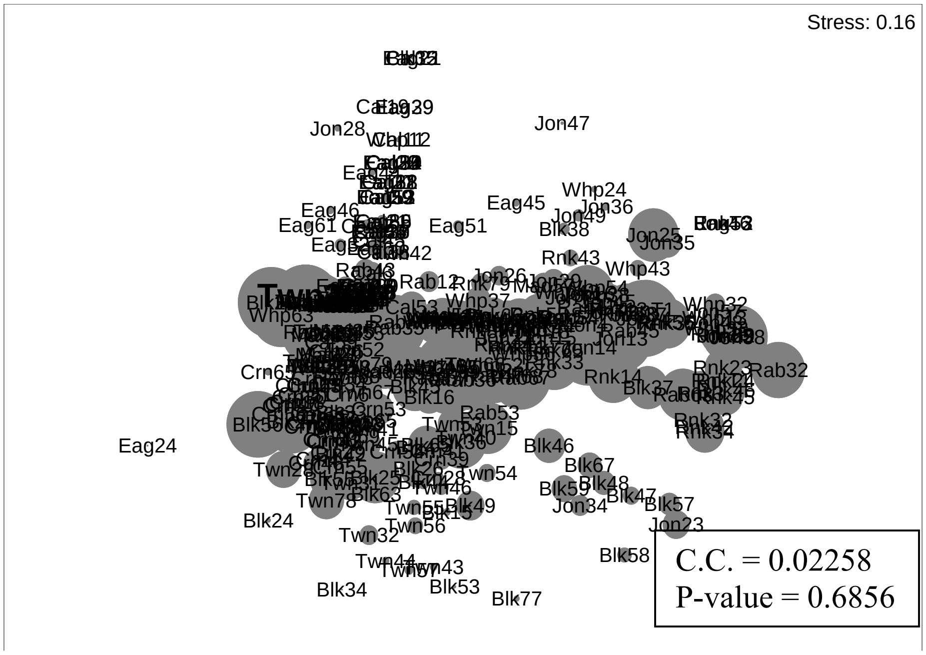


FIG. 78. Florida Bay Spring 1997 nMDS ordination plots with "Total Seagrass" and "Total Macroalgae" density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.


Fall 1997: Total Seagrass

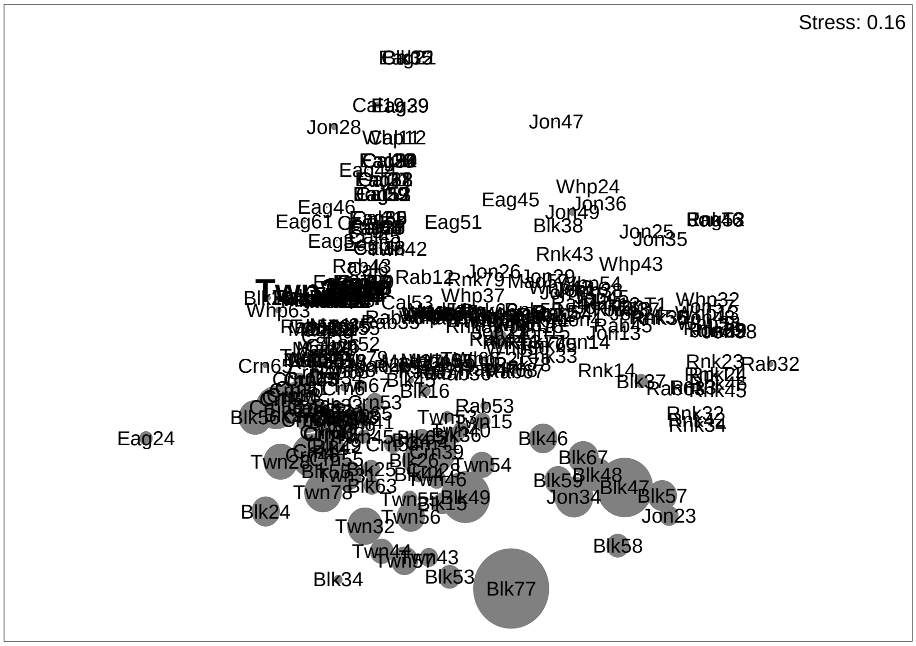
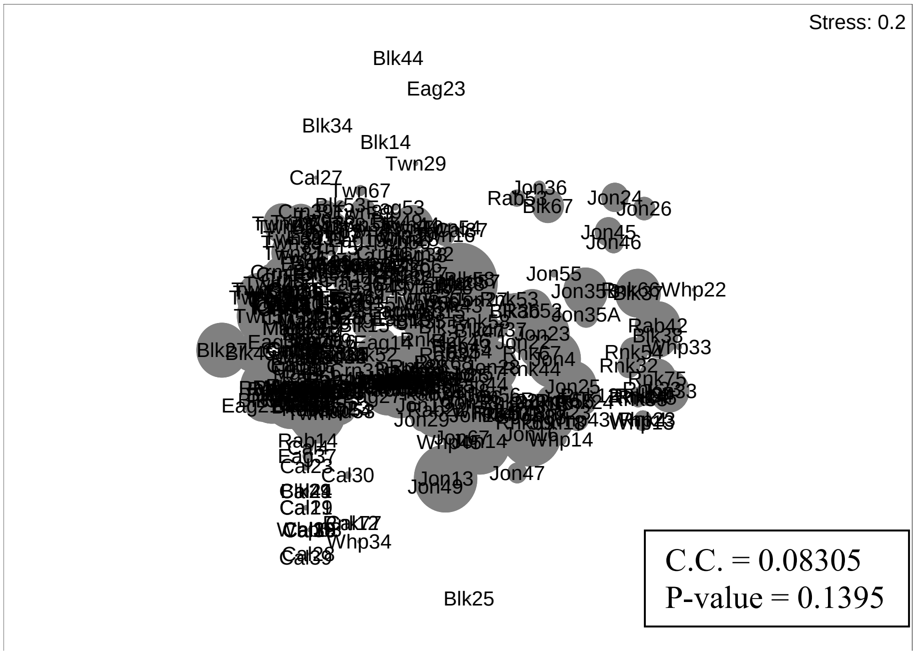

Fall 1997: Total Macroalgae

FIG. 79. Florida Bay Fall 1997 nMDS ordination plots with "Total Seagrass" and "Total Macroalgae" density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Spring 1998: Total Seagrass



Spring 1998: Total Macroalgae

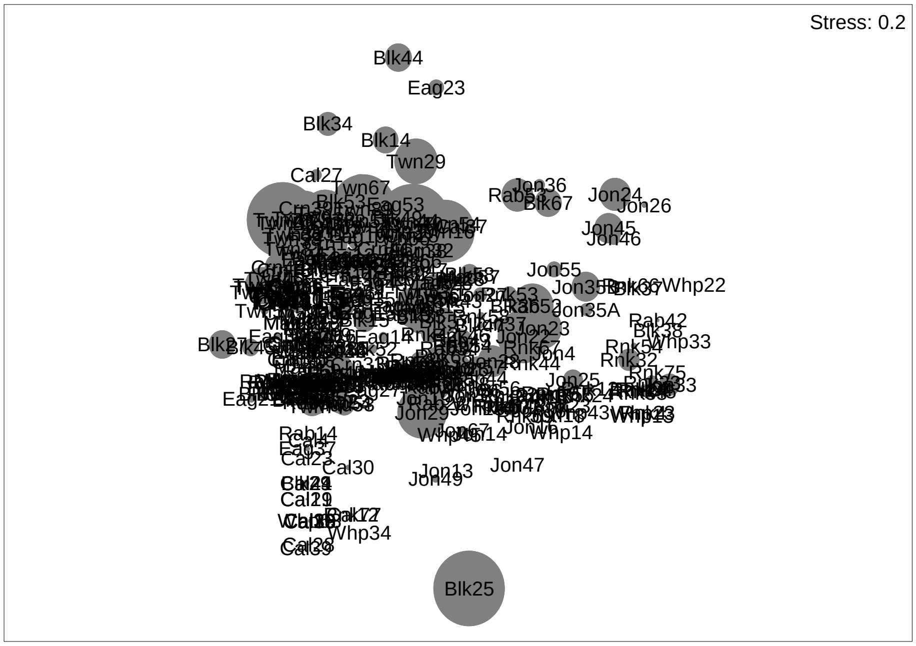
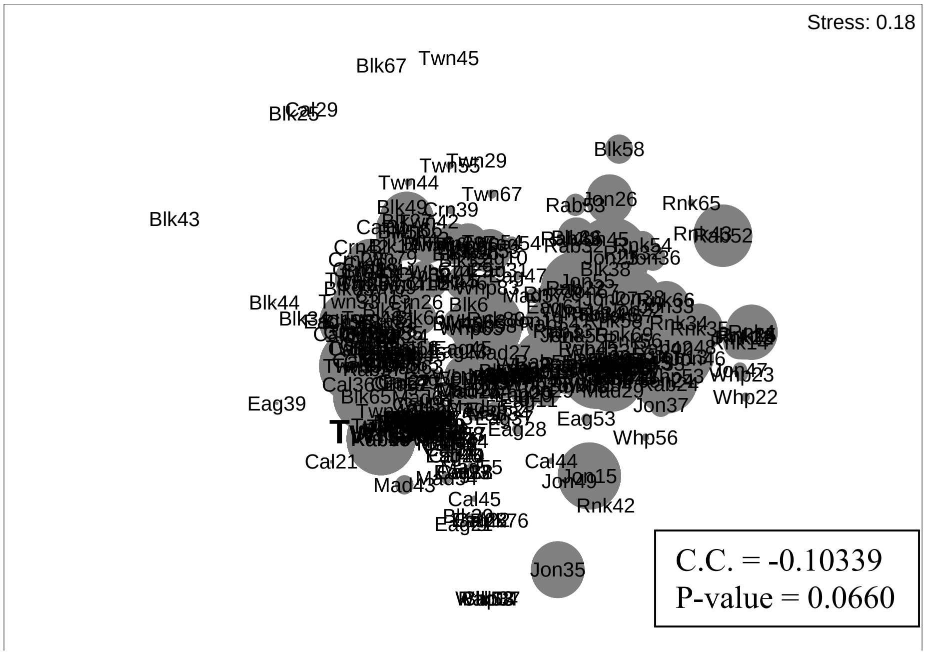


FIG. 80. Florida Bay Spring 1998 nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Fall 1998: Total Seagrass



Fall 1998: Total Macroalgae

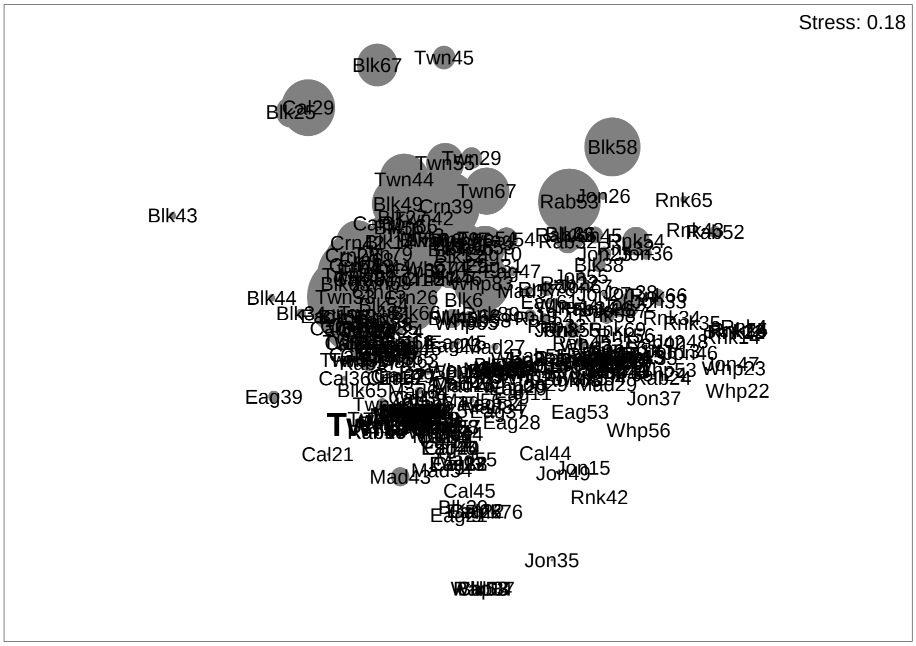
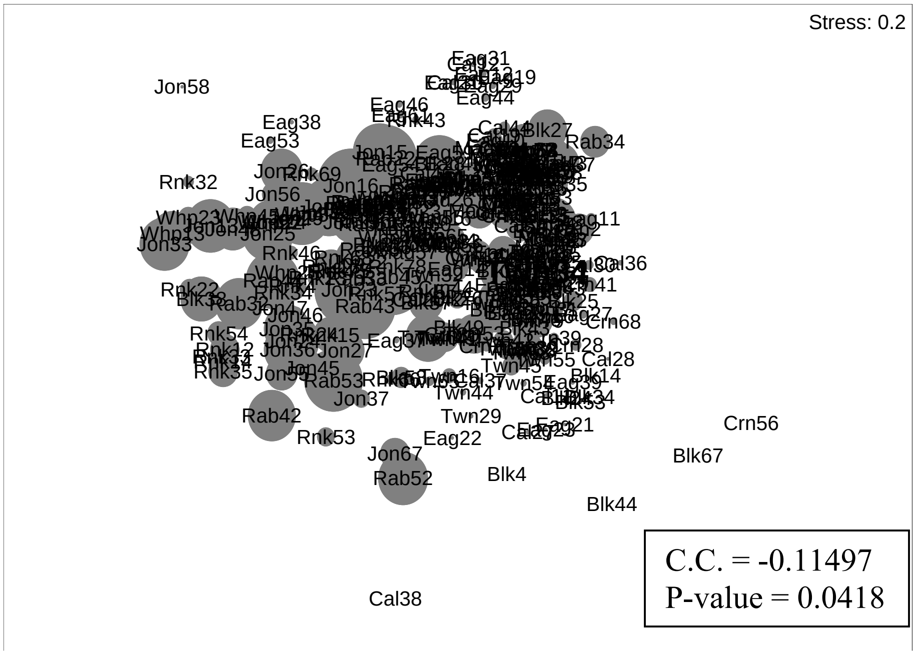


FIG. 81. Florida Bay Fall 1998 nMDS ordination plots with "Total Seagrass" and "Total Macroalgae" density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Spring 1999: Total Seagrass



Spring 1999: Total Macroalgae

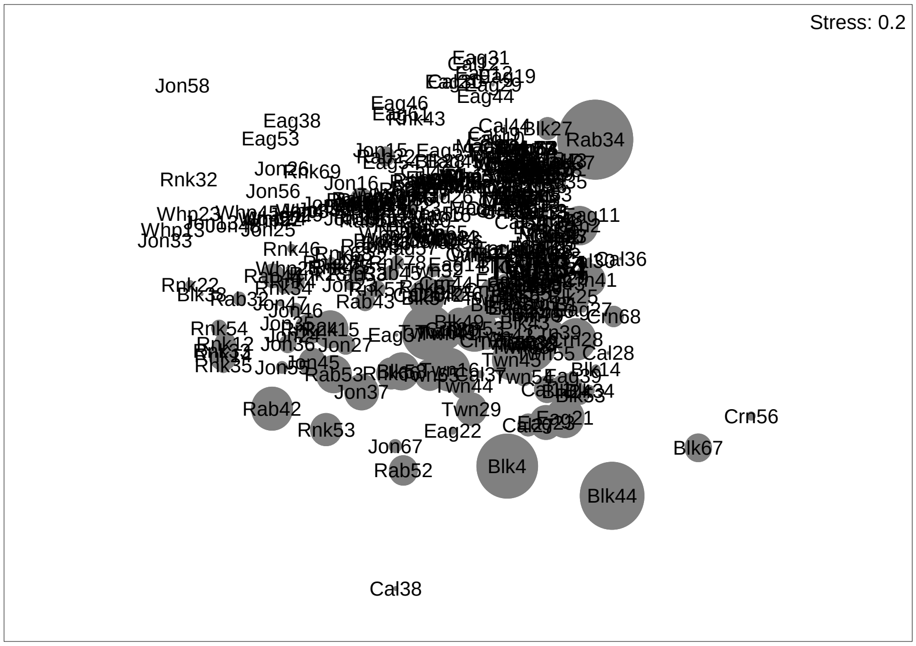
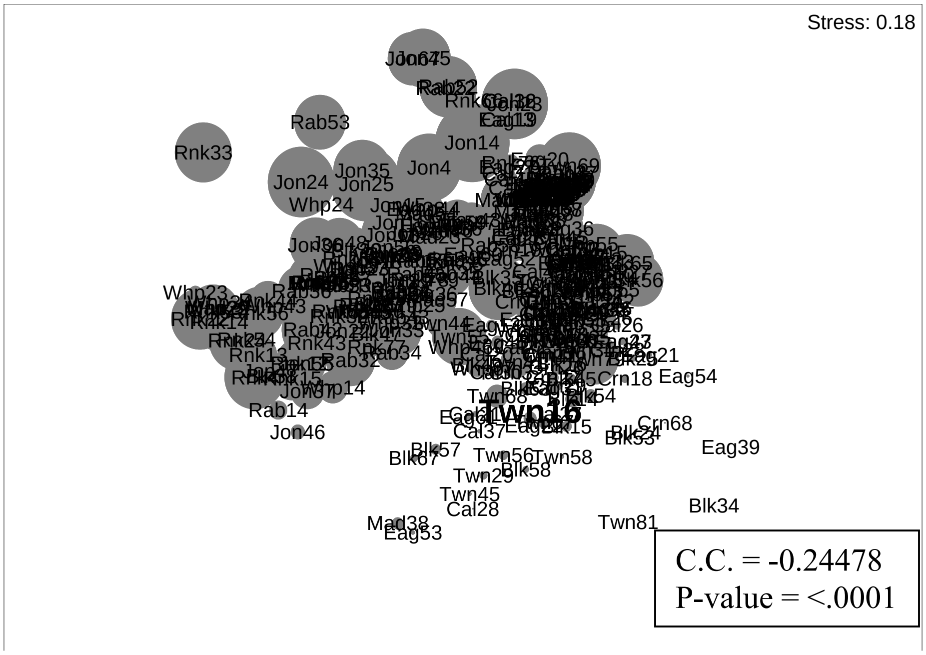


FIG. 82. Florida Bay Spring 1999 nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Fall 1999: Total Seagrass



Fall 1999: Total Macroalgae

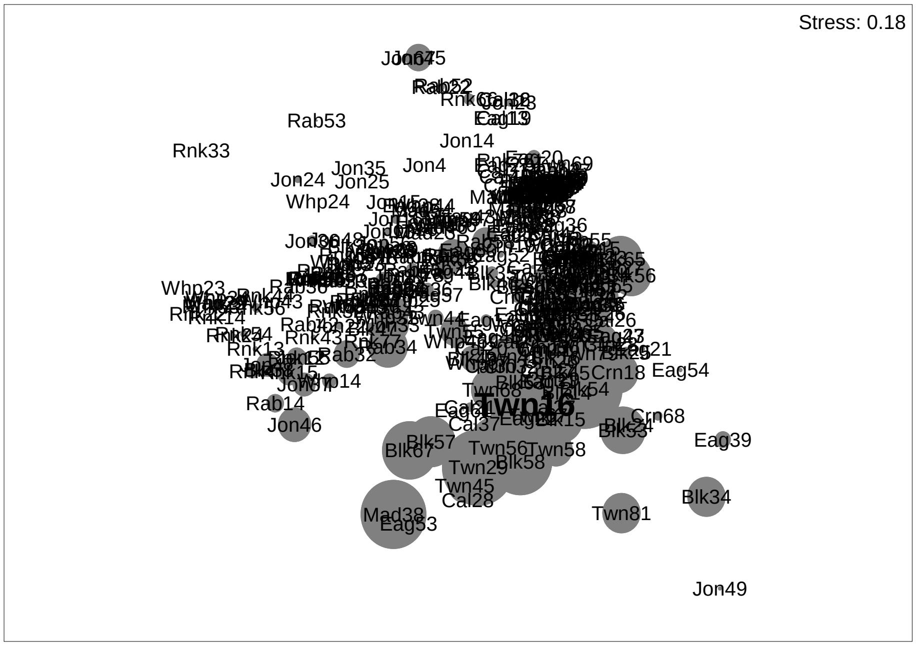
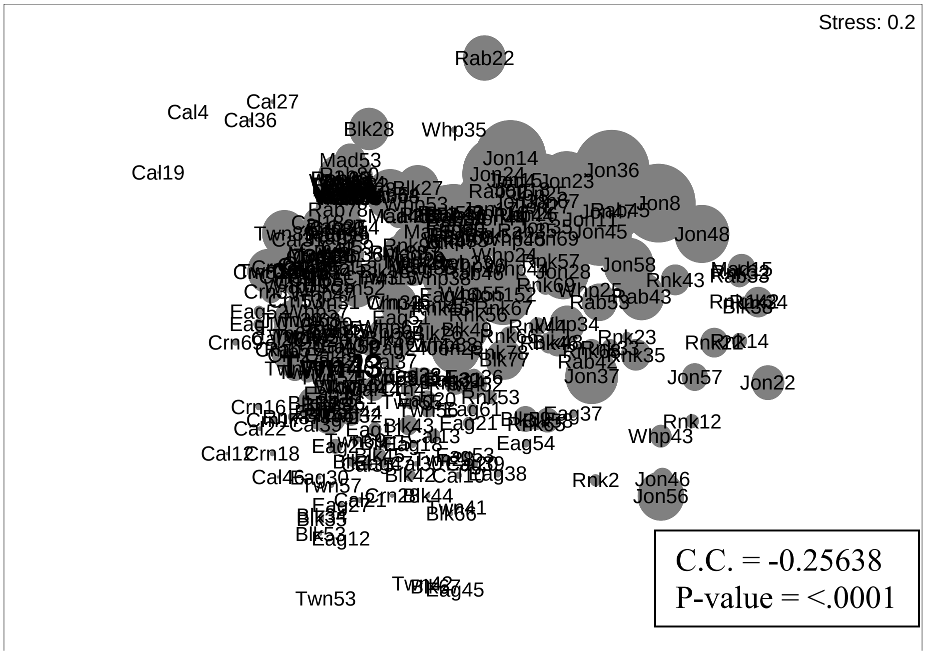


FIG. 83. Florida Bay Fall 1999 nMDS ordination plots with "Total Seagrass" and "Total Macroalgae" density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Spring 2000: Total Seagrass



Spring 2000: Total Macroalgae

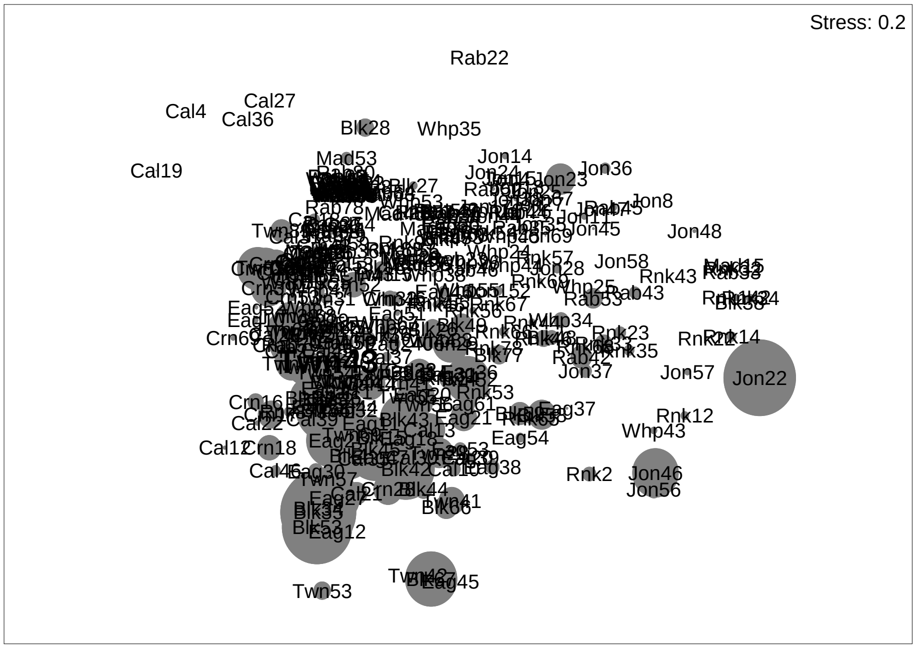
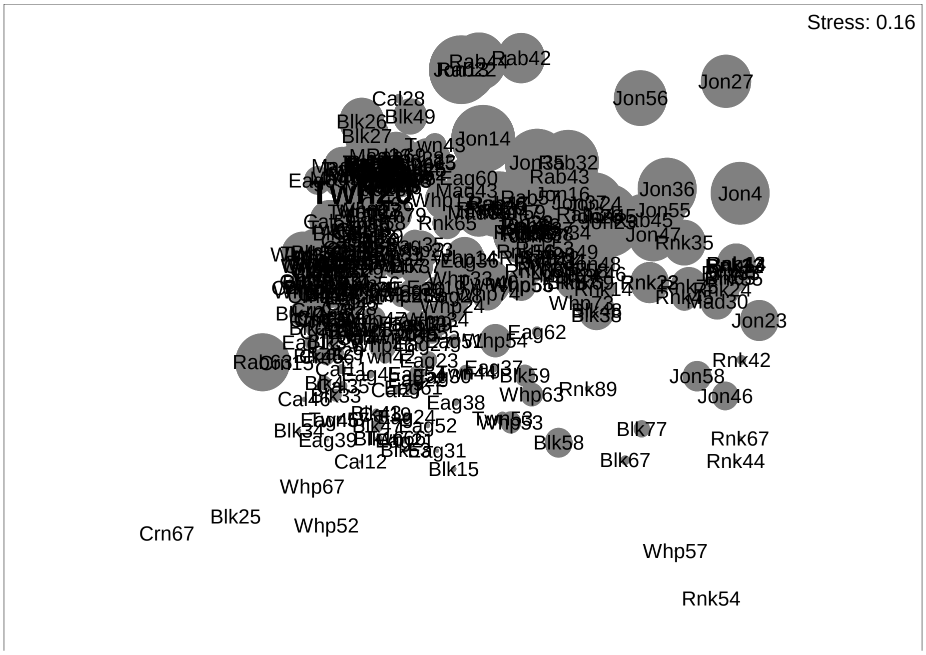


FIG. 84. Florida Bay Spring 2000 nMDS ordination plots with "Total Seagrass" and "Total Macroalgae" density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Fall 2000: Total Seagrass



Fall 2000: Total Macroalgae

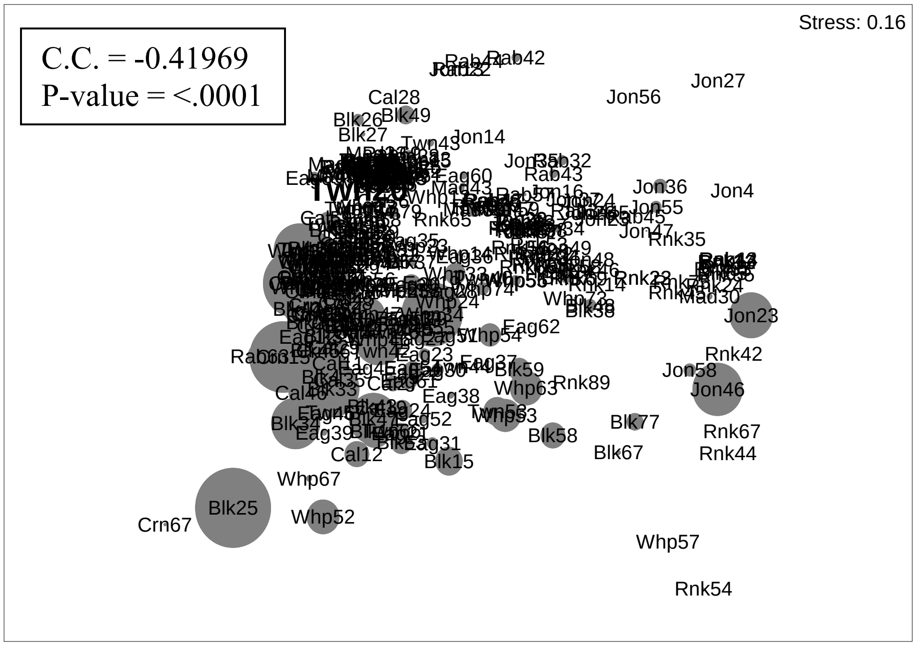
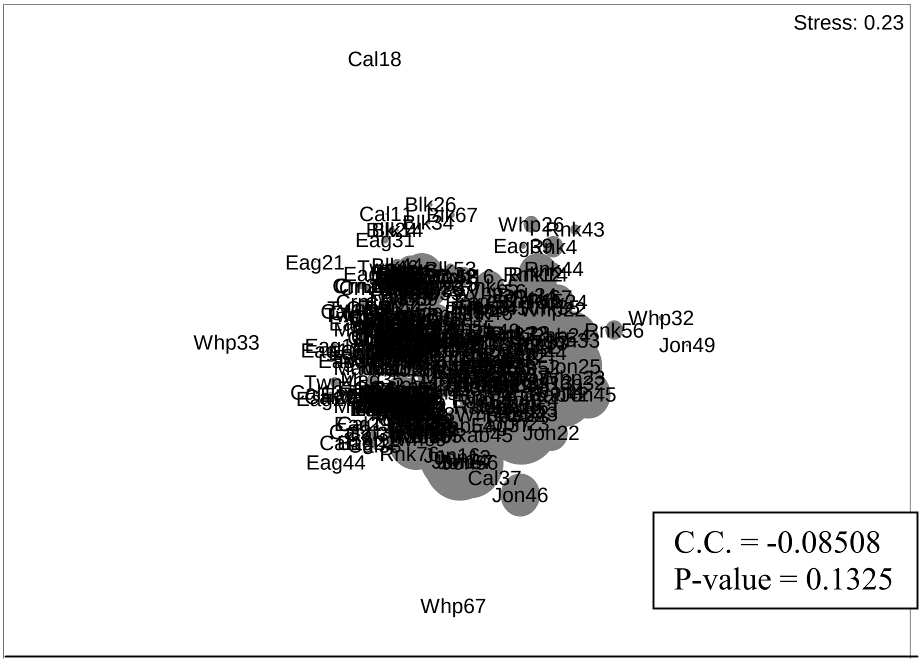


FIG. 85. Florida Bay Fall 2000 nMDS ordination plots with "Total Seagrass" and "Total Macroalgae" density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.



Spring 2001: Total Macroalgae

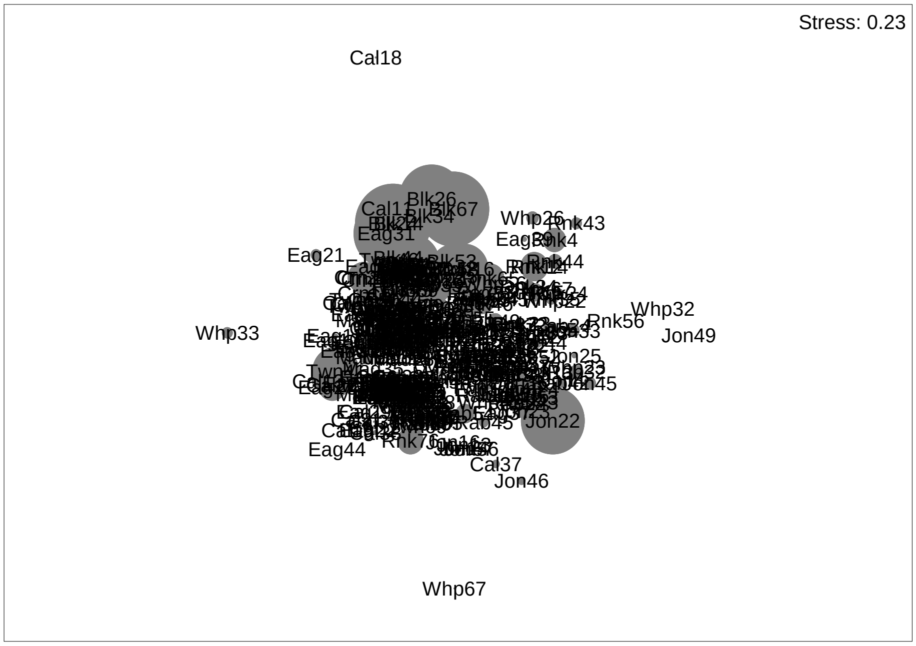
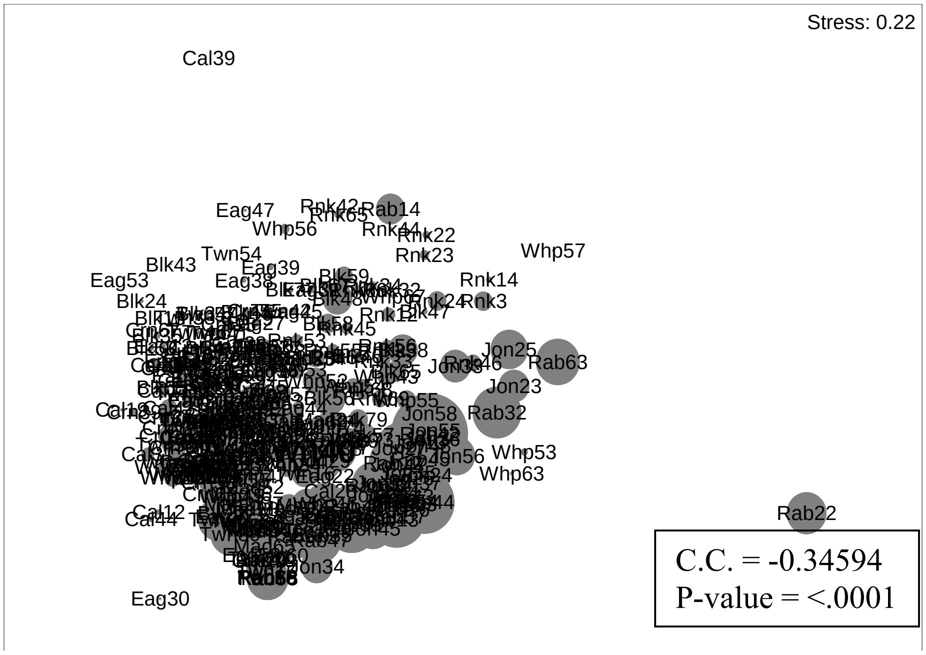


FIG. 86. Florida Bay Spring 2001 nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Spring 2002: Total Seagrass



Spring 2002: Total Macroalgae

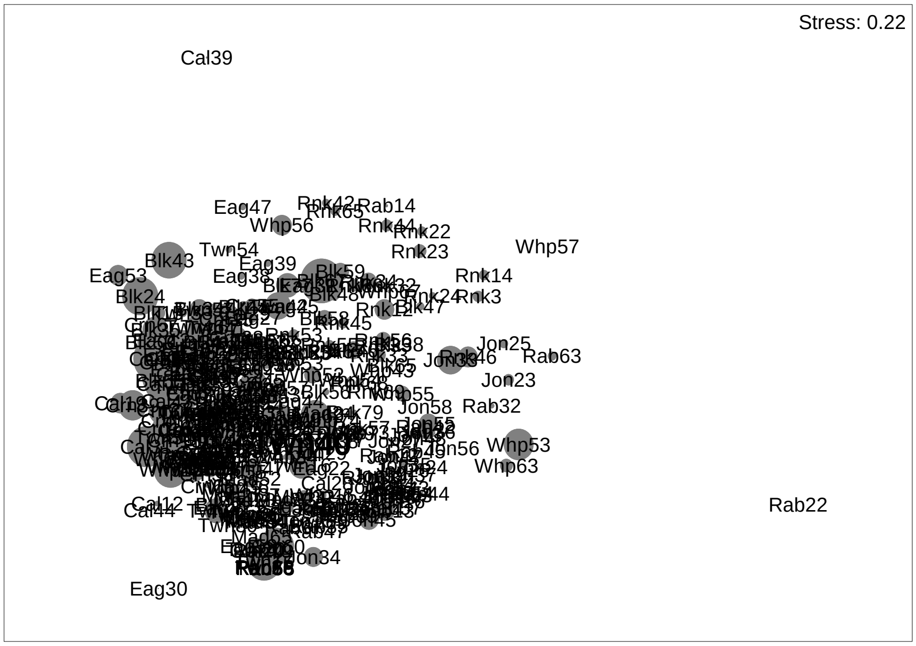
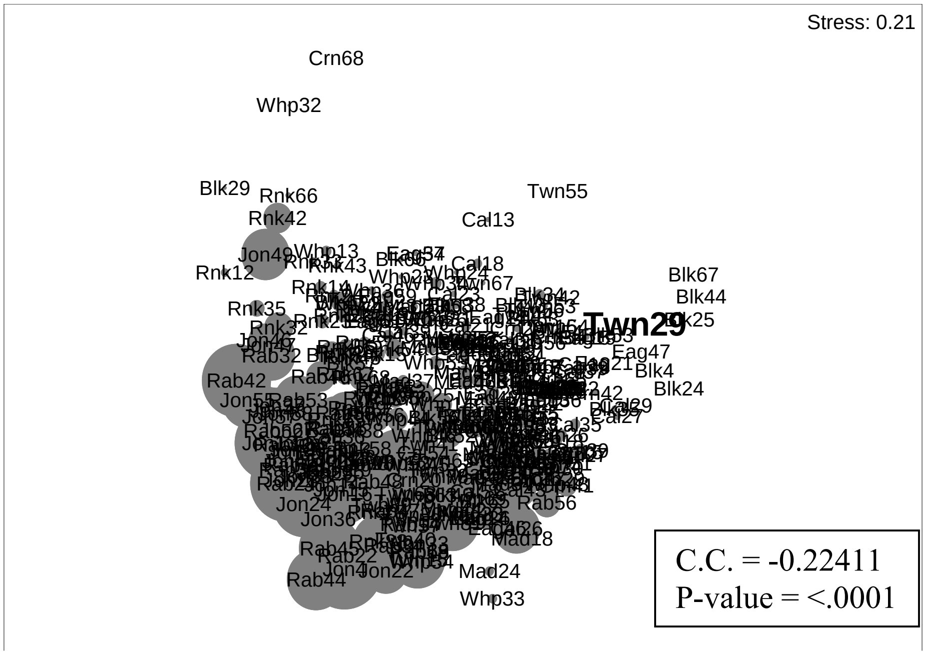


FIG. 87. Florida Bay Spring 2002 nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Fall 2002: Total Seagrass



Fall 2002: Total Macroalgae

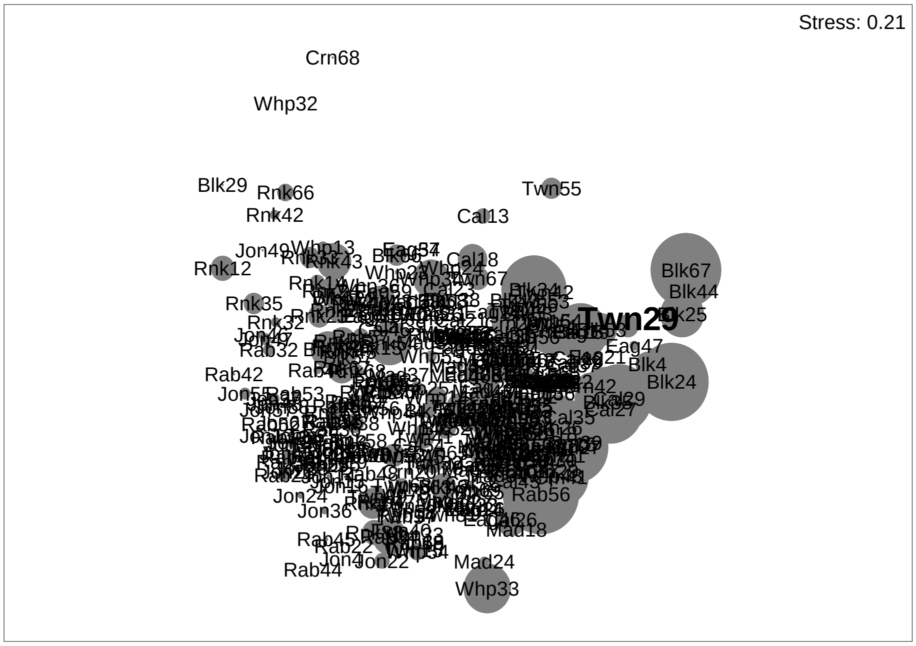
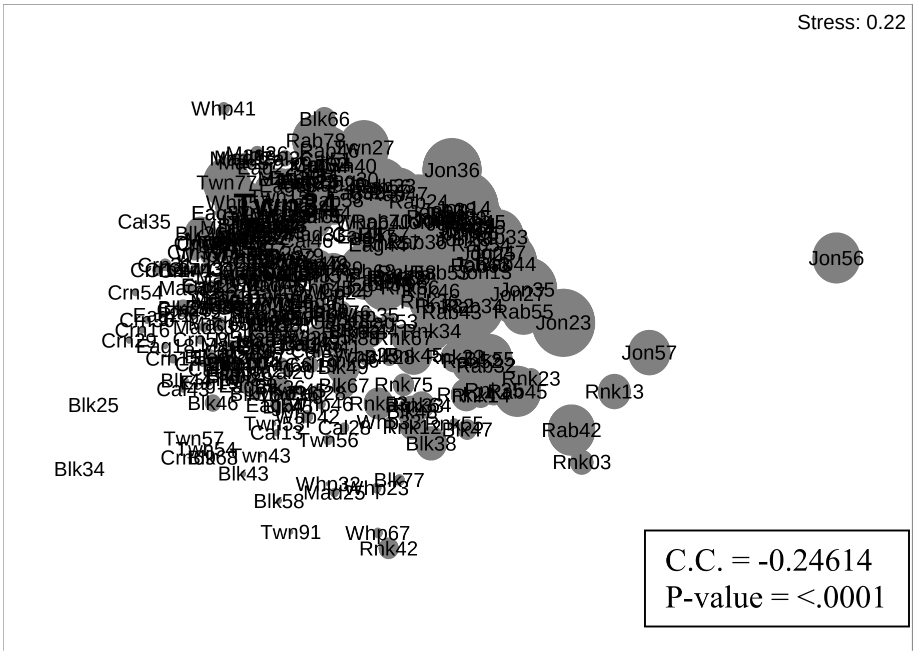


FIG. 88. Florida Bay Fall 2002 nMDS ordination plots with "Total Seagrass" and "Total Macroalgae" density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Spring 2003: Total Seagrass



Spring 2003: Total Macroalgae

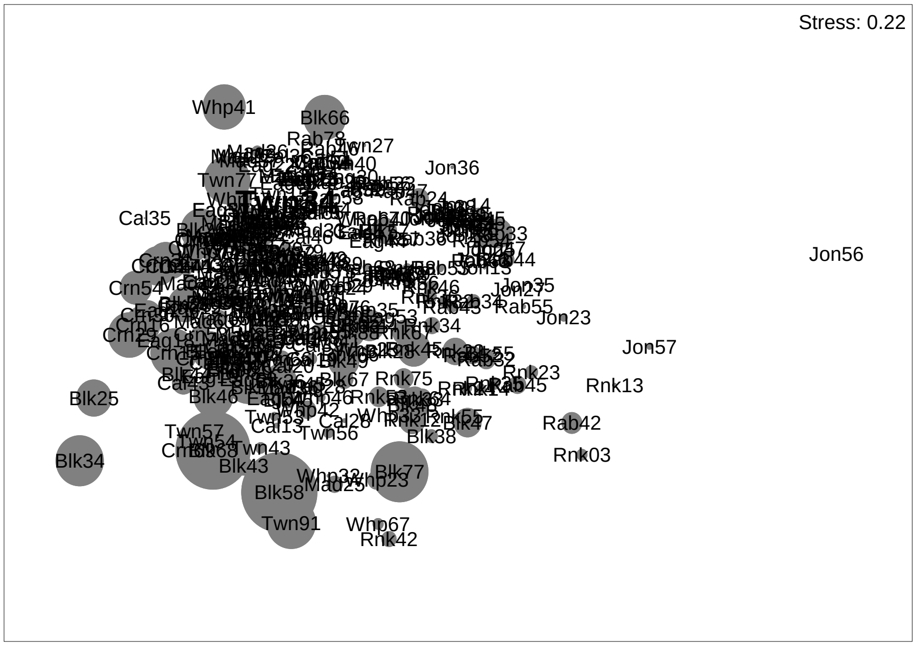
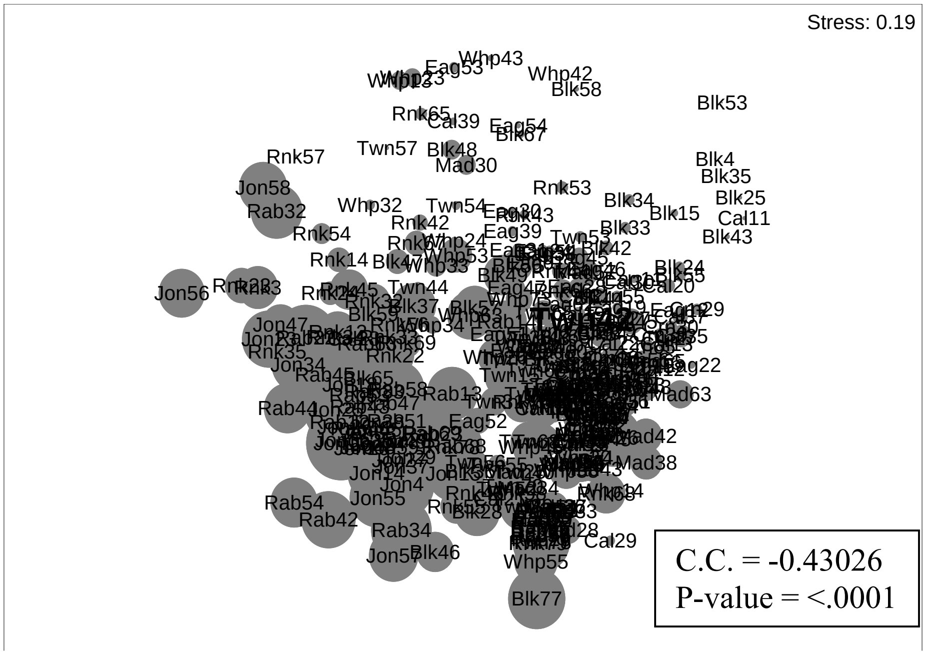


FIG. 89. Florida Bay Spring 2003 nMDS ordination plots with "Total Seagrass" and "Total Macroalgae" density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Fall 2003: Total Seagrass



Fall 2003: Total Macroalgae

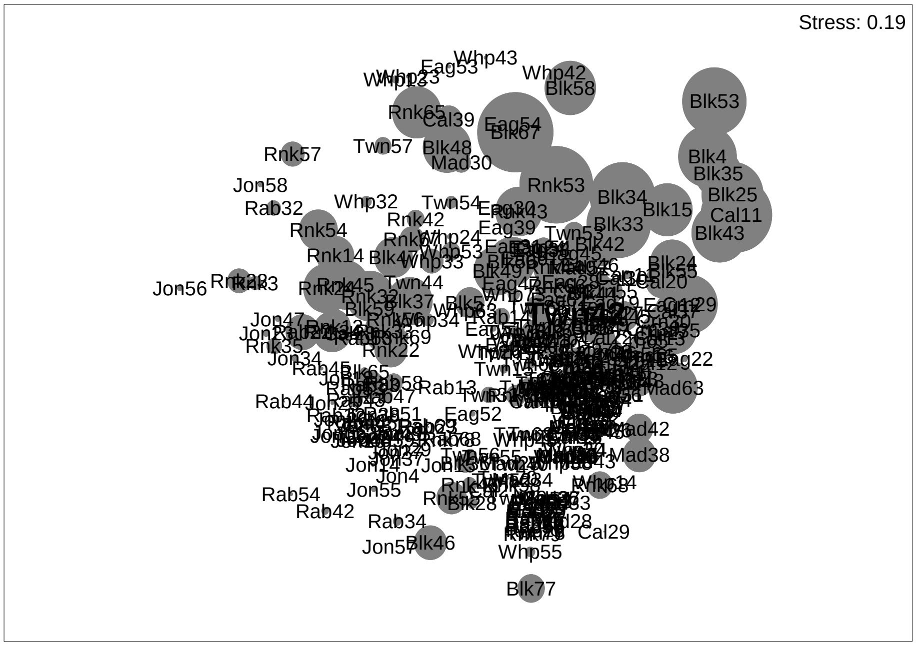
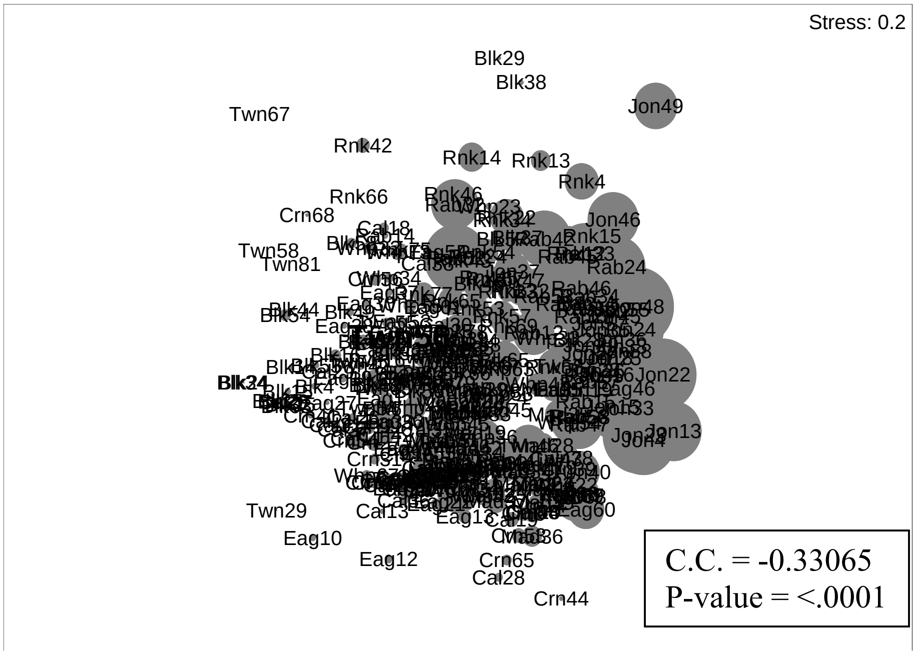


FIG. 90. Florida Bay Fall 2003 nMDS ordination plots with “Total Seagrass” and “Total Macroalgae” density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

Spring 2004: Total Seagrass



Spring 2004: Total Macroalgae

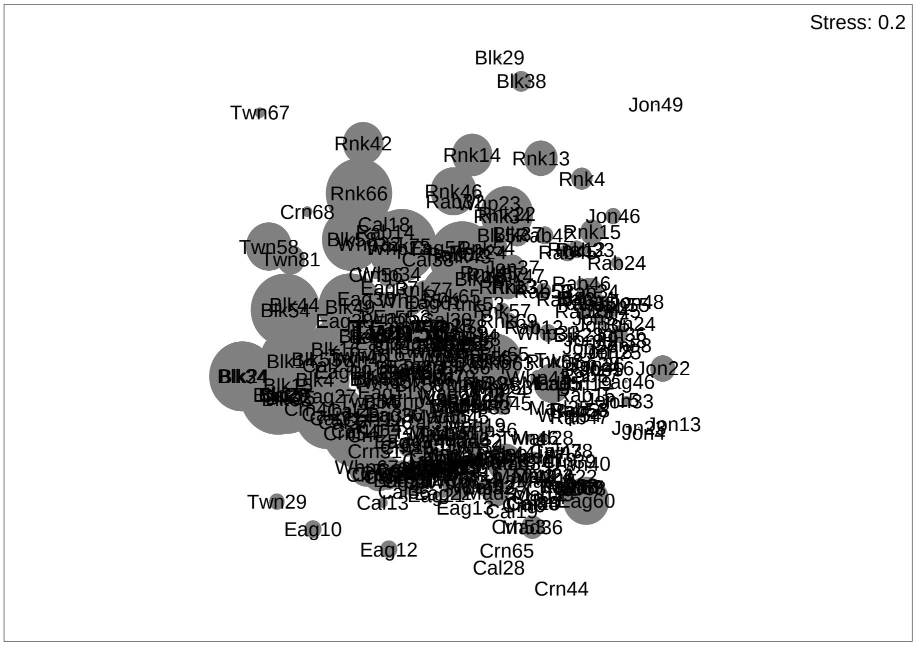


FIG. 91. Florida Bay Spring 2004 nMDS ordination plots with "Total Seagrass" and "Total Macroalgae" density overlays. The size of the gray bubbles is relative to density. Inset gives Spearman correlation coefficient and significance value.

strength of the correlation between that environmental/physical variable and the distribution of the macrophytes along its axis. The length of the vectors generally corresponds with significance (ie. the longest vector corresponds to the most significant variable), but on occasion they do not correspond. Instead the length indicates the strength of the correlation in one direction, but the most significant variable is having the most affect on the overall spread and distribution of the macrophytes, even though it may be shorter.

During spring 1995 sampling, CCA results indicate that water depth had the most statistically significant effect on the distribution of macrophytes (FIG. 92 and TABLE 26). It had both the strongest correlation with the distribution of macrophytes along its particular axis, as well as the strongest overall influence on the distribution of the macrophytes. Although this effect was found to be significant, the lambda value gives the variance explained by depth, which was only 2%. This indicates that there is some other environmental or physical factor exerting much more influence on the distribution of macrophytes that is not accounted for as part of the FHAP data set. None of the other environmental variables had a significant effect on macrophyte distribution during spring 1995, nor did any of the environmental variables show a significant effect on the distribution of macrophytes during fall 1995 sampling. Based on macrophyte distribution along the environmental vectors, it was seen that during spring 1995 sampling, *Halodule* and *Penicillus* responded to depth similarly in their distribution, as did *Thalassia* and *Caulerpa*. *Halimeda* and *Penicillus* also responded to depth similarly, and so did *Acetabularia* and *Batophora*. Although the macrophytes are arranged in ordination space along the other vectors as well in accordance with how they are responding to those variables, their similarity in distribution will not be discussed unless the environmental variable influence was statistically significant.

Spring 1996 macrophyte distribution was not significantly influenced by any of the tested environmental variables, but fall 1996 distribution was. In this case temperature was the most significant factor, although the amount of variance it accounted for was still very low (3%). Along the temperature axis, none of the macrophytes responded particularly similarly to one another, with the exception of *Sargassum* and the drift reds, which had the least amount of space separating them perpendicular to the temperature vector (FIG. 93 and TABLE 26).

Monte Carlo tests showed that spring 1997 macrophyte distribution was, on the other hand, significantly influenced by three of the four variables tested, although the variability they accounted for was still low enough to suggest that some other factor was having a greater influence on their distribution than any recorded by FHAP (FIG. 94 and TABLE 26). Nonetheless, water depth was most significantly correlated to the distribution of macrophytes, followed by visibility and then temperature. Based on their distribution along each of the vector axes, it was discernible that groups of macrophytes were responding to the different variables similarly. In this case, *Halimeda*, *Acetabularia*, and *Syringodium* responded to visibility nearly identically, as did *Batophora, Penicillus* and *Sargassum*. *Halodule* and *Halophila* were also separated by a short distance along that axis, indicating that they were also responding to visibility in a similar manner to one another (ie. they were highly correlated along that axis with little space separating them perpendicular to the visibility vector). Along the depth axis, *Syringodium* and *Penicillus*

TABLE 26. Monte Carlo Permutation test results showing the lambda value, P-value, and F-ratio for each environmental/physical variable during each sampling event. *indicates significance at α#0.05

	Variable	Lambda	P-value	F-ratio		Variable	Lambda	P-value	F-ratio
Sp 1995	Depth	0.02	0.008*	3.04	F 1995	Depth	0	0.908	0.33
	Vis	0	0.38	1.32		Sal	0	0.84	0.31
	Sal	0.01	0.722	0.65		Vis	0.01	0.972	0.15
						Temp	0	0.992	0.1
Sp 1996	Temp	0.01	0.138	1.63	F 1996	Temp	0.03	0.016*	5.8
	Depth	0	0.31	0.45		Vis	0.01	0.318	1.03
	Sal	0.01	0.688	0.39		Depth	0.01	0.198	1.55
	Vis	0	0.626	0.24		Sal	0.01	0.67	1
Sp 1997	Depth	0.02	0.012*	4.21	F 1997	Depth	0.04	0.002*	8.51
	Vis	0.01	0.002*	3.47		Sal	0	0.112	1.71
	Temp	0.01	0.028*	2.42		Vis	0.01	0.476	1.42
	Sal	0	0.944	0.24		Temp	0	0.8	0.42
Sp 1998	Depth	0.01	0.014*	3.33	F 1998	Vis	0.01	0.034*	3.12
	Temp	0.01	0.06	2.71		Sal	0.01	0.1	1.61
	Vis	0.01	0.352	0.84		Depth	0.01	0.296	1.41
	Sal	0	0.602	0.53		Temp	0	0.252	0.57
Sp 1999	Depth	0.02	0.004*	4.7	F 1999	Temp	0.04	0.016*	9.35
	Vis	0.01	0.026*	3.15		Vis	0.01	0.008*	3.34
	Temp	0.01	0.108	1.81		Depth	0.01	0.43	1.25
	Sal	0.01	0.178	1.48		Sal	0	0.484	1.03
Sp 2000	Depth	0.02	0.002*	4.6	F 2000	Vis	0.01	0.016*	2.4
	Sal	0.01	0.062	2.18		Temp	0.01	0.21	2.59
	Temp	0	0.228	1.43		Depth	0.01	0.134	2.06
	Vis	0.01	0.448	0.62		Sal	0	0.526	0.58
Sp 2001	Sal	0.04	0.002*	9.96					
	Temp	0.01	0.062	1.9					
	Depth	0.01	0.376	1.35					
	Vis	0	0.092	1.06					
Sp 2002	Sal	0.01	0.006*	2.8	Fall 2002	Depth	0.01	0.276	1.78
	Depth	0.01	0.086	2.05		Vis	0	0.444	1.42
	Vis	0	0.406	0.84		Sal	0.01	0.162	1.61
	Temp	0.01	0.686	0.72		Temp	0	0.522	0.9
Sp 2003	Depth	0.01	0.008*	3.76	Fall 2003	Depth	0.01	0.012*	2.76
	Sal	0.01	0.026*	2.1		Sal	0.01	0.03*	2.18
	Temp	0.01	0.094	1.65		Vis	0	0.454	0.81
	Vis	0	0.102	1.36		Temp	0	0.598	0.81
Sp 2004	Sal	0.02	0.002*	5.08					
	Depth	0.01	0.066	1.8					
	Vis	0	0.594	1.06					
	Temp	0	0.82	0.56					

responded similarly, as did *Batophora* and *Acetabularia* and to a certain extent *Halodule*, which were all closely related to *Halimeda* along that axis. Along the temperature axis,*Thalassia* and *Sargassum* responded similarly to one another, and were both somewhat similar to *Halodule*. *Halimeda*, *Acetabularia*, and *Batophora* were also tightly correlated along this axis, as were *Syringodium* and *Penicillus*, and the drift reds and *Halophila*. *Caulerpa* was placed on the outer limits of this ordination as an artifact of its rarity during this sampling period.

Water depth was again the most influential factor in the distribution of macrophytes during fall 1997 sampling (FIG. 94 and TABLE 26). *Halodule*, *Syringodium*, and *Caulerpa* responded to depth similarly at this time, as did *Thalassia*, *Halimeda*, and *Batophora*.

During spring and fall 1998 sampling, water depth and visibility, respectively, were found to be the only significant variables affecting the macrophyte distribution (FIG. 95 and TABLE 26). *Penicillus*, *Acetabularia*, and *Halodule* responded similarly to depth, as did the drift reds and *Thalassia* during spring 1998. Macrophytes that were placed at the edge of this ordination are again an artifact of their rarity in the data set for this particular sampling event. Fall 1998 showed *Thalassia* and *Batophora* responding to visibility similarly, as well as *Halodule* responding similarly to *Penicillus*, and *Halimeda* responding somewhat similarly to *Caulerpa*.

Water depth and visibility were again the significant variables affecting the macrophyte distribution during spring 1999, and fall 1999 macrophyte distribution was most significantly affected by temperature and visibility (FIG. 96 and TABLE 26). Along the depth axis on the spring 1999 CCA plot, *Halimeda* and *Penicillus* behaved similarly, as did *Halodule* and *Caulerpa* to a certain extent. *Thalassia*, *Batophora*, and *Acetabularia* also responded similarly to depth during this sampling event. Response to visibility, on the other hand, was similar between *Penicillus*, *Batophora*, and the drift reds, as well as between *Halodule* and *Halimeda*. The fall 1999 response to temperature was highly correlated between *Syringodium* and the drift reds, between *Halimeda* and *Acetabularia*, and between *Thalassia*, *Batophora*, *Penicillus*, and *Halodule.* Response to visibility was similar between *Thalassia*, *Halimeda*, and the drift reds, and between *Syringodium*, *Acetabularia*, and *Batophora*, as well as between *Caulerpa*, *Penicillus*, and *Acetabularia*. The variance actually accounted for by these variables was always low (TABLE 26).

Spring 2000 macrophyte distribution was only significantly correlated to water depth, and fall 2000 distribution only significantly correlated to visibility and in each case a minimal percent of the variance was actually accounted for by these variables (FIG. 97 and TABLE 26). Distribution along the depth axis in the spring 2000 CCA plot indicates that *Thalassia* and *Sargassum*, *Acetabularia* and *Syringodium*, and *Halimeda* and *Halodule* all responded to depth similarly. The fall 2000 distributional response to visibility shows similarities is response behavior among *Thalassia*, *Halodule*, and *Caulerpa*, the drift reds and *Halimeda*, and *Halophila*, *Penicillus*, and *Batophora*.

The distribution of macrophytes during spring 2001 was only significantly affected by salinity (FIG. 98 and TABLE 26). Distances between macrophytes along the salinity vector indicated that *Batophora* and *Acetabularia* responded similarly, as did *Thalassia* and the drift reds, and *Caulerpa* and *Syringodium*.

Salinity was still the only variable found to significantly affect the distribution of macrophytes in spring 2002 but it was not significant in fall 2002, nor were any of the other measured variables (FIG. 99 and TABLE 26). Distribution along the salinity vector on the spring 2002 CCA plot grouped *Halimeda* and *Caulerpa*, *Halodule* and the drift reds, *Batophora* and *Penicillus*, and *Acetabularia* and *Sargassum* according to their responses.

During both spring and fall 2003, salinity as well as water depth had significant affects on macrophyte distributions (FIG. 100 and TABLE 26), although again, a small amount of the variance was actually accounted for by these variables, meaning some other unmeasured variable was controlling macrophyte distribution moreso than salinity and depth at this time. During spring 2003, macrophyte distribution along the depth vector indicates that the following macrophytes were behaving similarly to one another: *Penicillus* and *Caulerpa*, *Batophora* and *Halodule*, *Halimeda* and *Syringodium*, and *Thalassia*, *Sargassum*, and *Acetabularia*. Spatial arrangement along the salinity vector indicates that *Halimeda* and *Caulerpa*, and *Batophora* and the drift reds were responding similarly. During fall 2003, few macrophytes were distributed similarly based on water depth, with the exception of *Batophora*, *Acetabularia*, and *Thalassia*, but many were correlated along the salinity vector. These included *Thalassia*, *Penicillus*, *Syringodium*, *Sargassum*, and *Caulerpa*.

Spring 2004 macrophyte distribution was only significantly correlated to salinity (FIG. 101 and TABLE 26). *Halimeda*, *Syringodium*, *Thalassia*, and the drift reds, as well as *Penicillus* and *Halodule*, and *Batophora* and *Acetabularia* behaved similarly to one another within their groups in response to salinity.

While macrophytes filling similar ecological roles repeatedly responded to environmental variables similarly, such as *Acetabularia* and *Batophora*, and *Halimeda* and *Penicillus*, the overall trend seen as a result of this analysis was that visibility and water depth were the driving forces in macrophyte distribution during the earlier years of FHAP sampling. Visibility stopped having a significant influence by spring 2001 when salinity became the most significant driving force in macrophyte distribution.

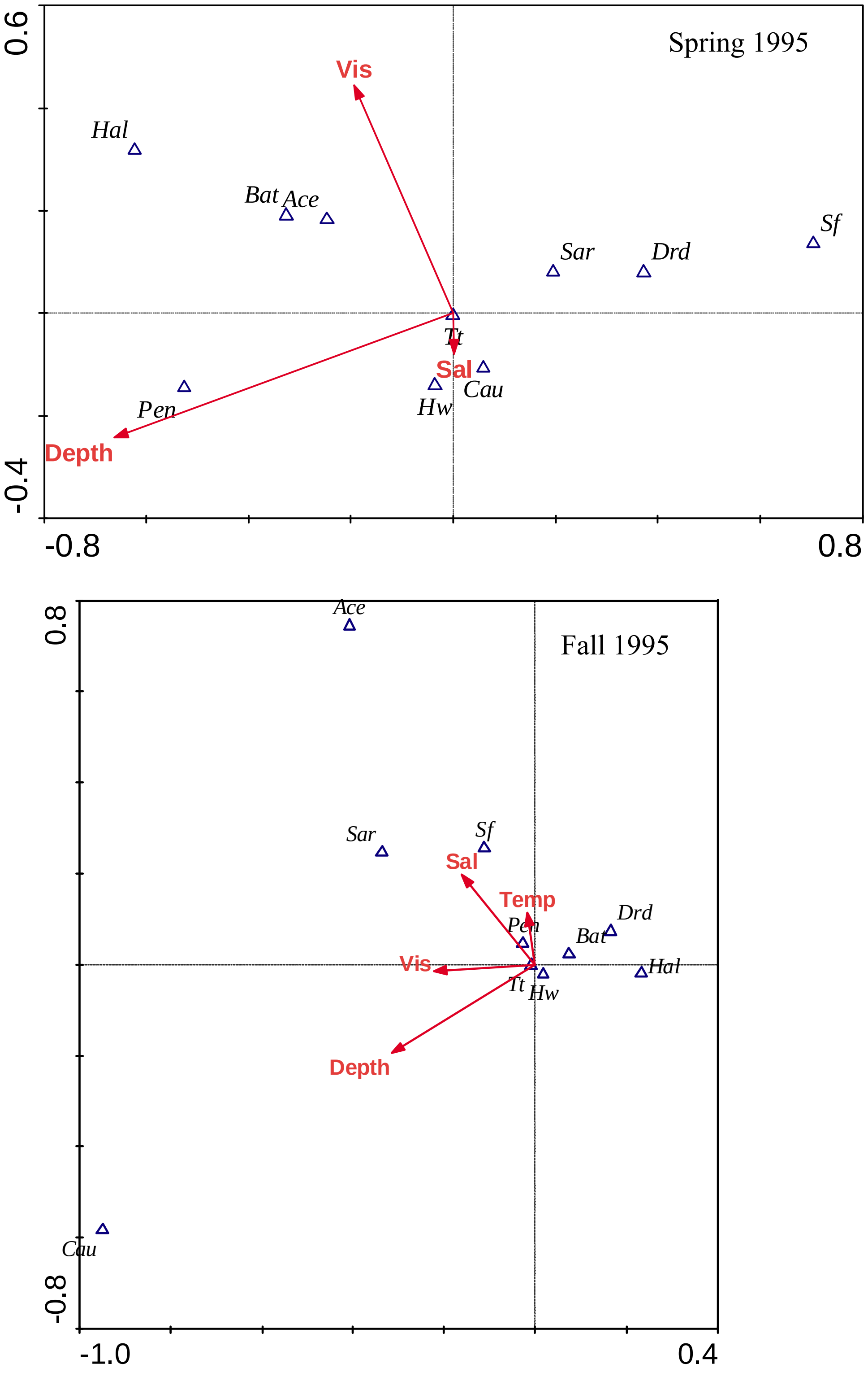
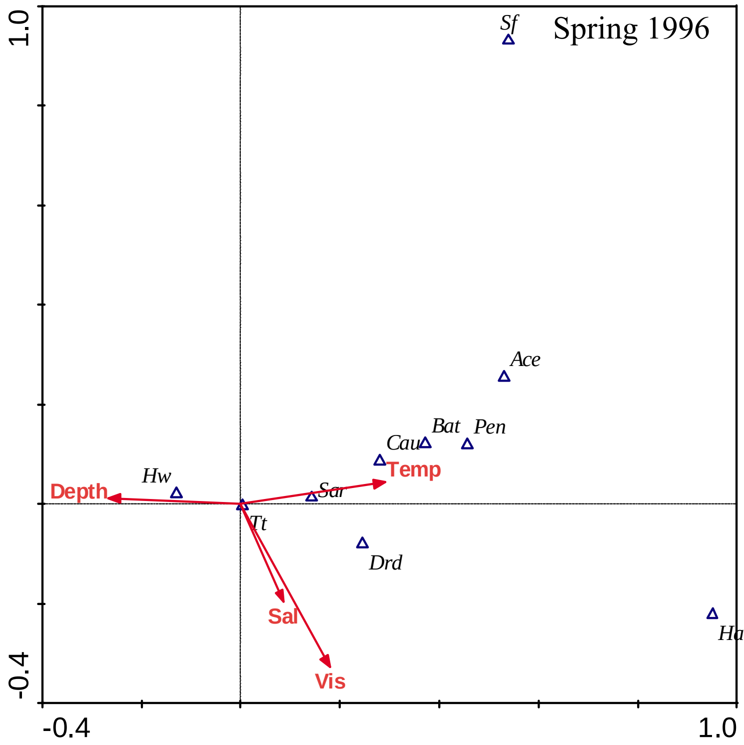


FIG. 92. Spring and Fall 1995 CCA plots.



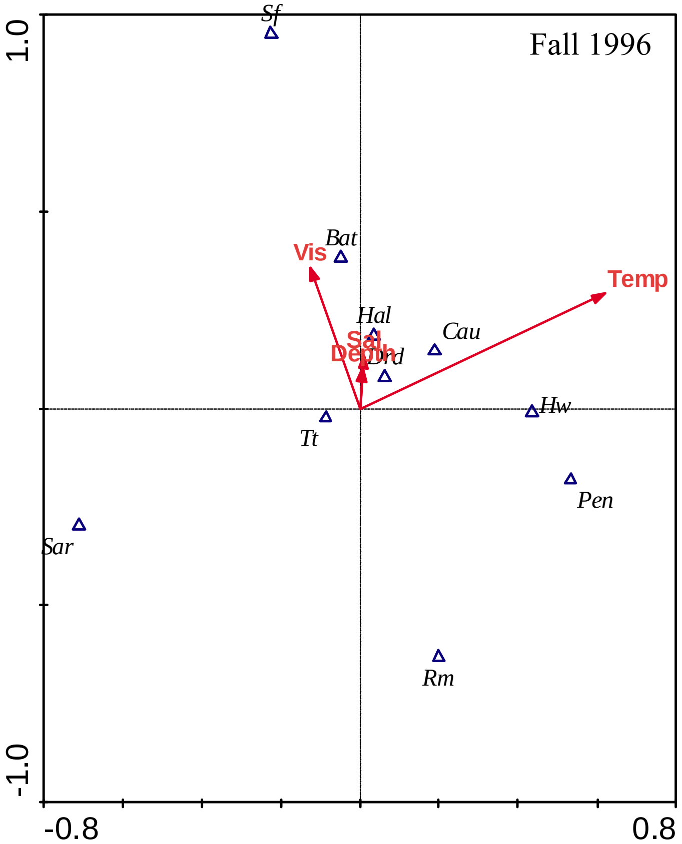
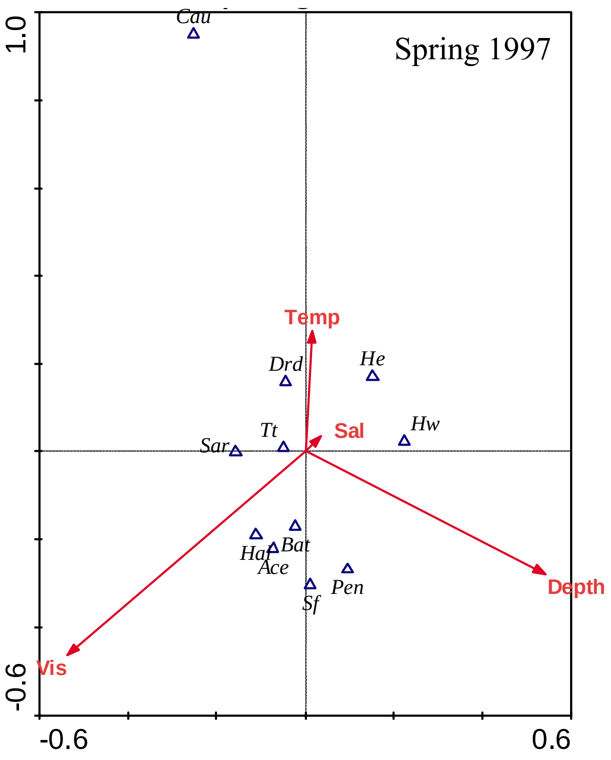


FIG. 93. Spring and Fall 1996 CCA plots.



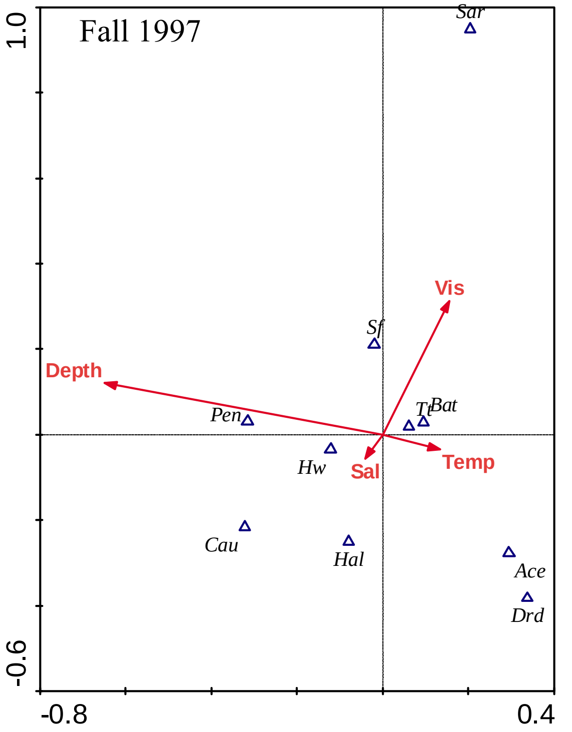


FIG. 94. Spring and Fall 1997 CCA plots.

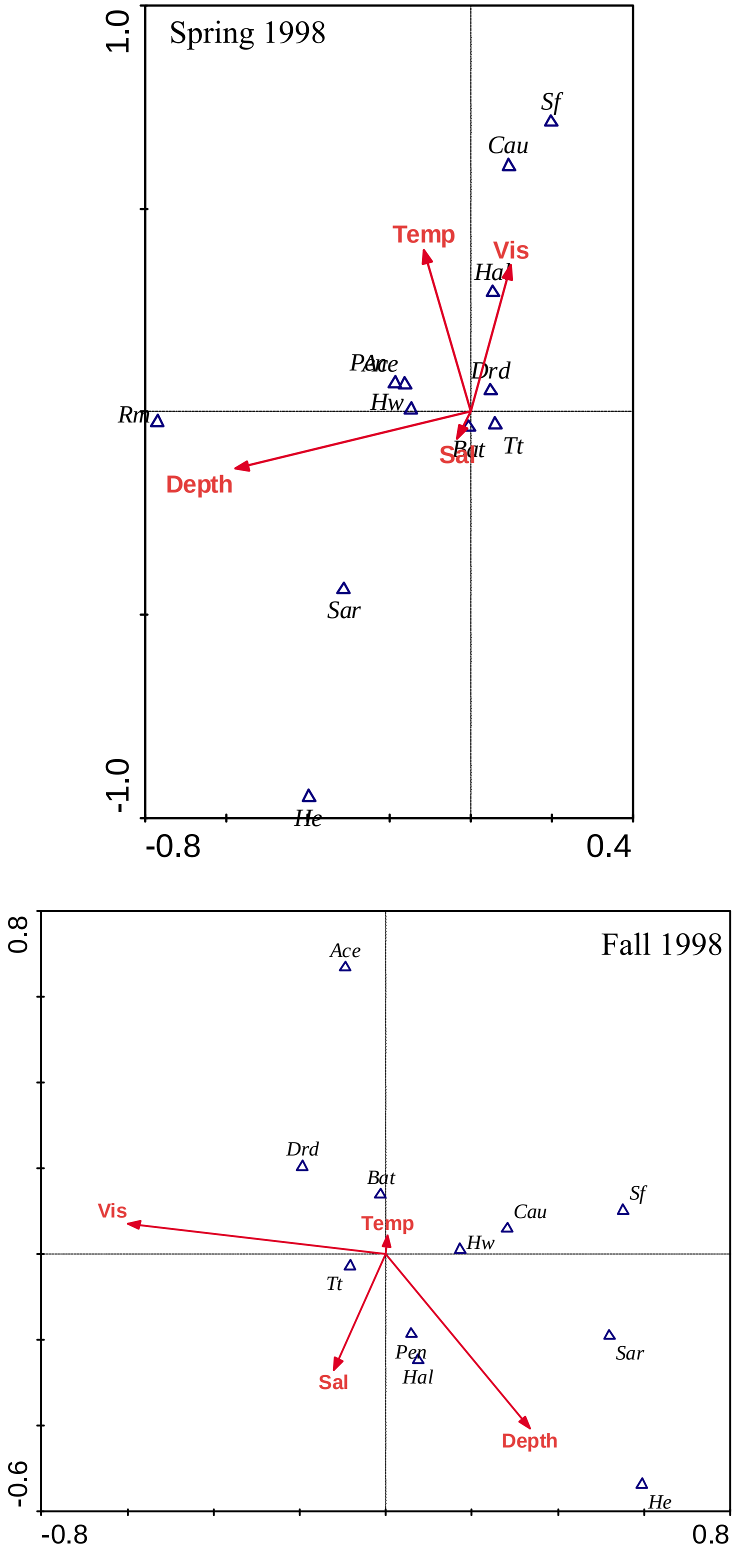
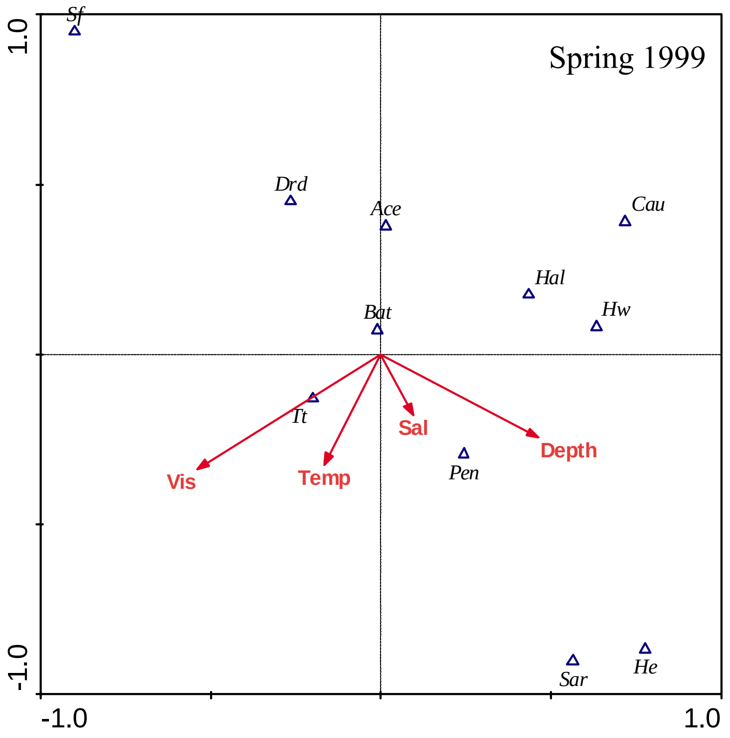


FIG. 95. Spring and Fall 1998 CCA plots.



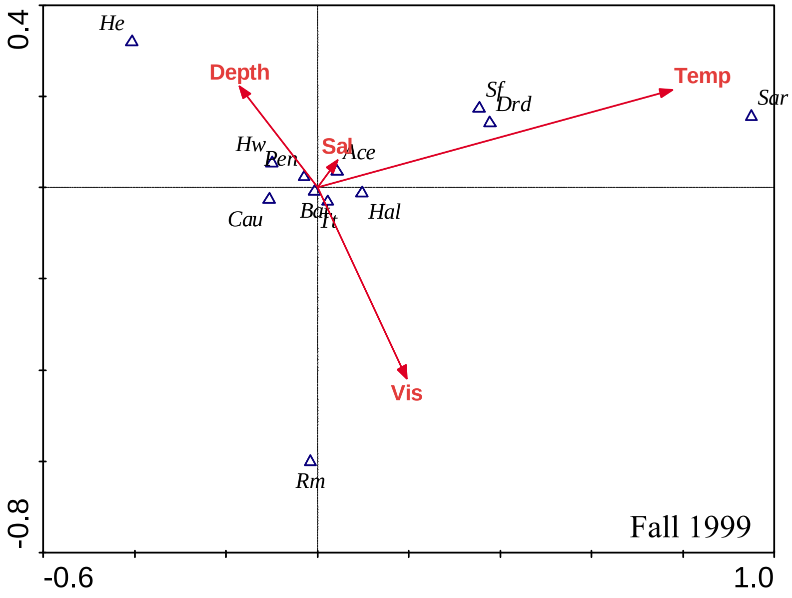


FIG. 96. Spring and Fall 1999 CCA plots.

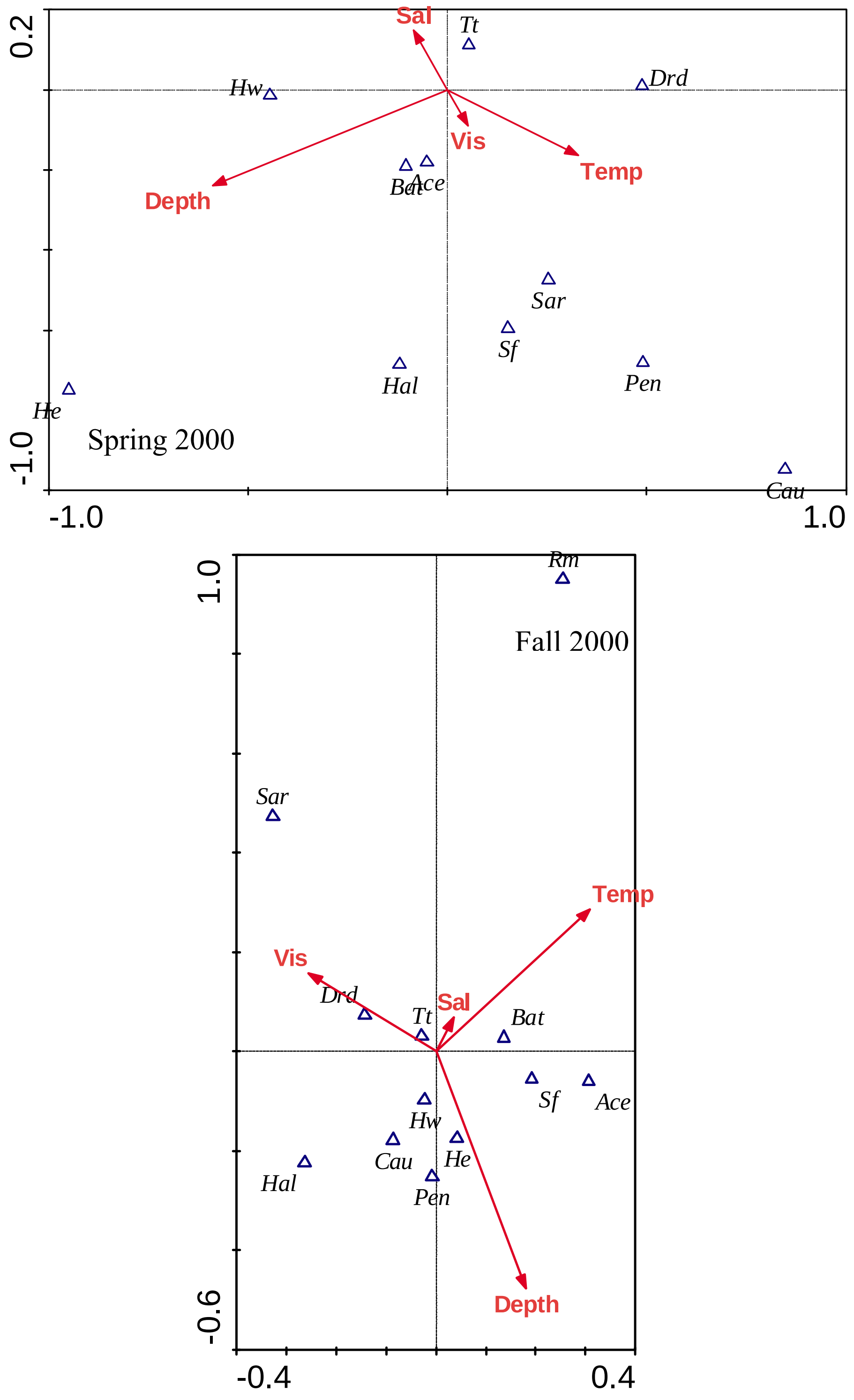


FIG. 97. Spring and Fall 2000 CCA plots.

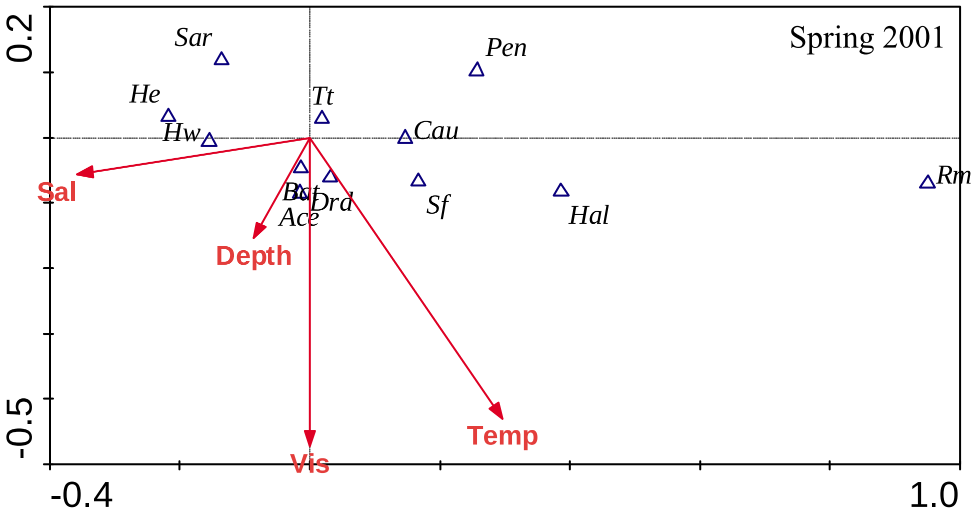


FIG. 98. Spring 2001 CCA plot.

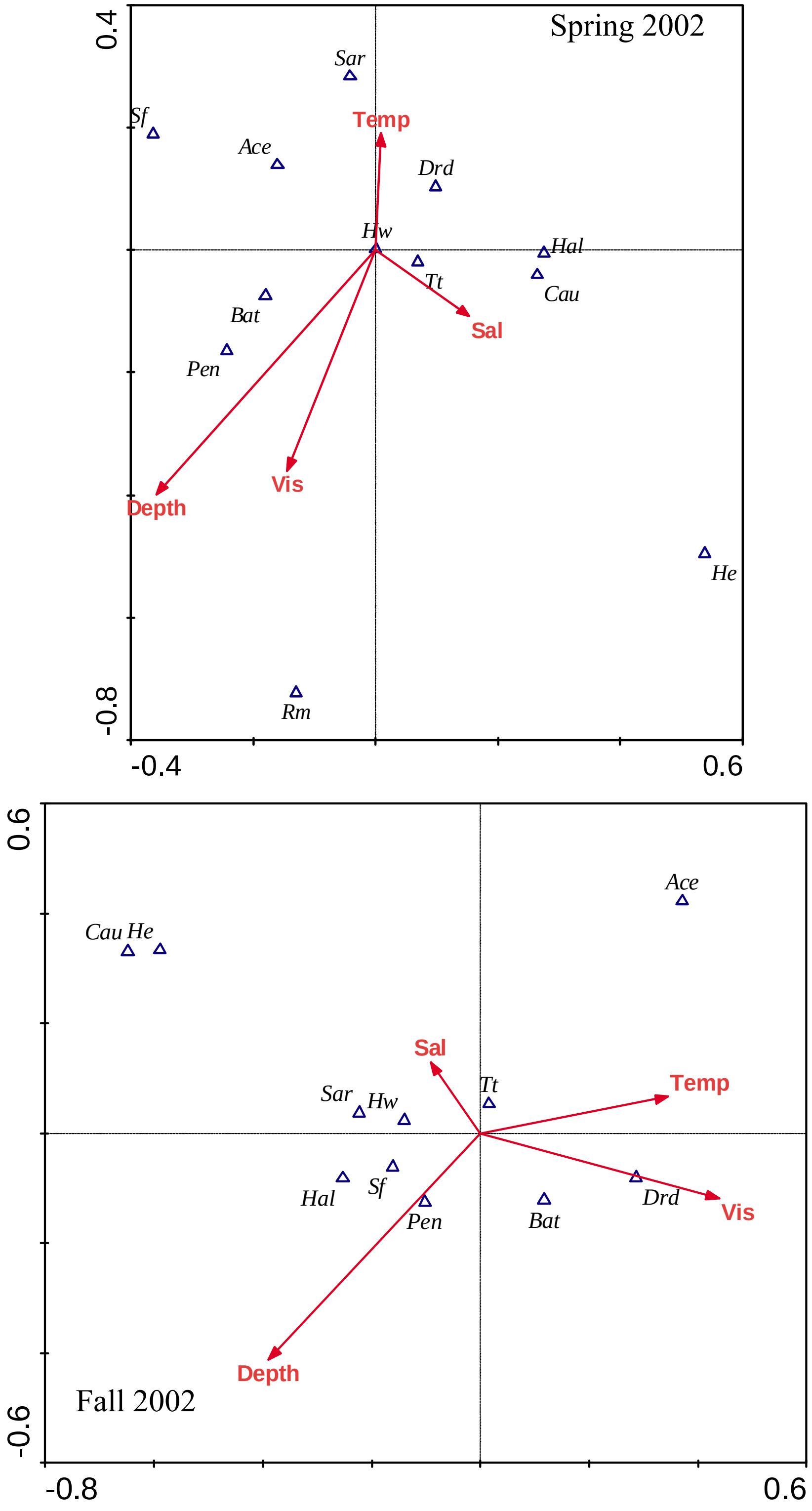


FIG. 99. Spring and Fall 2002 CCA plots.

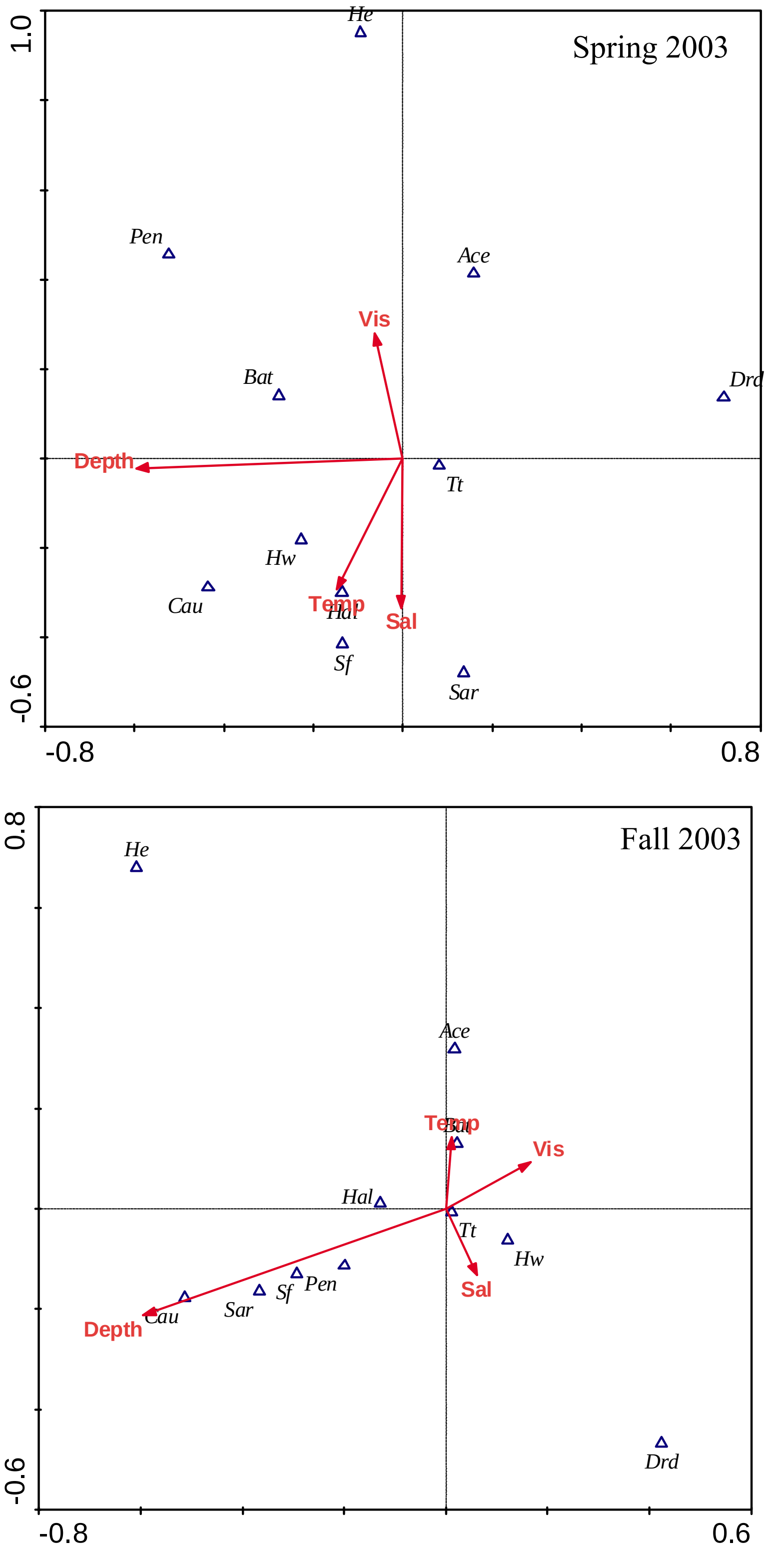


FIG. 100. Spring and Fall 2003 CCA plots.

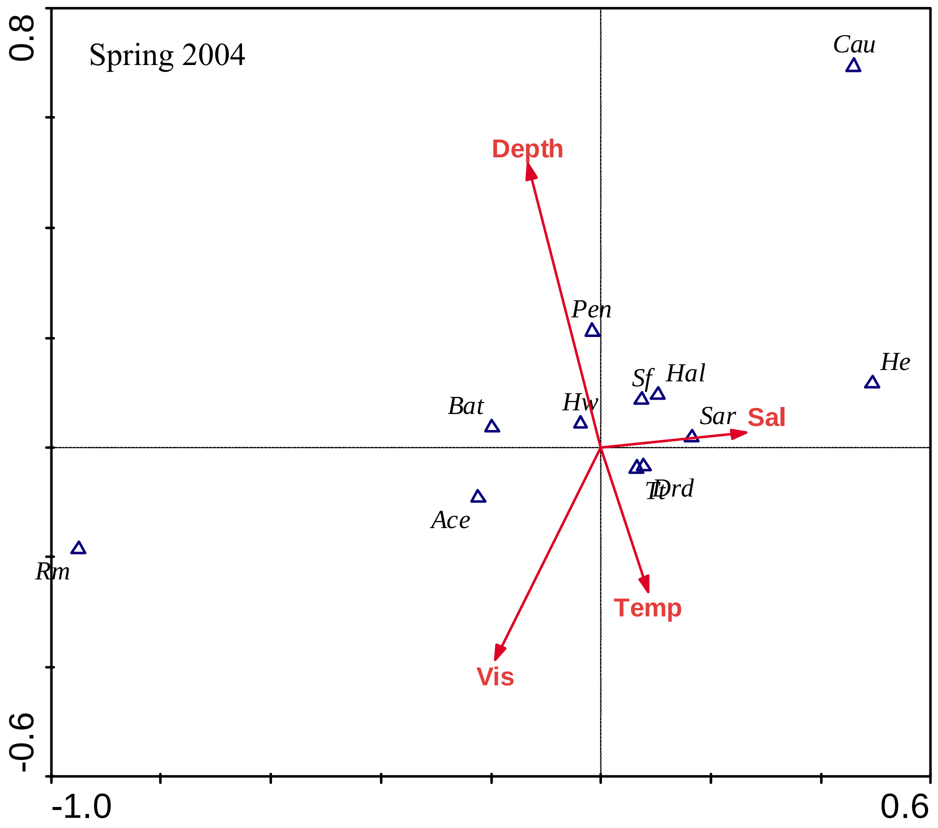


FIG. 101. Spring 2004 CCA plot.

DISCUSSION

FHAP data were analyzed at the bay-scale using weighted means and pooled data to determine if macrophyte density has changed in Florida Bay since 1995. Assessing change in the distribution and density of macrophytes at the bay-scale rather than the basin scale accounted for the size of each basin, which was not considered in the previous basin-scale assessment (Chapter 1). An increase in macrophyte density in a larger basin represents a far greater overall increase in that plant than would an equivalent increase in density in a smaller basin.

Thalassia remained the dominant macrophyte in Florida Bay between 1995 and 2004. The oscillating patterns seen in *Thalassia* density at the basin scale were apparent at the bay scale as well. Although density oscillated, overall *Thalassia* distribution and abundance was relatively constant over the course of the study. *Halodule* and *Syringodium* increased in density by spring 2004 and both exhibited bay-scale trends similar to and driven by those that were seen in the western basins, as neither were abundant enough throughout the rest of bay for this effect to be masked. Neither *Thalassia*, *Halodule*, nor *Syringodium* exhibited discernible trends in intra-annual variability.

Halophila and *Ruppia* were only seen occasionally in Florida Bay basins sampled by FHAP. Chapter One results showed that *Halophila* occurred in the western basins where lower light conditions, to which *Halophila* is more adapted (Durako et al. 2002), were more common. *Ruppia* was observed in areas more likely to receive freshwater input because it is a plant more acclimated to lower salinities than are found throughout the majority of the bay. *Ruppia* could potentially increase in distribution and density throughout the bay because of the Everglades Restoration Plan which is re-engineering or eliminating the water control structures in south Florida in order to mimic a more natural water flow through the Everglades (http://www.evergladesplan.org). This activity will increase the amount of freshwater delivered to Florida Bay, potentially decreasing the salinity and making conditions more favorable for plants such as *Ruppia* (Fourqurean et al. 2003, Kahn and Durako 2005).

As a group, macroalgae increased in the bay over the course of the study and several macroalgae surpassed the seagrasses, with the exception of *Thalassia*, in terms of density and distribution. *Batophora* increased in density more than any other macroalgae and was the second most abundant macrophyte in Florida Bay by 2004. Basin scale results (Chapter One) showed that, like *Acetabularia*, it increased significantly in the central basins but was virtually absent in the western basins. Although their spatial distributions were similar, *Batophora* colonized areas in which *Acetabularia* remained sparse, such as Crane and Whipray Basins, demonstrating its superior colonizing abilities. *Batophora* is holocarpic and maintains reproductive populations throughout the year although recorded reproductive activity is greatest in the fall (Morrison 1984). It exhibited some seasonality at the basin scale, but at the bay-scale it seemed only to exhibit linear increases in density, possibly suggesting that it became reproductive at different times of the year in different basins.

Acetabularia increased in both frequency and density from spring 1995 to spring 1998 and subsequently remained stable, though continued to exhibit dramatic intra-annual variation with spring densities much higher than fall densities. Although *Acetabularia* plants are reproductive throughout the year (Morrison 1984), evidence presented in Chapter One suggests that most of the population becomes reproductive sometime during the summer between June and September, as it was observed in higher densities when sampling took place in the spring, but then was much more sparse when sampling was conducted again in the fall. This could also potentially indicate intolerance to high summer temperatures and salinities, although nothing was found in the literature to support this possibility.

Caulerpa was observed in Blackwater Sound and the western basins, and was more dense during spring sampling, possibly due to its affinity for lower light conditions and higher growth rates during this time of year (O'Neal and Prince 1988, Collado-Vides and Robledo 1999). While it exhibited some intra-annual variability, it did not show any increasing or decreasing trends at either basin or bay scales.

Halimeda increased in several individual basins, particularly in the western area of the bay, as well as in Blackwater Sound in the east, and this increase was reflected at the bay scale. *Penicillus*, another calcareous macroalgae, also exhibited a bay-scale increase in density and frequency, but the majority of this increase took place in north-central basins: Rankin, Whipray, and Eagle. While *Halimeda* was rarely observed in Whipray, Madeira, Eagle, Calusa, or Crane, *Penicillus* was recorded throughout the bay. The difference in spatial extent exhibited by these two calcareous greens may be attributed to the fact that *Halimeda* is more acclimated to shallow water (less than one meter), deep sediments (more than one meter), higher current velocities, and dense *Thalassia,* while *Penicillus capitatus* exhibits higher growth rates in deeper (more than 3 meters) water, shallow sediment depths (from 5-20 cm), low currents and areas of sparse

Thalassia (Back 1979). The conditions favorable to *Penicillus* are found throughout the bay, but the conditions favorable to *Halimeda* are found primarily in the western basins.

Sargassum, a drift algae, was relatively insignificant in abundance in the bay throughout the duration of the study period. It was observed in basins more closely connected to the Everglades – potentially responding to freshwater input and salinity drops, or to increased nutrients from direct run-off in these areas. Because *Sargassum* is a marine algae (Lapointe 1995), its presence in these areas is more likely due to increased nutrients or because of its drifting nature – and consequently to wind patterns.

Finally, the drift reds, primarily composed of *Laurencia poiteii,* were highly variable throughout the bay. In terms of overall density, they constituted the third most abundant macrophyte in the bay, behind *Thalassia* and *Batophora*. Higher densities generally occurred in the more northern basins as well as in Blackwater Sound, but they were present throughout the bay during the study period. Bay-scale analysis indicated that drift red algae exhibit dramatic intra-annual variation with much higher densities and frequencies observed in the spring, concurrent with timing of peak densities found by Virnstein and Carbonara (1985) in the Indian River Lagoon, FL. After a decline from spring 1995 to fall 1995, there was an increasing trend in both frequency and density from spring 1996 to spring 2000. After this time, drift red density declined to just below their original relative density. Spring 2000 and spring 2002 showed large increases in density but only moderate increases in frequency, suggesting that while drift reds were not much more widely distributed, they were observed in larger quantities during these sampling events, possibly attributable to spikes in nutrient availability at those times. In fact, besides spring 2000 and spring 2002, spring and fall densities, though much different from one another, remained nearly constant over the course of the study.

Based on experimental evidence, Fourqurean and Rutten (2003) developed a successional model which suggests that if the south Florida ecosystems become more eutrophic, slow growing seagrasses will eventually be replaced by fast growing seagrasses which will eventually be replaced by macroalgae (benthic and epiphytic), which in turn will eventually be replaced by phytoplankton. Had bay scale analysis of the FHAP data been completed prior to basin-scale analysis, this model would have been accepted as the most likely scenario explaining the sequence of events occurring in Florida Bay. Bay scale data, particularly Figures 62 through 73, exhibit these trends. *Thalassia* appeared to have remained relatively stable while *Halodule* and *Syringodium* and several of the macroalgae increased.

However, having examined changes in macrophyte density and distribution in the ten basins individually, I feel confident in ruling out the general eutrophication of Florida Bay as an explanatory mechanism for this phenomenon. Basin scale results indicated that the increases in *Halodule* and *Syringodium* were isolated to the western basins. Although the trend was masked at the bay scale due to its dominance of the entire ecosystem, *Thalassia* also only increased in these basins. The increase in *Halimeda* density was primarily driven by trends in the western basins as well. These macrophytes did not, however, exhibit increases in density in the east-central and northeastern basins which were not affected by the 1987 *Thalassia* die-off. For this reason, and because they follow the typical post-disturbance successional model (Zieman 1982), it is more likely that the bay scale changes were a reflection of recovery of the western basins.

Recovery though does not explain the increased density of macroalgae in the central and northeastern basins because macrophytes in these basins were not affected by the mass die-off in 1987 (Robblee et al. 1991). Three other possible explanations can be explored and these include increased space availability, increased nutrient availability, and a lack of grazers. Because the seagrasses have not decreased in these basins since 1995, it is not likely that macroalgae were simply responding to increased space availability. An increased nutrient regime is likely, due to the upstream efforts to restore natural water flows through the Everglades and increased coastal development, but according to the experimentally based eutrophication model (Fourqurean and Rutten 2003), an increase in macroalgae would be preceded by an increase in seagrasses, first slow growing (*Thalassia*) and then fast growing seagrasses (*Halodule* and *Syringodium)*. Because of *Syringodium's* perpetual absence in the central and northeastern basins (except Blackwater Sound), it would not necessarily be expected that *Syringodium* follow this model. *Thalassia* and *Halodule*, however, are fairly common in these areas and had increased nutrients become available, they theoretically would have increased in density before the macroalgae, and this was not the case.

As indicated in Chapter One, because of the decline in the suitability of Florida Bay as fisheries and nursery habitat subsequent to the die-off (Butler et al. 1995), in addition to extensive recreational fishing pressure (Tilmant 1989), herbivorous fish have likely declined in Florida Bay. Larger herbivores such as the green sea turtle and manatee also once flourished in the bay (Jackson 2001, Thayer et al. 1984) but now their numbers have dwindled and it is very rare to witness either. Without these grazers, macroalgae are likely to exhibit increased densities, as is the case on many Caribbean coral reefs. A coral disease decreased the numbers of living corals in the Caribbean drastically, and macroalgae have exploited this newly-available space, preventing the recruitment of juvenile coral and re-establishment of coral on the reefs. Lack of grazer activity as a result of overfishing and the decline of herbivorous urchins, as opposed to increased nutrients, has been implicated as the major controlling factor for the macroalgal increase (Hughes et al. 1999). It is therefore not without precedent that lack of top-down control from grazers may be responsible for the increased macroalgae abundance in Florida Bay.

Having determined the extent of bay-scale change in macrophyte density, as well as the extent of intra-annual variability, another goal of this study was to determine if seagrass dynamics are correlated with macroalgal dynamics. Spearman Rank Order Correlation Analysis suggested that the same trends held true as in Chapter One. Although more Spearman Rank Order Correlations were detected when analyzing the Braun-Blanquet data at the bay scale, these are probably artifacts of the extensiveness of the data set and due to chance as opposed to biological or ecological significance *Thalassia* was generally negatively correlated to all other macrophytes, while *Halodule*, *Halophila*, and *Syringodium* were positively correlated to one another on most occasions. These three seagrasses, particularly *Halodule* and *Syringodium*, are pioneering species that rapidly colonize areas where *Thalassia* has been denuded (Williams 1990, Zieman 1982). Their positive correlations could therefore be attributed to their simultaneous presence and increase in the same areas.

Seagrass abundances fluctuated between being positively and negatively correlated with macroalgae abundances. As a group, the macroalgae were positively correlated with one another on most occasions. As was the case at the basin scale, exceptions did apply. However, the two most apparent relationships at the basin level were also found at the bay scale. *Acetabularia* and *Batophora* were repeatedly positively correlated, as were *Halimeda* and *Penicillus*. Although *Batophora* exploited areas that *Acetabularia* did not, and likewise for *Penicillus* and *Halimeda*, both pairs are closely related to one another and have somewhat similar substrate and possibly environmental requirements. In Card Sound, Bach (1979) found higher growth rates for *P. capitatus* in deeper waters with shallower sediments, and with low currents and sparse *Thalassia*; and found *Halimeda incrassata* more acclimated to shallower water with deeper sediments, more *Thalassia* and higher currents. FHAP results were similar to these trends at the basin-scale, but at the bay-scale their patterns in distribution and density were similar enough for them to be positively correlated on many occasions.

At the basin-scale, *Caulerpa* was often positively correlated to *Thalassia*. At the bay-scale, however, correlations between the two were infrequent and when they did occur, they were negative. This is probably explained by the extensive distribution of *Thalassia* in areas of the bay that exclude *Caulerpa* (shallow, high light areas). In the majority of the bay, *Thalassia* is much less dense than it is in the western basins where it can provide shade for *Caulerpa* (O'Neal and Prince 1988, Collado-Vides and Robledo 1999) and where it exhibited positive correlations. *Thalassia* is not dense enough in the remainder of the bay to support large stands of *Caulerpa*, therefore creating negative correlations when the data were pooled.

The repeatedly negative correlation between *Batophora* and the pioneering species of seagrasses at the bay scale was also exhibited at the basin-scale. Despite its small stature, *Batophora* showed the most dramatic increase in distribution and density of any of the macrophytes. Over the course of the study, it colonized almost all areas of the bay, with the exception of Johnson and Rabbit Key Basins – the basins in which *Halodule* and *Syringodium* were most dynamic. The lack of hard substrate (shells or sand) in these basins may also have played a role in inhibiting its colonization of this area.

Non-Metric Multidimensional Scaling was employed in conjunction with Total Seagrass and Total Macroalgae density overlays to show how basin macrophyte communities separated out and also to show the extent of hetero- or homogeneity within the bay. nMDS ordination plots exhibited spatially exclusive distributional patterns for the two groups of macrophytes. In terms of spatial distribution, pooling of the data yielded the same general trends as seen repeatedly at the basin scale. Total Seagrass distribution and Total Macroalgae distribution were generally mutually exclusive; and eleven times out of eighteen this negative correlation was statistically significant using Spearman Rank Order Correlation Analysis. The majority of these significantly negative correlations took place during the more recent years of FHAP sampling. The bay fluctuated between being relatively heterogeneous and relatively homogeneous based on station separation within the plots. Because of the large number of stations ordinated on one plot, it was difficult to discern clumps of stations belonging to one basin to determine if the basins were supporting different community assemblages. Stations located on the outskirts of the ordination varied over time, although stations from Blackwater Sound were routinely on the perimeter during the earlier years of sampling. Blackwater has been previously regarded as a representative of the bay as a whole (Hackney and Durako 2004). All taxa seen throughout the rest of the bay are represented in Blackwater most likely because of its physical heterogeneity: there is a great range of depth, sediment type and water quality within this basin which supports a variety of different macrophyte taxa.

A shift from non-significant to significant difference in the Total Seagrass and Total Macroalgae distributions took place in spring 1999. After that sampling event, the spring of 2001 was the only subsequent sampling event not to exhibit a significant difference in the two groups of macrophytes. This trend towards spatially exclusive behavior suggests that as macroalgae increased in the bay, areas that previously supported lower levels of macroalgae interspersed within seagrasses were later supporting higher levels of one or the other, possibly due to competition. Overlap in areas supporting moderate densities of both groups was seen during all sampling events.

The macrophyte community composition in Florida Bay during spring 2001 was uncharacteristically homogeneous according to the ordination plot – there was a very high degree of clustering with few outliers, and no significant difference between total seagrass and total macroalgae. This high degree of homogeneity coincided with a spike in salinity. Relatively high salinities were also recorded during the prior fall 2000 sampling in many basins. Many macrophytes exhibited uncharacteristically low densities in spring 2001. These same species also exhibited high densities during either spring or fall 2000, exacerbating the subsequent decrease. *Thalassia* peaked in fall 2000 – a period of high salinity in much of the bay, and then dropped in spring 2001. *Halodule* density also decreased, but *Syringodium* does not appear to have been affected. *Acetabularia* was low during both fall 2000 and spring 2001, and *Batophora* was unusually dense in fall 2000 and then much less dense in spring 2001. *Caulerpa* does not appear to have been affected, and *Halimeda* only slightly so with somewhat lower densities during those two sampling events. *Penicillus* was less dense during both fall 2000 and spring 2001, but *Sargassum* did not change. Finally, the drift reds spiked in density in spring 2000 but were much lower in density n spring 2001. Having examined the spikes in salinity and drop in densities of several of the macrophytes, the tight community clustering seen in the spring 2001 nMDS plot could have been attributed to macrophyte responses to the two-season salinity change. It appears that hyper-salinity stress may have caused decreased densities of many of the plants, thus making the bay's macrophyte communities more homogeneous.

Spring 2001 was also unusual in terms of Canonical Correspondence Analysis, which was used to determine if any of the physical variables measured by FHAP had a significant affect on macrophyte distribution. CCA showed that depth and visibility/water clarity were the initial driving forces in macrophyte distribution in Florida Bay from 1995-2000 and that many of the macroalgae grouped together in their functional and ecological roles in their response behavior to these physical variables. By spring 2001, visibility was no longer a significant driving force in macrophyte distribution. This change corresponded to a general decrease in turbidity and resulting increase in water clarity throughout the bay. Once the bay's waters cleared, salinity, and also water depth, were the most significant variables affecting macrophyte distribution, with salinity alone being the significant variably affecting distribution in spring 2001.

Because both water depth and water clarity significantly affected macrophyte distribution prior to spring 2001 and then depth and salinity affected distribution after spring 2001, water depth appears to be an important factor controlling distribution, although it rarely accounted for more than a few percent of the variability. This suggests that another environmental variable is having more influence on distribution than depth alone and that that factor is related to depth. One such parameter that co-varies with water depth is sediment type/sediment depth. Water depth and sediment depth increase along a northeast to southwest gradient (Zieman et al. 1989). Sediments in the northeast are more characteristically sandy and shelly with bedrock outcrops and gradually become more muddy towards the southwest. Different sediment/substrate types and sediment depths support different macrophytes, but due to lack of FHAP data regarding sediments, water depth was found to be the variable affecting distribution.

Salinity did not influence distribution significantly until spring 2001 – a year in which a large increase in salinity was detected in many basins. Salinity affected distribution during every subsequent sampling event except fall 2002, which interestingly yielded a spike above normal in salinity. Analysis of that sampling event, however, did not find any of the variables for which FHAP has data to be a significant factor controlling macrophyte distribution. Salinity was also very high during fall 2000 sampling. Although it seems that salinity affected macrophyte distribution in spring 2001 (as seen by a drop in density in many of the macrophytes), it is not altogether clear why it didn't have an effect the previous fall when the actual increase occurred. It could potentially be attributed to a delayed response, as has been observed in shading studies (Hall et al. 1991). Macrophyte distributions may not respond to acute salinity changes so were not actually affected until the following spring, when salinity was also high, suggesting significant community responses occurred only after hypersalinity conditions persisted. This may also have been the case with the fall 2002 increase in salinity – it appears that several macrophytes decreased slightly in density the following spring 2003, possibly again attributable to preceding hypersalinity conditions. Salinities were not hypersaline during spring 2003 sampling, but salinity significantly influenced distribution. These patterns suggest the existence of a lag in response to salinity and a possible dose-time threshold to cause significant community-level responses.

In conclusion, FHAP data suggest seagrass dynamics in the western basins represent a recovery of the system following the 1987 die-off. Increased macroalgae in the central and northeastern parts of the bay is most likely attributable to a decrease in grazer activity or increased nutrients, although due to a lack of seagrass response, the latter does not seem likely. Without experimental evidence and additional data, neither explanation is definite.

Because seagrasses remained stable throughout the central and eastern portions of the basins, it does not appear that the observed increase in macroalgae had a negative affect on seagrass density. Results from nMDS do however indicate that where there are higher densities of either seagrasses or macroalgae, there are lower densities of the other, while moderate densities of each co-occur. Thus, it appears that macroalgae are exploiting areas devoid of seagrass or with lower seagrass densities rather than preventing colonization by seagrasses.

CCA results showed that water depth or some variable coupled to depth are important in macrophyte distribution. It was also seen that spikes in salinity and more persistent hypersalinity conditions are capable of impacting macrophyte density and distribution significantly and should therefore continue to be monitored as the efforts of the CERP continue.

CCA results explained very little of the variability but did find depth to be a significant factor controlling macrophyte distribution on most occasions. Because of this, I believe that recording sediment type and depth, which change along the same gradient as water column depth, should be added to the FHAP sampling regime. General trends in sediment type and distribution are insufficient as the bottom of Florida Bay is so extensively heterogeneous that deep mud and rocky outcrops are often seen at the same station.

This dataset will provide an excellent resource to south Florida water managers as it provides a baseline of information and trends regarding all of the macrophytes regularly observed in Florida Bay. Changes to the Everglades hydrology will likely result in changes in Florida Bay and with this data set as a reference, the ecological effects of these changes will be more readily detected.

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