

MORPHOMETRIC VARIABILITY AND ALLOMETRIC RELATIONSHIPS IN THE  
SEAGRASS *THALASSIA TESTUDINUM* IN FLORIDA BAY

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## ABSTRACT

Morphometric variability and allometric relationships were investigated in the seagrass *Thalassia testudinum* in Florida Bay in 1998 and 1999. *Thalassia testudinum* is the dominant seagrass in this perturbed estuary and is important to its ecology. In this study I describe the trends and patterns of the morphometric characteristics of *T. testudinum* in ten basins in Florida Bay at two spatial scales in two sampling seasons. At the larger scale examined, only mean leaf number showed a significant interannual difference. Distributions of shoot-specific variables were more sensitive to interannual variation; however, both shoot-specific and area-specific characteristics have a high degree of variability at both levels examined. Certain morphometric parameters grouped together consistently and led me to define four ecological zones, similar to ecological zones defined in other studies based upon physical and other characteristics. The results of this study confirm that spatial heterogeneity in the distribution, abundance, and physical characteristics of *T. testudinum* support the concept of these ecologically distinct regions. Also, the results demonstrate the plasticity of *T. testudinum* morphology and the significant control that the physical and chemical environment of Florida Bay exert on this morphology. Density had little effect on the morphology of *T. testudinum*, which is similar to results reported for other clonal plants. However, density had a slight but significant negative correlation with leaf number; this was the only evidence of self-thinning seen. Age and water depth also had little effect on *T. testudinum* morphology. The results demonstrate that leaf area index can be used to estimate standing crop (and by extension productivity) and total shoot biomass of *T. testudinum* in Florida Bay. Leaf area index explained 97% of the variance in standing crop. The data compiled here show that some of the shoot-specific and area-specific characteristics of *T. testudinum* in

Florida Bay are strongly related and may prove to be useful descriptors of the architecture of this important seagrass.

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## CHAPTER 1

### INTERANNUAL AND SPATIAL MORPHOMETRIC VARIABILITY OF *THALASSIA TESTUDINUM*

#### INTRODUCTION

Seagrasses are rhizomatous marine angiosperms that form beds of varying density. As the dominant communities in many coastal environments of tropical and subtropical zones (den Hartog 1970) and as the climax communities in these systems (den Hartog 1977), seagrass beds fulfill several functions. Seagrasses stabilize bottom sediments, form structural substrate for epiphytic growth, provide nursery habitat and shelter to many organisms, and, most importantly, fix large amounts of carbon by photosynthesis which becomes available via direct herbivory and the detrital food web, both within the system and by export to other systems (den Hartog 1977, Borum & Wium-Andersen 1980, Zieman 1982, Thayer et al. 1984, Kenworthy et al. 1988, Duarte 1989). Yet, these important habitats often are affected by catastrophic mortality events (Kemp et al. 1983, Orth & Moore 1983, Cambridge et al. 1986, Larkum & West 1990), and recently a worldwide decline in the areal extent of seagrass beds has been observed (Short and Wyllie-Echevernia 1996, Duarte 2002).

In the South Florida region, total seagrass habitat is estimated to be more than 17,000 km<sup>2</sup> of semicontinuous beds (Fourqurean et al. 2002). Seagrasses are both the dominant biological community and the dominant physical feature of Florida Bay (Durako et al. 2002), the shallow, triangular lagoon south of the Florida peninsula. The dominant seagrass within this area is turtlegrass, *Thalassia testudinum* Banks ex König (Hydrocharitaceae), which usually occurs in dense, highly productive beds (Patriquin

1973). Seagrass beds (dominated by *T. testudinum*) cover more than 80% of the area of Florida Bay which is within Everglades National Park (Zieman et al. 1989). The shallow distribution and close proximity to the land/sea interface of these seagrass beds cause them to be sensitive to changes in the nearshore marine environment. Therefore, the distribution, abundance, and condition of seagrasses may be indicative of the health of Florida Bay.

These habitats are crucial for the productivity of fisheries and wildlife in this area (Zieman et al. 1989); the distribution of many faunal species is closely linked to seagrass meadows (Thayer & Chester 1989, Thayer et al. 1999); and changes in faunal communities of seagrass-covered mud banks in Florida Bay are associated with changes in their habitat (Matheson et al. 1999). One such change is the rapid and widespread mortality of *T. testudinum* in Florida Bay since 1987 (Robblee et al. 1991, Durako 1994, Fourqurean & Robblee 1999).

A number of stress-inducing agents have been proposed as the cause of this mass mortality, including unusually high salinities and temperatures, reduced freshwater input from the Everglades watershed, reduced frequency of tropical storms, sulfide toxicity, self-shading and chronic hypoxia of *T. testudinum* roots and rhizomes caused by biomass accumulation, an epidemic of a pathogenic marine slime mold (*Labyrinthula* sp.), or a combination of one or more of these factors (Robblee et al. 1991, Carlson et al. 1994, Durako & Kuss 1994, Durako 1994, Fourqurean & Robblee 1999). The resultant die-off of *T. testudinum* has contributed to eutrophication and increased turbidity in the Florida Bay system, which has led to a system-wide disturbance that threatens the stability of this valuable ecosystem (Butler et al. 1995). Examples such as this emphasize the importance of seagrass habitats and the key role they play in coastal ecosystems. This realization has

led to increased efforts to quantify seagrass annual productivity and growth dynamics to gain insight into the health of entire systems (Duarte et al. 1994, Durako 1995).

Seagrasses grow by reiteration of both horizontal and vertical rhizome internodes, leaf clusters, and roots (den Hartog 1970, Tomlinson 1974). In *Thalassia testudinum*, rhizomes (long-shoots) creep horizontally with branches at regular intervals that give rise to erect short-shoots with strap-shaped blades and anchoring roots (Patriquin 1973, Tomlinson & Vargo 1966, Duarte et al. 1994). Growth occurs in the apical meristem, the source of all plant biomass in seagrasses (Tomlinson 1974). Seagrasses are clonal plants; in *T. testudinum*, individual short-shoots and their blades comprise ramets, which are physically connected along the rhizome and which are physiologically integrated to comprise the genet, or genetic individual (Tomasko & Dawes 1989). Patriquin (1973) demonstrated how the internodal length of rhizomes can be used to determine plant age. Duarte et al. (1994) and Durako & Duarte (1997) further refined reconstructive aging techniques for *T. testudinum* using plastochrone intervals (the time interval between the formation of two successive leaves) in both rhizomes and short-shoots. Other structural and dynamic characteristics of *T. testudinum* include leaf width, leaf length, number of leaves per short-shoot, leaf area, number of leaf scars, leaf productivity, and leaf turnover (which are shoot-specific characteristics, along with plastochrone interval); area-specific characteristics include short-shoot and rhizome-apical densities, leaf area index, leaf productivity, and biomass (Durako 1995). Many of these characteristics appear suitable for evaluating the ecological condition of *T. testudinum* (Durako 1995).

As a clonal plant, vegetative growth is the dominant method of expansion of *Thalassia testudinum* beds (Tomlinson 1974, Zieman 1975), and recovery of seagrass beds from chronic decline depends to a large part on horizontal rhizome growth (Duarte

& Sand-Jensen 1990a). Rhizome growth is in turn dependent on the products of photosynthesis that result from the development of leaf-bearing shoots (Duarte & Sand-Jensen 1990b, Fourqurean & Zieman 1991). Although green photosynthetic leaves account for only 10 to 45 % of the total biomass of seagrasses (Brouns & Heijs 1986, Zieman 1982, Fourqurean & Zieman 1991), above-ground production is more easily assessed than below-ground biomass because of the accessibility of the leaves (van Tussenbroek 1995, 1998). Biomass of individual leaves is dependent on leaf area (Wahbeh 1984), and leaf dimensions (which comprise leaf area) are affected by environmental conditions and reproductive effort (McMillan 1978, Hulings 1979, McMillan & Phillips 1979, West & Larkum 1979, Durako & Moffler 1985, Dawes & Tomasko 1988, Harrison & Durance 1992, Lee & Dunton 1997). Phillips & Lewis (1983) specifically correlated leaf width with environmental stress and observed that seagrasses occur over ecological, spatial, and temporal gradients where plant characteristics (such as leaf dimensions) are correlated with environmental factors. Durako (1995) also observed that changes in structural characteristics, such as leaf length, width, and shoot-specific leaf area, may indicate response to environmental conditions at intermediate time scales between acute and chronic stress.

This study attempts to describe the trends and patterns of the morphometric characteristics of *Thalassia testudinum* in ten basins within Florida Bay during two sampling seasons. *Thalassia testudinum* is of interest because it is the most abundant seagrass species in the areas of Florida Bay examined, and it is usually considered the dominant primary producer in late-successional or climax seagrass communities (Patriquin 1973). *Thalassia testudinum* is one of the most studied seagrasses; however, the size of the dataset in this study is large. The null hypothesis examined was that the



morphometric characteristics of *T. testudinum* were constant across the bay. This hypothesis was tested by comparing shoot-specific and area-specific characteristics of *T. testudinum* in Florida Bay at the two spatial scales.

## METHODS

### Study area

This study was based on field collections in Florida Bay (ca. 25E05N, 81E45W), the shallow, seagrass-dominated lagoon which separates the Florida Keys from the southern tip of the Florida Peninsula (Fig. 1). The lagoon is triangular with mud banks that divide the Bay into 49 basins while restricting circulation and dampening tidal influence (Robblee et al. 1991; see Fourqurean & Robblee 1999 for a detailed description of Florida Bay). The samples were collected within Everglades National Park (ENP) over a range of habitat types and distances. The average water depth in the 2000 km<sup>2</sup> area within ENP is ca. 1 m but varies from less than 1 m to about 3 m (Schomer and Drew 1982). Although seagrass communities cover most of the Bay, community development increases in a strong gradient from the enclosed northeastern sections of the bay to the more open western sections (Zieman et al. 1989). *Thalassia testudinum* occurs in both monospecific and mixed-species seagrass beds throughout the Bay; in the northeast, communities are dominated by mostly sparse beds of *T. testudinum* with localized denser areas, but increasingly dense beds of *T. testudinum* are often intermixed with the

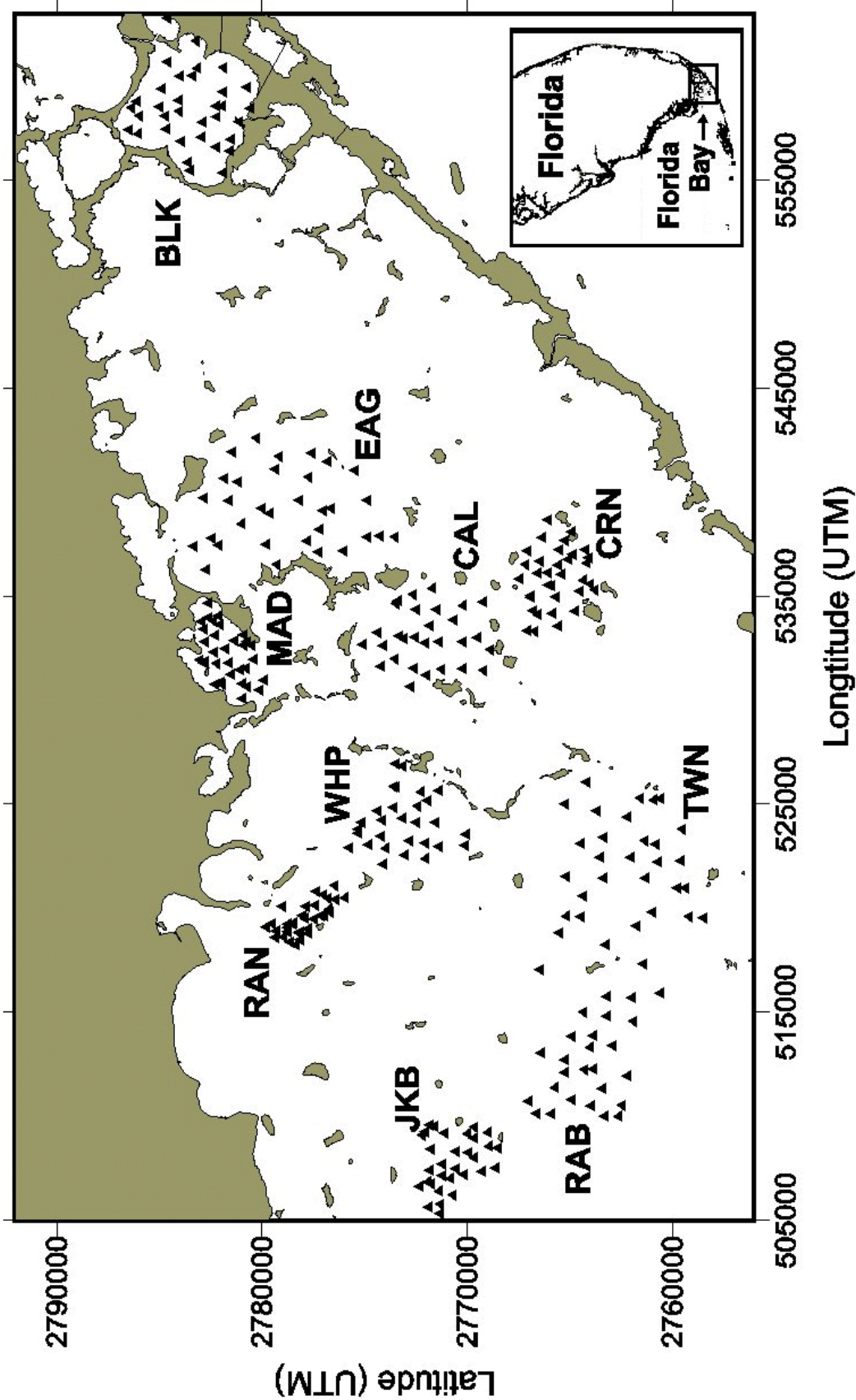


Figure 1. Florida Bay showing the locations of sites sampled in 1998 and 1999.

seagrasses *Halophila wrightii* Aschers., *Syringodium filiforme* Kützinger, and *Halophila engelmannii* Aschers. toward the west. Salinity and water clarity are highly variable throughout the Bay (Zieman 1982). As a negative estuary, the Bay is normally subject to periods of hypersalinity (Boyer et al. 1999), and increased light attenuation due to microalgal blooms and resuspended sediments has become apparent in recent years in many parts of the Bay (Stumpf et al. 1999). After a period of extremely high salinities in 1989-1990, Zieman et al. (1999) found mean salinity in the Bay from 1991-1995 to oscillate between 29 and 32 psu in winter and between 35 and 39 psu in summer. The waters of Florida Bay historically have been clear, but water clarity in the Bay is subject to broad regional and temporal differences. Turbidity has increased in the years since the *T. testudinum* die-off; Fourqurean & Zieman (1991) found diffuse light attenuation to be generally low in the Bay (mean  $k_d = 0.5 \text{ m}^{-1}$ ) prior to 1990, but in 1993-1994  $k_d$  ranged from 0.7 to  $2.8 \text{ m}^{-1}$  (Phlips et al. 1995). Light attenuation is generally greatest in the eastern and south-central regions of the Bay and lowest in the north-central and western regions (Phlips et al. 1995). Water temperature is more constant among basins, but it shows much seasonal variation due to the shallow nature of the Bay (Zieman 1982). Fine-grained to muddy-sand carbonate sediments increase in depth in a gradient from northeast to southwest (Zieman et al. 1989).

### Sampling methodology

Collections were made during the spring sampling of the Florida Bay Fish Habitat Assessment Program (FHAP) in May 1998 and May 1999. FHAP was established in 1995 to assess status and trends in the benthic fish habitat of Florida Bay as part of a multi-agency coordinated monitoring program implemented in this area to detect and

avert regional-scale seagrass loss (Fourqurean et al. 2002). FHAP proposes to accomplish this by providing spatial assessment and resolution of both intra- and inter-annual variability in the macrophyte (seagrass and macroalgae) communities of the Bay and by providing change data to monitor responses to environmental and anthropogenic perturbations of this system. Spatial assessment of the Bay is achieved by examining the species distribution and relative abundance of macrophytes at a baywide scale. Sampling is conducted twice-yearly during the spring (May) and early fall (October) in ten of the 49 basins (Table 1), which represent a continuous gradient across the Bay. Each basin is subdivided into 28 to 33 fixed, tessellated hexagonal grids from within which station locations are randomly chosen to yield a total of about 320 stations per sample period (Fig. 1); these stations are located using a handheld GPS. This sampling design results in systematic random sampling, with sampling effort scaled to the size of the basin, and provides suitable spatial data for interpolation (see Durako et al. 2002 for a detailed description of the FHAP sampling design).

For this study *Thalassia testudinum* was collected as part of the quantitative assessment of the benthic macrophyte communities during the 1998 and 1999 spring FHAP sampling; the 1998 sites were revisited in 1999. A core sample (177 cm<sup>2</sup>) was taken in the first of four Braun-Blanquet visual sample quadrats at each station. Thus, each spring sample consisted of over 300 core samples. Water depth and temperature, salinity, and secchi depth were recorded at each station. Plant material from the cores was washed free of sediment in the field, stored in plastic bags, and frozen for subsequent

Abbreviation	Basin
BLK	Blackwater Sound
CAL	Calusa Key
CRN	Crane Key
EAG	Eagle Key
JKB	Johnson Key
MAD	Madeira Bay
RAB	Rabbit Key
RAN	Rankin Lake
TWN	Twin Key
WHP	Whipray Bay

Table 1. List of sampled basins and their abbreviations in Florida Bay.

analysis. After thawing, seagrasses were sorted by species, short-shoot density (number  $\text{m}^{-2}$ ) was determined from the material in each core, the plant material was rinsed in 10% HCl to remove carbonates, and leaves were scraped carefully with a razor blade to remove epiphytes. Epiphyte loads were not quantified. Only those cores with live *T. testudinum* short-shoots (those with intact green blades) were analyzed for this study; dead short-shoots and dead rhizome material were discarded, and those short-shoots which were alive but without green blades (white or brown and crispy short-shoots with immature, white blades) were noted but not used in this analysis. In 1998 a total of 318 cores were collected; of these, 211 (66%) contained live *T. testudinum* short-shoots. Of the 314 cores taken in 1999, 232 (74%) contained at least one live short-shoot. For each live short-shoot, the number, length (cm) from point of attachment to the short-shoot leaf tip, and width (cm) just above the sheath (a protective covering consisting of dead leaves) of all green blades were recorded, and the shoot age in plastochrone intervals (the number of leaf scars plus the number of green and white blades) was calculated.

Green leaves (above-ground biomass) were dried to constant weight at 60EC and weighed to obtain standing crop ( $\text{g m}^{-2}$ ). Live short-shoot and live rhizomes and roots (white or brown and crispy) were also dried to constant weight (60EC) and weighed to obtain below-ground biomass ( $\text{g m}^{-2}$ ). These data were used to generate two types of characteristics of *T. testudinum*, shoot-specific characteristics and area-specific characteristics. Shoot-specific characteristics are leaves  $\text{shoot}^{-1}$ , maximum shoot leaf length, mean shoot leaf length, maximum leaf width, shoot-specific leaf area (the sum of the leaf area of a short-shoot,  $\text{cm}^2$ ), and shoot age (leaf scars  $\text{shoot}^{-1}$ ). Area-specific characteristics are short-shoot density, leaf area index (LAI, mean shoot-specific leaf area

× short-shoot density,  $\text{m}^2 \text{m}^{-2}$ ), standing crop ( $\text{g m}^{-2}$ ), and the ratio of above- to below-ground biomass.

### Statistical analyses

Samples from both years were used in morphometric analyses to assess year-to-year changes in shoot-specific and area-specific characteristics at two spatial scales: the Bay level and the basin level. Thus, within-year and between-year variability of the Bay was described, as was the variability between years of each basin. Graphical and statistical analyses were performed on the data both to visualize and quantify trends in each measured parameter. Morphometric characteristics were compared with a two-tiered approach. First, for each year the range and distribution of each characteristic was described and analyzed for both spatial scales; distributions were binned into appropriate classes. Significance ( $D_{\max} > 0.05$ ) of changes in these distributions between 1998 and 1999 was determined using the Kolmogorov-Smirnov Two-sample test (which does not require normality). Second, paired *t*-tests were used to assess baywide differences in the six shoot-specific characteristics and in the four area-specific characteristics between 1998 and 1999. Data were log transformed if necessary to approach normality and homogeneity of variance; however, Mann-Whitney Rank Sum analyses were used in lieu of *t*-tests when data could not be transformed to meet these assumptions. The criterion for significant differences was  $p < 0.05$ . Due to large variances within cores for some of the variables and because of the possible relatedness of the individual ramets, data from the short-shoots within each core were averaged prior to subsequent analysis. As a result, each core was considered as a replicate and each short-shoot within a core as a

subsample. Box-and-whisker diagrams were created for each morphometric characteristic in each basin to depict the distribution of data around the mean and median. Paired *t*-tests and Mann-Whitney Rank Sum tests were used to assess differences in the morphometric characteristics between 1998 and 1999. In addition, differences among basins were tested with a one-way ANOVA, after which basins were grouped into similar subsets using Duncan's Multiple Range tests for each variable to assess trends within the Bay.

After these tests were performed, some patterns became evident. Certain basins consistently grouped together into similar Duncan's subsets. To assess the statistical significance of these patterns, principal component analysis (PCA) was used to extract principal components from the means of the data and to further group the ten basins into four zones or regions based on biological similarities, such as those suggested by Zieman et al. (1989), Philips et al. (1995), or Boyer et al. (1999). Differences among the four zones were tested with a second series of one-way ANOVAs of the zone-pooled data. Zones were then grouped into similar subsets using Duncan's Multiple Range tests for each variable to confirm the independent assortment of the zones suggested by the PCA results. All statistical tests were performed using the SAS statistical program (SAS, Cary, NC) or SigmaStat (Jandel Scientific, San Rafael, CA).

## RESULTS

### Physical parameters



Physical data from 300+ sites collected in 1998 and 1999 are presented in Table 2. Mean salinity and temperature were both higher in 1999 while average secchi depth was similar between the years.

#### Biological Parameters

Morphometric characteristics of *Thalassia testudinum* in Florida Bay in 1998 and 1999 are summarized in Table 3. In this table, data from all ten basins were pooled for each year. Large ranges were measured and standard deviations generally were high due to the wide spatial sampling plan. Leaf width and leaf number exhibited the lowest variation in the pooled data, each with a standard deviation of about 30%. The other characteristics had standard deviations from 60% to in excess of the mean. The means of all shoot-specific characteristics increased from 1998 to 1999, except leaf number, which decreased. If the short-shoots within each core were treated as individuals (resulting in the high sample sizes reported in Table 3), each of the shoot-specific characteristics displayed significant interannual differences (Mann-Whitney Rank Sum tests,  $p < 0.001$  for all except shoot leaf area,  $p = 0.003$ ). However, if each core was treated as a replicate, only leaf number exhibited a significant difference from 1998 to 1999; shoots had 4% fewer leaves in 1999 ( $p < 0.005$ ). Area-specific characteristics were not significantly different between 1998 and 1999 ( $p > 0.05$ ).

Parameter Mean (Range)						
Year	Basin	n	Depth (cm)	Salinity (‰)	Temperature (EC)	Secchi (cm)
1998	BLK	34	236.5 (175 - 305)	27.3 (25.6 - 28.4)	30.8 (30.1 - 31.9)	236.5 (175 - 305)
	CAL	29	201.6 (140 - 225)	36.7 (33.7 - 38.0)	28.8 (28.2 - 29.4)	190.3 (30 - 225)
	CRN	34	197.9 (110 - 230)	35.9 (34.1 - 37.8)	27.3 (25.4 - 28.6)	192.6 (100 - 230)
	EAG	32	188.3 (165 - 218)	25.6 (22.8 - 28.4)	29.8 (29.2 - 30.7)	166.5 (80 - 218)
	JKB	32	149.5 (65 - 190)	34.9 (34.5 - 35.8)	28.3 (27.0 - 30.7)	141.4 (65 - 185)
	MAD	33	113.4 (55 - 137)	33.3 (28.0 - 35.4)	30.7 (29.7 - 32.1)	111.5 (55 - 137)
	RAB	28	183.0 (60 - 245)	34.9 (34.1 - 36.8)	26.9 (25.5 - 31.4)	164.3 (60 - 240)
	RAN	34	118.7 (50 - 140)	35.6 (35.2 - 36.5)	28.5 (27.7 - 29.5)	109.7 (50 - 140)
	TWN	31	212.7 (130 - 270)	35.3 (34.3 - 36.5)	29.0 (27.9 - 30.7)	212.4 (130 - 270)
	WHP	31	157.7 (80 - 205)	37.6 (36.8 - 38.7)	26.8 (25.4 - 28.3)	149.2 (70 - 205)
	All Basins	318	175.5 (50 - 305)	33.6 (22.8 - 38.7)	28.7 (25.4 - 32.1)	167.3 (30 - 305)
1999	BLK	34	217.5 (160 - 275)	36.3 (36.0 - 36.8)	29.8 (29.1 - 31.2)	217.5 (160 - 275)
	CAL	29	205.9 (140 - 235)	39.8 (39.3 - 40.2)	30.0 (29.1 - 31.0)	187.3 (130 - 235)
	CRN	34	188.5 (75 - 220)	39.2 (39.0 - 39.5)	28.5 (26.9 - 29.4)	187.8 (75 - 220)
	EAG	32	174.7 (145 - 220)	35.3 (33.3 - 37.3)	30.4 (29.9 - 32.3)	174.7 (145 - 220)
	JKB	31	134.7 (40 - 180)	36.4 (35.4 - 37.1)	29.3 (28.5 - 30.2)	133.1 (40 - 180)
	MAD	33	100.6 (60 - 125)	39.9 (39.4 - 40.3)	29.0 (27.9 - 30.7)	93.8 (60 - 125)
	RAB	27	179.3 (60 - 250)	36.9 (36.4 - 37.8)	31.1 (29.9 - 33.1)	176.1 (60 - 250)
	RAN	34	119.9 (70 - 140)	37.2 (34.9 - 38.3)	30.7 (27.9 - 33.2)	112.4 (60 - 140)
	TWN	31	208.4 (135 - 265)	37.8 (36.7 - 39.2)	29.2 (28.4 - 30.1)	208.4 (135 - 265)
	WHP	29	161.6 (80 - 190)	38.7 (35.8 - 40.0)	29.0 (28.0 - 30.7)	157.2 (80 - 190)
	All Basins	314	168.5 (40 - 275)	37.8 (33.3 - 40.3)	29.7 (26.9 - 33.2)	164.4 (40 - 275)

Table 2. Physical data from 300+ sites in ten basins in Florida Bay in May 1998 and May 1999.

Table 3. Summary of structural characteristics of *Thalassia testudinum* in Florida Bay in 1998 and 1999, all samples combined. The median value is given in parentheses for leaf scars shoot<sup>-1</sup> (shoot age) because of the skewed nature of most age data.

Year	Characteristic	n	Mean (Median)	STD	Range
<b>Shoot-specific characteristics</b>					
1998	Leaves shoot <sup>-1</sup>	1494	3.29	1.082	1 - 7
1999	Leaves shoot <sup>-1</sup>	1622	3.15	1.045	1 - 9
1998	Max leaf length (cm)	1494	11.27	7.143	0.1 - 45.2
1999	Max leaf length (cm)	1622	12.01	6.880	0.1 - 58.5
1998	Mean shoot leaf length (cm)	1494	8.60	5.398	0.1 - 34.5
1999	Mean shoot leaf length (cm)	1622	8.93	4.980	0.1 - 37.6
1998	Max leaf width (cm)	1494	0.48	0.168	0.1 - 1.4
1999	Max leaf width (cm)	1622	0.52	0.174	0.1 - 1.1
1998	Leaf area shoot <sup>-1</sup> (cm <sup>2</sup> )	1494	17.39	21.371	0.02 - 250.3
1999	Leaf area shoot <sup>-1</sup> (cm <sup>2</sup> )	1622	18.03	19.228	0.04 - 179.1
1998	Leaf scars shoot <sup>-1</sup>	1494	33.89 (30.0)	19.429	4 - 159
1999	Leaf scars shoot <sup>-1</sup>	1622	36.41 (32.0)	19.817	3 - 138
<b>Area-specific characteristics</b>					
1998	Short-shoots m <sup>-2</sup>	211	400.76	333.930	56.6 - 1754.6
1999	Short-shoots m <sup>-2</sup>	232	394.01	351.840	56.6 - 2037.6
1998	LAI (m <sup>2</sup> m <sup>-2</sup> )	211	0.697	0.893	0.008 - 5.304
1999	LAI (m <sup>2</sup> m <sup>-2</sup> )	232	0.710	0.969	0.007 - 6.682
1998	Standing crop (g m <sup>-2</sup> )	211	27.56	33.521	0.38 - 183.95
1999	Standing crop (g m <sup>-2</sup> )	232	27.30	35.242	0.28 - 205.80
1998	Above-ground:below-ground biomass	211	0.14	0.129	0.006 - 0.921
1999	Above-ground:below-ground biomass	232	0.12	0.096	0.003 - 0.642

## Distributions

The distributions of shoot-specific and area-specific characteristics of *Thalassia testudinum* in Florida Bay in 1998 and 1999 are shown in Figures 2 to 6; distributions within basins are shown in Figures 7 to 12. At the Bay level, leaf number and leaf width had slightly positively skewed but otherwise fairly uniform distributions. All other distributions at the Bay level were positively skewed. Distributions at the basin level were variable.

Leaves per shoot declined from 1998 to 1999 in the Bay (Table 2), and the distribution of leaf number at the Bay level followed that trend with a negative shift (Fig. 2A). The change in the distribution of leaf number was significant ( $D_{\max} > D_{0.05}$ ). Within-basin comparisons of the leaves per shoot distributions (Fig. 7) between 1998 and 1999 showed that although leaf number declined in seven of ten basins, a significant difference occurred between the two years only at Rabbit Key Basin. The modal class in the Bay for both years was three leaves per shoot, and about 70% of the total short-shoots in the Bay had between three and four leaves. At the basin level, the majority of shoots also had three to four leaves; however, about 80% of the shoots in Johnson Key Basin had four to six leaves while more than 70% in Eagle Key Basin had only two to three leaves.

The distribution of shoots with wider leaves was significantly higher in 1999 than in 1998 at the Bay level (Fig. 2B). Twin Key, Rankin Lake, and Whipray Basins all exhibited significant increases in shoot abundance with increasing width (Fig. 8); five of the other seven basins displayed insignificant positive shifts in distribution. About 80% of shoots in the Bay had leaves from 0.3 to 0.6 cm wide; the modal class for both years was 0.4 cm. Leaf width in the basins was much more variable, with Johnson Key, Rabbit

Key, and Rankin Lake Basins having a greater amount of shoots with wide leaves and Crane Key, Calusa Key, and Eagle Key Basins having shoots with thinner blades.

The distributions of maximum leaf length and mean leaf length were similar. The maximum leaf length (Fig. 3A) of more than 50% of shoots within the bay was between 6 and 14 cm while about 50% of shoots had a mean shoot length (Fig. 3B) of 4 to 10 cm. Both maximum leaf length and mean shoot leaf length displayed significant positive distribution shifts from 1998 to 1999 at the bay level. The modal class of maximum length was 8 - 10 cm in 1998 but increased to 10 - 12 cm in 1999; the mode of mean length displayed a similar shift from the 6 - 8 cm size class in 1998 to the 8 - 10 size cm class in 1999. Within-basin comparisons of maximum length (Fig. 9) and mean length (Fig. 10) distributions showed that, like width, length was variable at the basin level; Madeira Bay, Crane Key, Calusa Key, and Eagle Key Basins had positively skewed distributions while those of the other basins were more symmetrical. Johnson Key Basin had bimodal distributions of maximum length. Significant differences in the distributions of maximum leaf length and mean length were detected between the two years at Whipray and Calusa Key Basins, both of which were positive shifts. Six of the remaining eight basins and five of eight had insignificant positive shifts in maximum leaf length and mean length, respectively.

Nearly 60% of the shoots in the Bay had shoot-specific leaf areas between 5 and 15 cm<sup>2</sup> (Fig. 4A). The modal class in both years was 5 - 10 cm<sup>2</sup>, but there was a significant shift towards greater area in 1999. As at the Bay level, the distributions in the basins in general were also positively skewed, but those of Rabbit Key Basin and Rankin Lake were more symmetrical and those of Johnson Key again were bimodal. The

majority of basins also displayed positive interannual shifts, although only that of Whipray Basin was significant.

The distributions of leaf scars indicate a low representation of very young shoots (those with few leaf scars) at both Bay (Fig. 4B) and basin (Fig. 11) levels. The distributions at the Bay and basin levels were similar and positively skewed. About 50% of the shoots in the Bay had 50 leaf scars or less, and in both sampling seasons the modal age class was 20 - 25 leaf scars. The Bay had a significantly older population in 1999. Most of the basins also had older shoots in 1999, although this demographic shift was significant at the basin level only in Whipray and Crane Key Basins.

Changes in the distributions of all four area-specific characteristics were insignificant at the Bay level. Because of relatively small sample sizes and large variances, plots of the distributions of area-specific characteristics at the basin level were not generated. The pattern of the distribution of shoot density was similar between 1998 and 1999 (Fig. 5A). Nearly 60% of cores had six or fewer shoots in both years ( $< 350$  shoots  $\text{m}^{-2}$ ), and the modal class for both years was the smallest size class (1-2 shoots  $\text{core}^{-1}$ , or ca. 115 shoots  $\text{m}^{-2}$ ). There was a negative shift in the ratio of above- to below-ground biomass from 1998 to 1999 (Fig. 5B); the modal class was 0.075 - 0.10 in 1998 compared to 0.05 - 0.075 in 1999. This difference, however, was insignificant. The distributions of standing crop (Fig. 6A) and leaf area index (Fig. 6B) were similar; both distributions were positively skewed. The modal class in 1998 and 1999 for standing crop was 10 - 20  $\text{g m}^{-2}$ , and about 50% of sites in the bay had less than 30  $\text{g m}^{-2}$  standing crop. During both years the modal class of leaf area index was 0.2 - 0.4  $\text{m}^2 \text{ m}^{-2}$ ; very few sites had leaf area indices greater than 1.0  $\text{m}^2 \text{ m}^{-2}$ .

Figure 2. Interannual comparisons of the distributions of number of leaves shoot<sup>-1</sup> (A) and maximum leaf width (B) of short-shoots of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 (n = 1494) and shaded bars represent 1999 (n = 1622). Significant differences in distributions between years were seen in both plots based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ); asterisks (\*) indicate in which group significant  $D_{\max}$  occurred.



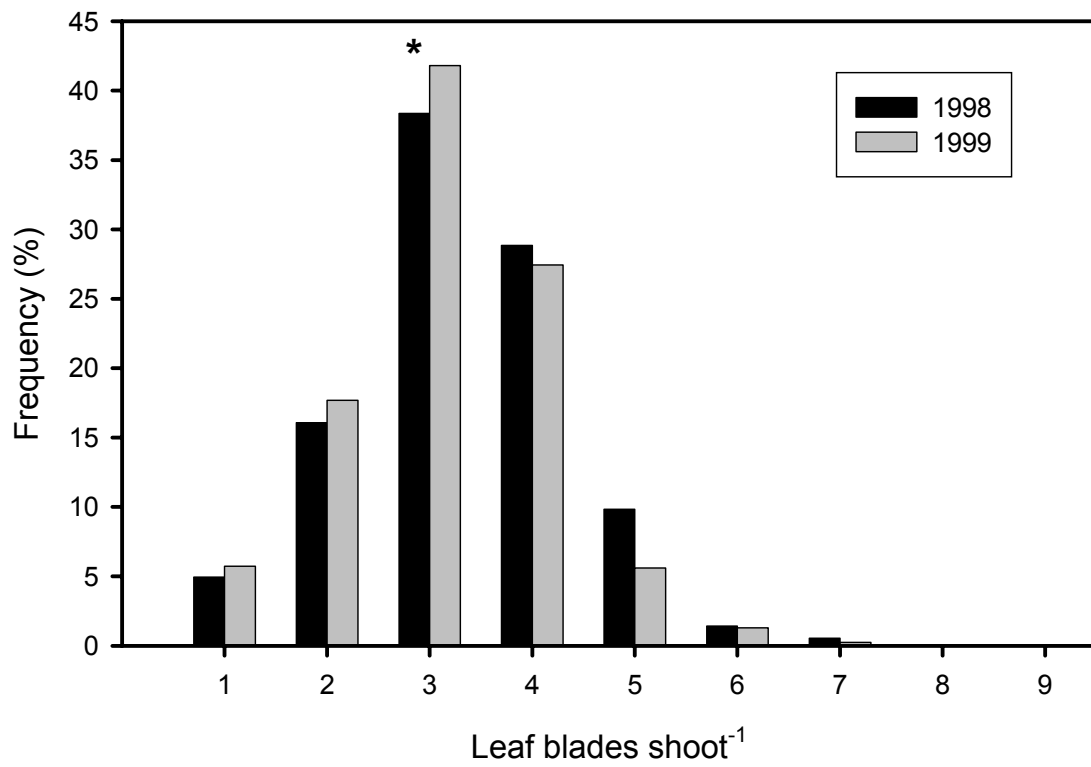
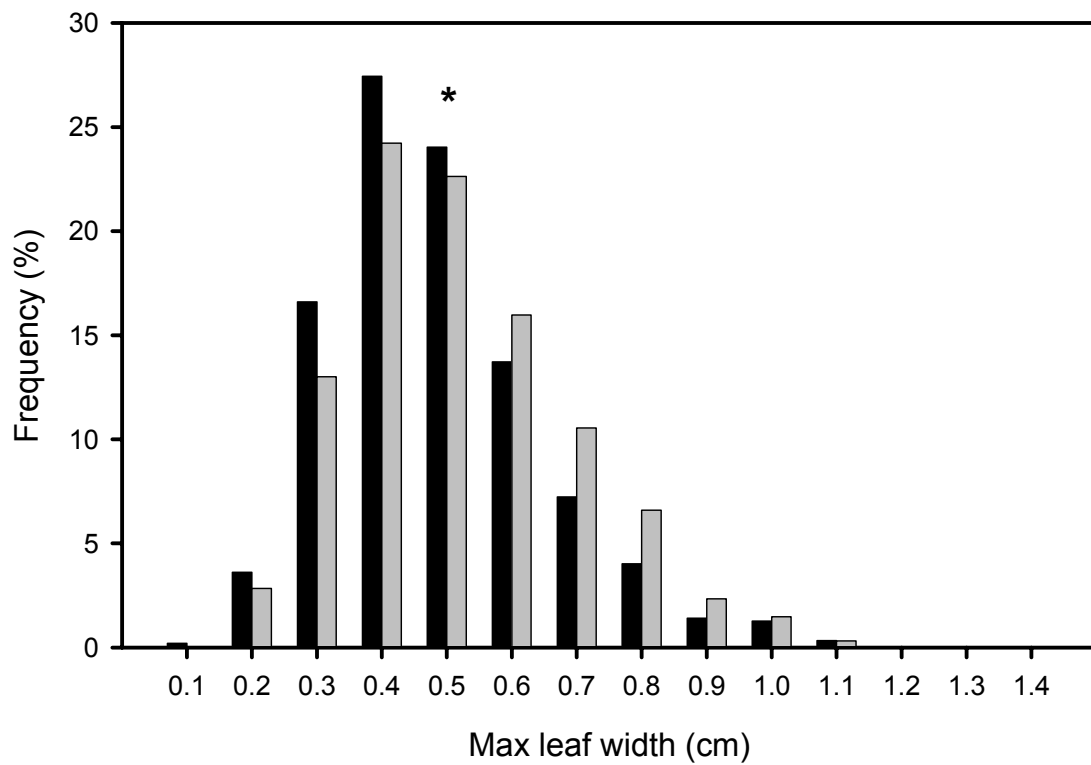
**A****B**

Figure 3. Interannual comparisons of the nested distributions of maximum leaf length (A) and mean shoot leaf length (B) of short-shoots of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 (n = 1494) and shaded bars represent 1999 (n = 1622). Significant differences in distributions between years were seen in both plots based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ); asterisks (\*) indicate in which group significant  $D_{\max}$  occurred. Both maximum length and mean length were binned into 2 cm size classes.

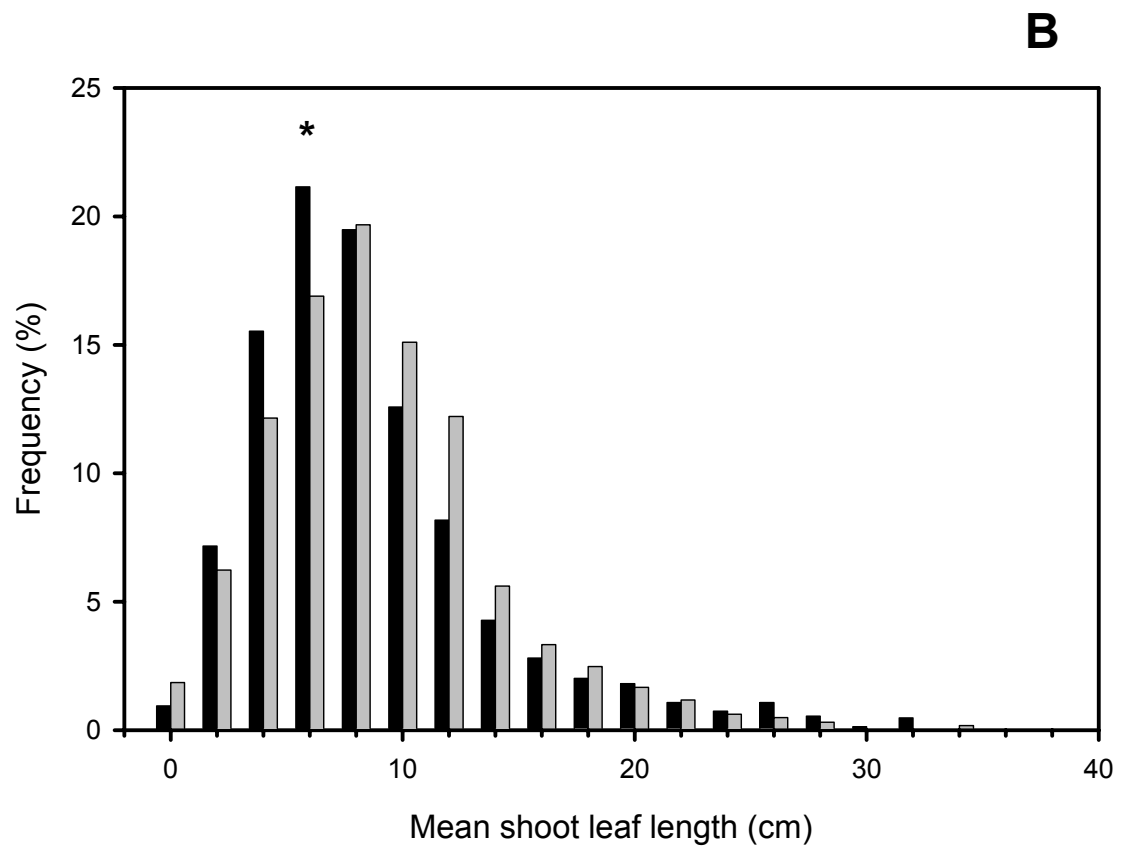
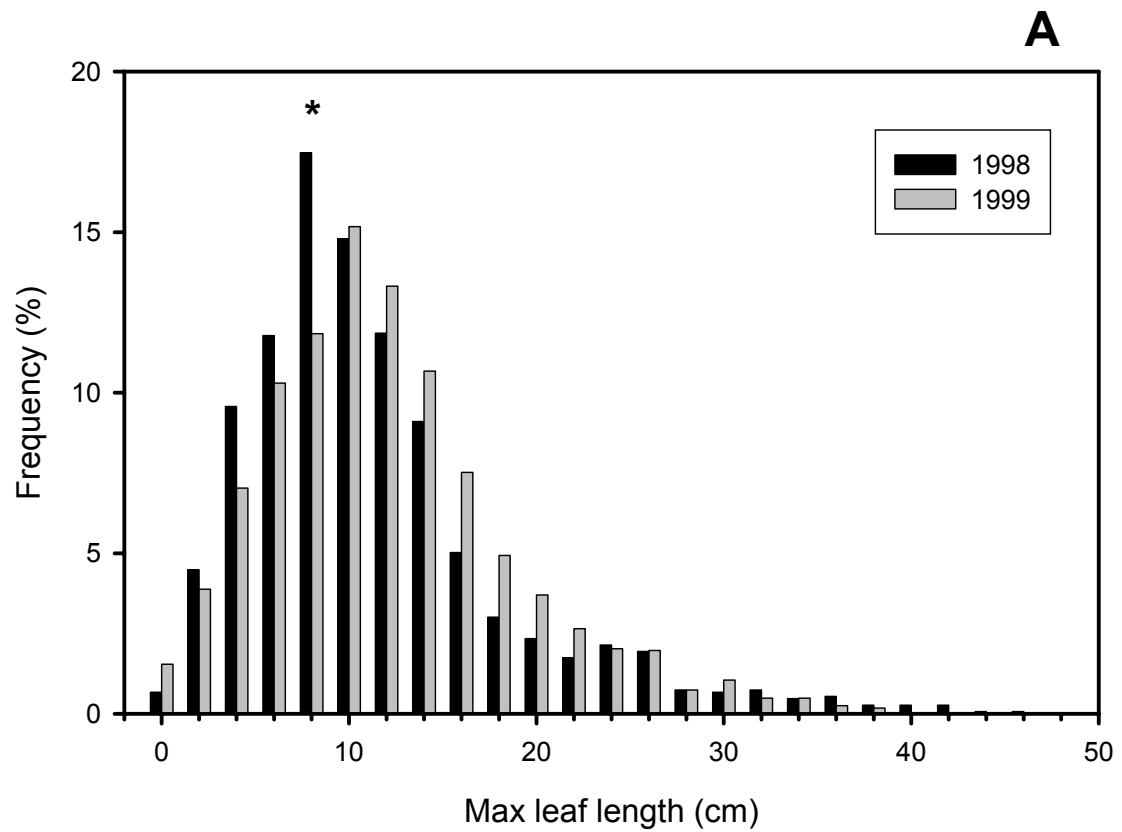


Figure 4. Interannual comparisons of the nested distributions of shoot-specific leaf area (A) and age (total number of leaf scars) (B) of short-shoots of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 (n = 1494) and shaded bars represent 1999 (n = 1622). Significant differences in distributions between years were seen in both plots based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ); asterisks (\*) indicate in which group significant  $D_{\max}$  occurred. Leaf area was binned by 5 cm<sup>2</sup> and age was binned by 5 scars.

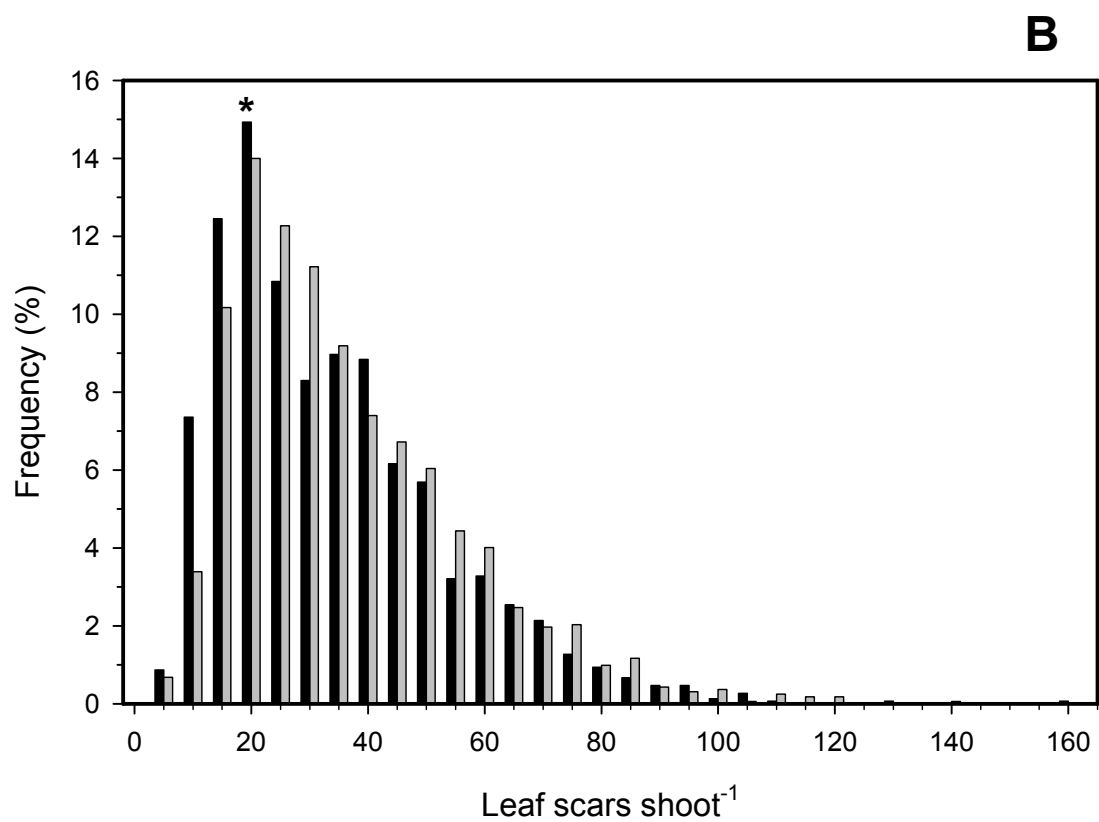
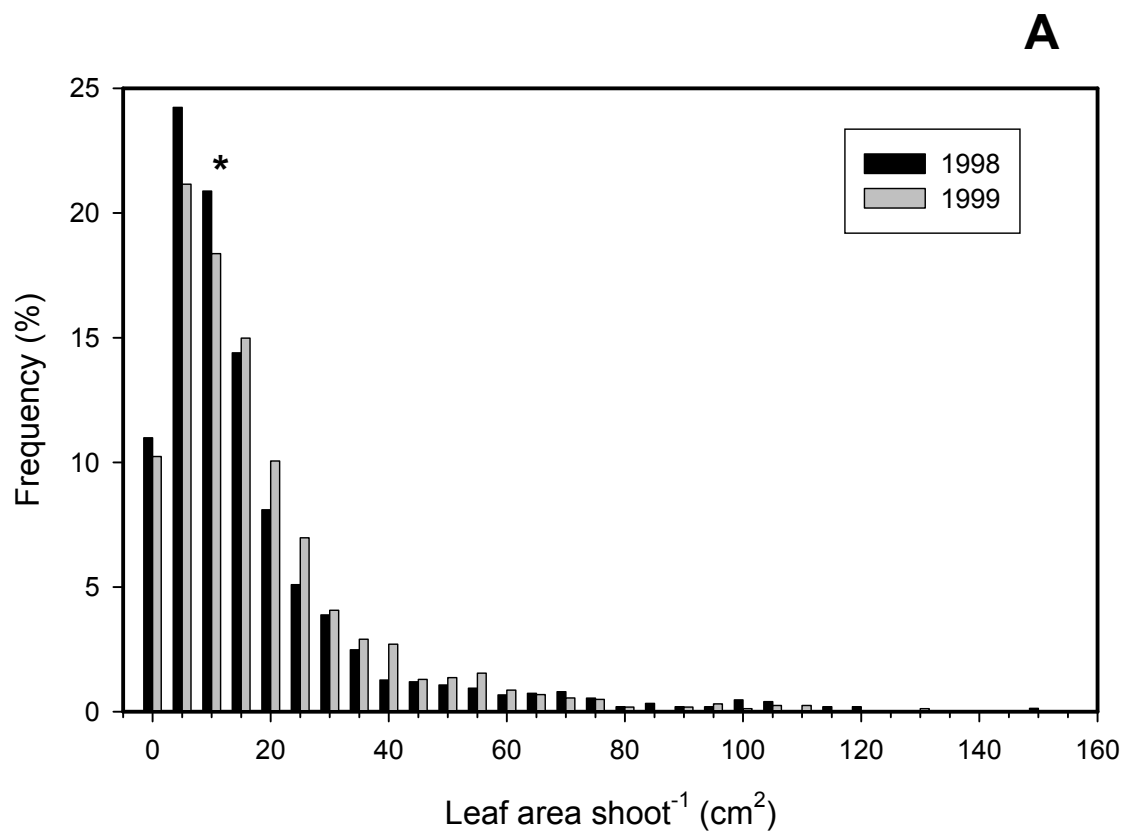


Figure 5. Interannual comparisons of the nested distributions of density (A) and above-ground:below-ground biomass (B) of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 (n = 211) and shaded bars represent 1999 (n = 232). There were no significant differences in distributions between years in either plot based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} < D_{0.05}$ ). Density was binned by  $\sim 115$  individuals  $\text{m}^{-2}$  and above-ground:below-ground biomass was binned by 0.025.

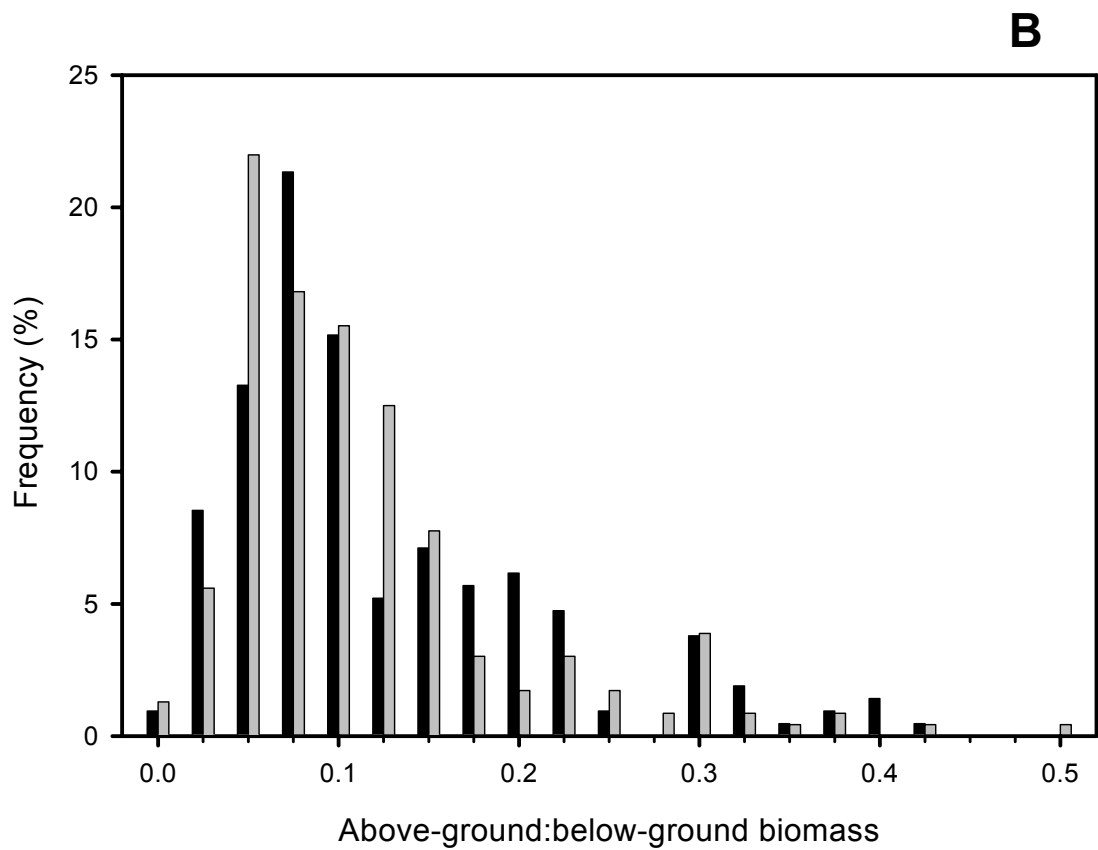
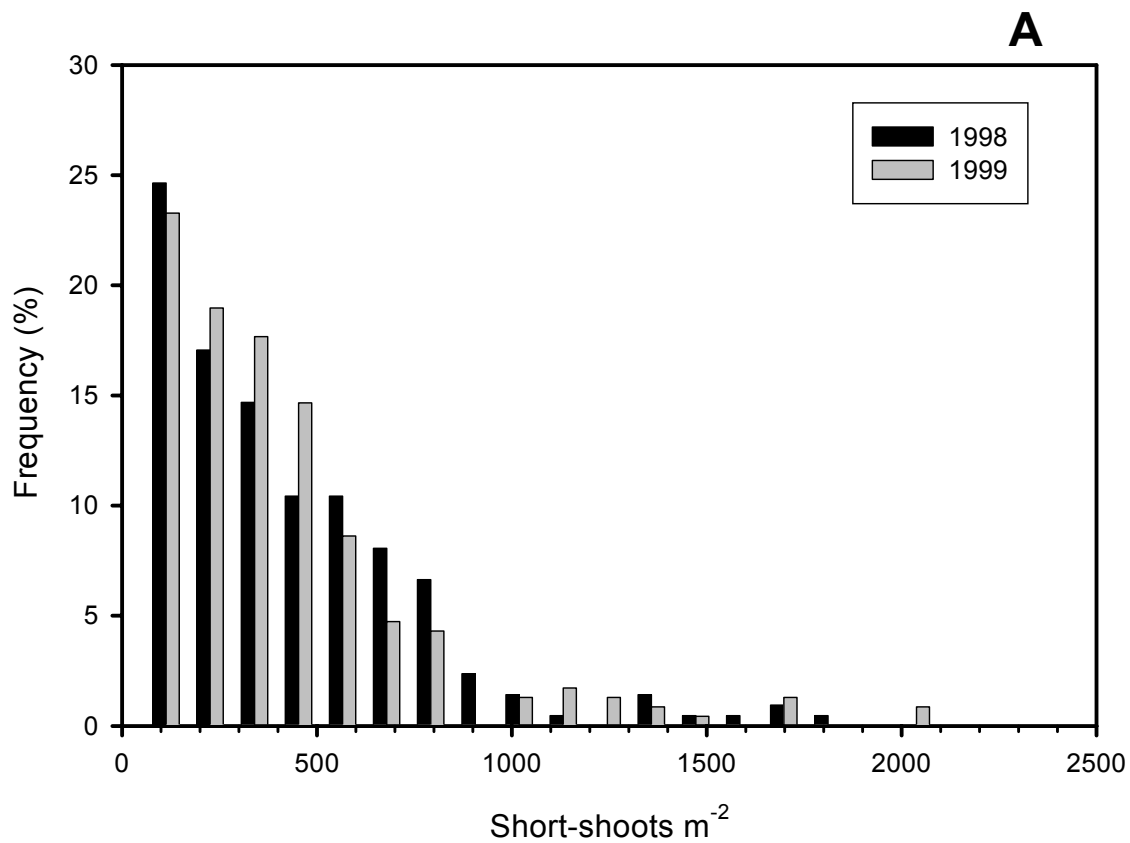


Figure 6.  
Interan

nual comparisons of the nested distributions of standing crop (A) and leaf area index (B) of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 (n = 211) and shaded bars represent 1999 (n = 232). There were no significant differences in distributions between years in either plot based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} < D_{0.05}$ ). Standing crop was binned by  $10 \text{ g m}^{-2}$  and leaf area index was binned by  $0.2 \text{ m}^2 \text{ m}^{-2}$ .



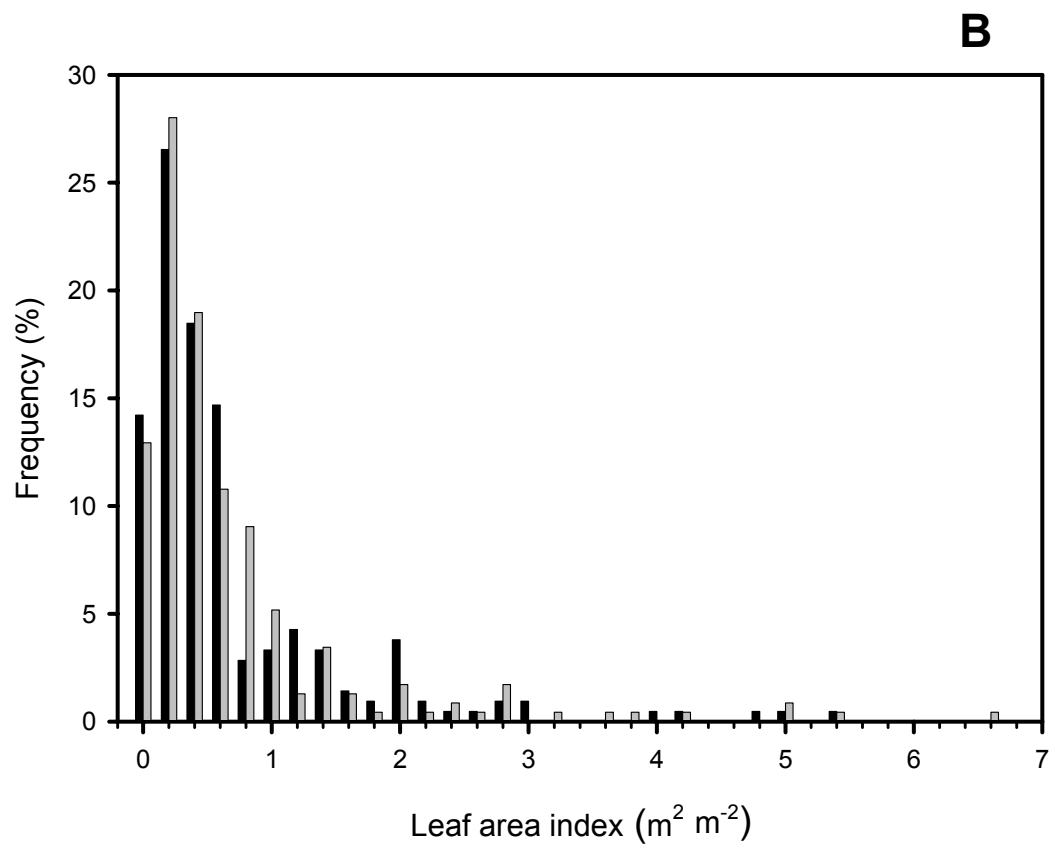
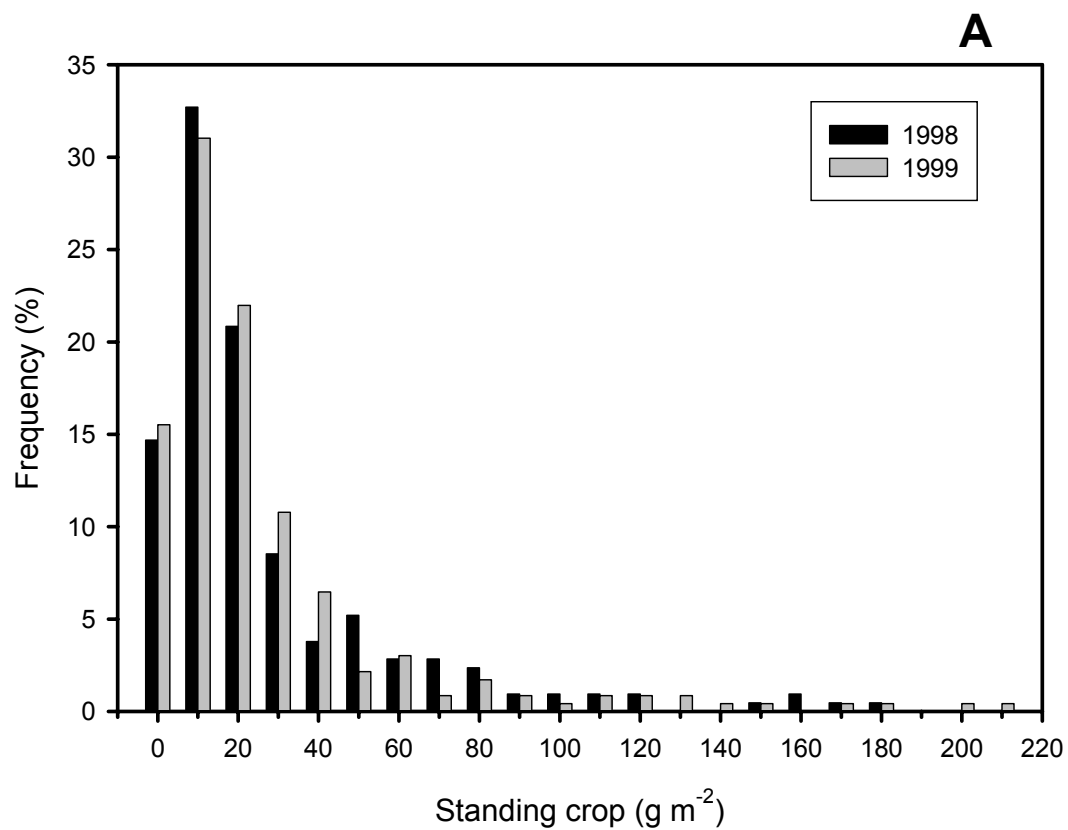


Figure 7. Interannual comparisons of the distributions of number of leaves shoot<sup>-1</sup> of *Thalassia testudinum* in ten basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant interannual differences in basin distributions based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ).

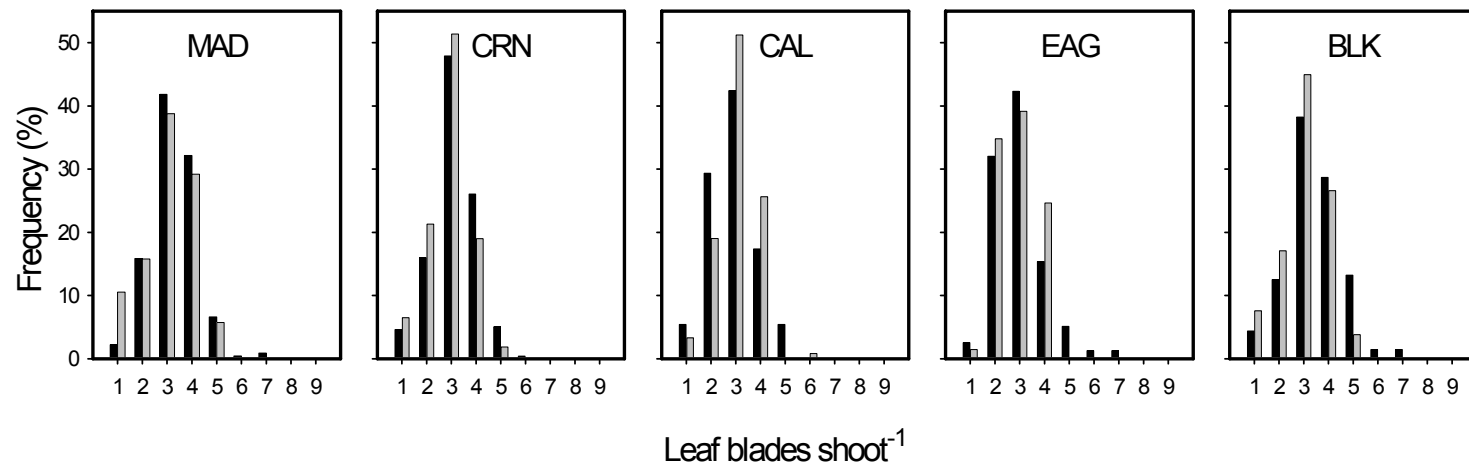
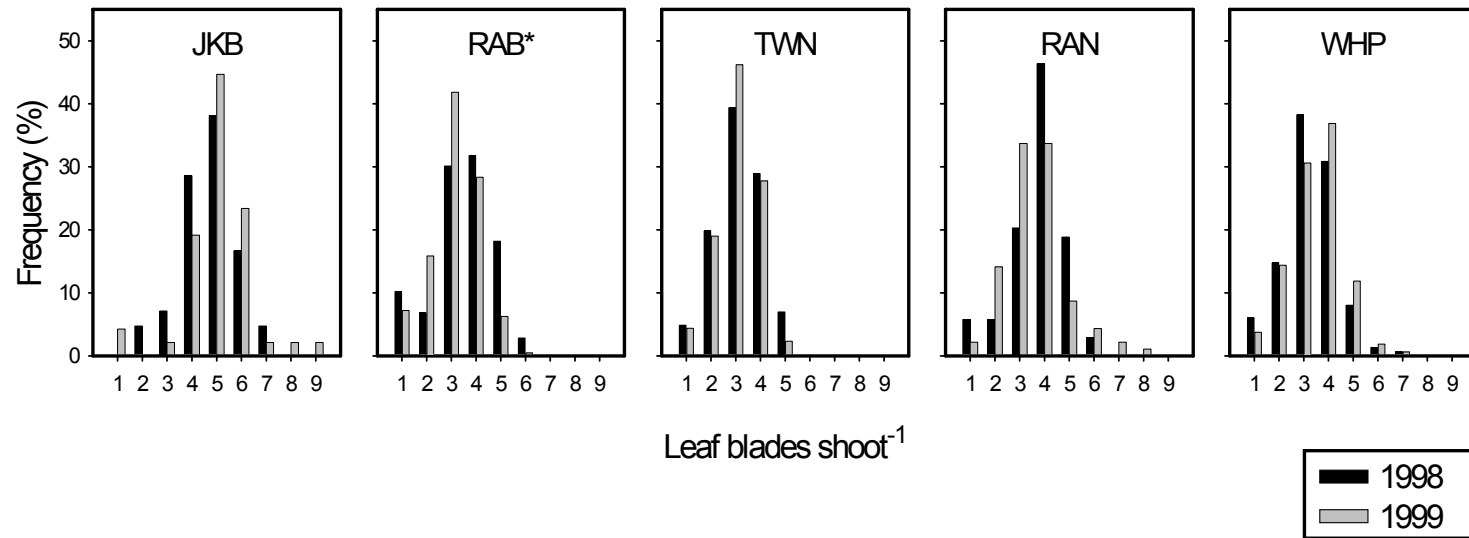


Figure 8. Interannual comparisons of the distributions of maximum leaf width of short-shoots of *Thalassia testudinum* in ten basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant interannual differences in basin distributions based on Kolmogorov-Smirnov Two-sample tests (  $D_{\max} > D_{0.05}$  ).

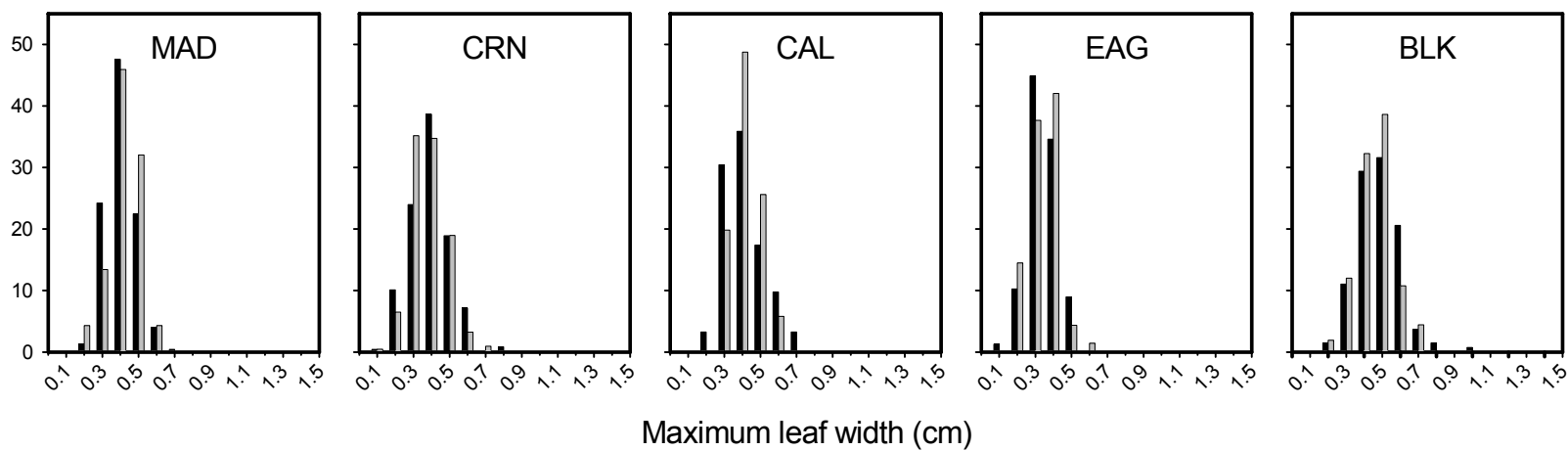
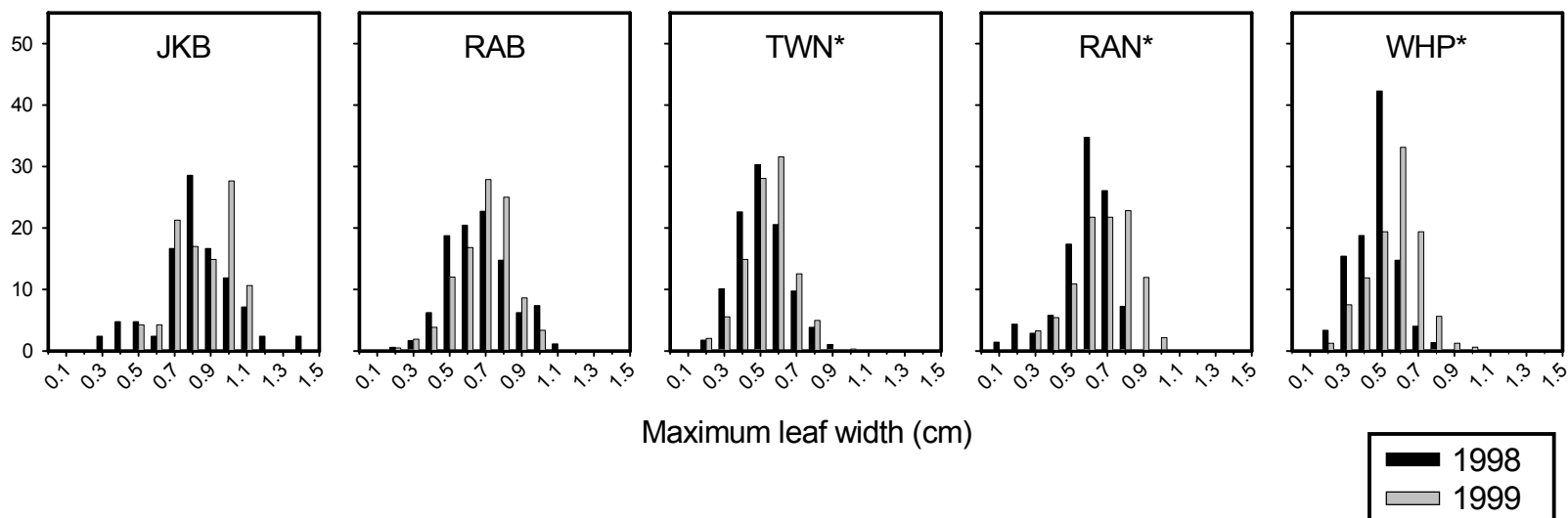


Figure 9. Interannual comparisons of the nested distributions (size class = 2 cm) of maximum leaf length of short-shoots of *Thalassia testudinum* in ten basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant interannual differences in basin distributions based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ).

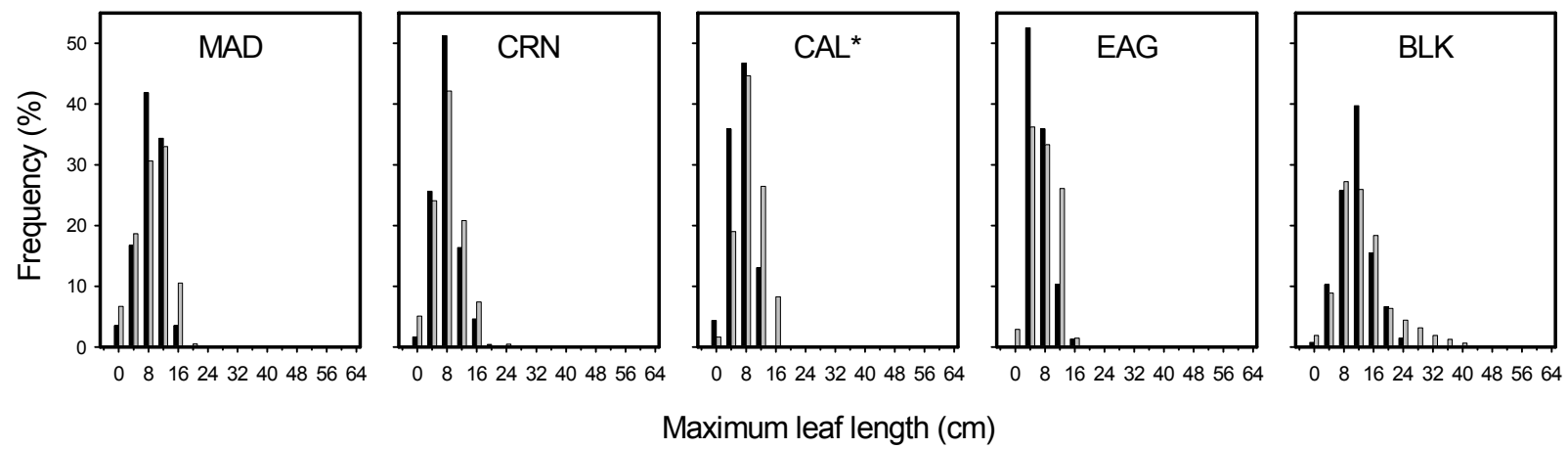
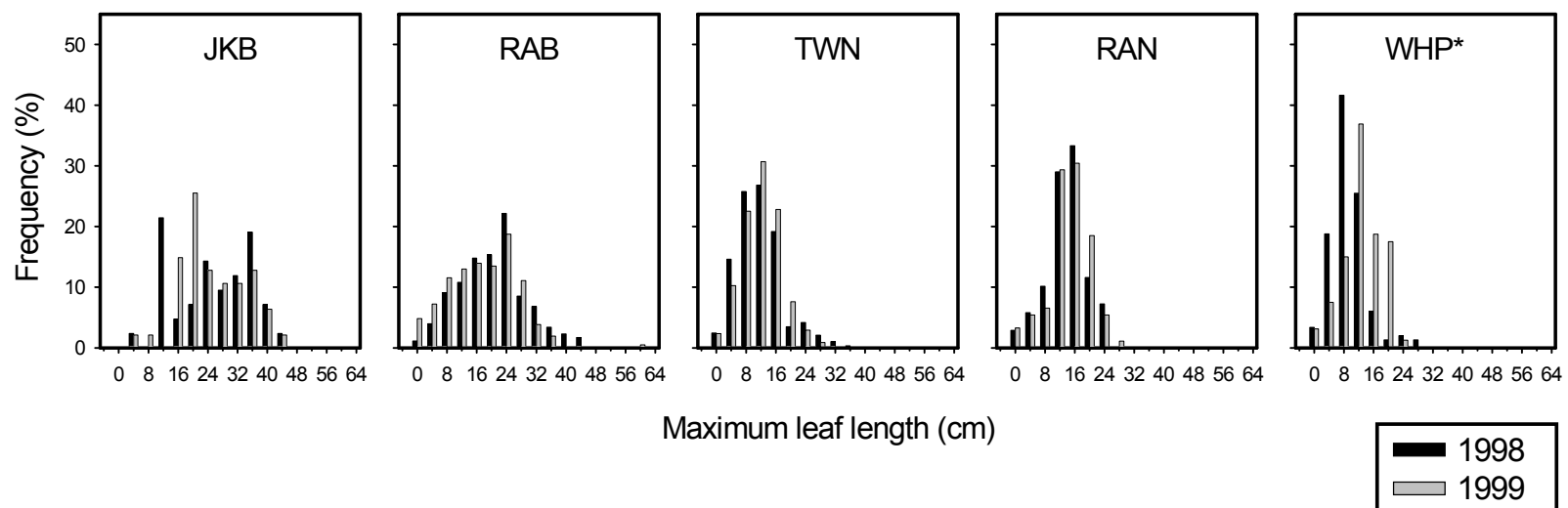


Figure 10. Interannual comparisons of the nested distributions (size class = 2.5 cm) of mean leaf length of short-shoots of *Thalassia testudinum* in ten basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant interannual differences in basin distributions based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ).



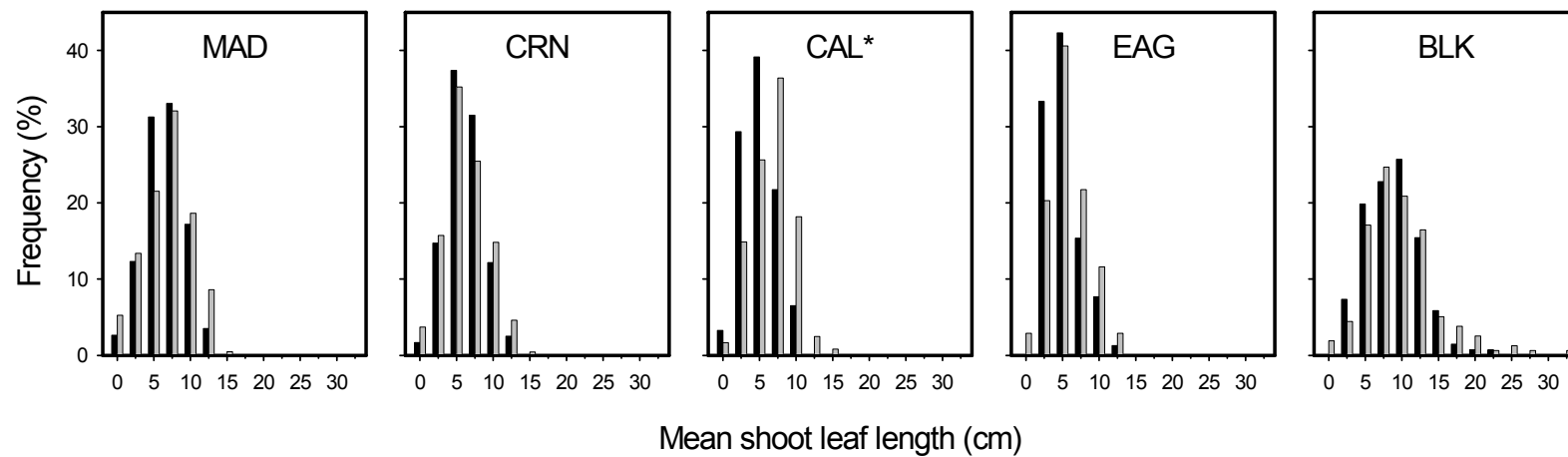
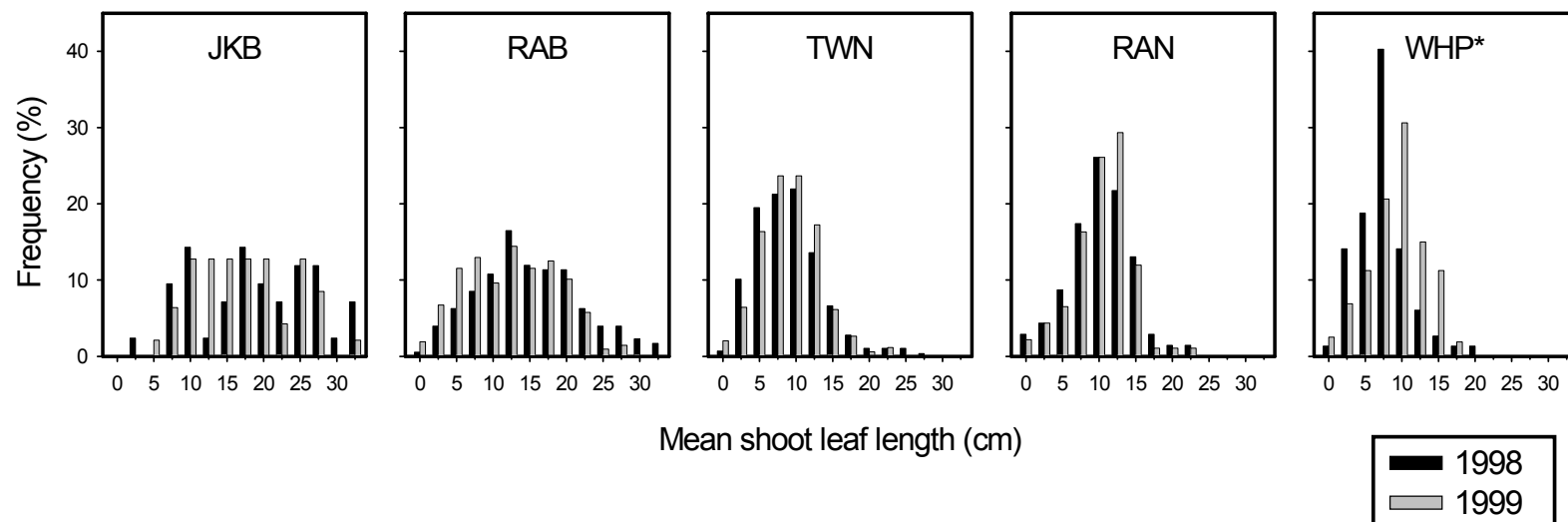


Figure 11. Interannual comparisons of the nested distributions (size class = 10 cm<sup>2</sup>) of shoot-specific leaf area of short-shoots of *Thalassia testudinum* in ten basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant interannual differences in basin distributions based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ).

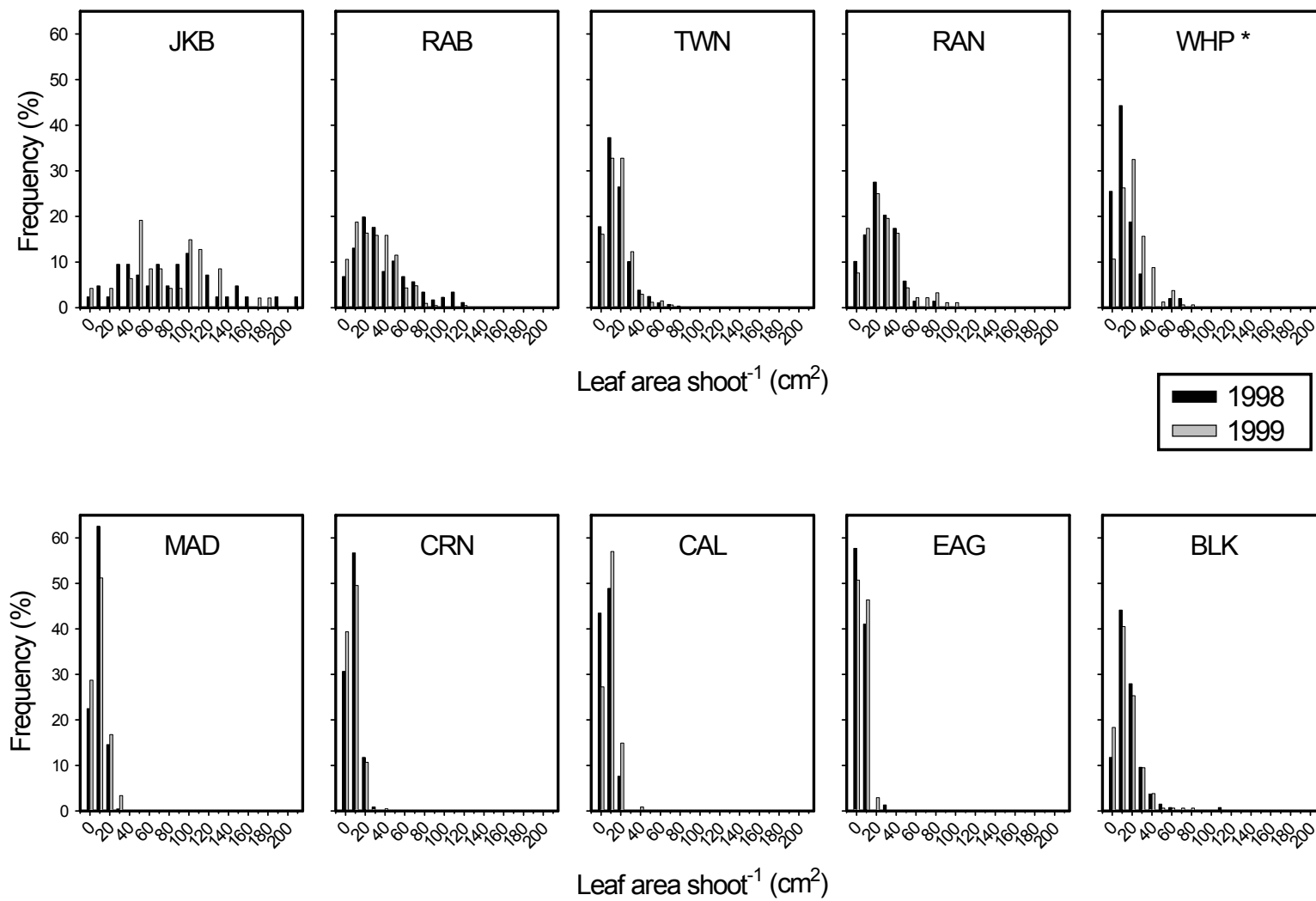
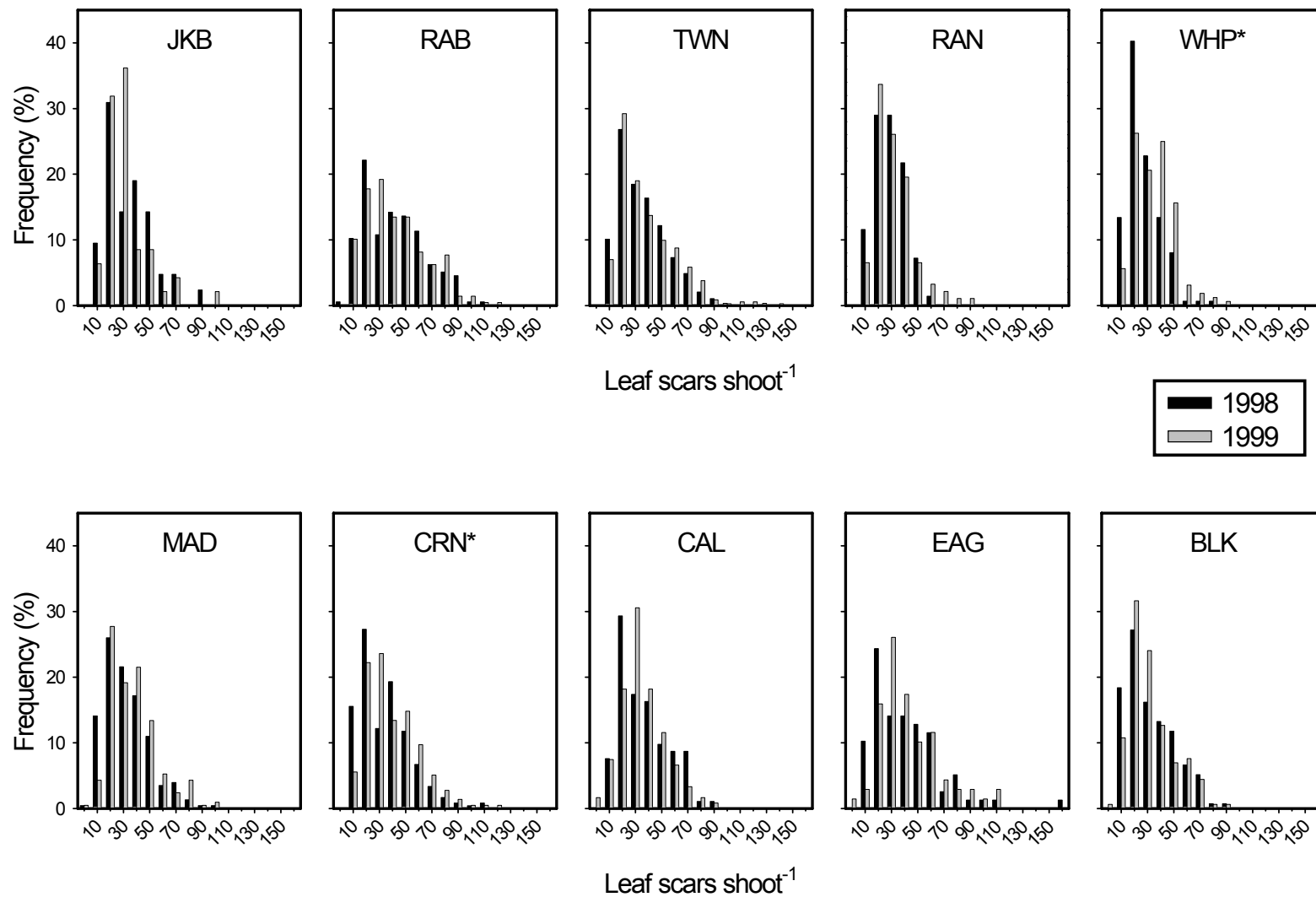


Figure 12. Interannual comparisons of the nested distributions (size class = 10 scars) of short-shoot age (total number of leaf scars) of *Thalassia testudinum* in ten basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant interannual differences in basin distributions based on Kolmogorov-Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ).



## Box-and-whisker plots

Box-and-whisker plots of *Thalassia testudinum* shoot-specific and area-specific characteristics in the ten sampled basins in Florida Bay in 1998 and 1999, along with asterisks indicating significant interannual differences within basins (results of Mann-Whitney Rank Sum tests or *t*-tests) are shown in Figures 13 to 22. Similar subsets based on Duncan's Multiple Range tests are indicated by letters. Mean values for the entire Bay are shown for comparison. These plots are of core means. In general, these plots followed the trends seen in the plots of the distribution of morphometric characteristics. The similarity in spatial pattern among five of the six shoot-specific characteristics, leaves per shoot (Fig. 13), leaf width (Fig. 14), maximum leaf length (Fig. 15), mean shoot leaf length (Fig. 16), and shoot-specific leaf area (Fig. 17), is striking. With few exceptions, the means and medians of these five parameters tended to increase in a gradient from Eagle Key basin in the northeast to Rabbit Key and Johnson Key Basins in the southwest. Blackwater Sound (in the northeast) and Twin Key Basin (in the south-central Bay) were notable exceptions. Three of the area-specific characteristics (excluding density) also followed this general trend; density (Fig. 19) increased in a gradient from the northeast to a high in the central Bay from where it decreased toward the southwest. Although leaf area index (Fig. 20) and standing crop (Fig. 21) are greatly influenced by density, these characteristics are also affected by shoot-specific characteristics and reflected those trends, as did the ratio of above- to below-ground biomass (Fig. 22).

Short-shoots in Johnson Key Basin had significantly more leaves than in all other basins in 1998 and 1999 (Fig. 13). Otherwise, no other basin was significantly distinct from any other, and, excluding Johnson Key, leaf number was fairly uniform

across the Bay in both years. In 1998, Calusa Key in the east had the fewest leaves per shoot (3.0) and Johnson Key had the most (4.4), nearly 50% more leaves per shoot than in Calusa. In 1999, Johnson Key again had the most leaves per shoot (5.3) while the shoots of Crane had the least (2.8), a difference of almost 100%. Shoots in Blackwater Sound, Crane Key Basin, and Madeira Bay had significantly fewer leaves in 1999 than in 1998.

Leaf width was more specific to regions within the Bay (Fig. 14). In both sampling seasons leaves in the western Bay (Johnson Key, 0.8 cm; Rabbit Key, 0.7 cm) on average were as much or more than twice as wide as those in the eastern Bay (Eagle Key, Calusa Key, Crane Key, Madeira Bay, 0.3 - 0.4 cm). Leaves of shoots in the central Bay (and in Blackwater Sound) were of intermediate width. Only leaves in Whipray Basin displayed a significant interannual difference, but an increase in width was seen throughout the Bay in 1999.

Maximum leaf length (Fig. 15), or canopy height, was much greater in western Johnson Key and Rabbit Key Basins in 1998 (more than 20 cm) than in basins to the east (less than 15 cm). The mean of the longest leaves in Johnson was 24 cm, four times the mean of the longest leaves in Eagle (5.9 cm). Again, the four eastern basins had the shortest canopy height, and leaf length increased towards the southwest. In 1999 a decline in maximum length in Johnson Key and Rabbit Key Basins (significant in Rabbit), combined with increases in all other basins (significant in Calusa and Whipray), made this characteristic slightly less variable across the Bay than in 1998. As in the previous year, shoots in Johnson had the longest leaves and Eagle the shortest.

Mean shoot leaf length (Fig. 16) showed a similar pattern as maximum length. Short-shoots in Johnson had the longest leaves on average (more than 16 cm). The four

eastern basins (excluding Blackwater) had the shortest leaves (less than 7 cm) in both years, about 35% as long as the leaves in Johnson Key Basin. Like with maximum length, leaves in Calusa and in Madeira were significantly longer in 1999 than in 1998, and those in Rabbit were significantly shorter.

Changes in leaf length were reflected in the plots of shoot-specific leaf area (Fig. 17). Shoots in Johnson had much greater total area (79.6 cm<sup>2</sup> in 1998, 74.3 cm<sup>2</sup> in 1999), almost twice that of the shoots in Rabbit and more than an order of magnitude greater than the shoots in Eagle. Shoots in Whipray and Calusa had significantly greater specific leaf areas in 1999 while leaf area decreased in Rabbit.

Short-shoots in Eagle Key Basin had the most leaf scars (a mean of more than 40 scars per shoot) compared to those in other basins in both 1998 and 1999 (Fig. 18). Eagle Key shoots had nearly 40% more leaf scars than those of Whipray and Rankin, the basins with the youngest shoots in 1998 and 1999, respectively. Seven of the ten basins showed an increase in the number of leaf scars per short-shoot, but the increases were only significant in Madeira and Whipray Basins.

Although *Thalassia testudinum* mean short-shoot density decreased in the Bay in 1999 compared to 1998 (Table 2), this decrease was statistically insignificant, and *T. testudinum* was more widespread in 1999. Twin Key Basin had the highest density in both years, about 650 shoots m<sup>-2</sup> (Fig. 19). In 1998, Johnson had the lowest density (170 shoots m<sup>-2</sup>), and in 1999 Eagle had the lowest density (178 shoots m<sup>-2</sup>), both of which were about 25% that of Twin. Six of the ten basins displayed insignificant decreases in density while the other four had insignificant increases.

Leaf area index increased in a gradient from the northeast (not including Blackwater Sound) to the southwest; LAI was greatest in the western basins of Johnson



Key and Rabbit Key in both sampling years, more than ten times that of the basin with the lowest value, Eagle Key (Fig. 20). In 1998 leaf area index was  $1.69 \text{ m}^2 \text{ m}^{-2}$  in Rabbit and  $0.12 \text{ m}^2 \text{ m}^{-2}$  in Eagle, and in 1999 LAI was  $1.75 \text{ m}^2 \text{ m}^{-2}$  in Johnson and  $0.11 \text{ m}^2 \text{ m}^{-2}$  in Eagle. A statistically insignificant increase in LAI was seen in the Bay as a whole from 1998 to 1999, but the only basin which showed a significant change (an increase) between years was Calusa.

The plots of *Thalassia testudinum* standing crop closely mirror those of leaf area index (Fig. 21). Again, the lowest values were seen in the northeast (Eagle Key Basin,  $4\text{-}5 \text{ g m}^{-2}$  in both years) and the highest in the west (ca.  $65 \text{ g m}^{-2}$  in Rabbit in 1998 and ca.  $60 \text{ g m}^{-2}$  in Johnson in 1999). There was no significant change in standing crop in the Bay between 1998 and 1999, and again, the only significant difference at the basin level was an increase in Calusa.

Above-/below-ground biomass ratio showed similar trends as well with a maximum in the southwest and a minimum in the northeast (Fig. 22). Shoots in Johnson Key Basin had the highest ratio in both years (ca. 30% above-ground biomass), and shoots in Madeira Bay and Crane Key Basin had the lowest ratios (less than 10% above-ground biomass). The Bay showed an insignificant decrease in this ratio from 1998 to 1999, a trend probably driven by significant decreases in Crane, Madeira, and Rabbit; Rankin was the only basin which showed a significant increase between years.

Figure 13. Number of leaves per individual of *Thalassia testudinum* short-shoots in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different means within a year based on Duncan's multiple range test. Basins marked with an asterisk (\*) exhibited significant differences between years based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.

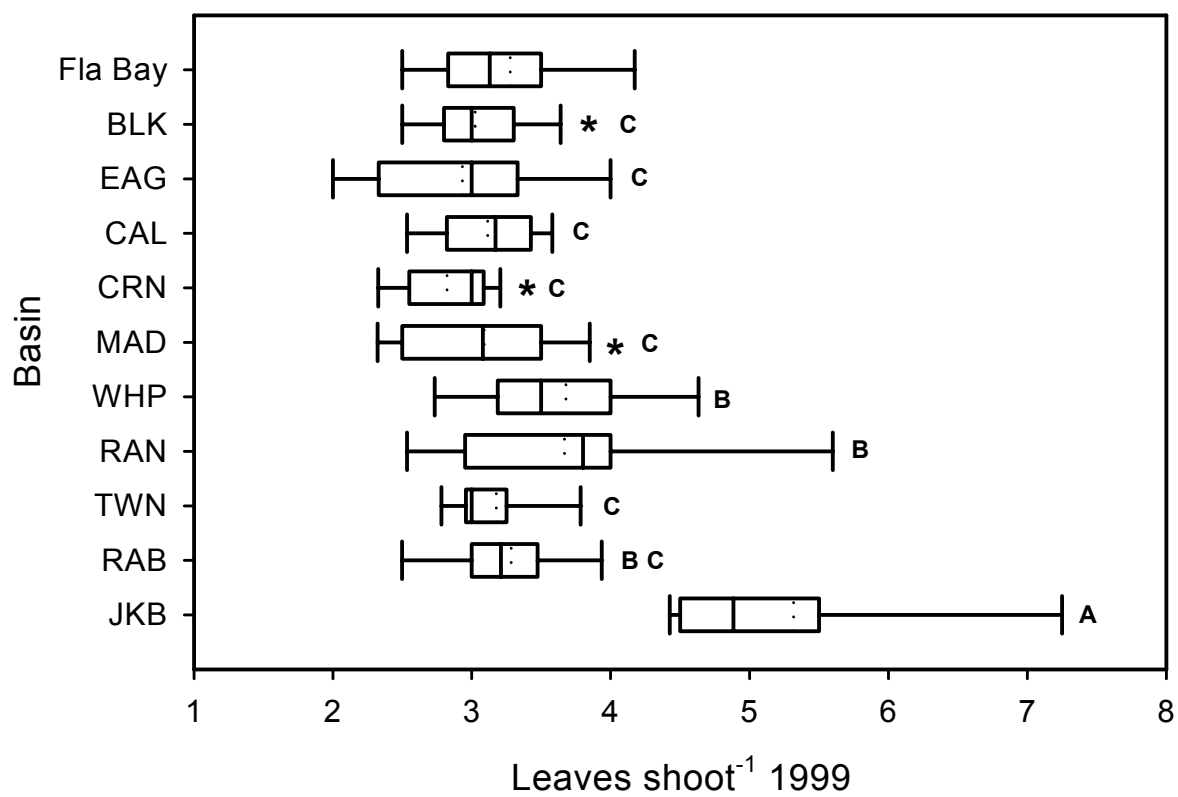
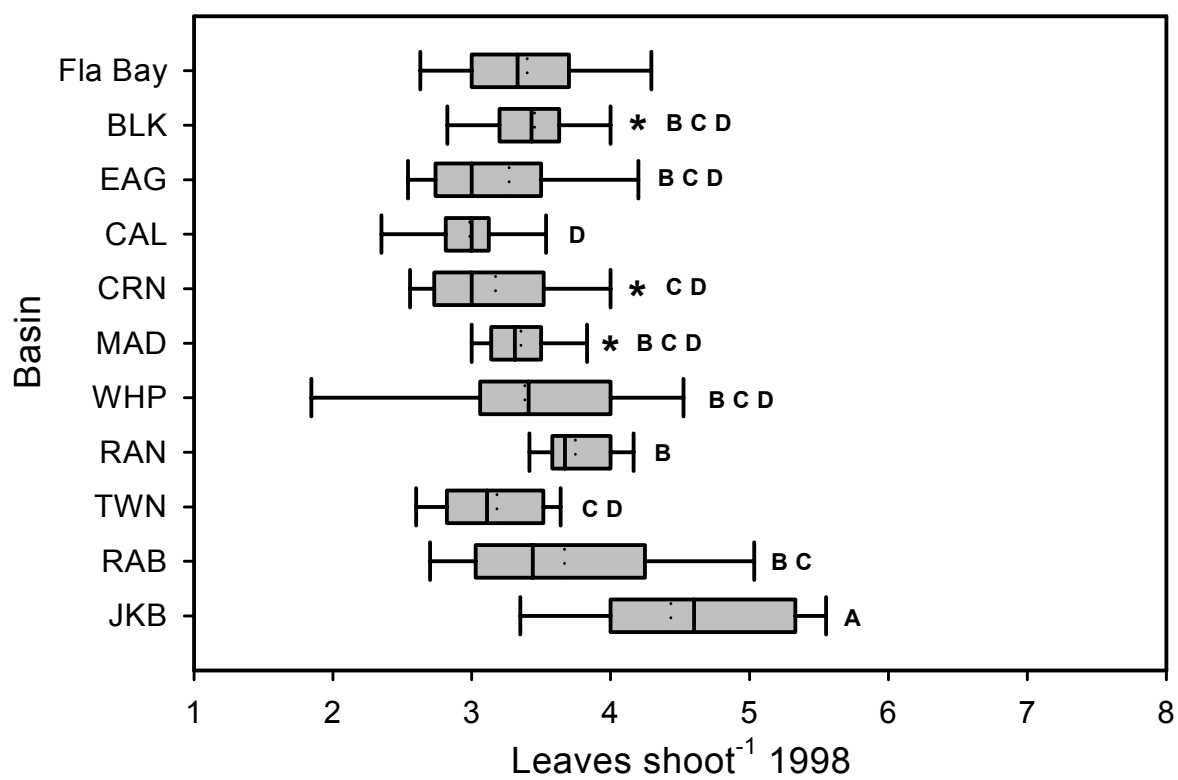


Figure 14. Maximum leaf width of short-shoots of *Thalassia testudinum* in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different means within a year based on Duncan's multiple range test. Basins marked with an asterisk (\*) exhibited significant differences between years based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.

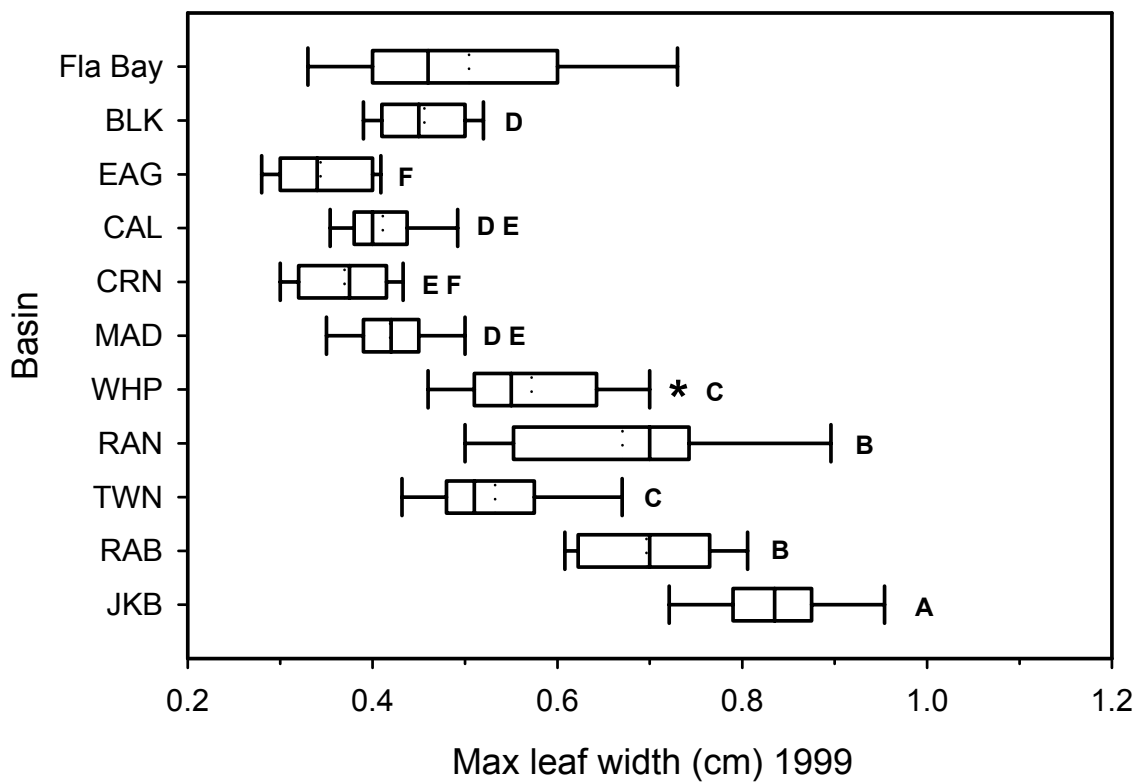
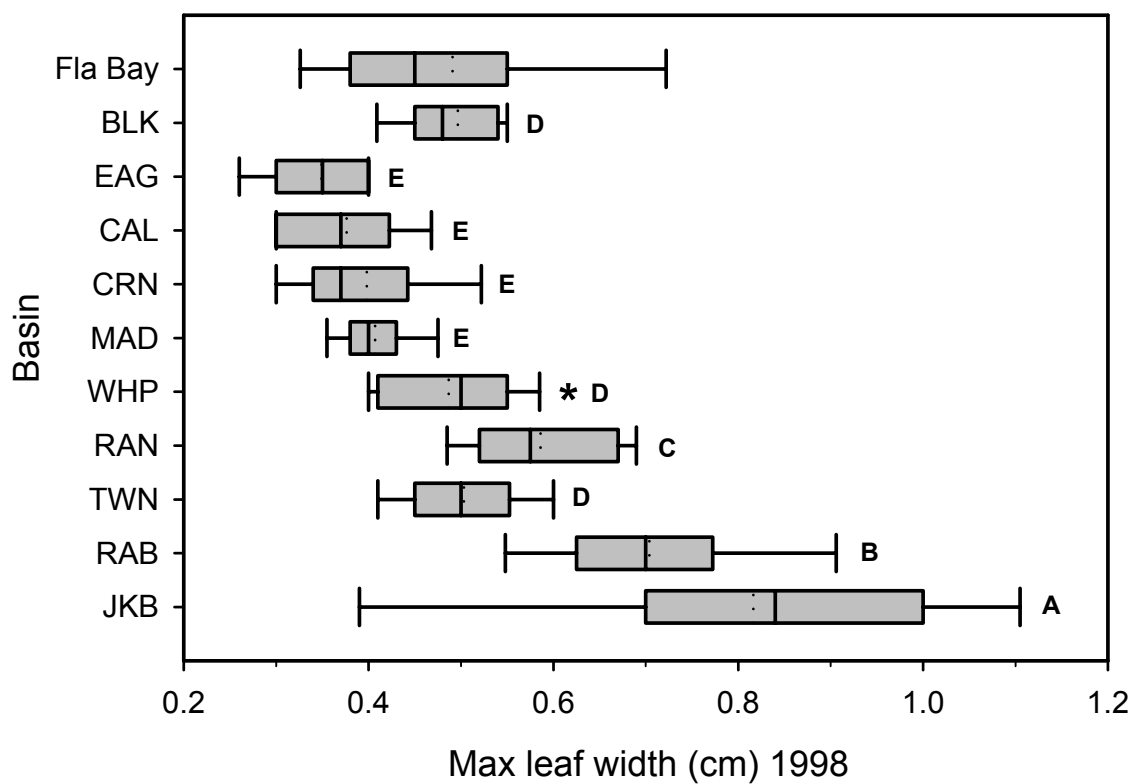


Figure 15. Maximum leaf length of short-shoots of *Thalassia testudinum* in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different means within a year based on Duncan's multiple range test. Basins marked with an asterisk (\*) exhibited significant differences between years based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.

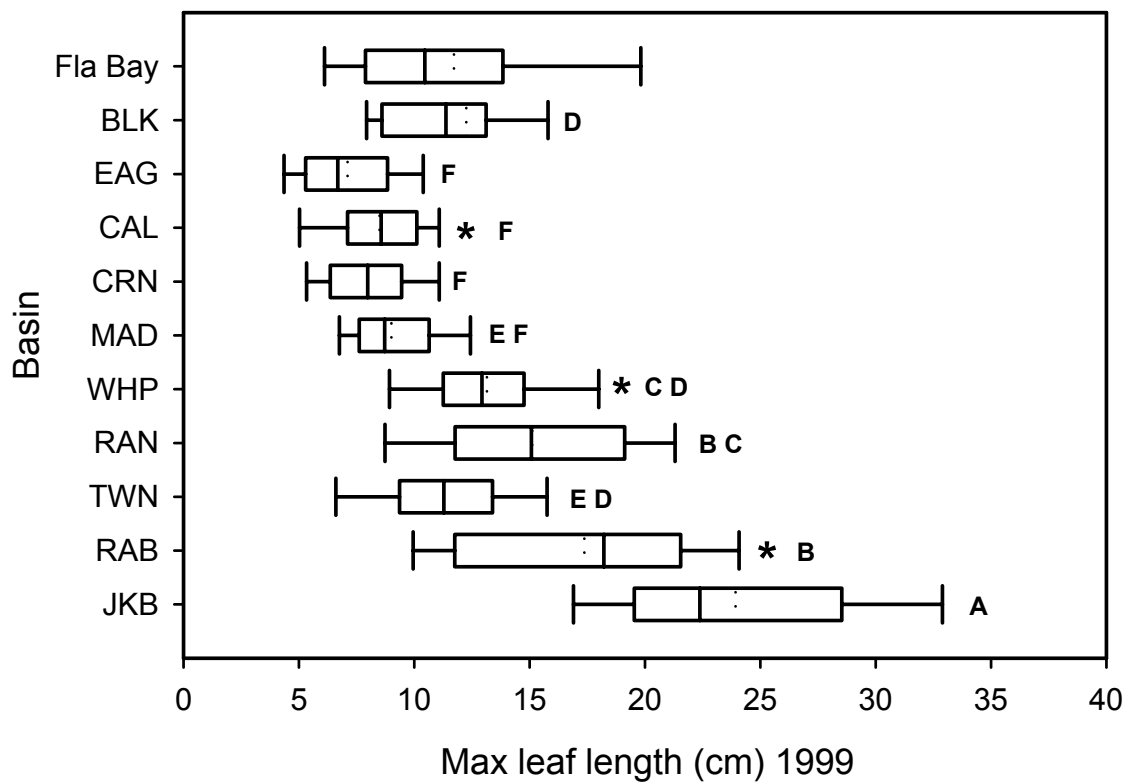
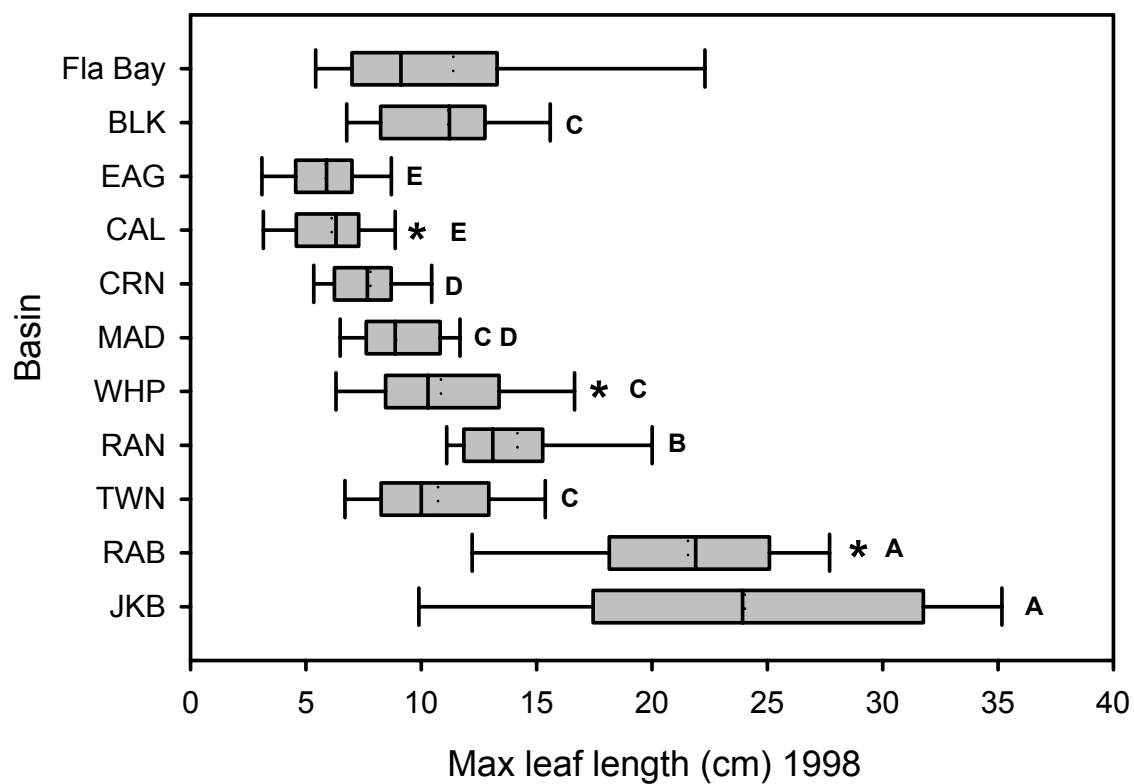


Figure 16. Mean shoot leaf length of short-shoots of *Thalassia testudinum* in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different means within a year based on Duncan's multiple range test. Basins marked with an asterisk (\*) exhibited significant differences between years based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.



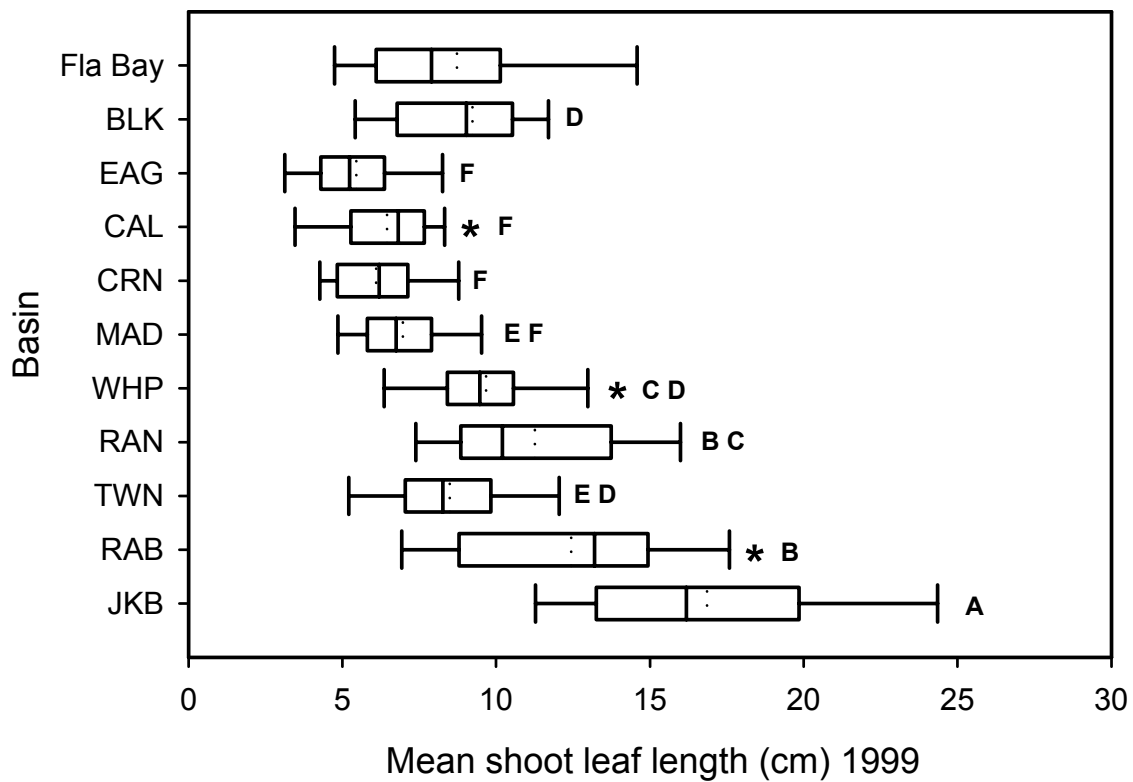
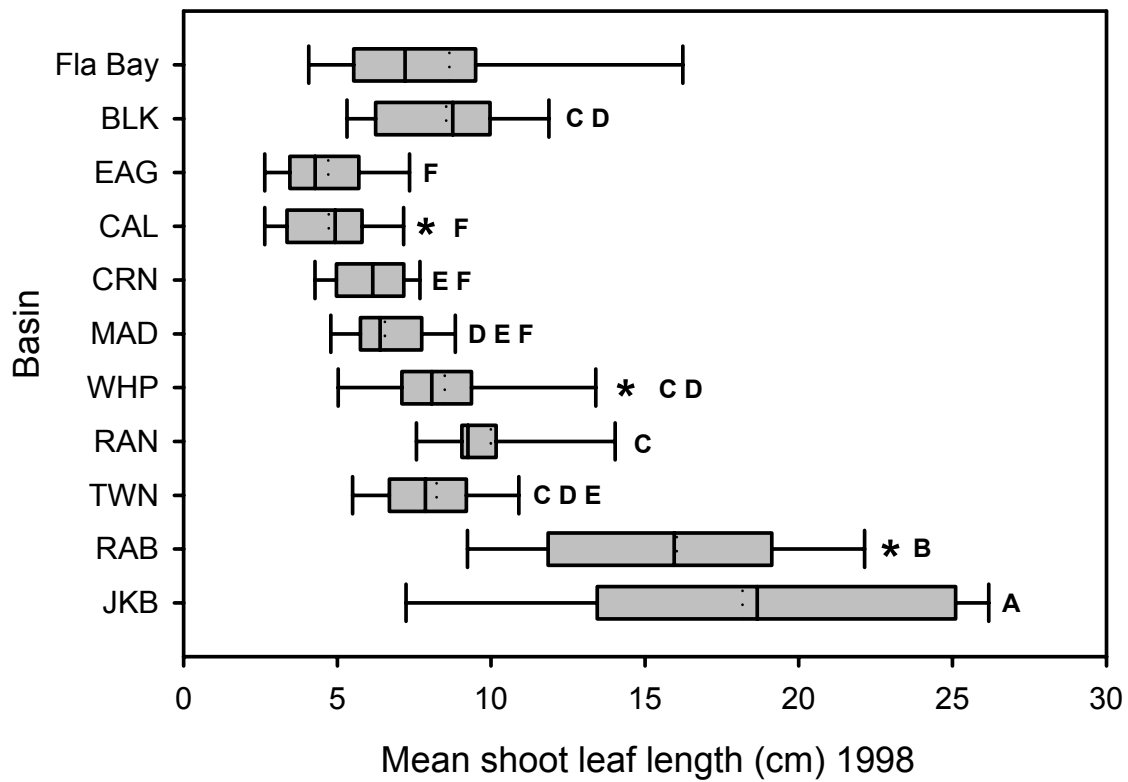


Figure 17. Shoot-specific leaf area of short-shoots of *Thalassia testudinum* in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different means within a year based on Duncan's multiple range test. Basins marked with an asterisk (\*) exhibited significant differences between years based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.

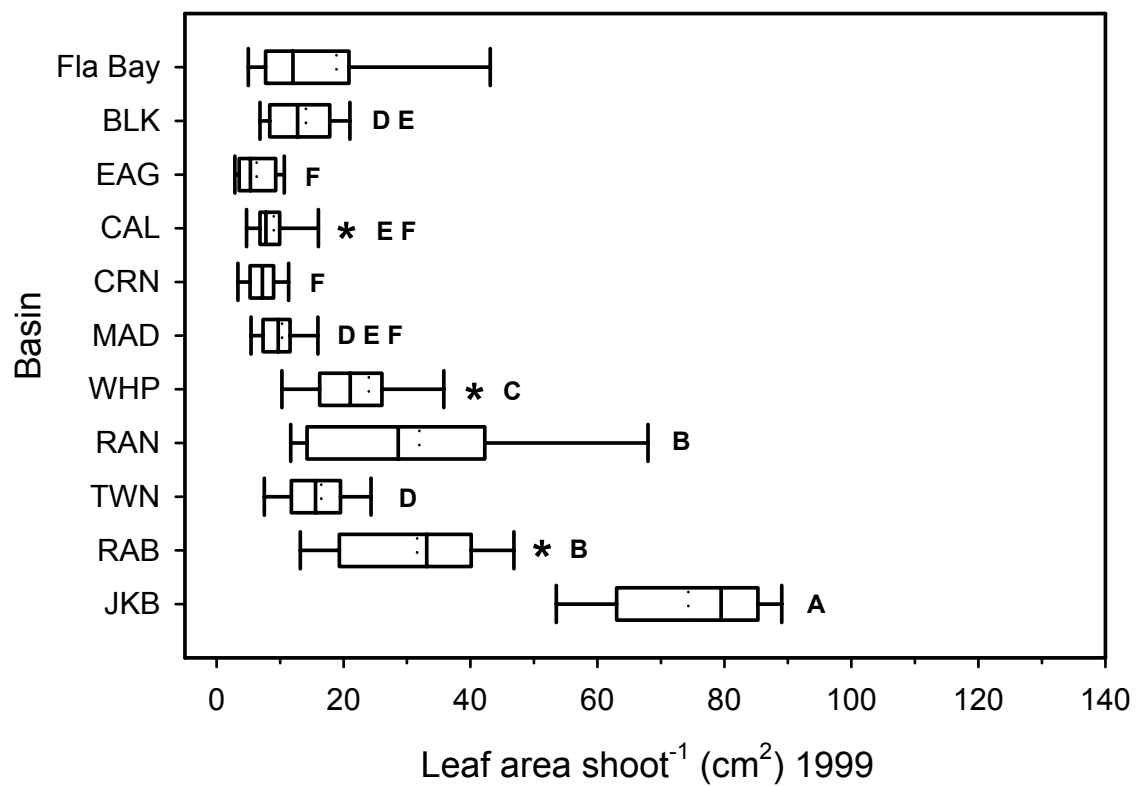
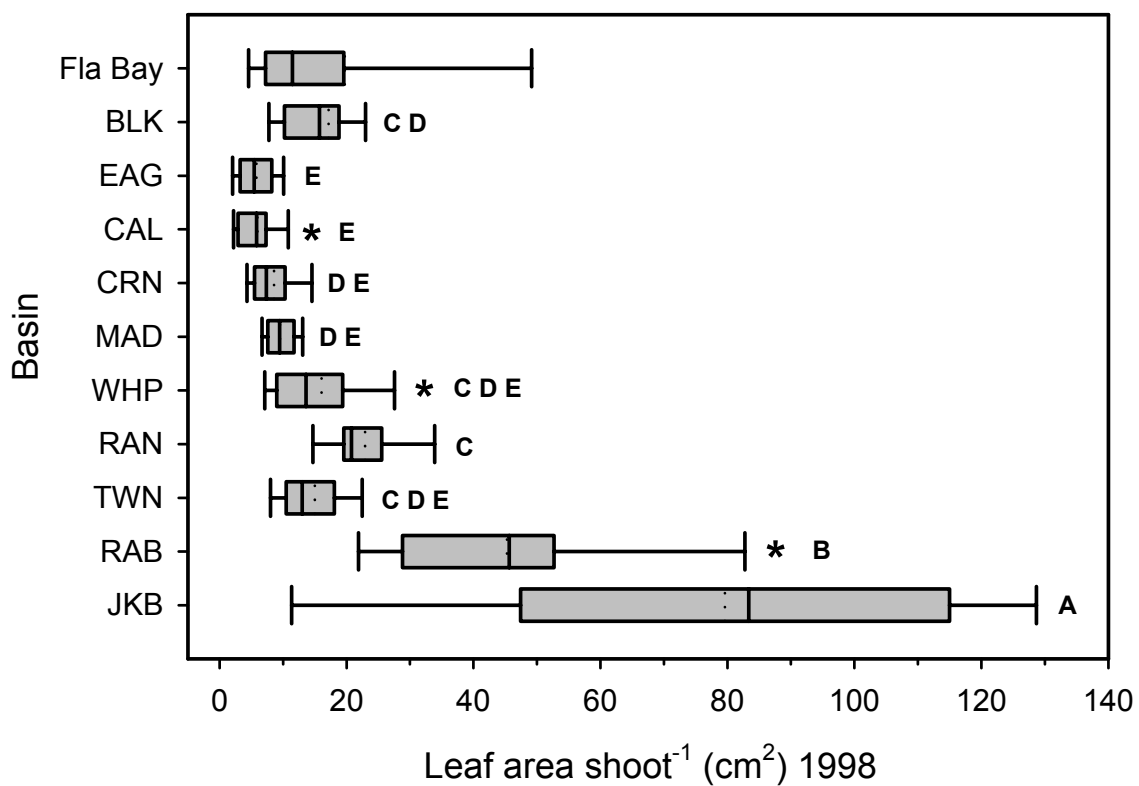


Figure 18. Age (number of scars + number of green and white leaves) of *Thalassia testudinum* short-shoots in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different means within a year based on Duncan's multiple range test. Basins marked with an asterisk (\*) exhibited significant differences between years based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.

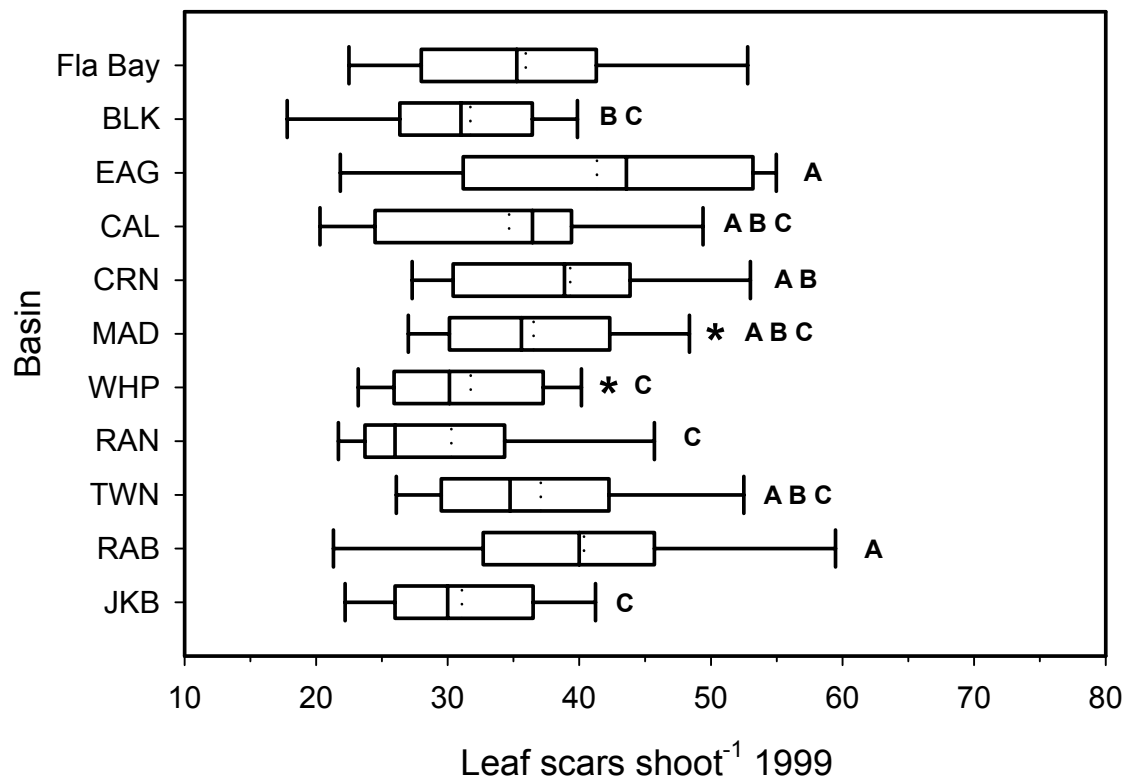
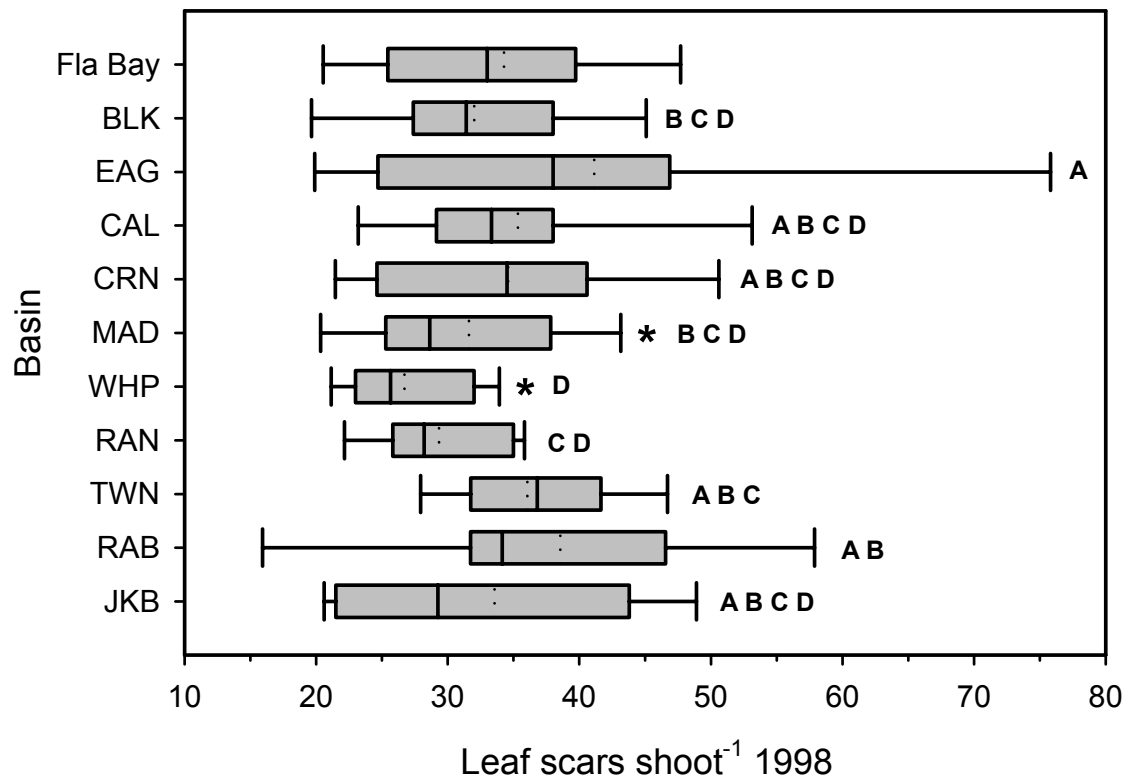


Figure 19. Density (number of individuals  $\text{m}^{-2}$ ) of *Thalassia testudinum* short-shoots in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different mean densities within a year based on Duncan's multiple range test. Interannual differences between basins were not significant based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.

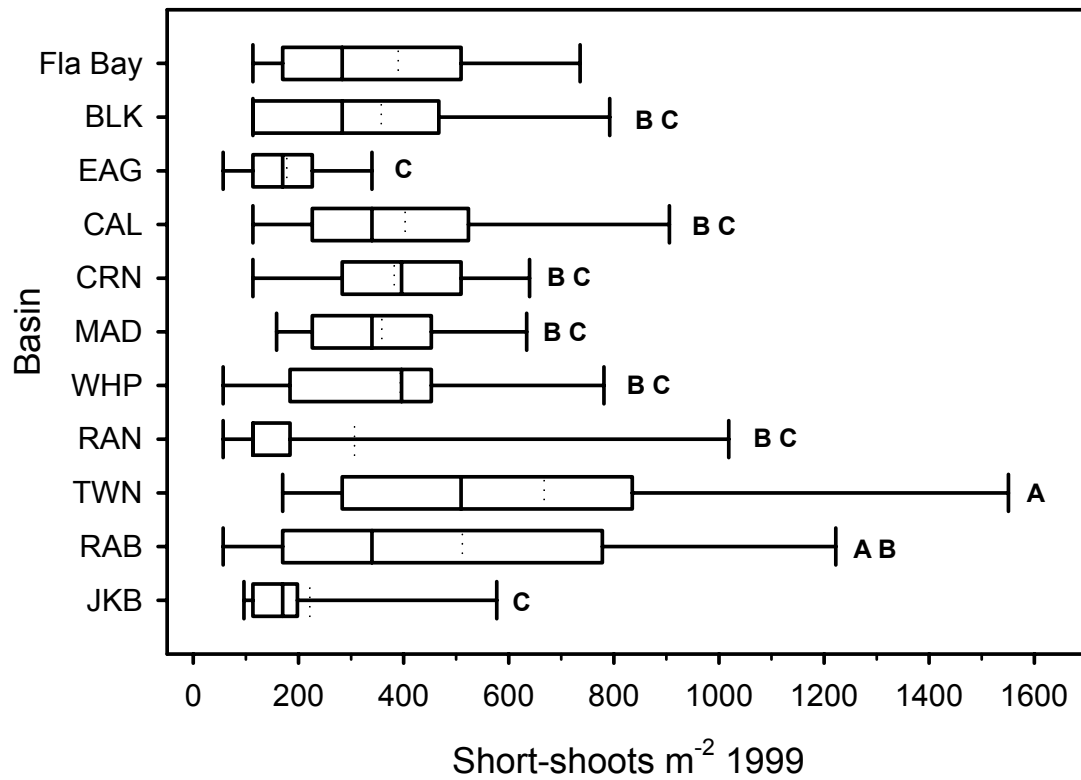
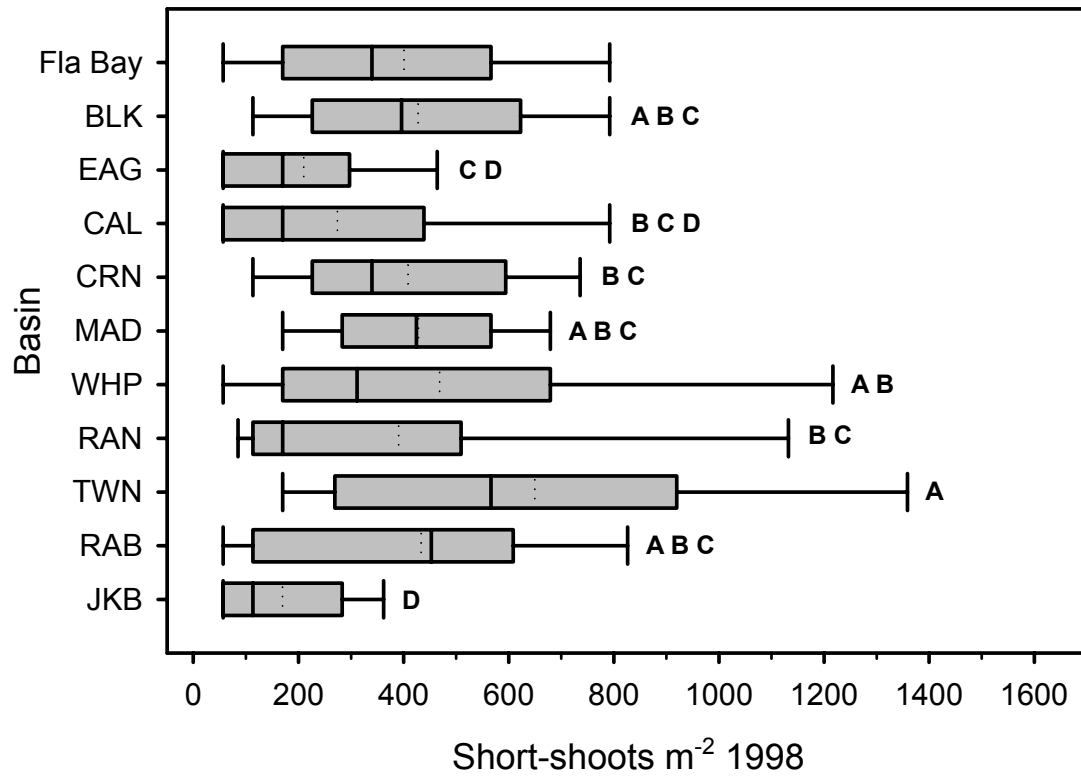


Figure 20. Leaf area index of *Thalassia testudinum* in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different means within a year based on Duncan's multiple range test. Basins marked with an asterisk (\*) exhibited significant differences between years based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.



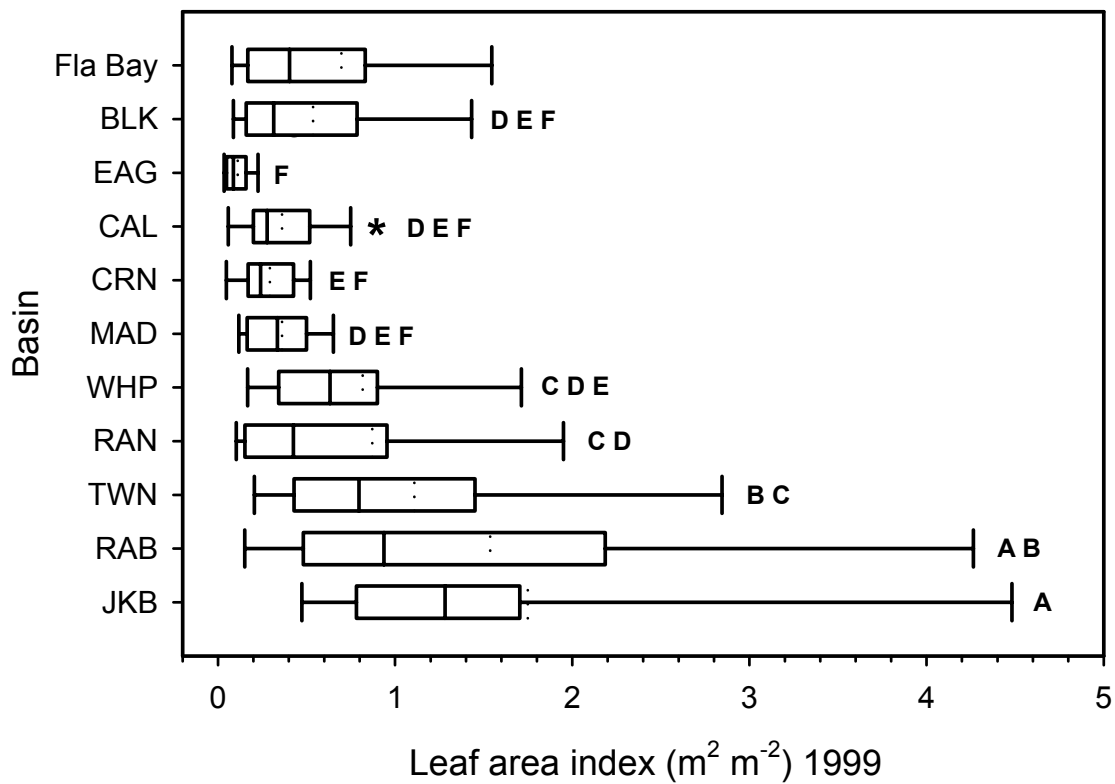
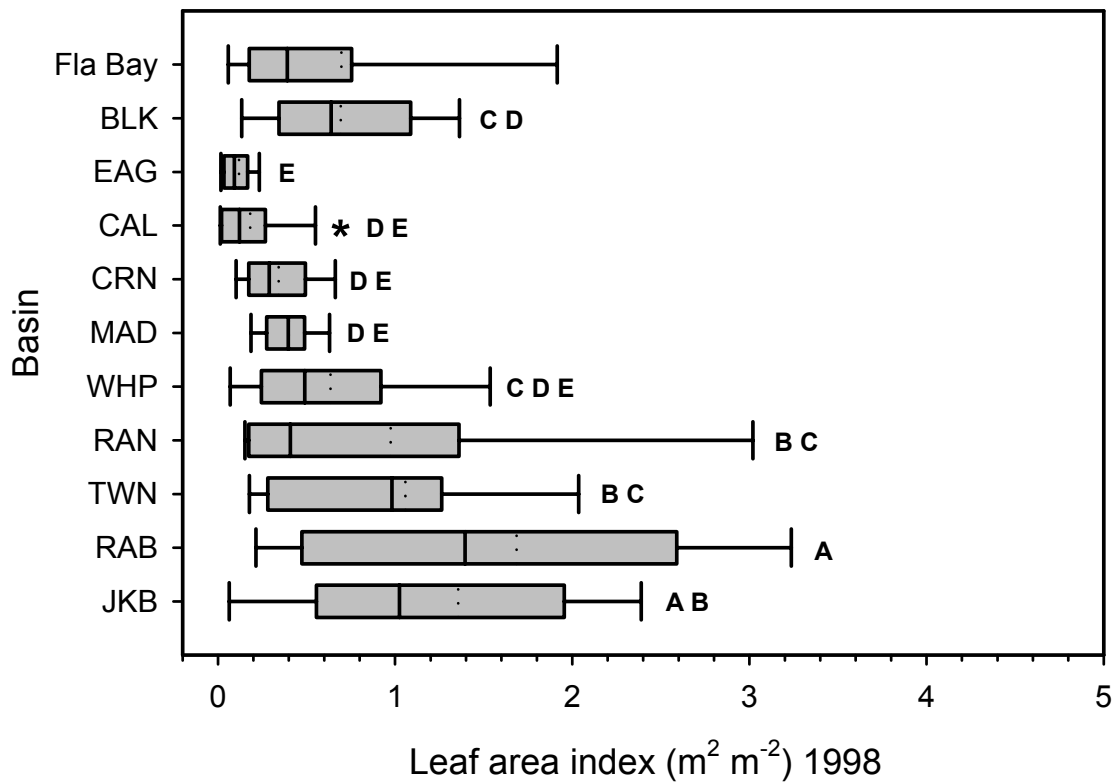


Figure 21. Standing crop of *Thalassia testudinum* in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different means within a year based on Duncan's multiple range test. Basins marked with an asterisk (\*) exhibited significant differences between years based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.

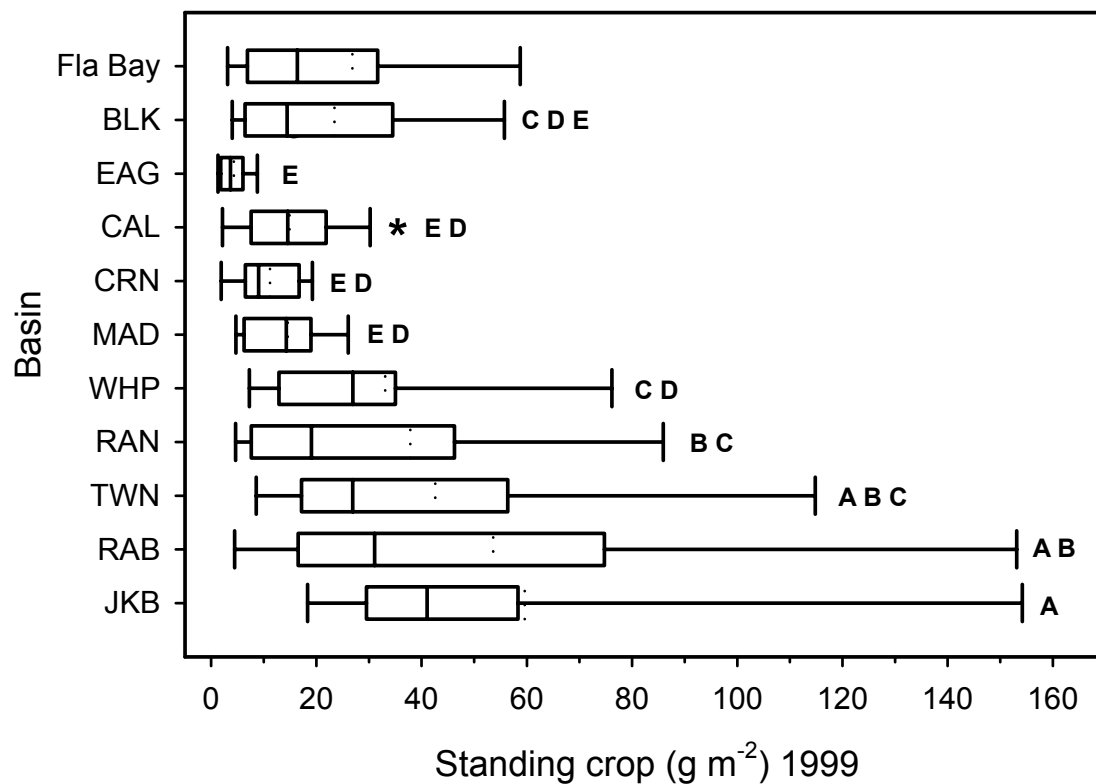
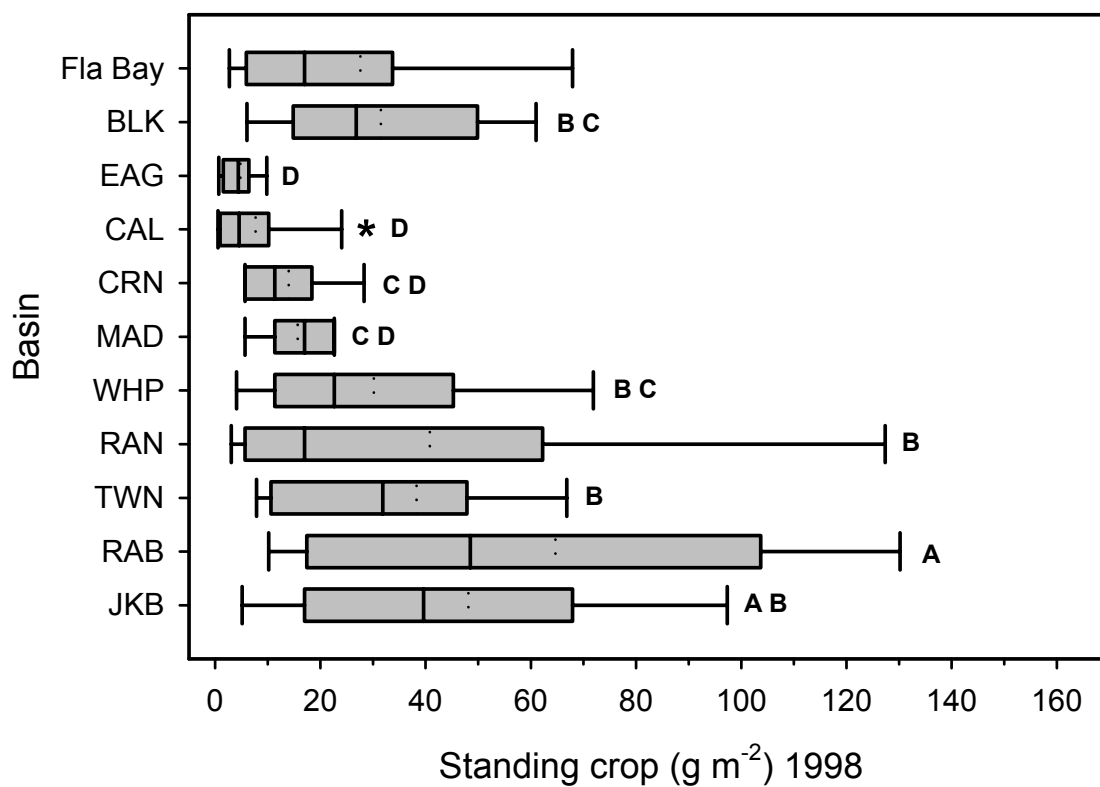
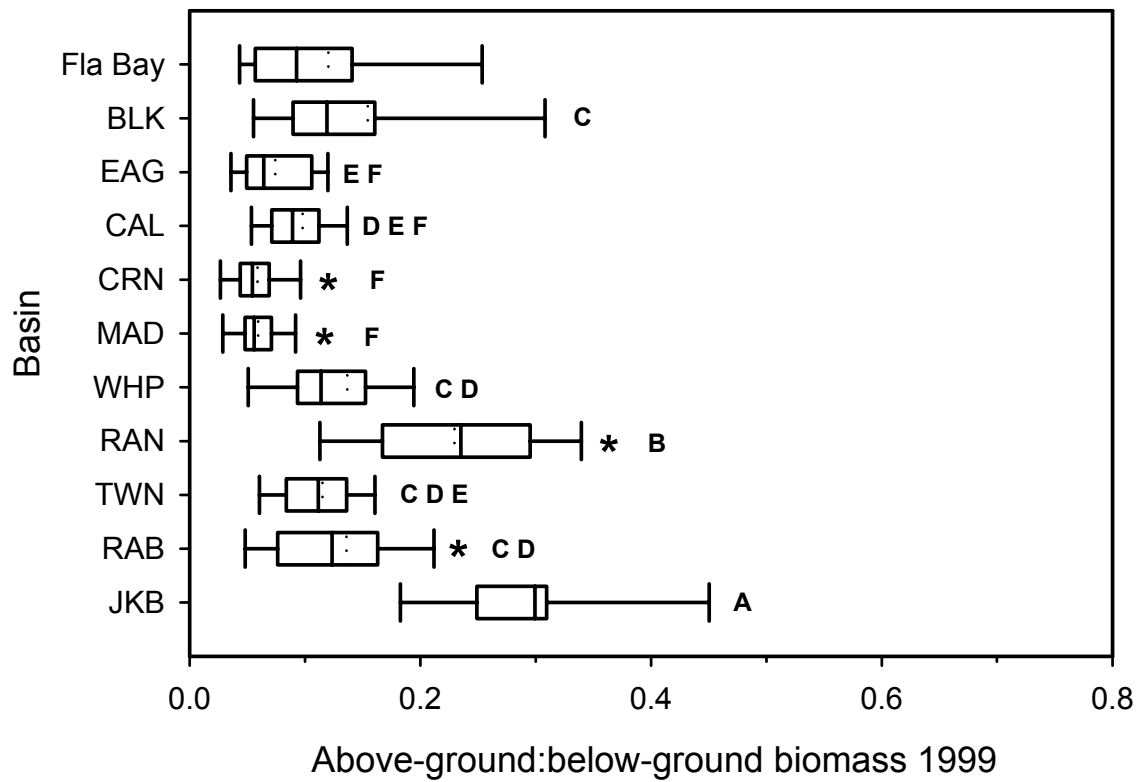
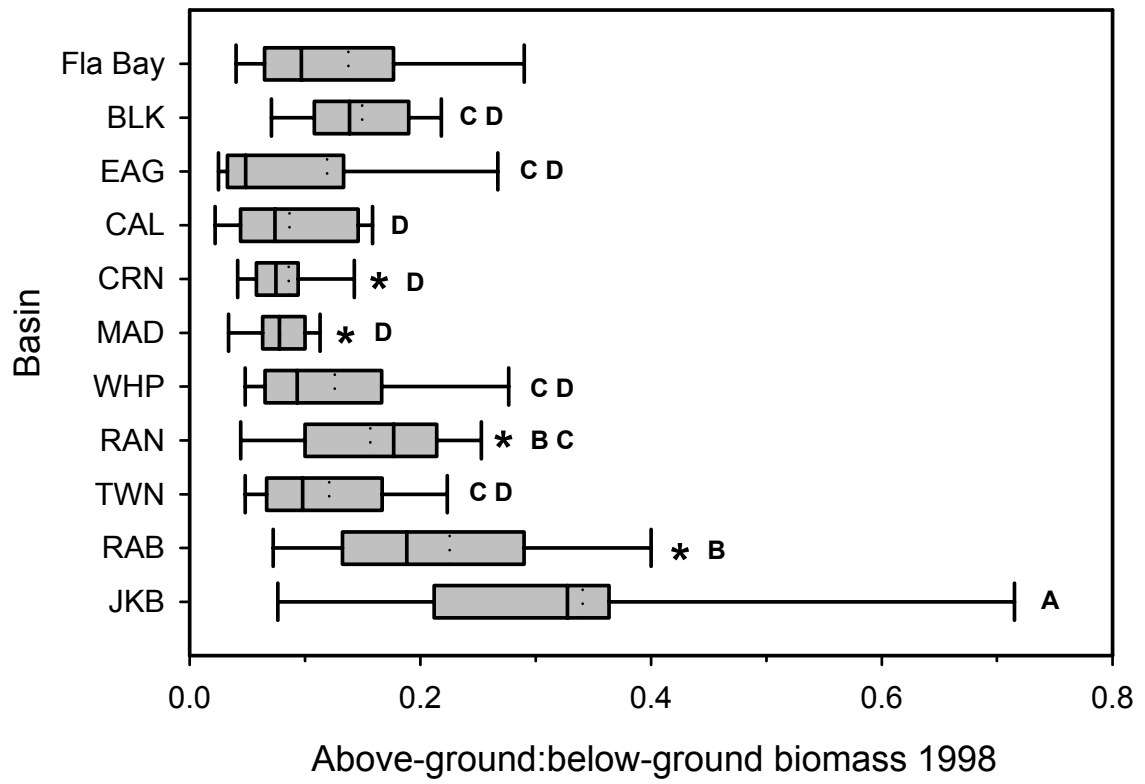


Figure 22. Ratio of above- to below-ground biomass of *Thalassia testudinum* in ten basins in Florida Bay in 1998 and 1999. Basins with the same letter designation did not have significantly different means within a year based on Duncan's multiple range test. Basins marked with an asterisk (\*) exhibited significant differences between years based on Mann-Whitney rank sum tests or student's *t*-tests. Box and whisker diagrams: boxes enclose interquartile range, vertical line within box represents median, dashed vertical line represents mean, whisker caps represent the 5th and 95th percentiles. Values for Florida Bay shown for comparison.



## Principal component analysis

Principal component analysis confirmed that certain basins grouped together frequently as indicated in Duncan's tests of variables; these results are shown in Fig. 23. In 1998 the first principal component (PC1) explained 53% of the variance and the second principal component (PC2) explained 21% of the variance; these composite variables captured 74% of the variation in the original data. In 1999 the first principal component (PC1) explained 52% of the variance and the second principal component (PC2) explained 23% of the variance; these composite variables captured 75% of the variation in the original data. The basin groupings were used to divide Florida Bay into four areas which exhibited similar trends for the variables examined. The Eastern Bay community consisted of Eagle Key, Madeira Bay, Calusa Key, and Crane Key Basins. The Central Bay community consisted of Blackwater Sound, Rankin Lake, and Whipray Basin; although geographically Blackwater Sound is in northeastern Florida Bay, statistically it grouped most often with Rankin Lake and Whipray Basin and not with the other eastern basins examined. The Western Bay community consisted of Rabbit and Twin Key Basins. Finally, Johnson Key Basin in the northwest was consistently significantly different from the other groupings and thus was placed as its own community.

Results of one-way analyses of variance for shoot-specific and area-specific characteristics for 1998 and 1999 among the pooled data for the communities identified by principal component analysis and Duncan groupings of similar subsets are shown in Table 4. All shoot-specific and area-specific characteristics displayed significant differences at the level of the Bay. The Johnson Key community was significantly different in both years from the other three communities in the number of leaves per

shoot, leaf width, leaf length, average shoot leaf length, and shoot leaf area. In 1998, *Thalassia testudinum* did not show significant differences among the Central Bay, Western Bay, and Eastern Bay communities in the number of leaves per shoot. In 1999, *T. testudinum* in the Central Bay and Western Bay did not show significant differences in leaf number, and leaf number in the Western Bay and Eastern Bay was not significantly different. All four communities were significantly different from each other in both sampling seasons in maximum leaf width, maximum leaf length, mean shoot leaf length, and shoot-specific leaf area. In 1998, the Western Bay, Eastern Bay, and Johnson Key communities were similar to each other in leaf scars per shoot, and in 1999 the Western and Eastern Bay communities were in similar subsets of leaf scars and the Central Bay and Johnson Key communities were in similar subsets.

Significant trends in area-specific characteristics among communities were less obvious but still present. Short-shoot density was highest in the Western Bay and lowest in Johnson Key. In 1998, the Johnson Key community had significantly different short-shoot density from all other communities; the Western Bay and Central Bay communities were similar, and the Central Bay was also similar to the Eastern Bay. In 1999, the Western Bay community was significantly different from the other communities in shoot density, and the Central Bay, Eastern Bay, and Johnson Key communities were not significantly different from each other. Leaf area index was highest in the Western Bay and Johnson Key communities. In 1998, leaf area index was similar in the Western Bay and Johnson Key communities while the Central and Eastern Bay communities were distinct. In 1999, leaf area index was distinct in the Western Bay and Johnson Key communities while the Central and Eastern Bay communities were in a homogenous subset. As with LAI, standing crop was highest in the Western Bay and

Johnson Key, intermediate in the Central Bay, and lowest in the Eastern Bay. In both sampling years *Thalassia testudinum* did not show significant differences in standing crop between the Western Bay and Johnson Key communities while the Central Bay community and the Eastern Bay community were distinct subsets. The ratio of above-/below-ground biomass was highest in both sampling seasons in the Johnson Key community and lowest in the Eastern Bay community; in 1998 the Western and Central Bay communities were a similar subset while in 1999 all four communities were significantly different from each other.



Figure 23. Results of principal component analysis (PCA) on shoot-specific and area-specific characteristics of *Thalassia testudinum* in Florida Bay in 1998 (A) and 1999 (B) with groupings into communities of biological similarity. Eastern Bay community = Eagle Key, Calusa Key, Crane Key, and Madeira Bay Basins; Central Bay community = Rankin Lake, Whipray Basin, and Blackwater Sound; Western Bay community = Rabbit Key and Twin Key Basins; Johnson Key community = Johnson Key Basin

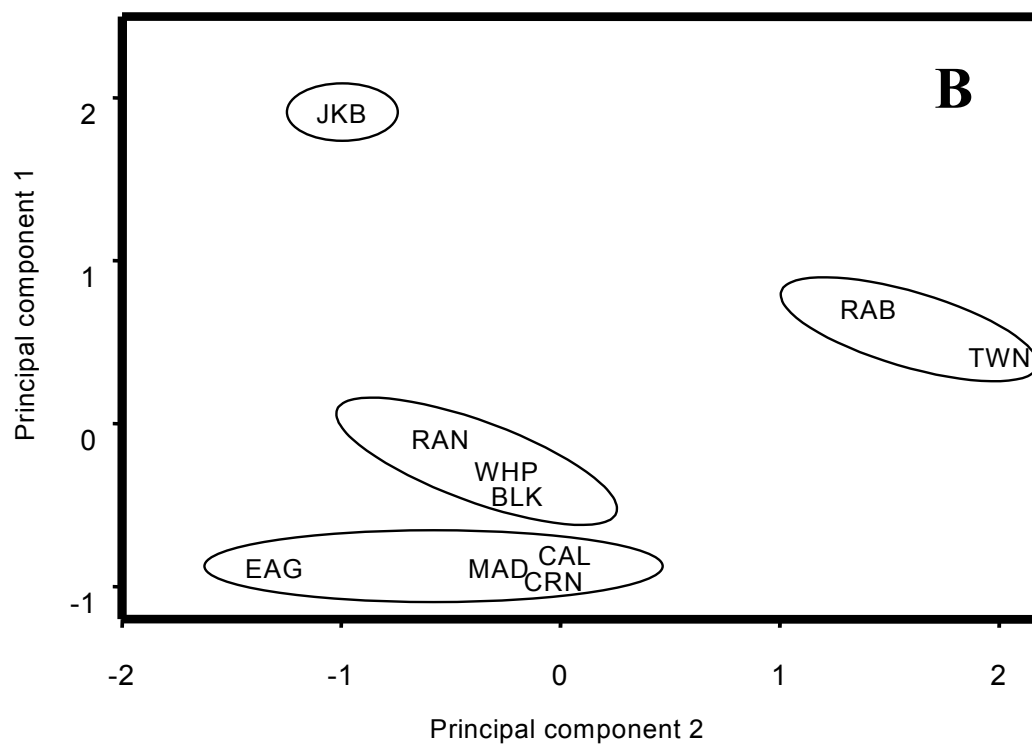
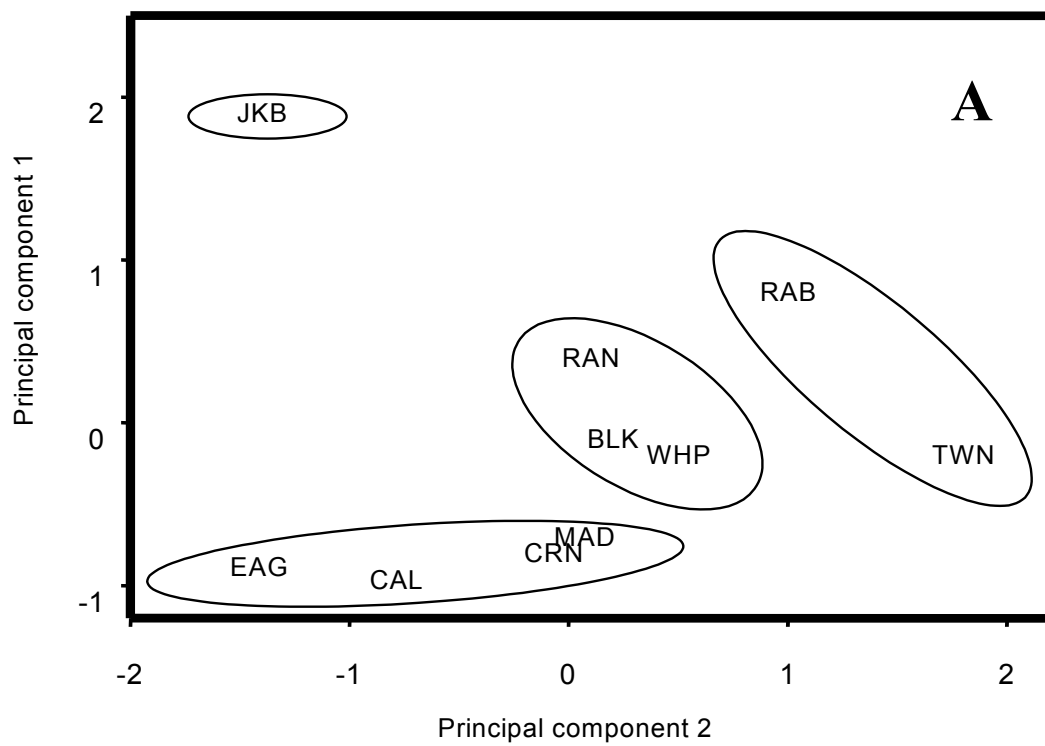


Table 4. Results of one-way analysis of variance to test for spatial differences in shoot-specific and area-specific characteristics of *Thalassia testudinum* between four communities in Florida Bay in 1998 and 1999, followed by Duncan's Multiple Range tests for comparisons between communities (homogenous subsets at  $p = 0.05$ ).

Jkb = Johnson Key Basin community, West = Western Bay, Cent = Central Bay, East = Eastern Bay

Year	Characteristic	One-Way Analysis of Variance			Duncan's Homogenous Subsets			
		n	<i>F</i>	<i>P</i>				
Shoot-specific characteristics								
1998	Leaves shoot <sup>-1</sup>	211	12.4	<0.001	Jkb	<u>Cent</u>	<u>West</u>	<u>East</u>
1999	Leaves shoot <sup>-1</sup>	232	39.3	<0.001	Jkb	<u>Cent</u>	<u>West</u>	<u>East</u>
1998	Max leaf width	211	81.4	<0.001	Jkb	West	Cent	East
1999	Max leaf width	232	113.6	<0.001	Jkb	West	Cent	East
1998	Max leaf length	211	64.9	<0.001	Jkb	West	Cent	East
1999	Max leaf length	232	63.7	<0.001	Jkb	West	Cent	East
1998	Mean shoot leaf length	211	63.3	<0.001	Jkb	West	Cent	East
1999	Mean shoot leaf length	232	61.5	<0.001	Jkb	West	Cent	East
1998	Leaf area shoot <sup>-1</sup>	211	82.5	<0.001	Jkb	West	Cent	East
1999	Leaf area shoot <sup>-1</sup>	232	128.0	<0.001	Jkb	West	Cent	East
1998	Leaf scars shoot <sup>-1</sup>	211	3.6	0.015	<u>West</u>	<u>East</u>	<u>Jkb</u>	Cent
1999	Leaf scars shoot <sup>-1</sup>	232	6.4	<0.001	<u>West</u>	<u>East</u>	<u>Cent</u>	<u>Jkb</u>
Area-specific characteristics								
1998	Short-shoots m <sup>-2</sup>	211	6.8	<0.001	<u>West</u>	<u>Cent</u>	<u>East</u>	Jkb
1999	Short-shoots m <sup>-2</sup>	232	9.5	<0.001	West	<u>Cent</u>	<u>East</u>	<u>Jkb</u>
1998	LAI	211	25.2	<0.001	<u>West</u>	<u>Jkb</u>	Cent	East
1999	LAI	232	23.5	<0.001	Jkb	West	<u>Cent</u>	<u>East</u>
1998	Standing crop	211	23.8	<0.001	<u>West</u>	<u>Jkb</u>	Cent	East
1999	Standing crop	232	21.0	<0.001	<u>Jkb</u>	<u>West</u>	Cent	East
1998	Above-ground: below-ground biomass	211	22.7	<0.001	Jkb	<u>West</u>	<u>Cent</u>	East
1999	Above-ground: below-ground biomass	232	45.6	<0.001	Jkb	Cent	West	East

## DISCUSSION

Morphometric characteristics of seagrasses vary significantly both among and between populations and at many spatial scales due to environmental and other causes (McMillan 1978, Bak 1980, Duarte 1991, de Heij & Neinhuis 1992, Alcoverro et al. 1995). Florida Bay is not a uniform environment (Phlips et al. 1995, Boyer et al. 1997, 1999), and the morphometric characteristics of *Thalassia testudinum* varied at the two spatial scales of the Bay examined in this study. However, these characteristics exhibited similar ranges relative to other areas in Florida Bay (Zieman et al. 1989, Durako 1995, Zieman et al. 1999, Hall et al. 1999), the Florida Keys (Tomasko & Lapointe 1991), Biscayne Bay, Florida (Irandi et al. 2002), Cockroach Bay, Florida (Rose & Dawes 1999), Bermuda (South 1983), and Mexico (Gallegos et al. 1993, van Tussenbroek 1995). Because seagrass morphometrics can also vary seasonally (Duarte 1989, Alcoverro et al. 1995, Durako 1995, van Tussenbroek 1998, Irandi et al. 2002), the effect of seasonal variation was minimized in this study with year-to-year comparisons of samples taken at approximately the same time of year. Any interannual differences observed are probably due to differences in winter temperatures and seasonal rainfall amounts between 1998 and 1999.

Of the characteristics of *Thalassia testudinum* measured in 1998 and 1999, only mean leaf number showed a significant (though minimal) interannual difference at the Bay level. Seasonality is the greatest source of variation in short-shoot leaf number of *T. testudinum* (Durako 1995). Most seagrass communities, including those of *T. testudinum*, achieve maximum biomass in summer (Dawes et al. 1985, Duarte 1989), usually as a result of increased shoot size (not increased density) in larger seagrass

species (Marbá et al. 1996). The distributions of all measured shoot-specific characteristics showed interannual differences, but the Kolmogorov-Smirnov Two-sample test used is more sensitive to changes in distribution around the median; these differences were probably a seasonal effect as they were fairly consistent across the characteristics measured. In Florida Bay, seasonality has little or no effect on short-shoot density but does affect standing crop and other shoot-specific characteristics (Zieman et al. 1999). Area-specific (density-dependent) characteristics showed no interannual difference in this study.

Shoot-specific and area-specific characteristics of *Thalassia testudinum* had high degrees of variability in Florida Bay, at both the Bay level and at the level of individual basins. These characteristics were not constant across Florida Bay; thus, the null hypothesis is rejected. The results of these analyses confirm those of earlier studies in illustrating an increase in *T. testudinum* abundance from northeastern to southwestern Florida Bay (Zieman et al. 1989, Hall et al. 1999). In addition, short-shoots were generally larger and had more leaves in the western basins. Leaf number and size decreased in a gradient from west to east, following trends in phosphorus availability (Fourqurean et al. 1992a, 1992b), sediment depth (Zieman et al. 1989), and iron concentration (Chambers et al. 2001). Three of the four area-specific characteristics (standing crop, leaf area index, and above-/below-ground biomass) measured showed essentially the same trend; short-shoot density was slightly more uniform across the Bay.

The large variability in morphometric characteristics of *Thalassia testudinum* seen in this study, even at relatively small scales, is not unusual in seagrass systems (Onuf 1996, Kaldy & Dunton 2000, Lee & Dunton 2000). The ranges of measured morphological characteristics were relatively large but were within reported values for

this species. This study attempted to address variation among sites by using widespread spatial sampling; the site-specific differences in *T. testudinum* characteristics observed are most likely regulated by differences in environmental parameters. Seagrass growth is regulated by light availability, temperature, and nutrient supply. Local environmental conditions probably form micro-habitats in Florida Bay that account for differences in biomass patterns among sites. Clonal plants often display morphological plasticity, which may be adaptive by allowing them to persist in a wide range of environmental conditions (Hutchings 1988). *Thalassia testudinum* has shown phenotypic plasticity in its leaf dimensions (van Tussenbroek 1996). In addition to responding to seasonal effects, leaf characters of *T. testudinum* and other seagrasses have been correlated with several environmental factors, including salinity (Phillips 1960, Dawes et al. 1985), low light availability because of depth (McMillan & Phillips 1979) and turbidity (Phillips & Lewis 1983, Lee & Dunton 1997), latitude (McMillan 1978), nutrient availability (Short 1983, Lee & Dunton 2000), freshwater input (Irlandi et al. 2002), and possibly intra- and inter-specific competition (Rose and Dawes 1999, Davis and Fourqurean 2001). Standing crop and density can also respond to the same factors. Seagrass characteristics involve so many interactive factors that causality of any one characteristic by any one environmental factor is difficult to determine (Short 1983).

The relatively low proportion of above- to below-ground biomass (~15%) of *Thalassia testudinum* compared to other seagrass species in Florida Bay accounts for its high light requirements (Fourqurean & Zieman 1991), and it also may be indicative of phosphorus limitation (Pérez et al. 1995). The values measured in this study (14% and 12% in 1998 and 1999, respectively) are similar to values reported by Iverson & Bittaker (1986) for southern Gulf of Mexico beds in and around Florida Bay and slightly lower

than those reported by Fourqurean & Zieman (1991), but these measurements were taken before maximum leaf biomass was reached in mid-summer (Dawes et al. 1985). This ratio is a function of density and leaf area, and it can be influenced by either factor. Some of the highest ratios of above- to below-ground biomass were seen in Johnson Key Basin and Rankin Lake. Although short-shoot densities were relatively low in Rankin Lake and Johnson Key Basin ( $< 200$  shoots  $m^{-2}$ ) compared to other basins in the Bay, the short-shoots in these areas were leafier. Short-shoots here had more leaves on average than those in other basins (Fig. 13), their leaves were among the widest (Fig. 14) and longest (Figs. 15 and 16), and they had high shoot-specific leaf areas (Fig. 17). These basins have been affected by die-off (Durako 1995, Hall et al. 1999) and chronic turbidity (Phlips & Badylak 1996); the increased ‘leafiness’ of shoots in chronically turbid areas such as these may indicate a morphological response to light limitation (Dawes & Tomasko 1988).

To facilitate characterization and study of this valuable community, many investigators have divided Florida Bay into distinct subenvironments or ecological zones, including those based on bank morphology and dynamics (Wanless and Taggett 1989), benthic plant communities (Zieman et al. 1989), water quality (Boyer et al. 1999), and light availability for planktonic and benthic primary production (Phlips et al. 1995). Zieman et al. (1989) used macrophyte distribution, standing crop, and productivity, along with sediment type and depth and water depth, to divide the Bay into six ecological regions with similar biological and physical characteristics. They included two other seagrass species and four types of macroalgae in addition to *Thalassia testudinum*, which was the most abundant macrophyte. Phlips et al. (1995) used regional differences in light attenuation to define four ecological zones in the Bay, and Boyer et al. (1999) divided



the Bay into three ‘zones of similar influence’ based on water quality data. These three schemes are similar in that they all have groupings of western, central, and eastern basins in some fashion.

The consistent groupings of morphometric parameters in a gradient across the Bay I saw in this study led me to define four ecological zones, based on shoot-specific and area-specific characteristics of *Thalassia testudinum*. The results of this study confirm that spatial heterogeneity in the distribution, abundance, and physical characteristics of a single seagrass species, *T. testudinum*, supports the concept of ecologically distinct regions in Florida Bay. In addition, the results demonstrate the plasticity of *T. testudinum* morphology and the significant control that the physical and chemical environment of the Bay exerts on this morphology. The four zones I have defined (Johnson Key community, Western Bay community, Central Bay community, and Eastern Bay community) are most similar to the four zones of Phlips et al. (1995). The Johnson Key community corresponds to the West region of Phlips et al., the Western Bay community to the South-Central region, the Central Bay community to the North-Central region, and the Eastern Bay community to the East region. The most obvious exception of my classification scheme compared to that of Phlips et al. (1995) and the others is my inclusion of Blackwater Sound with the Central Bay community. This basin is very diverse. Blackwater Sound is subject to the influence of freshwater flow from the C-111 canal and also to oceanic influence due to its proximity to various cuts that lead to the Atlantic; it has the deepest areas of any of the studied basins; it has areas of extremely clear water as well as very turbid areas near the Intracoastal Waterway; it has localized areas of shallow coarse sediments, deeper fine sediments, and bedrock outcrops; it has a variety of macroalgae; and four species of seagrass are present. In short, Blackwater

Sound is a microcosm of Florida Bay. Geographically, Blackwater Sound is in the East, but biologically, in regards to the characteristics of *T. testudinum*, it is most similar to Rankin Lake and Whipray Basin in the central interior of Florida Bay, which also share many of the same environmental characteristics. The box and whisker diagrams of shoot-specific and area-specific characteristics of *T. testudinum* (Figs. 13-22) and the principal component analysis of biological traits (Fig. 23) demonstrate how short-shoots in Blackwater Sound were similar to those found in central Florida Bay. The case of Blackwater Sound succinctly illustrates how measurement of *T. testudinum* morphology, distribution, and abundance over larger spatial scales can indicate to some degree the ecological status of this ecosystem.

In conclusion, a snapshot of abundance and biomass characteristics of *Thalassia testudinum* taken at the Bay level in Florida Bay will mask the extreme variability of these characteristics within the Bay at the basin level. In this study, the variability among basins of shoot-specific and area-specific characteristics of *T. testudinum* was much greater than the inter-annual variation. The degrees of phenotypic and community variability within a single seagrass species collected at similar times illustrate the environmental heterogeneity of the Bay. These local sources of variation could be missed if samples were taken at fewer sites across the Bay. Additional research is needed to define regional differences in patterns of nutrient cycling and input, freshwater and tidal mixing effects, and sediment resuspension and algal blooms and how these various factors affect the regional trends in the morphology of *T. testudinum*. Seagrass systems generate some of the highest rates of primary productivity measured in marine systems (e.g.,  $8 \times 10^5$  metric tons year<sup>-1</sup>, 1700 metric tons day<sup>-1</sup> in Florida Bay, Zieman et al. 1989) and provide refuge for small consumers (Thayer et al. 1984, Matheson et al. 1999).

Changes in these systems can have cascading effects on other organisms and other systems (Butler et al. 1995). Because of the fundamental roles that seagrasses play in support of fish and wildlife resources and in maintenance of water quality, it is essential to document trends in seagrass populations. Morphometric characteristics of seagrasses are relatively easy to collect and provide evidence of environmental stress within coastal habitats. Detailed, long-term monitoring of these sensitive habitats reveals long- and short-term patterns at various spatial scales and permits prediction of future changes. Continued monitoring of the seagrasses in Florida Bay is warranted, especially as management measures are imposed upon the ecosystem that could have unforeseen and unintended consequences on the benthic macrophyte and associated communities.

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## CHAPTER 2

### ALLOMETRIC RELATIONSHIPS AND PATTERNS DUE TO DENSITY, AGE, AND DEPTH IN *THALASSIA TESTUDINUM*

#### INTRODUCTION

*Thalassia testudinum* Banks ex König is one of the most important seagrass species in the Gulf of Mexico and Caribbean. This seagrass consists of horizontal rhizomes, which branch at regular intervals, and vertical rhizomes, which are erect, leaf- and root-bearing short-shoots (den Hartog 1970, Tomlinson 1974). Seagrass growth is regulated by light availability, temperature, sediment depth, nutrient supply, and salinity (Phillips 1960, McMillan and Phillips 1979, Dennison 1987, Short 1987, Zieman et al. 1989, Duarte 1991a, Fourqurean et al. 1992a, 1992b, Czerny and Dunton 1995, Chambers et al. 2001). Under optimal conditions, *T. testudinum* forms dense meadows where crowding can lead to intra-specific competition for resources, including sunlight. This competition can lead to self-thinning in monospecific stands of non-clonal plants, which is characterized by a negative linear relationship between biomass and density (Yoda et al. 1963, Weller 1987, Lonsdale 1990). However, clonal plants are not thought to self-thin (Hutchings 1979, Pitelka 1984, except see de Kroon and Kalliola 1995). Clonal plants may respond to crowding due to increasing density by inhibiting shoot development (de Kroon and Schieving 1990, van Tussenbroek et al. 2000) or by reaching and maintaining a maximum size of shoots or leaves which avoids self-shading and results in the allocation of more resources to below-ground storage organs (Givnish 1982, Westoby 1984).

*Thalassia testudinum* is a clonal plant. Because of the clonal nature of seagrasses, vegetative growth by rhizome elongation is the dominant method of expansion of *T. testudinum* into areas of disturbance or decline (Tomlinson 1974, Zieman 1975). Rhizomes are non-photosynthetic and thus must be supported in their development by photosynthetic products from the green leaves (Tomlinson and Vargo 1966). Leaves are of fundamental functional importance to green plants (Givnish 1982). Seagrasses and other plants often respond to environmental changes by increasing or decreasing size and/or number of their leaves. Because of their variation in form and phenology, the resultant implications for allocation to above- or below-ground biomass and whole plant growth, and not least importantly, their accessibility, leaves provide excellent opportunities for comparative studies (Givnish 1987). Leaf size and area may be affected by shoot density under crowded conditions as competition for light becomes a limiting factor (White 1981), and biomass density has been correlated with the influence of plants on the extinction of light within stands (Owens et al. 1968, Duarte and Kalff 1987). Stands with high biomass density are more prone to self-shading (Duarte and Kalff 1990). Givnish (1982) reported that for terrestrial species found only in dense herbaceous cover when competitors were close relatives or clones, smaller leaves than would be expected were observed. Density-based changes have also been observed in the leaves of seagrasses (Dawes and Tomasko 1988, Durako 1995).

Allometry, the study of size-correlated variations in organic form and process (Niklas 1994), has received less attention in plants than in animals (Bond and Midgley 1988). However, Nielsen and Sand-Jensen (1990) reported that the knowledge of allometric relationships within plant species has important ecological implications and

might indicate to what extent a system is limited by environmental factors. Duarte (1991b) further suggested that allometric relationships may provide a basis for prediction of species succession patterns and seagrass productivity from simple morphometric characteristics.

The seagrass die-off event that began in 1987 in Florida Bay appears to have been at least in part density dependent; dense beds of *Thalassia testudinum* within protected basins appeared to be most severely affected by die-off (Robblee et al. 1991, Hall et al. 1999). In this study I examined changes in *T. testudinum* morphology in relation to shoot density, shoot age, and depth, as well as the allometric relationships among various shoot-specific and area-specific characteristics of *T. testudinum*. The null hypotheses examined were that *T. testudinum* morphology was not affected by changes in shoot density, shoot age, and depth and that none of the physical characteristics of *T. testudinum* were related to each other. These hypotheses were tested by comparison with analyses of variance and linear regressions.

## METHODS

*Thalassia testudinum* was collected in Florida Bay in May 1998 and May 1999. A total of 443 cores were examined in this study, 211 cores containing 1493 short-shoots in 1998 and 232 cores containing 1622 short-shoots in 1999. Only those cores which contained mature, live short-shoots (those with photosynthetic green blades) were included in the analyses. These same core samples were used for the statistical analyses performed for the text of this chapter.

## Statistical analyses

One-way ANOVA's were used to test baywide differences in the effects of shoot density, water depth, and short-shoot age on shoot-specific and area-specific characteristics of *Thalassia testudinum*. Data were log transformed to approach normality and homogeneity of variance; however, data from 1998 and 1999 were analyzed separately because a normal distribution could not be attained when data from both years were grouped together for these analyses. The criterion for significant differences was  $p < 0.05$ . After these tests were performed, the effects of density, depth, and shoot age on *T. testudinum* were further examined using Spearman Rank Order correlation and regression analyses. Analyses were performed on log-transformed data. Spearman Rank correlations were used to assess the effect of density on characteristics of *T. testudinum* in lieu of linear regressions because the data could not be transformed to meet the assumptions of normality and homogeneity of variance. The criterion for significant differences for both of these tests was  $p < 0.05$ . Again, as in Chapter 1, data from the short-shoots within each core were averaged prior to subsequent analysis due to the large variances within cores and to the potential relatedness of the individual ramets.

Allometric relationships between variables in *Thalassia testudinum* were described using linear regression analysis of log-transformed data. Data from 1998 and 1999 were pooled in these analyses because they met the assumptions of normality and homogeneity of variance. Relationships were deemed significant if  $p < 0.05$ . The strength of relationships obtained (if significant) was described by the coefficient of determination ( $r^2$ ), and their precision was described by the standard error of the regression estimate. Variables not defined in Chapter 1 are total shoot biomass ( $\text{g m}^{-2}$ , combined weight of above- and below-ground biomass), above-ground individual shoot

weight (g, the average of the ratio of standing crop and short-shoot density within a core), and total shoot weight (g, the average of the ratio of combined above- and below-ground biomass and short-shoot density). These measurements were obtained as by Duarte and Kalff (1987).

## RESULTS

Results of one-way analyses of variance of the effects of *Thalassia testudinum* shoot density, water depth, and *T. testudinum* shoot age on shoot-specific and area-specific characteristics in Florida Bay in 1998 and 1999 are shown in Table 5. In 1998 (Table 5A), the only measured parameters that showed any significant effect from the independent variables were *T. testudinum* standing crop and the ratio of above-/below-ground biomass; short-shoot density had a significant effect on standing crop and short-shoot age had a significant effect on the biomass ratio. In 1999 (Table 5B), all of the measured parameters except leaf area index were affected significantly by at least one of the independent variables (the effect of shoot density on leaf area index was not measured because this parameter is a function of density). The number of leaves per shoot was affected by both shoot density and shoot age. Both maximum leaf length and mean leaf length were affected by shoot age. Water depth had a significant effect on both leaf width and shoot-specific leaf area. As in 1998, short-shoot density had a significant effect on standing crop, and shoot age had a significant effect on the biomass ratio.

Results of Spearman Correlations between shoot density and morphometric and biomass characteristics of *Thalassia testudinum* are shown in Table 6. In both sampling seasons the only measured parameters that showed any correlation with density were the number of leaves per shoot and standing crop. In both years, leaf number was negatively

correlated with shoot density (1998: Spearman coefficient = -0.167,  $p = 0.015$ ; 1999: Spearman coefficient = -0.159,  $p = 0.015$ ), and standing crop was positively correlated with shoot density (1998: Spearman coefficient = 0.693,  $p = 0$ ; 1999: Spearman coefficient = 0.677,  $p = 0$ ). Maximum and mean leaf length, leaf width, leaf area, and the ratio of above-/below-ground biomass showed no correlation with density.

Results of linear regressions between water depth and morphometric and biomass characteristics of *Thalassia testudinum* are shown in Table 7. In 1998, there were no significant relationships between any of the measured parameters and water depth. In 1999, however, maximum leaf width ( $r^2 = 0.025$ ,  $p = 0.017$ ) and shoot-specific leaf area ( $r^2 = 0.02$ ,  $p = 0.03$ ) were both negatively associated with water depth. Turtlegrass shoot density, the number of leaves per shoot, maximum and mean leaf length, leaf area index, standing crop, and above-ground:below-ground biomass showed no association with water depth in either year.

Results of linear regressions between shoot age and morphometric and biomass characteristics of *Thalassia testudinum* are shown in Table 8. In 1998, the only measured parameter that showed a significant relationship with shoot age was the ratio of above-ground to below-ground biomass ( $r^2 = 0.041$ ,  $p = 0.003$ ). This relationship was also significant in 1999 ( $r^2 = 0.085$ ,  $p < 0.001$ ). This ratio decreased with increasing age. The only other parameters which showed significant relationships with shoot age in 1999 were leaves per shoot ( $r^2 = 0.019$ ,  $p = 0.034$ ), maximum leaf length ( $r^2 = 0.025$ ,  $p = 0.016$ ), and mean leaf length ( $r^2 = 0.019$ ,  $p = 0.034$ ), all of which were negative relationships.



## Allometric relationships in *Thalassia testudinum*

Results of linear regressions between various morphometric and biomass characteristics of *Thalassia testudinum* are shown in Table 9. Leaf area index was highly correlated with standing crop (Eq. 1,  $r^2 = 0.969$ ,  $p < 0.001$ ); it was less strongly related to total shoot biomass (Eq. 2,  $r^2 = 0.698$ ,  $p < 0.001$ ). Shoot density was significantly related to standing crop (Eq. 3,  $r^2 = 0.509$ ,  $p < 0.001$ ) and total shoot biomass (Eq. 4,  $r^2 = 0.712$ ,  $p < 0.001$ ); however, density was not a significant indicator of individual above-ground shoot weight (Eq. 13,  $p = 0.879$ ) or total individual shoot weight (above- and below-ground biomass, Eq. 14,  $p = 0.913$ ). Shoot density was negatively correlated with leaf number (data not shown); the relationship was significant but very minor ( $r^2 = 0.01$ ). There was also a small but significant relationship between density and leaf length ( $r^2 = 0.01$ , data not shown). Not surprisingly, shoot-specific leaf area was strongly related to mean leaf length (Eq. 10,  $r^2 = 0.860$ ,  $p < 0.001$ ) and to maximum leaf width (Eq. 6,  $r^2 = 0.849$ ,  $p < 0.001$ ). Maximum leaf width was also strongly related to maximum leaf length (Eq. 7,  $r^2 = 0.666$ ,  $p < 0.001$ ) and mean leaf length (Eq. 8,  $r^2 = 0.647$ ,  $p < 0.001$ ). Although significant, the relationships between mean leaf length and standing crop (Eq. 5), leaf area index (Eq. 9), and above-/below-ground (Eq. 11) biomass were relatively weak (all  $r^2 < 0.50$ ), as were the relationships between maximum leaf width and these same variables (data not shown). Of the measured variables, shoot-specific leaf area was the most reliable morphometric indicator of above-ground:below-ground biomass (Eq. 12,  $r^2 = 0.515$ ,  $p < 0.001$ ).

Table 5. Summary of main effects  $F$  values and significance levels as determined by type III sum of squares in one-way (independent variables: shoot density, water depth, and shoot age) ANOVAs on shoot-specific and area-specific characteristics of *Thalassia testudinum* in Florida Bay in 1998 (A) and 1999 (B). Significant effects ( $p < 0.05$ ) are highlighted with bold type.

# A

Characteristic- 1998	Error Source	df	MSE	<i>F</i>	<i>P</i>
Leaves shoot-1	Short-shoot density	1	0.026	2.64	0.106
	Water depth	1	0.015	1.57	0.211
	Short-shoot age	1	0.022	2.27	0.133
	Error	209	0.010		
Max leaf length (cm)	Short-shoot density	1	0.085	1.48	0.226
	Water depth	1	0.171	3.01	0.084
	Short-shoot age	1	0.161	2.83	0.094
	Error	209	0.057		
Mean leaf length (cm)	Short-shoot density	1	0.112	2.08	0.151
	Water depth	1	0.111	2.05	0.153
	Short-shoot age	1	0.151	2.80	0.096
	Error	209	0.054		
Max leaf width (cm)	Short-shoot density	1	0.000	0.01	0.929
	Water depth	1	0.020	1.12	0.292
	Short-shoot age	1	0.014	0.77	0.381
	Error	209	0.018		
Shoot-specific leaf area (cm <sup>2</sup> )	Short-shoot density	1	0.118	0.73	0.393
	Water depth	1	0.328	2.05	0.153
	Short-shoot age	1	0.010	0.06	0.802
	Error	209	0.161		
Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	Short-shoot density	N/A	N/A	N/A	N/A
	Water depth	1	0.049	0.14	0.705
	Short-shoot age	1	0.050	0.15	0.702
	Error	209	0.341		
Standing crop (g m <sup>-2</sup> )	<b>Short-shoot density</b>	<b>1</b>	<b>34.575</b>	<b>223.20</b>	<b>&lt;0.001</b>
	Water depth	1	0.046	0.14	0.704
	Short-shoot age	1	0.032	0.10	0.750
	Error	209	0.320		
Above-/below-ground biomass	Short-shoot density	1	0.020	0.16	0.688
	Water depth	1	0.002	0.02	0.890
	<b>Short-shoot age</b>	<b>1</b>	<b>1.041</b>	<b>8.80</b>	<b>0.003</b>
	Error	209	0.123		

# B

Characteristic- 1999	Error Source	df	MSE	<i>F</i>	<i>P</i>
Leaves shoot <sup>1</sup>	<b>Short-shoot density</b>	<b>1</b>	<b>0.103</b>	<b>9.93</b>	<b>0.002</b>
	Water depth	1	0.041	3.90	0.050
	<b>Short-shoot age</b>	<b>1</b>	<b>0.048</b>	<b>4.56</b>	<b>0.034</b>
	Error	230	0.011		
Max leaf length (cm)	Short-shoot density	1	0.032	0.76	0.385
	Water depth	1	0.043	1.00	0.318
	<b>Short-shoot age</b>	<b>1</b>	<b>0.248</b>	<b>5.96</b>	<b>0.015</b>
	Error	230	0.042		
Mean leaf length (cm)	Short-shoot density	1	0.018	0.49	0.484
	Water depth	1	0.050	1.37	0.242
	<b>Short-shoot age</b>	<b>1</b>	<b>0.166</b>	<b>4.62</b>	<b>0.032</b>
	Error	230	0.036		
Max leaf width (cm)	Short-shoot density	1	0.000	0.02	0.895
	<b>Water depth</b>	<b>1</b>	<b>0.095</b>	<b>5.80</b>	<b>0.017</b>
	Short-shoot age	1	0.010	0.61	0.435
	Error	230	0.017		
Shoot-specific leaf area (cm <sup>2</sup> )	Short-shoot density	1	0.006	0.04	0.834
	<b>Water depth</b>	<b>1</b>	<b>0.625</b>	<b>4.79</b>	<b>0.030</b>
	Short-shoot age	1	0.487	3.71	0.056
	Error	230	0.131		
Leaf area index (m <sup>2</sup> - <sup>2</sup> )	Short-shoot density	N/A	N/A	N/A	N/A
	Water depth	1	0.638	2.44	0.120
	Short-shoot age	1	0.054	0.21	0.651
	Error	230	0.261		
Standing crop (g m <sup>-2</sup> )	<b>Short-shoot density</b>	<b>1</b>	<b>29.478</b>	<b>226.35</b>	<b>&lt;0.001</b>
	Water depth	1	0.620	2.43	0.121
	Short-shoot age	1	0.043	0.16	0.685
	Error	230	0.256		
Above-/below-ground biomass	Short-shoot density	1	0.232	2.31	0.130
	Water depth	1	0.002	0.02	0.889
	<b>Short-shoot age</b>	<b>1</b>	<b>1.997</b>	<b>21.57</b>	<b>&lt;0.001</b>
	Error	230	0.101		

Year	Characteristic	P	Correlation
			Coefficient
1998	Leaves shoot <sup>-1</sup>	0.015	-0.167
1999	Leaves shoot <sup>-1</sup>	0.015	-0.159
1998	Max leaf length (cm)	0.371	
1999	Max leaf length (cm)	0.788	
1998	Mean leaf length (cm)	0.230	
1999	Mean leaf length (cm)	0.910	
1998	Max leaf width (cm)	0.601	
1999	Max leaf width (cm)	0.704	
1998	Shoot-specific leaf area (cm <sup>2</sup> )	0.301	
1999	Shoot-specific leaf area (cm <sup>2</sup> )	0.908	
1998	Standing crop (g m <sup>-2</sup> )	0.0	0.693
1999	Standing crop (g m <sup>-2</sup> )	0.0	0.677
1998	Above-/below-ground biomass	0.899	
1999	Above-/below-ground biomass	0.101	

Table 6. Relationships between density and morphometric and biomass characteristics of *Thalassia testudinum* in Florida Bay in 1998 (n = 211) and 1999 (n = 232). Data are results of Spearman Rank Order Correlations of log<sub>10</sub> of shoot density (independent variable) vs. log<sub>10</sub> leaves shoot<sup>-1</sup>, max leaf length, mean shoot leaf length, max leaf width, shoot leaf area, standing crop, and the ratio of above- to below-ground biomass. Only significant effects (p < 0.05) are shown. Variables with a positive correlation coefficient increase with the independent variable and variables with a negative correlation coefficient decrease with the independent variable.

Year	Dependent Variable	Slope	F	P	r <sup>2</sup>
1998	Shoot density	0.169	0.77	0.380	0.004
1999	Shoot density	-0.003	0	0.930	0
1998	Leaves shoot <sup>-1</sup>	-0.059	1.57	0.212	0.007
1999	Leaves shoot <sup>-1</sup>	-0.090	3.90	0.050	0.017
1998	Max leaf length (cm)	-0.198	3.01	0.084	0.014
1999	Max leaf length (cm)	0.091	1.00	0.318	0.004
1998	Mean leaf length (cm)	-0.160	2.05	0.153	0.010
1999	Mean leaf length (cm)	-0.099	1.37	0.242	0.006
1998	Max leaf width (cm)	-0.068	1.12	0.292	0.005
<b>1999</b>	<b>Max leaf width (cm)</b>	<b>-0.137</b>	<b>5.80</b>	<b>0.017</b>	<b>0.025</b>
1998	Leaf area shoot <sup>-1</sup> (cm <sup>2</sup> )	-0.275	3.97	0.153	0.010
<b>1999</b>	<b>Leaf area shoot<sup>-1</sup> (cm<sup>2</sup>)</b>	<b>-0.350</b>	<b>4.79</b>	<b>0.030</b>	<b>0.020</b>
1998	Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	-0.106	0.14	0.705	0.001
1999	Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	-0.354	2.44	0.120	0.011
1998	Standing crop (g m <sup>-2</sup> )	-0.103	0.15	0.704	0.001
1999	Standing crop (g m <sup>-2</sup> )	-0.349	2.43	0.121	0.010
1998	Above-/below-ground biomass	0.023	0.02	0.890	0
1999	Above-/below-ground biomass	-0.020	0.02	0.889	0

Table 7. Relationships between depth and morphometric and biomass characteristics of *Thalassia testudinum* in Florida Bay in 1998 (n = 211) and 1999 (n = 232). Data are results of linear regressions of log<sub>10</sub> of water depth (independent variable) vs. log<sub>10</sub> shoot density, leaves shoot<sup>-1</sup>, max leaf length, mean shoot leaf length, max leaf width, shoot leaf area, leaf area index, standing crop, and the ratio of above- to below-ground biomass. Significant effects (p < 0.05) are in boldface type.

Year	Dependent Variable	Slope	F	P	r <sup>2</sup>
1998	Leaves shoot <sup>-1</sup>	0.067	2.27	0.133	0.011
<b>1999</b>	<b>Leaves shoot<sup>-1</sup></b>	<b>-0.092</b>	<b>4.53</b>	<b>0.034</b>	<b>0.019</b>
1998	Max leaf length (cm)	-0.180	2.83	0.094	0.013
<b>1999</b>	<b>Max leaf length (cm)</b>	<b>-0.209</b>	<b>5.92</b>	<b>0.016</b>	<b>0.025</b>
1998	Mean leaf length (cm)	-0.174	2.80	0.096	0.013
<b>1999</b>	<b>Mean leaf length (cm)</b>	<b>-0.171</b>	<b>4.57</b>	<b>0.034</b>	<b>0.019</b>
1998	Max leaf width (cm)	0.053	0.77	0.381	0.004
1999	Max leaf width (cm)	-0.042	0.581	0.447	0.003
1998	Leaf area shoot <sup>-1</sup> (cm <sup>2</sup> )	-0.045	0.06	0.802	0
1999	Leaf area shoot <sup>-1</sup> (cm <sup>2</sup> )	-0.292	3.63	0.058	0.016
1998	Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	0.100	0.147	0.702	0.001
1999	Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	0.109	0.248	0.619	0.001
1998	Standing crop (g m <sup>-2</sup> )	0.071	0.076	0.783	0
1999	Standing crop (g m <sup>-2</sup> )	0.097	0.203	0.653	0.001
<b>1998</b>	<b>Above-/below-ground biomass</b>	<b>-0.468</b>	<b>8.83</b>	<b>0.003</b>	<b>0.041</b>
<b>1999</b>	<b>Above-/below-ground biomass</b>	<b>-0.594</b>	<b>21.32</b>	<b>&lt;0.001</b>	<b>0.085</b>

Table 8. Relationships between shoot age and morphometric and biomass characteristics of *Thalassia testudinum* in Florida Bay in 1998 (n = 211) and 1999 (n = 232). Data are results of linear regressions of log<sub>10</sub> of shoot age (independent variable, leaf scars shoot<sup>-1</sup>) vs. log<sub>10</sub> leaves shoot<sup>-1</sup>, max leaf length, mean shoot leaf length, max leaf width, shoot leaf area, leaf area index, standing crop, and the ratio of above- to below-ground biomass. Significant effects (p < 0.05) are in boldface type.

Eq.	$Y$	$X$	$b_0$	$b_1$	$r^2$	$SE_{\text{slope}}$	$SE_{\text{log est}}$	$P$
(1) Standing crop		LAI	1.589	0.970	0.969	0.008	0.095	<0.001
(2) Total shoot biomass		LAI	2.533	0.694	0.698	0.022	0.251	<0.001
(3) Standing crop		Shoot density	0.456	1.007	0.509	0.047	0.379	<0.001
(4) Total shoot biomass		Shoot density	1.527	1.003	0.712	0.030	0.245	<0.001
(5) Standing crop		Mean leaf length	-0.384	1.735	0.463	0.089	0.397	<0.001
(6) Shoot-specific leaf area		Max leaf width	1.971	2.675	0.849	0.054	0.149	<0.001
(7) Max leaf length		Max leaf width	1.453	1.382	0.666	0.047	0.129	<0.001
(8) Mean leaf length		Max leaf width	1.306	1.296	0.647	0.046	0.126	<0.001
(9) Leaf area index		Mean leaf length	-2.054	1.810	0.490	0.088	0.392	<0.001
(10) Shoot-specific leaf area		Mean leaf length	-0.376	1.671	0.860	0.032	0.143	<0.001
(11) Above-/below-ground biomass		Mean leaf length	-1.944	1.045	0.433	0.066	0.254	<0.001
(12) Above-/below-ground biomass		Shoot-specific leaf area	-1.717	0.633	0.515	0.029	0.235	<0.001
(13) Individual shoot wt. (aboveground)		Shoot density	N/A	N/A	N/A	N/A	N/A	0.879
(14) Individual shoot wt. (total)		Shoot density	N/A	N/A	N/A	N/A	N/A	0.913

Table 9. Relationships between morphometric and biomass characteristics of *Thalassia testudinum* in Florida Bay in 1998 and 1999 (data combined,  $n = 444$ ). Data are results of linear regressions of  $\log_{10}$  values described by equations of the form  $Y = b_1X + b_0$ . The strength of the relationship is characterized by the coefficient of determination ( $r^2$ ), their precision by the standard error of the log-transformed regression estimates ( $SE_{\text{log est}}$ ), and the uncertainty about the regression slope is described by the standard error of the slope ( $SE_{\text{slope}}$ ). Significance is indicated by  $p < 0.05$ .



## DISCUSSION

Close relationships have been observed between rhizome biomass and shoot density and between shoot density and shoot biomass in *Thalassia testudinum* (Gallegos et al. 1993, Hall et al. 1999) and other species (Duarte and Sand-Jensen 1990a, Duarte 1991b). Increases in shoot density and shoot biomass generally are associated with greater leaf biomass in plants (Jacobs 1979, West and Larkum 1979, Larkum et al. 1984, Harrison and Durance 1992). Seagrass growth conditions in localized areas can be improved by increased patch size and density that contribute to a positive feed-back process (McRoy and Lloyd 1981, Fonseca et al. 1983). As density of *T. testudinum* increases, sedimentation rates increase and deposited sediments are stabilized, which helps create a relatively low-energy environment with improved water clarity even more conducive to seagrass growth (Zieman 1982, Onuf 1996). However, as plants become larger, self-shading can occur, and higher densities can become disadvantageous because of competition for light (Lee and Dunton 2000). Therefore, changes in density can result in changes in seagrass characteristics.

Under optimal conditions, *Thalassia testudinum* forms vast, dense meadows, often in monoculture (Zieman 1982). Monocultures are often characterized by density-dependent mortality as an increase in biomass is associated with a decrease in plant density (Westoby 1984, Weller 1987, Lonsdale 1990). However, *T. testudinum* is a clonal plant, and Hutchings (1979) showed that most clonal plants do not show self-thinning. Olesen and Sand-Jensen (1994) reported that self-thinning was relatively unpronounced in natural stands of *Zostera marina*, another clonal seagrass. Similarly, in the present study, density had very little effect on shoot-specific and area-specific characteristics of *T. testudinum*. Standing crop and total shoot biomass were both

correlated with density, results which are similar to those reported for *T. testudinum* and for other seagrass species (Backman and Barilotti 1976, Duarte and Sand-Jensen 1990a, Gallegos et al. 1993, Hall et al. 1999, Laugier et al. 1999). Shoot density was positively associated with standing crop and total shoot biomass (Table 8, Eq. 3,  $r^2 = 0.51$ , Eq. 4,  $r^2 = 0.71$ , respectively). The density/standing crop relationship is not as strong as those reported for *T. testudinum* by Hall et al. (1999) of  $r^2 = 0.62 - 0.74$  and Gallegos et al. (1993) of  $r^2 = 0.92$ . This could be due to a seasonality effect, or to the fact that in the present study only those cores with live, mature short-shoots were included in the statistical analysis. Cores with no *T. testudinum* short-shoots were not included, which can affect density estimates; in addition, immature, or “dormant,” short-shoots were not counted (van Tussenbroek et al. 2000). The number of leaves per shoot decreased with increasing density (Table 5); linear regression of short-shoot density against blade number was also significant with a negative slope ( $r^2 = 0.02$ , data not shown). These trends were significant but minor, similar to that seen by South (1983) in a study of *T. testudinum* beds in the Bahamas, and they suggest some self-thinning at the within-shoot level. In areas of high density in the Mexican Caribbean, *T. testudinum* had shorter, thinner blades than in areas of lower density (van Tussenbroek 1998). However, foliar weight/shoot did not vary with density (van Tussenbroek et al. 2000), which is similar to the results of the present study (Table 8, Eq. 13). Gallegos et al. (1993) found that *T. testudinum* short-shoots in a densely-populated lagoon in Mexico had significantly more leaves than in a nearby, less-disturbed area; however, this area was eutrophic. Shoot density had little or no effect on the other area-specific and shoot-specific characteristics examined in the present study, contrary to what might be expected among rhizomatous herbaceous plants (Jacobs 1979, Givnish 1982, Olesen and Sand-Jensen 1994, van Lent

and Vershuure 1994, van Tussenbroek 1998, Olesen et al. 2002). Duarte and Kalff (1987) reported that various marine and freshwater macrophytes displayed inverse relationships between density and plant weight. In the present study, however, density had no effect on individual above-ground shoot weight or total individual shoot weight (Table 8, Eqs. 13 and 14). This finding is significant because it indicates that no short-shoot self-thinning is occurring in this population. If self-thinning was occurring, declining shoot density should be accompanied by an increase in biomass and constant or increasing LAI (de Kroon and Kalliola 1995).

Water depth can affect physical characteristics of *Thalassia testudinum*, usually as a result of decreased light availability (McMillan and Phillips 1979, Dawes and Tomasko 1988, Tomasko and Dawes 1990). Increased ‘leafiness’ of *T. testudinum* is the common response to light reduction (Dawes and Tomasko 1988); however, in the present study depth had little effect on the plant characteristics measured (Table 6). This could be due to the generally low rate of light attenuation and small range of depth (about 250cm) in the basins studied in Florida Bay, which may not be great enough to detect morphometric differences in *T. testudinum* caused by decreasing irradiance due to depth. The maximum depth of seagrasses is controlled by light availability (Duarte 1991a), and attenuation of light results in declines in density and biomass. In Florida Bay, however, *T. testudinum* growing at depths of 3m and less (as in the sites in the present study) may not be light limited (Fourqurean and Zieman 1991). In 1999 depth had a small but significant negative effect on leaf width and shoot-specific leaf area, results which are similar to the observations of Lee and Dunton (1997) but contrary to other observed effects of depth on these characteristics in *T. testudinum* (Dawes and Tomasko 1988) and in other species (Bulthuis and Woelkerling 1983). The present results could be due to

chance or may be an artifact caused by salinity differences, which have been shown to effect leaf width in *T. testudinum* (Moore 1963, Zieman 1975, Zieman 1982, Dawes et al. 1985, Irlandi et al. 2002). In the present study leaf width significantly correlated with shoot-specific leaf area ( $p < 0.001$ ,  $r^2 = 0.849$ ). Leaf length, number, and width may increase in seagrass species with depth (Hulings 1979), but in some cases leaf width decreases with depth (Lee and Dunton 1997). Although water depth is significantly related to density of seagrasses, and *T. testudinum* density is usually higher in shallow water (Iverson and Bittaker 1986, Hall et al. 1999, Fourqurean et al. 2002), the results of the present study do not indicate an effect on shoot density of depth. Again, the narrow range of depths encountered and the relatively shallow study sites may mask any effect of depth on *T. testudinum* shoot density in the basins of Florida Bay. Similarly, leaf area index, a function of density and shoot-specific leaf area, correlates with depth (Dawes and Tomasko 1988), but no correlation was seen in the present study. The present results are similar to those for *Heterozostera tasmanica* reported by Bulthuis and Woelkerling (1983) in Australia. Standing crop should reflect the same patterns in relation to depth as density and LAI and in fact has been shown to be correlated with light availability (Lee and Dunton 1997), but statistical analyses of the present data showed no correlation between standing crop and depth. Above-ground:below-ground biomass ratios are predicted to increase when light is limiting to herbaceous plants (Hunt and Nicholls 1986). This ratio increases with depth in *T. testudinum* (Dawes and Tomasko 1988, Kaldy and Dunton 2000), but again the present study showed no relationship with depth. Not surprisingly, shoot-specific and area-specific characteristics of *T. testudinum* in the ten basins studied in Florida Bay showed none of the patterns expected with large changes in depth.

Age can affect physical characteristics of seagrasses. Individual short-shoots of *T. testudinum* can survive ten years or more (Patriquin 1973). Leaf width has been shown to increase with age in *T. testudinum* (Zieman 1975), and a narrowing of leaves precedes shoot death (Gallegos et al. 1993). Johnstone (1979) found that leaf width increases with age in *Enhalus acoroides*, an Indo-Pacific seagrass, and explained leaf polymorphism to be a function of age more than environmental factors. In the Mediterranean seagrass *Cymodocea nodosa*, leaf number per shoot and leaf length increase with shoot age to a plateau (Duarte and Sand-Jensen 1990a). Few significant correlations between age and shoot morphometrics were seen in the present study, however (Table 7). Although leaves per shoot and leaf length significantly decreased with increasing age in 1999, the regression lines were nominal. Allocation of biomass with shoot age was the only consistent significant relationship seen. As shoots aged, more resources were allocated to belowground biomass. Although the regression coefficients were low ( $r^2 < 0.10$ ), this pattern is expected, as the first leaves on vertical shoots are produced rapidly (Patriquin 1973) so that surface area is exposed for photosynthetic production. Age structure of seagrasses are often characterized by low numbers of very young shoots, many shoots less than one year old, and declining numbers of older shoots (Duarte et al. 1994), a pattern which was displayed by the populations in the present study (see Chapter 1).

Correlative increases in standing crop, leaf area index, leaf area, and other morphometric characteristics that have been reported for other seagrass species (Duarte and Sand-Jensen 1990a, 1990b) were not observed in the present study, perhaps as a result of the more uniform distribution of the stands of *T. testudinum* examined as opposed to the patchy distributions of seagrasses examined in other studies in which

patch edges were compared with patch interiors. Although Florida Bay is a disturbed estuary, in the basins studied *T. testudinum* exists in fairly stable, climax communities. Cores were collected throughout the basins without regard to location within a particular stand.

The most important findings in the present study are the allometric relationships exhibited among various shoot-specific and area-specific characteristics. Historically, standing crop has been the primary measure of comparison among seagrass systems because of the relative ease of sampling (Zieman 1982). Although wide variations of standing crop are characteristic for seagrass beds (Duarte 1989, Durako 1995, Hall et al. 1999, Durako et al. 2002), even localized, temporary changes in standing crop can cause significant changes in density, diversity, and abundance of associated faunal assemblages (Bell and Westoby 1986, Holmquist et al. 1989, Sogard et al. 1989, Thayer and Chester 1989, Matheson et al. 1999, Thayer et al. 1999). Despite a wide range of sediment properties and water depth, standing crop of *Thalassia testudinum* may be used to estimate productivity within a region, which is easier than traditional methods of productivity assessment (Zieman et al. 1989). Also, standing crop is important to note when describing optical qualities of the water column because light attenuation within the canopy is dependent on above-ground biomass density (Enríquez et al. 2002). Collection and analysis of standing crop is nevertheless laborious and time-consuming. In addition, in Florida Bay below-ground biomass of *T. testudinum*, which is difficult to collect in an accurate manner in deep or hard sediments, accounts for up to 90 % of total biomass (Zieman 1982, Durako 1995, Chapter 1). Equations 1 and 2 in Table 8 indicate that leaf area index can be used to estimate standing crop and total shoot biomass (above- and below-ground biomass combined) in Florida Bay. Leaf area index explained 97% and

69% of the variance in standing crop and total shoot biomass, respectively. In this study, leaf area index was shown to be an even more accurate indicator of standing crop and total shoot biomass than shoot density alone, which explained 51% and 71% of the variance, respectively. Standing crop, in turn, has been shown by Zieman et al. (1989) to have a linear relationship with areal leaf productivity for *T. testudinum* in Florida Bay ( $r^2 = 0.92$ ). Therefore, it is possible that measurements of leaf area index can be made in lieu of biomass collection to determine standing crop and productivity. However, studies are required to relate leaf area index to productivity over wide spatial and temporal scales such as in the Zieman et al. (1989) study.

Although within-species variability in some seagrass morphometric characteristics (seen in Chapter 1) is often similar in magnitude to that between species (Duarte 1991a), the data compiled here show that some of the shoot-specific and area-specific characteristics of *Thalassia testudinum* in Florida Bay are strongly related and might prove to be useful descriptors of the architecture of this important seagrass. In *Zostera marina*, leaf length and width are correlated (Bak 1980), and the data in the present study reveal that leaf width is linearly related to leaf length in *T. testudinum* (Table 8, Eqs. 7 and 8). Plants which have the longest leaves usually also have the widest leaves. This finding is probably driven by the trends discussed in Chapter 1. Standing crop as well as size of individual shoots of *T. testudinum* generally increase from the northeast to the southwest in Florida Bay in response to increasing sediment depth (Zieman et al. 1989) and nutrient availability (Fourqurean et al. 1992a, 1992b, Chambers et al. 2002). Leaf width is easy to determine, even in the field, and is also an accurate indicator of shoot-specific leaf area (Table 8, Eq. 6), a value which is tedious to obtain, usually in the lab. Mean leaf length explains 86 % of the variability in shoot-

specific leaf area (Table 8, Eq. 10), which is similar to that of leaf width (85 %). Leaf width is easier to measure than mean leaf length, however, especially in areas of high disturbance or exposure where leaves may be broken. Mean leaf length is also indicative of other shoot-specific characteristics, although the relationships are not as strong (Table 8, Eqs. 5, 9, and 11). In areas where underground biomass is difficult to obtain or if destructive sampling is not desired, shoot-specific leaf area can be used to estimate roughly the ratio of above- to below-ground biomass (Table 8, Eq. 12,  $r^2 = 0.52$ ).

In general, the null hypotheses concerning the effects of density, depth, and shoot age on *Thalassia testudinum* morphology were accepted; there were no consistent significant effects by these variables on the samples examined. However, allometric relationships were seen in some of the characters tested, and the null hypothesis that none of the physical characteristics of *T. testudinum* are correlated is rejected.

In summary, the results demonstrate the interrelatedness of the architectural components of *Thalassia testudinum*. These results also demonstrate that while habitat conditions play an important role in determination of *T. testudinum* size, growth, and productivity, *T. testudinum* can show great variation in its physical characteristics, even within the same bed. Despite the clonal growth paradigm of seagrass population dynamics, sexual reproduction plays a significant role in seagrass community development (Durako and Moffler 1987, Duarte and Sand-Jensen 1990a, Gallegos et al. 1992). Genetic variability may also play a role in seagrass biomass variability. Even at small scales (<1 m), *T. testudinum* does not grow exclusively in monoclonal patches (Davis et al. 1999). However, by using some of the relationships outlined in this study, researchers may be able to gain a rapid insight into the status of seagrasses in a large area without extensive, destructive sampling and time-consuming laboratory work.



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