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# Size–frequency patterns in morphometric characteristics of the seagrass *Thalassia testudinum* reflect environmental variability

John W. Hackney, Michael J. Durako\*

Department of Biological Sciences, Center for Marine Science, University of North Carolina at Wilmington,  
5600 Marvin Moss Ln, Wilmington, NC 28409, USA

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## Abstract

Patterns of variability in structural characteristics of the seagrass *Thalassia testudinum* were investigated in 10 basins across Florida Bay, Florida, USA. *T. testudinum* is the dominant seagrass in this perturbed subtropical estuary and changes in its ecological condition are being used as a one of the response metrics for the Comprehensive Everglades Restoration Program (CERP). Patterns in the size–frequency distributions of a suite of morphometric and biomass characteristics were compared at two spatial scales (Bay and basin) and between the two sample years (1998 and 1999). Size–frequency distributions of shoot-specific and area-specific characteristics were more sensitive to both inter-annual and among-basin variation than measures of central tendency because of the high degree of variability at both spatial scales. Distributions of several parameters consistently grouped together into three or four pattern types. These pattern groups were spatially very similar to regions previously defined based upon biological, physical, chemical, and geological characteristics. The results of this study confirm that spatial heterogeneity in the size–frequency distributions of morphometric and biomass characteristics of *T. testudinum* support the concept of ecologically distinct regions within Florida Bay. The results also demonstrate the sensitivity of size–frequency distributions to differences in environmental factors and the significant control that the physical and chemical environment of Florida Bay exerts on *T. testudinum* morphology.

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## 1. Introduction

Seagrasses form communities that often dominate the hydroscares of many coastal environments. Their shallow distribution and close proximity to the land/sea interface causes these marine angiosperms to be sensitive to changes in coastal watersheds that affect the nearshore marine environment. Healthy seagrass beds are highly productive and they increase

habitat complexity and stability compared with un-vegetated areas. Seagrass production, biomass, and structure support coastal fisheries via direct herbivory and detrital food webs within the beds and through export to adjacent systems. They also stabilize sediments, increasing optical water quality, form structural substrate for epiphytic growth, and provide nursery habitat and shelter to many organisms (den Hartog, 1977; Borum and Wium-Andersen, 1980; Zieman, 1982; Thayer et al., 1984; Kenworthy et al., 1988; Duarte, 1989).

In Florida Bay, seagrasses are both the dominant biological community and the dominant submerged

\* Corresponding author. Tel.: +1-910-962-2373;

fax: +1-910-962-2410.

E-mail address: durakom@uncw.edu (M.J. Durako).

physical feature (Durako et al., 2002; Fourqurean et al., 2002). Seagrass beds dominated by turtlegrass, *Thalassia testudinum* Banks ex König (Hydrocharitaceae), cover more than 80% of the area of Florida Bay within Everglades National Park (Zieman et al., 1989). The recent widespread die-off of *T. testudinum* in Florida Bay (Robblee et al., 1991; Fourqurean and Robblee, 1999) has contributed to eutrophication and increased turbidity in the Bay, which, in turn, has led to system-wide changes that threaten the stability of this valuable ecosystem (Butler et al., 1995). Because *T. testudinum* is a benthic, long-lived clonal plant requiring high light availability (i.e., clear water), the distribution, abundance, and condition of this species may be indicative of the “health” of Florida Bay (Durako et al., 2002). Thus, any change in this species’ ecological condition, which may be affected by water quality changes associated with the Comprehensive Everglades Restoration Program (CERP), is one of the central issues being considered by environmental managers.

Several structural and dynamic characteristics of *T. testudinum* have been investigated for use as indicators of ecological condition. These 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 (LAI), leaf productivity, and biomass (Durako, 1995). Leaf area, biomass of leaves (which 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 and Phillips, 1979; West and Larkum, 1979; Durako and Moffler, 1985; Dawes and Tomasko, 1988; Harrison and Durance, 1992; Lee and Dunton, 1997). Phillips and Lewis (1983) correlated leaf width in *T. testudinum* with environmental stress and observed that this structural characteristic changed in response to environmental factors. Durako (1995) also observed that changes in structural characteristics, such as leaf length, width, and shoot-specific leaf area, reflected responses of *T. testudinum* to environmental conditions. In all these previous studies, changes in measures of central tendencies (mean or median values) of the characteristics were assessed.

This paper describes the trends and patterns of size–frequency distributions of a suite of morphometric and biomass characteristics of *T. testudinum* in 10 basins within Florida Bay, during two sampling seasons. In a related paper, we used a hierarchical statistical approach to compare measures of central tendencies in these variables (Hackney and Durako, submitted for publication). Those analyses indicated only one significant inter-annual difference at the Bay scale, but they did reveal that the 10 sampled basins consistently grouped into four statistically-defined ecological zones. Here, size–frequency distributions of shoot-specific and area-specific characteristics of *T. testudinum* in Florida Bay were compared between the two sampling years at both the Bay and basin scales. The distributions of most of the structural characteristics also fell into three-to-four groups. In addition, size–frequency distribution data were more sensitive in detecting statistically-significant inter-annual variation at both the Bay and basin scales, suggesting that this may be a better alternative approach to detecting temporal change in monitoring and assessment programs than comparisons of means or median values.

## 2. Methods

Sampling was conducted in Florida Bay (ca. 25°05'N, 81°45'W), a shallow, seagrass-dominated estuary which separates the Florida Keys from the southern tip of the Florida Peninsula (Fig. 1). Florida Bay is comprised of a series of mud banks that divide the Bay into 49 shallow basins and which restrict circulation and dampen tidal influence (see Fourqurean and Robblee, 1999 for a detailed description of Florida Bay). *T. testudinum* was collected during the spring sampling of the Florida Bay Fish Habitat Assessment Program (FHAP) in May 1998 and May 1999. FHAP is a long-term status and trends assessment program and one of several multi-agency coordinated monitoring programs implemented in the south Florida region to detect changes in regional-scale seagrass distribution and abundance (Fourqurean et al., 2002). Sampling in FHAP is conducted in 10 of the 49 basins in Florida Bay (Fig. 1). Each basin is subdivided into 28–33 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).

Stations were located using GPS. Water depth and temperature, salinity, and secchi depth were recorded at each station.

For this study, *T. 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 single PVC core sample (177 cm<sup>2</sup>) was taken at each station. Plant material from the cores was washed free of sediment in the field, stored in plastic bags, and frozen for subsequent analysis. After thawing, seagrasses were sorted by species, short-shoot density (number m<sup>-2</sup>) 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. 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 60 °C and weighed to obtain standing crop (g m<sup>-2</sup>). Live short-shoot and live rhizomes and roots (white or brown and crispy) were also dried to constant weight (60 °C) and weighed to obtain below-ground biomass (g m<sup>-2</sup>). 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 per shoot, 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, cm<sup>2</sup>), and shoot age (leaf scars per shoot). Area-specific characteristics are short-shoot density, leaf area index (mean shoot-specific leaf area x short-shoot density, m<sup>2</sup> m<sup>-2</sup>), standing crop (g m<sup>-2</sup>), and the ratio of above- to below-ground biomass.

Morphometric and biomass characteristics were compared with a two-tiered statistical approach. First, for each year the range and distribution of each characteristic was described and analyzed for the Bay scale; distributions were binned into appropriate

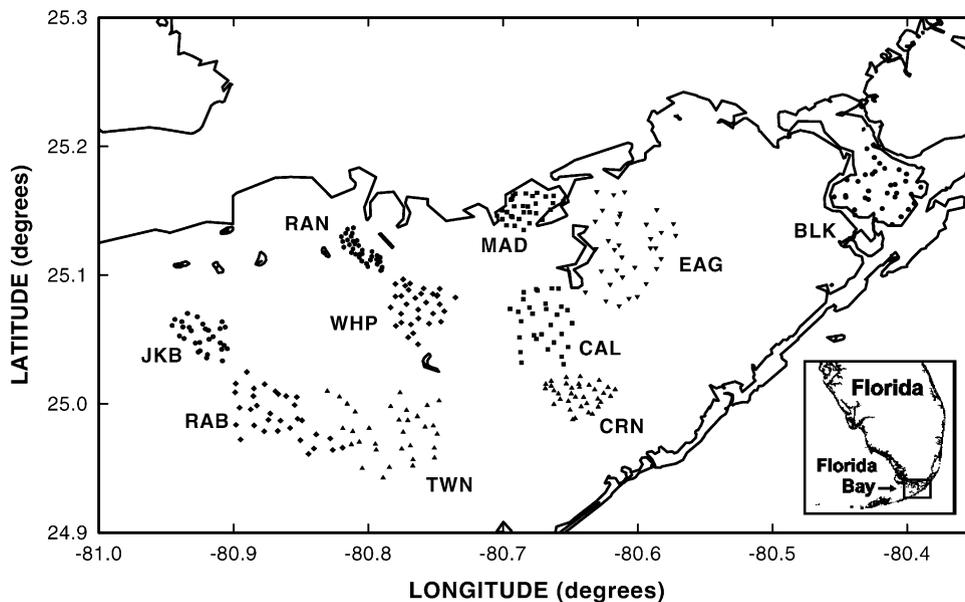


Fig. 1. Florida Bay showing the locations of sites sampled in 1998 and 1999.

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, the range and distribution of each characteristic was described and analyzed for each basin. Distributions

were again binned into appropriate classes and significance ( $D_{\max} > 0.05$ ) of changes in these distributions between 1998 and 1999 was determined using the Kolmogorov–Smirnov Two-sample test. The criterion for significant differences was  $P < 0.05$ . All statistical tests were performed using the SAS statistical

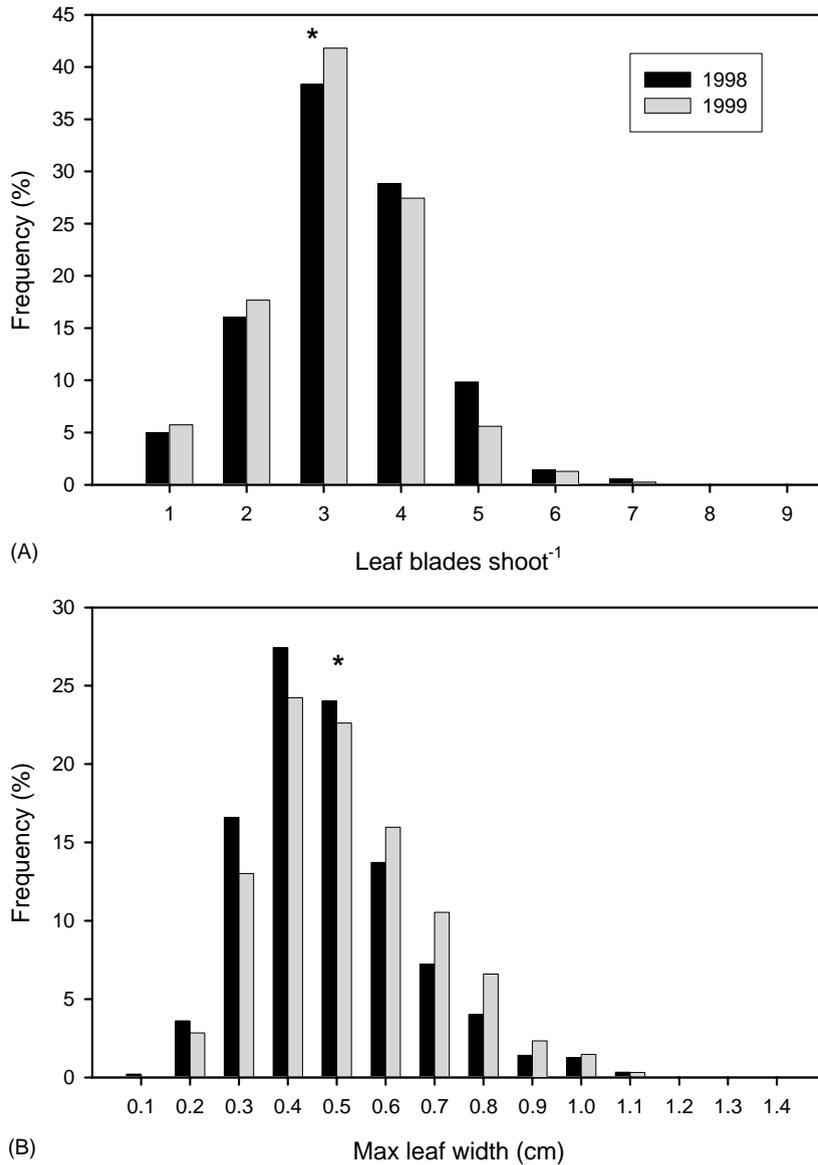


Fig. 2. Inter-annual comparisons of the distributions of number of (A) leaves per shoot and (B) maximum leaf width of short-shoots of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 ( $n = 1494$ ) and shaded bars represent 1999 ( $n = 1622$ ). Significant differences in distributions 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.

program (SAS, Cary, NC) or SigmaStat (Jandel Scientific, San Rafael, CA).

### 3. Results

At the Bay level, leaf number and leaf width had slightly positively skewed but otherwise fairly uniform distributions. All other morphometric character distributions at the Bay level were positively skewed. Distribution patterns at the basin level were highly variable.

Leaves per shoot, at the Bay scale, exhibited a significant ( $D_{max} > D_{0.05}$ ) negative shift in distribution from 1998 to 1999 (Fig. 2A). Within-basin comparisons of the leaves per shoot distributions (Fig. 3) between 1998 and 1999 showed that although leaf

number declined in seven of 10 basins, a significant difference occurred between the 2 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 in the central Bay also had three to four leaves; however, about 80% of the shoots in Johnson Key Basin, in the northwest, had four to six leaves while more than 70% in Eagle Key Basin, in the east, had only two to three leaves. Shoots in Crane and Calusa Basins mostly had 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 abundance

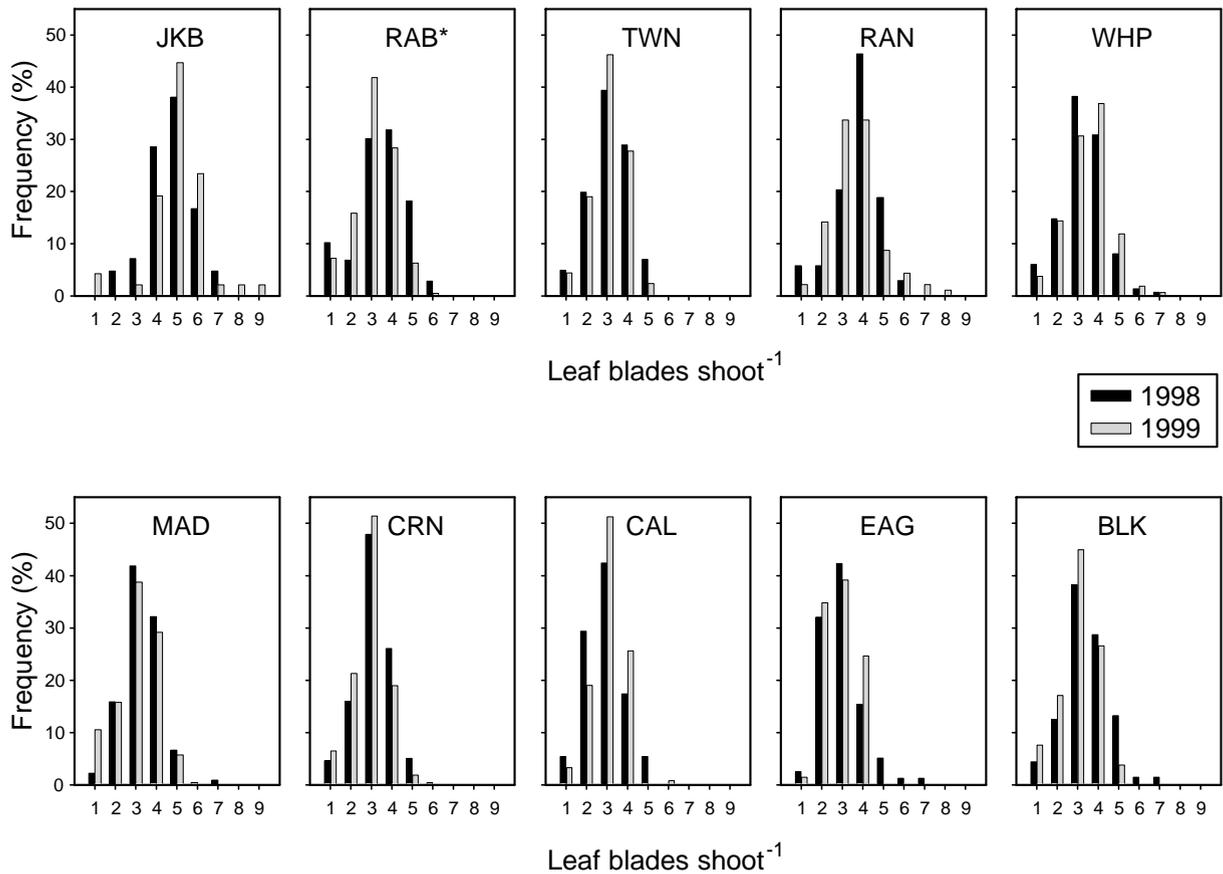


Fig. 3. Inter-annual comparisons of the distributions of number of leaves per shoot of *Thalassia testudinum* in 10 basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant inter-annual differences in basin distributions based on Kolmogorov–Smirnov Two-sample tests ( $D_{max} > D_{0.05}$ ).

of shoots with increased widths (Fig. 4); five of the other seven basins displayed insignificant positive shifts in distribution. At the Bay scale, about 80% of shoots had leaves from 0.3 to 0.6 cm wide; the modal class for both years was 0.4 cm. Leaf width at the basin scale was much more variable, with Johnson Key, Rabbit Key, and Rankin Lake Basins in the west having a greater amount of shoots with wide leaves and Crane Key, Calusa Key, and Eagle Key Basins in the east having shoots with thinner blades. Mid-Bay basins and Blackwater Sound had mostly shoots with intermediate width leaves.

The size–frequency distributions of maximum leaf length and mean leaf length were similar. The maximum leaf length (Fig. 5A) 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. 5B) of 4–10 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 cm class in 1999. Within-basin comparisons of maximum length (Fig. 6) and mean length (Fig. 7) distributions showed that, like width, length was highly 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 was unique in having bimodal distributions of maximum length. Significant differences in the distributions of maximum leaf length and mean length were detected between the 2 years at Whipray and Calusa Key Basins, both of which were positive shifts. Six of the remaining

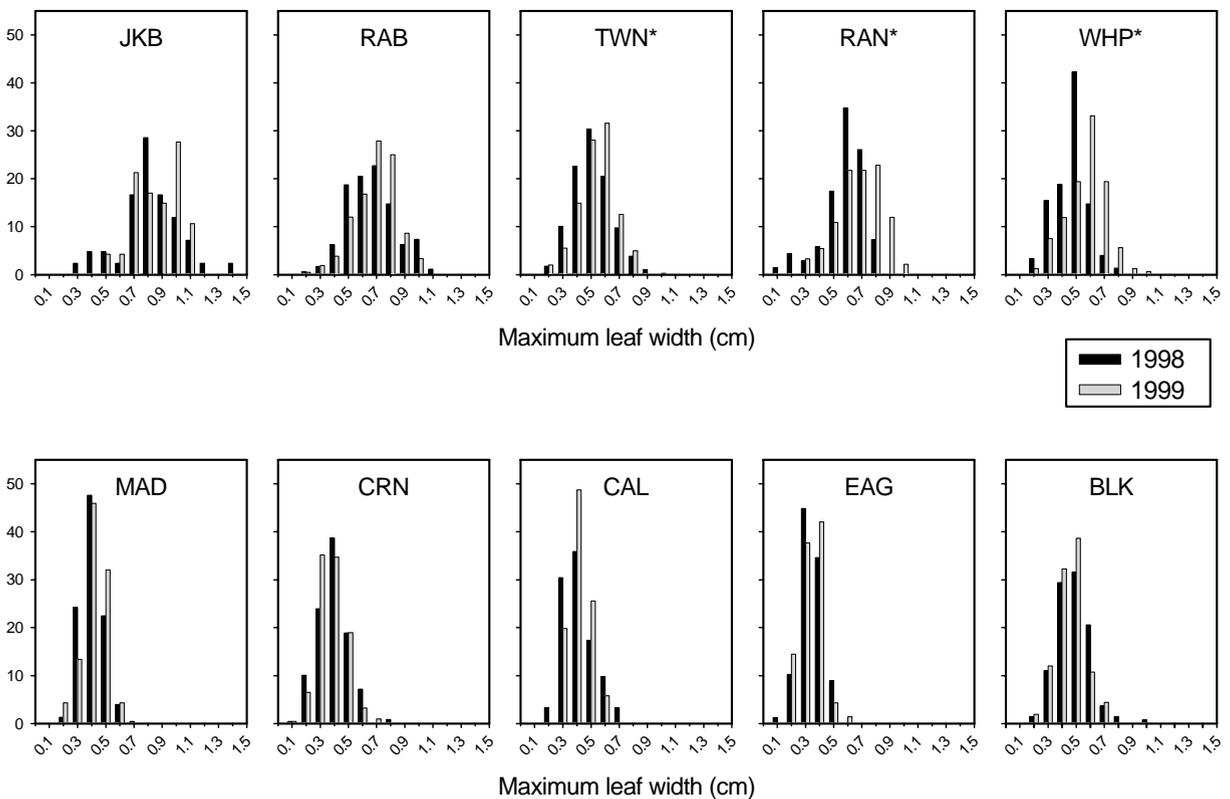


Fig. 4. Inter-annual comparisons of the distributions of maximum leaf width of short-shoots of *Thalassia testudinum* in 10 basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant inter-annual differences in basin distributions based on Kolmogorov–Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ).

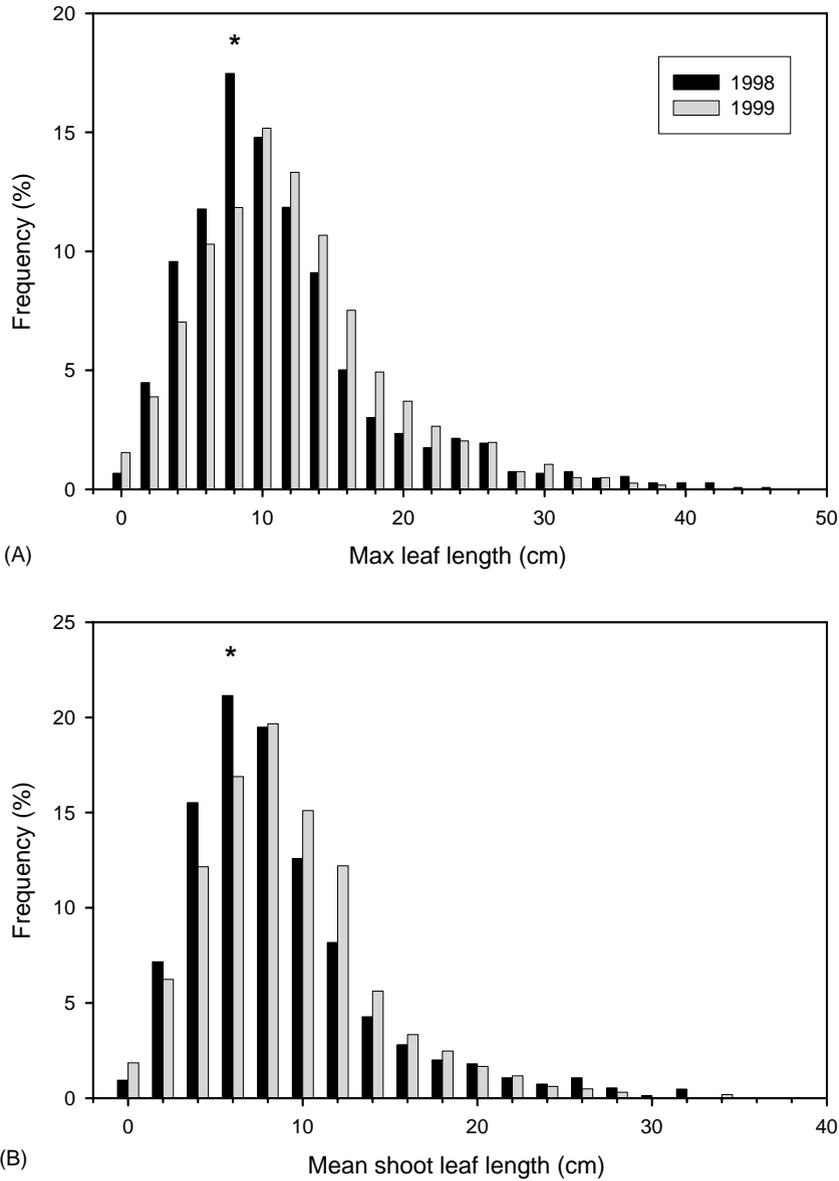


Fig. 5. Inter-annual comparisons of the nested distributions of (A) maximum leaf length and (B) mean shoot leaf length of short-shoots of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 ( $n = 1494$ ) and shaded bars represent 1999 ( $n = 1622$ ). Significant differences in distributions 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.

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. 8A).

The modal class in both years was 5–10 cm<sup>2</sup>, but there was a significant shift towards greater shoot-specific leaf area in 1999. As at the Bay level, the distributions in the basins were generally also positively skewed, but those of Rabbit Key Basin and Rankin

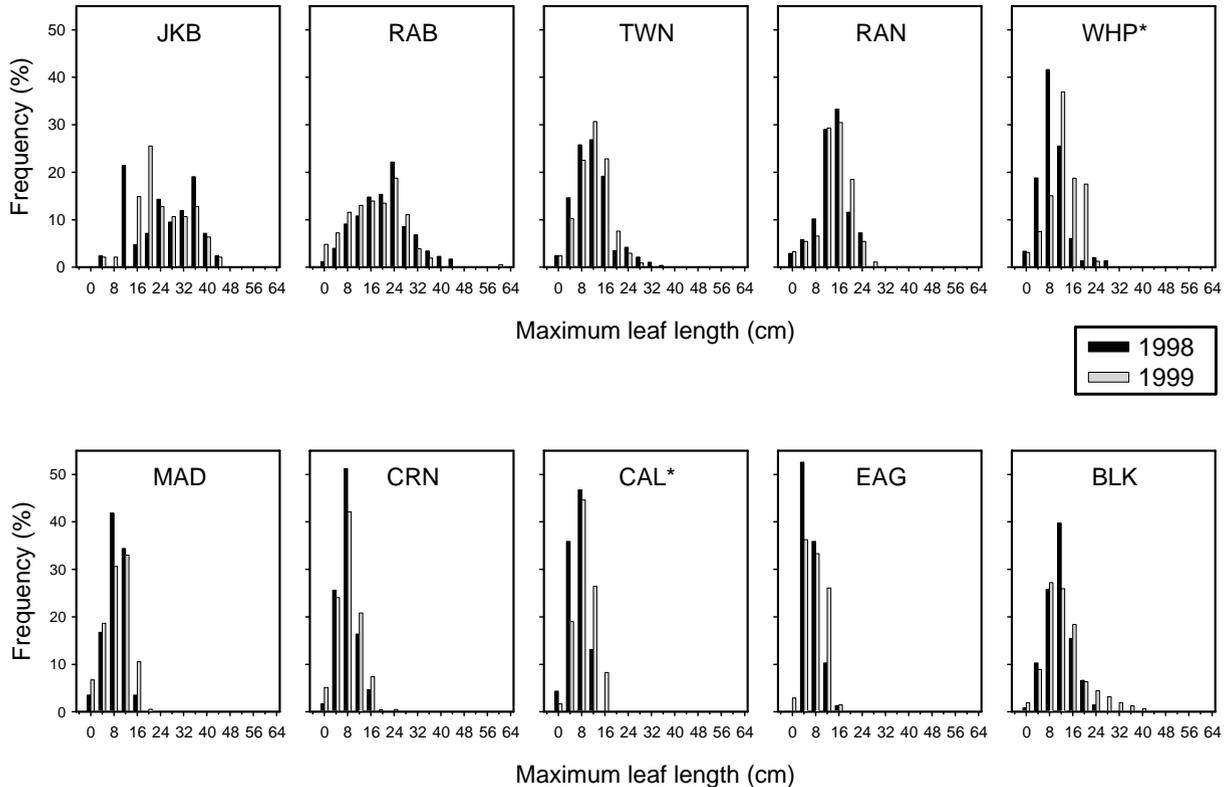


Fig. 6. Inter-annual comparisons of the nested distributions (size class = 2 cm) of maximum leaf length of short-shoots of *Thalassia testudinum* in 10 basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant inter-annual differences in basin distributions based on Kolmogorov–Smirnov Two-sample tests ( $D_{\max} > D_{0.05}$ ).

Lake were more symmetrical and those of Johnson Key again were bimodal (Fig. 9). The eastern basins, Eagle, Calusa, Crane Key Basins, and Madiera Bay had the lowest shoot-specific leaf areas. 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. 8B) and basin (Fig. 10) 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 population at the Bay scale was significantly older in 1999. Although most of the basins also had a shift towards more older shoots in 1999, 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 scale. 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 distribution pattern of shoot density, at the Bay level, was similar between 1998 and 1999 (Fig. 11A). Nearly 60% of cores had six or fewer shoots in both years ( $<350$  shoots  $m^{-2}$ ), and the modal class for both years was the smallest size class (1–2 shoots per core, or ca. 115 shoots  $m^{-2}$ ). There was a negative shift in the ratio of above- to below-ground biomass from 1998 to 1999 (Fig. 11B); 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. 12A) and leaf area index (Fig. 12B) were similar; both distributions were positively skewed. The modal class in 1998 and 1999

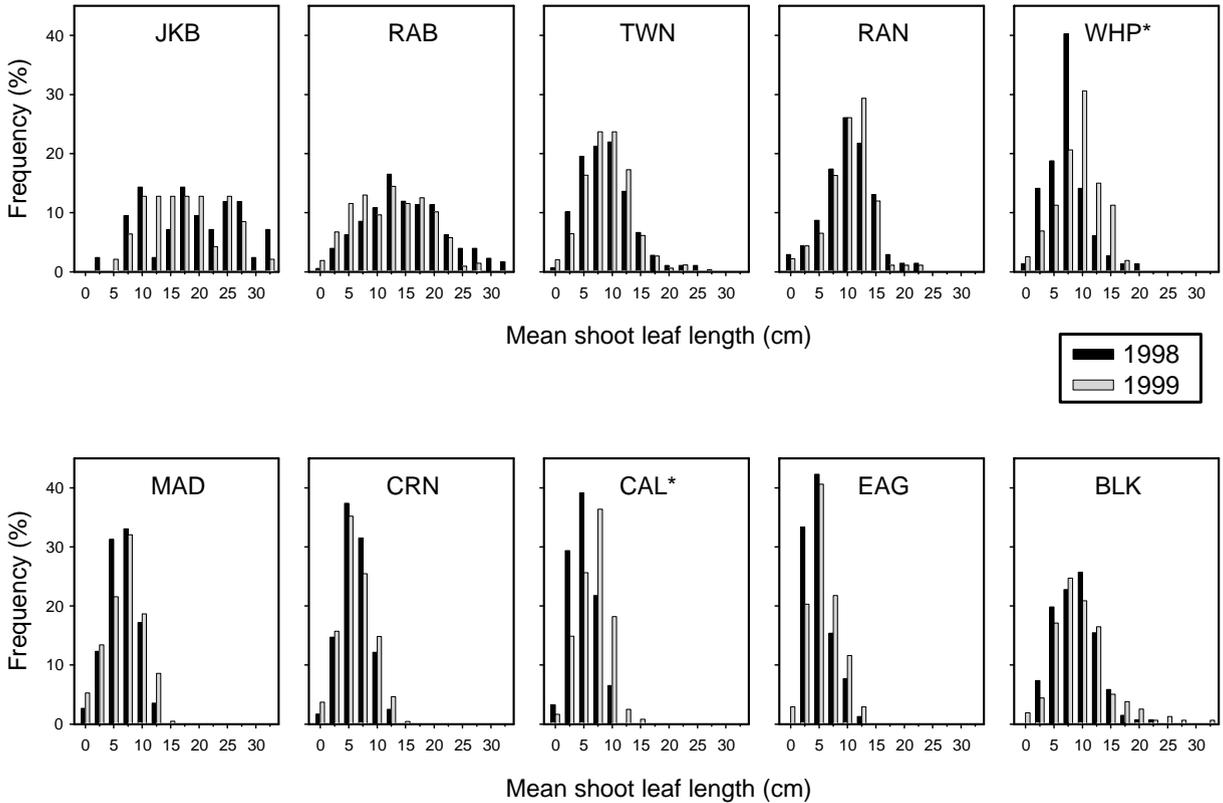


Fig. 7. Inter-annual comparisons of the nested distributions (size class = 2.5 cm) of mean leaf length of short-shoots of *Thalassia testudinum* in 10 basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant inter-annual differences in basin distributions based on Kolmogorov–Smirnov Two-sample tests ( $D_{max} > D_{0.05}$ ).

for standing crop was 10–20 g m<sup>-2</sup>, and about 50% of sites in the Bay had less than 30 g m<sup>-2</sup> standing crop. During both years the modal class of leaf area index was 0.2–0.4 m<sup>2</sup> m<sup>-2</sup>; very few sites had leaf area indices greater than 1.0 m<sup>2</sup> m<sup>-2</sup>.

**4. Discussion**

Structural characteristics of seagrasses may vary significantly among and between populations and at varying spatial scales (McMillan, 1978; Bak, 1980; Duarte, 1991; de Heij and Neinhuis, 1992; Alcoverro et al., 1995). Size–frequency distributions of morphometric and biomass characteristics of *T. testudinum* in Florida Bay exhibited significant inter-annual variability at the two spatial scales examined in this study. However, these characteristics exhibited similar

ranges relative to other areas in Florida Bay (Zieman et al., 1989, 1999; Durako, 1995; Hall et al., 1999), the Florida Keys (Tomasko and Lapointe, 1991), Biscayne Bay, Florida (Irlandi et al., 2002), Cockroach Bay, Florida (Rose and Dawes, 1999), Bermuda (South, 1983), and Mexico (Gallegos et al., 1993; van Tussenbroek, 1995). The effect of seasonal variation, which can be significant (Duarte, 1989; Alcoverro et al., 1995; Durako, 1995; van Tussenbroek, 1998; Irlandi et al., 2002), was minimized in this study with year-to-year comparisons of samples taken at approximately the same time of year.

All shoot-specific morphometric and biomass characteristics of *T. testudinum* showed significant inter-annual differences in size–frequency distributions, at the Bay level. In contrast, only leaf number per shoot showed a significant (though minimal) inter-annual difference between means, at

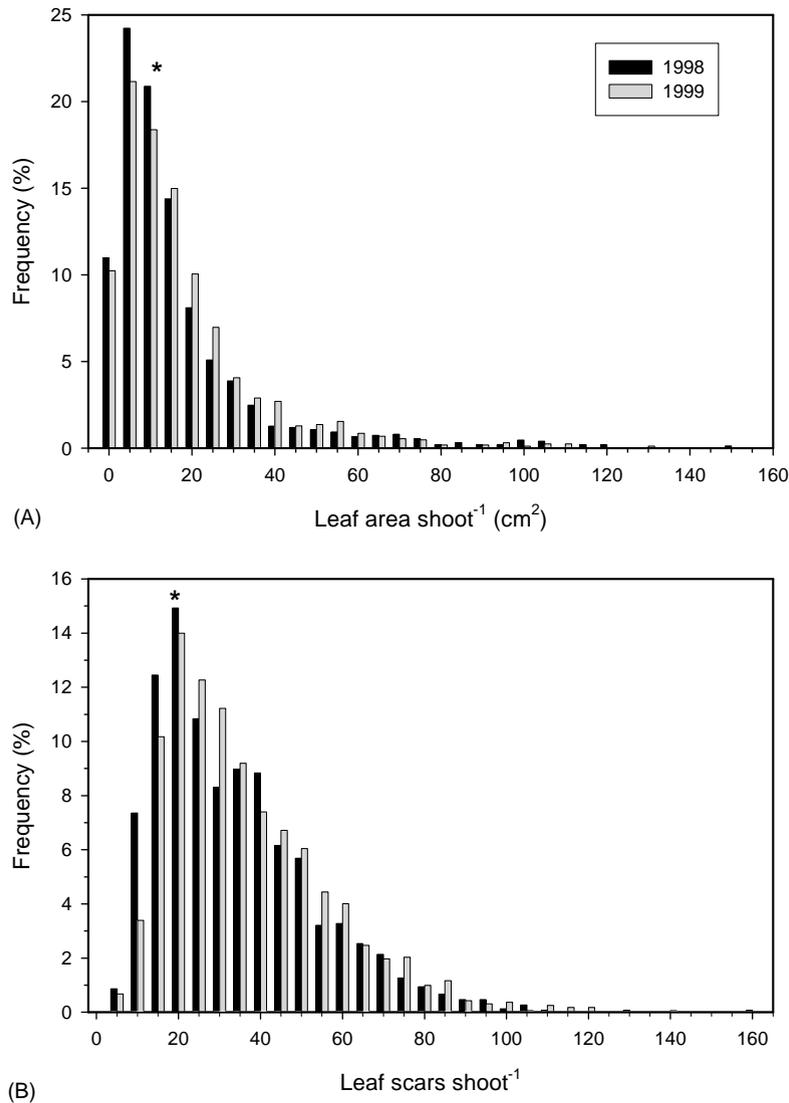


Fig. 8. Inter-annual comparisons of the nested distributions of (A) shoot-specific leaf area and (B) age (total number of leaf scars) of short-shoots of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 ( $n = 1494$ ) and shaded bars represent 1999 ( $n = 1622$ ). Significant differences 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.

the Bay level (Hackney and Durako, submitted for publication). Both analyses were done on the same dataset, suggesting that size–frequency distributions and the Kolmogorov–Smirnov Two-sample test are more sensitive for detecting changes in seagrass structural characteristics. The Kolmogorov–Smirnov Two-sample test also has the advantage of not re-

quiring data to be normally distributed, a frequent problem in monitoring data. The significant positive shifts detected in most of the parameter distributions in 1999 probably reflect both the higher salinities (Bay mean = 37.8 in 1999 versus 33.6 in 1998) and water temperatures (Bay mean = 29.7 °C in 1999 versus 28.7 °C in 1998), compared to 1998.

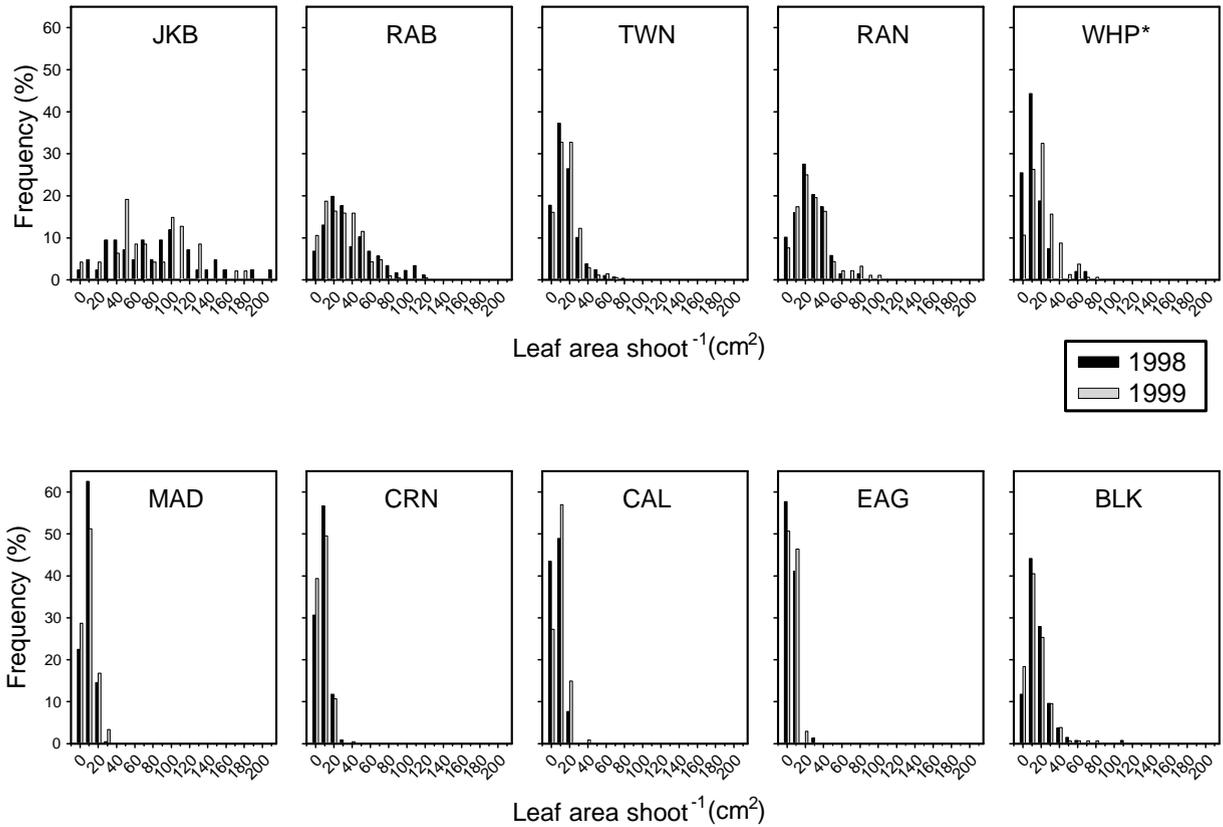


Fig. 9. Inter-annual comparisons of the nested distributions (size class = 10 cm<sup>2</sup>) of shoot-specific leaf area of short-shoots of *Thalassia testudinum* in 10 basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant inter-annual differences in basin distributions based on Kolmogorov–Smirnov Two-sample tests ( $D_{max} > D_{0.05}$ ).

The conditions in 1999 were, evidently, more favorable for this subtropical marine seagrass species. In contrast, area-specific (density-dependent) characteristics showed no inter-annual differences in their size–frequency distributions in the present study. Similarly, seasonality has little or no affect on the area-specific characteristic of mean short-shoot density in Florida Bay, but significant seasonal variation in mean standing crop and other shoot-specific characteristics may occur (Durako, 1995; Zieman et al., 1999).

The distributions of shoot-specific and area-specific characteristics of *T. testudinum* were highly variable in Florida Bay, at the level of individual basins. Short-shoots were generally larger and had more leaves in the western basins. Leaf number and size decreased from west to east and the 10 basins generally exhibited three to four groupings of size–frequency

distribution patterns. Standing crop, leaf area index, and above-/below-ground biomass showed essentially the same trend, however, short-shoot density was slightly more uniform across the Bay. The large variability in morphometric characteristics of *T. testudinum* seen in this study, even at relatively small scales, is not unusual in seagrass systems (Onuf, 1996; Kaldy and Dunton, 2000; Lee and Dunton, 2000). Although size distributions of the measured morphological characteristics were relatively large, they were within reported values for this species.

This study attempted to address large-scale variation among sites by using widespread spatial sampling. The consistent geographic clustering (with the exception of Blackwater Sound, see below) of the basin level patterns in the size–frequency distributions of *T. testudinum* morphometric and biomass

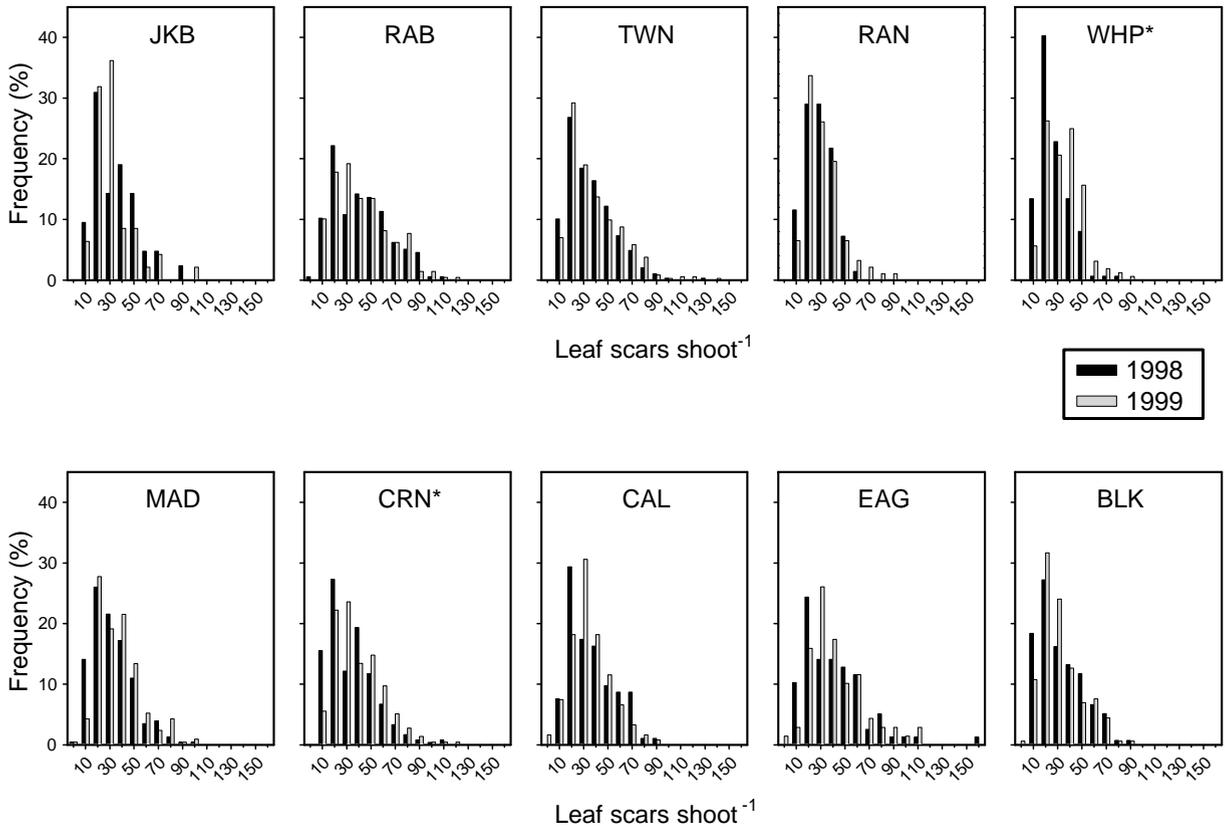


Fig. 10. Inter-annual comparisons of the nested distributions (size class = 10 scars) of short-shoot age (total number of leaf scars) of *Thalassia testudinum* in 10 basins in Florida Bay. Black bars represent 1998 and shaded bars represent 1999. Asterisks (\*) indicate significant inter-annual differences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

characteristics suggest they are likely regulated by landscape-scale differences in environmental parameters such as salinity, light availability, temperature, sediment depth, and nutrient supply. Using a discriminant function model, Fourqurean et al. (2003) recently demonstrated that mean salinity, salinity variability, light availability, sediment depth, and mean nutrient concentrations were important predictor variables for seagrass species occurrence and abundance in Florida Bay. Our data suggests that there is also a linkage between environmental variability and intra-specific plant structure. *T. testudinum* is known to exhibit phenotypic plasticity in its leaf dimensions that have been correlated with several environmental factors, including freshwater input (Irlandi et al., 2002), salinity (Dawes et al., 1985), nutrient availability (Short, 1983; Lee and Dunton, 2000), low

light availability (McMillan and Phillips, 1979) and turbidity (Phillips and Lewis, 1983; Lee and Dunton, 1997), latitude (McMillan, 1978), and intra- and inter-specific competition (Rose and Dawes, 1999; Davis and Fourqurean, 2001).

Several previous investigators have divided Florida Bay into distinct sub-environments or ecological zones based on bank morphology and dynamics (Wanless and Taggett, 1989), benthic plant communities (Zieman et al., 1989), light availability for planktonic and benthic primary production (Phlips et al., 1995), and water quality (Boyer et al., 1997). 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

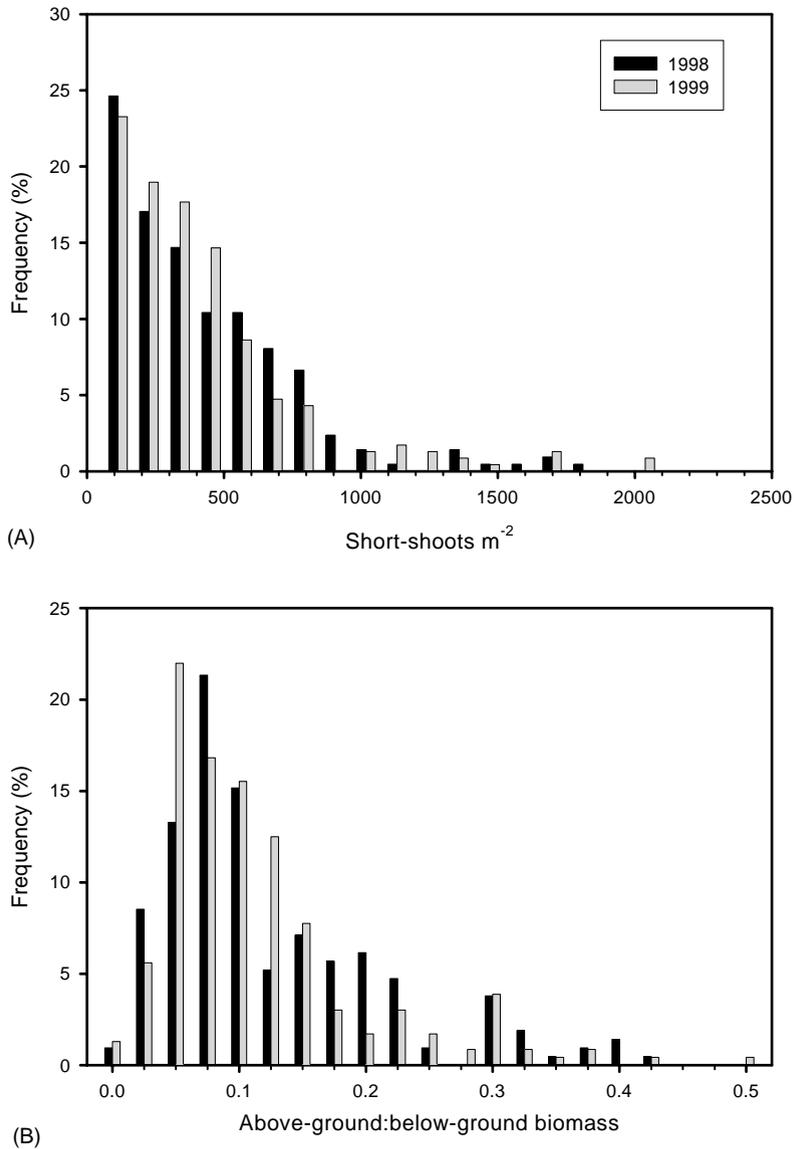


Fig. 11. Inter-annual comparisons of the (A) nested distributions of density and (B) above-ground:below-ground biomass of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 ( $n = 211$ ) and shaded bars represent 1999 ( $n = 232$ ). There were no significant differences in distributions between years in either plot based on Kolmogorov–Smirnov Two-sample tests ( $D_{\max} < D_{0.05}$ ). Density was binned by  $\sim 115$  individuals  $m^{-2}$  and above-ground:below-ground biomass was binned by 0.025.

four types of macroalgae, in addition to *T. 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.

Consistent groupings of the means and medians of morphometric and biomass parameters in a gradient across the Bay led to the definition of four ecological communities, based on shoot-specific and

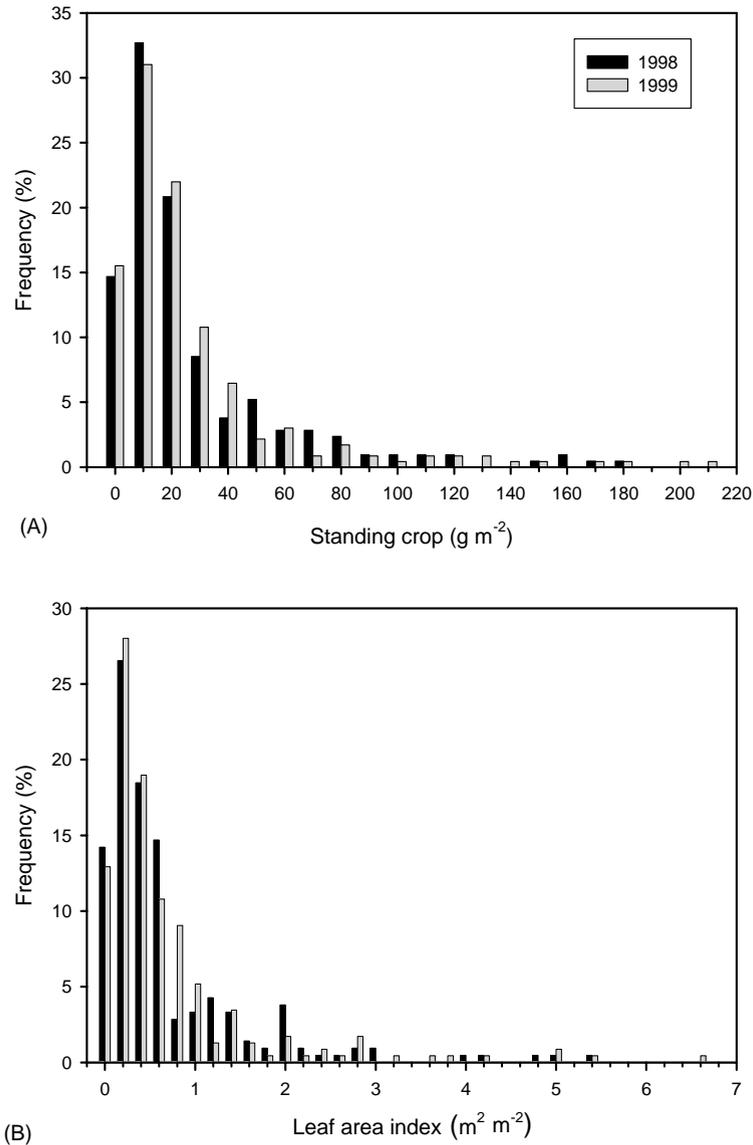


Fig. 12. Inter-annual comparisons of the nested distributions of (A) standing crop and (B) leaf area index of *Thalassia testudinum* in Florida Bay. Black bars represent 1998 ( $n = 211$ ) and shaded bars represent 1999 ( $n = 232$ ). There were no significant differences in distributions between years 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  $0.2 \text{ m}^2 \text{m}^{-2}$ .

area-specific characteristics of *T. testudinum* (Hackney and Durako, submitted for publication). Basin-level patterns in the size–frequency distributions of these structural characteristics examined in this study confirm that the 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 species' morphology. The four

community types defined by structural variability in *T. testudinum* (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 (Rabbit and Twin Key Basins) to the South-Central region, the Central Bay community (Rankin Lake, Whipray Bay, and Blackwater Sound) to the North-Central region, and the Eastern Bay community (Madeira Bay and Calusa, Crane, and Eagle Key Basins) to the East region. The most obvious geographic anomaly to this community-classification scheme compared to that of Phlips et al. (1995) and the others is the 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 several cuts connected to the Atlantic. Blackwater Sound has the deepest areas of any of the studied basins (305 cm depth); it has areas of extremely clear water as well as 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 of the five species of seagrass occurring in Florida Bay are present in the Sound. Thus, Blackwater Sound is a microcosm of Florida Bay and it is, biologically, with regard to the characteristics of *T. testudinum*, most similar to Rankin Lake and Whipray Basin in the central interior of Florida Bay.

In conclusion, the intra-annual variability among basins of shoot-specific and area-specific characteristics of *T. testudinum* was much greater than the inter-annual variation. The degree of structural variability within a single seagrass species collected at similar times illustrates the biological responses to the environmental heterogeneity of Florida Bay. These local sources of variation would be missed if only measures of central tendency were assessed, if samples were taken at fewer sites across the Bay, or if samples were pooled. The results shown here indicate that regional environmental differences significantly affect regional trends in the morphology of *T. testudinum*. The seagrasses in Florida Bay generate some of the highest rates of primary productivity measured in marine systems (e.g.,  $8 \times 10^5$  metric tons per

year, 1700 metric tons per day, Zieman et al., 1989) and they provide refuge for small consumers (Thayer et al., 1984; Matheson et al., 1999). Changes in these ecosystems can have cascading effects on other organisms and other systems (Butler et al., 1995). Thus, it is essential to track the ecosystem health of seagrass communities.

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