Decadal Changes in Seagrass Distribution and Abundance in Florida Bay

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ABSTRACT: The Florida Bay ecosystem has changed substantially in the past decade, and alterations in the seagrass communities have been particularly conspicuous. In 1987 large areas of Thalassia testudinum (turtlegrass) began dying rapidly in western Florida Bay. Although the rate has slowed considerably, die-off continues in many parts of the bay. Since 1991, seagrasses in Florida Bay have been subjected to decreased light availability due to widespread, persistent microalgal blooms and resuspended sediments. In light of these recent impacts, we determined the current status of Florida Bay seagrass communities. During the summer of 1994, seagrass species composition, shoot density, shoot morphometrics, and standing crop were measured at 107 stations. Seagrasses had been quantified at these same stations 10 yr earlier by Zieman et al. (1989). T. testudinum was the most widespread and abundant seagrass species in Florida Bay in both 1984 and 1994, and turtlegrass distribution changed little over the decade. On a baywide basis, T. testudinum density and biomass declined significantly between surveys; mean short-shoot density of T. testudinum dropped by 22% and standing crop by 28% over the decade. T. testudinum decline was not homogeneous throughout Florida Bay; largest reductions in shoot density and biomass were located principally in the central and western bay. Percent loss of T. testudinum standing crop in western Florida Bay in 1994 was considerably greater at the stations with the highest levels of standing crop in 1984 (126-215 g dry wt m⁻²) than at the stations with lower levels of biomass. While turtlegrass distribution remained consistent over time, both the distribution and abundance of two other seagrasses, Halodule wrightii and Syringodium filiforme, declined substantially between 1984 and 1994. Baywide, H. wrightii shoot density and standing crop declined by 92%, and S. filiforme density and standing crop declined by 93% and 88%, respectively, between surveys. Patterns of seagrass loss in Florida Bay between 1984 and 1994 suggest die-off and chronic light reductions were the most likely causes for decline. If die-off and persistent water-column turbidity continue in Florida Bay, the long-term future of seagrasses in the bay is uncertain.

Introduction

Seagrasses are characteristic of shallow coastal waters worldwide; however, few areas contain

meadows as extensive as those found in Florida Bay (Iverson and Bittaker 1986; Zieman et al. 1989). Seagrass beds, dominated by *Thalassia testudinum* Banks ex König (turtlegrass), historically covered most of the subtidal mud banks and basins in Florida Bay (Zieman et al. 1989). South Florida sea-

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grasses provide food and/or shelter to numerous fish and invertebrate species in the region, including the economically important pink shrimp, stone crab, and spiny lobster (Davis and Dodrill 1989; Holmquist et al. 1989a; Thayer and Chester 1989; Tilmant 1989; Robblee et al. 1991). A variety of wading birds as well as endangered species such as bald eagles, manatees, crocodiles, and sea turtles also depend, in part, on seagrass communities (Holmquist et al. 1989b; Mazzotti 1989; Boesch et al. 1993). Declines in seagrass habitat or changes in the species composition of seagrasses within Florida Bay could have serious consequences for the economy and ecology of South Florida (Robblee et al. 1991; Thayer et al. 1994; Thayer et al. 1999).

During the past decade, many components of the Florida Bay ecosystem have changed substantially, and alterations in the seagrass communities have been particularly conspicuous (Boesch et al. 1993; Butler et al. 1993; Fourgurean and Robblee 1999). Extensive areas of Thalassia testudinum began dying rapidly during the summer of 1987, particularly in western Florida Bay (Robblee et al. 1991). Although the rate has slowed considerably, turtlegrass die-off continues in many parts of the bay. The patchy mortality characteristic of die-off is very different from the gradual thinning and loss of seagrasses due to increased water-column turbidity experienced in many other parts of the world. In T. testudinum meadows affected by die-off there is often a sharp transition between die-off patches and visually healthy seagrasses. Factors that may contribute to T. testudinum die-off are physiological stressors such as elevated water temperature and prolonged hypersalinity, excessive seagrass biomass leading to increased respiratory demands, hypoxia and sulfide toxicity, and disease. The causative mechanism behind die-off remains incompletely understood (Robblee et al. 1991; Carlson et al. 1994; Durako 1994; Durako and Kuss 1994; Fourgurean and Robblee 1999).

While die-off appears to affect only turtlegrass, an ecosystem change relevant to all Florida Bay seagrass species is the widespread decline in water clarity that began in 1991 (Boyer et al. 1999; Stumpf et al. 1999). This increased light attenuation is due principally to microalgal blooms and resuspended sediments, and is most severe in the western and central bay (Phlips et al. 1995; Phlips and Badylak 1996). Environmental changes that lead to reductions in available light have been implicated in seagrass declines worldwide (Peres and Picard 1975; Cambridge and McComb 1984; Orth and Moore 1984; Giesen et al. 1990; Dennison et al. 1993; Onuf 1994). Thus, the turbid conditions that have become apparent in many parts of Florida Bay over the past few years may also negatively affect seagrasses (Thayer et al. 1994; Phlips et al. 1995; Fourqurean and Robblee 1999).

Because seagrasses have been subject to several major ecosystem changes in the recent past, we determined the current status of Florida Bay seagrass communities. During the summer of 1994, seagrass species composition, shoot density, shoot morphometrics, and standing crop were measured at more than 100 stations in Florida Bay. Seagrasses had been quantified at these same stations 10 yr earlier by Zieman et al. (1989) to establish a baseline for long-term monitoring of Florida Bay macrophyte communities. Revisiting the stations sampled in 1984 enabled us to update information regarding the distribution and abundance of seagrass communities in Florida Bay, and provided us with the unique opportunity to assess changes that have occurred since the onset of turtlegrass die-off and persistent water-column turbidity.

Materials and Methods

SEAGRASSES

Seagrasses were quantitatively sampled during June 1994 at 107 stations distributed throughout most of Florida Bay (Fig. 1; see Fourqurean and Robblee 1999 for a detailed description of Florida Bay). As previously stated, seagrasses at these stations were sampled by Zieman et al. (1989) in the summer of 1984. Four seagrass cores (15 cm diameter) were obtained at each station by haphazardly choosing sampling locations several meters off the bow, stern, port, and starboard of the boat. Cores were washed free of sediment in the field, stored in plastic bags, and frozen for subsequent analysis. In the laboratory, seagrasses were sorted by species, and short-shoot density and standing crop were determined from the material in each core. Plant material for standing crop (leaf dry weight m^{-2}) estimates was washed in 10% HCl, dried at 60°C, and weighed. The number of blades per shoot, and blade lengths and widths were determined for Thalassia testudinum shoots. Sediment depth was measured at each station with a stainless steel probing rod, and water depth was measured with a PVC pole marked in 1-cm increments.

STATISTICAL ANALYSES

Paired *t*-tests were used to assess baywide differences in shoot density, blade lengths, number of blades per shoot, and standing crop between summer 1984 and 1994. Wilcoxon-Signed-Rank analyses were used in lieu of *t*-tests when data could not be transformed to meet assumptions of normality. Stations were initially divided into three depth categories (0.25-1.25 m, > 1.25-2.25 m, and > 2.25m) to assess differences in seagrass parameters with



Fig. 1. Florida Bay showing the locations of the 107 study sites. Areas with coarse stippling represent carbonate mud banks. Finely stippled areas represent islands and the mainland.

respect to water depth in 1984 and 1994. One-way ANOVA revealed the latter two depth categories were not significantly different from each other and stations with depths >1.25 m were combined; t-tests were used to assess differences in seagrass parameters with respect to the two water depth categories (≤ 1.25 m versus > 1.25 m) for 1984 and 1994. Mann-Whitney Rank Sum analyses were used in lieu of *t*-tests when data could not be transformed to meet assumptions of normality and homogeneity of variance. Two-way ANOVA was used to investigate possible date \times depth interactions. The effect of water depth on % change in Thalassia testudinum standing crop between 1984 and 1994 was assessed by Mann-Whitney Rank Sum analysis. Relationships between sediment depth and seagrass density and standing crop in 1984 and 1994 were explored by linear regression analysis.

Zieman et al. (1989) divided Florida Bay into six regions based principally on the distribution and abundance of macrophyte communities (Fig. 2; see Zieman et al. 1989 for a detailed description of these regions). Paired t-tests and Wilcoxon-Signed-Rank analyses were used to assess differences in shoot density, blade lengths, number of blades per shoot and standing crop between summer 1984 and 1994 within each region. No attempt was made to address differences in seagrass parameters among regions due to the substantial variation in number of stations within regions (range = 8-37).

Initial turtlegrass die-off was reported to occur primarily in the densest seagrass beds in western Florida Bay (Robblee et al. 1991). Stations in western Florida Bay were divided into three density categories based on the 1984 standing crop (low biomass: 10–50 g dry wt m⁻², n = 19; medium biomass: 51–125 g dry wt m⁻², n = 26; and high biomass: 126–215 g dry wt m⁻², n = 20). Kruskal-Wallis one-way ANOVA on ranks was used to assess differences in percent biomass change among the three standing crop categories measured in 1994. Dunn's multiple comparison procedure was used to isolate treatments where significant differences occurred. Stations with mean standing crops < 10 g m⁻² in 1984 were not included in the analysis due to extreme variation in percent change.

Results

BAYWIDE CHANGES IN SEAGRASS COMMUNITIES

Thalassia testudinum

Thalassia testudinum was the most widespread and abundant seagrass species in Florida Bay during both 1984 and 1994 (Table 1). Turtlegrass distribution changed little over the decade; *T. testudinum* was present at 102 stations in 1984 and at 99 stations in 1994. Geographic patterns of *T. testudinum* abundance (i.e., short-shoot densities and leaf standing crop) were also similar between surveys. Shoot densities were generally lowest in northeastern Florida Bay, and increased toward the southwest, where highest densities were observed (Fig. 3a,b). Shoot density was positively associated



Fig. 2. Location and extent of ecological regions within Florida Bay based on macrophyte distribution and abundance (after Zieman et al. 1989).

with standing crop (1984: $r^2 = 0.62$, p < 0.001; 1994: $r^2 = 0.74$, p < 0.001); geographic patterns in turtlegrass standing crop followed those for density (Fig. 4a,b). Geographic variation in *T. testudinum* abundance in Florida Bay corresponds to a gradient of increasing sediment depth from northeast to southwest (see Zieman et al. 1989). Turtlegrass shoot density (1984: $r^2 = 0.35$, p < 0.001; 1994: r^2 = 0.30, p < 0.001) and standing crop (1984: $r^2 =$ 0.34, p < 0.001; 1994: $r^2 = 0.30$, p < 0.001) were positively related to sediment depth in both years

Table 1. Percent occurrence, short-shoot densities and standing crop of seagrasses in Florida Bay in 1984 and 1994.

| | Species | | |
|-----------|-------------------|----------------------------------|-------------------|
| | Thalassia | Halodule | Syringodium |
| % Occur | rence $(n = 107)$ | | |
| 1984 | 95.3 | 47.7 | 11.2 |
| 1994 | 92.5 | 13.1 | 3.7 |
| Baywide S | Standing Crop (g | dry wt m ⁻² \pm SE) | |
| 1984 | 63.9 ± 5.5 | 3.8 ± 1.1 | 4.1 ± 1.7 |
| 1994 | 46.0 ± 4.0 | 0.3 ± 0.2 | 0.5 ± 0.3 |
| Standing | Crop Where Pres | sent (g dry wt m ⁻² | ±SE) |
| 1984 | 67.1 ± 5.6 | 7.5 ± 2.0 | 36.8 ± 10.8 |
| 1994 | 48.2 ± 4.1 | 0.6 ± 0.4 | 5.6 ± 3.7 |
| Baywide S | Shoot Density (# | $m^{-2} \pm SE$) | |
| 1984 | 694.7 ± 47.5 | 267.5 ± 80.0 | 83.3 ± 34.9 |
| 1994 | 539.3 ± 49.5 | 22.5 ± 11.0 | 5.6 ± 3.8 |
| Shoot De | nsity Where Pres | ent (# $m^{-2} \pm SE$) | |
| 1984 | 720.5 ± 47.8 | 550.1 ± 156.0 | 742.4 ± 245.3 |
| 1994 | 565.7 ± 50.5 | 42.5 ± 22.1 | 49.5 ± 31.8 |

(Fig. 5). Relationships between turtlegrass abundance and sediment depth observed in 1984 closely resembled those observed in 1994.

The ranges in mean shoot density and standing crop remained similar at the 107 stations over the decade (1984: 0-2133 shoots m⁻² and 1994: 0-2137 shoots m^{-2} ; 1984: 0-215 g dry wt m^{-2} and 1994: 0–185 g dry wt m⁻², respectively). However, abundance was lower at many of the stations in 1994 than in 1984 (Figs. 3c, 4c), and on a baywide basis, Thalassia testudinum density and biomass declined significantly between surveys. Mean shortshoot density of T. testudinum in Florida Bay dropped by 22% (694.7 \pm 47.5 to 539.3 \pm 49.5 shoots m^{-2} , p < 0.001) and standing crop by 28% over the decade (63.9 \pm 5.5 to 46.0 \pm 4.0 g dry wt m^{-2} , p < 0.001) (Table 1). When considering only the 102 sites where turtlegrass occurred, mean density fell from 720.5 \pm 47.8 shoots m⁻² to 565.7 \pm 50.5 shoots m⁻² (p < 0.001) and standing crop from 67.1 \pm 5.6 g dry wt m⁻² to 48.2 \pm 4.1 g dry wt m⁻² (p < 0.001). T. testudinum decline was not homogeneous throughout the bay; most of the stations with the largest reductions in shoot density and biomass were located in central and western Florida Bay (Figs. 3c and 4c). Although there was a significant decline baywide, turtlegrass abundance actually increased at a number of stations from 1984 to 1994, especially in the eastern bay.

The mean number of turtlegrass blades per shoot did not change during the decade (2.6 ± 0.8) in 1984 versus 2.6 ± 0.7 in 1994, p = 0.269; range



Fig. 3. Short-shoot densities (# m⁻²) of *Thalassia testudinum* in 1984 (a) and 1994 (b) at the study locations within Florida Bay. Percent change in *T. testudinum* shoot density at the study locations (c).

of 107 stations: 1.9–4.1 in 1984, and 1.7–5.2 in 1994). The range in blade length was also consistent over time (3.2–31.7 cm in 1984, and 3–31.0 cm in 1994); however, on a baywide basis, mean blade length declined by 28% between surveys (12.1 \pm 0.8 cm to 8.7 \pm 0.4 cm, p < 0.001).

Mean turtlegrass density was significantly higher in shallow (≤ 1.25 m, n = 47) versus deep (> 1.25 m, n = 60) waters of Florida Bay in 1984 (932.0 ± 70.5 versus 508.9 ± 53.4 shoots m⁻², p = 0.001) and in 1994 (779.2 ± 88.5 versus 351.4 ± 41.3 shoots m⁻², p = 0.019). Results were similar for leaf standing crop (shallow versus deep: 85.8 ± 8.1 g dry wt m⁻² versus 46.8 ± 6.8 g dry wt m⁻², p < 0.001 in 1984, and 63.0 ± 6.6 g dry wt m⁻², p < 0.001 in 1994). Although *T. testudinum* abundance varied significantly with both date (1984 versus 1994) and water depth (shallow versus deep), results of two-way AN-OVA revealed no significant date × depth interaction for shoot densities (p = 0.734) or standing crop (p = 0.494). Neither *T. testudinum* blade length (shallow versus deep: 12.5 ± 1.0 cm versus 10.8 ± 0.9 cm, p = 0.208 in 1984, and 8.6 ± 0.5



Fig. 4. Standing crop (g dry wt m⁻²) of *Thalassia testudinum* in 1984 (a) and 1994 (b) at the study locations within Florida Bay. Percent change in *T. testudinum* standing crop at the study locations (c).

cm versus 8.9 ± 0.7 cm, p = 0.73, in 1994) nor number of blades per shoot (shallow versus deep: 2.7 ± 0.1 versus 2.6 ± 0.1 , p = 0.421 in 1984, and 2.6 ± 0.1 versus 2.6 ± 0.1 , p = 0.972 in 1994) varied significantly with water depth.

Percent change in *Thalassia testudinum* standing crop in western Florida Bay in 1994 varied significantly with regard to levels of leaf biomass in 1984 (p = 0.004; Fig. 6). Mean biomass reduction in 1994 was considerably greater at stations with high levels of standing crop in 1984 (52% decline) than at stations with medium levels of standing crop in 1984 (12% decline). Leaf biomass at stations in the low biomass category in 1984 remained almost unchanged over the decade (0.5% increase).

Halodule wrightii Ascherson

Halodule wrightii (shoalgrass) was less widespread than Thalassia testudinum in Florida Bay in 1984, occurring at only 48% of the stations surveyed (Table 1). Short-shoot densities generally increased from eastern to western Florida Bay, and maximum *H. wrightii* abundance was reached in the northwestern bay in both 1984 and 1994 (Fig. 7a,b).



Fig. 5. Linear regressions showing the relationship bewteen *Thalassia testudinum* short-shoot density $(\# m^{-2})$ and sediment depth (cm) at the study locations in 1984 and 1994, and between *Thalassia testudinum* standing crop (g dry wt m⁻²) and sediment depth (cm) in 1984 and 1994.



Fig. 6. Percent change in *Thalassia testudinum* standing crop in 1994 with respect to 1984 biomass category.

While turtlegrass distribution remained consistent over time, shoalgrass distribution declined substantially between surveys. In 1994, H. wrightii was found at only 12% of the sampling locations, and at considerably reduced abundances (Fig. 7c). Baywide, mean short-shoot density dropped from 267.5 ± 80.0 shoots m⁻² to 22.5 ± 11.0 shoots m⁻² between surveys (p < 0.001; range = 0-6400 shoots m^{-2} in 1984, and 0-962.2 shoots m^{-2} in 1994). Patterns for standing crop closely followed those for density: shoalgrass leaf biomass declined from 3.8 ± 1.1 g dry wt m⁻² in 1984 to 0.3 ± 0.2 g dry wt m⁻² in 1994 (p < 0.001; range = 0-87.5 \ddot{g} dry wt m⁻² in 1984, 0–21.3 g dry wt m⁻² in 1994). When considering only the 52 sites where shoalgrass occurred, mean density fell from 550.1 \pm 156.0 shoots m⁻² to 42.5 \pm 22.1 shoots m⁻² (p < 0.001), and standing crop from 7.5 ± 2.0 g dry wt m^{-2} to 0.6 ± 0.4 g dry wt m^{-2} (p < 0.001) over the decade.

Syringodium filiforme Kutzing

The distribution of Syringodium filiforme (manatee grass) was the most limited of the three seagrass species in Florida Bay. In summer 1984 S. filiforme was present at only 12 stations in western Florida Bay (Table 1 and Fig. 8a). A decade later,

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Fig. 7. Short-shoot densities ($\# m^{-2}$) of *Halodule wrightii* in 1984 (a) and 1994 (b) at the study locations within Florida Bay. Percent change in *H. wrightii* shoot density at the study locations (c).

S. filiforme was restricted to four stations, and at considerably reduced abundances (Fig. 8b,c). Mean short-shoot density fell 93% between surveys, from 83.3 \pm 34.9 shoots m⁻² to 5.6 \pm 3.8 shoots m⁻² (p < 0.001, range = 0-2366.7 shoots m⁻² in 1984, and 0-382.1 shoots m⁻² in 1994). Results were similar for standing crop, which declined from 4.1 \pm 1.7 g dry wt m⁻² in 1984 to 0.5 \pm 0.3 g dry wt m⁻² in 1994, p = 0.003 range = 0-99.3 g dry wt m⁻² in 1984, and 0-19.2 g dry wt m⁻² in 1994), an 88% reduction. When considering only the stations where manatee grass oc-

curred, mean density fell from 742.4 \pm 245.3 shoots m⁻² in 1984 to 49.6 \pm 31.8 shoots m⁻² in 1994 (p = 0.001), and standing crop from 36.7 \pm 11.3 g dry wt m⁻² in 1984 to 4.3 \pm 2.1 g dry wt m⁻² in 1994 (p = 0.017).

REGIONAL CHANGES IN SEAGRASS COMMUNITIES Thalassia testudinum

Regional analyses again illustrated an increase in turtlegrass abundance from northeastern to southwestern Florida Bay (Fig. 9a,b). Mean shoot densities of *Thalassia testudinum* generally declined in

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Fig. 8. Short-shoot densities $(\# m^{-2})$ of *Syringodium filiforme* in 1984 (a) and 1994 (b) at the study locations within Florida Bay. Percent change in *S. filforme* shoot density at the study locations (c).

all regions except the East Central region between 1984 and 1994 (Fig. 9a). Densities became significantly lower in the Mainland ($p = 0.047, 474.0 \pm 151.1$ shoots m^{-2} in 1984 versus 206.4 \pm 63.6 shoots m^{-2} in 1994), Interior ($p = 0.010, 714.1 \pm 80.8$ shoots m^{-2} in 1984 versus 422.3 \pm 96.9 shoots m^{-2} in 1994) and Gulf ($p = 0.001, 809.0 \pm 66.8$ shoots m^{-2} in 1984 versus 560.0 \pm 82.0 shoots m^{-2} in 1994) regions between surveys. Results for standing crop resembled those for density (Fig. 9b); however, declines in biomass over the decade were significant only in the Gulf region (p < 0.001,

101.1 \pm 9.0 g dry wt m⁻² in 1984 versus 58.7 \pm 6.6 g dry wt m⁻² in 1994). Discrepancies in the amount of reduction in density versus biomass within particular regions appeared to reflect corresponding changes in blade length between surveys (Fig. 9c). Mean blade length fell by 32% in the Gulf region between 1984 and 1994 (18.2 \pm 1.2 cm versus 12.5 \pm 0.8 cm, p < 0.001), but by only 18% and 19.5%, respectively, in the Interior (11.7 \pm 1.0 cm versus 9.6 \pm 0.8 cm, p = 0.007) and Mainland regions (9.7 \pm 1.4 cm versus 7.8 \pm 0.5 cm, p = 0.222). Blade lengths also became significantly shorter in



Fig. 9. Thalassia testudinum short-shoot densities $(\# m^{-2})$ (a), standing crop (g dry wt m⁻²) (b), blade lengths (cm) (c), and blades per shoot (d) in 1984 and 1994 within the six ecological regions of Florida Bay.

the Atlantic region over the decade (p < 0.001, 11.8 \pm 0.8 cm versus 7.9 \pm 0.5 cm). Number of blades per shoot did not differ between surveys in any region of Florida Bay (Fig. 9d).

Halodule wrightii

Halodule wrightii was present in all regions of Florida Bay in 1984 but was abundant only in the Mainland, Interior, and Gulf regions. Shoalgrass abundance generally became lower in all regions from 1984 to 1994 (Fig. 10). As with turtlegrass, H. wrightii shoot densities declined significantly in the Gulf region between surveys (p < 0.001, $350.2 \pm$ 110.2 shoots m⁻² in 1984 versus 7.7 \pm 4.2 shoots m⁻² in 1994). Patterns were similar for shoalgrass standing crop, which decreased by more than 97%in the Gulf region over the decade (p < 0.001, 5.8 \pm 1.6 g dry wt m⁻² in 1984 versus 0.2 \pm 0.1 g dry wt m⁻² in 1994). Standing crop also decreased significantly from 1984 to 1994 in the Northeast region (p = 0.016, 0.63 \pm 0.3 g dry wt m⁻² in 1984 versus 0.04 ± 0.04 g dry wt m⁻² in 1994).

Syringodium filiforme

Syringodium filiforme was present only in deeper waters of the Gulf region in both 1984 and 1994 (Fig. 11). The abundance of manatee grass in this region of Florida Bay decreased significantly over the decade. S. filiforme density declined from 240.8 \pm 96.5 shoots m⁻² in 1984 to 16.1 \pm 10.7 shoots m⁻² in 1994 (p = 0.003), and standing crop from 11.9 \pm 4.6 g dry wt m⁻² in 1984 to 1.4 \pm 0.8 g dry wt m⁻² in 1994 (p = 0.003).

Discussion

Although the Florida Bay ecosystem changed considerably between 1984 and 1994, *Thalassia testudinum* continued to be the dominant seagrass species in the bay, and its distribution at the study locations remained almost unchanged between surveys. Spatial patterns of turtlegrass abundance did not change over the decade; shoot densities and standing crop continued to increase from the northeastern to southwestern bay following gradients in sediment depth (Zieman et al. 1989) and phosphorus availability (Fourqurean et al. 1992). *T. testudinum* shoot density and biomass fell significantly over the decade, especially in western and central Florida Bay.

A variety of factors may have influenced turtlegrass decline in Florida Bay between 1984 and 1994, but the most likely causes for loss were *Thal*assia testudinum die-off (most extensive from 1987 to 1990), and decreased water clarity due to sedi-

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Fig. 10. Halodule wrightii short-shoot densities $(\# m^{-2})$ (a), and standing crop (g dry wt m⁻²) (b) in 1984 and 1994 within the six ecological regions of Florida Bay.

ment resuspension and phytoplankton blooms (1991–1997). Establishing the relative contribution of die-off versus reduced light availability to the turtlegrass decline observed here is problematic because 1) die-off was patchily distributed, thus there was no accurate way to identify stations where die-off actually occurred, and 2) long-term data regarding light conditions in Florida Bay are scarce since water clarity was of little concern prior to 1991. Although it is not possible to definitively establish cause and effect relationships, examining observed patterns of seagrass loss in Florida Bay relative to expected patterns of decline from turtlegrass die-off (see Robblee et al. 1991; Durako et al. 1994) and decreased light availability (see Peres and Picard 1975; Cambridge and McComb 1984; Orth and Moore 1984; Giesen et al. 1990; Dennison et al. 1993; Onuf 1994) lends insight. If the majority of seagrass deterioration in Florida Bay



Fig. 11. Syringodium filiforme short-shoot densities (# m 2), and standing crop (g dry wt m $^{-2}$) in 1984 and 1994 within the six ecological regions of Florida Bay.

between 1984 and 1994 was due to die-off, one would expect to see 1) declines in T. testudinum primarily in western and central Florida Bay, 2) greatest mortality in very dense turtlegrass beds, located mainly in shallower water along basin margins, 3) patchy rather than widespread declines in T. testudinum abundance in western and central Florida Bay, and 4) no decline in Halodule wrightii or Syringodium filiforme, which apparently were not affected by the die-off. If reduced light availability were responsible for most turtlegrass decline, then one would expect to see 1) T. testudinum declines in regions that were unaffected by die-off, 2) widespread reductions in turtlegrass density and biomass rather than localized declines, and 3) larger T. testudinum declines in deeper water due to increased light attenuation with depth. Although T. testudinum may require higher levels of irradiance for survival than *H. wrightii* or *S. filiforme* (Fourqurean 1992), given sufficient light reduction, one would also expect to see 4) deterioration of *H.* wrightii and *S. filiforme* as well as *T. testudinum*, and 5) more severe losses in *H. wrightii* and *S. filiforme* than in *T. testudinum* because of the smaller belowground reserves in the former two species (Hall et al. 1991; Czerny and Dunton 1995). Patterns of seagrass loss in Florida Bay between 1984 and 1994 were partially consistent not only with predictions associated with die-off, but also with those expected from chronic light reduction.

Thalassia testudinum shoot density and standing crop decreased substantially in western and central Florida Bay in areas where both die-off (Robblee et al. 1991) and light reduction (Phlips et al. 1995; Boyer et al. 1999; Stumpf et al. 1999) occurred between 1984 and 1994. However, large turtlegrass losses also occurred in locations with no reported die-off, but where water clarity had deteriorated since 1991. These results concur with those of Zieman et al. (1999), who found T. testudinum abundance declined at both die-off and control (no dieoff) stations in the western bay from 1989 to 1995. In addition, the distribution and abundance of Halodule wrightii and Syringodium filiforme declined drastically during the 10-yr period. Such declines in seagrass abundance are commonly observed as the result of decreased light availability in estuaries worldwide (Peres and Picard 1975; Cambridge and McComb 1984; Orth and Moore 1984; Giesen et al. 1990; Dennison et al. 1993; Onuf 1994). Along with substantial reductions in shoot density and biomass, T. testudinum blades became shorter in Florida Bay over the decade. T. testudinum blade lengths have been shown to decline significantly in response to experimental shading (75% reduction of ambient light) in Tampa Bay, Florida (Carlson and Acker 1985). Experimental light reductions of > 50% also caused declines in blade lengths of Posidonia sinuosa Cambridge and Kuo (Neverauskas 1988; Gordon et al. 1994), a seagrass that is structurally similar to T. testudinum (i.e., both seagrass species have relatively large belowground reserves, Czerny and Dunton 1995). However, significant declines in T. testudinum blade lengths also occurred in the Atlantic region of Florida Bay, where light levels appeared to have changed very little between 1984 and 1994 (Phlips et al. 1995; Boyer et al. 1999; Stumpf et al. 1999) but where die-off was present. These results suggest that die-off probably played a role in turtlegrass decline in Florida Bay over the decade, but that increased light attenuation was also an important controlling factor.

Our findings regarding *Thalassia testudinum* decline in shallow (≤ 1.25 m) versus deep (> 1.25 m) water raises questions concerning the role of

light reduction in Florida Bay seagrass loss. Turtlegrass shoot density and standing crop declined significantly in both shallow and deep water between 1984 and 1994, but the relative amount of decline was not substantially greater in deep than in shallow water. These results would seem inconsistent with reports of seagrass loss due to reduced light in many other estuaries, where declines were generally most severe in the deepest growing seagrasses (Orth and Moore 1983; Cambridge and Mc-Comb 1984; Giesen et al. 1990; Dennison et al. 1993; Onuf 1994; Fletcher and Fletcher 1995). Larger and more rapid declines were measured at the deep versus the shallow edge of a T. testudinum meadow in Tampa Bay, Florida, in response to experimental shading (60-65% reduction of ambient light; Hall et al. 1991). In the aforementioned systems, the maximum depth of seagrasses was controlled by light availability, thus any reduction in the amount of light reaching the deepest growing seagrasses should have resulted in declines in density and biomass. This was not the case in western and central Florida Bay, where before 1991, T. testudinum growing at approximately 3 m (the deepest stations sampled in these surveys) was not lightlimited (see Fourqurean and Zieman 1991). Perhaps T. testudinum declines that occurred in Florida Bay between 1984 and 1994 were no greater in deep than in shallow water because, prior to the turbidity increases that began in 1991, T. testudinum meadows in the deeper areas of western and central Florida Bay were well above the light-limited maximum depth. The more pronounced declines in deeper versus shallower water typically seen in response to decreased water clarity may not have been evident after only 3 yr due to the high belowground reserves and long life-spans of T. testudinum short-shoots. Recruitment and mortality rates of T. testudinum short-shoots estimated in 1994 using reconstructive aging techniques (see Durako 1994) indicated that density declines should become larger in deeper (> 1 m) versus shallower (≤ 1 m) water in western Florida Bay (Durako unpublished data). The pattern of equal decline in both shallow and deep sites may be the consequence of two separate causes of decline in T. testudinum: an early loss in mostly shallow water (Robblee et al. 1991) due to the poorly understood die-off phenomenon, followed by a subsequent loss in deeper water attributable to chronic light reduction.

The differences in percent change in 1994 *Thal-assia testudinum* standing crop among 1984 biomass categories were dramatic. The remarkably large decline in standing crop at stations in the high biomass category was consistent with previous accounts concerning the primary locations affected

by die-off in western Florida Bay. The prevalence of die-off in dense T. testudinum beds may be related to hypoxia and sulfide toxicity in combination with reduced photosynthetic rates due to blade damage caused by a slime mold (Labyrinthula sp.) (Durako and Kuss 1994), which has been isolated from T. testudinum in die-off patches (Porter and Muehlstein 1989). Sulfide levels in Florida Bay are quite high relative to other Florida estuaries (Carlson et al. 1994), and seagrasses must translocate photosynthetically produced oxygen to belowground tissues to avoid the effects of hypoxia and sulfide toxicity. T. testudinum may be more vulnerable to sulfide-induced hypoxia than Halodule wrightii or Syringodium filiforme due to its high ratio of belowground to aboveground biomass (Fourqurean and Zieman 1991; Carlson et al. 1994). Blade lesions produced by Labyrinthula sp. reduce T. testudinum photosynthesis, making it more susceptible to hypoxia and sulfide toxicity, which is generally considered the proximal cause of death in die-off (Durako and Kuss 1994; Fourgurean and Robblee 1999). Infection of T. testudinum by Labyrinthula sp. in Florida Bay appears to be density dependent, and is quite likely transmitted by leafto-leaf contact (see Muehlstein 1992), perhaps explaining the predominance of die-off in dense beds. Environmental stressors that weaken seagrasses (e.g., elevated water temperatures and hypersalinity) may increase the probability of infection by Labyrinthula (Short et al. 1988). While these results suggest die-off contributed to the significantly higher percent losses measured in T. testudinum beds with high levels of standing crop, the areal extent of T. testudinum decline measured in 1994 exceeded regions of reported die-off. Lower photosynthetic rates due to widespread light reduction also may have played a role in the larger declines measured in the dense T. testudinum beds of western and central Florida Bay. Reduction in available light by resuspended sediments and algal blooms likely depressed turtlegrass photosynthesis and subsequent translocation of oxygen to the rhizosphere, and could have lead to T. testudinum decline through increased effects of hypoxia and sulfide toxicity (see Goodman et al. 1995). Dense T. testudinum beds might also have been more acutely affected by reduced light than sparser beds as the result of greater self-shading.

The seagrasses Syringodium filiforme and Halodule wrightii also declined in Florida Bay over the decade, but unlike Thalassia testudinum, S. filifome and H. wrightii declined at almost every station where they occurred in 1984. Declines in all seagrass species within the bay and larger declines in S. filifome and H. wrightii than in T. testudinum suggest decreased water clarity contributed to seagrass losses 457

in Florida Bay between 1984 and 1994. The declines in S. filiforme and H. wrightii in western and central Florida Bay were probably related to the increased light attenuation that has occurred in these areas since 1991 (Phlips et al. 1995; Boyer et al. 1999; Stumpf et al. 1999). Both Robblee et al. (1991) and Thayer et al. (1994) suggested that H. wrightii rapidly colonized die-off patches in western Florida Bay. However, during subsequent visits to their study sites in 1993, Thayer et al. (1994) found no seagrasses in previous die-off patches. These authors suggested that the decreased water clarity that began in 1991 limited seagrass recolonization in die-off areas. While declines in H. wrightii in western Florida Bay appear to be related to increased light attenuation, shoalgrass abundance also decreased at a number of stations in eastern Florida Bay where the light climate appears to have changed very little during the past decade (Phlips et al. 1995; Boyer et al. 1999; Stumpf et al. 1999). Zieman et al. (1989) suggested long-term reduction of freshwater inflow may have played a role in the decline of shoalgrass in eastern Florida Bay during the past several decades. Higher, more stable salinities may promote T. testudinum over H. wrightii, especially in areas of clear water. T. testu*dinum* abundance actually increased at a number of stations in eastern Florida Bay between 1984 and 1994, supporting the suggestion of Zieman et al. (1989). Reduced phosphorus availability due to less freshwater inflow over many decades also might be involved in the decline of H. wrightii in eastern Florida Bay (Powell et al. 1989). It must be noted that we compared two snapshots of Florida Bay seagrass communities taken 10 yr apart. Because H. wrightii distribution and abundance can vary substantially over short time periods (Zieman 1982; Thayer et al. 1994; Fourgurean et al. 1995), and S. filiforme was encountered at only a few stations, declines in these seagrasses might be attributed to random variation or seasonal fluctuations in abundance. However, the magnitude and extent of H. wrightii and S. filiforme declines between 1984 and 1994 suggest seagrass losses were the result of significant environmental change rather than random effects.

The patchy distribution of die-off in Florida Bay coupled with the haphazard placement of stations in 1984 may have influenced our ability to assess the full extent of die-off in the decline of *T. testudinum*. For example, only two of the 107 stations we surveyed were located in Rankin Lake (see Fig. 1), which was one of the basins most severely affected by die-off. Thus, the chance of encountering stations in die-off patches was lower than would be expected with a more widespread controlling factor like reduced light. Even if increased light

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attenuation rather than die-off was the direct factor leading to T. testudinum loss at most stations in the present study, die-off probably played a major role in seagrass decline through its secondary effects on water clarity. T. testudinum die-off in western Florida Bay led to extensive areas of exposed sediments, which apparently caused the widespread turbidity now present in this region (Phlips and Badylak 1996; Stumpf et al. 1999). In addition, nutrients released to the water column through the remineralization of dying seagrasses and sediment resuspension in central Florida Bay may have contributed to algal bloom development. Die-off and persistent water column turbidity continue to affect seagrasses in Florida Bay, and recent observations (Durako and Hall unpublished data) indicate continued dramatic losses of T. testudinum in western Florida Bay. The long-term future of seagrasses in Florida Bay is uncertain.

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