

Seagrass Die-off in Florida Bay: Long-term Trends in Abundance and Growth of Turtle Grass, *Thalassia testudinum*

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ABSTRACT: Beginning in late 1987 Florida Bay experienced a large and unprecedented die-off of *Thalassia testudinum*. The die-off occurred only in stands of dense *T. testudinum*. We initiated an experimental monitoring effort in 1989 to attempt to ascertain the causes of this die-off phenomenon. From 1989 to 1995 the abundance and productivity of *T. testudinum* was measured at five stations associated with the seagrass die-off and three stations where no die-off had occurred (including one on the seaside of Key Largo, outside of Florida Bay). Early in the study the salinity was very high, exceeding 46 psu, but it has decreased to 29–38 psu in recent years. Seagrass standing crop and either short-shoot density or mass per short shoot declined at nearly all stations, including the stations without die-off (unaffected stations). Over the course of the study, areal productivity declined at three die-off stations; but mass-specific productivity increased at all die-off stations and one unaffected station. Seasonality was pronounced; detrended standardized residuals showed responses for all of the seagrass parameters to be greater than the yearly mean in spring and summer and less than the mean in fall and winter. Detrended residuals also showed decreased productivity to be correlated with increased salinities in the summer despite a long-term record of declining salinities. We propose a conceptual model of the seagrass die-off phenomenon. We document that salinity does contribute to stress on *T. testudinum* in Florida Bay, but salinity is believed to be only one contributing factor to the loss of seagrasses. The documented increase in the mass-specific productivity of *T. testudinum* over the period 1989–1995 suggests seagrasses are growing rapidly in Florida Bay by 1995; we predict that the loss of *T. testudinum* may be slowing down and that recovery is possible.

Introduction

In late 1987, fishing guides reported the beginning of a large and apparently unprecedented die-off of the seagrass *Thalassia testudinum* Banks ex König in Florida Bay, Florida (M. Collins, and R. Ruoff personal communications). In 1991 it was estimated that over 4,000 ha of seagrass beds had been denuded, and an additional 23,000 ha were affected to a lesser degree (Robblee et al. 1991). Mortality of seagrasses has continued since 1991 but at a slower pace (Carlson et al. 1994; Durako and Kuss 1994; Thayer et al. 1994). The causes of this mortality are still not well understood, but

stresses caused by such factors as high salinity, high temperature, sulfide toxicity, self-shading and hypoxia (caused by biomass accumulation), and infection by the slime mold (*Labyrinthula* sp.) are hypothesized to play a role (Robblee et al. 1991). General cultural eutrophication of the water column, so often the cause of seagrass mortality around the world (e.g., Orth and Moore 1983; Cambridge and McComb 1984; Giesen et al. 1990), has not been a contributing factor to the recent die-off in Florida Bay (Fourqurean et al. 1993).

Subsequent to the initial die-off of seagrasses in 1987, Florida Bay has experienced a number of environmental changes. The historically clear water of central and western Florida Bay has become turbid. Prior to 1990, diffuse attenuation of light

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in the water column of Florida Bay was generally low (mean $k_d = 0.5 \text{ m}^{-1}$, Fourqurean and Zieman 1991); in 1993–1994, k_d ranged from 0.7 to 2.8 (Phlips et al. 1995). This increase in light attenuation is linked to two co-occurring phenomena in Florida Bay: phytoplankton blooms and increased sediment resuspension. Persistent algal blooms have been present in central and western Florida Bay since 1991 (Phlips and Badylak 1996). These ecological changes are having effects on higher trophic levels as well. Blooms of unicellular cyanobacteria have been implicated in the mass mortality of sponges in Florida Bay, which provide the primary habitat for juvenile spiny lobster (Hunt and Herrnkind 1993). The algal blooms and increased turbidity have decreased the amount of light reaching seagrasses in Florida Bay (Phlips et al. 1995), causing a secondary loss of seagrasses due to chronic low light stress when light levels drop below 10% of surface levels (Duarte 1991). By 1992, these algal blooms and turbidity plumes had expanded from local to regional scale, covering over 1000 km² (Stumpf et al. 1999). The marked changes in the Florida Bay ecosystem following the die-off demonstrate the consequences of seagrass loss. Understanding the factors causing the mortality of *Thalassia testudinum* is imperative for the proper stewardship of the ecosystem.

Thalassia testudinum is a marine angiosperm and, although tolerant of moderate salinity fluctuations, it thrives in a fairly narrow salinity range (McMillan and Moseley 1967). Zieman (1975a) reported that productivity of *T. testudinum* was maximum at salinities of 28–30 psu, and declined at both higher and lower salinity. Coincident with the initial die-off of seagrasses in Florida Bay (1987), a regional drought caused the water in the center of Florida Bay to become hypersaline (> 35 psu). By 1989, the salinity of a large part of Florida Bay exceeded 50 psu (Fourqurean et al. 1992). Exacerbating the drought was the diversion of fresh water from the Everglades for flood control, agriculture, and urban water use (Light and Dineen 1994). As much as 70% of the historical flow may have been diverted (Smith et al. 1989). The coincidence of hypersalinity and seagrass die-off led to the hypothesis that the hypersalinity of Florida Bay was a major contributor to the mortality of *T. testudinum*.

In this paper we present the results of long-term monitoring of seagrass abundance and productivity from Florida Bay. These data were collected from sites in areas influenced by the seagrass die-off, as well as from sites from areas as yet unaffected. We document trends, both long-term and seasonal, in abundance and growth of *Thalassia testudinum* in Florida Bay. We explore the relationship of water column salinity to abundance and

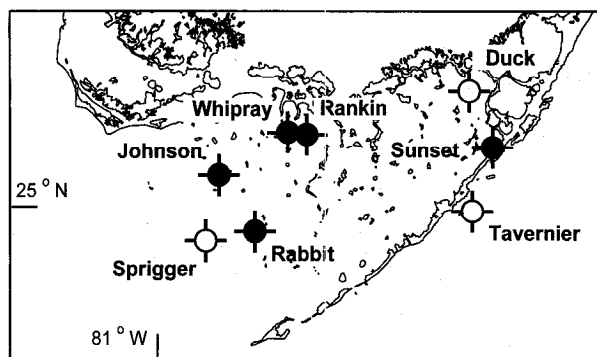


Fig. 1. Map of Florida Bay indicating station locations. Closed symbols represent stations in areas affected by seagrass die-off, open symbols are unaffected stations distant from the die-off.

growth of *T. testudinum* in Florida Bay by comparison of the time series of salinity and seagrass productivity. We present a conceptual model describing the factors leading up to the initial loss of seagrasses in Florida Bay (1987), as well as the factors leading to the subsequent ecosystem-level changes that followed seagrass die-off and that continue to-day.

Materials and Methods

STUDY LOCATION

Florida Bay is a shallow embayment located south of the Florida peninsula and west of the Florida Keys (Fig. 1). Historically, it has been an area containing dense seagrass beds (Zieman et al. 1989). Average water depth is ca. 1 m in the 2,000 km² portion of Florida Bay bounded on the west by shallow carbonate mud banks and the Everglades National Park (ENP) boundary. Stations were located in the areas of Florida Bay experiencing die-off of *Thalassia testudinum* and in areas distant from the areas of die-off (unaffected stations) (Fig. 1). These unaffected stations served as quasi-control stations. They were subject to similar environmental variations as the die-off stations but did not show any signs of die-off. Sampling began in 1989 at four stations located near the initial core die-off areas: Rankin Lake, Rabbit Key Basin, Johnson Key Basin, and Sunset Cove, and an unaffected station, Duck Key. Another die-off station was established in 1990 in Whipray Basin, and additional unaffected stations were established near Tavernier Key (outside of Florida Bay) in 1990 and Sprigger Bank in 1991.

Each of the stations in the die-off area was located in an apparently healthy *Thalassia testudinum* bed within 20 m of a recently denuded seagrass die-off area. Previous to the die-off event, all of the die-off sites had been dense, monospecific *T. tes-*

tudinum beds. The water column remained very clear (k_d ca. $0.2\text{--}0.5\text{ m}^{-1}$, Fourqurean and Zieman unpublished data) during the initial stages of the die-off event, with pronounced increases turbidity in 1992–1993, especially in the central and western bay areas more affected by die-off (Boyer et al. 1999). As the die-off progressed, exposing newly bared sediment subject to resuspension, epiphytic loading on the seagrass blades became heavy (J. W. Fourqurean personal observations). The unaffected stations were remote from the initial die-off areas. Duck Key is in the northeastern bay and is an area of sparse seagrass. Tavernier Key is outside of Florida Bay on the seaward side of Key Largo. Sprigger Bank is at the southwestern edge of Florida Bay and initially was remote from all die-off. Water clarity overlying the Sprigger Bank unaffected site has declined in response to turbidity increases and algal blooms in Florida Bay that have been prevalent since 1991 (Phlips and Badylak 1996). All die-off and unaffected stations were 1–2 m deep, except for Tavernier, which was 3 m deep.

FIELD SAMPLING METHODS

After their initial establishment, sites were revisited 2–6 times per year through September 1995. During each visit, measurements were made of short-shoot density, standing crop, leaf morphology (length and width), and the productivity of *Thalassia testudinum*. Temperature and salinity were recorded on each visit. Productivity was measured using the leaf-mark method (Zieman 1974). Six $20\text{ cm} \times 20\text{ cm}$ quadrats were arbitrarily placed in a *T. testudinum* bed and all shoots within the quadrats were marked at the base of the leaves with a needle. The plots were revisited 10–14 d later and harvested by pulling up the short-shoots with leaves intact. These were placed in plastic bags, placed over ice, and transported to the laboratory for processing. In the laboratory, each shoot was thoroughly washed to remove major fouling then the shoots were cut off at the sediment level and each blade was measured for length, width, and length-at-mark, according to age (from the youngest blade to the oldest). Epiphytes were removed by careful scraping and acidification in 5% HCl of the blades. We did not quantify the epiphyte loads. The seagrass samples were then thoroughly rinsed, oven-dried at 60°C , and weighed.

The parameters used in this analysis were standing crop (g m^{-2}) = mass of living attached green leaves; short-shoot density (ss m^{-2}); short-shoot mass (g ss^{-1}) = mass of living attached green leaves per short shoot; shoot-specific productivity ($\text{mg ss}^{-1} \text{d}^{-1}$) = mass of green leaves produced per short shoot per day; mass-specific productivity (mg

$\text{g}^{-1} \text{d}^{-1}$) = mass of green leaves produced per gram of standing crop per day; and areal productivity ($\text{g m}^{-2} \text{d}^{-1}$) = mass of green leaves produced per square meter of seagrass bed.

STATISTICAL ANALYSES

Data from the six replicate quadrats at each station were averaged prior to subsequent analysis. The data collected at each station were assessed for long-term trends using linear regression. Trends were deemed significant if the probability that the slope was different from zero was greater than 95% in a two-tailed test. Analysis of variance (ANOVA) was used to test for differences between seagrass abundance and growth estimates at die-off and unaffected sites. We used $p \leq 0.05$ as the criterion for significant differences. For tests of seasonality, the data for each station were detrended using the results of the long-term trend analysis, and the residuals were calculated. For each station, the residuals were standardized by dividing them by the value predicted by the long-term trend; in the absence of a significant long-term trend the data were divided by the grand mean of the data for the station. Data were categorized by season (winter, spring, summer, and fall), and differences among seasons were tested using ANOVA. The effect of salinity on seagrass abundance and growth was investigated with linear regression, with salinity as the independent variable, and the standardized residuals as the dependent variables.

Results

SALINITY TRENDS

At the beginning of the study, salinity was very high in Florida Bay. The mean salinity for all stations exceeded 46 psu in early 1990 (Fig. 2) and a high of 59 psu was recorded in Rankin Lake in 1989–1990. The mean salinity was above 40 psu until the fall of 1991; subsequently, mean salinity has oscillated between mean winter values of 29 and 32 psu, and mean summer values of 35 and 39 psu.

COMPARISON OF DIE-OFF AND UNAFFECTED STATIONS

The abundance and productivity of *Thalassia testudinum* was different at the die-off sites compared with the unaffected sites (Table 1). Averaged over the period of sampling, *T. testudinum* was more abundant at the die-off sites than at the unaffected sites. Standing crop at the die-off sites was about double that of the unaffected sites, and short-shoot density was 50% higher at the die-off sites. The seagrasses from the unaffected areas grew faster than those from the die-off sites. Individual short-shoots were more productive at the unaffected stations than the die-off stations ($2.5 \pm 0.3 \text{ mg ss}^{-1}$

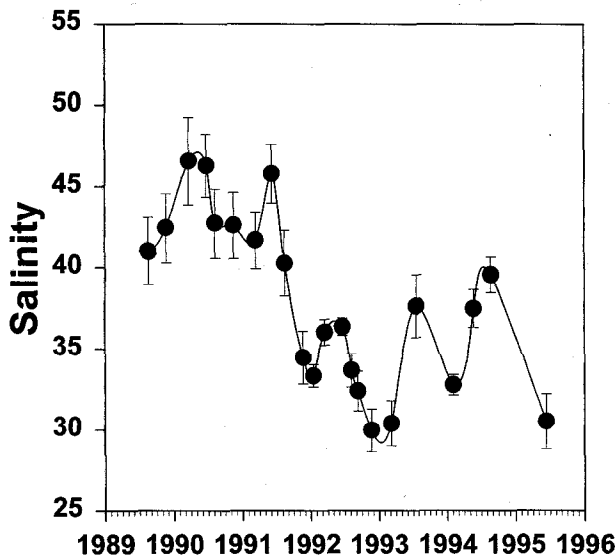


Fig. 2. Average salinity (psu) for all stations in Florida Bay for each sampling date. Error bars are ± 1 SE.

d^{-1} versus $1.7 \pm 0.2 \text{ mg ss}^{-1} \text{ d}^{-1}$, respectively). Mass-specific productivity was also higher at unaffected sites than the die-off sites ($16.9 \pm 0.7 \text{ mg g}^{-1} \text{ d}^{-1}$ versus $14.1 \pm 0.5 \text{ mg g}^{-1} \text{ d}^{-1}$, respectively). Despite the higher growth rates at unaffected sites, the die-off sites had greater areal production than the unaffected owing to initially denser seagrass beds at the die-off sites. The biomass of short-shoots was not significantly different at die-off and unaffected sites.

LONG-TERM TRENDS IN SEAGRASS ABUNDANCE

Abundance of *Thalassia testudinum* decreased over the sampling period at both die-off and unaffected sites, although at quite different rates. Four of the five die-off stations had a similar rate of loss of standing crop (Table 2). The long-term trend in standing crop at Johnson Key Basin, Rabbit Key Basin, Rankin Lake, and Sunset Cove was between $-14.1 \text{ g m}^{-2} \text{ yr}^{-1}$ and $-23.8 \text{ g m}^{-2} \text{ yr}^{-1}$, while there was no significant change in standing crop at the Whipray Basin site. Two of the three unaffected stations also had significant losses of standing crop; the trends at Duck Key and Sprigger Bank were $-6.4 \text{ g m}^{-2} \text{ yr}^{-1}$ and $-14.7 \text{ g m}^{-2} \text{ yr}^{-1}$, respectively. Three of five of the die-off stations showed a reduction in short-shoot density: Johnson Key Basin, Rankin Lake, and Rabbit Key Basin had long-term trends between $-81 \text{ ss m}^{-2} \text{ yr}^{-1}$ and $-121 \text{ ss m}^{-2} \text{ yr}^{-1}$. Whipray Basin, the only site that did not have a significant standing crop loss, had a significant increase in short-shoot density ($+84 \text{ ss m}^{-2} \text{ yr}^{-1}$). Of the unaffected sites, only Tavernier Key had a significant trend in short-shoot density ($-67 \text{ ss m}^{-2} \text{ yr}^{-1}$). The average mass of short shoots

TABLE 1. Comparison of abundance and growth estimates of *Thalassia testudinum* at die-off and unaffected sites. Means of all observations from 1989 to 1995 (± 1 SE). Significant differences between die-off and unaffected sites are indicated by different letter superscripts.

	Die-off Sites	Unaffected Sites
Standing crop (g m^{-2})	94.2 ± 5.5^a	50.2 ± 8.2^b
Short-shoot density (ss m^{-2})	768 ± 33^a	518 ± 49^b
Short-shoot mass (g ss^{-1})	117 ± 10^a	139 ± 15^a
Shoot-specific productivity ($\text{mg ss}^{-1} \text{ d}^{-1}$)	1.74 ± 0.21^a	2.47 ± 0.31^b
Mass-specific productivity ($\text{mg g}^{-1} \text{ d}^{-1}$)	14.1 ± 0.5^a	16.9 ± 0.7^b
Areal productivity ($\text{g m}^{-2} \text{ d}^{-1}$)	1.22 ± 0.08^a	0.84 ± 0.13^b

decreased at Rabbit Key Basin and Whipray Basin, the two die-off sites that did not have a significant negative trend in short-shoot density.

On average the die-off sites had a density of ca. 1000 ss m^{-2} in 1989; by 1995 the average density had decreased to ca. 600 ss m^{-2} (Fig. 3a). Unaffected sites on average also decreased in density (900 ss m^{-2} in 1990 to 400 ss m^{-2} in 1995). The standing crop of *Thalassia testudinum* decreased sharply at die-off sites, from ca. 200 g m^{-2} in 1989 to ca. 50 g m^{-2} in 1995, while standing crop at the unaffected sites was more constant (Fig. 3b).

LONG-TERM TRENDS IN SEAGRASS PRODUCTIVITY

There were no significant trends in the shoot-specific productivity at any of the unaffected or die-off sites (Table 2). Conversely, there were significant increases in the mass-specific productivity at all of the die-off stations, ranging from an increase of $1.3 \text{ (mg g}^{-1} \text{ d}^{-1}) \text{ yr}^{-1}$ at Rabbit Key Basin and Sunset Cove to $2.6 \text{ (mg g}^{-1} \text{ d}^{-1}) \text{ yr}^{-1}$ at Whipray Basin. A similar increase in mass-specific productivity was found at one of the unaffected stations (Tavernier Key). Areal productivity, a function of standing crop and mass-specific productivity, decreased significantly at three of five die-off stations. There were no significant trends in areal productivity at the unaffected stations.

While there were no significant long-term trends in the shoot-specific productivity, there was substantial variability at both die-off and unaffected sites (Fig. 4a). At the unaffected sites, mean shoot-specific productivity ranged from $< 1 \text{ mg ss}^{-1} \text{ d}^{-1}$ to $> 6 \text{ mg ss}^{-1} \text{ d}^{-1}$, while the range at die-off sites was somewhat lower ($< 1 \text{ mg ss}^{-1} \text{ d}^{-1}$ to $> 3 \text{ mg ss}^{-1} \text{ d}^{-1}$). The significant increases in mass-specific productivity at all of the die-off sites can be clearly seen in the averages of the die-off stations (Fig. 4b). In 1989, mass-specific productivity averaged ca. $12 \text{ mg g}^{-1} \text{ d}^{-1}$ at the die-off sites; by 1995 it had increased to an average of ca. $20 \text{ mg g}^{-1} \text{ d}^{-1}$. The

TABLE 2. Long-term trends in *Thalassia testudinum* abundance and growth estimates for each site. Values are the trend slope estimate (± 1 SE) in units yr^{-1} . NS: linear trend not significant at $p \leq 0.05$.

	Standing Crop (g m^{-2})	Short-Shoot Density (ss m^{-2})	Short-Shoot Mass (mg ss^{-1})	Shoot-specific Productivity ($\text{mg ss}^{-1} \text{d}^{-1}$)	Mass-specific Productivity ($\text{mg g}^{-1} \text{d}^{-1}$)	Areal Productivity ($\text{g m}^{-2} \text{d}^{-1}$)
Die-off stations						
Johnson Key Basin	-22.3 ± 4.3	-121 ± 16.6	NS	NS	1.4 ± 0.5	-0.21 ± 0.09
Rabbit Key Basin	-23.8 ± 3.9	NS	-15.3 ± 3.1	NS	1.3 ± 0.4	-0.19 ± 0.08
Rankin Lake	-14.1 ± 6.2	-81 ± 37	NS	NS	2.0 ± 0.4	NS
Whipray Basin	NS	84 ± 33	-8.9 ± 3.7	NS	2.6 ± 0.8	NS
Sunset Cove	-19.6 ± 4.2	-97 ± 20	NS	NS	1.3 ± 0.5	-0.20 ± 0.09
Unaffected stations						
Duck Key	-6.4 ± 2.3	NS	-7.9 ± 2.1	NS	NS	NS
Sprigger Bank	-14.7 ± 5.2	NS	NS	NS	NS	NS
Tavernier Key	NS	-67 ± 14	NS	NS	1.8 ± 0.7	NS

apparent increase in the mass-specific productivity in the unaffected sites was driven by the addition of the Sprigger Bank station in March 1991; it had significantly higher mass-specific productivity than the Duck Key or Tavernier Key unaffected sites.

A significant decrease in standing crop out-

weighed a significant increase in mass-specific productivity at the die-off sites, resulting in a net loss in areal productivity at the die-off sites from 1989 to 1995 (Fig. 4c). Die-off sites were producing ca. $2.5 \text{ g m}^{-2} \text{d}^{-1}$ in 1989, but by 1995 this average

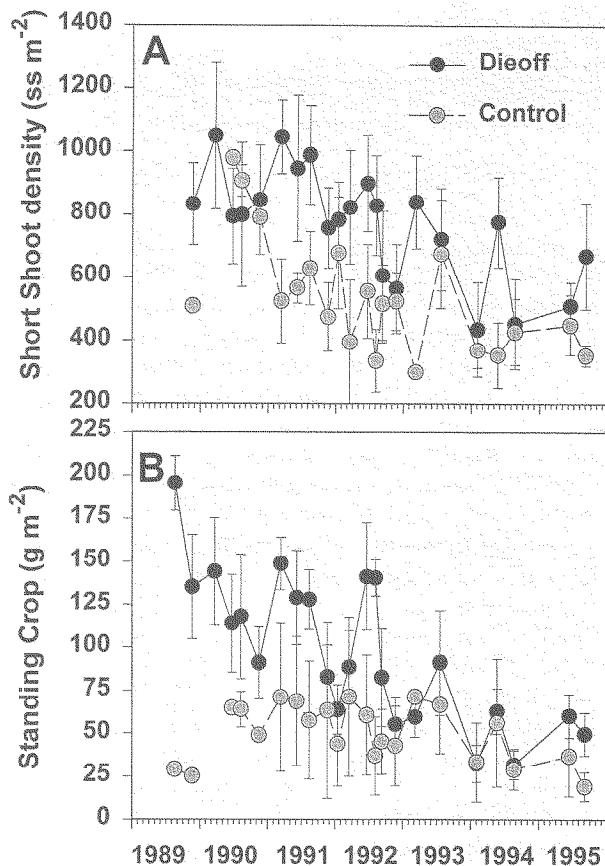


Fig. 3. *Thalassia testudinum*. Average abundance at die-off (black symbols) and unaffected (gray symbols) sites. Each point is the mean of all stations at that sampling interval; error bars are ± 1 SE. (a) Short-shoot density (short-shoots m^{-2}). (b) Standing Crop (g m^{-2}).

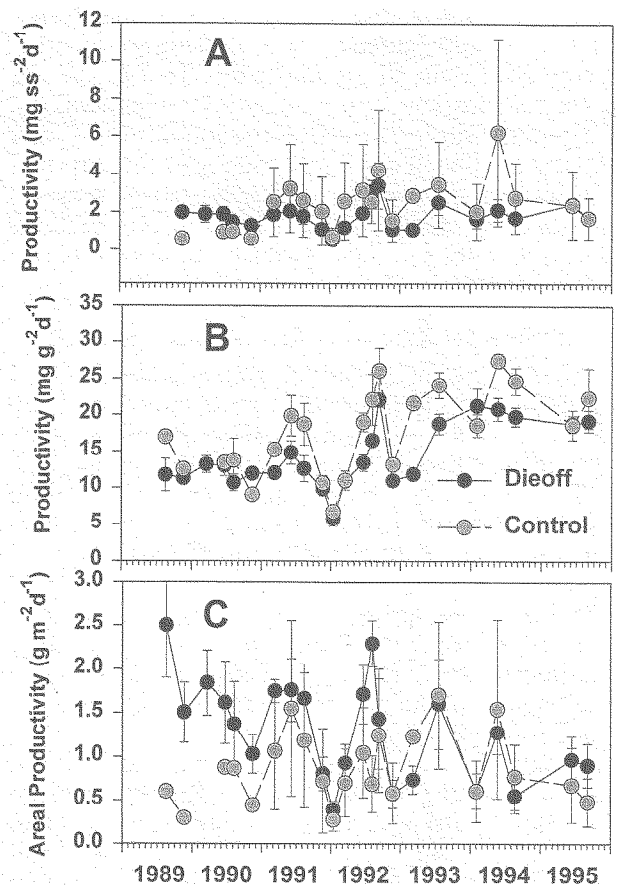


Fig. 4. *Thalassia testudinum*. Average productivity at die-off (black symbols) and unaffected (gray symbols) sites. Each point is the mean of all stations at that sampling interval; error bars are ± 1 SE. (a) Short-shoot specific productivity ($\text{mg (short-shoot)}^{-1} \text{m}^{-2} \text{d}^{-1}$). (b) Mass-specific productivity ($\text{mg g}^{-1} \text{d}^{-1}$). (c) Areal productivity ($\text{g m}^{-2} \text{d}^{-1}$).

TABLE 3. Seasonality and treatment effects on abundance and productivity of *Thalassia testudinum*. Results of ANOVA, testing for the effects of both treatment (die-off versus unaffected sites) and season (winter, spring, summer, and fall) on the standardized residual of the abundance and productivity parameters. Effects significant at $p \leq 0.05$ are in boldface type.

Parameter	n	Error Source	df	MSE	F	p
Short-shoot density	153	TREATMENT	1	0.007	0.10	0.76
		SEASON	3	0.068	0.88	0.45
		TREATMENT \times SEASON	3	0.089	1.15	0.33
Standing crop	158	TREATMENT	1	0.025	0.17	0.68
		SEASON	3	1.210	8.26	0.00
		TREATMENT \times SEASON	3	0.207	1.41	0.24
Short-shoot mass	153	TREATMENT	1	0.029	0.30	0.58
		SEASON	3	0.590	6.08	0.00
		TREATMENT \times SEASON	3	0.040	0.42	0.74
Short-shoot specific productivity	153	TREATMENT	1	0.323	2.21	0.14
		SEASON	3	1.210	22.19	0.00
		TREATMENT \times SEASON	3	0.207	0.49	0.67
Mass-specific productivity	158	TREATMENT	1	0.141	1.99	0.16
		SEASON	3	1.233	27.40	0.00
		TREATMENT \times SEASON	3	0.172	2.43	0.07
Areal productivity	159	TREATMENT	1	13.37	0.42	0.52
		SEASON	3	31.33	0.98	0.40
		TREATMENT \times SEASON	3	29.73	0.93	0.43

productivity had decreased substantially, to $< 1 \text{ g m}^{-2} \text{ d}^{-1}$. Areal productivity at the unaffected sites was quite variable, but there was no net change in areal production at the unaffected sites over the course of this study.

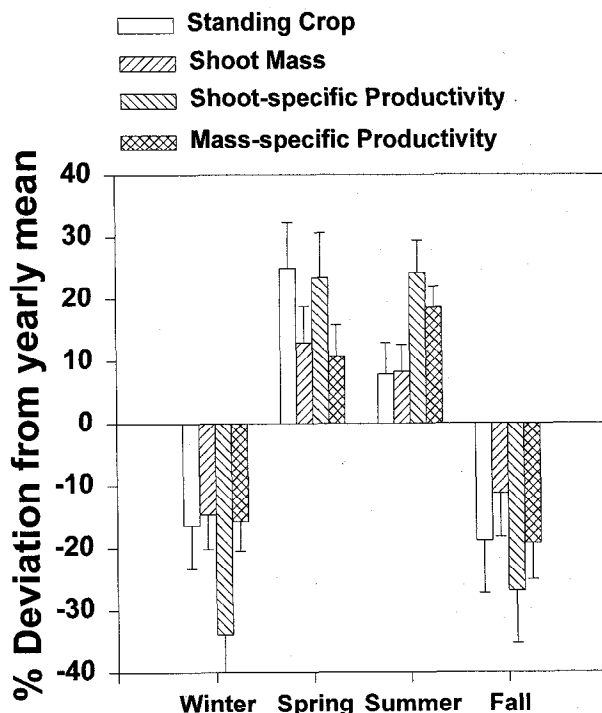


Fig. 5. *Thalassia testudinum*. Seasonality of abundance and productivity parameters. Standardized residuals of each parameter are grouped by season. Error bars are $\pm 1 \text{ SE}$.

SEASONALITY OF SEAGRASS ABUNDANCE AND PRODUCTIVITY

Much of the variation about the long-term trend in abundance and productivity of *Thalassia testudinum* (Figs. 3 and 4) could be explained by seasonality. The season in which the data were collected had a significant effect on the sign and magnitude of the deviation from the long-term trend for standing crop, short-shoot mass, short-shoot specific productivity, and mass-specific productivity, but not for short-shoot density or areal productivity (Table 3). Die-off and unaffected sites had similar residuals: neither the main effect of treatment nor the interaction term (treatment by season) were significant for any measure of abundance or growth (Table 3).

The standardized residuals are a measure of the fractional deviation of a measurement from the yearly average. Standing crop, short-shoot mass, short-shoot specific productivity, and mass-specific productivity exhibited similar seasonal patterns in their standardized residuals: negative deviation from the yearly mean in winter and fall, and positive deviations in spring and summer (Fig. 5). Shoot-specific productivity had the highest amplitude of deviation. In winter, shoot-specific productivity was an average of 33% lower than the yearly average, while in summer it was 25% greater. Short-shoot mass was considerably less variable than shoot-specific productivity, varying only $\pm 15\%$ seasonally. Standing crop peaked in spring.

EFFECT OF SALINITY ON SEAGRASS PRODUCTIVITY

Overall between 1989 and 1995, salinities in Florida Bay declined (Fig. 2). Three phases in sa-

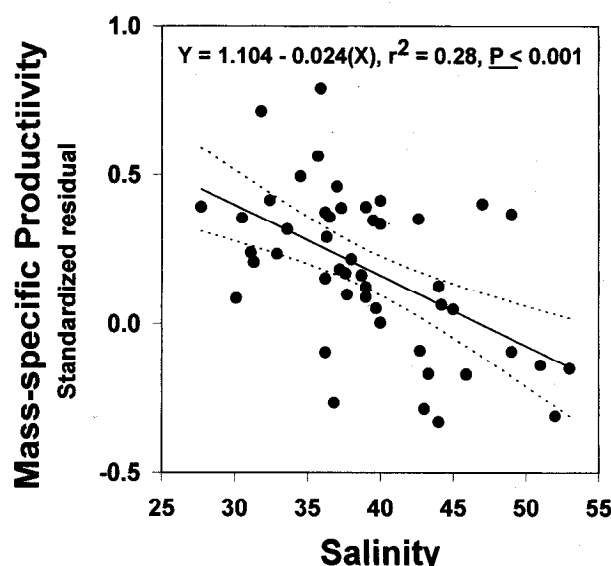


Fig. 6. *Thalassia testudinum*. Relationship between summer standardized residuals in mass-specific productivity and salinity. Solid line is the regression described by the equation on the figure, dotted lines are 95% confidence interval of the regression equation.

linities were seen during this time: a high salinity period from 1989 to mid 1991, a rapid decline from mid 1991 to late 1992, and a slow increase from 1993 to 1995. Seagrass short-shoot density and standing crop declined between 1989 and 1995 (Fig. 3 and Table 2), although in a more linear pattern, and mass-specific productivity increased (Fig. 4 and Table 2). Both salinity and seagrass abundance and productivity had a seasonal component to their variation.

Simple correlations of salinity with seagrass abundance and productivity were significant (results not presented), but are the result of the strong long-term trends in the datasets. Seagrass abundance responds to salinity over long time scales so we did not test for correlations between abundance and salinity at the collection time. In order to test for the effect of salinity on *Thalassia testudinum* productivity in the presence of the correlated time series, we used salinity as a predictor of the standardized residuals for each productivity parameter. Owing to the seasonal dependence of the sign of the standardized residuals, we segregated the data by season before analysis. For the summer season, the magnitude of standardized deviation of mass-specific productivity was significantly correlated with salinity (Fig. 6), with higher salinities leading to reduced production of *T. testudinum*. We found no significant correlations in other seasons. We also found no correlations between standardized residuals of short-shoot-specific or aerial productivity and salinity for any season.

Discussion

GENERAL TRENDS IN FLORIDA BAY SEAGRASSES

Seagrass beds in Florida Bay have continued to decline in density and biomass since the die-off event began in 1987. At the five sites we monitored immediately adjacent to areas that had been denuded by seagrass die-off, seagrass density declined an average of 43 ss m⁻² yr⁻¹ (Fig. 3a). This translated to a loss in standing crop of 16 g m⁻² yr⁻¹ (Fig. 3b). Only one site, Whipray Basin, did not exhibit declines in density and standing crop of *Thalassia testudinum*. We suspect that no decline in seagrass density was recorded at this site because major losses of biomass occurred there prior to our monitoring efforts (Zieman et al. 1989, unpublished data). During the period 1989–1995, *T. testudinum* density at Whipray Basin increased by 84 ss m⁻² yr⁻¹. The general decline in standing crop of seagrasses was not limited to the sites adjacent to areas that experienced the catastrophic die-off. The two unaffected sites in Florida Bay, Duck Key and Sprigger Bank, also had significant decreases in seagrass standing crop over the period from 1989 to 1995. Our results for Florida Bay corroborate the predictions of continued decline in seagrass density by Durako (1994) based on the demographics of the *T. testudinum* populations at Johnson, Rabbit Key Basin, and Rankin Lake in 1989–1990. Further, our results indicate that seagrass beds in Florida Bay have fared poorly whether or not they were near a site of catastrophic die-off.

In contrast to the loss in seagrass density and standing crop, we found that mass-specific productivity increased markedly from 1989 to 1995 at the die-off sites. In 1989 mass-specific productivity was ~ 12 mg g⁻¹ d⁻¹; this increased steadily to around 20 mg g⁻¹ d⁻¹ in 1995. The average yearly increase for all stations was 1.7 mg g⁻¹ d⁻¹. This increase in mass-specific productivity is not a departure from a long-term mean, but instead indicated a return to the rates of production prior to the die-off in 1983–1984, at which time mass-specific *Thalassia testudinum* productivity averaged 22 mg g⁻¹ d⁻¹ across Florida Bay (Zieman et al. 1989). Historical data on mass-specific productivity are remarkably constant in unimpacted *T. testudinum* beds in south Florida, with a range of 18 mg g⁻¹ d⁻¹ to 24 mg g⁻¹ d⁻¹ in studies of productivity from Biscayne Bay to the Lower Keys (Zieman 1968, 1975b, 1982). It is probable that the factors responsible for reducing the mass-specific productivity near the die-off sites at the beginning of this study (self-shading due to overcrowding, some environmental stress, or a combination) are reduced or are no longer present.

The increases in mass-specific productivity of seagrasses in Florida Bay occurred at the same time that transmission of light to the bottom was decreasing dramatically. Turbidity increased in the bay in 1991, leading to an increase in the diffuse attenuation coefficient of the water column from $< 0.5 \text{ m}^{-1}$ before 1990 (Fourqurean and Zieman 1991) to a high of 2.8 m^{-1} in 1993–1994 (Phlips et al. 1995; see also Boyer et al. 1999). This increase in attenuation of light in the water column resulted in as much as a tenfold reduction in light at 1 m, the average depth of seagrass beds in Florida Bay. Despite these drastic reductions in light reaching the canopy, seagrass mass-specific productivity increased. We attribute this increase in mass-specific productivity to a thinning of the seagrass canopy and the subsequent decrease in light attenuation within the plant canopy. It is also possible that mass-specific productivity increased because of physiological adaptation to the changing environmental conditions. For example, *Thalassia testudinum*, like most plants, responds to decreased light availability by increasing the amount of chlorophyll in leaf tissue (Wigginton and McMillan 1979; Czermy and Dunton 1995); increased chlorophyll content increases photosynthetic efficiency at low light levels. Increased mass-specific productivity may have also been a result of recovery of *T. testudinum* from a pathogen; *Labyrinthula* infection has been shown to decrease the photosynthetic capacity and rate of *T. testudinum* (Durako and Kuss 1994). Whatever the cause, the increase in mass-specific productivity in spite of the increases in turbidity bodes well for the survival of Florida Bay seagrasses.

Despite increasing productivity on a mass-specific basis over the period 1989–1995, areal productivity of *Thalassia testudinum* decreased at three of five die-off sites. This can be explained by a decrease in short-shoot density at the Johnson Key Basin and Sunset Cove sites; however, at Rabbit Key Basin there was no significant trend in short-shoot density. Rather, short-shoots of *T. testudinum* at Rabbit Key Basin, as defined by mass, became smaller over the period of study. Similarly, short-shoot size decreased at the Whipray Basin site, but this was offset by the increase in short-shoot density, resulting in no net trend in the areal productivity at that site. The decrease in short-shoot size at Rabbit Key Basin and Whipray Basin may be an indication of recruitment of new shoots to the population (Durako 1994).

THE ROLE OF SALINITY IN THE FLORIDA BAY SEAGRASS DIE-OFF

Our data (Fig. 6) suggest summer hypersalinity depressed the mass-specific production of *Thalassia*

testudinum in Florida Bay. Even as yearly mean salinity decreased from 1989 to 1995, salinity was consistently high (> 35 psu) during summer months (Fig. 2). Only during summer was there a significant effect of salinity on seagrass productivity. It is possible salinity stress on *T. testudinum* during summer may be sufficient to cause seagrass death, or that there is a strong interaction with other stressors such as high temperature and high sulfide levels (Carlson et al. 1994). Perhaps these stresses in combination with summertime maximum growth rate and recruitment increased mortality of *T. testudinum* shoots in Florida Bay. A more general effect of salinity on seagrass productivity may be masked by the temporal pattern of salinity from 1989 to 1995; however, during 1987–1991 Florida Bay was chronically hypersaline. Fourqurean et al. (1993) reported that for a 14-mo period in 1989–1990, the central core of the bay had salinities greater than 50 psu, with maximum salinities in the center of the bay over 60 psu. From 1991 onward, Florida Bay was only hypersaline in the summer months (Fig. 2), hence the lack of detectable salinity effects on productivity in other seasons. As *T. testudinum* is a stenohaline marine plant (McMillan and Mosely 1967; Zieman 1975a), it is reasonable to hypothesize hypersalinity as a causative agent in the initial seagrass die-off that occurred during this period. Salinity-related diebacks of seagrasses have been reported in Florida Bay in the past (Tabb et al. 1962).

Historically, salinity has been variable in Florida Bay, with periodic episodes of hypersalinity as severe as that recorded in 1989–1990 occurring every 15–20 yr (Finucane and Dragovich 1959; Tabb et al. 1962; M. B. Robblee unpublished data). Yet there have been no reports of the widespread mortality of *Thalassia testudinum* across Florida Bay before 1987; the earlier events reported by Tabb et al. (1962) affected only small areas, which quickly recovered. Rankin Lake and Rabbit Key Basin were the first areas where die-off was documented in 1987. Mean yearly salinity at Rankin Lake at this time was > 40 psu; this salinity may have been deleterious to *T. testudinum*. In contrast, mean yearly salinity at Rabbit Key Basin was only 36–38 psu (well within the range of normal salinity for *T. testudinum* communities) when the die-off began at that site. By the fall of 1987, however, salinity at the Rabbit Key Basin station was as high as 44 psu because of the anomalously dry autumn of 1987 (Orlando et al. 1997). Whether these salinities could have initiated a die-off in Rabbit Key Basin is unclear: the time course of response of *T. testudinum* to stressful salinity has not been well studied.

These observations combined with the significant negative effect of salinity on productivity (Fig.

6) suggest that salinity of Florida Bay may have played a significant role in the 1987–1991 seagrass die-off. However, it is also evident that salinity by itself cannot account for all of the pattern in the initial seagrass die-off or the subsequent environmental changes in Florida Bay. Below, we briefly present a conceptual model that attempts to describe the possible mechanisms for the seagrass community changes in Florida Bay since 1987. We recognize that many of the tenets of this model have not been well tested as yet; we present the model as a framework for guiding future research into the recent ecological changes of the Florida Bay ecosystem.

A CONCEPTUAL MODEL OF SEAGRASS DIE-OFF IN FLORIDA BAY

In 1962, Tabb et al. (1962) described a small-scale version of the major changes in the Florida Bay environment that began in 1987:

"...under hypersaline conditions (above 45–59 ppt) the turtle grass, *Thalassia testudinum* is adversely affected. The blades of the "grass" die back and thus expose the bottom muds. If high salinity periods persist for periods of 3–5 months the turtle grass cover of Florida Bay becomes reduced by defoliation so that wind scour reaches the marl muds and turbidity increases markedly. Such turbidity conditions further limit the numbers of species that may be found in the region beyond that already reduced by hypersalinity."

The 1987 die-off event began similarly: geographically distinct basins were affected by the loss of *Thalassia testudinum*. Following 1987, major changes in bottom cover and water clarity spread across western and central Florida Bay: *T. testudinum* continued to die-off in basins adjacent to the original die-off sites (Robblee et al. 1991) and water clarity decreased in the region (Phlips et al. 1995; Boyer et al. 1999). We propose that the most recent seagrass die-off event was qualitatively different and more spatially extensive than events described by Tabb et al. (1962) because the seagrass communities that existed at the beginning of the recent die-off were likely quite different from the ones in the previous decades. Over the period 1960–1987 there was a slow change in the seagrass communities of Florida Bay, which resulted in very dense beds of *Thalassia testudinum* in western Florida Bay (see below). These dense beds became overcrowded and unstable. A series of stresses (including, but not limited to, salinity stress) caused the die-off of the dense *T. testudinum* beds; once these beds succumbed to these stresses, water clarity decreased as nutrients were released from decaying seagrass biomass and newly unstable sedi-

ments. This led to decreased light availability, which further stressed seagrasses.

Tabb et al. (1962) described the structure of the seagrass beds in extreme western Florida Bay as being controlled by turbidity and salinity fluctuation. In turbid areas prone to large salinity swings, seagrasses were "stunted exhibiting sparse growth" (Tabb et al. 1962); as a result of turbidity and salinity stresses, large areas of Florida Bay became dominated by *Halodule wrightii*. In clearer waters more removed from freshwater discharge, seagrasses were larger and uniformly dense, and the beds were dominated by *Thalassia testudinum*. By the late 1970s, fishing guides were noticing changes occurring in western Florida Bay seagrass communities (M. Collins, R. Martin, and R. Ruoff personal communications). Numerous areas that in previous decades had been dense *H. wrightii* beds had become colonized by *T. testudinum*, and areas that were *T. testudinum*–*H. wrightii* mixes had become monospecific stands of *T. testudinum* (described in Zieman 1982, p. 90–91). These anecdotal observations are supported by a survey of seagrass beds in Florida Bay in the 1970s, which documents that *H. wrightii* or a *H. wrightii*–*T. testudinum* mix was more common in much of the northern bay where the die-off would occur (Schmidt 1979). By 1984, *T. testudinum* was the dominant seagrass in the region (Zieman et al. 1989). The density of *T. testudinum* continued to increase through the 1980s: in a 1988–1989 resurvey of 40 stations sampled by Zieman et al. (1989) in 1984, the mean standing crop of seagrass had increased. For example, standing crop increased by 50% at Johnson Key Basin and by nearly 200% at Rabbit Key Basin during the period 1984 to 1989 (Fig. 7). After the initiation of the seagrass die-off in 1987–1989, standing crop decreased steadily at both of those sites (Table 2 and Figs. 3 and 7). These observations and data suggest the seagrass communities that experienced the die-off in 1987 likely had a different species composition and density than those communities documented by Tabb et al. (1962).

Stressors that have been recognized (Robblee et al. 1991) to have potentially played a vital role in the 1987 die-off are hypersalinity of overlying seawater; increased temperature stress; imbalance in the ratio of photosynthesis to respiration; sulfide toxicity; disease; and eutrophication of overlying water. A few of these stressors have begun to be evaluated, while others remain to be investigated. We have presented data that suggests salinity does have a negative impact on seagrass productivity (Fig. 6), but that salinity alone is not a sufficient explanation of the die-off. General cultural eutrophication of the water column, so often the cause of seagrass mortality around the world, can not ac-

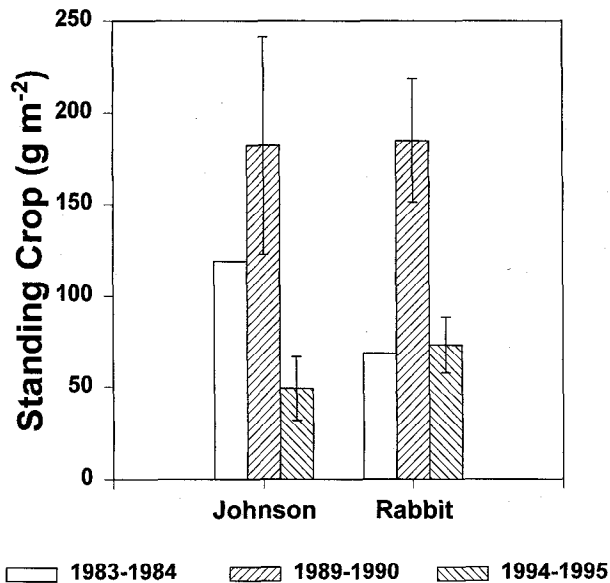


Fig. 7. *Thalassia testudinum*. Comparison of summer standing crop at the Rabbit Key Basin and Johnson Key Basin sites for three time periods: 1983–1984 (data from Zieman et al. 1989), 1989–1990, and 1994–1995

count for the seagrass die-off since the decline in water clarity and increases in nutrient concentrations did not occur until 1991, well after the death of the seagrasses (Fourqurean et al. 1993; Boyer et al. 1999). Evidence is mounting that hypoxia and sulfide toxicity play an important role in the initiation of the die-off (Carlson et al. 1994). Infections of *Thalassia testudinum* by the pathogenic slime mold *Labyrinthula* spp. are more prevalent from areas near seagrass die-off, and the infection reduces the ability of *T. testudinum* to photosynthesize (Durako and Kuss 1994). Less well-studied are the roles of high temperature and the combined effects of multiple stressors in the die-off.

Data from our monitoring program confirm the continued loss of seagrass biomass and primary production in Florida Bay during the period 1989–1995. In contrast to these losses, we have documented an increase in the mass-specific productivity of *Thalassia testudinum* in Florida Bay over the same interval. This increase in growth rate suggests the stresses on seagrasses in Florida Bay have lessened over the monitoring period, despite a general decrease in the water clarity of the system. We propose that the lessening of stress on *T. testudinum* is a direct consequence of the loss of seagrass biomass from Florida Bay. This loss of biomass may be a return to a historical average condition, in which *T. testudinum* is less dominant in the system. In addition, stress on these continentally influenced seagrasses has lessened with the breaking of the drought beginning in 1991 and continuing to

the present. Our observations and our conceptual model predict the loss of seagrasses from Florida Bay may be slowing and that the ecosystem is reaching a new equilibrium.

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