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Effects of Two Hurricanes on *Syringodium filiforme*, Manatee Grass, Within the Loxahatchee River Estuary, Southeast Florida

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ABSTRACT: In September 2004, the Loxahatchee River Estuary was affected by Hurricanes Frances and Jeanne, which resulted in a monthly rainfall record of 610 mm and abnormally high freshwater discharges to the system. The occurrence, density, and biomass of *Syringodium filiforme* in the Loxahatchee River Estuary declined significantly following the September 2004 storms based on 15 mo of pre-hurricane monitoring and 12 mo of post-hurricane monitoring. Throughout post-hurricane monitoring, *S. filiforme* showed no sign of recovery, though *Halophila johnsonii* increased considerably during the post-hurricane period. Freshwater discharges resulting from the September 2004 hurricanes lowered minimum daily salinity values to near zero and increased standard deviation of daily salinity values to 11‰. Extremely low minimum daily salinity values and high daily salinity fluctuations likely resulted in the observed decline of *S. filiforme*. We advise the use of minimum daily salinity values when assessing seagrass habitat suitability or when modeling the effects of alternative water management scenarios.

Introduction

Estuaries receive considerable attention from local stakeholders and natural resource managers because they provide essential nursery habitats that support the development of larval and juvenile fish and invertebrates (Montague and Ley 1993; Fourqurean et al. 2003; Lirman and Cropper 2003). Seagrasses are identified as a critical component of most estuaries because they provide food and refuge from predation for numerous economically and ecologically important species (Holmquist et al. 1989; Zieman et al. 1989; Montague and Ley 1993). Seagrasses are recognized as key components of estuarine productivity (Short et al. 1993; Fourqurean et al. 2001) and have been identified as biological indicators of water quality and ecosystem health. In particular, seagrasses are highly dependent upon suitable water clarity and light transmission (Dennison et al. 1993; Kemp et al. 2004), with water column chlorophyll concentration and turbidity being two of the most important factors causing light attenuation (Gallegos 1994). Some seagrass species, such as *Syringodium filiforme*, manatee grass, appear susceptible to lowered salinities and excessive salinity fluctuations (Montague and Ley 1993; Provancha and Scheidt 2000; Lirman and Cropper 2003).

In June 2003, the Loxahatchee River District partnered with the South Florida Water Management District and initiated a 3-yr monitoring effort to document pre-restoration conditions (i.e., distribution, species composition, density, and biomass) of seagrasses in the Loxahatchee River Estuary. Because seagrasses have been deemed a valued ecosystem component, they will be used to assess restoration success following modified freshwater inflows resulting from the Comprehensive Everglades Restoration Project and the Northwest Fork Restoration Plan (CERP 2001; SFWMD 2006). In September 2004 the study area was affected by Hurricanes Frances and Jeanne. Fourqurean and Rutten (2004) have shown hurricanes negatively affect seagrasses through mechanical stress (i.e., wind and wave damage), while others suggest altered water quality, especially lowered salinities, may significantly affect seagrasses (Lirman and Cropper 2003). Our objective was to evaluate the effects of the September 2004 hurricanes on the occurrence, density, and biomass of *S. filiforme* within the Loxahatchee River Estuary.

Study Area

The Loxahatchee River Estuary encompasses approximately 400 ha and drains a watershed of approximately 700 km^2 located in northeastern Palm Beach County and southeastern Martin County, Florida, USA. Freshwater discharges into the estuary from the North Fork, Northwest Fork, and Southwest Fork. The hydrology of the basin has been substantially altered by flood control efforts since the 1950s. Ongoing restoration efforts seek to increase freshwater discharge into the Northwest Fork and decrease the magnitude of freshwater discharge into the Southwest Fork. These altered freshwater discharges must maintain or enhance the ecological integrity of downstream reaches (i.e., estuary) and valued ecosystem components within

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*Corresponding author; tele: 561/747-5700; fax: 561/747-9929; e-mail: albrey@loxahatcheeriver.org the estuary such as oysters and seagrasses (SFWMD 2006).

Materials and Methods

Seagrasses, including *S. filiforme*, were sampled monthly from June 2003 through September 2005 in the Loxahatchee River Estuary at two sites (North Bay [NB] 26°57′01.7″N, 80°05′36.9″S; Sand Bar [SB] 26°56′53.1″N, 80°05′57.3″S). Permanent seagrass monitoring transects were established at these sites in June 2003 based on the spatial distribution of persistent *S. filiforme* beds. NB is located within a small cove on the north side of the estuary and has the highest richness of seagrasses and macroalgae among our sample sites. The NB site has three north-south transects 100 m in length and one east-west transect 100 m in length. The SB site is more centrally located and more strongly influenced by freshwater discharges as they pulse out of the system. Seagrasses were sampled at the SB site along three east-west transects 50 m in length and two north-south transects 100 m in length. NB and SB transect depths range from 0.1 to 1 m at mean tide level.

Monthly from June 2003 through September 2005, divers assessed the occurrence of *S. filiforme* by positioning a 0.0625-m^2 (25 × 25 cm) quadrat every 1 m along each transect. In each quadrat, the presence (or absence) of *S. filiforme* was noted. Divers also enumerated *S. filiforme* shoot density each month at the NB and SB sites in twelve 0.0625-m^2 quadrats randomly located within each seagrass bed.

Aboveground and belowground biomass of *S. filiforme* was assessed quarterly by collecting six 0.0144-m^2 (12 × 12 cm) cores randomly located within the seagrass bed at each seagrass sampling site. Cores were taken to a depth of approximately 15 cm. In the laboratory, seagrasses were separated by species and into living aboveground and belowground components. Samples were dried in an 80°C oven for 3–5 d and dry weights were recorded to the nearest 0.0001 g. For the present analysis, whole plant biomass (sensu Short et al. 1993) was assessed by combining aboveground and belowground living biomass.

In addition to the *S. filiforme* monitoring, water quality was evaluated at the NB and SB seagrass sites, and freshwater discharge into the system was recorded. Throughout the study, temperature, conductivity, salinity, dissolved oxygen, pH, turbidity, chlorophyll *a*, and photosynthetic available radiation (PAR) were recorded monthly at the time of seagrass sampling in the channel adjacent to each seagrass site. Starting in April 2004 salinity and temperature were recorded every 15 min at the NB site using a Hydrolab Minisonde 4a positioned at seagrass canopy height (c. 25 cm off the bottom). Supplemental water quality samples, including water color, were collected every other month in the channel adjacent to the NB seagrass site (i.e., Riverkeeper Station 40). Water quality samples were processed following Standard Methods by the Loxahatchee River District's Wildpine Laboratory, which is certified under the National Environmental Laboratory Accreditation Program. PAR was assessed by taking 3 replicates using 3 LI-COR spherical sensors (4 π) simultaneously located at 20, 50, and 100 cm below the water surface. Data were recorded on a LI-COR LI-1400 data logger. Light attenuation coefficient (K_d) was calculated as the slope of natural log transformed PAR values regressed against depth. Following Kemp et al. (2004), the percent of light passing through the water column to seagrasses (PLW) was calculated as $PLW = 100\exp[(-K_d)(Z)]$, where K_d is the light attenuation coefficient and Z is the depth of seagrass growth. Freshwater discharge into the Southwest Fork was recorded continuously at the S-46 structure, while freshwater discharge into the Northwest Fork was recorded continuously at Lainhart Dam. Discharge from the North Fork generally contributes approximately 6% of mean daily flow into the estuary and was not assessed during this period (SFWMD 2006).

Results

Hurricanes Frances and Jeanne affected the Loxahatchee River watershed in September 2004 with high winds, heavy rainfall, and excessive freshwater runoff. Both Frances (category 2) and Jeanne (category 3) made landfall approximately 60 km to the north of the Loxahatchee River Estuary. Though both storms exerted hurricane force winds on the estuary, Frances appears to have generated the greatest wind stress with sustained winds of 130 km h^{-1} measured in Jupiter, Florida.

Hurricanes Frances and Jeanne delivered a combined 610 mm of rainfall and resulted in excessive freshwater discharge to the estuary (Fig. 1), which negatively affected the salinity regime, light attenuation, and water quality in the Loxahatchee River Estuary. Freshwater discharges resulting from the hurricanes severely depressed water column salinity at the NB site (Fig. 1) and throughout the estuary (Loxahatchee River District unpublished data). During the 38-d period immediately following the hurricanes, minimum daily salinity was $< 17‰$ for 30 out of 38 d, with 17 continuous days of minimum salinity values below 17‰. During the same period, minimum daily salinity was $< 10‰$ for 18 out of 38 d, with 11 continuous days of minimum salinity values below 10‰. PAR samples in September, October, and November 2004 showed the percent

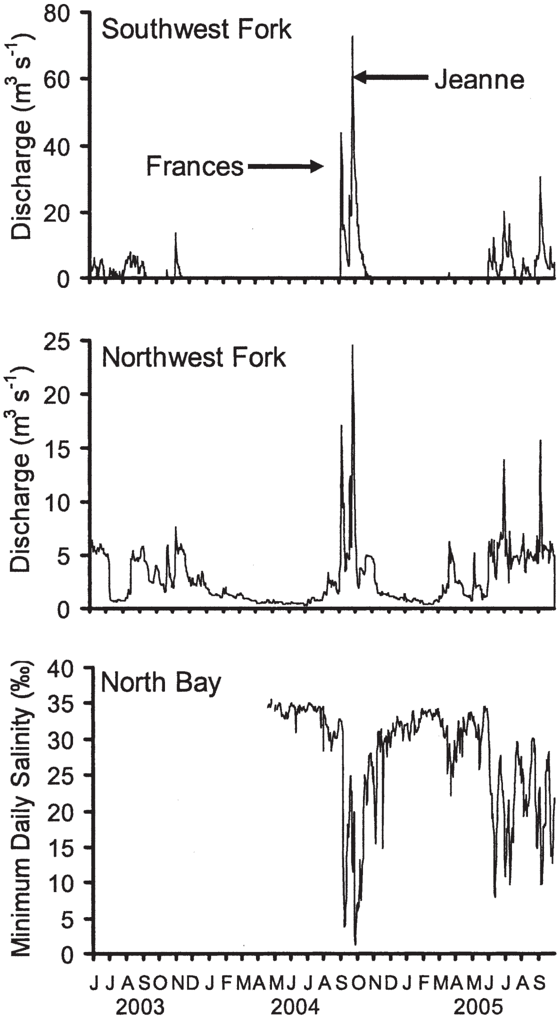

Fig. 1. Two hurricanes (Frances and Jeanne) affected the Loxahatchee River and estuary in September 2004. Elevated rainfall resulted in excessive mean daily discharges ($m^3 s^{-1}$) down the Southwest Fork and the Northwest Fork, and resulted in substantial declines in the salinity regime, shown as minimum daily salinity, of the estuary as recorded at the North Bay seagrass sampling site. Southwest Fork discharge was measured at S-46, and Northwest discharge was measured at Lainhart Dam. The dry season is November-April, while the wet season is May-October.

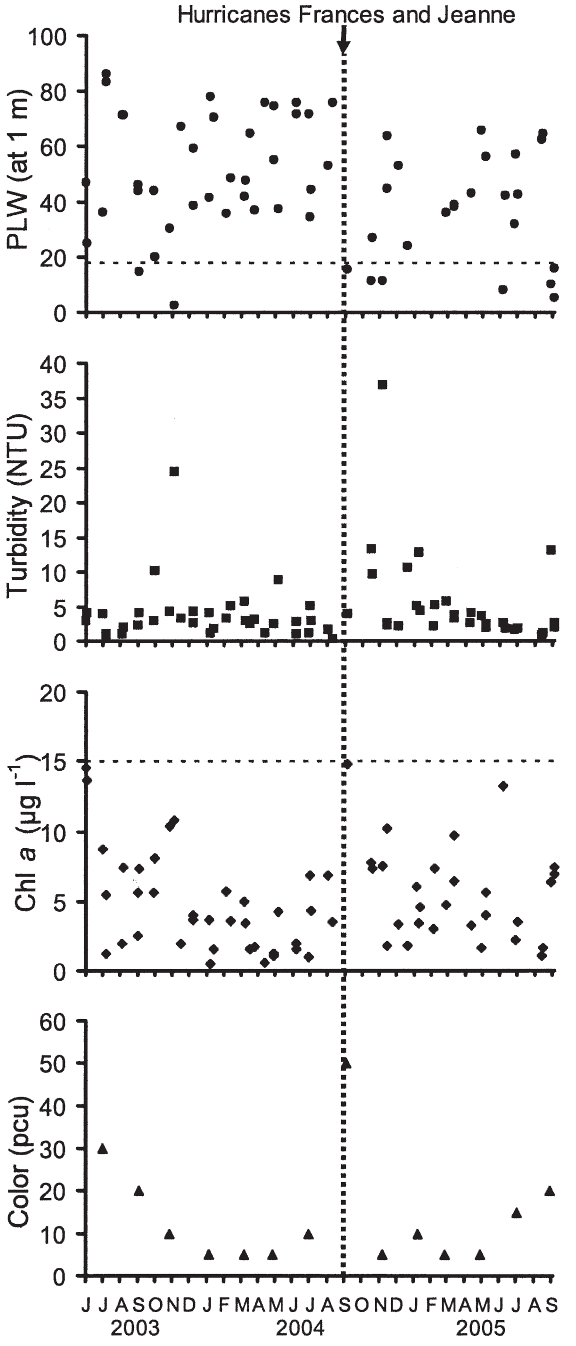

Fig. 2. Observed values reveal apparent short-term effects of Hurricanes Frances and Jeanne on percent of light (photosynthetically active radiation, PAR) transmitted through the water column to the depth of seagrass growth (PLW), turbidity, chlorophyll *a* concentrations, and water color. The dotted horizontal line in the PLW and chl *a* panels represent the minimum water quality thresholds for submerged aquatic vegetation established in Dennison et al. (1993) and Kemp et al. (2004).

of light reaching seagrasses (PLW) to be highly variable following the hurricanes with three of the six observations below the minimum light requirement for *S. filiforme* (i.e., < 19.2%; Dennison et al. 1993), though one PAR sample in October and two PAR samples in November showed PLW values well above the light requirements for *S. filiforme* (Fig. 2). Chlorophyll *a* concentration increased in September immediately following Hurricane Frances; note that all observed chlorophyll *a* concentrations were below the water quality threshold of 15 $\mu g\ l^{-1}$ used to define habitat requirements for submerged aquatic vegetation survival (Dennison et al. 1993;

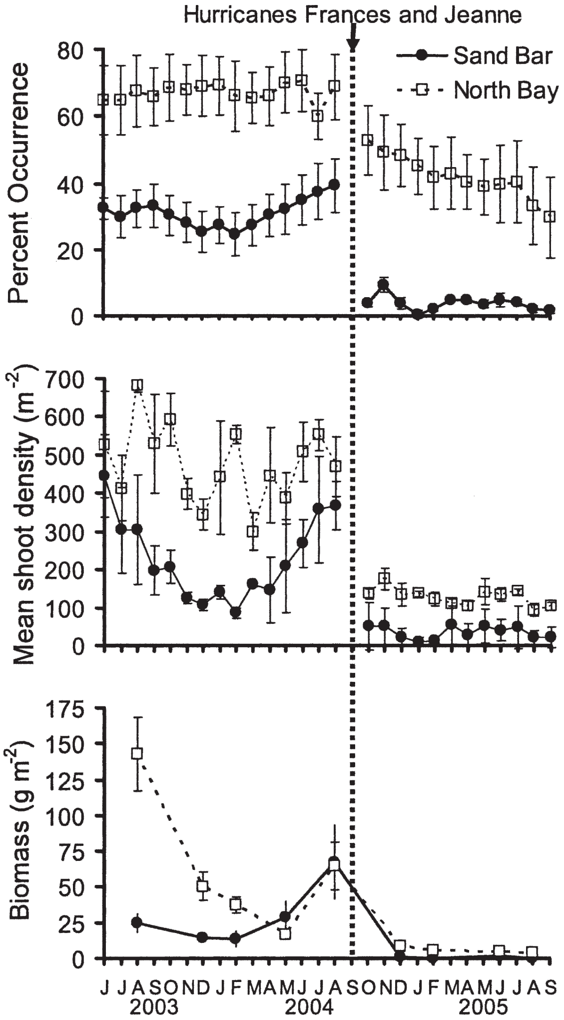

Fig. 3. *Syringodium filiforme* shows a pronounced decrease in percent occurrence, i.e., fraction of quadrats occupied, shoot density, and total (aboveground + belowground) dry weight biomass following September 2004, when two hurricanes affected the Loxahatchee River Estuary. Even 12 mo after the hurricanes *S. filiforme* showed no sign of recovery. Note that field data were not collected during September 2004 when the hurricanes made landfall. Error bars represent ± 1 SE.

Kemp et al. 2004). Turbidity in the water column at the seagrass sampling sites is generally below 5 NTU, but ranged up to approximately 13 NTU 1 mo following the hurricanes. The maximum turbidity value observed was 36.9 NTU measured nearly 2 mo after the hurricanes, while turbidity fell to 2.3 NTU approximately 1 wk later. Discharge of highly stained freshwater into the estuary resulted in water color increasing from 10 pcu to approximately 50 pcu immediately following Hurricane Frances, with water color values returning to normal by November.

Based on 15 mo of pre-hurricane monitoring and 12 mo of post-hurricane monitoring, the occurrence, density, and biomass of *S. filiforme* in the Loxahatchee River Estuary declined significantly following September 2004. The SB site showed an immediate and drastic reduction in the occurrence of *S. filiforme* (Fig. 3), while the NB site showed a smaller immediate loss and a prolonged gradual reduction in the occurrence of *S. filiforme* over the following 12 mo. Throughout the 12 mo of post-hurricane monitoring, *S. filiforme* did not show any appreciable recovery in occurrence at either sampling site; during this same period the occurrence of *Halophila johnsonii*, Johnson's seagrass, increased from $< 10\%$ (immediately following the hurricanes) to $> 60\%$ (12 mo post-hurricanes) at both sampling sites.

S. filiforme shoot density declined immediately following the September 2004 hurricanes. Pre-hurricane monitoring revealed a substantial amount of temporal (i.e., seasonal) and spatial variability in shoot density prior to the hurricanes. Immediately after and throughout the 12 mo post-hurricane monitoring period shoot densities remained a small fraction of the pre-disturbance levels (Fig. 3).

In the 15 mo prior to the September 2004 hurricanes, *S. filiforme* biomass showed obvious seasonal periodicity (especially at the NB site) with peaks occurring during the summertime quarterly samples (August). Following the 2004 hurricanes, we did not observe a seasonal peak in living *S. filiforme* biomass accumulation (Fig. 3). The substantial decline of total (aboveground + belowground) *S. filiforme* biomass following September 2004 was largely a result of and paralleled the observed declines of *S. filiforme* occurrence and shoot density.

Discussion

The occurrence, density, and biomass of *S. filiforme* declined substantially following the September 2004 hurricanes. Variability in species composition and spatial extent of seagrass communities in the Loxahatchee River Estuary has been observed and documented by local agencies since the 1980s. The present study shows the effect of the September 2004 hurricanes on *S. filiforme* based upon 15 mo of pre-hurricane and 12 mo of post-hurricane data.

The hurricanes of 2004 resulted in hurricane force winds and elevated freshwater discharges, both of which appear to have affected *S. filiforme*. Seagrass occurrence and density was reduced immediately following the hurricanes (Fig. 3a, note especially the SB site). Similar to findings of Fourqurean and Rutten (2004), our observations suggest mechanical thinning due to hurricane force winds was responsible for some of the immediate loss of *S. filiforme* leaves. Mechanical thinning alone can not explain all of the *S. filiforme* declines we observed. *S. filiforme* at the NB site showed a gradual reduction in occurrence over the 12 mo following the storms. We did not observe any meaningful burial or erosion of seagrasses during post-hurricane monitoring, as observed in offshore seagrass patches in the Florida Keys following a hurricane (Fourqurean and Rutten 2004).

We suggest extremely low minimum daily salinity values and high daily salinity fluctuations in the estuary likely resulted in the observed decline of *S. filiforme* in the Loxahatchee River Estuary. Based on a 25-yr period of record, mean monthly rainfall within the Loxahatchee watershed during September was 230 mm, while mean monthly freshwater discharges into the estuary from the Northwest and Southwest Forks averaged 10.9 $m^3 s^{-1}$ during the same 25-yr period. The September 2004 hurricanes yielded approximately 610 mm of rainfall in the Loxahatchee watershed, which resulted in freshwater discharges into the estuary that peaked at over 113.3 $m^3 s^{-1}$ and averaged 36.8 $m^3 s^{-1}$ for the month (see Fig. 1). We suggest these discharges and the resultant effects on the salinity regime were the dominant proximal cause of the significant declines in the occurrence, density, and biomass of *S. filiforme*.

Previous research has shown that *S. filiforme* thrives in salinities between 22–35‰ (Phillips 1960), but is generally not found at sites with salinity < 17‰ (Zimmerman and Livingston 1976), though salinities of 10‰ may be tolerated for short periods (Phillips 1960). Unfortunately, Phillips (1960) did not define short periods, but subsequent microcosm-based experiments have shown *S. filiforme* to be stressed after 14 d at 10‰ (Lirman and Cropper 2003). Seagrasses, in particular *S. filiforme*, are susceptible to excessive salinity fluctuations (Montague and Ley 1993; Provancha and Scheidt 2000; Lirman and Cropper 2003). Montague and Ley (1993) found seagrass biomass was not significantly related to mean salinity, but they showed seagrass biomass was significantly and negatively affected by salinity variability, measured as standard deviation of bottom salinity. They also suggested that seagrasses may be most harmed when measured salinity drops below 10‰ (i.e., minimum salinity < 10‰), and that seagrasses should be completely absent when the standard deviation of salinity exceeds 15‰. In the Loxahatchee River Estuary in situ salinity measurements taken every 15 min at the NB seagrass site (at seagrass canopy height) revealed that standard deviation of daily salinity is strongly and negatively correlated with observed minimum daily salinity ($n = 492$ d, standard deviation of daily salinity $= -0.274\times$(minimum daily salinity) $+ 9.998$; $r^2 = 0.94$; $p < 0.001$). Salinity variability increased as minimum daily salinities decreased; both of which are known to be harmful to *S. filiforme*. Freshwater discharges resulting from the September 2004 hurricanes lowered minimum daily salinity values to 2‰ (Fig. 1), and at the exact same time (28 September 2004) increased standard deviation of daily salinity values to 11‰—a worst case scenario for seagrasses according to Montague and Ley (1993). While hurricane related discharges severely depressed water column salinity values throughout the estuary during the ebb tide, the close proximity of the NB and SB seagrass sites to the mouth of the estuary permitted salinity values to rebound significantly during the flood tide. We advise the use of minimum daily salinity values when assessing seagrass habitat suitability or the effects of water management practices, because minimum daily values appear to be more meaningful and conservative than mean daily salinity values in well-flushed estuaries.

While the hurricanes had a measurable effect on light attenuation, chlorophyll *a*, turbidity, and water color, it appears that the magnitude and duration of these effects may not have been sufficient to cause the observed declines in seagrasses. Freshwater discharges resulting from the hurricanes altered light attenuation and related aspects of water quality known to constrain seagrass survival and productivity, though these effects appear to have been short lived (Fig. 2). Post-hurricane PAR measurements indicate the percent of light passing through the water column to seagrasses was intermittently below 19.2%, i.e., the minimum light requirement for *S. filiforme* (Dennison et al. 1993), until mid November, at which point light attenuation appears to have returned to normal (minimum values > 24%). While these values are lower than the minimum requirements for *S. filiforme*, light attenuation is known to be both temporally and spatially variable in estuaries (Dennison et al. 1993), and it appears that observed increases in light attenuation was not of sufficient magnitude or duration to cause the observed declines in seagrasses (Czerny and Dunton 1995; Longstaff and Dennison 1999; Beal and Schmit 2000). Field based observations in the Loxahatchee River Estuary did not show any correlation between the spatial pattern of *S. filiforme* loss and transect depth contours, which would be expected if light attenuation was the primary cause of seagrass loss. Because *S. filiforme* and *Halodule wrightii* have similar minimum light requirements (Dennison et al. 1993; Beal and Schmit 2000; Carlson et al. 2003), we would have expected *H. wrightii* to decline similarly to *S. filiforme* if light attenuation was the proximal cause of the *S. filiforme* decline. *H. wrightii* showed a minimal decline at both the NB and SB sampling sites immediately following the hurricanes and rebounded to pre-hurricane occurrence values within 2 mo following the hurricanes. *H. wrightii* maintained its pre-hurricane occurrence values throughout the 12 mo post-hurricane monitoring period (Loxahatchee River District unpublished data). We conclude that increased light attenuation did not drive the observed losses of *S. filiforme* in the Loxahatchee River Estuary following the 2004 hurricanes.

We remain uncertain as to the cause of the extended decline in the percent occurrence of *S. filiforme* at the NB site. It is possible that the gradual reduction in the occurrence of *S. filiforme* at the NB site over the 12 mo following the hurricanes was caused by the primary stressor (i.e., lowered minimum salinity and high salinity fluctuation). It appears more plausible that the long-term decline resulted from a secondary stressor such as sulfide toxicity or disease acting on stressed *S. filiforme* (sensu Carlson et al. 1994).

The reduction of *S. filiforme* occurrence, density, and biomass immediately after the hurricanes does not appear unusual (Provancha and Scheidt 2000; Fourqurean and Rutten 2004), but more research is needed to determine the precise mechanisms leading to the observed declines in *S. filiforme*. Mechanical stress (i.e., thinning) is most pronounced in open ocean environments with high wave energy (Fourqurean and Rutten 2004), while altered salinity regimes, in the form of extremely low minimum daily salinity values and high daily salinity fluctuations, may be most deleterious in well-flushed estuaries (present study). We advise the use of minimum daily salinity values when assessing seagrass habitat suitability or when modeling the effects of alternative water management scenarios in well-flushed estuaries such as the Loxahatchee River Estuary.

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