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Hypersalinity During Regional Drought Drives Mass Mortality of the Seagrass *Syringodium filiforme* in a Subtropical Lagoon

Sara S. Wilson[1,2] · Kenneth H. Dunton[1]

Abstract Seagrasses are sensitive to local environmental conditions such as salinity, the underwater light environment, and nutrient availability. To characterize seagrass coverage and condition, as well as to relate changes in community structure to local environmental and hydrologic conditions, we monitored seagrass communities in the Upper Laguna Madre (ULM), Texas annually from 2011 to 2015. In 2011 and 2012, the lagoon was dominated primarily by *Halodule wrightii*, with mixed meadows of *H. wrightii* and *Syringodium filiforme* located in the northwest of our study area. By 2013, the expansive *S. filiforme* meadows had disappeared and the species was restricted to the northernmost reaches of the lagoon. The *S. filiforme* mortality occurred following an extended period of extremely high salinity (salinities 50–70) during a regional drought. Continuous measurements of underwater photosynthetically active radiation and stable carbon isotopic signatures of seagrass blade tissues did not suggest light limitation, and *H. wrightii* N/P molar ratios near 30:1 were not indicative of nutrient limitation. Based on the absence of strong evidence for light or nutrient limitation, along with the known tolerance of *H. wrightii* for higher salinities, we conclude that hypersalinity driven by regional drought was likely the major driver behind the observed *S. filiforme* mortality. With a substantial portion of the global seagrass distribution threatened by drought in the next 50 years, the increased frequency of hypersaline conditions is likely to exacerbate stress in seagrass systems already vulnerable to the effects of rising water temperatures, eutrophication, and sea level rise.

Keywords Seagrass · *Syringodium* · Hypersalinity · Laguna Madre · Monitoring

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Introduction

Seagrass community structure is strongly regulated by a variety of environmental conditions. Changes in abiotic factors such as temperature, light, nutrients, and salinity can cause decreases in seagrass cover and productivity (e.g., Burkholder et al. 2007; Collier and Waycott 2014) and negatively impact the provision of ecosystem services (Cullen-Unsworth and Unsworth 2013), biogeochemical cycling (Marbà et al. 2007; Fourqurean et al. 2012), and ultimately bottom-up effects on marine food webs (Heck et al. 2008). Seagrass mortality has frequently been attributed to anthropogenic impacts related to water quality, such as increased turbidity from dredging (Onuf 1994), eutrophication (Burkholder et al. 2007), and mechanical damage (e.g., "prop scars"; Martin et al. 2008).

Future climate projections show both decreased precipitation and increasingly frequent drought conditions in areas such as the Mediterranean Sea, the Gulf of Mexico, and southwest Australia (IPCC 2014), all regions that support expansive seagrass meadows (Green and Short 2003). An increase in drought frequency and intensity can potentially alter salinity regimes in estuarine bays and coastal waters, which would negatively impact resident seagrass communities (Short and Neckles 1999). Drought conditions arise during extended periods of decreased precipitation when freshwater inflow to

estuaries slows or ceases completely, which can result in hypersaline (salinity > 35) conditions in estuarine systems that have restricted exchange to the coastal ocean (Montagna et al. 2013; Palmer and Montagna 2015).

Exposure to salinities beyond an optimal range (typically 30–40) is problematic for seagrasses because key metabolic processes such as photosynthesis, the production of new leaves, and nutrient uptake can be compromised (Short and Neckles 1999; Touchette 2007). Additionally, warm hypersaline water does not contain as much dissolved oxygen as normal seawater, which can lead to elevated levels of toxic hydrogen sulfides in seagrass soils as biological oxygen demands increase (Borum et al. 2005; Koch et al. 2007b). Multiple water quality stressors in a system already strained by hypersaline conditions are therefore potentially fatal for seagrasses. In fact, the combination of elevated temperature, low freshwater inflow, and hypersalinity are hypothesized to have been the cause of a major seagrass die-off in Florida Bay, USA (Zieman et al. 1999; Borum et al. 2005; Koch et al. 2007c).

One area predicted to experience increasingly frequent drought conditions is south Texas, which was recently faced with its most extreme drought on record in over a century (Cayan et al. 2010; Hernandez and Uddameri 2014; Romero-Lankao et al. 2014). This region includes the frequently hypersaline waters of the Laguna Madre, an expansive linked-lagoon system sheltered by barrier islands, which supports over 68,000 ha (~ 170,000 acres) of seagrass meadows (Dunton et al. 2011). Starting in 2012, we observed a massive die-off of the seagrass *Syringodium filiforme* in the Upper Laguna Madre (ULM). The event occurred amidst stable meadows of *Halodule wrightii* during an extended period of hypersalinity (salinities 50–70).

The major objective of this study was to examine the potential drivers of the *S. filiforme* decline in ULM in an attempt to explain how changing environmental conditions alter seagrass community structure. We examined continuous salinity and underwater light level records from a nearby permanent monitoring station (see Dunton 1994), along with indices of seagrass cover to examine whether local hydrology was a driver of *S. filiforme* declines. We also examined seagrass tissue elemental composition (C/N/P ratios) to assess nutrient availability. Variations from the "seagrass Redfield ratio" of 550:30:1 (Atkinson and Smith 1983; Duarte 1990) are often used to infer nutrient availability, which was investigated along with stable carbon isotopic ratios ($\delta^{13}C$) to examine possible light limitation (Grice et al. 1996; Hemminga and Mateo 1996; Hu et al. 2012). Overall, this study demonstrates the efficacy of coupling a seagrass monitoring program with environmental datasets to assess estuarine ecosystem structure and investigate the potential drivers behind observed community changes.

Methods

Site Description

The Texas coast is characterized by a network of semi-enclosed estuarine bays located behind barrier islands that run parallel to the shore. We monitored seagrasses along the entire Texas coast from 2011 to 2015 (data available at www.texasseagrass.org), including the ULM system (Fig. 1). The northern portion of ULM lies adjacent to Corpus Christi Bay, with Packery Channel as the nearest open connection to the Gulf of Mexico. Expansive agricultural and ranch lands are located west of the lagoon, characterized by flat terrain. Freshwater inflows to ULM from the west (through tributaries draining into Baffin Bay) are low because minimal precipitation rates are exceeded by high evaporation rates (Tunnell and Judd 2002; Schoenbaechler and Guthrie 2011). To the east of ULM is Padre Island and undeveloped Padre Island National Seashore. To the south, the Gulf Intracoastal Waterway (ICW) cuts through a large expanse of wind-tidal flats which separate the Laguna Madre into two parts (Upper and Lower). ULM is characterized by relatively clear water and shallow depths (~ 1 m with the exception of the ICW), and waters in the lagoon are primarily wind-mixed (Tunnell and Judd 2002; Solis and Powell 1999). Historically, limited freshwater inflows coupled with long water residence times (up to 350 days) and high evaporation rates created extremely high salinities throughout the lagoon (Solis and Powell 1999). However, construction of the ICW in 1949 and Packery Channel in 2006 has increased water mixing in ULM and helped to moderate salinities in recent years (Tunnell and Judd 2002; Onuf 2007). ULM supports vast meadows of *H. wrightii*, and mixed meadows of *H. wrightii* and *S. filiforme* were first observed in the northern part of the lagoon in 1988, which Quammen and Onuf (1993) predicted may have been the beginning of a *S. filiforme* "invasion" into ULM. Previous work in Lower Laguna Madre has shown expansive *H. wrightii* meadows outcompeted and subsequently replaced by *S. filiforme* and then by *Thalassia testudinum* (McMahan 1968; Merkord 1978; Quammen and Onuf 1993).

Monitoring Design

Our monitoring followed a restricted random sampling design to ensure even coverage across the study region while still maintaining random station selection (Dunton et al. 2011; Neckles et al. 2012). To generate the sampling stations, maps from the National Oceanic and Atmospheric Administration's 2004/2007 Benthic Habitat Mapping program (http://coast.noaa.gov/digitalcoast/data/benthiccover/) were used to create a shapefile delineating seagrass extent along the Texas coast. Grids of tessellated hexagons (each side 750 m for a total area of ~ 1.46 km^2) were overlaid onto the shapefile, with hexagon

Fig. 1 The Upper Laguna Madre, Texas. Inset shows locations of randomly assigned permanent monitoring stations within the grid of tessellated hexagons
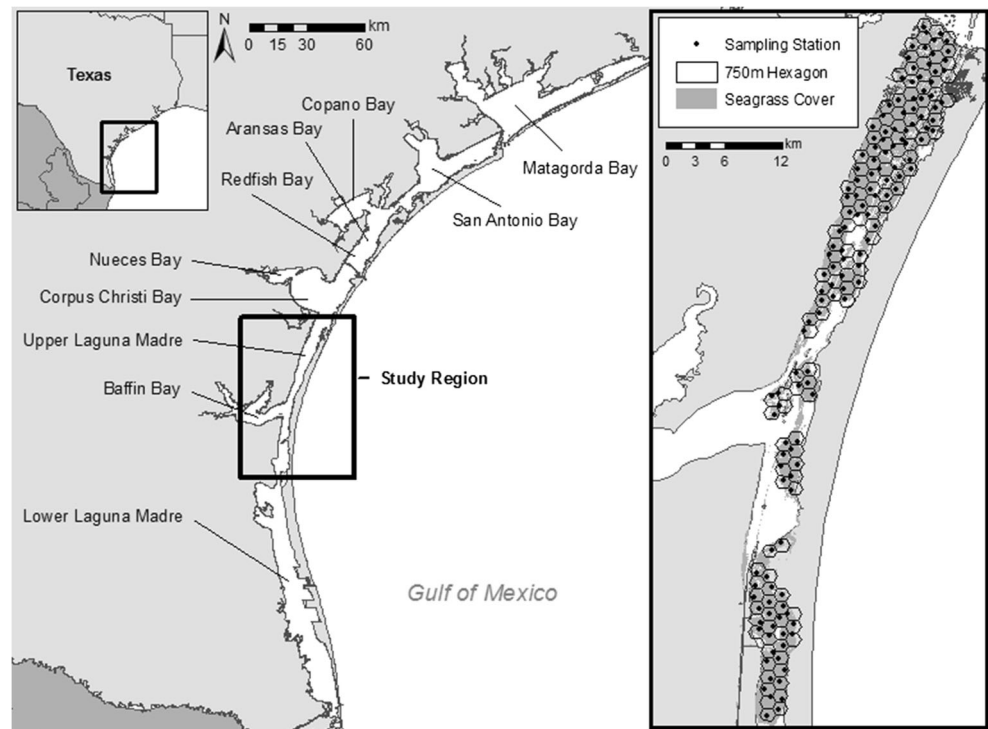
side length chosen to adequately represent the study area. One sampling station was assigned within each hexagon that contained > 50% seagrass cover according to the benthic habitat shapefile. A random number generator was used to assign latitude and longitude coordinates of the station within each hexagon (Fig. 1, inset). This design resulted in a total of 144 sampling stations in ULM.

Sampling Methods

From 2011 to 2015, annual sampling was conducted from late summer to early fall during the time of peak seagrass biomass, beginning at the northernmost stations and working south. Sampling efforts employed two to four personnel and occurred in July or August, typically spanning 3–5 days each year. Sampling was conducted by airboat, which minimized travel time between sites and allowed access to areas of the lagoon that would have been difficult to reach with an outboard motor due to shallow water depths. Generally, sampling took place on days with little cloud cover and winds below 25 km h^{-1}.

Following the methods of Neckles et al. (2012), each sampling station was defined as a circle 10 m in diameter around the assigned coordinates to account for the length of the boat and limitations in GPS accuracy. At each station, water quality and clarity measurements (data available at http://www.texasseagrass.org) were made before entering the water to minimize sediment re-suspension. Visual assessments of seagrass percent cover were made underwater at four ordinal points around the vessel using a 0.25-m^2 PVC quadrat frame

subdivided into 100 cells with monofilament line based on methods from Neckles et al. (2012). Percent cover measurements were always made by an experienced field technician to ensure accuracy. If *H. wrightii* (the most common species in our study area) was present at the station, a small tissue sample (consisting of shoots from multiple plants) was collected randomly by hand and stored on ice for transport back to the laboratory for tissue elemental analyses.

Long-Term Hydrologic Measurements

Continuous measurements of underwater conductivity and temperature were recorded at our permanent monitoring station LM-151 (27.35° N, 97.37° W; see Dunton 1994) using a HOBO U24-002-C conductivity logger (Onset, Bourne, MA). Conductivity was converted to salinity and calibrated with biweekly in situ measurements from a YSI 6920 datasonde (YSI, Yellow Springs, OH) using HOBOware's Conductivity Assistant software. To bolster our dataset, we also obtained continuous salinity data from two National Park Service monitoring stations in the ULM—Bird Island (27.86730°, −97.63364°) and Baffin Bay (27.29702°, −97.40491°)—collected with a YSI 6600 datasonde. Prior to data analyses, we averaged hourly salinity readings into daily values. Continuous measurements of underwater irradiance from the LM-151 station were measured by a subsurface light meter using methods from Dunton (1994) and transformed into total daily quantum flux (mol photons m^{-2} day^{-1}) for this analysis.

H. wrightii tissue samples from 2011 were processed from every station, and a random subset (approximately half) of the

tissue samples from 2012 to 2013 was processed to address time and cost constraints. Dried samples were weighed into tin capsules and analyzed for C and N content and isotopic composition on a Finnigan MAT Delta Plus continuous flow isotope ratio mass spectrometer coupled to a Carlo Erba 1500 elemental analyzer at the University of Texas Marine Science Institute. Isotope values are expressed in delta (δ) notation:

$$\delta^{13}C\ (\text{‰}) = \left[\left(R_{sample}\big/R_{standard}\right)-1\right] \times 1000 \tag{1}$$

where R is $^{13}C/^{12}C$ and the standard reference is Vienna Pee Dee Belemnite. Based on internal standards, which were run every 12th sample, instrumental analytical error was ± 0.2‰. Seagrass leaf P was analyzed with a Shimadzu UV-2401 Recording Spectrophotometer using modified methods from Chapman and Pratt (1961).

Spatial and Statistical Analyses

Seagrass cover changes through time were analyzed with a Friedman rank sum test and pairwise Wilcoxon multiple comparisons with a Bonferroni correction because the distributions of cover data were strongly bimodal (many instances of 0 and 100%) and did not meet the assumptions of normality required for parametric statistics. We also assessed continuous underwater light availability using a Friedman test followed by pairwise Wilcoxon tests with a Bonferroni correction. Since there was no significant difference between years for salinity collected at NPS stations and LM-151, we averaged the three continuous records and analyzed changes through time with a Kruskal-Wallis test followed by Wilcoxon multiple comparisons with a Bonferroni correction. All statistical procedures were done in R 3.3.2 (R Core Team) and results considered significant at $\alpha = 0.05$.

We used inverse-distance weighting interpolation to generate a continuous surface of seagrass cover, with predicted values for unsampled points based off the values of nearby sampled points, weighted by distance (Shepard 1968). We used 12 sampling stations identified from a variable search radius to generate a predicted value at each unknown point (100 m^2). Creating a map that shows both seagrass distribution and cover changes for the entire sampling area provides critical information for future monitoring and management efforts. All spatial analyses were performed in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA).

Results

The seagrass community in ULM is generally dominated by *H. wrightii*, with mixed meadows of *H. wrightii* and *S. filiforme* observed in 2011 and 2012 in the northwest part of our study area. By 2013, the *S. filiforme* had been almost

completely replaced by *H. wrightii*, which drove the significant changes observed across years in both *H. wrightii* and *S. filiforme* cover (Friedman $p < 0.0001$ for both; Fig. 2). *H. wrightii* cover from 2012 to 2013 was significantly greater than all other years (Friedman $p < 0.0001$ for both; Fig. 3). *S. filiforme* cover decreased significantly from 14.4 ± 2.4% (mean ± SE) in 2012 to 0.4 ± 0.1% in 2013 (Wilcoxon $p < 0.0001$), increased slightly to 1.7 ± 0.7% in 2014, and then increased significantly to 3.7 ± 1.0% in 2015 (Wilcoxon $p < 0.05$).

There were significant differences in ULM salinity from 2008 to 2015 (Kruskal-Wallis $p < 0.0001$). Annual salinities were significantly different from each other in all years, except 2011 where salinities were not different from 2008 or 2014 (Fig. 4). A distinct trend of increasing salinities was observed over a 4-year period, from a low of 31.4 ± 0.4 in 2010, to a peak of 50.0 ± 0.2 in 2013 (Fig. 4). Generally, salinities were above that of average seawater (~ 35), indicative of a hypersaline system. As expected, average monthly measurements were more variable (Fig. 5) but still showed a strong pattern of increasing salinity over the period from 2010 to 2014. There was an extended period of low (< 30) salinity from August 2010 to March 2011 and a long period of high (~ 50+) salinity from September 2012 to October 2013. Additionally, ULM experienced hypersaline (salinities > 35) conditions for 1023 days in a row (April 19, 2011 through February 05, 2015) during our study.
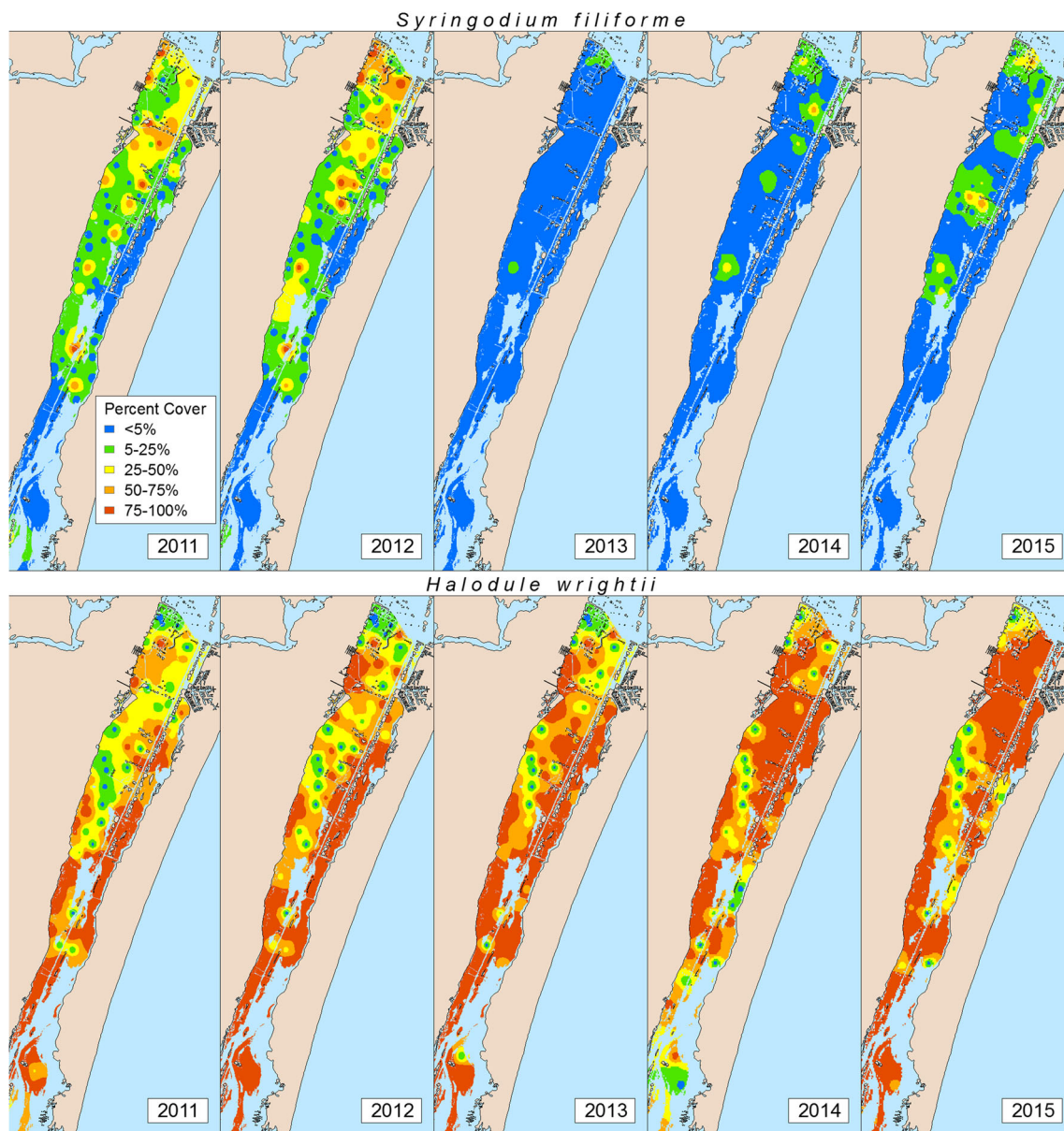
Underwater light significantly varied through time (Friedman $p < 0.0001$). Generally, 2009–2012 had significantly higher daily PAR values (14.3 ± 0.6, 11.9 ± 0.5, 16.1 ± 0.5, 10.3 ± 0.4 mol photons m^{-2} day^{-1}, respectively) than 2013–2015 (7.8 ± 0.3, 7.7 ± 0.3, 7.1 ± 0.3 mol photons m^{-2} day^{-1}, respectively; Fig. 6).

There were significant changes in *H. wrightii* C/N, C/P, and N/P molar ratios from 2011 to 2013 (Kruskal-Wallis $p < 0.0001$ for all). C/N was significantly higher in 2012 (22.5 ± 0.4) and 2013 (22.1 ± 0.3) compared to 2011 (20.5 ± 0.3; Table 1). C/P was significantly lower in 2012 (755.8 ± 25.6) and 2013 (728.5 ± 20.4) than in 2011 (893.1 ± 20.6), as was N/P (2011 43.6 ± 0.9; 2012 33.7 ± 1.1; 2013 33.2 ± 1.0). There were also significant changes in *H. wrightii* $\delta^{13}C$ from 2011 to 2013 (Kruskal-Wallis $p = 0.0001$). *H. wrightii* $\delta^{13}C$ increased significantly from 2011 (− 11.3 ± 0.1‰) to 2012 (− 10.4 ± 0.2‰), then decreased significantly in 2013 (− 11.2 ± 0.2‰; Table 1).

Discussion

Environmental Drivers of *Syringodium* Decline

We observed a dramatic decline in ULM *S. filiforme* populations during our monitoring in 2013, with the decline

S y r i n g o d i u m   f i l i f o r m e

Percent Cover
- <5%
- 5-25%
- 25-50%
- 50-75%
- 75-100%

2011   2012   2013   2014   2015

H a l o d u l e   w r i g h t i i

2011   2012   2013   2014   2015

Fig. 2 Changes in interpolated percent cover of *S. filiforme* and *H. wrightii* in Upper Laguna Madre from 2011 to 2015

persisting through 2014 and 2015. *H. wrightii* populations in the same area remained stable during this time, even increasing in percent cover significantly during 2012 and 2013. This phenomenon presented the opportunity to examine the drivers behind *S. filiforme* mortality within an otherwise healthy seagrass meadow. Utilizing local environmental datasets (salinity and underwater light) was critical for our analysis, as we were able to examine temporal seagrass coverage and condition trends in the context of estuarine water quality.

It has been well established that *S. filiforme* cannot tolerate high salinities or salinity fluctuations as effectively as *H. wrightii*, although most of these studies were conducted during a short period of time and under highly controlled

conditions (McMillan and Moseley 1967; McMahan 1968; Lirman and Cropper 2003). Peak leaf elongation rates for *S. filiforme* occur at salinities of 25 (Lirman and Cropper 2003), and previous laboratory studies using *S. filiforme* harvested from Texas bays found that plant growth ceased after being exposed to salinities between 45 and 52.5 for less than 30 days (McMillan and Moseley 1967; McMahan 1968). Given these findings, our data suggests that the 13 months (September 2012 to October 2013) of extremely high salinities (> 50) in ULM were the major driver behind *S. filiforme* mortality which began by summer 2013. In contrast, *H. wrightii* populations, whose salinity tolerance is much higher than *S. filiforme* (McMillan and Moseley 1967; McMahan 1968; Lirman and Cropper 2003; Ferreira et al.

Fig. 3 Percent cover of
S. filiforme and *H. wrightii* in
Upper Laguna Madre from 2011
to 2015. Note the difference in *y*-
axes. Asterisks indicate
significant differences between
years from pairwise Wilcoxon
multiple comparison tests run for
each species
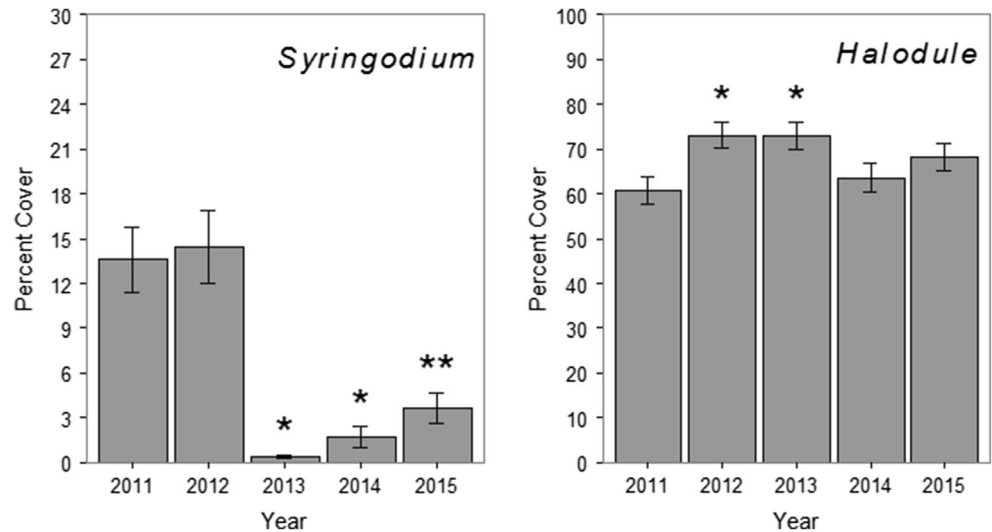
2017), survived this period and did not appear to experience
any adverse effects from the hypersaline conditions.

The effects of salinity stress on seagrasses have frequent-
ly been demonstrated in aquarium and mesocosm experi-
ments, where seagrasses subjected to salinity stress typical-
ly exhibit changes in osmolality, decreases in leaf growth
and shoot density, and higher mortality (Lirman and
Cropper 2003; Koch et al. 2007a; Ruíz et al. 2009;
Fernández-Torquemada and Sánchez-Lizaso 2011). Both
the rate and the duration of salinity changes to which
seagrasses are exposed can influence their condition or pro-
ductivity, and seagrasses are better able to respond to grad-
ual salinity changes rather than rapid "pulse" changes
(Koch et al. 2007b; Griffin and Durako 2012). It is therefore
not surprising that systems which experience frequent pe-
riods of hypersalinity, such as Florida Bay and the Laguna
Madre, nevertheless support expansive seagrass meadows
(Quammen and Onuf 1993; Lee et al. 2006). This study
provides a unique in situ example of how hypersaline

conditions have re-structured an expansive seagrass mead-
ow in a very short period of time.

There are two compelling pieces of evidence for why light
limitation has not likely played a role in the *S. filiforme* mor-
tality that we observed. First, underwater light levels during
this study were within normal ranges for ULM (Dunton 1994),
a system already documented to support healthy *S. filiforme*
populations (Onuf 2007; this study). Secondly, we observed
H. wrightii persistence in areas where *S. filiforme* mortality
occurred. Studies in Texas, Florida, and Bermuda have consis-
tently demonstrated that *H. wrightii* and *S. filiforme* have very
similar minimum light requirements for growth (Dunton 1994;
Onuf 1994; Kenworthy and Fonseca 1996; Manuel et al. 2013)
and light levels were sufficient for *H. wrightii* growth in the
same area. While a significant decrease in *H. wrightii* δ^{13}C
values from 2012 to 2013 may suggest lower light availability
in 2013 after the *S. filiforme* mortality, these data must be
interpreted with caution as seagrass δ^{13}C values can change
based upon their light environment in as little as 30 days (e.g.,

Fig. 4 Salinity in Upper Laguna
Madre averaged from hourly
measurements at LM-151 and
National Park Service stations
from 2008 to 2015. Letters indi-
cate significant differences be-
tween years ($\alpha = 0.05$) from
Wilcoxon multiple comparison
tests
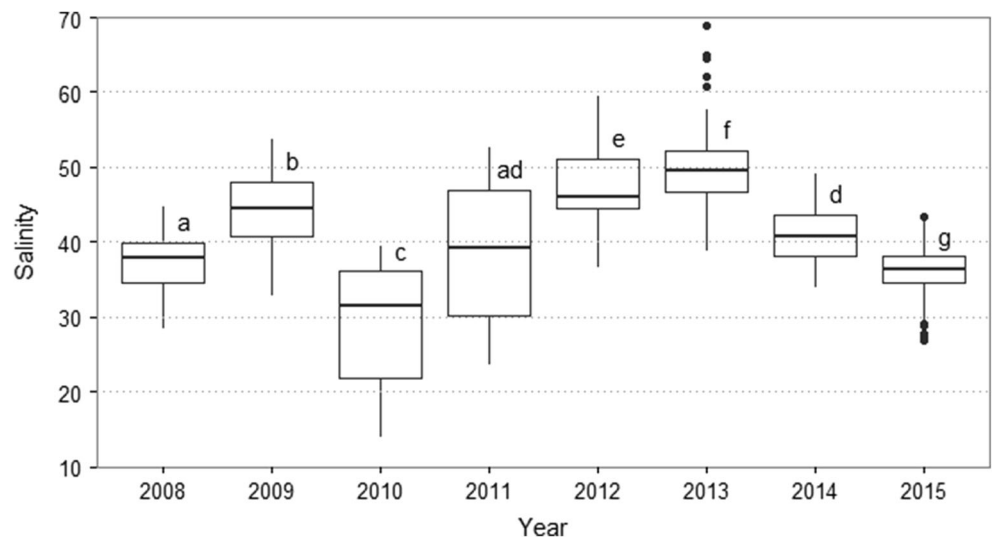
Fig. 5 Monthly measurements of Upper Laguna Madre salinity from National Park Service Baffin and Bird stations and our LM-151 station from June 2008 to February 2016 (boxplots), superimposed over *S. filiforme* cover during our monitoring (gray bars). The dashed line indicates average salinity of seawater (35). Note low salinities (< 20) in late summer 2010 from Hurricane Alex and note extended periods of very high (> 50) salinity from January to July 2013 at all stations
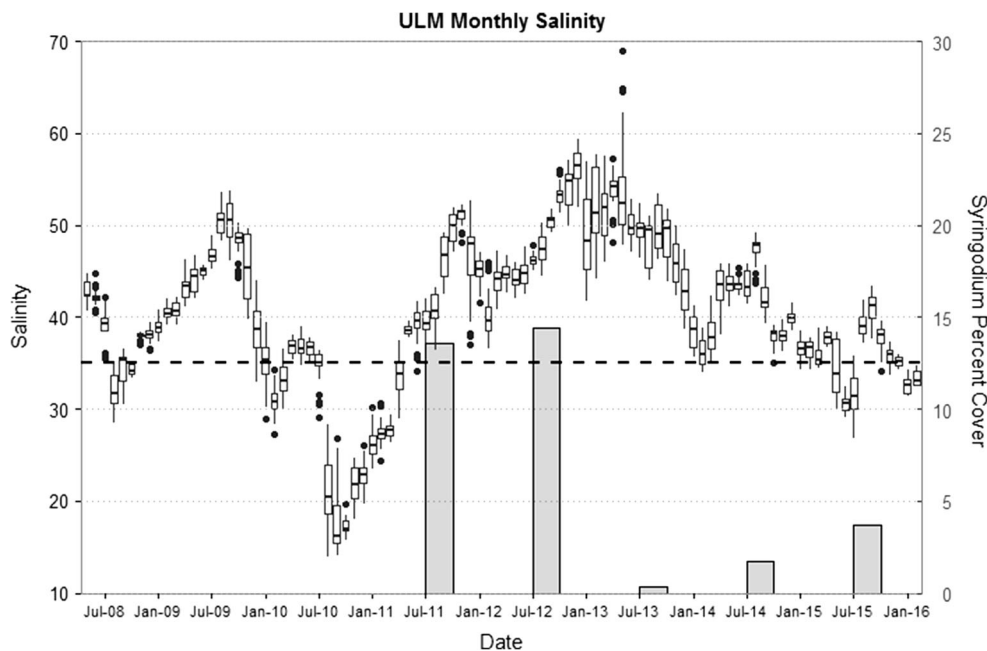

Grice et al. 1996). Instead, it is more likely that our carbon isotopic measurements are responding to greater self-shading as *H. wrightii* coverage increased from 2012 to 2013.

Although we did not analyze *S. filiforme* tissue, the elemental stoichiometry of *H. wrightii* provides some insight to nutrient availability in ULM during our study. Molar N/P ratios of seagrasses under N or P limitation will deviate from ∼ 30:1 in a manner proportional to the degree of nutrient limitation the plant experiences (Atkinson and Smith 1983; Duarte 1990; Fourqurean and Zieman 2002). While N/P ratios of 43.6:1 in 2011 may indicate some P limitation, we did not detect nutrient limitation for *H. wrightii* during the period of *S. filiforme* decline in 2012 and 2013. In fact, N/P ratios near 30:1 in 2012 and 2013 indicate adequate nutrient availability, at least for *H. wrightii* harvested in summer. While *H. wrightii* and *S. filiforme* have slightly different optimal C/N/P ratios

given their morphological and physiological differences (e.g., Atkinson and Smith 1983; Campbell and Fourqurean 2009), it is unlikely that *S. filiforme* is responding to nutrient limitation through extensive and widespread mortality in the presence of healthy populations of *H. wrightii*. Additionally, our nutrient data did not provide evidence of eutrophication, as chlorophyll *a* and light attenuation coefficient (k_d) values were relatively low and within normal ranges for this system (data available at www.texasseagrass.org).

A potential cause of seagrass decline not addressed in our study was sulfide toxicity. Warm and hypersaline waters can increase biological oxygen demands while also holding less dissolved oxygen, thereby increasing toxic porewater sulfide concentrations via elevated sediment sulfate reduction rates (Koch and Erskine 2001; Borum et al. 2005). The combination of high temperature, hypersalinity, and elevated

Fig. 6 Average daily quantum flux of photosynthetically active radiation (PAR) from 2008 to 2015 from the LM-151 station. Letters indicate significant differences between years ($\alpha = 0.05$) from pairwise Wilcoxon multiple comparison tests. The dashed line indicates average daily PAR at this station from 1989 to 1992 as reported in Dunton (1994)
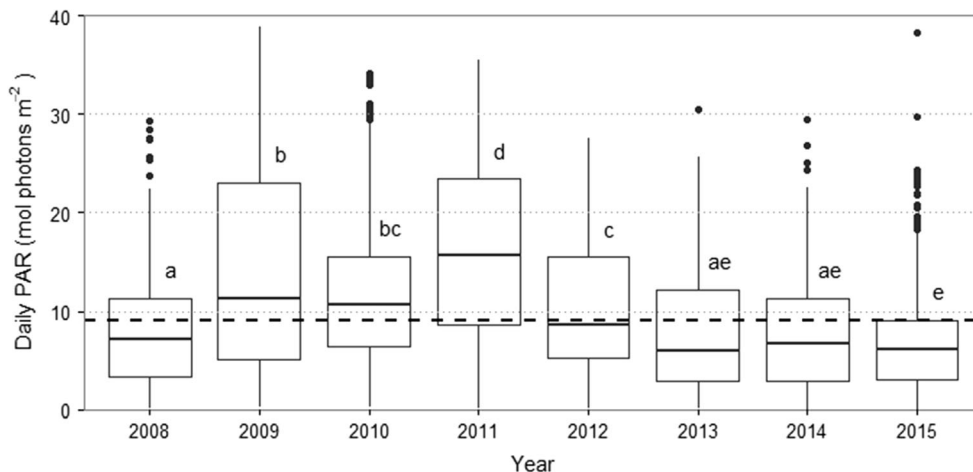
Table 1 Molar C/N, C/P, and N/P and δ¹³C (‰) values for *H. wrightii* in ULM from 2011 to 2013

Year	C/N	C/P	N/P	$\delta^{13}C$
2011	20.5 ± 0.3	893.1 ± 20.6	43.6 ± 0.9	− 11.3 ± 0.1
2012	22.5 ± 0.4*	755.8 ± 25.6*	33.7 ± 1.1*	− 10.4 ± 0.2*
2013	22.1 ± 0.3*	728.5 ± 20.4*	33.2 ± 1.0*	− 11.2 ± 0.2

Values reported as means ± SE

*Significant differences for each parameter across years from Wilcoxon multiple comparison tests

porewater sulfide levels has been experimentally shown to trigger *T. testudinum* die-offs (Koch and Erskine 2001), and this same trifecta of stressors has been hypothesized as a major driver behind the extensive seagrass die-offs in Florida Bay that began in 1987 (Zieman et al. 1999; Borum et al. 2005; Koch et al. 2007c).

Did sulfide toxicity play a role in the decline of *S. filiforme*? Cambridge et al. (2012) found that susceptibility to sulfide stress varied between several seagrass species, though these differences were not attributed to differences in plant size. Instead, they noted that for species like *S. isoetifolium*, which has relatively large lacunae in the aerenchyma tissue, morphology may control the degree of gas transport and thus a species' relative susceptibility to sulfide toxicity (Cambridge et al. 2012). Similarly, Holmer et al. (2009) found that *S. filiforme* was less susceptible to sulfide intrusion than *T. testudinum* and suggested that its ability to maintain high internal oxygen concentrations may make it a successful pioneer species in areas with high sulfide concentrations. While some studies suggest that *Syringodium* is more tolerant to sulfide intrusion than other seagrasses, we cannot present direct evidence to either support or refute whether sulfide toxicity contributed to observed *S. filiforme* declines in ULM.

Ecological Consequences of *Syringodium* Decline

The *S. filiforme* population crash in 2013 is especially interesting in a historical context, as Laguna Madre has traditionally supported monospecific *H. wrightii* meadows and *S. filiforme* was not observed in ULM until 1988 (McMahan 1968; Merkord 1978; Quammen and Onuf 1993; Onuf 2007). *S. filiforme* is recognized as a later successional species than *H. wrightii* in nutrient limited environments (Fourqurean and Rutten 2003), and an assessment in 1998 suggested a slow takeover by *S. filiforme* in northern ULM, where meadows had substantially expanded over the previous decade since the prior assessment in 1988 (Quammen and Onuf 1993; Onuf 2007). However, in an estuary that experiences such dynamic salinity shifts as Laguna Madre, it is possible that *S. filiforme* may never establish a permanent population, so perhaps persistence of the historically dominant *H. wrightii* populations should be prioritized by resource managers. In fact, several studies conducted in Laguna Madre indicate that local fauna may prefer *H. wrightii* meadows over *S. filiforme* or *T. testudinum* meadows (McMahan 1970; Mitchell et al. 1994; Rooker and Holt 1997; Tolan et al. 1997). Significant increases in *H. wrightii* coverage documented in ULM may increase habitat quality of the Laguna Madre for many local species.

Since the 2013 die-off, *S. filiforme* re-expansion into northwest ULM will inevitably occur if salinities continue to decrease. Small patches of parent meadows in northwest ULM should contribute greatly to *S. filiforme* expansion, as this species is characterized by high rhizome lateral expansion rates (up to 1 m annually; Short et al. 1993; Gallegos et al. 1994). *S. filiforme* seed banks in Laguna Madre have been shown to germinate after up to 4 years of dormancy, so remnant seed banks could also facilitate re-colonization (McMillan 1981). Our monitoring data from 2014 and 2015
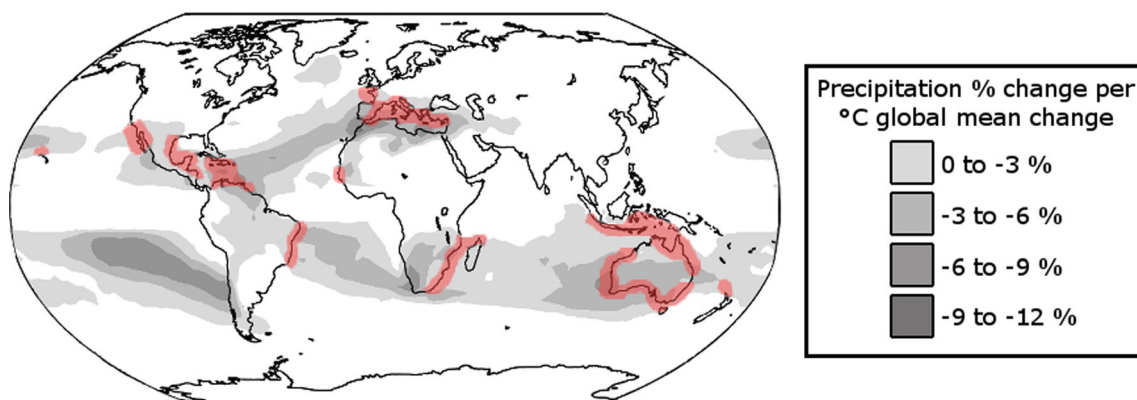
Fig. 7 Prediction of areas which will experience changes in seagrass community structure or persistence due to drought. Gray shading indicates areas predicted to experience decreased precipitation from 2081 to 2100 as compared to 1986–2005 (adapted from IPCC 2013).

Red shading indicates seagrass meadows present in areas where drought is expected to occur based on known global seagrass distribution (Green and Short 2003). Areas with red shading are exaggerated in extent for visibility at the global scale of the map

indicate that *S. filiforme* coverage has already expanded slightly since 2013. However, if regional drought persists and again drives salinities > 50 for an extended time period, *S. filiforme* populations may be knocked back again, compromising any advances in distribution and possibly indicating a "boom and bust" cycle for this species in ULM. The *Syringodium* mortality documented in this study occurred amidst a healthy *Halodule* meadow, but if the onset of drought conditions had been postponed and *Syringodium* had successfully outcompeted and displaced *Halodule* as was documented previously in the Lower Laguna Madre (Quammen and Onuf 1993; Onuf 2007), the impact of this die-off could have been much more severe.

Impacts of Drought on Seagrass Communities

We present evidence of *S. filiforme* mortality within stands of healthy *H. wrightii* attributed strictly to in situ hypersalinity driven by both regional drought and basin hydrology, and our study serves as one example for how drought conditions impact seagrass community structure. Drought, and more specifically hypersalinity, has recently been implicated as a factor contributing to seagrass loss in another shallow estuarine system as well. Large areas of *T. testudinum* mortality in Florida Bay, USA occurred in summer 2015 during sustained high salinities (50–60) and water temperatures (35–38 °C; Hall et al. 2016). In addition to producing hypersaline conditions, droughts have also been shown to impact seagrasses via lower rainfall and thus reductions in freshwater inputs to estuaries resulting in decreased nitrogen delivery, leading to seagrass loss (Hirst et al. 2016; Hirst and Jenkins 2017). Still other indirect (e.g., mutualism breakdown; deFouw et al. 2016) or unknown (Ball et al. 2014) impacts of drought conditions have been linked to seagrass loss around the world.

Despite the very recent work discussed above, drought as a major threat to seagrass communities in the future has been virtually overlooked at a global scale (except see Short and Neckles 1999). The past several decades have been marked by an accelerated worldwide decline of seagrasses (Short and Wyllie-Echeverria 1996; Orth et al. 2006; Waycott et al. 2009). Many areas that support extensive seagrass communities are also areas predicted to experience decreases in precipitation over the next century (Fig. 7), which could lead to more frequent or severe drought events. Not surprisingly, many of these areas including the Gulf of Mexico, the northern coast of Venezuela, the southwest coast of Africa, and both the southwest and southeast coasts of Australia are areas home to vulnerable or nearly threatened seagrass species (Short et al. 2011). As noted above, drought conditions can produce a variety of stressors for seagrasses at the landscape scale, few if any of which have straightforward or simple mitigation solutions. Ensuring adequate freshwater delivery to help alleviate abnormal hypersaline conditions, along with

maintaining open connections of barrier-island estuaries to the adjacent ocean are strategies that may help to moderate salinities during periods of drought to help prevent seagrass loss. Ultimately, drought and regional climate change in general will undoubtedly influence and shape coastal environments worldwide, especially those already vulnerable to stressors such as frequent hypersalinity, rising water temperatures, eutrophication, or sea level rise.

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