Gulf and Caribbean Research

Volume 34 | Issue 1

2023

Detecting Trends in Abundance and Distribution of Seagrasses in Lake Worth Lagoon, Palm Beach County, Florida

James R. Kerfoot Jr. Union University, jkerfoot@uu.edu

Samantha N. Jones Union University, samantha.jones@my.uu.edu

Michael H. Schiebout Union University, mschiebout@uu.edu

Beth Orlando Palm Beach County Environmental Resources Management, borlando@pbcgov.org

Follow this and additional works at: https://aquila.usm.edu/gcr

Part of the Terrestrial and Aquatic Ecology Commons

To access the supplemental data associated with this article, CLICK HERE.

Recommended Citation

Kerfoot, J. R. Jr., S. N. Jones, M. H. Schiebout and B. Orlando. 2023. Detecting Trends in Abundance and Distribution of Seagrasses in Lake Worth Lagoon, Palm Beach County, Florida. Gulf and Caribbean Research 34 (1): 43-59. Retrieved from https://aquila.usm.edu/gcr/vol34/iss1/7 DOI: https://doi.org/10.18785/gcr.3401.07

This Article is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in Gulf and Caribbean Research by an authorized editor of The Aquila Digital Community. For more information, please contact aquilastaff@usm.edu.

GULF AND CARIBBEAN



Volume 34 2023 ISSN: 2572-1410



Published by

THE UNIVERSITY OF SOUTHERN MISSISSIPPII.

GULF COAST RESEARCH LABORATORY

Ocean Springs, Mississippi

DETECTING TRENDS IN ABUNDANCE AND DISTRIBUTION OF SEAGRASSES IN LAKE WORTH LAGOON, PALM BEACH COUNTY, FLORIDA

James R. Kerfoot, Jr.1*, Samantha N. Jones1, Michael H. Schiebout1, and Beth Orlando2

¹Union University, Department of Biology, 1050 Union University Drive, Jackson, TN 38305;

²Palm Beach County Environmental Resources Management, 2300 North Jog Road – 4th Floor, West Palm Beach, FL 33411–2743; *Corresponding author, email: jkerfoot@uu.edu

ABSTRACT: Over the past 15 years, seagrass community stability has varied in estuaries throughout Florida. This study sought to model potential patterns of physiochemical parameters and community composition that may correlate with the fluctuation of seagrass populations in Lake Worth Lagoon (LWL), Palm Beach County, FL over time (2007-2019). Seven transects and 4 polygon areas throughout the LWL were established and stratified along a north-south gradient. Sites were sampled annually (May-August) for water quality, seagrass and macroalgal abundance, and community composition. Models developed to explain macrophyte abundance and composition were assessed using Akaike Information Criterion. Interaction between year and site best explained seagrass abundance and community composition in transect and polygon sites. Transect data revealed that seagrass and macroalgae declined after 2012 and continued until barely detected after 2016. This die off was not consistent for all transects and there was site variability in annual dissolved oxygen, nitrate, phosphate, and salinity levels. Polygon sites exhibited a shift in community composition after 2013, initially dominated by seagrass species *Syringodium filiforme* and *Halodule wrightii* before transitioning in 2012-2013 to *Halophila decipiens* and *Caulerpa* spp. Central lagoon sites transitioned to communities devoid of nearly all vegetative species. The loss of seagrass and the change in community composition could be explained by a transient dry period in 2012 and a subsequent inflow of freshwater. These events (sudden drought followed by an increase in freshwater) likely compounded the stress on the system between 2011-2014, leading to a drastic change in seagrass community.

KEY WORDS: Regional Variability; AIC; Community Composition; Halodule wrightii; Halophila decipiens

INTRODUCTION

Seagrass beds have been recognized as one of the most productive biological communities in the world and their presence is crucial for sustaining marine ecosystems (Zieman et al. 1989, Laboy–Nieves 2009). Seagrass beds are vital to estuarine health by providing food web structure, aiding in nutrient cycling, influencing water flow, and stabilizing sediment (Orth et al. 2006a, Short et al. 2011). Unfortunately, there has been a drastic worldwide decline in seagrasses for the past several decades, and most recently this decline has also been occurring in Florida (Durako 1994, Waycott et al. 2009, Unsworth et al. 2015). Congruent with this severe decline in seagrass meadows, especially in the Northern Hemisphere, marine environments have also experienced detrimental effects including increased ocean acidification, sediment erosion, and loss of marine species (Schlueter 1998, Hughes et al. 2009, Short et al. 2011, Hendriks et al. 2014). Initial conclusions suggest global warming (Waycott et al. 2009, Short et al. 2011), sedimentation (Longstaff and Dennison 1999, Erftemeijer and Lewis 2006), eutrophication (McGlathery 2001, Wall et al. 2013, Tiling and Proffitt 2017) and introduced species (Baldwin and Lovvorn 1994, Jun Bando 2006, Willette and Ambrose 2012) may be major drivers in this seagrass decline. Many studies have investigated what environmental factors and anthropogenic influences could be causing the depletion of seagrass meadows (see Carlson et al. 1994, Longstaff and Dennison 1999, Erftemeijer and Lewis 2006). For example, it was estimated that ~81% of seagrasses lost in Tampa Bay, FL were due to the combined impacts of increased turbidity and the physical removal and burial of seagrasses during dredging (Erftemeijer and Lewis 2006). Changing freshwater delivery compounded with elevating temperatures and a period of low tropical activity have been implicated in the declining seagrass beds of Florida Bay by increasing porewater sulfide concentrations through sediment mixing that caused chronic hypoxia of seagrass roots and rhizomes (Carlson et al. 1994, Durako 1994).

Spatial and temporal variability in seagrass community composition and productivity have been well documented in local and regional systems of Florida (Zieman 1975, Dawes et al. 1985, Fourqurean et al. 2001). Some seagrass bed communities seem to be thriving with stable population numbers while others seem to be declining and unstable (Orth et al. 2006a). Vital seagrass populations have been fluctuating in abundance along the east coast of Florida for over 2 decades and the processes (abiotic, biotic, or combinations of each) that govern declines and rebounds are not well understood (Fourqurean and Robblee 1999, Kemp 2000, Provancha and Scheidt 2000, Crigger et al. 2005).

Lake Worth Lagoon (LWL), an estuary in Palm Beach County, Florida, is comprised of several different kinds of habitats including non-vegetated mud and sand flats, seagrass, and fringing mangroves (Buzzeli et al. 2018). Crigger et al. (2005) present a conceptual ecological model and extensive series of working hypotheses designed to investigate the critical linkages between ecological stressors and attributes of LWL. The total area of seagrass communities has fluctuated from a high of 1,730 ha in 1940 to a low of 65 ha in a 1975 survey, eventually rebounding to 660 ha in 2001 (Crigger et al. 2005). Current reports indicate another decline in the seagrass communities of LWL (Orlando et al. 2016, Buzzeli et al. 2018). Buzzeli et al. (2018) documented variability in water quality parameters throughout the lagoon and laid the groundwork to explore the links between water quality parameters and seagrass communities in LWL. Abiotic (temperature, salinity, pH, turbidity, ammonia levels, etc.), biotic (community composition of seagrass and macroalgal species), and combinations of these factors can be important contributors to the fluctuation of seagrass communities in LWL. The goal of this study was to investigate a subset of that conceptual ecological model, focusing on the fluctuations of seagrass communities in established portions of LWL. This study aims to investigate the relationship of community composition and seagrass decline to water quality variables in LWL over a 13 y (2007-2019) period. Specifically, this study explores possible correlations that changing abiotic factors may have on the fluctuations observed in these communities.

MATERIALS AND METHODS

Lake Worth Lagoon, FL, is 32.2 km long between North Palm Beach and Ocean Ridge, extending west to east from Lake Okeechobee to the Atlantic Ocean and contains 2 inlets connecting to the Atlantic Ocean, Lake Worth (Palm Beach) Inlet and South Lake Worth (Boynton Beach) Inlet. The LWL watershed is about 181,299 ha, which considers all canals that flow into LWL (Florida Department of Environmental Protection 2016). The waters of the northern lagoon are the clearest, aided by tidal flows from the Lake Worth Inlet. Water quality declines through the lagoon's central and southern segments, which are characterized by limited flushing, with water residence times up to 13 d, compounded by ongoing contributions of nutrient–laden discharges from drainage canals carrying runoff from the expansive watershed (Palm Beach County 2021).

Two different methods were employed to collect seagrass and macroalgae abundance data. One method used 6 transects placed at different locations within the lagoon. The other method used randomly placed quadrats within 4 polygon areas throughout the lagoon. This community abundance data was collected by the Palm Beach County Department of Environmental Resources Management (PBC-ERM, FL). Water quality parameters were not collected directly from transect/polygon sites; however, each transect and polygon site was paired with PBC-ERM water quality stations closest to each over the same timeframe (Table 1, Figure 1). At each water quality station dissolved oxygen (mg/L), pH, salinity, nitrate (mg/L), phosphate (mg/L), ammonia (mg/L), temperature (°C), conductivity (µS/ cm), turbidity (NTU), secchi depth (m), and total suspended solids (mg/L) levels were measured using standard equipment. Due to the discontinuity of the recording of some of the parameters between transect and polygon sites, not all the water quality parameters were used for the separate transect and polygon analyses (i.e., ammonia, conductivity, turbidity, and total suspended solids; Table 2). For transect/polygon sites paired with 2 or more water quality stations, measurements were averaged and used in the analyses. For each dataset (transect and poly**TABLE 1.** Water quality stations in Lake Worth Lagoon, FL paired with transects and polygon sites used in the analyses. Figure 1 gives the exact locations of each transect, polygon site, and water quality station.

Transect	Water Quality Station
1	LWL1, LWL2
2	LWL13
4	LWL8
5	LWL13
6	LWL11
8	LWL10
9	LWL16, LWL17, LWL18
Polygon Sites	Water Quality Station
C17A	LWL4
C17B	LWL2
C51B	LWL10
C51C	LWL11

TABLE 2. Water quality parameters used (•) in analyses for transects and polygonal areas.

Water Quality Parameter	Transects	Polygon Sites
Ammonia	•	
Conductivity	•	
Dissolved Oxygen	•	•
pH	•	•
Salinity	•	•
Secchi Depth	•	•
Temperature	•	•
Nitrate	•	•
Phosphate	•	•
Total Suspended Solids		•
Turbidity	•	

gon) the dimensionality of the water quality data was reduced with a principle components analysis (PCA) and the resulting components used in subsequent analyses as proxies (Mickle et al. 2010).

Transect Sites

Transects were sampled annually between May and August for the 13-y period (2007-2019). Only transects that had continuous annual vegetation data were used and included transects 1, 2, 5, 6, 8, and 9 (Figure 1). Transect length ranged from 30.48 m long (transects 1, 6, and 8) to 60.96 m (transects 2, 5, and 9) (Coastal Eco-Group, Inc. 2016). Three 1 m² quadrats were placed equidistant along each transect with percent coverage of total seagrass and macroalgae recorded, regardless of species. For each quadrat the percent coverage was converted to Braun-Blanquet scores (BB) and averaged for each transect for each year (Table 3). The transect dataset included 234 quadrat recordings over the 13-y timeframe (6 transects x 3 quadrats x 13 y = 234 quadrats). Mean seagrass and macroalgae BB scores for each transect and year combination were calculated by averaging the 3 quadrats per year per transect. This allowed for congruency between the vegetation data and the water quality data for subsequent analyses, particularly the PCA.



FIGURE 1. Sampling sites in Lake Worth Lagoon, Palm Beach County, FL. The north section of the lagoon is on the left and the south section of the lagoon on the right. Blue teardrop symbol–water quality stations; Purple wave symbol–transects; Green square symbol–polygon.

Halophila johnsonii, Caulerpa sertularioides, Caulerpa prolifera, and unidentified benthic algae species were documented at each quadrat. The polygon area dataset included 4,739 quadrat recordings over the 11–y timeframe (polygon quadrat totals: 1,293 [C17A]; 1,288 [C17B]; 1,085 [C51B]; and 1,073 [C51C]).

Model Development Transect Analysis

Akaike's Information Criterion (AIC) adjusted for small sample size was used to assess the relative importance of competing candidate models for explaining seagrass BB scores among sites and years. Twenty-nine candidate models were constructed based on expected interactions between water quality variables, community variables, and possible temporal and spatial patterns (Supplementary Table S1). Variables in the models were categorized as water quality (PCA axis scores, PC1 and PC2), community (mean macroalgae BB scores), temporal (month and year), and spatial (transect). Within each of these categories of variables, 6 models were developed that only included individual variables (i.e., month only, year only, transect only, PC1 only, PC2 only, and macroalgae BB only). Twenty-one models were developed based on one or more variables from 2 categories to depict combinations and interactions between them (e.g., water quality + spatial, temporal x macroalgae, etc., Supplementary Table S1). A null model (no variables) and a global model (including all variables) comprised the final models used in the analyses. Models with low ΔAIC_{and} and high Akaike weights (w) have the best combination of parsimony (fewer variables) and fit (accuracy) for explaining

Polygon Sites

To monitor the presence or absence of specific seagrass and macroalgal species, PBC–ERM constructed 4 polygon sites that allowed species level resolution to be used in investigating seagrass community composition. Polygon sites were sampled multiple times throughout the year (1–6 times per year, averaging 4 times a year) between 2009 and 2019. The polygons were 0.405–0.809 ha areas and corresponded to PBC–ERM areas C17A, C17B, C51B, and C51C (Figure 1). Thirty 1 m² quadrats were randomly placed in each polygonal area, and percent coverage of specific seagrass and macroalgae species were recorded. The abundance of *Halodule wrightii, Syringodium filiforme, Thalassia testudinum, Halophila decipiens, Halophila englemannii*,

TABLE 3. The Braun–Blanquet scores, indicating percent cover of seagrasses, used in this study.

Braun—Blanquet Score	Description
0	Absent
0.1	Solitary Individual
0.5	Sparse and < 5%
1	Numerous, but < 5%
2	5%-25%
3	25%-50%
4	50%75%
5	75%–100%

mean seagrass BB scores (Burnham and Anderson 2006). Only models with a $w_i > 10\%$ of the highest w_i were interpreted.

Polygon Analysis

A separate AIC_c analysis was conducted to assess the relative importance of competing candidate models for explaining community composition in polygon areas. Initially the community data had percentages of species-level seagrasses and macroalgae for each quadrat and the dimensionality of the community data was reduced with a PCA. The resulting community PC1 score was used as the response variable in the AIC_c analysis. Like the transect analysis, models were developed based on expected interactions between water quality, depth, and possible temporal and spatial patterns (Supplementary Table S1). A total of 31 candidate models were used in the AIC_c analysis to assess the quality of each to predict the community PC1 scores (response variable). Variables in the models were categorized as water quality (PCA axis scores, PC1 and PC2), temporal (month and year), and spatial (polygon site and depth). Within each of these categories of variables, 6 models were developed that only included individual variables (i.e., month only, year only, site only, PC1 only, PC2 only, and depth only). Twentythree models were developed based on one or more variables from 2 categories to depict combinations and interactions between them (Supplementary Table S1). A null model (no variables) and a global model (including all variables) comprised the final models used in the analyses. The same criterion of low ΔAIC_{c} and high Akaike weights (w) for the transect analysis was used for the polygon area analysis.

Post-hoc Data Analysis

Post—hoc analyses were conducted on the transect and polygon data after the top 10% of the respective AIC_c analyses revealed which candidate models yielded the best explanation for either mean seagrass BB scores (transect data) or community PC1 scores (polygon data). All transect data met parametric assumptions of normality and homoscedasticity and were analyzed using a 2–way multivariate analysis of variance (MANO-VA) of water quality data (response variables) between years and transect sites (independent variables) followed by a series of ANOVAs to investigate which water quality variables are driving significant differences in the MANOVA tests. A subsequent Tukey pairwise comparison between individual years (2007–2019) and their associated water quality PC1 scores was done to visualize groupings between years.

For the polygon data the AIC_c results indicated the interaction between year and polygon sites (independent variables) explained the most variation in community PC1 scores (response variable). Due to the non-normal nature of the community PC1 scores a Scheirer-Ray-Hare (SRH) Analysis was run on the polygon AIC, results. The SRH is a non-parametric equivalent to the parametric two-way analysis of variance. A separate 2-way MANOVA was conducted on normally distributed polygon water quality data to test for significant differences in water quality variables (response variables) between years (2009–2019) and polygon sites (independent variables) followed by a series of 2-way ANOVAs to investigate which water quality variables are driving significant differences in the MANOVA tests. A subsequent Tukey pairwise comparison between individual years (2009–2019) and their associated water quality PC1 scores was done to visualize groupings between years. All analyses were performed using the R statistical computing package (R Core Team 2020) at an α -level of 0.05 where appropriate.

Results

Transect Data

The transect water quality PCA results highlight variation in the water quality data for each transect over time (Figure 2). Principle components 1 and 2 explained 58.03 % of the total



FIGURE 2. Transect water quality PCA for Lake Worth Lagoon, FL with PC1 and PC2 accounting for 58.03% of the variation in the dataset. Water quality variables that loaded heaviest are represented on the x and y axes. Individual transects are represented by various shapes and colors. White-northern gradient; Grey-central gradient; Black-southern gradient. Transect 1-□; Transect 2-•; Transect 5-▲; Transect 6-▲; Transect 8-●; Transect 9-■. Numbers inside shapes correspond to the year that data point represents (i.e., 12 = 2012). Transect 2 and transect 5 water quality points are very similar and overlap in the PCA. The dashed line demarcates that all the 2012 data points occur on the right side only.

TABLE 4. Explanatory models, AIC_c statistics, and weights (w_i) for the response variables. Only models with a weight >10% of the best model were interpreted and listed. Model numbers match list in Supplementary Table **S1**. BB–Braun–Blanquet scores indicate percent cover of seagrasses.

Response Variable	Number	Variables	AIC	∆AIC	w _i
Mean Seagrass BB	11	Year x Transect	170.3	0.0	0.648
	12	Month + Year x Transect	172.0	1.7	0.281
Mean Community PC1	17	Month + Year x Site	10,328.70	0.0	1.000

variation in the data points (42.95% and 15.08%, respectively). For PC1 loadings, phosphate, ammonia, and nitrate loaded strongly on the positive aspect of the axis whereas conductivity, salinity, and pH measures loaded high on the negative aspect of the axis. For PC2, secchi depth and dissolved oxygen loaded strongly on the positive aspect whereas temperature, turbidity, and pH loaded strongly on the negative aspect. Transects 1, 2,

and 5 each show smaller variability in PC1 scores over time compared with transects 6, 8, and 9 (Figure 2). Consequently, because water quality data were collected from water quality stations that overlapped between transects 2 and 5, the PC1 and PC2 scores for transects 2 and 5 are identical except for data from 2017, where scores are very similar. Across the majority of transects, water quality data for 2012, 2013, and 2014 tend to reveal elevated phosphorous, nitrates, and ammonia as well as reductions in salinity and pH compared with other years in the dataset (Figure 2, see demarcation line). The transect water quality PCA indicates 2 major findings: (1) there is variability in physiochemical structure between transects, and (2) water quality structure at each transect does not remain stable through time, with the parameters changing considerably in 2012, but reverting to early dataset levels by 2015/2016.

The AIC_c indicated that the most parsimonious model of mean seagrass BB score included the interaction between year and transect (model 11, $w_i = 0.648$, Table 4). The interaction between year and transect in the model indicates that the relationship of mean seagrass BB score with year is transect dependent. Starting in 2007 all 6

FIGURE 3. Mean (± se) Braun–Blanquet (BB) scores for transect data in Lake Worth Lagoon, FL. A. Seagrass (closed circles) and macroalgae (open circles). BB scores across all transects over time. B. Mean seagrass BB scores for individual transects over time. White-northern gradient; Greycentral gradient; Black-southern gradient. Transect 1 – □; Transect 2-•; Transect 5-▲; Transect 6-▲; Transect 8-•; Transect 9-■.

transects had some seagrass, with transect 6 beginning the dataset with the most and transect 2 having the least (Figure 3A—B). There is considerable fluctuation in seagrass BB scores for transects between 2010–2011 (Figure 3A—B, with transects 1, 5, and 8 increasing and transects 6 and 9 decreasing). There is a dramatic decline in seagrass BB score for all transects between 2012–2013 (Figure 3A). By 2013–2014 transects 5, 6, and 9 had no seagrass present, and

transects 2 and 8 lost seagrass completely by 2016 (Figure 3B). Although the seagrass BB score is reduced at transect 1 during 2013–2014, it rebounds in 2015 and maintains its seagrass abundance through 2019 (Figure 3B). Transects 2 and 5 have a resurgence of seagrass BB score by 2019, albeit very low. In general, towards the end of this dataset (2016–2019), seagrass abundance declined drastically in the central (transects 6 and



TABLE 5. Results of the analyses on transect water quality data in Lake Worth Lagoon, FL. A. The results of the 2–way MANOVA. The treatment of year groups consists of 2007–2012 and 2013–2019. B. Post–hoc ANOVA analyses. * represents significant differences between year groups. C. Mean ± se water quality variables for years 2010, 2011, and 2012. These years represent the period that a significant fluctuation in seagrass species across the lagoon occurred.

Independent Variable	df	Wilk's	F	num d	f denom df	Р
Year	12	0.00025	6.53	72 120	410.55	< 0.000
Transect	5	0.03771	4.96	36 50	235.96	< 0.000
Post—hoc Analyses						
Water Quality Variable		df	F	Р		
Ammonia (mg/L)						
Year		12	7.063	< 0.0001 *		
Transect		5	7.575	< 0.0001 *		
Conductivity (µ5/ citi)		12	16 060	< 0.0001 *		
Transact		5	8 966	< 0.0001 *		
Dissolved oxygen (mg/L)		5	0.700	- 0.0001		
Year		12	6.953	< 0.0001 *		
Transect		5	6.735	< 0.0001 *		
Nitrate (mg/L)						
Year		12	4.045	0.0001 *		
Transect		5	7.053	< 0.0001 *		
Phosphate (mg/L)						
Year		12	8.385	< 0.0001 *		
Transect		5	9.670	< 0.0001 *		
рН						
Year		12	17.602	< 0.0001 *		
Transect		5	9.209	< 0.0001 *		
Salinity						
Year		12	17.854	< 0.0001 *		
Transect		5	9.110	< 0.0001 *		
Secchi depth (m)						
Year		12	4.492	< 0.0001 *		
Transect		5	14.320	< 0.0001 *		
Temperature (°C)		10	00.005			
Year		12	22.085	< 0.0001 *		
Iransect		5	7.998	< 0.0001 *		
Iurbidity (NIU)		10	0.001	0.0170*		
Year		12	2.291	0.01/8^		
Irancoct		3	∠ا.Ծاک	< 0.0001 "		

Water Quality Variable	2010	0	201	11	2012			
Ammonia (mg/L)	1.283E-02 ±	1.2220E-03	3.167E-03 ±	2.959E-03	2.717E-02 ±	1.083E-02		
Conductivity (µS/cm)	45,388.17 ±	2,750.890	54,711 ±	339.941	38,466 ±	2,290.109		
Dissolved oxygen (mg/L)	6.44 ±	0.127	6.31 ±	0.090	6.77 ±	0.293		
Nitrate (mg/L)	5.317E-01 ±	4.3544E-02	2.700E-01 ±	2.338E-02	5.050E-01 ±	5.909E-02		
Phosphate (mg/L)	4.500E-02 ±	5.272E-03	3.300E-02 ±	5.347E-03	5.067E-02 ±	6.417E-03		
рН	8.15 ±	0.022	7.90 ±	0.026	7.87 ±	0.033		
Salinity	29.22 ±	1.946	36.07 ±	0.255	24.48 ±	1.531		
Secchi depth (m)	1.63 ±	0.284	1.42 ±	0.164	1.43 ±	0.194		
Temperature (°C)	31.48 ±	0.251	30.48 ±	0.239	28.87 ±	0.525		
Turbidity (NTU)	3.78 ±	0.393	3.42 ±	0.794	4.13 ±	1.219		

8) and southern (transects 2, 5, and 9) portions of the lagoon, but seagrass abundance maintained or increased in the northern portion (i.e., transect 1).

With the sharp decline in seagrass BB score in 2012, a 2-

way MANOVA was used to re—examine the water quality data. The MANOVA indicated significant differences between years and transects in the combined water quality data (Year analysis: Wilk's $_{12}$ = 0.00025, p < 0.0001, Table 5A). A series of

post-hoc ANOVAs revealed significant differences in ammonia, conductivity, dissolved oxygen, nitrate, phosphate, pH, salinity, secchi depth, temperature, and turbidity levels between years and transect sites (Table 5B). Investigating water quality in the years surrounding the fluctuations in seagrass BB score (Table 5C), ammonia, conductivity, and salinity increased from 2010 to 2011 and then decreased in 2012. Macroalgae BB score increased between 2010 and 2012, with a dramatic drop in 2013. Over the same period dissolved oxygen, nitrate level, phosphate level, and turbidity decreased from 2010 to 2011 and then increased in 2012. Temperature and pH steadily decreased between 2010 and 2012 at the transect sites. The Tukey pairwise comparison of mean environmental PC1 scores across years showed specific groupings of the years, with 2011 and 2013 being complete opposites in their mean PC1 scores and grouping differently from each other (Figure 4A).

Model 12 (Table 5A) also explained some of the variability in mean seagrass BB score ($w_i = 0.2807$), which included both



FIGURE 4. Mean $(\pm se)$ environmental PC1 scores from 2007–2019 for Lake Worth Lagoon, FL. A. Transects. B. Polygons. Letters above the columns indicate similarity between mean environmental PC1 scores for years with the same letter combination.

temporal variables (year and month) and transect. When investigating the means for the significant physiochemical variables in the 2–way MANOVA, general monthly trends included increasing ammonia, nitrate, phosphate, and temperature from May through August; and decreasing conductivity and salinity from May through August (Supplemental Table S2).

Polygon Data

To describe species-level community structure, the first 2 principle components of the community PCA for the polygon data explained 34.27% of the total variation between quadrats (Figure 5). Syringodium filiforme, T. testudinum, unidentified algae species, H. decipiens, C. sertularioides, and C. prolifera loaded highest on PC1 axis (Figure 5). The community PCA revealed high variability in seagrass and algal community PC1 scores over time for polygon sites C17A and C17B (northern polygons) compared with reduced variation at sites C51B and C51C (central polygons). On the PC2 axis, T. testudinum, S. filiforme, H. wrightii, H. johnsonii, and C. sertularioides loaded highest. In general, sites C17A and C17B had high variabilities through time in their community structure compared with sites C51B and C51C. The interesting V-shape of the PCA graph of the community data (Figure 5) is an effect of how the PCA rotates the data and the constraints of the data, namely that there are many zeros in the large dataset. Even with the limitation of this type of data, the PCA does provide a basic summary of the communities present at polygon sites over time.

The polygon water quality PCA indicated variation in water quality variables between polygon sites (Figure 6A–D). The first 2 principle components accounted for 52.80% of the total physiochemical variation between polygon sites. Sites vary along the PC1 axis, with C17A and C17B (Figure 6A, B) having similar water quality characteristics and a smaller variability compared with C51B and C51C (Figure 6C, D) which have similar water quality characteristics but a larger variability over the 11-y dataset. All sites had a similar variability in PC2 axis scores through time. Most of the polygon sites had an increase in dissolved oxygen and secchi depth measures with reductions in temperature, pH, and total suspended solids early in the dataset (2009-2012) compared with later in the dataset (2014-2019; Figure 6A–D). Sites C51B and C51C showed increased nitrate and phosphate levels between 2010–2014 (Figure 6C - D), while nitrate and phosphate levels remained constant and low at C17A and C17B.

The AIC_c indicated that the most parsimonious model of mean community PC1 scores included the interaction between temporal and spatial variables ($w_i = 1.000$, Table 4). Mean community PC1 scores plotted over time by polygon site show that site C17A and C17B changed dramatically over the 11–y dataset, whereas C51B and C51C communities mirrored each other and were stable in their composition through time (Figure 7). A post–hoc SRH analysis using year, site, and year x site (per the AIC_c outcome) revealed significant differences in mean community PC1 scores between years (H₁₀ = 2753, p < 0.001), between sites (H₃ = 246, p < 0.001), and the interaction between year and site (H₃₄ = 785, p < 0.001). The significant interaction between year and site is very evident for site C17A. In 2009,



FIGURE 5. The polygon community PCA for Lake Worth Lagoon, FL with PC1 and PC2 accounting for 34.27% of the variation in the dataset. The red vectors (arrows) represent loadings of the 9 macrophyte species in the dataset and which direction caused increases in those species. The observed V effect is most noticeable when the sampling units cover a long ecological gradient and those at the end of the gradient have few species in common (Quinn and Keough 2002).

C17A had a community dominated by S. filiforme, algae species, H. wrightii, and occasionally T. testudinum and maintained that community through 2013 (Table 6). The community dynamically shifted in 2014, switching to a community consisting of H. decipiens and macroalgae (C. sertularioides and C. prolifera; Figure 7, Table 6). At site C17B, H. wrightii, algae species, and H. johnsonii dominate until 2013, then switched to a H. wrightii, H. decipiens, macroalgae dominated system (Figure 7, Table 6). Polygons C51B and C51C were dominated by H. johnsonii and H. decipiens or H. johnsonii and H. wrightii, respectively, through 2013, however, the vegetation community decreased dramatically afterward, and was non-existent by 2016 for both sites (Table 6). In general, when investigating the first (2009) and last years (2019) in the dataset, there was a shift from S. filiforme and H. johnsonii to H. decipiens and macroalgae species in the northern portion of the lagoon (Figure 8).

With the large fluctuation in community structure around 2012, a 2-way MANOVA was used to re-examine the water quality data. The 2-way MANOVA indicated that there was a significant difference between years, between polygon sites, and the interaction between polygon site and year (Table 7A). The post-hoc ANOVAs showed significant differences for each water quality variable by year and polygon site as well (Table 7B). Investigating the water quality variables across sites between 2010 and 2012, nitrate levels, phosphate levels, salinity, and temperature increased from 2010 to 2011 and then diminished in 2012 (Table 7C). Dissolved oxygen and pH maintained steady levels during this period, whereas secchi depth decreased by 2012, likely a result of increases in total suspended solids between 2010 and 2012 (Table 7C). The Tukey pairwise comparison of mean environmental PC1 scores across years showed specific groupings of the years, with 2011 not grouping with any other year, and being completely opposite in PC1 score with 2012 (Figure 4B).

Investigating the transect and polygon water quality PCAs (Figures 2 and 6) indicated northern sites, compared with central and southern sites, had less variable water quality conditions over time with reference to PC1 scores. Years 2011–2012 had an increase in nutrients (especially nitrate and phosphate) in central and southern sites in comparison to 2013–2014 (2011–2012: Central_{nitrate} = $0.45 \pm 0.074 \text{ mg/L}$; Central_{phosphate} = $0.06 \pm 0.006 \text{ mg/L}$; Southern_{nitrate} = $0.38 \pm 0.077 \text{ mg/L}$; Southernphosphate = $0.03 \pm 0.006 \text{ mg/L}$; 2013 – 2014: Central_{nitrate} = $0.69 \pm 0.064 \text{ mg/L}$; Central_{phosphate} = $0.07 \pm 0.007 \text{ mg/L}$; Southern_{nitrate} = $0.58 \pm 0.022 \text{ mg/L}$; Southern_{phosphate} = $0.08 \pm 0.012 \text{ mg/L}$).

DISCUSSION

Having both transect and polygon data allowed for an investigation of changes in community composition at slightly different levels of resolution. The transect data separated vegetation cover broadly into 2 categories: seagrasses and algae, while the polygon data was more precise in that it divided, when possible, the vegetation percent cover into individual species. Similar conclusions can be drawn from both levels of resolution, indicating that the system has been impacted by changes in abiotic factors.

Seagrass beds can survive over a range of environmental conditions but typically occur in low energy zones. Factors determining their local distributions include light penetration (Laboy–Nieves 2009), temperature (Campbell et al. 2006, Waycott et al. 2009), salinity (Zieman 1975, Greve and Binzer 2004, Laboy–Nieves 2009), turbidity (Duarte et al. 1997, Laboy–Nieves 2009), depth (Greve and Binzer 2004, Laboy–Nieves 2009), and nutrient/run–off pollution (Durako 1994, Haynes et al. 2000, York et al. 2017). The ability to tolerate and adapt to changing water quality parameters can be an ultimate determinant of biotic composition and interactions in a system. Temper-



Figure 6. Individual water quality PCA graphs for each polygon site in Lake Worth Lagoon, FL. PC1 and PC2 scores account for 53.92% of the variation. Red vectors (arrows) represent loadings of water quality variables and which direction caused increases in those variables. The number next to the shapes indicate the year that point represents. A. Polygon site C17A. B. Polygon site C17B. C. Polygon site C51B. D. Polygon site C51C.



FIGURE 7. Mean community PC1 scores over time at polygon sites in Lake Worth Lagoon, FL. Polygon sites are represented as ○- C17A; □- C17B; •- C51B; ▲- C51C. Macrophyte species are characterized along the y-axis, with their placement indicating where they fit along the continuum based on PC1 loadings. The inset is a table depicting the results of the Scheirer-Ray-Hare analysis.

atures > 35°C inhibit photosynthesis and cause seagrass species to experience critical thermal stress (Ralph 1998, Campbell et al. 2006). Some tropical seagrass species increase photosynthesis (i.e., become more tolerant) with increasing water temperatures, including Cymodocea rotundata, C. serrulata, H. uninervis, and T. hemprichii as compared to other tropical species such as H. ovalis, Zostera capricorni, and Syringodium isoetifolium, but if the temperature exceeds 35°C, breakdown of photosynthetic enzymes occurs. All species suffer effects of episodic changes in temperatures up to 45°C (Campbell et al. 2006). McGlathery (2001) and Hauxwell et al. (2001) have assessed the influence of biotic factors such as macroalgal blooms on seagrass mortality. Nutrient run-off from stormwater and freshwater sources due to urban, industrial, and agricultural development cause an increased presence of macroalgae and cyanobacterial blooms which limit light availability to seagrasses, reducing their biomass and causing further damage to the diversity and habitat of seagrass meadows (McGlathery 2001, Tiling and Proffitt 2017).

Both transect and polygon modeling analyses revealed that the most parsimonious models included interactions between spatial and temporal variables to explain seagrass abundance and community structure. Fluctuations in seagrass abundance or their dominance in community structure depended upon year, and specific years seemed to influence certain sites more than others. Pivotal years appear to be 2010, 2011, and 2012, where water quality patterns and seagrass abundance shifted and are very notable for some transects.

For the transects, the water quality variables changed between 2010–2012 with nitrate, phosphate, and turbidity levels rising while pH and salinity levels declined. This shift possibly had an impact on the seagrass and macroalgae percent coverage in the transects because both showed decreases in mean BB scores during this time, seagrass more so than macroalgae although this was transect—specific. To best understand why these changes have occurred in both the transect and the polygon sites, it is essential to discover what happened between the years 2010 and 2012 to investigate these changes.

Buzzeli et al. (2018) found greater freshwater discharge into LWL in the wet seasons in the years 2013–2015, after lagoon lows in freshwater input during 2011–2012. It is conceivable that there was a synergistic effect between the drought stress and the increased freshwater input that followed on the seagrass system (Sherwood et al. 2016). Also, lagoon transect sites impacted by canals C–51 (central transects) and C–16 (southern

TABLE 6. Ranked dominant species at each polygon site in the Lake Worth Lagoon, FL over time. 1–most dominant; 2–second dominant; 3–third dominant. *–Years with < 3 ranks at a site imply that the next dominant species was <5%. Years completely devoid of species are represented by dashed lines (——).

Polygon	Site: C	C17A								Polygo	n Site: (C17B							
Year	H. decipiens	H. englemanni	H. johnsonii	H. wrightii	S. filiforme	T. testudinum	C. sertularioides	C. prolifera	Algae species	Year	H. decipiens	H. englemanni	H. johnsonii	H. wrightii	S. filiforme	T. testudinum	C. sertularioides	C. prolifera	Algae species
2009				3	1				2	2009			3	1					2
2010				3	1				2	2010			3	2					1
2011				3	2				1	2011			3	2					1
2012					1	3			2	2012			2	1					3
2013				3	1	2				2013			3	1					2
2014	1			2	3					2014	3		2	1					
2015	1							3	2	2015	2		3	1					
2016	1						3	2		2016	2			1				3	
2017	1							3	2	2017	2			1				3	
2018	1			2				3		2018	2			1			3		
2019	1			2					3	2019	2			1					3
Polygon	Site: C	C51B								Polygo	n Site: (C51C							
Year	H. decipiens	H. englemanni	H. johnsonii	H. wrightii	S. filiforme	T. testudinum	C. sertularioides	C. prolifera	Algae species	Year	H. decipiens	H. englemanni	H. johnsonii	H. wrightii	S. filiforme	T. testudinum	C. sertularioides	C. prolifera	Algae species
2009	1		3						2	2009			1	2					
2010	3		2						1	2010			2	3					1
2011	3		2						1	2011			2	3					1
2012	2		1						3	2012			1	2					3
2013										2013			1	*					
2014	*									2014			*						
2015	1									2015	*		*						*
										2016									
2016	*									2010									
2016 2017	*								*	2018			*						*
2016 2017 2018	*								*	2018 2017 2018			*						*

transects) showed considerable decreases in salinity and increases in total nitrates, total phosphorous, turbidity, and total suspended solids over the 9-y study that overlaps the datasets used here (Buzzeli et al. 2018). Conversely, sites closest to canal C-17 (northern transects) remained relatively stable over the study period (Buzzeli et al. 2018). This major perturbation in reduced freshwater flow during 2011–2012, followed by a larger than normal freshwater input during 2013–2015, may have set up conditions favoring either a community dominance switch in northern locations or a complete decimation of vegetational communities in central and southern locales, or both, as our data suggest. For instance, the polygon data depicted a change in community composition with a notable shift occurring in the northern sites from seagrass-dominated communities to macroalgae-dominated ones, while central polygon sites dramatically lost most of their vegetation after 2012.

Freshwater input introduces more nutrients from agricultural and urban sources into the watershed (Rudnick et al. 1999). Seagrass species do not necessarily need high levels of nitrogen or phosphorus in the substrate to thrive and increases in either may disturb established communities by allowing opportunistic species (such as macroalgae) a once unavailable niche (Greve and Binzer 2004). In support of this, our polygon data illustrated that a radical community shift occurred at site C17A with certain seagrass species no longer dominating and macroalgae species becoming the dominant species. The results of the transect and polygon water quality PCAs showed northern sites, compared with central and southern sites, had less variable water quality conditions over time (with reference to PC1 scores), which can provide stability of community structure. The increase in nutrients (especially nitrate and phosphate) in central and southern sites during 2013–2014 may have tipped the threshold balance, especially following a stressful year of reduced inflow in 2011-2012 (Buzzeli et al. 2018). Additional stress on the system includes an increase in pH, temperature, and total suspended solids through time lagoon-wide, which



FIGURE 8. Re–envisioned plot of the original polygon community PCA (see Figure 5). Only 2009 (open circles) and 2019 (closed triangles) data are plotted to visualize the community change over the 11y timeframe. The red vectors (arrows) represent loadings of the 9 macrophyte species in the dataset and which direction caused increases in those species. The white arrow depicts the community composition shift.

could continue to cause community decline, reduced community resilience, altered species, and transformed system (lagoonal) function. Nutrients delivered by freshwater sources have been known to stimulate macroalgae growth on seagrass beds where they will eventually outcompete seagrass in that system (Krupp et al. 2009). It has been shown that even moderate nutrient loading can reach a certain threshold making the water quality conditions favorable enough for a community switch where macroalgae species compete with seagrass and may even become dominant (Krupp et al. 2009), as was shown in portions of our dataset. Long-term continuous input of nutrients to established seagrass beds are known to cause a change in dominant seagrass species, perhaps through its influence on competition. For example, it was shown that a transition from a T. testudinum-dominated to a H. wrightii-dominated community was dependent on the timing of colonization of H. wrightii and the increase in nutrient input to the system (Fourgurean et al. 1995). This switch persisted for 8 y after the nutrient addition. Thalassia testudinum re-established dominance eventually through its ability to thrive on nutrient levels below the requirements of H. wrightii (Fourgurean et al. 1995).

Some seagrass species (H. wrightii, T. testudinum, and Ruppia

maritima) can adapt to increases in salinity, with species tolerating large increases from ambient to hypersaline conditions. Higher salinity levels are thought to be tolerated during gradual increases rather than pulsed events (Koch et al. 2007). Additionally, seagrasses that are adapted for growth in river outlets or estuarine habitats (e.g., *Zostera marina* and *Z. noltii*), where salinity can change rapidly, have been shown to exhibit higher tolerances to changes in salinity (Greve and Binzer 2004). High levels of salinity (2012) followed by the freshwater input into the LWL system (2013) and the subsequent increase in salinity (2015–2019) for many of the sites may have been too rapid for the once dominant seagrass species there.

A major cause of seagrass degradation is reduction in water clarity which can be caused by increased nutrient loading and turbidity. For example, it is estimated that ~81% of seagrasses were lost in Tampa Bay, FL between 1876–1976 due to the combined impacts of increased turbidity and the physical removal or burial of seagrasses during dredging (Erftemeijer and Lewis 2006). Turbidity can reduce light penetration to benthic communities and become lethal to seagrasses by preventing proper photosynthesis. Concurrently, both a significant reduction in secchi depth and a significant increase in turbidity occurred in **TABLE 7.** Results of the analyses on polygon water quality data in Lake Worth Lagoon, FL. A. The results of the 2-way MANOVA. The treatments were year groups (2009–2012 and 2013–2019), polygon site, and their interaction. df-degrees of freedom; num-numerator; denom-denominator. B. Post-hoc ANOVA analyses. * represent significant differences within treatments. C. Mean ± se for the water quality variables for years 2010, 2011, and 2012, years that represent a significant fluctuation in seagrass community across sites.

A	Independent Variable	df W	ilk's F	num df	denom df	Р	
	Year Group	10 0.0	0341 176.	317 100	29238	< 0.0001*	
	Polygon Site	3 0.2	2858 212.	568 30	11982	< 0.0001*	
	Year Group x Polygon Site	30 0.	1230 31.9	927 300	38849	< 0.0001 *	
в							
Ľ	Post—hoc Analyses Water Quality Variable	df	F	Р			
	Dissolved oxygen (mg/L)						
	Year Group	10	81.174	< 0.0001*			
	Polygon Site	3	65.608	< 0.0001 *			
	Year Group x Polygon Site	30	17.331	< 0.0001 *			
	Nitrate (mg/L)						
	Year Group	10	96.719	0.4062			
	Polygon Site	3	523.941	< 0.0001*			
	Year Group x Polygon Site	30	27.824	< 0.0001*			
	Phosphate (mg/L)						
	Year Group	10	249.447	< 0.0001*			
	Polygon Site	3	956.291	< 0.0001*			
	Year Group x Polygon Site	30	35.805	< 0.0001*			
	pH						
	Year Group	10	421.934	< 0.0001*			
	Polygon Site	3	466.332	< 0.0001*			
	Year Group x Polygon Site Salinity	30	33.875	< 0.0001*			
	Year Group	10	136.450	< 0.0001*			
	Polygon Site	3	360.005	< 0.0001*			
	Year Group x Polygon Site Secchi depth (m)	30	6.473	< 0.0001*			
	Year Group	10	242.095	< 0.0001*			
	Polygon Site	3	128.461	< 0.0001*			
	Year Group x Polygon Site Temperature (°C)	30	37.507	< 0.0001*			
	Year Group	10	98.512	< 0.0001*			
	Polygon Site	3	9.103	< 0.0001*			
	Year Group x Polygon Site	30	4.773	< 0.0001*			
	TSS (mg/L)						
	Year Group	10	174.874	< 0.0001*			
	Polygon Site	3	345.599	< 0.0001*			
	Year Group x Polygon Site	30	30.655	< 0.0001*			
С	Water Quality Variable	2	2010		2011	2012	
	Nitrato (mg/l)	1 7875 00	+ 14045 02	6 2025 02		3 507E 02 ± 2 545E	
	Phosphate (mg/L)	1.707E-02	+ 3140E-03	6.202E-03	$3 \pm 4.4320-04$ $3 \pm 1.8450 04$	$3.307 L = 02 \pm 2.303 E = 0$ $1.486E = 02 \pm 71.43E 0$	ວ3 ງ∡
	Dissolved ovvrgen (mg/L)	1.240L-02	± 0.047	0.07 8L=0.	$1 \pm 0.031 = 0.04$	1.400L-02 ± 7.142L-0	<i>J</i> 4
	nH	0.90 707	+ 0.047	2.12	$+ \pm 0.031$	0.70 ± 0.000	
	Solinity	7.7/ 20 2 1	± 0.000 + 0.187	33.00	5 ± 0.004 5 ± 0.107	7.73 ± 0.009 29.45 + 0.358	
	Secchi denth (m)	∠7.JI 1 3 1	+ 0.018	1 22	2 + 0.10	118 + 0.012	
		24 40	+ 0.230	1.32 26 AC	2 ± 0.014 2 + 0.1/8	21.67 ± 0.012	
	TSS (mg/l)	511	+ 0166	5 50	0.140	735 ± 0.100	
	100 (119/ 1/	5.14	_ 0.100	5.50		7.00 ± 0.200	

2012 compared with the prior years and certainly influenced the light availability for photosynthesis. Additionally, an increase in total suspended solids can be detrimental to seagrass by impacting their cuticle layer and reducing gas exchange or by smothering through burial (Erftemeijer and Lewis 2006).

•

Based on the polygon data, total suspended solids significantly increased at sites in 2012 compared with prior years, perhaps contributing to the decrease of seagrass at those sites through suffocating the macrophytes. In a very promising reversal, as turbidity and chlorophyll concentration decreased since the mid-1970s in Tampa Bay, there has been an estimated gain of about 6,319 ha in seagrass area between 2002-2016, roughly a 60% increase (McCarthy et al. 2018, Handley and Lockwood 2020). With continued efforts to develop the best water management practices and a greater public awareness of water usage and water quality surrounding the LWL, it may be possible to reduce the influence of nutrient runoff, sediment loading, and turbidity in this system to allow it to rebound to prior seagrass community composition and abundance (Palm Beach County 2021).

Seagrasses require on average ~11% of surface light for longterm survival (Duarte 1991, Longstaff and Dennison 1999); however, there is considerable variability for minimum light requirements reported for different seagrass species (range: 2.5 -37% of surface light; see Erftemeijer and Lewis 2006). Longstaff and Dennison (1999) assessed how pulsed turbidity events, resulting in disruptions in the amount of light received, affected Halodule pinifolia and Halophila ovalis survival. Interestingly, results indicated variation in tolerance to low light levels, and greater tolerance seemed to be conferred by increased photoadaptive responses (Longstaff and Dennison 1999). Seagrasses can change the chlorophyll a to b ratio and increase chlorophyll content while increasing canopy height and shoot length to compete for limited canopy space; however, these adaptations seem species-specific and might be short-term proximate responses (Longstaff and Dennison 1999). While adaptive physiology was not tested here, the polygon dataset indicates that some species persist, whereas others recede or invade a changed waterscape, suggesting some species are more adaptive than others. For example, at the northern sites H. wrightii tended to dominate the community structures throughout the dataset, while S. filiforme receded in its prominence during the fluctuation in water quality parameters. During the S. filiforme recession, H. decipiens and Caulerpa spp. entered the community and increased their prominence. This is a shift from larger, greater underground biomass, and longer-lived species (S. filiforme and T. testudinum) to smaller canopy species (Halophila spp.; Buzzeli et al. 2018). Halophila decipiens, H. wrightii and H. johnsonii were initially dominant in central sites, but have been extirpated over time, perhaps indicating that the large variation in water quality conditions during 2010–2013 and the return to pre-perturbation levels were just too much for them to tolerate. Additionally, this could indicate that seed production, seed viability, or seed germination decreased in these ruderal species following the changes. Seed bank production in general for seagrasses show high levels of variability (Hammertrom et. al. 2006, Orth et al. 2000, Gu et al. 2022) and water quality conditions, unsuitable substrate, burial depth, and predation have been shown to negatively impact seed viability (Orth et al. 2006b). Consequentially, changes in salinity are known to decrease germination rates (Gu et al. 2022) or cause suboptimal germination times that could lead to negative effects on seedling morphology and growth (e.g., reduced number of leaves per seedling and reduced maximum seedling leaf length, Xu et al. 2016), ultimately impacting the survival of these species.

This could point to the ability of *Halophila* spp. to tolerate and adapt to small deviations of water quality parameters (i.e., the smaller temporal variations in water quality at northern sites), while larger variations in water quality parameters may have surpassed their physiological limits (i.e., larger temporal variations in water quality at central sites).

Investigations of competition for light, space, and nutrient resources between the macrophyte species in LWL would be beneficial for future research. This would allow for a better understanding of the influence of biotic interactions in establishing communities within this lagoon, especially interactions between *H. wrightii*, *Caulerpa* spp., and *Halophila* spp., particularly during the dominance switch in the northern portions of the lagoon. Given optimal environmental conditions, studies have shown that some macrophytes can rapidly expand, displacing other species in as little as 10–12 weeks (Willette and Ambrose 2012) or out–perform others after disturbances (Baldwin and Lovvorn 1994, Jun Bando 2006).

Investigations of the physiological tolerances of many of the seagrass and macroalgal species linked to specific water quality parameters in this study are lacking. When investigating reasons for phenotypic variation in populations of T. testudinum across environmental gradients in the Gulf of Mexico, it was shown that stable environments (less fluctuating in temperature, salinity, and water clarity) resulted in increases in blade size, biomass, and horizontal expansion, whereas unstable environments (higher fluctuations in temperature, salinity, and water clarity) resulted in increased flowering and earlier age at flowering (McDonald et al. 2016). A better understanding of physiological tolerances of Halophila and Caulerpa spp. would enhance our insight into what degree abiotic factors are regulating the system. Within the northern, central, and southern segments of LWL there is documented variability in depth, area, volume, and flushing times (Buzelli et al. 2018). Although not studied here, perhaps flushing rates, depth, and volume in various portions of the lagoon may play a role in buffering certain regions and their biotic communities from short-term (annual) changes in water quality. It may also be advantageous to examine to what degree freshwater inflow results in increased siltation in different segments of the lagoon, which could be contributing to seagrass decline. Even though increased nutrient levels from freshwater input have been shown to be related to increases in nutrient loading and macroalgae blooms (Krupp et al. 2009), these may not be the only consequences of freshwater input.

As with many ecological systems, it is difficult to pinpoint one specific driver contributing to community change, but we can document the time during which major changes occurred. This macrophyte community change appears to be related to changes in pH, nutrient levels, and salinity levels. Portions of the lagoon were impacted differently, likely due to variations in substrate, starting community, depth, wave action, and specific abiotic conditions (e.g., temperature regimes and dissolved oxygen levels). Future data collection should continue and would benefit from collecting water quality data linked to the precise transect or polygon sites to aid in calibrating the influence of abiotic factors in driving community structure. Continued monitoring can provide a metric to assess regional capacities for community resilience in the lagoon. This will help answer the overarching question of whether the LWL vegetation can transition back to one dominated by seagrasses or is the new ecological regime preventing previous communities from being established?

ACKNOWLEDGMENTS

We thank Palm Beach County Environmental Resources Management for the use of their collected data from the transect and polygon sites in Lake Worth Lagoon, Palm Beach County, FL. We also thank E. Anderson, A. Madison, M. Bolyard, and anonymous reviewers for their valuable input to this manuscript. This work was supported in part through generous funding from The Henry Foundation and Union University's Undergraduate Research Grant program.

LITERATURE CITED

- Baldwin, J.R. and J.R. Lovvorn. 1994. Expansion of seagrass habitat by exotic Zostera japonica, and its use by dabbling ducks and brant in Boundary Bay, British Columbia. Marine Ecology Progress Series 103:119–127. http://doi.org/10.3354/ meps103119
- Burnham, K.P. and D.M. Anderson. 2006. Model selection and multimodel inference: A practical information—theoretical approach, 2nd ed. Springer–Verlag, New York, NY, USA, 515 p. https://doi.org/10.1007/b97636
- Buzzeli, C., Z. Chen, P. Doering, and A. Khan. 2018. Assessment of freshwater inflow and water quality for an urbanized, subtropical estuary (Lake Worth Lagoon, Florida, USA). Marine Technology Society Journal 52:19–31. https://doi. org/10.4031/MTSJ.52.4.2
- Campbell, S.J., L.J. McKenzie, and S.P. Kerville. 2006. Photosynthetic responses of seven tropical seagrasses to elevated seawater temperature. Journal of Experimental Marine Biology and Ecology 330:455–468. https://doi.org/10.1016/j. jembe.2005.09.017
- Carlson, P.R., Jr., L.A. Yarbro, and T.R. Barber. 1994. Relationship of sediment sulfide to mortality of *Thalassia Testudinum* in Florida Bay. Bulletin of Marine Science 54:733–746. http:// pascal-francis.inist.fr/vibad/index.php?action=getRecordDet ail&idt=4213623
- Coastal Eco–Group, Inc. 2016. Lake Worth Lagoon Fixed Transect Seagrass Monitoring: Cumulative Report 2015. Technical Report. Palm Beach County Department of Environmental Resources Management, Deerfield Beach, FL, USA, 170 p.
- Crigger, D.K., G.A. Graves, and D.L. Fike. 2005. Lake Worth Lagoon conceptual ecological model. Wetlands 25:943–954. https://doi.org/10.1672/02775212(2005)025[0943:LWLCE M]2.0.CO;2
- Dawes, C.J., M.O. Hall, and R.K. Riechert. 1985. Seasonal biomass and energy content in seagrass communities on the west coast of Florida. Journal of Coastal Research 1:255–262. https://journals.flvc.org/jcr/article/view/77259
- Duarte, C.M. 1991. Seagrass depth limits. Aquatic Botany 40:363-

377. https://doi.org/10.1016/0304-3770(91)90081-F

- Duarte, C.M., J. Terrados, N.S.R. Agawin, M.D. Fortes, S. Bach, and W.J. Kenworthy. 1997. Response of a mixed Philippine seagrass meadow to experimental burial. Marine Ecology Progress Series 147:285–294. https://doi.org/10.3354/ meps147285
- Durako, M.J. 1994. Seagrass die–off in Florida Bay (USA): Changes in shoot demographic characteristics and population dynamics in *Thalassia testudinum*. Marine Ecology Progress Series 110:59–66. https://doi.org/10.3354/meps110059
- Erftemeijer, P.L.A. and R.R. Lewis, III. 2006. Environmental impacts of dredging on seagrasses: A review. Marine Pollution Bulletin 52:1553–1572. https://doi.org/10.1016/j.marpolbul.2006.09.006
- Florida Department of Environmental Protection. 2016. Lake Worth Lagoon–Palm Beach Coast Watershed. Arquivo.pt. https://arquivo.pt/wayback/20160517001525/http:/www. protectingourwater.org/watersheds/map/lake_worth_lagoon_palm_beach_c/. (Accessed 9/15/2021).
- Fourqurean, J.W. and M.B. Robblee. 1999. Florida Bay: A history of recent ecological changes. Estuaries 22:345–357. https://doi.org/10.2307/1353203
- Fourqurean, J.W., G.V.N. Powell, W.J. Kenworthy, and J.C. Zieman. 1995. The effects of long-term manipulations of nutrient supply on competition between seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. Oikos 72:349–358. https://doi.org/10.2307/3546120
- Fourqurean, J.W., A. Willsie, C.D. Rose, and L.M. Rutten. 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. Marine Biology 138:341–354. https://doi.org/10.1007/s002270000448
- Greve, T.M. and T. Binzer. 2004. Which factors regulate seagrass growth and distribution? In: J. Borum, C.M. Duarte, D. Krause–Jensen, and T.M. Greve, eds. European Seagrasses: An Introduction to Monitoring and Management. The M&MS Project, European Union, University of Copenhagen, Denmark, p. 19–23.

- Gu, R., J. Statton, S. Rahmawati, R. Hovey, Y. Zhou, J. Tang, S. Yu, and G.A. Kendrick. 2022. Seed bank dynamics and quality in the seagrass *Halophila ovalis* along estuarine salinity gradients—a case in the Swan—Canning Estuary. Frontiers in Marine Science 9:1025615. https://doi.org/10.3389/ fmars.2022.1025615
- Hammerstrom, K.K., W.J. Kenworthy, M.S. Fonseca, and P.E. Whitfield. 2006. Seed bank, biomass, and productivity of *Halophila decipiens*, a deepwater seagrass on the west Florida continental shelf. Aquatic Botany 84:110–120. https://doi. org/10.1016/j.aquabot.2005.08.002
- Handley, L. and C. Lockwood. 2020. Florida statewide status and trends. In: L. Handley and C. Lockwood, eds. Seagrass Status and Trends Update for the Northern Gulf of Mexico: 2002 –2017. Final Report to the Gulf of Mexico Alliance for Contract No.: 121701–00, Ocean Springs, MS, USA, p. 42–73.
- Hauxwell, J., J. Cebrián, C. Furlong, and I. Valiela. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. Ecology 82:1007–1022. https://doi.org/10.1890/0012–9658(2001)082[1007:MCCT EZ]2.0.CO;2
- Haynes, D., P. Ralph, J. Prange, and B. Dennison. 2000. The impact of the herbicide diuron on photosynthesis in three species of tropical seagrass. Marine Pollution Bulletin 42:288–293. https://doi.org/10.1016/S0025–326X(00)00127–2
- Hendriks, I.E., Y.S. Olsen, L. Ramajo, L. Basso, A. Steckbauer, T.S. Moore, J. Howard, and C.M. Duarte. 2014. Photosynthetic activity buffers ocean acidification in seagrass meadows. Biogeosciences 11:333–346. https://doi.org/10.5194/ bg-11-333-2014
- Hughes, A.R, S.L. Williams, C.M. Duarte, K.L. Heck, Jr., and M. Waycott. 2009. Associations of concern: Declining seagrasses and threatened dependent species. Frontiers in Ecology and the Environment 7:242–246. https://doi.org/10.1890/080041
- Jun Bando, K. 2006. The roles of competition and disturbance in a marine invasion. Biological Invasions 8:755–763. https://doi.org/10.1007/s10530–00503543–4
- Kemp, W.M. 2000. Seagrass ecology and management: An introduction. In: S.A. Bortone, ed. Seagrasses: Monitoring, Ecology, Physiology, and Management. CRC Press, Boca Raton, FL, USA, p. 1–8.
- Koch, M.S., S.A. Schopmeyer, C. Kyhn–Hansen, C.J. Madden, and J.S. Peters. 2007. Tropical seagrass species tolerance to hypersalinity stress. Aquatic Botany 86:14–24. https://doi. org/10.1016/j.aquabot.2006.08.003
- Krupp, L.S., J. Cortés, and M. Wolff. 2009. Growth dynamics and state of seagrass *Thalassia testudinum* in the Gandoca– Manzanillo National Wildlife Refuge, Caribbean, Costa Rica. Revista de Biología Tropical 57:187–201. http://www. scielo.sa.cr/scielo.php?script=sci_arttext&pid=S0034– 77442009000500017&lng=en&nrm=iso.
- Laboy–Neives, E. 2009. Environmental profile and management issues in an estuarine ecosystem: A case study from Jobos Bay, Puerto Rico. In: E. Laboy–Neives, F. Schaffner, and A.G. Abdelhadi, eds. Environmental Management, Sustainable De-

velopment and Human Health. Taylor and Francis, London, UK, p. 361–397.

- Longstaff, B.J. and W.C. Dennison. 1999. Seagrass survival during pulsed turbidity events: The effects of light deprivation on the seagrasses *Halodule pinifolia* and *Halophila ovalis*. Aquatic Botany 65:105–121. https://doi.org/10.1016/S0304– 3770(99)00035–2
- McCarthy, M.J., F.E. Muller–Karger, D.B. Otis, and P. Méndez–Lázaro. 2018. Impacts of 40 years of land cover change on water quality in Tampa Bay, Florida. Cogent Geoscience 4:1422965. https://doi.org/10.1080/23312041.2017.1422956
- McDonald, A.M., P. Prado, K.L. Heck, Jr., J.W. Fourqurean, T.A. Frankovich, K.H. Dunton, and J. Cebrian. 2016. Seagrass growth, reproductive, and morphological plasticity across environmental gradients over a large spatial scale. Aquatic Botany 134:87–96. https://doi.org/10.1016/j.aquabot.2016.07.007
- McGlathery, K.J. 2001. Macroalgal blooms contribute to the decline of seagrass in nutrient—enriched coastal waters. Journal of Phycology 37:453–456. https://doi.org/10.1046/j.1529– 8817.2001.037004453.x
- Mickle, P.F., J.F. Schaefer, S.B. Adams, and B.R. Keiser. 2010. Habitat use of age 0 Alabama shad in the Pascagoula River drainage, USA. Ecology of Freshwater Fish 19:107–115. https://doi.org/10.1111/j.1600–0633.2009.00395.x
- Orlando, B., E. Anderson, and L.A. Yarbro. 2016. Summary report of Lake Worth Lagoon. In: L. Yarbro and P.R. Carlson, eds. Seagrass Integrated Mapping and Monitoring Report No. 2. Fish and Wildlife Research Institute Technical Report TR–17, version 2, Fish and Wildlife Research Institute, St. Petersburg, FL, USA, p. 246–254. http://hdl.handle.net/1834/41129
- Orth, R.J., M.C. Harwell, E.M. Bailey, A. Bartholomew, J.T. Jawad, A.V. Lombana, K.A. Moore, J.M. Rhode, and H.E. Woods. 2000. A review of issues in seagrass seed dormancy and germination: Implications for conservation and restoration. Marine Ecology Progress Series 200:277–288. https://doi.org/10.3354/meps200277
- Orth, R.J., T.J.B. Carruthers, W.C. Dennison, C.M. Durate, J.W. Fourqurean, K.L. Heck, Jr., A.R. Hughes, G.A. Kendrick, W.J. Kenworthy, S. Olyarnik, F.T. Short, M. Waycott, and S.L. Williams. 2006a. A global crisis for seagrass ecosystems. Bioscience 56:987–996. https://doi.org/10.1641/0006– 3568(2006)56[987:AGCFSE]2.0.CO;2
- Orth R.J., M.C. Harwell, and G.J. Inglis. 2006b. Ecology of seagrass seeds and seagrass dispersal processes. In: A.W.D. Larkum, R.J. Orth, and C.M. Duarte, eds. Seagrasses: Biology, Ecology, and Conservation. Springer, Dordrecht, Netherlands, p. 111-133.
- Palm Beach County. 2021. Lake Worth Lagoon Management Plan 2021. http://discover.pbcgov.org/erm/Publications/LWLManagementPlan 2021.pdf. (Accessed 9/15/2021).
- Provancha, J.A. and D.M. Scheidt. 2000. Long-term trends in seagrass beds in the Mosquito Lagoon and northern Banana River, Florida. In: S.A. Bortone, ed. Seagrasses: Monitoring, Ecology, Physiology, and Management. CRC Press, Boca Raton, FL, USA, p. 177–196.

- Quinn, G.P. and M.J. Keough. 2002. Principal components and correspondence analysis. In: G.P. Quinn and M.J. Keough, eds. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK, p. 443–458.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R–project.org/
- Ralph, P.J. 1998. Photosynthetic response of laboratory cultured Halophila ovalis to thermal stress. Marine Ecological Progress Series 171:123–130. https://doi.org/10.3354/meps171123
- Rudnick, D.T., Z. Chen, D.L. Childers, and T.D. Fontaine. 1999. Phosphorus and nitrogen inputs to Florida Bay: The importance of the Everglades watershed. Estuaries 22:398–416. https://doi.org/10.2307/1353207
- Schlueter, M.A. 1998. Gene flow and genetic diversity of turtle grass, *Thalassia testudinum*, banks ex könig, in the lower Florida Keys. Aquatic Botany 61:147–167. https://doi.org/10.1016/ S0304–3770(98)00063–1
- Sherwood, E.T., H.S. Greening, A.J. Janicki, and D.J. Karlen. 2016. Tampa Bay estuary: Monitoring long-term recovery through regional partnerships. Regional Studies in Marine Science 4:1–11. https://doi.org/10.1016/j.rsma.2015.05.005
- Short, F.T., B. Polidoro, S.R. Livingstone, K.E. Carpenter, S. Bandeira, J.S. Bujang, H.P. Calumpong, T.J.B. Carruthers, R.G. Coles, W.C. Dennison, P.L.A. Erftemeijer, M.D. Fortes, A.S. Freeman, T.G. Jagtap, A.H.M. Kamal, G.A. Kedrick, W.J. Kenworthy, Y.A. La Nafie, I.M. Nasution, R.J. Orth, A. Prathep, J.C. Sanciangco, B. van Tussenbroek, S.G. Vergara, M. Waycott, and J.C. Zieman. 2011. Extinction risk assessment of the world's seagrass species. Biological Conservation 144:1961–1971. https://doi.org/10.1016/j.biocon.2011.04.010
- Tiling, K. and C.E. Proffitt. 2017. Effects of Lyngbya majuscula blooms on the seagrass Halodule wrightii and resident invertebrates. Harmful Algae 62:104–112. https://doi.org/10.1016/j. hal.2016.11.015
- Unsworth, R.K.F., C.J. Collier, M. Waycott, L.J. Mckenzie, and L.C. Cullen–Unsworth. 2015. A framework for the resilience of seagrass ecosystems. Marine Pollution Bulletin 100:34–46. https://doi.org/10.1016/j.marpolbul.2015.08.016

- Wall, C.C., C.J. Gobler, B.J. Peterson, and J.E. Ward. 2013. Contrasting growth patterns of suspension—feeding molluscs (*Mercenaria mercenaria*, *Crassostrea virginica*, *Argopecten irradians*, and *Crepidula fornicate*) across a eutrophication gradient in the Peconic Estuary, NY, USA. Estuaries and Coasts 36:1274– 1291. https://doi.org/10.1007/s12237–013–9632–1
- Waycott, M., C.M. Duarte, T.J. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, K.L. Heck, Jr., and A.R. Hughes. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Science 106:12377–12381. https:// doi.org/10.1073/pnas.0905620106
- Willette, D.A. and R.F. Ambrose. 2012. Effects of the invasive *Halophila stipulacea* on the native seagrass *Syringodium filiforme*, and associated fish and epibiota communities in the eastern Caribbean. Aquatic Botany 103:74–82. https://doi.org/10.1016/j.aquabot.2012.06.007
- Xu, S.C., Y. Zhou, P.M. Wang, F. Wang, X.M. Zhang, and R.T. Gu. 2016. Salinity and temperature significantly influence seed germination, seedling establishment, and seedling growth of eelgrass *Zostera marina*. PeerJ 4:e2697. https://doi. org/10.7717/peerj.2697
- York, P., T. Smith, R. Coles, S. McKenna, R. Connolly, A.D. Irving, E.L. Jackson, K. McMahon, J.W. Runcie, C.D.H. Sherman, B.K. Sullivan, S.M. Trevathan–Tackett, K.E. Brodersen, A.B. Carter, C.J. Ewers, P.S. Lavery, C.M. Roelfsema, E.A. Sinclair, S. Strydom, J.E. Tanner, K.V. Dijk, F.Y. Warry, M. Waycott, and S. Whitehead. 2017. Identifying knowledge gaps in seagrass research and management: An Australian perspective. Marine Environmental Research 127:163–172. https://doi.org/10.1016/j.marenvres.2016.06.006
- Zieman, J.C. 1975. Seasonal variation of turtle grass, *Thalassia testudinum* König, with reference to temperature and salinity effects. Aquatic Botany 1:107–123. https://doi.org/10.1016/034–3770(75)90016–9
- Zieman, J.C., J.W. Fourqurean, and R.L. Iverson. 1989. Distribution, abundance, and productivity of seagrasses and macroalgae in Florida Bay. Bulletin of Marine Science 44:292–311. http://pascal-francis.inist.fr/vibad/index.php?action=getRe cordDetail&idt=19736176