Functional implications of changes in seagrass species composition in two shallow coastal lagoons

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ABSTRACT: While the consequences of losing seagrass meadows are well known, there is less information on the functional implications of changes in seagrass species composition. In this study, we use data from a long-term monitoring project in shallow lagoons on the Florida Gulf Coast to assess changes in the functional attributes of seagrass beds during a shift in seagrass species composition. We compare seagrass beds in 2 neighboring lagoons with different trends: one where the composition changed from 100 % *Halodule wrightii* to a mixed bed with up to 60 % *Ruppia maritima*, and one where the species composition remained unchanged. Our results indicate that the partial replacement of *H. wrightii* by *R. maritima* did not alter seagrass biomass m⁻², detrital biomass m⁻², benthic gross primary production, or benthic respiration. However, there was a small positive effect on benthic net primary production. While seagrass biomass m⁻² declined at both sites, the emergence of *R. maritima* increased the amount of available habitat through rapid expansion. Overall, our data suggest that shifts between 2 seagrass species with similar morphology, but different ecological strategies, may have little impact on the ecosystem services of seagrass beds in shallow coastal lagoons.

KEY WORDS: *Ruppia maritima* · *Halodule wrightii* · Seagrass · Species shift · Ecosystem metabolism

INTRODUCTION

Seagrass beds are important, yet vulnerable components of coastal ecosystems. They provide habitat for a wide range of organisms (Orth et al. 1984), improve water quality by stabilizing sediments (de Boer 2007), and are an important sink for carbon on a global scale (Fourqurean et al. 2012). However, they are sensitive to effects of human activities, such as dredging (Gonzalez-Correa et al. 2005), physical disturbances (Sargent et al. 1995), and the excessive input of nutrients and organic matter from coastal watersheds (Burkholder et al. 2007). During the last century, many coastal regions have experienced large decreases in seagrass cover (Waycott et al. 2009). In addition, there have been several reports of

changes in seagrass species composition throughout the United States (Quammen & Onuf 1993, Provan-cha & Scheidt 2000, Johnson et al. 2003, Cho et al. 2009, Lopez-Calderon et al. 2010, Moore et al. 2013). While the effects of loss of seagrass cover are well described, there is less information on the functional implications of changes in the dominant seagrass species. Biomass, production, and the fate of production can vary significantly between different species (Duarte 1991, Cebrian et al. 1997). As such, it is possible that changes in seagrass species composition can influence the role of seagrass beds in coastal ecosystems.

Halodule wrightii and *Ruppia maritima* are widespread and abundant along the coast of the Gulf of Mexico. These 2 seagrass species are morphologi-

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cally similar and often occur in mixed beds, but they have different ecological strategies: *R. maritima* can be classified as a colonizing species, while *H. wrightii* is closer to an opportunistic seagrass species (Kilminster et al. 2015). Colonizing seagrasses have the ability to quickly establish themselves in new areas, but their biomass can fluctuate significantly over time (Pulich 1985, Cho et al. 2009, Kilminster et al. 2015). They quickly reach sexual maturity and produce large amounts of seeds (Bonis et al. 1995). In the case of *R. maritima*, these seeds can remain dormant for extended periods of time (Kantrud 1991) and are able to survive passage through the digestive system of waterfowl and fish, which favors long-distance dispersal of the plants (Agami & Waisel 1988, Charalambidou et al. 2003).

Opportunistic species also have the ability to colonize new areas, but they tend to form meadows that are more persistent over time and have greater resistance to physiological disturbances than purely colonizing species (Kilminster et al. 2015). *H. wrightii* is a perennial seagrass that maintains a high level of productivity under a wide variety of light, nutrient, and salinity conditions (Dunton 1996). In the Gulf of Mexico, *H. wrightii* forms overwintering populations that exhibit more consistent growth rates and allocate a larger fraction of total biomass to roots and rhizomes compared to *R. maritima* (Dunton 1990, Kantrud 1991, Antón et al. 2009).

Both *H. wrightii* and *R. maritima* tolerate a wide range of salinities, ranging from nearly fresh water to >50 psu (Dunton 1990, Kantrud 1991, Doering et al. 2002, Koch et al. 2007). However, *R. maritima* is able

to outcompete *H. wrightii* when salinity is low (Provancha & Scheidt 2000). When both species are present along an estuarine gradient, *R. maritima* will often dominate in brackish areas, while *H. wrightii* is more abundant at higher salinities (Montague & Ley 1993, Adair et al. 1994).

Many studies have documented changes in species composition due to disturbances in these tropical New World seagrass beds. Grazing, variability in freshwater input, and modified nutrient regimes have caused changes in seagrass species composition in Laguna Madre (Quammen & Onuf 1993), Lake Pontchartrain (Cho & Poirrier 2005), and the Florida Keys (Peterson et al. 2002, Fourqurean et al. 1995, Herbert & Fourqurean 2008, Herbert et al. 2011). However, there are relatively few studies that directly measured changes in functional attributes of seagrass beds during a shift from one dominant seagrass species to another (Peterson et al. 2002).

In this study, we use long-term data from 2 small coastal lagoons with different trends in seagrass species composition to explore functional consequences of a change from a *H. wrightii*- to a *R. maritima*-dominated seagrass bed. We employ a paired BACI design to test (1) if the change from *H. wrightii* to *R. maritima* did affect aboveground biomass m^{-2} , belowground biomass m^{-2} , and detritus m^{-2} at our sites and (2) if the change from *H. wrightii* to *R. maritima* did affect benthic net primary production, benthic gross primary production, and benthic respiration at our sites. Testing these hypotheses will provide insights on potential impacts of shifts in the dominant seagrass species on carbon cycling, carbon storage, and habitat characteristics of seagrass beds in shallow coastal lagoons.

MATERIALS AND METHODS

We used data from a long-term study in 2 shallow coastal embayments, located in the Perdido Bay area, Florida, along the north central Gulf of Mexico: Kees Bayou (30.310°N, 87.469°W) and State Park (30.308°N, 87.403°W). These 2 sites are relatively close to each other and experience similar weather patterns (Fig. 1). State Park is the site with the least amount of human disturbance. This shallow lagoon is entirely surrounded by salt marsh and maritime forest, with no residential development adjacent to its shoreline or in its watershed. State Park is on average 0.4 m deep, has a surface area of 15 600 m^2 , and is approximately 50% covered with *Halodule wrightii*. This site is connected to both Big Lagoon

Fig. 1. Location of the 2 study sites, Kees Bayou (KB) and State Park (SP), near Perdido Bay FL, USA

and a brackish inland lake surrounded by wetlands. Kees Bayou has residential development on the northern and the eastern sides of the lagoon, while the southern and western sides are bordered by salt marsh. Kees Bayou is on average 0.47 m deep, has a surface area of 27 400 m², and is connected to Lower Perdido Bay by a small channel that passes through a nearby lagoon. At the start of our project, in 2000, 5 % of Kees Bayou was covered by a small bed of *H. wrightii* (Stutes et al. 2007). By 2012, up to 48 % of the bottom was covered by a mixed bed of *H. wrightii* and *Ruppia maritima*. Kees Bayou is more enclosed than State Park and is more affected by freshwater inflow due to its closer proximity to Perdido Bay.

State Park and Kees Bayou were sampled 4 to 5 times per year from September 2000 to January 2012. For each sampling round, both sites were sampled within a 10 d interval on days with <10 % cloud cover. At each site, 5 cores (15 cm diameter, 10 cm deep) were randomly collected in the seagrass bed (Fig. 2). The cores were sieved through a 0.5 mm mesh, stored on ice, and transported to the lab for further analysis. In each core, shoots of *R. maritima* and *H. wrightii* were counted to determine shoot density for both seagrass species. Living plant material (rhizomes with at least 1 green shoot attached) was sorted into above-ground biomass and belowground biomass. Dead plant material was counted as detritus. The detrital fraction is likely an overestimation because it contains pieces of rhizome and shoots that were broken off when they were cut with the corer. Each fraction was measured as ash-free dry weight m⁻². Temperature, salinity, and dissolved oxygen were measured using handheld units (YSI-85 or Hach HQ40d). Light inten-

sity in the air, just beneath the surface, and on the bottom was measured using a pair of Licor-193 with spherical bulbs and a data-logger.

From December 2001 to September 2003 and from January 2005 to January 2012, we measured daytime community metabolism using short (3 to 5 h) field incubations with clear/dark BOD bottles and benthic chambers (Stutes et al. 2007, Cebrian et al. 2008, 2009, Antón et al. 2009, 2011). For each site visit, 10 pairs of clear and dark benthic incubation chambers and 5 sets of clear and dark BOD bottles were randomly placed within the seagrass beds and incubated through solar noon (Fig. 2). We measured oxygen concentrations at the start and the end of the bottle incubations using a handheld oxygen meter (WTW OXI 197 or Hack LDO). Benthic chambers were measured at the end of the incubation by extracting water from the center of each chamber through a sample port using a 60 ml syringe with an attached tube. The water was carefully transferred to a small BOD bottle and measured using the handheld oxygen meters. The average oxygen concentrations measured in the bottles immediately after filling were used as the initial oxygen concentration in the benthic chambers. We used the mean change in oxygen concentration over time from the chamber incubations to calculate benthic daytime net primary production (BNPP) and benthic daytime community respiration (BR), based on Eqs. (1) & (2). The mean change in oxygen concentration for the clear and dark bottles (Eqs. 3 & 4) was subtracted from the chamber values to correct for the head-volume enclosed in the chambers.

$$\text{BNPP} = V[(F_c - I)/dt - P_c]/A \quad (1)$$

$$\text{BR} = V[(F_d - I)/dt - P_d]/A \quad (2)$$

$$P_c = \text{average} [(FB_c - IB_c)/dt] \quad (3)$$

$$P_d = \text{average} [(FB_d - IB_d)/dt] \quad (4)$$

In Eqs. (1) & (2), V is the volume of water enclosed in the chambers (l), F_c is the final oxygen concentration in the clear chamber incubations (mg l^{-1}), F_d is the final oxygen concentration in the dark chamber incubations (mg l^{-1}), I is the initial oxygen concentration (mg l^{-1}), A is the surface enclosed by the chambers (m^2), P_c is the mean change in oxygen concentrations during the clear bottle incubations (mg l h^{-1}), and P_d is the mean change in oxygen concentrations during the dark bottle incubations (mg l h^{-1}). In Eqs. (3) & (4), FB_c is the final oxygen concentration in the clear bottles (mg l^{-1}), FB_d is the final oxygen concentration in the dark bottles (mg l^{-1}), IB_c is the initial oxygen concentration in the clear bottles (mg l^{-1}), and IB_d is the initial oxygen concentrations in the

Fig. 2. Illustration of a sample event in State Park lagoon in 2012. When a site was sampled, 10 pairs of benthic incubation chambers were placed at random locations inside the seagrass bed, 5 core samples were taken haphazardly, and environmental data was collected at 6 stations throughout the site. T: temperature; Sal: salinity; DO: dissolved oxygen

dark bottles (mg l^{-1}). Daytime gross primary production (BGPP) was calculated as the sum of BNPP and the absolute value of BR for each pair of chambers.

The percentage of seagrass cover in each of the lagoons was assessed by analyzing aerial and satellite pictures with ArcMap 10. Pictures were geo-referenced, and the shapes of the lagoons and seagrass patches were digitized as polygons. In 2011, measurements were ground-truthed by tracing the contour of the seagrass patches in both lagoons using a real-time kinematic global positioning system (RTK). The relative size of the seagrass patches was calculated as the quotient of the areal extent of the seagrass patches and the size of each lagoon.

To address our main questions, we used an approach similar to a paired BACI design (Stewart-Oaten et al. 1986): we calculated the differences in average biomass and metabolism between the 2 sites for each sample event and compared the means of these differences before and after the emergence of *R. maritima* in Kees Bayou using Welch's 2-sample *t*-tests (Stewart-Oaten et al. 1986). All data were tested for additivity, normality, and equality of variance. If necessary, data were log-transformed to meet the assumption of additivity (Stewart-Oaten et al. 1986). All statistics were calculated using Minitab 14.

RESULTS

The environmental characteristics of the water column showed significant variability over time in both State Park and Kees Bayou. Temperature (range: 6.45 to 33.75°C) and salinity (range: 3.24 to 31.59) varied significantly over seasonal timescales (Fig. 3). Salinity showed a large variability over inter-annual timescales, as it was related to the mean river discharge into Perdido Bay (Fig. 3). There was no difference in temperature and dissolved oxygen between State Park and Kees Bayou. However, salinity was significantly lower in Kees Bayou (19.96 ± 0.66 ; mean $\pm$ SE) than in State Park (23.10 ± 0.61 , paired *t*-test: $t = -6.56$, $p < 0.001$), which is likely due to its closer proximity to river discharge. Dissolved oxygen concentrations also changed on a seasonal timescale (range: 3.68 to 13.19 mg l^{-1}). Daily changes in dissolved oxygen were more pronounced during summer, when water temperatures were high (range: 0.41 to 9.37 mg l^{-1} in Kees Bayou during July 2011, measured during a short-term deployment of a YSI-6600).

From 2004 to 2012, the seagrass bed in Kees Bayou underwent marked changes (Fig. 4). The size of the seagrass bed increased, from approximately 10%

Fig. 3. (a) Temperature of the water column and (b) dissolved oxygen in State Park (white) and Kees Bayou (black). (c) River discharge from the Perdido River. (d) Salinity in State Park (white) and Kees Bayou (black). Grey bands indicate periods of high river discharge

Fig. 4. (a) The seagrass bed in State Park was relatively stable. (b) The seagrass bed in Kees Bayou expanded over time. Darker colors indicate seagrass patches dominated by *H. wrightii*, lighter colors indicate patches dominated by *R. maritima*

cover in December 2004 to 48% cover in January 2012. During that time, the species composition changed from a homogeneous bed of *Halodule wrightii* to a mixed bed dominated by *Ruppia maritima* (up to 60% *R. maritima*; Fig. 5). The seagrass bed in State Park was more stable. The size of the seagrass bed remained more or less constant at 50% cover (Fig. 4), and the species composition remained the same (almost 100% *H. wrightii*; Fig. 5). The change in species cover occurred after a period of low salinity in Kees Bayou and high river discharge into Perdido Bay (Fig. 3).

Fig. 6 illustrates that average aboveground and belowground biomass m^{-2} was higher in State Park compared to Kees Bayou but that average biomass m^{-2} declined in both sites (Table 1). These trends were mirrored by the averaged metabolism data (Fig. 6). The *t*-tests comparing paired differences between the sites before and after January 2006 indicate that aboveground biomass m^{-2} , belowground biomass m^{-2} , and BGPP declined equally in State Park and Kees Bayou (Table 2, Fig. 7). The relative difference in BNPP did change significantly over time (Table 2), indicating that the decline in BNPP was more pronounced at State Park. However, the *t*-test was only significant after removing an outlier from the analysis ($-125.2 \text{ mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$ in June 2002, not shown on Fig. 7). Fig. 6 illustrates that detrital biomass m^{-2} and BR were higher in State Park than in Kees Bayou. The *t*-tests comparing relative differences between sites before and after January 2006

Fig. 5. Change in species composition in State Park (white) and Kees Bayou (black), expressed as the percentage of *Ruppia maritima* shoots per core sample, averaged per year. Before and after indicate the periods before and after the emergence of *R. maritima* in Kees Bayou. Error bars represent standard error

showed no significant effect for either BR or detritus m^{-2} , but the *p*-value for detritus m^{-2} was relatively small ($p = 0.051$). After January 2006, there was a bigger spread in the differences between the sites for detrital biomass m^{-2} , as indicated by indicated by Fig. 7 (Levene's test: $p = 0.006$).

DISCUSSION

Changes in seagrass species composition can alter the role of seagrass beds in coastal ecosystems. Dif-

Fig. 6. Changes in (a) aboveground biomass (AB), (b) belowground biomass (BE), (c) detritus, (d) benthic net primary production (BNPP), (e) benthic gross primary production (BGPP), and (f) benthic respiration (BR) in State Park (white) and Kees Bayou (black), before (years 2000–2005) and after (2006–2012) the shift in species composition in Kees Bayou. Error bars represent standard error

ferent seagrass species have different morphology and growth rates, which influence the amount of food and shelter available to epifauna and fish communities associated with seagrass beds (Hyndes et al.

2003, Micheli et al. 2008, Ray et al. 2014). Differences in growth rates, above/belowground biomass ratios, and leaf turnover rates have the potential to influence herbivory (Cebrian & Duarte 1998), accumulation of refractory detritus (Cebrian et al. 1997), and the export of organic matter from seagrass beds to adjacent ecosystems (Mateo et al. 2006). Nevertheless, our data indicate that certain seagrasses may be functionally equivalent. The comparison of structural and functional attributes of seagrass beds in State Park and Kees Bayou suggests that the substitution of *Halodule wrightii* by *Ruppia maritima* in Kees Bayou had little impact on ecosystem services.

Aboveground biomass m^{-2} and belowground biomass m^{-2} declined equally in both sites, so we cannot attribute the decline to the change in species composition in Kees Bayou. It is more likely that both sites were impacted by an external factor, such as changes in environmental drivers or an increase in nutrient load. The overall lower seagrass biomass m^{-2} in Kees Bayou was probably due to different site characteristics, such as sediment composition or flushing rate. These factors can affect seagrass growth through changes in nutrient availability and sediment sulfide concentrations

(Valiela et al. 1997, de Boer 2007). It is somewhat surprising that the emergence of *R. maritima* did not have a stronger impact on seagrass biomass m^{-2} , as *R. maritima* and *H. wrightii* have different life strate-

Table 1. Average, standard error and sample size for biomass, detritus and metabolism of all sample events in each lagoon from 2000–2005 and 2006–2012

	Year	State Park			Kees Bayou		
		Mean	SE	n	Mean	SE	n
Aboveground biomass (g AFDW m^{-2})	00–05	38.1	5.4	29	26.1	4.0	29
	06–12	16.8	2.1	26	13.7	1.4	26
Belowground biomass (g AFDW m^{-2})	00–05	100.5	9.3	29	74.5	7.2	29
	06–12	46.8	3.6	26	31.3	3.2	26
Detritus (g AFDW m^{-2})	00–05	396.2	16.4	27	207.9	11.7	27
	06–12	438.1	35.6	25	168.8	8.2	25
Net primary production (mg $\text{O}_2 \text{m}^{-2} \text{h}^{-1}$)	00–05	87.6	13.0	15	48.7	7.6	15
	06–12	26.4	8.9	26	18.1	8	26
Gross primary production (mg $\text{O}_2 \text{m}^{-2} \text{h}^{-1}$)	00–05	160.4	14.4	15	98.6	9.6	15
	06–12	110.9	11.6	26	67.2	8.8	26
Respiration (mg $\text{O}_2 \text{m}^{-2} \text{h}^{-1}$)	00–05	71.5	11.9	15	49.3	5.4	15
	06–12	85.4	9.2	26	47.7	4.8	26

Table 2. Welch's 2-sample *t*-test comparing the paired differences between the sites for aboveground biomass (AB), belowground biomass (BE), detritus (DET), benthic net primary production (BNPP), benthic gross primary production (BGPP), and benthic respiration (BR) between 2000–2005 and 2006–2012. AB and BR were log transformed to meet the assumption of additivity. SP: State Park; KB: Kees Bayou. **p* < 0.05 (changes are considered significant)

Variable	df	<i>t</i>	<i>p</i>
log(SP AB) – log(KB AB)	52	1.35	0.181
SP BE – KB BE	48	1.25	0.216
SP DET – KB DET	33	2.02	0.051
SP BNPP – KB BNPP	19	1.54	0.140
SP BNPP – KB BNPP (outlier removed)	20	2.5	0.021*
SP BGPP – KB GPP	18	0.87	0.398
log(SP BR) – log(KB BR)	28	0.36	0.724

gies. In monotypic beds of *H. wrightii*, the biomass of roots and rhizomes, averaged over a growth cycle, typically comprises 55 to 86 % of the total biomass on a per m² basis (Table 3). In mixed beds and in monotypic *R. maritima* beds, these values tend to be a lot lower: annual averages of belowground biomass range between 23 and 65 % of total biomass (Table 3). The contribution of belowground biomass to total biomass did not differ much between the monotypic seagrass bed in State Park and the mixed seagrass bed in Kees Bayou: between 2006 and 2012, belowground biomass comprised approximately 74 % of the total biomass in State Park and 68 % in Kees Bayou. The lack of a strong

Fig. 7. Paired differences between State Park SP and Kees Bayou KB for (a) log mean aboveground biomass (AB), (b) belowground biomass (BE), (c) detritus (DET), (d) benthic net primary production (BNPP), (e) benthic gross primary production (BGPP), and (f) log benthic respiration (BR)

Table 3. Aboveground biomass (AB), belowground biomass (BE), and the contribution of BE to total biomass of *Halodule wrightii* (Hal) and *Ruppia maritima* (Rup), averaged over the entire study period, in previous studies that spanned ≥ 1 entire growing seasons (mean $\pm$ SE). The input values for these calculations were extracted from figures, using the open source program WebPlotDigitizer (Rohatgi 2011)

Source	Site	Year	Species	AB	BE	Total	BE as % of total biomass	Sample events
Sordo (2011)	Paranagua Bay (Brazil)	2004–2005	Hal	3 $\pm$ 1	16 $\pm$ 4	19 $\pm$ 5	86 $\pm$ 34	6
Kowalski (2009)	Laguna Madre – LLM 107 (TX, USA)	1995–1997	Hal	31 $\pm$ 3	150 $\pm$ 14	181 $\pm$ 15	83 $\pm$ 10	19
This study	State Park (AL, USA)	2006–2012	Hal	17 $\pm$ 2	47 $\pm$ 4	64 $\pm$ 5	74 $\pm$ 2	26
This study	Kees Bayou (AL, USA)	2000–2005	Hal	26 $\pm$ 1	75 $\pm$ 7	101 $\pm$ 3	73 $\pm$ 3	29
This study	State Park (AL, USA)	2000–2005	Hal	38 $\pm$ 5	100 $\pm$ 9	138 $\pm$ 13	73 $\pm$ 2	29
Pulich (1985)	Laguna Madre (TX, USA)	1982	Hal	103 $\pm$ 22	269 $\pm$ 11	373 $\pm$ 32	72 $\pm$ 7	9
Burd (2001)	Laguna Madre – LM 151 (TX, USA)	1989–1997	Hal	86 $\pm$ 8	187 $\pm$ 17	272 $\pm$ 22	69 $\pm$ 8	41
This study	Kees Bayou (AL, USA)	2006–2012	Hal + Rup	14 $\pm$ 1	31 $\pm$ 3	45 $\pm$ 4	68 $\pm$ 2	26
McGovern (2007)	West Point aux Pines (AL, USA)	2006	Hal	13 $\pm$ 3	25 $\pm$ 5	38 $\pm$ 8	65 $\pm$ 19	13
Antón et al. (2009)	Sandy Bay (AL, USA)	2005–2006	Hal + Rup	14 $\pm$ 2	27 $\pm$ 4	41 $\pm$ 6	65 $\pm$ 14	14
Short (2006)	Tamandare (Brazil)	2002–2005	Hal	44 $\pm$ 9	77 $\pm$ 9	121 $\pm$ 15	63 $\pm$ 11	11
Dunton (1996)	East Flats – NEF (TX, USA)	1989–1994	Hal	97 $\pm$ 11	161 $\pm$ 11	258 $\pm$ 15	62 $\pm$ 6	29
Pulich (1985)	Redfish Bay (TX, USA)	1982	Hal	113 $\pm$ 20	169 $\pm$ 22	282 $\pm$ 41	60 $\pm$ 12	8
Cho & Poirrier (2005)	Lacombe (LA, USA)	2000–2002	Rup	33 $\pm$ 6	44 $\pm$ 4	77 $\pm$ 8	57 $\pm$ 8	26
Cho & Poirrier (2005)	Fontainebleau (LA, USA)	2000–2002	Rup	33 $\pm$ 9	42 $\pm$ 3	75 $\pm$ 11	56 $\pm$ 9	27
Dunton (1996)	San Antonio Bay – GBP (TX, USA)	1989–1994	Hal	27 $\pm$ 5	33 $\pm$ 3	60 $\pm$ 7	55 $\pm$ 11	25
Cho & Poirrier (2005)	Lincoln (LA, USA)	2000–2002	Rup	53 $\pm$ 10	51 $\pm$ 5	103 $\pm$ 14	49 $\pm$ 8	27
McGovern (2009)	Bayou la Batre – deep (AL, USA)	2006	Rup	9 $\pm$ 1	8 $\pm$ 1	16 $\pm$ 3	48 $\pm$ 11	9
Pulich (1985)	Redfish Bay (TX, USA)	1982	Hal + Rup	92 $\pm$ 11	79 $\pm$ 7	172 $\pm$ 17	46 $\pm$ 6	20
McGovern (2009)	Point aux Pines – deep (AL, USA)	2006	Rup	13 $\pm$ 2	10 $\pm$ 1	23 $\pm$ 2	45 $\pm$ 6	11
McGovern (2009)	Bayou la Batre – shallow (AL, USA)	2006	Rup	12 $\pm$ 3	9 $\pm$ 2	21 $\pm$ 5	43 $\pm$ 12	9
Cho & Poirrier (2005)	Herbes (LA, USA)	2000–2002	Rup	60 $\pm$ 16	42 $\pm$ 5	102 $\pm$ 20	41 $\pm$ 10	27
McGovern (2009)	Point aux Pines – shallow (AL, USA)	2006	Rup	22 $\pm$ 5	15 $\pm$ 1	37 $\pm$ 6	40 $\pm$ 8	12
McGovern (2009)	Bayou Heron – shallow (AL, USA)	2006	Rup	9 $\pm$ 2	6 $\pm$ 1	15 $\pm$ 3	39 $\pm$ 10	12
McGovern (2009)	Bayou Heron Island – shallow (AL, USA)	2006	Rup	27 $\pm$ 8	14 $\pm$ 2	41 $\pm$ 10	34 $\pm$ 9	12
McGovern (2009)	Bayou Heron – deep (AL, USA)	2006	Rup	26 $\pm$ 6	11 $\pm$ 2	37 $\pm$ 8	30 $\pm$ 9	11
Pulich (1985)	Laguna Madre (TX, USA)	1982	Rup	52 $\pm$ 9	19 $\pm$ 2	71 $\pm$ 9	27 $\pm$ 4	10
McGovern (2009)	Bayou Heron Island – deep (AL, USA)	2006	Rup	53 $\pm$ 20	16 $\pm$ 3	69 $\pm$ 22	23 $\pm$ 8	9

effect of the introduction of *R. maritima* on aboveground and belowground biomass m^{-2} could be related to environmental conditions in our sites. After January 2006, the total seagrass biomass m^{-2} in State Park and Kees Bayou was relatively low compared to other *H. wrightii* and *R. maritima* beds along the Gulf of Mexico (Table 3), indicating that both seagrass beds were growing in suboptimal conditions.

Net ecosystem metabolism is the net effect of production and respiration for all biological components in an ecosystem. A positive value indicates that the system is autotrophic, which means that the combined photosynthesis rate of all biological components exceeds the community respiration rate. A negative value is an indicator of a heterotrophic system, where community respiration exceeds *in situ* primary production (Smith & Hollibaugh 1997, Caffrey 2004). Our measurements of benthic net ecosystem metabolism are based on *in situ* daytime incubations, under standardized conditions (<10% cloud cover, incubations over solar noon), and as such, they cannot be used to accurately determine the trophic status of the seagrass beds. Another caveat is that we do not have measurements of seagrass biomass within the metabolism incubation chambers, so we cannot link measurements from individual chambers to the biomass of primary producers enclosed. However, our metabolism data can be used to compare values among lagoons and over time.

There was no significant change in relative differences

in BGPP between the lagoons before and after January 2006. However, our data indicate that the decline in BNPP was bigger in State Park than in Kees Bayou. The similarity between average seagrass biomass and average primary production suggests that the lower values after January 2006 are the result of an overall decline in photosynthetic biomass. Between 2006 and 2012, BGPP in seagrass beds in State Park and Kees Bayou was relatively low compared to values from other studies with similar methods (Murray & Wetzel 1987, Ziegler & Benner 1998, Antón et al. 2009). This further strengthens the hypothesis that both seagrass beds were growing in suboptimal conditions.

BR and detrital biomass m^{-2} followed a different trajectory compared to seagrass biomass and primary production. This suggests that a significant fraction of the dead organic matter in the sediment was coming from external sources, such as the surrounding marshes and the seagrass beds outside the lagoons. This is not surprising, as *R. maritima* and *H. wrightii* are both fast-growing seagrass species with high leaf turnover rates (Kantrud 1991, Virnstein 1982). Such species often have small pools of refractory detritus because they lose a large fraction of their production to herbivory and recycle most of their residual detrital production (Cebrian et al. 1997, Cebrian & Duarte 1998).

The total amount of seagrass habitat increased after the emergence of *R. maritima* in Kees Bayou, as the area of the bed increased from 10.7 % to 48.2 % of the lagoon surface between 2004 and 2012. This change could have influenced the overall food web within the lagoon, as infaunal and epifaunal communities often differ between seagrass beds and adjacent bare sediments (Orth et al. 1984, Ferrero-Vicente et al. 2011). However, a separate study comparing fish, macroinvertebrate, and epifaunal communities found little difference between Kees Bayou, State Park, and 4 other nearby lagoons with varying levels of seagrass cover (McDonald et al. 2016). This could be attributed to habitat redundancy between seagrass beds and fringing marshes or to the shallow depth of these lagoons, which limits access for large predators (McDonald et al. 2016).

CONCLUSION

A shift between 2 early successional seagrass species with similar morphology had little impact on the ecosystem services of seagrass beds in 2 shallow coastal lagoons. The partial replacement of *Halodule*

wrightii by *Ruppia maritima* did not alter biomass m^{-2} , detritus m^{-2} , BGPP, or BR. However, there was a small positive effect on BNPP. In addition, the emergence of *R. maritima* increased the amount of available habitat through rapid expansion. The small differences in seagrass biomass and metabolism indicate that *R. maritima* provided similar habitat as *H. wrightii*. This pattern suggests that changes in the dominant seagrass species do not always have a large effect on ecosystem services provided by seagrass beds. Despite their different life strategies, *H. wrightii* and *R. maritima* may be functionally equivalent when growing in suboptimal conditions.

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