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Chelsea M. Hester
University of West Florida

Heather M. Smith
University of West Florida

Marie E. Head
University of West Florida

Holly Langsten
University of West Florida

Samantha Linder
University of West Florida

et al.

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Comparing Productivity and Biogeochemistry of Native and Transplanted *Thalassia testudinum* and *Halodule beaudettei* in Big Lagoon, Florida, USA

CHELSEA M. HESTER, HEATHER M. SMITH, MARIE E. HEAD, HOLLY LANGSTEN, SAMANTHA LINDER, ELLEN MANOR, JOEL NORMAN, LINDSAY SARTORY, AND JANE M. CAFFREY

Seagrasses provide ecosystem services such as nursery habitats, refuge, and biogeochemical cycling. However, because seagrass communities are in decline, restoration efforts have increased. The seagrass restoration and monitoring programs at the Florida Department of Environmental Protection (FDEP) transplanted plugs of salvaged seagrasses from dock and marine construction sites. In this study, we used a 2-yr-old FDEP transplant site at Big Lagoon, Pensacola, FL, to compare primary production, respiration, and nutrient fluxes in mixed seagrass beds of *Thalassia testudinum* (turtle grass) and *Halodule beaudettei* (shoal grass) with intact, native beds of these seagrasses. We placed light and dark incubation chambers in native and transplanted seagrass beds on 10 different days during the growing season between May and Oct. to measure fluxes of oxygen, nitrate (NO_3), dissolved inorganic phosphate (DIP), and ammonium (NH_4^+). This study found no significant differences in the fluxes of any of the nutrients measured or in the production or respiration rates of native vs transplanted seagrass beds. The most significant environmental factor influencing net community production was light level. Nutrient fluxes were very low and variable, although there were consistent ammonium uptake and nitrate release early in the growing season. This rapid convergence in seagrass function by the transplanted beds to rates similar to those of native beds was likely the result of several factors, including use of plugs for restoration and planting adjacent to existing, healthy beds.

INTRODUCTION

Seagrasses are an important component of shallow marine ecosystems. They provide important services, such as food, protection, habitat, and nursery, for a variety of fauna, as well as sediment stabilization, carbon production, and export (Orth et al., 2006). Recent studies have also demonstrated that carbon sequestration by seagrass beds can be higher than that of other coastal environments (Duarte et al., 2013; Greiner et al., 2013), which is consistent with the high rates of primary production observed in these habitats. Seagrass beds also play an important role in nutrient cycling (Orth et al., 2006; McGlathery et al., 2007). Primary production and nutrient cycling are critical to the long-term success of seagrass beds. Nutrients such as nitrate, nitrite, ammonium, and phosphate are essential for the growth of seagrasses, although different seagrass species have differing nutrient uptake rates or requirements. In oligotrophic systems, retention and recycling of nutrients is critical for maintaining the health of beds. In Gulf of Mexico seagrass beds, the climax community of *Thalassia testudinum* is efficient at recycling and retaining nutrients,

particularly phosphorus, while *Halodule beaudettei* (formerly *Halodule wrightii*) can colonize and outcompete *T. testudinum* when nutrient and freshwater input are high (Fourqurean et al., 1995; Herbert et al., 2011).

Seagrass beds have declined globally as a result of anthropogenic changes such as physical modification, impaired water quality, overfishing, invasive species, and global climate change (Short and Wyllie-Echeverria, 1996; Orth et al., 2006; Waycott et al., 2009). The largest cause of seagrass decline is anthropogenic pollution from point and nonpoint sources (Ralph et al., 2006). Nutrient loading is also linked the rapid decline of seagrass beds; in all regions, an excess of nutrients or sediments in seagrass communities is the most common and significant cause of decline (Orth et al., 2006). Thus, there has been an increasing emphasis on restoration (Fonseca et al., 1998; Orth et al., 2006; Fonseca, 2011).

An important goal of restoration is to create seagrass beds that are functionally equivalent to natural beds. Evaluating the success of restored seagrass beds has commonly focused on metrics related to seagrass biomass, such as percent survival, shoot counts, stem density, and percent cover (Fonseca et al., 1998; Fonseca, 2011).

Fig. 1. Map of study area in Big Lagoon, FL, showing sampling sites for native (Na) and transplanted (Tr) seagrass beds.

Habitat use by fish and invertebrates has also been compared in restored and natural beds (Sheridan, 2004). However, few restoration projects have evaluated microbial processes, and we were unable to find any studies comparing primary productivity and respiration in restored seagrass beds and natural beds. In restored seagrass beds of different ages, primary productivity and respiration increased with age of bed (Rheuban et al., 2014). In one study, 7 yr after restoration, nitrogen fixation in restored eelgrass beds was similar to rates observed in mature meadows (Cole and McGlathery, 2012). In contrast, the microbial

community structure in restored seagrass beds was less complex than in reference beds (Bourque et al., 2015). More productive beds have higher standing crops (Zieman et al., 1989), which should result in higher net community productivity, gross primary productivity, and dissolved nutrient fluxes. Productivity within the beds also has important implications for nutrient recycling, retention, and carbon sequestration within the system.

Primary productivity, respiration, and sediment-water nutrient fluxes were compared between restored and adjacent native seagrass beds of mixed *T. testudinum* and *H. beaudettei*. We were

TABLE 1. Temperature, salinity, dissolved oxygen (DO), nutrient concentration, and light measurements from Big Lagoon, FL. Mean light levels from readings every 15 min over the duration of the incubation. Concentrations less than the MDL value for that nutrient are indicated with a “less than” symbol (<) and the determined MDL value. n.d. indicates no data.

Date	Temperature, °C	Salinity	DO, mg/L	NO ₃ ⁻ , μM	NH ₄ ⁺ , μM	DIP, μM	Mean light, μE/m ² /sec	% Surface irradiance	Light attenuation, per meter
Early									
18 May 2011	24.6	28.4	7.87	<0.27	<0.07	<0.05	n.d.	n.d.	n.d.
19 May 2011	23.2	25.7	6.95	<0.27	0.00	0.057	716	77	0.500
20 May 2011	24.3	26.8	8.49	<0.27	<0.07	<0.05	831	58	1.19
Peak									
16 June 2011	28.5	20.0	5.33	<0.27	0.33	<0.05	1,020	91	0.360
24 June 2011	30.3	24.9	4.16	<0.27	0.076	0.076	451	68	1.56
1 July 2011	30.6	25.5	7.42	<0.27	1.2	0.11	767	80	0.930
8 July 2011	31.1	25.9	3.06	<0.27	0.41	<0.05	338	61	2.01
Late									
10 Sep. 2011	26.6	18.2	7.97	0.44	<0.07	0.070	n.d.	n.d.	n.d.
23 Sep. 2011	27.3	27.0	5.91	0.50	0.77	<0.05	308	82	0.770
21 Oct. 2011	22.3	25.0	11.9	<0.27	0.42	0.24	945	89	2.01

interested in determining whether there were consistent differences between the beds as well as in how environmental conditions influence productivity, respiration, and nutrient fluxes. Because restored seagrass beds often have lower percent cover and lower belowground biomass than do healthy native beds (Fonseca et al., 1998), we hypothesized that restoration sites would have lower primary productivity, respiration, and less nutrient uptake compared to native beds.

Study area.—The Florida Department of Environmental Protection (FDEP) restoration program included salvage of seagrasses from locations for which permits for dock construction or other marine construction projects have been issued. These salvaged seagrasses were then transplanted to sites adjacent to existing healthy beds to maintain seagrass coverage within the region. For this study, we chose an FDEP transplant site Big Lagoon, FL, which was planted in Jan. 2009. All experiments and samples were collected from Big Lagoon, FL (30°18.5'N, 87°23'W), a lagoonal system connected to Pensacola Bay and Perdido Bay to the east and west, respectively (Fig. 1). Big Lagoon is approximately 11.3 km long and 1.5 km wide, with an average depth of 5 m and a tidal range of about 0.7 m (Johnson et al., 2005). Sediments are primarily sand, and the average salinity is 24 PSU. The dominant seagrass species in Big Lagoon are *H. beaudettei* and *T. testudinum*, with *H. beaudettei* being more dominant at shallow depths and *T. testudinum* more dominant at depth. Most of the seagrasses grow close to the shoreline, with a maximum depth of approximately 2 m (Johnson et al.,

2005). In Jan. 2009, approximately one hundred 12-inch cores of *T. testudinum* and *H. beaudettei* were transferred to our study site from other areas in Big Lagoon impacted by bridge construction as part of an FDEP restoration project. The initial area of the transplant site was 5.83 m², but the bed had grown to 18.49 m² by the summer of 2011. Both *H. beaudettei* and *T. testudinum* were present at the transplant site, while *H. beaudettei* dominated at the native site. Seagrass cover in this region is above 60% (Stutes et al., 2007). Stem densities of *H. beaudettei* were similar at both sites, ~1,613/m², while *T. testudinum* was about 370/m² at the transplant site and less than 12/m² at the native site (J. M. Caffrey, unpubl.). At the time of the study, the restoration site had intermingled with the native bed.

METHODS

Plexiglas benthic chambers were used to measure in situ benthic oxygen and nutrient fluxes in the seagrass beds. Chambers were deployed between the hours of 0900 hr and 1500 hr, and three water samples from inside the domes were collected at hourly intervals following an initial hour-long incubation. Chambers were deployed on three dates early in the growing season (May), four times during peak growing season (June and July), and three times late in the growing season (Sep. and Oct.). The dome volume was 27.044 liters, with a coverage area of 0.213 m². These are the same chambers used by Allison (2006) and have internal acrylic vanes connected by a threaded rod to exterior hemispherical cups to allow stirring of the

chamber from water currents or manually. Pairs of light and dark domes were placed in the native (Na) bed and in the transplanted (Tr) bed during each visit over the growing season. We placed the domes haphazardly in the seagrass beds in approximately the same two locations every visit. Water in the chamber was manually mixed by slowly rotating cups for 5 min before measuring dissolved oxygen concentrations. We collected 60 ml of water from the chambers, which was filtered through GF/F filters, frozen, and later analyzed for NH_4^+ , NO_3^- , and dissolved inorganic phosphate (DIP). Oxygen concentrations were measured using a YSI multimeter Pro 2030. A Data Logger Li-1400 4 pi light meter was used to measure percent surface irradiance in the overlying water and to monitor bottom irradiance over the course of the incubation. During the course of the 3-hr incubation, the water depths were relatively constant in this microtidal system. We also recorded temperature, salinity, and dissolved oxygen using a YSI multimeter Pro 2030 and collected water samples for nutrient analyses from the overlying waters (Table 1). The two seagrass beds used in this study were marked and were in close proximity to one another, allowing us to use one set of data for the overlying water conditions.

DIP was analyzed using the standard ammonium molybdate method and read in a 5-cm cell at 885 nm in a spectrophotometer (Parsons et al., 1984). We used a modification of the methods of Holmes et al. (1999) to determine NH_4^+ concentrations using 4 ml of working reagent of sodium sulfite, borate buffer, and orthophthaldialdehyde and 2 ml of sample. Nitrate analysis was carried out using the spongy cadmium method (Jones, 1984). We determined the method detection limit (MDL) for each nutrient using an online calculator (http://www.chemiasoft.com/mdl_by_epa.html) based on the Environmental Protection Agency method for detection of MDL, 40 CFR Part 136, Appendix B, revision 1.11.

We calculated rates of respiration and net community productivity (NCP) of the Na and Tr seagrass beds based on changes in dissolved oxygen concentrations. Respiration is reported as a negative value. These rates were calculated per the area of the domes per hour. Nutrient fluxes were calculated in the same manner. Gross production (GP) was calculated by subtracting respiration rates from NCP and multiplying by day length. This assumes that the hourly rates are proportional to the daily rates. Oxygen fluxes were converted to carbon fluxes using a PQ ratio of 1.2 and an RQ ratio of 1. Annual carbon fixation was calculated assuming that GP in April was the same as May and that rates in Aug. were the average of

the July and Sep. rates. We performed two statistical analyses to examine the differences between restored and native sites as well as the role of other factors, such as season (early, peak, and late) or light level (light vs dark). Analyses were performed on rank order data because the rates were not normally distributed. A two-factor analysis of variance was used to compare NCP and respiration rates between the sites (transplant vs native) and seasons (early, peak, and late). For the nutrient flux data, we used a GLM procedure to compare restored and native, season, and light vs dark incubations. Correlation analyses were performed to examine the relationships between rate measurements and the environmental parameters measured. As a result of inclement weather conditions on May 19th, samples were only collected at two time points on that day.

RESULTS

Environmental conditions during this study were variable, with temperatures ranging from a low of 22.3°C in Oct. to a high of 31.1°C in July (Table 1). Salinity ranged from 18.2 to 28.4 PSU (Table 1). Light levels were high in these shallow beds, with a percent surface irradiance exceeding 50% on all sampling dates. June 16th had the highest average light availability (1,020 $\mu\text{E}/\text{m}^2/\text{sec}$) and the highest percent surface irradiance (91%). September 23rd had the lowest light availability (308 $\mu\text{E}/\text{m}^2/\text{sec}$), and May 20th had the lowest percent surface light (58%) (Table 1).

Nutrient concentrations in the overlying water (OW) were generally low (Table 1). Overlying water NO_3^- concentrations were below detection limits for all sampling dates in May, June, July, and Oct. Concentrations were higher in September, at about 0.5 μM NO_3^- . Ammonium concentrations ranged from below the detection limit of 0.07 μM to a maximum concentration of 1.2 μM . Overlying water DIP concentrations were greatest in Oct., at 0.24 μM , but were generally below or just above the detection limit.

The native and transplanted beds had similar respiration rates (Fig. 2), with an overall average of -140 ± 32 mg $\text{O}_2/\text{m}^2/\text{hr}$ and -138 ± 22 mg $\text{O}_2/\text{m}^2/\text{hr}$ in Na and Tr beds, respectively. While respiration rates were greater in Na than in Tr beds, this difference was not significant ($P = 0.91$). The Na beds had a higher average net community productivity (288 ± 44 mg $\text{O}_2/\text{m}^2/\text{hr}$) than the Tr beds (226 ± 41 mg $\text{O}_2/\text{m}^2/\text{hr}$), although this difference was not significant ($P = 0.21$) (Fig. 2). The greatest net productivity occurred in the Na beds and the lowest net productivity occurred in the Tr beds, both on June 16th. Net community productivity was significantly

Fig. 2. Net community production and respiration (mg O₂/m²/hr), ammonium, nitrate, and DIP flux (μM/m²/hr) in native and transplanted seagrass beds in light and dark domes.

correlated with light ($r = 0.84$, $P = 0.01$; Fig. 3) and water column dissolved oxygen concentration ($r = 0.71$, $P = 0.02$); all other correlations with NCP were insignificant (Appendix 1). Respiration rates were significantly correlated with DIP fluxes ($r = 0.57$, $P = 0.09$; Appendix 1). Gross production was highest in May (2.3 g C/m²/d) and lowest in Sep. (1.2 g C/m²/d). Annual production for the growing season (April to Oct.) was 438 g C/m²/yr.

All nutrient fluxes were low and variable. There were no significant differences in any nutrient fluxes between the Na and Tr beds or between the light and dark incubations (Fig. 2). However, there were some significant seasonal differences, with significantly higher and positive nitrate fluxes early in the growing season compared to the peak growing season, when fluxes were near zero ($P = 0.03$). Late in the growing season, nitrate fluxes were positive in the light domes and negative in the dark domes. On average, nitrate fluxes were positive and slightly lower in the incubations of the Tr beds (1.82 ± 4.57 μM/m²/hr) compared to those of the Na beds (2.87 ± 3.73 μM/m²/hr). Nitrate and DIP fluxes were positively correlated ($r = 0.68$, $P = 0.03$). Overall, average DIP fluxes were positive in the Na beds (0.97 ± 1.04 μM/m²/hr) but negative in the Tr beds (-0.30 ± 0.88 μM/

m²/hr). This trend was most often produced early in the growing season. Ammonium fluxes increased over the season, with significantly lower ammonium fluxes early in the season compared to peak or late in the growing season ($P = 0.08$). On average, ammonium fluxes were negative in the Na beds (-2.98 ± 4.72 μM/m²/hr) and positive in the Tr beds (5.19 ± 5.94 μM/m²/hr) (Fig. 2). Ammonium fluxes were negatively correlated with average light levels ($r = -0.70$, $P = 0.05$) and with DIP fluxes ($r = -0.59$, $P = 0.01$). We found no other significant correlations between nutrient fluxes and environmental variables (Appendix 1).

DISCUSSION

The results from this study suggest that within 2 yr transplanted seagrasses attained rates of net community production, respiration, and nutrient fluxes that were similar to those of native seagrass beds. Several factors may be contributing to this. The first is that the site was restored using plugs with intact plants containing sediments, roots, and rhizomes, increasing the potential vegetative growth by the plants. In addition, the existing microbial community associated with the rhizosphere was included in the plugs. Secondly, the

Fig. 3. Net community productivity ($\text{mg O}_2/\text{m}^2/\text{hr}$) and average light level ($\mu\text{E}/\text{m}^2/\text{sec}$) in Big Lagoon native and transplanted seagrass beds. Regression line for transplanted domes excludes circled point.

restoration site was adjacent to existing healthy beds, so that water depth and light levels were appropriate for seagrass growth, which resulted in an expansion of the transplanted bed over time and similar stem densities of *H. beaudettei* between transplanted and native beds. Third, the sediment type from both restored and native beds were similar (predominantly sand). Finally, evaluating differences between the treatments (native vs transplant) was a challenge as a result of the high variability in rates. However, coefficients of variability in NCP and respiration from this study were similar to those measured in the studies of Nagel (2007), Stutes et al. (2007), and Yarbrow and Carlson (2008), between 5% and 50%. In general, nutrient fluxes in this study were very low and, thus, highly variable, often having coefficients of variation as high as 300%, similar to results from Ziegler and Benner (1999) and Yarbrow and Carlson (2008).

The factors described above may have resulted in a more rapid convergence between restoration and native seagrass beds compared to that associated with other restoration sites, where many years to decades may be required for cover and productivity at restoration sites to converge with native beds (McGlathery et al., 2012; Bell et al., 2014). Our results also contrast with studies monitored just 1 yr postrestoration that showed significant differences in infauna community structure, pore-water nutrients, sediment texture

(Bourque and Fourqurean, 2014), and microbial community structure (Bourque et al., 2015) between restored and reference sites. While this study suggests that few differences exist between the restored and native beds in Big Lagoon, studies at other locations as well as longer term monitoring of these perennial species are critical in order to unequivocally determine whether restored seagrass beds have the same critical ecosystem services, such as primary production and nutrient recycling, as native beds.

Productivity and respiration rates from this study reflect the entire seagrass community, as in the work of Murray and Wetzel (1987), Yarbrow and Carlson (2008), and Eyre et al. (2011b). In studies that have examined individual components, epiphytes, water column phytoplankton, and benthic algae comprise a significant fraction of the total production (Murray and Wetzel, 1987; Moncreiff et al., 1992). For example, in Mississippi Sound, epiphytes accounted for 46% of the total productivity, while *H. wrightii* blades accounted for only 13% (Moncreiff et al., 1992; Table 2). In Big Lagoon, epiphyte biomass on seagrasses can be significant, often exceeding $0.5 \mu\text{g chlorophyll } a/\text{cm}^2$ (J. M. Caffrey, unpubl.), which may have accounted for our high productivity rates compared to other locations. Although we did not measure the productivity of each constituent, previous measurements of gross benthic microalgal primary production in

TABLE 2. Net community productivity (NCP) and respiration in seagrass beds showing average ($\pm$ SE) or range (mg O₂/m²/hr).

Location	Seagrass species of study	Depth, m	Season	NCP, mg O ₂ /m ² /hr	Respiration, mg O ₂ /m ² /hr	Reference
Big Lagoon, FL, U.S.A.	Mixed <i>Thalassia testudinum</i> and <i>Halodule beaudettei</i>	0.5	May-Oct.	257 $\pm$ 43	-139 $\pm$ 27	This study
Big Lagoon, FL, U.S.A.	<i>Halodule wrightii</i>	0.3-0.7	Annual	-44 to 154	-45 to -173	Stutes et al. (2007)
Pensacola Bay, FL, U.S.A.	Bare sediment	1-2.3	June-Sep.	70 $\pm$ 22	-23 $\pm$ 4.7	Murrell et al. (2009)
Florida Bay, U.S.A.	<i>Thalassia testudinum</i>	0.5	May-Nov.	86-285	-202 to -86	Yarbro and Carlson (2008)
Florida Bay, U.S.A.	<i>Thalassia testudinum</i>		June-Aug.	219-1,419	-651 to -159	Nagel (2007)
Mississippi Sound, U.S.A.	Epiphytes	<2	Annual	275		Moncreiff et al. (1992)
	Phytoplankton			142		
	Sand microflora			103		
Chesapeake Bay, VA, U.S.A.	<i>Halodule wrightii</i>			78		
	<i>Zostera marina</i> with epiphytes	0.5-1.0	Annual	-80 to 480	-400 to -100	Murray and Wetzel (1987)
	Plankton			-50 to 380	-200 to -30	
	Sediment			0-170	-80 to -10	
Virginia Coastal Bays, U.S.A.	<i>Zostera marina</i>	1-2	June-July		-181 $\pm$ 43	Hume et al. (2011)
	<i>Zostera marina</i>	1-2	Annual		-276 to -183	Rheuban et al. (2014)
Lake Macquarie, Australia	<i>Zostera capricornii</i>	0.5-4	Feb.	-13 $\pm$ 16	-54 $\pm$ 19	Eyre and Ferguson (2002)
Moreton Bay, Australia	<i>Zostera capricornii</i>	1.7	Jan.	155 $\pm$ 12	-155 $\pm$ 11	Eyre et al. (2011b)

Fig. 4. Conceptual model of nitrogen cycling in seagrass beds. Solid lines represent diffusive fluxes between sediment and water column. Dashed lines represent plant uptake or release. Dotted lines represent microbial processes.

Big Lagoon ranged from 15 to 155 mg C/m²/hr (Bucolo et al., 2008), which are less than estimated community gross production (42 to 242 mg C/m²/hr) from this study.

The dominant factor driving primary productivity in the seagrass beds was ambient light level (Fig. 3), with no indication of saturation of gross productivity, as has been observed with other aquatic macrophytes (Binzer et al., 2006; Rheuban et al., 2014). Productivity of seagrass beds in Big Lagoon was also comparable to that of prior studies that took place in Mississippi (Moncreiff et al., 1992), Virginia (Murray and Wetzel, 1987; Hume et al., 2011), south Florida (Nagel, 2007; Yarbrow and Carlson, 2008), and Australia (Eyre and Ferguson, 2002; Eyre et al., 2011b), but much higher than rates measured in *H. beaudettei* patches in the region (Stutes et al., 2007) (Table 2). Since short-term studies can overestimate actual productivity rates, especially if they are performed in very productive times of the year, such as summer, during which seagrass productivity can be as much as 90% higher than in winter (Kaldy and Dunton, 2000), it is necessary to adjust for seasonal changes when estimating annual productivity rates of seagrass communities (Herzka and Dunton, 1997). Our study was conducted between May and Oct. and does not include either the early spring portion of the growing season or winter and fall, when the plants are dormant.

The low nutrient concentrations in the water column and low benthic fluxes suggest efficient retention of nutrients within this system. Benthic

nutrient fluxes integrate the nutrient uptake by the plant community and transformations by the microbial community (Fig. 4). Again, benthic nutrient fluxes were similar between the Na and Tr beds, with both showing stronger seasonal changes than differences between the sites. Mineralization of organic matter results in release of NH₄⁺ and DIP. These then become available for plant uptake, are released to the water column, or, in the case of NH₄⁺, may be oxidized to nitrate by nitrifying prokaryotes. Pore-water NH₄⁺ and DIP concentrations in Big Lagoon seagrass beds were often five to 10 times higher than in overlying water concentrations (A. Smith and J. M. Caffrey, unpubl.). This suggests that plant uptake reduced the flux of NH₄⁺ and DIP out of sediments. Nitrification may also lead to lower NH₄⁺ fluxes. Significant NO₃⁻ fluxes out of the sediment on three occasions were an indication of nitrification, which has been found to be significant in other seagrass sediments (Iizumi et al., 1980; Caffrey and Kemp, 1990; Hermann et al., 2008). Alternatively, submarine groundwater discharge with high NO₃⁻ groundwater from adjacent uplands might enhance NO₃⁻ fluxes out of the sediments.

Benthic nutrient fluxes were generally very low over the course of this study and had a smaller range in rates compared to bare sediments in Pensacola Bay (Murrell et al., 2009; Smith and Caffrey, 2009; Table 3). Rates in Big Lagoon were comparable to measurements from other beds of *H. beaudettei* (Cotner et al., 2004; Yarbrow and

TABLE 3. Benthic nutrient fluxes in seagrass beds after Yarbrow and Carlson. n.d. indicates no data. Range in rates in $\mu\text{M}/\text{m}^2/\text{hr}$.

Location	Seagrass species	NH_4^+ flux	NO_3^-	DIP flux	Reference
Big Lagoon, FL, USA	Mixed <i>Thalassia testudinum</i> and <i>Halodule beaudettei</i>	-37 to 22.7	-26.6 to 26	-2.9 to 5.8	This study
Pensacola Bay, FL, USA	Bare sandy sediments	-45.7 to 73.4	-52.3 to 47.4	-10.9 to 10	Murrell et al. (2009); Smith and Caffrey (2009)
Florida Bay, FL, USA	<i>Thalassia testudinum</i>	0.5-5.9	0.2-2.5	n.d.	Nagel (2007)
Florida Bay, FL, USA	<i>Thalassia testudinum</i>	-21 to 54	n.d.	-2.8 to 1.8	Yarbrow and Carlson (2008)
Florida Bay, FL, USA	<i>Halodule wrightii</i>	-5.8 to 2.4	n.d.	-0.1 to 1.2	Yarbrow and Carlson (2008)
Baffin Bay, TX, USA	<i>Halodule wrightii</i>	-9.2 to 15	n.d.	-3.7 to 11	Cotner et al. (2004)
Laguna Madre, TX, USA	<i>Thalassia testudinum</i>	-9.5 to 12.8	-0.04 to 0.25	Undetectable	Ziegler and Benner 1999
Bermuda	<i>Thalassia testudinum</i>	n.d.	n.d.	-0.04 to 0.3	Jensen et al. (1998)
Yaquina Bay, OR, USA	<i>Zostera japonica</i>	-14.1	-68.9	-1.6	Larned (2003)
Ishigaki Island, Japan	<i>Thalassia hemprichii</i>	-37 to 22.7	64-79	n.d.	Miyajima et al. (2001)
Sulawesi Island, Indonesia	Mixed <i>Thalassia hemprichii</i> and <i>Euthalys acoroides</i>	4.3	n.d.	1.6	Erftemeijer and Middleburg (1993)
Puttalam Lagoon, Sri Lanka	Mixed <i>Cynodorean rotundata</i> and <i>Euthalys acoroides</i>	n.d.	n.d.	23-110	Johnson and Johnstone (1995)
Lake Illawarra, Australia	<i>Ruppia megacarpa</i>	0.08-2.6	-0.06 to 0.31	-0.04 to 0.03	Qu et al. (2003)
Lake Macquarie, Australia	<i>Zostera capricornii</i>	0-100	0	0-3	Eyre and Ferguson (2002)
Moreton Bay, Australia	<i>Zostera capricornii</i>	-8 to 15	-1.2 to 0	0.12	Eyre et al. (2011b)
Moreton Bay, Australia	<i>Zostera capricornii</i>	-50 to 100	-10 to 0	-5 to 10	Eyre et al. (2011a)
Moreton Bay, Australia	<i>Halophila</i> spp.	-75 to 0	-20 to 0	-2 to 2	Eyre et al. (2011a)
Sounion, Greece	<i>Posidonia oceanica</i>	-3.3 to 29.6	-5.8 to 11.7	-9.6 to 5	Apotolaki et al. (2010)
Revellata Bay, Spain	<i>Posidonia oceanica</i>	-240 to 5.5	-20.6 to 4.1	-58 to -0.08	Gobert et al. (2002)
Ria Formosa, Portugal	<i>Zostera noltii</i>	-92 to 27	-63 to -30	-9 to -8	Asmus et al. (2000)

Carlson, 2006; Table 3). However, NH_4^+ fluxes from these studies were considerably lower than rates in beds of *T. testudinum* in Florida Bay or temperate beds of *Zostera marina* (Table 3). Our results contrast with those of most seagrass studies that show significant differences between light and dark nutrient fluxes. For example, Ziegler and Benner (1999) observed release of NH_4^+ to the overlying water in the dark and uptake in the light in mixed seagrass beds consisting of *T. testudinum*, *H. wrightii*, and *Syringodium filiforme*. However, in this study, fluxes of NO_3^- , DIP, or NH_4^+ were not significantly different between light or dark incubations.

In conclusion, our study found no significant difference between the native and transplanted mixed seagrass beds of *H. beaudettei* and *T. testudinum* as well as in high rates of annual gross production. These results indicate that the FDEP seagrass restoration program was successful in Big Lagoon and that subtropical seagrass beds restored

using plugs and planted adjacent to existing beds may relatively rapidly acquire the functions found in native beds. As a result of seagrass decline worldwide and the limited success of current restoration techniques, further research using different physical, chemical, and biological parameters as a measurement of seagrass health is necessary to understand the steps needed to create successful seagrass restoration programs.

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APPENDIX 1. Correlation coefficients (top value) and probabilities (bottom value) of fluxes and water quality parameters. Probabilities of <0.05 are italicized and bolded, those <0.1 are bolded.

	Respiration	Net community production	Nitrate flux	DIP flux	Ammonium flux
Temperature	−0.14 0.70	−0.54 0.11	−0.10 0.78	−0.36 0.31	0.39 0.27
Salinity	0.38 0.28	0.02 0.97	−0.02 0.95	−0.10 0.80	−0.21 0.57
Dissolved oxygen concentration	0.32 0.37	0.71 0.02	−0.21 0.55	0.23 0.52	−0.16 0.67
Nitrate concentration	−0.27 0.45	−0.42 0.22	0.09 0.81	−0.13 0.73	0.24 0.50
Ammonium concentration	0.26 0.47	−0.06 0.88	−0.36 0.31	−0.49 0.15	0.41 0.23
DIP concentration	0.13 0.72	0.39 0.26	−0.53 0.11	−0.01 0.98	0.25 0.48
Mean light	0.14 0.75	0.84 0.01	−0.27 0.52	0.35 0.39	− 0.70 0.05
Respiration		0.33 0.35	0.47 0.17	0.57 0.09	−0.33 0.35
Net community production			−0.18 0.62	0.10 0.79	−0.27 0.46
Nitrate flux				0.68 0.03	−0.41 0.24
DIP flux					− 0.59 0.07

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- CENTER FOR ENVIRONMENTAL DIAGNOSTICS AND BIOREMEDIATION AND DEPARTMENT OF BIOLOGY, UNIVERSITY OF WEST FLORIDA, 11000 UNIVERSITY PARKWAY, PENSACOLA, FLORIDA 32514. Send reprint requests to JMC. Date accepted: February 8, 2016.