Benthic metabolism across a gradient of anthropogenic impact in three shallow coastal lagoons in NW Florida

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ABSTRACT: Seagrasses are being lost at alarming rates worldwide, most often due to anthropogenic effects, but few reports have examined how seagrass loss affects the metabolism of coastal ecosystems. Here, we address this question by comparing both areal and system-integrated daytime benthic metabolic rates across 3 lagoons in the North Central Gulf of Mexico that display varying levels of abundance of the shoalgrass *Halodule wrightii* (i.e. from 64% of the bottom covered with shoalgrass down to between 4 and 0%), partially due to contrasting anthropogenic pressures. When comparing the 2 shoalgrass-containing lagoons, shoalgrass patches featured higher areal rates of gross primary production (GPP) and respiration (R), and, to a lesser extent, higher rates of net production (NP), than did bare sediment. These results were robust despite across-lagoon differences in percentage cover and areal biomass of shoalgrass and benthic microalgae (i.e. the lagoon with less cover also had lower areal shoalgrass biomass in the shoalgrass patches and higher areal microalgal chlorophyll *a* concentrations in the sediment). We did not find any consistent differences in the metabolic rates of bare sediment across the 3 lagoons, despite the fact that areal microalgal chlorophyll *a* concentrations in bare sediment increased as shoalgrass abundance decreased across the 3 lagoons. System-integrated rates of benthic GPP and R were higher in the lagoon with the highest shoalgrass cover when compared with the lagoons with little or no shoalgrass; but, surprisingly, system-integrated rates of benthic NP did not differ significantly across lagoons. This result suggests that the large decrease in shoalgrass abundance across the lagoons examined does not greatly affect the lagoon's potential capacity for accumulation and/or export of organic carbon. It also underlines the importance of deriving system-integrated estimates to properly understand how decreasing seagrass abundance can alter the daytime metabolism of coastal systems.

KEY WORDS: Seagrass · *Halodule wrightii* · Benthic microalgae · Eutrophication

INTRODUCTION

Seagrass meadows have been recognized over the past few decades as important components of coastal ecosystems (Halliday 1995, Asmus & Asmus 2000). They serve as valuable habitat (Virnstein et al. 1983) and nursery sites (Carr & Adams 1973, Heck & Orth 1980, Orth et al. 1984, Sogard & Able 1991, Connolly 1994) for many larval and juvenile species, some of which are commercially important (Pollard 1984, Halliday 1995). Seagrass beds are also among the most productive ecosystems (Daehnick et al. 1992, Duarte & Chiscano 1999, Kaldy & Dunton 2000), peaking at approximately 15 g C m^{-2} d^{-1} (Phillips & McRoy 1980, Touchette & Burkholder 2000), and thus have the potential to accumulate or export large amounts of bio-

mass and/or detritus (Bach et al. 1986, Vahatalo & Soendergaard 2002). They offer abundant physical structure and refuge for many organisms, which results in high levels of secondary production and a complex set of plant-animal interactions (Jernakoff et al. 1996). They also stabilize sediments (Fonseca 1989) with their dense roots and rhizomes and cause increased particle flux to sediments by slowing water movement (Dauby et al. 1995, Terrados & Duarte 2000). This, in concert with the fact that seagrasses have a near worldwide distribution (Hemminga & Duarte 2000), signifies their importance as a nearshore habitat.

Seagrasses are also important contributors to the metabolism of coastal ecosystems. Due to their abundance and the myriad organisms associated with them, coastal seagrass meadows are significant drivers of oxygen and carbon dynamics (Dunton 1996, Barron et al. 2004, Santos et al. 2004, Clavier et al. 2005). The study of system metabolism is important to ascertain whether a system is a source or sink of carbon and oxygen and to understand its role in ecosystem-scale budgets. System metabolism sets a maximum limit to the capacity of the system to export organic matter and act as a trophic resource for neighboring systems (Hemminga et al. 1996, Asmus & Asmus 2000, Santos et al. 2003). In addition, the dynamics of system metabolism may also be indicative of the extent of the system's dependence on internal recycling vs. imported resources. As systems become more autotrophic (i.e. carbon fixation increasingly higher than carbon consumption), net accumulation of photosynthetically-fixed carbon and nutrients within the system should also increase, and recycling of photosynthetically-fixed carbon and nutrients should decrease, which would render the system more dependent on imported nutrients for maintaining its productivity (Cebrian & Valiela 1999).

Under natural conditions, seagrasses often exhibit remarkable resilience and can thrive in environments subject to large fluctuations in temperature, salinity, turbidity, and energy on an annual, if not daily, basis (Touchette & Burkholder 2000). Nevertheless, throughout the last 2 decades there have been many reports of severe declines in seagrass abundance worldwide (Orth & Moore 1983, Durako 1994, Short & Tomasko et al. 1996, Wyllie-Echeverria 1996, Asmus & Asmus 2000). Human impacts, both direct and indirect, such as dredging, eutrophication, pollution, and salinity stress, are often the origin of significant seagrass decline (Phillips & McRoy 1980, Orth & Moore 1983, Short et al. 1995, Tomasko et al. 1996, Livingston et al. 1998, Borum et al. 2005). Though the mechanisms surrounding the above impacts have been studied at length (e.g. reduction of light, increased nutrients, sediment toxicity, and disease), few efforts have focused on how decreasing seagrass abundance affects benthic daytime metabolism in coastal ecosystems.

It is generally accepted that seagrass meadows are normally net autotrophic (Dunton 1996, Hemminga & Duarte 2000, Barron et al. 2004, Santos et al. 2004). Thus, in benthic coastal systems that are seagrass-dominated, one could argue that the degree of autotrophy decreases as seagrasses decline. However, contrary to this line of thinking, concomitant changes in the abundance of other primary producers, such as macroalgae and benthic microalgae, can also significantly influence benthic daytime metabolism within coastal systems and compensate for, even overcome, the impact of seagrass decline (Murray & Wetzel 1987, Cahoon 1999). Associated changes in organism abundance sheltered and/or fed by the primary producers, which greatly influence respiration (R), will also affect benthic daytime metabolism as the assemblage of dominant primary producers shifts.

In this article, we investigate how system-integrated daytime benthic metabolism changes with declining shoalgrass *Halodule wrightii* abundance across 3 coastal lagoons of the North Central Gulf of Mexico. Specifically, we ask 4 questions: (1) How does areal daytime metabolism of shoalgrass patches differ from that of bare sediment populated with benthic microalgae? (2) Do those differences hold across lagoons with contrasting relative abundances of shoalgrass patches and bare sediment? (3) How does areal daytime metabolism of bare sediment change across lagoons with decreasing or no shoalgrass? (4) What are
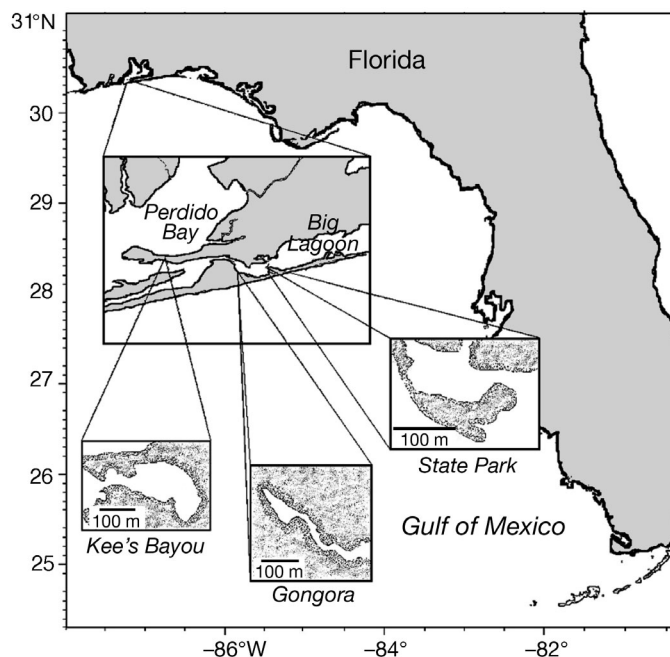

Fig. 1. Study sites located in NW Florida, USA

the consequences for system- (i.e. lagoon-) integrated benthic daytime metabolism and how does this system-integrated benthic metabolism differ across lagoons with decreasing shoalgrass abundance? Answering these questions improves our understanding of how the alteration of primary producer assemblages affects benthic daytime metabolism of coastal ecosystems. Further, this research offers insight as to how declining seagrass abundance could affect metabolic processes in coastal systems and possible ecological and ecosystem-scale ramifications, such as food availability and carbon sequestration.

MATERIALS AND METHODS

Study sites. The 3 lagoons studied (State Park, Kee's Bayou and Gongora) are located within Perdido Bay, Florida, USA (Fig. 1). The lagoons are moderate in size and, as typically found for other coastal lagoons, they are shallow and connected to a sound through a relatively narrow mouth (Fig. 1). Despite having similar physical characteristics (Fig. 2), they feature contrasting *Halodule wrightii* (shoalgrass) cover, ranging from total absence in Gongora to 4.2% ± 0.4 (mean ± SE) of the bottom covered in Kee's Bayou to 64.5% ± 1.0 in State Park (Fig. 3). Other than shoalgrass patches and bare sediment, no other benthic primary producer community types (e.g. macroalgal stands) were encountered in the lagoons during the period studied.

The differences in shoalgrass cover probably result, at least partially, from parallel differences in human impacts on the lagoons (Table 1). The State Park site, as the name indicates, resides within Big Lagoon State Park, Florida (30.308° N, 87.403° W) and represents the most pristine lagoon with the least amount of human alteration. It is entirely surrounded by salt marsh (predominantly *Juncus roemerianus*) and maritime forest with no residential development. Shoalgrass patches are dominant in terms of percent bottom coverage, with the rest corresponding to sandy sediment (Fig. 3).

Kee's Bayou (30.313° N, 87.469° W) is developed on the northern and eastern sides (i.e. condominium complex and houses) and bordered by marsh vegetation on
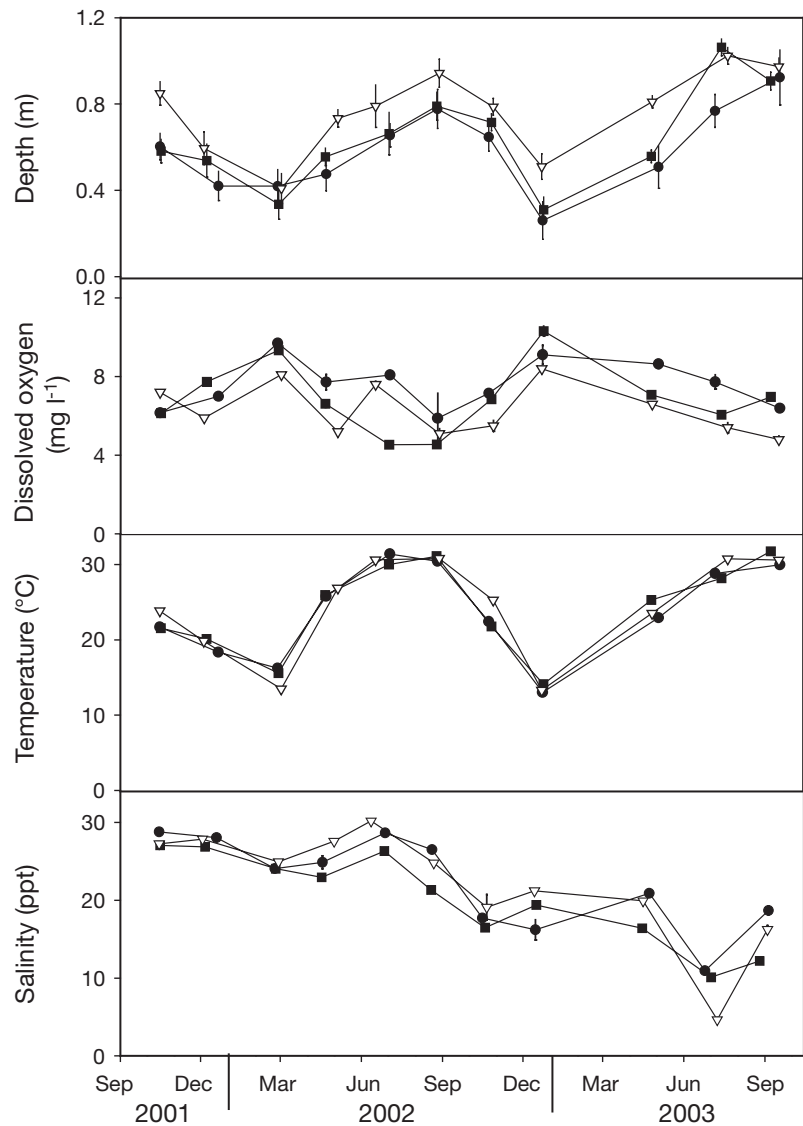

Fig. 2. Selected physical parameters in the 3 lagoons measured throughout the study period. Data are mean (± SE). (●) State Park, (■) Kee's Bayou, and (▽) Gongora

the southern and western sides. Shoalgrass patches cover only a small fraction of the bottom in Kee's Bayou, with the rest being a range of muddy and sandy sediment types (Fig. 3). Along with possibly higher runoff from surrounding human development, the narrower, more convoluted mouth of this lagoon, through reduced exposure to the open sound, could account for the finer sediment in this lagoon—especially when compared to the mouth of the State Park. Fine sediment is generally more dynamic than coarse sediment, which can lead to adverse conditions for shoalgrass growth by frequently burying leaves and/or exposing rhizomes and roots (Mills & Fonseca 2003). In fact, we observed numerous episodes of leaf burial and rhi-
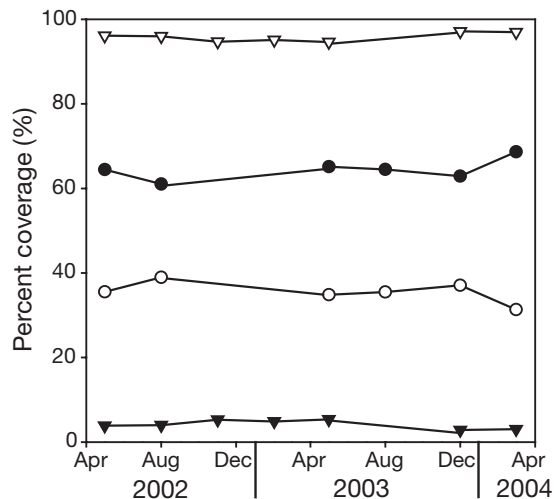
Fig. 3. Percentage of bottom covered with shoalgrass patches or bare sediment in State Park and Kee's bayou as determined through aerial photography. Circles: State Park; triangles: Kee's Bayou. Closed symbols: shoalgrass coverage; open symbols: bare sediment

zome exposure in this lagoon throughout the duration of the study. Finer sediment and resulting higher resuspension rates by wind and wave action could also result in a more turbid water-column and less light availability at the bottom for shoalgrass growth (Table 1). In addition, a 2 m wide canal that runs along the center of the lagoon is periodically dredged for navigation, which could also negatively affect the shoalgrass at this site. Kee's Bayou, in part due to human development around the lagoon, also receives higher nitrogen inputs than does State Park, but the higher nitrogen input does not result in higher concentrations of water-column chlorophyll in Kee's Bayou when compared to State Park (Table 1).

Finally, Gongora (30.305° N, 87.424° W) is bordered by residential development on its northern and eastern sides and by marsh vegetation on the southern and western sides. In addition, a culvert that serves as a

flushing point for an 18-hole golf course discharges at the northern tip of the lagoon. The lagoon has no shoalgrass and the sediment ranges from mostly sand at the mouth to a fine mud upstream. The lagoon is periodically dredged along its central axis for navigation, which, given the narrow, spindle shape of the lagoon, should have a large negative effect on any potential seagrass recruitment and growth. Gongora, in part due to larger surrounding human development, also receives higher nitrogen loads than the pristine State Park, which could lead to the higher water-column chlorophyll levels and lower light availability for shoalgrass growth observed in the former site (Table 1). The combination of intense disturbance caused by dredging and reduced light availability imposed by high water column chlorophyll concentrations could account for the lack of shoalgrass in Gongora.

Metabolism measurements. To quantify daytime benthic metabolism, we measured change in dissolved oxygen concentration within clear and dark acrylic benthic chambers incubated under ambient light conditions. The chambers were bell-shaped, with a diameter of 17.5 cm and a height of 16.0 cm, encompassing 0.032 m^2 of bottom area. They were inserted into the sediment up to a pre-marked insertion point on the chamber (2.5 cm from the bottom edge) to enclose a final water volume of 3.0 l, giving the chambers a very small perimeter-to-volume ratio. Chamber volume was set in the lab prior to deployment and was viewed as a compromise between insertion depth and adequate volume to reduce chamber-wall effects. After a field trial, a set of 10 chambers was randomly sampled to assure that volume enclosed within each chamber averaged 3.0 l and did not vary with reuse. On each sampling day, we haphazardly placed 10 pairs of chambers within shoalgrass patches and 10 pairs on bare sediment in State Park and Kee's Bayou, with each pair containing one clear and one dark chamber. Ten pairs of chambers were placed on each sampling date on the bare sediment of Gongora. To capture the gradient in sediment nature found in the lagoon (see above), the pairs were placed haphazardly at locations regularly distributed from the mouth to the upstream end.

We recorded the times at which we started and finished deploying the benthic chambers, which normally took approximately 1 h. These noted times, along with the total number of chamber pairs deployed, allowed us to estimate the start time of incubation for each pair of chambers. In addition, we filled 5 clear and 5 dark 300 ml

Table 1. Water-column transparency, total dissolved nitrogen loading rate, water-column chl *a* concentrations, and particulate organic matter (POM) measured for the lagoons studied. Data are for the entire duration of the study (mean ± SE), except nitrogen loading rates (June 2003 to June 2004; parentheses: inputs from houses [septic tanks, lawn fertilizer] and point sources [e.g. drainage culvert from golf course adjacent to Gongora site])

Study site	Transparency (%)	N loading (kg N ha^{-1} yr^{-1})	chl *a* (µg l^{-1})	POM (mg l^{-1})
State Park	53.4 ± 5.0	4.2 (0)	4.1 ± 0.4	6.0 ± 0.3
Kee's Bayou	43.1 ± 6.1	25.7 (9.9)	5.5 ± 0.5	6.9 ± 0.3
Gongora	43.8 ± 8.3	27.7 (14.2)	11.5 ± 1.9	7.6 ± 0.4

BOD bottles with water from the study site while the chambers were being deployed. Water from the mid water-column (i.e. between 20 and 40 cm deep) near the first pair of chambers was collected and carefully siphoned into the bottles from the bottom to avoid any bubble formation. Immediately after filling the bottles, we measured water oxygen concentration for each bottle using a high-sensitivity field oxygen meter (WTW OXI 197) attached to a stirring probe (Stir-Oxy G probe) and recorded the time of reading. The bottles were subsequently anchored to the bottom near the first pair of chambers for incubation. The average value of these initial oxygen concentrations in the bottles was taken as the initial concentration for the chambers (see Eqs. 1 & 2).

Chambers and bottles were incubated for approximately 4 h encompassing solar noon on sunny days in order to maximize system dynamics. At the end of the incubation period, a 60 ml sample of water was pulled out of the chamber using a syringe and attached tubing inserted through a 1 cm diameter access port. The water sample was taken at approximately mid-distance into the chamber headwater. The water was then transferred to a 60 ml BOD bottle and the oxygen concentration read with the oxygen meter and the time of reading recorded. We did not stir the water within the chambers during incubation. Previous work (Huettel & Gust 1992) has shown that stirring during incubations on porous sediments, such as the sediment found in our study sites, may generate substantial porewater flows, profoundly biasing O_2 concentrations in the overlying water and thus influencing metabolism measurements. However, in the absence of stirring, the dissolved O_2 produced or consumed due to benthic microalgal or shoalgrass metabolic processes may not uniformly mix throughout the chamber due to diffusion gradients. In turn, such gradients could also bias measurements. This, however, should not be a significant concern, since our 60 ml water samples were taken at approximately mid-chamber in an attempt to homogenize the chamber and break gradients that could have formed during incubation. To confirm this, we took aliquots (i.e. several measurements taken within the same chamber) regularly and haphazardly throughout the 2 yr that this project lasted. Aliquots were always very similar (i.e. within 10 to 15% of each other), thereby demonstrating that any possible stratification within the chambers was of no significant consequence for our metabolism measurements, particularly in view of the large range covered by the values obtained (see also Stutes et al. 2006). A further concern that could lead to depressed estimates of oxygen production or consumption in the chambers is that lack of stirring could allow gradients in dissolved compounds to develop around leaf surfaces and the sediment surface, thus slowing exchange with the water column and possibly limiting metabolic processes (Touchette & Burkholder 2000). This caveat should be considered when comparing our measurements with other results in the literature, but it should be of no consequence for our conclusions because they are based on the relative differences in oxygen production or consumption between shoalgrass patches and bare sediment. The extent of underestimation of oxygen production/consumption committed with our technique should apply similarly to both types of substratum.

We also measured the oxygen concentration in the 300 ml BOD bottles at the end of the incubation period, recorded the time of the reading, and subtracted the mean change in oxygen concentration within the bottles for clear or dark bottles from the total change (i.e. integrating the bottom and enclosed headwater) measured in each clear or dark chamber in order to examine benthic processes only (see Eqs. 1 & 2).

For each clear chamber, we calculated benthic community net production (NP, in mg C m^{-2} h^{-1}), and for each dark chamber, benthic community respiration (R, in mg C m^{-2} h^{-1}), as:

$$NP = VC\,[(F_C - I)/t - P_C]/A \qquad (1)$$
$$R = VC\,[(F_D - I)/t - P_D]/A \qquad (2)$$

where V is the volume of water enclosed in the chamber (in l), C is the conversion factor from oxygen to carbon, F_C and F_D are the final oxygen concentrations (mg O_2 l^{-1}) in the clear and dark chambers, I is the mean initial oxygen concentration in the chamber obtained from the bottles (mg O_2 l^{-1}, see above), t is the incubation period (h), P_C and P_D are the mean changes in oxygen concentration recorded for clear and dark bottles (mg O_2 l^{-1} h^{-1}; see above), and A is the area of the incubation chamber (m^2). The conversion factor for NP is 0.344 mg C mg O_2^{-1}, based on a photosynthetic quotient of 1.2 and respiratory quotient of 1, and the conversion factor for R is 0.375 mg C mg O_2^{-1} based on a respiratory quotient of 1 (Strickland & Parsons 1972). Finally, benthic community gross primary production (GPP; mg C m^{-2} h^{-1}) was calculated as the difference between NP and R, which, since R is always a negative value, corresponds to GPP = NP + |R|. This approach assumes that respiration rates in the dark equal respiration rates in the light, which may not be the case. For instance, for microalgae light respiration rates are often higher than dark respiration rates due to a variety of mechanisms, including photoacclimation (Grobbelaar et al. 1992, Herzig & Dubinsky 1992). If that was of significant consequence in our study, our values could underestimate GPP in shoalgrass patches and bare sediment, since benthic microalgae are prominent in both bottom types. Nevertheless, the differences in GPP between the 2 bottom types, on which

our conclusions are based, should be robust, particularly in view of the large magnitude of those differences.

System-integrated benthic metabolism. To examine the impact of differences in areal metabolic rates (i.e. rates per m² of shoalgrass patch or bare sediment) across lagoons and relative cover by each of the 2 bottom types (shoalgrass patches and bare sediment) on system-integrated benthic daytime metabolism, we derived weighted rates of benthic GPP, *R* and NP for each lagoon as:

$$\text{Weighted rate} = (\text{SR} \times \text{SC}) + (\text{BSR} \times \text{BSC}) \quad (3)$$

where SR and BSR are the mean areal metabolic rates for shoalgrass patches and bare sediment (i.e. rates per m² of shoalgrass patch or bare sediment), respectively, for the entire study duration (i.e. average of all single measurements), and SC and BSC are the mean fractions of total bottom covered by shoalgrass or bare sediment, respectively, (and error terms), for all the estimates based on aerial photography (see Fig. 3). Flights used to determine this were restricted to a maximum of 300 m due to logistics. In order to reduce artifacts due to oblique viewing, the altitude and direction of the flights were kept consistent. The photographs were scanned using a 12-bit scanner and color corrected using Adobe Photoshop 7.0. Percent cover was then estimated using Sigma Scan Pro 4.0. Values of percent cover could not be derived on some dates dues to reduced water column clarity. In Gongora, weighted rates simply equaled the mean areal rates for bare sediment because there was never any shoalgrass present.

Benthic producer biomass. To gain further insight into differences in metabolic rates between bottom types (shoalgrass patches vs. bare sediment) within and across lagoons, we also measured the biomass of the 2 main types of benthic primary producers in our study sites, i.e. shoalgrass (plus epiphytes) and benthic microalgae.

Shoalgrass biomass was sampled using a 15.5 cm inner-diameter PVC core that was inserted into the sediments to a depth of 12 cm to ensure collection of all below-ground biomass. Samples were bagged and stored on ice for transport to the lab where they were frozen at –10°C until processed. Once thawed, the samples were rinsed through a 500 µm sieve and all seagrass material was sorted out. Seagrass biomass was separated into above- and below-ground compartments, dried at 60°C until constant weight was achieved and then combusted at 500°C to determine the ash free dry weight (AFDW) per unit area (g AFDW per m² of bottom). On each sampling date, we took 5 cores within patches haphazardly chosen in the lagoon (only in State Park and Kee's Bayou).

We used chlorophyll *a* (chl *a*) concentration as an indicator of benthic microalgal biomass (Daehnick et al. 1992). To accomplish this, we sampled the sediment using a 2.5 cm diameter corer and sliced the top 1 cm sediment layer into a centrifuge tube, which was stored on ice and transported to the lab. In the lab, the samples were frozen at –80°C until processed. Upon thawing, chlorophyll was extracted for a 24 h period with 25.0 ml of acetone (Strickland & Parsons 1972). Chl *a* concentrations were measured fluorometrically with a Turner Designs Model TD-700 fluorometer using acidification (1N HCl) to correct for the presence of phaeopigments. Chlorophyll values were standardized to sediment area (mg chl *a* m⁻² of sediment). On each sampling day, one core was taken adjacent to each pair of benthic chambers incubated on bare sediment, for a total of 10 cores per lagoon per sampling day.

Measurements of metabolism and biomass were obtained during sampling periods approximately every 6 to 8 wk from October 2001 to August 2003. Less than 10 d separated sampling events for all 3 lagoons within a sampling period. Incubation and biomass measurements were taken on the same day every time a lagoon was sampled.

Water quality. In order to examine site differences in water quality, water column physical parameters were also recorded during this period on the same dates as the measurements of producer biomass and rates of metabolism. These parameters include bulk water column dissolved oxygen (mg l⁻¹), salinity (ppt), and temperature (°C) measured using a YSI 85 multiprobe; water-column transparency (defined as percentage of incident light to the amount of light reaching the benthos) using a pair of Li-Cor 193sa sensors and data logger; and depth (m) using a standard meter stick. Measurements were taken for each sampling period at the same 4 points within each lagoon near the mouth, near the upstream edge, and on both sides of the lagoon.

In addition, both particulate and dissolved parameters were determined through discrete water samples taken at the above mentioned points, plus 2 additional random points within each lagoon. These variables include dissolved nitrogen species determined using colorimetric techniques on a Skalar autoanalyzer, water column particulate chl *a* using the above-mentioned fluorometric method, and particulate organic matter (POM) as calculated by loss on ignition (LOI).

In addition to these static measurements of water quality, nitrogen loading rates for each lagoon were calculated from all likely sources, including tidal, atmospheric, and watershed inputs over the course of a year. Tidal and atmospheric inputs have been derived

using our own measurements of tidal volume exchange, rainfall, and total dissolved nitrogen concentration in tidal and rainwater obtained every 6 wk from June 2003 to June 2004. Watershed inputs were derived using the model described by Valiela et al. (1997) after assessment of land use in the watersheds. All water quality data reduction can be found in Fig. 2 and Table 1.

Statistical analyses. To address our Questions (1) and (2) — whether areal metabolic rates differ between shoalgrass patches and bare sediment and, if so, how those differences hold across lagoons with differing levels of shoalgrass abundance — we used a mixed 3-way ANOVA, with lagoon (State Park and Kee's Bayou) and bottom type (shoalgrass patches and bare sediment) as 2 fixed factors and time as the random factor. The analysis of the second fixed factor (bottom types) addresses Question (1), and the analysis of the interaction term between bottom type and lagoon (to reveal whether differences are lagoon-dependent) addresses Question (2).

To address Question (3) (whether areal metabolic rates of bare sediment vary across lagoons with differing shoalgrass cover) we used a mixed 2-way ANOVA with lagoon (State Park, Kee's Bayou and Gongora) as the fixed factor and time as the random factor. Differences in shoalgrass and benthic microalgal areal biomass among lagoons were also analyzed similarly, with a mixed 2-way ANOVA, but only with State Park and Kee's Bayou for shoalgrass biomass. Post-hoc tests between the 3 lagoons were done using 1-way ANOVA and pairwise Tukey tests if no significant interaction terms were found.

The requirements of data normality and homoscedasticity required by ANOVA were tested with the Chi-square procedure (test for normality) and Bartlett's test (test for homoscedasticity). In some cases, even after log-transforming the data, normality and/or homoscedasticity was not reached. ANOVA is considered a robust technique against violations of normality and/or heteroscedasticity, particularly with balanced designs with high data replication (Zar 1999). To further increase test robustness, when log-transformations failed to achieve normality and/or homoscedasticity, we reduced the significance level ($\propto$ value in the test) from 0.05 to 0.01 to minimize the chances of committing Type I error (Underwood 1997). All statistics were analyzed using Minitab 13.0 (SPSS).

To address our fourth question, how system-integrated benthic daytime metabolism differs across the 3 lagoons, we first derived the SEs of the weighted metabolic rates calculated with Eq. (3). For each weighted rate in State Park and Kee's Bayou, the standard error was derived as (Bevington 1969):

$$SE_{rate} = (SE^2_{(SR \times SC)} + SE^2_{(BSR \times BSC)})^{1/2} \qquad (4)$$

where

$$SE_{(SR \times SC)} = [(SE_{SR} \times SE_{SC})^2 + (SR \times SE_{SC})^2 + (SC \times SE_{SR})^2]^{1/2} \qquad (5)$$

$$SE_{(BSR \times BSC)} = [(SE_{BSR} \times SE_{BSC})^2 + (BSR \times SE_{BSC})^2 + (BSC \times SE_{BSR})^2]^{1/2} \qquad (6)$$

and SR, SC, BSR and BSC are as explained for Eq. (3).

Once the SEs were calculated, the df of each standard error was calculated using the Welch procedure (Welch 1947):

$$df\ SE_{(SR \times SC)} = SE^4_{(SR \times SC)}/[(SR^4 \times SE^4_{SC}/df\ SE_{SC}) + (SC^4 \times SE^4_{SR}/df\ SE_{SR})] \qquad (7)$$

$$df\ SE_{(BSR \times BSC)} = SE^4_{(BSR \times BSC)}/[(BSR^4 \times SE^4_{BSC}/df\ SE_{BSC}) + (BSC^4 \times SE^4_{BSR}/df\ SE_{BSR})] \qquad (8)$$

$$df\ SE_{rate} = SE^4_{rate}/[(SE^4_{(SR \times SC)}/df\ SE_{(SR \times SC)}) + (SE^4_{(BSR \times BSC)}/df\ SE_{(BSR \times BSC)})] \qquad (9)$$

Second, we calculated the 99% confidence interval (CI) of the weighted rate as (Zar 1999):

$$99\%\ CI = weighted\ rate \pm t_{0.01\ (2),df} \times SE_{rate} \qquad (10)$$

where df corresponds to the result of Eq. (9) or the df of the weighted metabolic rate. Finally, we compared the weighted values and 99% CIs of GPP, R and NP across the 3 lagoons and determined if significant differences existed at $\alpha \leq 0.01$.

RESULTS

Benthic metabolism

Comparison of bottom types across lagoons

In the 2 shoalgrass-vegetated lagoons, GPP was higher for shoalgrass patches than for bare sediment (Fig. 4, Table 2). Indeed, throughout the course of the study GPP ranged from 31.3 ± 16.2 to 107.7 ± 9.6 mg C m^{-2} h^{-1} (mean ± SE) in State Park and from 30.0 ± 6.6 to 68.4 ± 7.9 mg C m^{-2} h^{-1} in Kee's Bayou for shoalgrass patches, whereas for bare sediment it ranged from 9.5 ± 3.2 to 67.9 ± 7.0 mg C m^{-2} h^{-1} in State Park and from 1.3 ± 1.7 to 55.0 ± 5.0 mg C m^{-2} h^{-1} in Kee's Bayou. Higher GPP for shoalgrass patches did not depend on the lagoon or sampling time considered (i.e. no significant interaction between bottom type and lagoon or between bottom type and time). A significant opposing interaction was found between lagoon and time, indicating that benthic GPP tended to decrease over the course of the study in Kee's Bayou while slightly increasing in the State Park (Fig. 4, Table 2).
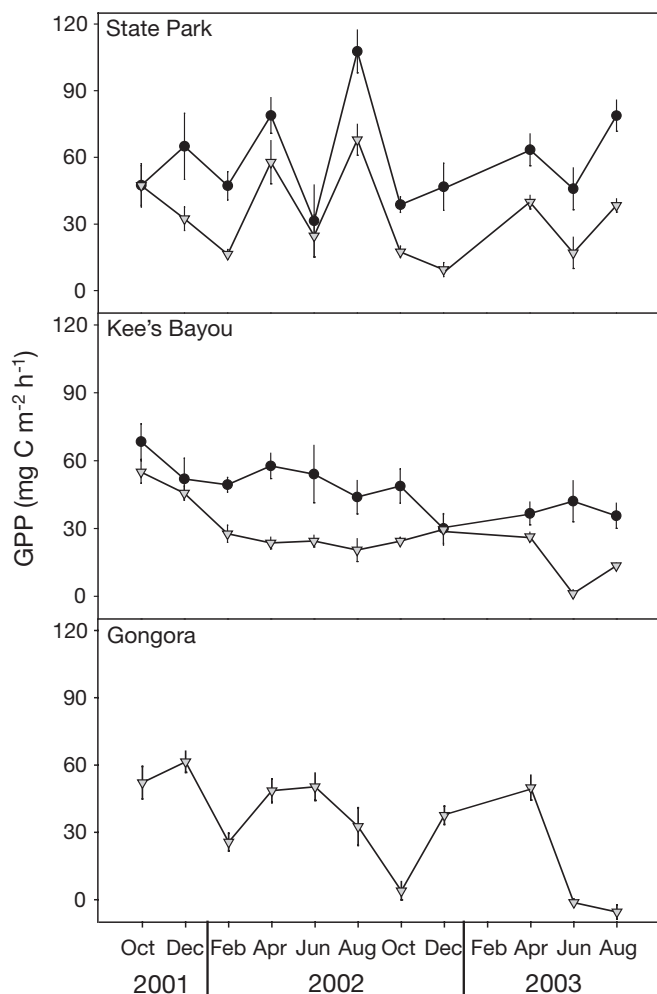
Fig. 4. Gross primary production (GPP) in shoalgrass patches (●) and bare sediment (▽) in the 3 lagoons studied. Data are mean ± SE

R in the 2 shoalgrass-vegetated lagoons was higher for shoalgrass patches than for bare sediment. In both State Park and Kee's Bayou (Fig. 5, Table 2), *R* for bare sediment was often low (<20 mg C h^{-1} m^{-2}), but reached levels of 43.2 ± 2.3 and 32.0 ± 3.8 mg C h^{-1} m^{-2} (mean ± SE) in State Park and Kee's Bayou, respectively (Fig. 5). In contrast, *R* for shoalgrass patches ranged from 13.7 ± 1.8 to 63.2 ± 2.4 mg C h^{-1} m^{-2} in State Park and from 12.7 ± 2.9 to 36.4 ± 7.1 mg C h^{-1} m^{-2} in Kee's Bayou. In addition, no significant interaction was found between bottom type and lagoon or bottom type and time, indicating higher *R* of shoalgrass patches was generally consistent regardless of the lagoon or sampling time considered. Finally, a significant opposing interaction was found between lagoon and time; benthic *R* displayed high values from February 2002 to October 2002 in State Park, but slightly depressed values during that period in Kee's Bayou (Fig. 5, Table 2).

Results for benthic NP in the 2 shoalgrass-vegetated lagoons were similar to those found for GPP and *R*; NP was higher for shoalgrass patches than for bare sediment (Fig. 6, Table 2), with that difference being independent of the lagoon or sampling time considered (i.e. no significant interaction between bottom type and lagoon or bottom type and time), and there was a significant opposing interaction between lagoon and time as benthic NP tended to decrease with time in Kee's Bayou, but to slightly increase with time in State Park (Fig. 6, Table 2). The magnitude of the difference in NP between shoalgrass patches and bare sediment, as indicated by the *F*-ratio of the bottom type factor in the ANOVA test, was smaller than the magnitude of the difference in either GPP or *R* (Table 2). This indicates that shoalgrass patches generally show higher NP than bare sediment, but to a lesser extent than they show higher GPP and *R*.

Comparison of bare sediment across lagoons

No consistent differences in GPP were found for bare sediment across the 3 lagoons compared (Fig. 4, Table 3). When the bare sediments of the 3 lagoons

Table 2. Mixed 3-way ANOVAs to compare rates of metabolism between shoalgrass patches and bare sediment in the 2 shoalgrass-vegetated lagoons (State Park and Kee's Bayou). *Significant (significance, α, was reduced from 0.05 to 0.01 when transformed data did not satisfy assumptions of normality and/or homoscedasticity. See 'Statistical analyses' for details)

| Factor	*F*	p
GPP		
Time	1.1	0.43
Lagoon	2.0	0.18
Bottom Type	95.3	<0.0001*
Time × Lagoon	5.3	0.007*
Time × Type	0.7	0.73
Type × Lagoon	0.8	0.40
Time × Lagoon × Type	1.7	0.07
R		
Time	0.9	0.57
Lagoon	0.8	0.39
Bottom Type	110.2	<0.0001*
Time × Lagoon	16.2	<0.0001*
Time × Type	0.8	0.62
Type × Lagoon	0.1	0.82
Time × Lagoon × Type	1.5	0.13
NP		
Time	1.2	0.38
Lagoon	0.2	0.68
Bottom Type	17.6	0.0002*
Time × Lagoon	5.7	0.006*
Time × Type	0.9	0.55
Type × Lagoon	1.6	0.23
Time × Lagoon × Type	1.5	0.15
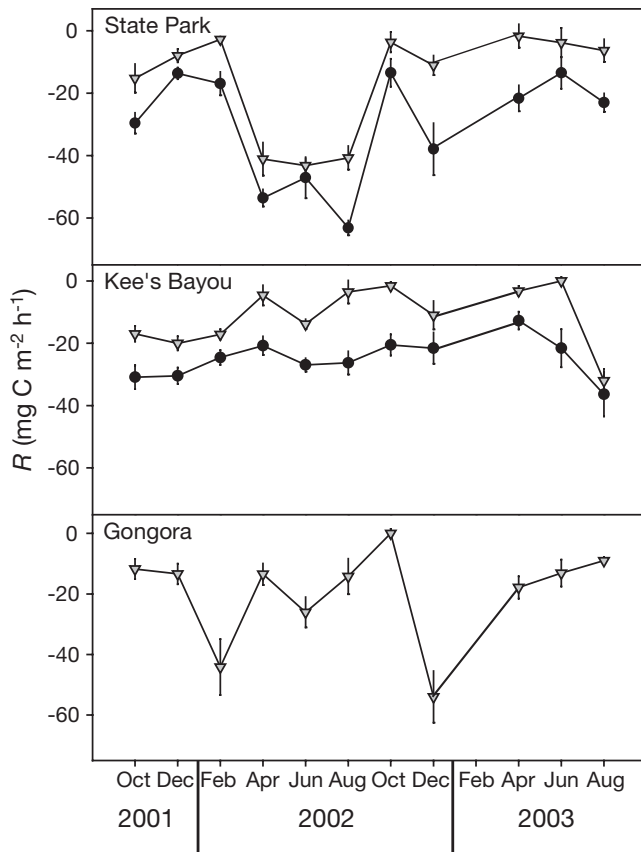
Fig. 5. Respiration (R) in shoalgrass patches (●) and bare sediment (▽) in the 3 lagoons studied. Data are mean ± SE

were examined simultaneously, GPP decreased with time, although that tendency was not statistically significant. These temporal changes, however, were largely contingent upon the lagoon considered, as revealed by the strong interaction found between lagoon and time. Namely, GPP for bare sediment in State Park oscillated throughout the course of the study and only showed a small overall decrease with time. In Kee's Bayou and Gongora, the overall decrease was larger than in State Park, but more uniform (i.e. less temporal oscillation) in Kee's Bayou than in Gongora (Fig. 4). As a consequence, although consistent differences across lagoons were not found, differences in GPP for bare sediment across lagoons were found during certain times throughout the course of the study.

R for bare sediment also did not vary across lagoons in any consistent way (Fig. 5, Table 3). A strong opposing interaction was found between lagoon and time; R for bare sediment varied largely across sampling dates in the 3 lagoons, but it displayed increased values from February to October 2002 in State Park and reduced values in Kee's Bayou during the same period. Thus although no consistent differences across

lagoons were found, R for bare sediment differed across lagoons at certain times (e.g. from February to October 2002) during the study.

The results obtained for NP when bare sediment was compared across the 3 lagoons were similar with those obtained for GPP (Fig. 6, Table 3). First, no consistent differences were found across the lagoons. Second, there was a marginally significant tendency for NP to decrease over time in the 3 lagoons, but the shape of that decrease was largely dependent on the lagoon considered. Thus, differences in NP for bare sediment across lagoons could also be found at certain times during the course of the study.

Comparison of system-integrated benthic production rates across lagoons

System-integrated benthic GPP was higher in State Park than in Kee's Bayou (Fig. 7), as one might expect when considering State Park's larger percentage of
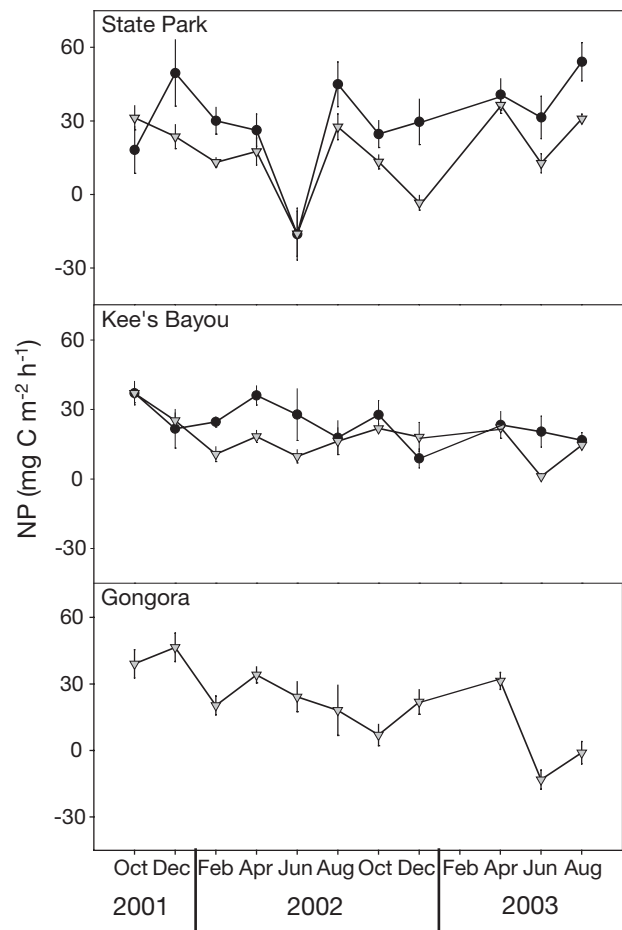

Fig. 6. Net production (NP) in shoalgrass patches (●) and bare sediment (▽) in the 3 lagoons studied. Data are mean ± SE

Table 3. Mixed 2-way ANOVAs for the comparison of bare sediment metabolism across lagoons. *Significant (significance, α, was reduced from 0.05 to 0.01 when transformed data did not satisfy assumptions of normality and/or homoscedasticity. See 'Statistical analyses' for details)

Factor	F-value	p-value
GPP		
Time	2.7	0.03
Lagoon	0.8	0.49
Time × Lagoon	8.1	<0.0001*
R		
Time	1.0	0.50
Lagoon	0.8	0.49
Time × Lagoon	12.1	<0.0001*
NP		
Time	2.4	0.05
Lagoon	0.4	0.68
Time × Lagoon	5.6	<0.0001*

total bottom shoalgrass covereage and the higher values of areal GPP found for shoalgrass patches than for bare sediment when the 2 lagoons were compared. System-integrated benthic GPP was also higher in State Park than in Gongora, but it did not differ significantly between Kee's Bayou and Gongora.

System-integrated benthic R was greater in State Park than in Kee's Bayou (Fig. 7), which is also to be expected from the larger percentage of total bottom covered by shoalgrass in the former lagoon and the higher values of areal R found for shoalgrass patches than for bare sediment when the 2 lagoons were compared. However, system-integrated benthic R in Gongora did not differ significantly from the value calculated for either of the other 2 lagoons.

In clear contrast to the results obtained for GPP and R, system-integrated benthic NP did not differ across the 3 lagoons examined. Values of system-integrated benthic NP followed the same visual pattern as for GPP and R (Fig. 7), with State Park showing the highest value, Kee's Bayou the lowest value and Gongora the intermediate value, but the values were not statistically different from each other. Power analysis was employed in order to rule out the chances of committing a Type II error, and comparisons were determined to be quite robust with $1 - \beta$ values greater than 0.99 for each comparison.

Benthic producer biomass

Shoalgrass total biomass (including above- and below-ground compartments) varied widely over the 2 yr sampling period (Fig. 8). The highest values were found in State Park during the first year of sampling,
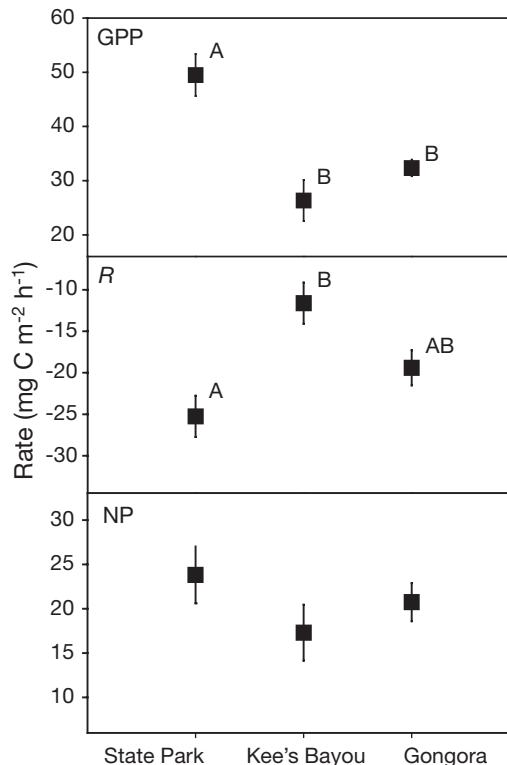

Fig. 7. System-integrated (weighted) rates of benthic GPP, R, and NP. Bars: SE of weighted rate as derived with Eqs. (4), (5), & (6) (see 'Statistical analyses'). Letters: significant differences (p ≤ 0.01) as obtained with Eq. (7) (see 'Statistical analyses')

which often exceeded 150 g AFDW m^{-2}, and peaked at 220.4 ± 60.5 g AFDW m^{-2} in August 2002. During that first year, Kee's Bayou displayed lower values of total shoalgrass biomass, which ranged from 49.7 ± 9.3 to 140.9 ± 26.2 g AFDW m^{-2}. However, the 2 lagoons showed similar values of total biomass during the second year of sampling, with values ranging from 54.4 ± 12.2 to 104.0 ± 21.3 g AFDW m^{-2} for State Park and 41.6 ± 10.3 to 113.4 ± 15.7 g AFDW m^{-2} for Kee's Bayou. Indeed, there was a significant interaction between lagoon and time, pointing to the large differences in total biomass found between the 2 lagoons in the first year but not in the second year (Table 4). These results were similar to those observed for aboveground biomass only; despite large temporal variability, State Park displayed higher values of biomass during the first year of sampling than did Kee's Bayou, but not during the second year (Fig. 8, Table 4). On average, aboveground biomass represented approximately 25% of total shoalgrass biomass.

Benthic microalgal chl a concentrations in bare sediment also varied widely over the 2 yr sampling period in the 3 lagoons (Fig. 9, Table 4). Similar to the patterns for shoalgrass biomass, significant differences in ben-
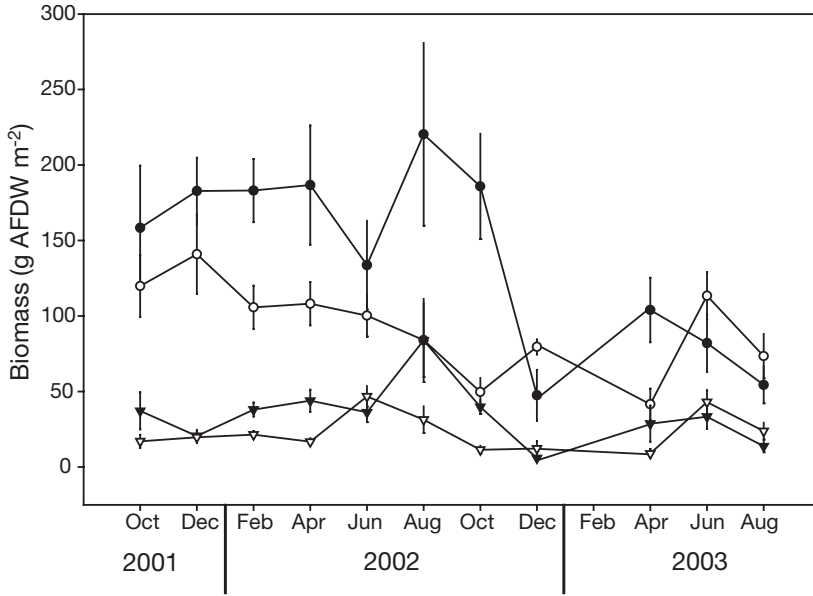
Fig. 8. Total (circles) and above-ground (triangles) shoalgrass biomass in State Park (solid symbols) and Kee's Bayou (open symbols). Data are mean ± SE

DISCUSSION

The areal metabolic rates measured for shoalgrass patches and bare sediment in the three lagoons we examined were similar, respectively, to the rates obtained in other shoalgrass and bare sediment systems in the Gulf of Mexico (Shoalgrass: Heffernan & Gibson 1983, Morgan & Kitting 1984, Clavier et al. 2005; Bare Sediment: Daehnick et al. 1992, Moncreiff et al. 1992) although other studies have reported higher rates (Murray & Wetzel 1987, D'Avanzo et al. 1996, Ziegler & Benner 1998, Kaldy et al. 2002), which could be partially due to differences in methodology. In addition, areal rates of daytime community GPP, *R*, and NP were all higher for shoalgrass patches than for bare sediment in the two vegetated lagoons. This is in accordance with several previous reports that also found higher rates of GPP, *R* and NP in seagrass beds than in the open sediment (Heffernan & Gibson 1983, Murray & Wetzel 1987, Daehnick & Sullivan 1989, Pollard & Kogure 1993). For instance, Murray & Wetzel (1987) measured rates of GPP that were nearly five times higher for seagrass beds than for bare sediment alone, and Pollard & Kogure (1993) measured substantially higher NP in seagrass patches than in bare sediment when adequate light was available.

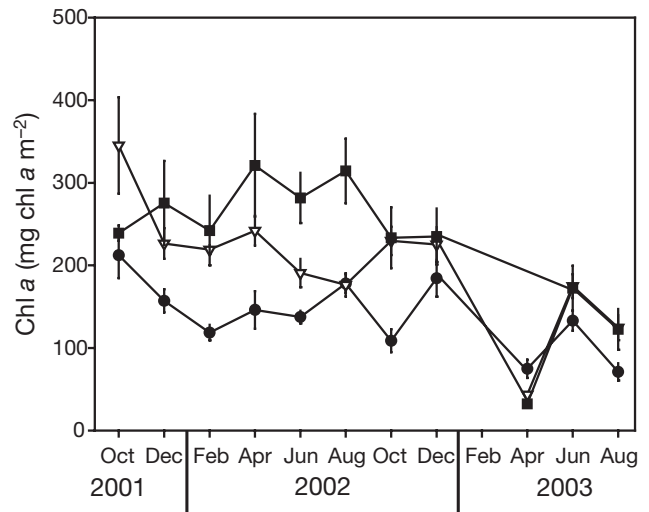The higher areal rates of GPP documented here for shoalgrass patches compared to bare sediment mainly

thic microalgal chl *a* concentrations occurred across lagoons during the first year of sampling, but not during the second year (i.e. highly significant interaction between lagoon and time). During the first year, benthic microalgal chl *a* concentration was highest at Gongora, intermediate at Kee's Bayou, and lowest at State Park (1-way ANOVA comparing the lagoons in the first year, p <0.01, Tukey-test for all pairwise comparisons, p < 0.01). During the second year, benthic microalgal chl *a* remained low and similar in the 3 lagoons.

Table 4. Mixed 2-way ANOVAs for comparison of total (below- plus above-ground) and above-ground shoalgrass biomass, and benthic microalgal chl *a* concentration across lagoons. *Significant (significance, α, was reduced from 0.05 to 0.01 when transformed data did not satisfy the assumptions of normality and/or homoscedasticity. See 'Statistical analyses' for details)

Factor	*F*	p
Total shoalgrass biomass		
Time	1.6	0.25
Lagoon	7.3	0.02
Time × Lagoon	2.5	0.01*
Above-ground shoalgrass biomass		
Time	1.6	0.23
Lagoon	3.5	0.09
Time × Lagoon	2.8	0.005*
Benthic microalgal chl *a* conc.		
Time	6.4	<0.0001*
Lagoon	11.9	<0.0001*
Time × Lagoon	2.7	<0.0001*

Fig. 9. Benthic microalgal chl *a* concentration in State Park (●), Kee's bayou (∇), and Gongora (■). Data are mean ± SE

result from the much larger biomass of primary producers found in the patches. In our 2 lagoons with shoalgrass, areal values of primary producer biomass expressed in carbon units (based on a AFDW to carbon conversion factor of 0.44 mg C mg AFDW^{-1} for shoalgrass leaves and epiphytes and 0.37 mg C mg AFDW^{-1} for roots and rhizomes; J. Stutes unpubl. data) ranged from at least 3-fold to one order of magnitude higher for shoalgrass patches than for bare sediment, depending on the C to chl a conversion used for benthic microalgae, which can range from 10 (MacIntyre et al. 2002) to 100 g C g chl a (Gasol et al. 1997, MacIntyre et al. 2002). This difference is conservative because sediment microalgae within the shoalgrass patches were not included in the calculation. The biomass of benthic microalgae that inhabit bare sediments turns over several times faster than that of shoalgrass (Moncreiff et al. 1992, Cebrian et al. 1999). However, the much larger areal primary producer biomass in shoalgrass patches compared to bare sediment far outweighs the differences in turnover, leading to higher rates of GPP for shoalgrass patches than for bare sediment.

The higher areal R rates for shoalgrass patches when compared to bare sediment documented in this study most likely result from larger areal primary producer biomass (Murray & Wetzel 1987, Daehnick & Sullivan 1989), higher organism abundance utilizing the patches for shelter and food (Morgan & Kitting 1984, Heck et al. 2003a), higher sedimentation of detritus and subsequent decomposition (Gacia et al. 2003, Barron et al. 2004), and the contribution by non-photosynthetic shoalgrass belowground biomass (Pollard & Kogure 1993, Touchette & Burkholder 2000). Bare sediments can attain higher areal R rates than seagrass beds in eutrophic estuaries (D'Avanzo et al. 1996) or when subject to intense sedimentation of organic matter (Livingston et al. 1998), but this is not the case in our lagoons.

Of particular ecological importance is that shoalgrass patches yield a greater surplus of photosynthetically fixed carbon (i.e. NP) than bare sediment in our study, yet the magnitude of that difference is less than the magnitude of the difference in absolute carbon fixation (i.e. GPP) or in R. Hence, shoalgrass patches feature on slightly higher areal rates of NP than bare sediment when compared to the large differences recorded for both GPP and R. The reason lies in the interaction between GPP and R in both types of bottom; shoalgrass patches have higher areal rates of GPP than does bare sediment, but also disproportionately higher areal rates of R, which agrees with previous comparisons (Barron et al. 2004, Gacia et al. 2005).

Higher areal rates of GPP, R and, to a lesser extent, NP for shoalgrass patches than for bare sediment were consistent throughout the course of our study even though all three areal metabolic rates varied widely throughout the study period. Yet, despite these large temporal oscillations, areal metabolic rates for bare sediment tended to be lower than for shoalgrass patches for the entire duration of the study. In contrast to these results, other studies have shown a large influence of seasonality on the relative differences in metabolic rates between open sediment and seagrass beds, with those differences becoming larger during late spring and early summer as seagrass metabolic rates peak to a greater extent than do bare sediment rates (Heffernan & Gibson 1983, Murray & Wetzel 1987, Kaldy et al. 2002).

In our study, shoalgrass patches tend to have higher areal metabolic rates than do bare sediments regardless of the lagoon considered. This is interesting considering that State Park demonstrated higher areal shoalgrass biomass values than Kee's Bayou during the first year of the study, but lower values of areal benthic microalgal chl a concentrations. Since producer biomass is a major driver of metabolic rates (Sand-Jensen & Borum 1983, Barron et al. 2004, Bostroem et al. 2004), one could have expected smaller metabolic differences between shoalgrass patches and bare sediment in Kee's Bayou than in State Park, at least during the first year of the study. Contrary to this expectation, the comparison between State Park and Kee's Bayou indicates that areal metabolic differences between shoalgrass patches and bare sediment remain unaltered despite decreased shoalgrass abundance, both in terms of areal biomass and total cover in the lagoon, and increased areal benthic microalgal chl a concentrations from State Park to Kee's Bayou.

We failed to find any consistent differences in areal metabolic rates for bare sediment among the 3 lagoons. Throughout the course of the study, the lagoons maintained steady relative bottom cover for shoalgrass patches and bare sediment, from 100% bottom cover by bare sediment in Gongora to approximately 96% in Kee's Bayou to approximately 36% in State Park. In addition, areal microalgal chl a concentrations in bare sediment was higher in Gongora than in the other two lagoons, and higher in Kee's Bayou than in State Park, during the first year of the study. Differences in microalgal chl a concentrations may partially result from differences in nitrogen loading from the surrounding watershed (D'Avanzo et al. 1996, Havens et al. 2001). Nevertheless, areal rates of GPP, R, and NP for bare sediment did not vary consistently across the lagoons despite statistically significant differences in areal microalgal chl a concentrations during the first year of study. Significant metabolic differences across lagoons were restricted to a number of sampling dates during the course of the study and did not follow any pattern. Our comparison shows that,

despite large differences in areal benthic microalgal chl *a* concentrations and relative cover by shoalgrass patches or bare sediment, areal metabolic rates for bare sediment remain similar overall in the three lagoons examined. The large temporal variability found in the metabolic rates of bare sediment in the three lagoons could partially account for the lack of consistent significant differences among the lagoons.

When areal values of benthic metabolic rates were scaled using cover measurements to derive weighted benthic metabolic rates for the entire lagoon, State Park exhibited higher weighted rates of benthic GPP than Kee's Bayou and Gongora. This is not surprising considering the higher areal rates of GPP for shoalgrass patches when compared to bare sediment and the much larger shoalgrass cover in State Park than in the other 2 lagoons. This indicates that, per weighted square meter, the bottom at State Park fixes approximately twice as much carbon through photosynthesis as does the bottom at Kee's Bayou and Gongora. In contrast, Kee's Bayou and Gongora did not show significantly different weighted rates of benthic GPP, probably due to the small differences in shoalgrass cover between the two lagoons (4% of the bottom in Kee's Bayou and nil in Gongora) and the lack of overall significant differences in areal metabolic rates for bare sediment across lagoons.

Weighted rates of benthic *R* were also higher in State Park than in Kee's Bayou, but they did not differ significantly between State Park and Gongora. This latter result was unexpected. Based on (1) the contrasting differences in shoalgrass cover found between State Park and Gongora, (2) the higher areal *R* rates found for shoalgrass patches than for bare sediment when the two lagoons with shoalgrass were compared, and (3) the lack of significant differences in overall areal *R* rates for bare sediment among the three lagoons, we expected higher weighted benthic *R* rates in State Park than in Gongora. This unexpected result mainly stems from the extremely high areal *R* rates measured in February and December 2002 for bare sediment at Gongora. While still not forcing significant differences in overall areal *R* rates for bare sediment across the 3 lagoons, those extreme values did seemingly increase the weighted rate of benthic *R* at Gongora enough to render it not significantly different from the weighted rate at State Park. Weighted rates of benthic *R* did not differ between Kee's Bayou and Gongora which, again, is probably due to the small differences in shoalgrass cover between the two lagoons and the lack of overall significant differences in areal metabolic rates for bare sediment across lagoons. Although our measurements only refer to daytime rates, this result could also hold for daily scales (i.e. day and nightime).

Most surprising, however, is that weighted rates of benthic NP did not differ significantly across lagoons despite greater areal rates observed for shoalgrass patches than for bare sediment and the much larger shoalgrass cover in State Park than in Kee's Bayou and Gongora. Power analysis of the comparisons confirms that the tests are quite robust with a $1 - \beta$ exceeding 0.99 in every case. The explanation partly lies in the reduced magnitude of the differences in areal NP between shoalgrass patches and bare sediment in comparison to the differences observed in areal GPP and *R*. Shoalgrass patches tend to exhibit higher areal rates of NP than do bare sediments, but to a lesser extent than their higher rates of GPP and *R*. As a consequence, weighted rates of benthic NP, unlike weighted rates of benthic GPP and *R*, do not differ significantly across the 3 lagoons examined.

The lack of significant differences in weighted rates of benthic NP across the 3 lagoons is not obvious from visual inspection of the differences in areal NP between shoalgrass patches and bare sediment and in shoalgrass cover across the lagoons. Because areal rates of NP are higher for shoalgrass patches than for bare sediment, and State Park has much higher shoalgrass cover than the other 2 lagoons, one could easily misinterpret those results to suggest that State Park has higher system-integrated rates of benthic NP (i.e. mg C weighted m^{-2} h^{-1}) than the other 2 lagoons, which is not the case. This underscores the need to derive system-integrated estimates to properly understand how changing benthic mosaics can alter the daytime metabolism, and important resulting implications, of coastal systems.

Also, the lack of significant system-integrated differences in benthic NP when comparing a system dominated by shoalgrass (State Park) with 2 systems with little or nonexistent shoalgrass cover (Kee's Bayou and Gongora) may have important implications. Because NP represents the excess of photosynthetically-fixed carbon that is not consumed by local producers and consumers, higher levels of NP should correspond to a greater potential capacity for the system to accumulate and/or export organic carbon. Indeed, systems with large levels of NP are often important sinks of organic carbon and/or can export large amounts of organic carbon to neighboring systems (Suchanek et al. 1985, Hemminga et al. 1996, Santos et al. 2003). On this basis, the decreasing levels of shoalgrass abundance across State Park to Kee's Bayou to Gongora do not seem to largely impact the potential capacity for the lagoons to accumulate and/or export organic carbon, since their system-integrated benthic NP did not vary significantly. Our results do have the caveat of being limited to daytime measurements alone, but shoalgrass patches may likely feature higher night time *R* rates

than bare sediment due to decomposition of the significant detrital pool and the fauna associated with this (Moriarty et al. 1986, Eyre & Ferguson 2002) and, thus, daily areal NP rates would become less different between shoalgrass patches and bare sediment, which would have reinforced the lack of significant differences in system-integrated benthic rates of NP as shoalgrass patches are replaced with bare sediment in the three lagoons compared. These results suggest that, as seagrass is lost in coastal systems, accumulation of organic carbon in the system and export to adjacent systems may not be as drastically altered as other system properties, such as the provision of shelter and food to many juvenile fish species and invertebrates by seagrass patches (Morgan & Kitting 1984, Connolly 1994, Duffy et al. 2001, Heck et al. 2003b).

This remains as an untested possibility for at least 3 reasons. First, the system-integrated benthic net excess of photosynthetically-fixed carbon not respired by producers and consumers during the time length of our incubations (i.e. from 3 to 5 h) should decompose faster over longer time periods in Kee's Bayou and Gongora than in State Park. Shoalgrass organic matter, which is more refractory than microalgal organic matter (Dawes 1986, Havens et al. 2001, Moncreiff & Sullivan 2001, Eyre & Ferguson 2002), is far less abundant in the former lagoons. Differences in long-term rates of organic matter decomposition should influence carbon accumulation in these systems (Cebrian 2002). Second, processes such as water-column metabolism and organic exchange through tidal export need to be considered to fully evaluate carbon accumulation in the lagoons (D'Avanzo et al. 1996, Gazeau et al. 2005). Third, seagrass leaves and benthic microalgae have different levels of buoyancy and are exported out of coastal systems through different means (Asmus & Asmus 2000, Hyndes & Lavery 2005). Thus, despite having similar levels of system-integrated benthic NP, the 3 lagoons examined may export and/or accumulate different quantities of organic carbon.

In conclusion, in accordance with past reports of the same and other seagrass species, shoalgrass patches in 2 lagoons of the North Central Gulf of Mexico display higher areal rates of daytime GPP, R and NP than does bare sediment. The differences in areal metabolic rates between shoalgrass patches and bare sediment in these lagoons are robust to the large opposing differences in shoalgrass abundance, both in terms of total bottom cover and areal biomass within the patches, and in areal microalgal chl a concentrations in bare sediment observed between the lagoons. In addition, we did not observe any consistent differences in areal metabolic rates for bare sediment when comparing these 2 lagoons and a third one that has no shoalgrass, despite the fact that areal microalgal chl a concentra-

tions in bare sediment increases as shoalgrass abundance decreases among the lagoons. Finally, the results obtained when comparing system-integrated benthic metabolic rates (i.e. combining areal rates and cover by each bottom type) among the 3 lagoons do not always correspond with the results observed with areal rates. The lagoon with the most shoalgrass most often has higher system-integrated benthic rates of GPP and R than the other 2 lagoons, but similar rates of NP. Thus, the decreasing trend in shoalgrass abundance among the 3 lagoons examined seems of limited importance for the lagoon's potential capacity to accumulate and/or export organic carbon, in contrast with the large impact that seagrass loss may have for other ecosystem properties. These results exemplify the need to obtain system-integrated estimates, and not solely areal measurements, to accurately evaluate how decreasing levels of seagrass abundance can alter the daytime metabolism of coastal ecosystems.

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