

ABSTRACT

Title of Dissertation: PLANT-SEDIMENT INTERACTIONS AND
BIOGEOCHEMICAL CYCLING FOR SEAGRASS
COMMUNITIES IN CHESAPEAKE AND FLORIDA
BAYS

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Seagrasses are prominent, productive components of shallow coastal ecosystems worldwide. The role of seagrasses in biogeochemical cycling varies widely across ecosystems, and this is due in large part to the complex interactions and feedbacks among processes controlling dynamics of carbon, oxygen, nutrients, and dissolved organic matter (DOM). This dissertation examines the importance of the keystone seagrass species, *Thalassia testudinum*, to biogeochemical cycling at the community and ecosystem levels in Florida Bay. The research presented here also describes the consequence of disturbances, such as shifts in species composition and seagrass dieback, on biogeochemical processes in both Florida and Chesapeake Bays. In Florida Bay, *T. testudinum* was shown to stimulate sediment microbial activities and benthic production of oxygen, inorganic nitrogen, and DOM relative to adjacent benthic communities without seagrass but containing benthic microalgae. Strong diel patterns in net fluxes of these solutes in both communities underscore the importance of photosynthesis. Ecosystem-level production (P) and respiration (R) rates were also enhanced in *T. testudinum* communities. Clear seasonal and

regional variations in P and R were evident across Florida Bay, with lowest rates reported in the northern regions. Seagrass dieback had a negative effect on sediment nitrification rates and net ecosystem production (P-R) at one site in Florida Bay, and loss of seagrass habitat may result in significant changes to biogeochemical budgets within this system. In mesohaline Chesapeake Bay, the ephemeral submersed plant species, *Ruppia maritima* was also shown to stimulate organic production, nutrient cycling, and sediment biogeochemical processes compared to benthic communities without seagrass; however, the more persistent native species, *Potamogeton perfoliatus*, had an even greater impact on these processes. Collectively, the results of this research reveal the potential significance of seagrass to biogeochemical cycling in Chesapeake and Florida Bays and suggest that disturbances, such as seagrass dieback or shifts in species composition, may substantially alter biogeochemical budgets within these systems.

PLANT-SEDIMENT INTERACTIONS AND BIOGEOCHEMICAL CYCLING FOR
SEAGRASS COMMUNITIES IN CHESPEAKE AND FLORIDA BAYS

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DEDICATION

To Mark Gould,
who, through his friendship and teachings,
inspired in me a love of science &
a desire to share it with others

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CHAPTER 1: Introduction

Seagrass communities are among the most productive in the biosphere and are of high ecological importance in many coastal environments. Because seagrass communities often serve as crucial nursery habitats for a variety of commercially important species (Lubbers et al. 1990, Connolly 1994, Heck et al. 1995, Polte & Asmus 2006), these highly productive ecosystems often are of significant economical value in addition to their ecological importance (McArthur & Boland 2006). These vascular plants inhabit diverse environments, ranging from temperate to tropical climates and from brackish to marine waters worldwide.

Seagrass communities also tend to be sites of enhanced biogeochemical cycling, and their influence on these processes can occur through both indirect and direct mechanisms. The physical structure of plant leaves impedes water flow within the seagrass bed (Fonseca et al. 1982, Verduin & Backhaus 2000), resulting in enhanced deposition and trapping of particulate organic matter (Ward et al. 1984, Gacia & Duarte 2001). The import of allochthonous organic matter, combined with the retention of senescing plant material, provide rich sources of organic substrate for microbial degradation and nutrient cycling within the seagrass sediments (e.g., Kenworthy et al. 1982, Kennedy et al. 2004). The physiology of the plants, themselves, may also influence sediment biogeochemical cycling (Fig. 1.1). Excretion of dissolved organic matter (DOM) in the form of labile, photosynthetic metabolites from plant roots to the surrounding sediment (e.g., Penhale & Smith 1977, Wetzel & Penhale 1979, Moriarty et al. 1986, Kaldy et al. 2006) (see Appendix) can stimulate heterotrophic processes such as nitrogen fixation (Moriarty & O'Donohue 1993, McGlathery et al. 1998) and sulfate reduction (Blaabjerg & Finster 1998, Holmer et al. 2001, Calleja et al. 2006). While enhanced nitrogen fixation can benefit seagrasses through a greater availability of inorganic nitrogen in seagrass sediments (Hansen et al. 2000), stimulation of sulfate reduction associated with DOM excretion can lead to the accumulation of sulfide, a

potential phytotoxin (Erskine & Koch 2000). Release of oxygen from plant roots can ameliorate this effect by precluding the accumulation of sulfide in the rhizosphere (Lee & Dunton 2000) (see Appendix). Root excretion of oxygen can also stimulate nitrification (Iizumi et al. 1980, Caffrey & Kemp 1990) and consequently, coupled nitrification-denitrification, by creating an oxidized zone around the roots in otherwise anoxic sediments (Frederiksen & Glud 2006). The balance between these relatively complex seagrass-sediment interactions can have important implications to both seagrass survival and community biogeochemical cycling.

In addition to their impact on sediment biogeochemistry, seagrasses can also influence biogeochemical cycling in the overlying water column (Fig. 1.1). Release of photosynthetically-derived O₂ from plant leaves to the surrounding water can support both benthic and pelagic heterotrophic processes (e.g., Moriarty et al. 1986, e.g., Chin-Leo & Benner 1991). Nutrient fluxes from seagrass sediments tend to be relatively low due to direct assimilation of inorganic nutrients through plant leaves (Short & McRoy 1984, Hemminga et al. 1999, Lee & Dunton 1999), tight recycling of sediment nutrients (Blackburn et al. 1994, Ziegler & Benner 1999a, Hansen et al. 2000), and the relative low nutrient content of decomposing plant material (e.g., Peduzzi & Herndl 1991). The relatively low rates of nutrient exchange across the sediment-water interface may limit phytoplankton growth in the overlying water (Risgaard-Petersen & Ottosen 2000). Under some circumstances, DOM production in seagrass communities can be relatively high (Velimirov 1986, Ziegler & Benner 1999, Eyre & Ferguson 2002). Although this DOM may derive from degradation of particulate organic matter, correlations with photosynthetic activity (Ziegler & Benner 1999) suggest that substantial fractions of DOM production arise from leaf excretion of dissolved organic compounds during photosynthesis (e.g., Wetzel & Penhale 1979). DOM release from the benthos may support bacterial production in the water column overlying seagrass beds representing a

microbial link between seagrass production and planktonic food webs (Moriarty & Pollard 1982, Chin-Leo & Benner 1991, Ziegler & Benner 1999b).

The influence of seagrasses on biogeochemical cycling often extends beyond the plant bed to the ecosystem level. Seagrass photosynthesis can represent a substantial contribution to overall ecosystem production. The balance between production and respiration within these communities provides an index of the trophic status and the availability of autochthonous organic matter for export to adjacent regions (e.g., Kemp et al. 1997, Barron et al. 2004). Positive net ecosystem production (NEP), where production exceeds respiration, indicates net autotrophy, while net heterotrophy is characterized by negative NEP (i.e., production < respiration). The trophic status of seagrass communities can vary both seasonally and across ecosystems. Despite high productivity, ecosystem production and respiration are often relatively balanced in seagrass communities (e.g., D'Avanzo et al. 1996, Ziegler & Benner 1998, Santos et al. 2004) (see Appendix). Although seagrasses and their associated microalgae are highly productive (e.g., Hemminga & Duarte 2000), instances of net heterotrophy have been reported previously (Barron et al. 2004, Caffrey 2004). High respiratory demands of plant tissue, combined with enhanced microbial decomposition of trapped POM, can result in net heterotrophy evolving over time after initial colonization (Barron et al. 2004). The trophic status of seagrass ecosystems can be influenced by factors such as light and nutrient availability and organic matter inputs.

Since the mid-20th Century, coastal environments worldwide have experienced significant losses in seagrass abundance and distribution (Orth & Moore 1983, Cambridge & McComb 1984, Larkum & West 1990, Pulich & White 1991, Robblee et al. 1991). Disturbances from both natural (e.g., hurricanes, disease, and grazing) and anthropogenic (e.g., dredging and nutrient and sediment loading) causes have been indicated as responsible for seagrass decline (Kemp et al. 1983, Larkum & West 1990,

Short & Wyllie-Echeverria 1996, Orth et al. 2006). In Florida Bay, dramatic losses of *Thalassia testudinum* populations in the late 1980's are thought to have arisen from a combination of natural and anthropogenic causes, including hypersalinity, sulfide toxicity, disease, and altered watershed hydrology and tidal exchange with adjacent coastal waters (Robblee et al. 1991, Carlson et al. 1994, Durako & Kuss 1994). Initial losses of seagrass populations in Florida Bay were followed by phytoplankton blooms and enhanced sediment resuspension that led to a secondary seagrass dieback (e.g., Fourqurean & Robblee 1999). Although some recovery of *T. testudinum* populations has occurred in recent years, incidents of seagrass dieback still occur (Zieman et al. 1999). In other estuaries, such as Chesapeake Bay, seagrass decline is generally attributed to increased anthropogenic nutrient inputs leading to decreased water clarity through stimulation of phytoplankton blooms epiphytic algal growth (Kemp et al. 1983). While the causes of seagrass decline in ecosystems such as Florida and Chesapeake Bays have been widely investigated, the consequences of these disturbances on biogeochemical cycling are poorly understood.

In this dissertation I investigate the role of seagrasses in biogeochemical cycling and the complex interactions controlling the dynamics of carbon, O₂, nutrients, sulfide, and DOM (Fig. 1.1). The central goals of this dissertation were to: 1) evaluate the importance of the keystone seagrass species, *T. testudinum* to biogeochemical cycling at the community and ecosystem levels in the subtropical Florida Bay system; 2) describe the consequence of disturbances, such as seagrass dieback on biogeochemical processes; and 3) investigate how these interactions between seagrass and biogeochemical processes may affect restoration of native submersed plant species in Chesapeake Bay.

In the first research chapter (Chapter 2), I employed a stratified research approach, ranging from plant-sediment interactions to benthic and open-water fluxes, to

determine the degree to which O₂, nutrient and DOM cycling were enhanced by the presence of *T. testudinum*. Using similar techniques, Chapter 3 focused on investigating the impact of seagrass dieback on biogeochemical cycling through comparison between healthy and disturbed communities in shallow (bank) and deeper (basin) habitats. The goal of Chapter 4 was to determine the influence of *T. testudinum* on net ecosystem metabolism and describe regional and seasonal variations in ecosystem metabolism at sites dominated by *T. testudinum* throughout Florida Bay. These studies were designed to enhance understanding of the importance of seagrass dieback to biogeochemical cycling and metabolism in Florida Bay and related shallow coastal systems. Information gained from these studies will also aid in developing biogeochemical budgets and provide insight into controls and fates of inorganic and organic nutrients within this ecosystem. In the final research chapter (Chapter 5), I quantitatively compare the relative roles of two submersed plant species in biogeochemical cycling in the mesohaline region of Chesapeake Bay. Specifically, I compare effects of the opportunistic species, *Ruppia maritima*, and the more stable species *Potamogeton perfoliatus*, on key biogeochemical processes and investigate how a recent resurgence of the former species might stimulate the restoration of the latter plant leading to enhanced and stable nutrient, oxygen and carbon dynamics within this region. The dissertation closes with a brief synthetic chapter that summarizes and integrates the key findings of this study and the implications for environmental management in Florida and Chesapeake Bays.

LITERATURE CITED

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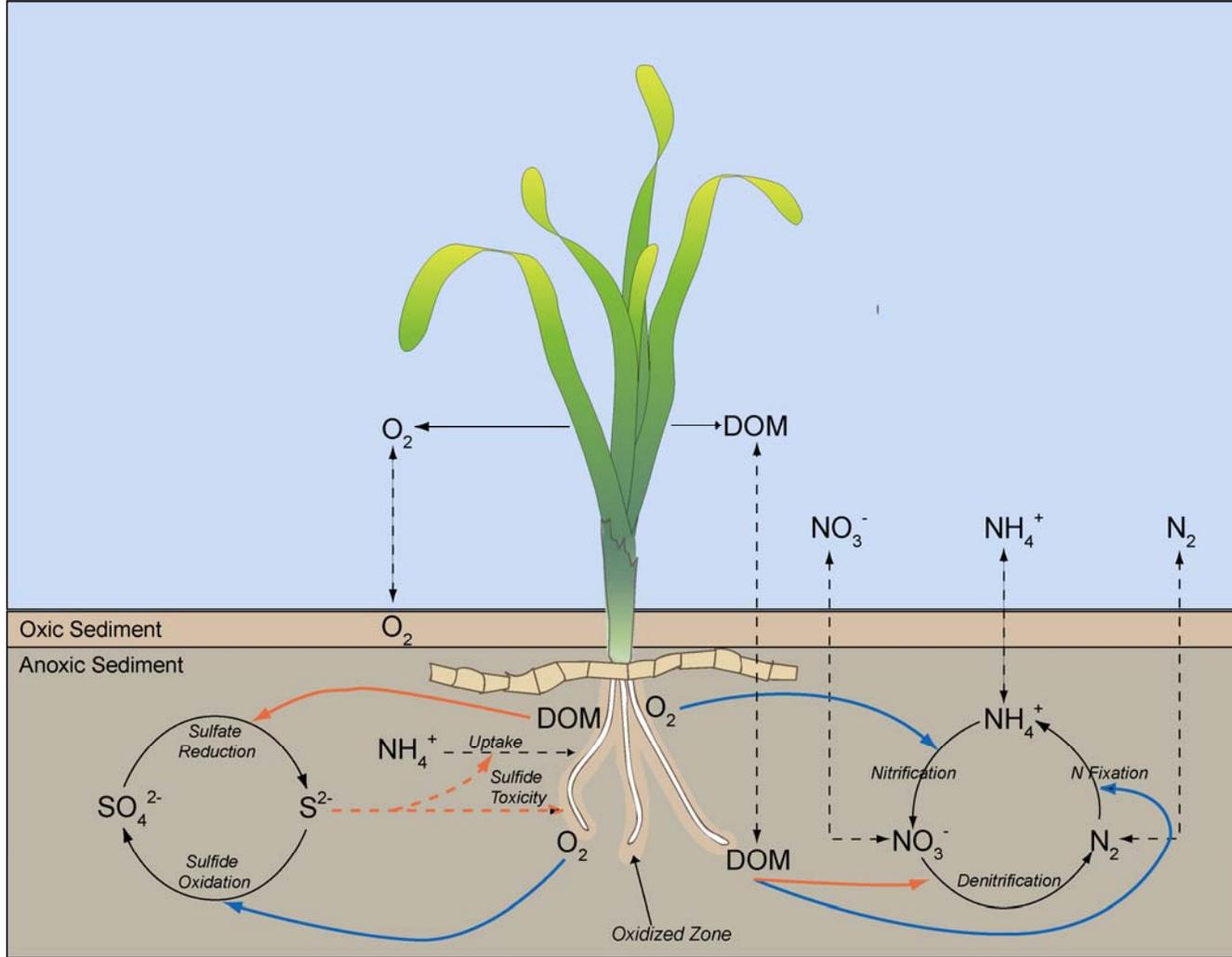


Fig. 1.1. Conceptual diagram of complex plant-sediment interactions and biogeochemical cycling in seagrass beds. Blue arrows represent positive feedback mechanisms, while red arrows represent negative feedback mechanisms.

**CHAPTER 2: Influence of *Thalassia testudinum* on biogeochemical cycling
at diel and seasonal scales in Florida Bay, USA**

ABSTRACT

Thalassia testudinum is the most dominant species of seagrass in Florida Bay, but little is known about how this submersed plant influences biogeochemical cycling within this system. The objective of this study was to determine the influence of *T. testudinum* on community O₂, nutrient, and DOM cycling compared to adjacent “bare” sediment containing microalgae but no seagrass in a small Florida Bay cove over 2003-2004. Diel and seasonal variations in biogeochemical cycling were determined from concentration changes in the open-water and from fluxes measured in intact core incubations. Sediment microbial activities (e.g., ammonification, nitrification) and sediment porewater concentrations of nutrients and sulfide were also measured in June 2004. Clear diel patterns observed in O₂, inorganic nitrogen, DOC, and DON concentrations emphasize the importance of benthic photosynthesis in both communities. Rates of O₂ production, NH₄⁺ regeneration, and DOC production were significantly enhanced in the *T. testudinum* community relative to bare sediments, and this difference was most pronounced in summer. Vertical profiles of O₂ and NH₄⁺ concentrations in the water column over the diel period revealed that the benthos was the source of remineralized nitrogen in the seagrass community. DOC production in the light was attributable to seagrass O₂ production, but rates of DOC production often exceeding photosynthetic C-fixation, suggesting that enhanced deposition and degradation of particulate organic matter may also be an important source of DOC. Brief periods of hypoxia within the seagrass canopy at night combined with high sediment sulfide concentrations revealed a potential vulnerability of *T. testudinum* to seagrass dieback during summer. The results of this study illustrate the potential importance of *T. testudinum* to biogeochemical cycling in Florida Bay and imply that seagrass dieback could have a significant impact on nutrient and organic carbon cycling within this system.

INTRODUCTION

Seagrasses represent a key ecological component of shallow coastal ecosystems worldwide, providing crucial habitat for many fish and invertebrate populations (e.g., Lubbers et al. 1990, Heck et al. 1995, West & King 1996). These vascular plant communities tend to be sites of enhanced sedimentological and biogeochemical processes including deposition (Ward et al. 1984, Gacia & Duarte 2001) and benthic decomposition (e.g., Kenworthy et al. 1982, Pollard & Moriarty 1991) of particulate organic matter. In addition, seagrass metabolism stimulates nitrogen fixation (e.g., Capone 1983, Welsh et al. 1997, McGlathery et al. 1998), coupled nitrification-denitrification (Caffrey & Kemp 1990, Risgaard-Petersen & Jensen 1997), phosphorus cycling (Fourqurean et al. 1992, Azzoni et al. 2001), and sulfate reduction (Blaabjerg & Finster 1998, Hansen et al. 2000) in the plant rhizosphere. The mechanisms by which seagrasses influence these processes vary with sediment composition, ranging from iron-rich clastic sediments that dominate many temperate coasts to iron-deplete carbonate sediments common in tropical regions (Erftemeijer & Middelburg 1993, Holmer et al. 2005). Although in recent years there has been an increasing emphasis on studies of seagrass-biogeochemistry interactions, most of these have been in temperate regions.

Seagrass beds influence biogeochemical cycling in both sediment and overlying water, and many of these interactions are driven by plant photosynthetic activity, thereby producing distinct diel variations in concentrations of key substrates and metabolites. For example, clear diel cycles of dissolved inorganic carbon and dissolved oxygen in the water column (Odum 1957, Frankignoulle & Distèche 1984, D'Avanzo et al. 1996) and associated sediment porewaters (Pedersen et al. 1998, Lee & Dunton 2000) have been reported for many seagrass beds. Although assimilation of nutrients is not strictly linked to photosynthesis in seagrasses (e.g., Touchette & Burkholder 2000), light/dark

differences in leaf and root uptake may contribute to diel variations in dissolved inorganic nitrogen and phosphorus in sediment interstitial and overlying water (Borum et al. 1989, Lee & Dunton 1999). In contrast, leaf exudation of dissolved organic matter (DOM) has been directly linked to photosynthetic production of simple metabolites, resulting in daytime increases in water column DOM concentrations (Velimirov 1986, Ziegler & Benner 1999). Photosynthetically-derived DOM translocated from plant leaves to roots may be excreted from plant roots to the surrounding sediment (Wetzel & Penhale 1979, Holmer et al. 2001, Kaldy et al. 2006), where it fuels microbial processes such as sulfate reduction (e.g., Isaksen & Finster 1996, e.g., Holmer & Nielsen 1997, Hansen et al. 2000), nitrogen fixation (O'Donohue et al. 1991, Welsh et al. 1997, Welsh et al. 2000), and denitrification (Blackburn et al. 1994, Risgaard-Petersen & Jensen 1997). Similarly, O₂ transported from leaves to roots through internal gas spaces, or lacunae, may ultimately diffuse into the surrounding sediments (Caffrey & Kemp 1991, Pedersen et al. 1998, Jensen et al. 2005, Frederiksen & Glud 2006). Oxidation of the rhizosphere from root release of O₂ can influence biogeochemical processes by enhancing nitrification at depth (Caffrey & Kemp 1991), reducing availability of PO₄³⁻ in iron-rich sediments (e.g., Wigand et al. 1997), and precluding rhizosphere accumulation of toxic anaerobic metabolites such as sulfide (Pedersen et al. 1998, Lee & Dunton 2000).

Florida Bay is a shallow, marine ecosystem dominated by dense, highly productive seagrass communities with *Thalassia testudinum* as the most prevalent species. This system is characterized by numerous carbonate mudbanks that limit water exchange throughout the bay and iron-depleted calcareous mud sediments which contribute to strong P-limited conditions for plant growth (e.g., Fourqurean et al. 1992, Armitage et al. 2005). Despite the relatively low external inputs of nutrients, seagrass communities in Florida Bay are highly productive (Zieman et al. 1989), suggesting that plant growth relies on autochthonous sources and internal recycling of inorganic

nutrients. In recent years, dieback events have led to widespread loss of *T. testudinum* throughout the Bay (Robblee et al. 1991). Although there is substantial information on distribution and production of this seagrass species in Florida Bay (e.g., Fourqurean et al. 2001), and there are several hypotheses regarding the causes of dieback (e.g., Durako & Kuss 1994, Zieman et al. 1999), there is surprisingly little information to suggest how dieback may affect biogeochemical cycling with this system.

The purpose of this study is to present an integrated study that explores differences in concentrations and fluxes of key substrates and metabolites in *T. testudinum* beds and “bare” (i.e., not inhabited by seagrass) sediments. This study focused on diel variations in concentrations and fluxes to emphasize effects of benthic photosynthesis. In addition, this study examines seasonal variations in seagrass effects on these processes. It is anticipated that information generated in this study will provide a basis for understanding how *T. testudinum* dieback affects integrated biogeochemistry within Florida Bay.

METHODS

Site description. This study was conducted at a shallow (~2 m depth) site on the NE edge of Florida Bay (Sunset Cove, FL) near Key Largo, FL, USA. Within the cove, there is large, relatively contiguous seagrass bed dominated by *Thalassia testudinum*. Adjacent to this seagrass bed, is a large (~ 500 m²) unvegetated area that is colonized by benthic microalgae (referred to as “bare”), which form a dense mat over the sediment surface. Because the majority of Florida Bay sediments are dominated by seagrasses (Zieman et al. 1989), it is often difficult to find these two communities in close proximity and at similar depths. Consequently, Sunset Cove represented an ideal location in which to compare biogeochemical cycling between these two communities.

Measurements and samples taken within the seagrass bed were collected at least 30 m from the edge of the bed in order to minimize edge effects.

Open water measurements. Direct continual measurements of dissolved O₂ concentrations in the water column overlying the *T. testudinum* bed and adjacent bare sediments were obtained in August and November 2003, and in January, March, June, and August 2004. Open water dissolved O₂ concentrations, temperature, and salinity were recorded at 10-min intervals over continuous 3-12 d periods using a multi-parameter data logging system (YSI 600 XLM) equipped with pulsed-O₂ electrodes, thermistors, and conductivity sensors. Instruments were deployed at each site at a depth of 1.25 m (approx. 0.75 m above the sediment surface), so that the sensor within the seagrass was situated just above the plant canopy. Additional instruments were positioned just above the sediment surface within the seagrass bed for all deployments and within the bare area (June 2004 only). Instrument fouling was not observed over the deployment. Ambient irradiance was measured throughout the study using Odyssey™ Photosynthetic Irradiance Meters (Dataflow Systems Inc.) that were deployed directly adjacent to the oxygen sensors.

Vertical variations in dissolved O₂ concentrations were measured in the *T. testudinum* bed during morning, early afternoon, and late evening in June 2004. Oxygen concentrations were measured at depths of 0, 50, 100, 150, 170, and 180 cm from the water surface using a hand-held dissolved O₂ meter (YSI™ Model 55). Within the seagrass bed, depths at 150, 170, and 180 cm coincided with the top of the canopy, half way below the canopy and the sediment surface, respectively.

Concurrent with measurements of diel variations of O₂ concentrations, we also quantified diel fluctuations of dissolved NH₄⁺, NO₃⁻, PO₄³⁻, DOC and DON concentrations in the water column overlying both vegetated and bare areas. Water samples were

collected by syringe from clear, flexible tubing that was permanently fixed at depths adjacent to the O₂ sensors. Samples were collected at 3 h intervals over a 2-3 d period during the YSI deployment, filtered (0.7- μ m ashed GF/Fs), and immediately frozen for subsequent analysis (see below). In June 2004, we collected additional samples for NH₄⁺ analysis at depths of 0.5, 1.0, and 1.75 m in the water column of the *T. testudinum* bed throughout the study.

Benthic fluxes. In January and June 2004, replicate intact seagrass plant and sediment units (n=3) were collected within the *T. testudinum* bed and in the adjacent bare area using clear acrylic cylindrical cores (dia = 15 cm, h = 47 cm). Each core contained approximately 15 cm height of sediment column that was overlain by approximately 30 cm of water column. In order to reduce light penetration through the side of the core into the sediment column, an opaque, reflective covering was placed around the sediment column so that only the water column of the core received light. Within 4 h of collection, cores were placed randomly in flow-through incubators under ambient temperature conditions and were covered with neutral-density screening to simulate *in situ* light conditions. The cores were aerated using aquarium pumps to ensure full O₂ and CO₂ saturation of the water column and were allowed to equilibrate overnight in the incubators prior to beginning the experiment.

At dawn of the following morning, the cores were sealed with clear acrylic lids to remove any gas headspace. To ensure proper mixing of the water column, each core was fitted with a magnetic stirbar that was continuously rotated via a central motor-driven magnetic turntable, and seagrass leaves were gently repositioned so as not to interfere with the stirbar. Water samples collected from each core were replaced simultaneously by an equal volume of ambient water. Water samples for O₂ and N₂ gases were taken during the first 4 h after dawn (light) and for several hours after dusk

(dark) at 30–45 min intervals, while water samples for NO_3^- , NH_4^+ , PO_4^{3-} , DOC and DON were taken at 2–3 h intervals over the course of the incubation (~24 h). Water samples for dissolved solutes were filtered (0.7- μm ashed GF/F filters) and immediately frozen. The short intervals between water sampling for dissolved gas analysis allowed for time-course measurements prior to the formation of any bubbles in the cores during the experiment, as gas bubble evolution during plant photosynthesis may interfere with sample analysis (Kana et al. 1994). After gas sample collection in the light, the cores were unsealed and aerated to maintain O_2 and CO_2 at saturation in the water column. The cores were resealed prior to dusk to measure changes in gas concentrations during the dark.

Following the incubation, subsamples for sediment chlorophyll-a concentrations were collected from surface (0–1 cm) sediments in each core and were immediately frozen for subsequent analysis. Plant biomass was obtained by gently rinsing core contents through a 0.5-cm mesh screen to remove all sediment. Biomass samples were stored in a refrigerator for up to 48 h and were sorted into live and dead, above- and belowground tissues. All plant biomass was dried at 60°C to a constant weight, ground, and analyzed for C, H, N, and P content (Short 1990).

Sediment porewaters. In June 2004, sediment porewater dialysis samplers ("peepers", Wigand et al. 2001) were deployed to measure vertical profiles of porewater solute concentrations within the *T. testudinum* bed and in an adjacent bare area. Peepers were composed of a PVC stake (25 x 2.5 x 3 cm) with 5 sampling ports of 1.9 cm in diameter. Prior to deployment, each port was filled with N_2 -sparged distilled water and covered with a 125 μm Nitex™ screen overlaying a 0.2 μm polycarbonate membrane. To ensure that the membrane and screen remained in place, a PVC plate with holes that corresponded to the sampling ports was affixed to the stake using 12 Teflon screws.

Peepers were transported to each site in N₂-sparged distilled water to minimize oxidation of the porewater. Sediment peepers were inserted into the sediment to yield average sediment sampling depths of 1.5, 4.5, 7.5, 11.5, and 16.5 cm. To avoid tearing of the membrane, an empty stake was driven into the sediment, withdrawn, and a peeper was placed in the resulting hole. Replicate peepers (n = 3) were deployed at each site for approximately 7-10 d. Immediately after retrieval, peepers were rinsed with distilled water to remove excess sediment. Samples were extracted by puncturing the membrane with a stainless steel needle affixed to a 10-mL graduated syringe and filtered through a 0.45 μm syringe filter. A portion of each sample was treated with diamine for sulfide analysis (Cline 1969) while the remaining sample was immediately frozen for subsequent NH₄⁺ analyses.

Sediment microbial activities. In addition to measuring *in situ* sediment porewater concentrations, vertical profiles of ammonification, sulfide production, nitrification and belowground biomass were measured at each site in June 2004. Intact sediment cores (n=3) were collected from the bare (no seagrass) and *T. testudinum* (plants and sediment) communities, and sediments were partitioned into 3-cm sections to a depth of 15 cm, yielding 5 sections (0-3, 3-6, 6-9, 9-12, and 12-15 cm). Previous observations revealed that the majority (75-90%) of root and rhizome biomass was found in the top 15 cm of sediments. Each section was sorted by hand to separate plant biomass and remove macrofauna and shells. Plant biomass was rinsed, separated into live and dead tissues and dried at 60°C for 48 h to generate depth profiles of root/rhizome biomass. The remaining sediment was homogenized and used to determine sediment water content and bulk density of each section, as well as to determine rates of biogeochemical processes.

Rates of ammonification and sulfate reduction were measured using a technique described by Aller and Yingst (1980) in which packed tubes of sediment are incubated anaerobically and the accumulation of NH_4^+ and S^{2-} is measured over time.

Homogenized sediment from each depth was packed into triplicate 15 mL polycarbonate centrifuge tubes, which were incubated anaerobically in sulfidic mud for 10 d. At 1, 7 and 10 d, one replicate from each depth was centrifuged and the resulting supernatant was filtered (0.45- μm). A portion of the supernatant was treated with diamine for sulfide analysis (Cline 1969), while the remaining portion was frozen for subsequent NH_4^+ analysis.

Potential nitrification rates were measured as the production of NO_3^- over time in aerobic sediment slurries (Caffrey & Kemp 1990). Approximately 1 g of sediment from each section was incubated in 25 mL of filtered (0.7 μm) site water contained in a 50 mL polycarbonate centrifuge tube. Each tube was amended with NH_4Cl to bring NH_4^+ concentrations to 1 mM. Slurries were continuously mixed using a shaker table to maintain aerobic conditions for 40 h at 25°C. At 2 and 40 h, slurries from replicate flasks were centrifuged and the water was filtered (0.45 μm) and frozen for subsequent NO_3^- analysis. Previous experiments indicated that nitrification rates were linear over a 48 h period (data not shown).

Nutrient Analyses. NH_4^+ , PO_4^{3-} , and $\text{NO}_3^- + \text{NO}_2^-$ samples were analyzed colorimetrically following Parsons et al. 1984. DON concentrations were obtained by subtracting inorganic nitrogen from total nitrogen concentrations, which were determined colorimetrically after persulfate digestion (Parsons et al. 1984). DOC concentrations were determined by high temperature catalytic oxidation (Sugimura & Suzuki 1988). Samples for plant tissue nutrients were dried at 60°C for 48 h, ground, and analyzed following Aspila et al. (1976). Sediment samples for chlorophyll-a analysis were thawed,

extracted with 90% acetone for 24 h and analyzed using a Turner Fluorometer (Parsons et al. 1984).

Water samples taken during flux experiments for N₂ and O₂ gases were collected in 8 mL glass vials, immediately preserved with mercuric chloride (HgCl₂), capped, and stored in an ambient water bath. The samples were analyzed within two weeks of collection by measuring changes in the ratios of O₂:Ar and N₂:Ar using a membrane inlet mass spectrometer (Kana et al. 1994). Because of the absence of headspace within the cores, changes in water column O₂ and N₂ concentrations in the light and dark were attributed to processes associated with the plants, sediments, and overlying water column. Increases in O₂ in the light and dark were attributed to photosynthetic and respiratory processes, respectively. Increases in dark N₂ concentrations were attributed to release of N₂ from the sediments associated with denitrification (Kana et al. 1994).

Calculation of rates. In order to compare open water to benthic flux cores, flux rates for both techniques for O₂, NO₃⁻, NH₄⁺, PO₄³⁻, DOC and DON were determined by calculating the slope of the regression for changes in concentration over time in both light and dark periods. Significant, linear trends were observed in almost all cases. Positive fluxes represent a net flux (net production) from the plants and/or sediment into the water column, or net production, whereas negative flux rates represent a net flux into the plants and/or sediment (or net consumption). Estimates of net daily production were calculated based on the number of hours of daylight or darkness for the specific days of the experiments.

Continuous records of dissolved O₂ concentrations, temperature, and salinity were used to calculate water column daytime production and nighttime respiration in both the *T. testudinum* and bare communities (e.g., Odum & Hoskins 1958). Nighttime respiration (R) and apparent daytime production (P_a) were estimated from the decline in

O₂ concentrations from dusk to dawn and from increases in O₂ observed from the daily minimum to daily maximum concentrations. Assuming hourly respiration rates were the same over the course of 24 h, gross photosynthetic production P_g was estimated as the sum of hourly P_a and R (absolute values) adjusted for the daylight period of the day. Volumetric rates (mmol m⁻³ d⁻¹) were converted to vertically-integrated rates (mmol m⁻² d⁻¹) by multiplying by the water column depth. Rates then were corrected for O₂ exchange across the air-water interface assuming a constant air-sea exchange rate of 0.5 g O₂ m⁻² h⁻¹ (atm)⁻¹, a reasonable estimate for shallow estuaries (Kremer et al. 2003) in the absence of local wind data (Kemp & Boynton 1980). The difference between P_a and R is equal to net ecosystem production (NEP) for a given day.

RESULTS

Water column concentrations & variability

Water Column Characteristics

Water column temperatures in Sunset Cove varied seasonally from ~20°C in January to ~30°C in August (Table 2.1). A wide range of salinities was recorded throughout the year with salinities as low as 25 in January and as high as 41 in August (Table 2.1). Daily integrated irradiance at 1.5 m depth in the water column ranged from 9.48 to 44.7 mol m⁻² d⁻¹ throughout the year with peak annual irradiances observed in June 2004 (data not shown).

O₂ Cycling

Throughout this study, clear diel and seasonal patterns in oxygen concentrations were evident in both the *T. testudinum* and bare (no seagrass) communities. On a daily basis, O₂ concentrations in the water column overlying the seagrass bed peaked in late afternoon (e.g., Fig. 2.2a), several hours after peak irradiance. Lowest O₂

concentrations occurred just before dawn. Similar patterns were observed in the bare community, with oxygen production beginning later in the day compared to the vegetated community (e.g., Fig. 2.2a). Because of malfunctions in the O₂ sensors, O₂ concentrations in November 2003 (*T. testudinum* only) and January 2004 were not recorded and, therefore, are not included in the following results.

Oxygen concentrations in the water column overlying the *T. testudinum* and bare communities ranged from 103 – 344 μM and from 52.1 – 164% saturation (Table 2.1). Maximum O₂ concentrations and percent O₂ saturation were significantly higher ($p < 0.03$) within the *T. testudinum* community relative to the bare community. Oxygen concentrations exhibited considerably more variation within the seagrass bed (CV = 20.6%) compared to bare sediments (CV = 13.5%). Greater variability in O₂ concentrations was also observed below the seagrass canopy (CV = 30.5%) relative to that above the canopy (Fig. 2.2b) and daily minima in both O₂ concentration and percent saturation minima were significantly lower ($p < 0.0001$) below the seagrass canopy. During summer months, O₂ concentrations below the seagrass canopy before dawn dipped to 3 mg L⁻¹ (~50% saturation) and occasional excursions to as low as 2 mg L⁻¹ (~25% saturation) (e.g., Fig. 2.2b). Peak daily oxygen concentrations at both sites were significantly higher in March 2004 ($p < 0.0001$) compared to all other months.

Rates of *in situ* apparent primary production (P_a), or integrated daytime O₂ production, ranged from 82 to 532 mmol O₂ m⁻² d⁻¹, and mean rates varied throughout the year. Rates were significantly higher in the *T. testudinum* community compared to bare sediments ($p < 0.0001$), and rates at both sites were highest in summer months (Table 2.2). P_a was positively correlated with daily integrated irradiance for both the *T. testudinum* ($r^2 = 0.35$, $p < 0.001$) and bare communities ($r^2 = 0.17$, $p < 0.04$).

Nighttime respiration (R) rates also varied seasonally, and daily rates ranged from 59.5 to 244 mmol O₂ m⁻² d⁻¹ (Table 2.3). Compared to bare sediments, the *T.*

testudinum community had significantly higher rates of R in August 2003 ($p < 0.003$), August 2004 ($p < 0.004$), and November 2004 ($p < 0.0001$). Highest rates of R were observed in summer months, with rates significantly lower ($p < 0.0001$, Tukey HSD) in March 2004 compared to other months. Hourly respiration rates were positively correlated with temperature in both vegetated ($r^2 = 0.51$, $p < 0.0001$) and bare ($r^2 = 0.35$, $p < 0.02$) communities and temperature-specific rates were significantly higher (ANCOVA, $p < 0.0001$) in the *T. testudinum* community.

Net ecosystem O₂ production (NEP) rates were consistently positive across seasons at both sites, indicating net autotrophy throughout the year. Highest rates of NEP were observed in March (Veg only) and June 2004 and rates were significantly higher in the vegetated community in June ($p = 0.05$), August ($p = 0.02$) and November 2004 ($p < 0.0001$) relative to bare sediments. Similarly, ratios of P_a to R were greater than 1 throughout the year at both sites. However, there were no significant differences in P_a:R values between the two sites over the year.

Dissolved Inorganic Nutrient Cycling

In situ inorganic nitrogen concentrations in the water column varied substantially over the course of the year, with concentrations ranging from 0.9 – 20.4 μM and 0.1 – 4.1 μM for NH₄⁺ and NO₃⁻, respectively. In November 2003, January 2004, and March 2004, NH₄⁺ concentrations were significantly lower ($p < 0.0001$) in the water column overlying the *T. testudinum* bed relative to the bare community (Table 2.1). However, concentrations below the seagrass canopy were significantly higher ($p < 0.0001$) than above the canopy. Sampling of the water column at 4 depths in the seagrass bed (below canopy, at the canopy, above the canopy, and in the water column) revealed vertical variations in NH₄⁺ concentrations in June 2004, with highest concentrations

found below the canopy (Fig. 2.3). There were no significant differences in NO_3^- concentrations between the two communities (Table 2.1) or in relation to position above or below the seagrass canopy.

I observed clear and consistent diel patterns in both NH_4^+ (e.g., Fig. 2.4b) and NO_3^- concentrations in the water column, with net consumption occurring during the day and net production, or regeneration, occurring at night. Benthic consumption (light fluxes) and regeneration (dark fluxes) of inorganic nitrogen were typically higher in the *T. testudinum* community compared to the bare community, and rates were highest in summer months (Tables 2.2 & 2.3). In August 2003 and June 2004, NH_4^+ regeneration rates were significantly higher ($p < 0.036$) in the *T. testudinum* community compared to bare sediments (e.g., Fig. 2.5). Furthermore, during all months, NH_4^+ regeneration rates were significantly higher ($p = 0.03$) below the seagrass canopy compared to above the canopy. Net fluxes of inorganic nitrogen were not significantly different from zero during fall and winter months outside of the primary plant growing season.

Throughout much of this study, dissolved PO_4^{3-} concentrations were extremely low and below the detection limit ($< 0.07 \mu\text{M}$) of analyses. While no consistent diel patterns in PO_4^{3-} concentrations were evident, we did frequently observe brief peaks in concentrations as high as $0.9 \mu\text{M}$ in the water column over both vegetated and bare sediments (e.g., Fig. 2.4c). In all cases, these pulses in PO_4^{3-} were followed by sharp declines in concentrations, so that concentrations were below detection within 2 hours after the pulse.

DOM Cycling

In situ water column DOC and DON concentrations ranged from 269 – 753 μM and 32 – 74 μM , respectively. DOC concentrations were significantly ($p < 0.0001$)

higher in the *T. testudinum* bed compared to the bare community, whereas DON concentrations were similar ($p = 0.50$) between the two communities (Table 2.1). No significant difference ($p > 0.05$) existed in DOC and DON concentrations measured above versus below the seagrass canopy.

Clear diel variations in DOC (e.g., Fig. 2.4d) and DON concentrations were observed at both sites during this study. Fluxes of DOC and DON were positive during the day and negative at night (Tables 2.2 & 2.3). Throughout the year, production of DOC was significantly higher ($p < 0.0002$) in the *T. testudinum* community relative to the bare community (e.g., Fig. 2.5). During summer months (August 2003 and June 2004), DOC consumption was also significantly higher ($p < 0.04$) in vegetated versus bare communities (e.g., Fig. 2.5). While the net daily production of DOC was positive over an annual cycle at both sites, net DOC production was significantly lower ($p < 0.01$) in the bare community. The difference between DON fluxes in the two communities was more variable, as rates at the bare site often equaled those in the *T. testudinum* bed (Tables 2.2 & 2.3). The magnitude and direction of net fluxes of DON were also highly variable at both sites throughout the year and no consistent relationship was evident between vegetated and bare communities. Although concentrations did not differ significantly, production of both DOC and DON were significantly higher ($p < 0.007$) below the seagrass canopy compared to above the canopy.

Benthic core fluxes

Benthic O₂ Fluxes

Oxygen fluxes measured in benthic cores in the light and dark ranged from 2.61 to 15.2 mmol O₂ m⁻² h⁻¹ and -2.01 to -13.9 mmol O₂ m⁻² h⁻¹, respectively. Both O₂ production and respiration were significantly higher ($p < 0.002$) in *T. testudinum* relative to the bare sediments (Table 2.4, Fig. 2.5). In vegetated sediments, production

increased (Fig. 2.6a) and respiration significantly ($p < 0.003$) increased from January to June (Table 2.4). Daily net O_2 production was greater in the *T. testudinum* compared to the bare community, but this difference was not significant ($p < 0.1096$). Negative net O_2 production was observed only in June in the bare sediments.

For the *T. testudinum* community, O_2 production per unit plant biomass increased significantly ($p < 0.03$) from January ($25.2 \pm 2.57 \mu\text{mol } O_2 \text{ g (dry wt)}^{-1} \text{ h}^{-1}$) to June ($47.3 \pm 6.01 \text{ mmol } O_2 \text{ g (dry wt)}^{-1} \text{ h}^{-1}$). Similarly, biomass-specific respiration rates were significantly higher ($p < 0.0005$) in June ($48.3 \pm 2.82 \mu\text{mol } O_2 \text{ g (dry wt)}^{-1} \text{ h}^{-1}$) compared to January ($17.3 \pm 1.19 \mu\text{mol } O_2 \text{ g (dry wt)}^{-1} \text{ h}^{-1}$). In bare sediments, there was no significant difference in O_2 production or respiration relative to sediment chlorophyll-a concentrations between the two seasons.

Benthic Fluxes of Dissolved Inorganic Nitrogen

Inorganic nitrogen fluxes in benthic flux cores followed similar patterns to *in situ* rates observed in the open-water, with consumption primarily observed in the light and production typically observed in the dark. Rates of benthic NH_4^+ consumption and regeneration ranged from -23.4 to $-161 \mu\text{mol } NH_4^+ \text{ m}^{-2} \text{ h}^{-1}$ and 11.2 to $496 \mu\text{mol } NH_4^+ \text{ m}^{-2} \text{ h}^{-1}$, respectively. In June, both daytime consumption and nighttime regeneration of NH_4^+ were significantly higher ($p < 0.02$) in *T. testudinum* sediments relative to bare sediments (Fig. 2.5). Benthic fluxes of NO_3^- varied from -21.6 to $19.5 \mu\text{mol } NO_3^- \text{ m}^{-2} \text{ h}^{-1}$ in the light and -9.43 to $21.5 \mu\text{mol } NO_3^- \text{ m}^{-2} \text{ h}^{-1}$ in the dark and consumption was significantly higher ($p < 0.04$) in vegetated communities (Table 2.4). In vegetated sediments, benthic fluxes of both NH_4^+ and NO_3^- increased significantly ($p < 0.04$) from January to June (Table 2.4, e.g., Fig. 2.6b & c). Only NH_4^+ regeneration and NO_3^- consumption increased significantly ($p < 0.05$) from January to June in bare sediments (Table 2.4). Net fluxes of

inorganic nitrogen integrated over the diel cycle were either negative (net consumption) or zero for both communities in January and June (Table 2.4).

Benthic DOM fluxes

Diel patterns in benthic fluxes of DOC and DON in the *T. testudinum* sediments were clear, with production in the light and consumption occurring in the dark (Table 2.4). In bare sediments, DON fluxes were more variable as production was sometimes observed in the dark and vice versa. Overall, these communities exhibited a wide range in rates of both DOC production (408 to 7424 $\mu\text{mol DOC m}^{-2} \text{ h}^{-1}$) and consumption (-351 to -5349 $\mu\text{mol DOC m}^{-2} \text{ h}^{-1}$), however these rates were similar to those reported in a *T. testudinum* community in Texas (Ziegler & Benner 1999). DON production and consumption ranged from -325 to 660 $\mu\text{mol DON m}^{-2} \text{ h}^{-1}$ and 391 to -1096 $\mu\text{mol DON m}^{-2} \text{ h}^{-1}$, respectively. Production rates for both DOC and DON were significantly higher ($p < 0.03$) in the *T. testudinum* compared to the bare community (Table 2.4). Rate of consumption for both DOC and DON were also typically lower in the bare community, however these differences were not significant. The magnitude of benthic DOC and DON fluxes did not exhibit a consistent seasonal pattern (e.g., Fig. 2.6d).

Plants, sediments & microbial processes

Plant Biomass & Nutrient Content

T. testudinum biomass and plant tissue nutrient content collected in benthic flux cores varied from January to June 2004. Aboveground biomass was lower in June ($238 \pm 33.6 \text{ g (dry weight) m}^{-2}$) compared to January ($322 \pm 21.4 \text{ g m}^{-2}$), although this difference was not significant ($p = 0.08$). In contrast, belowground biomass increased significantly ($p = 0.02$) from January ($714 \pm 74.3 \text{ g m}^{-2}$) to June ($1025 \pm 60.0 \text{ g m}^{-2}$).

Similarly, the ratio of belowground to aboveground biomass increased significantly ($p = 0.03$) from January (2.2 ± 0.23) to June (4.5 ± 0.88). Total plant biomass in June ($1263 \pm 26 \text{ g m}^{-2}$) was also significantly greater ($p < 0.04$) compared to total biomass in January ($1036 \pm 83 \text{ g m}^{-2}$).

Both nitrogen and phosphorus content in *T. testudinum* tissues decreased from January to June. Nitrogen content of aboveground tissues decreased significantly ($p = 0.005$) from January ($2.50 \pm 0.04\%$) to June ($1.96 \pm 0.08\%$). Belowground tissue nitrogen content was also lower in June (1.34 ± 0.08) compared to January (1.77 ± 0.16), although this difference was marginally insignificant ($p = 0.07$). Ratios of carbon to nitrogen (C:N) in above- and belowground tissues ranged from 15.2 – 20.5 and 18.3 – 30.7, respectively, with ratio decreasing significantly ($p < 0.03$) in both tissues from January to June.

The difference in phosphorus content in aboveground tissues was marginally insignificant ($p = 0.06$) between the two months, with lower content in June ($0.092 \pm 0.005\%$) relative to January ($0.107 \pm 0.003\%$). Phosphorus content of belowground tissues was significantly higher ($p < 0.05$) in January ($0.075 \pm 0.013\%$) relative to June ($0.032 \pm 0.006\%$). Mean carbon to phosphorus (C:P) ratios in aboveground tissues increased, albeit marginally insignificantly, ($p = 0.06$), from 795 ± 24.6 in January to 935 ± 46.5 in June. Similarly, C:P ratios in belowground tissues increased two-fold ($p = 0.06$) from 1154 ± 207.5 in January to 2770 ± 600.2 in June. Ratios of N:P in both above- and belowground tissues decreased from approximately ~50 to ~25 from January to June.

Sediment Chlorophyll-a

Sediment chlorophyll-*a* concentrations in benthic flux cores varied from 20 – 253 mg chl-*a* m^{-2} and concentrations were significantly higher ($p < 0.01$) in bare relative to vegetated sediments. Concentrations in vegetated sediments increased from 48 ± 16

mg chl-*a* m⁻² in January to 70 ± 27 mg chl-*a* m⁻² in June. Sediment chlorophyll-*a* concentrations also increased from 120 ± 18 mg chl-*a* m⁻² in January to 174 ± 60 mg chl-*a* m⁻² in June. Differences in concentrations between January and June were not significant for either site.

Sediment Water Content & Bulk Density

Sediment water content ranged from 63 – 88% of sediment weight and decreased with increasing depth in the sediment. Conversely, sediment bulk density increased with depth, ranging from 0.12 – 0.50 g cm⁻³. Both sediment water content and bulk density were statistically similar (*p* > 0.05) between vegetated and bare sediments.

In Situ Sediment Porewater Concentrations

Sediment porewater concentrations of NH₄⁺ and S²⁻ sampled from both vegetated and bare sediments in June 2004 ranged from 36 to 473 μM and 26 to 1753 μM, respectively (Fig. 2.7). Mean NH₄⁺ concentrations were slightly higher in vegetated sediments, however, there was no significant difference (*p* = 0.18) in concentration compared to bare sediments (Fig. 2.7a). In contrast, mean S²⁻ concentrations were significantly higher (*p* < 0.0001) in vegetated relative to bare sediments and, unlike in bare sediments, concentrations appeared to increase between 0 and 9 cm in depth (Fig. 2.7b).

Sediment Microbial Activities & Root Biomass

Vertical profiles of ammonification in June 2004 were generally similar between the two communities. Sediment ammonification rates ranged from 0.01 – 1.15 μmol NH₄⁺ g (dry sediment)⁻¹ d⁻¹. A subsurface peak in ammonification was observed in

vegetated sediments; however rates at this depth were not significantly different ($p = 0.13$) from rates in bare sediments. Vertically-integrated rates of ammonification in *T. testudinum* sediments ($11.4 \pm 2.62 \text{ mmol m}^{-2} \text{ d}^{-1}$) exceeded rates in bare sediments ($7.91 \pm 1.08 \text{ mmol m}^{-2} \text{ d}^{-1}$), although this difference was not significant ($p = 0.29$). Sulfide production in the sediment ranged from 0.03 to $1.10 \text{ } \mu\text{mol S}^{2-} \text{ g (dry sediment)}^{-1} \text{ d}^{-1}$ and rates were significantly higher ($p < 0.03$) in vegetated sediments at depths of 9-12 and 12-15 cm. Sediment nitrification rates ranged from 0.40 to $2.8 \text{ } \mu\text{mol g (dry sed)}^{-1} \text{ d}^{-1}$ and rates were higher, although not significantly ($p > 0.17$), in surficial (0-6 cm) sediments of the *T. testudinum* bed relative to bare sediments (Fig. 2.8). A depth profile of belowground biomass in the *T. testudinum* bed revealed an absence of roots and rhizome in surficial (0-3 cm) sediments and a subsurface peak in biomass at 6-9 cm in depth (data not shown). However, no clear relationship existed between these processes and belowground biomass in vegetated sediments.

DISCUSSION

Influence of *T. testudinum* on O₂ production, respiration and cycling

On a daily basis, *T. testudinum* influenced diel variations in dissolved O₂ concentrations to a greater extent than communities dominated by benthic microalgae (bare). This is evidenced by higher maxima and lower minima in O₂ concentrations with the *T. testudinum* community. Oxygen concentrations in the seagrass bed exhibited greater overall variation over short time intervals (~ 1-2 h) compared to the bare sediments, and variability below the seagrass canopy was greater than above (e.g., Fig. 2.2). This variability was likely the result of the oscillation of plant leaves due to wave action, which led to the release and subsequent mixing of water trapped within the canopy with the overlying water column (e.g., Koch & Gust 1999). Within both communities, mid-day plateaus in O₂ concentrations were frequently observed. A

number of mechanisms may be responsible for these patterns, including 1) water column depletion of inorganic nutrients or carbon dioxide needed to support photosynthesis (Koch 1994, Touchette & Burkholder 2000), 2) supersaturation of O₂ driving air-sea exchange rates (e.g., Kremer et al. 2003) and/or enhanced photorespiration (e.g., Downton et al. 1976, Sondergaard 1980) and 3) high rates of respiration in daytime due to enhanced production and excretion of labile photosynthates (Ziegler & Benner 1999).

Nighttime O₂ concentrations within the canopy were significantly lower than concentrations above the canopy and short periods (~ 1-2 h) of hypoxia (O₂ concentrations < 3.0 mg L⁻¹) were observed in summer months (e.g., Fig. 2.2b). The physical structure of plant leaves reduces water flow through the canopy, resulting in increased diffusive boundary layers, and consequently lower vertical diffusion rates within the plant canopy (e.g., Koch 1994). At night, high plant and sediment respiratory demands combined with a reduction in water exchange with the overlying water column can lead to depletion of O₂ concentrations in the water beneath the canopy. Because the diffusion of O₂ from plant leaves to belowground tissues at night is largely dependent on nighttime O₂ concentrations within the canopy (Pedersen et al. 1998, Greve et al. 2003), low O₂ concentrations may inhibit nighttime aerobic respiration in belowground tissues and lead to intrusion of phytotoxic compounds, such as sulfide, into plant tissues (Borum et al. 2005, Frederiksen et al. 2006, Holmer et al. 2006). Hence, in beds of high plant density where water velocity is limited and diffusive boundary layers are thick (Binzer et al. 2005), extended periods of low O₂ concentrations within the canopy could be detrimental to plant survival.

Oxygen produced in seagrass leaves has three possible fates: 1) release to the water column within the canopy, 2) respiration in plant leaves or 3) translocation to belowground tissues, where it supports aerobic respiration. When O₂ concentrations in

plant roots are higher than concentrations in the surrounding sediment, diffusion of O₂ from plant roots can occur, resulting in oxidation of rhizosphere sediments (Pedersen et al. 2004, Frederiksen & Glud 2006). While photosynthesis fuels O₂ excretion during the day, diffusion of O₂ from the water column into leaves at night appears to be important for sustaining root O₂ release through the night (Pederson et al. 1998, Greve et al 2003). Excretion of O₂ oxidizes sulfide, a known phytotoxin, in the rhizosphere, reducing the potential for its intrusion into plant tissues (Pedersen et al. 2004, Borum et al. 2005). Lee and Dunton (2000) attributed daytime reductions in sediment sulfide concentrations to release of photosynthetically-derived O₂ from *T. testudinum* roots. In this study, sulfide concentrations in *T. testudinum* sediments were near the high (~1 mM) end of the range concentrations reported for Florida Bay (Carlson et al. 1994). While *T. testudinum* appears to be relatively tolerant of high sulfide concentrations (~6 mM), prolonged exposure to high concentrations can adversely affect plant metabolic processes (Erskine & Koch 2000), and, when combined with other factors, such as high temperature and hypersalinity, may ultimately inhibit plant survival (Koch & Erskine 2001, Koch et al. 2007). Furthermore, extended periods of reduced light availability, such as those associated with wind-driven turbidity events or eutrophication (e.g., algal blooms, siltation), may reduce plant photosynthetic capacity, and thus, root O₂ release, and these conditions may increase the risk of sulfide intrusion into plant tissues (Calleja et al. 2006). Diffusion of S²⁻ from porewaters into seagrass roots is most likely to be important under hypoxic conditions within the plant canopy (Borum et al. 2005), as was observed in Sunset Cove water during August (Fig. 2.2b). Thus, these *T. testudinum* beds may be highly vulnerable to sulfide stress, particularly under high temperature conditions in summer (e.g., Koch et al. 2007).

Two methods, diel variations of *in situ* concentrations and sediment core incubations, were used to measure net fluxes of O₂, NH₄⁺, NO₃⁻, PO₄³⁻, DOC and DON in

this study. Patterns and rates of all solute fluxes measured in core incubations generally matched those inferred from concentration changes in the open-water (Fig. 2.5). Relative variance for the rates measured in flux cores tended to be lower than open-water rates, reflecting the more controlled experimental conditions in the former (e.g., Petersen et al. 2003), and in several cases (e.g., NH_4^+ flux), differences associated with seagrass effects were substantially more robust in core data. In general, however, rates from core incubations were lower than those from contemporaneous *in situ* observations (Fig. 2.5), possible due to unrealistically low mixing in core mesocosms (e.g., Fonseca & Kenworthy 1987). Other processes potentially contributing to lower rates in flux cores include rapid depletion of nutrients, CO_2 , and other substrates needed to support metabolic processes. In addition, flux cores do not account for processes occurring in the water column above the seagrass canopy. Although planktonic processes are more dominant in relatively eutrophic coastal ecosystems like Chesapeake Bay (Kemp et al. 1997), they are generally less important in low nutrient systems such as Florida Bay (Fourqurean & Robblee 1999), and this assumption is supported by low rates of planktonic respiration and production measured previously in Sunset Cove (Cornwell, pers. comm.). However, while rates obtained from benthic flux cores may tend to underestimate rates *in situ*, benthic flux measurements are often more convenient than *in situ* measurements and they may be useful for elucidating differences between treatments when complex interactions are involved.

The comparison between *T. testudinum* and bare sediments revealed higher rates of community O_2 production and this difference was most pronounced during summer months, when seagrass production was at its peak. Seagrasses themselves are, in part, responsible for this difference, but phytoplankton, epiphytes, benthic microalgae, and macroalgae may also contribute significantly to production within these communities (Pollard and Moriarty 1991, Moncreiff et al. 1992, Kaldy et al. 2002). In the

eastern region of Florida Bay, phytoplankton concentrations are typically low and measurements of planktonic O₂ cycling have been less than 5% of rates seen in the benthos (Cornwell, pers. comm.). Based on observed carbon content of plant leaves in January (32.75%) and June (33.2%), and assuming daily leaf turnover rates of 0.005 d⁻¹ and 0.02 d⁻¹ for January and June, respectively (Frankovich and Zieman 2005), I estimated leaf carbon production to be 0.5 g C m⁻² d⁻¹ in January and 1.6 g C m⁻² d⁻¹ in June. Benthic carbon production can also be estimated from O₂ production in benthic flux cores using a photosynthetic quotient of 1.0 and the assumptions that daytime and nighttime respiration rates are equal. Additionally it is assumed that dark respiration rates in cores collected in the “bare” area reflect all non-seagrass associated respiration in vegetated cores, as respiration rates measured in cores collected from between plants within the seagrass bed (i.e., containing no intact seagrass plants) were typically in close agreement relative to rates measured in cores collected from the bare (unvegetated) area in Sunset Cove (Cornwell pers. comm., data not shown). Despite lower sediment chlorophyll-*a* concentrations relative to the bare area, the abundance of organic matter within the seagrass bed fuels similar respiration rates for “bare” sediments within the bed, thus indicating adjacent bare (unvegetated) area respiration rates provide reasonable estimates for non-seagrass associated respiration rates. Incorporating all of the aforementioned assumptions, this reasoning leads to rates of 1.1 and 1.8 g C m⁻² d⁻¹ in January and June 2004, respectively. This comparison suggests that seagrass leaf production represented approximately 50% and 90% of total C production in January and June, respectively. Kaldy et al. (2002) estimated that *T. testudinum* was responsible for ~35% of community production in Lower Laguna Madre, where benthic macroalgae are abundant and contribute another 33-42% to the total community production. Benthic macroalgae were observed within the seagrass bed in Sunset Cove, but were not abundant, and thus, may not contribute substantially to production within this community.

The contribution from benthic microalgae was probably small, since sediment chlorophyll-*a* concentrations were significantly lower within the seagrass bed and benthic microalgal O₂ production in this site has been shown to be ~90% lower within the seagrass bed compared to the bare sediments (Burton-Evans 2005). Epiphytic contributions to production were also likely small, as epiphytic chlorophyll concentrations are typically some of the lowest in the Bay at less than 50 µg chl-*a* g⁻¹ of seagrass leaves (Frankovich and Fourqurean 1997). Thus, based on these measurements, it appears that *T. testudinum* is the dominant contributor to total ecosystem production within Sunset Cove seagrass beds; however the relative contribution varies seasonally.

While seagrasses may be responsible for the majority of community production within the *T. testudinum* bed, relatively high rates of production were also observed for the bare community. Benthic microalgal community O₂ production in the light ranged from 5 to 65% of contemporaneous rates observed in the adjacent *T. testudinum* community. The production rates are relatively high compared to benthic microalgal communities in other shallow estuaries and can probably be attributed to the high light availability with this system (Burton-Evans 2005). However, because seagrasses dominate as much as 90% of Florida Bay sediments (Zieman et al. 1989), benthic microalgae probably do not contribute significantly to total ecosystem production in Florida Bay.

Throughout the year, the metabolism of the *T. testudinum* community in Sunset Cove was net autotrophic, and the magnitude of net community production varied seasonally. Observed rates of net community production in the *T. testudinum* community were high, ranging from 21 to 181 mmol C m⁻² d⁻¹, but were within the range of rates reported in other seagrass systems (Hemminga and Duarte 2000). Previously reported rates of net community production in two different *T. testudinum* communities were considerably lower (0 to 75 mmol C m⁻² d⁻¹) (Ziegler & Benner 1998, Calleja et al.

2006) than rates observed in Sunset Cove. The trophic status of seagrass beds can vary across systems and seasons (Barron et al. 2004, Caffrey 2004), as well as with environmental conditions such as light availability (Calleja et al. 2006), with instances of net heterotrophy frequently observed. The high water clarity, and hence, high light availability may be responsible, in part, for the high rates of net O₂ production observed in Sunset Cove.

Influence of *T. testudinum* on nutrient cycling

The clear diel patterns in inorganic nitrogen concentrations suggest that photosynthetic production in both the *T. testudinum* and benthic microalgal communities strongly influenced nitrogen cycling through direct assimilation from the water column. The difference between the two communities was most pronounced during peak seagrass production in summer months, when rates were significantly higher in the *T. testudinum* community (Tables 2.2 & 2.4). The high rates of daytime NH₄⁺ consumption observed during summer months were likely the result of high N demand by seagrasses (Fig. 2.5). Seagrass N demand, estimated from daytime net O₂ production in benthic flux cores and assuming a photosynthetic quotient of 1.0 and plant carbon content of 33% dry weight, was approximately 7.4 and 9.3 mmol N m⁻² d⁻¹ in January and June, respectively. However, measured rates of daytime NH₄⁺ consumption from the water column (Table 2.2) accounted for only 10% in January and 22% of calculated plant N demand in June. The seagrasses in Sunset Cove therefore must be assimilating most of their N from the sediment in order to meet nutritional demands. Rates of net NH₄⁺ regeneration (net efflux from the sediments) measured at night in benthic flux cores were also higher in summer compared to winter months (Table 2.4). Assuming that nighttime NH₄⁺ regeneration rates were constant throughout the diel period and that there were no other sources of NH₄⁺ (e.g., N fixation) within the community, total NH₄⁺ regeneration

equaled ~ 7.7 and $10.0 \text{ mmol N m}^{-2} \text{ d}^{-1}$ in January and June, respectively. The close agreement between the plant N demand and estimated NH_4^+ regeneration is somewhat surprising, but not entirely unexpected as seagrass communities often exhibit tight recycling of nutrients (Duarte 1995). High calculated N demand in June may have been met by ammonification associated with decomposing plant material in seagrass sediments, as estimates of vertically-integrated ammonification within these sediments equaled approximately $11 \text{ mmol NH}_4^+ \text{ m}^{-2} \text{ d}^{-1}$.

Nitrogen fixation in seagrass communities can also meet a significant fraction of plant N demand (e.g., O'Donohue et al. 1991, e.g., Moriarty & O'Donohue 1993), but this process was not measured in this study. The contribution of N fixation to N pools in seagrass beds in Florida Bay is poorly understood. Rates of N fixation in benthic microalgal communities in Sunset Cove varied seasonally, ranging from 0.019 to $0.146 \text{ mmol N m}^{-2} \text{ d}^{-1}$ (Nagel 2004), far below the calculated seagrass demand. These rates most likely underestimate N fixation rates within the seagrass sediments, as organic matter production in seagrass beds is thought to enhance N fixation relative to bare sediments (Welsh et al. 1997, McGlathery et al. 1998, Hansen et al. 2000). Detailed experiments exploring N fixation rates in Florida Bay *T. testudinum* sediments are necessary in order to ascertain the relative contribution of N fixation to both overall N cycling and seagrass N demand in Florida Bay.

This remarkably tight coupling between O_2 cycling and NH_4^+ regeneration in *T. testudinum* beds of Sunset Cove can also be examined more directly in order to provide insight as to the source of organic matter driving NH_4^+ regeneration. Nighttime net regeneration of NH_4^+ in benthic flux cores was positively related to respiration ($y = 17x + 6.1$, $r^2 = 0.81$, $p = 0.01$) in the *T. testudinum* community. The slope of the regression reveals a ratio of O_2 respiration to NH_4^+ regeneration of approximately 17. Assuming a photosynthetic quotient ($\text{CO}_2:\text{O}_2$) equal to 1, the ratio of respiration to NH_4^+ regeneration

falls well within the range of carbon to nitrogen ratios (C:N ~15-20) observed in plant leaves in Sunset Cove. This similarity suggests that the source of organic matter fueling NH_4^+ regeneration was likely detrital seagrass material (Holmer et al. 2004).

The relatively elevated rates of benthic NH_4^+ regeneration combined with high sulfide production compared to bare sediments in June imply high sediment organic matter pools in the *T. testudinum* community. Based on these rates, one would expect higher sediment porewater NH_4^+ concentrations in vegetated sediments. This was not the case, however, as NH_4^+ concentrations were only slightly elevated in seagrass sediments. High plant N demand provides an explanation for this unexpected pattern. In systems where water column nutrient concentrations are low, seagrass assimilate the majority of nitrogen needed to support growth through plant roots (Short & McRoy 1984, Touchette & Burkholder 2000). As indicated in previous calculations, the lower porewater NH_4^+ concentrations likely reflect the relatively high demand for nutrients in the *T. testudinum* sediments.

Rates of net benthic NO_3^- production at night in *T. testudinum* sediments in June were surprisingly high ($180 \mu\text{mol m}^{-2} \text{d}^{-1}$), and rates exceeded those observed in bare sediments. High rates imply that there is a significant source of NO_3^- within these sediments. Release of NO_3^- -rich groundwater can contribute to effluxes of NO_3^- from estuarine sediments (Valiela et al. 1991, Staver et al. 1996), but surveys along the Keys in Florida Bay suggest that groundwater NO_3^- of terrestrial origin (e.g., septic systems) does not significantly contribute to water column NO_3^- concentrations offshore (Lapointe & Clark 1991). It is probable, therefore, that the source of NO_3^- production is within seagrass sediments. Root O_2 release creates rhizosphere microhabitats for obligate aerobic bacteria, such as nitrifiers, and may lead to enhanced nitrification in seagrass sediments (Caffrey and Kemp 1990). Since nitrification at depth within sediments depends on availability of O_2 (Ottosen et al. 1999), vertical profiles of nitrification within

seagrass sediments may also provide an indication of the degree to which the plants oxidize surrounding sediments through root oxygen release. Enriquez et al. (2001) attributed positive redox anomalies in *T. testudinum* sediments to seagrass photosynthetic activity and, several studies (e.g., Caffrey and Kemp 1990) have shown enhanced nitrification rates in vegetated relative to bare sediments. In this study, nitrification rates in June were marginally enhanced in *T. testudinum* sediments (Fig. 2.9), and rates did not appear to be correlated with belowground biomass. Since aerobic sediment slurries are meant to maximize growth conditions for nitrifying bacteria, estimates of nitrification determined from aerobic slurries tend to overestimate rates measured using other methods (Henriksen & Kemp 1988). However, removal of plant roots from sediments used in aerobic slurries could result in underestimation of nitrifying bacteria, as these bacteria often grow in close association with or attached to plant roots. In fact, during removal of roots from the sediments, a conglomeration of sediment, or plaque, was observed attached to plant roots. Consequently, it is possible that nitrification rates measured using sediment slurries in this study may have underestimated *in situ* rates. Further measurements of nitrification using alternative methods (e.g., isotope pairing) may provide a more accurate estimate of rates.

For both the bare and seagrass communities, net fluxes of NH_4^+ and NO_3^- , over the diel cycle were zero or slightly negative throughout most of the year. These communities, however, served as net sinks of inorganic nitrogen during summer months when plant production was highest. This pattern is typical of nutrient-limited systems and indicates tight recycling of inorganic nitrogen within these communities (Duarte 1995). The relationship between open water O_2 and NH_4^+ concentrations measured over the course of the year was negative ($y = -29.9x + 298$, $r^2 = 0.36$, $p < 0.0001$), suggesting high N demand within these communities. Burton-Evans (2005) concluded that the thick benthic microalgal mats present in the bare area in Sunset Cove

essentially served as a barrier to effluxes of NH_4^+ from the sediment, a common finding in benthic microalgal communities (Sundback & Graneli 1988, McGlathery et al. 2001, Miyajima et al. 2001). From the results of this study it is clear that both *T. testudinum* and benthic microalgae are efficient for reducing inorganic N concentrations in the water column.

The low concentrations and absence of diel patterns in PO_4^{3-} concentrations observed in this study are indicative of tight recycling of P in tropical carbonate sediments (e.g., McGlathery et al. 1994). Although there were no discernible diel patterns in PO_4^{3-} concentrations in this study, I did observe brief pulses in PO_4^{3-} concentrations throughout the year. These pulses may have originated from sediment resuspension caused by wind disturbance or bioturbation that subsequently led to the release of PO_4^{3-} from the sediment to the overlying water column. Sediment resuspension during wind events in Florida Bay can lead to sharp increases in PO_4^{3-} concentrations in the water column and, subsequent stimulation of phytoplankton productivity (Lawrence et al. 2004). The rapid decline in concentrations following these pulses was likely the result of uptake by phytoplankton and benthic autotrophs, or rapid sediment re-adsorption (Lawrence et al. 2004). While much of eastern Florida Bay is considered to be PO_4^{3-} -limited (Fourqurean et al. 1992, Zhang et al. 2004), wind or physical disturbance of the sediments may be important for releasing PO_4^{3-} to the water column and ultimately supporting plant growth. Dissolved organic phosphorus (DOP) may also be an important component of the phosphorus cycle in seagrass communities (Ziegler et al. 2004); however little data exist regarding the abundance and cycling of DOP within Florida Bay.

Influence of *T. testudinum* on DOM cycling

Net production of DOC was observed only during the day, and production rates were higher in the *T. testudinum* relative to the benthic microalgal community. Rates of net benthic DOC production during the light measured in flux cores in Sunset Cove were generally higher ($5 - 100 \text{ mmol m}^{-2} \text{ d}^{-1}$) than rates reported in a *T. testudinum* community in Texas ($0 - 18 \text{ mmol m}^{-2} \text{ d}^{-1}$) (Ziegler & Benner 1999), but were similar to those I observed in a *T. testudinum* bed in Rabbit Key in Florida Bay (Ch. 3). Higher rates of DOC production observed within the plant canopy indicate that the source of DOC release originated from within seagrass bed. Seagrasses are known to excrete a fraction of photosynthetically-fixed carbon as DOC from both leaves and belowground tissues (e.g., Wetzel and Penhale 1979). Release of DOC from plant roots could lead to the accumulation of DOC in sediment porewater (Koepfler et al. 1993), and could ultimately lead to enhanced effluxes of DOC from the sediment to the overlying water. While photosynthetic activity is a key factor contributing to DOC excretion, nutrient availability may also influence root DOC release. When nutrient limitation limits plant growth to a greater extent than light limitation, plants produce simple carbohydrates in excess of what can be used to support growth or respiration (Lambers et al. 1998). These excess photosynthates may be sequestered as storage polysaccharides for use when growth is no longer nutrient-limited (Alcoverro et al. 2001), or may be excreted to the external environment (Welsh et al. 1997). Thus, when plants are nutrient-limited, such as those in Sunset Cove, and carbohydrate reserves are high, root DOC excretion rates may be higher than when plant growth is nutrient replete. Release of fermentation by-products from anaerobic root respiration under hypoxic conditions (Smith et al. 1984) and leaching and decomposition of senescing or detrital plant material (Kenworthy et al. 1989, Opsahl & Benner 1993) may also result in DOC production and subsequent efflux from the sediment.

Daytime rates of DOC production were high and often equaled or exceeded carbon fixation associated with measured O₂ production, implying allochthonous sources of DOC to this community. Barron et al. (2004) reported similar findings and suggested that the high rates of DOC production were attributable to enhanced trapping of particulate organic matter within seagrass beds. The physical structure of plant leaves reduces water flow through the canopy (Fonseca et al. 1982), resulting in enhanced deposition of particulate organic matter (e.g., seston, phytoplankton) with seagrass beds (e.g., Ward et al. 1984, Gacia et al. 1999, Kennedy et al. 2004). In the case of Florida Bay, where phytoplankton concentrations are relatively low, imports of resuspended benthic microalgal mats, macroalgae or mangrove detritus are likely sources of allochthonous organic matter to seagrass communities. Indeed, during summer periods of high production, benthic microalgal mats from bare areas were observed floating at the water surface as a result of the formation of O₂ bubbles within the mat (MacIntyre et al. 1996, Nagel pers. obs.). Once in the water column, these mats were subject to lateral transport from wave action, and were observed to be subsequently deposited within the seagrass bed, where DOC produced from the decomposition of benthic microalgae within these mats may have contributed to the overall high observed rates of DOC production.

Because there are numerous possible sources of DOC, partitioning of DOC sources within these communities is difficult and was not a focus of this study. The clear diel patterns in DOC concentrations provide indirect evidence that seagrass production is responsible for the diel variations in DOC concentrations. Increases in the ratio of DOC:DON concentrations during daylight hours support seagrass exudation as the source of diel DOC variability (Fig. 2.9), since photosynthetic exudates are primarily simple carbohydrates (Moriarty et al. 1986, Koepfler et al. 1993, Blaabjerg et al. 1998). Ziegler and Benner (1999) also provided indirect evidence that DOC excretion from

seagrasses was responsible for diel DOC variability. However, rates of DOC excretion from live plants measured in laboratory experiments are consistently low, averaging less than 10% of plant carbon production (e.g., Wetzel & Penhale 1979). Epiphytes and benthic microalgae are frequently abundant in seagrass communities and are also known to excrete DOC during photosynthesis (Wetzel & Penhale 1979). Thus, it is possible that laboratory experiments on seagrasses alone underestimate light-mediated release of DOC within these communities. In addition, photodegradation of particulate organic matter can also contribute to daytime increases in DOC concentrations (Ziegler & Benner 2000), but it is not known to what degree this process influenced DOC production in this study.

The large pools of DOC produced may support microbial processes within these communities. Bacterioplankton C demand within a *T. testudinum* meadow has been shown to represent as much as 50% of NEP (Ziegler & Benner 1998) and may account for the high rates of nighttime DOC consumption observed in this study.

Photodegradation by solar radiation may also contribute to loss of DOC; however, this process appeared to play only a minor role in DOM cycling in a similar system (Ziegler and Benner 1999). In addition to supporting microbial processes, production of chromophoric DOM (CDOM) from detrital *T. testudinum* material is thought to absorb potentially harmful solar radiation (Stabenau et al. 2004). Because of the relatively low nutrient content and palatability of seagrass tissues, it is often thought that there are few direct linkages (i.e., grazers) between seagrasses and higher trophic levels (e.g., Duarte & Cebrian 1996). However, microbial consumption of DOC produced in the *T. testudinum* community may represent a link to higher trophic levels (Thresher et al. 1992, Lopez et al. 1995, Jones et al. 2003). This could occur either directly through consumption of seagrass-derived DOC (Blum & Mills 1991, Peduzzi & Herndl 1991, Jones et al. 2003, Kaldy et al. 2006) or indirectly through consumption of deposited

particulate matter (Barron et al. 2004) and microalgal-DOC release (Penhale & Smith 1977). In a recent study using ^{13}C -tracers, Kaldy et al. (2006) demonstrated a direct linkage between *T. testudinum* and sediment microbes and estimated that nearly all of sediment microbial carbon demand was met by a combination of direct DOC exudation and remineralization of detrital plant material within the seagrass bed. Thus, although bacterial productivity was not directly measured in this study, the observed high rates of nighttime DOC consumption were likely supporting bacterial carbon demand in both the sediment and overlying water column of the *T. testudinum* bed.

DON concentrations within both the bare and *T. testudinum* communities exhibited diel variability similar to DOC and rates represented as high as 90% of total nitrogen fluxes. Several studies have reported the release of DON from both benthic microalgal (e.g., Tyler et al. 2003) and seagrass (e.g., (Jorgensen et al. 1981) communities. Both photosynthetic production (Jorgensen et al. 1981) and leaching and decomposition of seagrass (Twilley et al. 1985, Pedersen et al. 1999) and microalgal material are potential sources of DON. Large effluxes of DON, such as those observed in August 2004, may be associated with the hydrolysis product of decomposing organic matter (Burdige & Zheng 1998) within seagrass beds (Eyre & Ferguson 2002). Although the composition of DON varies, dissolved free amino acids (DFAA) and urea often represent small, but important, fractions of nitrogen within the DON pool. The high rates of DON consumption combined with low ratios of DOC:DON consumption observed at night (Fig. 2.9) within the *T. testudinum* bed may be the result of preferential dark assimilation of DON by photosynthetic and microbial organisms within the community (Eyre & Ferguson 2002). While it is not known if seagrasses themselves are capable of assimilating DON, numerous studies have shown that benthic microalgae (Hansen et al. 2000, Tyler et al. 2003), macroalgae (Tyler et al. 2001) and bacteria (Jorgensen et al. 1981, Lopez et al. 1995) consume DON. Furthermore, benthic algae have been shown

to significantly mediate effluxes of DON from the sediment (Tyler et al. 2003) and may be responsible, in part, for the high rates of DON consumption observed. The lack of net DON production over the diel cycle suggests that the DON pool has a high turnover rate and that DON may be an important source of nitrogen for algal autotrophic production within this nutrient-limited system. The high rates and clear diel patterns illustrate the potential importance of DON to overall nitrogen cycling as well as the role of benthic primary producers in regulating DON cycling within these communities.

Synthesis and Implications

Given the apparent influence of *T. testudinum* on biogeochemical processes observed in this study and the dominance of *T. testudinum* throughout Florida Bay, it is clear that this species has a high potential for influencing biogeochemistry within this system (Fig. 2.10). The clear diel patterns and enhancement of processes relative to benthic microalgal communities illustrate the importance of *T. testudinum* in regulating O₂, nitrogen, and DOM cycling. The influence of these plants on nutrient cycling combined with high rates of organic production and potential for storage suggest that these plants may contribute significantly to C and N budgets in Florida Bay.

Recent dieback events have led to the loss of seagrass habitat and it appears that, of all seagrass species in Florida Bay, *T. testudinum* is the most susceptible to dieback (Robblee et al. 1991). Complex interactions between nighttime water column O₂ concentrations, internal O₂ pressure, temperature, salinity, and sediment sulfide concentrations likely play a role in plant susceptibility to dieback. The periodic hypoxia within the seagrass canopy concurrent with the high sediment sulfide concentrations that I observed indicates a potential vulnerability of *T. testudinum* in Sunset Cove to seagrass dieback during summer months. This could result in the formation of additional bare areas in Sunset Cove, which, in turn, could increase the relative importance of

benthic microalgal communities in biogeochemical cycling within this region. The results of this study suggest that seagrass dieback would represent a loss of a significant contributor to biogeochemical cycling in Florida Bay.

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Table 2.1. Average (\pm SE) concentrations of *in situ* O₂, NH₄⁺, NO₃⁻, DOC and DON and mean (\pm SE) temperature and salinity in the water column of *T. testudinum* (Veg) and bare communities in Sunset Cove, FL 2003-2004. “nd” indicates that no data are available.

Site	O ₂	NH ₄ ⁺	NO ₃ ⁻	DON	DOC	T	Salinity
Aug '03							
Veg	182 \pm 1.9	3.28 \pm 0.10	0.32 \pm 0.02	59.1 \pm 1.43	452 \pm 19.1	29.9 \pm 0.03	36.3 \pm 0.01
Bare	188 \pm 1.2	3.22 \pm 0.12	0.36 \pm 0.02	51.7 \pm 1.29	435 \pm 14.7	29.8 \pm 0.05	36.5 \pm 0.01
Nov '03							
Veg	nd	3.62 \pm 0.06	1.61 \pm 0.16	40.6 \pm 0.81	414 \pm 12.2	23.5 \pm 0.20	26.7 \pm 0.09
Bare	232 \pm 1.2	4.53 \pm 0.17	1.35 \pm 0.03	45.6 \pm 1.31	337 \pm 9.3	24.1 \pm 0.02	26.8 \pm 0.01
Jan '04							
Veg	nd	3.18 \pm 0.06	1.24 \pm 0.03	46.7 \pm 0.94	480 \pm 11.1	nd	nd
Bare	nd	3.41 \pm 0.18	1.29 \pm 0.04	43.6 \pm 0.73	450 \pm 10.8	20.1 \pm 0.04	25.7 \pm 0.11
Mar '04							
Veg	247 \pm 1.4	1.40 \pm 0.06	nd	nd	nd	23.2 \pm 0.04	28.2 \pm 0.01
Bare	239 \pm 1.6	2.24 \pm 0.12	nd	nd	nd	22.8 \pm 0.05	28.1 \pm 0.01
Jun '04							
Veg	206 \pm 2.5	3.33 \pm 0.12	1.50 \pm 0.18	48.7 \pm 0.82	361 \pm 9.4	31.1 \pm 0.02	36.3 \pm 0.04
Bare	202 \pm 2.1	3.37 \pm 0.13	1.36 \pm 0.16	50.9 \pm 0.76	343 \pm 8.4	31.1 \pm 0.02	36.8 \pm 0.01
Aug '04							
Veg	206 \pm 1.8	4.48 \pm 0.53	0.45 \pm 0.05	49.6 \pm 1.28	479 \pm 24.6	31.5 \pm 0.03	40.6 \pm 0.01
Bare	183 \pm 1.2	5.09 \pm 1.04	0.42 \pm 0.02	49.9 \pm 1.34	436 \pm 15.8	31.4 \pm 0.03	38.2 \pm 0.01

Table 2.2. Light (daytime) fluxes ($\text{mmol m}^{-2} \text{d}^{-1}$, mean \pm SE) of *in situ* O_2 , NH_4^+ , NO_3^- , DON, and DOC within the water column of *T. testudinum* (vegetated) and bare communities in Sunset Cove, FL in 2003-2004. “nd” indicates no data are available for that month.

	O_2	NH_4^+	NO_3^-	DON	DOC
Aug '03					
Veg	208 \pm 9.16	-2.09 \pm 0.27	-0.31 \pm 0.07	10.9 \pm 1.97	530 \pm 71.6
Bare	101 \pm 23.3	-1.67 \pm 0.34	-0.19 \pm 0.05	12.7 \pm 1.12	110 \pm 29.9
Nov '03					
Veg	nd	-0.78 \pm 0.12	-0.16 \pm 0.06	5.97 \pm 1.73	245 \pm 4.31
Bare	53.6 \pm 4.64	-0.53 \pm 0.16	-0.10 \pm 0.05	18.5 \pm 8.83	173 \pm 48.9
Jan '04					
Veg	nd	-0.83 \pm 0.17	-0.49 \pm 0.12	14.1 \pm 0.40	107 \pm 51.1
Bare	nd	-0.79 \pm 0.11	-0.12 \pm 0.04	9.00 \pm 2.84	100 \pm 39.1
Mar '04					
Veg	143 \pm 8.24	-0.57 \pm 0.07	nd	nd	nd
Bare	75.6 \pm 15.7	-1.75 \pm 0.75	nd	nd	nd
Jun '04					
Veg	183 \pm 13.5	-2.48 \pm 0.42	-1.87 \pm 0.67	15.2 \pm 3.40	197 \pm 48.4
Bare	117 \pm 11.7	-1.71 \pm 0.39	-1.81 \pm 0.83	7.27 \pm 2.29	61.7 \pm 20.1
Aug '04					
Veg	194 \pm 2.84	-5.43 \pm 0.62	-0.57 \pm 0.10	40.2 \pm 27.3	339 \pm 47.5
Bare	68.7 \pm 14.9	-4.34 \pm 1.19	-0.16 \pm 0.06	24.9 \pm 16.4	173 \pm 69.3

Table 2.3. Dark (nighttime) fluxes ($\text{mmol m}^{-2} \text{d}^{-1}$, mean \pm SE) of *in situ* O_2 , NH_4^+ , NO_3^- , DON, and DOC within the water column of *T. testudinum* (vegetated) and bare communities in Sunset Cove, FL in 2003-2004. “nd” indicated no data are available for that month.

	O_2	NH_4^+	NO_3^-	DON	DOC
Aug '03					
Veg	-67.6 ± 3.23	0.90 ± 0.17	0.17 ± 0.05	-22.0 ± 5.80	-144 ± 34.8
Bare	-37.9 ± 4.21	0.27 ± 0.07	0.13 ± 0.04	-23.7 ± 10.9	-41.2 ± 17.4
Nov '03					
Veg	nd	0.53 ± 0.11	0.27 ± 0.04	-5.40 ± 1.07	-90.3 ± 31.2
Bare	-46.3 ± 4.80	0.80 ± 0.43	0.33 ± 0.10	-11.1 ± 3.77	-77.9 ± 34.5
Jan '04					
Veg	nd	0.71 ± 0.14	0.24 ± 0.05	-6.46 ± 0.38	-49.9 ± 10.8
Bare	nd	0.69 ± 0.23	0.13 ± 0.02	-9.23 ± 3.43	-29.4 ± 11.6
Mar '04					
Veg	-69.8 ± 4.24	0.61 ± 0.09	nd	nd	nd
Bare	-65.4 ± 4.84	1.42 ± 0.49	nd	nd	nd
Jun '04					
Veg	-88.6 ± 5.52	1.03 ± 0.13	2.49 ± 1.02	-14.6 ± 1.67	-54.0 ± 8.67
Bare	-70.2 ± 3.08	0.36 ± 0.00	1.00 ± 0.06	-6.65 ± 1.52	-9.31 ± 3.14
Aug '04					
Veg	-96.1 ± 13.4	5.87 ± 2.09	0.37 ± 0.15	-23.1 ± 14.8	-130 ± 12.3
Bare	-44.5 ± 13.0	1.69 ± 0.47	0.08 ± 0.03	-36.6 ± 9.01	-111 ± 20.6

Table 2.4. Light, dark, and net fluxes ($\text{mmol m}^{-2} \text{d}^{-1}$, mean \pm SE) of O_2 , NH_4^+ , NO_3^- , DON, and DOC from benthic flux cores taken from *T. testudinum* and bare communities in Sunset Cove, FL in January and June 2004.

	O_2		NH_4^+		NO_3^-		DON		DOC	
	Veg	Bare	Veg	Bare	Veg	Bare	Veg	Bare	Veg	Bare
<i>January</i>										
Light	94 \pm 15	47 \pm 5.4	-0.74 \pm 0.08	-0.69 \pm 0.07	-0.08 \pm 0.03	-0.11 \pm 0.02	2.4 \pm 1.1	1.0 \pm 0.3	49 \pm 7.1	27 \pm 3.5
Dark	-69 \pm 1.4	-35 \pm 5.9	0.28 \pm 0.06	0.15 \pm 0.01	0.06 \pm 0.02	-0.03 \pm 0.05	-7.8 \pm 3.1	-6.8 \pm 3.3	-13 \pm 3.7	-6.0 \pm 0.9
Net	25 \pm 16	11 \pm 0.5	-0.46 \pm 0.07	-0.53 \pm 0.08	-0.02 \pm 0.05	-0.14 \pm 0.06	-5.4 \pm 3.8	-5.8 \pm 3.1	35 \pm 3.6	21 \pm 4.3
<i>June</i>										
Light	157 \pm 28	42 \pm 6.3	-1.96 \pm 0.22	-0.75 \pm 0.23	-0.23 \pm 0.03	-0.14 \pm 0.03	8.3 \pm 0.4	-1.1 \pm 2.5	60 \pm 20	24 \pm 9.4
Dark	-123 \pm 11	-47 \pm 4.4	2.73 \pm 1.25	0.28 \pm 0.05	0.18 \pm 0.01	0.08 \pm 0.04	-5.6 \pm 2.6	-0.7 \pm 2.7	-31 \pm 13	-18 \pm 5.3
Net	34 \pm 28	-4.7 \pm 1.9	-0.37 \pm 0.04	-0.48 \pm 0.22	-0.05 \pm 0.04	-0.04 \pm 0.07	2.6 \pm 3.0	-1.9 \pm 3.2	28 \pm 8.0	6.3 \pm 14

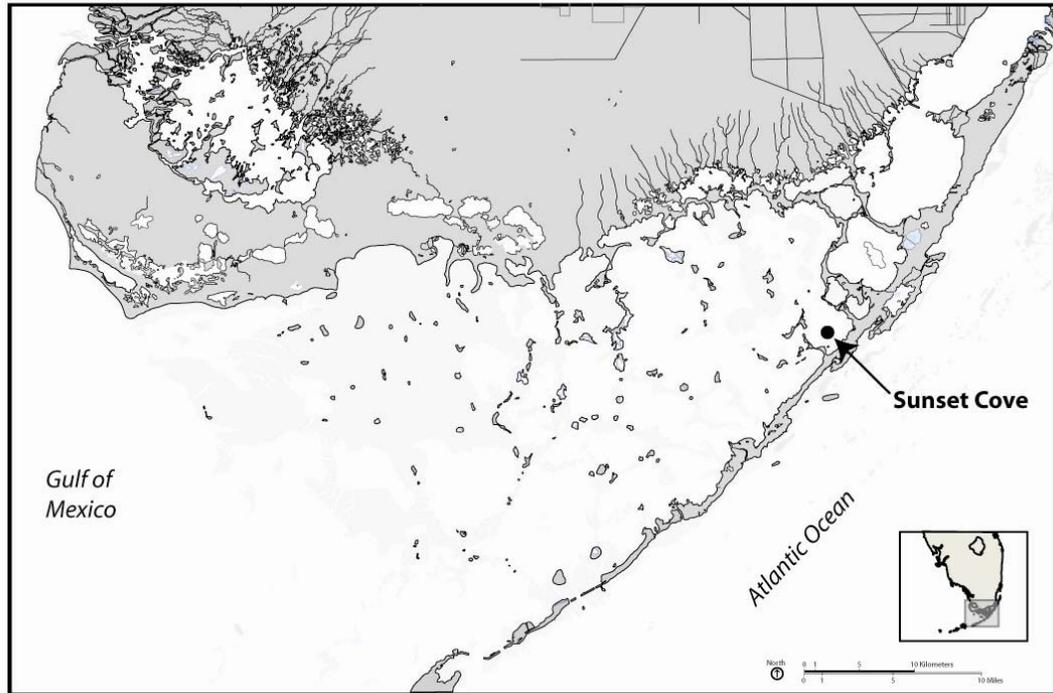


Fig 2.1. Map of field study site in Sunset Cove, Florida, USA.

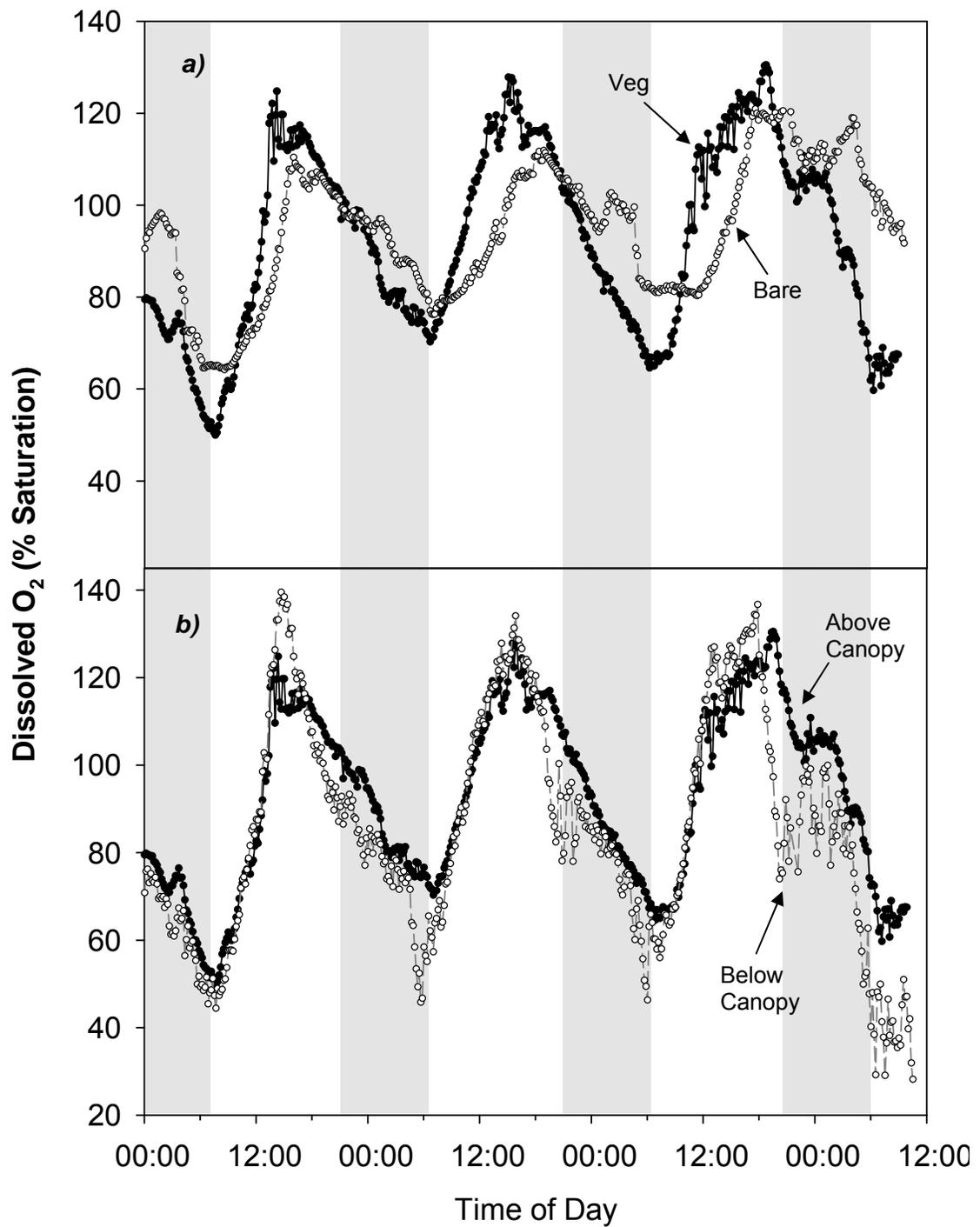


Fig 2.2. Diel variations in percent saturation of dissolved O₂ concentrations within *T. testudinum* (Veg) (filled symbol) and bare communities (open) (A) in August 2003. (B) Variations in percent saturation of dissolved O₂ concentrations above (filled symbol) and below (open symbol) the canopy in a *T. testudinum* bed in August 2003. The shaded areas indicated nighttime hours.

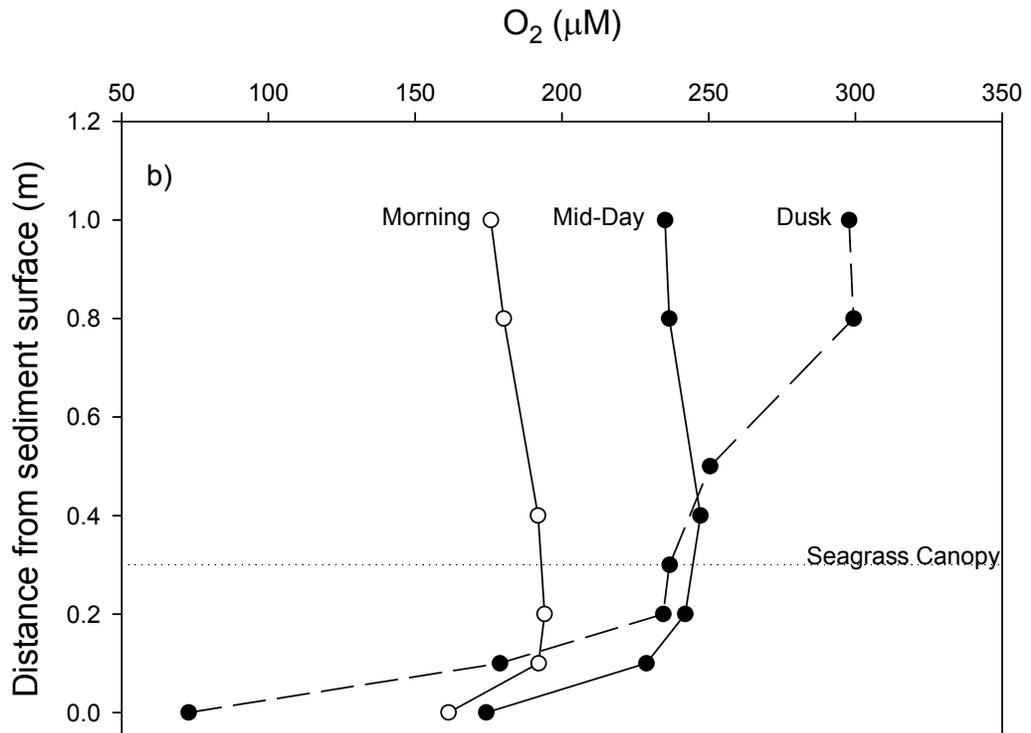
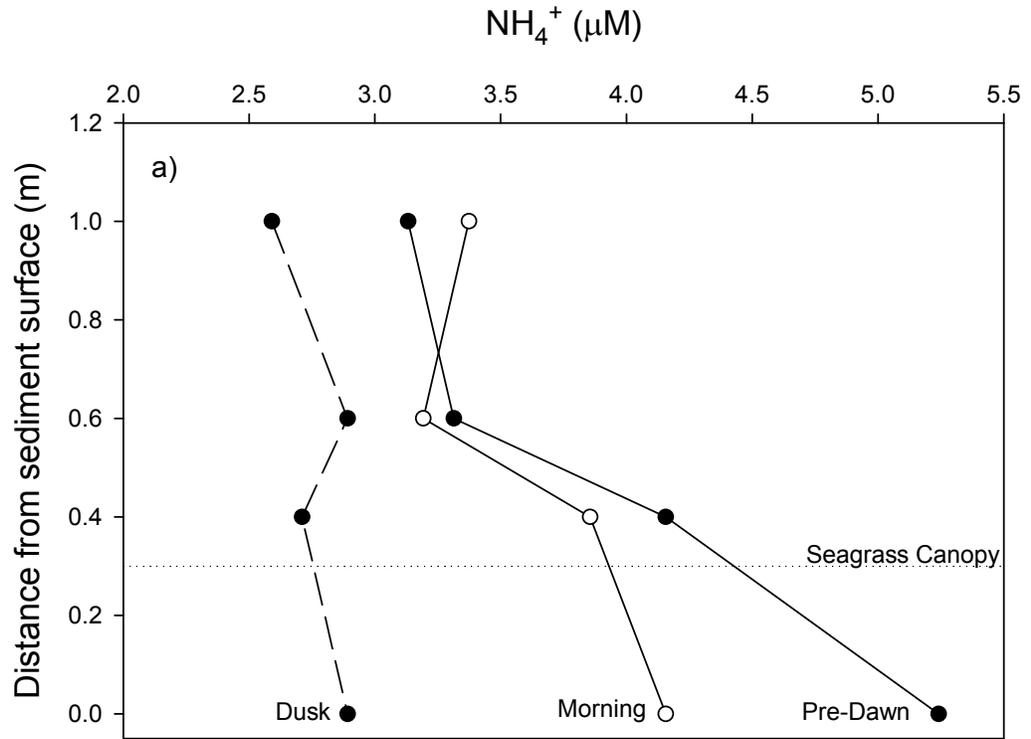


Fig. 2.3. Diel variations in vertical profiles of NH_4^+ (a) and O_2 (b) concentrations (μM) in the water column of a *T. testudinum* bed in June 2004. NH_4^+ concentrations were measured in the morning (09:30), at dusk (21:00), and at pre-dawn (03:30). O_2 concentrations were measured in the morning (09:30), at mid-day (13:00), and at dusk (21:00). The dotted line represents the depth above the sediment surface at which the top of canopy was found.

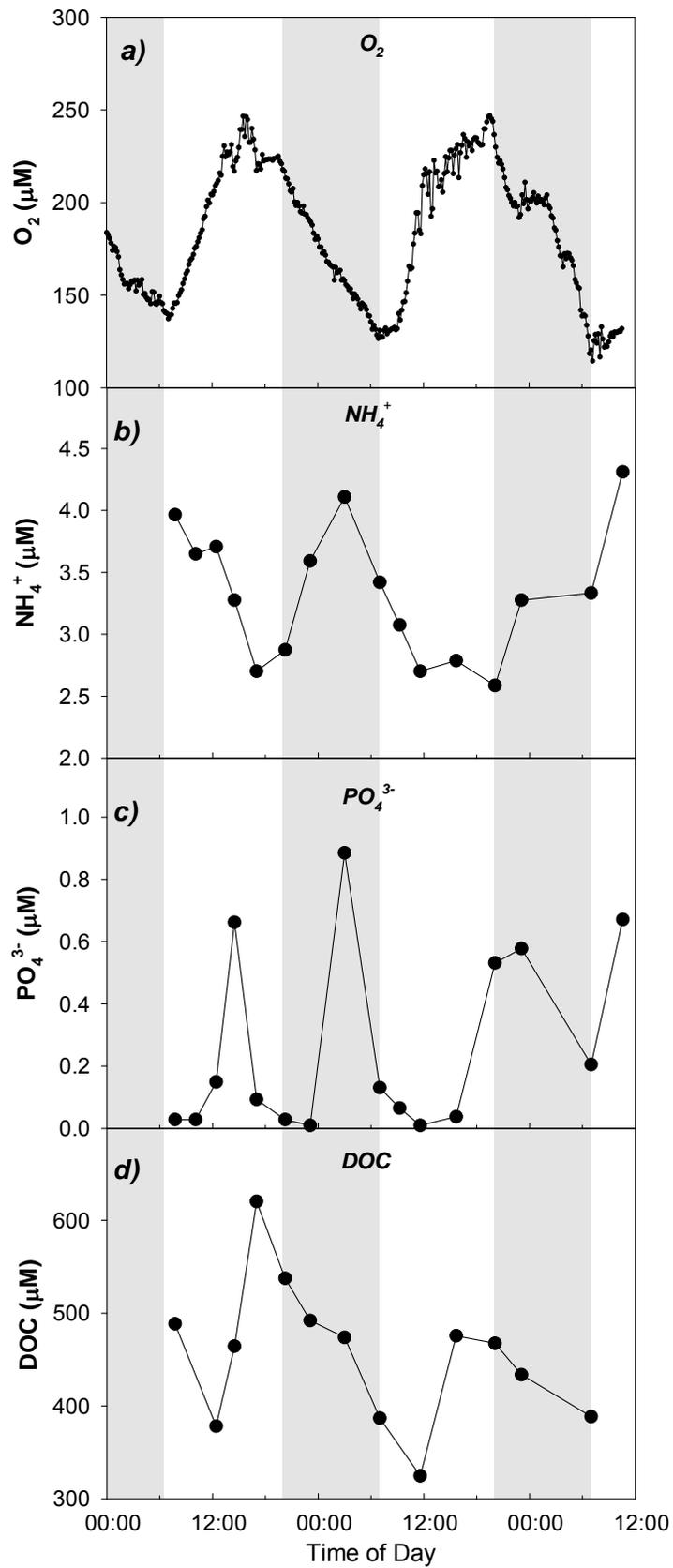


Fig 2.4. Diel variations in O_2 (A) NH_4^+ (B), PO_4^{3-} (C), and DOC (D) concentrations (μM) in the water column overlying a *T. testudinum* bed in August 2003. Shaded areas represent nighttime hours. Note the different scales on the right-hand y-axis for each panel.

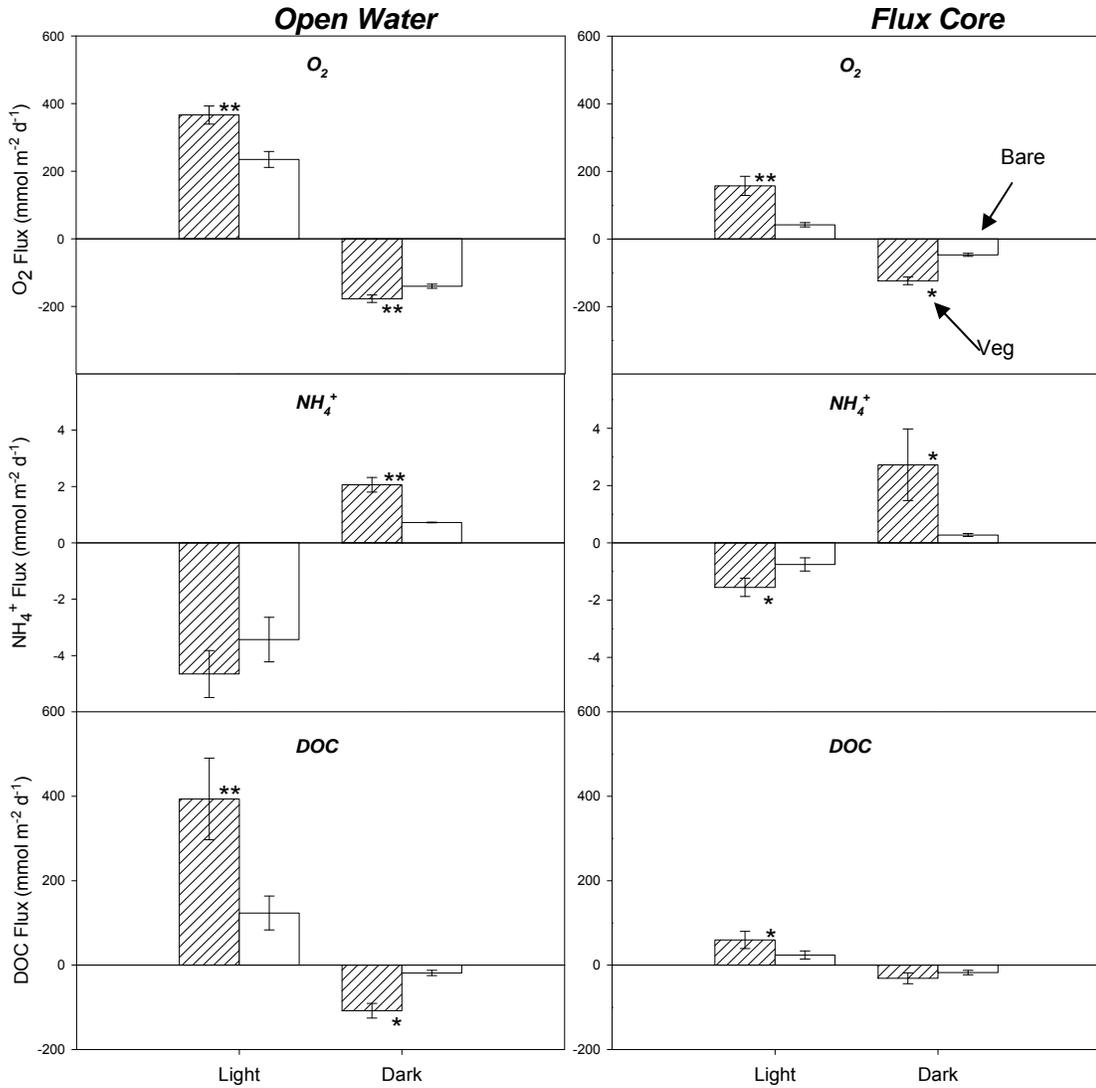


Fig 2.5. Comparison of light and dark flux rates (mean \pm SE) for O_2 (upper), NH_4^+ (middle), and DOC (lower) measured in the open water (left panel) versus benthic flux cores (right panel) in *T. testudinum* (hatched bars) and bare (open bars) communities. Significant differences between vegetated and bare communities are denoted by an '*' ($p < 0.05$) or '**' ($p < 0.01$).

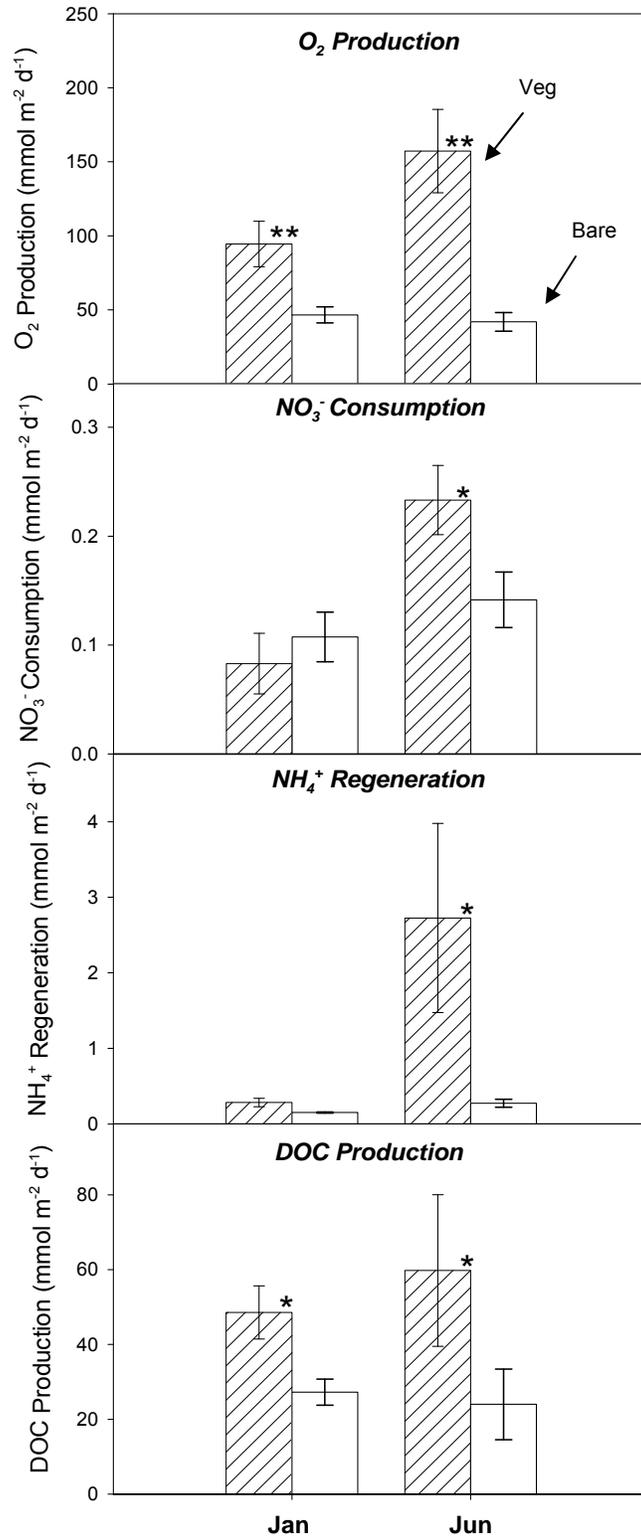


Fig 2.6. Seasonal variations (mean \pm SE) in O₂ production (a), NO₃⁻ consumption (b), NH₄⁺ regeneration (c), and DOC production (d) in *T. testudinum* (hatched) and bare communities (open) in January and June 2004. Rates were measured in benthic flux cores and have units of mmol m⁻² d⁻¹. Significant differences between vegetated and bare communities are denoted by an “*” (p < 0.05) or “**” (p < 0.01).

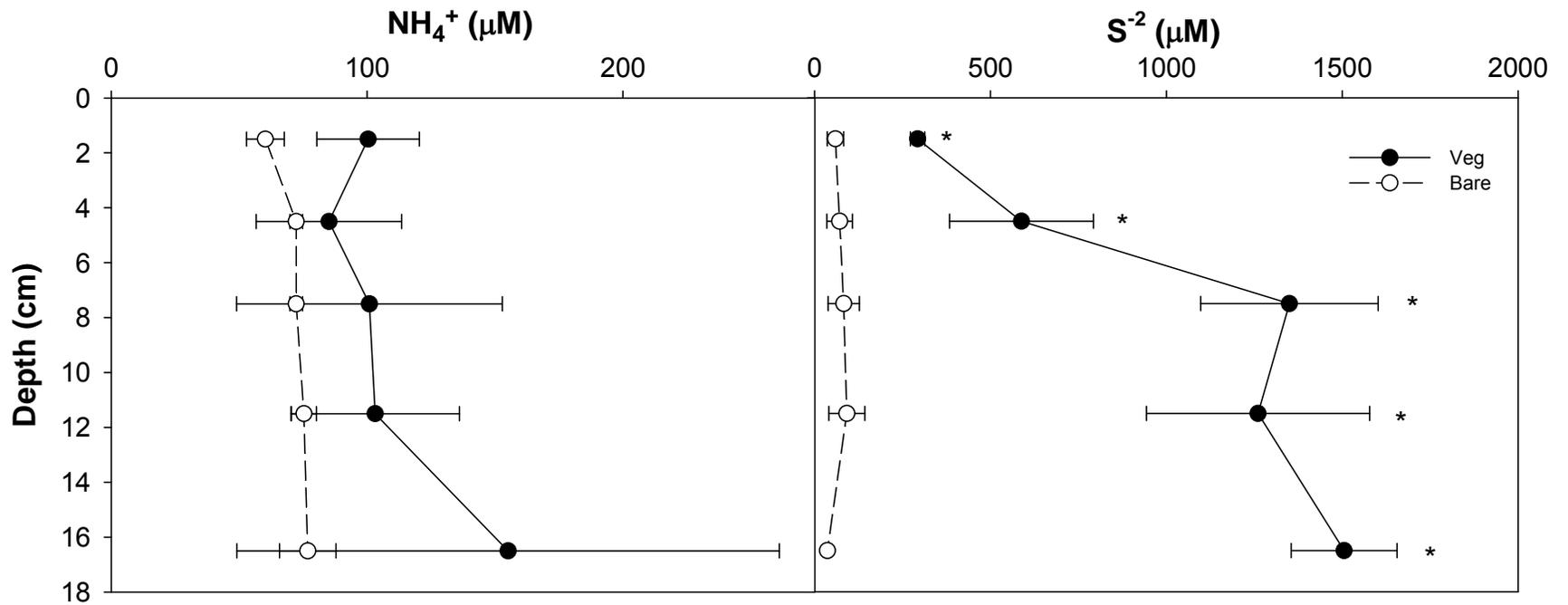


Fig 2.7. Vertical variations (mean \pm SE) in sediment porewater NH_4^+ (a) and S^{2-} (b) concentrations in a *T. testudinum* bed (filled symbol) and bare (open) sediments in June 2004. Note the different scales on the x-axes. An “*” indicates a significant difference ($p < .0001$) between concentrations in vegetated and bare communities.

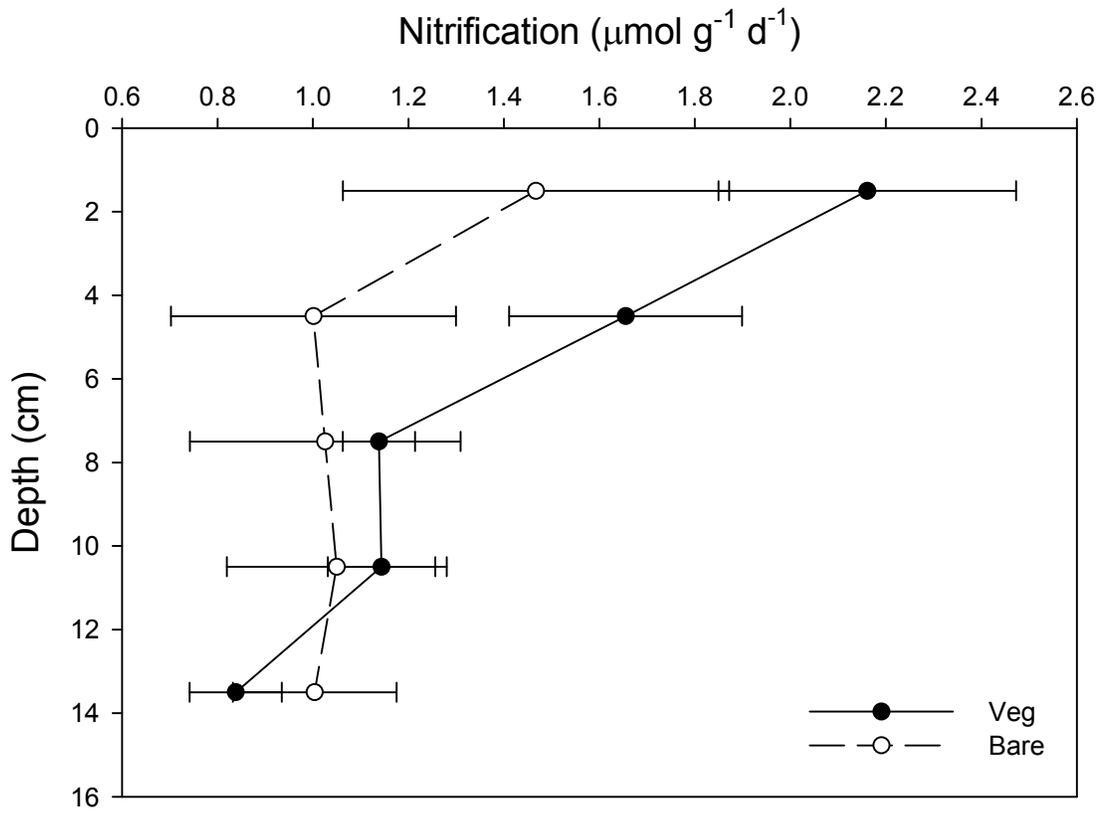


Fig 2.8. Vertical variations (mean \pm SE) in sediment nitrification ($\mu\text{mol g}^{-1} \text{d}^{-1}$) in a *T. testudinum* bed (filled symbol) and bare sediments (open) in June 2004. Note the scale.

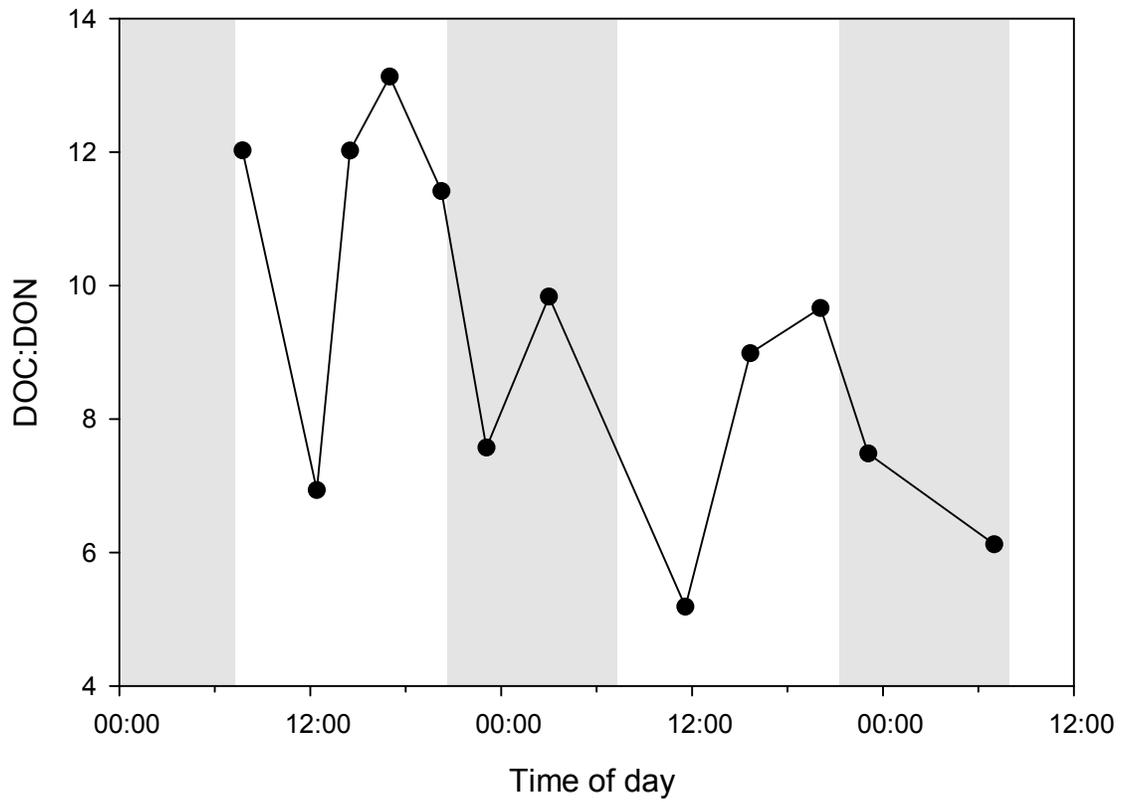


Fig 2.9. Diel variations in the ratio of DOC:DON concentrations in the *T. testudinum* community in August 2003. Shaded areas indicate nighttime hours.

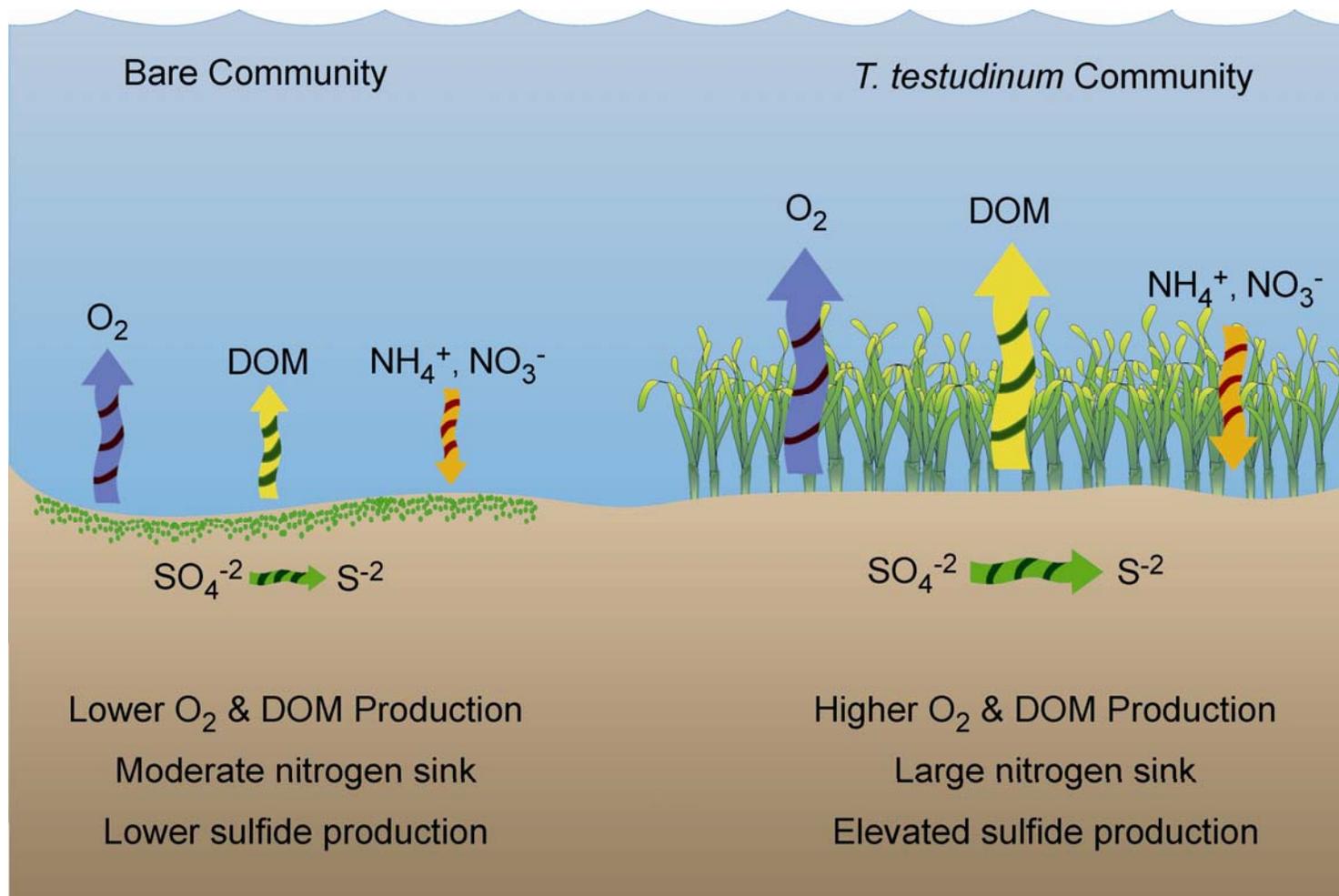


Fig 2.10. Comparison of the relative influence of *T. testudinum* and benthic microalgal (bare) communities on biogeochemical cycling.

CHAPTER 3: A comparative study of biogeochemical processes in bank and basin *Thalassia testudinum* beds in Florida Bay: Implications for seagrass dieback

ABSTRACT

Seagrasses are a prominent feature of most of the major basins of the Florida Bay ecosystem, occupying both deeper sediments within the basins and shallower mud banks that separate basins. Recent dieback events have led to losses of seagrass habitat and associated plant effects on biogeochemical cycling in Florida Bay. The goal of this study was to quantify differences in plant characteristics and biogeochemical cycling in basin and bank *Thalassia testudinum* communities and to assess the consequences of dieback on sediment biogeochemical processes at sites near Barnes and Rabbit Keys in Florida Bay. Plant and sediment characteristics, and benthic fluxes of O_2 , NH_4^+ , NO_3^- , and dissolved organic carbon and nitrogen across the sediment-water interface were measured using intact core incubations in both bank and basin communities. Sediment microbial activities and open-water estimates of ecosystem-level production and respiration were measured during an active dieback event in Barnes Key. Higher porewater ammonium concentrations in bank sediments, along with elevated plant tissue N levels, suggest that enhanced POM trapping and nitrogen regeneration rates tend to support higher plant production in bank habitats. However, benthic fluxes of inorganic nitrogen and dissolved organic matter did not reveal any discernible differences between bank and basin communities. Seagrass dieback during summer months at Barnes Key led to the stimulation of sulfate reduction and ammonification and the accumulation of sulfide in sediment porewaters. Bank communities were characterized by high sediment sulfide concentrations, flocculent sediments, and dense stands of seagrass plants, all of which may make these *T. testudinum* beds more vulnerable to dieback compared to beds in adjacent basin habitats. In general, seagrass dieback resulted in lower nitrification rates, presumably due to reduced rates of oxygen production and excretion from roots to surrounding sediments and associated higher sulfide concentrations. Consequently, seagrass

dieback led to reduced ecosystem-level O₂ production, increased community respiration and a negative balance between ecosystem production and respiration (i.e., net heterotrophy). Results of this study suggest that summertime seagrass dieback had a negative effect on plant-sediment interactions and biogeochemical cycling in Barnes Key. While the seagrass community exhibited a recovery during the winter months, the effect of dieback on biogeochemical cycling may nonetheless have lasting impact on these processes over the annual cycle.

INTRODUCTION

Seagrasses are highly productive, dominant features in many shallow, coastal environments. In addition to providing habitat for a complex assemblage of organisms (Lubbers et al. 1990, Connolly 1994, West & King 1996), seagrass communities can also influence biogeochemical cycling on both local (Caffrey & Kemp 1990, Lee & Dunton 2000, Risgaard-Petersen & Ottosen 2000, Azzoni et al. 2001) and system-wide scales (Kemp et al. 1984). Enhanced deposition (e.g., Ward et al. 1984), trapping (e.g., Gacia & Duarte 2001) and degradation of particulate organic matter increase water clarity and fuel regeneration of inorganic nutrients (e.g., Kenworthy et al. 1982, Harrison 1989, Pollard & Moriarty 1991). Excretion of both O₂ (e.g., Sand-Jensen et al. 1982) and dissolved organic matter (DOM) (e.g., Penhale & Smith 1977, Wetzel & Penhale 1979) from plant leaves may affect primary production, respiration, and nutrient cycling in the overlying water column. Root release of O₂ may enhance processes such as nitrification (e.g., Caffrey & Kemp 1991) and may also oxidize phytotoxic, reduced metabolites, such as sulfides, thus preventing their accumulation in the rhizosphere and plant tissues (Pedersen et al. 1998, Lee & Dunton 2000). Root release of DOM (Wetzel & Penhale 1979, Koepfler et al. 1993, Kaldy et al. 2006) may stimulate anaerobic microbial processes including ammonification (Caffrey & Kemp 1990, Lopez et al. 1995) and sulfate reduction (e.g., Holmer et al. 2001).

Florida Bay is a large, shallow estuary that has historically supported extensive populations of seagrasses. The bay is subdivided into numerous shallow (< 3 m) basins by a series of interconnected carbonate mudbanks that restrict water advection between adjacent basins (Powell et al. 1989). Basins are typically characterized by shallow, consolidated sediments comprised of well-sorted material, whereas banks are characterized by deeper, less consolidated, fine sediments (Holmquist et al. 1989). While seagrasses appear to thrive in both basin and bank sediments, plant

characteristics and overall biomass may differ between these sediments (Zieman et al. 1999) and these differences may, in turn, lead to differences in sediment biogeochemical rates between bank and basin seagrass communities.

In the late 1980's, Florida Bay experienced a large, unprecedented dieback of *T. testudinum* (Zieman et al. 1989, Robblee et al. 1991), which led to the formation of large unvegetated patches of sediment throughout the bay. Initial losses of seagrass occurred on the margins of the banks and progressed down into basin communities (Robblee et al. 1991). Following the initial dieback, intense phytoplankton blooms and increased sediment resuspension led to secondary dieback by reducing the amount of light available for seagrass growth (Phlips et al. 1995). While the dieback rate has slowed considerably since the mid-1990s, *T. testudinum* communities in various regions of the bay (e.g., Barnes Key) continue to exhibit signs of active dieback. Most of the hypothesized mechanisms regarding the cause of seagrass dieback involve interactions between seagrass plants and sediment biogeochemical cycling of organic matter and nutrients. Factors that may have contributed to dieback include hypersalinity, hyperthermia (Zieman et al. 1999), hypoxia and sulfide toxicity (Carlson et al. 1994, Borum et al. 2005), and pathogenic infection (Durako & Kuss 1994).

In this study, I sought to quantify general differences in plant characteristics and sediment biogeochemistry between basin and bank *T. testudinum* communities in Florida Bay. In addition, I investigated the consequences of seagrass dieback on sediment biogeochemical cycling in Barnes Key. Although there is substantial information and speculation as to the cause of dieback, there is very little known about its consequences on sediment nutrient cycling. Accumulation and decomposition of plant organic matter associated with dieback may lead to enhanced ammonification and sulfate reduction. Also, stressed plants experiencing dieback symptoms may exhibit lower productivity, and consequently release less O₂ and DOM to the rhizosphere. A

reduction in amount of free oxygen in the sediments may lead to lower nitrification-denitrification rates and changes in porewater sulfide pools.

METHODS

Site description and study design. Florida Bay is a large (2200 km²) shallow marine ecosystem occupying the area south of the Everglades and northwest of the Florida Keys (Fig. 3.1). The system is characterized by clear, oligotrophic water columns and carbonate sediments that support extensive populations of seagrass and benthic macroalgae. Numerous natural mudbank formations and small mangrove islands restrict water exchange within the bay, resulting in the development of discrete, shallow basins that often have distinct salinity and nutrient regimes compared to adjacent basins.

This study was focused in two adjacent basins, Rabbit Key and Barnes Key, located in the central region of Florida Bay (Fig. 3.1). At both sites, mean water depths were approximately 2 m in the basins and 0.5 m on the banks. Although both sites were dominated by nearly monospecific *Thalassia testudinum* meadows, the seagrass communities in the two basins were quite different. The seagrass in Rabbit Key were relatively healthy and dense, extending in a continuous meadow from the center of the basin onto the banks. Seagrasses in Barnes Key were also quite dense, however, plant beds on the bank appeared less healthy and were interrupted by large (~ 1 – 5 m diam.) unvegetated areas that apparently evolved from periods of active dieback (Fourqurean & Robblee 1999). These two locations provided an ideal natural experiment for comparing seagrass communities and associated biogeochemical processes on the banks versus basins, as well as in healthy communities versus those experiencing dieback.

Throughout this study, I employed a stratified research approach to investigate a combination of small-scale and large-scale processes. In July 2001, I examined differences in general plant (e.g., biomass, tissue nutrient content, leaf length and leaf

width) and sediment (e.g., bulk density and sediment porewater nutrient content) characteristics along a 4-point transect from the basin to the bank in Rabbit Key. Benthic nutrient fluxes and depth profiles of sediment microbial activities were measured in both basin and bank *T. testudinum* communities at Barnes Key and Rabbit Key in January and June 2003. Sediment microbial activities and porewater nutrient concentrations were also measured at Barnes Key in September 2002 during a period of active dieback. In addition, we analyzed continuous observations of dissolved O₂ at both sites during a 5-day period in August 2003 to estimate daytime O₂ production, respiration, and net ecosystem production in *T. testudinum* communities.

Biomass characteristics. Estimates of plant biomass were obtained by collecting replicate (n = 3) plant-sediment cores (diam. = 15.25 cm, h = 40 cm) from each site. Upon collection, plant biomass was gently rinsed with freshwater through a 0.5 cm mesh screen to remove all sediment and epiphytic material. Biomass samples were stored in a refrigerator for up to 48 h and were sorted into live and dead, above- and belowground tissues. All plant biomass was dried at 60°C to a constant weight, ground, and analyzed for tissue C, H, N, and P content (Short 1990). Leaf length (cm) and width (cm) were also measured on plants collected in Rabbit Key in July 2001.

Sediment characteristics. Water content and bulk density were determined for sediments collected from each site. Sediment cores (diam. = 15 cm) were sectioned into 3-cm vertical intervals to a depth of 15 cm. Plant biomass and shells were removed from each section and the remaining sediment was gently homogenized. A known volume of sediment was packed into a 50-mL polycarbonate centrifuge, weighed, and dried at 60°C to constant weight. Once dry, the sediments were reweighed and sediment water content was determined by the difference between wet and dry weight.

Bulk density was calculated by dividing sediment dry weight (g) by wet sediment volume (mL).

On select occasions, sediment porewater concentrations were determined by extraction of sediment cores (diam. = 10.2 cm) collected at each site. Cores were sectioned into depth intervals of 0-0.5, 0.5-1, 1-2, 2-3, 3-5, 5-7, 7-9 and 9-11 cm under a N₂ atmosphere to maintain redox conditions within each section. Sediment from each section was packed into a 50 mL polycarbonate centrifuge tube and was centrifuged at 3000 rpm for 10 min to separate porewater from the sediment. The resulting supernatant was filtered (0.45 µm) and frozen for subsequent NH₄⁺ and PO₄³⁻ analyses (Parsons et al. 1984). Prior to freezing, a 1 mL sub-sample of the filtered porewater was treated with diamine and stored at room temperature for sulfide analysis (Cline 1969).

Benthic nutrient fluxes. Sediment cores were collected from seagrass communities on the bank and basin of each site within a 1-week period during both winter (January) and peak summer growing season (June) of 2003. Replicate intact plant and sediment cores (n=3) were collected from each site using clear acrylic cylindrical cores (diam. = 15 cm, h = 47 cm). Each core contained approximately 15 cm of sediment height that was overlain by approximately 20 cm of water column. Immediately upon collection, each core was fitted with a rubber boot and sealed with a stainless steel hose clamp to prevent leakage of sediment. Cores were placed randomly in flow-through incubators under ambient temperature within 4 h of collection. Leaves and shoots were cleaned of loosely attached epiphytic material by hand, and plant material that had been severed during collection was also removed. The cores were then filled with site water to replace any that had been displaced during transport and were aerated using aquarium pumps to ensure full oxygen saturation of the water column. One layer of neutral-density screening was placed over each incubator to simulate natural light levels. The cores

were then allowed to equilibrate for a minimum of 8 h in the incubators prior to the beginning of the experiment.

After midnight, the cores were gently sealed with clear acrylic lids to remove headspace and bubbles. Water column mixing was achieved by fitting each core with a magnetic stirbar that was continuously stirred via a central motor-driven magnetic turntable. Water samples were collected from a sampling port on the lid with simultaneously addition of site water to replace sample water volume. Water samples for O₂ and N₂ gases were taken at 30-45 min intervals beginning at approximately 4 h before dawn (dark) and continuing until approximately 4 h after dawn (light). Water samples for NO₃⁻, NH₄⁺, PO₄³⁻, dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) were taken at 1 h intervals over the entire course of the incubation. With this experimental design, we were able to measure both light and dark fluxes as well as the transition between them without disrupting plant and microbial circadian rhythms. The short intervals between gas sampling precluded the formation of bubbles in the cores during the experiment, as bubbles may have interfered with sample analysis (Kana et al. 1994).

Water samples taken during the incubation for N₂ and O₂ gases were collected in 8 mL glass vials, immediately treated with mercuric chloride (HgCl₂), capped, and stored in ambient water. The samples were analyzed within two weeks of collection for the appearance/ disappearance of O₂ and N₂ relative to Ar concentrations in the water column using a membrane inlet mass spectrometer (Kana et al. 1994). Because of the absence of headspace within the cores, changes in water column O₂ and N₂ concentrations in the light and dark were attributed to processes associated with the plants, sediments, and overlying water column. Increases in O₂ in the light and dark were attributed to photosynthetic and respiratory processes, respectively. Increases in

dark N_2 concentrations were attributed to release of N_2 from the sediments signifying denitrification (Kana et al. 1998).

Water samples for NH_4^+ , NO_3^- , PO_4^{3-} , DOC, and DON concentrations were passed through ashed 0.7- μm GF/F filters and were immediately frozen. Nitrate and total nitrogen samples were analyzed colorimetrically after cadmium-catalyzed reduction of NO_3^- to NO_2^- (Parsons et al. 1984). NH_4^+ and PO_4^{3-} samples were also analyzed colorimetrically following Parsons et al. (1984). DON concentrations were obtained by subtracting inorganic nitrogen from total nitrogen concentrations. DOC concentrations were determined using a Shimadzu TOC 5000 analyzer (Sugimura & Suzuki 1988). Flux rates were determined by calculating the slope of the regression for changes in concentration over time in both light and dark periods. Significant, linear trends were observed in almost all cases. Positive fluxes represent a net flux from the plants and/or sediment into the water column, while negative flux values represent a net flux into the plants and/or sediment.

Following the incubation, cores were sampled for sediment chlorophyll-*a* and plant biomass. Sediment chlorophyll-*a* samples were collected by inserting a cut-off plastic syringe (diam. = 0.7 cm) to a depth of 1 cm and extruding the sediment into a foil-wrapped 15-ml polycarbonate centrifuge tube. Sediment samples were immediately frozen and were analyzed within 1-2 months of sample collection. Sediment samples for chlorophyll-*a* analysis were thawed, extracted with 90% acetone for 24 h and analyzed using a Turner Fluorometer (Parsons et al. 1984). Following sediment sample collection, plant biomass was processed according to the procedures outlined above.

Sediment microbial activities. In addition to conducting sediment-water exchange experiments, vertical profiles of sediment microbial activities and belowground biomass distribution were measured at each site in September 2002 (Barnes only) and January,

June and August 2003. Intact plant and sediment cores (n=3) were partitioned into 3-cm sections to a depth of 15 cm to yield 5 sections at average depths of 1.5, 4.5, 7.5, 10.5, and 12.5 cm. Previous observations revealed that the majority (~75-90%) of root and rhizome biomass at these sites was found in the top 15 cm of sediments (Nagel, pers. obs.). Each section was sorted by hand to remove plant biomass, macrofauna, and shells. Plant biomass was processed as outline above to generate depth profiles of root/rhizome biomass. The remaining sediment was gently homogenized and used to determine sediment water content and bulk density of each section, as well as to determine rates of potential nitrification and ammonification.

Ammonification rates were determined using a technique described by Aller and Yingst (1980) in which the accumulation of NH_4^+ over time is measured in packed tubes of anaerobically-incubated sediment. Homogenized sediment from each depth-interval was packed into triplicate 15 mL polycarbonate centrifuge tubes, which were incubated anaerobically in sulfidic mud for 10 d. At 1, 7 and 10 d, one replicate from each depth was centrifuged and the resulting supernatant was filtered (0.45- μm) and frozen for subsequent NH_4^+ analysis (Parsons et al. 1984).

Potential nitrification rates were measured as the production of NO_3^- over time in aerobic sediment slurries following Caffrey and Kemp (1990). Approximately 1 g of sediment from each section was incubated in 25 mL of filtered (0.7- μm) site water in a 50 mL polycarbonate centrifuge tube. Each tube was amended with NH_4Cl to bring NH_4^+ concentrations to 1 mM. Slurries were continuously mixed using a shaker table to maintain aerobic conditions for 24-48 h at 25°C. At 2 and 40 h, slurries from replicate flasks were centrifuged and the water was filtered (0.45- μm) and frozen for subsequent NO_3^- analysis (Parsons et al. 1984). Previous trials indicated that nitrification rates were linear over a 48 h period (data not shown).

Ecosystem production and respiration. To further investigate differences in the *T. testudinum* communities in Rabbit and Barnes Keys, I obtained continuous measurements of dissolved O₂ concentrations in the water column overlying the seagrass beds over a 5-d period in August 2003. Open-water dissolved O₂ concentrations, temperature, and salinity were recorded at 10-min intervals over this period using a multi-parameter data logging system (YSI 600 XLM) equipped with pulsed-O₂ electrodes, thermistors, and conductivity sensors. Instruments were deployed at each site at a depth of 0.75 m above the sediment surface (approx. 1.5 m below the water surface) so that they were situated just above the seagrass canopy. Instrument fouling was not observed during the deployment.

Continuous records of dissolved O₂, temperature, and salinity were used to calculate daytime apparent production (P_a) and nighttime dark respiration (R) (e.g., Odum & Hoskins 1958). Assuming hourly respiration rates are the same during the day and night, I calculated a nominal rate of gross photosynthetic production P_d as the sum of hourly P_a and R (absolute values) adjusted for the daylight period of the day. Volumetric rates were converted to vertically-integrated rates by multiplying by the water column depth and vertically-integrated rates were corrected for O₂ exchange across the air-water interface assuming a constant air-sea exchange rate of 0.5 g O₂ m⁻² h⁻¹ (atm)⁻¹. A constant air-sea exchange rate can be used in the absence of local wind data (Kemp & Boynton 1980) and 0.5 g O₂ m⁻² h⁻¹ (atm)⁻¹ is a reasonable estimate for shallow estuaries (Kremer et al. 2003). The diel integral of P_a and R provides a measure of net ecosystem production (NEP), which can be used to indicate the trophic status of the system. Positive values of NEP represent net autotrophy, whereas negative values represent net heterotrophy.

RESULTS

Variations in biomass and sediment properties

Biomass characteristics

In general, *T. testudinum* biomass was higher and exhibited more variability in bank communities relative to basin communities (Table 3.1). Both aboveground biomass ($p < 0.026$) and total dead biomass ($p < 0.025$) were significantly higher in bank versus basin communities. Aboveground biomass remained fairly constant or increased slightly from winter to summer in the basin communities. In contrast, bank communities exhibited a decline in aboveground biomass over this same time period at both sites. Overall, aboveground biomass was statistically similar ($p < 0.19$) between Barnes Key and Rabbit Key regardless of season. However, both belowground biomass ($p < 0.002$) and total biomass ($p < 0.003$) were significantly higher in Barnes Key compared to Rabbit Key (Table 3.1). Furthermore, there was a greater abundance ($p < 0.05$) of dead material in Barnes Key relative to Rabbit Key.

In September 2002, an active dieback event occurred on the bank in Barnes Key. Plant leaves appeared yellow and unhealthy, and minor agitation caused many shoots to separate entirely at the meristem. Necrotic lesions were also observed on many leaves. While biomass in the basin did not vary between January and September, overall belowground biomass on the bank was lower, although not significantly, in September (850 ± 257 g dry wt m^{-2}) compared to January (1217 ± 150 g dry wt m^{-2}) (Table 3.1). Depth profiles of belowground biomass followed a similar pattern, with lower biomass at all sediment depths in September (Fig. 3.2). Belowground biomass was significantly lower in September at intervals of 3-6 cm ($p < 0.016$) and 6-9 cm ($p < 0.05$) relative to biomass in January.

Plant morphology and biomass characteristics also differed between bank and basin communities. Leaf length ($p < 0.003$) and width ($p < 0.01$) significantly increased

along a transect from basin to bank in Rabbit Key (Fig. 3.3). Root to shoot ratios decreased significantly ($p < 0.05$) along this same transect, with a greater proportion of total biomass in belowground tissues in the basin relative to the bank. This pattern of longer leaves and lower root to shoot ratios on the bank was also regularly observed throughout the year at both Rabbit and Barnes Keys (Table 3.1).

Leaf nutrient content between basin and bank communities was more variable. Nutrient content in *T. testudinum* leaves ranged from 26.6 - 37.1%, 0.76 - 2.96%, and 0.03 - 0.18% for C, N, and P, respectively, well within the range of values previously reported for Florida Bay (Fourqurean et al. 1992). In July 2001, *T. testudinum* plants collected from Rabbit Key bank had higher nitrogen and phosphorus content relative to basin plants (Fig. 3.4), and this difference was statistically significant ($p < 0.05$) for belowground tissues. A similar trend was observed in plants collected in January and June 2003 from Barnes Key and in June 2003 in Rabbit Key, but these differences were not significant ($p > 0.05$). Ratios of C:N, N:P, and C:P showed considerable variability, ranging from 13.9-45.6, 18.8-79.3, and 497-2431, respectively. Plant nutrient content (%N and %P) and C:N and C:P were significantly higher ($p < 0.005$) in January relative to June 2003.

Sediment characteristics

At both sites, bank sediments were typically less consolidated with significantly lower bulk densities ($p < 0.0001$) and higher sediment water content ($p < 0.0001$) compared to basin sediments (e.g., Fig.3.5). Bulk densities increased with sediment depth and ranged from 0.08 to 0.30 g cm⁻³ and 0.21 to 0.69 g cm⁻³ on the banks and basins, respectively. Mean sediment water content ranged from 75 – 92% on the banks and 54 – 84% in the basins, with water content decreasing with increasing sediment

depth (Fig. 3.5). There were no significant differences in either bulk density or sediment water content between Rabbit and Barnes Keys.

Porewater nutrients were lowest in the basins and increased gradually toward the banks at all sites. In general, sediment porewater NH_4^+ , S^{2-} , and PO_4^{3-} concentrations were 2-4 fold higher at all depths in bank sediments compared to basin sediments (Fig. 3.6) and NH_4^+ and S^{2-} concentrations were significantly higher ($p < 0.001$) on the bank. Relatively high concentrations of NH_4^+ ($\sim 400 \mu\text{M}$) and PO_4^{3-} ($\sim 5 \mu\text{M}$) were observed at depth in bank sediments at both sites (Fourqurean et al. 1992). Sulfide concentrations were also high ($\sim 1.5 \text{ mM}$) in bank sediments but these values are well within the range of concentrations reported by other studies in Florida Bay (e.g., Carlson et al. 1994). In addition, porewater nutrient NH_4^+ and S^{2-} concentrations were significantly higher ($p < 0.03$) in Barnes banks sediments during an active dieback event in September 2002 relative to the following June (Fig. 3.7).

Patterns in relationships between porewater constituents varied between the two sites. Porewater NH_4^+ concentrations were positively related to PO_4^{3-} concentrations at both sites (Fig. 3.8a); however, the slope of the regression of NH_4^+ on PO_4^{3-} was 2-fold higher in Rabbit ($y = 112x + 22$, $r^2 = 0.66$, $p < 0.0001$) compared to Barnes Key ($y = 53x + 158$, $r^2 = 0.50$, $p < 0.0001$). Positive relationships were also observed between NH_4^+ and S^{2-} ($y = 0.17x + 17$, $r^2 = 0.36$, $p < 0.0001$) (Fig. 3.8b) concentrations and between PO_4^{3-} and S^{2-} concentrations ($y = 0.002x - 0.091$, $r^2 = 0.57$, $p < 0.0001$) (Fig. 3.8c) at Rabbit Key. In contrast, the considerable variability in these relationships at Barnes Key rendered them non-significant.

Sediment microbial activities

Nitrification activity ranged from 0 to $89 \text{ nmol cm}^{-3} \text{ d}^{-1}$, and rates were significantly higher ($p < 0.0001$) in basin sediments relative to those collected on the bank.

Nitrification potential on the bank in Barnes Key during the dieback event in September was significantly lower ($p < 0.009$) than rates observed in January (Fig. 3.9). Seasonal variability was observed on the bank at both sites with highest rates occurring in August. Basin communities exhibited little variability in nitrification activity throughout the year. There was no significant difference in nitrification activity between Barnes and Rabbit Keys in January and June 2003.

Ammonification rates ranged from 4.3 to 538 $\text{nmol cm}^{-3} \text{d}^{-1}$, with rates in Barnes Key significantly exceeding ($p < 0.043$) those in Rabbit Key. Similar to nitrification, seasonal patterns were also observed in ammonification rates. At all sites, rates were significantly higher ($p < 0.0001$) in August relative to January and June. On the bank in Barnes Key, ammonification rates were significantly higher ($p < 0.0001$) in September during the dieback event compared to other months.

Patterns in benthic production and respiration

Patterns in benthic O_2 cycling were consistent across both seasons at both sites, with production observed in the light and consumption observed in the dark (Table 3.2). Benthic O_2 production (P_a = net daytime O_2 release) and respiration (R = net O_2 consumption in dark) as measured in sediment core incubations ranged from 0.7 to 10.2 $\text{mmol m}^{-2} \text{h}^{-1}$ and 1.6 to 6.4 $\text{mmol m}^{-2} \text{h}^{-1}$, respectively. These rates compare well to similar rates measured in *T. testudinum* communities (Ziegler & Benner 1998). At both Barnes and Rabbit Key, significantly higher ($p < 0.05$) rates of benthic O_2 production were observed in January compared to June (Table 3.2). Neither benthic O_2 production nor respiration differed significantly ($p > 0.10$) between bank and basin communities. Biomass-specific rates of benthic community production (P/B) and respiration (R/B) ranged from 0.9 to 10.4 $\mu\text{mol O}_2 \text{g}^{-1} \text{dry weight h}^{-1}$ and 1.5 to 6.2 $\mu\text{mol O}_2 \text{g}^{-1} \text{dry weight h}^{-1}$, respectively. In general, P/B decreased slightly and R/B increased slightly, albeit

insignificantly, from January to June. The lowest values of P/B were observed in June on the bank in Rabbit Key. Photosynthetic O₂ production and respiration were not consistently correlated with plant biomass within or across sites.

In general, benthic communities associated with *T. testudinum* at Barnes and Rabbit Key were net autotrophic over the diel cycle, with mean P_a:R ratios greater than 1.0 (Table 3.1). Net daily benthic O₂ production in these communities ranged from -36 to 98 mmol O₂ m⁻² d⁻¹, and mean rates were significantly lower ($p < 0.01$) on the bank in Rabbit in June compared to January (Table 3.1). P_a:R ratios were lower in June despite higher overall O₂ production. The only instance of net heterotrophy (P_a:R = 0.3) in these communities occurred in June 2003 on Rabbit Key bank.

Benthic nutrient fluxes

Bottom water column concentrations of NH₄⁺ and NO₃⁻ (initial values in flux core incubations) ranged from 0.7 to 10.7 μM and 0.06 to 10.1 μM, and no consistent differences were observed in concentrations between the two sites. Benthic fluxes of inorganic nitrogen were highly variable, with no clear patterns in consumption or production over the diel cycle during either January or June. Ammonium fluxes ranged from -131 to 46 μmol m⁻² h⁻¹ in the light and -399 to 97 μmol m⁻² h⁻¹ in the dark. Nitrate fluxes showed similar variability, ranging from -39 to 103 μmol m⁻² h⁻¹ and -246 to -1.3 μmol m⁻² h⁻¹ in the light and dark, respectively. There were no significant differences in fluxes of inorganic nitrogen between bank and basin communities, Barnes and Rabbit Key, or January and June 2003. The vast majority of mean net fluxes of NH₄⁺ and NO₃⁻ were negative, ranging from -1.62 to 0.03 mmol m⁻² d⁻¹ for NH₄⁺ and -0.76 to -0.03 mmol m⁻² d⁻¹ for NO₃⁻. Concentrations of PO₄³⁻ were below detection limits at all sites so that no fluxes could be calculated.

Net denitrification, as measured by dark N_2 flux, was observed in June at both Rabbit and Barnes Keys. Mean rates in June ranged from 61 to 267 $\mu\text{mol } N_2 \text{ m}^{-2} \text{ h}^{-1}$ and there were no significant differences ($p > 0.05$) in rates between sites or between bank and basin communities. Rates of net denitrification in January were not significantly different from zero at either site.

Benthic fluxes of DOM

Like fluxes of inorganic nitrogen, benthic fluxes of DOC and DON in *T. testudinum* communities were highly variable over the course of the day and there were no consistent differences between sites or between bank and basin communities (Table 3.2). In January, I observed DOC production during the day and consumption at night at nearly all sites. However, the pattern in June was less clear as DOC production occurred during the day at some sites and during the night at other sites (Fig. 3.10). Benthic DON fluxes were typically more variable and were not consistently coupled with DOC production and consumption. The absence of clear diel patterns in production and consumption of DOC and DON as well as an apparent uncoupling between the two are in direct contrast with similar studies measuring fluxes in *T. testudinum* communities in Sunset Cove, Florida Bay (Table 3.2) (Chapter 2). Production and consumption of both DOC and DON appeared to be fairly balanced, as *T. testudinum* communities in Barnes and Rabbit Key exhibited neither net production nor consumption of DOC or DON over the diel period.

Ratios of DOC fluxes to DON fluxes ranged from 0.43 - 102 and were significantly higher ($p < 0.0002$) in Rabbit Key relative to ratios observed in Barnes Key. Similarly, ratios of DOC to O_2 production were significantly higher ($p < 0.025$) in Rabbit Key relative to Barnes Key, ranging from 0.03 to 20. Both DOC:DON ($p < 0.004$) and DOC: O_2 ($p < 0.025$) significantly higher in June compared to January at both sites.

From January to June, the ratio of DOC:DON increased from 3.2 ± 0.9 to 17 ± 6.3 in Barnes Key and 22 ± 9.6 to 57 ± 9.7 in Rabbit Key. Ratios of DOC:O₂ followed a similar trend increasing from 0.17 ± 0.05 to 1.16 ± 0.4 and 0.75 ± 0.43 to 5.8 ± 3.0 from January to June in Barnes Key and Rabbit Key, respectively.

O₂ Cycling & Net Ecosystem Production

Deployment of dissolved O₂ sensors in August 2003, revealed strong diel variations in O₂ concentrations in the water column overlying *T. testudinum* communities at both sites in Florida Bay (Fig. 3.11). Concentrations ranged from 0.13 – 0.21 mmol O₂ L⁻¹ in Barnes Key and 0.17 – 0.32 mmol O₂ L⁻¹ in Rabbit Key, and mean O₂ concentrations over the 5 d period were significantly lower ($p < 0.0001$) in Barnes Key (0.16 ± 0.001 mmol O₂ L⁻¹) compared to Rabbit Key (0.23 ± 0.002 mmol O₂ L⁻¹). Percent saturation of dissolved O₂ in the water column was also lower ($p < 0.0001$) in Barnes Key, ranging from 64 – 112% (mean = $85.0 \pm 0.45\%$). Oxygen concentrations in Rabbit Key ranged from 86 – 166% (mean = $121 \pm 0.80\%$) of saturation. Temperature (~29.8°C) and salinity (~38.4 ppt) were similar between the two sites over the 5 d period.

Rates of apparent daytime production (P_a) and nighttime respiration (R) varied from day to day at both sites in Florida Bay, ranging from 50 to 338 mmol O₂ m⁻² d⁻¹ and 100 to 192 mmol O₂ m⁻² d⁻¹, respectively. While mean nighttime respiration rates were similar ($p < 0.1299$) between the two sites, mean P_a was significantly higher ($p < 0.045$) in Rabbit compared to rates measured in Barnes Key (Fig. 3.11). Lowest daily rates of P_a coincided with days of lowest integrated irradiance (e.g., Fig. 3.9). Overall, these rates compare well with rates reported in previous studies that were conducted in similar *T. testudinum* communities (Ziegler & Benner 1998).

Rates of net ecosystem production (NEP) in *T. testudinum* communities at both sites exhibited day-to-day variability (Table 3.3) and rates ranged from -72 to 172 mmol O₂ m⁻² d⁻¹. Daily NEP rates in Rabbit Key were positive and P_a:R ratios were greater than 1.0 (Table 3.3) In contrast, negative NEP rates and P_a:R ratios were less than 1.0 on three of the days in Barnes Key (Table 3.3). Mean values of both NEP and P_a:R were significantly lower ($p < 0.0001$) in Barnes Key relative to Rabbit Key.

DISCUSSION

Implications of bank and basin characteristics for seagrass dieback

The abundance of shallow basins isolated by interconnected carbonate mudbanks are a prominent feature of the unique geological setting of Florida Bay. *T. testudinum* is widely distributed throughout Florida Bay, covering both basin and bank sediments (Zieman et al. 1989). Basins are characterized by deeper water and a shallow layer of consolidated sediments overlaying the bedrock, whereas bank sediments are typically deeper and less consolidated. Banks appear to be sites of sediment focusing, and, in this study, water content was higher and bulk density was lower in bank sediments, indicating a lesser degree of consolidation in these sediments (Fig. 3.12). This pattern of sediment focusing from deeper basins to the shallower banks is unusual for shallow coastal environments (Colman et al. 2002). Although it is unclear whether physical or biological processes are responsible for initiating mudbank formation, it is apparent that seagrasses may be influential for mudbank development and stability (Ginsburg 1956, Prager and Halley 1999). Seagrasses may play a role in mudbank development and stability by: 1) attenuating wave energy and enhancing deposition of fine particles (Ginsburg 1958, Prager & Halley 1999); 2) binding and stabilizing the sediment surface (e.g., Ginsburg 1956); and 3) supporting organisms

such as mollusks which contribute to biogenic production of carbonate sediments (Bosence 1989, Prager & Halley 1999).

Differences in sediment characteristics and water depth between banks and basins may influence the growth and productivity of *T. testudinum* in Florida Bay (e.g., Zieman et al. 1989). A survey of plant morphology and tissue nutrient content revealed clear differences between bank and basin *T. testudinum* communities (Fig. 3.12). Mean length and width of seagrass leaves increased (Fig. 3.2) and plant tissue C:N decreased (Fig. 3.3) along a transect from the basin to bank, suggesting higher nutrient availability (Powell et al. 1989) in bank sediments. Indeed, porewater NH_4^+ and PO_4^{3-} concentrations were significantly higher in bank sediments (Fig. 3.6). Enhanced trapping of particulate organic matter on the banks relative to the basins (Ginsburg 1958) could lead to higher rates of nutrient regeneration on the banks (Kenworthy et al. 1982), and consequently, elevated porewater nutrient concentrations. Bank communities also had a greater abundance of dead plant material (Table 3.1). Decomposition of this plant material could also stimulate nutrient regeneration within these communities (Harrison 1989, Holmer et al. 2001).

In addition to stimulating nutrient regeneration, enhanced trapping and degradation of organic matter may fuel sulfate reduction in bank sediments (Fig. 3.12). Porewater sulfide concentrations were significantly elevated on the banks relative to basin sediments (Fig. 3.6), implying higher rates of sulfate reduction in these sediments. The accumulation of sulfide, a potent phytotoxin, has been recognized as causing mortality in seagrass beds (e.g., Carlson et al. 1994) and intrusion of sulfide into plant tissues can negatively impact plant metabolic processes (Goodman et al. 1995, Koch & Erskine 2001). Hyperthermia and decreased water column O_2 concentrations due to high sediment respiratory demands on the bank relative to the basin (Table 3.2) may further increase seagrass susceptibility to sulfide toxicity (e.g., Koch et al. 2007).

Intrusion of sulfide into *T. testudinum* tissues has been shown to occur at night when water column and internal plant O₂ concentrations are low (Borum et al. 2005). Consequently, high sediment sulfide concentrations on bank sediments may pose a threat to seagrass survival.

Observations of initial seagrass dieback in Florida Bay suggest that it initiated in bank communities before radiating outward to basin communities (Robblee et al. 1991). Seagrass dieback may result from complex interactions with overcrowding leading to increased susceptibility to disease (Durako 1994), hypersalinity, hyperthermia, and sulfide toxicity (Zieman et al. 1999, Koch et al. 2007). Once loss of seagrass habitat occurs, the flocculent sediments on the bank may be readily susceptible to resuspension, which can lead to further loss of seagrasses through reduction in water clarity (e.g., Kelble et al. 2005). Resuspension of bank sediments may also stimulate productivity of bacteria and phytoplankton in the water column, through release of nutrients and DOM stored in sediment to the overlying water (Lawrence et al. 2004, Zhang et al. 2004). Stimulation of planktonic productivity contributes to further reductions in water clarity, representing a negative feedback mechanism for seagrass survival (Zieman et al. 1999). Thus, the inherent properties of bank communities, such as high sediment sulfide concentrations and respiratory demand and readily resuspended sediment may make them more vulnerable to experience dieback events compared to basin communities.

Comparison of benthic fluxes in Barnes and Rabbit Keys

Benthic O₂ fluxes in the *T. testudinum* exhibited clear diel patterns but did not consistently differ between bank and basin communities or between Rabbit and Barnes Key. Although net O₂ production in these communities increased from January to June, P_a:R ratios decreased over this time, indicating an increased importance of heterotrophic

processes in summer. During a dieback event in August 2003, open-water estimates of both P_a and NEP were significantly lower at the *T. testudinum* community in Barnes Key compared to the relatively healthy seagrass bed in Rabbit Key (Fig. 3.11). Percent saturation of O_2 in the water column rarely reached above 100% and negative values of NEP were measured on 3 out of 4 days. Negative values of NEP and P_a :R ratios < 1.0 imply that heterotrophic processes were dominating ecosystem metabolism during dieback. This is consistent with higher sediment respiratory demands associated with a greater abundance of decomposing plant material in dieback areas (Carlson et al. 1994). Furthermore, a shift to net heterotrophy implies that there may be little excess O_2 available to support oxidation of rhizosphere sediments (Gacia et al. 2005), resulting in a greater potential for sulfide intrusion into plant tissues (Borum et al. 2005). Positive values of NEP measured in January and March 2004 revealed an apparent return to net autotrophy in Barnes Key (data not shown) (Chapter 4). The influence of short-term, seasonal seagrass dieback on net ecosystem metabolism did not appear to extend into winter and spring, but could influence annual estimates of ecosystem production.

Fluxes of inorganic nitrogen were highly variable in the *T. testudinum* communities in Rabbit and Barnes Key (Table 3.2). In a similar study located in eastern Florida Bay (Sunset Cove, Chapter 2), clear diel patterns were observed in N fluxes, with consumption (net influx) consistently observed during the day and regeneration (net efflux) observed at night. While the reason for this lack of agreement is not clear, it is possible that processes other than plant uptake (e.g., enhanced degradation of organic matter) are involved in regulating N cycling at Rabbit and Barnes Keys.

The high net daily uptake rates of NH_4^+ observed in both January and June suggest relatively high N demand within the *T. testudinum* communities in Rabbit and Barnes Key. The lack of seasonal variation in net daily NH_4^+ fluxes may be indicative of strong N-limitation of plant productivity at these sites. Investigations of plant tissue

nutrient content in Florida Bay have shown strong spatial gradients in N content, with N-limitation more prominent in western regions of Florida Bay (Fourqurean et al. 1992, Armitage et al. 2005). Located in the central and western regions, respectively, both Barnes and Rabbit Keys are considered to be N-limited, which could account for the high rates of N uptake. Lower plant N content in June at both sites implies that seagrasses were subject to a higher degree of N limitation in summer; however, N uptake in flux cores did not reflect this pattern.

Phosphate concentrations were below detection limits throughout this study, and this is typical of the high degree of P-limitation observed in seagrass communities in carbonate sediment environments (e.g., Short et al. 1990, Fourqurean et al. 1992). Carbonate sediments are generally a sink for P, thereby reducing P availability in the water column for autotrophs (Jensen et al. 1998, Koch et al. 2001, McGlathery et al. 2001). Enhanced carbonate dissolution through root excretion of O_2 may be a source of P for seagrasses in Barnes and Rabbit Key (Burdige & Zimmerman 2002). Wind-resuspension of relatively nutrient-replete sediments is another potential source of P to seagrass communities in Florida Bay (Lawrence et al. 2004, Zhang et al. 2004). Relationships between porewater NH_4^+ and PO_4^{3-} suggest that Rabbit Key sediments were more P-limited compared to sediments in Barnes Key (Fig. 3.8).

DOC production within *T. testudinum* communities at Barnes and Rabbit Keys generally occurred during the daytime, indicating a potential link to plant O_2 production (Fig. 3.10). Fluxes in DON were more variable and did not appear to be coupled with DOC production. The apparent uncoupling between DOC and DON production is in contrast to patterns observed in a *T. testudinum* community in Sunset Cove (Chapter 2). This pattern implies that DOC and DON were derived from disparate sources, which might include direct exudation of simple photosynthates from seagrass plants (Penhale & Smith 1977, Moriarty et al. 1986), release of free amino acids from senescing plant

material within the beds (Jorgensen et al. 1981), and leaching from deposited organic matter (Barron et al. 2004, Holmer et al. 2004). The lower ratios of DOC:DON fluxes in Barnes Key indicate a comparatively larger DON pool relative to Rabbit, which may fuel both heterotrophic processes and microalgal production in the water column (Chin-Leo & Benner 1991).

Consequence of seagrass dieback to sediment biogeochemistry

In early September 2002, an active dieback event occurred on the bank in Barnes Key. Plant leaves on the bank were brown with necrotic lesions and leaves were observed to detach readily from the apical meristem, a pattern consistent with other observations of seagrass dieback (Zieman et al. 1999). Lower belowground biomass and greater abundance of dead material on the bank in September relative to subsequent months provided further evidence of dieback (Table 3.1). The larger pool of decomposing organic matter appeared to stimulate sulfate reduction in these sediments, as porewater sulfide concentrations were significantly higher in September relative to June (Fig. 3.7). Carlson et al. (1994) attributed high sediment sulfide concentrations prior to a dieback event to the death and decomposition of belowground tissues before evidence was visible in plant shoots. Porewater NH_4^+ and PO_4^{3-} concentrations and sediment ammonification rates were also elevated in September, providing further evidence of larger organic matter pools in bank sediments.

Seagrass dieback appeared to have a negative effect on sediment nitrification rates in September (Fig. 3.9). The lower rates of nitrification observed during the dieback event could be indicative of lower root O_2 release from plant roots. Submersed plants have been shown to excrete O_2 from plant roots into surrounding sediments (Sand-Jensen et al. 1982, Smith et al. 1984, Thursby 1984, Kemp & Murray 1986, Pedersen et al. 1998, Jensen et al. 2005, Frederiksen & Glud 2006). Oxygen released

from plant roots may derive from plant photosynthesis during the day (e.g., Smith et al. 1984) or may diffuse into plant leaves from the surrounding water column at night (e.g., Pedersen et al. 1998). When internal O₂ concentrations are high, O₂ that has diffused through the lacunae, or internal gas space, to plant roots can diffuse into the surrounding sediments, creating an oxidized zone around the roots inhabiting anoxic sediments (Caffrey & Kemp 1991, Jensen et al. 2005, Frederiksen & Glud 2006). Oxidation of rhizosphere sediments provides a microhabitat for obligate aerobic nitrifying bacteria and lead to enhanced nitrification in seagrass sediments (Caffrey & Kemp 1990). However, high sulfide concentrations observed during the dieback event could have led to inhibition of nitrification through toxicity, as nitrifying bacteria are highly sensitive to sulfide toxicity (Joye & Hollibaugh 1995). Inhibition of nitrification can also result from a reduction or loss of the oxic microzone around plant roots. This pattern may be common in highly sulfidic sediments where sulfide oxidation (Lee & Dunton 2000, Holmer & Laursen 2002), a process that can represent a large sink for O₂ in the root zone, consumes O₂ necessary to support nitrifying bacteria. A few studies have suggested that internal O₂ stress also may contribute to loss of the oxidized zone around plant roots and may arise from high plant respiratory demands or low O₂ concentrations in the overlying water column, such as was observed during a dieback event in August 2003 (Fig. 3.11). Under these conditions, intrusion of toxic sulfide into plant tissues (Pedersen et al. 2004, Borum et al. 2005, Calleja et al. 2006, Frederiksen et al. 2006) occurs, representing a negative feedback effect in which sulfide intrusion causes further internal O₂ stress and further reduces favorable conditions for nitrifying bacteria. Reduced nitrification in these sediments could lead to reductions in denitrification, which could have implications for nitrogen cycling within these communities. However, the recovery in seagrass root biomass and nitrification rates in January suggest that the influence of localized dieback on these processes may be short-lived.

Synthesis

Seagrass communities on mudbanks in Florida Bay are sites of enhanced biomass production and nutrient availability relative to basin communities. However, the enhanced deposition, retention, and remineralization of organic matter fuels sulfate reduction within these communities, which may prove to be detrimental to plant survival. Remineralization of decomposing plant material during seagrass dieback led to further accumulation of sulfide in sediment porewaters in bank sediments. High sulfide concentrations may also have led to the reduction or elimination of the oxidized zone around the rhizosphere. This, combined with a reduction in belowground biomass, may explain the observed reductions in nitrification rates during seagrass dieback. Seagrass communities in Barnes Key exhibited a shift in ecosystem production from net heterotrophy during the active dieback event to net autotrophy in winter. Recoveries in biomass, nitrification rates, and net ecosystem production in subsequent months suggest that the influence of seagrass dieback on biogeochemical cycling in Barnes Key was temporary. However, seagrass dieback may have a significant effect on annual estimates of biogeochemical rates in areas where seasonal dieback occurs. Investigations into the influence of dieback on biogeochemical processes such as nitrogen fixation and denitrification may provide further insight into the importance of *T. testudinum* on these processes.

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Table 3.1. Mean aboveground (AG), belowground (BG), total live and dead biomass (g dry wt m⁻²), root to shoot ratios (R/S), benthic net daily O₂ production (mmol m⁻² d⁻¹), production (P/B) and respiration (R/B) per unit biomass (μmol g⁻¹ h⁻¹), and ratios of production to respiration (P_a:R) for *T. testudinum* communities in Barnes Key and Rabbit Key. Biomass samples were collected from bank and basin communities in January 2003 and June 2003 at both sites and also in September 2002 at Barnes Key. "nd" indicates that no data are available.

Site	AG	BG	Total Live	Total Dead	R/S	Benthic NEP	P/B	R/B	Benthic P _a :R
Barnes									
<i>Bank</i>									
Sep	301 ± 64.7	850 ± 257	1150 ± 55.2	1460 ± 287	2.7 ± 0.4	nd	nd	nd	nd
Jan	397 ± 2.29	1217 ± 150	1615 ± 148	815 ± 44	3.1 ± 0.4	14.5 ± 10.5	4.0 ± 0.35	2.4 ± 0.2	1.7 ± 0.1
Jun	314 ± 41.2	1404 ± 93.8	1718 ± 117	1273 ± 147	4.6 ± 0.6	26.6 ± 19.6	3.3 ± 0.34	2.9 ± 0.7	1.3 ± 0.4
<i>Basin</i>									
Sep	221 ± 36.5	1017 ± 158	1239 ± 194	560 ± 47	4.6 ± 0.1	nd	nd	nd	nd
Jan	205 ± 15.6	1150 ± 69.9	1355 ± 320	1018 ± 111	5.7 ± 0.8	38.1 ± 6.4	6.1 ± 1.04	2.9 ± 0.5	2.1 ± 0.1
Jun	246 ± 40.0	1104 ± 226	1350 ± 266	692 ± 185	4.4 ± 0.3	46.8 ± 8.1	5.5 ± 1.89	3.8 ± 1.3	1.5 ± 0.1
Rabbit									
<i>Bank</i>									
Jan	303 ± 53.5	1028 ± 102	1331 ± 131	896 ± 94	3.6 ± 0.7	42.7 ± 11.4	5.1 ± 0.62	1.9 ± 0.2	2.7 ± 0.3
Jun	149 ± 34.9	637 ± 52.4	786 ± 87.3	513 ± 301	4.7 ± 1.0	-26.9 ± 5.64	2.3 ± 0.96	4.7 ± 0.4	0.3 ± 0.1
<i>Basin</i>									
Jan	189 ± 30.4	698 ± 107	887 ± 137	588 ± 92	3.7 ± 0.2	15.8 ± 7.7	5.0 ± 1.08	2.7 ± 0.1	1.8 ± 0.3
Jun	280 ± 33.6	583 ± 120	863 ± 88.6	663 ± 260	2.2 ± 0.7	28.5 ± 36.2	4.9 ± 2.84	2.7 ± 0.6	2.2 ± 1.4

Table 3.2. Mean (\pm SE) rates of light and dark fluxes of NH_4^+ ($\mu\text{mol m}^{-2} \text{h}^{-1}$) and O_2 , DOC, and DON ($\text{mmol m}^{-2} \text{h}^{-1}$) in bank and basin *T. testudinum* communities in Florida Bay. Fluxes were measured in intact plant-sediment cores collected in Barnes Key and Rabbit Key Basins (2003).

Site	O_2		NH_4^+		DOC		DON	
	Jan.	Jun.	Jan.	Jun.	Jan.	Jun.	Jan.	Jun.
Barnes								
Bank								
<i>Light</i>	6.58 \pm 1.10	5.75 \pm 0.81	-73.3 \pm 29.2	23.7 \pm 12.0	-0.80 \pm 0.32	-7.75 \pm 1.76	-0.27 \pm 0.04	-0.53 \pm 0.14
<i>Dark</i>	-4.45 \pm 0.45	-4.86 \pm 0.85	58.2 \pm 19.7	-177 \pm 111	2.58 \pm 0.72	10.49 \pm 5.83	-0.27 \pm 0.04	1.02 \pm 0.52
Basin								
<i>Light</i>	8.11 \pm 1.04	6.50 \pm 0.72	12.7 \pm 11.4	-35.7 \pm 27.5	1.87 \pm 0.77	4.97 \pm 2.99	-0.60 \pm 0.21	0.55 \pm 0.32
<i>Dark</i>	-3.94 \pm 0.46	-3.90 \pm 0.62	-38.4 \pm 13.4	-124 \pm 24.4	-0.90 \pm 0.25	0.36 \pm 5.51	0.30 \pm 0.08	-1.71 \pm 0.79
Rabbit								
Bank								
<i>Light</i>	6.98 \pm 1.53	1.62 \pm 0.51	-22.6 \pm 7.67	-26.9 \pm 8.86	0.79 \pm 0.27	-8.12 \pm 3.70	0.27 \pm 0.05	0.12 \pm 0.03
<i>Dark</i>	-2.62 \pm 0.51	-4.65 \pm 0.59	10.4 \pm 23.8	37.9 \pm 19.7	-2.42 \pm 1.00	17.06 \pm 1.46	-0.19 \pm 0.11	-0.40 \pm 0.17
Basin								
<i>Light</i>	4.21 \pm 0.65	4.00 \pm 2.30	-13.6 \pm 5.857	-19.8 \pm 8.39	5.28 \pm 2.91	-8.05 \pm 0.51	0.18 \pm 0.09	0.17 \pm 0.02
<i>Dark</i>	-2.35 \pm 0.25	-2.43 \pm 0.78	-44.0 \pm 21.9	7.32 \pm 0.80	-4.15 \pm 2.39	8.25 \pm 5.01	0.36 \pm 0.26	-0.18 \pm 0.13

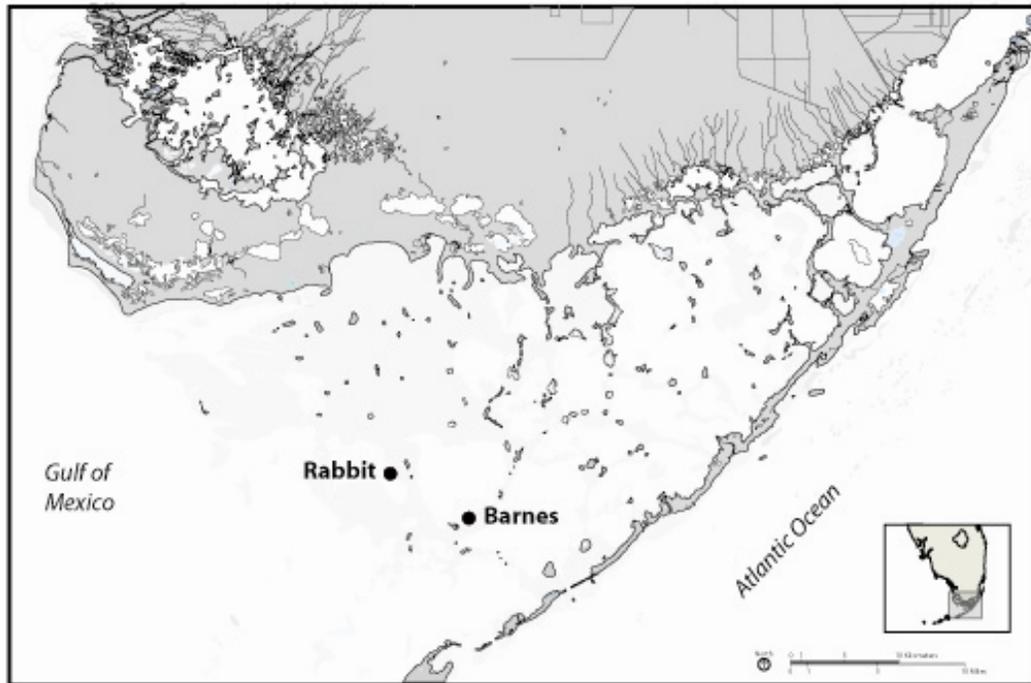


Fig 3.1. Map of Florida Bay showing study sites in Rabbit Key and Barnes Key.

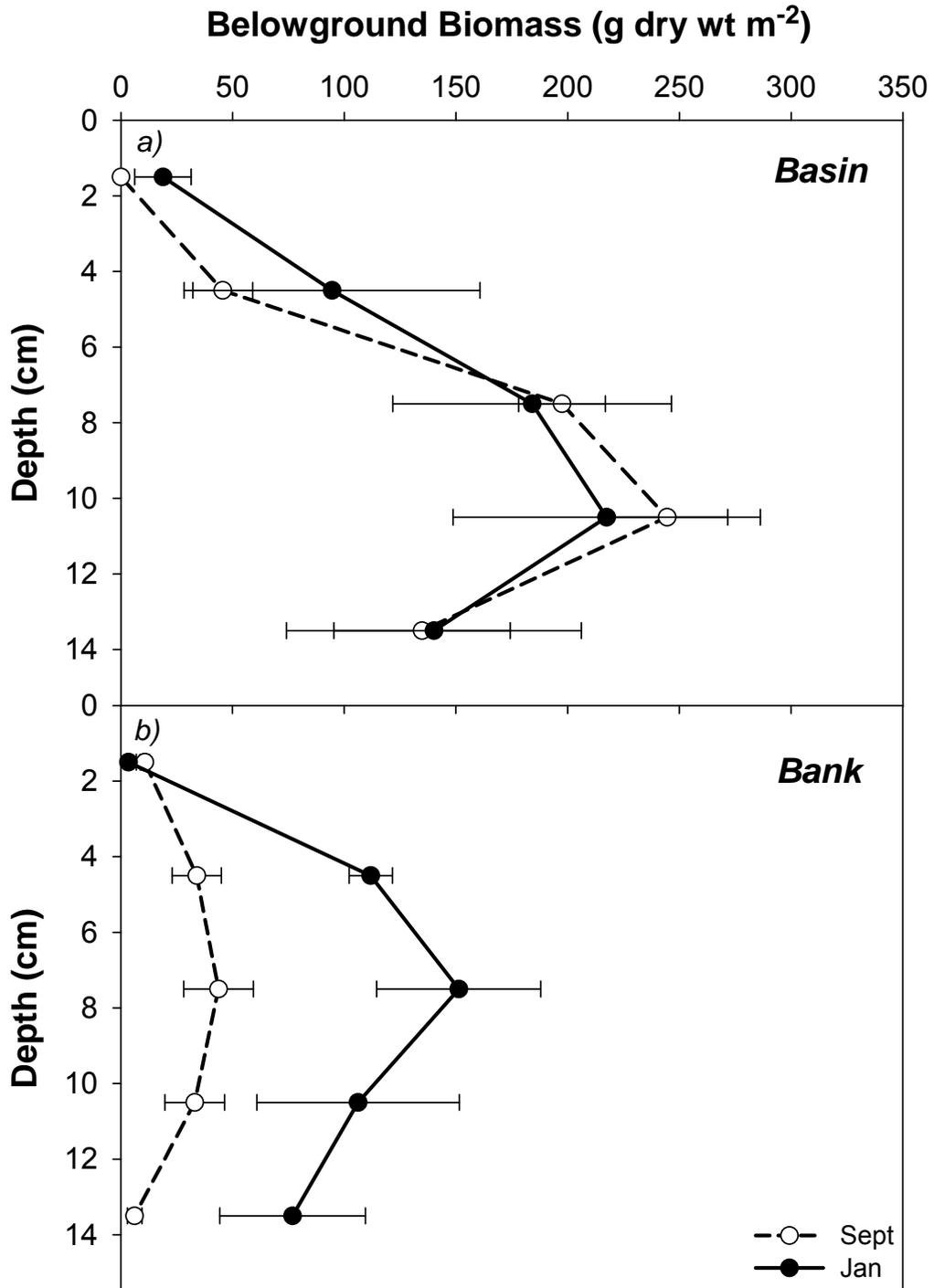


Fig 3.2. Vertical profiles of belowground biomass in sediments collected from (a) basin and (b) bank *T. testudinum* communities in Barnes Key. Open symbols correspond to an active dieback period in September 2002, while filled symbols correspond to a recovery period in January 2003.

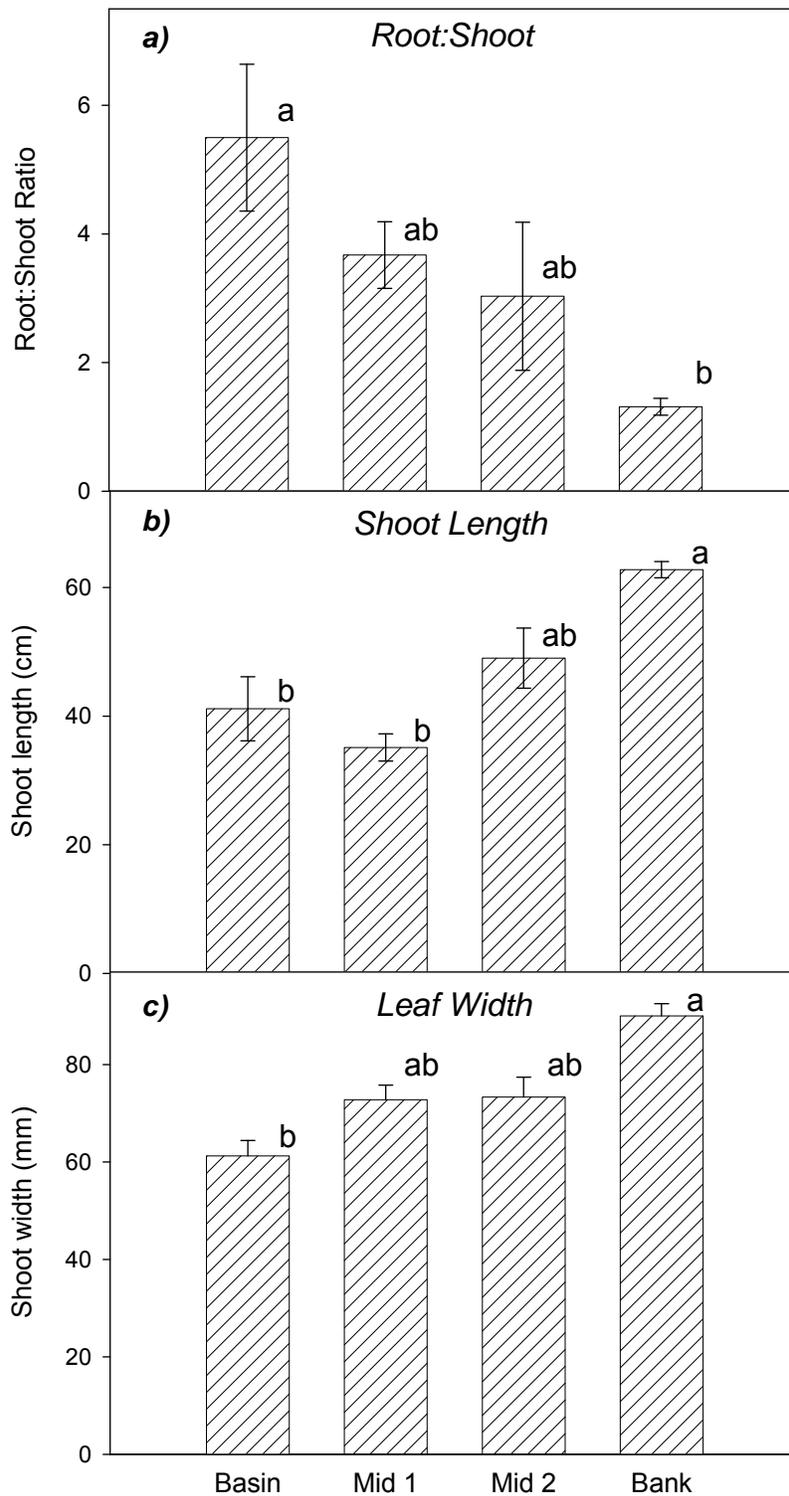


Fig. 3.3. Mean root:shoot ratios (a), shoot length (cm) (b), and leaf width (mm) (c) at 4 stations along a transect from the center of the basin to the bank in Rabbit Key in July 2001. Differences in lowercase letters indicate significant differences at $p < 0.05$.

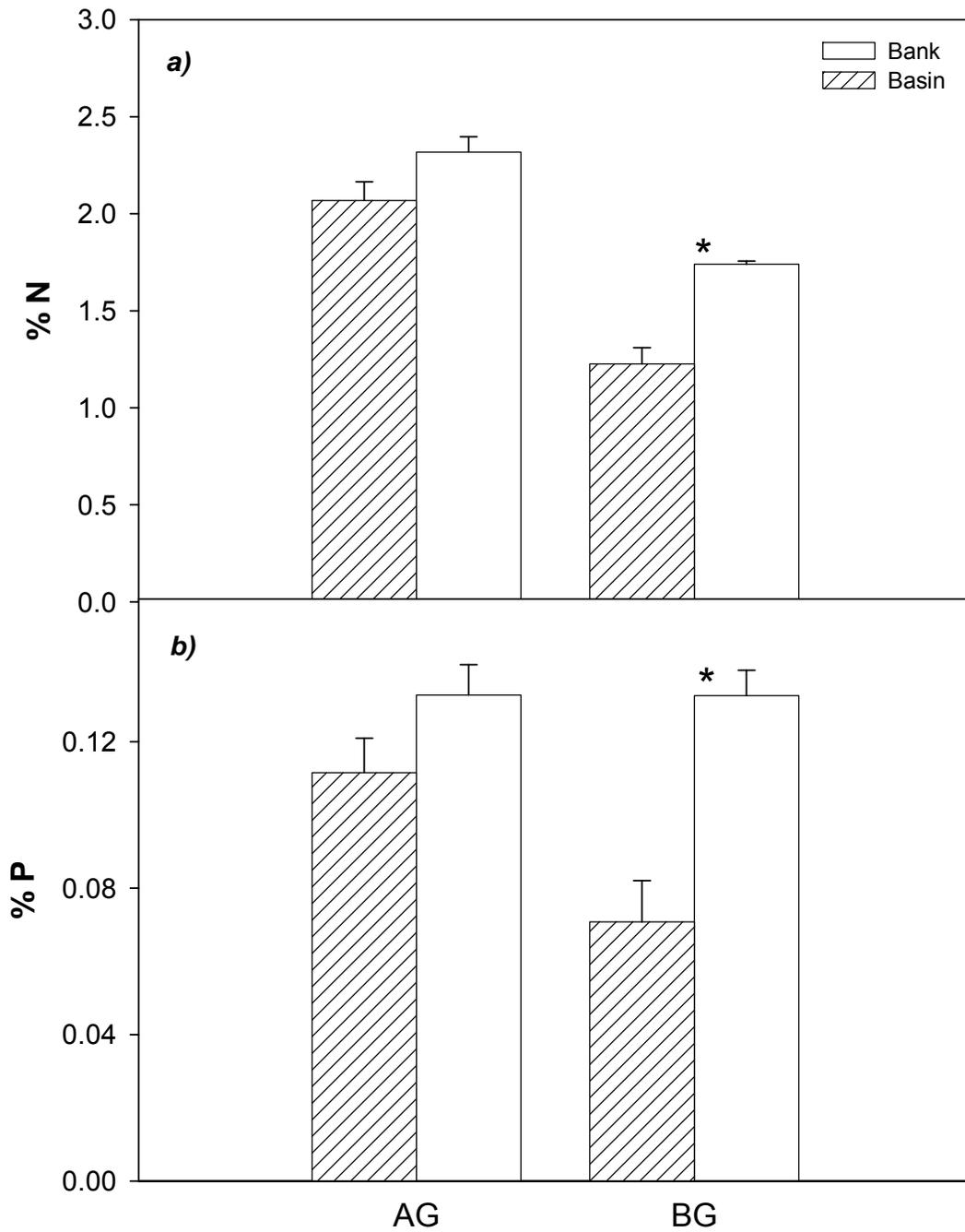


Fig. 3.4. Percent nitrogen (a) and (b) phosphorus content in aboveground (AG) and belowground (BG) *T. testudinum* tissues collected from basin (hatched) and bank (open) communities in Rabbit Key in July 2001. An “*” indicates a significant difference at the $p < 0.05$ level.

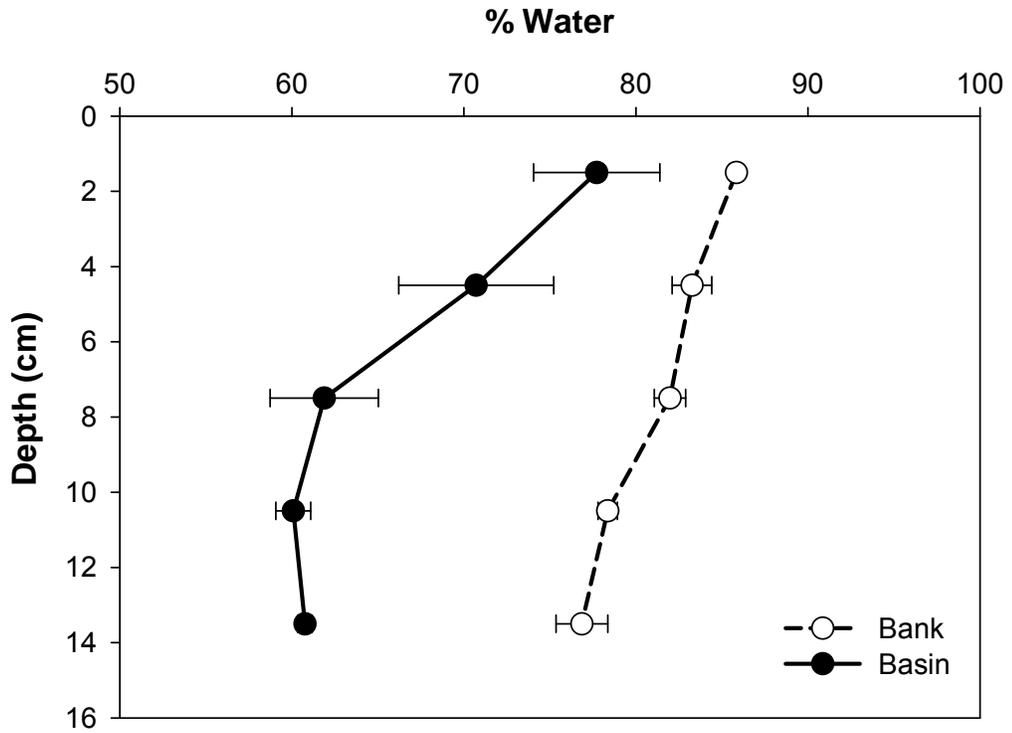


Fig 3.5. Example of depth profiles of sediment water content (% water) for bank (open symbol) and basin (filled) sediments in Barnes Key in January 2003.

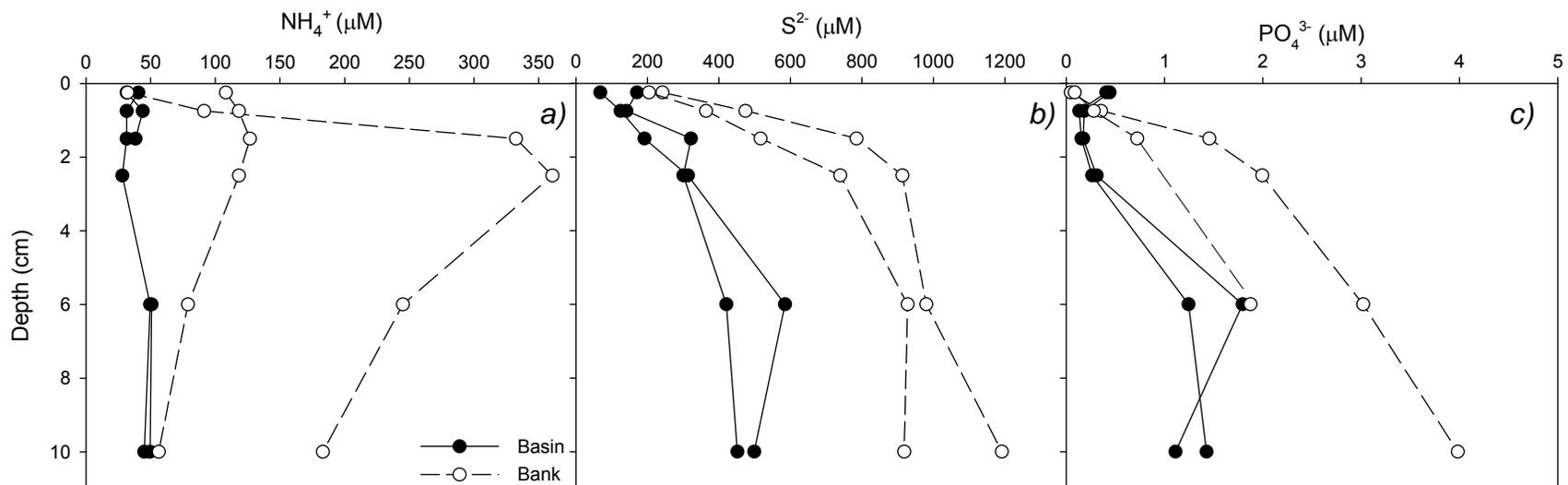


Fig. 3.6. Replicate sediment porewater profiles of (a) NH_4^+ , (b) S^{2-} , and (c) PO_4^{3-} in basin (solid line) and bank (dashed line) *T. testudinum* communities in Rabbit Key July 2001.

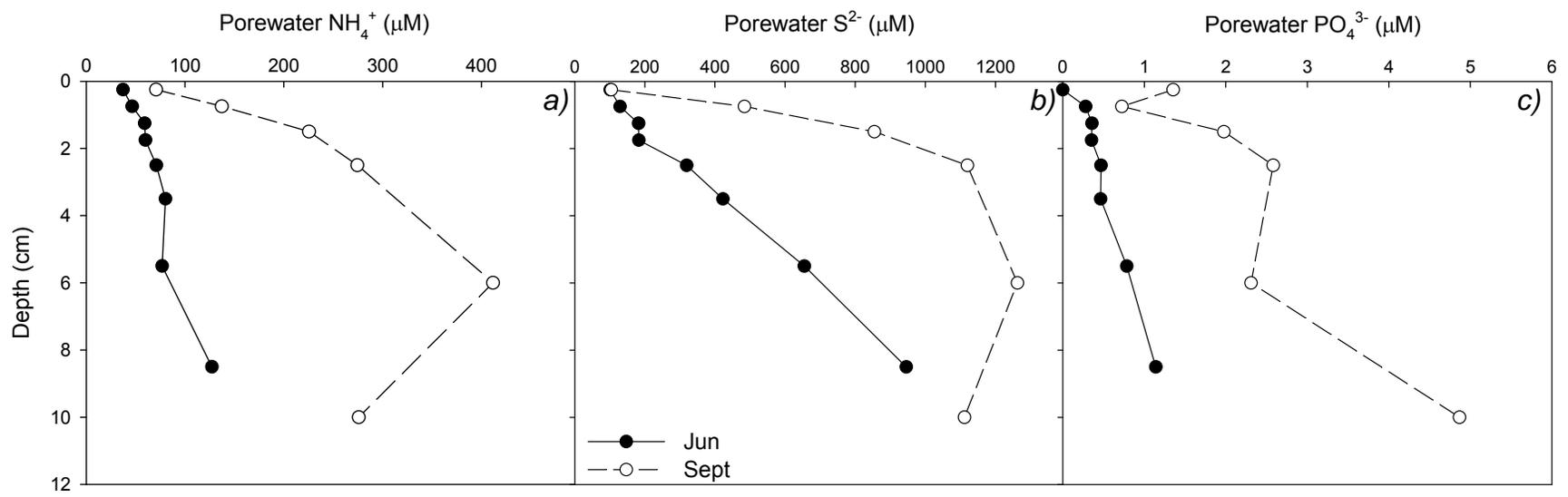


Fig. 3.7. Sediment porewater profiles of (a) NH_4^+ , (b) S^{2-} , and (c) PO_4^{3-} in June 2003 (solid line) and September 2002 (dashed line) in *T. testudinum* communities on the bank in Barnes Key.

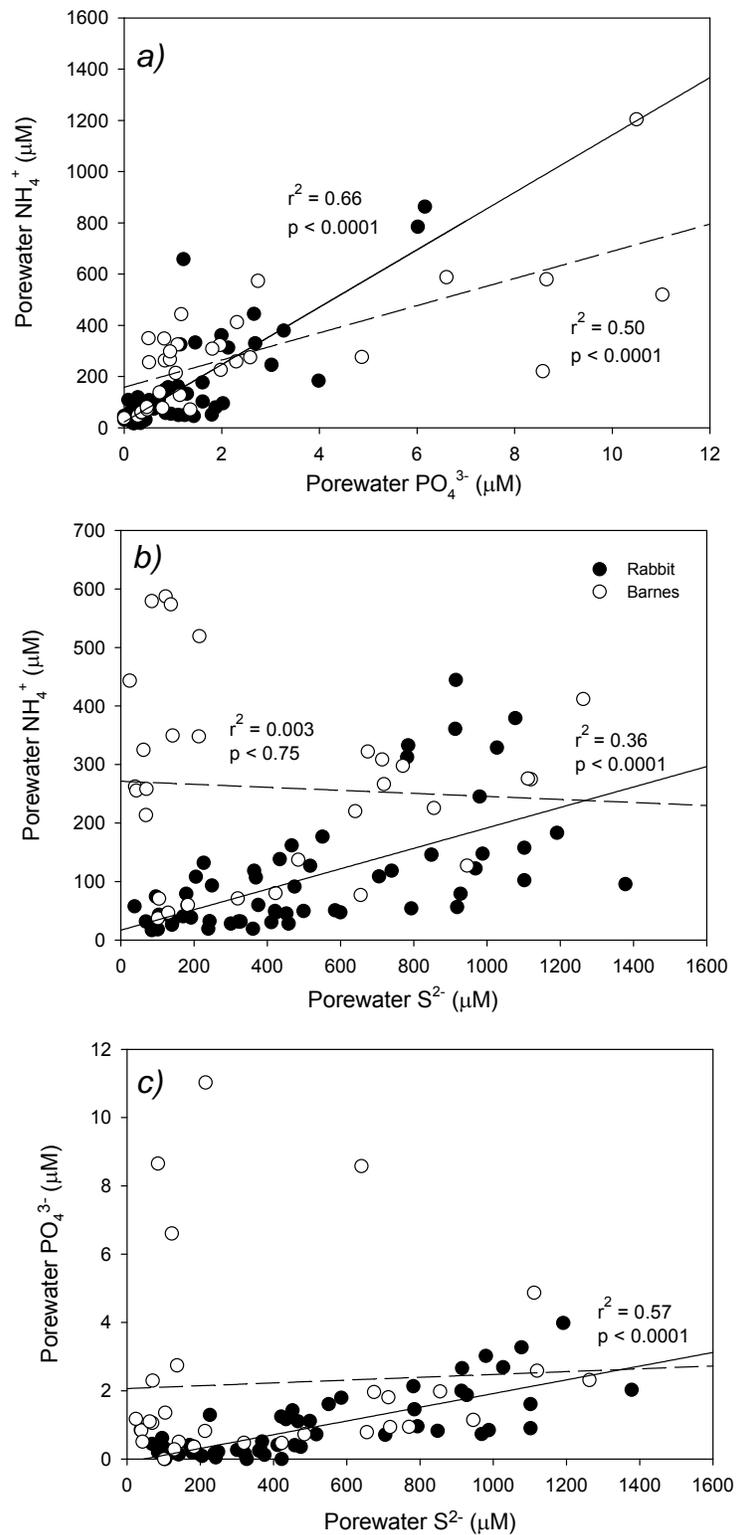


Fig. 3.8. Relationships between porewater (a) NH_4^+ and PO_4^{3-} , (b) NH_4^+ and S^{2-} , and (c) PO_4^{3-} and S^{2-} in Barnes Key (open symbols) and Rabbit Key (closed) from 2001-2003. Solid lines represent linear regression results for Rabbit Key data, whereas dashed lines represent regression lines for Barnes Key data.

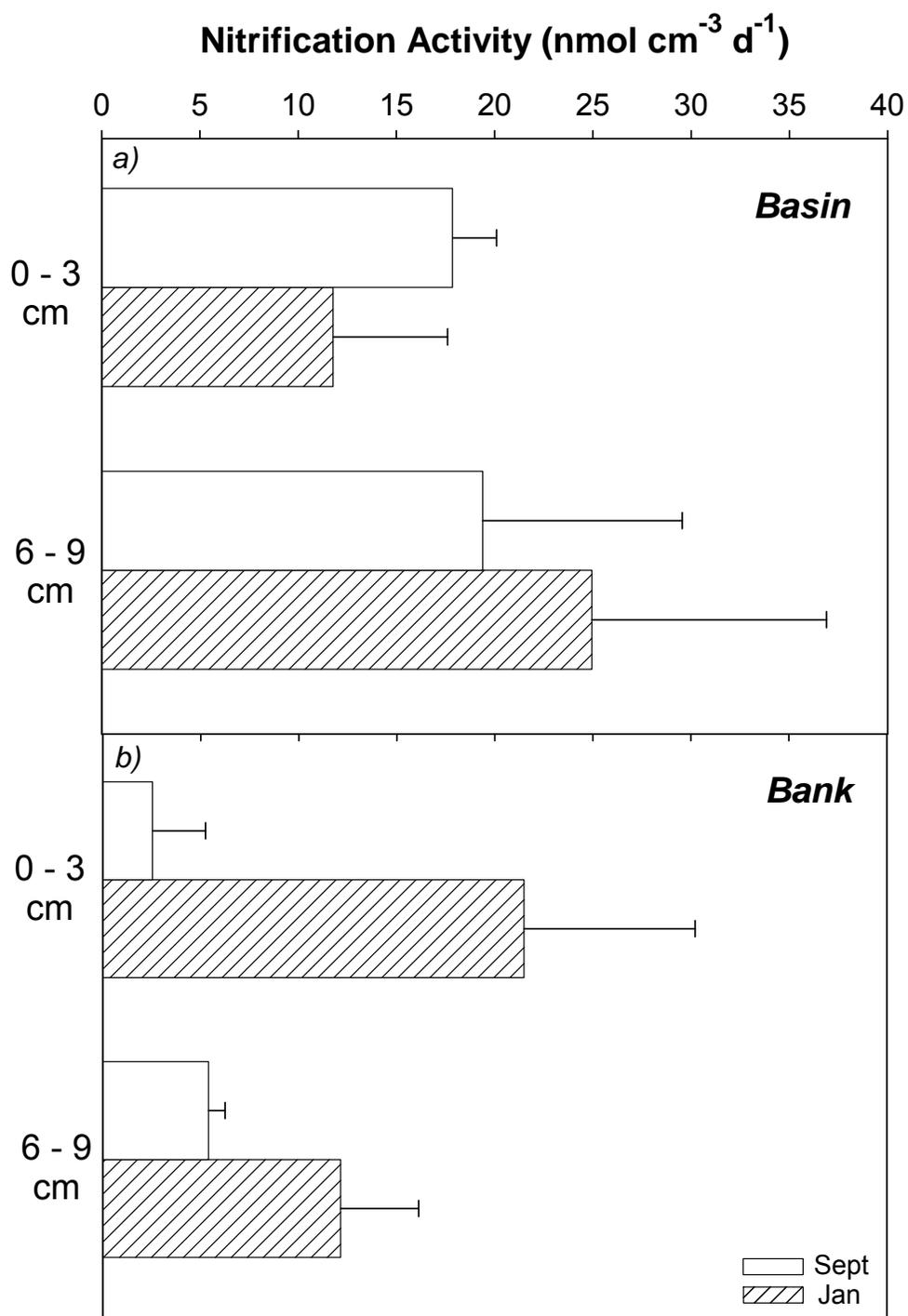


Fig 3.9. Nitrification activity in surficial (0-3 cm) and root zone (6-9 cm) sediments collected from (a) basin and (b) bank *T. testudinum* communities in Barnes Key. Open bars correspond to an active dieback period in September 2002, while hatched bars correspond to a recovery period in January 2003.

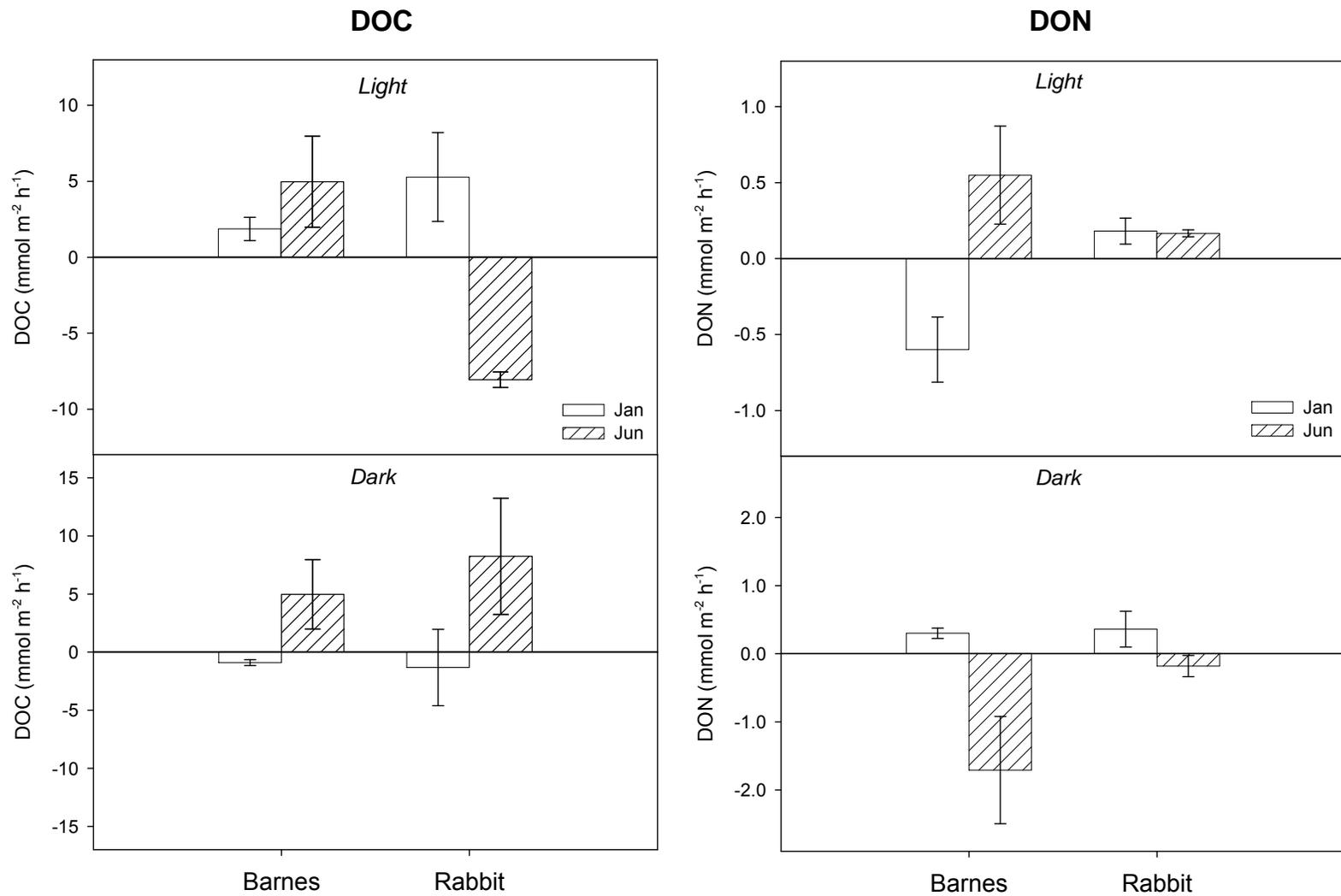


Fig 3.10. Light (above) and dark (below) fluxes of DOC (left) and DON (right) measured in Barnes Key and Rabbit Key *T. testudinum* communities in Florida Bay. Fluxes were measured in January (open) and June 2003 (hatched) and have units of mmol m⁻² h⁻¹.

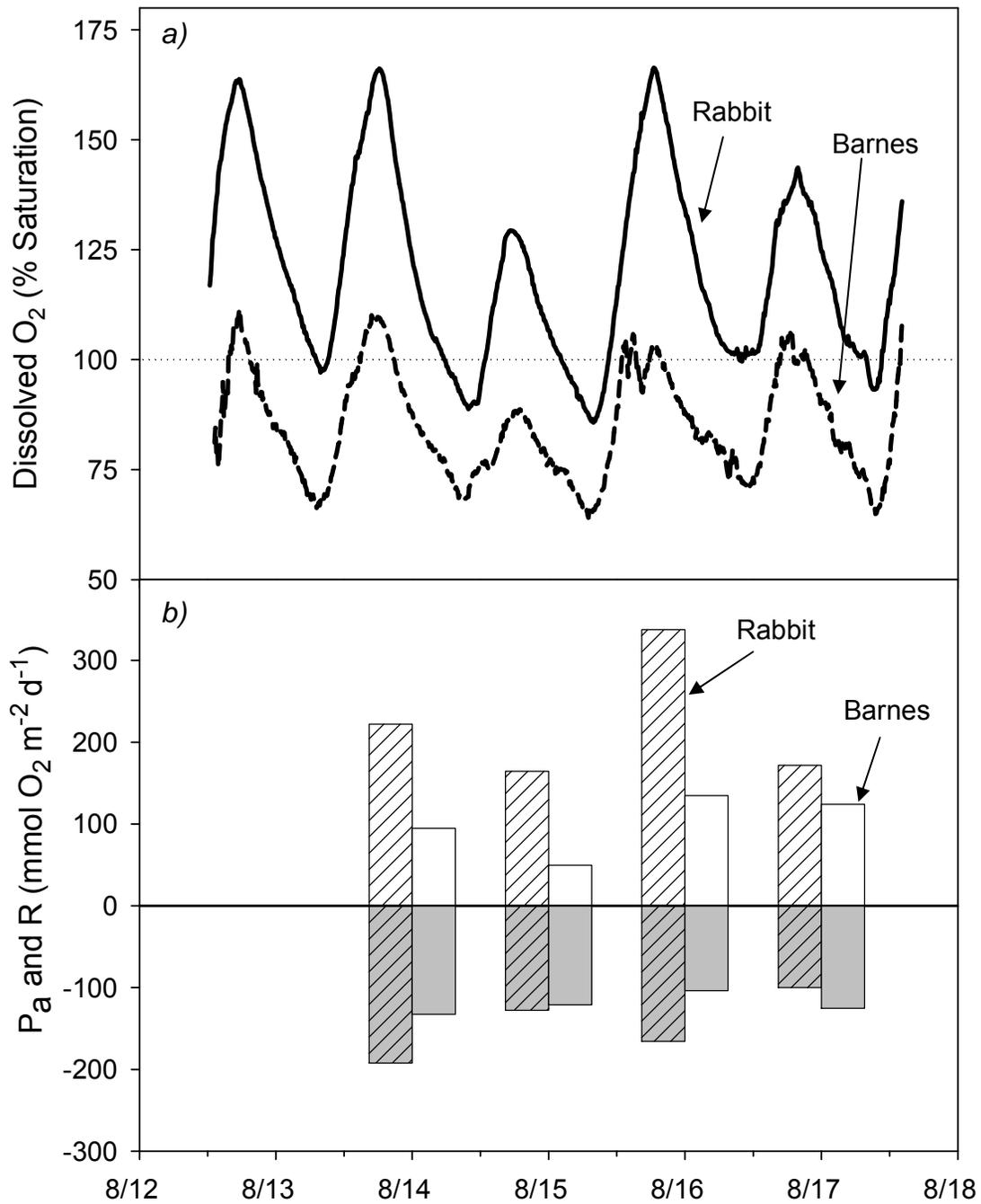


Fig. 3.11. (a) Continuous time course of dissolved O₂ (% saturation) in Rabbit Key Basin (solid line) and Barnes Key Basin (dashed line). The horizontal dotted line indicates 100% saturation over a 5 d period in August 2003. (b) Daily rates of P_a and R (shaded bars) (mmol O₂ m⁻² d⁻¹) in Rabbit (hatched) and Barnes Key (open bars).

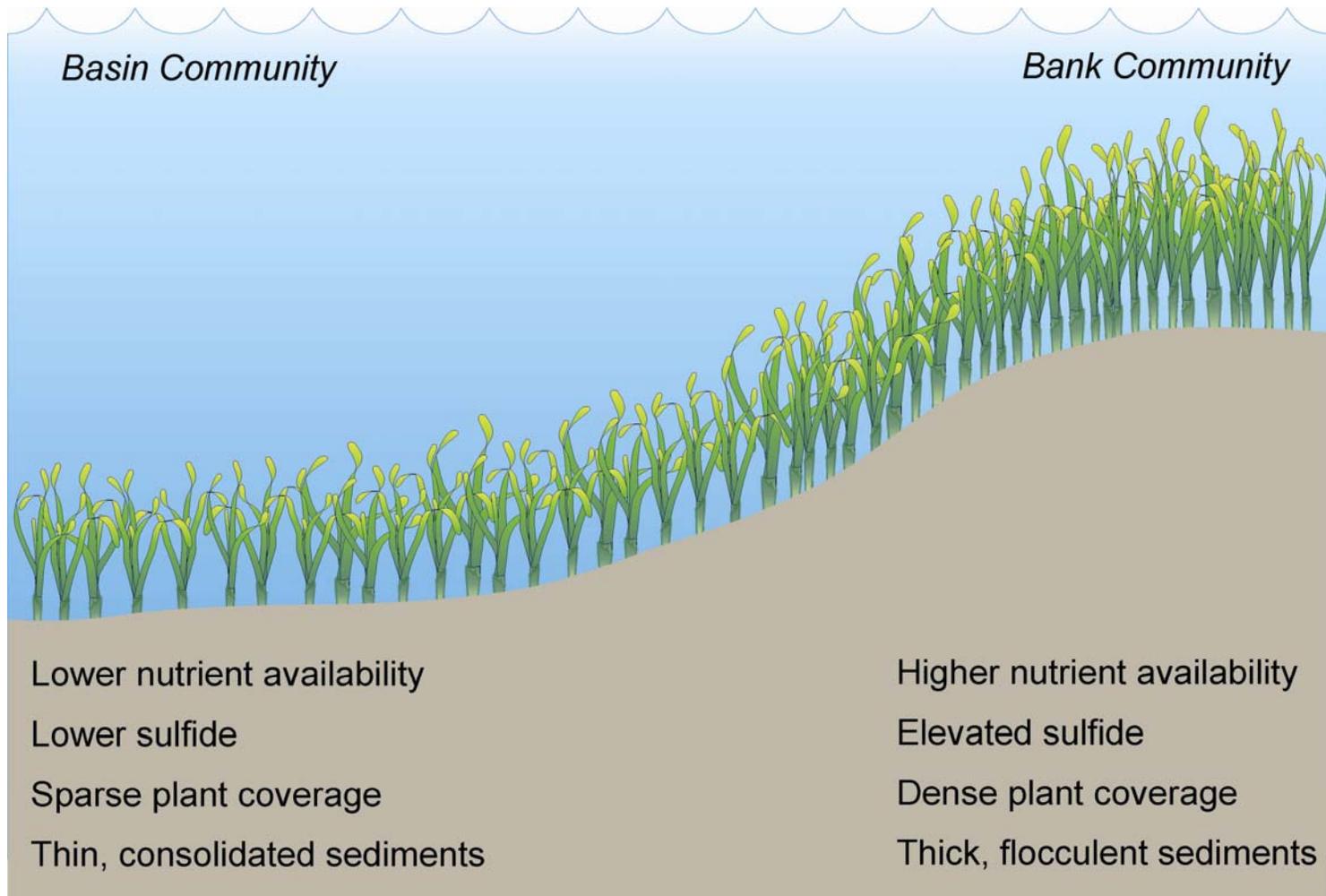


Fig. 3.12. Comparison of plant and sediment characteristics in basin and bank *T. testudinum* communities in Florida Bay.

**CHAPTER 4: Seasonal and regional variations in net ecosystem production
in *Thalassia testudinum* communities throughout Florida Bay**

ABSTRACT

Florida Bay is a unique, shallow ecosystem dominated by the seagrass, *Thalassia testudinum*, and characterized by a series of mudbanks that isolate basins, which often exhibit distinct water quality and environmental conditions. This study describes daily and seasonal variations in ecosystem-level photosynthetic production and respiration and how these processes are influenced by the presence of *T. testudinum*. Seasonal measurements were made over a two year period at five sites representing the major regions (Eastern, Northern, Central, and Western) in Florida Bay. Ecosystem production and respiration were also measured at an additional site in the Central region that has experienced dieback in recent years. Open-water dissolved O₂ concentrations measured continuously for consecutive days were used to estimate daytime apparent production (P_a), nighttime respiration (R), gross production (Pg), and net ecosystem production (NEP). Vertical profiles of dissolved O₂ concentrations within a seagrass bed showed distinct vertical gradients and diel patterns, with lowest O₂ concentrations observed below the seagrass canopy at night and highest concentrations below the canopy during the day. Rates of P_a were significantly higher in a *T. testudinum* community relative to adjacent “bare” sediments without seagrass (but containing benthic microalgal communities). In contrast, NEP did not differ between the two communities, presumably as a result of higher respiratory demand in the seagrass bed relative to bare sediments. Estimates of P_a and NEP varied both seasonally and regionally, ranging from 28.1 to 266 mmol O₂ m⁻² d⁻¹ and -56.3 to 116 mmol O₂ m⁻² d⁻¹, respectively. In general, these variations are consistent with observed variability in light, temperature, salinity, and nutrient regimes. Highest rates were observed in *T. testudinum* communities in the Eastern and Western Regions of the Bay. Seagrass beds were net autotrophic (P_a:R > 1.0) at all sites throughout most of the year; however, net heterotrophic conditions (P_a:R < 1.0) were encountered in a few instances, possibly

reflecting disturbance. The results of this study illustrate the importance of *T. testudinum* to NEP in Florida Bay and underscore the need to account for regional variations in annual biogeochemical budgets for Florida Bay.

INTRODUCTION

There has been longstanding interest in measuring the balance between daytime net primary production (P_a) and respiration (R) to quantify the potential for export of organic matter in aquatic ecosystems (e.g., Kenney et al. 1988, Kemp et al. 1997, Smith & Hollibaugh 1997) and to assess ecosystem trophic status (Odum 1956). In net autotrophic systems, where $P_a > R$, organic matter is available for burial, harvest, or export. Conversely, in net heterotrophic systems, where $P_a < R$, organic matter must be imported to support ecosystem respiration. Thus, net ecosystem production (NEP), or the difference between P_a and R , is a useful index for determining the trophic status of an ecosystem. There are many factors that regulate NEP in shallow, coastal ecosystems. These factors include availability of inorganic nutrients, water residence time, and inputs and bioavailability of organic matter (Hopkinson & Vallino 1995, Kemp et al. 1997).

Seagrass communities are often a highly productive component of shallow, aquatic ecosystems. The contribution of seagrasses to total ecosystem production, however, may vary both seasonally and across systems (Nixon 1972, Murray & Wetzel 1987, D'Avanzo et al. 1996, Ziegler & Benner 1998). Estimates of P_a and R in seagrass communities are typically obtained by measuring changes in dissolved oxygen (O_2) or total inorganic carbon (TCO_2) concentrations in either the open-water (e.g., Odum 1956) or in chamber incubations (e.g., Ziegler & Benner 1998). Although both techniques have their strengths and drawbacks, the open-water approach provides a truly integrated measure of ecosystem production and respiration (Odum & Wilson 1962).

Florida Bay is a unique, marine ecosystem dominated by extensive seagrass communities, with *Thalassia testudinum* as the primary species (Zieman et al. 1989). This large, shallow system is characterized by carbonate mudbank formations that

partition the bay into numerous, discrete basins and limit advective exchange throughout the bay (Powell et al. 1989). Although the predominance of calcium carbonate sediments leads to phosphorus (P) limitation for seagrass production throughout much of the bay, there are strong gradients in nitrogen (N) and P limitation, with P-limitation occurring in the eastern regions of the bay and N-limitation becoming more dominant in the western regions of the bay (Fourqurean & Zieman 2002, Armitage et al. 2005). Sources of nutrients to Florida Bay include exchange with the Gulf of Mexico and Atlantic Ocean shelf, atmospheric deposition, and freshwater inputs (runoff and groundwater) from the Florida Keys and Everglades (Rudnick et al. 1999). Sources of N and P into Florida Bay from the Everglades represent a small (< 15%) fraction of total inputs and are predominately organic in composition (Rudnick et al. 1999). Because shallow coastal ecosystems with high organic nutrient inputs tend to be net heterotrophic (Kemp et al. 1997), it is possible that net heterotrophy may occur in seagrass communities in Florida Bay where organic nutrients are the dominant form of nutrient inputs.

Since the late 1980's, regions of Florida Bay have been experiencing seagrass dieback (e.g., Robblee et al. 1991, Zieman et al. 1999). Indirect evidence suggests that the loss of seagrass has resulted in liberation of inorganic nutrients from the benthos to overlying water, allowing intense phytoplankton blooms to occur (Boyer et al. 1999, Fourqurean & Robblee 1999). In addition, the accumulation and degradation of plant material within dieback areas may have led to a large efflux of organic nutrients from the benthos, possibly enhancing heterotrophic microbial activity in the water column (Bugden et al. 1998) and contributing further to net heterotrophy in dieback areas.

Given the predominance of seagrass communities and unique physiography of Florida Bay, the purpose of this study was to: 1) explore the role of *Thalassia testudinum*

in ecosystem production by direct comparison with rates measured in adjacent unvegetated (bare) communities; and 2) to assess regional and seasonal variations in P_a , R and NEP in *T. testudinum* communities along an east-west transect in Florida Bay throughout 2003-4. Estimates of P_a and R were obtained from diel cycles in continuous measurements of O_2 concentrations in the open-water of five basins distributed across Florida Bay during winter, spring, summer, and fall in 2003 and 2004.

METHODS

Site description. Florida Bay is a shallow, sub-tropical estuary bordered to the north by Everglades National Park and by the nearly contiguous islands of the Florida Keys to the south and east. This partially-enclosed, marine ecosystem is open to the Gulf of Mexico to the west and has limited exchange with Atlantic Ocean through a series of channels between the Keys (Smith 1994). Inputs of freshwater runoff from the Everglades (Shark River Slough, Taylor Slough, and C-111 Canal) are relatively minor due to water management practices upstream. Tidal range throughout the bay is also minimal, as physiographic formations (e.g., mudbanks and mangrove islands) limit exchange with the Gulf of Mexico (Holmquist et al. 1989). A series of natural, carbonate mudbanks divides the bay into numerous shallow (< 2 m) basins, further reducing advective exchange within the system (Powell et al. 1989). The result is that basins often exhibit distinct differences in nutrient and salinity profiles relative to adjacent basins.

Measurements of community O_2 cycling in *T. testudinum* beds were collected in 5 distinct basins located in 4 regions (Northern, Western, Central and Eastern) of Florida Bay (Fig. 4.1). These sites were chosen to provide representative spatial coverage in distinct zones identified in previous studies (e.g., Zieman et al. 1989, Boyer et al. 1997)

and to investigate rates along an east-west transect in Florida Bay. Northern Florida Bay (Little Madeira) is heavily influenced by relatively nitrogen-replete, organic-rich freshwater inputs from Taylor River Slough into Little Madeira Bay (Rudnick et al. 1999). The Eastern Region (Sunset Cove) of Florida Bay tends to be relatively P-limited, but may receive nutrient inputs in the form of runoff from the Florida Keys (Lapointe & Clark 1991). Western Florida Bay (Rabbit) is influenced by advective exchange with the relatively P-rich water of the Gulf of Mexico, whereas Central Florida Bay (Rankin) tends to fall in between the nutrient profiles of the eastern and western regions of the bay (Rudnick et al. 1999). An additional site, Barnes Key, which is located in the southern part of the Central Region, experienced an active dieback event in August 2003. Rates were also measured at an additional site in unvegetated (bare) area (~500 m² diameter) adjacent to the *T. testudinum* bed in Sunset Cove to provide a comparison between the two communities. The average depth of the *T. testudinum* beds in Rankin and Little Madeira was ~1 m, while depth at the other sites was ~2 m.

Open-water measurements of P_a and R. Continuous measurements of open-water temperature, salinity, and dissolved oxygen (DO) concentrations were obtained using instrument packages (YSI 600 XLM) equipped with thermistors, conductivity sensors and pulsed-O₂ electrodes. At all sites, instruments were deployed at 0.75 m above the sediment surface, so that within the *T. testudinum* beds, the instruments were situated just above the seagrass canopy. Only one instrument was deployed at each site, excluding Sunset Cove, where an additional instrument was deployed mid-way between the sediment surface and the top of the seagrass canopy. Measurements were recorded at 10-min intervals over a series of 3-12 day periods in August and November 2003, and January, March, June, and November 2004. Measurements at Rabbit North did not commence until November 2003. On two occasions (June and August 2004), multiple sensors were

deployed within a 50 m radius in the *T. testudinum* bed in Sunset Cove to estimate spatial variability in O₂ concentrations.

Vertical variations in dissolved O₂ concentrations were measured in both the *T. testudinum* and bare communities during morning, early afternoon, and late evening in June 2004. Oxygen concentrations were measured at depths of 0, 50, 100, 160, 170, 180 and 210 (bare only) cm from the water surface with a hand-held dissolved O₂ meter (YSI™ Model 55). Within the seagrass bed, depths at 160, 170, and 180 cm coincided with the top of the canopy, half way below the canopy and the sediment surface, respectively.

Photosynthetically available irradiance (PAR) was measured at each site using a hand-held LICOR LI-1000 2π quantum sensor. PAR attenuation coefficients were estimated from measurements made at approximately 0.25 to 0.5 m depth intervals beginning at the water column surface at least 1 time during peak daily irradiance. Ambient irradiance in the air was recorded continuously at 15-min intervals at the National Park Service station in Key Largo, near the Sunset Cove site. PAR was also monitored continuously in the *T. testudinum* bed in Sunset Cove using a submersible Odyssey™ Light Meter (Dataflow Systems PTY, LTD) that was deployed adjacent to the YSI sensor. Continuous measurements of irradiance were integrated hourly and summed over a 24 h period to yield a daily integrated irradiance (mol m⁻² d⁻¹).

Records of O₂ concentrations were used to estimate daytime production and nighttime respiration. Nighttime respiration (R) was estimated from the decline in O₂ concentrations from dusk to dawn. Apparent daytime production (P_a) was estimated from increases in O₂ from the daily minimum to the maximum concentration and gross daytime production (P_g) was calculated from the sum of R and P_a (Hagy, J., pers. comm.), assuming that rates of respiration were constant throughout the daytime and nighttime hours. Vertically-integrated rates were computed by multiplying volumetric rates by the depth of the

water column. Rates were corrected for O₂ exchange across the air-water interface using an air-sea exchange coefficient of 0.5 g O₂ m⁻² h⁻¹ (atm)⁻¹, a value within the range of those reported for other shallow coastal bays (Kremer et al. 2003). Although air-sea exchange coefficients vary with wind speed (Raymond & Cole 2001), a constant value for air-sea exchange can be used in the absence of local wind data (Kemp & Boynton 1980). Despite day-to-day variability in light and temperature, continuous measurements made over 3-10 d periods tend to provide representative estimates of P_a and R (Kenney et al. 1988). This approach has been used successfully in shallow water systems dominated by seagrass (Ziegler & Benner 1998), macroalgae (D'Avanzo et al. 1996), and benthic microalgal communities (Kenney et al. 1988). The difference of O₂ production in daylight (P_a) minus O₂ consumption at night (R) is equal to net ecosystem production (NEP) for a given day.

Seasonal and annual estimates of rates were also calculated for each site. Rates from August 2003 and January, March and November 2004 were integrated over a 3 month period to estimate seasonal rates for Summer, Winter, Spring, and Fall, respectively. In Barnes, rates from early June 2004 were used in the absence of data from March 2004 and, consequently, this rate may overestimate the actual mean spring rate. Data from benthic flux cores in January 2004 at Sunset Cove were used to estimate Winter rates at this site. While benthic flux cores give reasonable estimates of P_a and R, they may underestimate open-water rates (Ziegler & Benner 1998). Annual rates were calculated from seasonal rates integrated over the entire year. Photosynthetic and respiratory quotients of 1.0 (1 mol CO₂: 1 mol O₂) were used to convert rates from oxygen to carbon units (Kemp et al. 1997).

In November 2003, programming errors in the YSI instruments resulted in O₂ concentrations being recorded at 10-h rather than 10-min intervals at a few sites (Rabbit North, Rabbit South and Sunset Cove). For these sites, I estimated P_a and R using changes in O₂ concentrations between two measurements, where the measurements coincided with dawn and dusk. In this manner I obtained 3 estimates of both P_a and R over the course of

the deployment. While this technique may not be ideal, previous studies have shown that this technique produces reasonable estimates of metabolic rates in seagrass beds (Odum & Hoskins 1958).

On a few occasions, “drift” in O₂ concentrations were observed, resulting in considerably lower concentrations and smaller amplitudes in diel patterns between the beginning and the end of the instrument deployment. Whether this drift was related to instrument fouling or failure is unclear. However, there was no obvious fouling on the sensors during any deployment. Data exhibiting clear evidence of drift were omitted from this analysis.

RESULTS

Mean water temperatures in *T. testudinum* beds in Florida Bay ranged from ~20° to 31° C over the annual cycle (Table 1) with highest values observed in summer months. Salinities at all sites in Florida Bay ranged from ~5 to 48, with the highest salinity recorded in Rankin in June 2004 (Table 4.1). Little Madeira exhibited the largest range (~5 to 36) in salinities as well as the lowest values recorded across the basins. Throughout this study, lowest salinities were observed in November 2003. In contrast, maximum annual salinities appeared to vary with location within the bay. For example, maximum salinities were recorded in November 2004 at Sunset Cove, whereas salinity was highest in June 2004 at the remainder of the sites. These patterns are similar to patterns observed previously (Boyer & Briceno 2005) and may be attributable to higher than average precipitation in Fall 2003 and lower than average precipitation throughout 2004. Light attenuation coefficients ranged from 0.27 to 5.6 m and were typically higher at Little Madeira and Rankin relative to the other sites. Highest values at all sites were measured during November 2003 and November 2004.

Dissolved O₂ concentrations exhibited clear diel patterns and varied both seasonally and across basins (Fig. 4.2). Concentrations ranged from 116 to 325 mM O₂ throughout the study (Table 4.1) and both minimum and maximum O₂ concentrations typically occurred during daytime hours (e.g., Fig. 4.2). Percent saturation of O₂ in the water column also varied seasonally (Table 4.1), ranging from 50 to 166% saturation. Concentrations were highest in the January and March 2004; however, the daily range in concentrations was greatest in summer months (e.g., Fig. 4.2a). Lowest mean values of both concentration and percent saturation were recorded at Barnes in August 2003 and November 2004 (Table 4.1). Dramatic declines in O₂ concentrations were observed at Little Madeira throughout the year and these declines were significantly ($p < 0.05$) and negatively correlated with salinity intrusion events. Spatial variability in concentrations in the *T. testudinum* bed in Sunset Cove was minimal at the 50-m scale in both June and August 2004 (data not shown).

Clear vertical and temporal patterns were observed in vertical profiles of O₂ concentrations throughout a day in the water column overlying the *T. testudinum* bed and bare sediments in June 2004. At both sites, concentrations in the top 1 m of the water column increased from morning to late evening (Fig 4.3). Concentrations varied little with depth at the unvegetated site, excluding a sharp decrease in concentrations beginning approximately 20 cm above the sediment surface in the early evening (Fig 4.3c). Oxygen concentrations were also relatively uniform in the top 1 m of the water column overlying the *T. testudinum* bed. However, sharp gradients in O₂ concentrations were observed in mid-afternoon and at dusk, with lowest concentrations observed at the sediment surface (Fig 4.3b & c). Lowest O₂ concentrations were observed in late evening below the seagrass canopy, when a 3-fold drop in concentrations was observed (Fig 4.3c).

Estimates of P_a , R , and P_g in *T. testudinum* communities varied seasonally as well as across basins. Rates of P_a were typically greater than estimates of R and ranged from 28.1 to 265 mmol O_2 m^{-2} d^{-1} and 23.4 to 203 mmol O_2 m^{-2} d^{-1} , respectively. Throughout the year, rates of P_g , P_a , and R were significantly higher ($p < 0.05$) in summer (June and August) compared to other months. Across all of the basins, the *T. testudinum* community in Sunset Cove exhibited significantly higher ($p < 0.05$, Tukey HSD) rates of P_g and P_a compared to other sites (Table 4.2). Lowest rates of P_g , P_a , and R were observed at Rankin and Little Madeira (Table 4.2). Excluding November 2003, rates of P_g both and R were significantly higher ($p < 0.05$) in the *T. testudinum* community at Sunset Cove compared to rates in the adjacent bare community (Fig. 4.4) and estimates of P_g , P_a , and R were all significantly greater ($p < 0.02$) below the seagrass canopy relative to above the canopy (data not shown). In addition to seasonal variability, day-to-day variations in rates were observed at each site throughout the year, and this variability was more pronounced in estimates of P_a relative to R .

In general, environmental conditions explained much of the variability in estimates of P_g , P_a , and R , but relationships differed among sites. For example, P_g was significantly ($p < 0.03$) and positively related to irradiance at most sites (Rankin, Little Madeira, and Sunset Cove) (e.g., Fig. 4.5a & b) and, these relationships were marginally insignificant ($p < 0.10$) at Rabbit and Barnes. Similarly, variations in temperature significantly ($p < 0.0002$) explained variability in R at Rankin, Rabbit, and Sunset Cove (e.g., Fig.4.6). Variability in the air-sea exchange coefficients used to calculate rates had little influence ($< 5\%$ change) on rates at sites < 1 m depth (e.g., Fig. 4.7b) and only a marginal effect ($< 25\%$ change) on rates at sites of 1 m in depth (e.g., Fig. 4.7a).

Estimates of NEP also varied across basins (Table 4.2), ranging from -56.3 to 116 mmol O_2 m^{-2} d^{-1} , with highest rates of NEP observed in Sunset Cove. Like P_a , rates varied seasonally, however there were no consistent seasonal patterns across basins.

Mean values of NEP were typically positive or not significantly different from zero, indicating either net production of O₂ or no net change in O₂ (Table 4.2). On some occasions, mean values of NEP were negative, indicating net consumption of O₂ (Table 4.2). Mean ratios of P_a:R within each basin were greater than 1.0 at all sites throughout the year, excluding August 2003 in Barnes, and highest ratios were observed in Little Madeira (Fig. 4.8a). Across all sites, there was a positive linear relationship between P_a and R and the slope of the linear regression line was also greater than 1.0 (Fig. 4.8b). There was no significant difference ($p > 0.10$) in NEP and ratios of P_a:R between the *T. testudinum* and bare communities in Sunset Cove. Annual estimates of NEP ranged from 4.5 to 136 mol C m⁻² yr⁻¹ and Sunset Cove exhibited the highest rates (Table 4.3).

DISCUSSION

Diel patterns in O₂ concentrations

Clear diel patterns in dissolved O₂ concentrations were observed in the water column over *T. testudinum* communities during this study, and these diurnal variations are consistent with those observed in numerous previously reported studies (Odum 1957, Murray & Wetzel 1987, Moriarty et al. 1990, Leverone 1995, Ziegler & Benner 1998). Minimum O₂ concentrations, however, typically occurred after sunrise the onset of O₂ production often not initiated until 2-3 h after dawn. This time lag in O₂ production could arise from mechanisms related to plant physiology and hydrological conditions. The light compensation point, or the irradiance at which photosynthesis begins, does not likely coincide with dawn, and the time of day at which the light compensation point is reached may depend on water clarity over the seagrass bed. Although Florida Bay waters typically have a high degree of water clarity (Phlips et al. 1995), sediment resuspension during wind events and periodic microalgal blooms may contribute to increased light attenuation (Lawrence et al. 2004). Furthermore, O₂ evolution from the

plant leaves to the surrounding water column may not occur simultaneously with the initiation of plant photosynthesis due to lacunal storage of O₂ (Kemp et al. 1986). High respiratory demand of belowground tissues during nighttime hours could result in low partial pressure of O₂ in the plant lacunae until photosynthesis begins (Greve et al. 2003). Indeed, measurements of O₂ partial pressure in *T. testudinum* meristems in Florida Bay were lowest before sunrise and were hyposaturated relative to the water column at night (Borum et al. 2005). Accumulation of O₂ in the lacunae to sufficient levels in response to the O₂ deficit created during the night could result in as long as a 30 min delay in evolution of O₂ to the water column (Kemp et al. 1986). Another source of delay may arise from the advective exchange of O₂ produced within the canopy to the overlying water column, which is, in turn, dependent on water flow within the seagrass bed (Koch & Gust 1999, Binzer et al. 2005). Thus, one of or a combination of these factors may have contributed to the delay in O₂ production observed in *T. testudinum* communities in this study.

Peak O₂ concentrations also occurred during daytime hours, with the initial decline in concentrations beginning in the afternoon several hours after peak irradiance. The decline in O₂ concentrations during daylight hours is like the result of heterotrophic processes overtaking autotrophic production during the day and this is supported by the decline in hourly rates of daytime net production, P_a, during early afternoon (data not shown). Potential causes of this decline in O₂ production could stem from carbon or nutrient limitation during peak photosynthesis or corresponding high rates of photorespiration (Touchette & Burkholder 2000). However, these processes were not measured and would require further investigation to ascertain how these processes contributed to the observed depression in rates.

Diel variations in O₂ concentrations in the water column of seagrass beds have been widely used to estimate production and respiration in seagrass communities

(Odum & Hoskins 1958, Odum & Wilson 1962, Nixon 1972, Ziegler & Benner 1998).

While this technique is not without criticism, measurements of dissolved O₂ concentrations are relatively simple and provide reasonable estimates of total ecosystem production compared to other methods (Ziegler & Benner 1998). In this study, estimates of daytime apparent production, P_a, were calculated from the rate of change in O₂ concentrations between the daily minimum and maximum concentrations, rather than between concentrations at dawn and dusk. This approach produces relatively conservative estimates of P_a and may slightly overestimate 24-h production.

Exchange of gases across the air-sea interface presents another potential source of error in calculating P_a and R using the open-water approach (e.g., Gazeau et al. 2005). Air-sea exchange coefficients vary with wind speed and fetch, and both of these factors may vary over the course of a day. For this study, I assumed that air-sea exchange rates were constant for all sites over the deployment of the sensors, but this approach does not account for variability in air-sea exchange associated with varying wind speed and direction (Kremer et al. 2003). Higher wind velocities increase turbulence, and thus, air-sea exchange, which can lead to overestimation of respiration rates (Ziegler & Benner 1998). Wind fetch may also factor into air-sea exchange depending on the relative position of nearby mangrove islands to the direction of the wind. Wind speed and direction were not measured directly in this study, but the use of variable air-sea exchange coefficients in calculations did not substantially alter estimates of rates within these communities (Fig. 4.7). Although the calculation of rates did not appear to be very susceptible to varying air-sea exchange, the incorporation of *in situ* air-sea exchange coefficients estimated from local wind data could reduce the potential for error associated with using a constant value.

Influence of *Thalassia testudinum* on ecosystem production

Throughout the year, *T. testudinum* communities exhibited significantly higher rates of both P_a and P_g relative to adjacent bare sediments in Sunset Cove. While the seagrass plants themselves are largely responsible for this difference, other benthic autotrophs, including epiphytes and benthic micro- and macroalgae, found in these communities may have contributed to the elevated rates of production (Murray & Wetzel 1987, Moncreiff et al. 1992, Kaldy et al. 2002). Benthic microalgae exhibited high rates of productivity in areas without seagrass in Sunset Cove and have been shown to contribute significantly to ecosystem production in seagrass communities (Jensen & Gibson 1986, Santos et al. 2004). However, benthic microalgae were less abundant within the seagrass bed (Burton-Evans 2005), presumably because of shading, and thus, may not have contributed significantly to ecosystem production. Phytoplankton were also unimportant, as the contribution of plankton to O_2 production has been shown to be insignificant (< 5%) within this community (Cornwell, pers. comm.). However, increased nutrient loading could stimulate phytoplankton and algal productivity and could result in a shift in the relative dominance of other autotrophs to primary productivity (Armitage et al. 2006) within these seagrass communities.

Net ecosystem production, NEP, was positive over the year in both communities, indicating net autotrophy. In contrast to elevated rates of daytime O_2 production in the *T. testudinum* community, NEP did not differ significantly between the two communities (Fig. 4.4). This pattern may be explained by higher respiratory demands within the seagrass bed relative to the bare community. Enhanced deposition and trapping of organic matter and senescing plant material (Ward et al. 1984, Gacia & Duarte 2001) combined with elevated production of dissolved organic matter (Ziegler & Benner 1999, Barron et al. 2004) in seagrass communities stimulates heterotrophic microbial processes in both the sediment and overlying water column (Chin-Leo & Benner 1991,

Velimirov & Walenta-Simon 1993), resulting in higher community respiratory demand. The physical structure of seagrass leaves provide habitat for epiphytic bacteria (Kirchman et al. 1984, Barnabas 1992) and other heterotrophic fauna (e.g., Hall & Bell 1993, Edgar et al. 1994), which also contribute to higher respiratory demand within these communities. Strong gradients in O₂ concentrations within the seagrass canopy (Fig. 4.3) in combination with higher rates of R below the canopy (Ch. 2) provide evidence of the higher respiratory demand in the *T. testudinum* community relative to adjacent bare sediments.

Regional variations in P_g and NEP

Rates of gross primary production, P_g, observed in *T. testudinum* communities in Florida Bay were relatively high compared to rates reported for other seagrass communities but were similar to rates reported in *T. testudinum* communities elsewhere (Odum & Hoskins 1958, Odum & Wilson 1962, Ziegler & Benner 1998). Despite seasonal variability, clear regional patterns in P_g emerged, with lowest rates observed in the Northern and Central Regions and highest rates observed in the Western Region (Fig. 4.9). The high rates of P_g observed at Rabbit Key Basin (Western Region) may be explained by advective exchange with the relatively P-rich water of the Gulf of Mexico (Boyer et al. 1999) which may, in turn, stimulate production relative to the P-limited sites in the Northern and Central Regions. Rates were also high at Sunset Cove in the Eastern Region, a region typically considered to be P-limited. Situated in close proximity to the Florida Keys, it is possible that Sunset Cove may receive nutrient inputs in the form of freshwater runoff or groundwater seepage from the Florida Keys leading to high rates of P_g that may not be representative of other communities in the Eastern Region. However, water column nutrient concentrations, and in particular P, decrease rapidly offshore of the Keys (Lapointe & Clark 1991) and water column PO₄³⁻ concentrations

were typically below detection limits throughout this study (Ch. 2). Furthermore, N:P ratios of plant tissues in Sunset Cove tend to be higher (~50) than ratios of plants at Rabbit (~30) (see Chapters 1 & 2), suggesting that seagrasses in Sunset Cove were relatively P-limited. Explorations as to whether the nutrients supporting growth in Sunset Cove were derived from autochthonous versus allochthonous sources (e.g., stable isotope studies, Fourqurean et al. 2005) would be useful in determining the degree to which proximity to the Keys influences production in Sunset Cove.

The relative abundance or spatial coverage of seagrasses within these basins could also explain differences in P_g . Presumably, sites with greater *T. testudinum* abundance should exhibit higher rates of P_g (Duarte 1989). A comparison of rates reported here (Table 4.2) to Braun-Blanquet abundance data for Rankin and Rabbit Keys in 2003-04 (courtesy of FWRI/UNCW South Florida Fisheries Habitat Assessment Program) supports this pattern. P_g was positively correlated to plant abundance ($r = 0.79$, $p < 0.05$, Spearman's Rho correlation) at these sites, suggesting that some of the variations in P_g were associated with overall plant abundance (data not shown). However, additional data regarding plant abundance for the other sites are needed to ascertain whether this pattern held across the bay.

There are several environmental factors, including water quality variables such as temperature, salinity, water clarity, and nutrient availability, that may regulate P_g in seagrass communities in Florida Bay. Although limited data related to environmental conditions (e.g., temperature, salinity, irradiance) were collected in this study, it was possible to compare contemporaneous seasonal and regional water quality data obtained from the SERC-FIU Water Quality Monitoring Network (Boyer & Briceno 2005) with rates of P_g measured in this study for sites in Little Madeira, Rankin Key, Rabbit Key, and Barnes Key. Strong correlations were evident between P_g and temperature, turbidity, and salinity (Table 4.4). Across all of the sites, surface temperature appears to

have driven much of the seasonality observed in rates, as variations in temperature were significantly correlated ($r = 0.57$, $p < 0.01$) with P_g .

Variations in turbidity were negatively correlated ($r = -0.57$, $p < 0.01$) with P_g , suggesting that reductions in light availability associated with increased turbidity resulted in depressions in plant productivity (e.g., Fourqurean et al. 2003). Furthermore, day-to-day and seasonal variations in irradiance measured in this study explained 15-65% of the variability in P_g observed in *T. testudinum* communities (e.g., Fig. 4.5). While it is likely that much of the turbidity within Florida Bay was related to tripton (non-algal particulate matter) concentrations in the water column (e.g., Kelble et al. 2005), phytoplankton abundance (e.g., Philips et al. 1995) may have contributed to light attenuation at Rankin Key. Of all of the sites, phytoplankton abundance, as determined from chlorophyll-*a* concentrations, was highest at Rankin Key, and there was a strong positive correlation ($r = 0.91$, $p < 0.0001$) between turbidity and chlorophyll-*a* (Boyer & Briceno 2005) at this site. The highest degrees of light attenuation observed across the sites consistently occurred at Little Madeira (Table 4.1), and the water column at Little Madeira was typically turbid and laden with tannins. The low degree of water clarity, however, did not appear to be correlated ($r = 0.005$) with reductions in P_g at this site, indicating that the *T. testudinum* plants in Little Madeira may be adapted to low-light conditions (e.g., Kraemer & Hanisak 2000). It is not clear whether events such as phytoplankton blooms (Philips et al. 1995), sediment resuspension (Lawrence et al. 2004) or high concentrations of chromophoric dissolved organic matter (Stabenau et al. 2004) contributed to increased turbidity throughout this study; however reductions in water clarity associated with projected hydrological changes to the Everglades-Florida Bay watershed (Fourqurean et al. 2003) may lead to light-limiting conditions for plant production within this ecosystem in the future.

Salinity was also positively correlated ($r = 0.67$, $p < 0.001$) with variations in P_g . Variability in salinity occurred over both regional and seasonal scales (e.g., Table 4.1), owing to restricted advective exchange between basins for the former and variations in evaporation over the annual cycle for the latter. While, *T. testudinum* is tolerant of prolonged exposure to salinities much higher than those observed in this study (Koch et al. 2007), rapid changes in salinity may temporarily increase plant respiratory demands (Jagels 1983), leading to short-term reductions in plant production. Rapid (~2-3 h) increases in salinity were frequently observed in Little Madeira. This basin is a fairly isolated embayment with minimal freshwater input from Taylor River Slough to the north and limited exchange with an adjacent basin to the South. The relatively rapid increases in salinity suggest increased advective or wind-driven exchange with the adjacent basin leading to the intrusion of higher salinity water into Little Madeira (e.g., Sanford & Boicourt 1990). This rapid (~2-3 h) increase in salinity may have induced physiological stress (Koch & Erskine 2001) on the seagrass plants in Little Madeira, resulting in the observed temporary depression in P_g (see Appendix).

Although nutrient availability certainly regulates plant production in Florida Bay to some extent (e.g., Powell et al. 1989, e.g., Fourqurean et al. 1992), analysis of water column nutrient concentrations did not reveal any significant correlations between nutrient availability and P_g (Table 4.4). In fact, P_g was negatively correlated, albeit weakly (Table 4.4), with total N and P concentrations across all of the sites. This pattern suggests that plant metabolism in these communities regulates nutrient concentrations in the overlying water column. The high leaf affinity for nitrogen at low water column concentrations (Lee & Dunton 1999) results in reduced nutrient efflux from these communities and leads to lower overall nutrient concentrations in the overlying water column. This pattern is supported by observations in the *T. testudinum* community in Sunset Cove (Ch. 2), as plant leaves intercepted and removed ammonium from the

water column within and directly above the canopy by as much as 50% over the diel cycle. Furthermore, sediment nutrients may be a better predictor for P_g in this system as *T. testudinum* likely obtains most of its nutrients needed to support growth via assimilation from the sediment through belowground tissues (Lee & Dunton 1999, Nielsen et al. 2006).

Although seagrass communities are often considered as highly productive, several studies have reported instances of both a balance between P_a and R (D'Avanzo et al. 1996, Ziegler & Benner 1998, Santos et al. 2004, Gacia et al. 2005) and instances of net heterotrophy (Barron et al. 2004, Caffrey 2004) in seagrass ecosystems (see Appendix). This apparent incongruity arises from high plant respiratory demands combined with enhanced heterotrophic activity within these communities. There were a few instances where heterotrophic processes seemed to overcome autotrophic production in *T. testudinum* communities in Florida Bay. The majority of these instances appear to be related to increased turbidity during wind resuspension events observed during these periods (Kelble et al. 2005). In Barnes Key, an active dieback event occurred in August 2003, as evidenced by the abundance of yellowing leaves and necrotic lesions as well as reduced overall coverage (Nagel, J. pers. obs.). The negative rates of NEP combined with P_a :R ratios < 1 suggest that heterotrophic processes dominated ecosystem metabolism during the dieback event. Seagrass dieback appears to have had only a temporary impact on NEP in Barnes Key, since rates rebounded to positive values in subsequent months. This pattern of apparent seasonal recovery from seagrass dieback at Barnes Key was also observed in 2002-2003, when plant biomass increased significantly in winter following a dieback event observed during the summer (see Chapter 3). While the cause of the dieback in Barnes Key is not clear, prolonged dieback events and further loss of seagrasses could result in a shift from net autotrophy to net heterotrophy within this basin.

While a few instances of net heterotrophy (i.e., negative values of NEP) did occur throughout the year in this study (Table 4.2), *T. testudinum* communities in Florida Bay appear to be net autotrophic throughout most of the year and this is consistent with reports from other seagrass communities (Hemminga & Duarte 2001, Barron et al. 2004, Gazeau et al. 2005). The magnitude of both NEP and values of $P_a:R$ varied regionally. *T. testudinum* communities in Sunset Cove and Rabbit Key exhibited the highest rates of NEP, but the $P_a:R$ ratios indicate that these communities were only slightly autotrophic or are in balance with respect to P_a and R (Fig. 4.8a). Lowest overall rates of P_a and R were observed in Little Madeira, however, $P_a:R$ ratios at this site were the highest recorded for any region. With the inputs of organic-rich nutrients from Taylor River Slough and high light attenuation relative to other basins (Kelble et al. 2005), it might be expected that the heterotrophic processes dominate NEP in Little Madeira (Kemp et al. 1997). The positive net NEP and high $P_a:R$ ratios indicate that this community is clearly net autotrophic, suggesting that inputs of organic matter from the Everglades may not be as important for regulating NEP in Little Madeira as originally thought. Projected changes to the hydrological regime in the Everglades will redirect and increase water flow through Taylor River Slough into Little Madeira (Fourqurean et al. 2003), which could increase inputs of organic matter and the relative importance of heterotrophic processes to ecosystem production in Little Madeira in the future.

The results of this study represent a unique contribution to the knowledge of the role of *T. testudinum* in production, respiration, and NEP in Florida Bay. Despite regional variability in rates, annual estimates of NEP (Table 4.3) and $P_a:R$ ratios (Fig. 4.8b) suggest that *T. testudinum* communities in Florida Bay were net autotrophic over the course of the year. These annual estimates represent a first-cut look at regional differences in the bay and may be useful for calculating a bay-wide budget. Direct measurements of air-sea exchange coefficients, spatial coverage of seagrasses, and

advective exchange between basins are necessary to improve these estimates and aid in the construction of a bay-wide estimate of ecosystem production. Projected changes to Everglades hydrology will increase freshwater inputs to the Bay and could alter the balance between production and respiration within this system. The information gleaned from this study provides a baseline to which future estimates of ecosystem production in Florida Bay can be compared.

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Table 4.1. Mean (\pm SE) Dissolved O₂ concentrations (μ M), percent oxygen saturation (% Sat), range in % saturation, temperature ($^{\circ}$ C), salinity, and light attenuation coefficients (k_d , units = m^{-1}) in *Thalassia testudinum* beds throughout Florida Bay in 2003-4. "nd" indicates that no data are available for that month.

Site	O ₂	% Saturation	% Saturation Range	T	Salinity	k_d
Little Madeira						
Aug '03	226 \pm 0.82	102 \pm 0.41	82 - 134	29.8 \pm 0.04	11.3 \pm 0.05	nd
Nov '03	240 \pm 0.54	94 \pm 0.21	62 - 105	24.1 \pm 0.03	4.93 \pm 0.03	1.91
Jan '04	269 \pm 0.65	104 \pm 0.24	79 - 128	20.1 \pm 0.04	15.4 \pm 0.12	0.82
Mar '04	245 \pm 0.70	100 \pm 0.28	62 - 135	23.0 \pm 0.05	16.2 \pm 0.03	1.27
Jun '04	181 \pm 1.26	94 \pm 0.68	56 - 147	30.5 \pm 0.03	35.4 \pm 0.01	0.91
Nov '04	204 \pm 0.61	92 \pm 0.27	58 - 114	26.4 \pm 0.02	36.0 \pm 0.08	5.65
Rankin						
Aug '03	194 \pm 1.34	102 \pm 0.74	72 - 155	29.7 \pm 0.03	39.9 \pm 0.01	nd
Nov '03	228 \pm 0.76	97 \pm 0.35	76 - 120	23.9 \pm 0.03	20.0 \pm 0.04	0.76
Jan '04	246 \pm 0.89	105 \pm 0.37	84 - 127	20.6 \pm 0.05	32.0 \pm 0.01	0.44
Mar '04	229 \pm 0.87	100 \pm 0.41	78 - 136	21.2 \pm 0.04	33.6 \pm 0.02	0.95
Jun '04	188 \pm 1.17	105 \pm 0.69	66 - 159	30.5 \pm 0.03	47.8 \pm 0.02	0.95
Nov '04	nd	nd	nd	25.7 \pm 0.02	36.4 \pm 0.04	0.84
Rabbit						
Aug '03	231 \pm 1.45	121 \pm 0.80	86 - 166	29.9 \pm 0.03	38.5 \pm 0.01	nd
Nov '03	219 \pm 7.16	99 \pm 3.38	78 - 128	24.3 \pm 0.25	31.8 \pm 0.06	0.87
Jan '04	247 \pm 0.61	107 \pm 0.27	90 - 123	20.4 \pm 0.03	33.5 \pm 0.01	0.26
Mar '04	241 \pm 0.90	106 \pm 0.72	85 - 126	22.9 \pm 0.05	35.0 \pm 0.01	0.41
Jun '04	202 \pm 0.98	108 \pm 0.54	74 - 146	30.4 \pm 0.02	41.1 \pm 0.02	0.38
Nov '04	186 \pm 0.67	89 \pm 0.34	73 - 108	26.3 \pm 0.02	36.1 \pm 0.02	0.64
Barnes						
Aug '03	163 \pm 0.81	85 \pm 0.45	64 - 112	29.7 \pm 0.03	38.4 \pm 0.01	nd
Nov '03	245 \pm 1.03	112 \pm 0.31	90 - 137	24.2 \pm 0.03	31.9 \pm 0.01	0.55
Jan '04	246 \pm 0.90	106 \pm 0.42	87 - 138	20.4 \pm 0.03	32.3 \pm 0.01	0.66
Mar '04	213 \pm 0.99	94 \pm 0.24	77 - 125	22.3 \pm 0.05	34.2 \pm 0.01	0.48
Jun '04	207 \pm 0.74	111 \pm 0.41	77 - 145	30.2 \pm 0.02	42.4 \pm 0.01	0.51
Nov '04	166 \pm 0.89	81 \pm 0.46	52 - 112	26.3 \pm 0.02	39.1 \pm 0.02	0.54
Sunset Cove						
Aug '03	175 \pm 1.35	90 \pm 0.72	50 - 131	29.9 \pm 0.03	36.3 \pm 0.00	nd
Nov '03	246 \pm 6.87	108 \pm 2.95	88 - 125	23.5 \pm 0.20	26.7 \pm 0.09	0.27
Jan '04	nd 0.00	nd	nd	nd	nd	0.89
Mar '04	263 \pm 0.70	116 \pm 0.33	86 - 154	23.2 \pm 0.04	28.2 \pm 0.01	0.26
Jun '04	202 \pm 1.11	106 \pm 0.61	66 - 153	31.1 \pm 0.02	36.3 \pm 0.04	0.51
Nov '04	195 \pm 0.71	97 \pm 0.36	52 - 142	26.2 \pm 0.02	40.4 \pm 0.01	1.03

Table 4.2. Rates (mean \pm SE) of NEP, P_a , P_g , and R (mmol O₂ m⁻² d⁻¹) in *Thalassia testudinum* beds throughout Florida Bay in 2003-4. “n” indicates the number of days over which the parameters were measured, and “nd” indicates that no data are available for that month. An “*” next to sites in November 2003 indicates that rates were calculated from changes between minimum and maximum O₂ concentrations available for those sites (see methods).

Site	P_a	R	P_g	NEP	n
Little Madeira					
Aug '03	73.9 \pm 14.1	36.7 \pm 7.84	117 \pm 22.7	37.1 \pm 8.00	4
Nov '03	39.1 \pm 8.96	38.8 \pm 10.8	71.2 \pm 15.0	0.27 \pm 11.0	7
Jan '04	56.2 \pm 8.14	32.3 \pm 8.15	82.6 \pm 11.0	23.9 \pm 11.0	6
Mar '04	72.7 \pm 9.44	57.3 \pm 7.44	130 \pm 9.75	15.5 \pm 13.8	12
Jun '04	nd	nd	nd	nd	nd
Nov '04	66.3 \pm 9.88	53.7 \pm 11.2	113 \pm 11.35	12.6 \pm 17.2	12
Rankin					
Aug '03	101 \pm 22.1	83.8 \pm 8.41	196 \pm 31.9	20.3 \pm 14.1	4
Nov '03	62.1 \pm 8.57	62.0 \pm 4.81	114 \pm 9.16	-0.94 \pm 9.81	7
Jan '04	72.5 \pm 10.0	50.3 \pm 3.41	114 \pm 8.57	22.3 \pm 13.8	5
Mar '04	68.0 \pm 10.5	55.4 \pm 3.51	123 \pm 12.3	7.50 \pm 9.79	5
Jun '04	99.8 \pm 10.5	81.6 \pm 5.65	208 \pm 10.5	18.2 \pm 13.6	5
Nov '04	nd	nd	nd	nd	nd
Rabbit					
Aug '03	224 \pm 40.0	146 \pm 20.3	398 \pm 57.5	77.6 \pm 32.7	4
Nov '03*	126 \pm 9.28	117 \pm 12.3	229 \pm 2.78	23.8 \pm 15.8	3
Jan '04	85.8 \pm 12.3	60.4 \pm 5.19	135 \pm 10.9	25.4 \pm 15.4	5
Mar '04	110 \pm 12.0	110 \pm 8.83	220 \pm 10.7	-35.0 \pm 17.2	6
Jun '04	208 \pm 5.95	133 \pm 4.37	385 \pm 8.32	74.4 \pm 7.32	7
Nov '04	89.0 \pm 9.20	111 \pm 3.50	188 \pm 7.83	-22.5 \pm 11.5	4
Barnes					
Aug '03	107 \pm 16.1	113 \pm 9.02	242 \pm 13.6	-20.0 \pm 22.2	6
Nov '03	129 \pm 23.7	68.1 \pm 16.8	185 \pm 34.6	61.1 \pm 18.8	5
Jan '04	82.6 \pm 8.09	81.2 \pm 8.34	149 \pm 5.99	1.38 \pm 15.1	6
Mar '04	nd	nd	nd	nd	nd
Jun '04	166 \pm 11.7	86.2 \pm 6.01	281 \pm 17.1	79.8 \pm 10.2	7
Nov '04	69.0 \pm 9.77	107 \pm 5.71	164 \pm 12.3	-37.6 \pm 14.8	3
Sunset Cove					
Aug '03	247 \pm 15.3	181 \pm 16.6	461 \pm 6.71	33.6 \pm 39.4	4
Nov '03*	128 \pm 16.9	101 \pm 18.2	229 \pm 22.0	26.7 \pm 27.4	3
Jan '04	nd	nd	nd	nd	nd
Mar '04	217 \pm 13.5	111 \pm 9.21	329 \pm 22.5	106 \pm 5.54	12
Jun '04	238 \pm 16.2	170 \pm 16.6	464 \pm 34.4	68.8 \pm 14.4	8
Nov '04	176 \pm 19.0	149 \pm 15.2	305 \pm 26.9	27.6 \pm 19.0	11

Table 4.3. Seasonal ($\text{mol C m}^{-2} \text{ mo}^{-1}$) and annual ($\text{mol C m}^{-2} \text{ yr}^{-1}$) estimates of NEP, P_a , P_g , and R in *Thalassia testudinum* beds throughout Florida Bay.

Site	P_a	R	P_g	NEP
Little Madeira				
<i>Winter</i>	1.69	1.13	2.48	0.72
<i>Spring</i>	2.23	1.18	3.99	0.47
<i>Summer</i>	2.27	0.97	3.60	1.14
<i>Fall</i>	1.19	1.76	2.16	0.01
<i>Annual</i>	22.1	15.1	36.7	7.01
Rankin				
<i>Winter</i>	2.18	1.51	3.41	0.67
<i>Spring</i>	2.09	1.70	3.77	0.23
<i>Summer</i>	3.10	2.57	6.03	0.62
<i>Fall</i>	1.88	1.88	3.46	-0.03
<i>Annual</i>	27.7	23.0	50.0	4.48
Rabbit				
<i>Winter</i>	2.57	1.81	4.06	0.76
<i>Spring</i>	3.39	3.37	6.74	-1.07
<i>Summer</i>	6.87	4.49	12.2	2.38
<i>Fall</i>	3.83	3.55	6.93	0.72
<i>Annual</i>	50.0	39.7	89.8	8.37
Barnes				
<i>Winter</i>	2.48	2.44	4.47	0.04
<i>Spring</i>	5.09	2.64	8.60	2.45
<i>Summer</i>	3.29	3.47	7.41	-0.61
<i>Fall</i>	3.92	2.06	5.62	1.85
<i>Annual</i>	44.3	31.8	78.3	11.2
Sunset Cove				
<i>Winter</i>	6.52	3.34	9.88	3.18
<i>Spring</i>	7.31	5.20	14.2	2.11
<i>Summer</i>	7.59	5.56	14.1	1.03
<i>Fall</i>	3.88	3.07	6.96	0.81
<i>Annual</i>	75.9	51.5	136	21.4

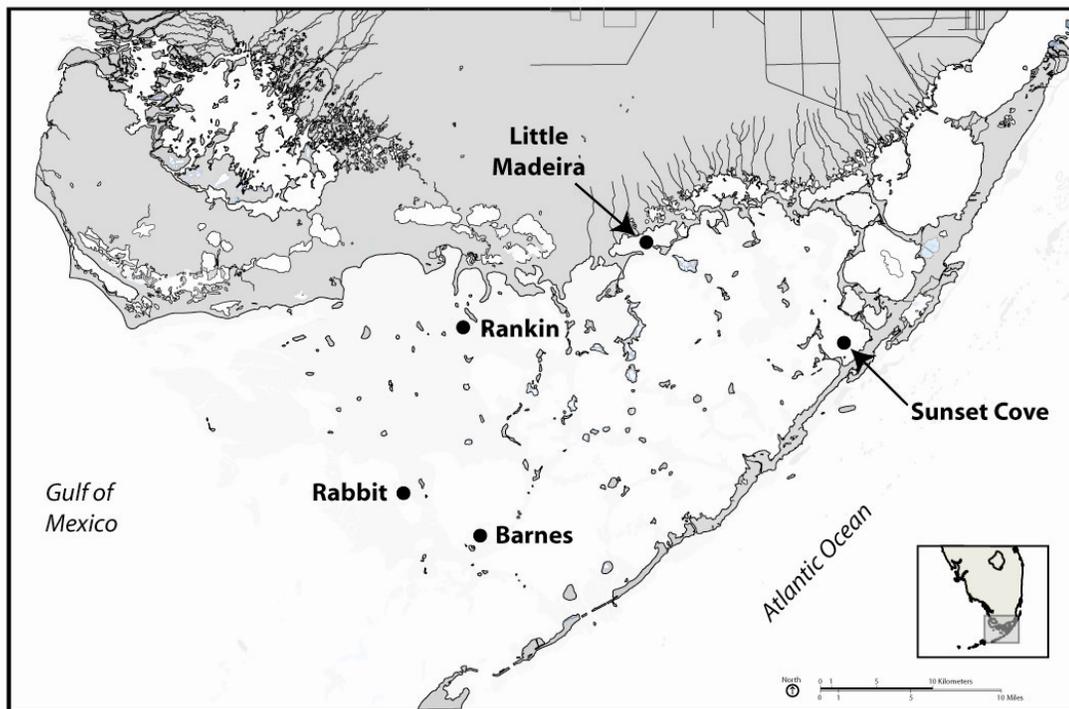


Fig. 4.1. Map of field study sites in Florida Bay.

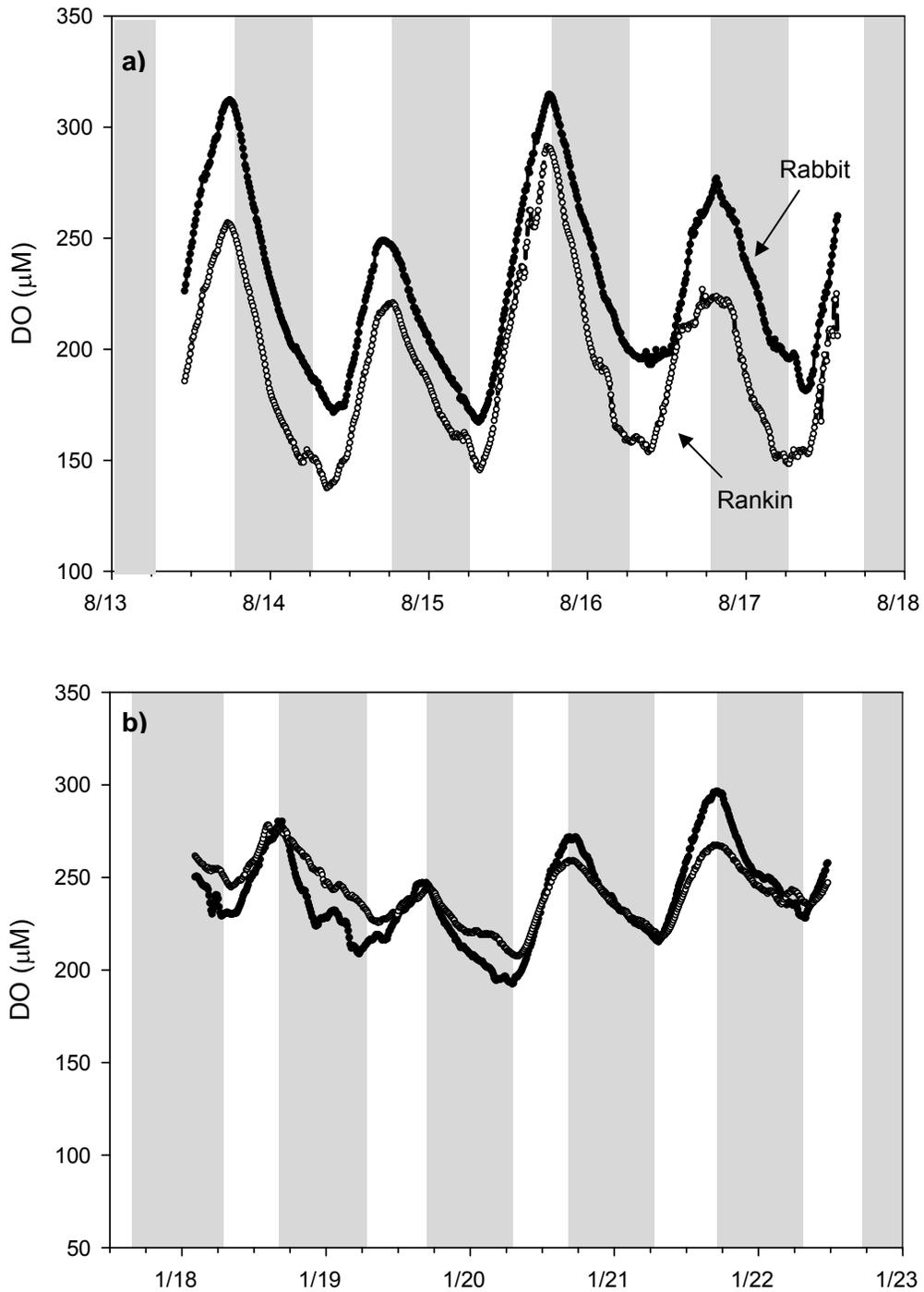


Fig. 4.2. Example of diel variation in continuous O_2 concentrations (μM) in Rankin (open symbol) and Rabbit (solid) in August 2003 (a) and January 2004 (b). Shaded areas indicated nighttime hours.

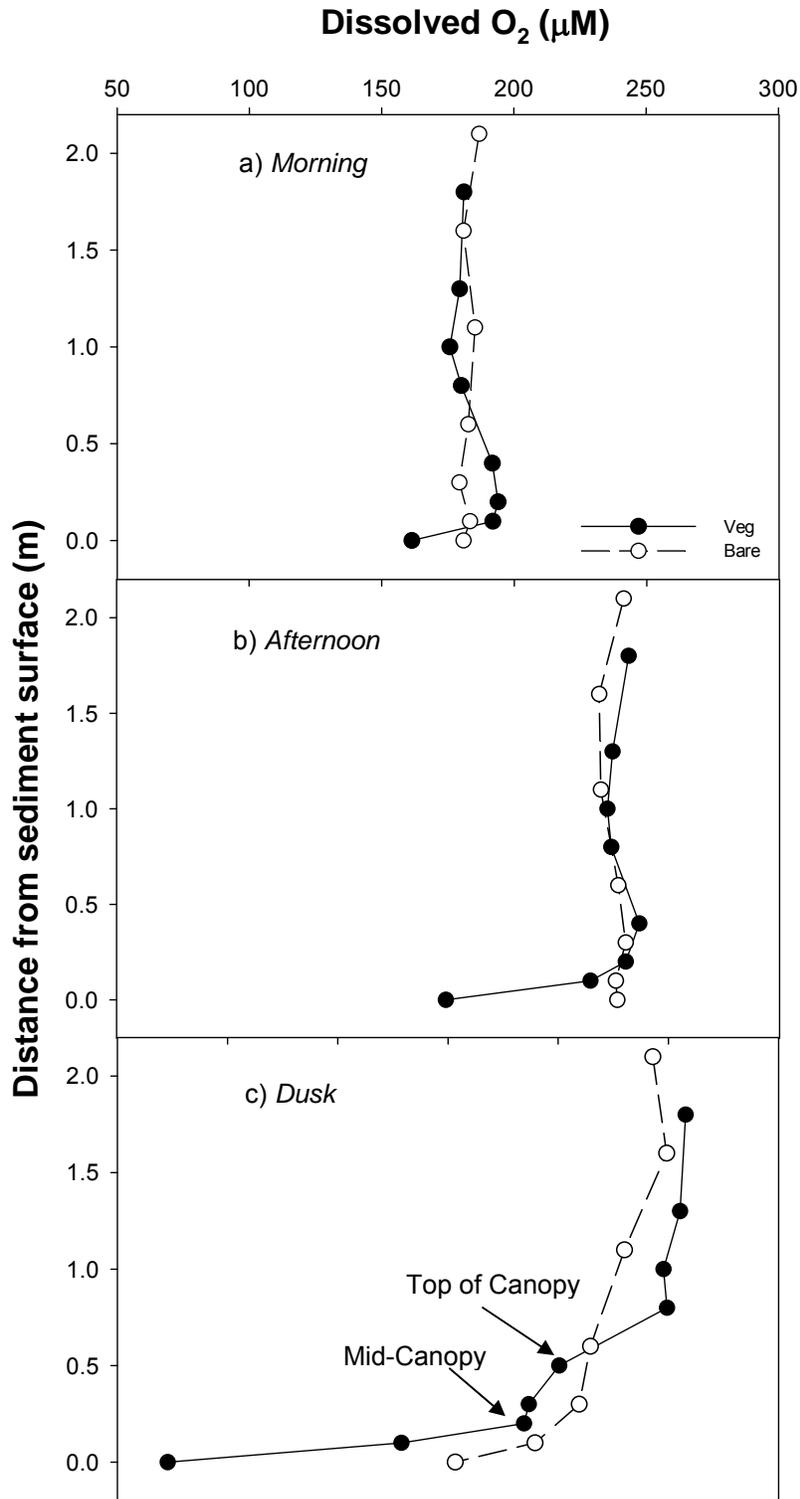


Fig 4.3. Vertical profiles of water column O₂ concentrations (µM) in a *Thalassia testudinum* bed and adjacent bare area at Sunset Cove in June 2004 during the morning (a), mid-afternoon (b), and at dusk (c). Depth on the y-axis is presented as distance from the sediment surface in meters.

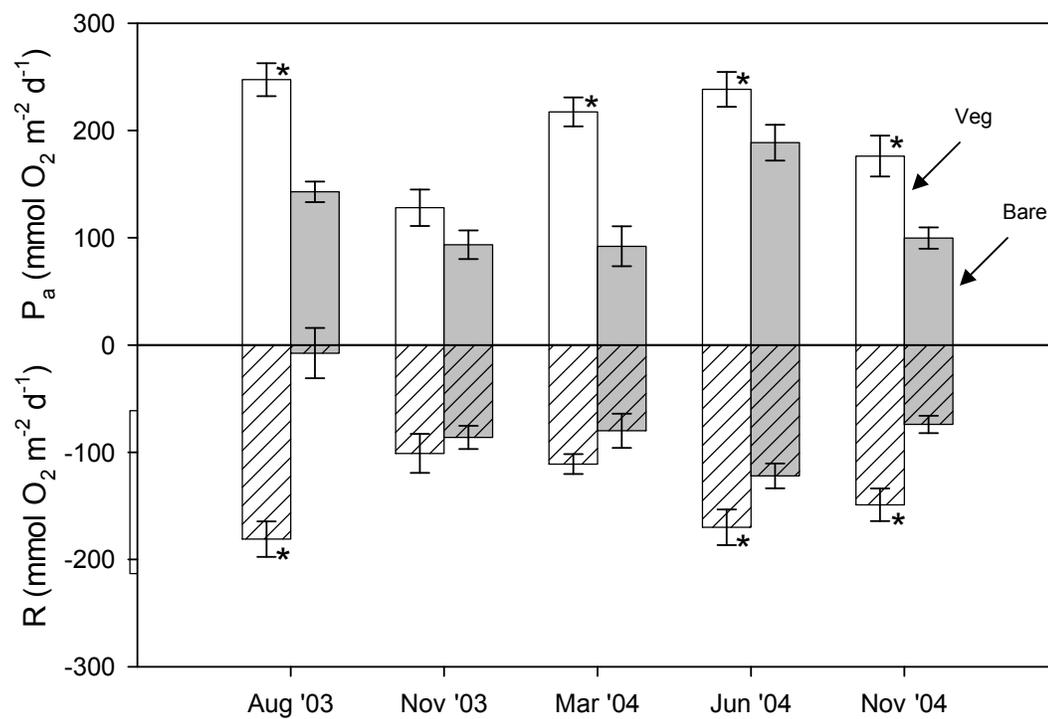


Fig. 4.4. Seasonal variations in mean (\pm SE) rates of P_a (open) and R (hatched bars) in a *T. testudinum* bed (white bars) and bare area (gray bars) in Sunset Cove in 2003-2004. An “*” indicates a significant difference at $p < 0.05$ between the sites for each rate.

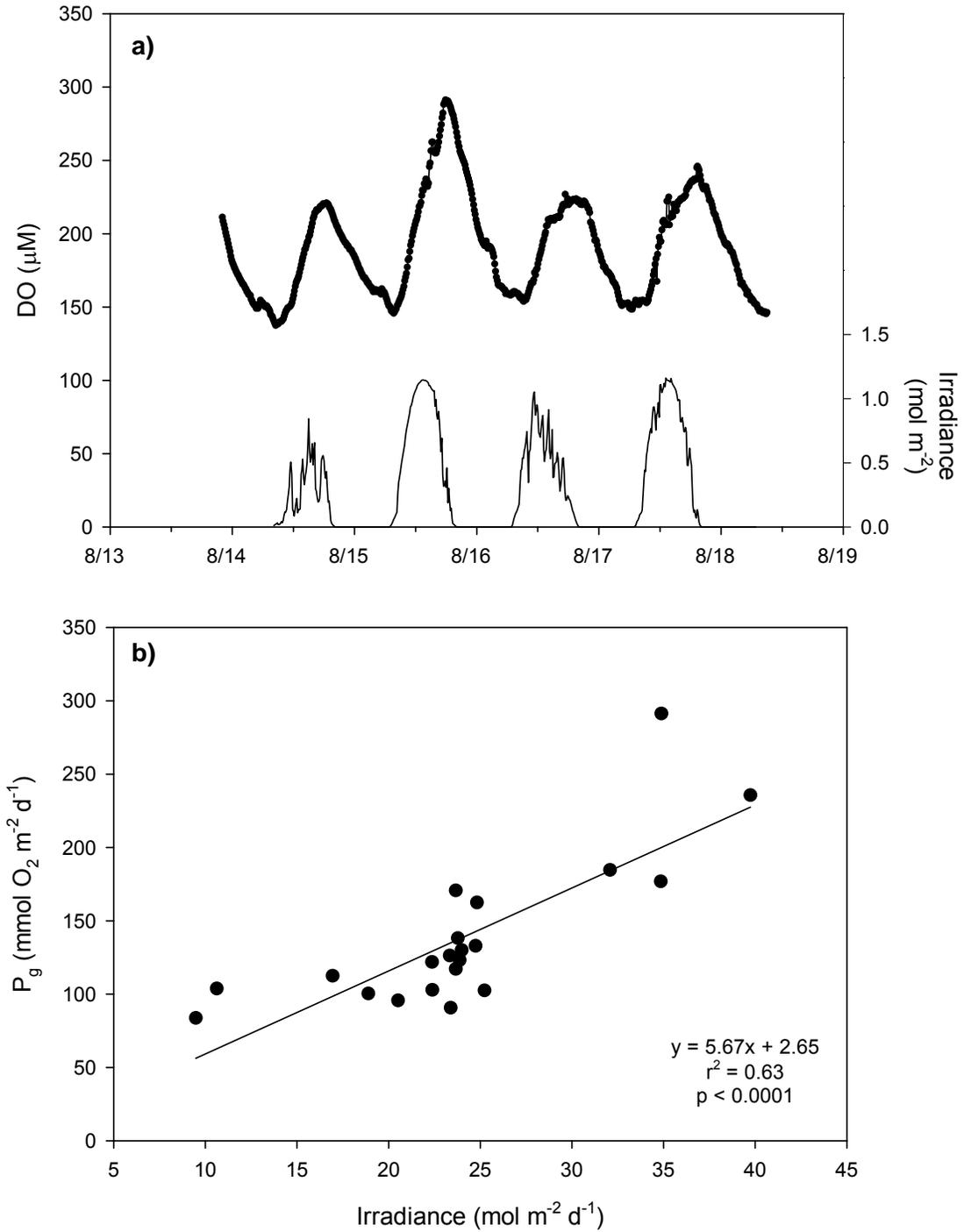


Fig. 4.5. (a) Diel variations in dissolved O_2 concentrations (μM) (bold line) and irradiance in a *T. testudinum* bed in Rankin during August 2004. (b) Linear regression of P_g ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) on irradiance in Rankin throughout 2003-4.

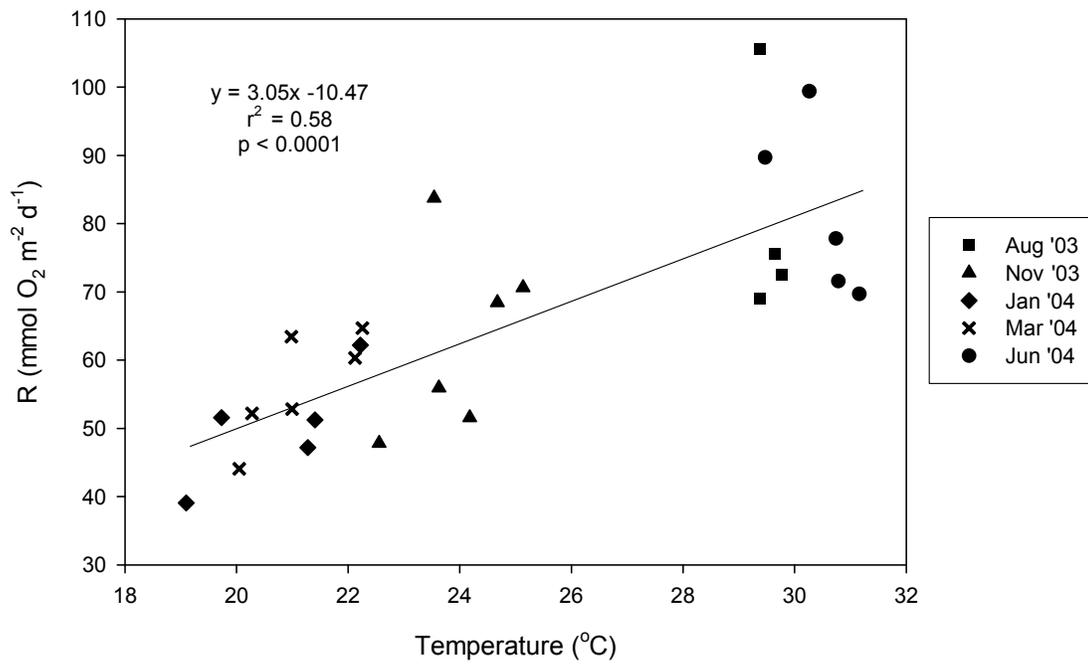


Fig. 4.6. Linear regression of nighttime respiration (mmol O₂ m⁻² d⁻¹) versus temperature (°C) in a *Thalassia testudinum* bed at Rankin in 2003-4.

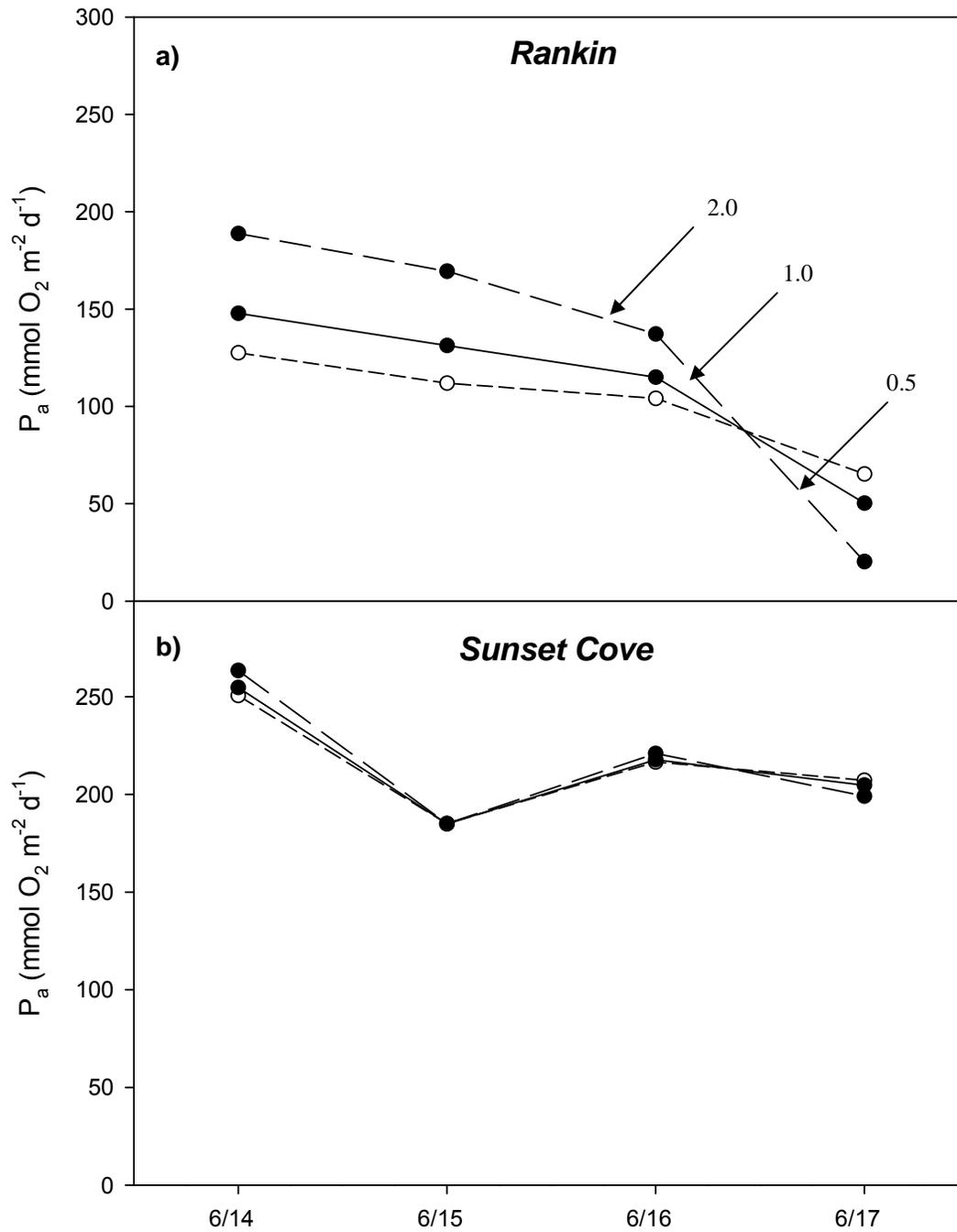


Fig. 4.7. Example of daily variations in P_a (mmol O_2 m^{-2} d^{-1}) at Rankin (a) and Sunset Cove (b) in response to variable air-sea exchange coefficients of 0.5, 1.0, and 2.0 g O_2 m^{-2} h^{-1} at 100% Saturation.

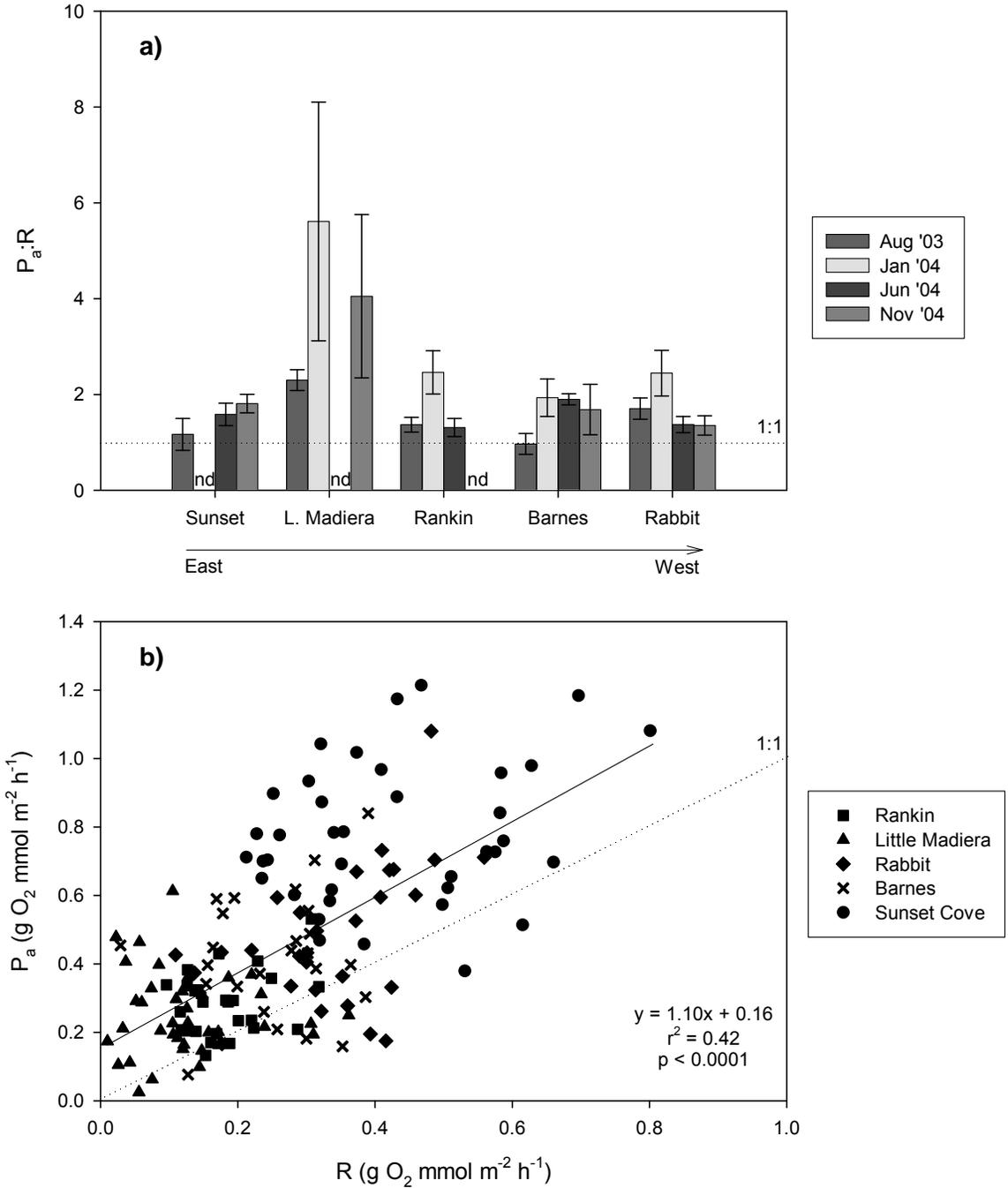


Fig. 4.8. (a) Seasonal variations in mean (\pm SE) ratios of $P_a:R$ in *T. testudinum* communities along an east-west transect in Florida Bay. (b) Linear regression of $P_a:R$ for all *T. testudinum* communities in Florida Bay. The dotted lines in both (a) and (b) represent a $P_a:R$ ratio of 1.

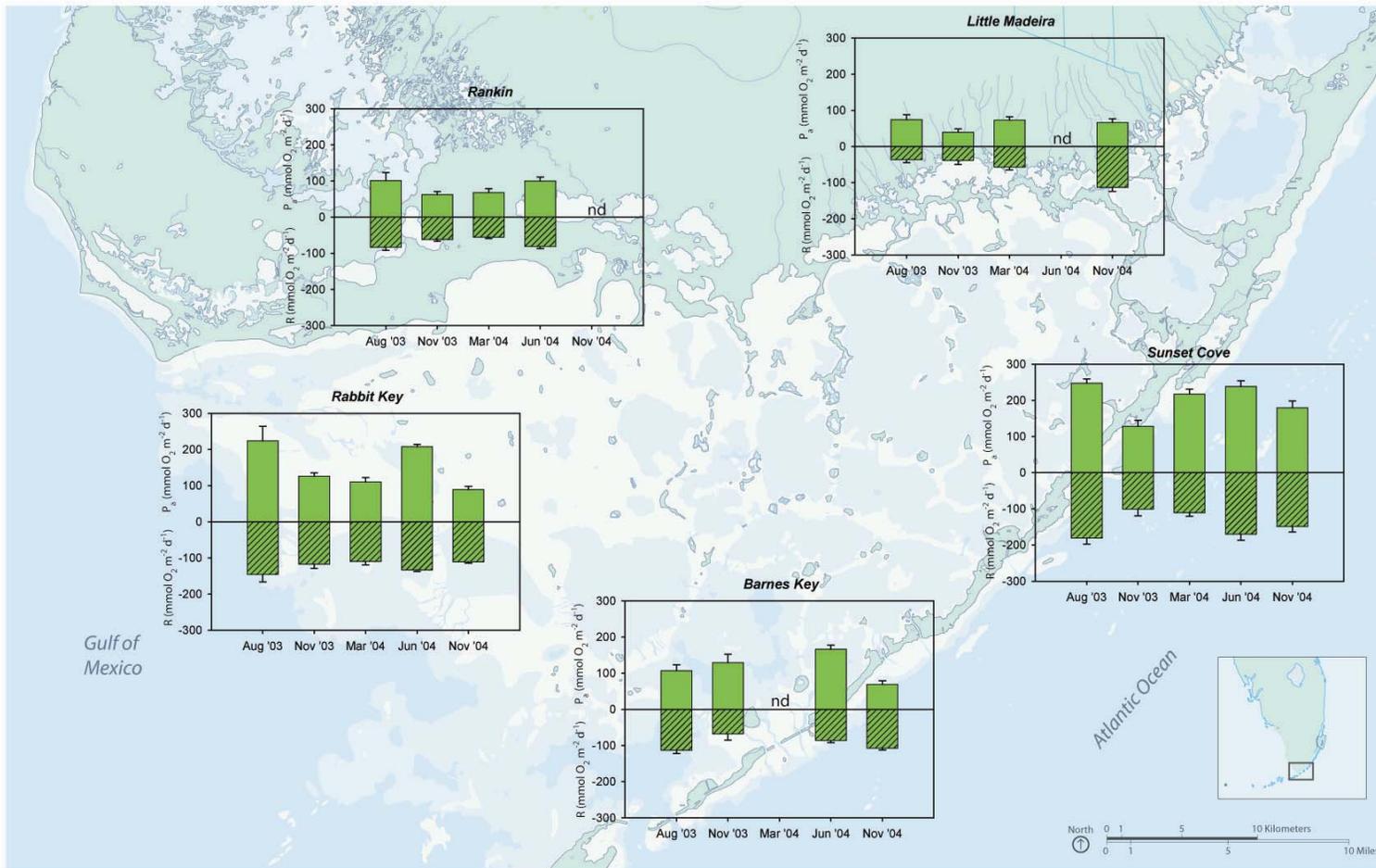


Fig. 4.9. Regional variations in P_a and R (hatched) ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) at 5 sites across Florida Bay in 2003-2004.

CHAPTER 5: Influence of the submersed plants *Ruppia maritima* and *Potamogeton perfoliatus* on biogeochemical cycling in Chesapeake Bay, USA

ABSTRACT

This study examines how organic production, nutrient cycling and related sediment biogeochemical processes in mesohaline Chesapeake Bay are affected by the submersed plants *Ruppia maritima* and *Potamogeton perfoliatus*. I also investigated differences in the influence of the vegetative and reproductive growth forms of *R. maritima* on these processes. I compared sediment porewater concentrations, potential nitrification and sediment-water exchange rates of O₂, N₂, NH₄⁺, dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) in plant communities versus adjacent unvegetated areas. Clear diel trends were observed in all benthic fluxes and many of these processes were positively related to plant biomass. In general, benthic fluxes and biogeochemical processes were enhanced in plant communities relative to adjacent unvegetated sediments colonized by benthic microalgae. Vegetated communities were significant sources of both DOC and DON to the overlying water column over a diel cycle and DOC production represented ~10-200% of photosynthetic production within these communities. Lower rates of biomass-specific O₂ production and nitrification and higher sediment porewater concentrations of NH₄⁺ and sulfide were observed in reproductive compared to vegetative *R. maritima* communities. Highest rates of net community O₂ production and coupled nitrification-denitrification were observed in *P. perfoliatus* compared to *R. maritima* communities. These results illustrate the biogeochemical importance of *R. maritima*, which is presently one of the most abundant submersed plants in Chesapeake Bay. Restoration of *P. perfoliatus* would further improve water quality conditions through the greater influence of this submersed plant on trapping and recycling nutrients and enhancing denitrification.

INTRODUCTION

Chesapeake Bay was once home to a diverse and abundant community of submersed aquatic plants (Orth & Moore 1983). In the mid 1960's, degradation of water quality associated with eutrophication led to an unprecedented decline in these communities throughout the Bay (Kemp et al. 1983, Twilley et al. 1985). Significant ecological consequences were associated with the loss of submersed plants, which provide food and habitat to diverse fish and invertebrates (Orth & Vanmontfrans 1987, Lubbers et al. 1990, Heck et al. 1995, Polte & Asmus 2006), enhanced sediment trapping (Ward et al. 1984, Gacia & Duarte 2001) and stimulate biogeochemical processes (e.g., Caffrey & Kemp 1990). Similar patterns of plant loss and ecosystem response have been described for numerous coastal environments worldwide (Short & Wyllie-Echeverria 1996, Orth et al. 2006).

The decline in submersed aquatic plant abundance in Chesapeake Bay led to the development of vast unvegetated shoals throughout the estuary. During the last two decades, many of these areas have been colonized by the native euryhaline species, *Ruppia maritima*, resulting in a modest recovery in total plant abundance, particularly in the mesohaline region (www.vims.edu/bio/sav). *Ruppia maritima* has two growth forms, a vegetative form, in which shoots (15-20 cm) can create dense meadows that occupy a small fraction of the water column, and a reproductive form, characterized by longer shoots (40-100 cm) that produce canopies at high densities (Silberhorn et al. 1996). This ruderal species has the ability to rapidly colonize unvegetated sediments and maintain its presence in disturbed environments for extended periods of time (Dunton 1990, Johnson et al. 2003). Despite its widespread distribution, there has been considerable interannual variability in both bed size and shoot density for *R. maritima* in this region (Schulte 2003). Other

historically abundant species, such as *Potamogeton perfoliatus*, remain scarce in this estuarine region.

Although the growth and survival of submersed aquatic plants often depends on environmental conditions in sediments and overlying water (Koch 2001, Kemp et al. 2004), submersed estuarine plants such as *Ruppia maritima* and *Potamogeton perfoliatus*, may play an active role in sediment biogeochemical cycling. Plant-enhanced deposition of particulate organic matter (Ward et al. 1984, Gacia & Duarte 2001) fuels microbial-mediated organic decomposition and resultant regeneration of inorganic nutrients (Kenworthy et al. 1982). Root release of O₂ to the rhizosphere (Sand-Jensen et al. 1982, Thursby 1984, Kemp & Murray 1986, Frederiksen & Glud 2006) may enhance aerobic microbial processes, such as nitrification (Caffrey & Kemp 1990). Root excretion of dissolved organic matter (DOM) to porewaters (Moriarty et al. 1986, Kaldy et al. 2006) may stimulate microbial processes such as nitrogen fixation (Welsh et al. 1996, McGlathery et al. 1998) and sulfate reduction (Holmer & Nielsen 1997, Blaabjerg & Finster 1998, Hansen et al. 2000). Although enhanced sulfate reduction can result in accumulation of phytotoxic sulfide in the porewaters (Goodman et al. 1995, Koch & Erskine 2001), root O₂ release can counteract this effect by oxidizing sulfide in the rhizosphere and preventing accumulation of sulfide to toxic concentrations (Lee & Dunton 2000). In addition, photosynthetically-derived DOM is released directly from plant leaves to the surrounding water (e.g., Wetzel & Penhale 1979) where it supports elevated bacterioplankton production (Moriarty et al. 1990, Chin-Leo & Benner 1991).

In this study, I compare how organic production, nutrient cycling and sediment biogeochemistry are influenced by stands of *Ruppia maritima* and *Potamogeton perfoliatus* in contrast to adjacent reference sites without submersed vascular plants. In addition, I investigate the effects of the vegetative versus

reproductive growth forms of *R. maritima*. I hypothesize that differences in growth and reproductive strategies, canopy structures, and belowground biomass allocations between these species and growth forms affect their interactions with biogeochemical processes in associated sediments and water columns.

METHODS

Site description. Measurements of sediment biogeochemical processes were conducted during the summers of 2003 and 2004 at study sites containing *Ruppia maritima* and *Potamogeton perfoliatus* beds located in the mesohaline region of Chesapeake Bay (Fig. 5.1). These sites were selected after careful review of historical distribution data (www.vims.edu/bio/sav) and field reconnaissance to provide beds of similar persistence (i.e., present 10 out of last 20 years), but different vegetation type (e.g., dominated by vegetative or flowering, reproductive shoots) and dominant species (viz., *R. maritima* or *P. perfoliatus*). Mean water depth at all sites was approximately 1.0 m (mean sea level), and salinity ranged from 8 – 12 at the *R. maritima* sites and 7 – 9 at the *P. perfoliatus* site.

Over the course of this study, I sampled two pairs of *Ruppia maritima* beds in mesohaline Chesapeake Bay. In July 2003, I sampled two *R. maritima* beds of similar size (~5 ha) located at the mouth of Eastern Bay on the eastern shore of the Chesapeake Bay (Fig. 5.1). The bed in Claiborne Cove (38° 50.103'N 76° 16.750' W) was dominated by non-flowering, vegetative shoots of *R. maritima* with only a few flowering, reproductive shoots observed over the entire bed. In contrast, the majority of *R. maritima* shoots in Ferry Cove (38° 45.986'N 76° 19.770' W) were reproductive, with many shoots extending to the water surface. In July 2004, I sampled two different *R. maritima* beds of similar size (~ 25 ha) located in Broad Creek (Fig. 5.1), a tributary of the Choptank River. Plants in Elberts Cove (38° 44.170' N, 76° 13.124'

W) were predominantly reproductive shoots, whereas those in Neavitt Cove (38° 43.074' N 76° 16.391' W) were comprised by only vegetative shoots. With the exception of Ferry Cove, plant density was typically highest in the interior of the bed and gradually tapered off toward the outer edges.

As no *Potamogeton perfoliatus* beds were present in the Choptank River region in 2003-04, I collected samples from a *P. perfoliatus* bed located in the Severn River (39° 02.081' N, 76° 31.901' W) on the western shore of the Chesapeake Bay (Fig. 5.1). The Severn River bed was large (~ 24 ha), and dense (100% coverage), with most shoots reaching the water surface. Density was highest in the center of the bed and only slightly lower on the edges, forming a distinct boundary between vegetated and unvegetated areas.

Benthic fluxes. In each experiment, sediment cores were collected from each site during peak growing season (late June – early July). Replicate intact plant and sediment units (n=3) were collected using clear acrylic cylindrical cores (dia = 15 cm, h = 47 cm) in each of the following locations: (1) the interior of the bed (inside), (2) 5-10 m from the edge of the bed (edge), and (3) outside of the bed in an unvegetated area within 25-50 m of the edge (unveg). Each core contained approximately 15 cm of sediment column that was overlain by approximately 20 cm of water column. Immediately upon collection, each core was fitted with a rubber boot at the base and sealed with a stainless steel hose clamp to prevent leakage of sediment. Cores were then transported to the laboratory where they were placed randomly in flow-through incubators under ambient temperature within 4 h of collection. Leaves and shoots were cleaned of loosely attached epiphytic material, and loose plant material was also removed. The cores were then filled with site water to replace any that had been lost during transport and were aerated using aquarium pumps to ensure full O₂

and CO₂ saturation of the water column. Neutral-density screening was placed over each incubator to simulate natural light levels. The cores were then allowed to equilibrate overnight in the incubators prior to the beginning of the experiment.

At dawn the following morning, the cores were sealed with clear acrylic lids to remove any gas headspace. To ensure proper mixing of the water column, each core was fitted with a magnetic stirbar that was continuously rotated via a central motor-driven magnetic turntable. Water samples were collected from a sampling port on the lid while an equal volume of site water was simultaneously added to replace sample water. Water samples for O₂ and N₂ gases were taken during the first 4 h after dawn (light) and for several hours after dusk (dark) at 30-45 min intervals, while water samples for NO₃⁻, NH₄⁺, PO₄³⁻, dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) were taken at 2-3 h intervals over the course of the incubation. The short intervals between gas sampling allowed time-course measurements prior to the formation of any bubbles in the cores during the experiment, as bubbles may interfere with sample analysis (Kana et al. 1994). After gas sample collection in the light, the cores were unsealed and aerated to maintain O₂ and CO₂ at saturation in the water column. The cores were resealed prior to dusk to measure changes in gas concentrations during the dark following the same protocol that was used at dawn.

Water samples taken during the incubation for N₂ and O₂ gases were collected in 8 mL glass vials, immediately treated with mercuric chloride (HgCl₂), capped, and stored in an ambient water bath. The samples were analyzed within two weeks of collection using a membrane inlet mass spectrometer (Kana et al. 1994) to measure changes in O₂ and N₂ relative to Ar concentrations in the water column. Because of the absence of headspace within the cores, changes in water column O₂ and N₂ concentrations in the light and dark were attributed to processes

associated with the plants, sediments, and overlying water column. Increases in O_2 in the light and dark were attributed to photosynthetic and respiratory processes, respectively. Increases in dark N_2 concentrations were attributed to release of N_2 from the sediments associated with denitrification (Kana et al. 1998).

Water samples for NH_4^+ , NO_3^- , PO_4^{3-} , DOC, and DON concentrations were passed through ashed 0.7- μm GF/F filters and were immediately frozen. NH_4^+ , PO_4^{3-} , and $NO_3^-+NO_2^-$ samples were analyzed colorimetrically following Parsons et al. 1984. DON concentrations were obtained by subtracting inorganic nitrogen from total nitrogen concentrations, which were determined colorimetrically after persulfate digestion (Parsons et al. 1984). DOC concentrations were determined by high temperature catalytic oxidation (Sugimura & Suzuki 1988).

Following the incubation subsamples for solid phase pools of sediment C, H, N and P and sediment chlorophyll-a were collected from each core. Samples for solid phase nutrients and sediment chlorophyll-a were collected using a cut-off plastic syringe (0.7 cm dia) that was inserted to a depth of 1 cm and were immediately frozen for subsequent analysis. Samples for solid phase nutrients were dried at 60°C for 48 h, ground, and analyzed following Aspila et al. (1976). Sediment samples for chlorophyll-a analysis were thawed, extracted with 90% acetone for 24 h and analyzed using a Turner Fluorometer (Parsons et al. 1984).

After sediment samples had been collected, plant biomass was obtained by gently rinsing core contents through a 0.5 cm mesh screen to remove all sediment. Biomass samples were stored in a refrigerator for up to 48 h and were sorted into live and dead, above- and belowground tissues. Aboveground biomass from Ferry Cove and Elberts Cove was further separated into vegetative and reproductive tissues. All plant biomass was dried at 60°C to a constant weight, ground, and analyzed for tissue C, H, N, and P content (Short 1990).

Sediment microbial activities. In addition to conducting benthic flux experiments, vertical profiles of potential nitrification and belowground biomass distributions were measured at each site. Intact plant/sediment cores (n=3) were collected from each site and were partitioned into 1.5-cm sections to a depth of 6 cm to yield 4 sections (0-1.5, 1.5-3, 3-4.5, and 4.5-6 cm). Previous observations revealed that the majority of root and rhizome biomass was found in the top 6 cm of sediments. Each section was sorted by hand to separate plant biomass and remove macrofauna and shells. Plant biomass was rinsed, separated into live and dead tissues and dried at 60°C to constant weight (~48) h to generate depth profiles of root/rhizome biomass. The remaining sediment was homogenized and used to measure sediment water content and bulk density of each section, as well as to determine rates of potential nitrification.

Potential nitrification rates were measured as the production of NO_3^- over time in aerobic sediment slurries (Caffrey & Kemp 1990). Approximately 1 g of sediment from each section was incubated in 25 mL of filtered (0.7 μm) site water in a 50 mL polycarbonate centrifuge tube. Each tube was amended with NH_4Cl to bring NH_4^+ concentrations to 1 mM. Slurries were continuously mixed using a shaker table to maintain aerobic conditions for 24 to 48 h at 25°C. At 2 and 40 h, slurries from replicate flasks were centrifuged and the water was filtered (0.45 μm) and frozen for subsequent NO_3^- analysis. Previous experiments indicated that nitrification rates were linear over a 48 h period (data not shown).

Sediment porewaters. In 2004, sediment porewater dialysis samplers ("peepers", Wigand et al. 2001) were deployed at Elberts Cove, Neavitt, and Severn sites to measure vertical profiles of porewater solute concentrations along a transect from inside, through the edge, and outside of the bed in an adjacent unvegetated area.

Peepers were composed of a PVC stake (25 x 2.5 x 3 cm) with 5 sampling ports of 1.9 cm in diameter. Prior to deployment, each port was filled with N₂-sparged distilled water and covered with a 125 μm Nitex™ screen overlaying a 0.2 μm polycarbonate membrane. To ensure that the membrane and screen remained in place, a PVC plate with holes that corresponded to the sampling ports was affixed to the stake using 12 Teflon screws. Peepers were transported to each site in N₂-sparged distilled water to minimize oxidation of the porewater. Sediment peepers were pushed into the sediment to yield average sediment sampling depths of 1.5, 4.5, 7.5, 11.5, and 16.5 cm. To avoid tearing of the membrane, an empty stake was driven into the sediment, withdrawn, and a peeper was placed in the resulting hole. Replicate peepers (n = 3) were deployed at each point along the transect (e.g., inside, edge, and unveg) and remained in the sediment for approximately 7-10 d. Immediately after retrieval, peepers were rinsed with distilled water to remove excess sediment. Samples were extracted by puncturing the membrane with a stainless steel needle affixed to a 10-mL graduated syringe and filtered through a 0.45 μm syringe filter. A portion of each sample was treated with diamine for sulfide analysis (Cline 1969) while the remaining sample was immediately frozen for subsequent NH₄⁺, NO₃⁻, and PO₄³⁻ analyses.

RESULTS

Plant characteristics

There were substantial differences in biomass and plant characteristics between vegetative and reproductive *Ruppia maritima* beds. In general, reproductive beds had significantly more aboveground biomass ($p < 0.0001$), and consequently higher shoot to root ratios ($p < 0.04$), compared to beds dominated by

vegetative shoots (Table 5.1). Within the former beds, reproductive shoots represented approximately 40% (Elberts Cove) and 60% (Ferry Cove) of aboveground biomass. Although plant nutrient content varied from site to site, reproductive shoots consistently had lower nitrogen content and higher C:N ratios relative to vegetative shoots, with C:N ratios for reproductive and vegetative shoots ranging from approximately 17-24 and 14-18, respectively. Phosphorous content followed a similar pattern, with mean C:P ratios of approximately 800 and 500 for reproductive and vegetative shoots, respectively.

There were also differences in both bed and plant characteristics between the *Potamogeton perfoliatus* and reproductive *Ruppia maritima* beds. Aboveground biomass was significantly ($p < 0.0001$) higher in the *P. perfoliatus* bed (232.25 ± 43.97 g dry wt m^{-2}) compared to all other *R. maritima* beds excluding the densest reproductive *R. maritima* bed at Elberts Cove (Table 5.1). Although, *P. perfoliatus* shoots were significantly ($p < 0.0001$) longer than reproductive *R. maritima* shoots, shoot to root ratios were not significantly different between *P. perfoliatus* and reproductive *R. maritima* beds (Table 1). In addition, plant tissue nutrient content was higher and C:N and C:P ratios were lower in the *P. perfoliatus* bed relative to the reproductive *R. maritima* bed (data not shown). Regardless of plant species or vegetation type, total biomass was significantly higher ($p < 0.03$) on the inside compared to the edge of the bed at all sites, excluding the *P. perfoliatus* bed in Severn ($p < 0.09$) (Table 5.1). There were, however, no consistent patterns observed in plant N and P content between plants collected on the edge relative to the interior of the beds (data not shown).

Sediment characteristics

Patterns in sediment chlorophyll-*a* concentrations, nutrients, and physical properties along transects from the interior of the bed to adjacent unvegetated areas varied from site to site. Sediment chlorophyll-*a* concentrations were similar across the transect in the vegetative *Ruppia maritima* sites (Claiborne and Neavitt). In Ferry Cove (reproductive *R. maritima*) sediment chlorophyll-*a* concentrations were significantly higher ($p < 0.0085$) in unvegetated areas relative to the inside and edge of the bed (Table 2). A similar pattern of lower sediment chlorophyll-*a* concentrations in the interior of the bed was observed at the Severn River site (*Potamogeton perfoliatus*), however differences between the vegetated and unvegetated areas were not statistically significant ($p < 0.1476$) (Table 5.2). In contrast, sediment chlorophyll-*a* concentrations in Elberts Cove (reproductive *R. maritima*) decreased significantly ($p < 0.05$) along the same transect (Table 5.2), with concentrations highest in the interior of the bed.

Clearer patterns were observed in both physical and chemical sediment characteristics across sites and transects. In general, sediment water content decreased significantly ($p < 0.0001$) and bulk density increased significantly ($p < 0.0037$) along a transect from vegetated to unvegetated areas regardless of vegetation type or species (Table 5.2). Sediment C:N ratios were significantly higher ($p < 0.023$) in vegetated areas compared to unvegetated areas (for Ferry and Claiborne sites where data were available, Table 5.2), reflecting the difference in C:N content of the dominant primary producers in these areas (i.e., algae versus vascular plants). Vegetation type may have further influenced sediment characteristics. Sediments in reproductive *Ruppia maritima* beds had consistently lower water content and higher bulk density compared to vegetative *R. maritima* beds (Table 5.2), although these differences were not statistically significant. In 2003, sediment

C:N ratios were slightly higher in the reproductive *R. maritima* community relative to the vegetative community (Table 5.2), but this trend was not observed in 2004.

There was considerable variability in sediment porewater concentrations of NH_4^+ , PO_4^{3-} , and S^{2-} across the sites. While depth profiles in unvegetated sediments showed little variation, profiles in vegetated areas revealed subsurface peaks in concentrations and greater overall variability. Porewater concentrations of NH_4^+ ($p < 0.0138$), PO_4^{3-} ($p < 0.0065$), and S^{2-} ($p < 0.0273$) were all significantly higher in reproductive *Ruppia maritima* sediments relative to adjacent unvegetated sediments (Figs. 5.2 & 5.3). Similarly, NH_4^+ and S^{2-} concentrations were higher and PO_4^{3-} concentrations were significantly higher ($p < 0.0001$) in *Potamogeton perfoliatus* sediments compared to unvegetated areas (Figs. 5.2 & 5.3). This pattern was not observed in vegetative *R. maritima* sediments, which often had lower concentrations relative to unvegetated areas. Ammonium and PO_4^{3-} concentrations were lower and S^{2-} concentrations were significantly ($p < 0.0012$) lower in vegetative *R. maritima* sediments compared to adjacent unvegetated sediments. Across sites, NH_4^+ , PO_4^{3-} , and S^{2-} concentrations were highest in the reproductive *R. maritima* compared to the other sites (Figs. 5.2 & 5.3). Patterns along transects from inside to the edge of vegetated areas were not consistent among sites.

Nitrification Activity

Potential nitrification rates ranged from 20 to 756 $\text{nmol cm}^{-3} \text{d}^{-1}$ and were significantly ($p < 0.03$) higher in vegetated areas compared to unvegetated areas at 3 of the 5 sites. Depth profiles of nitrification activity in unvegetated areas declined with increasing depth. In contrast, nitrification rates in vegetated areas often peaked below the sediment surface (e.g., Fig. 5.4a) and nitrification was positively correlated with root/rhizome biomass in sub-surface sediments (Fig. 5.4b). While highest rates

of nitrification were observed in surface sediments colonized by *Potamogeton perfoliatus*, nitrification rates at depth were similar between *P. perfoliatus* and both forms of *Ruppia maritima*. There was no significant difference in nitrification rates between vegetative and reproductive *R. maritima* communities.

Benthic fluxes

Time-course changes in nutrient concentrations during core incubations generally exhibited clear diel patterns. Relatively linear rates of change were observed during the first 6 to 8 hours of daylight and nighttime with a transition period in between (e.g., Fig. 5.5a). In almost all cases, significant trends were obtained for changes in concentration during these initial light and dark periods, allowing rates to be calculated from the slope of the regression (e.g., Fig. 5.5b). Most of the measured PO_4^{3-} fluxes were, however, not significantly different from zero. Increases in concentrations represent net fluxes into the water column, while negative rates represent net fluxes into the plants and/or sediment. It should be noted that changes in a given parameter were attributed to the entire community (i.e., plants, sediment, plankton) rather than to one component of the community. Differences between vegetated and unvegetated cores were, however, attributed to the presence of the plants themselves. There were no consistent patterns in fluxes along transects from inside to the edge of the beds across all of the sites.

Community O₂ Cycling

Benthic O₂ production in the light (P_L) and respiration in the dark (R_D) ranged from 0.7 to 28.1 and 2.3 to 15.2 mmol m⁻² h⁻¹, respectively. Unvegetated sediments exhibited significantly lower rates of O₂ production ($p < 0.0001$) and respiration ($p < 0.0001$) compared to vegetated sediments. Net O₂ production and respiration in

unvegetated sediments ranged from 8 to 54% and 27 to 62%, respectively, of rates found in adjacent vegetated sediments (Table 5.3). While O₂ production was significantly related to sediment chlorophyll-*a* concentrations in unvegetated sediments ($r^2 = 0.63$, $p < 0.0007$), respiration was not significantly correlated with sediment chlorophyll-*a* concentrations ($r^2 = 0.15$, $p < 0.1791$).

Photosynthetic O₂ production and respiration were significantly correlated with aboveground biomass in all vegetated communities, and the slopes of these relationships represent biomass-specific rates (Fig. 5.6). Vegetative *Ruppia maritima* shoots exhibited higher, rates of O₂ production per unit biomass (180 μmol O₂ g⁻¹ dry wt h⁻¹) compared to both reproductive *R. maritima* and *Potamogeton perfoliatus* shoots (107 μmol O₂ g⁻¹ dry wt h⁻¹) (Fig. 5a), although this difference was not statistically significant ($p < 0.32$). Biomass-specific respiration, however, was significantly lower for *P. perfoliatus* (15.6 μmol O₂ g⁻¹ dry wt h⁻¹, $p < 0.0025$) and there was no difference in biomass-specific respiration (61.3 μmol O₂ g⁻¹ dry wt h⁻¹) between the two growth forms of *R. maritima* (Fig. 5.6b).

Community O₂ production in the light was significantly ($p < 0.0004$) higher in the *Potamogeton perfoliatus* community relative to all *Ruppia maritima* communities, excluding Elberts Cove (Table 5.3). In contrast, community respiration was highest in the reproductive *R. maritima* communities (Table 5.3). The *P. perfoliatus* community was net autotrophic ($P_L > R_D$) over the diel cycle with a P:R ratio of approximately 2.8, and daily net O₂ production (228 ± 20 mmol m⁻² d⁻¹) was significantly higher ($p < 0.0001$) than rates in either vegetative or reproductive *R. maritima* communities. There was considerable variability in net community production between the two types of *R. maritima* communities. Net autotrophy was observed in Elberts Cove (100.8 ± 40 mmol O₂ m⁻² d⁻¹, P:R = 1.7), a reproductive *R.*

maritima community, and Claiborne, a vegetative community ($91.2 \pm 7.2 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, P:R = 2.2) In contrast, *R. maritima* communities in Ferry Cove (reproductive) and Neavitt (vegetative) were net heterotrophic ($P_L < R_D$) over the diel cycle, with rates of -12 ± 7.2 (P:R = 0.68) and $-33.6 \pm 12 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (P:R = 0.68), respectively. Net O_2 production in unvegetated communities exhibited similar variability, as sediments with relatively low chlorophyll-a concentrations ($< 70 \text{ mg chl m}^{-2}$) were net heterotrophic, whereas sediments with high chlorophyll-a concentrations ($> 100 \text{ mg chl m}^{-2}$) were generally net autotrophic (Tables 5.2 & 5.3). Estimates of community metabolism obtained from open-water continuous O_2 measurements (Odum 1956) in Elberts Cove in July ($156 \pm 24 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) (data not shown, Appendix) compare well to estimates obtained using the closed-core system ($100 \pm 40 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) reported in this study.

Inorganic nitrogen fluxes

Benthic fluxes of NH_4^+ were always negative in the light and positive in the dark, ranging from -87 to $-250 \text{ } \mu\text{mol m}^{-2} \text{ h}^{-1}$ and 18 to $530 \text{ } \mu\text{mol m}^{-2} \text{ h}^{-1}$, respectively. While there were no consistent patterns between species or vegetation type, vegetative sites exhibited significantly higher rates of both consumption (light, $p < 0.0020$) and regeneration (dark, $p < 0.0398$) of NH_4^+ compared to unvegetated sites (Table 5.3). Ammonium regeneration was positively correlated to aboveground biomass at all *Ruppia maritima* sites (Fig. 5.7). In contrast, there was no significant correlation between NH_4^+ regeneration and plant biomass in the *Potamogeton perfoliatus* site. No clear patterns emerged in dark NH_4^+ consumption versus biomass at any site, suggesting that other components of the community (e.g., epiphytes, bacteria) may also be important. The magnitude of night time benthic

NH_4^+ releases were lower than daytime consumption rates at all sites, resulting in net consumption of NH_4^+ over the 24-hr day (Table 5.3).

Fluxes of $\text{NO}_3^- + \text{NO}_2^-$ were small and followed similar patterns to NH_4^+ , with net consumption in the light and net efflux in the dark. However, unlike NH_4^+ fluxes, no significant differences in $\text{NO}_3^- + \text{NO}_2^-$ fluxes were observed between vegetated and unvegetated areas in either the light or dark. Nitrate + nitrite fluxes ranged from -226 to -1 $\mu\text{mol m}^{-2} \text{h}^{-1}$ in the light and -2 to 199 $\mu\text{mol m}^{-2} \text{h}^{-1}$ in the dark. In addition, there was no discernible pattern in $\text{NO}_3^- + \text{NO}_2^-$ fluxes between any of the submersed plant communities. Patterns in net daily $\text{NO}_3^- + \text{NO}_2^-$ flux were variable across sites, with most sites exhibiting either net consumption or no net change in $\text{NO}_3^- + \text{NO}_2^-$ concentrations over the course of the day.

Denitrification

Mean rates of net denitrification, as estimated by dark N_2 production, ranged from 155 to 741 $\mu\text{mol m}^{-2} \text{h}^{-1}$ in submersed plant communities and -134 to 232 $\mu\text{mol m}^{-2} \text{h}^{-1}$ in unvegetated sediments. Rates in vegetated communities significantly exceeded rates in unvegetated sediments ($p < 0.0048$). Denitrification was higher in the *Potamogeton perfoliatus* community relative to *Ruppia maritima* communities; however this difference was not statistically significant. Net denitrification was observed in unvegetated sediments only at Severn and Ferry Cove, the two sites with the highest sediment chlorophyll-a values. Denitrification was positively related to aboveground biomass and sediment chlorophyll-a in *R. maritima* and unvegetated communities, respectively (Fig. 5.8).

Fluxes of dissolved organic matter

Benthic DOC fluxes were always positive in the light, ranging from 0.2 to 16.5 mmol m⁻² h⁻¹. In the dark, benthic DOC fluxes were almost always negative (net consumption), with rates ranging from -3.3 to 29.1 mmol m⁻² h⁻¹. While, in some cases, rates of benthic DOC production or consumption in unvegetated areas equaled or exceeded rates observed in vegetated areas, daily net DOC fluxes in vegetated areas were consistently positive and significantly higher ($p < 0.0016$) than rates observed in unvegetated areas (Table 5.3). Mean net DOC production in vegetated areas ranged from 16 to 92 mmol m⁻² d⁻¹, whereas mean net DOC fluxes in unvegetated areas ranged from -117 to 10 mmol m⁻² d⁻¹. DOC production and consumption were not consistently related to plant biomass, vegetation type, or species across sites.

In vegetated areas, benthic DON fluxes followed similar patterns to those observed in DOC fluxes, with production in the light and consumption in the dark (Table 5.3). The directions of DON fluxes in unvegetated areas were more variable, with rates in the light ranging from -1.7 to 0.61 mmol m⁻² h⁻¹ and rates in the dark ranging from -0.31 to 1.2 mmol m⁻² h⁻¹. While there were no clear differences between plant species or vegetation type, net DON production in the light was higher, although not significantly ($p < 0.0786$), in vegetated areas compared to unvegetated areas. In addition, vegetated communities were consistently net productive over the diel cycle with respect to DON, whereas net daily DON fluxes were often negative in unvegetated areas (Table 5.3).

Although there was considerable variability across sites, consistent relationships were evident between O₂ and DOC fluxes. The DOC:O₂ ratio for daytime benthic production in *Ruppia maritima* communities was 1.53 ± 0.34 . The DOC:O₂ ratio for dark consumption was lower at 0.58 ± 0.11 (Fig. 5.9a). These

values were considerably lower in the *Potamogeton perfoliatus* community, with DOC production and consumption comprising $32 \pm 14\%$ and $48 \pm 12\%$ of O_2 production and respiration, respectively. In unvegetated areas, DOC production and consumption represented $152 \pm 42\%$ and $125 \pm 25\%$ of O_2 production and respiration, respectively. Similar patterns were observed for DON production and consumption relative to O_2 fluxes (Fig. 5.9b).

Ratios of DOC:DON fluxes were highly variable across sites. Mean ratios of DOC:DON fluxes in the light were similar for reproductive *Ruppia maritima* (12.2 ± 3.7) and *Potamogeton perfoliatus* (5.5 ± 1.3) communities, but were 2-4 fold higher for vegetative *R. maritima* communities (29.3 ± 12.3). This difference was less pronounced for the ratio of dark DOC:DON fluxes, with only slightly higher ratios in vegetative *R. maritima* communities (17.6 ± 5.7) relative to reproductive *R. maritima* (6.8 ± 1.9) and *P. perfoliatus* communities (11.4 ± 5.9).

DISCUSSION

Variations in nutrient cycling across plant beds

In this study, I sought to quantify differences in sediment nutrient cycling processes along transects from outside through the edge and into the interior of *Ruppia maritima* beds. As a water mass flows across a submersed plant bed, dissolved nutrients tend to be assimilated directly from the water column and concentrations of suspended particles tend to decline as they sink from the water and are trapped within the plant canopy (Bulthuis 1984, Ward et al. 1984, Gacia & Duarte 2001). Particulate organic matter settles to the sediment surface, where it may fuel regeneration of inorganic nutrients, and solutes are assimilated by plants to support production. Depending on the relative balance among rates of nutrient trapping, recycling and uptake, sediments within the plant bed may have higher (e.g.,

Kenworthy et al. 1982) or lower (e.g., Short 1983) nutrient concentrations compared to unvegetated sediments. Canopy friction tends to cause velocities to decline as water flows over the plant bed, potentially resulting in lower rates of particle trapping and nutrient uptake in the interior of large beds (e.g., Moore 1996). Thus, it might be hypothesized that plant tissue nutrient concentrations and sediment nutrient regeneration are elevated on the edge of the bed relative to the interior. In this study, plant nutrient content was typically highest on the edge of the beds, indicating that plants on the edge are exposed to higher nutrient concentrations than those found inside the bed. In contrast, plant biomass and shoot:root ratios tended to be higher in the interior of *R. maritima* beds, suggesting that these plants benefit from being sheltered from hydrodynamic stress (e.g., Schanz et al. 2003). However, I did not observe any consistent differences in either benthic fluxes or sediment porewater concentrations along the transect from the edge of the bed through the interior. It appears that many physical and biotic factors interact to regulate differences in nutrient cycling from the edge to interior of these beds.

Influence of *Ruppia maritima* on net ecosystem production

Overall, both O₂ production and respiration in these *Ruppia maritima* communities were high and are similar to rates reported for other Chesapeake Bay submersed plant species, such as *Zostera marina* (Wetzel & Penhale 1983). Clear diel patterns in O₂ cycling were observed at all sites, with net O₂ production occurring during the day and net respiration occurring at night, and rates were significantly higher in *R. maritima* communities compared to unvegetated sediments. Elevated rates in vegetated communities are the result of both the direct effects of plant metabolism and indirect effects associated with plant enhanced production and respiration in epiphyte and sediment communities (Murray & Wetzel 1987).

Whereas gross O₂ production was consistently and significantly higher in vegetated communities relative to unvegetated sediments, patterns in net daily O₂ production, or net ecosystem production (NEP), were more variable. NEP did not appear to be related to vegetation type (Table 5.3), as some vegetative and reproductive communities exhibited net autotrophy (positive NEP, P:R > 1) and others exhibited net heterotrophy (negative NEP, P:R < 1). This pattern is consistent with other studies that have demonstrated seasonal and spatial variability in net ecosystem production in submersed aquatic plant communities (Murray & Wetzel 1987, Moncreiff et al. 1992, Ziegler & Benner 1998, Gazeau et al. 2005). In this study, when the community was net autotrophic, net O₂ production was comparable between vegetative and reproductive *Ruppia maritima* communities. A possible explanation for this pattern is that, despite lower overall biomass, vegetative *R. maritima* communities exhibited higher biomass-specific O₂ production compared to reproductive communities. The incidence of net heterotrophy in *R. maritima* communities may reflect higher respiratory demands associated with enhanced trapping of allochthonous particulate organic matter and related heterotrophic activity (Kemp & Boynton 1984, Barron et al. 2004). While net O₂ production was similar between the two communities, the higher biomass and vertical structure in reproductive communities may provide greater quality habitat for fish and other estuarine organisms (e.g., Worthington et al. 1992). The abundant physical structure in reproductive beds may also lead to enhanced water clarity and particle deposition compared to vegetative beds (e.g., Ward et al. 1984).

Submersed plant effects on DOM

In this study, DOC and DON cycling in submersed plant beds followed clear diel patterns suggesting a link between plant photosynthesis and DOM production.

Several studies have shown that exudation of DOC by submersed aquatic plants is largely associated with plant photosynthesis and may represent ~10% of plant production (Wetzel & Penhale 1979, Sondergaard 1981). DOC production in this study was observed only during the light, suggesting that DOC production may indeed have been linked to plant photosynthesis. However, DOC production in this study ranged from ~10-200% of community O₂ production, indicating that sources other than plant photosynthesis must have been involved (e.g., Barron et al. 2004). Ultraviolet solar radiation has been shown to contribute to the degradation of plant material and release of DOC in aquatic plant beds during daylight hours (Ziegler & Benner 2000, Stabenau et al. 2004). In addition, daytime excretion of DOC from plant roots to sediment porewaters (Koepfler et al. 1993) also may have contributed to a net efflux from the sediment.

Overall, vegetated communities were significant sources of DOC to the overlying water column. The lability of DOC released from these communities, and consequently the potential for export, may vary depending on the mechanism of production. DOC released as photosynthetic exudates tend to be small molecular weight compounds that may be readily available for microbial utilization (Wetzel & Penhale 1979, Sondergaard 1983). Indeed, several studies have shown that bacterial activity in submersed aquatic plant beds varies over the diel cycle and is synchronized with plant photosynthesis (Moriarty & Pollard 1982, Chin-Leo & Benner 1991). Compounds released from leaching and degradation of plant material may have varied lability. Soluble compounds, such as monomeric carbohydrates, that are leached during initial stages of tissue decomposition are relatively labile and consequently may have rapid turnover rates (Kenworthy et al. 1989, Blum & Mills 1991, Peduzzi & Herndl 1991). Remaining plant tissue decomposes more slowly

and leads to the release of higher molecular weight compounds, such as cellulose and lignins, which are relatively resistant to degradation (Kenworthy & Thayer 1984).

Net production of DON was also high and represented the dominant form of dissolved N released from submersed plant communities in this study. Excretion of amino acids from plant leaves and roots during photosynthesis may have contributed to DON pools in the overlying water column (Jorgensen et al. 1981). Leaching from decomposing plant tissue also may have contributed significantly to DON pools (Jorgensen et al. 1981, Pedersen et al. 1999). The net consumption of inorganic nitrogen combined with the net production of DON demonstrates the importance of these communities for binding inorganic nutrients into organic material.

While the results of this study demonstrated diel variation in DOC and DON fluxes, these fluxes may also vary seasonally (Velimirov 1986, Ziegler & Benner 1999). This study was conducted during the growing season when plant production was at its peak. It might be expected that, as the growing season ends, the contribution of photosynthetic production to DOC and DON pools would decline relative to the contribution from tissue decomposition and this shift could lead to changes in DOM bioavailability. Regardless of the source, production of DOC and DON represents a significant component of the overall C and N balance within these systems. Furthermore, plant-derived DOC and DON generation may support enhanced bacterial production (Moriarty et al. 1990, Chin-Leo & Benner 1991, Kaldy et al. 2006), representing a link between these plants and higher trophic levels (e.g., Peduzzi & Herndl 1991, Thresher et al. 1992).

Influence of *R. maritima* on sediment biogeochemical cycling

Several studies have provided evidence of enhanced biogeochemical cycling in submersed aquatic plant sediments (e.g., Kenworthy et al. 1982, e.g., Caffrey &

Kemp 1990), and this appeared to be the case for *Ruppia maritima* communities in this study. Ammonium regeneration was higher in *R. maritima* sediments compared to unvegetated sediments, and this process was positively correlated to plant biomass. Despite enhanced NH_4^+ regeneration, however, these communities were net sinks with respect to NH_4^+ , suggesting tight recycling of nutrients within these plant-sediment systems. A previous study also found higher rates of daytime NH_4^+ uptake in sediments inhabited by *R. megacarpa* compared to unvegetated sediments (Dudley & Walker 2000). Patterns in sediment porewater NH_4^+ concentrations were more variable, as NH_4^+ concentrations were, respectively, higher in reproductive *R. maritima* sediments and lower in vegetative *R. maritima* sediments relative to adjacent unvegetated sediments. This discrepancy between reproductive and vegetative *R. maritima* communities may be indicative of the balance between enhanced NH_4^+ regeneration and plant NH_4^+ assimilation in these communities, with NH_4^+ regeneration exceeding plant uptake in reproductive communities and plant NH_4^+ assimilation exceeding regeneration in vegetative communities. Long, reproductive shoots likely attenuate water flow and enhance particle deposition to a greater extent than short, vegetative shoots (e.g., Ward et al. 1984), resulting in larger pools of organic matter in reproductive bed sediments. Hence, remineralization of this organic matter, and thus, NH_4^+ regeneration rates are higher in reproductive communities.

In all instances, both nitrification and denitrification rates were higher in *Ruppia maritima* communities relative to unvegetated areas. These processes were positively related to aboveground biomass, suggesting a link between oxygen release to the rhizosphere and coupled nitrification-denitrification (e.g., Caffrey & Kemp 1990). Greater O_2 production per unit biomass in vegetative *R. maritima* relative to reproductive communities may have resulted in higher root O_2 excretion

rates and, thus, a larger fraction of oxidized sediments at depth. This conclusion is also supported by previous studies that demonstrated that root release of O_2 in submersed plants is inversely related to the length of vertical shoots (Kemp & Murray 1986). Because nitrifying bacteria require O_2 to produce nitrate and are inhibited by S^{2-} production (Henriksen & Kemp 1988, Joye & Hollibaugh 1995), higher rates of root O_2 excretion tend to enhance nitrification in the rhizosphere. This may explain both the lower S^{2-} concentrations (Lee & Dunton 2000) and higher nitrification rates in the vegetative *R. maritima* communities.

In contrast, denitrification rates were similar between the two *Ruppia maritima* communities with differing predominant growth forms. Denitrification, an anaerobic process, is primarily dependent on organic matter supply and nitrate availability. If nitrification and denitrification are coupled, it might be expected that the higher nitrification rates observed in vegetative *R. maritima* communities would have led to enhanced denitrification. However, it is possible that organic matter supply could have been limiting denitrification in vegetative sediments, as evidenced by the relatively low S^{2-} concentrations. In the reproductive *R. maritima* communities, S^{2-} concentrations, and presumably organic matter supplies, were higher, whereas nitrification rates were lower, indicating that denitrification may have been limited by nitrate supply. An alternative explanation might involve environmental differences between the sites that would favor a larger fraction of NO_3^- being reduced back to NH_4^+ (e.g., Binnerup et al. 1992). In any case, these patterns suggest a complex relationship between coupled nitrification-denitrification and organic matter supply in these *R. maritima* communities.

Rates of primary production and nutrient uptake in unvegetated areas in this study were relatively high (e.g., Nilsson et al. 1991, Rizzo et al. 1992), suggesting that benthic microalgae may be important contributors to these processes in shallow

waters of the mesohaline Chesapeake Bay. In areas where sediment chlorophyll-*a* concentrations were high, rates of O₂ production in unvegetated sediments represented as much as 50% of O₂ production observed in vegetated sediments. As in other studies (e.g., Sundback & Miles 2000), I observed high rates of uptake of inorganic nitrogen and DON and little to no denitrification in benthic microalgal communities. Such patterns suggest that these communities serve as a net sink for nitrogen within this system, but do not contribute to nitrogen removal via denitrification.

In contrast to benthic microalgae, the structure and physiology of submersed vascular plants allows them to have a greater influence on physical and biogeochemical processes. The physical structure of plant leaves reduces water flow across the bed (Gambi et al. 1990), resulting in enhanced deposition of particulate organic matter and reduction of sediment resuspension (Ward et al. 1984, Terrados & Duarte 2000). High biomass and nutrient re-adsorption from senescing plant tissues (Borum et al. 1989) results in higher potential for retention and storage of nutrients within these vascular plant communities relative to benthic microalgal communities. Additionally, plant roots extend deeper into the sediment where root release of O₂ contributes to oxidized sediments at depth. Oxidation of subsurface sediments increases the volume of sediments available to support nitrifying bacterial activity, which may, in turn, enhance rates of denitrification (Caffrey & Kemp 1990, Ottosen et al. 1999).

Ruppia maritima* vs. *Potamogeton perfoliatus

While both plant species affect biogeochemical cycling through similar mechanisms, in this study, *Potamogeton perfoliatus* had a greater influence on these processes compared to *Ruppia maritima* (Fig. 5.10). Whereas biomass-specific O₂

production was similar between the two species, respiration per unit biomass was lower for *P. perfoliatus*, resulting in higher net O₂ production per unit biomass compared to reproductive *R. maritima*. Furthermore, both net community O₂ production and aboveground biomass in the *P. perfoliatus* community were approximately twice those of reproductive *R. maritima* communities. Greater biomass may enhance particulate organic matter deposition in plant beds (e.g., Ward et al. 1984), and higher O₂ production would tend to support higher rates of O₂ (Caffrey & Kemp 1991, Frederiksen & Glud 2006) and DOC release to the rhizosphere (Koepfler et al. 1993). Surficial nitrification and integrated denitrification rates were both also enhanced in *P. perfoliatus* sediments relative to rates measured in *R. maritima* sediments. Higher nitrification rates in *P. perfoliatus* sediments may have been the result of higher biomass-specific O₂ production, and consequently, higher O₂ release rates from plant roots (e.g., Sand-Jensen et al. 2005). Lower porewater S⁻² concentrations support this hypothesis. Indeed, estimates of root O₂ release rates measured in split-compartment hydroponic chambers were approximately 19% and 10% of leaf production in *P. perfoliatus* and *R. maritima*, respectively (J. Nagel, Appendix). Thus, plant stimulation of nitrification and denitrification in *P. perfoliatus* sediments may result in higher net rates of nitrogen loss (Caffrey & Kemp 1990, Hemminga et al. 1991) compared to rates in *R. maritima* sediments. Despite differences in biomass and O₂ production, DOM cycling rates were similar between *R. maritima* and *P. perfoliatus* communities, and both communities were net sources of DOM to the overlying water.

The ability of these two species to influence biogeochemical processes on larger spatial and temporal scales is, in part, dependent upon the reproductive ecology and physiology of each species. For example, with its prolific production of viable seeds and high growth potential (Stevenson et al. 1993, Silberhorn et al.

1996), *Ruppia maritima* is capable of rapidly recolonizing unvegetated sediments (Verhoeven 1979, Dunton 1990, Johnson et al. 2003). Despite its opportunistic nature, there has been considerable variability in the abundance and persistence of *R. maritima* beds in mesohaline Chesapeake Bay during the last two decades (Schulte 2003). Thus, the contribution of *R. maritima* to net ecosystem production and biogeochemical cycling in this region may vary considerably from year to year. Unlike *R. maritima*, *Potamogeton perfoliatus* does not reproduce effectively by seed but relies largely on vegetative propagation to maintain and expand its distribution (Philbrick & Les 1996). However, once established in an area, *P. perfoliatus* can form dense beds that are stable over long time periods (Goldsborough & Kemp 1988). Hence, with its enhancement of biogeochemical processes and potential for long-term bed stability, *P. perfoliatus* may have greater overall impact on biogeochemical cycling in this region. In addition, *P. perfoliatus* may provide higher quality habitat for estuarine organisms compared to other species, such as *R. maritima* (Heck 1984, Lubbers et al. 1990).

Results of this study illustrate the importance of *Ruppia maritima* to biogeochemical cycling in mesohaline Chesapeake Bay. Enhancement of biogeochemical processes through plant-sediment interactions may represent a positive feedback through which *R. maritima* modifies its environment to benefit its own survival and propagation. Direct nutrient assimilation, stimulation of nitrification-denitrification, and enhanced trapping of suspended particles can improve water clarity and reduce nutrients available for phytoplankton and epiphytes. Ultimately, this will provide better growth conditions both for *R. maritima* and for other submersed aquatic plant species. Although its distribution is variable, mean areal coverage of *R. maritima* in mesohaline regions of Chesapeake Bay has increased markedly in recent years (www.vims.edu/bio/sav). This natural recovery is probably

largely attributable to prolific production and wide dispersal of seeds by *R. maritima*. Submersed plant cover in this region is, however, still well below historic levels, and other more stable native species remain scarce (Kemp et al. 2004). Thus, areas in mesohaline Chesapeake Bay currently occupied by *R. maritima* may be ideal locations for focusing initiatives to restore other native species, such as *Potamogeton perfoliatus*, which might further improve water quality conditions through even greater effects on particle trapping, nutrient recycling and denitrification in a more stable habitat.

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Table 5.1. Mean (\pm SE) aboveground and belowground plant biomass (g dry wt m⁻²), shoot to root ratios, and shoot lengths (cm) of *Potamogeton perfoliatus* (Severn), reproductive *Ruppia maritima* (Elberts and Ferry), and vegetative *Ruppia maritima* (Neavitt and Claiborne) collected in 2003 and 2004. Measurements were taken inside and on the edge of each bed.

Site	Aboveground	Belowground	Shoot:Root	Shoot Length
<i>Severn</i>				
Inside	232.3 \pm 44.0	27.4 \pm 0.6	8.6 \pm 1.8	46.0 \pm 5.8
Edge	125.2 \pm 23.3	26.3 \pm 1.9	4.7 \pm 0.6	27.5 \pm 3.3
<i>Elberts</i>				
Inside	101.4 \pm 4.6	37.7 \pm 7.2	4.7 \pm 0.8	29.8 \pm 1.7
Edge	51.2 \pm 8.6	33.3 \pm 2.4	1.7 \pm 0.2	32.9 \pm 5.7
<i>Ferry</i>				
Inside	47.5 \pm 12.9	3.4 \pm 1.0	18.5 \pm 8.1	26.2 \pm 2.2
Edge	95.8 \pm 6.8	18.9 \pm 7.9	7.3 \pm 2.7	27.8 \pm 1.3
<i>Neavitt</i>				
Inside	22.7 \pm 4.2	16.0 \pm 7.2	2.4 \pm 1.1	12.7 \pm 0.8
Edge	4.9 \pm 0.8	2.6 \pm 0.7	2.0 \pm 0.3	7.1 \pm 0.6
<i>Claiborne</i>				
Inside	36.2 \pm 7.7	12.9 \pm 3.3	3.1 \pm 0.8	12.3 \pm 0.7
Edge	2.4 \pm 0.3	1.5 \pm 0.2	1.8 \pm 0.5	7.6 \pm 0.6

Table 5.2. Mean (\pm SE) sediment water content, bulk density (g m^{-3}), C:N ratios, nitrogen content and sediment chlorophyll-*a* concentrations (mg chl m^{-2}) for *Potamogeton perfoliatus* (Severn), reproductive *Ruppia maritima* (Elberts and Ferry), and vegetative *Ruppia maritima* (Neavitt and Claiborne) beds. Measurements were taken on the inside and edge of the beds as well as in adjacent bare areas. Dashes (---) indicate that there are no data for that site.

Site	% H ₂ O	Bulk Density	Sed C:N	Sed % N	Sed Chl- <i>a</i>
<i>Severn</i>					
Inside	29.9 \pm 0.64	1.17 \pm 0.03	---	---	195.5 \pm 63.7
Edge	---	---	13.19 \pm 0.91	0.037 \pm 0.000	346.6 \pm 74.7
Bare	26.7 \pm 2.00	1.42 \pm 0.03	---	---	412.3 \pm 89.6
<i>Elberts</i>					
Inside	27.4 \pm 0.43	1.30 \pm 0.04	9.63 \pm 0.19	0.024 \pm 0.001	153.9 \pm 11.6
Edge	---	---	11.20 \pm 0.85	0.023 \pm 0.001	116.4 \pm 37.4
Bare	22.2 \pm 0.62	1.39 \pm 0.04	---	---	50.9 \pm 10.2
<i>Ferry</i>					
Inside	0.29 \pm 0.02	1.14 \pm 0.04	---	---	169.4 \pm 40.4
Edge	0.21 \pm 0.01	1.38 \pm 0.03	9.80 \pm 0.47	0.063 \pm 0.002	218.0 \pm 22.4
Bare	0.22 \pm 0.01	1.38 \pm 0.03	6.51 \pm 0.45	0.032 \pm 0.005	419.7 \pm 16.3
<i>Neavitt</i>					
Inside	30.6 \pm 0.25	1.22 \pm 0.09	11.16 \pm 0.61	0.024 \pm 0.001	102.6 \pm 41.5
Edge	---	---	12.31 \pm 1.13	0.025 \pm 0.002	102.3 \pm 56.8
Bare	25.3 \pm 0.21	1.33 \pm 0.05	---	---	62.5 \pm 20.7
<i>Claiborne</i>					
Inside	0.32 \pm 0.01	1.08 \pm 0.02	---	---	270.3 \pm 53.9
Edge	0.30 \pm 0.01	1.18 \pm 0.02	7.14 \pm 0.08	0.049 \pm 0.003	256.4 \pm 38.8
Bare	0.28 \pm 0.01	1.20 \pm 0.02	6.04 \pm 0.35	0.044 \pm 0.001	289.7 \pm 54.9

Table 5.3. Light, dark, and net fluxes ($\text{mmol m}^{-2} \text{h}^{-1} \pm \text{SE}$) of O_2 , NH_4^+ , DON and DOC in *Potamogeton perfoliatus* (Severn), reproductive *Ruppia maritima* (Elberts, Ferry Cove), and vegetative *Ruppia maritima* (Neavitt, Claiborne) beds and adjacent bare areas in mesohaline Chesapeake Bay.

	O_2		NH_4^+		DON		DOC	
	Veg	Unveg	Veg	Unveg	Veg	Unveg	Veg	Unveg
<i>Severn</i>								
Light	27.0 ± 9.3	4.5 ± 10.6	-0.12 ± 0.02	-0.12 ± 0.05	0.73 ± 0.04	0.38 ± 0.05	4.1 ± 1.2	4.4 ± 2.0
Dark	-11.2 ± 0.7	-3.1 ± 0.4	0.09 ± 0.03	0.07 ± 0.02	-0.56 ± 0.10	-0.18 ± 0.13	-4.7 ± 2.5	-4.2 ± 0.8
Net	9.5 ± 0.8	1.0 ± 0.7	-0.03 ± 0.01	-0.03 ± 0.02	0.20 ± 0.03	0.13 ± 0.05	1.3 ± 0.6	0.4 ± 1.2
<i>Elberts</i>								
Light	18.5 ± 4.3	1.4 ± 0.4	-0.17 ± 0.06	-0.09 ± 0.01	0.67 ± 0.04	-0.74 ± 0.06	5.6 ± 2.4	5.9 ± 1.9
Dark	-12.7 ± 2.2	-6.0 ± 1.1	0.10 ± 0.02	0.02 ± 0.01	-0.63 ± 0.29	-0.69 ± 0.13	-4.0 ± 1.3	-17.6 ± 5.8
Net	4.2 ± 1.7	-2.0 ± 0.6	-0.07 ± 0.02	-0.04 ± 0.00	0.13 ± 0.05	-0.72 ± 0.33	1.2 ± 0.7	-4.9 ± 2.8
<i>Ferry</i>								
Light	10.1 ± 1.8	5.4 ± 0.6	-0.27 ± 0.08	-0.09 ± 0.04	1.30 ± 0.22	0.53 ± 0.06	5.6 ± 2.7	0.5 ± 0.1
Dark	-13.2 ± 2.6	-3.5 ± 0.2	0.53 ± 0.16	0.11 ± 0.02	-1.83 ± 0.25	-0.76 ± 0.25	-3.3 ± 0.9	-0.8 ± 0.1
Net	-0.5 ± 0.3	1.3 ± 0.3	-0.03 ± 0.03	0.00 ± 0.03	0.30 ± 0.08	-0.19 ± 0.10	2.3 ± 1.7	-0.2 ± 0.1
<i>Neavitt</i>								
Light	5.4 ± 0.4	1.7 ± 0.2	-0.19 ± 0.02	-0.10 ± 0.04	0.70 ± 0.20	-0.25 ± 0.05	7.9 ± 3.5	2.6 ± 0.5
Dark	-9.5 ± 0.6	-3.2 ± 0.3	0.14 ± 0.02	0.07 ± 0.04	-0.37 ± 0.05	-0.27 ± 0.04	-5.7 ± 2.7	-2.8 ± 0.4
Net	-1.4 ± 0.5	-0.6 ± 0.3	-0.04 ± 0.01	-0.02 ± 0.03	0.21 ± 0.10	-0.01 ± 0.01	1.7 ± 0.7	0.1 ± 0.4
<i>Claiborne</i>								
Light	12.7 ± 0.7	6.5 ± 0.8	-0.25 ± 0.05	-0.10 ± 0.05	0.41 ± 0.09	-0.19 ± 0.03	8.8 ± 3.0	2.2 ± 1.2
Dark	-6.8 ± 0.6	-4.2 ± 0.6	0.17 ± 0.06	0.07 ± 0.04	-0.27 ± 0.02	-0.15 ± 0.09	-2.0 ± 0.5	-1.4 ± 2.4
Net	3.8 ± 0.3	1.6 ± 0.5	-0.06 ± 0.02	-0.02 ± 0.01	0.10 ± 0.06	0.03 ± 0.03	3.8 ± 1.4	-1.1 ± 0.2

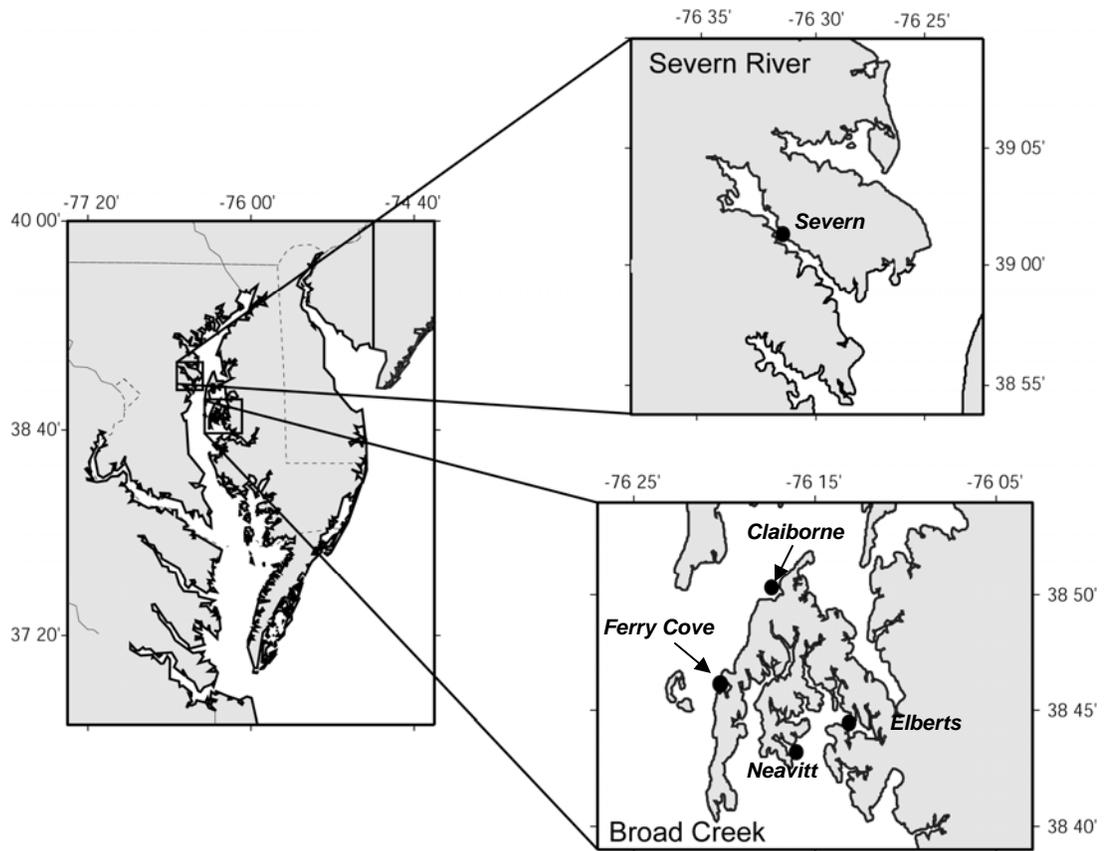


Fig. 5.1. Study sites in mesohaline Chesapeake Bay. Four *Ruppia maritima* beds were sampled in Broad Creek and one *Potamogeton perfoliatus* bed was sampled in the Severn River.

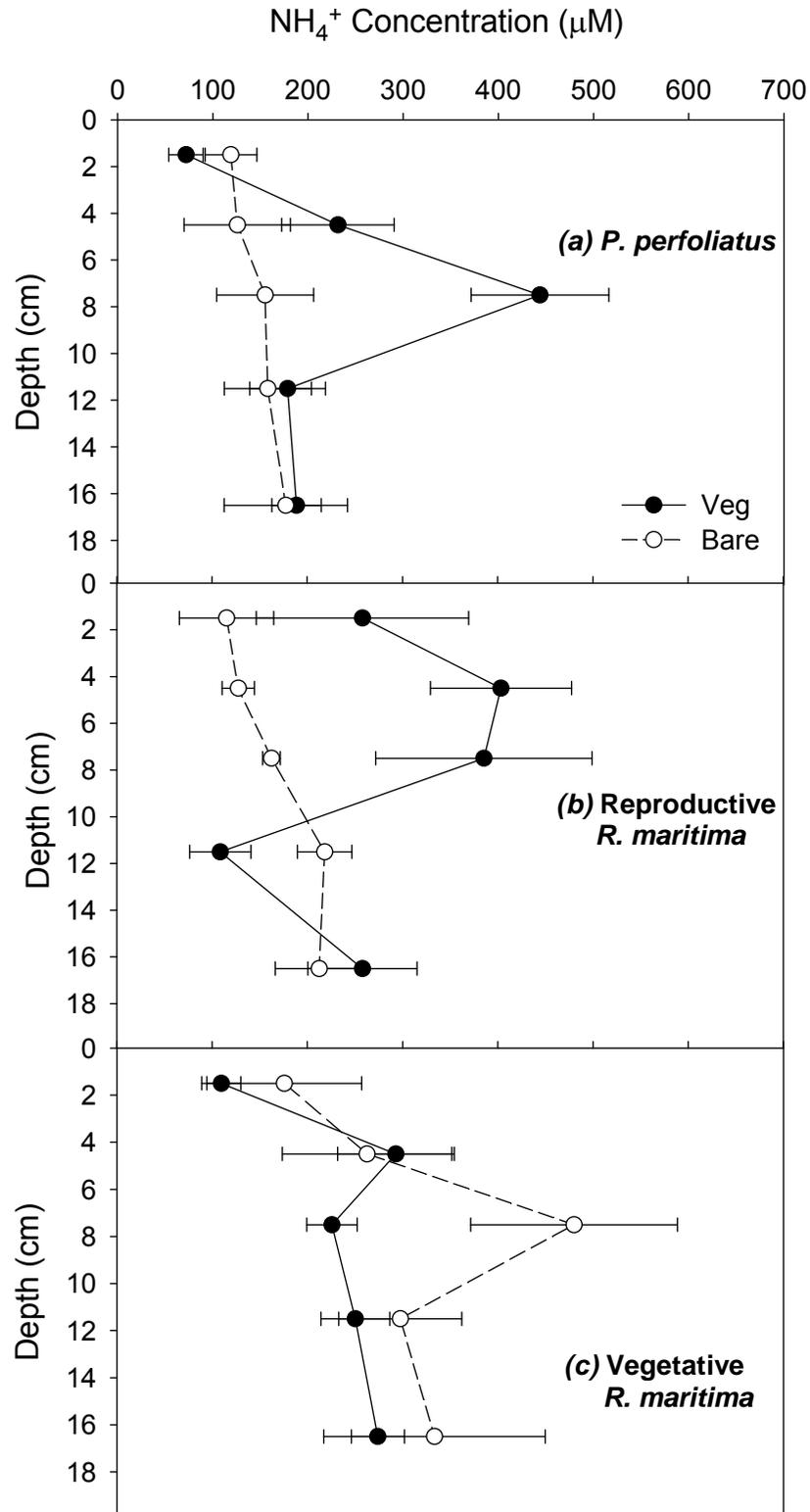


Fig. 5.2. Depth profiles of porewater NH_4^+ concentrations in vegetated (filled symbol) and adjacent bare areas (open) in *Potamogeton perfoliatus* (a), reproductive *Ruppia maritima* (b), and vegetative *Ruppia maritima* (c) communities. Each point represents a 3 cm depth interval with x-axis standard error bars.

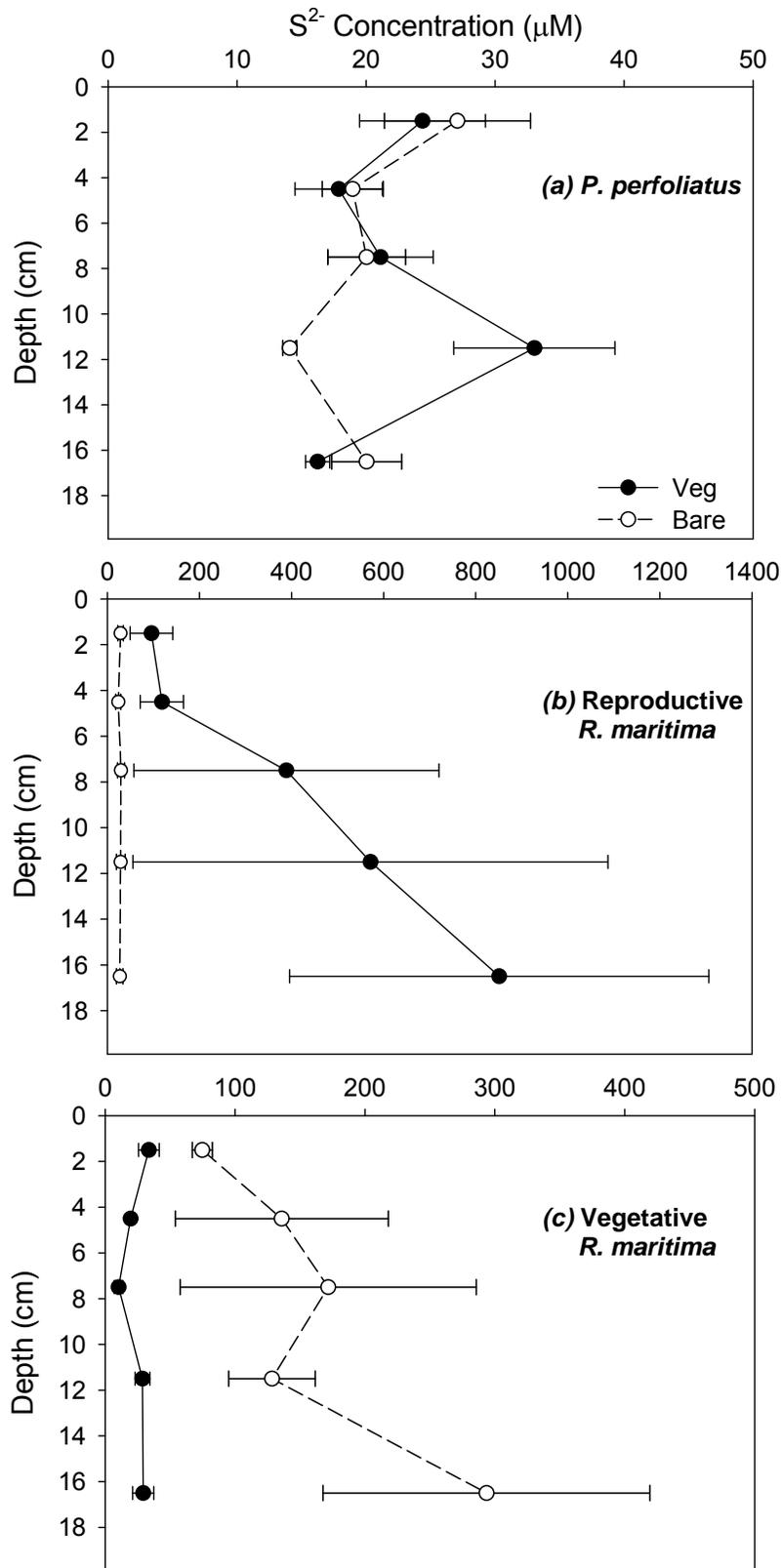


Fig. 5.3. Depth profiles of porewater sulfide concentrations in vegetated and adjacent bare areas in *Potamogeton perfoliatus* (a), reproductive *Ruppia maritima* (b), and vegetative *Ruppia maritima* (c) communities.

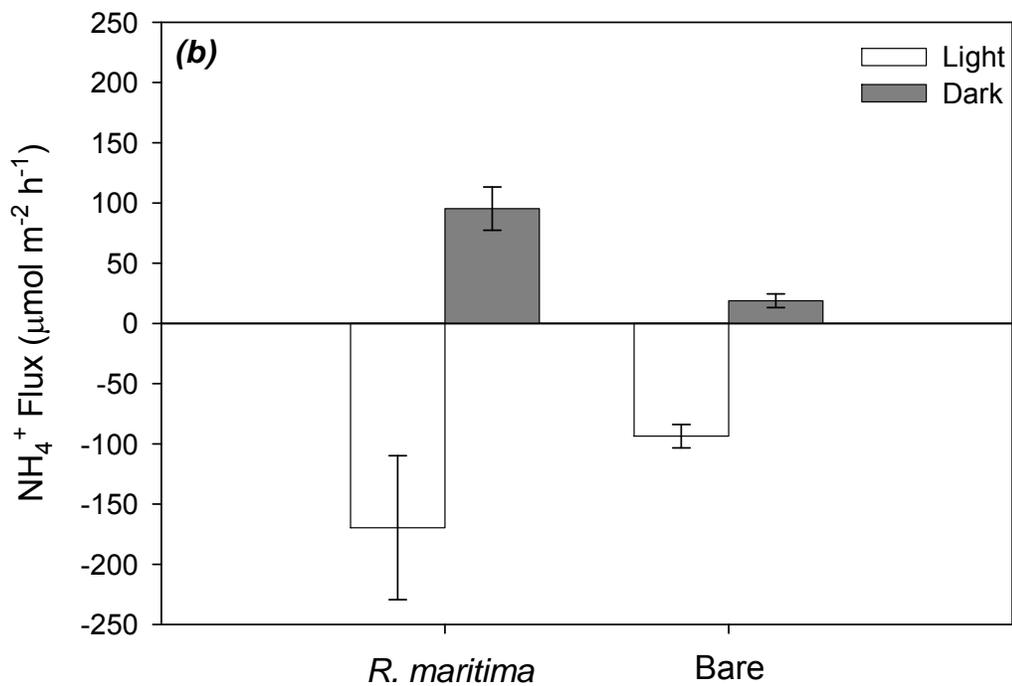
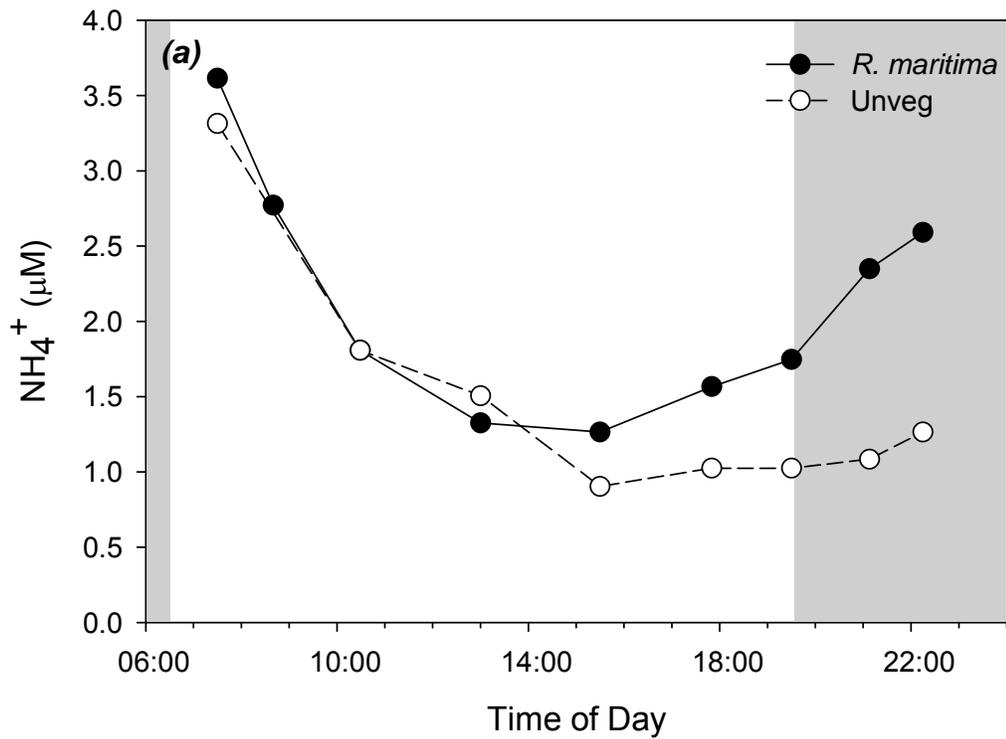


Fig. 5.5. (a) Diel trends in NH_4^+ concentrations during flux core experiments in *Ruppia maritima* (filled circle) and bare (open) communities. Gray bars along y-axis indicate dark periods. (b) Example of net NH_4^+ flux in light (open) and dark (filled) periods for *Ruppia maritima* and bare communities.

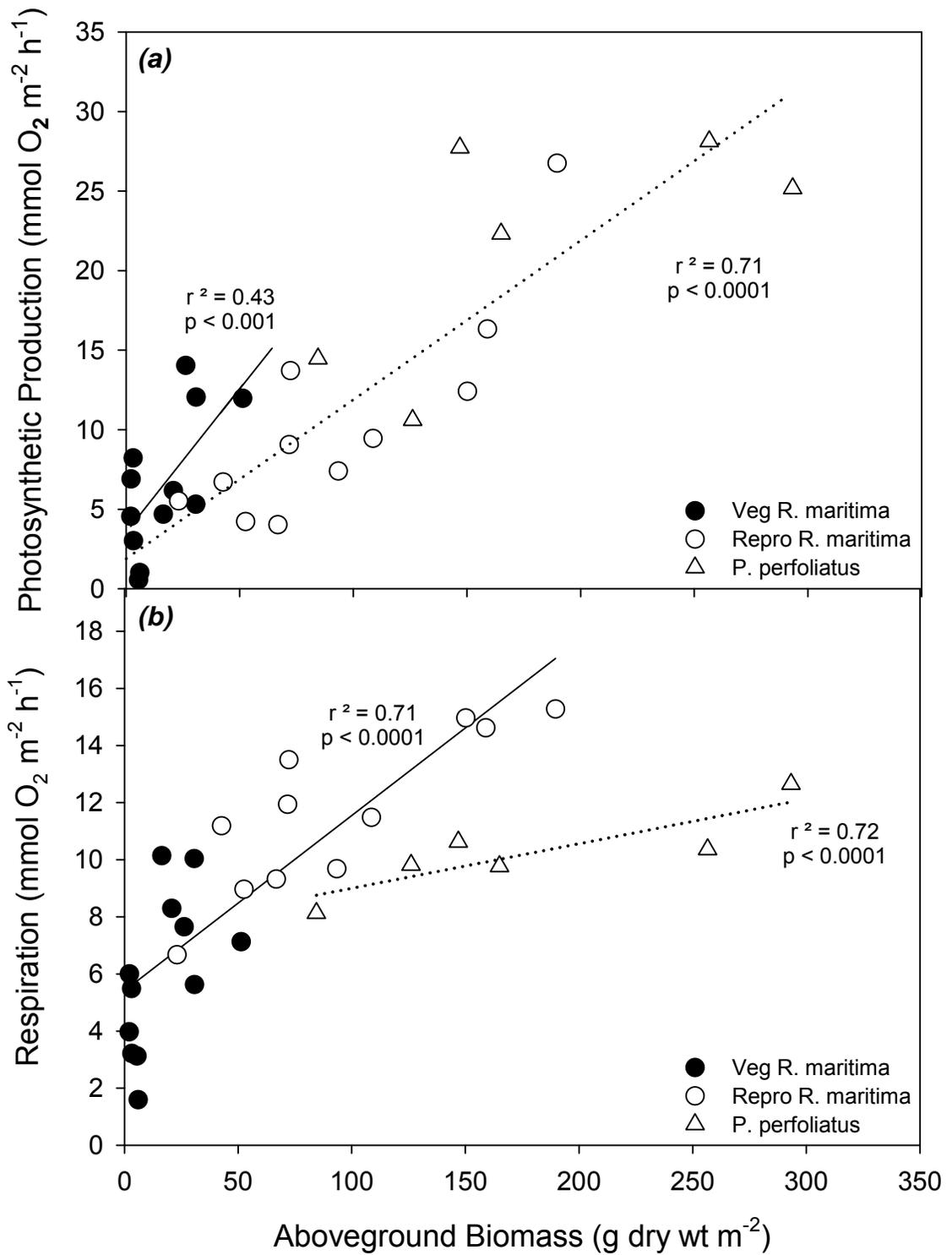


Fig. 5.6. Biomass-specific photosynthetic O₂ production (a) and respiration (b) in vegetative (filled circle) and reproductive (open circle) *Ruppia maritima* beds and *Potamogeton perfoliatus* beds (triangle).

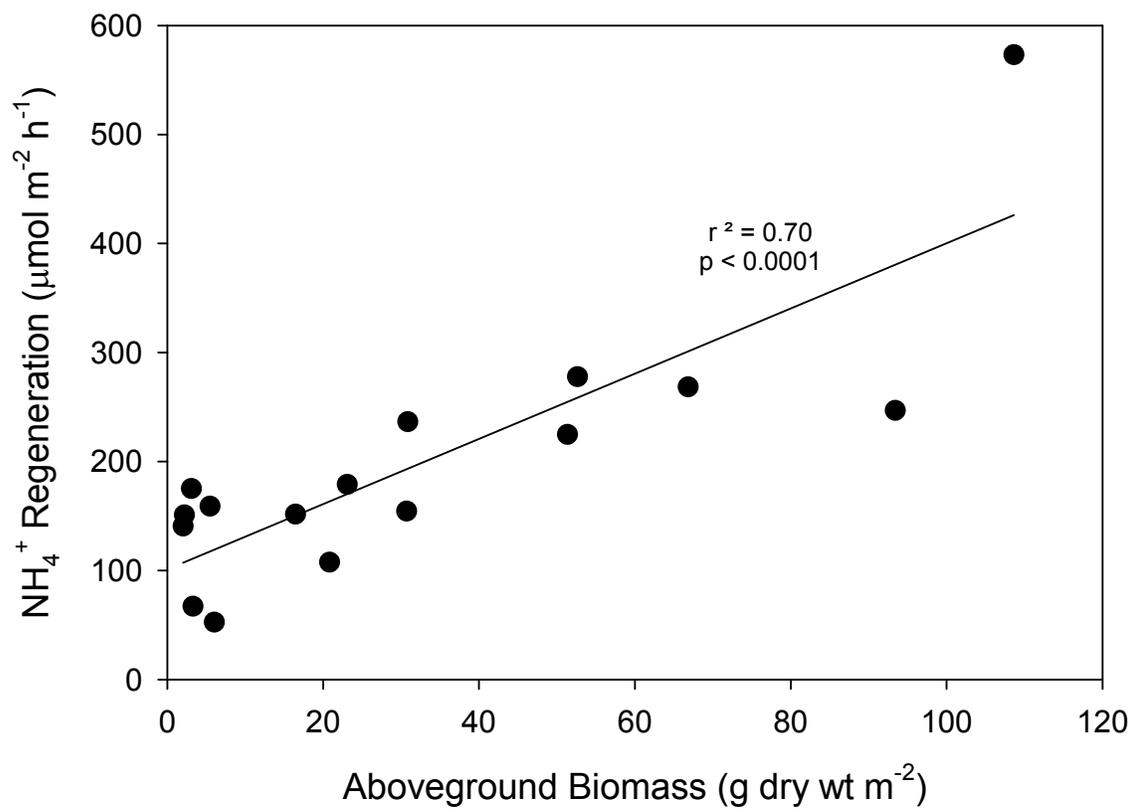


Fig. 5.7. Linear regression of ammonium regeneration (dark NH₄⁺ flux) vs. aboveground biomass in *Ruppia maritima* communities.

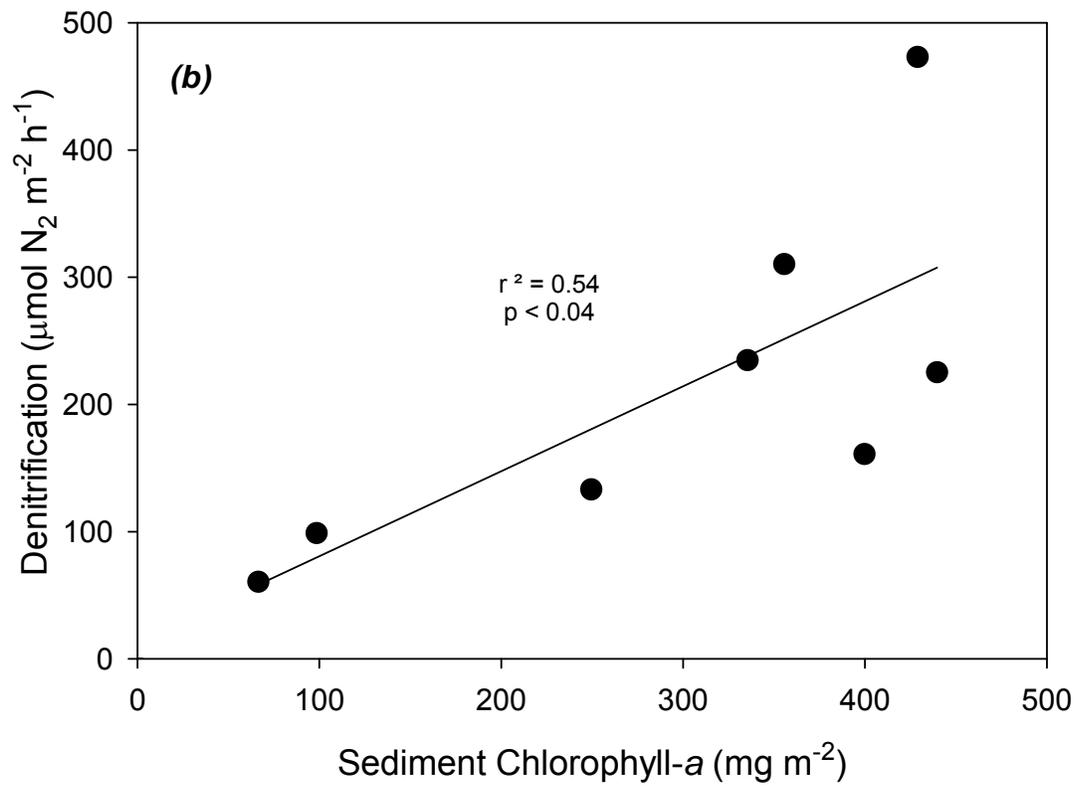
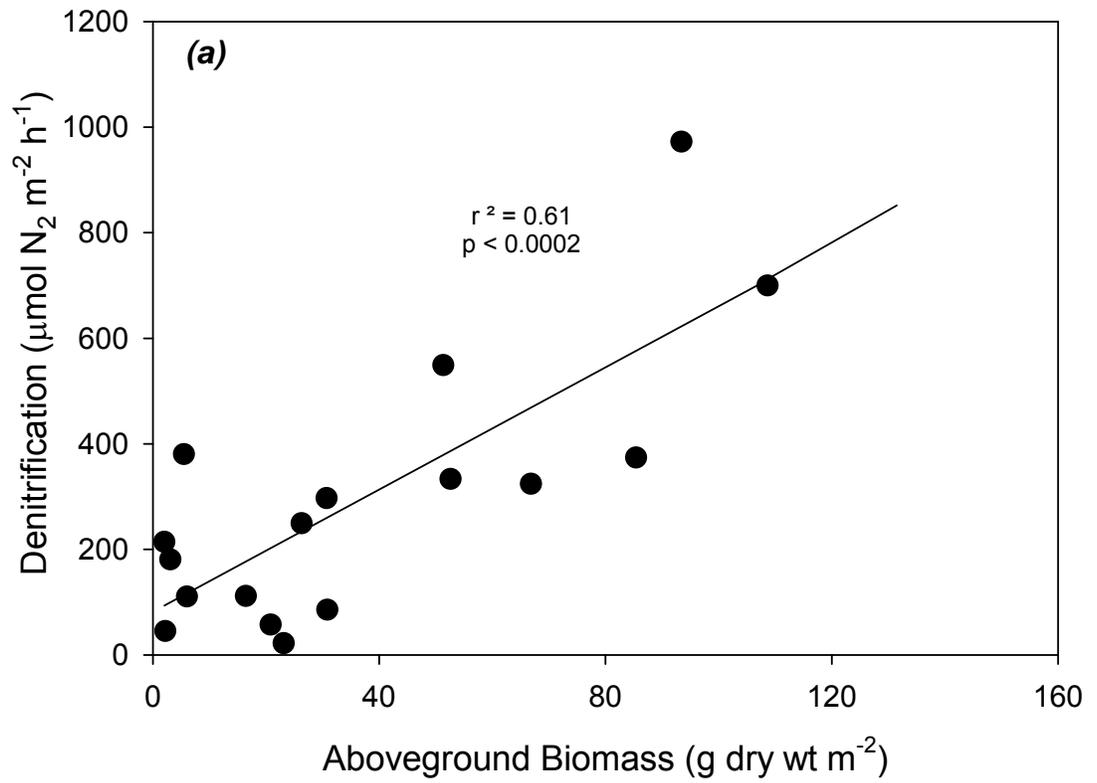


Fig. 5.8. Denitrification (dark N_2 flux) vs. aboveground biomass in *Ruppia maritima* communities (a) and sediment chlorophyll-a in bare communities (b).

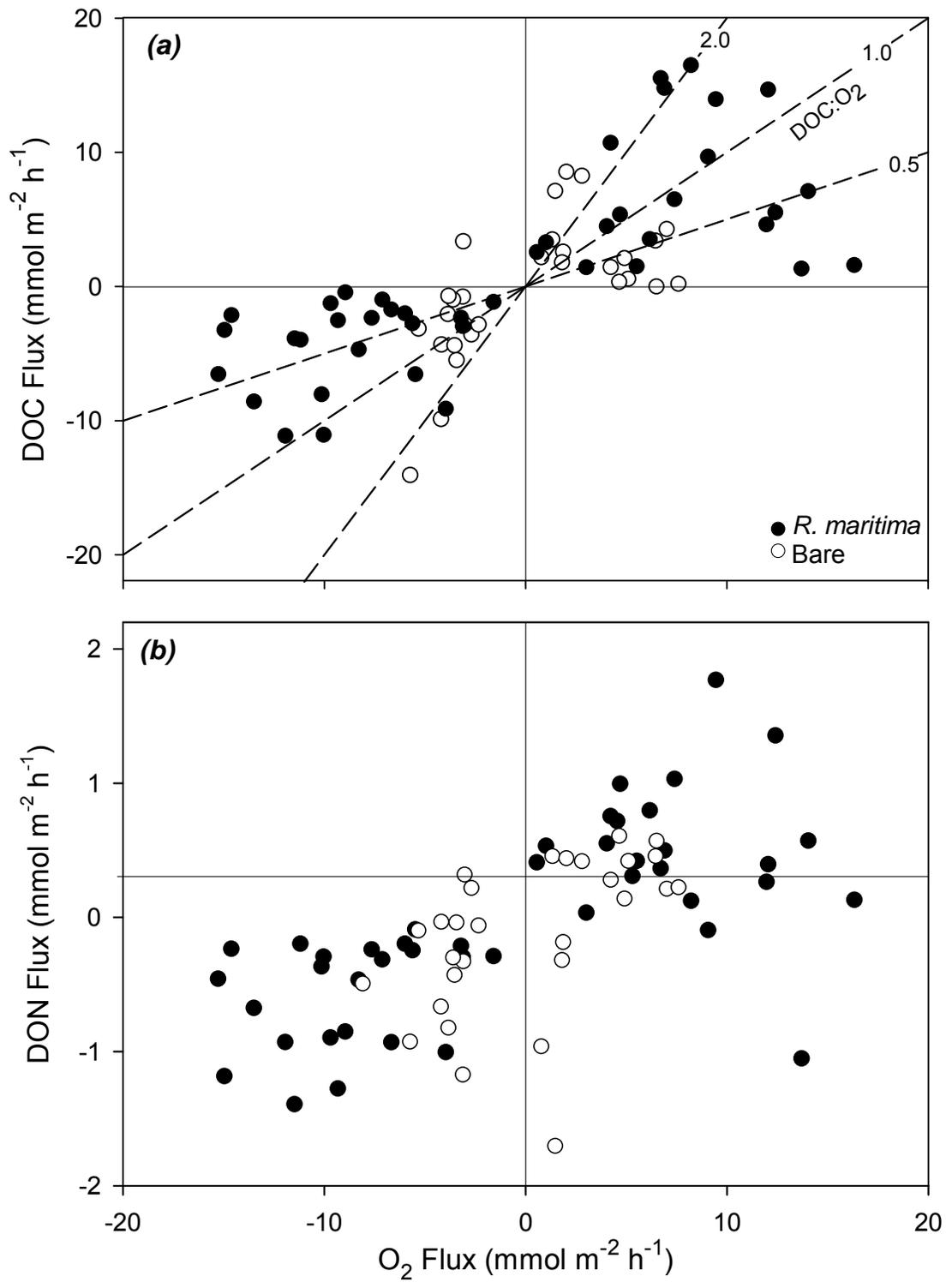


Fig. 5.9. DOC (a) and DON (b) fluxes vs. O_2 fluxes in *Ruppia maritima* (filled circle) and adjacent bare communities (open). Positive fluxes represent production or efflux, whereas negative fluxes represent consumption or influx. Dashed lines in (a) indicate ratios of DOC: O_2 flux of 0.5, 1.0, and 2.0.

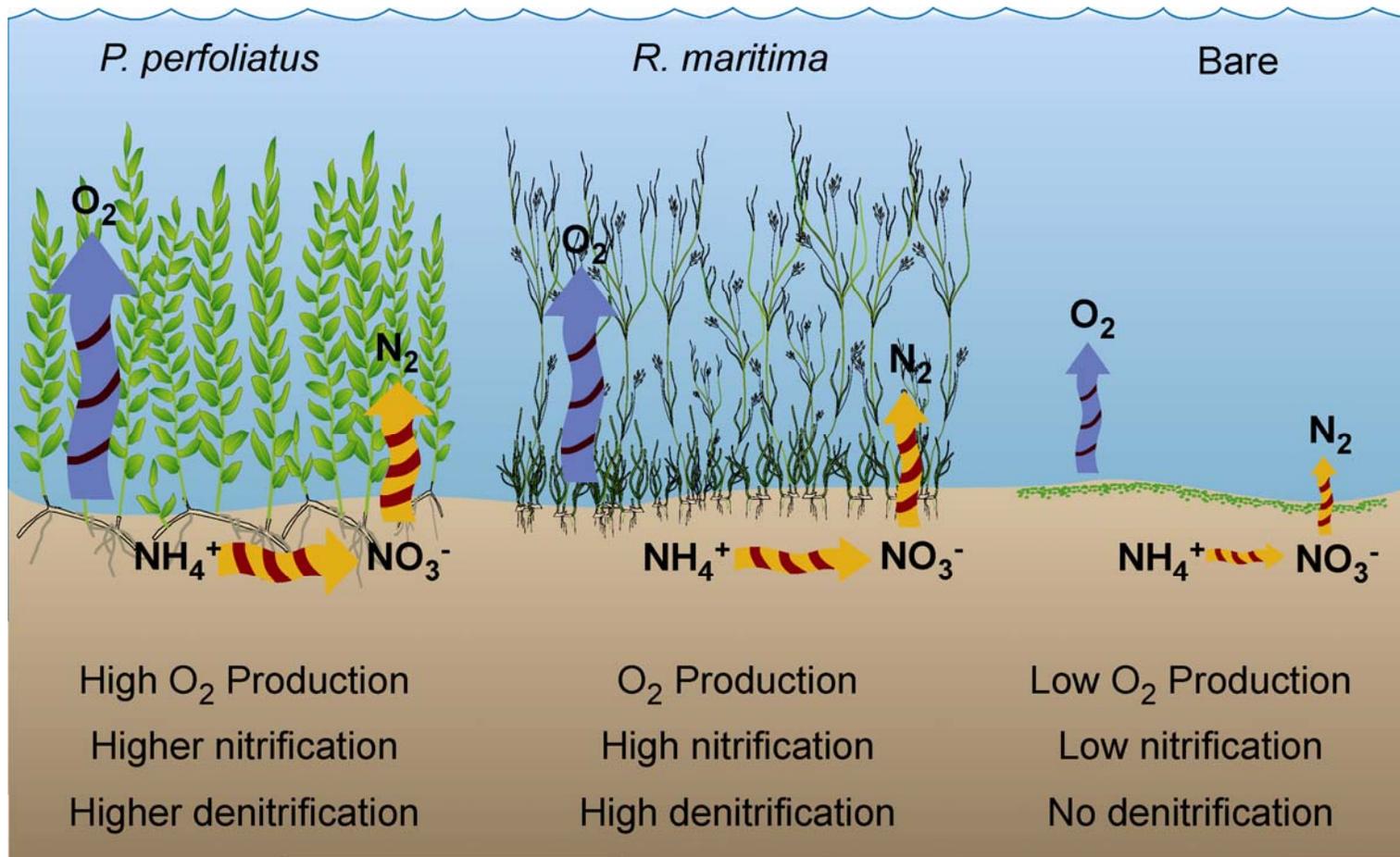


Fig. 5.10. Comparison of relative influences of *P. perfoliatus*, *R. maritima*, and bare communities on biogeochemical processes in mesohaline Chesapeake Bay.

CHAPTER 6: Conclusions and synthesis

Results of this research quantify how specific seagrasses beds in Chesapeake and Florida Bays significantly enhance key biogeochemical processes in sediments and overlying water compared to “bare” (containing microalgae but no seagrass) benthic communities. Seagrass primary production enhanced DOC release and inorganic nitrogen consumption in the daytime as well as nighttime consumption of O₂ and DOC and release of inorganic nitrogen, thereby underscoring the importance of plant photosynthesis in regulating these processes. Observed enhancement of nitrification in seagrass sediments appears also to be derived from plant production and associated root release of O₂ into the surrounding sediments. Elevated porewater S²⁻ and NH₄⁺ concentrations and enhanced sulfide production and ammonification measured in *R. maritima* and *T. testudinum* sediments emphasize the importance of these beds as sites of organic enrichment. The high rates of DOC production in these beds often exceeded photosynthetic carbon production further suggesting the tendency of these seagrass communities to trap and bind particulate organic matter. The relative importance of these species to annual biogeochemical budgets may, however, differ between the two ecosystems, as submersed plants in mesohaline Chesapeake Bay senesce from late fall to early spring, whereas *T. testudinum* persists year-round in Florida Bay.

Although biogeochemical rates were enhanced by all three seagrass species studied, differences emerged in relation to their relative influence on some processes. Of the 3 species of submersed plants studied in this research, *P. perfoliatus* exhibited the greatest influence on O₂ cycling. Rates of daytime apparent O₂ production (P_a) and net ecosystem production (NEP) measured during peak growing season (June/July) were highest in the *P. perfoliatus* community, followed by *R. maritima*, and *T. testudinum*. These differences may be, in part, explained by relationships between plant biomass and P_a and respiration (R). Biomass-specific O₂ production rates were similar (~100 μmol O₂ g⁻¹ (dry wt) h⁻¹) for both *R. maritima* and *P. perfoliatus*, but these rates

were 2-fold higher than those for *T. testudinum*. Lowest rates of biomass-specific respiration were observed for *P. perfoliatus* ($\sim 15 \mu\text{mol O}_2 \text{ g}^{-1} (\text{dry wt}) \text{ h}^{-1}$), whereas rates for *R. maritima* and *T. testudinum* were ~ 3 times higher than *P. perfoliatus*.

Morphological differences between these plants are one possible explanation of these patterns. *P. perfoliatus* is a canopy-forming species, with the majority of its biomass devoted to aboveground tissues and root to shoot biomass ratios < 1.0 . Conversely, the majority of plant biomass in the meadow-forming species, *T. testudinum*, is invested in belowground tissues (root:shoot > 1.0). Because O_2 is required to support aerobic metabolism in belowground tissues (Smith et al. 1984), the higher relative proportion of belowground tissues in *T. testudinum* represents a larger sink of O_2 for this species relative to *P. perfoliatus*. *R. maritima* was intermediate between these other two species in terms of both root to shoot ratios and net biomass-specific O_2 production.

While the communities studied in this research were all generally net autotrophic, the role of these submersed plants in NEP may also vary seasonally and regionally, as was the case in Florida Bay. Regional and seasonal variations in temperature, salinity, light, and nutrient regimes appear to regulate the balance between production and respiration in these systems. Because of the relatively high turbidity and phytoplankton abundance leading to low water clarity and high concentrations of suspended POC, submersed plant communities in Chesapeake Bay tend to be POC sinks more prone to net heterotrophy than those in the relatively clear, low productivity waters of Florida Bay.

Estimates of nitrification rates also differed between seagrass communities in the two ecosystems. Nitrification rates were higher in *R. maritima* and *P. perfoliatus* sediments in Chesapeake Bay relative to those colonized by *T. testudinum* in Florida Bay. Higher rates of nitrification in *R. maritima* and *P. perfoliatus* sediments may enhance denitrification (Caffrey & Kemp 1990, Ottosen et al. 1999), a process which can lead to removal of inorganic nitrogen from the system (Hemminga et al. 1991, Cornwell

et al. 1999). This process may be especially important for ameliorating the effects of high inorganic nitrogen loading in eutrophic systems such as Chesapeake Bay. In contrast, high porewater sulfide concentrations in the relatively iron-deplete carbonate sediments of Florida Bay may have inhibited nitrification (Henriksen & Kemp 1988, Joye & Hollibaugh 1995), and consequently denitrification, in Florida Bay *T. testudinum* sediments. Indeed, no net denitrification, measured as dark N₂ flux, was observed in *T. testudinum* sediments throughout this research. Further investigations into the direct influence of submersed plant species on denitrification and nitrogen fixation would provide valuable insight into the role of these plants in larger scale N cycling within these systems.

Given the importance of seagrasses to biogeochemical cycling documented here, loss of seagrass habitat and shifts in species composition could substantially alter biogeochemical budgets within these systems. A seagrass dieback event observed in Florida Bay led to a reduction in nitrification, enhancement of sulfide production, and a shift in NEP from net autotrophy to net heterotrophy. Although this event may have been limited to summer months, the consequences of seagrass dieback may have a lasting impact on biogeochemical cycling over the annual cycle. Projected changes to watershed hydrology may further impact biogeochemical cycling in Florida Bay by causing shifts in benthic communities and the relative abundance of the more euryhaline seagrasses *R. maritima* and *Halodule wrightii* at the expense of *T. testudinum* (Fourqurean et al. 2003).

Shifts in species composition may have affected biogeochemical cycling in mesohaline Chesapeake Bay, as *P. perfoliatus*, the historically dominant, stable species, had a greater influence on these processes relative to *R. maritima*, the now abundant but ephemeral, opportunistic species. Recent efforts to restore submersed plant populations and diversity in Chesapeake Bay have met with limited success, and the

factors influencing transplant survivorship are not well understood. Knowledge regarding plant interactions with biogeochemical cycling, such as gained from this research, could be useful for improving restoration strategies. For example, direct nutrient assimilation, stimulation of nitrification-denitrification, and enhanced trapping of suspended particles in *R. maritima* beds can improve water clarity and reduce nutrients available for phytoplankton and epiphytes. Thus, establishing plant transplants near or within *R. maritima* beds may increase survival and improve restoration success; however, further investigations are required to test this hypothesis.

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APPENDICES

Appendix I. Compilation tables of relevant rates reported previously in peer-reviewed literature.

Table I.a. O₂ excretion rates expressed as a rate ($\mu\text{mol g}^{-1}$ (dry weight) h^{-1}) and as a percentage of net primary production (NPP) from submersed aquatic plant roots.

Species	O ₂ Release		Reference
	$(\mu\text{mol mg}^{-1} \text{h}^{-1})$	% NPP	
Freshwater Plants			
<i>Egeria densa</i>	0.072	-	Sorrell & Dromgoole 1987 ^a
<i>Isoetes lacustris</i>	0.044	39.0	Sand-Jensen et al. 1982 ^a
<i>Lobelia dortmanna</i>	0.163	93.0	Sand-Jensen et al. 1982 ^a
<i>Lobelia dortmanna</i>	0.017	50.0	Sand-Jensen and Prahl 1982 ^a
<i>Littorella uniflora</i>	0.036	-	Christensen et al. 1994 ^a
<i>Littorella uniflora</i>	0.033	28.0	Sand-Jensen et al. 1982 ^a
<i>Myriophyllum verticillatum</i>	0.059	-	Carpenter et al. 1983 ^a
<i>Potamogeton crispus</i>	0.098	2.0	Sand-Jensen et al. 1982 ^a
<i>Potamogeton friesii</i>	0.035	2.0	Sand-Jensen et al. 1982 ^a
<i>Potamogeton pectinatus</i>	0.037	4.0	Sand-Jensen et al. 1982 ^a
<i>Potamogeton perfoliatus</i>	0.038	5.4	Kemp & Murray 1986 ^a
<i>Potamogeton perfoliatus</i>	0.099	9.0	Caffrey & Kemp 1991 ^{a,b}
Estuarine and Marine Plants			
<i>Cymodocea rotundata</i>	0.0002	-	Pederson et al. 1998 ^a
<i>Halophila ovalis</i>	0.077	-	Connell et al. 1999 ^a
<i>Ruppia maritima</i>	0.078	-	Ihursby 1984 ^a
<i>Zostera marina</i>	0.009	3.2	Caffrey & Kemp 1991 ^{a,b}
<i>Zostera marina</i>	0.002	-	Iizumi et al. 1980 ^a
<i>Zostera marina</i>	0.003	1.0	Sand-Jensen et al. 1982 ^a
<i>Zostera marina</i>	0.007	1.2	Smith et al. 1984

^aRates determined using split-compartment hydroponic chambers

^bRates determined using *in situ* O₂ microelectrodes

Table I.b. DOC excretion rates expressed as a percentage of net primary production (NPP) from submersed aquatic plant leaves and roots.

Species	DOC excretion (% NPP)		Method ¹	Reference
	Leaves	Roots		
<i>Cymodocea rotundata</i>	--	7.0	Hydroponic	Holmer et al. 2001
<i>Cymodocea serrulata</i>	0.2	--	Hydroponic	Roberts & Moriarty 1987
<i>Halodule wrightii</i>	0.5 - 1.4	0.03 - 0.7	Hydroponic	Wetzel & Penhale 1979
<i>Halodule wrightii</i>	1.0	6.0 - 17.0	Intact sediment	Moriarty et al. 1986
<i>Posidonia oceanica</i>	0 - 3.0	--	Intact sediment	Velimirov 1986
<i>Syringodium isoetifolium</i>	0.9	--	Hydroponic	Roberts & Moriarty 1987
<i>Thalassia hemprichii</i>	--	5.4	Hydroponic	Holmer et al. 2001
<i>Thalassia testudinum</i>	1.3	--	Hydroponic	Brylinsky 1979
<i>Thalassia testudinum</i>	0.3	8.0	Hydroponic	Wetzel & Penhale 1979
<i>Thalassia testudinum</i>		15.0 - 30.0	Intact sediment	Kaldy et al. 2006
<i>Zostera capricorni</i>	1.0	--	Hydroponic	Roberts & Moriarty 1987
<i>Zostera capricorni</i>	--	6.0 - 10.0	Intact sediment	Moriarty & Boon 1989
<i>Zostera capricorni</i>	--	8.0 - 18.0	Indirect	Hansen et al. 2000
<i>Zostera marina</i>	--	2.0 - 4.0	Indirect	Blaabjerg et al. 1998
<i>Zostera marina</i>	1.2	--	Hydroponic	Penhale & Smith 1977
<i>Zostera marina</i>	4.9 - 2.7	0.5 - 2.7	Hydroponic	Wetzel & Penhale 1979
<i>Zostera marina</i>	2.2	--	Hydroponic	Kirchman 1984

¹Hydroponic refers to ¹⁴C measurements in split-compartment hydroponic chambers

Intact sediment refers to ¹⁴C measurements in cores with plants/sediments intact

Indirect refers to estimates of root DOC release needed to support observed sulfate reduction rates

Table I.c. Rates of apparent daytime production (P_a), nighttime respiration (R), and net ecosystem production (NEP) for seagrass communities using either open water or discrete (i.e., benthic chambers). Rates are expressed as $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$.

Species	P_a	R	NEP	Method	Reference
<i>Cymodocea nodosa</i>	7.0 - 49.3	1.01 - 83.7	-71.5 - 14.6	Discrete	Barron et al. 2004
<i>Cymodocea nodosa</i>			-7.81 - 16.6	Discrete	Gacia et al. 2005
<i>Posidonia oceanica</i>			-24.7 - 88.8	Discrete	Gazeau et al. 2004
<i>Ruppia maritima</i>	161	112	49.0	Open water	Murray & Wetzel 1987
<i>Ruppia maritima</i>	129 - 444	163 - 316	-33.6 - 101	Discrete	This study
<i>Ruppia maritima</i>	74.7 - 246	44.7 - 162	0 - 138	Open water	This study
<i>Thalassia hemprichii</i>	75.0 - 367	117 - 425		Discrete	Ertemeijer et al. 1993
<i>Thalassia testudinum</i>	118 - 157	51.9 - 82.1	66.5 - 74.6	Discrete	Calleja et al. 2006
<i>Thalassia testudinum</i>	94.3 - 157	69.1 - 123	25.2 - 34.7	Discrete	This study
<i>Thalassia testudinum</i>	62.1 - 247	32.5 - 170	-37.6 - 106	Open water	This study
<i>Thalassia testudinum</i>	120 - 1050	168 - 675	262 - 750	Open water	Odum et al. 1959
<i>Thalassia testudinum</i>	125 - 938	134 - 615	75.0 - 390	Open water	Odum 1964
<i>Thalassia testudinum</i>	259 - 1300	200 - 1175	-306 - 253	Open water	Reyes & Merino 1991
<i>Thalassia testudinum</i>	56.0 - 366	103 - 381		Open water	Ziegler & Benner 1998
<i>Zostera marina</i>	197	94.0	103	Open water	Murray & Wetzel 1987
<i>Zostera marina</i>	91.0	113	-22.0	Open water	Nixon & Oviatt 1972

Appendix II. Photosynthesis-Irradiance curves for *Thalassia testudinum* along a transect at Barnes Key in Sept. 2002.

Photosynthesis-irradiance curves were obtained for *T. testudinum* leaves collected along a transect from the basin to the bank during an active dieback event in Barnes Key (Sept. 2002). Intact plants were collected by coring from beds in Barnes Key and were transported back to the Key Largo Ranger Station. Apical 10-cm sections of *T. testudinum* leaves were placed in ambient seawater in BOD incubation bottles. Replicate bottles (n=2) were then incubated at various light levels ranging from 0 to 600 μE for ~ 2.5 h. Water samples were then collected for dissolve O_2 gas analysis (see Chapter 2 for methods) and rates were reported as change in O_2 concentration per gram (dry weight) of plant material per h.

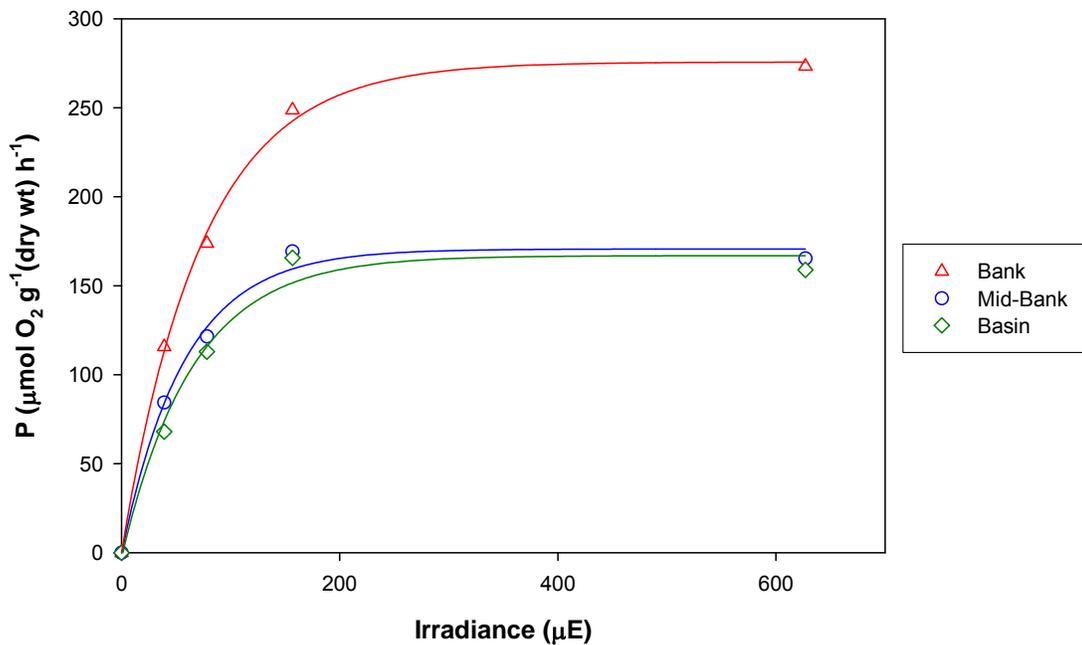


Fig II.a. Photosynthesis-irradiance curves for *T. testudinum* leaves collected along a transect from basin to bank in Barnes Key 2002.

Appendix III. Variations in production and respiration in *T. testudinum* communities in Florida Bay

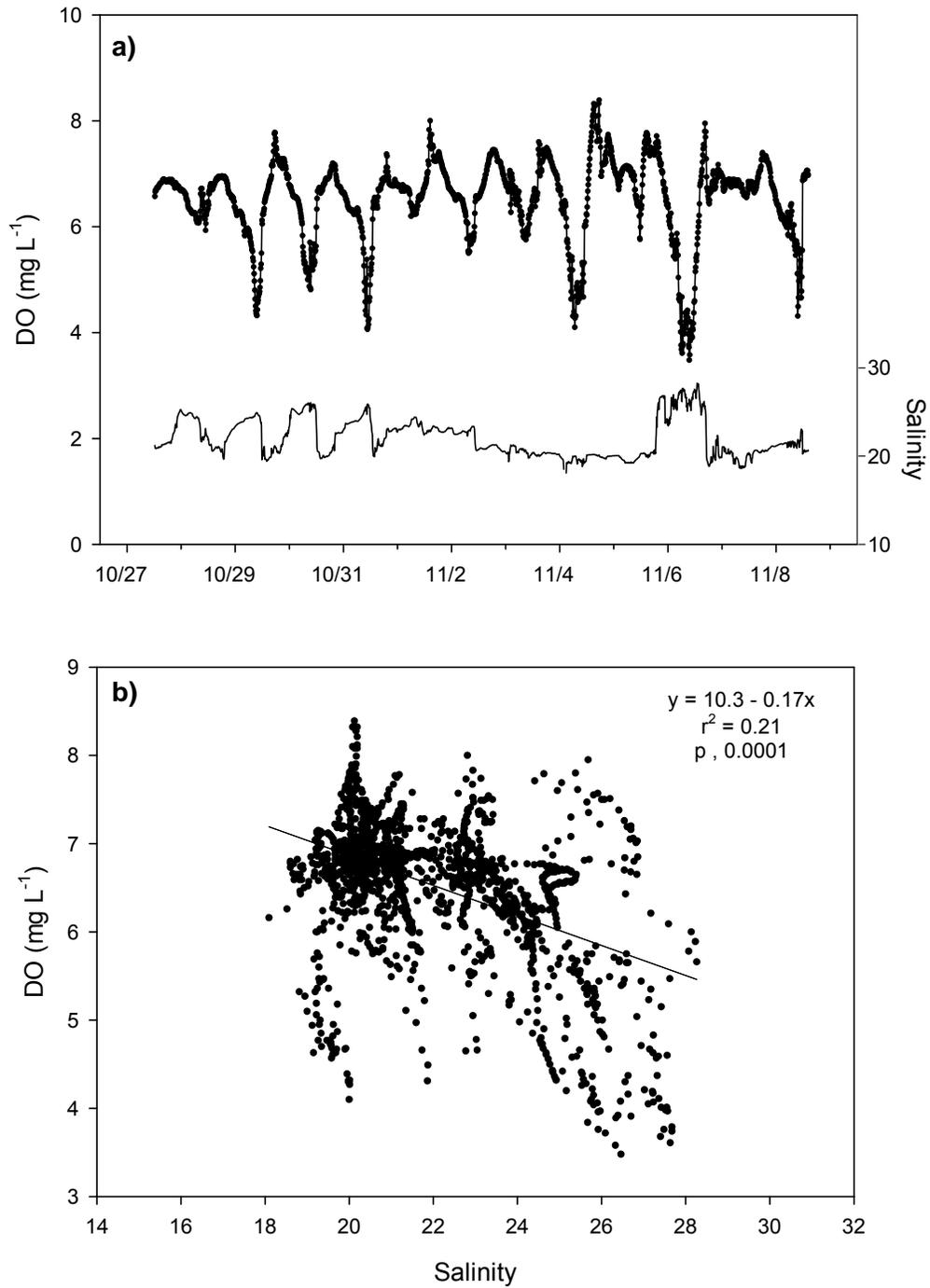


Fig. III.b. (A) Diel variations in DO concentrations (mg L⁻¹) and salinity in Little Madeira in Fall 2004. (B) Linear regression of DO on salinity.

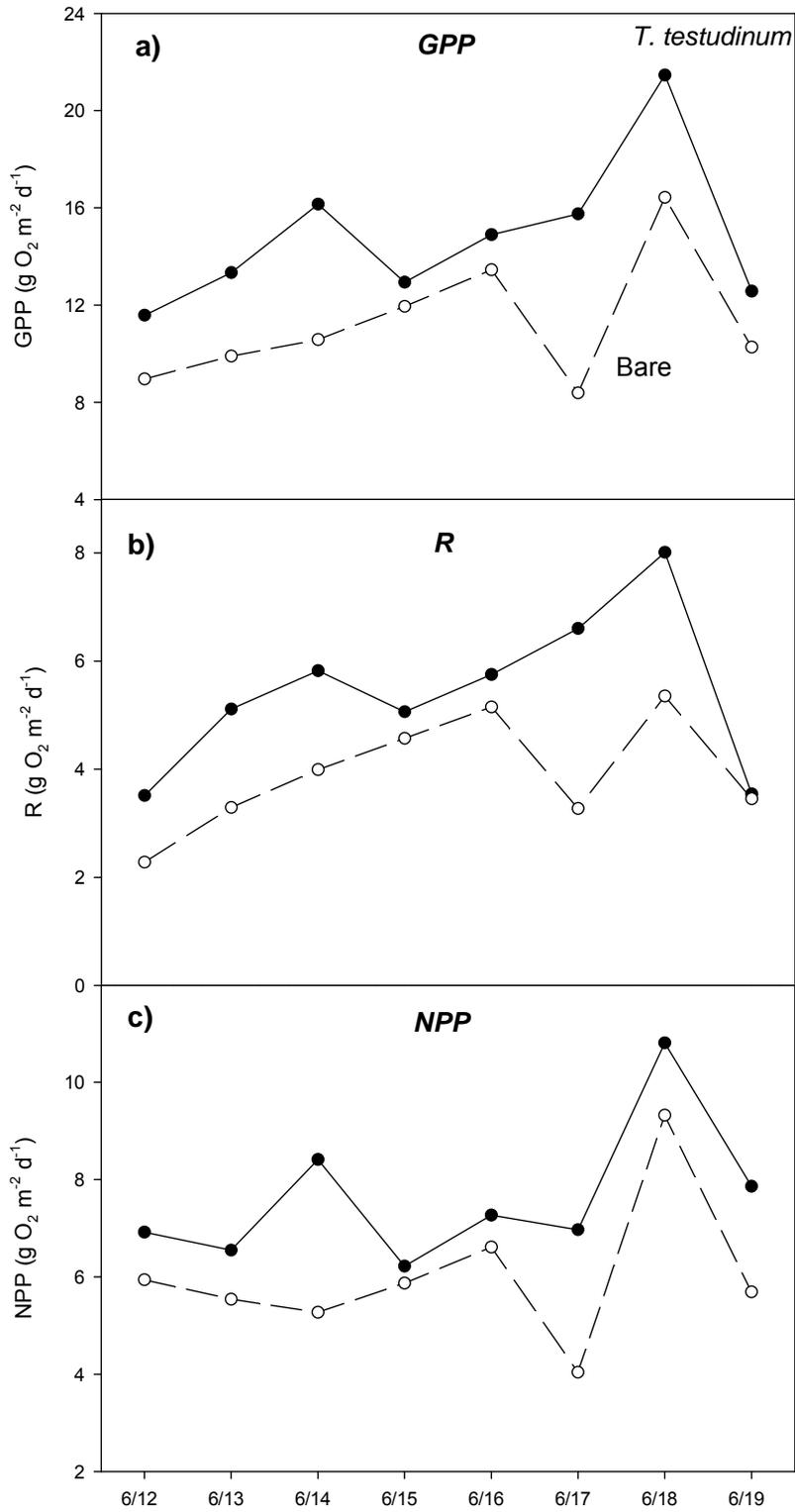


Fig. III.b. Diel variations in GPP (a), R (b), and NPP (c) in a *T. testudinum* bed (solid) and bare area (open) in Sunset Cove in June 2004.

Appendix IV. Leaf and root O₂ release by *Thalassia testudinum*, *Potamogeton perfoliatus*, reproductive *Ruppia maritima*, and vegetative *R. maritima*.

Leaf and root O₂ excretion rates for each species were determined using split-compartment hydroponic chambers (n=3). Plants were collected from field populations and were maintained in artificial seawater adjusted to the appropriate field salinity until the experiments began. Three plants were placed in each chamber so that the leaves and roots were isolated from each other and no water exchange occurred between the compartments. Each compartment was filled with artificial seawater and was fitted with a magnetically-driven stirbar to aid in circulation. Root compartments were covered with aluminum foil to prevent light from reaching the roots. Experiments were conducted in an environmental chamber set at constant irradiance (1100 μE) and temperature (25°C) beginning with 1-3 of dark incubation followed by several hours of light incubation. Water samples for dissolved O₂ gas analysis (see methods Ch. 2) were collected at 30-40 min intervals from sampling ports set into each compartment.

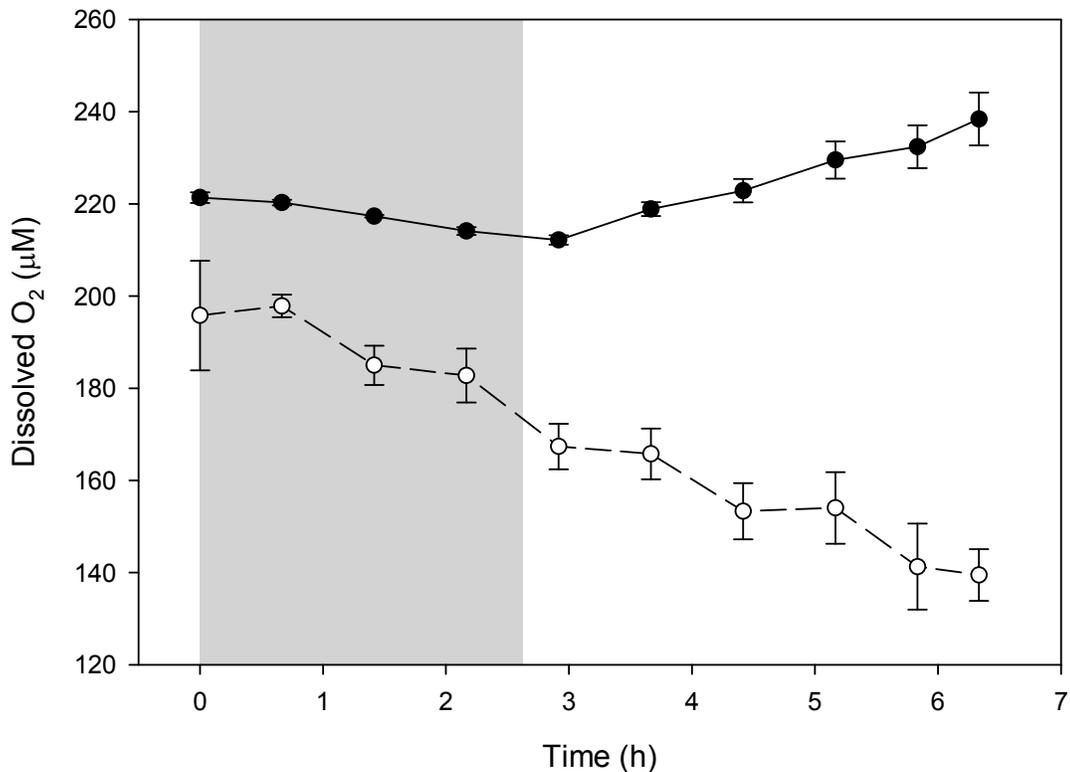


Fig. IV.a. Light/dark variations in dissolved O₂ concentrations (μM) measured in leaf (solid) and root (open symbol) compartments of split-compartment hydroponic chambers for *T. testudinum*. The shaded area represents the dark incubation, whereas white areas represent light incubation.

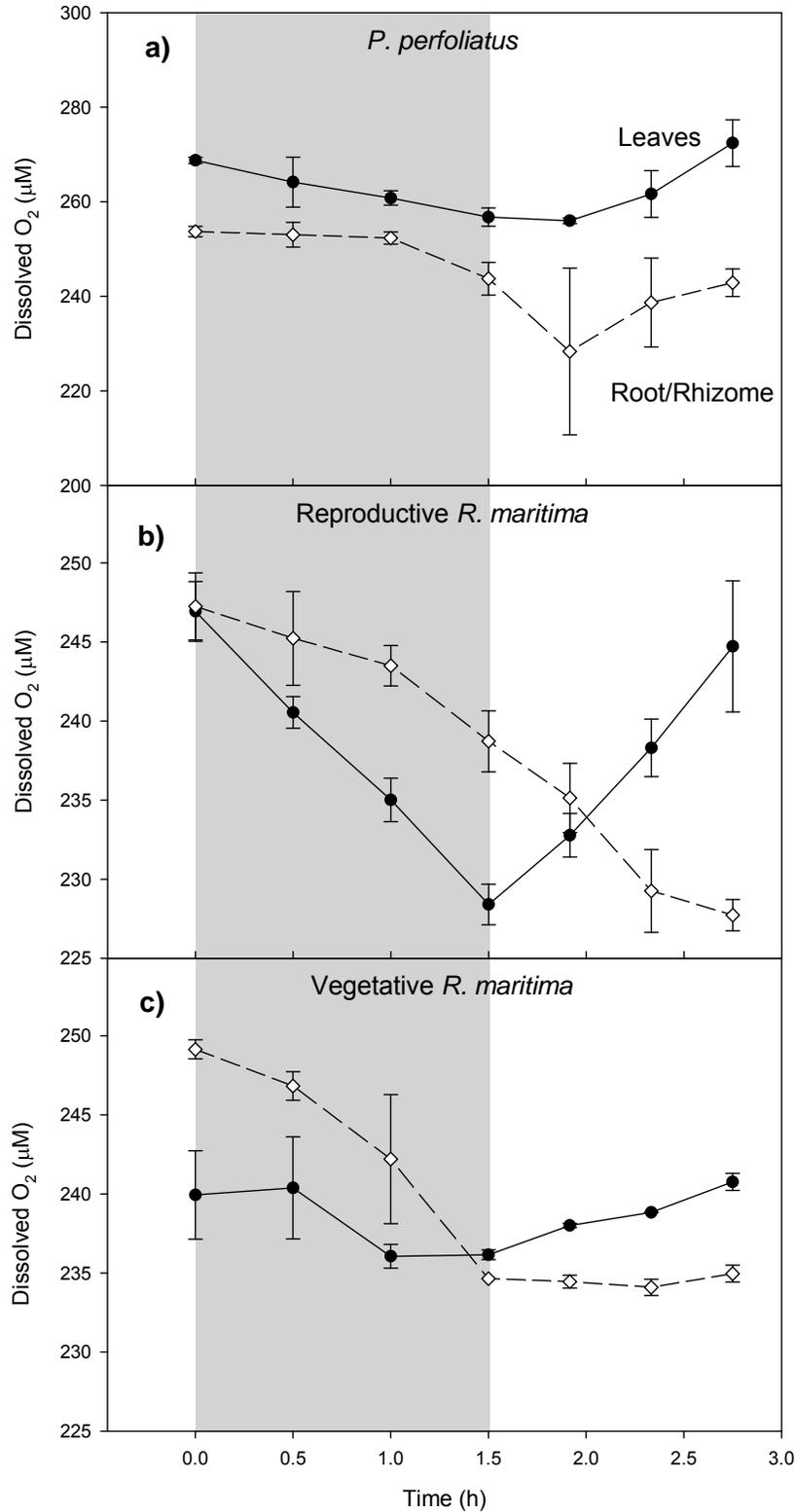


Fig IV.b. Light/dark variations in dissolved O₂ concentrations (µM) measured in leaf (solid) and root (open symbol) compartments of split-compartment hydroponic chambers for (a) *P. perfoliatus*, (b) reproductive *R. maritima*, and (c) vegetative *R. maritima*. The shaded area represents the dark incubation, whereas white areas represent light incubation. Note the different scales.

Appendix V. Diel variations in dissolved O₂ concentrations and net ecosystem production in reproductive *Ruppia maritima* and bare communities July 2004.

Diel variations in dissolved O₂ concentrations were measured in a reproductive *R. maritima* and bare community in mesohaline Chesapeake Bay in July 2004. Continuous measurements of open-water temperature, salinity, and dissolved O₂ concentrations were obtained using instrument packages (YSI 600 XLM) equipped with thermistors, conductivity sensors and pulsed-O₂ electrodes. Instruments were deployed at 0.75 m above the sediment surface. One instrument was deployed at each site and measurements were recorded at 10-min intervals over a series of 7 days. Daily estimates of gross primary production (P_g), respiration (R_n), and net ecosystem production (NEP) were calculated for each site using methods reported in Chapter 2.

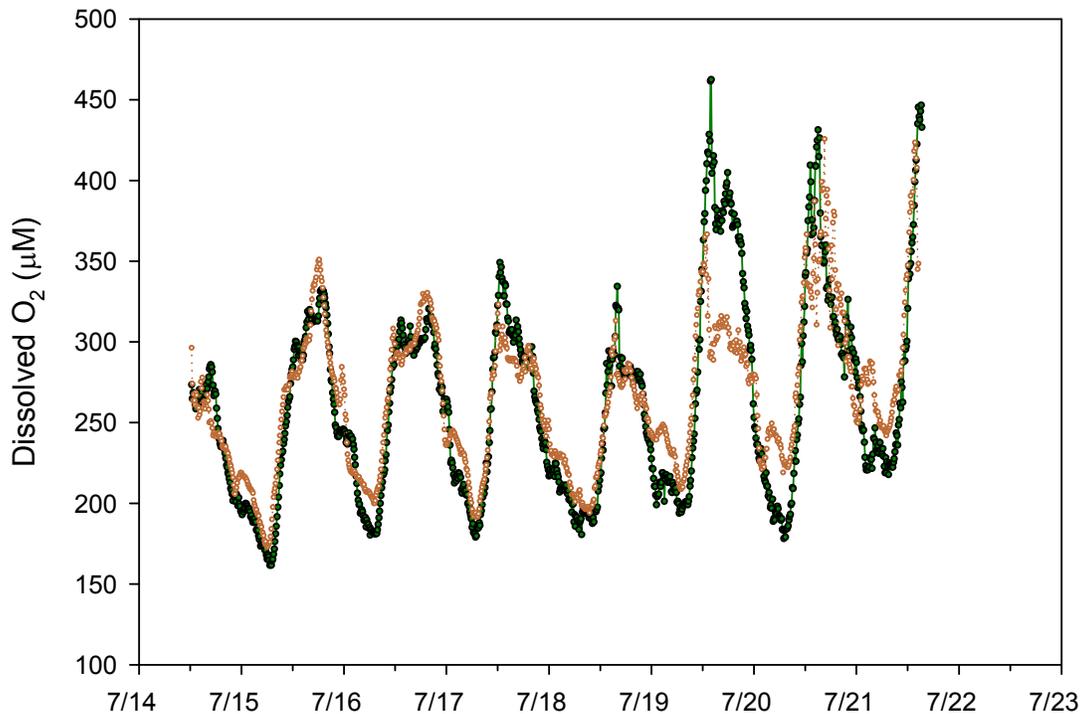


Fig. V.a. Diel variations in open-water dissolved O₂ concentrations (µM) measured in reproductive *R. maritima* (green) and bare (brown) communities in mesohaline Chesapeake Bay in July 2004.

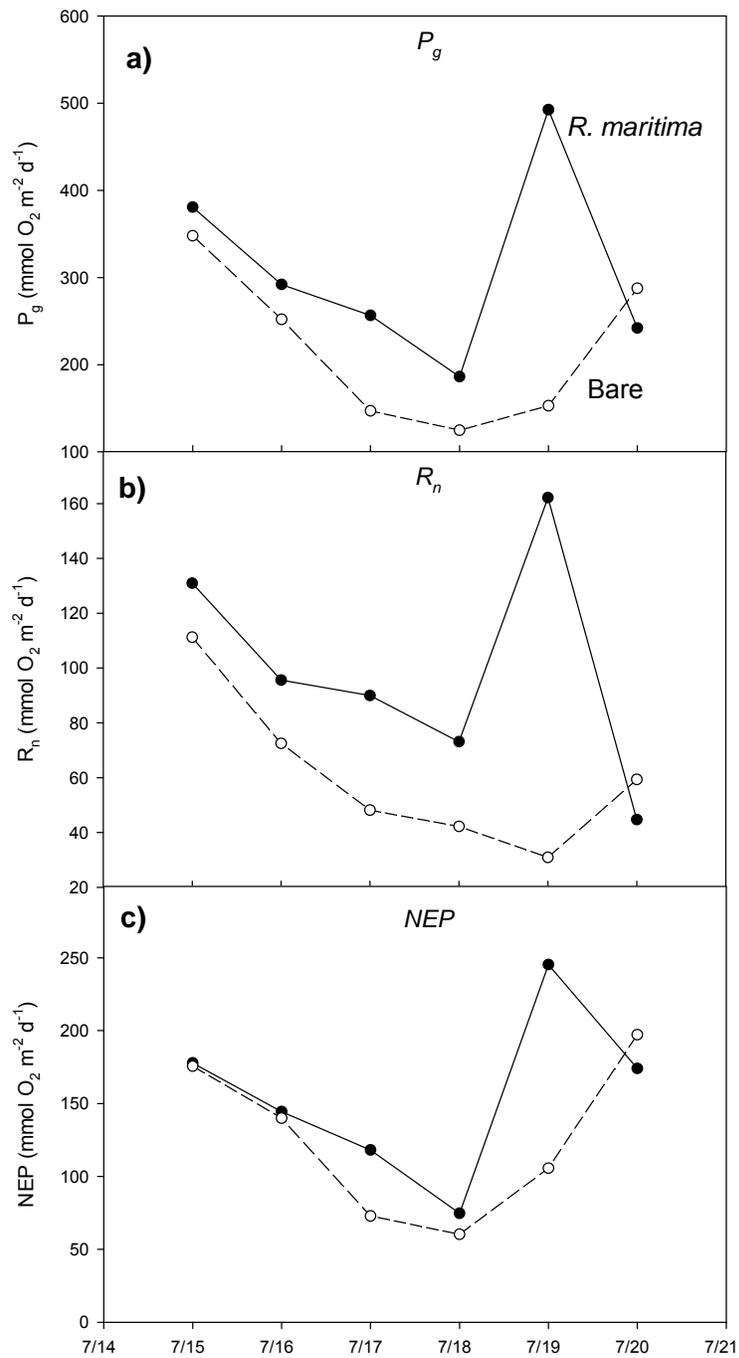


Fig. V.b. Diel variations in gross primary production (P_g), respiration (R_n), and net ecosystem production (NEP) in a reproductive *R. maritima* (filled) and bare (open symbol) community in mesohaline Chesapeake Bay in July 2004. Note the different scales on the y-axis

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