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Effects of nutrient enrichment and shading on sediment primary production and metabolism in eutrophic estuaries

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ABSTRACT: The impact of anthropogenic eutrophication on the productivity and metabolism of estuarine sediments has received relatively little attention. In this study, we investigated the separate and combined effects of decreased light availability and sediment nutrient enrichment, 2 of the most important impacts of anthropogenic eutrophication, on sediment primary production and metabolism in 2 eutrophic subestuaries of Weeks Bay (Alabama, USA), seasonally, over a year. We found a significant effect of shading on both sediment primary production and metabolism, mostly due to decreased photosynthetic rates of benthic microalgae coupled with simultaneous increases in sediment respiration rates. The ratio of mean production in non-shaded plots to that in shaded plots was close to 1 and tended to occur at natural bottom light intensities <100 µmol m^{-2} s^{-1} during the summer experiments, whereas higher light intensities tended to increase the ratio (i.e. higher values under non-shaded conditions). The ratio tended to decrease and become closer to 1 at the highest values of light intensity recorded (>600 µmol photons m^{-2} s^{-1}). Nutrient enrichment had little effect on sediment primary production and metabolism in the estuarine sites studied; however, in some instances nutrient enrichment influenced the negative effects of reduced light on sediment net production. The results demonstrate that the impact of light reduction on sediment primary production and metabolism in a turbid, nutrient-rich estuary is greater than that of additional sediment nutrient enrichment.

KEY WORDS: Sediment · Microphytobenthos · Metabolism · Primary production · Nutrient enrichment · Light limitation · Eutrophication

INTRODUCTION

Benthic microalgae, also termed microphytobenthos, are ubiquitous in subtidal and intertidal estuarine sediments. They live in the upper few millimeters of the sediment in shallow ecosystems and exhibit diel vertical migration within this layer. Benthic microalgae play a number of important roles in estuarine ecosystems. They produce extracellular polymeric substances that are an important carbon source for bacteria and grazers, and aid in the stabilization of sediments (Wolfstein & Stal 2002). This sediment stabilization helps to reduce resuspension and thus the erosion of estuarine bottoms (Miller et al. 1996). Benthic microalgae are also intermediaries in many biogeochemical processes in estuaries, and thus important components of sediment carbon and nutrient cycling and exchange with the water column (Baillie 1986, Rizzo et al. 1992). Further, benthic microalgae have been shown to contribute significantly to the total primary production of estuaries (de Jonge 1992, MacIntyre & Cullen 1995) in view of the large area they normally cover (i.e. sedi-

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ment flats) and their significant areal productivity rates (in g C m^{-2} h^{-1}). Indeed, several studies have documented that in shallow estuarine environments benthic microalgae can achieve areal productivity rates that are at least 20% that of phytoplankton (Daehnick et al. 1992, Moncreiff et al. 1992, Schreiber & Pennock 1995) and at least 25% that of macrophytes and epiphytes (Moncreiff et al. 1992). Because of their high contribution to total estuarine primary production, benthic microalgae are also important trophic resources for many local and external consumers (Middelburg et al. 2000, Carman & Fry 2002).

As a result of the increasing occupation of coastal watersheds by humans, the discharge of nutrients into coastal waters is also increasing (Nixon 1995, Howarth et al. 2002). This process, known as anthropogenic eutrophication of coastal ecosystems, is one of the most pervasive worldwide environmental impacts imposed by humans (NRC 1994, Jackson et al. 2000, Tilman et al. 2001), and its effects on the biota of coastal ecosystems have received considerable attention. For instance, it is well known that increased nutrient loading often leads to blooms of phytoplankton and/or filamentous benthic macroalgae (e.g. reviews by Duarte 1995, Borum & Sand-Jensen 1996, Cloern 2001) which, in turn, may exert a series of positive (e.g. enhanced refuge, food and recruitment) and negative (e.g. anoxia, predator attraction, high sulfide concentrations) impacts on benthic infauna (e.g. Rafaelli et al. 1998, Norkko et al. 2000, Franz & Friedman 2002). The effects on other benthic macrophytes, such as seagrasses and large bulky macroalgae, are often negative and include anoxia (Sfriso et al. 1992, Krause-Jensen et al. 1999), adverse biogeochemical conditions (Van Katwijk et al. 1997) and light limitation (Short et al. 1995, Hauxwell et al. 2001), which may involve substantial loss of these macrophytes (Silberstein et al. 1986, Short & Wyllie-Echeverria 1996, Hauxwell et al. 2003). Nevertheless, relatively little research has been done on the effects of eutrophication on the primary production and metabolism of sediments inhabited by microalgae (Barranguet et al. 1998, Hillebrand & Sommer 2000a,b, Hillebrand et al. 2002). This is an important aspect in view of the worldwide occurrence and persistence of eutrophication and of the numerous important ecological roles of benthic microalgae.

Anthropogenic eutrophication may involve positive and/or negative effects on benthic microalgal communities depending on (inter alia), the interaction between nutrients and light availability during and following increased nutrient loads. For instance, in shallow, well-illuminated sediments, where nutrient limitation of microalgal growth occurs, higher anthropogenically induced nutrient loads could stimulate benthic primary production if light availability at the sediment surface remains high. Research in the Baltic Sea has shown that microphytobenthic biomass increases after nutrient enrichment under conditions of high irradiance (Hillebrand et al. 2000). Dizon & Yap (1999) found that the biomass and photosynthetic yield of coral reef microphytobenthic communities also increased with elevated levels of nitrogen and phosphorus input. Conversely, in nutrient-rich, turbid estuaries where light limitation of microphytobenthic growth frequently occurs, higher water-column attenuation and decreased light availability at the bottom resulting from eutrophication should have a greater effect on benthic primary production than increased nutrient availability. Meyercordt & Meyer-Reil (1999) compared microphytobenthic primary production in a highly eutrophied and turbid coastal lagoon with that in a moderately eutrophied coastal lagoon, and showed that light limitation in the highly eutrophied lagoon was detrimental to microphytobenthic primary production.

The objective of the present research was to determine the separate and combined effects of sediment nutrient enrichment and decreased light availability (2 of the most important processes that often accompany anthropogenic eutrophication) on sediment primary production and metabolism at 2 nutrient-rich, turbid estuarine sites within Weeks Bay (Alabama, USA). We hypothesized that further enrichment of the already nutrient-rich sediment would have little effect on primary production and metabolism, whereas decreased light availability would have a considerably negative impact. This research contributes to our understanding of how further increases in nutrient availability and reductions in light availability would affect eutrophic estuarine benthic systems, and provides information useful for environmental management of these systems.

MATERIALS AND METHODS

Study sites. Weeks Bay is a small estuarine embayment on the eastern shore of Mobile Bay, Alabama (Fig. 1). The embayment is shallow (mean water depth = 1.4 m) and has a small tidal range of 0.3 to 0.5 m. Weeks Bay is fed primarily by the Fish River from the north and the Magnolia River from the east, although there are several smaller tidal streams that drain into the bay. Following intense rainfall, freshets can replace the water within the bay within 2 to 3 d, although the water is normally renewed every 3 d through tidal forcing (Schroeder et al. 1990, 1992). Thus, the salinity of Weeks Bay is strongly controlled by the Mobile River system, and to a lesser extent by the Weeks Bay watershed. The sediments are a mix-

ture of clay and silt, with a surface layer mainly comprised of sandy clay loam and organic soil (Haywick et al. unpubl. data).

Studies were conducted at 2 sites within the bay between October 2002 and July 2003. The first site (Magnolia) was on the SE shoreline near the mouth of the Magnolia River, and the second (Reserve) was on the NW shoreline within a smaller embayment of the estuary (Fig. 1). Both intertidal regions were dominated by the cordgrass *Spartina alterniflora* Loisel and *S. cynosuroides* (L.) Roth, and the black needlerush *Juncus roemerianus* Scheele. The sediments at Magnolia were mainly composed of sand, while those at Reserve were dominated by organic unconsolidated mud, despite some seasonal variability in sediment composition in both sites.

Weeks Bay is characterized by a turbid water column arising from high concentrations of suspended sediments resulting from resuspension during wind events, discharge from the Fish and Magnolia Rivers, as well as tidal inputs from Mobile Bay (Miller-Way et al. 1996). Schreiber & Pennock (1995) reported high levels of light extinction in the water column of Weeks Bay, with attenuation coefficients ranging between 1 and 7.5 m^{-1}. In addition, a 4 yr series of surveys by Pennock et al. (2001) showed that nutrient concentrations in the water column of Weeks Bay are generally higher than in many other estuarine systems (Cebrian & Valiela 1999). Furthermore, preliminary measurements indicated that sediment porewater nutrient concentrations are higher than in other systems (Worm et al. 2000).

At both sites, all experiments were conducted on bare subtidal sediments. Water depth varied with season and site, from 0.1 m in winter to 1.2 m in spring/summer at Magnolia and from 0.2 m in fall/winter to 0.8 m in spring/summer at Reserve. The microphytobenthic community of the sites is dominated by several diatom genera: *Achnanthes*, *Amphora*, *Navicula*, *Nitzschia* and *Pleurosira* (S. Phipps pers. comm.). Polychaetes, such as *Hobsonia florida*, *Laeonereris culveri* and *Eteone*, comprise the most abundant group of macrofauna in the sediment (Miller-Way et al. 1996). Due to considerable and frequent resuspension, benthic diatoms are also often present in the water-column (S. Phipps pers. comm.), along with pelagic diatoms, several species of rotifers and copepods, numerous commercially important fishes, and invertebrates such as blue crabs and penaeid shrimps (Miller-Way et al. 1996).

Experimental design. The effects of sediment light-availability (i.e. shading) and nutrient enrichment on sediment primary production and metabolism were tested seasonally (in October 2002, February 2003, May 2003 and July 2003) at the 2 study sites. Experimental plots were 1 m^2 PVC frames placed 30 ± 2 cm above the sediment surface; 10 of these frames were covered with a black shade cloth (Aquacenter), while 10 remained uncovered. The shade cloth reduced light intensity at the sediment surface by about 50% compared to unshaded conditions. The cloths were cleaned carefully by hand throughout each experiment to minimize any increase in shading from build-up of mud and detritus on the cloth. Furthermore, the sediment under 10 of the frames (5 shaded and 5 unshaded) was enriched several times throughout the experiment (see next subsection). Therefore, each experiment involved a 2-factorial manipulation with 4 treatments: (1) natural light and nutrient availability, (2) reduced light and natural nutrient availability, (3) natural light and enhanced nutrient availability and (4) reduced light and enhanced nutrient availability. Each treatment had 5 replicates (i.e. five 1 m^2 frames). Replicates of the 4 treatments were grouped into 5 rows, with each row containing 1 replicate of each treatment randomly located within the row. Adjacent plots (both within and across rows) were 1.5 m apart. This design minimized the impact of unknown environmental heterogeneity on our results (Sokal & Rohlf 1995, Quinn & Keough 2002). Each experiment was run for 6 d.

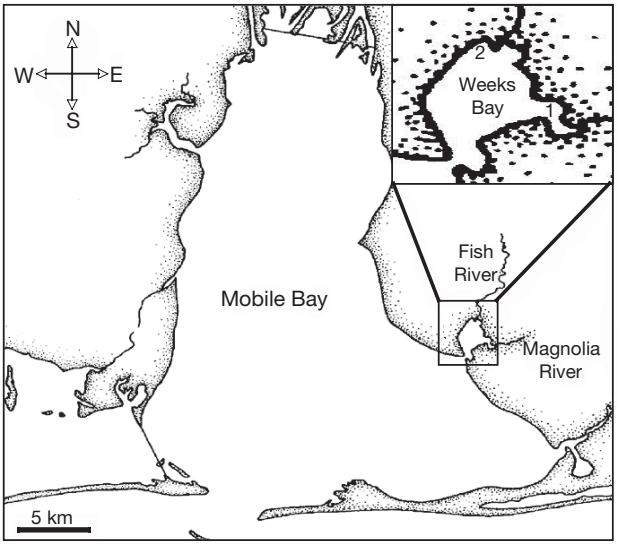

Fig. 1. Study sites at Weeks Bay, Alabama. 1: Magnolia; 2: Reserve

Sediment nutrient enrichment. Prior to starting our experiments in fall 2002, we measured ambient nitrogen and phosphorus concentrations in the sediment porewater of the 2 study sites (see next subsection). For each site, and based on the ambient porewater concentrations and information on sediment density and porewater content, we calculated a nitrogen addition per plot that represented a 70× increase relative to the average ambient concentration. Then, using the esti-

mated porewater nitrogen concentration in the fertilized plots and the average ambient phosphorus concentration in the porewater, we calculated the quantity of phosphorus required to be added to each plot at each site such that the final concentrations in the sediment porewater immediately after fertilization would approximate the 17:1 nitrogen:phosphorus molar ratio corresponding to the internal ratio of microphytobenthos (Hillebrand & Sommer 1999). Because ambient nitrogen:phosphorus molar ratios in the sediment porewater were much greater than 17:1, phosphorus addition represented a more than 70× increase relative to ambient concentrations (i.e. 150× at Magnolia and 400× at Reserve). Final values were 3.15 g N and 0.445 g P per plot at Magnolia and 4.47 g N and 0.66 g P per plot at Reserve each time nutrients were added in the fall experiments. Nutrient additions were made on Days 0 and 2 during these experiments. This fertilization procedure was intended to maintain elevated, stoichiometrically-balanced nutrient availability throughout the experiments, and was based on levels of enrichment reported in previous papers (Worm et al. 2000), knowledge of sediment resuspension rates in our study area (S. Phipps pers. comm.), and the stoichiometric ratio of microphytobenthos (Hillebrand & Sommer 1999).

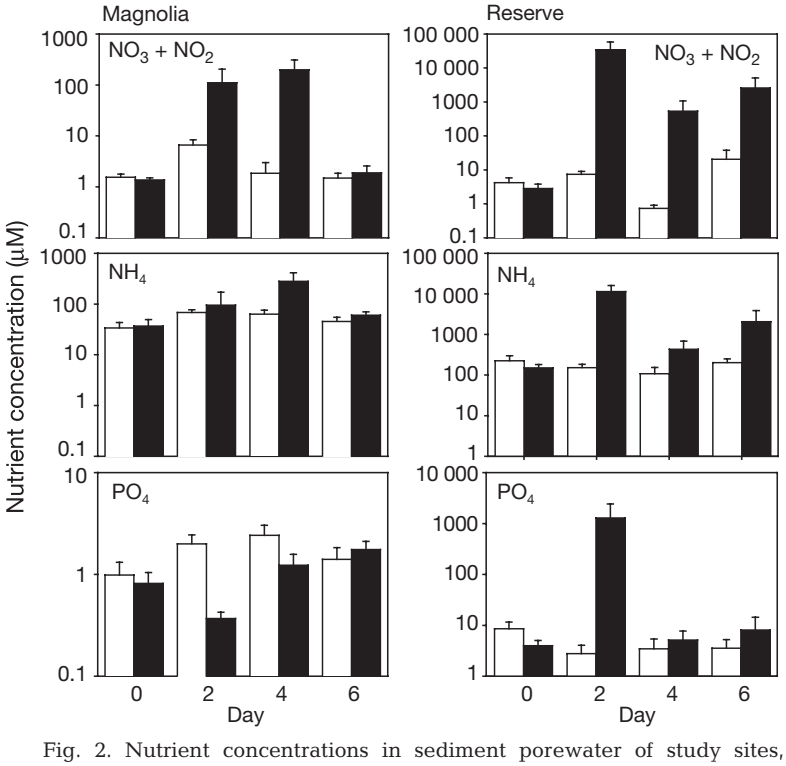

Fig. 2. Nutrient concentrations in sediment porewater of study sites, regardless of shading treatment (shaded and non-shaded pooled) during 2002 fall experiment. Data are means + SE (n = 10). Open bars and black bars are non-fertilized and fertilized plots, respectively. Concentrations are log-transformed

Nitrogen and phosphorus were added in a quick-release form of solid commercial-grade ammonium-nitrate (17% ammoniacal nitrogen, 17% nitrate nitrogen, Royster-Clark) and super phosphate (46% P_2O_5, Agribusiness), respectively. Each set of nutrients was subdivided into 5 equal amounts and packaged into 2.5 cm diameter packets made of nylon stocking. These were then carefully buried to a depth of approximately 10 cm at the 4 corners and center of each fertilized plot; 1 measurement of nutrient porewater concentrations was taken per plot on Days 0, 2, 4 and 6 of the fall experiment at each site. Samples on Days 0 and 2 were taken before burying the nutrient packets. The samples were taken and processed as detailed in next subsection.

Examination of the porewater nutrient concentrations for the fall experiments revealed that, in general, concentrations remained higher in the fertilized plots at the 2 sites through Day 4, but that differences tended to fade on Day 6 (Fig. 2, Table 1). Therefore, in order to ensure increased, stoichiometrically-balanced nutrient availability in the fertilized plots throughout the experiments, we fertilized again on Day 4 in all experiments performed during the other seasons, but with only half the amount of nutrients added on Days 0 and 2. Thus, the final quantities added per plot in February 2003, May 2003 and July 2003 were 3.15 g N and 0.445 g P per plot at Magnolia, and 4.47 g N and 0.66 g P per plot at Reserve, on Days 0 and 2, and 1.58 g N and 0.223 g P per plot at Magnolia, and 2.24 g N and 0.33 g P per plot at Reserve, on Day 4. We also measured porewater nutrient concentrations on Days 0 (before burying the packets) and 6 in each of these 3 seasons. One measurement was taken per plot in each site as described below. While nutrient concentrations remained similar between fertilized and non-fertilized plots on Day 0, fertilized plots tended to show higher values on Day 6 (Table 1), indicating that our enrichment procedure generally provided increased, stoichiometrically balanced nutrient availability in the treatment plots throughout the experimental period.

Porewater nutrients. Porewater nutrient samples were collected using a porewater sampler consisting of an 8 cm long piece of rigid aquarium tubing with holes drilled at regular intervals and attached to a 60 ml syringe. The tubing was inserted into the sediment and the porewater drawn up into the syringe and taken back to the laboratory for processing. All samples were filtered through 0.45 µm glass-fiber filters

Table 1. Comparison of porewater nutrient concentrations between non-fertilized and fertilized plots at study sites for Days 4 and 6 in fall experiments and Day 6 in all other experiments. Values are p-values of Student's *t*-test (H_o: concentration non-fertilized ≥ concentration fertilized). *p ≤ 0.05, **0.1 ≥ p > 0.05

Site	Day	$NO_3 + NO_2$	NH_4	PO_4
Fall				
Magnolia	4	0.01*	0.07**	0.93
	6	0.14	0.43	0.14
Reserve	4	0.01*	0.04*	0.25
	6	0.11	0.27	0.36
Winter				
Magnolia	6	0.01*	0.06**	0.03*
Reserve	6	0.02*	0.75	0.90
Spring				
Magnolia	6	0.05*	0.13	0.01*
Reserve	6	0.20	0.01*	0.01*
Summer				
Magnolia	6	0.18	0.07**	0.03*
Reserve	6	0.03*	0.03*	0.34

(Ahlstrom) and analyzed for nitrate, nitrite, ammonium and phosphate according to standard colorimetric methods (Strickland & Parsons 1972) using a skalar SAN$^+$ autoanalyzer. Porewater nutrients were measured on Days 0 and 3 of the experiment.

Sediment primary production. Sediment primary production was measured using the ^{14}C uptake method of Van Raalte et al. (1974) for sediment-associated algae, with some modifications (Moncreiff et al. 1992). Incubations were performed *in situ*. Sediment cores were taken with a 2.5 cm diameter corer. For each core, the top 1 cm of sediment was sliced onto a silicone stopper and stopper and sediment were plugged into an incubation quartz tube of the same diameter: the sediment was gently pushed 1 cm above the top of the collection core, the bottom of the quartz core was pressed firmly over the top rim of the collection core, and the top cm of sediment was transferred onto the silicone stopper by sliding the quartz tube onto the stopper. This procedure minimized the possible disturbance associated with slicing and transferring of the top 1 cm of sediment to the incubation tube. We added 3 µCi of $NaH^{14}CO_3$ to 10 ml of filtered site seawater, and gently spiked the solution into the tube by trickling along the tube wall. We took 3 cores from each experimental treatment, each of the 3 cores being taken from a different plot (i.e. 3 complete rows of the 5 were sampled). In addition, in all of the plots of one of the rows selected, a second tube containing the isotope and dichlorophenyl dimethyl urea (DCMU) at a concentration of 10^{-5} M was incubated along with the isotope-only tube. DCMU is a natural herbicide which inhibits the operation of Photosystem II and active carbon uptake (Legendre et al. 1983). Thus, the tubes that received DCMU acted as 'blanks' for the determination of photosynthetic uptake of ^{14}C (i.e. uptake in the isotope-only tubes minus uptake in the DCMU tubes). The tubes were then sealed with top silicone stoppers and cable ties, stabilized with wire frames to ensure adequate anchorage to the bottom, returned to the same plots from which they were originally taken, and incubated for 4 to 5 h. When anchoring the tubes, care was taken to level off the incubated sediment with the surrounding sediment. At the end of the incubation period, ^{14}C uptake was stopped by the addition of buffered 4% formalin, and the samples transported to the laboratory for further processing. The incubations all occured around solar noon and under sunny conditions. When weather permitted, they were carried out on Days 2, 4 and 6.

In the laboratory, the samples were washed from the incubation tubes with 50 ml of 2% HCl onto 0.45 µm cellulose nitrate filters (Whatman); this process also removed all unincorporated and sediment-bound ^{14}C. The filter and sediment were placed in 50 ml polypropylene centrifuge tubes for digestion (accomplished with the addition of 10 ml of concentrated HNO_3 [reagent grade] per tube) and incubated in a fume hood for 12 h. The digested samples were centrifuged for 10 min at 1000 rpm, and 1 ml of the supernatant of each sample was added to 9 ml of 0.75 M tris buffer (ICN Biomedicals). Finally, 0.5 ml of this combination was added to 4.5 ml of scintillation cocktail (EcoLume) and the number of scintillations counted over 5 min using a Packard Tri-Carb 2500-TR scintillation counter. Count rates were given in disintegrations per minute (dpm), which were then converted to values of primary production (PP, in mg C m^{-2} sediment h^{-1}) following (Leach 1970, Strickland & Parsons 1972):

$$PP = [(S - D) \times V \times Alk \times CT \times DF]/(t \times dpm_a \times A)$$

where S is the dpm of the sample with no DCMU, D is the average dpm of the 4 DCMU samples on a given day (see below), V is the volume incubated in the tube (0.01 l), Alk is the alkalinity of the water incubated (mg C l^{-1}), CT is a correction term for the difference between ^{12}C and ^{14}C isotopic masses (1.064), DF is the dilution factor (200), t is the incubation time (h), dpm_a is the absolute activity added in the incubation tube (6.66×10^6 dpm), and A is the area of the incubated sediment (m^2). Alkalinity was determined by measuring the concentration of dissolved inorganic carbon in the water column at each site during each experimental week. Water-column samples were collected in 20 ml glass vials 2 d before incubation (e.g. samples for incubations on Day 2 were collected on the deployment day and samples for incubations on Days 4 and 6

were collected on Days 2 and 4, respectively), stored on ice, and returned to the laboratory for processing. Concentrations of dissolved inorganic carbon were determined using a Shimadzu TOC-5000 fitted with a non-dispersive infrared detector. On each experimental day at each site, duplicate samples were run and the mean value was used in the above equation. Since dpm in the DCMU incubations were generally low and similar, the 4 DCMU samples measured on each day were averaged as a single value.

Sediment metabolism. To measure how nutrient enrichment and decreased light availability affected sediment metabolism, we recorded changes in dissolved oxygen concentration inside transparent and opaque chambers placed over the sediment surface. The chambers were made of clear plastic and were cylindrical, measuring 18.4 cm in diameter and 21.6 cm in height. Some of the transparent chambers were painted with several coats of flat black paint to make them completely opaque. On each sampling day, 1 transparent and 1 opaque chamber were placed within each plot and anchored onto the bottom such that only the top 15 cm of the chamber was above the sediment surface. Thus, these metabolism measurements integrated the sediment and the overlying 15 cm (i.e. height of incubation chamber) of water column, which often contains much resuspended sediment (Shaffer & Sullivan 1988, de Jonge & van Beusekom 1992, S. Phipps & M. Sullivan pers. comm.).

Before deploying the chambers, the sediment surface was checked for large animals (i.e. crabs, hermit crabs, oysters) and pieces of debris, which were removed when present. Incubation time was between 3 and 5 h. All incubations were around solar noon and always in sunny conditions. When weather permitted, incubations were carried out on Days 2, 4 and 6. At the end of each incubation period, water samples were removed from the chambers with a 60 ml syringe and attached tubing by inserting the tubing through a 1.0 cm diameter hole at the top of the chamber (this had remained capped throughout the incubation period). Care was taken to draw water from approximately the middle of the chamber. After collection, the water was gently transferred to a 50 ml BOD bottle and the oxygen concentration read with a field oxygen probe (WTW Oxi 197i/StirrOx G, WTW Measurement Systems). Prior to beginning the incubations, at least 3 measurements of the initial oxygen concentration in the water column were taken near the incubation area. Sediment net production (NP, in mg C m^{-2} sediment h^{-1}) corresponds to the difference between final and initial oxygen concentrations in the transparent chambers, sediment respiration (R, in mg C m^{-2} sediment h^{-1}) to the difference in the dark chambers. They were calculated by following:

$$NP = [(F - I)/t] \times C \times H \times P_{con}$$
$$R = [(F - I)/t] \times C \times H \times R$$

where F and I are the dissolved oxygen concentrations (mg l^{-1}) at the end and start of the incubation, t is the incubation time (h), C is the conversion factor of liters to m^3, H is the height of the water column in the chamber (0.15 m), P_{con} is the oxygen/carbon conversion factor for sediment net production (0.344 mg C mg^{-1} oxygen based on a photosynthetic quotient of 1.2 and a respiratory quotient of 1: Strickland & Parsons 1972), and R is the oxygen/carbon conversion factor for sediment respiration (0.375 mg C mg^{-1} oxygen based on a respiratory quotient of 1: Strickland & Parsons 1972). Finally, sediment gross primary production was calculated as the difference between net production and respiration (mg C m^{-2} sediment h^{-1}).

Hydrographic conditions. On each sampling date, we also measured photosynthetically active radiation (PAR) at the sediment surface (both as absolute amount and as percentage of incident light at the air–water interface), water-column temperature, salinity and dissolved oxygen concentration. Measurements were taken adjacent to the experimental plots (<5 m) around midday. On some days, a second PAR reading was made at the end of the benthic chamber incubation period. PAR was measured using a LICOR quantum irradiance meter equipped with air and underwater sensors fitted to 4π cells (LICOR). Temperature, salinity and dissolved oxygen were measured at the water surface and right above the sediment using a YSI Model 85 meter (Yellow Springs Instrument). On a few days, we also took PAR measurements beneath a number of shaded frames.

Water-column nutrient (nitrate, nitrite, ammonium and orthophosphate) concentrations and phytoplankton biomass were also measured on Days 0 and 6 adjacent to the experimental plots. We took 6 replicate water samples from approximately mid-depth, and stored them on ice for transport to the laboratory for analysis. Samples were filtered through a 0.45 µm glass-fiber filter (Pall Life Sciences), the filtrate was collected in duplicate nalgene bottles, and both filter and filtrate were stored at −80°C until processing. Phytoplankton biomass was measured as chlorophyll *a* according to the fluorometric technique of Parsons et al. (1984). Water-column nutrient concentrations were determined using a Skalar SAN^+ autoanalyzer.

Statistical analyses. We used a 3-way fixed-factor ANOVA (Sigmastat, Version 2.03, SPSS) to investigate the effects of light reduction and nutrient enrichment on sediment primary production and metabolism. Day (2, 4 or 6) is considered as the third fixed factor. The reasons are 2-fold. First, even though we repeatedly sampled the same plots, we targeted a dif-

ferent sediment location each time we took a new sample from a given plot. As a result, most probably completely new organisms entered the incubation quartz tubes or benthic chambers each time the plot was sampled. Therefore, successive samples within the same plot were not co-depended due to repeated inclusion of the same organisms, thus rendering a repeated-measures design with time as the repeated-measure factor, inappropriate (Mead 1992, Quinn & Keough 2002). Second, our intent was to examine the effects of the 6 d manipulation at 3 times intervals that approximately corresponded to 3 successive generations of the benthic microalgae in the sediment community studied. Thus, measurements were made every 2 d after initiation of the experiments, since 2 d roughly correspond to the turnover time of benthic microalgal populations (Cebrian 1999). Thus, time can be interpreted as a fixed factor, with the 2 d measurement intervals serving as a proxy for successive populations (Sokal & Rohlf 1995, Zar 1998). All data were tested for normality and homogeneity of variance and, where necessary, transformed to meet these requirements.

RESULTS

Hydrographic conditions

Water-column depth was higher in spring and summer and lower in fall and winter (Table 2) , consistent with the seasonality in water depth observed in shallow coastal systems of the NE Gulf of Mexico (Schroeder et al. 1992). Our depth measurements varied from 0.4 to 1.2 m at Magnolia and from 0.2 to 1.2 m at Reserve. Water temperature and salinity also showed clear seasonal oscillations. At Magnolia, temperature ranged from 14.8 in the winter to 31.3°C in late summer–early fall, and from 10.3 to 30.9°C for the same seasons at Reserve. Salinity was lower in the spring and summer, coinciding with the rainy season, ranging from ca. 0 to 14.3 at Magnolia, and from 0.1 to 11.9 at Reserve.

Dissolved oxygen concentrations in the water column were high (generally >7 mg l^{-1}) at the 2 sites throughout the year, and tended to be highest in the winter (Table 2). Water-column nutrient and chlorophyll *a* concentrations were also high at the 2 sites and

Table 2. Hydrogrphic conditions at study sites. Data are means ± SE (with range in parentheses). PAR: photosynthetically active radiation

Depth (cm)	Temp. (°C)	Salinity	Dissolved oxygen (mg l^{-1})	Water-column chl *a* (µg l^{-1})	Bottom PAR (µmol photons m^{-2} s^{-1})	Trans-mittance (%)	Water-column nutrients (µmol l^{-1}) $NO_3 + NO_2$	NH_4	PO_4
Magnolia									
Fall									
67.8 ± 6.3 (50.0–80.0)	24.6 ± 1.0 (20.5–31.3)	8.7 ± 0.7 (6.4–14.3)	9.9 ± 0.4 (8.1–11.7)	51.7 ± 5.0 (31.7–76.5)	208.2 ± 42.8 (63.0–302.2)	17.1 ± 2.1 (10.2–24.6)	3.8 ± 0.5 (0.2–6.5)	0.7 ± 0.1 (0.2–1.4)	0.3 ± 0.06 (0.1–0.7)
Winter									
57.0 ± 6.1 (40.0–68.0)	17.0 ± 0.6 (14.8–19.0)	9.8 ± 0.6 (7.7–11.9)	14.5 ± 0.9 (12.0–18.5)	58.9 ± 5.7 (33.9–99.6)	537.9 ± 326.9 (98.0–1507.0)	29.6 ± 10.8 (15.5–61.8)	22.13 ± 6.605 (0.4–48.3)	0.2 ± 0.03 (0.1–0.4)	0.1 ± 0.01 (0.04–0.2)
Spring									
94.0 ± 7.9 (67.0–115.0)	28.3 ± 0.02 (27.3–29.6)	2.7 ± 0.1 (2.3–2.9)	7.6 ± 0.2 (6.9–8.2)	28.1 ± 2.2 (21.0–45.0)	212.0 ± 34.5 (79.8–301.9)	8.6 ± 1.6 (4.1–14.2)	12.4 ± 1.0 (7.9–17.4)	1.0 ± 0.2 (0.3–1.8)	0.16 ± 0.01 (0.1–0.2)
Summer									
88.0 ± 8.8 (60.0–120.0)	29.4 ± 0.4 (27.6–30.8)	0.2 ± 0.1 (0.0–0.5)	7.6 ± 0.8 (5.2–11.1)	36.0 ± 1.9 (25.9–45.5)	86.0 ± 20.9 (27.9–157.9)	3.6 ± 0.7 (1.2–5.6)	10.2 ± 1.8 (1.5–16.2)	1.5 ± 0.3 (0.3–2.6)	0.8 ± 0.2 (0.2–1.6)
Reserve									
Fall									
44.2 ± 8.6 (23.0–74.0)	21.6 ± 0.6 (17.8–24.5)	10.1 ± 0.5 (7.9–11.9)	10.5 ± 0.6 (7.6–13.3)	24.4 ± 2.1 (16.9–36.6)	537.0 ± 225.9 (5.0–1450.0)	26.0 ± 9.8 (0.3–62.1)	14.7 ± 1.9 (6.7–21.2)	0.5 ± 0.1 (0.2–0.7)	0.1 ± 0.002 (0.1–0.12)
Winter									
59.0 ± 7.2 (43.0–92.0)	12.7 ± 0.67 (10.3–15.3)	8.57 ± 0.27 (8.0–10.0)	11.6 ± 0.7 (9.0–15.5)	9.9 ± 1.0 (5.4 -15.3)	589.6 ± 233.6 (65.0–1450.0)	32.5 ± 7.4 (15.6–59.7)	26.1 ± 2.7 (0.4–37.5)	1.5 ± 0.5 (0.1–6.8)	0.06 ± 0.01 (0.01–0.1)
Spring									
77.6 ± 3.5 (70.0–90.0)	24.7 ± 0.2 (23.8–25.5)	1.2 ± 0.1 (0.9–1.3)	9.9 ± 0.2 (9.3–10.6)	53.5 ± 5.4 (30.4 -79.8)	126.5 ± 59.5 (7.8–330.0)	5.4 ± 2.2 (0.4–12.7)	5.7 ± 1.668 (0.1–12.4)	0.5 ± 0.06 (0.3–1.0)	0.08 ± 0.007 (0.06–0.14)
Summer									
98.6 ± 7.3 (76.0–120.0)	27.8 ± 0.9 (24.1–30.9)	0.15 ± 0.02 (0.1–0.2)	8.9 ± 0.6 (7.4–11.3)	17.8 ± 4.2 (2.3–35.5)	27.6 ± 9.6 (5.6–59.0)	1.3 ± 0.4 (0.4–2.7)	2.2 ± 0.6 (0.03–4.8)	0.5 ± 0.1 (0.1-1.0)	0.1 ± 0.005 (0.09–0.15)

Table 3. Results of 3-way ANOVA of sediment primary production (measured at ^{14}C uptake) for each experiment at each site. Numbers correspond to p-value for each factor in ANOVA. *p ≤ 0.05, **0.1 ≥ p > 0.05

Factor	Magnolia			Reserve		
	Winter	Spring	Summer	Winter	Spring	Summer
Day	<0.001*	0.010*	<0.001*	0.376	0.674	0.002*
Light	0.004*	<0.001*	<0.001*	0.011*	0.097**	0.909
Nutrients	0.267	0.380	0.265	0.203	0.128	0.909
Day × Light	0.503	0.979	<0.001*	0.143	0.324	0.130
Day × Nutrients	0.969	0.273	0.014*	0.387	0.260	0.479
Light × Nutrients	0.626	0.835	0.658	0.404	0.425	0.180
Day × Light × Nutrients	0.988	0.687	0.276	0.501	0.452	0.971

did not show any clear seasonal patterns. PAR at the bottom, both as absolute amount and as percentage of incident light at the water surface, was higher in fall and winter and lower in spring and summer, consistent with the seasonality observed in water-column depth. In particular, summer PAR values were extremely low, averaging 86 (4% of surface light) and 28 (1% of surface light) µmol photons m^{-2} s^{-1} at Magnolia and Reserve, respectively (Table 2).

Sediment primary production

Sediment primary production varied among sampling days in all the experiments at Magnolia, but only in the summer experiment at Reserve (Table 3, Fig. 3). At Magnolia, reduced light availability decreased primary production on all sampling days in the winter and spring experiments, but only on Day 6 in the summer experiment. At Reserve, reduced light depressed primary production on all sampling days in the winter and spring experiment, although the effect was marginal in the latter. Nutrient enrichment did not affect primary production, regardless of site and season, except for a minor increase in the differences among sampling days in the summer experiment at Magnolia.

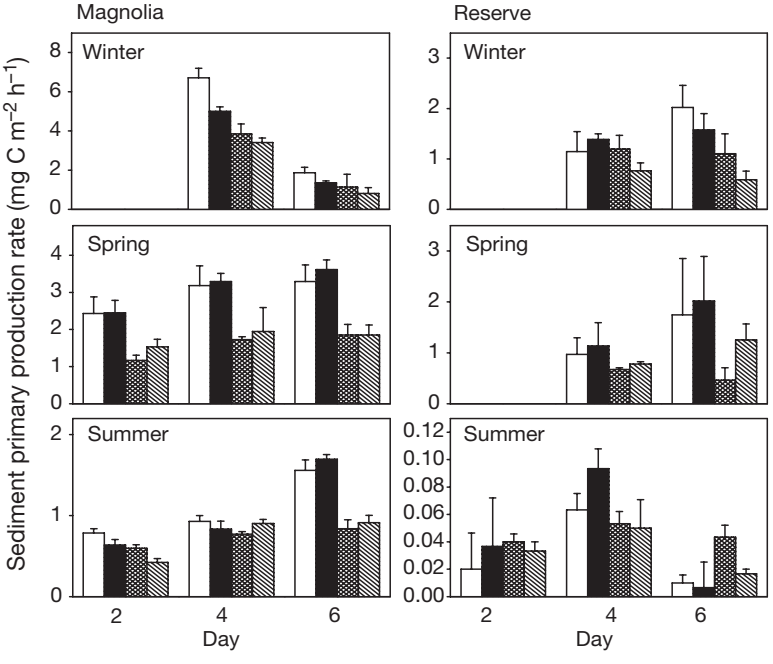

Fig. 3. Effects of shading and nutrient enrichment on sediment primary production (measured as ^{14}C uptake) at study sites. Data are means + SE (n = 5). (□) No shading, no nutrient enrichment; (■) no shading, nutrient enrichment; (▩) shading, no nutrient enrichment; (▨) shading, nutrient enrichment

Sediment metabolism

Gross primary production of the sediment varied among sampling days in the spring and summer experiments at Magnolia and in the fall and spring experiments at Reserve (Table 4, Fig. 4). At Magnolia, decreased light availability reduced gross production on all sampling days in the fall experiment and on Days 2 and 6 in the spring experiment. At Reserve, decreased light depressed gross production on Day 6 in the fall experiment and on all sampling days in the winter and spring experiments, although the effect was not strong. Nutrient enrichment had no effect in any season or site.

Sediment respiration generally varied substantially among sampling days, with large differences at the 2 sites for all experiments, except for the spring experiment at Magnolia (Table 5, Fig. 5). Reduced light availability increased respiration on all sampling days in the fall experiments at Magnolia and Reserve, and only marginally in the spring experiment at Reserve. Nutrient enrichment had no effect on respiration regardless of site or season.

Sediment net production also generally varied among sampling days, particularly at Reserve, and fluctuated between positive and negative values, depending on the interplay between gross primary production and respiration (Table 6, Fig. 6). At Magnolia, net production decreased with decreasing light availability on all sampling days in the fall experiment, and on Days 2 and 6 in the spring experiment. At Reserve, reduced light decreased net production on Day 6 in the fall experiment and on all sampling days in the spring experiment. In addition, as found for gross production and respiration, nutrient enrichment had no effect on net production in any site or season, except for a tendency for greater reduction in net production in the non-fertilized than in the fertilized shaded plots on Day 6 of the fall experiment at Reserve.

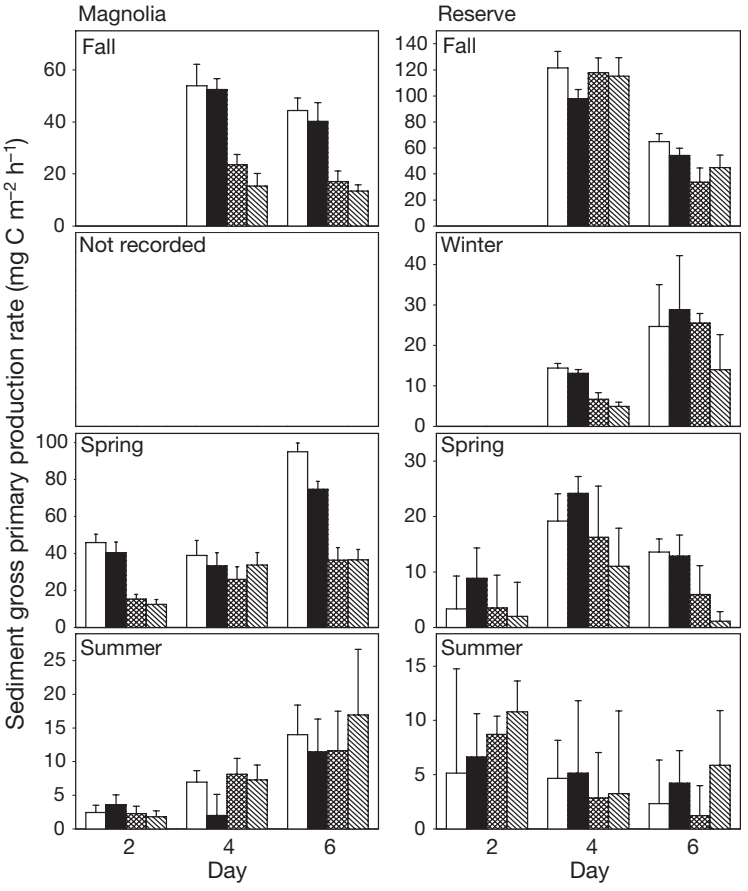

Fig. 4. Effects of shading and nutrient enrichment on gross primary production of sediment at study sites. Data presentation and shading as in Fig. 3

DISCUSSION

This study has shown a significant negative effect of shading on sediment primary production in the 2 estuarine sites examined. Measured as oxygen production, reduced light availability decreased primary production at the 2 sites in the fall, winter and spring experiments, although in 2 of the experiments the decrease only occurred on 1 or 2 sampling days (i.e. significant interaction between day and light treatments). Measured as ^{14}C uptake, reduced light availability decreased primary production on Day 6 of the summer experiment at Magnolia and on all sampling days in the winter and spring experiments at the 2 sites, although the decrease tended to be less important at Reserve (i.e. $0.01 \leq p \leq 0.10$).

Reduced light availability also affected sediment metabolism. Shading increased sediment respiration on all days in the 2 fall experiments and in the spring experiment at Reserve, albeit only marginally in spring. The increase in sediment respiration with shading could be partially due to higher mortality of and/or exudation by benthic microalgae under conditions of low light availability and subsequent use of microalgal particulate

Table 4. Results of 3-way ANOVA for gross primary production of sediment for each experiment at each site. na: not available. $^{*}p \leq 0.05$, $^{**}0.1 \geq p > 0.05$

Factor	Magnolia				Reserve			
	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer
Day	0.425	na	<0.001*	0.057**	<0.001*	0.171	0.003*	0.417
Light	<0.001*	na	<0.001*	0.491	0.043*	0.057**	0.035*	0.795
Nutrients	0.199	na	0.504	0.750	0.967	0.176	0.848	0.535
Day × Light	0.742	na	0.002*	0.269	0.015*	0.884	0.608	0.726
Day × Nutrients	0.485	na	0.545	0.618	0.335	0.326	0.875	0.927
Light × Nutrients	0.308	na	0.324	0.264	0.120	0.172	0.295	0.853
Day × Light × Nutrients	0.291	na	0.537	0.559	0.378	0.214	0.912	0.979

Table 5. Results of 3-way ANOVA of sediment respiration for each experiment at each site. *p ≤ 0.05, **0.1 ≥ p > 0.05. na: not available

Factor	Magnolia				Reserve			
	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer
Day	<0.001*	na	0.795	<0.001*	0.021*	<0.001*	0.004*	<0.001*
Light	0.020*	na	0.235	0.177	0.006*	0.775	0.080**	0.185
Nutrients	0.282	na	0.303	0.838	0.244	0.368	0.580	0.208
Day × Light	0.712	na	0.552	0.626	0.137	0.745	0.540	0.126
Day × Nutrients	0.205	na	0.267	0.937	0.418	0.298	0.935	0.645
Light × Nutrients	0.382	na	0.278	0.465	0.414	0.164	0.287	0.172
Day × Light × Nutrients	0.987	na	0.415	0.537	0.976	0.182	0.867	0.658

and dissolved detritus by decomposers (De Jonge & Colijn 1994, Barranguet et al. 1997). In addition, with the exception of the experiment in winter at Reserve, sediment net production decreased with decreasing light availability, at least on 1 of the sampling days, in all the fall and spring experiments. All the decreases observed in net production with decreased light availability coincided with concomitant decreases in gross primary production and, for the fall experiment at Magnolia and the fall and spring experiments at Reserve, also with concomitant increases in respiration, although those increases were sometimes only marginal (0.05 < p ≤ 0.1). Thus, the decreases in sediment net production observed with reduced light availability in our study appear to be a consequence of depressed photosynthetic rates of benthic microalgae (i.e. lower rates of sediment gross primary production) and, generally, simultaneous increases in sediment respiration rates.

The apparent light-limitation of sediment primary production caused by our shading treatment during the experiments in the fall, winter and spring is further supported by a comparison of our measurements of natural light intensity at the sediment surface with published photosynthesis–irradiance curves for benthic (microalgal) communities. The mean values of natural light intensity recorded at the sediment surface during the fall, winter and spring experiments ranged from 208 to 538 µmol photons m^{-2} s^{-1} at Magnolia and from 127 to 590 µmol photons m^{-2} s^{-1} at Reserve. Thus, since the shading treatment reduced light availability by 50%, the mean values of light intensity at the sediment surface under the shaded frames should have ranged from approximately 104 to 269 µmol photons m^{-2} s^{-1} at Magnolia and from 63 to 295 µmol photons m^{-2} s^{-1} at Reserve during the experiments in the fall, winter and spring, which is consistent with the number of direct light measurements we took at the sediment surface under the shaded frames. Published values of the minimum light intensity at which microphytobenthic photosynthesis saturates usually range from 300 to 500 µmol photons m^{-2} s^{-1} (Pinckney & Zingmark 1991, 1993, Blanchard & Montana 1992, Blanchard & Gall 1994, Wolfstein & Hartig 1998). This suggests that, during the fall, winter and spring experiments, our shading treatment frequently reduced light availability below saturating levels for microphytobenthic photosynthesis and thus significantly depressed sediment primary production.

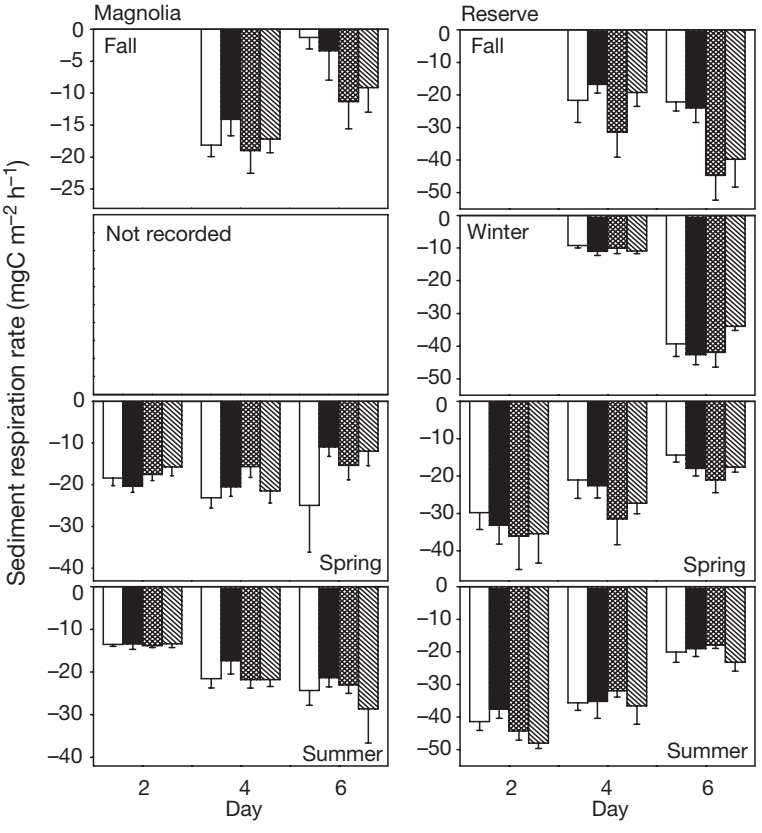

Fig. 5. Effects of shading and nutrient enrichment on sediment respiration at study sites. Data presentation and shading as in Fig. 3

Table 6. Results of 3-way ANOVA of sediment net production for each experiment at each site. *p ≤ 0.05, **0.1 ≥ p > 0.05. na: not available

Factor	Magnolia				Reserve			
	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer
Day	0.292	na	<0.001*	0.561	<0.001*	<0.001*	<0.001*	<0.001*
Light	<0.001*	na	<0.001*	0.551	<0.001*	0.158	<0.001*	0.529
Nutrients	0.287	na	0.917	0.669	0.236	0.627	0.973	0.855
Day × Light	0.504	na	0.005*	0.782	<0.001*	0.619	0.682	0.904
Day × Nutrients	0.532	na	0.848	0.762	0.151	0.863	0.733	0.789
Light × Nutrients	0.301	na	0.504	0.443	0.027*	0.814	0.625	0.240
Day × Light × Nutrients	0.244	na	0.992	0.698	0.100**	0.771	0.883	0.955

In contrast, shading did not have an important effect on sediment primary production in the summer experiments. (We did not find any effects of shading on primary production when measured as oxygen production in either of the 2 summer experiments and, when measured as ^{14}C uptake, we only found a negative effect on Day 6 at Magnolia). The low natural levels of light intensity measured at the sediment surface during the summer experiments may help explain why we found almost no negative effect of shading in that season. During the summer experiments, natural light intensity at the sediment surface ranged from 28 to 158 µmol photons m^{-2} s^{-1} (average 86 µmol) at Magnolia and from 6 to 59 µmol photons m^{-2} s^{-1} (average 28) at Reserve. These low light levels would allow little microphytobenthic production even without experimental shading during the summer compared with the experiments in the other seasons (as supported by our measurements). More importantly, and based on photosynthesis–irradiance curves published for other microphytobenthic communities (Hargrave et al. 1983, Pinckney & Zingmark 1991, 1993, Blanchard & Montagna 1992, Blanchard & Gall 1994, Wolfstein & Hartig 1998, Dodds et al. 1999, Blackford 2002), the additional 50% reduction in light availability imposed by our shading treatment (on average from 86 to 43 µmol photons m^{-2} s^{-1} at Magnolia and from 28 to 14 µmol photons m^{-2} s^{-1} at Reserve) would only cause a small additional reduction in the rate of absolute microphytobenthic photosynthesis relative to the reduction observed for the experiments in the other seasons. Such a small decrease in absolute microphytobenthic production could have easily remained undetected in our experiment, since it would probably have been overridden by physical and biological differences among the experimental plots such as sediment and organism patchiness, benthic microalgal species composition, detrital input from the adjacent marsh and sediment resuspension.

Thus, the response of sediment primary production to shading at our study sites is dependent on the natural levels of light intensity at the sediment surface. When

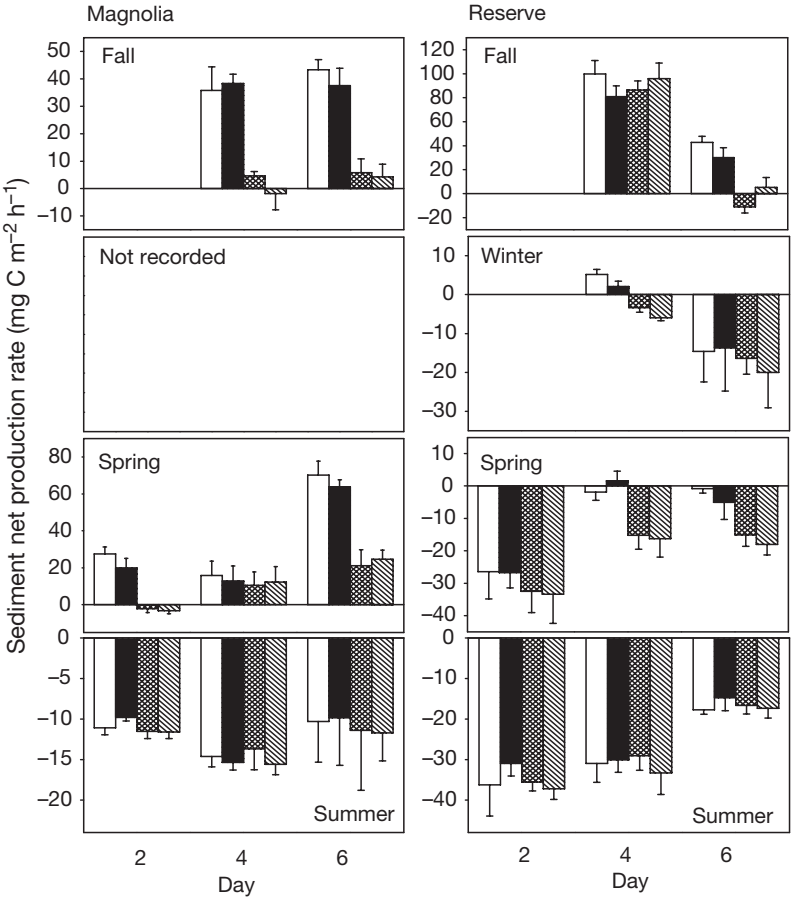

Fig. 6. Effects of shading and nutrient enrichment on sediment net production at study sites. Data presentation and shading as in Fig. 3

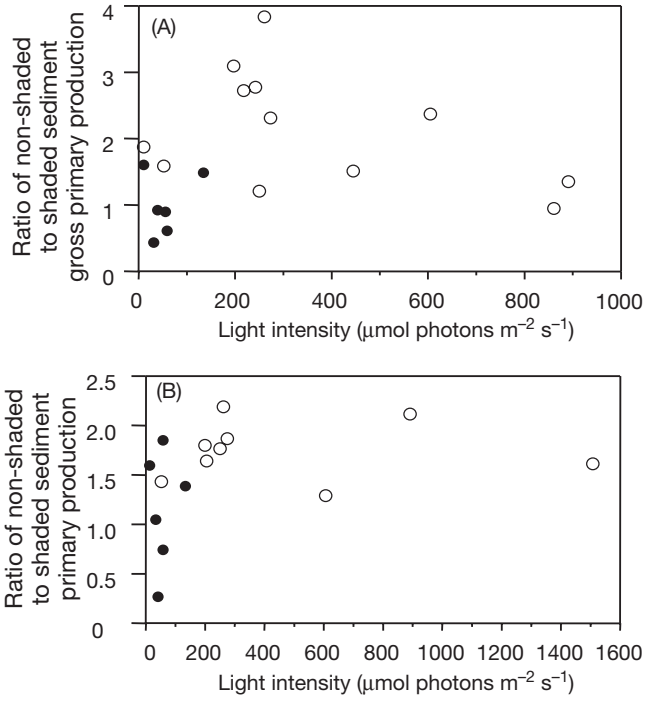

Fig. 7. Mean ratios of (A) gross primary production (measured as oxygen production) of non-shaded to shaded sediment and (B) primary production (measured as ^{14}C uptake) of non-shaded to shaded sediment versus natural (i.e. non-shaded) light availability at sediment surface. Each data point represents a day when incubations were performed (see text). For each day, the 5 fertilized and 5 non-fertilized replicates subjected to same shade treatment were grouped to calculate mean values, since fertilization did not affect response of either variable to shading. (●) Summer experiments; (○) all other experiments

natural light availability for microphytobenthos remained >100 µmol photons m^{-2} s^{-1} (normally the case during the fall, winter and spring experiments), a 50% decrease in light availability generally caused a significant reduction in sediment primary production. In contrast, when natural availability remained <100 µmol photons m^{-2} s^{-1} (the normal situation during the summer experiments), a further 50% reduction in light availability did not normally lead to a significant decrease in primary production. To further demonstrate this trend, we calculated the ratio of mean production in non-shaded plots to that in shaded plots for each day on which the incubations were done, and plotted the ratios versus the natural light intensity measured at the sediment surface on that day (Fig. 7). Fig. 7 shows that ratios relatively close to 1 (i.e. similar production under non-shaded and shaded conditions) generally occurred at intensities <100 µmol m^{-2} s^{-1}, and accordingly mostly during the summer experiments, whereas the ratio tended to increase (i.e. higher values under non-shaded conditions) with higher intensities. It is interesting that the ratios seemed to decrease and become closer to 1 at the highest values of light intensity recorded (>600 µmol photons m^{-2} s^{-1}), especially when primary production was measured as oxygen production, suggesting some photoinhibition of microphytobenthic photosynthesis and/or little effect of shading, since the sediment under the shaded frames would still receive near-saturating intensities. The response of sediment primary production to natural light availability is shown by the shading experiments in Fig. 7B; this could, if other important factors such as nutrients and temperature do not limit production severely, be a general feature of estuarine systems subject to ample fluctuations in bottom light availability.

In sharp contrast with the important impact of shading, nutrient enrichment had little effect on sediment primary production and metabolism at the estuarine sites studied. We found that nutrient enrichment only slightly increased the negative effects of reduced light on sediment net production on Day 6 of the fall experiment at Reserve (i.e. greater reduction in net production in the non-fertilized than in the fertilized shaded plots), and sediment primary production measured as ^{14}C uptake among sampling days in the summer experiment at Magnolia. It is interesting that, despite the fact that we applied nutrients in a stoichiometrically balanced ratio and compensated somewhat for the apparent natural phosphorus imbalance for microphytobenthic growth, we observed little impact of our nutrient addition on sediment primary production and metabolism. The minor role of sediment nutrient enrichment in our experiments probably stems, at least in part, from 2 characteristics of the study sites. First, natural light availability at the sediment surface, even in the fall and winter, often appears to be limiting for microphytobenthic photosynthesis, and this could mask any positive impact of nutrient addition (Barranguet et al. 1998, Meyercordt & Meyer-Reil 1999). Second, the sites feature high ambient nutrient concentrations in the sediment porewater, which would mean that addition of supplementary nutrients would have little impact. At Magnolia, nitrogen ($NH_4 + NO_3 + NO_2$) ranged from 2.4 to 125.1 µmol l^{-1} (median = 42.1 µmol l^{-1}) and phosphorus from 0.1 to 18.6 µmol l^{-1} (median = 0.8 µmol l^{-1}) in the sediment porewater of the non-fertilized plots in our experiments (values obtained by pooling together measurements on Day 0, see 'Materials and methods'). At Reserve, nitrogen ranged from 6.8 to 842.4 µmol l^{-1} (median = 111 µmol l^{-1}) and phosphorus from 0.11 to 120.1 µmol l^{-1} (median = 4.7 µmol l^{-1}). Indeed, perhaps with the exception of phosphorus concentrations at Magnolia, these values appear to be saturating for microphytobenthic growth under adequate light and temperature, based on

growth–nutrient relationships for microalgae developed in laboratory experiments (see review by Smayda 1997).

The quantities of nitrogen and phosphorus applied per fertilized plot in all experiments were calculated from the mean ambient concentrations measured prior to starting the fall experiment. This, however, does not affect the conclusion that nutrient addition is of little consequence for sediment primary production and metabolism at our study sites. First, our enrichment always represented a substantial increase relative to ambient concentrations (i.e. measurements on Day 0 prior to adding nutrients at the specific site and season). Second, we generally found an ambient relative deficiency in phosphorus in the sediment porewater (i.e. mean nitrogen:phosphorus molar ratio considerably higher than 17 for concentrations measured on Day 0), but nutrients were always added to the fertilized plots at an approximately 15 to 16 nitrogen:phosphorus molar ratio. Therefore, had relative phosphorus availability been limiting for microphytobenthic production, we should have found a significant impact on sediment primary production and metabolism in the fertilized plots at least under adequate light and temperature levels.

The methods used to measure sediment primary production and metabolism have inherent limitations, but these limitations should not affect our conclusions significantly. Specifically, the water enclosed in the benthic chambers was not stirred during the incubations. This could have led to reduced oxygen exchange between the sediment and the overlying 15 cm water column in the chamber and, thus, to underestimates of sediment primary production and respiration. In addition, we did not spike ^{14}C directly into the pore spaces of the top 1 cm of sediment incubated in the quartz tubes, which could also have resulted in underestimates of sediment primary production. However, these limitations were common to all our experimental treatments, and thus the differences observed between our experimental treatments should be indicative of the true impact of light reduction and nutrient addition on the variables measured. Thus, in the experiments where both types of measurements were made, the results obtained with primary production measured as oxygen production matched closely those obtained as ^{14}C uptake.

The results of this study have important implications for the management of Weeks Bay and other eutrophic, turbid estuaries: We have shown that a short-term (<1 wk), small-scale (1 m^2 bottom area) 50% reduction in incident light generally depresses sediment primary production at the 2 study locations examined, except during the summer experiments. The 2 locations examined are at opposite ends of Weeks Bay and differ in sediment type (sand at Magnolia, unconsolidated mud at Reserve) and ambient sediment primary production (usually higher at Magnolia), but a substantial depression of production due to a 50% reduction in light availability was a consistent feature of both sites. Therefore, because water-column characteristics (i.e. high nutrient and chlorophyll *a* concentrations, substantial turbidity and light extinction, and seasonal salinity, temperature and oxygen concentrations) at our 2 sites are similar to those at many other locations in Weeks Bay (Pennock et al. 2001), the negative effect of short-term, small-scale shading on sediment primary production could be a general feature of this system. This suggests that the deployment of permanent or temporary man-made structures in Weeks Bay, such as docks, fishing piers or mooring platforms, would adversely affect sediment primary production in the bay. Other anthropogenically-induced activities that can significantly reduce the amount of light reaching the sediment, such as dredging (e.g. de Jonge 1983, de Jonge & de Jonge 2002) and the promotion of phytoplankton blooms through increased nutrient loading, could also have a detrimental effect on sediment primary production through light limitation of microphytobenthic photosynthesis. In turn, depressed microphytobenthic productivity could have a negative impact on the many important functions of these communities in estuarine systems, such as sediment stabilization, chemical recycling and food provision (e.g. de Jonge & van Beusekom 1992, 1995). In contrast, sediment nutrient enrichment does not seem to have any major consequences for sediment primary production in this already eutrophic estuarine system. These results and the suggested consequences for management could also be applicable to other eutrophic, turbid estuaries.

In conclusion, we have demonstrated that, in accordance with our initial hypothesis, the impact of light reduction on sediment primary production in a turbid, nutrient-rich estuary is more important than the impact of additional nutrient enrichment. In view of the importance of microphytobenthic communities for coastal systems and the pervasive, worldwide eutrophication of these systems, similar experiments in oligotrophic, high-light locations are required. The results of such experiments would probably differ from ours, since a greater role of nutrient enrichment would be expected for pristine locations. Elucidating how communities of benthic microalgae respond to increased eutrophication across a gradient of initial trophic conditions is important for environmental management of this problem.

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