

Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon

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ABSTRACT: In shallow coastal systems where most of the seafloor lies within the photic zone, benthic photoautotrophy is likely to play a key role in regulating carbon and nitrogen cycling. We measured dissolved inorganic carbon exchanges in seasonal microcosm incubations to determine the relative importance of benthic (with and without macroalgae) and water column metabolism at 3 sites located along a nutrient gradient in a coastal barrier-island lagoon on the eastern shore of Virginia. When coupled with data on *in situ* biomass, the incubations clearly indicated a seasonality in the dominance of primary producers at the sites, with benthic primary producers being the most important early and late in the growing season and phytoplankton dominating following a mid-summer period of macroalgal decay and the release of algal-bound nutrients to the water column. The benthos was always net autotrophic, and differences in community metabolism at the 3 sites appeared to be largely due to variation in macroalgal biomass. Macroalgae accumulated to a greater extent in the mid-lagoon and accounted for up to 96% of benthic production. The water column was net heterotrophic throughout the lagoon except following the mid-summer macroalgal collapse, when phytoplankton biomass was highest at the 2 sites closest to the mainland. Benthic microalgal production also increased in importance following the macroalgal decline, suggesting that competition for light and possibly nutrients limited benthic microalgal production when macroalgal densities were high. Overall, there was a distinct seasonality in patterns of total metabolism within the bay, where all sites were net autotrophic in the spring and summer and net heterotrophic in the fall. Up to 8 g N m⁻² accumulated in macroalgal biomass throughout spring and early summer at the mid-lagoon shoal site, slowing nutrient transport through the lagoon. Nutrient turnover rates were higher during the period when phytoplankton and benthic microalgae were the dominant primary producers. This study illustrates the functional importance of different primary producer communities to carbon metabolism and to the temporary retention of nutrients in lagoonal land-margin ecosystems.

KEY WORDS: Lagoon · Metabolism · Autotrophy · Heterotrophy · Carbon · Nitrogen · Macroalgae · Phytoplankton · Microalgae · Chlorophyll

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INTRODUCTION

Coastal lagoons and bays constitute a major type of land margin ecosystem on most continents, yet surprisingly little is known about the fate and transport of nutrients entering shallow lagoons compared to large,

deep estuaries (Boynton et al. 1996). Nutrient inputs to coastal lagoons are typically lower than to river-dominated estuaries (Nixon 1982, Boynton et al. 1996). However, changes in land use and increased human populations have also resulted in problems associated with eutrophication in coastal lagoons (Sfriso et al. 1992, Valiela et al. 1992, 1997, Boynton et al. 1996). Like deep estuaries, these shallow bays and lagoons, which normally are highly productive, function as

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important buffer zones that can reduce or remove nutrients on their transit from land to sea. The impact of nutrient inputs and their retention as they pass through shallow-water systems depend on the metabolism of both autotrophs and heterotrophs within the systems as well as physical transport rates.

The benthos is a critical component of coastal lagoons and bays. In these systems, most of the seafloor lies within the photic zone, and production of seagrasses, macroalgae and benthic microalgae typically exceeds that of phytoplankton (Borum & Sand-Jensen 1996). Uptake and temporary retention of nutrients in plant biomass, burial of recalcitrant organic matter, and the effects of autotrophic metabolism (oxygen release and nitrogen uptake) on denitrification all influence the transport of nutrients through these shallow-water systems. Fast-growing, opportunistic macroalgae with 'boom and bust' cycles tend to proliferate where nutrient enrichment is high (e.g., McComb & Humphries 1992, Sfriso et al. 1992, Valiela et al. 1992, 1997). At high densities, these macroalgae can function temporarily as a 'filter' by intercepting dissolved nutrient fluxes from the sediments to the overlying water, thereby reducing nutrient availability for phytoplankton growth (Thybo-Christesen & Blackburn 1993, McGlathery et al. 1997). Release of plant-bound nutrients following senescence may subsequently stimulate phytoplankton and bacterial metabolism in the water column. Likewise, nutrient assimilation and photosynthetic oxygenation of the sediments by benthic microalgae may control nutrient fluxes at the sediment-water interface (Blackburn & Henriksen 1983, Risgaard-Petersen et al. 1994, Reay et al. 1995, Sundbäck et al. 2000). High rates of benthic metabolism also can lead to oxygen supersaturation and to episodes of oxygen depletion throughout the water column (e.g., Sfriso et al. 1992, Valiela et al. 1992, Boynton et al. 1996).

The trophic status of the benthic or pelagic communities (measured as the difference between primary production and total respiration, i.e. autotrophy vs heterotrophy) may thus be indicative of the rates and pathways of carbon (C) and nitrogen (N) cycling in coastal systems. In addition, total metabolism integrates the benthic and pelagic components and provides useful information on the functional linkage between coastal ecosystems and adjacent systems (watershed and coastal ocean), that is, the degree to which the system is an importer or exporter of nutrients and organic matter. Most metabolism studies to date have been performed in relatively deep coastal systems where the dominant autotrophs are phytoplankton. In shallow-water systems, benthic photoautotrophy is likely to be a key driver of total metabolism (Kenney et al. 1988, D'Avanzo et al. 1996, Carmouze et

al. 1998). Data on the trophic status of shallow lagoons and bays are equivocal, with some showing balanced metabolism or slight autotrophy either on a seasonal or annual basis (Reyes & Merino 1991, D'Avanzo et al. 1996, Carmouze et al. 1998) and others indicating heterotrophy (Nowicki & Nixon 1985, Flores-Verdugo et al. 1988). There is also evidence of both seasonal and interannual variations in patterns of autotrophy and heterotrophy (Kenney et al. 1988, Carmouze et al. 1998). Clearly, much of this variation is driven by key physical factors such as water residence time (Kenney et al. 1988, Knoppers et al. 1991) and by changes in biomass and species composition of the dominant autotrophs (Oviatt et al. 1986, Knoppers et al. 1991). Understanding the integrated response to changing activities in the watershed is key to establishing how these coastal systems function in transporting or retaining nutrient and organic matter inputs at the land-sea interface.

In this study we measured benthic and pelagic metabolism on a seasonal basis (spring, summer, fall) at 3 sites along a nutrient gradient in a shallow lagoon lying between the mainland and barrier islands on the eastern shore of Virginia. Since we were particularly interested in quantifying the relative contribution of the different autotrophic communities (phytoplankton, macroalgae, benthic microalgae) to total carbon metabolism at the 3 sites, we used microcosm incubations to distinguish metabolism of the benthic community (with and without macroalgae) from that of the water column. Several recent studies have used a similar microcosm incubation technique in shallow lagoons (Carmouze et al. 1991, 1998, Rizzo et al. 1996, Viaroli et al. 1996). The main questions we asked in this study were: (1) Are the benthic and pelagic communities at the study sites net autotrophic or net heterotrophic? (2) Are there differences across the nutrient loading gradient? This was part of a larger study aimed at understanding how the lagoon functions as a 'filter' to retain or remove reactive nitrogen in its transport across the land margin.

METHODS

Site description. Hog Island Bay is a shallow coastal lagoon (~100 km²) on the eastern shore of Virginia and is part of the Virginia Coast Reserve (VCR) Long Term Ecological Research (LTER) Site (Fig. 1). It is bordered on the west by the Delmarva Peninsula and on the east by barrier islands, a typical feature of the Atlantic and Gulf coasts. Other than the main channel (Great Machipongo Channel) that empties into the Atlantic Ocean, the lagoon is shallow (<1–2 m at mean low water [MLW]) with a semi-diurnal tidal range of

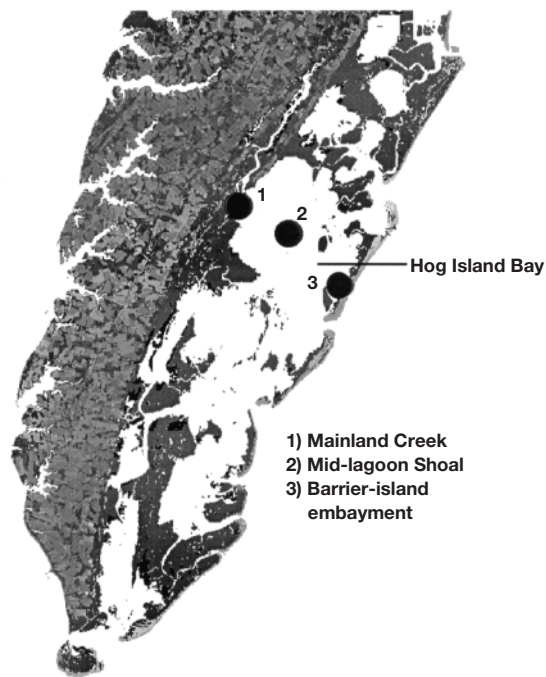


Fig. 1. Site map of Hog Island Bay, which lies within the Virginia Coast Reserve on the eastern shore of the Delmarva Peninsula. The 3 sites represent a gradient in nutrient loading across the lagoon

~1.2–1.5 m. Approximately 50% of the surface area of the lagoon is <1 m at MLW, and there are extensive exposed mudflats. The VCR lagoons were formerly vegetated with seagrasses, but they disappeared in the 1930s and have only recently been rediscovered in small, isolated patches. Like many coastal embayments, inputs of freshwater are relatively low and enter the lagoon primarily via groundwater. The shallow aquifer is also the main source of nutrients to the lagoon (Reay et al. 1992, Anderson et al. 1997); enrichment of groundwater is primarily the result of agricultural activities, which represent 55% of the Hog Island Bay watershed area (442 km²) (Bohlke & Denver 1995, Hamilton & Helsel 1995). Atmospheric inputs into the bay are probably also important (Paerl et al. 1990), although they remain to be quantified.

Three sites were sampled along a transect across Hog Island Bay from the mainland to the barrier island (Fig. 1). The sites were in the shallow (<1 m MLW) regions that dominate the lagoon and are as follows: (1) a mainland site adjacent to a fringing marsh tidal creek, 'Creek'; (2) an open-water shoal site located mid-lagoon that con-

tained numerous relict oyster reefs, 'Shoal'; and (3) a back-barrier embayment site near the southern end of Hog Island, 'Hog'. Characteristics of the sites are shown in Table 1. The transect represents a gradient in nutrient loading, as reflected in the water column nutrient concentrations, in the sediment organic and nitrogen contents, and in the macroalgal tissue nitrogen content (see Table 3). The sediments ranged from fine-grained silt at the Creek site to coarse sand at the Hog site. All sites received sufficient light to support benthic photosynthesis. On an annual basis, for a mean depth of 1 m, about 11 to 18% of incident irradiance reached the lagoon bottom. Benthic microalgae and macroalgae occurred at all sites, with *Ulva lactuca* and *Gracilaria tikvahiae* being the most abundant macroalgal taxa.

Benthic and water column metabolism. We estimated production and respiration at each site in October 1997 and May and August 1998 from changes in dissolved inorganic carbon (DIC) concentrations in microcosm incubations of: (1) water column only, (2) sediment+water column, and (3) sediment+macroalgae+water column ($n = 3$ for each treatment per site) in outdoor flowing seawater tables. The water column treatment was used both to determine water column activity and to correct the DIC measurements in the sediment and sediment+macroalgae treatments for water column metabolism. For the sediment+macroalgae treatment, the added macroalgal biomass varied among individual cores and was equivalent to 70–200 gdw m⁻², which is within the range of natural field densities (K.J.M. et al. unpubl. data, see Fig. 7b).

The microcosms consisted of 10 × 30 cm transparent cores with magnetic stirrers attached to the clear, acrylic core tops. The stirrers mixed the water column continuously at 60 rpm without disturbing the sediment. The cores contained 12 cm of sediment and ~18 cm of overlying water. Sediment cores and *Ulva lactuca* were collected from each site and held

Table 1. Physical and chemical characteristics of the 3 sites in Hog Island Bay. Data are annual averages (\pm SE) of samples taken in all 4 seasons. dw: dry weight

	Creek	Shoal	Hog
Water column nutrients (μ M)			
DIN	4.4 \pm 0.9	2.3 \pm 2.5	1.2 \pm 0.4
DON	15.4 \pm 1.9	12.1 \pm 3.7	11.8 \pm 1.6
DIP	1.4 \pm 0.2	0.8 \pm 0.1	0.5 \pm 0.1
Sediment organic content (% dw)	3.8 \pm 0.2	2.1 \pm 0.3	0.48 \pm 0.3
Sediment N content (% dw)	0.11 \pm 0.00	0.03 \pm 0.00	0.01 \pm 0.00
Sediment molar C:N	14.4 \pm 1.7	11.76 \pm 1.4	12.9 \pm 4.1
Sediment bulk density (g cm ⁻³)	0.89 \pm 0.09	1.51 \pm 0.15	1.78 \pm 0.07
Light extinction, k (m ⁻¹)	2.2 \pm 0.6	1.9 \pm 0.8	1.7 \pm 0.7

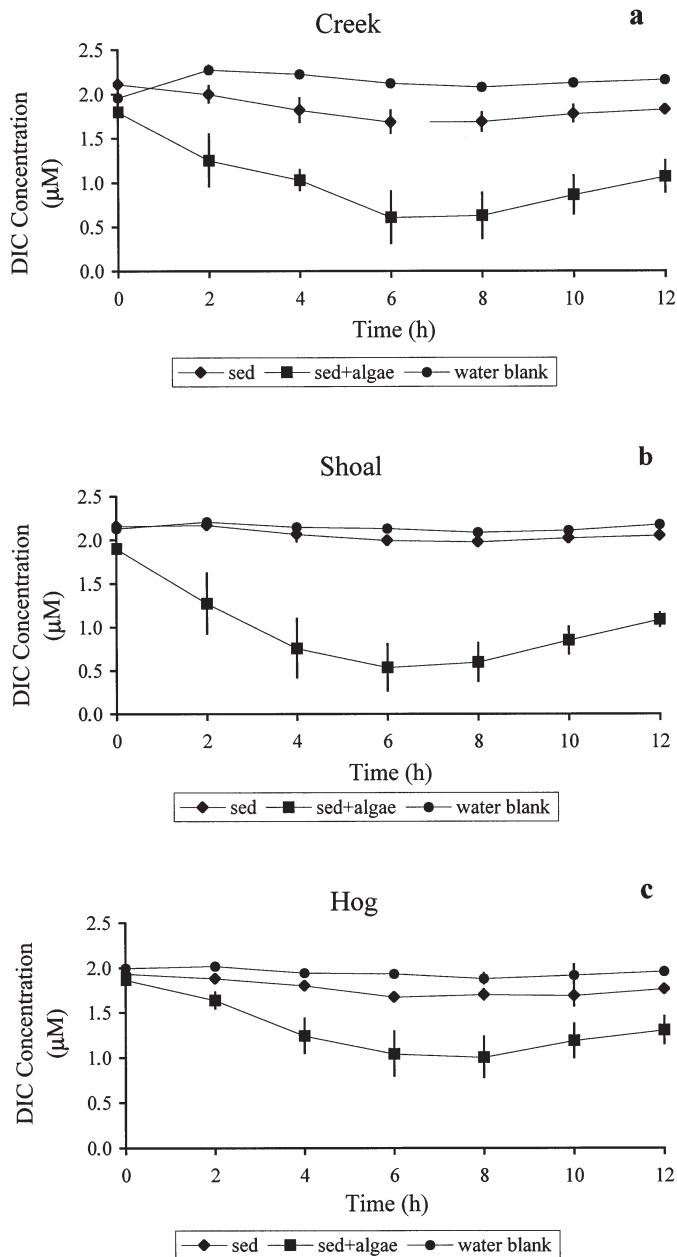


Fig. 2. Typical dissolved inorganic carbon (DIC) exchange during the microcosm incubations, showing uptake of DIC in the light during the first 6 h followed by DIC production in the subsequent 6 h dark period. The treatments are sediment, sediment+macroalgae and water blank. The slopes of the depletion and production curves indicate that DIC was not limiting to primary production during these short incubations

overnight in the seawater tables; the flowing seawater was used only to maintain *in situ* temperatures and did not mix with the sediment or water inside the microcosms. The incubations were initiated the following morning by replacing the overlying water of the microcosms with water collected from each site. Additional cores were set up with a water column only. Incident

irradiance varied between 700 and 1200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ during the light incubations. These levels are similar to those measured during the same months in the field (K.J.M. et al. unpubl. data), and exceed typical light saturation values for photosynthesis of both benthic microalgae (Rizzo et al. 1996) and the dominant macroalgae in Hog Island Bay (Henley & Ramus 1989, Peckol & Rivers 1996).

Water samples were collected at the start of the incubation and then at 2 h intervals during the initial 6 h light incubation and the subsequent 6 h dark incubation. All DIC samples were filtered (0.45 μm , Gilman Supor) prior to storage in 13 ml Hungate tubes (Bellco Glass Inc., Vineland, NJ), and were kept in a refrigerator until they were analyzed within 4 wk using a LiCor 6252 infra-red gas analyzer. Storage tests of estuarine water have shown that this procedure gives accurate DIC measurements for samples obtained within 6 wk (I.C.A. unpubl. data). Production or consumption of DIC was determined from the change in concentration versus time. Our measurements showed that there was a linear change in DIC concentrations, and indicated that DIC did not become limiting to primary producers during the short incubation (Fig. 2). Changes in DIC in the light and dark incubations represent whole community metabolism, and reflect the balance between DIC consumption/production by autotrophs and production by zooplankton, benthic fauna and bacteria during the incubation period. We also measured dissolved oxygen (DO) concentrations and temperature using an Orbisphere multichannel DO detector, but found that this gave a less accurate estimate of production and respiration because the water rapidly became supersaturated and formed bubbles in the light. Nutrient fluxes across the sediment-water interface and rates of sediment N mineralization and immobilization were also measured and are reported by Anderson et al. (unpubl.). Changes in dissolved inorganic N (DIN) concentrations of the water column treatment showed that DIN concentrations, although low, did not become depleted during the 6 h light incubations due to phytoplankton uptake (Fig. 3). Thus there is no clear evidence that 'bottle effects' (i.e. separating the water column from the benthos) underestimated water column metabolism in our short-term closed incubations (Kemp & Boynton 1980).

Sediment and water column chlorophyll a. At the end of the incubation, 1 sediment subsample from each of the cores in the sediment+water column treatments was analyzed for chlorophyll *a* (chl *a*) ($n = 3$ for each site). In addition, chl *a* was sampled in triplicate at all sites in July. The top 0 to 1 cm of the sediment was removed using a small corer (3.98 cm^2) and frozen for later analysis. Chl *a* concentration was determined according to the protocol of Lorenzen (1967), as modi-

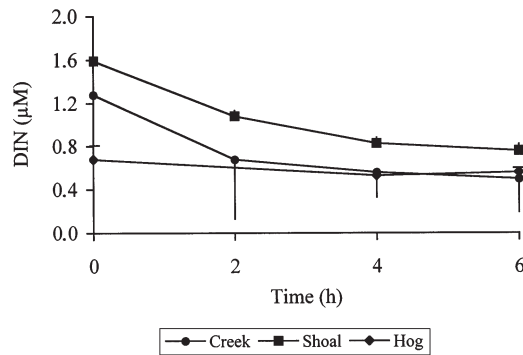


Fig. 3. Typical changes in DIN concentrations during water column incubations for the 3 sites in Hog Island Bay. The linear change in concentration indicates that DIN did not become depleted during the 6 h light and dark incubations

fied by Pinckney & Zigmark (1994) to include extraction of the unground sediment sample with a solvent mixture of 45% methanol, 45% ethanol, and 10% deionized water, at -15°C for >1 wk. Water column chl *a* was determined in triplicate in the water collected at each site for the incubations using the method of Shoaf & Lium (1976). Samples of 5 ml were filtered through GF/F filters, and the filters were extracted in a solution of 45% acetone, 45% dimethyl sulfoxide (DMSO), and 10% deionized water. Extraction took place in the dark for 24 h.

Macroalgal biomass and elemental content. The *Ulva lactuca* used in the incubations was rinsed free of epiphytes with deionized water, freeze-dried and weighed. Duplicate subsamples of the tissue were ground into a fine powder with a mortar and pestle and analyzed for C and N content using a Carlo Erba NA 2500 elemental analyzer. To relate our benthic metabolism measurements from the microcosms to the natural algal densities at each site, we estimated macroalgal biomass and the amount of bare sediment area (with microalgae only) from June 1998 to June 1999 at 6 locations in the lagoon, 2 of each representing creek, mid-lagoon shoal, and back-barrier embayment sites. This was part of a larger effort to establish a long-term data set on primary producer biomass and distribution in the lagoon as part of the VCR LTER program (K.J.M. et al. unpubl. data). For the purposes of the present study, we assumed that the seasonal metabolism measurements could be directly related to seasonal variation in macroalgal biomass. At each location, macroalgae were collected haphazardly within a 0.15 m^2 circular core cast ($n = 6$ to 8 at each location, for a total of 12 to 16 replicates per site). The collected plants were sorted by species, rinsed with both lagoon water and deionized water, and carefully cleaned of attached epiphytes. Samples were then freeze-dried to a constant weight for biomass determination.

Estimating *in situ* benthic metabolism. Attempts to relate laboratory measurements of benthic production or nutrient uptake directly to *in situ* rates are problematic because of the assumption that production is constant per unit biomass. We corrected our DIC metabolism measurements from the microcosm studies for both the shading effects within the macroalgal mat (Krause-Jensen et al. 1996, Peckol & Rivers 1996, McGlathery et al. 1997) and the macroalgal shading of the sediment surface at the measured densities of macroalgae at each site. Without accounting for these processes, we would likely overestimate benthic metabolism at our 3 sites. To make the correction, we used a straightforward procedure that involved 3 basic steps: (1) we calculated macroalgal metabolism in the microcosms by subtracting the sediment metabolism from the sediment+macroalgae treatments, (2) using field data on macroalgal biomass at each site, we factored in self-shading within the macroalgal mat to reliably estimate *in situ* macroalgal metabolism per m^2 , and (3) we estimated sediment metabolism at each site (per m^2) based on the microcosm measurements (sediment treatment) and the shading of the sediment surface by macroalgae at each site.

We used 2 relationships in our calculations. First, we defined a function to describe the variation in benthic microalgal metabolism with varying densities of macroalgae overlying the sediment surface (Fig. 4a). When the macroalgal biomass measured at a particular location was zero, the *in situ* sediment metabolism was determined to equal the rates measured in the sediment microcosms for that site. At very high macroalgal densities (Fig. 4a), we assumed that complete shading of the sediment surface eliminated microalgal production, and daily DIC metabolism rates were calculated from the measured dark DIC production rates averaged over a 24 h period. We defined this complete shading of benthic microalgae to occur at macroalgal densities above 300 gdw m^{-2} based on the relationship found by Krause-Jensen et al. (1996) between macroalgal biomass and light attenuation. In a sensitivity analysis of our method, we found that adjusting this critical biomass to 200 or 400 gdw m^{-2} changed our results by $<3\%$. As a first approximation, we have assumed a negative linear relationship in microalgal production with increasing macroalgal densities between these maximum and minimum values (Fig. 4a). Although vertical profiles of microalgal production with depth in bare sediments are known to be curvilinear (McIntyre et al. 1996), there is little information on how depth-integrated production varies with macroalgal coverage (Sundbäck et al. 1996). We used this linear relationship to determine sediment microalgal metabolism in the sediment+macroalgae microcosms and subtracted this

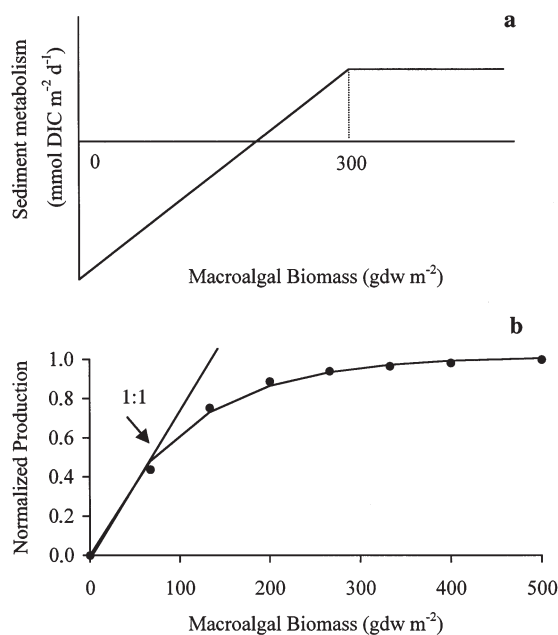


Fig. 4. Two models used to correct benthic community metabolism measurements for (a) shading of benthic microalgal production by macroalgae overlying the sediment surface and (b) self-shading within the macroalgal mat. The relationship in (b) is derived from the variation in production with depth in macroalgal mats reported in Krause-Jensen et al. (1996), and is normalized to maximum production (per unit area) at high macroalgal densities. The 1:1 line represents the production rate with no shading effects where production increases proportionately to biomass

value to obtain an estimate of macroalgal metabolism. The second relationship we used adjusted macroalgal production for self-shading within the macroalgal mat (Fig. 4b). Studies have shown the reduction of macroalgal productivity with exponentially decreasing light availability within macroalgal mats for *Chaetomorpha linum* (Krause-Jensen et al. 1996) and for *Cladophora vagabunda* and *Gracilaria tikvahiae* (Peckol & Rivers 1996). Although the degree of light attenuation varies among species, the production-biomass relationship of Krause-Jensen et al. (1996) should give a reasonable first-order estimate of *in situ* density-dependent production in the mixed-species mats, and is clearly more accurate than assuming constant production rates per unit biomass. A fit to the data of Krause-Jensen et al. (1996) gives $y = 1 - \exp(-0.00804x)$ ($R^2 = 0.99$) where y is the production rate normalized to maximum production at high biomass and x is the biomass (gdw m^{-2}). Using our biomass data as input, we adjusted our production rates for self-shading. To account for differences between macroalgal densities in the microcosms and *in situ* densities, we determined a scaling factor:

$$F = [1 - \exp(-0.00804x_{\text{field}})] / [1 - \exp(-0.00804x_{\text{microcosm}})] \quad (1)$$

This factor is multiplied by the average macroalgal metabolism in the microcosms for each site to obtain an estimate of *in situ* macroalgal metabolism at that site. For example, if the average macroalgal biomass in the microcosms for a site was 150 gdw m^{-2} and the biomass measured in the field was 500 gdw m^{-2} , the scaling factor F is calculated to be 1.4 (Fig. 4b). In other words, when the macroalgal biomass increases from 150 to 500 gdw m^{-2} , the production (per unit area) will increase by a factor of 1.4. This example shows how important it is to include the effect of shading in this scaling process. If not included, scaling based on biomass alone would give a factor of 3.3 ($500/150$); this is equivalent to using the 1:1 line shown in Fig. 4b. At low densities ($<50 \text{ gdw m}^{-2}$), the scaling factor makes little difference in the total metabolism calculation, because self-shading within the macroalgal population is of less importance and production increases proportionately with biomass. The final step in our procedure was to estimate *in situ* sediment metabolism. We did this in the same way as for the microcosms using the relationship shown in Fig. 4a, but in this case we used the measured *in situ* macroalgal biomass to account for shading at each site.

This scaling process can be summarized by the following equation:

$$M_t = (M_c - M_{s1})F + M_{s2} \quad (2)$$

where M_t is the total *in situ* benthic metabolism, M_c is the metabolism measured in the sediment+macroalgae microcosms, M_{s1} is the sediment metabolism rate in the microcosms corrected for the shading effect of macroalgal biomass, F is the scaling factor correcting for differences in the biomass in the field relative to that in the microcosms, and M_{s2} is the sediment metabolism rate *in situ* taking into account the shading effect of measured densities of macroalgae. The term $(M_c - M_{s1})F$ represents the calculated *in situ* macroalgal metabolism and this is simply added to the *in situ* sediment metabolism rate to obtain an estimate of total benthic metabolism. We made this calculation of total benthic metabolism for each replicate field measurement of macroalgal biomass, or bare area if macroalgae were absent (12 to 16 per site). All metabolism measurements are reported in $\text{mmol DIC m}^{-2} \text{ d}^{-1}$.

Statistical analysis. Differences in metabolism between sites were tested using 2-way ANOVA with site and time as main factors. Comparisons among microcosm treatments (light vs dark) and *in situ* primary producer biomass (by site) were made using 1-way ANOVA. Differences were accepted as significant at $p < 0.05$.

RESULTS

Community production and respiration

Differences between light and dark microcosm incubations averaged over the 3 seasons (spring, summer, fall) clearly showed significant autotrophic production by the benthic macroalgal and microalgal populations at all sites ($p < 0.002$; Fig. 5b,c). Net production rates for the sediment + macroalgae community measured in the light incubations ranged from 23.1 to 30.6 $\text{mmol C m}^{-2} \text{h}^{-1}$, and dark respiration rates ranged from 9.9 to 12.4 $\text{mmol C m}^{-2} \text{h}^{-1}$ (Fig. 5c). Overall, there were no significant differences in either net production or dark respiration rates between sites ($p = 0.23$ and $p = 0.73$; Fig. 5c). For the incubations with sediment only, average net production rates in the light were about 5-fold smaller than when macroalgae were present (3.7 to 6.6 $\text{mmol C m}^{-2} \text{h}^{-1}$; Fig. 5b). Respiration rates also were lower, approximately 3-fold less than in sediment incubations containing macroalgae (0.9 to 2.7 $\text{mmol C m}^{-2} \text{h}^{-1}$; Fig. 5b). Net production rates and dark respiration rates for the sediment cores were not significantly different between sites ($p = 0.58$ and $p = 0.57$). For the water column, differences between light and dark incubations were insignificant when averaged over the seasons ($p = 0.79$, 0.57 and 0.87 for Creek, Shoal and Hog sites; Fig. 5a). Phytoplankton production was only evident in August at all sites (Fig. 6a) when DIC consumption in the light decreased with distance from the mainland (27.8 ± 3.1 , 15.8 ± 8.9 and 12.9 ± 3.1 $\text{mmol DIC m}^{-2} \text{h}^{-1}$ for the Creek, Shoal and Hog sites).

Net primary production rates of macroalgae in the microcosms are shown in Table 2, and are comparable to rates reported in the literature. Analysis of the macroalgal tissue showed that there was a general decrease in %N content from the Creek to the Hog site (Table 3), indicating a gradient of high to low N availability from the mainland seaward. At all sites, the lowest tissue N content was found in May, when the growth demand for N relative to the N supply was probably the highest.

The hourly metabolism rates from the microcosms were scaled to the number of light and dark hours for each sampling period to calculate daily net metabolism rates for each community on a per m^2 basis. Seasonal differences in metabolism were evident for all autotrophic components of the system (Fig. 6). The water column was heterotrophic or in balance in the spring and fall and was autotrophic in the summer (Fig. 6a). At all sites, the water column was most heterotrophic in the fall. There were no differences in water column metabolism between sites in any season (site \times time; $p = 0.93$). Sediments were slightly auto-

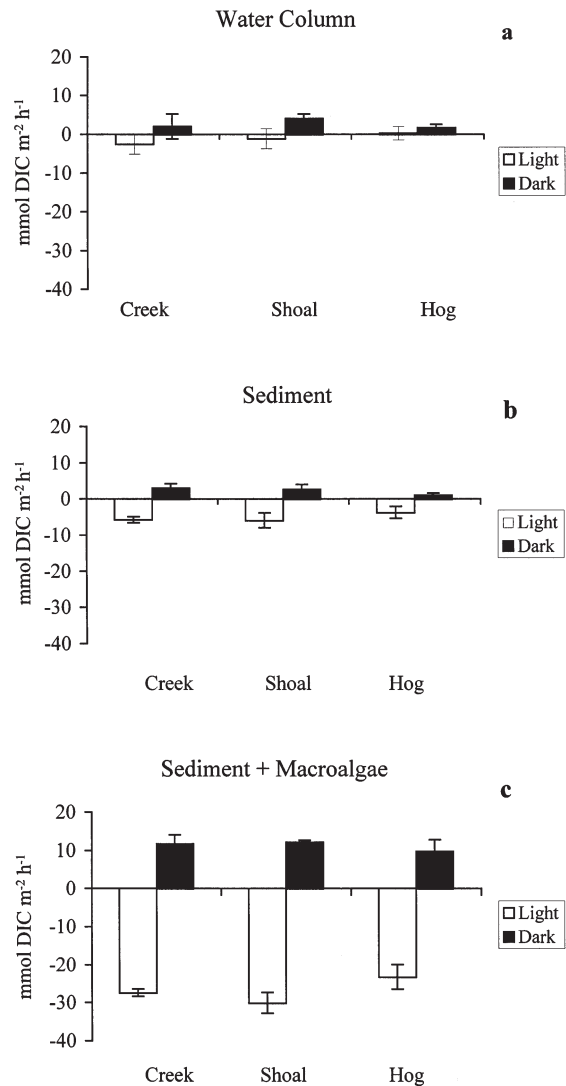


Fig. 5. Seasonal averages of light and dark microcosm incubations for the (a) water column, (b) sediment, and (c) sediment+macroalgae. The benthic metabolism values are corrected for water column activity. The water column metabolism rates are calculated for a depth of 1 m. Values are calculated as the average of the seasonal (spring, summer, fall) means ($n = 3$ for each season). The error bars (SE) represent variation between the seasons

trophic or in balance in the spring and fall at all sites and were more markedly autotrophic in mid-summer, with average rates of $100 \text{ mmol C m}^{-2} \text{d}^{-1}$ (Fig. 6b). In all the seasons sampled, daily net sediment metabolism was similar between the sites (site \times time; $p = 0.15$). The benthic community in the microcosms containing macroalgae was always strongly autotrophic, with highest rates in mid-summer when temperature and light conditions were conducive to growth, and lowest rates in fall (Fig. 6c). At the biomass densities used in the microcosms, maximum rates of daily net

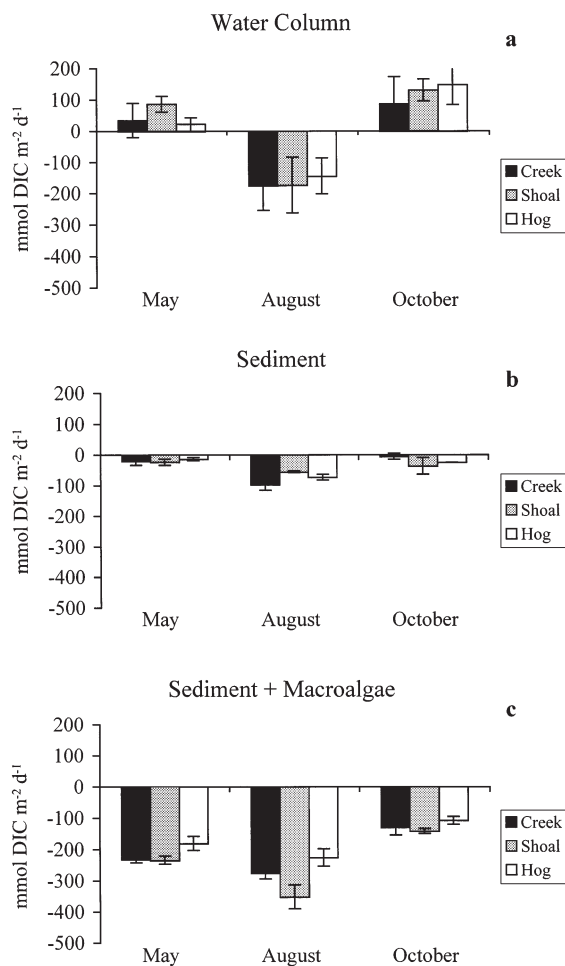


Fig. 6. Daily metabolism rates determined from the microcosms for the (a) water column, (b) sediment, and (c) sediment+macroalgal communities calculated from light and dark incubations and normalized to the number of light and dark hours each month. The water column metabolism rates are calculated for a depth of 1 m. Values represent means ($n = 3$) ± 1 SE

production were about 4 to 5 times higher than those for the benthic microalgal community.

Autotroph biomass

Macroalgal biomass was highly variable throughout the lagoon, with densities ranging from 0 to 650 gdw m⁻² during the year. There was a distinct seasonal pattern in biomass, with an early summer peak followed by a decline in biomass by late summer at all sites, and a subsequent accumulation through the fall and winter months until the next summer peak (Fig. 7b). Biomass was always highest at the mid-lagoon Shoal site ($p < 0.003$), and thick (30 cm) mats developed in localized

areas in early summer. In these areas, the macroalgal collapse led to a temporary period of anoxia throughout the water column and a significant flux of macroalgal-bound nutrients to the water column (Tyler et al. 2001). The macroalgal decline at all sites was followed by increase in water column chl *a* (Fig. 7a). Water column chl *a* concentrations were typically lower at the Hog Island embayment site than at the Creek and Shoal sites ($p = 0.06$). In July, water column chl *a* concentrations reached a high of 12 $\mu\text{g l}^{-1}$ at the Creek and Shoal sites, and a lower peak of $\sim 5 \mu\text{g l}^{-1}$ at the Hog Island site furthest offshore. In October, concentrations

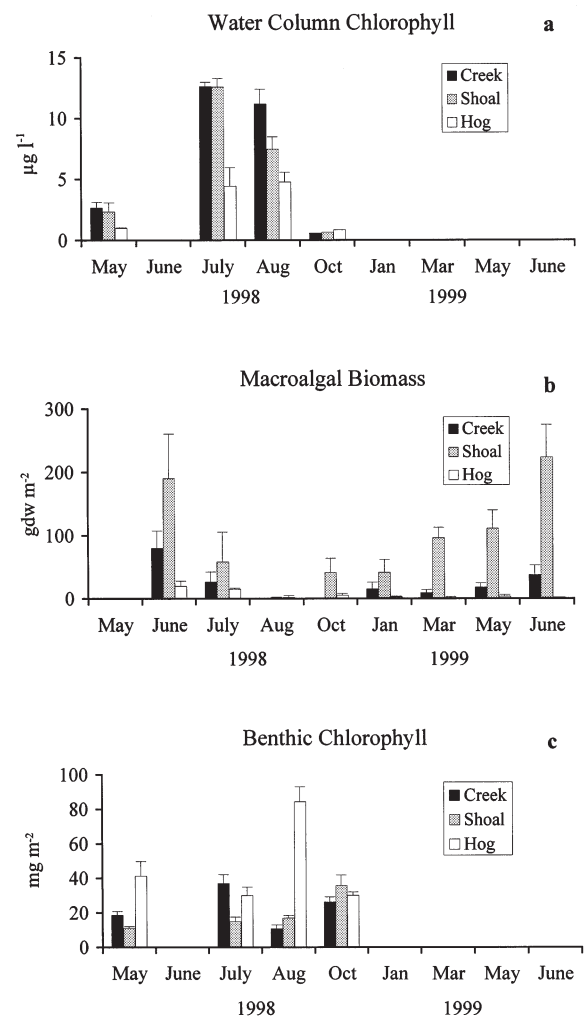


Fig. 7. Distribution of primary producer biomass at the 3 sites in Hog Island Bay. Water column (a) and sediment (b) chlorophyll values were determined from samples used for the metabolism incubations. Benthic macroalgal distribution (c) was determined at 2 locations for each site (6 to 8 replicate measurements at each location) throughout the year. Values are means ($n = 3$ for water column and sediment chlorophyll, and $n = 12$ to 16 for macroalgal biomass). Error bars represent ± 1 SE

Table 2. Comparison of macroalgal production rates (chlorophytes)

Site	Species	Production (mmol C gdw ⁻¹ h ⁻¹)	Source
Hog Island Bay, Virginia, USA	<i>Ulva lactuca</i>	0.1–0.26 ^a	This study
Roskilde Fjord, Denmark	<i>Chaetomorpha linum</i>	1–1.1 ^b	McGlathery & Pedersen (1999)
Kertinge Nor, Denmark	<i>Chaetomorpha linum</i>	0.06 ^c	Krause-Jensen et al. (1996)
Waquoit Bay, Massachusetts, USA	<i>Cladophora vagabunda</i>	0.25–0.67 ^d	Peckol & Rivers (1996)
Harrington Sound, Bermuda	<i>Cladophora prolifera</i>	0.04 ^e	Lapointe & O'Connell (1989)
Beaufort, North Carolina, USA	<i>Ulva rotunda</i>	1.5–2 ^f	Henley & Ramus (1989)

^aMicrocosm incubations in outdoor flowing seawater table
^bLaboratory incubation in growth chamber
^cLaboratory flow-through experiment in growth chamber
^dField incubation
^eOutdoor flowing seawater system, O₂ production values converted to C fixed using photosynthetic quotient of 1
^fIncubation in outdoor flowing seawater table, O₂ production values converted to C fixed using photosynthetic quotient of 1

Table 3. Macroalgal tissue carbon and nitrogen content (x ± SE). Values represent % of algal dry weight

Site	%C	%N	C:N (molar)
Creek			
May	32.0 ± 0.78	1.8 ± 0.14	20.3 ± 1.09
August	33.1 ± 0.39	2.2 ± 0.15	17.8 ± 1.11
October	31.6 ± 0.43	3.6 ± 0.06	10.1 ± 0.16
Shoal			
May	24.6 ± 2.14	1.5 ± 0.13	19.6 ± 0.21
August	32.6 ± 0.37	2.2 ± 0.17	17.7 ± 1.29
October	30.6 ± 2.10	2.7 ± 0.19	13.3 ± 0.52
Hog			
May	30.6 ± 1.50	0.80 ± 0.05	44.7 ± 1.48
August	30.5 ± 1.6	1.1 ± 0.15	33.6 ± 3.28
October	27.9 ± 1.47	1.8 ± 0.15	18.4 ± 2.23

were <1 µg l⁻¹ at all sites (Fig. 7a) and remained at low levels during much of the winter (K.J.M. et al. unpubl. data). Sediment chl *a* was variable at all sites and showed no clear trend in concentration between months (Fig. 7c). Despite the usefulness of chl *a* concentrations as an index of photosynthetic potential of benthic microalgal populations, we found no strong relationship between chl *a* concentrations and either net production in the light incubations or daily net production in individual cores (R² = 0.019 and 0.043, respectively; p > 0.05).

Benthic versus pelagic community metabolism

Daily *in situ* benthic community metabolism calculated from the core incubations and extrapolated to field densities of macroalgae and the proportion of bare sediment colonized by microalgae showed that

the benthic community at all 3 sites in the lagoon was net autotrophic (Fig. 8). Rates of DIC consumption ranged from a low of 6 mmol C m⁻² d⁻¹ at the mainland Creek site in the fall to a high of 179 mmol C m⁻² d⁻¹ at the mid-lagoon Shoal site in late spring. There were significant differences between the sites during all 3 seasons sampled (site × time; p < 0.0001). Rates of DIC consumption were generally highest at the Shoal site, except in the late summer following the macroalgal collapse, when net autotrophic metabolism was highest for the benthic community at the Creek site. At the Shoal site, the benthic community was most strongly net autotrophic in May as macroalgal biomass accumulated in dense mats. Net autotrophy of the benthic community declined following the macroalgal crash, and then increased again in the fall as macroalgae returned to the site (Fig. 8, Table 4). About 85% of the benthic production in late summer following the macroalgal collapse could be attributed to sediment microalgal metabolism (Table 4). At the mainland Creek site, daily DIC consumption in the spring was lower than the Shoal site, largely due to the lower macroalgal biomass. Benthic microalgae contributed the most to benthic autotrophy at this nearshore site in the late summer and fall (Table 4). Rates of benthic metabolism were relatively low at the Hog site, and net autotrophy could be attributed largely to the activity of the sediment microalgae during all 3 seasons sampled (Table 4). It was only in August, when the macroalgae had declined at the 2 sites closest to the mainland, that benthic production at the embayment site was relatively high.

For comparison with the benthic community, we scaled the daily DIC fluxes from the water column microcosms to a m² basis using an average water column height of 1 m for the 3 sites. There were no significant differences in water column metabolism between

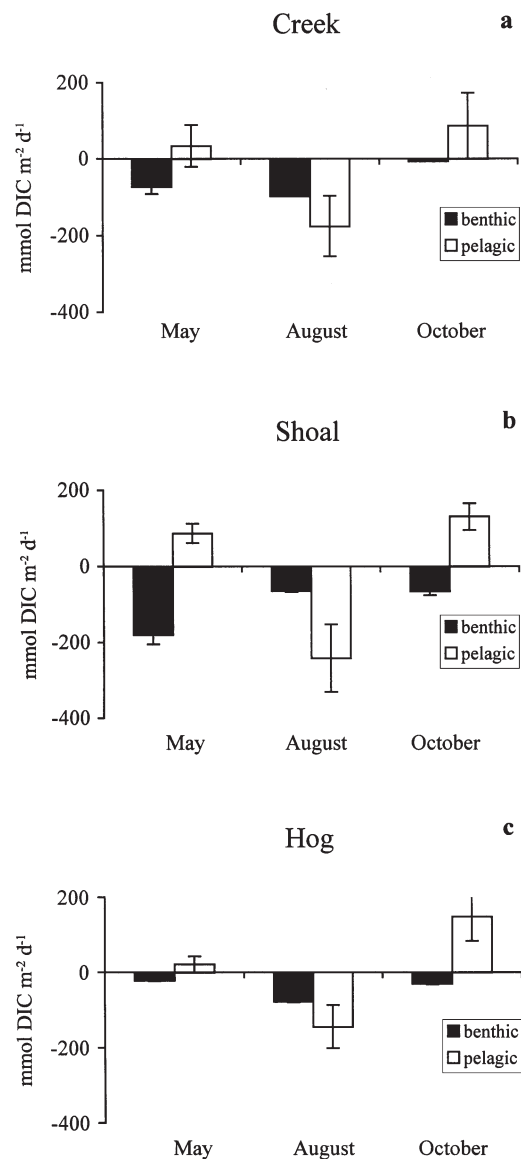


Fig. 8. Benthic vs pelagic metabolism at each site during the spring, summer and fall ($x \pm SE$, $n = 3$). Benthic metabolism was calculated based on the DIC exchange rates determined from the microcosm incubations, *in situ* measurements of macroalgal biomass and bare area colonized by benthic microalgae only. In scaling from the microcosm to *in situ* rates, benthic metabolism was corrected for both self-shading within the macroalgal mat and shading of the benthic microalgae by macroalgae overlying the sediment surface. Water column metabolism was based on a water column height of 1 m

the sites during the sampling periods (site \times time; $p = 0.79$). The water column at all 3 sites was net heterotrophic in the spring and even more so in the fall (Fig. 8). It was only following the collapse of the macroalgae in late summer that the water column at all 3 sites was net autotrophic.

Table 4. Percentage of benthic production accounted for by macroalgae and sediment microalgae

Month	Site	Microalgae (% of benthic production)	Macroalgae (% of benthic production)
May	Creek	14	86
	Shoal	4	96
	Hog	62	38
August	Creek	98	2
	Shoal	85	15
	Hog	99	1
October	Creek	72	28
	Shoal	32	68
	Hog	81	19

DISCUSSION

Benthic versus pelagic metabolism

In shallow coastal estuaries and lagoons, where much of the sediment surface is within the euphotic zone, benthic photoautotrophy is recognized as playing an important role in nutrient, oxygen and DIC exchanges across the sediment-water interface (e.g., Rizzo et al. 1996, Viaroli et al. 1996, McGlathery et al. 1997, Valiela et al. 1997, Sundbäck et al. 2000). In Hog Island Bay, about 50% of the sediment area is <1 m depth at MLW, with these shoal areas supporting highly productive benthic microalgal and macroalgal communities. The microcosm incubations described here, coupled with data on *in situ* macroalgal biomass, and sediment and water column chlorophyll, clearly indicate a seasonality in the dominance of primary producers at the sites, with benthic primary producers being the most important early and late in the growing season and phytoplankton dominating following a mid-summer period of macroalgal decay and release of algal-bound nutrients into the water column. Strong water column heterotrophy in the fall indicated that this peak in phytoplankton production was short-lived.

There were clear differences in benthic metabolism among the 3 sites studied, which reflected a gradient in nutrient availability. Since production of macroalgal communities is known to be stimulated by nutrient inputs (Nilsson et al. 1991, Valiela et al. 1997), and the light attenuation values indicated sufficient light availability to support algal photosynthesis at all sites (Table 1), we might expect the highest rates of benthic production to occur at the nearshore Creek site. However, we found that the mid-lagoon Shoal site generally had the highest rates of benthic production, with these differences being related to variation in macroalgal densities between the sites. Macroalgae accumu-

lated to the greatest extent at the Shoal site, probably due to physical transport of drifting macroalgae and entrapment by exposed oyster bars in the shoal areas. This is a physically dynamic system, where each year over 30 extratropical storms occur with magnitudes sufficient to elevate tides above astronomical norms (Hayden et al. 1999), generating waves and storm surges. At the more protected barrier island embayment site, the macroalgae were more limited by N availability, production rates were relatively low, and biomass also remained low throughout the year. Sediment microalgae accounted for the majority of benthic production (62 to 99%) at this site during the spring through fall. Despite high nutrient levels at the near-shore Creek site, macroalgal populations also accumulated to a lesser extent than in the mid-lagoon. This may be partly due to episodes of high light attenuation from resuspension of the fine silty sediments during windy periods.

A mid-summer decrease in macroalgal biomass occurred throughout the lagoon, even where populations were sparse, which suggests that light limitation within dense macroalgal mats was not the only mechanism contributing to the decline. It is likely that increased respiratory demands from high summer temperatures resulted in net decomposition. Other possible mechanisms could be increased grazing pressure (Geertz-Hansen et al. 1993, Giannotti & McGlathery 2001) or advection of macroalgae onto the marshes and mudflats or out to the coastal ocean.

Regardless of the specific mechanism responsible for the macroalgal decline observed, it is clear that it was associated with an increase in water column chlorophyll and phytoplankton production. Our results are consistent with other studies showing dominance of macroalgae over phytoplankton in shallow coastal lagoons and bays, punctuated by periodic shifts to phytoplankton dominance (Sfriso et al. 1992, Valiela et al. 1992, Riisgaard et al. 1995). Such low phytoplankton production has been attributed to nutrient competition between macroalgae and phytoplankton (Fong et al. 1993, Thybo-Christesen & Blackburn 1993, McGlathery et al. 1997) and to water residence times shorter than phytoplankton duplication times (Valiela et al. 1997). At low-to-moderate nutrient loading rates, macroalgae can sustain maximum growth rates for longer periods of time than phytoplankton because their nutrient storage capacity offsets the need for a constant nutrient supply (Fong et al. 1993, Pedersen & Borum 1996). Stored nutrients in phytoplankton can only sustain maximum growth for a day or less, whereas growth by ephemeral macroalgae such as *Ulva*, *Cladophora* and *Chaetomorpha* can be sustained by stored nutrients for at least 5 d (Borum 1996). Macroalgae also can uncouple sediment remineraliza-

tion from water column activity by intercepting nutrient fluxes across the sediment-water interface and thereby reducing the amount of nutrients available for phytoplankton production (Thybo-Christesen & Blackburn 1993, McGlathery et al. 1997). Similarly, the benthic microalgal community may function as a 'filter' to control the flux of dissolved nutrients from the sediment to the overlying water column (Risgaard-Petersen et al. 1994, Reay et al. 1995, Sunbäck et al. 2000). In Hog Island Bay, the sediments were not a significant source of inorganic nitrogen to the water column during the seasons studied despite high mineralization rates (Anderson et al. unpubl.). This suggests that bacterial and/or benthic microalgal assimilation and/or denitrification rates were high. Although sediments are generally considered to be a significant internal source of nutrients in shallow coastal systems, several studies have shown that sandy sediments which support productive microalgal communities may be net sinks of dissolved nutrients during certain times of the year (Nilsson et al. 1991, Rizzo et al. 1992, Sunbäck et al. 2000). It is likely that benthic primary producers in Hog Island Bay relied, at least in part, on water column N to meet their growth demands and that there was competition with phytoplankton for water column nutrients during the spring and early summer when growth rates were high. Following the release of both DIN and DON to the water column from senescing macroalgae, phytoplankton production would be stimulated either by direct uptake or by indirect assimilation following bacterial mineralization of DON in the water column.

Benthic microalgal production also increased in importance following the macroalgal decline at all 3 sites, suggesting that competition for light limited benthic microalgal production occurred when macroalgal densities were high. Surprisingly, there have been few direct studies of resource competition between mat-forming macroalgae and benthic microalgae (Sunbäck et al. 1990, 1996). Persistent, dense macroalgal mats would be expected to affect production of sediment microalgal communities by reducing light levels and by creating anoxic conditions at the sediment surface. At lower densities, or when macroalgae are floating in the water column and do not create intense shading and/or bottom water anoxia, sediment microalgal production would not be as strongly influenced (Sunbäck et al. 1996).

Patterns of autotrophy and heterotrophy

It is difficult to scale hourly metabolism rates obtained from enclosed microcosm incubations of the sediment or water column to total metabolism, because

sampling may not be representative and/or because 'bottle effects' might lead to resource limitation during the incubations (Kemp & Boynton 1980). On the other hand, *in situ* 'open water' techniques to estimate total system metabolism may be difficult to apply in hydrologically complex lagoonal ecosystems where water residence times can vary significantly in different parts of the lagoon (Oliveira & Baptista 1997). We do not have concurrent total metabolism measurements using the 'open water' method at our 3 sites for comparison. However, since the water column in our study is shallow and well-mixed, we would expect to find a reasonable correspondence between the microcosm incubations and 'open-water' measurements (Kemp & Boynton 1980). In addition, changes in DIC and DIN concentrations during our water column incubations did not show signs of C or N limitation that would have led to underestimation of metabolism. Our estimates of total daily metabolism at our sites fall within the range of those reported for other coastal lagoons (Table 5). Nonetheless, we restrict our discussion to the general patterns of trophic status at the 3 sites studied.

There was a distinct seasonality in patterns of system autotrophy and heterotrophy at all sites within Hog Island Bay, where all sites were net autotrophic in the spring and summer and net heterotrophic in the fall. This is in general agreement with other recent studies in shallow coastal lagoons that have shown a shift from

net autotrophy during spring and summer months to net heterotrophy in winter regardless of whether the systems were phytoplankton or macrophyte dominated (Carmouze et al. 1991, 1998, Reyes & Merino 1991). These patterns can be driven by either biological or physical processes. Carmouze et al. (1998) suggested that the seasonal switch from autotrophy to heterotrophy in several subtropical lagoons in Brazil was driven by low phytoplankton activity in the winter as temperature and irradiance levels became less conducive to growth. Conversely, Reyes & Merino (1991) attributed strong winter heterotrophy in a macrophyte-dominated tropical lagoon to resuspension and rapid degradation of organic-rich sediments during winter storms. In Hog Island Bay, the pattern of autotrophy and heterotrophy at the 3 sites appeared to be linked, at least in part, to macroalgal metabolism, either directly, when macroalgal biomass was high in the spring and early summer, or indirectly as nutrients released from the decomposition of macroalgae temporarily stimulated phytoplankton production and bacterial metabolism in the water column. Whatever the specific mechanism, it appears that a seasonal shift between net autotrophy and heterotrophy may be a common feature of coastal lagoons (Knoppers et al. 1991). Such a shift also has been found in a mesocosm experiment, where there was a seasonal pattern of autotrophy during the winter-spring diatom bloom and

Table 5. Comparison of daily metabolism measurements in coastal lagoons. Reported values integrate sediment and overlying water column

Location	Season	Metabolism (mmol C m ⁻² d ⁻¹)	Dominant plant community	Source
Hog Island Bay, Virginia, USA	Spring	-92 to 1 ^a	Macroalgae/ benthic microalgae	This study
	Summer	-305 to -221 ^a	Macroalgae/ phytoplankton	This study
	Fall	65 to 118 ^a	Macroalgae/ benthic microalgae	This study
Barro Lagoon, Brazil	Summer	-11 ^b	Phytoplankton	Carmouze et al. (1998)
	Winter	37 ^b	Phytoplankton	Carmouze et al. (1998)
Newport River Estuary, North Carolina, USA	Winter	12 to 31 ^c	Phytoplankton	Kenney et al. (1998)
	Spring	-17 ^c	Phytoplankton	Kenney et al. (1998)
	Summer	-24 ^c	Phytoplankton	Kenney et al. (1998)
	Fall	-17 ^c	Phytoplankton	Kenney et al. (1998)
Borjorquez Lagoon, Yucatan, Mexico	Range	-306 to 213 ^d	Seagrass/ macroalgae	Reyes & Merino (1991)
	during year	-188 to 128 ^d	Phytoplankton/ macroalgae	Reyes & Merino (1991)

^aDiel changes in DIC in microcosm incubations in outdoor flowing seawater table at 3 stations
^bDiel changes in CO₂ in entire water column (free water and in plexiglass tubes with and without sediments) at 1 location
^cDiel changes in O₂ measured in water column at mid-depth at 1 station on samples taken with a horizontal van Dorn bottle
^dDiel changes in O₂ measured at 2 depths in water column at 4 stations

heterotrophy during summer and early fall when the diatoms were likely nutrient (silica) limited (Oviatt et al. 1986). The strong fall heterotrophy in Hog Island Bay reflects both low benthic autotrophy and high pelagic heterotrophy, the latter probably due to nutrient limitation of phytoplankton coupled with high bacterial metabolism. Low temperatures in the fall also may have decreased autotrophic metabolism of both benthic and pelagic communities. Kemp et al. (1997) also described a period of net heterotrophy in the fall in the lower Chesapeake Bay and attributed this to nutrient limitation and the seasonal input of seagrass detritus.

Implications for fate and retention of N in Hog Island Bay

Assimilation by macroalgae and other autotrophs in Hog Island Bay represents a temporary retention of nutrients within the system unless significant burial or export of particulate organic matter occurs. The degree to which retention of nutrients in plant biomass slows nutrient transport to the coastal ocean will depend largely on the tissue nutrient content and turnover time of the primary producers. Nutrient turnover rates are highest for phytoplankton and benthic macroalgae (low C:N content and rapid growth rates), moderate for ephemeral macroalgae, and lowest for perennial macroalgae and seagrasses (high C:N and slower growth rates) (Buchsbaum et al. 1991, Enriquez et al. 1993). The dominance of fast-growing ephemeral macroalgae and phytoplankton over seagrasses in enriched lagoons can feed back to accelerate nutrient cycling rates such that nutrient retention time is decreased. Nutrients that are released upon senescence can be reassimilated by other autotrophs or bacteria, exported as dissolved inorganic or organic forms, or denitrified.

In order to relate C metabolism to N assimilation by the different primary producer communities within Hog Island Bay, we calculated the N required to support autotrophic production based on our measurements of carbon metabolism and tissue C:N. We used our measured values for macroalgal C:N, the Redfield C:N ratio of 6.6 for the water column, and a C:N ratio of 9, reported by Sundbäck et al. (2000) for the benthic microalgal communities in similar shallow-water sediments. In the spring, macroalgae were the strongest sink for N at the 2 sites closest to shore, with N assimilation rates ranging from 3.1 to 9.5 mmol N m⁻² d⁻¹. Nutrients accumulated in macroalgal biomass throughout the spring and early summer; we calculated the total N pool accumulated by algae prior to their decline to be 129 mmol N m⁻² at the nearshore

Creek site and 571 mmol N m⁻² at the mid-lagoon Shoal site. This large capacity for nutrient retention in macroalgal tissue clearly was only temporary. Tyler et al. (2001) measured flux rates of dissolved organic and inorganic N and calculated that at the mid-lagoon Shoal site, where dense macroalgal populations collapsed, it would take <2 wk for the macroalgal material to be completely remineralized. It was only immediately following the macroalgal decline at all sites throughout the lagoon that the water column and benthic microalgal communities became a strong sink for N. Assimilation rates were high (6.0 to 10.6 mmol N m⁻² d⁻¹ for the benthic microalgal community and 21.8 to 26.4 mmol N m⁻² d⁻¹ for the water column), but since turnover rates also were high and the peak in production was short-lived, nutrient retention by these communities was shorter than for the macroalgae. Seagrasses have recently returned as isolated patches in some lagoons of the Virginia Coast Reserve. If this trend continues and seagrasses recolonize Hog Island Bay and replace benthic algae as the dominant primary producers, we would expect an increase in the retention of nutrients in slowly degradable seagrass tissue. Clearly, the character and composition of the autotrophic community plays a key role in determining the extent to which these shallow coastal estuaries and lagoons function as a filter to temporarily retain or permanently remove nutrients in their trajectory from the land to the coastal ocean.

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