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Abstract

Coastal lagoons are a common land-margin feature worldwide and function as an important filter for nutrients entering from the watershed. The shallow nature of lagoons leads to dominance by benthic autotrophs, which can regulate benthic–pelagic coupling. Here we demonstrate that both microalgae and macroalgae are important in controlling dissolved inorganic as well as organic nitrogen (DIN and DON) fluxes between the sediments and the water column. Fluxes of nitrogen (NH_4^+, NO_3^-, DON, urea, and dissolved free and combined amino acids [DFAA, DCAA]) and O_2 were measured from October 1998 through August 1999 in sediment cores collected from Hog Island Bay, Virginia. Cores were collected from four sites representing the range of environmental conditions across this shallow lagoon: muddy, high-nutrient and sandy, low-nutrient sites that were both dominated by benthic microalgae, and a mid-lagoon site with fine sands covered by dense macroalgal mats. Sediment–water column DON fluxes were highly variable and comparable in magnitude to DIN fluxes; fluxes of individual compounds (urea, DFAA, DCAA) often proceeded simultaneously in different directions. Where sediment metabolism was net autotrophic because of microalgal activity, TDN (total dissolved nitrogen) fluxes, mostly comprised of DIN, urea, and DFAA, were directed into the sediments. Heterotrophic sediments, including those underlying macroalgal mats, were a net source of TDN, mostly as DIN. Macroalgae intercepted sediment–water column fluxes of DIN, urea, and DFAA, which accounted for 27–75% of calculated N demand. DON uptake was important in satisfying macroalgal N demand seasonally and where DIN concentrations were low. Up to 22% of total N uptake was released to the water column as DCAA. Overall, macroalgae assimilated, transformed, and rereleased to the water column both organic and inorganic N on short (minutes–hours) and long (months) time scales. Microalgae and macroalgae clearly regulate benthic–pelagic coupling and thereby influence transformations and retention of N moving across the land–sea interface.

Coastal lagoons, like deep estuaries, process nutrients traveling from coastal watersheds across the land margin to the open ocean. The shallow nature of lagoonal estuaries leads to a high ratio of surface area to water volume and the benthos is usually within the photic zone. As a result, benthic primary production is often more important than pelagic production, and sediment mineralization of nutrients may drive overall biogeochemical cycling (Martens 1982; Sand-Jensen and Borum 1991; Anderson et al. 2003). Seagrasses, macroalgae, and microalgae are the dominant benthic primary producers in these shallow systems (Sand-Jensen and Borum 1991). As human inputs of nitrogen (N) to shallow coastal systems increase, there is often a shift in the dominant group of producers, from seagrasses to macroalgae, and perhaps eventually to phytoplankton where nutrient loading and water residence time are both sufficiently high (Valiela et al. 1997). Because microalgae and macroalgae are capable of rapid nutrient uptake, particularly in comparison to seagrasses, their presence at the sediment surface influences the movement of dissolved nutrients across the sediment–water interface. Although the influence of benthic algae on benthic–pelagic coupling of dissolved inorganic N (DIN) has been well studied (Sundback and Graneli 1988; Rizzo 1990; Krause-Jensen et al. 1996; McGlathery et al. 1997), the impact of these important primary producers on dissolved organic N (DON) fluxes is not well understood.

DON, which enters coastal systems via freshwater input and atmospheric deposition, often makes up a large proportion of the dissolved N in seawater (Sharp 1983). Sediment fluxes of recycled N also are a potentially important source of DON to the water column, although the magnitude of DON fluxes in shallow estuaries can vary widely (Hopkinson 1987; Dollar et al. 1991; Tyler et al. 2001). Measurements of bulk DON, however, mask the dynamics of individual compounds, which vary widely in molecular weight

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Table 1. Characteristics of the four sites in Hog Island Bay. Water column concentrations are the annual mean, range, and percent of the total dissolved nitrogen (TDN) pool made up by each compound from samples collected at the time of core collection for flux experiments. Macroalgal biomass, benthic microalgal Chl *a*, sediment % N, and sediment C : N were measured within a week of each flux experiment and also represent the annual mean and range.

		Willis Wharf		Creek		Shoal		Hog	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
TDN	μmol L^{-1}	22.2	12.7–45.7	15.7	9.1–30.0	10.7	7.0–14.2	9.0	4.8–13.8
NH_4^+	μmol L^{-1}	4.3	0.5–14.4	2.7	0.5–8.6	0.8	0.0–2.5	0.7	0.0–2.4
	% TDN	15	3–31	14	4–29	7	0–17	7	0–17
NO_3^-	μmol L^{-1}	2.5	1.1–5.7	1.7	0.4–5.0	0.6	0.0–1.1	0.7	0.0–1.5
	% TDN	11	7–15	10	3–17	6	0–13	8	0–14
DON*	μmol L^{-1}	15.4	10.0–25.7	11.3	7.5–16.4	9.3	6.2–13.0	7.6	4.5–10.8
	% TDN	73	56–83	76	55–89	87	75–97	85	73–97
Urea	μmol L^{-1}	1.0	0.4–2.3	1.0	0.3–2.0	0.4	0.2–0.7	0.4	0.2–0.8
	% TDN	4	3–6	6	2–108	4	2–8	6	2–8
DFAA*	nmol L^{-1}	216	79–425	59.2	24–106	157	39–156	123	56–218
	% TDN	1	0–5	0	0–1	2	0–3	1	1–2
DCAA*	nmol L^{-1}	2178	1346–2986	1277	407–2013	1265	736–1200	1013	705–1217
	% TDN	12	5–21	10	3–25	12	8–18	12	8–17
		4							
Biomass†	g dw m^{-2}		0–11	2	0–6	157	28–306	8	3–25
Chl *a*†	mg m^{-2}	36	14–63	26	12–40	30	13–40	69	37–101
% N†		0.11	0.09–0.13	0.11	0.09–0.15	0.04	0.00–0.08	0.01	0.00–0.01
C : N†		12	9–19	12	9–17	13	7–19	19	11–38
Sediment type			Mud		Mud		Fine sand		Sand

* DON, dissolved organic nitrogen; DFAA, dissolved free amino acids; DCAA, dissolved combined amino acids.
† McGlathery et al. unpubl. data.

and bioavailability (Burdige and Zheng 1998). For example, bioavailable compounds such as amino acids and urea may make up a significant portion of the DON pool and contribute to the benthic flux of DON (Boucher and Boucher-Rodoni 1988; Lomstein et al. 1989; Burdige and Zheng 1998). In addition, these small, labile organic compounds may represent an important source of N for both heterotrophic and autotrophic microorganisms, as well as for benthic plants (Jorgensen 1982; Admiraal et al. 1984; Lomstein et al. 1989; Keil and Kirchman 1993; Nilsson and Sundback 1996; Rondell et al. 2000). In the work presented here, we investigated the role of the two dominant groups of benthic primary producers, macroalgae and microalgae, in regulating sediment–water column exchanges of DIN, bulk DON, and specific labile DON compounds (dissolved free and combined amino acids [DFAA, DCAA], urea) in Hog Island Bay, a shallow lagoon on the Virginia coast.

Methods

Site description—Hog Island Bay, located within the Virginia Coast Reserve LTER site, is a typical back-barrier lagoonal estuary extending westward from the Delmarva Peninsula, Virginia (Fig. 1). Of the total benthic surface area of the lagoon (15,085 ha), 37% is intertidal marshes and flats and 46% is less than 2 m deep at mean low water (MLW) (Oertel 2001). Recent numerical model results indicate that residence times of individual water parcels within the lagoon are spatially highly variable and range from 1 to 21 d, with an average of 16 d (D. Fugate pers. comm.). The small creeks that drain the agricultural watershed contain high concentrations of dissolved N, primarily as DIN, resulting largely from nutrient-enriched groundwater and to a lesser extent from overland flow after rain events (Neikirk 1996; J. Wu unpubl. data). Atmospheric deposition is also a potentially important source of DIN and DON to the system. There is a gradient of nutrient inputs and sediment organic matter across Hog Island Bay from the mainland to the islands, with the highest concentrations of dissolved N and sediment organic matter found closest to the mainland (McGlathery et al. 2001).

Seagrasses have been locally extinct since the 1930s, so that benthic macroalgae and microalgae are the dominant primary producers. The dominance of each of these functional groups of primary producers varies across the lagoon and shifts throughout the year (McGlathery et al. 2001). Macroalgal biomass, which is dominated by *Gracilaria tikvahiae*, *Bryopsis plumosa*, and *Ulva lactuca*, peaks in July. Phytoplankton may exhibit a peak in productivity following the decline in macroalgal biomass (McGlathery et al. 2001). Benthic microalgal productivity has been shown to range from 4% to 99% of total benthic productivity, with highest rates in the late summer (McGlathery et al. 2001).

Samples were collected from four shallow subtidal sites (<1 m at MLW) that represent the range of environmental conditions within Hog Island Bay (Fig. 1). Descriptive characteristics of each site are given in Table 1. Closest to the mainland, the Willis Wharf (WW) site was located near the head of Parting Creek, a small tributary of Machipongo Channel. Historically, shellfish processing plants were located here and more recently, aquaculture facilities discharge water into the creek. The Creek site was located on the mar-

gin of a small secondary tidal creek (~5 m across) flowing through a well-developed *Spartina alterniflora* marsh. Macroalgal biomass was generally low at both of these sites (<10 g dry weight [dw] m^{-2}, McGlathery et al. 2001; McGlathery et al. unpubl. data). The Shoal site was located mid-lagoon in proximity to a series of relict oyster reefs, which provide an attachment site for macroalgae and serve as a barrier, trapping floating macroalgae. All sampling took place in the fine-grained sandy sediments just to the east of the reefs. Macroalgal biomass at Shoal was an order of magnitude higher than at the other sites, with patchy mats >650 g dw m^{-2} (McGlathery et al. 2001). A back-barrier site located at the southern end of Hog Island (Hog) was characterized by coarse-grained, low-organic-content sands and macroalgal biomass similar to Creek, but microalgal chlorophyll *a* [Chl *a*] that was often 2× higher than elsewhere in the lagoon (McGlathery et al. 2001).

N flux measurements—Sediment–water column fluxes of dissolved nitrogen were measured in polycarbonate core tubes (8 cm i.d.; 12 cm sediment, 18 cm water column) in October 1998 and January, March, May, June, and August 1999. In July of 1999, an additional experiment was conducted at Shoal only, in an attempt to capture the high fluxes previously observed following the crash of the macroalgal mats. The macroalgae did not exhibit the massive die-off as in previous years, however, and biomass declined more slowly. Measurements from this month are included in figures, but were not included in statistical analyses to maintain an equal number of samples between sites. Sediment cores, water, and *U. lactuca* were collected from each site by hand, transported to the laboratory in Charlottesville, Virginia, and held overnight in a Conviron® environmental growth chamber at ambient temperatures. Stoppers were removed from the cores overnight to allow gas exchange with the air.

At the initiation of the experiment, the overlying water was siphoned from each core and carefully replaced with unfiltered seawater taken from each site. Experimental treatments (sediment only, sediment + algae, and water blanks) were run in triplicate. *U. lactuca* biomass in the cores, equivalent to 50–85 g dw m^{-2}, approximated the mean monthly biomass in the lagoon (42.9 ± 82.1 g dw m^{-2}, McGlathery et al. unpubl. data). To simulate conditions in the field, macroalgae were positioned at the sediment surface and held in place by a small disk of clear plastic netting (1 mm mesh). A small magnetic stir bar was then suspended from a flexible metal holster in each core and the core was capped with an acrylic top. All air bubbles were released through a small hole in the top and a rubber stopper was inserted to seal the chamber. Cores were placed in random sequence in filled aquaria in the environmental chamber. The water column of each core was gently stirred (~60 rpm) throughout the experiment to prevent the build-up of concentration gradients at the sediment–water column interface. Fluxes were measured over a 12-h period (6 h light [~550 μmol photons m^{-2} s^{-1}], 6 h dark) at ambient field temperatures. Dissolved oxygen (DO) and temperature were measured and samples for ammonium (NH_4^+) and nitrate + nitrite (NO_3^- + NO_2^-) were collected at 3-h intervals; samples for urea, amino acids, and total dissolved nitrogen (TDN) were collected at 6-h intervals. DO was measured using an Orion Model 842 meter with a self-stirring probe. Water samples were collected with a syringe and cores were refilled with an equal volume of water before recapping. The cores were darkened by covering aquaria with aluminum foil immediately after the 6-h sampling. All nutrient samples were filtered immediately (Gelman Supor, 0.45 μm) and frozen with the exception of NH_4^+ and urea samples, which were analyzed within 3 h of collection. Samples for amino acid analysis (20 ml) were filtered through mixed cellulose ester filters using gentle vacuum pressure and frozen. Macroalgal thalli from sediment + algae cores were removed after the experiment, rinsed briefly with deionized water, patted dry, and frozen. Samples were lyophilized, ground to homogeneity, and C and N contents were measured using a Carlo Erba NA 2500 Elemental Analyzer.

Nutrient analyses—Ammonium was measured using the phenol–hypochlorite method (Solorzano 1969). Nitrate + nitrite was measured using an Alpkem ''Flow Solution'' Autoanalyzer (Perstorp 1992). Urea was measured using the method described by Goeyens et al. (1998) and TDN was measured as NO_3^- after alkaline persulfate digestion in precombusted sealed ampoules as described in Tyler et al. (2001). DFAA concentrations were determined by precolumn derivatization with *o*-phthaldialdehyde, separation by high-performance liquid chromatography (HPLC) using a two-eluent gradient (eluent 1: 80% NaAc buffer, 19% HPLC-grade methanol, 1% tetrahydrofuran; eluent 2: 80% HPLC-grade methanol, 20% NaAc buffer; Alltech Guard Column and Adsorbosphere OPA HR Separator Column), and detection by fluorescence (Jones et al. 1981). Total dissolved amino acids were measured after hydrolysis of 1-ml water samples in pre-ashed ampoules. One milliliter of 12N HCl was added, the ampoule was sealed and heated to 100°C for 24 h (Pedersen et al. 1999). The ampoules were then opened and dried in a vacuum desiccator. After redissolution in 2 ml of nanopure water, samples were analyzed as described above. DCAA were calculated as the difference between total and free amino acids. Nanopure water blanks were run through the entire filtration, storage, and analysis procedures for both DFAA and DCAA to evaluate and allow correction for contamination. Standard abbreviations are used for all amino acids. Pro was not detected using this method and because of co-elution with an unidentified compound, Val was not satisfactorily resolved. Asn and Gln are converted to Asp and Glu, respectively, by the hydrolysis procedure and are reported together. Amino acid concentrations are expressed as mol L^{-1} N.

Flux calculations—Fluxes were estimated on the basis of the change in water column concentration over time as described in Tyler et al. (2001). Water blanks were used to correct sediment and sediment + algae treatments for water column activity. Likewise, *U. lactuca* uptake and release were calculated by subtracting the average sediment flux from the site and then dividing by the biomass of macroalgae in each core. Daily fluxes were calculated using the number of hours of light or dark on the day of the experiment. Annual sediment fluxes were calculated for each site by mul-

tiplying each individual replicate by the number of days in the ''season'' that it represents. One randomly selected replicate from each season was chosen and these six estimates were summed, yielding an annual flux rate. This was repeated for the two remaining replicates, and the resulting three annual estimates were averaged to give a single annual flux rate and error estimate. Although these calculations assume that the variance across sampling times was equal, which may not be true, it allows for an estimate of the potential variability in the annual flux rates. Annual macroalgal uptake was calculated similarly, by multiplying the measured uptake rate for each season (as mmol g dw^{-1} d^{-1}) by the corresponding local biomass (g dw m^{-2}; McGlathery et al. unpubl. data). This calculation assumes that the relation between measured uptake and biomass is linear, which is likely true at low biomass (equal to or less than biomass used in experiment). However, at the higher biomass occasionally found in the field, all sediment release of NO_3^-, NH_4^+, and urea would be consumed by the lower portion of the mat (McGlathery et al. 1997). Thus multiplying our calculated uptake rate by the biomass found in dense mats would greatly overestimate in situ macroalgal uptake. To compensate for this, the extrapolation of measured uptake rates to field conditions was modified when field biomass was greater than that used in our experiments (Shoal site, January 1999 through August 1999) and both rates are presented in the text. In our incubation cores, N available for macroalgal uptake was derived from two sources, sediment and water column. We assumed that the sediment contribution to macroalgal N demand was equal to the measured daily sediment efflux, regardless of macroalgal biomass. The water column contribution was calculated as the difference between measured uptake and the sediment flux (total uptake − sediment flux = water column N uptake). To obtain the total areal uptake of N by macroalgae in situ, the water column N uptake rate was multiplied by the field biomass and this value then added to the areal sediment flux (total areal uptake = [water column N uptake × biomass] + sediment flux). Our closed experimental system may underestimate the water column N availability found in the field where tides continually bring in new nutrients.

Statistical analyses—The influence of macroalgae on daily sediment fluxes was analyzed across all sites and dates using a one-way analysis of variance (ANOVA). Light–dark differences in hourly flux rates and hourly uptake rates were analyzed similarly. Differences between sites and dates were analyzed using a two-way ANOVA (three sites × six dates), and significant differences between sites or dates were determined using Tukey's HSD post hoc test. Pearson correlation analysis was used to identify significant relations between sediment flux rates and water temperature measured in this experiment, and macroalgal biomass, benthic Chl *a*, and sediment N and C : N content (Table 1). Relations between algal uptake rates and water temperature and algal tissue N were also analyzed using this method.

Results

Site characteristics—Water column dissolved N concentrations clearly show the pattern of decreasing N availability

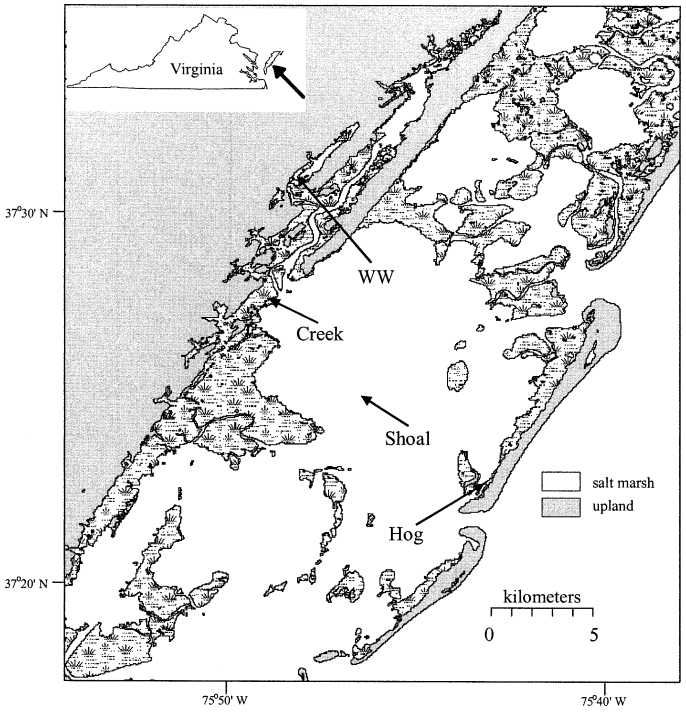

Fig. 1. Map showing the location of Hog Island Bay on the Delmarva Peninsula, Virginia and the four sites used in this study.

across the lagoon (Table 1), with highest concentrations at WW and lowest at Hog. Overall, DON was 55–97% of the N pool, and was proportionately greater at Hog and Shoal than at Creek and WW. DCAA concentrations were comparable with NH_4^+ and NO_3^-; urea concentrations were slightly lower and DFAA very low relative to the other components. The most common DFAA (>4 mole %) in the water column were Ser (11%), His (20%), Gly (14%), Arg (13%), Asp (7%), Glu (6%), and Ala (4%) (Fig. 2A). Because these percentages are based on concentrations of amino acid N, the relative importance of N-rich amino acids, such as His and Arg, increases. The most abundant DCAA (Fig. 2B) were Gly (26%), Ala (14%), His (12%), Thr (9%), Asp (9%), Ser (8%), Glu (7%), and Arg (5%). Temporally, TDN concentrations were highest in late summer and lowest in winter and spring. *U. lactuca* tissue N generally reflected the spatial and temporal variability in water column nutrients; highest tissue N was found at the mainland sites and there was a uniform decrease during spring, followed by an increase in summer at all sites except Hog (Fig. 3).

Sediment fluxes—Differences in sediment fluxes generally divided the sites into two groups: WW and Hog; Creek and Shoal. On an annual basis, sediments at Hog and WW were net autotrophic (2.7 ± 0.3 and 4.3 ± 0.3 mol O_2 m^{-2} yr^{-1}, respectively); Creek was approximately in metabolic balance (−0.1 ± 0.4), and Shoal was net heterotrophic (−1.3 ± 0.2 mol O_2 m^{-2} yr^{-1}; Table 2). WW and Hog sediments were net autotrophic throughout the year; Creek sediments were autotrophic only in October and August, and Shoal sediments only in October (Fig. 4). Maximum net heterotrophy of Shoal sediments underlying macroalgal mats coincided

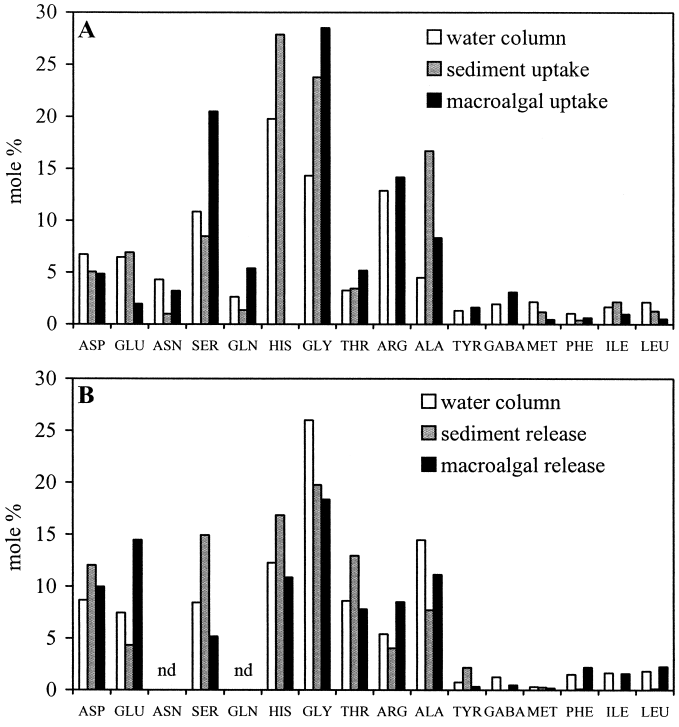

Fig. 2. Mol % N for (A) water column standing stock, sediment, and macroalgal uptake of dissolved free amino acids and (B) sediment and macroalgal of dissolved combined amino acids. A zero value indicates that no release or uptake of this amino acid was measured except where noted as ''nd''; these amino acids are not recovered after hydrolysis as described in the Methods.

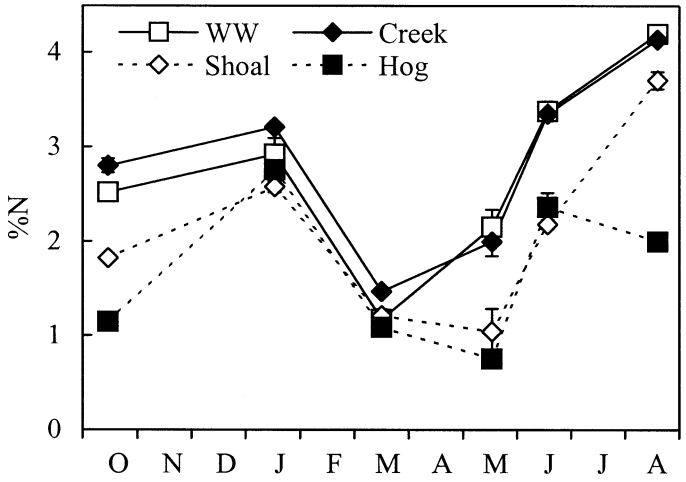

Fig. 3. Tissue N content of *Ulva lactuca* used in experiments (%N ± SE).

with maximum macroalgal biomass. Overall, the sediment DO flux correlated negatively with macroalgal biomass and positively with benthic Chl *a* and temperature (Table 3).

The average daily TDN fluxes (all sampling periods weighted equally) showed a similar grouping of sites; Creek and Shoal sediments produced a net efflux (220 and 276 μmol m^{-2} d^{-1}, respectively) and autotrophic WW and Hog sediments a net influx (-816 and -243 μmol m^{-2} d^{-1}, respectively; Table 2). Overall fluxes were highest during the summer months (Fig. 4). Annual fluxes (sampling periods time-weighted) also divided the sites into two groups: TDN efflux at Creek and Shoal (82 ± 21 and 66 ± 29 mmol m^{-2} yr^{-1}, respectively) and influx at WW and Hog (-299 ± 9 and -51 ± 16 mmol m^{-2} yr^{-1}, respectively; Fig. 5). However, the individual components of the flux often behaved differently from the net TDN flux, with uptake and release of different compounds occurring simultaneously.

On an annual basis, Creek and Shoal sediments consumed DON and released DIN. The NH_4^+ released from the Creek sediments was 94% of the total N efflux (153 mmol m^{-2} yr^{-1}). Similarly, at Shoal, NH_4^+ (65%) was also the primary component of the N efflux (247 mmol m^{-2} yr^{-1}), with urea (32%) and DCAA (2%) exhibiting only short-term importance. Of the total DON influx, 23% was identified at the Creek (urea = 4%, DFAA = 7%, DCAA = 11%) and only 1% at the Shoal (as DFAA). At WW and Hog, DIN was the dominant component of the influx (NH_4^+ = 39%, NO_3^- = 12% at WW; NH_4^+ = 25%, NO_3^- = 31% at Hog); unknown DON compounds were also important (49% and 43% at WW and Hog, respectively), but DFAA were not (<1%). The small efflux of N from the sediments at these sites (efflux = 4 and 34 mmol m^{-2} yr^{-1}, for WW and Hog, respectively) was made up of urea (100% at WW; 39% at Hog) and DCAA (61% at Hog).

There were substantial seasonal differences at all sites, resulting in high variance of the mean daily fluxes (Table 2; Fig. 4). The highest NH_4^+ effluxes were in summer at Creek and Shoal, while there was still a net influx of both NH_4^+ and NO_3^- at WW and Hog. Total DON fluxes were generally directed into the sediments during the warmer months at all sites except WW in June. DON release occurred in October and January at Hog and in October at Shoal and was predominantly made up of urea. The daily DIN, total DON, and TDN fluxes were all highly negatively correlated with the sediment DO flux (Table 3). The daily NH_4^+ flux was also negatively correlated with sediment Chl *a* and positively with macroalgal biomass in the field (Table 3). Overall, no significant seasonal trends in sediment urea uptake or release were observed and it was only a substantial component of the flux at Hog and Shoal. However, the release of urea and DON were both proportional to the C:N of the sediments (Table 3). DFAA fluxes were generally small relative to the total DON flux, with little variability between sites. The only large release of DFAA was observed at Shoal and Hog in January; at all other sites and times the fluxes of all DFAA, except Arg, Tyr, and γ-aminobutyric acid (GABA), were directed into the sediments (Fig. 2A). DCAA fluxes exhibited high variability across the lagoon, and differences between sites were seen only between WW and Hog; there was no interpretable pattern of DCAA release relative to season. Overall, only GABA and Ile were taken up as DCAA by the sediments (mean DCAA uptake = 1.9 μmol m^{-2} d^{-1}) and all other amino acids were released (mean DCAA release = 27.3 μmol m^{-2} d^{-1}; Fig. 2B). Sediment NH_4^+ release and DFAA uptake were much greater in the dark (Fig. 6). Individual DFAA also showed distinct light–dark differences, with significantly greater dark uptake of the most abundant DFAA (data not shown).

Table 2. Analysis of variance results and average daily flux rate for each site (μmol m^{-2} d^{-1} N ± SE; n = 15 for amino acids and 18 for all other values). A positive number denotes a flux out of the sediment; a negative number indicates a flux into the sediment. Significantly different subsets (Tukey's HSD post hoc test) for the site comparison are denoted by the different letters given beneath the overall means.

		F	df	Willis Wharf	Creek	Shoal	Hog
DO†	site	33.3****	3	7±2	−1±2	−3±1	12±2
	date	10.8***	5	a	b	b	a
	site×date	5.6***	15				
NH_4^+	site	39.7***	3	−327±104	418±90	384±126	−78±29
	date	2.3	5	a	b	b	c
	site×date	7.0***	15				
NO_3^-	site	10.5***	3	−115±36	9±47	6±13	−80±27
	date	12.6***	5	a	b	b	a
	site×date	6.3***	15				
DON†	site	1.3	3	−361±141	−122±146	−45±154	−137±152
	date	7.0***	5	a	a	a	a
	site×date	3.5***	15				
Urea	site	3.6*	3	−4±22	−1±26	189±82	32±31
	date	1.2	5	a	a	b	ab
	site×date	0.9	15				
DFAA†	site	1.5	3	−36.3±14.8	−13.8±14.4	−13.6±16.0	−11.8±16.2
	date	4.4**	4	a	a	a	a
	site×date	2.4*	12				
DCAA†	site	3.1*	3	−48.6±46.3	49.9±51.4	19.1±28.0	74.9±34.3
	date	1.5	4	a	ab	ab	b
	site×date	5.3***	12				
TDN†	site	19.1***	3	−816±187	220±177	276±166	−243±156
	date	8.2***	5	a	b	b	c
	site×date	3.6***	15				

* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

† DO, dissolved oxygen; DON, dissolved organic nitrogen; DFAA, dissolved free amino acids; DCAA, dissolved combined amino acids; TDN, total dissolved nitrogen.

Influence of macroalgae on sediment fluxes—Where macroalgal biomass was high at Shoal, the annual benthic (sediment + macroalgae) TDN fluxes were controlled by macroalgal uptake and release of N (Fig. 5). At Shoal, net TDN fluxes decreased by 112–619 mmol m^{-2} yr^{-1} (first number adjusted for high biomass) because of macroalgal uptake. In contrast, at WW, Creek, and Hog, low macroalgal biomass had little impact on the net benthic TDN flux (additional uptake = 17, 19, and 8 mmol m^{-2} yr^{-1}, respectively). On an annual basis at Shoal, the benthos (including macroalgae) imported DIN and DFAA and exported DCAA and bulk DON (Fig. 5). The same trend was seen in the daily measurements, as shown in Fig. 4. Macroalgae intercepted DIN and urea fluxes to the water column, and benthic uptake of DFAA and release of DCAA were greater in the presence of macroalgae. Averaged over all sites and dates, the sediment + macroalgae treatment resulted in a >500 μmol m^{-2} d^{-1} change in the NH_4^+ flux and >100 μmol m^{-2} d^{-1} change in the urea flux (Fig. 7). Uptake of NO_3^- and DFAA from the water column increased two- to threefold in cores with macroalgae (Fig. 7). All DFAA were taken up by *U. lactuca*, except His (Fig. 2A). Total benthic DON uptake was less in sediment + algae cores, but not significantly so because of high variability. However, the DCAA flux, which was insignificant in sediment-only cores, averaged 191 ± 36 μmol m^{-2} d^{-1} in cores with macroalgae.

Macroalgal uptake and release, corrected for the sediment fluxes, also varied between dark and light; uptake of NH_4^+ and NO_3^- were higher in the light, whereas uptake of urea and DFAA were higher in the dark (Fig. 6). The uptake of all individual amino acids was greater in the dark, but only significantly so for Glu, Asn, Thr, Arg, Tyr, GABA, and Phe. DCAA were released only in the light; although all DCAA were released, Gly (18%), Glu (14%), Ala (11%), His (11%), and Ser (5%) were the most abundant (Fig. 2B). The average daily macroalgal uptake (as DIN, urea, and DFAA) at each site varied significantly across the lagoon, from 24.6 μmol g dw^{-1} d^{-1} at Creek, to 15.8 and 13.4 at WW and Shoal, and 3.2 at Hog (Table 4). NH_4^+, NO_3^-, and urea uptake were all correlated with the N content of algae (Table 3). The relative importance of DON for macroalgae increased as DIN availability decreased: DIN was the majority of the uptake at WW and Creek; DIN uptake also was dominant at Shoal, but urea contributed a greater percentage; at Hog, DIN was only one-third of total uptake and DON contributed the remainder (Table 4). There was a general trend of increasing DCAA release from the macroalgae as the N content of the algae decreased (Tables 3, 4). Averaged across all sites, this release was equivalent to 22% of the total uptake of N by the macroalgae. NH_4^+ uptake was greater during the warmer months and DFAA uptake was greater during the colder months (Table 3).

Discussion

The observed patterns of benthic uptake and release of nitrogen show clearly that within Hog Island Bay the dom-

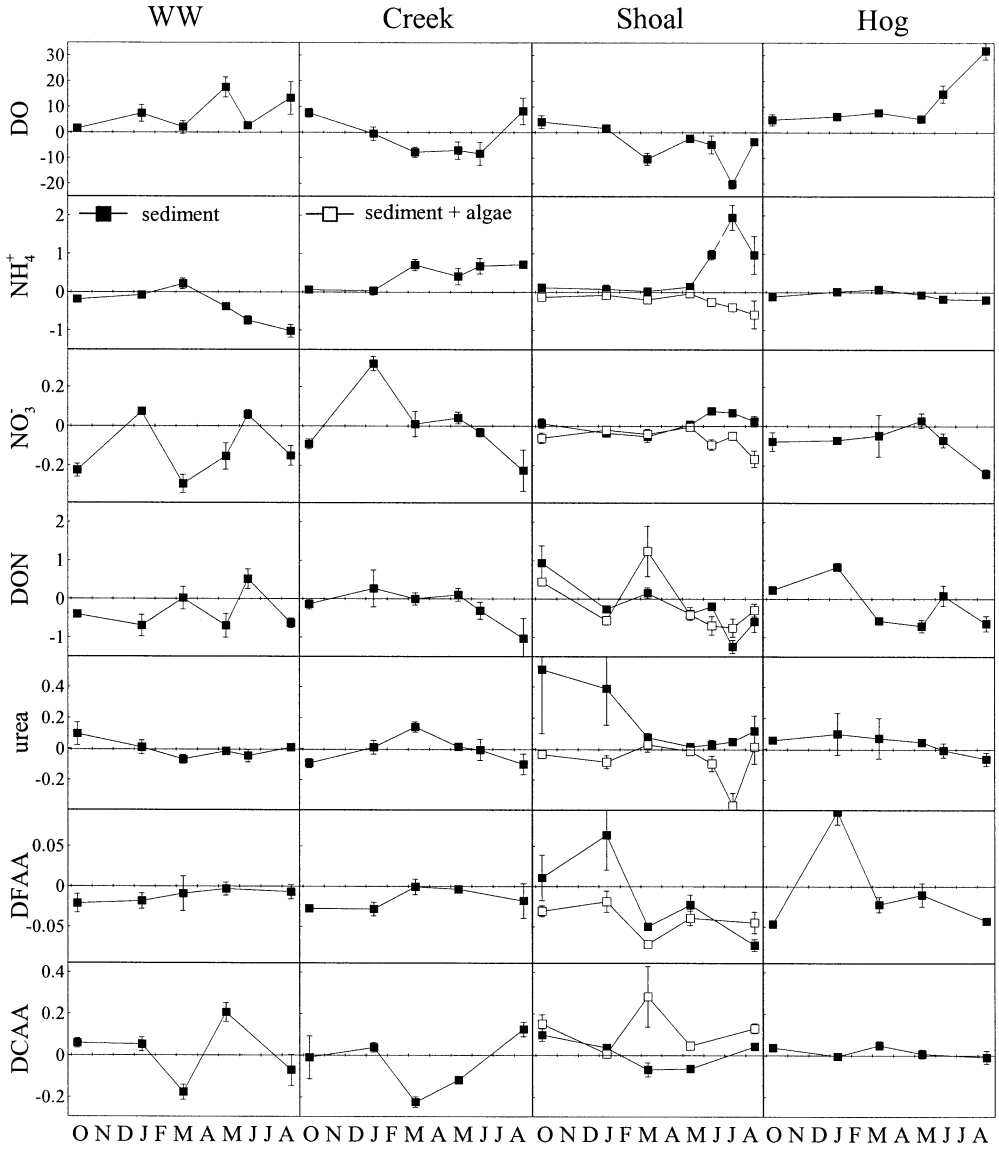

Fig. 4. Daily sediment and sediment + algae fluxes (mmol m^{-2} d^{-1} N ± SE) of dissolved oxygen, ammonium, nitrate + nitrite, dissolved organic nitrogen, urea, dissolved free amino acids, and dissolved combined amino acids across Hog Island Bay. Fluxes measured in sediment + algae cores are shown for the Shoal site only. Positive values indicate a flux from the benthos to the water column; negative values indicate a flux from the water column to the benthos.

inant primary producers, either benthic microalgae or macroalgae, control benthic–pelagic coupling. Where sediments were net autotrophic (WW and Hog) the sediments were a TDN sink and microalgae were likely to be the most important factor controlling TDN fluxes. Where sediments were net heterotrophic (Creek and Shoal) the sediments were a TDN source. At Shoal, dense macroalgae overlying the sediment surface caused the total benthos (sediments + macroalgae) to be a TDN sink, in spite of relatively high sediment N release.

Sediment fluxes and the influence of benthic microalgae—The daily sediment NH_4^+ and NO_3^- flux rates in Hog Island Bay were low (−1.2–2.0 mmol m^{-2} d^{-1} NH_4^+ and −0.4–0.4 mmol m^{-2} d^{-1} NO_3^-) compared to those observed in similar shallow estuaries (−8.1–15.6 mmol m^{-2} d^{-1} NH_4^+, 0–0.1 mmol m^{-2} d^{-1} NO_3^-, Nowicki and Nixon 1985; Rizzo 1990; Rysgaard et al. 1996; Anderson et al. 2003). The high variability we observed in daily DON fluxes in Hog Island Bay appears to be typical of coastal sediments. Small values of DON uptake by sediments also have been observed in some moderately shallow estuaries (−0.3 mmol m^{-2} d^{-1}; Dollar et al. 1991), but others have found DON fluxes directed out of the sediments (0.2–3.9 mmol m^{-2} d^{-1}; Hopkinson 1987; Lomstein et al. 1998). The same variability has been found in deeper estuaries, where in some cases DON was an important component of the TDN efflux (Lomstein et al. 1989; Blackburn et al. 1996) and in others it was small or insig-

Table 3. Results of Pearson correlation analysis. Values are the Pearson correlation coefficient (r). n = 60 for AA and 72 for all other components.

	Sediment flux					Macroalgal uptake/release	
	Biomass	Chl *a*	Temperature	Sediment C : N	DO flux	Temperature	Tissue % N
DO†	−0.35**	0.30**	0.28*	0.18			
NH_4^+	0.47***	−0.33**	0.01	−0.20	−0.52***	−0.59***	−0.60***
NO_3^-	0.22	−0.07	−0.36**	−0.12	−0.42***	−0.06	−0.30*
DON†	−0.10	−0.04	−0.20	0.33*	−0.30**	−0.04	−0.41**
Urea	0.11	−0.01	−0.09	0.32*	−0.20	0.16	−0.28*
DFAA†	−0.25	−0.05	−0.45***	−0.06	−0.02	0.35*	0.10
DCAA†	0.04	−0.07	0.19	0.11	0.25	−0.20	−0.41*
TDN†	0.23	−0.22	−0.22	0.09	−0.57***	−0.45***	−0.67***

* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

† DO, dissolved oxygen; DON, dissolved organic nitrogen; DFAA, dissolved free amino acids; DCAA, dissolved combined amino acids; TON, total dissolved nitrogen.

nificant (Burdige and Zheng 1998). The relatively low fluxes of both DIN and DON that we observed were consistent with previous work in Hog Island Bay, which demonstrated that bacterial immobilization and microalgal uptake were capable of removing all mineralized N, in spite of high mineralization rates (Anderson et al. 2003). Because sediment DIN fluxes were negligible or directed into the sediments in the previous study, phytoplankton in the water column had a greater effect on water column nutrients than the benthos (Anderson et al. 2003). It is likely that in the earlier study, when the sediments were autotrophic at all sites (McGlathery et al. 2001), microalgae were more important in consuming sediment-derived DIN than in the present study when the sediments at Creek and Shoal were net heterotro-

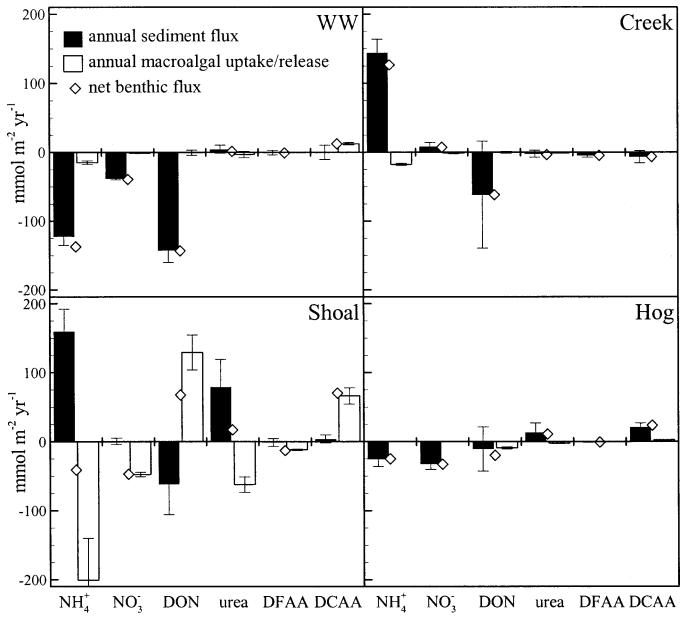

Fig. 5. Calculated annual sediment–water column fluxes, areal macroalgal uptake/release (corrected for high biomass as described in the text), and net benthic flux (sum sediment flux + macroalgal uptake/release) across Hog Island Bay. Positive numbers represent a release from the benthos to the water column. All values are in mmol m^{-2} yr^{-1} N ± SE.

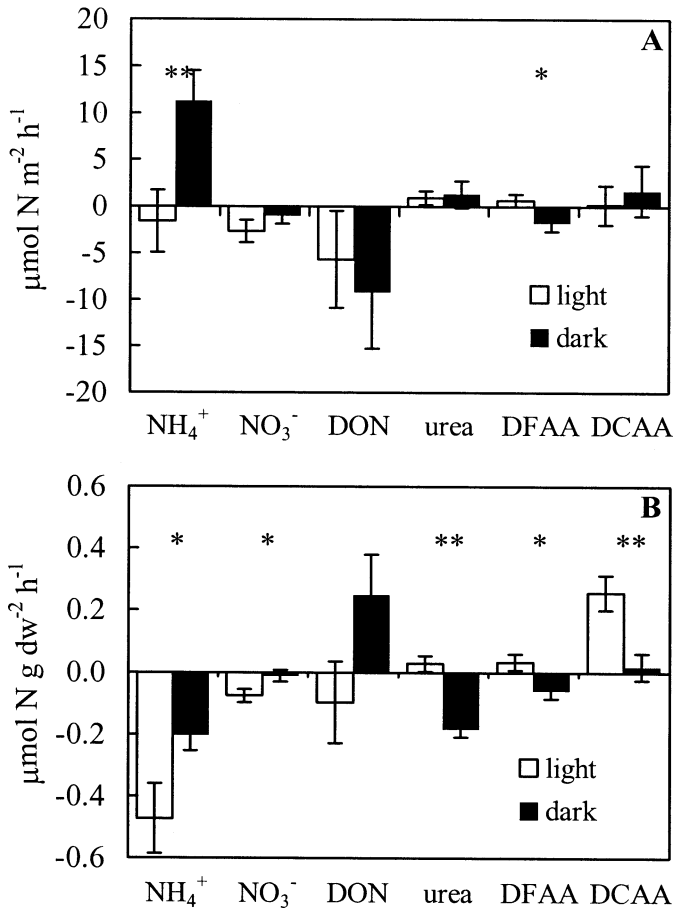

Fig. 6. Comparison between light and dark (A) sediment fluxes and (B) macroalgal uptake/release of dissolved nitrogen. Error bars = SE; n = 72 each for light and dark for all measurements except amino acids, where n = 60. *, significant difference between treatments at $P < 0.05$; **, significant difference at $P < 0.01$. A positive value indicates a flux from the benthos/algae to the water column; a negative value indicates a flux into the benthos/algae from the water column.

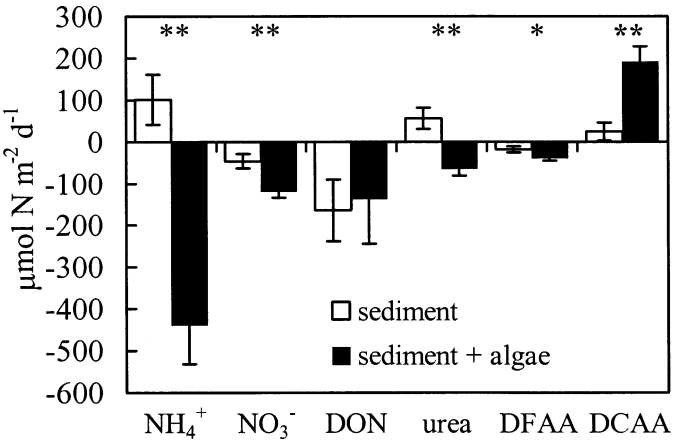

Fig. 7. Comparison between sediment and sediment + algae treatments. All units are in μmol m^{-2} d^{-1} N ± SE. $n = 72$ for each treatment for all components except amino acids, where $n = 60$. *, significant difference between treatments at $P < 0.05$; **, significant difference at $P < 0.001$. A positive value indicates a flux from the benthos to the water column; a negative value indicates a flux into the benthos from the water column.

phic and we observed a more significant release of DIN from these sediments.

The lack of a clear relation between DIN and DON fluxes and either sediment type or organic content (Fisher et al. 1982; Nowicki and Nixon 1985) in Hog Island Bay is likely due to the strong influence of the primary producers. Benthic microalgal mediation of DIN fluxes is evident in the significantly lower light fluxes at all four sites and the correlation between NH_4^+ and NO_3^- influxes (at Hog and WW) and both DO production and benthic Chl *a* (NH_4^+ only). NH_4^+ may be removed from the water column directly by microalgae and also by nitrifiers stimulated by microalgal DO production (An and Joye 2001). Microalgae also prevent NH_4^+ efflux to the water column both by direct uptake and by creating a redox ''filter'' from photosynthetic O_2 production (Sundback and Graneli 1988). Even though net heterotrophy at Creek and Shoal suggests a less active microalgal community at these sites, the daytime NH_4^+ fluxes were reduced by 50% and 23%, respectively, over the nighttime fluxes. The light–dark differences in DIN efflux that we observed were equal to and higher than those measured in a shallow Rhode Island lagoon (25% reduction, Nowicki and Nixon 1985). Previous estimates of microalgal N demand at these sites were high (7.4–16.1 mmol m^{-2} d^{-1} N; Anderson et al. 2003); however, in the present study the sediment NH_4^+ efflux at Creek and Shoal indicates that nitrogen mineralization exceeded microalgal demand, the redox filter effect, and denitrification. The higher summertime DIN fluxes that we observed at Creek and Shoal are common in temperate estuaries (Fisher et al. 1982; Rizzo 1990). Substrate for the continual release of mineralized N from organic-rich Creek sediments from March through August was probably supplied by buried macroalgae (pers. obs.) or seepage of DIN-enriched groundwater entering through the creekbank (Neikirk 1996).

The correlation between the DO efflux and DON influx, although not as clear across sites as for DIN, suggests a temporal importance of microalgal DON uptake consistent with Rondell et al. (2000), who showed utilization of small DON compounds by microbial mat communities dominated by cyanobacteria. Additionally, microalgal DO production may stimulate uptake of dissolved organic compounds by sediment heterotrophs. In general, DON fluxes are quite difficult to interpret because a single value represents the net flux of hundreds of compounds. At best we have identified 10–40% of the DON pool as urea and amino acids. Although this leaves the bulk of the pool to be identified, a closer examination of the individual compounds provides more information than bulk DON fluxes alone.

The overall range of urea fluxes measured in this study (−0.2–1.3 mmol m^{-2} d^{-1}; mean = 0.05) was comparable with the few other measurements of urea fluxes in both shallow (2.1 mmol m^{-2} d^{-1}; Boucher and Boucher-Rodoni 1988) and deep systems (0.01–0.7 mmol m^{-2} d^{-1}; Lomstein et al. 1989; Blackburn et al. 1996), as well as in Hog Island Bay (Tyler et al. 2001). Even when sediment organic C : N is high and mineralized N is rapidly immobilized by sediment bacteria, hydrolysis of detritus at the sediment surface may still lead to a positive flux of DON (Lomstein et al. 1998). This flux may be comprised of small, labile compounds such as amino acids and urea (Burdige and Zheng 1998), as we observed at Hog and Shoal in the fall when high sediment C : N coincided with an efflux of DON, which at Shoal was comprised of urea and DCAA. Except for the high release

Table 4. Average daily uptake and release of dissolved N (μmol g dw^{-1} d^{-1} N ± SE) by *Ulva lactuca* for each site. Positive values indicate a release from the macroalgae to the water; negative numbers indicate uptake by the macroalgae from the water or sediment. Percent contribution to total uptake is indicated in parentheses.

	NH_4^+	NO_3^-	DON†	Urea	DFAA†	DCAA†	DON*
WW	−12.7±3.1 (79)	−1.2±0.6 (7)	−6.9±3.6	−1.6±0.9 (10)	−0.4±0.4 (2)	5.1±0.8	−0.2 (1)
Creek	−20.0±5.1 (81)	−2.3±1.0 (9)	3.3±2.7	−1.9±0.8 (8)	−0.4±0.2 (2)	3.7±2.6	8.9
Shoal	−9.7±2.5 (73)	−1.0±0.4 (7)	2.7±3.4	−2.3±0.8 (17)	−0.4±0.3 (3)	2.7±1.2	7.6
Hog	−0.4±0.3 (11)	−0.9±0.3 (25)	−3.2±3.5	−1.2±0.9 (34)	−0.6±0.3 (18)	1.5±0.8	−0.5 (13)

DON* = DON − (urea + DFAA + DCAA) and represents the ''unknown'' fraction of the DON pool. $n = 15$ for AA and 18 for all other components.
† DON, dissolved organic nitrogen; DFAA, dissolved free amino acids; DCAA, dissolved combined amino acids.

at Shoal in October, sediment DCAA fluxes were erratic, not correlated with any other fluxes or predictor variables, and did not appear to be influenced by microalgae. Total, hydrolyzable amino acids may make up a high percentage of sediment pore-water TDN in some cases (20–70%, Henrichs et al. 1984; 30–40%, Burdige and Martens 1988), but in Hog Island Bay DCAA were not predictably released to the water column.

Microalgae (cyanobacteria) can survive with only urea as a N source and are capable of uptake in both the light and dark, with somewhat reduced uptake in the dark (Rondell et al. 2000). The capacity for dark uptake may explain why we did not observe light–dark differences in sediment fluxes, and precludes a distinct conclusion that microalgae prevent urea fluxes to the water column. However, the greater release of urea with lower DO production during the colder months suggests decreased uptake during this period. Further, microalgal uptake in Hog Island Bay may prevent the high summertime urea fluxes measured by Boucher and Boucher-Rodoni (1988). There was often a great deal of variability associated with a positive urea flux among individual cores; this heterogeneity may be due to the patchy distribution of bioturbating infauna (Lomstein et al. 1989) or benthic microalgae.

Even though DFAA were only a small proportion of water column and sediment influxes of TDN (0–5%) in Hog Island Bay, these highly labile compounds have such rapid turnover that low concentrations or fluxes may not be indicative of relative importance (Hagstrom et al. 1984), particularly at the time scale of our experiments (6 h). Uptake rates of His, Gly, and Ala were much greater than their relative concentration in the water column, suggesting some preferential uptake. His, which had the highest uptake on the basis of the mole % of N, contains 4 N atoms, making it a valuable N source, even at low concentrations. Gly and Ala are aliphatic neutral amino acids, with small side chains, possibly making them easier to assimilate than some of the larger amino acids. The DFAA uptake that we observed contrasts with DFAA release measured in the shallow Kysing Fjord, Denmark (1300 μmol m^{-2} d^{-1}; Jorgensen 1982) or somewhat deeper Cape Lookout Bight, North Carolina (52–257 μmol m^{-2} d^{-1}; Burdige and Martens 1990). Although we may have slightly underestimated the DFAA flux since we did not measure Lys, Val, Pro, or the nonprotein amino acids β-aminoglutaric acid, ornithine, or taurine, some of which may be important components of sediment fluxes (Jorgensen 1982; Burdige and Martens 1990), the higher-sediment organic matter in Cape Lookout Bight (3–5% organic C, 0.5% N; Burdige and Martens 1988) or water column nutrients in Kysing Fjord (Jorgensen 1982) may also have contributed to the positive DFAA fluxes measured in these more nutrient-enriched estuaries. Moreover, anoxia may limit DFAA mineralization within organic-rich sediments and foster an efflux (Henrichs et al. 1984), but DO production was generally high in Hog Island Bay, except at Shoal and Creek in the summer, and aerobic mineralization at the sediment surface may have decreased the DFAA flux to the water column. The high gross mineralization rate at our sites (0.9–6.5 mmol m^{-2} d^{-1} N; Anderson et al. 2003) further indicates that DFAA could have been consumed within the sediments by bacteria (Lomstein et al. 1998) or microalgae, which are capable of both light and dark DFAA uptake (Jorgensen 1982; Admiraal et al. 1984; Nilsson and Sundback 1996). Dark uptake of DFAA may provide a competitive advantage to buried microalgae (Nilsson and Sundback 1996). Consistent with this prediction, we observed a significantly greater dark influx of DFAA and the greatest DFAA uptake occurred at WW, where DO production was high. The greater dark uptake suggests that microalgal uptake may have been important, but uptake by heterotrophic microbes was also a probable contributor to the net influx from the water column.

Influence of macroalgae on benthic–pelagic coupling—It is clear that on an annual basis, macroalgal uptake controlled the movement of DIN, urea, and DFAA between the sediment and water column at Shoal and may thereby uncouple sediment–water column interactions. In phytoplankton-dominated estuaries, sediments may contribute 28–35% of the N to support new primary production (Fisher et al. 1982). In this study, the efflux of DIN and urea was sufficient to meet 27–75% of the macroalgal uptake (second number adjusted for high biomass). Some additional N was likely supplied by recycling within the macroalgal mat (McGlathery et al. 1997; Trimmer et al. 2000). The increase in tissue N observed at Shoal in late summer, which corresponded to high NH_4^+, NO_3^-, and urea uptake, was likely due to the seasonal release of N from these sediments.

The N uptake rates reported here (NH_4^+, 0–5 μmol g dw^{-1} h^{-1}) are much lower than the maximum uptake rates reported for an opportunistic green macroalga such as *U. lactuca* (V_{max} for NH_4^+ = 138 μmol g dw^{-1} h^{-1}; Fujita 1985), but probably are more representative of true field uptake because of the low water column concentrations present in Hog Island Bay. Macroalgal N demand (as measured uptake) was met by several forms of dissolved N, with DON playing an increasingly important role as DIN availability decreased. When DIN (generally as NH_4^+) was readily available in the warmer months, it constituted the majority of uptake (75% of mean uptake, all sites). Nonetheless, urea (12%) was more important than NO_3^- (9%) overall and was more important seasonally than either NH_4^+ or NO_3^-. Mean DFAA uptake was also very low (3% of total), but likewise temporally important during colder months. Other studies have shown temporal importance of urea (Bronk and Glibert 1993) and DFAA (Mulholland et al. 2002) in satisfying the N demand of phytoplankton. In addition, Admiraal et al. (1984) showed that diatoms were capable of more rapid DFAA uptake at times of low DIN availability.

Where DIN concentrations were lowest, at the Hog site, DFAA and urea comprised nearly 90% of the total annual uptake of known compounds (-3.6 mmol m^{-2} yr^{-1} as DIN, urea, and DFAA). If we include uptake of ''unknown'' DON compounds (-8.4 mmol m^{-2} yr^{-1}), it is evident that DON provided nearly all of the macroalgal N demand. Little is known about the uptake kinetics or importance of DON to macroalgae (Lobban and Harrison 1997), but uptake rates of urea and DFAA by *U. lactuca* can be substantial (Tyler unpubl. data) and growth of macroalgae using urea can be equivalent to those using DIN (e.g., Navarro-Angulo and Robledo 1999). Recently, the importance of DON in nutri-

ent-poor ecosystems has received greater attention, and it has been suggested that plants growing in these depauperate environments may be better adapted to use DON, rather than DIN (Van Breeman 2002). If this is true, then the Hog macroalgae may be better acclimated to, or have induced uptake mechanisms for, DON uptake. *U. lactuca* appeared to assimilate all measured DFAA (except His), and Gly and Ser in particular were selectively taken up relative to their water column concentrations. This contrasts with sediment uptake, where His was an important component of the DFAA influx. The higher uptake rates of DFAA and urea in the dark are difficult to explain, particularly because water column release was not greater (data not shown). However, as proposed for microalgae, dark uptake may provide a competitive advantage when DIN concentrations are low or during turbidity events.

Accumulations of macroalgae at the mid-lagoon Shoal site appeared to control both seasonal and interannual variability in N fluxes. During July 1998, patches of the macroalgal bloom crashed, releasing very high quantities of both DON and DIN to the water column (Tyler et al. 2001) and stimulating phytoplankton production (McGlathery et al. 2001); this episodic release was not observed during the present study, despite higher biomass in the summer of 1999. The high-sediment O_2 consumption, DON uptake, and DIN release during July 1999 suggest that the sediments beneath the dense macroalgal mat were heterotrophic and all available DON was rapidly mineralized to DIN. Trimmer et al. (2000) showed enhanced rates of mineralization beneath macroalgal mats, which can lead to high nutrient concentrations within the mat (McGlathery et al. 1997). The sustained sediment release that we observed in the absence of macroalgae (sediment-only cores) indicates that mineralized macroalgal detritus was slowly released from the sediments as DIN and DON during our incubations. In the previous year, when patches of the dense macroalgal mat at the Shoal crashed, we observed an efflux of DIN only where the overlying mat crashed (Tyler et al. 2001), in spite of high mineralization rates beneath the living mat nearby (Anderson et al. 2003). This suggests that interannual variability in microalgal activity, macroalgal biomass, and other factors leading to mat persistence may ultimately govern N release from the sediments. In addition to supplying organic matter for mineralization within the sediments, macroalgal mats have other potential impacts on benthic–pelagic coupling. Dense mats decrease light availability at the sediment surface (>90%; Krause-Jensen et al. 1996), which may inhibit microalgal growth and explain the inverse relation between macroalgal biomass and both sediment Chl *a* and sediment DO production. A possible decrease in microalgal activity beneath macroalgal mats due to shading may foster a greater release of N to the water column. In addition, like microalgae, the diel shifts in redox at the sediment surface induced by DO production and consumption may influence N fluxes. For example, anoxia beneath the mat may prevent nitrification and thereby increase the NH_4^+ flux from the sediments to the overlying macroalgal mat. Our calculated macroalgal N uptake may be an underestimate of in situ conditions because it does not account for the longer-term effect of macroalgae reducing light and oxygen at the sediment surface, which would stimulate sediment N release. However, the impact on benthic–pelagic coupling remains the same and by intercepting sediment–water column N fluxes, macroalgal mats may outcompete phytoplankton for sediment-derived nutrients (McGlathery et al. 1997; Valiela et al. 1997).

In our previous work, we documented a large DON release by living macroalgae; in the presence of macroalgae, benthic DON release was >250% higher (Tyler et al. 2001). In the current study, the variability in total DON fluxes was sufficiently high that there was not a significant effect of the macroalgae on the fluxes. However, we found that the mean benthic flux of DCAA increased nearly eightfold in the presence of macroalgae, which corroborates our previous work (Tyler et al. 2001) and gives new information on the nature of ''leaked'' organic matter. The higher release of DCAA in the light suggests that this release is a photosynthetically driven process, although Harlin and Craigie (1975) found no difference in light–dark DON release rates for a brown macroalgae. Phytoplankton may release 25–41% of DIN uptake as DON on short time scales (Bronk et al. 1994) and much of this release may be DFAA and DCAA (Flynn and Berry 1999). Jorgensen (1982) found increased water column DFAA in the presence of *U. lactuca*, but based on the amino acid composition concluded that the DFAA were exudates from bacteria stimulated by algal DON release. It is possible that this algal DON release may have been DCAA. In the current study, macroalgal DCAA release was 22% of the total N taken up, indicating a substantial loss of N to the water column. Whereas in some cases the DCAA in estuarine waters may not be available for bacterial utilization (Keil and Kirchman 1993), others have suggested that DCAA are an important substrate for bacterial growth (Hagstrom et al. 1984). If the released DCAA are bioavailable, these exudates will fuel heterotrophic activity in the waters surrounding a macroalgal mat (Valiela et al. 1997) and increase the oxygen demand. This rapid release of N suggests that macroalgal N turns over at two different rates after uptake: a rapid release as DCAA (and other compounds) and a slower release during senescence. The rapid uptake and release indicates that actual uptake is greatly underestimated if based solely on tissue N.

In conclusion, our work has shown that because of temporal and spatial variability in benthic primary producers, the relative role of the benthos in regulating sediment–water column fluxes can vary considerably from year to year and even over short distances in a small, shallow lagoon. Autotrophic sediments with abundant microalgae took up dissolved N; conversely, heterotrophic sediments, particularly those beneath macroalgal mats, released dissolved N. DIN, primarily as NH_4^+, was the dominant and most predictable component of the sediment–water column N flux, but DON was also an important constituent of fluxes and dominated the water column TDN pool. Likewise, macroalgal N demand was met primarily by elevated sediment DIN fluxes in the summer, but when DIN standing stocks and fluxes were low, small DON compounds, such as urea and DFAA, were important N sources. Where dense macroalgal mats occur, algae controlled benthic–pelagic coupling of TDN by intercepting DIN fluxes and subsequently rereleasing DON to the water column. Release of DCAA and other DON compounds

by living macroalgae may lead to elevated heterotrophic activity in the water column of macroalgal-dominated lagoons. The primary producers in a shallow estuary such as Hog Island Bay are clearly important in determining the transformations and retention of N passing from the land through the lagoon and out to the coastal ocean.

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