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RESEARCH ARTICLE

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Ingestion and assimilation of nitrogen from benthic sediments by three species of coral

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Abstract We quantified the nitrogen and enzyme hydrolyzable amino acid (EHAA) concentrations of sediments prior to and after corals sloughed, ingested, and egested sediments layered onto their surfaces, for the three coral species *Siderastrea siderea*, *Agaricia agaricites*, and *Porites astreoides* in Jamaica. The percent nitrogen of the sediments egested by all three species was lower than in the sediments available to the corals. Additionally, the sediments sloughed (not ingested) by *A. agaricites* and *P. astreoides* were lower in percent nitrogen, while the sediments sloughed by *S. siderea* had the same percent nitrogen as that of the available sediments. The percent nitrogen of the sediments sloughed and egested by *P. astreoides* showed significant negative and positive relationships, respectively, to increasing sediment loads, while the percent nitrogen of the sediments sloughed and egested by both *S. siderea* and *A. agaricites* showed no relationship to sediment load. EHAA concentrations were not significantly different between the sloughed and available sediments but were significantly lower in the sediments egested by *S. siderea* and *A. agaricites* (EHAA concentrations were not measured for *P. astreodies* sediment fractions). Comparisons of the nitrogen and EHAA concentrations in the sloughed and egested sediments to what was available prior to coral processing show that maximum ingestion was between 0.1 and 0.2 μg N μg^{-1} coral N cm^{-2} and between 0.5 and 0.6 μg EHAA·cm^{-2}. Maximum assimilation efficiencies were estimated to be 30–60% of the available nitrogen. The data show that corals ingest and alter the nitrogen concentration of particles that land on their surfaces. The corals' abilities to process these sediments, and the sediments' possible contributions to coral nutrition, are discussed based on these results.

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Introduction

There has been a considerable amount of research into the effects of sediments on corals, specifically the effects of increased turbidity and the ability of corals to reject sediments deposited onto their surfaces (see review by Rogers 1990). Although both suspended and settling sediments are thought to affect corals negatively, some studies suggest that suspended sediments, which reduce light levels important for zooxanthellae photosynthesis, are more stressful to corals than those that settle onto coral surfaces (Dodge and Vaisny 1977; Bak 1976; Tomasick and Sander 1985).

Several recent studies show that corals feed on, and benefit from, suspended and sedimenting particles (Anthony 1999a, 1999b; 2000; Anthony and Fabricius 2000; Mills et al. 2004). Likewise, corals can sort sediments on their surfaces and remove specific particles (Mills and Sebens 1997). These studies indicate that both suspended and downward-fluxing sediments can be a source of nutrition to corals. However, these studies investigated only suspended sediments (<100 μm) or those freshly settling out of the water column. Sediments that settle onto coral surfaces are a combination of both newly produced and resuspended particles. Surficial sediments contain substantial organic material, and microorganisms, and thus can be a source of nutrients including carbon, nitrogen, and/or phosphorus. Storm

events or strong currents can resuspend surficial sediments and thus make them available to corals. Here we test the hypothesis that benthic sediments layered onto the surfaces of corals are ingested and the nitrogen assimilated, and thus the processed sediments are lower in nitrogen and amino acid content. We define sediment processing as ingestion, sloughing of sediments off the coral surfaces, and egestion of ingested sediments.

To test our hypothesis, we layered field-collected reef surface sediments onto three species of coral, *Siderastrea siderea*, *Agaricia agaricites*, and *Porites astreoides*, and collected the sediments after they were sloughed and egested by the corals. The nitrogen content and enzyme hydrolyzable amino acids (EHAA) of the available (layered onto coral surfaces), sloughed, and egested sediments were analyzed and compared. Additionally, differences in the total amount of sediments ingested were determined, and nitrogen assimilation efficiencies were estimated.

Materials and methods

Coral collection and maintenance

Colonies of the scleractinian corals *S. siderea*, *A. agaricites*, *and P. astreoides* were collected at Red Buoy Reef, Discovery Bay, Jamaica, West Indies (Fig. 1) during January to April 1995 from a depth of 10–16 m. All three species are broadly distributed on Caribbean reefs and can be found in backreef and lagoonal locations where sediment loads can be substantial. Corals were brought to the Discovery Bay Marine Laboratory and held in running seawater tanks no longer than 2 weeks before being used in experiments. If drastic changes in colony appearance were noticed (lightening or darkening of pigmentation) the colonies were not used and new colonies were collected. Colony sizes were 22.1 ± 5.48, 28.0 ± 9.99, and 35.8 ± 9.54 cm^2 for *S. siderea* ($n = 7$), *A. agaricities* ($n = 8$), and *P. astreoides* ($n = 6$), respectively; surface area of each colony was measured using the aluminum foil technique of Marsh (1970).

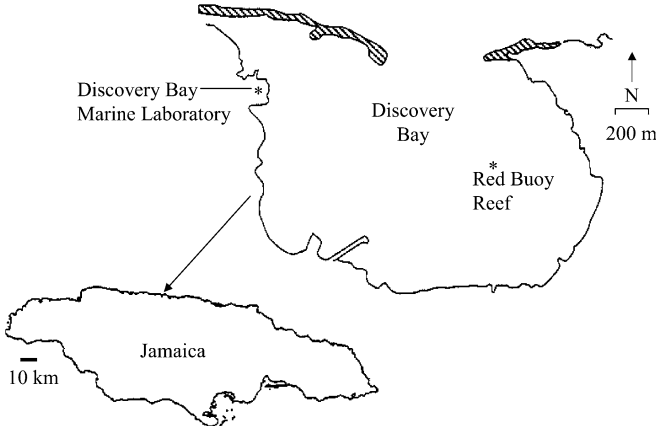

Fig. 1 Map of Discovery Bay, Jamaica with the locations of the Discovery Bay Marine Laboratory and Red Buoy Reef, the site of sediment and coral collections, indicated by *asterisks*. The *arrow* indicates the location of Discovery Bay on the North shore of Jamaica

Sediment collection and preparation

Sediments were collected at Red Buoy Reef the morning of each experiment using the wide ends of 60-ml syringes to scoop the top 1–5 mm of sediments. These samples represent surficial sediments that are resuspended during storm events then settle onto coral surfaces. The sediments were filtered through aquarium netting to remove particles > 2.0 mm and collected in a 200-ml screw-top plastic beaker with a Plexiglas wall bisecting the bottom third of the beaker. The remaining head-space in the beaker was filled with 0.2 μm filtered seawater (FSW) before it was capped tightly and gently inverted several times. The sediment was allowed to settle (15 min) into the two sections at the bottom providing two equal samples of sediment and the overlying water was siphoned off. The sediments from one section were siphoned into a pre-weighed 15-ml centrifuge tube to be used in the feeding experiments while the sediments remaining in the beaker were again split into two equal portions and collected into pre-weighed 15-ml centrifuge tubes. The tubes were centrifuged to pellet the sediment, the overlying water was decanted, and the wet weights of the sediments were determined. One centrifuge tube was filtered onto pre-weighed and pre-combusted 4.7 cm GF/F filters (450°C for 4.0 h), placed into pre-combusted foil envelopes, dried at 60°C, and stored in a desiccator until elemental nitrogen analysis could be performed. The second sediment sample was dried at 60°C and stored frozen until EHAA analysis was performed.

Sediment processing experiments

Corals were placed into small rectangular flow chambers with flow generated by a paddle wheel (Fig. 2). They were allowed to acclimate to flow speeds of approximately 5 cm s^{-1} (measured by video traces of suspended *Artemia* cysts) for approximately 30 min. Once acclimated, the flow was briefly turned off while the sediments were carefully layered onto the surface of the coral colony (Fig. 2). The sediments for the feeding experiments were pre-weighed (wet weight) and evenly spread over the surface of the coral. Loads varied from 11.7 to 53.0, 0.9 to 50.8, and 0.1 to 42.7 mg cm^{-2} for *S. siderea, A. agaricites,* and *P. astreoides*, respectively. The flow was turned on again and the corals were allowed to process the sediments (2–4 h). Afterward, colonies were removed from the flow chambers and suspended upside down in egestion chambers (500 ml) filled with 0.45 μm FSW for 10–12 h to facilitate egested sediments falling off coral surfaces (Fig. 2). In preliminary experiments, no egestion was observed after this time period. After

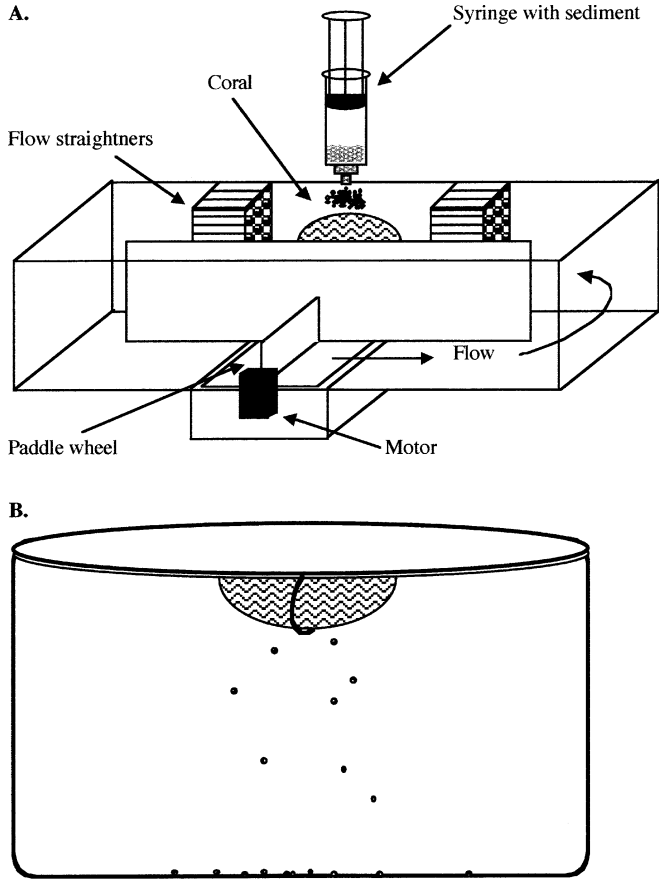

Fig. 2 Flow (**A**) and egestion (**B**) chambers used in the coral sediment-processing experiments

the egestion period, the corals were removed from the chambers and air-dried.

The sediments sloughed and egested by the corals were allowed to settle (approximately 1 h) in their respective chambers and were then siphoned from the bottom of the chambers. The sediments were split as above, placed into separate pre-weighed 15-ml centrifuge tubes, and centrifuged at high speed. The overlying water was then decanted and the wet weights of the sediments recorded. Sediment wet weights were converted to dry weights using the following regression equations determined for Red Buoy Reef sediments, one for wet weights < 0.5 mg and a second for wet weights > 0.5 mg:

$$<0.5 \text{ mg: } y = -0.17 + 0.54x \quad r^2 = 0.90$$

$$> 0.5 \text{ mg: } y = 0.0014 + 0.6x \quad r^2 = 0.98$$

Following centrifugation, the sloughed and egested sediments were resuspended in 0.2 μm FSW, sub-sampled, and filtered onto pre-weighed and pre-combusted 2.5-cm GF/F filters for elemental nitrogen analysis. The filters were placed into pre-combusted foil envelopes and dried at 60°C. The remaining sloughed and egested sediments were centrifuged again, the overlying water decanted, and the samples stored frozen until EHAA analysis.

All samples for elemental analysis were placed in a desiccator with an open bowl of concentrated HCl for 24 h to remove carbonates, then dried again and stored in a desiccator until analysis. Prior to analysis, all samples and standards (acetanilide, 10.36% N) were loaded into pre-combusted (900°C for 1 h) nickel sleeves. Elemental analysis was performed at the analytical services laboratory of the University of Maryland's Horn Point Laboratory using an Exeter Analytical, Inc. (EAI) CE-440 elemental analyzer.

Sediment EHAA were extracted using the method of Mayer et al. (1995). Briefly, samples collected for EHAA analysis were freeze-dried and 0.1 g of each was measured into 1.5 ml plastic centrifuge tubes. Bacterial activity was inhibited by adding 1 ml of 0.1 *M* phosphate buffer (pH 8) containing 0.1 *M* sodium arsenate and 0.1 m *M* pentachlorophenol, and the samples were vortexed and then cooled at 6°C for 1 h. Next, 0.1 ml of Proteinase-K (Sigma no. P8044) was added, final concentration 100 $\mu g \cdot ml^{-1}$, and the samples were placed in the dark on a shaking incubator table at 37–39°C for 3 h. Afterward, the samples were centrifuged at high speed to pellet sediments, and the supernatant was removed and placed into a 1.5-ml centrifuge tube. Trichloroacetic acid (TCA) (0.1 ml of 100%) was then added to the sediment samples and they were refrigerated for 30 min. The sediments were again centrifuged (13,000×g for 5 min) to remove precipitated macromolecules, and the supernatant, containing the low molecular weight compounds (EHAA), was placed into 0.8-ml glass tubes. Ultra high purity HCl (0.8 ml) was then added and the tubes were sealed under N_2. Finally, the samples were heated in a dry bath at 110°C for 24 h and stored frozen until analysis.

EHAA analysis was carried out by adding 0.1 ml of each sample to a glass test tube containing 2 ml of pH 10 boric acid buffer and 0.1 ml of 6 N NaOH. The samples were capped, vortexed, and allowed to stand at room temperature for 1 h. Aliquots (0.4 ml) were added to cuvettes containing 2 ml of the boric acid buffer, and 0.4 ml of o-Phthalaldehyde (OPA) reagent was then added. Samples were next vortexed and allowed to stand 1–5 min, and their fluorescence was then measured using a spectrofluorometer (excitation: 340 nm, emission: 455 nm). The OPA reagent was made by adding 0.5 g OPA (Sigma P1378) to 2.5 ml methanol and crushing to dissolve. The OPA/methanol solution was then added to 500 ml of OPA buffer [30 g boric acid, 3.5 ml Brij 35 solution (Sigma 430AG-6), and 2.5 g ethylenediaminetetracetic acid (EDTA)–Na salt]. The buffer was brought up to 1 l using deionized water, the pH was adjusted to 9.8–10.0 with potassium hydroxide (KOH) pellets, and then 5 ml of 2-mecaptoethanol (Sigma M6250) was added.

The nitrogen and EHAA per sediment dry weight (DW) were compared using two-factor analyses of covariance (ANCOVAs) to determine if species and sediment fractions (available, sloughed, and egested) differed with sediment load as a covariate. The

Bonferroni/Dunn means comparison test was used to identify differences between species. Additionally, relationships between nitrogen content of the sediment fractions and sediment load were investigated using linear regressions. The data were arcsine square-root transformed to meet normality assumptions.

Results

Nitrogen concentrations (micrograms N·per milligram DW) of sediment collected at or near sites of coral collection during 1994 and 1995 show great variability in sediment nitrogen content (Fig. 3). Each bar represents an individual sample of benthic surficial sediments collected from haphazardly chosen locations at Red Buoy Reef. Concentrations can be very different on the same day (e.g. 19 January 1994 range 0.94–7.03 μg N·mg^{-1} DW and at different times of year. The average (± SE) concentration of the 1994 samples was 1.41 ± 0.33 μg N·mg^{-1} DW, and that of the 1995 samples was 0.69 ± 0.22 μg N·mg^{-1} DW.

Sediment-processing experiments

The percent nitrogen of the available, sloughed, and egested sediment fractions was not linearly related to sediment load for either *S. siderea* or *A. agaricites* (Table 1). By contrast, the percent nitrogen of the sediment sloughed by *P. astreoides* was negatively related to increasing sediment loads, while the egested *P. astreoides* sediments showed a positive relationship to sediment load.

The proportions of available nitrogen in the sloughed and egested sediments were negatively related to increasing sediment loads for sediments egested by *S. siderea* and *A. agaricites*, and those sloughed by *P. astreoides* (Table 1). No relationship between the proportion of available nitrogen and sediment load was recorded for the sediments sloughed by *S. siderea* and *A. agaricites* or for those sediments egested by *P. astreoides* (Table 1).

The percent nitrogen was significantly different among the sediment fractions, but not among species (Table 2, Fig. 4A). The available fraction had the

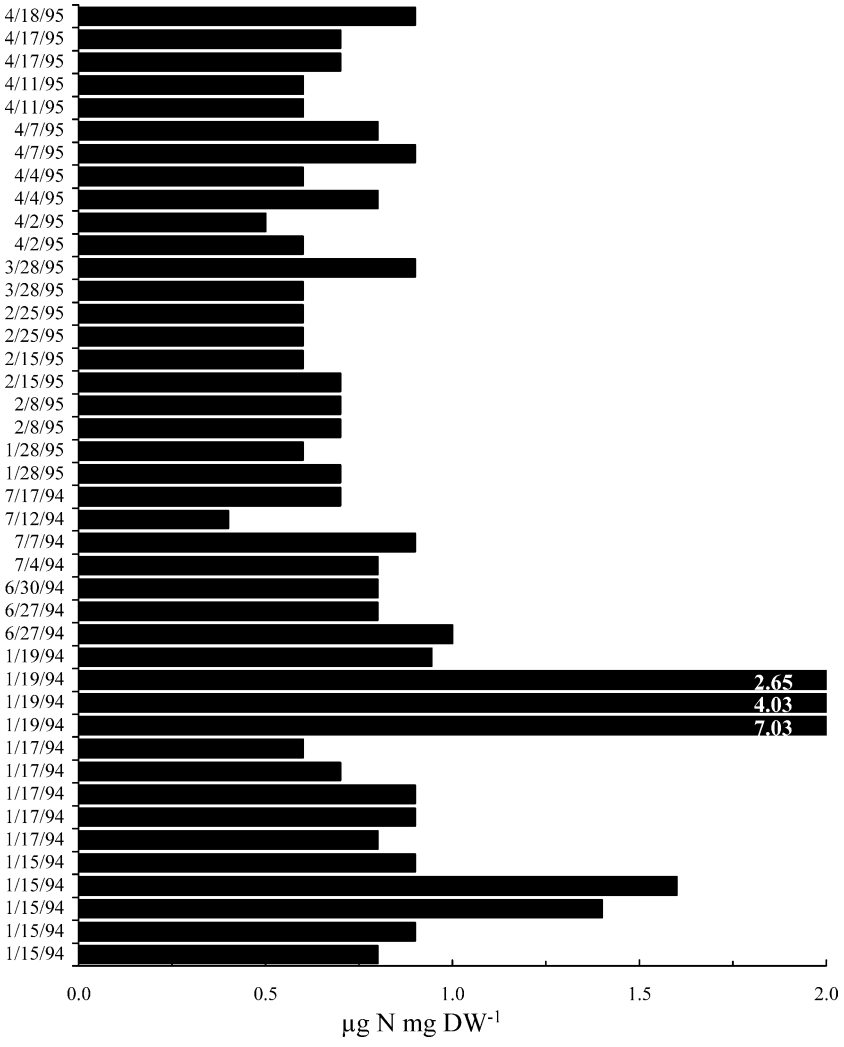

Fig. 3 Nitrogen concentrations of Red Buoy Reef benthic sediments sampled between 15 January 1994 and 18 April 1995

Table 1 Least squares linear regressions between sediment load and the sediment parameters percent nitrogen and micrograms nitrogen·per microgram nitrogen available ($\alpha = 0.05$) for the three coral species *Siderastrea siderea*, *Agaricia agaricites*, and *Porites astreoides*

	Sediment fraction	Intercept	Slope	r^2	Number	*F*-value	*P*-value
Percent N							
S. siderea	Available	0.024	4.53×10^{-5}	0.44	7	3.95	0.10
	Sloughed	0.024	6.57×10^{-5}	0.19	5	0.71	0.46
	Egested	0.011	-8.77×10^{-6}	0.005	7	0.03	0.88
A. agaricites	Available	0.028	-5.95×10^{-5}	0.10	8	0.69	0.44
	Sloughed	0.015	-1.33×10^{-4}	0.19	8	1.37	0.29
	Egested	0.013	-7.83×10^{-5}	0.24	6	1.28	0.32
P. astreoides	Available	0.026	-4.37×10^{-5}	0.49	4	1.93	0.30
	Sloughed	0.014	-1.01×10^{-4}	0.95	5	57.65	0.005
	Egested	0.012	2.12×10^{-4}	0.81	5	12.70	0.04
μg N·μg^{-1} N available							
S. siderea	Sloughed	0.127	-1.20×10^{-3}	0.60	5	4.44	0.13
	Egested	0.038	-3.90×10^{-4}	0.73	7	13.48	0.01
A. agaricites	Sloughed	0.071	-1.08×10^{-3}	0.19	7	1.21	0.32
	Egested	0.046	-5.90×10^{-4}	0.78	5	11.17	0.04
P. astreoides	Sloughed	0.059	-1.02×10^{-3}	0.98	4	128.86	0.008
	Egested	0.053	-3.29×10^{-4}	0.56	4	2.56	0.25

Table 2 Two-factor analyses of covariance comparing percent nitrogen, micrograms nitrogen per microgram nitrogen available, and micrograms enzyme hydrolyzable amino acid (EHAA) per milligram sediment of the three sediment fractions among species with sediment load as a covariate. The data were transformed by taking the inverse sine of the square root of the data as proportions, and the error mean square was used as the denominator in all *F*-value calculations

Source of variation	*df*	Mean square	*F*-value	*P*-value	Significance
Percent N					
Species	2	7.65E−06	0.99	0.38	NS
Sediment fraction	2	2.97E−04	38.84	0.0001	**
Sediment load	1	2.23E−07	0.029	0.87	NS
Species*Sediment fraction	4	1.79E−05	2.33	0.07	NS
Species*Sediment load	2	1.12E−05	1.46	0.25	NS
Sediment fraction*Sediment load	2	7.19E−06	0.94	0.40	NS
Species*Sediment fraction*Sediment load	4	1.87E−05	2.44	0.06	NS
Error	37	7.65E−06			
μg N·μg N available^{-1}					
Species	2	0.01	1.16	0.34	NS
Sediment fraction	1	0.004	7.99	0.01	*
Sediment load	1	0.004	7.92	0.01	*
Species*Sediment fraction	2	0.001	2.40	0.12	NS
Species*Sediment load	2	1.02E−05	0.30	0.74	NS
Sediment fraction*Sediment load	1	0.001	1.43	0.25	NS
Species*Sediment fraction*Sediment load	2	6.99E−06	0.02	0.99	NS
Error	20	4.67E−04			
μg EHAA per mg sediment					
Species	1	0.282	2.534	0.13	NS
Sediment fraction	2	0.027	0.245	0.78	NS
Sediment load	1	0.003	0.027	0.87	NS
Species*Sediment fraction	2	0.026	0.233	0.79	NS
Species*Sediment load	1	0.098	0.879	0.36	NS
Sediment fraction*Sediment load	2	0.091	0.814	0.46	NS
Species*Sediment fraction*Sediment load	2	0.020	0.181	0.84	NS
Error	21	0.111			

* $P < 0.05$; ** $P < 0.001$

highest percent nitrogen ($0.07 \pm 0.002\%$, average ± SE), followed by the sloughed sediments ($0.03 \pm 0.006\%$). The egested sediments contained the lowest percent nitrogen ($0.02 \pm 0.002\%$). There was no statistical difference detected among species when the percent nitrogen of the sloughed sediment was compared (*S. siderea*: $0.07 \pm 0.004\%$, *A. agaricites*: $0.014 \pm 0.002\%$, *P. astreoides*: 0.017 ± 0.002). With respect to the proportion of available nitrogen in the sloughed and egested sediment fractions, significant differences were not detected among species but were recorded among sediment fractions and sediment load (Table 2, Fig. 4B). Sloughed sediments contained the greater proportion of available nitrogen compared with the egested sediments (0.36 ± 0.18 μg N·μg^{-1} N available vs 0.18 ± 0.03 μg N·μg^{-1} N available).

The EHAA concentration of the available sediments was not different from that sloughed by *S. siderea* or *A. agaricites*. However, the egested sediments for both corals had increased EHAA concentrations relative to available and sloughed sediment fractions, though not significant by ANCOVA analysis (Table 2, Fig. 4C). All sediment fractions from the *A. agaricites* experiments had higher concentrations of EHAAs than did the sediments in the *S. siderea* experiments, including the available sediments (Fig. 4C). There was a 3.3-fold

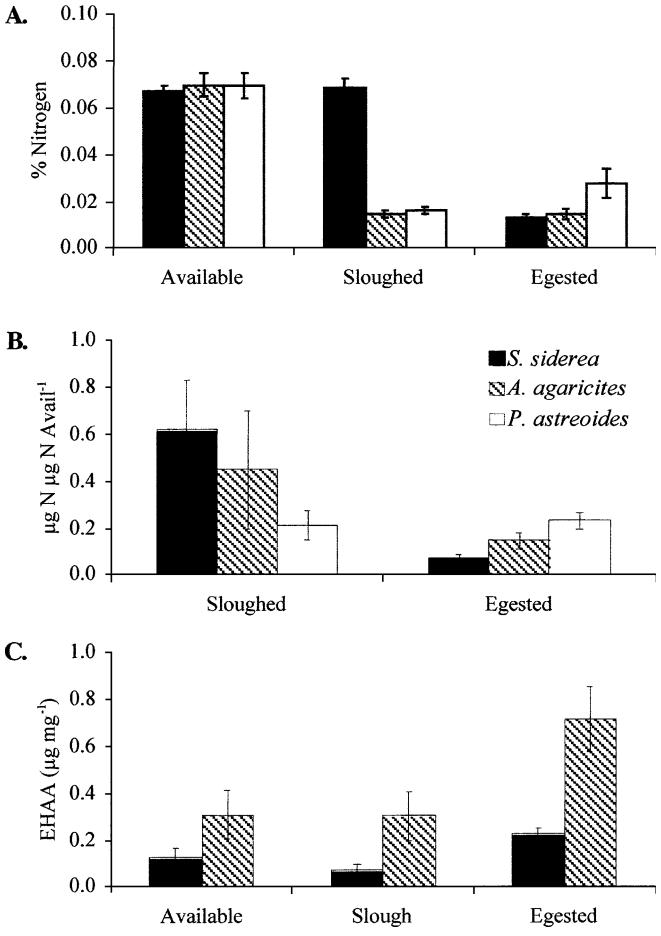

Fig. 4 Mean (± SE) **A** percent nitrogen, **B** nitrogen relative to the total nitrogen available, and **C** enzyme hydrolyzable amino acid (EHAA) of the different sediment fractions processed by the three coral species, *Siderastrea siderea*, *Agaricia agaricites*, and *Porites astreoides*

increase between the sloughed and egested EHAA concentrations of the *S. siderea* sediments and a 2.4-fold increase between those sloughed and egested by *A. agaricites*. The EHAA concentrations of the different sediment fractions were compared to the corresponding sediment nitrogen concentrations for both species (Table 3). The EHAA concentrations of the available sediments were positively related to the total nitrogen content, with higher nitrogen concentrations relating to higher EHAA concentrations (i.e. a greater percentage of organic material). In contrast, the EHAA concentrations of the sloughed sediments from *A. agaricites* and egested sediments from both species were not significantly related to the total nitrogen content in these sediment fractions.

We also compared nitrogen concentrations, EHAA concentrations, and EHAA nitrogen (EHAA N) of the sediments available to, and processed by, the coral species (Fig. 5). EHAA concentrations in the available sediments were approximately a quarter of total nitrogen concentrations. The EHAA N was $3.6 \pm 0.53\%$ of the total nitrogen in the sediments available to the corals, assuming EHAA N was 16% of the EHAA mass (Mayer et al. 1986). The percentage of total nitrogen attributable to EHAA N increased in sediments sloughed by *A. agaricites* and egested by both species (*S. siderea* sloughed: $1.27 \pm 0.25\%$, egested: $48.02 \pm 11.75\%$; *A. agaricites* sloughed: $28.55 \pm 9.52\%$, egested: $88.83 \pm 22.95\%$).

S. siderea ingested the greatest amount of sediment per area (10.24 ± 5.46 mg cm^{-2}, average ± SE), while *A. agaricites* and *P. astreoides* ingested statistically similar amounts (3.47 ± 4.46 and 4.82 ± 6.22 mg cm^{-2}, respectively; ANCOVA, $df = 2$, $F = 6.28$, $P < 0.05$; Fig. 6A). Likewise, *S. siderea* ingested a greater amount of nitrogen (5.58 ± 3.73 µg N cm^{-2}) per coral surface area than did either *A. agaricites* (2.43 ± 3.12 µg N cm^{-2}) or *P. astreoides* (3.37 ± 4.35 µg N cm^{-2}; ANCOVA, $df = 2$, $F = 6.24$, $P = 0.01$; data not presented). When the amounts of nitrogen ingested per area were normalized to total colony biomass per area (micrograms N cm^{-2}) no significant differences were found among species (Fig. 6B). *A. agaricites* ingested 0.17 ± 0.23 µg N (µg N cm^{-2})$^{-1}$, while *P. astreoides* ingested 0.07 ± 0.13 µg N (µg N cm^{-2})$^{-1}$, and *S. siderea* ingested 0.09 ± 0.07 µg N (µg N cm^{-2})$^{-1}$. Likewise, ingestion of the sediment EHAAs per coral surface area were not significantly different between *S. siderea* (0.55 ± 0.32 mg cm^{-2}) and *A. agaricites* (0.45 ± 0.57 mg cm^{-2}; Fig. 6C).

Discussion

Surficial sediments on coral reefs contain bacteria, microbial exudates, protozoa, interstitial invertebrates,

Table 3 Least squares linear regression between sediment nitrogen content (micrograms per milligram) and EHAA content (micrograms per milligram) for the different sediment fractions

Sediment fraction	Intercept	Slope	r^2	Number	*F*-value	*P*-value
Available	−0.106	0.384	0.386	11	5.66	0.04
S. siderea						
Sloughed[a]						
Egested	0.118	1.709	0.146	5	0.52	0.53
A. agaricites						
Sloughed	0.272	0.122	0.100	8	0.06	0.81
Egested	0.49	1.127	0.040	4	0.096	0.79

[a] Statistical analysis not performed for this sediment fraction

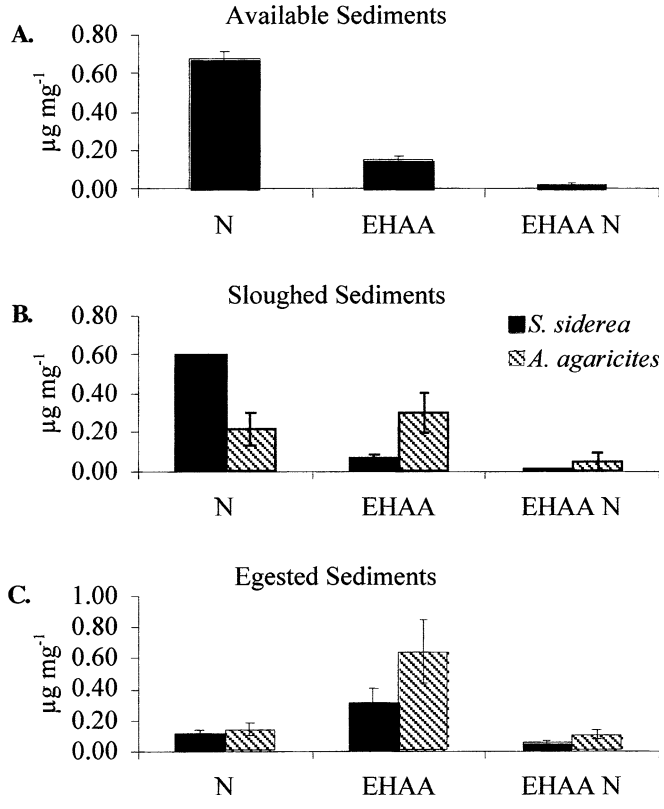

Fig. 5 Comparison of the nitrogen, EHAA, and EHAA N (EHAA nitrogen) concentrations in the **A** available, **B** sloughed, and **C** egested sediment fractions

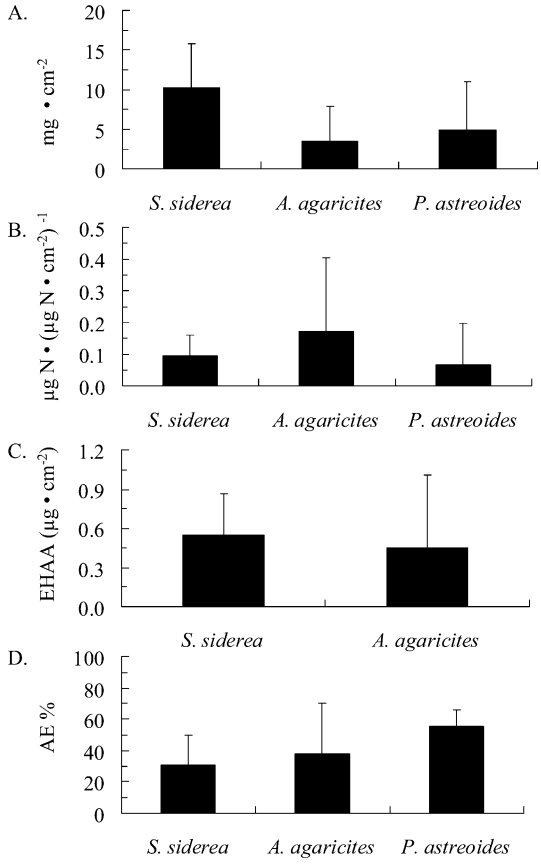

Fig. 6 Mean (±SE) **A** dry weight, **B** nitrogen, and **C** EHAA ingested; and **D** assimilation efficiency (AE) for the three coral species investigated

microalgae, sorbed organic matter, and detrital organic matter (Lopez and Levinton 1987) that are all potential sources of food to corals. Sediment-associated flagellates and ciliates, for example, have been identified as potential sources of nutrition (Alongi 1990). Benthic sediments are available to corals only if they are resuspended and then settle onto coral surfaces, a process shown to be influenced by both reef wind regimes (Larcombe et al. 1995) and the activity of benthivorous fish (Yahel et al. 2002). In addition to resuspended sediments, freshly settling particles are possible sources of nutrition as well. Reefs are areas of high mucus production, which facilitates the aggregation of particles that settle onto coral surfaces, and reef fishes produce feces that are a food source for some reef organisms (Bailey and Robertson 1982; Robertson 1982; Rothans and Miller 1991). Meyer and Shultz (1985) recorded average particulate organic carbon deposition by grunts of 164–251 mg m^{-2}·day^{-1} onto *Porites furcata* and *Acropora palmata* colonies, and the maximum fecal production coincided with periods of highest coral growth rates. Likewise, detritus settling over corals along the Great Barrier Reef can have up to 20% of its nitrogen in labile biochemicals (proteins, lipids, or carbohydrates; Dommisse 2001); and Crossman et al. (2001) have shown that detritus from epilithic algal communities contains a significant amount of protein amino acids and argue this is an important food source for grazing reef fishes.

Benthic suspension feeders utilize these different sources of particulate matter as sources of nutrition. Sponges, ascidians, gorgonians, and soft and hard corals have been shown to ingest phytoplankton (Fabricius et al. 1995; Ribes et al. 1998; Widdig and Schlichter 2001), ciliates (Coma et al. 2001), bacteria (Bak et al. 1998; Gast et al. 1998), zooplankton (Sebens et al. 1998), and both particulate (Anthony 1999a; Mills et al. 2004) and dissolved organic matter (Yahel et al. 2003; Ferrier 1991). Such sessile suspension feeders have been considered the ultimate opportunistic consumers because of their ability to utilize seston of many types and sizes (Coma et al. 2001). The ascidian *Halocynthia papillosa* and the gorgonian *Paramuricea clavata* obtained 92 and 96% of their ingested carbon from detrital matter, respectively. Likewise, Fabricius and Dommisse (2000) found that water downstream of alcyonacean soft corals was significantly depleted of chlorophyll, particulate organic carbon, and particulate phosphorus. Therefore it is not too surprising to find that scleractinians can utilize resuspended sediments as a source of nitrogen.

The sediments used here varied in their nitrogen content, averaging 0.08 µg N mg^{-1}, and at times containing >2 µg N·mg^{-1}. EHAAs were approximately 0.03% of the available sediment by weight, but the EHAA N was 3.5% of the available nitrogen. We

sampled sediments from the top layer (1–5 mm) of deposited matter, which may have included a high percentage of recently settled particulate matter and detritus, and thus greater amounts of labile nitrogen than particulate matter that had been part of the sediments for a longer period of time. These surficial sediments are also those most likely to be resuspended and to settle onto coral surfaces.

The decreased percent nitrogen of the sediments egested by *Siderastrea siderea, Agaricia agaricites,* and *Porites astreoides* suggest that these corals are removing nitrogen from sediments that land on their surfaces. The sediments sloughed by *P. astreoides* and *A. agaricites* were also lower in percent nitrogen, indicating that these two species may be selectively ingesting particles with a higher nitrogen content, or stripping the sediment of organic nitrogen during the sloughing process. However, even when percent nitrogen does not change during sediment processing, it is still possible that corals are ingesting sediments nonselectively. Evidence from recent work shows that some corals can ingest and assimilate carbon from suspended particulate matter (SPM; Anthony 1999a; Anthony 2000; Anthony and Fabricius 2000), as well as nitrogen from particulate matter collected in sediment traps (Mills et al. 2004), and that these sediments may contribute as much, and at times more, carbon and nitrogen to some corals' nutritional budgets as other particulate sources. This study is the first that measures changes in the nitrogen content of benthic sediments layered onto coral surfaces and suggests they too are a source of nutrition for corals.

For both *S. siderea* and *A. agaricites*, increasing sediment load resulted in egested sediment fractions with a lower proportion of available nitrogen. The data suggest that either the assimilation efficiencies of these corals also increased and/or that the corals' selectivity for particles high in nutritional "quality" (higher percent nitrogen, more labile) decreased. Mills and Sebens (1997) found that as sediment loads increased, the corals *S. siderea* and *A. agaricites* removed potentially nutritious experimental particles (*Artemia* cysts) from sediments with decreasing efficiency. Likewise, Anthony (1999a) measured decreasing particulate organic carbon assimilation efficiencies with increasing concentrations of SPM for four species of coral. Thus, we propose that, as sediment loads increased in our experiments, selective ingestion of particles with high nutritional "quality" decreased. The result was that sediments of poor "quality" (low percent nitrogen, more refractory) were ingested and subsequently egested; thus they contained a lower proportion of the available nitrogen.

Sediments sloughed by *P. astreoides* also contained a lower percent nitrogen, and lower proportion of available nitrogen as sediment loads increased, but the percent nitrogen of the egested fractions was positively related to increasing sediment loads. The negative relationship between percent nitrogen and sediment load for the sloughed sediments suggests that, at higher sediment loads, this coral's selective ability to remove particles high in nitrogen content increased. This is not intuitive, but the contrasting positive relationship measured between the percent nitrogen of the egested fraction and increasing sediment loads supports this. As sediment loads increased, a high selectivity of nitrogen-rich particles would lead to sloughed sediments with a low percent nitrogen, and possibly, egested sediments with a higher percent nitrogen than available, if assimilation efficiencies decreased under higher sediment loads as is suggested with suspended particulate matter (Anthony 1999a).

P. astreoides colonies make a mucus sheet over their surface that collects particles and is then sloughed with the assistance of wave action (Lewis and Price 1975; Coffroth 1990). In contrast, the other two species use fluid mucus strands to collect sediments that are then transported to colony edges by cilia where gravity and wave action remove them (Lewis and Price 1975, 1976). Coffroth (1990) investigated the biochemical make-up and nutritional quality of both fluid mucus and mucus sheets from poritid corals in the Caribbean and found that they are composed mainly of carbohydrates and proteins. Mucus sheets contained a higher ash content, bacterial abundances, chlorophyll *a* concentration, and lower C:N ratios than fluid mucus and were considered to contribute negligibly as a nutrient source on reefs. Likewise, the production of mucus sheets by poritid corals was determined to be a minor portion of coral production (Edmunds and Davies 1986; Coffroth 1990). Little is known as to how mucus sheets affect the ability of poritid corals to process sediments on their surfaces, but *P. asteroides* has been described as using tentacles only, and not mucus, when feeding on particulate matter (Lewis and Price 1975). On the other hand, *A. agaricites* uses mucus nets or filaments alone, and *S. siderea* uses both tentacles and mucus to capture particulate matter. The use of mucus for feeding on particulate matter layered over a coral's surface would likely bind particles of differing nutritional quality. Tentacles alone, though, may allow *P. astreoides* to be more selective than either *S. siderea* or *A. agaricites* when sloughing sediments and may result in only particles high in organic nitrogen being ingested, thus accounting for the differences measured in percent nitrogen of sediments sloughed and egested by *P. astreoides* as sediment loads increase.

The processing of sediments by the corals altered the EHAA concentrations, with egested sediments having higher EHAA concentrations than the available sediments. The result that neither the sloughed nor the egested sediments showed any significant relationship to the nitrogen concentrations of these fractions supports this. The mucus utilized by both *S. siderea* and *A. agaricites* during the ingestion and egestion process may have increased EHAA concentrations of the egested sediments. Ducklow and Mitchell (1979) found coral mucus to be composed of varying levels of protein (5–

59%), as did Meikle et al. (1988; 9–70%). Both studies found that the amino acid composition of coral mucus was similar among several coral species, but that amino acid concentrations were different. Both *S. siderea* and *A. agaricites* utilize mucus when feeding on particulate matter (Lewis and Price 1975), and thus the nitrogen and EHAA concentrations of the processed sediments measured here include any mucus added by the corals. While the corals seem to have added amino acids to the egested sediment fractions, the total EHAAs sloughed and egested is less than the total EHAAs available for both species, suggesting that the corals ingested, and possibly assimilated, the difference.

Maximum nitrogen assimilation efficiencies (AE_N) can be estimated by summing the nitrogen in the sloughed and egested sediments and comparing this to the nitrogen of the available sediments initially provided to the coral. Making the assumption that the difference is assimilated nitrogen, the corals studied here varied in their sediment nitrogen assimilation efficiencies (Fig. 6D). *S. siderea* assimilated approximately 31% of the nitrogen associated with these sediments, while *A. agaricites* and *P. astreoides* assimilated 55–74% of the nitrogen associated with the sediments. The amount of nitrogen ingested per coral tissue nitrogen content was highest for *A. agaricites* relative to the other two species (Fig. 6B) but was not significantly different among species. High organic carbon assimilation efficiencies were reported for corals feeding on suspended particulate matter (64–94%) for concentrations ranging from 1 to 30 mg l^{-1} (Anthony 1999a); these measurements were likely overestimates due to the specificity of the radioactive label ^{14}C to the live portion of the SPM. Our AE_N estimates were not made using labels specific to one portion of the sediments but were calculated from bulk nitrogen differences between available and coral-processed sediments (sloughed plus egested). We made no measurements of nitrogen loss to the water in dissolved forms, but the release of dissolved nitrogen by corals was assumed to be small (Szmant et al. 1990) due to the uptake of catabolic nitrogen products by the coral's symbiotic zooxanthellae. However, layering sediments over the coral's surface may have resulted in a stress that caused the coral to release some dissolved nitrogen. It certainly results in the production of mucus, which contains proteins and amino acids (Ducklow and Mitchell 1979; Means and Sigleo 1986; Meikle et al. 1988). Thus, our estimates of assimilation efficiency are likely overestimates and are presented here as maximum efficiencies. Additionally, the nitrogen assimilation estimates calculated here would be overestimates if the corals retained particles longer than the 10- to 12-h egestion period. Our preliminary experiments found this to be sufficient time for all visible particles to be released. Nevertheless, egestion of zooplankton can take longer (K.P. Sebens, personal observation); therefore, the assimilation efficiencies reported here must be considered carefully. It should also be noted that egested material may contain added mucus or bacteria that have populated these particles while in the coelenteron and thus the egested material may be high in percent nitrogen even when much of the ingested sediment nitrogen has been assimilated into coral tissue.

In addition to coral-mediated changes in sediment nitrogen, reef sediments are sites of active microbial communities that can remineralize particulate nitrogen (Williams et al. 1985; Capone et al. 1992). Capone et al. (1992) measured ammonification rates of 6 μmol N m^{-2} h^{-1} corresponding to 12% of the sediment particulate organic nitrogen (PON) pool per day. If such rates result from the transformation of PON, our estimates of coral N uptake through the ingestion of sediments are too high. However, the corals might still utilize this nitrogen. Schaffelke (1999) has shown that tropical species of *Sargassum* benefit from the particulate layer that covers the thalli; growth rates were up to 180% higher when particles were present. It is proposed that the epiphytic microbial community remineralizes the particulate nutrients and creates a nutrient-rich boundary layer that the alga can then utilize. The same can be hypothesized for the microbial community associated with the coral surface, as well as with the sediments that settle onto the coral.

Although available nitrogen forms a small proportion of the deposited total nitrogen pool relative to nitrogen in suspended particulate matter, the total amount of organic matter in surficial sediments can be greater than that in the water column (Nixon and Pilson 1983). Sediments, however, can contain high proportions of refractory nitrogen (Lopez and Leviton 1987), and detritus can have high concentrations of humic materials (Rice 1982) that may not be bioavailable to consumers. While much of the sedimentary organic matter is refractory, some is available for assimilation by macro-consumers ingesting the sediment particles. Normally, sediment feeders absorb at least 15% of the organic matter present in ingested sediments (Lopez and Levinton 1987), and ingested detritus can be an important source of energy and nutrients (Findlay and Tenore 1982). We show here that the processing and ingestion of benthic sediments by three species of corals alter the N and EHAA content of the sediments in a way that indicates the corals obtain nutrition from these sediments. Likewise, maximal assimilation efficiencies for sediment-associated nitrogen are relatively high. In conclusion, the ingestion of benthic sediments that become resuspended and land on coral surfaces may be an important source of nitrogen to some coral species.

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