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ABSTRACT

The sediments of the turbulent backreef area of Teague Bay, St. Croix, U.S.V.I., were examined for grain size, concentrations of inorganic nitrogen dissolved in sediment pore waters, Eh, organic carbon, rates of ammonium production, and fluxes of NH_4^+ and $NO_3^- + NO_2^-$ from the sediments. The sediments were mostly oxidized and characterized by low N concentrations (typically <5 μM) and low organic carbon (<0.6%). Local pockets of higher HH_4^+ concentrations were correlated with reducing sediments. The mean ammonification rate was 41.2 $\mu mol/l$ sediment/d. Ammonium fluxes were highly variable, predominantly positive, with a mean of 71 $\mu mol/m^2$-d. Nitrate + nitrite fluxes were more erratic and had a mean of -5 $\mu mol/m^2/h$. The ammonification rate was used to predict an ammonium flux which compared well with the mean measured flux. The occurrence of lower-than-predicted fluxes and of NH_4^+ concentrations up to 79 μM in reducing sediments could indicate that nitrification coupled to denitrification occurred in certain areas of the backreef and that nitrogen was lost from the ecosystem. The nitrogen requirements for two benthic macroalgae (Caulerpa sertulariodes, Acanthophora spicifera) found on the backreef were calculated from biomass, oxygen productivity, and C/N data. Comparison of the requirements to the NH_4^+ production rate and benthic N fluxes revealed that the algae are probably N-limited when growing on the backreef. A nitrogen fixation rate was measured for Caulerpa and its associated epibiota using an acetylene reduction technique. The range of rates measured was 102-329 ug N/g dry weight-h, which could supply a significant proportion of Caulerpa's N requirement, assuming an efficient mechanism exists for transferring the fixed N.

RESUME

Les sédiments de la zone agitée d'arrière récif de Teague Bay, situé en mode battu, St. Croix, U.S. Virgin Islands ont été étudiés pour déterminer la granulométrie, la concentration en azote dissous inorganique dans les eaux interstitielles, l'Eh, le carbone organique, le taux de production d'ammonium et le flux de NH_4^+ et $NO_3^- + NO_2^-$. Les sédiments sont pour la plupart oxydés et caractérisés par une faible concentration en azote (<5 μm) et en carbone organique (<0.6%). Les concentrations locales élevées en NH_4^+ sont corrélées aux sédiments réduits. Le taux moyen d'ammonification est de 41.2 $\mu mol/l$ de sédiment/jour. Les flux d'ammonium sont très variables, généralement positifs avec une moyenne de 71 $\mu mol/m^2/jour$. Les variations des flux de $NO_3- + NO_2-$ sont plus "erratiques" et ont une moyenne de -5 $\mu mol/m^2$-jour. Le taux d'ammonification a été utilisé pour prévoir le flux d'ammonium, celui-ci correspondant parfaitement à la valeur moyenne mesurée. L'existence de flux inférieurs à ceux prévus, et la présence de concentrations en NH_4^+ supérieures à 75 μM dans les sédiments réduits semble indiquer qu'il y a une nitrification couplée à une dénitrification dans certaines régions de l'arrière récif et qu'il y a une perte d'azote pour l'écosystème. Les besoins en azote pour deux macro-algues benthiques (Caulerpa sertulariodes, Acanthophora spicifera) de l'arrière récif ont été calculés à partir de la biomasse, de la production d'oxygène, et les données du rapport C/N. La comparaison des besoins en azote avec le taux de production de NH_4^+ ainsi que le flux d'azote depuis le sédiment révèlent que ces algues sont limitées en ressource azotée lorsqu'elles croissent sur l'arrière récif. Le taux de fixation d'azote par les Caulerpes et leurs épiphytes associés a été mesuré par la méthode de "l'acétylène". Les taux s'étendent de 102 à 329 ug N/g de poids sec/heure pouvant fournir une proportion significative des besoins en azote des Caulerpes, ce qui permet de suggérer qu'il existerait un mécanisme de transfert de l'azote fixe.

INTRODUCTION

Consideration of nitrogen regeneration is of vital importance to understanding coral reef ecosystem function. Our general objective was to investigate aspects of nitrogen cycling in coral reef sediments in a discrete area of reef in order to define spatial heterogeneity within the sediments and to determine if the area was representative of reef environments previously described. We chose to study the backreef sediments of Tague Bay barrier reef system, located on the northeast shore of St. Croix, U. S. Virgin Islands (64° 36'W; 17° 46'N). This reef system has been described previously (Adey, 1975, 1978, Adey and Burke, 1976). Here, the solid reef framework of Acropora palmata ends abruptly on the backreef giving way to a coral rubble pavement covered by a veneer of sediments and scattered coral heads. This pavement extends from the reef framework to 10-50 m into the lagoon. The demarcation between lagoon and backreef sediments is obvious: sediment depth abruptly increases, grain size is noticeably finer, seagrasses grow. Compared to the wealth of organisms associated with the solid reef framework, the backreef sediments appear biologically barren. Refuge from predators is scarce and the sediments, subjected to the turbulence of ocean swells breaking over the reef, are unstable. The physical regime may minimize deposition of organic matter from the reef into the sediments and this low input should be reflected in the occurrence of oxidized sediments, low concentrations of inorganic nitrogen in sediment pore waters, and low rates of nitrogen remineralization and fluxes from the sediment.

Our specific objectives were: (1) to determine the distribution of inorganic nitrogen in the sediments, (2) to measure directly rates of ammonium production and the release of nitrate+nitrite and ammonium from the sediments, and (3) to assess the N requirements for productivity of two common backreef macroalgae.

METHODS

In April 1982 and December 1983, two line transects situated within 20 m of each other were set across the bottom in 1.2 to 3m of water. The transects ran perpendicular to the landward edge of Tague Bay barrier reef. One transect (T1) was 59 m long and the other (T2) was 24 m long. Duplicate sampling stations were situated every 2m along the transects.

A wire probe was used to determine sediment depth. The top 10 cm or less of sediment were collected and analysed for grain-size (Folk, 1974). Sedimentary organic carbon (OC) was measured in the top 2 cm of sediment (Gaudette et al., 1974).

Miniature diffusion chambers (50 ml) were used to collect sediment pore waters in the top 5 cm of sediment. Chambers remained in the sediment for 11 days, time sufficient for external concentrations to equilibrate with internal ones (Williams et al., 1985). Ammonium (Koroleff, 1976) and nitrate+nitrite (Strickland and Parsons, 1972) concentrations, Eh, and

pH were determined on the collected pore waters.

Fluxes of ammonium and nitrate+nitrite from the sediment were measured under opaque PVC chambers. The chambers enclosed 0.049 m^2 of sediment and 8-11 l of overlying water and were stirred magnetically. Samples of water in the chambers were taken at 0, 2, 4, and 24 h and analysed for ammonium and nitrate+nitrite . Fluxes were calculated as the slope of the line of concentration versus time, using chamber volumes and areas for unit area conversion.

To determine ammonification (rate of ammonium production), sediment was collected to a maximum depth of 10 cm but average of <5 along T1 near the flux study sites. The collected sediment was placed under a N_2 atmosphere into 50 ml opaque glass test tubes which were then capped. Test tubes were incubated at in situ temperature (26°C) in the laboratory. Ammonium concentrations (n=6 tubes) in pore waters and adsorbed to sediments (Rosenfeld, 1979) were determined the initial day and subsequently 6 times during the next 5 weeks. Porosity was calculated using the weight loss of wet sediment upon drying at 90°C and assuming an average carbonate sediment density of 2.84 g/cm^3 (Milliman, 1974). The net rate of ammonium production is defined as the product of m times porosity, where m is the slope of the regression of pore water concentrations in the incubated sediments against time.

All Caulerpa sertularioides was collected from 90 one m^2 quadrats placed end to end over flat areas of the backreef sediments, after first assessing visually that it was the most common macroalga. In 20 of these quadrats all other macroalgae were also collected. Algae were separated, identified, dried at 90°C, and weighed. Individual plants of Acanthophora spicifera, another common alga, were collected for biomass determination.

Primary productivity of C. sertularioides and A. spicifera were measured using an O_2 light-dark bottle method (Strickland and Parsons, 1972). Obvious epiphytes were removed from the macroalgae. Incubations proceeded in situ from 1030-1230 h. Oxygen productivity was converted to carbon assuming a photosynthetic quotient of 1.2.

The N_2 fixation activity of C. sertularioides and its associated epibiota was assessed using an acetylene reduction technique (Burris, 1974) in a 3 h incubation, during which time the rate of C_2H_4 production was constant. Controls using seawater but no Caulerpa and seawater + Caulerpa but no acetylene were also run. Preliminary experiments determined that 15% C_2H_2 resulted in maximum production of C_2H_4. Ethylene produced was corrected for C_2H_2 solubility (Flett et al., 1976). A conversion of 4:1 mols $C_2H_2:N_2$ was used (Graham et al., 1980). Carbon and N content of the Caulerpa used in these experiments was analysed in a Perkin-Elmer 240B elemental analyzer.

RESULTS

Mean sediment depth was 8.9±8.4 cm with a maximum of 20 cm,

but <5 cm in the first 11 m next to the reef. Mean grain sizes ranged from 0.58-2.24 phi (coarse to fine sands) and became progressively finer away from the reef. Organic C had a mean value of 0.34% by weight and showed no correlation with grain size or distance from the reef (r<0.25) (Fig. 1).

Redox potential (Eh) of sediment pore waters ranged from -180 to +499 and pH from 7.3-8.1 (Fig. 2). These values fell into two basic groups where 67% of the sites were oxidized

with Eh (r=0.66). Ammonium and nitrate+nitrite were uncorrelated with each other and both were uncorrelated with OC. Sites within less than 30 cm of each other could vary by as much as 30 μM.

Fluxes were measured over sediments having low Eh and higher ammonium concentrations and visibly free of biota including algal mats. The changes in ammonium concentrations over time in the benthic flux chambers were typically linear (r>0.7). Ammonium fluxes from the
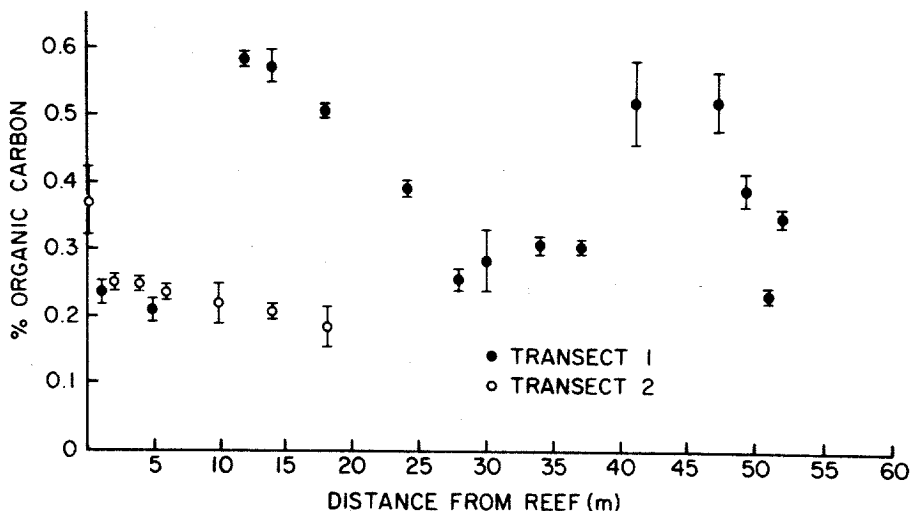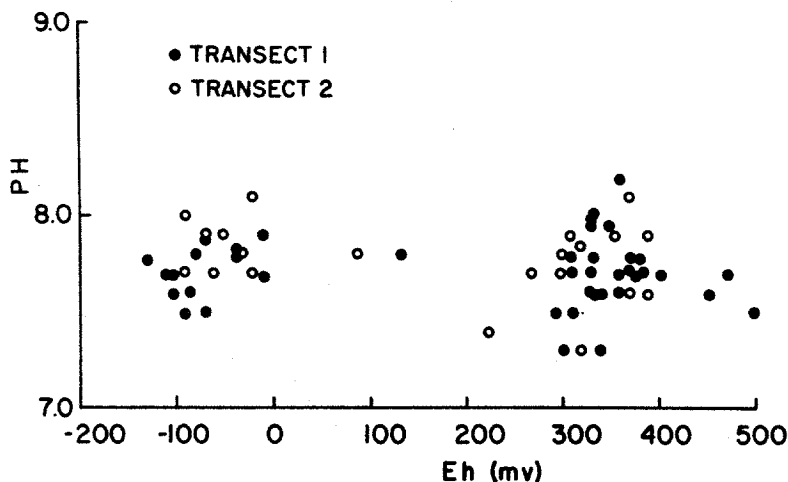

Fig. 1: Organic C. Mean ± 1 standard deviation

Fig. 2: Redox potential (Eh) and pH of pore waters

(Eh>+300) and the rest were reducing (Eh<0). Eh correlated poorly with grain size, OC, and position on the transects (r<0.15).

Concentrations of dissolved inorganic N were low; 83% of the nitrate+nitrite and 60% of the ammonium samples were less than 5μM. Mean concentrations were 2.78±2.58 μM nitrate-nitrite and 10.0±14.9 ammonium, ranging from 0-39.8 and 0-79 respectively (Fig. 3). Ammonium concentrations were correlated inversely

sediments were positive except for three cases where there was no net flux and two in which concentrations declined in the chambers. Ammonium fluxes were highly variable, ranging from -90 to 372 μmol N/m²/h with a mean of 71. Changes in nitrate+nitrite concentrations in the chambers were more erratic than ammonium In half of the 24 experiments, there were no clear linear changes in concentrations over time. Reporting only the measurements which

were linear, the mean nitrate+nitrite flux
was -5 μmol·N/m²/h, ranging from -131 to +141.
The fluxes represented net rates including
any uptake of N by benthic organisms. The
opaque chambers would minimize benthic uptake.
Obviously, negative fluxes indicated that benthic
uptake occurred.

The net rates of ammonium production

adsorption. Ammonium turnover times were
calculated from the ammonification rate,
porosity, and pore water ammonium concentrations,
assuming a steady state condition. Turnover
times ranged from 0-1.06 d with a mean of 0.14.
Sixty % of the sites had turnover times less
than 0.07 d.

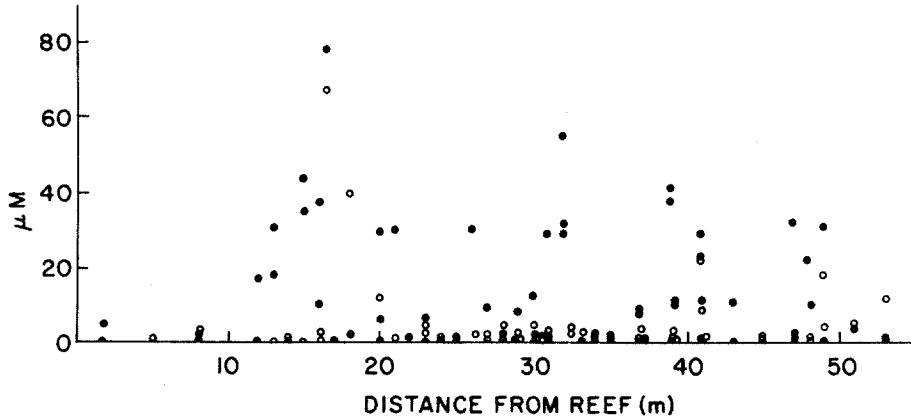Total macroalgal biomass averaged 391 g

Figure 3: Concentrations of N dissolved in pore waters. Ammonium = closed circles;
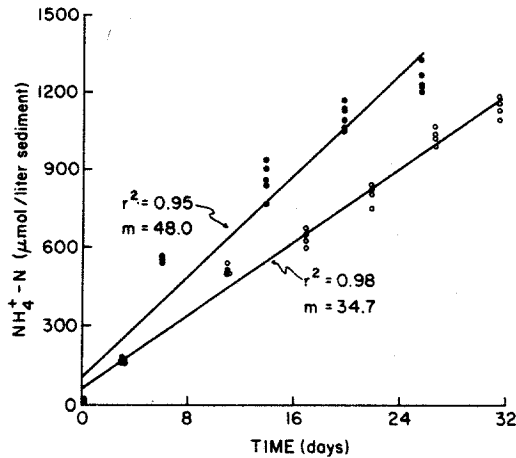nitrate+nitrite = open circles

Figure 4: Results of two independent ammonification experiments

determined in two separate experiments were
not significantly different, thus experiments
were combined to give a rate of 41.2 μmol/l
sediment/d (Fig. 4). At the low pore water
ammonium concentrations found in the backreef
sediments, ammonium adsorption to sediments
was negligible. The ammonification rate
therefore was uncorrected for ammonium

dry/m² of which Caulerpa sertulariodes comprised
0-75%. C. sertulariodes occurred in only 26%
of the 90m² sampled, averaging 164 g/m² (dry
weight). Other macroalgae occurring were
Laurencia poitei, Dictyopteris jamaicensis,
Jania sp., Dictyota dichotoma, and Penicillus
flabellum.

The gross productivities of C. sertulariodes

and _Acanthophora spicifera_ were 0.77 ± 0.52 mg C/g/h (dry weight) (n=28) and $3.94+2.04$ (n=3) respectively. Estimates of nitrogen fixation associated with _Caulerpa_ were 26.8 ± 20.5 μmol N/g/h (dry weight).

DISCUSSION

Tague Bay backreef sediments are a spatially heterogeneous environment of generally low dissolved nitrogen pools but contain local pockets of reducing sediments having higher ammonium concentrations. Although there was a wide range of pore water inorganic nitrogen concentrations, most sampling sites had concentrations <5 μM. Benthic N fluxes on the backreef fell into the lower range of values reported from temperate coastal areas (Klump and Martens, 1983). Ammonification rates also fell among the lower values measured in primarily silica-clastic anoxic sediments (Blackburn, 1979; Klump and Martens, 1983), or modelled for carbonate sediments (Hines and Lyons, 1982). Ammonification rates on the backreef may be limited by organic input to the sediment, given the physical regime of the area which would not promote deposition of organic matter and the low values of OC measured.

In roughly one-third of the sampling sites, local concentrations of >30 μM ammonium or nitrate+nitrite were found. Distribution of these pockets of higher nutrient concentrations was uncorrelated with grain size or OC but ammonium concentrations were inversely correlated with Eh. The occurrence of high ammonium/low Eh conditions is surprising in the turbulent physical regime of the backreef where sediment redistribution appears to occur frequently. There was no obvious relationship between the distribution of these areas and growth of sediment-stabilizing algae such as _Caulerpa_ and _Halimeda_. Low Eh and high ammonium concentrations did occur under a bloom of a Chrysophycean alga and often where filaments of _Crouania_ sp., a microscopic red alga, tended to bind sediment grains. These observations suggest that microalgae may stabilize the

sediments and allow formation of zones wherein the rate of diffusion or production of O_2 is lower than that of benthic community respiration. These areas may be zones of enhanced N remineralization because remineralization of N from organic matter proceeds most completely under anoxic conditions (Parnas, 1975). In addition, the potential for denitrification exists in these areas. The Eh-pH conditions are within environmental limits of denitrifying bacteria (Baas Becking _et al._, 1960). We estimated a N_2 flux from the sediments to see if the value would be a reasonable denitrification rate. We calculated a production-predicted flux from our ammonification rate assuming that at steady state, ammonium production equals the amount of N diffusing from the sediments (Aller, 1980) and using a production zone of 5 cm. Because the ammonification experiment proceeded under anoxia, remineralization would proceed most completely and thus the predicted flux rate would represent a total potential flux. The predicted N_2 flux, then, is equal to the total predicted N flux minus the measured ammonium plus nitrate+nitrite fluxes. The range in expected N_2 fluxes thus calculated was $30-152$ μmol/m^2/h, which falls among reported rates for denitrification (Klump and Martens, 1983). We therefore suggest a loss of N from this reef ecosystem may occur. Direct measurement of denitrification should become a research priority because conservation of N in coral reef systems is suspected to be critical to the function of the ecosystem.

Finally, we investigated the relative value of the various sources of N we measured for the productivity of two common algae growing on the backreef (Table 1). We calculated a N requirement of 192 nmol/plant/h for _Caulerpa sertulariodes_ using its mean productivity, a mean C/N of 17.71, and its mean individual biomass. The mean N_2 fixation rate was far in excess of this requirement, assuming a mechanism exists for transfer of fixed N to the macrophyte. For comparison with other available sources of N, it was necessary to estimate the area of sediment occupied by a

Table 1. Nitrogen requirements and sources for 2 benthic macroalgae. Dry weights used

REQUIREMENTS	SOURCES
Caulerpa sertulariodes	
Productivity: 0.77 mg C/g/h	N_2 Fixation: 1.66 μmol N/plant/h
C/N: 17.7	Benthic N Flux: 213 nmol/plant/h
Mean Plant Biomass: 61.9 mg	Sediment NH_4^+ Production: 300 nmol/plant/h
N Requirement: 192 nmol/plant/h	
Acanthophora spicifera	
Productivity: 3.94 mgC/g/h	
C/N: 16.5	Benthic N Flux: 114 nmol/plant/h
Mean Plant Biomass: 363.4 mg	Water Column Flow: 1.5 μmol/plant/h
N Requirement: 6.2 μmol/plant/h	

typical plant by using horizontal projections of mean plant length and width, or cm^2. The mean ammonium flux from this area would be 213 nmol/h. Caulerpa can also take up sediment ammonium via its rhizoids (Williams, 1984). This ability enables the plant to access the 300 nmol N/h produced as ammonium in the rhizosphere of a typical plant (sediment depth of rhizosphere = 5 cm). These comparisons suggest there is sufficient nitrogen to support an even higher productivity by Caulerpa and that light or some other factor is limiting to its productivity.

We calculated a N requirement of 6.2 µmol/plant/h for Acanthophora spicifera using its mean productivity, a C/N of 16.5 (Atkinson and Smith, 1983), and the mean individual biomass. The projected horizontal area covered by an average plant was estimated to be 16 cm^2. The mean benthic N flux over this area would be 114 nmol/h, which is only 2% of the N requirement. Unlike Caulerpa, Acanthophora has no rhizoids for uptake of sediment nutrients and thus is probably restricted to utilising N in the water column. An average flow rate of 5.1 cm/s and maximum water concentrations of 0.1 µM-N would deliver roughly 1.5 µmol/h across a typical plant. While we did not measure the potential for N_2 fixation activity associated with the alga, our other calculations suggest that Acanthophora productivity may be N-limited and that benthic N regeneration is unlikely to be significant in terms of the plant's N requirements. In nature, therefore, the productivity should be directly proportional to the flow rate.

In summary, the backreef sediment environment of Tague Bay is in general one of relatively low inorganic N concentrations, but having localized areas of higher concentrations. Rates of N regeneration were low, even in the sediments having low Eh and higher ammonium concentrations. The often turbulent physical regime of the area probably contributes to this characterization and may result in the very low macroalgal biomass found, either directly or indirectly by causing nutrient limitation. Sediment N regeneration can provide a significant portion of the N requirements of rhizoid-bearing algae of low productivity, such as Caulerpa, and probably also of microscopic algae intimately associated with sediment grains. For other benthic macroalgae, sediment nitrogen sources are probably insignificant.

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