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REPORT

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Nutrient uptake by coral-reef microatolls

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Abstract We measured rates of ammonium and phosphate uptake into 12 microatolls at One Tree reef lagoon, Australia, on 14 occasions over a range of seasonal and meteorological conditions from 1993 to 1995. Nine of the microatolls were spiked with ammonia and/or phosphate every low tide (2.5–4 h) during low- (15-month) and high- (13-month) loading periods. The remaining three microatolls that were not spiked with nutrient served as reference conditions. Ammonium concentrations were elevated from an average background of 0.7 to 11 μM NH_4 during the low-loading period and 36 μM NH_4 during the high-loading period, resulting in a loading to the benthos of 3.5 and 18 mmol NH_4 m^{-2} low $tide^{-1}$. Phosphate concentrations were elevated from an average background of 0.2 to 2.3 and 5.1 μM PO_4 during low- and high-loading periods, respectively, resulting in a loading of 0.66 and 3.9 mmol PO_4 m^{-2} low $tide^{-1}$. Ammonium and phosphate concentrations decreased significantly over low-tides, and uptake rates were proportional to concentrations (first-order). The average uptake-rate constant, S ($m\ s^{-1}$), for ammonium and phosphate did not differ between the two loading periods but was highly variable. Averaged over both loading periods, S for ammonium was $129 \pm 74 \times 10^{-6}$ $m\ s^{-1}$ and S for phosphate was $67 \pm 39 \times 10^{-6}$ $m\ s^{-1}$. At background nutrient concentrations, estimated nutrient-uptake rates were 7.8 mmol NH_4 m^{-2} day^{-1} and 1.2 mmol PO_4 m^{-2} day^{-1}. Excretion rates—calculated from the mean difference in uptake rates measured in reference and nutrient-enriched microatolls—were estimated to be 4.3 mmol NH_4 m^{-2} day^{-1} and 0.9 mmol PO_4 m^{-2} day^{-1}. We reason and suggest that nutrient uptake rates in these microatolls were close to mass-transfer limited rates. We conclude that nutrient uptake into coral reefs can behighly dynamic, varying 10-fold spatially and temporally.

Keywords Coral reef · Nutrient uptake · Mass transfer · ENCORE · Ammonium · Phosphate

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Introduction

Uptake rates of inorganic nutrients (NH_4, PO_4, NO_3, SiO_3) into coral reef communities have been difficult to measure in situ. Earlier workers from the 1920s to 1980s hypothesized rapid net changes in nutrient concentrations across coral-reef flats, but discovered that nutrient concentrations remain nearly constant. This result led to suggestions of ''tight'' and ''rapid' recycling of nutrients through symbiotic relationships (Johannes and Project Symbiosis Team 1972), as well as rapid recycling of nutrients between heterotrophs and autotrophs through the water column [Pilson and Betzer (1973); see Atkinson (1988) for a review].

During the 1980s, field and laboratory experiments revealed that maximal rates of phosphate uptake were relatively slow compared to advective fluxes; typical reefs flats could only remove very small percentages of nutrients flowing across them [$< 5\%$; Atkinson (1992)]. This fact indicated that recycling of nutrients through the water column could only occur on scales of hundreds of meters and certainly was not rapid. It became evident that nutrient concentrations do not change across most reefs, simply because reefs cannot remove those nutrients fast enough.

To observe nutrient uptake in the field at ambient concentrations, water must reside over a shallow (~1-m) reef community for at least several hours. The water must be shallow so that uptake results in measurable

changes in nutrient concentrations within relatively short periods of time. It is unusual to find shallow, ponded water over typical high-biomass reef communities, so it has been difficult to make measurements of nutrient uptake under natural conditions.

In the 1990s, nutrient-uptake experiments were performed in flumes to determine the rate-limiting step for nutrient uptake into coral-reef benthos. Nutrient-uptake rates into experimental assemblages of coral-reef benthos are limited by diffusion through concentration-depleted boundary layers adjacent to these benthic surfaces; that is, nutrient uptake is mass-transfer limited (Atkinson and Bilger 1992; Baird and Atkinson 1997).

Nutrient-uptake rates for these experimental assemblages are positively correlated to nutrient concentration and water velocity, and can be quantified using a relatively simple equation:

$$m = St \times U_b \times [C_b - C_o],$$

where m is the nutrient-uptake rate in mass per area per time, St is a dimensionless rate constant called the Stanton number, U_b is water velocity, and C_b is the concentration in the bulk water. C_o is the idealized average nutrient concentration at the collective surfaces of the organisms; C_o is assumed to be negligible under strict definition of mass-transfer limitation, but is probably in most cases some significant percentage of C_b (Bilger and Atkinson 1995).

The Stanton number, St, is a somewhat confusing constant for non-engineers; it represents a dimensionless ratio of uptake into a benthic surface compared to the rate of advection of a substance past the surface. St is typically a very small number—around 10^{-4} for shallow coral reefs—and quantifies the mass transfer between the benthos and the overlying water flow. St is strongly a function of the form-drag and skin-friction of the benthic community, and can be parameterized by a friction factor (c_f), which is a measure of the energy dissipated by benthic surface friction under steady flows (Bilger and Atkinson 1992; Kays and Crawford 1993). Thus, ''rough'' benthic surfaces with highly branched, rigid organisms, such as coral, dissipate more energy than ''smooth'' surfaces, giving higher St and higher uptake rates (Baird and Atkinson 1997; Thomas and Atkinson 1997).

The product of St and U_b is expressed as the uptake-rate constant, S, which can either be derived from engineering literature on heat and mass transfer, or measured directly. S for flume studies on coral-reef assemblages with moderate water velocities (4–39 cm s^{-1}) range approximately an order of magnitude, between 20 and 200×10^{-6} m s^{-1} or between ~2 and 20 m day^{-1} (Bilger and Atkinson 1995).

There are, however, no published data sets of S derived from in situ measurements of nutrient uptake [except for a respiration-normalized constant of Atkinson (1987)]. Two obvious questions arise: (1) are uptake rate constants, S, for field studies similar to flume studies, and (2) are these uptake constants variable, as mass-transfer limitation would imply?

The ENCORE (Enrichment of Nutrients on a Coral Reef Experiment) project included measurements of nutrient uptake into 12 coral microatolls within One Tree reef lagoon, Australia, providing a comprehensive database to determine nutrient-uptake rates into natural coral-reef communities. This paper is the first study to report values of S for nutrient uptake in the field, and compare those constants with laboratory and flume experiments. Measurements of physical parameters to calculate mass-transfer limited rates, such as water velocity and surface friction, were not part of the ENCORE study; thus we cannot in this paper prove whether the microatolls are mass-transfer limited.

Methods

Experimental design

The detailed design of ENCORE is given in Larkum and Steven (1994). Briefly, 12 microatolls of similar size, volume, and benthic composition were used as natural, replicated subsystems (Fig. 1 and Table 1). The microatolls are all located in the northern end of the One Tree reef lagoon (23°30′S, 152°06′E) and are grouped in three clusters, demarcated by the surrounding lagoon morphology. During low tide, the perimeter of coral isolates a shallow pool (< 1 m) inside each microatoll for 2.5–4 h from the surrounding lagoon, thus forming clearly defined boundaries. Twice daily, during low tide, each of the 12 microatolls received one of four nutrient treatments: either the addition of NH_4 (+N), PO_4 (+P), NH_4 and PO_4 combined (+N+P), or no nutrient addition (reference, –N–P). The nine nutrient-enriched microatolls were fertilized using automated ''nutrient-dispensing units'' that discharged concentrated nutrients through multiple pipe outlets distributed through the microatolls (Koop et al. 2001). Thus, organisms growing naturally, or transplanted into the microatoll basins, were maintained in natural environmental conditions, but subjected to nutrient-enriched waters during low-tide periods.

The 28-month experiment was divided into a low-loading period (LL, September 1993–December 1994), followed by a high-loading period (HL, January 1995–February 1996). Throughout the low-loading period, concentrated NH_4 (as NH_4Cl) and PO_4 (as KH_2PO_4) were added every low tide as a single pulse to the water body within the microatoll basin to achieve initial concentrations of 10 μM NH_4 and 2 μM PO_4. During the high-loading period, nutrients were added three times every low tide (~37 min apart) to sustain elevated concentrations of 20 μM NH_4 and 4 μM PO_4.

Microatoll characteristics

The basins of the microatolls vary from oblong to elliptical, are often convoluted, and have volumes of 27–323 m^3 at low tide (Table 1, Fig. 1). The southeast walls of the microatolls are well developed (1–2 m wide), while the northerly walls can be thin and uneven. The height of the inside wall of the microatolls varies from 0.5–0.9 m, with the deeper microatolls occurring in the northwest sector of One Tree reef lagoon (6, 11, 12). The planar surface area of the microatoll basins are 107–829 m^2 and the volume-to-area ratios of the microatolls vary from 0.30–0.64 (Table 1).

Most of the coral and algal biota are distributed along the inside walls. Mean cover of scleractinian corals ranges from 6–26%, with greater biomass occurring in the deeper microatolls. The most abundant coral colonies are encrusting (*Porites lichen*, *P. murrayensis*, *Goniopora tenuidens*, *Favites abdita*, *Platygyra sinensis*, and *Goniastrea retiformis*) and small-branching (*Acropora bushyensis*, *A. palifera*, *Pocillopora damicornis*, *Stylophora pistillata*, and *Seriatopora hystrix*) species. Stands of staghorn-branching corals

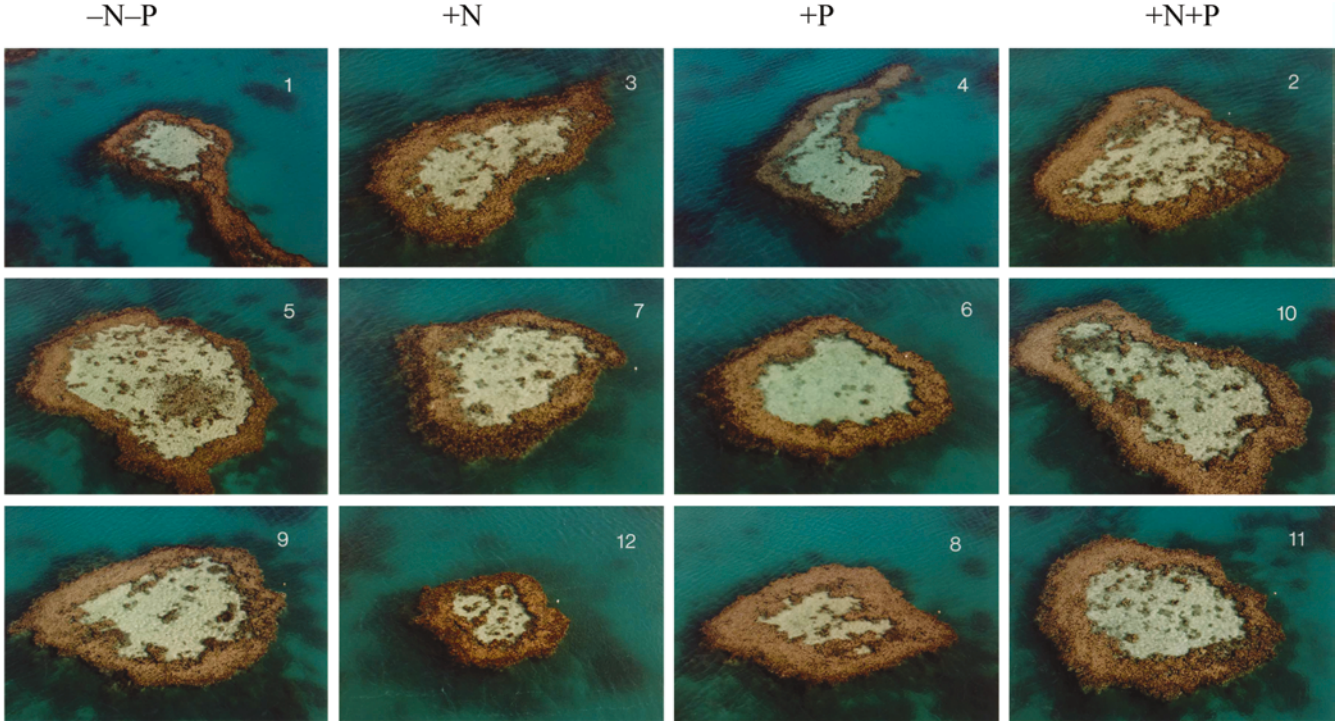

Fig. 1 Oblique aerial photographs showing overall morphology of the 12 microatolls and ordered vertically by nutrient treatment. Refer to Table 1 for dimensions

(*A. aspera*, *A. nobilis*, and *A. longiciathus*) are common in the deeper microatolls where they proliferate along the southern walls. Coralline algae (*Lithophyllum* spp. and *Porolithon* spp.) cover up to 12% of the walls. Macroalgae, mainly *Laurencia* spp., *Chlorodesmis fastigiata*, *Turbinaria ornata*, and *Caulerpa* spp., are seasonal, but low in cover (~2%). The epilithic algae community covers all other substrate.

The bottoms of the microatolls are predominantly sand (40–60%), with small outcrops of dead coral covered in biota. Live coral cover is 5–18% and is comprised mainly of stands of branching corals such as *Acropora grandis* and *A. pulchra*. Also distributed on the bottom of the microatolls during the experiment were plastic racks holding a variety of coral, soft coral, and algae species transplanted from adjacent areas [see Larkum and Steven (1994) for project details].

Wind is the primary force controlling water motion within the microatolls, once they become isolated from the lagoon. Winds, originating from the southeast and northwest varied from 0.5–7.2 m s^{-1} during the study (Table 2).

Sampling nutrient concentrations

To measure rates of nutrient depletion, microatoll waters were sampled 4–11 times during each low-tide period (Table 2). Replicate water samples were taken from three locations within each microatoll by drawing water along PVC pipes (14 mm i.d.) using a bilge pump. The inlets of the pipes were mounted on poles ~0.2 m above the substratum to minimize sediment resuspension. To ensure a representative sample, 5–10 L was flushed through each pipe before retaining a final volume of 5 L. Sub-samples for nutrient analysis were taken with a 100-mL syringe, and filtered through 0.45 μm minisart filters into bottles. Bottles were rinsed with filtrate, before retaining 50 mL for analysis. Wind direction and speed (m s^{-1}), cloud cover (oktas), and sea surface temperature (°C) were recorded at each sampling period.

Table 1 Microatoll dimensions: depth, area, and volume of the microatolls were measured using a TOPCON Electron Distance Instrument

Treatment	Microatoll no.	Depth (m)	Microatoll basin area			Volume (m^3)	Vol: A_{bottom} (m)
			Wall (m^2)	Bottom	Total		
–N–P	1	0.76	37	184	221	60	0.33
	5	0.50	50	779	829	323	0.41
	9	0.58	30	209	239	76	0.37
+N	3	0.60	27	166	193	61	0.36
	7	0.58	28	185	213	74	0.40
	12	0.80	29	107	136	46	0.43
+P	4	0.65	45	381	426	135	0.36
	6	0.85	47	238	284	152	0.64
	8	0.51	17	90	107	27	0.30
+N+P	2	0.54	31	255	286	93	0.36
	10	0.67	39	270	209	130	0.48
	11	0.75	35	174	136	90	0.52

On 9 days during the low-loading period, nutrient samples in each of the 12 microatolls were collected immediately after the addition of nutrients and at hourly intervals thereafter, until the tide rose and inundated the microatolls with lagoonal water (see Table 2 for sampling times and conditions). Samples for nutrient analysis were stored on ice and returned to the laboratory where they were analyzed immediately for NH_4 and PO_4 using standard spectrophotometric techniques.

On 5 days during high loading (Table 2), nutrient samples were collected at ~15-min intervals, prior to and following the three nutrient additions. With increased sampling frequency, it was logistically possible to only sample four to six microatolls on the same low tide. Samples were analyzed within 2 weeks for NH_4, NO_3, and PO_4 on a segmented flow autoanalyzer at the Queensland Department of Health, Brisbane.

Calculations

For each sampling period, the mean ($n = 3$) concentration of NH_4 and PO_4 in each microatoll was plotted against time, t. The uptake-rate constant, S, was calculated as the slope of ln N or P vs. t, multiplied by the microatoll volume (V) to area (A) ratio. This approach assumes the excretion rate during the uptake period is constant. Nutrient loading (L) per low tide was estimated as the amount of nutrient added to the background nutrient concentration, minus the final nutrient concentration at the end of low tide, multiplied by the V to A ratio (Table 3). We did not use initial concentrations in the above nutrient-loading calculation because the error due to initial patchiness is variable and difficult to estimate.

Results

Ammonium

Ammonium loading into reference (–N–P) microatolls during the 2.5- to 4-h low-tide periods averaged (±SD) 0.18 ± 0.06 mmol N m^{-2}. In N-enriched (+N, +N+P) microatolls, NH_4 loading averaged 3.6 ± 0.55 mmol N m^{-2} in low loading, and 17.6 ± 3.2 mmol N m^{-2} in high loading (Table 3). NH_4 concentrations in –N–P microatolls significantly decreased ($F_{1,80} = 31$, $p < 0.0001$) from 1.1 ± 0.2 to 0.4 ± 0.4 μM N and averaged 0.7 ± 0.7 μM N (Table 3, Fig. 2A). NH_4 concentrations

Table 2 Microatoll sampling dates, times, and prevailing weather conditions. Wind speed and direction were recorded with a hand-held anemometer. Sea surface temperatures are the mean daily temperatures recorded by in-situ dataloggers in each microatoll

	Date	Cumulative nutrient loading days	Microatolls sampled	No. of samples	Sample time	Wind speed (m s^{-1})	Wind direction	Temperature (°C)
Low loading	25/09/93	24	1–12	4	1000–1425	3.4	SE	22.2
	27/09/93	26	1–12	4	1145–1540	7.2	SE	21.8
	23/11/93	83	1–12	4	1048–1347	3.1	N	24.1
	24/11/93	84	1–12	4	1215–1425	6.5	N	24.6
	20/06/94	292	1–12	4	1206–1438	3.6	SE	21.8
	21/06/94	293	1–12	4	1230–1500	5.9	SE	21.4
	22/06/94	294	1–12	4	1300–1545	3.4	SE	21.9
	17/09/94	381	1–12	4	1145–1417	0.5	NW	24.3
	19/09/94	383	1–12	4	1230–1500	5.4	NW	23.4
High loading	25/03/95	570	7, 8, 9, 10	10	1040–1336	1.5	SE	28.1
	27/03/95	572	7, 9, 10	10	1300–1530	2.9	SE	27.4
	22/07/95	689	1–6	11	0955–1415	1.8	SE	20.0
	23/07/95	690	1–6	11	1035–1428	5.9	NW	20.9
	20/10/95	779	6, 10–12	9	1130–1435	6.5	SE	22.9

Table 3 Summary statistics of NH_4 (*N*) and PO_4 (*P*) concentrations, uptake-rate constants (*S*), and loading (*L*) in reference (*–N–P*), low-loading (*LL*), and high-loading (*HL*) phases. In LL, initial concentrations were measured immediately after nutrient additions, whereas in HL, initial concentrations were measured after the third nutrient addition

	Concentration								S			L		
	Initial			Final			Mean							
	n	Mean ±SD	Range	*n*	Mean ±SD	Range	*n*	Mean ±SD	*n*	Mean ±SD	Range	*n*	Mean ±SD	Range
	(mmol m^{-3})								(10^{-6} m s^{-1})			(mmol m^{-2} low $tide^{-1}$)		
NH_4														
–N–P	54	1.1 ± 0.18	0.2–4.0	48	0.4 ± 0.4	0.1–1.6	214	0.7 ± 0.7	41	60 ± 29	12–130	33	0.18 ± 0.06	0.06–0.33
+NLL	54	10.7 ± 5.0	2.0–19.8	52	0.9 ± 0.8	0.1–3.6	216	4.4 ± 4.9	47	131 ± 69	32–306	47	3.57 ± 0.55	2.47–4.56
+NHL	12	36.2 ± 21.9	8.5–80.3	12	11.3 ± 10.2	1.0–30.3	128	18.6 ± 19.4	16	125 ± 88	26–352	11	17.64 ± 3.16	12.75–22.66
PO_4														
–N–P	54	0.2 ± 0.1	0.1–0.4	54	0.2 ± 0.1	0.1–0.3	216	0.2 ± 0.1	30	13 ± 5	4–23	27	0.02 ± 0.01	0.00–0.04
+PLL	47	2.3 ± 1.0	0.9–4.5	54	0.5 ± 0.3	0.1–1.5	216	1.0 ± 0.9	47	63 ± 36	9–214	45	0.66 ± 0.20	0.23–1.10
+PHL	12	5.1 ± 2.8	1.1–12.0	12	2.4 ± 1.6	0.2–4.7	131	3.3 ± 2.6	16	80 ± 46	25–153	10	3.86 ± 0.90	2.38–5.74

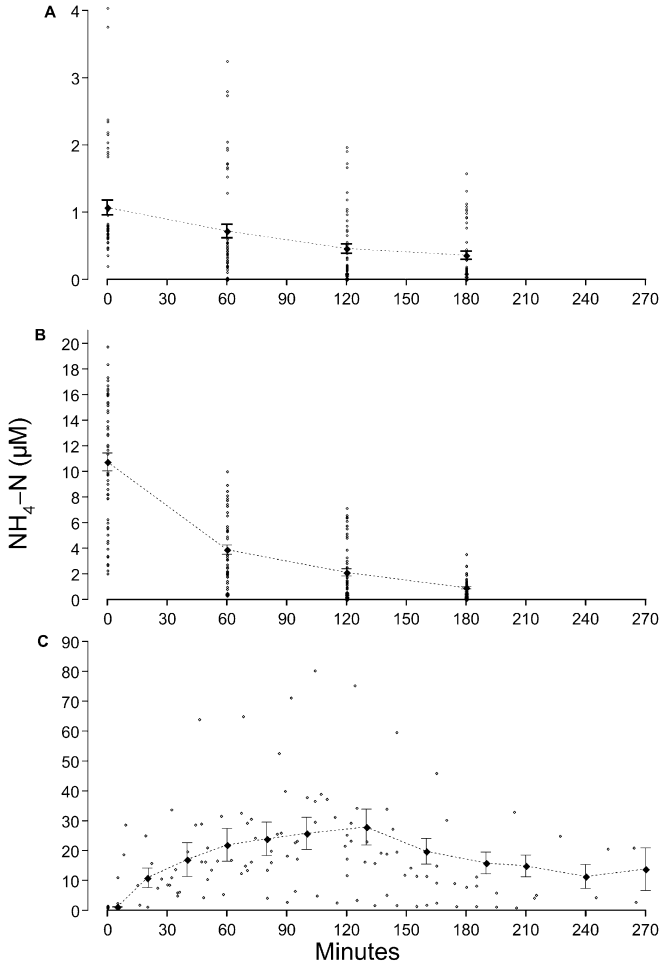

Fig. 2 NH_4 concentrations measured in –N–P (**A**) and N-enriched microatolls during low (**B**) and high (**C**) loading. Data are the composite of nine sampling dates in low loading and five in high loading (Table 2). The mean (±SE) of these data are plotted as *diamonds*. During low loading, nutrients were added every low tide as a single pulse to the water body within the microatoll basin; during high loading, nutrients were added thrice at ~37-min intervals

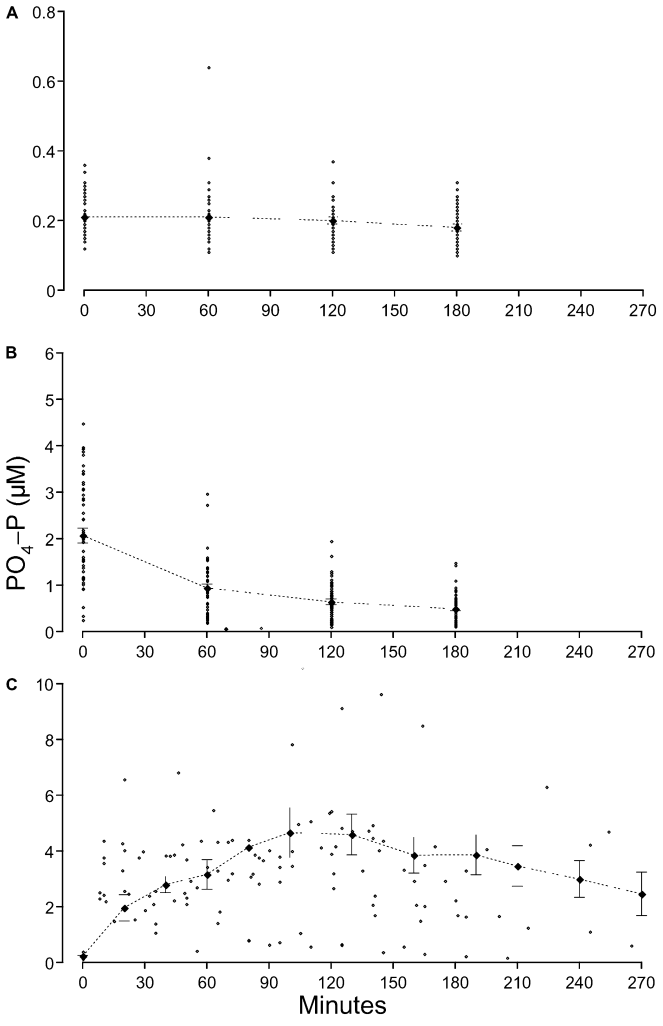

Fig. 3 PO_4 concentrations measured in –N–P (**A**) and P-enriched microatolls during low (**B**) and high (**C**) loading. Data are the composite of nine sampling dates in low loading and five in high loading (Table 2). The mean (± SE) of these data are plotted as *diamonds*. During low loading, nutrients were added every low tide as a single pulse to the water body within the microatoll basin; during high loading, nutrients were added thrice at ~37-min intervals

in the N-enriched microatolls during low loading significantly decreased ($F_{1,92} = 246$, $p < 0.0001$) from 10.7 ± 5.0 to 0.9 ± 0.8 μM N and averaged 4.4 μM N (Table 3, Fig. 2B); similarly, during the high-loading period, NH_4 also significantly decreased ($F_{1,31} = 7.3$, $p = 0.011$) from 36.2 ± 21.9 to 11.3 ± 10.2 μM N and averaged 18.6 μM N (Table 3, Fig. 2C). In all cases NH_4 was removed from the water column and taken up by the benthos. Ammonium uptake-rate constants (S_N) averaged (±SD) $60 \pm 29 \times 10^{-6}$ m s^{-1} for –N–P microatolls, $131 \pm 69 \times 10^{-6}$ m s^{-1} for low-loading conditions, and $125 \pm 88 \times 10^{-6}$ m s^{-1} for high-loading conditions (Table 3). S_N of individual microatolls did not vary significantly between low and high loading (t-tests, $p = 0.1702$–0.9183), giving an overall mean S_N of 129×10^{-6} m s^{-1}. Thus, NH_4 uptake, m, calculated at background concentrations (0.7 μM N) was 7.8 mmol m^{-2} day^{-1}.

Phosphate

Phosphate loading into microatolls over low tide averaged (±SD) 0.017 ± 0.009 mmol m^{-2} in –N–P, 0.66 ± 0.20 mmol m^{-2} in low loading, and 3.9 ± 0.90 mmol m^{-2} in high loading. PO_4 concentrations in –N–P microatolls showed no consistent trends and averaged 0.20 ± 0.1 μM P (Table 3, Fig. 3A). Phosphate concentrations in P-enriched (+P, +N+P) microatolls significantly decreased ($F_{1,88} = 98$, $p < 0.0001$) during the low-load period from 2.3 ± 1.0 to 0.5 ± 0.3 μM (Table 3, Fig. 3B), whereas during high loading, phosphate concentrations rose with each successive nutrient addition, reaching an average maximum concentration of 5.1 ± 2.8 μM P, and subsequently decreasing significantly ($F_{1,81} = 65$, $p < 0.0001$) to an

average of 2.4 ± 1.6 μM P (Table 3, Fig. 3C). Phosphate uptake-rate constants (S_P) averaged $13 \pm 5 \times 10^{-6}$ m s^{-1} for –N–P microatolls, and for P-enriched microatolls, $63 \pm 36 \times 10^{-6}$ m s^{-1} for low loading and $80 \pm 46 \times 10^{-6}$ m s^{-1} for high loading (Table 3). S_P of individual microatolls did not vary significantly between low and high loading (t-tests, $p = 0.2985$–0.9977), and combined had a mean S_P of 67×10^{-6} m s^{-1}. The average phosphate uptake at background concentrations (0.2 μM P) was 1.2 mmol m^{-2} day^{-1}.

Discussion

These results clearly show that nutrients were removed from the water in the microatolls. Other studies demonstrate that biological uptake and assimilation were the principal fate of these nutrients (Steven 2000). The reported uptake rate constants, S, for reference (–N–P) microatolls are much lower than S for low- and high-loading periods. Assuming the lowered net uptake is simply a result of uptake and excretion being closely balanced at low concentration, an excretion rate of the benthic communities in the microatolls can be calculated by equating net uptake rate in the –N–P patch-reefs to gross uptake less excretion:

$$S_R \cdot [NH_4 \text{ or } PO_4]_R = S_L \cdot [NH_4 \text{ or } PO_4]_R - Excretion\ Rate$$

where the subscripts $_R$ and $_L$ refer to data from reference and nutrient-loaded microatolls, respectively. For these estimates, we assume that the excretion rate is constant during the low-tide period; neither uptake kinetics nor internal nutrient pools are changing significantly during this brief period, so we believe this assumption is warranted and consistent with previous studies. Using data from Table 3, daily excretion rates are estimated to be 4.3 mmol NH_4 m^{-2} day^{-1} and 0.86 mmol PO_4 m^{-2} day^{-1}.

Measured nutrient concentrations and uptake-rate constants were highly variable, both between days and among microatolls (Fig. 4, Table 3). Variation among microatolls resulted from intrinsic differences in their physical dimensions (i.e., surface area, volume) and construction (i.e., "leakiness"), biological composition, and local hydrodynamic conditions. In particular, microatoll 11 had substantially higher S_N and S_P than other microatolls (Fig. 4).

On any one day, uptake rates were more similar among the 12 microatolls than rates measured in the same microatoll on different days. S_N of N-enriched microatolls varied significantly between days ($F_{13,44} = 5.88$, $p < 0.0001$), but not among microatolls on the same day ($F_{4,45} = 0.98$, $p = 0.580$). Similarly, S_P of P-enriched microatolls varied more among days ($F_{13,40} = 1.89$, $p = 0.067$) than among microatolls on the same day ($F_{4,40} = 0.66$, $p = 0.780$).

A principal source of this daily variation was, we believe, due to differences in water velocities and mixing characteristics within the microatolls; these conditions were driven primarily by the prevailing wind speed and direction. On very still days (< 1.5 m s^{-1} wind speed), nutrient concentrations were initially patchy (i.e., high initial replicate variability), often exceeded desired concentrations, and had enhanced uptake rates. At wind speeds greater than 7 m s^{-1}, surface water was sometimes driven over the northerly rim, or flushed through the porous matrix of the microatolls, resulting in low initial concentrations. However, on moderately windy days (1.5–6.5 m s^{-1} wind speed), nutrients mixed quickly within the water volume, resulting in excellent first-order regression fits of the data (note curvature in Fig. 2B,C and Fig. 3B,C; mean $R^2_{adj} = 0.92$, $n = 209$). Under these conditions, S_N varied significantly with wind speed (Fig. 5A; $R^2_{adj} = 0.853$, $p < 0.0001$, $n = 31$), but no such relationship could be established for S_P (Fig. 5B; $R^2_{adj} = 0.058$, $p < 0.1137$, $n = 28$). Measured S_N significantly correlated ($r = 0.919$, $n = 31$, $p < 0.0001$) with S_N predicted from estimates of water velocity (2% of wind speed) and roughness [using previous published mass-transfer correlations, Thomas and Atkinson (1997)]. Measured and predicted S_P was not correlated ($r = 0.3101$, $n = 28$, $p < 0.1083$).

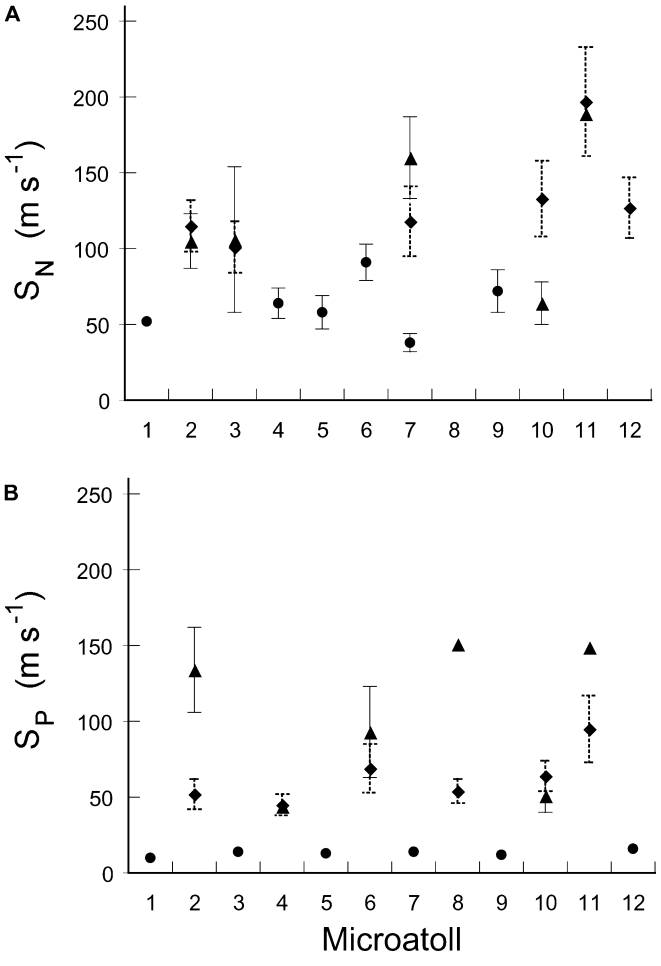

Fig. 4 Average (± SE) microatoll uptake-rate constants S_N (**A**) and S_P (**B**) measured under reference (*black circles*), low-loading (*diamonds*), and high-loading (*triangles*) conditions

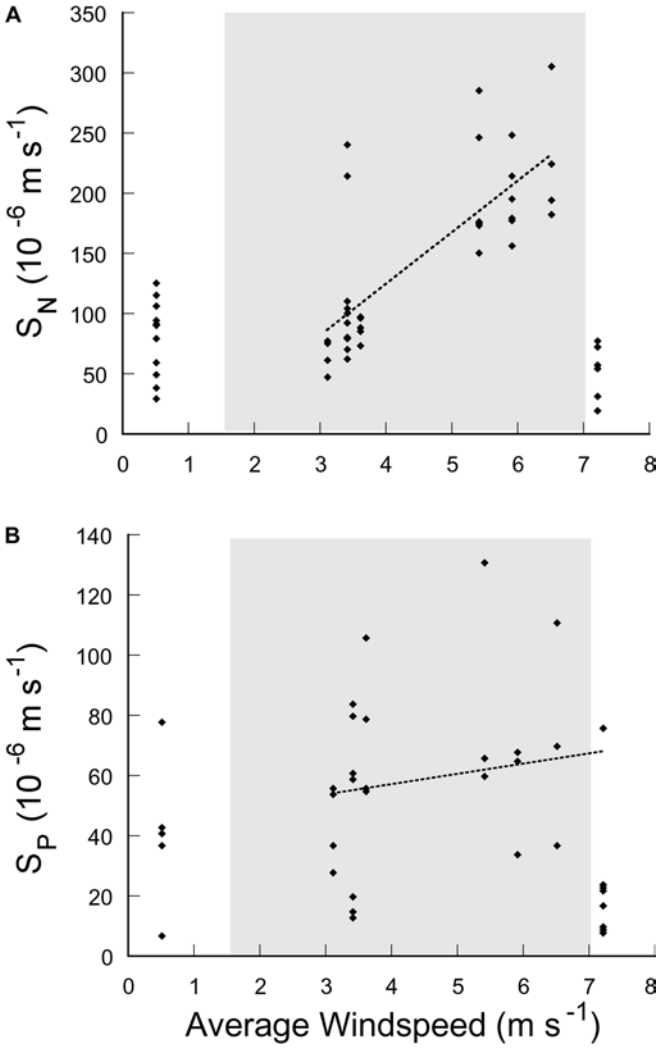

Fig. 5 S_N (**A**) and S_P (**B**) of nutrient-enriched microatolls during low loading plotted against average wind speed. Data within the range of moderate wind speeds (1.5–6.5 m s^{-1}) are shown in the *shaded box* with lines of best fit: $S_N = 75.21 + 47.61X$, $R^2_{adj} = 0.853$, $n = 31$, $p < 0.0001$; $S_P = 32.38 + 6.71X$, $R^2_{adj} = 0.058$, $n = 28$, $p < 0.1137$

S for experimental coral-reef communities in flumes range 26–147×10^{-6} m s^{-1} for NH_4 and 5–60×10^{-6} m s^{-1} for PO_4, over a range of water velocities from 4–39 cm s^{-1} (Bilger and Atkinson 1995). S for this study (Table 3) compares very well to flume S; S_N ranges 26–352 and averages 129×10^{-6} m s^{-1}, and S_P ranges 9–214 and averages 67×10^{-6} m s^{-1}.

In microatolls with simultaneous measurements of N and P uptake (+N+P), measured S_N was also significantly correlated to S_P ($r = 0.56$, $n = 29$, $p = 0.0016$). The ratio of average S_N: S_P was 2.1 ± 0.23 ($n = 29$). If nutrient uptake is mass-transfer limited, then the NH_4 uptake should be 2.2 times greater than PO_4 uptake because NH_4 ions diffuse faster than PO_4 ions (Bilger and Atkinson 1992).

Limited data from the high-loading period also show that uptake rates following the final third nutrient addition were ~3 times slower than uptake rates following the first nutrient addition. This is consistent with S being near mass-transfer limited rates because nutrient loading decreases S (Bilger and Atkinson 1995). For example, Bilger and Atkinson (1995) showed that increases in nutrient loading to 25–50 mmol N m^{-2} day^{-1} decreased S about three-fold. In the present study, the high loading treatment was about 17.6 mmol N m^{-2} per loading period or about 35 mmol N m^{-2} day^{-1}, consistent with the previous flume data.

We suggest that the rates of nutrient uptake in the microatolls may be close to mass-transfer limitation for the following reasons: (1) nutrient-uptake rates, m, are proportional to concentration (first-order); (2) S, the first-order uptake-rate constant, is positively correlated to wind speed (which is positively correlated to water motion); (3) S is similar in magnitude to S in flume studies, in which uptake rates were shown to be mass-transfer limited; (4) S_N are ~ twice S_P, confirming the different diffusivities of NH_4 and PO_4; and (5) in the high-loading period sequential additions over the course of a low tide decreased both S_N and S_P. Thus, we suggest that the reported order of magnitude variability in the uptake rate constants, S, for both NH_4 and PO_4, may be directly related to changes in the physical environments of the microatolls. Differences in water velocity, rather than biological or physical differences, appear to be the dominant source of this variation in S. We conclude that nutrient input, one of the basic factors limiting the quantity and quality of organic production, is highly variable spatially and temporally, maintaining a range of habitats for the diversity of coral reef autotrophs.

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