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Effects of Water Velocity on Respiration, Calcification, and Ammonium Uptake of a *Porites compressa* Community[1]

M. J. Atkinson, E. Kotler, and P. Newton[2]

ABSTRACT: Colonies of *Porites compressa* Dana were placed in a 10-m-long flume to form a community of coral. Ammonium uptake (N uptake) rate, respiration rate, and calcification rate were measured at different water velocities, ranging from 1 to 57 cm sec^{-1}. N uptake was proportional to concentration from 20 to 0.15 μM N. The first-order rate constant for N uptake varied from 6.8 to 15.6 day^{-1}, only an average of 2.1 times over a 10-fold change in water velocity. First-order rate constants for respiration were less than those for N uptake and ranged from 4.8 to 6.6 day^{-1}. Respiration rate and calcification rate were not correlated with water velocity. The relative turnover of N compared with oxygen (O_2) indicates that 94–98% of N flux must be retained within this coral community.

Uptake rates of phosphate (P) into algal reef-flat communities are positively correlated with water velocity and show a consistent enhancement above that predicted by correlations of mass-transfer from the engineering literature (Atkinson and Bilger 1992). The explanation for the correlation between uptake rate and water velocity is that increased water velocity thins diffusive boundary layers adjacent to organisms. Diffusion of P through these boundary layers can be the rate-limiting step for uptake into communities of coral reef benthos; that is, P can be "mass-transfer limited."

Several preliminary uptake experiments with nitrate and ammonium also showed uptake rates consistent with mass-transfer limitation. A U.S.–Israel Workshop was organized to understand more fully the responses of hermatypic corals to elevated nitrate-ammonium concentrations. Workshop participants studied effects of N enrichment on the composition of zooxanthellae and host (such as carbon : nitrogen : phosphorus [CNP] ratios, amino acids, protein, and enzymes) and growth parameters of zooxanthellae and coral (such as zooxanthellae growth, coral calcification, and photosynthesis). In view of our previous results on the effects of water velocity on P uptake rates (Atkinson and Bilger 1992), we wanted to measure uptake rates of ammonium into a community of hermatypic coral over a range of water velocities and determine whether the uptake rate is mass-transfer limited. (We use the term ammonium uptake even though actual uptake of ammonium by coral can be as ammonia [NH_3].) We also wanted to determine the maximum N-uptake rate, so as to calculate N turnover by the coral community. In addition to N uptake, we also measured two other metabolic rates that have been suggested to be affected by water velocity, calcification and respiration. Respiration rates were useful to calculate the relative turnover of oxygen (O_2) and carbon (C) with that of N. This analysis would indicate the relative amount of N retained by symbiosis between zooxanthellae and host tissue, and how this amount of "retained-N" would change with water velocity.

To be mass-transfer limited, the rate of uptake must have first-order kinetics (rate of uptake is directly proportional to concentration), and the first-order rate coefficient must

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[2] Hawaii Institute of Marine Biology, University of Hawaii, P.O. Box 1346, Kaneohe, Hawaii 96744.

be directly proportional to velocity by a root of 0.5 to 0.8 (Bilger and Atkinson 1992) (that is, $k \sim U_b$ exp [0.5 to 0.8], where k is the first-order rate coefficient and U_b is the velocity in the bulk of the flow, or bulk velocity). Exponents <0.5 are possible, but do not strictly adhere to the algebraic definition of mass-transfer limitation (Bilger and Atkinson 1992). The algebraic definition of mass-transfer limitation requires that the surface concentration of nutrient is negligible compared with the concentration of the bulk water.

MATERIALS AND METHODS

Specimens of *Porites compressa* Dana were collected from the Coconut Island reef flat, Hawaii Institute of Marine Biology, brought to the island, and then placed in an experimental flume, 10 m long, 0.35 m high, and 0.35 m wide (see Atkinson and Bilger [1992] for a discussion of the design of the flume and the formation of side-wall and bottom momentum boundary layers). The experimental community covered 2.1 m^2 (6 by 0.35 m) of the 8-m-long test area of the flume. Water was recirculated through the flume throughout the experiments. Water velocities past the experimental community were controlled from 1 cm sec^{-1} to about 57 cm sec^{-1}. The ratio of water volume to planar surface area of the test area of the flume for these experiments was 0.62 m.

Colonies of *P. compressa* were cleaned of epiphytes and incubated for 4 days in the flume at water velocites of 10 cm sec^{-1} before respiration rates were measured. Daytime respiration rates were measured by placing 4-mil black plastic over the entire flume and measuring changes in O_2 concentration over the next 4–8 hr. O_2 concentration was measured with an O_2 meter (YSI model 58), calibrated to Winkler titrations ($n = 22$, $r^2 = 0.96$). The O_2 probe was mounted in the bulk flow of water over the upstream end of the test benthos. Respiration rates were measured over 10 days from 26 July to 9 August 1991.

N-uptake rates and calcification rates were measured over 7 days during the workshop, 22 to 29 August 1991. Each experiment began in the morning and ended by about 1700 hr. This ensured that both N uptake and calcification were measured through a daylight period. Each morning before the experiment began, coral colonies, side walls, and bottom of the flume were picked clean of epiphytes. This procedure ensured that there were few epiphytes or bacterial films on the walls that could have contributed to N uptake or calcification. After this daily cleaning, the flume was filled with fresh seawater and an ammonium sulphate spike was added over a 1-min period at maximum water velocity to bring the initial concentrations to near 20 μM N. This technique ensured rapid mixing of the spike into the recirculating seawater. Initial water samples were taken after 20 min. Approximately 7–10 water samples were taken throughout the day. During each sampling period, about 10 1-liter subsamples of flume water were siphoned into a bucket. This procedure reduces noise in the data, apparently produced by patches of nutrients in the flume water. The duration of subsampling was the time period for three transits of the water around the flume, which varied from 3 to 24 min depending on the speed of the water. A subsample of the water in the bucket was taken with a 150-ml syringe, and this water was filtered through a GF/C in-line filter into a Nalgene bottle for storage. The subsample of water for nutrients was frozen within 15 min of collection. The water sample for measurement of total alkalinity was left at room temperature. PO_4^{3-}, NO_3^-, NH_4^+, and SiO_4^{4-} were measured on a Technicon II Autoanalyzer, with standard Technicon industrial methods as modified by Walsh (1989). Total alkalinity was determined using the intercept of the linear regression between titrated acid and pH change between pH of 4 and 3 (Edmond 1970). At least 20 points were used in the regression. Our precision using this technique, based on triplicate sampling, was 0.003 meq $liter^{-1}$. Calcification rate is the rate of change of total alkalinity divided by two (Smith and Kinsey 1978, Atkinson and Grigg 1984). Water velocities in the flume were measured by placing a neutrally bouyant

scintillation vial upstream of the community and timing its movement through 6 m of the 8-m test section. Control rates were measured with no organisms in the flume on 29 August. These rates included gas exchange for O_2 and NH_3 and any uptake by bacterial or algal films.

RESULTS

Over the range of O_2 concentrations (3–425 μM O_2), respiration rates were proportional to concentration ($r^2 = 0.996$–1.000, $n = 5$; Table 1). However, the first-order rate coefficient for O_2 uptake, k_O, was not significantly correlated to water velocity, indicating that O_2 uptake is probably not controlled by diffusive boundary layers. The mean k_O was 5.4 day^{-1} $\pm$ 0.7, $n = 8$; the percentage standard deviation was only 13% over a range in water velocities from 1.0 to 36.1 cm sec^{-1} and throughout 14 days. The rate constant for the control, which was measured at the end of the experiments, was 0.46 day^{-1}, only 9% of the mean value. A respiration rate for this community can be calculated by multiplying the mean k_O, 5.4 day^{-1}, times the saturation concentration of 200 μM O_2: 5.4 day^{-1} $\times$ 200 μM O_2 = 1080 mM day^{-1}. Taking the volume to surface area ratio of 0.62 m, the per planar area respiration rate is 670 mmol O_2 m^{-2} day^{-1}.

TABLE 1

SUMMARY OF RESPIRATION EXPERIMENTS ON THE *Porites compressa* COMMUNITY IN THE FLUME

DATE	TIME	VELOCITY (cm sec^{-1})	O_{2i} (μM)	O_{2f} (μM)	k_O (day^{-1})
26 July	9.67–15.72	4.2 $\pm$ 0.26	209	31	6.6
29 July	10.00–15.67	36.1 $\pm$ 1.2	203	44	5.6
31 July	9.77–15.65	5.1 $\pm$ 0.25	200	38	6.2
1 Aug.	9.43–16.47	5.0 $\pm$ 0.20	200	21	5.0
2 Aug.	11.25–15.63	9.3 $\pm$ 0.10	209	78	4.9
5–6 Aug.	15.07–10.97	4.8 $\pm$ 0.09	425	3	5.5
6–7 Aug.	16.65–09.03	1.0 $\pm$ 0.05	325	3	4.8
8–9 Aug.	17.83–09.62	1.0 $\pm$ 0.06	281	3	4.8
Control					
9–11 Aug.	16.34–10.50	4.0 $\pm$ 0.18	188	125	0.46

NOTE: The control experiment without coral, 9–11 August, lasted 2 days. "Time" is the start-end decimal time of day; O_{2i} is the initial O_2 concentration and O_{2f} is final; k_O is the first-order rate coefficient (slope of ln O_2 versus day); r^2s are all above 0.996.

TABLE 2

SUMMARY OF AMMONIUM UPTAKE EXPERIMENTS ON THE *Porites compressa* COMMUNITY IN THE FLUME

DATE	TIME	VELOCITY (cm sec^{-1})	$NH_4^+{}_i$ (μM)	$NH_4^+{}_f$ (μM)	k_N (day^{-1})	r^2 $n = 8$	$CaCO_3$ (mmol m^{-2} day^{-1})	r^2 $n = 10$
22 Aug.	10.78–15.50	47.6 $\pm$ 2.1	18.30	1.70	12.7	0.99	314	0.99
23 Aug.	9.42–17.07	5.6 $\pm$ 0.8	18.41	1.26	7.34	0.95	361	1.00
24 Aug.	9.50–16.00	5.6 $\pm$ 0.6	20.94	3.33	6.84	1.00	333	1.00
25 Aug.	9.00–16.00	28.5 $\pm$ 1.6	18.90	0.79	12.7	0.97	430	1.00
26 Aug.	11.75–15.50	50.6 $\pm$ 2.0	1.11	0.15	13.5	0.99	—	—
27 Aug.	9.50–16.00	56.9 $\pm$ 3.2	21.91	0.41	15.6	0.99	314	0.99
Control								
29 Aug.	9.75–16.47	36.9 $\pm$ 1.0	20.03	17.46	0.47	0.92	13	0.06

NOTE: The control experiment without coral was on 29 August. "Time" is the start-end decimal time of day. $NH_4^+{}_i$ is the initial ammonium concentration and $NH_4^+{}_f$ is final; k_N is the first-order rate coefficient (slope of ln NH_4^+ versus day). Calcification rate is a linear rate and summarized under $CaCO_3$; r^2s for NH_4^+ uptake and $CaCO_3$ are listed after the rate.

Calcification rates were constant throughout the day ($r^2 = 0.993$–0.998; Table 2) and were also not a function of water velocity. The mean calcification rate was 350 mmol $CaCO_3$ m^{-2} day^{-1} $\pm$ 0.048, $n = 5$. The control rate was 13 mmol $CaCO_3$ m^{-2} day^{-1} ($r^2 = 0.063$), only 3.8% of the mean rate. Both respiration and calcification rates are close to metabolic standards for coral reef flats (Kinsey 1985), indicating that the flume community represents a healthy coral assemblage.

Rates of N uptake were proportional to ammonium concentration from 20 to 0.15 μM N ($r^2 = 0.972$ to 0.998); an example of an N uptake experiment is shown in Figure 1. The first-order rate coefficient for N uptake, k_N, was positively correlated to water velocity (Table 2, Figure 2): k_N was 7.3 and 6.8 day^{-1} at 5.6 cm sec^{-1} and 12.7 day^{-1} and 15.6 day^{-1} at 47.6 and 56.9 cm sec^{-1}, respectively. The k_N value for the control measurement was 0.47 day^{-1}, only 6.9% of the minimum observed rate and 3% of the maximum rate. A 10-fold increase in water velocity only increased N uptake 2.1-fold. At 0.15 μM ammonium, there was no apparent net uptake of ammonium (experiment of 26 August, Table 2), indicating that uptake rate of N equaled the release rate of N.

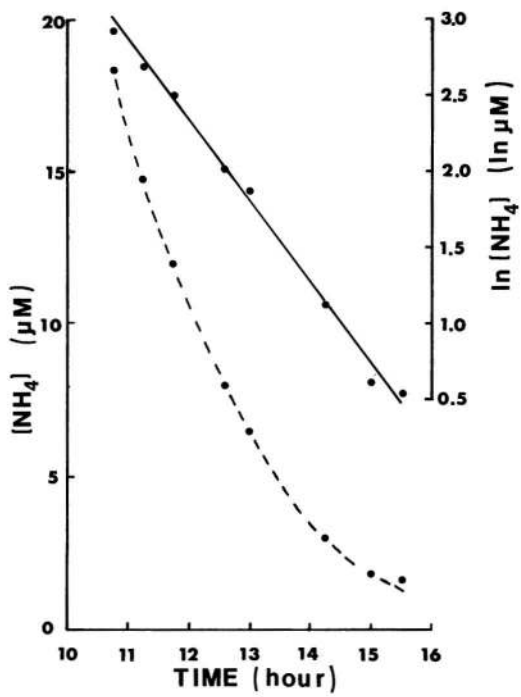

FIGURE 1. Dashed line: ammonium concentration versus time of day for experiment on 22 August (Table 2). Experiments began in the morning with initial concentrations near 20 μM N and continued until 1600 hr. Solid line: ln [NH_4^+] for the same experiment. The slope of the straight line is the first-order rate constant, k_N, for this experiment. The first-order rate constants are reported in Table 1 for O_2 and Table 2 for ammonium.

P concentration in the flume experiments decreased only slightly from initial concentrations of 0.15–0.21 to 0.09–0.20 μM P (Table 3). Similarly, Si concentrations began at 7.65–9.62 and changed to 2.99–9.25 μM Si. In all but one instance, Si decreased. In contrast, $NO_3 + NO_2$ significantly increased from initial concentrations of 0.29–0.63 to final concentrations of 0.63–1.44 μM N. During the experiment where no ammonium was injected into the flume (experiment of 26 August), NO_3 significantly decreased from 0.50 to 0.17 μM N. These results indicate that NO_3 is produced during high ammonium concentrations, but is removed from the water when ammonium concentrations are low.

DISCUSSION

It is well known that hermatypic corals retain or recycle N relative to C (Rahav et al. 1989). The relative turnover of N and C can be estimated for the corals in these experiments. A release rate of ammonium from the coral community can be calculated by assuming that uptake of ammonium equals release of ammonium at 0.15 μM N (experiment of 26 August, Table 2). Uptake rate (and release rate) is therefore equal to k_N x (0.15 μM N). Taking the largest rate coefficient in Table 2, 15.6 day^{-1} at 56.9 cm sec^{-1}, the maximum release rate of ammonium from the experimental coral community in the flume was 1.4 mmol N m^{-2} day^{-1}. The calculated respiration rate of these corals at 200 μM O_2 was 670 mmol m^{-2} day^{-1}. Assuming a respiratory quotient (C/O_2) of 1.0, the C : N ratio

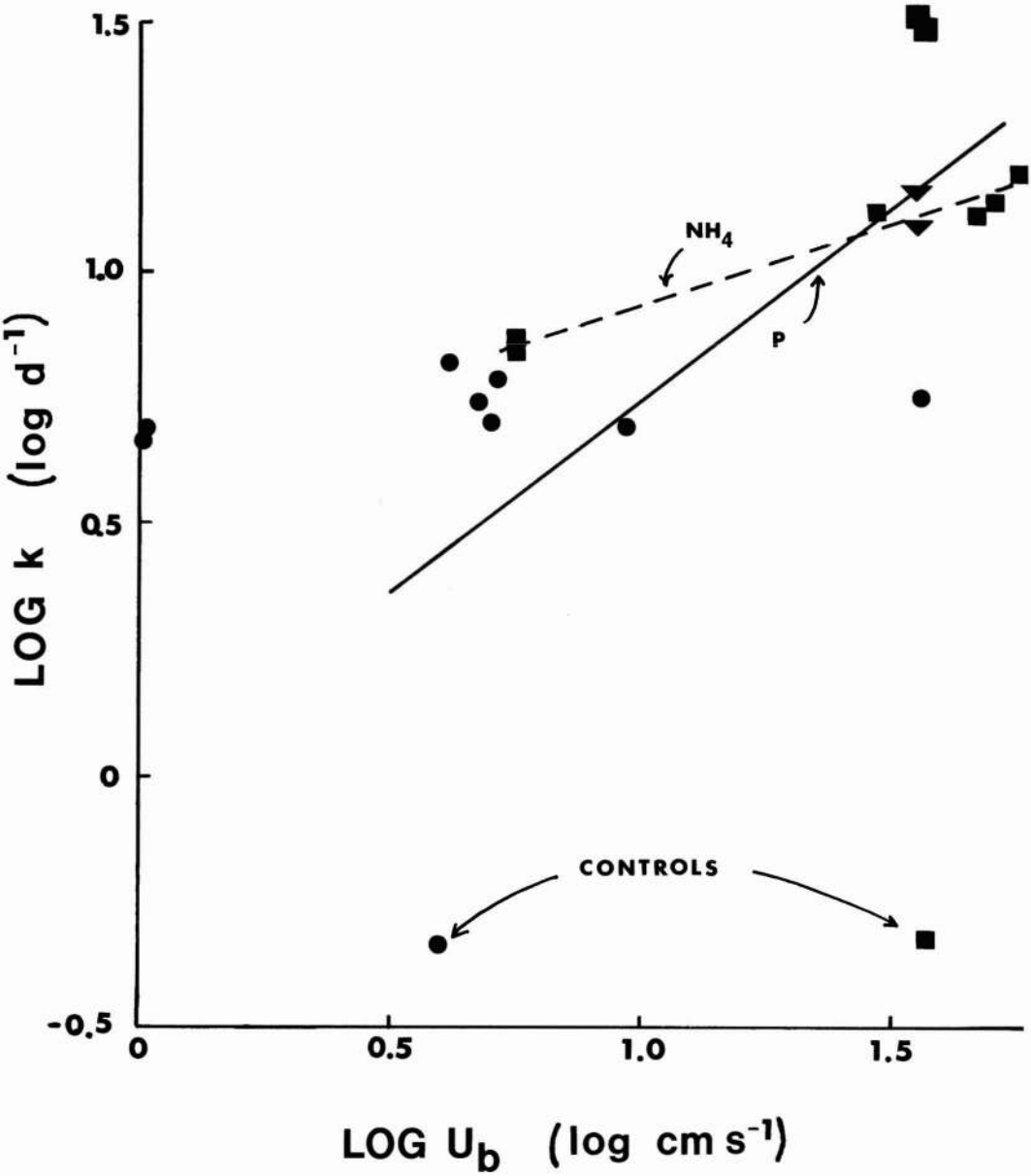

FIGURE 2. First-order rate constants versus water velocity. The solid line is the relationship between P uptake (k_P) into a mixed algal community and water velocity (Atkinson and Bilger 1992). The dashed line connecting the solid squares shows the relationship between ammonium uptake (k_N) and water velocity for our experiments with *Porites compressa*. The solid circles show O_2 uptake, k_O, for these experiments. The large solid squares show ammonium uptake, k_N, for a mixed algal community in the flume. The solid triangles show NO_3 uptake into a mixed algal community.

TABLE 3

INITIAL AND FINAL CONCENTRATIONS, C_o and C_t, RESPECTIVELY, OF NUTRIENTS IN THE AMMONIUM UPTAKE EXPERIMENTS

			PO_4		$NO_3 + NO_2$		Si	
DATE	HOUR	VELOCITY (cm sec^{-1})	C_o	C_t	C_o	C_t	C_o	C_t
22 Aug.	4.72	47.6	0.20	0.09	0.54	1.05	7.80	6.25
23 Aug.	7.65	5.6	0.17	0.14	0.56	1.25	8.14	5.30
24 Aug.	6.50	5.6	0.15	0.20	0.43	1.44	8.96	7.65
25 Aug.	7.0	28.5	0.20	0.17	0.63	0.96	7.65	4.48
26 Aug.	3.75	50.6	0.20	0.13	0.50	0.17	9.14	2.99
27 Aug.	6.5	56.9	0.21	0.20	0.29	0.63	8.96	4.10
Control								
29 Aug.	6.72	36.9	0.19	0.13	0.63	0.83	9.62	9.25

of release from the corals was 478 (670/1.4). C : N ratios of host tissue for control corals from this workshop (Muller-Parker et al. 1994) were from 5 to 7; zooxanthellae C : N ratios varied from 7 to 20 depending on the ammonium concentration of the incubation water. If organic substrates of catabolism have C : N ratios of 7, then 98% of N flux is retained within the coral; similarly, if C : N ratios are 20, then 94% of N flux is retained. This calculation was based on the fastest uptake rate constant, assuming ambient concentrations of 0.15 μM. There was only a 2.4-fold change in the uptake rate constant with water velocity, so water velocity had little effect on these conclusions. At least 10-fold changes in N uptake would be required to support the flux of ammonium without large changes in N retention within corals. Rahav et al. (1989) showed that recycled N from host tissue accounts for >90% of the zooxanthellae N demand in *Stylophora pistillata* Esper. Our results corroborate those findings.

Both calcification and respiration rates were not significantly correlated to water velocity. It is not surprising that calcification is not correlated to water velocity. It is difficult to imagine concentration-depleted diffusive boundary layers of Ca, considering that seawater is ca. 10 mM Ca. Furthermore, the production of CO_3 is controlled within corals and is probably not directly related to the pH of the overlying water. Previous observations that community calcification is correlated to water velocity (Kinsey 1985) are probably a result of changes in community structure or some other indirect effect of water velocity, such as increased nutrient uptake.

Respiration did not appear to be affected by water velocity in this community. Apparently in this study the rates of O_2 uptake were not fast enough to develop diffusive boundary layers around the coral (Newton and Atkinson 1991). Note that the first-order rate constants for O_2 uptake (Table 1, Figure 2) are almost three-fold lower than the rate constants for ammonium uptake (Table 2, Figure 1).

N uptake is limited by diffusion through diffusive boundary layers. N uptake is first order and positively correlated to the bulk water velocity. The increase in k_N with water velocity, however, was less than expected. Normally for turbulent flow, the increase would be 0.7–0.8 root, or $\log k = 0.8 \log U_b$ (Bilger and Atkinson 1992). A 10-fold change in water velocity would increase k 6.3-fold, not just 2.1-fold as in these experiments. Given our data, the slope between $\log k_N$ and $\log U_b$ is only about 0.3. This value is too low to conclude definitely that N uptake is mass-transfer limited.

Figure 2 shows our results compared with some previously published results. The solid line is the best line representing P uptake versus water velocity from Atkinson and Bilger (1992). The dashed line connects values of k_N

for the low-velocity experiments of our study with values for the high-velocity experiments. Note that k_N is two to three times above k_P at the lower velocities. This result is to be expected for mass-transfer limited rates, because diffusion of ammonium through water (hence the boundary layers) is three times faster than that of P (Li and Gregory 1974). However, at the higher velocities, N uptake into this coral community is about the same as P uptake into the mixed coral-algal community. There are two plausible explanations for this result. The first is that the concentration of ammonium at the surface of the organisms is a substantial percentage of the concentration in the bulk flow. This would result in a decreased effect of velocity on N uptake. The other explanation is that coral branches force water into more interstitial spaces than would otherwise occur, giving enhanced uptake at lower velocities. This explanation is unlikely, because a two- to threefold uptake rate above P uptake is expected. It is apparent that these explanations need further research to verify whether coral morphology in a mixed community alters the relative uptake of nutrients at different velocities.

An interesting pattern in metabolic rates is illustrated in Figure 2; O_2 uptake is near mass-transfer limited rates but shows no significant effects with changes in velocity; in contrast, N and P uptake have larger rate coefficients and are therefore closer to the mass-transfer limit. We suggest that respiration probably cannot be maintained at a mass-transfer limited rate because low water velocities would then stress or kill microorganisms living in the boundary layer. The reduced flux of O_2 would continually limit the activity of these organisms. Thus the observed community respiration rate is sustained at the highest level without becoming strongly water velocity–dependent. Organisms probably shunt intracellular energy to nutrient-uptake mechanisms that allow the fastest nutrient uptake under all conditions; thus they take advantage of the high water velocity by increasing nutrient uptake. We believe further experimentation will show that other coral or coral-algal communities have similar metabolic patterns.

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