PHOSPHATE-UPTAKE OF EXPERIMENTAL CORAL AND ALGAL COMMUNITIES UNDER STEADY VERSUS OSCILLATORY FLOW

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ABSTRACT

Relationships between nutrient-uptake and net carbon production are variable on reefs. Nutrient-uptake appears to be governed by diffusion of nutrients through nutrient-depleted boundary layers near the surfaces of autotrophs. Nutrient-uptake may occur at different rates under steady and oscillatory flows because the boundary layers may be different. Rates of phosphate-uptake were measured for five experimental communities, two coral and three algal, for a total of 24 experiments. Uptake rate constants (S) ranged from 0.82 to 6.9 m day^{-1} over water velocities of 10 to 50 cm s^{-1}. Uptake was proportional to water velocity and was close to mass-transfer limitation. Phosphate-loading rates, between 0.22 and 1.9 mmol m^{-2} day^{-1}, were typical of natural loading. Excretion rates increased over time and ranged from 0 to 2.1 mmol m^{-2} day^{-1}. S was not significantly different under steady versus oscillatory flow. The rate of phosphate-uptake may be enhanced by nitrogen-loading.

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INTRODUCTION

CORAL REEF COMMUNITY METABOLISM

Autotrophs combine the nutrients phosphorus and nitrogen with inorganic carbon to produce organic matter, according to the following unbalanced equation:

$$HPO_4^{2-} + yNO_3^- + xCO_2 + H^+ + H_2O \text{ -------> } (CH_2O)_x(NH_3)_yH_3PO_4 + O_2 \quad (1)$$

(Stumm and Morgan 1981). This equation can be balanced for benthic autotrophs with an average C:N:P ratio of 550:30:1 (Atkinson and Smith 1983). This ratio is five- to ten-fold higher than the C:N:P for phytoplankton (106:16:1; Redfield *et al.* 1963), meaning that compared to phytoplankton, benthic algae fix five- to ten-fold more grams of carbon per gram of phosphorus. The mechanisms controlling these C:N:P ratios are not fully understood.

Primary production by coral reefs is dominated by benthic algae, whereas production in the open-ocean is dominated by phytoplankton. This fact, combined with the difference in C:N:P ratios, explains why coral reef communities have a much higher rate of carbon-fixation compared to open-ocean communities, even though both communities fix a comparable amount of nutrients (Atkinson and Falter 2003).

Primary production by coral reef autotrophs is nutrient-limited (Atkinson 1988), but narrow barrier and fringing reefs remove only a small fraction of the nutrients from the water column (Atkinson 1992). The flux of phosphate is small because a physical mechanism limits the rate of nutrient-uptake; reef autotrophs are not always able to take up nutrients at a maximum biologically-determined

rate. During times of high biological demand, the rate of nutrient-uptake is limited by molecular diffusion through a nutrient-depleted boundary layer at the surface of the organism, which is termed mass-transfer limitation (Bilger and Atkinson 1992).

Mass-Transfer Limitation

Mass-transfer theory is based on well-established engineering literature that describes the transfer of dissolved compounds between fluids and reactive surfaces. Empirical mass transfer relationships for naturally-rough biological surfaces have not been developed, so the empirical heat transfer relationship for *rough surfaces in fully-developed turbulent flow has been adapted to naturally-*rough biological surfaces such as coral reefs (Bilger and Atkinson 1992). The following theory, which explains this empirical relationship, has been successfully used to describe nutrient-uptake by coral reef communities (Bilger and Atkinson 1992, Atkinson and Bilger 1992, Atkinson *et al.* 1994, Bilger and Atkinson 1995, Larned and Atkinson 1997, Thomas and Atkinson 1997, Baird and Atkinson 1997, Atkinson *et al.* 2001, Denny and Wethey 2001, Falter 2002).

Boundary layers are formed whenever a fluid interacts with a solid. The "no-slip" condition, which states that at the fluid-solid interface fluid particles have zero velocity and adhere to the surface, causes the formation of a velocity gradient (Kundu 1990). The velocity gradient is responsible for boundary layer formation. A sublayer within the total boundary layer, called the momentum boundary layer, forces the creation of a concentration boundary layer.

Nutrients pass through the concentration boundary layer by the process of molecular diffusion. The flux of nutrients is proportional to the bulk water velocity and nutrient concentration. As velocity increases and as concentration in the bulk fluid increases, the rate of diffusion increases. Mathematically, the flux (J, μmol m^{-2} s^{-1}) is given by

$$J = StU_b([C]_b - [C]_w) \quad (2)$$

where U_b is the bulk flow velocity (cm s^{-1}), $[C]_b$ is the concentration of the nutrient in the bulk fluid (μM), $[C]_w$ is the concentration of the nutrient at the wall (μM), and St, the Stanton number, is a dimensionless number that combines measures of friction, viscosity, shear stress, and the diffusivity of the nutrient (Bilger and Atkinson 1992). The terms encompassed in St give an overall measure of the physical parameters that influence the character of the boundary layer. The extreme application of Equation (2) at $U_b = 0$ is not encountered in the real world; release of photosynthetically-produced oxygen bubbles and thermal convection caused by differential solar heating do not allow for zero flow.

When uptake is limited by mass-transfer, biological demand for nutrients is very high and therefore C_w is assumed to be negligible. The parameters St and U_b can be combined into S, the first-order uptake rate constant, according to the following equation.

$$J_i = S\,[C]_b \quad (3)$$

S increases proportionately with U_b because $S = S_tU_b$. For experimental coral reef communities in steady-flow flumes (Bilger and Atkinson 1992, Atkinson and Bilger 1992, Atkinson *et al.* 1994, Bilger and Atkinson 1995, Larned and Atkinson

1997, Thomas and Atkinson 1997) and for the wave-driven Biosphere 2 coral reef biome (Atkinson *et al.* 2001) it has been demonstrated that S's for nitrogen and phosphate are proportional to U_b.

STEADY VERSUS OSCILLATORY FLOW

The physics of boundary layers may be different under steady and oscillatory flows (Kundu 1990, Nielson 1992). There is some evidence that compared to steady flow, oscillatory flow enhances the rates of net primary production (Carpenter et al. 1991) and nitrogen-fixation by algal turfs (Williams and Carpenter 1998). In addition, Kinsey (1979) and Dennison and Barnes (1984) documented that rates of new production in coral reef communities are greatest on the fore-reef slope, which correlates to the maximum wave energy. Using the dissolution of plaster molds, Falter (2002) found that rates of mass transfer were 1.4-2.0 times higher under oscillatory flow in the field than under steady flow in a flume, although the author noted that some of this difference may be due to different turbulence structures of the flow fields.

HYPOTHESIS

The following null hypothesis was tested in this study:

> The slope of S versus U_b is not significantly different for steady versus oscillatory flow.

If nutrient-uptake is limited by diffusion through a boundary layer, and if boundary layer structure is different under steady and oscillatory flow, then rates of nutrient-uptake should be different under these flow regimes.

METHODS

Nutrient enrichment experiments were performed on experimental coral reef communities under varying flow conditions. In all, 24 experiments were conducted on five communities over a one-year period. Phosphate was increased above the ambient level and then the decrease in aqueous phosphate concentration over time was measured. It has been demonstrated that the decrease in aqueous phosphate corresponds to active uptake by autotrophs, not adsorption (Atkinson 1981). Control experiments were performed with an empty flume and with dead coral skeletons to confirm this finding.

Phosphorus was used for the nutrient spike, as opposed to nitrogen, because 1) phosphorus may be the limiting nutrient on coral reefs since fixation of atmospheric nitrogen relieves nitrogen limitation (Atkinson 1992), 2) the biogeochemical pathways of phosphorus are less complicated than nitrogen (Stumm and Morgan 1981), 3) phosphorus is accumulated in the calcium carbonate structure of reefs and therefore reefs may be a sink for phosphorus (Atkinson and Falter 2003), and 4) C:P compositional ratios of autotrophs are high and variable on reefs; determining the rate kinetics of phosphorus-uptake is important in interpreting this fact.

In addition to testing the null hypothesis, an objective of this work was to learn how to experiment successfully with communities in a new wave-flume. To this end, the methods evolved over the course of the study as we learned more about how communities functioned in the flume. Different types of communities

and different sampling regimes were tested. Because of the evolving methods, multiple data analysis techniques were required.

FLUME SET-UP

An indoor wave-flume was constructed at the Hawaii Institute of Marine Biology (HIMB) *Coconut Island, Hawaii in the summer of 2002 (Figure 1) for the* purpose of comparing biogeochemical reactions under steady and oscillatory flow. The 1.5 m^3 flume, with 0.9 m^2 test section and 18 m total flow path, is capable of steady flows from a motorized propeller or oscillatory flow from a motorized piston system. Six 400-watt metal halide bulbs placed in three reflective hoods (brand: PFO Lighting) provided light to the communities. The light hoods were placed approximately 30 cm above the flume top. Timers turned on the lights from 6:30 to 18:30 daily for communities 1 to 4 and from 4:30 to 20:30 for Algae Community 3. Seawater from Kaneohe Bay was pumped into the flume from the HIMB plumbing system. The flume has a sand filter (Purex Triton, model no. SM-20-3) which was sometimes used to filter incoming water.

COMMUNITY COLLECTION

The first two communities (Coral Community 1 and Coral Community 2) *were predominately coral heads and the second two communities* (Algae Community 1 and Algae Community 2) were predominately algal-covered coral rubble. Coral Community 1 (12 August to 20 September 2002; Figure 2) and Coral Community 2 (23 September to mid October 2002; no figure) were collected from a shallow (~1m) near-shore area at HIMB named the "coral garden." Most of the coral heads in this area were taken from other areas of

Figure 1. Wave-flume at HIMB. Flume was constructed in Summer 2002 and is capable of producing steady and oscillatory flow. The 18-m flow path flume can contain a volume of 1.5 m^3 and has a test section area of 0.9 m^2. Metal halide bulbs provide lighting to the indoor system.

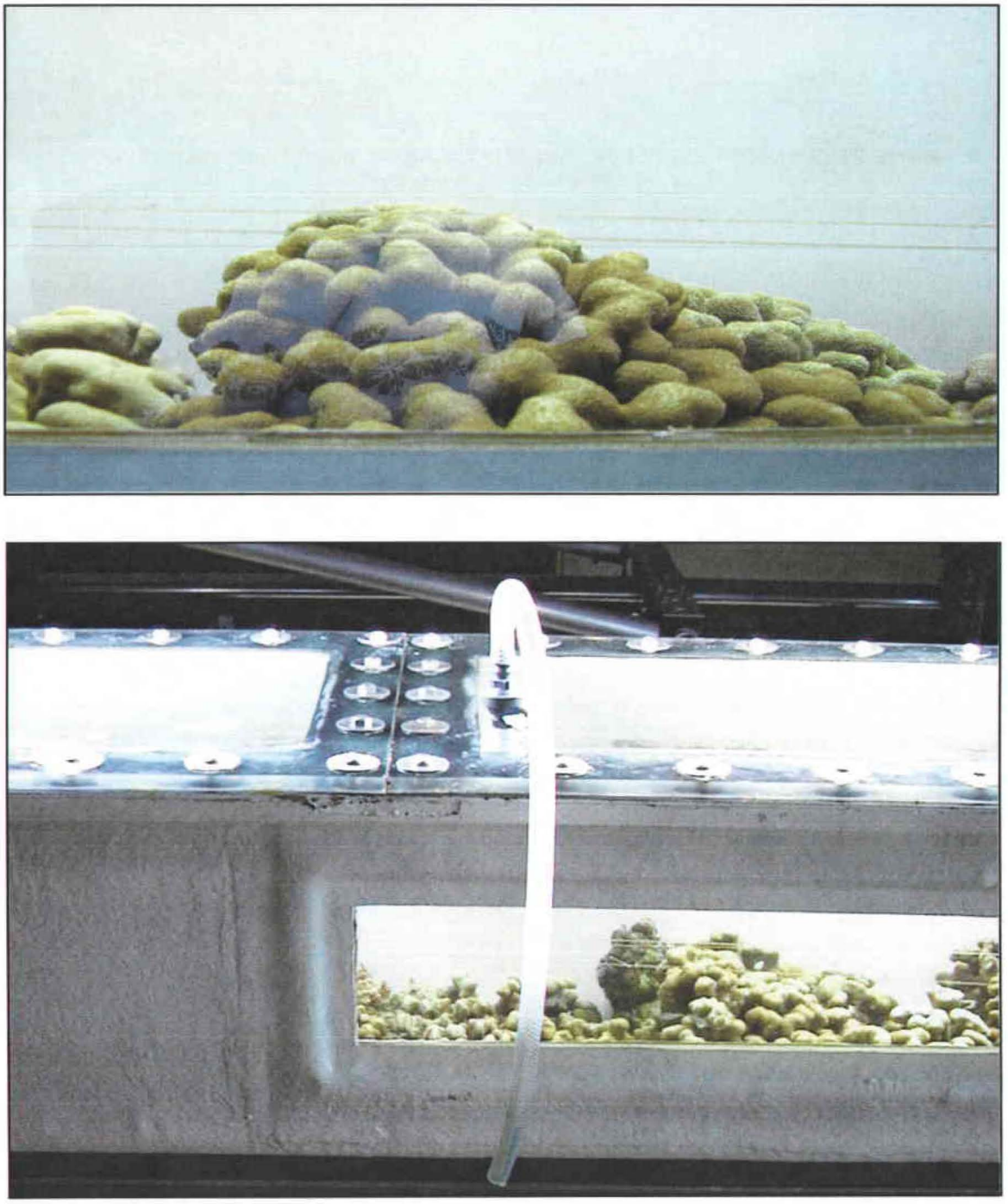

Figure 2. Coral Community 1. This community was collected on 12 August 2002 from the "coral garden" at HIMB. *Porites compressa* was the dominant coral species and *Pocillopora damicornis* was also present. Coral Community 2 (not shown) was collected from the same area on 23 September 2002 and had similar composition.

HIMB or Kaneohe Bay, used in past experiments, and then placed in the "coral garden" prior to collection for this experiment. Coral heads were shaken underwater to remove excess sediment and fauna, placed in buckets, carried to the flume, and then immediately placed inside the flume, which was partially filled with seawater. Corals were submerged during the transfer from the reef flat to flume. Corals were packed in the flume and tethered down with monofilament line to minimize movement during oscillatory flow. Movement of corals was not a problem during steady flow. Corals were predominately *Porites compressa* with a few *Pocillopora damicornis* and associated algae, sponges, worms, and crabs. Although Coral Community 1 was placed back into the "coral garden," care was taken to use different heads for Coral Community 2.

Algae Community 1 (17 to 25 January 2003; Figure 3) was algal-covered coral rubble collected from a shallow (~1m) sand bottom area approximately 10 m offshore of crescent beach at HIMB. This community was dominated by turf algae and had little macroalgae. Algae Community 2 (2 April 2003 to 7 May 2003; Figure 4) and Algae Community 3 (14 July 2003 to 24 July 2003; Figure 5) were algal-covered rubble from the sandy, 1 m deep back-reef of Checker Reef in Kaneohe Bay. Algae Communities 2 and 3 had considerably more macroalgae than did the Algae Community 1. Dominant species were *Acanthophora specifera*, *Gracilaria salicornia*, *Dictyosphaeria cavernosa*, *Centroceras clavulatum*, *Caulerpa racemosa*, *Padina sanctae-crucis*, *Sargassum echinocarpum*, and *Coelothrix irregularis* (John Huisman, University of Hawaii Department of Botany, personal communication). According to oxygen

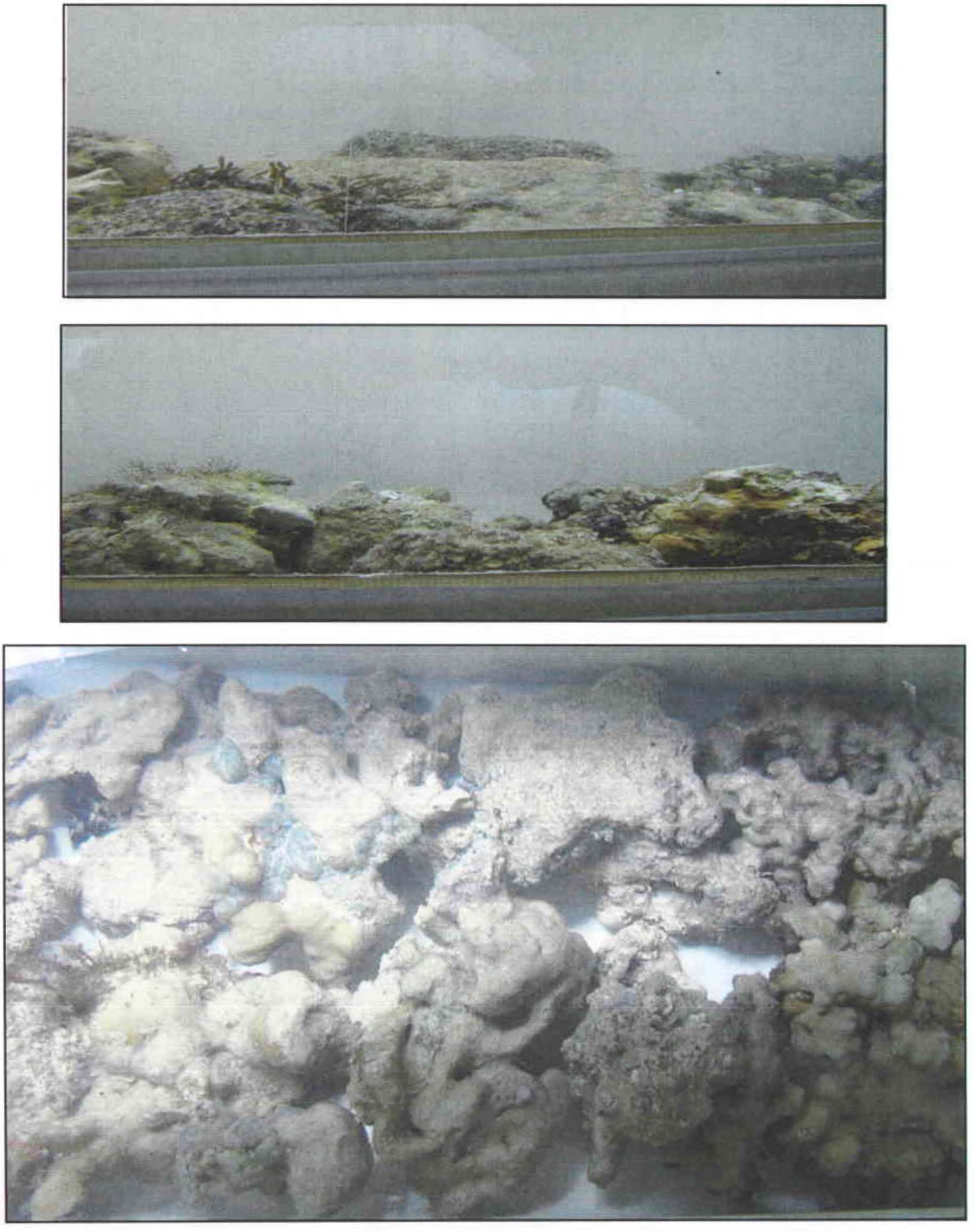

Figure 3. Algae Community 1. This community was collected on 17 January 2003 from a ~1 m deep sand bottom area ~10 m offshore of Coconut Island. Turf algae were more abundant than macroalgae.

Figure 4. Algae Community 2. This community was collected on 2 April 2003 from the ~1m deep backreef of Checker Reef in Kaneohe Bay. Species included *Acanthophora specifera, Gracilaria salicornia, Dictyosphaeria cavernosa, Centroceras clavulatum, Caulerpa racemosa, Padina sanctae-crucis, Sargassum echinocarpum,* and *Coelothrix irregularis.*

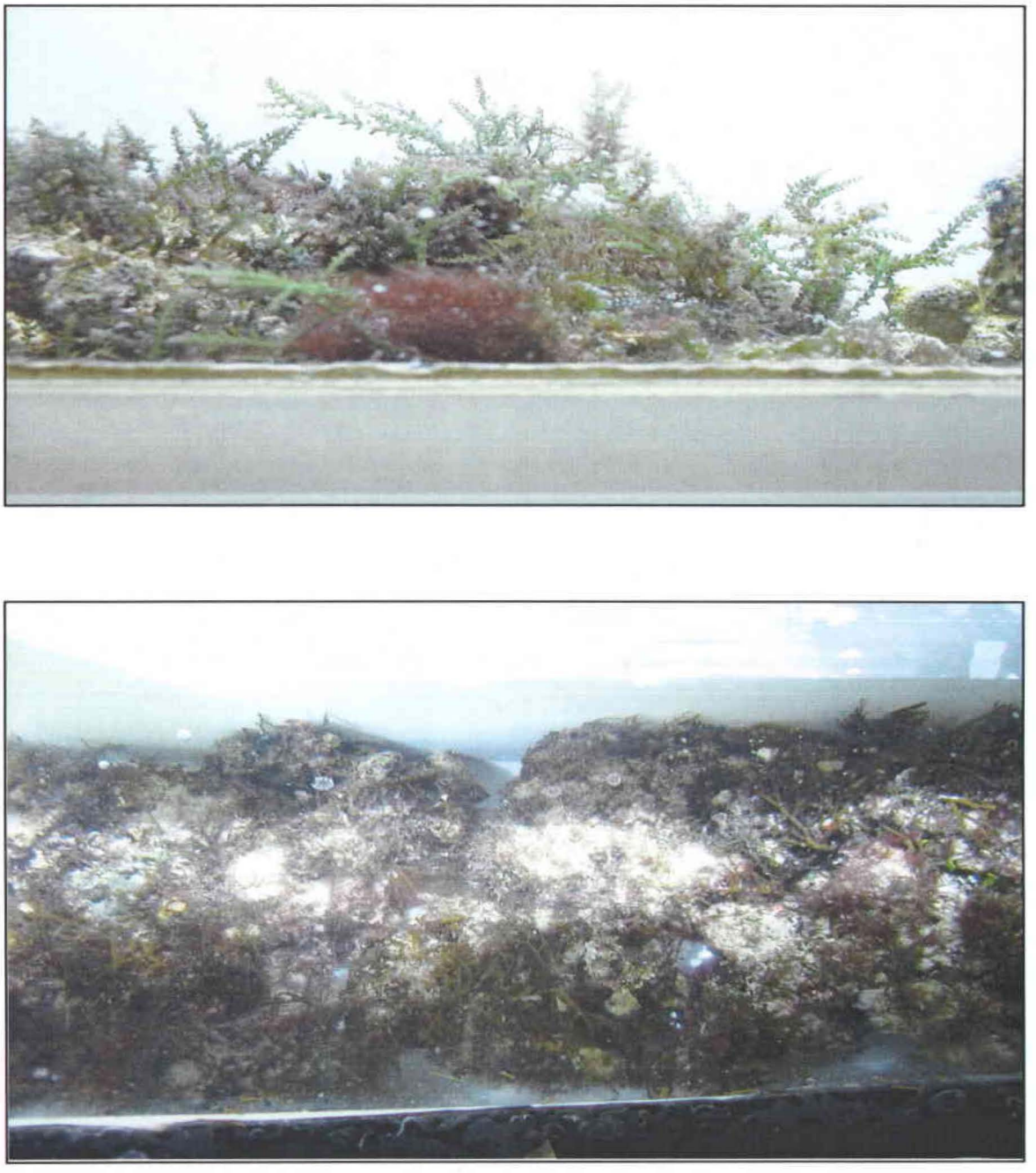

Figure 5. Algae Community 3. This community was collected on 14 July 2003 from the ~1m deep backreef of Checker Reef in Kaneohe Bay. Species were similar to Algae Community 2 (see Figure 4 for list).

measurements, the production to respiration (P/R) ratio of Algae Community 2 was 2.6, revealing the dominantly autotrophic nature of the community. P/R is typically greater than unity for algal turfs (Kinsey 1985).

After each community was placed in the flume, fresh seawater was allowed to flow through the system. The seawater was filtered for Coral Communities 1 and 2 and for Algae Community 3, but due to concerns of starving suspension feeders, the seawater was unfiltered for Algae Communities 1 and 2. Between experiments, bulk water velocity was ~5 cm s^{-1} for Coral Communities 1 and 2, ~25 cm s^{-1} for Algae Communities 1 and 2, and ~50 cm s^{-1} for Algae Community 3.

FLOW MEASUREMENTS

For steady flow, bulk water velocity (U_b) was determined by timing neutrally buoyant particles as they traveled the length of the flume in the main flow of water. Five to ten particles were timed for each experiment. The particles were on the order of <0.5 cm and were mainly plant detritus.

For oscillatory flow, U_b was determined by the equation $U_b = 2X/T$, where X is the excursion amplitude and T is the period. X was obtained by averaging the greatest distance traveled by neutrally buoyant particles in both directions. T was obtained by timing the particles or the rotation of the motor-arm. Velocities used in this study are within 10-20% of velocities measured by an acoustic doppler velocitimeter (ADV).

NUTRIENT ADDITION EXPERIMENTS

Phosphate, in the form KH_2PO_4, was weighed, placed into a one liter Nalgene bottle, and diluted to one liter with filtered seawater. The concentrated solution of phosphate was poured into the back standpipe of the flume (see Figure 1). The one-liter container was rinsed three times with flume seawater and the wash water was poured into the standpipe. In later experiments, nitrogen was added to the community to keep it healthy (Table 1). Nitrogen was added in the form of NH_4Cl, using the same technique as phosphate.

Mixing experiments using KH_2PO_4 in an empty flume showed that the mixing time of the flume is approximately 10 minutes for steady flow and 25 to 50 minutes for oscillatory flow, depending on velocity. Based on this, the first few samples were not used in the determination of the uptake rate constants. Water samples were taken at periodic intervals through the middle sample port. For Coral Communities 1 and 2, samples were unfiltered and taken directly from the sample port. After flushing the port tubing for approximately one minute, acid-washed Nalgene bottles were rinsed with three aliquots of sample and then filled with 100mL of water. For Algae Communities 1, 2, and 3, samples were filtered and taken from a bucket (Figure 6). The middle sample port was allowed to drip into a clean bucket for a specified amount of time: 1 minute for Algae Community 1 and 30 minutes to 1 hour for Algae Communities 2 and 3. A 140-mL syringe was rinsed with sample, an in-line filter with 2.4 cm Whatman GF/C filter paper (Whatman no. 1822 024) was cleaned with sample, the sample bottle was rinsed with three aliquots of filtered sample, and then the sample bottle was filled. The

Community[a]	Experiment[b]	Flow[c]	Velocity[d]	Seawater Filtered[e]	Sample Filtered[f]	NH_4Cl[g]	Time[h]	[P][i]			Uptake Rate[j]		r^k
								Before	Begin	End	S	error	
Coral Community 1 (8/12/02)	x020814	S	50	Y	N	N	390	0.23	15.64	11.08	2.1	0.3	--
	x020817	O	25	Y	N	N	680	0.10	3.15	1.86	4.3	0.8	--
	x020820	O	15	Y	N	N	480	0.21	7.14	4.71	1.1	0.3	--
	x020824	O	25	Y	N	N	1445	0.12	4.26	0.93	4.3	2.5	--
	x020830	S	25	Y	N	N	4105	0.12	2.59	0.32	1.5	0.1	0.2
	x020902	S	25	Y	N	N	4328	0.10	2.30	0.57	--	--	--
	x020909	S	50	Y	N	N	6645	0.14	2.29	0.23	1.8	0.7	0.4
Coral Community 2 (9/23/02)	x020925	S	25	Y	N	N	7180	0.00	2.60	0.05	3.5	0.0	--
	x021002	O	25	Y	N	N	4596	NaN	3.40	0.79	1.4	0.4	1.0
	x021007	O	25	Y	N	N	5932	0.14	2.86	0.91	0.82	0.1	0.6
Algae Community 1 (1/17/03)	x030118	S	20	N	Y	N	1816	0.00	1.01	0.09	3.1	0.3	--
	x030124	S	20	N	Y	N	1595	0.04	0.88	0.17	4.0	0.7	0.2
Algae Community 2 (4/2/03)	x030404	S	50	N	Y	Y	1595	0.04	1.17	0.00	6.9	0.4	--
	x030409	S	25	N	Y	Y	1574	0.09	1.08	0.05	5.3	0.8	0.0
	x030414	S	10	N	Y	Y	1440	0.09	1.42	0.19	4.0	1.1	0.8
	x030421	O	50	N	Y	Y	1390	0.06	1.61	0.32	3.9	0.3	1.2
	x030428	O	25	N	Y	Y	1451	0.08	2.05	0.26	4.1	1.0	1.8
	x030505	O	10	N	Y	Y	1533	0.04	1.81	0.33	5.0	1.3	2.1
Algae Community 3 (7/14/03)	x030715	O	50	Y	Y	Y	300	0.14	1.47	0.60	6.5	0.3	--
	x030716	S	50	Y	Y	Y	300	0.16	1.30	0.70	6.5	0.4	--
	x030718	O	10	Y	Y	Y	300	0.07	1.11	0.48	5.5	0.3	--
	x030719	S	10	Y	Y	Y	300	0.02	0.92	0.55	4.5	0.3	--
	x030722	S	50	Y	Y	Y	300	0.06	1.12	0.63	6.0	0.5	--
	x030723	O	50	Y	Y	Y	300	0.03	1.25	0.58	5.6	0.2	--

Table 1. Summary of experimental methods and results. Notes: a) Collection date is given in parentheses. b) Experiments are named after the start date given in YYMMDD. c) S = steady, O = oscillatory. d) Units of cm s^{-1}. e) Y = yes, N = no; refers to seawater coming into flume filtered by sand filter. f) Refers to filtration of sample through GFC filter. g) Refers to the addition of ammonium chloride during experiment. h) Duration of experiment (min). i) Concentration of phosphate (uM) before nutrient spike, after nutrient spike is mixed throughout flume, and at the end of the experiment. j) First-order uptake rate constant (m day^{-1}) with standard error. k) Excretion rate in (mmol m^{-2} day^{-1}).

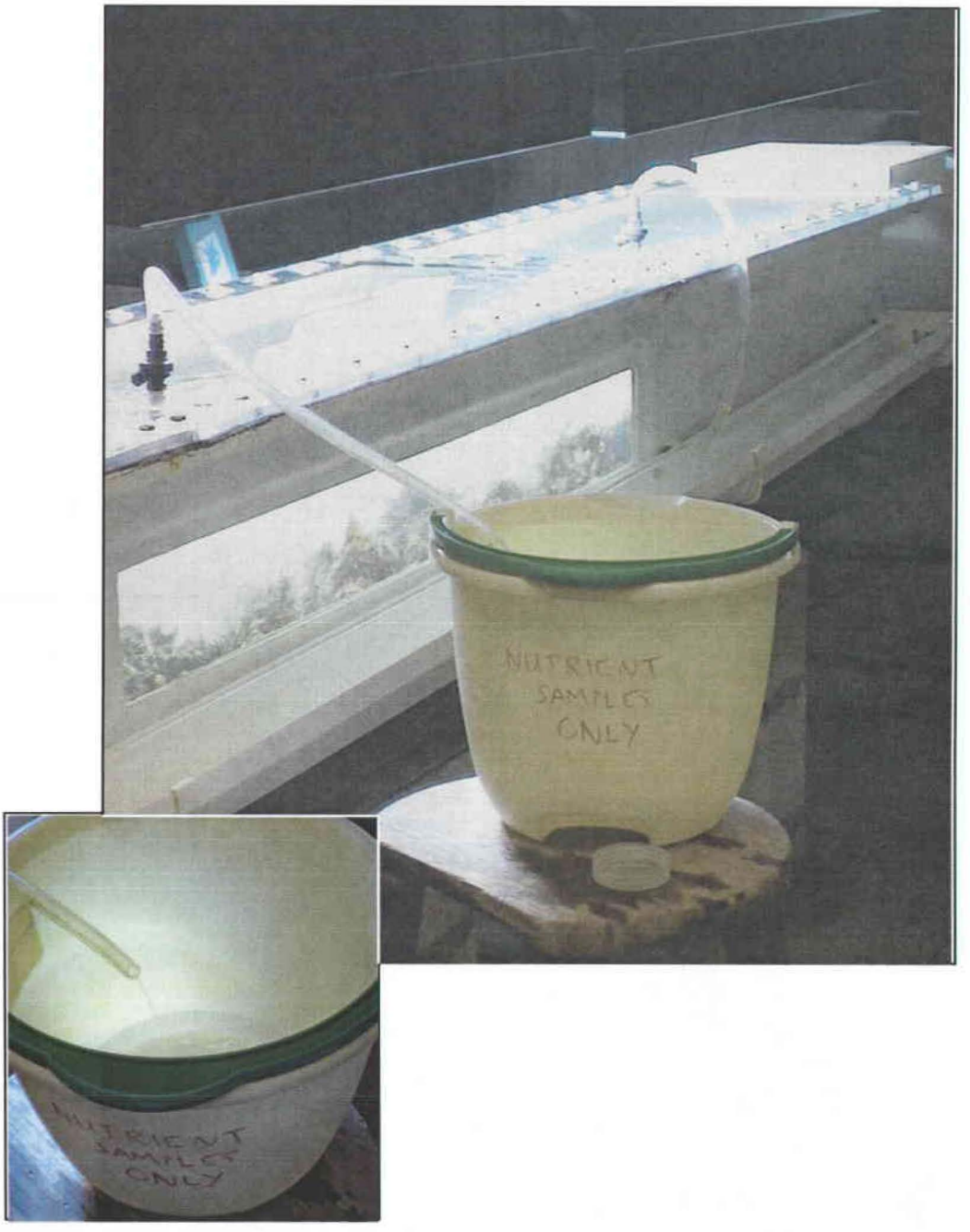

Figure 6. Sampling apparatus for experiments with Algae Communities 1, 2, and 3. Water samples were taken through the middle sample port of the flume into a bucket through plastic tubing. Flume water was allowed to drip into the bucket slowly to allow for temporal and spatial homogenization. Subsamples were taken from the bucket with a 140-mL syringe with an in-line filter.

subsampling technique used in the latter experiments was aimed at reducing patchiness of the water, but no patchiness was observed and comparison of filtered to non-filtered samples showed no significant difference. In all cases, sample bottles were frozen after collection in a laboratory freezer.

PHOSPHATE ANALYSIS

Samples were thawed at room temperature or in a water bath immediately prior to analysis. The concentration of dissolved phosphate was determined using the method "Determination of reactive phosphorus" developed by Strickland and Parsons (1968). This method involves forming a phospho-molybdate complex under acidic conditions. Analyses were performed on a Brinkman PC 800 Colorimeter with 880 nm wavelength and 5 cm pathlength absorption cell.

DATA ANALYSIS

Two mathematical techniques were used to calculate the first order rate constant, S. Ideally, the mathematical model that best fits these types of experiments calculates both uptake and excretion terms. A calculation of the uptake rate constant and a release rate was accomplished using a nonlinear, least-squares fitting program in Matlab based on the equation:

$$Y = (Y_0 - r/k)e^{-k/t} + r/k \qquad (4)$$

where Y is the concentration of phosphate, Y_0 is the initial concentration of phosphate, r is the release rate (mmol m^{-3} min^{-1}), and k is the rate constant of nutrient-uptake.

In some experiments, there was insufficient data evenly spread throughout the experiment to warrant using a non-linear equation with two terms. Other experiments had a very large value of r that disallowed the calculation of S by the above equation. A second approach used the initial drop in concentration to calculate the uptake rate, but ignored the part of the curve near the asymptote that is only useful for calculating r. When r is removed, k is determined using a nonlinear fitting program in Matlab based on the following equation.

$$Y = Y_0 e^{-k/t} \tag{5}$$

In both cases, S, the area-normalized first-order uptake rate constant, is k times the volume of the flume divided by planar surface area of the test community in the flume. Planar surface area, as opposed to reactive surface area, is used because of the simplicity of measurement, although it is an underestimate of the true reactive surface area of the community. Planar area has been used throughout the literature on mass-transfer limited processes, and so the rates obtained in this study may be compared to previously reported values.

RESULTS

CONTROL EXPERIMENTS

Two control experiments were performed to confirm that the decrease in phosphate concentration was due to biological uptake, not adsorption. Phosphate was added to an empty flume (no organisms) and to a community of dead *Porites Compressa* skeletons. In both cases, the phosphate concentration remained constant; no decrease in phosphate concentration could be detected.

CORAL COMMUNITY 1

A total of seven experiments were conducted on Coral Community 1 over a period of 28 days (see Table 1 for a summary of all results). This community appeared healthy for the first two weeks and then paled in color thereafter. The community may have declined for a variety of reasons. First, the incoming seawater was filtered for this community, meaning any suspension feeders had a low supply of food. Second, the artificial lighting may not have been sufficient for the coral community. Third, and most likely, no nitrogen was added to the water. The community was relying on the nitrogen in the ambient seawater flowing in from the HIMB pipe system. The nitrogen concentration of this water was not measured and remains unknown. The lack of sidewall algal growth in the coral communities, as compared to the algae that were given nitrogen, may be evidence of lack of nitrogen.

Uptake of phosphate is apparent as the phosphate concentration decreased over time (Figure 7). An uptake rate for the experiment that began on September 2, 2002 cannot be calculated because of insufficient data, so this

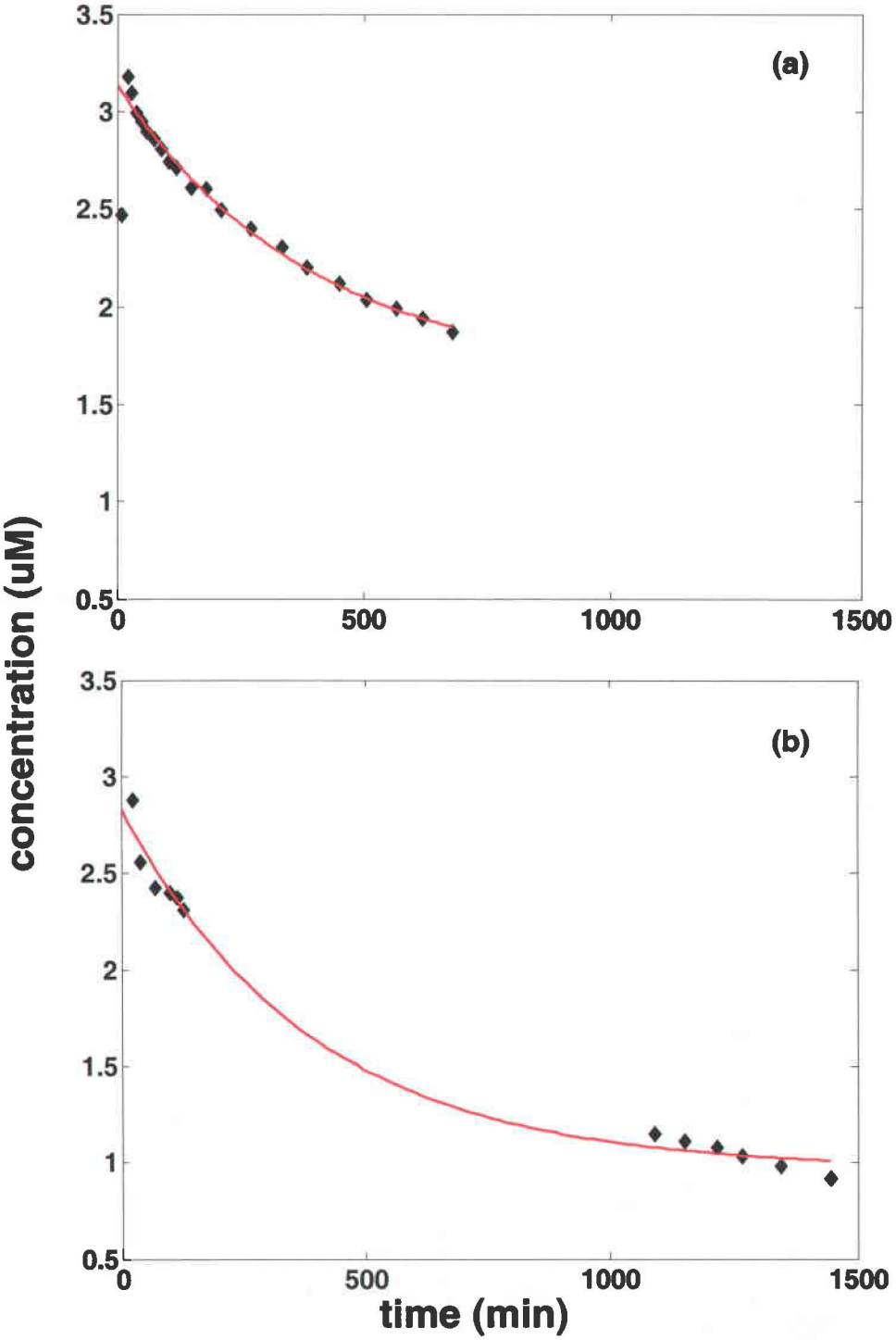

Figure 7. Example uptake curves for Coral Community 1. Experiment x020817 is shown in (a) and experiment x020824 is shown in (b). S was calculated with an excretion term for (a) but without an excretion term for (b); S was 4.3 m day^{-1} for both experiments.

experiment was omitted from the analysis. For the other six experiments, S ranged from 1.1 to 4.3 m day^{-1} at water velocities of 15 to 50 cm s^{-1}. For both steady and oscillatory flow, there is an increase in S with U_b (Figure 8).

CORAL COMMUNITY 2

A total of three experiments were conducted on Coral Community 2 over a period of 14 days. The community began bleaching soon after it was placed in the flume and after the third experiment it was discovered that a nudibranch colony had infested the coral and killed most of it. Bleaching may have also been induced by the factors listed under Coral Community 1. The uptake rates for these experiments decreased over time and were 3.5, 1.4, and 0.82 m day^{-1} at 25 cm s^{-1}, revealing the demise of this community. These experiments were omitted from analysis due to the severe bleaching.

ALGAE COMMUNITY 1

Two experiments were performed on Algae Community 1 with 7 days in between the experiments. This community appeared to be healthy and algal growth was apparent, especially since the flume was not cleaned between experiments. Phosphate concentration decreased over time following a first-order relationship. Both experiments were done in steady mode and the uptake rates were 3.1 and 4.0 m day^{-1} at 20 cm s^{-1}.

ALGAE COMMUNITY 2

Six experiments were performed with Algae Community 2 over a period of 33 days. The community appeared to be healthy throughout the experiments and algal growth was observed. Phosphate concentration decreased over time

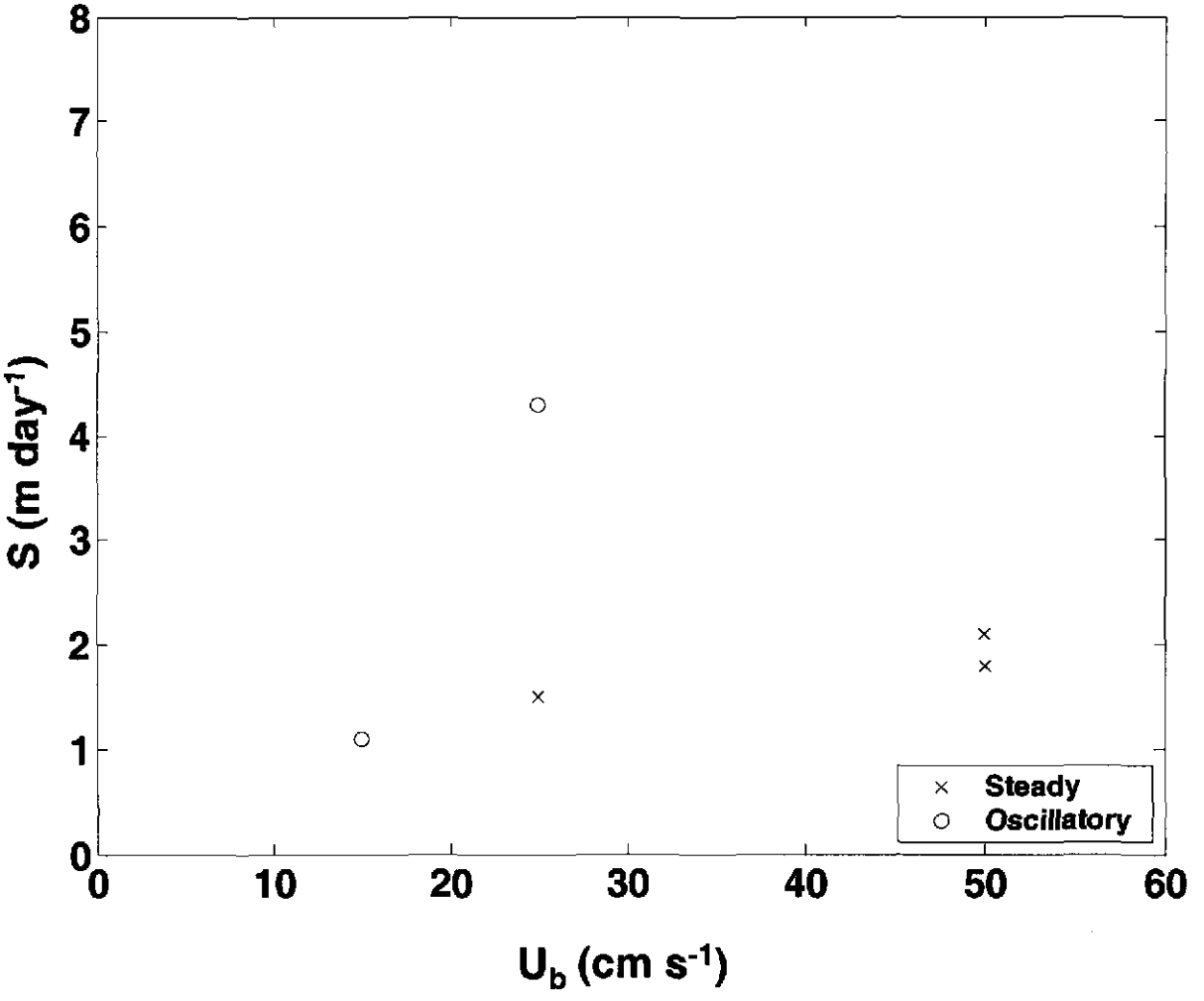

Figure 8. S versus U_b for Coral Community 1. There is an increase in S with U_b for both steady and oscillatory flow.

following a first-order relationship (Figure 9). S ranged from 3.9 to 6.9 m day^{-1} at water velocities of 10 to 50 cm s^{-1} (Figure 10).

ALGAE COMMUNITY 3

Three pairs of experiments were performed with Algae Community 3 over a period of nine days. Each pair of experiments included a steady and an oscillatory experiment, both done at the same water velocity. The first pair is shown in Figure 11. The community was exposed to oscillatory flow at 50 cm s^{-1} between each pair in an effort to keep biomass constant; minimal growth was observed on the sides of the flume and changes in the biomass of the benthos were not apparent. S values ranged from 4.5 to 6.5 m day^{-1} at water velocities of 10 and 50 cm s^{-1} (Figure 12). A paired t-test failed to show a significant difference in uptake under steady versus oscillatory flow.

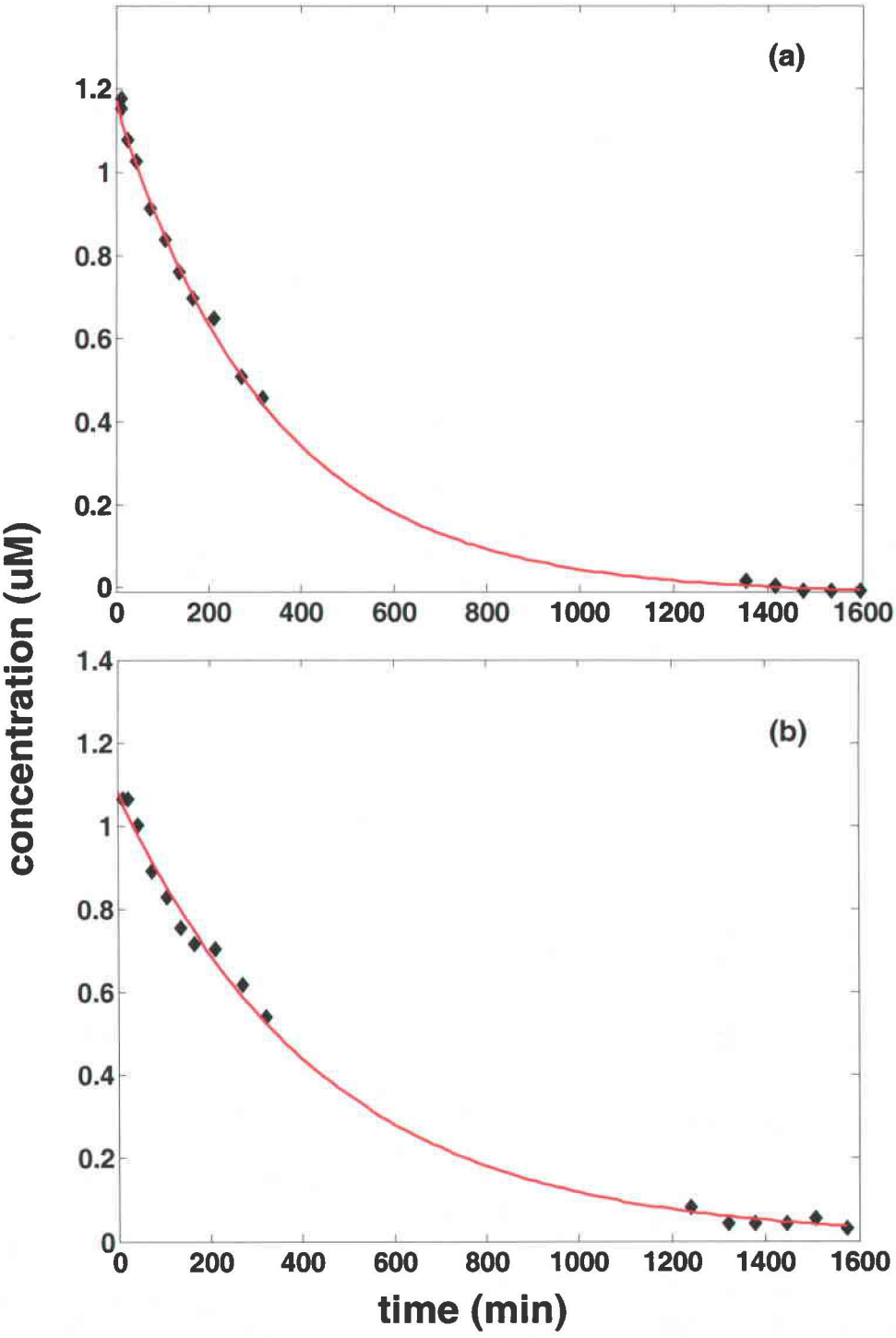

Figure 9. Example uptake curves for Algae Community 2. Both experiments were conducted in steady flow; x030404 (a) was conducted at a higher velocity and showed a higher uptake rate than x020409(b; 50 and 25 cm s^{-1} and S of 6.9 m day^{-1} and 5.3 m day^{-1}).

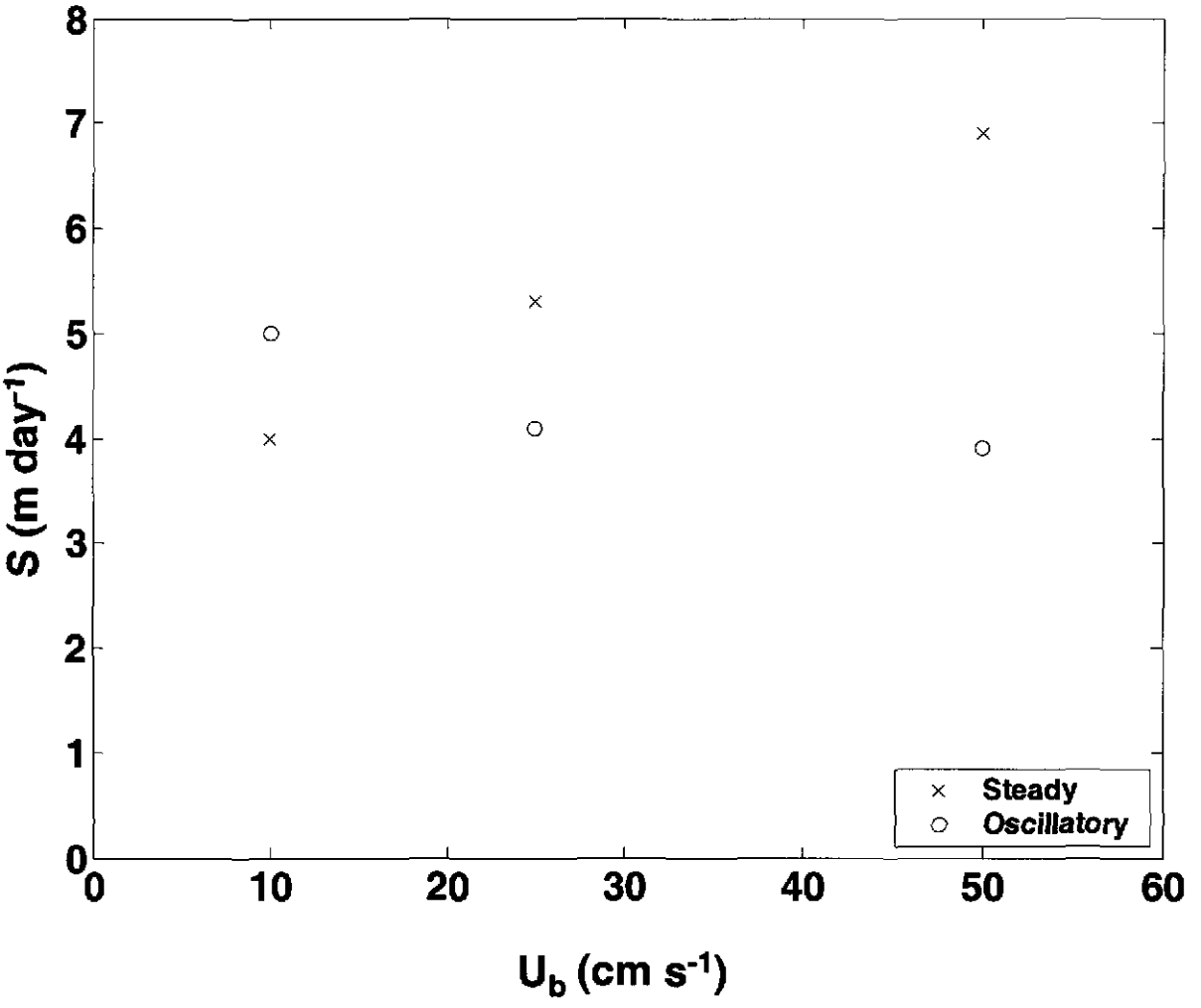

Figure 10. S versus U_b for Algae Community 2. There is an increase in S with U_b for steady flow. Changes in reactive surface area are probably responsible for the varying response of S to U_b for oscillatory flow.

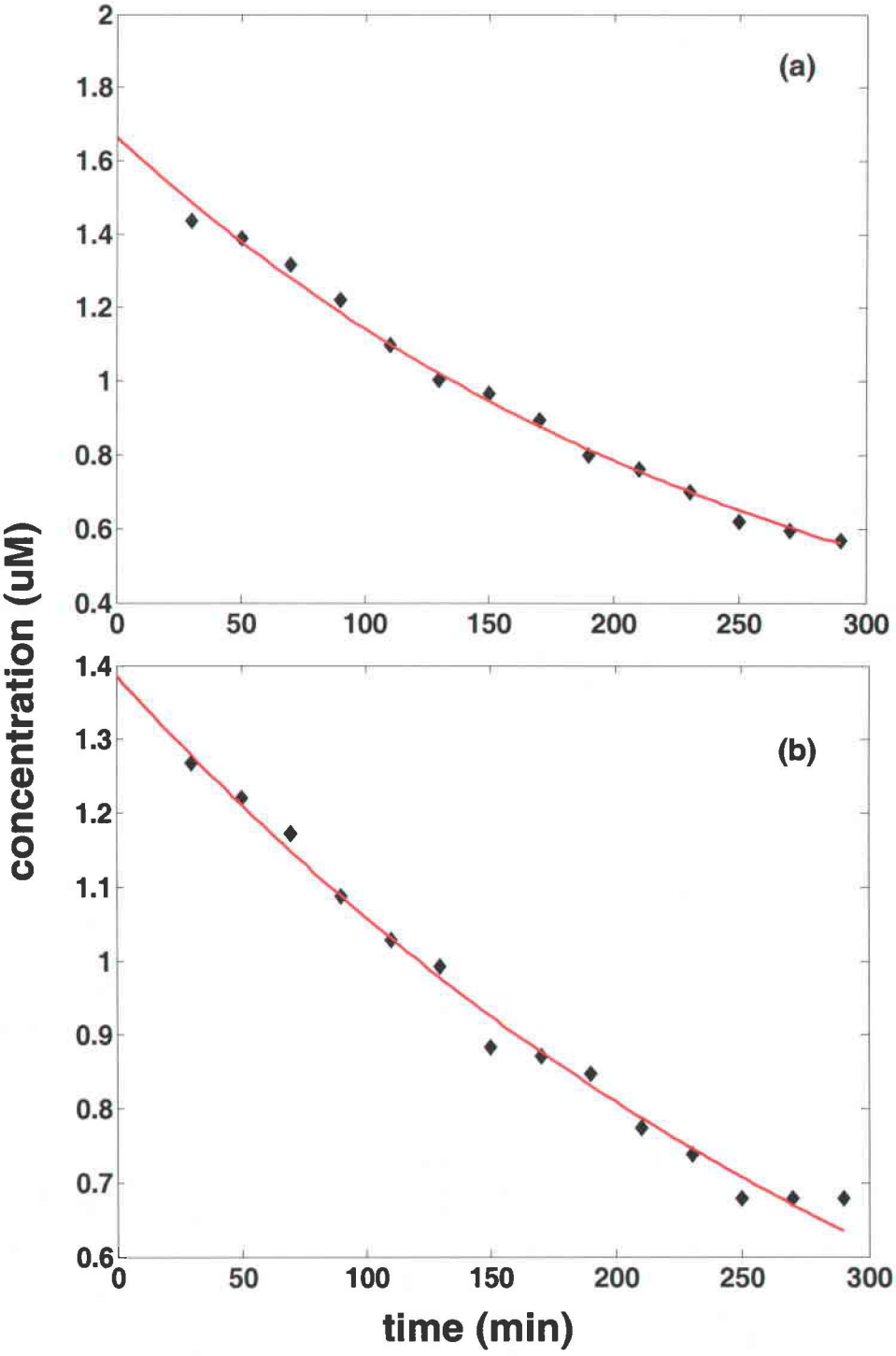

Figure 11. Example uptake curves for Algae Community 3. Experiment x030715 is shown in (a) and experiment x030716 is shown in (b). Both experiments were conducted at 50 cm s^{-1} and both had uptake rates of 6.5 m day^{-1}, eventhough (a) was oscillatory flow and (b) was steady flow.

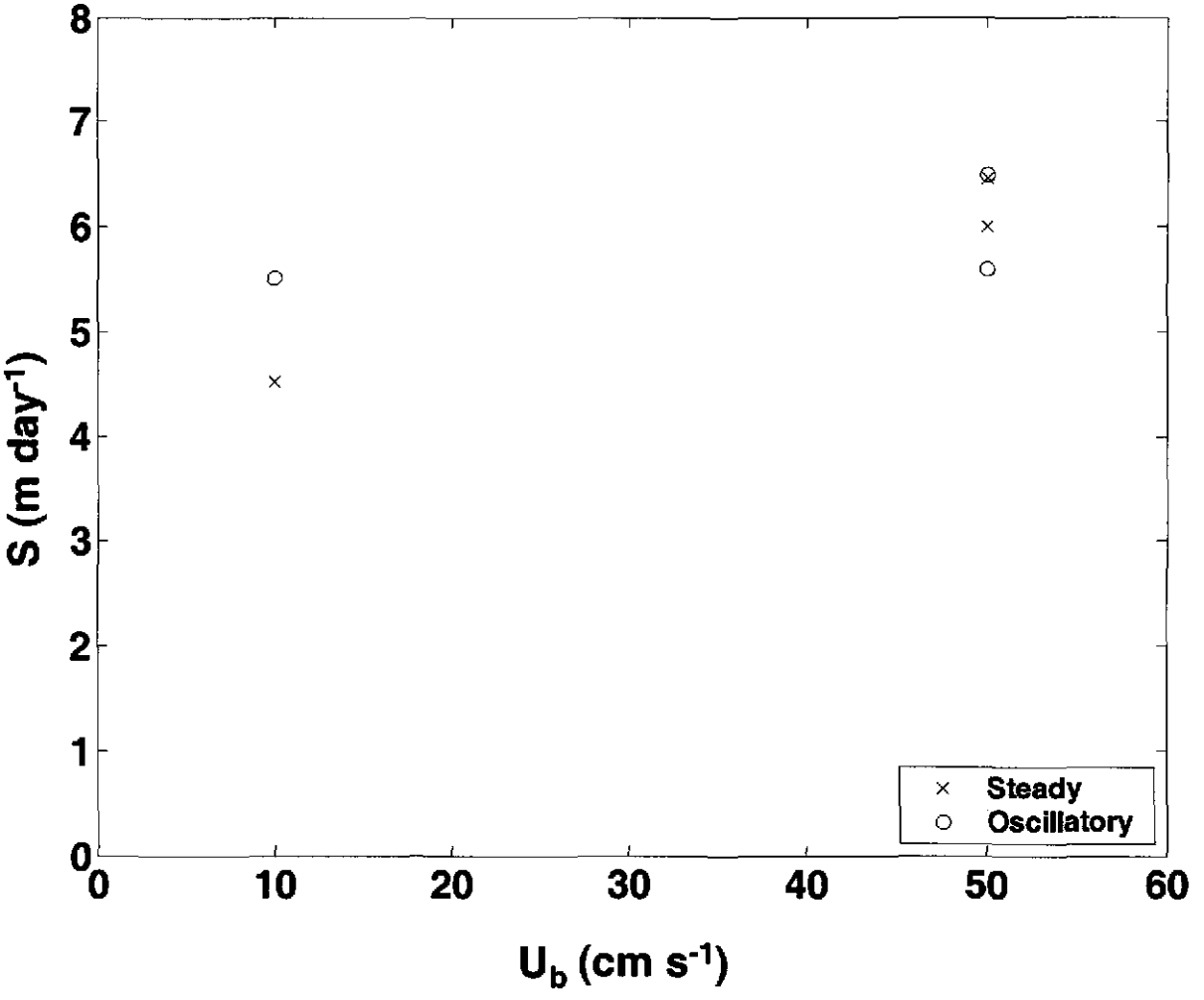

Figure 12. S versus U_b for Algae Community 3. There is an increase in S with U_b for both steady and oscillatory flow if values of S at the same velocity are averaged.

DISCUSSION

MASS-TRANSFER LIMITATION

To evaluate the hypothesis, nutrient-uptake must be close to the mass-transfer limit, i.e., S is proportional to U_b. Coral Community 1 and Algae Community 3 show weak, linear relationships between S and U_b (see Figures 8 and 12). The experiments on Algae Community 1 were conducted at the same velocity so this test for mass-transfer limitation cannot be performed. The first three experiments on Algae Community 2 show an increase in S with U_b (see Figure 10), but the last three experiments were more influenced by reactive surface area effects, as discussed below. It appears that the communities were close enough to mass-transfer limitation to evaluate the hypothesis.

If the communities were completely limited by mass-transfer at all times, then a stronger correlation of phosphate-uptake to water velocity would be expected. The variablility in the response of phosphate-uptake to water velocity is on the same order as past studies. A re-evaluation of literature data (Atkinson and Bilger 1992, Bilger and Atkinson 1995, Larned and Atkinson 1997, and Steven and Atkinson 2003) shows that phosphate-uptake does not correlate to water velocity as well as ammonia-uptake. This may be interpreted to mean that the biological demand for phosphorus is less consistent than for nitrogen. Light, oxygen, and nutrient-loading may have affected the biological demand for phosphate in the communities of this study.

Light

Theoretically, a community may have lowered biological demand for nutrients if the quantity and/or quality of light are sub-optimal. Artificial lighting for the flume was chosen based on published light-saturation data. Photosynthesis-irradiation curves can give a measure of the quantity of photons required for coral to reach the maximum rate of photosynthesis (P_{max}). Unfortunately, flow is not considered when calculating P_{max} and the true amount of required photons may be higher than reported in the literature (Bob Carpenter, personal communication); therefore, the lighting for the flume may not provide enough photons for the communities to reach P_{max}. In addition, the measured photon output of the flume lights averages 350 to 400 $\mu E\ m^{-2}\ s^{-1}$, which is less than expected based on the manufacturer's claims. The length of daylight was increased for Algae Community 3 from 12 to 16 hours. No significant increase in S was observed, but an even greater increase in the length of daylight may increase S. This possibility will be tested in future flume experiments.

Quality of light, i.e. spectral distribution of the light, may also be inadequate. Spectra indicate that the flume light is multi-peaked (Figure 13) and does not mimic the smooth spectra of sunlight. A new lighting system for the flume is currently being developed to address the issues of quantity and quality of light.

Oxygen

Although insufficient oxygen could cause a community to operate at lower than mass-transfer limited rates, it appears that enough oxygen was available to

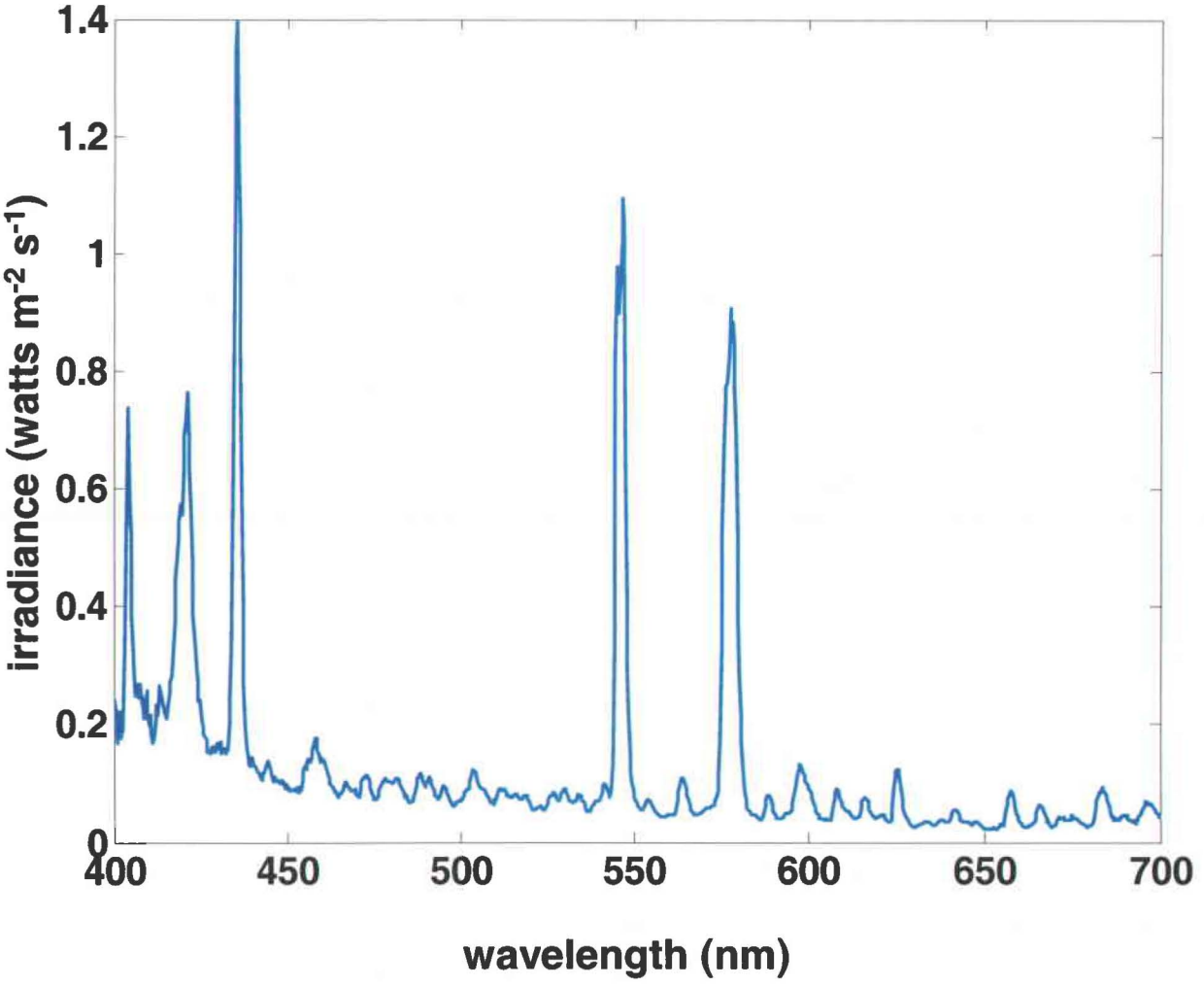

Figure 13. Spectrum of photosynthetically-available light produced by flume lighting. Six 400-watt metal halide bulbs hang over the flume in refelective hoods. The spectrum is multi-peaked and does not match the smooth spectrum of natural sunlight.

these communities. Measurement of dissolved oxygen of Algae Community 2 over a 24-hour period revealed that the peak oxygen concentration was found at the end of the light period (252 μM O_2) and the lowest concentration was at the end of the dark period (115 μM O_2); these results are expected. Net primary production (NPP) was 300 mmol C m^{-2} day^{-1}, while the respiration rate was 190 mmol C m^{-2} day^{-1}. Assuming that the respiration rate is constant over the 24-hour period, gross primary production (GPP) was 500 mmol C m^{-2} day^{-1}, close to the average production rate for reef-flat coral/algal zones, 600 mmol C m^{-2} day^{-1} (Kinzie 1985).

Nutrient-Loading

Excessive phosphate-loading can depress phosphate-uptake rates (Bilger and Atkinson 1995). All communities experienced phosphate-loading rates comparable to *in situ* conditions and below loading rates that have been shown to depress phosphate-uptake. Loading rates were between 0.29 and 1.9 mmol P m^{-2} day^{-1} for Coral Community 1 and between 0.22 to 0.52 mmol m^{-2} day^{-1} for the algae communities. Steven and Atkinson (2003) found that phosphate-loading was 1.2 mmol m^{-2} day^{-1} at background nutrient concentrations and that S did not significantly vary for an individual microatoll between "low loading" (1.3 mmol m^{-2} day^{-1}) and "high loading" (7.8 mmol m^{-2} day^{-1}). Larned and Atkinson (1997) showed that phosphate-loading at a maximum of 4 mmol day^{-1} was not too high as evidenced by the fact that tissue concentrations of phosphorus did not increase during successive runs. Phosphate-loading did significantly decrease S in Bilger and Atkinson (1995) when loading rates reached up to 7 mmol m^{-2} day^{-1}.

Compared to these literature values, the experiments conducted in this study had acceptable phosphate-loading conditions.

While excessive phosphate-loading lowers the rate of phosphate-uptake, nitrogen-loading may increase the rate of phosphate-uptake. This new idea is supported by data in this study and in the literature. In the present study, it was observed that the addition of ammonia correlated to a near-doubling of the phosphate-uptake rate. This finding spurred a re-analysis of literature data.

Bilger and Atkinson (1995) interpreted a large increase in phosphate-uptake rate to be caused by phosphate starvation, but a closer examination of the data reveal that nitrogen-loading may have increased the phosphate-uptake rate. During the phosphate starvation period, nitrogen-loading was increased 3-4 times for a few days. The following phosphate-uptake rates were elevated by 2-3 times. To separate the effect of nitrogen-loading from phosphate starvation, it is necessary to look at a second time period in which the community was relatively starved for phosphate but nitrogen-loading was low. Phosphate-uptake rates were not elevated after this period of time, lending evidence to the idea that nitrogen-loading was responsible for the observed increase in phosphate-uptake. Interestingly, Steven and Atkinson (2003) documented that for the microatolls of One Tree Reef Lagoon, Australia, the uptake of phosphate was correlated to the uptake of ammonia, but not correlated to wind speed, which was used as a proxy for water motion.

When the results from this study, the Bilger and Atkinson 1995 study, and the Steven and Atkinson 2003 study are plotted on Figure 14, the correlation

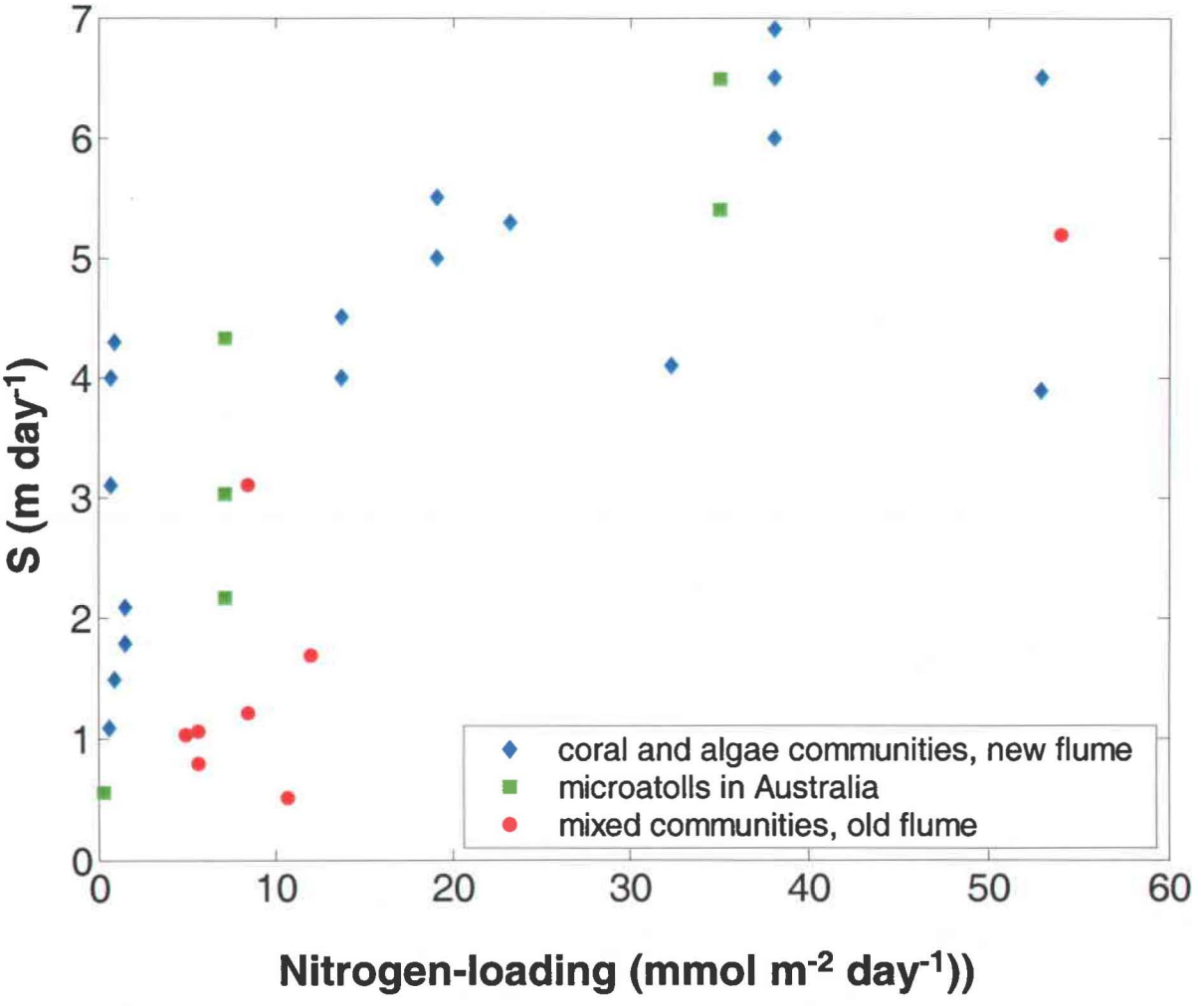

Figure 14. The effect of nitrogen-loading on phosphate-uptake. The addition of nitrogen increases phosphate-uptake rate until a threshold of 30 mmol N m^{-2} day^{-1}. Phosphate-uptake reaches a maximal, mass-transfer limited rate of 6 to 7 m day^{-1}. Blue diamonds, this paper; green squares, Steven and Atkinson 2003; red circles, Bilger and Atkinson 1995.

between phosphate-uptake and nitrogen-loading is apparent. Note that Figure 14 does not correct for three factors that affect S, namely velocity, phosphate-loading rate, and community type, so considerable scatter is expected. Figure 14 shows that as nitrogen-loading increases, so does phosphate-uptake, until a level at which increases in nitrogen-loading do not result in further increases in phosphate-uptake. This maximal value of S is probably the mass-transfer limited uptake rate, which may only be reached if nitrogen-loading is sufficient. The maximal, mass-transfer limited phosphate-uptake rate is about 6 to 7 m day^{-1} (see Figure 14). The importance of nitrogen-loading will be revisited later in this discussion.

Steady versus Oscillatory Flow

A difference in phosphate-uptake under steady versus oscillatory flow was not observed; therefore, the null hypothesis is accepted. The methods for Algae Community 3 were the most finely-tuned to test the hypothesis, and the results failed to show a significant difference. Instead, it was observed that phosphate-uptake was approximately constant under steady and oscillatory flow.

Algae Community 2 demonstrated enhanced uptake under steady flow for two of the three velocities (see Figure 10 and Table 1), which is the opposite result of what was expected; however, it is likely that this is a result of increasing biomass of the algae on the benthos and sidewalls of the flume. Since the planar surface area of the community is used to normalize S, changes in biomass and the resulting changes in reactive surface area are not included in the

calculations. To understand the reactive surface area effect in Algae Community 2, it is helpful to first look at Algae Community 1.

The purpose of these experiments on Algae Community 1 was to see whether there is a significant difference in S as the community acclimates to the flume environment. The flume was not cleaned between experiments and biomass growth was observed. The S for the second experiment was 30% higher than for the first experiment. This can be used as an estimate of the effect of reactive surface area on S, which is approximately a 30% increase in S over one week at the nutrient concentrations and flow parameters of these experiments. Algal growth rate was observed to be larger for Algae Community 2, suggesting a greater than 30% increase, but the sidewalls were cleaned during the Algae Community 2 experiments; these counterbalancing factors allow an approximation of 30%.

The first three experiments on Algae Community 2 were conducted under steady flow in order of decreasing velocity. Although the walls were partially cleaned between experiments, reactive surface area increased from x030404 to x030414. Assuming 30% artificial increase as discussed above, S for x030414 (10 cm s^{-1}) should have been about 2.6, meaning that the slope of S vs. U_b for steady flow should have been more steep.

Algae Community 2 was collected from a relatively low-energy environment and was only exposed to steady flow until after the third experiment. When the flow was changed to oscillatory, wave action drastically decreased the reactive surface area by breaking off large fronds of macroalgae and scrubbing

algae from the sidewalls. It is likely that the community had less reactive surface area for the oscillatory, 50 cm s^{-1} experiment (x030421) than for the steady, 50 cm s^{-1} experiment (x030404), which explains why S is lower for the oscillatory experiment.

The last three experiments on Algae Community 2 were conducted under oscillatory flow in order of decreasing velocity. As velocity and therefore wave scrubbing decreased, reactive surface area increased. This explains why S did not increase with velocity as expected.

It is unlikely that the biomass of the community for the oscillatory, 10 cm s^{-1} experiment (x030505) was the same as for the steady, 10 cm s^{-1} experiment (x030414), but the relative biomasses were not determined. Comparison of the 10 cm s^{-1} experiments suggests a wave enhancement factor of 1.3, but it is unclear whether this enhancement is real.

The reactive surface area effect discussed above was not important to the coral communities because 1) the wave motion was not ever large enough to break pieces of coral and 2) sidewall growth was minimal in the coral communities, presumably because no nitrogen was added. There is one pair of experiments on Coral Community 1 that might be used to evaluate whether there is an enhancement due to oscillatory flow: x020824 and x020830 (see Table 1 and Figure 8). It appears that the oscillatory experiment, x020824, has an S almost three fold larger than the steady experiment, x020830; however, the error bounds on S for x020824 are anomalously large and forbid the comparison of this pair of experiments.

The methods for Algae Community 3 reflect what was learned about the reactive surface area effect. Pairing experiments, with 24 hours between the start of experiments in a pair, allowed for better comparison of flow regimes. By subjecting the community to intense wave action on the first day in the flume and between each pair, biomass was maintained at a nearly constant level. Phosphate-uptake was constant under steady and oscillatory flow for Algae Community 3.

These experiments are the first attempt to directly compare nutrient-uptake by experimental communities under steady and oscillatory flow. The outcome of this study may have been different if a parameter other than bulk flow speed was used as a basis of comparison between steady and oscillatory flow. The wave-enhancement of metabolic processes found in past studies may be more directly attributed to a physical parameter other than flow type, such as turbulence, large-scale roughness, and drag. For example, as noted by Atkinson *et al.* (2001), the turbulent dissipation of energy caused by drag caused from large coral knolls in the Biosphere cannot be produced in a flume. S in the Biosphere community may be higher than experimental communities in flumes because of differences in large-scale roughness.

There is current debate over what scales of roughness affect S. Only one study reports S for an *in situ* community (Stevens and Atkinson 2003), but since water velocity was not measured, it is unknown how this value of S compares to experimental communities. Falter (2002) placed gypsum molds in the field and found that their rates of dissolution were 1.4 to 2.0 fold higher than the rates of

dissolution in a steady-flow flume; multiple physical parameters vary from field to flume, only one of which is flow type. Turbulence, large-scale roughness and drag, and other physical parameters that could affect boundary layer formation, and thereby affect nutrient-uptake, should be studied in future experiments.

NUTRIENT EXCRETION

The excretion term r could be calculated for long experiments with reasonable excretion rates (see Table 1). Calculated r's ranged from 0 to 2.1 mmol m^{-2} day^{-1}. This agrees with the *in situ* community at One Tree reef lagoon, Australia, which has an r of 0.9 mmol m^{-2} day^{-1} (Steven and Atkinson 2003).

There is not enough data to evaluate a trend in r for Coral Communities 1 and 2 and Algae Community 1. Excretion increased with each successive experiment on Algae Community 2 (Figure 15). Excretion of nutrients by a community could increase over time if the community was loaded excessively or if the heterotroph to autotroph ratio of the community changed over time. Nutrient-loading is probably not the cause of the observed increase in r since nutrient-loading was not excessive (see above discussion). It is more likely that Algae Community 2 experienced an increase in the abundance of heterotrophic organisms. The observed accumulation of detritus in the flume could harbor bacteria that excrete phosphorus back into the water.

METHOD DEVELOPMENT

Part of the emphasis of this study was to develop a method to cultivate and experiment with coral reef communities in the new flume. With each new community, lessons were learned and methods changed. The communities'

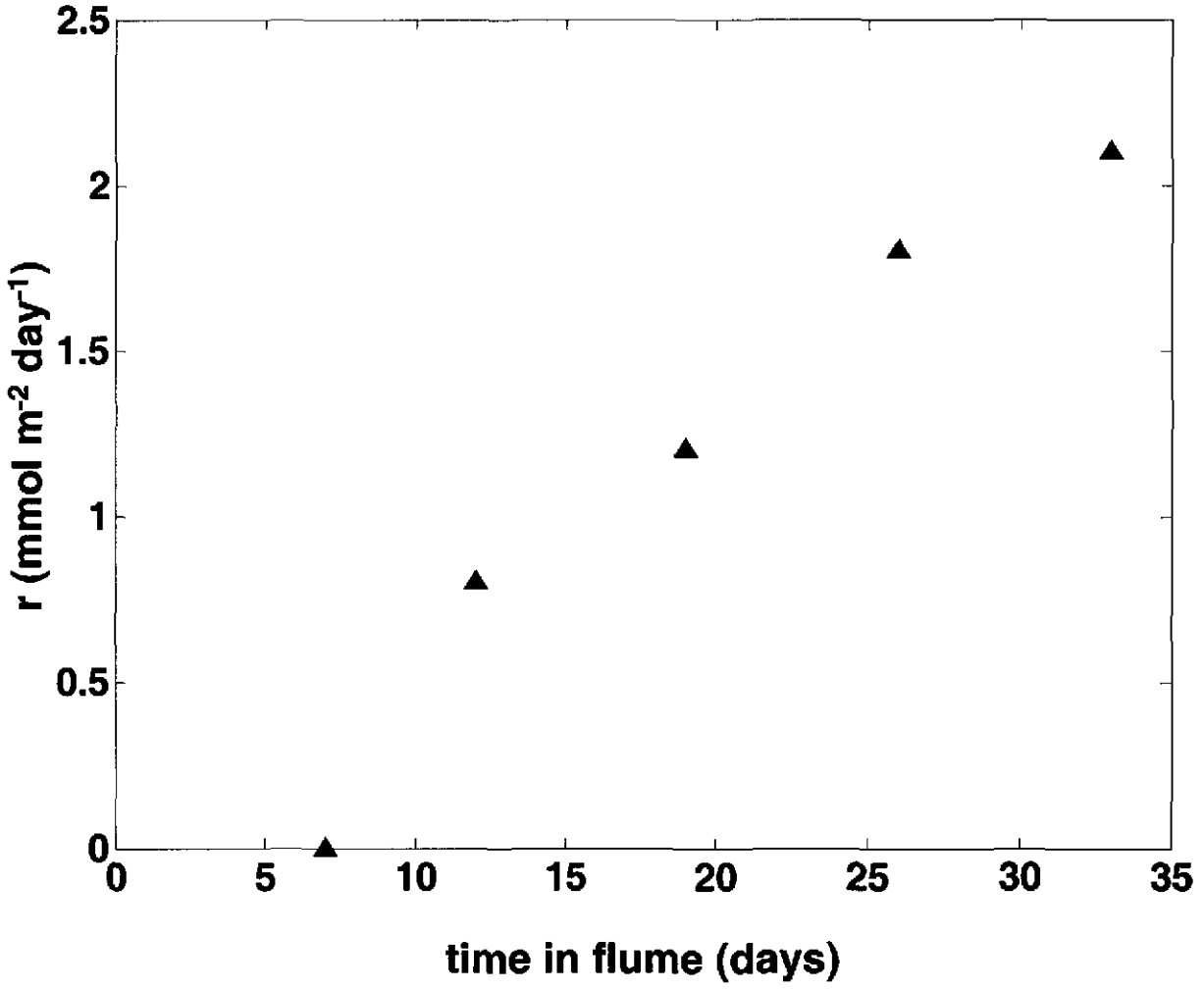

Figure 15. Excretion rate versus time for Algae Community 2. Excretion rate increased with time, probably due to increased heterotrophic bacteria living in detritus that accumulated in the flume over time.

average S increased over time (average S = 2.5, 3.6, 4.9, and 5.8 m day^{-1}), probably in response to evolving methods that improved the health of the communities.

Important method developments included: 1) the addition of nitrogen, 2) decreased experiment length, 3) pairing experiments to aid comparison, and 4) exposing the community to high energy between experiments. It is suggested that nitrogen and phosphorus be added together in future experiments. It is also suggested that the duration of experiments be minimized so that phosphate-loading can be kept at acceptable levels. Also, it is encouraged to minimize the time that a community is in the flume. It is desirable to keep the communities close to their *in situ* species composition and structure and the longer a community is in the flume, the more it adapts to the artificial environment. Excretion of nutrients may increase with the duration of time that a community is in the flume.

To compare uptake rates under different flow regimes, it is suggested that experiments be paired and that the community be exposed to the highest level of momentum transfer before every experiment. Ideally, changes in reactive surface area should be measured and then used to normalize S, but this is not practical. Instead, the community may be brought to a quasi-replicable community structure and biomass by exposure to high energy, such as high-velocity wave action.

The methods presented here still need improvement. Lighting needs to be adjusted to more closely mimic natural sunlight. Additionally, bulk flow speed

may not be the best parameter to compare steady and oscillatory flows. The difference in boundary layer formation under these flow regimes may be due to a physical parameter such as turbulence. Measurements of turbulence by an ADV may more accurately describe flow conditions than U_b and may be a better measure for evaluating the hypothesis.

It is important to note that the observed increase in average S from Coral Community 1 to Algae Community 3 may be partially due to the switch from coral- to algae-dominated communities. In other words, community composition may be important in determining S. It is possible that coral communities take-up nutrients at a slower rate than algae communities because of a physical characteristic of the community, such as roughness. A second possibility is that the observation of greater S for algae is an artifact of flume conditions. The coral communities may have had relatively low values of S because of greater sensitivity to light fields or nitrogen availability. The connection between community composition and nutrient-uptake is explored further in the "Comparison with Past Studies" section.

COMMUNITY PRODUCTION FROM S

NPP of a community may be estimated by measuring S if the phosphate concentration, P/R ratio, and C:P ratio of the community are known. Using average literature values for the preceding three quantities allows the calculation of the rate of NPP given an average S. For Algae Community 2, the average S was 4.9 m day^{-1}, which equates to 440 mmol C m^{-2} day^{-1}. This agrees remarkably with 500 mmol C m^{-2} day^{-1} calculated by measuring oxygen (see above)

considering all of the averages used in the calculation. Conversely, it is possible to back-calculate the S required to sustain measured GPP in the field. An uptake rate of 6.7 m day^{-1} equates to the average GPP measured for reef-flat coral/algal zones, 600 mmol C m^{-2} day^{-1} (Kinzie 1985).

COMPARISON WITH PAST STUDIES

Overall, S ranged from 1.1 to 6.9 m day^{-1} over a U_b range of 10 to 50 cm s^{-1} (excluding Coral Community 2). These results fall within the range of S's reported in the literature: 0.4 to 13 m day^{-1} over a U_b range of 4 to 58 cm s^{-1} (Atkinson and Bilger 1992, Bilger and Atkinson 1995, Larned and Atkinson 1997, Atkinson *et al.* 2001, Steven and Atkinson 2003; Figure 16).

Community type appears to have a large influence on S, perhaps because of roughness characteristics. As roughness increases, reactive surface area also increases, but changes in reactive surface area are not accounted for in the calculation of S. Algae-dominated communities (shown in green in Figure 16) have a similar response to velocity. A best-fit linear regression through the algae communities (Line A) gives an intercept value of 2.9 m day^{-1} for zero velocity. This correspondence is particularly interesting since these experiments were *done in three extremely different environments; some were done in the new* flume described herein, some were done in a one-way recirculating flume (Larned and Atkinson 1997), and one was a control experiment done in a small aquarium under zero flow, which gave an uptake rate of 2.3 m day^{-1}.

Coral-dominated communities (shown in red) fall below Line A, but this is possibly due to problems in cultivation of these communities (see previous

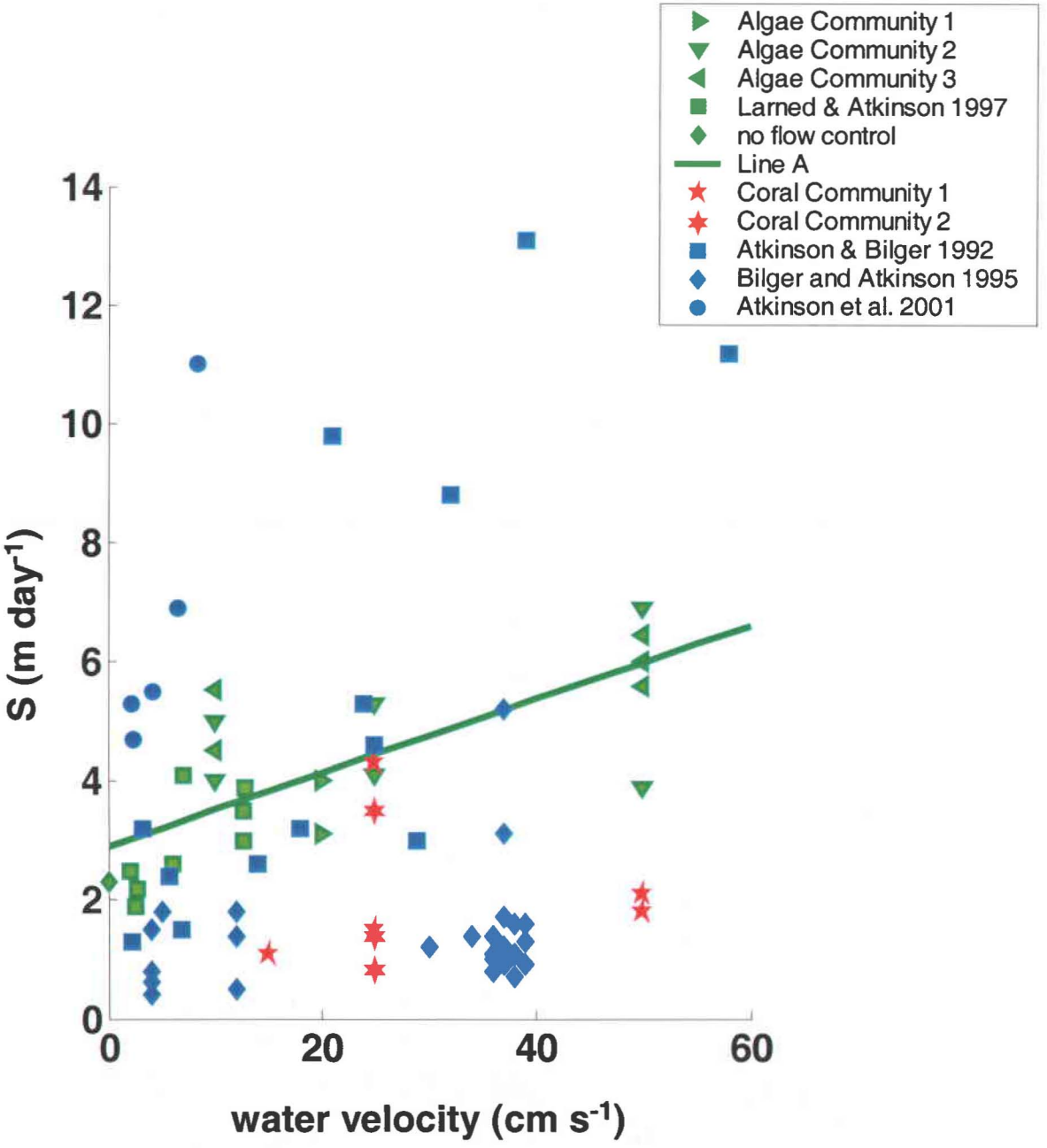

Figure 16. Results from this study compared to published data from past studies. Algae-dominated communities are shown in green, coral-dominated communities are shown in red, and mixed coral and algae communities are shown in blue. Line A represents the linear regression for the algae-dominated communities. Response of S to U_b seems dependant on community composition, community size, and nutrient- loading history.

section, "Method Development"). These findings should not be used to generalize S for coral communities.

Mixed algae and coral communities (shown in blue) have varied responses to velocity partly due to different experimental conditions and possibly also due to different community composition. Bilger and Atkinson (1995) data plot below Line A because those communities had depressed S as a result of excessive phosphorus-loading. Atkinson and Bilger (1992) experimented upon two communities, both of which were reported to have similar community composition. One community had much higher uptake rates (blue squares above Line A) than the other (blue squares at and below Line A). The difference in these two communities is not explained by the authors and is not apparent. Since the communities were both experimented upon in the same flume under similar velocities, there are no obvious differences in the physical characteristics of the communities. The difference may be due to nitrogen-loading effects; nitrogen was added sporadically if the community looked "unhealthy" (Atkinson, personal communication) but nitrogen additions are not documented in the publication.

The Biosphere 2 community (Atkinson *et al.* 2001) appears to have anomalously high values of S; the authors suggest that the anomaly is due to 1) wave action or 2) the large coral knolls in the Biosphere community may create a much larger drag than can be produced in flumes. In light of the results of this study, the second suggestion seems most probable and agrees with the findings of Falter (2002) who found enhanced mass-transfer in the field compared to the flume. Alternatively, the elevated values of S may be due to nitrogen-loading

effects; the concentration of nitrogen in the Biosphere is approximately twice ambient nitrogen concentrations (Atkinson *et al.* 2001).

PHOSPHATE-UPTAKE IN THE FIELD

It appears that phosphate-uptake occurs at mass-transfer limited rates in the field. As discussed above, Figure 14 shows that the maximal, mass-transfer limited phosphate-uptake rate is reached only if nitrogen-loading is sufficient, i.e. greater than 30 mmol N m^{-2} day^{-1}. Total (particulate and dissolved) nitrogen-loading in the field over a coral reef is approximately 30 mmol m^{-2} day^{-1}(Ribes *et al.* 2003), so it appears that nitrogen availability will not limit phosphate-uptake in the field.

The mass-transfer limited phosphate-uptake rate is about 6 to 7 m day^{-1} (see Figure 14 and above discussion). Three separate estimates of phosphate-uptake in the field converge on this value of S: 1) as discussed above, average GPP of a coral reef ecosystem equates to S of 6.7 m day^{-1}, 2) phosphate-loading in the field is approximately 1 mmol P m^{-2} day^{-1} (Steven and Atkinson 2003), which equates to an S of 7 m day^{-1} using the equation Loading = S x [P], and 3) phosphate-uptake was measured directly for the Kaneohe Bay Barrier Reef to be 7 m day-1 (Falter 2002). These numerical similarities suggest that phosphate-uptake occurs at mass-transfer limited rates in the field.

THE LINK BETWEEN UPTAKE KINETICS AND STOICHIOMETRY

As stated in the introduction, the mechanisms that determine C:N:P ratios have not been determined. The N:P ratio is partially explained through mass-transfer theory. The rate-limiting step to nutrient-uptake is molecular diffusion. If

the concentrations of ammonia and phosphate were equal, then the ratio of ammonia- to phosphate-uptake would occur at a ratio of about 2:1, based on the diffusivities of these molecules. The concentrations of ammonia and phosphate are not equal, however, because there is a larger supply of nitrogen than phosphorus. In addition to nitrogen-fixation (Atkinson 1992), there is a high rate of uptake of particulate nitrogen (10-30 mmol particulate N m^{-2} d^{-1}) compared to particulate phosphorus (0.6 mmol particulate P m^{-2} d^{-1}; Ribes *et al.* 2003). Sponges take-up particulate nutrients, remineralize them, and release dissolved nutrients (Ribes *et al.* 2003), which are later available for uptake by the autotrophs.

Because the concentration of phosphorus is much lower than that of nitrogen, and because uptake rates are proportional to concentration under mass-transfer theory, the rate of phosphate-uptake is low relative to nitrogen-uptake. This leads to the observed benthic autotroph N:P ratio of 30:1. It is interesting to note that the measured *in situ* nutrient-loading rates (30 mmol N m^{-2} day^{-1} and 1 mmol P m^{-2} day^{-1}) correspond to the N:P ratio.

NUTRIENT LIMITATION

It is not known whether nitrogen or phosphorus is limiting to primary production on reefs. This discussion suggests that phosphorus may be the macronutrient that limits primary production on reefs. The supply of phosphorus is less than that of nitrogen, so the phosphate-uptake rate is lower than that of nitrogen. This hypothesis, that phosphorus is limiting to production on reefs, should be tested in the near future.

CONCLUSION

The data presented herein do not support the idea that phosphate-uptake operates at different rates under steady versus oscillatory flow. Phosphate-uptake for typical reef flat communities appears to become mass-transfer limited rates of 6 to 7 m day^{-1}. I suggest that these rate constants are not achieved without sufficient loading of N, 10-30 mmol m^{-2} d^{-1}. Phosphate-uptake is likely occurring at mass-transfer limited rates in the field.

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