

## A novel flume for simulating the effects of wave- and tide-driven water motion on the biogeochemistry of benthic reef communities

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### Abstract

We present a new flume for simulating the effects of both steady and oscillatory flow on the biogeochemical fluxes to coral reef communities based on a modified U-tube design. The flume is designed to recreate the in situ characteristics of a wide range of flows generated by wind, waves, and tides through two configurations. In the first configuration, a propeller driven by a 12-V DC motor generates steady, unidirectional flow speeds of 5 to 70 cm s<sup>-1</sup>. In the second configuration, a piston driven by a 1500-W AC motor is used to generate oscillatory flows that are 5–12 s in period and have root-mean-square flow speeds of up to 50 cm s<sup>-1</sup>, thus simulating the kinematics of real surface gravity waves in coral reef environments. Experimental coral reef communities are housed in a 3-m long test section covered with acrylic windows and lit with either 400- or 1000-W metal halide lamps generating photosynthetically active radiation (PAR) irradiances of up to 1000 μEin m<sup>-2</sup> s<sup>-1</sup>. The ratio of the volume of water in the flume to the projected area occupied by the experimental communities ranges from 1.1 to 1.7 m, making possible the expedient measurement of chemical fluxes to and from experimental reef communities. The total cost of the flume is just under \$20,000 US for materials and approximately 700 person-hours of labor.

### Introduction

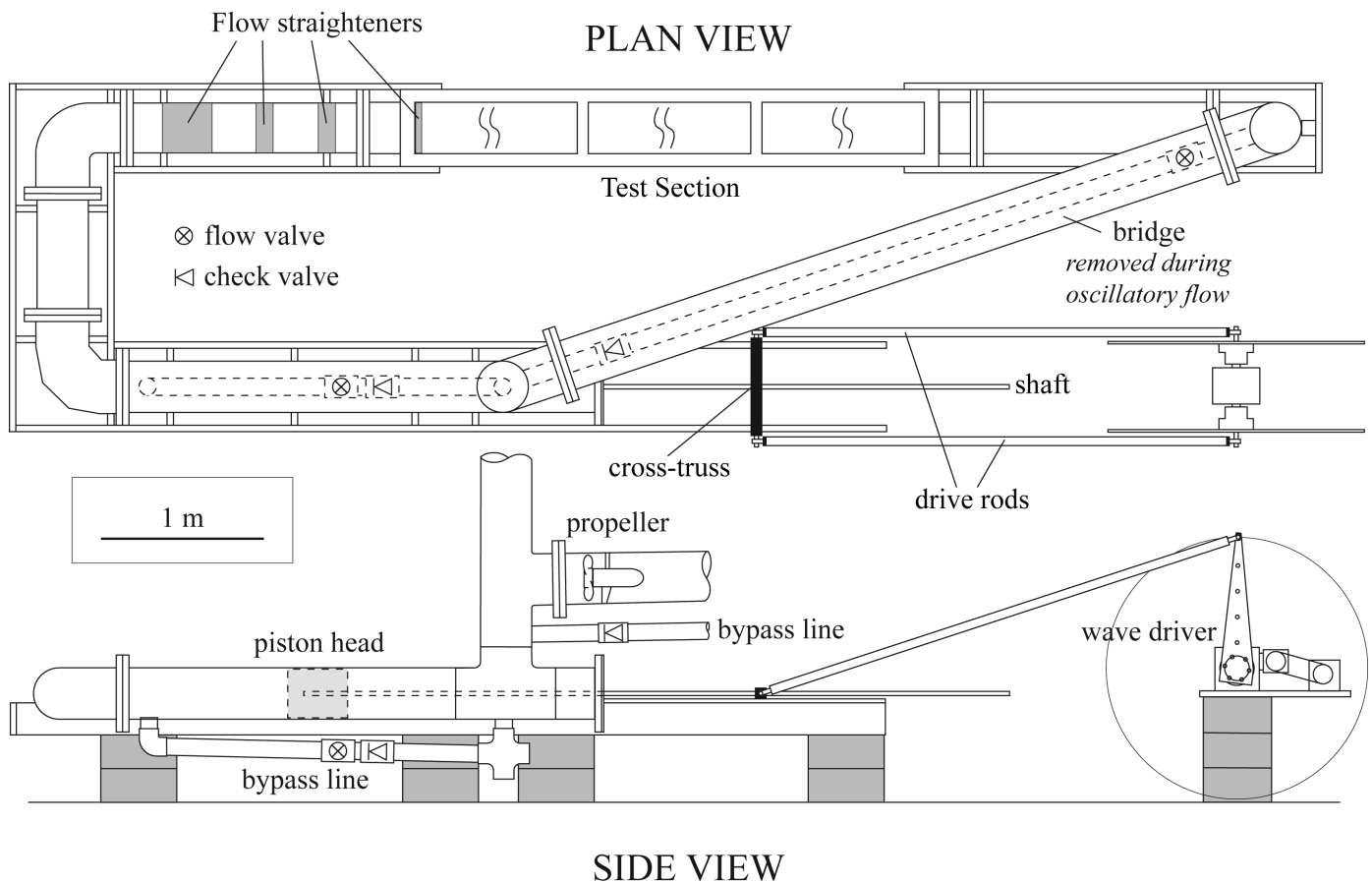
Research conducted over the past two decades has shown that water motion is a critical variable affecting the growth and metabolism of reef biota. Reef coral and algae exposed to increased water motion exhibit higher rates of photosynthesis and respiration (Carpenter et al. 1991; Dennison and Barnes 1988; Larkum et al. 2003; Lesser et al. 1994; Patterson et al. 1991; Sebens 2003; Williams and Carpenter 1998), nitrogen fixation (Carpenter et al. 1991; Williams and Carpenter 1998), and nutrient uptake (Atkinson and Bilger 1992; Atkinson et al. 2001; Larned and Atkinson 1997; Steven and Atkinson 2003; Thomas and Atkinson 1997). Water motion can also affect rates of particle capture by reef coral (Fabricius et al. 1995; Fabricius et al. 1998; Sebens et al. 1998; Sebens et al. 1997). Few studies have examined the effects of wave-driven, oscillatory

motion on the metabolism of living benthic organisms (Carpenter et al. 1991; Thomas and Cornelsen 2003; Williams and Carpenter 1998). Experimental flumes used in these studies, however, were limited by the range of flow speeds that could be generated as well as by their inability to reproduce periods of oscillation within the range of most surface gravity waves found in near-shore environments (5–16 s). Oscillatory flow resulting from the propagation and transformation of surface gravity waves can be the dominant source of water motion in shallow reef communities (e.g., Hearn et al. 2001; Munk and Sargent 1954; Nelson 1996; Young 1989). Maximum mass transfer rates of dissolved metabolites such as HPO<sub>4</sub><sup>2-</sup>, NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, O<sub>2</sub>, and CO<sub>2</sub> to and from benthic reef communities can be much greater under oscillatory flow than under steady flows of equal magnitude. Enhancement of mass transfer rates under oscillatory flow can vary with wave velocity, period, and orbital excursion amplitude (Falter et al. 2005; Lowe et al. 2005; Reidenbach et al. 2006).

The in situ measurement of chemical fluxes to and from coral reef communities would be ideal; however, most often the actual fluxes are too small relative to either the volume transport of water over the reef or to rates of horizontal mixing to generate significant estimates from spatial and temporal changes in the chemistry of the ambient water (Atkinson and Smith 1987). Artificial enclosures, such as fences, domes,

### Acknowledgments

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**Fig. 1.** Schematic of flume from both the plan and side views. All dimensions are drawn to scale.

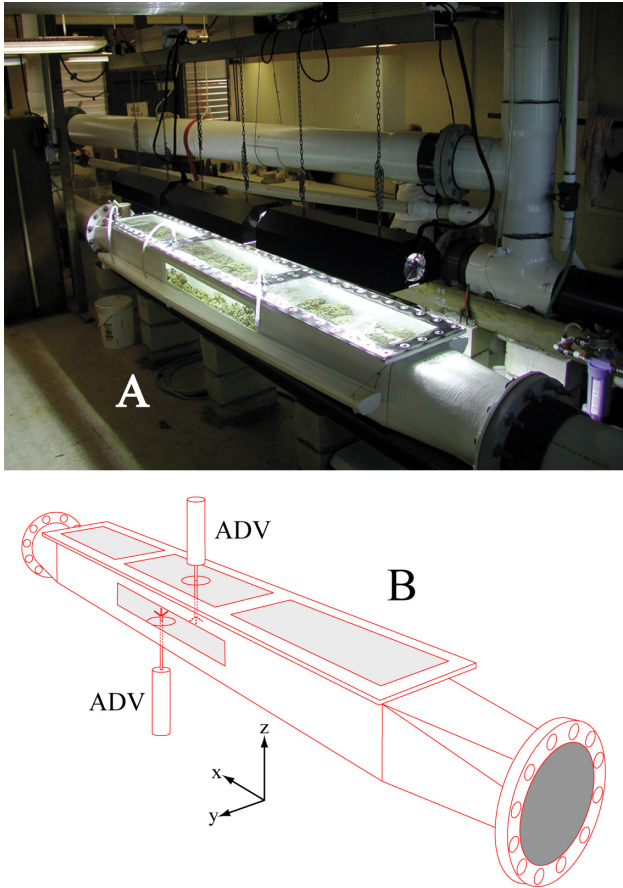
flumes, and tents, have been used to retain a control volume of water in contact with benthic reef communities, thereby increasing the metabolic signal in the water (Atkinson and Grigg 1984; Boucher et al. 1998; Yates and Halley 2003). Unfortunately, simple field enclosures fail to properly simulate the natural movement of water and thus fail to control the thickness and variability of benthic boundary layers.

Wave and current flumes originally designed purely for the study of fluid mechanics can be modified and adapted for the study and maintenance of living organisms while simulating the full range of flow conditions to which coral reef communities are exposed. We have developed such a flume capable of generating oscillatory flows of 5 to 12 s in period with root-mean-square (rms) flow speeds of up to  $50 \text{ cm s}^{-1}$  as well as steady, unidirectional flow speeds of up to  $70 \text{ cm s}^{-1}$ . These are flow speeds greater than most conventional wave-current flumes can generate. What further distinguishes this flume, other than the range of flow speeds it can generate, is that it is specifically designed for the measurement of important metabolic processes such as growth, net production, respiration, nutrient uptake and release, and calcification. It has also been designed to control for important environmental variables

other than flow, such as light and water chemistry, which can greatly affect the growth and metabolism of living organisms.

### Materials and procedures

**Main flume body**—The basic design of the flume is that of a U-shaped tube (see Gaylord et al. 1994) with the middle part of the U bent 180 degrees to fit inside our laboratory at the Hawaii Institute of Marine Biology (Figures 1 and 2). The main body of the flume is constructed from 0.3-m diameter, schedule 40 PVC pipe. The two upright standpipes of the flume rise 2.4 m above the middle section of the flume, which is 12.2 m long. The volume of water within the flume can vary from 1.0 to  $1.5 \text{ m}^3$  depending on the water level inside the standpipes. The maximum planar surface area occupied by the experimental community within the test section of the flume is  $0.9 \text{ m}^2$ , resulting in flume volume to community area ratios of between 1.1 and 1.7  $\text{m}^3$ . We have found that volume to surface area ratios of between 1 and 3 are well suited for conducting controlled metabolic experiments on other coral reef communities (Bilger and Atkinson 1995; Thomas and Atkinson 1997; Atkinson et al. 1999). It can easily be shown from the basic momentum equations that the natural period of oscillation



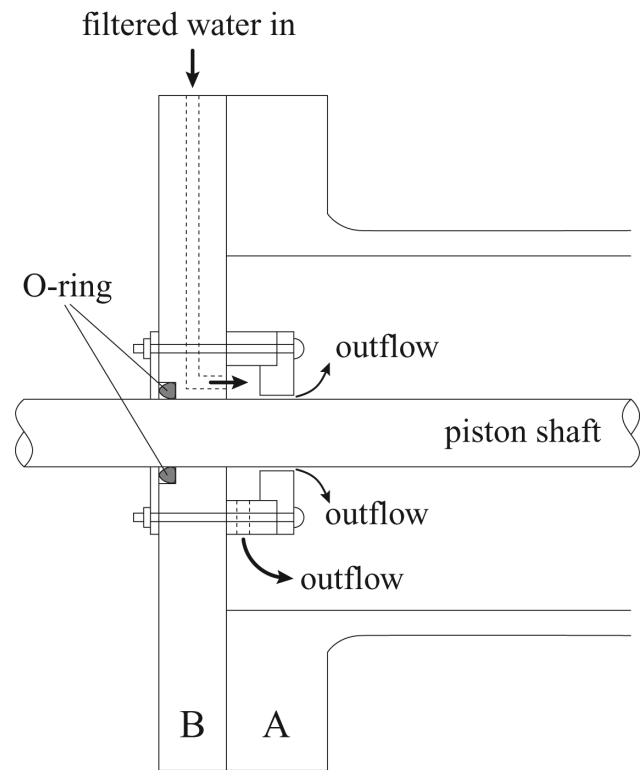
**Fig. 2.** (A) Image of the flume as viewed from the corner opposite the wave maker (see Figure 1). The test section is shown in the foreground with the two standpipes, bridge, and bypass lines evident in the background. (B) Drawing of test section showing possible top- and bottom-mounted positions for an ADV. The axes shown represent the coordinate system into which flows within the flume are decomposed.

( $T_n$ ) within a U-tube is a function of the total length of water from the free surface in one standpipe to the free surface in the opposite standpipe ( $L$ ),

$$T_n = 2\pi \sqrt{\frac{L}{2g}} \quad (1)$$

where  $g$  is the rate of gravitational acceleration. Ignoring frictional damping, minor differences between the cross-sectional area of the pipe and test section, and using  $L \approx 15$  m, Eq. 1 gives  $T_n \approx 5.5$  s.

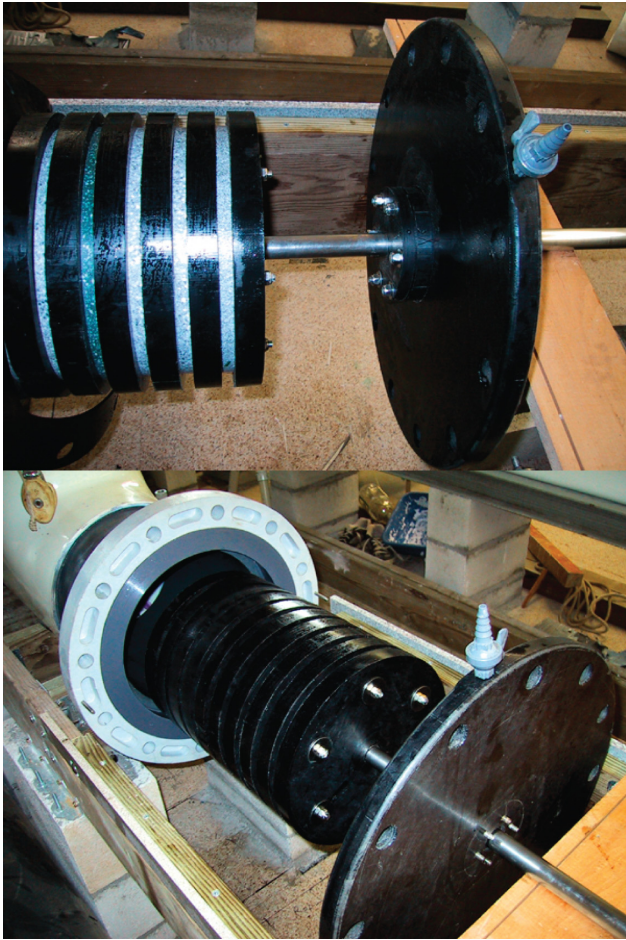
**Oscillatory flow generation**—Oscillatory flow is generated by a mechanical piston inside the pipe section of the flume. The piston is driven by a 1500-W output electric motor (Baldor Electric) with a variable output of up to 1800 rpm (30 Hz). A tachometer inside the motor provides feedback to a variable-speed motor controller so that a constant period of oscillation can be maintained. The driveshaft of the motor is coupled to a 150:1 reduction gear (Emerson Power Transmission), thus generating cyclical motion of  $\leq 0.2$  Hz or periods of  $\geq 5$  s. Two



**Fig. 3.** Schematic of piston seal. An o-ring compressed by an external plate provides a watertight seal on the piston shaft. Filtered water flows into the piston seal chamber, where it is then allowed to flow into the main area of the piston chamber around the piston shaft and through a small release port to ensure that no debris gets between the moving shaft and the o-ring. All dimensions were drawn to scale except for the vertical scales of the piston chamber flange (A) and the piston chamber flange cover (B).

steel cranks connected to two hubs mounted on the reduction gear drive the piston shaft by means of two aluminum drive rods. Spherical rod-end bearings attached to both ends of the drive rods inhibit the development of torsional stress on the entire drive system that could result from less than perfect alignment of the drive system components.

The piston shaft consists of a 2.5-cm diameter, 4-m long stainless steel rod, and is the only metal component of the flume in contact with the water. This makes the flume well suited for use with seawater. The shaft enters the flume through an internal housing with a shaft seal mounted on the outside wall (Figure 3). A small 100-W pump is used to draw water from inside the flume and through a 10- $\mu$ m fabric filter, after which it is flushed into the interior of the shaft seal housing, across the piston shaft, and back into the main body of the flume. Flushing the housing with filtered seawater from the flume ensures that hard debris suspended within the test section will not score the shaft seal and cause it to leak. The shaft is attached to the drive system by a cross-truss connected to the free end of each drive rod (Figure 1). The cross-truss rides along two level slide rails made from Corian (for con-



**Fig. 4.** Image of piston head pulled outside the piston chamber. The black plates are made from high-density polyethylene (HDPE). The gray plates are made from Corian.

venience) to support the horizontal movement of the piston and shaft. We were concerned that debris (sand, coral, and coral rubble) from the test section could migrate to the piston chamber and become jammed between the piston head and chamber wall. Therefore, we used a 3-mm diameter brass shear pin inserted through the center of the piston shaft to connect the shaft to the cross-truss. This was done as a safety measure so that if the piston head were ever to seize, the shear pin would break, decoupling the motor from the piston. The cross-truss would then be allowed to move freely without requiring movement of the shaft.

The piston head is constructed from alternate layers of 1.25-cm Corian and 2.5-cm thick high-density polyethylene (HDPE) sheet (Figure 4), with the diameter of the HDPE disks being ~2 cm greater in diameter than the Corian disks. The corrugated design of the piston head retards the movement of water between the piston head and chamber wall and obviates the need for a perfectly cylindrical piston chamber or a perfectly machined piston head. Nonetheless, the piston chamber was constructed from 0.3-m diameter, schedule 80 PVC pipe rather

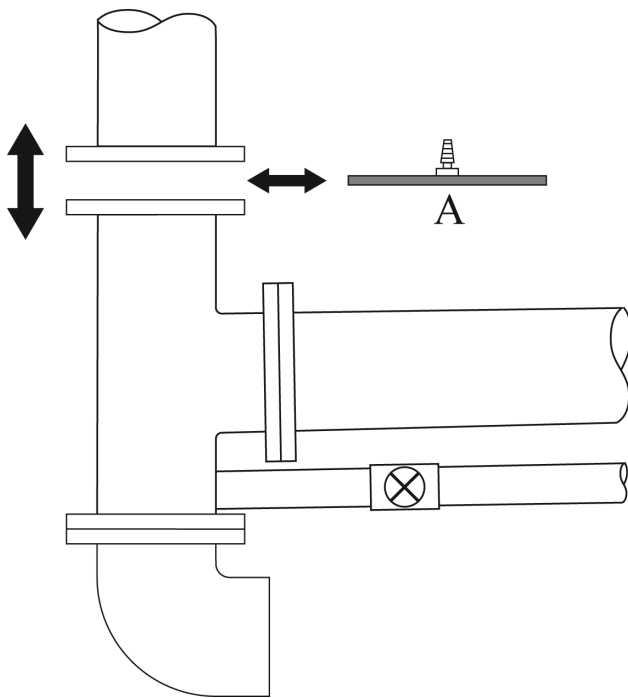
than schedule 40 pipe because the dimensions of the heavier schedule 80 pipe are less irregular and deviate less from a perfect cylinder. The larger-diameter disks comprising the piston head were constructed from HDPE because these disks contact the chamber walls. HDPE is a very smooth and slightly pliable material and thus an excellent material to use as a bearing surface. We believe that is generally good to use a material similar to Corian for the smaller-diameter disks because it provides strength and rigidity to the piston head and is close to being neutrally buoyant. Constructing a piston head from material that is close to neutrally buoyant minimizes wear on the bottom of the piston head and piston chamber by minimizing the weight of the piston head in water.

Holes drilled into the crank allow the piston excursion amplitude,  $A_p$  (defined as the maximum distance traversed by the piston head), to be set at discrete lengths of 0.3, 0.6, 0.9, 1.2, and 1.5 m. Because of differences in the cross-sectional area of the test section relative to the cross-sectional area of the piston chamber, these  $A_p$  values correspond to excursion orbital amplitudes in an empty test section ( $A_o$ ) of 0.2 to 1.1 m. Because flow inside the flume is sinusoidal, the rms flow speed in the test section  $U_{rms}$  can be directly related to the excursion length and wave period  $T$  by

$$U_{rms} = \frac{\pi}{\sqrt{2}} \frac{A_o}{T} \quad (2)$$

The ability to measure biogeochemical reactions presented design constraints in addition to those necessary for generating wave-driven flow. The most important modification to the basic U-tube design is the addition of bypass lines: one 10-cm diameter pipe connecting the two standpipes, and another 10-cm diameter pipe connecting the two ends of the piston chamber (Figure 1). The living community in the test section of the flume is the only chemically reactive component of the flume, and the net current provided by the bypass lines allows the living community to interact with the entire water mass. Check valves mounted in both pipes ensure the net flow of water in a direction moving from the piston chamber to the test section, but not in the opposite direction (Figure 1). Ball valves mounted adjacent to the check valves allow the net flow to be throttled so that the resulting net flow is kept below 10% of the maximum flow speed. The release or uptake of metabolites by the experimental community in the test section can thus be evenly distributed over the entire water mass, reducing the formation of chemical gradients and patchiness in the water. Inhomogeneities in the composition of the flume water would complicate both sampling and interpretation of the experimental data. In comparison, maintaining a homogeneous chemical composition of the entire water mass under steady flow is typically not a problem.

*Steady flow generation*—Many reef communities can still be exposed to predominantly quasi-steady, unidirectional currents rather than wave-driven oscillatory flow. These currents can be tidally driven or result from wave set-up in the surf



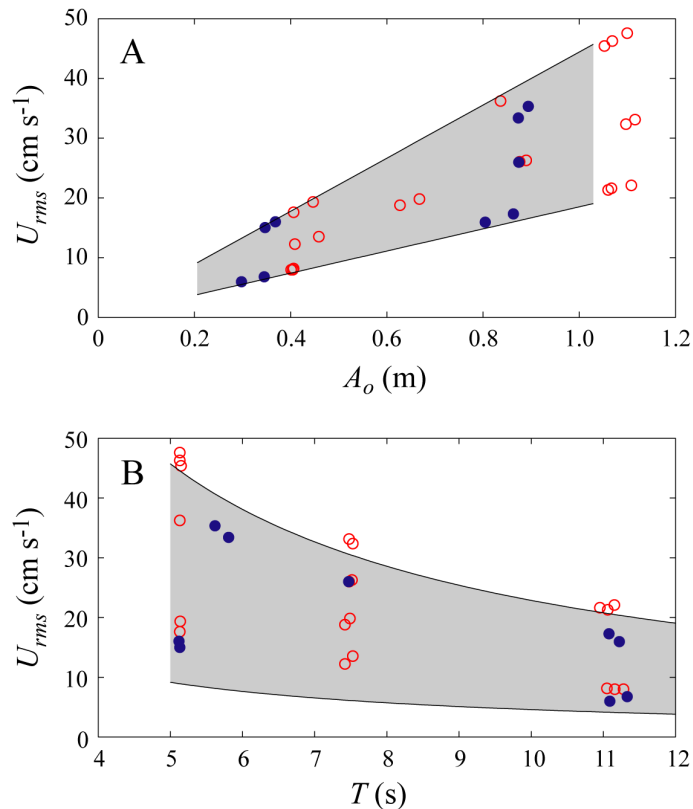
**Fig. 5.** Schematic of the break in the second standpipe used to reduce the presence of free oscillations under steady flow. Under steady flow, the standpipe is separated, and a cap fitted with a valve (A) to vent trapped air is bolted to the bottom flange.

zone (Hearn and Parker 1988; Symonds et al. 1995; Tait 1972). The flume presented here can be reconfigured to generate steady, unidirectional flow speeds of up to  $70 \text{ cm s}^{-1}$  within the test section. In this mode, the piston is pulled all the way back to the shaft seal end, where the piston is out of the flow path of water moving from the standpipe into and through the piston chamber. A small, 12-V electric “trolling” motor inside the standpipe bridge is run by a variable DC power supply to generate unidirectional flow (Minn Kota, Mankato, MN, USA). Finally, the standpipe opposite of the piston chamber is separated at a flange and capped to prevent free oscillations of the water inside the flume (Figure 5). These oscillations of water in the standpipe create fluctuations in the flow that can interfere with measurements of turbulence inside test section. The flume can be converted between unidirectional and oscillatory mode in approximately 2 hours while the experimental reef community remains completely submerged. Hence, differences in the mode of flow on community metabolism rates can be determined without disturbing the live organisms residing in the test section.

**Test section**—The main body of the test section consists of a closed, rectangular channel that is 3 m long, 0.3 m wide, and 0.35 m high, constructed from 1-cm thick fiberglass (Figures 1 and 2). Transition segments at the ends of the test section convert the flow cross-section from the circular shape of the pipe to the rectangular shape of the middle test section with less than 7-degree grades along each of the sidewalls. This is done

to minimize flow disturbance, recirculation, and turbulence generation within the transition. In addition, a set of sequential flow straighteners are mounted in the pipe upstream of the flume to reduce the effects of swirl and turbulence generated in the 90-degree elbows upstream (Figure 1). The purpose of this flow-straightening system is to break the swirl and large-scale turbulent eddies into progressively smaller eddies. This accelerates the rate at which turbulence is dissipated, minimizing the amount of free-stream turbulence reaching the test section. The first straightener consists of two flat pieces of 3-mm thick, 30-cm long PVC sheet oriented vertically and horizontally within the pipe, forming a cross-shaped profile in the direction of flow. The second and third set of flow straighteners are made from packed sections of 7.5-cm and 4-cm diameter PVC pipe 15 cm long. Finally, after passing through the transition of the test section, the flow is forced through a grid 2.5 cm deep with 1.5-cm spacing before entering the working section of the test section.

The top of the specimen section is sealed with three separate acrylic windows 1.2 cm thick to allow for illumination of the experimental communities. Each window is secured with 32 10-mm diameter stainless steel bolts positioned at 10-cm intervals and sealed against a flat gasket, 10 cm wide, which runs along all sides of the window frame. This many fasteners are needed to seal the windows against the maximum weight of 725 kg pressing on each of the windows when the standpipes are filled to the top. Light is provided to the experimental communities by six 1000-W metal halide bulbs in reflective hoods (Sunlight Supply and Venture Lighting International) with intensities of up to  $\sim 1000 \mu\text{Ein m}^{-2} \text{ s}^{-1}$  of photosynthetically active radiation (PAR). These light levels are saturating or near-saturating for benthic reef autotrophs at both the organismal and community scales (Carpenter 1985; Chalker 1981; Gattuso et al. 1996; Williams and Carpenter 1990). Alternatively, six 400-W metal halide bulbs (PFO Lighting) provide illumination of  $\sim 400 \mu\text{Ein m}^{-2} \text{ s}^{-1}$ . Light intensities inside the test section can be varied by choice of lamp wattages and adjusting the height above test section at which the lamps hang. Illumination from metal halide lights differs from that of natural sunlight in that most of the light is emitted in discrete wave bands rather than in a smooth, continuous spectrum. Light levels in the flume are measured using a LI-COR model 192-SA spherical PAR sensor (LI-COR Biosciences) with the bottom half of the spherical sensor covered so that only downwelling irradiance is measured. To monitor changes in the opacity of the acrylic windows and in the output of the metal halide bulbs, light measurements are performed while the flume is empty but with the windows in place. Attenuation of the light field in the water is negligible given the shallow depth of the flume and the clarity of the tropical seawater used in our experiments. A  $0.1 \times 3 \text{ m}$  acrylic window built into the side of the flume allows for observation during the course of an experiment when lighting precludes observation from the top window.

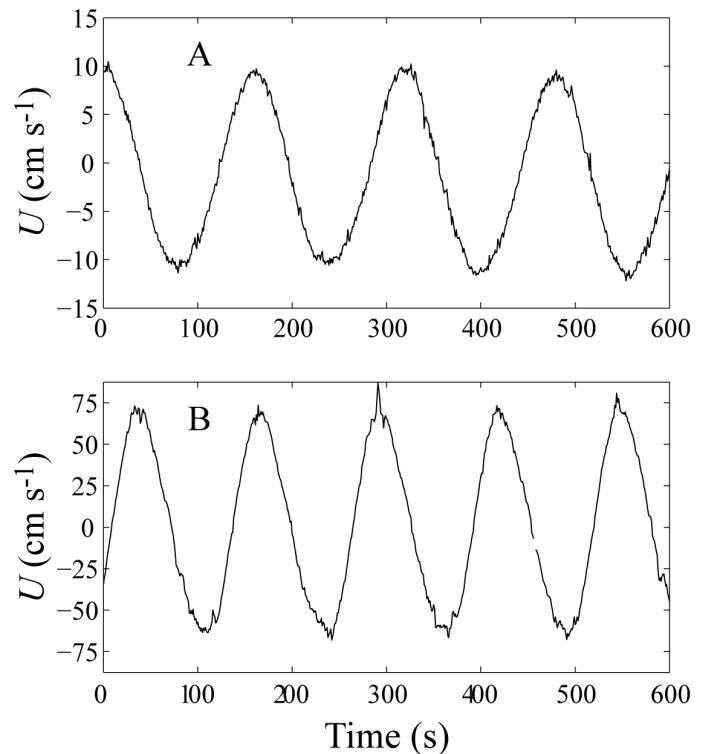


**Fig. 6.** Flow speeds (rms) generated under oscillatory flow in the test section when filled with an experimental reef community ( $\circ$ ) or without ( $\bullet$ ) as a function of excursion amplitude (A) and wave period (B). The gray area denotes the range of flow conditions that the flume can support when the test section is unoccupied. Flow speeds are slightly higher when the test section contains living organisms or other experimental materials owing to a reduction in the effective cross-sectional area of the test section.

Measurement of flow inside the flume is performed using a Nortek NDV Acoustic Doppler Velocimeter (ADV) equipped with a 3-component downward-looking probe. The probe of the ADV is mounted through the bottom of the test section using a special collar that locks around the probe shaft and against the surface of the flume (Figure 2B). Gaskets on both locking surfaces create seals to prevent leakage from this through-hull fitting. If lighting of the test section through one of the windows is not required, the ADV can be mounted through an acrylic window (Figure 2B). The compact design of this model of ADV (1.4-cm shaft diameter), and the fact that flow velocities are sampled 5 cm from the probe head, ensures minimal disturbance of the flow field during measurement.

### Assessment

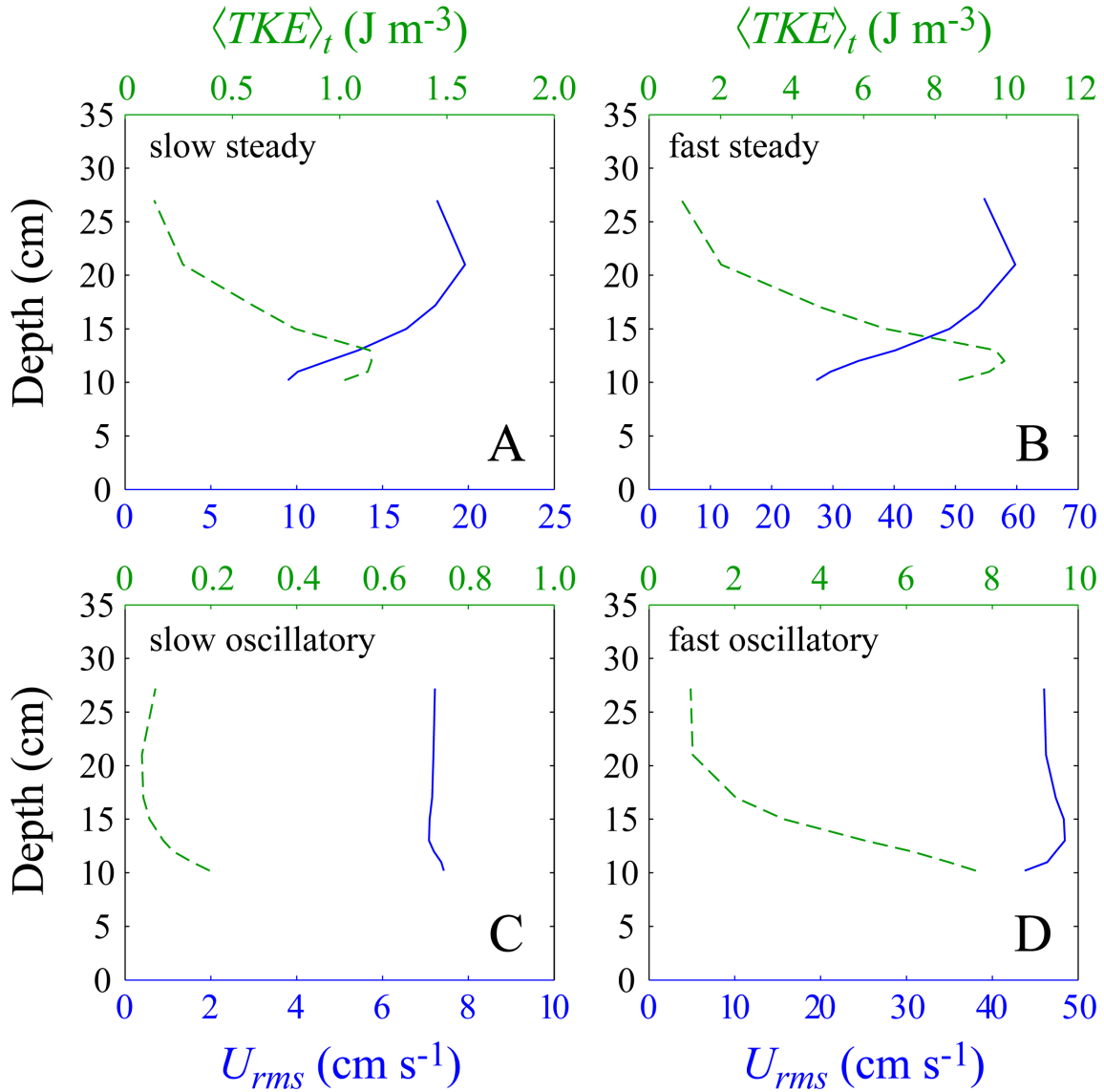
*Flow in the test section*—The present flume design is capable of generating root-mean-square (rms) oscillatory flow speeds of up to  $50 \text{ cm s}^{-1}$  using different combinations of piston excursion amplitude and wave period. However, not all com-



**Fig. 7.** Sample plots of flow velocity along the direction of the test section vs. time under slow oscillatory flow ( $T = 6.4 \text{ s}$ ,  $A_o \approx 0.25 \text{ m}$ ) (A) and fast oscillatory flow ( $T = 5.1 \text{ s}$ ,  $A_o \approx 1.1 \text{ m}$ ) (B) measured 22 cm off the bottom. The high-frequency irregularities in each of the time series are the result of turbulent fluctuations in the flow. A community of living coral was present inside the test section when these measurements were made.

binations of flow speed, period, and excursion amplitude are possible with the present design (Figure 6). For example, for  $T > 10 \text{ s}$ ,  $U_{rms}$  cannot exceed  $25 \text{ cm s}^{-1}$  due to limitations in the maximum excursion amplitude that can be generated. The tachometer feedback circuit on the wave generator ensures that wave period varies between cycles by less than 2%, and the geometry and length of the drive system creates a wave signal that deviates from a perfect sinusoid by no more than a few percent (Figure 7). Profiles of  $U_{rms}$  over an experimental coral community under oscillatory flow are nearly uniform with depth under both slow and fast flow (Figure 8), with the exception of a near-bottom flow speed maximum under both conditions, as predicted by wave boundary layer theory (Nielsen 1992).

Steady, unidirectional flows of up to  $70 \text{ cm s}^{-1}$  have been created in the flume (data not shown); however, we were unable to create flows  $< 5 \text{ cm s}^{-1}$  due to intermittent performance of the motor at very low power. It is possible to lower the minimum steady flow by using a different motor, but we have not yet found a need to generate such low flows. Profiles of flow speed over the same community under unidirectional flow are not as vertically uniform as under oscillatory flow, indicating that thicker boundary layers form under unidirec-



**Fig. 8.** Profiles of rms flow speed (—) and time-averaged turbulent kinetic energy (---) over an experimental coral community under slow steady flow (A), fast steady flow (B), slow oscillatory flow ( $T = 6.4$  s,  $A_0 \approx 0.25$  m) (C), and fast oscillatory flow ( $T = 5.1$  s,  $A_0 \approx 1.1$  m) (D). The roughness height of the coral community varies from 8 to 12 cm based on the maximum height of each piece of coral.  $z = 0$  is defined as the bottom of the test section.

tional flow (Figure 8). Variations in mean flow speed near the top of the test section indicate that there is a ~10% uncertainty in how  $U_\infty$  over the experimental community is defined under unidirectional flow.

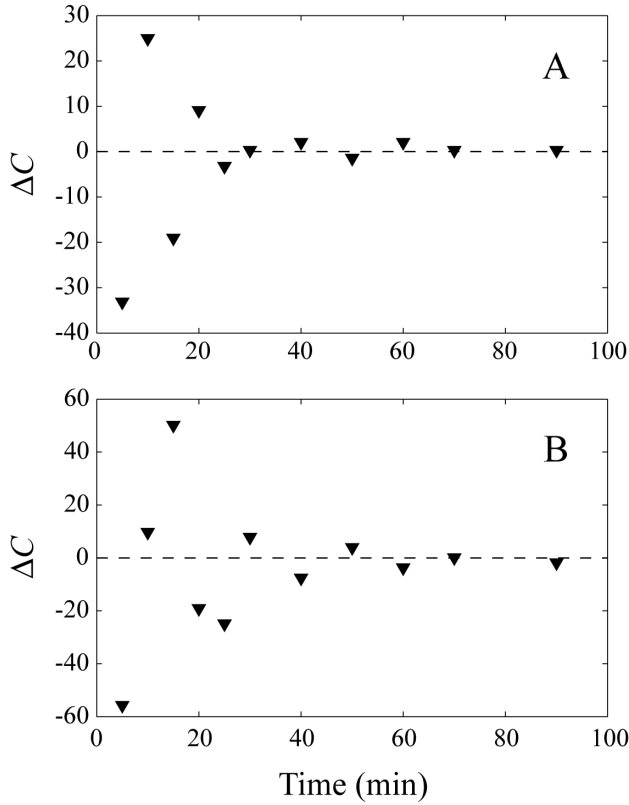
Under all flow conditions, there is typically a 5- to 10-fold increase in the turbulent kinetic energy (TKE) from ~10-15 cm above the coral community to near the top of the coral community. This result indicates that turbulence near the experimental coral is primarily generated by the direct interaction of the community with the flow section, and not by turbulence generated by the interactions of the flow with the sidewalls or elbows of the flume. Time-averaged TKE was calculated from

the turbulent flow data along each axis ( $x, y, z$ ) (Figure 2B) as

$$\langle TKE \rangle_t = \frac{1}{2} \rho \left( \langle u'^2 \rangle_t + \langle v'^2 \rangle_t + \langle w'^2 \rangle_t \right) \quad (3)$$

where  $\langle \rangle_t$  represent averaging with respect to time,  $\rho$  is the density of the water in the flume, and  $u'$ ,  $v'$ , and  $w'$  represent turbulent flow fluctuations in the  $x$ ,  $y$ , and  $z$  directions, respectively.

For the steady, unidirectional flow experiments, turbulent velocities  $u'(t)$  were calculated by subtracting the time-averaged velocity  $\langle U \rangle_t$  from the measured instantaneous velocities  $U(t)$ . In oscillatory flow experiments,  $U(t)$  can be decomposed into three components,



**Fig. 9.** Concentration of a dissolved tracer released at a single point in the flume vs. time under oscillatory flow where  $U_{rms} = 10 \text{ cm s}^{-1}$  (A) and  $U_{rms} = 40 \text{ cm s}^{-1}$  (B). Concentrations are reported as the difference from the asymptotic concentration in percent

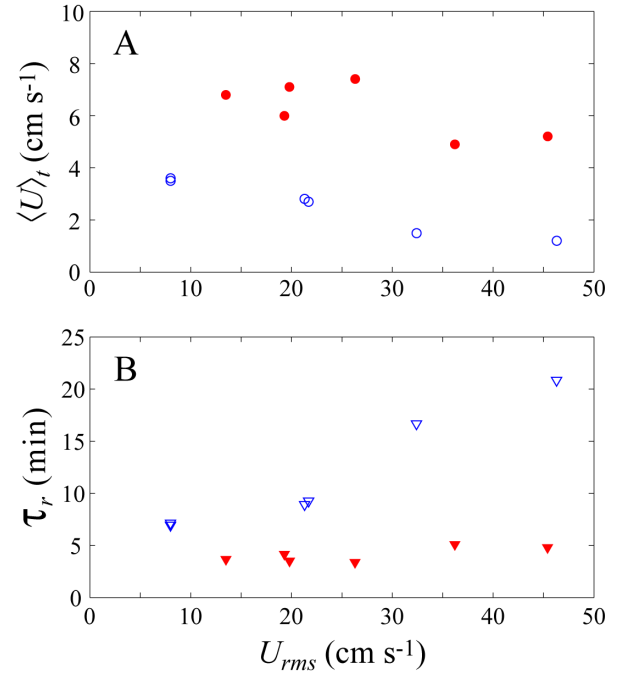
$$\left( \Delta C = \frac{C(t) - C_{\infty}}{C_{\infty}} \right).$$

Both bypass valves were open halfway during each of these tests. The test section of the flume was filled with coral rubble while these data were taken.

$$U(t) = \langle U \rangle_t + \tilde{u}(t) + u'(t) \quad (4)$$

where  $\tilde{u}(t)$  is the sinusoidal oscillatory component of the flow;  $u'(t)$  can be calculated by difference using Eq. 4. Because the oscillatory flow generated in the flume is highly consistent in its form and periodicity,  $\tilde{u}(t)$  will by definition vary only with the phase of the oscillatory flow; thus  $\tilde{u}(t)$  can be calculated by averaging instantaneous velocities of the same phase.

**Mixing and recirculation**—The time required for a chemical signal released at one point of the flume to become completely homogenized (i.e., vary by < 5%) throughout the entire volume of the flume under oscillatory flow was ~30 min for  $U_{rms} = 40 \text{ cm s}^{-1}$  and ~60 min for  $U_{rms} = 10 \text{ cm s}^{-1}$  (Figure 9), and less than 15 min under all unidirectional flow speeds. We define these measurements as the mixing time of the flume ( $\tau_m$ ). We define the recirculation time ( $\tau_r$ ) as the time required for a water parcel to transit the full length of the flume ( $\tau_r = L/\langle U \rangle_t$ , where  $L = 18 \text{ m}$  for steady flow and  $L = 15 \text{ m}$  for oscillatory flow).  $\tau_r$  varies



**Fig. 10.** Time-averaged flow speed (A) and recirculation time (B) vs. rms flow speed under oscillatory flow when both bypass valves are half open ( $\nabla$ ) and fully open ( $\blacktriangledown$ ).

between just 0.5 and 5 min under unidirectional flow ( $6 \leq U \leq 50 \text{ cm s}^{-1}$ ) and between 3 and 21 min under oscillatory flow, depending on the state of the bypass valves (Figure 10).

To better justify the importance of using bypass lines to mix and recirculate the water inside the flume, we can estimate the time required to mix the water in the flume just by turbulence alone. The turbulent eddy diffusivity ( $D_e$ ) inside the flume can be related to the diameter of the flume pipe ( $d_p$ ) as well as  $u'_{rms}$  (Fischer et al. 1979)

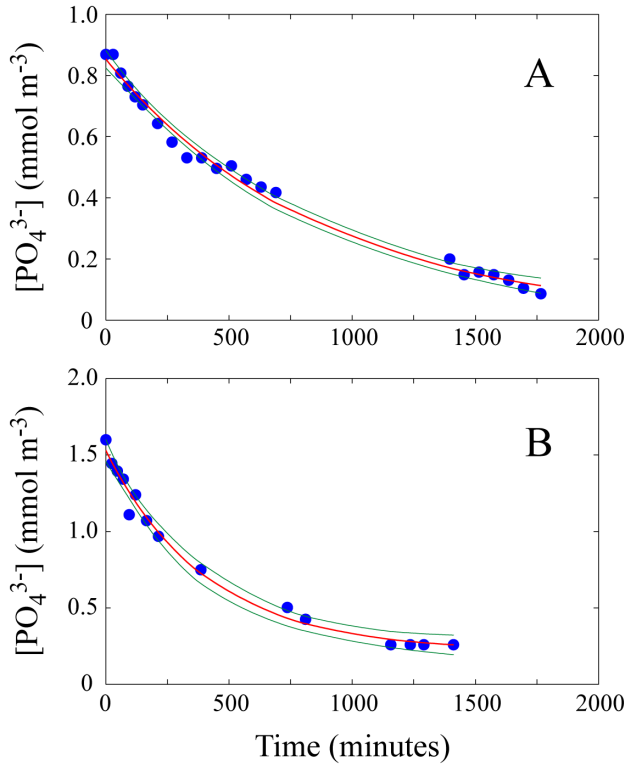
$$D_e \approx 0.15 u'_{rms} d_p \quad (5)$$

where the value of 0.15 is an empirically measured constant. Given an rms velocity of  $25 \text{ cm s}^{-1}$  and a background turbulence intensity of ~10% in the flume (data not shown),  $D_e$  would then be  $\sim 0.001 \text{ m}^2 \text{ s}^{-1}$ . The time scale for mixing the entire flume just by turbulent dispersion alone can be estimated by the following expression

$$\tau_e \approx \frac{L^2}{2 D_e} \quad (6)$$

where  $L$  is the length of the flume. For  $L = 15 \text{ m}$  and  $D_e \approx 0.001 \text{ m}^2 \text{ s}^{-1}$ ,  $\tau_e$  would be roughly 30 h.

**Flux measurements**—The time scale at which changes occur in the mass of a compound within the flume depends on both the mass flux and the volume of water inside the flume. For example, both theory and practice have shown that nutrient uptake by coral reef communities is first-order with respect to concentra-



**Fig. 11.** Uptake of dissolved phosphate by experimental communities of coral rubble covered with turf and macroalgae under steady flow at 20 cm s<sup>-1</sup> (A) and oscillatory flow at 25 cm s<sup>-1</sup> (B). Solid red lines denote fitted curves of the form  $P(t) = P_0(1 - e^{-kt}) + r/k$ ; green lines represent the 95% confidence limits for these fits. Values of  $S$  calculated from these data along with their 95% confidence limits are  $S = 2.7 \pm 0.5$  m d<sup>-1</sup> ( $r^2 = 0.99$ ,  $n = 19$ ) for steady flow and  $S = 4.1 \pm 1.0$  m d<sup>-1</sup> ( $r^2 = 0.99$ ,  $n = 12$ ) for oscillatory flow (see text for details).

tion. The first-order differential equation balancing changes in the total mass of a nutrient in the flume,  $N_i$ , with the uptake is

$$\frac{dN_i}{dt} = V \frac{d[N_i]}{dt} = -S_i [N_i] A_c \quad (7)$$

where  $S_i$  is the mass transfer coefficient of nutrient  $i$ ,  $A_c$  is the planar area occupied by the community, and  $V$  is the volume of the flume. Whereas  $A_c$  represents the area in the test section taken up by community,  $S_i$  is a function of the total bioactive surface area of the community interacting with the flume water. The solution of Eq. 7 gives an exponential function whose decay constant,  $k_N$ , is equal to

$$k_N = \frac{S_i A_c}{V} \quad (8)$$

A typical nutrient mass transfer coefficient of 5 m d<sup>-1</sup> and a volume to community area ratio of 1.25 m would yield a first-order decay constant of 4 d<sup>-1</sup>, or an equivalent half-life for the nutrient in the flume of ~4 h. If the volume of the flume relative to the experimental area were quadrupled, the half-life of

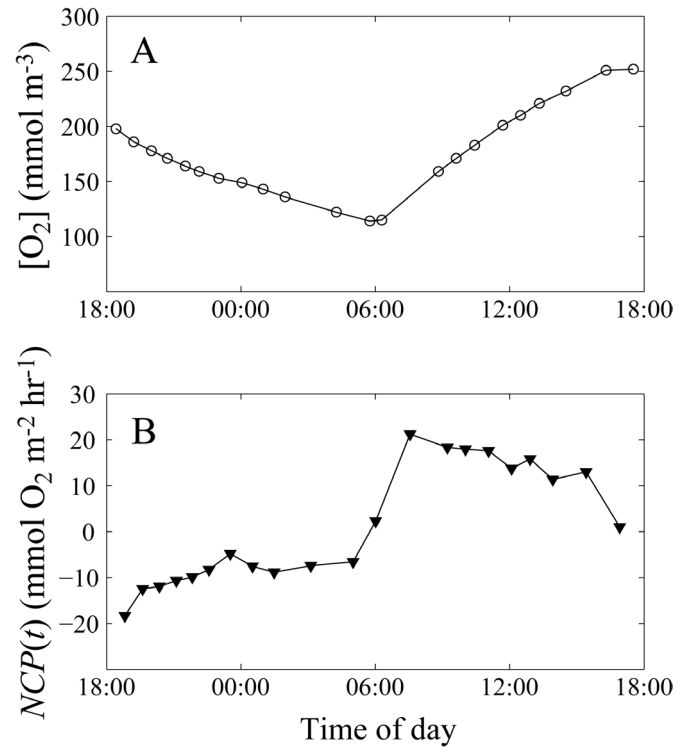
a nutrient being taken up by the community would be increased by a factor of 4 ( $\tau_{1/2} = \frac{V \ln 2}{S_i A_c}$ ). Larger ratios of  $V$  to  $A_c$  could be used when designing the test section as long as it is understood that the time scale for each experiment will increase.

Net community production can also be estimated from the change in oxygen per unit time and the area to volume ratio

$$\frac{d[O_2]}{dt} = NCP \cdot PQ \cdot \frac{A_c}{V} \quad (9)$$

where  $PQ$  is the photosynthetic quotient. Additionally, community calcification rates could also be measured in this flume based on changes in the partial pressure of dissolved CO<sub>2</sub> gas, total alkalinity, total dissolved inorganic carbon, and/or pH, although we have not yet made such measurements.

Experimental communities consisting of coral rubble, 10-15 cm in height and 10-20 cm in width, and covered with turf and macroalgae yielded estimates of phosphate mass transfer coefficients similar to those obtained in other flumes (Figure 11). Nonetheless, phosphate uptake appears to be ~30% higher under oscillatory rather than steady flow at comparable  $U_{rms}$ , consistent with dissolution of plaster (gypsum) blocks under steady and oscillatory flow (Falter et al. 2005; Lowe et al. 2005;



**Fig. 12.** Dissolved oxygen concentration (A) and instantaneous net community production  $[NCP(t)]$  (B) vs. time under oscillatory flow ( $U_{rms} = 0.2$  m s<sup>-1</sup>,  $T = 7.4$  s) for an experimental community of algal-covered coral rubble at an irradiance of 400  $\mu\text{Ein m}^{-2} \text{s}^{-1}$ .  $NCP(t)$  was calculated based on a flume volume of 1.1 m<sup>3</sup> and an experimental community planar area of 0.9 m<sup>2</sup>, and assuming a photosynthetic quotient ( $\Delta O_2 / \Delta CO_2$ ) of  $\approx 1$  (Kinsey 1985).

**Table 1.** Budget for the material costs spent in building the flume.

Component	Cost, US\$
Piping	
Schedule 40 pipe	600
Schedule 80 pipe	340
Minor pipe	50
Flanges with gaskets	1170
90-degree elbows	1125
Tees	1500
Ball and check valves	634
Cement and primer	80
Pipe fasteners	330
Support structure	
Wood board	82
Concrete hollow tile	94
Quick mixing concrete	275
Ratchet and tackle (to lift cross-pipe)	75
Miscellaneous hardware	200
Oscillatory flow generation	
Motor with controller	1500
Reduction gear	1820
Cranks and hubs	900
Drive rods and cross-truss	180
Piston shaft and head	367
Shaft seal and filter assembly	120
Pump for shaft seal filter assembly	160
Steady flow generation	
12-V DC trolling motor	120
Variable power supply	250
Test section	
Custom-built test section	4740
Artificial lighting	2400
Miscellaneous parts	100
Total	19,212

Reidenbach et al. 2006). Diel changes in dissolved oxygen concentration were around 7-8  $\mu\text{M h}^{-1}$  in the dark and around 10-11  $\mu\text{M h}^{-1}$  in the light (Figure 12). Lighting during these experiments was 12 hours on/12 hours off. The effect of such consistent lighting can be seen in the near-constant slopes of  $[\text{O}_2]$  versus time and near constant rates of net production under both light and dark conditions (Figure 12). Integration of the diel oxygen curves assuming a PQ of 1.0 (Kinsey 1985) gives rates of dark respiration of 220  $\text{mmol C m}^{-2} \text{d}^{-1}$ , rates of gross primary production of 300  $\text{mmol C m}^{-2} \text{d}^{-1}$ , and a production to respiration ratio of 1.36 (Figure 12). These values are consistent with natural, low-relief, algal-dominated communities (Kinsey, 1985).

*Cost*—The material costs of constructing the flume were just under \$20,000 U.S. (Table 1). We estimate that ~700 person-hours of labor are required to construct the flume. This amount is roughly equivalent to two people working 3 days a week for 3 months.

## Discussion

The dimensions of the test section are the most important criteria around which the rest of the flume is designed. Reef organisms are centimeters to meters in size. We wanted a test section that allowed experimenting with communities consisting of elements 5 to 20 cm in height. These communities can consist of anything—turf algae, encrusting calcareous algae, and macroalgae; branching and lobate hard coral; active particle feeders such as sponges, ascidians, and tunicates; or passive filter feeders such as gorgonians and sea fans. To have a flume with a sufficiently large test section and the capacity to generate a wider range of flow speeds requires a larger wave generator than can be found in most conventional wave-current flumes. Otherwise, the entire flume could have been scaled down and an alternative form of oscillatory flow generation could have been used. U-tube-type wave flumes smaller and simpler than this one have already been used for the study of marine macrophyte biomechanics (Gaylord et al. 1994). We chose a U-tube design because it is easier to recreate wave orbital velocities and periods typically found on coral reefs with a U-tube design than with a free-surface wave generator. As an example, a 10-s period wave with a  $U_{rms}$  of 25  $\text{cm s}^{-1}$  would require a free surface wave that was ~1 m high and ~20 m long. A flume incorporating a free-surface wave generator creating waves of this size would need to be much larger than the design presented here, increasing by many times the construction cost, time, and space needed. Furthermore, such a flume would inevitably contain a much larger mass of water, requiring the use of larger experimental communities and/or longer experimental times, thereby increasing the cost and time of conducting experiments.

One limitation of the present flume design is the inability to generate fast flows with long periods (e.g.,  $U_{rms} > 25 \text{ cm s}^{-1}$  for  $T > 10 \text{ s}$ ) (Figure 6). The entire flume could also be lengthened to increase the natural period of oscillation so that it is easier to simulate longer-period waves such as those derived from open ocean swells ( $T > 10 \text{ s}$ ). For this to occur, however, the stroke length of the piston would also have to increase proportionally to generate higher  $U_{rms}$  at the longer  $T$ . Longer stroke lengths would require an even larger wave-maker but would improve the ability for wave period and flow speed to be independently controlled. Scaling up the size of the present flume and wave generator is not all that impractical; however, we believe that the design presented here is a prudent compromise between economy of size, economy of cost, and performance. Another limitation inherent to the design of a U-tube flume is that the top of the working section must always be below the free surface of the water in the standpipes. This requires that the test section of the flume be covered and sealed during all experiments. As such, access to the test section is more restricted than in an open-top flume, and an hour or more is needed to completely remove and then securely refasten the windows covering the test section. We have not found these limitations inhibitory in terms of the kind of

experiments we can conduct, but it does make the flume difficult to use for "quick" experiments.

As stated above, many variables such as water motion, light, temperature, and water chemistry influence the growth and metabolism of reef organisms. Experimental mesocosms, such as the flume shown here, provide a good approach for studying how these factors interact to influence the overall ecology of reef organisms and reef communities. To relate the results of such experiments to real reef communities living under in situ conditions in a quantifiable or predictive way, it is necessary to simulate the wide range of physical and chemical environments in which these organisms live. If the various forcing variables are not properly scaled and simulated, then interpretation of the metabolic response of the organisms and communities to varying environmental conditions will likely be incorrect. We believe that the flume design presented here represents an important step toward conducting properly simulated experiments, especially with regard to the wide range of flow conditions to which coral reef communities are exposed.

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