

Mass transfer limitation of photosynthesis of coral reef algal turfs

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Abstract Algal turfs are the major primary producing component on many coral reefs and this production supports higher levels in the complex reef trophic web. Rates of metabolism of algal turfs are related positively to water motion, consistent with limitation by the diffusion of a substance through a boundary layer. Based on engineering mass transfer theory, we hypothesized that photosynthesis of algal turfs is controlled by rates of mass transfer and responses of photosynthesis to increasing flow speed should be predicted by engineering correlations. This hypothesis was tested in ten experiments where photosynthesis was estimated in a flume/respirometer from changes in dissolved oxygen at eight flow speeds between 0.08 and 0.52 m/s. Flow in the flume and over the reef at Kaneohe Bay, Oahu, Hawaii was estimated using hot-film thermistor and electromagnetic current meters. Rates of photosynthesis were related positively to flow in all experiments and plots of the log of the average Sherwood number (Sh_{meas}) versus log Reynolds number (Re_D) for each

experiment are lower than predicted for mass transfer through a turbulent boundary layer. Algal turf-covered plates are characterized as hydrodynamically transitional to fully rough surfaces and the lower than predicted slopes suggest that roughness reduces rates of mass transfer. A negative correlation between algal turf biomass and slopes of the $\log Sh_{meas}$ - $\log Re_D$ plots suggests that mass transfer to algal turfs is affected significantly by the physical structure of the algal community. Patterns of photosynthesis based on changes in dissolved oxygen and dissolved inorganic carbon concentrations (DIC) indicate that the flow speed effect is not the result of increased flux of oxygen from the algal turfs, and combined with the short response time to flow speed, suggest that DIC may limit rates of photosynthesis. Although there are differences between flow in the flume and flow over algal turfs on the reef, these results suggest that photosynthesis is controlled, at least in part, by mass transfer. The chemical engineering approach provides a framework to pose further testable hypotheses about how algal canopy height, flow oscillation, turbulence, and substratum roughness may modulate rates of metabolism of coral reef algal turfs.

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Introduction

Coral reefs are among the most productive ecosystems in the ocean. Despite numerous studies of the factors that influence rates of metabolism of reef organisms and communities, considerable uncertainty and debate remain about the relative importance of nutrient and light limitation in the control of reef primary production (Barnes and Devereux 1984; Larkum and Koop

1996; Szmant 1996), the degree to which reefs are closed or open systems (Atkinson 1987; Smith and Kinsey 1988), and the relative importance of bottom-up processes versus the top-down control of primary producer abundance by herbivores (Hatcher 1996). This latter point has been highlighted by alternative views of the causes of shifts in community structure on many reefs (especially in the Caribbean) from coral to algal domination (Hughes 1994; Lapointe 1997; Hughes et al. 1999).

On many reefs the major primary producing component is comprised of free-living algae that form a thin veneer over dead coral substrata (Marsh 1976; Carpenter 1986). Algal turf communities (Hatcher 1982) are diminutive, with canopy heights generally <1 cm, but are diverse assemblages with representatives from up to five algal divisions (Scott and Russ 1987; Hackney et al. 1989). Rates of photosynthesis of reef algal turfs are affected by several environmental factors including light (Carpenter 1985), water motion (Carpenter et al. 1991), and nutrient concentrations (Williams and Carpenter 1988). For shallow portions of many coral reefs, where much of the primary production occurs, light probably is not limiting except in areas of very high spatial heterogeneity (Adey and Steneck 1985). Rates of photosynthesis by reef algal turfs and macroalgae are enhanced significantly by water motion (Carpenter et al. 1991; Larkum et al. 2003) and similar patterns have been demonstrated for rates of nitrogen fixation (Carpenter et al. 1991; Williams and Carpenter 1998). Metabolic and nutrient uptake processes of other reef organisms and coral reef communities also have been shown to be related positively to flow speed (Patterson et al. 1991; Atkinson and Bilger 1992; Bilger and Atkinson 1992; Falter et al. 2004). Furthermore, physical and biological disturbance can alter the biomass and architecture of the turf community (Carpenter 1986) affecting the flow environment over and within algal turfs (Carpenter and Williams 1993), and thereby indirectly influence algal turf metabolism.

The results of these studies suggest that boundary layer dynamics and mass transfer of materials to and from the surfaces of organisms are critical in modulating rates of material exchange and metabolism of reef communities. Clearly, a better understanding of how flow affects algal turf metabolism is fundamental to resolving debate about the relative importance of, and the relationship between, bottom-up and top-down processes in coral reef environments.

Here we present the engineering approach to mass transfer and relate it to measured rates of photosynthesis of coral reef algal turfs. We test the hypothesis that rates of photosynthesis are related positively to

water flow speed and put these results in the context of the flow environment over the reef. Based on engineering theory, we then calculate predicted rates of mass transfer to a rough surface and compare them to the measured flux rates to reveal any inconsistencies that might elucidate unique properties of mass transfer to biological surfaces.

Engineering mass transfer approach

Mass and heat transfer at surfaces have been addressed rigorously in the engineering literature (White 1988; Kays and Crawford 1993). Engineering correlations have been used successfully to describe mass transfer processes at the seafloor (Dade 1993) and for reef organisms and communities (Patterson et al. 1991; Bilger and Atkinson 1992; Baird and Atkinson 1997; Baird et al. 2004; Falter et al. 2004, 2005). As fluid moves over surfaces, momentum is extracted from the fluid through friction and a gradient in flow speed is established over the surface that is called the momentum boundary layer. Analogously, if mass is transferred at a surface by the uptake of a compound, gas, or ion from the bulk fluid, a gradient in concentration is established over the surface; this is the diffusive boundary layer. Delivery of mass to the surface by diffusion is described by Fick's first Law of Diffusion (flux = $-D_m [dC/dx]$), where D_m is the coefficient of diffusion for the compound, gas, or ion in the fluid and dC/dx is the concentration gradient over the diffusive boundary layer. As a result, at a constant bulk concentration, flux is inversely proportional to the thickness of the diffusive boundary layer. The relationship between the momentum (MBL) and diffusive boundary (DBL) layers is given by $DBL/MBL = Sc^{-0.33}$, where Sc is the Schmidt number, which is the ratio of the diffusivity of momentum to the diffusivity of the compound, gas, or ion in question. For molecules that are relevant to photosynthesis, values of Sc in seawater at 25°C are 423 for O_2 and 797 for HCO_3^- (calculated from values of D_m and ν given in Ramsing and Gundersen 2001).

Momentum and diffusive boundary layer characteristics are related to the type and speed of fluid motion, the distance the fluid moves over the surface, the surface roughness, and the steadiness of the flow (White 1994). Both types of boundary layers decrease as flow speed increases but how they decrease depends on whether the flow is laminar or turbulent. Characteristics of the flow surrounding an object are related to the Reynolds number (Re), defined as $U_\infty L/\nu$, where U_∞ is the freestream flow speed, L is the characteristic dimension of the object, and ν is the kinematic viscosity

of the fluid. Re represents the ratio of inertial and viscous forces that are acting on the fluid. Fluids with $Re < 10^5$ (over a smooth flat plate) usually are laminar and become turbulent at $Re > 5 \times 10^5$. As a fluid flows steadily over a surface, the boundary layer grows and its thickness is a function of the local Re (Re_x), defined as $U_\infty x/\nu$, where x is the distance downstream from the leading edge of the surface. The thickness of a boundary layer over a smooth flat plate is $\approx 5(Re_x)^{-0.5}$, and in turbulent flow is $\approx 0.37(Re_x)^{-0.2}$. Laminar boundary layers become turbulent when $Re_x > 10^5$ to 10^6 . Over smooth surfaces turbulent boundary layers consist of a thin viscous sublayer adjacent to the surface, a transition zone, and an outer region that is fully turbulent. In the presence of surface roughness the viscous sublayer disappears. Unsteady flows introduce a temporal component to boundary layer formation and growth and can result in the periodic disruption of established boundary layers (White 1994).

Diffusive boundary layers may represent a significant resistance to the flux of mass to and from the surfaces of benthic organisms. If the compound, gas, or ion is taken up and used immediately in a metabolic process, then diffusion across the boundary becomes the rate-limiting step and the process is mass transfer limited (Bilger and Atkinson 1992). In this case, the metabolic rate should be a function of flow speed to either the ~ 0.5 (laminar) or ~ 0.8 (turbulent) power.

To make analyses dimensionless, previous approaches to relate rates of mass transfer to fluid motion have used the Sherwood number (Sh , Patterson et al. 1991) or the Stanton number (St , Bilger and Atkinson 1992). Sh is defined as $h_m W/D_m$, where h_m is the mass transfer coefficient, W is the characteristic dimension of the organism, and D_m is the coefficient of diffusion for the compound, gas, or ion. The mass transfer coefficient is calculated from the metabolic rate per unit area divided by the concentration gradient ($C_b - C_o$) between the bulk fluid (C_b) and the wall (C_o , site of exchange). Sh represents the metabolic rate in a dimensionless form and is the ratio of convection-assisted mass transfer to exchange by diffusion alone. Sh is related to St as,

$$Sh = St Sc Re \quad (1)$$

where

$$St = m/U_\infty(C_b - C_o) \quad (2)$$

where m is the metabolic rate or uptake rate per unit area. As a result, either Sh or St can be used to examine relationships between metabolism and water motion.

However, these engineering correlations are for mass transfer to hydrodynamically smooth surfaces. Hydrodynamic roughness is quantified by the roughness Reynolds number, Re_k , defined as $u_* k'/\nu$, where u_* is the shear velocity, k' is the height of the roughness elements, and ν is the kinematic viscosity of the fluid. Surfaces with $Re_k > 70$ are considered fully rough, those with $Re_k < 6$ are smooth, and surfaces with $6 > Re_k > 70$ are transitionally rough (Kays and Crawford 1993). For rough surfaces, a more appropriate formulation of St is given by Kays and Crawford (1993) as:

$$St_{\text{rough}} = (c_f/2) / [0.9 + (c_f/2)^{0.5}/St_k] \quad (3)$$

where

$$St_k^{-1} = 5.19 Re_k^{0.2} Sc^{0.44} - 8.48 \quad (4)$$

and,

$$c_f^{-1} = \left(1.14 - 2.0 \log \left(k'/D_h\right)^2\right) \quad (5)$$

and is similar to correlations presented by Dade (1993). St_k in Eqs. 3 and 4 represents the Stanton number for the roughness elements. In Eqs. 3 and 5, c_f is the coefficient of friction for a rough surface and D_h is the hydraulic diameter ($4 \times$ cross-sectional area/perimeter) of a noncircular tube. These formulas were developed empirically primarily for engineering surfaces with abiotic roughness elements. For these surfaces roughness enhances mass transfer at low Re but has a negative effect with increasing Re (Yaglom and Kader 1974; Dade 1993).

Using this approach for rough surfaces, St_{rough} can be calculated from Eq. 3 and predicted values of Sh calculated from Eq. 1. According to mass transfer theory and empirical data from engineering applications, Sh is related to flow as, $Sh = aRe^b$ (White 1988), where a is a constant and b is an exponent that varies according to the type of boundary layer. The exponent assumes a value of 0.5 if exchange occurs through a laminar boundary layer and a value > 0.67 if the boundary layer is turbulent (White 1988). As discussed by Patterson et al. (1991), Sh can be calculated locally for a specific patch of an organism or community, or calculated for the entire organism or community, in which case it becomes an average estimate of mass transfer. Sh used here will always refer to the average Sh . Positive slopes of plots of $\log Sh$ versus $\log Re$ are consistent with mass transfer limitation and their value indicates whether mass transfer is occurring through a laminar or turbulent boundary.

Based on this chemical engineering approach to mass transfer, we tested the hypothesis that rates of photosynthesis of coral reef algal turfs are mass transfer limited. As a result, we predicted that rates of photosynthesis are related positively to flow speed and that this relationship should be described by engineering correlations.

Materials and methods

Study site

The study was conducted on the barrier reef enclosing Kaneohe Bay, Oahu, Hawaii (21°28'N, 157°48'W) using the facilities of the Hawaii Institute of Marine Biology (University of Hawaii). The reef is approximately 5 km long and the reef flat is up to 2 km wide. Water flow across the reef is dominated by wind-driven waves and swell that bring water to the reef with nutrient concentrations typical of tropical oceanic waters (Bathen 1968; Atkinson 1987). Study areas were located on the upstream portion of the reef flat at 1–2.5 m depth (Fig. 1). The seaward reef flat is

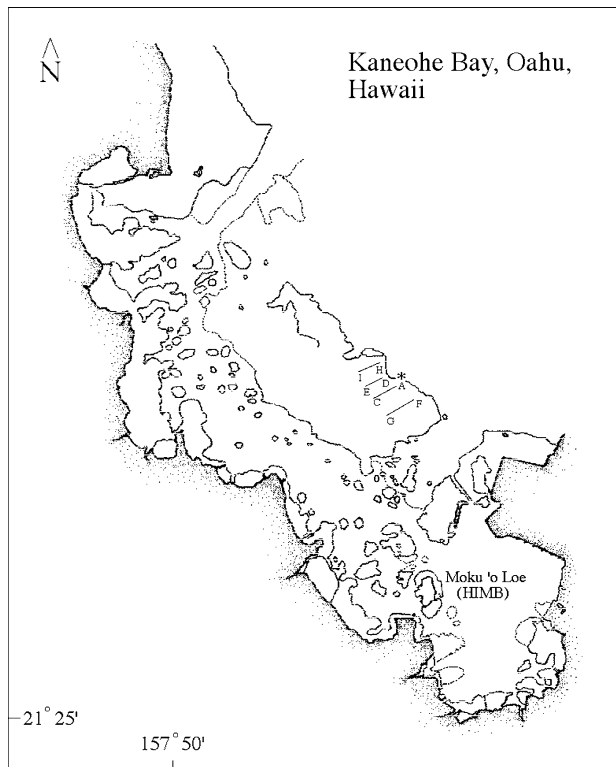


Fig. 1 Map of Kaneohe Bay, Oahu, Hawaii with approximate locations of flow transect endpoints given by letters. The location of the algal turf plates on the Kaneohe Bay barrier reef is shown by an asterisk

dominated by coral rubble and consolidated pavement with scattered “bommies” of the corals *Porites lobata*, *Montipora flabellata*, and *Pocillopora meandrina*. The majority of the rubble and pavement substratum is covered by algal turfs with occasional macroalgae (primarily *Dictyopteris* spp., *Sargassum* spp., and *Turbinaria ornata*). Canopy heights of algal turfs on the upstream reef flat range from <1 to 8 mm with a mean height of 2.7 mm (± 0.9 SD, $n = 340$).

Algal turf communities used in experiments developed on >400 plates ($7.5 \times 8.5 \times 1$ cm³) cut from the coral *Porites lobata*. Plates were attached to PVC racks and affixed to the reef at 1.5–2 m depth. Algal communities were established for >9 months prior to use in experiments.

Flume/respirometer design

Rates of photosynthesis of algal turfs were estimated in a flume/respirometer that is a modification of a design by Vogel and LaBarbara (1978). The flume is constructed of a rectangular, UV-transparent acrylic working section ($11 \times 10 \times 110$ cm) mated (at an 8° angle) to a circular (7.6 cm, I.D.) PVC return section (Fig. 2). The total volume of the flume is 27.8 l (± 0.03 SD, $n = 5$). Flow in the flume is driven by a propellor attached to a 1/90 hp DC motor mounted and sealed in the downstream portion of the return section. Motor speed and direction are regulated by a motor controller circuit. For unidirectional flow, the water is driven by the propellor ~2.9 m downstream through the circular return section before entering the working section of the flume. Flow straighteners (10 cm length) constructed from polycarbonate with rectangular, aligned openings (0.5×1 cm) are located at the upstream and



Fig. 2 Photograph of flume/respirometer inside the temperature-controlled reservoir. The working section is UV-transparent acrylic and is $11 \times 10 \times 110$ cm in dimension. Algal turf-covered plates sit in a depression in the floor of the flume and a hot-film thermistor flow probe is located 0.8 cm above the plates

downstream ends of the working section. Access to the working section is provided by two ports located 20 cm from each end. The ports are sealed with o-rings and secured with stainless spring-loaded fasteners. A depression ($8 \times 26 \times 1.2$ cm) in the center of the floor of the working section allows placement of three, algal turf-covered coral plates (191.3 cm^2 area) flush with the bottom of the flume. Sealable ports in the side of the working section allow placement of a hot-film thermistor flow probe and an o-ring sealed port in the return section accommodates an oxygen probe. The lower portion of the flume is submerged in a temperature-controlled reservoir (volume ~ 500 l) to minimize temperature changes inside the flume. During a typical run, temperature inside the flume varied $\ll 1^\circ\text{C}$ from ambient seawater temperature. In order to detect changes in dissolved oxygen during experiments the flume is sealed and filled completely with seawater. The design and dimensions of the flume are a compromise between hydrodynamic considerations (Nowell and Jumars 1987) and the need to minimize volume for respirometry measurements.

Flow in the flume

Flow in the flume was characterized using a hot-film thermistor flow probe (Model 1269 W, TSI, St Paul, MN, USA) and video analysis of particle movement. Flow profiles across the center of the working section were conducted at three heights (0.8, 3, and 5 cm) at two flow speeds (low 0.08 m/s, high 0.42 m/s) above bare coral plates placed in the well in the bottom of the flume. At each height, the flow probe was positioned at five locations across the flume (between 1.75 and 8.75 cm from the wall). At each location, flow was sampled at 10 Hz for 2 min; the voltage output from the flowmeter was converted to a digital signal (Analog Devices 6B-12, Norwood, MA, USA) and stored using data acquisition software (Labtech Notebook Pro 8, Labtech Technologies Corp., Wilmington, MA, USA). Flow probes were calibrated in the flume from the results of simultaneous video analysis of particle movement (see below). All measurements were made using unidirectional flow in the flume.

Shear velocities (u_*) within the flume were estimated from vertical profiles of flow speed estimated by analyzing the movement of neutrally buoyant particles (hydrated brine shrimp cysts). Using slit illumination (1 mm slit width) from above, particles along the centerline of the flume (above bare coral plates) were videotaped (Sony FX710 Hi-8) at each of ten flow speeds between 0.08 and 0.60 m/s. At each flow speed, minimum of five video frames were captured (Video-

Spigot, SuperMac Technology, Sunnyvale, CA, USA) and analyzed using NIH Image 1.55 software. Measurements of the movement of a minimum of 100 particles among the five video frames for each flow speed were made at heights from < 0.01 to 10 cm above the plates. Assuming a logarithmic relationship between the time-averaged flow speed and height above the bottom of the flume, values of u_* were estimated from the slope of the ln height-flow speed relationship multiplied by von Kármán's constant (0.41, Denny 1988).

Flow in the field

Flow over the Kaneohe Bay barrier reef was characterized at several spatial and temporal scales. At the largest spatial and longest temporal scales, flow was measured at the endpoints of four transects that were established over a 1.5 km section of the reef. The transects were perpendicular to the reef with the upstream ends just behind the breaking waves on the reef crest with the opposite ends 100–150 m downstream. Flow was measured simultaneously at the ends of each transect using paired InterOcean S4 electromagnetic current meters (InterOcean, Inc., San Diego, CA, USA) mounted 0.5 m above the substratum on concrete bases. Temporal scales of sampling ranged from continuous (at 2 Hz) over a 24 h period, to 20 min (at 2 Hz) out of every 6 h for 6 days period. Flow was measured across a transect for 2 months at a time and the current meters then were moved to a new transect.

Flow also was estimated at smaller spatial and temporal scales using a hot-film thermistor flow probe to measure flow speed profiles above the substratum (Carpenter and Williams 1993) at the endpoints of three of the four transects (Williams and Carpenter 1998). At each location, algal turf canopy height ($n = 5$) was measured within 3 mm of where the flow probe was closest to the substratum. Estimates of u_* were made from the slopes of the relationship (for points within the log layer) between the time-averaged flow speeds at each height above the substratum and the natural logarithm of the heights above the substratum, multiplied by von Kármán's constant.

Photosynthesis/flow experiments

To test the hypothesis that photosynthesis of reef algal turfs is mass transfer limited and related to water flow speed, we estimated rates of photosynthesis of algal turfs at eight flow speeds in the flume/respirometer in ten experiments. For each experiment, three algal turf-covered plates were collected randomly from the field,

cleaned of encrusting organisms on the sides and bottom, and placed in the depression in the bottom of the flume. Inert putty (Sculpey III, Polyform Products, Schiller Park, IL, USA) was used to position the plates so that their upper surfaces were flush with the floor of the flume. Algal turfs extended above the flume floor by 0.5–2 mm. The flume was filled with filtered seawater (20 μm nominal) and sparged with N_2 to reduce oxygen concentration to < 75% saturation. For each experiment, rates of photosynthesis were estimated at eight flow speeds (0.08, 0.11, 0.14, 0.27, 0.32, 0.42, 0.47, 0.52 m/s) in a random order. These flow speeds were chosen to represent the range of flow speeds that are encountered most frequently on the Kaneohe barrier reef (see below). The lowest flow speed was limited by the minimum rotation speed of the flume motor. At each flow speed, algal turfs were allowed to acclimate for 5 min at the new flow speed prior to initiating sampling. Flow speeds were set according to a prior calibration of motor speed (see above) and were measured (at 0.1 Hz) during experiments using a hot-film thermistor flow probe located in the center of the flume working section, 5 cm above the algal turfs.

Rates of photosynthesis were estimated from changes in dissolved oxygen (sampled at 0.1 Hz, Nester Instr., Millville, NJ, USA) at saturating (Carpenter and Williams, unpublished data) photon flux densities of natural sunlight between 600 and 1,500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ over an incubation time of 15 min. Photon flux densities were controlled using neutral density screening. Oxygen concentrations never exceeded 90% saturation, which minimized oxygen bubble formation. Rates of oxygen evolution were estimated from least-squares regressions of oxygen concentration over time. The response of the oxygen probe was independent of flow speed (data not shown).

Values of Sh_{meas} were calculated for each flow speed from Eq. 6,

$$Sh_{\text{meas}} = (mW)/[D_m(C_b - C_0)] \quad (6)$$

where m is the rate of oxygen evolution per area per time, C_b is the bulk oxygen concentration at the beginning of the experiment, C_0 is the oxygen concentration at the site of photosynthesis (which was assumed to be zero), W is the total length of the algal-covered plates along the axis of water flow, and D_m is the coefficient of diffusion for oxygen in seawater at 28°C.

Following incubations, plates were sampled randomly for ash-free dry mass (AFDM, $n = 5$ per plate, $n = 15$ per experiment), chlorophyll a content ($n = 5$ per plate, $n = 15$ per experiment), and algal turf canopy height ($n = 10$ per plate, $n = 30$ per experiment).

Samples for AFDM and chl. a were 1 cm^2 in size and included encrusting and endolithic algae that were scraped from the coral plate (Carpenter 1986). AFDM was estimated as the mass lost by combusting samples at 550°C for 4 h. Chlorophyll a content was estimated spectrophotometrically after extracting pigments in 90% acetone for 24 h in the dark at 4°C, and using the equations of Jeffrey and Humphrey (1975).

Control experiments were conducted in both the light ($n = 3$) and dark ($n = 3$) with bare coral plates and filtered seawater in the flume at each of two flow speeds (0.04–0.42 m/s). Incubation times were increased to 30 min in order to detect small changes in dissolved oxygen concentrations.

Photosynthetic quotient experiments

To equate rates and patterns of photosynthesis based on oxygen evolution to carbon uptake and fixation, we conducted experiments to estimate the photosynthetic quotients (PQ, moles of oxygen evolved per mole of carbon fixed) for reef algal turfs. In two experiments with randomly selected algal turf-covered plates, rates of photosynthesis were estimated simultaneously from changes in dissolved oxygen, as described previously, and by changes in dissolved inorganic carbon (DIC) concentrations at six flow speeds between 0.8 and 0.52 m/s. Flow speeds were chosen in a random order. Concentrations of DIC were estimated using the pH–total alkalinity method (Smith and Kinsey 1978). Replicate 30 ml seawater subsamples were taken from the flume at the beginning and end of each incubation and pH and total alkalinity were determined within a 2 h period. Total DIC concentrations were calculated using equations from Smith and Kinsey (1978) and dissociation constants from Skirrow (1975). Although it has not been demonstrated which form(s) of DIC are utilized by algal turf species, the demonstrated absence of photorespiration (Hackney and Sze 1988) and the elevation in pH above ten accompanying photosynthesis (Larkum et al. 2003) suggest that bicarbonate might be the major form of carbon used by turf species (Maberly 1990; Larkum et al. 2003). The pH–TA method estimates the total concentration of all carbon forms in seawater.

Results

Theoretical considerations of flow in the flume

Flow in the flume can be described in general terms as flow inside a rectangular tube. Using equations for tube

flow (Kays and Crawford 1993) and substituting the hydraulic diameter (D_h) for the diameter of the tube, the Reynolds numbers (Re_D) describing flow in the flume can be estimated. Values of Re_D varied between 0.89 and 5.80×10^4 (Table 1) and indicate that flow in the flume is turbulent. Onset of turbulence for pipe flow occurs at $Re_D \approx 0.23 \times 10^4$ (Kays and Crawford 1993). Turbulence in the flume is generated (in part) by the propellor and while some of this turbulence is dampened by the flow straighteners, the characteristics of the flow entering the working section likely are more complex than predicted from simple engineering models.

An additional consideration of flow inside the working section of the flume is the entry length. A momentum boundary layer continues to grow until the boundary layers over all surfaces meet in the center of the pipe; at this point (the entry length) velocity profiles over the surfaces are stable and the flow is referred to as fully developed. Predicted entry lengths are longer for laminar than for turbulent flows and increase with flow speed in both cases. For the laminar case, the ratio of the entry length to D_h can be >100 (requiring a flume with an equivalent D_h to be >10 m in length to achieve fully developed flow), while for turbulent flow this ratio is <10 (Kays and Crawford 1993). For the turbulent flow in our flume, the velocity profiles are $\sim 70\%$ developed by the time the flow reaches the plates at the lowest flow speed and $\sim 42\%$ developed at the highest flow speed. As a result, boundary layers will not be formed fully and this should present conditions that will provide conservative estimates of the effects of boundary layers on algal metabolism.

Flow in the flume

Water flow in the plate area of the working section of the flume does not vary greatly between the walls of

Table 1 Flow speeds used in flume experiments, calculated Re_D (using D_h) and predicted turbulent momentum boundary layer thicknesses for each flow speed

Flow speed (m/s)	Re_D	Turbulent BL (m)
0.08	0.89×10^4	0.019
0.11	1.23×10^4	0.018
0.14	1.56×10^4	0.017
0.27	3.01×10^4	0.015
0.32	3.57×10^4	0.015
0.42	4.68×10^4	0.014
0.47	5.24×10^4	0.013
0.52	5.80×10^4	0.013

Boundary layer thicknesses are calculated for the upstream edge of the plates in the flume using equations in Denny (1988) for flat plate boundary layers

the working section or among the heights measured above the plates (Fig. 3). Flow patterns are similar at low (0.08 m/s) and high (0.42 m/s) flow, although at low speed there is increased cross-sectional variation at the highest height (5 cm) above the plates. These patterns of flow speed suggest that algal turfs on the coral plates in the flume are experiencing similar flow environments.

Vertical flow speed profiles from video analysis of particle movements demonstrate steep gradients in flow speed close to the substratum in the bottom of the flume. The steepness of these gradients is described by values of u_* that estimate the shear stress exerted on the bottom (Denny 1988). Estimates of u_* ranged from 0.008 to 0.057 m/s and are linearly and positively related to the freestream flow speed (U_∞) in the flume (Fig. 4). The mean value of u_* over all flow speeds was $\approx 0.11U_\infty$.

One estimate of turbulence is the root mean square (RMS) of the flow (Denny 1988; Patterson et al. 1991). The RMS of flow speeds in the flume, as measured by

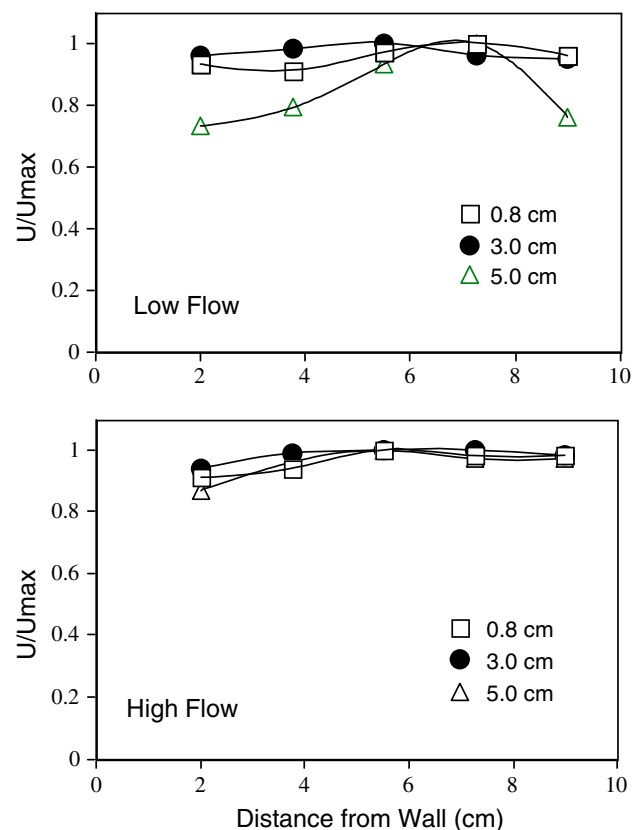


Fig. 3 Normalized flow speed profiles across the center of the working section of the flume at three heights (0.8, 3.0, and 5.0 cm) above bare coral plates at low (0.08 m/s) and high (0.42 m/s) flow speeds. Flow speed was estimated using a hot-film thermistor flow probe sampling at 10 Hz for 2 min at each location

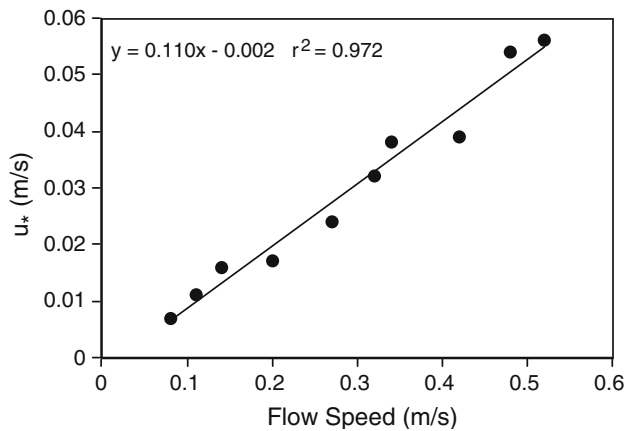


Fig. 4 Estimates of shear velocities (u_*) for ten flow speeds in the flume. Values of u_* were estimated from analysis of the movement of neutrally buoyant particles at different heights above bare coral plates

the hot-film thermistor flow probe, increases linearly with freestream flow speed (Fig. 5) with a maximum value of ~ 0.2 m/s.

Flow in the field

The dominant direction of net flow over the Kaneohe Bay barrier reef is from the NE (30° – 60° magnetic) and this wind and wave-driven flow pumps water over the shallow reef crest onto the reef flat. Over all transects and times, mean flow speeds varied from 0.22 to 0.26 m/s at upstream sites and 0.15–0.19 m/s at downstream sites. The maximum range of flow speed over all sites was 0–2 m/s. A typical distribution of flow speeds over a 6 days period (sampled for 20 min at 2 Hz out of each 6 h period) at an upstream site

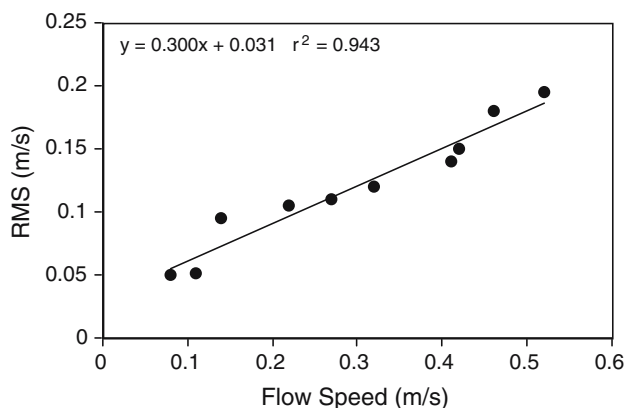


Fig. 5 Estimates of turbulence (RMS root mean square) of flow in the flume at ten flow speeds. RMS at each flow speed was calculated from flow speeds measured in the center of the working section over bare coral plates using a hot-film thermistor flow probe sampling at 10 Hz for 2 min at each location

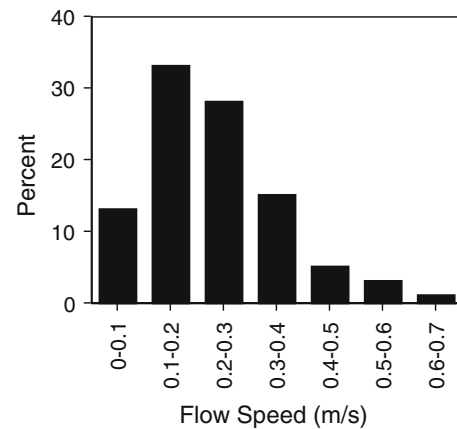


Fig. 6 A typical flow speed-frequency histogram for an upstream location (site A) on Kaneohe Bay barrier reef flat as measured by an S4 current meter. Sampling of flow was at 2 Hz for 20 min in each 6 h period for 6 days

(Fig. 6) indicates that $>90\%$ of the flow speeds are <0.5 m/s. Flow speed-frequency histograms for downstream ends of the transects were skewed further toward lower flow speeds (Carpenter and Williams, unpublished data). The mean flow speeds from the field are in the middle of the range of flow speeds used in the flume experiments. No estimates of turbulence in the field can be extracted from the S4 data due to the slow sampling rate.

Profiles of flow speed above the reef substratum indicate steep gradients in flow speeds (Table 2; Williams and Carpenter 1998), which were best fit ($r^2 > 0.8$) by a relationship that does not include roughness height (Denny 1988). Estimates of u_* varied from 0.004 to 0.077 m/s and the mean value (\pm SD) of u_* over all profiles was $\approx 0.09U_\infty$ (± 0.04). Mean algal canopy heights surrounding the sites of the flow profiles ranged from 1 to 3.8 mm. Based on the data presented by Williams and Carpenter (1998), values of u_* are correlated positively with algal turf canopy height in the vicinity of the flow speed profiles (partial correlation analysis, $r = 0.39$, $P < 0.05$). The ratio of u_*/U_∞ also was correlated positively with algal canopy height (partial correlation analysis of arcsin-transformed data, $r = 0.74$, $P < 0.01$). Estimates of turbulence (RMS) of the oscillatory flow speeds 5 cm above the reef substratum varied from 0.05 to 0.57 m/s with an average of 0.28 m/s. These estimates of turbulence are for flow speeds not velocities.

Photosynthesis/flow experiments

Algal turfs used in the experiments had mean canopy heights that ranged from 1.1 to 1.8 mm, AFDM ranging from 9.4 to 18.6 mg/cm^2 , and chlorophyll *a* content

Table 2 Mean algal canopy heights, freestream flow speeds (U_∞), and estimates of shear velocities (u_*) for each of 29 flow profiles measured on the Kaneohe Bay barrier reef flat

Site	Algal canopy height (mm)	U_∞ (m/s)	u_* (m/s)
I-1	2.4	0.27	0.014
I-2	1.4	0.29	0.040
I-3	1.4	0.28	0.028
I-4	2.2	0.37	0.018
I-5	1.4	0.24	0.017
H-6	1.8	0.12	0.008
H-7	1.8	0.23	0.017
H-8	1.0	0.41	0.035
H-9	2.2	0.46	0.042
H-10	1.4	0.32	0.004
G-1	2.4	0.18	0.017
G-2	2.0	0.49	0.004
G-3	1.4	0.37	0.035
G-4	2.2	0.25	0.036
F-1	1.4	0.15	0.012
F-2	1.8	0.23	0.015
F-3	1.6	0.12	0.010
F-4	3.6	0.21	0.026
A-1	2.6	0.43	0.037
A-2	3.8	0.63	0.065
A-3	3.4	0.58	0.077
A-4	2.2	0.40	0.056
C-1	2.4	0.21	0.031
C-2	2.0	0.23	0.030
C-3	3.0	0.18	0.026
C-4	2.6	0.23	0.024
A-6	1.4	0.43	0.022
A-7	2.4	0.41	0.038
A-8	2.0	0.43	0.057

ranging from 2.7 to 4.5 $\mu\text{g}/\text{cm}^2$ (Table 3). Coefficients of determination for the regressions of O_2 concentration versus time for the experiments ranged from 0.81 to 0.98. Rates of photosynthesis of algal turfs increased as a function of flow speed in all experiments and ranged from 3 to 32 $\text{mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ (Fig. 7). Rates increased by an average of a factor of ~ 3 between flow speeds of 0.08 and 0.52 m/s.

Table 3 Mean (\pm SE, $n = 3$) algal canopy height, ash-free dry mass (AFDM), and chlorophyll *a* content of algal turfs used in each of the ten photosynthesis-flow experiments

Exp. no.	Canopy height (mm)	AFDM (mg/cm^2)	chl. <i>a</i> ($\mu\text{g}/\text{cm}^2$)
1	1.3 \pm 0.3	14.2 \pm 1.8	3.4 \pm 0.8
2	1.8 \pm 0.1	12.5 \pm 2.6	3.6 \pm 1.1
3	1.1 \pm 0.2	9.4 \pm 0.9	4.1 \pm 0.7
4	1.2 \pm 0.4	11.9 \pm 3.1	3.5 \pm 0.3
5	1.6 \pm 0.2	16.0 \pm 2.4	3.2 \pm 0.2
6	1.3 \pm 0.2	11.3 \pm 2.0	2.7 \pm 0.6
7	1.3 \pm 0.2	13.5 \pm 2.2	4.4 \pm 0.5
8	1.7 \pm 0	9.8 \pm 0.4	4.5 \pm 0.6
9	1.5 \pm 0.2	14.2 \pm 3.1	3.2 \pm 0.3
10	1.5 \pm 0.2	18.6 \pm 7.6	3.9 \pm 1.5

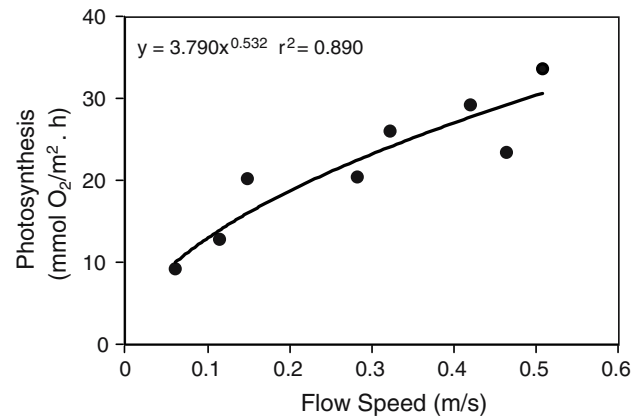


Fig. 7 Results of a typical experiment (Exp. 3) estimating algal turf photosynthesis (normalized to area) at eight flow speeds. Curve fit is a power function

The narrow range of algal canopy heights and the resulting c_f values resulted in little variation in the predicted values of St_{rough} and Sh_{pred} between experiments (Table 4). However, Sh_{meas} calculated from the estimated rates of photosynthesis exhibited greater variation. Ratios of $Sh_{\text{meas}}:Sh_{\text{pred}}$ varied from 0.21 to 1.31 and generally were highest at low Re_D and decreased with increasing Re_D (Table 4).

Plots of the logarithms of the average Sh_{meas} versus $\log Re_D$ for each experiment (Fig. 8) demonstrate a strong relationship between photosynthesis and flow speed but have slopes that are lower than predicted for mass transfer through a turbulent boundary layer (White 1988). The slopes of the $\log Sh_{\text{meas}}-\log Re_D$ plots range from 0.27 to 0.64 and all regressions are significant statistically. There is a negative and significant correlation ($r = -0.65$, $P < 0.05$) between the slopes of the $\log Sh_{\text{meas}}-\log Re_D$ plots and the AFDM of the algal turfs and a weak and negative correlation ($r = -0.31$, $P > 0.05$) between slopes and the coefficients of variation (CV) of algal turf canopy heights. There is no correlation ($r = -0.01$) between slopes of the plots and oxygen concentrations in the flume.

Regressions of oxygen concentration versus time in both light and dark control experiments had zero slopes at both low and high flow speeds. This suggests that rates of metabolism of microorganisms in the flume are negligible compared to rates of algal turf photosynthesis.

Photosynthetic quotient experiments

Rates of photosynthesis based on oxygen evolution ranged from 11.81 to 38.16 $\text{mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$. Photosynthetic rates of the same algal turfs based on changes

Table 4 Flow speeds, pipe Reynolds numbers (Re_D), mean algal canopy heights, coefficients of friction (c_f), roughness Reynolds numbers (Re_k), Schmidt numbers (Sc), Stanton numbers for the roughness elements (St_k), Stanton numbers for rough surfaces (St_{rough}), predicted Sherwood numbers (Sh_{pred}), measured Sherwood numbers (Sh_{meas}), and the ratios of $Sh_{meas}:Sh_{pred}$ for each flow speed for each experiment

Flow speed (m/s)	Re_D	Can. height (m)	c_f	Re_k	Sc	St_k	St_{rough}	Sh_{pred}	Sh_{meas}	$Sh_{meas}:Sh_{pred}$
Exp. 1										
0.08	8,919	0.0013	0.010	12	410	0.00891	0.00057	2,089	2,581	1.24
0.11	12,264	0.0013	0.010	17	410	0.00832	0.00054	2,701	3,306	1.22
0.14	15,609	0.0013	0.010	21	410	0.00790	0.00051	3,280	4,313	1.31
0.27	30,102	0.0013	0.010	41	410	0.00687	0.00045	5,567	4,326	0.78
0.32	35,677	0.0013	0.010	49	410	0.00663	0.00044	6,384	5,818	0.91
0.42	46,826	0.0013	0.010	64	410	0.00626	0.00041	7,946	5,242	0.66
0.47	52,400	0.0013	0.010	72	410	0.00611	0.00040	8,698	4,292	0.49
0.52	57,974	0.0013	0.010	79	410	0.00599	0.00040	9,436	4,202	0.45
Exp. 2										
0.08	8,919	0.0018	0.011	17	410	0.00831	0.00057	2,091	1,942	0.93
0.11	12,264	0.0018	0.011	23	410	0.00776	0.00054	2,703	1,470	0.54
0.14	15,609	0.0018	0.011	29	410	0.00737	0.00051	3,282	3,848	1.17
0.27	30,102	0.0018	0.011	57	410	0.00642	0.00045	5,566	3,538	0.64
0.32	35,677	0.0018	0.011	67	410	0.00619	0.00044	6,380	4,460	0.70
0.42	46,826	0.0018	0.011	88	410	0.00585	0.00041	7,939	4,756	0.60
0.47	52,400	0.0018	0.011	99	410	0.00571	0.00040	8,690	3,778	0.43
0.52	57,974	0.0018	0.011	110	410	0.00559	0.00040	9,425	4,372	0.46
Exp. 3										
0.08	8,919	0.0011	0.010	10	410	0.00923	0.00057	2,090	1,874	0.90
0.11	12,264	0.0011	0.010	14	410	0.00862	0.00054	2,702	2,563	0.95
0.14	15,609	0.0011	0.010	18	410	0.00819	0.00051	3,283	4,082	1.24
0.27	30,102	0.0011	0.010	35	410	0.00712	0.00045	5,574	4,127	0.74
0.32	35,677	0.0011	0.010	41	410	0.00687	0.00044	6,392	5,256	0.82
0.42	46,826	0.0011	0.010	54	410	0.00648	0.00041	7,957	5,863	0.74
0.47	52,400	0.0011	0.010	61	410	0.00633	0.00041	8,712	4,730	0.54
0.52	57,974	0.0011	0.010	67	410	0.00620	0.00040	9,451	6,759	0.72
Exp. 4										
0.08	8,919	0.0012	0.010	11	410	0.00906	0.00057	2,089	1,616	0.77
0.11	12,264	0.0012	0.010	15	410	0.00846	0.00054	2,701	2,692	1.00
0.14	15,609	0.0012	0.010	20	410	0.00804	0.00051	3,281	4,290	1.31
0.27	30,102	0.0012	0.010	38	410	0.00699	0.00045	5,570	5,205	0.93
0.32	35,677	0.0012	0.010	45	410	0.00674	0.00044	6,387	3,821	0.60
0.42	46,826	0.0012	0.010	59	410	0.00637	0.00041	7,951	5,616	0.71
0.47	52,400	0.0012	0.010	66	410	0.00622	0.00041	8,704	5,257	0.60
0.52	57,974	0.0012	0.010	73	410	0.00609	0.00040	9,442	5,228	0.55
Exp. 5										
0.08	8,919	0.0016	0.011	15	410	0.00852	0.00057	2,090	1,616	0.77
0.11	12,264	0.0016	0.011	21	410	0.00796	0.00054	2,701	2,692	1.00
0.14	15,609	0.0016	0.011	26	410	0.00756	0.00051	3,280	4,290	1.31
0.27	30,102	0.0016	0.011	51	410	0.00658	0.00045	5,564	5,205	0.94
0.42	46,826	0.0016	0.011	79	410	0.00599	0.00041	7,939	5,616	0.71
0.47	52,400	0.0016	0.011	88	410	0.00585	0.00040	8,690	5,257	0.60
0.52	57,974	0.0016	0.011	97	410	0.00573	0.00040	9,426	5,228	0.55
Exp. 6										
0.08	8,919	0.0013	0.010	12	410	0.00891	0.00057	2,089	706	0.34
0.11	12,264	0.0013	0.010	17	410	0.00832	0.00054	2,701	2,420	0.90
0.14	15,609	0.0013	0.010	21	410	0.00790	0.00051	3,280	1,965	0.60
0.27	30,102	0.0013	0.010	41	410	0.00687	0.00045	5,567	2,805	0.50
0.32	35,677	0.0013	0.010	49	410	0.00663	0.00044	6,384	2,786	0.44
0.42	46,826	0.0013	0.010	64	410	0.00626	0.00041	7,946	2,783	0.35
0.47	52,400	0.0013	0.010	72	410	0.00611	0.00040	8,698	2,912	0.33
0.52	57,974	0.0013	0.010	79	410	0.00599	0.00040	9,436	4,872	0.52
Exp. 7										
0.08	8,919	0.0013	0.010	12	410	0.00891	0.00057	2,089	1,377	0.66
0.11	12,264	0.0013	0.010	17	410	0.00832	0.00054	2,701	1,202	0.44
0.14	15,609	0.0013	0.010	21	410	0.00790	0.00051	3,280	2,184	0.67

Table 4 continued

Flow speed (m/s)	Re_D	Can. height (m)	c_f	Re_k	Sc	St_k	St_{rough}	Sh_{pred}	Sh_{meas}	$Sh_{meas}:Sh_{pred}$
0.27	30,102	0.0013	0.010	41	410	0.00687	0.00045	5,567	1,598	0.29
0.32	35,677	0.0013	0.010	49	410	0.00663	0.00044	6,384	1,703	0.27
0.42	46,826	0.0013	0.010	64	410	0.00626	0.00041	7,946	1,654	0.21
0.47	52,400	0.0013	0.010	72	410	0.00611	0.00040	8,698	2,321	0.27
0.52	57,974	0.0013	0.010	79	410	0.00599	0.00040	9,436	3,766	0.40
Exp. 8										
0.08	8,919	0.0017	0.011	16	410	0.00841	0.00057	2,091	207	0.10
0.11	12,264	0.0017	0.011	22	410	0.00786	0.00054	2,702	1,478	0.55
0.14	15,609	0.0017	0.011	28	410	0.00746	0.00051	3,281	2,400	0.73
0.27	30,102	0.0017	0.011	54	410	0.00649	0.00045	5,565	3,152	0.57
0.32	35,677	0.0017	0.011	64	410	0.00626	0.00044	6,379	2,491	0.39
0.42	46,826	0.0017	0.011	84	410	0.00592	0.00041	7,938	1,919	0.24
0.47	52,400	0.0017	0.011	94	410	0.00578	0.00040	8,690	2,684	0.31
0.52	57,974	0.0017	0.011	103	410	0.00566	0.00040	9,425	2,909	0.31
Exp. 9										
0.08	8,919	0.0015	0.011	14	410	0.00864	0.00057	2,089	1,234	0.59
0.11	12,264	0.0015	0.011	19	410	0.00807	0.00054	2,701	1,424	0.53
0.14	15,609	0.0015	0.011	25	410	0.00766	0.00051	3,280	2,374	0.72
0.27	30,102	0.0015	0.011	47	410	0.00667	0.00045	5,565	2,772	0.50
0.32	35,677	0.0015	0.011	56	410	0.00643	0.00044	6,380	3,496	0.55
0.47	52,400	0.0015	0.011	83	410	0.00593	0.00040	8,692	3,003	0.35
0.52	57,974	0.0015	0.011	91	410	0.00581	0.00040	9,428	2,809	0.30
Exp. 10										
0.08	8,919	0.0015	0.011	14	410	0.00864	0.00057	2,089	1,083	0.52
0.11	12,264	0.0015	0.011	19	410	0.00807	0.00054	2,701	1,382	0.51
0.14	15,609	0.0015	0.011	25	410	0.00766	0.00051	3,280	2,027	0.62
0.27	30,102	0.0015	0.011	47	410	0.00667	0.00045	5,565	2,293	0.41
0.32	35,677	0.0015	0.011	56	410	0.00643	0.00044	6,380	1,961	0.31
0.42	46,826	0.0015	0.011	74	410	0.00607	0.00041	7,940	2,200	0.28
0.47	52,400	0.0015	0.011	83	410	0.00593	0.00040	8,692	2,189	0.25
0.52	57,974	0.0015	0.011	91	410	0.00581	0.00040	9,428	2,539	0.27

in DIC concentration ranged from 14.54 to 40.70 mmol C m⁻² h⁻¹. The linear relationship between photosynthetic rates based on the two methods suggests that the PQ is not affected by flow speed and has a value very

near unity (Fig. 9). These results also demonstrate that the effect of flow speed on algal turf photosynthesis is not an artifact of estimating photosynthesis from changes in dissolved oxygen (Table 5).

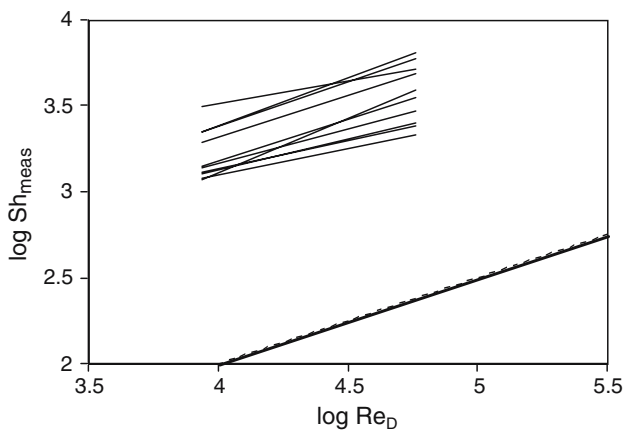


Fig. 8 Plots of $\log Sh_{meas}$ – $\log Re_D$ for each of the ten photosynthesis-flow experiments (solid lines). The predicted relationship between $\log Sh_{meas}$ – $\log Re_D$ for mass transfer through a laminar boundary (slope = 0.50) is shown by the heavy solid line

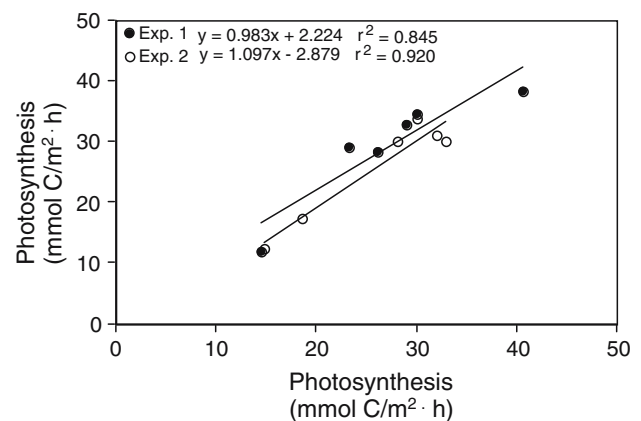


Fig. 9 Plots of photosynthesis of reef algal turf communities based on simultaneous estimation by changes in dissolved oxygen and changes in DIC concentrations in two experiments

Table 5 Slopes, coefficients of determination (r^2), and levels of significance for least squares regressions of $Sh_{\text{meas}}-Re_D$ plots for all ten experiments

Exp. no.	Slope	r^2	P
1	0.27	0.56	0.030
2	0.49	0.66	0.010
3	0.56	0.86	0.001
4	0.53	0.75	0.006
5	0.31	0.72	0.016
6	0.64	0.68	0.007
7	0.48	0.58	0.050
8	0.33	0.43	0.040
9	0.49	0.76	0.009
10	0.40	0.78	0.005

Discussion

Mass transfer limitation of photosynthesis

Rates of algal metabolism have been shown previously to be a function of water motion (Wheeler 1980; Carpenter et al. 1991; Koch 1993; Stevens and Hurd 1997; Williams and Carpenter 1998), caused by the transport of nutrients and gases across diffusive boundary layers surrounding the algae (Wheeler 1982). In coral reef environments, where rates of metabolism per unit area are among the highest of any biological community, the use of chemical engineering models and correlations has led to insights into how flow modulates processes that control rates of metabolism and uptake of reef organisms and communities (Atkinson and Bilger 1992; Bilger and Atkinson 1992; Patterson 1992; Baird and Atkinson 1997). Use of these models involves extrapolations to much higher Sc than in typical engineering applications (Bilger and Atkinson 1992). Nevertheless, using these approaches, rates of photosynthesis and respiration of reef corals (Patterson et al. 1991; Lesser et al. 1994) and rates of nutrient uptake by reef communities (Atkinson and Bilger 1992; Thomas and Atkinson 1997; Falter et al. 2004) have been demonstrated to be affected significantly by water flow in ways that are consistent with mass transfer theory. Application of engineering models has led to predictions about the effects of organism size, geometry, and substratum roughness on the performance of individual organisms and whole communities (Falter et al. 2005). In cases where inconsistencies have appeared between predictions of engineering theory and empirical results (e.g., higher than predicted maximal rates of mass transfer), unique characteristics of living systems, such as cilia and/or mucous-covered surfaces or fine-scale interactions between adjacent structures, have been proposed to influence the dynamics of the interface

between the fluid environment and reef organisms (Bilger and Atkinson 1992). As a result, this approach has led to testable hypotheses about fundamental processes that modulate reef metabolism.

The biomass, chlorophyll *a* content, and rates of photosynthesis for algal turfs in Kaneohe Bay used in our experiments are within the ranges reported for other algal turf communities (Carpenter 1986; Klumpp and McKinnon 1992). The results presented here strongly support the hypothesis that rates of photosynthesis of coral reef algal turfs are controlled by mass transfer over an entire range of realistic, unidirectional flow speeds. Although changes in O_2 were used to estimate photosynthetic rates, the effects of flow speed on patterns of photosynthesis is not the result of increasing flux of photosynthetically generated O_2 away from the algal turfs because the same effect of flow speed is observed when photosynthesis is estimated by changes in DIC concentration. If increased flux of O_2 were responsible for the pattern, the effect of flow speed should decrease as the bulk concentration of O_2 increases, which would increase the concentration gradient across the diffusive boundary layer and increase flux. However, photosynthetic rates were estimated at flow speeds that were ordered randomly with respect to O_2 concentration in the flume and there was no correlation between O_2 concentration and the effect of flow speed on photosynthetic rates.

For the same reasons, the flow speed effect is not the result of the alleviation of inhibition of photosynthesis by high O_2 concentrations within the algal turfs. There is no evidence that high O_2 concentrations result in photorespiration in algal turf species (Hackney and Sze 1988). These results suggest that photosynthesis is mass transfer limited by either nutrients or DIC. The short response time (min) of the effect of flow speed indicates that DIC limitation is more likely than nutrient limitation, since the latter would require time for enzyme synthesis. This interpretation is consistent with previously published results based on measurements of pH and oxygen profiles over coral reef algal turfs at smaller spatial scales (Larkum et al. 2003). Longer term growth of algal turfs likely is limited by nutrient availability.

Slopes of the $\log Sh_{\text{meas}}-\log Re_D$ plots are lower than predicted for mass transfer through a turbulent boundary layer despite flow in the flume being nearly fully turbulent. There are two possible explanations for this pattern, which are not mutually exclusive. One explanation is that the assumption that C_0 is zero is erroneous and that slopes of the $\log Sh_{\text{meas}}-\log Re_D$ plots are reduced as the diffusive flux of O_2 is reduced across a lowered concentration gradient. Bilger and Atkinson

(1995) found such an effect of nutrient loading on the values of mass transfer exponents (equivalent to the slopes of the above relationships) for both phosphorus and ammonium uptake.

A second factor likely to result in lower than predicted slopes of the $\log Sh_{\text{meas}}-\log Re_D$ relationships is the effect of roughness. Although we attempted to minimize the effects of substratum roughness by growing algal turfs on uniformly flat coral plates, the algal turf filaments are roughness elements that extend from the surfaces of the flat plates and may alter flow near the substratum. The algal turfs in the flume experiments varied in canopy height from 1 to 4 mm and at flow speeds between 0.08 and 0.52 m/s, Re_k varies from ~10 to 240. For a mean algal canopy height of 1.4 mm, Re_k varies from ~1 to 85.

In our experiments, values of Sh_{meas} were highest at $17 < Re < 29$, consistent with predictions from engineering surfaces. The effects of roughness on mass transfer have been well studied for engineering surfaces with regular abiotic roughness elements. Mass transfer to these surfaces (with $Sc \sim 500$) is enhanced at $6 < Re_k < 30$ and decreases at values of $Re_k > 40$ (Dade 1993). At high Re , mass transfer to rough surfaces can be lower than that to smooth surfaces (Yaglom and Kader 1974). The decrease in mass transfer to surfaces at high Re_k has been explained by the cavity vortex hypothesis (Dipprey and Sabersky 1963), where the exchange of mass within cavities between roughness elements is controlled by diffusion to the surface from recirculating flow cells between the elements and the frequency that these cavities are flushed (see Dade 1993 for a review). This exchange is retarded with increasing Re_k , as either the height of the roughness elements increases (thus deepening the cavities between elements), and/or as u_* increases and the flow cells are flushed with increasing frequency. Increasing Re_k from near 0 to ~30 results in an increase in mass transfer as the viscous sublayer thins and eventually disappears over the roughness elements. However, with further increases in Re_k , the mean flow near the surface is slowed by the roughness elements and viscous ponding occurs between them and reduces mass transfer to the surface (Dade 1993).

The negative correlation of the slopes of the $\log Sh_{\text{meas}}-\log Re_D$ plots with the AFDM of the algal turfs indicates that algal biomass alters mass transfer to the turfs. For a fully turbulent boundary layer over a flat plate, mass transfer rates are predicted to increase as a 0.8 power of Re . Since similar predictions hold for cylindrical geometries (White 1988), if algal turfs are viewed as upright cylinders that vary in length (canopy height) and density (number of filaments/area), mass

transfer to algal turfs should follow similar patterns. Algal turfs consist of patches of packed cylinders with some patches being transitionally or fully rough, while interspersed patches are hydrodynamically smooth. Algal turfs with increased AFDM most likely have increased densities of filaments (as well as higher canopy heights) rather than increased canopy heights alone. This is supported by the lack of correlation between AFDM and mean canopy height for algal turfs on the plates and may partially explain the relationship between AFDM and the mass transfer relationship with flow in algal turfs. The negative correlation of algal biomass with the slopes of the $\log Sh_{\text{meas}}-\log Re_D$ plots suggests that as biomass increases, mass transfer may occur increasingly through a semi-stagnant boundary layer within cavities formed by algal turf filaments.

Patterns of flow and mass exchange within and between biotic roughness elements such as algal turf filaments undoubtedly are more complicated than for regularly spaced and similarly shaped abiotic roughness (Falter et al. 2005). Additionally, algal turf filaments are deformable in flow and together with patchiness in filament density and height, may add unknown effects on flow between elements and rates of mass transfer. While there is general agreement between patterns of mass transfer and Re_k in algal turfs and those predicted for abiotic surfaces, the higher than predicted values of Sh_{meas} (in some experiments) and the lower than predicted slopes of the $\log Sh_{\text{meas}}-\log Re_D$ relationships suggest that the effect of the micro-architecture of living surfaces (e.g., algal filament height and density) on mass transfer relationships requires further investigation. Since algal turf canopy height and biomass are controlled primarily by either biological (Carpenter 1986) or physical (Cheroske et al. 2000) disturbance, this provides an indirect link between disturbance and the modulation of reef algal community metabolism (Carpenter 1986; Williams and Carpenter 1997).

Water flow over algal turfs in the flume and field

The extrapolation of the results presented here on the effects of water flow on algal turf photosynthesis to algal turfs growing on reefs depends on how closely the flow environment in the flume simulates the relevant parameters of flow conditions in the field (Nowell and Jumars 1987). There are numerous constraints when investigating such a complex problem and we made several simplifications in our initial approach. Metabolic rates were estimated in a sealed flume to control and replicate the flow environment during experiments. The reliable estimation of metabolic rates over

short time periods placed constraints on the volume/(metabolically active area) ratio of the flume and the size dimensions of the flume were scaled accordingly. A second simplification in our approach was to conduct the experiments using unidirectional flow. The intent in this initial study was to address the effects of water flow speed on algal metabolism under relatively simple conditions that could be replicated and evaluated using mass transfer correlations. The results of these studies will serve as the basis for proposing realistic, testable hypotheses about the effects of turbulence, flow oscillation, and algal canopy height on the mass transfer limitation of photosynthesis. A third simplification was to minimize the effects of larger scale (>10 cm) substratum roughness by using algal turfs on uniform coral plates. While substratum roughness may enhance mass transfer to surfaces, this study attempted to establish a baseline of information about the effects of flow without the confounding effects of other factors such as larger scale substratum roughness while maintaining the roughness created by algal turf filaments. The relevant scales of roughness on the Kaneohe Bay barrier reef span a minimum of three orders of magnitude (mm to m) and, while the effects of roughness at the coral colony scale are of potential interest and importance for mass transfer processes, their effects are beyond the scope of the current study.

Despite the simplification in our approach, the flow regime in the flume was similar in many ways to flow over algal turf-covered substrata in the field. The range of flow speeds used in the flume experiments (0.08–0.52 m/s) was within the range of freestream flow speeds that algal turf communities encounter on the reef (majority of flow speeds were between 0 and 0.5 m/s). A more important descriptor of near-substratum turbulent flow is the shear velocity, which ranged from 0.008 to 0.057 m/s in the flume and from 0.004 to 0.077 m/s in the field flow profiles indicating that there was gross similarity between flow regimes in the flume and field. The positive correlations of both u_* and the ratio of u_*/U_∞ with algal turf canopy height in the field is further evidence that the physical structure of algal turfs affects the local flow environment. Spatial variation in mean algal turf canopy heights on the reef flat occurs over a factor of ~ 4 and is associated with variation in values of u_*/U_∞ over an order of magnitude. Since both algal canopy height and u_* affect values of Re_k , at a mean freestream flow speed of 0.2 m/s, spatial variation in Re_k would be expected over a range of 2–121. As a result, spatial variation in the physical structure of the algal community may result in Re_k values on either side of the range ($17 < Re_k < 29$) where maximum rates of mass transfer

and photosynthesis occurred in the flume experiments. These predictions suggest that widespread spatial variation in algal turf photosynthesis occurs on the reef due to the interactions between water flow and algal turf canopy height, which is determined primarily by disturbance.

Not surprisingly, estimates of turbulence for flow in the flume were lower than those for field flow with the maximum turbulence in the flume approaching the mean estimates of turbulence in the field. The maximum length scales of turbulence in the flume are a function of the upstream flow straighteners which break-up larger-scale turbulent eddies. The effects of larger-scale turbulence on the mass transfer limitation of photosynthesis are not known.

The scaling of the flume resulted in partially developed boundary layers over the algal turf covered plates. To achieve fully developed flow in a flume with the same D_h , the length of the working section would need to be 1.4–2.4 times longer. The effect of partially developed boundary layers on patterns of photosynthesis-flow relationships should be an underestimate of the degree of mass transfer limitation because exchange of mass is occurring through a thinner diffusive boundary layer than would be present under fully developed flow. Although flow in the field is oscillatory, at typical wave periods of 5–12 s and mean flow speeds of 0.25 m/s, there is sufficient time for boundary layers to develop fully before they are interrupted by a change in flow direction. As a result, the patterns demonstrated in the flume should be applicable to (subject to the caveats above), and perhaps underestimates of, mass transfer control of algal turf photosynthesis in the field.

Hydrodynamics and reef metabolism

Our results, combined with previous studies, suggest that hydrodynamic processes are fundamental in the modulation of nutrient uptake by reef benthos (Atkinson and Bilger 1992; Thomas and Atkinson 1997; Falter et al. 2004), metabolism and feeding of reef corals (Patterson et al. 1991; Helmuth and Sebens 1993), and rates of nitrogen fixation and photosynthesis by reef algal turf communities (Carpenter et al. 1991; Williams and Carpenter 1998). While the role of water motion has been appreciated for some time, only recently has a new paradigm emerged positing the fundamental importance of the dynamics of the organism–fluid interface in controlling rates of reef metabolism across spatial and temporal scales. The results of these studies have implications for understanding the controls and constraints on maximum rates of reef metabolism and represent a shift away from the

paradigm that reefs are independent of the surrounding oceanography (Smith and Kinsey 1988).

The use of engineering correlations to explore relationships between the flow environment and metabolism of algal turf communities appears promising. Testable predictions for algal turfs arising from these models include the effect of turbulence generated by unsteady flows, and the effect of large-scale roughness on rates of mass transfer (and therefore metabolism). This approach also provides a context in which to frame hypotheses and make predictions of experimental responses about what factor(s) result in the mass transfer limitation of algal turf photosynthesis.

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