

## Effects of nonlocal turbulence on the mass transfer of dissolved species to reef corals

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### Abstract

We examined the importance of nonlocal turbulence to the mass transfer of dissolved species from both cylinders and models of reef coral. Solid gypsum cylinders and gypsum-coated model coral were dissolved in an outdoor flume at mean flow speeds of 4.5 and 10 cm s<sup>-1</sup>. Three model corals were used: two branched forms of the genera *Acropora* and *Pocillopora*, and one lobate form of the genus *Platygyra*. Turbulence intensities ( $Tu$ ) were measured as the ratio of the standard deviation of the time-variant flow to the mean.  $Tu$  of between 5% and 55% were created independently of the mean flow by pumping water through two vertical arrays of jets. Mass transfer coefficients increased by 10–70% with turbulence intensity for all forms at both mean flow speeds considered ( $p < 0.05$ ); however, mass transfer coefficients for the branched coral were not as sensitive to changes in turbulence intensity as for the lobate coral. Results for the cylinders were consistent with the engineering literature and indicate that the effects of turbulence intensity on mass transfer become weaker when branch size or flow speed (or both) become very small. Turbulence intensities measured around experimental coral communities and above naturally occurring reef communities typically vary between 15% and 35%. Assuming an average turbulence intensity of around 25%, then ignoring the effects of nonlocal turbulence altogether would result in uncertainties in mass transfer coefficients of at most  $\pm 10\%$  for the lobate coral form and  $\pm 5\%$  for the branched coral forms. Measuring external turbulence in bulk flows is not necessary for most evaluations of biogeochemical rates in benthic reef systems.

For more than a decade it has been well known that water motion plays an important role in controlling rates of benthic metabolism and material exchange. Higher water motion can increase rates of photosynthesis, respiration, and nitrogen fixation in reef coral, turf algae, and macroalgae (Carpenter et al. 1991; Lesser et al. 1994; Sebens 2003). Rates of nutrient uptake by coral, turf algae, and macroalgae can also increase with greater water motion (Atkinson and Bilger 1992; Thomas and Atkinson 1997; Atkinson et al. 2001). The primary mechanism by which water motion can affect rates of metabolite transfer is through modulation of the concentration boundary layers adjacent to the active surfaces of benthic organisms. When the biochemical demand for a particular metabolite by an organism is high enough, the convective transfer of dissolved metabolites across the concentration boundary layer becomes the rate-limiting step or is “mass-transfer limited” (Bilger and Atkinson 1992). Estimates of nutrient

fluxes to natural reef communities have been made in the field using principles of convective mass transfer derived from both theory and controlled experimentation (Atkinson 1992; Baird et al. 2004; Falter et al. 2004). Our ability to make such in situ predictions is essential for understanding how rates of nutrient uptake, photosynthesis, respiration, and other metabolic processes vary within and between reefs. This knowledge is crucial to understanding the general ecology of coral reef communities.

To better understand the role that water motion plays in regulating fluxes of dissolved materials to coral reef organisms and communities, we must first understand how rates of convective mass transfer to naturally rough surfaces vary under the wide variety of flows to which reef communities are exposed. Unfortunately, it is still not fully clear to what detail we need to understand, characterize, and measure water motion, because natural flows are often the sum of multiple fluid dynamics subject to entirely different forcings (e.g., tides, upwelling, gravity waves, internal waves, buoyancy-driven flow, etc.) and operate on different space scales and time scales. For example, the prevalence of surface waves in many coral reef environments (Munk and Sargent 1954; Hearn and Parker 1988; Young 1989) raised questions of whether rates of mass transfer under wave-driven, oscillatory flow were greater than under steady, unidirectional flow (Carpenter et al. 1991). Subsequent studies have demonstrated that rates of dissolved species mass transfer were enhanced under wave-driven, oscillatory flow, with the degree of enhancement depending on the morphology of the forms and the kinematics of the wave (Falter et al. 2005; Lowe et al. 2005a; Reidenbach et al. 2006a).

### Acknowledgments

We thank Jim Fleming for assistance in the construction of the turbulence generators, Mark Baird for assistance and suggestions during preliminary experiments, Rob Rivers at All Pool & Spa for refurbishing a 30-year-old pool pump and thus maintaining the continuity of the experiments, Sandy Chang for her assistance collecting some of the data, and Jane Culp who inspired these experiments.

This research was supported by grant OCE04-53117 from the National Science Foundation.

This is Hawaii Institute of Marine Biology contribution 1246 and School of Ocean and Earth Science and Technology contribution 6972.

Many reef organisms and communities are typically rough, or distinctively nonstreamlined in their morphology, such that even the modest movement of water past their forms can incur separation of flow resulting in locally generated turbulent boundary-layer flows. The eddies generated by this interaction then advect and mix into the surrounding water column, creating time-variant fluctuations superimposed on the mean flow, which increase the mixing and transport of both mass and momentum. It is the aggregate effect of communities of rough, reef organisms living in concert with other nonliving, roughness features (e.g., rocks, ledges, sand ripples, etc.) over a large expanse of benthos that creates the turbulence experienced by the benthos as a whole (Reidenbach et al. 2006b). To what extent does this nonlocal turbulence affect rates of dissolved species mass transfer to individual reef organisms? Here we define nonlocal turbulence as the turbulence incident to a solid surface generated by upstream roughness features. This is in contrast to the turbulence generated at the solid-liquid interface by the direct interaction of a roughness element with the surrounding mean flow. Nonlocal turbulence can be generated at different scales, such as by adjacent branches within the same coral colony or between adjacent colonies and organisms within a larger reef community. The engineering literature tells us that nonlocal turbulence can double to quadruple rates of convective mass transfer to flat plates and smooth cylinders at the same mean flow speed (Kestin and Wood 1971; Maciejewski and Moffat 1992b; Sanitjai and Goldstein 2001). However, these studies have focused exclusively on heat and mass transfer for simple geometric surfaces under flows and boundary conditions that are grossly different from those governing the convective mass transfer of dissolved species to and from benthic organisms.

The role that nonlocal turbulence plays in controlling the mass transfer of dissolved species to benthic communities is far from clear. We know that coral and other sessile benthic organisms often live under predominantly turbulent flow conditions. Several studies have suggested that nonlocal turbulence could play some unknown role in the mass transfer of dissolved species to benthic communities (Thomas and Cornelisen 2003; Falter et al. 2005; Reidenbach et al. 2006a), whereas other studies have hypothesized that levels of turbulence in the water column (i.e., nonlocal) are in fact the critical fluid property determining rates of mass transfer (Hearn et al. 2001; Baird et al. 2004). None of these points of view, however, have ever been explicitly tested let alone verified. As a consequence, the potential role of nonlocal turbulence has been the source of much informal speculation and criticism in studies of benthic metabolism. Turbulence generated by wall and entrance effects in experimental flumes and flow chambers as well as in turbulent wakes generated by grids, cages, blunt objects, or even other organisms and their appendages, often has been used to challenge the validity of various experimental designs. These concerns, however, have not been issued without some basis. It is well established that turbulence structure plays a very important role in benthic ecology with regard to the encounter and detection of odor plumes (Finelli et al. 1999; Mead et al. 2002; Weissburg et al. 2002),

fertilization of freely released gametes (Denny and Shibata 1989; Denny et al. 2002; Crimaldi and Browning 2004), patterns of larval settlement (Crimaldi et al. 2002), uptake of organic particles by active filter feeders (Frechette et al. 1989), and fluxes of dissolved materials from sediment beds (Santschi et al. 1991; Dade 1993; Lorke et al. 2003).

What levels of turbulent water motion are found in and around coral reef communities? At present there are few measurements of near-bottom turbulence over coral reefs. This is partly due to the effort, expensive equipment, and expertise necessary to make such measurements. Proper measurement of turbulence in the field is not trivial, and is currently an active area of research in the field of near-shore physical oceanography. This is especially true in the presence of random waves that can make it difficult to discriminate turbulent fluid motions from the time-variant fluid motions of the waves themselves (Benilov and Filyushkin 1970; Shaw and Trowbridge 2001). If nonlocal turbulence does play a critical role in determining rates of mass transfer to reef communities, then the flow environments surrounding reef communities will need to be characterized with much greater effort and detail than is commonly done. Before committing the resources to make such an effort we must first ask what is the quantitative importance of nonlocal turbulence in controlling fluxes of dissolved nutrients and other metabolites from one community to another and from one environment to another? The larger motivation for the present study, however, is to improve our understanding how water motion shapes the ecology of corals and other sessile benthic organisms beyond what is currently known.

We examined the effects of varying levels of incident turbulence intensity on rates of dissolved species mass transfer from model reef corals. Plaster cylinders and model corals were dissolved in experimental flows where both mean flow speed and turbulence intensity were varied independently. The results of these experiments were then compared with the range of turbulence intensities found in and around coral reef organisms and communities in order to assess how rates of dissolved species mass transfer may respond to natural and experimental variation in levels of turbulent water motion.

*Background*—An effective approach for describing mass transfer from a liquid to solid surfaces involving both diffusion and convection is by relating the flux of a species ( $J$  in  $\text{mmol m}^{-2} \text{d}^{-1}$ ) to the difference between the concentration of that species in the bulk fluid ( $C_b$  in  $\text{mmol m}^{-3}$ ) and at the solid-liquid interface ( $C_s$ ), and the mass transfer coefficient ( $\beta$  in  $\text{m s}^{-1}$ )

$$J = \beta(C_b - C_s) \quad (1)$$

In essence, Eq. 1 relates the transport rates given by the conservation equations (continuity, momentum, and species) in terms of the boundary conditions and a convective mass transfer coefficient,  $\beta$ . In the engineering literature,  $\beta$  is most often defined on the basis of fluxes normalized by the total surface area available for heat and mass transfer; however, for rough surfaces of variable total surface area,

$\beta$  is often defined on the basis of fluxes normalized to the plan or projected area. Mass transfer is often described using a nondimensional variable called the Sherwood number (Sh) that incorporates  $\beta$ , which in turn, is often expressed as a function of two other nondimensional variables: the Reynolds number (Re) and Schmidt number (Sc).

$$\text{Sh} \equiv \frac{\beta L}{D} \quad (2)$$

$$\text{Re} \equiv \frac{UL}{\nu} \quad (3)$$

$$\text{Sc} \equiv \frac{\nu}{D} \quad (4)$$

where  $U$  is the mean flow speed of the fluid ( $\text{m s}^{-1}$ ),  $L$  is a characteristic length scale (m),  $\nu$  is the kinematic viscosity of the fluid ( $\text{m}^2 \text{s}^{-1}$ ), and  $D$  is the diffusivity of the dissolved species exchanging at the solid-liquid boundary ( $\text{m}^2 \text{s}^{-1}$ ). A common expression used for estimating Sh averaged around the circumference of a cylinder is provided by Churchill and Bernstein (1977)

$$\text{Sh} = 0.3 + \frac{0.62\text{Re}^{1/2}\text{Sc}^{3/4}}{[1 + (0.4/\text{Sc})^{2/3}]^{1/4}} \quad (5)$$

where  $L$  is taken as the cylinder diameter ( $d$ ). For the range of fluid characteristics relevant to the mass transfer of dissolved species to and from living benthic communities ( $\text{Re} > 100$  and  $\text{Sc} > 400$ ), Eq. 5 can be simplified to the following expression:

$$\text{Sh} = 0.62\text{Re}^{1/2}\text{Sc}^{1/3} \quad (6)$$

Equation 6 can be rearranged using Eqs. 2–4 to show the inherent dependency of  $\beta$  on the physical variables  $U$ ,  $d$ , and  $D$

$$\beta \propto \frac{U^{1/2}D^{2/3}}{d^{1/2}} \quad (7)$$

For coral reef communities, Bilger and Atkinson (1992) proposed using heat and mass transfer correlations for rough surfaces provided by Dipprey and Sabersky (1963) and Dawson and Trass (1972) to estimate the first-order uptake rate coefficient  $S$  directly from fundamental physical and nondimensional variables where  $S \equiv J/C_b$ . Nutrient uptake is considered mass-transfer limited when the concentration at the surface ( $C_s$ ) is very small in comparison to the concentration in the bulk fluid ( $C_s \ll C_b$ ), and thus,  $S \rightarrow \beta$  (Eq. 1). The correlations proposed by Bilger and Atkinson (1992) have been shown to be effective in predicting rates of nutrient mass transfer to both experimental (Atkinson and Bilger 1992; Thomas and Atkinson 1997) and naturally occurring (Falter et al. 2004) coral reef communities. Falter et al. (2004) showed that given the range of flows and roughness heights found for

most reef communities, and the values of Sc for dissolved metabolites ( $>400$ ), these heat and mass transfer correlations could be simplified into the following relationship:

$$\beta = \Gamma u_* \text{Re}_k^{-0.2} \text{Sc}^{-0.6} \quad (8)$$

where  $\Gamma$  is an empirical constant,  $u_*$  is the friction velocity, and  $\text{Re}_k$  is the Reynolds roughness number.  $\text{Re}_k$  is defined as

$$\text{Re}_k \equiv \frac{u_* k}{\nu} \quad (9)$$

where  $k$  is the roughness height of the reef community. The expression shown in Eq. 8 can be rearranged to show the dependency of  $\beta$  on the important dimensional quantities of interest (see Falter et al. 2004)

$$\beta \propto U^{0.8} D^{0.6} \quad (10)$$

Prior studies of heat and mass transfer to both flat plates and cylinders have shown that the enhancement in Sh due to turbulence is a function of the product of the turbulence intensity (Tu) and Re (Kestin and Wood 1971; Simonich and Bradshaw 1978; Sanitjai and Goldstein 2001)

$$\frac{\text{Sh}}{\text{Sh}_0} = f(\text{Tu Re}) \quad (11)$$

where  $\text{Sh}_0$  is Sh for an incident flow in which the turbulence intensity is zero and the flow is laminar. Tu is defined as the ratio of the root-mean-square (rms) average turbulent flow speed ( $q_{\text{rms}}$ ) to the mean flow speed ( $\bar{U}$ )

$$\text{Tu} \equiv \frac{q_{\text{rms}}}{\bar{U}} \quad (12)$$

where  $q$  is calculated from the turbulent flow velocities in the x, y, and z directions ( $u'$ ,  $v'$ , and  $w'$ , respectively) according to

$$q = \sqrt{\frac{1}{3}(u'^2 + v'^2 + w'^2)} \quad (13)$$

Calculating Tu this way rather than using flow data from just one axis avoids the need to assume that the turbulence is isotropic (Lowery and Vachon 1975). We can further define the enhancement of Sh or  $\beta$  due to turbulence intensity based on the left-hand term in Eq. 11

$$E_{\text{Tu}} = \frac{\text{Sh}}{\text{Sh}_0} \quad (14)$$

In this study we vary mean flow and turbulence (hence turbulence intensity) and measure the enhancement of the mass-transfer coefficient for several forms of coral and cylinder geometries under different levels of turbulence intensity relative to the case where turbulence is absent.

## Methods

**Facilities and measurements**—All experiments were conducted in an outdoor flume at the Hawaii Institute of Marine Biology, on Coconut Island, Oahu, Hawaii. This flume has been described in greater detail elsewhere (Atkinson and Bilger 1992); however, it consists of two adjacent rectangular channels 12 m long, 40 cm wide, and 30 cm deep connected at one end with a 180° turn and at the other with a 1.5-m-deep well housing a 12V DC variable-speed propeller used to generate mean flow. To generate turbulence, water is pumped from the flume channel opposite of the test section using a 500-watt (3/4 horsepower) pump and forced through two 2-cm-diameter pipes each with 2-mm holes drilled at ~1.1-cm intervals in each pipe creating two vertical arrays of jets (Fig. 1). The two sets of jets are directed inward, perpendicular to the mean flow direction. Turbulence intensity was varied by increasing or decreasing the distance downstream from the jets upstream (Maciejewski and Moffat 1992a). All flow measurements were made at 25 Hz using a Nortek NDV acoustic Doppler velocimeter (ADV) equipped with a three-dimensional sideways-looking probe mounted on a mobile frame so that flow characteristics could be measured at any x, y, and z position within the flume test section (Fig. 1). Turbulence velocities were calculated by detrending each velocity time-series using a linear regression in each of the x, y, and z directions and defining  $u'$ ,  $v'$ , and  $w'$ , respectively, by the residuals.

Our experiments were designed to independently control mean flow and turbulence levels separately and uniformly, so that we could properly evaluate the importance of nonlocally generated turbulence on rates of mass transfer to benthic reef communities. Thus, experimental turbulent flows used in this study were mechanically generated with jets rather than through the interaction of a mean flow with a naturally rough reef community. Our jet-generated turbulence simulated the spectral characteristics of naturally generated turbulence (Fig. 2).

Liquid gypsum plaster was prepared by mixing No. 1 pottery plaster (US Gypsum) with water in a 5:4 ratio (volume plaster to volume water) for 1–2 min. The plaster was either poured into PVC molds to make solid cylinders or used to coat the model corals. Two cylinder geometries were used in this study: one 5 cm in diameter and 10 cm in height, and another 1.6 cm in diameter and 15 cm in height. All cylinders were soaked in still seawater for 1 h, allowed to sit for 30 min in air, and then weighed before being dissolved in an experiment. After being dissolved under natural seawater in the flume, all cylinders were again allowed to sit for 30 min in air, and then weighed. The difference in the weights of the wet cylinders before and after dissolution were converted to dry-weight losses using a mass ratio of dry to wet plaster equal to 0.64 (Falter et al. 2005).

Model coral (Energy Savers Unlimited) 12–13 cm in height, 15–18 cm wide, and 12–14 cm deep of the genera *Platygyra*, *Pocillopora*, and *Acropora* were coated with plaster to create mass transfer surfaces that closely

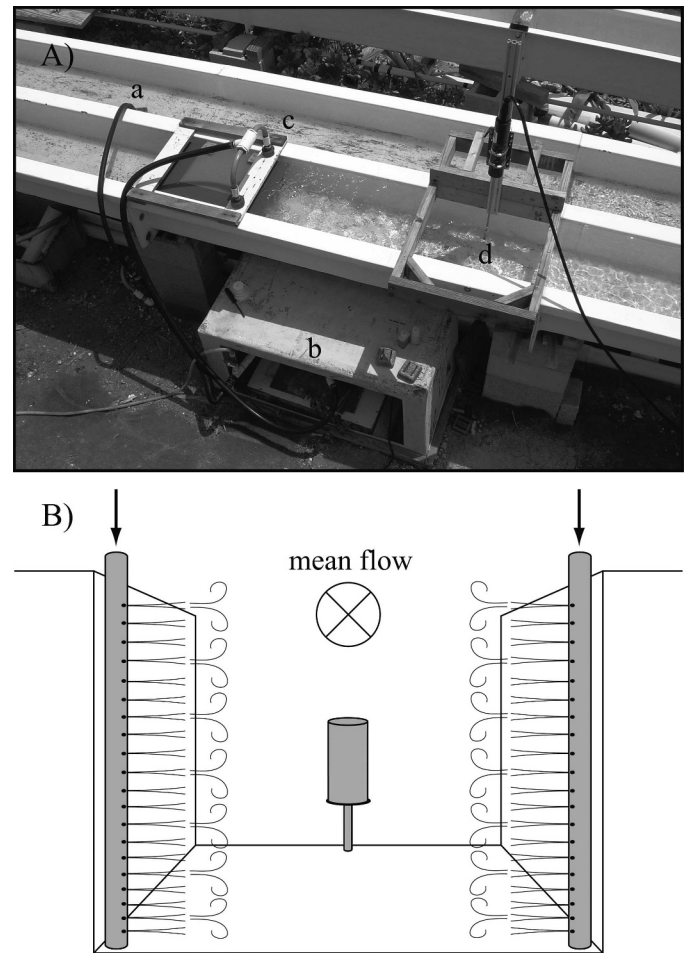


Fig. 1. (A) To generate turbulence, water was pumped from the flume channel opposite of the test section (a) using a 500-watt pump (b) and forced through two linear arrays of jets on either side of the flume test section (c). Flow measurements downstream of the turbulence source were made using an ADV with a three-dimensional sideways-looking probe vertically mounted on a mobile frame (d). (B) Downstream view of turbulent jets and location of mounted form inside the working section of the flume (cylinder shown). Note that the mean flow is generated by a propeller elsewhere in the flume and not by the forcing of water through the turbulent jets.

mimicked the morphology of living coral (Fig. 3). Synthetic model coral was used rather than natural, carbonate coral skeletons because (1) they provide the use of multiple replicates of the same exact coral morphology, which greatly facilitated experimental productivity; (2) they are lighter than real coral heads, thereby providing more sensitive mass-dependent measurements; and (3) unlike carbonate skeletons, they are impermeable to the adsorption and desorption of water, which could complicate measurements of dissolution by weight loss. After being initially coated, all corals were dried in an oven for 48 h at 50°C and then weighed. Plaster-coated corals were then dissolved under natural seawater in the flume from 40 to 400 min, depending on the flow conditions, resulting in dry-weight losses of 9 to 25 g. To estimate uncertainty in the weight-loss method, four corals of the exact same

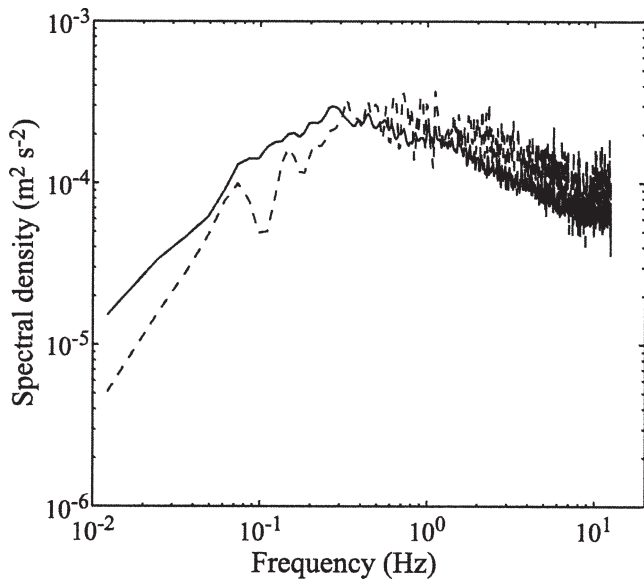


Fig. 2. Variance-preserving spectral density of  $q$  (see Eq. 13) spatially averaged over flow incident to an experimental form (solid line,  $df = 216$  for each point shown) and at 1 cm above a 3-m-long experimental community of *Porites compressa* skeletons  $\sim 10$  cm in height (dashed line,  $df = 24$  for each point shown). For both spectra,  $\bar{U} = 10 \text{ cm s}^{-1}$  and  $Tu = 28\%$ .

morphology were coated and dried according to the procedure above, soaked in still seawater for 30 min, dried in the oven for 48 h, and then weighed again.

**Experimental design**—All model coral and the 5-cm-diameter cylinders were dissolved at two predominant nominal mean flow speeds:  $\bar{U} = 4.5$  and  $10 \text{ cm s}^{-1}$ . The 1.6-cm-diameter cylinders, however, were dissolved only when  $\bar{U} = 4.5 \text{ cm s}^{-1}$ . For the  $\bar{U} = 10 \text{ cm s}^{-1}$  experiments,  $\beta$  was measured at  $Tu$  of around 5%, 13%, 30%, and 50% whereas for the  $\bar{U} = 4.5 \text{ cm s}^{-1}$  experiments, replicate measurements of  $\beta$  were made only under a low  $Tu$  of around 10% and a high  $Tu$  of around 55%. All forms were mounted in the center of the flume, 5 cm off the bottom to remove them from any potential bottom boundary-layer effects (e.g., velocity defects and higher turbulence levels) and to ensure the exposure of the forms to spatially homogeneous mean and turbulent flow fields. Prior experiments showed that mean flows reached their approximate free-stream values at heights  $>4$  cm off the bottom in an empty flume when  $\bar{U} > 4 \text{ cm s}^{-1}$ . The bottom faces of all coral were cleaned of their plaster coatings and the bottom faces of all cylinders were covered to exclude these surfaces from contributing to dissolution. For the model coral, measurements of  $\bar{U}$ ,  $q$ , and  $Tu$  were made on a  $3 \times 3$  grid 15 cm wide and 10 cm high centered on the upstream face of the coral perpendicular to the direction of flow before and after each experiment. Values of  $\bar{U}$ ,  $q$ , and  $Tu$  were then averaged over each of these grids to generate a singular value for each whole coral. For the cylinders, measurements of  $\bar{U}$ ,  $q$ , and  $Tu$  were made in a three-point profile 10 cm high for the 5-cm-diameter cylinders and 15 cm high for the 1.6-cm-diameter cylinders centered on

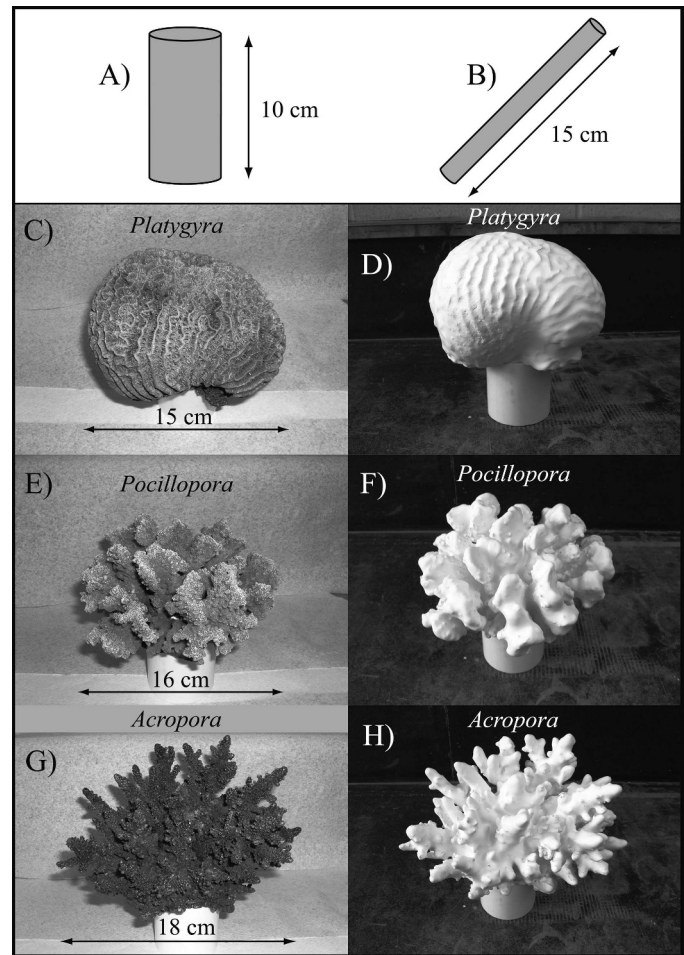


Fig. 3. Drawings of the (A) 5-cm-diameter and (B) 1.5-cm-diameter model cylinder geometries. Images of the three model corals with and without plaster coatings: (C, D) *Platygyra*, (E, F) *Pocillopora*, and (G, H) *Acropora*.

the upstream face of the cylinders before and after each experiment. Values of  $\bar{U}$ ,  $q$ , and  $Tu$  were then averaged over each of these profiles to generate a singular value of  $\bar{U}$ ,  $q$ , and  $Tu$  for each whole cylinder.

**Estimation of mass transfer coefficients**—Mass transfer coefficients for  $\text{Ca}^{2+}$  can be calculated from the dry-weight lost from each form ( $\Delta M_{\text{dry}}$ ) according to

$$\beta = - \frac{\Delta M_{\text{dry}}}{MW_{\text{gyp}} \Delta t A_f \Delta C} \quad (15)$$

where  $MW_{\text{gyp}}$  is the molecular weight of gypsum ( $172.2 \text{ g mol}^{-1}$ ),  $\Delta t$  is the time taken to dissolve the form,  $A_f$  is the surface area of the form, and  $\Delta C$  is the concentration difference across the boundary layer ( $20.8 \text{ mol m}^{-3}$ ; Falter et al. 2005). For cylinders,  $A_f$  was calculated on the basis of the average height and diameter of the cylinders measured before and after being dissolved. Equations 2 and 15 were then used to calculate  $Sh$  for all cylinders by taking the diameter as the characteristic length scale. We did not measure  $A_f$  for the corals because we were

only interested in the effects of varying flow conditions (i.e.,  $Tu$ ) on mass transfer from each coral form individually. Therefore, we calculated spatially integrated mass transfer coefficients ( $\beta^*$ ) for the coral forms that were independent of surface area where

$$\beta^* = \beta \cdot A_f \quad (16)$$

We also calculated  $\beta^*$  for each of the cylinders in order to compare results from the cylinders with those from the coral forms. For the mass transfer of dissolved species with the same diffusivity to/from forms of the same size and shape,  $E_{Tu}$  (Eq. 14) can be defined solely in terms of either  $\beta$  or  $\beta^*$  rather than  $Sh$ .

$$E_{Tu} \equiv \frac{\beta}{\beta_o} = \frac{\beta^*}{\beta_o^*} \quad (17)$$

Because of slight variations in temperature and mean flow speed during experiments, all measurements of  $\beta$  and  $\beta^*$  were normalized to a standard temperature of 25°C and a standard  $\bar{U}$  of either 4.5 or 10 cm s<sup>-1</sup> according to Eq. 7 for the cylinder and Eq. 10 for the coral. Average temperatures for all experiments varied between 23° and 27°C leading to corrections in  $\beta$  and  $\beta^*$  of only  $\pm 5\%$  for all forms. For the nominal  $\bar{U} = 10$  cm s<sup>-1</sup> experiments, actual  $\bar{U}$  varied between 9.5 and 10.7 cm s<sup>-1</sup>, whereas for the nominal  $\bar{U} = 4.5$  cm s<sup>-1</sup> experiments, actual  $\bar{U}$  varied between 4.0 and 5.1 cm s<sup>-1</sup>. Corrections in  $\beta$  and  $\beta^*$  and for actual versus nominal flow speeds were  $\pm 5\%$  for  $\bar{U} = 10$  cm s<sup>-1</sup> experiments and  $\pm 10\%$  for  $\bar{U} = 4.5$  cm s<sup>-1</sup> experiments.

Changes in the dry mass of the blank plaster coral forms ( $\pm 95\%$  CI) were  $-0.3 \pm 0.5$  g for the cylinders,  $-0.7 \pm 0.9$  g for the *Platygyra*,  $-1.2 \pm 1.5$  g for the *Pocillopora*, and  $-1.0 \pm 1.4$  g for the *Acropora* ( $n = 4$  for all forms). This translated into uncertainties of between 5% and 15% in estimates of  $\beta$  for individual coral forms, and between 2% and 5% in estimates of  $\beta$  for individual cylinders. Because in all cases the mean weight loss was not significantly greater than zero, no blank weight losses were subtracted during any of the experiments.

## Results

For the  $\bar{U} = 10$  cm s<sup>-1</sup> experiments,  $\beta^*$  increased with  $Tu$  for all coral forms and the 5-cm cylinders ( $r^2 = 0.55$ – $0.89$ ,  $p < 0.05$ ; Fig. 4). For these experiments, the sensitivity of mass transfer rates to nonlocal sources of turbulence can be quantified by comparing the incremental increase in turbulent enhancement per added increment of turbulence intensity using the definition given in Eq. 17

$$\frac{dE_{Tu}}{dT_u} = \frac{1}{\beta_o^*} \frac{d\beta^*}{dT_u} \quad (18)$$

It is easy to see that the quantity on the right-hand side of Eq. 18 can be calculated for each of the forms by taking

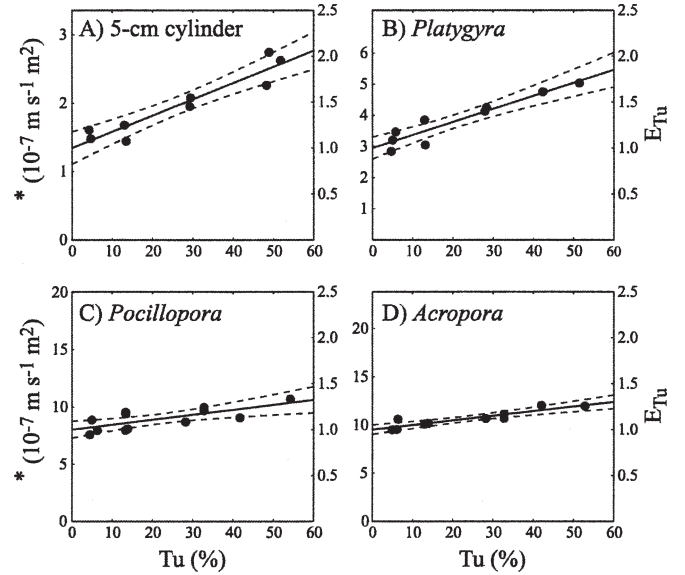


Fig. 4. Integral mass transfer coefficients ( $\beta^*$ , left y-axes) and turbulent enhancement ( $E_{Tu}$ , right y-axes) versus  $Tu$  for all forms in the  $\bar{U} = 10$  cm s<sup>-1</sup> experiments. Solid lines represent best-fit linear regression whereas dashed lines represent 95% confidence intervals on regression predictions. (A) Five-centimeter-diameter cylinders:  $\beta^* = 2.4Tu + 1.3$  ( $n = 9$ ,  $r^2 = 0.89$ ). (B) *Platygyra*:  $\beta^* = 4.2Tu + 2.9$  ( $n = 9$ ,  $r^2 = 0.89$ ). (C) *Pocillopora*:  $\beta^* = 4.3Tu + 8.0$  ( $n = 12$ ,  $r^2 = 0.55$ ). (D) *Acropora*:  $\beta^* = 4.8Tu + 9.5$  ( $n = 10$ ,  $r^2 = 0.83$ ).  $E_{Tu}$  were calculated by dividing values of  $\beta^*$  for each form by their respective regression y-intercepts. A value of  $E_{Tu} = 1$  represents no enhancement.

the ratio of their best-fit regression slopes of  $\beta^*$  versus  $Tu$  ( $d\beta^*/dT_u$ ) to their best-fit y-intercepts ( $\beta_o^*$ ).  $dE_{Tu}/dT_u$  For the 5-cm cylinder, *Platygyra*, *Pocillopora*, and *Acropora* forms were ( $\pm 95\%$  CI):  $1.8 \pm 0.6$ ,  $1.4 \pm 0.4$ ,  $0.5 \pm 0.3$ , and  $0.5 \pm 0.2$ , respectively (Fig. 4). Thus,  $\beta$  for the branched corals (*Acropora* and *Pocillopora*) were less sensitive to changes in  $Tu$  than for either the lobate *Platygyra* coral or the 5-cm cylinders. For the  $\bar{U} = 4.5$  cm s<sup>-1</sup> experiments,  $\beta^*$  for all forms increased significantly from  $Tu$  of  $\sim 10\%$  to  $Tu$  of  $\sim 55\%$  ( $p < 0.05$ ; Table 1). For these experiments, we quantified the sensitivity of  $\beta^*$  to changes in  $Tu$  by comparing the ratio of  $\beta^*$  at high and low  $Tu$  (Table 1). Mass transfer coefficients for branched coral forms were still less sensitive to changes in  $Tu$  than for the lobate coral form at this flow speed ( $p < 0.05$ ), but not less sensitive than for the 5-cm cylinders. Mass transfer coefficients for the 1.6-cm cylinders were the least sensitive of any form to changes in  $Tu$  (Table 1).

Turbulent enhancement for all cylinders in this study increased linearly with  $TuRe$  ( $r^2 = 0.95$ ; Fig. 5). The regression predicted a turbulent enhancement of only 1.04 for  $TuRe = 0$ , results consistent with the heat and mass transfer literature. For all coral forms, there was no significant difference between  $E_{Tu}$  at  $\bar{U} = 4.5$  cm s<sup>-1</sup> and at  $\bar{U} = 10$  cm s<sup>-1</sup> (Table 1).

Table 1. Mass transfer coefficients for all forms at  $\bar{U} = 4.5 \text{ cm s}^{-1}$  at low and high turbulence and the resulting enhancement due to turbulence ( $\beta_{\text{high}}^*/\beta_{\text{low}}^*$ ) along with their uncertainty at the 95% confidence level and number of replicates ( $n$ ). The ratio of  $\beta_{\text{high}}^*$  to  $\beta_{\text{low}}^*$  at  $\bar{U} = 10 \text{ cm s}^{-1}$  was estimated from the regression equations in Fig. 4 for the corresponding Tu from the  $\bar{U} = 4.5 \text{ cm s}^{-1}$  experiments.

Form	$n$	Tu	$\bar{U} = 4.5 \text{ cm s}^{-1}$		Tu	$\beta^* (\times 10^{-7} \text{ m s}^{-1} \text{ m}^{-2})$	$\beta^* (\times 10^{-7} \text{ m s}^{-1} \text{ m}^{-2})$	$(\beta_{\text{high}}^*/\beta_{\text{low}}^*)$	$\bar{U} = 10 \text{ cm s}^{-1}$ $(\beta_{\text{high}}^*/\beta_{\text{low}}^*)$
			$\beta^* (\times 10^{-7} \text{ m s}^{-1} \text{ m}^{-2})$	$\beta^* (\times 10^{-7} \text{ m s}^{-1} \text{ m}^{-2})$					
1.6-cm Cylinder	3	11	0.85 ± 0.03	0.87 ± 0.05	54	1.10 ± 0.07	—	1.64 ± 0.18	
5-cm Cylinder	2	11	0.95 ± 0.08	1.23 ± 0.08	56	1.28 ± 0.13	—	1.71 ± 0.18	
<i>Platygyra</i>	2	11	2.0 ± 0.3	3.3 ± 0.3	57	1.70 ± 0.27	—	1.23 ± 0.12	
<i>Pocillopora</i>	2	8	5.3 ± 0.5	7.4 ± 1.0	61	1.40 ± 0.23	—	1.22 ± 0.06	
<i>Acropora</i>	2	11	6.5 ± 0.4	8.6 ± 1.1	49	1.32 ± 0.18	—	—	

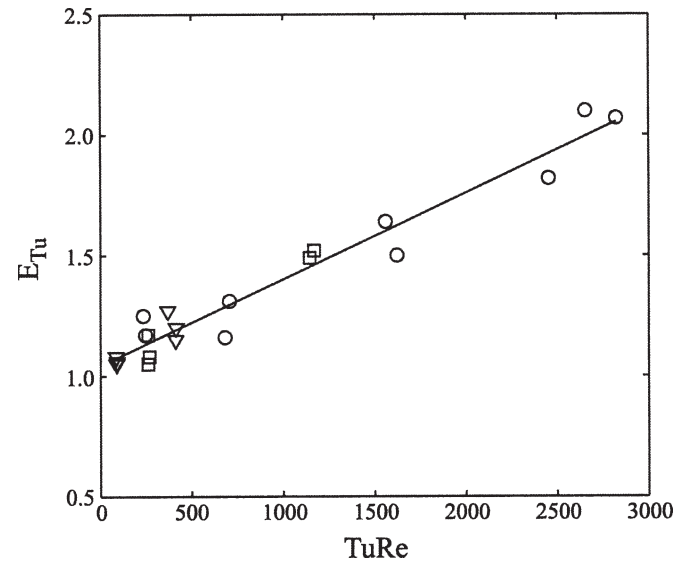


Fig. 5.  $E_{\text{Tu}}$  versus  $\text{TuRe}$  for cylinders used in this study:  $d = 1.6 \text{ cm}$  and  $\bar{U} = 4.5 \text{ cm s}^{-1}$  (triangles);  $d = 5 \text{ cm}$  and  $\bar{U} = 4.5 \text{ cm s}^{-1}$  (squares);  $d = 5 \text{ cm}$  and  $\bar{U} = 10 \text{ cm s}^{-1}$  (circles). Equation for the line shown is  $y = 3.58 \times 10^{-4}x + 1.04$  ( $n = 20$ ,  $r^2 = 0.95$ ). A value of  $E_{\text{Tu}} = 1$  represents no enhancement.

### Discussion

*Branch scale*—Smaller branches can exchange dissolved metabolites faster per unit skeletal weight than larger branches because of a higher ratio of tissue surface area to skeletal volume. Assuming coral branches can be modeled as long cylinders, then the surface area per length of branch is proportional to the diameter of the branch ( $d$ ) while the volume of skeletal biomass per length of branch is proportional to  $\sim d^2$ ; thus, the metabolite exchange rate per skeletal biomass scales by  $\sim 1/d$ . This is a fundamental benefit of having branched versus lobate growth forms. Equation 7 indicates that mass-transfer rates per unit surface area (i.e.,  $\beta$ ) scale by  $1/\sqrt{d}$  demonstrating an additional advantage of thinner branch size. Thus, total rates of mass transfer per branch skeletal volume should scale by  $d^{-3/2}$ . Our results ( $\text{Sc} = 1,250$ ) in conjunction with prior literature on heat and mass transfer ( $\text{Sc} < 3$ ) indicate that the influence of nonlocal turbulence on  $\beta$  for the entire cylinder decreases as the cylinder diameter  $d$  decreases. Sanitjai and Goldstein (2001) suggested that nonlocal turbulence has a stronger effect on cylinders at higher Re (and hence larger  $d$  at the same flow speed) due to thinner boundary layers, a greater tendency for transition (laminar  $\rightarrow$  turbulent), and increased reattachment of flow following separation of the streamlines from the cylinder surface. As a consequence, nonlocal turbulence should have less of an effect on rates of mass transfer to individual branches as the branch diameter gets smaller. For example: a 1-cm-diameter cylindrical branch exposed to an interior mean flow of  $10 \text{ cm s}^{-1}$  with a Tu equal to 5% would have an Re of around 1,000 and an TuRe of 50. The same branch exposed to the same interior mean flow, but with

a very high Tu of 50%, would still have a TuRe of only 500. Thus,  $\beta$  for this same branch under these very different turbulent flow conditions should differ by only 20% or less (Fig. 5).

Real coral branches are not as smooth as the cylinders or the gypsum-coated skeletons used in this study. The millimeter-scale roughness features that are generally present on living coral were absent from the forms used in these experiments. Mass transfer to rough surfaces are always higher than to smooth surfaces at the same Re (Yaglom and Kader 1974; Zhao and Trass 1997; Lolija 2005). Enhancement due to roughness may increase in regions of transitional flow, but generally decreases with both increasing flow speed and absolute roughness height. As turbulent boundary layers develop, turbulent perturbations of the viscous sublayer become less dependent upon turbulence created by the surface roughness, and more dependent upon turbulence generated in the boundary layer above leading to diminished enhancement (Dawson and Trass 1972). We expect that increasing nonlocal turbulence would act in a similar manner to that of an increasingly turbulent boundary layer, causing mass transfer to these surfaces to behave as if they were occurring at higher Re and  $Re_k$  than calculated from the mean flow. Thus, increasing nonlocal turbulence would diminish the added mass transfer that millimeter-scale roughness would give above that found for a smooth surface. Falter et al. (2005) studied the effects of added millimeter-scale and centimeter-scale surface roughness features to the mass transfer of bluff, rectangular bodies ( $6 \times 6 \times 12 \text{ cm}^3$ ) exposed to in situ flows on natural coral reefs and found that when normalized to total surface area, mass-transfer rates were comparable for all forms: smooth and rough. These results indicated no particular enhancement in mass-transfer rates by small-scale roughness beyond that created by the added surface area inherent to the geometry of the roughness elements. We believe, on the basis of the above considerations, that the interaction of surface roughness and nonlocal turbulence will not greatly affect mass-transfer rates for coral branches. Consequently, we expect that millimeter-scale roughness elements on living coral branches will not make them more sensitive to nonlocal turbulence. It is more likely that such small-scale roughness will make living branches even less sensitive.

*Colony scale*—We had thought mass-transfer rates for whole colonies of branched corals would be most sensitive to changes in incident turbulence intensity as a result of increased turbulence intensity driving greater exchange of momentum between the interior spaces of the coral and the ambient flow. Branched corals have a much greater amount of surface area than do lobate corals of roughly the same size; therefore, any process that would increase flow between the branches should greatly increase the total mass transfer for the entire form. Thus, mass transfer to branched corals should be more dynamic with respect to variations in the surrounding flow. The larger-scale pressure gradients associated with turbulent accelerations could have provided one possible means for driving flow into and within the interior space of the branches following

a mechanism analogous to the action of surface wave-driven on-flow within submerged canopies (Lowe et al. 2005b). We assumed that only turbulent accelerations resulting from eddies larger than that of the entire coral form would be spatially coherent enough to induce flow between branches. For our experiments that length scale ( $L$ ) was 10 cm and corresponded to a time-scale of  $\sim L/\bar{U}$  or  $\sim 1$  s. We estimate an rms-turbulent acceleration of  $6.3 \text{ cm s}^{-2}$  at the relevant length scales from spectra measured at a mean flow of  $10 \text{ cm s}^{-1}$  and an intermediate turbulence intensity of 30% once turbulent fluctuations  $>1$  Hz have been filtered out. For comparison, the rms-orbital acceleration under a shallow-water wave whose rms-orbital speed ( $U_{\text{rms}}$ ) was equal to  $10 \text{ cm s}^{-1}$  (equal to the higher mean flow treated in this study) and whose period ( $T$ ) were between wind waves and ocean swell (e.g.,  $\sim 10$  s) would be  $\sim 2\pi U_{\text{rms}}/T$  or  $6.3 \text{ cm s}^{-2}$ . Thus, flow accelerations due to turbulence can be comparable to those induced by passing gravity waves. We did not measure enhancement in mass-transfer rates from turbulence similar to that suggested for some wave-driven flows ( $>2$ , Lowe et al. 2005b; Reidenbach et al. 2006a). This may be because turbulent flow speeds are typically only a fraction of mean flow speeds.

*Community scale*—Our experimental design considered the effects of nonlocal turbulence on isolated coral colonies. Flow within the interior spaces of isolated, branched coral colonies will be attenuated leading to significant reductions in potential interior mass transfer rates (Chamberlain and Graus 1975; Reidenbach et al. 2006a). Nonetheless, there can still be significant penetration of the mean flow into the interior space of isolated colonies driven by the pressure gradient setup from the large-scale separation of flow around the entire form (Chamberlain and Graus 1975). In this sense, branched coral colonies living in sparse aggregations (a case that is more typical than not on coral reefs) may behave like porous bluff bodies. In contrast, coral colonies living in dense aggregations may behave more like submerged rigid canopies. A true coral canopy is developed when the spacing of the individual colonies is on the order of the colony height or closer and the horizontal expanse of the aggregation is greater than roughly 10 times the canopy height. The latter requirement is necessary to keep the canopy interior isolated from the kind of horizontal penetration of pressure-driven flow experienced by isolated coral colonies living or colonies in small clusters. Under the spatial arrangement necessary to form true coral canopies; and under steady, unidirectional flow, shear-generated turbulence is the only substantial mechanism left by which momentum can be transported into the canopy interior (Raupach et al. 1996; Ghisalberti and Nepf 2002). Inflections in the velocity profile near the tops of the canopies generate Kelvin-Helmholtz instability waves, which are particularly effective at vertical momentum transport due to their high associated Reynolds stresses in comparison with more typical boundary-layer turbulence. These instability waves can then propagate, facilitating the vertical exchange of momentum between canopy

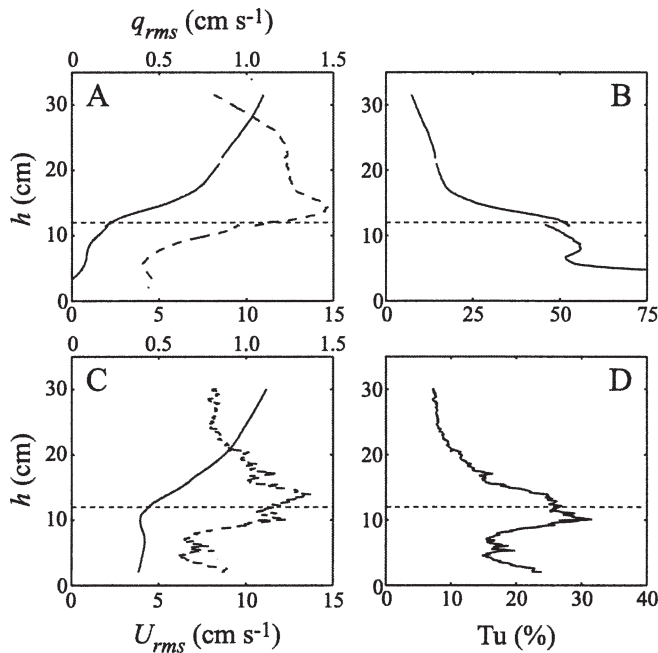


Fig. 6.  $U_{rms}$  (solid line) and  $q_{rms}$  (dashed line) versus depth between two coral heads in an experimental community of *Porites compressa* under (A) steady, unidirectional flow and (C) under an oscillatory flow with a period of 2.1 s. Measurements shown were made by particle imaging velocimetry at the Environmental Fluid Mechanics Laboratory at Stanford University (Lowe 2005). (B) Tu versus depth calculated for the same flow conditions shown in A. (D) Tu versus depth calculated for the same flow conditions shown in C. The height of the community is 12 cm as indicated by the horizontal dashed line in each plot.

elements farther downstream. Thus, highly coherent, large-scale, nonlocal turbulence could play a more important role in mass transfer to coral living in canopies under steady, unidirectional flow than our data indicate. This mechanism may be even more important for submerged, flexible vegetative canopies under free-stream flow speeds that exceed the threshold at which waving of the canopy occurs, further enhancing the vertical exchange of momentum (Ackerman and Okubo 1993; Ghisalberti and Nepf 2002). Still, the production of instability waves by shear is a weak mechanism for driving the exchange of metabolites when compared with the action of wave-driven oscillatory flow on interior mass transfer rates in both isolated coral colonies (Reidenbach et al. 2006a) and model coral canopies (Lowe et al. 2005b).

Although mean flow within coral canopies can be highly attenuated, turbulence intensities between roughness elements can be much higher than above the bed due to both shear and wake production (Fig. 6). For wave-driven, oscillatory flow, within-bed values of Tu vary from 15% to 30% and reach maximum values near the tops of the roughness elements. In the case of steady, unidirectional flow; within-bed values of Tu can exceed well over 50%, increasing with depth in the rough bed. Consequently, local rates of mass transfer deep within the bed should be much greater than expected if only local mean flow speeds were considered. However, these anomalous values of Tu are

driven not by large increases in  $q_{rms}$ , but rather from large reductions in the mean flow  $\bar{U}$ ; a property typical for canopy flows (e.g., Ghisalberti and Nepf 2002; Raupach et al. 1996). For example, the integral of the mass transfer coefficient over the depth of the canopy ( $\int \beta_o$ ) neglecting any enhancement due to turbulence and should be proportional to the integral of  $\bar{U}^{0.8}$ , or  $\int \beta_o = c \int \bar{U}(z)^{0.8} dz$  where  $c$  is an arbitrary constant of proportionality. If we assume a turbulent enhancement for the *P. compressa* canopy shown in Fig. 6 similar to that of the *Pocillopora* models used in this study (Fig. 4C), then the resulting depth-integrated, turbulence-enhanced canopy mass-transfer coefficient  $\int \beta$  would be equal to  $c \int \bar{U}(z)^{0.8} \cdot E_T(Tu(z)) dz$  or  $1.32 \int \beta_o$ . However, if we were to assume a substantially lower average Tu inside the same *P. compressa* canopy of only 25% (a value typical for flows both above real reefs and between coral canopies under oscillatory flow), then  $\int \beta$  would equal  $1.13 \int \beta_o$ . Thus, by assuming an average Tu of only 25% for the interior *P. compressa* canopy, mass transfer to the entire coral would be underestimated by only ~16%. We do not consider this difference to be very important in light of other physical and biological factors. First, there is generally less available bioactive surface area deeper in the coral canopy than at the exterior, which would make these low  $\bar{U}$ -high Tu environments even less numerically important than suggested above. Second, light levels deep within the interior of coral canopies can be substantially reduced compared with those of ambient values (Falkowski et al. 1990). Without ample light, it may not be possible for photoautotrophic tissues to maintain a high enough biochemical demand to reach rates of mass-transfer limitation, regardless of the physics of their local flow environment. It is very possible that despite various mechanisms for injecting momentum into the interior of coral canopies, these surfaces are still not contributing much to the exchange of metabolites for the entire canopy and that most of the metabolite exchange occurs near the top of submerged coral canopies. We believe this should be the subject of future investigation.

*Turbulence intensities over real reefs*—There are few in situ measurements of turbulence intensity made either within or above natural coral reefs. Data we have collected from a high-energy, wave-dominated reef flat indicate a relatively constant Tu of 20–25% just above the reef surface due to a strong correlation between turbulent and mean flow speeds (Fig. 7). Reidenbach et al. (2006b) measured a Tu of 20–35% at heights of 10 and 30 cm above fringing reefs in the Gulf of Eilat under steady, unidirectional flow speeds of 10–20 cm s<sup>-1</sup>. Assuming that turbulence intensities in and around both experimental and natural reef communities typically vary between 15% and 35% and average around 25%, then ignoring turbulence intensity altogether would result in uncertainties in  $\beta$  of at most  $\pm 10\%$  for the lobate coral, and at most  $\pm 5\%$  for the branched coral (Fig. 4). These results indicate that nonlocal turbulence generated by rough bottoms is not providing a substantial mechanism with which to greatly affect rates of mass transfer to reef organisms and communities and, therefore, how these rates will vary from one hydrodynamic

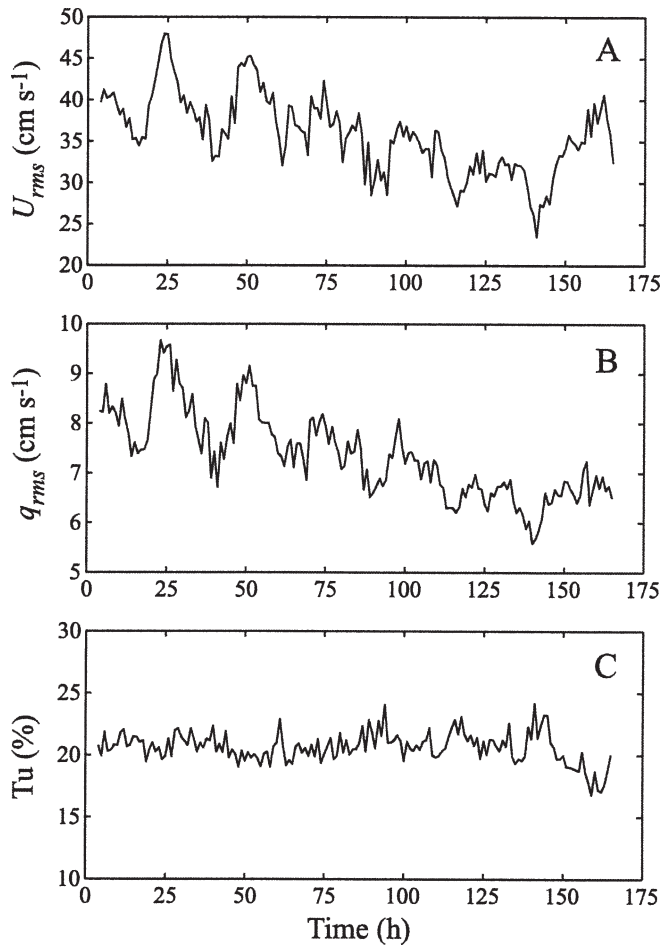


Fig. 7. (A)  $U_{rms}$ , (B)  $q_{rms}$ , and (C) Tu measured 30 cm off the bottom on the Kaneohe Bay Barrier Reef flat, roughly 50 to 100 m landward of the surf zone ( $21.5^{\circ}\text{N}$ ,  $157.8^{\circ}\text{W}$ , depth = 2 m). See Lowe et al. (2005a) for additional experimental details.

environment to the next. For example, in our study, a 10-fold increase in Tu (5%→50%) resulted in a 60% increase in mass transfer for the lobate coral and a 25% increase in mass transfer for the branched coral, whereas a 10-fold increase in mean near-bottom flow speeds should increase rates of mass transfer to coral communities by more than 500% (Eq. 10).

Hearn et al. (2001) proposed that turbulence in the boundary layer above reef communities was the physical mechanism controlling the minimum mixing length scale, and therefore, the thickness of diffusive boundary layers. It appears, however, that turbulence in the water column above the reef bottom cannot control rates of nutrient and metabolite mass transfer to the benthos. Although mass transfer to reef coral may be taking place through turbulent boundary layers, this transfer occurs almost entirely from the interaction of each roughness element with its own local mean flow field. Turbulence structure can play an important but indirect role in affecting rates of mass transfer by reducing velocity defects in the boundary layer and increasing the spatially averaged mean flow to which reef organisms and communities are exposed; however,

these effects will be explicitly manifest in the shape of mean velocity profiles. Ultimately, it is much more the spatial structure of the mean flow, rather than that of the turbulence itself, which controls rates of mass transfer to reef coral.

*Implications for future studies*—Profiles of turbulence have been used to estimate the in situ uptake of organic particles by benthic communities (Genin et al. 2002). This is made possible only because particle concentration gradients are sometimes large enough to be measured synoptically with turbulent motions allowing for the direct estimates of material fluxes. For dissolved species, however, the thicknesses of the concentration boundary layers are considerably smaller: tens to hundreds of microns thick (Kuhl et al. 1995; Larkum et al. 2003; Falter et al. 2005) making their direct measurement for entire organisms or communities both difficult and questionable at best. Furthermore, the collection and interpretation of turbulence data in situ is far from a simple procedure. Given that turbulent flow speeds are only 20–30% of the mean flow, the presence of even modest wave motion can confound accurate measurement of turbulent fluctuations (Benilov and Filyushkin 1970; Shaw and Trowbridge 2001). The measurement of turbulence in situ requires a much greater amount of instrumentation, expertise, and effort than simply measuring the mean flow, which at present, can be performed with a single instrument and minimal post-processing of the data.

We believe that further study of turbulence over benthic communities will lead to greater understanding of how hydrodynamics affects the general ecology of benthic organisms, and that additional data on turbulence structure over coral reefs should still be collected. Nonetheless, our results should help simplify experiments on the metabolism of benthic organisms in which water motion is an important environmental consideration, but not necessarily the subject of direct interest. If the purpose is to assess, compare, or just control for the exchange of important dissolved chemical species between organisms and communities under varying natural or experimental flows, then measuring the turbulent components of water motion is not necessary. Flumes and flow chambers designed specifically to measure rates of metabolism need not be very quiescent, and should probably aim for turbulent intensities between 10% and 20%. There are still other criteria for the proper design of flumes and flow chambers intended for the measurement of benthic metabolism (Nowell and Jumars 1984; Falter et al. 2006), but artifacts due to background turbulence is not one of them. We recommend that flows around benthic organisms and communities be measured at frequencies high enough to capture wave-orbital motion ( $\geq 1$  Hz), and only if such wave motion is present.

We conclude that nonlocal turbulence increases rates of dissolved species mass transfer to reef coral, and that the degree of turbulent enhancement varies with the morphology of the form. However, mass-transfer rates to the roughest and most complex forms (i.e., branching) were the least sensitive to changes in nonlocal turbulence. Our

results indicate that mass-transfer rates are still driven much more by variation in mean flow speed than by direct interaction of the turbulence itself with the organisms' concentration boundary layers. Consequently, natural variations in turbulence intensity in and around reef coral are not likely large enough to substantially affect variation in rates of uptake or release (or both) of dissolved nutrients and other dissolved metabolites.

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Received: 1 May 2006

Accepted: 17 September 2006

Amended: 28 September 2006