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Mass-transfer limitation of nutrient uptake by a wave-dominated reef flat community

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Abstract

Maximum rates of phosphate, nitrate, and ammonium uptake by a reef flat community were estimated from rates of frictional dissipation that were calculated from the attenuation of waves propagating over the Kaneohe Bay Barrier Reef flat. Time-averaged flow speeds across the entire study area ranged from 0.08 to 0.22 m s^{-1}. Observed decreases in wave energy fluxes and near-bottom orbital velocities gave a mean estimate for the bottom friction coefficient (c_f) of 0.22 ± 0.03. Friction coefficients were used to estimate nutrient mass-transfer coefficients of 5–9 m d^{-1} for phosphate and 9–16 m d^{-1} for ammonium and nitrate. Wave heights offshore of Kaneohe Bay were also used to estimate an annual phosphate mass-transfer coefficient of 8 ± 2 m d^{-1}. This value is similar to a published value of 9 ± 2 m d^{-1} that was determined from measured changes in phosphate concentrations across the reef flat. We conclude that rates of phosphate uptake by the Kaneohe Bay Barrier Reef flat community are occurring near the limits of mass transfer.

Net primary production is a major pathway by which mass and energy flow into coral reef ecosystems. The uptake of dissolved nutrients is often the rate-limiting step for net primary production in marine ecosystems. Thus, a knowledge of the kinetics of nutrient uptake by coral reef communities is necessary for assessing how nutrient loading rates change in response to natural or anthropogenic increases in nutrient concentrations. Bilger and Atkinson (1992) proposed that nutrient uptake by shallow reef communities was limited by mass transfer, the physical transfer of nutrients across concentration boundary layers covering the surfaces of reef autotrophs. These authors used mass-transfer correlations for rough surfaces taken from the engineering literature to correlate maximum rates of nutrient uptake with the frictional characteristics of experimental reef communities. Subsequent studies demonstrated the ability of such mass-transfer correlations to predict nutrient uptake kinetics for experimental reef communities within closed, recirculating flumes (Atkinson and Bilger 1992; Bilger and Atkinson 1995; Thomas and Atkinson 1997) and a large experimental mesocosm (Atkinson et al. 2001). The results of these studies made it clear that shallow-water reef communities are capable of taking up nutrients from the water column at rates that are limited by mass transfer. However, it had not yet been demonstrated whether in situ rates of nutrient uptake by natural reef communities were occurring near the limits of mass transfer.

Typically, in situ measurements of nutrient fluxes to coral reefs rely on monitoring changes in the concentration of nutrients in water slowly moving across shallow reef communities and, as such, are unable to discriminate between gross rates of nutrient uptake and rates of nutrient release. Because shallow-water reef communities are composed of both autotrophic and heterotrophic organisms, pathways for nutrient release must also exist wherever there are pathways for nutrient uptake. Problems of dilution due to mixing and advection prevent the introduction of tracers to directly measure gross nutrient uptake rates (Atkinson and Smith 1987). Furthermore, most reef communities live in water that is too deep or of too short a residence time to make a significant measurement of any nutrient flux at all. Mass-transfer correlations provide a means for estimating gross nutrient uptake rates to coral reef communities, or at least maximum uptake rates, where direct measurements are not possible. There have been few estimates of in situ nutrient mass-transfer rates for natural reef communities, and the few estimates available have relied on inadequate physical and experimental information necessary for predicting nutrient mass-transfer rates (Atkinson 1992; Atkinson and Bilger 1992; Baird et al. in press). This has resulted in very large discrepancies (up to a factor of 40) between predicted and observed rates of nutrient uptake (Atkinson 1987; Bilger and Atkinson 1992).

In the present article, we reconsider the estimation of maximum nutrient mass-transfer rates to a wave-dominated, natural reef flat community on the Kaneohe Bay Barrier Reef, Oahu, Hawaii, based primarily on an improved understanding of the flow conditions and frictional roughness of the reef flat community. First, we will review mass-transfer theory and the results of experiments from the literature on nutrient mass transfer to coral reefs. Next, we will describe the means by which we parameterized and quantified the

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frictional roughness and flow characteristics of the Kaneohe Bay Barrier Reef flat on the basis of observations of wave attenuation across the reef flat. Using the above information, we demonstrate that observed net rates of phosphate uptake by the Kaneohe Bay Barrier Reef flat are comparable to maximum rates of gross phosphate uptake predicted from empirical mass-transfer correlations and are, therefore, not anomalously high (Bilger and Atkinson 1992).

Background: coral reef mass-transfer relationships

Mass-transfer theory states that the molar flux of a given species, J_i, to a surface under a given set of flow conditions can be related to the concentration of that species at the surface, $[C_i]_s$, and in the bulk fluid $[C_i]_b$, by the molar mass-transfer coefficient, S_i:

$$J_i = S_i([C_i]_b - [C_i]_w) \tag{1}$$

where J_i is defined to be positive for describing nutrient uptake. Under the assumption of $[C_i]_b \gg [C_i]_w$, then the molar flux approaches a maximum mass-transfer rate of

$$J_{i,\max} = S_i[C_i]_b \tag{2}$$

The mass-transfer parameterization used by Atkinson et al. (Bilger and Atkinson 1992; Baird and Atkinson 1997; Thomas and Atkinson 1997) was based on the dimensionless Stanton number, St_i, which relates S_i to the flow speed of the ambient fluid, U:

$$S_i = \mathrm{St}_i U \tag{3}$$

Dade (1993) generalized an expression for St_i on the basis of the heat-transfer correlations of Dipprey and Sabersky (1963) as well as the mass-transfer correlations of Dawson and Trass (1972)

$$St_i = \frac{c_f/2}{1 + \sqrt{(c_f/2)}\,(\gamma \mathrm{Re}_k^a \mathrm{Sc}_i^b - 8.48)} \tag{4}$$

where c_f is the friction coefficient, which relates the magnitude of benthic shear stress, τ_b, to U:

$$\tau_b = \frac{1}{2} c_f \rho U^2 \tag{5}$$

where Re_k is the Reynolds roughness number, defined as

$$\mathrm{Re}_k \equiv \frac{u^* k}{\nu} \tag{6}$$

where k is the roughness height, ν is the kinematic viscosity of the fluid, and u^* is the friction velocity, defined as

$$u^* \equiv \sqrt{\frac{\tau_b}{\rho}} \tag{7}$$

Sc_i is the Schmidt number of specific dissolved nutrient i and is defined as the ratio of the kinematic viscosity of the fluid to the molecular diffusivity of that nutrient (D_i) in the fluid ($\mathrm{Sc}_i \equiv \nu/D_i$). Sc measurements for dissolved inorganic nutrients in waters around coral reefs are typically >500.

The empirical constants a, b, and γ in Eq. 4 are taken from the heat-transfer relationship for rough surfaces provided by Dipprey and Sabersky (1963) and the mass-transfer relationship for rough surfaces provided by Dawson and Trass (1972). The heat-transfer correlation of Dipprey and Sabersky extends to higher Re_k values than does the mass-transfer correlation of Dawson and Trass (2,400 vs. 120); however, the correlation of Dawson and Trass extends to higher values of Sc than the Dipprey and Sabersky correlation extends for the heat-transfer equivalent of Sc (4,600 vs. 6). Using a value of $a = 0.2$ taken from the more relevant high Re_k data of Dipprey and Sabersky (1963), a value of $b = 0.58$ taken from the more relevant high Sc data of Dawson and Trass (1972); under the assumption that the roughness heights of most reefs are typically ≥ 0.01 m, bulk flow velocities are ≥ 0.02 m s^{-1}, and values of c_f are no less than one fifth the minimum published value (0.005), Re_k for most reef environments should be no less than $\sim 10^2$. This means that the term involving Re_k and Sc dominates the denominator of Eq. 4. The value of 8.48 in the denominator of Eq. 4 contributes $<2\%$ to the calculation of St; thus, Eqs. 3 and 4 can be combined and simplified into a semiempirical equation predicting S_i for benthic communities from observed flow and frictional characteristics

$$S_i \approx \Gamma \frac{\sqrt{c_f/2}}{\mathrm{Re}_k^{0.2} \mathrm{Sc}_i^{0.58}} U \tag{8}$$

where Γ is an empirical constant.

Mass-transfer coefficients measured from the uptake of ammonium by experimental reef communities (Thomas and Atkinson 1997) are in very good agreement with coefficients obtained from the dissolution of gypsum-coated corals (Baird and Atkinson 1997), as described by the functional relationship given in Eq. 8 (Fig. 1). These results demonstrate not only that nutrient uptake by experimental reef communities occurs at the limits of mass transfer but that uptake rates could be predicted using existing mass-transfer relationships. If Eq. 8 is dimensionalized, then the following proportionality results:

$$S_i \propto \frac{c_f^{0.4} U^{0.8} D_i^{0.58}}{k^{0.2} \nu^{0.38}} \tag{9}$$

D_i for a specific dissolved nutrient, and ν can be calculated on the basis of the salinity and temperature of sea water (Li and Gregory 1974). Equations 8 and 9 demonstrate that S_i is a function of the roughness of a community, the diffusivity of the species in question, and the ambient flow conditions. Field measurements of c_f and U, along with estimates of k based on the frictional roughness and wave excursion amplitude, will be used in Eq. 8 to predict the maximum gross uptake rates of phosphate, ammonium, and nitrate across the Kaneohe Bay Barrier Reef flat.

Methods

Site description—Kaneohe Bay is located on the northeast, or windward, side of the island of Oahu, Hawaii. The Kaneohe Bay Barrier Reef is $\sim$2 km wide and 10 km long, running northwest to southeast along the entrance of Kaneohe Bay (Fig. 2). The depth of the reef flat ranges from <1 to $\sim$3 m, shoaling toward the back reef and away from chan-

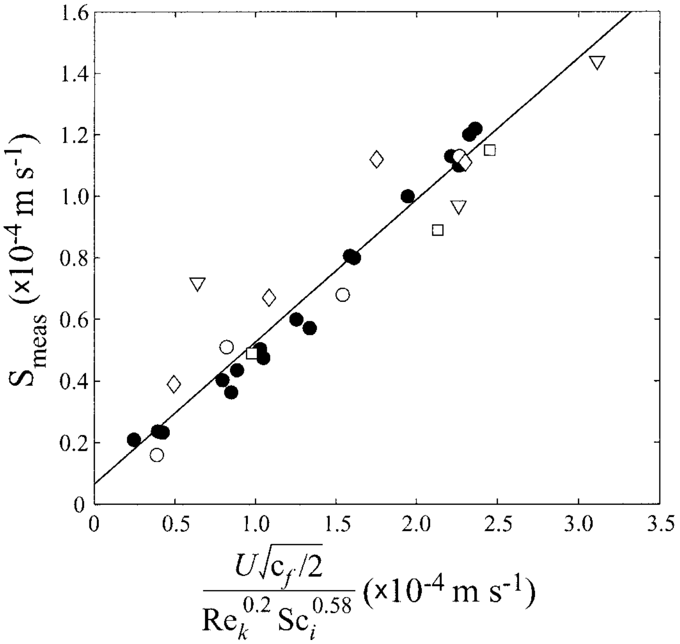

Fig. 1. Measured mass-transfer coefficients derived from gypsum-coated coral skeletons (black symbols) as well as from ammonium uptake by experimental reef communities (white symbols) consisting of high-relief coral rubble overgrown with turf and macroalgae (squares), low-relief coral rubble overgrown with turf and macroalgae (circles), *Porites compressa* (triangles), and *Pocillopora damicornis* (diamonds) vs. the quotient term in Eq. 8. See text for definitions of nondimensional variables. The model II regression shown is $y = 0.46x - 6 \times 10^{-6}$ ($r^2 = 0.92$, $n = 31$).

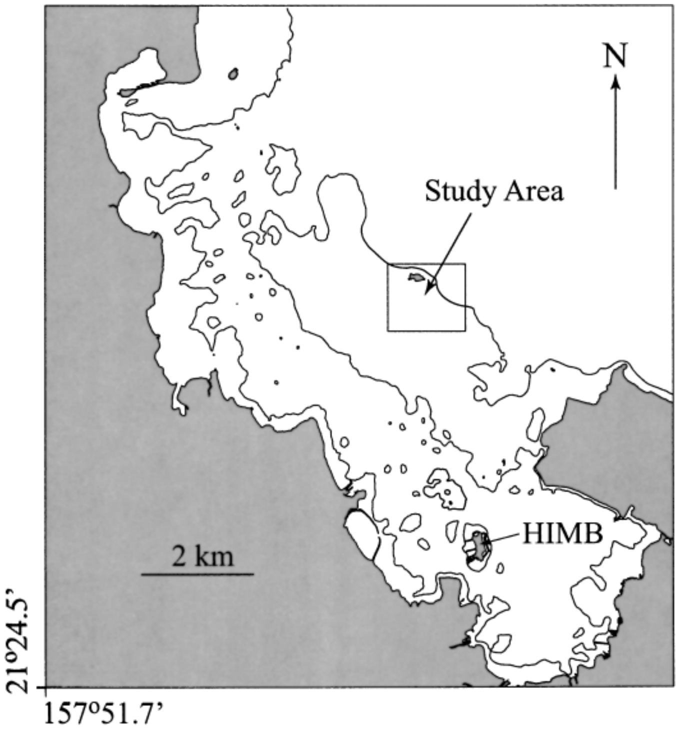

Fig. 2. Kaneohe Bay, Oahu, Hawaii. The Kaneohe Barrier Reef and patch reefs are outlined by 4-m isobaths.

nels bounding each side of the reef to the middle of the reef flat. There are two primary sources of wave energy impinging on the Kaneohe Bay Barrier Reef: (1) wind waves 6–10 s in period generated by trade winds that blow out of the east to northeast year round but are most consistent during the summer, and (2) ocean swells 10–14 s in period that originate from the north to northwest only during the winter months (October–April).

Wave characteristics were measured within a specific study area located toward the center and front of the reef flat (Fig. 3). This specific area was chosen in consideration of the following hydrodynamic characteristics. First, changes in wave height appeared to be greatest in areas of the reef flat closer to the fore reef than to the back reef, providing the most robust estimates of changes in wave energy flux. Second, wave fronts moving across this area, and extending some hundreds of meters on either side of the area, were observed to be nearly parallel and indicated only one predominant direction (Fig. 3). As a consequence, a one-dimensional linear array could adequately characterize losses in wave energy by monitoring changes in wave energy flux along a line in the direction of predominant wave propagation. Third, wave transformations within the study area should be dominated by dissipation due to bottom friction—the specific process with which we are interested in quantifying.

The study area was also chosen in consideration of the following biogeochemical characteristics. First, it was an area where measurements of ambient nutrient concentrations, estimates of phosphate uptake rate coefficients, and estimates of gross community production and respiration had already been made (Webb 1977; Atkinson 1987; M.J.A. unpubl. data). Second, the substrate of the study area consists almost entirely of hard limestone populated mainly with groups of turf, macroalgae, and coralline algae with little sand. Therefore, it represents a nearly complete bioactive and autotrophic surface with few areas of minimal metabolic activity (Kinsey 1985). Common genera of macroalgae within the study area include *Acanthophora, Asparagopsis, Dictyota, Halimeda, Padina, Sargassum,* and *Turbinaria.* The study area is also sparsely populated with heads of *Pocillopora meandrina, Pocillopora damicornis* and *Porites lobata* (≤0.3 m); however, corals represent less than a few percent of the bottom cover within the study area. Descriptions of the reef flat community made here are consistent with prior descriptions made by Atkinson (1981*b*) and later by Chun-Smith (1994), which indicates that the composition and morphology of the bottom community has remained largely unchanged.

Wave height measurements—Wave heights across the reef flat were measured on three different days corresponding to three different levels of incident wave activity during the summer of 2001 (10 and 16 August and 4 September). The dates used throughout the present article represent the days that instruments were taken from the water. These measurements were made during the summer, to ensure that the directional spectrum of waves incident to the Kaneohe Bay Barrier Reef would have only one source—the trade winds.

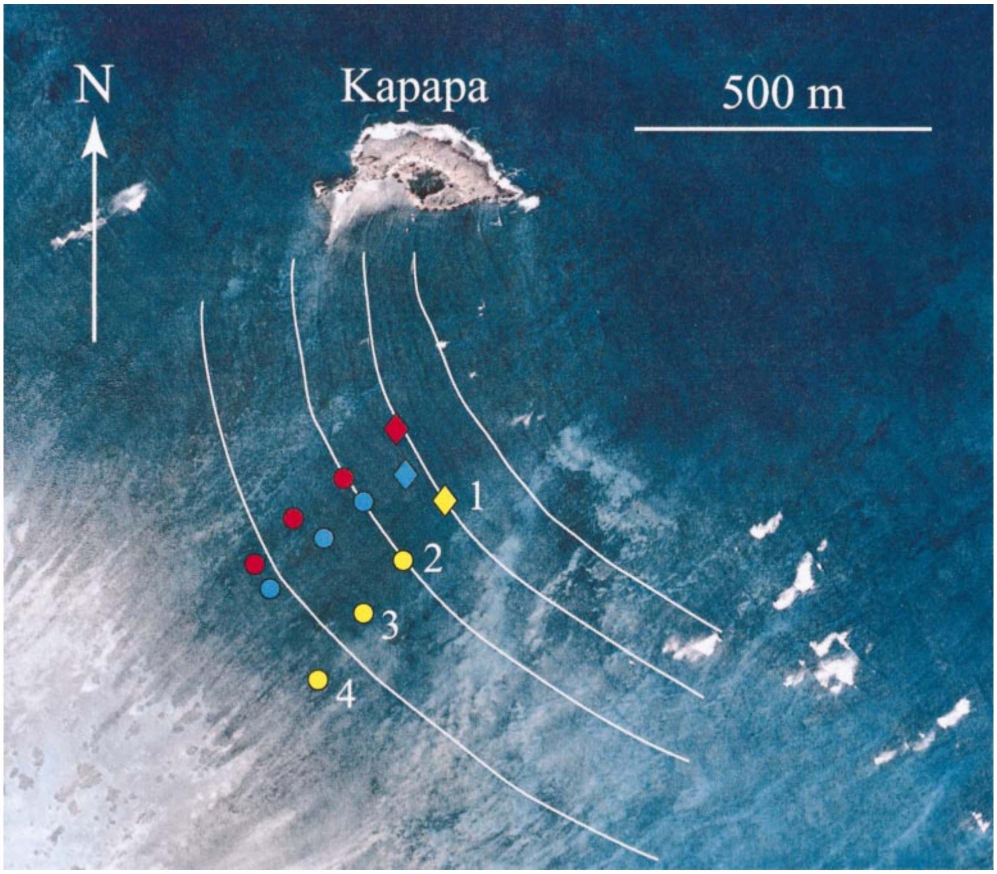

Fig. 3. Instrument locations on the Kaneohe Bay Barrier Reef flat for August 10 (red), August 16 (cyan), and September 4 (yellow). Stations were numbered according to distance from the fore reef. Diamonds represent stations where both a current meter and a pressure sensor were deployed (Sta. 1). Circles mark stations where only a pressure sensor was deployed (Sta. 2–4). The dark color of the study area indicates nearly 100% coverage of the benthos with algae. Select wave fronts are highlighted in white. Aerial image taken by the AURORA hyperspectral imaging sensor.

On each day, four Seabird SBE-26 pressure sensors (Seabird Electronics) were deployed ~100 m apart in a linear array following the direction of predominant wave propagation, with the first sensor located ~50 m from the back of the surf zone (Fig. 3). All pressure sensors were intercalibrated. The purpose of allowing space between the back of the breaking zone and the first station of the array was to allow broken waves to fully reform and to prevent the measurement of wave energy fluxes in an area that is prone to secondary breaking. In addition, the landward extent of the breaking zone can migrate in accordance with tidal changes in the depth of the reef flat. All pressure sensors were deployed on the bottom and programmed to sample at 2 Hz in 15-min bursts every half-hour, yielding 1,800 samples per burst. Each deployment lasted ~1 d, yielding 40–43 wave bursts per deployment. The one-sided power spectral densities for wave height were calculated from the pressure sensor data using linear wave theory (Dean and Dalrymple 1991). Each burst was treated as a single record, and the resulting spectra from each burst was band-averaged by 10 fundamental frequencies into bands 1/90 Hz wide. Rms-wave heights, H_{rms}, were calculated for each burst from the total spectral energy during each burst (Horikawa 1988).

Average H_{rms} values outside the Kaneohe Bay Barrier Reef were measured every half-hour by a directional wave buoy (Datawell) deployed ~5 km off the Mokapu Peninsula, southeast of Kaneohe Bay (21°24.9′N, 157°40.7′W).

Velocity measurements—A MAVS-3 three dimensional current meter (NOBSKA) was deployed 1 m away from the pressure sensor closest to the fore reef on each of the 3 d (Fig. 3). The current meter was zero-calibrated in still water before each deployment and mounted in a free-standing, weighted tripod with its sensor positioned 0.5 m off the bottom. Data from the *u* and *v* axes (i.e., the two horizontal axes) of the current meter were used to estimate the predominant direction of wave propagation by identifying the first principal component axis of horizontal velocity for each wave burst.

Results

Wave heights—The mean significant heights of waves outside Kaneohe Bay during sampling were 1.3 m (10 August), 1.1 m (16 August), and 0.9 m (4 September). These values were lower than the mean daily significant wave height of 1.4 m over the 2-yr period between August 2000 and June 2002, because offshore wave heights are generally

Table 1. Mean and range (m) of rms-wave heights (H_{rms}) for each day at each station. The ranges are given by the minimum and maximum burst value from each deployment. Stations are ordered with increasing distance from the fore reef (Fig. 3).

	10 Aug		16 Aug		4 Sep	
Sta.	Mean	Range	Mean	Range	Mean	Range
1	0.40	0.35–0.45	0.30	0.20–0.38	0.23	0.18–0.27
2	0.27	0.23–0.31	0.24	0.14–0.32	0.19	0.13–0.24
3	0.18	0.14–0.22	0.20	0.10–0.28	0.12	0.07–0.17
4	0.16	0.12–0.20	0.13	0.05–0.21	0.09	0.05–0.14

higher during winter. H_{rms} values decreased 0.15–0.25 m across the reef flat from the most seaward to most landward stations (Table 1). Differences in H_{rms} values across the reef flat among the 3 d varied according to differences in H_{rms} values outside Kaneohe Bay. Mean wave-height spectral densities across the reef flat appeared to be distributed in a single-peaked band from 0.05 to ~0.35 Hz (Fig. 4). The peak in wave energy density for stations closest to the breaking zone occurred between 7 and 8 s in period on each of the 3 d, corresponding to peak periods in the near shore wave field.

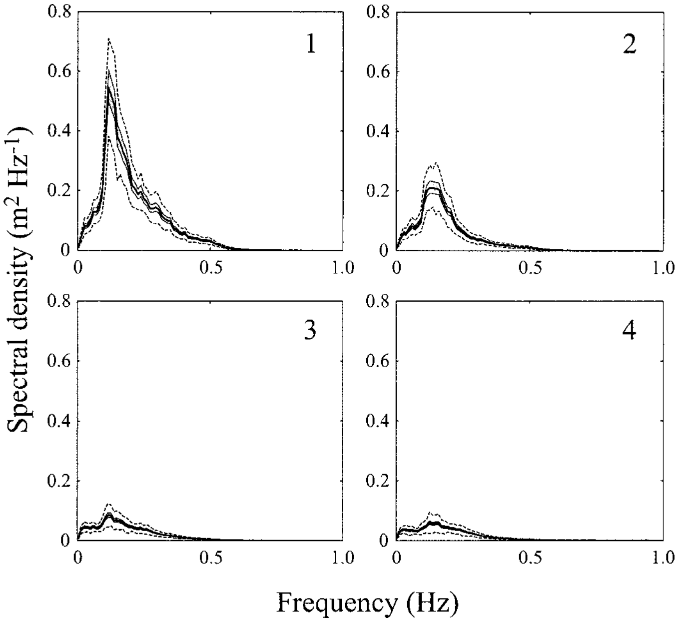

Fig. 4. Power spectral densities of surface wave height for each of the four stations on 10 August 2001. Mean spectra are given by the thick black line. The gray regions represent the 95% confidence interval for the mean spectra. The dashed lines represent one standard deviation for all spectra. Stations are ordered with increasing distance from the fore reef (see Fig. 3).

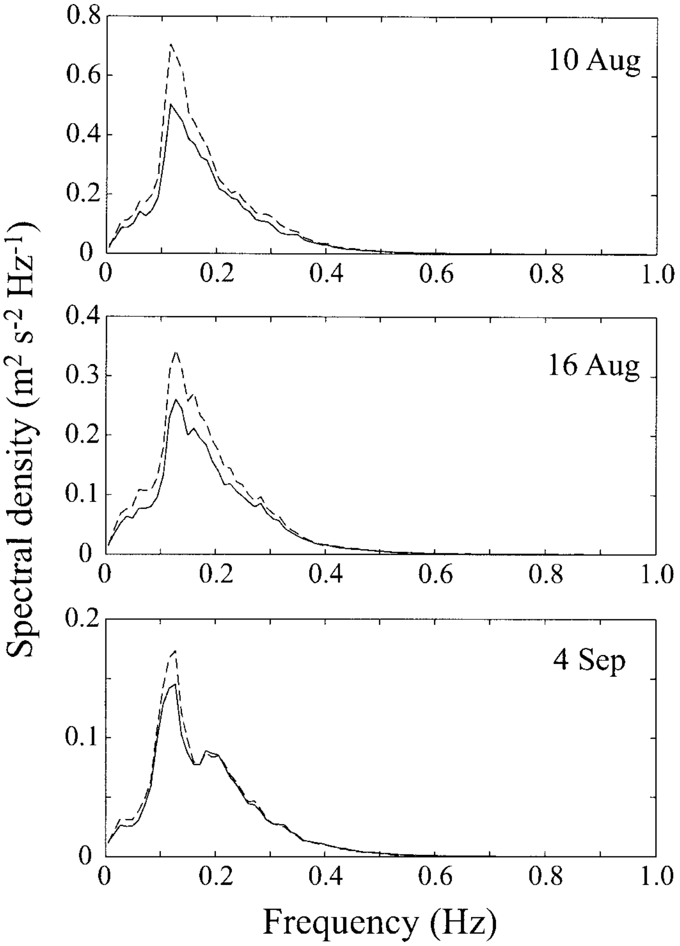

Fig. 5. Mean power spectral densities of near-bottom horizontal velocities for 10 and 16 August and 4 September 2001 as measured directly with a current meter (solid line) and predicted from pressure sensor measurements using linear transformations.

Wave-orbital velocities—Spectral densities of wave induced, and horizontal flow velocities were calculated from the current meter data by adding spectra calculated from both the *u* and *v* axes. The resulting spectra were similar in shape and magnitude to those predicted by linear transformation of the pressure sensor data (Dean and Dalrymple 1991; Fig. 5). However, spectral densities calculated from the current meter data were lower than those derived from the pressure sensor data, especially for the highest spectral densities and for the more energetic days. On the basis of data and estimates of the friction coefficient presented here, horizontal flow speeds should be >99% their potential flow values at a distance of ~0.5 m from the bottom (Nielsen 1992; Hearn 2001). Isobe (1983) showed that observed orbital velocities under shallow-water waves propagating over a gently sloping bottom were lower than those predicted from linear theory. For the present data, measured wave-orbital velocities were 5–10% lower than those predicted by linear theory. Our data indicate that the corrections to shallow-water wave orbital velocities predicted from linear theory depend on the magnitude of the spectral density and not on its frequency ($r^2 = 0.98$, $n = 11{,}257$), which is suggestive of a missing nonlinear correction. Regardless, these results demonstrate the utility of using linear theory for relating wave orbital velocities and pressure under nonlinear waves in shallow water and are consistent with the results of prior studies (Guza and Thornton 1980). Near-bottom horizontal velocities were predicted at all sites from the pressure sensor

Table 2. Mean and range (m s^{-1}) of time-averaged, near-bottom horizontal flow speeds $\langle U_t \rangle_t$ for each day at each station. The ranges are given by the minimum and maximum burst value from each deployment. Stations are ordered with increasing distance from the fore reef (Fig. 3).

	4 Aug		16 Aug		4 Sep	
Sta.	Mean	Range	Mean	Range	Mean	Range
1	0.214	0.191–0.233	0.164	0.133–0.185	0.116	0.100–0.131
2	0.167	0.147–0.188	0.148	0.104–0.179	0.119	0.099–0.136
3	0.126	0.107–0.126	0.137	0.092–0.162	0.086	0.062–0.112
4	0.119	0.098–0.139	0.102	0.058–0.132	0.081	0.057–0.104

data using empirical correction of the wave-orbital velocities predicted by linear wave theory. Time-averaged, near-bottom horizontal flow speeds ($\langle U_h \rangle_t$, where $U_h \equiv |\vec{U}_h|$) varied between 0.08 and 0.22 m s^{-1}, decreasing with increasing distance from the fore reef and with decreasing H_{sig} outside Kaneohe Bay (Table 2). These horizontal flow speeds are typical of other shallow-water reef environments (Munk and Sargent 1954; Atkinson et al. 1981; Hearn and Parker 1988; Nelson 1996; Helmuth et al. 1997; Sebens et al. 1998).

Cross-reef currents—Mean cross-reef currents ($\langle \vec{U}_h \rangle_t$) were calculated from mean horizontal velocities over each 15-min burst, which removed oscillatory wave orbital motions by averaging. Cross-reef currents were typically <0.02 m s^{-1} for each of the three deployments; therefore, wave-current interactions were not considered in the treatment of wave transformations and bottom friction.

Wave energy fluxes—Waves propagating in shallow water develop a nonlinear wave form (Dean and Dalrymple 1991). For shallow-water waves, cnoidal wave theory provides the best description of wave dynamics and kinematics (Horikawa 1988). Isobe (1985) simplified the description of finite-amplitude waves in shallow water using first-order cnoidal wave theory and provided the following expression for the wave energy flux, F:

$$F = f_2 \rho g H^2 \sqrt{gh} \tag{10}$$

where ρ is the density of sea water, g is the gravitational acceleration constant, H is the wave height, and h is the depth of the water. The value of the parameter f_2 depends on the degree to which the wave form is nonlinear. The shape and energy of a shallow-water wave can be fully described by its associated cnoidal functions; however, Isobe (1985) created a simple table for the value of f_2 that was based on a wave-shape parameter called the shallow-water Ursell number, Us, which is defined as

$$\mathrm{Us} \equiv \frac{gHT^2}{h^2} \tag{11}$$

where T is the wave period. Higher values of Us represent increasingly nonlinear wave forms. F and Us were calculated using the peak spectral period, and H_{rms} was determined from each burst of measurements.

Corrections for wave flux divergence—Increases in the flux of wave energy along the direction of wave propagation can occur because of the presence of energy sources such as wind stress and from convergence caused by refraction. Decreases in the flux of wave energy along the direction of propagation can occur from energy sinks such as breaking and bottom dissipation and from divergence of wave fronts caused by refraction and diffraction. The area that we studied was chosen to be well inside the limits of the breaking zone so that wave breaking could not be a factor in changing wave energy fluxes. Substantial changes in wave height and wave energy density occurred over tens to hundreds of meters. This is much too small a fetch for the predominant trade winds to add significant amounts of energy to surface waves propagating across the study area; therefore, wind inputs were also neglected.

There was some evidence of the spreading of wave fronts due to refraction near the back side of Kapapa Island as well as over a slightly shallower part of the reef flat adjacent to the study area (Fig. 3). The resulting apparent decrease in wave energy flux can be estimated by conserving the total flux of energy along the length of an arc between adjacent wave-ray paths (Dean and Dalrymple 1991). Thus, the predicted wave energy flux at one point along the wave-ray path can be estimated from the wave-energy flux at a point upstream by their respective radii of curvature, R_i

$$F_{i+1} = F_i \frac{R_i}{R_{i+1}} \tag{12}$$

where the subscripts i and $i + 1$ represent adjacent stations. The expected change in wave energy flux due to refraction would then be given as

$$\Delta F_r = F_i \left(1 - \frac{R_i}{R_{i+1}} \right) \tag{13}$$

Changes in wave-energy fluxes due to bottom friction, ΔF_{bf}, were then estimated from the observed differences in wave energy fluxes, ΔF, by subtracting the effects of refraction according to

$$\Delta F_{bf} = \Delta F - \Delta F_r \tag{14}$$

The predominant direction of wave propagation (and wave energy flux) was nearly constant throughout each deployment (Fig. 6). More than 93% of the wave energy flux occurred along one axis on all 3 d. The direction of predominant wave propagation rotated ~15° over an arc distance of ~150 m at the most seaward stations of the reef flat (Fig. 6). This would indicate an initial radius of curvature (R_o) of ~600 m in the shape of the propagating wave fronts ($R_o = [150/15] \times [180/\pi]$). This is consistent with visual interpretation of propagating wave fronts from an aerial photograph of the Kaneohe Bay Barrier Reef, which indicates that $R_o \approx$ 1,000 m near the most seaward stations and decreases towards the back of the reef flat (Fig. 4). On the basis of the above considerations, R at the most seaward stations was taken to be 800 m. Although this approach to estimating the wave-energy flux divergence due to refraction is simplistic, the data presented here indicate that this process typically

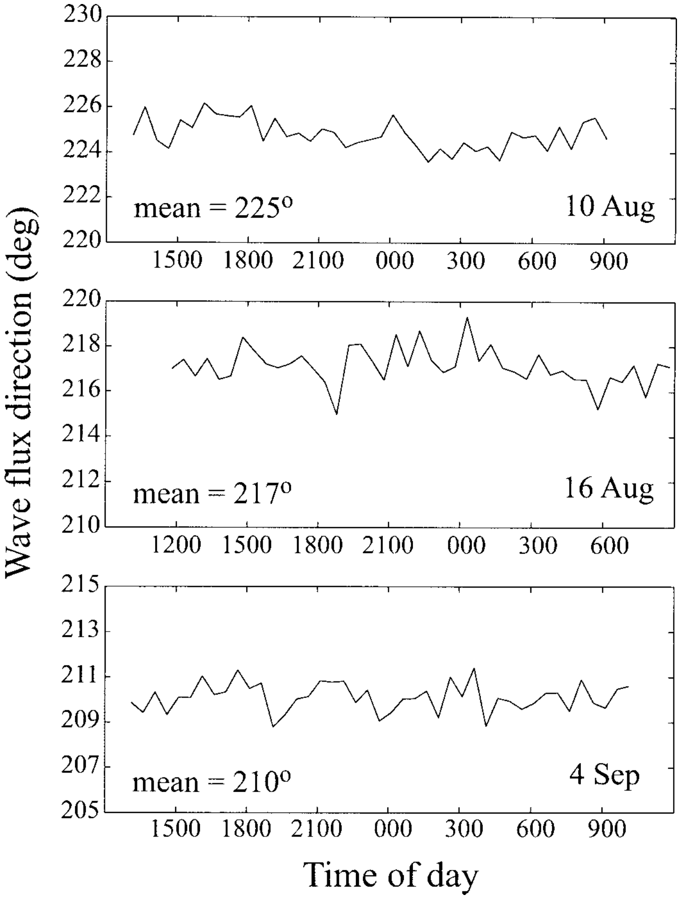

Fig. 6. Principal direction of wave propagation determined from the current meter on 10 and 16 August and 4 September 2001. The principal axis carried >93% of the variance in flow speed on all 3 d.

contributed, at most, only 20–30% of the observed decline in wave-energy fluxes across the study area ($\Delta F_r/\Delta F$).

Estimating c_f *from rates of frictional dissipation*—Because there was only one predominant direction of wave propagation within the study area, the spatial divergence in wave energy fluxes could be reduced to a one-dimensional problem

$$\frac{\partial F}{\partial r} = -\varepsilon_{bf} - \frac{\partial F_r}{\partial r} \tag{15}$$

where r is a coordinate position along the direction of wave propagation. ε_{bf} is the areal rate of wave energy dissipation due to bottom friction (defined to be a positive number) and $(\partial F_r/\partial r)$ is the wave energy flux divergence due to refraction. The total rate of wave energy dissipation can be taken as the product of the total bottom stress with the near-bottom horizontal flow velocity, $\vec{U}_h$,

$$\varepsilon_{bf} = \vec{\tau}_b \cdot \vec{U}_h \tag{16}$$

where $\vec{\tau}_b$ is the total bottom stress, which includes all dissipative forces associated with wave-bottom interactions and is modeled here using a single quadratic friction law that is the vector equivalent of Eq. 5.

Combining Eqs. 14, 15, and 16; time-averaging over the length of each burst; and space-averaging over the distance between instruments gives the following expression:

$$\frac{\langle \Delta F_{bf} \rangle_t}{\Delta r} = \frac{1}{2} c_f \rho \langle |U_h^3| \rangle_{t,x} \cos \phi \tag{17}$$

where ϕ is the phase lag between the maximum bottom shear stress and the maximum bottom flow speed. $\langle |U_h^3| \rangle_{t,x}$ was calculated as the mean of $\langle |U_h^3| \rangle_t$ from each adjacent pair of stations, which is equivalent to assuming that $\langle |U_h^3| \rangle_t$ varied linearly between stations. Because flow measurements were made only at the most seaward station of each array, $\langle |U_h^3| \rangle_t$ was estimated from the pressure sensor data using linear theory followed by empirical correction to the linear transfer function as described earlier. There was generally excellent agreement between estimated values of $\langle |U_h^3| \rangle_t$ based on pressure sensor measurements and those calculated directly from the current meter data at the most seaward stations ($y = 1.02x + 0.0005$; $r^2 = 0.95$, $n = 126$).

Eq. 17 is analogous to an expression first proposed by Jonsson (1966) that relates the average rate of energy dissipation due to bottom friction to the maximum flow velocity in simple harmonic flow, [$\vec{U} = U_m \sin(\omega t)$]:

$$\langle \varepsilon_{bf} \rangle_t = \frac{2}{3\pi} f_e \rho U_m^3 \tag{18}$$

where U_m is the maximum flow speed. Jonsson (1966) defined f_e on the basis of energy dissipation to distinguish it from the friction factor f_w used for relating the maximum bottom shear stress to U_m. For turbulent flow over relatively small roughness elements, this phase lag is only ~25° (Jonsson 1966, 1980), and cos ϕ is already close to unity. If the phase lag between the maximum shear stress and U_m is neglected, then $c_f \equiv f_e$, because $\langle |\vec{U}| \vec{U} \times \vec{U} \rangle_t = (4/3\pi) U_m^3$. A review of the literature indicates that there should be little difference between f_e and c_f for surfaces with friction coefficients >0.05 (Nielsen 1992). Furthermore, the literature review by Nielsen (1992) revealed that $f_w \approx f_e$ for turbulent, oscillatory flow over rough bottoms within the variability of experimental data. For the present article, we assume that ϕ is negligible and that $c_f \approx f_w \approx f_e$. Therefore, we choose to use c_f as the characteristic friction coefficient in order to be consistent with prior literature describing nutrient mass transfer to coral reef communities.

Equation 17 can be rearranged to give the expression

$$\frac{2 \langle \Delta F_{bf} \rangle_t}{\rho \Delta r} = c_f \langle |U_h^3| \rangle_{t,x} \tag{19}$$

where the left-hand term was regressed against $\langle |U_h^3| \rangle_{t,x}$ to get a best estimate of $c_f = 0.22 \pm 0.02$ ($p < 0.05$, $r^2 = 0.91$, $n = 338$) for the study area of the reef flat (Fig. 7). Changes in the wave energy flux between the last two stations of the array on August 10 were not included in the regression, because they appear to cluster away from the other data lying near the regression line. This is likely because of nonlocal inputs of wave energy from the area of the Kaneohe Bay Barrier Reef northwest of Kapapa Island on this most energetic day. The northwest half of the reef flat is deeper (2–3 m) than areas of the reef flat southeast of Kapapa Island

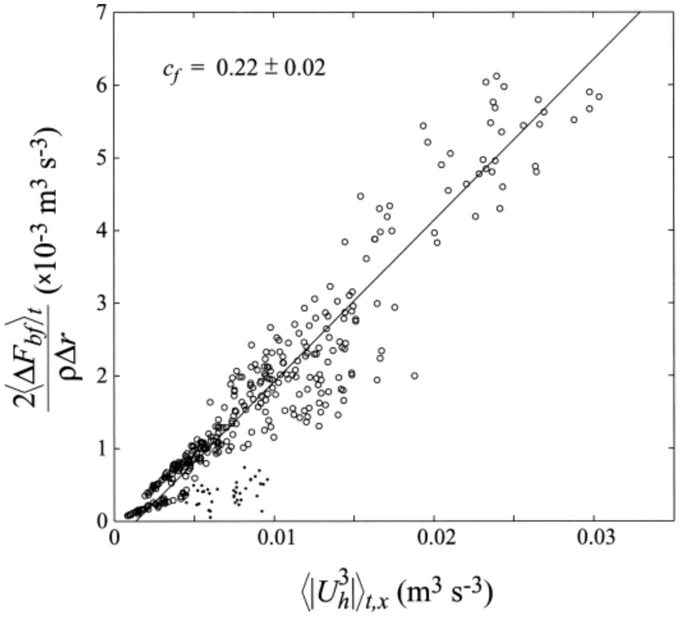

Fig. 7. Values for the left-hand term in Eq. 25 vs. $\langle |U_h^3| \rangle_{t,x}$ averaged between all stations on all days (circles) except from between Sta. 3 and 4 on 10 August (dots). See text for derivation. Model II regression gives the equation $y = 0.22x - 0.0003$ ($r^2 = 0.91$, $n = 338$), where the value of the slope gives the best estimate of c_f.

and could have allowed for the transmission of wave energy to the most landward station, where observed wave energy densities would be higher than expected. Separation of the data from all 3 d into three pairs of stations with increasing distance from the fore reef indicated that c_f did not vary significantly with distance across the study area ($p < 0.025$). Uncertainty in the estimate of c_f for the reef flat community can also come from uncertainty in the radii of curvature for the diverging wave fronts (Eq. 13). However, an uncertainty of ±200 m in the radii of curvature estimated here translates into an equivalent uncertainty in the value of c_f of ±0.01. As a consequence, the total uncertainty in c_f is ±0.03 or ±14%.

Estimation of k *based on* $\mathrm{c_f}$—Estimates of k based on c_f can be obtained from the literature on turbulent, oscillatory flow over rough surfaces. Conditions across the study area met the criteria for rough, turbulent, oscillatory flow (Kamphuis 1975) on the basis of the estimated friction factors and relevant Reynolds numbers. Nielsen (1992) reanalyzed various experimental data on the friction generated by oscillatory flow over rough surfaces and gave the empirical expression

$$c_f = \exp\left[5.5\left(\frac{k}{A}\right)^{0.2} - 6.3\right] \qquad (20)$$

where k is the roughness height as described before and A is the horizontal orbital excursion amplitude. For the data presented here, the rms-orbital amplitude, A_{rms}, varied from 0.2 m at the most back-reef stations to 0.6 m at the most fore-reef stations. Using the value of c_f estimated before and a mean A_{rms} of 0.4 m for the study area, we derived an average k for the study area of 0.2 m from Eq. 20. This result was consistent with visual observations of the study area made in the field.

Table 3. Estimates of mass transfer coefficients for dissolved phosphate (S_P), as well as nitrate and ammonium (S_N, in m d^{-1}) for the Kaneohe Bay Barrier Reef flat, using the regression result shown in Fig. 1. Uncertainties in reported values vary between 0.7 and 0.9 m d^{-1} for S_P and between 1.2 and 1.5 m d^{-1} for S_N. The diffusivity of dissolved phosphate was calculated as the weighted average of the diffusivities of dissolved phosphate species on the basis of their relative abundance in sea water (Li and Gregory 1974; Morel 1983). Values for species diffusivity and ν were estimated based on measured temperatures and a salinity of 35. The roughness height, k, was assumed to be 0.2 m (see text for details).

	Sta.			
Date	1	2	3	4
S_P				
10 Aug	7.1	6.0	4.9	4.7
16 Aug	5.8	5.4	5.2	4.2
4 Sep	4.5	4.7	3.7	3.6
S_N				
10 Aug	12.1	10.2	8.3	8.0
16 Aug	9.9	9.2	8.8	7.1
4 Sep	7.7	8.0	6.3	6.1

Estimates of nutrient mass-transfer coefficients—Mass-transfer coefficients for dissolved phosphate, nitrate, and ammonium uptake by the Kaneohe Bay Barrier Reef flat community were calculated on the basis of the regression shown in Fig. 1. Mean daily values for the nutrient mass-transfer coefficients across the study area were estimated for each station over the entire duration of each deployment (Table 3) and ranged 3.6–7.1 m d^{-1} for phosphate (S_P) and 5.9–12.0 m d^{-1} for ammonium and nitrate (S_N). The reported uncertainty in c_f would translate into uncertainty in S of ±5%, or about ±0.5 m d^{-1} for $\mathrm{S_P}$ and ±0.8 m d^{-1} for S_N at 95% confidence.

Discussion

Frictional roughness of the reef flat—The friction coefficient for the Kaneohe Bay Barrier Reef flat reported here ($c_f = 0.22 \pm 0.02$) is comparable with c_f estimated for other reefs such as Ala Moana Reef, Hawaii ($c_f = 0.28 \pm 0.05$; Gerritsen 1981) and John Brewer Reef, Great Barrier Reef ($c_f = 0.15 \pm 0.02$; Nelson 1996). Kajiura (1968) proposed a theoretical limit of $c_f = 0.25$ for $A/k < 1.67$. However, in reviewing a greater number of experimental data sets, Jonsson (1980) indicated that a constant value of $c_f = 0.30$ should be used for $A/k < 1.57$. The estimate of c_f reported here is close to this asymptotic limit—that is, of order 0.1 as opposed to being of order 0.01. The comparably high values of c_f for this and other reefs may result from the scale of their roughness heights being similar in magnitude to wave orbital excursion amplitudes. Furthermore, it is clear from Eq. 20 and the results of other studies (e.g., Grant and Madsen 1982) that the amount of frictional dissipation increases with greater roughness height. Smyth and Hay (2002) found that rates of frictional dissipation over rough beds could be an order of magnitude higher than rates of frictional dissipation over flat bottoms. This implies that rates of frictional dissipation across a larger area could be highly localized over larger roughness elements (such as coral heads) provided the bottom surrounding such roughness elements is much flatter. The morphology of our study area appeared to be relatively homogeneous on a larger scale (>10 m), albeit irregular on a local scale (<1–3 m), with roughness heights varying from ~0.05 to 0.3 m. Therefore, we believe that the dissipation of wave energy due to bottom friction was distributed somewhat evenly across the reef flat and that our estimate of an average roughness height based on existing wave friction models is reasonable. This may not be the case for smooth reef bottoms (e.g., algal pavements) populated with large coral heads, in which more conventional models of bottom friction could break down.

Table 4. Estimates of mass-transfer coefficients for dissolved phosphate (S_P), as well as nitrate and ammonium (S_N, in m day^{-1}) for the Kaneohe Bay Barrier Reef flat using values provided in Table 3 and adjusting for enhancement under oscillatory flow. Uncertainties in adjusted mass transfer coefficients vary between 1.5 and 2 m d^{-1} for S_P and between 2.5 and 3.5 m d^{-1} for S_N.

	Sta.			
Date	1	2	3	4
S_P				
10 Aug	9	8	7	7
16 Aug	8	7	7	6
4 Sep	6	7	5	5
S_N				
10 Aug	15	13	12	11
16 Aug	13	12	12	10
4 Sep	11	11	9	9

Estimates of S *from existing mass-transfer correlations*—The mass-transfer correlations used by Atkinson et al. were developed under steady flow. Dissolution of artificial rough plaster forms on the reef flat and in flumes showed that rates of nutrient mass transfer should be ~1.3–1.4 times higher under oscillatory flow than under steady flow (Falter 2002). These results are consistent with enhancement of N_2 fixation in turf algal communities under oscillatory flows (Williams and Carpenter 1998) and ammonium uptake by sea grasses (Thomas and Cornelisen 2003). The exact mechanisms responsible for differences in mass transfer under steady and oscillatory flow are not yet certain; they cannot be explained by increased drag (Sarpkaya and Isaacson 1981) but may be the result of increased turbulence under oscillatory flow (Hearn et al. 2001; Thomas and Cornelisen 2003). It is also possible that the acceleration of water over rough surfaces may help destabilize the viscous sublayer adjacent to the rough surfaces, thereby diminishing the thickness of the concentration boundary layer. Regardless, differences in mass-transfer rates under steady and oscillatory flow are minor compared with variation in mass-transfer rates due to flow speed alone across reef environments (factor of 1.3 vs. ~5). In the present study, mass-transfer coefficients for the reef flat community were predicted on the basis of steady flow conditions and need to be corrected for oscillatory flow. As a consequence, values for the mass-transfer coefficients shown in Table 3 were adjusted to reflect rates of nutrient mass transfer under wave-dominated flow conditions on the Kaneohe Bay Barrier Reef flat (Table 4).

Mass-transfer correlations for rough surfaces used by Atkinson and coworkers were developed in the absence of form drag. Form drag results from the separation of flow streamlines from the surfaces of an object leading to the formation of turbulent eddies and is likely the dominant source of bottom drag over coral reef communities. The mass transfer of dissolved solutes, however, occurs across concentration boundary layers tens to hundreds of microns thick (Shashar et al. 1996; Falter 2002; Larkum et al. 2003) and is probably spread over the entire surface area of reef communities, not just the largest roughness scales on which bottom drag primarily depends. Nonetheless, these mass-transfer correlations successfully predicted rates of mass transfer for experimental reef communities, which are characterized by high frictional roughness (c_f = 0.05–0.2; $\mathrm{Re}_k \approx 10^3$–$10^5$), and high Sc (500–1,500; Baird and Atkinson 1997; Thomas and Atkinson 1997). There may be no direct causal relationship between bottom drag and nutrient mass transfer. However, reef communities with greater morphological roughness (or rugosity) will typically have greater reactive surface area and increased turbulence production, both of which could increase overall rates of mass transfer to the benthos. Values of U_h, c_f, k, Re_k, and Sc for the Kaneohe Bay Barrier reef flat community were similar in scale to those used in prior flume experiments, so the application of an empirical mass-transfer relationship derived from flume results to the reef flat is appropriate.

Comparison of S_P *with prior estimates and measurements of phosphate uptake*—Atkinson (1987) measured changes in phosphate concentrations across the same region of the Kaneohe Bay Barrier Reef flat once a month for an entire year and estimated a mean net phosphate uptake rate coefficient (S_{Pnet}) of 9 ± 2 m d^{-1}. This estimate was based on a mean cross-reef volumetric transport of 0.06 m^3 s^{-1} m^{-1} determined from the movement of drogues and dye patches. Daily mean rms-wave heights impinging on the Kaneohe Bay Barrier Reef over a 2-yr period during this study averaged 1.4 m. As a consequence, estimates of S_P made from data taken on 10 August 2001, with $H_{\mathrm{rms}} = 1.3$, are likely to be close to the annual average S_P for the reef flat community. S_P on 10 August 2001 was 8 ± 2 m d^{-1} (Table 4). That S_P (calculated in the present study) and S_{Pnet} (determined by actual changes in phosphate) are similar indicates that rates of phosphate uptake by this reef flat community operate near the physical limits allowed by mass transfer. Previously, Bilger and Atkinson (1992) had substantially underestimated phosphate mass-transfer rates to the Kaneohe Bay Barrier Reef flat (S_P = 0.26 m d^{-1}). This was partly because the frictional characteristics of coral reef communities had not been measured at the time of their study. In addition, Bilger and Atkinson (1992) used mean flow velocity, or net flow speed, as their velocity scale for estimating S_P, because St is conventionally defined based on net volumetric flow rates. However, the authors had alluded to possible enhancement to mass-transfer rates due to wave-orbital motion. We now know that mean flow speed and not mean velocity is the more relevant flow scale for defining mass-transfer rates under nonsteady flows (Falter 2002; Thomas and Cornelisen 2003).

Dissolved NH_4^+ *and* NO_3^- *mass transfer: N versus P limitation*—Mass-transfer coefficients for ammonium and nitrate should be ~1.7 times greater than for phosphate, because the diffusivities of these compounds are higher. Combined ammonium and nitrate concentrations in most reef environments are typically only three times higher than dissolved phosphate concentrations (D'Elia and Wiebe 1990; Atkinson and Falter 2003); thus, maximum N : P uptake ratios can only be 5 : 1–9 : 1 (3–5 times 1.7), yet N : P ratios of most reef macrophytes are 20 : 1–40 : 1 (Atkinson and Smith 1983). There must be some other source of nitrogen subsidizing their growth.

The dissolved inorganic N : P ratio (N = ammonium + nitrate, P = phosphate) of ocean water coming into Kaneohe Bay is 4.4 (Atkinson 1981*b*). If we include organics in this N : P ratio, then it is 17.4, because most of the dissolved nitrogen exists as organic nitrogen. Clearly, under the assumption of the above mass-transfer relationships, dissolved inorganic nitrogen cannot be the only source of nitrogen for reef autotrophs. Either the Kanoehe Bay barrier reef is strongly dependent on organic nitrogen or there is some other source of nitrogen such as nitrogen fixation or nitrogen from organic particles supplying the demand for fixed nitrogen. On the basis of our results from the Biosphere mesocosm (Atkinson et al. 2001), we believe that rate kinetics for organic nitrogen uptake are much too slow for significant amounts of organic nitrogen to be removed. In fact, the concentration of organic nitrogen is the same over the reef as it is coming onto the reef (Atkinson 1981*a*), so that there must be another source of nitrogen. Ribes et al. (2003) showed that the uptake and removal of particles by sponges and ascidians can account for a very large flux of nitrogen. Indeed, the uptake of particles has long been cited as an important source of additional nutrition to coral reef communities (Glynn 1973; Johannes and Gerber 1974; Fabricius et al. 1998; Sebens et al. 1998; Yahel et al. 1998). The remineralization of particulate nitrogen is sufficient to increase dissolved nitrate and ammonia over the reef. As phosphate decreases over the reef, apparently at a mass-transfer–limited rate, nitrogen increases, giving rise to dissolved N : P ratios >30 : 1. Thus, we believe that uptake of both nitrate and ammonia are operating at mass-transfer–limited rates but that they cannot be observed because of the remineralization of particulate nitrogen. Unfortunately, we do not yet have enough data to estimate the flux of nitrogen from nitrogen fixation (Wiebe et al. 1975; Wilkinson et al. 1984; Larkum et al. 1988).

Relationship between carbon and phosphorus assimilation in reef flat communities—Estimates of gross community production for the Kaneohe Bay Barrier reef range 1,000–1,500 mmol C m^{-2} d^{-1} (Webb 1977; M.J.A. unpubl. data). These rates are not unexpected, given the high metabolic performance of seaward reef flats in high-energy environments (Kinsey 1985). These estimates of gross primary production, along with other estimates from the coral reef literature, could be even 50% higher than reported, given recent evidence for enhanced respiration by reef autotrophs during the daytime (Langdon et al. 2003) and under increased flow (Sebens 2003). Typical C : P ratios of macrophytes from the Kaneohe Bay Barrier reef flat are 600 : 1–800 : 1 (Atkinson and Smith 1983; Chun-Smith 1994). Multiplying these ratios by the phosphate uptake rate (determined above from wave dissipation; 0.06–0.08 mmol $m^{-3} \times 8$ m day^{-1} = 0.5–0.7 mmol P m^{-2} d^{-1}) yield estimates for average net primary production ~300–600 mmol C m^{-2} d^{-1}. Thus, at most, only 20–40% of the total carbon fixed by this reef flat community can be used for net primary production and is ''limited,'' or controlled, by rates of nutrient mass transfer. For the reef to achieve even this amount of net primary production, nearly all phosphate removed by this reef flat must be incorporated into new plant growth.

If rates of net primary production within shallow coral reef communities are limited by rates of nutrient uptake, then it is possible that net primary production is greatest in those areas of the reef where the dissipation of energy is the greatest: the shallow fore reef and near fore-reef zones of the reef flat. This is even more likely considering that (1) increased water motion enhances rates of photosynthesis in reef coral and alga (Dennison and Barnes 1988; Carpenter et al. 1991; Patterson et al. 1991), and (2) rates of gross and net community production decrease with increasing distance from the reef crest (Barnes and Devereux 1984; and Kinsey and Davies 1979). More recently, Russ (2003) found that rates of algal productivity, grazing, and grazer biomass were greatest on the reef crest, where the dissipation of flow energy is usually highest. There has been mounting evidence that water motion is a fundamental factor that drives temporal and spatial variability in reef productivity and metabolism. We believe water motion to be as important an environmental variable as light and temperature in defining the ecology of coral reef communities.

We conclude that rates of phosphate uptake by the Kaneohe Bay Barrier Reef flat community are occurring near the limits of mass transfer. These conditions are supported by the net release of fixed nitrogen on the reef flat.

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