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REPORT

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A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves

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Abstract Mass-transfer rates between water and benthos are derived based on the dissipation of energy by the benthic communities of coral reefs. Roughness of the benthic communities causes currents and waves to dissipate energy on reef flats at rates which far exceed ocean values of energy dissipation. The derivation here shows that first-order rate constants for nutrient uptake are (1) proportional to energy dissipation to the 0.25 root, (2) proportional to the bottom shear stress to the 0.4 root, and (3) proportional to current speed to the 0.75 root (decreasing to the 0.4 root under extreme wave activity). The shear stress, thus nutrient uptake, is positively correlated to the large-scale roughness, and to excess wave height (above the breaking height) of incoming waves. These causal relationships between nutrient-uptake rates and dissipation of energy support the general observations of reef zonation and reef metabolic rates, and are the paramount reason that coral reefs can maintain high productivity in low-nutrient tropical waters.

Keywords Ocean modeling · Friction · Nutrient uptake · Coral reefs · Hydrodynamics · Biosphere 2 · Kaneohe Bay

Introduction

Coral reef flats have high areal gross productivity which rivals the most productive ecosystems (Sargeant and Austin 1954; see Hatcher 1988, 1990 for a good background review). They are marvelous architectures of life which can thrive in the very low nutrient waters of tropical seas, where a coral reef is reputed to be the marine equivalent of an "oasis in the desert." Darwin originally posed the question of how these richly diverse ecosystems could persist in the barren waters of tropical oceans. He stated the question, and supplied an answer (Darwin 1842): he simply reasoned that they must obtain "their nutrition" from the neighboring ocean because reefs grow best at their margins, at the interface between ocean waves and quiescent lagoons. Darwin observed many prograding reefs of the Pacific atolls. He also reasoned that coral reefs, being animal in nature, must consume food material from the neighboring ocean. On this basis, Yonge (1940) expected to measure increases of inorganic phosphate near reefs, as an indication of net excretion by animals (in particular the Ribbon Reefs of the Northern Great Barrier Reef), but instead measured no change in phosphate concentration. Through the 1940s to 1970s, the paradigm shifted – coral reefs were determined to be largely plant dominated (Odum and Odum 1955; Odum 1971), not animal. The unusual fact, however, was that there was no apparent removal of nutrients as water crossed reef flats (Odum and Odum 1955; Pilson and Betzer 1973). This is the crux of the present-day "Darwin paradox": how can a system maintain high productivity, in low-nutrient water, without apparently removing nutrients from the water? Munk and Sargent (1954) actually supplied the answer in an obscure publication: they reasoned there was such a great demand for nutrients by the living forms, creating depleted boundary layers, that the "scrubbing action of the waves" was required to thin boundary layers. They concluded that the reef communities exposed to waves had maximum nutrient uptake and would grow best, supporting the contentions of the early naturalists. Their suggestion was ignored, however, and by 1970 the dogma emerged that "recycling" must occur very tightly, both through symbiotic relationships and between close autotrophic-heterotrophic relation-

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ships to sustain the rapid flux of nutrients (Pomeroy 1970; Johannes et al. 1972). Pilson and Betzer (1973) even reasoned that this recycling must be highly synchronous to maintain the relatively constant concentrations of nutrients observed across reef flats. This recycling paradigm fits nicely with H.T. Odum's belief that autocatalytic systems maximize power output (rate of energy transfer) by recycling. By the 1980s it was obvious, however, that the uptake rates of phosphate (^{32}P experiments) were much slower than expected. Less than 5% of phosphate advecting across, or through, most reefs could be removed from the water (Atkinson 1987; Atkinson and Smith 1987; Atkinson 1992). A simple explanation of the Darwin paradox emerged: coral reefs obtained nutrients as fast as they could and fixed carbon at relatively high C:N:P ratios, not considered by earlier workers (Atkinson and Smith 1983; Atkinson 1988). One did not need to invoke esoteric or exotic sources of nutrients, e.g., groundwater (D'Elia et al. 1981), large tides (Thompson and Golding 1981), upwelling (Andrews and Gentien 1982), and endolithic upwelling (Rougerie et al. 1992) to explain reef productivity.

By the 1990s it was evident that if diffusion through nutrient-depleted boundary layers limited the rates of nutrient uptake, then nutrient uptake for a given nutrient concentration had to be dependent on water velocity and, more precisely, on shear stress (the force exerted by bottom drag on the water). Bilger and Atkinson (1992) borrowed empirical studies from the engineering literature on heat and mass transfer to parameterize this problem. Those publications introduced the Stanton number to reef ecology, showing nutrient uptake per area (denoted by m) was proportional to the Stanton number (St) multiplied by bulk velocity (U_b) and bulk concentration (C_b), i.e., $m = St \times U_b \times C_b$. The Stanton number times velocity has dimensions of a velocity and is a first-order rate constant, denoted by S, which is now widely reported. A series of flume studies (Atkinson and Bilger 1992; Atkinson et al. 1994; Baird and Atkinson 1997; Thomas and Atkinson 1997) and field studies (Atkinson et al. 2001; Steven and Atkinson, unpublished data) describes first-order rate constants, S, for PO_4, NO_3, and NH_4 uptake into communities of coral reef benthos. The effect of water velocity on nutrient uptake has also been found in other plant species (Larned and Atkinson 1997).

There are two observations in those data sets which are especially germane to the present study. Firstly, the calculations of Bilger and Atkinson (1992) consider the uptake of PO_4 over the Kaneohe Bay barrier reef to be "anomalously high" (the title of their paper) compared to empirical relationships derived from mass-transfer literature for engineering surfaces. Secondly, recent work in the wave-driven coral reef mesocosm at Biosphere 2 (Atkinson et al. 2001) also indicates an enhancement of S above the expected engineering values. It is further noted that Thomas and Atkinson (1997), and Baird and Atkinson (1997) clearly showed that roughness did affect mass transfer of coral but nevertheless their values remained low compared to field values. One major factor in these differences in measured S is evidently the role of gravity waves.

The present paper introduces a derivation of the first-order rate constants for nutrient uptake, S, from purely physical parameters, not relying on empirical studies of the heat and mass-transfer literature. The advantage of this approach is twofold:

1. We can include effects of waves and wave setup, and so simulate typical field conditions;
2. We can get better insight into the controlling parameters on reefs.

The present approach is new and relies only on quantities calculated in standard numerical models of dissipation of energy in the ocean. It is intended to be both physically transparent and allow mass-transfer coefficients to become a commonplace prediction of any shallow-water model which includes a determination of the turbulent-energy dissipation rate per unit mass (denoted in this paper by ϵ). The present paper does not itself employ numerical models to determine the turbulent dissipation rate, but instead uses a simple analytical determination of ϵ based on the shear stress over the reef. This analytical approach is a "generation-dissipation balance", although it reasonably assumes that the vertical diffusion of turbulence through the water column is also very strong. In this way, the paper proceeds to calculate the dependence of the mass-transfer coefficients on important physical parameters of the reef. The turbulent-energy dissipation rate per unit mass ϵ is calculated in all ocean models which employ some sort of turbulent closure system. An example is the widely used level 2½ scheme introduced by Mellor and Yamada (1982).

Molecular diffusive boundary layer

Over most of the water column, turbulence dominates the mixing of nutrients, but turbulence becomes ineffective at very small spatial scales (e.g., Lazier and Mann 1989). Nutrients can only be transported at such scales by the action of molecular diffusion. The "diffusive boundary layer" which surrounds the surfaces of corals (or benthic communities) is illustrated in Fig. 1. Molecular diffusivity for nutrients is many orders of magnitude weaker than values for typical vertical mixing by turbulence in the ocean, or over a coral reef. So, the diffusive boundary layer acts as a "barrier" which nutrients must penetrate in order to be absorbed by the coral or benthic community. The thickness of the diffusive boundary layer decreases as the turbulence of the water column increases, so that the barrier effect is much less in turbulent waters, and conversely, becomes very large in basins which have little turbulence. An example of the latter is given by Hearn and Robson (2000).

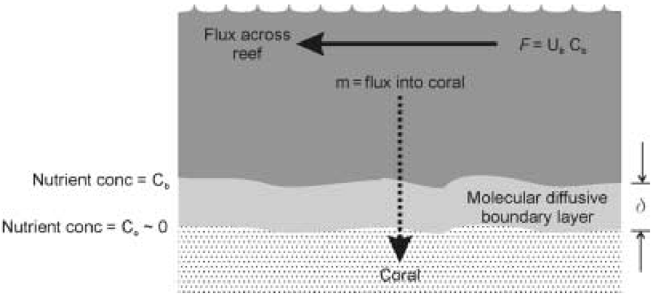

Fig. 1 The role of the diffusive boundary layer. U_b is the bulk water velocity over the reef, C_b the bulk concentration of nutrients, F the advected nutrient flux density, and m the flux of nutrients into the coral

A central idea is that the demand for nutrients by corals, and other benthic plants of the reef flat, is so high (e.g., Atkinson 1988) that concentrations of nutrients in the diffusive boundary layer will adjust to provide the maximum possible flux of nutrients to the coral. If the demand for nutrients by the coral is suddenly "turned on" in a model of the diffusive boundary layer, the plant will deplete the nutrients within that layer. At the outer boundary of the layer, the concentration will remain at the ambient bulk concentrations C_b, characteristic of water over the reef, because beyond the layer there is very strong mixing due to turbulence. This process of nutrient depletion within the layer will continue until a steady state is reached This will involve a nutrient concentration which decreases linearly with distance from the outer edge of the layer to the surface of the plant. Increasing the nutrient demand reduces the steady-state concentration at the plant until it reaches a value which is very close to zero. At that stage, the transport of nutrients through the layer has reached a maximum (since the concentration gradient is then maximal). It is this maximum transport through the layer which is used to derive the nutrient-uptake coefficients S in this paper. A discussion of the nutrient concentration at the surface is given by Bilger and Atkinson (1995).

Nutrient-uptake coefficient and the Stanton number

The maximum nutrient absorption, or uptake flux, m, into the coral is written as

$$m = SC_b \tag{1}$$

where C_b is the bulk concentration of nutrients in the water column. For simplicity in this paper S will be referred to as the "nutrient-uptake coefficient", and this term is equivalent to "mass-transfer constant" or "first-order rate constant". S is given by the theory of the section above and Fig. 1 as

$$S = D/\delta \tag{2}$$

where D is the molecular diffusivity of the nutrient, δ is the thickness of the diffusive boundary layer, and C_b is the concentration of nutrients at the outer edge of the layer, i.e., in the "bulk" of the water column. The nutrient flux, F, as shown in Fig. 1, which is being transported horizontally across the coral reef by the advective velocity, U_b, across the reef, is

$$F = C_b U_b \tag{3}$$

The Stanton number St (Bilger and Atkinson 1995) is defined as

$$S_t \equiv m/F \tag{4}$$

so the Stanton number is the fraction of the flux of nutrients passing over the reef which is absorbed by the reef. The Stanton number is usually very small for a reef, ranging from 10^{-5} to 10^{-4}. It is evident from Eqs. (1) to (4) that

$$S_t = S/U_b \tag{5}$$

The Stanton number controls the rate at which the nutrient concentration in a parcel of water decreases with distance x as it propagates across the reef. This can be readily proved by noting that the nutrient absorption from the parcel over a distance dx is mdx/U_b per unit area where, by Eq. (1), $m = SC_b$. The nutrient concentration per unit area of the water column is hC_b (where h is the water depth), so that $hdC_b = -SC_b dx/U_b$, and hence integrating,

$$C_b = C_b^0 \exp(-xSt/h) \tag{6}$$

with C_b^0 the concentration at $x = 0$. This means that the decay of nutrients across a reef depends on the Stanton number divided by depth. However, the determination of the nutrient-uptake coefficient, S, from St by using Eq. (5) requires a value for the across-reef advective speed U_b. If St/h varies over the path of the water particle, the exponent in Eq. (6) is replaced by the integral $-\int_0^x (St/h)dx$.

Thickness of the diffusive boundary layer and the $\epsilon^{1/4}$ law

The diffusive boundary layer thickness, δ, is controlled by the rate, ϵ, at which turbulent energy descends down the Richardson (1922) cascade, to become "small scale" and finally be dissipated as heat. Because the flow occurs at very high Reynolds numbers, at sufficiently small scales the turbulent eddies are isotropic and so there is a "universal equilibrium range" (Kolmogorov 1962) in which all turbulent fields are statistically similar provided that they are scaled by the Kolmogorov (1962) length. Turbulent fluctuations will still be detectable in nutrient concentrations at spatial scales which are smaller than the Kolmogorov length, because the molecular diffusivity of nutrients D is many orders of magnitude smaller than the molecular viscosity ν. Hence, for nutrients the appropriate length scale is given by the Batchelor (1967) length,

$$\delta \equiv \left(\nu D^2/\varepsilon\right)^{1/4} \tag{7}$$

Hence, Eq. (2) becomes

$$\begin{aligned} S &= A\varepsilon^{1/4} \\ A &\equiv \left(\frac{D^2}{\nu}\right)^{1/4} \end{aligned} \tag{8}$$

and this will be called the $\epsilon^{1/4}$ law. The nutrient-uptake coefficient, S, is proportional to the fourth root of ϵ, the energy dissipation rate per unit mass. The $\epsilon^{1/4}$ law is the cornerstone of the theoretical development of this paper. At first sight, $\epsilon^{1/4}$ seems a very weak dependence, and to produce an increase in S of a factor of ten requires ϵ to increase by 10^4. Of all the parameters which affect turbulent energy dissipation in the ocean, the surface roughness of the coral reef community is probably the one most likely to be responsible for the high values of ϵ necessary to produce the relatively high values of S on coral reefs.

Hydrodynamics of coral reefs

Turbulent energy dissipation on reefs arises from both the effect of across-reef current and the loss of energy from surface gravity waves. Furthermore, currents and surface gravity waves are intimately connected on reefs for two reasons. The first reason is that the major currents on reefs are driven by waves breaking on the fore-reef. This is not exclusively the case, and currents on reefs may also be driven by tidal flows and wind stress. However, such flows are of secondary importance and not central to the basic morphology of coral reefs, which is built around processes associated with wave forcing. Wave stress has long been recognized as the quintessential physical forcing function for coral reefs, determining many aspects of their ecology (e.g., Bradbury and Young 1981; Dollar 1982; Hatcher et al. 1987; Roberts et al. 1992).

Waves breaking on the fore-reef (Fig. 2) raise the elevation of the water surface by an amount $\Delta\eta$ at the front of the reef flat (commonly called the wave "setup"). The value of the wave setup $\Delta\eta$ depends on the height of incoming waves, as detailed in the discussion below and Eq. (16), but for the present we note that it is typically some tens of centimeters, i.e., 0.1 to 0.5 m. If there is an open lagoon behind the reef, the water surface at the back of the reef is very close to that of the open ocean. Consequently, the wave setup produces a strong downward slope of the water surface from the front to the back of the reef flat. The strength of this gradient depends on the width of the reef, a (the distance from the front to the back of the reef flat). This width is usually a few hundred meters, although some exceptional reef flats are wider (e.g., Kaneohe Bay which is about 1,500 m wide). So the usual magnitude of the surface slope is about 0.1 m in a hundred meters. On the reef flat, there is almost no wave-breaking because the total height of the water column decreases by, at most, a fraction of a meter. This means that the pressure gradient produced by the slope of the surface must be balanced by the friction between the flow and the reef (because the Coriolis force is very much smaller).

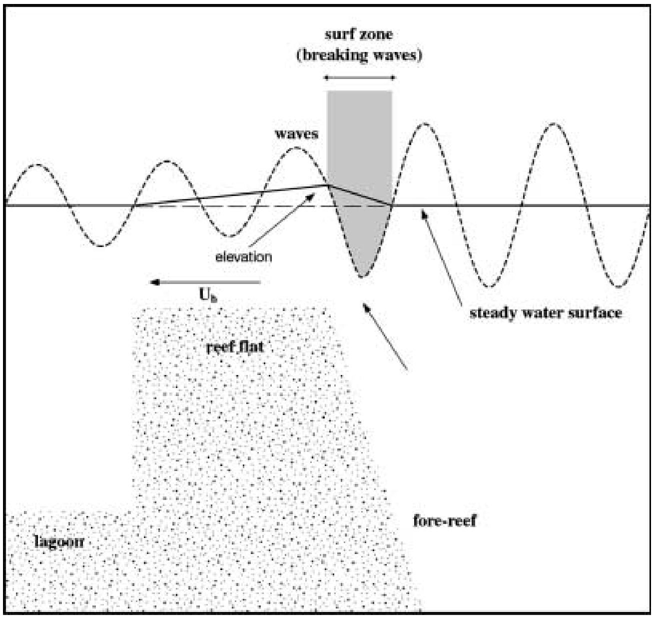

Fig. 2 A schematic of water flow across a reef flat. U_b is the bulk velocity of flow across the reef

The balance between the slope of the water surface and friction, which occurs on the reef flat, is very common in shallow waters (see, for example, Csanady 1982). Reefs, however, are unique in terms of the magnitude of the slope of the water surface. For example, a typical wind-driven bay of depth 5 m would have a surface slope of $0.2\ \mathrm{m}^2$ in 100 km for a wind of $10\ \mathrm{m\ s}^{-1}$. The flow of water down the surface slope of a coral reef involves a loss of potential energy which is then dissipated by friction into turbulent energy. This is always the case for a surface slope, but for a reef the dissipation of energy occurs in a very short distance and so gives a large energy dissipation per unit mass (denoted here by ϵ).

The total conversion of potential energy to turbulent kinetic energy over the reef flat means that the pressure gradient over the reef flat must, as already indicated, be balanced by frictional stress, i.e.,

$$\tau = \rho g h \frac{\Delta\eta}{a} \tag{9}$$

where ρ is the density of seawater, g the acceleration due to gravity, h the mean water depth over the reef, a the width of the reef, and $\Delta\eta$ is the wave setup at the front of the reef flat, i.e., the change in the surface elevation across the reef flat. If the frictional stress on a reef were similar to that of water flowing at the same speed over a smooth sandy bottom, only a small fraction of the potential energy from the surface slope could be dissipated to turbulence. Conversion of the energy to turbulence requires the much greater bottom roughness characteristic of reef crests.

The frictional forces on a reef flat can be treated by the concept of the "rough surface", widely used in turbulence theory (e.g., Pope 2000). Rough surfaces in the ocean experience extreme surface stress and consequently are usually smoothed by erosion, but calcifying organisms of coral reefs grow to offset that process and maintain roughness. This extreme roughness gives drag coefficients two orders of magnitude higher than for sand (Roberts et al. 1992; Nelson 1994, 1996; Thomas and Atkinson 1997; Lugo-Fernadez et al. 1998). For conventional quadratic friction, it is straightforward to determine the energy dissipation rate per unit mass, ϵ, over the reef as $C_d u^3/h$ where C_d is the bottom drag coefficient. So it is instructive to compare the energy dissipation on a reef with that in a macrotidal system where currents can reach values of 0.5 to 1 m s^{-1} (and may well exceed those on a coral reef). Coral reefs are shallower than typical macrotidal systems, but the major reason that ϵ is so much higher for a reef is that C_d is several orders of magnitude larger. This effect is further enhanced by the influence of surface gravity waves on a reef. The surface slope of the water over the reef, and hence the energy flow, is originally supplied by the incoming surface gravity waves on the fore-reef. So input of turbulent energy on reef flats by the across-reef current is some three orders of magnitude higher than anywhere else in the ocean. This comparison includes turbulent energy input by the most severe wind and tidal motions (e.g., Fischer et al. 1979), and it has its root cause in the extreme roughness of reefs.

The turbulent energy dissipation is not distributed evenly over the water column above the bottom. Instead, ϵ increases near to the roughness elements of the benthic surface in inverse proportion to the maximum size of eddies in the turbulence field and is given by $\kappa\ d_c$ (Prandtl 1925). Here κ is von Kármán's constant (0.4), and d_c is the roughness length for coral. So, if τ is the stress at the reef surface, the energy dissipation rate per unit mass within a roughness length of the surface has the form

$$\varepsilon = (\tau/\rho)^{3/2}/\kappa d_c \tag{10}$$

and this is based on the theory of the logarithmic boundary layer which is founded on measurements of flow near a rough wall.

Coefficient of friction and roughness length

A coefficient of friction, C_d, can be estimated from a roughness length of d by

$$C_d \sim \left[\kappa \Big/ \ln\left(\frac{h}{d}\right)\right]^2 \tag{11}$$

Hence, for example, the friction coefficient $C_d = 0.0025$, commonly associated with sand, corresponds to d of the order of a few millimeters. It follows from Eq. (11) that an increase in C_d by some arbitrary factor (let us call this factor α) is produced by an increase of roughness length from d to say d^* where

$$d* = h\left(\frac{d}{h}\right)^{1/\sqrt{\alpha}} \tag{12}$$

So, if a coral reef has a friction coefficient C_d, which is two orders of magnitude larger than sand, i.e., $\alpha \sim 100$ and d/h is of order 0.005, it follows that d^* must be about 50% of h. This means that the only way of achieving such high drag coefficients is for the roughness length to be an appreciable fraction of the water depth. This is entirely consistent with most measurements of roughness lengths of coral reef communities, which show values of d_c/h from 0.1 to 1 (Roberts et al. 1992; Nelson 1994, 1996; Baird and Atkinson 1997; Thomas and Atkinson 1997; Lugo-Fernadez et al. 1998). Interestingly, C_d is dependent on the ratio of roughness to total depth which provides a natural scaling law for experiments in flumes (Atkinson and Bilger 1992).

The $\tau^{3/8}$ law for dependence of absorption on stress

The turbulence which is generated over a reef by the rough surface is so great that the turbulent energy is rapidly mixed. Thus, the dissipation is characteristic of the mean generation rate over the whole water column, so that Eq. (10) is generalized slightly (by averaging over the water column) to

$$\varepsilon = (\tau/\rho)^{3/2}\frac{\ln(d_c/h)}{\kappa h} \tag{13}$$

The logarithmic factor in Eq. (13) is of order 1, because the roughness length of coral $d_c \sim h$ over the large hydrodynamic length scales in which turbulence is mixed. Hence, substituting Eq. (13) in the $\tau^{1/4}$ law (Eq. 8) gives

$$\begin{aligned} S &= B\tau^{3/8} \\ B &\equiv \left[\frac{D^2 \ln(d_c/h)}{\upsilon\rho^{3/2}\kappa h}\right]^{1/4} \end{aligned} \tag{14}$$

known as the $\tau^{3/8}$ law for the dependence of S on bottom stress τ, or approximately $\tau^{0.4}$. The dependence of S on $\tau^{0.4}$ is corroborated by the data of Thomas and Atkinson (1997), and Baird and Atkinson (1997), and this is shown in Fig. 3. Using Eq. (9) to determine τ from the head difference $\Delta\eta$ gives

$$S = \left[\left(gh\frac{\Delta\eta}{a}\right)^{3/2}\frac{D^2 \ln(d_c/h)}{\upsilon\kappa h}\right]^{1/4} \tag{15}$$

Wave created stress and the $\Omega^{3/8}$ law

The wave setup on a reef, or the head difference across the reef flat, can be determined from the height of

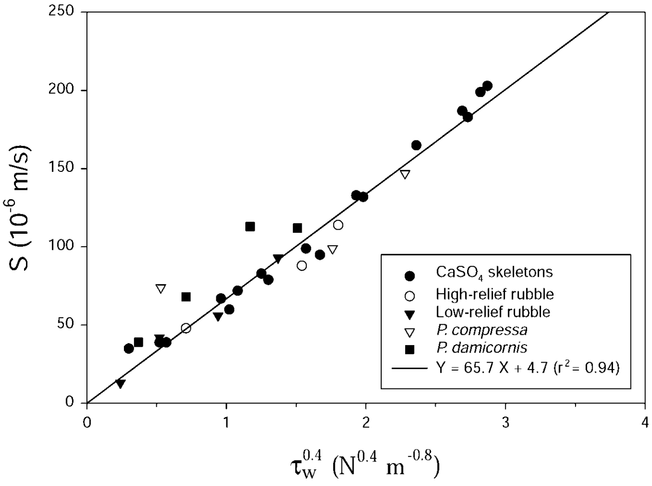

Fig. 3 Assemblages of coral, macroalgae, and turf-covered rubble were placed in a flume and exposed to steady, unidirectional flow velocities ranging from 0.02 to 0.5 m s^{-1}. Change in head across the experimental community was measured to determine the drag, or shear stress τ_w exerted by the community on the flowing water (NH_4^+, Thomas and Atkinson 1997; dissolution of gypsum-coated coral skeletons, Baird and Atkinson 1997). The nutrient-uptake coefficients (*S*) measured in these different experiments were normalized by scaling them to the diffusivity of NH_4^+ and compared to the measured shear stress raised to the 0.4 power. The regression is a model II linear regression

incoming waves *H*. The maximum height of surface gravity waves which can propagate through a water column of depth *h* is usually taken to be some fraction γ of *h*, i.e., the maximum wave height is γh. In reality, the value of γ depends on the slope of the bottom and decreases as the slope decreases, i.e., a rapidly sloping bottom can support higher waves than a very flat bottom of the same depth (Young 1989; Hardy and Young 1991; Nelson 1994, 1996). However, for the present purposes, it is sufficient to take γ as a constant of value about 0.8. Details of the corresponding calculations of wave setup on reefs when γ is considered to vary are given by Hearn (1999). It is useful to define an "excess wave height" by $\Omega = H - \gamma h$, so that wave breaking only occurs if $\Omega > 0$. It was shown by Tait (1972) that the steady-state wave setup at the front of a coral reef is proportional to this excess wave height, i.e.,

$$\begin{aligned}\Delta\eta &= \Gamma\Omega \\ \Gamma &\equiv \frac{1}{\gamma\left[1+\left(8/3\gamma^2\right)\right]}\end{aligned} \tag{16}$$

Note that the Tait (1972) result allows for non-linear terms in the continuity equation on the fore-reef and should not be linearized. There is, however, an approximation in Eq. (16) which assumes that the fore-reef is very steep, so that some "set down" of the surface in the surf zone can be ignored. This slightly affects the value of Γ.

The Tait (1972) result leads with Eq. (9) to

$$\tau = \frac{\rho g h \Gamma}{a}\Omega \tag{17}$$

Substituting Eq. (17) in Eq. (13) gives

$$\varepsilon = \left(\frac{gh\Gamma\Omega}{a}\right)^{3/2}\frac{\ln(d_c/h)}{\kappa h} \tag{18}$$

and so, using the $\epsilon^{1/4}$ law (Eq. 8), Eq. (18) leads to a law connecting the nutrient-uptake coefficient with the excess wave height Ω:

$$\begin{aligned}S &= C\Omega^{3/8} \\ C &\equiv \left[\frac{D^2\ln(d_c/h)}{\upsilon\kappa h}\right]^{1/4}\left(\frac{gh\Gamma}{a}\right)^{3/8}\end{aligned} \tag{19}$$

Kaneohe Reef (Bathen 1968) has a width $a \sim$1,500 m and, using standard values of $D = 7\times10^{-10}$ m^2 s^{-1} for PO_4, $\nu = 0.94\times10^{-6}$ m^2 s^{-1} with $d_c = 0.1$ m, and for $H = 1.5$ m and $h = 0.5$, the predicted nutrient-uptake coefficient, *S*, is 94×10^{-6} m s^{-1}, remarkably close to the observed value, 102×10^{-6} m s^{-1}, obtained by multiplying the observed *St* by the cross-reef water velocity of 0.06 m s^{-1} (Bilger and Atkinson 1992). This value can also be compared, for example, with $S = 1\times10^{-8}$ m s^{-1} for the blades of the giant kelp *Macrocystis* (Wheeler 1978, 1980). Notice that the present theory for Kaneohe Reef gives a value of $\epsilon \sim 10^{-2}$ W kg^{-1} whereas levels of turbulence elsewhere in the ocean very rarely exceed 10^{-4} W kg^{-1}.

Following a water particle over the reef, and monitoring nutrient concentration, Eq. (6) shows that the logarithm of bulk concentration C_b should decrease linearly with distance at a rate *St*/*h*. The values calculated above for *S* are of order 10^{-4} m s^{-1}, so using $U_b \sim 0.2$ m s^{-1} as a typical flow velocity over a reef gives a typical Stanton number *St* of 5×10^{-4}. So, if $h \sim 1$ m, the distance over the reef for the nutrient concentration to decrease to $1/e$, i.e., 37% of its initial value, is $h/St \sim 2$ km. Few reefs are wide enough to exhibit such nutrient depletion. According to Eq. (5), the Stanton number is higher on reefs with lower flow velocities U_b, although that may imply smaller excess wave height Ω (which would offset the increase).

Quadratic friction and the $U_b^{3/4}$ law

Although the nutrient-uptake coefficient *S* has already been determined from the dissipation rate ϵ, the bottom stress τ and the excess wave height Ω, finding the dependence of the mass transfer *S* on the bulk flow velocity U_b over the reef requires information on the variation of τ with U_b. During steady turbulent flow over a rough surface in the absence of wave motion,

$$\tau = \rho C_d U_b^2 \tag{20}$$

where C_d is the friction drag coefficient. This is the widely used law of "quadratic" friction and it is worthwhile to recall the reason for this quadratic dependence. In non-turbulent flow, such as the flow of a gas dominated by molecular viscosity, all stresses are proportional to speed of flow. In turbulent flow, however, stresses are generated by the effect of the flow on the turbulent field. For flow over a rough surface, this turbulence is created by the flow itself and so the law becomes quadratic. Substituting Eq. (20) into the $\tau^{3/8}$ law (Eq. 14) leads to

$$S = DU_b^{3/4}$$
$$D \equiv \left[C_d^{3/2}\frac{D^2\ln(d_c/h)}{\upsilon\kappa h}\right]^{1/4} \tag{21}$$

and this $U_b^{3/4}$ law matches the flume results of Atkinson and Bilger (1992), as shown in Fig. 4. Using the quoted flume value (Atkinson and Bilger 1992) of $C_d = 0.01$ gives $\log S = -3.5 + 0.75 \log U_b$ which is plotted in Fig. 4, comparing well with their data. For quadratic friction, the Stanton number can now be expressed directly in terms of U_b, using Eqs. (5) and (21), as $St = DU_b^{-1/4}$.

Wave enhancement of friction on a reef

Waves on reefs are an important aspect of energy dissipation and play an intimate part in the energy dissipation process and clearly affect roughness. Understanding the role of waves is fundamental to the hydrodynamics of reefs, which underpins all of the present theory.

It has been well known for two decades that the effect of surface gravity waves in shallow water is effectively to increase roughness, and there are many observational studies of this effect (Grant and Madson 1979; Grant et al. 1984). The reason for this increase in roughness, or C_d, is akin to form-drag (which is due to separation between individual roughness elements resulting in spatially varying pressure gradients). Therefore, for a given current flowing over the reef, the presence of waves increases the turbulent energy dissipation, and hence the nutrient-uptake coefficient, S. A controlling factor for the effect of waves on roughness is the thickness of the wave boundary layer, which is the distance which the periodic wave stress at the surface of the reef can penetrate into the water column during a time comparable to half the wave period. For normal coastal situations, this thickness is much smaller than the water depth, so that the only effect of waves is to increase apparent bottom roughness, i.e., the value of C_d. However, reefs may be so rough that a significant part of the water column lies inside the wave boundary layer. In such a situation, the turbulence created by the interaction of the waves with the rough bottom would affect much of the water column. Inside the wave boundary layer, the effect of the waves is maximal and the usual quadratic friction law is replaced by a linear relation (Hearn 1999). This linear form is a consequence of the interaction of the bulk residual current U_b with the turbulence due to the waves passing over the rough bottom. When U_b becomes greater than the particle speed associated with the wave, this linear "wave" friction law is replaced by the usual quadratic law.

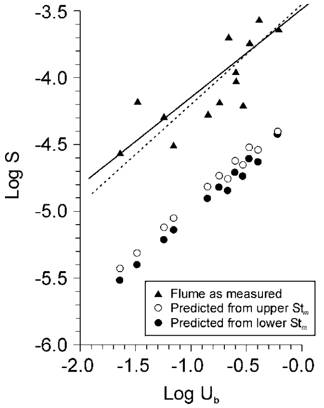

Fig. 4 Log$S$ (nutrient-uptake coefficient) for phosphate versus logU_b (water velocity). *Triangles* are measurements, and *circles* are predictions using different approximations of the Stanton number (denoted by St_m) from Atkinson and Bilger (1992). The *continuous line* is a best fit to measurements and has a slope 0.76. The *broken line* is the present theory (no fitting); slope = 0.75 from Eq. (21)

A consequence of such a linear friction law is that U_b becomes proportional to τ and hence, by Eq. (17), proportional to Ω. This contrasts with the usual quadratic friction law in which U_b is proportional to the square root of τ and hence proportional to $\Omega^{0.5}$. Data on currents and wave height from Ningaloo Reef (Hearn and Parker 1988) show a least-squares best fit of 0.90 for the exponent n in a Ω^n law for U_b, confirming a nearly linear relation between excess wave height and current. This linear law is also confirmed by data from Pagès and Andrefouët (2001) and, considering data from the Tuamotu Archipelago, Andréfouët et al. (2001) state that from the long-term record, it appears that the daily average cross-reef current over Mururoa atoll reef is linearly related to the offshore wave height (Tartinville and Rancher 2000). It is to be emphasized that the waves are acting in two ways in such a situation: firstly, they are partially breaking to produce a wave setup which creates a pressure gradient and secondly, they are propagating over the reef to produce turbulence. However, very importantly, this latter process (which influences friction) does not vary with incoming wave height. The thickness of the wave boundary layer is controlled by the roughness of the surface because it is dependent on the turbulent diffusivity near the surface of the reef. So, the observations from Ningaloo Reef (and elsewhere) may suggest that the roughness of the reef is sufficient for the wave boundary layer to penetrate through most, or a significant part of the water column. Even if that does not occur, the waves will enhance the apparent roughness above the top of the wave boundary layer. The situation of a wave boundary layer penetrating throughout the water column is itself familiar from the linear friction law found in macro-tidal waters. In that case, the penetration is due to the wave period being replaced by the tidal period which is much longer (12.4 h). For both a coral reef and a macro-tidal sea, the resultant linear law is a consequence of the residual current interacting with the turbulence created by the oscillatory currents (Csanady 1982). An important caveat is necessary here in that the spatial scales of coral reefs may affect the dynamics of the wave boundary layer. The transition from a quadratic to linear friction law produces a change in the $U_b^{3/8}$ law for nutrient-uptake coefficient, S, represented by Eq. (21) with the exponent p in U_b^p decreasing from $p=3/4$ to $p=3/8$ as the wave boundary layer gets thicker.

Summary

The derivation in this paper indicates that the roughness of benthic communities and the wave forcing of currents on coral reefs create strong turbulent energy dissipation leading to high mass-exchange rates. The theory provides the following results, which are strongly supported by published measurements. The nutrient-uptake coefficient, S, is

1. proportional to shear stress to the 0.4 root (data in Fig. 3),
2. proportional to water velocity to the 0.75 root, $U_b^{3/4}$, under conditions where waves are not forcing the mean flow, in agreement with data in Fig. 4 from Atkinson and Bilger (1992),
3. predictable for the flume results of Atkinson and Bilger (1992), and the Kaneohe Bay field results of Atkinson (1987) and Bilger and Atkinson (1992).

The observed values of drag coefficient for coral imply that the ratio of roughness length to depth is of order 0.1 to 1, indicating that coral reefs have a natural roughness unrivaled by other structures. This roughness has presumably evolved as being advantageous to nutrient uptake but it also increases net stress on the coral which can lead to mechanical damage, especially during storms (e.g., Done 1992; Dollar and Tribble 1993), so that there is necessarily some optimum roughness (Baird 1996) which may be greater for corals in the lagoon (which are more protected from wave action).

To determine nutrient-uptake rates, the present theory does not need to make any assumption regarding the form of the friction law on reef flats, and uses the $\Omega^{3/8}$ law (Eq. 19), where Ω is the excess wave height defined as $\Omega = H - \gamma h$, h is the depth of water over the reef, H is the height of incident waves, and γ is a fraction usually taken to be 0.8. If, however, currents over the reef are used for prediction of uptake, it is necessary to know the form of the friction law and appropriate values of drag coefficient. The present derivation of uptake-rate coefficients has the turbulent-energy dissipation rate per unit mass ϵ as its central parameter. Because ϵ can be derived directly from measurements of the turbulence spectrum over a reef flat, we anticipate that the predictions of the present model will be evaluated with such field data.

The above results indicate that shallow systems with large roughness elements can achieve maximal nutrient-uptake rates. The large dissipation of energy is a result of large-scale roughness elements and not dependent on micro-topographies. Nutrient-uptake rates are further enhanced by wave motion, due to an increase in the dissipation of energy under oscillatory flow. Simply, waves appear to increase the roughness or drag of the benthic communities for the same mean flows. We suggest that fore-reef environments and reef crests are sustaining a much higher flux of nutrients (and probably other compounds) than back-reef areas. These results are consistent with observations by many biologists that "reefs grow best at their margins". These results also give a physical understanding to the basic zonation of reef flats (Kinsey 1985), where fore-reefs and reef crests have a relatively high net production of organic material (P/R ratios $\gg 1$), requiring a net input of nutrients, and support net heterotrophic communities downstream. Clearly, the wave-exposed areas achieve a high uptake of nutrients to support plant growth, often turf algae. Kinsey originally suggested (personal communication during his PhD defense) that this characteristic zonation in metabolism was physically controlled, but there has been little direct understanding of the fundamental processes. The high dissipation of energy by these communities is the paramount cause for reef communities achieving such high gross primary production in low-nutrient tropical waters.

Finally, it is anticipated that the $\epsilon^{1/4}$ law, i.e., the fourth root of turbulent dissipation, introduced by the present paper will allow many numerical models, which are presently being applied to reefs, to calculate nutrient-uptake rates, or exchange rates of other compounds which are mass-transfer limited, furthering our understanding of the basic ecology, zonation, and biogeochemistry of coral reefs. A consequence of the importance of turbulence, through waves and current speed, to the rate of nutrient uptake on coral reefs, is that this rate must show considerable temporal variability on the time scale of the weather band, i.e., 7 to 10 days.

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