Hydrodynamics of Coral Reefs

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Abstract

The geometric complexity of coral reefs leads to interesting fluid mechanics problems at scales ranging from those of coral colonies or even branches a few millimeters in diameter up to whole reefs that can be kilometers in horizontal extent. In many cases, both at the colony and reef scale, unsteady flows, usually due to surface waves, behave very differently than do steady flows for which the coral structures may appear to have quite high resistance to any flow through their interior. Allowing for this difference, engineering formulae for mass transfer describe well the uptake of nutrients by corals, although a priori determination of hydrodynamic roughness of corals and coral reefs is not yet possible. Surface wave-driven flows are a common feature of many coral reefs and appear to follow predictions of theories based on radiation stress gradients. However, comparisons to observations have been relatively limited, and there is some question as to the role played by Stokes drift in these flows. Like other near-shore environments, internal waves and flows driven by horizontal buoyancy gradients can also be important.

INTRODUCTION

Coral reefs provide a wide and varied habitat that supports some of the most diverse assemblages of living organisms found anywhere on Earth (Darwin 1842). Since Odum & Odum (1955), it has been known that reefs represent islands of enormous productivity because they are efficient at trapping nutrients, zooplankton, and possibly phytoplankton from the surrounding waters (Yahel et al. 1998). This highlights the primary connection between reef function and health and hydrodynamic processes. Recent work has highlighted how flow-mediated mass transfer may also prevent coral bleaching (Nakamura & van Woesik 2001), the loss of symbiotic algae (the zooxanthallae) from the tissue of the coral polyps that can lead to death of the corals (Hoegh-Guldberg 1999).

The hydrodynamics of coral reefs and coral colonies entails a wide range of scales of fluid motions, starting with the largest scales characterizing flow such as eddies produced by island wakes, smaller depth-scale turbulent features determined by reef topography, and finally the smallest scales of flow, those comparable to single coral colonies. I use this hierarchy of scales as a basis for organizing this review, starting with the smallest scales and finishing at the largest scales. Due to space constraints, important topics like the role of wave-induced coral breakage in shaping reefs, or the value of reefs as natural breakwaters, are left for others to review. In a like fashion, an excellent review of work on the physical oceanography of reefs prior to 1990 can be found in Andrews & Pickard (1990).

FLOW AT THE SCALE OF A CORAL COLONY

Most of the reef-building corals are modular organisms, i.e., each coral is a colony consisting of numerous, interconnected, identical modules, called polyps. The coral grows by extending its carbonate skeleton and adding more polyps. As **Figure 1** shows, this "design concept" is highly diverse, with some corals taking branching forms, some foliated and some massive.

Given the geometric complexity of corals, it is somewhat more difficult to define their size except perhaps in terms of the size of the box required to contain a given colony. With this definition, the coral colony size can vary from 10^{-3} to 30 m^3. Other measures can also be defined, e.g., the ratio of the total surface area of the coral to the plan-form area of the box that contains it. This ratio is important in that it defines the amount of surface area of coral per unit area of reef across which mass transfer can occur (Falter et al. 2005). One means to obtain this information, at least for smaller colonies, is to obtain a complete three-dimensional map of the colony by X-ray tomography (Kaandorp et al. 2003). Using this approach, the area ratio is five for the branching coral shown in **Figure 2*a*** (S. Chang, personal communication). This colony structure allows for enhanced mass flux to the colony within limits discussed below. In comparison, this ratio would be close to one for most engineered surfaces, although the complex structures used to cool microprocessors must achieve a similar enhancement to keep laptops like the one used to write this article from catching fire!

Most, if not all, of the work on colony-scale hydrodynamics has focused on branching corals. Chamberlain & Graus (1975) carried out flow visualization studies

Figure 1

Coral reef on the north shore of Moorea, F.P. (Photo by A. Santoro.)

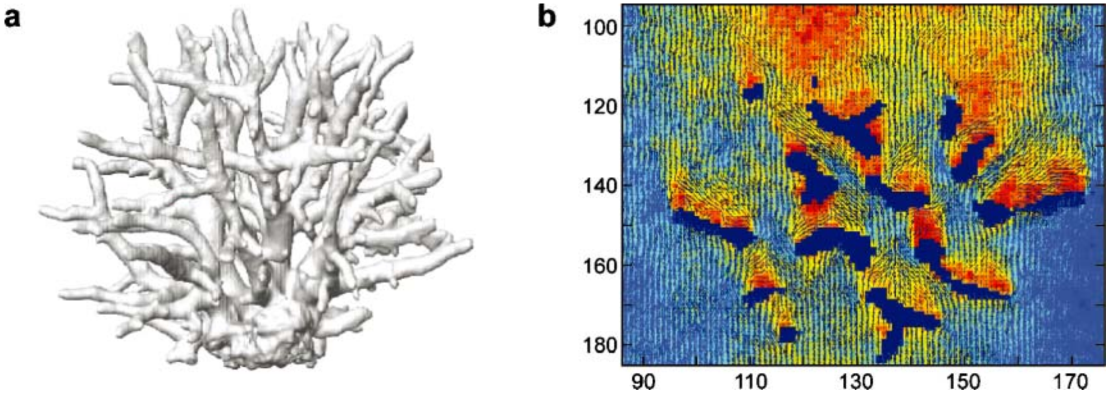

Figure 2

(*a*) As seen by X-ray tomography: *Stylophora pistillata*, low velocity morphology (Chang et al. 2004, Reidenbach et al. 2006a). (*b*) Flow inside the coral shown in (*a*) as measured by Magnetic Resonance Velocimetry (MRV). This is a horizontal plane taken near mid-height using the MRV technique of Elkins et al. (2003). Image courtesy of S. Chang and C. Elkins.

using both real coral specimens and arrays of cylindrical rods, finding that much of the flow that approaches branching corals is diverted around and over the coral. As expected, coral geometries with denser branching tend to divert more flow to the exterior, whereas coral geometries with sparser branching allow more flow through the interior (Reidenbach et al. 2006a). Examining flows inside the coral colony has proved difficult since the outer branches block both optical and acoustic access to the interior. However, recent work (Elkins et al. 2003) (**Figure 2*b***) using magnetic resonance velocimetry (MRV), which is not obstructed by the solid matrix, reveals the complex details of the interaction of wakes from upstream branches encountering downstream branches that leads to blocking of interior flows (S. Chang & C. Elkins, unpublished data).

The flow through the coral colony is different in the presence of waves. In experiments with several species and morphologies of branching coral, Reidenbach et al. (2006a) confirmed the steady flow behavior discussed above by looking at the dissolution of small gypsum plugs (a proxy for velocity) placed throughout the coral colony interiors. When waves were added, the velocities inside the colony were inferred to be similar to those outside the colony, leading to a wave enhancement of interior mass transfer. Lowe et al. (2005b,c) confirmed this behavior for arrays of cylinders serving as a simple model of a coral, showing that the enhancement depends on the Keulegan-Carpenter number (Dean & Dalrymple 1991),

$$\mathrm{Kc} = \frac{U_w}{\omega S}, \tag{1}$$

where U_w is the wave orbital velocity, ω is the frequency, and S is the cylinder spacing. Kc represents the ratio of the orbital excursion to object geometry, in this case the cylinder spacing. When Kc is large, the flow is drag dominated and velocities inside the colony are much lower than in the free stream. In contrast, when Kc is small, the interstitial flow is inertia dominated and interior velocities more nearly match exterior ones, and total mass transfer is enhanced over that of steady flows.

Unlike engineered structures, corals are living structures that respond to flow in complex ways that can alter their physical structure. For example, flow variations inside the colony may induce localized calcification and a specific preferential growth form (Kaandorp et al. 2003, 2005; Kaandorp & Kübler 2001; Lesser et al. 1994), or may lead to branch orientation that optimizes nutrient uptake or prey capture (Helmuth & Sebens 1993). Veron & Pichon (1976) show examples of the resulting flow-related intraspecific plasticity variability. Amatzia Genin of the Steinitz Lab in Israel has carried out simple experiments demonstrating the effect of flow on morphology in which coral of a given species and flow environment is exposed in situ to higher flow velocities using underwater pumps (see Reidenbach et al. 2006a). The effect of this flow change is to make the coral skeleton almost uniformly thicker, thus reducing the size of the spaces between the branches.

For branching corals this connection should be complicated by the fact that the distribution and rates of mass transfer for flow through and over corals depends on the details of separation from the branches and subsequent reattachment on downstream branches. Separated and reattached flows cause large variations in local heat (and mass) transfer such that heat transfer and momentum can be decoupled (Vogel & Eaton 1985). Using lattice Boltzmann methods to solve the complicated interior flow problem, and assuming that local growth is limited by diffusion to the structure (diffusion limited accretion), Kaandorp and colleagues (Kaandorp et al. 2003, 2005; Kaandorp & Kubler 2001) predict structures that are quite similar in appearance to branching corals.

However, although the qualitative appearance is correct, there is no doubt that the devil is in the details. For example, to correctly predict mass transfer of nutrients to the corals, the thin diffusive boundary layers on the coral branches must be resolved. For most nutrients of interest, which have Schmidt numbers $\mathrm{Sc} = \nu/D$ that are O(1000), scalar boundary layers can be expected to be a factor of $\mathrm{Sc}^{1/3} \sim 10$ times smaller than any local viscous boundary layers (see e.g., Kays & Crawford 1993). For example, for a 1 cm diameter (d) branch with a flow (U) of 10 cm/s, the viscous boundary layer thickness will be $\delta_v \sim (\nu d/U)^{1/2} \sim 0.03$ cm, and so a numerical model of mass transfer to this branch would need to resolve layers that are 3×10^{-3} cm thick. Thus, a grid for a typical coral colony with a linear dimension of 10 cm would have of the order of $3000^3 \sim 10^{10}$ grid points. Even with immersed boundary methods (Chang et al. 2004, Iaccarino & Verzicco 2003) this is still out of reach, although it does seem that computing mass transfer for $\mathrm{Sc} \sim 1$, which would only require 10^7 grid points, may be attainable and interesting.

However, there is also biology to consider! The fact that the observed change in branch thickness with increased flow is nearly uniform suggests the possible importance of internal translocation of nutrients, photosynthates, etc. in the tissue layer that connects the polyps of a given colony (Rinkevich & Loya 1983). Were there no translocation, presumably the geometric modifications would be entirely localized, as modeled by Kaandorp and colleagues. Thus, it seems that to produce a "virtual coral" would require coupling the challenging flow model with appropriate spatially explicit models of the biology of the polyps. In any case, although a convincing determination of the mechanism(s) involved remains to be produced, the fact that flow velocity affects morphology seems incontrovertible.

BOUNDARY LAYER FLOW OVER REEFS: FLOWS AT THE 1- TO 10-M SCALE

At scales of 1 to 10 m, the most obvious physical feature of coral reefs is that they are remarkably rough, having bottom drag coefficients, C_D, that are typically ten times larger (or more) than the canonical value of 0.0025 found for muddy or sandy sea beds (Lugo-Fernandez et al. 1998b, Roberts et al. 1975). Baird & Atkinson (1997) report values of equivalent sand grain roughness, $k_s = 0.28$ m, for flows in a flume filled with coral skeletons, although McDonald et al. (2006) found that, in part, this large apparent roughness was due to the fact that laboratory experiments in flows of limited depth force significant amounts of flow through the corals rather than over it as with deeper flows. Measurements of wave damping over the reef flat at Kane'ohe Bay reported in Falter et al. (2004) and Lowe et al. (2005a), as well as measurements of wave setup reported in Tait (1972) and Gerritsen (1980), gave similar values.

Reidenbach et al. (2006) found that $k_s = 1$m for nonwavy flow over the fringing reef in Eilat.

As is common in the study of geophysical boundary layers (see e.g., Lueck &Lu 1998), these values of k_s are essentially determined by choosing k_s, so that observed velocity profile u(z) best fits the law of the wall

$$u(z) = \frac{u_*}{\kappa} \ln\left(\frac{30z}{k_s}\right). \tag{2}$$

Here $\kappa = 0.41$ is the von Karman constant and z is the height above the bed. At least for steady flows, this appears to be justified: Reidenbach et al.'s (2006b) simultaneous measurements of velocity profiles and turbulent stresses at several heights above the bed match the law of the wall, as well as indicate that the rate of dissipation of turbulent kinetic energy is nearly in balance with its rate of production, as would be expected in a canonical rough-wall turbulent boundary layer. However, although there have been various approaches to directly measuring the real roughness of reefs, e.g., by draping chains or measuring a dense array of heights, there is currently no accepted way of measuring reef roughness that can be translated into values of C_D or k_s.

The challenge of predicting drag on coral reefs derives from their geometric complexity and how the colony-scale flows combine with the effects of other nearby roughness (rocks, sponges, etc.). Drawing the analogy to canopy flows (Ghisalberti & Nepf 2004, Raupach & Thom 1981), particularly urban canopy flows (see Britter & Hanna 2003, Coceal & Belcher 2004), Lowe et al. (2005b) show how the drag on an array of cylinders, a crude model of a coral reef, depends on the ratio of the spacing, S, of the cylinders to their diameter, D. For steady flows, this leads to good predictions of the overall drag on the array, at least for the range of cylinder spacing ($1 < S/D < 3$) studied. When applied to the fields of coral bommies found on many Indo-Pacific reefs, Lowe et al.'s analysis suggests spatially averaged drag coefficients that can be O(1).

As noted above, corals differ in one important respect to most canopy flows in that many coral reefs are subject to surface waves such that the predominant flows are not steady. As a result, for coral pavements, i.e., extensive canopies made from corals, the steady limit results in weak flows inside the canopy. In the high-frequency limit, wave velocities inside the canopy are nearly identical to those above the canopy. Nonetheless, from the standpoint of predicting drag, Lowe et al. (2005a) found that relations appropriate to other simpler forms of roughness adequately predict the frequency dependence of damping on their reef. However, lacking a suitable treatment of how the multiscaled roughness of the reef affects drag, these results may not be easily generalized to other reefs, at least in a predictive sense.

As a consequence of this large roughness, and because of the complex nature of the corals, i.e., a structure that maximizes surface area per volume, reefs have much higher mass transfer rates per unit area than most engineered substrates. Bilger & Atkinson (1992) were the first to attempt to use engineering mass transfer correlations (e.g., Dipprey & Sabersky 1963) to predict rates of nutrient (principally phosphate) uptake by reefs. Setting aside unsteadiness for the moment, there are two key aspects of mass transfer to reefs: (*a*) reefs have large values of the roughness Reynolds number

$k^+ = u_* k_s/\nu$, and (*b*) nutrients of interest have large values of Sc, i.e., O(1000). Lacking appropriate data, Bilger & Atkinson (1992) combined the high k^+ but low Sc ($Sc = 7$) results of Dipprey & Sabersky (1963) with the low k^+ but high Sc results of Dawson & Trass (1972). Initially, it appeared that mass transfer was much greater than would be expected based on flow over rough walls (Atkinson & Bilger 1992). However, later work (Falter et al. 2004, 2005) that accounts for the fact that waves are the dominant motion on the reefs and in the tanks that Atkinson and colleagues studied shows that the mass transfer relation (shown in **Figure 3**)

$$St = \frac{\dot{m}}{\rho U_0 C_0} = \lambda \frac{C_D^{0.5}}{(k^+)^{0.2}\, Sc^{0.6}}, \tag{3}$$

where $\dot{m}$ is the mass flux per unit area, St is the Stanton number, C_0 is the free stream nutrient concentration, U_0 is the free stream velocity = the wave orbital velocity when waves are dominant, and λ is an O(1) constant, fit all of the mass transfer data both from real reefs and from coral assemblages located in flumes (Baird & Atkinson 1997, Thomas & Atkinson 1997).

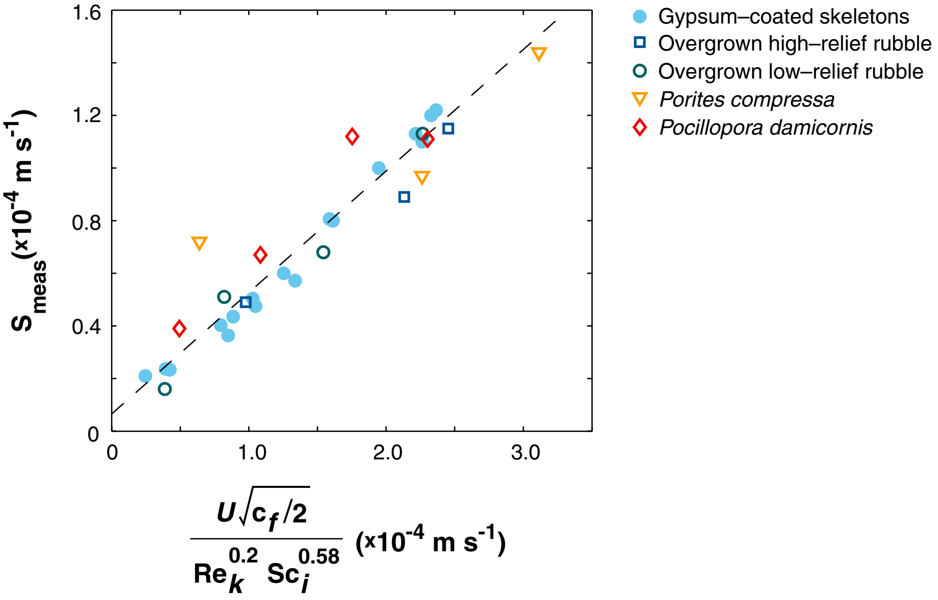

Figure 3

Mass transfer to coral colonies and reefs measured by Falter et al. (2004) and shown in their figure 1. Note that in this plot $Re_k = k^+$ and that the plot is given in dimensional terms. The filled symbols represent experiments with gypsum-coated skeletons whereas the open symbols refer to ammonium uptake by experimental reef communities 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*). Please see Falter et al. (2004) for an explanation of the symbols. Copyright 2004 by the American Society of Limnology and Oceanography.

There are three caveats to this fit: (*a*) The surface area available for mass transfer per unit area of reef must be accounted for. As discussed above, this ratio may be five or more for dense coral canopies (Falter et al. 2005). (*b*) The value of C_D in the wavy case is the one required to match the observed damping of waves (Falter et al. 2004, Hearn et al. 2001). (*c*) This implies that nutrient uptake is linked directly to the wave climate of the reef; there is still a factor 1.3–.5 enhancement due to oscillatory motion that has been included (Falter et al. 2005, Lowe et al. 2005c, Reidenbach et al. 2006a).

The factor of $(k^+)^{-0.2}$ appearing in Equation 3 implies that as roughness increases, mass transfer is reduced. This factor represents the sheltering of lower parts of the surface by the higher parts of the roughness elements, i.e., that velocities and hence mass transfer are higher near the tops of the roughness than in the troughs between the roughness elements (Dipprey & Sabersky 1963). Given the high interior resistance of branching corals to flow, this model seems applicable to both isolated coral colonies as well as continuous canopies of coral, although for waves, the velocity enhancement seen in laboratory experiments may mean that the constant of proportionality in Equation 3 may also depend on an appropriately defined value of Kc, as does the drag (Lowe et al. 2005c).

Turbulence produced by the coral reef also affects the rate particulates suspended in the water column that can be grazed by the overall reef community (Frechette et al. 1988, Genin et al. 2002). Because rougher boundaries lead to higher rates of mass transfer, they also make grazing more efficient. It seems possible that as a reef grows and becomes rougher, it can support denser assemblages of other benthic organisms, e.g., sponges or boring bivalves, i.e., richer benthic communities that add to the diversity of life on the reef. On the other hand, in nonwavy flows, individual colonies may see diminishing returns as they become progressively more "shaded" by their neighbors. The hypothesis that these two effects can come into balance on some reefs is an interesting one that deserves an experimental test (A. Genin, personal communication).

REEF-SCALE FLOWS: FLOWS AT SCALE OF 100 M TO 1000 M

Wave-Driven Flows over Coral Reefs

In many coral reef lagoons, surface wave–driven flows often (but not always) dominate. Of all areas of research connecting corals and hydrodynamics, the topic of wave-driven flows has probably received the most attention, beginning with pioneering studies by Von Arx (1954) and Munk et al. (1949), which consider flushing of reef lagoons by wave-driven flows over the fringing reef to more recent work examining wave transformation and wave forcing of flows over and along fringing reefs (Andréfouët et al. 2001; Angwenyi & Rydberg 2005; Gourlay & Colleter 2005; Hardy & Young 1996; Hearn 1999; Kraines et al. 1998, 1999; Lowe et al. 2005a; Lugo-Fernandez et al. 1998a,b; Prager 1991; Roberts et al. 1975; Roberts & Suhayda 1983; Symonds & Black 2001; Symonds et al. 1995; Tartinville & Rancher 2000; Young 1989). The basic idea (Munk & Sargent 1948, Young 1989) is that incident waves break on the

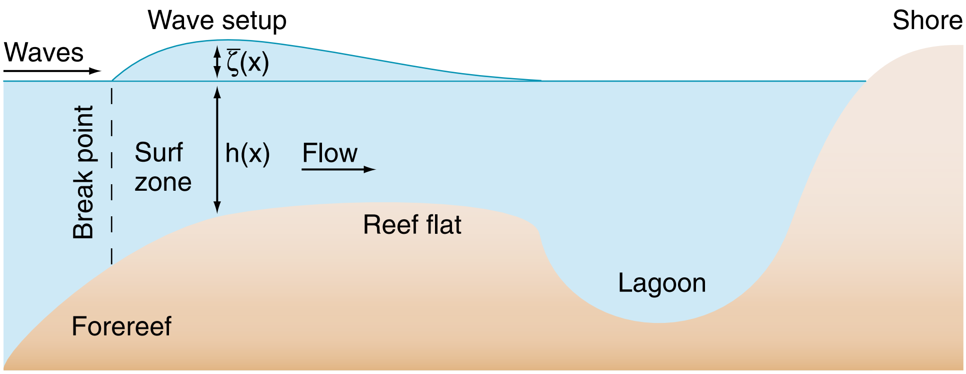

Figure 4

Definition sketch for wave-driven flow over a reef and into a lagoon. (Redrawn from Hearn 1999; courtesy of R. Lowe.)

offshore face of the reef and push water onto the reef flat and then into the lagoon (if there is one; see **Figure 4**).

Symonds et al. (1995) and Hearn (1999) present observations showing this connection. For example, Hearn (1999) found (with significant scatter) that induced cross-reef currents were linearly proportional to offshore wave height. In a remarkable series of lab experiments studying wave-driven flows over reefs, Gourlay (1996a,b) varied both mean water level relative to the reef flat level incident wave height, finding two regimes of flow behavior: (*a*) reef-top control: When the mean water level is sufficiently far above the reef flat, the reef flat flow is in a friction-pressure gradient balance; (*b*) reef-rim control: When the mean water level is at or below the (raised) reef flat, a hydraulic control at the lagoon end of the flat determines the depth of the overall flow. In the latter case, wave breaking occured on the fore-reef and the wave-driven flow was due to swash running up and onto the reef flat. Note that in Gourlay's experiments the reef flat was relatively smooth (no roughness elements) in these experiments, and so the rim-control flows may be less relevant to real reefs.

All models of wave-driven flows over reefs (e.g., Gourlay & Colleter 2005, Hearn 1999, Symonds et al. 1995) are based on the idea first advanced by Longuet-Higgins & Stewart (1962) that spatial gradients in wave radiation stress, i.e., the depth-integrated momentum flux (including pressure forces) associated with propagating waves, appears as a body force acting on the mean (wave averaged – marked with an overbar) flow. Thus, they should be quite similar in dynamics to longshore flows on beaches forced by incident waves (Lentz et al. 1999). As presented in Mei (1989), including radiation stresses, the momentum equations governing the horizontal flow can be written as

$$\frac{\partial U_j}{\partial t} + U_i \frac{\partial U_j}{\partial x_i} = -g\frac{\partial \bar{\zeta}}{\partial x_j} - \frac{1}{\rho(\bar{\zeta} + h)}\frac{\partial S_{ij}}{\partial x_i} - \frac{\tau_j^B}{\rho(\bar{\zeta} + h)}, \tag{4}$$

where $U_i = U_i^E + U_i^S$ is the ith component of the Lagrangian mean velocity, written here as the sum of the depth-averaged Eulerian mean velocity and depth-averaged Stokes drift velocity (Longuet-Higgins 1969), $\overline{\zeta}$ is the deviation of the free surface from mean sea level (MSL), h is the depth of the bottom below MSL, S_{ij} is the radiation stress tensor (given below), and τ_i^B is the mean (wave-averaged) bottom stress. For waves propagating in the x_1 direction (normal to shore) with amplitude A, wave number k, Longuet-Higgins & Stewart (1962) show that

$$S_{11} = \frac{\rho g A^2}{4}\left(1 + \frac{4kh}{\sinh(2kh)}\right). \tag{5}$$

Thus, as waves shoal (changing kh), there will be variations in S_{11} that may drive currents (Longuet Higgins 1970) or result in the setup of the free surface (Bowen et al. 1968). Note that Equation 4 applies to Lagrangian, not Eulerian, mean velocities. Although the contribution of the Stokes drift to the overall flow may be negligible for longshore flows on a beach, this may not be true for flows over reefs in which the mean Eulerian flow and Stokes drift are coaligned.

Symonds et al. (1995) were the first to apply these ideas to computing wave-forced flow on reefs, analyzing the case of a simple geometry in which the offshore section was represented as a plane beach while onshore of the break was a constant depth reef flat. Waves were assumed to shoal and then break when the critical breaking criterion $A = \Gamma h/2$, where the constant $\Gamma \approx 0.8$ was derived from experiments examining waves on beaches. In this model, offshore of the break, there is a set down of the water surface, because the approximate momentum balance reads (x_1 directed positive offshore)

$$g\frac{\partial\overline{\zeta}}{\partial x_1} \approx -\frac{1}{\rho(\overline{\zeta}+h)}\frac{\partial S_{11}}{\partial x_1}, \tag{6}$$

with $\partial S_{11}/\partial x_1 < 0$. Within the breaker zone itself, there is a setup of the free surface since Equation 6 still holds (c.f. Hearn 1999), but with $\partial S_{11}/\partial x_1 > 0$. If there were no reef flat, then there would be a setup of the water surface just like on beaches (Gerritsen 1980, Tait 1972).

Inshore of the break the water surface slopes down from its high point at the end of the break to the water level in the lagoon, which is assumed to be the same as offshore, driving a flow with

$$g\frac{\partial\overline{\zeta}}{\partial x_1} \simeq -\frac{\tau_j^B}{\rho(\overline{\zeta}+h)} = -\frac{C_D\overline{u\,|u|}}{\rho(\overline{\zeta}+h)} \approx -r\frac{U}{h}. \tag{7}$$

Here the drag is expressed as the average of the instantaneous bottom friction, including both mean flow and waves or, for analytical convenience, using a linearized friction model (Hearn 1999, Symonds et al. 1995). Because the waves are assumed not to change in this region (not always a good assumption; see Lowe et al. 2005a), there is no radiation stress gradient on the reef flat. Like most circulation models, Equation 7 is closed by choosing bottom friction coefficients to best match observations. These will be relatively large owing to the roughness of the reef (Lugo-Fernandez et al. 1998b) and will be a function of the wave orbital velocity (Hearn 1999). Again, whatever the roughness, the subtle point that the model predicts Lagrangian mean velocities complicates things because the friction formulations are expressed in terms of the Eulerian means.

Model results from Symonds et al. (1995) compare well with currents measured on John Brewer reef, a small reef located in the Great Barrier Reef complex, although significant differences, possibly attributable to other forcing, remain (Symonds & Black 2001). Lugo-Fernandez et al. (1998b) use a model similar to that of Symonds et al. to successfully hindcast sea level changes on Tague Reef in the Caribbean. Hearn's (1999) comparisons are more limited, for example citing one observation from Kane'ohe Bay, Hawaii. In contrast, Gourlay & Colleter's (2005) modeling does an excellent job of matching Gourlay's earlier observations. In this case, it is evident that the control offered by laboratory experiments usefully isolates the effects of geometry on wave-driven flows.

Hearn's analysis points out an important aspect of wave-driven flows over reefs: When the depth over the reef is shallow, flows will be weak because friction is strong, whereas when the depth over the reef is large, flows will be weak because of limited breaking and hence small radiation stress gradients (see also Gourlay & Colleter 2005). Thus, there will be a depth at which the wave-driven flow is a maximum. Moreover, tidal variations in depth will produce tidal variations in mean flows over the reef.

Although useful in their simplicity, the assumptions made by Symonds et al. and Hearn. may not always be valid. For example, both models assume that $\overline{\zeta}$ is zero at the end of the reef flat, whereas, in reality, the water level must rise in the lagoon to drive flow out through passes in the reef back to the ocean. These additional features, e.g., tides, setup in the lagoon, radiation stresses on the reef flat, are easily dealt with in two- and three-dimensional circulation models. To date, these models have generally used relatively simple wave models, i.e., ones that include refraction and wave breaking only, and used the resulting wave field to calculate radiation stress gradients to force mean flows (Kraines et al. 1998, 1999; Prager 1991; Symonds & Black 2001; Tartinville & Rancher 2000). In both two-dimensional and three-dimensional models (Tartinville et al. 1997), the radiation stress gradient is applied as a body force. The comparison between observations (which have generally been limited) and modeling looks promising, and has permitted estimation of important biogeochemical hydrodynamic measures such as Lagoon residence time (Tartinville et al. 1997). More sophisticated approaches to predicting wave dynamics, e.g., Boussinesq wave models (Skotner & Apelt 1999) or models accounting explicitly for effects of large bottom slope on wave propagation (Massel & Gourlay 2000), have also been used, albeit only to look at the waves alone.

Nonetheless, the bottom line is that, unlike the case for beaches (Lentz & Raubenheimer 1999), measurements of mean free surface changes have not been done in conjunction with current measurements as would be needed to definitively test any of the models discussed above. Conversely, given the issue of Eulerian (what is measured) and Lagrangian (what is predicted) means, it seems that observations of waves and wave-driven flows on coral reefs might also lead to new insights into fundamental aspects of the way waves and mean flows interact.

Flows Driven by Tides and Buoyancy

Much of the work on large-scale reef hydrodynamics has focused on the role reef geometry plays in determining patterns and rates of horizontal transport, particularly that of the larvae of coral reef fish and other organisms (Black 1993, Cowen et al. 2000). These larger-scale processes are only slightly, if at all, influenced by waves. Wolanski and colleagues at the Australian Institute of Marine Sciences have focused on inter-reef transport in the Great Barrier Reef complex, showing how flows in this region reflect the separate influences of shelf waves (Wolanski & Bennett 1983) and tides (Wolanski 1983). One of their more general results is the importance of reef roughness in generating large-scale vorticity. Field observation, laboratory work, and computation (see Wolanski et al. 1994) clarify that flow around isolated reefs generates substantial vertical vorticity organized as large, reef-scale eddies, more or less like those one sees shed by any bluff body. However, several twists emerge in "shallow" water: Most notably, over the bottom of the surrounding ocean these eddies develop secondary flows formally analogous to those that arise through Ekman layer dynamics (Wolanski et al. 1984).

On the basis of Wolanski's work, we might expect that less dramatic variations in topography associated with larger-scale patchiness of the reefs will likewise lead to the generation of vertical vorticity and hence of more complicated secondary flows, particularly those involving onshore-offshore exchanges. For example, if the longshore flow encounters a region of high roughness, it should diverge offshore; if it encounters a region of low roughness it should accelerate and entrain offshore fluid. As an extreme example of this effect, spectacular residual flows have been seen in lagoon-atoll reef systems like that at Enewetak (Atkinson et al. 1981), where the channels through the fringing reef can be the site of remarkably strong tidal currents.

Pointing to the strong coupling of hydrodynamic and biochemical processes, as well as to the importance of oceanic stratification, Leichter et al. (1996, 2003) observed significant transport of nutrients by internal waves from deep water onto Conch Reef on the Southeast Florida Shelf. These observations showed large-amplitude internal waves generated tidally that propagated onshore, shoaled, and broke. The details of the generation mechanism are currently unclear, but there is evidence that Leichter et al. may be observing the nonlinear near-shore behavior of the cross-Florida strait internal seiche (Niiler 1968). Besides transporting nutrients, these waves also move cold water up the shelf; the resulting periodic cooling events may help to forestall bleaching during times when water temperatures might otherwise exceed the bleaching threshold (Riegl & Piller 2003).

The steep topography of reefs can also lead to baroclinic exchange flows through the mechanisms known as differential heating or cooling (Monismith et al. 2006, Symonds & Gardiner-Garden 1994). When heated (by the sun) or cooled (mostly by evaporation), the shallow near-shore waters of the reef will heat or cool more rapidly than deeper waters offshore, leading to onshore-offshore temperature gradients and, hence, baroclinic pressure gradients. Neiman et al. (2004) observed gravity currents produced by cooling of the reef off Aqaba on the eastern shore of the northern Red Sea, finding that these could result in the significant export into the phytoplankton-derived carbon in the deeper waters of the Gulf of Aqaba. Monismith et al. (2006) documented both heating and cooling flows on the Eilat reef, finding that the momentum balance is mainly steady and inertial and advective heat transport are dominant (Sturman et al. 1999), although bottom friction and unsteadiness in the thermal forcing can also be important. The inertial scaling gives a sheared cross-shore flow, ΔV, that varies as

$$\Delta V \sim \beta^{-1/3} \left(\frac{\alpha\, g\, \widetilde{H}\, h}{\rho\, c_p} \right)^{1/3}, \tag{8}$$

where β is the bottom slope, α is the thermal expansivity, $\widetilde{H}$ is the surface heat flux, h is the local depth, ρ is the fluid density, and c_p is the heat capacity. The effects of unsteadiness and bottom friction are secondary, generally acting to weaken the exchange flow, especially when the longshore flow is strong. Like internal wave upwelling, one can speculate that these convective flows provide a mechanism for locally reducing the thermal stress that can lead to bleaching (Hoegh-Guldberg 1999), as well as enhancing physical connectivity between the reef and ocean.

Although it has received scant attention, the flow of stratified fluid over a reef should be expected to produce relative strong vertical mixing for even relatively slow mean flows, meaning that reefs may be good sites for studying bottom mixed-layer dynamics, including sloping boundary layer dynamics (Garrett et al. (1993), or turbulence dynamics in stratified fluids. One of the clearest observations of boundary mixing in the ocean is that reported in Wolanski (1987) for flow in the lee of a coral island.

SUMMARY

Corals and coral reefs exemplify organisms and ecosystems that are shaped by flow. At the smallest scales, the hydrodynamics of flow through and over very complicated bodies determines local mass transfer and, in ways yet to be determined, morphology of the coral skeleton. Seen at larger scales, the carbonate framework that coral polyps manufacture appears to be a very rough surface, one that promotes mass transfer between the overlying water and the organisms of the reef, significantly damps surface waves, and, of course, provides a rich habitat for a wide variety of organisms. At the scale of the reef as a whole, coral reefs are similar to other near-shore coastal environments, e.g., sandy beaches or kelp forests on rocky shores, in that flows can be driven by various combinations of tides, buoyancy, and internal and surface waves. Remarkably, it appears that reefs can be excellent (and pleasant!) laboratories in which to study these processes. Because the geometries are different from those of more commonly studied systems, i.e., beaches, work on reefs should be expected to yield new insights into the dynamics of coastal flows more generally.

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