

Flow effects on benthic grazing on phytoplankton by a Caribbean reef

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Abstract

We present measurements of flows and fluxes of phytoplankton to Conch Reef, Florida, a Caribbean reef dominated by sponges and soft corals, located in 15 m of water offshore of Key Largo. Vertical profiles of chlorophyll *a*, a proxy for phytoplankton biomass, showed a near-bed depletion, indicating the existence of concentration boundary layers. Along with simultaneous measurements of velocity profiles, near-bed turbulence, and temperature stratification, these profiles were used to compute α , the mass transfer velocity of phytoplankton to the bed (i.e., the flux to the bed normalized by near-bed concentration). The α value ranged from -40 to $+130$ m d^{-1} , with a significant linear positive relationship with shear velocity. The median value of $\alpha = 48 \pm 20$ m d^{-1} is larger than would be expected, given the observed population of filter-feeding sponges. Nonetheless, these large values of α are consistent with values found recently for another coral reef as well as for a soft bottom estuarine community. Taken as a whole, these measurements indicate that reefs with large roughness and/or energetic currents should be able to support higher biomasses of benthic organisms than would low relief reefs or reefs in sluggish waters.

Many coral reefs are considered “islands of high productivity” in “oceanic deserts,” surrounded by oligotrophic waters where nutrients are scarce (Sargent and Austin 1954; Erez 1990; Levinton 1995). This seemingly paradoxical situation is thought to arise because coral reefs are efficient at trapping nutrients, bacteria, zooplankton, and phytoplankton from the surrounding waters (Ayuki 1995; Yahel et al. 1998; Holbrèque et al. 2006) and so can balance the nutrients required for primary production and their leakage offshore (Genin et al. 2009). Because many reefs depend on suspended particles and dissolved nutrients trapped from the flowing water, their functioning may be regulated by the hydrodynamics.

For example, uptake rates of phosphate and ammonium by reef-flat communities can be limited by flow-mediated mass transfer (Atkinson and Bilger 1992), as can oxygen fluxes to and from coral colonies (Patterson et al. 1991; Finelli et al. 2006). In the case of reef communities, rates of mass transfer to reefs (or individual reef organisms) can be expressed as a function of the turbulent shear stress at the bed, the roughness of the reef, and the molecular diffusivity of the material being transferred (Atkinson and Bilger 1992).

The removal of dissolved or suspended materials (e.g., nutrients, phytoplankton) by benthic organisms leads to a

nutrient-depleted region near the bed (i.e., the formation of a concentration boundary layer). In concentration boundary layers, downward, vertical turbulent mixing replaces material (e.g., nutrients) removed near the bed (Butman et al. 1994). The formation of concentration boundary layers has been documented in the field over several communities, including lacustrine sponge communities (Pile et al. 1997), mussel beds (Ackerman et al. 2001), soft bottom infauna in San Francisco Bay (Jones et al. 2009), and coral reefs (Yahel et al. 1998; Genin et al. 2009). Using the control volume method, Genin et al. (2009) measured flow-dependent grazing rates of chlorophyll *a* (Chl *a*) that varied from 0 to ~ 20 m d^{-1} . Notably, both Genin et al. (2009) and Jones et al. (2009) find statistically significant relationships between grazing rates and flow.

Variation in grazing rates between different ecosystems can be due to both abiotic factors, such as shear velocity, topographic roughness, and the concentration of dissolved nutrients, and biological traits, such as the concentration of plankton in the water and the type and abundance of benthic planktivores. The main objective of this study was to measure benthic grazing on phytoplankton by a Caribbean coral reef where phytoplanktivores such as sponges, gorgonians, and soft corals are highly abundant and where the currents are strong, comparing this grazing with similar measurements recently reported by Genin et al.

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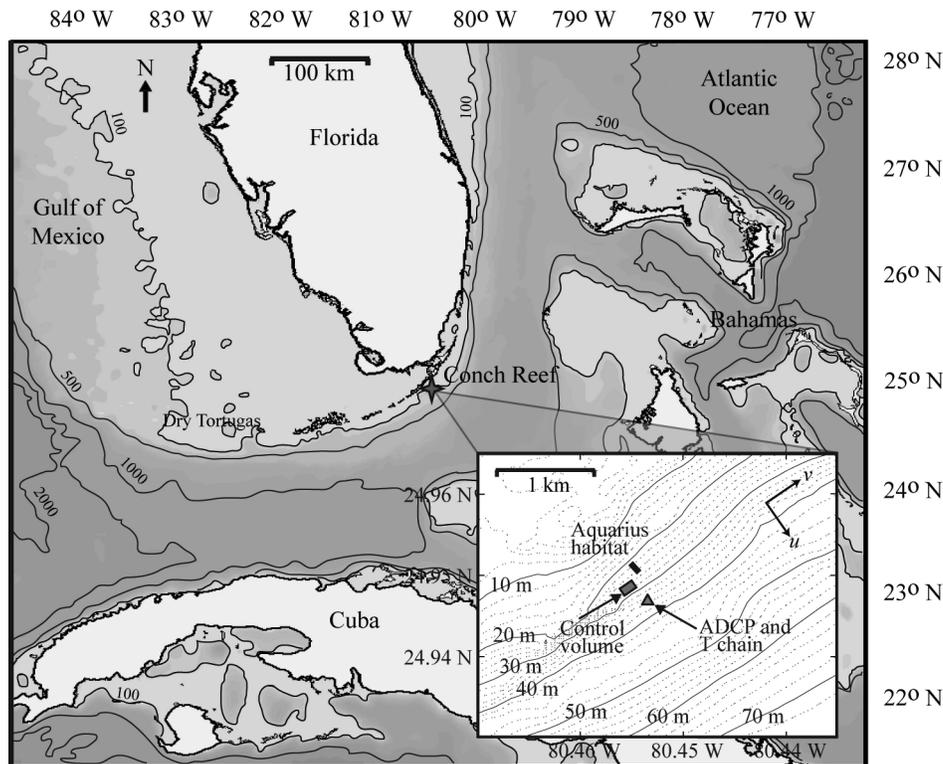


Fig. 1. Site location, including detail of the *Aquarius* region, including control volume location. The 32-m isobath station with an ADCP and thermistor (T) chain is also referred to as Deep S4.

(2009) from an Indo-Pacific, stony-coral-dominated reef, where such phytoplanktivores are markedly less abundant and where the currents are substantially weaker.

In the following sections we will show that the Conch Reef grazing rates are greater than those seen on the Eilat Reef, but they appear to show a similar dependence on flow. We hypothesize that the higher biomass of grazers on Conch Reef may reflect the fact that currents at Conch Reef are more energetic than those over the Eilat Reef and, thus, can support higher fluxes of phytoplankton biomass to the benthos.

Methods

The measurements were made at Conch Reef (24°59'N, 80°25'W), 8 km southeast of Key Largo in the Florida Keys (Fig. 1), using the National Oceanic and Atmospheric Administration (NOAA) underwater laboratory, *Aquarius* (see <http://www.uncw.edu/aquarius/>). Benthic communities at Conch Reef consist primarily of soft corals, sponges, and benthic macroalgae (Jaap 1984; Southwell et al. 2008). Scleractinian corals are present but generally are not abundant, with typical coverage reported to be 10% or less (Gardner et al. 2003). Typical roughness of the reef, including the larger sponges and soft corals, is on the order of 0.3 m, although the tops of the tallest sponges, *Xestospongia muta*, as well as rocky outcrops can be as much as 1 m above the bed.

Flows at Conch Reef are predominantly along-shore (ca. southwest to northeast) at speeds that are typically 0.1–0.3 m s⁻¹, and flows vary in response to changes in the position of the core of the Florida Current and with changes in the climate of shoaling internal waves (Leichter et al. 1996; Davis et al. 2008). Cross-shore flows and short-term temperature variability are mostly driven by internal waves (Leichter et al. 1996; Davis et al. 2008). While typically measuring a few centimeters per second, cross-shore velocities can be as high as 0.3 m s⁻¹ during energetic internal wave events.

In July 2005 we deployed three upward-looking, 1200-KHz Teledyne RD Instruments acoustic Doppler current profilers (ADCPs) and a string of Seabird SBE39 temperature loggers (at 0, 4, 8, and 12 m above bed [mab]) on a plateau in 15 m of water ca. 100 m southwest of *Aquarius*. Nortek Vector Acoustic Doppler Velocimeters (ADV) were mounted on a small sawhorse frame with sampling volumes positioned at 0.25, 0.6, 1.5, and 3.0 mab. The ADVs were cabled to *Aquarius* and their data were transmitted via wireless Ethernet to computers onshore in Key Largo for data logging. A summary of the instrument deployment is given in Table 1, and the physical layout of the instruments is shown in Fig. 2. Details of the deployments, data acquisition, and instrument specifications can be found in Davis (2008).

In measuring grazing we chose to focus on phytoplankton for two reasons: from a biogeochemical point of view,

Table 1. Instrument deployment.

| Instrument | Details | Location |
|---------------------------|------------------------------------|----------------------------|
| 600-KHz RDI ADCP | 3–27 mab; 2-m bins | Deep S4 (32-m depth) |
| 1200-KHz RDI ADCP (×3) | 1.1–12.1 mab; 0.25-m bins | Control volume, 15-m depth |
| Thermistor chain (SBE 39) | 1, 3, 6, 9, 12, 18, 21, 24, 27 mab | Deep S4, 32-m depth |
| Thermistor chain (SBE 39) | 0, 4, 8, and 12 mab | Control volume, 15-m depth |
| Nortek Vector ADV | 0.3, 0.6, 1.5, and 3 mab | Control volume, 15-m depth |

benthic consumption of phytoplankton over fore-reefs exposed to open-water currents is almost entirely an import of allochthonous nutrients, and logistically the quantification of phytoplankton biomass is relatively simple using the concentration of extracted Chl *a* (Holbrèque et al. 2006; Genin et al. 2009).

Concentrations of Chl *a* were typically less than 1 mg m⁻³. Chl *a* measurements were made by collecting 600-mL samples of water through an array of four lines of samplers attached to taut-line moorings and connected via 9.5-mm inner diameter plastic tubing to a sampling box located at 24 m in depth (Fig. 3). Originally designed to provide data for the control volume (CoVo) method described by Genin et al. (2009), the sampling ports were distributed over the depth, with a higher density of samplers near the bottom in order to resolve the concentration boundary layer. The CoVo was aligned with its long axis aligned north to south, reflecting the orientation of the local topography where it was deployed. The sampling box was connected to the surface via a reinforced hose, thus creating a net suction of 2.4 atm for the 20 sample lines that were connected to the box. Originally, two boxes were built, sampling from 40 lines (10 on each mooring), but as a result of equipment failure, only one box was operational, making it possible to sample no more than 20 lines. Thus, on each corner of the CoVo we had sample intakes at heights of 0.02, 0.3, 1.0, 2.0, and 9.5 mab. While the sample lines were designed to be identical in length, making the frictional loss and, thus, the flow rate in each line as similar as possible, small drip irrigation valves were added to enable flow rates to be

adjusted by divers in situ to match the filling rates of all samples.

Operationally, the box was first purged of water using air from a scuba cylinder; next, individual sample bottles were placed inside the box by divers; the box was closed and then allowed to return to atmospheric pressure; and, finally, the sample line valves were opened, allowing the sample bottles to be filled over a 30-min period to average out turbulent fluctuations in concentration. Once the bottles were filled, they were transported by divers to the surface for immediate filtration of 300 mL per sample, first through a 65- μ m nylon mesh and then by a 0.7- μ m GF/F filter. With its nominal 0.7- μ m pore size, this filter retained almost all phytoplankton cells, including *Prochlorococcus* (A. Post unpubl.). Immediately after filtration, the filters were immersed in 90% acetone solution for 24 h, cold (4°C), dark extraction, followed by a fluorometric measurement of Chl *a* and phaeopigments using the acidification method with a precalibrated fluorometer (10-AU-005, Turner Designs), as described in Yahel et al. (1998).

Results

The period during which our grazing rate measurements were made (17–19 July 2005 = days 198–200) was unusual in that it coincided with a period of weak currents and relatively little internal wave activity (Fig. 4), an apparent consequence of Hurricane Dennis, a Category 4 storm, which passed over the eastern Caribbean between 06 July and 09 July (days 187–190). The hurricane produced a significantly deeper mixed layer throughout the region (Manzello et al. 2007), reducing temperature variability due to internal waves at the relatively shallow depths of the Conch Reef.

Despite the relatively weak internal wave activity during the period of our experiments, some of the sampling runs were made during periods of internal wave-induced stratification and cross-shore flows (Fig. 5). Overall, current velocities varied between 0 and 35 cm s⁻¹. Currents in the CoVo (15 m in depth) were well correlated with, but weaker than, those at the deeper (32-m) station, in contrast to the common assumption that velocities on reefs are weaker at depth (Lesser 2006). Flow speeds at 1 mab during our water sampling varied between 1 and 15 cm s⁻¹.

The few internal wave cooling events that occurred during the experiment created weak, transient stratification. Given limited (0 and 4 mab) near-bed temperature resolution, to estimate the potential importance of stratification, we calculated the Richardson number using near-bottom shear and stratification (Turner 1973)

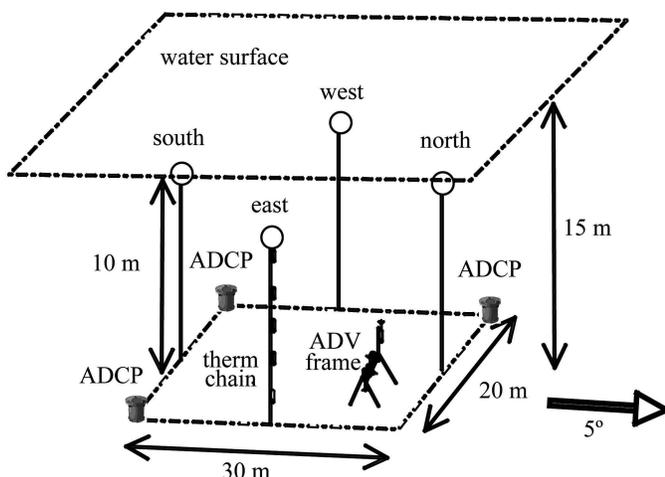


Fig. 2. Instrument layout in control volume. The arrow points north; the CoVo was aligned approximately north-south.

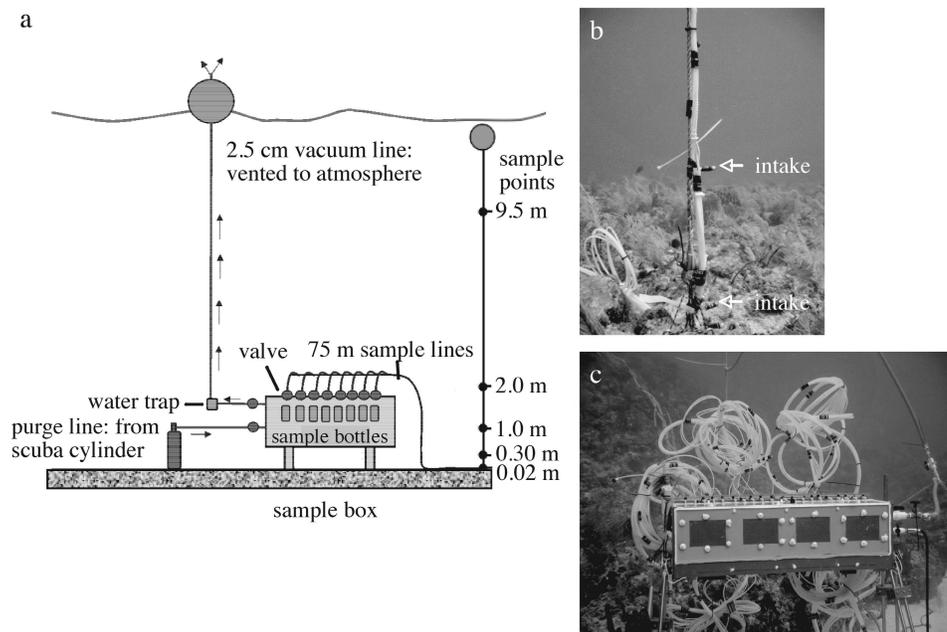


Fig. 3. Samplers and pump setup: (a) sketch; (b) detail of sampling port; and (c) the sampling box.

$$Ri = \frac{N^2}{S^2} \approx \frac{1}{\rho} \frac{\Delta\rho g}{\Delta z} \left(\left(\frac{\partial U}{\partial z} \right)^2 + \left(\frac{\partial V}{\partial z} \right)^2 \right)^{-1} \quad (1)$$

where $\Delta\rho$ was computed using the difference between the temperatures at 0 and 4 mab, so that the change in height above bed z , $\Delta z = 4$ m, and the velocity shears below 2 mab were computed as the difference between ADCP speeds measured at 1 and 2 mab.

Using Eq. 1, we estimate that during only two of the sample runs did Ri exceed 0.25 (i.e., for nearly all of the runs, the near-bottom samplers were probably within the bottom well-mixed layer, rendering applicable the law of the wall [Reidenbach et al. 2006] as a description of near-bed flows). As described below, this assumption is important for the use of eddy diffusivities to calculate fluxes to the bed.

The depth-averaged Chl a concentration varied substantially in time and space during the runs (Fig. 6). Regardless of flow direction, the east and south sampling lines consistently recorded higher concentrations than did the north and west lines. Chl a data at each height above the bed were averaged with data at the corresponding height in all moorings, yielding an average vertical profile for each run, in essence using the multiple profiles to help average out some of the effects of small-scale spatial heterogeneity. These profiles (Fig. 7) show a reduction of Chl a concentration near the bed (i.e., the existence of concentration boundary layers over the reef). This trend is most clearly seen in the overall average profile (Fig. 8), showing a near-bed reduction in concentration of approximately 10% relative to 1–2 mab.

While the vertical resolution of the Chl a profiles along their upper portion was poor, the data indicate a decline of

Chl a concentration near the sea surface, probably as the result of a lower Chl a :carbon ratio at that strongly illuminated layer (Geider et al. 1997). While the decrease in Chl a concentrations with height above 1 mab is indicative of sedimentation effects, this is not likely given the sinking velocities of the small (diameter [d] $< 1 \mu\text{m}$) phytoplankton (e.g., *Synechococcus* and *Prochlorococcus*) that typically comprise the phytoplankton community of oligotrophic waters such as those of the Florida Straits (Lindell and Post 1995; Holbrèque et al. 2006). This can be justified using the results of Eppley et al. (1967), whose plot of sinking velocity vs. cell size (their fig. 3) indicates that for the $d \sim 1 \mu\text{m}$, $W_s < 0.1 \text{ m d}^{-1}$ (i.e., far less than the values of α we calculated from our data). We will return to this point below. Consistent with enhanced benthic grazing, the concentration of phaeopigments, a product of Chl a digestion by grazers (Welshmeyer and Lorenzen 1985), was higher near the bed (Fig. 9). Since phaeopigments are also produced by bacterial cell lysis (Bianchi et al. 2002), their increase near the bed could have been partly due to resuspension of phaeopigment-rich particles.

Determination of the grazing rate—Data from the 14 CoVo runs can be used to determine grazing rates using the Reynolds averaged scalar conservation equation for dissolved or suspended materials:

$$\frac{\partial C}{\partial t} + \nabla \cdot (\vec{U}C) - \frac{\partial}{\partial z} (W_s C) \cong - \frac{\partial}{\partial z} (\overline{w\epsilon}) \quad (2)$$

in which uppercase variables are Reynolds (time) averages of the concentration (C) and velocity [$\vec{U} = (U, V, W)$], lowercase variables represent turbulent fluctuations of concentration (c) of the suspended material, and where

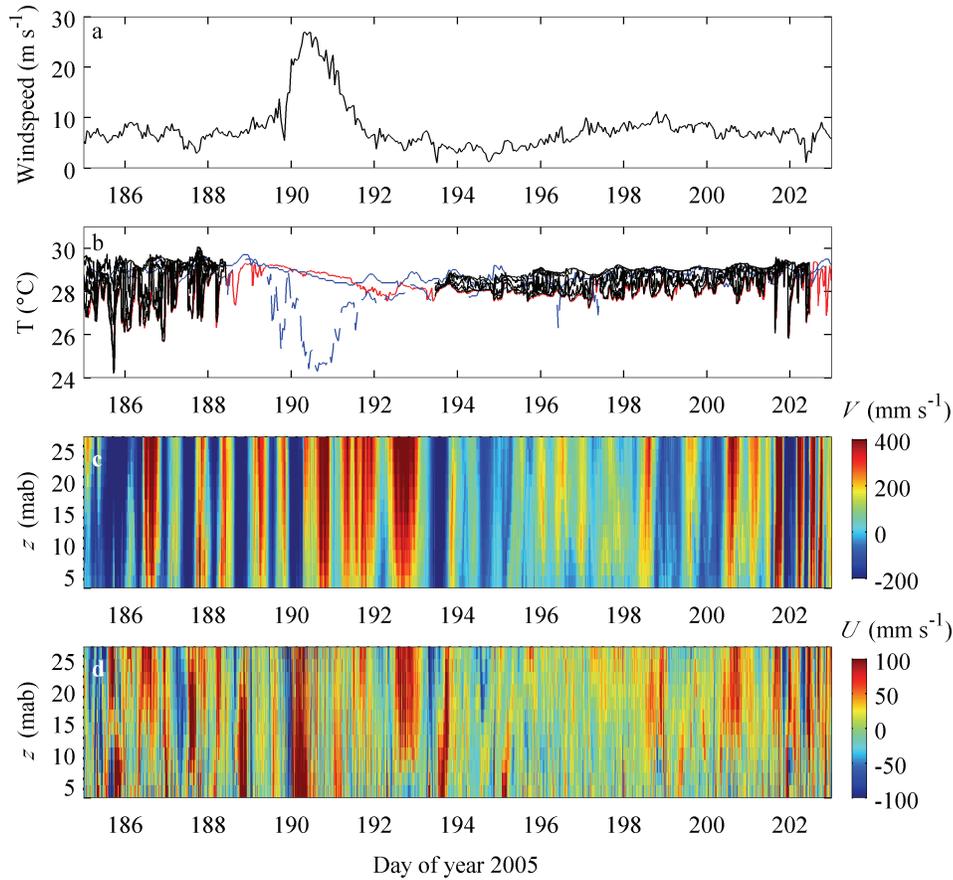


Fig. 4. Conditions at Conch Reef, July 2005: (a) wind speed measured at Sand Key Reef (NOAA Station SANF1); (b) temperatures measured at the 32-m-deep site on Conch Reef by the thermistor chain (solid line) and by the ADCP (red line), on the surface at Sand Key (dashed blue line), and in the air at Sand Key (solid blue line); (c) alongshore velocity at the 32-m site; and (d) cross-shore velocity at the 32-m site. Note that the thermistor chain was removed from the water between days 188 and 194 to prevent its damage by Hurricane Dennis.

velocity $\vec{u} = (u, v, w)$, W_s is the settling velocity of the suspended material, t is time, z is height above the bed, and the overbar in the last term represents the time average of the vertical flux of the suspended material. Note that W is generally assumed to be small so that it can be neglected (Savarese et al. 1997). When applied to phytoplankton, Eq. 2 neglects growth, respiration, and grazing in the water column (Genin et al. 2009). As discussed in Butman et al. (1994), benthic grazing is usually represented as a vertical flux to the bed at velocity α :

$$-W_s C + \overline{w\bar{c}} = -W_s C - \varepsilon_t \frac{\partial C}{\partial z} = -\alpha C_0 \quad (3)$$

where all variables, C , $\overline{w\bar{c}}$, and $\partial C/\partial z$ are evaluated at $z = 0$ and where C_0 is the concentration at some reference height above the bed. The representation of grazing in terms of C_0 is different than what is used in the mass-transfer literature, in which the flux is usually written in terms of the free-stream concentration. This is done because C tends to vary over the whole water column such that there is no free-stream concentration. In some cases, C_0 is taken to be the concentration at the bed, C_b , although this form cannot be

used to represent grazing at the bed (see Eq. 7). In practical terms, since C usually varies by ca. 10–20%, at most, at practical measurement heights, the exact choice of the concentration for normalization of the grazing flux does not significantly influence the computation of α from data.

Assuming a log-profile (i.e., the law of the wall) for the time-averaged velocities and a linear near-bed stress profile, the eddy diffusivity, ε_t , can be written for the region near the bed as follows (Fischer et al. 1979):

$$\varepsilon_t = \kappa U_* z \quad (4)$$

where $\kappa = 0.4$ is the von Karman constant and where the shear velocity is defined in terms of the bed stress, $u_*^2 = C_D(U_1^2 + V_1^2)$, computed using a drag coefficient, C_D , and the speed measured 1 m above the bed. The basis for assuming that law-of-the-wall diffusivities apply is the measurement of the boundary layer structure reported in Reidenbach et al. (2006). They showed that flow over a similarly rough coral reef obeyed the law of the wall in terms of turbulence dynamics (e.g., the dependence of turbulence dissipation rates on shear velocity and height matched predictions based on the law of the wall).

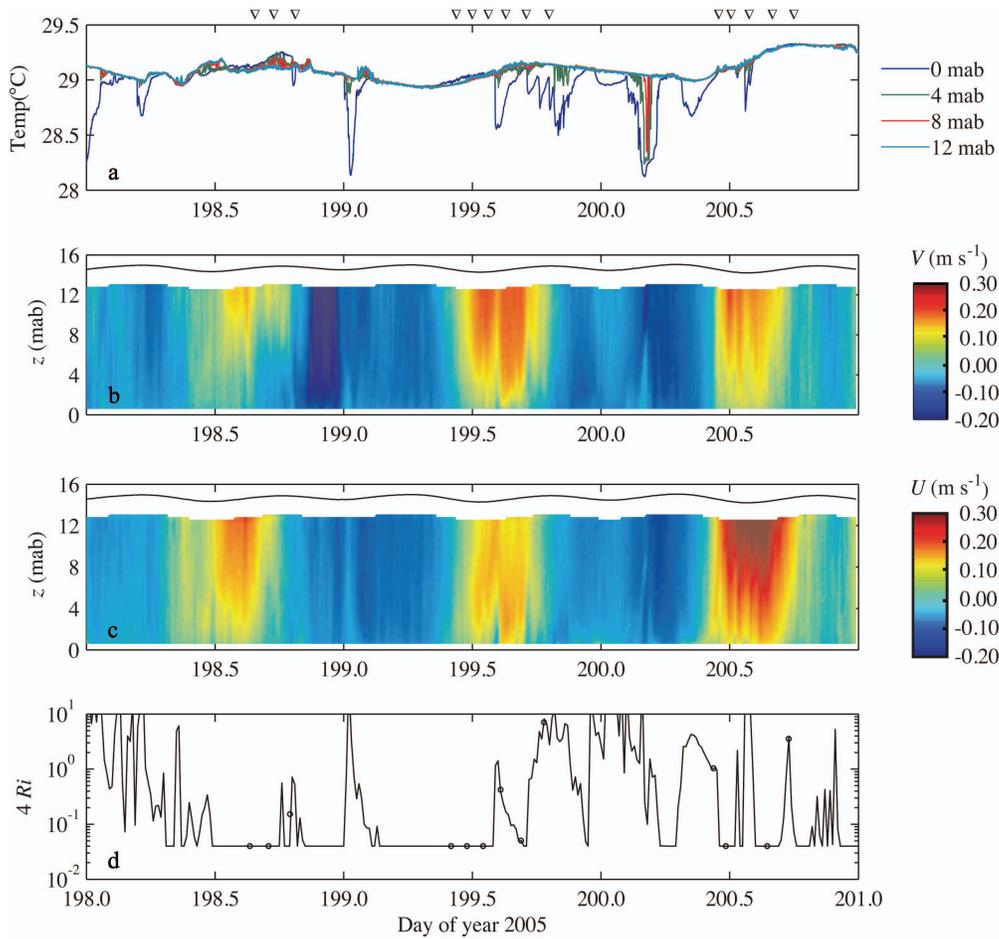


Fig. 5. Flow conditions in control volume during grazing experiments: (a) temperatures—line colors shown in the legend mark the heights of the thermistors; (b) north velocity; (c) east velocity; and (d) near-bottom stability (open circles mark times of sample runs). The nablas above (a) mark times of the CoVo runs.

In the absence of grazing, Eq. 3 yields the Rouse profile (Vanoni 2006),

$$C(z) = C(z_r) \left(\frac{z}{z_r} \right)^{-W_s/\kappa u_*} \quad (5)$$

where $C(z_r)$ is the concentration measured at height z_r . It is possible to fit the decline in concentration between 1 and 2 mab with Eq. 5 and $W_s = 10 \text{ m d}^{-1}$. However, this is ca. 100 times larger than the largest values reported by Eppley et al. (1967) for $1\text{-}\mu\text{m}$ phytoplankton cells and so is not likely to explain this aspect of the observations.

There are two methods by which Eqs. 2 and 3 can be used to compute α . Both assume steady state. The first is the CoVo approach described by Genin et al. (2009), a method that uses integration of Eq. 2 over a box extending from the bed to the water surface. The flux to the bed is computed from the difference between the horizontal advective fluxes into and out of the box or control volume. The second approach (Ackerman et al. 2001) is to compute α using Eqs. 3 and 4 (i.e., to measure the concentration gradient and to assume both a sinking velocity and an eddy diffusivity based on measured shear velocities).

The sampling arrays were intended to enable us to compute fluxes using the CoVo method; however, attempts at calculating α using this method gave inconsistent results because the south and east sampling arrays showed concentrations that were consistently substantially different than the north and west arrays, regardless of flow direction. This bias appears to occur because of the proximity of the south and east moorings to the edge of the plateau, where they often sampled offshore water that had not passed over the reef. In effect, the array of samplers did not adequately resolve the concentration field on the faces of the CoVo, thus rendering the method inaccurate. Therefore, to minimize sampling requirements, CoVos must be sited in locations that are reasonably spatially homogeneous.

To compute grazing rates, we used instead Eqs. 3 and 4 (with $W_s = 0$). One approach to computing α from data is to write Eq. 3 in finite difference form as

$$\alpha \simeq \frac{1}{C_b} \left(\frac{\kappa u_*}{2} (z_1 + z_2) \frac{C_2 - C_1}{z_2 - z_1} \right) \quad (6)$$

where C_1 and C_2 are the concentrations at heights z_1 and z_2 , respectively. However, as pointed out to us by one of the

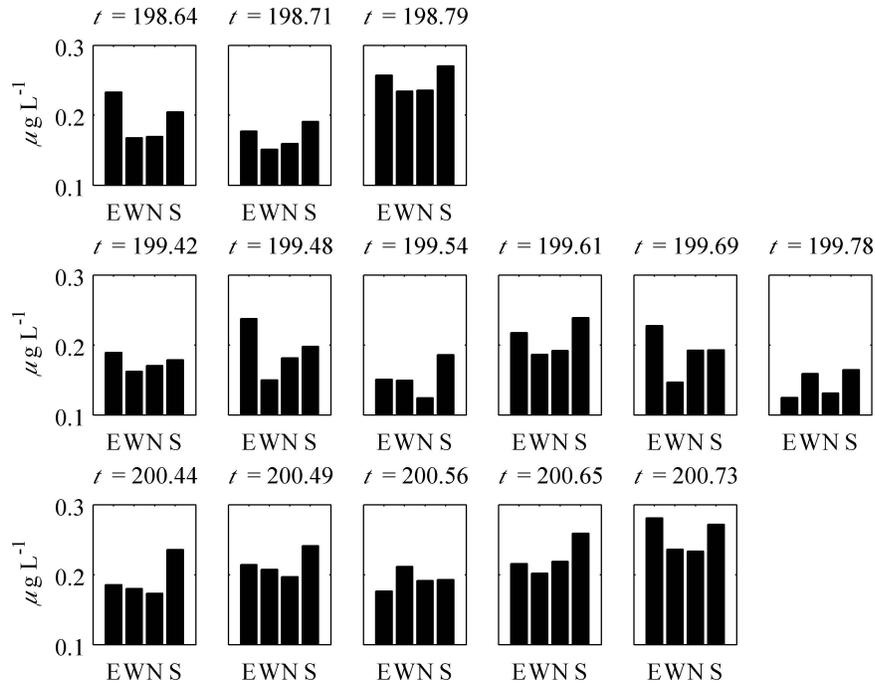


Fig. 6. Spatial variation of depth-averaged Chl *a* concentrations. The first row shows runs from 17 July 2005, the second runs from 18 July 2005, and the third runs from 19 July 2005. Letters refer to the sampling line (east, west, north, and south) to which each bar applies.

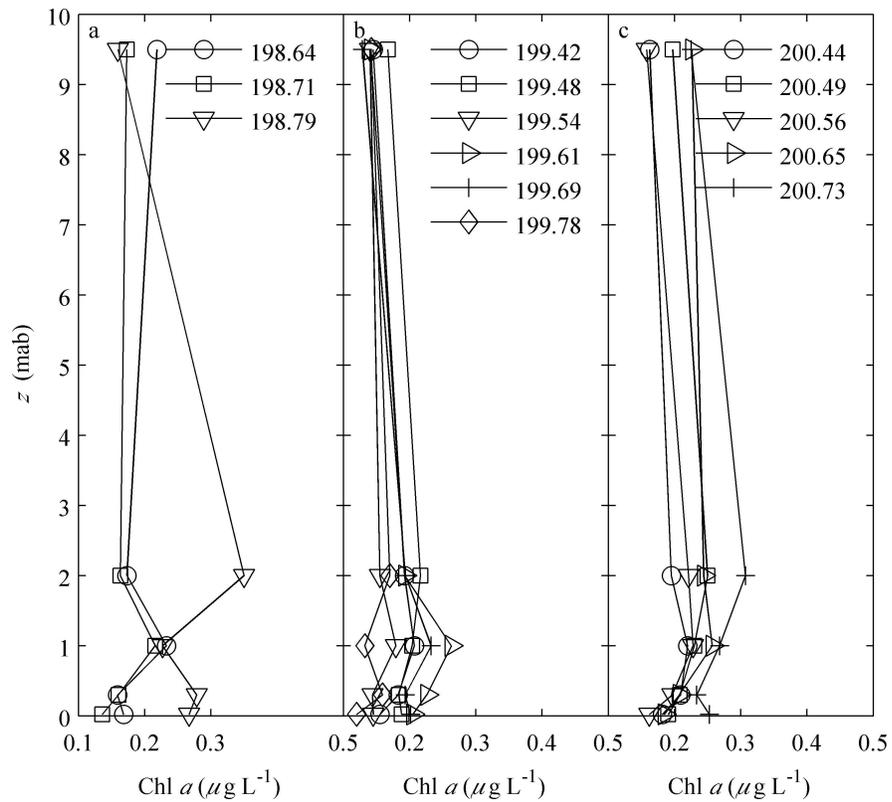


Fig. 7. Average Chl *a* profiles from each run: (a) 17 July; (b) 18 July; and (c) 19 July. Times as indicated in legends.

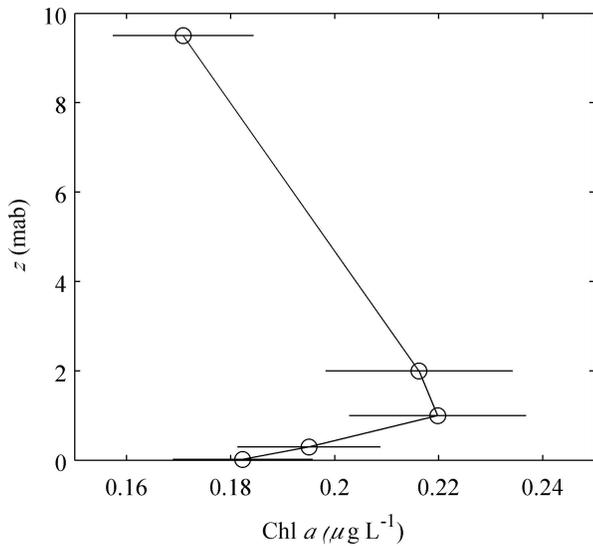


Fig. 8. Average profile for Chl *a* concentration over all locations and all runs. The symbols mark the averages of all 14 runs; the error bars show the uncertainty in the mean at the 95% confidence level.

referees, and as described in Jones et al. (2009), if the flux to the bed is assumed to be independent of height, Eq. 3 can be integrated to find

$$C = C_b + \frac{\alpha C_b}{\kappa u_*} \log\left(\frac{z}{z_c}\right) \quad (7)$$

where we have chosen C_b to be the concentration at height z_c . Jones et al. (2009) found α by fitting Eq. 7 to their measured concentration profiles. In this case,

$$\alpha = \kappa u_* \frac{(C_2 - C_1)}{C_b} \left[\log\left(\frac{z_2}{z_1}\right) \right]^{-1} \quad (8)$$

The ratio of the estimate in Eq. 8 to that in Eq. 6 is approximately $1/2 \log(z_2/z_1)$ if $z_2 \gg z_1$. Based on the profiles shown in Figs. 7 and 8, we chose $z_1 = 0.02$ mab and $z_2 = 1$ mab, so that this ratio would be approximately 2. However, the profiles we observed are not particularly well described by Eq. 7; indeed, as seen in Fig. 8, the profile in the bottom meter appears to be nearly linear. This pattern may be the effect of the rough bottom topography at Conch Reef and, more importantly, of tall suspension feeders such as the common barrel sponges *Xestospongia muta* (Southwell et al. 2008), whose feeding takes place over a finite region above the bed.

Thus, a more complete model of grazing would be one in which the flux takes the form

$$\begin{aligned} \kappa u_* z \frac{dC}{dz} &= \alpha C_0 (a + b(z/h_c)) \quad z \leq h_c \\ &= \alpha C_0 \quad z > h_c \end{aligned} \quad (9)$$

(i.e., there is a layer near the bed of thickness h_c in which the grazing takes place such that the fraction a of the total grazing takes place at the bed and the fraction b is

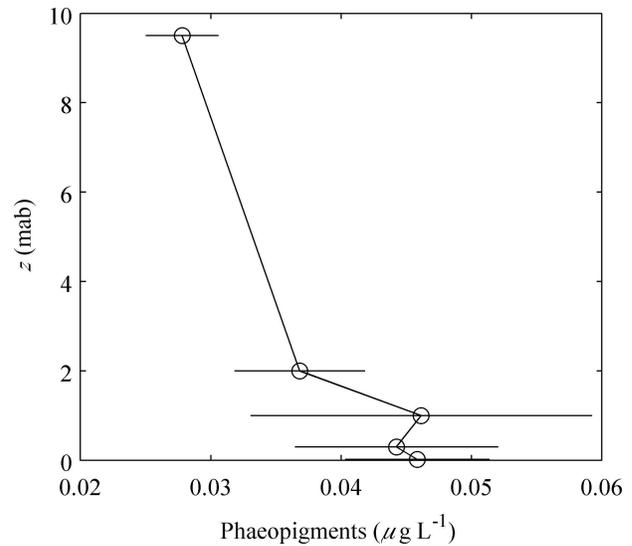


Fig. 9. Average profile for phaeopigment concentration. The symbols mark the averages of all 14 runs; the error bars show the uncertainty in the mean at the 95% confidence level.

distributed uniformly over the depth). Note that $a + b = 1$. We have written Eq. 9 in terms of αC_0 , taking C_0 to be the concentration at $z = h_c$ because as seen in Eq. 7, the bed concentration is not defined for the case $a \neq 0$. Equation 9 can be integrated to find

$$\begin{aligned} C &= C_0 \left(1 + \frac{\alpha}{\kappa u_*} \left\{ a \ln\left(\frac{z}{h_c}\right) - b \left(1 - \frac{z}{h_c}\right) \right\} \right) \quad z \leq h_c \\ C &= C_0 \left(1 + \frac{\alpha}{\kappa u_*} \ln\left(\frac{z}{h_c}\right) \right) \quad z > h_c \end{aligned} \quad (10)$$

If $a = 1$, the grazing is concentrated at the bottom, and the profile is logarithmic over the entire depth. On the other hand, if $b = 1$, the grazing is all distributed over the bottom layer, and the concentration varies linearly in this layer and logarithmically above. Sample profiles with $(C_0, \alpha, u_*, h_c) = (0.205, 50 \text{ m d}^{-1}, 1.2 \text{ cm s}^{-1}, 0.5 \text{ m})$ and $a = 1$ or $b = 1$ are shown in Fig. 10. These values of the parameters have been chosen to match the average of the observed data. Clearly, the case $a = 1$ does not match the observations, whereas the case $b = 1$ matches well. Note that for the case $b = 1$, we can compute the total grazing flux as

$$Flux \simeq \kappa u_* h_c \left. \frac{dC}{dz} \right|^{z=h_c} \simeq \kappa u_* h_c \frac{\Delta C}{\Delta z} \quad (11)$$

For $h_c = 0.5$ m, the values of α computed using Eq. 11 are the same as those that would be computed using the finite difference expression, Eq. 6. A second plausible fit (not shown) has $(C_0, \alpha, u_*, h_c) = (0.22, 75 \text{ m d}^{-1}, 1.2 \text{ cm s}^{-1}, 1 \text{ m})$ and a flux that measures twice that which would be computed using Eq. 6. Values of $h_c < 0.5$ tend to show too much curvature in the C profile near the bed. Moreover, the heights of soft corals and sponges in the CV were typically in the 0.5 to 1-m range. Thus, values of h_c in the range of 0.5 to 1 m would seem to be plausible. Finally, numerical integration of Eq. 9, including $W_s = 5 \text{ m d}^{-1}$

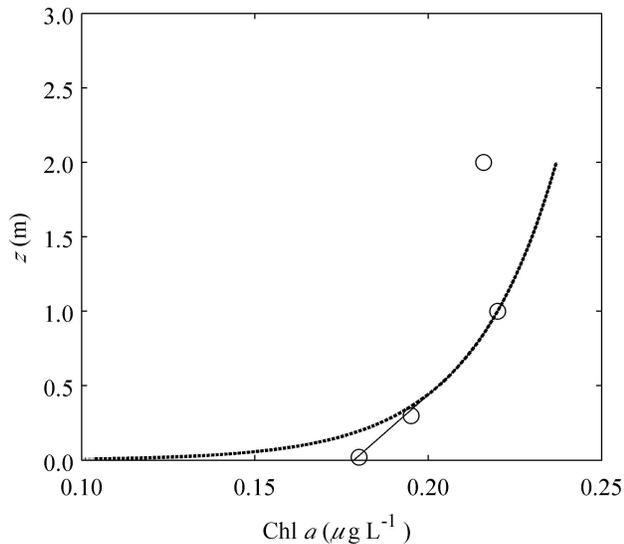


Fig. 10. Model calculations of Chl *a* profiles including distributed grazing. Average data from all runs are shown as open circles; theory with all the grazing occurring on the bottom is represented by the dashed line, whereas theory with all of the grazing being distributed over a layer of 0.5-m thickness is represented by the solid line. C_0 and α have been chosen to match the observations.

(not shown), differed little in the bottom boundary layer from the profile computed assuming $W_s = 0$.

In light of the discussion above, it would appear that our values of α may have a systematic uncertainty of $\pm 50\%$ with the two models bounding the simple finite difference values (Eq. 6), with the data better matching the model with distributed grazing. Thus, in the absence of more detailed information about grazing distributions, and possibly the details of near-bed mixing in canopy-type flows, we decided that the simplest approach would be to use Eq. 6. Pursuing this approach, the shear velocity was computed using a value of $C_D \approx 0.017 \pm 0.0006$, determined from least-squares fitting of the ADV stress measurements at 0.6 mab with the ADCP speed at 1 mab. The precision of C_D is much greater than the individual stress estimates, which we estimate to be $\pm 50\%$ (Davis 2008). The median grazing rate from these calculations was $\alpha = 48 \pm 20 \text{ m d}^{-1}$, with the uncertainty at the 95% level estimated using bootstrapping. Note that α values show a significant ($p = 0.013$) linear correlation with u_* ($r = 0.64$; Fig. 11). This reflects the fact that the group $1/C_0 (C_2 - C_1) = 0.2 \pm 0.085$ (95% level) was effectively constant, with no significant dependence of this group on u_* .

Discussion

The values of α shown in Fig. 11 can be compared with an estimate of grazing by sponges alone, based on information on their abundance and pumping rates, measured at Conch Reef by Southwell et al. (2008). In order to estimate the total pumping rates by sponges per square millimeter of reef, we use the data of Southwell et al. to calculate the allometric relationships ($r^2 = 0.93$) between the volume (V) of the individual sponge and its pumping

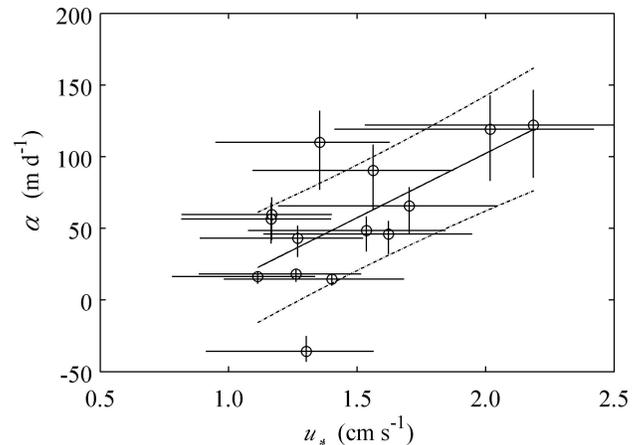


Fig. 11. Result for grazing rate, α , as a function of u_* . The dashed lines mark the 95% confidence intervals for the linear regression (solid line). Uncertainties in α and u_* are based on an estimated uncertainty of $\pm 50\%$ in the measured Reynolds stresses.

rate (Q), thus

$$Q = 282 V^{0.93} \quad (12)$$

Using Eq. 12 and benthic survey data, we found a grazing rate of 24 m d^{-1} due to sponges, about half of which is accounted for by large barrel sponges (*Xestospongia muta*). This value is lower than the $\alpha = 48 \pm 20 \text{ m d}^{-1}$ found in this study. Recall, however, that the individual-based calculations did not account for other benthic phytoplanktivores, such as soft corals, gorgonians, bivalves, tunicates, and worms.

A lower grazing rate, $\alpha \approx 20 \text{ m d}^{-1}$, and a similar discrepancy, with a lower estimate (5.6 m d^{-1}) based on the abundance and pumping rate of benthic phytoplanktivores, were found by Genin et al. (2009) for the coral reef of Eilat in the Red Sea. It is not surprising that grazing is higher on Conch Reef, given the much higher abundance of grazers (sponges, bivalves, and tunicates). In a like fashion, the data given in Savarese et al. (1997) give $\alpha \approx 13 \text{ m d}^{-1}$ for a dense assemblage of sponges in Lake Baikal. The lower grazing values obtained from the abundance and pumping rates of benthic phytoplanktivores can be explained by the fact that neither passive filter feeders (e.g., gorgonians, soft corals, polychaetes, bryozoans) nor some abundant active filter feeders (e.g., bivalves, tunicates) were included in the benthic survey used in our calculations.

The values of α that we obtained for Conch Reef equate to a removal process for the whole 15-m water column, with a time constant of 0.1–0.3 d. Given that typical doubling times for phytoplankton growth in the oligotrophic waters of the Florida Keys might be 1–2 d (Fiechter and Mooers 2007), it appears that benthic grazing on the reef is faster than local primary production and so requires the import of organic carbon to the reef from offshore waters. Given that the reef is ca. 300 m wide, this equates to a required flow across the reef per unit length of reef of $300 \text{ m} \times 0.0012 \text{ m s}^{-1} (100 \text{ m}^{-1}) \approx 0.4 \text{ m}^2 \text{ s}^{-1}$, comparable to, but smaller than, the value we estimate from our ADCP data, $1.4 \text{ m}^2 \text{ s}^{-1}$ (Davis 2008). Nonetheless, this also points

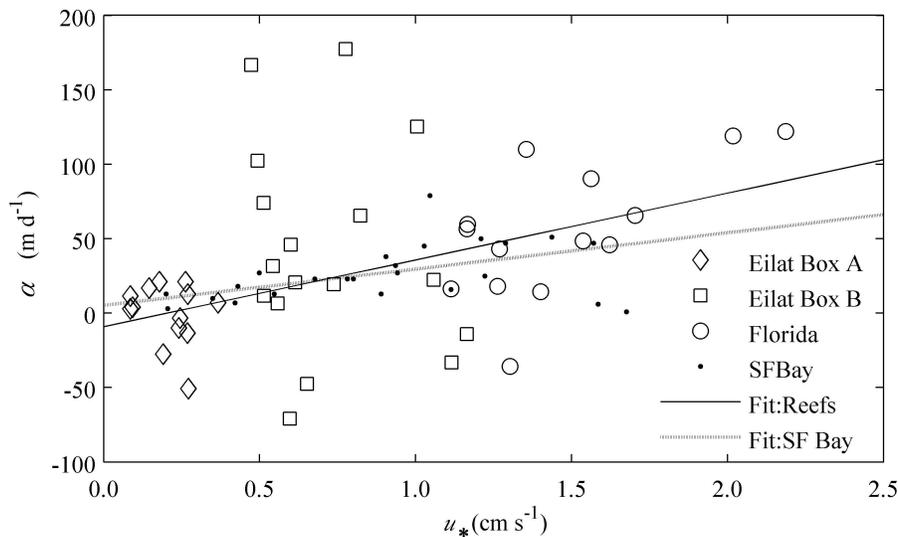


Fig. 12. Grazing data from Eilat (open diamonds and squares), Florida (open circles), and San Francisco Bay (closed diamonds). The solid line represents the best-fit line from robust regression for the combined reef data, whereas the dashed line represents the best-fit line from robust regression for the San Francisco Bay soft bottom community.

out the importance of the internal waves observed at Conch Reef: they increase offshore–onshore exchange and especially the supply of plankton-rich waters to the reef from the deeper subsurface maximum of phytoplankton biomass (Leichter et al. 1996).

Benthic grazing rates similar to those observed at Conch Reef were found by Jones et al. (2009) for a soft bottom benthic community in San Francisco Bay ($\alpha \approx 40 \text{ m d}^{-1}$ for $u_* \approx 1.5 \text{ cm s}^{-1}$). It should be noted that the CoVo-based estimate of Jones et al. was in good agreement with the rate computed using profiles and the law of the wall, reassuring the adequacy of the latter approach, which was used in this study. This point is further supported by comparing the grazing rates measured at all three sites—Conch Reef, Eilat, and San Francisco Bay (Fig. 12). Robust linear regression (Maronna et al. 2006) carried out using the curve-fitting toolbox in MatlabTM shows that for the combined Florida and Eilat data at the 95% level, $\alpha = (-14 \pm 21) + (61 \pm 25)u_*$, where α is given in meters per day and u_* is given in centimeters per day. In this case, robust fitting is useful in reducing the effect of the high noise in the Eilat data, noise that appears to be due to the lack of averaging of the samples (Genin et al. 2009). This relation is similar to what we find for the soft bottom case, although it appears that grazing by the reef community is more strongly dependent on u_* . The stronger dependency may reflect active pumping by sponges, which tends to increase near-bed mass fluxes as well as the canopy-like nature of the reef roughness, which permits flow in and amongst the roughness elements, further enhancing mass transfer.

Strictly speaking, α determined as above or by the CoVo method is a measurement of the flux to the bed and so *could* reflect deposition rather than grazing. However, given that anything deposited on the bed would tend to be resuspended, with the rate of resuspension increasing with flow velocity, one would not expect to see fluxes to the bed that

increase with flow. Thus, we argue that the fluxes we observed are indeed the results of grazing.

Examining our results in terms of food web dynamics (Lesser 2006), it is important to note that the phytoplankton we sampled are by no means the only, perhaps not even the major, source of organic carbon for the Conch Reef benthos. Trussell et al. (2006) and Lesser (2006) found that heterotrophic bacteria dominated the biomass of particles grazed by sponges during their experiments at Conch Reef. In contrast, for water samples taken at several locations in the Florida Keys, Hoch et al. (2008) found that bacteria constituted about 30% of the planktonic biomass (expressed as carbon), as did Holbrèque et al. (2006) for a reef atoll in the Indian Ocean. In any case, since fluxes are normalized by concentration, we can use the measured Chl *a* as a ‘tracer’ for computing the grazing velocity α . The value of α so obtained will be a lower bound, since measured fluxes include implicitly the efficiency of particle retention, which can depend on particle size (Pile et al. 1997) or other cell characteristics (Yahel et al. 2009). Thus, for situations in which complete measurements of particulate organic carbon are available (i.e., not just phytoplankton), our results can be used to evaluate the total flux of carbon to the bed from planktonic particles.

Despite the substantial difference between benthic communities, bottom roughness, etc., when mass flux is scaled by u_* , phytoplankton flux to the reefs does not appear to be very different from that to a muddy soft bottom community. As Atkinson and colleagues have found to be the case for nutrients, and as found in small flume by Ribes and Atkinson (2007), this shows that hydrodynamic processes can limit the flux of plankton to the benthos. While the mass transfer rate is also a function of the concentration of particles in the water, given that larger roughness produces higher rates of mass transfer, as the benthos becomes more rugged, it can support a higher

biomass of grazers. Likewise, more energetic flow environments would also appear to be able to support higher benthic biomass. Support for this hypothesis comes from the fact that flows on Conch Reef are, in general, several times faster than flows on the Eilat Reef, enabling the support of a biomass of grazers on Conch Reef that is several times larger than that on the Eilat Reef.

Our measurements of grazing on Conch Reef consistently show the presence of concentration boundary layers over the reef. Combining these data with measurements of near-bed flows and turbulence, we find benthic grazing rates that are flow dependent. Thus, as seen for mass transfer of nutrients to the reef, the flux of phytoplankton biomass depends on flow, because mixing near the bed controls transfer to grazers. As a consequence, the roughness of the reef, an intrinsic feature of coral reefs, influences coupling of the reef to the ocean above (i.e., the rougher the reef, the higher will be the flux of any suspended materials to the reef). Thus, it would appear that reefs with large roughness and/or energetic currents should be able to support higher biomasses of benthic organisms than would low-relief reefs, or reefs in sluggish waters.

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References

- ACKERMAN, J. D., M. R. LOEWEN, AND P. F. HAMBLIN. 2001. Benthic-pelagic coupling over a zebra mussel reef in western Lake Erie. *Limnol. Oceanogr.* **46**: 892–904.
- ATKINSON, M. J., AND R. W. BILGER. 1992. Effects of water velocity on phosphate uptake in coral reef-flat communities. *Limnol. Oceanogr.* **37**: 273–279, doi:10.4319/lo.1992.37.2.0273
- AYUKI, T. 1995. Retention of phytoplankton and planktonic microbes on coral reefs within the Great Barrier Reef, Australia. *Coral Reefs* **14**: 141–147, doi:10.1007/BF00367231
- BIANCHI, T. S., C. ROLFF, B. WIDBOM, AND R. ELMGREN. 2002. Phytoplankton pigments in Baltic Sea seston and sediments: Seasonal variability, fluxes, and transformations. *Estuar. Coast. Shelf Sci.* **55**: 369–383, doi:10.1006/ecss.2001.0911
- BUTMAN, C. A., M. FRECHETTE, W. R. GEYER, AND V. R. STARCZAK. 1994. Flume experiments on food-supply to the blue mussel *Mytilus-edulis*-L as a function of boundary-layer flow. *Limnol. Oceanogr.* **39**: 1755–1768, doi:10.4319/lo.1994.39.7.1755
- DAVIS, K. A. 2008. Dynamics of internal waves on the Southeast Florida shelf: Implications for cross-shelf exchange and turbulent mixing on a barrier reef system. Ph.D. thesis. Stanford Univ.
- , J. J. LEICHTER, J. L. HENCH, AND S. G. MONISMITH. 2008. Effects of western boundary current dynamics on the internal wave field of the Southeast Florida shelf. *J. Geophys. Res.* **113**: C09010, doi:10.1029/2007JC004699
- EPPLEY, R. W., R. W. HOLMES, AND J. D. H. STRICKLAND. 1967. Sinking rates of marine phytoplankton measured with a fluorometer. *J. Exp. Mar. Biol. Ecol.* **1**: 191–208, doi:10.1016/0022-0981(67)90014-7
- EREZ, J. 1990. On the importance of food sources in coral reef ecosystems, p. 411–418. *In* Z. Dubinsky [ed.], *Coral reefs*. Elsevier.
- FIECHTER, J., AND C. N. K. MOOERS. 2007. Primary production associated with the Florida Current along the East Florida Shelf: Weekly to seasonal variability from mesoscale-resolution biophysical simulations. *J. Geophys. Res.* **112**: C12002, doi:10.1029/2006JC003576
- FINELLI, C. M., B. S. T. HELMUTH, N. D. PENTCHEFF, AND D. S. WETHEY. 2006. Water flow influences oxygen transport and photosynthetic efficiency in corals. *Coral Reefs* **25**: 47–57, doi:10.1007/s00338-005-0055-8
- FISCHER, H. B., E. J. LIST, R. C. Y. KOH, J. IMBERGER, AND N. H. BROOKS. 1979. Mixing in inland and coastal waters. Academic Press.
- GARDNER, T. A., I. M. CÔTÉ, J. A. GILL, A. GRANT, AND A. R. WATKINSON. 2003. Long-term region wide declines in Caribbean corals. *Science* **301**: 958–960, doi:10.1126/science.1086050
- GEIDER, R. J., H. L. MACINTYRE, AND T. M. KANA. 1997. Dynamic model of phytoplankton growth and acclimation: Responses of the balanced growth rate and the chlorophyll *a*: carbon ratio to light, nutrient-limitation and temperature. *Mar. Ecol. Prog. Ser.* **148**: 187–200, doi:10.3354/meps148187
- GENIN, A., S. G. MONISMITH, M. A. REIDENBACH, G. YAHIEL, AND J. R. KOSEFF. 2009. Intense benthic grazing in a coral reef. *Limnol. Oceanogr.* **54**: 938–951.
- HOCH, M. P., K. S. DILLON, R. B. COFFIN, AND L. A. CIFUENTES. 2008. Sensitivity of bacterioplankton nitrogen metabolism to eutrophication in sub-tropical coastal waters of Key West, Florida. *Mar. Pollut. Bull.* **56**: 913–926, doi:10.1016/j.marpolbul.2008.01.030
- HOLBRÈQUE, F., B. DELESALLE, J. BLANCHOT, Y. MONTEL, AND C. FERRIER-PAGÈS. 2006. Picoplankton removal by the coral reef community of La Prévoyante, Mayotte Island. *Aquat. Microb. Ecol.* **44**: 59–70, doi:10.3354/ame044059
- JAAP, W. C. 1984. The ecology of the South Florida coral reefs: A community profile. U.S. Fish and Wildlife Service FWS/OBS-82/08. 138 p.
- JONES, N. L., J. K. THOMPSON, K. R. ARRIGO, AND S. G. MONISMITH. 2009. Hydrodynamic control of phytoplankton loss to the benthos in an estuarine environment. *Limnol. Oceanogr.* **54**: 952–969.
- LEICHTER, J. J., S. R. WING, S. L. MILLER, AND M. W. DENNY. 1996. Pulsed delivery of sub-thermocline water to Conch Reef (Florida Keys), by internal tide bores. *Limnol. Oceanogr.* **41**: 1490–1501, doi:10.4319/lo.1996.41.7.1490
- LESSER, M. P. 2006. Benthic-pelagic coupling on coral reefs: Feeding and growth of Caribbean sponges. *Mar. Ecol. Prog. Ser.* **328**: 277–288.
- LEVINTON, J. S. 1995. Marine biology. Oxford Univ. Press.

- LINDELL, D., AND A. F. POST. 1995. Ultraphytoplankton succession is triggered by deep winter mixing in the Gulf of Aqaba (Eilat), Red Sea. *Limnol. Oceanogr.* **40**: 1130–1141, doi:10.4319/lo.1995.40.6.1130
- MANZELLO, D. P., M. BRANDT, T. B. SMITH, D. LIRMAN, J. C. HENDEE, AND R. S. NEMETH. 2007. Hurricanes benefit bleached corals. *Proc. Natl. Acad. Sci. USA* **104**: 12035–12039, doi:10.1073/pnas.0701194104
- MARONNA, R. A., R. D. MARTIN, AND V. J. YOHAI. 2006. Robust statistics: Theory and methods. Wiley.
- PATTERSON, M. R., K. P. SEBENS, AND R. R. OLSON. 1991. In situ measurements of flow effects on primary production and dark respiration in reef corals. *Limnol. Oceanogr.* **36**: 936–958, doi:10.4319/lo.1991.36.5.0936
- PILE, A. J., M. R. PATTERSON, M. SAVARESE, V. I. CHERNYKH, AND V. A. FIALKOV. 1997. Trophic effects of sponge feeding within Lake Baikal's littoral zone. 2. Sponge abundance, diet, feeding efficiency, and carbon flux. *Limnol. Oceanogr.* **42**: 178–184.
- REIDENBACH, M. A., S. G. MONISMITH, J. R. KOSEFF, G. YAHIEL, AND A. GENIN. 2006. Boundary layer turbulence and flow structure over a fringing coral reef. *Limnol. Oceanogr.* **51**: 1956–1968.
- RIBES, M., AND M. J. ATKINSON. 2007. Effects of water velocity on picoplankton uptake by coral reef communities. *Coral Reefs* **26**: 413–421, doi:10.1007/s00338-007-0211-4
- SARGENT, M. C., AND T. S. AUSTIN. 1954. Organic production of an atoll. *US Geol. Soc. Prof. Paper* **260**: E293–E300.
- SAVARESE, M., M. R. PATTERSON, V. I. CHERNYKH, AND V. A. FIALKOV. 1997. Trophic effects of sponge feeding within Lake Baikal's littoral zone. 2. In situ pumping rates. *Limnol. Oceanogr.* **42**: 171–178, doi:10.4319/lo.1997.42.1.0171
- SOUTHWELL, M. W., J. B. WEISZ, C. S. MARTENS, AND N. LINDQUIST. 2008. In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. *Limnol. Oceanogr.* **53**: 986–996.
- TRUSSELL, G. C., M. P. LESSER, M. R. PATTERSON, AND S. J. GENOVESE. 2006. Depth-specific differences in growth of the reef sponge *Callyspongia vaginalis*: Role of bottom-up effects. *Mar. Ecol. Prog. Ser.* **323**: 149–158, doi:10.3354/meps323149
- TURNER, J. S. 1973. Buoyancy effects in fluids. Cambridge Press.
- VANONI, V. A. 2006. Sedimentation engineering: Theory, measurements, modeling, and practice, 2nd ed. American Society of Civil Engineers.
- WELSCHMEYER, N. A., AND C. J. LORENZEN. 1985. Chlorophyll budgets: Zooplankton grazing and phytoplankton growth in a temperate fjord and the Central Pacific gyres. *Limnol. Oceanogr.* **30**: 1–21, doi:10.4319/lo.1985.30.1.0001
- YAHIEL, G., D. MARIE, P. G. BENINGER, S. ECKSTEIN, AND A. GENIN. 2009. In situ evidence for pre-capture qualitative selection in the tropical bivalve *Lithophaga simplex*. *Aquat. Biol.* **6**: 235–246, doi:10.3354/ab00131
- , A. F. POST, K. FABRICIUS, D. MARIE, D. VAULOT, AND A. GENIN. 1998. Phytoplankton distribution and grazing near coral reefs. *Limnol. Oceanogr.* **43**: 551–563, doi:10.4319/lo.1998.43.4.0551

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