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Intense benthic grazing of phytoplankton in a coral reef

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Abstract

Grazing on phytoplankton by a section of the fringing coral reef in Eilat, the Gulf of Aqaba, Red Sea, was studied using the control-volume approach, a direct, nonintrusive technique common in engineering studies. Concentrations of chlorophyll *a* were measured using four vertical arrays of pumps, 10 pumps on each, that defined an imaginary box (i.e., the control volume), extending from the bed to surface, overlying a section of the sloping fore-reef >100 m^2 in size. Concurrent velocity measurements were made at the center of the box using a vertical array of acoustic current meters. Together, the concentration and velocity measurements allowed us to compute phytoplankton fluxes in and out of the control volume. While phytoplankton patchiness and other turbulent variations in concentration introduced significant variability, mass balances of fluxes into and out of the box indicate a flow-dependent grazing rate of approximately 10 m d^{-1} to 20 m d^{-1}. This value was larger than, but not statistically different from, values derived from an "a priori estimate" (calculated based on the density and feeding rates of benthic grazers) and an estimate computed from the observed near-bed gradient of Chl *a*. Phytoplankton grazing is a principal pathway through which allochthonous nutrients are imported to the reef community from the flowing water.

Coral reefs flourish in oligotrophic, nutrient-poor waters. Nevertheless, reefs are some of the most productive ecosystems in the ocean, with benthic gross production characteristically an order of magnitude higher than that of nearby ambient waters (Sargent and Austin 1954; Hearn et al. 2001; Atkinson and Falter 2003). Such a striking difference in the productivity of juxtaposed communities has initiated numerous studies searching for significant sources of nutrients that may explain the maintenance of high productivity at the reef (reviewed by Erez 1990; Hearn et al. 2001; Atkinson and Falter 2003). Earlier studies (Odum and Odum 1955; Pomeroy 1970) demonstrated the important energetic subsidy provided by ocean currents and tides to overall reef productivity, but later the focus shifted to the role of recycling (Erez 1990). However, even if recycling is highly efficient, a substantial import is required to account, at the very least, for the export ("leak") of nutrients from the reef. This is especially true for the outer sections of fringing reefs which are constantly flushed with currents (Hatcher 1997). This export consists of both dissolved and particulate matter (Charpy and Charpy-Roubaud 1991; Delesalle et al. 1998, Hata et al. 1998), including the release of eggs and larvae to the open waters (Hamner et al. 2007) and predation by pelagic nekton on reef organisms.

An important, continuous source for nutrients is a direct uptake of dissolved inorganic nitrogen (N) and phosphorus (P) from the flowing waters by corals and other benthic autotrophs (Atkinson and Bilger 1992). This uptake, a mass-transfer–limited process (Baird and Atkinson 1997; Hearn et al. 2001; Steven and Atkinson 2003), may be sufficient to fully account for the demand for P (Bilger and Atkinson 1992). However, because the N : P ratio of reef autotrophs is much higher than the Redfield ratio, additional sources of nitrogen (e.g., fixation or particle grazing) must be important (Atkinson and Falter 2003). While in some special locations intermittent pulses of upwelling (Wolanski and Delesalle 1995), internal bores (Liechter et al. 2003), and seaward flow of underground waters (Paytan et al. 2006) can augment the supply of dissolved inorganic nitrogen to the reef; the indirect import of nitrogen via planktivory by benthic suspension feeders may exceed all other sources (Richter et al. 2001; Ribes et al. 2003, 2005). For this heterotrophic pathway to be effective, benthic plankton feeders should abound, their feeding rates should be high and, in the case of long reefs, the reef must be exposed to reef-ward currents that constantly replenish depleted waters. All three conditions are expected to be found over the outer, exposed sections of coral reefs, where coral cover is typically high and benthic plankton feeders are abundant (Glynn 1973; Hamner et al. 1988).

Earlier measurements of plankton flux to the reef were based on simple comparisons of plankton concentrations up- and down-stream of coral reefs (Glynn 1973; Yahel et al. 1998; Fabricius and Dommisse 2000). However, the complex near-bottom flow hampered reliable quantitative interpretation of the measurements, and findings from

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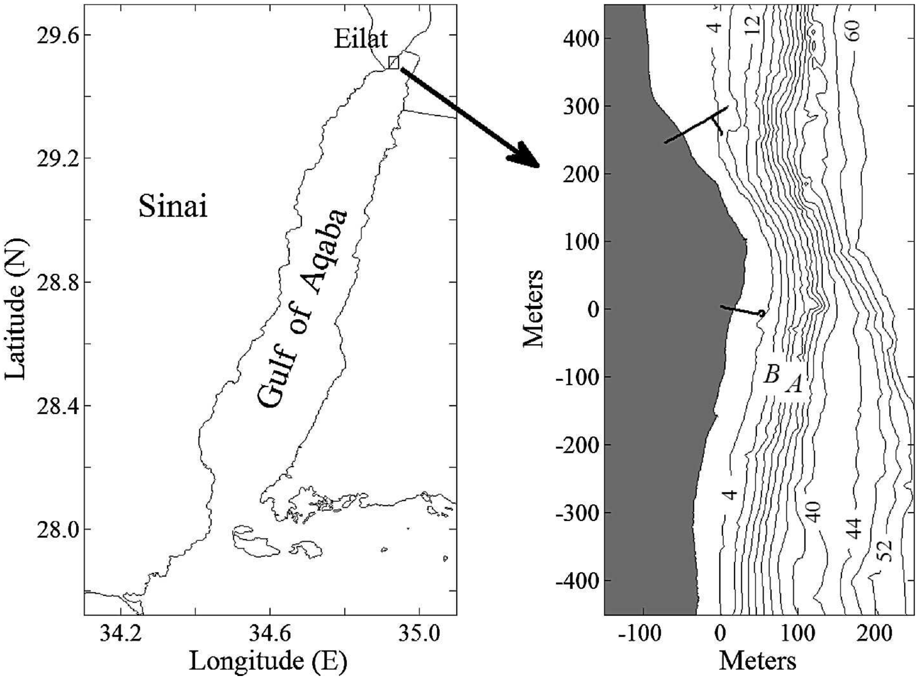

Fig. 1. The location of our study site in Eilat, northern Gulf of Aqaba, Red Sea (left panel) and the detailed bathymetry of the reef slope near sites *A* and *B* (right panel) are shown. The bathymetric chart in the right panel was rotated so that the top of the plot is oriented toward the northeast (45°NE). The two thick lines protruding to sea (right panel) indicate the piers of the Interuniversity Institute (south) and the Coral Reef Observatory (north). Contour depths are shown in meters. (Based on unpublished bathymetric survey carried out in 2000 by D. Fong and M. Reidenbach.)

unique situations (e.g., channels or perforated reefs) may be idiosyncratic. The use of a large, recirculating flume allowed Atkinson et al. (reviewed in Atkinson and Falter 2003) to measure the rates of nutrient uptake and plankton grazing (Ribes et al. 2003, 2005; Ribes and Atkinson 2007) by artificial assemblages of benthic fauna collected at the coral reef in Kaneohe Bay, Hawaii. Yet, those flume measurements have not been validated in situ.

In general, an in situ quantification of mass fluxes across the water–bottom interface is a major objective in studies of benthic–pelagic coupling, from shallow reefs and freshwater habitats to the deep sea. Such measurements are relatively straightforward where changes in concentrations are accurately measured under conditions of fairly homogeneous or confined flow, such as in streams (Asmus and Asmus 1991), channels (Fabricius and Dommisse 2000), or downstream of perforated reefs (Fabricius et al. 1998). In most benthic habitats, however, such measurements become highly complex (Nishihara and Ackerman 2007) because lateral boundaries are open, velocities are vertically sheared; turbulent mixing is sometimes strong (Gross and Nowell 1983); and the concentrations of the commodities of interest usually change with distance from the bottom (O'Riordan et al. 1993; Yahel et al. 1998). Various techniques have been used to overcome those difficulties. One such technique, the "chamber" experiment, uses measurements of concentration changes occurring in a watertight container with single specimens or a small section of the benthic community (Hopkinson et al. 1991; Smith and Kaufmann 1999). However, this intrusive method introduces serious artifacts because it is size-limited, blocks natural flows, and prevents food replenishment. Another common technique is the use of Lagrangian measurements, i.e., measuring changes in water properties along the path of a parcel-tracking drogue (Barnes and Lazar 1993; Fabricius and Dommisse 2000). Underlying this approach are restrictive assumptions that the drogue should track the flow and that point measurements of concentration adequately represent the entire water column. The occurrence of steep velocity and concentration boundary layers render this technique unusable in the vast majority of benthic habitats.

To circumvent these problems, we set out to apply the "control volume" approach, a standard engineering technique (Street et al. 1996), in order to measure the flux of phytoplankton from the flowing water to an open reef community, growing on an exposed, outer slope.

Study site

The study was carried out in summer 1999 at two sites (Fig. 1, sites *A* and *B*) on the sloping fore-reef in front of the Steinitz Marine Biology Laboratory in Eilat, Israel (29°36′N, 34°56′E), northern Gulf of Aqaba, Red Sea. Site *A* was located at a mean depth of 13 m where the bottom slope was 27°, while site *B* was located at a mean depth of

9 m where the slope was 18°. At both reef sites, coral cover was approximately 14%, with a typical topographic relief of the order of 0.5 m (Reidenbach et al. 2006). The local reef community was described by Fishelson (1971), Benayahu and Loya (1977), and Yahel et al. (2002). Briefly, the reef was dominated by stony corals and a diverse guild of phytoplanktivores, including sponges, bivalves, ascidians, actinians and polychaetes (*see* Results). Benthic algae were sparse, particularly during summer, the season during which this study was carried out. Lagrangian measurements made by Barnes and Lazar (1993) aboard a floating raft over the subtidal reef flat near our study site indicated a gross primary productivity of 12.3 g C m^2 d^{-1}.

Background information on the oceanographic and meteorological conditions at the site are available from the Israel National Monitoring Program of the Gulf of Eilat (http://www.iui-eilat.ac.il/NMP/). The sea-level tide is semidiurnal, with amplitude ranging from 0.25 m to 1 m. Moderate winds with an average speed of approximately 4 m s^{-1} are oriented predominantly along the axis of the Gulf from the northeast. The region is extremely arid, with an average rainfall of 3 cm y^{-1}. High evaporation rates (0.5–1 cm d^{-1}) result in latent heat fluxes as large as 400 W m^{-2} (Monismith et al. 2006). During summer, the surface-mixed layer usually does not exceed 30 m depth. Sea-surface temperatures vary annually between 21°C and 27°C with a corresponding range of air temperature between 10°C and 45°C. The pelagic ecosystem is unique for the world's warm oceans due to an unusually weak stratification during summer and a remarkable convective mixing, reaching hundreds of meters in depth, in winter (Genin et al. 1995). Consequently, both the planktonic and coral reef communities undergo strong seasonality, shifting from oligotrophic conditions with severe nutrient limitation and a dominance of *Prochlorococcus* and *Synechococcus* during the warm months (June–October) to mesotrophic conditions with a dominance of eukaryotic ultraphytoplankton in winter–spring (Genin et al. 1995; Lindell and Post 1995; Al-Najjar et al. 2007).

The current regime near Eilat was studied by Genin and Paldor (1998), Berman et al. (2003), and Monismith and Genin (2004). The small-scale flow over the reef at our site was studied concurrently with this work by Reidenbach et al. (2006). During the warm season (May–October), when the water column is stably stratified, the predominant longshore currents are associated with semidiurnal internal tides and vary between 0 cm s^{-1} and 20 cm s^{-1}.

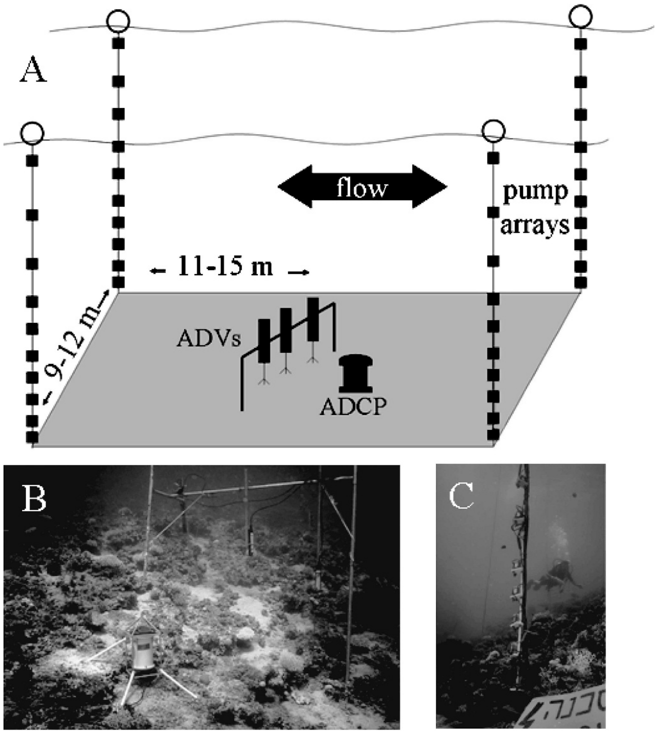

Fig. 2. (A) A sketch of the control volume (CoVo) used in this study is shown. The size of the CoVo "floor" was 114 m^2 and 106 m^2 at sites *A* and *B*, respectively, with the longer axis oriented parallel to the direction of the dominant (longshore) current. (B) The current meters deployed at the center of the CoVo are pictured, showing the up-looking ADCP and the frame holding the three down-looking ADVs. (C) The pump array at one of the four CoVo corners is pictured, showing 7 of the 10 pumps and the attachment of the pipes to the mooring line.

Methods

Control volume—In situ measurements of phytoplankton grazing by the entire coral-reef community were made using an approach referred to in the engineering fluid mechanics literature (Street et al. 1996) as a "control volume" (hereafter CoVo). Underlying this approach was the designation of a small section of the reef as the CoVo's "floor" (114 m^2 and 106 m^2 at sites *A* and *B*, respectively), with its four imaginary "walls" extending from bottom to surface (Fig. 2). Since no flux of phytoplankton occurs across the air–water interface (the CoVo's "ceiling"), the net integrated flux of phytoplankton through the four walls gives the value of grazing at the bottom.

Under conditions of no benthic grazing, the evolution equation for phytoplankton biomass in a water parcel flowing across the CoVo should consider advection, turbulent mixing, net production, and zooplankton grazing (Cloern 1991):

$$\frac{\partial C}{\partial t}+U\frac{\partial C}{\partial x}+V\frac{\partial C}{\partial y}+W\frac{\partial C}{\partial z}-W_s\frac{\partial C}{\partial z}\cong-\frac{\partial\overline{w'c'}}{\partial z}+(\mu-g_z)C \qquad (1)$$

where C is the mean (Reynolds averaged) concentration of chlorophyll *a* (hereafter Chl *a*); U, V, and W are respectively the mean longshore, cross-shore, and vertical velocities; W_s is the sinking rate of phytoplankton cells; $\overline{w'c'}$ is the turbulent flux of Chl *a*; μ is the net rate of growth (d^{-1}); and g_z is the rate of grazing by zooplankton (also d^{-1}). Since the phytoplankton community is dominated by minute cells (more than 90% of the biomass are cells <8 μm; Yahel et al. 1998), we assume that on the time scale it takes the water to cross the CoVo (minutes) W_s is insignificant. We also assume that to first order, $\mu \approx g_z$. Thus, the material derivative (the rate of change following the fluid motion) can be calculated using this equation:

$$\frac{D}{Dt} = \frac{\partial}{\partial t} + U\frac{\partial}{\partial x} + V\frac{\partial}{\partial y} + W\frac{\partial}{\partial z} \qquad (2)$$

Equation 1 can be approximated using this equation:

$$\frac{DC}{Dt} \cong -\frac{\partial \overline{w'c'}}{\partial z} \qquad (3)$$

i.e., following the motion of a water parcel, C can change via turbulent mixing. If C, U, and V were nearly uniform over the depth, then integration of Eq. 3 from the reef to the water surface would allow us to calculate the flux to the bed using the following equation:

$$H\frac{D\langle C\rangle}{Dt} \cong \overline{w'c'}\Big|^{z=0} = -\text{flux to the bed} = -\alpha\langle C\rangle \qquad (4)$$

where H is water depth, $\langle C\rangle$ is the depth-averaged concentration, and $a > 0$ is the grazing velocity (Koseff et al. 1993). We note that because near-bed concentrations can be less than $\langle C\rangle$, α is not necessarily the same as the actual rate of water processing by the benthic community (Wildish and Kristmanson 1997), and given the complexity of the reef topography, the bed elevation $z = 0$ is placed at the lowest level below which nearly all the grazing takes place.

Equation 4 is commonly used as the basis for Lagrangian sampling schemes in which one follows a drogue and tries to repeatedly sample the same water parcel so as to approximate the left-hand side of Eq. 4 (Barnes and Lazar 1993). However, if the water column is sheared, the velocity at a single depth is not representative of the effects of advection, and Eq. 4 is no longer accurate.

An alternative approach to Eq. 4 is to integrate Eq. 3 over a fixed volume, the "control volume" (Street et al. 1996). In this case, the evolution of the mass of Chl *a* in the volume is described by the Reynolds transport theorem, stating that for conservative substances the accumulation or depletion of mass in the CoVo is balanced by the difference in fluxes through its faces. In the present case (Fig. 2), where the CoVo extends from the bottom to a surface through which there is no flux (=sea surface), the Reynolds transport theorem gives this equation:

$$\frac{d}{dt}\iiint_V C\,dV = -\iint_{S_v}\left(\vec{U}C\right)\times\vec{n}\,dS_v - \iint_{S_B}\alpha C\,dS_B \qquad (5)$$

where V is the volume of the CoVo, S_v is the surface area of the CoVo's vertical "walls", $\vec{n}$ is a unit normal vector pointing locally out of the CoVo, and S_B is the area of the bottom where the flux is assumed to be entirely due to benthic grazing.

Since it is not possible to measure velocities and concentrations everywhere in the CoVo, we must approximate Eq. 5 using limited measurements. In the experiments discussed below, we had four profiles of C, measured on the corners of the box-like CoVo and one profile of U at the center (Fig. 2). For this case, we evaluated the Reynolds transport theorem based mass balance using this equation:

$$V\frac{d\langle C\rangle}{dt} + \sum_{i=1}^{4} B_i \int_0^H V_i^n C_i dz = -\alpha S_B\langle C\rangle \qquad (6)$$

where B_i is the width of the ith face, V_i^n and C_i are respectively the vertically varying velocity normal to (positive outwards) and the concentration at the center of the ith face. We computed C_i by linear interpolation of the concentrations measured along the two vertical lines that bounded a given face. The average concentration in the CoVo $\langle C\rangle$ was computed as the average of the four measured concentration profiles:

$$\langle C\rangle \cong \frac{1}{4H}\sum_{i=1}^{4}\int_0^H C_i dz \qquad (7)$$

In all of the work reported below, we further simplified Eq. 6 by assuming that the concentration field was approximately steady, thus neglecting the contribution of the first term on the left hand side of Eq. 6. We will return to the implications of this assumption in the Discussion section. Thus, our estimate of grazing is computed using this equation:

$$-\frac{1}{S_B\langle C\rangle}\sum_{i=1}^{4} B_i \int_0^H V_i^n C_i dz \cong \alpha \qquad (8)$$

Water samples were collected using 40 submerged aquarium pumps (AT-2220, Atman), 10 on each of the four corners (Fig. 2A,C). The water was pumped to the shore through forty pipes, each 100-m long and 12 mm in diameter, one for each pump. Due to friction in the long pipes, the flow rate at the outlet was ~1 L min^{-1}. To minimize disturbance to the ambient flow, the pipe from each pump was attached to the mooring line (Fig. 2C), extending vertically to the surface, where the 10 pipes from each mooring were bundled together, floating on the sea surface to shore. Custom-built manifolds were used so that we could collect water samples simultaneously from all 40 pipes (photo 4 in Genin et al. 2002). Thereby, a single "run" consisted of the four simultaneous profiles of Chl *a*, one at each corner of the CoVo. The corresponding information on the currents for each run was obtained by calculating a single profile of the average currents during 10 min preceding the water sampling, measured at the center of the CoVo.

The sampled water (~300 mL) was pre-filtered through a 100-μm mesh wrapped around each pipe outlet to remove zooplankton and fragments of benthic algae, and collected in pre-measured, individually marked glass flasks. The samples were immediately transferred to the laboratory, filtered on glass microfiber (GF/F) filters and analyzed for Chl *a* using 24-h cold (5°C) extraction in a 90% acetone solution buffered with magnesium carbonate ($MgCO_3$) as in Yahel et al. (1998). The filtration of the 40 samples was always completed within 1.5 h after collection. Chl *a* concentration in the acetone extraction was measured using the nonacidification method with a TD 700 fluorometer (Turner Design). Phaeophytin concentrations were also measured for some of the samples using the acidification method with a AU-10 fluorometer (Turner Design). Both fluorometers were calibrated prior to the experiment and checked for electronic drift during the experiment with a solid standard. An identical processing of daily pairs of samples taken approximately 1 min apart at the sea surface at a fixed point 300 m north of the study site during 1999–2000 ($n = 214$ pairs) indicated that the analytical precision of our method, measured as the average deviation of the pair from its mean, was 5 ng Chl *a* L^{-1} (coefficient of variation <2%). Throughout this study we used Chl *a* concentration as a surrogate for phytoplankton carbon, based on a Chl *a*:C ratio of 1:60 found at our study site by Yahel et al. (1998).

A total of 13 runs (520 Chl *a* samples) from site *A* and 17 runs (680 Chl *a* samples) from site *B* were used in the analysis. An additional six runs (hereafter "control runs") were carried out at site *A* after covering the reef under the CoVo with a clear plastic sheeting, effectively isolating the benthic community from the overlying waters (*see* fig. 2 in Reidenbach et al. 2006). A total of nine runs with erratic profiles of Chl *a*, or with strongly sheared currents, or with currents which reversed or markedly changed during the 10 min before the sampling time were excluded from the analysis.

Current measurements—An array of current meters was used to measure velocity and turbulence throughout the water column near the center of each CoVo (Fig. 2A,B). This array consisted of three Acoustic Doppler Velocimeters (ADV, Sontek) and an Acoustic Doppler Current Profiler (ADCP, 600 KHz, RDI, Teledyne). The ADVs were attached to a tripod positioned to measure the current at 0.1 m, 0.3 m, and 1.0 m above bottom (mab). The ADCP was programmed to profile the water column in 0.5 m bins between 1.5 m above the bottom to approximately 1 m below the surface. The ADVs measured the velocity at a rate of 25 Hz, while the ADCP recorded the velocity every 10 s by averaging 40 equally-spaced measurements. The velocity measurements were rotated into longshore (45°NE) and cross-shore components. Details of the current-meter deployments and associated results can be found in Reidenbach et al. (2006).

Benthic survey—A survey of the benthic community contained within the CoVo at the two sites was carried out between 29 December 1999 and 12 January 2000. The two main objectives of this survey were to characterize the benthic community and to calculate an "a priori estimate" of α based on the integration of the abundance of benthic phytoplankton grazers and their measured grazing rate. The latter parameter was based on a concurrent study (Yahel 2003; Yahel et al. 2005) during which we measured the pumping rate of each taxon (Table 1) and the efficiency by which phytoplankton is removed from the water it filters. The contribution of cryptic fauna to benthic grazing was calculated based on values reported by Yahel et al. (2006) for grazing by exposed ("bare") rocky substrate.

The abundance of benthic suspension feeders at site *A* was measured at three different scales: (1) Large specimens (sponges, colonial tunicates, and stony coral infected with *Lithophaga*) were counted over the entire CoVo bottom. (2) Sponges and tunicates with large (>2 mm in diameter) excurrent aperture were counted in a grid of 1 × 1-m quadrats placed 3 m apart across the entire CoVo area. In addition, a visual estimate of the total percentage of cover of live animals, mostly corals, was made in each quadrat. (3) Smaller suspension feeders, primarily endolithic sponges, were counted in the lower leftmost ninth of each quadrat (0.111 m^2). The density of the coral-boring *Lithophaga* was estimated using two-level sampling (Pielou 1978) of their host corals and careful counts of their abundance in subsamples of the corals' branches. Other minute (<5-mm) phytoplanktivores, such as polychaetes, bryozoa, and other cryptic suspension feeders (Yahel et al. 2006), were not counted in our survey. Due to logistic limitations, the survey at site *B* consisted of only counts of large specimens, as described in item 1.

Results

Time series of water temperature, currents, and Chl *a* concentration during the experiment are shown in Fig. 3. The experiment coincided with the start of late-summer water cooling, where water temperature steadily decreased from 28°C at the start of the experiment to 25.5°C at its end. The wind during our experiment was always toward the southwest, with a mean velocity of nearly 4 m s^{-1}. Due to the short fetch between the northern end of the Gulf and our study site, the surface waves during our experiment were small, 20–50 cm in height. The semidiurnal longshore currents (~10 cm s^{-1}, Fig. 3B), were typical for the summer period (Genin and Paldor 1998). Limited profiling of temperature and salinity (not shown) indicated that these velocities were adequate to vertically mix the water column over the reef. Profiles of the mean flow speed at the two sites (Fig. 4) show the vertical shear expected for turbulent flow over a rough surface. Reidenbach et al. (2006) showed that velocity was distributed logarithmically with height and that the roughness length for flow over this reef was ~1 cm, leading to a drag coefficient of $C_D = 0.01$, implying that the shear velocity, u_*, was ~10% of the depth-averaged velocity. The cross-shore velocities (Fig. 3C) show a diurnal cycle in which weak upwelling and seaward surface flow occur when the water is warming, and weak downwelling and shoreward flow on the surface during cooling (Monismith et al. 2006). Finally, throughout this period, depth-averaged Chl *a* concentrations varied from 120 ng L^{-1} to 210 ng L^{-1} (Fig. 3D), values typical of summer conditions in the Gulf of Aqaba (Genin et al. 1995).

Concentrations of Chl *a* decreased, and those of phaeopigments increased near the bottom (Fig. 4), as expected when the concentration boundary layer (CBL) is formed due to benthic grazing. The concentration of Chl *a* near the bottom (<1 mab) was on average (±SE) 2.8 (±0.8) ng L^{-1} lower than in the 1-m layer above (1.2–2.2 mab), while the corresponding increase in phaeopigments was 3.15 (±0.9) ng L^{-1}. A pair-wise comparison using the average profiles of different runs (i.e., the average of the four CoVo pump arrays in each run) indicated that the magnitude of the near-bottom decrease in Chl *a* was not

Table 1. (A) - Average (SD) density of small active suspension feeders, their phytoplankton clearance rate, and their relative contribution to the total clearance rate by the suspension feeders included in the benthic survey at site *A* (n=45). The names of the host corals are indicated for the boring bivalve *Lithophaga*. (B) – The total number of exhaling apertures (e.g., oscula) of large active suspension feeders at site *A* and their total clearance rates and relative contribution to the total measured for that site. The calculations of clearance rate are based on measurements of pumping rates and phytoplankton removal efficiencies of active suspension feeders made by Yahel (2003) and Yahel et al. (2003, 2005) at the coral reef of Eilat.

A) Small active suspension feeders	Density (No. m^{-2})	Clearance rate (L m^{-2} h^{-1})	Relative Contribution (%)
Bivalves			
Lithophaga in *Montipora*	1.67 (5.98)	0.26 (0.16)	0.2
Lithophaga in *Cyphastrea*	1.51 (3.91)	0.05 (0.12)	0.0
Lithophaga in *Goniastrea*	0.31 (1.46)	0.11 (0.51)	0.1
Lithophaga in *Stylophora*	3.00 (7.57)	0.10 (0.24)	0.1
Lithophaga in *Astreopora*	2.16 (8.79)	0.75 (3.06)	0.7
Lithophaga in *others*	0.07 (0.45)	0.004 (0.01)	0.0
Tridacna	0.04 (0.30)	0.16 (1.06)	0.1
Pedum sp.	0.40 (2.68)	1.73 (11.6)	1.6
Lithophaga malacana	0.44 (1.10)	2.31 (5.7)	2.1
Astrea	0.02 (0.15)	0.10 (0.64)	0.1
Chama	0.27 (0.75)	1.15 (3.24)	1.0
Sponges			
Subarites	0.36 (1.07)	3.66 (11.0)	3.3
Mycale	1.24 (2.70)	5.95 (12.9)	5.4
Cliona 2–4 mm	8.38 (15.4)	8.86 (16.2)	8.1
Cliona <1 mm	305.93 (538.8)	40.55 (71.4)	36.9
sponge 2–4 mm	4.00 (5.10)	4.23 (5.40)	3.9
sponge <1 mm	40.62 (162.9)	5.38 (21.6)	4.9
Tunicates			
Halocynthia gangelion	0.76 (1.85)	2.70 (6.60)	2.5
Didemnum	0.69 (2.38)	1.11 (3.84)	1.0
other colonial tunicates	0.80 (3.40)	1.29 (5.48)	1.2
other solitary tunicates	0.18 (0.49)	0.87 (2.40)	0.8
	Total	81.3 (80.2)	74.1

B) Large active suspension feeders	Exhaling apertures		Clearance rate (L m^{-2} h^{-1})	Relative contribution (%)
	Total count	No. m^{-2}		
Bivalves				
Lithophaga simplex	363	3.19	1.11	1.0
Lithophaga eritrea	78	0.69	0.13	0.1
Sponges				
Subarites clavatus	274	2.41	25.19	22.9
Cliona sp.	195	1.71	1.64	1.5
Tunicates				
Didemnum candidum	10	0.09	0.16	0.1
Theonella swinhoei	3	0.03	0.25	0.2
		Total	28.47	25.9

significantly different from the corresponding increase in phaeopigments ($p > 0.7$, paired t-test) and that the two trends were significantly correlated (Pearson $r = 0.37$, $p < 0.03$). Consequently, the Chl a : Phaeo ratio decreased from an average value (±SE) of 3.6 (±0.09) in the upper layer to 3.3 (±0.09) at the 1-mab layer.

The CoVo runs indicated an average grazing rate (±SE) of 510 (±200) ng Chl a s^{-1} at site *A* (bottom area = 114 m^2) and 430 (±300) ng Chl a s^{-1} at site *B* (106 m^2). Grazing rates at the two sites were not significantly different ($p > 0.6$, paired t-test), and together they were significantly different from zero ($p < 0.04$, t-test, $n = 30$). Considering a Chl a : carbon (C) ratio of 1 : 60 at our study site (Yahel et al. 1998), the average (±SE) grazing rate was 0.22 (±0.1) g C m^{-2} d^{-1}. Using the Redfield C : nitrogen (N) ratio for phytoplankton at our study site (R. Yahel, G. Yahel, and A. Genin unpubl. data), the average import of nitrogen to the reef community via this grazing was 2.8 mmol N m^{-2} d^{-1}. The rate of grazing in the "control" runs, when the reef was covered with a clear plastic sheeting, were five-fold smaller and not significantly different from zero (0.04 ± 0.1 g C m^{-2} d^{-1}, $p > 0.6$, t-test, $n = 6$). Figure 5 presents the average grazing rates at each site and during the control runs in terms of α calculated based on the average Chl a concentration in the water column during each run, as defined in Eq. 8. The overall average (±SE) of α was 20 (±8) m d^{-1} ($n = 30$).

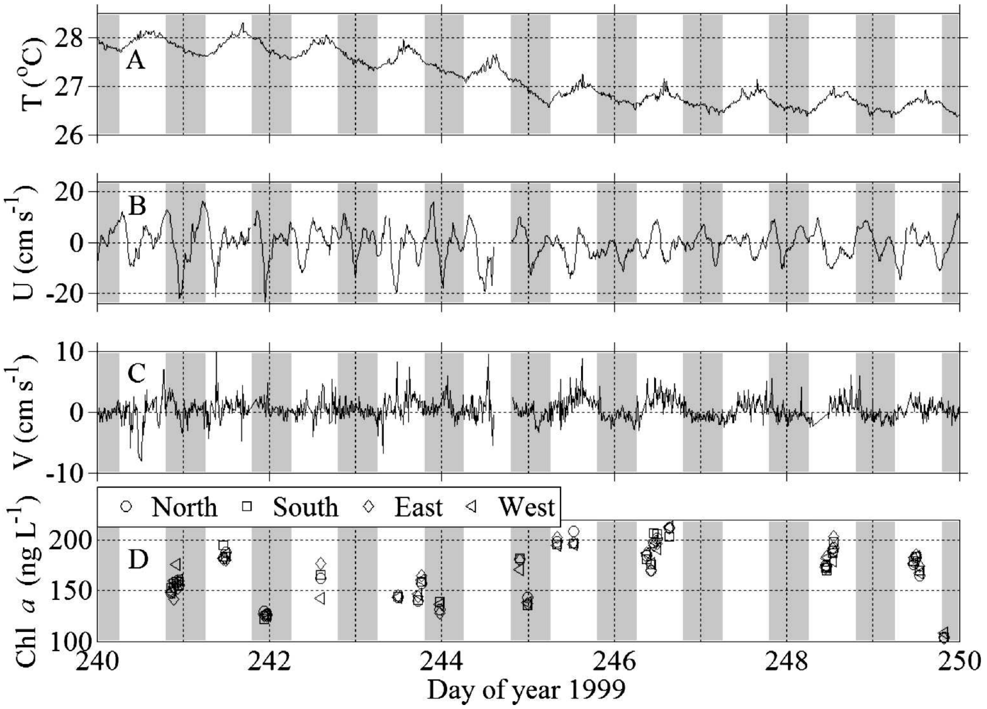

Fig. 3. Time series of (A) sea-surface temperature, (B) depth-averaged, longshore velocity with positive values indicating northeastward currents, (C) vertical shear in cross-shore flow with positive values indicating water flowing offshore at the surface and onshore near the bottom, and (D) depth-averaged concentrations of Chl *a* at the north, south, east, and west corners of the control volume are shown. Shaded bars indicate night time.

The correlation between α and the mean flow (U_b) and the mean velocity shear ($\partial U/\partial z$) in the lowermost 1 m above bottom were low (0.46 and 0.51, respectively) but significant ($p < 0.05$; Fig. 6A,B), whereas the correlation between α and u_* (Fig. 6C) was not significant ($p > 0.05$). This likely reflects the large uncertainty (±20%, Reidenbach et al. 2006) in determining u_*. The relationships between grazing and flow were further corroborated by the significant difference (Mann–Whitney *U*-test, $p < 0.001$) of grazing rate (a) between runs with weak (<7 cm s^{-1}) and stronger currents (Fig. 6).

The community at site *A* was dominated by medium-sized (>2 cm^2) stony corals (11.8 ± 17.1 colonies m^{-2}) that do not directly feed on phytoplankton, but some of their symbionts do (e.g., *Lithophaga* spp.). Pumping rates by active suspension feeders ranged from 0.02 mL s^{-1} in minute boring animals to 3.83 mL s^{-1} in the large sponges *Theonella swinhoei* and *Subarites clavatus*. The efficiency by which those suspension feeders removed phytoplankton from the water they filtered ranged from 22% in the *Tridacna* spp. to over 70% in some sponges and tunicates (Yahel 2003; Yahel et al. 2003, 2005). The density of suspension feeders at site *A*, their phytoplankton clearance rate and their relative contribution to the removal of phytoplankton from the water is reported in Table 1. The a priori estimate of grazing rate at site *A*, a sum of clearance rate by active suspension feeders (109.8 L m^{-2} h^{-1}; Table 1) and the exposed rocks (125 L m^{-2} h^{-1}; Yahel et al. 2006), yielded a value of $a = 5.6$ m d^{-1}, substantially lower than, however not statistically different from ($p > 0.08$, *t*-test) the CoVo-based value.

Discussion

In terms of C, the benthic grazing rate of 0.22 g C m^{-2} d^{-1} measured in the coral reef of Eilat was intense; it was equivalent to a removal of the total phytoplankton produced daily per square meter in the oligotrophic waters off the reef (Reiss and Hottinger 1982; D. Iluz unpubl. data). Because the coral reef in Eilat is constantly flushed with "new" water originating from the open sea (Monismith et al. 2006) and because the residence time of the water over the ~1-km–long fringing reef in Eilat is a few hours, i.e., much shorter than phytoplankton generation time, phytoplankton grazing by the reef is, by and large, an import of allochthonous food, rather than recycling. For phytoplankton having a C : N ratio close to Redfield, which is the case for phytoplankton at our study site (R. Yahel, G. Yahel, and A. Genin unpubl. data), the grazing rate we measured constitutes an import of 2.8 mmol N m^{-2} d^{-1}. This import of allocthonous N by grazing can balance the "leak" of dissolved inorganic N downstream (2.5 mmol N m^{-2} d^{-1}, T. Korpal, 1991). These findings agree with the results of a flume experiment with an artificial assembly of corals and benthic suspension feeders in Hawaii (Ribes et al. 2003, 2005; Ribes and Atkinson 2007). However, the nitrogen flux measured by Ribes et al. (2005) and Ribes and

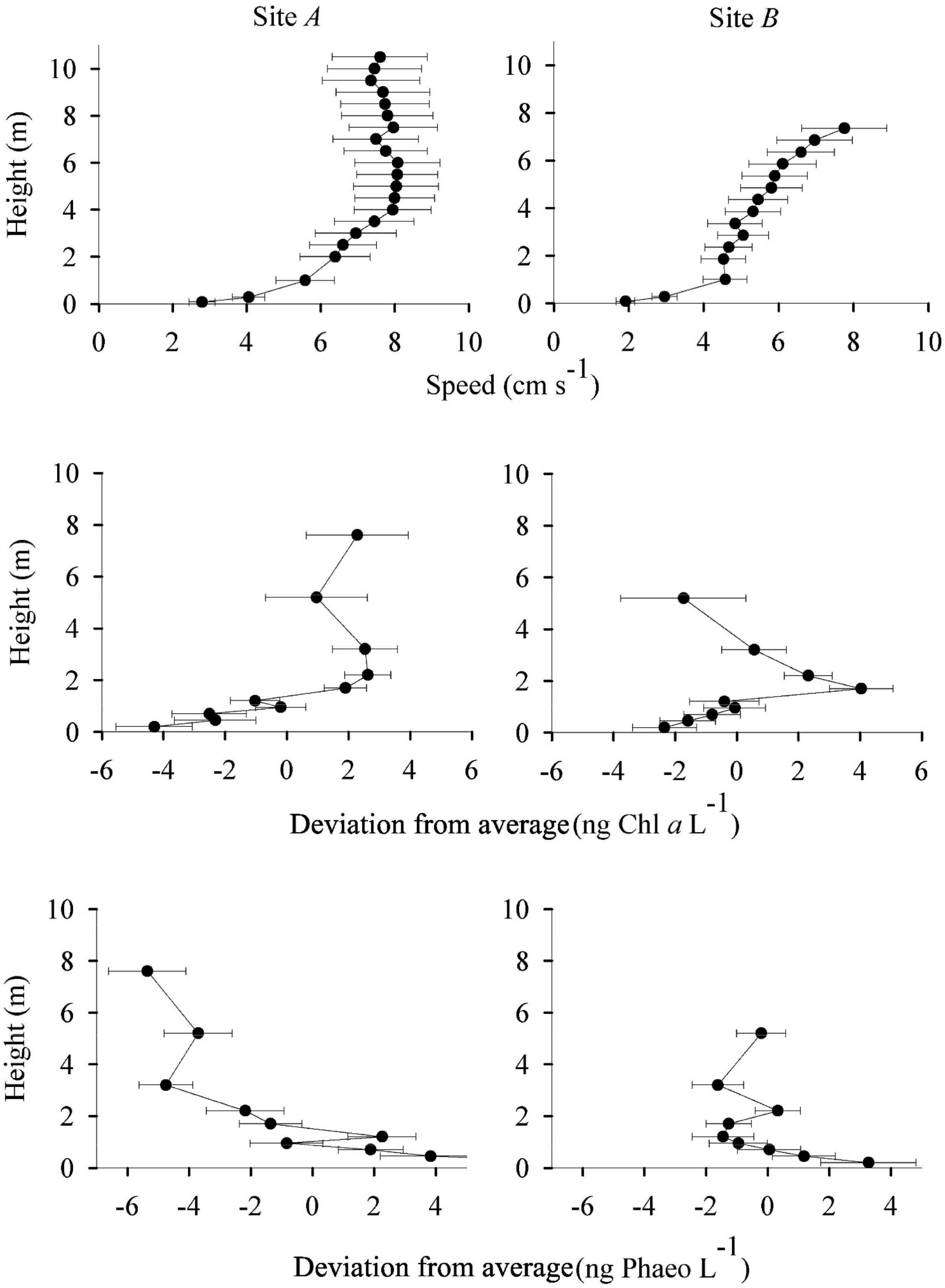

Fig. 4. Average (±SE) profiles of flow speed (top panels), chlorophyll *a* (middle panels), and phaeopigments (bottom panels) at sites *A* (left) and *B* (right) are shown. Chlorophyll and phaeopigment profiles are presented as the deviation of the measurements at different heights from the depth-averaged concentration of their respective profiles.

Atkinson (2007) in the flume was five times higher than the import inferred from our in situ CoVo measurements. Since the plankton biomass, expressed in terms of C, was roughly the same in both studies ($\sim 10^{-2}$ g C m^{-3}), the difference in grazing was most probably due to the much higher density of suspension feeders in their flume, which had 100% coral cover and >5% cover of sponges, ascidians, and actinians (Ribes et al. 2003). Our long-term measurements of currents and temperatures in Eilat (Genin and Paldor 1998; Monismith and Genin 2004, Monismith et al. 2006) indicate that neither upwelling (Wolanski and Delesalle 1995) nor internal bores (Leichter et al. 2003) are common at our study site. The import of N from terrestrial sources was also expected to be insignificant because the local climate is extremely arid and no rivers are found in the region. Hence, phytoplanktivory may be the principal pathway through which allochthonous N is imported to the reef. Note however, that the rate of N fixation at the reef (Wiebe et al. 1975; Lesser et al. 2004), a challenging measurement for the

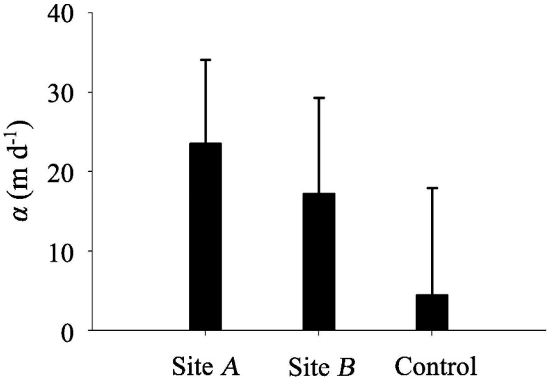

Fig. 5. Average (±SE) grazing rates (α) expressed in terms of clearance rate (m^3 of water cleared by 1 m^2 of reef community per day) at the nonmanipulated reef at sites *A* and *B* and during the control run at site *A* are shown.

scale of the whole community (Atkinson and Falter 2003), is yet unknown.

Aside from grazing, the observed depletion of phytoplankton from waters flowing over the reef could be partially due to passive settling of cells baffled by the reef framework, especially during periods with weak currents. Yet, if eventually mineralized, grazing and settling should be biogeochemically equivalent because both are a form of import of allochthonous N from the flowing water to the benthic community. The following information, however, indicates that grazing, rather than passive settling, was the dominant process: (1) the near-bottom depletion of Chl *a* coincided with an equivalent increase in phaeopigments (Fig. 4), a product of grazing (Welschmeyer and Lorenzen 1985); (2) the depletion of phytoplankton increased with water velocity (Fig. 6), rather than decreasing as expected for passive settling; (3) neither a decrease in Chl *a* nor an increase in phaeopigments was observed over sandy (reefless) bottom (*see* figure 4 in Yahel et al. 1998); and (4) our flume experiments (Yahel et al. 2006) showed that Chl *a* depletion that occurred in water flowing over freshly collected gravel and rocky substrate no longer persisted after the grazers were killed by baking the substrates.

That the a priori estimate of α calculated based on the benthic survey was lower than (however, not significantly different from) the CoVo-based value (5.6 m d^{-1} vs. 20 m d^{-1}, respectively) can be partly explained by the fact that the taxa on which the a priori estimate was based did not include soft corals (Fabricius et al. 1998). Cavity-dwelling fauna (Richter et al. 2001), and small, nonmolluscan epifauna (e.g., bryozoans, hydrozoans, and polychaetes) were the dominant passive suspension feeders at our study site with a mean (±SD) density of 1.9 ± 3.1 colonies m^{-2}. Note, however, that part of the grazing by the latter group was included in the value attributed to "exposed rocks."

Another likely reason for the large difference between the a priori and CoVo estimates was the large uncertainty of the latter (SE = ±8.1 m d^{-1}). A key shortcoming of our implementation of the CoVo was the measurements' high sensitivity to patchiness because the water samples were taken nearly instantaneously (1 min to fill a sampling bottle) and because all 40 samples across the CoVo were taken simultaneously. While this approach offers the advantage of creating a "snap shot" of the chlorophyll concentration, it rendered the grazing measurements most sensitive to spatial variability (patchiness) of the measured parameter. To overcome that problem, the open-reef CoVo runs were replicated as many times as logistically possible (17 times at site *A* and 13 times at site *B*). Unfortunately, such a high number of replicates was impossible for the control because of concern for the well-being of the reef under the plastic sheeting. The limited duration (18 h) of the sheeting cover allowed a total of six runs, during which phytoplankton patchiness was, unfortunately, noticeable. The high variance and ensuing weak statistical power probably accounts for the statistically insignificant difference between the control and the open-reef runs, in spite of the fact that the average grazing in the latter was five times higher.

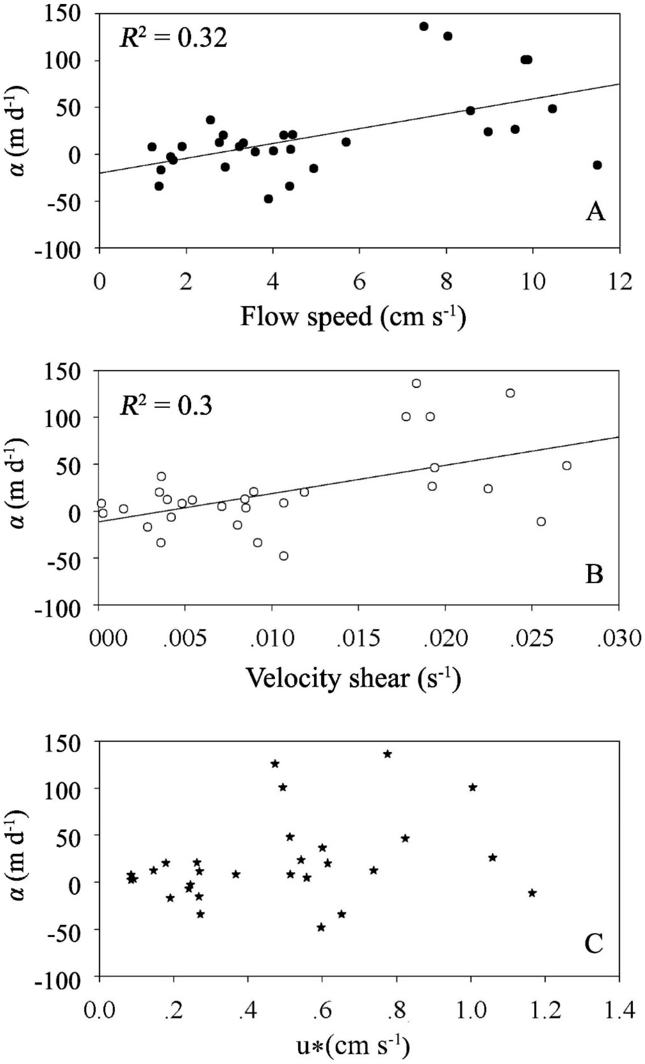

Fig. 6. Grazing rate (*a*) vs. (A) flow speed at 1 mab, (B) velocity shear across the 1 m boundary layer, and (C) u_* are shown.

Our in situ findings parallel those of Atkinson et al. (Atkinson and Bilger 1992; Ribes et al. 2005; Ribes and Atkinson 2007), showing that nutrient uptake by the reef community can be mass-transfer limited. Indeed, we can examine the observed variation in a with velocity in light of mass-transfer theory as applied to coral reefs by Bilger and Atkinson (1992), Baird and Atkinson (1997), and Falter et al. (2004). Following Bilger and Atkinson (their eq. 12), we can write α in the following way:

$$\alpha = \mathrm{St}\, U_b \tag{9}$$

where U_b is the velocity far from the boundary. St is the Stanton number, a nondimensional number that can depend on the roughness of the wall to which mass transfer is taking place, u_*, fluid viscosity (v), and diffusivity through the Schmidt number of the substance being transferred ($\mathrm{Sc} = v\ \mathrm{D}^{-1}$). The linear dependence of α on U_b shown in Fig. 6 implies $\mathrm{St} \approx 1.1 \times 10^{-3}$, whereas taking the mean of ($\alpha = U_b^{-1}$) gives $\mathrm{St} \approx 6 \times 10^{-4}$, values similar to but larger than those reported by Ribes and Atkinson (2007). These values of St are several orders of magnitude larger than what would be expected from diffusion of phytoplankton-sized cells (Ribes and Atkinson 2007), probably reflecting an enhancement of mass transfer by active filter feeders (e.g., sponges, bivalves, and ascidians) which generate incurrent and excurrent flows that can augment mass-transfer in a highly depleted CBL (O'Riordan et al. 1993; Vogel 1994).

A noticeable outcome of the intense benthic grazing was the near-bed depletion of phytoplankton (Fig. 4). As expected, the sharp decrease of Chl a in the benthic boundary layer coincided with an equivalent increase in phaeopigments, a product of chlorophyll digestion (Welschmeyer and Lorenzen 1985). Similar CBLs above dense communities of benthic suspension feeders were found in both temperate communities (Frechette and Bourget 1985; Dolmer 2000; Ackerman et al. 2001) and coral reefs (Yahel et al. 1998, 2005). The depletion intensity near the bed can be characterized using the steepness of the concentration gradient (Wildish and Kristmanson 1997). To the extent that gradient-diffusion models can describe flows near complex roughness such as that of a coral reef, we can compute a second estimate of the grazing flux using this equation:

$$\alpha = \frac{K_z}{\langle C \rangle}\frac{\partial C}{\partial z} = \frac{\kappa u_* z}{\langle C \rangle}\frac{\partial C}{\partial z} \tag{10}$$

where K_z is the vertical turbulent diffusivity, and $\kappa = 0.41$ is the von Karman constant. Based on an average near-bed gradient for all of our data of $\sim 3.7\ \mu\mathrm{g\ m^{-4}}$, an average u_* of 0.005 m s^{-1}, and $\langle C \rangle = 0.17$ mg Chl a m^{-3} at $z = 1$ m, the expected value of α is ~4 m d^{-1}. This estimate is close to the a priori estimate (5.63 m d^{-1}) and is lower than the CoVo-based value of 20 ($\pm$8.1) m d^{-1}; however, neither value is significantly different from the latter (t-test, $p > 0.05$). Laboratory observations made over canopies, i.e., arrays of large roughness elements, suggest that standard formulations of mixing coefficients may underestimate actual scalar fluxes near the tops of the roughness elements (Coppin et al. 1986). The major advantage of the CoVo approach is that no such assumptions are necessary.

Our estimate of phytoplankton grazing of 20 m d^{-1} compares well with reported values of α in other coral reefs, ranging from 7 m d^{-1} to 26 m d^{-1} in the aforementioned flume (Ribes et al. 2005; Ribes and Atkinson 2007), but lower than the 42 m d^{-1} reported for a channel reef by Fabricius and Dommisse (2000).

Limits to the resolution of the technique, especially those imposed by the low Chl a concentrations and the complex nature of the flow and related mixing near the reef, seem to obscure the relationship between the gradient and flow, i.e., we would expect that gradients would decrease with increasing flow. This can be seen using a simple theory for the CBL. Assume that we have a CBL of thickness δ, across which there is a change in concentration ΔC. We define α via the inferred flux to the bed such that, in terms of the real "pumping" rate ϕ (m d^{-1}), we have the following:

$$\begin{aligned}\alpha C_0 = \varphi(C_0 - \Delta C) = \mathrm{flux} = \kappa u_* z\frac{\partial C}{\partial z} = \beta\kappa u_* \delta\frac{\partial C}{\delta}\\ = \beta\kappa u_* \Delta C\end{aligned} \tag{11}$$

where β is an O(1) constant. Thus, solving for $\Delta C / C_0$ we find the following:

$$\frac{\Delta C}{C_0} = \frac{\varphi}{\varphi + \beta\kappa u_*} \tag{12}$$

Thus, for increasing flow speed, $\Delta C / C_0$ should decrease, as observed by O'Riordan et al. (1995) in their laboratory experiments with model bivalve beds. We can also compute α as a function of flow speed and actual pumping using Eq. 11:

$$\frac{\alpha}{\varphi} = \frac{\beta\kappa u_*}{\varphi + \beta\kappa u_*} \tag{13}$$

suggesting that, for weak flows ($\beta\kappa u_* \ll \phi$), the following is true:

$$\frac{\alpha}{\phi} \approx \frac{\beta\kappa u_*}{\phi} \tag{14}$$

Whereas, for strong flows ($\beta\kappa u_* \gg \phi$), the following is true:

$$\frac{\alpha}{\phi} \approx 1 \tag{15}$$

For constant ϕ, under conditions of slow flow, the grazing rate is expected to be limited by hydrodynamics and should increase with flow speed, whereas for fast flows, mixing does not control exchange to the bed. Our experiments fall in the former regime because α is a function of U (Fig. 6). This analysis also points out the importance of coral roughness, since an increase of C_D for a given U increases u_* and thus increases α for a given value of the intrinsic grazing rate ϕ. The connection between roughness and grazing rate suggests that, as the reef becomes more developed in terms of larger corals, and hence larger roughness and wall shear stress, it can also support more intense grazing. This prediction has yet to be tested.

In addition to vertical variations in phytoplankton concentration associated with grazing on the reef, horizontal variations between the reef and offshore must also exist. Conceptually, if the reef acts like a sink for allochthonous phytoplankton, there must be exchange between the offshore and the reef. If this was only associated with longshore flows, then based on our results, one would expect to see a significant longshore variation in phytoplankton concentration, with the highest concentrations observed where water from offshore first encounters the reef and a gradual decline down current. However, neither a longshore gradient in phytoplankton concentration nor a corresponding change in the abundance of benthic suspension feeders is seen along the fringing reefs in Eilat and other parts of the Gulf of Aqaba (Yahel et al. 1998; A. Genin unpubl. data). The lack of such gradients can be fully explained by the prevalence of substantial diurnally varying cross-shore currents (Monismith et al. 2006). During the summer, differential, depth-dependent warming of the shallow water column during the day forces an offshore flow aloft and a shoreward flow near the bottom, and this trend reverses during the cooling period at night (Fig. 3C). The occurrence of such buoyancy-driven, cross-reef currents at other coral reefs (Boden 1952; Neimann et al. 2004) suggests that this circulation can be a key mechanism for replenishing depleted waters over benthic communities on shallow slopes.

The CoVo results are based on the assumption that $d\langle C\rangle/dt \approx 0$. If there were no grazing, but only unsteady changes in concentration due to patchiness, for example, we would infer the following:

$$\frac{H}{\langle C\rangle}\frac{d\langle C\rangle}{dt} = \alpha_{\mathrm{app}} \tag{16}$$

where α_{app} is the apparent grazing rate we would derive from the differences of fluxes through the faces of the CoVo. This short-term unsteadiness may be attributed to the patchiness of the plankton as it passes through the CoVo, since, in the absence of grazing or vertical mixing, the advection equation reduces to the following:

$$\frac{\partial C}{\partial t} \cong -U\frac{\partial C}{\partial x} \tag{17}$$

Thus, spatial variations in C will appear as temporal variations in fixed measurements.

The error implied by Eq. 17 was evaluated using a repetitive, high-resolution set of Chl *a* samples available from a related study carried out ~40 m north of site *B* soon after our field experiment (G. M. Raid, A. K. M. Farrah, and A. Genin unpubl. data). Once every 2 weeks during an 8-week period (October–December 1999), 16 Chl *a* measurements were taken at 15-min intervals during two 4-h periods: one during the day, the other during the night. Each measurement consisted of duplicate water samples, processed for extracted Chl α as in this study. All the samples were taken at 0.75 m above bottom (8-m depth). The time derivative in Eq. 17 was estimated using simple differences of the measured concentrations using this equation:

$$\frac{d\langle C\rangle}{dt} \approx \frac{C(t_2)-C(t_1)}{t_2-t_1} \tag{18}$$

Samples were taken sequentially at times t_1 and t_2. The average (±SE) value of α_{app} calculated for all pairs of consecutive measurements ($n = 231$ pairs) was -2 (± 4) m d^{-1}, i.e., substantially lower than the value of the CoVo-based *a* and not significantly different from zero ($p > 0.5$, *t*-test). Nevertheless, patchiness can considerably increase the "noise" of the CoVo measurements. Therefore, the CoVo approach requires to replicate the runs many times or to use an integrating sampling protocol that averages out temporal variation. That the gradient-flux estimate of α, which is not subject to the vagaries of patchiness, is of the same magnitude as the CoVo estimate, adds confidence in the latter value, which is the average of 30 replicated runs.

To reduce the noise, we recommend the use of samplers that slowly collect the water over a long period (e.g., 30 min), thereby averaging out the patchiness in the water flowing across the CoVo. That is, the sampler should continuously draw water for a period that is much longer than the time it takes a water parcel to cross the CoVo yet is sufficiently short so that no changes in the concentration of the measured parameter occur within the sampler (e.g., due to mortality or production). Following the completion of this study and the realization of the patchiness-related problem, we developed an effective technique to average out patchiness by using small submerged pumps that slowly trickled water (3 L h^{-1}) into inflatable infusion bags (1 L in volume). The flow rate into the bag was set by attaching an irrigation dripper (in line, 4 L^{-1} h^{-1}, nonregulated, Netafim) to the tube between the pump and the infusion bag. Fig. 7 shows an example of the patch-averaging capability of this technique in a trial carried out at the coral reef 40 m north of site *B* on 1 September 2008 (*see* Fig. 7 caption for details). The standard deviation due to patchiness during our sampling was 3–8 times larger than the analytical precision of the chlorophyll measuring technique. For logistic reasons, we could not re-deploy the CoVo setup in order to make additional runs using our new patch-averaging technique.

The in situ CoVo method overcomes key problems associated with past measurements of grazing, including the artifacts of flumes (McDonald et al. 2006) and the inability to track water parcels in a strongly sheared boundary layer using a Lagrangian drifter. Furthermore, the control-volume method is free from assumptions about the flow, i.e., the absence of velocities normal to the boundary at the height of the corals, or the applicability of gradient-diffusion models near a complex, rough surface. However, these advantages come at the price of an inherently low signal-to-noise ratio. If a large CoVo is chosen to maximize potential signal, then spatial variability in concentration, benthic communities, and flow may dominate the measurements, whereas, with small CoVos, the change in concentration may not be adequately resolved by existing analytical approaches. Patch-averaging samplers like the one we developed (Fig. 7) can considerably increase the measurements' signal-to-noise ratio. Together with the recent improvements in analytical instrumentation, the CoVo approach should become a

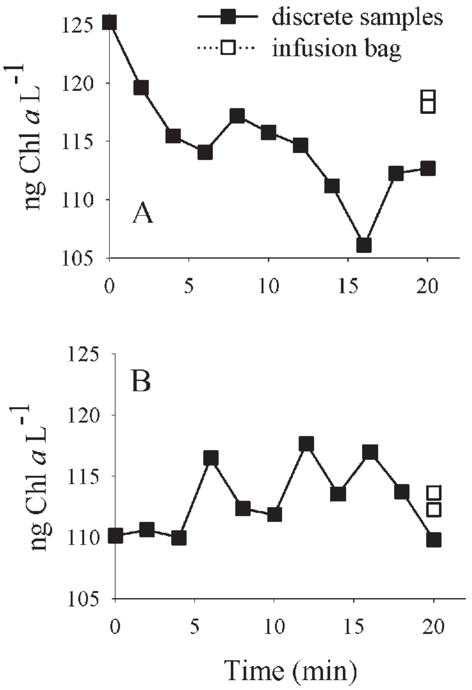

Fig. 7. An example of the patch-averaging technique, comparing the variation of Chl *a* during two 20-min–long time series (A and B), each consisting of 11 discrete samples (filled squares), and the Chl *a* in the corresponding patch-averaging samples (open squares) obtained at a 3-m depth (1 mab) in the coral reef of Eilat on 1 September 2008. The discrete samples in each series were taken every 2 min using a submerged pump (6 L min^{-1}) that delivered the water to a nearby pier (Fig. 1), where the sample bottles (300-mL) were filled. The corresponding patch-averaging sample was obtained at the same place with a small submerged pump that continuously trickled the water (0.05 L min^{-1}) into an inflatable infusion bag during the same 20-min interval. Two samples (300-mL) were taken from each infusion bag, showing that the analytical precision of our Chl *a* measurement was 3–8 times tighter than the ambient variation (patchiness) during the corresponding time series.

useful technique to measure in situ fluxes of key particulate and dissolved commodities (e.g., nutrients, oxygen, organic carbon, and inorganic carbon) between flowing waters and benthic communities in coral reefs, temperate reefs, kelp forest, and perhaps the deep sea.

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