Flow enhances photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water

Tali Mass[a,b,1], Amatzia Genin[a,b], Uri Shavit[c], Mor Grinstein[d], and Dan Tchernov[a,b,2]

[a]H. Steinitz Marine Biology Laboratory, Interuniversity Institute for Marine Sciences, Eilat 88103, Israel; [b]Department of Evolution, Systematics and Ecology, Alexander Silberman Institute of Life Sciences, Hebrew University of Jerusalem, Jerusalem 91904, Israel; [c]Civil and Environmental Engineering, Technion, Haifa 32000, Israel; and [d]Institutes of Earth Sciences, Hebrew University of Jerusalem, Jerusalem 91904, Israel

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Worldwide, many marine coastal habitats are facing rapid deterioration due in part to human-driven changes in habitat characteristics, including changes in flow patterns, a factor known to greatly affect primary production in corals, algae, and seagrasses. The effect of flow traditionally is attributed to enhanced influx of nutrients and dissolved inorganic carbon (DIC) across the benthic boundary layer from the water to the organism however, here we report that the organism's photosynthetic response to changes in the flow is nearly instantaneous, and that neither nutrients nor DIC limits this rapid response. Using microelectrodes, dual-pulse amplitude-modulated fluorometry, particle image velocimetry, and real time mass-spectrometry with the common scleractinian coral *Favia veroni*, the alga *Gracilaria cornea*, and the seagrass *Halophila stipulacea*, we show that this augmented photosynthesis is due to flow-driven enhancement of oxygen efflux from the organism to the water, which increases the affinity of the RuBisCO to CO_2. No augmentation of photosynthesis was found in the absence of flow or when flow occurred, but the ambient concentration of oxygen was artificially elevated. We suggest that water motion should be considered a fundamental factor, equivalent to light and nutrients, in determining photosynthesis rates in marine benthic autotrophs.

photorespiration | coral | seagrass | algae | RuBisCO

The exchange rate of dissolved nutrients, oxygen, and inorganic carbon between sessile organisms and the ambient water is in many cases inversely proportional to the thickness of the diffusive boundary layer (DBL). Because increasing flow speed makes the DBL thinner (1–3), a positive correlation is often found between flow speed and key physiological processes that depend on the uptake of solutes, such as photosynthesis, respiration, growth, and calcification (1, 2, 4, 5). Perhaps the most fundamental of these processes is photosynthesis (6). Enhancement of photosynthesis by flow has been documented in numerous marine benthic autotrophs, including corals (2, 4, 6, 7), algae (8, 9), and seagrasses (10, 11). Traditionally, this enhancement is explained in terms of flow-dependent influx of nutrients and dissolved inorganic carbon (DIC), key elements in the biosynthesis of cell components and as the terminal electron acceptor of the carboxylation pathway, respectively (6–12). However, a recent study showed that the uptake of nutrients by aquatic macrophytes was slower than their diffusion across the boundary layer, indicating that uptake rather than diffusion controls mass transfer, regardless of water velocity (13). Furthermore, for nutrients to become functional in photosynthesis, the molecules must first be assimilated and incorporated in the photosynthetic units, a process that typically takes hours to complete (14), making a role in the fast response of photosynthesis to flow unlikely (5). For DIC to affect this process, the availability of inorganic carbon should limit photosynthesis when flow is absent. Whereas several studies have shown that CO_2 enrichment enhances photosynthesis in some macroalgae (15, 16) and seagrasses (17), other studies inferred no DIC limitation under the pH of seawater, at which the ambient concentration of HCO_3^- exceeds 2 mM (11, 12, 18, 19).

In this study, we tested an alternative explanation, namely, that photosynthesis is affected by the flow-dependent efflux of oxygen from the organism, rather than by the influx of dissolved elements from the water to the organism. There are two possible pathways by which oxygen accumulation inhibits photosynthesis (2, 4): (i) photorespiration, involving enhanced oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) (20), and (ii) the production and accumulation of reactive oxygen species (ROS) (4) through such processes as the Mehler reaction (21, 22). The latter pathway is most pronounced under conditions of extreme temperatures or excessive light (4). Photorespiration is expected to occur when the internal concentration of oxygen is sufficiently high to effectively compete with CO_2 as the substrates of RuBisCO (23), a key enzyme in photosynthetic carbon assimilation.

The objective of this study was to elucidate the mechanism through which flow affects photosynthesis in species belonging to the three main groups of marine benthic autotrophs: the scleractinian coral *Favia veroni*, the seagrass *Halophila stipulacea*, and the macroalga *Gracilaria cornea*.

Results and Discussion

In all three species studied, the onset of flow led to significantly (several-fold) enhanced photosynthesis and a substantial (32%–45%) reduction of oxygen concentration inside the organisms (Fig. 1). Differences between flow and no-flow conditions were highly significant ($P < 0.001$ for each taxon, t test). Incubation of the organisms in a real-time mass spectrometer into which a spike of the isotope $^{18}O_2$ was injected produced increased net photosynthesis under flow conditions compared with no-flow conditions (an average of 3.5 times higher in the coral, 1.9 times higher in the alga, and 2.5 times higher in the seagrass; Fig. 1*D*), and lower respiration, measured based on the decline in $^{18}O_2$, under flow conditions in all three species. The [flow]:[no-flow] ratios of both photosynthesis and respiration were significantly different from 1.0 ($P < 0.001$ and < 0.01, respectively, t test; Fig. 1*D*). The photosynthetic response to the onset of flow was nearly instantaneous (Fig. 1 *A* and *B*). Although, as discussed above, this rapidity makes a role of nutrient influx unlikely, we tested that possibility by directly measuring photosynthesis under no-flow conditions but with high nutrient concentrations. No effect

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[1]To whom correspondence should be addressed. E-mail: tali.mass@mail.huji.ac.il.

[2]Present address: Marine Biology Department, Leon H. Charney School of Marine Sciences, University of Haifa, Haifa 31905, Israel.

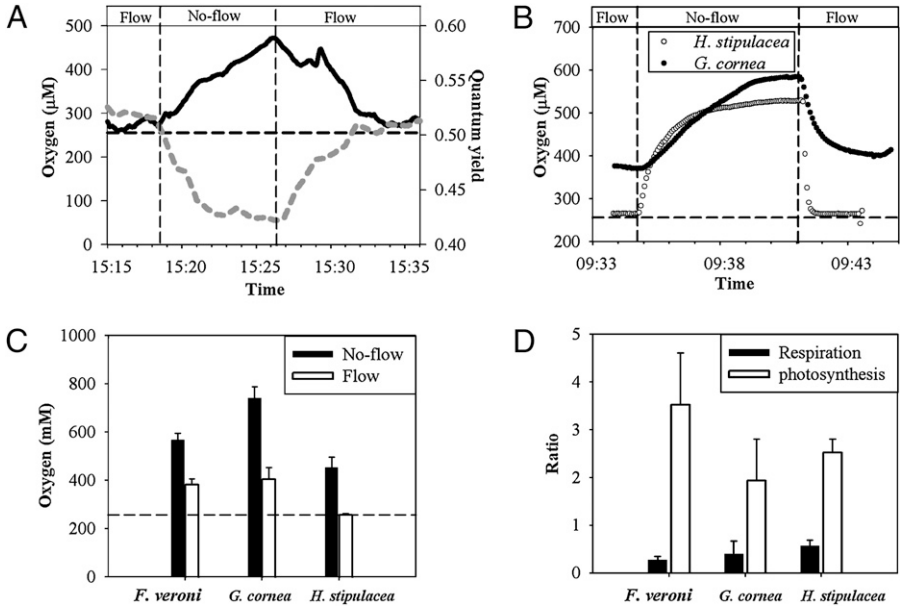

Fig. 1. Effects of flow on oxygen, respiration, and photosynthesis. (*A*) Changes in internal concentration of oxygen (solid line) and quantum yield (dashed line) in *F. veroni* following the onset of flow and its cessation. (*B*) A similar trend of increasing oxygen concentration inside the organism after the cessation of flow and decreasing oxygen concentration after resumption of flow in *G. cornea* (full circles) and *H. stipulacea* (open circles). (*C*) Average (SEM) oxygen concentration inside *F. veroni* ($n = 14$; 2 colonies), the alga *G. cornea* ($n = 8$; 3 specimens), and the seagrass *H. stipulacea* ($n = 5$; 2 plants) under no-flow (solid bars) and flow (open bars) conditions. The dashed horizontal lines indicate ambient oxygen concentration (256 μM). (*D*) Average (SEM) ratios of net photosynthesis (open bars) and respiration (solid bars) between the respective rate with flow and that with no flow ($n = 5$, 3, 3 for *F. veroni*, *G. cornea*, and *H. stipulacea*, respectively).

of the added nutrients on photosynthesis was found ($P > 0.2$, Wilcoxon's signed-rank test, $n = 3$ for each species). Similarly, a doubling of the concentration of HCO_3^- concentration in the incubation chamber (under no-flow conditions) had no effect on photosynthesis in either species ($P > 0.2$, Wilcoxon's signed-rank test, $n = 3$ for each species). Note that our finding that neither nutrients nor DIC affected photosynthesis refers to the short-term effect of flow. Over the long term, the flow-dependent influx of elements, especially nutrients, can have a significant effect on an organism's growth and productivity (1).

The mean flow speed, measured by particle imaging velocimetry (PIV) at 2.5 cm above the surface, was 13.2 cm s^{-1} for the coral, 20.6 cm s^{-1} for the alga, and 4.5 cm s^{-1} for the seagrass (Fig. 2). The corresponding maximum turbulent kinetic energy (TKE), calculated based on the streamwise and vertical components, was 12.7 $cm^2\ s^{-2}$ for the coral, 20.1 $cm^2\ s^{-2}$ for the alga, and 3.03 $cm^2\ s^{-2}$ for the seagrass (Fig. 2*B*). These values fall well within the range of currents in the natural habitats of the three species (24).

Time series of oxygen concentration inside the coral after the onset of flow exhibited the expected Fickian behavior, with an immediate response at the coral–water interface and a delayed response at depths of 0.8 and 1.5 mm inside the tissue (Fig. 3*A*). Integration of the profiles shown in Fig. 3*A* showed that the efflux of oxygen from the coral after the initiation of flow was ~2 μmol $O_2\ m^{-2}\ s^{-1}$. This is a conservative estimate, because it does not account for the net production of oxygen inside the organism. This value was ≈6.6 times higher than the efflux under no-flow conditions (~0.3 μmol $O_2\ m^{-2}\ s^{-1}$), calculated based on the gradient of oxygen concentration outside the coral (~130 mol $O_2\ m^{-4}$; Fig. 3*B*) and its molecular diffusion coefficient ($2.35 \cdot 10^{-9}\ m^2\ s^{-1}$). A corresponding assessment of the above difference in mass fluxes, based on measurements of the dissolution of gypsum spheres (25), indicated that the mass flux in the aquarium was 10.92 times higher under flow conditions than under no-flow conditions, whereas the corresponding difference in the mass spectrometry chamber was 10.09; that is, the effect of the pump on the mass flux over the organism in the aquarium was almost identical to that of the stirrer in the mass spectrometry, both exhibiting realistic flow conditions.

The augmentation of oxygen efflux by flow should be localized, affecting the organism's sections exposed to strong flow. Such localization is expected to be especially important in corals, where photosynthesis increases the pH and in turn supports calcification (26, 27). Thus, it is not surprising that flow has a pronounced effect on skeletal growth of stony corals (28). The persistent maintenance of low internal oxygen concentration by flow also reduces the risk of bleaching in corals living under conditions of strong flow (29). Indeed, initial signs of bleaching sometimes can be seen in the inner parts of branching corals (e.g., fig. 3A in ref. 30), where flow is relatively weak (31).

Two possible pathways can explain the negative effect of high oxygen on photosynthesis under no-flow conditions: the Mehler ascorbate peroxidase reaction (21, 22) and photorespiration (23). Because the Mehler reaction releases hydrogen peroxide (H_2O_2) to the cytoplasm, the addition of catalase, an enzyme that decomposes H_2O_2 to water and oxygen, could be used to test its occurrence, by measuring oxygen concentration after catalase is added to the water. In none of the species examined did the addition of catalase lead to an increase in oxygen concentration. This finding indicates a minor contribution, if any, of the Mehler reaction under no-flow conditions. Note, however, that photorespiration also produces H_2O_2, but here the peroxide is enclosed within the peroxisome, where it is detoxified by autoproduced catalase (32–34).

We conclude that photorespiration, driven by the use of oxygen instead of CO_2 as the substrate for RuBisCO, was the principal cause of the decline in photosynthesis under no-flow conditions. Whereas the species examined had different types of RuBisCO with differing affinities to CO_2 and O_2 (23), in all three species low internal oxygen enhanced photosynthesis (Fig. 1*D*).

If the efflux of oxygen affected photosynthesis, then we would expect the effect of flow to be less pronounced (possibly undetectable) when oxygen concentration in the ambient water is artificially raised (2). Indeed, the elevated oxygen concentration

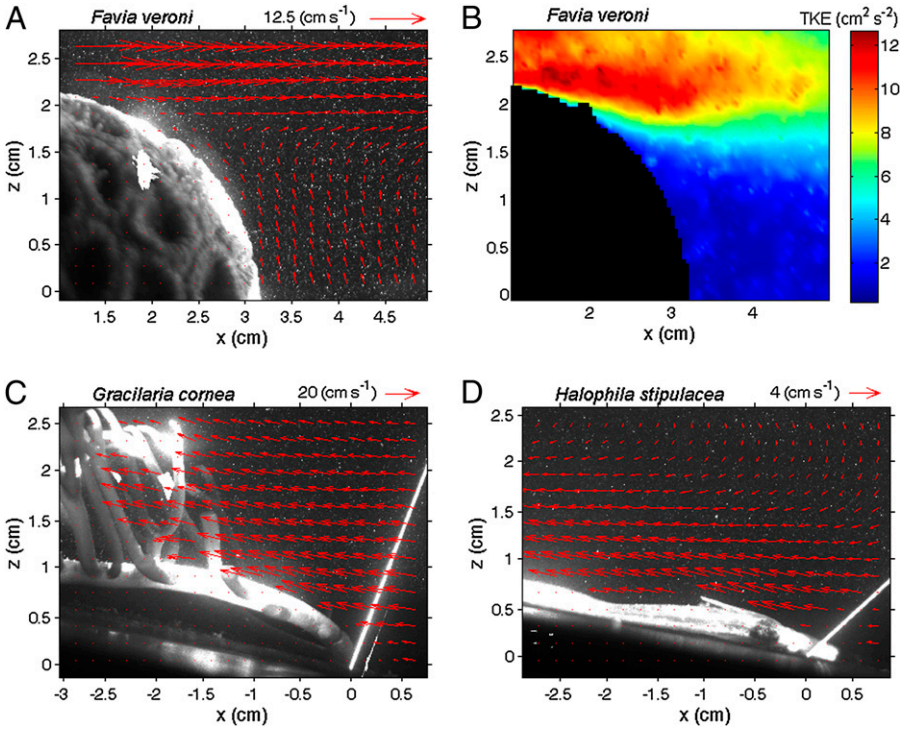

Fig. 2. The velocity field near *F. veroni* (*A*), *G. cornea* (*C*), and *H. stipulacea* (*D*), measured by PIV. To improve visual clarity, only every forth vector is shown. (*B*) The corresponding TKE near the coral.

in the incubation chamber [retaining the normal concentration of HCO_3^- (2.3 mM) and pH (8.2)] nullified the flow-driven enhancement of photosynthesis (Fig. 4). In the coral and seagrass, the hyperoxic conditions even caused respiration to exceed photosynthesis (Fig. 4). The effect of elevated oxygen concentration in the incubation chamber, and the differences in this effect among the species, were highly significant ($P < 0.001$, two-way ANOVA, $n = 3$ specimens for each of the three species). The level of oxygen concentration causing compensation (photosynthesis = respiration) was 440 μM in the coral and 600 μM in the seagrass, whereas concentrations as high as 1200 μM were still below the compensation threshold for the alga. Thus, of the three species examined, the photosynthetic system of *G. cornea* appears to be the least sensitive to elevated oxygen concentration.

The finding that the effect of flow on photosynthesis operates at the level of RuBisCO and photorespiration justifies the consideration of flow as a key environmental factor determining primary production in marine benthic communities, perhaps equivalent in importance to light and nutrients. Past changes in current forcing, such as the intensification of winds and currents during glacial periods (35, 36), could have affected benthic productivity in coral reefs, kelp forests, and other coastal habitats. The magnitude of such changes is yet to be assessed at the community and ecosystem levels, however. Given the positive relationships between photosynthesis and calcification in corals (37), exposure to flow may locally ameliorate the predicted deterioration of coral reefs due to ocean acidification (38).

Methods

The scleractinian coral *F. veroni* and the seagrass *H. stipulacea* were collected by scuba divers at depths of 2–15 m in the Red Sea coral reef in front of the H. Steinitz Marine Biology Laboratory, Eilat, Israel (29°30′ N, 34°56′ E). The red alga *G. cornea* was obtained from the National Center for Mariculture in Eilat.

The microelectrode and PIV measurements were carried out in an aquarium (18 × 16 × 30 cm) under conditions of average seawater temperature (25 °C) and moderate light intensity (350 μmol photons m^{-2} s^{-1}). The light source was a halogen lamp (21V, 150W) fitted with a collimating lens and fiberoptics (MI-150; Dolan Jenner). This light intensity was weaker than the level required for maximum photosynthesis (39) at the depths at which the organisms were collected. A small aquarium pump (5 L min^{-1} capacity; Atman AT-301) was used to generate flow. The pump outlet was aligned so that the flow streamlines surrounded the representative species in a symmetric pattern, measured near the organisms using PIV, as described below.

Oxygen Microelectrode. Point measurements and profiles of oxygen concentration within the organism's tissues and across its diffusive boundary layer were measured using a Clark-type O_2 needle microelectrode (1.1-mm tip diameter; OXN; Unisense), attached to a custom-built picoampere meter (Keithley). Data were recorded using LabVIEW version 6.1 for Windows (LTR Publishing). The microelectrode was inserted into the organism's tissue at an angle of ~135°–145° relative to the flow direction using a manual micromanipulator (XYZ hydraulic; Narishige) under a dissecting microscope. The microelectrode was calibrated at 25 °C in air-saturated and zero concentration (nitrogen-flushed) seawater.

Calculation of Oxygen Efflux. The efflux of oxygen under flow conditions was calculated using time series of oxygen concentrations measured after the onset of flow at the surface of *F. veroni* and 0.8 and 1.5 mm inside its body (Fig. 3*B*). A numerical trapezoidal spherical integration was used to calculate the amount of oxygen (Δm) that was depleted from the coral tissue during the first 15 seconds of flow, using the following equation:

$$\Delta m = \int_{R_i}^{R_o} c(t=0)4\pi r^2 dr - \int_{R_i}^{R_o} c(t=15s)4\pi r^2 dr, \qquad (1)$$

where the concentrations c at $t = 0$ and $t = 15$ s are assumed to be linear at each segment (0–0.8 mm and 0.8–1.5 mm); $c = ar + b$, where a and b are the linear regression coefficients for each segment; and R_i and R_o are the inner and outer radii of each segment. The depleted amount of oxygen was divided by time (15 s) and coral surface area (0.012 m^2; coral radius, 30.9 mm), yielding an estimated oxygen efflux following the onset of flow.

Photosynthesis and Respiration. Measurement of net production, gross production, and light-dependent consumption of oxygen in the three species were measured under normal and elevated concentrations of oxygen, nutrients, and HCO_3^- using membrane inlet mass spectrometry. This instrument uses mem-

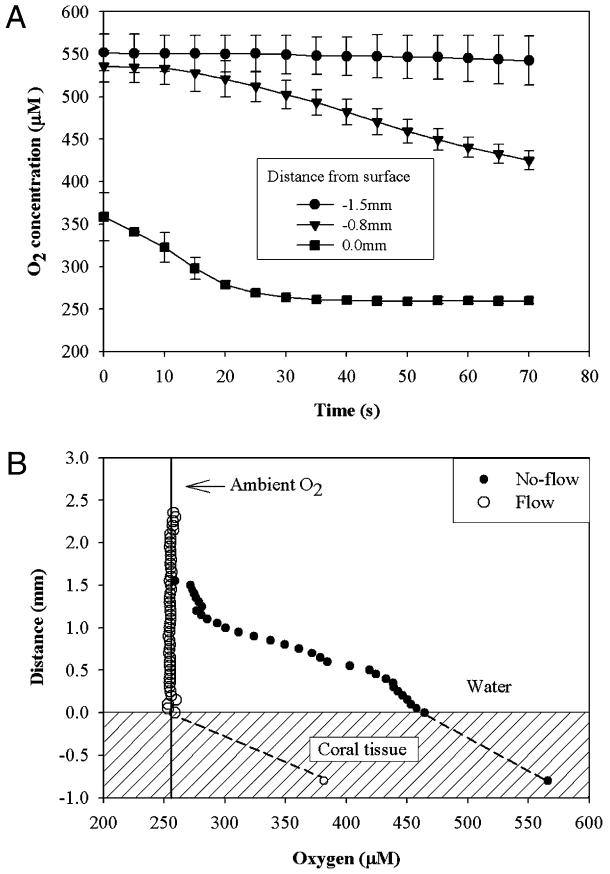

Fig. 3. Changes in oxygen concentration with time and distance near the interface between *F. veroni* and the water. (*A*) Average time series (n = 2–3 series) of oxygen changes during the first 70 s after at the onset of flow, at the coral–water interface, and 0.8 and 1.5 mm inside the coral. (*B*) Average profile of oxygen concentration outside and inside *F. veroni* under flow and no-flow conditions (n = 4 and 7 profiles, respectively).

brane inlet system attached to a Prisma QMS-200 quadrapole mass spectrometer (Pfeiffer Vacuum), with closed ion source and electron multiplier detector that measures the concentrations of the target elements ($^{16}O_2$ and $^{18}O_2$) and two reference elements (^{14}N and ^{40}Ar) every 5 s in a small (3.3 mL), custom-made chamber containing a small specimen of the target species. Photosynthesis was calculated based on the evolution rate of $^{16}O_2$ in the chamber water, whereas respiration was calculated based on the decline in $^{18}O_2$ after a spike of this element was added to the water (amounting to ~1% of the total dissolved oxygen). All of the measurements were replicated with three specimens of each species, under flow and no-flow conditions, both under dark and light conditions (40). Flow was generated in the chamber using a small stirrer. The temperature of the seawater in the chamber was maintained at 25 °C using a water jacket connected to a temperature-controlled water bath. A 150-W cold light source (Schott KL 1500) was used for illumination at a level of 500 μmol photons m^{-2} s^{-1}. The oxygen sensor was calibrated under conditions of oxygen saturation and zero concentration (nitrogen-flushed).

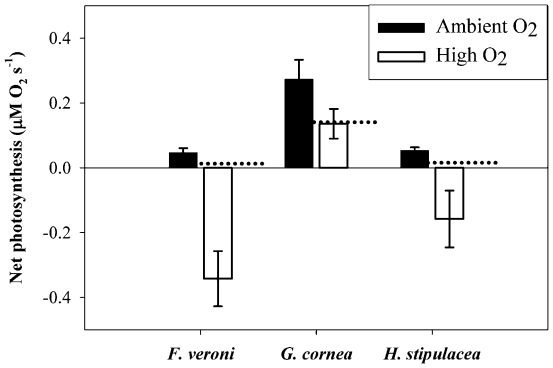

Fig. 4. Average (SEM) net photosynthesis under flow conditions in water with normal (solid bars) and supersaturated (200%–500%; open bars) concentrations of oxygen (n = 3 for all three species). The horizontal dotted lines indicate the expected net photosynthesis under conditions of no flow and normal oxygen concentration, calculated based on Fig. 1*C*.

Photosynthesis Efficiency. Measurements of quantum yield of photosystem II were made in the *F. veroni* using dual-pulse amplitude modulated fluorometry (PAM), as described previously (41). The device's fiberoptics was positioned ≈5 mm from the organism's surface at an angle of ~45° relative to the flow direction, 4–5 cm from the oxygen microsensor. No PAM measurements were possible for the alga and seagrass because of their undulating motion under flow conditions.

Particle Image Velocimetry. PIV (42) is a noninvasive optical measurement technique that provides two-dimensional, two-component, instantaneous velocity fields obtained by comparing the positions of particles in pairs of images recorded with a double-shutter imaging system. For this study, we used natural seawater particles illuminated with a two Nd:YAG pulsed-laser system (Twins ULTRA PIV-200 laser; Big Sky), emitting 200 mJ per pulse. One thousand image pairs were acquired for each specimen along a vertical plain near the vicinity of the microelectrode insertion point. Each image pair generated ≈5,400 velocity vectors, used to obtain mean velocity and TKE, as shown in Fig. 2.

Gypsum Dissolution Measurements. The gypsum dissolution technique (25) was used to assess the difference of mass flux between the flow and no-flow conditions. Six replicated runs were carried out in the aquarium, three with pump-generated flow identical to that used for the microelectrode experiment and three in still water. In each run, a molded sphere of gypsum, 6.2 cm in diameter (similar to that of the studied coral), was put for 16.8 h attached on short (2 cm) stands. Similarly, six replicated runs were carried out in the mass spectrometry chamber, three runs with the stirrer-generated flow and three in still water. Here the clods were cylinders (7 mm diameter, 15 mm tall), and the run lasted 2.0 h. To avoid saturation of dissolved gypsum during the experiment, the water was replaced every 10 min. In both experiments, the dissolution rate was calculated based on the decline in the clods' dry weight.

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1. Atkinson MJ, Bilger RW (1992) Effects of water velocity on phosphate uptake in coral reef-flat communities. *Limnol Oceanogr* 37:273–279.
2. Finelli CM, Helmuth BST, Pentcheff ND, Wethey DS (2006) Water flow influences oxygen transport and photosynthetic efficiency in corals. *Coral Reefs* 25:47–57.
3. Kays WM, Crawford ME (1980) *Convective Heat and Mass Transfer* (McGraw-Hill, New York).
4. Lesser MP (1996) Elevated temperatures and ultraviolet radiation cause oxidative stress and inhibit photosynthesis in symbiotic dinoflagellates. *Limnol Oceanogr* 41:271–283.
5. Patterson MR, Sebens KP, Olson RR (1991) In situ measurements of flow effects on primary production and dark respiration in reef corals. *Limnol Oceanogr* 36:936–948.
6. Hoogenboom MO, Connolly SR (2009) Defining fundamental niche dimensions of corals: Synergistic effects of colony size, light, and flow. *Ecology* 90:767–780.
7. Dennison WC, Barnes DJ (1988) Effect of water motion on coral photosynthesis and calcification. *J Exp Mar Biol Ecol* 115:67–77.
8. Carpenter R, Williams S (2007) Mass transfer limitation of photosynthesis of coral reef algal turfs. *Mar Biol* 151:435–450.
9. Koehl MAR, Alberte RS (1988) Flow, flapping, and photosynthesis of *Nereocystis luetkeana*: A functional comparison of undulate and flat blade morphologies. *Mar Biol* 99:435–444.
10. Enriquez S, Rodriguez-Roman A (2006) Effect of water flow on the photosynthesis of three marine macrophytes from a fringing-reef lagoon. *Mar Ecol Prog Ser* 323:119–132.
11. Larkum AWD, Drew E, Ralph P (2006) *Seagrasses: Biology, Ecology and Conservation*, eds Larkum AWD, Orth RJ, Duarte CM (Springer, Dordrecht, The Netherlands), pp 323–345.

12. Lesser MP, Weis VM, Patterson MR, Jokiel PL (1994) Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): Diffusion barriers, inorganic carbon limitation, and biochemical plasticity. *J Exp Mar Biol Ecol* 178:153–179.
13. Nishihara GN, Ackerman JD (2009) Diffusive boundary layers do not limit the photosynthesis of the aquatic macrophyte, *Vallisneria americana*, at moderate flows and saturating light levels. *Limnol Oceanogr* 54:1874–1882.
14. Lehniger AL (1978) *Biochemistry* (Worth, New York).
15. Borowitzka MA, Larkum WD (1976) Calcification in the green alga *Halimeda*, III: The sources of inorganic carbon for photosynthesis and calcification and a model of the mechanisms of calcification. *J Exp Bot* 27:879–893.
16. Gao K, McKinley K (1994) Use of macroalgae for marine biomass production and CO_2 remediation: A review. *J Appl Phycol* 6:45–60.
17. Zimmerman RC, Kohrs DG, Steller DL, Alberte RS (1997) Impacts of CO_2 enrichment on productivity and light requirements of eelgrass. *Plant Physiol* 115:599–607.
18. Burris JE, Porter JW, Laing WA (1983) Effects of carbon dioxide concentration on coral photosynthesis. *Mar Biol* 75:113–116.
19. Goiran C, Al-Moghrabi S, Allemand D, Jaubert J (1996) Inorganic carbon uptake for photosynthesis by the symbiotic coral/dinoflagellate association, I: Photosynthetic performances of symbionts and dependence on sea water bicarbonate. *J Exp Mar Biol Ecol* 199:207–225.
20. Goldsworthy A (1970) Photorespiration. *Bot Rev* 36:321–340.
21. Asada K (2000) The water–water cycle as alternative photon and electron sinks. *Philos Trans R Soc Lond B* 355:1419–1431.
22. Mehler AH (1957) Studies on reactions of illuminated chloroplasts, I: Mechanism of the reduction of oxygen and other Hill reagents. *Arch Biochem Biophys* 33:65–77.
23. Jordan DB, Ogren WL (1981) Species variation in the specificity of ribulose biphosphate carboxylase/oxygenase. *Nature* 291:513–515.
24. Reidenbach MA, et al. (2006) The effects of waves and morphology on mass transfer within branched reef corals. *Limnol Oceanogr* 51:1134–1141.
25. Falter JL, Atkinson MJ, Coimbra CFM (2005) Effects of surface roughness and oscillatory flow on the dissolution of plaster forms: Evidence for nutrient mass transfer to coral reef communities. *Limnol Oceanogr* 50:246–254.
26. Furla P, Galgani I, Durand I, Allemand D (2000) Sources and mechanisms of inorganic carbon transport for coral calcification and photosynthesis. *J Exp Biol* 203:3445–3457.
27. Schneider K, Erez J (2006) The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. *Limnol Oceanogr* 51: 1284–1293.
28. Veron J, Pichon V (1976) *Scleractinian of Eastern Australia, Monograph 1: Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae* (Australian Institute of Marine Science, Townsville, Australia).
29. Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866.
30. Rowan R, Knowlton N, Baker A, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* 388:265–269.
31. Chang S, et al. (2009) Flow inside a coral colony measured using magnetic resonance velocimetry. *Limnol Oceanogr* 54:1819–1827.
32. Asada K (1999) The water–water cycle in chloroplasts: Scavenging of active oxygens and dissipation of excess photons. *Annu Rev Plant Physiol Plant Mol Biol* 50:601–639.
33. Badger MR, et al. (1998) The diversity and coevolution of Rubisco, plastids, pyrenoids, and chloroplast-based CO_2-concentrating mechanisms in algae. *Can J Bot* 76: 1052–1071.
34. Robert G, et al. (2009) Apoplastic superoxide level in wheat protoplast under photooxidative stress is regulated by chloroplast redox signals: Effects on the antioxidant system. *Plant Sci* 177:168–174.
35. Praetorius SK, McManus JF, Oppo DW, Curry WB (2008) Episodic reductions in bottom-water currents since the last ice age. *Nat Geosci* 1:449–452.
36. Toggweiler JR, Russell J (2008) Ocean circulation in a warming climate. *Nature* 451: 286–288.
37. Barnes DJ, Chalker BE (1990) *Ecosystems of the World: Coral Reefs*, ed Dubinsky Z (Elsevier, Amsterdam), pp 109–131.
38. Silverman J, et al. (2009) Coral reefs may start dissolving when atmospheric CO_2 doubles. *Geophys Res Lett* 36:L05606.
39. Mass T, et al. (2007) Photoacclimation of *Stylophora pistillata* to light extremes: Metabolism and calcification. *Mar Ecol Prog Ser* 334:93–102.
40. Canvin DT, et al. (1980) Oxygen exchange in leaves in the light. *Plant Physiol* 66: 302–307.
41. Schreiber U, Bilger W, Neubauer C (1994) *Ecophysiology of Photosynthesis*, eds Schulze ED, Caldwell MM (Springer, Heidelberg), pp 49–70.
42. Raffel M, Willert CE, Wereley ST, Kompenhans J (2007) *Particle Image Velocimetry: A Practical Guide* (Springer-Verlag, Berlin).