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REPORT

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Effects of water flow on growth and energetics of the scleractinian coral *Agaricia tenuifolia* in Belize

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Abstract The branching scleractinian coral *Agaricia tenuifolia* is abundant on reefs in Belize, over an exceptionally broad range of depth, flow regime, and irradiance. Photosynthesis and respiration of coral branches were measured over a range of irradiance and unidirectional flow speeds (1–10 cm s^{-1}) using a small-volume respirometry chamber designed for flat coral branches. Respiration rate increased significantly with flow speed; however, there was no significant effect of flow on either α or P_{max}, indicating that this coral could thus carry out maximum photosynthesis even at very low flow. This result contrasts with published results for other coral species that experience a significant increase in net photosynthesis with flow speed. Growth rates of *A. tenuifolia* were measured using branch fragments in a variety of reef habitats, over a range of water flow speeds. Growth rates were comparable over most habitat types, across a depth range of 1–15 m. Compared to 1 m, flow and irradiance at 15 m decreased to less than 20% and less than 50%, respectively. Reduced growth was observed only at 24-m depth, and in low-flow microhabitats (concavities) at 15 m. Transplants to 1 m, in the surf zone, also had reduced growth and were the only group to suffer significant colony mortality. At 8- and 15-m depth, growth rate of flat coral branches was not affected by orientation (parallel or perpendicular to flow) or shading. Compared with studies of other species, *A. tenuifolia* displays an ability to utilize a greater range of habitats and flow speeds, suggesting that it may have specific adaptations that allow it to tolerate very low flow conditions.

Keywords *Agaricia tenuifolia* · Coral energetics · Photosynthesis · Coral growth · Water flow

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Introduction

Determining the factors that affect the distribution of reef corals along gradients of wave action and depth is of great importance to understanding coral reef community structure. Studies of water flow on coral biology concentrated originally on stress and breakage of corals in high flow, and on the resulting modifications of form (Done 1982; Graus and MacIntyre 1989). Recent studies have further demonstrated the importance of water flow in modulating physiological processes in corals, enhancing photosynthesis by symbiotic algae, and increasing respiration rates of coral tissue (Dennison and Barnes 1988; Patterson et al. 1991; Patterson 1992; Atkinson et al. 1994; Lesser et al. 1994; Bruno and Edmunds 1998). Water flow affects the encounter rate of corals with particles, including zooplankton, and thus ingestion rates of particulate material (Sebens 1997; Sebens et al. 1997, 1998; Fabricius et al. 1995), and uptake of dissolved nutrients by corals (Atkinson and Bilger 1992; Thomas and Atkinson 1997) and is also important in aiding sediment removal from coral surfaces (Rogers 1990). Thus, some corals grow more rapidly when flow increases (Jokiel 1978; Montebon and Yap 1997; Kuffner 2001). However, field studies examining the effects of water flow on coral growth and physiological performance are lacking.

Many studies of water flow on coral reefs have measured current speeds and net flows over whole reefs, yet few have considered flow as it is experienced by the corals themselves. Adequate information on water movement near coral surfaces, in a variety of reef zones, has not been available until recently (Sebens and Johnson 1991; Helmuth and Sebens 1993; Johnson and Sebens 1993; Sebens and Done 1992). Such studies indicate that water flow at moderate depths on the forereef, and in lagoonal or backreef environments, is usually well below speeds that are optimal for particle capture, photosynthesis, or nutrient uptake (Sebens 1997). Wave-induced flow in shallow reef zones provides conditions conducive to maximum photosynthesis, capture of particles, and uptake of nutrients, and this is where the fastest growing corals generally dominate. Here, we investigate the effects of water flow on respiration and photosynthesis by a common Caribbean coral, *Agaricia tenuifolia*. We also relate these controlled measurements to growth rate data collected in the field, over a range of microhabitats.

The upright plating coral, *A. tenuifolia*, is abundant in habitats from shallow exposed reefs to extremely protected lagoons in Belize, spanning a very broad range of physical conditions, especially water flow and irradiance. The structure of *A. tenuifolia* aggregations displays a wide diversity of morphologies, particularly in spacing between branches (Helmuth et al. 1997a, 1997b). Coring studies by Aronson and Precht (1997) and Aronson et al. (1998, 2002) found that staghorn coral, *Acropora cervicornis*, was the spatial dominant on lagoonal edge reefs in Belize for up to 3,000 years. This condition persisted until the late 1980s, when populations were destroyed by an outbreak of white band disease (Aronson et al. 1998). The community then switched to one dominated by *A. tenuifolia*. In late 1998, this system was again upset by a mass mortality caused by a bleaching event, coincident with an increase in sea surface temperature (Aronson et al. 2000). Levels of mortality due to bleaching in Belize were highest in areas in and near to the Pelican Cays, areas characterized by low water flow (Helmuth et al. 1997a; Shyka and Sebens 2000). Such observations suggest that increased levels of bleaching may have been exacerbated directly through flow-mediated effects on coral physiology (Patterson and Price 1992), or indirectly if reduced water motion led to localized increases in water temperature via solar heating.

Our previous studies examined the links between morphology, environmental conditions, and physiology of the *A. tenuifolia* symbiosis in habitats varying in water flow and mean irradiance. Decreased branch spacing limits mass transfer between coral tissues and water, but branch spacing was linked most closely to ambient light levels (Helmuth et al. 1997a). In general, spacing between branches increased with depth (and decreasing light) on the forereef; however, mangrove lagoon-edge habitats with very low flow but high irradiance also produced colonies with tight interbranch spacing. Decreased irradiance within aggregations also had a large effect on vertical extent of tissue on branches, zooxanthellae density, and pigment composition (Helmuth et al. 1997b). While decreased spacing between branches significantly affects water flow and mass transfer to coral tissues, this coral appears very tolerant of such low flow conditions, in marked contrast to coral species examined previously (e.g. Dennison and Barnes 1988; Patterson et al. 1991; Lesser et al. 1994; Rex et al. 1995).

In this study, we examined the coupled effects of water flow and light level on photosynthesis and respiration of coral and algal tissue using respirometry chambers in flowing seawater aquaria. We also used field growth (transplant/explant) experiments to determine the effects of depth, irradiance, and flow on growth rates of *A. tenuifolia* in a variety of habitats. These experiments took advantage of microhabitat variation including convexities (high flow), flat surfaces (moderate flow), and concavities (low flow) at a given depth, all having the same irradiance and water conditions (temperature, nutrients).

Materials and methods

Photosynthesis and respiration

Three respirometry chambers (Plexiglas 2×6×10 cm, 300 ml) were connected to submersible pumps (Rule 800 gph) with variable input voltage (1–12 V DC; Fig. 1) and water from each chamber cycled past a polarographic oxygen membrane electrode connected to an Oxygraph three electrode system (Hansatech Instruments, Norfolk, England, UK). Oxygen diffusion through the plastic tubing was not measurable in 30-min laboratory tests, and thus

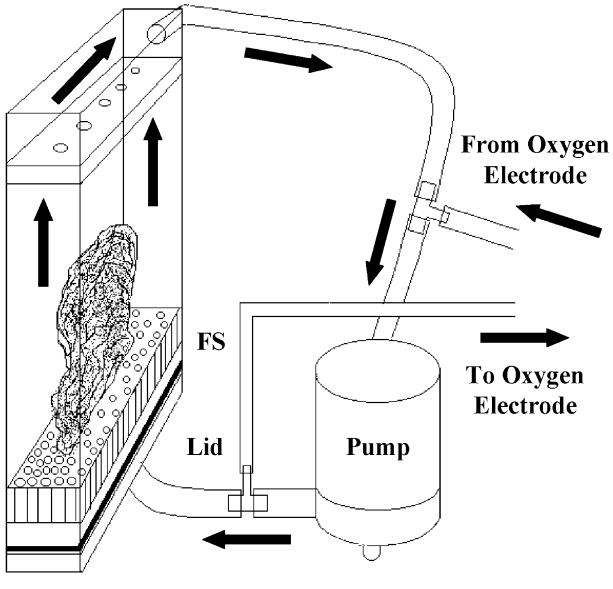

Fig. 1 Apparatus used to produce unidirectional turbulent flow over plates of *A. tenuifolia*. A submersible pump circulates water from bottom to top of the rectangular Plexiglas chamber. Flow straighteners (FS) in the bottom of the chamber distribute flow evenly across the chamber. Tubing upstream and downstream of the pump circulates flow to oxygen sensors. The apparatus was completely submerged in a large water bath to control temperature and provide water for flushing the chamber

was considered negligible during experimental runs. Mean flow speeds ranged from 1 to 10 cm s^{-1}, measured by timing water movement through chambers with coral present. Flow was unidirectional in the chambers, although the small space between coral and chamber walls produced fully turbulent flow that was not of equal speed across the chamber.

Corals were collected, attached to slit PVC pipe racks, and returned to the same depth for tissue recovery over 3–5 days in March 2000. *A. tenuifolia* branches (4×4×0.5 cm) were taken from ten widely separated colonies at 1–2 m depth off Carrie Bow Cay, Belize (16°48.0'N, 88°05.0'W). Corals were transferred to the laboratory and mounted inside chambers, each within a flowing seawater bath (beige plastic container, 40 L). Temperature was monitored in the bath, and in respirometry chambers when water was flushed out. Branches were oriented upright, as in field aggregations, and chamber orientation was adjusted as the angle of the sun changed to achieve approximately equal lighting on both branch sides. A LiCor LI192SA planar underwater sensor (PAR 400–700 nm) was mounted in the same position as the coral chamber, facing the container wall. Data were collected during periods with few or no clouds (noon ± 3 h) and irradiance (photosynthetic photon flux density) was logged each minute. Light reduction by nylon screens and by the Plexiglas chamber walls was determined with the same sensor.

Corals were acclimated and tested at full morning irradiance, then shaded by one to four layers of screen over the chambers. For consistency, light was progressively decreased simulating increasing cloud cover or dusk. Respiration was measured after corals had experienced several hours of darkness. When oxygen concentration changed by more than 10–15% of ambient, the chamber was flushed with new seawater. Laboratory tests showed that changing the pressure of water contacting the oxygen sensor shifted the calibration by only a few percent. Oxygen flux could thus be calculated accurately a few minutes after flushing or changing flow speed. High flow rates in the tubing leading to the oxygen sensor were found to be critical for accurate readings. Controls were run with empty chambers at each flow speed, with or without light, just before experimental runs.

Oxygen flux was measured at flow speeds of 2, 5, 8, and 10 cm s^{-1} and a full range of irradiances (0–1,400 μM m^{-2} s^{-1}). Saturating light levels ($P_{max,}$ I > 700 μM m^{-2} s^{-1}) were used for further flow comparisons. A lower speed (1 cm s^{-1}) was added when it was noted that P_{max} was high even at 2 cm s^{-1}. Temperature in the chambers increased between flushes; time between flushes was limited to keep temperatures at 28.0 ± 1.5 °C. At the end of each experiment, each coral was photographed, polyps counted, and then bisected. One half was used for zooxanthellae counts and chlorophyll determinations [methods in Helmuth et al. (1997b)], and the other was dried for total CHN analysis. Surface area was determined from photographs (NIH Image software).

Field growth experiments

Field experiments examined growth rates over the full extent of physical conditions experienced by populations of *A. tenuifolia* at this site. In January 1992 a study was initiated to assess the effect of depth on growth rate. Branches were collected and returned to each depth from 8 to 24 m (explants); branches from 8 m were moved to 15- and 24-m sites (transplants). Multiple branches were collected from a colony and each branch was exposed to a different treatment (e.g. depth, microhabitat). Branches were trimmed to 4–5 cm wide and 6–8 cm long, then were clamped into PVC pipe racks (3-cm diameter, 30- to 40-cm length) slit along one side (3-mm slit width). A wide-tip screwdriver was used to spread the PVC, a branch base was inserted and the screwdriver removed, allowing the PVC to apply pressure (Fig. 2). This method is rapid and obviates the need for epoxy or other invasive attachment methods. Branches from four colonies were mounted in each rack, with racks 3–10 m apart. The PVC rack was attached tightly to the reef using cable ties to concrete nails or through coral rock. Branches were mounted upright, with broad sides facing the dominant flow direction.

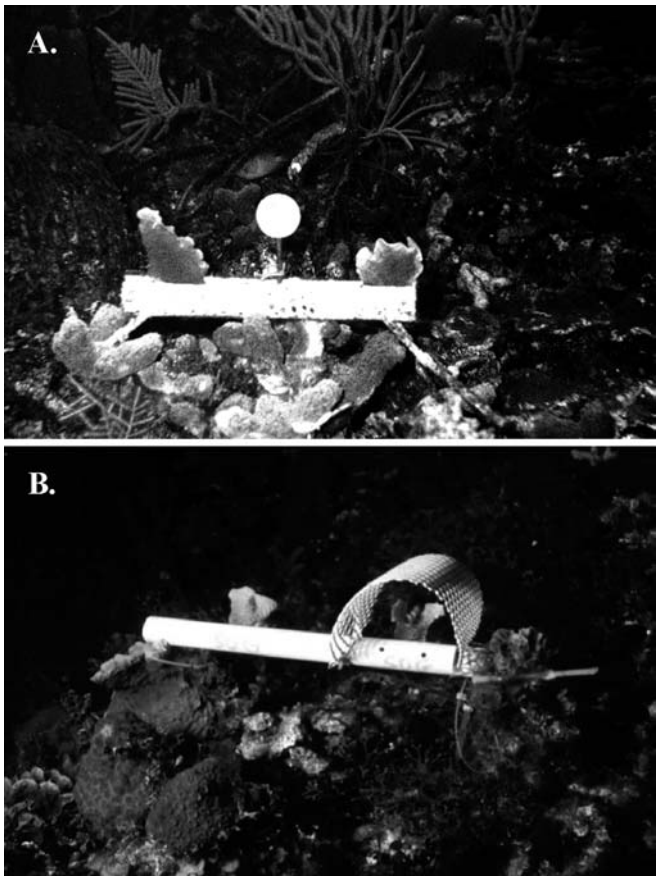

Fig. 2 **A** Growth transplant of two *A. tenuifolia* plates clamped in slit PVC pipe, with a plaster sphere in the center for a 2-day flow measurement. **B** Growth transplant of *A. tenuifolia* under a light reduction grid, with an adjacent control. PVC pipes are approximately (**A**) 20 and (**B**) 25 cm long

We tested the effects of varying flow at a single (8-m) depth using microhabitat variation. Convex surfaces (buttress tops) experience greater flow than concave surfaces (valleys), and flat surfaces provide intermediate flow speeds. Transplanted corals thus experienced different flow speeds, but the same irradiance and water conditions (temperature, nutrient concentration). The effect of branch orientation was tested at a single depth (12 m) by orienting explants parallel or perpendicular to flow. Corallum ridge orientation (raised skeleton between rows of polyps) was also manipulated among explants. Ridges are generally horizontal in the field, but can be found oriented vertically at colony edges.

Experiments were retrieved in April 1992, corals were photographed, and skeletal growth was measured on branches removed from the PVC rack using buoyant weight (in seawater). Changes in skeletal weight were expressed as absolute weight gained and as weight gained relative to initial weight (percent) to control for the variance in initial weight. In this coral, branches grow by adding length and width with little change in plate thickness. Therefore, weight is a good proxy for surface area and weight gain relative to initial weight is linear with weight gain relative to coral surface area. Weight gain was used because it can be determined much more accurately and quickly than surface area, detecting weight changes of less than 1% (Davies 1995). Buoyant weight measures skeletal weight alone; the tissue contribution is negligible. Differences in tissue growth among treatments were thus not examined and our growth rates apply only to skeletal increase.

We repeated the depth study during March to July 1994, and included three shallower (1-m depth) habitats: two on the forereef and one in the backreef environment. We also repeated the flow microhabitat study on large *A. tenuifolia* buttresses at 8-m depth

and at 15 m, where flow speeds were less than at 8 m. Observations indicated that branches sticking out of large aggregations at 8 m experienced high flow, branches within the aggregations experienced less flow, and those in closed channels within the aggregations received the least flow. Open channels experienced strong upward movement of water from deep within the aggregation (induced flow), as well as eddy penetration from above. All weight changes (1992, 1994) were standardized to 110-day rates (i.e. to the longest deployment). Analysis of variance was performed using SigmaStat version 2.03; all data sets were tested for normality and for homogeneity of variance.

We added a partial shade treatment (8 and 15 m) during June to July 1994 to determine whether light could be limiting growth at those depths. Two branches from the same colony were mounted in a PVC rack, with one branch shaded underneath a curved sheet of Vexar mesh (0.8-cm openings). The mesh was oriented to provide shade along the path of the sun (east/west), which reduced irradiance by approximately 30%, as measured by a LiCor spherical (4 pi) sensor in shallow water (Fig. 2). The open ends of the mesh shade were oriented to the prevailing flow, north to south at this site.

Water flow measurements

Two Interocean S4 recording electromagnetic current meters were used to characterize near-mainstream flow 50 cm off the substratum in unobstructed reef locations [methods in Helmuth and Sebens (1993); Sebens and Done (1992); Helmuth et al. (1997a)]. Meters were deployed over a depth gradient of 1–30 m (Fig. 3), placed 5–10 min at each depth during SCUBA dives, to provide a depth transect of flow within a 1- to 2-h period, on days with different surface wave and current conditions. The meters collected data in two dimensions every 0.5 s; the mean of these data is a measure of total water movement past a given point (irrespective of direction) rather than net flux. Flow 50 cm off the substratum is directly relevant to suspension feeders such as gorgonians, or tall mounding and branching corals. However, many coral polyps are on mounds and branches a few to tens of centimeters off the substratum. Based on our previous studies (Helmuth and Sebens 1993, unpublished data) flow at 5–10 cm off the substratum is often equal to or only slightly less than the flow at 50 cm in oscillatory flow.

Dissolution of plaster spheres over 1–2 days was used as an integrated measure of water movement at each transplant/explant rack (Muus 1969; Jokiel and Morrissey 1993; Rex et al. 1995). Plaster spheres (3 or 5 cm in diameter) were fabricated in a Plexiglas mold, embedded with 5-cm screws. Underwater, spheres were screwed into the slit top of each PVC pipe rack (Fig. 2), placing the sphere at the same height as the coral branches. For calibration, groups of three to five plaster spheres were mounted on T-shaped PVC racks, with spheres 50 cm off the bottom and within one lateral meter of the S4 meters in low and high flow habitats. Calibrations were carried out at the field site because plaster dissolution rate depends on temperature, turbulence, and type of flow [oscillatory, unidirectional; Porter et al. (2000)]. Turbulence near the bottom (around racks) can be higher than at the S4 meter; thus even the field calibrations provide only approximate measures of mean flow speed. However, plaster dissolution is an excellent proxy for mass flux, which depends on flow speed, type, and turbulence (Porter et al. 2000).

Results

Coral energetics

Corals in flow chambers displayed typical P/I curves, with few discernable differences among flow speeds (Fig. 4). Maximum photosynthetic rates (P_{max}) were achieved at 500–700 μM photons m^{-2} s^{-1} and above, and compensation occurred around 100 μM m^{-2} s^{-1} for these corals (from very shallow habitats, 1–2 m depth). There was no indication of photoinhibition, although photosynthesis at the highest irradiance used (>1,100 μM photons m^{-2} s^{-1}) was slightly less than at 900–1,000. Orientation of the flat branches in chambers, as in the field, did not allow maximum possible illumination of any coral (i.e. full sun on a flat side).

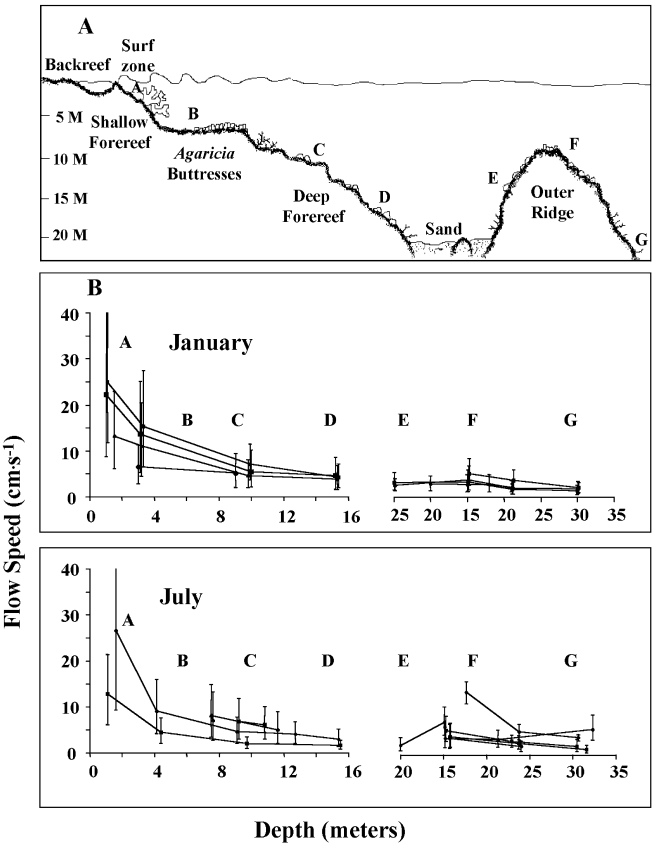

Fig. 3 **A** Reef profile at Carrie Bow Cay, showing backreef, forereef slope (*A–D*), sand channel, and outer ridge with landward- (*E*) and seaward-facing (*F*, *G*) reef slopes. *Letters* correspond to locations of flow measurements. **B** Flow profiles for Carrie Bow Cay (S4 meter, instantaneous 0.5-s data, 5 min mean ±SD) at 0.5 m above unobstructed reef surfaces on 4 days in January and July 1992. Separate profiles are provided for the inner forereef slope and for the outer ridge

Oxygen flux data were fit to the parameters of the hyperbolic tangent function [$P_{net} = P_{max} \tanh(\alpha I P_{max}^{-1}) + R$; Chalker (1981);Table 1), where P_{max} is light-saturated gross photosynthesis, α is light-harvesting efficiency, I is irradiance, R is respiration (negative), and $I_k = P_{max}/\alpha$. Net photosynthesis is calculated as $P_{net} = P_{gross} + R$. Mean dark respiration rates (R) were calculated for each flow group; then P_{max} and a were determined as best fits to oxygen flux versus irradiance by Levenburg–Marquardt least squares iterative nonlinear minimization (TableCurve 2D 4.0, SPSS Inc., Chicago, Illinois). Coral respiration during photosynthesis is probably maximized by high intracellular oxygen concentration, and thus may be flow independent

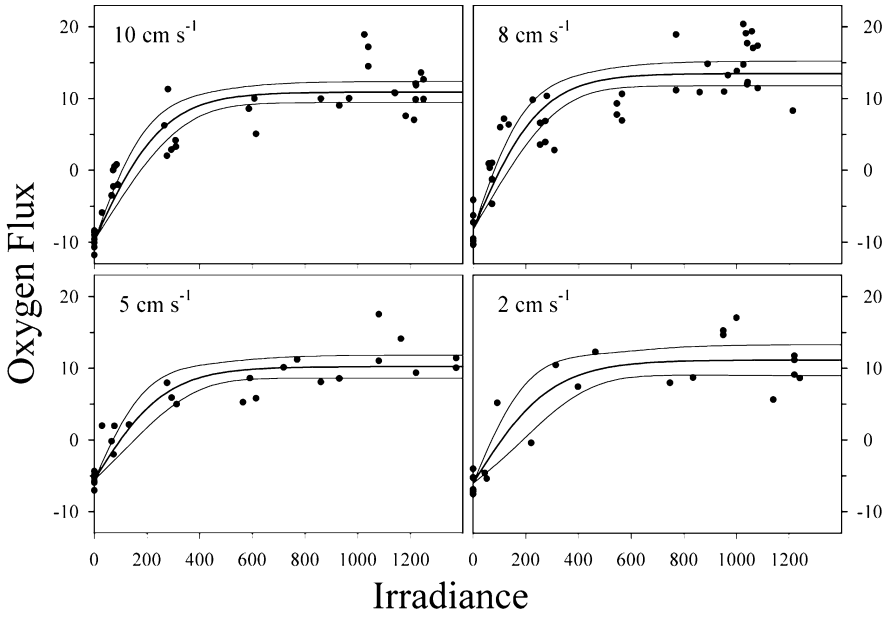

Fig. 4 Photosynthesis and respiration (R, at irradiance = 0) by *A. tenuifolia* at four flow speeds, over a range of irradiance (I). *Outer* (*narrow*) *lines* represent 95% confidence interval around best fit *center* (*thicker*) *line*

and overestimated by dark respiration. Gross P_{max}, which incorporates the dark respiration rate for each group, is best viewed as a parameter used for curve fitting rather than a true estimate of P_{max} gross. On the other hand, P_{max} net represents true maximum net photosynthetic rate, as measured during these experiments.

ANOVA and Student Neuman Keuls multiple comparison tests were performed on P_{max} and α values from the curve fitting procedure, using the resulting SE, for the six corals tested at all irradiance levels. There was a significant effect of flow category on P_{max} net ($F = 3.18$, $p < 0.03$), with the 8 cm s^{-1} group slightly higher and significantly different from the 2 and 10 cm s^{-1} groups. However, there was not a consistent trend of increasing P_{max} with flow. The ANOVA showed no significant treatment effect for α ($F = 1.35$, $p = 0.26$). Power of the P_{max} test (at $p = 0.05$) was 0.534, and of the α test was 0.114. P_{max} (at $I > 700$ μM m^{-2} s^{-1}) for all 10 coral specimens (Fig. 5) showed no significant effect of flow over flow speeds of 1–10 cm s^{-1} (linear regression, $R^2 = 0.034$, $p = 0.126$). We repeated these analyses normalizing to total nitrogen (i.e. tissue), polyp number, and chlorophyll (data not presented). Results when normalized to tissue and polyp number were essentially identical to those using surface area, but there was much more variability within each data set when normalized to these parameters.

Respiration in the dark was affected by flow speed (Fig. 5) (linear regression, $R^2 = 0.462$, $p = 0.0001$) and respiration at 2 cm s^{-1} was about half that at 10 cm s^{-1}. At low irradiance (50–100 μM m^{-2} s^{-1}), the flow effect disappeared, and there were no differences among rates of net production at any of the four flow speeds tested (linear regression, $R^2 = 0.002$).

Rates of photosynthesis and respiration are expressed per unit coral surface area in this study, but, for conversion purposes, we provide mean values (±SD) for

Table 1 Best fit parameter values of the hyperbolic tangent function for oxygen flux data, from corals tested at each of four flow speeds, and for all groups combined. *Numbers in parentheses* are standard errors. R^2 and *N* photo (sample size) are for calculations of P_{max} and α (slope at low irradiance). Respiration (*R*) was determined using all dark runs; it is presented and used as a negative value; P_{max} net = P_{max} gross + R. Calculated values of I_k [intersection of $y = P_{max}$ (gross) and $y = \alpha I + R$] are also given. *N resp* Sample size for respiration mean. Units are nmol oxygen min^{-1} cm^{-2} coral surface for P_{max} and respiration, nmol oxygen †mol $photons^{-1}$ for α, and †mol photons min^{-1} cm^{-2} for I_k. Note that P_{max} gross values, incorporating dark respiration, are used for curve fitting only, not as estimates of true P_{max} gross (see text)

	Flow speed category				
	2 cm s^{-1}	5 cm s^{-1}	8 cm s^{-1}	10 cm s^{-1}	All data
Respiration	–6.04 (0.57)	–5.56 (0.93)	–8.26 (0.91)	–9.77 (0.46)	–7.53 (0.45)
P_{max} net	11.14 (1.04)	10.22 (0.79)	13.49 (0.85)	10.91 (0.73)	11.72 (0.45)
P_{max} gross	17.18 (1.04)	15.78 (0.79)	21.75 (0.85)	20.68 (0.73)	19.25 (0.45)
α	0.058 (0.014)	0.059 (0.011)	0.085 (0.011)	0.079 (0.010)	0.071 (0.006)
$I_k (= P_{max}/a)$	296	267	256	262	271
R^2	0.856	0.857	0.817	0.875	0.828
N photo	17	21	37	32	107
N resp	6	6	7	7	26

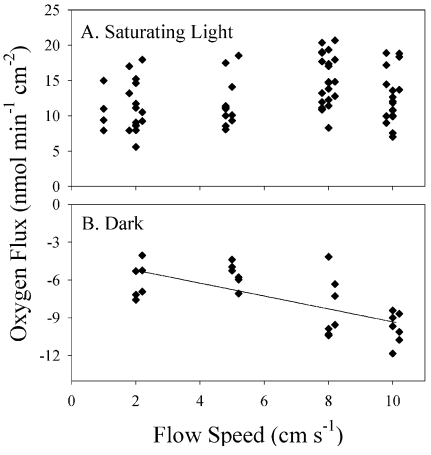

Fig. 5 **A** Rates of light-saturated photosynthesis (at >700 μmol m^{-2} s^{-1}) by ten coral plates tested at five flow speeds on subsequent days (*vertical rows of points*) under nearly identical conditions. Rates of oxygen flux are not different among flow speed categories by regression (see text). **B** Rates of dark respiration by six coral plates tested at four flow speeds under nearly identical conditions; these rates increased significantly (more negative) with flow speed by regression analysis (see text)

several other coral biomass and algal pigment measures. The corals used in these experiments ranged from 6.5–15.9 polyps cm^{-2} of skeleton (mean 11.5). Total nitrogen content was 500 ± 132 μg cm^{-2}, which converts to approximately 3.48 mg protein and 4.98 mg total ash-free dry weight of tissue per cm^2 [based on percent protein for anemone tissue, Shick (1991)]. Chlorophyll *a* was 10.64 ± 4.30 μg cm^{-2}, chlorophyll c_2 was 3.84 ± 1.46 μg cm^{-2}, and total carotenoids were 19.05 ± 8.05 μg cm^{-2} coral surface area. Using data in Helmuth et al. (1997b) for this site and depth, zooxanthellae densities were estimated from our chlorophyll *a* data as $7.41 \pm 4.16 \times 10^5$ zooxanthellae cells cm^{-2}, averaging regions from 0–5 cm from the branch tip.

Field growth experiments

Coral growth was compared as relative and absolute weight change for statistical analyses (SigmaStat v.2.03; Table 2). Dry weights of branches used in all experiments were 12–18 g; typical growth of 30% over 3 months thus represents an addition of 3.6–5.4 g dry weight per branch and maximum growth was triple that rate. Coral explants at 8–24 m exhibited growth rates that differed by less than 15% between the most rapid growth, at 12-m depth, and the slowest, at 24 m (Fig. 6). Corals transplanted from 8 m to 15- or 24-m depth grew at rates similar to those originating at 15 or 24 m (ANOVA; Table 2). The only significant difference among all 1992 growth rates was between the 24-m group and the groups at 8- and 12-m depth [Student Neuman Keuls (SNK) multiple comparisons test, $p < 0.05$]. In 1994, there was no significant effect of depth for 1–15 m. However, growth rates at 1 m on the forereef were much lower than in all other habitats, and mortality was high (50%); growth at 24 m was lower than at 15, 8, and 1 m (SNK test, $p < 0.05$). Depth ANOVAs had statistical power ranging from 0.54 to 1.00 (Table 2).

Corals mounted on buttress tops (convex) and on flat and concave surfaces (high, medium, and low flow microhabitats, respectively) at 8-m depth did not show differences in growth rate among groups in 1992 (Table 2), nor was there an effect of colony origin. In 1994, there was no significant colony effect, but there was a significant treatment effect; corals transplanted to the concave (low flow) microhabitats grew about 40% less rapidly than did those on flat substrata (Fig. 7A, Table 2). Corals on convexities (high flow) had intermediate growth rates at 15-m depth. Plaster dissolution rates in the convex and flat surface microhabitats were not different (see below), and thus these microhabitats could be considered the same flow treatment. ANOVAs testing flow and colony effects had statistical power values from 0.05–0.77 and 0.41–0.96, respectively (Table 2). In 1992, corals oriented perpendicular or parallel to flow (at 12 m, flat surfaces) had no difference in growth rates for either skeletal ridge orientation (Table 2). Power of ANOVAs for orientation was low (0.05–0.17) and thus the lack of significant difference should be interpreted cautiously.

A. tenuifolia buttresses at 6- to 8-m depth also provide a range of flow microhabitats. In 1994 there was no significant difference in growth rates among branches (explants) in any microhabitat type at this depth, including open or closed channels or outside aggregations (Fig. 7, Table 2). However, there was a significant colony effect; explants from one colony grew at a slower rate than those from the other three colonies in all microhabitats (SNK test, $p < 0.05$). Statistical power was 0.72–0.90 for colony effects and 0.05 for flow (Table 2). The lack of statistical differences among flow groups should thus be considered accordingly. Shading did not affect growth rates in short-term (3-week) transplants; there were no significant differences between growth of shaded and unshaded explants at 8-m or at 15-m depth, although the power of these tests ranged from only 0.14–0.26 (1994; Table 2). In centers of aggregations, the effect of reduced irradiance could be much greater than in these isolated branch experiments; it is thus still possible that irradiance can limit growth at either depth.

Flow environment

S4 meter recordings indicate that deep reef habitats (e.g. 30 m) generally had mean flow speeds less than 5 cm s^{-1}. Flow was unidirectional, with small wave-induced oscillatory elements. Flows increased from 30-m to 1-m depth, with oscillatory flow dominating at 15 m and shallower [Fig. 2 ; see also Helmuth et al. (1997a)]. Mean flows at 1-m depth on the forereef were between 20 and 30 cm s^{-1}; maximum flow speeds were more than twice

Table 2 ANOVA results comparing growth rates and plaster sphere dissolution rates (SigmaStat v. 2.03). *Symbols following year* indicate change per unit initial weight (*w*), or absolute change (*a*) in coral weight. Depth of measurement (*m*) and factors tested in one-way or two-way ANOVAs are listed, followed by degrees of freedom, *F* statistics, and *p* value for each factor and for their interaction.The power of each test (at $\alpha = 0.05$) is provided for each factor and for their interaction. *n* Pattern of missing data prevents interaction test. *Bold P values* indicate significance (at $\alpha \leq 0.05$). *Orien* Orientation (parallel, perpendicular); *Trans* transplant from 8 m to 15 or 24 m; *batch* batches of plaster spheres deployed on two or three separate days; *M* March; *J* July; *res* residual

Year	Depth	Factor		Degrees of freedom				F statistic			*p* value			Power		
	(m)	F1	F2	F1	F2	Res	1×2	F1	F2	1×2	P1	P2	1×2	F1	F2	1×2
Coral growth rate																
92w	All	Depth	–	3	–	45	–	5.50	–	–	**0.003**	–	–	0.86	–	–
92a	All	Depth	–	3	–	45	–	3.30	–	–	**0.029**	–	–	0.54	–	–
92w	8	Flow	Colony	2	3	24	6	0.67	2.85	1.47	0.521	0.059	0.231	0.05	0.41	0.16
92a	8	Flow	Colony	2	3	24	6	0.52	7.69	0.64	0.604	**0.001**	0.698	0.05	0.96	0.05
92w	12	Orien	Colony	3	4	12	8	0.73	0.75	n	0.550	0.576	n	0.05	0.05	n
92a	12	Orien	Colony	3	4	12	8	1.81	0.53	n	0.199	0.714	n	0.17	0.05	n
92w	8, 15	Trans	–	1	–	9	–	0.61		–	0.456	–	–	0.05	–	–
92a	8, 15	Trans	–	1	–	9	–	0.003	–	–	0.960	–	–	0.05	–	–
92w	8, 24	Trans	–	1	–	9	–	0.77	–	–	0.400	–	–	0.05	–	–
92a	8, 24	Trans	–	1	–	9	–	3.78	–	–	0.080	–	–	0.32	–	–
94w	All	Depth	–	5	–	107	–	11.26	–	–	**0.001**	–	–	1.00	–	–
94a	All	Depth	–	5	–	107	–	25.19	–	–	**0.001**	–	–	1.00	–	–
94w	15	Flow	Colony	2	3	22	6	4.73	1.19	0.25	**0.020**	0.335	0.953	0.62	0.08	0.05
94a	15	Flow	Colony	2	3	22	6	6.05	4.08	0.59	**0.008**	**0.019**	0.738	0.77	0.64	0.05
94w	8	Flow	Colony	2	3	25	6	0.81	6.33	0.77	0.456	**0.002**	0.601	0.05	0.90	0.05
94a	8	Flow	Colony	2	3	25	6	0.04	4.83	0.63	0.957	**0.009**	0.705	0.05	0.76	0.05
94w	8, 15	Shade	Depth	1	1	14	1	3.10	1.02	0.07	0.100	0.331	0.801	0.26	0.05	0.05
94a	8, 15	Shade	Depth	1	1	14	1	1.94	1.62	0.34	0.186	0.224	0.569	0.14	0.10	0.05
Plaster sp#here dissolution rate																
92	All	Depth	Batch	3	2	122	n	118.4	146.0	n	**0.001**	**0.001**	n	1.00	1.00	n
92	8	Flow	Batch	2	2	46	4	21.68	108.6	0.93	**0.001**	**0.001**	0.458	1.00	1.00	0.05
92	12	Orient	Batch	2	1	25	n	2.73	98.84	n	0.085	**0.001**	n	0.32	1.00	n
94	15 M	Flow	–	2	–	19	–	8.01	–	–	**0.003**	–	–	0.89	–	–
94	15 J	Flow	–	2	–	27	–	7.31	–	–	**0.003**	–	–	0.87	–	–
94	All M	Depth	–	4	–	34	–	71.62	–	–	**0.001**	–	–	1.00	–	–
94	All J	Depth	–	4	–	28	–	44.27	–	–	**0.001**	–	–	1.00	–	–
94	8 J	Flow	Batch	2	1	38	2	0.92	103.9	0.12	0.409	**0.001**	0.883	0.05	1.00	0.05
94	8 M	Flow	–	2	–	21	–	7.70	–	–	**0.003**	–	–	0.88	–	–
94	8 J	Shade	–	1	–	17	–	0.70	–	–	0.415	–	–	0.04	–	–
94	15 J	Shade	–	1	–	26	–	1.50	–	–	0.232	–	–	0.09	–	–

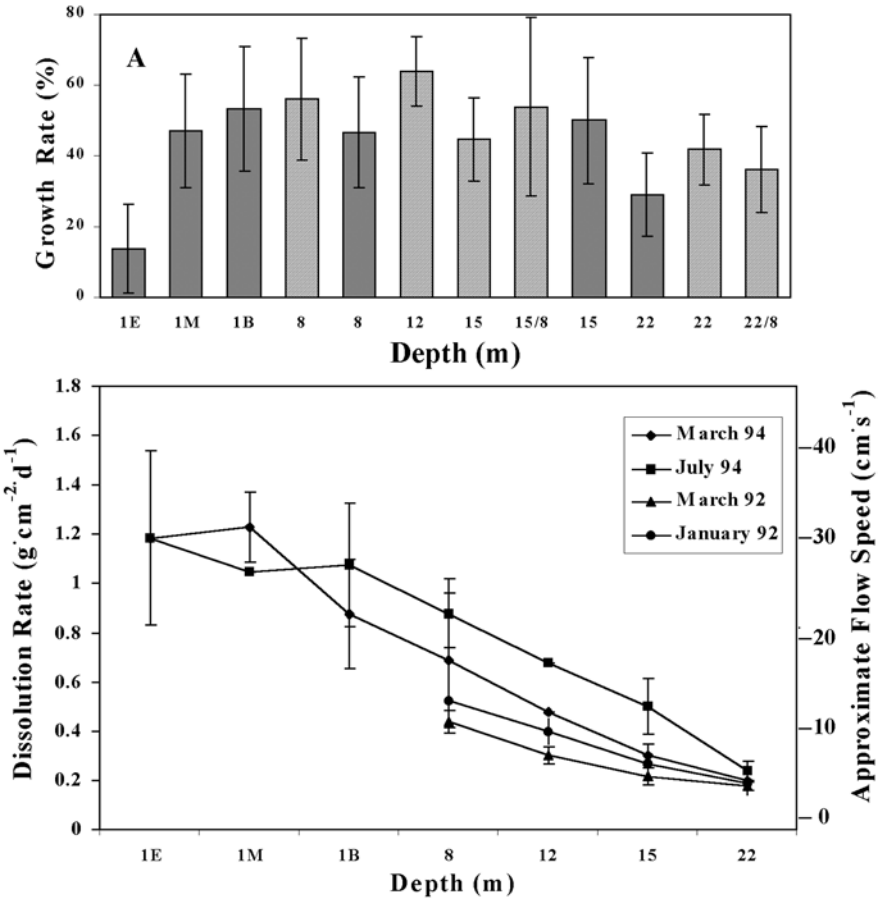

Fig. 6 **A** Growth rate (mean ± SD) as grams added per initial gram of skeleton (percent) of *A. tenuifolia* transplants ($N = 6$–8 each) along a depth gradient measured over 3 months (110 days) during 1992 (*crosshatched bars*) and 1994 (*shaded darker bars*). *15/8* and *24/8* indicate transplants from 8-m depth to 15- and 24-m depth, respectively. **B** Plaster sphere dissolution rates (mass loss, g cm^{-2} day^{-1}) for five spheres (mean ± SD) at each depth (*above*). *B* Backreef at 1-m depth; *E* exposed forereef at 1-m depth; *M* moderately exposed forereef at 1-m depth. Approximate flow speeds are from calibration of dissolution rates to S4 meter mean flow speeds in the same habitats, and in still water

mean flows and exceed 100 cm s^{-1} in the surf zone under high wave conditions (> 1.5 m height). Plaster sphere dissolution rates in deep reef habitats were one fifth those at the shallowest sites (Fig. 6) and backreef habitats had dissolution rates about 30% lower than the forereef at the same depth. In July 1992 and March 1994, dissolution rates at all depths differed significantly from each other (Table 2; ANOVA, SNK test, $p < 0.05$). Statistical power for this analysis was high (close to 1.0).

At 15-m depth, convexities and flat surfaces had dissolution rates about 20% higher than adjacent concavities in 1992, and about 30% higher in 1994. In July 1992, rates for convex surfaces at 8 m were significantly higher than for either flat or concave surfaces (SNK test, $p < 0.05$) (Table 2). In July 1994, 15-m sites showed a significant effect of microhabitat, with concave surfaces differing from convex, and convex from flat surfaces (SNK test, $p < 0.05$). Shaded explants had dissolution rates equal to those of control explants at 15 m and 8 m (Table 2). There was no difference in dissolution rate for explant racks with corals oriented perpendicular or parallel to flow in 1992 (Table 2). The power of ANOVA was high for flow comparisons (> 0.80), but was low for shading and orientation tests (0.05–0.32).

On *A. tenuifolia* buttresses at 8 m (1994), dissolution differed by about 10–15% between unobstructed (outer) transplants and those within aggregations. In July 1994 there were no differences among open and blocked channels within aggregations, or those outside aggregations. In March 1994, outer sites had significantly greater dissolution rates than those in closed and open channels, which were in turn indistinguishable (ANOVA, SNK test, $p < 0.05$). The statistical power for March was high (0.88), but that for July was much lower (0.05; Table 2).

Discussion

Reef topography provides corals with a broad range of flow environments, from very low unidirectional flow on the deep reef, to breaking waves in the surf zone. *A. tenuifolia* spans this entire range, and can be the most abundant coral both on the shallow forereef and in extremely low flow conditions along mangrove lagoon edges (Aronson and Precht 1997; Shyka and Sebens 2000; Aronson et al. 2002). Previous research (Dennison and Barnes 1988; Patterson and Sebens 1989; Patterson et al. 1991; Rex et al. 1995) showed that increased water motion reduces the boundary layer over coral tissues (thus oxygen and/or bicarbonate transport) and determines rates of photosynthesis by zooxanthellae and respiration of coral and algal tissue. This effect was also observed in *A. tenuifolia* for dark respiration, but not for net photosynthesis at any irradiance. In contrast to species examined previously, this coral appears much

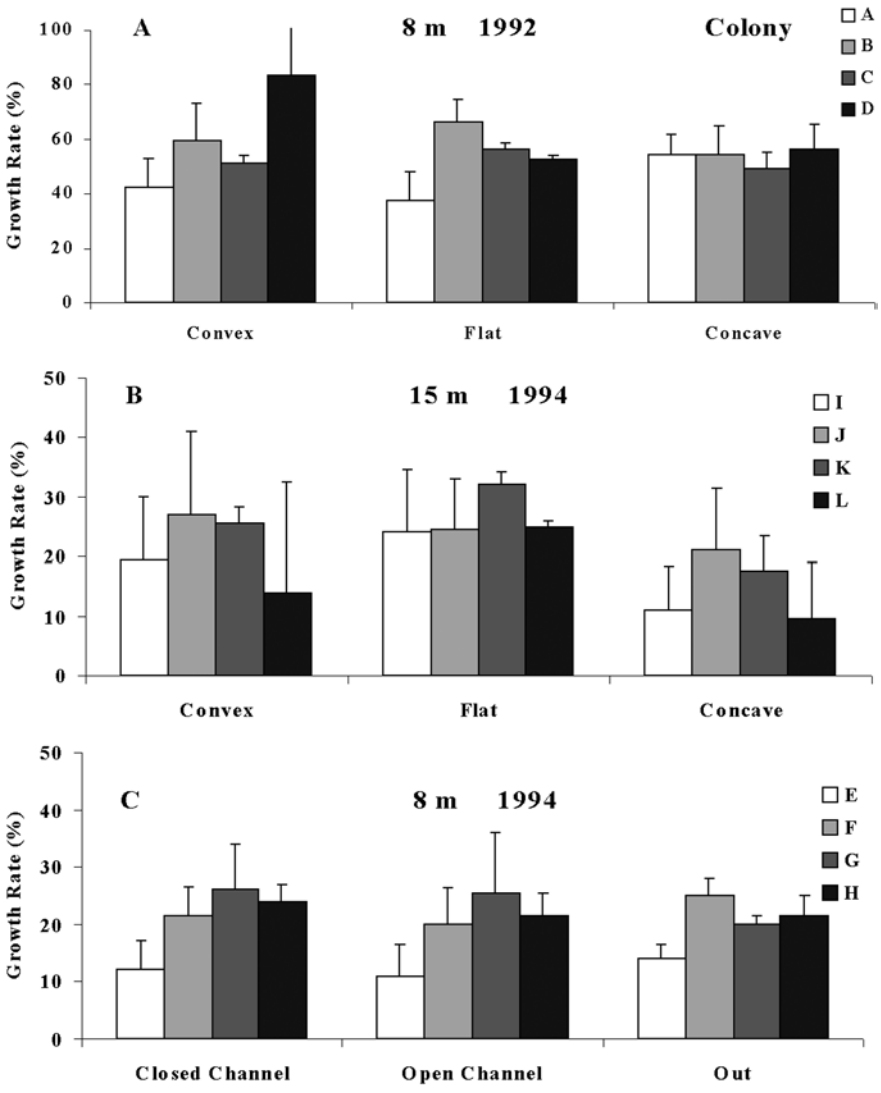

Fig 7 Growth rates (1992, 1994) of *Agaricia* transplants ($N = 6$ each) on convex, flat, and concave surfaces (high, moderate, and low flow microhabitats) at **A** 8 m, **B** 15 m, and **C** in four locations at 8 m on *Agaricia* buttresses. *Out* outside aggregations; *Open* inside aggregation with open channels; *Closed* inside aggregation with closed channels. Growth rates are grams added per initial gram of skeleton (percent) over 3 months (110 days). *Error bars* are one standard deviation. *Letters* indicate individual colonies from which transplants originated. ANOVA results (Table 2) indicate a significant colony effect, but no differences among treatment groups at 8 m (1992 and 1994). At 15 m there were no differences among colonies, but the flow treatments were significant; concave (low flow) transplants had growth rates significantly less than the flat (medium flow) group (1994)

more tolerant of low flow speeds; high levels of both photosynthesis and growth occurred over an extreme range of flow regimes. This tolerance may also explain why living tissue on lower regions of branches is able to withstand the very low flow and mass flux observed and predicted inside *A. tenuifolia* colonies with tight branch spacing (Helmuth et al. 1997a).

Corals depend on several sources of energy and nutrients, including zooplankton (Sebens et al. 1996, 1998; Heidelberg et al. 1997), particulate material (Mills and Sebens 1997; Anthony 1999), and dissolved nutrients (Shyka and Sebens 2000). Water movement provides corals with prey, and aids in nutrient transfer across the boundary layer above coral tissues (Thomas and Atkinson 1997), but also has negative effects that may limit coral distribution to certain reef habitats (Sebens 1997). For these reasons, we expect corals experiencing a wide range of flow speeds to show a similarly wide range of physiological and growth responses. This is especially true when irradiance also varies markedly, as occurs along the depth gradient at Carrie Bow Cay (Helmuth et al. 1997a, 1997b) or within aggregations. *A. tenuifolia* is able to capture particles at rates (Helmuth and Sebens, unpublished) similar to those measured for other species of this genus (Helmuth and Sebens 1993) and can even capture live zooplankton in field experiments (Sebens, unpublished), although not at rates comparable to some other branching species (Sebens et al. 1996, 1998). Growth rate responses to flow reflect the sum of flow effects on particle capture, nutrient uptake, photosynthesis, and respiration. Since dark respiration increases with flow, and photosynthesis does not, these corals might be expected to grow somewhat slower in high flow, as was observed at 1 m on the forereef. However, this energetic deficit may be countered by increased rates of particle capture and bicarbonate and nutrient uptake with increasing flow speed.

Water flow near reef surfaces

Flow regimes on reefs are diverse and arise from a number of separate processes. Corals and other sessile organisms on reefs live within a boundary layer that is

generally turbulent, not laminar. The velocity profile across this layer depends on surface roughness, shape of roughness elements, and mainstream flow above that surface (Shashar et al. 1996, reviewed by Denny 1988). Both waves and currents generate substantial flow on reefs. Oscillatory flow generated by waves (collapsed wave orbitals) prevents the buildup of a steady-state momentum boundary layer, as found in unidirectional flow (currents). Furthermore, corals on exposed (e.g. convex) surfaces may experience high flows at the same time that those in concavities and within aggregations (Chamberlain and Graus 1975; Helmuth et al. 1997a) experience severely reduced flow.

Development of a diffusional boundary layer over an organism inhibits particle, gas, or nutrient movement across that layer (Patterson and Sebens 1989; Patterson et al. 1991; Patterson 1992; Thomas and Atkinson 1997). For example, in laboratory flume studies of small mounding corals in unidirectional flow (Gardella and Edmunds 2001), flow at the level of coral polyps and tentacles was about half that 4 cm higher, and the flow profile (shear velocity, U*) was affected by surface roughness. Highly turbulent and/or oscillatory flows of low to moderate speed are likely to be more beneficial to passive suspension feeders than less turbulent but higher flows. For the same amount of water passing by a given point, the former type of flow provides greater rates of mass flux [e.g. plaster spheres, Porter et al. (2000)].

Strong near-substratum flows increase the probability of organism dislodgment, however, and coral colonies with high surface-area-to-volume ratios (Porter 1976) are more likely to suffer dislodgment. There is thus a clear tradeoff between high surface area [per unit volume or tissue biomass, Sebens (1997)] for uptake, and risk of partial or complete mortality. Corals that maximize the former may benefit greatly during periods without severe storms, but suffer disproportionately when hurricane-level storms arrive.

At Carrie Bow Cay, as at other wave-exposed reef locations (e.g. Sebens and Done 1992), high flow speeds are experienced by corals in the surf zone and on the shallow forereef. Even under moderate wave conditions, such flows can be in the 20- to 40-cm s^{-1} range, which may be near the optimum for particle capture (Helmuth and Sebens 1993; Sebens et al. 1997, and unpublished data) and uptake of dissolved substances (Patterson et al. 1991) by at least some corals. Most other reef habitats, especially those deeper than about 5 m, usually experience flow speeds that can be considered limiting for particle capture, nutrient uptake, and energetics of the coral symbiosis. This is not true of all reefs or reef habitats, especially when there are strong subsurface tidal or longshore currents (Roberts and Suhayda 1983; Sebens and Done 1992). Strong subsurface flows also accompany internal tidal bores (Leichter et al. 1996, 1998), which can transport deep-water nutrients and zooplankton to certain depth zones on coral reefs.

Photosynthesis and respiration

Photosynthesis by *A. tenuifolia* occurred at near maximal rates at flow speeds of 1–10 cm s^{-1}, and respiration in the dark was enhanced by flow. This result differs from previous studies where flow was found to have a strong positive effect on photosynthesis (Dennison and Barnes 1988; Patterson et al. 1991; Lesser et al. 1994; Rex et al. 1995). The effect on respiration is as expected, and has been found for other anthozoans (Patterson and Sebens 1989; Patterson et al. 1991; Rex et al. 1995; Bruno and Edmunds 1998). The almost complete nocturnal depletion of oxygen near coral surfaces in low flow (Shashar et al. 1993; Kuhl et al. 1995; Gardella and Edmunds 1999) ensures that metabolic rates are reduced under such conditions. This effect is particularly evident within branch aggregations (Bruno and Edmunds 1998).

During the day, even at low irradiance, oxygen production by zooxanthellae is much greater than is used for algal and animal respiration, and oxygen is exported; respiration will then be at a maximum at any flow speed (Edmunds and Dubinsky 1988; Shick 1990) and only flow effects on photosynthesis should be important. Flow limitation of bicarbonate diffusion into coral tissues, rather than oxygen removal, is likely to be limiting for corals in low flow (Patterson et al. 1991; Lesser et al. 1994), although oxygen concentration can be very high near photosynthesizing tissue surfaces in low flow (deBeer et al. 2000). Corals using ciliary tracts for feeding or sediment removal [e.g. *Agaricia*, Lewis and Price (1975, 1976)], may be able to stir the boundary layer enough during low flow conditions to remove some of this limitation. This does not, however, explain the flow effect on respiration.

Growth of *Agaricia tenuifolia*

Growth rates measured for *A. tenuifolia* in this study are high for corals in general (Hubbard and Scaturo 1985), and remained high even when branches were transplanted into the lowest flow conditions on the Carrie Bow Cay forereef. Somewhat reduced growth was observed only under the low flow/low irradiance conditions that occur at 24 m, close to the lower depth limit for this species, and in low flow microhabitats (concavities) at 15-m depth. This reduction in growth rate with depth is minimal compared to the reduction in water motion measured by either electromagnetic flow meters or plaster sphere dissolution. It is also minimal compared to the more than 60% reduction in light expected at 24-m depth (Helmuth et al. 1997a). However, most transplanted coral branches were isolated, and thus were exposed to the greatest ambient flow and light available at each depth, similar to small colonies or edge branches in colonies with wide branch spacing. Branches in the centers of aggregations, even with wide spacing, experience greatly reduced flow, mass flux (Helmuth et al.

1997a), and irradiance (Helmuth et al. 1997b), all of which could limit growth.

Growth rates even higher than those measured on the shallow forereef at Carrie Bow Cay were measured for explants along mangrove lagoon edges in the Pelican Cays, Belize, a very low flow environment with enhanced dissolved nutrient concentrations and high irradiance (Helmuth et al. 1997a; Shyka and Sebens 2000). Such colonies exhibit tight branch spacing (Helmuth et al. 1997a) and show reduced growth rates only in microhabitats with mean flow speeds less than about 2 cm s^{-1} (Shyka 2000). The negative effects of flow limitation on particle capture and uptake of dissolved substances may be offset, however, by greater availability of dissolved or particulate nutrients in certain low flow locations (Shyka and Sebens 2000).

In large aggregations, branches of *A. tenuifolia* are usually oriented perpendicular to the dominant direction of flow, especially in centers and along sides of colonies. Orienting broadside to flow increases turbulence around branches, but also increases drag (Patterson 1980). The aggregating growth form of this species, where multiple genotypes intermingle to form monospecific stands, reduces the probability of mortality from drag-induced breakage (Chornesky 1991) and allows persistence in high flow habitats where it might otherwise be destroyed by storm waves. Our transplant experiments using isolated branches showed that orientation did not affect growth rate at 12-m depth, where large aggregations are common. At 8-m depth, transplants in exposed locations and within aggregations had similar growth rates. Even partially blocked channels within aggregations provided an environment conducive to rapid growth. It thus appears that wave-induced flow over the surface of such aggregations provides sufficient flow between branches to allow high growth rates. However, this is probably not the case for other corals that attempt to penetrate aggregations of *A. tenuifolia*. The tight interbranch spacing may create an environment that *A. tenuifolia* can tolerate, but which excludes its competitors, primarily *Porites porites* and *Acropora cervicornis*.

Turbulent eddies form behind each branch perpendicular to flow and probably sweep downward into aggregations deep enough to contact all living tissue. Colonies with tighter branch spacing have living tissue only a short distance down each branch, indicating that either flow or light, or both, become limiting in regions distant from branch tips (Helmuth et al. 1997a, 1997b). Colonies with unobstructed channels (50 cm or more deep) between branches experience induced flow upward along branches, based on our video recordings of particles moving upward rapidly through such channels during the passage of waves over the colony. The respirometry chambers used here were designed to mimic this type of flow, unidirectional and upward along each branch.

Transplants at 8- and 15-m depth did not show significant differences in growth rate in shaded (30% light reduction) and unshaded conditions. Although these were short term compared to all others, growth was still substantial (2–4%) in both treatments. This indicates that corals not in aggregations, or at edges of aggregations, could be receiving enough irradiance at these depths to achieve high rates of growth. Within aggregations, light reduction is much more severe, e.g. over 80% at 8–12 cm below branch tips, and can be limiting (Helmuth et al. 1997b). Chamber experiments (Fig. 4) indicate that *A. tenuifolia* can achieve close to its maximum photosynthetic rate at 300–400 μM m^{-2} s^{-1}. Light measurements at 7-m depth at Carrie Bow Cay were approximately 50% of surface irradiance, and at 17 m around 35% (Helmuth et al. 1997a). Therefore, isolated coral branches at the depths of our 8-m and 15-m transplants would experience irradiances over 300 μM m^{-2} s^{-1} for much of the day, even in our experimental shading treatment. The relatively low values of I_k (Table 1) for this species help explain its ability to grow rapidly even in deep reef zones, where branch spacing is relatively wide, and within tight aggregations in shallow zones.

Transplants at 1-m depth on the exposed forereef showed reduced growth rates and a high rate of mortality, even though transplant racks remained tightly attached and transplanted corals could not have scraped each other or touched the substratum nearby. Transplants in slightly less exposed forereef sites did much better, with low mortality and high growth, as did corals just inside the reef crest in the backreef environment at the same depth. The reason for high mortality on the shallow forereef (surf zone) is unknown. One possibility is that flow was excessively high and thus inhibited capture of particles and/or caused elevated respiration in the dark. Another possibility is that resuspension of sand or other solid material during storms abraded or broke the transplants. Some were dead in place, and a few were broken off at the transplant rack level, indicating that drag or projectiles could have caused mortality. Whole branch mortality was extremely rare in all other transplant groups.

A. tenuifolia can be the spatially dominant coral in environments as disparate as the shallow forereef just under breaking waves (Rützler and MacIntyre1982; Chornesky 1991; Aronson and Precht 1995) to the edges of quiet mangrove-circled lagoons in the Pelican Cays (Shyka 2000; Shyka and Sebens 2000). *Acropora cervicornis* is the only other coral species with a similar distribution; before being decimated by hurricanes, then disease (Aronson and Precht 1997; Aronson et al. 1998), this species was more abundant than *A. tenuifolia* on the same lagoon edges, and also formed large thickets on the shallow forereef at Carrie Bow Cay (Rützler and MacIntyre 1982). Both corals exhibit rapid growth, have small polyps, and high tissue-surface-to-total-biomass ratios (Sebens 1997). They can be thought of as energy maximizers, presenting the greatest possible coral tissue area to the overlying water, per unit coral tissue mass. This is an efficient growth form for capture of light,

particles, zooplankton, and dissolved nutrients from seawater (Sebens 1997); however, it is also a growth form susceptible to damage during severe storms.

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