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Environmental versus intrinsic determination of colony symmetry in the coral *Pocillopora verrucosa*

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ABSTRACT: The morphology of corals is strongly dependent on environmental conditions. Different morphologies can be induced by flow and light due to their effects on respiration, production, calcification and prey capture. Yet, colonies of many branching corals exhibit a radial symmetry, possibly indicating an intrinsic determination of colony morphology. The scleractinian coral *Pocillopora verrucosa* (Ellis and Solander, 1786) is a common species in the Red Sea, displaying striking flow-dependent plasticity in colony morphology. Branches of this coral are thicker and more compact in habitats exposed to stronger flow, but the colonies are usually radially symmetric. The objective of this study was to experimentally examine whether the colony symmetry in this species is determined by intrinsic or extrinsic factors. Six corals were exposed *in situ* for 4 mo to a unidirectional flow generated with submerged pumps, creating asymmetric flow, stronger at the side facing the pump. The up-current side of the corals developed higher concentrations of chlorophyll and proteins, greater density of zooxanthellae, and displayed a more compact morphology and longer linear extension. While asymmetry in photosynthesis and photosynthates may disappear due to within-colony translocation, our findings on asymmetry in skeletal growth and morphology indicate that environmental conditions generate lasting asymmetry in corals. Current measurements indicate that the ubiquitous symmetry observed in *P. verrucosa* is apparently due to a corresponding symmetry in the flow.

KEY WORDS: Flow · Zooxanthellae · Chlorophyll · Morphology · Red Sea

INTRODUCTION

The morphology of corals is strongly affected by light and water motion (Goreau 1959, Dustan 1975, Foster 1979, Bottjer 1980, Lesser et al. 1994, Bruno & Edmunds 1997, Helmuth et al. 1997, Muko et al. 2000, Vermeij & Bak 2002, Iwase et al. 2008) due to their remarkable effect on the corals' respiration, production, calcification and prey capture (Dennison & Barnes 1988, Patterson et al. 1991, Sebens & Johnson 1991, Mass et al. 2007). Yet, colonies of many branching corals exhibit a radial symmetry, possibly indicating an intrinsic determination of colony morphology (Loya 1976, Rinkevich 2002).

Symmetry develops under intrinsic control if materials produced in one part of the colony (e.g. due to faster flow) are effectively translocated to other parts (Rinkevich 2002). Symmetry can also develop when new branches are added according to strict architectural rules, termed 'genetic blueprint' by Rinkevich (2002), regardless of differences in the physiological state of different branches (Rinkevich 2002, Shaish et al. 2006, 2007). The claim that colony morphology is determined intrinsically was originally proposed by Loya (1976), who noted that broken branches in *Stylophora pistillata* grew faster than intact ones.

Alternatively, if the shape of the colony is determined mostly by environmental conditions (hereafter 'extrinsic control') (Kaandorp 1999), symmetry of the colony will reflect symmetry of environmental conditions: the colony may be asymmetric when one side of the colony consistently experiences different environ-

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mental conditions than another, and radial symmetry can develop if the governing factors around the coral are symmetric.

The objective of this study was to experimentally examine the relative importance of intrinsic and extrinsic factors in determining the colony symmetry in *Pocillopora verrucosa*.

MATERIALS AND METHODS

A flow-manipulation experiment was carried out from 4 September 2006 to 16 January 2007 at 8 m depth in the coral reef off the H. Steinitz Marine Biology Laboratory, Eilat, Israel (Red Sea, 29° 30′ N, 34° 56′ E). This reef is part of a 5 km stretch of coastline containing reef interspersed with open sand regions devoid of corals. The reef is dominated by hermatypic corals. Soft corals, anemones, sponges, tunicates and polychaetes are also common (Fishelson 1971). The currents at the study site are predominantly oriented parallel to the shore line with an average near-bottom flow speed of ~5 cm s^{-1} (Genin & Paldor 1998). Semidiurnal reversals of flow direction occurred during May to October, whereas lower frequency reversals (period of several days) are dominant during winter (Monismith & Genin 2004).

Our study focused on the scleractinian coral *Pocillopora verrucosa* (Ellis and Solander, 1786) a common species in a variety of reef environments of the Red Sea. The coral displays striking morphological variations related to flow: branches are thick and compact in habitats exposed to high flow conditions, becoming thinner and open in protected habitat (Veron & Pichon 1976).

Experimental setup. Seven colonies of *Pocillopora verrucosa* growing at the reef at 7 to 9 m depth were carefully transplanted on 4 September 2006 to 7 transparent, flow-manipulation chambers (Fig. 1). Each chamber was an upside-down U-shaped box (wall height 0.4 m, ceiling dimension 0.5 × 0.5 m) made of transparent Plexiglas bolted to an opaque PVC base. Each single coral colony was glued at the center of the chamber. The experimental setup consisted of 4 pairs of 2 chambers (one chamber was left unused for this experiment), with the pumps in each pair oriented in opposite directions (Fig. 1). The 2 Plexiglass walls separating the chambers in the pair effectively prevented any within-pair cross-chamber effect on flow conditions. The 2 open ends in all chambers were oriented perpendicular to the direction of the prevailing long-shore currents, effectively shielding the coral from the ambient flow. The flow was intensified by an underwater pump with its outflow oriented onto the coral through a 50 cm long, 10.1 cm diameter PVC pipe (Fig. 1) (see Genin et al. 1994). Thereby, the coral was exposed to a unidirectional flow, creating asymmetric flow conditions with stronger current at the up- than down-current side (hereafter 'up-current' and 'down-current', respectively). The pumps were attached near the chambers so that the distal end of each pipe was 25 cm away from the up-current side of the coral, exposing the coral to flow intensity in the range of 15 to 20 cm s^{-1}, substantially stronger than the ambient current (~5 cm s^{-1}). The distance between the pump and coral was determined based on flow measurements carried out in a 2 m long flume using an Acoustic Doppler Velocimeter (ADV-Ocean, Sontek). The ADV was attached on a frame above the flume, set to measure the flow speed ~1 cm in front of the upstream edge of a coral skeleton which was similar in size to the corals used in the experiment.

The flow intensity at the coral's outer surface at 4 different sides (up-current, down-current, left, right) was visually observed with fluorescein dye and assessed using the gypsum dissolution technique (Doty 1971). Small gypsum casts were made in 1.5 ml Eppendorf tubes as described by Goldshmid et al. (2004), using 98% $CaSO_4$-0.5H_2O (Gesher Gypsum). The dissolution of the casts, used as a proxy of mass flux (Jokiel & Morrissey 1993), was measured by simultaneously posi-

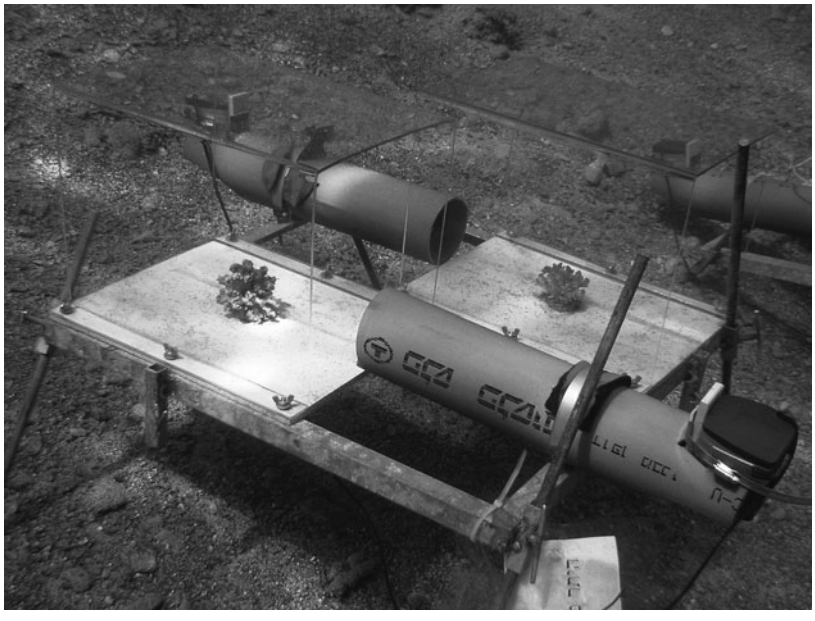

Fig. 1. Underwater setup of flow-manipulation experiment showing 2 units each consisting of a transparent, upside down U-shape box (40 × 40 × 30 cm) and a pump attached to a 50 cm long, 10.1 cm diameter pipe directed at the coral

tioning in the coral 4 gypsum casts, one at each side, for 6 h. The dissolution of the cast at each side was normalized by dividing the absolute dissolution (g) by the average of all 4 casts from the same coral (hereafter 'Dissolution Index'). The measurements were repeated 4 times in November to December 2006.

The corals were retrieved, 2 corals per day, on 15 to 17 January 2007, 98 to 100 d after the starting date. Immediately after retrieval, the corals were transferred to the laboratory and within 5 min the tissue was removed with an airbrush connected to a reservoir of filtered seawater (0.20 µm filter) from 3 fragments from each of the up- and down-current sides of each colony. The density of zooxanthellae in the collected fluid was determined by microscopic counts using a hemocytometer, 10 replicate counts per sample. Chlorophyll *a* (chl *a*) was measured by filtering 3 replicates of 2 to 5 ml of the slurry through Whatman GF/C (1.2 µm) filters followed by 24 h, cold (4°C), dark extraction in 90% acetone. A spectrophotometer (Ultraspec 2001 Pro, Biochrom) was used to determine the concentration of chl *a* in the extract (Jeffrey & Humphrey 1975). The total protein content in the tissue was determined using the Bradford method (Bradford 1976). Coral surface area was determined using Methylene Blue dye as described by Hoegh-Guldberg (1988) except that instead of the repetitive shaking, the excess dye was removed with air jet with a fixed flow from a scuba tank equipped with a pressure gage. The measurements were replicated 3 times per coral fragment, yielding a coefficient of variation (CV) of 17.3%. Values of zooxanthellae density and concentration of chl *a* and protein are reported per unit area.

At the onset of the project all colonies were dyed with Alizarin Red *in situ* in order to examine the development of morphological differences between the up- and down-current sides. The occurrence of such differences was assessed by measuring the skeletal linear extension of new branches and by visual counting of the number of protruding 'bumps' (Fig. 2) per projected surface (viewed from above) on branches which grew during the experiment. The linear extension of a branch was recorded by measuring with a caliper the distance between the alizarin mark and the tip of the branch's most distant extension (N = 3 to 12 branches per side in each of the 6 corals). A 'bump' was defined as a protruding skeleton that had 2 polyps along its stem (i.e. 2 polyps high). Protruding features that were ≤3 polyps high were defined as a 'branch' (see Fig. 2). The projected surface of a branch was calculated by measuring the lengths of its major (longest) axis and the axis perpendicular to it, as seen when looking directly down at the branch top (Fig. 2).

To assess the degree of morphological symmetry of *Pocillopora verrucosa*, we measured the 2 orthogonal

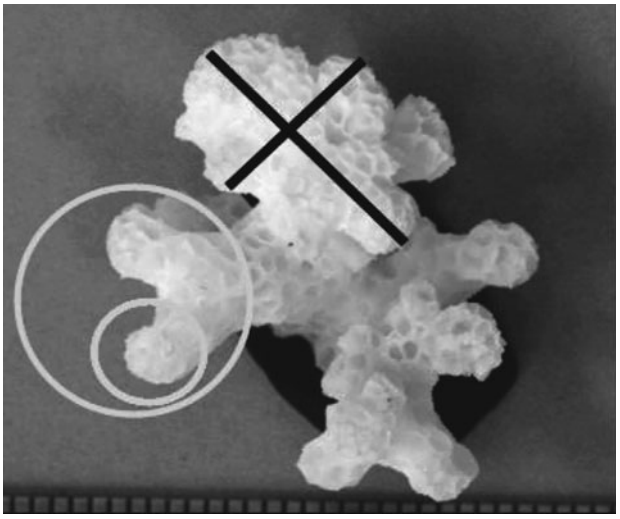

Fig. 2. Example of a 'bump' (2 polyps high, small circle) and a branch (≤3 polyps high, large circle) of the newly grown part of a coral in the flow manipulation experiment (viewed from above). The perpendicular black lines are an example of the 2 diameters used to calculate the branch's projected area, assuming an ellipsoid shape

diameters of all the *P. verrucosa* colonies (N = 46) found along a belt transect 100 × 1 m in size at 8 m depth at the Interuniversity Institute of Marine Sciences (IUI) reef. The 2 diameters were oriented so that one was parallel to the long-shore direction (the main axis of the ambient flow) and the other perpendicular to it. The ratio between the 2 diameters was used as a proxy of the colony's circular symmetry.

The symmetry of the flow over the reef was assessed using 4 yr of current measurements obtained by Genin & Paldor (1998) at our study site from 1988 to 1991. The currents were measured using an electromagnetic current meter (S4, InterOcean) deployed 12 m below the surface at 38 m water depth, ~150 m seaward of our study site.

Statistical analyses. The differences in the content of chl *a*, zooxanthellae density, and chl *a* per zooxanthellae between the up- and down-current sides (N = 3 fragments per side per coral) were tested by 2-way ANOVA (factors: coral, side) using STATISTICA 7.1 (StatSoft) after verifying homogeneity of variances using Cochran's Test. The homogeneity of variance for those 3 variables was obtained by log transforming the raw values. The variance of protein was not homogeneous, regardless of transformation. Therefore, the comparison of up- vs. down-current sides for this variable was made using a randomization test as follows. The 6 measurements obtained for each coral (3 fragments from the up- and 3 from the down-current sides) were ranked based on their protein concentration (rank 6 = highest concentration). The sum of ranks of

the 3 up-current branches was calculated for each coral and then pooled from all 6 corals into a single value, the 'total sum of ranks' of the up-current side. The same procedure was then simulated 100 000 times using random ranking. To reject H_0 (that protein concentrations in the up-and down-current sides were not different) at a significance level of $p < 0.05$, using a 2-sided test, the observed 'total sum of ranks' should be greater than the value demarcating the highest 2.5% or smaller than the value demarcating the lowest 2.5% of the 100 000 simulated values.

RESULTS

ADV measurements in the flume indicated that the flow speed at the down-current side of the coral was ~2 cm s^{-1}.

Visual observations with fluorescein dye indicated that (1) without the pumps, the water around the corals within the chambers was nearly stagnant, and (2) with the pumps working, there was no discernible effect of the flow generated in one chamber on the flow in its paired chamber.

Two weeks after the start of the flow manipulation experiment, while the intensified flow was ~10 cm s^{-1}, all the colonies started to bleach at the down-current side. The pump valves were therefore reset to generate a stronger flow (15 to 20 cm s^{-1} at the corals' up-current edge; ~2 cm s^{-1} at the down-current side). Consequently, all but one colony recovered, reducing to 6 the total number of colonies used in this experiment.

Dissolution at the up-current side was significantly stronger than at the down-current side (mean ± SE = 1.235 ± 0.014 and 0.652 ± 0.016 at the up- and down-current sides, respectively; paired *t*-test, $t = 21.468$, $p < 0.0001$, df = 30) (Fig. 3).

Up-current coral tissue at the end of the experiment contained a significantly higher concentration of chl *a* per zooxanthellae (Fig. 4a), higher chl *a* per surface area (Fig. 4b), greater density of zooxanthellae (Fig. 4c) (2-way ANOVA, $F_{1,29}$ = 18.098, 44.281, 9.2002 respectivly, n = 6, $p < 0.005$ for all), and more protein per surface area (Fig. 4d) (randomization test, 2-sided, $p < 0.05$) than the down-current side.

The linear extension of the branches during the 98 to 100 d of the experiment was significantly higher (1-way ANOVA, $F_{1,68} = 37.092$, $p < 0.0001$) at the up-current side than at the down-current side (0.49 ± 0.18 and 1.03 ± 1.47 cm, respectively) (Fig. 5a). The number of bumps per projected area was significantly lower at the up-current side (1-way ANOVA, $F_{1,81} = 31.992$, $p < 0.001$), so that the coral branches at that side appeared to be more bulky and less slender (Fig. 5b).

In situ, the projected outline of *Pocillopora verrucosa* colonies (viewed from above) exhibited a circular symmetry, with the ratio between long- and cross-shore diameters not significantly different from unity (paired

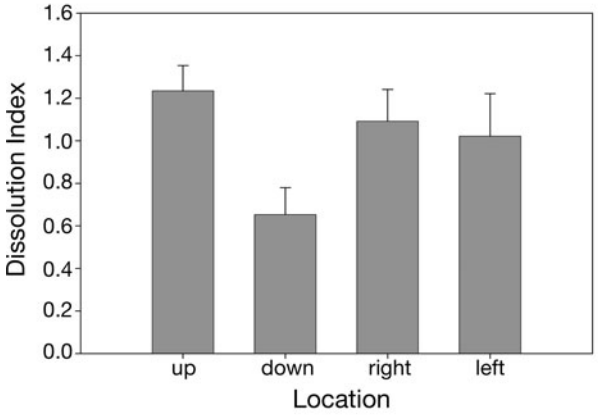

Fig. 3. Average gypsum Dissolution Index of small clots inserted for 6 h between the branches of the corals in the flow-manipulation experiments at the up-current, down-current, left and right sides of the colony (N = 4 runs, 7 corals in each; error bars = SD)

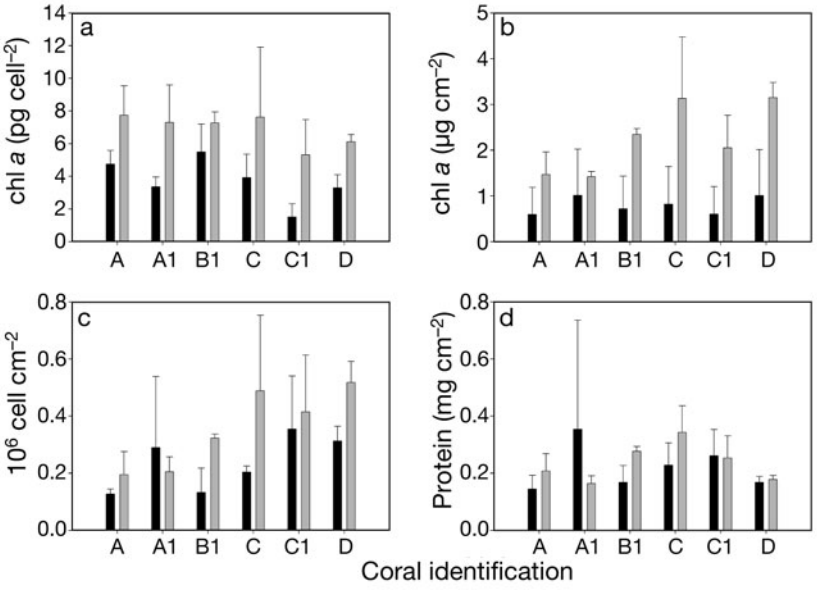

Fig. 4. *Pocillopora verrucosa*. Average concentration of (a) chl *a* per zooxanthella, (b) chl *a* per area, (c) zooxanthellae per area, and (d) protein per area after 4 mo of flow manipulation at the up-current (gray bars) and down-current (black bars) sides (N = 3 branches at each side of each of the 6 corals; error bars = SD). The difference between the 2 sides was statistically significant for all 4 parameters (see 'Results')

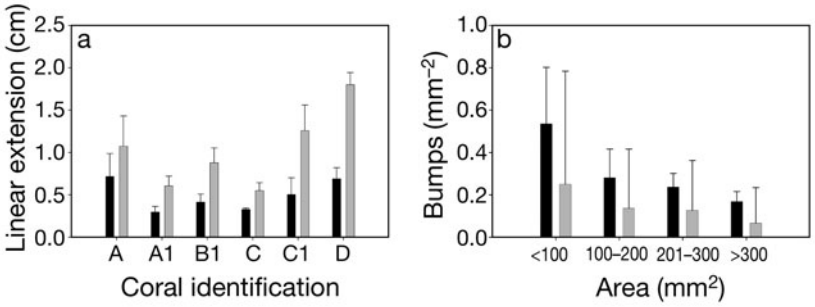

Fig. 5. *Pocillopora verrucosa*. Flow-driven morphological asymmetry. (a) Average linear extension of branches and (b) density of 'bumps' (see Fig. 2 for definition) at the down-current (black bars) and up-current (gray bars) sides of the corals exposed to unidirectional flow (N = 3 branches at each of the up- and down-current sides of each of the 6 corals). The difference between the 2 sides was statistically significant for all 4 parameters (1-way ANOVA, $p < 0.001$)

t-test, $t = 1.602$, $p > 0.1$, df = 45). The mean (± SD) of the long- and cross-shore diameters were 16.9 (± 7.3) and 16.2 (± 7.3) cm, respectively (Fig. 6).

The frequency distribution of the long-shore currents in Eilat during the 4 yr of measurements showed an almost perfect symmetry, with 48.2% of the energy density oriented southward and 47.6% northward (Fig. 7), with the rest of the energy (4.2%) oriented in the cross-shore directions.

DISCUSSION

Asymmetric flow generates a corresponding asymmetry in the morphology and tissue composition of *Pocillopora verrucosa*. Within 4 mo, the up-current side grew faster, became more 'bulky' and had higher concentrations of zooxanthellae, chl *a* and protein. Finelli et al. (2007) showed that enhanced flow created an intracolony asymmetry in photosynthesis rate in the stony corals *Porites porites* and *Siderastrea siderea.* A similar asymmetry in zooxanthellae was found in the soft coral *Sinularia flexibilis* by Khalesi et al. (2007). Flow-induced enhancement of skeletal growth was observed in *Pocillopora damicornis* (Nakamura & Yamasaki 2005, Suzuki et al. 2007) and *Stylophora pistillata* (Nakamura & Yamasaki 2005). Using unidirectional flow in models simulating mass flux-dependent growth in corals, Kaandorp et al. (1996) showed a development of strong skeletal asymmetry, similar to that shown in a photograph of *Acropora reticulate* in Vogel (1981). *A. cervicornis* colonies that grew in an exposed reef developed more 'bushy' and denser branches than those growing in a protected lagoon (Bottjer 1980).

Rates of respiration, primary production and nutrient uptake are flow-dependent (Thomas & Atkinson 1997); therefore, enhanced flow can augment the growth of both zooxanthellae (Nakamura et al. 2003) and their host (Dennison & Barnes 1988). The higher density of chl *a* and zooxanthellae found at the corals' up-current side could have been due to enhanced nutrient uptake, as such an increase is typical for corals grown in waters with high nutrient concentrations (Thomas & Atkinson 1997).

At the initial phase of our experiment, when the pumps were set to generate slow flow (10 and 0.5 cm s^{-1} at the up- and down-current sides, respectively),

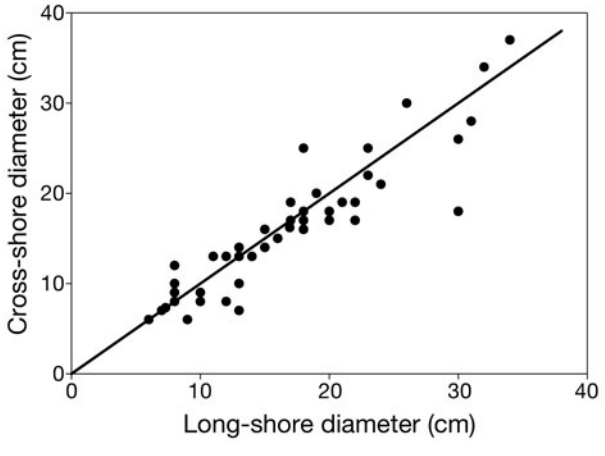

Fig. 6. *Pocillopora verrucosa*. Radial symmetry in the coral reef of Eilat, comparing the colony diameters in the direction parallel to the shore line (long-shore, the main axis of the ambient currents) and that in the cross-shore direction. The ratio between the 2 axes (solid line) was not significantly different from unity (paired *t*-test, $p > 0.1$, N = 46)

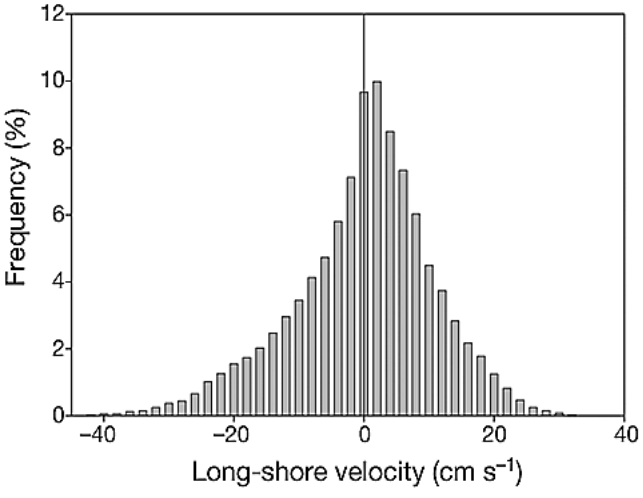

Fig. 7. Frequency distribution of different current velocities (in bins of 2 cm s^{-1}) in the long-shore direction at 12 m depth near the coral reef of Eilat from 1988 to 1991. Positive values indicate northeastward current

the corals started to bleach at the down-current side. Since the corals in our experiment were protected from the ambient flow by transparent Plexiglass walls, the only source of discernable flow was the pump. Hence, the bleaching at the initial phase may indicate that lack of currents causes stress, and possibly mortality, in *Pocillopora verrucosa*. Once the flow was reset to a stronger level, all but one of the corals recovered. Nakamura & van Woesik (2001) and Nakamura (2003) previously pointed out the important relation between bleaching and flow. A recent study by Carpenter & Patterson (2007) showed an intracolony asymmetry in photosynthetic efficiency within colonies of *Montastrea annularis* when the coral was exposed to an elevated temperature and unidirectional flow.

While asymmetry in photosynthesis and its products may disappear due to within-colony translocation (Oren et al. 1997), our findings indicate that asymmetry in environmental conditions generates lasting morphological and physiological asymmetry in corals. The overall symmetry observed in *Pocillopora verrucosa* can be determined by a corresponding symmetry in the flow, rather than by intrinsic control by the coral. The gypsum dissolution in the corals exposed to the manipulated current (Fig. 3) indicated that while the strongest mass flux occurred over the up-current side, the coral's lateral sides were also exposed to strong flow, only slightly weaker than the up-current. Hence, the semidiurnal reversal of currents in the coral reef of Eilat (Fig. 7) (Genin & Paldor 1998, Monismith & Genin 2004) is expected to induce a nearly-perfect circular symmetry of mass flux over coral colonies, generating a corresponding symmetry in their morphology (Fig. 6).

The results of our experiment with *Pocillopora verrucosa* contradict the claim that coral morphology at the level of the whole colony is 'predetermined', lacking plasticity (Shaish et al. 2007). Rinkevich's (2002) conclusion that a 'genetic blueprint' of colonial organisms is activated to ensure the alleged 'rules for species-specific landscape' does not hold for the branching coral *P. verrucosa* in Eilat. In our study, flow determined both the colony symmetry and the morphological characteristics of the individual branches, corroborating the conclusion that exposure to flow was responsible for the striking morphological differences found in *P. damicornis* in reefs exposed to different levels of flow intensity (see Fig. 1.1 in Kaandorp & Kuebler 2001). A visual survey of different coral reefs in the Gulf of Aqaba (A. Genin unpubl. data) indicated the occurrence of similarly striking morphological differences in *Stylophora pistillata*.

Note that we do not propose that genetics does not play a role in determining the morphological characteristics of corals. The large degree of flow-related plasticity may indeed be determined by a yet unknown set of plasticity-related genes (Pigliucci 1996). Our experiments, as well as the aforementioned examples of environment-related intraspecific plasticity in coral morphology (see 'Introduction'), indicate that skeletal growth in corals does not necessarily follow rigid 'blueprints' or predetermined 'species-specific landscapes' as proposed by other studies (Rinkevich 2002, Shaish et al. 2006, 2007).

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