

# Factors Controlling the Expansion Behavior of *Favia favus* (Cnidaria: Scleractinia): Effects of Light, Flow, and Planktonic Prey

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**Abstract.** Colonies of the massive stony coral *Favia favus* were exposed to different flow speeds and levels of light, and to the addition of zooplankton prey. The relative importance of each factor in controlling polyp expansion behavior was tested. The coral polyps fully expanded when they were exposed to low light intensity ( $0\text{--}40\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ ) and high flow speed ( $15\ \text{cm s}^{-1}$ ), regardless of prey presence. They also partially expanded under low and medium light ( $40\text{--}80\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ ) at medium flow speed ( $10\ \text{cm s}^{-1}$ ). The corals expanded their polyps only when they were exposed to light levels below compensation irradiance ( $I_{\text{com}}$ : light level at which photosynthesis = respiration), which was determined to be about  $107 \pm 24\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ .

The results presented here indicate that high flow, low light, and the presence of planktonic prey induce coral expansion. There is a hierarchy of response to these stimuli, in which light level and flow speed are dominant over prey presence. Coral response to these three factors is probably due to the relative importance of gas exchange and zooplankton prey.

## Introduction

Diel patterns of polyp expansion and contraction vary between species of anthozoans, including reef-building corals (Kawaguti, 1954; Porter, 1974; Lasker, 1979), gorgonians (Wainwright, 1967), and sea anemones (Pearse, 1974; Sebens and DeRiemer, 1977). Most reef corals expand their tentacles nocturnally, but some expand continuously or only during the day (Abe, 1939; Porter, 1974; Lasker, 1979).

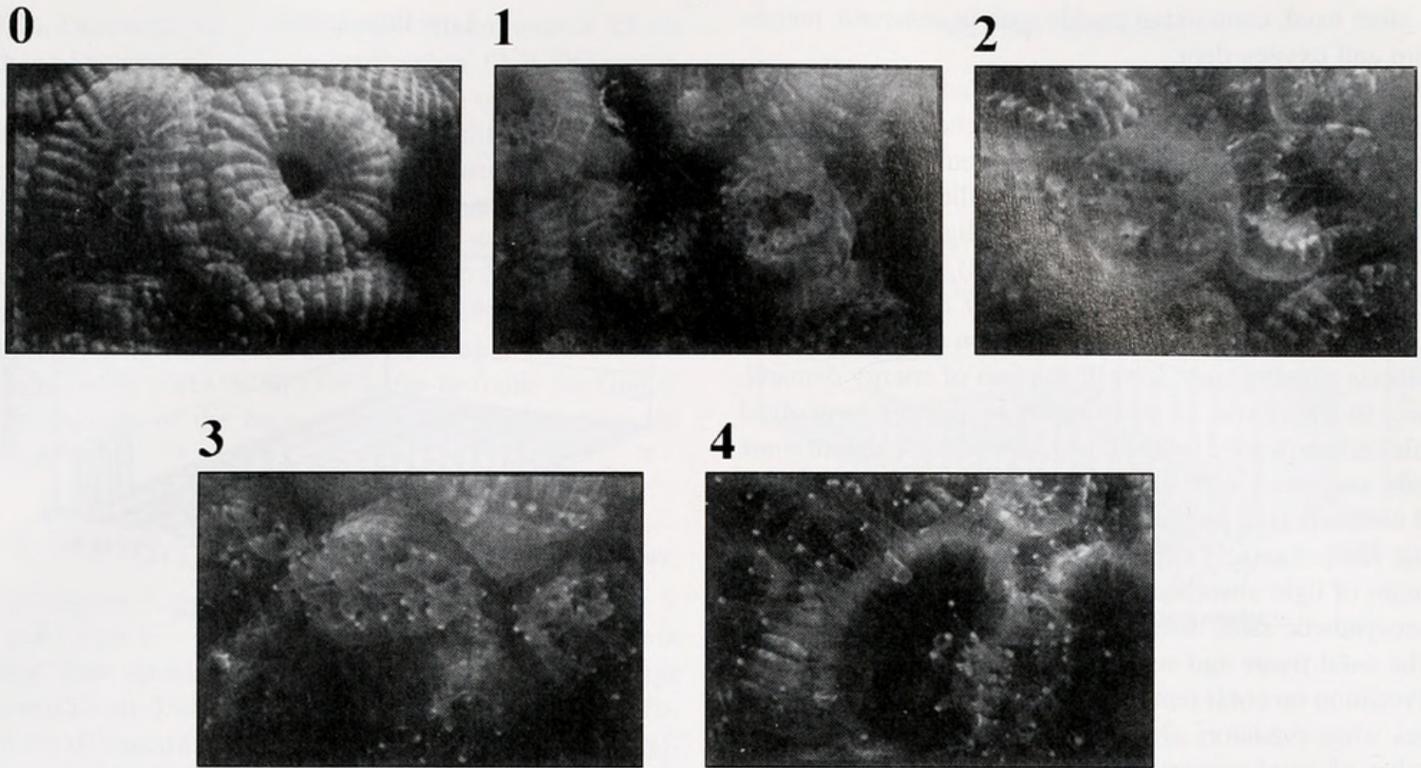
Corals that expand tentacles at night remain open until dawn, but a beam of light or mechanical stimulation may cause them to contract immediately (Abe, 1939). Sea anemones show a similar range of behavior. Structures containing high densities of zooxanthellae (such as pseudotentacles and column vesicles) may expand under conditions favorable for photosynthesis, whereas structures that contain few or no zooxanthellae (such as feeding tentacles) contract under these conditions (Sebens and DeRiemer, 1977). In the stony coral *Plerogyra sinuosa*, vesicles with high zooxanthellae density expand only during daytime, and feeding tentacles expand at night (Vareschi and Fricke, 1986). Likewise, polyps of the encrusting gorgonian *Erythropodium caribbaeorum* have pinnate tentacles with dense populations of zooxanthellae that do not function in nocturnal feeding and are expanded during the day (Sebens and Miles, 1988). It is assumed that, since such structures contract when their main function is impeded, their expansion involves some form of energy cost. When feeding tentacles themselves contain dense populations of zooxanthellae, they serve both functions of prey capture and photosynthesis, and generally are expanded continuously.

Zooplankton prey are most abundant at night on coral reefs (Sorokin, 1990), so it has been assumed that most corals expand their tentacles nocturnally in order to capture prey (Porter, 1974; Lewis and Price, 1975). Tentacular expansion also is affected by water flow, which reduces the thickness of the boundary layer over tissues and enhances gas exchange (Shashar *et al.*, 1993). Increases in water flow result in higher (approximately doubled) rates of respiration by sea anemones, stony corals, and soft corals (Patterson and Sebens, 1989; Patterson *et al.*, 1991).

The effect of flow on respiration is likely to be magnified when the exposed tissue surface area is increased by extension of either tentacles or specialized column structures.

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**Figure 1.** Levels of tentacle expansion in colonies of the stony coral *Favia fava*. Five levels were arbitrarily designated as follows: 0 = full contraction, 1 = 25% expansion, 2 = 50% expansion, 3 = 75% expansion, 4 = 100% expansion. Each score refers to a whole coral colony.

Low flow rate limits the diffusion of materials in the water column to and from coral tissues, thereby regulating and reducing metabolic rates (Patterson and Sebens, 1989; Patterson *et al.*, 1991), zooxanthellae productivity (Dennison and Barnes, 1988; Shick, 1990; Patterson *et al.*, 1991), and nutrient uptake (Atkinson and Bilger, 1992). Oxygen builds up to high levels within and above coral tissue surfaces during the day as a result of photosynthesis, and is extremely depleted near those surfaces at night due to respiration; both gradients are reduced, improving delivery of dissolved substances to and from tissues, with even small increases of flow speed (Shashar and Stambler, 1992; Kuhl *et al.*, 1995; Shashar *et al.*, 1996).

Polyp size, tentacle morphology, and tissue surface area vary widely among coral species, and all three factors contribute to prey encounter and capture rate. Porter (1976) suggested that large polyps with elongate tentacles specialize in zooplankton capture, at the expense of high surface area conducive to photosynthesis. However, more recent evidence shows that certain small-polyped corals are able to capture almost the same size range of prey as do those with larger polyps, and actually have much higher rates of prey capture per unit biomass because of the high surface area of the tentacles that they expose to moving water (Sebens, 1987a). The small-polyped coral *Madracis mirabilis* captures 30 times more zooplankton per coral biomass than does the much larger-polyped *Montastrea cavernosa* (Sebens *et al.*, 1996). The biomass of polyps of *M. mirabilis* is

only 1/90th of the biomass of *M. cavernosa* polyps, but an equal biomass of *M. mirabilis* colony has 12 times the tentacular surface area of a *M. cavernosa* colony.

A primary cost associated with expansion in corals is increased respiration, facilitated by a larger surface area of tissue in contact with the overlying water, including water inside the coelenteron, than in contracted corals. Polyp expansion is energy consuming, in that it is achieved by pressurization of the coelenteron. Pressurization is brought about by ciliary pumping of water into the coelenteron, which acts on the viscoelastic material of the polyp wall (Barnes, 1987).

Rates of respiration are known to be significantly reduced in contracted corals (Brafield and Chapman, 1965; Pearse, 1974; Robbins, and Shick, 1980; Lasker, 1981). The magnitude of this difference depends on ambient oxygen concentration (Beattie, 1971; Sassaman and Mangum, 1972, 1973, 1974; Shumway, 1978) and on the ratio of expanded to contracted tissue area, rather than being a simple response to low external oxygen concentration alone. Contraction may be a means of producing a low oxygen concentration in the coelenteron, resulting in lower metabolic rates and in savings of energy or carbon regardless of the external oxygen level (Sebens, 1987b). In contrast, expansion may aid in the diffusion of excess oxygen away from photosynthesizing coral tissues, thus reducing local hyperoxia and its negative effect on metabolic rates or damage due to superoxide radicals (Lesser and Shick, 1989; Shick, 1991). On

the other hand, contraction could result in anaerobic metabolism and oxygen debt.

The effects of polyp expansion and contraction on gas exchange and on the key metabolic processes of photosynthesis and respiration are unknown in stony corals. In some cases, photosynthesis contributes all of the required carbon for corals, as in the shallow-water, high-light-adapted *Stylophora pistillata* (Falkowski *et al.*, 1984), whereas in low-light-adapted *S. pistillata* (Falkowski *et al.*, 1984) and in other coral species that depend mostly on predation, photosynthesis supplies only a small fraction of energy demand. Since, in the course of photosynthesis, oxygen is evolved while carbon dioxide is consumed, it is possible that in some corals and other zooxanthellate organisms, the extension and contraction of tentacles is tightly coupled to photosynthetic rates. Tentacle expansion status in corals affects the amount of light absorbed by the zooxanthellae, and in turn photosynthetic rates determine  $O_2$  and  $CO_2$  concentrations in the coral tissue and surrounding waters.

Predation on coral tentacles may cause their retraction at times when predators are active. However, a considerable number of coral species with zooxanthellate tentacles expand during the daytime when many coral predators (*e.g.*, chaetodontid fish) are active, suggesting that predation on tentacles is not a currently active selective force on these behavioral patterns.

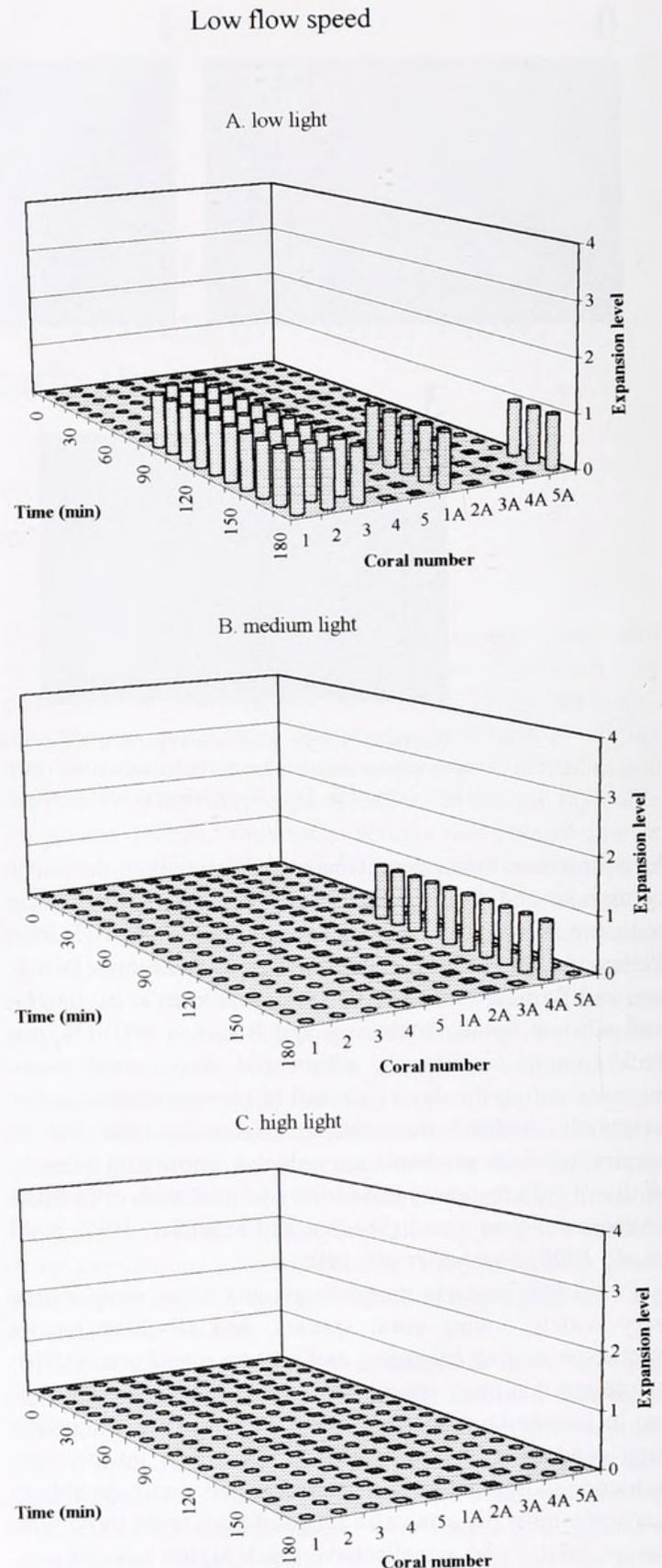
On coral reefs at Eilat (Gulf of Aqaba, northern Red Sea), colonies of the massive stony coral *Favia fавus* expand their tentacles only after sunset and remain open until sunrise (O. Levy, unpub. obs.). In the present study, we determined the relative importance of flow speed, photosynthetically active radiation (PAR), and planktonic prey availability in controlling tentacle expansion behavior in *Favia fавus*.

## Materials and Methods

### Coral collection and flow tank setup

Colonies of the common coral *Favia fавus* were collected from the reef adjacent to the Interuniversity Institute for Marine Science at Eilat, Israel, northern Red Sea, from depths of 5–7 m. Individuals of this species were chosen for study because they are abundant on coral reefs at Eilat, their polyps are large (about 1 cm diameter) and easy to observe, and they exhibit regular diel behavior under laboratory conditions. The collected coral colonies, each up to 10 cm diameter, were transferred to the laboratory and placed in shallow tanks supplied with running seawater for 10 h of acclimation before experiments were begun. New corals were collected for each combination of experimental treatments.

Experiments on tentacle expansion behavior were performed in two 25-l recirculating flow tanks; procedures were based on those described by Vogel and LaBarbera



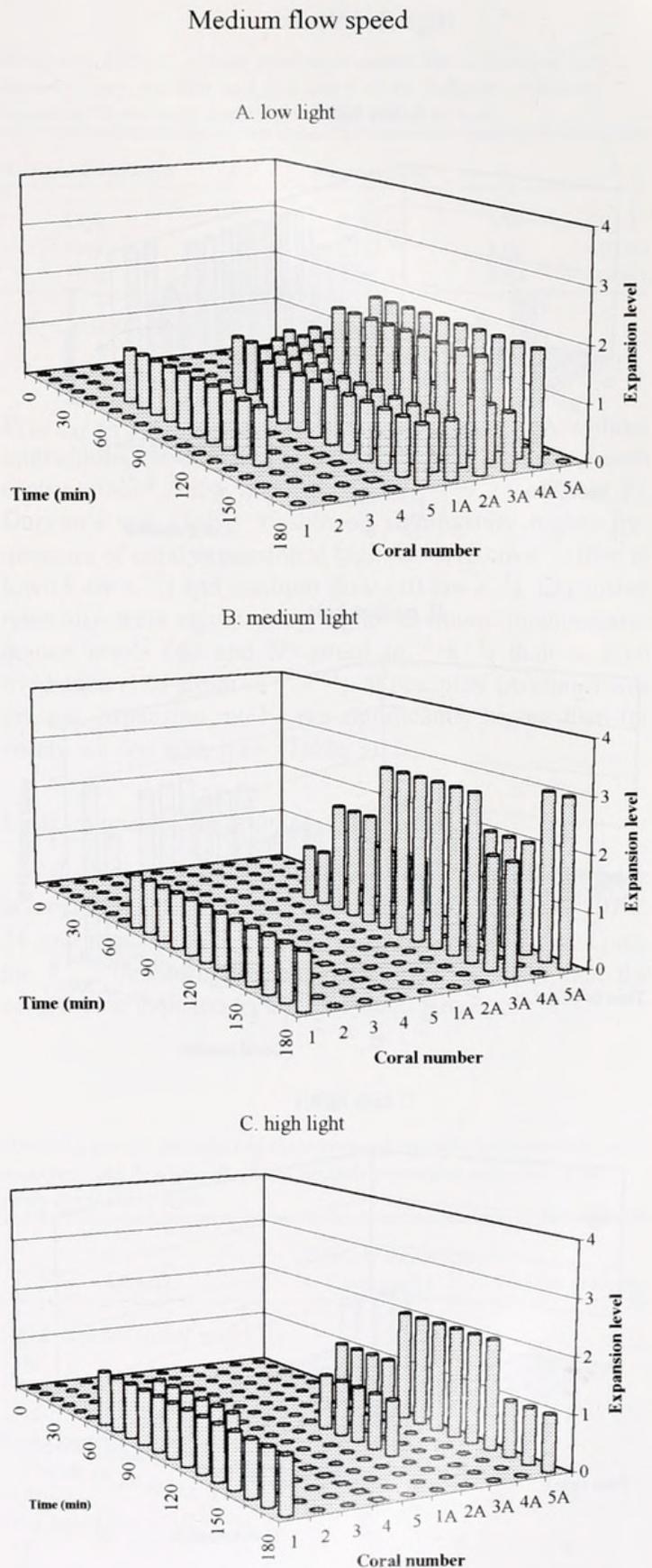
**Figure 2.** Tentacle expansion behavior of the stony coral *Favia fавus* at low flow ( $5 \text{ cm s}^{-1}$ ), with variation in light intensity and prey presence (*Artemia* nauplii). Corals marked with A were fed *Artemia* after 90 min. (A) Light intensity  $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . (B) Light intensity  $80 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . (C) Light intensity  $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

(1978). Each tank was 100 cm long  $\times$  10 cm wide  $\times$  25 cm high, and seawater was circulated with a 12-V DC motor. Electronic function generators, consisting of computer programs that were interfaced through a digital-to-analog circuit, controlled the motor speed. Flow speed was measured by following the movement of brightly illuminated particles that were added to the water. Particle movements were recorded using a video camera (Sony CCD 2000E, Hi8 PAL system) with a close-up lens. Flow velocity was measured as described by Trager *et al.* (1990), using a videocassette recorder (Sony EVO-9800P) for frame-to-frame tracking of the movement of the back-lit particles suspended in the flowing water.

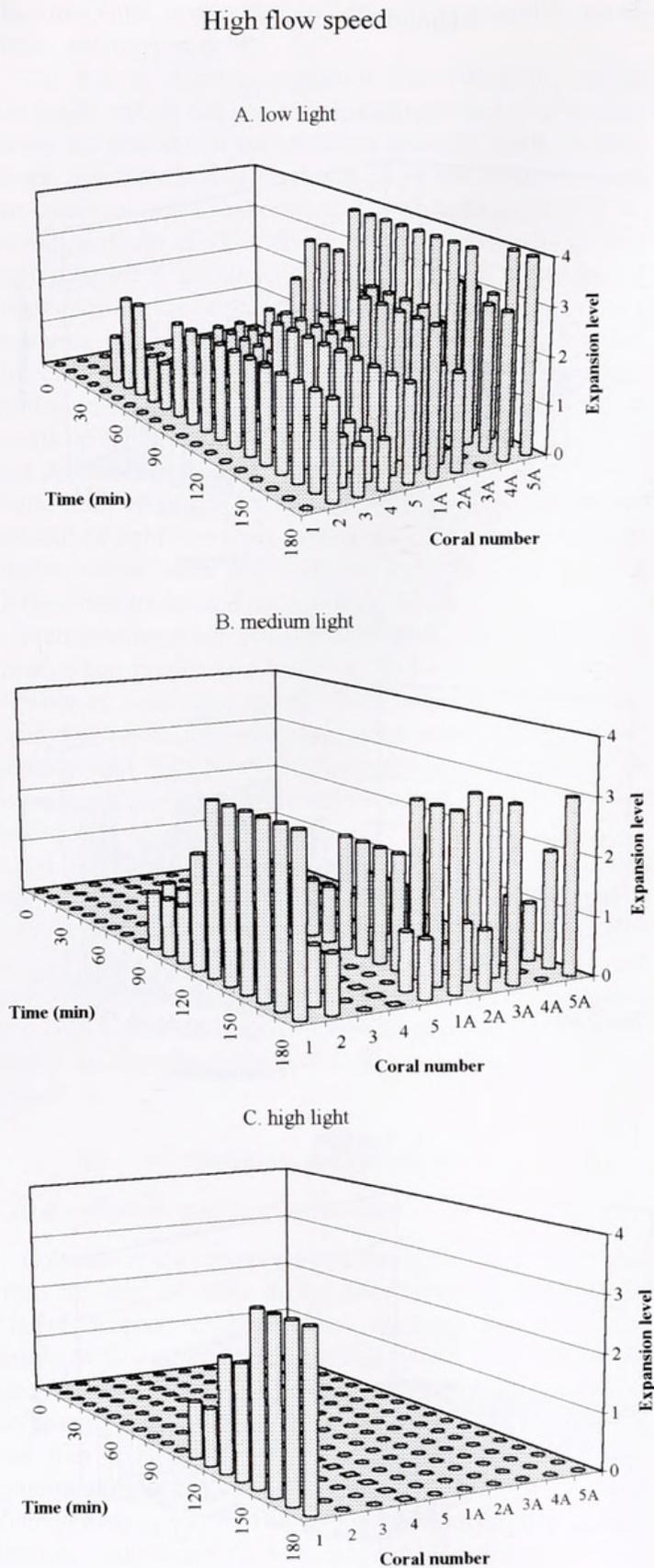
#### Coral expansion experiments

Colonies of *F. favus* were tested at three flow speeds: 5, 10, and 15  $\text{cm s}^{-1}$ . These speeds were selected as similar to natural flow speeds on coral reefs at Eilat, which range between about 5 and 20  $\text{cm s}^{-1}$  (Genin *et al.*, 1994). For each set of experiments, 20 colonies were used; five corals were placed in each of four tanks. Two of the tanks served as controls with no flow, while in the other two tanks flow was generated as described above. Halogen lamps coupled to fiber optics were set above all four tanks within each experiment, and three light irradiance levels were tested—40, 80, and 120  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (equivalent to 40, 80, and 120  $\mu\text{E m}^{-2} \text{s}^{-1}$ ). Irradiance was measured as photon flux, with a QSI-140 quantum scalar irradiance meter. Temperature was maintained at  $24 \pm 0.1^\circ\text{C}$ . Each experiment lasted 180 min, and coral expansion behavior was recorded every 10 min. The tanks were rinsed between experiments. In feeding experiments, freshly hatched *Artemia* nauplii were added *ad libitum*. Tentacle expansion of *F. favus* was scored on a scale based on Lasker (1979), ranging from 0 to 4, where 0 represents 0% expansion (full contraction), 1 is 25% expansion, 2 is 50% expansion, 3 is 75% expansion, and 4 is 100% expansion (Fig. 1). Each score refers to a whole coral colony (Fig. 1).

The first set of three experiments was conducted at a flow speed of 5  $\text{cm s}^{-1}$ , with three levels of irradiance (40, 80, 120  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). In one of the two tanks with water flow, and in one of the control tanks without flow, *Artemia* nauplii serving as zooplankton prey were added after 90 min. In the second set of three experiments, the flow speed was set to 10  $\text{cm s}^{-1}$ , and the last set of three experiments was run with new colonies of *F. favus* at a flow speed of 15  $\text{cm s}^{-1}$ . Thus, in the three sets of experiments, corals were exposed to all possible combinations of water flow, light intensity, and prey presence. The corals were replaced with new colonies in each experiment to avoid changes in behavior with experience. At the beginning of all experiments, the tentacles of the *F. favus* colonies were contracted (Fig. 1).



**Figure 3.** Tentacle expansion behavior of the stony coral *Favia favus* at medium flow (10  $\text{cm s}^{-1}$ ), with variation in light intensity and prey presence (*Artemia* nauplii). Corals marked with A were fed *Artemia* after 90 min. (A) Light intensity 40  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . (B) Light intensity 80  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . (C) Light intensity 120  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .



**Figure 4.** Tentacle expansion behavior of the stony coral *Favia favus* at high flow ( $15 \text{ cm s}^{-1}$ ), with variation in light intensity and prey presence (*Artemia nauplii*). Corals marked with A were fed *Artemia* after 90 min. (A) Light intensity  $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . (B) Light intensity  $80 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . (C) Light intensity  $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

We assessed possible interaction effects between light intensity, prey presence, and flow speed on tentacle expansion behavior in *F. favus* by performing three-way ANOVA tests on the results.

#### Determination of light compensation point ( $I_{com}$ )

The light compensation point for *F. favus* was determined by measuring coral respiration in a closed system (Haramaty *et al.*, 1997). Photosynthesis (under different light intensities) and dark respiration were measured as changes in oxygen concentration, using a Clark-type  $\text{O}_2$  electrode (YSI 5331) (Dubinsky *et al.*, 1987). Measurements were made in a double-walled, cylindrical 230-ml chamber filled with filtered seawater (GF/C  $0.45 \mu\text{m}$ ). Temperature was maintained at  $24 \pm 0.1^\circ\text{C}$ . The water in each respirometry chamber was stirred by a magnetic bar beneath a perforated plate supporting the coral. An oxygen electrode detected the rate of oxygen decline in the chamber with an amplifier, which was connected to a data logger (Furier, Israel), coupled to an oxygen meter. Oxygen uptake was measured in the dark for 30 min, and then light intensity was increased, in steps of 30 min, to 10, 40, 80, 120, and  $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

Colony surface area was measured by covering each coral colony with plasticene, then removing the cover and spreading it flat. The outline of the plasticene sheet was then copied onto aluminum foil and cut; surface area was determined by the weight of the foil in relation to the weight of a piece of foil of known surface area (Marsh, 1970). For calculation of light compensation point ( $I_{com}$ ), we used computer software attached to the data logger, and the inverse quadratic equation for unit surface area, as described by Ben-Zion and Dubinsky (1988).

## Results

### *Coral expansion behavior*

The expansion behavior of *F. favus* colonies varied with each combination of stimuli. In the first set of experiments at low flow speed ( $5 \text{ cm s}^{-1}$ ) under low irradiance levels ( $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ), the coral tentacles expanded only partially with or without the addition of *Artemia nauplii* (Fig. 2A), up to level 1 (25%) (Fig. 1). Most tentacles remained fully contracted under medium irradiance level (Fig. 2B); when prey were added, only one coral responded and expanded up to level 1 (25%). In the control tanks with no water flow, the corals remained contracted during the entire 180 min of the experiment. When corals were exposed to higher irradiance ( $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ), tentacle expansion did not occur at all, and the corals remained contracted during the entire experiment (180 min) (Fig. 2C). The same response occurred in the two control tanks in which corals were exposed to no flow at  $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

Table 1

Three-way ANOVA, with interactions among the variables of light intensity, prey presence, and flow speed on the behavior of tentacle expansion in the stony coral *Favia fавus* after 180 min

Source of variation	DF	Mean square	F	P
Light	2	3298.61	6.55	<0.01
Prey	1	2777.77	5.52	<0.05
Light × Prey	2	1173.61	2.33	Not significant
Flow	2	5361.11	10.65	0.001
Light × Flow	4	1027.77	2.04	Not significant
Prey × Flow	2	694.44	1.38	Not significant
Light × Prey × Flow	4	590.27	1.17	Not significant

$P < 0.0001$ ,  $F_{(17,89)} = 3.54$ .

In the second set of experiments at intermediate water flow rate ( $10 \text{ cm s}^{-1}$ ), at a low light intensity of  $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , and in the absence of *Artemia* nauplii, two corals expanded up to level 1 (25%). When *Artemia* nauplii were added, four corals expanded their tentacles—two to level 1 (25%) and two up to level 2 (50%) (Fig. 3A). In the control tanks with no flow, all corals remained contracted during the entire experiment, even when prey was added. When light intensity was increased to  $80 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , only three corals responded. Two colonies out of the group fed with *Artemia* expanded to level 3 (75%); the third colony from the unfed group expanded only to level 1 (25%) (Fig. 3B). No expansion responses occurred in the two control groups at  $80 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . At high light intensity ( $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and intermediate flow speed, only four corals expanded their tentacles slightly, two in the *Artemia*-fed group and two in the non-fed group (Fig. 3C). Again, there was no expansion response by the control corals.

In the third set of experiments run at high flow speed ( $15 \text{ cm s}^{-1}$ ), with low irradiance ( $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ), most of the corals showed positive response and expanded their tentacles. In the group fed with *Artemia*, four corals responded: two fully expanded to level 4 (100%), and two opened to level 3 (75%).

In the non-fed group, four corals responded: two expanded to level 1 (25%), and the other two expanded up to level 2 (50%) (Fig. 4A). In the two control groups, with no flow, the corals remained contracted during the entire experiment. Similar responses occurred at medium light intensity  $80 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (Fig. 4B), but no expansion response occurred in the two (no-flow) control groups. Only one coral expanded its tentacles to level 3 (75%) when light irradiance was increased to  $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , and all the corals, including those in the other control groups, remained contracted during the entire 180 min (Fig. 4C).

A three-way ANOVA of expansion behavior with the three variables tested (light, flow, and prey) revealed no significant interactions between the variables ( $P < 0.0001$

Table 2

Three-way ANOVA, without interaction among the variables of light intensity, prey presence, and flow speed on the behavior of tentacle expansion in the stony coral *Favia fавus* after 180 min

Source of variation	DF	Mean square	F	P
Light	2	3298.61	5.96	<0.01
Prey	1	2777.77	5.02	<0.005
Flow	2	5361.11	9.69	<0.001

$P < 0.0001$ ,  $F_{(5,84)} = 7.27$ .

$F_{(17,89)} = 3.54$ ) (Table 1). A three-way ANOVA without interactions showed significant variation in expansion with each variable ( $P < 0.0001$ ,  $F_{(5,84)} = 7.27$ ) (Table 2). Duncan's test (Table 3) showed significantly higher frequencies of coral expansion at high flow ( $15 \text{ cm s}^{-1}$ ) than at low ( $5 \text{ cm s}^{-1}$ ) and medium flow ( $10 \text{ cm s}^{-1}$ ). Expansion rates also were significantly higher at low-to-medium irradiance levels ( $40$  and  $80 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) than at high irradiance ( $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). When prey (*Artemia*) was present, expansion rates were significantly higher than for corals not fed with prey (Table 3).

#### Light compensation point ( $I_{com}$ )

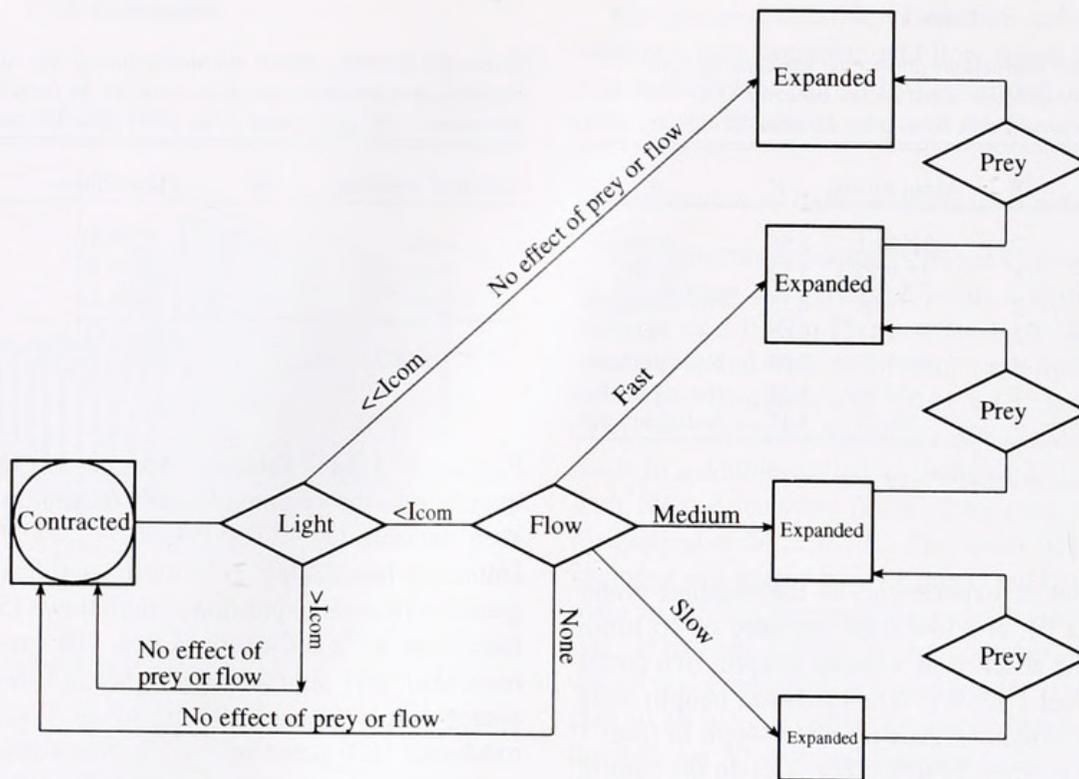
Calculation of the P/I curve revealed that the irradiance level needed to achieve compensation in *F. fавus* was  $107 \pm 24 \mu\text{mol m}^{-2} \text{ s}^{-1}$  ( $n = 5$  corals tested). We calculated only the  $I_{com}$ , therefore the maximum light intensity that the corals were exposed to was only  $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

Table 3

Duncan's test on the effect of three types of stimuli (light intensity, prey presence, and flow speed) on the tentacle expansion behavior of the stony coral *Favia fавus*

Stimulus	Tentacle expansion (mean %)	Duncan grouping
Light intensity ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )		
40	27.5	A
80	19.16	A
120	6.66	B
Prey ( <i>Artemia</i> nauplii)		
Present	23.33	A
Absent	12.22	B
Flow speed ( $\text{cm s}^{-1}$ )		
5	5	B
10	16.66	B
15	31.66	A

Maximum coral expansion occurred when light intensity was low ( $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ), prey were present, and water flow speed was high ( $15 \text{ cm s}^{-1}$ ). See Fig. 1 for description of % tentacle expansion. Means with the same letter are not significantly different at  $P = 0.05$ .



**Figure 5.** A conceptual diagram of tentacle expansion behavior in the stony coral *Favia fava* in response to different levels of light intensity, flow speed, and the addition of prey (*Artemia nauplii*). Maximum tentacle expansion occurred at dark. At low irradiance, under the compensation point ( $I_{com}$ ), corals will expand with correlation to the flow rate. Furthermore, the addition of prey can enlarge tentacle expansion response in those conditions. At high irradiance level, above  $I_{com}$  the tentacles remain contracted regardless of the presence of neither flow nor prey. In still water the corals remain contracted.

## Discussion

We demonstrate here the relative importance of light, flow, and zooplankton prey in controlling the expansion behavior of a stony coral. Although previous studies have examined these factors separately, the present study is the first to test all three factors simultaneously and to elucidate that prey presence is of secondary importance to light and flow in inducing the expansion of coral tissue.

Several reports have demonstrated that stony corals and sea anemones expand their tentacles in the presence of food (Mariscal and Lenhoff, 1968; Reimer, 1970, 1971; Lewis and Price, 1975). Electrophysiological studies using suction electrodes in the coral *Meandrina meandrites* have shown that repeated stimulation of the nerve net evokes oral disk expansion and tentacle extension, similar to the expansion behavior that normally occurs at night when the corals feed (McFarlane, 1978). It is assumed that the nervous responses occur due to prey stimulation of chemoreceptors, as described for the mushroom coral *Heliofungia actiniformis* by McFarlane and Lawn (1991). Flow also is known to cause expansion by corals; high flow speed increases both the potential for encountering planctonic prey and the mass transfer rate of dissolved gases and nutrients (Sebens *et al.*, 1997).

Our analysis of three variables simultaneously shows that each factor has an impact on the expansion behavior of *F. fava*, but that flow and light are the main triggers. Maximum tentacle expansion in *F. fava* corals occurred with high flow, low irradiance, and the addition of prey (Fig. 4A). When there was no addition of prey, but light intensity remained low and flow velocity high, the corals responded and expanded their tentacles up to 75%. Positive responses also occurred in medium flow, with medium light (Fig. 3A, B), but there was almost no response at all when light intensity was maximal ( $120 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), regardless of flow speed or prey presence.

At high flow, the benefits of flow to photosynthesis are greater than the costs associated with increased respiration, thus energy available to the coral for growth and reproduction is greater, up to some asymptote, with increasing flow speed (Patterson *et al.*, 1991; Patterson, 1992). Coral energetics depend upon tissue expansion state, which alters both the surface area exposed to flow and the thickness of the tissue layers through which materials diffuse. In high-speed flow environments, flow modulation of coral energetics is minimal. When water flow is low, dense branches or other morphologies that increase the total volume and thickness of a colony's diffusional boundary layer may negatively

affect the coral's energy balance. In low-flow environments, the diffusional boundary layer may become severely limiting to metabolic processes; corals in these environments show morphologies that maximize the exposure of their tissue surfaces to flow (Lesser *et al.*, 1994; Sebens *et al.*, 1997).

We suggest that expansion behavior in zooxanthellate corals relates to their energy equilibrium between heterotrophy and autotrophy. The expanded tentacles of *F. fавus* corals have low densities of zooxanthellae and may produce a self-shadow on the rest of the coral tissue that contains dense algae (O. Levy, unpub. obs.). Thus, under conditions of high light, expansion may lead to a decrease in overall photosynthetic rate and an increase in coral metabolic rate, resulting in a net loss of energy.

The expansion responses that we observed here lead us to propose a hierarchy of response to the three variables examined. According to our results, in still water, corals will not expand their tentacles even if light and prey levels vary (Fig. 5). When the light level is too high (over  $I_{com}$ ), they also will not expand, even when flow and prey vary. When light levels are low ( $<I_{com}$ ), the expansion behavior depends on conditions of flow and prey (Fig. 5). Finally, if no prey is present, the corals will still expand, but only if light is low and flow speed is medium to high. Therefore, the coral's response to prey presence is secondary to its response to light and flow.

This relative importance of different environmental factors in controlling tentacular expansion (Fig. 5) may apply to many coral species, which, like the colonies of *F. fавus* tested here, have low densities of algae in their tentacles and are known for their nocturnal expansion behavior. However, these results probably do not apply to corals that contain high algal densities in their tentacles and thus would benefit from expansion when light levels are high.

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