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Bleaching of the coral *Oculina patagonica* by *Vibrio* AK-1

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ABSTRACT: Bleaching in stony corals is the result of a disruption of the symbiosis between the coral hosts and photosynthetic microalgal endosymbionts (zooxanthellae). Coral bleaching may be induced by a variety of environmental stimuli, including increased seawater temperature. Large-scale bleaching episodes have been suggested to be linked to global warming. We have discovered that coral bleaching, in this case, bleaching of the Mediterranean coral *Oculina patagonica*, is caused by a bacterial infection and that water temperature is a contributing factor. The causative agent, *Vibrio* AK-1, was present in 28 bleached *O. patagonica* examined, but absent from 24 healthy (unbleached) corals. The *Vibrio* sp. was isolated in pure culture, characterized microbiologically, and shown to cause bleaching when inoculated onto unbleached corals. An increase in seawater temperature may influence the outcome of bacterial infection by lowering the resistance of the coral to infection and/or increasing the virulence of the bacterium. When inoculated with 10^6 *Vibrio* AK-1 ml^{-1} at 26°C, bleaching began at around 10 d and affected more than 80% of the corals after 44 d. Bleaching did not occur under the same conditions in the presence of antibiotics or if the temperature was lowered to 16°C.

KEY WORDS: Coral · Bleaching · Bacterial infection · *Vibrio* · *Oculina* · Mediterranean

INTRODUCTION

Coral bleaching, the disruption of symbioses between corals and microalgae (zooxanthellae; Brown et al. 1995), is a problem that threatens coral reefs throughout the world. Coral bleaching events of unprecedented frequency and global extent were reported in the 1980s and early 1990s (Goreau 1990, Glynn 1991a, Hoegh-Guldberg & Salvat 1995). The subject is of concern because of mortality and local extinctions associated with large-scale bleaching episodes (Glynn 1991b), the fact that bleaching episodes have increased dramatically in frequency and intensity within the past decade (D'Elia et al. 1991), and speculation about possible links to global warming (Jokiel & Coles 1990, Glynn 1991b, 1993, Smith & Buddemeier 1992, Buddemeier & Fautin 1993). A number of causes have been suggested for bleaching, including elevated temperatures (Jokiel & Coles 1977, 1990, Gates 1990, Glynn 1990, Glynn & D'Croz 1990, Gates et al. 1992, Fitt & Warner 1995) and increased irradiance (Glynn et al. 1992, Gleason & Wellington 1993, Shick et al. 1995).

Buddemeier & Fautin (1993) have suggested that coral bleaching is a normal regulatory process by which genetic variation among the zooxanthellae is allowed. Bleached coral reefs generally have a patchy appearance due to the irregular distribution of bleached colonies (Glynn et al. 1985). Edmunds (1994) suggested that the reef-wide spatial distribution of bleached coral colonies is the result of the distribution of bleaching-susceptible clonal genotypes. Despite these efforts, little progress has been made in understanding why some corals bleach while others do not (Edmunds 1994).

Although bacteria are known to be abundant and active around corals and in the coral surface microlayer (Sorokin 1973, Mitchell & Chet 1975, Ducklow & Mitchell 1979, Ritchie & Smith 1994), little information exists on the structure, composition and maintenance of the bacterial community. The surface of living corals is covered by a mucoid material. This surface mucopolysaccharide layer provides a matrix for bacterial colonization, allowing for the establishment of a 'nor-

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mal bacterial community' which may be characteristic of a particular coral species (Mitchell & Chet 1975, Ducklow & Mitchell 1979, Rublee et al. 1980, Segel & Ducklow 1982, Ritchie et al. 1994).

Recently, Kushmaro et al. (1996) indicated that bleaching of the coral *Oculina patagonica* is caused by bacterial infection. *O. patagonica* was first observed in the Mediterranean in 1966 and was presumed to be an immigrant species accidentally introduced from South America (Zibrowius 1974). Recent surveys show that *O. patagonica* is abundant in wide areas along the Israeli coast of the Mediterranean at a depth range of 1 to 50 m. Most of the bleached colonies have been found in patchy formations at depths of 1 to 6 m. The number of bleached colonies increased rapidly from late May to September following rising sea temperatures reaching 29°C (Fine & Loya 1995). Bleaching of *O. patagonica* was first observed in the summer of 1993 and since then has been continuously monitored. In this paper, we present data on the isolation and characterization of *Vibrio* AK-1 and on the ability of this bacterium to infect and cause bleaching of *O. patagonica* under laboratory conditions.

MATERIALS AND METHODS

Collection and maintenance of the corals. Intact colonies of the coral *Oculina patagonica* were collected during the summer of 1995 from a depth of 1 to 3 m at 3 sites along the Mediterranean coast of Israel (see Table 2). Seawater temperature at time of collection was 25 to 26°C. Within 1 to 2 h of collection, each colony was split into several pieces and placed into 2 l aerated aquaria containing filtered seawater (0.45 µm) that were maintained at 25°C. The aquaria were illuminated with a fluorescent lamp at 12 h light:12 h dark intervals. Coral pieces were allowed to recover and regenerate for 15 d before the start of each experiment. If any piece failed to heal (complete cover of damaged skeleton by new tissue), it was discarded and not used in any experiment.

***Vibrio* AK-1 sampling and isolation.** Small pieces of bleached and unbleached corals collected as described above (in all, 28 samples were taken from bleached corals and 24 samples from unbleached corals) were placed in sterile tubes and brought to the laboratory within 2 h. The mucous surface layer of each piece was removed with a sterile loop, diluted into sterile seawater, streaked onto Marine Agar (18 g Marine Broth, Difco MA 2216, 9 g NaCl and 18 g Difco Bacto Agar, per 1 l of deionized water) and incubated at 30°C for 3 d. The dominant colony types were restreaked onto Marine Agar to obtain pure cultures. These strains were subsequently tested for their pathogenic effect on healthy *Oculina patagonica*. The only strain able to induce bleaching, referred to as AK-1, was subsequently characterized as belonging to the genus *Vibrio* (Farmer & Hickman-Brenner 1992). The presence of strain *Vibrio* AK-1 was determined by its characteristic colony morphology, cellular morphological pattern and antibiotic sensitivity pattern.

Characterization of *Vibrio* AK-1. Strain *Vibrio* AK-1 was routinely cultivated on Marine Agar or Marine Broth at 30°C. Gram reaction, cell morphology and motility were determined microscopically. Scanning electron microscopy was performed on healthy and bleached coral pieces as well as on pure cultures of *Vibrio* AK-1. Biochemical tests (indole production, nitrate from nitrite, acidification of glucose, arginine dihydrolyase, oxidase, esculine hydrolysis, gelatinase and β-galactosidase) were performed by api-20 NE (micromethod tests for the identification of Gram-negative rods, Bio Merieüx SA, Marcy-Ietoile, France). The standard api-20 NE method was used except that the media were adjusted to 3% NaCl. Growth and acid production were measured on TCBS Agar (Difco) which contains sucrose. Salt tolerance was determined in Nutrient broth (Difco) containing 0 to 12% NaCl. Sensitivity to antibiotics (10 µg ampicillin, 15 µg erythromycin, 10 µg penicillin-G, 30 µg tetracycline, 30 µg kanamycin and 10 µg streptomycin, each applied to a paper disc) was determined after incubation for 24 h at 30°C on Marine Agar. Sensitivity to 30 µg per disc of the *Vibrio*-specific compound Vibriostatic 0129 (Sigma), was determined as described above. Vibriostatic 0129 is 2,4-diamino-6,7-diisopropylpteridine. This compound specifically inhibits the growth of bacteria of the genus *Vibrio*. Microbial fatty acid profile was analyzed using the MIDI/Hewlett Packard microbial identification system (Analytical Services Inc., Williston, VT, USA).

Laboratory bleaching experiments. Three types of experiments were performed. In the first set of experiments bleached and healthy corals were put together in 3 aerated 2 l aquaria and maintained at 25 and 17°C.

In the second set of experiments, 10 µl containing 5×10^6 cells ml^{-1} of *Vibrio* AK-1 were placed on each of 5 healthy corals and the corals were then put into separate aerated aquaria maintained at 25°C. For a control, 5 corals were inoculated with 10 µl of sterile medium rather than bacteria and placed in separate aquaria. To determine if the *Vibrio* AK-1 supernatant fluid was toxic to coral, a 24 h culture was centrifuged at $12\,000 \times g$ for 20 min and filtered through a 0.2 µm membrane filter. The supernatant (10 µl) was applied to corals as described above.

The third set of experiments was carried out without removing the corals from 2 l aerated aquaria. In the first test, conducted at 26°C, 3 aquaria, each containing 6 colonies of *Oculina patagonica* corals, were inoculated with *Vibrio* AK-1 to a final bacterial cell density

of 5×10^6 cells ml^{-1}. Two additional aquaria, each containing 6 colonies, served as controls. In the second test, 3 aquaria, each containing 6 colonies of *O. patagonica* maintained at 16°C and 25°C, were inoculated with *Vibro* AK-1 to a final bacterial cell density of 5×10^5 cells ml^{-1}. For the antibiotic experiments, 100 mg l^{-1} of kanamycin and 100 mg l^{-1} of penicillin-G) were added to 1 infected aquarium. A control aquarium was treated in exactly the same manner except that it was inoculated with sterile medium in place of bacteria.

Determination of bleaching and histology. Percentage of bleaching was determined qualitatively by visual observation of corals in the laboratory and the field. Quantitative measurements were obtained by counting the number of algae directly from histological sections of bleached and unbleached coral tissue samples. Coral tissue samples were fixed in 4% formaldehyde solution in seawater for 24 h, rinsed in fresh water and transferred to 70% ethanol for preservation. Decalcification was carried out using a solution of 1:1 (v:v) formic acid (initial conc. 42.5%) and sodium citrate (initial conc. 20%) for 24 h. After decalcification, the tissue was rinsed in water and transferred to 70% ethanol. The dehydrated tissue was embedded in paraffin. Sequential cross-sections of the tissue were mounted on glass slides, and were stained with hematoxylin and eosin. These histological sections were examined through a Nikon light microscope at a magnification of 1000× using a calibrated eye piece micrometer.

Table 1. Characteristics of *Vibrio* sp. strain AK-1

Test	Result
Colonies on Marine Agar	Cream colored, 5 mm diameter after 3 d
Colonies on TCBS Agar	Yellow, 5 mm diameter after 3 d
Cell morphology	Rod, 1.1 × 0.5 mm
Gram stain	Negative
Motility	Positive
Flagella	Polar
Growth on Vibriostatic 0129	Negative
Growth on 2 to 4% NaCl	Positive
Biochemical tests	
Indole production	–
Nitrate from nitrite	+
Acidification of glucose medium	+
Arginine dihydrolase	+
Oxidase	+
Esculin hydrolysis	+
Gelatinase	–
β-galactosidase	+
Antibiotic sensitivity	+[a]

[a]Sensitive to ampicillin, erythromycin, penicillin-G, tetracycline, kanamycin and streptomycin

RESULTS

Isolation and characterization of *Vibrio* AK-1

During a survey of bacteria present in the mucus of different species of corals, we observed that there was a unique colony type associated with bleached *Oculina patagonica*. This bacterium, referred to as strain AK-1, was isolated in pure culture by dilution of a mucus sample from a bleached coral in sterile seawater, streaking onto Marine Agar and incubation at 30°C for 3 d. Under these conditions, strain AK-1 yielded characteristic cream-colored colonies. The strain was further purified by cloning onto Marine Agar.

The characteristics of strain AK-1 are summarized in Table 1. It is a Gram-negative, motile, rod-shaped bacterium that contains a polar flagellum (Fig. 1a). These properties, together with its ability to form yellow colonies on TCBS Agar and its sensitivity to Vibriostatic 0129, define strain AK-1 as a marine species of the genus *Vibrio* (Farmer & Hickman-Brenner 1992). Based on the antibiotic sensitivities, biochemical tests and carbon compound utilization, as well as the fatty acid profile (data not shown), strain AK-1 appears to be a new species of *Vibrio*.

Distribution of *Vibrio* AK-1 on *Oculina patagonica*

The initial observation that led us to consider the role of *Vibrio* AK-1 in bleaching of the coral *Oculina patagonica* was the presence of large aggregates of rod-shaped bacteria on the border between bleached and unbleached zones at the tentacular rim (Kushmaro et al. 1996). These bacteria were also seen surrounding released zooxanthellae on the surface of bleached corals (Fig. 1b). No bacterial aggregates were seen on unbleached tissues.

During summer 1995 a systematic microbiological examination of bleached and unbleached coral colonies was performed at 3 sites on the Mediterranean coast of Israel. At Tel Aviv and Hedera, about 90% of the coral populations were bleached. The coral population at Achziv showed no sign of bleaching. *Vibrio* AK-1 were isolated from all 28 samples taken from bleached corals and were absent from all 24 samples taken from unbleached corals (Table 2).

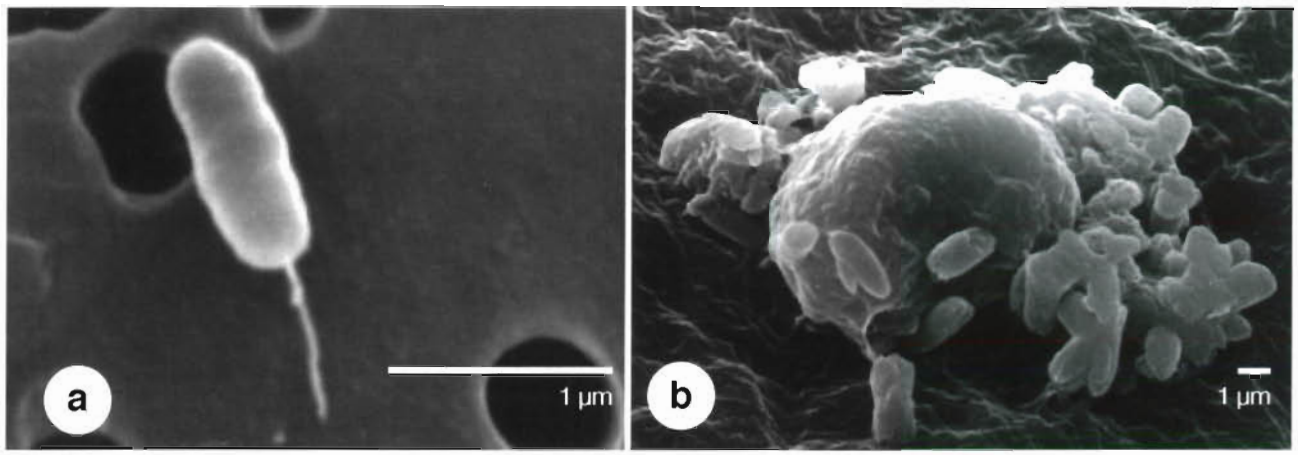

Fig. 1. *Vibrio* AK-1 and *Oculina patagonica*. Scanning electron micrograph of (a) *Vibrio* AK-1 with polar flagella, and (b) rod-shaped bacteria surrounding a zooxanthellae on the surface of coral *O. patagonica*. Scale bar = 1 µm

Induction of bleaching of healthy *Oculina patagonica* by bleached corals

To test if there was a transmissible bleaching agent (first set of experiments), bleached and healthy corals were put together in aerated 2 l aquaria and maintained at 25 and 17°C. At 25°C, all the healthy corals showed observable bleaching after 20 d. Bleaching was not observed in the healthy corals at 17°C. Furthermore, at 17°C, the bleached corals began to show signs of recovery.

Infection of *Oculina patagonica* with *Vibrio* AK-1 in aquaria

Two types of laboratory infection experiments were performed that demonstrate that pure cultures of *Vibrio* AK-1 infect *Oculina patagonica* and cause bleaching. In the second set of experiments, 10 µl of resuspended cells of *Vibrio* AK-1 (5×10^6 ml^{-1}) were placed onto each of 5 healthy corals, and then the corals were put into separate aerated 2 l aquaria maintained at 25°C. All the corals showed bleaching at the site of inoculation after 6 to 8 d. In a control experiment, in which 10 µl of sterile medium was used in place of bacteria, no bleaching was observed even after 40 d. Bleaching was due to the bacterial cells, not an extracellular metabolite, because filtration of the *Vibrio* AK-1 culture through a 0.2 µm membrane filter led to an inactive cell-free supernatant.

In the third set of experiments, *Vibrio* AK-1 was inoculated into the water of 2 l aerated aquaria containing the corals Corals were not removed from aquaria for this procedure. In the first test, conducted at 26°C, 3 aquaria were infected with 5×10^6 *Vibrio* AK-1 cells ml^{-1} and 2 additional aquaria served as controls (Fig. 2). In all 3 experimental aquaria there was observable bleaching after 10 d, which by 44 d had spread over most of the corals. Tissue retraction was observed after 52 d, followed by the death of the colonies within a few days. The corals in the control aquaria (no added bacteria) remained healthy for 52 d, at which time the test was concluded. A visual comparison of an infected and a control coral is presented in Fig. 3.

Vibrio AK-1 was also able to cause bleaching when inoculated at a density of 5×10^5 cells ml^{-1} into aquaria maintained at 25°C. Each aquarium contained 6 *Oculina patagonica* corals and the experiment was carried out without removing the corals from 2 l aerated aquaria. Bleaching was determined after 44 d, qualitatively by visual observation and quantitatively by counting the number of algae directly from histological sections of bleached and unbleached tissue samples (Table 3). Bleaching was not observed (1) without addition of bacteria, (2) when the temperature of the

Table 2. *Oculina patagonica*. Sampling sites, coral condition and presence of *Vibrio sp.* strain AK-1 in bleached corals. Numbers in parentheses represent the number of corals examined microbiologically

Sampling site	Coral condition	*Vibrio* AK-1
Achziv (33° 02' N, 35° 05' E)	Normal (5)	Absent in all
Tel Aviv (32° 02' N, 34° 42' E)	Normal (12)	Absent in all
	30–50% bleached (14)	Present in all
	90% bleached (5)	Present in all
Hedera (32° 25' N, 34° 55' E)	Normal (7)	Absent in all
	30–50% bleached (9)	Present in all

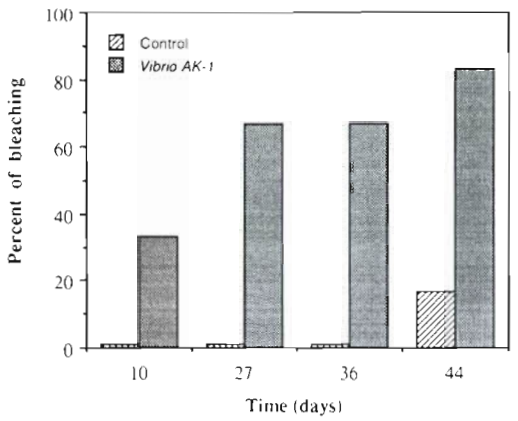

Fig. 2. *Oculina patagonica*. Percentage of bleaching due to *Vibrio* AK-1 infection at 26°C. Five aquaria, each containing 6 *O. patagonica* corals, were maintained at 26°C. Three of these aquaria were inoculated with *Vibrio* AK-1 at a bacterial cell density of 5×10^6 ml^{-1}. The 2 remaining control aquaria were treated in exactly the same manner except that they were inoculated with sterile medium in place of bacteria

aquaria was maintained at 16°C, or (3) in the presence of 100 mg l^{-1} of kanamycin and 100 mg l^{-1} of penicillin-G. The algae counts for the unbleached corals were similar in differing treatments (1.12 to 1.15 $\times$ 10^4 mm^{-2}) and did not differ significantly (1-way ANOVA, $p > 0.05$). After treatment with *Vibrio* AK-1 at 25°C for 44 d, the algae counts decreased significantly (1-way ANOVA, $p < 0.001$) in the 3 corals examined (53, 50 and 37 %) compared to the average algae counts of the unbleached corals.

DISCUSSION

We showed that *Vibrio* AK-1 caused bleaching of *Oculina patagonica* at 25 and 26°C, but not at 16°C. This is consistent with the observation (Fine & Loya 1995) that the bleaching occurs naturally in the summer, when seawater temperatures rise to an average of 26°C and reach a maximum of 29°C, and recovery occurs during winter, when water temperature decreases to 16°C.

Several authors have reported on the patchy spatial distribution and spreading nature of coral bleaching (Fisk & Done 1985, Oliver 1985, Ogden & Wicklund 1988, Glynn 1990, Jokiel & Coles 1990, D'Elia et al. 1991, Hagman & Gittings 1992, Lang et al. 1992, Edmunds 1994). It has been argued that the random mosaic patterns of bleaching observed in coral colonies is difficult to attribute solely to environmental stress, since neighboring regions of the colony must be exposed to the same extrinsic conditions (Hayes & Bush 1990). The progression of observable changes that take place during coral bleaching are reminiscent of developing microbial biofilms on other biological tissues (Hoyle et al. 1993) or inorganic surfaces (Huang et al. 1995). Ritchie et al. (1994) demonstrated a shift in the structure of bacterial communities from *Pseudomonas* sp. to *Vibrio* sp. when *Montastrea annularis* became bleached. In the coral *Oculina patagonica* we demonstrated that *Vibrio* AK-1 appeared on all samples that were taken from bleached corals. Although we observed that bleaching was due to the bacterial cells themselves and not extracellular prod-

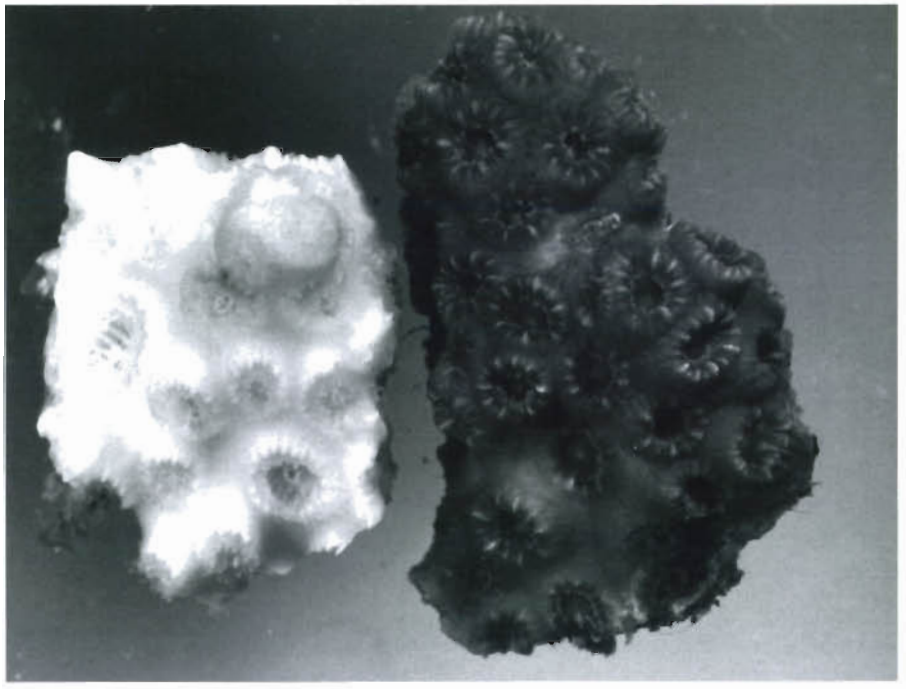

Fig. 3. *Oculina patagonica*. Bleached coral 44 d after infection with 5×10^6 *Vibrio* AK-1 cells ml^{-1} at 26°C (left) and healthy coral (right). Magnification 4×

Table 3. *Oculina patagonica*. Infection with *Vibrio* AK-1 in aerated aquaria. Each aquarium contained 6 colonies. The algae counts represent the average ± SE for 1 coral. Ten histological sequential cross-sections were analyzed for each coral

Treatment	Visual observation	Algae counts from 1 mm^2 histological section ($\times 10^4$)
5×10^5 cells ml^{-1} of *Vibrio* AK-1, 25°C	90% bleaching	0.54 ± 0.03 0.57 ± 0.02 0.72 ± 0.02
5×10^5 cells ml^{-1} of *Vibrio* AK-1, 16°C	No signs of bleaching	1.13 ± 0.04
5×10^5 cells ml^{-1} of *Vibrio* AK-1, 25°C, antibiotic (100 mg l^{-1} of kanamycin and penicillin-G)	No signs of bleaching	1.12 ± 0.04
Control (no inoculum), 25°C	No signs of bleaching	1.15 ± 0.04

ucts in the supernatant, we propose that bleaching might be a result of extracellular toxins produced locally at the site of infection.

An early attempt to understand the mechanism for the bleaching on a Panamanian coral reef, coincident with the prolonged 1983 El-Niño warming event (Glynn et al. 1985), showed that normally colored colonies receiving bleached colony portions in grafts remained in a healthy state. In the gastrodermis of the bleached *Pavona varians* and *Pocillopora elegans*, colonies suspected of being bacteria were observed. Cryofractured samples of these tissues revealed the presence of spherical to rod-shaped bacteria-like objects in the gastrodermal cells, sometimes occupying zooxanthellae vacuoles, in both coral species (Glynn et al. 1985). The authors concluded that thermal stress may be responsible for the coral deaths. However, it is difficult to exclude an infectious agent without knowing the mode of transmission or the minimum infectious dose. In acroporid corals afflicted with white band disease, Peters et al. (1983) discovered unusual, Gram-negative, rod-shaped bacteria living in aggregates in the calicoblast epidermis lining the gastrovascular canals. In our experiments we observed that the pathogenic bacteria on the bleached coral were highly concentrated at the borderline between the bleached and healthy tissue. Few bacteria were present over most of the bleached surface.

Buddemeier & Fautin (1993) hypothesized that coral bleaching is a natural adaptive mechanism which provides an opportunity for the host coral to be repopulated with a different type of zooxanthellae. Stress conditions tend to favor coral-algae combinations which are resistant to the stress. In support of this hypothesis, it has been demonstrated that the same species of coral can form symbiotic relationships with different taxa of zooxanthellae (Rowan & Knowlton 1995). We further suggest that the coral-algae combinations that would be selected are those that are resistant to bacterial infection. Coral bleaching followed by selection of new coral-algae combinations may be one of the mechanisms by which *Oculina patagonica* develops resistance to *Vibrio* AK-1.

Our findings show that bleaching of the coral *Oculina patagonica* along the Mediterranean coast of Israel is caused by a bacterial infection. An increase in the temperature of seawater can influence the outcome of the bacterial infection in at least the following 2 ways: lowering the resistance of the coral to infection and/or increasing the virulence of the bacterium. The doubling times of *Vibrio* AK-1 in Marine Broth at 15, 20, 25 and 30°C were 240, 95, 60, and 40 min, respectively (authors' unpubl. data). The higher growth rate of *Vibrio* AK-1 at elevated temperatures may, at least in part, be responsible for the observed effect of temperature on coral bleaching.

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