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Ultraviolet radiation prevents bleaching in the Mediterranean coral *Oculina patagonica*

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ABSTRACT: The causative agent of bleaching in the coral *Oculina patagonica* in the Mediterranean Sea is *Vibrio shiloi*. The bacterium becomes more virulent with increasing seawater temperature, resulting in extensive coral bleaching (80 to 90 %) every summer in 1 to 6 m depth. However, colonies in shallow water (0 to 80 cm depth) showed negligible bleaching, despite being exposed to higher temperatures (ca 2°C) than the deeper water corals. Fragments transplanted from 4 m depth to a shallow reef flat (< 30 cm depth) in May showed no bleaching during the summer months, whereas intact colonies at 4 m and fragments transplanted to that depth from the reef flat underwent extensive bleaching. The concentration of *V. shiloi* was very high ($> 2 \times 10^4$ cm⁻²) in bleached fragments at 4 m, whereas in non-bleached fragments from the reef flat, *V. shiloi* could not be detected. When *O. patagonica* was infected with *V. shiloi* in laboratory aquaria and subsequently exposed to sunlight, the intracellular bacteria were rapidly killed, aborting the infection and preventing bleaching. However, when the infected corals were protected from ultraviolet (UV) light, the intracellular *V. shiloi* multiplied and the coral bleached. We present here for the first time evidence for prevention of coral bacterial bleaching by UV radiation (UVR).

KEY WORDS: Corals · *Oculina patagonica* · Bleaching · UV · *Vibrio shiloi* · Mediterranean

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INTRODUCTION

Coral bleaching, the disruption of the symbiotic association between coral hosts and their symbiotic photosynthetic algal endosymbionts, threatens coral reefs throughout the world (Hoegh-Guldberg 1999, Wilkinson et al. 1999). Coral bleaching is often linked to global climate change, especially elevated seawater temperature (Glynn 1991, 1993, Brown 1997, Hoegh-Guldberg 1999) and high solar irradiance (Jokiel 1980, Lesser et al. 1990, Gleason & Wellington 1993, Glynn 1993). The latter is known to negatively affect photosynthesis, growth of zooxanthellae (Lesser & Shick 1989) and survival of epifauna (Jokiel 1980, Siebeck 1988). Gleason & Wellington (1993) transplanted

colonies of *Montastrea annularis* from 24 m to 18 and 12 m, either exposing them to ambient irradiance or screening them from ultraviolet radiation (UVR, 280 to 400 nm). They found that colonies transplanted to a shallower depth were paler and revealed lower densities of zooxanthellae compared with shielded colonies at the same depth, and concluded that it was the higher UVR that had affected the corals. This led to a series of studies on the effect of high UVR on cultured zooxanthellae (Banaszak & Trench 1995, Lesser 1996) and dinoflagellates living within various cnidarian tissues (Lesser & Shick 1989, Kinzie 1993, Banaszak & Trench 1995). A range of anti-UVR protective mechanisms were demonstrated for the cnidarian host and symbiotic dinoflagellates including mycosporin-like amino acids (MAA), fluorescent pigments (Salih et al. 2000) and active oxygen scavenging systems (Shick et al. 1996). Although several investigators have suggested that elevated levels of UVR have been instru-

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mental in causing bleaching, field evidence for a primary role of UVR has been circumstantial (Hoegh-Guldberg 1999).

Bleaching of *Oculina patagonica* was first recorded along the Israeli coast in summer 1993 (Fine & Loya 1995). Since then, 80 to 90 % of coral colonies exhibit bleaching during the summer months when water temperature reaches a maximum of 29 to 30°C, and then recover in the winter (Kushmaro et al. 1998). When analyzing a disease affected by environmental factors, it is critical to appreciate the difference between cause and causative agent. In the case of the coral *O. patagonica* in the Mediterranean, the causative agent for bleaching is the bacterium *Vibrio shiloi* (Kushmaro et al. 1996, 1997), whereas the environmental cause of the disease is increased seawater temperature (Kushmaro et al. 1998). The increased seawater temperature results in expression of virulence genes in the bacterium, leading to adhesion of the bacterium to a β -D-galactoside receptor on the coral surface (Toren et al. 1998), penetration and multiplication of the bacterium in the coral tissue (Banin et al. 2000a,b), and production of toxins and killing of the intracellular algae (Ben-Haim et al. 1999, Rosenberg et al. 1999).

The initial observation that led to this study was the low level of coral bleaching in tidal pools and reef flats compared to corals in deeper water, despite higher surface seawater temperature (SST) in shallow waters. Experiments described here indicate that UV light in solar radiation kills *Vibrio shiloi*, which is present within the coral tissue, and aborts the infection and subsequent bleaching.

MATERIAL AND METHODS

Field experiments. We have been continuously monitoring bleaching of *Oculina patagonica* since 1993 (Kushmaro et al. 1998, Fine unpubl.). In the present study, we focused on bleaching of colonies inhabiting the reef flat (<30 cm depth), very shallow tide pools (30 to 80 cm depth) and, for comparison, bleaching of colonies inhabiting depths of 1 to 6 m. The study was carried out off the coast of Sdot-Yam, Israel. Monthly (June to December 2000) observations for percentage of bleaching were performed on 40 tagged colonies on the reef flat, 40 in tide pools and 200 at depths of 1 to 6 m. Colonies that were visually estimated to exceed 10 % bleached living surface area were scored as bleached colonies.

SST data at 6 m and in the tide pools were obtained using Onset Stow Away data-loggers (sampling once every hour).

To test the hypothesis that solar radiation may affect coral bleaching, 24 colonies at 4 m depth and 24

colonies on the reef flat were tagged during mid-May 2000, a few weeks before the seawater temperature rises abruptly and *Oculina patagonica* colonies undergo bleaching (Kushmaro et al. 1998). Two fragments from each colony were cored out using a stainless-steel corer ($r = 1.5$ cm, fragment surface area = 7.0 cm²). One set of fragments was glued and tagged near their intact mother colony as controls and the second set of fragments was used for reciprocal transplantation between 4 m depth and the reef flat. The state of bleaching of the intact colonies and the fragments was monitored monthly. In August 2000, 8 transplanted core fragments from 4 m and 8 from the reef flat were collected and examined for presence of *Vibrio shiloi* using specific polyclonal antibodies (Banin et al. 2000b). Total counts and CFU (colony forming units) were performed using fluorescence microscopy and Marine agar (DIFCO), respectively.

Laboratory experiments. To test the hypothesis that solar radiation may protect corals from bacterial-induced bleaching, 40 fragments of healthy *Oculina patagonica* (each ca 3 cm²) were infected with 4.2×10^4 *Vibrio shiloi* ml⁻¹ in a 2 l aquarium. After 3 d in the laboratory aquarium under a 12:12 h light:dark regime, 20 of the infected fragments were placed in an aquarium in direct sunlight (+UV) while an additional 20 were placed in another aquarium in direct sunlight, but shielded from UVR (-UV) with a 5 mm Plexiglas cover which blocks 100 % of UVR (280 to 400 nm) but transmits 95 % of the visible light (400 to 700 nm). The average irradiation at 12:00 h for UVA (320 to 400 nm) and UVB (280 to 320 nm) was 28.8 and 1.7 J s⁻¹ m⁻² respectively. Ten coral fragments (5 -UV and 5 +UV), uninfected with *V. shiloi*, were cultured under the same conditions as control. The aquaria were aerated and maintained at $28 \pm 0.5^\circ\text{C}$ in a water bath. At the indicated times, coral fragments were assayed for internal *V. shiloi* by the gentamycin invasion assay, using specific *V. shiloi* antibodies (Banin et al. 2000b).

RESULTS

Field observations

Bleaching of *Oculina patagonica* colonies was found to be depth dependent. The observed bleaching rate varied from an average of $3.6 \pm 1.5\%$ ($n = 40$) on the reef flat to $11.4 \pm 4\%$ ($n = 40$) in the tide pools and up to an average of $84 \pm 10\%$ ($n = 200$) at a depth of 1 to 6 m (Fig. 1). The percentage of colonies undergoing bleaching increased dramatically at depths greater than 0.5 m (Fig. 1). No change in percentage of bleaching was detected between 1 and 6 m depth.

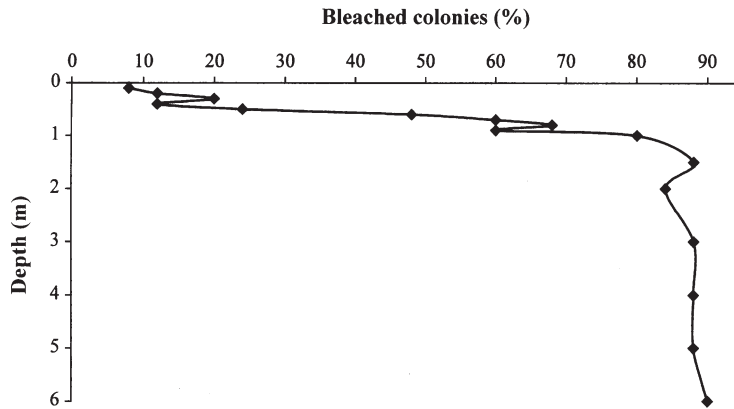


Fig. 1. *Oculina patagonica*. Bleaching along a depth gradient, from the reef flat (<30 cm depth) down to tide pools (30 to 80 cm) and at 1 to 6 m

Temperature data patterns

As revealed from the temperature record retrieved from the data loggers at 6 m and in a tide pool (30 to 80 cm depth), in summer, during bleaching events (May to October), the monthly mean SST in shallow tide pools is ca 2°C higher than that at a depth of 6 m (Fig. 2A). From October to December, an opposite trend in SST was detected, with higher SST at a depth of 6 m compared with that in the tide pool. Furthermore, the daily amplitude in the tide pools is much wider (over 2°C) than that at 6 m (ca 0.5°C) (Fig. 2B). Maximum temperature in tide pools and on the reef flat reached 32°C for a period of a few hours, whereas the temperature at the same time at 6 m depth was 28.5°C (Fig. 2B). The maximum daily temperature at 6 m during the summer months was lower than the minimum daily temperature in the tide pools (Fig. 2B).

Transplantation experiment

In the transplantation experiment, only 8% of the intact colonies ($n = 24$) on the reef flat showed negligible dimensions of bleaching (i.e. ca 5.0% of the colony's surface area appeared bleached, Fig. 3, a). The same result was obtained for the control fragments ($n = 24$) on the reef flat (Fig. 3, b). However, all *Oculina patagonica* fragments ($n =$

24) transplanted from the reef flat to 4 m depth underwent substantial bleaching (100% of the fragments) with an average bleached surface area of $32 \pm 23\%$ (Fig. 3, c). At 4 m depth, 96% of the intact colonies and control fragments underwent bleaching, with a $35 \pm 25\%$ bleached surface area in both cases (Fig. 3, d,e). In contrast, only 8% of the fragments transplanted from 4 m to the reef flat underwent negligible bleaching of ca 5% bleached surface area (Fig. 3, f).

Vibrio shiloi was not detected in any of the 8 non-bleached fragments transplanted from 4 m to the reef flat, whereas in the 8 bleached fragments transplanted from the reef flat to 4 m the total counts varied from 8×10^6 to 2×10^8 cells cm^{-2} of coral fragment (Table 1).

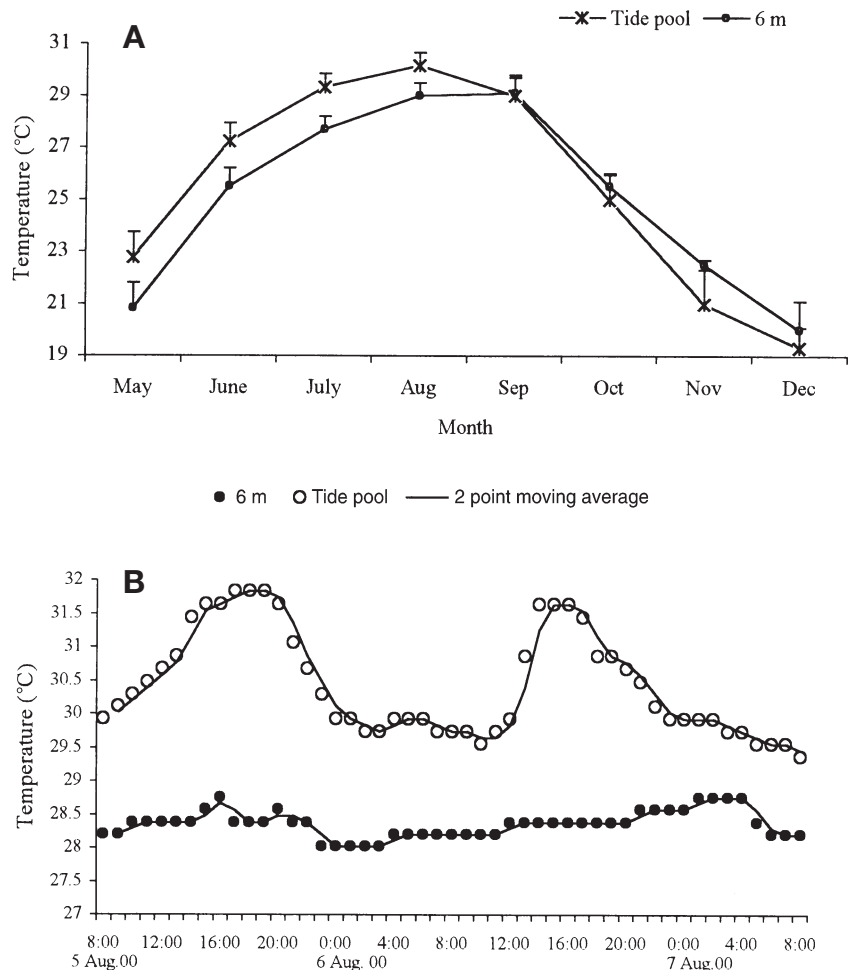


Fig. 2. Seawater temperature. (A) Monthly averages (May to December) in tide pools and at 6 m depth during the bleaching season of *Oculina patagonica*. (B) Daily temperature (sampled every h) in a tide pool and at 6 m depth during 48 h in August 2000. Data presented as 2 point moving average

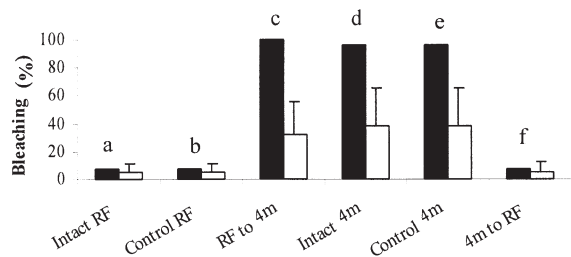


Fig. 3. *Oculina patagonica*. Percentage (\pm SD) of bleached colonies (black bars) and bleached living surface area (blank bars) of intact colonies (a, d) and fragments transplanted to the reef flat (RF, f) and to 4 m depth (c), and control fragments (b, e)

Aquarium experiments

In the laboratory aquarium experiments, none of the 20 fragments of healthy *Oculina patagonica* infected with 4.2×10^4 *Vibrio shiloi* ml^{-1} and subsequently exposed to direct sunlight (+UV) showed any signs of bleaching (Fig. 4). In contrast, the 20 fragments infected with *V. shiloi* and exposed to direct sunlight but shielded from UV (–UV) showed a total loss of pigmentation after 10 d, the hallmark of the bleaching disease. Uninfected control fragments exposed to sunlight under the same conditions showed no bleaching, regardless of whether or not they were covered with Plexiglas (Fig. 4). After 8 h exposure to unfiltered solar radiation, the number of *V. shiloi* per coral had

Table 1. Colony forming unit (CFU) and total counts of *Vibrio shiloi* in core fragments of *Oculina patagonica* after transplantation. B = bleached, NB = non-bleached

Sample ^a	Visual observation	CFU (cm ²)	Total count (cm ²)
1	B	2×10^5	Not detected
2	B	3.5×10^5	1.1×10^8
3	B	2×10^4	8×10^6
4	B	2×10^4	8×10^7
5	B	4×10^5	2×10^8
6	B	5×10^5	1×10^7
7	B	3×10^4	3×10^7
8	B	1×10^6	8×10^7
9	NB	Not detected	Not detected
10	NB	Not detected	Not detected
11	NB	Not detected	Not detected
12	NB	Not detected	Not detected
13	NB	Not detected	Not detected
14	NB	Not detected	Not detected
15	NB	Not detected	Not detected
16	NB	Not detected	Not detected

^aSamples 1 to 8 are cores transplanted from the reef flat to 4 m depth. Samples 9 to 16 are cores transplanted from 4 m to the reef flat

decreased by 97 % to 6×10^5 cm^{-2} coral fragment (Fig. 5). After 10 h, they were no longer detectable (i.e. $<10^5$). In the aquarium protected from UV light, the number of *V. shiloi* inside the coral increased to 2.5×10^7 per coral after 6 h and then remained relatively constant for at least 1 wk (Fig. 5). A comparison of the rate of UV killing of *V. shiloi* in the coral epidermis compared to that in seawater (data not presented) at the same depth (30 cm) indicated that the coral provided little, if any, protection to the pathogenic bacteria.

DISCUSSION

In the present study, we clearly demonstrate that in *Oculina patagonica* along the Mediterranean coast of Israel, UVR prevents bleaching. This is at variance with previous reports that UVR may be one of the causes of coral bleaching (Jokiel 1980, Lesser et al. 1990, Gleason & Wellington 1993, Glynn 1993). Most evidence indicates that elevated temperature is the major cause of mass bleaching events (Hoegh-Guldberg 1999). The cause for bleaching of *O. patagonica* in the Mediterranean is also temperature (Kushmaro et al. 1998). Moreover, while 80 to 90 % of *O. patagonica* colonies undergo bleaching during the summer months in the eastern Mediterranean, no bleaching of that species has ever been recorded in the western Mediterranean (Fine 2001), where summer temperatures are much lower ($<22^\circ\text{C}$). Kushmaro et al. (1998) demonstrated that colonies exposed to a temperature of 29°C did not bleach if the causative bleaching pathogen was not present, whereas bleaching occurred slowly at 20°C and rapidly at 29°C in the presence of the pathogen.

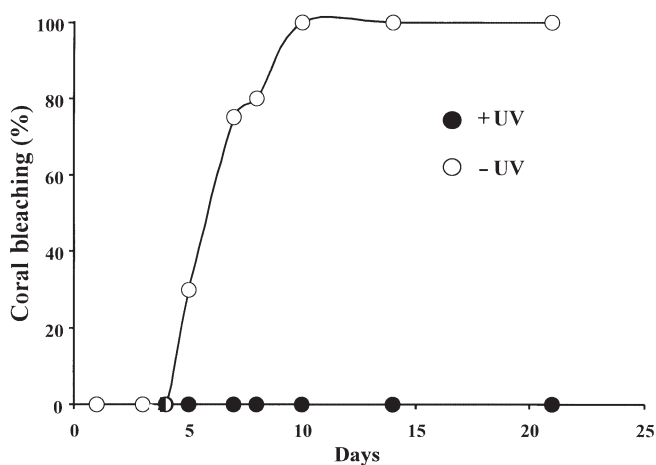


Fig. 4. *Oculina patagonica*. Effect of solar radiation on the bleaching of the coral by the pathogenic bacteria *Vibrio shiloi*

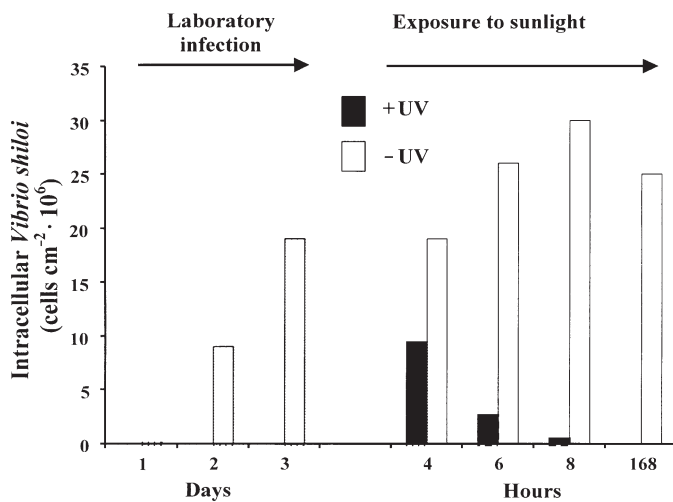


Fig. 5. *Oculina patagonica*. Effect of solar radiation on *Vibrio shiloi* inside the coral host ectodermis as determined by fluorescence microscopy

Toren et al. (1998) demonstrated that bleaching of *Oculina patagonica* is temperature regulated via production of the adhesin required for adhesion of *Vibrio shiloi* to its host coral. Accordingly, at higher temperatures, bacterial synthesis of the adhesin results in efficient adhesion to the coral and subsequently high bleaching. At winter temperatures (16°C) the adhesin is not produced by the bacterium and no infection takes place. In addition to adhesion, intracellular growth of the bacteria and toxin production are also temperature dependent (Banin et al. 2000a,b).

According to the data retrieved from the temperature data loggers at 6 m and in tide pools (<80 cm), temperature at shallower depths is ca 2°C warmer than at 6 m during the summer months (Fig. 2A). The temperature on the reef flat and tide pools is greatly influenced by tide cycle and amplitude; hence, on a daily scale, *Oculina patagonica* colonies in tide pools experience temperatures 4°C above that at 6 m (especially during low tide) for a period of several hours (Fig. 2B). Even at high tide when temperature in the shallows approaches that at 6 m, the latter will still be ca 1°C colder (Fig. 2B). Thus, a much higher bleaching percentage would be expected in these warmer shallows than at 6 m. Ironically, the opposite is true. As revealed in the present study, colonies of *O. patagonica* inhabiting the reef flat exposed to high water temperature and irradiance underwent a much lower bleaching rate than colonies at a depth of 1 to 6 m (Fig. 1).

Brown et al. (2000) provided data on the bleaching pattern of *Goniastrea aspera*, a shallow-water Indo-Pacific coral. They reported that corals exposed to high solar radiation prior to maximum seawater temperature were protected from bleaching. They explain their

data by suggesting that 'experience can shape coral bleaching patterns.' More specifically, they state that exposure to high solar radiation caused the corals to become more tolerant to the combined stress of temperature and solar radiation. Similar observations were reported by Loya et al. (2001) at Sesoko Island, Japan, where juvenile *Acropora* colonies in the intertidal zone survived bleaching events despite being exposed to high irradiance during summer midday low tides. This survival is especially intriguing in view of the mass mortality observed in coral colonies of the same species in deeper water of the same locality. The data presented in this paper suggest a novel testable hypothesis, i.e. the reason some coral species do not bleach under high solar irradiance may be because coral-bleaching bacteria are destroyed under such conditions.

Due to the possibility that corals present in shallower water intrinsically differ from deeper water corals (i.e. may contain different clades of zooxanthellae), the transplantation experiment was performed. When fragments of *Oculina patagonica* colonies were transplanted from 4 m depth to the reef flat, they did not bleach, although their intact mother colony did (Fig. 3). Consistent with the visual observations on bleaching were the low numbers of the causative bleaching agent *Vibrio shiloi* detected in transplanted fragments from 4 m to the reef flat (Table 1). All the data support the contention that in the case of *O. patagonica*, UVR is lethal to the causative agent of bleaching.

Lyons et al. (1998) reported that bacteria in the surface microlayer of the coral *Montastrea faveolata* receive some protection from UVR. In the case of *Vibrio shiloi* in *Oculina patagonica*, in order to achieve successful colonization the bacteria must multiply at a rate higher than their elimination by solar radiation. Since the doubling time of *V. shiloi* in *O. patagonica* at 28°C is ca 6 h (Kushmaro et al. 1997), for *V. shiloi* to bleach *O. patagonica*, the coral must be at a depth where UVR is low enough to enable a half-life of the bacterium to exceed 6 h. In the Mediterranean Sea off the coast of Israel in the summer, this would correspond to a depth of ca 1 m.

Salih et al. (2000) reported a protective mechanism in which fluorescent pigments (FPs) serve as sunscreens and enhance the resistance of corals to bleaching during periods of heat stress. Coral colonies in shallower water, exposed to higher solar radiation, were much more reflective due to higher concentrations of FPs (Salih et al. 2000). Fluorescent pigments may be one of the mechanisms allowing *Oculina patagonica* and its endosymbionts to inhabit reef flats and survive the high intensity solar radiation. However, because bacteria are haploid and generally highly sensitive to UVR, much more so than algae or

corals, high solar radiation kills the pathogen and thereby prevents bleaching.

The healing effect of UV on diseases caused by pathogenic bacteria is known in other systems. Liltved & Landfald (2000) reported that viability of fish pathogenic bacteria was rapidly reduced when exposed to sunlight. A 99.9% inactivation was observed after 2 h exposure. The variable effect of UV on marine bacteria has also been reported by Joux et al. (1999). Clearly, more research is necessary before generalizing on the effect of UV on the possible prevention of coral diseases and their general health.

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