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SYNERGISTIC EFFECTS OF UVR AND TEMPERATURE ON THE SURVIVAL OF AZOOXANTHELLATE AND ZOOXANTHELLATE EARLY DEVELOPMENTAL STAGES OF SOFT CORALS

Dafna Zeevi-Ben-Yosef and Yehuda Benayahu

ABSTRACT

The interaction between ambient water temperature and UVR and its possible effect on the survival of coral early life-history stages was investigated in the Red Sea soft corals *Heteroxenia fuscescens* Eherenberg, 1834, and *Rhytisma fulvum fulvum* Forsskål, 1775. Planulae and azoo- and zooxanthellate polyps were obtained from colonies collected from the coral reefs at Eilat (Gulf of Aqaba, northern Red Sea). Survival of the different developmental stages under different UVR regimes was examined in the laboratory and monitored every 12 hrs until 50% survival (i.e., LD_{50}) was attained. Maximal LD_{50} value for *H. fuscescens* planulae under exposure to UVR was only 70 hrs whereas the unexposed planulae showed 100% survival over the same time period. Survival of Azooxanthellate primary polyps of *H. fuscescens* increased with higher temperatures under UVR exposure, and zooxanthellate polyps had higher rates of survival than azooxanthellate polyps at 26 °C. *Rhytisma fulvum fulvum* planulae had higher survival rates compared to those of *H. fuscescens* planulae, and azoo- and zooxanthellate primary polyps. Our results demonstrate that UVR and elevated temperature may have a synergistic effect on the survival of soft corals at early life-history stages. In addition, Mycosporine-like amino acids (MAAs) may have played a role in the survival of the different juvenile stages of the two studied species.

Despite growing evidence that UV radiation is of major biological significance in tropical waters (Shick and Dunlap, 2002; Drohan et al., 2005; Harley et al., 2006), its effects on the larval stages of benthic coral reef organisms have not been adequately investigated. Because of their small size (optical radius), rapid rates of cell proliferation, and lack of protective covering, planktonic embryos and larvae of many marine invertebrates are likely to be at risk of damage by UVR (Laurion and Vincent, 1998; Adams and Shick, 2001). UVR has been shown to decrease survivorship of eggs and planula larvae of the broadcast-spawning stony corals *Acropora palmata* Lamarck, 1816, *Montastraea annularis* Ellis and Solander, 1786, and *Montastraea franksi* Ellis and Solander, 1786, (Wellington and Fitt, 2003; Gleason et al., 2006). In a laboratory experiment planulae of the stony coral *Porites astreoides* Lamarck, 1816, showed a settlement preference for reduced UV radiation regions (Gleason et al., 2006). UV radiation was also shown to cause damage to a number of aquatic larvae (Shick and Dunlap, 2002). For example, exposure of the larval and adult stages of the copepod *Acartia clausii* Giesbrecht and of *Daphnia magna* Strauss, 1820 (Cladocera) to UVR reduced their survival, and had long-term effects such as decreased fecundity and reproduction (Karanas et al., 1981; Huebner et al., 2006). To avoid or overcome such deleterious effects, many marine invertebrates, including corals (Michalek-Wagner, 2001; Shick and Dunlap, 2002; Zeevi-Ben-Yosef et al., 2006), have developed UV sunscreening and UV damage repair mechanisms (see also Shick and Dunlap, 2002).

Several studies have addressed the possible synergy between two environmentally critical factors: namely, ambient temperature and high irradiance (Lesser et al., 1990; Drollet et al., 1994; Lesser, 1997; Michalek-Wagner, 2001; Lesser and Farrel, 2004).

During the past two decades, both acute and chronic bleaching of corals have occurred on a dramatically increased scale and intensity, and have been correlated with high sea surface temperature anomalies (e.g., Aronson et al., 2000; Loya et al., 2001; Douglas, 2003; Berkelmans et al., 2004; Donner et al., 2007). The recognized multiple biological effects of bleaching include reduced coral growth, calcification, and possibly also reduced reproductive output and increased mortality (review by Hughes et al., 2003; Lesser, 2007). Among the factors that induce bleaching in corals, a possible synergistic interaction between temperature and light, both in the visible and the UV region, has received the most attention (Lesser et al., 1990; Drollet et al., 1994; Lesser, 1996; Lesser and Farrel, 2004). To date, however, the synergistic effects of UVR and temperature on marine larval stages have not been adequately investigated.

Throughout the Indo-Pacific region, soft corals (Octocorallia, Alcyonacea) constitute a major benthic component and are regarded as the second most important component after the stony corals (Fabricius, 2005). Zeevi-Ben-Yosef et al. (2006) showed that the concentration of palythine, which is the most prominent UVR-absorbing compound in soft corals, known as a Mycosporine-like amino acid (MAA) (Michalek-Wagner and Willis, 2001), declined in UV-protected colonies of the soft coral *Heteroxenia fuscescens* Eherenberg, 1834, mainly in shallow water and during the summer period. MAAs were present in both azoo- and zooxanthellate early developmental stages of this soft coral (Zeevi-Ben-Yosef et al., 2008). It is thus suggested that UVR plays a major role in regulating MAA biosynthesis. This, together with the ability to alter the concentration of palythine as a response to environmental changes (Zeevi-Ben-Yosef et al., unpubl. data), may indicate that colonies of *H. fuscescens* are well-adapted for protection against UVR.

In the current study, we determined the nature of the interaction between ambient seawater temperature and UVR and its possible effect on the survival of early developmental stages of two species of Red Sea soft corals. Specifically, the study dealt with the effects following exposure of azoo- and zooxanthellate planulae and primary polyps to UVR at different temperatures**.** We chose as a model system two zooxanthellate soft corals, *H. fuscescens* and *Rhytisma fulvum fulvum* Forsskål, 1775, which incorporate both azoo- and zooxanthellate early life history stages in their life cycle. Our study was designed to expand our understanding of the synergistic effect of UVR and temperature on the survival of soft coral larvae at different developmental stages, including in relation to their symbiotic state.

Methods

Studied Organisms and Collection of Planulae.—The two studied soft corals were obtained from the coral reef across from the Interuniversity Institute for Marine Sciences at Eilat (IUI) (Gulf of Aqaba, northern Red Sea). *Heteroxenia fuscescens* (family Xeniidae) is a hermaphroditic planula-brooder which releases azooxanthellate planulae nearly year-round (Benayahu, 1991; Ben-David-Zaslow et al., 1999). Colonies of *H. fuscescens* were collected from a depth of 3–8 m from November 1998 through August 2001. In the laboratory they were placed in containers with running seawater, at a flow rate of 2 L min^{-1}. Prior to sunset, each colony was transferred to a separate aerated aquarium, and examined the following morning for the presence of planulae (see also Ben-David-Zaslow et al., 1999). The released planulae were collected with a Pasteur pipette into 250 ml PVC containers filled with Millipore-filtered (0.2 μm) seawater (FSW) to avoid bacterial contamination. Embryos of *R. f. fulvum* (family Alcyoniidae) were removed from surface-brooded colonies (see Benayahu and

Loya, 1983) at 3 m depth in July 1999 and 2001. Samples were kept in the laboratory in aerated FSW until achieving the mature azooxanthellate planula stage and then maintained as above. The planulae of the two species were air transported to Tel Aviv for further experiments.

Development of Primary Polyps.—Planulae of *H. fuscescens* and *R. f. fulvum* maintained in 0.45 μm Eilat FSW settled and initiated normal metamorphosis to primary polyps 10–14 d after release (Ben-David-Zaslow, 1994; Yacobovitch et al., 2003). In Tel Aviv, the planulae of each species were placed separately into 24-well tissue culture plates, 3 planulae per well, filled with 3 ml 0.45 μm FSW (72 planulae per plate). The plates were placed inside incubators (MRC- LE509) at a temperature corresponding to the ambient seawater temperature at the time the experiments were conducted. To obtain zooxanthellate primary polyps of *H. fuscescens* and *R. f. fulvum*, freshly isolated algal cells from colonies of each species were obtained by homogenization and centrifugation following the methodology described by Yacobovitch et al. (2003). The symbionts were introduced into each well upon initiation of metamorphosis, yielding a final concentration of $5–7 \times 10^{-4}$ algal cells ml^{-1}. Half of the FSW in each well was changed every other day for both azoo- and zooxanthellate primary polyps throughout the experiments. The initial number of planulae introduced into a given plate and the percentage of successful metamorphosis into the primary polyp stage dictated the number of primary polyps used in the different assays.

Survival of Planulae Under Exposure to UVR.—To examine survival of planulae of *H. fuscescens* and *R. f. fulvum* under different UVR regimes, planulae were placed in 24-well tissue culture plates (3 planulae per well). Each well was filled with 3 ml 0.2 μm FSW. The number of wells used varied among the different experiments, ranging from 30 to 50 planulae for each plate. Each plate (containing an equal number of planulae) was considered a replicate. The plates were placed inside incubators under a 12L:12D lighting regime, at a temperature corresponding to the ambient Eilat seawater temperature when the colonies were collected (21–28 °C, Table 1). Exposure to controlled radiation levels was conducted by means of a Cole-Parmer 15-watt UV lamp (290–320 nm) and a Philips Cool White lamp (400–700 nm). The irradiances of UVB, UVA and PAR used for all experiments were 0.8, 3, and 14 W m^{-2} s^{-1}, corresponding to conditions measured at 3 m depth in Eilat during September 1999 (Zeevi Ben-Yosef et al., 2006). These radiation levels were adopted since they reflect the highest recorded values among all measurements conducted throughout the study period. The exposed replications (PAR+UVA+UVB) were covered with a polystyrene filter (2 mm thick) to remove wavelengths < 290 nm, not encountered in nature (Cullen and Lesser, 1991). The control plates (PAR) were covered with a PVC filter (3 mm thick) to remove wavelengths < 400 nm. The survival experiments were conducted at ambient temperature. To examine the effect of an experimental (different from ambient) temperature on the survival of *H. fuscescens* planulae under exposure to UVR, temperature in the incubator was altered in April 2001 from the ambient temperature of 23° to 21° and 26 °C, and in July 2001 from 28° to 21° and 30 °C (n = 3, 50 planulae per each temperature). Batches of planulae of *R. f. fulvum* were exposed to UVR at 26 °C (n = 3, 51 planulae each) and 25 °C as described above (Table 2). Survival of planulae was calculated separately for each plate under UVR exposure and experimental temperatures as the ratio between the number of planulae on a given monitoring date and their initial number in each plate. Survival and appearance of the planulae were monitored every 12 hrs until 50% survival was obtained (i.e., LD_{50}).

Survival of Primary Polyps Under UVR.—To examine the survival of azoo- and zooxanthellate primary polyps of the three studied soft coral species under exposure to different UVR regimes they were maintained and monitored as described above for planulae. Azoo- and zooxanthellate primary polyps of *H. fuscescens* were exposed to UVR from April 1999 to August 2001 at 22–28 °C, corresponding to the ambient seawater temperature when the respective batches of planulae were obtained (Table 1). Different batches of azoo- and zooxanthellate primary polyps of *R. f. fulvum* were exposed to UVR at various dates and temperatures.

Table 1. Details of experiments testing survival of early life history stages of *Heteroxenia fuscecsnes* obtained at different dates (with various ambient temperatures) to exposure to UVR at various experimental temperatures. For each date, the number of trials and number of animals in each trial are indicated. Azoox. = azooxanthellate primary polyps, Zoox. = zooxanthellate primary polyps.

Date	Stage	Ambient temp. (°C)	Experimental temp. (°C)	# of trials	# of animals in each trial
Mar. 1999	Planulae	21	21	1	30
Apr. 2001	Planulae	23	23	3	50
	Planulae	23	21	2	50
	Planulae	23	26	2	50
Jun. 2001	Planulae	24	24	3	50
Aug. 2001	Planulae	28	28	3	50
	Planulae	28	21	3	50
	Planulae	28	30	3	50
Apr. 1999	Azoox.	22	22	1	18
Oct. 1999	Azoox.	26	26	1	46
Apr. 2001	Azoox.	23	23	1	40
May 2001	Azoox.	23	23	1	40
Aug. 2001	Azoox.	28	28	1	24
May 1999	Zoox.	24	24	2	36, 48
Jun. 1999	Zoox.	26	26	1	47
Aug. 2001	Zoox.	28	28	2	30

Statistical Analysis.—Analysis of data was conducted using the statistical program SPSS, with the Kaplan-Meier estimator for survival analysis (Cox and Oakes, 1984). Survival of the different developmental stages was evaluated daily until LD_{50}, thereby obtaining repeated measurements with time for the same individuals. The dependent variable was latency to the first observation of mortality (survival time T) and was only positive. Another property of the dataset in our study was the presence of censored data: variable time had two different meanings, depending on the situation. When mortality was observed it provided the actual survival time, whereas for surviving individuals the variable time gave the duration of the experiment. An incomplete observation was termed censored (censor = 1 when mortality occurred during the observation time; otherwise censor = 0). Because the presence of incomplete data cannot be taken into account when traditional univariate methods are used, survival analysis offers a biostatistic method to contend with incomplete data (Marquenie et al., 2002). The starting point is the survival function $S(T) = Pr(T \geq t)$ which gives the probability of observing a survival time T that is larger than or equal to some value t. This survival curve can be estimated by the Kaplan-Meier estimator $\hat{S}(t)$. It takes into account information from all the observations, both censored and uncensored, and is defined by:

$$\hat{S}(t) = \Pi_{t(i) \leq t} \frac{n_i}{n_i - d_i}$$

where n_i is the number of objects at risk at time $t_{(i)}$ (rank-ordered survival times; $t_{(1)}$, $t_{(2)} < \ldots < t_{(m)}$, and d_i is the observed number of events (Cox and Oakes, 1984).

Differences among treatments (temperatures) were tested by using the Log-Rank test, a non-parametric method that is based on assigning a weight to the observations as a function of their ranking (Hosmer and Lemeshow, 1999).

Table 2. Details of experiments testing survivorship of early life history stages of *Rhytisma fulvum fulvum* obtained at different dates (with various respective ambient temperatures) in which exposure to UVR was conducted. For each date, the number of trials and number of animals in each trial are indicated. Azoox. = azooxanthellate primary polyps, Zoox. = zooxanthellate primary polyps.

Date	Stage	Temp. (°C)	# of trials	# of animals in each trial
Jul. 1999	Planulae	26	2	120
Jul. 2001	Planulae	25	3	50
Sep. 2001	Azoox.	26	1	32
Jul. 2001	Azoox.	28	1	24
Aug. 2001	Zoox.	28	2	15, 20

Results

The Soft Coral *Heteroxenia fuscescens*.—The results of the survival experiments of the different life-history stages of *H. fuscescens* are presented in Figure 1. All control groups survived throughout all the experiments, maintained their normal elongated form and behaviour unless mentioned otherwise, and therefore are not illustrated. For this study, onset of mortality was termed the critical point. The shortest period of time required to reach the critical point was 10 hrs, recorded at 21 °C, while the longest was 37.5 hrs at 28 °C (Fig. 1A). Prior to the critical point planulae lost their elongated form, became spherical, and attached to the bottom or the sides of the wells. These changes were followed, after ~12 hrs from the beginning of the experiments, by disintegration of the planulae. In all experiments the UVR-treated groups revealed a similar temporal pattern, with an initial phase of high survival that lasted 24 ± 9 cumulative hrs of exposure to UVR, followed by mortality of up to 50% (LD_{50}) within a period of 54 ± 9 cumulative hrs of exposure (total number of planulae = 660). Survival time of the planulae at 24 °C was significantly higher than at 23 °C (Fig. 2; Kaplan-Meier Survival analysis, Logrank tests, $P < 0.0001$). No significant differences were found between the survival of planulae at the ambient 23 °C and the two experimental temperatures (21° and 26 °C) (Figs. 2, 3A, Kaplan-Meier survival analysis, Logrank tests, $P = 0.0738$). Survival at an ambient temperature of 28 °C was significantly higher than survival obtained under the experimental temperatures of 21° and 30 °C (Fig. 3B; Kaplan-Meier survival analysis, Logrank tests, $P < 0.0001$).

Survival of azooxanthellate primary polyps of *H. fuscescens* showed high variability in the time elapsed until critical point was achieved under the tested temperatures, ranging between 6–37 hrs of exposure at a temperature range of 22–28 °C (Fig. 1B). The polyps then started to disintegrate, and LD_{50} was reached after 30–95.5 hrs of UVR exposure at the same range, respectively. After the first ca. 12 hrs of exposure the tentacles of these primary polyps contracted and their pulsation ceased. Some of them remained in this state for the remainder of the experiment (maximum 95.5 hrs). The control group in all experiments retained normal development. The survival of azooxanthellate primary polyps was significantly higher at 28 °C than at 26° and 23 °C, and was significantly higher at 26 °C than at 23 °C (Fig. 4A, Kaplan-Meier Survival analysis, Logrank tests; $P = 0.0038$).

The critical point for the zooxanthellate primary polyps was achieved after 8–40 hrs in the different experiments, and their LD_{50} was attained after 77–200 hrs of exposure (Fig. 1C). These values did not correspond to the experimental temperatures.

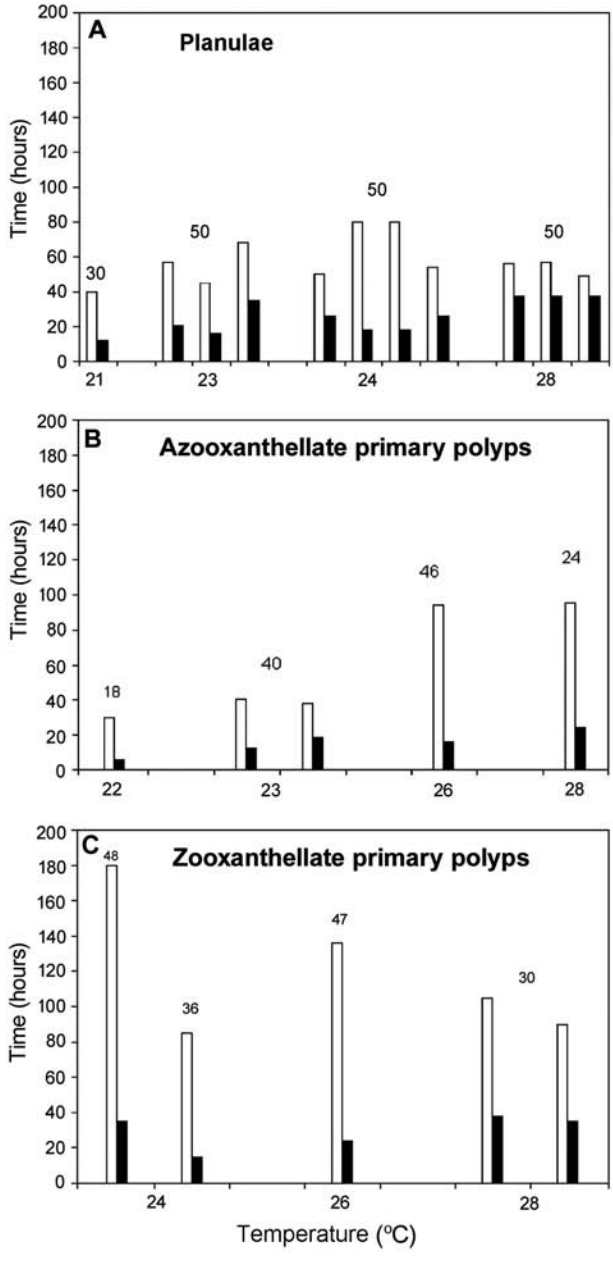

Figure 1. LD_{50} (time to 50% survival; open bars) and critical point (solid bars) values (in hours) of *Heteroxenia fuscescens* early life history stages: (A) planulae, (B) azooxanthellate primary polyps, and (C) zooxanthellate primary polyps exposed to UVR at different ambient temperatures. Number of tested animals is indicated above bars.

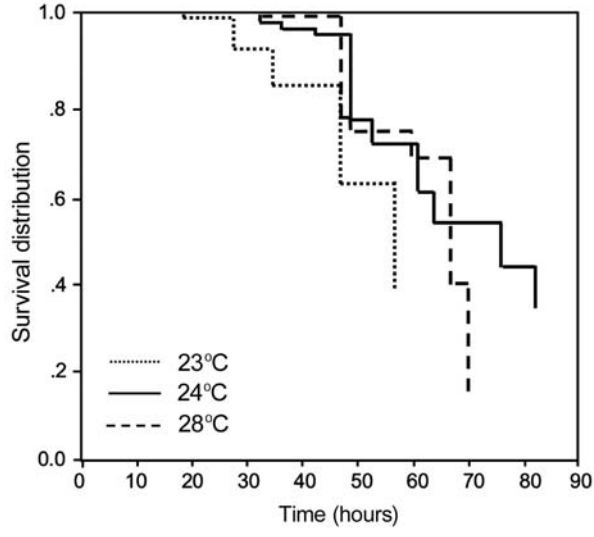

Figure 2. Survival distribution curves for UV-exposed *Heteroxenia fuscescens* planulae at three experimental temperatures.

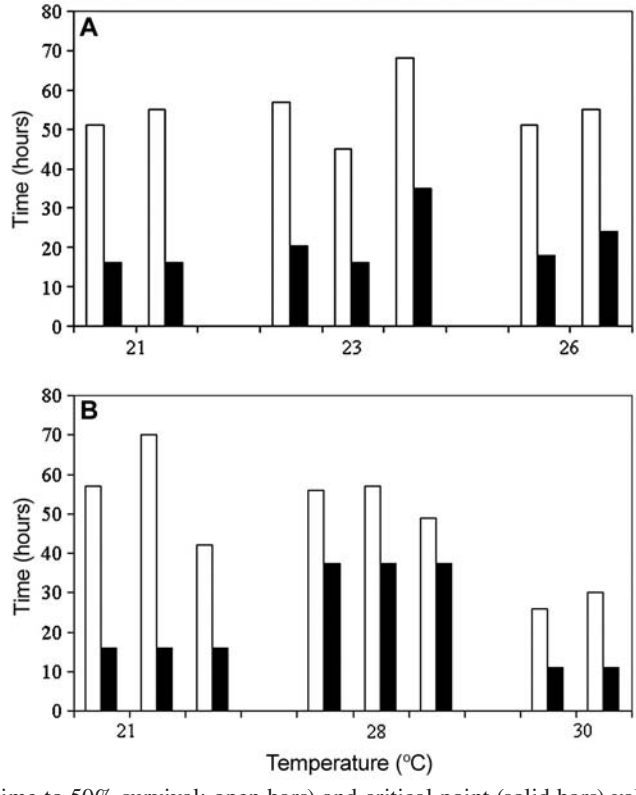

Figure 3. LD_{50} (time to 50% survival; open bars) and critical point (solid bars) values (in hours) for: (A) *Heteroxenia fuscescens* planulae obtained at ambient temperature 23 °C and tested at 21° and 26 °C, and (B) planulae obtained at ambient temperature 28 °C and tested at 21° and 30 °C. n = 50 planulae for each experiment.

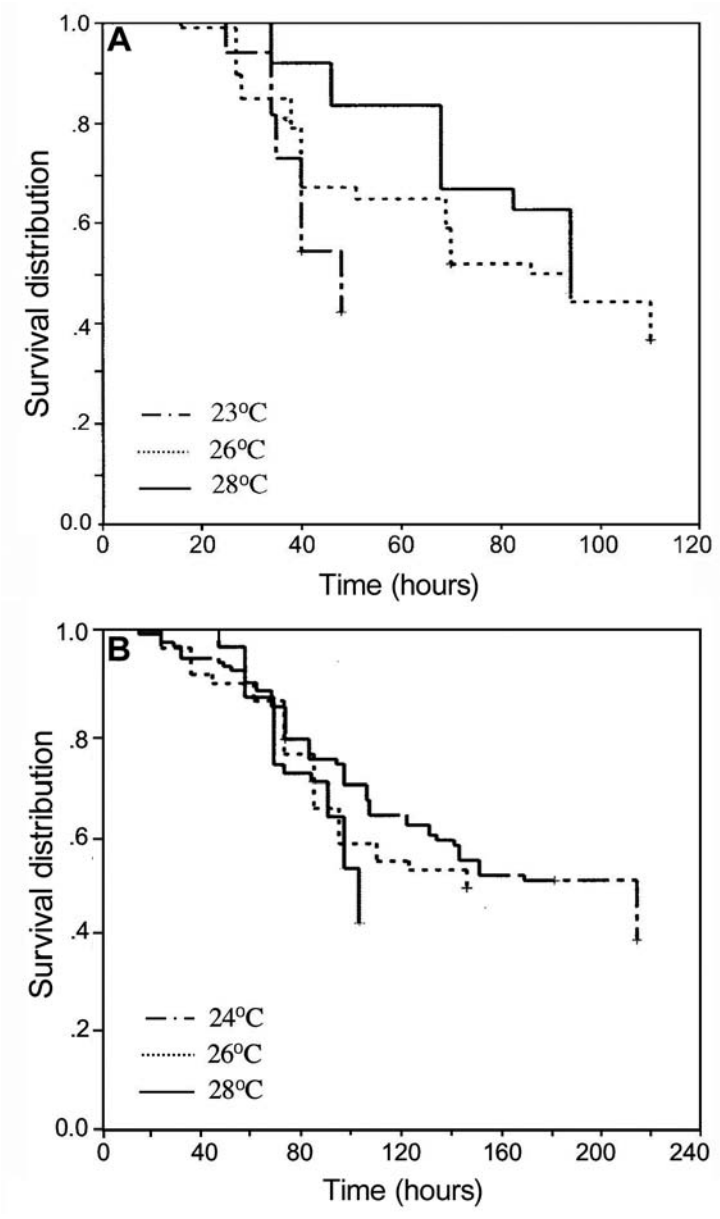

Figure 4. Survival distribution curves for UV-exposed primary polyps of *Heteroxenia fuscecsens* at three experimental temperatures; (A) azooxanthellate polyps and (B) zooxanthellate polyps.

Some of the zooxanthellate primary polyps contracted and ceased their pulsation. Mortality of the UVR-treated polyps took place gradually, reached $LD_{50,}$ and then continued through the end of each experiment. All of the control groups had high survival (> 90%). Survival of zooxanthellate primary polyps at all temperatures did not differ significantly (Fig. 4B; Kaplan-Meier Survival analysis, Logrank tests: P = 0.052).

Survival of planulae and azoo- and zooxanthellate polyps was compared in July and August 2001 under an ambient temperature of 28 °C and was significantly lower

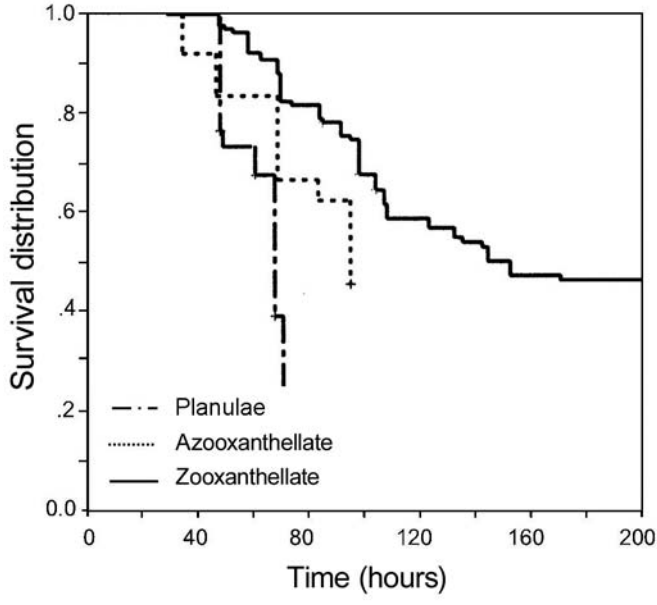

Figure 5. Survival distribution curves for *Heteroxenia fuscecsens* planulae, azooxanthellate primary polyps, and zooxanthellate primary polyps at ambient temperature 28 °C.

for the planulae than for the two types of polyps (Fig. 5; Kaplan-Meier Survival analysis, Logrank tests: $P < 0.0001$). No significant differences were found between the two types of polyps. At 26 °C, however, survival of the zooxanthellate primary polyps was significantly higher than for the azooxanthellate polyps (Kaplan-Meier Survival analysis, Logrank tests: $P = 0.0079$, data shown in Figs. 4A,B, 5). Survival of the planulae was significantly lower at 24 °C compared to zooxanthellate primary polyps, and at 23 °C, it was also significantly lower than the azooxanthellate polyps (Kaplan-Meier survival analysis, Logrank tests: $P < 0.0001$ and $P = 0.0005$, respectively).

The Soft Coral *Rhytisma fulvum fulvum*.—Planulae of *R. f. fulvum* reacted similarly in all UVR exposure experiments, exhibiting a slow decline in survival and high values of critical point and $LD_{50,}$ ranging between 30–64 and 217–460 cumulative hrs of exposure to UVR, respectively. The UVR-treated planulae retained their normal appearance throughout all experiments. Survival of the planulae at 26 °C was significantly higher than at 25 °C (Fig. 6; Kaplan-Meier Survival analysis, Logrank tests: $P = 0.0063$). The critical point for azooxanthellate primary polyps was achieved after 24 hrs of UVR exposure and their LD_{50} was 128 hrs at 26 °C and 95.5 hrs at 28 °C (Fig. 6). For the zooxanthellate primary polyps, the critical point was recorded after 30 hrs at 28 °C in both experiments, with LD_{50} of 170 and 135 hrs. Mortality also occurred in the control group and reached 65% of the initial number of polyps after 168 hrs of exposure. Survival of planulae at 26 °C was significantly higher than that of both the azoo- and zooxanthellate polyps (Kaplan-Meier survival analysis, Logrank tests: $P = 0.0001$). Survival of azooxanthellate primary polyps of *R. f. fulvum* was significantly lower compared to the zooxanthellate ones (Kaplan-Meier survival analysis, Logrank tests: $P = 0.0001$).

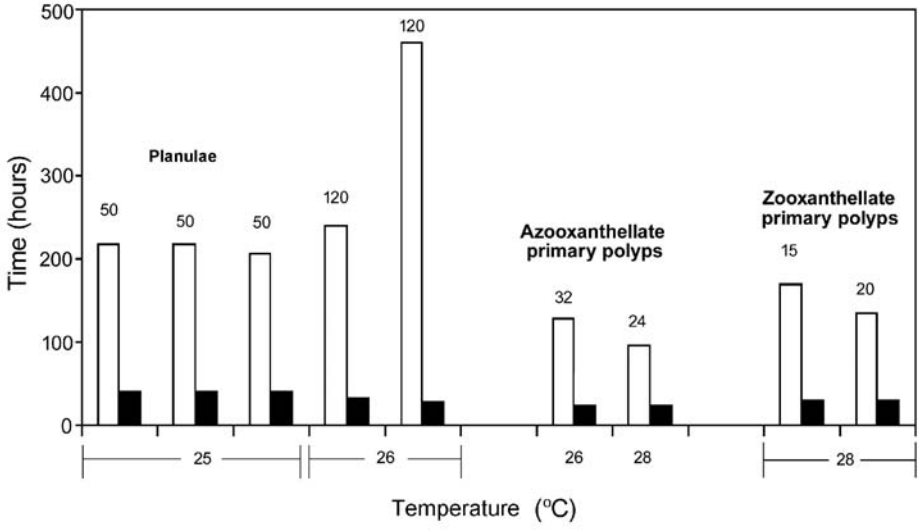

Figure 6. LD_{50} (time to 50% survival; open bars) and critical point (solid bars) values (in hours) of early life history stages of *Rhytisma fulvum fulvum*: (A) planulae, (B) azooxanthellate primary polyps, and (C) zooxanthellate primary polyps exposed to UVR at different ambient temperatures. Number of tested animals is indicated above bars.

Discussion

Here we present for the first time clear evidence for a relationship between the survival of early developmental stages of soft corals and UVR and seawater temperature. The azooxanthellate planulae of *H. fuscescens* were found to be the most sensitive life-history stage to UVR compared to the species' azoo- and zooxanthellate primary polyps at all dates and temperatures. Planulae release in *H. fuscescens* occurs nearly year-round, with higher rates in summer derived from the higher energy content of the parental colonies (Ben-David-Zaslow and Benayahu, 2000). In addition, the summer-released planulae are longer and weigh more compared to planulae from other seasons. The traits of planulae released under high ambient seawater temperatures may thus increase their fitness and survival under high UVR and temperature conditions (Ben-David-Zaslow and Benayahu, 1996, 2000).

Our study revealed the maximal LD_{50} value for *H. fuscescens* planulae under exposure to UVR to be only 70 hrs, whereas the unexposed planulae showed 100% survival for the same period. In a previous study, maximal LD_{50} for the same coral planulae was 37 d when kept under natural light conditions (Ben-David-Zaslow and Benayahu, 1996). UVR is thus an important contributory factor to decreasing planulae survival in this species. Previous studies have shown that UVR, and especially UVB, reduced survival of early developmental stages of various marine invertebrates, such as echinoderms (Adams and Shick, 2001; Karentz et al., 2004), gastropods (Carefoot et al., 1998; Wraith et al., 2006), crabs (Hovel and Morgan, 1999; Dattilo et al., 2005), and stony corals (Gleason and Wellington, 1995; Gleason and Fitt, 2003). However, those studies did not examine a possible synergistic effect of temperature and UVR. Such effects have been found in studies on bleaching of mature colonies of stony corals

(Lesser et al., 1990; Drollet et al., 1994; Lesser, 1997; Lesser and Farrel, 2006) and soft corals (Michalek-Wagner, 2001). Our results are the first to show the synergistic effect of temperature and UVR on the survival of early developmental stages of soft corals. In *H. fuscescens* and *R. f. fulvum*, the survival of planulae under UVR was higher at 24 °C than at 23 °C, but decreased at 28 °C. In the Gulf of Aqaba, the annual temperature range is between 21 °C in winter and 28 °C in summer (Yahel et al., 2005). Oxygen consumption by planulae of *H. fuscescens* at a temperature range of 15–30 °C has been found to be higher at elevated temperatures (0.9 and 0.5 µl hr^{-1}, respectively, Reichert, 2001). Furthermore, planulae exposed to UVR for 12 hrs had a higher oxygen consumption rate compared to the unexposed control at the same temperature (Reichert, 2001). It is thus possible that elevated temperatures, even within the normal range, act synergistically with UVR to reduce survival in planulae.

Azooxanthellate primary polyps of *H. fuscescens* had a high survival rate at higher temperatures under UVR exposure. Moreover, their survival rate was higher than that of planulae at all tested temperatures and similar to that of zooxanthellate polyps at 28 °C. On the other hand, zooxanthellate polyps of this soft coral had higher rates of survival than azooxanthellate polyps at 26 °C. Symbiotic zooxanthellae are a major component in determining the energy budget of coral hosts (Davies, 1991). Acquisition of symbiotic algae by primary polyps of *H. fuscescens* coincides with the development of their mouth opening (Yacobovitch et al., 2003). Yacobovitch et al. (2003) suggested that the significantly higher survival rate in the laboratory for zooxanthellate primary polyps of *H. fuscescens* as compared to azooxanthellate ones could be due to the symbiotic state. This may explain the higher survival of zooxanthellate primary polyps compared to the azooxanthellate ones under exposure to UVR at 26 °C. Consequently, at 28 °C, the survival of zooxanthellate primary polyps under exposure to UVR would be expected to be higher than that of azooxanthellate ones; yet no such significant differences in their survival rates at that temperature were obtained. High temperatures along with UVR can damage the coral-algal symbiosis (e.g., Drollet et al., 1994; Lesser, 1996; Lesser and Farrel, 2006). Michalek-Wagner (2001) showed a significantly greater loss in both zooxanthellae numbers and chlorophyll concentrations in the soft corals *Lobophytum compactum* Tixier-Durivault, 1956, and *Sinularia flexibilis* (Quoy and Gaimard, 1833), in the Great Barrier Reef (Australia), when an elevated temperature (32 °C, which is between 1 and 2 °C above the normal range), and UVR occurred in combination. In the Gulf of Aqaba, a temperature of 28 °C is at the upper end of the normal range (Genin et al., 1995). It is possible that in our study the exposure of zooxanthellate primary polyps of *H. fuscescens* to extreme temperature together with UVR damaged their zooxanthellae and consequently reduced their survival. The high survival rate of azooxanthellate polyps is also likely due to the presence of the UV-absorbing compounds (MAAs) detected in their tissue, which play a role in protection against UVR (Zeevi-Ben-Yosef et al., 2008).

Planulae of *R. f. fulvum* had higher values of critical point and cumulative hours of exposure compared to *H. fuscescens* planulae and their survival was higher than that of the azoo- and zooxanthellate primary polyps of the latter. The embryos of *R. f. fulvum*, which complete their development to azooxanthellate planulae on the surface of the female colony, detach 6 d after release and then settle on the reef (Benayahu and Loya, 1983). It is possible that they are exposed to higher levels of UVR during

embryogenesis while being surface brooded and are therefore more tolerant to UVR than *H. fuscescens* planulae, which are internally brooded. Zooxanthellate primary polyps of *Xenia umbellata* Lamarck, 1816, demonstrated a very low survival rate (12–16 hrs; Zeevi Ben-Yosef, 2003). This, together with the lower survival of *H. fuscescens* zooxanthellate primary polyps at higher temperatures, underscores the question: To what extent does symbiotic state contribute to the fitness of coral juvenile stages under such conditions? In a recent study, Zeevi-Ben-Yosef et al. (2008) showed that MAAs were present in all early developmental stages of *H. fuscescens,* including planulae, azoo- and zooxanthellate primary polyps, and concluded that the source of MAAs is not the symbiotic algae. The survival rate of a variety of early developmental stages of soft corals studied has indicated that planulae are the most sensitive while zooxanthellate polyps are the most resistant to UV radiation, thus correlating with their respective MAA concentrations (Zeevi-Ben-Yosef et al., 2008).

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