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Mycosporine-like amino acids in azooxanthellate and zooxanthellate early developmental stages of the soft coral *Heteroxenia fuscescens*

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Abstract

The ontogenetic changes of MAAs in the soft coral *Heteroxenia fuscescens* was studied in relation to their symbiotic state (azooxanthellate *vs.* zooxanthellate) under different temperature conditions in the Gulf of Eilat, northern Red Sea. The HPLC chromatograms for extracts of the planulae, azoo- and zooxanthellate primary polyps of *H. fuscescens* from all dates of collection yielded a single peak at 320 nm that has been identified as the compound palythine. Concentration of palythine in planulae at 23 °C was 7.57±1 nmol mg^{-1} protein and at 28 °C reached 17.29±1 nmol×mg^{-1} protein. Concentration of palythine in azooxanthellate primary polyps was 16.4±3 nmol×mg^{-1} protein and 28.37±2.8 nmol×mg^{-1} protein at 23 °C and 28 °C respectively. The palythine concentration for zooxanthellate primary polyps at 23 °C was 13±3 nmol×mg^{-1} protein and at 28 °C 32.7±2 nmol mg^{-1} protein. Palythine concentrations were significantly higher at 28 °C in the different animal groups and correlated linearly with the ambient collection temperature. This study shows for the first time that UVR and temperature act synergistically and affect the MAA levels of early life-history stages of soft corals.

Keywords: *Heteroxenia fuscescens*; Mycosporine-like amino acids; Planulae; Red Sea; Temperature

1. Introduction

Mycosporine-like amino acids (MAAs) are well-described UV-absorbing compounds that maximally absorb UVR between 309 and 360 nm and are ubiquitous among marine organisms (Dunlap and Shick, 1998; Shick and Dunlap, 2002). Concentration of MAAs correlates with UV exposure (Shick et al., 1999), often being highest in eggs, as in echinoderms (Chioccara et al., 1986; Adams and Shick, 1996), mollusks (Carefoot et al., 1998; Prezeslawski et al., 2005), sponges (Bandaranayake et al., 1997) and copepods (Tartarotti and Sommaruga, 2006). Cleavage of embryos of the sea urchin *Strongylocentrotus droebachiensis* was inhibited under exposure to UVR (Adams and Shick, 1996), while the MAAs found in embryos of *S. droebachiensis* were shown to protect them against UV-B-induced abnormalities during their development to the pluteus larval stage (Adams and Shick, 2001). Exposure of sea hare (*Aplysia dactylomela*) spawn to UVR reduced the hatching rate of its veligers, which was related to an MAA-poor diet (Carefoot et al., 1998). Planula–larvae of the stony coral *Agaricia agaricites* originating at a depth of 24 m had higher mortality as a result of UV-B radiation than its conspecifics at 3 m (Gleason and Wellington, 1995), a difference that was attributed to the three-fold higher concentration of MAAs in the former compared to the latter. UVR had a negative effect on planular settlement of the stony coral *Pocillopora damicornis* however, despite the differences in MAA concentrations, the origin of these planulae did not significantly affect their survival or settlement (Kuffner, 2001). Michalek-Wagner and Willis (2001a) found that in the eggs of the soft coral *Lobophytum compactum* the MAA levels were approximately three-fold higher than in their parent colonies, and suggested that this corroborated their function as photo-protectants in the planulae, which may experience extreme UV radiation while in the plankton.

Since MAA biosynthesis involves the shikimic acid pathway (Favre-Bonvine et al., 1987), a biochemical route not present in

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metazoans (Bently, 1990), in corals MAAs are presumed to originate in their symbiotic zooxanthellae (Dunlap and Chalker, 1986). Shick et al. (1999) provided the first evidence that inhibition of the shikimate pathway blocks UV-B-stimulated accumulation of MAAs in a coral. A later study however, showed that MAA synthesis and conversion of MAAs in planulae of the stony coral *Goniastrea retiformis* occurred in the absence of zooxanthellae, indicating a possible contribution of prokaryotes associated with the animal tissue to these processes (Yakovleva and Baird, 2005). Freshly isolated zooxanthellae from their hosts frequently have the same or similar MAA complement as the holobiont (intact symbiosis) or host tissues (Banaszak and Trench, 1995; Shick et al., 1995), reinforcing the notion that algal cells produce the MAAs. However, in some cases isolated zooxanthellae from MAA-containing holobionts lack MAAs (Banaszak and Trench, 1995; Ishikura et al., 1997). This, together with the inability of zooxanthellae to synthesize MAAs in culture (Banaszak and Trench, 1995; Banaszak et al., 2000), suggests that the MAAs may have another provenance. Assuming that invertebrates are unable to synthesize MAAs (an assumption not yet tested experimentally), and although a bacterial source cannot be discounted (Arai et al., 1992; Yakovleva and Baird, 2005), their trophic accumulation may constitute the major pathway of UV acclimation by nonsymbiotic reef consumers (Shick et al., 1992; Shick and Dunlap, 2002). Therefore, it is highly probable that the source of MAAs may vary among different organisms, including their early developmental stages.

Parental provision of MAAs to larvae is a common strategy for avoiding UV damage among taxa with planktonic larvae, such as *S. droebachiensis* (see: Adams and Shick, 1996; Adams and Shick, 2001), *A. dactylomela* (see: Carefoot et al., 1998) and the soft corals *L. compactum* and *Sinularia flexibilis* (see: Michalek-Wagner, 2001). Most symbiotic (zooxanthellate) cnidarians have aposymbiotic (azooxanthellate) juvenile stages early in their life cycle, preceding the symbiotic (zooxanthellate) ones (Benayahu, 1997; Yacobovitch et al., 2003). MAA presence and levels in the tissues of these different stages and their relevance to resistance to UVR has remained largely unexamined. For example, the azooxanthellate scyphistomae of the jellyfish *Cassiopeia xamachana* produced no MAAs even when exposed to UVR, whereas its zooxanthellate ephyrae and the adult medusa contained the same MAAs found in their zooxanthellae, though their resistance to UVR in the different stages was not examined (Banaszak and Trench, 1995). Interestingly, azooxanthellate planulae of *G. retiformis* showed a significant increase in the concentration of MAAs between three and seven days of age (Yakovleva and Baird, 2005). Thus, it could be that in those cases the source of MAAs was other than the symbiotic zooxanthellae.

Increase in ambient temperature results in a decreased capacity of zooxanthellae to process the excitation energy resulting from the dark reactions of photosynthesis (Jones et al., 1997), thus leaving zooxanthellae further sensitive to light and eventually leading to photoinhibition (Jones et al., 1997). Subsequent discarding of the thermally-damaged zooxanthellae by the host as a damage-limiting response (Michalek-Wagner and Willis, 2001b) may in turn affect its MAA concentration. Michalek-Wagner and Willis (2001a) showed reductions of 13 and 44% in MAA concentrations in eggs of moderately and heavily bleached colonies of *L. compactum*. Hence, the synergistic relationship between irradiance and elevated temperature, and its implications for MAA levels of different early life-history stages, offer an intriguing subject for study.

MAAs play a role in protecting early developmental stages of marine organisms against UVR in laboratory experiments (Carefoot et al., 1998; Adams and Shick, 2001), yet studies of UVR and the involvement of MAA protection on such stages among tropical corals are scant (Shick and Dunlap, 2002). Consequently, a comparison of MAA composition and UV-tolerance in the early developmental stages of corals is necessary before any meaningful correlations can be established. Hence, the present study hypothesized that the resistance of corals to UVR already exists in their early developmental stages by means of MAAs, whose presence is associated with the symbiotic algae. We also examined the concentration of MAAs in relation to ambient temperature in both azooxanthellate (planulae and primary polyps) and zooxanthellate (infected primary polyps) of the soft coral *Heteroxenia fuscescens* (see Yacobovitch et al., 2003). Adult colonies of this soft coral contain MAAs in relation to environmental changes in UVR (Zeevi Ben-Yosef et al., 2006). Thus, the present study was aimed at understanding the nature of the ontogenetic changes of MAAs in these animals in relation to their symbiotic state (azooxanthellate *vs*. zooxanthellate) under different temperature conditions.

2. Methods

2.1. Studied organisms and collection of planulae

The soft coral *H. fuscescens* (family Xeniidae) is a common reef dweller in the northern Red Sea and its life history is well documented. It is a hermaphroditic planula-brooder that releases azooxanthellate planulae nearly all year round (Benayahu, 1991; Ben-David-Zaslow et al., 1999). Mature colonies of *H. fuscescens* were collected from the coral reef (3–8 m deep) across from the Interuniversity Institute for Marine Sciences at Eilat (IUI) in April–August 2001, at ambient temperatures of 21°–28°C. In the laboratory they were placed in containers with running seawater, prior to sunset, and examined the following morning for the presence of planulae (see also Ben-David-Zaslow et al., 1999). The released planulae were transferred into 250 ml PVC containers filled with Millipore-filtered (0.2 μm) seawater (FSW) to avoid bacterial contamination and transported to Tel Aviv for further experiments.

2.2. Development of primary polyps

Planulae of *H. fuscescens* maintained in 0.45 μm Eilat FSW initiated normal metamorphosis 10–14 days after release, and subsequently successfully developed into primary polyps (see Yacobovitch et al., 2003). The planulae were placed in 24-well tissue culture plates, 3 planulae per well, filled with 3 ml 0.45 μm FSW (72 planulae per plate) and placed inside incubators (MRC-LE509) at a temperature corresponding to the ambient seawater temperature at the time of their release from the colonies. In order

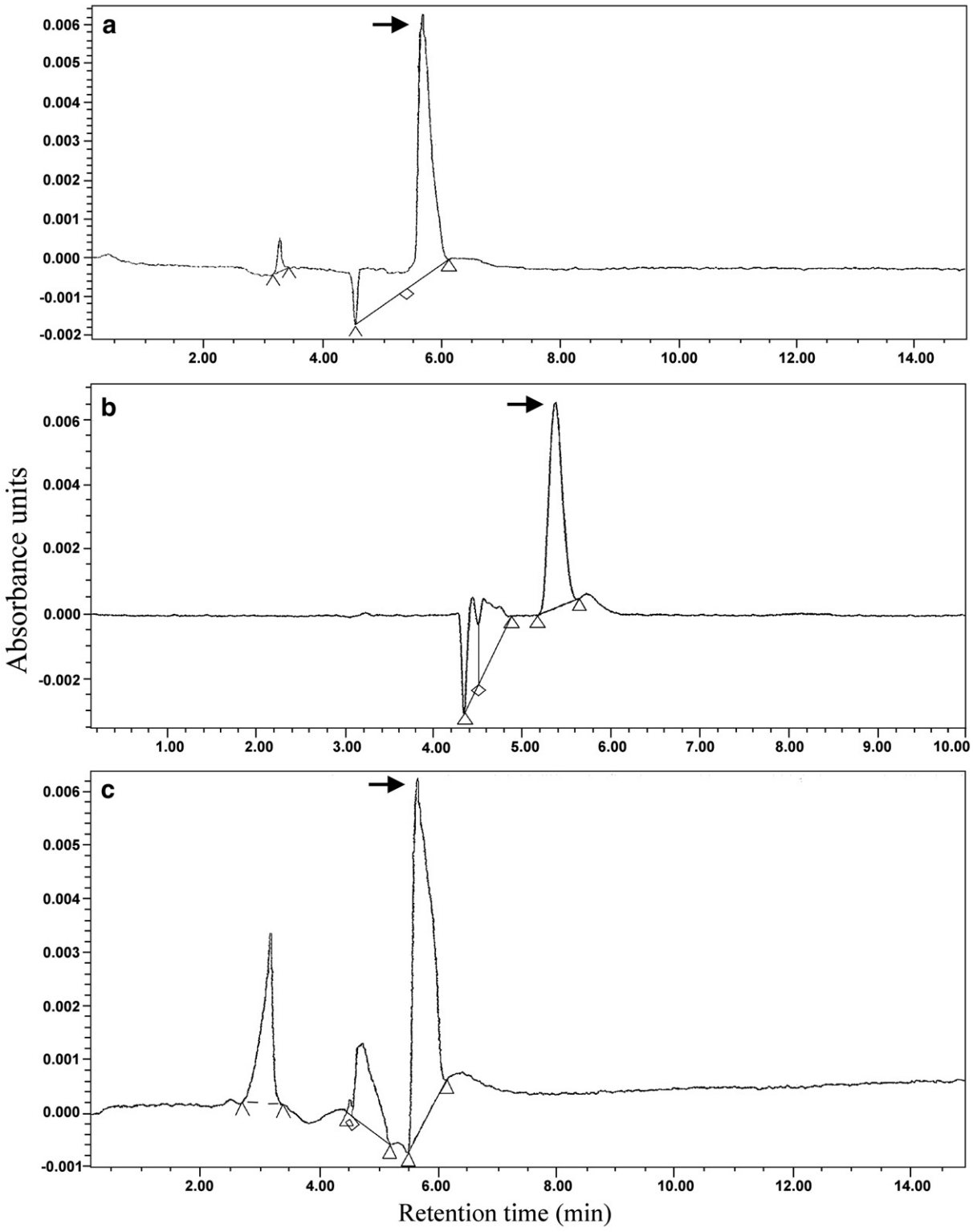

Fig. 1. *Heteroxenia fuscescens*: Typical HPLC chromatograms of planulae (a), azooxanthellate (b) and (c) zooxanthellate primary polyps. Arrow indicates the peak of the identified compound palythine.

to obtain zooxanthellate primary polyps of *H. fuscescens*, freshly isolated algal cells from the parental colonies were obtained by homogenization and centrifugation following the methodology described by Yacobovitch et al. (2003). The algal symbionts were introduced into each well upon initiation of metamorphosis, yielding a final concentration of $5–7\times10^{-4}$ algal cells $\times$ ml^{-1}. The initial number of planulae introduced into a given plate and the percentage of successful metamorphosis into the primary

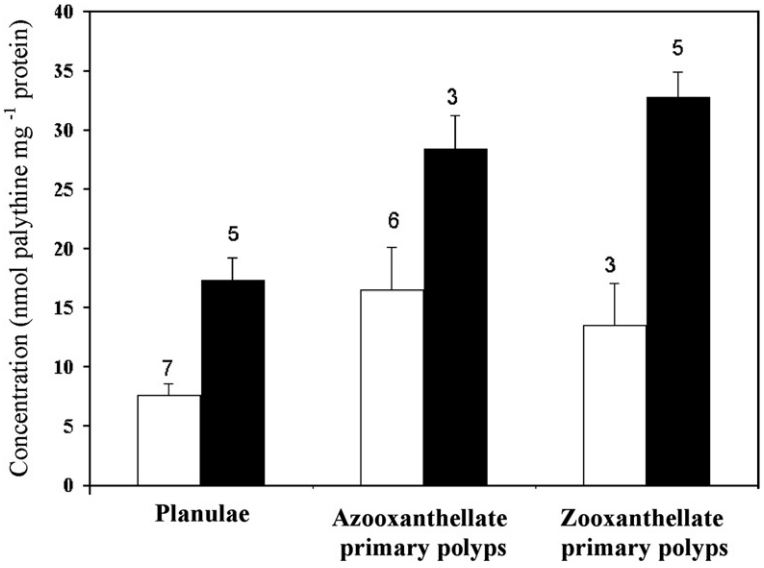

Fig. 2. *Heteroxenia fuscescens*: Concentration of palythine per mg protein in early life-history stages at ambient temperatures of 23 °C (blank bars) and 28 °C (black bars). Number of replications is indicated above bars (5 planulae each).

polyp stage dictated the number of primary polyps used in the different assays.

2.3. MAAs in early developmental stages

Planulae of *H. fuscescens* were obtained at ambient temperatures of 23° (April 2001) 24° (May 2001), 26° (September 2001) and 28 °C (July 2001). Some of the planulae were immediately frozen at −20 °C ($n \geq 3$ replicates for each temperature, 5 animals each). The rest of the planulae were reared in incubators at 23 °C (April 2001) and 28 °C (July 2001) corresponding to the ambient temperature at the collection time and then frozen at −20 °C ($n \geq 3$ replicates for each temperature, 5 animals each). All samples were homogenized and extracted in 100% methanol overnight at 4 °C. They were then centrifuged at 10,000 rpm for 5 min to remove tissue residue. The extracts were analyzed for presence of MAAs by HPLC (see Zeevi Ben-Yosef et al., 2006). MAAs were quantified by comparing the integrated HPLC peak to the standard and MAA concentration was normalized to protein concentration for each sample.

3. Results

The HPLC chromatograms for extracts of the planulae, azoo- and zooxanthellate primary polyps of *H. fuscescens* from all dates of collection (Fig. 1a–c) yielded a single peak at 320 nm, which has been identified as the compound palythine (see also Zeevi Ben-Yosef et al., 2006). Concentration of palythine in planulae at 23 °C was 7.57±1 nmol × mg^{-1} protein and at 28 °C reached 17.29±1 nmol × mg^{-1} protein (Fig. 2, $n=35$ and $n=25$ planulae, respectively). Concentration of palythine in azooxanthellate primary polyps was 16.4±3 nmol × mg^{-1} protein ($n=30$) and 28.37±2.8 nmol × mg^{-1} protein ($n=15$) at 23 °C and 28 °C respectively. The palythine concentration for

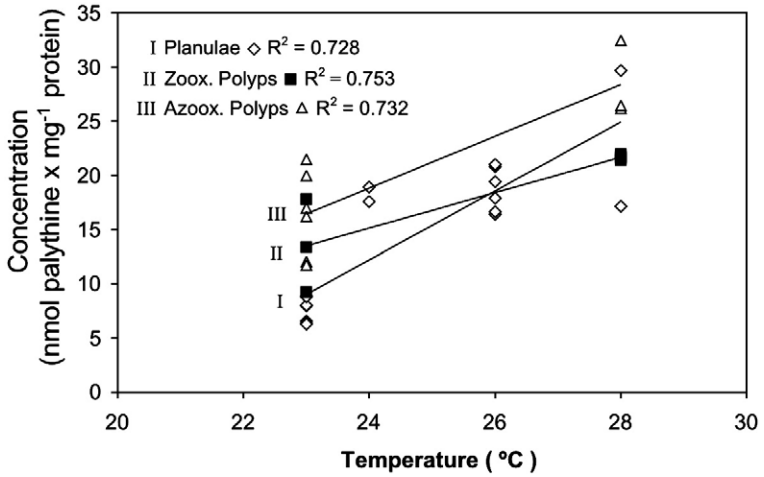

Fig. 3. *Heteroxenia fuscescens*: Linear correlation of palythine concentration in different early life-history stages in relation to ambient temperature.

zooxanthellate primary polyps at 23 °C was 13±3 nmol×mg^{-1} protein (n=15) and at 28 °C 32.7±2 nmol×mg^{-1} protein (n=25). Palythine concentrations were significantly higher at 28 °C in the different animal groups (Two-way ANOVA, $p<0.001$) but the interaction between stage and temperature was not significant (Two-way ANOVA, $p>0.05$). Post-hoc comparisons showed that the main difference in palythine concentrations was between the planulae and the two polyp groups and not between the azooxanthellate and zooxanthellate polyps. Palythine concentration in the three different animal groups correlated linearly with the ambient collection temperature (Fig. 3: planulae $R^2=0.728$, zooxanthellate polyps $R^2=0.757$ and azooxanthellate polyps $R^2=0.732$, p=0.001.

4. Discussion

To date, few studies have been conducted on the presence of MAAs in azooxanthellate or zooxanthellate early life-history stages of cnidarian hosts. Banaszak and Trench (1995) showed that in the ephyra and adult medusa of *C. xamachana*, the source of the MAAs is their symbiotic zooxanthellae. Yakovleva and Baird (2005) showed a significant increase in the concentration of MAAs between days 3 and 7 of development of azooxanthellate planulae of the stony coral *G. retiformis.* The present study revealed the MAA compound palythine in both the azooxanthellate and zooxanthellate early developmental stages of *H. fuscescens*, which contained even higher palythine levels than the planulae. Shick et al. (1999) provided firm evidence that MAA biosynthesis in the stony coral *Stylophora pistillata* originates from its symbiotic algae; while Yakovleva and Baird (2005) suggested that the biosynthesis of MAAs in *G. retiformis* might originate from symbiotic microorganisms. Therefore, our finding that azooxanthellate primary polyps contained higher palythine levels than the planulae and similar levels to the zooxanthellate polyps at 23 °C (see Fig. 2) is intriguing and may support the latter suggestion.

S. droebachiensis acquired free amino acids (FAAs) from seawater by active transport (Jeackle and Manahan, 1992), but did not acquire shinorine, the MAA most commonly found in sea urchin eggs (Adams and Shick, 2001). Uptake of dissolved organic matter (DOM) in the form of FAAs from seawater has been demonstrated for planulae (Ben-David-Zaslow and Benayahu, 2000) and mature colonies (Schlichter, 1982) of *H. fuscescens*. MAAs have been found in the medium of dinoflagellate cultures (Banaszak et al., 2000) and UV-absorbing compounds have been detected dissolved in seawater during plankton blooms (Vernet and Whitehead, 1996). Therefore, a possible source of the palythine for the azooxanthellate planulae and primary polyps of *H. fuscescens* might have been the filtered seawater used in the current study, or contributed by the symbiotic microorganisms as suggested by Yakovleva and Baird (2005), though this remains to be investigated.

In the present study, a relationship was found between high MAA levels and high ambient seawater temperature (i.e., 28 °C). These findings coincide with palythine concentrations in colonies of *H. fuscescens* which are significantly higher in summer than in the other seasons, particularly in shallow-reef water (Zeevi Ben-Yosef et al., 2006). We suggest a possible link between the mode of coral reproduction i.e., spawning, surface brooding and brooding (see also Benayahu, 1997) and the concentration of MAAs in their early developmental stages. Levels of MAAs in the spawned azooxanthellate eggs of *L. compactum* were found to be approximately three-fold higher than those in maternal tissue (~300 and ~1000 nmol×mg^{-1} protein respectively) (Michalek-Wagner and Willis, 2000a). Our study revealed that in planulae of *H. fuscescens* MAA concentration is much lower than that in mature colonies (17.29±1 and 130±40 nmol×mg^{-1} protein respectively (this study; Zeevi Ben-Yosef et al., 2006). Planulae of *H. fuscescens* are negatively buoyant and sink to the bottom immediately upon release (Ben-David-Zaslow and Benayahu, 1996), and hence are most probably less exposed to UV than the buoyant eggs of *L. compactum*. Interestingly, the planulae of the surface brooder *R. fulvum fulvum* (see Benayahu and Loya, 1983) has palythine levels higher than those of *H. fuscescens* planulae (117.5±12.5 *vs.* 17.29±1 nmol×mg^{-1} protein respectively). It is suggested that the surface-brooded embryos of *R. fulvum fulvum* are exposed to higher levels of UVR, especially in shallow water, compared to the internally-brooded embryos of *H. fuscescens,* thus explaining their respective concentrations of MAAs. Further, MAA concentration in eggs of *L. compactum* prior to spawning (Michalek-Wagner and Willis, 2000a) was more than five-fold higher than in embryos of *R. fulvum fulvum*, thus indicating a possible adaptive value of MAA concentration in relation to the mode of reproduction, which can also affect their survival under exposure to UVR (Zeevi Ben-Yosef, 2003).

The present findings contradict the original hypothesis of our study, which contended that the presence of zooxanthellae determines the levels of MAAs in the coral tissues, while supporting the findings of Yakovleva and Baird (2005) which indicated that presence or absence of MAAs do not relate to the presence of algal endosymbionts. Marine organisms also appear to receive protection against UVR through antioxidants, including uric acid, carotenoids, tocopherols, glutathione, ovothiols, gadusols, and ascorbic acid (reviewed by Shick et al., 1996; Dunlap et al., 2000). It is suggested, therefore, that in cases of low levels of MAAs such as those found in early azooxanthellate developmental stages of soft corals in comparison to their respective adults, the former might utilize alternative UVR protectors, whose exact nature remains to be studied.

5. Conclusions

This study demonstrated for the first time that UVR and temperature act synergistically and affect MAA levels of early life-history stages of soft corals. This underscores the significance of these compounds as UV protectors in the course of the life cycle of *H. fuscescens*. Furthermore, the link between MAA levels and different life-history stages demonstrates their ability to regulate MAA levels in response to ecological and environmental cues. In the soft coral studied, it would seem that the source of MAAs is not the alga partner of the symbiosis. The corals might acquire their MAAs independently from their diet, from the surrounding medium or from the associated symbiotic

microorganisms in the azooxanthellate stages, possibilities that demand further investigation.

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