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Postlarval chromatophores as an adaptation to ultraviolet radiation

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Abstract

It is now well established that ultraviolet radiation (UVR) may have detrimental, even lethal effects on zooplankters. Unlike copepods and other holoplankters, which may avoid UVR by undergoing diel vertical migration, larvae of many decapod crustaceans and fishes recruit to adult populations by remaining in near-surface waters during the daytime. Consequently, they are exposed to biologically damaging UVR. A possible adaptation in these larvae is chromatophores, which may absorb UVR by expanding in high light environments. The supposition is that expanded chromatophores more effectively absorb UVR, but there is some fitness cost to having expanded chromatophores in low light environments. Since the ratio of visible light to UVR in the water column changes as result of season, latitude, dissolved organic carbon, and a host of other factors, the benefits of chromatophores would be maximized if they responded specifically to UVR. The purpose of this study was to determine whether the chromatophores of crab postlarvae (megalopae) could expand in response to UVR. Megalopae of two species of crabs (*Cancer oregonensis*, *Telmessus cheiragonus*) were collected from large surface-swarms during mid-day as they recruited onshore in early May 1998 at Friday Harbor, Washington, USA. Dark-adapted megalopae (held in the dark for 8 h before experiments) were exposed to UVR (UVBR + UVAR, 280–400 nm), UVAR (320–400 nm), and light (400–1700 nm) in the laboratory. Chromatophores expanded after only minutes of exposure to UVR, UVAR, and light for both species. Two alternative hypotheses may explain why both harmful and comparatively benign wavelengths stimulated chromatophores to rapidly expand. First, larvae may not distinguish among different wavelengths, which, if true, would increase the vulnerability of these larvae to intensifying UVBR due to ozone depletion. Second, chromatophores have functions other than blocking UVR, such as crypsis and thermoregulation, and must respond to light for these other functions to operate.

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1. Introduction

The extensive diel vertical migrations undertaken by many holoplankters have generated considerable interest in the scientific community over much of this century. It is now widely accepted that this behavior minimizes predation by diurnally foraging planktivorous fishes and damage caused by ultraviolet radiation (UVR) (e.g., Hailstone, 1979; Luck and O'Brien, 1981; Gliwicz, 1986). While the migration is energetically expensive, lowering reproductive output, it is more adaptive than remaining in dangerous sunlit surface waters (DeMeester and Beenaerts, 1993; Duncan et al., 1993). In stark contrast to this paradigm, dispersing larvae of many decapod crustaceans and fishes are abundant near the sea surface in the daytime (e.g., Hunter et al., 1979; Morgan and Christy, 1996). Although this phenomenon has been documented many times, its direct contradiction to the prevailing paradigm has not received much attention from ecological and evolutionary biologists.

Larvae remaining in near-surface waters raise two questions: (1) why do they remain in this hostile environment; and (2) how can they remain there while other zooplankters cannot? A suggested answer to the first question is that remaining in surface waters enables larvae to migrate from larval nursery areas back to adult habitats. The distance between adult habitats and larval nursery areas can be as far as 100 km, and larvae generally cannot swim between these locales (reviewed by Boehlert and Mundy, 1988; Epifanio, 1988; McConaugha, 1988; Morgan, 1995; Shanks, 1995). Larvae complete these migrations by spending different amounts of time in opposing stratified currents (Morgan, 1995; Shanks, 1995; Young, 1995). They typically are advected from nearshore habitats by subsurface currents, and postlarvae are transported onshore in surface waters by winds and internal waves (Shanks, 1983, 1986, 1988; Goodrich et al., 1989; Matthews, 1995; Lobue, 1996; Morgan et al., 1996). Thus, postlarvae may spend more time in illuminated surface waters than do larvae, and as a result suffer greater exposure to predatory fishes and UVR (Morgan and Christy, 1996).

Morgan and Christy (1996) provided a possible answer to the second question, how some larvae can survive in sunlit surface waters. Complex chromatophore systems in decapod larvae may protect them from UVR without increasing their visibility to planktivorous fishes. Large dark chromatophores (melanophores) are often situated over vital organs. These chromatophores contain melanins, which are pigments that strongly absorb both visible light and UVR, and other pigments that absorb light of different wavelengths (Masthay, 1997). Crustaceans are more darkly pigmented in locales where they receive higher doses of UVR (e.g., Hebert and Emery, 1990; Hessen and Sorensen, 1990), and a photoproctective role for larval and adult chromatophores has been suggested (Pautsch, 1953; Coohill et al., 1970). Chromatophores are also polychromatic, tingeing larvae green, and may be situated beneath organs (Morgan and Christy, 1996). The greenish hue may reduce the contrast of larvae with the surrounding water column, making it more difficult for fishes to see larvae.

Chromatophores generally expand in high light environments and contract in low light environments (Pautsch, 1951; Johnson, 1974; Hunter et al., 1981). Therefore, fully expanded chromatophores could better protect larvae from UVR, but there could be some fitness cost to having expanded chromatophores in its absence. If UVR protection is indeed their primary function, the costs of having chromatophores would be minimized if they could respond specifically to UVR. This is particularly true since visible light is an imperfect surrogate marker for UVR.

The ratio of visible light to UVR varies across time and space in response to changes in depth, time of day, season, latitude, water composition, and weather (Jerlov, 1968; Smith and Baker, 1981; Cutchis, 1982; Madronich, 1993). UVR-responsiveness is important if larvae are to mount appropriate responses to a changing irradiance environment, and it will become even more important as levels of UVBR increase from continuing ozone degradation. Furthermore, the speed of the larval response is important, since the photic environment can change rapidly. However, the minimum time for larval chromatophores to respond to UVR is unknown.

The purpose of this study was to determine whether the chromatophores of crab postlarvae (megalopae) are capable of such a UV-specific response. Specifically, we tested chromatophore expansion after 10 and 20 min in response to UVR (UVBR, 280–320 nm or UVAR, 320–400 nm) and light (400–1700 nm).

2. Material and methods

2.1. Collection

This study was conducted using megalopae of two species of crabs that live on the Pacific coast of the USA, *Cancer oregonensis* (Dana)(Cancridae) and *Telmessus cheiragonus* (Tilesius) (Cheiragonidae). Both species were collected from a large surface swarm during mid-day as they recruited onshore. *Telmessus cheiragonus* megalopae were collected on 4 May 1998 and *C. oregonensis* megalopae were collected a week later. Both species were collected from docks at the Friday Harbor Laboratories, Washington, USA. Megalopae were identified using available taxonomic keys (Cordell and Escofet, unpublished). Identifications were verified by holding megalopae until they metamorphosed to the juvenile stage (Jenson, 1995). Megalopae of *C. oregonensis* were relatively lightly pigmented as compared to *T. cheiragonus,* and covered by approximately 20 chromatophores dorsally (Fig. 1). Megalopae of *T. cheiragonus* were quite dark, and covered by approximately 60 dorsal chromatophores (Fig. 2). Megalopae were kept for 1–2 weeks in 18.9-l buckets in a running seawater table (11–13°C) at the Friday Harbor Laboratories until experiments could be conducted. Lids shielded megalopae from direct light for 8 h before experiments began.

2.2. Experimental design

All experiments on *Cancer oregonensis* megalopae and the UVR experiment on *Telmessus cheiragonus* were conducted at night in a dark cold room maintained at 12°C

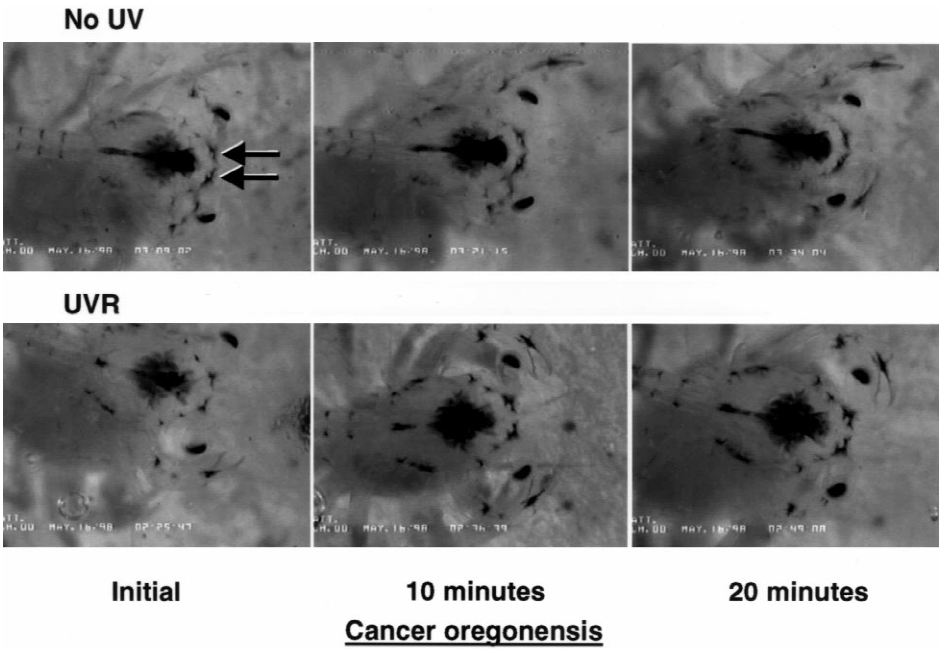

Fig. 1. Chromatophore size of two dark-adapted *Cancer oregonensis* megalopae after exposure for 10 and 20 min to No-UVR and UVR. The three images for each treatment are from the same individual. All images are at the same magnification. Arrows indicate the two chromatophores measured. See text for more explanation of the treatments.

to match the ambient temperature of seawater. The light experiment on *T. cheiragonus* megalopae was conducted at night in the laboratory, and microscope slides containing megalopae were held in seawater baths at 12°C. Experiments were conducted at night to allow better control of the light environment of the larvae. If endogenous rhythms influence chromatophore expansion, then we would expect responsiveness to be lower at night. Therefore, these measurements would provide conservative estimates of chromatophore response.

Before the night of the experiment, wells were created on microscope slides using silicon and were allowed to dry for 24 h. On the night of the experiment, megalopae were placed individually in a well with seawater under low-light conditions, and the slides were numbered to keep track of individuals during the course of the experiment. A cover slip was placed over the well to ensure that megalopae maintained the same orientation while still permitting limited movement. These glass coverslips blocked the lower portion of the UVBR range but allowed some UVBR to pass (Fig. 3). Slides were covered shielding megalopae from UVR and light both before and after experimental exposure. To record an image for later measurement, a slide was placed on the stage of a dissecting microscope that was equipped with a videocamera, and the megalopa was recorded for 1–2 s using a VHS videocassette recorder. A fiber optic light source was used to illuminate megalopae for recording. The slide was removed immediately from

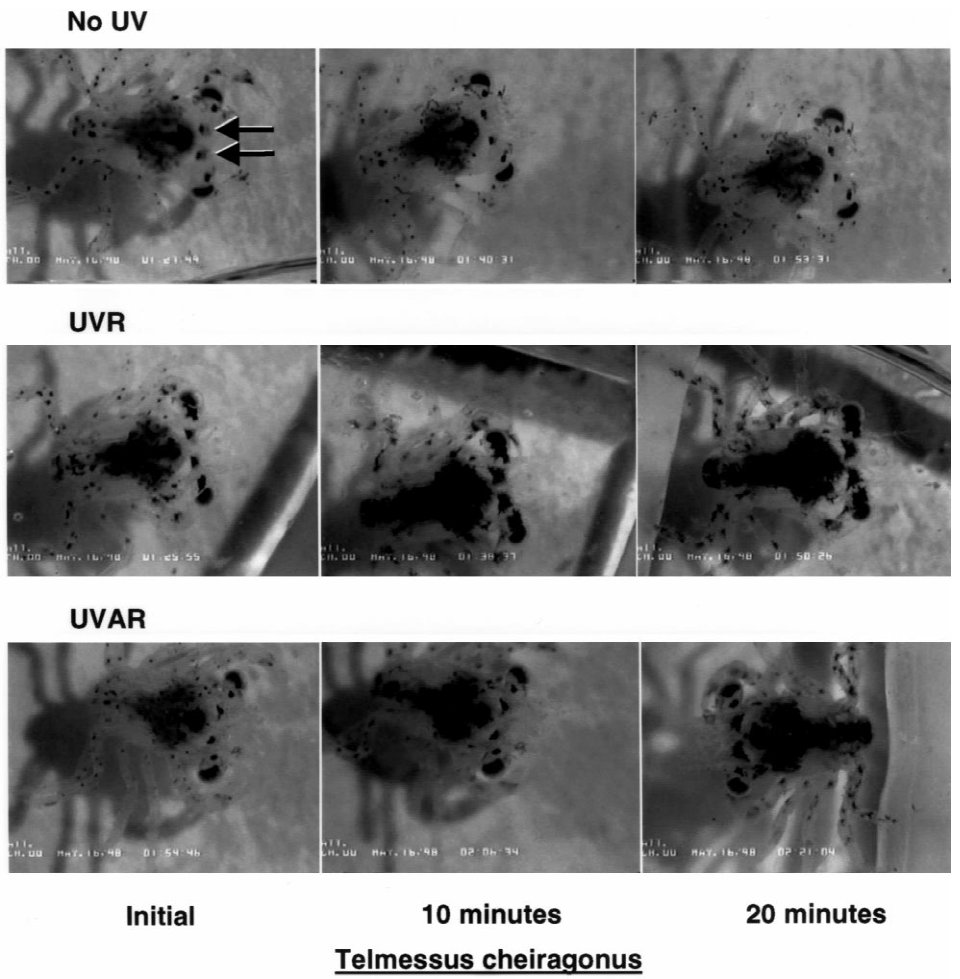

Fig. 2. Chromatophore size of three dark-adapted *Telmessus cheiragonus* megalopae after exposure for 10 and 20 min to No-UVR, UVR, and UVAR. The three images for each treatment are from the same individual. All images are at the same magnification. Arrows indicate the two chromatophores measured. See text for more explanation of the treatments.

the microscope stage and was covered again. After all megalopae were recorded, slides were chosen haphazardly and placed in the appropriate treatments. The starting times of treatments were staggered by 5 min to allow time to take measurements. Megalopae were exposed to a treatment for two 10-min periods. At the end of each period, megalopae were recorded using the previously described method.

2.3. Light experiments

In the first experiment, chromatophore responses to light were measured for both

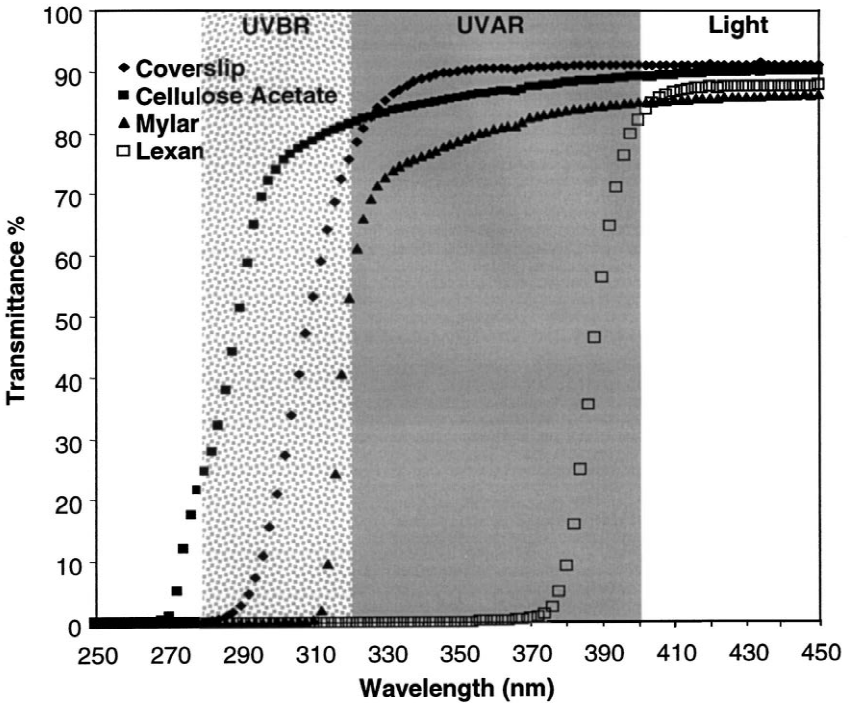

Fig. 3. Percent transmittance data for wavelengths from 250 to 450 nm (similar to the UVA-340 bulbs) for cellulose acetate, glass coverslip, lexan, and mylar.

species. Megalopae either were maintained in darkness, except when they were videotaped for 1–2 s, or they were exposed to light that was emitted by a fiber optics light. The fiber optics light produced light ranging from 400 to 1700 nm with a peak output at 1000 nm. Twelve megalopae of *C. oregonensis* were exposed to each treatment. Ten megalopae of *T. cheiragonus* were kept in the dark and 11 were exposed to light.

2.4. UVR experiments

In the second experiment, chromatophore responses to UVR were measured for *C. oregonensis* megalopae. Twenty-four megalopae were placed under a UVR lamp that held two UVA-340 bulbs (Q-Panel, Cleveland). Four months before our experiment bulb output was measured at 130–160 $\mu W/cm^2$ UVAR and 85–112 $\mu W/cm^2$ UVBR with a newly calibrated UVX Digital Radiometer (UVP, San Gabriel, CA, USA). The lamps generated a UV power spectrum similar to sunlight, emitting no radiation below 292 nm and only small amounts of visible light (Beasley et al., 1996). Megalopae were positioned approximately 50 cm below the lights. Half of the megalopae were placed

beneath a neutral density, cellulose acetate filter that transmitted UVR (Fig. 3). As a control, the other half of the megalopae were shielded from UVR by a 1-mm thick transparent Lexan sheet, which was opaque to UVR but transmitted longer wavelengths (Fig. 3) (Karentz and Lutze, 1990). One megalopa in the No-UVR treatment was mishandled during the experiment and was omitted from the analysis.

Chromatophore responses to UVR were measured for *T. cheiragonus* megalopae following the same protocol, except that a UVAR treatment was added. The objective was to determine whether chromatophores expanded upon exposure to UVBR, UVAR, or both. Because we were unable to measure the responses to UVBR directly, we estimated the response to UVBR as the difference in response to the UVR (UVAR and UVBR) and the UVAR treatments. A filter of 0.1-mm thick polyester film (Mylar, DuPont) screened UVBR but transmitted UVAR (Fig. 3). Six megalopae were placed in each treatment.

2.5. Measurement and analysis

All measurements were made on two chromatophores that were situated on the anterodorsal surface of the cephalothorax (Figs. 1 and 2). These chromatophores were chosen for several reasons. First, contrast between the chromatophores and surrounding body tissue was good. Other chromatophores appeared to expand more in response to radiation, but the poor contrast between chromatophores and underlying organs confounded measurements. Second, the chosen chromatophores were oriented parallel to the plane of focus, which increased the accuracy of measurements taken from two-dimensional images. Third, these chromatophores did not contact other chromatophores when fully expanded, allowing us to measure expansion of a single chromatophore.

NIH image analysis software (Scion Corporation) was used to quantify the area of chromatophores from recorded images. The density slice option in the software package was used to circumscribe chromatophores, and the highlighted area was measured in square micrometers using the auto-wand setting. A stage micrometer was used to calibrate these measurements. Change in chromatophore size after 10 min was calculated by subtracting initial chromatophore size from the chromatophore size after 10 min. Change in size after 20 min was calculated by subtracting initial chromatophore size from the chromatophore size after 20 min. To compare the two species percent change was calculated by dividing the change in chromatophore size by the initial size. A *t*-test compared the change in chromatophore area among treatments when assumptions of normality were met, and a Welch analysis of variance (ANOVA) was used when variances were unequal.

3. Results

3.1. Responses of chromatophores to light

Chromatophores of *Cancer oregonensis* megalopae expanded when exposed to light. Chromatophores of megalopae kept in the dark did not increase in area during the course

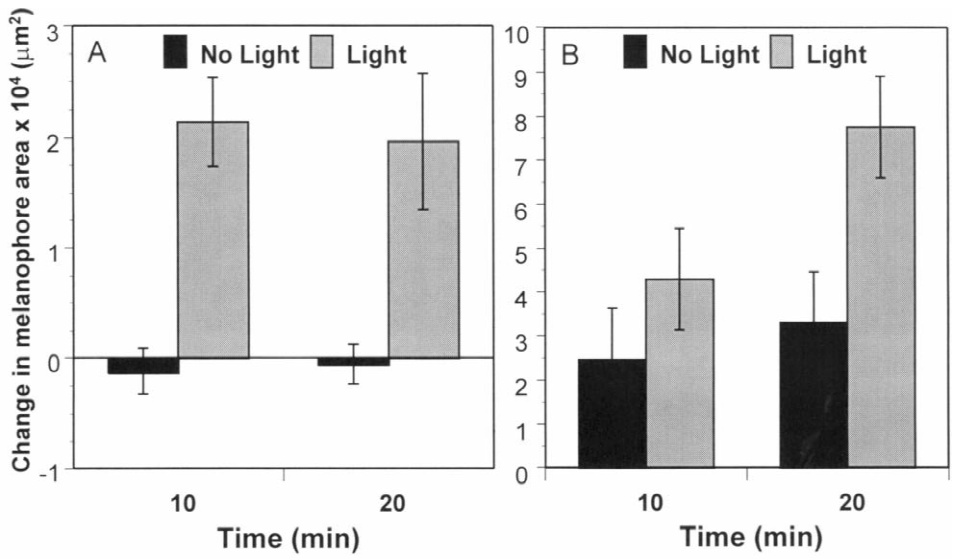

Fig. 4. Change in chromatophore area in response to light (400–1700 nm) for dark-adapted (A) *Cancer oregonensis* ($n = 24$) and (B) *Telmessus cheiragonus* ($n = 21$) megalopae after 10- and 20-min exposures. Error bars indicate standard error. See text for more explanation of the treatments.

of the experiment, whereas those exposed to light more than doubled in size during the first 10 min and did not increase thereafter (Fig. 4A). Chromatophores were fully expanded after 10 min of exposure. The change in chromatophore area of megalopae held in the dark and those exposed to light differed after 10 min (Welch ANOVA = 4.995, $P < 0.0001$) and 20 min (t-test = -3.148, $P = 0.008$) of exposure.

Chromatophores of *Telmessus cheiragonus* megalopae also expanded when exposed to light. As with *C. oregonensis* megalopae, the change in chromatophore area of *T. cheiragonus* megalopae exposed to light was more than twice as large as it was for megalopae maintained in darkness (Fig. 4B). Chromatophores of megalopae kept in the dark increased slightly after 10 and 20 min, whereas those exposed to light more than doubled in size after 10 min and tripled in size after 20 min. As with *C. oregonensis*, the change in chromatophore area of megalopae held in the dark and those exposed to light was different after 10 min (t-test = 3.214, $P = 0.005$) and 20 min (t-test = -3.831, $P = 0.001$).

3.2. Responses of chromatophores to UVR and UVAR

Chromatophores of *Cancer oregonensis* megalopae expanded when exposed to UVR (Figs. 1 and 5A). Chromatophores in the No-UVR treatment expanded slightly, probably because the UVA-340 bulbs emitted some light at wavelengths longer than those cut off by the lexan filter (Fig. 3). The change in chromatophore area was greater in the UVR than the No-UV treatment after 10 (Welch ANOVA = 2.282, $P = 0.04$) and 20 min of exposure (Welch ANOVA = 2.139, $P = 0.05$).

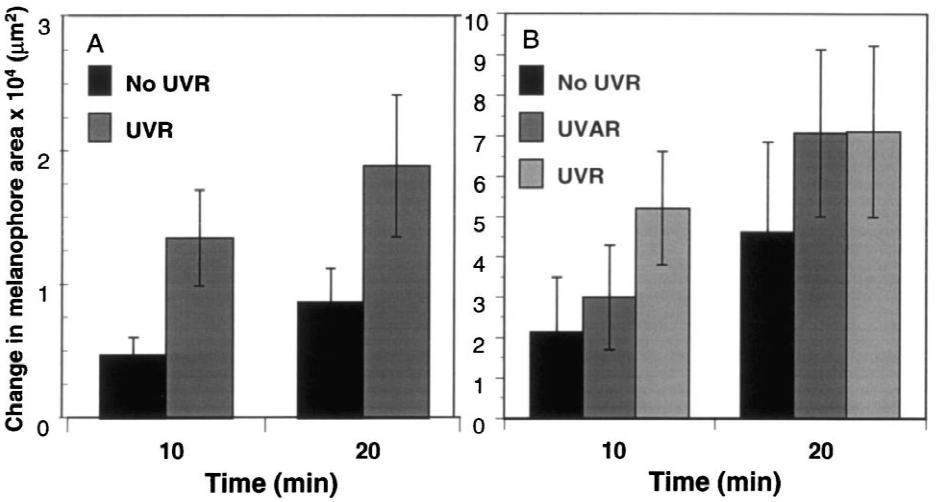

Fig. 5. Change in chromatophore area in response to UVR (280–400 nm) and UVAR (320–400 nm) for dark-adapted (A) *Cancer oregonensis* ($n = 23$) and (B) *Telmessus cheiragonus* ($n = 18$) megalopae after 10- and 20-min exposures. Error bars indicate standard error. See text for more explanation of the treatments.

Chromatophores of *Telmessus cheiragonus* megalopae also expanded in response to UVR (Figs. 2 and 5B). Chromatophores expansion was greatest in the UVR (UVAR and UVBR) treatment followed by the UVAR and No-UVR treatments in descending order. However, these differences were not significant after 10 min (Welch ANOVA = 1.728, $P = 0.23$) or 20 min (ANOVA = 1.709, $P = 0.21$) of exposure, probably due to small sample sizes ($n = 6$) and high variability. Nevertheless, chromatophore expansion (UVR/No UVR) was greater after 10 min for this species than it was for *C. oregonensis*, for which significant differences were obtained (Table 1).

3.3. Comparisons between species

The comparisons of chromatophore percent-change between *Cancer oregonensis* and

Table 1
Chromatophore area in the UVR and UVAR treatments relative to the No-UVR treatment[a]

Time	Treatment ratio	*Cancer oregonensis*		*Telmessus cheiragonus*	
		Ratio of means	Ratio of S.E.	Ratio of means	Ratio of S.E.
10	UVR:No UVR	2.12	2.69	2.45	1.04
	UVAR:No UVR	NA	NA	1.41	0.92
20	UVR:No UVR	2.20	2.11	1.54	0.95
	UVAR:No UVR	NA	NA	1.54	0.82

[a] Ratios were calculated to contrast chromatophore expansion by the two species upon exposure to UVR and UVAR. S.E. represents one standard error. See text for further explanation of the treatments.

Telmessus cheiragonus for the light and UVR treatments were not significantly different after 10 min (light–Welch ANOVA = 0.25, $P = 0.63$; UVR–Welch ANOVA = 2.07, $P = 0.17$) and 20 min (light–t-test = -1.08, $P = 0.2916$; UVR–Welch ANOVA = 1.71, $P = 0.21$).

4. Discussion

4.1. Response to UVR

Chromatophores of both species expanded in response to UVR, as has been reported for larvae of one species of shrimp (Pautsch, 1951) and two species of fish (Hunter et al., 1979, 1981). In these studies, responses were measured after an hour or more of exposure to UVR. In contrast, our study showed larval chromatophores expanded fully after only minutes of exposure to UVR, similar to UVR-responses of adult decapod chromatophores (Coohill et al., 1970).

The ability of postlarvae to adjust chromatophore size in response to both light and UVR suggests that they are adapted to changing levels of UVR during larval life. By responding to UVR directly, larvae are able to adjust chromatophore size appropriately as weather, time of day, latitude, season, and water composition change. As a result, larvae may effectively decrease UVR damage while dispersing over large distances. Furthermore, postlarvae detecting and responding to UVBR should be less vulnerable to ozone depletion as the amount of UVBR that penetrates marine waters increases relative to longer wavelengths.

The ability of larvae to detect UVR appears in several groups of marine organisms, including fish (Hunter et al., 1979, 1981), shrimp (Pautsch, 1951), crab (this study), and echinoids (Pennington and Emlet, 1986). Furthermore, many types of UVR absorbing compounds (sunscreens) are found in a diversity of marine organisms, from archaebacteria to algae to most invertebrates (review, Cockell, 1999). This suggests UVR plays an important role in the evolution of marine larvae.

4.2. Response to light

In addition to UVR, light stimulated chromatophores to expand. The response to light is typical for larval and postlarval chromatophores and has been shown for 12 of 13 species of decapod larvae (Keeble and Gamble, 1904; Pautsch, 1951, 1961, 1965, 1967; Lawinski and Pautsch, 1965; Nagabushanam, 1965; Rao, 1967; Nagabushanam and Sarojini, 1969; Johnson, 1974), all three species of crab megalopae (Johnson, 1974) and both species of fish larvae (Hunter et al., 1979, 1981) tested.

This common response to light prompts the question of why postlarvae are responding to light in addition to UVR. There are two alternative explanations. First, postlarvae may not be able to distinguish among different wavelengths, and may respond to a wide range of wavelengths. This could result from a physiological or evolutionary constraint on the response mechanisms, or weak selection for the ability to distinguish among wavelengths. While our study shows that postlarvae can respond to UVR and light

separately, we do not know if this represents an ability to distinguish between UVR and light, or merely a generalized response to total photon flux. Until we know more about the photoresponse mechanisms of postlarvae, it will be difficult to evaluate this hypothesis.

A second hypothesis is that chromatophores provide more than UVBR protection. One possibility is that chromatophores are effective in reducing the visibility of larvae to planktivorous fishes (Morgan and Christy, 1996). Chromatophores of some decapod larvae can match background colors (Pautsch, 1967) and others emit a blue–green hue, enabling larvae to reduce contrast with the surrounding environment (Morgan and Christy, 1996). Chromatophores are scattered along appendages and around the body, suggesting that disruptive coloration may be an effective camouflage (Morgan and Christy, 1996). Planktivorous fishes feed less effectively as light diminishes (Hobson and Chess, 1978; Zaret, 1980; Lazarro, 1987), and the need for expanded chromatophores would diminish accordingly. In addition, chromatophores might decrease the amount of UVR reflected by the larva decreasing predation by fishes that hunt by detecting UVR. As a result, postlarvae might be best adapted if they can respond to both light and UVR.

Larval chromatophores may also serve a thermoregulatory function. Pigmentation has been shown to warm the internal tissues of copepods (Byron, 1981), and adult crab chromatophores may regulate body temperature (Brown and Sandeen, 1948; Powell, 1962; Wilkens and Fingerman, 1965; Rao, 1969). Unlike adult crabs, larvae probably do not generally experience lethal temperatures, due to buffering by the surrounding water. Any increase in body temperature due to chromatophore expansion in response to light would thus have primarily positive effects, such as decreased development time. Most chromatophores occur on the dorsal surface, so those larvae swimming in a normal upright position would absorb sunlight most effectively. Chromatophores along the ventral surface would absorb backscattered radiation or incident radiation when larvae assume another orientation. Since chromatophores contract as light decreases, there may be a cost to expanded chromatophores in low light that overrides thermoregulatory function.

Megalopae of both study species were collected from a large surface swarm in broad daylight. Plankton surveys have recorded *Cancer* spp. megalopae in the neuston during the daytime, but they generally occurred deeper in the water column near mid-day on bright sunny days and in clear water when light intensities were highest (Shanks, 1986; Jamieson and Phillips, 1988; Shenker, 1988). Megalopae and larvae of other crabs and fishes also are abundant in the neuston during the daytime (McConaugha, 1988; Matthews, 1995; Lobue, 1996), especially in surface slicks generated by internal waves (Shanks, 1983, 1986, 1988). Postlarvae detecting and adjusting chromatophore size in response to UVR as well as light may be better adapted to changing environmental conditions during larval transport. This would be especially important as megalopae move to sunlit surface waters as they migrate to adult habitats.

None of the functions for chromatophores suggested above are mutually exclusive with a UV photoprotective function. The need for UV photoprotection in marine organisms is clear; UVR can kill decapod, fish, echinoid, and gastropod larvae (Ewald, 1912; Hunter et al., 1979, 1981; Damkaer et al., 1981; Damkaer and Dey, 1983;

Pennington and Emlet, 1986; Morgan and Christy, 1996; Hovel and Morgan, 1999; Hoffman pers. commun.) and damages DNA of marine organisms to depths of 20 m (Smith and Baker, 1979; Fleischmann, 1989; Karentz and Lutze, 1990). Moreover, small doses of UVR may have sublethal effects, increasing abnormalities and lengthening development times (Hunter et al., 1979; Anderson et al., 1993; Adams and Shick, 1996). In turn, these effects may increase predation or advection from appropriate adult habitats. Thus, the rapid and full expansion of larval and postlarval chromatophores following even brief exposure to UVR may be adaptive if it does, in fact, confer protection from the deleterious effects of UVR.

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