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Survival of marine larvae under the countervailing selective pressures of photodamage and predation

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Abstract

Unlike most zooplankters, larvae of decapod crustaceans and fish often are pigmented and may hatch and ascend to the sea surface during the day. Chromatophores possibly protect these larvae from ultraviolet radiation (UVR), but may increase their visibility to planktivorous fish. We exposed larvae of four species of tropical crabs to sunlight and to planktivorous fish in the field to address this paradox. Most lightly pigmented larvae of three species died from exposure to sunlight within 1 d, and 94–97.5% of them died after 2 d. The more darkly pigmented *Pachygrapsus transversus* larvae survived significantly better; only 57% of them died after 2 d of exposure to sunlight. These darkly pigmented larvae survived encounters with fish as well as or better than larvae of two other species that did not have large melanophores. Larval chromatophore systems may block UVR without greatly increasing the visibility of larvae to fish. Larvae that migrate from adult habitats to nursery grounds in surface waters throughout the day likely have chromatophore systems that are effective against both of these countervailing selective pressures; however, increasing UVR may stress larvae. The timing of larval release relative to the diel cycle was not related to the susceptibility of larvae to photodamage.

Visual predation in heterogeneous terrestrial and benthic habitats has resulted in distinctive variously colored prey that are inconspicuous in their native surroundings (McFall-Ngai 1990). In contrast, predators in the pelagic realm view their prey against a more homogeneous background, and most zooplankters look and behave somewhat alike. They are small and transparent, and migrate from productive surface waters during the day (McFall-Ngai 1990). These traits are believed to reduce predation by planktivorous fish (Hobson and Chess 1978; Zaret 1980; Lazarro 1987). Despite the prevalence of transparency, pigmented zooplankters occur in most marine habitats and deep lakes, where they descend from bright productive surface waters to dimmer deeper waters. This refuge is not available in shallow ponds, where bright red copepods often are replaced by inconspicuous pale green or blue morphs (Hairston 1979; Luecke and O'Brien 1981; Byron 1982). Pale morphs may not be widespread because they are more susceptible to photodamage from ultraviolet (UVR) radiation. In lakes that do not contain fish, heavily pigmented zooplankters remain in productive near-surface waters during the day and have higher reproductive outputs (De Meester and Beenaerts 1993; Duncan et al. 1993). Thus, zooplankters may minimize both predation and photodamage by avoiding brightly illuminated waters, but at the cost of reduced reproductive output.

Decapod crustaceans and fish are exceptional because their pigmented larvae often develop in sunlit surface waters where they are exposed to both predation and photodamage. This apparently paradoxical phenomenon is hard to explain. Numerous large melanophores (brown-black chromatophores) may protect these larvae from UVR (Hunter et al. 1981; Moser 1982), but they also should make larvae conspicuous to planktivorous fish. This paradox would be resolved if larvae possessed complex chromatophore systems that blocked UVR without increasing their visibility to fish. Many decapod larvae do have multicolored pigment systems that apparently enable larvae to change color and blue-green reflective pigments that obscure dark chromatophores. Although complex chromatophore systems were described long ago (e.g. Lebour 1928; Aikawa 1929), their possible significance has not been examined.

We investigated this paradox by measuring the survival of tropical larvae that were exposed to both UVR and planktivorous fish. UV intensities near the equator are twice as high as at temperate latitudes and are strong year-round (Calkins and Thordardottir 1980; Hardy and Gucinski 1989). UVR and visible light also penetrate more deeply in clearer tropical waters than in temperate waters (Lythgoe 1979; Calkins and Thordardottir 1980). Therefore, traits that protect surface-dwelling larvae from both UVR and planktivorous fish should be especially apparent in tropical species.

We chose to study four species of tropical intertidal crabs that have variously pigmented larvae (Fig. 1, Table 1). If UVR is an important cause of mortality, then more larvae exposed to UVR should die than those shielded from it, larvae with extensive melanophores should survive exposure to UVR better than larvae with small, lightly colored chromatophores, and larvae with large melanophores should be more likely to hatch during the day than lightly pigmented larvae. Many newly hatched larvae are positively phototactic or negatively geotactic (Thor-

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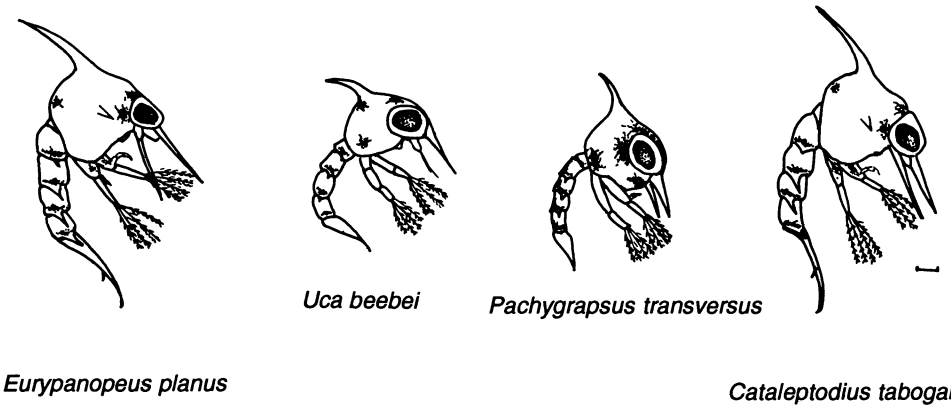

Fig. 1. Larvae of four species of crabs from Panama. Chromatophores are representations and do not reflect their precise location and number. Scale bar = 0.1 mm.

son 1964; Sulkin 1984; Forward 1988), and larvae having large melanophores may be better protected upon entering sunlit surface waters. Therefore, darkly pigmented *Pachygrapsus transversus* larvae should be less susceptible to UVR and more likely to hatch during the day than larvae of the other three species.

If chromatophores increase the vulnerability of larvae to planktivorous fish, then darkly or brightly pigmented larvae should be more conspicuous and eaten more often than lightly pigmented larvae. *Eurypanopeus planus* larvae should be eaten least often because they are transparent except for small black-green chromatophores that impart a green hue to the larva. If these traits reduce larval conspicuousness, then larvae may hatch during the day and ascend to well-lighted waters without experiencing heavy predation. Brownish yellow *Uca beebei* larvae should be intermediate in vulnerability, and red *Cataleptodius taboganus* and darkly pigmented *P. transversus* larvae should be most vulnerable to predation. These conspicuous larvae should hatch at night and avoid surface waters during the day to avoid predation.

Thus, mortality from the countervailing selective pressures of UVR and planktivorous fish should be inversely related to the amount and color of larval pigments. Darkly pigmented *P. transversus* larvae should be least susceptible to UVR but should be one of the two species most vulnerable to predation. In contrast, lightly pigmented *E. planus* larvae should be least vulnerable to predation but should be among the three species most vulnerable to UVR.

Methods

Timing of larval release—Ovigerous crabs of all four species were collected during low tides from intertidal habitats near Naos Marine Laboratory on the Pacific coast of Panama. Hatching patterns relative to the L/D cycle were determined in the field; the methods and results are described elsewhere (Morgan and Christy 1995). Briefly, ovigerous crabs of each species were isolated inside boxes anchored in the intertidal zone amid natural populations of the species. Boxes were covered with removable Plexiglas tops, and screened holes permitted water exchange. Water was pumped from boxes into a plankton net every 30 min while boxes were inundated. The study was concluded when all crabs inside the boxes released larvae. Because larval release was observed over a tidal cycle, the effects of tidal variation were reflected in day-night hatching patterns. Hatching was quantified by counting larvae in each sample or by measuring the amount of larvae volumetrically in graduated test tubes. The total

Table 1. Expected and observed susceptibilities of tropical crab larvae to photodamage and predatory fish relative to the color and size of larval chromatophores.

	Chromatophores		Suscept. to UVR			Suscept. to fish	
			Expected				
	Color	Size	Color	Size	Obs.	Expected	Obs.
Eurypanopeus planus	Black-green	Small	Low	High	High	Low	Low
Uca beebei	Brown-yellow	Small	Low	High	High	Low	Moderate
Pachygrapsus transversus	Dark brown–Yellow-green	Large	Low	Low	Low	High	Moderate
Cataleptodius taboganus	Red	Small	High	High	High	High	High

Table 2. Percentage of larvae released during daylight and darkness (1800–0600 hours) by four species of crabs that inhabit the intertidal zone along the Pacific coast of Panama. The brief crepuscular periods were considered darkness because light is further reduced underwater. Total number of crabs monitored—*n*; total number of days hatching was observed—days.

	Larvae released (%)			
	Daylight	Darkness	*n*	Days
Eurypanopeus planus	83.3	16.7	82	20
Uca beebei	97.6	2.4	129	14
Pachygrapsus transversus	64.7	35.3	134	16
Cataleptodius taboganus	6.4	93.6	30	10

number of crabs examined, duration of observation periods, and percentage of crabs releasing larvae in daylight and darkness are presented in Table 2.

Larvae were obtained by isolating and maintaining ovigerous crabs at ambient seawater conditions (~30°C and 35‰) in flowthrough outdoor tables from October–November 1987. Larval release overlapped biweekly for 2 or 3 d (1–3 d after full and new moons), so that newly hatched larvae of all species could be obtained on the same day and exposed simultaneously to UVR and planktivorous fish.

UV experiments—We exposed 54 newly hatched zoeae of each species to natural sunlight, shielded 54 of their siblings from UVR, and counted the number of larvae surviving in each treatment after 24 and 48 h. This exposure closely simulated that of free-living larvae at the sea surface to all wavelengths of UVR, which is important because UV-A irradiance may stimulate repair of tissues that have been damaged by UV-B irradiance—the most harmful form of UV light. Larvae from the same brood were allocated among treatments to reduce variance in survival. Larvae for each treatment were held separately in several clear plastic compartmented trays (21 × 1.3 × 3.5 cm). These trays were placed in two flowthrough seawater tables on the laboratory dock and exposed to direct sunlight throughout the day. Brown walls of the seawater tables were covered in sediment and algae, which limited reflection of UVR. One seawater table was shielded from UVR by a 6-mm-thick transparent acrylic plastic sheet that was opaque to UVR but transmitted 90% of light at longer wavelengths (Jokiel and York 1982). Replicate UV and no-UV treatments alternated between tanks to avoid unforeseen confounding effects in the two seawater tables. The plastic sheet was raised 10 cm from the top of the seawater tables to permit air to circulate. Seawater pumped from the Bay of Panama into the tables kept water inside the trays within 1°C of ambient seawater temperatures. Therefore, air cooling and high exchange rates of water prevented the UV-opaque sheet from inducing a greenhouse effect. Seawater tables overflowed so that trays floating on the surface would not be shaded by table walls. Lids of all trays were closed during occasional rain showers. Surviving larvae were counted 24 and 48 h after experiments began. Larvae were fed *Artemia* (Great Salt Lake brand) nauplii and provided with clean water daily.

The experiment was conducted four times: twice on clear sunny days and twice on overcast rainy days. The effect of UV intensity on larval survival was determined by comparing results of trials conducted on sunny and overcast days. However, UV intensity was not measured. Data were arcsin square-root-transformed, and the effects of UVR and weather on larval survival was analyzed by ANOVA.

Predation experiments—Feeding trials were conducted in the Bay of Panama in 19-liter (48 cm high × 27 cm diam) clear glass carboys to provide nearly natural lighting for fish to select prey. One hundred newly hatched larvae (<12 h old) of each species (400 larvae in total) were fed simultaneously to 30–40-mm-long (SL) silversides, *Hubbesia gilberti,* in each of 10 carboys. This fish was chosen because it is common along shorelines where these larvae are released and because silversides of this size commonly eat crab larvae (Morgan 1990). Fish were not fed 24 h before experiments to standardize hunger level. To accustom them to their surroundings, fish were placed individually in carboys with filtered seawater the night before they were fed larvae. Carboys were suspended either 0.5 or 2.5 m below the surface and within 100 m of shore. Silversides fed for 3–6 h between 0930 and 1630 hours. The length of time that fish fed was adjusted between trials to maximize the number of fish that consumed between 20 and 80% of the crab larvae. We did not include fish that ate too few crab larvae, due to stress for example, or too many crab larvae, causing larvae of only one species to remain, thereby obscuring preferences for the other species. Hence, we varied the duration of trials to standardize the number of larvae consumed; the number of trials conducted at each depth depended on how many replicates were excluded from analysis. Thirteen trials were conducted at 0.5-m depth and 20 trials at 2.5-m depth. Five trials at each depth were conducted concurrently. In addition, 100 larvae of each species were added to three carboys without fish and these carboys were suspended at each depth for 6 h. All larvae (100%) were recovered from fishless controls. Larvae were recovered by collecting them on a 230-μm-mesh sieve.

Data were log-transformed, and ANOVA was used to detect interspecific differences in larval survival at the two depths. We then did a planned comparison of mean larval survival among species.

Results

Timing of larval release—P. transversus, U. beebei, and *E. planus* commonly released larvae throughout the day, and *C. taboganus* primarily released larvae at night (Table 2). The timing of larval release relative to lunar, tidal amplitude, and tidal cycles is presented elsewhere (Morgan and Christy 1995). Briefly, larval release by all four

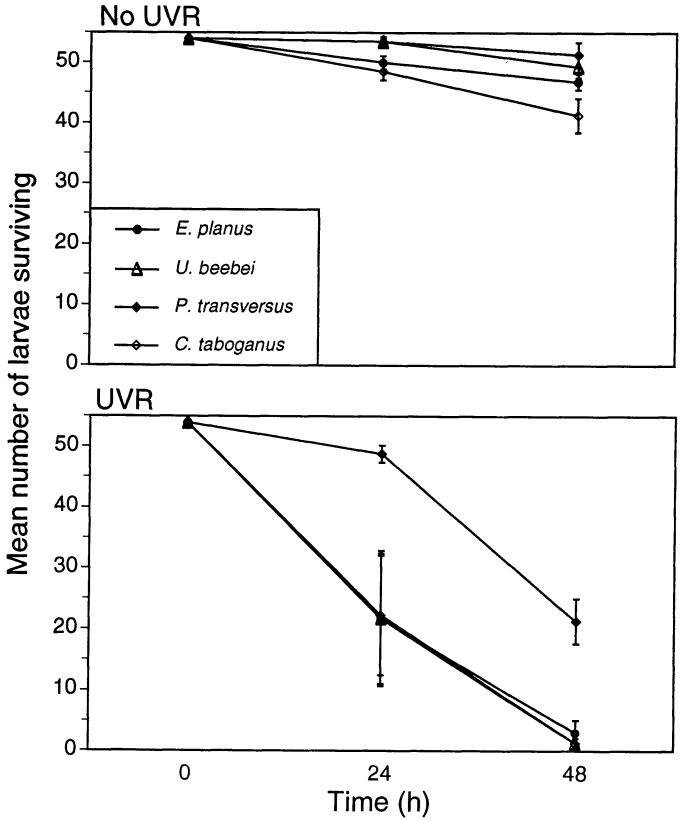

Fig. 2. Mean survival (±1 SD) of four species of crab larvae that were either exposed to sunlight or shielded from UVR for 48 h.

species peaked within 1 h of high tide. *E. planus* hatched asynchronously relative to the lunar and tidal amplitude cycles, and larval release by the other three species peaked biweekly within several days of spring high tides and new and full moons.

UV experiments—Most larvae died after 1 d of exposure to sunlight and survived well when they were shielded from UVR (Fig. 2, Table 3). After 2 d, 94.0–97.5% of *E. planus, U. beebei,* and *C. taboganus* larvae died from exposure to sunlight; only 8.8–23.6% of those shielded from UVR died. *P. transversus* larvae survived significantly better: 57% died when exposed to direct sunlight, whereas only 5.1% died when shielded from UVR. Therefore, UVR clearly is detrimental to crab larvae that occupy surface waters soon after they are released. Furthermore, larval survival was affected by UV intensity. Larvae of all species initially survived better on cloudy days than on bright, clear days, but even under cloudy conditions, few larvae survived after 2 d (Fig. 3, Table 3).

Interspecific differences in larval survival were not related to chromatophore color alone. Two of the three species bearing melanophores (*E. planus, U. beebei*) survived as poorly as did red *C. taboganus* larvae (Fig. 2, Table 3). However, large melanophores may enhance survival, because *P. transversus* larvae survived better than did larvae of the other three species that have small, variously colored chromatophores.

Table 3. ANOVA of the survival of four species of crab larvae that were either exposed to or shielded from UVR for 48 h on overcast and sunny days.

Source	df	MS	*F*	*P*
UVR	1	1,3081.53	912.00	<0.001
Weather	1	0.03	<0.01	0.963
Species	3	336.45	23.46	<0.001
UVR × weather	1	132.03	9.20	0.008
UVR × species	3	118.20	8.24	0.002
Weather × species	3	10.87	0.76	0.534
UVR × weather × species	3	9.03	0.63	0.604
Error	16	14.34		

Predation experiments—Results of feeding trials generally matched the predicted relationship between pigmentation and larval vulnerabilities (Table 1). However, the most darkly pigmented larvae (*P. transversus*) were not eaten most often (Fig. 4). Silversides ate significantly more red *C. taboganus* larvae than brown *U. beebei* or *P. transversus* larvae ($F = 10.14$; df = 1, 128; $P < 0.002$) or green *E. planus* larvae ($F = 26.31$; df = 1, 128; $P < 0.001$). Furthermore, fish preferred *U. beebei* and *P. transversus* larvae to *E. planus* larvae ($F = 7.45$; df = 1, 128; $P = 0.007$). Fish fed longer at 0.5 m than they did at 2.5 m (5.4±0.7 vs. 3.4±0.5 h), and they ate significantly more at the shallower depth ($F = 39.31$; df = 1, 124; $P < 0.001$). Although preferences of silversides for larvae of all four species did not differ significantly be-

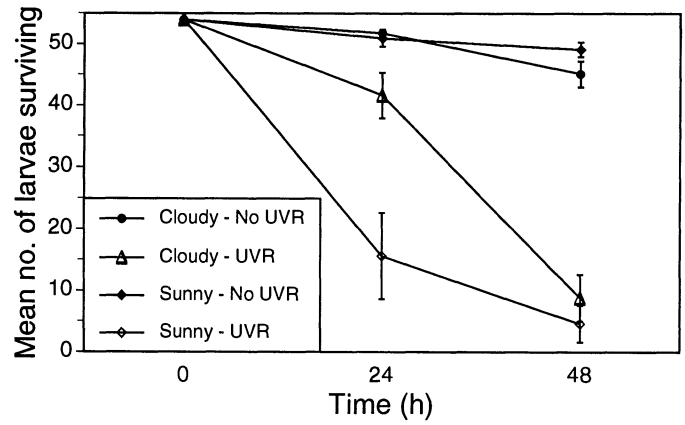

Fig. 3. Mean survival (±1 SD) of four species of crab larvae that were either exposed to sunlight or shielded from UVR for 48 h on cloudy and sunny days. Results were combined to emphasize the effect of weather conditions on survival (*see Table 3*).

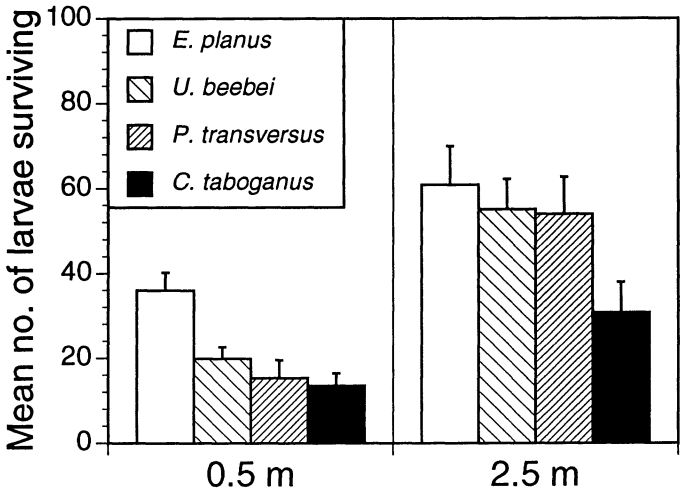

Fig. 4. Mean survival (±1 SD) of crab larvae that were fed to silversides, *Hubbesia gilberti*, 30–40 mm long for 3–6 h at depths of 0.5 and 2.5 m in the Bay of Panama.

tween depths ($F = 2.47$; df = 3, 124; $P = 0.07$), there was a tendency for more *U. beebei* and *P. transversus* larvae to be eaten at the shallower depth (Fig. 4).

Discussion

Chromatophore systems may enable larvae to disperse in surface currents without succumbing to the countervailing selective pressures of UVR and predation; chromatophores may block damaging radiation without greatly increasing the visibility of larvae to planktivorous fish. Thus, the seemingly paradoxical presence of conspicuous pigmented larvae in surface waters may be resolved by recognizing the complexity of larval chromatophore systems. This conclusion was derived from the following evidence.

Exposure to UVR rapidly killed crab larvae, but large melanophores apparently reduced mortality rates. Similar results have been obtained for fish larvae. Heavily melanic fish larvae survived exposure to UVR in the laboratory better than did species with more lightly pigmented larvae (Hunter et al. 1979, 1981; Moser 1982). These dark fish larvae develop closer to the sea surface and when seasonal UV intensities are higher than do species with less pigmentation. Chromatophores in both decapod and fish larvae often are situated over vital organs and may absorb UVR. These larvae also could have more UV-absorbing mycosporinelike amino acids, as do other marine organisms (Schick et al. 1992), or better photorepair mechanisms. When decapod larvae received an overdose of UVR, damaged tissues are repaired (Damkaer and Dey 1983). Thus, larval mortality from UVR has been demonstrated, and potential adaptations to reduce photodamage are evident.

Although the most darkly pigmented larvae were best protected from UVR, they should have been most visible to predators. However, fish ate *P. transversus* larvae least often. These larvae have a highly reflective blue-green layer that overlies and may mask large melanophores in the cardiac region. Furthermore, *P. transversus* larvae seem to change color between dark brown and yellow-green phases, but even in the dark brown phase, these polychromatic chromatophores tinge the larvae green. Larvae may darken when exposed to intense UVR in neustonic or near-surface waters while their blue-green reflective layers and greenish hue reduce their conspicuousness to fish. As UVR attenuates in deeper, less brightly lit waters, larvae may lighten and become even less visible to fish. Thus, changes in the selective regime of the upper water column may be accommodated by polychromatic pigment systems that protect larvae from UVR while reducing their conspicuousness to predatory fish.

Chromatophore masking may be common among crab larvae. Blue-green reflective layers are positioned above chromatophores in larvae of species other than *P. transversus* (Wear 1970). Even more widespread are polychromatic chromatophores that seem to have several color phases (Wear 1970; Webber and Wear 1981). Chromatophores of some larvae and postlarvae have been shown experimentally to respond to light (Nagabushanam 1965; Pautsch 1967; Johnson 1974) and match background colors (Pautsch 1967). In other species, chromatophores imbue larvae with an overall hue that differs from the individual colors of their chromatophore pigments (Table 1). For example, the black-green chromatophores of *E. planus* appear mostly black, but impart a distinct green cast to the larvae. These larvae were eaten least often, perhaps because their greenish color renders them cryptic against the background spectral radiance of coastal waters (Lythgoe 1979). Moreover, regardless of chromatophore color, all crab larvae we observed under artificial light emit a green iridescence that may result from light refracting through exoskeletons (Neville 1975), which could reduce the visibility of all crab larvae to planktivorous fish.

Selection for pigment systems that reduce the conspicuousness of larvae may be strong. Our feeding trials demonstrated that fish select the most conspicuous larvae rather than those defended by the longest spines. If long spines best protected crab larvae from planktivorous fish (Morgan 1989, 1990), then silversides should have eaten more poorly defended *U. beebei* and *P. transversus* larvae than well-defended *C. taboganus* and *E. planus* larvae. However, the two large spiny larval types were the most (*C. taboganus*) and least (*E. planus*) preferred prey, probably due to differences in their visibility. Conspicuous red *C. taboganus* larvae were eaten much more often than cryptic pale green *E. planus* larvae. Interspecific differences in antipredatory behaviors are unlikely to explain the results of feeding trials because crab larvae do not attempt to evade or escape fish (Morgan 1989, 1990).

Elaborate pigment systems may be common in species that develop near the sea surface because exposure to both countervailing selective pressures is high. Of the four study species, *P. transversus* likely remains highest in the water column during the day. The chromatophore systems of this species were most complex and best protected the

larvae from UVR while affording moderate protection from predatory fish. The high mortalities of the other three species suggest that none of these larvae normally is exposed to high doses of UVR. However, the relative vulnerabilities to planktivorous fish indicate that cryptic *E. planus* larvae occur highest in the water column during the day, and highly conspicuous *C. taboganus* larvae develop deepest in more dimly lit waters. Attempts to test these predictions by determining the vertical distributions of larvae in the plankton were thwarted because these species could not be distinguished readily from other larvae.

Although UVR may be an important selective factor for dispersive larvae, it may not directly affect reproductive timing by crabs. The timing of larval release relative to the diel cycle and the susceptibility of larvae to photodamage were not related. Larvae of *E. planus* and *U. beebei* that sometimes hatched during the day, survived as poorly as did larvae of *C. taboganus,* which hatched primarily at night. However, UVR may indirectly affect the timing of larval release. UV exposure may favor increased pigmentation, which increases the conspicuousness of larvae to fish and decreases the probability that larvae will be released during the day. Planktivorous fish generally do not feed on larvae at night (Hobson and Chess 1978; Morgan 1990); therefore, vulnerable larvae may be released when predatory fish are more easily avoided. Indeed, highly conspicuous red larvae of *C. taboganus* were eaten most often by fish and hatched only at night, whereas less conspicuous larvae (*E. planus, U. beebei, P. transversus*) were eaten less frequently and often hatched during the day.

Conclusion

Unlike pigmented holoplankters, many marine larvae may require dispersal in illuminated waters to complete their life cycles. By frequenting surface or near-surface waters, larvae may disperse from estuaries in outwelling waters and return by wind-driven surface currents, internal waves, and selective tidal stream transport (Shanks 1983; Epifanio 1988; McConaugha 1988). The proximity to the sea surface and the time spent there during the day varies among species and developmental stage, but clearly some species of crabs and fish cannot avoid UVR and planktivorous fish by migrating to deeper water during the day. Therefore, the importance of UVR as a selective factor should not be discounted despite the rapid attenuation of UVR in marine habitats (Baker and Smith 1982).

Although the deleterious effects of UVR on marine larvae and the photoprotective function of pigments were noted long ago (Ewald 1912; Dehorne 1918; Aboul-Ela 1958), the frequent dismissal of UVR as an important selective factor in the lives of zooplankters may have led to the failure of ecological theory to address the present paradox. Continued dismissal of UVR as an important mortality factor may be imprudent because most of the world's marine harvest relies on species, including many fish, crabs and lobsters, that develop at or near the sea surface where UV intensities are highest (Hardy 1982). Like frogs at high altitudes (Blaustein et al. 1994) and stream insect larvae (Bothell et al. 1994), these marine animals may be harbingers of the deleterious effects of ozone depletion. Although small increases in UVR may not kill larvae directly, they may need additional energy to produce protective pigments, repair damaged tissues, and migrate from productive surface waters. Longer development times may ensue and increase predation or advection from appropriate adult habitats. Detecting sustained declines in marine populations likely will be more difficult than in terrestrial and freshwater habitats due to notoriously variable larval recruitment. Consequently, the most pressing needs are for experimental measurements of UVR on larval survival and development in the field and on the ability of early developmental stages to repair or avoid photodamage.

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