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NOTE

# High survival of neustonic zoea I larvae of American lobster *Homarus americanus* following short-term exposure to ultraviolet radiation (280 to 400 nm)

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ABSTRACT: Ultraviolet radiation (UV-B = 280 to 320 nm; UV-A = 320 to 400 nm) is harmful to the planktonic early life stages of some marine organisms. In the Gulf of St. Lawrence, Canada, measurements of the diffuse attenuation coefficients have indicated that the maximum depth to which 10% of the surface energy penetrates at 310 nm is 3 m. Thus, organisms residing in this surface layer are exposed to UV radiation. During the summer spawning season (May to September), the first zoeal larval stages of the American lobster *Homarus americanus* are present in the first 2 m of the water column during the day. Thus, *H. americanus* larvae are exposed to UV radiation. We incubated stage I larvae of *H. americanus* under an artificial light source that simulated the irradiance conditions measured at a depth of 1 m in the Gulf of St. Lawrence waters near solar noon. Three spectral exposure treatments were used: (1) UV-B+UV-A+PAR; (2) UV-A+PAR; (3) PAR only. Larvae were irradiated for 4 d (2 h $d^{-1}$) and maintained thereafter under a natural photoperiod (fluorescent lamps) until first molt. Mortality was monitored daily throughout the experiment. There were no differences in mortality amongst the 3 spectral treatments. Larvae began dying at the same time and at the same rate independently of the spectral irradiation that they received. Thus, lobster larvae appear to be tolerant of short (2 h) exposures to UV radiation.

KEY WORDS: UV-B · UV-A · Ozone depletion · Estuary and Gulf of St. Lawrence · Secondary production

Although solar ultraviolet radiation (UV-B = 280 to 320 nm; UV-A = 320 to 400 nm) is rapidly attenuated in the water column, it can reach ecologically significant depths (Booth & Morrow 1997). In the estuary and Gulf of St. Lawrence (Québec, Canada), the depth to which 10% of the surface irradiance penetrates at 310 nm is approximately 3 m (Kuhn et al. 1999). During the summer, the water column in this region is characterized by a steep thermocline that develops at 10 to 30 m (Koutitonsky & Bugden 1991). This pronounced stratification, which coincides with periods of high incident solar radiation, acts as a physical barrier, trapping the early life stages of many planktonic organisms near the surface. Consequently, they are exposed to relatively high levels of solar UV-B radiation during the summer months.

The detrimental effects of enhanced UV-B radiation have been demonstrated for aquatic organisms at most trophic levels: bacterioplankton, phytoplankton and macrophytic algae, zooplankton, and ichthyoplankton (see reviews by Holm-Hansen et al. 1993, Siebeck et al. 1994, Häder 1997). Current levels of UV-B radiation are harmful to planktonic crustaceans. Higher mortality, a shift in the sex ratio, reduced fecundity, morphological malformations in the offspring and reduced developmental rates are among the negative effects reported (Karanas et al. 1981, Williamson et al. 1994, Chalker-Scott 1995, Cabrera et al. 1997, Hovel & Morgan 1999, Kouwenberg et al. 1999b).

Decapod crustaceans have complex life cycles with several planktonic larval stages prior to benthic settlement. This planktonic existence can last from days to weeks. In the American lobster *Homarus americanus*, which occurs along the northeast coast of North America (Cobb & Wahle 1994), hatching takes place over a 4 mo period from late May through September (Ennis 1995). In the Gulf of St. Lawrence, stage I lobster larvae are distributed between 0 and 1.6 m during the day (Hudon et al. 1986) and are, therefore, exposed to

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UV radiation. The fact that they are positively phototactic during this stage of their life history (Ennis 1995) suggests that they are well adapted to incident solar radiation. In this study, we tested the hypothesis that the neustonic stage I larvae of *H. americanus* are insensitive to current levels of UV radiation.

**Materials and methods.** Stage I larvae were obtained from lobsters captured at Iles de la Madeleine, Gulf of St. Lawrence, and maintained at the Maurice-Lamontagne Institute (Mont-Joli, Québec, Canada). Larvae were incubated in filtered seawater pumped from the Estuary of St. Lawrence (28.5 psu, 15°C) in 2 round incubators constructed of Nytex (800 µm mesh size). In order to avoid cannibalistic interactions, the incubators were designed so that each larva occupied its own compartment (48, 3 × 3 × 8 cm compartments in each incubator). The incubators were immersed in 10 l buckets filled with circulating seawater, which was changed daily and constantly aerated. This design allowed for water circulation through the incubation container. Larvae were fed daily with frozen *Artemia* (3 larva$^{-1}$). Any uneaten food (from the previous day) was removed from the incubator prior to the introduction of new food items.

Lobster larvae were irradiated under a custom-designed solar simulator (SS). The SS, which has been fully described and optically characterized in Kouwenberg et al. (1999a), consisted of two 1 kW Xenon-arc-lamps (SS-1000X, Spectral Energy, Westwood, NJ) outfitted with optical feedback amplifiers which maintained a constant output. The output optics of the 2 Xenon lamps (see Fig. 1 in Kouwenberg et al. 1999a) were oriented so that their radiative fields overlapped. Arc lamp 1 contained a standard mirror that reflected its entire spectral output (minus the infrared) through to the optics head. Arc lamp 2 contained a dichroic mirror which preferentially reflected wavelengths from 280 to 450 nm. The optics heads of the 2 arc lamps had filter holders into which combinations of optical filters could be inserted, allowing for a variety of spectral exposures and dose rates. The SS's output (that is, the dose rate) was adjusted to mimic that of a sunny summer's day near solar noon (Fig. 1A).

Three spectral exposure treatments were produced by covering two-thirds of each incubator (16 compartments—and lobster larvae—under each third) with different filter materials and leaving the third uncovered. Individuals covered with OP-2™ (Cyro Industries) were exposed only to photosynthetically active radiation (PAR = 400 to 700 nm) = PAR treatment; those covered with 0.05 mm thick type D Mylar™ (Dupont) received UV-A (320 to 400 nm) and PAR radiation = UV-A+PAR treatment; larvae in the unshielded treatment were exposed to the full simulated solar spectrum = UV-B+UV-A+PAR treatment (Fig. 1B). Since the

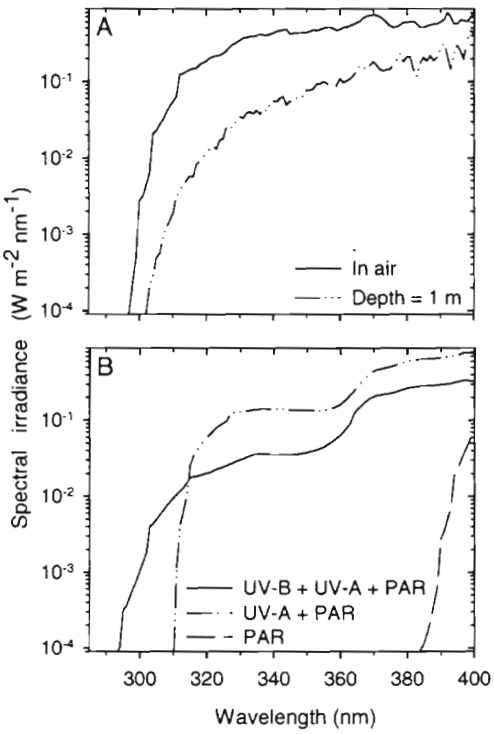


Fig. 1. Irradiance spectra (280 to 400 nm) (A) measured in the air under cloudless skies on 5 August 1996 at 13:05 h Eastern Daylight Time outside the Maurice-Lamontagne Institute, Mont-Joli, Québec, Canada (48° 38' 25.9" N, 68° 09' 21" W) and at 1 m in the Gulf of St. Lawrence (69° 22' 89" N, 48° 10' 39" W) and (B) for the unshielded (UV-B+UV-A+PAR), Mylar™ (UV-A+PAR) and OP-2™ (PAR) exposure treatments

radiative output of the SS was not spatially uniform, the spectral irradiance delivered to the larvae was slightly different at each incubation position in the incubator. However, owing to the small size of the compartments relative to the spectroradiometer's sensor, it was impossible to make spectral measurements for each of them. Instead, only 3 measurements (1 for each spectral treatment) were made (Fig. 1B) using an Optronic Laboratories (Orlando, Florida) OL-754-O-PMT scanning spectroradiometer.

The 48 larvae (all <18 h old and from the same parental cross) in each of the 2 identical Nytex incubators (that is, 2 replicates) were irradiated under the SS for 2 h (first one incubator then, 2 h later, the other) a day on each of 4 consecutive days. During the exposure period, the incubators were positioned so that the larvae were at a maximal depth of 1 cm. The exposure conditions were identical for both incubators.

Immediately after irradiation, larvae were reimmersed in the 10 l buckets filled with newly filtered circulating and aerated seawater in a temperature-controlled chamber. After removal of the filter material, they were illuminated under two 30 W Vita-lite® fluo-

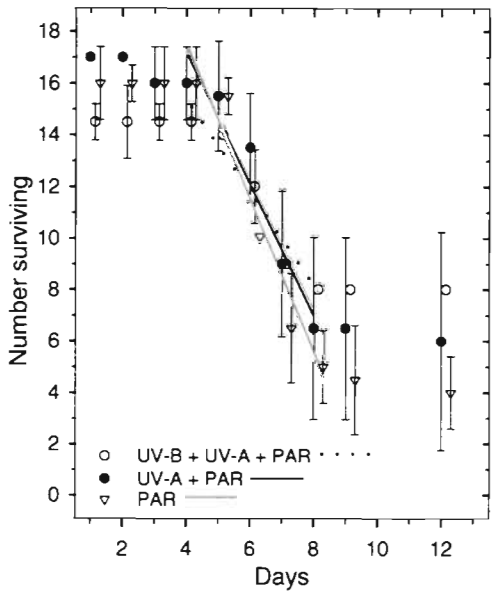


Fig. 2. Number (mean ± SD) of surviving zoea I larvae of American lobster *Homarus americanus* during and after a 4 d exposure (2 h $d^{-1}$) to a simulated solar spectrum. Day 1 (<18 h old larvae) was the first day of exposure and Day 4 the last. Regression lines were fit to the linear decline in survivorship between Days 4 and 8. Points on the *x*-axis have been offset slightly so that the error bars are more clearly visible

rescent lamps (Duro-test, Canada) placed 1.5 m from the larvae on a 10:14 h light:dark photoperiod.

Survival of each larva was monitored daily from the beginning of the experiment through the molt from zoea I to zoea II (at Day 12).

**Results and discussion.** Survival of lobster larvae was not affected by short-term exposure to UV radiation: the number of larvae still alive in the 3 spectral exposure treatments at Day 12 was not significantly different (SAS, Kruskal-Wallis Chi-Square Approximation Test: $\chi^2 = 3.6029$, df = 2, p = 0.1651). Mortality was minimal during the first 3 to 4 d of the experiment, rose significantly between Days 4 and 8, and then stabilized (Fig. 2). The mortality observed within each treatment (between Days 4 and 8) was compared by testing for homogeneity of slopes for the days versus mortality relationship (SAS, General Linear Model Procedure: $F = 3.06$, df = 2, p = 0.0654): there was no significant difference among the 3 spectral exposure treatments, indicating that UV irradiation was not the cause. Mortality in the early life stages of planktonic organisms is often high, since embryos and larvae are susceptible to a variety of physico-chemical and biological stressors (Morgan 1995, Richmond & Woodin 1996). Ecdyses are critical transitions in the life of larval forms (Rabalais & Gore 1985), so zoeae approaching molt are likely more sensitive to less than optimal incubating conditions. This might explain the relatively high mortality observed in all treatment groups between Days 5 and 8—as the larvae approached molt. Alternatively, the growth conditions that we provided might have been suboptimal, or the larvae could have contracted a disease. In any case, since all of the spectral exposure treatments exhibited the same mortality time-line, concluding that the mortality effect was not UVB-induced is tenable.

Some planktonic crustaceans are highly sensitive to UV-B radiation, while others are unaffected (Damkaer et al. 1980, Damkaer & Dey 1982, Dey et al. 1988, Saito & Taguchi 1995). At least to some extent, this difference in sensitivity to UV-B is related to pigmentation. Several authors have reported that pigmented species are more tolerant of UV-B radiation than are unpigmented forms (Ringelberg et al. 1984, Morgan & Christy 1996). However, the pigment composition in crustaceans, and its contribution to UV-B protection, is somewhat unclear. Most of the light-absorbing compounds present in crustacean chromatophores are carotenoid-derived substances, whose spectral absorption peaks lie in the visible waveband (Ghidalia 1985). Therefore, they are not a direct filter against UV-B radiation, but they can still protect cellular molecules from photo-oxidation (Siebeck et al. 1994). Carotenoid pigments are not synthesized by crustaceans but are taken up from the diet and incorporated into the cuticule (Herring 1972). Thus, stage I lobster larvae likely have only small amounts of this form of protective pigment. Other screening compounds might be present. Mycosporine-like amino acids (MAAs), which absorb UV radiation between 310 and 360 nm, have been found in marine planktonic and intertidal copepods, isopods, euphausids, and amphipods (Karentz et al. 1991). It is possible that such pigments are also present in lobster larvae.

At least one of the underlying causes of UV-B-induced mortality, particularly in the early life stages, appears to be damage to the DNA molecule (Hunter et al. 1981, Kouwenberg et al. 1999a,b). Thus, DNA repair mechanisms play an important role in determining an organism's tolerance to UV-B radiation (Zagarese et al. 1997). Photoreactivation, a widespread repair mechanism (Mitchell & Karentz 1993), is triggered by long-wave UV and visible wavelengths and it operates within a relatively short time span (Hearst 1995, Vetter et al. 1999). In our experiment, larvae received photoreactivating light immediately after each irradiation: this might act as a counterbalance to UV-B-induced damage, both in the context of this experiment, and in the wild.

The dose rate delivered to the uncovered treatment group by the SS was 0.221 W $m^{-2}$ in the UV-B and 11.5 W $m^{-2}$ in the UV-B+UV-A waveband: these values are comparable to the 0.151 and 10.48 W $m^{-2}$ measured

at 1 m in the lower estuary and Gulf of St. Lawrence (Kuhn et al. 1999). *Calanus finmarchicus* embryos exposed to this SS for only a few minutes exhibited significant UV-B-induced mortality (Kouwenberg et al. 1999b). Thus, the high survivorship of lobster zoea exposed under this SS indicates that they are, at the very least, far more tolerant of UV-B exposure than are *C. finmarchicus* embryos.

Although the total daily dose would be higher in nature than in this experiment (only 2 h of exposure per day), our results suggest that lobster larvae are well-adapted to the maximal dose rates of this geographic region. This is perhaps not surprising, given that this life history stage has evolved to a neustonic existence. More extensive experiments—using elevated levels of UV-B, longer exposures and a greater level of replication—are required to establish whether lobster larvae are susceptible to the increases in UV-B expected over the coming decades (Fergusson & Wardle 1998, Shindell et al. 1998, Montzka et al. 1999).

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