Impact of solar ultraviolet radiation on hatching of a marine copepod, *Calanus finmarchicus*

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ABSTRACT: The calanoid copepod *Calanus finmarchicus* is a key component of the zooplankton community in the estuary and Gulf of St. Lawrence, Canada. During the spring and summer months, *C. finmarchicus* eggs are released into the shallow (0 to 15 m) mixed surface layer, where they incubate for 1 to 3 d. Radiometric measurements in this region show that biologically significant levels of solar ultraviolet radiation (UV = 280 to 400 nm) penetrate into the mixed surface layer. Thus, *C. finmarchicus* eggs are potentially susceptible to UV-induced mortality. This possibility was evaluated by incubating *C. finmarchicus* eggs in an outdoor reservoir under natural sunlight. There were 3 spectral exposures regimes [UV-B (280–320 nm) + UV-A (320–400 nm) + PAR (400–700 nm); UV-A+PAR; PAR only]. Control groups were kept in the dark. Incubations were conducted at depths of 2 and 60 cm and the percentage of eggs that hatched was determined following 2 to 3 d exposures in 3 independent experiments. Both the UV-B+UV-A+PAR and the UV-A+PAR treatments exhibited low percent hatching compared to the PAR and dark treatments: UV radiation had a strong negative impact on *C. finmarchicus* eggs. Further, percent hatching in UV-B-exposed eggs was not significantly lower than that in eggs exposed to UV-A only: under natural sunlight, UV-A radiation appeared to be more detrimental to *C. finmarchicus* embryos than UV-B. UV penetration into the experimental reservoir was similar to that observed in estuarine waters of this region, but lower than the clearer waters of the Gulf of St. Lawrence. This suggests that, at current levels of exposure, UV radiation has a negative effect on *C. finmarchicus* eggs residing in the first few meters of the water column in this geographic region.

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

INTRODUCTION

Negative effects of solar ultraviolet-B (UV-B = 280 to 320 nm) radiation on bacterioplankton, phytoplankton and macrophytic algae, zooplankton, and ichthyoplankton have all been documented (see reviews by Holm-Hansen et al. 1993, Siebeck et al. 1994, Häder et al. 1995). However, the broader ecological impacts of UV-B remain unclear, as the processes involved are species- and life stage-specific (e.g. Dey et al. 1988, Zagarese et al. 1997), and there are substantial differences between short- and long-term effects (e.g. Bothwell et al. 1993, Cabrera et al. 1997). Moreover, indirect effects can also have significant consequences. For example, UV-B-induced changes in the fatty acid composition of phytoplankton can alter (reduce) its value as a food source for higher trophic organisms (Goes et al. 1994); increased pigmentation in response to UV-B exposure enhances predation risk (Hairsson 1979, Morgan & Christy 1996), and avoidance of the surface layers typically reduces prey encounter rate.

Although UV-B radiation is rapidly attenuated in the water column, it can reach ecologically significant depths (Booth & Morrow 1997). In the estuary and Gulf of St. Lawrence (Canada), measurements of the diffuse
attenuation coefficients for UV-B indicated maximum 10% depths (the depth to which 10% of the surface irradiance penetrates) of 3 m at 310 nm (Kuhn et al. 1999). During the summer, the water column in some regions of the St. Lawrence system is characterized by a steep thermocline (10 to 30 m) which separates the surface mixed layer from a cold intermediate layer (Koutitonsky & Bugden 1991). This pronounced stratification, which coincides with periods of high incident solar radiation, acts as a physical barrier constraining the (non- or minimally motile) early life stages of many planktonic organisms to the shallow mixed layer. Consequently, they may be exposed to relatively high levels of solar UV-B radiation during the summer months.

*Calanus finmarchicus* is a dominant species of the mesozooplankton community in these waters (de Lafontaine et al. 1991, Runge & Pleurde 1996). This copepod plays a key role in the pelagic food webs of the North Atlantic, since its eggs and nauplii are a predominant prey for larvae of several ecologically and economically important fish species. The first feeding larval stages of some stocks of redfish, cod and haddock feed almost exclusively on *Calanus* sp. eggs and nauplii (Kane 1984, Runge & de Lafontaine 1996). Females release their eggs in surface waters, mostly during the spring and summer months (March to September). More than 34% of the eggs are found in the first 4 m of the water column, where they may be exposed to UV radiation (Runge & de Lafontaine 1996, P. Kuhn pers. comm.).

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 altered developmental rates are among the negative effects reported (Karanas et al. 1981, Williamson et al. 1994, Chalker-Scott 1995, Cabrera et al. 1997, Kowenbenk et al. 1999). The role of UV-A radiation (320 to 400 nm) is not as clearly defined, although it appears to be involved in the photorepair of UV-B-induced damage (Sutherland 1981). However, several studies have demonstrated its deleterious effects on aquatic organisms (Cullen et al. 1992, Bothwell et al. 1994, Bass & Sistrun 1997, Williamson et al. 1997). Given that *Calanus finmarchicus* eggs are potentially at risk in their natural environment, we attempted to determine their tolerance to incident UV radiation. Our specific goal was to evaluate the impact of solar UV-B and UV-A radiation on hatching of *C. finmarchicus* eggs.

**MATERIALS AND METHODS**

Eggs were exposed to natural sunlight in a fiberglass reservoir 60 cm high and 122 cm wide (0.701 m³) placed on the grounds of the Maurice-Lamontagne Institute (MLI), Québec, Canada (48°38'25.9"N, 68°09'21.0"W). The reservoir contained seawater pumped from the St. Lawrence estuary and filtered through a series of quartz sand filters (0.8 to 1.2 mm grain size, allowing only particles of <20 to 40 μm to pass). Water in the reservoir was completely replaced approximately every hour.

**Radiometry.** Spectral irradiance (at 1 nm intervals) in the reservoir was measured at the beginning of each experiment using an OL754-O-PMT scanning spectroradiometer (Optronic Laboratories, Orlando, FL) outfitted with a WP470 submersible integrating sphere. Measurements were made at the locations in the reservoir where the incubation tubes were suspended (see below). The instrument was calibrated against a NIST-traceable 200 W tungsten-halogen standard lamp (Optronic Laboratories, model no. OL 752-10) prior to each set of measurements. Ambient terrestrial UV-B radiation (287 to 320 nm at 0.5 nm intervals) was recorded every 30 min by a Brewer MKIII double monochromator spectrophotometer (Sci-Tec Instruments Inc., Saskatoon, Saskatchewan) deployed on the roof of the MLI. The Brewer measurements were used to obtain total daily UV-B irradiant exposure during the course of each experiment.

**Experimental organisms.** *Calanus finmarchicus* females were collected from the St. Lawrence estuary by vertical haul (250 to 0 m) using a 1 m diameter zoo-plankton net (333 μm mesh) deployed at midday. Immediately after capture, gravid females were placed in 10 l buckets (50 copepods bucket⁻¹) filled with newly filtered seawater (0.2 μm pore size, salinity of 28 ± 1 psu), where they released their eggs. The buckets were maintained in a temperature-controlled chamber at 6.5°C. Females were fed once per day on the diatom *Skeletonema costatum* and the filtered seawater in the buckets was replaced every 2 d. This culture of *S. costatum* is not detrimental to hatching success in *C. finmarchicus* (Ban et al. 1997). For Expt 1, females were collected from the estuary 4 wk prior to the egg collections. For Expt 2, females were collected the day before the experiment and the eggs released that same night were those added to the incubation tubes. For Expt 3, eggs were collected from the Expt 2 females.

For each experiment, eggs were collected by siphoning most of the water from the buckets through a Tygon®, hose fitted with a Nytex filter (70 μm mesh size). Females released their eggs at night and eggs were, therefore, collected by 07:00 h so that they were all <6 h old. The remaining water containing the concentrated eggs was then gathered by gently pouring the contents of the bucket into a beaker. Samples were then transferred from the beaker to petri dishes. Eggs were sorted with a glass Pasteur micropipette under a binocular microscope and introduced into quartz incubation tubes (50 eggs tube⁻¹) that had been filled with filtered seawater. We could not filter out all of the fecal pellets pre-
sent in the water from the buckets since the pellets were approximately the same size as the eggs. Thus, there was some organic matter in the tubes together with the eggs. The incubation tubes were 10 cm long and had an inner diameter of 22 mm. They were sealed with plastic stoppers placed over both ends. Thus, there was no water circulation through the tubes.

**Incubation procedures.** Tubes were incubated in the reservoir at depths of 2 and 60 cm. The tubes were suspended horizontally (along their long axis) from racks and the eggs, which were negatively buoyant, rested on the bottom in 1 layer only. 3 spectral exposure treatments were used (at both depths) by covering some of the tubes with UV-blocking filters and leaving others uncovered. Tubes protected with 0.05 mm thick Mylar-D™ (Dupont) were exposed to UV-A and photosynthetically active radiation (PAR = 400 to 700 nm) = Mylar treatment. Those covered with OP-2™ (an acrylic sheet material manufactured by Cyro Industries) received only PAR radiation = OP-2 treatment. Unprotected tubes were exposed to the full solar spectrum = Quartz. The spectral exposure treatments produced by these materials were as expected (Fig. 1A).

In the first experiment, a subset of tubes was incubated simultaneously in a temperature-controlled room (at 7.5°C). They were wrapped with aluminium foil and considered as controls, although the experimental conditions were not identical: temperature was somewhat higher in the outdoor reservoir (9.8 ± 0.6°C at midday) and it fluctuated throughout the day. In Expts 2 and 3, dark controls were placed in the reservoir. However, in Expt 3, the control group was lost, so it could not be included in the analysis. Despite the inconsistencies in these dark control groups, the experiments did all have a consistent relative control—since the OP-2 treatment did not receive any UV radiation, it can also be considered as a control (within the context of an analysis of UV effects).

Three experiments were conducted during the summer of 1997. Details of these incubations are provided in Table 1. The difference in duration of the experi-

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**Table 1.** Duration of daytime (light) and nighttime (dark) exposures (approximations based upon sunrise and sunset times), total incident integrated UV-B irradiance during each experiment (from the Brewer instrument), and water temperature in the experimental reservoir during the outdoor incubations of *Calanus finmarchicus* eggs

<table>
<thead>
<tr>
<th>Expt</th>
<th>Incubation dates and times (1997)</th>
<th>Duration of daytime exposure</th>
<th>Duration of dark exposure</th>
<th>Total UV-B exposure (kJ m⁻²)</th>
<th>Mean temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>14 Jul, 14:45 h–16 Jul, 12:00 h</td>
<td>28 h 32 min</td>
<td>17 h 92 min</td>
<td>175</td>
<td>9.8 ± 0.62</td>
</tr>
<tr>
<td>2</td>
<td>6 Aug, 12:00 h–8 Aug, 09:00 h</td>
<td>25 h 42 min</td>
<td>18 h 48 min</td>
<td>145</td>
<td>9.7 ± 0.0</td>
</tr>
<tr>
<td>3</td>
<td>20 Aug, 12:30 h–23 Aug, 09:00 h</td>
<td>38 h 10 min</td>
<td>30 h 21 min</td>
<td>90</td>
<td>7.8 ± 0.4</td>
</tr>
</tbody>
</table>
RESULTS

Radiometry

The penetration of UV radiation into the reservoir’s water column was slightly greater than that recorded for estuarine waters of the St. Lawrence system (Fig. 2). This was to be expected, since the water input to the reservoir was filtered. However, penetration of UV radiation in the clearer Gulf of St. Lawrence waters was significantly higher than that of the reservoir (Fig. 2). There was essentially no measurable radiation (underwater) below 300 nm.

There was no clear and consistent relationship between daily incident UV-B irradiance and percent hatching in the UV-B-exposed treatment (Table 1, Fig. 3).

Response to solar exposure. In all 3 experiments, spectral exposure had a significant effect on the percentage of Calanus finmarchicus eggs that hatched (Table 2). In general, C. finmarchicus eggs exposed to natural UV radiation (Quartz and Mylar treatments) was not likely a result of their having died and quickly disintegrated, since in test trials it took longer than 2 to 3 d for dead eggs (killed by heat shock) to disintegrate.

Statistical analysis. The percentage of eggs that had hatched at the end of each experiment was calculated for each incubation tube. Percent hatching was arcsine transformed and 2-way ANOVAs (on spectral exposure and depth) were performed on each of the 3 independent experiments to test for any differences among treatments. Since the number of replicates differed amongst treatments, the cell size in these ANOVAs was unbalanced, and this reduced the statistical power of the analyses. If a significant difference was present, Bonferroni multiple comparison tests (Sokal & Rohlf 1995) were conducted in order to isolate the source(s).

<table>
<thead>
<tr>
<th>Expt</th>
<th>Effect</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>Spectral exposure</td>
<td>1</td>
<td>0.004</td>
<td>0.004</td>
<td>1.811</td>
<td>0.190</td>
</tr>
<tr>
<td></td>
<td>Depth</td>
<td>1</td>
<td>0.004</td>
<td>0.004</td>
<td>1.811</td>
<td>0.190</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>3</td>
<td>0.0013</td>
<td>0.0004</td>
<td>0.206</td>
<td>0.692</td>
</tr>
<tr>
<td>2</td>
<td>Spectral exposure</td>
<td>1</td>
<td>0.695</td>
<td>0.695</td>
<td>6.884</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td>Depth</td>
<td>1</td>
<td>0.695</td>
<td>0.695</td>
<td>6.884</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
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<td>0.186</td>
<td>0.066</td>
<td>0.728</td>
<td>0.543</td>
</tr>
<tr>
<td>3</td>
<td>Spectral exposure</td>
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<td>0.14</td>
<td>8.328</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Depth</td>
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<td>0.16</td>
<td>9.518</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>2</td>
<td>0.264</td>
<td>0.142</td>
<td>8.474</td>
<td>0.005</td>
</tr>
</tbody>
</table>

**Table 2. Summary of the 2-way ANOVAs performed on percent hatching of Calanus finmarchicus eggs exposed to natural UV radiation.** Percent hatching was tested against spectral exposure treatment (Quartz, Mylar, OP-2 and controls) and depth (2 and 60 cm) in each of the 3 experiments independently.
Table 3. Summary of the pairwise multiple comparison tests (Bonferroni t-test) performed on percent hatching of Calanus finmarchicus eggs exposed to natural UV radiation. The 3 experiments and the 2 different exposure depths, were analysed separately. When reading down the columns, any pairwise comparison for which different letters are listed were different at the alpha = 0.05 level of probability. For example, in Expt 1, hatching in the Dark and OP-2 treatments was not different but hatching in the OP-2 and Mylar treatments was exhibited lower hatching than those that were protected from UV (OP-2 and dark controls) (Table 3, Fig. 3). This was consistent for all experiments, and at both incubation depths, with the exception of Expt 3 at 60 cm (for which Mylar was not significantly different from OP-2) (Table 3). Further, hatching in UV-B-exposed eggs (Quartz treatment) was not significantly lower than that in eggs exposed to UV-A only (Mylar treatment), except in Expt 3 at 60 cm (Table 3, Fig. 3). Hatching in UV-A-exposed eggs was significantly lower than that in UV-protected eggs (OP-2), except in Expt 3 at 60 cm (Table 3).

There was no statistically discernible effect of incubation depth on percent hatching in Expt 1. In Expt 2, percent hatching in both the Mylar and the OP-2 treatments were lower at the surface than at 60 cm (Bonferroni t-test, p < 0.05). In Expt 3, only percent hatching in the Mylar treatment was significantly lower at the surface than at depth (Bonferroni t-test, p < 0.05).

DISCUSSION

The effects of solar irradiation on Calanus finmarchicus were investigated by Harvey (1930), who found that exposure to direct sunlight decreased their heartbeat. He also observed that blue light was more effective in reducing their heartbeat than either red or green. Several more recent studies have shown that UV-B radiation is harmful to planktonic crustaceans; for example, UV-B radiation decreased survival in copepods (Ringelberg et al. 1984, Dey et al. 1988), in euphausiids, in the larval stages of shrimp and crab.
Although wavelengths as long as 365 nm induce detectable levels of cyclobutane pyrimidine dimers (Setlow 1993), one of the main UV-B photo-products in the DNA molecule (Hearst 1995), the action spectrum for DNA damage indicates that the relative biological response to wavelengths beyond 310 nm is negligible (Setlow 1974).

In this study, there was a significant difference between the UV-exposed (Quartz and Mylar) and the UV-protected (OP-2 and dark controls) treatments: Calanus finmarchicus eggs were highly susceptible to artificial UV-B radiation, particularly in the 280 to 312 nm waveband. However, the exposure conditions in those experiments were different from those in the present work: integrated irradiance in the UV-B waveband was higher than for natural sunlight and eggs were only exposed to UV radiation for a short time (1 h day^{-1}). Nonetheless, the biological weighting function reported by Kouwenberg et al. (1999) reflects strong UV-B effects, as is typical for such weighting functions (Cullen & Neale 1997).

Another possibility is that eggs were killed by longer wavelengths of UV-A radiation. The effect of UV-A radiation on biological systems remains unclear (Sutherland et al. 1992). While its role in DNA photorepair has been well documented (Sutherland 1981, Hearst 1995, Mitani et al. 1996), fewer studies have demonstrated its deleterious effects on aquatic organisms. However, UV-A radiation inhibits photosynthesis in Antarctic diatoms and dinoflagellates, and in freshwater algae (Cullen et al. 1992, Bothwell et al. 1994). Furthermore, UV-A radiation induced a transitory decrease in the metabolic rate of the cichlid fish Cichlasoma nigrofasciatum (Winckler & Fidhiany 1996a), a lower hatching success in embryos of the Japanese medaka Oryzias latipes (Bass & Sistrun 1997) as well as increased mortality in eggs of the yellow perch Perca flavescens (Williamson et al. 1997) and in the freshwater copepod Boeckella gracilipes (Zagarese et al. 1997). Unlike UV-B, UV-A-induced damage does not result from direct absorption of photons by the DNA molecule (Beer et al. 1993). Although wavelengths as long as 365 nm induce detectable levels of cyclobutane pyrimidine dimers (Ahmed & Neale 1997). Pigments such as melanin or the carotenoids are known to act as free-radical scavengers and energy transducers (Hes- ter & Morel 1989 and references therein, Beer et al. 1995). Pigments such as melanin or the carotenoids are known to act as free-radical scavengers and energy transducers (Hesser 1994), but Calanus finmarchicus eggs are unpigmented. Moreover, interaction between UV and dissolved organic matter (DOM) present in the water can also produce reactive oxygen transients which subsequently have cytotoxic effects (Zepp et al. 1987). This mechanism of damage occurs over a relatively longer time frame than direct damage to DNA since it results from cumulative physiological stress. This might explain why Kouwenberg et al. (1999) did not find a UV-A effect: in those experiments, C. finmarchicus eggs received only 1 h of exposure to UV-A per day.

Percent hatching in the dark controls was lower than it is typical for Calanus finmarchicus eggs (approximately 80%, P. Joly pers. comm.). Salinity variations in the reservoir water during the exposure period would not have affected the eggs, since the tubes were closed. Temperature was not monitored throughout the day, but C. finmarchicus eggs are tolerant of a broad range of temperatures (-2 to 20°C, Marshall & Orr 1972)—they were not exposed to extremes in these experiments. One possible explanation for the low percent hatching is that the manipulations in-
volved in the collection and transfer of the eggs at the start of the experiments caused subtle damage to the egg membrane, even though eggs still appeared viable. In Expt 1, in which percent hatching was generally very low, a food quality problem could also be involved. The eggs used in this experiment came from females that had been fed exclusivley on Skeletonema costatum for approximately 6 wk. Although this diatom is not detrimental to the hatching success of C. finmarchicus (Ban et al. 1997), the monospecific diet could have had a negative impact on the biochemical composition of the eggs, and on their viability. The fact that the dark controls in this experiment were kept in the laboratory, yet still exhibited low percent hatching, suggests that the generally low percent hatching in all treatments was related to a problem in the quality of the eggs and not to the experimental conditions (such as low oxygen or disease) in the reservoir incubations.

If the eggs were stressed prior to the outdoor incubations, then any other stress factor (such as UV radiation) could have acted synergistically and exacerbated its effects. There are examples of synergism between UV-B radiation and pathogens (Kiesecker & Blaustein 1995), pH (Long et al. 1995), nutritional status of the exposed organism (Zellmer 1996) and pollutants (Joshi & Misra 1986). UV-A radiation can also interact synergistically with temperature (Winckler & Fidhiany 1996b) and pollutants (Kagan et al. 1987).

Depth affected percent hatching only in the Mylar and OP-2 treatments of Expt 2, and the Mylar treatment in Expt 3. Percent hatching was always lower at the surface. This difference probably results from the attenuation of UV light with depth (Fig. 1). More consistent depth-related differences were likely undetectable as a result of the high variability within each treatment and/or the low percent hatching.

In these experiments, Calanus finmarchicus eggs received ecologically realistic UV dose rates and daily UV doses. The wavelength-specific 10% depth penetrations in the reservoir were similar to those observed in this organism’s estuarine habitat (Fig. 2 and see Kuhn et al. 1999). However, 10% depths in the Gulf of St. Lawrence, where C. finmarchicus is also very abundant, are higher (Fig. 2). Thus, the UV impacts on C. finmarchicus eggs recorded here would underestimate those that might occur in the waters of the Gulf of St. Lawrence. Thus, eggs residing at depths of 0 to 4 m in the natural environments of this region are susceptible to UV radiation. However, our experimental design did not attempt to simulate the vertical mixing dynamics of the surface layer. In an experiment in which vertical cycling was simulated, Zagarese et al. (1998a,b) found that the freshwater cladoceran Ceriodaphnia dubia (a species capable of photorepair) was more susceptible to UV radiation when it was incubated at a fixed depth than when it was artificially mixed in the water column. On the other hand, Boeckella gracilipes, a species without the ability to photorepair, exhibited the opposite response. The difference was apparently due to the photorepair ability of C. dubia. This implies that both vertical mixing and the capacity for photorepair play a major role in the UV tolerance of planktonic organisms. If C. finmarchicus eggs are capable of photorepair, UV exposure would result in less severe net photodamage in their natural environment than the results presented here suggest. We have not as yet tested photoreactivation potential in C. finmarchicus eggs. However, other calanoid copepods do have this capacity (Naganuma et al. 1997, Zagarese et al. 1997).

The results of these experiments suggest that, at current levels of exposure, UV radiation (particularly UV-A) has a negative effect on Calanus finmarchicus eggs residing in the upper layers of the ocean. Additional information on the vertical distribution (at very fine scales in the upper 5 m of their water column) and mixing dynamics of C. finmarchicus eggs, and other planktonic organisms, is needed in order to assess the impact of UV radiation on these planktonic early life stages. The role of UV-A as a deleterious environmental parameter also needs to be more thoroughly investigated.

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