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# Biological weighting of ultraviolet (280–400 nm) induced mortality in marine zooplankton and fish. II. *Calanus finmarchicus* (Copepoda) eggs

**Abstract** The copepod *Calanus finmarchicus* Gunnerus is a key component of the planktonic food web in the Gulf of St. Lawrence, Canada. In this region, productivity-determining biophysical interactions occur in the upper 0 to 30 m of the water column. The eggs and nauplii of *C. finmarchicus* are found in this layer. Measurements of the diffuse attenuation coefficients for solar ultraviolet-B radiation (280 to 320 nm, UV-B) at various locations in this region indicated maximum 10% depths (the depth to which 10% of the surface energy penetrates) of 3 to 4 m at a wavelength of 310 nm. This represents a significant percentage of the summer mixed-layer water column: organisms residing in this layer are exposed to UV-B radiation. Laboratory experiments using a Xenon-arc-lamp based solar simulator revealed that *C. finmarchicus* embryos exposed to UV-B exhibited high wavelength-dependent mortality. The strongest effects occurred under exposures to wavelengths below 312 nm. A significant percentage of nauplii hatched from eggs exposed to these wavelengths exhibited malformations indicative of errors in pattern formation during embryogenesis. At the shorter wavelengths ($< 305$ nm), UV-B-induced mortality was strongly dependent on cumulative exposure. The biological weighting function (BWF) derived for UV-B-induced mortality in *C. finmarchicus* eggs is similar to that reported for naked DNA. This suggests that the UV-B-induced mortality effect on *C. finmarchicus* embryos is a direct result of DNA damage. There was no evidence of a detrimental effect of ultraviolet-A radiation (320 to 400 nm). Calculations based upon the BWF indicate that, under current noon surface irradiance, 50% of *C. finmarchicus* eggs located at or very near (within 10 cm) the ocean surface will be dead after 2.5 h of exposure. Under solar spectral irradiance simulating a 20% decrease in ozone layer thickness, this time drops to 2.2 h. These are first-order estimates based upon irradiance taken at a time of day during which the values would be maximal. Nonetheless, they illustrate the relative changes in UV-B effects that will result from ozone layer depletions expected over the coming decades. It is also important to point out that variability in cloud cover, water quality, and vertical distribution and displacement within the mixed layer, can all have a greater effect on the flux of UV-B radiation to which *C. finmarchicus* eggs are exposed than will ozone layer depletion at these latitudes.

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## Introduction

In early summer, the mixed layer in the northern Gulf of St. Lawrence and Labrador Shelf comprises the upper 0 to 15 m of the water column and is separated from an intermediate layer of colder water ($< 1$ °C) by a sharp thermocline (see references cited in Kouwenberg et al. 1999). This underlying cold water, and the density gradient associated with it, effectively confines biological productivity to the much warmer surface mixed layer (Therriault 1991). Measurements of the diffuse attenuation coefficients for solar ultraviolet-B radiation (280 to 320 nm, UV-B) at various locations in the Gulf of St. Lawrence indicate maximum 10% depths (the depth to which 10% of the surface energy penetrates at a given

wavelength) of 3 to 4 m at a wavelength of 310 nm (Kuhn et al. 1999). This represents a significant percentage of the summer mixed-layer water column.

The planktonic copepod *Calanus finmarchicus* is prominent in the mesozooplankton community of the Gulf of St. Lawrence and Labrador Shelf (Grainger 1963; de Lafontaine et al. 1991). *C. finmarchicus* females release their eggs near the surface, probably during the night and early morning (Runge and Plourde 1996). Thirty to fifty percent of these eggs are present in the surface 0 to 5 m (Runge and de Lafontaine 1996). Larvae of redfish (*Sebastes* spp.), a commercially important stock in the north-central Gulf of St. Lawrence, ingest egg and naupliar stages of *C. finmarchicus* in large numbers in early summer (Runge and de Lafontaine 1996). Later in the summer, these same larvae feed on *C. finmarchicus* nauplii and copepodites (J.A. Runge and Y. de Lafontaine, unpublished observations). Although never rigorously studied, the contribution of *C. finmarchicus* to the diet of larval Atlantic cod (*Gadus morhua*) spawned in the Gulf of St. Lawrence and on the Labrador Shelf is assumed to be similar in importance to the role of *C. finmarchicus* in the diet of arctonorwegian cod larvae in Norwegian coastal waters. This *C. finmarchicus*–redfish (and presumably cod) interaction in the northern Gulf of St. Lawrence occurs in the surface mixed layer.

Some marine copepods are negatively affected by current levels of UV-B radiation (Thomson 1986). UV-B-induced naupliar mortality, reduced survival and fecundity in females, and sex ratio shifts have all been reported (Karanas et al. 1979, 1981; Chalker-Scott 1995; Naganuma et al. 1997). Further, UV-B-induced damage to the DNA of crustacean zooplankton has been detected in samples collected from depths of up to 20 m (Malloy et al. 1997). The effect of UV-B radiation on the early life stages of *Calanus finmarchicus* has never been investigated.

As a consequence of the planktonic distribution of its early life stages, and the hydrography and bio-optics of the water columns in the northern Gulf of St. Lawrence, *Calanus finmarchicus* may be vulnerable to changes in incident UV-B radiation. And, if *C. finmarchicus* is at risk, so are the components of the pelagic food web which are dependent upon it. Here we investigate the potential for UV radiation (280 to 400 nm) to affect the survival and hatching success of eggs of this species. The specific goals of this study were to (1) evaluate the effect of UV radiation on mortality in *C. finmarchicus* eggs, (2) generate dose–response relationships and a biological weighting function (BWF) for the effect of UV on mortality in *C. finmarchicus* eggs, and (3) present a preliminary assessment of the potential impact of solar UV radiation on the early life stages of this key component of the planktonic food web.

## Materials and methods

The methods employed in conducting the experiments reported here are almost identical to those detailed in the preceding paper (Kouwenberg et al. 1999). Thus, they will be presented in abbreviated form, and readers will be referred to the appropriate sections of Kouwenberg et al. (1999) for complete details.

### Radiometry and general experimental procedures

Spectral irradiance was measured with an OL754-O-PMT scanning spectroradiometer (Optronic Laboratories, Orlando, Florida) and *Calanus finmarchicus* Gunnerus eggs were irradiated under a custom-designed Xenon-arc-lamp based solar simulator (SS) (Fig. 1 in Kouwenberg et al. 1999).

*Calanus finmarchicus* eggs were incubated in 150 mm high, 22 mm inner diameter glass tubes filled with 0.2 μm filtered seawater at 28 ± 1 psu (Fig. 1c in Kouwenberg et al. 1999). Eggs were negatively buoyant and so remained near the bottom of the tubes throughout the exposures. Since the irradiance measurements were made at the surface, and the eggs were incubated under 150 mm of water, calculations of irradiance-dependent mortality might have been underestimated. However, this was not the case: with an attenuation coefficient of 1 $m^{-1}$ (or less) for filtered water from the St. Lawrence estuary, and a water column of 150 mm, attenuation in the tubes due to absorbance would have been less than 1.5%.

A total of 34 incubation tubes, each containing approximately 100 *Calanus finmarchicus* eggs, were immersed in a water bath at 6 °C. The bottom of the incubation basin was fitted with a polyethylene holder which contained a slot for each of the incubation tubes. The holder was designed so that it could be positioned at exactly the same orientation under the SS during each exposure. This was important because the SS's output was not spatially uniform. Each incubation tube was covered with a 25 × 25 mm quartz substrate long-pass filter (Schott WG280, WG295, WG305, WG312, WG335, WG360, and GG400), for which the cut-off wavelength is as specified (Fig. 1d in Kouwenberg et al. 1999). There were five tubes for each cut-off filter treatment except for the WG360, which had four. Spectral irradiance [$E(\lambda)$, in W $m^{-2}$ $nm^{-1}$] was measured at 1 nm intervals (250 to 800 nm) under each of the cut-off filters at all 34 tube positions in the incubator. As a result of the spatially non-uniform output of the SS, each of the 34 tubes received a somewhat different dose rate (Fig. 2 in Kouwenberg et al. 1999) and, since the exposures were always of a set duration, a different dose (J $m^{-2}$). The combined filters – those in the SS's optics heads and those on top of each tube – eliminated all UV-C radiation (Figs. 1d and 2 in Kouwenberg et al. 1999). DNA-weighted biologically effective irradiance delivered to the tubes in the WG280, 295, 305, 312 and 335 treatments were calculated as the mean of all the tubes in each of these spectral exposure treatments and compared against natural solar irradiance (see Fig. 3 in Kouwenberg et al. 1999).

### UV irradiation experiments

*Calanus finmarchicus* females, collected from the lower St. Lawrence estuary on 4 September 1996, were maintained in 2 liter glass beakers filled with 0.2 μm filtered seawater (28 ± 1 psu) at 6 °C. Each beaker contained 10 to 15 females, which were fed twice each day on the diatom *Skeletonema costatum* for 1 week in order to increase egg production to maximum values. This strain of *Skeletonema* was not harmful to hatching success of *Calanus* spp. eggs (Ban et al. 1997). Eggs were collected no more than 6 h after being released by females. The embryonic period for *C. finmarchicus* at this temperature is approximately 3 d (McLaren et al. 1988).

There were four different experiments, identical except for the duration of UV exposure. Exposure times for Experiments 1 through 4 were: 2 h $d^{-1}$ for 2 d, 1 h $d^{-1}$ for 2 d, 1 h on 1 d, and 0.5 h on 1 d. The dose rate was the same for all experiments (see Fig. 3 in Kouwenberg et al. 1999). In between exposures, eggs were maintained on a 12 h light : 12 h dark photoperiod, illuminated by two 30 W Vita-Lite (Duro-Test Canada, Inc.) fluorescent tubes placed 1.5 m from the eggs. The spectral output of Vita-Lite lamps includes some long-wave UV-A (320 to 400 nm). The photosynthetically active radiation (PAR; 400 to 700 nm) output of these

lamps, at the position where the eggs were incubated, was 0.03 W m$^{-2}$. For each experiment, there was a control group of eggs drawn from the same population of females. The control group for Experiment 1 consisted of five tubes, each containing approximately 100 eggs, held at 6 °C in the dark. For the remaining experiments, the controls were four or five tubes held under 12 h light : 12 h dark photoperiod (as above).

On the third day following each experiment, the incubation tubes were inspected for the numbers of nauplii and unhatched eggs. Nauplii were examined individually and categorized as dead, alive but deformed (any clear structural abnormality, such as fused, asymmetrical or shortened appendages, etc.), or alive and normal.

### Derivation of the BWF for UV-induced mortality in Calanus finmarchicus eggs

The BWF for UV-induced *Calanus finmarchicus* egg mortality was derived following Rundel (1983) as modified and described by Cullen and Neale (1997).

Data on the differential survival of *Calanus finmarchicus* eggs exposed to varying amounts of UV radiation were fit to a simple exponential model the form of which is:

$$\frac{\text{Egg}(d)}{\text{Egg}(0)} = e^{-(H^* + M \cdot T)} \quad , \tag{1}$$

where Egg(0) is the number of live eggs in any one tube on Day 0, Egg(d) is the number of live eggs in that tube on Day d, $H^*$ (dimensionless) is the sample's biologically weighted radiant exposure, $M$ (s$^{-1}$) is a fitted parameter for non-irradiance dependent mortality and $T$ (s) is the total length of the experiment.

Biologically weighted radiant exposure was calculated as:

$$H^* = t_{uv} \cdot \sum_{\lambda=250}^{800} \varepsilon_H(\lambda) \cdot E(\lambda) \cdot \Delta\lambda \quad , \tag{2}$$

where $t_{uv}$ (s) is the total time of exposure to incident spectral irradiance, $\varepsilon_H(\lambda)$ (J m$^{-2}$)$^{-1}$ is the biological weighting coefficient for radiant exposure and $E(\lambda)$ (J m$^{-2}$ s$^{-1}$ nm$^{-1}$) is the incident irradiance at wavelength $\lambda$ (nm).

$\varepsilon_H(\lambda)$ was calculated according to:

$$\varepsilon_H(\lambda) = C \cdot e^{\{-[m_1 + m_2 \cdot (\lambda - 290)]\}} \quad , \tag{3}$$

where $m_x$ are fitted parameters and $C$ (J m$^{-2}$)$^{-1}$ is a proportionality constant, here equal to one (Cullen and Neale 1997).

The following data from the UV exposure experiments were used in the derivation: the number of healthy nauplii in each of the 34 treatment tubes for each day of the experiment, the corresponding spectral irradiance (250 to 800 nm) for that tube's position (and cut-off filter) under the SS, and the duration of the daily exposure. Results from the 280 and 295 nm cut-off filter treatment groups were excluded from the analysis because mortality in these two groups was almost 100% in all four experiments.

The BWF analysis produces a weighting for each wavelength, constrained only by the exponential form of Eq. 3; it is not restricted to the UV-B waveband. Further, results from every tube – and not the mean of the four or five tubes from each spectral exposure treatment – are included in the analysis.

## Results

### Viability of nauplii from UV-irradiated Calanus finmarchicus eggs

Most *C. finmarchicus* eggs exposed to the shorter UV-B wavelengths (280, 295 and 305 nm cut-off filter treat-

ments) did not hatch (Fig. 1). Even when exposed to UV-B for only 0.5 h, only a small percentage of the eggs hatched (Fig. 1) – of these, many nauplii were dead or deformed (Figs. 1, 2). The hatching success of eggs in the 312 nm long-pass filter treatment group was also affected, although not at the shortest exposure time (Fig. 1). However, many of the nauplii hatching from eggs in the 312 nm treatment group were dead or deformed (Figs. 1, 2). There was no significant difference (Student's *t*-test, $p > 0.05$) in the survival of eggs exposed to both UV-A radiation and visible light (335 and 360 nm treatment groups) and those exposed to visible light only ($> 400$ nm treatment group).

Naupliar viability data were replotted against total dose (unweighted) in order to more effectively assess the dose–response relationships between radiant exposure and mortality in *Calanus finmarchicus* eggs. There was essentially no survivorship in the 280 and 295 nm treatment groups, at even the lowest doses: *C. finmarchicus* eggs are extremely sensitive to UV-B exposure at these wavelengths (Fig. 3). The result was similar for the 305 nm treatment, although there was some hatching success at the lowest doses. However, the nauplii hatched from this group were mostly non-viable (Fig. 1). There was an inverse (seemingly exponential) relationship between total dose and naupliar survival in the 312 nm treatment group (Fig. 3), and most of the nauplii hatched in this group were also viable (Fig. 1). There was no relationship between total dose and naupliar viability in the 335, 360 and 400 nm groups (Fig. 3).

### BWF for Calanus finmarchicus egg mortality

The BWF for UV-induced mortality in *C. finmarchicus* eggs exhibits a typically steep decline against wavelength: the impact of UV-B is more than two orders of magnitude higher at 290 nm than at 320 nm (Fig. 4). Weightings in the UV-A waveband were essentially non-existent.

The principle of parsimony was applied in the BWF analysis: neither irradiance-independent mortality ($M$), nor a second-order term in the wavelength-dependent mortality ($m_3$), significantly improved the fits. Thus, they were not included in the final formulation. The exclusion of these terms is further justified in that $M$ was very low, 8.5 E-7 s$^{-1}$, suggesting that ancillary mortality was insignificant. The BWF parameters for the simplest form of the model, and for the model with a mortality term, are presented for completeness (Table 1).

## Discussion

### Viability of nauplii from UV-irradiated Calanus finmarchicus eggs

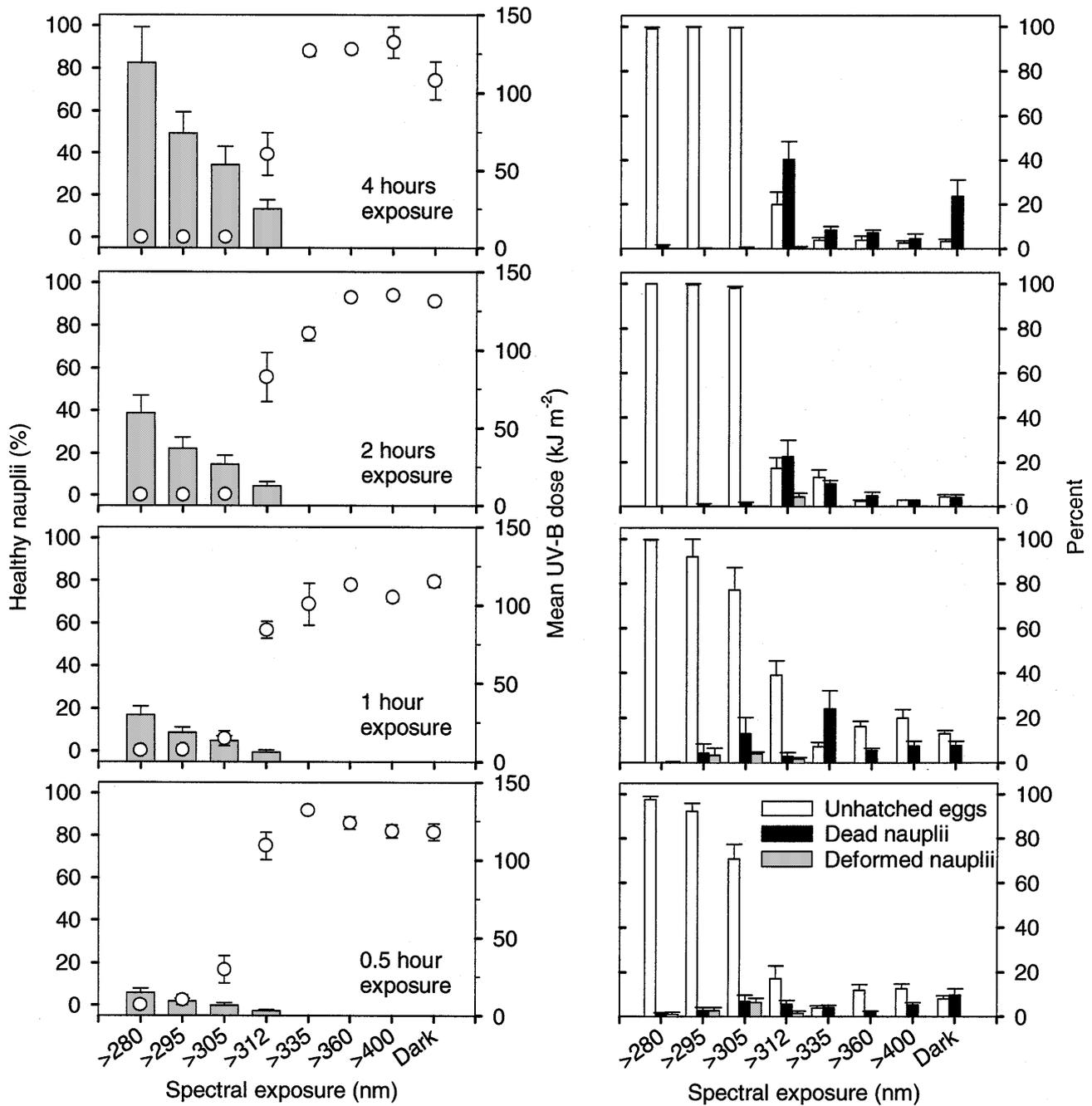UV-B radiation, particularly in the 280 to 312 nm waveband, had a strong negative impact on the survival

**Fig. 1** *Calanus finmarchicus*. Survival of eggs exposed to various spectral wavebands. Each panel on the left side of the figure presents the mean UV-B dose (*shaded bars*) and the proportion of healthy nauplii (*open circles*) hatching from eggs exposed to radiation greater than the specified cut-off wavelength (Fig. 2 in Kouwenberg et al. 1999). Exposure duration was different for each experiment, as noted in each panel. The panels on the right present the percentage of unhatched eggs and also the proportion of nauplii that hatched but were dead or deformed. Proportions are percentages of the initial number of eggs in each tube. Mean values ± standard error bars

**Table 1** Parameter values for the biological weighting function fit to *Calanus finmarchicus* egg mortality data ($M^*$ was set to zero)

| Parameter | Lower 95% | Fitted value | Upper 95% | $r^2$ |
|---|---|---|---|---|
| Without irradiance-independent mortality | | | | |
| $m_1$ | 6.380 | 6.697 | 7.014 | |
| $m_2$ | 0.120 | 0.139 | 0.158 | |
| $M^*$ | 0.000 | 0.000 | 0.000 | 0.740 |
| With irradiance-independent mortality | | | | |
| $m_1$ | 6.572 | 7.083 | 7.596 | |
| $m_2$ | 0.108 | 0.134 | 0.160 | |
| $M$ | 5.40E-07 | 8.50E-07 | 1.16E-06 | 0.756 |

of *C. finmarchicus* eggs, even over short exposure times (Fig. 1) and low total doses (Fig. 3). At the shorter wavelengths (<305 nm) UV-B-induced mortality was strongly dose-dependent. The mortality effect was less
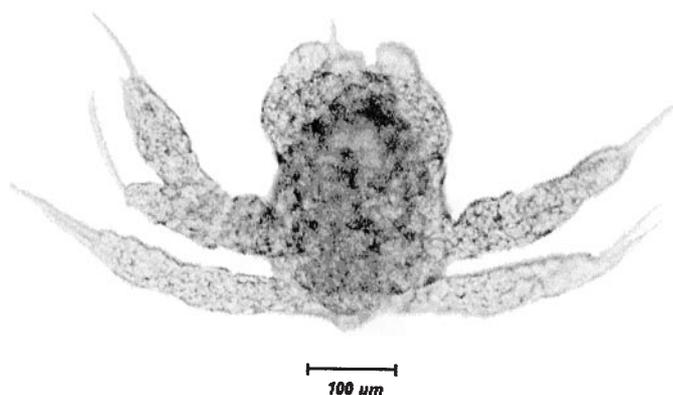
**Fig. 2** *Calanus finmarchicus*. Photomicrograph of a deformed nauplius. Nauplii with malformations such as – fused, asymmetrical or shortened appendages, abnormalities in appendage segmentation and configuration of setae – were typical

pronounced in the 312 nm treatment, and there was no effect in the 335, 360 and 400 nm treatment groups (Fig. 3). The spectral resolution of these results are the highest so far generated for a copepod. Nonetheless, similar dose-dependent effects have been reported for *Acartia clausii* irradiated under Westinghouse FS40 sunlamps (Karanas et al. 1979), and for several other species (Karanas et al. 1979, 1981; Thomson 1986; Dey et al. 1988; Naganuma et al. 1997).

Nauplii hatching from UV-B-irradiated eggs were often dead or deformed, even at low total exposure times (Fig. 1). The deformations observed (Fig. 2) – fused, asymmetrical or shortened appendages, abnormalities in appendage segmentation and configuration of setae – were similar to those reported in *Calanus helgolandicus* nauplii produced by females which had been grazing on diatoms reputed to be toxic (Poulet et al. 1995, e.g. their Fig. 4F). Deformations of this type are apparently the result of cellular anomalies during mitosis (Poulet et al. 1995). The observations reported here indicate that UV-B irradiation produces similar disruptions in pattern formation and/or morphogenesis. This contention is further supported by observations of UV-B-induced malformations in the planktonic pluteus larvae of the echinoid *Dendraster excentricus* (Pennington and Emlet 1986).

### BWF for *Calanus finmarchicus* egg mortality

The wavelength specificity of UV-induced mortality in *C. finmarchicus* eggs, as defined in the BWF (Fig. 4), exhibits a slope similar to that of the DNA action spectrum (Setlow 1974). This is consistent with the BWF reported for Atlantic cod eggs (Kouwenberg et al. 1999) and with the analysis of Hunter et al. (1981), who found that UV-B-induced mortality in northern anchovy (*Engraulis mordax*) was consistent with the DNA action spectrum. It seems likely, therefore, that UV-B-induced mortality in *C. finmarchicus* embryos results from DNA

damage. There was no significant effect of UV-A radiation in these experiments.

The BWF reported here for *Calanus finmarchicus* eggs was derived from their mortality response. Consequently, the weightings are in absolute units $(J\ m^{-2})^{-1}$ – as opposed to relative units – and, thus, egg mortality resulting from any given exposure can be predicted in absolute terms using Eq. 1. To the best of our knowledge, this is the first such BWF generated for a copepod.

A fundamental assumption for construction of an accurate dose-dependent BWF is the principle of reciprocity (Cullen and Neale 1997 and references cited therein). In the context of a UV-B exposure experiment, reciprocity holds if the effect of cumulative dose is the same regardless of the dose rate at which it was delivered. If reciprocity fails, a short intense exposure would result in a different effect than a long weak exposure to the same cumulative dose. In this latter case, evaluations of effect versus cumulative exposure (i.e. dose-dependence) cannot be applied outside the conditions (i.e. time scales) under which they were generated, and BWFs derived from such results would be less reliable and of more limited use.

This BWF was generated for the "net" effect of UV (the effect with photorepair – since eggs were incubated on a 12 h light : 12 h dark photoperiod in between UV exposures). Significant repair would compromise reciprocity. Since the photorepair abilities of *Calanus finmarchicus*, and their adherence to the principle of reciprocity, are as yet uninvestigated, the ecological relevance of the BWF in predicting UV-induced mortality for this species is not fully resolved. However, reciprocity held for Atlantic cod eggs irradiated under the same conditions, and despite the fact that they were incubated under fluorescent lamps in between UV exposures; i.e., they were allowed to repair damage, but the recovery was weak, even though the incubation conditions between exposures were benign. This suggests that the data used to derive the BWFs for both cod and *C. finmarchicus* were generated under ecologically relevant conditions and that the weightings, therefore, can be applied to realistic exposure scenarios. At the very least, this BWF can be considered as a starting point, indicative of the damage to DNA from UV-B.

### Ecological context

The results presented here indicate that *Calanus finmarchicus* may be sensitive to variation in incident UV-B radiation in subarctic regions of the northwestern Atlantic Ocean, including the Gulf of St. Lawrence and Labrador Shelf, where the cold intermediate layer sits just under the sea surface in early summer. In these regions, *C. finmarchicus* eggs, probably spawned near the surface at night or in the early morning (Runge and Plourde 1996), are constrained to develop in the warm surface waters above the sharp thermocline that typi-
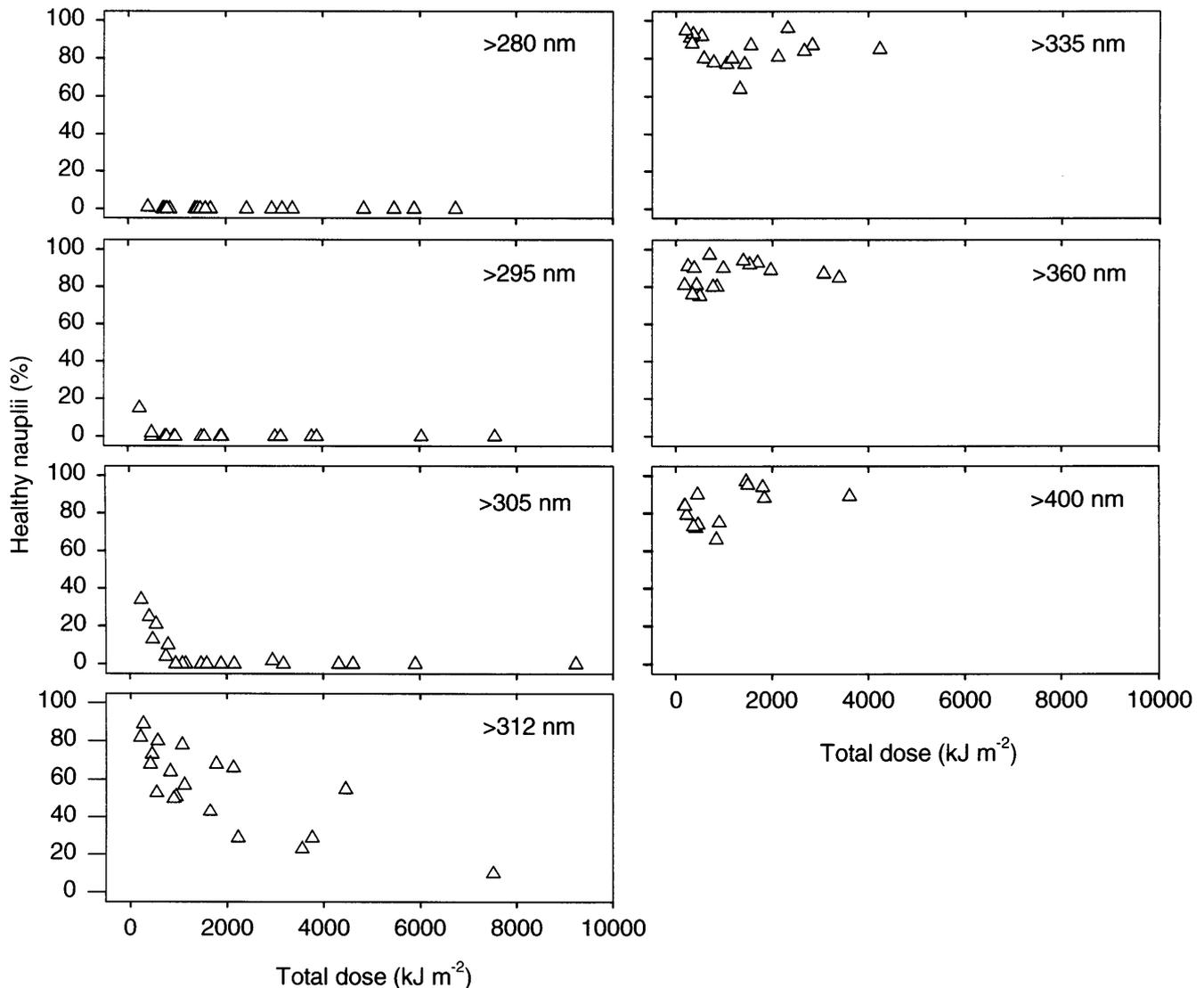
**Fig. 3** *Calanus finmarchicus*. Proportion of healthy nauplii hatching from eggs exposed to UV-B radiation for different durations. Data are presented as a function of the total (unweighted) dose delivered. Each frame presents the percentage of healthy nauplii produced for a treatment group that received radiation above the wavelength specified in the upper right hand corner. Total doses were calculated by integrating the spectral irradiances across wavelength (to 800 nm) and multiplying by the exposure time

cally commences at a depth of 10 to 15 m. Observations of *C. finmarchicus* egg distribution in the Laurentian channel show the majority of eggs residing in the surface layer (above 5 to 10 m) during daytime, where they hatch into the first naupliar stage 1 to 2 d after maternal release (depending upon ambient temperature: McLaren et al. 1988). Because *C. finmarchicus* eggs are negatively buoyant (Marshall and Orr 1955), those released in the cold intermediate layer (20 to 50 m), or those that sink into it from above, probably never return to the surface mixed layer. We hypothesize that these eggs are lost to the population (as well as to larval fish predators) because their development time in this cold water is pro-

hibitively long (> 6 d: McLaren et al. 1988). The high mortality exhibited by *C. finmarchicus* eggs after short exposures to UV-B implies that UV-B radiation may exert a countervailing selective pressure which favours release of eggs deeper in the water column or the production of negatively buoyant eggs: both would increase the probability of their loss to the cold intermediate layer.

Of the copepod species that predominate in subarctic planktonic communities, *Calanus finmarchicus* may be among those most vulnerable to UV-B radiation. *Calanus hyperboreus*, the other dominant calanoid copepod in the deep waters of the Gulf of St. Lawrence, releases eggs at depth in late winter through early spring (Conover 1988). Thus, their eggs are not exposed to UV-B radiation, although naupliar stages residing in the surface mixed layer later in spring and early summer might be. The calanoid copepod *Pseudocalanus* sp., and the cyclopoid copepod *Oithona* sp., carry their eggs until hatching; it is possible, therefore, that females protect their eggs from UV-B exposure by maintaining a depth
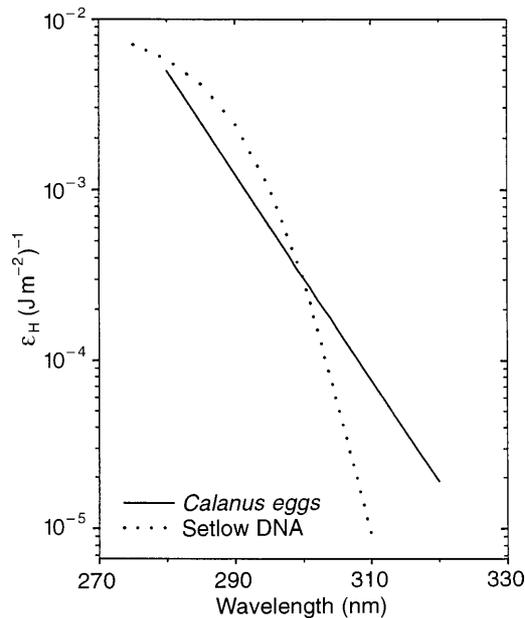
**Fig. 4** A biological weighting function (BWF) for egg mortality in *Calanus finmarchicus* (*continuous line*) and wavelength-dependence of damage to the naked DNA molecule (data drawn from Setlow 1974) (*dotted line*). The Setlow curve has been normalized against the BWF's value at 300 nm for ease of comparison

in the mixed layer below that to which UV-B penetrates. *Temora longicornis*, a calanoid copepod dominant on the shallow Magdalen Plateau in the southern Gulf of St. Lawrence, releases highly pigmented eggs into the water: although the photoprotective qualities of this pigment are presently unknown, they may protect eggs from UV-B-induced damage (see Ringelberg et al. 1984; Zellmer 1995; Zagarese et al. 1997). *Metridia longa*, another common calanoid species in the Gulf of St. Lawrence, although less abundant than *C. finmarchicus*, broadcasts unpigmented eggs and may also be susceptible to UV-B.

Exposure to UV-B radiation may be even more damaging than suggested by results on egg mortality alone. Even short (sub-lethal) exposures to UV-B produced a significant proportion of deformed first stage nauplii which were clearly non-viable. This was particularly significant in the 312 nm treatment, in which abnormal naupliar development accounted for approximately 30% of all non-viable progeny (eggs and nauplii) (Fig. 1).

### Predicting UV-B effects on the early life stages of *Calanus finmarchicus*

Any attempt to assess the impact of UV radiation on planktonic marine organisms requires that the wavelength-dependent biological effect of UV photons be known. That is, a relevant BWF – like that presented here for *C. finmarchicus* egg mortality – must be avail-

able (for more complete presentations of this issue see Cullen and Neale 1997; Kouwenberg et al. 1999).

Biologically weighted radiant exposure, $H^*$ (Eq. 2), is obtained by combining spectral irradiance and exposure time with the BWF for *Calanus finmarchicus* egg mortality. Using several spectra of solar irradiance – for a late summer day in the air and the same day after 20% ozone depletion (Fig. 5, Curves A and C, respectively) – allows a visual and quantitative comparison of the biologically effective irradiance that would be produced under each of these conditions (compare Curves B and D in Fig. 5). The salient feature of this graph is the large increase in biologically effective irradiance that results from only a small change in UV-B irradiance.

A more ecologically meaningful analysis is possible from Eq. 1 which, since the second-order mortality term ($M$) is zero, reduces to

$$\frac{\text{Egg}(d)}{\text{Egg}(0)} = e^{-H^*} \quad . \tag{4}$$

Under each of the above spectral irradiance conditions, the $H^*$ that yields, for example, Egg($d$)/Egg(0) = 0.5, is calculated. This value then allows the exposure time resulting in 50% egg mortality to be calculated (from Eq. 2). Under current noon surface irradiance, 50% of *Calanus finmarchicus* eggs located at or very near the ocean surface will be dead after 2.5 h of exposure. Under solar spectral irradiance simulating a 20% decrease in ozone layer thickness, this time drops to 2.2 h for eggs at the surface. These are, of course, first-order estimates based upon irradiance taken at a time of day during which the values would be maximal, and upon a worst case scenario BWF. Nonetheless, they illustrate the relative changes in UV-B impacts that will result from ozone layer depletions expected over the coming decades.

The depth at which eggs are suspended in the water column – and the diffuse attenuation coefficient for UV-B wavelengths exhibited by the water – will also affect their susceptibility to UV-B. We calculated (as above) that 50% of *Calanus finmarchicus* eggs incubated under 50 cm of water from the maritime estuary of the St. Lawrence River would be dead after 4.6 h of exposure to the noon-time sun – double the time calculated for the surface. In a similar exposure experiment with the freshwater calanoid copepod *Diaptomus* sp., significant mortality in eggs and nauplii was observed after near-surface exposures of 3 d or less (Williamson et al. 1994). These values are of the same order of magnitude as the above estimates, indicating that the calculations are at least reasonably realistic.

This study represents a first step in generating an ability to predict the ecological significance of UV-B radiation on *Calanus finmarchicus* early life stages in the estuary and Gulf of St. Lawrence. A more rigorous and realistic quantitative assessment of direct UV-B effects on the population dynamics of marine copepods requires data on the vertical distribution of early life stages in the mixed layer of the water column (with a greater
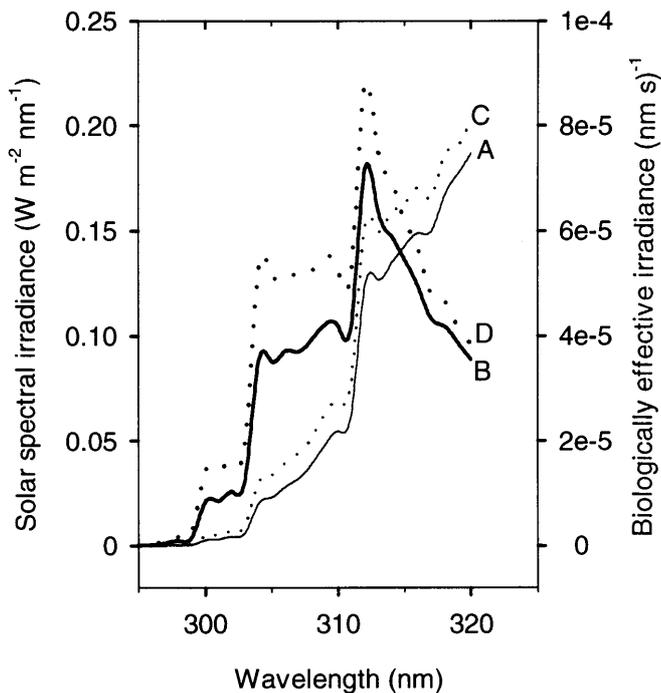
**Fig. 5** An illustration of how the biological weighting function (BWF) for *Calanus finmarchicus* egg mortality can be combined with measurements of spectral irradiance to estimate biologically effective irradiance at each wavelength [*A* solar spectral irradiance measured outside the Maurice-Lamontagne Institute, St. Flavie, Québec, Canada (48°38′25.9″N; 68°09′21.0″W) on 5 August 1996 under cloudless skies; *B* biologically effective irradiance under the spectral conditions illustrated in A; *C* solar spectral irradiance for 5 August 1996 corrected for a 20% ozone depletion (using a 50 level delta-Eddington radiative transfer model, Davies et al. 1999), *D* biologically effective irradiance under the spectral conditions illustrated in C]

resolution in the upper 10 m than currently exists), surface UV-B irradiance during the reproductive season, and subsurface spectral irradiance for waters supporting such eggs. A model to predict the vertical position of passive particles (such as eggs) in the mixed layer, and particularly their daily residence time near the surface under various weather conditions, is also necessary. All of these components would have to be incorporated into a simulation model that could then provide an assessment of UV-B effects on a population of eggs distributed throughout the mixed layer. Such a model, analogous to that recently published by Neale et al. (1998) for primary production in the Antarctic, is currently being developed.

Although there is clear evidence for detrimental effects of UV-B on crustacean zooplankton, some species appear to be highly resistant to UV-B (Thomson 1986; Saito and Taguchi 1995; Zellmer 1995; Cabrera et al. 1997; Zagarese et al. 1997). It is important to keep this in mind when discussing the potential impacts of UV-B on secondary production in aquatic ecosystems. Further, variability in cloud cover, water quality, and vertical distribution and displacement within the mixed layer, can all have a greater effect on the flux of UV-B

radiation to which *Calanus finmarchicus* eggs are exposed than will ozone layer depletion at these latitudes.

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