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Modeling the effects of ultraviolet radiation on embryos of *Calanus finmarchicus* and Atlantic cod (*Gadus morhua*) in a mixing environment

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Abstract

It is well established that ultraviolet radiation (UVR, 280–400 nm) harms aquatic organisms. Reductions in productivity have been reported for phytoplankton, ichthyoplankton, and zooplankton in incubations exposed to UVR. It is difficult, however, to estimate the effects of UVR in natural waters. Quantitative assessments of UVR effects on aquatic organisms require high-resolution measurements of solar irradiance and its attenuation in the water, spectral weighting functions for biological effects, and realistic descriptions of the distributions and vertical movements of particles in the water column. Using experimentally determined biological weighting functions for UV-induced mortality along with measurement-based models of solar irradiance and of vertical distributions of embryos as influenced by mixing, we modeled UVR-induced mortality in the early life stages of two key species in the upper estuary and Gulf of St. Lawrence, Atlantic cod (*Gadus morhua*) and the planktonic copepod, *Calanus finmarchicus. G. morhua* embryos are insensitive to UVR, with an average daily survival of ~99% over numerous environmental conditions. *C. finmarchicus* are considerably more vulnerable, with an average survival of 90% ± 12% (SD). Lowest modeled daily survival was 59% under ambient ozone and 49% under 50% ozone loss. A sensitivity analysis allowed us to examine the relative influences of hydrographic variability, meteorological conditions, and ozone depletion on UVR-induced mortality in *C. finmarchicus* embryos. The modeled hydrographic and meteorological conditions are a representative range of natural variability for the St. Lawrence region during the 1997 field season, with the exception of extreme ozone depletion (50%). Effects are expressed as relative change of survival normalized to survival under a reference simulation. Similar to other studies, water column mixing and water clarity have the most significant influence on embryo survivorship, with a 3%–80% increased chance of survival when in static, compared with mixed waters, and a 3%–46% increased chance of survival when in the darkest, compared with the clearest waters. Cloudy skies increase survivorship between 1%–30%, and ozone depletion of 50% can decrease survivorship by 9%. On average, ozone depletion decreases survival by 3% and of the factors considered has the smallest influence on mortality of *C. finmarchicus* embryos.

Long-term data on solar ultraviolet-B radiation (UVB, 280–320 nm) incident at the Earth's surface, although rare, indicate that over the past 10–15 yr, UVB levels have increased significantly in midlatitude areas (Crutzen 1992; Madronich et al. 1995; Wardle et al. 1997). Recent ozone losses over the Arctic have caused ozone thinning at midlatitudes (Bjorn et al. 1998; Fergusson and Wardle 1998), and Arctic losses, similar to those of the Antarctic in the early 1990s, are predicted for the years 2010–2019 (Shindell et al. 1998).

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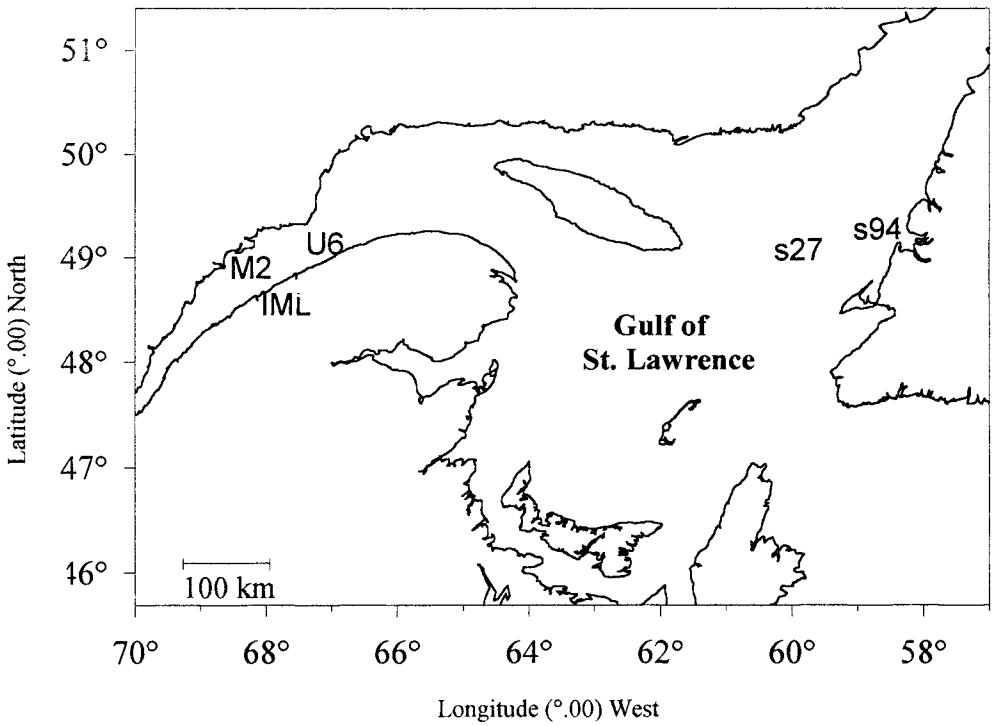

Fig. 1. The estuary and Gulf of St. Lawrence, Canada, showing station locations. High-resolution UVR measurements were made in the surface waters at Sta. M2, 27, and 94. Embryos of *G. morhua* were found at Sta. 27 and 94, and those of *C. finmarchicus* were found at Sta. 27 and M2. The vertical distribution of *C. finmarachicus* embryos was measured at Sta. U6 on 03 June 1997, at three depth strata (0–5, 5–10, and 10–30 m). IML (48°0.38'N, 68°0.09'W) is the location at which surface spectral irradiance measurements (286–350 nm) were made with a Brewer MK III scanning spectroradiometer.

phytoplankton (Cullen and Neale 1994; Herndl 1997), ichthyoplankton (Hunter et al. 1982; Williamson et al. 1997) and zooplankton (Williamson et al. 1994) in incubation experiments. It is more difficult, and therefore rare, to quantify the effects of ultraviolet radiation (UVR, 280–400 nm) in natural water columns subjected to vertical mixing (*see* Neale et al. 1998; Zagarese et al. 1998). In 1995, an extensive research program began with the aim of assessing quantitatively the effects of UVR on the early life stages of two ecologically important species in the upper estuary and Gulf of St. Lawrence (Fig. 1): Atlantic cod (*Gadus morhua*) and the planktonic copepod, *Calanus finmarchicus.* Toward this end, we combined experimental data for these two species into a model of natural water columns, including high-resolution measurements of irradiance and water attenuation, biological weighting functions for mortality, realistic vertical distributions of eggs (embryos), and vertical mixing of particles.

Both cod and *C. finmarchicus* are believed to be susceptible to UVR, since their embryos are found within the shallow mixed layer (0–15 m) that forms above a cold, intermediate layer during the spring and summer in the Gulf of St. Lawrence (Fortier et al. 1992; Runge and de Lafontaine 1996; Ouellet 1997). Female cod release positively buoyant eggs between March and June at depths >200m, which then ascend toward the surface over a period of 2–10 d, hatching ~14 days after release (Solemdal and Sundby 1981). Embryo ascension rate and final vertical distribution depend on factors such as embryo size, embryo composition and hydrography (Anderson and de Young 1995; Ouellet 1997). When wind speed is low, high embryo concentrations have been observed near the surface (Sundby 1983, 1991). Studies in the Gulf of St. Lawrence found maximum embryo densities at depths of 50–60 m, with 14%–55% of the embryos residing in the top 50 m (Ouellet 1997). *C. finmarchicus* females spawn from March to September. They release their embryos at the surface, probably during the night or early morning (Runge and Plourde 1996); embryos sink after release. Thirty to fifty percent of these embryos are typically found in the surface 5-m layer.

Outdoor incubation experiments have shown that embryos of *G. morhua* and in particular *C. finmarchicus* are vulnerable to ambient UVR at depths between 2 and 60 cm in tanks (Browman et al. 1999). However, these studies did not reproduce the natural radiation environment, where exposures of individual embryos to UVR are altered by changing environmental conditions: position in the water column as influenced by vertical mixing, water attenuation characteristics, and meteorological conditions. To assess the impact of ambient UVR, including levels expected from potential ozone loss, on embryos of these two species in their natural environment, we adopted an approach similar to that taken by Neale et al. (1998), who modeled photoinhibition of photosynthesis. Several components were combined into a mod-

el of UVR exposure: (1) a random walk model to estimate the vertical position of passive particles (embryos of *G. morhua* and *C. finmarchicus*) in the mixed layer; (2) surface down-welling irradiance measurements (290–350 nm) made with a Brewer MK III spectroradiometer at the Maurice Lamontagne Institute (IML; Fig. 1); (3) diffuse attenuation coefficients from 290 to 400 nm, measured for the different water masses in the estuary and Gulf of St. Lawrence (Kuhn et al. 1999); and (4) high-spectral-resolution (290–400 nm) biological weighting functions for UV-induced mortality in the two species (Kouwenberg et al. 1999*a*,*b*).

Methods

Model overview—The model describes vertical mixing, underwater irradiance, and biological responses to UVR. Individual particles, embryos of *G. morhua* and *C. finmarchicus*, are initially distributed uniformly in the modeled water column. They are vertically mixed every 20 s through the day according to a random walk diffusivity model. At each depth they are exposed to UV radiation, which was measured at the surface with a Brewer spectroradiometer, interpolated to match the 20-s mixing interval, and propagated to depth by use of measured diffuse attenuation coefficients. The radiant exposure for each embryo is weighted by a biological weighting function for mortality. Death occurs according to a probability that is a function of UV exposure, consistent with the underlying model of UV-induced mortality. At the end of the day, percentage of survival is calculated for the assemblage.

Physical model—Mixing regime: Random walk models are often used to simulate turbulent movement in marine environments (Falkowski and Wirick 1981; Franks and Marra 1994; Neale et al. 1998), with the movements of particles described as a function of diffusivity. These so-called naive models suffer from artifactual accumulation of particles in areas of low diffusivity. Visser's (1997) Lagrangian vertical mixing model is used here. It avoids particle stagnancy by including a nonrandom ''advective'' component. The vertical mixing model was used to trace changes in the depth distribution of either *G. morhua* or *C. finmarchicus* embryos through mixed layers of different depths (10, 30, or 50 m). Reflecting boundary conditions were imposed at the surface and bottom of the mixed layer. Two thousand embryos were used in the model simulations, and, to satisfy the criterion for Visser's more sophisticated model, a time step of 20 s was used. Mixing was forced by diffusivity, which corresponded to wind speeds of ~0–10 m s^{-1}. Consistent with Visser's formulation, the diffusivity profile has a subsurface maximum at 2 m.

G. morhua—For most model simulations, cod embryos were initially homogeneously distributed in the top 50 m of the water column. The embryos were either neutrally buoyant or ascended at a rate of 8.6 m day^{-1} (J. T. Anderson pers. comm.). For certain model simulations, all embryos were initially distributed in the top 5 m, with ascending buoyancy, to examine a worst-case scenario of high UVR exposure.

C. finmarchicus—To establish the diel vertical distribution of *C. finmarchicus* embryos in the St. Lawrence region, water samples were collected from three different strata at 08:00 and 15:00 h on 3 June 1997 (Sta. U6 in Fig. 1) aboard the C.S.S. *Parizeau.* From each stratum (0–5, 5–10, and 10–30 m), 15 m^3 of water were collected with a centifugal pump and filtered through a 73-μm mesh net submersed in sea water on deck. Samples were preserved in 4% formaldehyde. Subsamples were later analyzed for concentration of *C. finmarchicus* embryos.

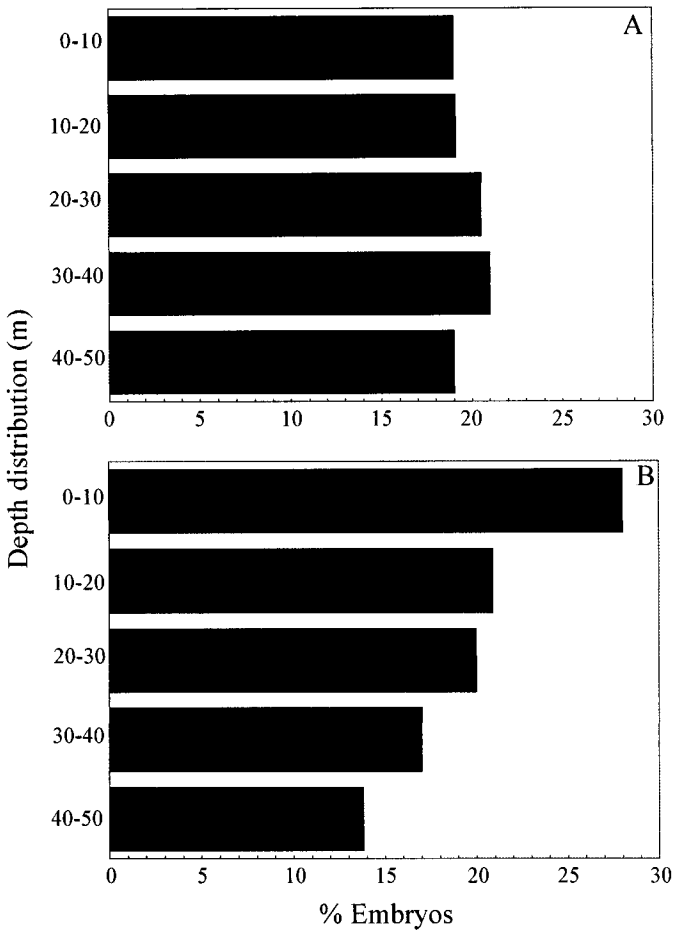

Fig. 2. Final modeled vertical distributions of *G. morhua* embryos after a day of mixing in a 50-m mixed layer, with wind speeds of 10 m s^{-1}, (A) neutral buoyancy, and (B) an ascending buoyancy of 8.6 m day^{-1}. Initially embryos are homogeneously distributed over the 50-m layer. At the end of the simulation 20% still remain in the top 10 m when the buoyancy is neutral and 28% when embryos have an ascending buoyancy.

Seventy percent of the embryos were observed in the top 5 m at 08:00, but only 20% were observed in the surface 5 m by midafternoon (Fig. 3A,B)—this is consistent with the hypothesis of a diel spawning rhythm at the surface, with negatively buoyant embryos. In the model simulations, *C. finmarchicus* embryos were initially distributed homogeneously in the top 5 m and assigned a sinking rate of 32 m day^{-1} (Marshall and Orr 1953).

Surface irradiance: Surface spectral down-welling irradiance measurements (286–350 nm), made hourly with a Brewer MK III spectroradiometer at the IML (Fig. 1), were used as above-water irradiances ($E[0^+, \lambda, t]$ W m^{-2} nm^{-1}).

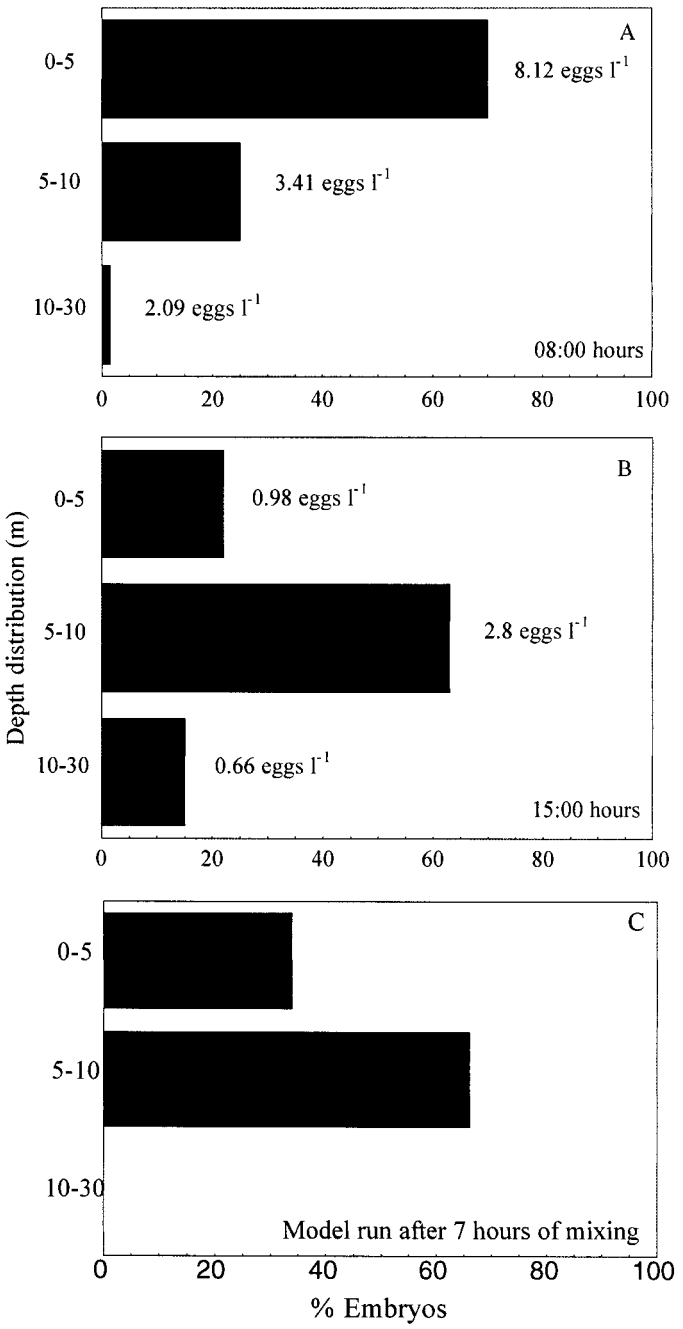

Fig. 3. Vertical distribution of *C. finmarchicus* embryos collected on 3 June 1997 at Sta. U6 aboard the C.S.S. *Parizeau* in the estuary of St. Lawrence (Fig. 1). Samples were collected at (A) 8:00 and (B) 15:00 h; wind speeds ranged from 7 to 15 m s^{-1}. (C) For embryos of *C. finmarchicus* with an initial uniform depth distribution confined to the upper 5 m to simulate hatching of eggs in the morning, a sinking rate of 32 m d^{-1}, a 10-m mixed layer, and 10 m s^{-1} wind speeds, after 7 h of mixing (same time period between field observations, A and B) 34% of the embryos remained in the top 5 m of the water column, and the majority of eggs (66 %) were distributed between 5–10 m.

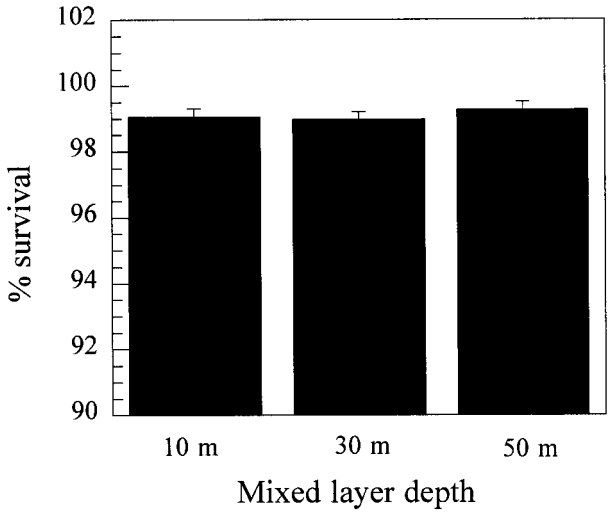

Fig. 4. The influence of mixed layer depth (10, 30, and 50 m) on *Gadus morhua* (Atlantic cod) embryo survival. Ten model simulations were run for each mixed layer depth, using clear sky irradiance, the clearest water (Sta. 27), ambient ozone, and 10 m s^{-1} windspeeds. There is no statistical difference between the survivorship of cod at the varying mixed layer depths, the average standard deviation is 0.25%.

Measurements from a clear (14 July 1997) and an overcast (19 July 1997) day were interpolated to 20-s intervals to match the model increments (daily totals shown in Fig. 6A). Ozone losses of 10%, 20%, 30%, 40%, and 50% were applied to $E[0^+, \lambda, t]$ by use of a delta-Eddington radiative transfer algorithm (Fig. 6E; Davies et al. 1999; note that the algorithm was extended to 500 nm). The delta-Eddington algorithm was also used to break $E[0^+, \lambda, t]$ into its diffuse and direct components. Assuming a flat sea surface, the below-surface irradiance ($E[0^-, \lambda, t]$) was calculated by applying a surface albedo of 6% to the diffuse component (Kirk 1994) and Fresnel reflectance and refraction to the direct component.

Subsurface irradiance: Irradiance at depth ($E[z, \lambda, t]$) was estimated by use of Beer's law,

$$E[z, \lambda, t] = E[0^-, \lambda, t]e^{-Kd(\lambda)z}. \quad (1)$$

Embryo depths (z; m) are output from the Langrangian vertical mixing model, and diffuse attenuation coefficients ($[Kd, \lambda]$ m^{-1}) were determined from high-resolution spectral down-welling irradiance measurements (290–400 nm) made at depths from 1 to 4 m in the estuary and Gulf of St. Lawrence by use of an Optronic Laboratories scanning spectroradiometer (Kuhn et al. 1999). For this work, $Kd(\lambda)$ are from stations at which embryos are typically found, Sta. 27 and 94 for cod and 27 and M2 for *C. finmarchicus*, were used (Figs. 1, 6C). It should be noted that scalar irradiance was not used in the model. Scalar irradiance is calculated by dividing down-welling irradiance by the average cosine ($\overline{\mu_b}$) for the down-welling irradiance (Kirk 1994). The average cosine is not well characterized for UVB wavelengths important in DNA damage, although it is known that $\overline{\mu_b}$ approaches 1.0 for waters with high ratios of absorption to scatter, characteristic of shorter wavelengths in high chro-

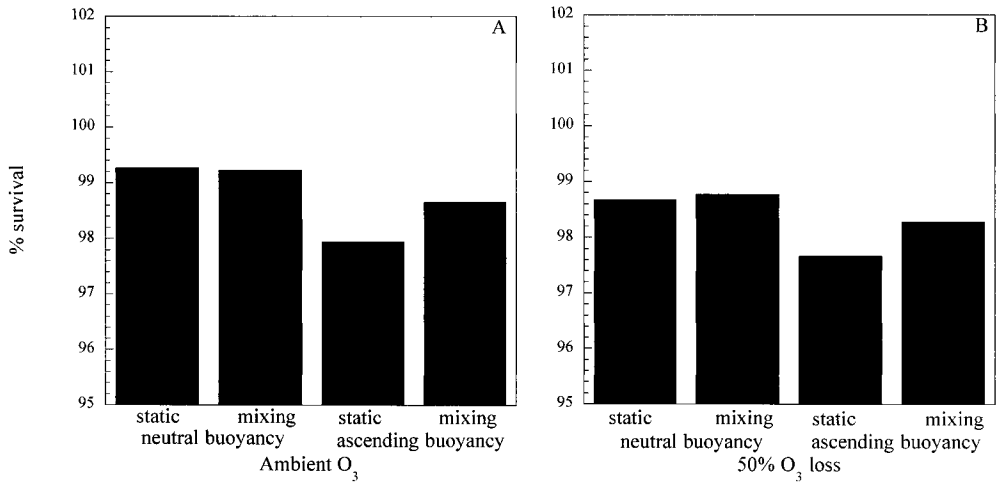

Fig. 5. Daily percentage of survival of *G. morhua* (Atlantic cod) embryos, averaged over all three mixing depths. Effects of egg buoyancy (neutral or ascending at 8.6 m day^{-1}), wind speed (0 or 10 m s^{-1}), and 50% ozone loss for the clearest waters (Sta. 27) under clear sky conditions. Standard deviations of 0.25% are shown.

mophoric dissolved organic matter (CDOM) water (Kirk 1994; Bannister 1992). Consequently, our estimates of DNA damage might be slight underestimates, especially for Sta. 27, a station with relatively low absorption in UV wavelengths. The full range of modeled parameters is listed in Table 1.

Model of UVR impact—Damage by UVR was quantified by use of biological weighting functions (BWFs, $\epsilon[\lambda]$ J^{-1}m^2), experimentally determined for mortality of both cod and *C. finmarchicus* embryos (Kouwenberg et al. 1999*a,b*). The BWFs are first-order exponential fits to a wavelength-dependent function relating the relative number of embryos surviving exposure to varying spectral UVR exposure (Rundel 1983; discussed by Cullen and Neale 1997). The weighting functions were developed for the ''net'' effect of UV, the effect with photorepair—since eggs were exposed to UVR during incubations under visible light on a 12-h light : 12-h dark photoperiods, with UV exposures superimposed during the light period. It should be cautioned that the contribution of photorepair and the adherence to the principle of reciprocity were not quantified for *C. finmarchicus;* however, reciprocity was tested and found to hold for cod eggs that were irradiated under the same conditions (*see* Kouwenberg et al. 1999*a,b*). Reciprocity holds only when repair is insignificant. Slopes for both cod and *Calanus* are similar to that of the action spectrum for DNA damage (Setlow 1974).

The probability of survival (S) at each time step is defined as

$$S = e^{-(H_{inh})} \tag{2}$$

where biologically weighted exposure (*Hinh;* dimensionless) was calculated for each time step by use of $\epsilon(\lambda)$ and irradiance at depth of embryo ($E[z, \lambda, t]$):

$$H_{\text{inh}} = \Delta t \sum_{\lambda=290}^{350} \epsilon(\lambda)E[z, \lambda, t]. \tag{3}$$

To determine survival at each time step, S is compared with a uniformly distributed random number ranging from 0 to 1 (after Murray and Jackson 1993). If S is less than the random number (more likely with large *Hinh*) the embryo dies; if it is greater or equal to the random number (smaller *Hinh*), it survives to the next time step. At the end of the day the percentage of surviving embryos is calculated.

The formulation in Eq. 2 is consistent with the assumption that, although many photons are absorbed before mortality occurs, the actual inactivating event is caused by only one of these photons (Jagger 1967). This simple ''one-hit'' model can be applied reasonably to more complicated processes involving several sensitive targets, as long as one ''hit'' can cause inactivation (Smith and Hanawalt 1969). The BWFs for our model were derived by use of one-hit kinetics, and the patterns of mortality were effectively described (Kouwenberg et al. 1999*a,b*), so it is the most appropriate kinetic model to use until evidence for a better model is obtained.

Results

Vertical distributions of embryos—In simulations of cod embryos evenly distributed in the 50-m surface layer at time 0, 20% of the total embryo number began the simulation in the top 10 m. By the end of a model run, 12 h later, by use of a 50-m mixed layer and a wind speed of 10 m s^{-1}, 20.4% were found in the top layer when embryos were assigned neutral buoyancy (Fig. 2A) and 28% (Fig. 2B) when the buoyancy was -8.6 m day^{-1} (embryos ascended). There are no in situ diel observations of vertical cod embryo distribution available to validate our model simulations.

The mixing portion of the model simulated the observed diel movement of *C. finmarchicus* embryos relatively well. For embryos initially distributed in the upper 5 m, a 10-m mixed layer, and 10 m s^{-1} wind speeds, after 7 h (same time period between field observations) 34% of the embryos remained in the top 5 m of the water column, and the majority

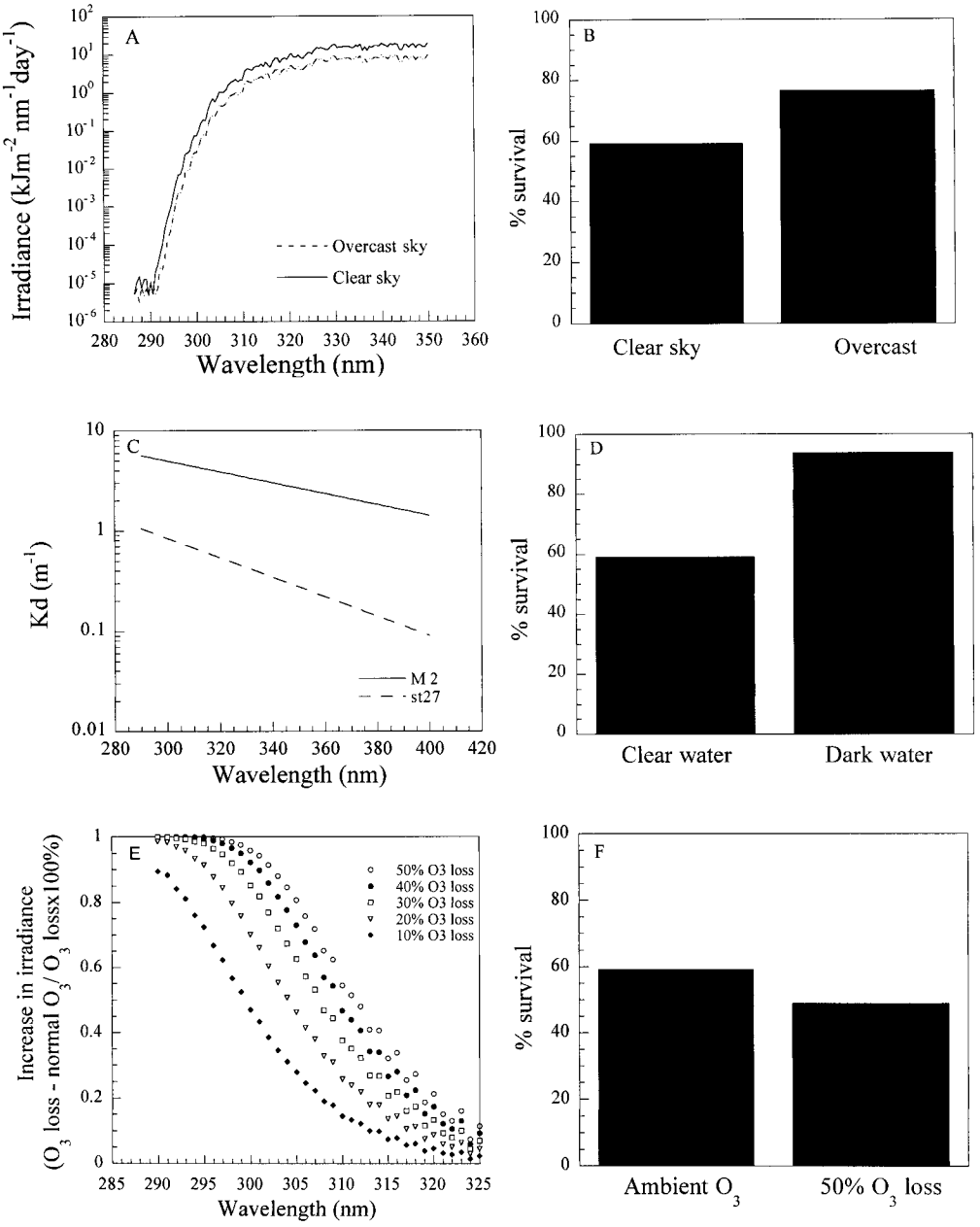

Fig. 6. A, C, and E show the physical conditions which produced corresponding (B, D, and F) model simulations of *C. finmarchicus* daily embryo survival, standard deviation. (A) Daily total irradiance for clear (14 July 1997) and overcast (19 July 1997) summer days, measured at IML with a Brewer MK III scanning spectroradiometer. (C) Diffuse attenuation coefficients for Sta. M2 and 27, locations shown in Fig. 1. (E) Increase in irradiance for a given O_3 loss, ambient O_3 was set to 350 Dobson units. Plots B, D, and F illustrate effects of cloud, water attenuation, and ozone loss, respectively. Model simulations are for a 10-m mixed layer, with a wind speed of 10 m s^{-1} (conditions which produced the lowest survival). Plots B and D are under ambient O_3 conditions.

of embryos (66%) were distributed between 5 and 10 m (Fig. 3C). This change in vertical distribution, strongly determined by the assigned sinking rate of 32 m d^{-1}, is close to the field observations on 3 June 1997 (Figs. 3A,B), which were made under similar windspeeds (7–15 m s^{-1}) and comparable mixed layer depth, as inferred from the sharp pycnocline which was observed at 10 m.

Mortality—Calculation showed that *G. morhua* embryos are insensitive to environmental UVR. For all combinations of model conditions (n = 72), the average survivorship ± standard deviation of *G. morhua* embryos is 99 ± 0.63%. Embryo survivorship was found to be insensitive to mixed layer depth; there were no significant difference in survivorship for the three depths of mixing (10, 30, and 50 m;

Table 1. Ranges of modeling parameters used for all simulations.

Species	Irradiance	O_3 loss (%)	*Kd* at 310 nm (m^{-1})	Initial embryo depth distribution (m)	Mixing windspeed ($m\ s^{-1}$)	Mixed layer depth (m)	Embryo sinking rate ($m\ day^{-1}$)
Gadus morhua	Clear–Cloudy	0, 50	Sta. 27 and 94 0.69, 1.0	0–50*	0, 10	10, 30, 50	0, +8.6
Calanus finmarchicus	Clear–Cloudy	0, 50	Sta. 27 and M2 0.69, 4.4	0–5	0, 10	10, 30, 50	−32

* For the ''worst case scenario,'' embryos were distributed in the top 5 m.

Fig. 4). The average standard deviation for all 30 model runs is 0.25%. Note that a standard deviation of 0.25% applies to all survival model output, since it represents the deviation of the models random number generator. Figure 5 shows the effects of embryo buoyancy, wind speed, and ozone loss, on survival of *G. morhua* embryos, under clear sky conditions and for the clearest waters (Sta. 27). Survivorship was always >97%, but differences were observed. Mixing and static conditions have similar impacts on embryos when they are neutrally buoyant, but when embryos have an ascending buoyancy, mixing increases survivability. Ozone loss decreases survival slightly in all cases.

The model indicates that cod in the estuary and Gulf of St. Lawrence are not sensitive to UVR. Even in the extreme case, in which all 2000 embryos are placed in the top 5 m and are positively buoyant, the number of embryos surviving is 94.5% day^{-1} under ambient ozone and 93.3% with 50% ozone loss. *C. finmarchicus*, however, are considerably more sensitive. Their average survivorship ($n = 48$) is $89.95 \pm 11.9\%$. Because the impact of UVR on cod was so minor, the subsequent sensitivity analysis refers to *C. finmarchicus* embryos only.

A sensitivity analysis allowed us to examine the relative influences of hydrographic variability, meteorological conditions, and ozone depletion on UVR induced mortality in *C. finmarchicus* embryos. The modeled conditions are a representative range of natural variability for the St. Lawrence region during the field study, with the exception of the extreme ozone depletion (50%). Normalized percentage differences,

$$\frac{\%\ \text{Survival(condition } a) - \%\ \text{Survival(condition } b)}{\%\ \text{Survival(condition } a)}, \quad (4)$$

for all modelled conditions are shown in Table 2. For completeness, the absolute percentage differences,

$$\%\ \text{Survival(condition } a) - \%\ \text{Survival(condition } b), \quad (5)$$

and the percentage survival for condition *a* have also been included. The following discussion refers to the normalized percentage differences (Eq. 4). Rate of water column mixing had the most significant impact on embryo survivorship. A static water column, opposed to one mixed at 10 $m\ s^{-1}$, increases the chance of embryo survivorship, on average, 27% for a 10-m mixed layer and 10% for a deep layer (30–50 m). Water clarity (defined as the down-welling attenuation coefficient) is the second most influencial factor on embryo survivorship, with an average increased chance of survival of 15% between the darkest and clearest waters (Sta. M2 and 27, respectively). Having a deep mixed layer (30–50m), as opposed to a shallow 10-m layer, increases embryo survivorship on average by 6%. Overcast sky conditions also increase survivorship by 6%. Ozone depletion decreases survival an average of 3.5% and of the factors considered has the smallest influence on mortality of *C. finmarchicus* embryos (Table 2).

The lowest *C. finmarchicus* survivorship, under ambient ozone levels occurred with a 10-m mixed layer and 10 $m\ s^{-1}$ winds (59%; Fig. 6). The influence of cloud, water attenuation, and ozone depletion for these mixing parameters are displayed in Fig. 6. The results are consistent with the sensitivity analysis shown in Table 2. Water attenuation has more of an impact than cloud cover and ozone loss. Survivorship increases from 59% in optically thin waters to 94% in optically thick (Fig. 6C,D). Cloud cover increases survival from 59% to 77% (Fig. 6A,B), and 50% ozone depletion decreases survival from 59% to 49% (Fig. 6E,F).

Discussion

G. morhua—The Atlantic cod embryos used to generate the BWF are insensitive to daily levels of UVR typical for the St. Lawrence region. Even in the worst-case scenario of embryos initially distributed in the surface 5 m, with an ascending buoyancy, mortality was only 6% day^{-1}. Physiological variability of the spawning adults (i.e., young vs. old, starved vs. well nourished) and stage of embryonic development affect UVR sensitivity (Kouwenberg 1999*a*). It is possible that BWFs created by use of embryos at different developmental stages and from other cod individuals (i.e., different stocks or genotypes) would be more sensitive to UVR. However, this study applied the more sensitive of two available BWFs. Embryos used to generate the weighting function were in middle gastrulation, a stage at which they are more susceptible to UVR exposure (Kouwenberg 1999*a*). Cod embryos are believed to be UVR resistant because they contain protective pigments that absorb UVR (Chioccara et al. 1980; Plack et al. 1981).

C. finmarchicus—These embryos are more sensitive to UVR than cod, consistent with the mortality and DNA damage BWFs for these two species (Kouwenberg 1999*a*,*b*). Variations in ozone, mixing depth, mixing rate, cloud cover, and water attenuation greatly influence predictions of *C. finmarchicus* embryo mortality. Although losses of atmospheric ozone always increase mortality, it is the least significant of

Table 2. Normalized percentage difference and absolute difference of survivorship for all model simulations for *C. finmarchicus* embryos. The percentage survival of the denominator of the normalized percentage of difference are included.

Source of variability	Measure of variability	Strongest effect (%)	Weakest effect (%)	Average effect (%)
Ozone loss	$\frac{\%S(amb) - \%S(50\%\ loss)}{\%S(amb)}$	9	0	3.4
	%S(amb) − %S(50% loss)	10.25	0	2.7
	%S(ambient)	59.05	100	92
Mixing rate*	$\frac{\%S(mix) - \%S(static)}{\%S(mix)}$	10 m: −79.4 30 m: −26.6	10 m: −2.8 30 m: −0.1	10 m: −27.2 30 m: −10.0
	%S(mix) − %S(static)	10 m: −38.8 30 m: −19	10 m: −2.7 30 m: −2.1	10 m: −17.1 30 m: −8.7
	%S(mix)	10 m: 48.8 30 m: 70.9	10 m: 97 30 m: 98	10 m: 78.9 30 m: 88.2
Mixing depth†	$\frac{\%S(deep) - \%S(shallow)}{\%S(deep)}$	32.1	0	6.29
	%S(deep) − %S(shallow)	23	0	5.5
	%S(deep)	71.8	100	86.4
Sky condition	$\frac{\%S(cloud) - \%S(clear)}{\%S(cloud)}$	30.2	0	6.1
	%S(cloud) − %S(clear)	21	0	4.9
	%S(cloud)	70	100	93.3
Water attenuation	$\frac{\%S(dark) - \%S(clear)}{\%S(dark)}$	46.4	3.2	14.6
	%S(dark) − %S(clear)	34.6	4.5	14.09
	%S(dark)	93.6	100	97.8

* Mix refers to 10 m s^{-1} windspeed. Difference between 30 and 50 m depths were negligible; thus, only 30 m results are shown.
† Deep mixing depth is considered to be 30 m.

the factors considered. This is consistent with results of Neale et al. (1998), in which they found that phytoplankton productivity in the Antarctic was negatively impacted more by physiological variation, mixing regime, and sky condition than by ozone depletion.

Our sensitivity analysis revealed that, of the factors studied, vertical mixing has the most influence on *C. finmarchicus* embryo survival. Under static conditions, the near-surface mortality rate (embryos h^{-1}) is lower as the day proceeds because mortality and sinking reduce the number of susceptible, viable embryos close to the surface. When wind-driven mixing is introduced, more embryos are carried up to shallow depths, increasing the rate of mortality. These results are consistent with Neale et al. (1998) and Zagarese et al. (1998) who found that mixing increases inhibition of photosynthesis and mortality in phytoplankton and copepods, respectively. The result applies to inactivation processes that are not repaired rapidly (Neale et al. 1998). This finding reinforces the suggestion that UVR incubation studies must consider vertical mixing when extrapolating experimental results to the natural world (Cullen and Neale 1994).

Our prediction that changes in water attenuation have a significant impact on *C. finmarchicus* mortality corroborate studies in freshwater ecosystems (Schindler et al. 1996; Williamson et al. 1996), which indicate that changes in chromophoric dissolved organic matter (CDOM) concentration, and therefore water attenuation, may be more important than stratospheric ozone depletion in regulating future levels of UVR. Similar results were found by Arrigo and Brown (1996), when they examined CDOM influences on primary productivity in the Southern Ocean, where ozone loss was as high as 50%. Any increase in water clarity would further exacerbate the impact of UVR. Such increases in UVR could be caused by reductions in dissolved organic carbon loading or photochemical fading of CDOM. The latter is a process by which humic material loses color across the entire absorption spectrum when exposed to sunlight (Zepp 1988; Miller 1994). Photochemical fading has interesting implications, since ozone depletion would enhance this process; irradiance in the UVB range is more effective than longer wavelengths at fading CDOM.

Results of this study indicate that UVR is a substantial source of daily water column mortality of *C. finmarchicus* embryos in the estuary and Gulf of St. Lawrence. Once released, the embryos are vulnerable for ~2 d, the time to hatching, depending on ambient temperature (McLaren et al. 1988). Because of their sinking properties, they would be most susceptible to UVR on the first day, as modeled here.

Although our results are for 2 d in July 1997, the clear sky results likely represent the most damaging meteorological conditions for the region, since solar irradiance is intense at this time of the year and the ambient ozone levels were similar to or less than values in March and in September of that year, as determined by the total ozone mapping spectrometer, which spans the spawning period of *C. finmarchicus* and cod. Furthermore, the use of irradiance calculated with a 50% ozone loss ensures that our analysis has not underestimated the potential damaging effects of UVR.

The effects of UVR may even be more damaging than our calculations with the one-hit embryo mortality BWF suggests, since sublethal exposures to UVB produced significant numbers of nauplii that were deformed and nonviable (Kouwenberg 1999*b*). These nauplii are treated as survivors, but they would not develop into adults. Also, the BWF for *Calanus* embryos was generated from experiments during which some photorepair may have occurred. In nature, rates of repair might be lower, especially during vertical mixing to depths where reactivating wavelengths do not penetrate effectively (Huot et al. 2000).

In addition to its possible influence on *C. finmarchicus* population dynamics, UVR may also impact food availability to Gulf of St. Lawrence fish larvae that feed on early life stages of *C. finmarchicus* and other copepod species (e.g., Runge and de Lafontaine 1996; Runge et al. 1999). It is not known at the present time whether embryos of other copepod species are also as sensitive. In any event, on the basis of the *Calanus* results presented here, we cannot rule out a significant impact of UVR on the productivity of the Gulf of St. Lawrence ecosystem. It should be cautioned, however, that the results of this model should not be used to make quantitative predictions without proper empirical validation. This would include careful investigation of repair processes (Jeffrey et al. 1996; Vetter et al. 1999); as previously discussed, the *Calanus* BWF did not quantify photorepair or reciprocity. The BWF experiments were, however, conducted under ecologically relevant conditions, where the embryos did have opportunity for repair, and should therefore be considered a starting point, indicative of the damage to DNA from UVB.

One could extend this model to other regions of the world by using appropriate water attenuation coefficients and irradiance measurements (or modeled values); however, the BWFs were developed for species in the Gulf of St. Lawrence and may not be representative of other populations.

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