

Assessing the Impacts of Solar Ultraviolet Radiation on the Early Life Stages of Crustacean Zooplankton and Ichthyoplankton in Marine Coastal Systems¹

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ABSTRACT: Over the past 10–15 years, solar ultraviolet B (UV-B, 290–320 nm) levels have increased significantly at mid-latitude areas of the Northern and Southern Hemispheres. These increases in UV-B are linked to reductions of stratospheric ozone. Although the variables that affect UV-B penetration into water columns are still under active investigation, there are typically strong correlations between dissolved organic carbon (DOC), chlorophyll *a* (chl *a*), and UV attenuation. This is particularly significant in the context of possible UV-B impacts on marine coastal systems, since DOC and chl *a* are usually much more highly concentrated in these waters than in the open ocean. Observations indicate that the early life stages of crustacean zooplankton and ichthyoplankton present in the first meter of coastal water columns (likely only a small percentage of the total population) are susceptible to UV-B radiation. Variability in cloud cover, water transparency (and the variables that affect it), and vertical distribution and displacement of organisms within the mixed layer have a greater effect on the flux of UV-B radiation to which plankton are exposed than will ozone layer depletion. Although exposure to UV-B can negatively affect planktonic organisms, such direct effects are likely minimal in coastal zones, and within the context of all the other environmental factors that produce the very high levels of mortality typically observed in their early life stages. Indirect effects (e.g., UV-B-induced reduction in the nutritional quality of the food base) have not as yet been adequately evaluated.

Introduction

Long-term data series on solar ultraviolet-B radiation (290–320 nm, UV-B) incident at the Earth's surface indicate that, over the past 10–15 years, UV-B levels have increased significantly at mid-latitude and high-latitude areas of the Northern and Southern Hemispheres (Crutzen 1992; Kerr and McElroy 1993; Madronich et al. 1995; Wardle et al. 1997). These increases in UV-B are linked to reductions of stratospheric ozone (Kerr and McElroy 1993; Madronich 1994; Madronich et al. 1995). Severe seasonal reductions in ozone layer thickness are not restricted to the Antarctic; dramatic depletions have also been recorded over the Arctic (Fergusson and Wardle 1998; Goutail et al. 1999; Dahlback 2001). As a result of air mass mixing, deep ozone depletion at these high latitudes tends to draw ozone north and southward, resulting in ozone thinning at middle latitudes (Björn et al. 1998; Fergusson and Wardle 1998; Goutail et al. 1999). Ozone layer depletion, and concomitant in-

creases in UV-B, are world-wide phenomena that are inextricably linked to global climatic change (sensu Staehelin et al. 2001).

In contrast to the meteorological database, high spectral resolution measurements of UV-B underwater are rare (reviewed in Kirk 1994; Booth and Morrow 1997; Franklin and Forster 1997). It is clear that UV-B penetrates to depths greater than is widely accepted, in some water columns dramatically so (Booth and Morrow 1997). Although the variables that affect UV-B attenuation are still under active investigation, dissolved organic carbon (DOC) and chlorophyll *a* (chl *a*) are key correlates (Scully and Lean 1994; Morris et al. 1995; Laurion et al. 1997; Kuhn et al. 1999).

A rapidly growing number of studies indicate that UV-B radiation, at current levels, is harmful to aquatic organisms and may reduce the productivity of marine ecosystems (e.g., Siebeck et al. 1994; Häder 1997; deMora et al. 2000; Hessen 2001). Such UV-B-induced reductions in productivity have been reported for phytoplankton, heterotrophs, and zooplankton, the key intermediary levels of marine food chains (Damkaer 1982; Thomson 1986; Cullen and Neale 1994; Chalker-Scott 1995; Smith and Cullen 1995; Booth et al. 1997; Häder 1997; Browman et al. 2000; Browman and Vetter 2001). Analogous studies on planktonic fish eggs and larvae indicate that exposure to levels of UV-

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B currently incident at the Earth's surface results in higher mortality that may lead to poorer recruitment to adult populations (Pommeranz 1974; Hunter et al. 1981, 1982; Williamson et al. 1997; Walters and Ward 1998; Zagarese and Williamson 2000, 2001; Lesser et al. 2001).

Since ozone layer depletion is expected to continue for many more years (albeit at a lower rate; Staehelin et al. 2001), the possible impacts of solar UV-B radiation on marine organisms and ecosystems are under active investigation (recently reviewed in Häder 1997; Browman et al. 2000; deMora et al. 2000; Hessen 2001). This paper assesses the potential impacts of ozone depletion-related increases in UV-B radiation on the early life stages of fishes in coastal ecosystems. Crustacean zooplankton are included in this analysis because of their key role as forage for fish larvae.

Overview of UV-B Optics in Marine Coastal Water Columns

Because the effects of UV radiation are strongly wavelength dependent (e.g., Williamson et al. 2001), accurate measurement of spectral irradiance is fundamental to any study on its biological impact. High resolution UV measurements are essential for the application of biological weighting functions (BWFs), especially for the shortest and most damaging wavelengths: 280–312 nm (Madronich 1993; Williamson et al. 2001). In order to make an assessment of the biological impacts of UV radiation on crustacean zooplankton and ichthyoplankton in coastal ecosystems, measurements of UV irradiance spectra are required.

A general optical characterization of water columns is obtained from diffuse attenuation coefficients (K_{dx}), which are calculated from empirical measurements of spectral irradiance at various depths. For comparative purposes, wavelength-specific 10% depths (the depth to which 10% of the below-surface irradiance penetrates) are often derived from the K_{dx} values. It is important to note that the choice of 10% depth is arbitrary—it is not based upon any correlation with biological impact. Measurements of K_{dx} for UV-B radiation in coastal zones indicate 10% depths of 1–4 m at a wavelength of 310 nm (Booth and Morrow 1997; Kuhn et al. 1999; Fig. 1). Ultraviolet-A radiation (320–400 nm, UV-A) reaches even greater depths. 10% penetration depths are generally smaller in estuarine waters than in clearer offshore waters. All of the values recorded from coastal waters fall near the middle of the rather broad range of 10% depth penetrations previously reported; at 310 nm, a 10% depth of 0.1 m was recorded by Scully and Lean (1994) in Lake Cromwell, Québec, and values as high as 20 m were observed for clear ocean waters

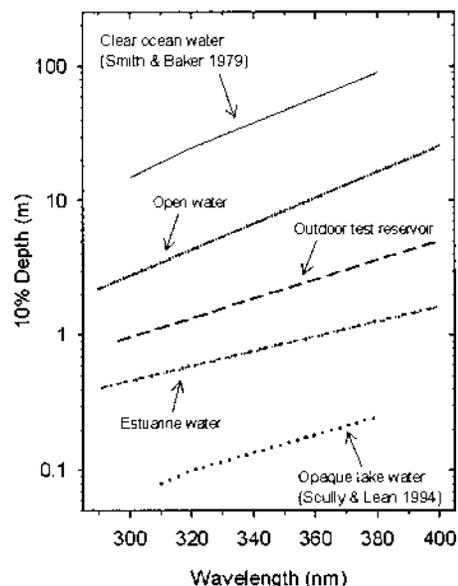


Fig. 1. Ten percent depth penetrations (the depth to which 10% of irradiance just below the surface penetrates) at selected locations in the estuary and Gulf of St. Lawrence, Canada. All values fall within the range reported by Scully and Lean (1994) for the highly UV-opaque Lake Cromwell, Québec, and Smith and Baker (1979) for extremely clear marine waters. (Modified from Browman et al. 2000).

by Smith and Baker (1979). Organisms residing in the near-surface layer could be exposed to biologically damaging levels of UV radiation.

In the estuary and Gulf of St. Lawrence, Canada, DOC was more highly correlated with K_d than was chl *a* (Kuhn et al. 1999). While this is perhaps the most common situation, in extreme cases chl *a* is highly correlated with UV attenuation (Stambler et al. 1997). In freshwater, DOC is the dominant factor in UV attenuation and chl *a* is most often unimportant (Scully and Lean 1994; Morris et al. 1995; Laurion et al. 1997). For most marine water types, there is a significant autocorrelation between DOC and chl *a*, making it difficult to determine their respective contributions to the diffuse attenuation coefficients. The slopes of these relationships imply that yellow substance, and therefore DOC, is important (Kuhn et al. 1999). Because of the mixed influence chl *a* and DOC have on UV attenuation in marine waters, seasonal changes in the relative concentrations of these parameters will significantly affect UV penetration. In this same sense, other factors that affect DOC and chl *a* over the long and short term—climate change, habitat destruction, acid rain, eutrophication of coastal zone waters—will greatly influence the level of UV to which marine organisms are exposed (Schindler et al. 1996; Schindler and

Curtis 1997; Gibson et al. 2000; Pienitz and Vincent 2000).

Overview of UV Impacts on Crustacean Zooplankton and Ichthyoplankton

DIRECT EFFECTS

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; Tartarotti et al. 2000; Lacuna and Uye 2001). 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). Eggs of *Calanus finmarchicus*, a prominent member of the mesozooplankton community throughout the north Atlantic, incubated under UV radiation exhibited low percent hatching compared to those protected from UV (Alonso Rodriguez et al. 2000). 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. In analogous experiments with Atlantic cod (*Gadus morhua*) eggs, exposure to UV-B produced a significant negative effect (Béland et al. 1999); UV-A had no negative effect on cod eggs.

Additional experiments using a solar simulator revealed high wavelength-dependent mortality in both *C. finmarchicus* and cod embryos exposed to UV (Kouwenberg et al. 1999a,b). The strongest effects occurred under exposures to wavelengths below 312 nm. At the shorter wavelengths (< 305 nm) UV-B-induced mortality was strongly dose-dependent, but (for both *C. finmarchicus* and cod) not significantly influenced by dose rate. The BWFs derived for UV-B-induced mortality in *C. finmarchicus* and cod eggs were similar in shape to the action spectrum for UV-B effects on naked DNA (Fig. 2). The wavelength-dependence of DNA damage was similar to that for the mortality effect (Browman et al. 2000; Browman and Vetter 2001). These observations suggest that UV-induced mortality in *C. finmarchicus* and cod eggs is a direct result of DNA damage.

These results indicate that *C. finmarchicus* may be sensitive to variation in incident UV radiation in subarctic regions of the northwest Atlantic Ocean. In these regions, and also in coastal zones, *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 thermocline. Observa-

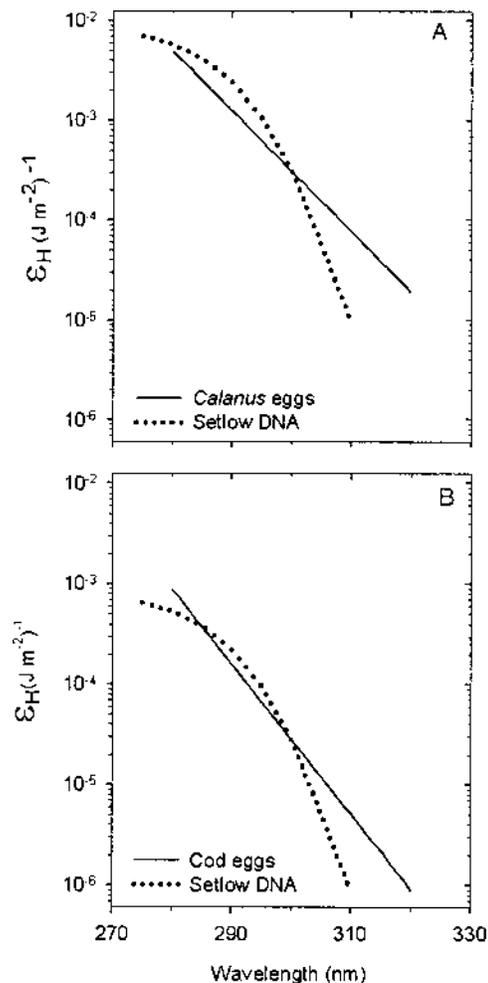


Fig. 2. A) Biological weighting function (BWF) for egg mortality in *Calanus finmarchicus* (solid line). B) BWF for egg mortality in Atlantic cod, *Gadus morhua* (solid line). In both panels, the wavelength-dependence of damage to the naked DNA molecule (data drawn from Setlow 1974) is superimposed as a dotted line. The Setlow curve was normalized against the BWF's value at 300 nm for ease of comparison. (Modified from Browman et al. 2000.)

tions of *C. finmarchicus* egg distribution in the Laurentian channel (Quebec, Canada) show the majority of eggs residing in the surface layer (above 5–10 m) during daytime, where they hatch into the first naupliar stage 1–2 d after maternal release.

Although *C. finmarchicus* appears susceptible to UV radiation, results from the few other species that have been studied are highly variable; some species suffer strong negative impacts, while others are resistant (Damkaer 1982; Thomson 1986; Dey et al. 1988; reviewed in Zagarese and Williamson 2000). The factors determining this susceptibility are many and complex, but include seasonality and location of spawning, vertical distribution, presence of UV screening compounds, and the ability

to repair UV-induced damage to tissues and the DNA molecule (e.g., Williamson et al. 2001).

The work of Marinaro and Bernard (1966), Pommeranz (1974), and Hunter et al. (1979, 1981, 1982) provided clear evidence of the detrimental effect of UV-B on the planktonic early life stages of marine fishes. Hunter et al. (1979), working with northern anchovy (*Engraulis mordax*) and Pacific mackerel (*Scomber japonicus*) embryos and larvae, reported that exposure to surface levels of UV-B could be lethal. Significant sub-lethal effects were also reported: lesions in the brain and retina, and reduced growth rate. The study concluded that, under some conditions, 13% of the annual production of northern anchovy larvae could be lost as a result of UV-B related mortality (Hunter et al. 1981, 1982). With the exception of a small (but rapidly growing) number of recent studies, little additional information has been generated for the effects of UV-B on ichthyoplankton. The results presented above for Atlantic cod substantiate earlier results on the lethal effects of UV-B on planktonic fish eggs. As is the case for copepods, the early life stages of fishes will be differentially susceptible to UV radiation and for the same reasons. Some studies conclude that UV effects will be significant (e.g., Williamson et al. 1997; Battini et al. 2000; Lesser et al. 2001), while others conclude that they will not (e.g., Kuhn et al. 2000; Dethlefsen et al. 2001; Steeger et al. 2001).

INDIRECT EFFECTS

The great majority of UV-B radiation research examines direct effects on specific organisms. The few studies that have investigated indirect effects illustrate how UV-B-induced changes in food-chain interactions can be far more significant than direct effects on individual organisms at any single trophic level (e.g., Bothwell et al. 1994; Williamson et al. 1999; and see discussion in Hessen et al. 1997). Recent investigations point to the possibility of such a food-chain effect in both marine and freshwaters; UV-B exposure (even at low dose rates) reduces the total lipid content of some microalgae (Arts and Rai 1997; Plante and Arts 1998; Arts et al. 2000) and this effect includes the polyunsaturated fatty acids (PUFA; Goes et al. 1994; Wang and Chai 1994; Hessen et al. 1997). For zooplankton and fish larvae, the only source of these fatty acids is dietary—since they cannot synthesize them de novo, they must be obtained through prey organisms (e.g., Goulden and Place 1990; Rainuzzo et al. 1997; Reitan et al. 1997; Sargent et al. 1997). Dietary deficiencies of these fatty acids are manifested in many ways. For example, in the freshwater Cladoceran *Daphnia* spp., growth rates are correlated with the sestonic content of eicosapentaenoic

acid (Müller-Navarra 1995a,b; De Lange and Van Donk 1997; Scott et al. 1999). In Atlantic herring (*Clupea harengus*), dietary deficits of essential fatty acids, in particular docosahexaenoic acid, reduces the number of rods in the eyes (Bell and Dick 1993) and also negatively affects the feeding of these fish under low light intensities (Bell et al. 1995; Masuda et al. 1998). Other negative consequences of essential fatty acid deficits have also been reported (e.g., Kanazawa 1997; Rainuzzo et al. 1997; Bell et al. 1998). A UV-B-induced reduction in the PUFA content of microalgae will be passed on to the herbivorous zooplankton that graze upon them, also decreasing the levels of this essential nutrient that are available to be taken up by fish larvae. Since fish larvae (and their prey) require these essential fatty acids for proper development and growth, such a reduction in the nutritional quality of the food base has potentially widespread and significant implications for the overall productivity and health of aquatic ecosystems.

Exposure to UV radiation, especially UV-B, has many harmful effects on animal health. These may result in poorer performance, or death, even though they are not directly induced by the UV exposure. UV-B suppresses both systemic and local immune responses to a variety of antigens, including micro-organisms (Hurks et al. 1994; Garssen et al. 1998). In addition to suppressing T-cell-mediated immune reactions, UV-B also affects nonspecific cellular immune defences. Recent studies demonstrate disturbed immunological responses in UV-B-irradiated roach (*Rutilus rutilus* L.); the function of isolated head kidney neutrophils and macrophages (immuno-responsive cells) were significantly altered after a single dose of UV-B (Salo et al. 1998). Natural cytotoxicity, assumed to be an important defence mechanism in viral, neoplastic, and parasitic diseases, was reduced. A single UV-B exposure decreased the ability of fish lymphocytes to respond to activators, and the reduction was still visible 14 d after the single exposure (Jokinen et al. 2001). This indicates altered regulation of lymphocyte-dependent immune functions. Exposure to UV-B induces a strong systemic stress response which is manifested in the fish's blood by an increased number of circulating phagocytes and elevated plasma cortisol levels (Salo et al. 2000a). Exposure to UV-A radiation induced some of the same negative effects on the immune system (Salo et al. 2000b). Since high cortisol levels induce immunosuppression in fishes (Bonga 1997) it is now clear that the effect of UV-B exposure on the immune system has both direct and indirect components. These findings strongly suggest that the immune system of fishes is significantly impacted by

exposure to a single, moderate-level dose of UV-B radiation. At the population level, such a reduction in immune response might be manifested as lowered resistance to pathogens and in increased susceptibility to diseases. The ability of the fish immune system to accommodate increases in solar UV-B radiation are unknown. It is possible that the immune system of young fishes is highly vulnerable to UV-B radiation because lymphoid organs are rapidly developing and critical phases of cell proliferation, differentiation, and maturation are occurring (Grace and Manning 1980; Botham and Manning 1981; Chilmonczyk 1992). It is also possible that exposure to ambient UV-B radiation impedes the development of the thymus or other lymphoid organs resulting in compromised immune defense later in life. The effect of UV radiation on the immune function of fish embryos and larvae, and on the development of the immune system, is unknown.

Other indirect effects of UV radiation are also possible. For species that spawn in the surface layer, UV-B may affect sperm quality (sensu Don and Avtalion 1993; Valcarcel et al. 1994) and affect fertilization rate and genome transfer. If UV reduces the productivity of protozoans and crustacean zooplankton there will be less prey available for fish larvae and other organisms that feed upon them.

Existing studies of UV-B impacts have almost all examined the effects of short-term exposure on biological end points such as skin injury (sunburn), DNA damage, development and growth rates, immune function, or outright mortality. Few studies have examined the potential effects of longer-term (low-level) UV-B exposures (but see Fidhiany and Winckler 1999). All of these indirect (and longer-term) effects of UV radiation have yet to be investigated.

An Overview of the Ecological Context

A quantitative assessment of direct UV-B effects on the population dynamics of the planktonic early life stages of marine organisms requires detailed information on vertical distributions in the mixed layer of the water column (with high resolution in the upper 10 m), surface UV-B irradiance during the reproductive season and subsurface spectral irradiance for waters in nursery areas (see Kuhn et al. 1999), biological weighting functions—which explicitly consider the possibility of photorepair—for the effect of UV-B radiation on mortality (see Kouwenberg et al. 1999a,b; Browman et al. 2000; Tartarotti et al. 2000; Grad et al. 2001), and a mathematical simulation 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 mete-

orological and hydrographic conditions. All of these components can be incorporated into a broader simulation model to provide an assessment of UV-B effects on a population of early life stages distributed (and circulating) throughout the mixed layer (see Neale et al. 1998, 2001; Kuhn et al. 2000; Neale 2001).

The model developed by Kuhn et al. (2000) incorporates all of the physical and biological information listed above and generates an absolute estimate of mortality under different meteorological and hydrographic conditions. As a result, the relative impacts of differing combinations of environmental conditions—for example, a typical clear versus a typical overcast sky; a typical clear versus a typical opaque coastal water column; current ambient versus realistically thinned ozone layer—can be evaluated (Kuhn et al. 2000).

For *C. finmarchicus* eggs in the estuary and Gulf of St. Lawrence, UV-B-induced mortality under all model scenarios ranged between < 1% and 51%, with a mean \pm SD of $10.05 \pm 11.9\%$ ($n = 48$ modelled scenarios). For cod, none of the model scenarios produced a UV-B-induced mortality greater than 1.2%, with a mean \pm SD of $1.0 \pm 0.63\%$ ($n = 72$ modelled scenarios). The most important determinant of survivorship (for both species) was water column transparency (Fig. 3). Even when ozone layer depletions of 50% were modelled, the effect on mortality remained far lower than that resulting from either thick cloud cover or opacity of the water column. Analogous simulation models constructed for phytoplankton (primary production) yielded similar interpretations of the relative effects of mixed layer depth, cloud cover, and ozone layer thickness on UV-induced impacts (Neale 2001; Neale et al. 2001). The simulation model of Huot et al. (2000) indicated that ozone thickness could in some instances be the single most important determinant of DNA damage in bacterioplankton.

Although these simulation model based predictions are instructive, data to parameterize such models are scarce, and it will be some time before we are in a position to make similar predictions for many species inhabiting a range of geographic locations. These models assume that the BWFs used to parameterize them do not seriously violate the principle of reciprocity (the Bunsen-Roscoe principle, De Gruijl et al. 1986; Coohill 1991; Buma et al. 1997; Cullen and Neale 1997; Browman et al. 2000; Zagarese and Williamson 2000; Browman and Vetter 2001; Grad et al. 2001). In the context of a UV 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

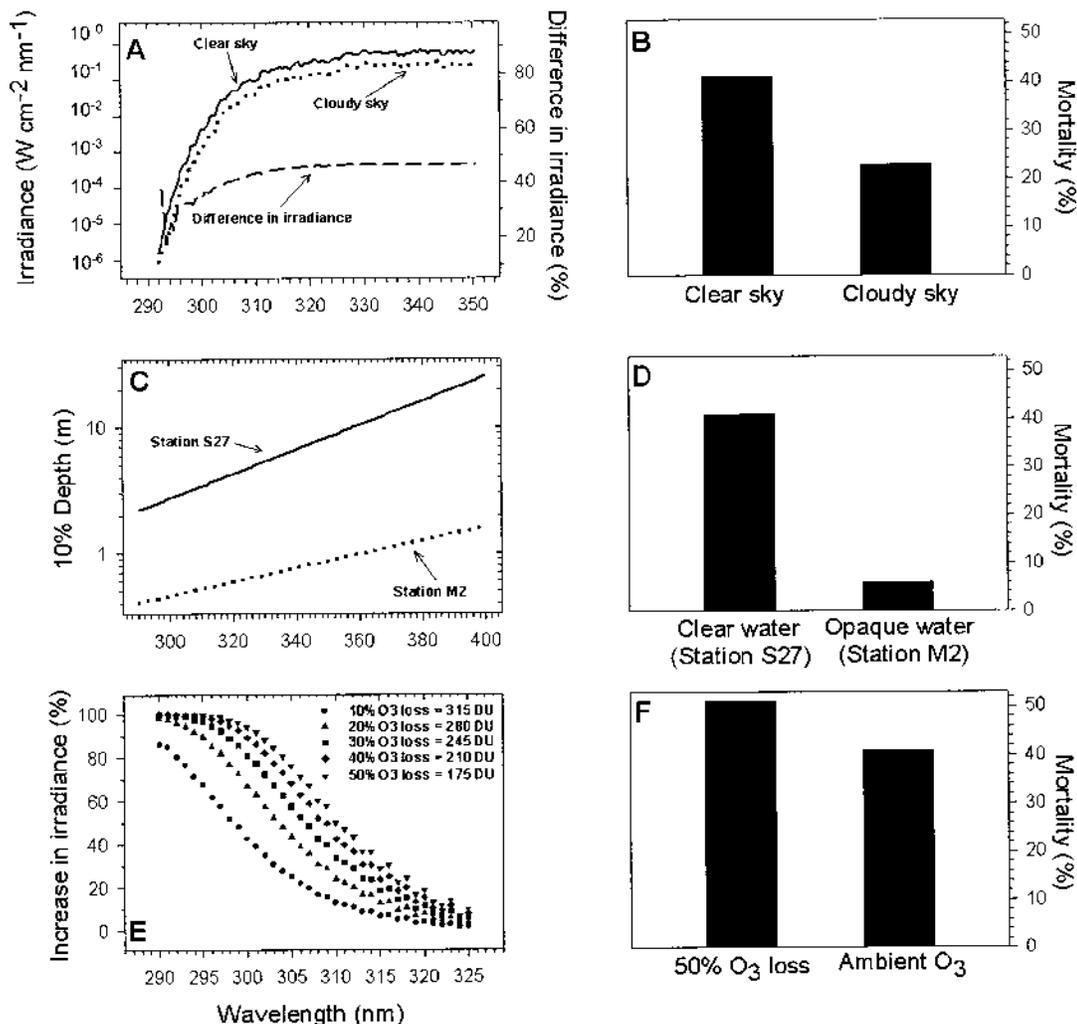


Fig. 3. Output of a mathematical simulation model (Kuhn et al. 2000) illustrating the relative effects of selected variables on UV-induced mortality in *Calanus finmarchicus* embryos. (A–B) Clear versus cloudy sky. When spectral irradiance is plotted on a log scale (as on the left y-axis of panel A, the difference between clear and cloudy skies appears small. When plotted as a percent (as on the right y-axis), the magnitude of the difference in irradiance becomes clearer. Even though the cloudy sky versus clear sky lines appear similar, the percent difference in the UV waveband is actually approximately 50%. (C–D) Clear versus opaque water column. The clear station (E–F) 50% thinning of ozone versus ambient ozone.

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. BWFs derived from such results would be less reliable and of limited use. The principle of reciprocity has not often been rigorously evaluated and, when it has, the results have been inconsistent (e.g., see the discussion in Browman et al. 2000; Grad et al. 2001). Reciprocity held under the conditions used to generate the BWFs employed in the Kuhn et al. (2000) model (Browman and Vetter 2001).

UV Impacts in the Coastal Zone

The Kuhn et al. (2000) simulation model provides an opportunity to assess the relative contributions of several key variables in determining the UV exposure of planktonic early life stages circulating in a mixed water column (Fig. 3). This analysis demonstrates that variability in cloud cover, water quality, and vertical distribution and displacement within the mixed layer, all have a greater effect on the flux of UV-B radiation to which the early life stages of zooplankton and fishes are exposed than will ozone layer depletion. All else being held equal, the most important determinant of

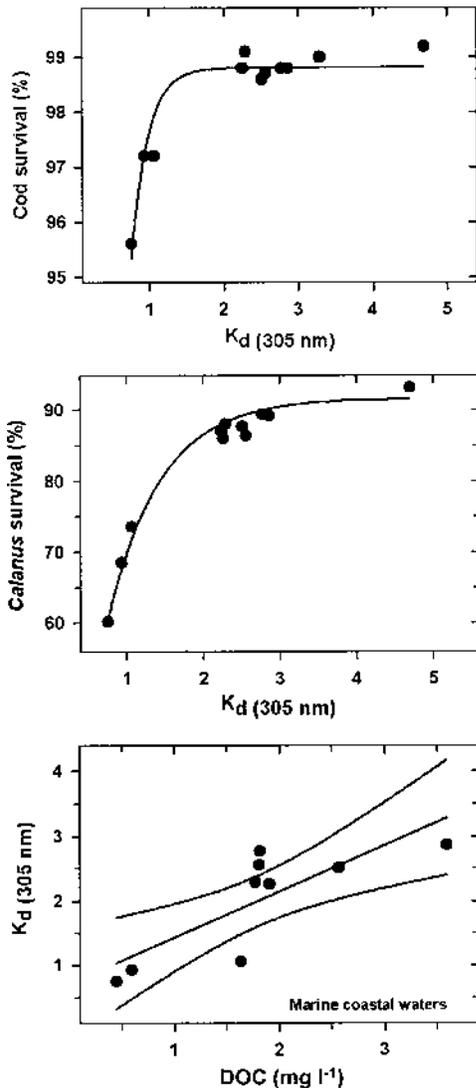


Fig. 4. Output of a mathematical simulation model (Kuhn et al. 2000): A) Dissolved organic carbon (DOC) versus diffuse attenuation coefficient (K_d) at 305 nm from field measurements in the estuary and Gulf of St. Lawrence, Canada. The straight line is the regression, the curved lines are the 95% confidence intervals. B) K_d at 305 nm versus modelled survival of *Calanus finmarchicus* embryos exposed to UV radiation in a mixed water column. C) K_d versus modelled survival of Atlantic cod (*Gadus morhua*) embryos exposed to UV radiation in a mixed water column.

UV-induced mortality was transparency of the water column (Fig. 3).

Since DOC and chl *a* are strongly correlated with the transparency of water columns to UV, it follows that the concentrations of these substances in coastal zones (usually very high) will be the overriding factor affecting UV-induced mortality. The Kuhn et al. (2000) simulation model supports this contention (Fig. 4). DOC levels in eutrophic coast-

al zones is often greater than 3–4 mg l⁻¹; the diffuse attenuation coefficients for UV-B associated with such levels (Fig. 4a) essentially protect *C. finmarchicus* and cod eggs from UV-induced mortality (Fig. 4b,c). In this context, DOC can be considered as a sunscreen for the organisms inhabiting eutrophic coastal zone waters. A recent report by Lesser et al. (2001) indicates that the early life stages of Atlantic cod may be susceptible to UV impacts in Gulf of Maine waters.

Closing Perspective

Although UV-B radiation can have negative impacts (direct effects) on crustacean zooplankton and ichthyoplankton populations, it must be viewed as only one among many environmental factors—bacterial and viral pathogens, predation, toxic algae—that produce the mortality typically observed in the planktonic early life stages of these organismal groups. For zooplankton and fish species whose early life stages are distributed throughout the mixed layer, it seems most likely that UV-B radiation would represent only a minor source of direct mortality for the population, and particularly in sunscreen-protected coastal zones. For those species whose early life stages are neustonic, there may be circumstances (albeit rare)—cloudless sky, thin ozone layer, no wind, calm seas, low nutrient loading—under which the contribution of UV-B radiation to the population's mortality could be much more significant. The impact of indirect effects have not as yet been adequately evaluated.

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