13 Impacts of Ultraviolet Radiation on Crustacean Zooplankton and Ichthyoplankton: Case Studies from Subarctic Marine Ecosystems

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13.1 Introduction

A rapidly growing number of studies indicate that solar ultraviolet B radiation (280–320 nm, UV-B), 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). Such UV-B-induced decreases in productivity have been reported for bacterioplankton, 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; Häder 1997). Analogous studies on the planktonic (often neustonic) early life history stages of crustacean zooplankton and ichthyoplankton, although much rarer, indicate that exposure to levels of UV-B currently incident at the earth's surface could result in higher mortality that may lead to poorer recruitment to the adult populations of marine and freshwater fishes (Pommeranz 1974; Hunter et al. 1981, 1982; Williamson et al. 1997; Walters and Ward 1998; Zagarese and Williamson 2000). This chapter focuses on the effects of UV (280–400 nm) radiation on crustacean zooplankton and ichthyoplankton in subarctic marine ecosystems.

The effects of UV radiation on these two trophic levels have been thoroughly reviewed in several recent primary publications and book chapters (e.g. Siebeck et al. 1994; Browman et al. 2000; Zagarese and Williamson 2000). Thus, we will not cover this same ground here. Rather, our material is presented as independent case studies. The first case study – conducted in Norway – applied molecular techniques to assess UV-induced DNA damage to the eggs and larvae of Arcto-Norwegian cod (*Gadus morhua*), incubated in situ. The second case study – conducted in Canada – used a combination of approaches to address the issue of UV-induced effects on the calanoid copepod *Calanus finmarchicus*, and on the eggs of Atlantic cod (*Gadus morhua*). Among other advantages, this format provides readers insight into the development and

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implementation of two research programs, in two parts of the world, which applied different approaches to address similar questions.

13.2 Case Study I – Lofoten, Norway

R.D. Vetter and colleagues from the Southwest Fisheries Science Center, La Jolla, California, USA, together with Osmond Holm-Hansen and associates at the Scripps Institution of Oceanography, La Jolla, have been collaborating with Professor Hans Christian Eilertsen and others at the Norwegian College of Fisheries, University of Tromsø, Tromsø, Norway, on a series of ongoing studies into the effects of UV radiation on phytoplankton, zooplankton and ichthyoplankton in high latitude environments. In this chapter, results on the ichthyoplankton portion of these studies will be summarized.

Unlike the Antarctic, the Arctic has significant areas of human settlement and a high dependence of indigenous peoples on marine resources. This is particularly true in northern Europe where the ocean currents and local climatology provide relatively mild ice-free conditions. Tromsø, Norway, is a city of more than 40,000 located at about 70° N latitude (roughly the equivalent latitude to the edge of the permanent ice pack in Antarctica). The city is a hub for year-round fisheries and aquaculture activities. Our investigations have combined experimental studies conducted at the University of Tromsø's

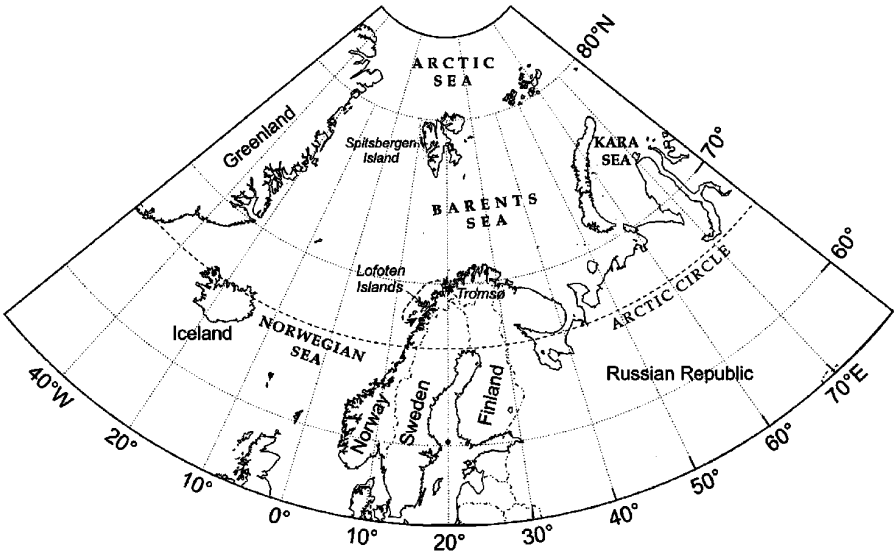

Fig. 13.1. Map of the case study I site near Lofoten, Norway

Center for Aquaculture (Havbruksstasjonen) on Ringvassøy in northern Norway, and field studies conducted in the Lofoten Islands (Fig. 13.1). Our studies have taken advantage of the aquaculture facilities at Havbruksstasjonen as a source of eggs and larvae of known parentage and age with which to carry out experiments. Although solar simulators are improving and provide a means of administering a precise and repeatable dose (e.g. Kouwenberg et al. 1999a,b), it is difficult to precisely match the vertical spectral attenuation, and diel changes in intensity and spectral character of natural light. This is particularly true at high latitudes where fish can experience 24 h of daylight during the summer months. Since we initially knew nothing about the nature of damage and the process and timing of photorepair in high latitude fishes, we elected to use natural solar radiation for all experiments. Thus, our studies focus on the effects of natural solar ultraviolet radiation on the early life history stages of the Arcto-Norwegian stock of cod (*Gadus morhua*).

13.2.1 Hydrographics of the Lofoten Area

The high latitude environment of northern Norway is the site of some of the most productive fisheries in the world. In Norwegian waters, cod leave the continental shelf and migrate to known spawning locations within coastal fjords. In these locations, cod congregate near the bottom and spawn repeatedly over the course of several weeks. In the Lofoten Islands, these spawning banks have been the location of traditional cod fisheries for the past 1000 years (Hjort 1914). Cod eggs are spawned at depth and the positively buoyant eggs gradually rise to the surface. The surface waters of the spawning banks contain vast quantities of eggs and newly hatched larvae. It is these early life stages, and the optical conditions, on the spawning banks, that have been the focus of our investigations into the effects of solar ultraviolet radiation on cod. Our observations have included a range of responses to UV exposure including behaviour, developmental delay, cell cycle changes, mortality, and DNA damage. All experimental studies have employed cod eggs and larvae spawned in captivity. All field and laboratory exposures have used natural sunlight.

13.2.2 The UV Environment of the Norwegian Coast

Frequent cloud cover punctuated by bright sunny days characterizes the maritime climate of northern Norway. Ozone thickness is clearly important with respect to long-term charges in the northern high latitude UV environment. Ozone thickness has been monitored by the University of Tromsø since

1935 and continues to be monitored to this day (Henriksen et al. 1992a,b, 1993, 1994). Atmospheric changes do seem to be occurring (IASC Report 1995) but have not been detected on the ground in Tromsø (Henriksen et al. 1992b; Stolarski et al. 1992). This may be due to the high incidence of cloud cover which is the primary determinant of daily changes in surface UV irradiance in these maritime environments (Lubin and Jensen 1995). In addition to surface irradiance, the UV environment of eggs and larvae is also determined by the UV-absorbing properties of seawater and the vertical

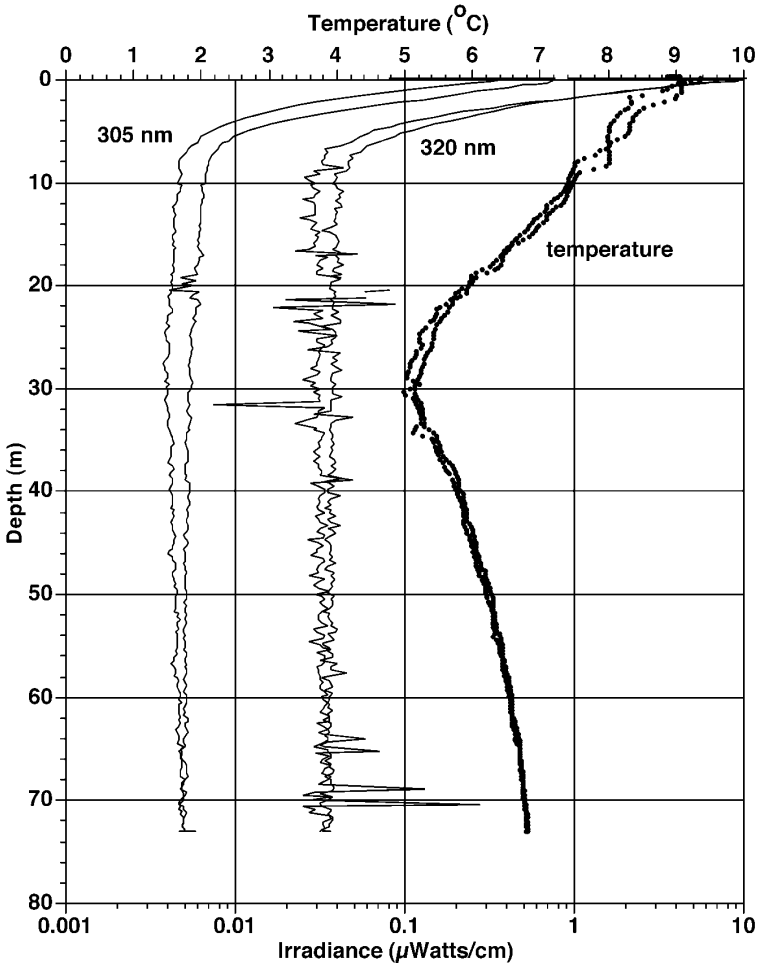

Fig. 13.2. Vertical profiles of temperature and the attenuation of UV irradiance at a spawning location in Austnesfjorden, Lofoten Islands, Norway, 7 June 1995. Measurements were made with a Biospherical Instruments PUV 500. UV-B at 305 nm was rapidly attenuated and was not detectable below 10 m

distribution of the eggs and larvae. Here, the unusual properties of fjords provide an environment different from the open waters of the Gulf of St. Lawrence study site of Browman and colleagues (Browman et al. 2000; this Chap.).

UV attenuation in surface waters is dependent upon living and dead particulate matter (generally in the form of sediments and phytoplankton), and the presence of dissolved organic compounds that absorb in the UV (Smith and Baker 1979; Kirk 1994; Kuhn et al. 1999). UV attenuation is typically exponential with depth in well-mixed surface waters. Unlike typical oceanic waters, the fjord environment often contains high amounts of freshwater runoff of recent terrestrial origin. This melt water can contain large amounts of surface sediments, which of course block and scatter all wavelengths. However, they also contain terrestrial plant organic matter (Gelbstoff) that has high specific absorbance in the UV. As a result, apparently clear fjord waters may have a high capacity to block UV. At our study sites, including the Lofoten Islands, UV-B was generally not detectable below 10 m (Helbling et al. 1996; Fig. 13.2).

In the protected fjord environment wind sheer is often reduced relative to nearby open water. When wind is low, mixing is weak, and buoyant eggs are free to float at-or-near the air-sea interface where UV dose is highest (Solemdal and Sundby 1981; Sundby 1983). Plankton tows taken near the surface in the Lofoten Islands often contain massive numbers of cod eggs and larvae.

13.2.3 UV Responses in Arcto-Norwegian Cod Eggs

13.2.3.1 Behavioural Responses

Behavioural responses to UV are not generally considered with respect to eggs, but to the extent that depth and the time of day at which eggs are released are regulated, they should be considered as potential responses of ecological importance. Large adult cod in sea pens will submerge on sunny days and remain near the surface on cloudy days, so it is not unreasonable to assume that they can sense and respond to the UV environment. There is some evidence that buoyancy in cod eggs can be regulated, and this would affect the potential for exposure to high doses near the sea surface. Buoyancy changes in response to environmental salinity have been observed (Thorsen et al. 1996) but no studies have yet been done that examine changes in spawning behaviour or egg properties in response to UV.

13.2.3.2 UV Blocking in the Egg

The leathery egg shell or chorion, as well as the fluid-filled perivitelline space and the developing embryo, can contain compounds that absorb UV light (Grant et al. 1980; Dunlap et al. 1995). While these compounds may serve other functions (Dunlap and Yamamoto 1995), it has been hypothesized that in some marine eggs they may serve to protect cellular function against UV damage in the developing embryo (Carefoot et al. 1998). Also, cod eggs float yolk side up so that the rapidly dividing cells of the embryo may be protected from downwelling irradiances by the more inert oil globule and yolk proteins.

One way to test the protective effects of the egg environment is to place developing eggs and newly hatched larvae in the same chamber and expose them to an identical regime of natural sunlight. If protection is important, the eggs should have lower mortality and sustain less DNA damage than the hatched embryos. In the Arcto-Norwegian cod, the egg clearly provides some

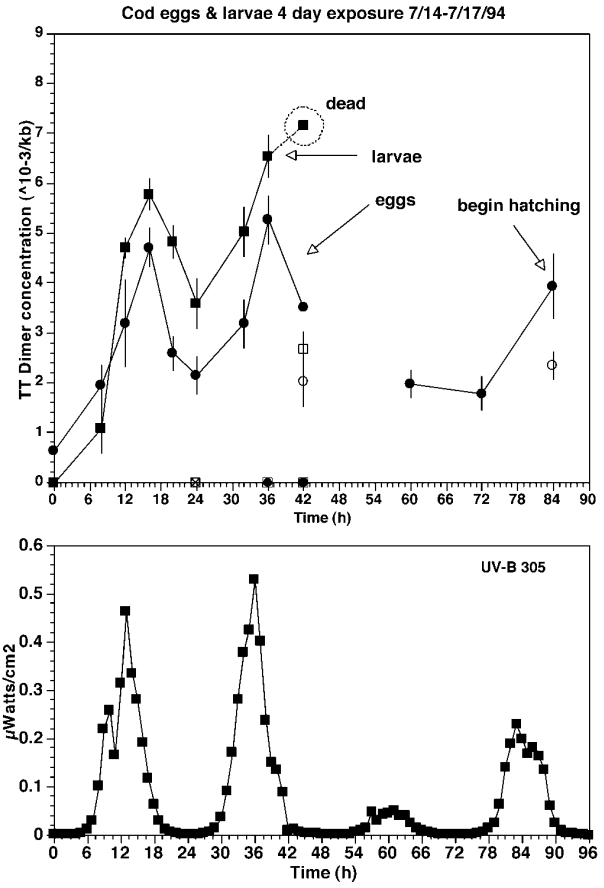

Fig. 13.3. Egg and larval differences. Eggs and newly hatched yolk-sac larvae were placed in a series of quartz cylinders and exposed to natural sunlight in an outdoor tank at the University of Tromsø, Aquaculture Station (70°N latitude). One cylinder containing several hundred eggs and larvae was harvested at different times of day and night. UV dose (305 nm), DNA damage as CPDs, and mortality were recorded. *Open symbols* are Mylar controls

protection (Fig. 13.3). Eggs consistently contained much fewer cyclobutane pyrimidine dimers (CPDs), a form of DNA damage caused only by UV-B radiation (Vetter et al. 1999). Mortality differences provide further evidence of the protective effects of the egg environment. In this preliminary experiment, all of the larvae died by the end of the second day (Fig. 13.3). The majority of eggs survived for two additional days and eventually hatched. Differential sensitivity in eggs and larvae (implying UV protection) is not a property of all fish eggs. Northern anchovy, *Engraulis mordax*, show little protective effect of the egg as evidenced by similar levels of CPDs in eggs and larvae (Vetter et al. 1999, 2001). Although the optical properties of the solid chorion have not been investigated, cod eggs are a source of some of the first described small molecular weight UV blocking compounds, including the aptly named gadusol (Grant et al. 1980).

13.2.3.3 Developmental Delay and Egg Mortality

In our early experiments we made no attempt to separate the effects of UV-B from UV-A (320–400 nm). In subsequent experiments, we included three treatments: visible, visible+UV-A, and visible+UV-A and B. UV-B was excluded with Mylar and UV-A and B were excluded with a "theater film" with a sharp cutoff at 400 nm. For these experiments 16.5-cm-diameter quartz cylinders that were 16.5 cm high were placed on end, on a flow-through water table, and exposed to a natural day–night regime. Each cylinder had 15 cm of useable depth with mesh screening on the bottom so that larvae or eggs were retained but water could exchange. Two or three replicates of each treatment were placed randomly on the water table. With this experimental design we took a closer look at the effects of UV-A and UV-B on the rates of embryonic development as well as mortality. Each day the numbers of dead eggs were counted and the stages of the developing embryos compared to published descriptions (Fossum 1986).

As in the preliminary experiments (Fig. 13.3), there was a clear effect of UV-B on mortality but there was no difference in mortality between visible and visible plus UV-A (Fig. 13.4). Examination of the developmental stages in treatments exposed to visible plus UV-A and B clearly showed that a sublethal response on developmental delay occurred on day 3 (Table 13.1), prior to the high mortality exhibited on day 4 (Fig. 13.4). There was no measurable effect of the visible plus UV-A treatment on mortality (Fig. 13.4). However, we did begin to see a sublethal effect of UV-A on developmental delay (Table 13.1). Our results for mortality agree quite well with the measurements and biological weighting functions of the Canadian studies (Kouwenberg et al. 1999a,b; Browman et al. 2000), which clearly show that UV-B is responsible for the main portion of the damage spectrum. Sublethal UV-A effects were not observed in the Canadian studies. The ecological significance of the UV-A-

Table 13.1. Effects of UVR on developmental rate of cod embryos. Developmental stages of day 3 and 4 embryos exposed to natural solar irradiance in late June 1996 at 70°N. Embryos exposed to Visible+UVA and B were delayed relative to other groups on day 3 and died on day 4 (see Fig. 13.4). Embryos exposed to Visible+UVA were developmentally delayed by day 4. Normal embryos hatch in ~14 days at 7–8 °C. Values are percentages of embryos in the stage indicated at top of table

Stage no.	14–15 Blastula	16 Beginning gastrula	17–18 Early gastrula	19 Middle gastrula	20 Early epiboly	21 Late epiboly	22–23 Blastopore closure
Day 3							
Visible	0.7	–	–	78.6	10.5	–	10.1
Visible+UVA	2.0	–	–	97.5	0.5	–	–
Visible+UVA and B	2.7	34.7	60.0	–	2.7	–	–
Day 4							
Visible	–	–	–	–	3.6	96.4	–
Visible+UVA	–	–	–	–	71.4	28.6	–
Visible+UVA and B	–	–	All died	–	–	–	–

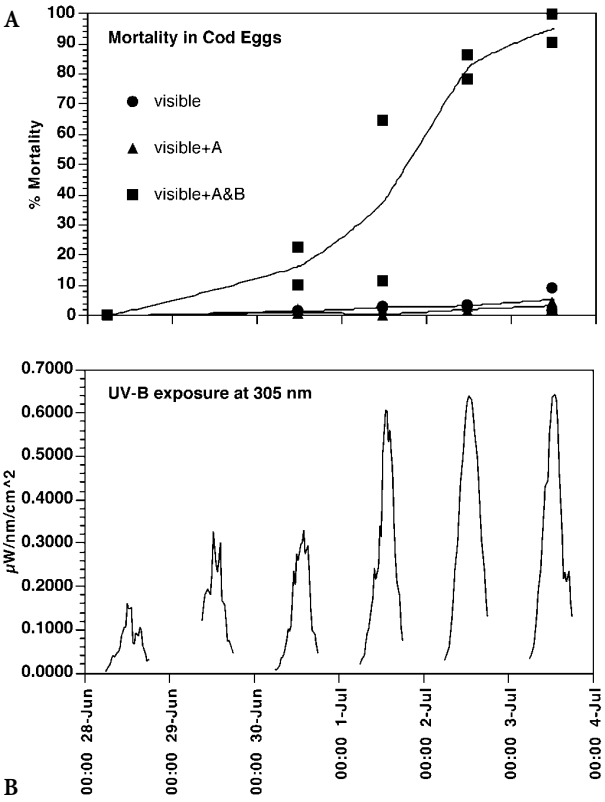

Fig. 13.4A,B. Effects on egg mortality. **A** Mortality of early embryos exposed to natural solar irradiances in late June-early July at 70°N latitude in 1996. *Symbols* are the values for each of two replicate cylinders and the *line* is drawn through the mean. **B** Solar irradiance was not constant for the 6 days of the experiment. Exposure to UVB resulted in almost complete mortality. UV-A had no measurable effect on mortality

induced developmental delay is not known but we stress that natural sunlight was used for our experiments so the results should at least be applicable to eggs floating near the surface (=15 cm).

13.2.4 UV Responses in Arcto-Norwegian Cod Yolk Sac Larvae

13.2.4.1 Behavioural Responses

We made no attempt to quantitatively measure behavioural responses to UV, but there did appear to be a clear response to UV-B. Cod yolk sac larvae are pigmented, and readily observable with the naked eye. When placed in the quartz cylinders on the outside wet table with three replicate treatments of visible, visible plus UV-A, and visible plus UV-A and B, larvae distributed themselves evenly throughout the vertical extent of the cylinder (15 cm) under the visible and visible+UV-A treatments. In the treatments exposed to visible+UV-A and B larvae were consistently found at the bottom of the cylinders, particularly at peak solar intensity. This was observable even on the first few days of the treatments when mortality or morbidity was not a factor.

13.2.4.2 Mortality Effects

In the preliminary experiments (Fig. 13.3), exposure to full natural summer sunlight at 70° N latitude was lethal. In more detailed experiments with better replication, we examined the effects of visible, visible+UV-A, and visible+UV-A and B on mortality and a variety of other biological properties (Fig. 13.5). In these experiments UV-B was 100 % lethal on day 5. We emphasize that this is not a cumulative dose experiment in the sense of the Canadian studies (Kouwenberg et al. 1999a,b; Browman et al. 2000), because daily dose varied with cloud conditions (Fig. 13.5B). Yolk sac larvae on day 6 showed a sudden increase in UV-A mortality after 2 days of high solar intensity (Fig. 13.5). This effect was observed even though the visible+UV-A treatment exhibited almost no DNA damage (data not shown). This result may have been due to exhaustion of yolk reserves because of higher energetic costs. Other causes such as peroxidative damage may have been a factor. Although this UV-A effect is of physiological interest, it is hard to imagine free swimming larvae (as opposed to buoyant eggs) remaining in the upper 15 cm of the ocean for 6 days in order to receive such an intense dose.

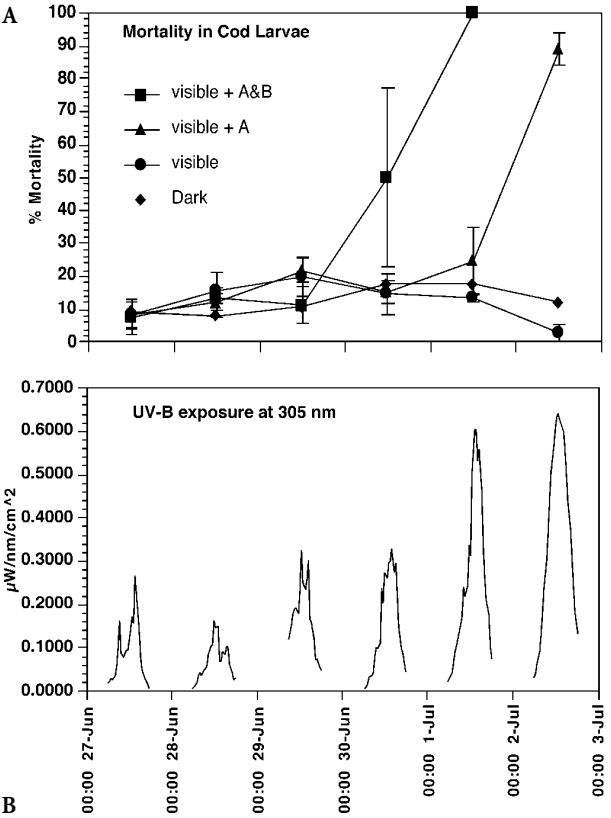

Fig. 13.5A,B. Effects on larval mortality. **A** Mortality of early embryos exposed to natural solar irradiances in late June-early July at 70°N latitude in 1996. *Symbols* are the means and standard deviations for three cylinders and the *line* is drawn through the mean. **B** Solar irradiance was not constant for the 6 days of the experiment. Exposure to UV-B resulted in complete mortality by day 5. UV-A had little effect until the last day where mortality was about 90 %

13.2.4.3 DNA Damage and Repair in Cod Larvae

The process of UV-specific DNA damage and repair has been followed in fish eggs and larvae via a chemiluminescent antibody detection system for the presence of cyclobutane pyrimidine dimers (CPDs) in DNA (Vetter et al. 1999 and references therein). The detection system is sensitive enough to measure DNA damage in a single larva exposed to natural amounts of sunlight. Although many forms of DNA damage can occur, CPDs appear to be formed by the direct absorption of photons into the DNA helix. In the simplest case two adjacent thymines on the same strand of DNA break their hydrogen bonds with the complementary adenines of the adjacent strand and bond with each other. Hence the name pyrimidine, or in this case, thymine dimer (Mitchell and Karentz 1993). This type of damage is repaired by a soluble enzyme, photolyase, which uses the energy in blue light to break the dimer and reform the correct complementary base pairing (Sancar 1996 and references therein). Other, potentially more dangerous forms of damage, such

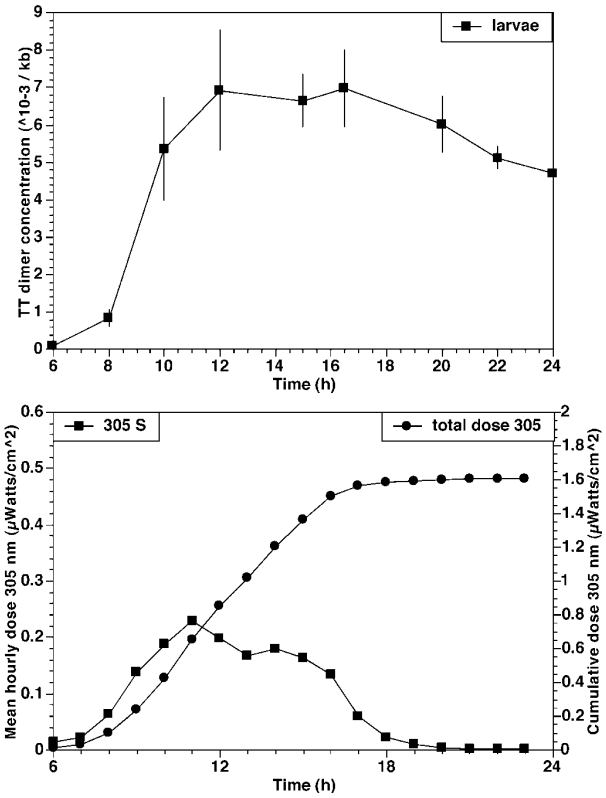

Fig. 13.6. Photorepair in cod larvae. Cod larvae began to accumulate DNA damage in the morning with a rapid increase by 10:00. On this cloudy day, UV-B peaked at 11:00. DNA damage levels approximate the cumulative dose curve rather than the dose rate up to 18:00 when no UV-B can be measured. Some photorepair occurred during the Arctic summer night when longer wavelength light is available

as 6–4 photoproducts, are also formed during the absorption of UV-B and these require more extensive excision repair (Mitchell 1988). The concentration of CPDs in an egg or larva gives a good indication of the depths to which UV-B can damage tissue under natural light and natural water column optics. The accumulation (or disappearance) of CPDs at different times of day is a good indicator of how a larva is damaged by solar UV-B (and also of its ability to repair damage). While the repair of CPDs does not mean there has been no lasting effect of damage on downstream gene expression or cellular energy balance, the accumulation of CPDs over several days is particularly problematic and suggests a very limited capacity to repair DNA damage. Surprisingly, light-dependent repair seems to be the only active form of CPD repair, so further repair ceases at night and commences again the following morning before new CPD formation outpaces repair on the following day (Vetter et al. 1999). An animal that repairs rapidly has a diel CPD curve centered at solar noon that approximates the diel dose-rate curve of solar intensity. An organism without any repair would have a sigmoidal curve that followed the cumulative solar dose curve (at least until DNA damage sites are

saturated). All larvae fall somewhere in between these two theoretical extremes. Anchovy closely approximate the dose-rate curve and do not accumulate CPDs from 1 day to the next. Cod show some capacity for photorepair but at much lower levels. CPD levels in cod larvae climb with the increase in total dose and dose rate as the solar zenith approaches; in the afternoon and early evening CPD levels remain high until midnight even though some repair is occurring (Fig. 13.6A). Cod larvae more closely approximate the cumulative dose curve rather than the dose rate curve (Fig. 13.6B). Cod larvae seem better able to keep up with repair at lower irradiances (cloudy days, deeper depths in water). Unlike the anchovy, in cod high concentrations of CPDs are often carried over into the following day (Fig. 13.3 and unpubl. data). It may be that the absolute levels of photolyase in cod are lower than in anchovy, but it could also be that the kinetics of photolyase enzyme activity, which is highly temperature sensitive, may be limited under the colder conditions of high latitude environments. This will be a productive area of future investigations.

13.2.5 In-Situ Measurements on the Lofoten Spawning Banks

13.2.5.1 DNA Damage Under Natural Conditions

Laboratory experiments were designed to mimic the worst case for natural populations, eggs and larvae living near the surface for an entire solar cycle. Clearly, most larvae occur deeper in the water column where UV light is quickly attenuated. To examine the effects of depth on DNA damage rates, we suspended larvae of known age with no previous exposure to UV light into the water column at Austnesfjord in the Lofoten Islands. Racks of quartz cylinders, each containing about 200 larvae, were suspended at 1, 3, 5 and 10 m in the water. Racks were placed in the water at midnight. Beginning at dawn, divers retrieved cylinders from the racks at 3-h intervals (Fig. 13.7A). The optical cast (Fig. 13.2) corresponds to this experiment. Cod larvae sustained measurable DNA damage under the optical conditions of the Lofoten spawning banks. Larvae at 1 m rapidly accumulated DNA damage (Fig. 13.7). The amounts of DNA damage at 3, 5 and 10 m were detectable but far lower than at 1 m. This agrees with the rapid attenuation of UV-B in the fjord waters. For cod, there was not a decrease in CPDs during the afternoon and evening, but there was for anchovy (Fig. 13.7). As with the laboratory exposures, this indicates that even though the anchovy sustain much greater levels of damage at the higher irradiances typical of temperate waters, they possess a much greater capacity for photorepair than the cod (Fig. 13.7B).

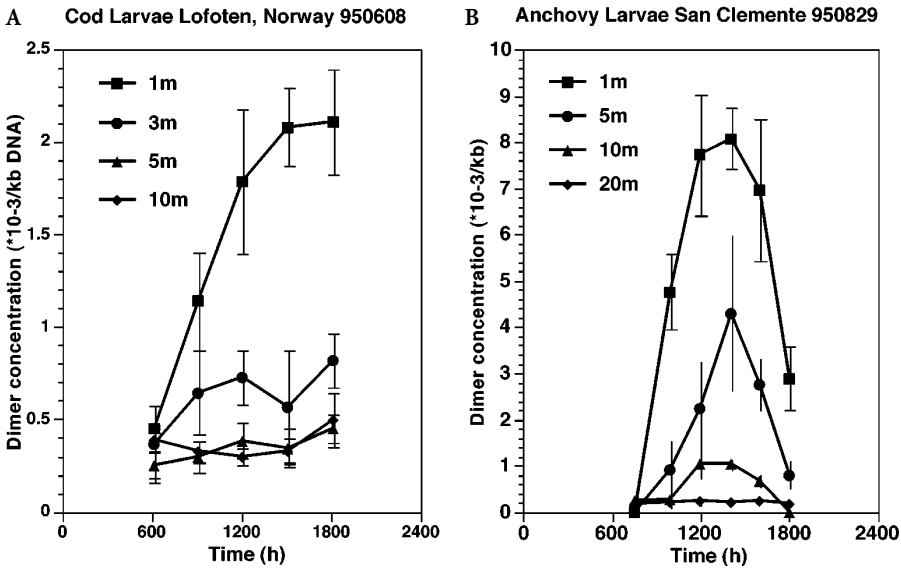

Fig. 13.7. A In-situ incubation of cod larvae. Cod yolk-sac larvae were suspended in quartz cylinders in the waters of Austnesfjorden, a spawning area in the Lofoten Islands, Norway. DNA damage was observed to a depth of 10 m. DNA damage accumulated throughout the afternoon with little evidence of photorepair. Optical characteristics and temperature are shown in Fig. 13.2. **B** In situ incubation of anchovy at 32° N latitude off San Diego, California, USA. UV dose was higher and so were DNA damage levels (note difference in axis) and damage occurred deeper in the water (note differences in depths of incubations). Despite higher levels of DNA damage, anchovy exhibited higher levels of photorepair in the afternoon

13.2.6 Summary of Case Study I

Cod eggs and larvae are damaged by UV-A and B and possess the typical means of repairing DNA damage via photorepair. While cod eggs and larvae clearly carry out photorepair, all of our experiments converge on the finding that the capacity for repair is low and not adequate for full repair before the onset of new damage on the following day (Figs. 13.3, 13.6, 13.7; and data not shown). This low capacity for photorepair can lead to a greater multi-day accumulation of DNA damage than currently observed for the temperate fishes we have studied (Vetter et al. 1999; Vetter, unpubl. data). Not enough fish larvae have been studied to make sweeping generalizations, but there are clearly species differences in rates of DNA damage and repair. These differences may account for why some larvae appear to conform to dose reciprocity while others do not (see Sect. 13.3.4.2.4). Dose reciprocity says that total cumulative dose rather than dose rate is what is important, i.e. two low

irradiance cloudy days will be equivalent to one high irradiance sunny day. In the northern anchovy, *Engraulis mordax*, a baseline level of CPDs remains after the first exposure but in general CPD levels do not accumulate over many days (Vetter et al. 1999). Anchovy larvae do not obey dose-reciprocity relationships (Hunter et al. 1982). Cod, with a more limited capacity for photorepair, accumulate damage over multiple days and adhere more closely to dose reciprocity under the conditions tested (Kouwenberg et al. 1999b). This is an important point of concern. Presently, cod appear to be adapted to the cloudy, highly attenuating waters of the Norwegian fjords. How they will adapt to higher levels of UV associated with reduced cloud cover or ozone thinning is unknown, but their capacity for adaptation can be studied. Photolyase, the enzyme responsible for photorepair in fishes, is inducible (Uchida et al. 1995), but the extent to which cod can change their photorepair capacity is the next area of priority research.

13.3 Case Study II – Estuary and Gulf of St. Lawrence, Canada

13.3.1 Hydrographics of the Study Area

In some regions of the Gulf of St. Lawrence (Fig. 13.8A), the late spring and summer water column shows a pronounced thermocline between 10 and 30 m (Petrie et al. 1988; Koutitonsky and Bugden 1991; Runge and de Lafontaine 1996; Fig. 13.8B). A cold intermediate layer (CIL, –1 to +1 °C), situated at depths of 30–100 m, separates the warm mixed layer near the surface (14–16 °C in summer) from the waters at depth (6 °C; Koutitonsky and Bugden 1991; Runge and de Lafontaine 1996; Gilbert and Pettigrew 1997; Fig. 13.8B). As a result of the spring-through-fall presence of this intermediate cold layer, the most important productivity-determining biophysical interactions occur in the upper 0–30 m of the water column (Therriault 1991; Ohman and Runge 1994; Runge and de Lafontaine 1996). During summer, the mixed layer in these waters is typically 10–15 m deep. The eggs and larvae of several commercially important marine invertebrates and fishes are found in this layer (Fortier et al. 1992; Runge and de Lafontaine 1996; Fig. 13.8C).

Following from the complete absence of information on levels of ultraviolet radiation (280–400 nm=UV) in the water columns of this region, and on the potential biological impacts of UV on the organisms present in the shallow mixed layer, the objectives of the research program reported in this second case study were to: (1) measure ambient levels of UV radiation and determine which variables most strongly affected its attenuation; and (2)

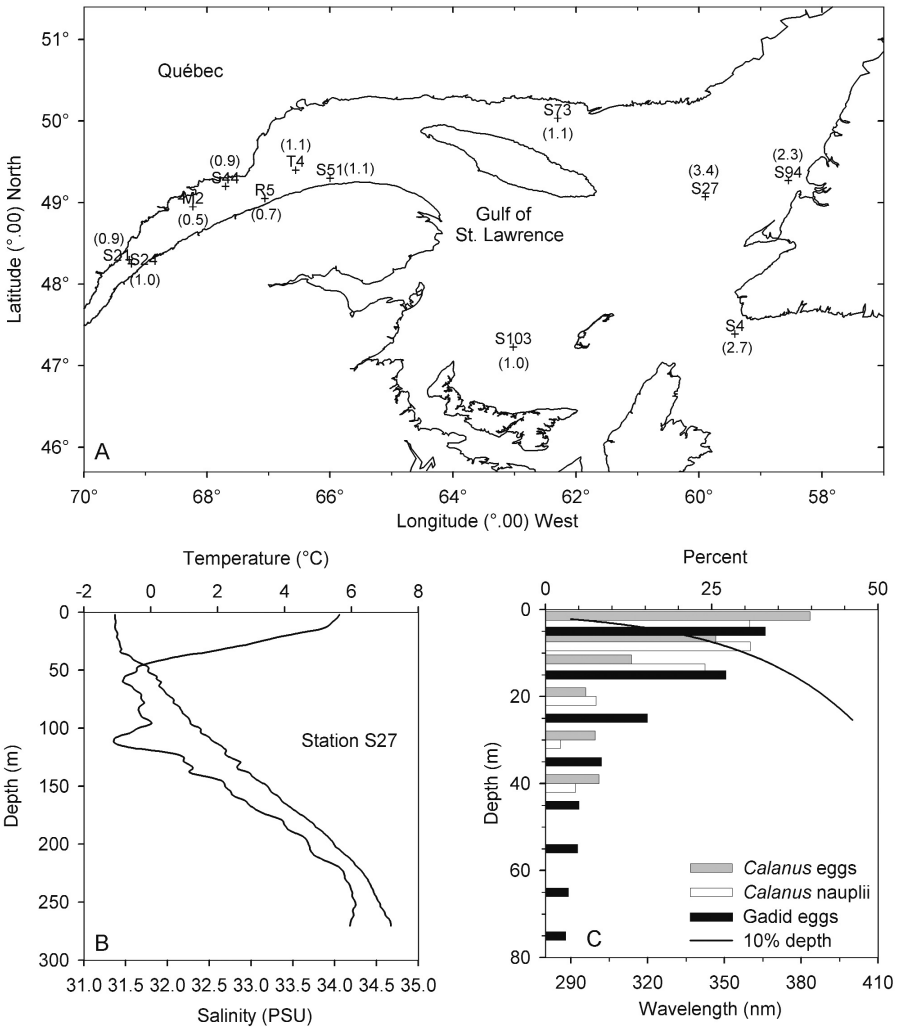

Fig. 13.8. A Map of the estuary and Gulf of St. Lawrence, Canada, showing the location of stations at which high resolution ultraviolet (290–400 nm) radiation measurements were made in the surface waters of the region. The *numbers in parentheses* next to each station position are the 10% depth penetrations (the depth to which 10% of irradiance just below the surface penetrates) at a wavelength of 310 nm. Water samples were obtained from these same stations and analysed for chlorophyll *a* and dissolved organic carbon content. **B** Vertical profiles for temperature and salinity – taken at station S27 on the map – illustrating the shallow spring-summer mixed layer. **C** Vertical distribution of *Calanus finmarchicus* eggs and nauplii, and gadid (including cod) eggs. The wavelength-specific 10% depth penetrations at station S27 (that with the clearest water) are superimposed over the egg vertical distributions in order to illustrate which percentage of the egg population is likely exposed to UV-B radiation. (Reprinted from Browman et al. 2000 with the permission of the publisher, Inter-Research)

investigate the potential impacts of UV radiation on species of crustacean zooplankton and fish whose early life stages are planktonic. A synthetic summary of these investigations is presented in the text that follows.

13.3.2 The UV Environment of the Gulf of St. Lawrence

Accurate measurement of spectral irradiance is fundamental to any study on the biological effects of UV radiation. 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). Thus, in order to make an assessment of the biological impacts of UV radiation on crustacean zooplankton and ichthyoplankton in the St. Lawrence, we had to first measure UV irradiance spectra at several geographic locations. To obtain a more general optical characterization of these waters, we also calculated diffuse attenuation coefficients ($K_{d\lambda}$) and 10 % depth penetrations (the depth to which 10 % of the below surface irradiance penetrates at any given wavelength) for these sites. Finally, we evaluated how DOC and chl *a* were related to $K_{d\lambda}$ in these water columns.

The methods employed in collecting the data reported in this, and in other sections of the text, will not be presented here. However, in each case, readers are directed to a source publication in which full details of the methods appear.

Station-averaged spectral flux at 300 nm was 1.1/E^3_Wm^2_nm just below the surface. Detectable fluxes just below the surface were measured at wavelengths as low as 294 nm (station T4; Fig. 13.8A). There was little variation in this lower wavelength limit among stations, 296±2 nm. At 300 nm, K_d values ranged from approximately 1 to 5/m, with corresponding 10 % depth penetrations of 2.3 and 0.4 m (Fig. 13.9). At 400 nm, K_d varied between 0.2 and 1.4/m and the 10 % depth penetrations were 21 and 1.4 m (Fig. 13.9). The 10 % depths were generally smallest in the estuary (stations M2, R5, S21, S24 and S44; Fig. 13.8A) and became greater in the clearer waters toward, and in, the Gulf (stations T4, S51, S73, S103, S27, S4 and S94; Fig. 13.8A). All values fall within the range of 10 % depth penetrations presented in the review article by Booth and Morrow (1997): at 310 nm a depth of 0.1 m was recorded by Scully and Lean (1994) in Lake Cromwell, Québec, Canada, and values as high as 20 m were reported for clear ocean waters by Smith and Baker (1979; Fig. 13.9).

The lowest DOC and chl *a* values – 0.448 g/m^3 and 0.05 µg/l, respectively – were measured at station S27 (sampled on 15 June 1997). The highest DOC value – 3.59 g/m^3 – was recorded at station S21 (sampled on 1 September 1997), and the highest chl *a* value – 2.02 µg/l – was recorded at station S44 (sampled on 30 August 1997; Kuhn et al. 1999). For all wavelengths, DOC was

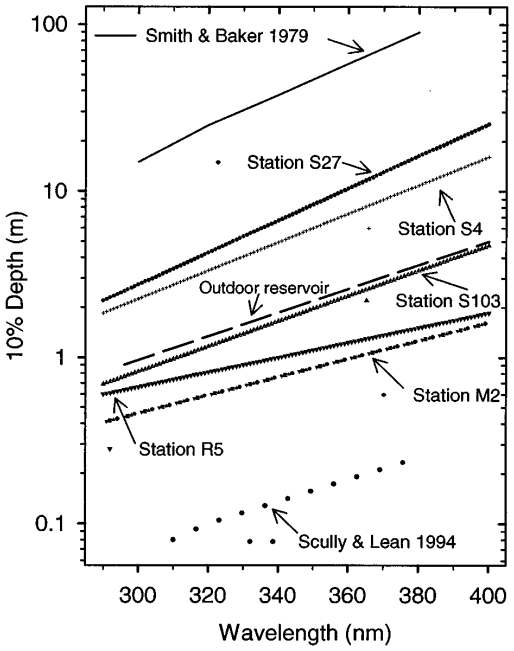

Fig. 13.9. Ten-percent depth penetrations (the depth to which 10 % of irradiance just below the surface penetrates) at selected stations in the estuary and Gulf of St. Lawrence. Station locations are plotted in Fig. 13.8A. All values fall within the range of values reported by Scully and Lean (1994) for the highly UV-opaque Lake Cromwell, Québec, Canada, and by Smith and Baker (1979) for extremely clear marine waters. (Reprinted from Browman et al. 2000 with the permission of the publisher, Inter-Research)

more highly correlated with K_d than was chl *a*. The average correlation coefficient between DOC and K_d was 0.81; between chl *a* and K_d, 0.73; and between chl *a* and DOC, 0.73. In other marine environments, 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). However, for most marine water types there is a significant auto-correlation between DOC and chl *a*, making it difficult to determine their respective contributions to the diffuse attenuation coefficients. However, 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.

These measurements indicate that potentially harmful levels of UV radiation penetrate into the summer mixed-layer water column in the upper estuary and Gulf of St. Lawrence. UV-A reaches even greater depths (Fig. 13.9). Thus, the early life history stages of the crustacean and fish species that are present in this shallow mixed layer may be impacted by UV radiation.

13.3.3 Species Studied

13.3.3.1 Copepod Study Species: *Calanus finmarchicus* Gunnerus

The planktonic copepod, *Calanus finmarchicus* Gunnerus, 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, and from early spring through fall (Runge and Plourde 1996). Thirty to 50 % of these eggs are present in the surface 0 to 5 m (Runge and de Lafontaine 1996; Fig. 13.8C). Larvae of redfish (*Sebastes* spp.), a commercially important stock in the north-central Gulf of St. Lawrence, ingest large numbers of the egg and naupliar stages of *C. finmarchicus* 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, unpubl. observ.). Although never rigorously studied, the contribution of *C. finmarchicus* to the diet of larval cod 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 Arcto-Norwegian cod larvae in Norwegian coastal waters. This *C. finmarchicus*-redfish (and presumably cod) interaction in the northern Gulf of St. Lawrence occurs in the shallow surface mixed layer.

13.3.3.2 Ichthyoplankton Study Species: Atlantic Cod

The reproductive season for Atlantic cod in the Gulf of St. Lawrence begins early in the spring (April) and continues through mid-summer (July; Ouellet et al. 1997). Spawning occurs in deep water (>200 m) and cod eggs, which are typically positively buoyant, ascend to the surface mixed layer over a period of 2 to 10 days (Solemdal and Sundby 1981; Anderson and de Young 1995; Ouellet 1997). Cod eggs are present in the 0–25 m depth stratum off the Newfoundland Shelf (Anderson and de Young 1995), off Greenland and Labrador (Brander 1994), on southern Georges Bank (Lough et al. 1996) and in the northern Gulf of St. Lawrence (Ouellet 1997; Fig. 13.8C). The specific proportion of the egg population present in this surface layer cannot be definitively quantified since the vertical distribution of cod eggs is dependent upon a number of variable and interacting factors (egg buoyancy, meteorological and hydrographic conditions, etc.). Nonetheless, when wind speed is low, the highest egg concentrations are observed in the upper 0 to 10 m of the water column (Solemdal and Sundby 1981). The early larval stages are also typically present, and often even closer to the surface (Anderson and de Young 1995).

13.3.4 Effects of UV-B on Crustacean Zooplankton and Ichthyoplankton

13.3.4.1 Outdoor Exposure Experiments

As a first step toward evaluating the potential effects of UV on *Calanus finmarchicus* and cod, we conducted a series of experiments in which eggs of both species were incubated under the sun, with and without the UV-B and/or UV-A wavebands. We wished to determine whether current levels of UV radiation at the ocean surface would have a detrimental effect on the early life stages of these species.

13.3.4.1.1 *Calanus finmarchicus*

C. finmarchicus eggs were negatively affected by ambient levels of solar UV radiation (Quartz and Mylar vs. OP-2 and Dark treatments; Fig. 13.10). Further, percent hatching in eggs exposed to both UV-B and UV-A (Quartz) was not significantly lower than that in eggs exposed to UV-A only (OP-2): under natural sunlight, UV-A radiation appeared to be more detrimental to *C. finmarchicus* embryos than was UV-B (Fig. 13.10). There was no consistent statistically discernible effect of incubation depth in these experiments (but see Alonso Rodriguez et al. 2000 for specific exceptions). These results were consistent across three independent experiments (only one of which is presented here), and were statistically discernible (Alonso Rodriguez et al. 2000).

It is possible that the low percent of hatching in these two treatments, the high variability among replicates, and the low statistical power resulting from several missing replicates, masked any difference in their response to UV-B exposure. Further, the Mylar material used in these experiments transmits some energy at the UV-B–UV-A transition (13 % transmission at 315 nm; 49 % at 320 nm), so the eggs in the Mylar treatments were exposed to some UV-B radiation. Given the high impact weightings for exposures at these wavelengths (see below), this amount of energy may have been enough to kill the eggs. It is possible, therefore, that wavelengths at the UV-B–UV-A transition are at least partly responsible for the low percent of hatching in the Quartz and Mylar treatments of our experiments. The boundaries of the UV-B and UV-A wavebands have been established based upon ozone absorption profiles (Lubin and Frederick 1991). Given the variety of biological and biochemical effects induced by UV radiation, all of them wavelength-dependent, it is not always appropriate, nor biologically relevant, to be bounded by these arbitrary limits.

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

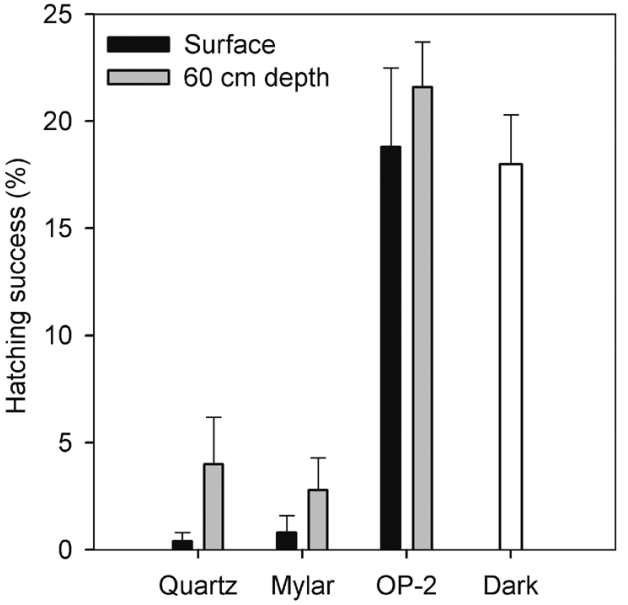

Fig. 13.10. Hatching success (means ± SEM) of *Calanus finmarchicus* eggs incubated outside of the Maurice-Lamontagne Institute, Mont-Joli, Québec, Canada (48° 38′ 25.9″ N, 68° 09′ 21.0″ W). Incubations were carried out at two depths: just below the surface and at 60 cm. Eggs were exposed to three light regimes. (1) UV-B+UV-A+PAR (PAR=photosynthetically active radiation). Eggs in this treatment (*Quartz*) – incubated in quartz tubes – were exposed to the complete solar spectrum. (2) UV-A+PAR. In this treatment (*Mylar*), UV-B was excluded by wrapping the quartz tubes with Dupont's 0.05-mm-thick type D Mylar. (3) PAR only. In this treatment (*OP-2*), UV-A and UV-B were eliminated by placing the quartz tubes under a 3-mm-thick piece of the acrylic sheet material OP-2 (Cyro Industries). Control groups (*dark*) were incubated in quartz tubes wrapped with aluminum foil. (Reprinted from Browman et al. 2000 with the permission of the publisher, Inter-Research)

(Karanas et al. 1979, 1981; Chalker-Scott 1995; Naganuma et al. 1997; Zagarese and Williamson 2000). Further, UV-B-induced damage to the DNA of crustacean zooplankton has been detected in samples collected from depths of down to 20 m (Malloy et al. 1997). This is the first investigation of the effects of UV radiation on the early life stages of *Calanus finmarchicus*, and there exist few data on UV-induced egg mortality in marine copepods with which to compare our results. Nonetheless, these screening experiments, and the results presented below from higher spectral resolution treatments, support the contention that UV is detrimental.

It is also possible that eggs were killed by longer wavelengths of UV-A radiation. The effect of UV-A radiation on biological systems remains unclear (Sutherland et al. 1992). While its role in DNA photorepair has been well documented (Sutherland 1981; Hearst 1995; Mitani et al. 1996), fewer

studies have demonstrated its deleterious effects on aquatic organisms. However, UV-A radiation inhibits photosynthesis in Antarctic diatoms and dinoflagellates, and in freshwater algae (Cullen et al. 1992; Bothwell et al. 1994). Furthermore, UV-A radiation induced a transitory decrease in the metabolic rate of the cichlid fish, *Cichlasoma nigrofasciatum* (Winckler and Fidhiany 1996), a lower hatching success in embryos of the Japanese medaka, *Oryzias latipes* (Bass and Sistrun 1997), as well as increased mortality in eggs of the yellow perch, *Perca flavescens* (Williamson et al. 1997) and in the freshwater copepod *Boeckella gracilipes* (Zagarese et al. 1997). Unlike UV-B, UV-A-induced damage does not result from direct absorption of photons by the DNA molecule (Beer et al. 1993). Although wavelengths as long as 365 nm induce detectable levels of cyclobutane pyrimidine dimers (Ahmed and Setlow 1993), one of the main UV-B photoproducts in the DNA molecule (Hearst 1995), the action spectrum for DNA damage indicates that the relative biological response to wavelengths beyond 310 nm is negligible (Setlow 1974).

UV-A radiation is absorbed by organic molecules other than DNA, such as proteins, lipids and RNA. The dissipation of the absorbed energy via photochemical reactions generates a variety of by-products (hydroxyl radicals, superoxide, hydrogen peroxide and singlet-state oxygen) which can accumulate and cause significant oxidative damage to cross-link membrane lipids and other cellular components (Lesser and Shick 1989 and references therein; Beer et al. 1993). Pigments such as melanin or the carotenoids are known to act as free-radical scavengers and energy transducers (Hessen 1994), but *Calanus finmarchicus* eggs are unpigmented. Moreover, interaction between UV and dissolved organic matter (DOM) present in the water can also produce reactive oxygen transients which subsequently have cytotoxic effects (Zepp et al. 1987). This mechanism of damage occurs over a relatively longer time frame than direct damage to DNA since it results from cumulative physiological stress. This might explain why Kouwenberg et al. (1999b) did not find a UV-A effect: in those experiments, *C. finmarchicus* eggs received only a 1-h exposure of UV-A per day. Further experiments are required to resolve the issues surrounding UV-B vs. UV-A effects.

13.3.4.1.2 Atlantic Cod

Cod embryos exposed to UV-B radiation (Quartz treatment) exhibited a higher rate of mortality, and greater cumulative mortality, than those shielded from UV-B (Mylar and OP-2 treatments; Fig. 13.11). These results were consistent across four experiments (only one of which is presented here), and were statistically discernible (Béland et al. 1999). UV-B-induced mortality at the surface was virtually 100 %, but that at 50 cm was negligible (at least in this experiment – but see Béland et al. 1999).

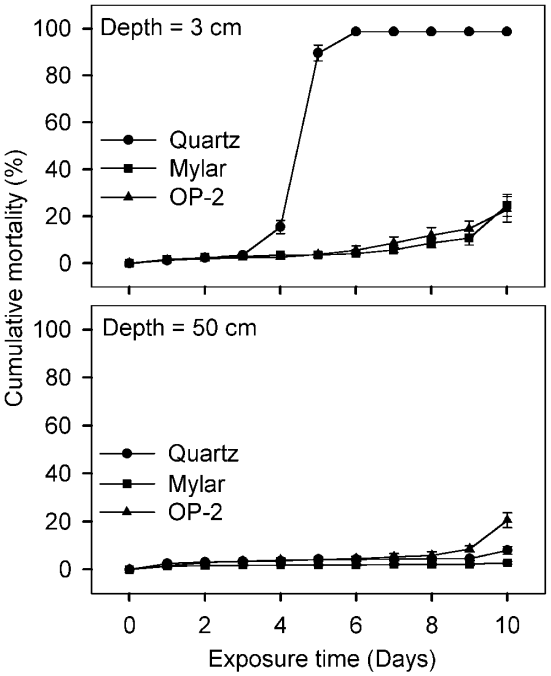

Fig. 13.11. Percent cumulative mortality (means ± SEM) in Atlantic cod (*Gadus morhua*) eggs incubated outside of the Maurice-Lamontagne Institute, Mont-Joli, Québec, Canada (48°38′25.9″N, 68°09′21.0″W). Incubations were carried out at two depths: just below the surface and at 50 cm. Eggs were exposed to three light regimes. (1) UV-B+UV-A+PAR (PAR=photosynthetically active radiation). Eggs in this treatment (*Quartz*) – incubated in quartz tubes – were exposed to the complete solar spectrum. (2) UV-A+PAR. In this treatment (*Mylar*), UV-B was excluded by wrapping the quartz tubes with Dupont's 0.05-mm-thick type D Mylar. (3) PAR only. In this treatment (*OP-2*), UV-A and UV-B were eliminated by placing the quartz tubes under a 3-mm-thick piece of the acrylic sheet material OP-2. (Cyro Industries; reprinted from Browman et al. 2000 with the permission of the publisher, Inter-Research)

Mortality of yellow perch (*Perca flavescens*) eggs, incubated in situ at various depths and under spectral exposure treatments similar to those reported here, was very high (>95 %), even at depths down to 0.8 m (Williamson et al. 1997). Observations from the few other studies on UV-B-induced mortality in fish eggs are also consistent with our results (Marinaro and Bernard 1966; Pommeranz 1974; Hunter et al. 1982; Zagarese and Williamson 2000).

Negative effects of UV-A on fishes have been documented (see the preceding section). Nonetheless, cod eggs were not negatively affected by exposure to UV-A radiation in our experiments: there were no clear differences in mortality in the UV-A+PAR (Mylar) treatment relative to the PAR only (OP-2) treatment (Fig. 13.11). This result is consistent with that

reported from higher spectral resolution experiments on UV-induced mortality in cod eggs: there was no clear negative effect of UV-A (see below and Kouwenberg et al. 1999a). As was the case for *Calanus finmarchicus*, further experiments on the effects of UV-A and visible light – both in inducing mortality and with respect to the balance between photodamage and photorepair – are required to resolve these issues.

The experiments reported here indicate that Atlantic cod eggs – at least those present in the first half-meter of the water column – are susceptible to UV-B radiation. However, the 10 % depths for UV penetration in the outdoor reservoir were less than those for regions of the Gulf of St. Lawrence where cod spawn (Fig. 13.9; and see Béland et al. 1999). This suggests that the impact of UV-B reported here is an underestimate of that which would be observed in the wild. This conclusion, however, must be carefully qualified.

Although the available information on the vertical distribution of cod eggs in this region is limited, it appears that most are not present in the upper 4 m of the water column (Ouellet 1997). Even if most cod eggs were present in the 0–15 m mixed layer of the northern Gulf of St. Lawrence water column, they would be in circulation and their daily residence time in the upper 4 m would depend upon meteorological and hydrographic conditions (among other things – see Solemdal and Sundby 1981). Short residence times, which appear likely, would further reduce the population-level impact of UV-B on cod eggs. These issues are taken up again below (Sect. 3.4.3).

13.3.4.2 Solar Simulator Experiments with *Calanus finmarchicus* and Atlantic Cod

The outdoor experiments described above allowed an assessment of whether exposure to current levels of UV-B, UV-A, or PAR had a detrimental effect on *Calanus finmarchicus* or cod eggs. However, the conclusions that can be drawn from broad-band screening experiments such as these are limited, and they cannot be used to make predictions about impacts that might occur under different conditions of spectral quality and intensity.

A number of factors make it difficult to predict the biological effect of UV-B radiation on aquatic organisms. For example, (1) the spectral composition and intensity of light reaching the earth's surface are highly variable, being affected by weather conditions, the thickness of the ozone layer, and air pollution, among other things (Graedel and Crutzen 1995; Varotsos et al. 1994; Madronich et al. 1995; Németh et al. 1996). This variability is both spatial and temporal. (2) The underwater light field is further affected by the wavelength-specific diffuse attenuation coefficients of water bodies, themselves highly variable, geographically, seasonally and annually (Piazena and Häder 1994; Laurion et al. 1997). (3) Photon absorption by the DNA molecule, by proteins,

by tissues and by whole organisms, is strongly wavelength-dependent, dropping off steeply above 300 nm (see the data reported by Setlow 1974; Coohil 1991; Cullen and Neale 1997; among others). Since the biological effectiveness of UV photons is inversely related to wavelength, and short-wave photons are strongly absorbed by organic molecules and sea water, relatively small changes in UV-B irradiance can lead to large changes in biological effect. (4) Ozone layer depletion will not affect the entire UV-B waveband equally. Rather, increases in UV-B associated with a thinning ozone layer will be mainly restricted to the 295–312 nm waveband: the most damaging wavelengths (Kerr and McElroy 1993; Graedel and Crutzen 1995; Madronich et al. 1995). Following from this, any attempt to assess the impact of UV-B radiation on planktonic marine organisms requires that the wavelength-dependent biological effect of UV-B photons be known. That is, a relevant BWF – like those presented here for *Calanus finmarchicus* and cod egg mortality (see below) – must be available (Cullen and Neale 1997 provide a thorough presentation of this issue).

The goals of the solar simulator (SS) experiments were to (1) evaluate the effect of UV radiation on mortality in the eggs of *Calanus finmarchicus* and Atlantic cod, with a higher degree of spectral resolution and irradiance control than is possible with screening experiments; (2) generate dose-response relationships and test the principle of reciprocity, which states that the UV-B-induced mortality effect on eggs will be dose but not dose *rate* dependent; (3) derive BWFs for the effect of UV on mortality in *C. finmarchicus* and Atlantic cod eggs; (4) evaluate DNA damage as a function of spectral exposure; and (5) present an assessment of the potential direct impact of solar UV radiation on the early life stages of *C. finmarchicus* and cod in the subarctic marine ecosystems of eastern Canada.

13.3.4.2.1 Wavelength-Dependent Mortality

UV-B radiation, particularly in the 280–312 nm waveband, had a strong negative impact on the survival of *Calanus finmarchicus* eggs, even over short exposure times (Fig. 13.12) and at low total doses. At the shorter wavelengths (<305 nm), UV-B-induced mortality was strongly dependent upon cumulative dose (Kouwenberg et al. 1999b). The mortality effect was less pronounced in the 312-nm treatment, and there was no effect in the 335-, 360- and 400-nm treatment groups (Fig. 13.12). The spectral resolution of these results is the highest so far generated for a copepod. Nonetheless, similar dose-dependent effects have been reported for *Acartia clausii* (Karanas et al. 1979) irradiated under Westinghouse FS40 sunlamps and for several other species (Karanas et al. 1979, 1981; Thomson 1986; Dey et al. 1988; Naganuma et al. 1997).

UV-B radiation, particularly in the 280–312 nm waveband, had a strong negative impact on the survival of Atlantic cod eggs (Fig. 13.13). This is

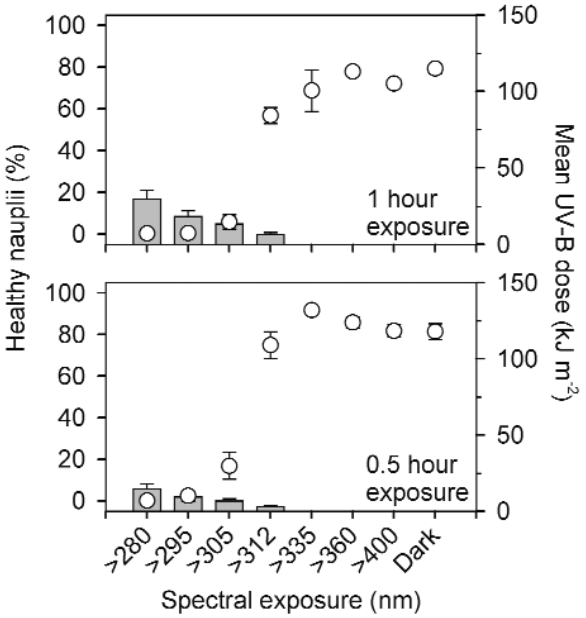

Fig. 13.12. Survival in *Calanus finmarchicus* eggs exposed to various spectral wavebands. *Open circles* are the mean (± SEM) proportion of healthy nauplii from eggs exposed to radiation greater than the specified cut-off wavelength. The *filled bars* represent the mean (± SEM) UV-B dose delivered under each of these spectral exposure treatments. Two exposure durations are presented, as noted in each panel. (Reprinted from Browman et al. 2000 with the permission of the publisher, Inter-Research)

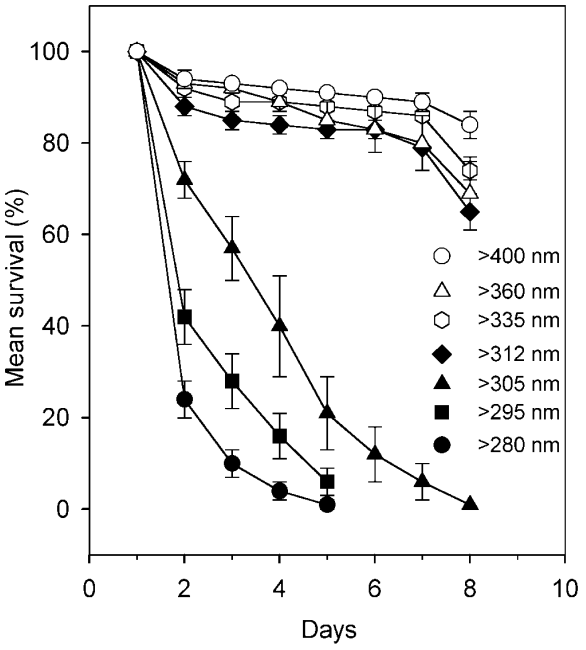

Fig. 13.13. Mean (± SEM) egg survival in Atlantic cod (*Gadus morhua*) eggs exposed to various spectral wavebands, without photorepair between exposures. Each *curve* represents the mortality induced by exposure to radiation greater than the cut-off wavelength indicated. *Open symbols* denote treatments that received UV-A and visible light, or visible light only. *Filled symbols* denote treatments that received radiation in the UV-B+exposed to various spectral wavebands of UV-A+visible wavebands. (Reprinted from Browman et al. 2000 with the permission of the publisher, Inter-Research)

consistent with observations on several other species (Marinaro and Bernard 1966; Pommeranz 1974; Hunter et al. 1982; Williamson et al. 1997), although these earlier studies do not provide the same spectral resolution. There was also evidence suggesting the presence of photorepair mechanisms in cod eggs (Kouwenberg et al. 1999a). Remediating effects of photorepair on UV-B-induced mortality, and DNA damage, have been reported for northern anchovy (*Engraulis mordax*) larvae (Kaup and Hunter 1981; Vetter et al. 1999; and see case study I). Mitchell et al. (1993) reported on DNA photorepair in UV-B-exposed platyfish (*Xiphophorus variatus*) and Mitani et al. (1996) observed that exposure to UV-A and blue light induced the production of cyclobutane pyrimidine dimer photolyase (involved in the repair of UV-B-induced DNA damage) in cultured cells of the goldfish (*Carassius auratus*). Similar results on photorepair were reported by Vetter et al. (1999) and in case study I of this chapter.

13.3.4.2.2 DNA Damage

Formation of cyclobutane pyrimidine dimers (CPDs) in DNA is one of the most common results of exposure to UV-B radiation. The formation of CPDs, and their repair, has been well-studied in fish cell lines, fish embryos and fish skin (Achey et al. 1979; Shima et al. 1981; Regan et al. 1983; Shima and Setlow 1984; Applegate and Ley 1988; Ahmed and Setlow 1993). Since the concentration of CPDs in an organism's DNA is directly related to UV-B exposure, they are potentially useful as UV-B-specific indicators of exposure in wild populations of fish larvae (Vetter et al. 1999). Thus, we undertook to describe the wavelength-specific effect of UV-B exposure on DNA damage in *Calanus finmarchicus* and cod eggs.

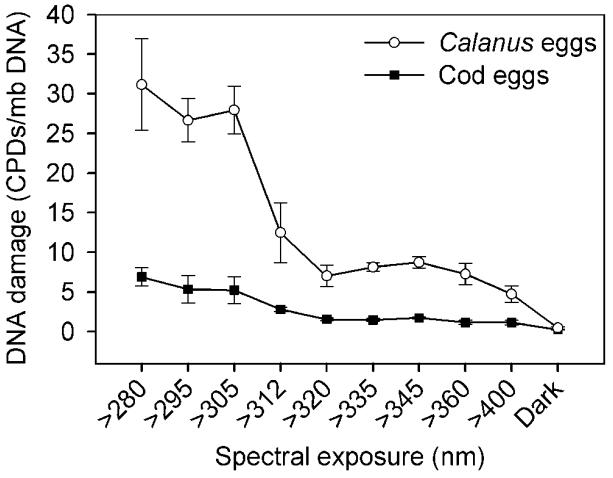

Fig. 13.14. Mean (± SEM) DNA damage in *Calanus finmarchicus* and Atlantic cod (*Gadus morhua*) eggs exposed to various spectral wavebands at the same dose rate and total dose. (Reprinted from Browman et al. 2000 with the permission of the publisher, Inter-Research)

UV-induced damage – as represented by CPD concentration per millibase of DNA – to the DNA in *Calanus finmarchicus* and cod eggs was highest in the WG280, WG295, WG305 and WG312-nm exposure treatments (Fig. 13.14). These were all significantly different from the other exposure treatments, and from the dark controls. CPD concentration in the UV-A exposure treatments was not significantly different from that in the dark controls (Fig. 13.14). These data indicate that *Calanus finmarchicus* eggs are significantly more susceptible to UV-B-induced DNA damage than are cod eggs. This likely reflects differences in the relative rates of damage and repair in these two organisms.

13.3.4.2.3 Biological Weighting Functions

The BWF for UV-induced mortality in *Calanus finmarchicus* eggs exhibits a typically steep decline against wavelength: UV impact is more than two orders of magnitude higher at 290 nm than at 320 nm (Fig. 13.15A). The scenario is similar for cod eggs: UV-induced mortality is almost two orders of magnitude higher at 300 nm than at 320 nm (Fig. 13.15B). Based upon these weightings, *C. finmarchicus* eggs appear to be significantly more sensitive to UV exposure than are cod eggs (cf. the two BWFs in Fig. 13.15). This is consistent with the DNA results presented in the previous section.

The wavelength-specific sensitivity of UV-induced mortality in *C. finmarchicus* and cod eggs, as defined in the BWFs, exhibits a slope consistent with that of the DNA action spectrum through 310 nm (Setlow 1974; Fig. 13.15A,B). Further, the wavelength weightings of the BWFs are consistent with the wavelength-dependence of DNA damage reported above. Following from this, it seems likely that UV-induced mortality in *C. finmarchicus* and cod eggs results from DNA damage which, if not repaired, causes mortal errors in embryogenesis and pattern formation. Weightings in the UV-A waveband were essentially non-existent for both BWFs (Fig. 13.15).

Hunter et al. (1981) related weighted UV-B exposure to the survival of northern anchovy eggs and larvae using several UV-B action spectra. They found that survival was best predicted when the UV-B exposure was weighted by the Setlow (1974) DNA action spectrum and this represents the first attempt to apply a BWF to UV-B-induced mortality in ichthyoplankton. BWFs such as those used by Hunter et al. (1981) yield only relative predictions – they tell us how much more (or less) mortality there will be for one spectral exposure vs. another. The BWFs reported here for *Calanus finmarchicus* and cod eggs were derived from the mortality response itself, as opposed to being chosen as the best predictor of relative mortality. Consequently, the weightings are in absolute units $(J\ m^{-2})^{-1}$. This allows differentiation of biological responses with the same spectral shape but for which the level of response is different (e.g. the DNA damage results presented in Fig. 13.14).

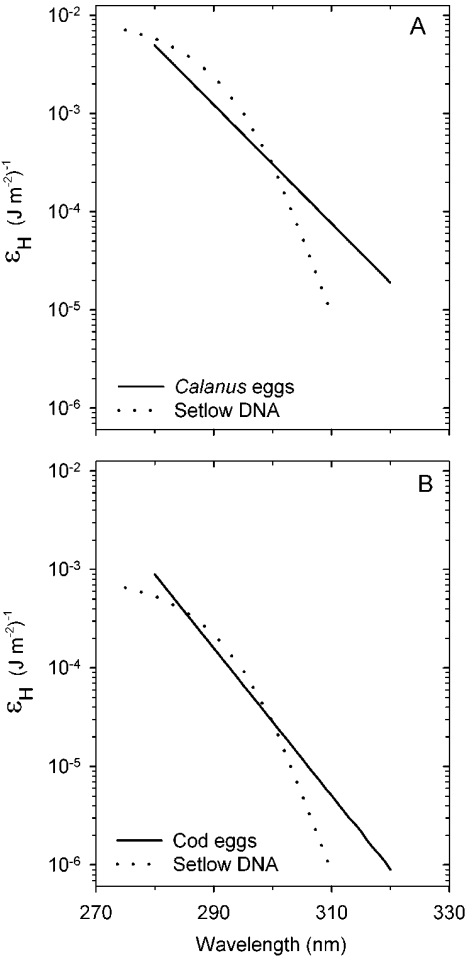

Fig. 13.15. A Biological weighting function (BWF) for egg mortality in *Calanus finmarchicus* (*solid line*). **B** BWF for egg mortality in Atlantic cod (*Gadus morhua*; *solid line*). In both panels, the wavelength-dependence of damage to the naked DNA molecule (data drawn from Setlow 1974) is superimposed as a *dotted line*. The Setlow curve was normalized against the BWF's value at 300 nm for ease of comparison. (Reprinted from Browman et al. 2000 with the permission of the publisher, Inter-Research)

The Hunter et al. approach would not allow for such a differentiation. As a result, egg mortality (in *absolute* terms) resulting from any given exposure (associated, for example, with different environmental conditions, such as ozone thinning) can be predicted (Kouwenberg et al. 1999a,b).

13.3.4.2.4 Reciprocity

One of the more important fundamental assumptions for construction of an accurate dose-dependent BWF is the principle of reciprocity (De Gruijl et al. 1986; Coohill 1991; Cullen and Neale 1997; Buma et al. 1997). 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 vs. 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. The principle of reciprocity has not often been rigorously evaluated and, when it has, the results have been inconsistent (see references cited above). Nonetheless, there was no discernible effect of dose rate on hatching of *Calanus finmarchicus* eggs exposed to three different cumulative doses each delivered at three different dose rates (Browman and St-Pierre 2001): reciprocity held. In an analogous experiment with cod eggs, reciprocity also held (see Kouwenberg et al. 1999a; Fig. 13.4). These radiative conditions were the same as those delivered in the experiments used to derive the BWFs. Further, reciprocity held despite the fact that the eggs were incubated under fluorescent lamps in between UV exposures, i.e. they were allowed to photorepair. Thus, the BWFs for *C. finmarchicus* and cod presented here can reasonably be applied to quantify the wavelength-specific impact of UV on the eggs of these species.

Hunter et al. (1981, 1982) present the only other assessment of the reciprocity principle for a marine fish. For northern anchovy larvae, and under relatively broad dose/dose rate exposures, reciprocity did not hold. The reasons for this inconsistency are unknown. However, one possibility is the difference in the relative duration of intense UV-B exposures vs. the time for repair. To the extent that repair dominates damage, reciprocity fails. When damage dominates, repair processes will not significantly compromise reciprocity. It is possible that the experiments reported here were generally consistent with reciprocity because the duration of exposure was relatively short – and so damage was dominant – while those of Hunter et al. (1981, 1982) were longer and less intense – and so repair was dominant. In evaluations of reciprocity, it is important to acknowledge that experiments conducted on different time scales may yield significantly different results.

13.3.4.3 A Simulation Model for UV-B-Induced Mortality

All of the preceding represents the building blocks necessary to predict the ecological significance of UV-B radiation on the population dynamics of planktonic organisms – in this case, the early life stages of *Calanus finmarchicus* and Atlantic cod in the Gulf of St. Lawrence. A more complete quantitative assessment of direct UV-B effects on these planktonic life stages requires further information and analysis, specifically: (1) detailed vertical distributions of eggs in the mixed layer of the water column (with high resolution in the upper 10 m); (2) surface UV-B irradiance during the reproductive season, and subsurface spectral irradiance for waters supporting

such eggs (see Kuhn et al. 1999); (3) biological weighting functions – which explicitly consider the possibility of photorepair (and, therefore, the absence of reciprocity) – for the effect of UV-B radiation on egg mortality (see Kouwenberg et al. 1999a,b); and (4) 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 meteorological 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 eggs distributed (and circulating) throughout the mixed layer (e.g. Neale et al. 1998). We have recently developed such a model (Kuhn et al. 2000).

The Kuhn et al. (2000) model 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, clear vs. overcast skies; clear vs. opaque water column; ambient vs. thinned ozone layer – can be evaluated. This is an individually based model, so it is run iteratively on several thousand eggs. The output is the percent of eggs that have died as a result of exposure to UV-B. Complete details of the model, and all of the scenarios evaluated, are reported in Kuhn et al. (2000).

13.3.4.3.1 Model Predictions

The simulation model presented above 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. For *Calanus finmarchicus* eggs, UV-B-induced mortality under all model scenarios ranged between <1 and 51 %, with a mean (± SD) of 10.05±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 (± SD) of 1.0±0.63 % (n=72 modelled scenarios). This result is consistent with the data presented above – *Calanus finmarchicus* eggs are more susceptible to UV-B radiation than are cod eggs.

The most important determinant of survivorship (for both species) was water column transparency (Fig. 13.16): even when ozone layer depletions of 50 % were modelled, the effect on mortality (Fig. 13.16F) remained far lower than that resulting from either thick cloud cover (Fig. 13.16B) or opacity of the water column (Fig. 13.16D). 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.

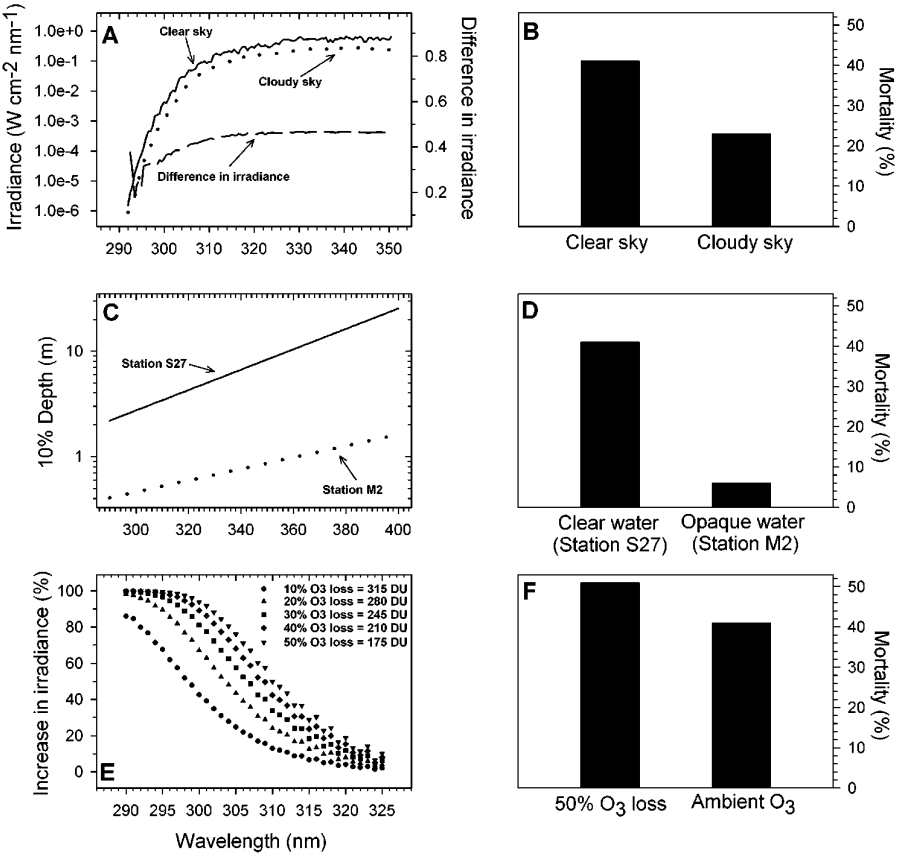

Fig. 13.16A–F. Output of a mathematical simulation model (Kuhn et al. 2000) illustrating the relative effects of selected variables on UV-induced mortality in *Calanus finmarchicus* embryos. **A, B** Clear vs. cloudy sky. When spectral irradiance is plotted on a log scale (as on the left *y*-axis of **A**), the difference between clear and cloudy skies appears small. However, when plotted as a percent (as on the right *y*-axis), the magnitude of the difference in irradiance becomes clearer. **C, D** Clear vs. opaque water column. **E, F** The clear station 50 % thinning of ozone vs. ambient ozone. (Modified from Kuhn et al. 2000)

Since DOC and chl *a* determine 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. 13.17). DOC levels in eutrophic coastal zones are often greater than 3–4 mg/l: the diffuse attenuation coefficients for UV-B associated with such levels (Fig. 13.17A) essentially protect *Calanus finmarchicus* and cod eggs from UV-induced mortality (Fig. 13.17B,C). In this context, DOC can be considered as a sunscreen for the organisms inhabiting eutrophic coastal zone waters (Browman 2002).

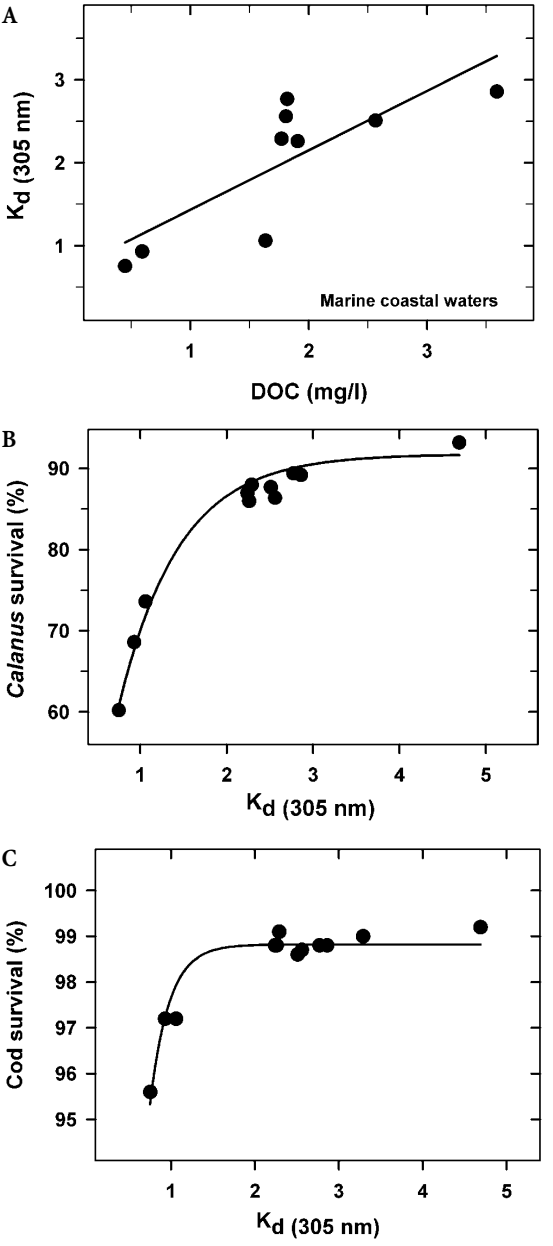

Fig. 13.17. A Dissolved organic carbon (DOC) vs. diffuse attenuation coefficient (K_d) at 305 nm from field measurements in the estuary and Gulf of St. Lawrence, Canada. **B** K_d at 305 nm vs. modelled survival of *Calanus finmarchicus* embryos exposed to UV radiation in a mixed water column. **C** K_d vs. modelled survival of Atlantic cod (*Gadus morhua*) embryos exposed to UV radiation in a mixed water column. (Modified from Browman 2002)

13.3.5 Ecological Context

13.3.5.1 Direct Effects of UV Radiation

13.3.5.1.1 Calanus finmarchicus

The results presented here indicate that *Calanus finmarchicus* may be sensitive to variation in incident UV radiation in subarctic regions of the northwest 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 typically 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 5–10 m) during daytime, where they hatch into the first naupliar stage 1 to 2 days after maternal release (depending upon ambient temperature; McLaren et al. 1988).

Exposure to UV-B radiation may be even more damaging to *Calanus finmarchicus* 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; Kouwenberg et al. 1999b; Fig. 13.1).

13.3.5.1.2 Atlantic Cod

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 number of recent studies (Malloy et al. 1997; Williamson et al. 1997; Freitag et al. 1998; Steeger et al. 1999; Vetter et al. 1999; Zagarese and Williamson 2000), very little additional information has been generated for the effects of UV-B on ichthyoplankton. The results presented here substantiate earlier results on the lethal effects of UV-B on planktonic

fish eggs and provide the first BWF and only the second assessment of the reciprocity principle generated for a marine fish.

13.3.5.2 Indirect Effects of UV Radiation

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 (PUFAs; 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; also see De Lange and Van Donk 1997; also see 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; also see 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, thereby 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 non-

specific 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 (immunoresponsive cells) were significantly altered after a single dose of UV-B (Salo et al. 1998). Further, 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 days after the single exposure (Jokinen et al. 2001). This indicates altered regulation of lymphocyte-dependent immune functions. Finally, 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. 2000). 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. Taken together, 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 is unknown. Further, the immune system of young fishes is likely 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 defence 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 example, for species that spawn in the surface layer, UV-B may affect sperm quality (*sensu* Don and Avtalion 1993; Valcarcel et al. 1994) and thereby affect fertilization rate and/or genome transfer. Also, 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. Finally, 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. To date, 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/or longer term) effects of UV radiation have yet to be investigated.

13.3.6. Summary of Case Study II and Parting Words of Caution

Eggs of *Calanus finmarchicus* and Atlantic cod were incubated under the sun, with and without the UV-B and/or UV-A wavebands. UV-exposed eggs exhibited low percent hatching compared to those protected from UV: UV radiation had a strong negative impact on *C. finmarchicus* eggs. Further, percent hatching in UV-B-exposed eggs was not significantly lower than that in eggs exposed to UV-A only: under natural sunlight, UV-A radiation appeared to be more detrimental to *C. finmarchicus* embryos than was UV-B. In analogous experiments with Atlantic cod eggs, exposure to UV-B produced a significant negative effect. However, UV-A had no negative effect on cod eggs. Additional experiments using an SS revealed high wavelength-dependent mortality in both *C. finmarchicus* and cod embryos exposed to UV. 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. Thus, at least within the limits of the exposures under which the BWFs were generated, reciprocity held. 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. Further, the wavelength-dependence of DNA damage was similar to that for the mortality effect. These observations suggest that UV-induced mortality in *C. finmarchicus* and cod eggs is a direct result of DNA damage. There was no evidence of a detrimental effect of UV-A radiation in these SS-derived results. A mathematical model that includes the BWFs, vertical mixing of eggs, meteorological and hydrographic conditions, and ozone depletion, indicates that UV-induced mortality in the *C. finmarchicus* egg population could be as high as 51 %, while the impact on the cod egg population was no more than 1 %.

It is important to point out that variability in cloud cover, water quality, and vertical distribution and displacement within the mixed layer, will likely all have a greater effect on the flux of UV-B radiation to which the eggs of zooplankton and fishes are exposed than will ozone layer depletion at these latitudes. Thus, although UV-B radiation *can* have negative impacts (direct effects) on crustacean zooplankton and ichthyoplankton populations, it must be viewed as only one amongst many environmental factors – bacterial and/or viral pathogens, predation, toxic algae, etc. – 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. However, for those species whose early life stages are neustonic, there may be circumstances (albeit rare) – cloudless sky, thin ozone layer, no wind, calm seas – under which the contribution of UV-B radiation to the

population's mortality could be much more significant. Simulation models such as that described here allow quantification, in a relative sense at least, of the direct contribution made by UV-B radiation to overall mortality under varying atmospheric and oceanographic conditions. The impact of indirect effects – which may well be of much greater import to marine populations and ecosystems – has yet to be evaluated.

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