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www.publish.csiro.au/journals/mfr *Marine and Freshwater Research*, 2004, **55**, 1–8

Differential tolerance to ultraviolet-B light and photoenzymatic repair in cladocerans from a Chilean lake

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Abstract. In the present study, the sensitivity of four coexisting cladoceran species to ultraviolet (UV)-B radiation was evaluated. First, the LD_{50} under conditions inhibiting the action of photoenzymatic repair was calculated by exposing cladocerans to different doses of UV-B light only. Animals in another treatment group were exposed to both UV-B and visible light, which allows for photoenzymatic repair. Photoenzymatic repair contributed significantly towards the degree of total tolerance to UV-B light in all groups of cladocerans, although the magnitude of the contribution varied among species. When no photoenzymatic repair was allowed, the most tolerant species was *Moina micrura*, followed by *Daphnia ambigua* and *Ceriodaphnia dubia*, with *Diaphanosoma chilense* being the most sensitive species. Under conditions permitting the action of photorepair, *M. micrura* was again the most tolerant species to UV-B light. *Ceriodaphnia dubia* showed an intermediate tolerance value, whereas *D. chilense* and *D. ambigua* were the least tolerant species, with no significant differences between them. Adults and juveniles of *C. dubia* differed in their sensitivity to UV-B light under conditions with and without photorepair.

Extra keywords: Chile, *Daphnia*, photoreactivation, toxicology, zooplankton.

Introduction

The thinning of the stratospheric ozone layer, which is currently taking place over polar and temperate latitudes (Madronich 1994), has resulted in increasing levels of ultraviolet (UV) radiation reaching the earth's surface that could, potentially, have deleterious effects on aquatic food webs (Williamson 1995). In recent years, many studies dealing with the ecological consequences of UV radiation on aquatic biota have been undertaken (Karentz *et al*. 1994), although most have been performed in marine systems (Smith 1989; Karentz *et al*. 1991; Holm-Hansen *et al*. 1993), with emphasis on phytoplankton. Because microalgae are at the base of aquatic food webs, evidence that UV can alter phytoplankton biomass or growth strongly suggests that the entire ecosystem could be affected. Several researchers have also reported significant effects of UV exposure on marine and freshwater zooplankton. In copepods, effects of UV-B on survival (Karanas *et al*. 1979; Dey *et al*. 1988; Tartarotti *et al*. 1999), fecundity (Karanas *et al*. 1981; Williamson *et al*. 1994; Cabrera *et al*. 1997) and population density (Cabrera and Pizarro 1994) have been demonstrated. Furthermore, considerable evidence shows that cladocerans are sensitive to sources of UV-B at natural intensities (Siebeck 1978; Siebeck and Böhm 1991, 1994; Hessen 1994; Siebeck *et al*. 1994; Zagarese *et al*. 1994; Hurtubise *et al*. 1998; Grad *et al*. 2001). However, most of these studies have focused on *Daphnia* species and less information is available on other groups of cladocerans.

Negative effects on the fitness of planktonic organisms caused by UV radiation are mostly attributable to damage of nucleic acids by exposure to UV-B at 280–320 nm. Nonetheless, planktonic animals have different biological strategies for dealing with natural doses of UV-B light. One strategy is the avoidance of harmful radiation via behavioral mechanisms, such as diel vertical migration (Siebeck and Böhm 1994; Leech and Williamson 2001; Rhode *et al*. 2001). Other strategies include those that confer tolerance to UV light (e.g. mechanisms allowing organisms to tolerate the effects of the radiation reaching the body surface). These tolerance mechanisms can be further subdivided into those that prevent damage through the action of photoprotective pigments and those that repair damaged DNA produced by radiation. Some zooplankton species possess pigmented surfaces to prevent damage. In cladocerans, these surfaces are mainly composed of melanin (Hebert and Emery 1990), whereas in copepods these surfaces consist principally of carotenoids or mycosporine-like amino acids (Hairston 1979; Siebeck *et al*. 1994; Tartarotti *et al*. 2001). The two main mechanisms of DNA repair are: (*1*) photoenzymatic repair (PER), which uses the enzyme photolyase and short-wave visible

10.1071/MF03027 1323-1650/04/020001

light as its source of energy (Sutherland 1981); and (*2*) the excision repair system, which does not require light (Sancar 1994). Although all known organisms possess the excision repair system, PER is considerably more effective and has been demonstrated to exist in many zooplanktonic species (Malloy *et al.* 1997).

The integrated effect of UV-B light on aquatic food webs involves complex processes and is not yet fully understood. Ultraviolet-B radiation decreases primary productivity and, therefore, alters the availability of basal resources. Furthermore, the results of several studies suggest that UV-B light can reduce the nutritional value of algae for herbivorous plankton (Arts and Rai 1997; De Lange and Van Donk 1997; Gulati and De Mott 1997; Scott *et al.* 1999), thus exerting detrimental effects on zooplankton reproduction and survival. The harmful effects of UV-B light on aquatic biota may be highly variable. This variability may result because the physical features of the system, such as light intensity and UV transparency of the water, vary over time. Furthermore, a particular organism may be able to change its sensitivity to UV light over different developmental states (Leech and Williamson 2000) and according to its microevolutionary and ontogenetic history.

Although interspecific differences in tolerance to UV light have been demonstrated among planktonic animals (Siebeck and Böhm 1991; Hurtubise *et al.* 1998; Leech and Williamson 2000; Wübben *et al.* 2001), much less is known about the underlying mechanisms that could explain such variance. In the present study we estimated the tolerance to UV-B light of four cladoceran species that are common inhabitants of lakes in central Chile. We assessed the relative importance of PER and photoprotective mechanisms on the tolerance of the species tested and, as a further objective, we tested for differences in the tolerance to UV-B light between two age classes in one of the species.

Materials and methods

All experiments were run under controlled conditions, using artificial light sources, at the Limnological Research Station of the Ludwig-Maximilians University of Munich (Seeon, Germany). The irradiation chamber (Fig. 1) consisted of a 1000-W xenon high-pressure arc lamp (sun simulator) and additional UV-B sources (Philips TL40 W/12, Philips, Eindhoven, The Netherlands; 275–365 nm, maximum 315 nm).

Biological material

Experiments were conducted on four species of pelagic cladocerans, namely *Daphnia ambigua*, *Ceriodaphnia dubia*, *Diaphanosoma chilense* and *Moina micrura*. These species inhabit Lake El Plateado in Valparaíso, Chile, as well as many other lakes in central Chile. Lake El Plateado is a small, eutrophic, monomictic temperate lake, with a maximum depth of 12 m. This lake exhibits strong vertical gradients of temperature and oxygen content during the warm season. Water transparency is highly variable on a seasonal time scale, with maximum photosynthetically active radiation (PAR) penetration during the austral summer. Further details regarding the limnological features of Lake El Plateado can be found in Ramos-Jiliberto *et al.* (1997, 1998). All cladocerans investigated in the present study were collected at this lake. Specimens of each species were isolated and cultured in the laboratory for approximately 4 months before experimentation. All specimens were provided with a monoculture of *Chlorella* sp. as a food source, which was isolated from the same system. In many previous experiments (unpublished results), *Chlorella* sp. has proved to be adequate for the survival, growth and reproduction of the species studied herein.

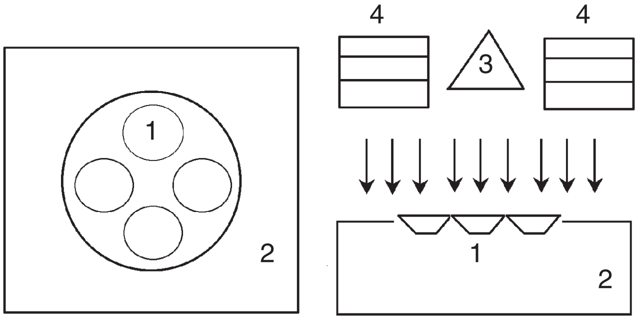

Fig. 1. Schematic representation of the irradiation chamber used in the present study. Left, as viewed from above; right, lateral view. Different parts of the system are as follows: (1), quartz vessels containing the cladocerans (including one control); (2), thermoregulated water bath; (3), solar simulator; (4), ultraviolet-B lamps.

Experimental animals were similar-sized adults from each species. We also used <48-h-old newborns individuals obtained from the third brood of same-aged mothers of the species *C. dubia*. Newborns of one species were included to obtain a wider range of responses and to explore the possible effects of age on the tolerance to UV-B light.

Experimental design

We performed two sets of experiments to measure the degree of tolerance to UV light (under conditions inhibiting or permitting PER). In each of the experiments, cladocerans were placed in groups of 10 individuals in open 5-cm diameter, 2.5-cm deep quartz dishes containing a few milliliters (approximately 1.5 cm depth) of filtered lake water (glass fiber filter of approximately 0.45 μm pore size). Temperature was kept constant at 20.0 ± 0.5°C. Three experimental groups and one control group were irradiated simultaneously in each of the approximately 100 trials (see Fig. 1). After each exposure treatment, organisms were kept in darkness in 80-mL beakers containing filtered lake water and food. The beakers were checked for mortality after 24 h. A total of approximately 4000 animals (approximately 3000 for the different treatments and 1000 for controls) were used in the experiments. We measured irradiance (UV-B dose rate) at the position where the cladocerans were placed in the chamber. For each of the two sets of experiments, the dose rate was kept constant (1.144 and 3.416 J s^{-1} m^{-2} for no-PER and PER experiments, respectively) and the exposure time was varied (from >0 to 180 min according to the different treatments).

Ultraviolet tolerance excluding PER

One set of experiments was designed to assess the tolerance of the organisms excluding the PER mechanism to UV-B light. In these experiments, species were exposed to the following UV-B doses: *Moina micrura* was exposed to 0.17, 0.34, 0.69, 1.03, 1.17, 1.37, 1.72 and 2.06 kJ m^{-2}; *Daphnia ambigua* was exposed to 0.17, 0.45 (two trials), 0.55 (three trials), 0.69 (three trials), 0.86, 1.03 (two trials), 1.37 (two trials), 1.78, 2.06 (two trials) and 4.12 kJ m^{-2}; *Diaphanosoma chilense* was exposed to 0.03, 0.07, 0.14 (two trials), 0.27 (two trials), 0.41, 0.55 and 0.86 kJ m^{-2}; *Ceriodaphnia dubia* was exposed to 0.17, 0.24, 0.34, 0.51, 0.69, 0.86 and 2.06 kJ m^{-2} (two trials); and *Ceriodaphnia dubia* newborns were exposed to 0.03, 0.07, 0.14 (two trials), 0.15 (two trials), 0.16 (two trials), 0.17 (two trials), 0.19 (two trials), 0.22 (two trials), 0.25 (two trials), 0.27 (two trials), 0.39, 0.51, 0.69 and 0.86 kJ m^{-2}.

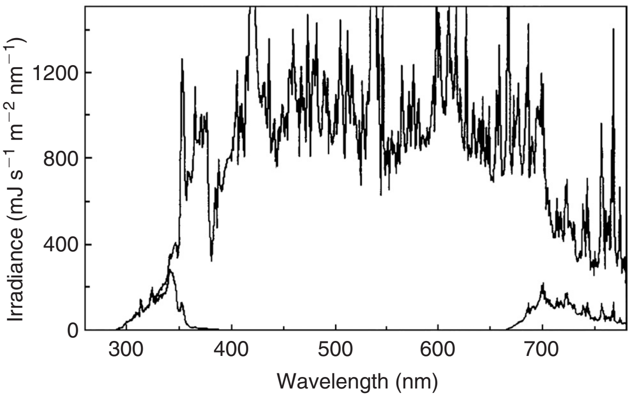

Fig. 2. Spectral composition of the radiation used in the experiments without photoenzymatic repair (PER; inner curves) and with PER (outer curve).

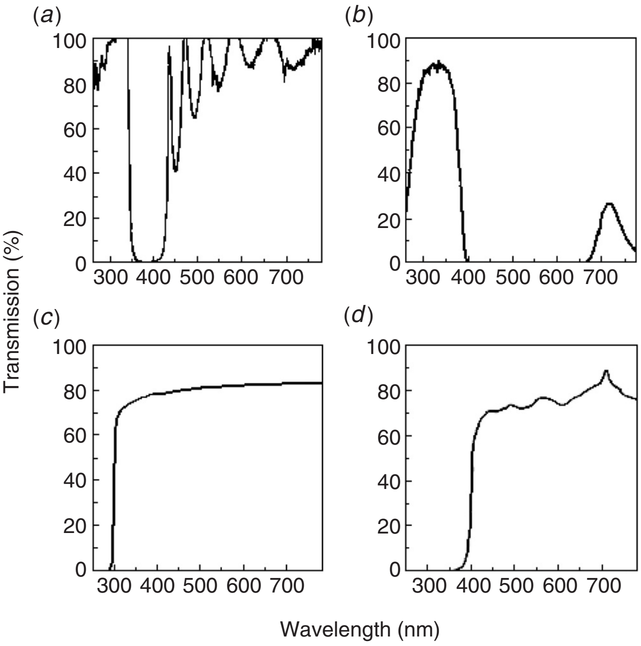

Fig. 3. Transmission spectra of the filters used in the experiments: (*a*) KIF, (*b*) UG11, (*c*) N125 and (*d*) polycarbonate.

For these treatments, the experimental organisms were exposed to a radiation spectrum including most of the UV-B and a short-wave fraction of UV-A, from 285 to 350 nm (Fig. 2; irradiance measured with a calibrated Bentham spectral radiometer, Bentham Instruments Ltd., Germany). This condition was achieved by using a combination of blocking filters (UG 11 + KIF + 2 × N125 = 'UV-B combination'). The UG 11 filter (Schott, Mainz, Germany) blocks the visible range, from 400 to 680 nm, the KIF filter (Schott) effectively blocks the 350–430 nm range and the N125 acetate filter blocks wavelengths shorter than 285 nm and, therefore, transmits only the UV-B to infrared (IR) range. For control tests, we used a polycarbonate filter that transmits only from the visible to the IR range. The controls allowed us to account for any source of mortality due to experimental factors other than the effect of UV-B. The transmission spectra of all filters were checked carefully using a Biochrom 4060 spectrophotometer (Biochrom Ltd, Cambridge, UK) and are shown in Fig. 3.

Ultraviolet tolerance including PER

In the second set of experiments, we measured the tolerance to UV light allowing for the PER mechanism. In these experiments, species were exposed to the following UV-B doses: *Moina micrura* was exposed to 1.35, 2.7, 5.4, 10.8, 21.6 and 32.4 kJ m^{-2}; *Daphnia ambigua* was exposed to 1.35, 2.7, 5.4, 7.2, 10.8 and 21.6 kJ m^{-2}; *Diaphanosoma chilense* was exposed to 1.35, 1.8, 2.7, 5.4, 10.8 and 21.6 kJ m^{-2}; *Ceriodaphnia dubia* was exposed to 1.08 (two trials), 1.35 (two trials), 2.7, 2.97, 5.4 (two trials), 10.8 and 21.6 kJ m^{-2}; and *Ceriodaphnia dubia* newborns were exposed to 0.72, 1.35, 2.7, 5.4, 10.8 and 21.6 kJ m^{-2}.

In these treatments, animals were irradiated under two foils of N125 blocking filters, thus being exposed to UV + visible light during the experimental period. Following this period, animals were maintained under the polycarbonate foils (blocking out the entire UV range) for an additional 20 min. Control animals were always exposed under polycarbonate foils.

Data analyses

Tolerance to UV-B was measured as the LD$_{50}$ (i.e. the UV-B light dose for 50% mortality). The LD$_{50}$ values and 95% confidence interval limits were calculated, after correcting for mortality in the controls, using the trimmed Spearman–Karber method (Hamilton *et al.* 1977). Significant differences were accepted if the 95% confidence limits did not overlap. The relative importance of PER relative to other protective mechanisms was measured through the dose-modification factor (DMF; ≥ 1), which is the ratio between the LD$_{50}$ with and without PER (Siebeck and Böhm 1991). Thus, a DMF value equal to 1 indicates that no PER is taking place and a DMF value of 2 indicates that tolerance to UV-B light of a species exhibiting PER is twofold greater than the tolerance of the same species without PER.

Results

The results of the different experiments are shown as dose–mortality curves in Fig. 4. All controls survived at a rate above 95% and were not plotted. Values of tolerance to UV-B light (measured as LD$_{50}$) and confidence limits are shown in Fig. 5. Values are provided in Table 1, together with DMF values.

All groups had significantly different sensitivities to UV-B light when no PER was allowed. Among adults, the most tolerant species was *M. micrura*, with an LD$_{50}$ value of 0.94 kJ m^{-2}, followed by *D. ambigua* (0.63 kJ m^{-2}) and *C. dubia* (0.31 kJ m^{-2}), whereas the most sensitive species was *D. chilense* (0.24 kJ m^{-2}). The sensitivity of newborn individuals of *C. dubia* differed from that of adults of the same species. Furthermore, newborns were the least tolerant of all the groups tested (0.16 kJ m^{-2}; see Table 1 for details).

Among cladocerans exposed simultaneously to UV and visible light, *D. chilense* (LD$_{50}$ = 2.94 kJ m^{-2}) and *D. ambigua* (2.85 kJ m^{-2}) were the least tolerant species, showing no significant differences between them. *Moina micrura* (10.8 kJ m^{-2}) was again the most tolerant species, whereas adults of *C. dubia* were intermediate in their tolerance to UV-B light (7.27 kJ m^{-2}). Tolerance to UV light of *C. dubia* newborns (3.32 kJ m^{-2}) was significantly lower compared with that of adults, but did not differ from that of *D. chilense* and *D. ambigua*.

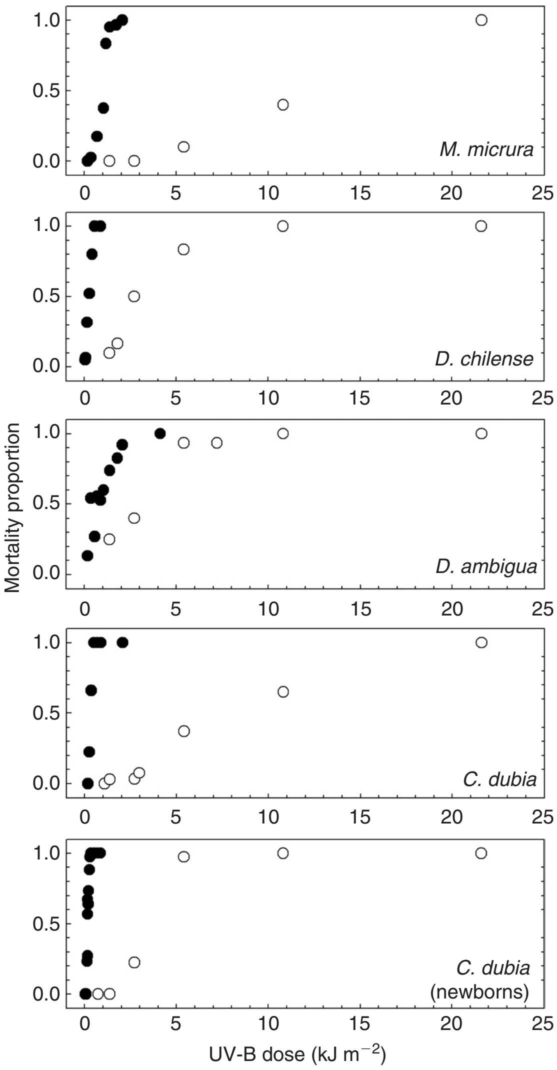

Fig. 4. Dose–mortality curves of cladocerans exposed to ultraviolet (UV)-B only (●), and UV + visible light (○).

In all species tested, tolerances to UV light differed with and without PER (Fig. 5). Table 1 shows the ratio of total tolerance (i.e. protection + PER) to tolerance without PER, demonstrating that PER is less effective, relative to protective mechanisms, in *D. ambigua* and that PER is most effective in *C. dubia* (for both adults and juveniles). *Moina micrura* and *D. chilense* had intermediate DMF values.

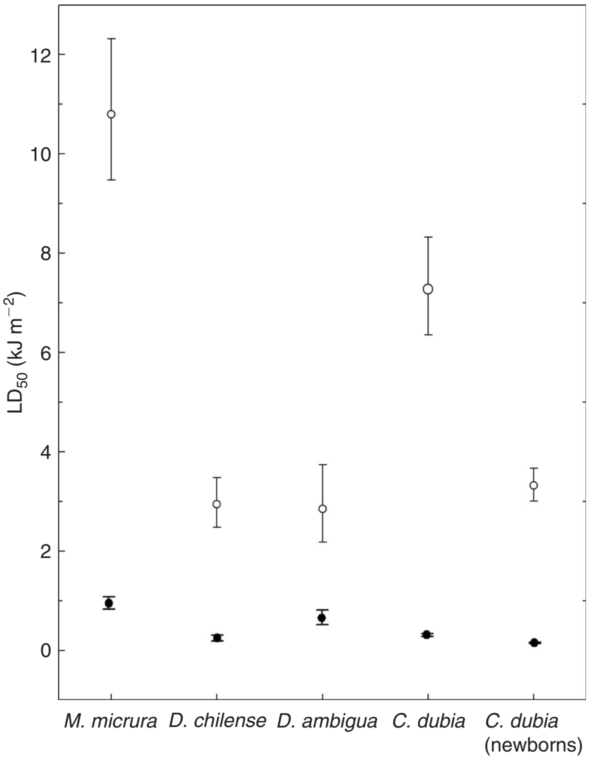

Fig. 5. Ultraviolet (UV)-B tolerance (LD$_{50}$ and confidence intervals) of cladocerans exposed to UV-B (●; error bars are not visible in some cases due to the ordinate scale) and UV + visible light (○).

Table 1. Tolerance to ultraviolet-B light of cladocerans, expressed as median lethal doses (LD$_{50}$) and their 95% confidence limits in experiments with and without photoenzymatic repair

	No photoenzymatic repair			Photoenzymatic repair			DMF
	n	LD$_{50}$ (kJ m^{-2})	95% CL	*n*	LD$_{50}$ (kJ m^{-2})	95% CL	
Moina micrura	280 (80)	0.94	0.86–1.03	180 (50)	10.8	9.47–12.32	11.49
Diaphanosoma chilense	280 (70)	0.24	0.20–0.28	150 (50)	2.94	2.48–3.48	12.25
Daphnia ambigua	638 (110)	0.63	0.54–0.74	170 (50)	2.85	2.18–3.74	4.52
Ceriodaphnia dubia	300 (70)	0.31	0.29–0.33	340 (70)	7.27	6.35–8.32	23.45
Ceriodaphnia dubia (newborns)	718 (140)	0.16	0.15–0.17	190 (50)	3.32	3.01–3.67	20.75

The number of experimental organisms used (*n*) is given, together with the number of control organisms (in parentheses).
The dose-modification factor (DMF) is the overall tolerance relative to tolerance due to photoprotective mechanisms.
CL, Confidence interval.

Discussion

Zooplankton use various strategies to avoid UV-B-induced DNA damage and consequent reduction in fitness. Behavioral avoidance by downward diurnal migration is very effective because light attenuates exponentially with depth, but it will only work in systems that are deep enough relative to UV penetration (e.g. deep lakes or shallower yet turbid lakes). However, if invertebrate predators also perform diel vertical migrations to avoid fish predators, this would produce a conflict between UV-B and predator avoidance of their zooplankton prey. Furthermore, if hostile conditions for zooplankton individuals occur in deeper water, such as the development of deep hypoxic layers in eutrophic lakes, zooplankton will be confined to surface waters (Hall 1964; Hanazato 1992; Massana *et al.* 1994). Moreover, diel vertical migration usually implies that zooplankton are exposed to low temperatures in deep waters, which represents an important cost in terms of slowed developmental rates (Loose and Dawidowicz 1994).

In any case, where behavioral UV-B avoidance is not feasible or is disadvantageous, tolerance mechanisms play a crucial role. Protective pigmentation and PER are important tolerance mechanisms, each of which has distinct ecological consequences. Pigmentation involves a trade-off between UV protection and predation risk, because animals with greater pigmentation are more vulnerable to predation by visual predators (Hansson 2000; Johnsen and Widder 2001). Photoenzymatic repair is temperature dependent and, consequently, its effectiveness will vary seasonally (Williamson *et al.* 2002). Ultimately, each individual organism will exhibit particular capabilities to avoid or tolerate (either through preventive protection or repair mechanisms) the harmful effects of UV-B, depending on genetic constraints, physiological state and environmental conditions.

In this study, we present experimental results that show differential UV-B sensitivities between coexisting cladocerans, differences in sensitivity between animals at different developmental stages and differential contributions of PER to UV tolerance. Between-species differences in tolerances to UV-B light attributable to photoprotection were significant in all cases (Table 1), with *M. micrura* being the most tolerant group, followed by *D. ambigua*, *C. dubia* and, finally, *D. chilense*. Photoenzymatic repair significantly increased UV-B tolerance by a factor of 5–23. *Daphnia ambigua* showed the weakest increment in tolerance to UV light with the addition of PER, whereas *C. dubia* showed the strongest increase. Tolerance to UV-B light including PER continued to be highest for *M. micrura*, followed by *C. dubia* and, finally, *D. chilense* and *D. ambigua*. We also found significant differences in tolerances to UV-B light between juvenile and adult *C. dubia*, both with and without PER. Interestingly, the DMF was similar for juveniles and adults.

Comparisons with the various tolerance values reported in the literature reveal that our results agree with those reported previously for invertebrates, despite considerable variation in experimental conditions and the species being studied. Siebeck and Böhm (1991) reported LD_{50} values for *Daphnia galeata* and *Daphnia pulex* of 0.08 and 0.07 kJ m^{-2}, respectively, in the absence of PER. In the same study, the authors provide LD_{50} values for corals, with no PER effects, which vary between 0.02 and 0.24 kJ m^{-2}. Our results using cladocerans give somewhat greater values of LD_{50}, ranging between 0.16 and 0.92 kJ m^{-2}. In contrast, Lacuna and Uye (2000, 2001) evaluated the degree of tolerance to UV-B light of two copepod species with low and high PER at different developmental stages (i.e. eggs and adults). Their results for low PER effects reveal LD_{50} values between 4.01 kJ m^{-2} (eggs) and 22.0 kJ m^{-2} (adult females), which are far greater than the values for cladocerans obtained in the present study. However, neither of the studies of Lacuna and Uye (2000, 2001) blocked the UV-A and visible spectra and, therefore, these results are not comparable with those of the present study.

The literature contains more information for UV-B tolerance allowing PER, probably because of the relative simplicity of the experimental setup. Siebeck and Böhm (1991) reported an LD_{50} of 0.39 kJ m^{-2} for *D. galeata* and 1.07 kJ m^{-2} for *D. pulex*. Lacuna and Uye (2000, 2001) found LD_{50} values ranging between 7.9 and 22.5 kJ m^{-2} for the copepod *Acartia omorii* and between 16.0 and 27 kJ m^{-2} for *Sinocalanus tenellus*. Hurtubise *et al.* (1998) report LD_{50} values ranging between 0.7 and 3.28 kJ m^{-2} for cladocerans, 3.19 kJ m^{-2} for amphipods and 15.12 kJ m^{-2} for ostracods. Wübben *et al.* (2001) give LD_{50} values for *D. carinata* (35.1 kJ m^{-2}), *Ceriodaphnia dubia* (36.7 kJ m^{-2}) and the copepod *Boeckella delicata* (32.8 kJ m^{-2}). Thus, the values obtained in the present study (2.18–9.47 kJ m^{-2}) fall within the range reported previously for invertebrates, and particularly for cladocerans. It should be noted that a large difference exists between the LD_{50} of *C. dubia* reported by Wübben *et al.* (2001) and our own estimation of 7.27 kJ m^{-2}. This difference could be explained, in part, by the different lamps used and particularly by the dose rate, which was higher in the present study. Nevertheless, the animals used in our experiments were collected from a turbid lake, whereas *C. dubia* was collected from a clearer water body by Wübben *et al.* (2001) and, therefore, a greater tolerance to UV light should be expected for those animals.

Dose-modification factor values of 5 and 14.7 have been shown for *D. galeata* and *D. pulex*, respectively (Siebeck and Böhm 1991). These authors reported DMF values for corals ranging between 5.2 and 7.3. These values are within the range of those reported herein, which range from 4.52 for *D. ambigua* to 23.45 for *C. dubia*. This confirms that PER is an important mechanism conferring UV-B protection in cladocerans, but that its magnitude varies considerably between species. Lacuna and Uye (2000, 2001) documented DMF values ranging between 1 and 3.9 for copepods, but these experiments did not remove PER radiation and, therefore, the DMF cannot be interpreted in the same way as in the present study.

The effects of age on the degree of tolerance to UV-B light were accounted for by Lacuna and Uye (2000, 2001), who showed that adult female copepods have a higher tolerance to UV and a lower DMF than earlier stages. Our results also demonstrated a significant increase in tolerance to UV-B with age, but with a difference in DMF of only approximately 10%. In addition to interspecific differences in UV-B tolerance seen in the present and previous studies, the consideration of stage, or age, dependence of UV-B tolerance makes it more difficult to translate results from simple laboratory experiments to real ecosystems. Interestingly, the tolerance to UV-B light including PER correlates with the intrinsic population growth rate of the respective groups, as measured under laboratory controlled conditions (life-table results, unpublished). This suggests that species that are most tolerant to UV-B radiation (in this case *M. micrura* and *C. dubia*) also have the greatest potential for growth and, therefore, they should be able to survive and reproduce better in surface waters. Therefore, surface-adapted species could take advantage of higher temperatures and possibly greater amounts of food found in the epilimnion, thereby increasing reproductive output enough to counterbalance the mortality exerted by visual predators (Stich and Lampert 1984). This topic should be investigated in a systematic way in future studies. In contrast, the two species with the lowest tolerance to UV light (*D. chilense* and *D. ambigua*) exhibit diel vertical migration at the study site (Ramos-Jiliberto and Zúñiga 2001; Ramos-Jiliberto *et al.* 2004), being located near the surface at night and at greater depths during the day. This suggests that the primary protective mechanism against radiation used by these species is the avoidance of UV light via behavioral mechanisms (either predator induced or not), avoiding the surface layers during daylight.

The overall impact of UV-B radiation in aquatic ecosystems is a complex process that affects multiple populations and multiple trophic levels and includes several interactions between populations and the physical environment itself (Siebeck *et al.* 1994; Williamson 1995). For example, when the tolerance of herbivores to UV-B light is lower than that of their algal food source, algal growth can be enhanced when the system is exposed to UV-B (Bothwell *et al.* 1994). Similarly, the outcome of competitive interactions could be altered under the pressure of UV-B when differences in the degree of tolerance to UV light exist among species within the same trophic level. Therefore, interspecific differences in sensitivity to UV should be considered when explaining and predicting community response to high levels of UV radiation.

Because the effectiveness of different mechanisms of avoidance of and tolerance to UV-B depend on the actual ecological scenario, the interspecific differences in sensitivity to UV-B light will probably vary over time and space. Furthermore, when trade-offs related to avoidance of and protection or repair from UV light occur, we expect that the net advantages of a given strategy will be dynamic, being related to predation pressure, water conditions and resource availability, among other factors.

Quantitative information on the degree of tolerance to UV-B light (e.g. LD_{50}) is valuable for assessing the potential damage of radiation on the target species. However, because this kind of result is strongly dependent on experimental conditions, as well as on the state of the organisms tested, generalising any particular result obtained in the laboratory to the natural complex world is not straightforward. For example, Siebeck and Böhm (1994) reported an LD_{50} value for *D. galeata* of 35 $\mathrm{kJ\,m^{-2}}$ under natural light, which is almost 100-fold higher than that reported by the same authors under artificial light sources. Therefore, comparisons between studies must be made with extreme caution. Comparative studies are much more informative and provide a qualitative basis for assessing how an environmental stressor could affect interactions within a structured population or a community. Future work oriented towards recognising the ecological consequences of UV radiation should strive to understand the mechanisms governing the complex effects of UV in ecological systems, particularly the indirect effect of UV radiation in food webs.

Acknowledgments

We sincerely thank Ralph Tollrian and an anonymous reviewer for helpful comments. Our research was supported by Volkswagen-Stiftung funds and a German Academic Exchange Service (DAAD) scholarship to R.R.J. The experimental work was greatly facilitated by O. Siebeck and the staff of the Limnological Research Station of Seeon, of the Ludwig-Maximilians University of Munich. The manuscript was finished with partial support from FONDECYT grant 3000051 to R.R.J and Research project 124.789 from the Univeridad Católica de Valparaíso.

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Manuscript received 20 February 2003; revised 4 August 2003; accepted 15 October 2003.