Phytoplankton and zooplankton response to ultraviolet radiation in a high-altitude Andean lake: short- versus long-term effects

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Abstract. Exclusion experiments on global UV (A and B) radiation and global UVB were performed in 460 l mesocosms with plankton communities from the oligotrophic Andean lake Laguna Negra (33°35'S–70°04'W; 2700 m a.s.l.). The experiments were run for 30 days during the summers of 1991–1992 and 1992–1993, and for 48 days in 1993–1994. When UVB radiation was allowed to enter into the mesocosms (full sun), the population of *Ankyra judayi* (Chlorophyta) reached the highest density, suggesting that this species can endure high levels of UV radiation. Concurrently, an increase in chlorophyll *a* concentration was observed in this treatment. The cladoceran *Chydorus sphaericus* and the rotifer *Lepadella ovalis* were strongly inhibited by UVB. Conversely, UVB radiation had no effect on the survival of the different life stages of the calanoid copepod *Boeckella gracilipes*, suggesting a species-specific difference in the sensitivity to solar UVB radiation. Moreover, no reduction in the number of copepod eggs per female and the number of nauplii produced was observed. Apparently, herbivory does not strongly affect phytoplankton abundance. Moreover, the phytoplankton species composition changed in the different treatments over the time. *Fragilaria construens* and *Fragilaria crotonensis* were dominant in those mesocosms where UVB was excluded. Populations fluctuated depending on their life cycles and the period of time they were exposed to UVB radiation. It is important to define the time scale of exclusion experiments, because different conclusions about the influence of UVB irradiance result from short-, medium- or long-term exposures.

Introduction

In the last 10 years, many studies have shown that the decrease in stratospheric ozone allows an increased flux of UVB radiation to reach the Earth's surface (Bojkov, 1995; Madronich *et al.*, 1995, and references therein). The ozone 'hole' extends into January and February, so that significant increases in UVB radiation can be expected at the surface over Antarctica during summer (Jones and Shalklin, 1995). Furthermore, evidence for an ozone 'hole' pertubation has been observed at 30° south (Kirchhoff *et al.*, 1996).

UVB has been shown to affect different cellular processes, such as the rate of carbon fixation, respiration and the biosynthesis of protective pigments (Carreto *et al.*, 1990; Cullen *et al.*, 1992; Smith *et al.*, 1992; Karentz *et al.*, 1994). Bothwell *et al.* (1994) studied the effect of UVB radiation on periphyton communities, and found a clear interaction between primary producers and herbivores in a shallow artificial running-water ecosystem. UVB radiation decreased the herbivore pressure, leading to increases in periphyton density. Effects were time dependent: the initial inhibitory effect of UV on algae was reversed after 3–4 weeks, and by 5 weeks total abundance [chlorophyll (Chl) *a*, cell number and cell biovolumes] was 2- to 4-fold greater than in communities protected from UV (Bothwell *et al.*,

1993). Damaging effects of UVB radiation have been reported for different freshwater zooplankton species (Zagarese *et al.*, 1994; Zellmer, 1995; and references therein). Williamson *et al.* (1994) observed a suppression of the reproduction of a freshwater copepod by UVB radiation down to 6 m in an oligotrophic lake. Zooplankton may avoid exposure to high levels of UVB by staying in deep water layers or by undergoing diel vertical migration (Damkaer, 1982). However, these strategies incur a physiological price (Orcutt and Porter, 1983; Stich and Lampert, 1984; Dawidowicz and Loose, 1992) or increase the risk of predatory losses (Stich and Lampert, 1981; Gliwicz, 1986). DNA repair pathways (e.g. photoreactivation), photoprotective compounds [mycosporine-like amino acids (MAAs)] or antioxidants like carotenoid pigments (e.g. astaxanthin), catalase and others occur in some crustaceans (Hairston, 1979, 1980; Byron, 1982; Ringelberg *et al.*, 1984; Karentz *et al.*, 1991; Smith *et al.*, 1992; Hessen, 1993, 1994). Far higher total carotenoid concentrations are observed in freshwater calanoid copepods than in cladocerans (Hebert and Emery, 1990; Hessen and Sorensen, 1990; Hessen, 1993, 1994). Cuticular melanization (direct sun blocking; probably antioxidant) is more likely in cladocerans of high altitudes and living under high solar radiation levels (Beaton and Hebert, 1988; Hebert and Emery, 1990; Hobaek and Wolf, 1991). Pigmentation of rotifers has also been reported (Dumont *et al.*, 1978; Modenutti, 1992), but its role in photoprotection is not yet known.

UVB radiation is a highly reactive component of the solar spectrum. Vincent and Roy (1993) suggested that solar UVB radiation has been a significant variable in the aquatic environment throughout evolutionary time, and photosynthetic organisms have developed a variety of defenses that allow them to avoid, screen, repair and otherwise protect their cells from long-term damage. Predictions of immediate and large-scale impairment of primary production in response to ozone depletion seem to be greatly exaggerated, and may lead to inappropriate monitoring strategies and measurement techniques (Vincent and Roy, 1993). Nevertheless, Blaustein *et al.* (1994) showed density declines in photolyase activity level in amphibians and Schindler *et al.* (1996) have shown an intimate linkage between climate warming, acid deposition and increasing exposure to UV radiation in boreal ecosystems. Thus, UVB radiation induces a variety of processes, including intracellular processes, as well as physical and chemical properties of water (Cabrera and Pizarro, 1994). Consequently, it is necessary to consider UVB radiation effects directly on biomolecules and indirectly on environmental changes that can affect the organisms.

The eventual impacts of increasing global UVB remain unknown, but predicting and (or) detecting the onset of such changes in the aquatic environment will require novel bioassay approaches and a commitment to long-term monitoring of community structure in representative freshwater and marine ecosystems. Most of the UVB studies to date have been reported from the northern hemisphere and none or few come from South America where ozone depletion is proceeding most rapidly. Experimental limnological enclosure studies allow the study of the effects of UV on plankton. Two important questions have been addressed with our experimental set-up. (i) How can plankton communities be affected by acute and chronic UVB radiation? (ii) Are all planktonic species

equally affected by UVB radiation? This paper describes such experiments carried out in a high-mountain lake in the southern hemisphere (Central Andes). Unprotected mesocosms were exposed to a natural higher UVB intensity characteristic of this latitude and altitude. These results are compared with those from mesocosms protected from UVB.

Method

Study site

Laguna Negra is a large, deep lake located at 2700 m a.s.l. in the Andes near Santiago, Chile (33°40′S–70°06′W; z_{max} 320 m, z_{mean} 94.7 m, surface area ~7 km^2 and volume 625 × 10^6 m^3).

Mesocosms

The experiments were performed during the summer seasons of 1991–1992, 1992–1993 and 1993–1994. The duration of the experiment was 30 days for the first 2 years and 48 days for the third. In the 30 day experiments, only Chl a and some taxonomic phyto- and zooplankton samples were examined. Six mesocosms (Femoglass, opaque material, outside wall gray in color and the inside close to white) were filled with 460 l of near-shore, surface lake water around midday 1 day before the experimental period started. The dimensions of the mesocosms were depth 1.0 m, and 1.0 and 0.7 m upper and bottom diameters, respectively. The mesocosms were located outside the lake at a distance of 12 m from the shoreline because the level of the lake was rising (snow melt) at that time of the year. No wall growth was observed during the experimental periods.

Radiation treatments

Three treatments were repeated with one mesocosm each in 1991–1992, and in duplicate mesocosms in the period of the 1992–1993 and 1993–1994 experiments.

Treatment 1 [photosynthetically active radiation (PAR)]. Mesocosms covered with 1.2 × 1.2 m Mylar + plexiglass sheets which selectively absorb UVA and UVB, but transmit PAR.

Treatment 2 (PAR + UVA). Mesocosms covered with 1.2 × 1.2 m Mylar which selectively absorbs UVB radiation, but transmits PAR plus UVA.

Treatment 3 (PAR + UVA + UVB). Mesocosms exposed to full sunshine, thus receiving all types of solar radiation (control).

The Mylar filters (polyester, 0.12 mm, type SH-71, made by S.K.C. Films Limited, Seoul, Korea) were replaced every 15 days because their optical properties changed. A gap of 20 cm was left between the cover and the upper border of the enclosure to allow air currents to circulate and to permit water removal. Before sampling at midday, temperature was measured with a submersible

thermocouple (Knick, Model Portamess 654, FRG) at three depths (surface, 40 cm and the bottom).

Radiation was measured with portable PUV-510 (air sensor) and PUV-500 (submersible) multichannel moderate band width filter instruments (Biospherical Instruments, Inc., San Diego, CA). Center wavelengths are ~308, 320, 340 and 380 nm, and band widths are ~10 nm full width at half maximum (Booth *et al.*, 1994). The air sensor has a center at 306 nm wavelength, the underwater sensor at 308 nm (these values were obtained from Biospherical Instruments Inc., San Diego, CA). Radiation received in Santiago (600 m a.s.l.) is the reference value for the mesocosms, due to the inaccessibility of the experimental site. Radiation at Laguna Negra was calculated from these values according to Cabrera *et al.* (1995) using an altitude effect at 306 nm of 10% km^{-1}. The data measured in the UVB range were corrected by an ad hoc inversion method according to Fuenzalida (submitted; see also Booth *et al.*, 1994). The UV extinction coefficient (K_d) in the lake and in the mesocosms was estimated by fitting exponential regressions.

Sampling counts and water chemistry

Water samples were taken at midday, using a transparent Van Dorn bottle (3 l volume) in a horizontal position from the surface layer, at intervals of not more
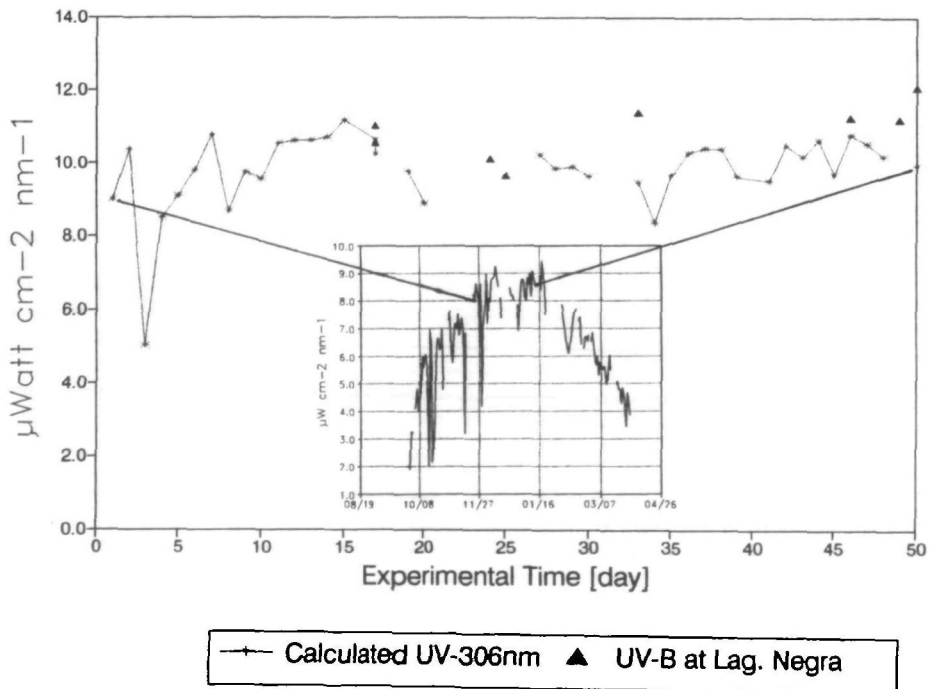
Fig. 1. Maximum daily UVB$_{306\,nm}$ values during the experiment in 1993–1994. Extrapolated from continuous measurements with PUV-510 (Biospherical Instruments Inc.) in Santiago (100 km northwest of the experimental site). The small panel shows half-year UVB$_{306\,nm}$ (daily maximum values) at Santiago City.

than 7 days. The mesocosms were not mixed before sampling. Chlorophyll *a* concentration (2 l) was measured in replicates using the method described by Jeffrey and Humphrey (1975). In the last year (1993–1994), phytoplankton were taken from the same water sample as Chl *a*, fixed immediately with Lugol, identified and counted using an inverted microscope, after settling in volumetric chambers following the methodology of Coon *et al.* (1987). At least 100 optical fields were counted (~1.0 cm³; Wild, 400× magnification).

At the end of the last experimental period (1993–1994), 48 l from each mesocosm were filtered through a 45 μm mesh size plankton net to determine zooplankton species composition and abundance. The mesocosms were stirred prior to zooplankton sampling. Samples were preserved in formaldehyde (3% final concentration), sedimented in an Utermöhl chamber and counted under an inverted microscope. Abundance, as well as the number of eggs and embryos for the cladocerans and the different life stages and the number of eggs for the copepods, were determined for the entire sample.

In 1993–1994, it was necessary to add 48 l of lake water to all the mesocosms, equivalent to 8.7% of the total volume, because the evaporation was high, in order to maintain the original water volume. Total nitrogen and phosphorus were determined in all the containers, from samples taken at days 1, 3, 26 and 45, utilizing standard methods (American Public Health Association, 1975).

Results

Ultraviolet radiation and PAR

In the 1993–1994 period, daily maximum extrapolated values of UVB$_{306\ nm}$ fluctuated between 11.19 and 5.01 μW cm^{-2} nm^{-1}, with a mean of 9.82 ± 1.03 μW
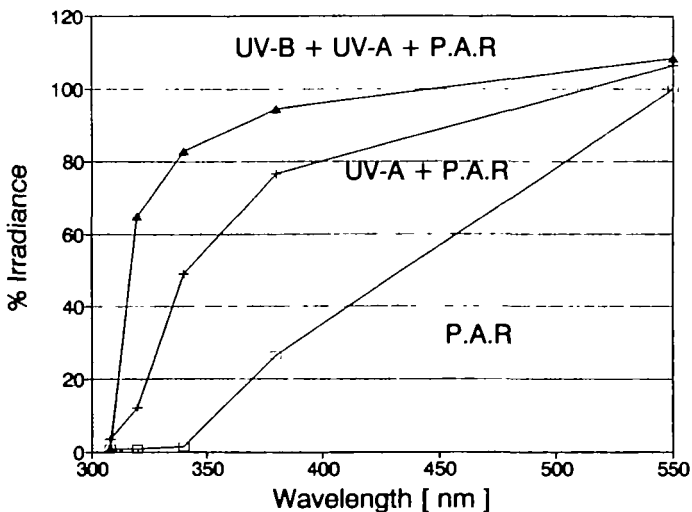
Fig. 2. Spectral irradiance measured inside the mesocosms (40 cm depth) with PUV-500 (Biospherical Instruments Inc.) at midday. Reference (100%) values were taken with PUV-510 (air sensor). PAR is a broad-band measurement, here it is referred to 550 nm.

cm^{-2} nm^{-1} (Figure 1); direct measurements at the mesocosm site are shown as triangles. This is the period with the highest UVB irradiance at this latitude and altitude in the southern hemisphere. UVB$_{306\ nm}$ radiation at Santiago (600 m a.s.l.) is shown from August 1993 to April 1994 (Figure 1).

Global (direct plus diffuse) UV radiation inside the mesocosm (at 0.4 m depth) is shown in Figure 2. The 100% represents the radiation received at the water surface. The quantities shown are in direct relation to the quality (absorption) of the filters used. The UV-exposed treatments received more PAR (8%) because of the reflection of the mesocosm wall.

To determine the amount of UV radiation that the planktonic organisms received in the lake, the penetration of different UV radiation and PAR was measured (Figure 3a and b). Extinction coefficients were calculated (Table I).
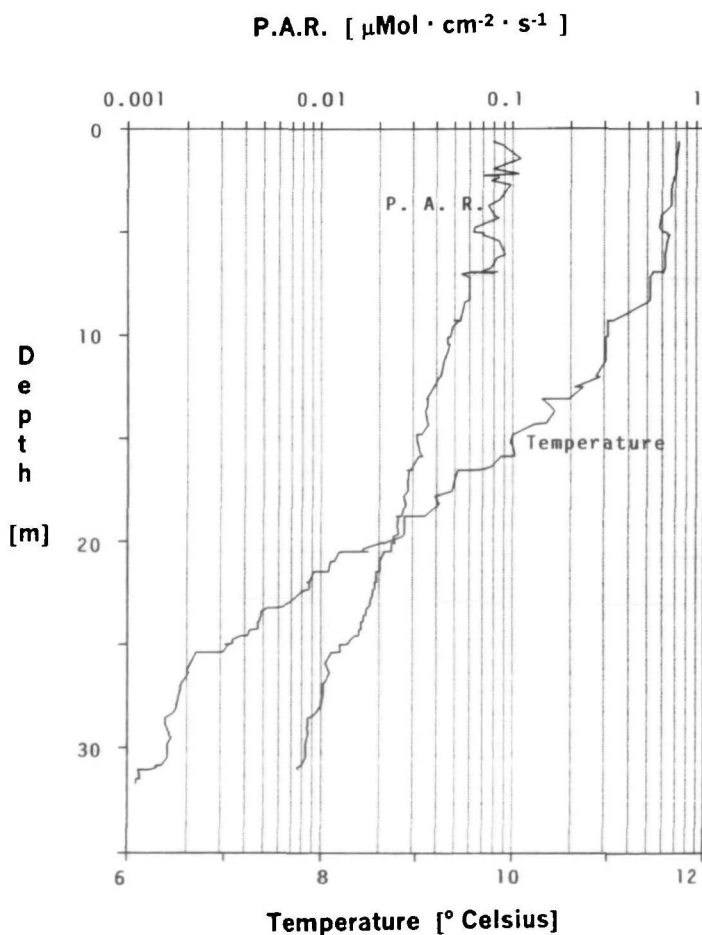

Fig. 3. (a)Vertical profiles of temperature and PAR measured with PUV-500 (Biospherical Instruments Inc.) in Laguna Negra (open water), December 1992.

Table I. Vertical attenuation coefficients for downward UVB irradiance of different wavelengths taken with PUV-500 (Biospherical Instruments Inc.) in Laguna Negra, November 1992. Incident radiation at the surface (I_o), UV is expressed in $\mu W\ cm^{-2}\ nm^{-1}$, PAR is expressed in $\mu mol\ cm^{-2}\ s^{-1}$. Correlation coefficient (K_d); n, number of pairs taken for correlation estimation and depth where 10% of I_o was reached

$K_d (k^a)$	$I_o{}^a$	r^2	n	$z (10\%\ I_o)$ m
308 nm = 0.186	6.960	0.998	152	12.3
320 nm = 0.192	45.637	0.972	177	13.0
340 nm = 0.160	77.277	0.988	202	15.4
380 nm = 0.109	99.448	0.987	192	22.0
PAR = 0.091	0.151	0.993	202	24.8

[a]Calculated from $I = I_o \times e^{-kz}$.
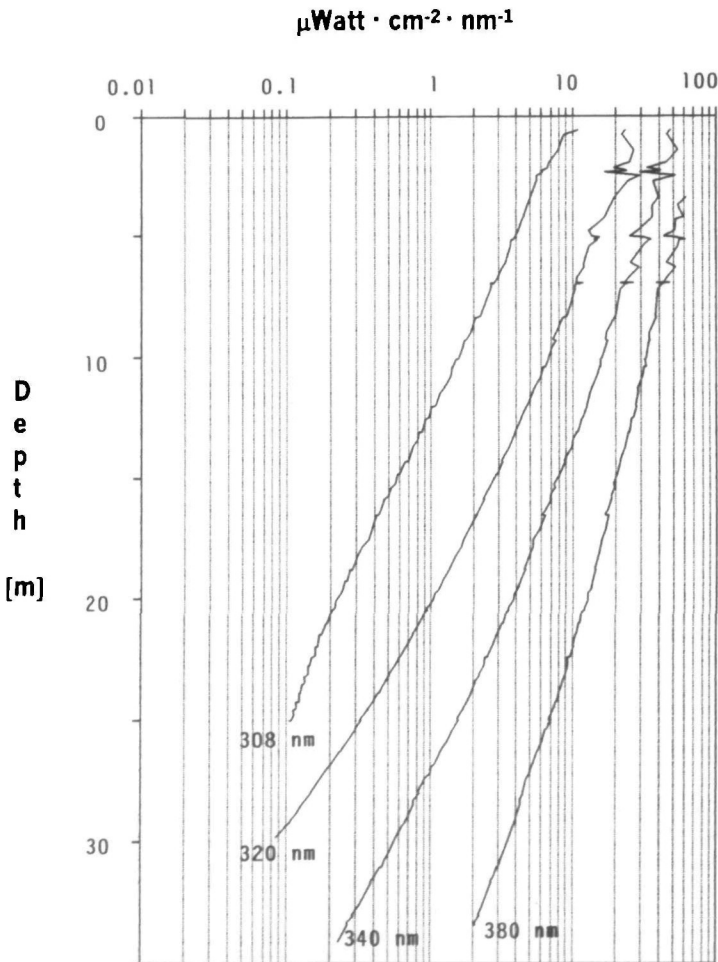
Fig. 3. (b) Vertical profiles of UV (308, 320, 340 and 380 nm) downward irradiance in Laguna Negra, December 1992.

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## Total nitrogen, total phosphorus and evaporation

The initial and final mean concentrations of total nitrogen were 141 ± 14 and 167 ± 42 µg l⁻¹, respectively, and the initial and final mean concentrations of total phosphorus were 0.83 ± 0.03 and 1.25 ± 0.00002 µg l⁻¹. These concentrations increased slightly during the experiments due to evaporation and refilling with unfiltered lake water.

Temperature

Midday temperatures fluctuated more in the mesocosms than in the lake (Figure 4). At the beginning of the 1993–1994 experimental period, the meso-cosms had 2 days (3 and 4) at 0°C (ice cover 10 cm thick), but the surface water of the lake never froze. The surface temperature of the lake water increased from 9.5 to 17°C between days 5 and 48 of the experiment. In general, the lake water was always cooler than inside the mesocosms at midday. For example, on day 12 the mesocosms were 16.5 ± 0.8°C, while the lake water temperature was only 12.5°C. The buffering influence of the lake water mass was observed. At the beginning of the experiment, the differences were largest because the mesocosms were far from the shoreline (12 m). Later, the temperatures of the mesocosms and the lake were very similar (Figure 4).

Phytoplankton biomass (chlorophyll a)

In the first year (1991–1992), in the presence of UV radiation, Chl a concentrations were higher than in UV-excluded mesocosms where Chl a concentrations
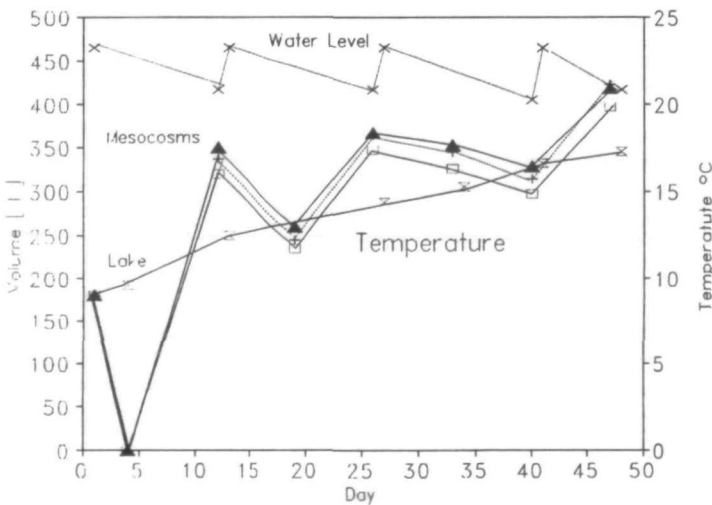

Fig. 4. Midday, mean temperature measured in the mesocosms and single measurement at the shore of Laguna Negra. The upper, dashed data line (x) represents the changes in the mesocosm water level due to evaporation and refilling during 1993–1994. The mesocosms at the beginning of the experimental period were placed at a distance of 12 m from the shore and finished close to it (1 m), because the surface of the lake rose during the experiment.

decreased. At the end of the experiment (day 30), all treatments had similar amounts of Chl *a* (Figure 5a).

However, in the other two summer periods (1992–1993 and 1993–1994), the pattern was different. In the presence of UVB, Chl *a* concentrations declined during the first 2 weeks. After this, they increased slightly to a maximum concentration at day 32 (Figure 5b). In 1993–1994, Chl *a* concentrations were not correlated with any biomass changes of the more abundant microalgal species.

However, when the experimental period was extended to 48 days, there was a general decrease in biomass in all treatments. At day 42, the same amount of Chl *a* was observed in all the mesocosms (Figure 5b), followed by an increase in
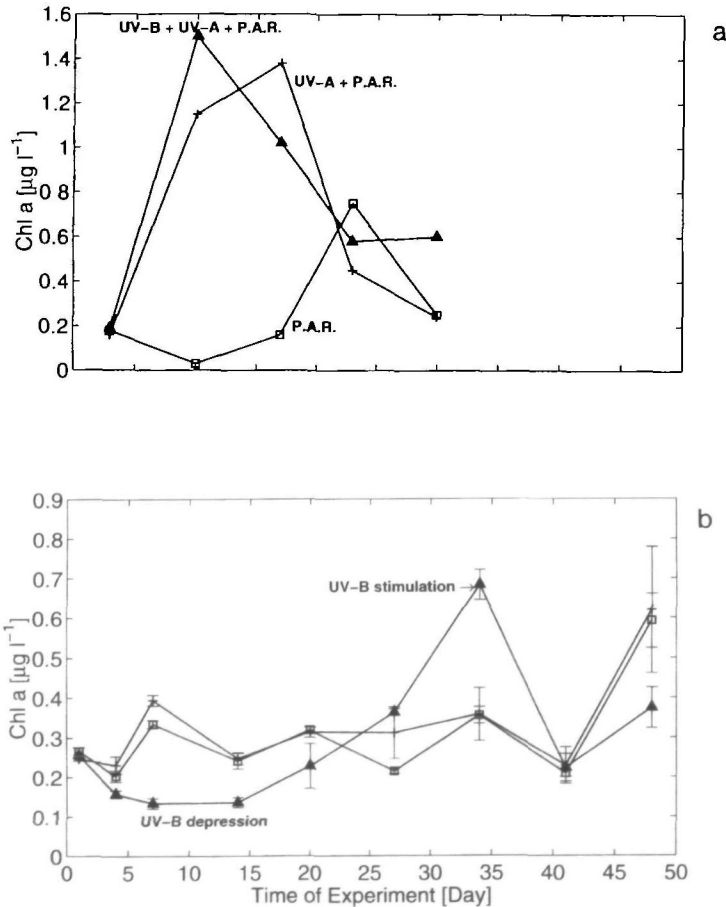
Fig. 5. (a) Changes in chlorophyll *a* for different treatments during the 1991–1992 mesocosm experiment (duration of 30 days). (b) Changes in chlorophyll *a* for different treatments during the 1993–1994 mesocosm experiment (duration of 48 days). Vertical bars represent the standard error. PAR treatment is represented by open squares, PAR + UVA treatment is represented by plus signs and PAR + UVA + UVB treatment is represented by solid triangles.

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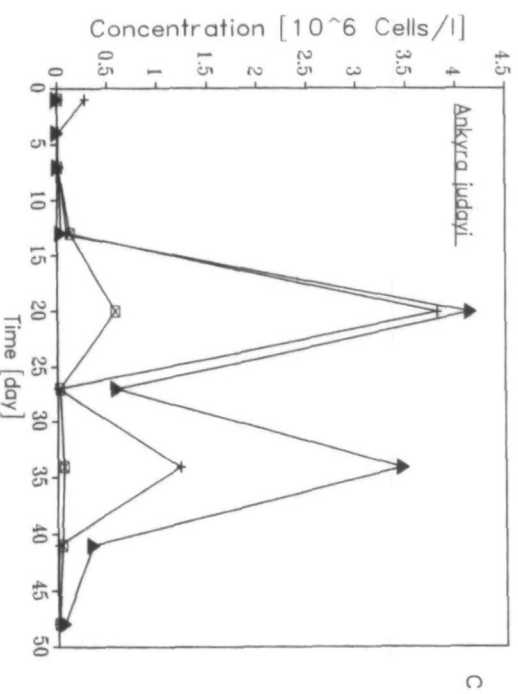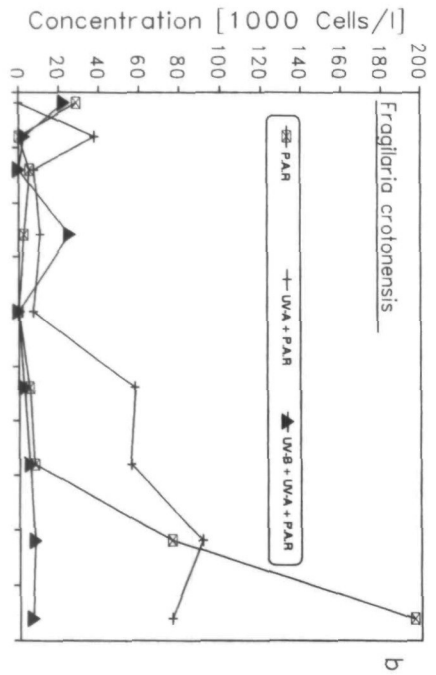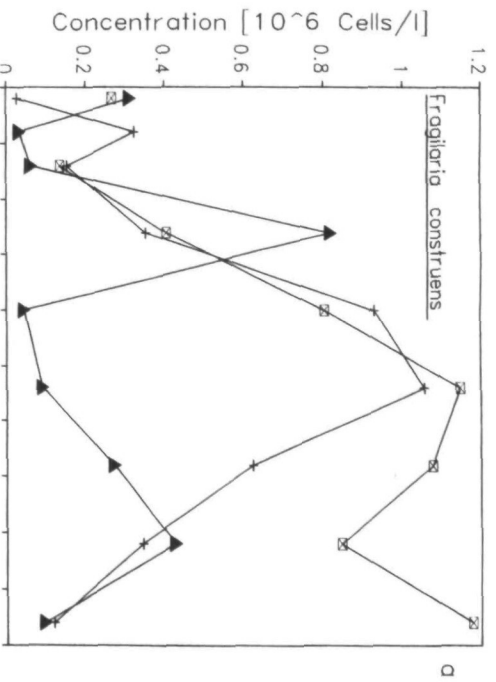
Chl *a* in all of them. Phytoplankton biomass at the end of the experimental period was greater than the initial concentration in three treatments.

When UVB and total UV were excluded, biomass remained relatively uniform (mean 0.3 ± 0.1 µg l^{-1}) during the experimental period, except at the end (days 38 and 48) where both UV exclusion treatments had double their initial values.

Generally, changes in Chl *a* concentration occurred, especially between day 7 and day 34 (1993–1994).

Phytoplankton dynamics

The more conspicuous phytoplankton components in the mesocosms were diatoms (*Fragilaria construens* and *Fragilaria crotonensis*) and Chlorophyceae (cf. *Ankyra judayi*). Other less represented groups were: *Cymbella* sp., *Achnanthes* sp., *Amphora* sp., *Elakatothrix* sp., *Navicula* sp., *Rhodomonas* sp. and *Palmelopis* sp.

In mesocosms exposed to full solar radiation, *F.construens* (Figure 6a) increased in concentration, from 0.3 (day 1) to 0.8×10^6 cells l^{-1} (day 13); after that, it decreased and then increased slightly again.

In the UVB-excluded mesocosms, *F.construens* increased in density until day 27, after which it declined continuously. In the PAR mesocosms, *F.construens* reached a maximum abundance after day 27. *Fragilaria crotonensis* (Figure 6b) was scarce during the experimental period in mesocosms exposed to full sun radiation, with densities around $5–10 \times 10^3$ cells l^{-1}. In mesocosms where UV radiation (A and B) was excluded, *F.crotonensis* increased six times; exclusion of only UVB led to close to 20 times more concentration (abundance) at the end of the experimental period.

Ankyra judayi was especially abundant in the mesocosms exposed to UVB radiation (full sun), where densities reached up to 4.0×10^6 cells l^{-1} on day 20 and 3.5×10^6 cells l^{-1} on day 34 (Figure 6c). In contrast, in the UV-excluded mesocosms, *A.judayi* reached only 1/8 of the maximum peaks (day 20).

Zooplankton

The mesocosms were filled with lake water from close to the shore; consequently, the species composition reflects the typical littoral zone, including the rotifers *Lepadella ovalis* Mueller 1768 and *Euchlanis dilatata* Ehrenberg 1932, and the cladoceran *Chydorus sphaericus* Mueller 1785. The pelagic (Zuñiga and Dominguez, 1977, 1978) calanoid copepod *Boeckella gracilipes* Daday 1901 was

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Fig. 6. (a) Concentration changes of *Fragilaria construens* in the three mesocosms during the 48 day experiment (1993–1994). (b) Concentration changes of *Fragilaria crotonensis* in the three mesocosms during the 48 day experiment (1993–1994). (c) Concentration changes of *Ankyra judayi* in the three mesocosms during the 48 day experiment (1993–1994).
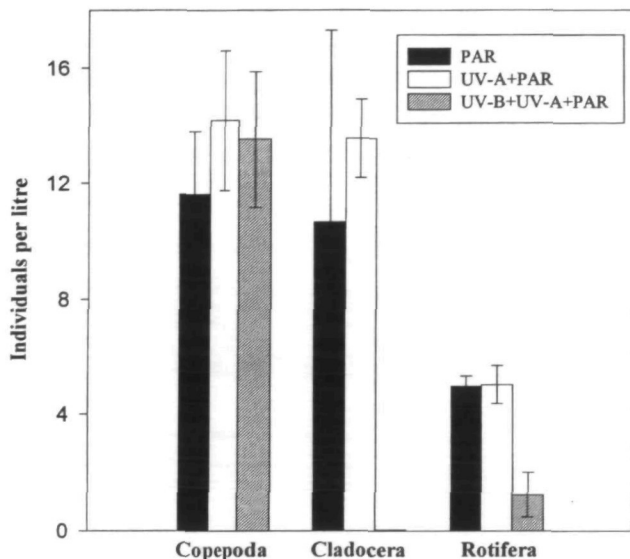
Fig. 7. (a) Mean abundance and standard deviation of the different zooplankton groups exposed to total solar radiation, UVA and PAR, and only PAR after long-term exposure of 48 days (1993–1994). Note that the value of *Chydora sphaericus* is 0.04 (± 2.97E-07) in the treatment exposed to UV (full sun).
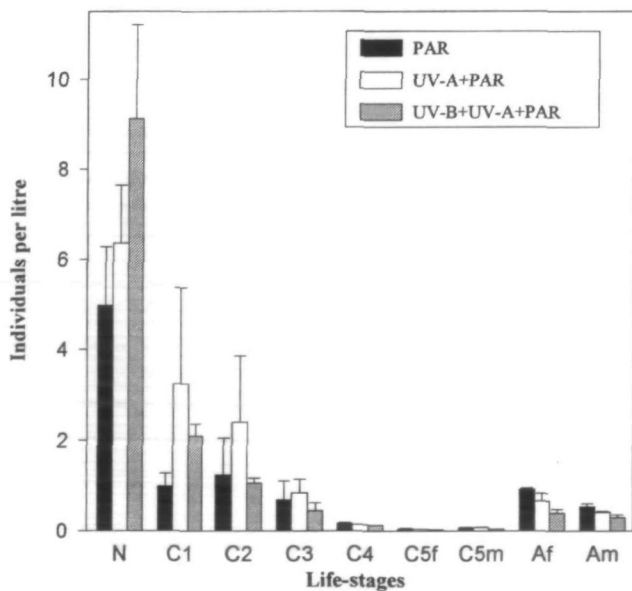
Fig. 7. (b) Mean abundance and standard deviation of the different life stages (nauplii, copepodids C1–C5, adult female and male) of *Boeckella gracilipes* in the three UV treatments after exposure of 48 days (1993–1994).

also present. The mean abundances (individuals per litre) of the most abundant species for the three treatments are shown in Figure 7a.

The differences in the values of variables were assessed with one-way ANOVA by post-hoc comparison (Scheffé test). Considering the three treatments for each zooplankton group, the following results are shown: copepods $P = 0.736$, cladocerans $P = 0.174$ and rotifers $P = 0.039$, the only group where significant differences were given.

The mean number of eggs per female *B.gracilipes* differed among the three treatments: 7.4 ($\pm$ 0.1) for full sun, 1.1 ($\pm$ 0.3) in the UV-excluded treatment and 2.3 ($\pm$ 0.7) in the UVB-shielded treatment. Maximum clutch size ranged from 23 eggs per ovigerous female in the treatment receiving total radiation to eight eggs in the UVB-excluded treatment (11 eggs in the UVA- and UVB-excluded treatment). The UV-excluded treatments had similar numbers of cladoceran eggs and embryos. Containers receiving UVA + PAR or only PAR had 0.15 ($\pm$ 0.01) and 0.3 ($\pm$ 0.07) eggs/embryos per female, respectively. No eggs, embryos or ephippia were observed in the mesocosms exposed to total solar radiation.

Discussion

The experimental site is receiving the highest UVB radiation reported, probably because of its altitude and the potential influence of the nearby antarctic ozone 'hole'. Herman *et al.* (1995), Kirchhoff *et al.* (1996) and Tocho *et al.* (1996) have shown events of low ozone over the southern tip of South America and ozone-poor air moving towards the north over the continent.

Penetration of light in Laguna Negra is similar to that of other very clear and colorless high-altitude lakes, including Lake Tahoe (Sierra Nevada, USA) and Lake Bessvatn (Norway) in which UVB penetrates almost as well as it does in the open ocean (Kirk, 1994). These lakes have lower concentrations of gilvin (the UV-absorbing dissolved yellow humic material) than other inland waters.

Owing to the remoteness of the study site, it was not possible to add filtered lake water to maintain the water level in the mesocosms (upper part of Figure 4), because of the small amount added (8.7% of the total volume) the influence on the mesocosm community structure may have been negligible.

As water temperature was similar in the different mesocosms throughout the experimental period, we assume that changes in the plankton communities result from different UV treatments.

Bothwell *et al.* (1994) demonstrated a higher grazing pressure in the UV-exposed treatment, this observation may explain the low Chl *a* concentration in the treatment receiving only PAR during 1991–1992.

In the extended period of the 1993–1994 experiment, maximum Chl *a* concentrations were observed in the UVB-exposed mesocosms on day 34 (Figure 5b), resulting from a gradual increase in Chl *a* over 14 days. This peak was double the Chl *a* concentration of the other treatments, suggesting UVB stimulation (adaptation?). However, apparently there is no good correlation between Chl *a* and phytoplankton concentration.

Ankyra judayi was especially abundant in the mesocosms exposed to UV radiation (full sun). High densities of this species may be attributed to the following: (i) they are Chlorococcales (Chlorophyceae), a group which has pigments which protect them from UV radiation; (ii) they are lance shaped, this may reduce radiation by reflection at cell wall and cell plasmatic membrane, and thus protect their nuclear material (DNA); this species was found close to the surface (10–20 cm) at midday; (iii) in unprotected (high-UVB) mesocosms, zooplankton concentrations were lower at the end of the experimental period (day 48) and, therefore, herbivore activity was probably lower. If *A.judayi* were a good food for zooplankters, this may explain why they were less abundant in mesocosms receiving only PAR, where higher densities of zooplankton were observed at the 48 day experiment.

Ankyra judayi seems to be more resistant to high levels of UVA and UVB radiation than the diatoms. The *A.judayi* from Laguna Negra is smaller (21 µm long, 0.8 µm wide) than the *Ankyra* sp. (60 µm long) reported by Reymond and Hegewald (1988); it is also smaller than the *A.judayi* (40 µm long) illustrated by Reynolds (1984). It appears that in very clear lakes (López, 1977; Richerson *et al.*, 1978; Coon *et al.*, 1987), small cells increase fastest and become dominant. Reynolds (1986) classified *Ankyra* as a summer species and said that they are more dependent on long perceived day lengths.

Cell size and morphology may determine the susceptibility of unicellular organisms to damage by UV radiation. Ionizing radiation experiments indicate that small cells and organisms are more sensitive to physical damage than larger ones. Karentz *et al.* (1991) and Karentz (1991) reported that the amount of DNA damage in Antarctic phytoplankton correlated with the morphometric characteristics (ratio of cell surface to cell volume) of individual species. In smaller cells, the distance between the cell surface and the nucleus (DNA) is shortened. The truncated light path reduces refraction and absorption by cytoplasmic components, and increases the amount of UV radiation entering the nucleus (Mitchell and Karentz, 1993). However, our results indicate that shape may be as important as the distance between the cell surface and the nucleus.

Numbers of the copepod *B.gracilipes* were the same in all treatments after the long-term exposure of 48 days. Neither nauplii and copepodids, nor adult females and males, were affected. Furthermore, the relative composition of the several life stages of *B.gracilipes* did not differ among the three treatments, suggesting no differentiated life-stage sensitivity (Figure 7b). Conversely, the cladoceran *C.sphaericus* was strongly reduced by UVB radiation (Figure 7a). *Chydorus sphaericus* showed no negative response when exposed to UVA and PAR. No significant differences in the treatments were given due to the high standard deviation in the PAR treatment. The difference in the abundance of the rotifers *L.ovalis* and the infrequent *E.dilitata* in the containers receiving total solar radiation compared to the treatments receiving UVA + PAR and PAR indicates that the rotifers were depressed by UVB radiation ($P = 0.039$).

The results from this experiment indicate that long-term exposure to *in situ* levels of solar radiation causes substantial effects on the zooplankton

populations, but with enormous variability among species. Different sensitivity to UVB radiation has been observed in different species (Siebeck, 1978; Siebeck and Böhm, 1994; Williamson *et al.*, 1994), life stages (Karanas *et al.*, 1979; Zellmer, 1995), in pigmented versus unpigmented morphs (Ringelberg *et al.*, 1984) and in different groups of one zooplankton species (Karanas *et al.*, 1981). *Boeckella gracilipes* shows the typical diel vertical migration pattern during summer in Laguna Negra; it is a slightly red-pigmented copepod with absorption peaks at 474 nm and in the UV range (334 and 380 nm) (Tartarotti *et al.*, personal communication). The abundance of *B.gracilipes* in the three treatments suggests that this copepod species is adapted to high solar radiation levels. The clutch size, number of eggs per female and the high abundance of the nauplii indicate that the reproduction of *B.gracilipes* is not impaired by UVB radiation. The occurrence of UVB-resistant phytoplankton in the containers receiving total solar radiation may be due to UV-absorbing compounds in these organisms, as observed in marine algae (Karentz *et al.*, 1991). These compounds may be transferred to *B.gracilipes*, thereby probably providing UV protection. A combination of photoprotection (antioxidants and MAAs) and repair mechanisms (e.g. photoreactivation) may play an important role in the survival of this species. High UVB tolerance was shown in *Boeckella gibbosa* after short-term (48 h) and long-term (24 days) incubation in solar radiation levels (Balseiro and Zagarese, 1994; Zagarese *et al.*, 1997). Williamson *et al.* (1994) observed a depression by UVB of the number of eggs per female *Diaptomus*, after an exposure for 3 days to *in situ* levels of solar radiation in an oligotrophic lake. However, an *in situ* experiment near the water surface for the same period showed a slightly higher mortality in *B.gracilipes* compared to the UVB-excluded control (Tartarotti *et al.*, personal communication). Siebeck and Böhm (1994) observed higher UVB tolerance in non-migrating compared to migrating *Daphnia* species. The littoral species *C.sphaericus*, found in summer in the whole water column close to the shore in Laguna Negra, was not present in water layers shallower than 1.5 m during the day (B.Tartarotti, unpublished). Zagarese *et al.* (1994) demonstrated UVB-induced mortality down to this depth in the cladoceran *Daphnia* of an oligotrophic lake. In the experiment, a natural behavioral avoidance response was lacking because of the depth of the containers. The results of the long-term exposure indicate that *C.sphaericus* is not able to survive high UVB radiation, in contrast to the migrating *B.gracilipes*. The rotifer *Keratella taurocephala* showed no response when exposed to solar radiation for 3 days in an oligotrophic lake (Williamson *et al.*, 1994), whereas the abundance of the rotifer *L.ovalis* shows a UVB impairment after long-term exposure.

It is clear that solar UVB radiation can alter both phyto- and zooplankton communities. The phytoplankton community, perhaps because of its greater diversity, is able to recover more rapidly. The phytoplankton community may be further aided by the fall in grazing pressure if zooplankton are negatively impacted by UVB, permitting UV-'resistant' phytoplankton species to reach high biomass levels.

Experimental period

This study is one of the first long-term experiments set up to observe the effects of *in situ* levels of UVB radiation on natural phyto- and zooplankton communities in the southern hemisphere during the ozone 'hole' period.

A short-term exposure (6–12 days) would have led to the conclusion that the phytoplankton biomass (Chl *a*) is strongly negatively impacted by UVB radiation and an experimental period of 26–33 days showed the reverse results.

The long-term results of this study showed the following. (i) It is important to monitor different parts of the plankton community in order to observe linkages under different UVB conditions. Information about bacteria and protozooplankton under different UV and light conditions is still needed. (ii) In very clear (oligotrophic) lakes, where UVB levels are high, especially resistant (*A.judayi*) or vulnerable (*C.sphaericus*) species could be used as environmental indicators in UVB monitoring programs. (iii) UVB exclusion experiments must be long term in order to permit the full expression of ecological events.

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References

American Public Health Association (1975) *Standard Methods for the Examination of Water and Waste Water*, 14th edn. APHA, New York.
Balseiro,E.G. and Zagarese,H.E. (1994) Distribución vertical y resistencia de *Pseudoboeckella gibbosa* a la radiación solar. In *I Congreso y III Reunión Argentina de Limnologia*. Tankay, I, pp. 91–92.
Beaton,M.J. and Hebert,P.D.N. (1988) Geographical parthenogenesis and polyploidy in *Daphnia pulex*. Am. Nat., 132, 837–845.
Blaustein,A.R., Hoffman,P.D., Hokit,D.G., Kiesecker,J.M., Walls,S.C. and Hays,J.B.(1994) UV repair and resistance to solar UV-B in amphibian eggs: a link to population declines? *Proc. Natl Acad. Sci. USA*, 91, 1791–1795.
Bojkov,R.D. (1995) *La Cambiante capa de Ozono*. Editado por la Organización Meteorológica Mundial y Programa de las Naciones Unidas para el Medio Ambiente, 32 pp.
Booth,C.R., Mestechnica,T. and Morrow,J.H. (1994) Errors in the reporting of solar spectral irradiance using moderate bandwidth radiometers: and experimental investigation. SPIE Vol. 2258 *Ocean Optics*, XII, 654–663.
Bothwell,M.L., Sherbot,D., Roberge,A.C. and Daley,R.J. (1993) Influence of natural ultraviolet radiation on lotic periphytic diatom community growth, biomass accrual and species composition: short-term *versus* long-term effects. *J. Phycol.*, 29, 24–35.
Bothwell,M.L., Sherbot,D.M.J. and Pollock,C.M. (1994) Ecosystem response to solar ultraviolet-B radiation: Influence of trophic-level interactions. *Science*, 265, 97–100.

Byron,E.R. (1982) The adaptive significance of calanoid copepod pigmentation: a comparative and experimental analysis. *Ecology*, **63**, 1871–1886.

Cabrera,S. and Pizarro,G. (1994) Changes in Chlorophyll *a* concentration, copepod abundance and UV and PAR penetration in the water column during the ozone depletion in Antarctic Lake Kitiesh 1992. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 123–134.

Cabrera,S., Bozzo,S. and Fuenzalida,H. (1995) Variation in UV radiation in Chile. *J. Photochem. Photobiol. B: Biol.*, **28**, 137–142.

Carreto,J.I., Carignan,M.O., Daleo,G. and De Marco,S.G. (1990) Occurrence of mycosporine-like amino acids in the red tide dinoflagellate *Alexandrium excavatum* UV-photoprotective compounds? *J. Plankton Res.*, **12**, 909–921.

Coon,T.G., López,M., Richerson,P.J., Powell,T.M. and Goldman,R. (1987) Summer dynamics of the deep chlorophyll maximum in Lake Tahoe. *J. Plankton Res.*, **9**, 327–344.

Cullen,J.J., Neale,P.J. and Lesser,M.P. (1992) Biological weighting function for the inhibition of phytoplankton photosynthesis by ultraviolet radiation. *Science*, **258**, 646–650.

Damkaer,D.M. (1982) Possible influences of solar UV radiation in the evolution of marine zooplankton. In Calkins,J. (ed.), *The Role of Solar Ultraviolet Radiation in Marine Ecosystems*. Plenum Press, New York, pp. 701–706.

Dawidowicz,P. and Loose,C.J. (1992) Metabolic costs during predator-induced vertical migration of *Daphnia*. *Limnol. Oceanogr.*, **37**, 665–669.

Dumont,H.J., Coussement,M. and Anderson,R.S. (1978) An examination of some *Hexarthra* species (Rotatoria) from Western Canada and Nepal. *Can. J. Zool.*, **56**, 440–445.

Fuenzalida,H. Measurement of solar UV irradiance with multichannel moderate bandwidth filter instruments. *Appl. Optic*, (submitted).

Gliwicz,M.Z. (1986) Predation and the evolution of diel vertical migration. *Nature*, **320**, 746–748.

Hairston,N.J., Jr (1979) The adaptive significance of color polymorphism in two species of *Diaptomus* (Copepoda). *Limnol. Oceanogr.*, **24**, 15–37.

Hairston,N.J., Jr (1980) The vertical distribution of diaptomid copepods in relation to body pigmentation. In Kerfoot,W.C. (ed.), *Evolution and Ecology of Zooplankton Communities*. University Press, Hanover, pp. 98–110.

Hebert,P.D.N. and Emery,C.J. (1990) The adaptive significance of cuticular pigmentation in *Daphnia*. *Funct. Ecol.*, **4**, 703–710.

Herman,J.R. *et al.* (1995) Meteor 3/total ozone mapping spectrometer observations of the 1993 ozone hole. *J. Geophys. Res.*, **10**, 2973–2983.

Hessen,D.O. (1993) DNA-damage and pigmentation in alpine and arctic zooplankton as bioindicators of UV-B radiation. *Verh. Int. Ver. Limnol.*, **25**, 482–486.

Hessen,D.O. (1994) *Daphnia* response on UV-light. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 185–195.

Hessen,D.O. and Sörensen,K. (1990) Photoprotective pigmentation in alpine zooplankton populations. *Aqua Fenn.*, **20**, 165–170.

Hobaek,A. and Wolf,H.G. (1991) Ecological genetics of Norwegian *Daphnia*. II. Distribution of *Daphnia longispina* in relation to short-wave radiation and water color. *Hydrobiologia*, **225**, 228–243.

Jeffrey,S.W. and Humphrey,G.F. (1975) New spectrophotometric equation for determining chlorophylls *a*, *b* and *c*1 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanz.*, **167**, 191–194.

Jones,A.E. and Shalklin,J.D. (1995) Continued decline of total ozone over Halley, Antarctica, since 1985. *Nature*, **376**, 409–411.

Karanas,J.J., Van Dyke,H. and Worrest,R.C. (1979) Midultraviolet (UV-B) sensitivity of *Acartia clausii* Giesbrecht (Copepoda). *Limnol. Oceanogr.*, **24**, 1104–1116.

Karanas,J.J., Worrest,R.C. and Van Dyke,H. (1981) Impact of UV-B radiation on the fecundity of the copepod *Acartia clausii*. *Mar. Biol.*, **65**, 125–133.

Karentz,D. (1991) Ecological considerations of Antarctic ozone depletion. *Antarct. Sci.*, **3**, 3–11.

Karentz,D., McEuen,F.S., Land,K.M. and Dunlap,W.C. (1991) A survey of mycosporine-like amino acid compounds in Antarctic marine organisms: Potential protection from ultraviolet exposure. *Mar. Biol.*, **108**, 157–166.

Karentz,D. *et al.* (1994) Impact of UV-B radiation on pelagic freshwater ecosystems: Report of working group on bacteria and phytoplankton. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 31–69.

Kirchhoff,V.W.J.H., Schuch,N.J., Pinheiro,D.K. and Harris,J.M. (1996) Evidence for an ozone hole perturbation at 30° south. *Atmos. Environ.*, **30**, 1481–1488.

Kirk,J.T.O. (1994) Optics of UV-B radiation in natural waters. *Arch. Hydrobiol. Beih, Ergebn. Limnol.*, **43**, 1–16.

López,M. (1977) Vertical and temporal distribution of phytoplankton populations of Lake Tahoe, California-Nevada. MS Thesis, University of California, Davis, CA.

Madronich,S., McKenzie,R.L., Caldwell,M.M. and Björn,L.O. (1995) Changes in ultraviolet radiation reaching the Earth's surface. *Ambio*, **24**, 143–152.

Mitchell,D.L. and Karentz,D. (1993) The induction and repair of DNA photodamage in the environment. In Young,A., Björn,L., Moan,J. and Nultsch,W. (eds), *Environmental UV Photobiology*. Plenum Press, pp. 345–377.

Modenutti,B. (1992) Summer population of *Hexarthra bulgarica* in a high elevation lake of South Andes. *Hydrobiologia*, **259**, 33–37.

Orcutt,J.D. and Porter,K.G. (1983) Diel vertical migration by zooplankton: Constant and fluctuating temperature effects on life history parameters of *Daphnia*. *Limnol. Oceanogr.*, **28**, 720–730.

Reymond,O. and Hegewald,E. (1988) A morphological and cytological assessment of *Paradoxia* and *Ankyra* (Chloroccoccales, Chlorophyceae). *Arch. Protistenkd.*, **135**, 167–172.

Reynolds,C.S. (1986) Experimental manipulations of the phytoplankton periodicity in large limnetic enclosures in Blelham Tarn, English Lake District. *Hydrobiologia*, **138**, 43–64.

Reynolds,C.S. (1984) *The Ecology of Freshwater Phytoplankton*. Cambridge University Press, Cambridge.

Richerson,P.J., López,M. and Coon,T. (1978) The deep chlorophyll maximum layer of Lake Tahoe. *Verh. Int. Ver. Limnol.*, **20**, 426–433.

Ringelberg,J., Keyser,A.L. and Flik,B.J.G. (1984) The mortality of ultraviolet radiation in a translucent and in a red morph of *Acanthodiaptomus denticornis* (Crustacea, Copepoda) and its possible ecological relevance. *Hydrobiologia*, **112**, 217–222.

Schindler,D.W., Curtis,P.J., Parker,B.R. and Stainton,M.P. (1996) Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature*, **379**, 705–708.

Siebeck,O. (1978) Ultraviolet tolerance of planktonic crustaceans. *Verh. Int. Ver. Limnol.*, **20**, 2469–2473.

Siebeck,O. and Böhm,U. (1994) Challenges for an appraisal of UV-B effects upon planktonic crustaceans under natural radiation conditions with a non-migrating (*Daphnia pulex obtusa*) and a migrating Cladoceran (*Daphnia galeata*). *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 197–206.

Smith,R.C. *et al.* (1992) Ozone depletion: ultraviolet radiation and phytoplankton biology in Antarctic waters. *Science*, **255**, 952–959.

Stich,H.B. and Lampert,W. (1981) Predator evasion as an explanation of diurnal vertical migration of zooplankton. *Nature*, **293**, 396–398.

Stich,H.B. and Lampert,W. (1984) Growth and reproduction of migrating and non-migrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. *Oecologia (Berlin)*, **61**, 192–196.

Tocho,J.O., Da Silva,L., Lifante,G., Cusso,F. and Jaque,F. (1996) Penetración del agujero de ozono en Sudamérica. *Invest. Cienc.*, **Febrero**, 68–73.

Vincent,W.F. and Roy,S. (1993) Solar ultraviolet-B radiation and aquatic primary production: damage, protection and recovery. *Environ. Rev.*, **1**, 1–12.

Williamson,C.E., Zagarese,H.E., Schulze,P.C., Hargreaves,B. and Seva,J. (1994) The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. *J. Plankton Res.*, **16**, 205–218.

Zagarese,H.E., Williamson,C.E., Mislivets,M. and Orr,P. (1994) The vulnerability of *Daphnia* to UV-B radiation in the Northeastern United States. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 207–216.

Zagarese,H.E., Williamson,C.E., Vail,T.L, Olsen,O. and Queimaliños,C. (1997) Long-term exposure of *Boeckella gibbosa* (Copepoda, Calanoida) to 'in situ' levels of solar UV-B radiation. *Freshwater Biol.*, in press.

Zellmer,I.D. (1995) UV-B-tolerance of alpine and arctic *Daphnia*. *Hydrobiolgia*, **307**, 153–159.

Zuñiga,L. and Dominguez,P. (1977) Observaciones sobre el zooplancton de lagos chilenos. *An. Mus. Hist. Nat. Valpo.*, **10**, 107–120.

Zuñiga,L. and Dominguez,P.(1978) Entomostracos planctónicos del lago Riñihue (Valdivia, Chile): distribución temporal de la taxocenosis. *An. Mus. Hist. Nat. Valpo.*, **11**, 89–95.