

# Positive effects of UV radiation on a calanoid copepod in a transparent lake: do competition, predation or food availability play a role?

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*Zooplankton tolerant to ultraviolet radiation (UVR) could be indirectly affected by UVR through interactions with UV-sensitive species in the same ecosystem. In Lake Giles, Pennsylvania, USA, the calanoid copepod Leptodiatomus minutus is more UVR tolerant than the cohabiting species Daphnia catawba and Cyclops scutifer. We asked whether L. minutus is affected by UV-induced mortality of a food competitor (D. catawba) or a predator of its nauplii (C. scutifer). We conducted two in situ enclosure experiments with six treatments: L. minutus alone, L. minutus + Daphnia and L. minutus + Cyclops in the presence and absence of UVR. There were few differences in survival among treatments in Experiment 1, which had enhanced food and a cumulative UVR (320 nm) dose of 9.3 kJ m<sup>-2</sup>. In Experiment 2, which had ambient food and a UVR (320 nm) dose of 20.0 kJ m<sup>-2</sup>, L. minutus survival and reproduction were higher in the +UVR compared to -UVR, regardless of competitors or predators. Chlorophyll a (Chl a) in Experiment 2 was higher in the +UVR than -UVR. While interactions between zooplankton species of differing UVR tolerances are potentially important, these results instead demonstrate that the beneficial UVR effect on L. minutus is independent of concurrent detrimental UVR effects on competitors and predators. Further research on the phytoplankton community is necessary to determine whether UVR alleviates bacterial competition, increases nutrient availability or affects phytoplankton by other mechanisms.*

## INTRODUCTION

Ultraviolet radiation (UVR) is recognized as an important biological stressor for many species in aquatic ecosystems (Williamson, 1996). It is, however, only one of many interacting selective pressures on zooplankton. Previous studies have examined the role of UVR within the context of pigmentation and predation pressure (Hairton, 1976; Hansson, 2000, 2004), food limitation (Stutzman, 2000), dissolved organic carbon (DOC) changes (Rautio and Korhola, 2002), and temperature changes (Williamson *et al.*, 2002). However, to our knowledge there have been few studies that examined how competitive and predatory interactions between

zooplankton species influence net UVR effects. The purpose of this study was to determine whether interactions with cohabiting zooplankton species affect the response of a calanoid copepod, *Leptodiatomus minutus*, to UV radiation.

While UVR is generally recognized to be biologically detrimental, its effects are variable depending on environmental conditions and the attributes of a particular species. Zooplankton cope with UVR by different mechanisms including photoprotection, DNA damage repair and behavioral avoidance; different species thus vary in their UV tolerance. In some studies of cohabiting calanoids and cladocerans, cladocerans were more UV sensitive than calanoids (Cabrera *et al.*, 1997; Leech and

Williamson, 2000). Because UV-tolerant species often interact with UV-sensitive species through competition or predation, UVR may have a direct effect on sensitive species, and consequently, an indirect effect on tolerant species. For example, in benthic lotic ecosystems UV-B can indirectly stimulate algal growth after several weeks by reducing chironomid herbivores (Bothwell *et al.*, 1994). We hypothesize that similar indirect effects involving trophic level interactions with other zooplankton species in a pelagic lake ecosystem can result in UVR actually benefiting a more UV-tolerant species.

*Leptodiatomus minutus* in Lake Giles, a high-UVR system in northeastern Pennsylvania (USA), is tolerant to UVR, although it can exhibit some UV sensitivity (Williamson *et al.*, 1994; Stutzman, 1999; Leech and Williamson, 2000). Two of the dominant coexisting zooplankton species in this lake are the cladoceran *Daphnia catawba* and the cyclopoid copepod *Cyclops scutifer*, which are both generally more UV sensitive than *L. minutus* (Leech and Williamson, 2000). *Daphnia catawba* may be a food competitor with *L. minutus*, as *Daphnia* can depress diatom abundance (Soto and Hurlbert, 1991), and the diets of diatoms and *Daphnia* may overlap (Sanders *et al.*, 1996). We reasoned that UV-induced mortality of *D. catawba* may enhance *L. minutus* survival and reproduction, especially if conditions are food limiting, as they often are in oligotrophic Lake Giles. *Cyclops scutifer* is known to prey on its own nauplii, as well as other copepod nauplii (Krylov, 1988). If conditions are food limiting for *C. scutifer*, causing it to prey on *L. minutus* nauplii, then *L. minutus* nauplii may be greater in the presence of UVR due to the UV-induced mortality of *C. scutifer*.

A further possible indirect effect on *L. minutus* is that food quality or quantity may be altered by UVR. Although some studies have demonstrated UVR inhibition of photosynthesis and primary productivity (Day and Neale, 2002), others have shown that phytoplankton communities can be stimulated by UVR (Cabrera *et al.*, 1997; Plante and Arts, 2000). Some phytoplankton species are UVR tolerant due to protective pigmentation and cell size and morphology (Cabrera *et al.*, 1997). Such UVR-tolerant species may be stimulated by UVR through release from competition with less tolerant bacteria (Plante and Arts, 2000) or phytoplankton. Thus, we reasoned that in addition to indirect effects at the grazer level, UVR could also affect *L. minutus* by enhancing primary producers. Here we test the combined hypotheses that UVR benefits *L. minutus* by harming its major food competitor (*D. catawba*), harming predators of its nauplii (*C. scutifer*), altering food availability [as evidenced by changes in chlorophyll *a* (Chl *a*) concentrations] or a combination of these factors.

## METHOD

The study was conducted in Lake Giles, located on the Pocono Plateau of northeastern Pennsylvania, USA (41°23' N, 75°06' W). Lake Giles is a transparent (summer 1% attenuation depth of 320 nm UV in 2003 = 5 m), acidic (pH = 5.6), oligotrophic lake with a DOC concentration of ~0.17 mM. Historically, Lake Giles has been even more UV transparent with 1% 320-nm attenuation depths >15 m (Williamson *et al.*, 1999). In addition to the calanoid copepod *L. minutus*, the zooplankton community in Lake Giles is dominated by *D. catawba*, *C. scutifer* and, to a lesser extent, the calanoid copepod *Aglaodiaptomus spatulocrenatus*. For the latter two species, only the copepodid stage was prevalent at the time of this experiment. Also present in lower abundances are *Diaphanosoma* spp. and *Polyphemus* spp.

Two similar *in situ* experiments were conducted during the summer of 2003. Each experiment had six treatments: *L. minutus* alone (control), *L. minutus* + *Daphnia*, and *L. minutus* + *Cyclops*, each in the presence and absence of UVR. The two control treatments had six replicates, and the four other treatments had five replicates. UVR was manipulated using two long-wave pass acrylic filters: OP-2 for the -UVR treatment (50% transmittance at 410 nm removes all 320-nm radiation) and OP-4 for the +UVR treatment (50% transmittance at 272 nm transmits all 320-nm radiation) (CYRO Industries). The acrylic filters were cut into 0.5 m × 1.0 m sections which were attached with cable ties to PVC frames of the same dimensions. Nylon netting tied to the underside of the frames supported two 3.8 L-sized polyethylene bags (Bitran) that were filled to a volume of 3.5 L.

For Experiment 1, we collected *L. minutus*, *Daphnia* and *Cyclops* on 18 June, the evening before experiment setup. We used a 202- $\mu$ m mesh net to collect one tow from 5 m depth to the surface and one tow from 20 to 14 m depth at 22:00. The depths, mesh size and collection time were chosen based on the known vertical distribution and size of the three species so the organisms could be easily separated. *Daphnia* and *L. minutus* were separated from the 0–5 m depth tow using a 363- $\mu$ m mesh cup. The <363- $\mu$ m size fraction was ~99% *L. minutus*, with a few small immature *A. spatulocrenatus*. This size fraction was used to stock all bags with *L. minutus*. The >363- $\mu$ m size fraction was used for the 'Daphnia addition', and it was ~95% *Daphnia*, with *A. spatulocrenatus* composing the remaining 5%. *Cyclops* was separated from the 14–20 m tows also using a 363- $\mu$ m mesh cup. The >363- $\mu$ m size fraction was ~90% *Cyclops*, with the remaining 10% consisting of *A. spatulocrenatus* copepodids and a few cladocerans. This fraction was used as the 'Cyclops addition'. Rotifers were not intentionally

included, but a few *Keratella taurocephala* were present in every size fraction. Each size fraction was diluted with ~2 L of Lake Giles water, and then equal aliquots of *L. minutus* and equal aliquots each of *Daphnia* and *Cyclops* were measured out. Because the 'Daphnia addition' and 'Cyclops addition' fractions included some *L. minutus*, initial *L. minutus* densities within these treatments were slightly elevated (1.2- to 1.3-fold) compared to control densities and natural daytime summer lake densities of ~42 *L. minutus* L<sup>-1</sup>. In contrast, concentrations of *Daphnia* and *Cyclops* in the competitor and predator treatments were elevated by 33- to 82-fold relative to the controls to maximize potential competitive and predatory effects. Summer daytime whole water column densities within Lake Giles are typically ~5 *Daphnia* L<sup>-1</sup> and 1–2 *Cyclops* L<sup>-1</sup>, but densities in specific vertical strata of the lake are often much higher than this.

Experiment 1 was set up on 19 June 2003 from 13:40 to 14:30. Each bag was filled with 3.5 L of 48- $\mu$ m filtered lake water collected from 1 m depth. All 32 bags received a *L. minutus* aliquot, and *Daphnia* and *Cyclops* aliquots were added to 10 bags each (5 +UVR and 5 -UVR). Because Lake Giles is highly oligotrophic and bag experiments can be stressful for zooplankton, concentrated WCR (Whiteacre Pond *Cryptomonas reflexa*), a culture of the alga *Cryptomonas reflexa* from Whiteacre Pond (Northampton County, PA, USA; 40°35' N, 75°22' W) grown in a modified MBL medium (Williamson and Butler, 1987), was also added to each bag, resulting in Chl *a* concentrations that were three times higher than the lake concentration of 0.35  $\mu$ g Chl *a* L<sup>-1</sup>. WCR was also added to six extra bags, from which six water samples were collected for initial time point data. Six aliquots of each zooplankton group were also preserved for the initial zooplankton data. The bags were placed between the acrylic covers and nylon netting on the frames, which were deployed at 0.5 m depth. Six days later, on 25 June the experiment was taken down from 10:20 to 12:00. All zooplankton within each bag were collected with a 48- $\mu$ m mesh and preserved with a sucrose formalin solution (10% of sample volume). Final water samples were also collected from each bag.

For Experiment 2, zooplankton tows were taken on 14 July 2003, the evening before set-up, using the same collection and separation methods as for Experiment 1. Set up for Experiment 2 took place on 15 July at 10:50–12:00, and the experiment was taken down 9 days later on 24 July 2003 from 9:00 to 12:00, using the same methods as Experiment 1. There were two important differences between the experiments. First, Experiment 2 was 3 days longer than Experiment 1, and the weather was sunnier, resulting in a doubled UVR dose in comparison to Experiment 2. Second, Experiment 2 received no WCR addition to observe responses of the zooplankton

under ambient food conditions, as opposed to enhanced food conditions.

In the laboratory, zooplankton were enumerated in their entirety using a Bogorov counting chamber, and water samples were filtered using GF/F (Whatman) filters, which were frozen for later Chl *a* analysis. Absorbance of the filtrate was measured on a UV-1601 Scanning Spectrophotometer (Shimadzu) to obtain absorption coefficients for 200–800 nm. Chl *a* was used to assess food availability. The frozen filtered chlorophyll samples were extracted with a 5:1 (volume : volume) mixture of 90% aqueous acetone with methanol (Pechar, 1987) for 24 h. The fluorescence of the extract was measured on a Sequoia-Turner Model 112 Fluorometer. The instrument was calibrated using chlorophyll extracts in 90% acetone that were measured spectrophotometrically. Chlorophyll concentrations were corrected for pheopigment using the acidification method (American Public Health Association, 1995).

In the field we also collected UVR, temperature and dissolved oxygen data. Temperature and dissolved oxygen data were measured at the beginning and end of each experiment with a YSI Model 58 Dissolved Oxygen Meter. Underwater UVR was measured with a BIC radiometer (Biospherical Instruments), which records downwelling solar irradiance at three UV wavebands centered at 305, 320 and 380 nm and photosynthetically active radiation [(PAR), 400–700 nm]. Incident solar irradiance data for the duration of the two experiments were available from a GUV 521 radiometer (Biospherical Instruments) stationed nearby at Lacawac Sanctuary (41°23' N, 75°18' W). This instrument records 15-min averages centered at 305, 320, 340, 380 nm and PAR. The GUV data for 320-nm irradiance were summed and integrated over the course of each experiment to obtain the cumulative amount of 320-nm UVR received at the lake surface. The cumulative exposure, in units of kJ m<sup>-2</sup>, was also converted to 'exposure days', a UVR metric that expresses the exposure level for the most biologically effective UV wavelength for zooplankton such as *Daphnia* (Williamson *et al.*, 1999, 2001). An exposure day is the amount of 320-nm radiation received at the water surface on a cloud-free day at summer solstice under 'normal' ozone conditions for the region (332 Dobson units, average for 15–25 June from 1997 to 2001, Earth Probe TOMS, R. McPeters, <http://toms.gsfc.nasa.gov/>). The 320-nm wavelength has been recognized as biologically important when both zooplankton mortality response and UV exposure at different wavelengths are considered (Williamson *et al.*, 2001). The 320-nm exposure day was estimated by using the modeling program RTBasic (Biospherical Instruments, San Diego, CA, USA). This program

estimates incident solar radiation for a given date, time and location. Other input parameters include ozone and cloud optical depth. Running this model at 15-min intervals on summer solstice during typical ozone conditions and zero cloud optical depth yielded a 320-nm dose of  $10.9 \text{ kJ m}^{-2} \text{ nm}^{-1}$  for the day. The measured cumulative 320-nm irradiance during our experiment was divided by this number to obtain 320-nm exposure days.

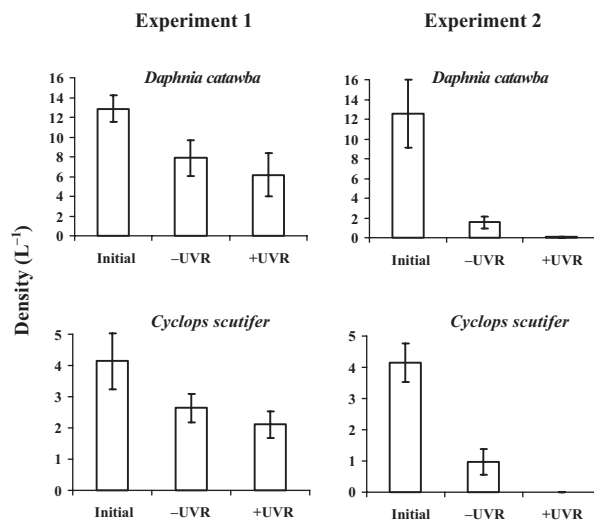
In addition to incident irradiance, cumulative UV-320 exposure received at the center of the +UVR experiment bags for each experiment was estimated using averaged  $K_{d320}$  values obtained from BIC data, the percent transmission of the OP-4 acrylics and Bitran bags (91.4 and 83.8%, respectively, obtained from spectrophotometric scans conducted in water) and the averaged dissolved absorption coefficient ( $a_{320}$ ) for all initial and +UVR treatments. Surface albedo was estimated to be 5% and was accounted for in the calculations.

Statistical analyses were performed using the software package SPSS 12.0 for Windows (Release 12.0.0; SPSS Inc.). Univariate two-way analysis of variance (ANOVA) tests (UVR  $\times$  *Daphnia* and UVR  $\times$  *Cyclops*) were conducted for Chl *a* concentrations and for each *L. minutus* group: females, males, copepodids, nauplii and egg ratios (mean number of eggs per female). To account for differences in initial numbers, the data were converted to percentage of mean initial numbers. Raw data were used for nauplii, because their initial numbers were close to zero. Transformations were not done, because a Kolmogorov–Smirnov test showed the converted data to be normally distributed. One-way ANOVA tests were conducted for UVR effects on *Daphnia* and *Cyclops*.

## RESULTS

In Experiment 1, there was no effect of UVR on *Daphnia* in the +*Daphnia* treatment ( $F_{1,7} = 0.364$ ,  $P = 0.563$ ) or on *Cyclops* in the +*Cyclops* treatment ( $F_{1,7} = 0.634$ ,  $P = 0.452$ ; Fig. 1). Both *Daphnia* and *Cyclops* densities declined by  $\sim 30\%$  during the experiment (Fig. 1). There were more nauplii in the +*Daphnia* than in the controls (Table I; Fig. 2). There was no significant effect of any treatments on Chl *a* (Fig. 3).

For Experiment 2, UVR had a significant effect on all *L. minutus* life stages (Table I). Survival and reproduction were higher in the presence of UVR than in the absence. Copepodids were not affected by *Daphnia* or *Cyclops*. The presence of *Daphnia* had a significant negative effect on females and egg ratios in both UVR treatments (Fig. 2; Table I). The presence of *Cyclops* had a significant negative effect on males and egg ratios in both UVR treatments (Table I; Fig. 2).



**Fig. 1.** Densities of *Daphnia catawba* in the +*Daphnia* treatments and *Cyclops scutifer* in the +*Cyclops* treatments during Experiments 1 and 2, expressed as mean  $\pm$  standard error ( $n = 5$ ). The levels of these species in the other treatments were close to  $0 \text{ L}^{-1}$ .

In the -UVR treatment *Daphnia* densities declined to  $1.54 \pm 0.57 \text{ L}^{-1}$ , which is below the typical lake density of  $\sim 5 \text{ L}^{-1}$ , and *Cyclops* densities declined to  $0.97 \pm 0.42 \text{ L}^{-1}$ , which is approximately lake density. Both species were virtually eliminated in the +UVR treatment. This negative effect of UVR was significant for *Daphnia* ( $F_{1,8} = 6.76$ ,  $P = 0.03$ ) but not for *Cyclops* ( $F_{1,8} = 4.16$ ,  $P = 0.08$ ). There were no significant interactions of UVR and *Daphnia* or UVR and *Cyclops* for any *L. minutus* group, indicating that *Daphnia* and *Cyclops* did not significantly alter the response of *L. minutus* to UVR.

Chl *a* concentrations increased during Experiment 2 and were higher in the +UVR treatments than in the -UVR treatments ( $F_{1,26} = 8.01$ ,  $P = 0.009$ ; Fig. 3). *Daphnia* and *Cyclops* additions had no significant effect on Chl *a*.

For Experiment 1, surface temperature was  $21.0^\circ\text{C}$  at the beginning of the experiment and was  $23.0^\circ\text{C}$  at the end of the experiment. The mixed layer extended to 2 m, and dissolved oxygen ranged from 8.8 to  $9.0 \text{ mg L}^{-1}$  throughout the mixed layer. The epilimnetic  $K_{d320}$  was  $1.85 \text{ m}^{-1}$  on 17 June 2003 and  $1.82 \text{ m}^{-1}$  on 30 June 2003. From summing and integrating the GUV data for 320-nm irradiance, we obtained  $27.3 \text{ kJ m}^{-2}$  as the cumulative amount of 320-nm UVR received at the lake surface over the 6-day experiment. This is equivalent to 2.5 320-nm exposure days. The average daily 320-nm dose received at the lake surface was  $4.24 \text{ kJ m}^{-2}$ , and the maximum daily dose was  $8.25 \text{ kJ m}^{-2}$ , received on 24 June.

In Experiment 2, the surface temperature was  $23.5^\circ\text{C}$  at the beginning and at the end and the mixed layer

Table I: Results from two-way analysis of variances (ANOVAs) testing the effects of ultraviolet radiation (UVR), *Daphnia* and *Cyclops* on the survival of *Leptodiptomus minutus* females, males and copepodids and on *L. minutus* nauplii and egg ratios (mean number of eggs per female)

Group	UVR	<i>Daphnia</i>	<i>Cyclops</i>
Experiment 1			
Females	NS	NS	NS
Males	NS	NS	NS
Copepodids	NS	NS	NS
Nauplii	NS	$F_{1,25} = 11.49, P = 0.002 (+)$	NS
Egg ratio	NS	NS	NS
Experiment 2			
Females	$F_{1,24} = 29.27, P = 0.000 (+)$	$F_{1,24} = 12.24, P = 0.002 (-)$	NS
Males	$F_{1,24} = 12.96, P = 0.001 (+)$	NS	$F_{1,24} = 6.98, P = 0.014 (-)$
Copepodids	$F_{1,24} = 44.27, P = 0.000 (+)$	NS	NS
Nauplii	$F_{1,24} = 22.53, P = 0.000 (+)$	NS	NS
Egg ratio	$F_{1,24} = 11.11, P = 0.003 (+)$	$F_{1,24} = 26.54, P = 0.000 (-)$	$F_{1,24} = 4.36, P = 0.048 (-)$

UVR, ultraviolet radiation. A (+) or a (-) indicates if the significant effect was positive or negative. NS indicates no significance at the  $\alpha = 0.05$  level. No significant interactions were observed.

extended to 5 m. Dissolved oxygen ranged from 8.0 to 9.0 mg L<sup>-1</sup> throughout the mixed layer. The epilimnetic  $K_{d320}$  was 1.38 m<sup>-1</sup> on 15 July 2003 and 1.31 m<sup>-1</sup> on 21 July 2003. The cumulative amount of 320-nm UVR received at the lake surface over the 9-day experiment was 54.9 kJ m<sup>-2</sup>, which is equivalent to 5.0 320-nm exposure days. The 320-nm UV in the control treatment was within 2% of the *Cyclops* and *Daphnia* treatments (Table II). The average daily 320-nm dose received at the lake surface was 5.49 kJ m<sup>-2</sup> and the maximum daily dose was 8.43 kJ m<sup>-2</sup>, received on 17 July.

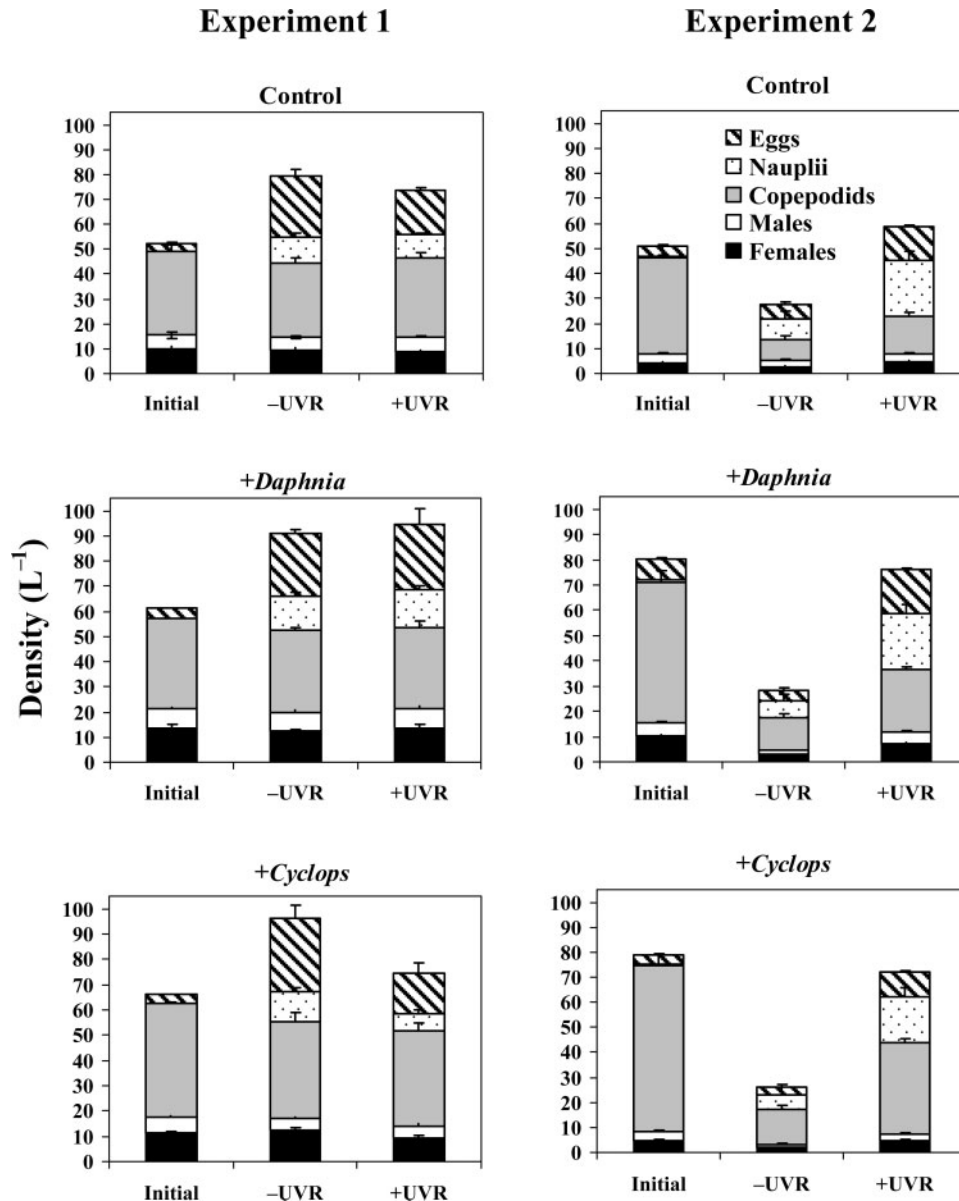
In Experiment 2, the >363- $\mu$ m size fraction from the deep tow that we used as the ‘*Cyclops* addition’ was ~50% *Cyclops*, with the remaining 50% consisting of diaptomid copepodids. The >363- $\mu$ m size fraction from the shallow tow that we used as the ‘*Daphnia* addition’ contained 80% *Daphnia*, with *L. minutus* composing ~15% of the biomass and *Diaphanosoma* spp. and *A. spatulocrenatus* composing the remaining 5%. Thus, initial *L. minutus* densities within the +*Cyclops* and +*Daphnia* treatments were elevated 1.5- to 1.8-fold compared to control densities and natural daytime summer lake densities of ~46 L<sup>-1</sup>.

## DISCUSSION

The competitor *Daphnia* and nauplii predator *Cyclops* negatively affected *L. minutus* survival and reproduction in Experiment 2 but did not influence the UVR response of *L. minutus*, as we hypothesized. Instead, this study demonstrates that while a low dose of UVR under

enhanced food conditions may have no apparent effect on *L. minutus*, a higher UVR dose under ambient food conditions appears to be beneficial. This beneficial effect of UVR was observed in the control treatments and thus is not necessarily dependent on the interactions with *Daphnia* or *Cyclops* that we hypothesized. An additional key finding was that Chl *a* levels increased more in the presence of UVR than in the absence. These results suggest that changes in food availability may be a stronger factor than zooplankton species interactions in the positive UVR effects on *L. minutus*. These results are consistent with prior studies that have demonstrated beneficial effects of UVR on the food supply of invertebrates (Cabrera *et al.*, 1997; De Lange *et al.*, 2003; Tank *et al.*, 2003) and have numerous implications related to how changes in the aquatic UVR environment may alter planktonic community structure.

There are several possible reasons why UVR had a positive effect in Experiment 2. The positive effect of UVR on Chl *a* suggests that *L. minutus* may benefit from UVR via indirect mechanisms at the primary producer level. UVR inhibition of both primary and bacterial production varies with factors such as season, depth and adaptation to sunlight (Carrillo *et al.*, 2002). In some microbial assemblages, UVR may increase the ratio of phytoplankton to bacteria (Plante and Arts, 2000). Such an increase in algae relative to bacteria may increase diaptomid copepod reproduction (Sanders *et al.*, 1996). UV-irradiated algae may affect zooplankton grazing rates, but the effect can be positive or negative, depending on the species of both phytoplankton and

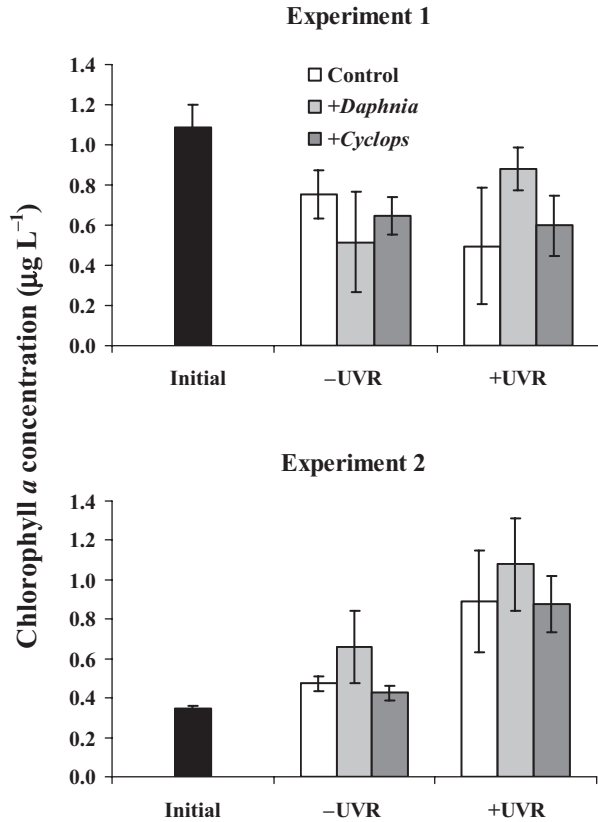


**Fig. 2.** Densities of *Leptodiptomus minutus* females, males, copepodids, nauplii and eggs in the control, +*Daphnia* and +*Cyclops* treatments during Experiments 1 and 2, expressed as mean  $\pm$  SE ( $n = 5$ ).

zooplankton and on the time scale of UVR stress (De Lange and Luerling, 2003). Cabrera *et al.* (Cabrera *et al.*, 1997) observed an increased Chl *a* concentration and altered phytoplankton community composition in the presence of UVR in a high-elevation lake mesocosm experiment, although the calanoid copepod in that experiment was not affected by UVR.

In addition to phytoplankton, it is also possible that bacteria were stimulated by photodegradation of DOC, making the DOC more biolabile and increasing the availability of inorganic nutrients that are often limiting

in oligotrophic, low-DOC Lake Giles. Numerous studies have demonstrated the importance of UVR in increasing DOC biolability (Moran and Zepp, 1997; De Lange *et al.*, 2003). In Experiment 2,  $a_{320}$  declined in the +UVR treatments, especially +UVR control, but increased in the -UVR treatments (Table II). This indicates that there was more photodegradation of dissolved substances in the +UVR, and probably a greater release of biolabile compounds, though previous studies suggest that this effect is minimal with the low-DOC Lake Giles water (De Lange *et al.*, 2003).



**Fig. 3.** Chlorophyll *a* (Chl *a*) concentrations in Experiments 1 (top) and 2 (bottom), expressed as mean  $\pm$  SE ( $n = 5$ ). Initial chlorophyll was measured from the lake water used to stock all bags, and chlorophyll was measured at the end of the experiment in every bag.

Both *Daphnia* and *Cyclops* experienced high mortality in Experiment 2. Potential contributing factors include the increased incubation time, UVR dose and high densities relative to food availability (Fig. 1). Despite

high mortality, *Daphnia* and *Cyclops* still affected *L. minutus* in both UVR treatments (Table I). The negative effects of *Daphnia* and *Cyclops* on *L. minutus* egg ratios in Experiment 2 indicate that both *Daphnia* and *Cyclops* may have decreased food availability for *L. minutus*. The edibility and quality of the phytoplankton and other microorganisms in the various treatments are unknown, but diaptomid egg ratios are known to be decreased by lower food availability (Williamson and Butler, 1987). Although Chl *a* increased from initial levels in all treatments, final concentrations were only  $\sim 1 \mu\text{g L}^{-1}$  or less (Fig. 3). The significant negative effect of *Daphnia* on *L. minutus* females and *Cyclops* on *L. minutus* males may also be related to low availability of nutritious food resources. The higher initial densities of *L. minutus* males and females that resulted from *Daphnia* and *Cyclops* additions are an unintended effect that may have contributed to lower availability of high-quality (in terms of edibility and/or nutritional status) food in these treatments compared to the controls.

During Experiment 2, copepodid mortality was quite high in both the +UVR and -UVR, whereas initial numbers of adults were maintained in the +UVR, and nauplii and egg production increased in both UVR treatments (Fig. 2). This may be due to a greater sensitivity to low food concentrations and/or quality for copepodids compared to other life stages. In laboratory experiments, diaptomid copepodids were affected more than nauplii by low food levels, probably due to the ability of nauplii to graze more efficiently on small phytoplankton (Elmore, 1982). Copepodids may also be more affected than other life stages by the low phosphorus levels in Lake Giles, which are typically  $< 1 \mu\text{g L}^{-1}$ . For example, *Diaptomus clavipes* raised on a phosphorus-sufficient diet matured, but on a phosphorus-deficient diet

*Table II: Dissolved absorption coefficients ( $a_{320}$ ) and cumulative 320-nm irradiance ( $E_{320}$ ) received at the center of the +ultraviolet radiation (+UVR) treatment bags in  $\text{kJ m}^{-2}$  and 320-nm exposure days, expressed as mean  $\pm$  standard error ( $n = 5$ )*

Treatment	Experiment 1			Experiment 2		
	$a_{320}$ ( $\text{m}^{-1}$ )	$E_{320}$ ( $\text{kJ m}^{-2}$ )	320-nm exposure days	$a_{320}$ ( $\text{m}^{-1}$ )	$E_{320}$ ( $\text{kJ m}^{-2}$ )	320-nm exposure days
Initial	$1.24 \pm 0.01$	NA	NA	$1.35 \pm 0.03$	NA	NA
+UVR control	$0.92 \pm 0.10$	9.34	0.86	$0.57 \pm 0.45$	20.00	1.84
+UVR + <i>Daphnia</i>	$0.85 \pm 0.00$	9.36	0.86	$1.08 \pm 0.03$	19.65	1.80
+UVR + <i>Cyclops</i>	$0.92 \pm 0.03$	9.34	0.86	$1.07 \pm 0.02$	19.65	1.80
-UVR control	$1.17 \pm 0.03$	NA	NA	$1.43 \pm 0.02$	NA	NA
-UVR + <i>Daphnia</i>	$1.07 \pm 0.01$	NA	NA	$1.47 \pm 0.04$	NA	NA
-UVR + <i>Cyclops</i>	$1.08 \pm 0.04$	NA	NA	$1.47 \pm 0.05$	NA	NA

NA, not applicable, because the -UVR treatments received no 320-nm irradiance.

reached only the CII copepodid stage (Villar-Argaiz and Sterner, 2002).

One limitation of this study is that each experiment provides data only at initial and final time points. Similar studies have demonstrated how UVR stimulation and suppression are dynamic processes resulting in different short-term and long-term effects on biota (Cabrera *et al.*, 1997; Vinebrooke and Leavitt, 1998). The stimulatory UVR effect on algae observed by Bothwell *et al.* (Bothwell *et al.*, 1994) did not appear until 3 weeks into the experiment, as this effect was dependent on the depression of chironomid grazers. Cabrera *et al.* (Cabrera *et al.*, 1997) observed a negative effect of UV-B on chlorophyll in the first few weeks of their experiment, but a stimulatory effect after 30 days. Another limitation is that in Experiment 2, the additions of *Daphnia* and *Cyclops* increased *L. minutus* adult and copepodid densities over control densities ~1.5- to 1.8-fold (Fig. 2), an effect that was difficult to control, given the dominance of the species and our desire to avoid handpicking and over-handling the zooplankton. However, we still obtained the desired *Daphnia* and *Cyclops* treatment effects, because initial densities were 12 *Daphnia* L<sup>-1</sup> and 4 *Cyclops* L<sup>-1</sup> within the respective treatments, while natural lake densities are 5 *Daphnia* L<sup>-1</sup> and 1 *Cyclops* L<sup>-1</sup>, and control densities were essentially zero. Thus, *Daphnia* and *Cyclops* densities were elevated much more than *L. minutus* in Experiment 2.

UVR has often been considered a universal stressor to aquatic systems. While interactions between zooplankton species of differing UVR tolerances are potentially important, these results instead demonstrate that UVR can have a beneficial effect on more UV-tolerant species such as *L. minutus* and that this effect is independent of the concurrent detrimental UVR effects on competitors or predators. The result of higher Chl *a* concentrations in the presence of UVR suggests that UVR may indirectly influence *L. minutus* through the phytoplankton community. These findings may have important implications for plankton community structure under conditions of environmental change. Further research of short- and long-term effects of UVR on zooplankton, the microplanktonic community and photochemical processes will be useful in determining the mechanisms and prevalence of UVR stimulation.

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