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Vertical migration mitigates UV effects on zooplankton community composition

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Running head: Defence mechanisms outweigh UV effects

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Abstract

Several zooplankton species are susceptible to ultraviolet radiation (UV), suggesting that UV may shape zooplankton community composition. Little is known, however, about the quantitative effects of long-term UV exposure in relation to biological processes. Therefore, we studied effects of UV on behaviour, population dynamics, and reproduction of several zooplankton taxa. We identified different strategies regarding daytime vertical distribution: a strong response to UV threat, illustrated by *Daphnia*; a weak, albeit significant response, such as in copepods; and lastly, a stationary position in a depth refuge, as in *Chydorus* and *Eurycercus*. The relative abundances of the different zooplankton species were similar and only *Daphnia* and copepod nauplii displayed a slight decrease in relative abundance in response to UV treatment. *Daphnia* also reacted to the UV threat by increasing resting egg production, whereas long-term population dynamics for all studied species were surprisingly similar between treatments, despite considerable differences in UV exposure for several months. We conclude that zooplankton communities at temperate latitudes are able to survive increased UV levels due to efficient defences, suggesting that future potential increases in UV radiation may result in only moderate impacts on zooplankton population dynamics and community composition.

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Introduction

A great number of factors may potentially affect the performance of organisms in aquatic ecosystems including temperature, light and nutrient availability. Ultraviolet radiation (UV) has recently also received a lot of attention since it may have negative effects on many aquatic taxa (Bancroft et al., 2007). UV is known to affect both behaviour (Rhode et al., 2001; Boeing et al., 2004; Hansson and Hylander, 2009a) and mortality rate (Hairston, 1979; Ringelberg et al., 1984) in zooplankton communities and is predicted to be an environmental issue of increasing prominence for future aquatic ecosystems (Brönmark and Hansson, 2002; Rautio and Korhola, 2002). Despite these predictions, little is known about the quantitative effects of long-term exposure to UV radiation on aquatic organisms, especially in relation to other processes occurring in natural systems (Siebeck et al., 1994). Several previous studies investigating zooplankton vertical migration have noted that it's causes may differ both temporally (within a system) and spatially (among lakes) (Leech and Williamson, 2000; Winder et al., 2004; Leech et al., 2005). Other studies have shown that the susceptibility of zooplankton to environmental factors such as UV radiation may be species-specific (Rhode et al., 2001; Hansson et al., 2007a). Some species of *Daphnia*, for example, are more vulnerable to UV than are several copepod species (Leech and Williamson, 2000; Hansson and Hylander, 2009b). This differential susceptibility has led some to argue that UV radiation could be structuring zooplankton communities (Williamson et al., 2001). However, since the UV threat co-varies with other parameters like temperature, food shortage, and fish predation, it is difficult to single out the UV effect (Marinone et al., 2006).

An important aim of the present study is to assess if an increase in the levels of long-term UV radiation exposure may affect population dynamics, reproduction and species diversity. We also aim at assessing the importance of UV as a structuring factor in relation to competition and behavioural defences like vertical migration. Previous studies on community response to UV have generally dealt with short time periods and entailed low statistical power (Cabrera et al., 1997; Delange et al., 1999). Furthermore, there is still a gap in knowledge on how UV affects species interactions, trophic relationships, and in the end, the community composition of aquatic systems (Sommaruga 2003). Therefore, we performed a long-term study (4 months) at elevated UV exposure where several zooplankton taxa were studied. We focused on behaviour (vertical migration) and population dynamics and the effects on zooplankton community composition.

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Method

A mesocosm experiment was performed in Lund, southern Sweden (55.67° N, 13.5° E) using 8 plastic cylinders (diameter 0.37 m, height 1.0 m) arranged randomly in two rows. A mixture of tap water (80 L) and filtered lake water (27 L from a nearby lake (Dalby Quarry); 50-μm mesh size) was added to each mesocosm, and the water was constantly and gently aerated. A certain volume of a mixture of zooplankton coming from Dalby Quarry and a small nearby pond was added to each mesocom giving an initial dominance of calanoid copepods (*Eudiaptomus gracilis*, approximately 56 L^{-1}) and *Daphnia* sp. (0.93 L^{-1}). Pre-cultured algal food (*Scenedesmus* sp. and *Clamydomonas* sp.) was added to each cylinder in original concentrations of approximately 120 000 cells mL^{-1} and 3 000 cell mL^{-1}, respectively. This food was added to the mesocosms once a week. Water from Dalby Quarry had an absorption coefficient of 2.0 and an attenuation depth of 1.6 m (320 nm, 1% remaining). The water in the mesocosms had an absorption coefficient of 9.4 and an attenuation depth of approximately 0.4 m. Two treatments (n=4) were applied, consisting of visible light (V) or the entire solar spectrum (UV). In addition to the natural sunlight, extra UV radiation was supplied with one fluorescent lamp placed above each cylinder. The fluorescent lamps (Philips, CLEO Performance, 80 W) were turned on for 16 hours each day, approximately between sunrise and sunset. The lamps have a spectrum with maximum intensity around 350 nm. For spectral composition of the same kinds of lamps see Hylander et al. (Hylander et al., 2009b). The UV radiation reaching the water surface of the cylinders was controlled by Plexiglas (Röhm GS 233) that screened out most of the UV radiation (i.e. the V-treatment; effectively cutting off radiation below ~370 nm), or by UV-transparent Plexiglas (Röhm GS 2458) that let both visible and UV radiation through (i.e. the UV-treatment). The lamps provided additional radiation to the UV treatment, adding approximately 40% extra UVA compared with ambient conditions (daily integrated values during a clear day); and the UV-blocking Plexiglas lowered UVA by circa 70% in the V treatment (Fig. 1). Experimental treatments also increased UVB radiation by approximately 30% in the UV treatment and reduced the exposure by approximately 100% in the V treatment (Fig. 1). For transmittance of the Plexiglas see Hansson et al. (Hansson et al., 2007). Ambient UVA and UVB radiation were also monitored (Fig. 1; UV sensors SUL 033 and SUL 240, connected to a logging meter IL 1400A, International Light). Ambient integrated daily UVA radiation was 58 (±23) J cm^{-2} day^{-1} and UVB was 1.2 (±0.2) J cm^{-2} day^{-1} (mean for the entire experimental period measured outside the experiment with the same sensors as above). To estimate penetration of UV into the water, absorbance at 320 nm (A_{320}) was regularly measured (Beckman DU 800

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spectrophotometer) in the surface waters of all cylinders. The diffuse attenuation coefficient (at 320 nm) and the attenuation depth (1%, 320 nm) were calculated using the relationship between the absorption coefficient at 320 nm and the diffuse attenuation coefficient (K_{320}, Kirk, 1994, Morris et al., 1995). The UV threat estimate of radiation still remaining at a depth of 0.1 m ($I_{0.1}$) was calculated (Hansson, 2004) from $I_{0.1}=I_0\, e^{(-K320*0.1)}$, where I_0 is the daily integrated UVA radiation from the sun and the fluorescent lamps. One of the main zooplankton groups in this study, *Daphnia*, has a receptor within the compound eye in the UVA spectrum (Smith and Macagno 1990) making UVA suitable for the threat estimate. In order to keep periphyton production down, the walls of the cylinders were swept with a brush once a week, which clouded the water for a couple of hours. Evaporation lead to reduced water levels and therefore we added new water every month.

Throughout the experiment surface oxygen, temperature and fluorescence were monitored (fluorescence was recalculated to chlorophyll with a standard curve; Turner Designs, Aquafluor Handheld Fluorometer/Turbidimeter). Chlorophyll a values ranged between 12 and 139 µg L^{-1} with a mean value of 40 µg L^{-1} for both treatments over the entire experiment, and there were no differences between treatments (RM ANOVA; $F_{1,6} = 0.7$; $p > 0.05$). A depth profile of chlorophyll was measured during a sunny day and there were no differences between treatments or between depths and no significant interaction (Treatment: Two-way ANOVA; $F_{1,12} = 0.8$; $p > 0.05$; depth: Two-way ANOVA; $F_{1,12} = 1.1$; $p > 0.05$; treatment x depth interaction: Two-way ANOVA; $F_{1,12} = 1.0$; $p > 0.05$). Temperature varied throughout the experiment from 9.5 - 27.1 ºC and there were no differences between treatments (Fig. 2; RM ANOVA; $F_{1,6} = 0.1$; $p > 0.05$). A depth profile of temperature was measured during a sunny day and there were no differences between treatments but approximately one degree Celsius lower temperature at the bottom compared with surface water (Treatment: Two-way ANOVA; $F_{1,12} = 0.6$; $p > 0.05$; depth: Two-way ANOVA; $F_{1,12} = 45.6$; $p < 0.05$). There was no significant interaction between treatment and depth (Two-way ANOVA; $F_{1,12} = 2.3$; $p > 0.05$). Also oxygen did not differ between treatments and ranged from 7.9 – 14.4 mg L^{-1} (Fig. 2; RM ANOVA; $F_{1,6} = 0.6$; $p > 0.05$). The phytoplankton community composition was also monitored in surface waters three times throughout the experimental period. The community was initially dominated by *Chlamydomonas* sp., *Scenedesmus* sp., *Rhodomonas* sp., *Fragillaria* sp., *Aphanothece* sp., and some Ankistrodesmacae. Eventually the diversity decreased, and *Scenedesmus* sp. and *Chlamydomonas* sp. became dominant, constituting approximately 90% and 6.5% of the total algal numbers, respectively. All other algal species constituted less than 1% of total algal

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abundance throughout the experiment. Regarding the abundances of all algal species present, there were no differences between treatments (two-way MANOVA, $F_{6,13} = 2.4$, $p > 0.05$). Depth profiles for phytoplankton species composition are not available but chlorophyll measurements indicate that there were no differences in algal biomass between depths and treatments (see above). Samples for nutrients were collected at the end of the experiment and analyzed according to standard methods (Tyler and Olsson 2001; ICP MS ELAN-600). Mean total phosphorous concentrations (± 1SD) were 57.8 (±51.6) and 44.3 (±30.4) in the V and UV treatments, respectively and there were no differences between treatments (t = 0.396, p > 0.05)

Experimental treatments started on 10-May and then zooplankton population dynamics and vertical migration were monitored approximately once a month, between 18-May and 5-Sept-2006, by collecting samples at noon from the surface (depth 0.1 m) and the bottom (depth 0.9 m) of the cylinders. A four-litre sample was taken from each level through tubing in the cylinder walls. The animals were retrieved on a 50 µm net and preserved with Lugol's solution. All zooplankton in the entire sample, i.e. not a subsample, were counted using a Petri dish with eight sub-chambers, each 26 × 33 mm (Nalge Nunc, USA), and a dissecting microscope. Each sampling also included counting of egg- and ephippia-carrying *Daphnia* (i.e. normal eggs and resting eggs).

Analysis of population dynamics, community composition, and reproduction was made by means of repeated measures ANOVA (RM ANOVA) on log- or angular-transformed data. Zooplankton densities were calculated from mean values of the 0.1 and 0.9 m samplings, and the total filtered volume from each sampling represents approximately 7.5% of the total water volume in the mesocosms. Vertical position, expressed as surface-to-bottom ratio, was assessed by regression analysis, plotted against the different UV threats (se threat estimate above, i.e. $I_{0.1}$). Note that each point in the regression analysis represents one mesocosm at one sampling date. Statistical analysis was performed in SPSS 15.0.

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Results

Community response and population dynamics

The number of zooplankton species and the proportions of the different species was rather similar when comparing the two treatments throughout the experiment (V and UV; Fig. 3). The most common taxa by numbers were *Chydorus* sp., *Daphnia* sp., calanoid copepods and copepod nauplii, whereas *Eurycercus* sp., cyclopoid copepods and rotifers occurred in lower abundances (Table 1). Community differences between treatments were small, although there was a significant negative effect of UV on the proportion of *Daphnia* sp. and copepod nauplii (RM ANOVA; $p \leq 0.05$; Table 2). The proportion of *Daphnia* of the total zooplankton population was higher in UV treatments in May but then decreased and was generally lower in the UV treatment than in the V treatment (Table 2; Fig. 3). Copepod nauplii relative abundance was generally lower in the UV treatment than in the V treatment throughout the entire experiment (Fig. 3). None of the zooplankton taxa showed any response in absolute density to the treatments (i.e. Number L^{-1}; RM ANOVA; $p > 0.05$; Table 2). *Daphnia* started (in May) at very low abundances (< 1 L^{-1}), but already in June it had reached between 10 and 30 individuals L^{-1} (Fig. 4). There was no overall treatment effect ($p>0.05$; Table 2), but a significant treatment by time interaction illustrated by higher numbers of *Daphnia* early in the season in the UV than in the V treatment. This was followed by a shift to higher absolute densities in the V treatment during September ($p<0.05$; Table 2; Fig. 4). *Chydorus* increased in abundance over time but did not display any differences in abundance between treatments over time (Fig. 4).

Behavioural responses to UV

Along a UV threat gradient some taxa, including *Eurycercus* sp., *Chydorus* and rotifers showed no behavioural response to UV radiation, whereas the depth distribution (expressed as surface-to-bottom ratio) of copepod nauplii, cyclopoid and calanoid copepods, and *Daphnia*, was inversely related to UV threat (Table 3; $p < 0.05$; Fig. 5). *Chydorus* sp. and *Eurycercus* sp. rarely visited surface waters, as indicated by a surface-to-bottom ratio below zero (Fig. 5).

Reproductive responses

The proportion of egg-carrying *Daphnia* increased from less than 5% to between 30 and 40% from June to September (Fig. 6). Overall, the proportion of egg-carrying females was lower in the UV treatment compared with the V treatment during June and July but there was a shift towards higher proportions in the UV treatment during August and September (Fig. 6; RM ANOVA; treatment*time; $F_{9,36} = 3.5$; $p < 0.05$). In contrast, the proportion of the *Daphnia* population that had induced ephippia (resting eggs) was always higher in the presence of UV

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radiation, compared to absence of UV (Fig. 6; means 8.7 and 5.0%, respectively; $F_{1,6} = 8.6$; $p < 0.05$; RM ANOVA).

Discussion

In open-water habitats of lakes and oceans, there are considerable temporal and spatial variations in mortality risk; organisms, such as zooplankton, use behavioural and morphological traits to meet these challenging variations (Hansson et al., 2007a; Hylander et al., 2009a, 2009b). Several factors, such as temperature (Loose and Dawidowitcz, 1994; Winder et al., 2003), pH, and food limitation (Gliwicz and Pijanowska, 1989; Winder et al., 2003), but also ultraviolet radiation (UV), have been shown to affect zooplankton mortality rate and behaviour (Tartarotti et al., 1999; Leech and Williamson, 2001; Williamson et al., 2001; Hansson et al., 2007a). UV is known to affect accumulation of UV protective compounds, behaviour and potentially also zooplankton community community (Alonso et al., 2004; Marinone et al., 2006; Hylander et al., 2009a, 2009b). Even though we applied an elevated UV level (both UVA and UVB) for several months in a shallow system (~1m) we only saw moderate effects on the zooplankton community composition and population dynamics. This indicates that the community is well adapted to handle changes in UV radiation through their natural UV defences. Zooplankton have a number of different defence mechanisms in response to UV radiation, including vertical migration, photoenzymatic repair and accumulation of UV protective compounds (Hansson and Hylander, 2009b).

The behavioural response (vertical migration) to increased UV radiation differed considerably among taxa and *Daphnia* showed the strongest response; although showing a less dramatic response, copepod nauplii, calanoid and cyclopoid copepods also spent more time at the surface under low UV threat, compared to high UV. *Chydorus* and *Eurycercus*, regardless of UV treatment, remained mainly at the bottom during daytime, as illustrated by the almost constant low surface-to-bottom ratio. Species spending most of the time at the bottom are decoupled from any UV threat; but they are also restricted to bottom waters during daytime, which may be a competitive disadvantage (Loose and Dawidowitcz, 1994). Accordingly, from our study three different strategies can be identified regarding daytime vertical distribution: strong response to the instantaneous UV-threat, illustrated by *Daphnia*; a weak, albeit significant response, such as in copepods and rotifers; and finally, a stationary position at depth as a refuge from UV radiation, such as by *Chydorus* and *Eurycercus*. Such taxon-specific differences have previously been identified for several other zooplankton taxa (Tartarotti et al., 1999; Boeing et al., 2004; Marinone et al., 2006; Obertegger et al., 2008).

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The strength of the behavioural response to UV has been attributed to the amount of photoprotective pigmentation, for example melanin and carotenoids, such that organisms with high amounts of pigments tend to have weaker behavioural responses compared to organisms with low amounts of pigments (Tollrian and Heibl, 2004; Hansson et al., 2007a; Obertegger et al., 2008; Hylander et al., 2009b). Melanin pigmentation in *Daphnia* from temperate regions is generally low (Hebert and Emery, 1990; Hansson et al., 2007a), which may explain the strong migratory response to UV threat that we observed in this study. Also differences in temperature and food availability may change vertical migration patterns (Orcutt and Porter, 1983; Johnsen and Jakobsen, 1987). In this study, there were no differences between treatments in surface chlorophyll a and temperature. The temperature was slightly lower deep down in the mesocoms but there were no significant interactions between depth and treatment. Furthermore, vertical position of different algal species was not studied but algal biomass (chlorophyll a) was evenly distributed throughout the water column and there were no effects of depth or treatment x depth interaction effects. Overall, this indicates that UV was the most important factor in explaining the vertical position of the animals.

Daphnia reproduction was altered by the treatments. Effects on the proportion of egg-carrying females were minor but the production of ephippia (resting eggs) increased upon UV exposure. This may reflect one of the costs associated with UV exposure in natural populations. Ephippia induction has previously been shown to be triggered by both abiotic and biotic factors, for example temperature, photoperiod, and food level (reviewed in Gyllström and Hansson, 2004). Diapause is generally assumed to arise as a way of escaping periods of harsh environmental conditions, but, to our knowledge, UV has not previously been shown to be an induction agent. Since UV varies temporally over hours, days, and seasons, it is likely that ephippia production would be beneficial as a way of escaping periods of intense radiation. In nature, *Daphnia* populations in rock pools with high solar exposure have been observed to have high occurrence of ephippia, but the phenomenon has not been quantified systematically (D.O. Hessen, Oslo, personal communication).

Long-term population dynamics were relatively similar between treatments for all taxa investigated; none showed any overall treatment response to increased UV radiation levels compared to non-UV treatments. Also the community composition was rather stable with the same number of species occurring in approximately the same proportions when comparing the UV and non-UV treatments. However, after several months small differences occurred with slightly lower relative abundance of copepod nauplii and *Daphnia* in the UV treatment, indicating that these two groups were negatively affected by the radiation. Others have

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suggested that zooplankton biodiversity and community composition could be structured by the UV environment (Williamson et al., 2001). It can be difficult, however, to single out the UV effect because of covariance with other factors such as temperature and food shortage (Marinone et al., 2006). *Daphnia* has previously been suggested to be more vulnerable to UV compared to copepods and rotifers (Leech and Williamson, 2000; Williamson et al., 2001; Leech et al., 2005). Our long-term study supports the vulnerability of *Daphnia* which occurred in lower proportions in the UV treatment and also induced more ephippia. UV effects were, however, of minor importance since the overall community composition was very similar between the UV and the non-UV treatment. This is illustrated by the marked similarity in intraspecific population dynamics when comparing treatments with and without UV radiation (Fig. 4). Finally, there was a significant treatment to time effect for *Daphnia* population dynamics. This may be due to high initial reproduction in the UV treatment as a stress response. However, later in the season ephippia production increased and the UV treatment population decreased more rapidly compared with the V treatment.

In terms of UV attenuation depth, the results are comparable with natural situations since the experimental depth penetration is in the same range as UV penetration in lakes from the same area (around 0.4 m 1% attenuation depth at 320 nm) (Hansson, 2004). UV attenuation due to chlorophyll may have been present even though seston, in contrast to DOC, generally contributes much less to UV attenuation (Scully and Lean, 1994). It is difficult to assess if the elevated experimental UV level is realistic compared to natural changes. Long-term time series of UV radiation reaching earth are scarce, but calculations indicate that there has been a 6 to 14% increase in UV irradiance at mid and high latitudes between 1980 and 2002 (UNEP/WMO, 2002). Also potential differences in spectral composition of UV produced by lamps and natural radiation make it difficult to compare the applied UV exposure to natural conditions. Even though the levels used in this experiment may have been higher than the observed natural change and that we applied them for several months, we observed only moderate zooplankton community effects. This leads to the conclusion that zooplankton communities, at least at the latitudes studied, are well adapted to UV changes, due to efficient defences like vertical migration and UV protective pigmentation (Tartarotti et al., 2001; Moeller et al., 2005; Persaud et al., 2007; Hansson and Hylander, 2009a; Hylander et al., 2009a, 2009b). Even if we applied elevated levels of UV compared with ambient levels, attenuation in the water was relatively high. In systems where UV penetrates to deeper depths it cannot be ruled out that UV may be a stronger structuring force for the zooplankton community, as suggested by Williamson et al. (Williamson et al., 2001) and Marinone et al.

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(Marinone et al., 2006). However, our study underlines the importance of allowing the organisms to use their inducible defences, in this case vertical migration, in order to assess the true net effect of UV on the community composition.

During recent years much research has focused on how predicted climate change, including alterations in temperature, rainfall (Suttle et al., 2007), as well as UV radiation (Williamson, 1995), may affect natural ecosystem processes. In our investigation of UV effects on freshwater zooplankton and responses in behaviour and community composition, we conclude that one component of global change (UV radiation) may to a large extent be overruled and buffered against by biological processes such as vertical migration. Even though we applied elevated levels of UV throughout a summer we only saw moderate community changes. *Daphnia* and copepod larvae were relatively less common in the UV treatment but differences were small. Both relative and absolute abundances for all other species were stable between treatments, which indicates that organisms that are able to use efficient UV defences (like vertical migration) will withstand elevated UV levels. Instead, alterations in other climatic variables and interspecific competition may have stronger effects on community dynamics.

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References

Alonso, C., Rocco, V., Barriga, JP., Battini, MA. and Zagarese, H. (2004) Surface avoidance by freshwater zooplankton: Field evidence on the role of ultraviolet radiation. *Limnol. Oceanogr.*, **49**, 225-232.

Boeing, WJ., Leech, DM., Williamson, CE., Cooke, S., Torres, L. (2004) Damaging UV radiation and invertebrate predation: conflicting selective pressures for zooplankton vertical distribution in the water column of low DOC lakes. *Oecologia*, **138**, 603-612.

Bancroft, B. A., Baker, N. J., and Blaustein, A.R. (2007) Effects of UVB radiation on marine and freshwater organisms: a synthesis through meta-analysis. *Ecol. Lett.*, **10**, 332-345.

Bronmark, C. and Hansson, LA. (2002) Environmental issues in lakes and ponds: current state and perspectives. *Environ. Conserv.*, **29**, 290-307.

Cabrera, S., Lopez, M. and Tartarotti, B. (1997) Phytoplankton and zooplankton response to ultraviolet radiation in a high-altitude Andean lake: short- versus long-term effects. *J. Plankton Res.*, **19**, 1565-1582.

De Lange, HJ., Verschoor, AM., Gylstra, R., Cuppen, JGM. and Van Donk, E. (1999) Effects of artificial ultraviolet-B radiation on experimental aquatic microcosms. *Freshwater Biol.*, **42**, 545-560.

Gliwicz, Z. M. and Pijanowska, J. (1989) The role of predation in zooplankton succession. In: Sommer, U. (ed.), *Plankton ecology: Succession in planktonic communities.* Springer-Verlag, Berlin, pp. 253-296.

Gyllstrom, M. and Hansson, L-A. (2004.) Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. *Aquat. Sci.*, **66**, 274-295.

Hairston, NG. (1979) Adaptive significance of color polymorphism in 2 species of *Diaptomus* (Copepoda). *Limnol. Oceanogr.*, **24**, 15-37.

Hansson, L-A. (2004) Plasticity in pigmentation induced by conflicting threats from predation and UV radiation. *Ecology*, **85**, 1005-1016.

Hansson, L-A. and Hylander, S. (2009a) Size-structured risk assessments govern Daphnia migration. *Proc. R. Soc. B*, **276**, 331-336.

Hansson, L-A. and Hylander, S. (2009b.) Effects of ultraviolet radiation on pigmentation, photoenzymatic repair, behavior, and community ecology of zooplankton. *Photoch. Photobiol. Sci.*, **8**, 1266-1275.

Hansson, L-A., Hylander, S. and Sommaruga, R. (2007) Escape from UV threats in zooplankton: A cocktail of behavior and protective pigmentation. *Ecology*, **88**, 1932-1939.

For Peer Review

Hebert, PDN. and Emery, CJ. (1990) The adaptive significance of cuticular pigmentation in daphnia. *Funct. Ecol.*, **4**, 703-710.

Hylander, S., Boeing, W. J., Granéli, W., Karlsson, J., von Einem, J., Gutseit, K. and Hansson, L-A. (2009a) Complementary UV protective compounds in zooplankton. *Limnol. Oceanogr.*, **54**, 1883-1893.

Hylander, S., Larsson, N. and Hansson, L-A. (2009b) Zooplankton vertical migration and plasticity of pigmentation arising from simultaneous UV and predation threats. *Limnol. Oceanogr.*, **54**, 483-491.

Johnsen, B. and Jacobsen, P. (1987) The effect of food limitation on vertical migration in Daphnia longispina. *Limnol. Oceanogr.*,. **32**, 873-880.

Kirk, JTO. (1994) Optics of UV-B radiation in natural waters. *Arch. Hydrobiol. Beih.*, **43**, 1-16.

Leech, DM., Padeletti, A. and Williamson, CE. (2005) Zooplankton behavioral responses to solar UV radiation vary within and among lakes. *J. Plankton Res.*, **27**, 461-471.

Leech, DM. and Williamson, CE. (2000) Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? *Ecol. Appl.*, **10**, 1530-1540.

Leech, DM. and Williamson, CE. (2001) In situ exposure to ultraviolet radiation alters the depth distribution of Daphnia. *Limnol. Oceanogr.*, **46**, 416-420.

Loose, CJ. and Dawidowicz, P. (1994) Trade-offs in diel vertical migration by zooplankton: The costs of predator avoidance. *Ecology,* **75**, 2255-2263.

Marinone, MC., Marque, SM., Suarez, DA., Dieguez, MDC., Perez, P., Rios, PDL., Soto, D. and Zagarese, HE. (2006) UV radiation as a potential driving force for zooplankton community structure in Patagonian lakes. *Photochem. Photobiol.*, **82**, 962-971.

Moeller, RE., Gilroy, S., Williamson, CE., Grad, G., Sommaruga, R. (2005) Dietary acquisition of photoprotective compounds (mycosporine-like amino acids, carotenoids) and acclimation to ultraviolet radiation in a freshwater copepod. *Limnol. Oceanogr.*, **50**, 427-439.

Morris, DP., Zagarese, H., Williamson, CE., Balseiro, EG., Hargreaves, BR., Modenutti, B., Moeller, R. and Queimalinos, C. (1995) The attentuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnol. Oceanogr.*, **40**, 1381-1391.

Obertegger, U., Flaim, G. and Sommaruga, R. (2008) Multifactorial nature of rotifer water layer preferences in an oligotrophic lake. *J. Plankton Res.*, **30**, 633-643.

For Peer Review

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.

Persaud, AD., Moeller, RE., Williamson, CE. and Burns, CW. (2007) Photoprotective compounds in weakly and strongly pigmented copepods and co-occurring cladocerans. *Freshwater Biol.*, **52**, 2121-2133.

Rautio, M. and Korhola, A. (2002) Effects of ultraviolet radiation and dissolved organic carbon on the survival of subarctic zooplankton. *Polar Biol.*, **25**, 460-468.

Rhode, SC., Pawlowski, M. and Tollrian, R. (2001) The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus Daphnia. *Nature*, **412**, 69-72.

Ringelberg, J., Keyser, AL.and Flik, BJG. (1984) The mortality effect of ultraviolet-radiation in a translucent and in a red morph of *Acanthodiaptomus-denticornis* (Crustacea, Copepoda) and its possible ecological relevance. *Hydrobiol.*, **112**, 217-222.

Scully, N.M. and Lean, DRS. (1994) The attenuation of ultraviolet radiation in temperate lakes. *Arch. Hydrobiol. Beih.*, **43**, 135-144.

Siebeck, O., Vail, TL., Williamson, CE., Vetter, R., Hessen, D., Zagarese, H., Little, E., Balseiro, E., Modenutti, B., Seva J. and Shumate, A. (1994) Impact of UV-B radiation on zooplankton and fish in pelagic freshwater ecosystems. *Arch. Hydrobiol. Beih.*, **43**, 101-114.

Smith, K.C. and Macagno, E.R. (1990) UV photoreceptor in the compound eye of *Daphnia magna*. *J. Comp. Physiol.* A., **166**, 597-606.

Sommaruga, R. (2003) UVR and its effects on species interactions. In Helbling, ER. and Zagarese, H. (eds.), *UV Effects in Aquatic Organisms and Ecosystems*. The Royal Society of Chemistry, Cambridge, pp. 485-508.

Suttle, KB., Thomsen, MA. and Power, ME. (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640-642.

Tartarotti, B., Cabrera, S., Psenner, R. and Sommaruga, R. (1999) Survivorship of *Cyclops abyssorum tatricus* (Cyclopoida, Copepoda) and *Boeckella gracilipes* (Calanoida, Copepoda) under ambient levels of solar UVB radiation in two high-mountain lakes. *J. Plankton Res.*, **21**, 549-560.

Tartarotti, B., Laurion, I. and Sommaruga, R. (2001) Large variability in the concentration of mycosporine-like amino acids among zooplankton from lakes located across an altitude gradient. *Limnol. Oceanogr.*, **46**, 1546-1552.

For Peer Review

Tollrian, R. and Heibl, C. (2004) Phenotypic plasticity in pigmentation in Daphnia induced by UV radiation and fish kairomones. *Funct. Ecol.*, **18**, 497-502.

Tyler, G. and Olsson, T. (2001) Concentrations of 60 elements in the soil as related to the soil acidity. *European Journal of Soil Science*, **52**, 151-165.

UNEP/WMO. (2002) Executive Summary, Scientific Assessment of Ozone Depletion: 2002. In: *Scientific assessment of ozone depletion: 2002*. World meteorological organization global ozone research and monitoring project. Report no. 47.

Williamson, CE. (1995) What role does UV-B radiation play in freshwater ecosystems? *Limnol. Oceanogr.*, **40**, 386-392.

Williamson, CE., Olson, OG., Lott, SE., Walker, ND., Engstrom, DR. and Hargreaves, BR. (2001) Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. *Ecology*, **82**, 1748-1760.

Winder, M., Buergi, HR. and Spaak, P. (2003) Seasonal vertical distribution of phytoplankton and copepod species in a high-mountain lake. *Arch. Hydrobiol*. 158, 197-213.

Winder, M., Spaak, P. and Mooij, WM. (2004) Trade-offs in *Daphnia* habitat selection. *Ecology*, **85**, 2027-2036.

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Tables

Table 1. Population dynamics (numbers L^{-1}) for all sampled zooplankton groups throughout the experiment. Mean values are given with standard error within brackets.

Table 2. Results from RM ANOVAs. A) Differences in community composition for the different species of zooplankton, i.e. the proportion in relation to the total zooplankton population (relative abundance). B) Differences in population dynamics (i.e. absolute abundance, Number L^{-1}) for the different zooplankton species.

Table 3**.** Results from regression analysis of surface to bottom ratios of different species of zooplankton at different UV threats.

Figure legends

Fig. 1. Daily UVA and UVB exposures measured weekly in ambient conditions and estimated in UV and V treatments. Net emission from fluorescent lamps is calculated as the emission coming from the lamps in a dark room minus shading from experimental setup and the transmission of the Plexiglass.

Fig. 2. Temperature (ºC) and oxygen levels (mg L^{-1}) throughout the experiment. Standard deviations are sometimes not visible.

Fig. 3. Community response: Relative abundance (%) of the different zooplankton species throughout the experiment (note that it is copepod nauplii). Treatments are visible light (V; panel A) or the entire solar spectrum (UV; panel B). Density estimates are based on a mean value from the 0.1 and 0.9 m samplings.

Fig. 4. Population dynamics: Mean abundances (number L^{-1}; ± 1SD) of the two most common species of zooplankton, *Daphnia* sp. and *Chydorus* sp. throughout the experimental period. Treatments are visible light (V) or the entire solar spectrum (UV). Density estimates are based on a mean value from the 0.1 and 0.9 m samplings.

Fig. 5.. Depth distribution of zooplankton (calanoid copepods, *Chydorus* sp., cyclopoid copepods, *Daphnia* sp., *Eurycercus* sp., copepod nauplii, and rotifers) expressed as surface-to-bottom ratio at different UV threats. Significant relationships are indicated by p-values.

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Treatments are visible light (V) or the entire solar spectrum (UV). Note that each point in the figure represents data from one mesocom at one sampling. The variability in UV threat that is seen within treatments is due to changes in ambient radiation and also changing absorption coefficients over time.

Fig. 6.. Mean proportion (%, ±1SD) egg- (A) and ephippia- (B) carrying *Daphnia* during the experiment. Treatments are visible light (V) or the entire solar spectrum (UV). Ephippia and egg production estimates are based on a mean value from the 0.1 and 0.9 m samplings.

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Table 1

V - treatment

Month	Calanoids	*Eurycercus*	*Chydorus*	Cyclopoids	Rotifers	*Daphnia*	Nauplii
May	19.8 (13.7)	0 0)	0.4 (0.2)	0.7 (0.3)	0 (0)	3.2 (1.9)	0 (0)
June	4.2 (1.6)	0 (0)	11.5 (2.1)	10.8 (5.9)	3.4 (2.5)	19.9 (4.7)	4.0 (0.9)
July	4.5 (1.8)	0.3 (0.1	59.5 (5.8)	3.8 (0.3)	0.6 (0.2)	15.0 (5.2)	14.7 (2.7)
Aug	0.1 (0.1)	3.0 (1.6)	34.3 (9.0)	6.6 (2.7)	0.3 (0.1)	8.5 (2.2)	19.6 (5.5)
Sep	0 (0)	5.0 (3.1)	19.6 (5.8)	4.6 (3.2)	2.9 (2.7)	22.7 (3.9)	21.4 (8.1)

UV - treatment

Month	Calanoids	*Eurycercus*	*Chydorus*	Cyclopoids	Rotifers	*Daphnia*	Nauplii
May	5.7 (1.6)	0 (0)	0.1 (0.02)	0.7 (0.2)	0 (0)	2.3 (1.0)	0 (0)
June	3.0 (1.0)	0 (0)	36.4 (19.1)	3.3 (0.3)	4.0 (2.5)	31.9 (6.9)	3.0 (1.1)
July	1.9 (0.6)	0.6 (0.2)	83.4 (1.8)	4.1 (0.9)	0.8 (0.4)	21.1 (7.8)	11.6 (3.4)
Aug	0.1 (0.04)	3.7 (1.4)	36.7 (20.4)	7.1 (2.2)	0.1 (0.04))	13.8 (2.7)	15.1 (3.2)
Sep	0.02 (0.02)	3.4 (1.8)	32.6 (29.8)	10.2 (5.5)	0.2 (0.1)	8.0 (3.7)	11.3 (6.6)

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Table 2.

A) Community response

	Treatment			Time			Time*treatment	
Zooplankton	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
Calanoid	0.3	0.596	1,6	16.4	0.005	1,6	0.1	0.782
Chydorus	0.4	0.569	1,6	14.1	0.005	1,7	0.4	0.608
Cyclopoid	<0.1	0.984	1,6	1.7	0.191	4,24	1.5	0.262
Daphnia	7.2	**0.037**	1,6	1.0	0.448	4,24	4.3	**0.009**
Eurycercus	0.2	0.71	1,6	12.8	<0.001	4,24	0.3	0.853
Cop. nauplii	5.9	**0.052**	1,6	19.2	<0.001	4,24	1.4	0.261
Rotifers	0.3	0.621	1,6	2.6	0.15	1,7	1.1	0.345

B) Population dynamics

	Treatment			Time			Time*treatment	
Zooplankton	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
Calanoid	3.1	0.130	1,6	3.3	0.114	1,6	0.2	0.719
Chydorus	<0.1	0.902	1,6	39.6	<0.001	1,9	1.8	0.219
Cyclopoid	0.2	0.695	1,6	5.4	0.003	4,24	1.1	0.369
Daphnia	<0.1	0.920	1,6	15.5	<0.001	4,24	2.9	**0.041**
Eurycercus	<0.1	0.821	1,6	11.1	0.001	4,24	0.4	0.835
Nauplii	2.6	0.155	1,6	31.1	<0.001	4,24	0.7	0.598
Rotifers	0.2	0.667	1,6	5.2	0.026	2,11	0.6	0.568

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Table 3.

Depth distribution

Zooplankton	Beta	r^2	df	p
Calanoid	-0.533	0.284	1,25	**0.004**
Chydorus	-0.254	0.065	1,35	0.129
Cyclopoid	-0.347	0.121	1,38	**0.028**
Daphnia	-0.728	0.53	1,38	**<0.001**
Eurycercus	-0.079	0.006	1,19	0.733
Copepod nauplii	-0.402	0.162	1,30	**0.022**
Rotifers	-0.319	0.102	1,21	0.137

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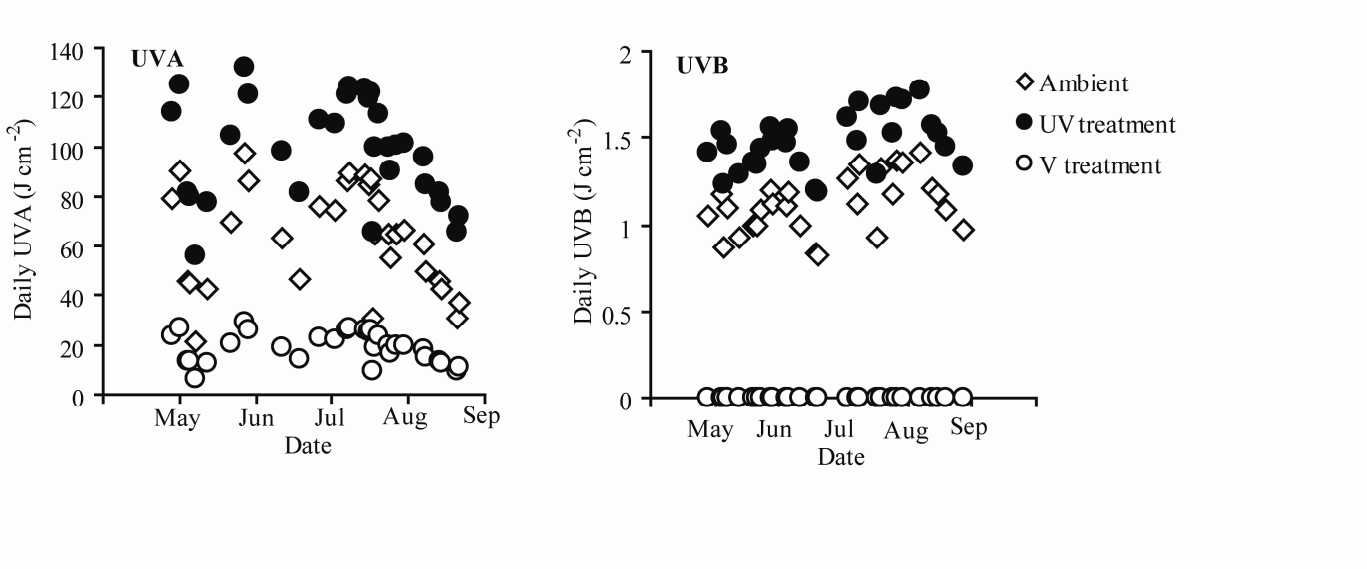

Fig. 1.

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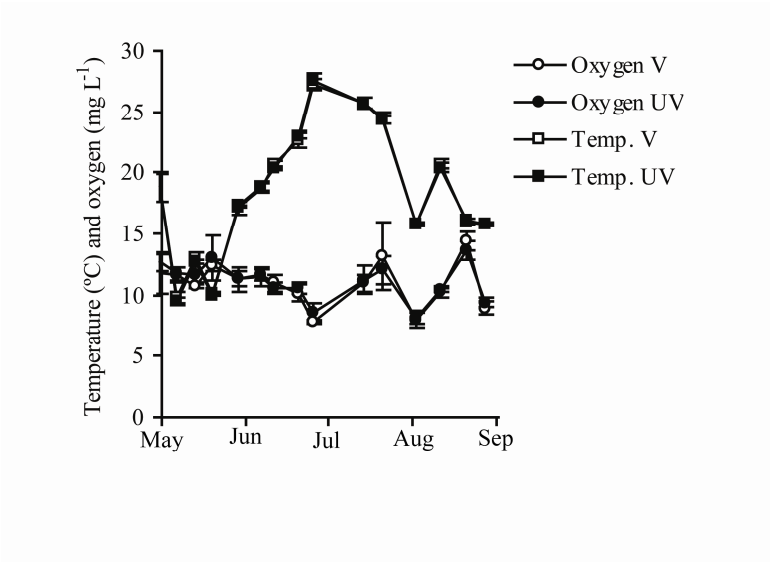

Fig. 2.

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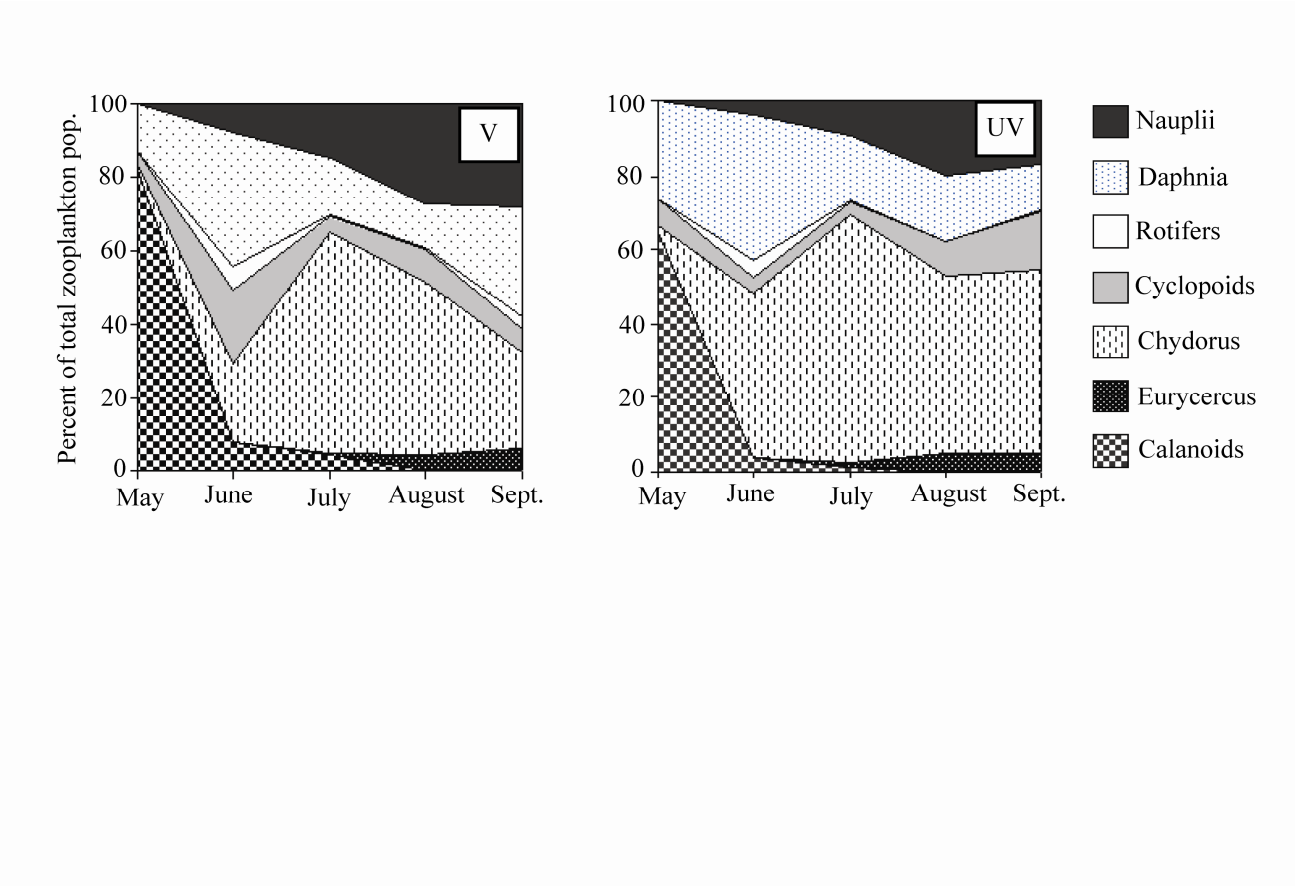

Fig. 3.

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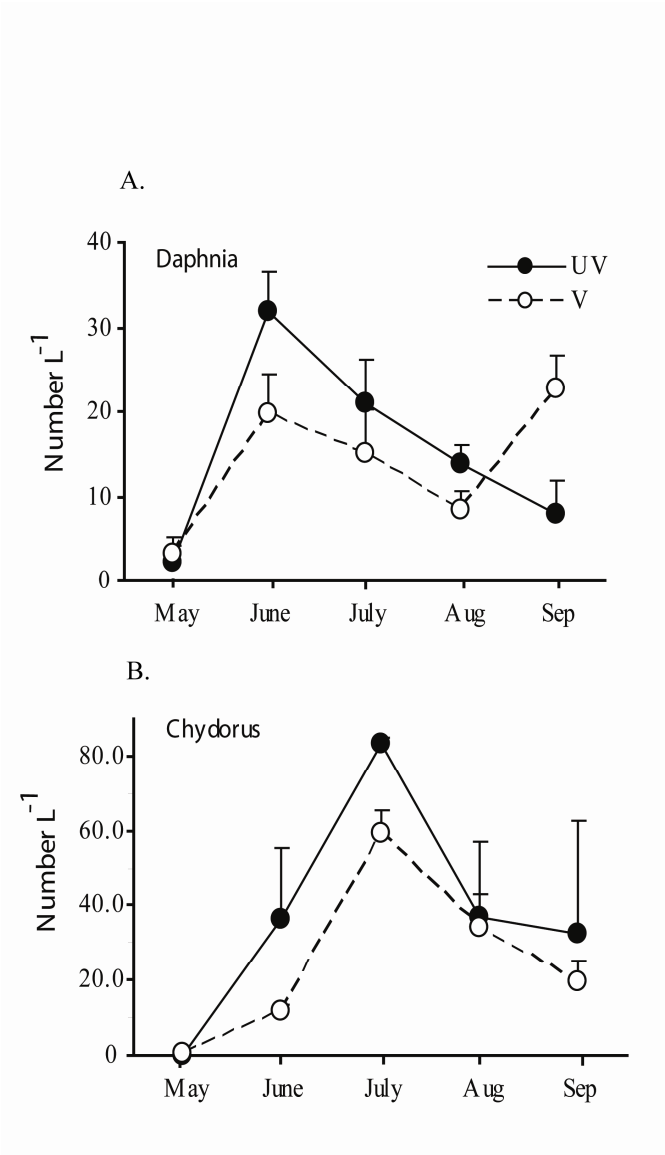

Fig. 4

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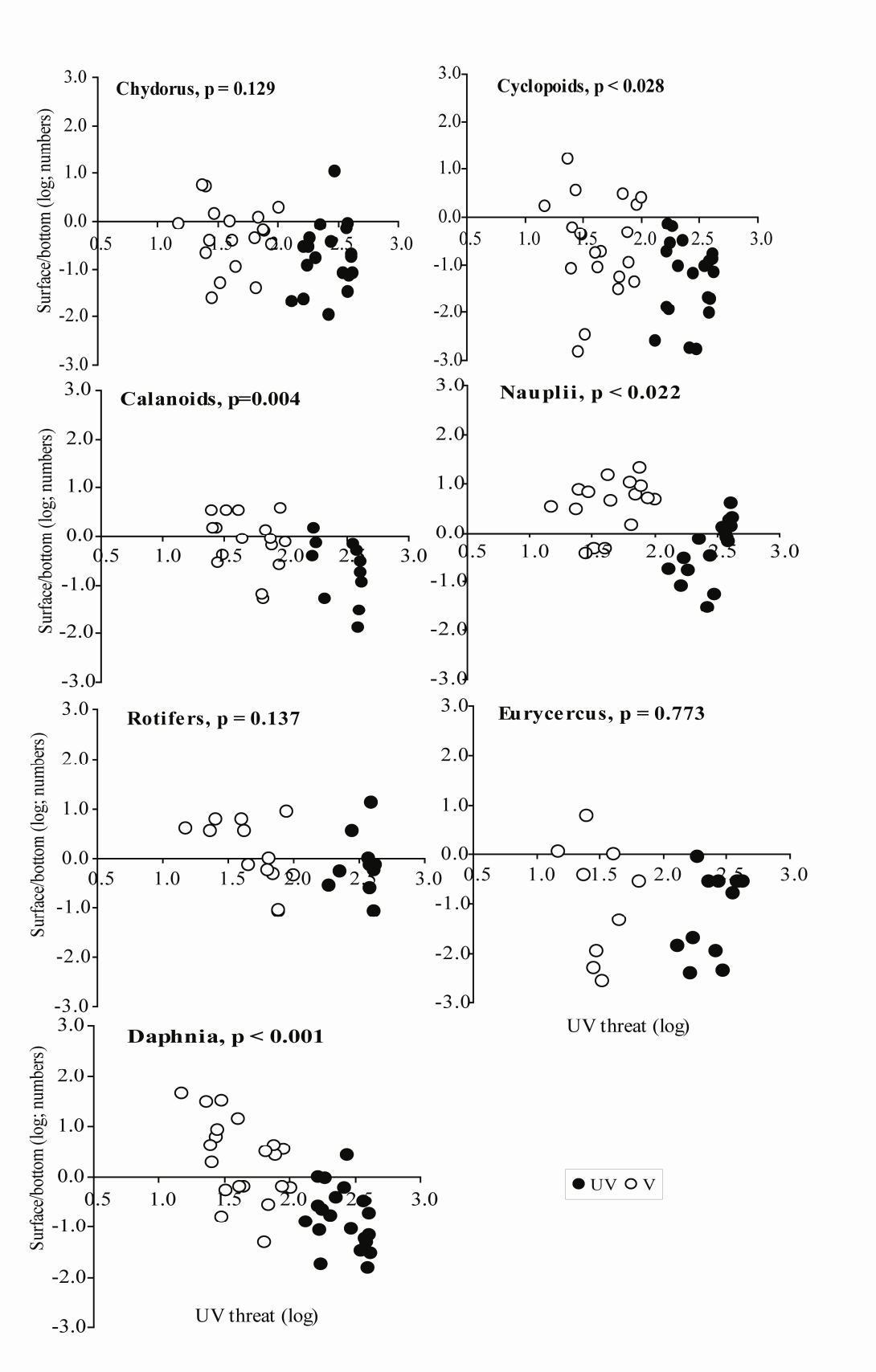
Chydorus, p = 0.129
Cyclopoids, p < 0.028
Calanoids, p=0.004
Nauplii, p < 0.022
Rotifers, p = 0.137
Eurycercus, p = 0.773
Daphnia, p < 0.001
Surface/bottom (log; numbers)
UV threat (log)
UV
V

Fig. 5.

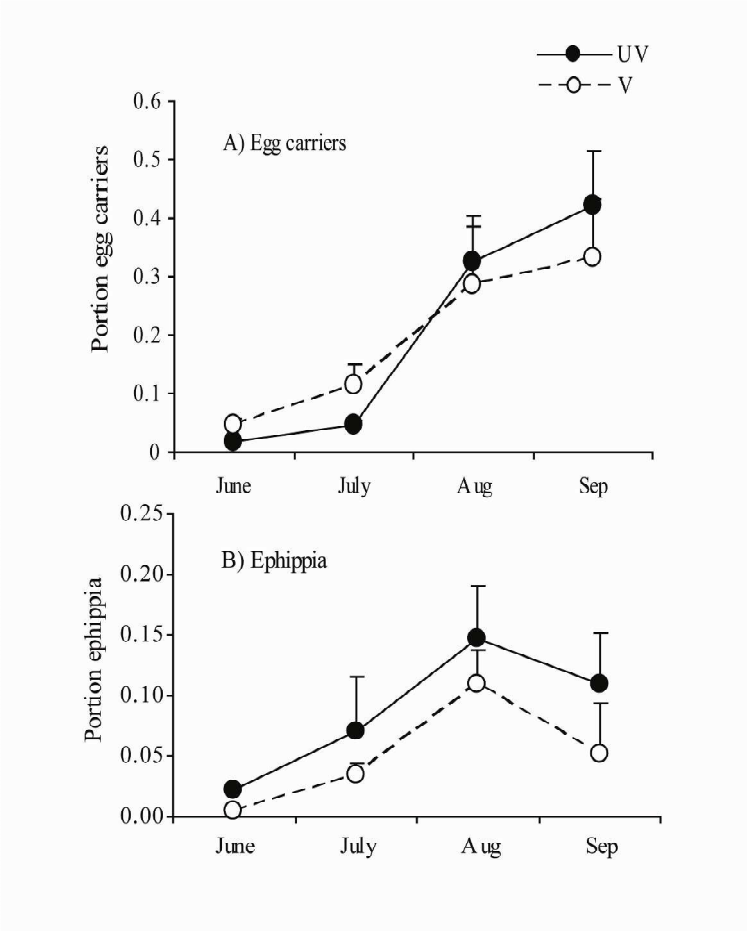
UV
V
A) Egg carriers
Portion egg carriers
0.6
0.5
0.4
0.3
0.2
0.1
0
June
July
Aug
Sep
B) Ephippia
Portion ephippia
0.25
0.20
0.15
0.10
0.05
0.00
June
July
Aug
Sep

Fig. 6.

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