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**Vertical migration mitigates UV effects on zooplankton
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Vertical migration mitigates UV effects on zooplankton community composition

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zooplankton , UV , community , vertical migration

Running head: Defence mechanisms outweigh UV effects

1
2
3 29 **Abstract**
4

5 30 Several zooplankton species are susceptible to ultraviolet radiation (UV), suggesting that UV
6 31 may shape zooplankton community composition. Little is known, however, about the
7 32 quantitative effects of long-term UV exposure in relation to biological processes. Therefore,
8 33 we studied effects of UV on behaviour, population dynamics, and reproduction of several
9 34 zooplankton taxa. We identified different strategies regarding daytime vertical distribution: a
10 35 strong response to UV threat, illustrated by *Daphnia*; a weak, albeit significant response, such
11 36 as in copepods; and lastly, a stationary position in a depth refuge, as in *Chydorus* and
12 37 *Eurycerus*. The relative abundances of the different zooplankton species were similar and
13 38 only *Daphnia* and copepod nauplii displayed a slight decrease in relative abundance in
14 39 response to UV treatment. *Daphnia* also reacted to the UV threat by increasing resting egg
15 40 production, whereas long-term population dynamics for all studied species were surprisingly
16 41 similar between treatments, despite considerable differences in UV exposure for several
17 42 months. We conclude that zooplankton communities at temperate latitudes are able to survive
18 43 increased UV levels due to efficient defences, suggesting that future potential increases in UV
19 44 radiation may result in only moderate impacts on zooplankton population dynamics and
20 45 community composition.
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46 Introduction

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

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

78

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 mesocosm 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 (\pm 23) J cm⁻² day⁻¹ and UVB was 1.2 (\pm 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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3 113 spectrophotometer) in the surface waters of all cylinders. The diffuse attenuation coefficient
4 114 (at 320 nm) and the attenuation depth (1%, 320 nm) were calculated using the relationship
5 115 between the absorption coefficient at 320 nm and the diffuse attenuation coefficient (K_{320} ,
6 116 Kirk, 1994, Morris et al., 1995). The UV threat estimate of radiation still remaining at a depth
7 117 of 0.1 m ($I_{0.1}$) was calculated (Hansson, 2004) from $I_{0.1} = I_0 e^{(-K_{320} \cdot 0.1)}$, where I_0 is the daily
8 118 integrated UVA radiation from the sun and the fluorescent lamps. One of the main
9 119 zooplankton groups in this study, *Daphnia*, has a receptor within the compound eye in the
10 120 UVA spectrum (Smith and Macagno 1990) making UVA suitable for the threat estimate. In
11 121 order to keep periphyton production down, the walls of the cylinders were swept with a brush
12 122 once a week, which clouded the water for a couple of hours. Evaporation lead to reduced
13 123 water levels and therefore we added new water every month.

14 124 Throughout the experiment surface oxygen, temperature and fluorescence were
15 125 monitored (fluorescence was recalculated to chlorophyll with a standard curve; Turner
16 126 Designs, Aquafluor Handheld Fluorometer/Turbidimeter). Chlorophyll a values ranged
17 127 between 12 and 139 $\mu\text{g L}^{-1}$ with a mean value of 40 $\mu\text{g L}^{-1}$ for both treatments over the entire
18 128 experiment, and there were no differences between treatments (RM ANOVA; $F_{1,6} = 0.7$; $p >$
19 129 0.05). A depth profile of chlorophyll was measured during a sunny day and there were no
20 130 differences between treatments or between depths and no significant interaction (Treatment:
21 131 Two-way ANOVA; $F_{1,12} = 0.8$; $p > 0.05$; depth: Two-way ANOVA; $F_{1,12} = 1.1$; $p > 0.05$;
22 132 treatment x depth interaction: Two-way ANOVA; $F_{1,12} = 1.0$; $p > 0.05$). Temperature varied
23 133 throughout the experiment from 9.5 - 27.1 °C and there were no differences between
24 134 treatments (Fig. 2; RM ANOVA; $F_{1,6} = 0.1$; $p > 0.05$). A depth profile of temperature was
25 135 measured during a sunny day and there were no differences between treatments but
26 136 approximately one degree Celsius lower temperature at the bottom compared with surface
27 137 water (Treatment: Two-way ANOVA; $F_{1,12} = 0.6$; $p > 0.05$; depth: Two-way ANOVA; $F_{1,12} =$
28 138 45.6; $p < 0.05$). There was no significant interaction between treatment and depth (Two-way
29 139 ANOVA; $F_{1,12} = 2.3$; $p > 0.05$). Also oxygen did not differ between treatments and ranged
30 140 from 7.9 – 14.4 mg L^{-1} (Fig. 2; RM ANOVA; $F_{1,6} = 0.6$; $p > 0.05$). The phytoplankton
31 141 community composition was also monitored in surface waters three times throughout the
32 142 experimental period. The community was initially dominated by *Chlamydomonas* sp.,
33 143 *Scenedesmus* sp., *Rhodomonas* sp., *Fragillaria* sp., *Aphanothece* sp., and some
34 144 Ankistrodesmaceae. Eventually the diversity decreased, and *Scenedesmus* sp. and
35 145 *Chlamydomonas* sp. became dominant, constituting approximately 90% and 6.5% of the total
36 146 algal numbers, respectively. All other algal species constituted less than 1% of total algal

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3 147 abundance throughout the experiment. Regarding the abundances of all algal species present,
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5 148 there were no differences between treatments (two-way MANOVA, $F_{6,13} = 2.4$, $p > 0.05$).
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7 149 Depth profiles for phytoplankton species composition are not available but chlorophyll
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9 150 measurements indicate that there were no differences in algal biomass between depths and
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11 151 treatments (see above). Samples for nutrients were collected at the end of the experiment and
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13 152 analyzed according to standard methods (Tyler and Olsson 2001; ICP MS ELAN-600). Mean
14
15 153 total phosphorous concentrations ($\pm 1SD$) were 57.8 (± 51.6) and 44.3 (± 30.4) in the V and
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17 154 UV treatments, respectively and there were no differences between treatments ($t = 0.396$, $p >$
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19 155 0.05)
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21 156 Experimental treatments started on 10-May and then zooplankton population dynamics and
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23 157 vertical migration were monitored approximately once a month, between 18-May and 5-Sept-
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25 158 2006, by collecting samples at noon from the surface (depth 0.1 m) and the bottom (depth 0.9
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27 159 m) of the cylinders. A four-litre sample was taken from each level through tubing in the
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29 160 cylinder walls. The animals were retrieved on a 50 μm net and preserved with Lugol's
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31 161 solution. All zooplankton in the entire sample, i.e. not a subsample, were counted using a
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33 162 Petri dish with eight sub-chambers, each 26 \times 33 mm (Nalge Nunc, USA), and a dissecting
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35 163 microscope. Each sampling also included counting of egg- and ephippia-carrying *Daphnia*
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37 164 (i.e. normal eggs and resting eggs).
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39 165 Analysis of population dynamics, community composition, and reproduction was made by
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41 166 means of repeated measures ANOVA (RM ANOVA) on log- or angular-transformed data.
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43 167 Zooplankton densities were calculated from mean values of the 0.1 and 0.9 m samplings, and
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45 168 the total filtered volume from each sampling represents approximately 7.5% of the total water
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47 169 volume in the mesocosms. Vertical position, expressed as surface-to-bottom ratio, was
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49 170 assessed by regression analysis, plotted against the different UV threats (see threat estimate
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51 171 above, i.e. $I_{0.1}$). Note that each point in the regression analysis represents one mesocosm at
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53 172 one sampling date. Statistical analysis was performed in SPSS 15.0.
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174 **Results**

175 **Community response and population dynamics**

176 The number of zooplankton species and the proportions of the different species was rather
177 similar when comparing the two treatments throughout the experiment (V and UV; Fig. 3).
178 The most common taxa by numbers were *Chydorus* sp., *Daphnia* sp., calanoid copepods and
179 copepod nauplii, whereas *Eurycerus* sp., cyclopoid copepods and rotifers occurred in lower
180 abundances (Table 1). Community differences between treatments were small, although there
181 was a significant negative effect of UV on the proportion of *Daphnia* sp. and copepod nauplii
182 (RM ANOVA; $p \leq 0.05$; Table 2). The proportion of *Daphnia* of the total zooplankton
183 population was higher in UV treatments in May but then decreased and was generally lower
184 in the UV treatment than in the V treatment (Table 2; Fig. 3). Copepod nauplii relative
185 abundance was generally lower in the UV treatment than in the V treatment throughout the
186 entire experiment (Fig. 3). None of the zooplankton taxa showed any response in absolute
187 density to the treatments (i.e. Number L⁻¹; RM ANOVA; $p > 0.05$; Table 2). *Daphnia* started
188 (in May) at very low abundances (< 1 L⁻¹), but already in June it had reached between 10 and
189 30 individuals L⁻¹ (Fig. 4). There was no overall treatment effect ($p > 0.05$; Table 2), but a
190 significant treatment by time interaction illustrated by higher numbers of *Daphnia* early in the
191 season in the UV than in the V treatment. This was followed by a shift to higher absolute
192 densities in the V treatment during September ($p < 0.05$; Table 2; Fig. 4). *Chydorus* increased
193 in abundance over time but did not display any differences in abundance between treatments
194 over time (Fig. 4).

195 **Behavioural responses to UV**

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

201 **Reproductive responses**

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

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3 208 radiation, compared to absence of UV (Fig. 6; means 8.7 and 5.0%, respectively; $F_{1,6} = 8.6$; p
4 < 0.05; RM ANOVA).
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8 211 **Discussion**

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10 212 In open-water habitats of lakes and oceans, there are considerable temporal and spatial
11 213 variations in mortality risk; organisms, such as zooplankton, use behavioural and
12 214 morphological traits to meet these challenging variations (Hansson et al., 2007a; Hylander et
13 215 al., 2009a, 2009b). Several factors, such as temperature (Loose and Dawidowicz, 1994;
14 216 Winder et al., 2003), pH, and food limitation (Gliwicz and Pijanowska, 1989; Winder et al.,
15 217 2003), but also ultraviolet radiation (UV), have been shown to affect zooplankton mortality
16 218 rate and behaviour (Tartarotti et al., 1999; Leech and Williamson, 2001; Williamson et al.,
17 219 2001; Hansson et al., 2007a). UV is known to affect accumulation of UV protective
18 220 compounds, behaviour and potentially also zooplankton community community (Alonso et
19 221 al., 2004; Marinone et al., 2006; Hylander et al., 2009a, 2009b). Even though we applied an
20 222 elevated UV level (both UVA and UVB) for several months in a shallow system (~1m) we
21 223 only saw moderate effects on the zooplankton community composition and population
22 224 dynamics. This indicates that the community is well adapted to handle changes in UV
23 225 radiation through their natural UV defences. Zooplankton have a number of different defence
24 226 mechanisms in response to UV radiation, including vertical migration, photoenzymatic repair
25 227 and accumulation of UV protective compounds (Hansson and Hylander, 2009b).

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28 228 The behavioural response (vertical migration) to increased UV radiation differed
29 229 considerably among taxa and *Daphnia* showed the strongest response; although showing a
30 230 less dramatic response, copepod nauplii, calanoid and cyclopoid copepods also spent more
31 231 time at the surface under low UV threat, compared to high UV. *Chydorus* and *Eurycerus*,
32 232 regardless of UV treatment, remained mainly at the bottom during daytime, as illustrated by
33 233 the almost constant low surface-to-bottom ratio. Species spending most of the time at the
34 234 bottom are decoupled from any UV threat; but they are also restricted to bottom waters during
35 235 daytime, which may be a competitive disadvantage (Loose and Dawidowicz, 1994).
36 236 Accordingly, from our study three different strategies can be identified regarding daytime
37 237 vertical distribution: strong response to the instantaneous UV-threat, illustrated by *Daphnia*; a
38 238 weak, albeit significant response, such as in copepods and rotifers; and finally, a stationary
39 239 position at depth as a refuge from UV radiation, such as by *Chydorus* and *Eurycerus*. Such
40 240 taxon-specific differences have previously been identified for several other zooplankton taxa
41 241 (Tartarotti et al., 1999; Boeing et al., 2004; Marinone et al., 2006; Obertegger et al., 2008).

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3 242 The strength of the behavioural response to UV has been attributed to the amount of
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5 243 photoprotective pigmentation, for example melanin and carotenoids, such that organisms with
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7 244 high amounts of pigments tend to have weaker behavioural responses compared to organisms
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9 245 with low amounts of pigments (Tollrian and Heibl, 2004; Hansson et al., 2007a; Obertegger et
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11 246 al., 2008; Hylander et al., 2009b). Melanin pigmentation in *Daphnia* from temperate regions
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13 247 is generally low (Hebert and Emery, 1990; Hansson et al., 2007a), which may explain the
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15 248 strong migratory response to UV threat that we observed in this study. Also differences in
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17 249 temperature and food availability may change vertical migration patterns (Orcutt and Porter,
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19 250 1983; Johnsen and Jakobsen, 1987). In this study, there were no differences between
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21 251 treatments in surface chlorophyll a and temperature. The temperature was slightly lower deep
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23 252 down in the mesocoms but there were no significant interactions between depth and
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25 253 treatment. Furthermore, vertical position of different algal species was not studied but algal
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27 254 biomass (chlorophyll a) was evenly distributed throughout the water column and there were
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29 255 no effects of depth or treatment x depth interaction effects. Overall, this indicates that UV was
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31 256 the most important factor in explaining the vertical position of the animals.

32 257 *Daphnia* reproduction was altered by the treatments. Effects on the proportion of egg-
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34 258 carrying females were minor but the production of ephippia (resting eggs) increased upon UV
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36 259 exposure. This may reflect one of the costs associated with UV exposure in natural
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38 260 populations. Ephippia induction has previously been shown to be triggered by both abiotic
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40 261 and biotic factors, for example temperature, photoperiod, and food level (reviewed in
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42 262 Gyllström and Hansson, 2004). Diapause is generally assumed to arise as a way of escaping
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44 263 periods of harsh environmental conditions, but, to our knowledge, UV has not previously
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46 264 been shown to be an induction agent. Since UV varies temporally over hours, days, and
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48 265 seasons, it is likely that ephippia production would be beneficial as a way of escaping periods
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50 266 of intense radiation. In nature, *Daphnia* populations in rock pools with high solar exposure
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52 267 have been observed to have high occurrence of ephippia, but the phenomenon has not been
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54 268 quantified systematically (D.O. Hessen, Oslo, personal communication).

55 269 Long-term population dynamics were relatively similar between treatments for all taxa
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57 270 investigated; none showed any overall treatment response to increased UV radiation levels
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59 271 compared to non-UV treatments. Also the community composition was rather stable with the
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272 same number of species occurring in approximately the same proportions when comparing the
273 UV and non-UV treatments. However, after several months small differences occurred with
274 slightly lower relative abundance of copepod nauplii and *Daphnia* in the UV treatment,
275 indicating that these two groups were negatively affected by the radiation. Others have

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3 276 suggested that zooplankton biodiversity and community composition could be structured by
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5 277 the UV environment (Williamson et al., 2001). It can be difficult, however, to single out the
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7 278 UV effect because of covariance with other factors such as temperature and food shortage
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9 279 (*Marinone et al., 2006*). *Daphnia* has previously been suggested to be more vulnerable to UV
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11 280 compared to copepods and rotifers (Leech and Williamson, 2000; Williamson et al., 2001;
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13 281 Leech et al., 2005). Our long-term study supports the vulnerability of *Daphnia* which
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15 282 occurred in lower proportions in the UV treatment and also induced more ephippia. UV
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17 283 effects were, however, of minor importance since the overall community composition was
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19 284 very similar between the UV and the non-UV treatment. This is illustrated by the marked
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21 285 similarity in intraspecific population dynamics when comparing treatments with and without
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23 286 UV radiation (Fig. 4). Finally, there was a significant treatment to time effect for *Daphnia*
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25 287 population dynamics. This may be due to high initial reproduction in the UV treatment as a
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27 288 stress response. However, later in the season ephippia production increased and the UV
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29 289 treatment population decreased more rapidly compared with the V treatment.

28 290 In terms of UV attenuation depth, the results are comparable with natural situations
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30 291 since the experimental depth penetration is in the same range as UV penetration in lakes from
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32 292 the same area (around 0.4 m 1% attenuation depth at 320 nm) (Hansson, 2004). UV
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34 293 attenuation due to chlorophyll may have been present even though seston, in contrast to DOC,
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36 294 generally contributes much less to UV attenuation (Scully and Lean, 1994). It is difficult to
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38 295 assess if the elevated experimental UV level is realistic compared to natural changes. Long-
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40 296 term time series of UV radiation reaching earth are scarce, but calculations indicate that there
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42 297 has been a 6 to 14% increase in UV irradiance at mid and high latitudes between 1980 and
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44 298 2002 (UNEP/WMO, 2002). Also potential differences in spectral composition of UV
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46 299 produced by lamps and natural radiation make it difficult to compare the applied UV
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48 300 exposure to natural conditions. Even though the levels used in this experiment may have been
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50 301 higher than the observed natural change and that we applied them for several months, we
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52 302 observed only moderate zooplankton community effects. This leads to the conclusion that
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54 303 zooplankton communities, at least at the latitudes studied, are well adapted to UV changes,
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56 304 due to efficient defences like vertical migration and UV protective pigmentation (Tartarotti et
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58 305 al., 2001; Moeller et al., 2005; Persaud et al., 2007; Hansson and Hylander, 2009a; Hylander
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60 306 et al., 2009a, 2009b). Even if we applied elevated levels of UV compared with ambient levels,
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308 307 attenuation in the water was relatively high. In systems where UV penetrates to deeper depths
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308 308 it cannot be ruled out that UV may be a stronger structuring force for the zooplankton
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309 309 community, as suggested by Williamson et al. (Williamson et al., 2001) and Marinone et al.

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3 310 (Marinone et al., 2006). However, our study underlines the importance of allowing the
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5 311 organisms to use their inducible defences, in this case vertical migration, in order to assess the
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7 312 true net effect of UV on the community composition.

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9 313 During recent years much research has focused on how predicted climate change, including
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11 314 alterations in temperature, rainfall (Suttle et al., 2007), as well as UV radiation (Williamson,
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13 315 1995), may affect natural ecosystem processes. In our investigation of UV effects on
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15 316 freshwater zooplankton and responses in behaviour and community composition, we conclude
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17 317 that one component of global change (UV radiation) may to a large extent be overruled and
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19 318 buffered against by biological processes such as vertical migration. Even though we applied
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21 319 elevated levels of UV throughout a summer we only saw moderate community changes.
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23 320 *Daphnia* and copepod larvae were relatively less common in the UV treatment but differences
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25 321 were small. Both relative and absolute abundances for all other species were stable between
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27 322 treatments, which indicates that organisms that are able to use efficient UV defences (like
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29 323 vertical migration) will withstand elevated UV levels. Instead, alterations in other climatic
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31 324 variables and interspecific competition may have stronger effects on community dynamics.

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36
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38
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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 ($^{\circ}C$) 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} ; $\pm 1SD$) 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., *Eurycerus* 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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3 482 Treatments are visible light (V) or the entire solar spectrum (UV). Note that each point in the
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5 483 figure represents data from one mesocom at one sampling. The variability in UV threat that is
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7 484 seen within treatments is due to changes in ambient radiation and also changing absorption
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9 485 coefficients over time.

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11 487 Fig. 6.. Mean proportion (% , $\pm 1SD$) egg- (A) and ehippia- (B) carrying *Daphnia* during the
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14 488 experiment. Treatments are visible light (V) or the entire solar spectrum (UV). Ehippia and
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16 489 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	<i>Eurycercus</i>	<i>Chydorus</i>	Cyclopoids	Rotifers	<i>Daphnia</i>	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	<i>Eurycercus</i>	<i>Chydorus</i>	Cyclopoids	Rotifers	<i>Daphnia</i>	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)

Table 2.

A) Community response

Zooplankton	Treatment			Time			Time*treatment	
	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
<i>Chydorus</i>	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
<i>Daphnia</i>	7.2	0.037	1,6	1.0	0.448	4,24	4.3	0.009
<i>Eurycerus</i>	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

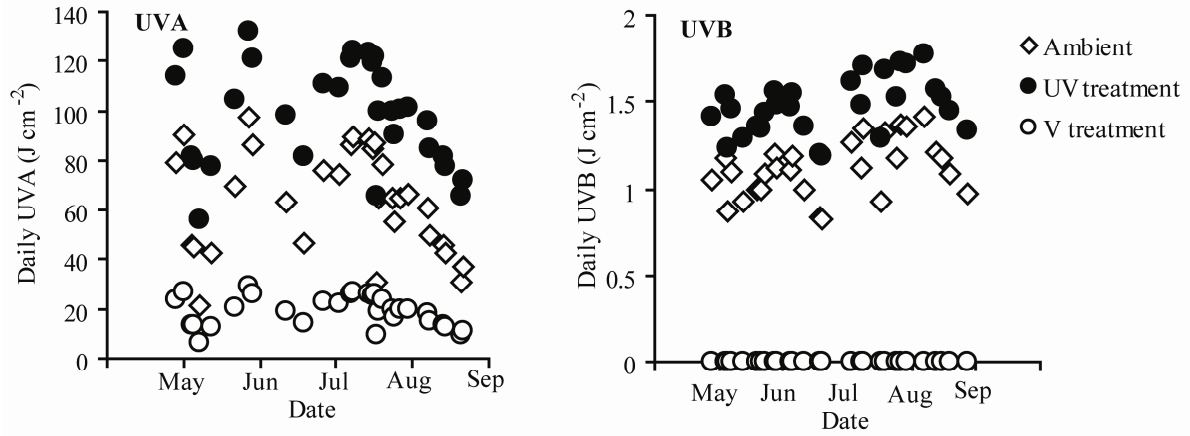
Zooplankton	Treatment			Time			Time*treatment	
	F	p	df	F	p	df	F	p
Calanoid	3.1	0.130	1,6	3.3	0.114	1,6	0.2	0.719
<i>Chydorus</i>	<0.1	0.902	1,6	39.6	<0.001	1,9	1.8	0.219
Cyclopoid	0.2	0.695	1,6	5.4	0.003	4,24	1.1	0.369
<i>Daphnia</i>	<0.1	0.920	1,6	15.5	<0.001	4,24	2.9	0.041
<i>Eurycerus</i>	<0.1	0.821	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

Table 3.**Depth distribution**

Zooplankton	Beta	r²	df	p
Calanoid	-0.533	0.284	1,25	0.004
<i>Chydorus</i>	-0.254	0.065	1,35	0.129
Cyclopoid	-0.347	0.121	1,38	0.028
<i>Daphnia</i>	-0.728	0.53	1,38	<0.001
<i>Eurycercus</i>	-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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3 Fig. 1.

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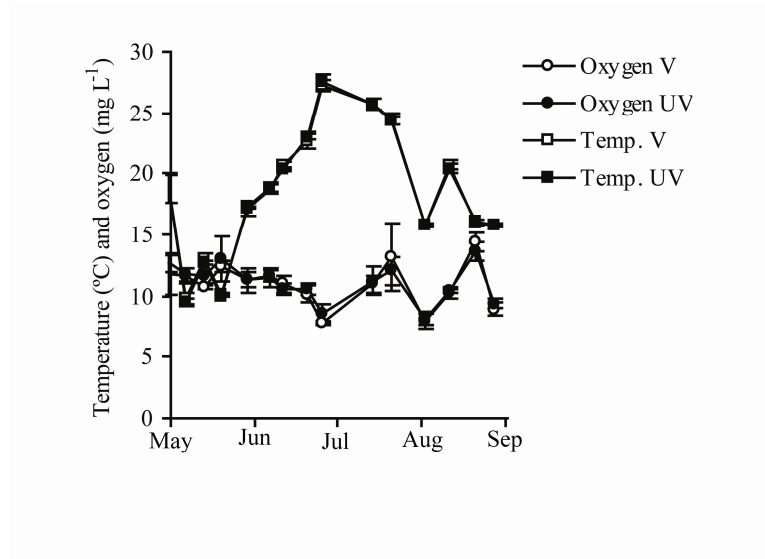
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Fig. 2.

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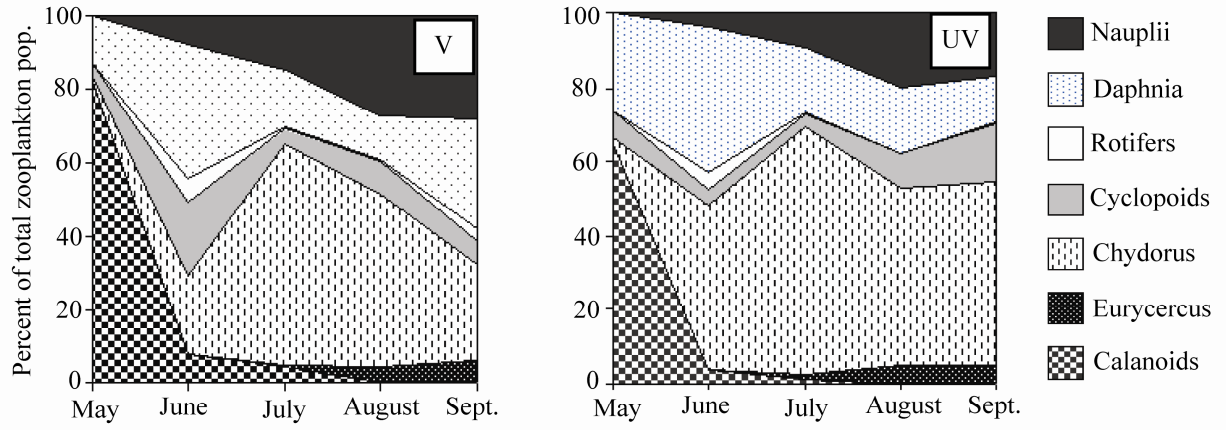


Fig. 3.

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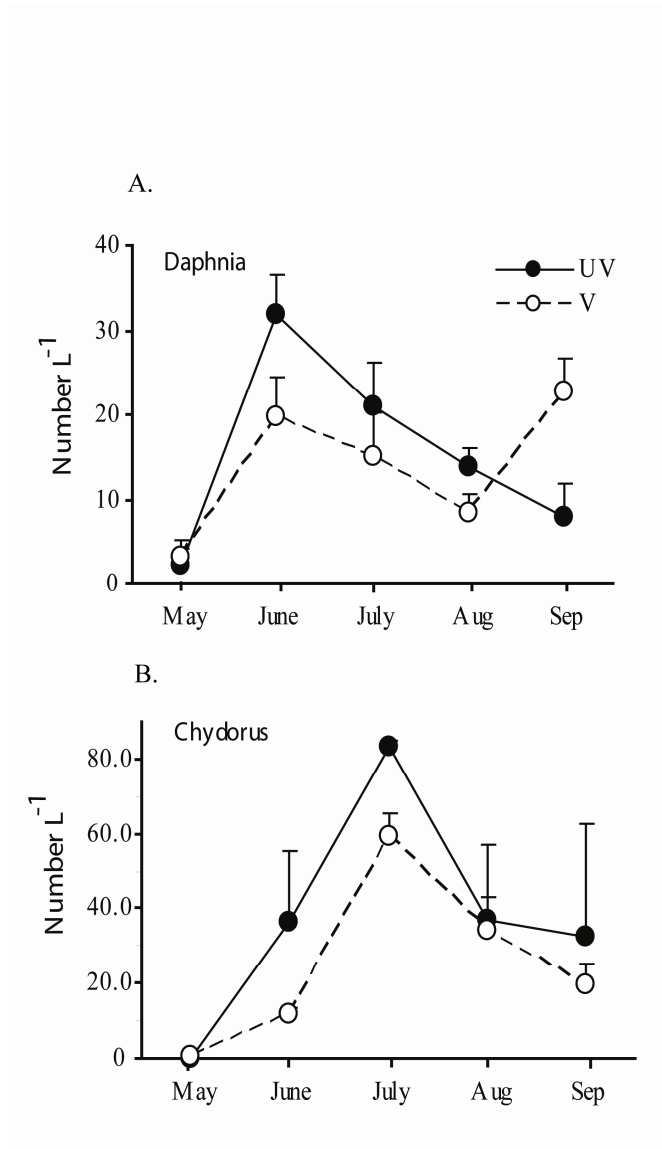


Fig. 4

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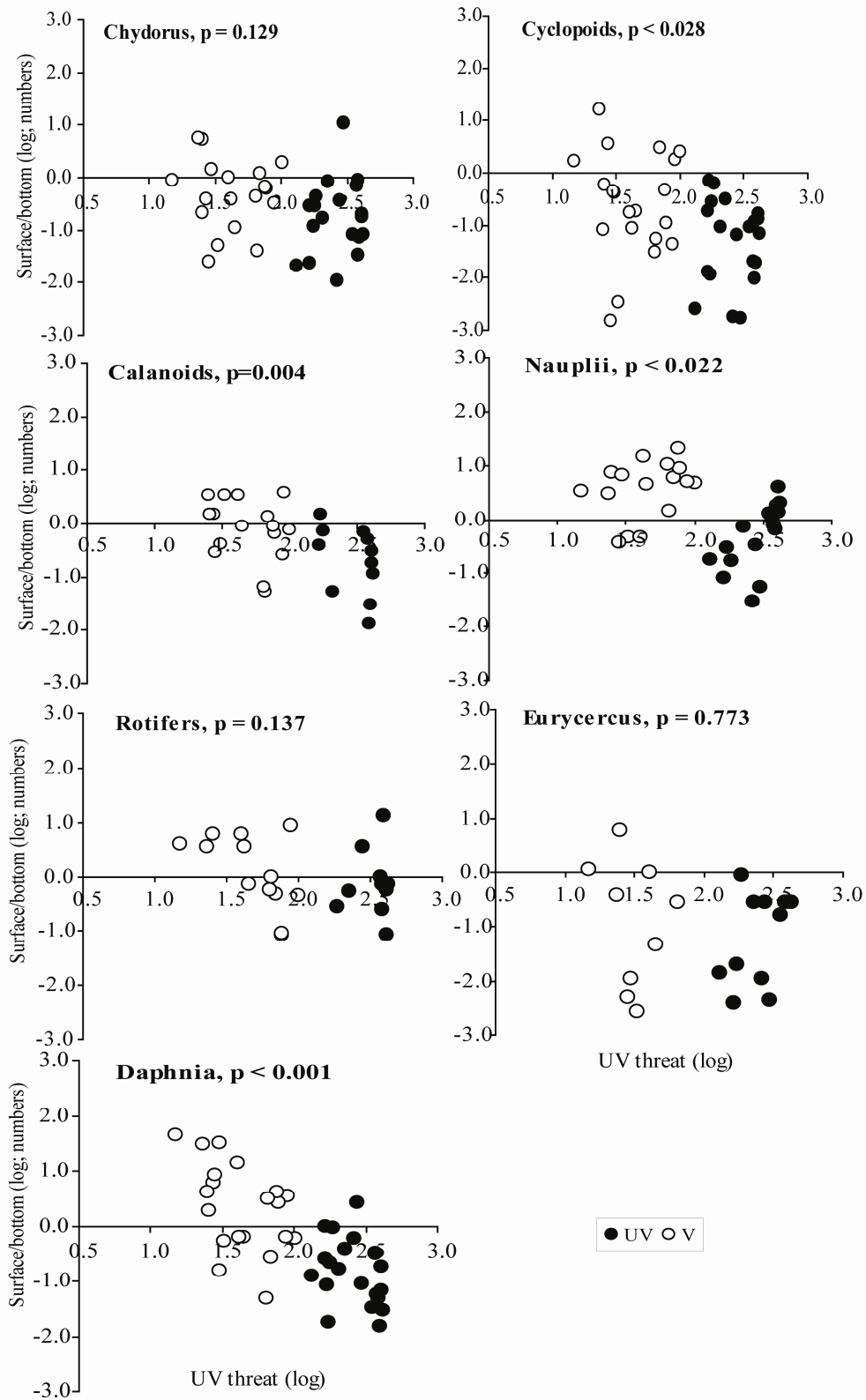


Fig. 5.

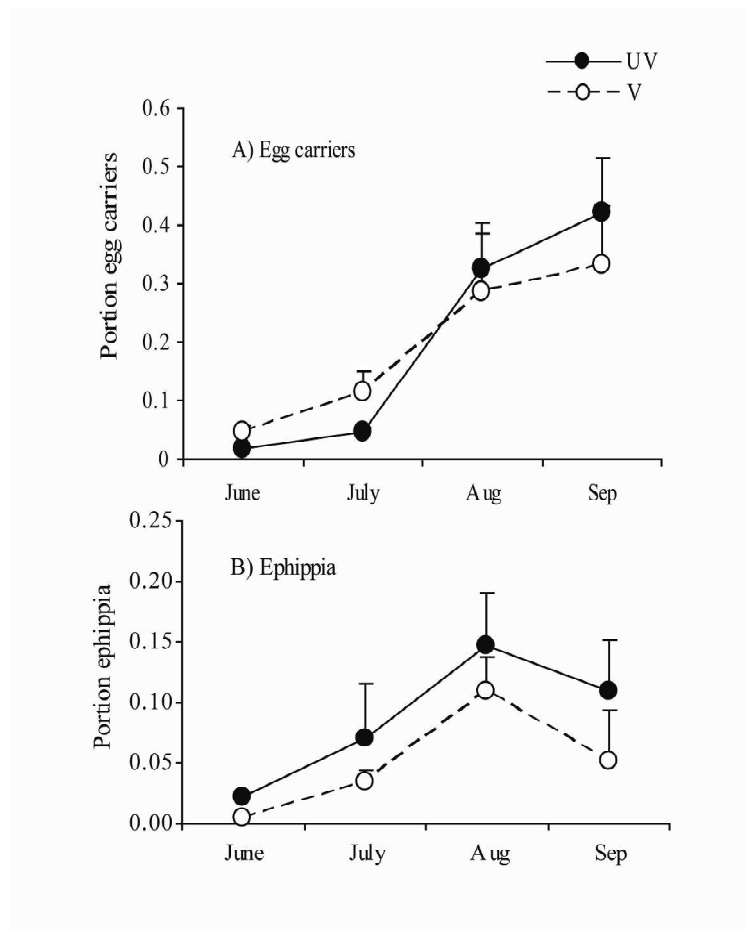


Fig. 6.