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Damaging UV radiation and invertebrate predation: conflicting selective pressures for zooplankton vertical distribution in the water column of low DOC lakes

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Abstract In nature most organisms have to manage conflicting demands of food gathering, predator avoidance, and finding a favorable abiotic environment (oxygen, temperature, etc.) in order to maximize their fitness. In the vertical water column of lakes with high solar ultraviolet radiation (UV) and invertebrate predators, zooplankton face two particularly strong and conflicting selective pressures. During daylight hours invertebrate predators often induce an upward vertical migration of zooplankton prey while potentially damaging UV forces a downward migration. We used 2.2 m long columns suspended vertically in a lake to conduct 2×2 factorial experiments to examine patterns of depth selection behavior by zooplankton in the presence and absence of both the invertebrate predator *Chaoborus* and UV. We hypothesized that *Chaoborus* and UV both affect the distribution of zooplankton and a combination of both factors would lead to a narrowing of depth distribution. We found that when *Chaoborus* were present zooplankton tended to be distributed at shallower depths in the columns, while in the presence of UV they exhibited a deeper distribution. *Chaoborus* themselves were always found near the bottom of the columns regardless of the UV treatment. Simultaneous exposure to predators and UV resulted in a peak of zooplankton (especially *Daphnia*

catawba) distribution at intermediate depths. In a significant number of cases, depth range was narrowed in response to *Chaoborus*, UV, or both.

Keywords Ultraviolet · *Chaoborus* · Vertical distribution · Vertical migration · Predator-prey overlap

Introduction

The distribution of organisms is limited by a number of biotic constraints (e.g., food availability, predator occurrence, competition) and abiotic tolerances (e.g., ecosystem size, oxygen, temperature, pH, minerals, nutrients). These elements influence food web complexity and food chain length (Resh and Barnby 1987; Post 2002). Rapid changes caused by human activities may further limit the range of certain species due to habitat destruction (Lin 2003), import of new invasive species (Carruthers 2003), eutrophication (Bakker and Berendse 1999), acidification (Corfield 2000; Driscoll et al. 2003), and climate change (Woodward and Rochefort 1991; Williams et al. 2002; Wichmann et al. 2003). In the recent past, the effects of climate change on ecosystems have been the focus of intense research. Climate change is expected to alter precipitation and increase temperature, atmospheric CO₂ concentrations, and ultra-violet radiation (UVR) (Chen et al. 2003). Those alterations resulting from climate changes may pose a threat to terrestrial (Kennedy 1995; Caldwell et al. 2003; Jones et al. 2003) as well as aquatic ecosystems (Band et al. 1996; Rouse et al. 1997; Day and Neale 2002). UVR that reaches the earth surface consists of UV-A (320–400 nm) and UV-B (280–320 nm), both of which can be potentially damaging to aquatic organisms. UV wavelengths of approximately 320 nm are the most biologically damaging to aquatic zooplankton *Daphnia* when one takes into account both the number of photons in incident sunlight and the lethal damage per photon (Williamson et al. 2001a).

A three-dimensional water column makes a complex and heterogeneous environment in which organisms have

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to balance many conflicting selective pressures. For example, while temperature and oxygen conditions are typically favorable at shallower depths for zooplankton (Kerfoot 1985), visual predation by fish in the surface waters can force diel vertical migration, which is the migration of zooplankton down into the colder, darker depths in the water column during daylight (Zaret and Suffern 1976; Stich and Lampert 1981). The selective pressure to migrate to deeper waters in the presence of visual predators is generally greatest on larger zooplankton species such as invertebrate predators like *Chaoborus*, which are consequently often found in deeper water layers during daytime (Luecke 1986; Dawidowicz et al. 1990; Tjossem 1990; Voss and Mumm 1999). *Chaoborus* (Diptera) spend most of their life-cycle as larvae in lakes and ponds. They go through four larval instar stages. The first two instars feed mainly on smaller zooplankton like rotifers, while the latter two instars are voracious predators on larger zooplankton crustaceans like copepods and cladocerans. The ingestible size spectrum is dependent on mouth gape size, which increases from smaller species like *Chaoborus punctipennis* and *C. flavicans* to *C. trivittatus* and *C. americanus* (Saether 1970). They are tactile ambush predators and can drastically alter zooplankton composition and abundance by intense predation pressure (Dodson 1972; Kajak and Rybak 1979; Yan et al. 1991; Benndorf et al. 2000; Ramcharan et al. 2001). Recent studies estimate that more than 90% of northern temperate lakes are inhabited by *Chaoborus* (Wissel 2001). Several studies have documented the ability of many zooplankton species to use a chemical (kairomone) exuded by *Chaoborus* spp. predators as a cue for the presence of this invertebrate predator, causing them to undergo an upward migration during daytime (Ohman et al. 1983; Dodson 1988; Neill 1990; Ramcharan et al. 1992; Nesbitt et al. 1996; De Meester et al. 1999).

An upward migration at day and downward migration at night was termed 'reverse vertical migration', in contrast to diel vertical migration. Reverse vertical migration results in a shallower vertical distribution of organisms during daytime in natural environments (Bayly 1986; Ohman 1990). Zooplankton exhibit upward migrations in response to *Chaoborus* mainly in fishless lakes, or lakes with a low abundance of fish (Bayly 1986). However, zooplankton may also exhibit upward migrations in lakes with high fish abundance on a seasonal basis. Stibor and Lampert (2000) show such a seasonal response to fish and *Chaoborus* kairomone for a life history response in *Daphnia*.

Recently, in situ experimental manipulations of natural solar ultraviolet radiation have demonstrated that zooplankton migrate to deeper depths in lakes in response to UV exposure (Leech and Williamson 2001; Rhode et al. 2001). This presents a set of conflicting selective pressures for zooplankton prey of *Chaoborus* in lakes with high levels of UV. While zooplankton in general exhibit a downward migration in the presence of high UV, *Chaoborus* predators trigger an upward migration during daytime. This raises the question of whether zooplankton

will migrate upward or downward in the presence of *Chaoborus* and UV. Does one response overwhelm or dominate the other? Or is the vertical habitat range over which the zooplankton can survive likely to be constricted due to these conflicting selective pressures?

Here we present the results of a set of controlled field experiments that examine how zooplankton cope with these opposing selective pressure of abiotic (UV) and biotic stressors (invertebrate predator—*Chaoborus*), and we make predictions on how projected increases of UV related to climate change might affect lake communities. The experiments involved suspending 2.2 m long UV-shielding and UV-transparent columns in the upper metalimnion of a high UV lake with the addition or exclusion of *Chaoborus* predators in order to examine the vertical distribution response of zooplankton. We expect that zooplankton respond accordingly to the two selective pressures by migrating down in response to UV and up in response to *Chaoborus*, which should lead to a narrowing in depth range at intermediate layers in the simultaneous presence of UV and *Chaoborus*. We then discuss where in nature we would expect the co-occurrence of high UVR and high abundance of *Chaoborus*, and their implications for zooplankton communities, especially in regard to climate change.

Materials and methods

Study site

Experiments were conducted in Lake Giles, located on the Pocono Plateau of northeastern Pennsylvania (41°23'N, 75°06'W). Lake Giles is an oligotrophic, acidic (pH=5.5), high UV system with a dissolved organic carbon concentration of about 1.0 mg l⁻¹ and a mean summer Secchi depth of 11–15 m. The lake is thermally stratified from late April through late October and remains well oxygenated at all depths throughout the year. The zooplankton community is dominated by *Leptodiatomus minutus*, *Cyclops scutifer*, and *Daphnia catawba*. Also present are *Aglaodiaptomus spatulocrenatus* (formerly *Diaptomus spatulocrenatus*), *Diaphanosoma* spp., *Polyphemus* spp. and a few rotifers in small numbers. The dominant *Chaoborus* species is *C. punctipennis* although *C. flavicans* is also present. Due to its oligotrophic and acidic status, Lake Giles has a restricted species list, with acid tolerant species like *D. catawba* dominating.

Light and temperature measurements

Temperature (Fig. 1a) and dissolved oxygen were measured using a YSI Model 57 Oxygen meter. Underwater light profiles of UV and PAR were taken with a Biospherical Profiling Ultraviolet Radiometer (PUV) 500 (Biospherical Instruments, San Diego, Ca., USA) on 18 June 2001. Diffuse attenuation coefficients (K_d , m⁻¹) were obtained from the slope of the linear regression of the natural logarithm of irradiance versus depth for each wavelength. The measured attenuation depth (depth to which 1% of surface irradiance penetrates) for 320 nm UV was 6.41 m in Lake Giles, with 17% of the surface UV at 320 nm penetrating to a depth of 2 m (top of the columns) and 5% down to 4 m (Fig. 1b).

Weather conditions on all days of the experiment were sunny and clear with an air temperature of 18°C and a surface water temperature of 21.5°C.

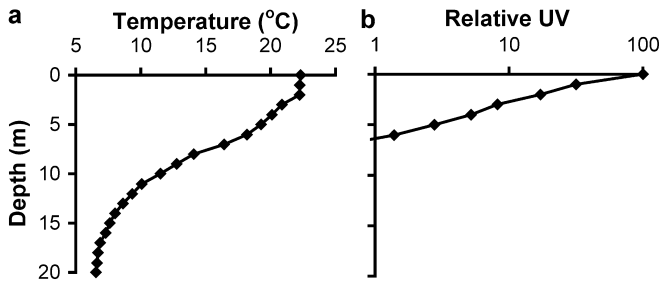


Fig. 1 a Temperature and b UV (at 320 nm as % of surface irradiance) profiles for Lake Giles on 18 June 2001

Experimental design

Acrylic columns (8 cm × 8 cm × 2.2 m long, total volume = 14 l) were constructed using UV-transparent (OP-4, 50% transmittance at 272 nm, CYRO Industries) and UV-blocking (OP-2, 50% transmittance at 410 nm, CYRO Industries) plastics. Columns consisted of 10 cm long sections at the top and bottom, and four 50 cm long sections in the middle. (Longer columns proved to be very difficult to manage in the field.) Each section was separated by a partition with a 3 cm hole in the center through which zooplankton could migrate freely. Directly below each partition was a hinged “trap door”, which hung open when the columns were suspended vertically. Each of the five trapdoors was attached to a single piece of durable Kevlar string, which when pulled, closed the doors simultaneously. A 2 cm diameter hole was located at the bottom of each section for removal of water and plankton. Holes were fitted with silicone stoppers during the experiment.

Preliminary experiments demonstrated that many zooplankton species swim downward regardless of light treatment at the surface. The strongest reaction to UVR was found when the columns were suspended in the upper metalimnion (between 2.0 and 4.2 m) in Lake Giles (Fig. 1a). We chose this depth for our subsequent experiments. In order to avoid shocking the animals by collecting them at darker depths during the day and bringing them to the surface, the experiments were set up at night and taken down in the late morning or early afternoon.

For the first experiment, *Chaoborus punctipennis* (78%) and *C. flavicans* (22%) were collected from a nearby lake (Lacawac) just before midnight on 12 June 2001 with a 2 mm mesh net towed from 10 m to the surface. *Chaoborus* were collected from Lake Lacawac because the abundance of *Chaoborus* was low in Lake Giles at the time of this experiment. The *Chaoborus* were kept in Lake Giles water near lake temperature in an incubator in the laboratory until the set-up of the experiment. The acrylic columns were filled with unfiltered epilimnion water by submerging them into the surface waters and suspended between 2.0 and 4.2 m in Lake Giles at 2200 hours EST on 13 June 2001. As the natural epilimnetic zooplankton densities at that time were high no additional zooplankton were added to the columns (Table 1). The experiment was set up in a 2×2 factorial design, with 6 UV-transparent columns and 6 UV-blocking columns. Thirty-five *Chaoborus* were introduced into the center (bottom of the third section) of each of six columns (three UV-transparent and three UV-blocking). These +UV and -UV columns were filled alternately to avoid sample bias. Once filled, the columns were attached to a floating rack and vertically suspended in the upper metalimnion of Lake Giles. At 1045 hours EST the next day, the trap doors were shut, and the contents of each section were emptied into pre-labeled sample cups and preserved in a 4% sucrose formaldehyde solution.

The second experiment began on 18 June 2001 at 1730 hours EST and ended on 19 June 2001 at 1305 hours EST. *C. punctipennis* were collected on 17 June 2001 near midnight from Lake Giles with the same methods as in the first experiment. *C. punctipennis* was the only species occurring at that time. Columns were filled with unfiltered epilimnion water and zooplankton were collected at 1945 hours EST with five tows using a 363 μm net towed from 5 m to the surface. The experimental set up was identical to that

Table 1 Mean ±1 SE zooplankton densities per liter in the experiments

	Experiment 1	Experiment 2
<i>D. catawba</i>	56.99±2.28	26.18±2.46
<i>Diaphanosoma</i>	4.94±0.51	1.30±0.21
<i>L. minutus</i>	25±1.08	11.23±0.89
<i>A. spatulocrenatus</i>	1.16±0.16	1.01±0.11
Copepodids	23.08±0.68	7.09±1.04
Nauplii	6.88±0.59	4.91±0.68
<i>Polyphemus</i>	7.42±3.35	0±0
<i>Chaoborus</i> ^a	2.41±0.07	1.99±0.07

^aDensities only for + *Chaoborus* treatments

described above. Zooplankton were introduced into the center section of each column and thirty *C. punctipennis* were added through this same section to half of the columns (three UV-transparent and three UV-blocking) (see Table 1 for zooplankton densities). Animals were allowed to migrate freely throughout the columns for approximately 15.5 h. Take down of the experiment started at noon the following day.

The total number of individuals of each species in each section of the columns was counted under a dissecting microscope in the laboratory.

Statistical methods

We tested the null hypothesis that there would be no difference in the vertical distribution patterns, mean depth or depth range among species in response to UVR, *Chaoborus*, or both. Statistical analysis was conducted with STATISTICA (StatSoft 2003). A Kolmogorov-Smirnov test (K-S test) was performed to detect differences in vertical distribution patterns of zooplankton taxa, followed by a Levene's test to identify differences in depth range (variance). Although violating the assumptions of normal distribution and homogeneous variances, we used a parametric approach to test for treatment effects on mean depth. A non-parametric test would have again combined the data from the columns for each treatment and viewed each individual as a replicate creating potential problems with pseudo-replication while a parametric approach maintained the experimental design. We feel that a combination of non-parametric (K-S and Levene's test) and parametric statistics was most appropriate to counteract the shortfalls of both methods. The mean depth of each species or taxonomic group in each column was determined by multiplying the number of individuals in each section of a column by the average depth of that section. These values were then summed and divided by the total number of individuals in the column. A multivariate analysis of variance (MANOVA) was performed with mean depths of the various zooplankton taxa as response variable and UV (absence/presence) and *Chaoborus* (absence/presence) as explanatory variables.

We discovered later that one column had been constructed with the wrong plastic on one side (UV transparent instead of UV blocking). Data from that column were excluded from the analysis, resulting in an unbalanced design.

Results

Daphnia catawba and *Leptodiptomus minutus* were the only species that showed significant differences in vertical distribution patterns in all treatments in both experiments ($P < 0.05$, K-S test) (Table 2). *D. catawba* responded

significantly to UV and *Chaoborus* in both experiments as reflected by differences in mean depths among treatments (Table 3, Fig. 2). In the absence of *Chaoborus*, UV induced *Daphnia* to be distributed 0.51 m deeper in both experiments. When *Chaoborus* were present, the response to UV was reduced to a depth difference of only 0.36 m and 0.29 m in the first and second experiments, respectively. *Chaoborus* forced *Daphnia* up 0.44 and

0.58 m in the +UV treatments and 0.29 and 0.51 m in the –UV treatments in the two experiments (Fig. 2). Despite a broader distribution in absence of UV and *Chaoborus*, the depth range was only significantly narrowed with *Chaoborus* as a predictive factor (Table 4, Fig. 3). In the presence of *Chaoborus*, the vertical distribution of *Daphnia* was skewed toward the top of the columns, while in the presence of *Chaoborus* and UV, *Daphnia* clustered at

Table 2 Vertical distribution of zooplankton taxa according to different treatments. +Ch indicates presence of *Chaoborus*, +UV presence of UV light, while –signs present absence of those factors. Letters that are listed in the same line mean that there is no significant difference among treatments, while letters in different lines indicate significant difference between values ($P < 0.05$, Kolmogorov-Smirnov test). The first half displays results from the first experiment, the second half from the second experiment

	+Ch / +UV	+Ch / –UV	–Ch / +UV	–Ch / –UV
<i>D. catawba</i>	A	B	C	D
<i>Diaphanosoma</i>	A	A B	B	C
<i>L. minutus</i>	A	B	C	D
<i>A. spatulocrenatus</i>	A	A	B	A
Copepodids	A	B	C	D
Nauplii	A	A	B	A
<i>Polyphemus</i>	A	B	A	B C
<i>Chaoborus</i>	A	A		
	+Ch / +UV	+Ch / –UV	–Ch / +UV	–Ch / –UV
<i>D. catawba</i>	A	B	C	D
<i>Diaphanosoma</i>	A B	A B	A	B
<i>L. minutus</i>	A	B	C	D
<i>A. spatulocrenatus</i>	A	A	B	A B
Copepodids	A	B	C	B
Nauplii	A	A	B	C
<i>Chaoborus</i>	A	A		

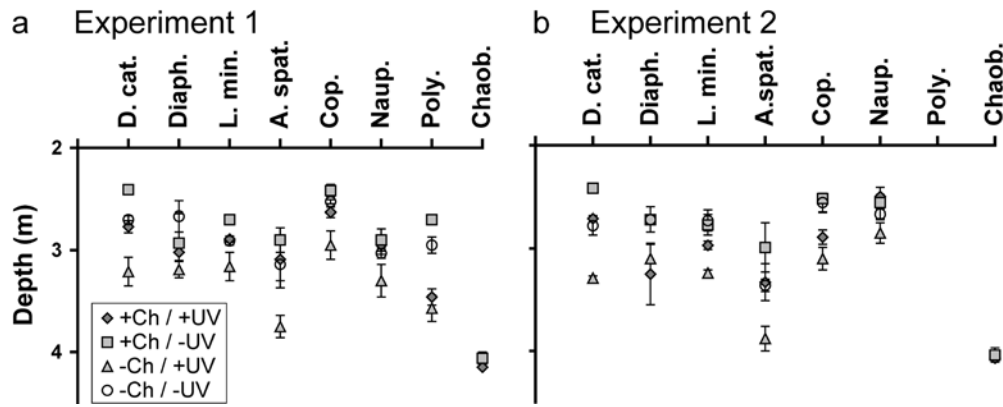


Fig. 2 Mean vertical distribution ± 1 SE for various zooplankton groups in experiment 1 (a) and experiment 2 (b). +Ch represents the treatments that included *Chaoborus*, -Ch the treatments that excluded *Chaoborus*, +UV are the columns that were transparent to ultraviolet radiation and -UV the columns that were UV blocking.

(*D. cat.* *Daphnia catawba*, *Diaph.* *Diaphanosoma*, *L. min.* *Leptodiaptomus minutus*, *A. Spat.* *Aglaodiaptomus spatulocrenatus*, *Cop.* Copepodids, *Naup.* Nauplii, *Poly.* *Polyphemus*; did not occur in experiment 2, *Chaob.* *Chaoborus*)

intermediate depths (Fig. 3). *Chaoborus* were located in the bottom of the columns regardless of UV treatment (Fig. 2). *L. minutus* also significantly changed mean depth in response to UV in both experiments and *Chaoborus* in the first experiment (Table 3, Fig. 2). The variance in vertical distribution (depth range) of *L. minutus* of the first experiment showed a similar pattern as that of *D. catawba* (Table 4).

Copepodids (90% *Leptodiaptomus minutus*) had different vertical distribution patterns than either species of the two adult calanoids (*Leptodiaptomus minutus* and *Aglaodiaptomus spatulocrenatus*) ($P < 0.05$, K-S test). Although they also showed a significant response to UV and

Chaoborus in at least one of the experiments (Table 3), they were distributed significantly shallower in general ($P < 0.05$, MANOVA, Fig. 2) and often exhibited less variance than adult copepods (Table 4). Thus copepodids were treated as a separate group. There were no other consistent differences among various life-history stages or sexes (adult females without eggs vs females with eggs, females vs males, adults vs juveniles) between experiments 1 and 2 except for *L. minutus*. Egg carrying female *L. minutus* showed a shallower distribution in all treatments than the females that did not carry eggs.

A. spatulocrenatus and nauplii usually showed a different vertical distribution pattern only in the -Ch / +UV treatment (Table 2). They tended to react significantly to UV only in the absence of *Chaoborus* and significantly to *Chaoborus* only in the presence of UV with a deeper or shallower mean vertical distribution, respectively (Fig. 2). Depth range was typically narrowed down in the +UV treatments (Table 4).

Table 3 P -values for mean depth of various zooplankton groups in response to the variables *Chaoborus* and UV light and their interaction as tested by MANOVA for first (top) and second (bottom) experiment; bold numbers indicate significant response ($P < 0.05$)

	<i>Chaoborus</i>	UV	<i>Chaoborus</i> \times UV
<i>D. catawba</i>	0.01	0.00	0.41
<i>Diaphanosoma</i>	0.77	0.07	0.17
<i>L. minutus</i>	0.02	0.03	0.75
<i>A. spatulocrenatus</i>	0.05	0.07	0.31
Copepodids	0.04	0.01	0.27
Nauplii	0.07	0.20	0.38
<i>Polyphemus</i>	0.10	0.00	0.50
<i>Chaoborus</i>		0.27	
	<i>Chaoborus</i>	UV	<i>Chaoborus</i> \times UV
<i>D. catawba</i>	0.00	0.00	0.10
<i>Diaphanosoma</i>	0.73	0.06	0.73
<i>L. minutus</i>	0.15	0.00	0.07
<i>A. spatulocrenatus</i>	0.02	0.02	0.59
Copepodids	0.23	0.00	0.37
Nauplii	0.03	0.52	0.21
<i>Chaoborus</i>		0.61	

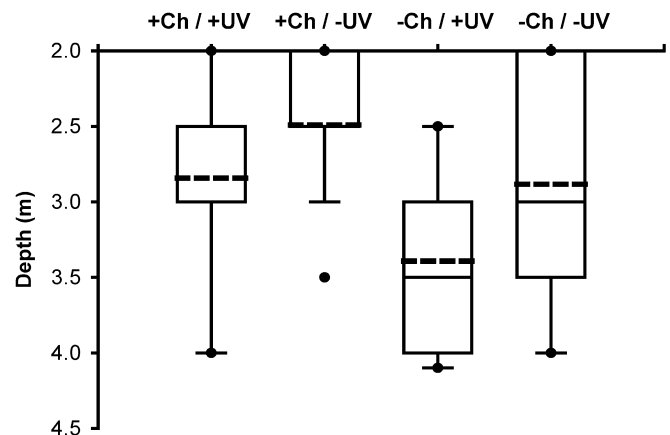


Fig. 3 Boxplots of vertical depth distribution of *Daphnia catawba* in experiment 2 in the presence (+) and absence (-) of *Chaoborus* (Ch) and UV. The solid line shows the median, the dashed line the mean. The box includes the 2nd and 3rd quartile, while the deviation bars represent the 10th and 90th percentiles and the dots the 5th and 95th percentiles

Table 4 Variance in depth distribution of zooplankton taxa according to different treatments. +Ch indicates presence of *Chaoborus*, +UV presence of UV light, while –signs present absence of those factors. Numbers that are listed in the same line mean that there is no significant difference among treatments, while numbers in different lines indicate significant difference between values ($P < 0.05$, Levene's test). Results from the first experiment appear in the first half of the table, results from the second experiment in the second half

	+Ch / +UV	+Ch / –UV	–Ch / +UV	–Ch / –UV
<i>D. catawba</i>	0.54	0.48	0.58	0.60
<i>Diaphanosoma</i>	0.53	0.62	0.61	0.57
<i>L. minutus</i>	0.49	0.59		0.57
<i>A. spatulocrenatus</i>	0.55		0.65	0.69
Copepodids	0.44	1.02	0.50	0.85
Nauplii	0.58	0.40	0.58	0.54
	0.58	0.53	0.54	
<i>Polyphemus</i>	0.44	0.44		0.64
		0.44	0.54	
<i>Chaoborus</i>	0.00			0.69
		0.09		
	+Ch / +UV	+Ch / –UV	–Ch / +UV	–Ch / –UV
<i>D. catawba</i>	0.49	0.36	0.60	0.63
<i>Diaphanosoma</i>	0.34	0.31	0.52	0.51
<i>L. minutus</i>	0.58	0.59	0.61	0.63
<i>A. spatulocrenatus</i>	0.45	0.62		0.72
	0.45		0.37	
Copepodids	0.56	0.55	0.63	0.58
Nauplii	0.49		0.64	0.53
		0.63		
		0.63		0.53
<i>Chaoborus</i>	0.06	0.11		

Consistent significant differences in the vertical distribution of *Diaphanosoma* were seen only between the –Ch / –UV and –Ch / +UV treatments (Table 2). Their mean depth response to UV approached significance in both experiments (Table 3) and depth range was most narrow in the +Ch / +UV treatment in the first experiment.

Polyphemus also showed significant differences in vertical distribution pattern among treatments (Table 2). They selected significantly deeper depths due to UV and narrowed their depth range in the presence of both UV and *Chaoborus* (Tables 3, 4, Fig. 2).

In general, the distribution of zooplankton taxa was shallowest in the treatment with *Chaoborus* that excluded UV (+Ch / –UV) (Fig. 2). Zooplankton stayed at intermediate depths in treatments that either included *Chaoborus* and UV or excluded both factors (+Ch / +UV, –Ch / –UV), while treatments with only UV (–Ch / +UV) usually drove zooplankton to the deepest depths. Significant responses to UV were always indicated by a downward movement and to *Chaoborus* by an upward

movement. There was a strong tendency for the depth variability to be highest in the treatments with neither *Chaoborus* nor UV (–Ch / –UV) (54% of all cases) and the vertical distribution to be narrowest in the treatments with *Chaoborus* and UV (+Ch / +UV) (47% of all cases) (Table 4). Sixty percent of the zooplankton taxa significantly narrowed their vertical distribution due to *Chaoborus* (46%), UV (43%), or both (11%).

Discussion

The results of this study confirm previous work demonstrating that damaging wavelengths of UV can cause a deeper depth distribution of zooplankton in lakes during the day (Leech and Williamson 2001; Williamson et al. 2001b) while the presence of *Chaoborus* can lead to a shallower distribution of zooplankton (Dodson 1988; Ramcharan et al. 1992; Nesbitt et al. 1996). While previous work on vertical migration in response to

Chaoborus and UV has focused primarily on *Daphnia*, we report the responses of a wide variety of zooplankton taxa to these two selective pressures. Of all the zooplankton taxa we looked at, the presence of UV photoreceptors has only been confirmed within the genus of *Daphnia* (Smith and Macagno 1990; reviewed by Leech and Johnsen 2003). To our knowledge, this is the first study to demonstrate a downward migration in response to UVR in *Diaphanosoma* and *Polyphemus*. Although no proof, this strongly suggests UV vision in those taxa. Remarkably, we detected a significant downward migration of several zooplankton taxa due to UVR even at a deeper depth. This shows that UVR by itself—without fish kairomone—might be able to force zooplankton down to depths of colder temperature, thus slowing egg development time (Bottrell 1975). In addition, this study is the first in situ test of how zooplankton respond to the simultaneous occurrence of these two conflicting selective pressures. We found that *Daphnia catawba* in particular exhibited a response that constrained it to a narrower portion of the vertical habitat in the experimental columns when both *Chaoborus* and UV were present compared to when *Chaoborus* and UV were excluded. In contrast, the various life history stages of the diaptomid copepods tended to be more variable in general. The predatory cladoceran *Polyphemus* responded only to UV, while the UV-effect on the herbivorous cladoceran *Diaphanosoma* was only detectable in the absence of *Chaoborus*. Lack of response might be explained by low mobility (nauplii) or insensitivity to the stressors. For example, *Polyphemus* might be fairly invulnerable to *Chaoborus* and, therefore, only reacts to UV, while the pigmented copepod *A. spatulocrenatus* only reacts to UV in the absence of *Chaoborus*. It may not be adaptive for *A. spatulocrenatus* to react to UV in the presence of a different environmental threat.

The experimental design that we used makes it difficult to clearly determine whether the shallower distribution of zooplankton in the presence of *Chaoborus* was due to behavioral avoidance, predatory consumption, or a combination of these two factors. In an attempt to address the potential importance of consumption versus behavioral avoidance in the two experiments reported here we estimated the predation rate of *Chaoborus* by subtracting the average number of prey in the columns with *Chaoborus* from the average number of prey in the columns without the invertebrate predator. There was no evidence of predation by *Chaoborus* on any of the zooplankton groups in the first experiment (ANOVA, $P > 0.25$). The same was true for most zooplankton groups in the second experiment except that there were fewer *Daphnia catawba* ($F_{1,7} = 23.85$, $P = 0.0018$), and *Diaphanosoma* sp. ($F_{1,7} = 8.24$, $P = 0.0240$) in the treatments that included *Chaoborus* (16 l^{-1} and 0.6 l^{-1} respectively) compared to the *Chaoborus*-free treatments (26 l^{-1} and 1.3 l^{-1} respectively). There was no difference in *Chaoborus* predation rates in the presence and absence of UV ($P > 0.5$). As noted in the results, *Diaphanosoma* and *Daphnia* both exhibited statistically significant distributional response to

Chaoborus, so for the responses that we observed in this study, consumption is likely to have contributed to their response. Whether the change in the distribution in response to *Chaoborus* is due to active avoidance or consumption, the net result is the same: a shallower distribution of the population. Where consumption is important, the consequences of these conflicting selective pressures are likely to be even more severe than would be the case with behavioral avoidance alone. In this environment the prey population is likely to decline, even to the point of elimination. The presence of similar vertical distribution responses of *Daphnia* in the two experiments suggests that vertical distribution responses are likely in nature whether or not consumption is a significant factor.

Another limitation of our study is that our experimental columns were only 2.2 m long and thus artificially constrained zooplankton to a narrower range of depths than are likely in deep lakes. In clear lakes with a high abundance of planktivorous fish the potentially conflicting selective pressures between invertebrate predators and UV are likely to be low or nonexistent because *Chaoborus* are likely to be forced to hide in the hypolimnion or sediment to avoid fish predation during daylight (Luecke 1986; Dawidowicz et al. 1990; Tjossem 1990; Voss and Mumm 1999). As kairomones degrade fairly quickly (Dodson 1988), zooplankton could migrate downward into the darker hypolimnion during the day to escape harmful UV and predation by visually foraging fish predators, and would have to protect themselves from *Chaoborus* only at night when the *Chaoborus* migrate out of the sediments. Similarly, lakes with a high dissolved organic carbon (DOC) concentration can absorb UVR within the first few centimeters and would likely not cause a conflict between UVR and *Chaoborus* (Scully and Lean 1994; Morris et al. 1995; Rautio and Korhola 2002). However, lakes with a DOC level as high as approximately 3 mg l^{-1} have been shown to have a weak but significant effect on vertical distribution of zooplankton (Clair et al. 2001).

In nature, we would expect this kind of conflict in any ecosystem in which diel vertical migration occurs due to UVR or reverse diel vertical migration takes place due to invertebrate predators. Despite the fact that many zooplankton species have evolved the characteristic to upwardly migrate during daytime in response to *Chaoborus* kairomone, this behavior has been studied mainly in the laboratory and reverse diel vertical migration in the field has received little attention. To date, the only thorough review on reverse diel vertical migration was by Bayly (1986), who reported 12 cases in lakes and cited 14 marine occurrences. The most thoroughly researched case that indicates that a conflict between *Chaoborus* and UVR could occur in nature was reported by Fedorenko (1975). This study shows a strong reverse vertical migration by the copepod *Diaptomus kenai* in an oligotrophic, fishless lake. He also reported that *C. americanus* and *C. trivittatus* co-occurred and *C. trivittatus* exhibited a strong normal diel vertical migration. Migration by *D. kenai* was most pronounced in October, at the peak abundance of 4th instar *Chaoborus* larvae. At noon the

copepod was distributed between 0 and 7 m and did not overlap with *Chaoborus* distribution (8–17 m). At midnight, *Diatomus* scattered between 0 and 20 m, while *Chaoborus* were mainly found in the top layer (0–8 m). Migration by 4th instar *Chaoborus* in fishless lakes has also been reported by Swift (1976). Fishless lakes are often in remote locations and much less studied than lakes that are inhabited by fish. We propose that there are more lakes that hold a substantial migrating *Chaoborus* population and are clear enough for UVR to penetrate to deeper depths in the water column. Morris et al. (1995) showed that the attenuation depth ($z_{1\%}$) for UVR at 320 nm is around 1 m for water with a diffuse attenuation coefficient (K_d) below 3.8 m^{-1} (correlates to a dissolved organic carbon (DOC) level of about $<2.5 \text{ mg l}^{-1}$). Out of the 65 lakes they studied in Alaska, Colorado, Pennsylvania and the Bariloche region of Argentina, about 45% were clear enough for UV-B₃₂₀ to penetrate between 1 m down to more than 10 m. For some shallow, low DOC lakes high fluxes of UVR penetrated the entire water column. Another example would be some of the Rocky Mountain lakes studied by Lamontagne et al. (1994), since most mountain lakes are clear and fishless, and *Chaoborus* species composition seems to depend on temperature. Similarly, acidified lakes often only support invertebrate predators and are so clear that UVR can penetrate deep into the water (Yan et al. 1985). Temporary ponds often do not support fish, and *Chaoborus* might be re-introduced from neighboring lakes on an annual basis. In that case, it is likely that migrating *Chaoborus* species will dominate those temporary ponds as a predator. Also, in lakes with few visual predators, *Chaoborus* species migrate to deeper depths throughout the day but can still exert a substantial predation pressure on zooplankton species at daytime (Berendonk and O'Brien 1996). In these systems zooplankton migration characteristics would conflict in the presence of the two opposite migrating requirements and may be confined to a narrow water layer to minimize predation and avoid damaging UV. Another situation where the combination of UVR plus *Chaoborus* could restrict zooplankton to a narrow depth interval would be a lake with low DOC that contained zooplankton that are vulnerable to *Chaoborus* but too small to be preyed upon by fish.

Both planktivorous fish and *Chaoborus* can have a strong, seasonally variable impact on zooplankton communities (Tollrian and Dodson 1999). In a mesotrophic lake in Germany, Stibor and Lampert (2000) showed that fish kairomone reduced size at first reproduction of *Daphnia hyalina* in July and August when fish predation is high but not later in the year. However, *Chaoborus* kairomone increased size at first reproduction only in September and October, when *Chaoborus* larvae are abundant. Although some studies have confirmed this behavior in terms of vertical migration (Connell 1978; Bayly 1986), the migration pattern was not viewed in light of the presence of various predators and the abundance of *Chaoborus* was not documented. Furthermore, *Chaoborus* have proven to be highly sensitive to UV light and,

therefore, avoid the surface layer during daytime (Williamson et al. 1999; Persaud and Yan 2003). So far only one study has attempted to compare sensitivity to UVR among different zooplankton taxa (Leech and Williamson 2000). *Chaoborus*, especially early larval instars, show higher mortality to UVR than other zooplankton taxa, resulting in forcing the *Chaoborus* further down into the water column than their prey items, even in some fishless lakes. This most probably results in the clustering of prey items at intermediate depths in nature in the same manner as was shown in our experiment.

Clustering at a narrow depth interval could lead to intense competition among zooplankton for the available food resources in this particular stratum. This type of indirect effect on food limitation might further aggravate the community stability. For example, there is evidence that *Daphnia pulex* has reduced UV-B tolerance at lower food concentrations (Zellmer 1996).

Inducible defenses, which can be expressed when predators are present, are common when both a cost (reduced fitness) and benefit (reduced predation) occur (Harvell 1990). Dawidowicz and Loose (1992) concluded that the cost of vertical migration due to fish kairomone can be linked to reduced growth in *Daphnia* when they are exposed to colder temperature during daytime. So far, no explanation has been offered to link costs of upward migration due to *Chaoborus* kairomone. We propose that the costs due to UVR exposure and enhanced competition are the zooplankton clustering within narrower depth refuge.

Penetration of UV increases rapidly in freshwater ecosystems with DOC levels below $1\text{--}2 \text{ mg l}^{-1}$ (Williamson 1996) and in clear lakes the euphotic zone (1% penetration level) of 320 nm UV can reach down to 33 m (Morris et al. 1995). Even slight increases in UV penetration into lake ecosystems may have additional confounding and indirect effects that could influence migration patterns of zooplankton. Moreover, at increased UV levels phytoplankton growth can be inhibited (Hessen and Van Donk 1994), digestibility of algae by *Daphnia magna* decreased (Van Donk and Hessen 1995), reproduction of *Diatomus* suppressed (Williamson et al. 1994), mortality of cladocerans (Williamson et al. 1994; Hurtubise et al. 1998) and *Chaoborus* (Persaud and Yan 2003) increased, and egg hatching success in fish decreased (Williamson et al. 1997). This diverse range of responses of planktonic organisms suggests that a more thorough understanding of the responses of various taxa (e.g. *Chaoborus* versus prey organisms) to UV is needed in order to make accurate predictions about the ecological results of changes in UV exposure (Williamson et al. 1999). Considering future increases in UV exposure due to stratospheric ozone depletion (Kerr and McElroy 1993) as well as enhanced lake clarity from photobleaching (Morris and Hargreaves 1997), lake acidification, and climate change (Schindler et al. 1996; Williamson et al. 1996; Yan et al. 1996), direct and indirect effects of UVR on aquatic communities have the potential to play an increasingly

dramatic role in variations in community structure both among and within lakes.

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