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Hansson, Lars-Anders

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LUND UNIVERSITY

PO Box 117  
221 00 Lund  
+46 46-222 00 00

## PLASTICITY IN PIGMENTATION INDUCED BY CONFLICTING THREATS FROM PREDATION AND UV RADIATION

LARS-ANDERS HANSSON<sup>1</sup>

*Institute of Ecology/Limnology, Lund University, Ecology Building, SE-223 62 Lund, Sweden*

**Abstract.** In a variable and unpredictable environment, phenotypic plasticity in morphology or behavior may considerably improve an organism's protection against environmental threats and thereby its fitness. Here I demonstrate that common freshwater organisms, copepods (Crustacea), show a plastic response by adjusting pigmentation level in relation to two environmental threats: ultraviolet radiation (UV) and predation. The red pigment in copepods, astaxanthin, reduces damage caused by UV radiation, but makes the organism more conspicuous, thereby exposing it to higher predation pressure. In a field survey of six lakes sampled monthly for 16 mo, I quantified UV and predation threat, as well as copepod pigmentation level. The relative threat ratio (UV/predation) was generally lowest during summer and highest during spring; this pattern was paralleled by pigmentation level among copepods. Moreover, the level of pigmentation among copepods in lakes with high predation pressure was lower than among those copepods in lakes with lower risk of predation. In a complementary experimental study performed under constant UV threat, calanoid copepods in the absence of predation threat responded with almost three times higher pigment levels, compared to those with fish present (caged). Hence, the correlative field survey and the mechanistic experiment together suggest that the level of pigmentation in copepods is an inducible and adjustable defense, governed by the aim to improve individual protection against prevailing threats from both predation and UV radiation.

**Key words:** copepod; limnology; phenotypic plasticity; pigment; predation; ultraviolet radiation; zooplankton.

### INTRODUCTION

All organisms, in both terrestrial and aquatic systems, are continuously faced with multiple sources of information about threats and opportunities in their environment; they need to handle this information and, as best they can, make compromises in behavior or morphology (Dodson 1989). To cope with these everyday environmental threats, many aquatic organisms have evolved morphological adaptations, such as spines in some fish (e.g., Hoogland et al. 1957), rotifer, and algal species, or behavioral adaptations, such as diel vertical migration among zooplankton (e.g., Stich and Lampert 1981, Rhode et al. 2001). While most adaptations are constitutive, that is, they are present throughout the organism's lifetime, some are induced only during periods when the threat is present. In the case of predation threat, such inducible defenses may be viewed as strategies in which nonlethal cues from predators, such as chemical substances, are utilized by prey as reliable predictors of the risk of predation. Inducible defenses allow organisms to reap the benefits of a defense, while saving potential costs associated with investment in the defense. The cue transferring information of a predation risk is generally thought to be a chemical substance released by the predator, al-

though few such chemicals have actually been identified (Boriss et al. 1999, Brönmark and Hansson 2000, von Elert and Pohnert 2000). These cues, and others like them, can be considered a "chemical information network" (Hansson 2000a), and their possible existence may have a profound impact on our understanding of ecological systems. This network of cues and induced adaptive responses suggests that organism interactions are not solely defined by direct encounters and feeding links, but may also include behavioral and morphological plasticity of the prey; higher level responses buffering against predicted effects from trophic feeding interactions.

Inducible defences may be especially beneficial in situations where several threats act simultaneously. A striking example of how an adaptation can be beneficial against one threat but simultaneously disastrous against another is pigmentation among freshwater copepods (Crustacea), common cosmopolitan freshwater zooplankters. The bright red pigmentation effectively protects the animal from being harmed by ultraviolet (UV) radiation (Hairston 1976). However, the pigment also makes the animal more conspicuous, increasing the risk of being captured by predators, such as fish.

Both predation and UV risks differ among lakes, depending on temporal variations in UV radiation reaching the water surface, the UV penetration through the water column, and on fish feeding rates, species composition, and biomass. Moreover, both threats vary

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<sup>1</sup> E-mail: Lars-Anders.Hansson@limnol.lu.se

temporally within a lake, depending on sun hours and angle and on fish feeding efficiency; the latter is mainly a function of temperature (Lessmark 1983, Persson 1986, Jobling 1994). Based on these concepts, it may be predicted that copepod pigmentation would be highest in those lakes that have high UV penetration and low predation pressure. Similarly, within each lake, pigmentation level may be predicted to be highest during periods when UV penetration is high; that is, when turbidity in the water of eutrophic lakes, as well as feeding efficiency by fish, are low. Hence, upon hypothesizing that copepods adjust their pigmentation level to the relative threat from UV and predation, we arrive at the somewhat counterintuitive prediction that pigmentation level should be highest during spring and fall, when UV penetration through the water is high and lower temperature reduces fish feeding rate.

In an intensive 16-mo survey of six lakes, I tested this hypothesis by estimating threats from UV radiation and fish predation and simultaneously quantifying copepod pigmentation. Further, in order to test if the mechanism behind patterns found in natural systems is a trade-off between threats from UV radiation vs. predation, I conducted an experimental study at constant UV threat but different predation threats. The specific hypothesis for this mechanistic study was that copepods decrease their photo-protective pigmentation in the presence of fish predation at constant UV radiation. Additionally, since UV radiation rapidly attenuates in water (Schindler et al. 1996), another plastic response by copepods would be to migrate downwards, thereby utilizing depth as a refuge from UV radiation. I experimentally tested this hypothesis by allowing, or not allowing, copepods to utilize the depth refuge. Hence, the present study consists of a field survey in which I have quantified the variation in pigment and threat levels (UV radiation and predation) and an experiment aimed at assessing the mechanisms behind these observed patterns, which may be morphological (changes in pigmentation level) and/or behavioral (vertical migration).

## MATERIAL AND METHODS

### *Lake descriptions*

The six lakes included in the field study are situated within a radius of 50 km from the city of Lund in southern Sweden (55.67° N, 13.5° E) and vary in size between 0.2 and 20.5 km<sup>2</sup> (Table 1). All lakes are meso- to eutrophic with summer (June to September) Secchi depths between 0.3 and 2.5 m and total phosphorus concentrations of 20–240 µg/L (Table 1).

### *Threat estimates*

The amount of radiation reaching a specific depth in a lake is a function of the extinction coefficient of light, which, in turn, is dependent on the absorption and scattering of radiation due to particle type and concentra-

tion. Eutrophic waters, which are high in chlorophyll and dissolved organic material (DOM), as well as brown waters, rich in humic substances, usually have the highest extinction coefficients. Photosynthetically active radiation (PAR) was measured at 0.0 and 0.4 m depth with a LI-COR Quantum Photometer (Li-185B) connected to an Li-192SB underwater sensor (LI-COR, Lincoln, Nebraska, USA). On each sampling date PAR was measured at 0.0 and 0.4 m depth and from these data the extinction coefficient for PAR ( $K_{PAR}$ ) was calculated for each sampling date and lake. The extinction coefficient was calculated from the relationship  $K_{PAR} = -\ln(I_{0.4}/I_{0.0})$ , where  $I_{0.4}$  and  $I_{0.0}$  are the light intensities at 0.4 m and at 0.0 m below the surface, respectively. In March, April, and May of 2000 absorbance at 320 nm (UVA-UVB) was also measured from water samples taken at 0–0.3 m depth and measured on a Beckman DU 800 spectrophotometer (Beckman, Fullerton, California, USA) at 320 nm. The absorption coefficient at 320 nm ( $a_{320}$ ) was calculated from the relation  $a_{320} = \ln(10^{abs})$  reported for a 1-m path length (Morris et al. 1995). The extinction coefficient for radiation at 320 nm ( $K_{320}$ ) was then calculated from  $K_{320} = 1.51(a_{320}) - 0.12$  (Morris et al. 1995). Based on this, a relation between  $K_{PAR}$  and  $K_{320}$  at each site was calculated:  $K_{320} = 18.52(K_{PAR}) + 7.03$  ( $n = 14$ ,  $r^2 = 0.69$ ). Solar irradiances reaching the water surface ( $I_0$ ) were obtained from the model “FASTRT” (available online)<sup>2</sup> after corrections for atmospheric ozone thickness using “Total Ozone Mapping Spectrometer” (TOMS; available online).<sup>3</sup> The model was run for surface downward irradiance at 320 nm. All calculations were made for Lund, Sweden (55.67° N, 13.5° E) and were based on the mean radiation during eight days before each sampling date (including the sampling date). Most of the lakes were partly frozen from mid-January to early March 2000, which may have led to an overestimation of the UV threat during this period.

Since the copepods were sampled in surface water at about 0 to 0.3 m, that is, the diameter of the net, the radiation (320 nm) reaching the middle of the sampling depth (0.15 m) was used as an estimate for the UV threat to copepods and was calculated from  $I_{0.15} = I_0 e^{(-K_{320} 0.15)}$ . Hence, this estimate of the relative UV threat to copepods includes both the seasonal variation in incoming radiation (which is generally low during winter and high during summer), as well as the temporal (within a lake) and spatial (among lakes) variation in attenuation through the water column. Such a calculation may provide a reliable estimate of the UV threat experienced by the copepods sampled.

The main planktivorous fish in southern Swedish lakes are generally roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) smaller than 150 mm. This was also

<sup>2</sup> URL: <http://www.itek.norut.no>

<sup>3</sup> URL: [http://toms.gsfc.nasa.gov/teacher/ozone\\_overhead.html](http://toms.gsfc.nasa.gov/teacher/ozone_overhead.html)

the case in the lakes included in my study, where this category constituted between 64% and 99% of the total biomass, except in Lake Krankesjön, where it constituted 41%. Therefore, the catch (in biomass) per unit effort (CPUE) of this category was used as an estimate of the relative predation pressure on zooplankton. Fish sampling was performed using two pelagial and two littoral sinking fyke nets (biological survey nets; Lundgrens, Stockholm, Sweden) applied parallel to the shore during 12 h. Each net is 42 m long and 1.5 m high and consists of 14 units of 3 m with different mesh sizes in random order ranging from 6.25 to 75.0 mm from knot to knot. Determination of fish biomass was based on one fishing occasion, performed in September 2000. The reason for fishing in September is that the young-of-the-year fish are then large enough to be caught and are thereby included in the biomass estimate, while temperature is still high enough to allow fish to feed. Although it may be argued that fishing once in each lake may not give an exact assessment of the fish biomass, it should be noted that the method used was standardized and performed in the same way in all lakes. Variables that may affect the predation pressure on zooplankton include fish species composition, size distribution, biomass, as well as temperature. Since the study was focused on the most efficient planktivores (roach and perch), the basis for calculations of predation pressure is similar among lakes with respect to fish species composition. The size distribution of fish was relatively similar among lakes with individual masses of  $28.5 \pm 8.0$  and  $33.0 \pm 8.5$  g (mean  $\pm$  1 SE) for roach and perch, respectively. Therefore, no compensation for differences in size distributions among lakes were made. Since temperature is a main determinant of fish foraging efficiency (Lessmark 1983, Persson 1986, Jobling 1994), and thereby of the predation pressure on zooplankton, the biomass was adjusted to a temperature–consumption rate function based on the empirical relationship between temperature and food consumption (measured as milligrams of zooplankton per gram of fish): consumption rate =  $0.2897e^{(0.1848 \text{ temp})}$  (Lessmark 1983). Besides temperature, fish biomass may fluctuate temporally due to, for example, mortality, growth, reproduction, and migration. The biomass of fish is generally at its maximum during August–September in temperate lakes (Appenzeller 1998). In order to compensate for temporal fluctuations in fish biomass, and thereby for predation threat to zooplankton, I used a long-term study on fish biomass fluctuations in Lake Constance, Germany (Appenzeller 1998). This study is based on echo sounding which allows biomass estimates irrespective of temperature effects on fish activity. Hence, net fishing, which is the most common method for biomass estimates, is not appropriate for temporal studies since fish activity, and thereby the catch efficiency, is strongly affected by temperature. The echo-sounding surveys performed by Appenzeller (1998) showed that the fish

biomass in February–March was only ~30% of that in August–September. Appenzeller estimated fish biomass in February, June, July, August, October, and November and, after interpolations for the months missing, I normalized the data set (the highest biomass was set to 1.0) and finally multiplied this with my own biomass estimates for each sampling occasion. Hence, I based the estimate of predation threat on biomass of perch (<150 mm) and roach, adjusted for temporal (seasonal) fluctuations in consumption rate, as well as for temporal variation in fish biomass within lakes. Such an estimate may provide an opportunity to compare spatial (among lakes) and temporal (seasonal) variations in predation threat on zooplankton.

The estimated UV and predation threats were normalized by assigning the highest value to 1.0 and the normalized values were then log transformed and combined in a ratio (UV/predation) and used as an estimate of the instantaneous relative threat from both UV and predation for each sampling date and lake. It should be noted that the way an organism experiences threats is difficult, or even impossible, to estimate, and I fully acknowledge that my approach to calculate relative UV and predation threats certainly has weaknesses. It should also be noted that the threat estimates are used to compare *relative* spatial and temporal variations among and within lakes sampled simultaneously and with identical methods, suggesting that comparisons or extrapolations outside this data set should be done with caution. However, despite shortcomings, the approach used offers a rare possibility for spatial (among lakes) and temporal (within lakes) estimates and comparisons of environmental threats, which then can be related to putative responses in organisms.

#### *Response estimates*

Astaxanthin is a red pigment identified as the major pigment component among copepods (Byron 1982). Copepods cannot synthesize it themselves, but have to ingest it through food (Hairston 1978). Astaxanthin has a strong quenching effect against singlet oxygen, as well as a strong scavenging effect against free radicals, which are products of UV-induced processes (Miki 1991) and are therefore efficient in protecting against photo-damage (Hairston 1980). There are also other UV-absorbing pigments, e.g., mycosporine-like compounds (Sommaruga and Garcia-Pichel 1999), which were not quantified here. In my field study, copepods were sampled in the surface water (0–0.3 m) with a 300- $\mu$ m net (diameter 0.3 m). Animals were then transported live to the laboratory in prefiltered water (Whatman GF/C) from each lake, which allowed for gut clearance of any algal pigment. The absence of chlorophyll peaks (665 nm) in both the field and experimental studies (Fig. 1) indicates that after this procedure the amount of algae in the guts of the copepods was negligible. Hence, pigments from recently consumed algae remaining in the guts have most probably not affected

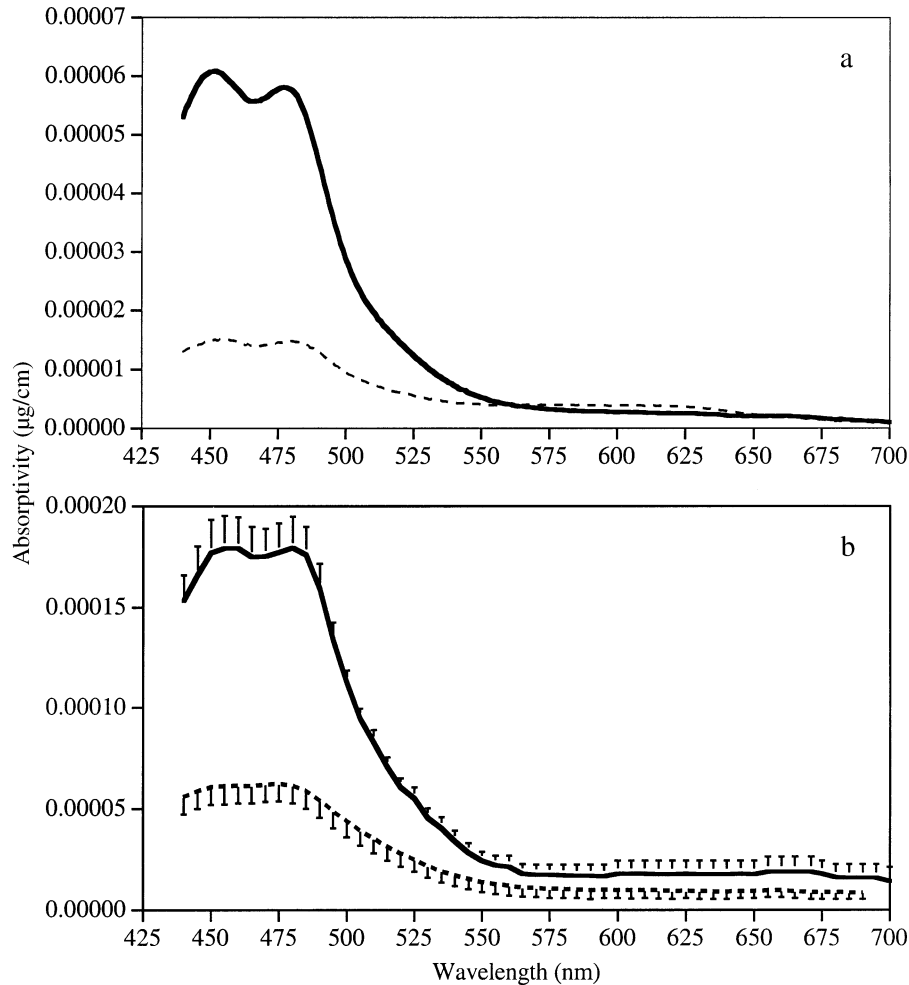


FIG. 1. Wavelength scans for calanoid (solid lines) and cyclopoid (dotted lines) copepods from (a) Lake Häljasjön in southern Sweden, May 2002, and (b) at the end of the laboratory experiment (means  $\pm$  1 SD;  $n = 3$ ). The scans show absorptivity ( $r$ ) of copepod tissue and were performed at intervals of 1 nm, but for clarity standard deviations are only presented for every 5 nm. Maximum absorbance for the photo-protective pigments is  $\sim$ 474 nm, and for algal chlorophyll it is 665 nm.

the results (Sommaruga and Garcia-Pichel 1999). At the laboratory, a subsample of about 100 individuals were counted and put in a plastic scintillation vial (25 mL). The subsample was then frozen followed by extraction with ethanol (96%) at room temperature for 12 h. A preliminary methodological test showed that freezing does not affect pigment level of copepods ( $t_4 = 0.3320$ , ns). Samples were disrupted using an ultrasonic converter (Heat Systems model CL4, Farmingdale, New York, USA; 20 kHz; 20 s in ice bath) and then centrifuged for 5 min at 3000 rpm. Quantification of the extracted red pigment in the supernatant was performed with a Beckman DU 800 spectrophotometer at 474 nm, which is the absorbance peak for the active pigment (Hairston 1979). All samples were also scanned at each wavelength from 440 to 700 nm (Fig. 1). The absorptivity ( $r$ ) of copepod tissue was calculated from  $r = \text{abs}_{320}/zC$ , where  $\text{abs}_{320}$  is from absor-

bance readings at 320 nm (Beckman DU 800 spectrophotometer),  $z$  is the path length (1 cm), and  $C$  is the dry mass of copepods in the sample (in micrograms).

#### Laboratory experiment

Twelve cylindrical polyethylene containers (height 1.0 m, diameter 0.57 m) were used in the experiment. The containers were filled with lake water and copper-free tap water (proportions 35:65); six of them were sealed off with 300- $\mu$ m nylon nets 0.3 m below water surface, excluding zooplankton from utilizing depth as a refuge from ultraviolet radiation. The penetration of 1% of the surface radiation was  $0.46 \pm 0.05$  m for 320 nm and  $1.06 \pm 0.13$  m for 380 nm, respectively (means  $\pm$  1 SD). Hence, below the net (0.3 m) only 5% and 12% of the 320 and 380 nm radiation remained, suggesting that access to depths beyond 0.3 m provided the animals with an efficient refuge from UV radiation.



This treatment was crossed with presence and absence of caged fish in a  $2 \times 2$  factorial design with three replicates, giving two treatments with depth refuge, but with fish (RF) and without (RN), and two treatments where zooplankton were unable to utilize the refuge, with fish (NF) and without (NN). The experiment was performed in a culture room with constant temperature and light conditions, ensuring that no environmental or seasonal variables affected the results. Mean water temperature ranged between  $15.0^\circ$  and  $16.4^\circ\text{C}$  during the experiment ( $15.6 \pm 0.3^\circ\text{C}$ , mean  $\pm 1$  SD,  $n = 36$ ). In the experiment, UV threat was measured as absorbance at 320 nm in each container on each sampling date. Incoming radiation to the water surface was measured with a UVA sensor (SUL 033, International Light, Newburyport, Massachusetts, USA) connected to a logging meter (IL 1400A, International Light). Calculations were similar to those performed in the field study.

The experiment started 19 April 2002 and ended 41 d later (30 May). Samplings were performed six times starting just after addition of the animals (pretreatment), day 0, and thereafter on days 3, 6, 18, 27, and 41. A combination of five cool white (36-W, Osram, Munich, Germany) and three UV (UVA-340, Q-Panel, Cleveland, Ohio, USA) lamps and a light:dark cycle of 13:11 h gave a nonlethal radiation dose (UVA =  $2.74 \pm 0.49$  W/m<sup>2</sup> and UVB =  $0.081 \pm 0.017$  W/m<sup>2</sup>). This corresponds to the radiation intensity at noon on a lightly clouded winter/spring day and is about one-tenth the UV radiation during a sunny summer day (UVA =  $27.8$  W/m<sup>2</sup> and UVB =  $0.28$  W/m<sup>2</sup>). The 1% attenuation depth for UV radiation at 320 nm was derived by first calculating the absorption coefficient in the same way as for the field study ( $a_{320} = \ln(10^{\text{abs}})$ ; Morris et al. 1995). Then the extinction coefficient ( $K_d$ ; per meter) was derived from the correlation between the absorption coefficient and  $K_d$  ( $r^2 = 0.94$ ; Laurion et al. 2000), and, finally, the 1% attenuation depth ( $Z_{1\%}$ ; in meters) was calculated according to:  $Z_{1\%} = 4.605/K_d$ . For comparison, the 1% penetration depth for 380 nm (UVA) was derived from the linear relationship between 320 and 380 nm ( $r^2 = 0.96$ ; Williamson et al. 1996).

The containers were randomly placed under the light panels and aerated from two aquarium pumps, each providing air to six containers. Roach (*Rutilus rutilus*), caught by electrofishing in one of the lakes included in the field study (Lake Krankesjön), were used in the fish treatments. The fish (1+, length =  $48.6 \pm 4.2$  mm, mean  $\pm 1$  SD,  $n = 30$ ) were allowed to feed on copepods for 24 h before they were put in free-floating net cages (165  $\times$  140  $\times$  125 mm) in the experimental containers. Mesh size was less than 0.2 mm ensuring no predation on zooplankton. Empty net cages were put in treatments without fish. Fish were taken out and allowed to eat copepods or replaced by recently fed individuals every 2–7 d. Until day 22 of the experiment two fish were kept in each cage; thereafter only one fish was used.

The day before starting the experiment, zooplankton were collected in one of the lakes included in the field survey (Lake Häljasjön) with a 300- $\mu\text{m}$  net. During spring, the zooplankton community in Lake Häljasjön consists almost exclusively of cyclopoid and calanoid copepods (>95%; by numbers). The animals were kept in lake water during the night and then mixed and portioned out to the containers at an initial concentration of  $120 \pm 56$  calanoid copepods/L and  $58 \pm 25$  cyclopoid copepods/L (means  $\pm 1$  SD). Every day, or in some cases every second day, additional food was provided to each container by means of about 0.5 L of algal culture (*Scenedesmus* spp. >80% by numbers). This was to ensure that food quantity and quality for zooplankton was similar in all treatments, since differences in algal astaxanthin concentration varies among, as well as temporally within, algal species (Boussiba 2000).

On each sampling date, water samples for assessment of UV absorption were taken for later analysis of absorbance at 320 nm on a Beckman DU 800 spectrophotometer. Surface water samples for zooplankton abundance and pigment determinations were taken from 0 to 0.3 m depth and poured through a 55- $\mu\text{m}$  net. Zooplankton were then kept in prefiltered water (Whatman GF/C) from the containers during at least 3 h. This procedure was performed in order to avoid feeding after sampling and to allow for gut evacuation, thereby avoiding algal pigments to be included in the analysis. That this procedure was successful is indicated by the absence of a chlorophyll peak (665 nm) in the wavelength scans (Fig. 1). Calanoid and cyclopoid copepods were counted and separated by hand under a dissecting microscope and thereafter frozen and analyzed in the same way as in the field study.

## RESULTS

### Field survey

The relative UV threat was generally highest from April to August and lowest from October to March (Fig. 2). During summer the mean UV threat was generally somewhat lower in the lakes with high rather than with low predation threat (Fig. 2). The depth to which 1% ( $Z_{1\%}$ ) of the surface radiation reached ranged between 0.1 and 0.9 m for 320 nm (UVA-UVB) and between 0.3 and 2.2 m for 380 nm (UVA; Table 1). In four of the lakes, the fish catches (catch per unit effort; CPUE) were similar, ranging between 2.4 and 3.6 kg (Table 1), and the predation threat in these lakes were categorized as low. In two of the lakes, Lake Vomb and Lake Sövedsjön, the CPUE was 9.0 and 5.2 kg, respectively (Table 1), and the predation pressure on zooplankton in these lakes was therefore categorized as high. In all lakes the predation threat on zooplankton was highest in August and lowest from October to April (Fig. 2). The relative threat ratio (UV/predation) generally showed maximum values during February to

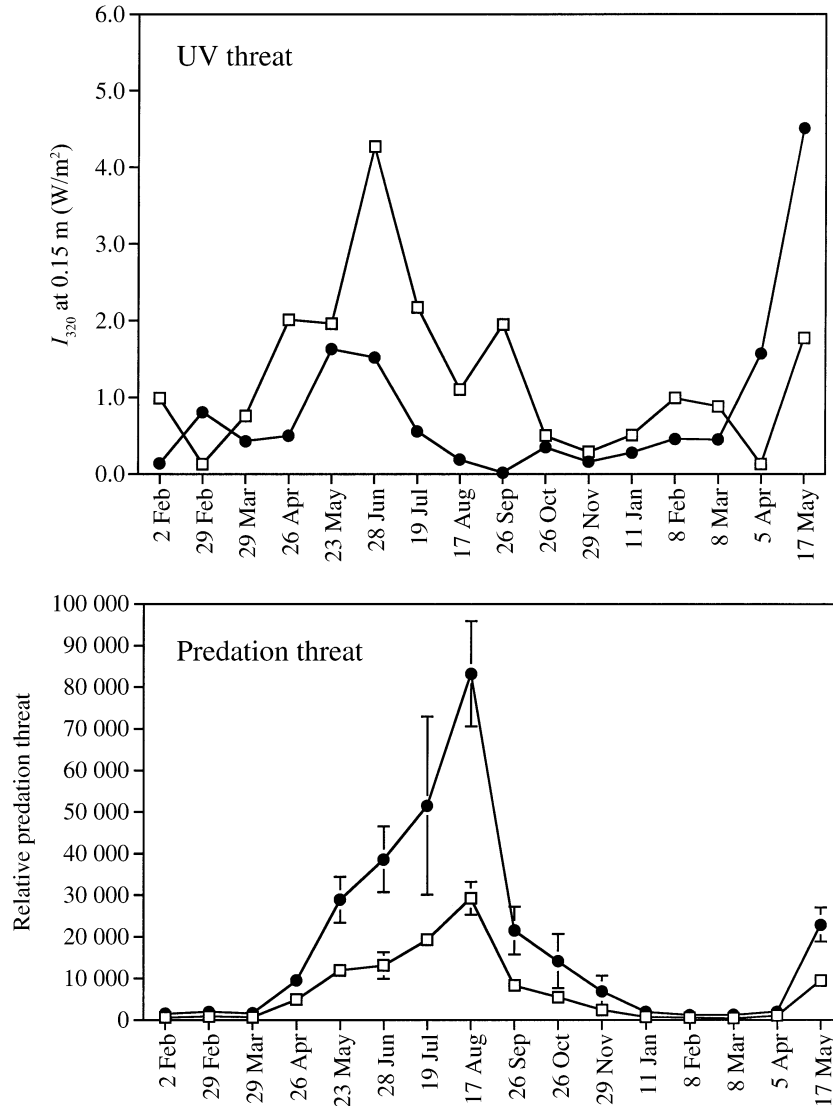


FIG. 2. Temporal variation in UV and predation threats (February 2000–May 2001) in lakes with high (filled symbols; Lakes Vomb and Sövesjön) and low (open symbols; Lakes Krankesjön, Dagstorpssjön, Ringsjön, and Häljasjön) predation pressure on copepods by fish. Bars indicate  $\pm 1$  SD. For clarity no error bars are shown for UV threats.

April during both years investigated and lower values from May to November (Fig. 3). The threat ratio was lower in lakes with high fish biomass than in lakes with low fish biomass ( $t_{89} = 2.854$ ,  $P < 0.006$ ), which was a result of higher predation pressure and a tendency for lower UV threat (Fig. 2).

The pigmentation among both calanoid and cyclopoid copepods generally showed a short maximum during a period between February and April and lowest values during summer (Fig. 3). The mean pigmentation level was higher for calanoid copepods in lakes with low predation threat rather than with high (seasonal mean = 1.0 and 0.65  $\mu\text{g}/\text{mg}$  dry mass [DM], respectively,  $t_{76} = 3.457$ ,  $P < 0.001$ ; Table 2). This was also the case with respect to cyclopoid copepods, showing

a mean pigmentation of 0.91  $\mu\text{g}/\text{mg}$  DM at low predation pressure and 0.66 at high ( $t_{82} = 3.160$ ,  $P < 0.003$ ; Table 2). The temporal fluctuations in pigmentation among both calanoid and cyclopoid copepods generally paralleled fluctuations in the threat ratio (UV/predation; Fig. 3). Moreover, combining all sampling occasions reveals a correlation between the relative threat ratio and the pigmentation level (Pearson's  $r = 0.42$ ,  $t_{151} = 5.706$ ,  $P < 0.001$ ; Fig. 4).

#### Laboratory experiment

The UV radiation intensity reaching the water surface in the laboratory experiment corresponded to a lightly clouded winter/spring day, ensuring that the UV dose was not lethal. The depth to which 1% of the

TABLE 1. Characteristics of the lakes in southern Sweden included in the field study.

Lake	Area (km <sup>2</sup> )	Maximum depth (m)	Mean depth (m)	Secchi depth (m)	Total phosphorus (μg/L)	CPUE <sup>†</sup> (g)	Z <sub>1%</sub> (320 nm) <sup>‡</sup>	Z <sub>1%</sub> (380 nm) <sup>‡</sup>
Low predation								
Dagstorpssjön	0.5	4	2.8	1.0–2.5	39–50	2832	0.11–0.13	0.30–0.35
Eastern Ringsjön	20.5	16	6.1	0.6–1.2	60–240	3630	0.11–0.22	0.28–0.55
Krankejsjön	4.2	3	1.5	1.2–2.1	22–56	2919	0.10–0.44	0.77–1.08
Häljasjön	0.2	10	5.6	NA	20–40	2405	0.12–0.93	0.33–2.23
High predation								
Sövdesjön	2.8	8	3.4	0.7–0.8	105–229	8993	0.10–0.23	0.26–0.53
Vombsjön	12.4	14	6.0	0.3–1.1	60–150	5194	0.11–0.32	0.30–0.78

Notes: Lakes are categorized as having low and high predation threats at fish catch per unit effort (CPUE) below 4000 g and above 5000 g, respectively. Values for physical and chemical data are given as summer ranges from June to September, except with respect to Z<sub>1%</sub>, which represent whole-year data. “NA” indicates that data are not available.

<sup>†</sup> Fish catch per unit effort of roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) smaller than 150 mm.

<sup>‡</sup> The range in depth penetration (in meters) for 1% of surface irradiation (Z<sub>1%</sub>) at 320 and 380 nm.

surface radiation reached ranged from 0.4 to 0.7 m for 320 nm and 1.0 to 1.7 m for 380 nm. Abundances of calanoid copepods did not differ among treatments or between surface and bottom during the experimental period (repeated-measures ANOVA,  $F_{5,15} = 1.877$ ,  $P$

> 0.10). Cyclopoid copepods, however, tended to prefer staying at the surface, at least during the first sampling occasions, leading to differences in abundances between surface and bottom samples (repeated-measures ANOVA,  $F_{5,15} = 3.474$ ,  $P < 0.008$ ). With respect

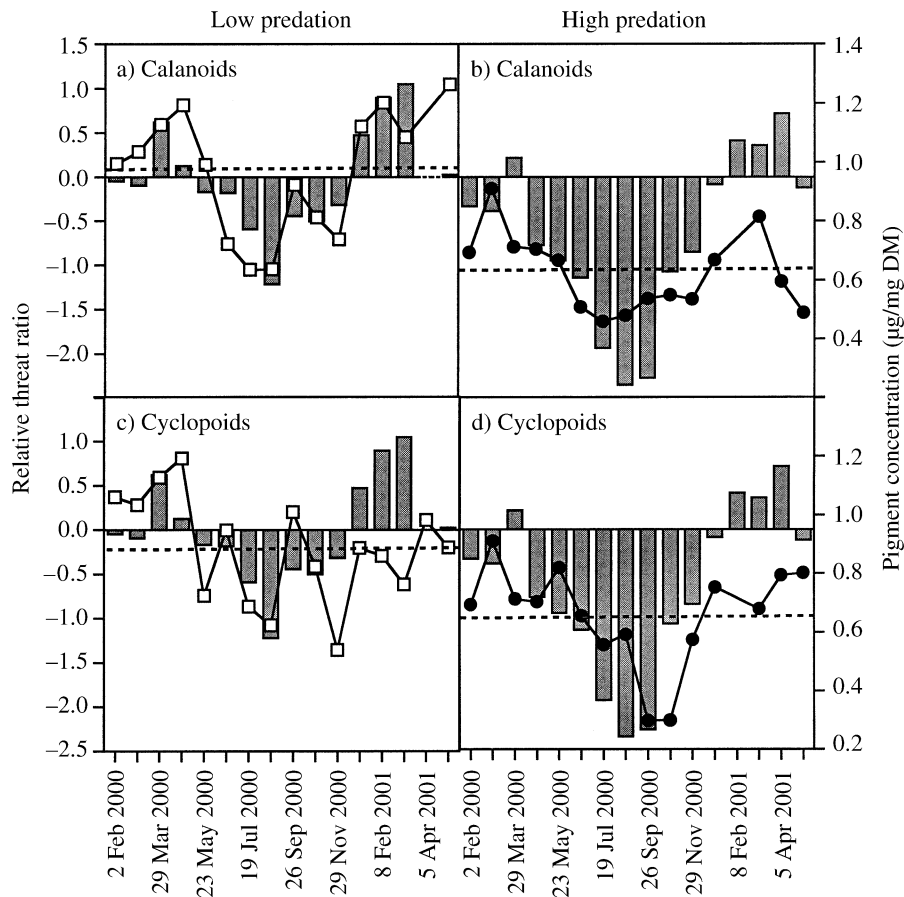


FIG. 3. Temporal variation (means) in relative threat ratio (UV/predation, dimensionless; bars) and pigmentation (lines and symbols; in micrograms of astaxanthin per milligram of dry mass [DM]) among (a, b) calanoid and (c, d) cyclopoid copepods in lakes with (a, c) low and (b, d) high fish predation. Dotted lines indicate seasonal means in pigmentation.



TABLE 2. Levels and temporal ranges in pigmentation (in micrograms of astaxanthin per milligram of dry mass) among calanoid and cyclopoid copepods in lakes with low and high predation pressure from February 2000 to May 2001.

Lake	Calanoid copepod pigmentation		Cyclopoid copepod pigmentation	
	Mean (SD)	Range	Mean (SD)	Range
Low predation				
Dagstorpsjön	1.34 (0.26)	0.96–1.72	1.20 (0.25)	0.83–1.55
Häljasjön	0.87 (0.21)	0.57–1.17	0.78 (0.25)	0.29–1.17
Krankesjön	1.07 (0.27)	0.62–1.52	0.88 (0.13)	0.62–1.07
Ringsjön	0.74 (0.40)	0.09–1.56	0.78 (0.35)	0.03–1.56
Mean	1.00 (0.29)	0.56–1.49	0.91 (0.25)	0.44–1.34
High predation				
Sövdesjön	0.66 (0.19)	0.35–0.98	0.63 (0.21)	0.28–1.00
Vombsjön	0.63 (0.19)	0.15–0.84	0.68 (0.20)	0.32–0.95
Mean	0.65 (0.19)	0.25–0.91	0.66 (0.21)	0.30–0.98

to pigmentation level (micrograms of astaxanthin per milligram DM) there was a treatment effect in calanoid copepods (repeated-measures ANOVA,  $F_{5,15} = 6.954$ ,  $P < 0.001$ ), but not for cyclopoid copepods (repeated-measures ANOVA,  $F_{5,15} = 1.428$ ,  $P > 0.10$ ). Contrast analyses (Fisher's PLSD) for calanoid copepods show that there were no differences between surface and bottom or within groups of treatments with and without fish (Table 3). Instead, the entire treatment effect was due to differences between treatments with and without fish (Table 3). Since the only treatment effect recorded among calanoid copepods was between fish and nonfish treatments, refuge and nonrefuge treatments were pooled, showing a 2.5 times higher (1.43 vs. 0.57  $\mu\text{g}/\text{mg DM}$ ) mean concentration of astaxanthin in treatments without fish over those with fish (repeated-measures ANOVA,  $F_{5,15} = 12.466$ ,  $P < 0.002$ ; Fig. 5). A similar pooling of data for cyclopoid copepods showed

no effect from fish (repeated-measures ANOVA,  $F_{5,15} = 1.203$ ,  $P > 0.10$ ), although there was a tendency toward higher pigmentation levels in the absence of fish in the beginning of the experiment (days 3 and 6; Fig. 5).

Copepod eggs are known to contain high amounts of pigments (Hairston 1979) and therefore I counted egg-bearing individuals in each treatment. With respect to calanoid copepods there were no differences in portion of egg bearers (repeated-measures ANOVA,  $F_{5,15} = 0.234$ ;  $P > 0.50$ ), whereas cyclopoid copepods, showing no differences in pigmentation, had a somewhat higher portion of egg bearers in the fish treatment (RF) than in the other treatments (repeated-measures

TABLE 3. Probability values for contrast analysis (Fisher's PLSD) on repeated-measures ANOVA including all treatments in the experiment.

Treatment	Calanoid copepods, $P$	Cyclopoid copepods, $P$
<b>RN<sub>S</sub>, RF<sub>S</sub></b>	<b>&lt;0.002</b>	NS
RN <sub>S</sub> , NN	NS	NS
<b>RN<sub>S</sub>, NF</b>	<b>&lt;0.012</b>	NS
RN <sub>S</sub> , RN <sub>B</sub>	NS	NS
<b>RN<sub>S</sub>, RF<sub>B</sub></b>	<b>&lt;0.001</b>	NS
<b>RF<sub>S</sub>, NN</b>	<b>&lt;0.002</b>	<b>&lt;0.013</b>
RF <sub>S</sub> , NF	NS	NS
<b>RF<sub>S</sub>, RN<sub>B</sub></b>	<b>&lt;0.002</b>	NS
RF <sub>S</sub> , RF <sub>B</sub>	NS	NS
<b>NN, NF</b>	<b>&lt;0.010</b>	NS
NN, RN <sub>B</sub>	NS	<0.050
<b>NN, RF<sub>B</sub></b>	<b>&lt;0.001</b>	NS
<b>NF, RN<sub>B</sub></b>	<b>&lt;0.008</b>	NS
NF, RF <sub>B</sub>	NS	NS
<b>RN<sub>B</sub>, RF<sub>B</sub></b>	<b>&lt;0.001</b>	NS

Notes: Statistics for the repeated-measures ANOVA are:  $F_{5,15} = 6.954$ ,  $P < 0.001$  and  $F_{5,15} = 1.428$ ,  $P > 0.05$  (NS), for calanoid and cyclopoid copepods, respectively. Boldface type indicates where differences are predicted according to hypotheses. Surface (subscript S) and bottom (subscript B) samples are from RN (Refuge/No fish) and RF (Refuge/Fish) treatments as well as NN (No refuge/No Fish) and NF (No refuge/Fish) treatments. Tests not significant at the 0.05 level are denoted "NS."

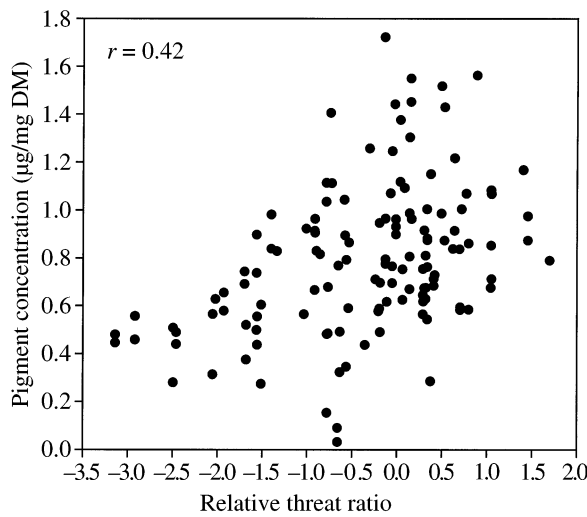


FIG. 4. Correlation between relative threat (UV/predation) and pigmentation level (in micrograms of astaxanthin per milligram of dry mass [DM]) for calanoid and cyclopoid copepods. (Pearson's  $r = 0.42$ ;  $t_{151} = 5.706$ ,  $P < 0.001$ ).

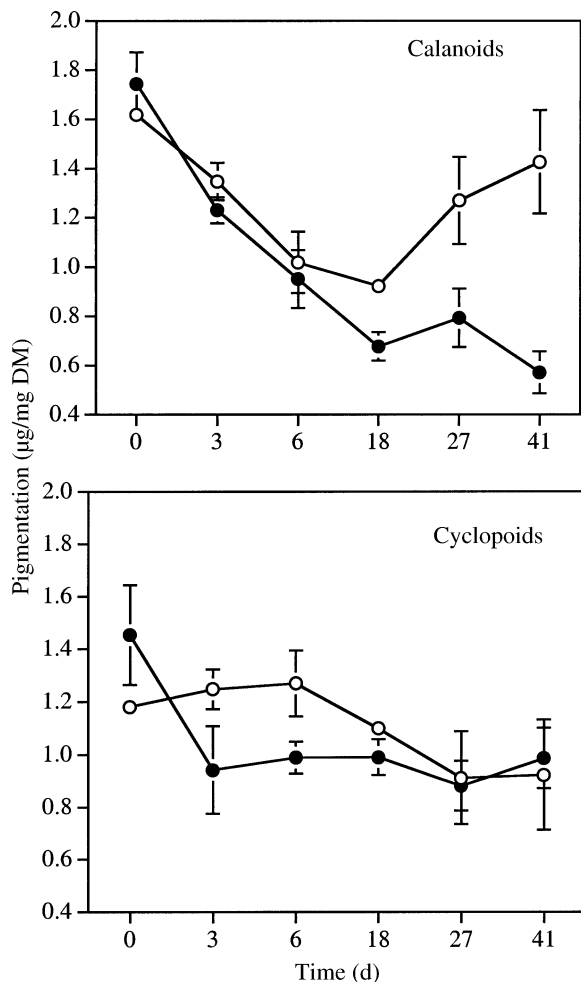


FIG. 5. Temporal changes in pigment content (in micrograms of astaxanthin per milligram of dry mass [DM]) of calanoid and cyclopoid copepods in experimental treatments with fish (filled symbols) and without fish (open symbols) (means  $\pm$  1 SD).

ANOVA,  $F_{5,15} = 3.945$ ;  $P < 0.036$ ; Tukey-Kramer post hoc test).

#### DISCUSSION

Phenotypic plasticity, which is the ability of a genotype to produce more than one alternative form of morphology or behavior in response to environmental conditions (West-Eberhard 1989), may strongly influence species interactions by changing individual growth rates and vulnerability to predation (van Buskirk and Schmidt 2000). Moreover, phenotypic plasticity may reflect spatial and temporal environmental fluctuations, as well as variations in species interactions, such as changes in predation pressure (Agrawal 2001). The plastic trait addressed here, pigmentation level among copepods, has several relevant properties: It varies globally by at least a factor of 10 (Hansson 2000b), and its levels are generally highest where the

ultraviolet radiation is high, such as in polar regions (Hairston 1979, Luecke and O'Brien 1981, Byron 1982, Hansson 2000b). However, in lakes where fish predation on zooplankton is high, the pigmentation level among copepods tends to be considerably lower than in fish-free lakes (Hairston 1979, Luecke and O'Brien 1981, Utne-Palm 1999, Hansson 2000b). In temperate regions, where the UV threat is lower than in polar regions, copepods generally accumulate less pigment than do those at higher latitudes (Hansson 2000b). Copepods may reduce the harm caused by UV radiation both morphologically, by adjusting the pigment level, and behaviorally, by migrating downwards in the water column. With respect to copepods, this behavioral response has been demonstrated in some (e.g., Hairston 1978, Zagarese et al. 1997), but not in other studies (Rocco et al. 2002). Cladocerans, on the other hand, seem to more generally utilize vertical migration to avoid UV radiation (Leech and Williamson 2000, Rhode et al. 2001). Besides these possibilities, zooplankton may also rely on photo-repairing enzyme systems, which, however, are very temperature dependent, having low efficiency at low temperatures (Williamson et al. 2002).

Despite the fact that UV threat is less pronounced in temperate regions, copepods seem to accumulate as much pigment as possible, given that they also have to face a threat from fish predation, a threat that varies considerably with time, as does UV radiation (Fig. 2). Combining the threats from UV radiation and fish predation into a "threat ratio" (UV/predation) may give us a relative estimate of the everyday life of copepods and the threat assessments they have to perform. Interestingly, this threat ratio tended to be highest in early spring (February to April; Fig. 3), which was generally also the case with the level of pigmentation both among cyclopoid and calanoid copepods, although the variation among lakes was considerable (Table 2). Thus, the level of astaxanthin pigment was not highest when incident UV radiation levels were highest, in July to August (Fig. 2); from the point of view of UV protection, this was not expected. One possible reason for this pattern is that, during summer, the turbidity in the water column is at its maximum due to algal growth, which may reduce the UV threat somewhat. Still, the UV threat was considerably higher during summer than during spring, fall, and winter (Fig. 2). An alternative explanation would be that as temperature increases, so does fish feeding efficiency, confronting the copepods with a higher predation pressure, especially for individuals that are more visible because of pigmentation, which would lead to a need to reduce pigmentation. This position is strengthened by the observation of higher mean pigmentation levels among both calanoid and cyclopoid copepods in lakes with low predation threat compared with those under high predation threat (Fig. 3, Table 2).

Several hypotheses have been advanced to explain variation in copepod pigmentation, including the view that it functions as a food reserve (Hallegraeff et al. 1978, Ringelberg 1980) or that the pigment offers cryptic coloration to deep-dwelling marine organisms exposed to bioluminescence (Herring 1972). Others have stated that the pigment is adaptive for cold-water copepods by absorbing heat from solar radiation, thereby allowing higher metabolism (Brehm 1938) or that the pigment functions as a photo-protectant against UV radiation (Hairston 1976). Most of these explanations lack experimental evidence, and Byron (1982) concluded that only the hypotheses of photo-protection (Hairston 1976) and increased metabolism (Brehm 1938) remain. Byron (1982) based his support for the latter explanation on a negative correlation between temperature and pigmentation ( $r_s = -0.49$ ; Byron 1982: Fig. 4). I found a tendency for a similar inverse relationship between temperature and pigmentation over time in the six lakes investigated ( $r = -0.20$ , NS). However, the explanation for this relation may not be a need for higher metabolism at lower temperatures, but instead a higher risk of predation at higher temperatures and therefore a need for a reduced pigmentation level; this explanation may also, upon reexamination, hold true for the lakes investigated by Byron (1982). Another argument against the view that pigmentation is induced by a metabolic need at low temperatures is that copepods in Arctic lakes, where temperatures are low and constant, may have pigmentation levels differing up to 10 times in magnitude (Hansson 2000b). Hence, among all the hypotheses put forward, the only one remaining is the suggestion that pigmentation functions as photo-protection against UV radiation (Hairston 1976).

Zooplankton cannot synthesize astaxanthin themselves, but receive it by feeding on algae. It may therefore be argued that copepod pigmentation simply mirrors algal astaxanthin concentration, which fluctuates temporally due to several environmental stresses (Boussiba 2000). Although I did not quantify algal pigment content, it is unlikely that these fluctuations explain the astaxanthin variation among copepods in the field study, since pigment changes in the same order of magnitude occurred in the laboratory experiment, where food levels and quality were similar in all treatments. Moreover, Hairston (1979) performed several laboratory and field studies and concluded that differences in pigmentation among copepods lies in individual regulation of metabolic uptake of dietary carotenoids. Similarly, Byron (1982) argued that phytoplankton pigment concentration is not limiting to pigmentation in calanoid copepods. Hence, both my laboratory experiment and earlier studies suggest that the build-up of pigmentation in copepods is to a large extent decoupled from the actual pigment concentration in the food.

The pigmentation level of copepods in Arctic lakes can be six times higher than that of copepods in temperate lakes (Hansson 2000b). Moreover, within a temperate lake pigmentation levels also range widely over the course of a year, as the results from my field study show (Table 2). These observations in natural systems may be explained, however, solely by selective predation on red morphs (Hairston 1979). A possible scenario may be that during summer, when predation pressure is high, the red morphs are preferred as food, leading to a reduction in the mean pigmentation of the population. Accordingly, copepods in lakes with high fish biomass should have lower levels of pigments than in lakes with low fish biomass, which was seen to be the case (Fig. 3). Although selective predation may be important for the patterns revealed in the field study, my complementary laboratory experiment shows that at similar UV threat, high pigmentation is counteracted by the presence of nonfeeding fish predators. Moreover, since the UV radiation in the experiment corresponded to a lightly clouded day during winter/spring, we would, based on data from Fig. 3, expect pigment values among calanoid copepods of about 0.7 and 1.2  $\mu\text{g}/\text{mg DM}$  at high and low predation threat, respectively (Fig. 3). The pigment concentrations among calanoid copepods at the end of the experiment were very close to the predicted, about 0.6 and 1.4  $\mu\text{g}/\text{mg DM}$  with and without predation threat, respectively (Fig. 5), further strengthening the mechanistic connection between the experimental results and the temporal variation in copepod pigmentation in the lakes. Hence, differences in pigmentation among calanoid copepods induced by experimental exposure, and not exposure, to fish cues were of the same order of magnitude as the seasonal variation recorded in natural systems. Together the studies suggest that pigmentation level is not merely a physiological response to changes in season or a population shift brought about by selective predation; rather, it is a balancing act between varying UV and predation threats that the copepod experiences at the level of the individual. The rapid decrease in pigmentation among calanoid copepods during the first 18 d of the experiment (Fig. 5) is most probably attributable to the lower UV threat in the laboratory compared to in the lake. The relatively lower UV threat may also partly explain why cyclopoid copepods showed no differences in pigmentation level between treatments, except for days 3 and 6 (Fig. 5). This does not, however, explain the relatively high pigment level among cyclopoid copepods in the fish treatment throughout the experiment (Fig. 5). The reason why cyclopoid copepods responded to fluctuations in threat ratios in natural systems, but not in the laboratory experiment, is unknown and has to be further investigated.

In the laboratory experiment, calanoid copepods were evenly distributed within the containers, suggesting that they did not actively take advantage of the depth refuge from UV radiation; this was also sug-

gested by Rocco et al. (2002) regarding Antarctic calanoids. Cyclopoid copepods, on the other hand, actually avoided the refuge from UV radiation; they had higher abundances at the surface than at the bottom of the containers, a distribution also found by Neill (1992). However, it may be argued that if individual animals move randomly within their allocated volume, the total daily dose of UV radiation would have been lower in containers with a depth refuge rather than those without, since only 5% and 12% of the surface radiation (320 and 380 nm, respectively) reached below 0.3 m (where the net was attached). If so, we would expect higher pigmentation levels in the nonrefuge treatments, which was not the case. Hence, neither calanoid nor cyclopoid copepods utilized the depth refuge in my experiment, which would have been an alternative strategy instead of increasing the pigment level (Zagarese et al. 1997, Rocco et al. 2002). This does not, however, imply that copepods are not using depth as a refuge in natural systems, since the relatively low UV radiation applied in my experiment may not have been intense enough to trigger vertical migration.

The evolution of phenotypic plasticity has been suggested to lead to success for those entering novel habitats, such as for invading species (Agrawal 2001). With respect to the plasticity in pigmentation among copepods, it may be predicted to improve the odds for survival in an environment where UV radiation is increasing, or eventually will, such as in high-latitude regions (Björn et al. 1998), where UV radiation has a detrimental effect on zooplankton (Rautio and Korhola 2002). Recently, a discussion has emerged regarding whether UV radiation actually affects aquatic organisms, since the optical characteristics of natural waters may protect them from UV-derived injuries, a debate that is especially pronounced regarding amphibians (e.g., Kiesecker et al. 2001, Palen et al. 2002). With respect to copepods, the UV radiation in my studies was not lethal, although nonlethal UV radiation may affect other properties, such as growth and reproduction. Hence, due to their plasticity in photo-protective pigmentation, copepods and possibly some species of *Daphnia* (Hessen 1996, Rautio and Korhola 2001) may be predicted to be more successful than many other zooplankton groups, as the ozone hole continues to grow (Pieintz and Vincent 2000). This notion is in line with recent field experiments showing that altered UV radiation affected the taxonomic composition by reducing abundances of some organisms, while leaving others, among them pigmented copepods, unaffected (Vinebrooke and Leavitt 1999). The ability to adjust the level of protective pigments may prove beneficial in several ways, such as allowing for utilization of shallower depths, thereby increasing the depth range and the access to algal food (Johnsen and Widder 2001). However, there may also be costs associated with pigmentation, which for *Daphnia* is manifested in delayed age at first reproduction and lower clutch size

(Weider 1987, Hessen 1996). In most freshwater and marine systems, copepods are common and often dominant, and thereby they often have strong ecological interactions. One reason for their competence may be their ability to respond with phenotypic plasticity in pigmentation level, thereby reducing mortality from both predation and UV radiation.

In conclusion, the present study supports the view that UV threat is a main determinant of copepod pigmentation (Hairston 1976). However, it also expands this explanation by showing that the predation threat experienced by the copepod reduces pigmentation from red to pale within the individual's lifetime. This suggests that copepods collect information about the relative risk of UV vs. predation and that individual animals continuously make threat assessments, which are manifested, both temporally within a specific lake and spatially among lakes, as a plasticity in pigmentation level.

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#### LITERATURE CITED

- Agrawal, A. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* **294**:321–325.
- Appenzeller, A. R. 1998. Seasonal variability patterns of acoustic estimates of fish biomass and fish size in a lake dominated by coregonids (Lake Constance). *Archiv für Hydrobiologie, Special Issues* **50**:227–236.
- Björn, L.-O., T. Callaghan, C. Gehrke, U. Johansson, M. Sonesson, and D. Gwynn-Jones. 1998. The problem of ozone depletion in northern Europe. *Ambio* **27**:275–279.
- Boriss, H., M. Boersma, and K. H. Wiltshire. 1999. Trimethylamine induces migration of waterfleas. *Nature* **398**:382.
- Boussiba, S. 2000. Carotenogenesis in the green alga *Haematococcus pluvialis*: cellular physiology and stress response. *Physiologia Plantarum* **108**:111–117.
- Brehm, V. 1938. Die Rotfärbung von Hochgebirgsseeorganismen. *Biological Reviews* **13**:307–318.
- Brönmark, C., and L.-A. Hansson. 2000. Chemical communication in aquatic systems—an introduction. *Oikos* **88**:103–110.
- Byron, E. 1982. The adaptive significance of calanoid copepod pigmentation: a comparative and experimental analysis. *Ecology* **63**:1871–1886.
- Dodson, S. 1989. Predator-induced reaction norms. *BioScience* **39**:447–452.
- Hairston, N. G. 1976. Photoprotection by carotenoid pigment in the copepod *Diaptomus nevadensis*. *Proceedings of the National Academy of Sciences* **73**:971–974.
- Hairston, N. G. 1978. Carotenoid photoprotection in *Diaptomus kenai*. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **20**:2541–2545.
- Hairston, N. G., Jr. 1979. The adaptive significance of color polymorphism in two species of *Diaptomus* Copepoda. *Limnology and Oceanography* **24**:15–37.
- Hairston, N. G. 1980. The vertical distribution of diaptomid copepods in relation to body pigmentation. Pages 98–110 in W. C. Kerfoot, editor. *Evolution and ecology of zooplankton communities*. American Society of Limnology



- and Oceanography Special Symposium 3. University Press of New England, Hanover, New Hampshire, USA.
- Hallegraeff, G. M., I. Mous, R. Veeger, G. Flick, and J. Ringelberg. 1978. A comparative study of the carotenoid pigmentation of zooplankton of lake Maarseveen (Netherlands) and of Lac Pavin (Auvergne, France). II. Diurnal variations in carotenoid content. *Comparative Biochemistry and Physiology* **60B**:59–62.
- Hansson, L.-A. 2000a. Synergistic effects of food web dynamics and induced behavioral responses in aquatic ecosystems. *Ecology* **81**:842–851.
- Hansson, L.-A. 2000b. Induced pigmentation in zooplankton: a trade-off between threats from predation and ultraviolet radiation. *Proceedings of the Royal Society of London Series B* **267**:2327–2331.
- Herring, P. J. 1972. Depth distribution of carotenoid pigments and lipids of some oceanic animals. I. Mixed zooplankton, copepods, and euphausiids. *Journal of the Marine Biological Association of the United Kingdom* **52**:179–189.
- Hessen, D. 1996. Competitive trade-off strategies in Arctic *Daphnia* linked to melanism and UV-B stress. *Polar Biology* **16**:573–579.
- Hoogland, R., D. Morris, and N. Tinbergen. 1957. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defence against predators (*Perca* and *Esox*). *Behaviour* **10**:205–236.
- Jobling, M. 1994. Fish bioenergetics. Fish and fisheries series 13. Chapman and Hall, London, UK.
- Johnsen, S., and E. A. Widder. 2001. Ultraviolet absorption in transparent zooplankton and its implications for depth distribution and visual predation. *Marine Biology* **138**:717–730.
- Kiesecker, J., A. Blaustein, and L. Belden. 2001. Complex causes of amphibian population declines. *Nature* **410**:681–683.
- Laurion, I., M. Ventura, J. Catalan, R. Psenner, and R. Sommaruga. 2000. Attenuation of ultraviolet radiation in mountain lakes: factors controlling the among- and within-lake variability. *Limnology and Oceanography* **45**:1274–1288.
- Leech, D., and C. Williamson. 2000. Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? *Ecological Applications* **10**:1530–1540.
- Lessmark, O. 1983. Competition between perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in south Swedish lakes. Dissertation. Lund University, Lund, Sweden.
- Luecke, C., and W. J. O'Brien. 1981. Phototoxicity and fish predation: selective factors in color morphs in Heterocope. *Limnology and Oceanography* **26**:454–460.
- Miki, W. 1991. Biological functions and activities of animal carotenoids. *Pure and Applied Chemistry* **63**:141–146.
- Morris, D. P., H. Zagareze, C. E. Williamson, E. G. Balseiro, B. R. Hargreaves, B. Modenutti, R. Moeller, and C. Queimalinos. 1995. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography* **40**:1381–1391.
- Neill, W. 1992. Population variation in the ontogeny of predator-induced vertical migration in copepods. *Nature* **356**:54–57.
- Palen, W. J., D. E. Schindler, M. J. Adams, C. A. Pearl, R. B. Bury, and S. A. Diamond. 2002. Optical characteristics of natural waters protect amphibians from UV-B in the U.S. Pacific Northwest. *Ecology* **83**:2951–2957.
- Persson, L. 1986. Temperature-induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): implications for coexistence between poikilotherms. *Journal of Animal Ecology* **55**:829–839.
- Pieintz, R., and W. Vincent. 2000. Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. *Nature* **404**:484–487.
- Rautio, M., and A. Korhola. 2001. UV-induced pigmentation in subarctic *Daphnia*. *Limnology and Oceanography* **47**:295–299.
- Rautio, M., and A. Korhola. 2002. Effects of ultraviolet radiation and dissolved organic carbon on the survival of subarctic zooplankton. *Polar Biology* **25**:460–468.
- Rhode, S., M. Pawlowski, and R. Tollrian. 2001. The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*. *Nature* **412**:69–72.
- Ringelberg, J. 1980. Aspects of red pigmentation in zooplankton, especially copepods. Pages 91–97 in W. C. Kerfoot, editor. *Evolution and ecology of zooplankton communities*. American Society of Limnology and Oceanography Special Symposium 3. University Press of New England, Hanover, New Hampshire, USA.
- Rocco, J., O. Oppezzo, R. Pizarro, R. Sommaruga, M. Ferraro, and H. E. Zagarese. 2002. Ultraviolet damage and counteracting mechanisms in the freshwater copepod *Boeckella poppei* from the Antarctic peninsula. *Limnology and Oceanography* **47**:829–836.
- Schindler, D. W., P. J. Curtis, B. R. Parker, and B. R. Stainton. 1996. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature* **379**:705–708.
- Sommaruga, R., and F. Garcia-Pichel. 1999. UV-absorbing mycosporine-like compounds in planktonic and benthic organisms from a high-mountain lake. *Archiv für Hydrobiologie* **144**:255–269.
- Stich, H.-B., and W. Lampert. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature* **293**:396–398.
- Utne-Palm, A. 1999. The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey. *Journal of Fish Biology* **54**:1244–1258.
- van Buskirk, J., and B. R. Schmidt. 2000. Predator-induced phenotypic plasticity in larval newts: trade-offs, selection, and variation in nature. *Ecology* **81**:3009–3028.
- Vinebrooke, R. D., and P. R. Leavitt. 1999. Differential responses of littoral communities to ultraviolet radiation in an alpine lake. *Ecology* **80**:223–237.
- von Elert, E., and G. Pohnert. 2000. Predator specificity of kairomones in diel vertical migration of *Daphnia*: a chemical approach. *Oikos* **88**:119–128.
- Weider, L. J. 1987. Life history variation among low-arctic clones of obligately parthenogenetic *Daphnia pulex*: a diploid-polyploid complex. *Oecologia* **73**:251–256.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* **20**:249–278.
- Williamson, C. E., G. Grad, H. De-Lange, S. Gilroy, and D. M. Karapelou. 2002. Temperature-dependent ultraviolet responses in zooplankton: implications of climate change. *Limnology and Oceanography* **47**:1844–1848.
- Williamson, C. E., R. Stemberger, D. Morris, T. Frost, and S. Paulsen. 1996. Ultraviolet radiation in North American lakes: attenuation estimates from DOC measurements and implications for plankton communities. *Limnology and Oceanography* **41**:1024–1034.
- Zagarese, H. E., M. Feldman, and C. E. Williamson. 1997. UV-B induced damage and photoreactivation in three species of *Boeckella* (Copepoda, Calanoida). *Journal of Plankton Research* **19**:357–367.