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UV avoidance of coregonid larvae

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Although several authors have shown that UV radiation can cause damage to fish larvae, the UV avoidance behaviour of larvae has received little attention. Larval coregonids are vulnerable to the recently enhanced UV levels because immediately after hatching in spring they show a distinct positive phototaxis. The behavior of three size groups of vendace (*Coregonus albula* (L.)) and whitefish (*Coregonus lavaretus* (L.) *s.l.*) larvae were studied under enhanced UV-B irradiation in the laboratory. In addition, field data from four coregonid lakes in Finland were analysed. Coregonid larvae avoided UV radiation both in the laboratory and field. The smallest vendace larvae were the most sensitive to changes in UV irradiation in the laboratory experiments. In the field, the avoidance behaviour was more pronounced in lakes with low dissolved organic carbon (DOC) concentrations than in a lake with a high DOC concentration.

Introduction

Due to stratospheric ozone depletion, the amount of UV-B radiation (280–315 nm) reaching the Earth's surface has increased during recent decades (Kerr & McElroy 1993, Austin *et al.* 1999). As a consequence, higher UV-B irradiances are entering water (Karentz & Bosch 2001). Solar UV-B radiation has caused damage to early developmental stages of fish (Hunter *et al.* 1981, Beland *et al.* 1999, Browman *et al.* 2000), shrimp (Wuebben 2000), crab (Hovel & Morgan 1999), amphibians (Merilä *et al.* 2000, Kiesecker *et al.* 2001), and other aquatic animals (Adams & Shick 2001).

Long-term prediction of future UV levels is uncertain but they may slowly recover to pre-ozone depletion levels during the next 50 years (Madronich *et al.* 1998). The predicted changes are highly variable with season. According to Reuder *et al.* (2001), the enhanced recent UV values in Central Europe during late winter and spring will persist for the next few decades. Until 2015, a further slight increase is predicted for springtime but during summer and autumn, the UV level may remain at recent levels. Taalas *et al.* (1996, 2000) suggested that, relative to 1979–1992 conditions, the 2010–2020 conditions will have a springtime enhancement of erythemal UV doses of up to 90% in the 60–90°N region. The corresponding maximum increases in the annual Northern Hemispheric UV doses are estimated to be 14% in 2010–2020, and 2% in 2040–2050.

The most severe effects of UV-B radiation on fishes are impaired larval development and decreased reproductive capacity (Häder *et al.*

1995). At high latitudes, the late-spring increases in UV-B exposure may affect some species because the UV-B enhancement occurs at critical phases of their development (Häder *et al*. 1995). For example, Kouwenberg *et al*. (1999) found that cod (*Gadus morhua*) embryos exposed in the laboratory to UV-B exhibited high wavelength-dependent mortality. The strongest effects occurred under exposure to wavelengths below 312 nm. However, there was no evidence of a detrimental effect of UV-A radiation (315–400 nm). Williamson *et al*. (1997) found detrimental effects of UV-B on eggs and spawning depth of yellow perch (*Perca flavescens*). Spawning took place much deeper in a high-UVR lake (median = 3.2 m) than in low-UVR lake (median = 0.4 m).

There are three main ways that fish larvae can cope with enhanced UV irradiation: DNA photorepair mechanisms, skin melanin pigmentation, and avoidance behaviour (e.g. Ahmed & Setlow 1993, Häkkinen *et al*. 2002). The distribution of fish larvae in the presence of UV radiation has been little studied although the UV radiation directed movements of other planktonic organisms have been well documented (e.g. Leech & Williamson 2001, Rhode *et al*. 2001). Speekmann *et al*. (2000) studied the vertical distribution of Pacific herring (*Clupea pallasi*) larvae under laboratory conditions. They found that 1-day-old Pacific herring larvae resided about 50 cm deeper in the presence of UV-B radiation than in the absence of UV-B. In addition, larvae displayed positive phototactic behaviour. In their study, 7-day-old larvae displayed less phototactic behaviour and in the absence of UV-B, resided at about 75 cm, while 14-day-old larvae resided even deeper, usually below 100 cm.

Recently, Kelly and Bothwell (2002) studied UV avoidance of newly hatched coho salmon (*Oncorhynchus kisutch*) alevins and two-month-old juveniles in outdoor chambers. Both age classes showed high selective avoidance of UV radiation (280–400 nm) under high solar intensities. Within the UV spectrum, coho responded significantly to UV-A radiation. Under lower solar intensities coho showed no spectral preference.

Vendace (*Coregonus albula* (L.)) and whitefish (*Coregonus lavaretus* (L.) *s.l.*) larvae are vulnerable to enhanced solar UV-B levels because immediately after hatching in spring, they show distinct positive phototaxis (Shkorbatov 1966). Newly hatched coregonid larvae aggregate in shallow littoral areas or in water layers near the surface in the pelagic zone (Karjalainen *et al*. 1998). This behaviour usually prevails for at least six weeks. By the end of the larval period, the phototaxis is replaced by more complicated behavioural patterns and responses to environmental factors (Shkorbatov 1966, Karjalainen *et al*. 2000).

Our objective was to study whether coregonid larvae are able to avoid enhanced UV-B radiation despite their positive phototaxis. In 2000 and 2001, we performed two experimental series in the laboratory to study the UV avoidance of vendace and whitefish larvae. In addition, vertical distribution of coregonid larvae was examined in relation to solar radiation in four Finnish lakes in 1996–2000 to study avoidance behaviour in the field.

Materials and methods

Avoidance experiments in the laboratory

Fertilised vendace (lake Vanajavesi stock in 2000 and lake Pyhäselkä stock in 2001) and whitefish (lake Pyhäselkä stock) eggs were incubated in glass jars until the larvae hatched in April 2000 and 2001. Three size groups of vendace larvae were used in experiments each year and three groups of whitefish larvae in 2001 were also used. In 2000, the mean total lengths ± S.D. of the vendace larvae in different groups were: (1) 12.7 ± 0.9 mm, (2) 18.8 ± 2.0 mm, and (3) 24.2 ± 2.7 mm. In 2001, the vendace groups were: (1) 9.4 ± 0.6 mm, (2) 11.2 ± 0.6 mm, and (3) 15.6 ± 1.1 mm. Whitefish groups were: (1) 12.6 ± 0.7 mm, (2) 13.7 ± 0.9 mm, and (3) 18.3 ± 1.3 mm. The developmental stage of larvae in the corresponding size groups was identical between vendace and whitefish in 2001.

Experimental series I

Experimental series were performed from 13 to 29 June 2000 at the University of Jyväskylä, Fin-

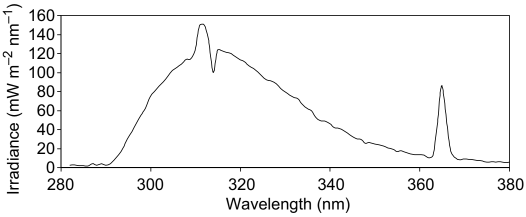

Fig. 1. Spectrum of UV-B lamp measured under cellulose diacetate foil.

land. Two glass aquaria (70 × 28 × 25 cm) were used in each experiment. They were placed side-by-side in a glass fibre pool (1 × 1 m). The circulating water in the pool served as a water bath which regulated the temperatures of the aquaria. A water layer of 5 cm was used in the aquaria to minimise the vertical movement of the larvae. There was no oxygenation in the aquaria. Grey tape was attached to the outside of the aquaria to increase the visibility of the aquarium wall for the larvae.

A visible light fluorescent tube (Philips TLD 36 W/950) and a Q-Panel UVB-313 fluorescent tube were attached above both aquaria. The spectrum of the UV-B lamp is given in Fig. 1. Two light zones of similar size were created in the aquaria. One included UV-B radiation whereas the other one did not. Because the UV-B lamps emitted UV-C radiation (200–280 nm) which is not present in the Earth's atmosphere, it was blocked by cellulose diacetate foil (Clarifoil, 0.13 mm thick). UV-C and UV-B radiation were blocked by Mylar-D foil (DuPont, 0.25 mm thick). Thus, half of an aquarium was covered with Mylar-D foil and the other half with cellulose diacetate.

Before the experiments, UV irradiation was measured at 21 points (10 cm intervals) with a Hamamatsu Photonic Multichannel Spectral analyser (model PMA-11), which measures the wavelength range 280–380 nm. Both UV-B and UV-A irradiation diminished markedly in the middle of the aquarium (Fig. 2). Unweighted UV-B irradiation varied from 51 to 978 mW m^{-2} and unweighted UV-A irradiation from 707 to 1443 mW m^{-2} at different measuring points. Because only the Hamamatsu Spectral analyser was accessible during the experiments, irradiance of visible light (400–800 nm) under cellulose diacetate and Mylar-D foil was measured afterwards with a Macam spectroradiometer (measuring range 280–800 nm). It was the same on both sides ranging from 12.3 W m^{-2} under cellulose diacetate to 12.4 W m^{-2} under Mylar-D foil. The spectra of the visible light are given in Fig. 3.

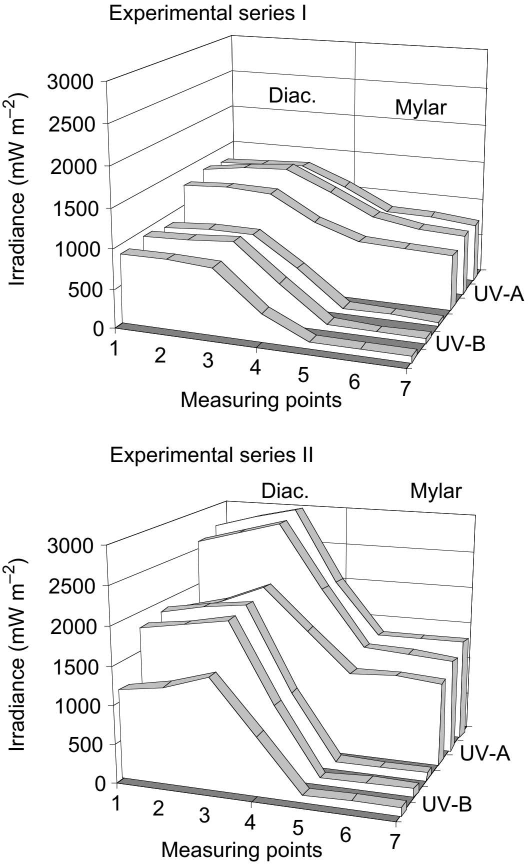

Fig. 2. Unweighted UV-A and UV-B irradiances in different measuring points in test aquarium in experimental series I and II. Three longitudinal measuring grids (left, middle, right) were used. The distance between single measuring points (1–7) in each grid was 10 cm.

Fifteen to twenty hours before the experiment, fifty vendace larvae were taken from the rearing aquarium and transferred into the test aquaria. The temperatures in the rearing and test aquaria were identical. The larvae were fed with *Artemia* nauplii just before the transfer. After the transfer the aquaria were covered with cellulose diacetate and Mylar-D foils. The order of the foils was randomised for every experiment and for both aquaria.

During both the habituation and experimental periods the pool was covered from the side by a

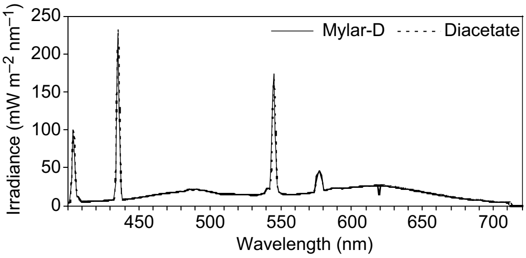

Fig. 3. Spectra of visible light under cellulose diacetate and Mylar-D foil. The spectra are almost identical so the spectrum under diacetate foil can be seen only in a few places.

curtain and it was illuminated with a Philips visible light fluorescent tube. The photoperiod was the same as in the rearing aquarium, 18 h light and 6 h dark.

One experiment included three phases: (1) the control phase without UV radiation, (2) the UV exposure phase, and (3) the recovery phase without UV radiation. The control and recovery phases each lasted for one hour and the exposure phase lasted for two hours. The experiment was repeated twice with two different groups for each larval size to produce four replicates. The position of the larvae was observed by eye every ten minutes. The observer did not know the order of the foils. The number of larvae below the Mylar-D and cellulose diacetate foil in both aquaria was counted through a small window in the curtain.

The mean percentages of larvae under the Mylar-D foil during the three phases in an experiment were calculated. Data were Arcsin-transformed prior to statistical analysis. Analysis of variance (ANOVA) followed by Tukey's test was used to compare differences between the three phases in the experiments and the three size groups of larvae. The dependent variable was the relative number of larvae under the Mylar-D foil and the independent factors were the phase variable and the size group variable.

The water temperature was measured at 21 points in each aquarium before and after the experiment. It did not change during the experiment. The mean temperature was 12.4 °C (± 0.2) in all experiments. There was no significant difference in temperature between different parts of an aquarium or between aquaria.

Experimental series II

Experimental series were performed from 8 April to 7 May 2001. Four glass aquaria (70 × 28 × 25 cm) were used in each experiment with a water layer of 5 cm. They were placed side by side in two glass fibre pools (1 × 1 m) with two aquaria in each pool. White plastic foil was attached to the bottom of the aquaria to increase the visibility of the larvae and on the sides to increase the visibility of the aquarium wall for the larvae.

A Philips visible light fluorescent tube and a Q-Panel UVB-313 fluorescent tube were attached above two aquaria. They served as test aquaria. Above two control aquaria, only a visible light fluorescent tube was attached. In the test aquaria, two different but similar-sized light zones were created. One included UV-B radiation whereas the other one did not. Again, half of an aquarium was covered with Mylar-D foil and the other half with cellulose diacetate.

The effect of Mylar-D and cellulose diacetate foils on the distribution of whitefish larvae was also studied under the visible light regime. The distribution did not differ significantly in aquaria with or without Mylar-D and cellulose diacetate foils (Paired *t*-test, $t_3 = 2.02$, $P > 0.05$). However, foils were used also above the control aquaria.

Irradiation was measured as in experiment I. Both UV-B and UV-A irradiation diminished markedly in the middle of the aquarium (Fig. 2). Unweighted UV-B irradiation varied from 91 to 2055 mW m^{-2} and unweighted UV-A irradiation from 1081 to 2996 mW m^{-2} at different measuring points.

At the beginning of the experiment, twenty vendace or whitefish larvae were taken from the rearing aquarium and transferred into the test and control aquaria. The temperatures in all the aquaria were identical. After the transfer, the test and control aquaria were covered with cellulose diacetate and Mylar-D foils and the pools were covered from the side by a curtain.

In the test (UV exposure) aquaria, there was a two hour habituation phase without UV irradiation and a two hour UV exposure phase. In the control aquaria (visible light regime), illumination was the same during the whole experiment. The experiment was repeated three times with three different groups of larvae for each size group to produce six replicates. The experiments were recorded with four digital video cameras (JVC TK-C1380E or Ikegami ICD-47E). A digital video recorder (Calibur Kalatel model DVMRe-4CS) was used to save the data. There was one video camera above each aquarium. The position of the larvae was observed both from the video film and with naked eye through a small window in the curtain every ten minutes. The number of larvae below the cellulose diacetate foil (UV-B exposure in test aquaria) in each aquarium was counted.

After the experiment the water temperature was measured in each aquarium. The mean temperature was 11.1 °C (± 2.2) in each experiment. There was no difference in temperature between different parts of an aquarium or between aquaria.

A paired-sample *t*-test (SPSS 10.0 for Windows) was used to compare the number of larvae under the Mylar-D foil in the test and control aquaria during the UV exposure phase. The test was performed for three size groups and for both species. The pairs were created using average values of control and exposure treatment in one experiment during UV exposure phase.

Vertical distribution in the field

The differences in the vertical distribution of coregonid larvae between sunny and cloudy periods were analysed from the field data gathered from lakes Paasivesi, Puruvesi, Onkamo and SW Pyhäjärvi in 1996–2000. Secchi depths varied from 3.3 to 8.0 m in the lakes and colour of water from 3 to 35 mg Pt l^{-1} (Table 1). The samples were collected by Bongo nets (Karjalainen *et al*. 1998, 2002) both in the littoral and pelagic zones.

Newly hatched vendace and whitefish larvae were collected immediately after ice-off that occurred between mid-April (SW Pyhäjärvi) and mid-May (Paasivesi, Onkamo). A jet-powered boat with two Bongo nets attached to its front was used. The depth of the water in the randomly selected sampling areas was more than 1 m.

In each sampling tow, one Bongo net gathered larvae from the vertical depth layer of 0–0.4 m and another net from the depth layer of 0.4–0.8 m. In the laboratory, the number of vendace and whitefish larvae in each tow was counted and the relative number of larvae caught by the upper net (0–0.4 m) was calculated. The surface percentages (SP = catch in the upper net/total catch in a tow) of vendace and whitefish larvae were used to compare the vertical distribution of larvae in sunny and cloudy periods.

Cloud cover was estimated visually during each tow and classified into nine (0–8) classes. These original cloud cover values were recoded into three cloud cover classes: CCC 1, no cloud cover (0–2); CCC 2, medium cloud cover (3–5); and CCC 3, full cloud cover (6–8). The cloud cover was used as an indirect estimate of the amount of UV irradiance. According to Seckmeyer *et al*. (1996), the transmittance of the cloud-layer is wavelength-dependent, ranging from 45% in the UV-A to 60% in the UV-B waveband. Thus, thick cloud cover considerably reduces UV irradiance. To make sure there

Table 1. Secchi depth, colour of water, width of the littoral zone and surface area of the four lakes studied. Lake Puruvesi consists of two separate lake basins. The data of water analyses are from the databases of the Finnish Regional Environmental Centres.

Lake	Secchi depth (m)	Colour (mg Pt l^{-1})	Average width of littoral zone (m)	Area (km^2)
SW Pyhäjärvi	3.3	15	65	154
Puruvesi				
Harvanselkä	8.0	5	29	132
Hummonselkä	7.0	10	36	184
Paasivesi	3.5	35	35	101
Onkamo	3.9	15	86	32

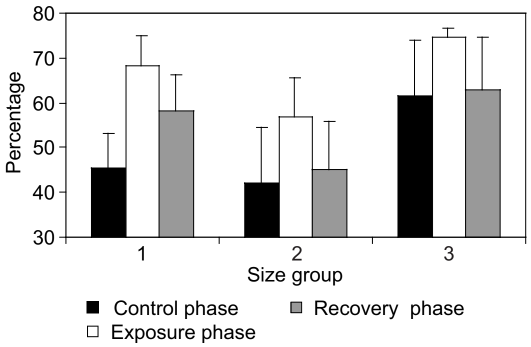

Fig. 4. Mean percentages (± S.D.) of vendace larvae under Mylar-D foil (UV-B cover) in experimental series I.

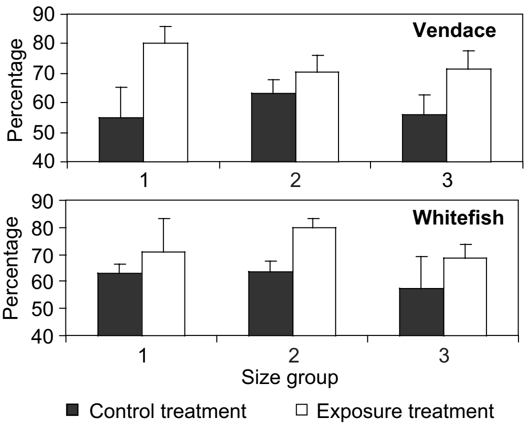

Fig. 5. Mean percentages (± S.D.) of vendace and whitefish larvae under Mylar-D foil (UV-B cover) during the UV exposure in experimental series II.

really were differences in UV irradiance during sampling periods, only CCC 1 and CCC 3 were compared in the analysis.

Before statistical analysis, the SPs were arcsin-transformed. There were no whitefish in lake Onkamo and thus, the analysis was made only for vendace larvae in this lake. Analysis of variance (ANOVA) was used to compare the SPs of vendace and whitefish larvae between two cloud cover classes and five years in each lake.

Results

UV avoidance in the laboratory experiments

In the experimental series I, the number of vendace larvae observed under UV-B cover differed both between phases (ANOVA: $F_{2,9} = 9.70$, $P < 0.05$) and among size groups ($F_{2,9} = 11.32$, $P < 0.05$). The control and recovery phase differed from the exposure phase (Tukey test: $P < 0.05$), but the control phase did not differ from the recovery phase (Tukey test: $P > 0.05$). In the UV exposure phase, the mean percentages of vendace larvae under UV-B cover for the three size groups were: (1) 68%, (2) 57%, and (3) 74% (Fig. 4). The relative number of small larvae under UV-B cover did not differ significantly from the number of medium-sized or large larvae (Tukey test: $P > 0.05$). However, the relative number of medium-sized larvae differed from that of large larvae (Tukey test: $P < 0.05$).

In the experimental series II, the number of vendace larvae in all three size groups was significantly higher in the exposure treatment under UV-B cover (Fig. 5) than in the control treatment (Paired *t*-test: $t_5 = 5.25$, $P < 0.05$, $t_5 = 2.65$, $P < 0.05$ and $t_5 = 3.72$, $P < 0.05$, respectively). For whitefish larvae, the number under UV-B cover was significantly higher during the UV exposure in size groups 2 and 3 (Paired *t*-test: $t_5 = 6.40$, $P < 0.05$ and $t_5 = 2.66$, $P < 0.05$, respectively). In size group 1 the difference was not significant ($t_5 = 1.53$, $P > 0.05$).

Vertical distribution in the field

In lakes Puruvesi, Onkamo, and SW Pyhäjärvi, the mean SPs of vendace larvae were higher in CCC 3 (cloudy) than in CCC 1 (sunny) (Fig. 6). The SPs differed significantly between CCCs in lakes Onkamo (ANOVA: $F_{1,226} = 112.49$, $P < 0.05$), Puruvesi ($F_{1,218} = 23.97$, $P < 0.05$) and SW Pyhäjärvi ($F_{1,429} = 20.46$, $P < 0.05$). They did not differ in lake Paasivesi (ANOVA: $F_{1,82} = 0.21$, $P > 0.05$). There were also differences in SPs between years in lakes Onkamo (ANOVA: $F_{4,223} = 3.69$, $P < 0.05$), Puruvesi ($F_{4,215} = 8.20$, $P < 0.05$) and SW Pyhäjärvi ($F_{4,426} = 13.76$, $P < 0.05$), whereas in lake Paasivesi SPs did not differ between years (ANOVA: $F_{4,79} = 1.42$, $P > 0.05$).

In lakes Puruvesi and SW Pyhäjärvi, the mean SPs of whitefish larvae were higher in CCC 3 than in CCC 1 (Fig. 6). The SPs did not differ between CCCs in lakes Paasivesi (ANOVA: $F_{1,36} = 2.18$, $P > 0.05$) and Puruvesi ($F_{1,112} = 1.29$, $P > 0.05$) but, in SW Pyhäjärvi the difference was statistically significant (ANOVA: $F_{1,332} = 12.94$, $P < 0.05$). Between study years SPs differed significantly in lakes Puruvesi (ANOVA: $F_{4,109} = 6.15$, $P < 0.05$) and SW Pyhäjärvi ($F_{4,329} = 10.72$, $P < 0.05$) but not in lake Paasivesi (ANOVA: $F_{4,33} = 0.74$, $P > 0.05$).

Discussion

Vendace and whitefish larvae showed a tendency to adjust their vertical position according to light conditions and avoid UV radiation in both laboratory experiments and lake data. Coregonid larvae escaped the UV radiation under UV-B cover under experimental conditions and in lakes they resided deeper during sunny periods than during cloudy periods.

The highest irradiances of UV were different in experimental series I and II. In series I, the highest unweighted irradiance of UV-B was 978 mW m^{-2} and that of UV-A 1443 mW m^{-2}. In series II, they were twice as high, 2055 mW m^{-2} (UV-B) and 2996 mW m^{-2} (UV-A), respectively. The highest dose rates of UV-B at Jokioinen, Finland, in the beginning of May in 2000 were 700–900 mW m^{-2} and dose rates of UV-A were 3900–4200 mW m^{-2} (J. Kaurola pers. comm.). This means that in our experiments the highest irradiance of UV-B in experimental series I was at the same level as the highest ambient levels in Finland in spring and in series II it was twice as high. Because ambient UV-B irradiances are expected to increase in the future especially in spring, they may be somewhere between the irradiances used in experimental series I and II. However, the spectrum of the UV-B lamp is somewhat different from that of sunlight, especially in the UV-A range. The highest UV-A irradiances in our experiments were lower than highest ambient levels.

Statistical analysis of experimental series I revealed that the only difference in relative number of vendace larvae under UV-B cover during the UV exposure phase was between medium-sized and large larvae. However, the difference in relative numbers between the consecutive control and exposure phase was highest in small larvae (68% – 45% = 23%). In medium-sized and large larvae it was 15% and 12%, respectively. In experimental series II, the largest difference in relative numbers of larvae under UV-B cover between the concurrent control and exposure treatment was also in small larvae. The difference was 25%. In large larvae it was 15% and in medium-sized larvae only 7%. In whitefish larvae the differences were 16%, 11%, and 8% in medium-sized, large and small larvae, respectively.

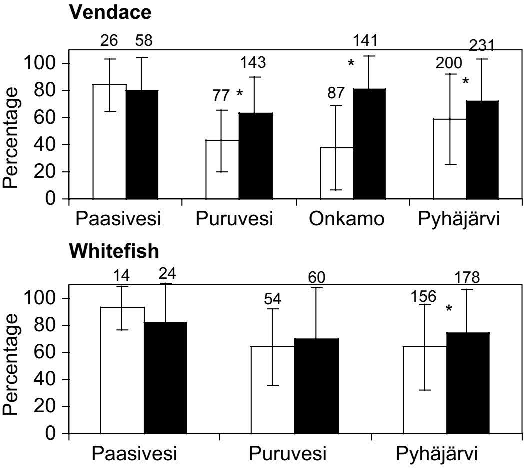

Fig. 6. Mean surface percentages (± S.D.) of vendace and whitefish larvae in different lakes in sunny (cloud cover class CCC 1, white bars) and cloudy (CCC 3, black bars) sampling periods. Number of tows and statistically significant differences (* = *t*-test $P < 0.05$) between the pairs are shown above the bars.

These results suggest that the smallest vendace larvae are the most sensitive to UV radiation of the species and size groups that we studied. It also seems that whitefish larvae are less sensitive to changes in UV irradiation than vendace larvae. Speekmann *et al.* (2000) noticed that the youngest Pacific herring larvae were the most sensitive to UV-B radiation. However, because older larvae in their study resided in deeper water in the absence of UV-B, it is possible that the UV-B radiation was insufficient to be detected or was less harmful to the older larvae. In our experiments, UV irradiation was the same to all size groups. On the other hand, Kelly and Bothwell (2002) did not find any difference in UV avoidance between newly hatched coho salmon alevins and two-month-old juveniles.

The attenuation depth of UV radiation in freshwater lakes depends primarily on the concentration of dissolved organic carbon (DOC) in the water (Morris *et al.* 1995, Bukaveckas & Robbins-Forbes 2000, Huovinen *et al.* 2000). For example, in some regions of North America 25% of the lakes have 1% attenuation depths for UV-B radiation (320 nm) on the order of 4 m or more. In other regions, 75% of the lakes have 1% attenuation depths for UV-B shallower than 0.5 m. Attenuation depths of UV-A radiation (380 nm) are about 2.5 times as deep as those for UV-B (Williamson *et al.* 1996). However, the DOC concentrations in the North American lakes studied at this time (0.88–10.68 mg l^{-1}) are somewhat lower than concentrations in Finland. Huovinen (2000) and Huovinen *et al.* (2000) measured the vertical attenuation of UV radiation in four humic lakes in Central Finland with DOC ranging from 5.2 to 16.0 mg l^{-1} and colour of water from 10 to 80 mg Pt l^{-1}. They found that the depth where the UV-B irradiance was reduced to 1% of the irradiance just beneath the surface varied from 0.12 to 0.57 m (315 nm) in the study lakes. The 1% penetration depth in the UV-A waveband was from 0.23 m to 1.08 m at 380 nm.

Of our study lakes, Puruvesi has the clearest water (colour 5–10 mg Pt l^{-1}, Table 1). According to Huovinen (2000), the 1% attenuation depth of UV-B radiation (315 nm) in this kind of lake is about 0.6 m. Thus, there may have been some UV-B radiation present in the lower water column (0.4–0.8 m). In all the other lakes the colour of water was so high (15–35 mg Pt l^{-1}) that UV-B radiation is present only in the upper water column (0–0.4 m). Furthermore, UV-A radiation (380 nm) is present in the lower water column in lakes Puruvesi, Onkamo, and SW Pyhäjärvi but not in Paasivesi.

The difference in percentages of vendace larvae at the lake surface between cloudy and sunny periods was greatest in lake Onkamo. In lake Paasivesi, the mean surface percentages of vendace larvae did not differ between cloud cover classes and surface percentages were even higher during sunny than cloudy periods. However, the colour of the water in lake Paasivesi was darker than in the other study lakes (35 Pt l^{-1} *vs.* 5–15 mg Pt l^{-1}) and the attenuation depth for UV radiation was lower. We conclude that vendace larvae did not have to change their vertical position in humic lake Paasivesi as much as in the other lakes to avoid high UV levels.The amplitude of vertical movement was probably so narrow (less than 40 cm) that it could not be detected in our study.

The percentages of whitefish larvae at the lake surface differed between cloudy and sunny periods only in SW Pyhäjärvi. They did not differ in lake Puruvesi, which had the clearest water of the study lakes. Similar to the situation for vendace larvae, the mean surface percentage in lake Paasivesi was higher during sunny than during cloudy periods. Because coregonid larvae are positively phototactic, it is possible that in humic lake Paasivesi where the attenuation of UV radiation is high, vendace and whitefish larvae are able to aggregate at the surface (top 40 cm) during sunny periods. In other clearer study lakes this may be impossible due to harmful irradiances of UV radiation.

There are several other factors than UV irradiation that may partly explain the vertical distribution of larvae in the field data. These factors include the vertical distribution of zooplankton, which are food for the coregonid larvae, wind-driven currents, and water temperature. For example, Leech and Williamson (2001) and Rhode *et al.* (2001) noticed that *Daphnia* species avoided UV radiation both under natural solar radiation and in laboratory exposures to UV. A large proportion of individuals migrated downward in the presence of UV radiation, whereas those in the UV-shielded treatments tended to remain closer to the surface. However, in our experimental series I and II coregonid larvae avoided UV radiation with no zooplankton in the water and similar avoidance behaviour is suggested to occur under field conditions as well.

The water temperature is low in Finnish lakes in spring when coregonid larvae hatch and the water column is not yet stratified. Therefore, during sunny periods surface water temperature is likely to rise. Because coregonid larvae prefer warmer water than is found in the lakes during hatching (Shkorbatov 1966), the vertical position of larvae should be closer to the surface during sunny periods than during cloudy periods. However, it was just the opposite in our data. The effect of wind-driven currents on the larvae is difficult to estimate, but the mean wind velocities in our lake sampling were only 2–4 m s^{-1}.

Our results indicated that coregonid larvae are capable of avoiding UV radiation, but we were unable to clarify whether UV-B or UV-A radiation is the major directive factor in avoidance behaviour of vendace and whitefish larvae. Microspectrophotometric analysis of spectral sensitivity of larval retinas would give important information about the ability of larval coregonids to sense UV radiation (e.g. Beaudet *et al*. 1993). However, in the field the perception of UV radiation is not necessarily needed. The avoidance of high visible light levels may help larvae in avoiding UV radiation.

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