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Metabolic depression in UV-B exposed larval coregonids

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Exposure to UV-B radiation has been found to have negative effects on fish, such as reduced survival and growth, but sublethal effects, such as metabolic costs of increasing UV-B irradiance, have received little attention. We studied the oxygen consumption rates of vendace and whitefish larvae under enhanced UV-B irradiance in the laboratory. In addition, we studied energy allocation for digestion and activity in whitefish larvae. UV-B exposure had no clear effect on the minimum or routine oxygen consumption rates of vendace larvae, but the metabolic scope of vendace larvae and the maximum oxygen consumption rates of both vendace and whitefish larvae decreased. In the allocation experiments, enhanced UV-B irradiance mainly decreased the oxygen consumption allocated for digestion in whitefish larvae. In the field, the direct impact of increased UV-B irradiance on coregonid digestion and growth will be negligible, but some indirect effects, such as increased risk of predation, are possible.

Introduction

Most studies of the effects of UV-B radiation (280–315 nm) on fish have focused on direct effects on growth and survival. Exposure to UV-B radiation has been found to have negative effects, including reduced embryonic survival (Williamson *et al*. 1997, Kouwenberg *et al*. 1999), reduced larval survival and growth (Hunter *et al*. 1979, 1981) and dermal damage (Blazer *et al*. 1997), although sensitivity varies widely between species and life history stages (Blazer *et al*. 1997, Kouwenberg *et al*. 1999, Steeger *et al*. 1999). In general, sublethal effects of UV-B radiation have received less attention. This is surprising because direct, lethal effects may on some occasions be ecologically less important than sublethal effects. One example of sublethal effects in animals is metabolic depression (Guppy & Withers 1999). It can be induced e.g. by toxicants (Jørgensen *et al*. 2001) or other abiotic factors, such as environmental oxygen concentration or temperature (Cech *et al*. 1979). Both abiotic and biotic (parasites, diseases) disturbances can decrease the metabolic scope due to depression of the maximum capacity.

In larval and juvenile fish, effects of swimming (e.g. Puckett & Dill 1984, Soofiani & Priede 1985, Dabrowski 1986, Kaufmann 1990), body mass (e.g. Karjalainen *et al*. 1995, Giguere *et al*. 1988), feeding (e.g. Mehner & Wieser 1994, Hunt von Herbing & White 2002) and temperature (e.g. Karjalainen *et al*. 1995, Hanel *et al*. 1996, Hunt von Herbing 2002) on metabolic costs have been studied intensively. Metabolic costs of increasing UV-B irradiance (Kerr

& McElroy 1993, Austin *et al*. 1999) have been studied very little, although metabolic disturbances may substantially affect larval growth and survival rates. Steeger *et al*. (2001) found no effect of enhanced UV-B irradiance on oxygen consumption rates in juvenile North Sea plaice (*Pleuronectes platessa*), but Freitag *et al*. (1998) noticed impairment of respiratory control in plaice larvae. To our knowledge the only clear evidence of UV induced metabolic depression in fish is presented by Winckler and Fidhiany (1999). They showed that enhanced UV-A (315–400 nm) irradiance caused general metabolic depression in convict cichlid (*Cichlasoma nigrofasciatum*) after long-term exposure.

During the larval phase, fish are the most vulnerable to high UV levels and make good subjects for UV studies. Most fish larvae are transparent having very little photoprotective pigmentation (Freitag *et al*. 1998). In addition, many fish larvae are positively phototactic and thus spend most of the time in the photic zone where UV irradiance is highest (Häder *et al*. 1995). Coregonid fish are widely distributed in the northern hemisphere and they have great commercial and recreational values in Scandinavian inland waters. Larvae hatch in spring when the highest irradiances are encountered in the northern hemisphere (Taalas *et al*. 2000, 2002), and spend several weeks after hatching in shallow littoral areas or in surface waters in the pelagic zone (Viljanen *et al*. 1995) where they may be exposed to episodes of high UV irradiance.

The aim of this study was to evaluate how predicted future UV-B levels might affect the oxygen consumption rates in vendace (*Coregonus albula*) and whitefish (*Coregonus lavaretus*) larvae, and what the consequences would be. We also studied the energy allocation for digestion (SDA) and activity under enhanced UV-B irradiance in whitefish larvae.

Material and methods

Routine rate experiments

We measured oxygen consumption of larval vendace (Lake Pyhäselkä stock) in a series of experiments using an intermittent-flow respirometer (Forstner 1983, Forstner *et al*. 1983) equipped with polarographic oxygen sensor (POS, YSI 5750). The respirometer system included three parallel acrylic swimming chambers. After each measurement, the oxygen electrode chamber and the fish chambers were flushed with fully aerated water. Bacterial oxygen consumption in the respirometer was measured at the beginning and at the end of each experiment and was subtracted from the total decline of oxygen. Water temperature and changes in air pressure during the measuring period were also taken into account for the calculations (according to Forstner & Gnaiger 1983).

Before the experiments, larvae were collected randomly from the rearing aquaria and transferred to the exposure aquaria (length 40 × wide 25 × height 20 cm). The temperature in both aquaria was equal. In every experiment, there was a control treatment without UV-B radiation and a UV-B exposure treatment. In the control treatment, UV-A radiation (Q-Panel UVA-340) and visible light (Philips TLD 36W/950 daylight) lamps were used and UV-B radiation produced by the UV-A lamps was blocked by a Mylar-D filter. In the UV-B exposure treatment, UV-A, visible light and adjustable UV-B lamps (Q-Panel UVB-313) were used and UV-C radiation (200–280 nm) produced by the UV-B lamps was blocked by a cellulose diacetate filter. During the three hour exposure, all treatments were replicated (two aquaria per treatment). The erythemal (CIE) weighted UV dose in the UV-B exposure treatment was 3.58 kJ m^{-2}.

In the rearing aquaria, larvae were fed *Artemia* nauplii *ad libitum*. Before the measurements, larvae were starved for 18 hours. Oxygen consumption of 10–60 (depending on the total mass, in every size group approximately 150 mg) vendace larvae sampled randomly from the exposure aquaria was recorded for 15 minutes in each chamber. The average rate during this period was extrapolated to an hourly value. Thus, each chamber represented one experimental unit. One experiment lasted for 24 hours yielding 24 hourly observations. The maximum (R_{max}) and minimum (R_{min}) oxygen consumption rates in these experiments were, respectively, the means of the three highest and three lowest values

obtained during the 24 hour period. The routine rate was the mean of all values obtained during the 24 hour period, excluding the values used for the maximum and minimum rates. The metabolic scope was the difference between maximum and minimum rates. The mean fresh mass (± S.D.) and developmental stages of larvae and water temperature in the experiments are shown in Table 1.

Maximum rate experiments

We measured maximum oxygen consumption rates (R_{max}) of larval vendace (Lake Pyhäselkä stock from the University of Joensuu hatchery) and whitefish (Rautalampi stock from the hatchery of Finnish Game and Fisheries Research Institute, Laukaa) exposed to different UV doses in a series of swimming respirometer experiments. The maximum oxygen consumption rates of the 3.58 kJ m^{-2} UV treatment were taken from the routine rate experiments. The same respirometer was used as in the routine rate experiments but the three parallel acrylic swimming chambers in the swimming respirometer had lower diameter than in the intermittent-flow respirometer. Thus, water flow and swimming speed of fish in the swimming respirometer were higher than in the intermittent-flow respirometer. The maximum oxygen consumption rates are, however, comparable between the different respirometer configurations. Karjalainen *et al*. (1995) have shown that after introduction into the respirometer chambers of intermittent-flow respirometer the metabolic rates of juvenile vendace and whitefish did not differ from the maximum values obtained in swimming the respirometer.

In every experiment, there was a UV-B exposure treatment and a control treatment without UV radiation. Therefore, in the exposure treatment the UV lamps were the same as in the routine rate experiments, but in the control treatment larvae were exposed only to visible light. Before the exposure, larvae were fed *Artemia* nauplii *ad libitum* to ensure that UV irradiation did not affect the quantity of food consumed. During the exposure, all treatments were replicated (four aquaria per treatment). The CIE weighted UV doses varied from 1.81 kJ m^{-2} to 3.65 kJ m^{-2} for vendace larvae, and from 1.37 kJ m^{-2} to 5.58 kJ m^{-2} for whitefish larvae (Table 1). The average daily dose in southern Finland in the beginning of May (between 2–8 day) was 1.66 kJ m^{-2} measured at Jokioinen (60.82°N, 23.50°E) 1998–2000, but maximum daily doses in May 2000 were ~3 kJ m^{-2} (J. Kaurola, Finnish Meteorological Institute, pers. comm.). The mean fresh masses (± S.D.), developmental stages of larvae and water temperatures in different experiments are shown in Table 1.

During the measurement period, a school of five fish sampled randomly from the exposure aquaria swam against the current and maximum oxygen consumption rates were recorded. The duration of the exercise and the water current (4–6 cm s^{-1}, approximately 2 BL s^{-1}) were adjusted according to the preliminary swimming tests with unfed larvae (Karjalainen *et al*. 2003). In both the maximum rate and energy allocation experiments, oxygen consumption was recorded for seven minutes in each chamber, and the aver-

Table 1. Fresh mass (mean ± S.D.) of whitefish and vendace larvae and water temperature in different experiments. Number of larvae are shown in parentheses and larval developmental stages (LDS) according to Luczynski *et al*. (1988) with Roman numerals. In experiment with CIE weighted UV irradiance of 3.58 kJ m^{-2} the fresh mass (± S.D.) was the mean of the three size groups used.

UV dose (kJ m^{-2})	Whitefish mg ± S.D. (*n*)	Vendace mg ± S.D. (*n*)	Temperature (°C)
1.37	30.8 ± 2.7 (12) VI–VII	–	14
1.81	35.4 ± 0.7 (6) VI–VII	16.1 ± 0.6 (3) V–VI	12
3.58		5.5 ± 3.7 (27) II–VI	12
3.65	24.7 ± 3.0 (24) V–VI	10.6 ± 1.4 (24) III–IV	14
5.35	26.6 ± 4.3 (16) V–VI	–	12
5.58	59.0 ± 7.1 (12) VIII–IX	–	14

age rate during this period was extrapolated to an hourly value. Thus, the group of fish was first intoduced into a chamber and after seven minutes they were taken out. This procedure was repeated three times with one-hour intervals and with the same group of fish. The mean value of the three repeated measurements was used for further analysis because there was no difference in oxygen consumption between the measurements (ANOVA: $p > 0.05$).

Energy allocation experiments

We examined energy allocation by larval whitefish (Rautalampi stock) for activity and digestion in two swimming respirometer experiments. First, larvae were starved for 15 hours. After that, half of the fish were fed *Artemia* nauplii for two to three hours and the other half remained without food before the oxygen consumption measurements. In experiment 1, only a high ration (*ad libitum*, ratio 2) was offered and in experiment 2, low (10% of fresh mass, ratio 1) and high (*ad libitum*, ratio 2) rations were offered. During the feeding period, all treatments were replicated (four aquaria per treatment). After the feeding period, one group of both fed and unfed fish was exposed to UV-B radiation for three and two hours in experiment 1 and 2, respectively. This ensured that UV-B eposure had no effect on the quantity of food consumed. The lamps used were as in the maximum rate experiments. The CIE weighted UV doses were 5.58 kJ m^{-2} and 5.35 kJ m^{-2} in experiment 1 and 2, respectively. After the exposure, oxygen consumption of 6–24 schools (five larvae per school) sampled randomly from the exposure aquaria was measured in the swimming chambers. The costs of digestion (R_{sda} = the post-prandial rise in the metabolic rate, SDA as in Jobling 1983) were calculated by subtracting the mean R_{max} of unfed larvae from the mean R_{max} of fed larvae.

Statistics

In the routine rate and allocation experiments, two-way ANOVA was used. The fixed factors in the routine rate experiments were UV treatment (with and without UV radiation) and measuring time, and in the allocation experiments UV treatment and food ration. In the maximum rate and allocation experiments, a mean value of three repeated measurements was used for analysis. In the maximum rate experiments, ANOVA was not used due to the differences between the two respirometer systems and because experiments were performed in separate sessions (three for vendace and five for whitefish larvae) during a longer time period. Instead, the difference in each experiment between control and exposure treatment was tested by the *t*-test. Regression analysis was then performed to estimate UV dose that affected maximum oxygen consumption rates of coregonid larvae. The regression analysis was performed for the combined data of vendace and whitefish larvae because only three UV doses were used for vendace larvae. The relative difference (RD) in the maximum oxygen consumption rates was calculated with the equation:

$$RD\% = [(\text{mean } R_{max} \text{ of the UV exposed larvae}) - (\text{mean } R_{max} \text{ of the control larvae})] / (\text{mean } R_{max} \text{ of the control larva}) \times 100.$$

Results

Routine rates

Both the maximum oxygen consumption rate (ANOVA: $F_{1,9} = 11.86$, $p < 0.01$) and the metabolic scope of vendace larvae were significantly ($F_{1,9} = 7.59$, $p < 0.05$) lower in the UV-B exposure treatment than in the control treatment without UV-B radiation (Fig. 1). The minimum and routine oxygen consumption rates were also slightly lower in the UV-B exposure treatment than in the control treatment, but the differences were not significant (ANOVA: $F_{1,9} = 0.78$ and 2.15 in maximum and routine rates, respectively, $p > 0.05$ in both cases).

Maximum rates

In the experiments with the CIE weighted UV dose of 3.65 kJ m^{-2} and above, the maximum oxygen consumption rates of whitefish larvae

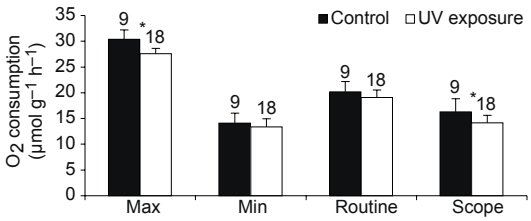

Fig. 1. Mean values for maximum, minimum and routine oxygen consumption rates and for metabolic scope of vendace larvae with and without UV-B radiation. Vertical lines represent the standard errors of the mean. Number of groups (10–60 larvae in a group) used are given above the bars. Significant ($p < 0.05$) differences between the control and exposure treatments are indicated with asterisks.

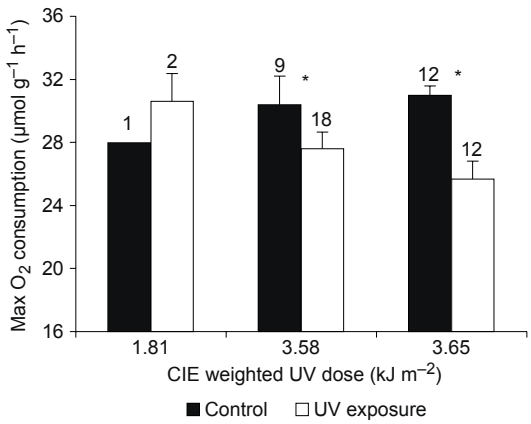

Fig. 3. Mean maximum oxygen consumption rates of vendace larvae after different UV exposures. Vertical lines represent the standard errors of the mean. Number of groups (five larvae in a group) used are given above the bars. Significant ($p < 0.05$) differences between the control and exposure treatments are indicated with asterisks.

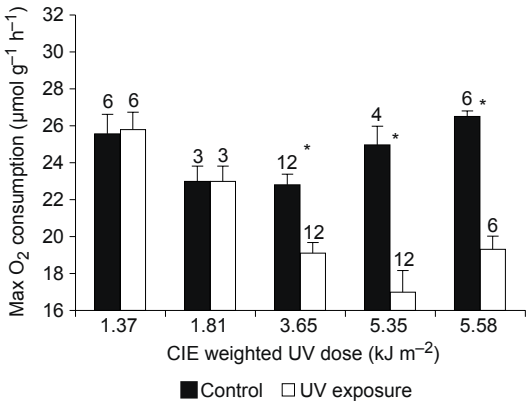

Fig. 2. Mean maximum oxygen consumption rates of whitefish larvae after different UV exposures (CIE weighted UV irradiance). Vertical lines represent the standard errors of the mean. Number of groups (five larvae in a group) used are given above the bars. Significant ($p < 0.05$, asterisk) differences between the control and exposure treatments are indicated with asterisks.

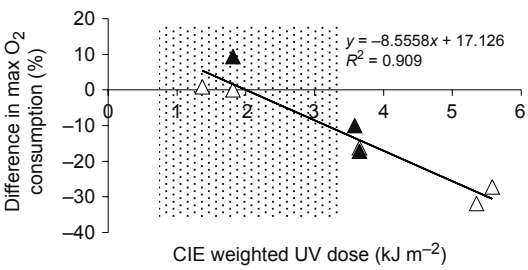

Fig. 4. Relative difference (RD% = [(mean R_{max} of the UV exposed larvae) – mean R_{max} of the control larvae)]/(mean R_{max} of the control larvae)) in the maximum oxygen consumption rates of vendace and whitefish larvae in relation to the CIE weighted UV irradiance. Grey area denotes the ambient daily UV doses in May.

were significantly (*t*-test: 3.65 kJ m^{-2} level: t_{22} = 4.53; 5.35 kJ m^{-2} level: t_{14} = 5.22; 5.58 kJ m^{-2} level: t_{10} = 9.17; $p < 0.05$ in all cases) lower in the exposure treatment than in the control treatment (Fig. 2). In the lower UV exposures, maximum oxygen consumption did not differ between the exposure and control treatments (*t*-test: 1.37 kJ m^{-2} level: t_{10} = 0.16; 1.81 kJ m^{-2} level: t_4 = 0; $p > 0.05$ in both cases). Whitefish larvae were exposed to lower and higher UV doses than vendace larvae.

In the highest UV doses used for vendace larvae, 3.58 and 3.65 kJ m^{-2}, the maximum oxygen consumption rates were significantly (3.58 kJ m^{-2} level: *see* routine rate experiments; *t*-test: 3.65 kJ m^{-2} level: t_{22} = 4.13, $p < 0.05$) lower in the exposure treatment than in the control treatment (Fig. 3). The maximum oxygen consumption rate and the statistical test result of the 3.58 kJ m^{-2} UV treatment were taken from the routine rate experiments.

The relative difference in the maximum oxygen consumption rates between UV-exposed and control larvae (all vendace and whitefish experiments included) increased significantly with increasing UV dose (Regression analysis: $F_{1,6}$ = 12.44, $p < 0.05$; Fig. 4). The highest change (–32%) was observed with a UV dose of 5.35 kJ m^{-2} for whitefish larvae.

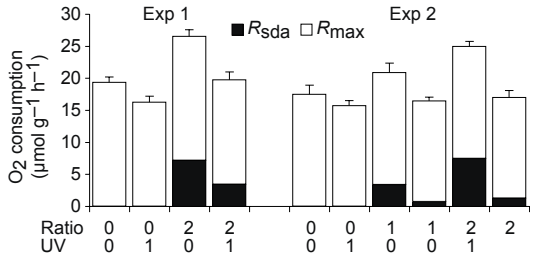

Fig. 5. Oxygen consumption rates of fed (ration 1 = low, and ration 2 = *ad libitum*) and unfed (ration = 0) larval whitefish without UV radiation (UV = 0) and under UV radiation (UV = 1) in the two swimming respirometer experiments. The costs of digestion (R_{sda}) and maintenance and activity ($R_{m + act}$) are given separately and the vertical lines represent the standard errors of the mean of the maximum oxygen consumption rates (R_{max}).

Allocation for activity and digestion

The maximum metabolic rate of the unfed larvae ($R_{m + act}$) was lower than that of the fed larvae ($R_{m + act + sda}$), and both the maximum rate and the digestion costs (R_{sda}) of the larvae fed the high ration were higher than those of the larvae fed the low ration (Table 2 and Fig. 5). UV radiation decreased the maximum rates in both experiments 1 and 2. Both the food ration (ANOVA: experiment 1: $F_{1,17} = 9.48$; experiment 2: $F_{3,62} = 9.38$; $p < 0.01$ in both cases) and UV radiation significantly (experiment 1: $F_{1,17} = 26.80$; experiment 2: $F_{1,62} = 14.03$; $p < 0.01$ in both cases) affected the maximum rates and in experiment 2, the interaction (ration × UV) was also significant ($F_{3,62} = 3.56$, $p < 0.05$). Thus, the decrease in the maximum metabolic rates in the larvae fed the high ration was higher (25%–30% reduction) than that in the larvae fed the low ration or without food (10%–20% reduction).

Under UV radiation, the digestion costs decreased much more (52%–83%) as compared with those in the control group, than did the activity and maintenance costs (10%–15%). Also, the SDA decreased more in the high than in the low ration treatment and the highest decrease in SDA (83%) was measured in the larvae fed the high ration in experiment 2. The constant swimming speed in the swimming chambers kept the activity (R_{act}) and maintenance costs (R_m) at a constant level.

Discussion

In our study, UV-B exposure under laboratory conditions had no clear effect on the minimum or routine oxygen consumption rates of vendace larvae, but the metabolic scope of vendace larvae and the maximum oxygen consumption rates of both vendace and whitefish larvae decreased. However, the doses needed to decrease the metabolic scope and the maximum oxygen consumption rates were higher than present ambient daily doses in Finland during the hatching of coregonids. Because UV irradiance in spring is expected to increase during the next few decades (Kerr & McElroy 1993, Austin *et al.* 1999), CIE weighted daily doses of 3–4 kJ m^{-2} are realistic (Taalas *et al.* 2000) at least during calm, sunny days and ozone depletion. Thus, positively phototactic (Bogdanova 1972, Karjalainen *et al.* 1998) coregonid larvae may occasionally be exposed to UV levels high enough to decrease their maximum

Table 2. Fresh mass and maximum oxygen consumption rate (number of cases in parentheses) of the fed (low or high ration) and unfed (no food) larval whitefish without UV radiation (no UV) and under UV radiation (with UV) in the swimming respirometer experiments. Asterisks and dashes indicate the significant ($p < 0.05$) and insignificant ($p > 0.05$) difference between the food rations, respectively.

Experiment	Fresh mass ± S.D. (mg)	Temp. (°C)	Maximum metabolic rate R_{max} ± S.D. (µmol g^{-1} h^{-1}) (*n*)				
			No food		Low Ration		High Ration
1: no UV	57.6 ± 4.0	14	19.4 ± 2.0 (6)	*	no data		26.5 ± 2.3 (6)
1: with UV	53.7 ± 4.1	14	16.3 ± 2.6 (6)	*	no data		19.8 ± 3.0 (6)
2: no UV	25.6 ± 4.8	12	17.5 ± 4.1 (8)	–	20.9 ± 4.9 (11)	*	25.0 ± 1.6 (4)
2: with UV	27.6 ± 3.8	12	15.7 ± 2.8 (12)	–	16.5 ± 3.1 (24)	–	17.0 ± 3.8 (12)

aerobic performance and metabolic scope.

Even short-term depression in maximum aerobic capacity has several disadvantages to larval fish in nature. After hatching, coregonid larvae have to swim continuously in order to stay in the photic zone (Karjalainen *et al*. 2002). In strong, wind-induced currents, decreased metabolic scope means that larvae are less able to stay in the photic zone where are the most abundant food resources and the water is warmer and better aerated than in the aphotic zone. If those circumstances prevail for a long period of time larvae may starve and mortality may increase.

On the other hand, rapidly growing larvae can use almost all of their available metabolic power for growth (Hunt von Herbing & White 2002). In this case, decreased metabolic scope from high UV doses decreases growth rate and prolongs the time spent in the small, vulnerable larval phase with high risk of predation (Miller *et al*. 1988). Lowered maximum oxygen uptake rate can also mean that under predation risk and during the postprandial metabolic peak, larvae do not have enough aerobic capacity to escape predators successfully (Conover & Schultz 1997). Thus, both lower growth rate and maximum aerobic capacity influence the larval survival probability.

Karjalainen *et al*. (2003) suggested that the energy budget of larval whitefish is additive, which means that each component of the budget has its own allocation and this specific capacity cannot be used for other purposes. In this study, UV radiation decreased the maximum aerobic capacity and mainly the oxygen consumption allocated for digestion in whitefish larvae. This suppression of digestion can be caused by direct disturbance of the digestive system (*see* below) or by compensatory (or competitive) effect on energy allocation. Compensatory allocation means that if a fish is swimming at its maximum speed, it cannot digest food simultaneously (Priede 1985). This may be inevitable under unfavourable conditions where metabolic scope is insufficient to cover all metabolic activities running simultaneously. According to Farrell *et al*. (2001), prolonged swimming in unfed adult chinook salmon (*Oncorhynchus tshawytscha*) reduces blood flow to the gut. They also suggest that, in fed fish, struggling may temporarily delay or decrease the intensity of digestive processes and thus delay food absorption and impair growth. In our experiments under high UV radiation, the energy allocated to digestion costs was suppressed (competitive effect) which can also be expected to impair growth in the long term. Enhanced UV-B irradiance (CIE weighted UV doses 3.65 and 6.15 kJ m^{-2}) also decreased the growth of whitefish larvae in a two-week rearing experiment (O. Ylönen & J. Karjalainen unpubl. data). Retarded growth was also noticed by Hunter *et al*. (1979, 1981) in larval northern anchovy, *Engraulis mordax*, exposed to enhanced UV-B irradiance.

The exact physiological mechanisms of the metabolic scope depression and disturbance in the oxygen consumption of the digestive system are unclear and need further research. We propose two possible explanations: (1) the mitochondrial capacity that supplies energy to the digestive system is decreased, or (2) regulation of blood circulation in the digestive system is disturbed. One way to investigate the depression of the digestive system capacity would be the method presented by Rønnestad *et al*. (2001). Their system can provide data for the gut absorbtion, oxidation and assimilation of nutrients and is based on the release, transfer and entrapment of metabolically produced $^{14}C\text{-}CO_2$ through manipulation of the water pH.

In conclusion, the highest daily UV doses in our allocation experiments will not be expected in Finnish lakes in the near future. Also in the future the lowest UV dose decreasing maximum oxygen consumption rate (3.58 kJ m^{-2}) will be realistic above the water surface only for a few days during spring. Moreover, because the water used in our laboratory experiments was very clear (colour of water 2.0 mg Pt l^{-1}; DOC concentration 2.0 mg l^{-1}) whereas in Finnish coregonid lakes the water is generally rather humic (colour of water 5–68 mg Pt l^{-1}, Häkkinen *et al*. 2003), the attenuation of UV radiation in lakes is much higher than in our experiments. Thus, in the field the direct effect of UV-B radiation on coregonid digestion and growth will probably be small, but some indirect effects, such as increased predation risk, can occasionally be expected. However, in clear ocean waters where UV-B radiation can penetrate down to 20 meters (Kirk 1994) UV-B radiation has the potential to disturb metabolic

processes of larval fish. These sublethal effects may then influence larval survival and diminish recruitment of wild fish stocks.

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