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ORIGINAL PAPER

Sub-lethal exposure to ultraviolet radiation reduces prey consumption by Atlantic cod larvae (*Gadus morhua*)

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Abstract Levels of ultraviolet-B radiation (UV-B: 280–315 nm) reaching the earth's surface have increased over the past few decades due to ozone depletion. It is well documented that exposure to UV-B radiation increases mortality in marine fish larvae. However, few studies have examined sub-lethal effects of UV-B radiation such as, for example, the possibility that it affects prey consumption by fish larvae. Atlantic cod larvae were exposed to a sub-lethal level of ultraviolet-B radiation (UV-B: 280–315 nm) for 15 h. After the exposure, rotifers (4/mL) were fed to cod larvae at three different post-exposure intervals (20 min, 3 and 6 h). Trials were replicated three times for each post-exposure interval. The number of rotifers in the gut and the percent of empty guts (number of fish with empty gut/number of fish examined × 100) were analyzed. Results were compared to those of unexposed fish (the control treatment). UV-B exposed cod larvae had consumed significantly fewer rotifers than control fish at all post-exposure intervals. There was no significant difference in the frequency of empty guts between fish in the UV-B treatment versus fish in the control treatment at any of the post-exposure time points (although the difference at 20 min post-exposure was borderline significant). These observations suggest that cod larvae exposed to sub-lethal levels of UV-B have lower net energy gain which may lead to reduced growth rate and possibly poorer survival.

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Introduction

Biologically deleterious UV-B radiation (280–315 nm) is one of the major environmental stressors in epipelagic marine ecosystems (Häder et al. 2011). The depth to which UV-B penetrates into oceanic waters varies over a wide range depending mainly upon the concentration of colored dissolved organic matter [e.g., Kjeldstad et al. (2003)]. In North European coastal waters, the depth of UV-B penetration to 10 % of the sea surface irradiance at 310 nm was 0.3–10.4 m (open coastal waters) and 0.08–6.1 m (fjord and estuaries) (Tedetti and Sempèrè 2006). In the waters of the estuary and Gulf of St. Lawrence, Canada, where cod eggs and larvae are abundant, the maximum 10 % depth (at 310 nm) was 3–4 m (Browman et al. 2000). Increasing levels of UV-B radiation at the earth's surface have been observed over the last few decades; this has been ascribed to depletion of the ozone layer (Kerr and McElroy 1993; Madronich et al. 1995; McKenzie et al. 2007). Higher levels of UV-B underwater were confirmed in regions over which there was significant ozone thinning (Tedetti and Sempèrè 2006).

Extensive research has been performed on the negative effects of UV-B radiation on pelagic marine fish eggs and larvae. Earlier studies demonstrated that current levels of UV-B radiation increased mortality of eggs and larvae in a variety of marine fish species such as Northern anchovy *Engraulis mordax*, Pacific mackerel *Scomber japonicus*,

red sea bream *Pagrus major*, black sea bream *Acanthopagrus schlegeli*, and Atlantic cod *Gadus morhua* (Hunter et al. 1979; Béland et al. 1999; Kouwenberg et al. 1999; Fukunishi et al. 2006). A recent meta-analysis of the effects of UV-B radiation on marine biota revealed that fish eggs and larvae—including Atlantic cod—exhibited among the steepest mortality response to UV-B (Llabrés et al. 2013).

In addition to outright lethal effects, sub-lethal effects of UV-B radiation on aquatic organisms have been receiving more attention recently [reviewed in Tucker and Williamson (2011)]. For instance, in larval fish, UV-B radiation causes slower growth, lesions in the eyes, brain, and skin, immune depression, increased oxygen consumption, and behavioral disorders (Hunter et al. 1979, 1981; McFadzen et al. 2000; Alemanni et al. 2003; Vehniänen et al. 2007; Jokinen et al. 2008). Laboratory experiments indicate that sub-lethal UV-B exposure negatively affects the digestion of food by fish larvae (Ylöen et al. 2004; Sharma et al. 2010). Sharma et al. (2010) exposed Indian major carp larvae, *Catla catla*, to a sub-lethal level of UV-B radiation every other day for 55 days and reported that levels of the digestive enzyme were significantly lower in UV-B treated fish compared to the control group. However, no studies have examined the effect of UV-B radiation on prey consumption by fish larvae.

Atlantic cod (*G. morhua*) is commercially important and they have been used as one of the model species to evaluate the effects of UV-B radiation on the early life stages of marine fish, since their early life stages are exposed to UV-B radiation [see Kuhn et al. (2000)]. Some of the negative effects of UV-B on cod larvae are increased mortality, DNA damage, and poor escape performance from a predator (Béland et al. 1999; Kouwenberg et al. 1999; Browman et al. 2000, 2003; Fukunishi et al. 2012). In marine fishes, survival during the early life stages largely determines recruitment success (e.g., Houde 1987). According to the modeling results of Köster et al. (2003), mortality during the larval period is the most important determinant of recruitment variability in Baltic cod. In addition, starvation-induced mortality in cod larvae is considered a major factor contributing to poor recruitment (Huwer et al. 2011). Therefore, we conducted an experiment designed to evaluate whether sub-lethal exposure to UV-B affects the prey consumption of cod larvae thereby possibly affecting feeding and growth.

Materials and methods

Fish husbandry

Fertilized cod eggs were collected from autumn-spawning broodstock at the Institute of Marine Research, Austevoll Research Station, Norway. They were incubated and reared in three 40 L polyethylene stock tanks. Filtered seawater was circulated at a flow rate of 20–25 L/h. Moderate aeration was provided. Two fluorescent light tubes (18W Osram Biolux 72) were placed 70 cm above the tanks and were kept on for 24 h a day throughout the rearing period. Fish were fed with rotifers four times a day at an abundance of 1.25–4 individuals per mL depending upon the age of the fish. 1.7–2 mL of algae paste (Rotifer Diet, Instant Algae, Reed Mariculture Inc., USA) was also added to each tank at feeding (the "green water" technique commonly used in intensive culture of cod). The water temperature was 10.4–12.4 °C. On the day of experiments, twenty individuals were randomly sampled from the tanks, anesthetized with MS222, and their standard length (mean ± SD) measured under a binocular microscope. The size of the 30 days post-hatch cod larvae used in these experiments was 8.73 ± 0.46 mm, $N = 20$. Fish were cared for in accordance with the principles and guidelines of the Norwegian Institute of Marine Research's Animal Care Committee (ID 3415).

Ultraviolet exposure

Rotifers were fed to cod larvae (4 ind./mL) in the stock tanks 1 h before the exposure treatments. Two polyethylene exposure tanks (40 L) were prepared, and three UV-A lamps (UV-A 340, Q-Lab corporation, USA) and three fluorescent lamps (Polylux XL F36w/830, General Electric, UK) were positioned 30 cm above them. These UV-A lamps also emit UV-B (280–315 nm). About 120 cod larvae were gently scooped (with a hand cup) from the stock tanks and were transferred to each exposure tank. After 10 min of acclimation, fish were exposed to a sub-lethal level of UV-B radiation (2.9 kJ/m^2/h) for 15 h (UV-B dose: 43.4 kJ/m^2). The control tank was covered with mylar-D film during the exposure to block UV-B radiation. The UV-B fluence rate applied in this experiment is lower than that of the maximum value measured in Bergen during the summer (3.9 kJ/m^2/h). The total UV-B dose in the UV-B treatment was approximately equivalent to that of 11 h daylight exposure (see Fukunishi et al. 2012). Thus, cod larvae were exposed to ecologically relevant levels of UV that were lower than the lethal dose rates/doses applied in other experiments with cod larvae (see Fig. 4 in Kouwenberg et al. 1999). In pilot experiments, we confirmed that no mortality was observed 24 h after these UV-B exposures (in 24 and 29 dph cod larvae). The overhead fluorescent lamps in the laboratory were off during the exposure. Therefore, after the UV-B exposure period, fish were kept in the dark until feeding experiments began. Additional details of the experimental setup and the spectral irradiance, dose, and

dose rate delivered to each treatment are described in Fukunishi et al. (2012).

Feeding experiment

To assess the effect of UV-B over time, feeding experiments were conducted after the exposure for both UV-B and control treatments. After the UV-B exposure, cod larvae were kept in the exposure tanks without any food for either 20 min, 3 or 6 h. After this time had passed, larvae were moved down the hall to another laboratory where they were placed in a glass tank (15 cm × 15 cm × 15 cm) filled with 2.5 L of filtered sea water and 0.1 mL of algae paste. The depth of water in the tank was 13 cm. The room and water temperature was 12 °C. Ceiling lamps (Polylux XL F36w/830, General Electric, UK) in the laboratory were on during feeding experiments. Eight fish were transferred from the exposure tank to an experimental tank (different tanks for each treatment) and acclimatized for 10 min. Rotifers were then added at an abundance of 4 individuals per mL. Fish were allowed to feed on rotifers for 1 h and were then euthanized with an overdose of MS222 and preserved in 70 % ethanol. Feeding experiments were run concurrently across 6 feeding tanks (3 tanks with UV-B exposed larvae and 3 tanks with control larvae) for each of the post-exposure times (i.e., after 20 min, 3 and 6 h in the dark). The experimental tanks were surrounded by a black curtain to minimize external disturbance. The number of rotifers in the guts of larvae was counted under a binocular microscope, and the average number present in the guts of fish that had consumed one or more rotifers was calculated. The percent of fish with empty guts was calculated as the number of larvae that had no rotifers in the gut divided by the total number of fish in the tank (8 individuals) multiplied by 100.

Statistical analysis

A nonparametric Mann–Whitney *U*-test was used to compare prey consumption between UV-B treatment and control at each post-exposure time point. We used a nonparametric Kruskal–Wallis ANOVA to assess differences in prey consumption between time exposures (within each treatment). A Steel–Dwass multiple comparison test was then used to determine which time exposure groups were significantly different.

Chi-square tests were performed to compare the frequency of empty guts between treatments. When a significant difference was identified, post hoc tests using Ryan's Method were performed to examine the difference in the frequency of empty guts among the three post-exposure time points for both treatments.

Results

The rotifers that we observed in the gut of cod larvae were recently eaten and almost undigested. Cod larvae in the UV-B treatment consumed fewer prey than control fish: the number of rotifers in the gut of UV-B exposed fish was significantly lower than that of control fish at all post-exposure time points (Mann–Whitney *U*-test, 20 min: $U = 67.5$, $N_1 = 14$, $N_2 = 20$, $P < 0.05$; 3 h: $U = 71$, $N_1 = 19$, $N_2 = 23$, $P < 0.01$; 6 h: $U = 132$, $N_1 = 23$, $N_2 = 23$, $P < 0.01$) (Fig. 1). The difference in the mean number of rotifers in the gut between the UV-B treatment and the control was twice as high after 6 h than after 20 min. Within the treatment groups and control, prey consumption at the 20 min time point was significantly lower than those at the 3 and 6 h time points (Kruskal–Wallis test, UV-B treatment: $H_2 = 9.96$, $P < 0.01$; control: $H_2 = 9.55$, $P < 0.01$, followed by the Steel–Dwass test, UV-B treatment: 20 min vs 3 h, $P < 0.05$; 20 min vs 6 h, $P = 0.01$; control: 20 min vs 3 h, $P = 0.01$; 20 min vs 6 h, $P < 0.05$), but there was no significant difference between the 3 and 6 h post-exposure time points in either the UV-B treatment or the control (Steel–Dwass test, UV-B treatment: $P > 0.05$; control: $P > 0.05$). There was no significant difference in the frequency of empty guts between fish in the UV-B treatment versus fish in the control treatment at any of the post-exposure time points (although the difference at 20 min post-exposure was borderline significant) (Chi-square test, 20 min: $\chi_1^2 = 3.63$, $P = 0.057$; 3 h: $\chi_1^2 = 3.05$, $P > 0.05$; 6 h: $\chi_1^2 = 0$, $P = 1$) (Fig. 2). The difference in the frequency of empty guts between the control and the UV treatment at 20 min, 3 and 6 h post-exposure were 21, 17, and 0 %, respectively. The frequency of empty guts in the UV-B treatment was significantly different among post-exposure time points (Chi-square test, $\chi_2^2 = 9.804$, $P < 0.01$) and there was a significant difference between 20 min and 6 h post-exposure time points (Ryan's Method multiple comparison test, $P < 0.05$). There was no significant difference in the frequency of empty guts among post-exposure time points in the control treatment (Chi-square test, $\chi_2^2 = 3.273$, $P > 0.05$).

Discussion

Atlantic cod larvae digest copepod nauplii in 30 min to 1.5 h at 5 °C, and therefore, their gut contents represent the summation of feeding over the previous 4 h (Tilseth and Ellertsen 1984; Lough and Mountain 1996). These gut clearance times are much shorter than the UV exposure period in our experiment (15 h). Further, soft-bodied rotifers are digested more rapidly than copepods (e.g.,

Karjalainen and Viljanen 1992; Sutela and Huusko 1994), and therefore, the rotifers that we observed in the guts of the larvae must have been eaten during the feeding experiments.

Exposure to sub-lethal levels of UV-B reduced the number of rotifers in the guts of cod larvae for up to 6 h after exposure (Fig. 1). In addition, the difference of prey consumption between larvae in the UV-B treatment and the control increased with post-exposure time. These results suggest that sub-lethal levels of UV-B exposure will reduce the food/energy intake of cod larvae for at least 6 h, and the effect was even more pronounced at 6 h of post-exposure. Further, although it was only marginally significant ($P = 0.057$), the frequency of empty guts in larvae from the UV-B treatment was higher compared to the control treatment at 20 min post-exposure (Fig. 2). Therefore, it is likely that sub-lethal exposure to UV-B radiation either decreased attack rate/capture success or the proportion of cod larvae that were actively feeding for at least 20 min after exposure. Since the number of hours of darkness can be less than 6 at more northern latitudes, this UV-B-induced effect on cod larvae might carry over to the next day. UV-B radiation caused slower growth in larval northern anchovy *Engraulis mordax* (Hunter et al. 1979) and juvenile Atlantic salmon *Salmo salar* (Jokinen et al. 2008). These earlier observations could have been due to decreased prey consumption induced by UV-B exposure.

Although our experiments were not designed to identify the mechanisms underlying these results, there are a several possible explanations. (1) Feeding motivation of cod larvae was suppressed by UV-B exposure. Sharma et al. (2010) reported that UV-B exposure decreased digestive enzyme

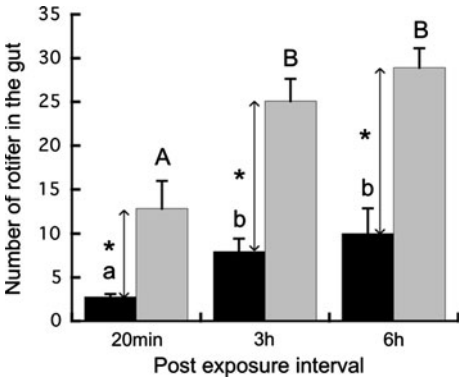

Fig. 1 Effects of UV-B exposure on prey consumption by cod larvae (*Gadus morhua*). The *black columns* denote the UV-B treatment and the *gray columns* the control. *Asterisks* indicate a significant difference between UV-B and control treatments (Mann–Whitney *U*-test, 20 min: $N_1 = 14$, $N_2 = 20$, $P < 0.05$; 3 h: $N_1 = 19$, $N_2 = 23$, $P < 0.01$; 6 h: $N_1 = 23$, $N_2 = 23$, $P < 0.01$). *Vertical bars* are standard errors. *Different letters* indicate significant differences in prey consumption among post-exposure time points (Kruskal–Wallis test, followed by the Steel–Dwass test, $P < 0.05$)

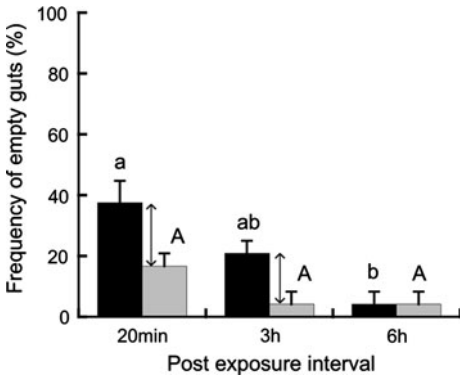

Fig. 2 Effects of UV-B exposure on the frequency of empty guts in cod larvae (*Gadus morhua*). The *black columns* denote the UV-B treatment and the *gray columns* the control. *Vertical bars* are standard errors. *Different letters* indicate significant differences in the frequency of empty guts among post-exposure intervals (Chi-square test, followed by the Ryan's Method multiple comparison test, $N = 24$, $P < 0.05$)

activity in Indian major carp (*Catla catla*) larvae. In white fish larvae [*Coregonus lavaretus* (L.)], the oxygen consumption allocated for digestion was decreased by UV-B (Ylöen et al. 2004). Therefore, it is possible that UV-B exposed cod larvae had lower appetite compared to control fish. (2) Feeding efficiency was decreased due to the loss of energy caused by UV-B exposure. In a previous study, we exposed cod larvae to sub-lethal levels of UV-B radiation in a manner analogous to the experiments reported here (Fukunishi et al. 2012). The escape distance and escape rate of cod larvae from a fish predator were decreased by UV-B radiation, suggesting that larvae had less metabolic scope than control fish that were not exposed to UV-B radiation. Alemanni et al. (2003) reported that sub-lethal levels of UV-B were stressful to juvenile rainbow trout *Oncorhynchus mykiss*. Their oxygen consumption, swimming activity, and restless behavior (e.g., rapid tail and fin movements) increased in the presence of UV-B radiation, leading to an overall loss of energy. Energy is also consumed when fish repair UV-B-induced DNA damage (Olson and Mitchell 2006). (3) UV-B damage in cod larvae changed their foraging behavior. Hunter et al. (1979) found that UV-B exposure induced lesions in the eyes of larval northern anchovy *Engraulis mordax*. Since cod larvae are visual feeders (Ellertsen et al. 1980), their feeding performance would be decreased if their eyes were affected by UV-B exposure.

In both the UV-B and control treatments, prey consumption increased with the amount of time that larvae had been fasting (Fig. 1). This is likely because the foraging motivation and hunger level of cod larvae increased with the time over which they had been without food (see Munk 1995; Ruzicka and Gallager 2006). The percentage of all larvae that had empty guts decreased over time in the

UV-B treatment (Fig. 2). On the other hand, the percentage of all larvae that had empty guts did not change over time in the control treatment. Further, the difference in the percentage of empty guts between larvae from the UV-B treatment and control decreased with post-exposure time, and the value at 6 h post-exposure was the same (4 %) in the UV-B treatment and control treatments. Thus, in addition to the possibility that longer fasting periods increase feeding motivation, this observation may also indicate recovery from UV-B damage. This interpretation is consistent with the observation that fish larvae can recover from UV-B-induced DNA damage (Malloy et al. 1997; Vetter et al. 1999; Dong et al. 2007). Further, Vehniänen et al. (2007) reported that pike larvae (*Esox lucius*) recovered from a UV-B-induced behavioral disorder after about one week.

In the natural environment, fish larval prey such as copepods are generally distributed in patches at abundances lower than that used in our experiment (Dower et al. 2002; Pepin et al. 2003). Therefore, the effect of UV-B radiation on prey consumption of cod larvae in the sea might be more pronounced than observed in our experiments simply because of a far lower prey encounter rate. Lower prey consumption by cod larvae, induced by exposure to relatively low levels of UV-B, could lead to a variety of negative consequences. For example, food limitation decreases growth rate and, thereby, increases the duration of vulnerable larval stages which in turn affects cumulative mortality (Houde 1978). Rice et al. (1987) demonstrated that starved bloater larvae (*Coregonus hoyi*) had poorer swimming capabilities and were more vulnerable to predation compared to similar sized fed larvae.

Sub-lethal levels of UV-B exposure reduced prey consumption of cod larvae. Since starvation mortality in cod larvae has a high potential to contribute to recruitment variability (Huwer et al. 2011), exposure to sub-lethal levels of UV-B radiation might have negative impacts on cod resources by decreasing larval competence. In our previous studies, we demonstrated that cod larvae exposed to sub-lethal levels of UV-B were more vulnerable to a fish predator (Fukunishi et al. 2012). Combined with the result reported here, this indicates that UV-B radiation could indirectly reduce survival of larval cod.

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