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Ontogeny of tolerance to and avoidance of ultraviolet radiation in red sea bream *Pagrus major* and black sea bream *Acanthopagrus schlegeli*

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ABSTRACT: Ontogenetic changes of tolerance to, and avoidance of, ultraviolet-B radiation (UV-B) were examined in red sea bream *Pagrus major* and black sea bream *Acanthopagrus schlegeli*. In the tolerance experiment, larvae and juveniles (age 13–46 days) were put in beakers, and were exposed to one of five different levels of UV-B radiation (1.8, 1.1, 0.2, 0.1, and 0 W/m^2) for one hour. Their survival rates were calculated either 12 or 24 h later. In the avoidance experiment, fish (age 3–49 days) were put in a long experimental tank, half of which was covered with UV-blocking film and placed under two levels of UV-B radiation (1.1 and 0.2 W/m^2), and their avoidance indices were calculated. Black sea bream had significantly better survival compared to red sea bream for most ages. Only black sea bream of ages 37 and 49 days showed significant avoidance of UV radiation under the higher level of UV-B, whereas both species did not show avoidance on any days at the lower level. The present results suggest that black sea bream are significantly better adapted to habitats with high UV-B radiation, than red sea bream, reflecting that back sea bream live in shallower waters through their early life stages.

KEY WORDS: **avoidance, behavioral ontogeny, black sea bream *Acanthopagrus schlegeli*, red sea bream *Pagrus major*, tolerance, UV-B radiation.**

INTRODUCTION

Levels of biologically active solar ultraviolet-B radiation (UV-B, 280–315 nm) reaching the Earth's surface have substantially increased during the past few decades because of the depletion of stratospheric ozone.[1–4] As ozone depletion continues in the mid-latitude regions of the Northern and Southern Hemispheres,[5] there is a strong possibility that UV-B radiation will increase further in the future. Although exact prediction is unavailable, Taalas *et al.*[6] proposed that enhanced UV doses may exist until the middle of the 21st century, and that springtime enhancement of harmful UV doses during 2010–2020 will be as much as 90% compared to the 1979–1992 conditions in the 60–90°N region. Because UV-B entering the water column is also increasing,[7] the negative effects of UV-B on the total aquatic ecosystem are potentially severe.

Planktonic eggs and larvae drifting near the sea surface have little or no swimming capability, and thus are vulnerable to UV-B radiation. A growing number of studies report that UV-B radiation leads to a decrease in survival rate[8–13] and hatching success,[8,12,14,15] plus produces lesions in the brain and retina or retarded growth and development,[8] and lesions of the skin.[16,17]

Recruitment success of marine fish generally depends on survival during the larval and early juvenile stages. Therefore, it is crucial to understand the processes affecting mortality at young stages so as to optimize utilization of fisheries resources. Although some studies have revealed that UV-B radiation has negative effects on copepods and fish eggs,[18–21] analogous studies on fish larvae and juveniles are scarce in species in Japanese coastal waters.

Red sea bream *Pagrus major* and black sea bream *Acanthopagrus schlegeli*, both sparids, are distributed from Hokkaido to Kyushu in Japan,[22]

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and are extremely important commercial species. Although both species can be found from the surface to the bottom of the sea, red sea bream larvae tend to dwell near the bottom, whereas black sea bream larvae concentrate near the surface.[23] Red sea bream settle on the bottom at around 10 m depth and shift their habitat from pelagic to benthic when they reach 12–15 mm in standard length (SL).[24,25] In contrast, black sea bream shift their habitat from pelagic as larvae, to the surf zone less than 1 m depth when they attain 6–7 mm SL.[23] This pattern implies that black sea bream are more likely to be exposed to higher levels of UV-B through the early life stages. Here it is hypothesized that black sea bream have a higher tolerance to UV radiation than red sea bream and thus are adapted to shallow-water environments. Therefore, the survival against and avoidance of UV-B radiation in larvae and juveniles of both species is examined here, with emphasis on developmental changes.

MATERIALS AND METHODS

Fish husbandry

Naturally spawned and fertilized red sea bream and black sea bream eggs were provided by the Kyoto Prefectual Sea-Farming Center on 25 May 2004. Eggs were transferred to the Fisheries Research Station of Kyoto University and were stocked into four transparent polycarbonate tanks (500 L), two tanks for each species. Stocking density was about 30 000 eggs for each tank.

Eggs of both species hatched on the next day, and thus it was possible to use larvae and juveniles with matching ages on each day of the experiment. From day 2, larvae of both species were provided with rotifers *Brachionus plicatilis* cultured with freshwater chlorella (Nama-Chlorella V12, Kurorera Kogyo, Tokyo, Japan) and enriched with commercial HUFA oil (Aquarun, BASF, Tokyo, Japan; and Marine Gloss, Nisshin Marinetech, Kanagawa, Japan). Rotifer density was maintained at 5 ind./mL. From day 15, *Artemia* spp. nauplii were provided at a density of 0.5 ind./mL, again with HUFA enrichment in addition to rotifers. On day 21 or later fish were fed with various sizes of formulated food (Kyowa A250, B400, and B700, Kyowa Hakko Kogyo, Tokyo, Japan) depending on their developmental stages, in addition to enriched *Artemia* but without rotifers. Twenty specimens of both species were sampled randomly from the rearing tanks at 1–9 day intervals, fixed with 10% neutralized formalin and were transferred to a 70% ethanol solution within 24 h. Their SLs were measured later. Rearing was conducted up to day 49, during which the water temperature ranged 18–24°C.

Radiometry

Field measurements of UV-B radiation were conducted using a portable photo-Radiometer (DO 9721, Delta OHM, Padua, Italy). Observations were made at the western part of Wakasa Bay (35°39′N, 135°24′E) on a sunny and clear day (24 May 2004) by the Research Vessel Ryokuyo-maru (Kyoto University, 8 t). UV-B radiation was measured above the sea surface twice per hour; the average of 1 s-interval measurement for 10 min was obtained in each observation. The maximum value recorded at 12:00 hours (1.1 W/m^2) was defined as level B for laboratory experiments. Observations were also conducted on the pontoon in the Fisheries Research Station of Kyoto University to define a lightly clouded level (level C, 0.2 W/m^2) and heavily clouded level (D, 0.1 W/m^2) depending on the cloud cover in May 2004.

Tolerance experiment

Red sea bream and black sea bream larvae and juveniles with matching ages were used to examine the developmental changes of tolerance against UV-B radiation. Fifty (13, 19, and 26 days old) or 25 (35 and 46 days old) individuals of both species were randomly selected from rearing tanks. Replicates of 10 or five individuals were placed in five 500 mL glass beakers filled with 500 mL filtered sea water for each species and acclimatized for 3 min. Distances from UV-B lights (TL 20 W/12 RS, Philips, Eindhoven, Netherlands; wavelength ~260–400 nm and maximum emission 306 nm) to beakers were adjusted by putting the beakers on different heights of concrete blocks (Fig. 1). Thus, each beaker was exposed to four different intensities of UV-B: (i) A, 1.8 W/m^2; (ii) B, 1.1 W/m^2; (iii) C, 0.2 W/m^2; and (iv) D, 0.1 W/m^2. UV-B intensity was measured just above the water surface using the same instrument as field observations. The penetration of UV-B from the side of the beaker was negligible, since it was only 0.05 W/m^2, even under condition A measured without sea water. Each value approximates the following conditions: (i) A, a value which is slightly higher than the UV-B level observed during early summer in Japan Sea, (ii) B, maximum value observed at the sea surface off the western part of Wakasa Bay on a sunny and clear day; (iii) C, a value measured on a lightly clouded day; and (iv) D, a value measured on a heavily clouded day. Further, control beakers covered with

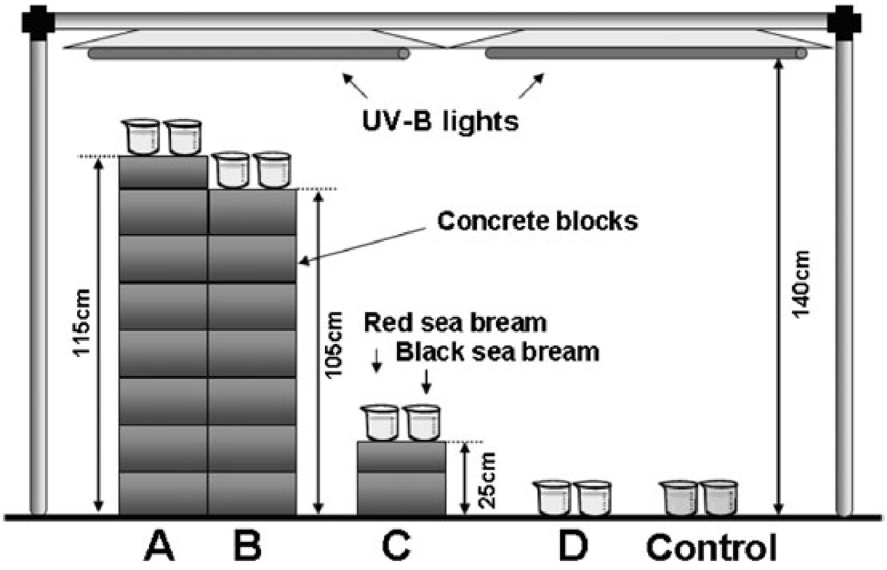

Fig. 1 Schematic drawing of tolerance experiment apparatus. Larvae and juveniles of red sea bream and black sea bream were put in beakers and were exposed to different UV-B radiation conditions.

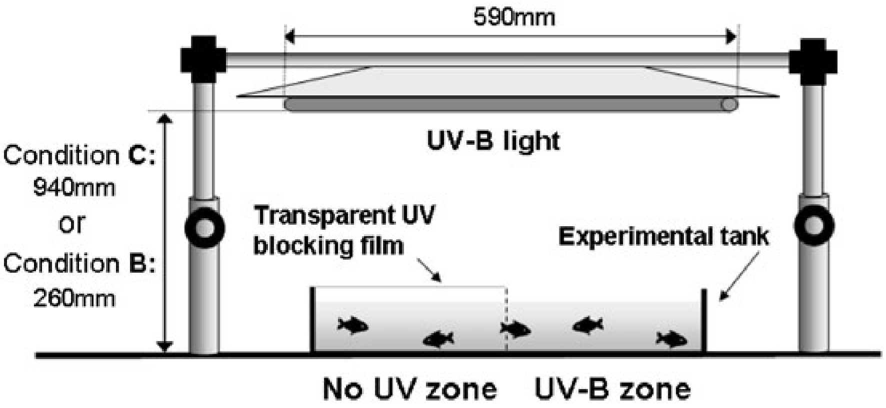

Fig. 2 Schematic drawing of avoidance experiment apparatus. The height of the UV-B light was adjustable, so the behavior of experimental fish could be observed under two different illumination conditions.

transparent UV-blocking film (UV-cut Clear Film XL-16, Mirareed, Tokyo, Japan) were also provided. This film blocks light less than 380 nm and allows 94% of visible light to penetrate. The experimental area (4 m^2) was enclosed with a black curtain in a temperature controlled room (28 m^2). After exposing UV under the above conditions for one hour, the beakers were immediately transferred to a water bath (85 cm × 90 cm × 20 cm) filled with sea water with the temperature kept the same as that of the rearing tanks. Live individuals were counted at 12 (13 and 19 days old) or 24 (26, 35 and 46 days old) hours later. Individuals that died during the experiment were removed from the beaker using a pipette to avoid deterioration of water quality. Mild aeration from an air stone was provided to each beaker for those of 35- and 43-days old fish. Four replicates were conducted for the 13-days old individuals and five replicates for the other ages of both species, from which the survival rate ± standard error was calculated. Temperature and dissolved oxygen of sea water in the beaker was not substantially different before and after the experiment.

Avoidance experiment

Larvae and juveniles of 3, 9, 15, 21, 29, 37 and 49 days old were used in the avoidance experiment. A transparent plastic experimental tank (54 cm × 8 cm × 8 cm, 6 cm water depth), half of which was covered with transparent UV-blocking film, was placed under the UV-B illumination (Fig. 2). Thus, one end of the experimental tank was exposed to UV-B radiation (UV-B zone) and the other side was not (No UV zone). The UV-B strength was set at the same level as either B (1.1 W/m^2) or C (0.2 W/m^2) in the tolerance experiment. The back of the experimental tank was covered with a black vinyl sheet. The experimental system was enclosed within a black curtain to minimize the effects of the observer. Ten (26, 35 and

46 days old) or five (13 and 19 days old) individuals of both species were randomly selected from rearing tanks, transferred into the experimental tank and were dispersed in both sides of the experimental tank as evenly as possible. Fish were acclimatized for 3 min. The behavior of larvae and juveniles was observed for 20 min through holes in the black curtain using a video camera (AI18CIR-AFM, Hoga, Kyoto, Japan) connected to a monitor. The number of larvae and juveniles in the No UV zone was counted every minute, from which the avoidance index was calculated as follows:

$$\text{Avoidance index} = \frac{\begin{pmatrix}\text{Cumulative number}\\ \text{of larvae or juveniles}\\ \text{in No UV-B zone}\end{pmatrix}}{\begin{pmatrix}\text{number of larvae or}\\ \text{juveniles stocked}\\ \text{in the aquarium}\end{pmatrix}\times\begin{pmatrix}\text{number of}\\ \text{counts} = 20\end{pmatrix}}$$

If the larvae or juveniles distributed randomly in the experimental tank during the 20 min period, the avoidance index is expected to be 0.5, and if they always avoided the UV-B radiation, it would be 1.0. The experiment was repeated four times with both species under the two illumination conditions, and the location of the No UV-B zone was changed for each trial.

Statistical analysis

A Student's *t*-test was used to compare the SL of matching ages between red sea bream and black sea bream. Average survival rates in the tolerance experiment were arcsine-transformed and compared between red sea bream and black sea bream, as well as the control and other conditions using a Student's *t*-test. ANOVA followed by a Tukey–Kramer honestly significant difference (HSD) multiple comparisons test, was also performed to compare different ages within the same species, using JMP statistical software (JMP, SAS Institute, Cary, NC, USA). A Student's *t*-test was applied to compare between each avoidance index value, and the value expected, according to random distribution, i.e. 0.5.

RESULTS

Fish husbandry

The mean SL between red sea bream and black sea bream was not significantly different up to day 15 ($P > 0.05$, Student's *t*-test). From day 19, the mean SL of red sea bream was significantly larger than that of black sea bream ($P < 0.05$) except for day 26 and 49 (Fig. 3).

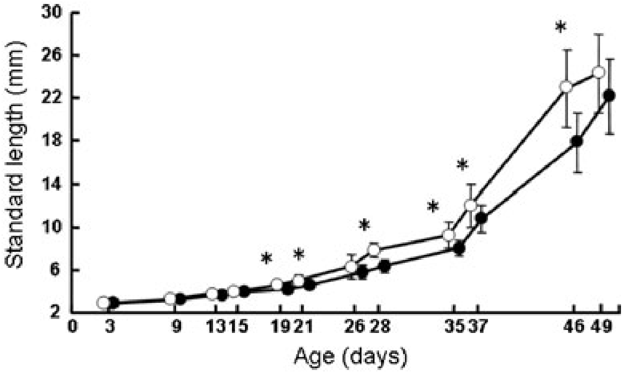

Fig. 3 Growth of red sea bream (○) and black sea bream (●) reared in the laboratory. Each value represents mean ± standard deviation ($n = 20$). Symbols with an asterisk (*) indicate a significant difference between the two species ($P < 0.05$, Student's *t*-test).

Tolerance experiment

Overall, the survival rate against UV-B radiation was higher in black sea bream compared to that of red sea bream (Fig. 4). Higher survival rates in black sea bream were observed for most ages for conditions A and B ($P < 0.05$, Student's *t*-test), whereas there was no significant difference between these two species in conditions C and D and the control.

For red sea bream, survival rates were low for A (0–28%) and B (20–44%), all of which were significantly lower than the control ($P < 0.05$, Student's *t*-test). This was not the case for C and D. Further, their survival rate was significantly different among ages only between day 35 and 46 for A ($P < 0.05$, HSD test), but no significant difference among ages was observed for B ($P > 0.05$, ANOVA).

In the case of black sea bream, mean survival rates for A were generally low (25–36%) except for day 19, and were significantly lower than the control ($P < 0.05$, Student's *t*-test) on day 26 and 46. For condition B, their survival rates were not significantly different from that of the control on all days ($P > 0.05$, Student's *t*-test). However, survival rates on day 35 were much lower than that of the control; the difference between condition B and the control was 28%, and the value on day 35 for B was also significantly lower than that on day 26 and 46 ($P < 0.05$, HSD test). Their survival rates for C and D were not significantly different compared to that of control ($P > 0.05$, Student's *t*-test).

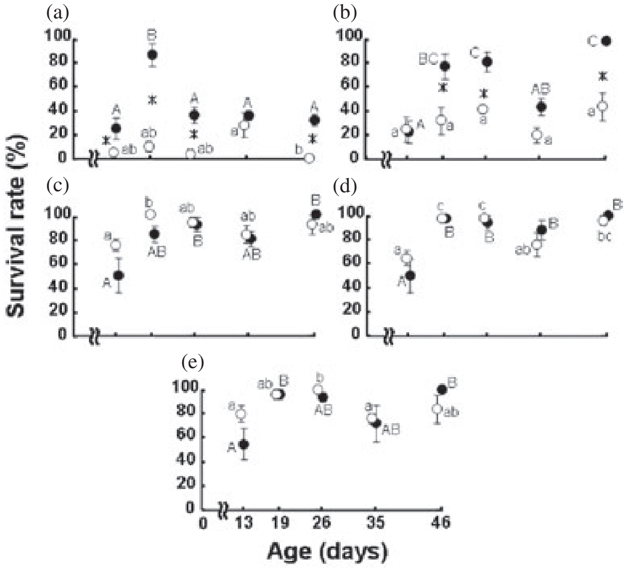

Fig. 4 Survival rates of red sea bream (○) and black sea bream (●) under different levels of UV-B radiation. (a) 1.8 W/m^2, (b) 1.1 W/m^2, (c) 0.2 W/m^2, (d) 0.1 W/m^2, (e) 0 W/m^2 (control). Each value represents mean ± standard error (age 13 days: $n = 4$, others: $n = 5$). ●: black sea bream; ○: red sea bream. Significant difference between red sea bream and black sea bream in the same age was represented by asterisks (*) ($P < 0.05$, *t*-test). Different letters indicate significant difference among ages for each species ($P < 0.05$, one way ANOVA followed by HSD test); large and small capitals represent black sea bream and red sea bream, respectively.

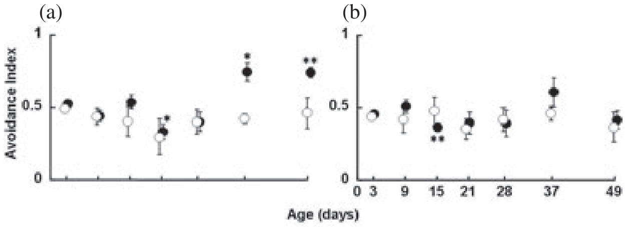

Fig. 5 Avoidance index of red sea bream (○) and black sea bream (●) under UV-B intensities of (a) 1.1 W/m^2, equivalent to sunny conditions in the field, and (b) 0.2 W/m^2, equivalent to cloudy conditions in the field. Each value represents mean ± standard error ($n = 4$). Significant difference between each value and 0.5 are represented by asterisks (*$P < 0.05$, **$P < 0.01$, Student's *t*-test).

Avoidance experiment

Black sea bream showed their avoidance of UV under condition B on day 37 and 49 (Fig. 5). When the UV lamp was turned on, the fish first showed disordered movement swimming back and forth in the experimental tank, then they started to gather at the side with the UV-blocking film, although some individuals occasionally strayed to the UV-exposed side. The avoidance index values of black sea bream larvae and juveniles under condition B were almost ≤0.5, the value expected in random distribution, up to day 28 (Fig. 5). The avoidance index values, however, increased to 0.75 on day 37 and to 0.74 on day 49, both of which were significantly different from 0.5 ($P < 0.01$ and <0.05, respectively, Student's *t*-test). Red sea bream did not show measurable avoidance on any days tested under the same conditions. Neither species showed significant avoidance under condition C; the avoidance indexes were close to, or slightly smaller than 0.5 for all ages.

DISCUSSION

Ecological implications of tolerance against UV

In our UV tolerance experiment, black sea bream showed significantly better survival than red sea bream for most ages tested under the two strongest levels of radiation (Fig. 4). This finding supports our hypothesis that black sea bream is more adapted to habitats with high UV compared to red sea bream.

The survival rates of red sea bream larvae and juveniles were consistently low under A and B conditions, and did not show developmental changes. This result implies that even the maximum ambient UV-B level (1.1 W/m^2) is potentially lethal for red sea bream larvae and juveniles, and might be responsible for substantial loss of their population if they stay near the surface.

In the case of black sea bream larvae and juveniles, although their survival rates in A were generally low, their survival rates in condition B were not significantly different from the control for all ages. This suggests that they are resistant to the maximum ambient UV-B level at present, but may suffer negative effects under the future UV-B levels predicted.

The survival rate of black sea bream on day 35 (8.1 ± 0.75 mm SL) under condition B was much lower (44%) compared to the trials on day 26 (82%), then it increased to 100% on day 43 (Fig. 4). Larvae of black sea bream at 8 mm SL are often found in the surf zone,[23] and their transformation from larvae to juveniles occurs from 9.0 to 11.0 mm SL.[24] Extensive morphological and physiological changes, such as reconstruction of the digestive system, occur during the metamorphosis period[24,25] and may be accompanied by a relatively low stress-resistant period,[26] resulting in low tolerance to UV radiation. Therefore, it is speculated that even black sea bream may suffer from UV-induced mortality at present UV levels if their metamorphosing larvae remain near the surface.

Although larvae of both species are found from near the surface to the bottom, red sea bream larvae tend to dwell near the bottom, where black sea bream concentrate near the surface in the daytime.[23] In their juvenile stage, red sea bream settle on the bottom at about 10 m depth and their habitat shifts from pelagic to benthic when they reach 12–15 mm SL.[27,28] Black sea bream, in contrast, shift their habitat from the pelagic to the surf zone at less than 1 m depth when they attain 6–7 mm SL.[23] They then appear often in extremely shallow water with grass eels near estuaries when they reach 10–11 mm SL.[29,30] Black sea bream therefore live in shallower areas with high UV-B levels all through their early life stages.

Hunter *et al.*[8] reported that northern anchovy *Engraulis mordax* larvae show higher UV-B induced mortality and lesions in brain and eye when compared to Pacific mackerel *Scomber japonicus*. Northern anchovy live in coastal waters, whereas Pacific mackerel occur in pelagic waters.[22] As pelagic waters are more transparent than coastal waters, Pacific mackerel may be better adapted to an environment with higher UV levels than northern anchovy. McFadzen *et al.*[17] showed that sole *Solea solea* larvae formed skin lesion at elevated levels of UV-B, whereas turbot *Scophthalmus maximus* larvae did not show lesions, reflecting that turbot larvae appear in the ichthyoplankton during mid-summer and live high in the water column, while and sole larvae are generally found in the spring in deeper water with less UV-B penetration.

Various mechanisms of UV-protection in fishes have been proposed. Lowe and Goodman-Lowe[31] founded that scalloped hammerhead shark *Sphyrna lewini* pups show a marked increase of photoprotective melanin when they shift their habitat from a deeper murky bay area to clear pelagic waters. Dunlap and Shick[32] reported that tropical and temperate fishes reduce photochemical damage by absorbing ultraviolet radiation with mycosporine-like amino acid in eyes, skin, and reproductive tissues. Northern anchovy eggs and larvae[33] and goldfish *Carassius auratus* embryos[34] restore DNA lesion through photorepair. Since the mechanism of UV protection may vary among species as well as their developmental stages, further histological and histochemical studies are required to understand the difference in UV tolerance between red sea bream and black sea bream.

Interspecies difference and ontogenetic changes of UV-avoidance

Black sea bream juveniles showed significant avoidance from UV-B radiation on day 37 (10.7 ± 1.2 mm) and 49 (22.1 ± 3.5 mm) under condition B (1.1 W/m^2), where red sea bream did not show avoidance from UV-B radiation on any of the days tested (Fig. 5).

As mentioned, black sea bream are found in extremely shallow water such as the surf zone when they attain 6–7 mm SL,[23] whereas red sea bream settle to the bottom at about 10 m depth when they reach 12–15 mm SL.[24,25] Although the surf zone and other shallow water areas have high a risk of UV damage, the surf zone is abundant in prey organisms and can be a good refuge from predators.[35] Therefore, in spite of the risk of high UV-B radiation, black sea bream juveniles shift their habitat to the surf zone. In our experiment they did not show avoidance of UV-B radiation for condition C (0.2 W/m^2), suggesting that they avoid UV only when it reaches a harmful level. Red sea bream, in contrast, shift their habitat to a deeper area where UV-B level is at a sublethal level, thus they would not require a capability for UV-avoidance.

Visual cell structures of fishes, in general, change with shifts of habitat to adapt to the new optical environment. For example, the single cones of red sea bream fuse to form twin cones and rods appear in the settlement stage, increasing the sensitivity to lower light level intensity environments.[36] Labrids such as the dwarf wrasse *Doratonotus megalepis* and creole wrasse *Clepticus parrae* develop UV-sensitive cones shortly after settlement.[37] Miyagi and Kawamura[38] reported that the retina of black sea bream adults shows no response to UV stimuli. Although histological changes of retina have not been studied in the present work, black sea bream might develop UV-sensitive cones in the early juvenile stage, then lose them with ontogenetic habitat changes. Browman and Hawryshyn[39] reported that rainbow trout *Oncorhynchus mykiss* juveniles lose their UV photosensitivity when they reach approximately 60 g.

Both newly emerged alevins and two-month-old juveniles of coho salmon *Oncorhynchus kisutch* show a high selective avoidance from solar UV radiation in river conditions under high solar intensities, whereas they show no spectral preference under lower solar intensities.[40] Vendace *Coregonus albula* and whitefish *Coregonus lavaretus* larvae avoid UV radiation despite their positive phototaxis, although whitefish are less sensitive to changes in UV irradiation than vendace, and they represent the smallest size group which were the most sensitive to UV under laboratory conditions.[41] Therefore, previous work as well as the present results suggest that the onset of UV avoidance differs depending on species, perhaps reflecting the requirement in their habitat.

In this work, avoidance was only studied only in the horizontal dimension. Speekmann *et al.*[42] however, demonstrated under laboratory conditions that 1-day-old Pacific herring *Clupea pallasi* larvae stay substantially deeper (≥60 cm) when UV-B radiation is present. Ylönen *et al.*[41] showed that vendace and whitefish larvae shift their vertical position in a lake deeper during sunny periods than during cloudy periods, to avoid UV radiation. Therefore, vertical avoidance of both species also needs to be considered in work on red sea bream and black sea bream.

Penetration of ultraviolet radiation in the coastal water column displays strong seasonal changes, depending on the marine environment such as chlorophyll pigments and dissolved organic materials,[43,44] and seasonal atmospheric changes such as the amount of cloud or small particles suspended in air (aerosols).[3] Therefore, careful consideration is required to assess the negative effect of ultraviolet radiation on fish larvae assemblage. Present results clearly show that tolerance to, and avoidance of, UV differs remarkably between two fish species in the same family. Excess UV radiation may thus change species composition in the fish community in the future.

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REFERENCES

1. Kerr JB, McElroy CT. Evidence for upward trends of ultraviolet-B radiation linked to ozone depletion. *Science* 1993; **262**: 1032–1034.
2. Madronich S, McKenzie RL, Caldwell MM, Björn LO. Changes in ultraviolet radiation reaching the Earth's surface. *Ambio* 1995; **24**: 143–152.
3. Madronich S, McKenzie RL, Björn LO, Caldwell MM. Changes in biologically active ultraviolet radiation reaching the Earth's surface. *J. Photochem. Photobiol. B. Biol.* 1998; **46**: 5–19.
4. Sasaki M, Takeshita S, Oyanagi T, Miyake Y, Sakata T. Increasing trend of biologically active solar ultraviolet-B irradiance in mid-latitude Japan in the 1990s. *Opt. Eng.* 2002; **41**: 3062–3069.
5. World Meteorological Organization (WMO). Scientific assessment of ozone depletion: 2002. *WMO Ozone Rep. 47*, WMO, Geneva 2002.
6. Taalas P, Kaurola J, Kylling A, Shindell D, Sausen R, Dameris M, Grewe V, Herman J, Damski J, Steil B. The impact of greenhouse gases and halogenated species on future solar UV radiation doses. *Geophys. Res. Lett.* 2000; **27**: 1127–1130.
7. Karentz D, Bosch I. Influence of ozone-related increases in ultraviolet radiation on Antarctic marine organisms. *Am. Zool.* 2001; **41**: 3–16.
8. Hunter JR, Taylor JH, Moser HG. Effect of ultraviolet irradiation on eggs and larvae of the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*, during the embryonic stage. *Photochem. Photobiol.* 1979; **29**: 325–338.
9. Hunter JR, Kaupp SE, Taylor JH. Effects of solar and artificial ultraviolet-B radiation on larval northern anchovy, *Engraulis mordax*. *Photochem. Photobiol.* 1981; **34**: 477–486.
10. Williamson CE, Metzgar SL, Lovera PA, Moeller RE. Solar ultraviolet radiation and the spawning habitat of yellow perch, *Perca flavescens*. *Ecol. Appl.* 1997; **7**: 1017–1023.
11. Béland F, Browman HI, Rodriguez CA, St-Pierre J-F. Effect of solar ultraviolet radiation (280–400nm) on the eggs and larvae of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 1999; **56**: 1058–1067.
12. Kouwenberg JHM, Browman HI, Cullen JJ, Davis RF, St-Pierre J-F, Runge JA. Biological weighting of ultraviolet (280–400nm) induced mortality in marine zooplankton and fish. I. Atlantic cod (*Gadus morhua*) eggs. *Mar. Biol.* 1999; **134**: 269–284.
13. Steeger H-U, Wiemer M, Freitag JF, Paul RJ. Vitality of plaice embryos (*Pleuronectes platessa*) at moderate UV-B exposure. *J. Sea Res.* 1999; **42**: 27–34.
14. Charron RA, Fenwick JC, Lean DRS, Moon TW. Ultraviolet-B radiation effects on antioxidants status and survival in the zebrafish, *Brachydanio rerio*. *Photochem. Photobiol.* 2000; **72**: 327–333.
15. Uye S. Effect of enhanced mid-ultraviolet (UVB) radiation on the reproduction of major marine fish populations. *Bull. Asahi Breweries Foundation* 2001; **14**: 115–124.
16. Blazer VS. Effects of ultraviolet-B radiation on fish: histologic comparison of a UVB-tolerant species. *J. Aquat. Anim. Health* 1997; **9**: 132–143.
17. McFadzen I, Baynes S, Hallam J, Beesley A, Lowe D. Histopathology of the skin of UV-B irradiated sole (*Solea solea*) and turbot (*Scophthalmus maximus*) larvae. *Mar. Environ. Res.* 2000; **50**: 273–277.
18. Naganuma T, Inoue T, Uye S. Photoreactivation of UV-induced damage to embryos of a planktonic copepod. *J. Plankton Res.* 1997; **19**: 783–787.
19. Lacuna DG, Uye S. Effect of UVB radiation on the survival, feeding and egg production of the brackish-water copepod, *Sinocalanus tenellus*, with notes on photoreactivation. *Hydrobiologica* 2000; **434**: 73–79.
20. Lacuna DG, Uye S. Influence of mid-ultraviolet (UVB) radiation on the physiology of the marine planktonic copepod *Acartia omorii* and the potential role of photoreactivation. *J. Plankton Res.* 2001; **23**: 143–155.

21. Saito H, Taguchi S. Influence of UVB radiation on hatching success of marine copepod *Paracalanus parvus s.* 1. *J. Exp. Mar. Biol. Ecol.* 2003; **282**: 135–147.
22. Masuda H, Amaoka K, Araga T, Ueno T, Yoshino T (eds.) *The Fishes of the Japanese Archipelago*. Tokaidaigaku Publications, Tokyo. 1984.
23. Kinoshita I, Tanaka M. Differentiated spatial distribution of larvae and juveniles of the two sparids, red and black sea bream, in Shijiki Bay. *Nippon Suisan Gakkaishi* 1990; **56**: 1807–1813.
24. Fukuhara O. Larval development and behavior in early life stages of black sea bream reared in the laboratory. *Nippon Suisan Gakkaishi* 1987; **53**: 371–379 (in Japanese).
25. Tanaka M. Studies on the structure and function of the digestive system in teleost larvae-III. Development of the digestive system during postlarval stage. *Jpn. J. Ichthyol* 1971; **18**: 164–174.
26. Ishibashi Y, Ozawa M, Hirata H, Kumai H. Ontogenic changes in various stress tolerances of larval and juvenile red sea bream *Pagrus major*. *Nippon Suisan Gakkaishi* 2003; **69**: 36–43 (in Japanese).
27. Tanaka M. Habitat change of red sea bream juvenile from pelagic to benthic life. *Suisan Doboku* 1979; **16**: 47–57 (in Japanese).
28. Tanaka M. The ecological studies on the larvae and juveniles of the red sea bream in Shijiki Bay-I. The horizontal distribution of the pelagic larvae and juveniles in and outside the Bay. *Bull. Seikai Reg. Fish. Res. Lab.* 1980; **54**: 231–258 (in Japanese).
29. Oshima Y. Seaweed bed and the protection of juvenile fish habitat. In: Japanese Society of Fisheries Science (ed.). *Overview of Fisheries Science.* Japan Society for the Promotion of Science, Xxxx. 1954; 128–181 (in Japanese).
30. Kinosita I. Ecological study on larvae and juveniles of sparine fishes occurring in surf zones of sandy beach. *Bull. Mar. Sci. Fish. Kochi Univ.* 1993; **13**: 21–99.
31. Lowe C, Goodman-Lowe G. Suntanning in hammerhead sharks. *Nature* 1996; **383**: 677.
32. Dunlap WC, Shick JM. Ultraviolet radiation-absorbing mycosporine-like amino acids in coral reef organisms: a biochemical and environmental perspective. *J. Phycol.* 1998; **34**: 418–430.
33. Vetter RD, Kurtzman A, Mori T. Diel cycles of DNA damage and repair in eggs and larvae of northern anchovy, *Engraulis mordax*, exposed to solar ultraviolet radiation. *Photochem. Photobiol.* 1999; **69**: 27–33.
34. Wiegand MD, Young DLW, Gajda BM, Thuen DJM, Rittberg DAH, Huebner JD, Loadman NL. Ultraviolet light-induced impairment of goldfish embryo development and evidence for photorepair mechanisms. *J. Fish. Biol.* 2004; **64**: 1242–1256.
35. Kinoshita I. Occurrence of larval and juvenile fishes in the surf zones facing Tosa Bay. *Kaiyo Seibutu* 1984; **35**: 409–415.
36. Kawamura G, Tuda R, Kumai H, Ohashi S. The visual cell morphology of *Pagrus major* and its adaptive changes with shift from pelagic to benthic habitats. *Nippon Suisan Gakkaishi* 1984; **50**: 1975–1980.
37. Lara MR. Morphology of the eye and visual acuities in the settlement-intervals of some coral reef fishes (Labridae, Scaridae). *Envir. Biol. Fish.* 2001; **62**: 365–378.
38. Miyagi M, Kawamura G. 1-response to UV stimulus and UV sensitive cones in marine fishes. *Nippon Suisan Gakkaishi* 2000; **66**: 195–199.
39. Browman HI, Hawryshyn CW. The developmental trajectory of ultraviolet photosensitivity in rainbow trout is altered by thyroxine. *Vision Res.* 1994; **34**: 1397–1406.
40. Kelly DJ, Bothwell ML. Avoidance of solar ultraviolet radiation by juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 2002; **59**: 474–482.
41. Ylönen O, Huuskonen H, Karjalainen J. UV avoidance of coregonid larvae. *Ann. Zool. Fennici* 2004; **41**: 89–98.
42. Speekmann CL, Bollens SM, Avent SR. The effect of ultraviolet radiation on the vertical distribution and mortality of estuarine zooplankton. *J. Plankton Res.* 2000; **22**: 2325–2350.
43. Kuwahara VS, Ogawa H, Toda T, Kikuchi T, Taguchi S. Variability of bio-optical factors influencing the seasonal attenuation of ultraviolet radiation in temperate coastal waters of Japan. *Photochem. Photobiol.* 2000; **72**: 193–199.
44. Kuwahara VS, Toda T, Hamasaki K, Kikuchi T, Taguchi S. Variability in the relative penetration of ultraviolet radiation to photosynthetically available radiation in temperate coastal waters, Japan. *J. Oceanogr.* 2000; **56**: 399–408.