Environ Biol Fish (2013) 96:13–20
DOI 10.1007/s10641-012-0017-2

Comparison of UV-B tolerance between wild and hatchery-reared juveniles of red sea bream (*Pagrus major*) and black sea bream (*Acanthopagrus schlegeli*)

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Received: 7 March 2011 / Accepted: 13 April 2012 / Published online: 28 April 2012

Abstract The amount of ultraviolet (UV)-B radiation reaching the sea surface has increased due to ozone depletion. Several laboratory studies have highlighted the negative impacts of UV radiation on fish using hatchery-reared specimens. However, potential differences in UV tolerance between wild and hatchery-reared fish have been given little consideration. Wild and reared juveniles of red sea bream and black sea bream were exposed to one of four different UV-B radiation levels (1.8; 1.1; 0.4; 0 W/m^2) for 4 h. Survival rate was measured every 2 h for a period of 24 h (red sea bream) or 48 h (black sea bream) following exposure. Wild and reared juvenile red sea bream were characterized by similar survival rate, with survival declining to almost 0 % 24 h after exposure at the 1.1 and 1.8 W/m^2 levels. In black sea bream, wild individuals showed significantly higher survival than reared fish in levels 1.1 and 1.8 W/m^2. Melanophore density was also measured since melanin absorbs UV radiation. Wild black sea bream showed higher melanophore density compared to reared individuals, while no such difference was observed in red sea bream. We conclude that wild black sea bream juveniles acquire higher UV tolerance partly by increasing melanophore density through exposure to UV radiation. Our results indicate that the predicted impacts of UV radiation on fish populations solely based on experimentation with hatchery-reared specimens may be overestimated for some species.

Keywords Ultraviolet radiation · Sparid fish · Interspecific comparison · Melanophores

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Introduction

Increasing ultraviolet-B (UV-B) radiation (280–315 nm) associated with ozone depletion has been reported not only in polar regions but also at mid-latitudes over the past few decades (Kerr and McElroy 1993; Madronich et al. 1998). For instance, the annual UV dose received at ground level increased by 5.5 % per decade over the 1979–2003 period in the Netherlands (12–52°N, 19–5°E) (den Outer et al. 2005). Because a fraction of UV-B radiation penetrates below the sea surface (Tedetti and Sempéré 2006), it is important to quantify the adaptation potential of marine fish to their changing environment. Substantial progress has been achieved

in the understanding of negative impacts of UV radiation on fish, especially in their early life stages. For instance, hatching deficiencies (Béland et al. 1999; Kouwenberg et al. 1999; Fukunishi et al. 2010), increased mortality (Hunter et al. 1979, 1981; Béland et al. 1999; Kouwenberg et al. 1999; Steeger et al. 1999; Fukunishi et al. 2006), DNA damage (Kouwenberg et al. 1999; Browman et al. 2003), malformations (Dong et al. 2007), eye, brain and skin lesions (Hunter et al. 1979; Blazer et al. 1997; McFadzen et al. 2000), retarded growth (Hunter et al. 1979; Jokinen et al. 2008) and immune depression (Jokinen et al. 2008; Markkula et al. 2009) have been documented in a variety of fish species. However, most of these studies have been conducted in the laboratory using hatchery-reared fish.

Experiments using hatchery-reared fish allow measuring processes on relatively high numbers of individuals of similar life history. However, hatchery-reared individuals do not always best represent the range of variability of a given species in terms of morphology, physiology and behaviour, as they develop in a controlled environment. For example, Boglione et al. (2001) reported that larval hatchery-reared gilthead sea bream (*Sparus aurata*) showed bone malformations, which are not observed in wild individuals. Lipid and highly unsaturated fatty acids (HUFA) composition of yellowtail (*Seriola quinqueradiata)* larvae was significantly different among wild and hatchery-reared individuals (Arakawa et al. 2002). Red sea bream juveniles that were extensively farmed in a semi-natural environment developed higher tolerance against anesthesia, drying, hypoxia and starvation relative to hatchery-reared individuals fed with enriched rotifers and *Artemia* (Tsumura and Yamamoto 1993). The swimming capacity of hatchery-reared red drum (*Sciaenops ocellatusn*) larvae was inferior to that of wild individuals at the same size (Smith and Fuiman 2004). Therefore, it is not necessarily appropriate to extrapolate to wild fish populations the effects of environmental factors derived from hatchery-reared individuals. In order to evaluate the impact of UV radiation on fish more precisely, it is important to consider the potential inferiority of hatchery-reared fish in evaluations of UV tolerance. However, little attention has been paid on this issue so far.

In a previous study, we reported that hatchery-reared juveniles of black sea bream, a fish species inhabiting the surf zone, were more tolerant to UV-B radiation than red sea bream juveniles, which are usually distributed in deeper waters (Fukunishi et al. 2006). The objectives of this study were to assess the potential differences of UV-B tolerance among wild and hatchery-reared individuals in these two closely-related species, and to verify the hypothesis that the general result observed in hatchery-reared fish 'black sea bream show higher UV tolerance than red sea bream' applies to wild fish as well. The density of melanophores was also measured in order to quantify the response of fish to UV, since melanin, the main component of melanophores, absorbs wavelengths of UV radiation and constitutes one of the main UV-protection mechanisms (Cockell and Knowland 1999).

Materials and methods

Sampling of wild juveniles

Wild red sea bream (*Pagrus major*) juveniles were collected using a beam trawl (2×0.3 m width and height, 3 mm mesh) towed on the bottom at a depth of ~10 m offshore Kanzaki Beach, Kyoto Prefecture. Sampling was conducted by the Research Vessel Ryokuyo-maru (Kyoto University) on 17 June 2008. Fish were stocked in a white opaque bucket with moderate aeration and were immediately brought to the Maizuru Fisheries Research Station (MFRS) of Kyoto University. The experiment was conducted on the following day.

Wild black sea bream (*Acanthopagrus schlegeli*) juveniles were sampled using a surf zone (<1.2 m) net in front of the MFRS from 18 July to 26 July 2008. Fish were kept in a light shielded container and were immediately transferred to the laboratory. Fish were kept in a 200 L black tank and fed with formulated food (Otohime S-2, Marubeni Nisshin Feed Co, Tokyo, Japan) twice a day until a sufficient number of fish had been collected (i.e. 36 individuals) to conduct the experiment.

Fish rearing

Naturally-spawned red sea bream and black sea bream eggs were provided by the Isikawa Prefectual Fisheries Research Center on 2 June 2008. They were transported to the MFRS and were stocked in two transparent circular tanks (500 L) for each species at a density of 30000 per tank. Eggs of both species

hatched on the next day. The hatching date was defined as 0 day post hatching (DPH). Fish were reared indoors at low photosynthetically active radiation (PAR) intensity and in the absence of UV radiation. Rotifers and *Artemia* enriched with Marine Gloss EX (Nissin Marinetech, Yokohama, Japan) and formulated food of various size (Kyowa B400, and B700, Kyowa Hakko Kogyo, Tokyo, Japan) were fed to larvae and juveniles twice a day, depending on their developmental stage. Rearing procedures for larvae and juveniles followed those detailed in Fukunishi et al. (2006). Water temperature in the stock tank ranged 18.3–23.8°C in red sea bream, and 18.1–25.1°C in black sea bream.

Experimental procedure

The experiment was conducted when hatchery-reared juveniles attained a similar size as wild juveniles in each species. The mean total length of wild and hatchery-reared red sea bream was 24.3±0.3 mm and 24.2±0.3 mm (44 DPH), respectively. For black sea bream, wild and hatchery-reared fish measured 40.5± 0.8 mm and 40.8±0.5 mm (73 DPH), respectively.

The apparatus of the experiment was set up in a temperature-controlled room (28 m^2), and the experimental area (4 m^2) was surrounded by black vinyl curtains. A water bath (20 cm×85 cm×90 cm) was set on the floor just under the fluorescent lamps (Toshiba: FLR40S W/M/36 White) on the ceiling. A hole (diameter: 15 mm) was made on one side of the water bath at a height of 8 cm from the bottom to drain seawater. Filtered seawater was circulated in the water bath and moderate aeration was provided. Water temperature was maintained at the same level as that of the stock tanks using a thermostat and a chiller. UV-B lamps (TL 20 W/12 RS, Philips, Eindhoven, Netherlands; wavelength 260–400 nm and maximum emission 306 nm) were hung above the water bath. Three different levels of UV radiation were provided (A: 1.8 W/m^2; B: 1.1 W/m^2; C: 0.4 W/m^2) by adjusting the distance from UV-B lamps to the water surface. Light measurements were made just above the water surface with a portable photoradiometer (DO9721, Delta Ohm, Padua, Italy). Each treatment approximated the following conditions: (A) a value higher than the UV-B level observed during early summer in Wakasa Bay, Sea of Japan; (B) the maximum UV-B radiation level observed at the sea surface off the western part of Wakasa Bay on a sunny and clear day; and (C) a value observed on a slightly cloudy day. Controls without UV exposure were also prepared. UV-C radiation emitted from UV-B lamps (less than 280 nm) was blocked by covering them with cellulose diacetate film [Clarifoil, Derby, England; the spectral transmittance is shown in Fukunishi et al. (2010)]. Each exposure section was separated vertically using transparent UV-blocking sheets to prevent light interference among treatments. Three juveniles were stocked in each mesh plastic container (1 L) set directly underneath the UV-B lamps in the water bath. The mesh (diameter: 5 mm) of the container kept the water level constant and similar to that of the water bath (8 cm), and allowed seawater to run through, providing enough oxygen to the fish. The number of replications (i.e. containers) at each UV level was 5 in both wild and hatchery-reared red sea bream, and 3 and 6 in wild and hatchery-reared black sea bream, respectively. Fish were exposed to UV-B for 4 h from 10:00 to 14:00. The cumulative UV dose at each level was A: 25,920 J/m^2, B: 15,840 J/m^2, C: 5,760 J/m^2 and Control: 0 J/m^2, respectively. The light regime of the fluorescent lamps in the room was set as L: D=12:12 (lights on from 6:00 to 18:00). The number of surviving individuals was counted every 2 h after the UV exposure and mean survival rate was calculated. The observation period of red sea bream and black sea bream lasted 24 h and 48 h, respectively. An individual was considered dead when gill ventilation was stopped. Individuals found dead during the experiment were immediately removed to avoid degradation of water quality. Standard length of fish was measured after the experiment with a digital caliper.

The density of melanophores

Pictures of the skin were taken from 10 randomly-selected areas over the lateral line using a digital camera connected to a binocular microscope (SMZ1500, SMZ15-LS-BD, Nikon, Japan). The mean density of melanophores (number/mm^2) was calculated. Five specimens from each species and origin (wild or hatchery-reared) were randomly sampled and analyzed.

Statistical analysis

Student's *t*-test was used to compare standard length among wild and hatchery-reared fish. Survival was assessed with the Kaplan-Meyer method and tested for significance by the log-rank test. An ANOVA complemented by the Tukey-Kramer HSD test was

performed to compare the density of melanophores among fish species and origins. All analyses were run under the JMP (Ver. 5.01J) statistical software (SAS Institute, Cary NC, USA).

Results

There was no significant difference in total length between wild and hatchery-reared individuals in either species (*t*-test, $P>0.05$).

Similar survival rate was observed among wild and hatchery-reared red sea bream juveniles for both A and B exposure levels (Fig. 1: a, b). In level A, all individuals died within 24 h after the exposure in both wild and hatchery-reared fish. Although a significant difference in mortality rate was found between wild and hatchery-reared fish (Kaplan-Myer method, log rank test, $P<0.05$), the time interval from the onset of death to 100 % mortality was 4 h in both origins (wild: 14–18 h, hatchery-reared: 16–20 h). Under level B exposure, mortality of wild and hatchery-reared fish at the end of the experiment was 93 % and 100 %, respectively, and did not differ significantly (Kaplan-Myer method, log rank test, $P>0.05$).

In black sea bream, wild individuals showed significantly higher survival than hatchery-reared ones in levels A and B (Kaplan-Myer method log rank test, $P<0.05$) (Fig. 1: c, d). Survival rate of hatchery-reared fish decreased gradually from about 20 h post-exposure and reached 100 % mortality at the end of the experiment. In contrast, survival rate of wild juveniles declined later than that of hatchery-reared fish in level A and 11 % of individuals survived until the end of the

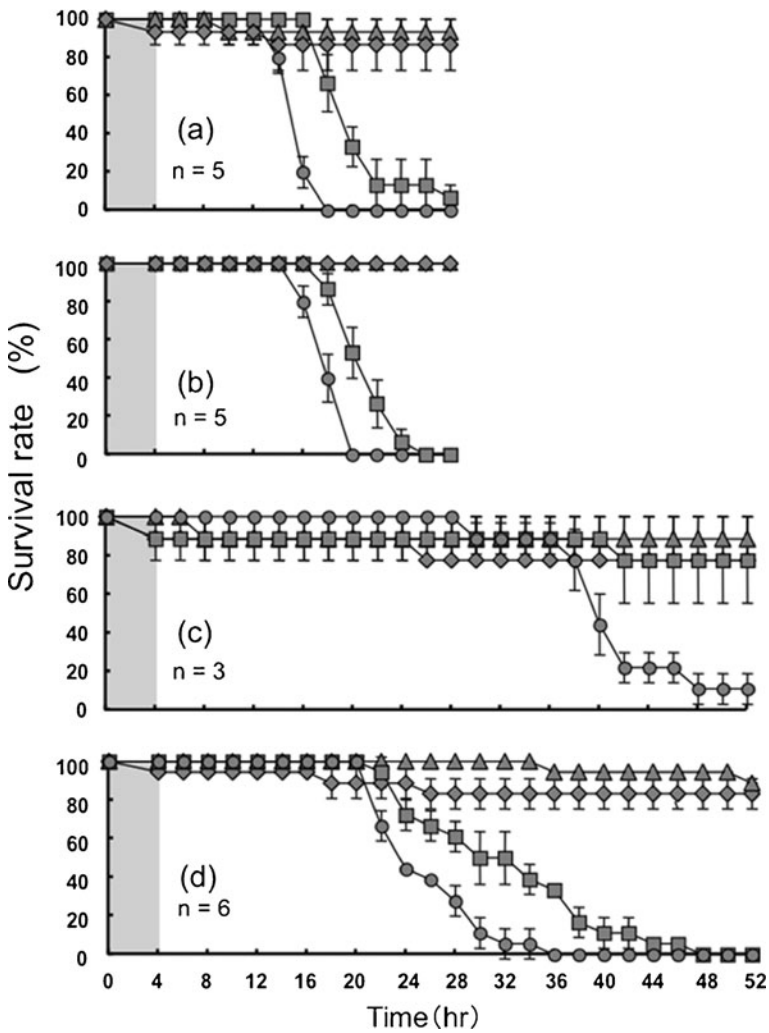

Fig. 1 Survival of hatchery-reared and wild juvenile red sea bream (*Pagrus major*) and black sea bream (*Acanthopagrus schlegeli*) under different levels of UV-B radiation. **a** wild red sea bream, **b** hatchery-reared red sea bream, **c** wild black sea bream, **d** hatchery-reared black sea bream. Circle symbols: Level A; rectangle symbols: Level B; triangle symbols: Level C; diamond symbols: Control. Each value represents the mean ± SE. The shaded area represents the UV exposure period

experiment. In level B, as many as 80 % of wild black sea bream survived.

Wild red sea bream showed poorer UV tolerance relative to wild black sea bream (Fig. 1: a, c). Survival was significantly different among species in level A and B, but not in level C and control (Kaplan-Myer method log rank test, $P<0.05$).

Mean melanophore density did not significantly differ between wild and hatchery-reared red sea bream (Tukey-Kramer HSD test, $P>0.05$) (Fig. 2). In contrast, wild black sea bream juveniles were characterized by a 40 % higher melanophore density than that of hatchery-reared fish (Tukey-Kramer HSD test, $P<0.05$). Both wild and hatchery-reared black sea bream showed a significantly higher melanophore density compared to that of red sea bream (Tukey-Kramer HSD test, $P<0.05$).

Discussion

There was a clear interspecific difference between red sea bream and black sea bream in both UV tolerance and melanophore density. In red sea bream, no significant difference was observed in UV tolerance between wild and hatchery-reared juveniles. Both experiments resulted in >90 % or 100 % mortality under high UV radiation levels A and B. Melanophore density did not significantly differ between origins either.

The main post-settlement habitat of red sea bream juveniles consists of sandy beaches of about 10 m depth (Tanaka 1985), in which most of the UV wavelengths are attenuated before reaching the bottom. Kuwahara et al. (2000) measured that the 1 % attenuation depth of UV-B was <10 m depth in similar coastal areas of Sagami Bay in summer. We therefore hypothesize that juvenile red sea bream do not need to develop high UV tolerance in their natural habitat.

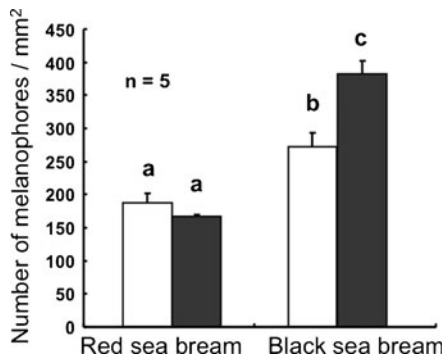

Fig. 2 Density of melanophores in hatchery-reared and wild juveniles for red sea bream (*Pagrus major*) and black sea bream (*Acanthopagrus schlegeli*). White and solid bars denote hatchery-reared and wild juveniles, respectively. Different letters represent significant difference among groups. Each value represents the mean ± SE

On the contrary, wild black sea bream juveniles showed superior UV tolerance to their hatchery-reared counterparts. All hatchery-reared individuals exposed to UV radiation level B died during the experiment, whereas 80 % of wild juveniles survived until the end of the experiment. These results indicate that wild black sea bream juveniles may tolerate short periods of UV radiation exposure corresponding to the maximum current level observed in the habitat.

Wild juveniles were characterized by a higher number of melanophores on the dorsal skin relative to hatchery-reared fish. Melanophore density increase due to environmental stress has been reported in other species. For example, medaka (*Oryzias latipes*) reared in a black tank developed more melanophores than those reared in a white tank (Sugimoto 1993). In this case, the adaptive significance is considered to be the cryptic coloration allowing fish to blend into the background. Hatchery-reared adult red sea bream are known for being tanned when cultured in outdoor shallow cages, resulting in a reduced market price. Therefore, covering cages is a common procedure among farmers to prevent the body color of fish from darkening. Adachi et al. 2005 reported that adult red sea bream reared in outdoor cages developed more melanophores compared to wild individuals or fish reared in light-shielded cages. These authors speculated that red sea bream exposed to sunlight were adapted to the UV radiation. Juvenile scalloped hammerhead shark (*Sphyrna lewini*) showed increased melanin concentration on the skin in response to an increase of solar radiation, leading to the reduction of transmittance in the UV-B wavelengths (Lowe and Goodman-Lowe 1996). Since black sea bream inhabit the surf zone with white background, increasing melanophores could result in increasing visibility to predators (Hansson 2004). Despite this potential disadvantage, wild black sea bream juveniles were darker and showed higher UV tolerance compared to individuals reared in transparent tanks. These results suggest that wild black sea bream juveniles develop a high UV tolerance partly by increasing the number of melanophores on the skin during development.

Potential intraspecific variability in UV tolerance should be considered as one of the reasons why UV tolerance of wild fish was superior to that of hatchery-reared black sea bream, since individuals characterized by higher UV tolerance may selectively survive in a UV-radiated environment. However, this possibility appears unlikely because UV tolerance variability among hatchery-reared black sea bream was relatively low. Maximum differences of surviving time among individuals in radiation level A and B were only 14 h and 26 h, respectively. In addition, the fact that the coefficient of variation of melanophore density was relatively small in both wild (0.12) and hatchery-reared fish (0.18) supports this interpretation, as the number of melanophores can fluctuate to adapt to light intensity.

It is also unlikely that any genetic characteristics of hatchery-reared black sea bream contributed to the low UV tolerance compared to the wild counterpart, because the fertilized egges we used in this study originated from a sub-population of 250 individuals captured in the Sea of Japan and so the domestication would hardly have occurred. Therefore, poorer UV tolerance in hatchery-reared fish should have resulted from certain rearing conditions in the hatchery.

Black sea bream is one of the most important target species for commercial stock enhancement in Japan and a cumulative total of 14 billion hatchery-reared black sea bream juveniles were released from 1977 to 2005 (Yamashita and Aritaki 2010). Our results indicate that hatchery-reared black sea bream juveniles with relatively low UV tolerance have already been released to the sea. Black sea bream are usually released in the coastal area near main fishering ports, which is different from the habitat of wild juveniles (i.e. surf zones). In general, water in the ports tends to be turbid due to anthropogenic factors. In addition, there are a number of artificial structures such as boats or docks. UV penetration in the water column may, thus, be relatively low, decreasing the probability that fish are exposed to high levels of UV radiation.

Survival of hatchery-reared black sea bream juveniles would have been higher than the value observed in the present experiment if the experiments were conducted with refuge or deeper containers. This is because hatchery-reared black sea bream juveniles can actively avoid artificial UV-B radiation when the UV intensity is high (1.1 W/m^2) (Fukunishi et al. 2006). Behavioural avoidance of solar UV radiation was also observed in juvenile coho salmon (*Oncorhynchus kisutch*) in outdoor experiments (Kelly and Bothwell 2002; Holtby and Bothwell 2008). Therefore, released black sea bream seedlings may also seek shady areas or select different habitats characterized by reduced UV radiation (e.g. deeper or more turbid environments) and thus they would not experience such a high mortality as obseved in the experiments. However if exploiting shallow surf zones with few shades along with wild juveniles, they would suffer higher vulnerability to the lethal and sub-lethal effects of UV radiation. Sub-lethal effects, consisting in delayed growth and increased infection rate due to weaker immune system (Jokinen et al. 2008), may contribute to the higher mortality of released fish in the natural environment. In the hatchery production process, black sea bream are usually reared in a room under relatively low PAR intensity and in the absence of UV radiation. We propose that exposing black sea bream seedlings to moderate UV radiation levels may increase melanophores on the skin and magnify UV tolerance prior to release.

Wild black sea bream juveniles inhabiting shallow areas with high UV radiation exposure exhibited higher UV tolerance compared to wild red sea bream juveniles distributing deeper in the water column in an environment with low UV radiation. This result supports our previous conclusions with hatchery-reared fish that ‘species inhabiting shallow areas with high UV radiation levels are well adapted to a high UV radiation environment’. In addition, black sea bream juveniles were characterized by higher melanophore density than red sea bream, both in hatchery-reared and wild fish. Thus, melanophores are likely one of the reason for the observed interspecific difference in UV tolerance between red sea bream and black sea bream.

In this study, hatchery-reared fish showed a lower UV tolerance relative to wild individuals. Although we only focused on the juvenile stage in the present experiment, such trends may also be associated with the larval stage. Further experiments using healthy live larvae captured in the natural environment are needed to assess the ontogeny of the adaptation to UV radiation. Overall, differences in UV tolerance observed between hatchery-reared red sea bream and black sea bream were also found in wild individuals. Therefore, we conclude that it is valid to use hatchery-reared fish to assess interspecific differences in UV tolerance potential. However, predicting UV impacts on wild fish populations solely based on experimentation with hatchery-reared specimens may lead to overestimation in some species.

Acknowledgments We thank the Ishikawa Prefectural Fisheries Center for providing red sea bream and black sea bream fertilized eggs, staff at Notojima Station, National Center for Stock Enhancement, Fisheries Research Agency, for providing rotifers, and the staff and students in MFRS for helping sampling of wild red sea bream and black sea bream. Comments from H. I. Browman and two anonymous reviewers substantially improved the quality of this manuscript. This study was supported by Grant-in-Aid for JSPS fellows (No. 203906).

References

Adachi K, Kato K, Wakamatsu K, Ito S, Ishimaru K, Hirat T, Murata O, Kumai H (2005) The histological analysis, colorimetric evaluation, and chemical quantification of melanin content in 'suntanned' fish. Pigment Cell Res 18:465–468

Arakawa T, Ishizaki Y, Chuda H, Shimizu K, Arimoto M, Takeuchi T (2002) Comparison of lipid classes and fatty acid compositions between hatchery reared and wild caught yellowtail *Seriola quinqueradiata* juvenile [in Japanese]. Bull Jap Soc Sci Fish 68:374–381

Béland F, Browman HI, Rodriguez CA, St-Pierre J-F (1999) Effect of solar ultraviolet radiation (280–400 nm) on the eggs and larvae of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 56:1058–1067

Blazer VS, Favacher DL, Little EE, Ewing MS, Kocan KM (1997) Effects of ultraviolet-B radiation on fish: Histologic comparison of a UV-B sensitive and UVB-tolerant species. J Aquat Anim Health 9:132–143

Boglione C, Gagliardi F, Scardi M, Cataudella S (2001) Skeletal descriptors and quality assessment in larvae and post-larvae of wild-caught and hatchery-reared gilthead sea bream (*Sparus aurata* L. 1758). Aquaculture 192:1–22

Browman HI, Vetter RD, Rodriguez CA, Cullen JJ, Davis RF, Lynn E, St Pierre JF (2003) Ultraviolet (280–400 nm)-induced DNA damage in the eggs and larvae of *Calanus finmarchicus* G. (Copepoda) and Atlantic cod (*Gadus morhua*). Photochem Photobiol 77:397–404

Cockell CS, Knowland J (1999) Ultraviolet radiation screening compounds. Biol Rev 74:311–345

den Outer PN, Slaper H, Tax RB (2005) UV radiation in the Netherlands: asessing long-term variability and trends in relation to ozone and clouds. J Geophys Res 110:D02203

Dong Q, Svobota K, Tiersch TR, Monroe WT (2007) Photobiological effects of UVA and UVB light in zebrafish embryos: evidence for a competent photorepair system. J Photochem Photobiol B Biol 87:137–146

Fukunishi Y, Masuda R, Yamashita Y (2006) Ontogeny of tolerance to and avoidance of ultraviolet radiation in red sea bream *Pagrus major* and black sea bream *Acanthopagrus schlegeli*. Fish Sci 72:356–363

Fukunishi Y, Masuda R, Yamashita Y (2010) Exposure of eggs to solar UV-B lead to reduced hatching rates in two sparid fishes, red sea bream (*Pagrus major*) and black sea bream (*Acanthopagrus schlegeli*). J Fish Biol 76:734–741

Hansson LA (2004) Plasticity in pigmentation induced by conflicting threats from predation and UV radiation. Ecology 85:1005–1016

Holtby LB, Bothwell ML (2008) Effects of solar ultraviolet radiation on the behaviour of juvenile coho salmon (*Oncorhynchus kisutch*): avoidance, feeding, and agonistic interactions. Can J Fish Aquat Sci 65:701–711

Hunter JR, Taylor JH, Moser HG (1979) 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 29:325–338

Hunter JR, Kaupp SE, Taylor JH (1981) Effects of solar and artificial ultraviolet-B radiation on larval northern anchovy, *Engraulis mordax*. Photochem Photobiol 34:477–486

Jokinen IE, Markkula ES, Salo HM, Kuhn P, Nikoskelainen S, Arts MT, Browman HI (2008) Exposure to increased ambient ultraviolet B radiation has negative effects on growth, condition and immune function of juvenile Atlantic Salmon (*Salmo salar*). Photochem Photobiol 84:1265–1271

Kelly DJ, Bothwell ML (2002) Avoidance of solar ultraviolet radiation by juvenile coho salmon (*Oncorhynchus kisutch*). Can J Fish Aquat Sci 59:474–482

Kerr JB, McElroy CT (1993) Evidence for upward trends of ultraviolet-B radiation linked to ozone depletion. Science 262:1032–1034

Kouwenberg JHM, Browman HI, Cullen JJ, Davis RF, St-Pierre J-F, Runge JA (1999) Biological weighting of ultraviolet (280–400 nm) induced mortality in marine zooplankton and fish. I. Atlantic cod (*Gadus morhua*) eggs. Mar Biol 134:269–284

Kuwahara VS, Ogawa H, Toda T, Kikuchi T, Taguchi S (2000) Variability of bio-optical factors influencing the seasonal attenuation of ultraviolet radiation in temperate coastal waters of Japan. Photochem Photobiol 72:193–199

Lowe C, Goodman-Lowe G (1996) Suntanning in hammerhead sharks. Nature 383:677

Madronich S, Mckenzie RL, Björn LO, Caldwell MM (1998) Changes in biologically active ultraviolet radiation reaching the Earth's surface. J Photochem Photobiol B Biol 46:5–19

Markkula E, Salo HM, Rikalainen K, Jokinen IE (2009) Long-term UVB irradiation affects the immune functions of carp (*Cyprinus carpio*) and Rainbow Trout (*Onchorhynchus mykiss*). Photochem Photobiol 85:347–352

McFadzen I, Baynes S, Hallam J, Beesley A, Lowe D (2000) Histopathology of the skin of UV-B irradiated sole (*Solea solea*) and turbot (*Scophthalmus maximus*) larvae. Mar Environ Res 50:273–277

Smith ME, Fuiman LA (2004) Behavioral performance of wild-caught and laboratory-reared red drum *Sciaenops ocellatus* (Linnaeus) larvae. J Exp Mar Biol Ecol 302:17–33

Steeger H-U, Wiemer M, Freitag JF, Paul RJ (1999) Vitality of plaice embryos (*Pleuronectes platessa*) at moderate UV-B exposure. J Sea Res 42:27–34

Sugimoto M (1993) Morphological color changes in the medaka, *Oryzias latipes,* after prolonged background adaptation:

II. Changes in the population and morphology of melanophores. Comp Biochem Physiol 104A:13–518

Tanaka M (1985) Factors affecting the inshore migration of pelagic larval and demersal juvenile red sea bream *Pagrus major* to a nursery ground. Trans Am Fish Soc 114:471–477

Tedetti M, Sempéré R (2006) Penetration of ultraviolet radiation in the marine environment. A review. Photochem Photobiol 82:389–397

Tsumura S, Yamamoto Y (1993) Rearing methods and healthy fry. In: Kitajima R (ed) Healthy fry for release, and their production techniques [in Japanese]. Koseisya-Koseikaku, Tokyo, pp 84–93

Yamashita Y, Aritaki M (2010) Stock enhancement of Japanese flounder in Japan. In: Watanabe W (ed) Daniels HV. Practical flatfish culture and stock enhancement. Wiley-Blackwell, Ames, pp 239–251