Chum salmon spawners do not respond to flickering near-UV radiation that could be used to drive away egg predators in spawning streams

Gunzo Kawamura1*, Norihiko Nakano2, Kazuhiko Anraku1 and Takaaki Nishi1

1Faculty of Fisheries, Kagoshima University, Kagoshima 890-0056, Japan.
2Graduate School of Fisheries Science, Hokkaido University, Hakodate 041-8611, Japan.

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Chum salmon (Oncorhynchus keta) eggs are eaten in large numbers by Japanese dace (Tribolodon hakonensis) in the spawning streams in Hokkaido. One way to reduce predation on salmon eggs might be to use flickering near-ultraviolet (UV) radiation at 386 nm, to which Japanese dace is known to react negatively. The effect of flickering near-UV on chum salmon was determined in this paper. Sexually mature chum salmon were examined for (i) retinal photoreceptors (corner single cones) sensitive to near-UV; (ii) behavioural responses to flickering radiation at near-UV (λmax 386 nm), green (λmax 524 nm), and red (λmax 618 nm); and (iii) near-UV transmittance through the cornea and lens. The chum salmon had complete square cone mosaics (four double cones around a central single cone and four single cones at the corners of the square) at the central sector of the retina. The corner single cones are the photoreceptors sensitive to near-UV. About 300 mature chum salmon did not respond to flickering near-UV radiation from light-emitting diodes in an indoor tank, but avoided flickering green light and red light. The eye lens of chum salmon almost totally blocked short wavelengths below 390 nm. Thus, despite having UV-sensitive photoreceptors in the retina, mature chum salmon can not respond to near-UV radiation because of the UV-blocking lens. We conclude that flickering near-UV radiation can be a feasible means to scare away the Japanese dace from the spawning streams without any influence on the chum salmon spawners in daytime as well as at night.

Key words: Chum salmon, ocular transmission, near-ultraviolet, corner single cones, egg predation, Japanese dace.

INTRODUCTION

The chum salmon (Oncorhynchus keta) has the widest geographical distribution among salmonids in the North Pacific Rim and there is current interest to protect and enhance the wild populations. Adults return to the natal river to spawn and across Japan, they enter rivers for spawning from September to December. Eggs are deposited in the stream gravel beds and hatch after 74 d at 6-7 °C and 125 d at 3.4 °C (Ochiai and Tanaka, 1986). The alevins reside in the gravel as they resorb their yolk and then emerge from the stream bottom after 2-3 months. During this time in the streams, chum salmon eggs and alevins are prey to a variety of fishes, particularly the Japanese dace (Tribolodon hakonensis) (Inukai, 1949).

One way to protect the wild populations of chum salmon is to reduce predation on eggs and alevins, and one way to do so is to influence the behaviour and movement of both the predator and the prey without physically handling them. Several technologies have been developed to elicit fish movement away from hazardous structures or situations. These technologies are referred to as sensory deterrent systems and among the possible stimuli, light appears to be most effective (Hadderingh, 1979; Hamel et al., 2008). Of course the response of the target species must be well known before a particular stimulus can be used to modify movement patterns in the spawning streams.

Microspectrophotometry revealed that the Japanese dace have eyes sensitive to the near-ultraviolet (UV)
wavelengths (Harosi and Hashimoto, 1983) and avoid flickering near-UV radiation in an outdoor tank even in daytime (Matsumoto, 2005). Indeed, flickering light is an effective fright stimulus for fishes (Kawamura et al., 2002; Richards et al., 2007; Oliveira Mesquita et al., 2008). Thus, flickering near-UV radiation could be used to drive Japanese dace away from chum salmon spawning streams. The question is: will flickering light drive away the chum salmon as well?

Mature chum salmon have cone cells also sensitive to near-UV (Beaudet et al., 1997) and it is possible that the spawners also avoid flickering near-UV. Salmonids are known to avoid flashing strobe lights during both day and night (Simenstad et al., 1999). Many fishes are UV sensitive when immature, but not when they mature. Newly hatched Atlantic salmon (Salmo salar) have retinas with complete square cone mosaics including the corneal single cones (Kunz et al., 1994). The corneal single cones disappear from the retina except along the dorsal periphery during the parr stage, over a year old, but reappear upon maturation (Flamarique, 2002). In the rainbow trout (O. mykiss), near-UV sensitive cones disappear from the ventral retina during smoltification but remain intact in the dorsal retina (Allison et al., 2003).

Retinas with near-UV sensitive photoreceptors allow the animal to see near-UV radiation if the ocular media (cornea, lens and humors) are UV-transparent. If a portion of the spectrum is absorbed by the ocular media, then vision at these wavelengths becomes impossible. Light-blocking pigments that absorb UV radiation have been found in the ocular media of many fishes (Siebeck and Marshall, 2001; Losey et al., 2003; White et al., 2004). The intact eyes of juvenile rainbow trout, cutthroat trout (O. clarki clarki) and sockeye salmon (O. nerka) are all electrophysiologically sensitive to near-UV (Parkyn and Hawryshyn, 2000). The transmittance of the ocular media of rainbow trout (Hawryshyn et al., 1989) and adult sockeye salmon (Flamarique, 2000) are high enough to allow these salmonids to see UV.

To determine if chum salmon spawners are sensitive to flickering near-UV radiation, we examined sexually mature chum salmon for (i) the presence of UV-sensitive corner single cones in the retina, (ii) behavioural response to flickering near-UV, green, and red light; and (iii) near-UV transmittance through the lens and cornea. If chum salmon are not sensitive to flickering near-UV, then the latter could be used in a sensory deterrent system in the spawning streams to drive away Japanese dace and reduce predation on chum salmon eggs and alevins.

**MATERIALS AND METHODS**

**Retinal histology**

Three freshly killed sexually mature chum salmon (two males and one female, 72-78 cm in total length), captured from the wild during their upstream migration by a salmon-trap set in the Toi River in Hakodate, Hokkaido, were obtained from the Toi Fisheries Coope-

**Transmittance through ocular media**

Four freshly killed chum salmon (three males, one female, 70-77 cm in total length) were obtained from a local supplier in Hakodate and the heads were transported in ice-water to the Faculty of Fisheries, Kagoshima University. Iceing and freezing have negligible effect on the transmission of fish lenses and cones (Thorpe et al., 1993; Losey et al., 2003). A 100-W xenon lamp provided sufficient UV radiation for transmittance through ocular media. Spectral transmittance was measured with a spectroradiometer (HSR-8100) over the wave band from 300 to 700 nm. The corneal preparation was mounted on a 0.9 mm thick glass slide on a micromanipulator (M-3333, Narishige Scientific Instrument Lab., Tokyo, Japan) with a magnet stand, and was then placed in front of the pinhole spectro-
Figure 1. Illustrations showing (A) the complete square cone mosaic found in central sector of the retina, and (B) different cone mosaic found in the peripheral sectors. CSC, corner single cone; DC, double cone; SC, central single cone. Double cones are larger and fewer at the central retina.

RESULTS

Distribution of UV-sensitive corner single cones

Double cones and central single cones were found in the entire retina of the chum salmon. Complete square cone mosaics, consisting of four double cones around a central single cone and four corner single cones at the corners were found only at the central sector of the retina (Figure 1a), in contrast to the irregular arrangement in the other sectors (Figure 1b). In all three chum salmon, corner single cones were absent in the nasal, dorso-nasal and ventro-nasal sectors, but had the highest density in the central retina (Table 1). The individuals varied in the presence and density of corner single cones elsewhere in the retina. Small numbers of corner single cones were present in the ventro-temporal sector in fish #1, in the dorso-temporal and ventral sectors in fish #2, and in the dorsal, dorso-temporal, temporal, and ventro-temporal sectors in fish #3 (Table 1).

Behavior toward flickering UV radiation

Left undisturbed, sexually mature chum salmon moved slowly, oriented in random directions, and distributed evenly in the tank. When exposed to near-UV radiation at flicker frequencies from 1 to 100 Hz, the fish showed no change in behaviour and slowly passed or hovered over the submerged light-emitting unit even at the highest near-UV radiation of 39.6 µW/cm² (Table 2). In contrast, fish exposed to flickering green light at intensity 11.0 µW/cm² slowly left and avoided the light-emitting unit, especially at the flicker frequency of 7 and 9 Hz. They showed a similar but weaker response to flickering red light at 7 and 9 Hz. Thus, flickering near-UV was neutral, whereas flickering green and red lights were deterrent to chum salmon.

Transmittance of cornea and lens

The cornea of all four chum salmon transmitted well the UV radiation at all wavelengths and transmittance increased with wavelength (Figure 2). The lens of chum salmon #1 transmitted at λmax 444 nm and down to wavelengths of 326-345 nm, but only at 11% of the highest value (Figure 2). Lens transmittance had λmax 492 nm in the three other chum salmon, but dropped steeply to only 9-37 % at 400 nm, 0.6-6.6 % at 390 nm, and could not be measured at 385 nm (Fig. 2).

DISCUSSION

The corner single cones are the UV-sensitive photoreceptors in salmonids (Flamarique, 2000). In the present study, chum salmon had complete square cone mosaics only at the central retina and had no or only a few corner single cones in the other retinal sectors. Beaudet et al. (1997) found both complete square cone mosaics and corner single cones over wider areas of the retina in mature chum salmon captured in British Columbia, Canada. Despite the individual variation and difference in the genetic population (Sato et al., 2004), it is clear that chum salmon has corner single cones at maturity.
Table 1. Density of corner single cones in different topographical sectors of the retina of three mature chum salmon.

<table>
<thead>
<tr>
<th>Chum salmon</th>
<th>Ratio of corner single cones to central single cones in 0.01 mm² of retina by sector</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dorsal</td>
</tr>
<tr>
<td>#1</td>
<td>0</td>
</tr>
<tr>
<td>#2</td>
<td>0</td>
</tr>
<tr>
<td>#3</td>
<td>0.08 (2/25)</td>
</tr>
</tbody>
</table>

Table 2. Response of sexually mature chum salmon to near-UV, green and red light at different flicker frequencies.

<table>
<thead>
<tr>
<th>Radiation wavelength</th>
<th>Trial</th>
<th>Intensity (µW/cm²)</th>
<th>Response patterns at flicker frequency (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>1-5</td>
</tr>
<tr>
<td>Near-UV (λmax 386 nm)</td>
<td>1</td>
<td>20.8</td>
<td>D</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>39.6</td>
<td>D</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>39.6</td>
<td>D</td>
</tr>
<tr>
<td>Red (λmax 618 nm)</td>
<td>1</td>
<td>31.2</td>
<td>D</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>41.3</td>
<td>D</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>41.3</td>
<td>D</td>
</tr>
<tr>
<td>Green (λmax 524 nm)</td>
<td>1</td>
<td>8.2</td>
<td>C only at 5</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>11.0</td>
<td>D</td>
</tr>
</tbody>
</table>

Response patterns: A. All fish slowly moved away from light-emitting unit and no fish remained in the test zone; B. Fish slowly moved away from light-emitting unit and 2 - 4 fish remained in the test zone; C. Several fish moved away but came back to the test zone; D. No change in distribution pattern and swimming speed.

Figure 2. Transmission spectra (at wavelength band from 320 nm to 600 nm) of the lens and cornea of four chum salmon specimens.
However, the mature chum salmon did not avoid flickering UV radiation, whereas they avoided flickering green light and slightly avoided the flickering red light. Chum salmon retina has peak sensitivity at 527 nm and much lower sensitivity at 618 nm (Munz and Beatty, 1965). Lack of behavioural response to UV radiation was due to the lens which cut off the near-UV radiation below 390 nm and made vision at these wavelengths impossible. The lens of chum salmon #1 was somewhat transparent to near-UV at 326-345 nm, possibly due to different concentrations of short-wave absorbing compounds within the lens (Thorpe et al., 1993), but the eyes of salmonoids have low sensitivity at these wavelengths (Flamarique, 2000). Similar low transmittance in the short wavelengths has been reported for whiting (Merlangus maelangus), keyhold cichlid (Aequidens maronii) and two-spotted goby (Gobiusculus flavescens) (Thorpe et al., 1993; Utne-Palm and Bowmarker, 2006) and also considered insignificant to vision and behaviour.

The presence of UV-blocking lens is not common among adult salmonids. Flamarique (2000) found that in sockeye salmon, near-UV wavelengths as short as 320 nm could reach the retina for visual processing. Parkyn and Hawryshyn (2000) found that juvenile rainbow trout, steelhead trout, cutthroat trout, and sockeye salmon were all sensitive to near-UV. Transmittance through the fish lens varies with the type and concentration of compounds that absorb short wavelengths, and the concentration increases with age (Thorpe and Douglas, 1993; Thorpe et al., 1993).

UV sensitivity of fish has also been shown by recordings of S-potentials (Furuse et al., 1999; Miyagi and Kawamura, 2000; Nakano et al., 2006) from the horizontal cells of inverted eyes, where the stimulus light is given straight to the retina without passing through the ocular media. UV sensitivity in fish eyes with UV-blocking ocular media is thus not properly shown by the S-potentials.

The evidence that the sexually mature chum salmon is not sensitive to near-UV implies that the use of flickering near-UV radiation can be an effective means to scare away the UV-sensitive Japanese dace in the spawning streams. The effectiveness of light stimuli in water varies with day or night use. In daytime, the background illumination often makes the stimulus light less effective (EPRI, 1994). However, the intensity of artificial near-UV radiation can be made higher than the naturally low near-UV radiation from the sun at the water surface (Jerlov, 1976). According to Matsumoto (2005), Japanese dace avoided flickering near-UV radiation even in daytime at illuminance of 330-3980 lx. Thus, we conclude that flickering near-UV can be a feasible way to scare away the Japanese dace from the spawning streams without any influence on the chum salmon spawners in daytime as well as at night.

Bell and Hoar (1950) found that short doses of intense UV-B radiation (wavelengths from 280-320 nm) caused high embryonic mortality and hatching defects in sockeye salmon (O. nerka). Flamarique and Harrower (1999) incubated sockeye salmon eggs under light backgrounds of different spectral composition (300-850 nm) and found that egg mortality was higher under UV-B and visible light than in the dark (control) and subsequent survival of alevins was lowest under UV-B treatment and highest in the dark. Thus, both UV-B and visible light are harmful to salmon embryos in the laboratory. Natural sunlight would also be harmful to salmon eggs in streams, were it not for the fact that salmon eggs and alevins stay under the gravel under water. The use of flickering near-UV (wavelength 386 nm) in a sensory deterrent system in salmon streams might harm salmon eggs and alevins, but this is unlikely because UV radiation is quickly absorbed by high levels of dissolved organic carbon (Lesser et al., 2001) and is negligible compared to the mortality due to predation by Japanese dace.

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REFERENCES


