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Exposure to solar radiation may increase ocular UV-filtering in the juvenile scalloped hammerhead shark, *Sphyrna lewini*

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Abstract Light energy is necessary for vision, but ocular tissues are subject to photodamage, and many vertebrates sequester UV-absorbant pigments in their pre-retinal ocular tissues, in part to minimize such damage. In this study (21 May–1 July 2001), juvenile scalloped hammerhead sharks, *Sphyrna lewini* (Griffith and Smith, 1834), were exposed to higher levels of solar radiation than they had previously experienced in the source habitat in the turbid waters of Kane'ohe Bay, Hawai'i, USA. Light transmission through the ocular media was measured in two individuals shortly after capture and in other individuals after 7, 14, 20, 27, and 41 days exposure to high light levels in a shallow, outdoor pen. Sharks from their usual habitat filtered a small proportion of the UV spectrum, but sharks exposed to greater solar radiation showed increased UV blocking in their corneal tissues, particularly at wavelengths below 310 nm. The proportion of UV blocked was relative to the duration of exposure. There were no changes attributable to exposure duration in transmission through the whole eye or lens, nor was there any clear pattern to variation in transmission through dorsal, ventral, anterior, and posterior quadrants of the cornea. Further experiments will be needed to confirm that this apparently rapid corneal adaptation to high light was due to the increased UV exposure.

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Introduction

Short-wavelength solar radiation in the ultraviolet range (UV, 280–400 nm) has well-documented deleterious effects on aquatic organisms (Zagarese and Williamson 2001), including free radical formation (Lesser et al. 2001), DNA damage (Vetter et al. 1999), epithelial lesions (Bullock 1988; Blazer et al. 1997), and cataract formation (Doughty et al. 1997). Adaptive mechanisms can be divided into behavioral means (e.g. habitat selection, Lowe and Goodman-Lowe 1996; Cockell and Knowland 1999), changeable corneal coloration (Kondrashev et al. 1986; Siebeck and Marshall 2000), pupil control (Gilbert et al. 1981), accumulation of blocking compounds (Lowe and Goodman-Lowe 1996; Zamzow and Losey 2002), and damage repair (Vetter et al. 1999). Mycosporine-like amino acids (MAAs) and several other compounds found in pre-retinal ocular tissues of fishes appear to aid in filtering high-energy, short-wavelength light (reviewed by Douglas and Marshall 1999). Douglas and Marshall (1999) observed that "...since ocular filters are usually found in animals living in high light levels, it is possible that they are the direct result of light exposure," and reported that goldfish raised under extreme high and low light conditions in the laboratory showed correspondingly high and low quantities of corneal pigmentation. However, Zamzow and Losey (2002) reported no effect of differential UV exposure on the ocular transmission of the teleost fish *Thalassoma duperrey* under quasi-natural conditions. Here, we describe the effects of solar radiation exposure on pre-retinal ocular transmission in juvenile scalloped hammerhead sharks, *Sphyrna lewini*.

Kane'ohe Bay, Oahu (Hawai'i; 21°30′N; 157°45′W) is a nursery ground for hammerhead shark pups (Clarke

1971). Kane'ohe Bay has a flat, silty bottom (8–15 m depth), interspersed with patch reefs extending to < 1 m of the surface. The pups are born and spend the early part of their life in the deep (~15 m), turbid waters of the bay (Holland et al. 1993), while the adults are pelagic, occupying clear, oceanic waters (Compagno 1984) where they are potentially exposed to higher levels of UV radiation. Although quantities of light with wavelengths < 400 nm penetrate clear, oceanic waters, these wavelengths attenuate quickly in turbid, coastal water (reviews by Jerlov 1976; Loew and McFarland 1990). Lowe and Goodman-Lowe (1996) report light measurements taken near midday under clear skies in Kane'ohe Bay (shallow measurements within the enclosure referred to below), and found that levels of UVR were 600 times greater at the depth of 1 m than at 15 m.

There has been comparatively little investigation into mechanisms for reducing the harmful effects of UV radiation in aquatic vertebrates. In fishes, filtration of short-wavelength light may occur within the cornea, humor, lens, or retina, with the final combination of filtration varying considerably among fish species (Douglas and Marshall 1999; Siebeck and Marshall 2001; Nelson et al. 2002; Losey et al., unpublished data). There is strong evidence that fishes exposed to natural levels of solar radiation, but prevented from regulating their exposure by behavioral means, suffer UV-induced damage (Bullock 1988; Zagarese and Williamson 2001), including damage to their visual systems. Teleost fishes such as labroids, tetraodontids, and hexagrammids possess corneas with spatially and/or temporally heterogeneous pigmentation (Kondrashev et al. 1986; Siebeck and Marshall 2000). Although the explanations for this observation remain speculative, these pigmentation patterns may be related in part to differences in the varying intensities of downwelling, sidewelling, and upwelling light (see also Lythgoe and Shand 1989).

We compared the transmission of light through the whole eye, lens, and cornea in juvenile scalloped hammerhead sharks (*Sphyrna lewini*) held for varying periods of time in shallow water with high levels of UV radiation. We also tested the hypothesis that spatial heterogeneity in corneal pigmentation would vary with exposure to solar radiation.

Materials and methods

Between 21 May and 1 July 2001, we captured 11 juvenile scalloped hammerheads, *Sphyrna lewini* (Griffith and Smith, 1834), by handline fishing in Kane'ohe Bay, Hawai'i, USA. Three males and eight females ranged in size from 39.0 to 44.3 cm fork length (42.5 mean, ± 1.7 SD) and represented young-of-the-year and juveniles < 2 years old. Nine sharks were placed in a shallow (< 2 m), outdoor holding pen at the Hawai'i Institute of Marine Biology (HIMB) immediately after capture, and held for 7–41 days (Fig. 1). Two sharks were sampled immediately upon capture (1 July 2001) from the deeper waters (~15 m) of the bay. The clear, shallow water of the holding pen was exposed to quantities of UV radiation significantly greater than the turbid channels in deeper portions of the bay from which the sharks were captured (Lowe and Goodman-Lowe 1996). While daily total UVR varied considerably during the duration of the study, there was a close correlation between the duration of exposure and the cumulative UVR (Fig. 1; $r = 0.998$, $Z = 9.40$, $P < 0.0001$). Sharks were fed to satiation three times per week on a diet of squid, mackerel, and herring. At intervals, sharks were removed from the holding pen at ~1200 hours, and euthanized immediately with an overdose of MS-222.

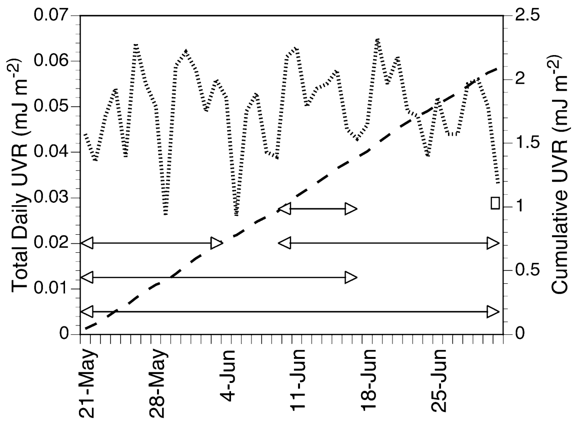

Fig. 1 Daily (*dotted*) and cumulative (*dashed*) above-surface measurements from the Eppley total ultraviolet radiometer at the HIMB weather station (Hawai'i Institute of Marine Biology, Kane'ohe, Hawai'i). *Arrows* represent capture, exposure, and sample dates (two sharks for each event, except for the period, 21 May–1 July 2001, where one shark was used). The *open square* represents capture and sample date for two sharks

After dissecting the left eye from each euthanized shark, we measured light transmission through the pre-retinal ocular media (whole eye, lens, and cornea) as in Losey et al. (2000). Briefly, (1) a small hole was cut through the sclera opposite the pupil and near the optic nerve; (2) the eye was mounted on an aluminum slide with the pupil over a 1.4 cm hole in the middle of the slide; (3) using a UV-transmitting 400 μm fiber optic probe mounted on a micromanipulator, we introduced light from a DT 1000 light source (range: ~200 to 750 nm) into the hole in the back of the eye; (4) light exiting the fiber optic probe and passing through the humors, lens, and cornea was measured using a collecting lens on the end of another fiber optic probe leading to an Ocean Optics S2000 spectrophotometer; (5) after measuring transmission through the whole eye, we measured transmission through the center of the isolated lens and the isolated cornea in a similar manner. We used an average of three scans for each transmission measurement, normalized these to 100% at the highest value below 501 nm, and identified the wavelength at which transmission reached 50% (T_{50}, Douglas 1989) for each eye, lens, and cornea.

To test the hypothesis that exposure to solar radiation would effect a detectable change in intra-ocular filtering, we compared transmission data from freshly caught sharks to individuals held in shallow water for 7–41 days. We compared the T_{50} values for the whole eye, lens, and cornea with both the duration of exposure (in days) and the total exposure to the UV component of the solar radiation (in mJ m^{-2}; 295–389 nm) using linear regression. UV irradiance data were obtained from the Eppley total ultraviolet radiometer at the HIMB weather station and represent above-surface measures of total irradiation (mean ± SD: 0.050 ± 0.009 mJ m^{-2} day^{-1}); thus the sharks experienced less actual radiation than reported, but the relative treatment is valid.

We also tested the hypothesis that corneal filtration in the hammerheads would be spatially heterogeneous in sharks exposed to increased solar radiation. We measured transmission as described above for each of four quadrants (dorsal, ventral, anterior, posterior) of the corneas taken from seven sharks, and compared the means using ANOVA. To test the hypothesis that the difference between the dorsal and ventral quadrants of the cornea changed as a function of radiation exposure, we compared the duration of exposure (in days) to the ratio of the dorsal quadrant T_{50} to the ventral quadrant T_{50} using linear regression.

All procedures were conducted in accordance with University of Hawai'i IACUC protocol 95-012.

Results and discussion

Because the duration of exposure and the accumulated UV radiation were so tightly correlated, results using either measure (days or mJ m^{-2}) are identical and we report only the results using duration of exposure (days). The quantity of short-wavelength light filtered by the corneas was positively and significantly correlated with the length of exposure ($R^2=0.58$, $F_{(1,9)}=12.64$, $P=0.01$; Fig. 2). No significant trends were observed for the whole eye ($R^2=0.17$, $F_{(1,8)}=1.59$, $P=0.24$) or the lens ($R^2=0.23$, $F_{(1,9)}=2.71$, $P=0.13$). Transmission through the dorsal, ventral, anterior, and posterior quadrants of the seven corneas tested were not significantly different ($F_{(3,17)}=0.090$, $P=0.96$, Fig. 3). The ratios describing the relative difference in transmission between dorsal and ventral quadrants also failed to support our hypothesis that the relative difference between these quadrants would change as a function of radiation exposure ($R^2=0.045$, $F_{(1,5)}=0.236$, $P=0.65$).

While the lens remained the limiting factor determining light transmission through the pre-retinal tissues (Fig. 4), the cornea, at least in this species, changed rapidly in response to environmental conditions. Sharks held in shallow water and exposed to solar radiation increased corneal filtration of short-wavelength light; the juvenile hammerheads occupying the turbid waters of the bay channels are less exposed to UV radiation and, thus, have little need for short-wavelength ocular filtration. The corneas observed in this study showed maximal absorbance (λ_{max}) around 273 nm, well below that of the MAAs or gadusol, a compound structurally similar to MAAs and found in some fish eggs (Cockell and Knowland 1999). Melanin, a pigment known to increase in dermal concentration in response to UV radiation (Lowe and Goodman-Lowe 1996), shows a more variable absorbance profile with $\lambda_{max}\cong260$ nm (Cockell and Knowland 1999). The identity of the pigment(s) responsible for short-wavelength filtration in hammerhead shark corneas remains to be determined. It is also unclear whether the putative changes in corneal T_{50} were due to increased pigment concentration or the acquisition of new pigments.

The observed increase in corneal filtration (296–306 nm) probably protects the lens from exposure to the shortest, most-damaging UV wavelengths that are known to cause cataracts (e.g. Zigman 1995). There are additional potential advantages to short-wavelength filtration, including reduced chromatic aberration or fine focusing ability (Douglas and Marshall 1999) and improved color constancy (Douglas and Marshall 1999; Dyer 2001), but it is difficult to see how these adaptations would drive the rapid changes observed in this study since the distribution of wavelengths reaching the retina was not altered by the corneal absorption.

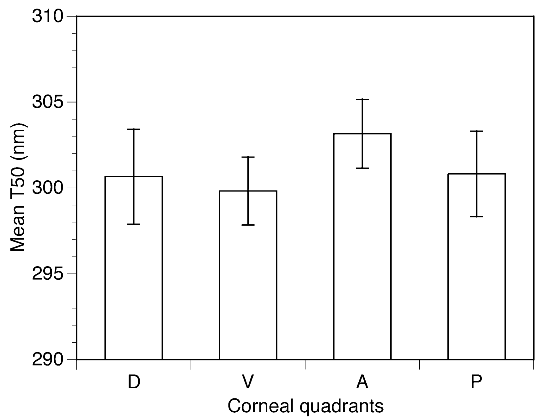

Fig. 3 *Sphyrna lewini*. Mean T_{50} (±SE) for corneal quadrants (*D* dorsal; *V* ventral; *A* anterior; *P* posterior); no significant differences ($n=7$)

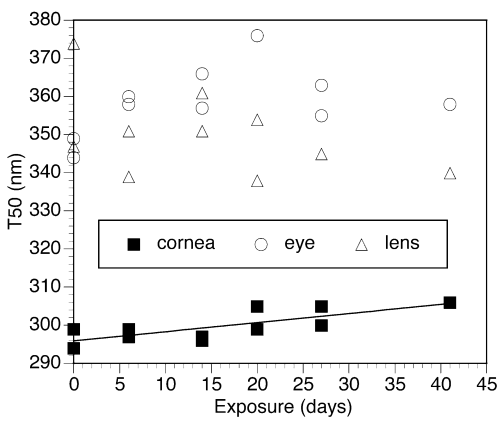

Fig. 2 *Sphyrna lewini*. Wavelength at which transmission was reduced to 50% (T_{50}) for the cornea, lens, and whole eye relative to duration of exposure

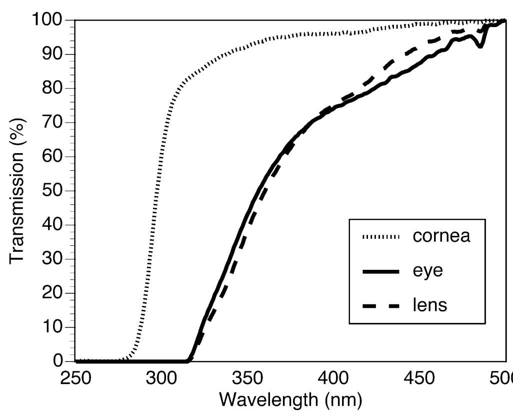

Fig. 4 *Sphyrna lewini*. Ocular transmission ("hammer07": total exposure = 14 days and 0.754 mJ m^{-2}); note that lens is limiting factor

While we observed no obvious aphakic spaces (these sharks were euthanized in full sun with their pupil dilation likely near their minimum), the pupillary aperture is elongate and it is possible that an aphakic gap exists under reduced light conditions. In such an instance, corneal short-wavelength filtration would provide some protection to the retina from light thus by-passing the lens. We cannot rule out the possibility that change in ocular transmission occurred as a result of diet or some other environmental factor associated with husbandry. Available evidence suggests that, for teleost fishes, the source of MAAs is dietary (Mason et al. 1998; Zamzow and Losey 2002), and the food supplied to the captive hammerheads was necessarily different from in the field, namely small fishes (Perciformes: Gobiidae, Scaridae) and crustaceans (Natantia: Alpheidae; Clarke 1971). Clearly this warrants further investigation by controlling the diet. Moreover, some individuals should be held in a shaded environment, under photic conditions matching their usual environment.

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