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Flicker electroretinography (ERG) was used to examine the in situ photopic (cone-photoreceptor based) spectral sensitivities of Green and Loggerhead Sea Turtles. Both species were responsive to wavelengths from 440–700 nm, and both had peak sensitivity in the long wavelength portion of the spectrum (~580 nm). For Loggerhead Sea Turtles, no measurable responses were obtained below about 440 nm, whereas reliable signals were seen for Green Sea Turtles at wavelengths down to 400 nm. Both species exhibited significant declines in sensitivity below 500 nm. The overall shapes of the spectral sensitivity functions were similar for the two species. These results support previous findings that sea turtles have well-developed photopic visual systems. The characteristics of these spectral sensitivity functions indicate that both species possess multiple cone photopigment types, and these, in conjunction with the presence of colored oil droplets, strongly imply a capacity for color discrimination. Comparative evaluation suggests that these turtles have modified their visual pigments from those of their terrestrial relatives to better suit the ambient conditions present in the shallow water, submarine environments that they typically inhabit.

MODERN sea turtles diverged from their terrestrial and freshwater relatives roughly 150 million years ago (Pritchard, 1997). They live an almost exclusively marine existence, returning to the ocean within a few hours of hatching and subsequently rarely returning to land. Sea turtles are currently distributed worldwide throughout the tropical and subtropical oceans, with some species occasionally ranging into higher, more temperate latitudes. Sea turtles occupy a variety of ecologic niches. For instance, adult Green Sea Turtles (*Chelonia mydas*) are generally found near shore feeding on plant and algal matter, whereas others, such as adult Loggerhead Sea Turtles (*Caretta caretta*) may stay farther offshore, diving deeper to forage on benthic invertebrates and fish (Bjorndal, 1997).

Anatomical examinations reveal that, in contrast to terrestrial and freshwater turtles, the eyes of sea turtles have round lenses, much like those found in fish, to compensate for the loss of corneal refraction under water (Walls, 1942; Ehrenfeld and Koch, 1967; Northmore and Granda, 1991). The spectral sensitivity of marine turtles is also different from that of their land-based relatives (Liebman and Granda, 1971; Granda and Dvorak, 1977). Microspectrophotometric (MSP) evaluations of Green Sea Turtle photoreceptors show that 11-*cis* retinal is used as the light sensitive chromophore component of sea turtle visual pigments; land based turtles typically use 3,4 di-dehydroretinal (Liebman and Granda, 1971; Loew and Govardovski, 2001). This substitution has the effect of substantially shifting the sensitivity of the longer wavelength sensitive visual pigments of marine turtles toward shorter wavelengths. MSP also reveals that the light-absorbing oil droplets present in marine turtle cone photoreceptors are different from those of terrestrial and freshwater turtles (Granda and Haden, 1970; Granda and Dvorak, 1977).

Although there is evidence that the visual sense is important to sea turtles throughout all stages of their life cycle (Ehrenfeld and Carr, 1967; Kingsmill and Mrosovsky, 1982; Lohmann et al., 1990), relatively little is known about their in situ visual sensitivities; most previous work has been directed at the individual photoreceptors. Because several conservation issues currently facing marine turtles can be related, at least in part, to the effects of anthropogenic light sources, there is a particular need for a better understanding of the visual abilities of living turtles (e.g., Witherington, 1991; Witzell, 1999). As a step in this direction, we have used a noninvasive technique, rapid-flicker electroretinography (ERG), to investigate the photopic (cone-photoreceptor based) visual sensitivities of two marine turtle species, Green and Loggerhead Sea Turtles. This type of ERG is particularly relevant to behavioral/conservation issues, because it reflects the actual sensitivity of the eyes of the animal, including the combined effects of the cone visual pigments, oil droplets, and other sources of intraocular scattering and absorption (e.g. cornea, lens). Rapid-flicker ERG was chosen over the single flash ERG technique previously used with Green Sea Turtles (Granda and O'Shea, 1972), because it is better

suited to isolating cone photoreceptor responses and thereby potentially providing a more accurate representation of in situ photopic sensitivity. Furthermore, by conducting parallel experiments with two species, we reasoned that, because the individual cone photopigments of the Green Sea Turtle have been previously measured, we could use the ERG measurements on Green Sea Turtles to draw more precise inferences about the photoreceptor complements of Loggerhead Sea Turtles.

Materials and Methods

Live adult (all greater than 30 years old) Green and Loggerhead Sea turtles were examined at SeaWorld, San Diego, California. Recordings were obtained from four Green Sea Turtles and six Loggerhead Sea Turtles. It was not possible to determine the gender of some of the turtles, but at least one male and one female were examined from each species. These animals were maintained in captivity in seawater exhibits before and after recording. All animal husbandry and experimental procedures were conducted according to protocols approved by the SeaWorld Institutional Animal Care and Use Committee (IACUC) and were overseen by the veterinary staff at SeaWorld.

Photopic (cone-photoreceptor based) spectral sensitivity was evaluated for each turtle in vivo using flicker electroretinography (ERG). For this examination, animals were removed from their holding pools and anesthetized with intravenous administration of ketamine (6.0–9.0 mg/kg) and metatomadine (0.1 mg/kg) injected transdermally into the dilation of the external jugular vein at the base of the head. Once anaesthetized, the turtles were positioned on a slant board that was placed on an adjustable surgical table, and the head position was stabilized through the use of padded restraints. Although the general anesthetic typically produced some degree of pupillary dilation, in some cases additional dilation was achieved by topical application of atropine and ophthalmic neosynephrine. The cornea was anesthetized by a topical application of proparacaine hydrochloride (0.5%) prior to the installation of a bipolar contact-lens electrode of the Burian-Allen configuration. After the experiments were completed, the effects of the anesthesia were partially reversed using atapamazole (0.1 mg/kg). In all cases, full recovery was achieved without incident.

The general technique used to record flicker ERGs has been described in detail elsewhere (Jacobs et al., 1996). In the present experiments, the eye was stimulated with a train of light pulses originating from a high-intensity (50-W tungsten-halide lamp) grating monochromator having a half bandpass of 15 nm. The light was imaged onto the retina in Maxwellian view in the form of a spot subtending 59 deg. The test light was temporally modulated with electromechanical shutters (Vincent Associates, Rochester, NY) as a square-wave pulse having a 25% duty cycle so as to achieve any desired flicker rate. The fundamental frequency component of the ERG response was extracted by filtering and this signal was averaged over a total of 50 presentations. Spectral sensitivity functions were measured using two techniques. In the first case, a flicker photometric procedure was employed in which the responses to the test light and those given to an interleaved reference light (achromatic, 14 log photons/sec/sr) that illuminated the same region of the retina and flickered at the same temporal frequency were compared. Over successive presentations, the intensity of the monochromatic test light was adjusted by changing the position of a 3.0-log unit neutral-density wedge until the light produced a response equal to that given to the fixed reference light. Repetition of this procedure for a range of different test wavelengths can be used to define a spectral sensitivity function (Jacobs and Neitz, 1987). In a second set of measurements, spectral sensitivity functions were similarly determined using a standard amplitude-criterion method. In this case, the intensity of the test light at each wavelength was adjusted over successive presentations until it produced a response with a constant amplitude of 3.2 μV.

ERG temporal response functions were also obtained. To accomplish this, the intensity of an achromatic (2850 K) flickering light was adjusted to produce a response having a criterion amplitude of 3.2 μV. This procedure was repeated for flickering lights varying in steps of 4 Hz from 4–40 Hz. For all of the spectral sensitivity and rate measurements, thresholds were determined twice for each test condition and these values subsequently averaged. All recordings were made under moderate photopic illumination produced by a mixture of indirect skylight and overhead fluorescent lighting that yielded an illuminance of 165 lux at the subject's eye.

Results

As recorded from the corneas of sea turtle eyes, flickering lights produced small but quite reliable ERG signals. For example, Figure 1A shows a representative intensity/response func-

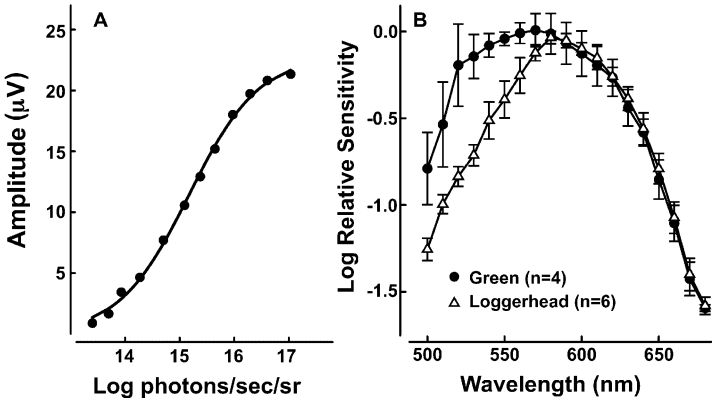

Fig. 1. (A) An example of a flicker ERG intensity/response function obtained from a Loggerhead Sea Turtle. The datapoints are mean amplitudes obtained from four presentations of an achromatic test light flickered at 20 Hz. The intensity of the stimulus is as specified at the cornea. The fitted line is a Michaelis-Menton function. The values of the three parameters for this fit are V_{max} = 22.9 μV; k = 15.2 log-photons/sec/sr; η = 0.68. These three index, respectively, voltage at saturation, intensity required for half-maximum amplitude, and a slope parameter. (B) Photopic spectral sensitivity curves for Green and Loggerhead Sea Turtles obtained with the flicker-photometric ERG procedure described in the text. The datapoints are mean values for the numbers of animals specified and the error bars represent ± 1 standard deviation. The datapoints have been interconnected with straight lines.

tion obtained from a Loggerhead Sea Turtle to 20 Hz flicker. The plotted points represent the mean amplitudes recorded for four successive presentations of the test light each of which in turn consisted of 50 stimulus cycles. The line fitted through the datapoints was derived from the Michaelis-Menton function, a metric typically used to account for intensity-response relationships for signals recorded early in visual systems, including photoreceptor responses recorded directly from cones of freshwater turtles (Granda and Dvorak, 1977). Although the peak amplitudes recorded under these flickering-light test conditions were modest in size (in the range of 20–50 μV), they were, as noted, highly reliable; for example, the SD values for the responses of Figure 1 averaged less than 1 μV across the full span of stimulus intensity.

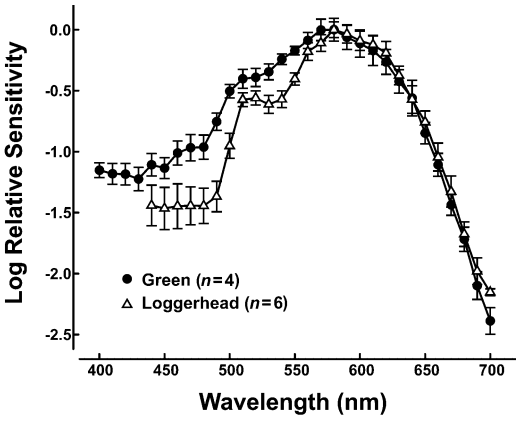

Fig. 2. Photopic spectral sensitivity curves for Green and Loggerhead Sea Turtles obtained from an amplitude-criterion procedure. The test light was flickered at 20 Hz. Other details are the same as for Figure 1B.

Figure 1B summarizes the spectral sensitivity functions obtained from 10 sea turtles as determined with ERG flicker photometry using 20-Hz flicker. The functions for both species peak at about 580 nm. The sensitivities of the two are indistinguishable from that point out to the longer wavelengths. However, the sensitivity curve for the Loggerhead Sea Turtles falls off more steeply toward the short wavelengths than does the equivalent function obtained from the Green Sea Turtles. With this technique it proved impossible to make sensitivity measurements for wavelengths shorter than about 500 nm. Note that the individual variability for each species over this spectral range is quite small with SD values averaging 0.1-log unit or less.

In an attempt to extend the spectral range of the spectral sensitivity functions, we also tested these same animals using the amplitude-criterion procedure. The results are shown in Figure 2, which again summarizes results obtained from the same 10 animals. With this procedure, it proved possible to obtain sensitivity measurements from 700 nm well down into the short wavelengths (400 nm and 440 nm for the Green and Loggerhead Sea Turtles, respectively). As for the flicker photometric results, both species

show a sensitivity peak at about 580 nm with a smooth (and equivalent) falloff in sensitivity to the longer wavelengths. To the shorter wavelengths the shapes of the functions for the two species are similar with a secondary peak at about 520 nm and a region of near constant sensitivity below about 500 nm. As in the flicker photometric spectral sensitivity functions, the Loggerhead Sea Turtles had consistently lower sensitivity to all of the test wavelengths shorter than the principal peak. It is also apparent that the variability among animals is larger for the shorter test wavelengths and that this is particularly marked for the Loggerhead Sea Turtles at wavelengths shorter than 500 nm. Variability within individuals remained relatively consistent across the spectral range examined.

All of the above measurements were made at a single temporal frequency (20 Hz). To examine the effects of temporal rate on sea turtle ERGs, we also measured thresholds for achromatic lights across a range of temporal frequencies. For both species, temporal sensitivity was maximal over a relatively broad range extending from about 8–16 Hz. Sensitivity at 4 Hz was only 0.25- to 0.5-log units below peak sensitivity. At flicker rates above 12–16 Hz, sensitivity gradually fell off to up to 36 Hz, where thresholds for both species were over 2.0-log units below peak values. At 40 Hz, no consistently reliable responses could be recorded and straight-line extrapolation of the frequency/sensitivity curve suggests that 40 Hz represents the high-frequency cutoff for both turtle species. For frequencies greater than the peak, the sensitivity of the Loggerhead Sea Turtles was consistently (but not dramatically) lower than for the Green Sea Turtles. This presumably reflects the lower sensitivity of the former species to shorter test wavelengths.

Discussion

Previous measurements of the spectral sensitivity of Green Sea Turtles have been made using a single-flash ERG technique (Granda and O'Shea, 1972). In both the dark- and light-adapted eye the spectral sensitivity functions had multiple peaks at about 600 nm, 520 nm, and 460 nm. The spectral sensitivities we measured for Green Sea Turtles are roughly similar to these earlier results, although the long wavelength peak is somewhat shorter in the present measurements (λ_{max} ~580 nm) and the short-wavelength peak is much less clearly defined. There are other differences between the two experiments, two of which are potentially important. The first is that the use of high frequency flicker ERG more securely isolates signals from cones than the single-flash procedure, even when the latter is conducted in a light-adapted eye. Thus, it is conceivable that some contributions from rods are represented in the earlier study's spectral sensitivity results. The relatively high frequency temporal responses of both species (up to 36 Hz) support the conclusion that our data are representative of cone photoreceptor responses (see Jacobs et al., 1996). Perhaps more important is the great difference in age of the turtles examined in the two experiments. In the earlier experiment, the turtles were very young (somewhere between two and 16 months of age; Granda and O'Shea, 1972). There are not sufficient records available to age our subjects accurately. The staff at SeaWorld indicates that they are all at least 30 years of age, and perhaps some turtles are substantially beyond that point. It is conceivable that with age the ocular components of sea turtle eyes (cornea, lens, etc.) become considerably less transmissive. In humans where age-related losses of ocular transmissivity have been extensively studied, these changes are often found to differentially filter out short wavelength ($\lambda < 500$ nm) energy (e.g., Weale, 1988). If this is also true for sea turtles, it might explain the differences in short wavelength sensitivity seen in the two studies. In any case, the results of the two studies suggest there may be differences in short-wavelength sensitivity between young and aged sea turtles.

Earlier MSP measurements revealed the presence of four types of photopigment in the retina of the Green Sea Turtles: a rod pigment with a 502 nm peak and three types of cone pigment with respective peak values (λ_{max}) of 440, 502, and 562 nm (Liebman and Granda, 1971). As is typical of many reptiles, as well as a number of amphibians, monotremes and fishes, the cone photoreceptors of the Green Sea Turtle also contain high-density oil droplets (Granda and Haden, 1970). Because these oil droplets are interposed in the optical pathway to the outer segments, if colored, they can serve to spectrally filter incoming light. In the Green Sea Turtle there are three classes of oil droplets, clear, yellow, and orange. They are selectively paired with the cone pigments to form what are potentially six spectrally discrete classes of receptor (Liebman and Granda, 1971). The net effect of these pairings is to effectively shift the spectral sensitivity of two of the cone classes to longer wavelengths. As in Granda and O'Shea (1972), the shifted positions of the two longer wavelength peaks in the Green Sea Turtle ERG sensitivity curve reflect this (Fig. 2).

The spectral sensitivity functions obtained from Loggerhead Sea Turtles are similar in shape to those derived for Green Sea Turtles, suggesting a similar cone pigment and oil droplet complement in the two species. Direct comparisons can be made for one of the cone pigments in the two species. This is because, as noted above, the oil droplets function as long-pass filters. The longest of these, the yellow droplets, show no detectable absorption for wavelengths longer than about 600 nm (Liebman and Granda, 1971). Consequently, the long wavelength limb of the spectral sensitivity functions should reflect principally the absorption properties of the longest of the cone pigments. To determine the spectral position of this pigment, we shifted a standard photopigment absorption function (Govardovskii et al., 2001) along the wavelength axis to determine what pigment position best accounted for the array of sensitivity values for test lights of all wavelengths 600 nm and longer. For the two estimates of sensitivity obtained for Green Sea Turtles (Figs. 1, 2), these peaks were at 563 and 559 nm, respectively. These values are very close to the position of the cone pigment directly measured with MSP (562 nm). A similar test of the two spectral sensitivities obtained from Loggerhead Sea Turtles yielded estimates of 562 and 563 nm. We conclude that these two species have in common their longest cone pigment. Given the uncertainties produced by oil droplet/pigment combinations described above, a similar comparison of other cone pigment positions is not possible, although the general similarity of the shapes of the spectral sensitivity functions strongly suggest that they too are the same for these two sea turtles.

In general, the retinas of most turtles (Walls, 1942; Granda and Dvorak, 1977), including the marine species (Granda and Dvorak 1977; Bartol and Musick, 2001) are cone dominated, with cone:rod photoreceptor ratios of 2:1 or more (Bartol and Musick, 2001). This is unlike other diving tetrapods, such as marine mammals that typically have large, rod-dominated eyes to maximize light capture, and a limited range of spectral sensitivity (Lavigne et al., 1977; Peichl et al., 2001; Levenson and Dizon, 2003). Similarly, many fish, particularly those inhabiting depths visited by the deeper diving turtles (> 100 m), are strongly adapted to maximize light sensitivity and exhibit evidence of reduced photopic visual abilities (Lythgoe, 1979; Bowmaker, 1995). This often includes a relatively narrow range of spectral sensitivity in comparison to similar, shallow water species (Bowmaker et al., 1994; Lythgoe et al., 1994). Qualitative evaluation of sea turtle visual systems suggests that these animals have largely retained diurnally adapted visual systems like those of their reptilian/avian relatives. Their broad spectral sensitivity corresponds well with the type of light available in relatively shallow, well-lit marine waters, rather than that of the dim, nearly monochromatic deep oceanic water (Kirk, 1994). They also have relatively small lenses (Northmore and Granda, 1991) and cone-dominated retinae with additional light filtering oil droplets (Granda and Haden, 1970; Bartol and Musick, 2001). Even the very deep diving Leatherback Sea Turtle (Eckert et al., 1989) does not possess a particularly large lens, which might be expected if these turtles were adapted for maximizing light capture (Northmore and Granda, 1991).

The presence of multiple functioning photoreceptor types also suggests that these turtles have retained the ability to make color discriminations. Such abilities are lost in sensitivity adapted marine mammals (Peichl et al., 2001; Levenson and Dizon, 2003) and fish from deeper water habitats (e.g., Bowmaker et al., 1994; Cowing et al., 2002) but are relatively common in diurnally adapted fish, birds, and other reptiles (Bowmaker, 1995; Yokoyama and Yokoyama, 1996). Color vision and the retinal circuitry that supports that capacity have been extensively studied in freshwater turtles. Evidence suggests that in these turtles the array of pigment and oil droplet combinations and the neural support provide a multidimensional color vision system that is probably at least tetrachromatic in nature (Neumeyer, 1998). Although both cone pigments and oil droplets differ for freshwater and sea turtles, the presence of multiple pigments and oil droplets in sea turtles strongly suggests that they are like their freshwater cousins in enjoying a color vision capacity. The nature of that capacity remains to be determined.

All these observations suggest that the vision of sea turtles is primarily suited for use in photopic conditions. However, there is also reason to conclude that the visual systems of sea turtles have been modified for use in the marine environment. In comparison to closely related terrestrial turtles, both species of sea turtle exhibited long wavelength sensitivity indicative of visual pigments that have been shifted toward the shorter wavelengths of light ($\lambda \leq 500$ nm) typically prevalent in marine environments (Kirk, 1994). The cone pigments of the Green and likely those of the Loggerhead Sea Turtles have λ_{max} 18 to 55 nm shorter in sensitivity than those of the land-based Red-Eared Slider (*Trachemys scripta elegans*; Liebman and Granda, 1971; Loew

and Govardovskii, 2001). Much of this sensitivity change is undoubtedly related to a shift in chromophore. The essentially identical long wavelength sensitive pigments of Green and Loggerhead Sea Turtles suggest that both species, and perhaps then all marine turtles, have made the chromophore substitution to retinal from 3,4 di-dehydroretinal (Granda and Dvorak, 1977). This same disparity is common between marine and freshwater fish species; marine fishes typically have retinal in their visual pigments and the corresponding short wavelength shift in sensitivity (Bowmaker, 1995).

The conclusion that sea turtle visual pigments are well-suited for use in relatively well-lit, shallow water marine environments concurs with the observed diving/foraging behavior of most species (Bjorndal, 1997). The photopic spectral sensitivities of these sea turtles are clearly different from those of the other diving tetrapod groups, as they are different from their nonmarine relatives.

In fact, the cone visual pigments of sea turtles are convergent in many ways with those of some of the tropical, shallow-water marine fish with which they share habitat. Both have multiple pigment types and a broad range of sensitivity but are short-wavelength shifted in sensitivity when compared to similar species from freshwater/terrestrial habitats (Lythgoe et al., 1994; Bowmaker, 1995; Losey et al., 2003). Indeed, considering the absence of reductions in photopic function for increased overall sensitivity seen in deep water fish and mammals, one might speculate that the visual sense may not be of great consequence to deep diving Loggerhead and Leatherback Sea Turtles when they venture to depths in excess of a few hundred meters, as they sometimes do (Eckert et al., 1989; Bjorndal, 1997). This remains to be determined.

However, it also important to consider the ecological and behavioral ramifications of visual stimuli when considering the significance of the sensitivity data presented here. The results from ERG are strictly a representation of the sensitivity of the eyes and do not reflect the behavioral significance that visual stimuli may contain. For example, although less sensitive to short wavelength lights, both Green and Loggerhead Sea Turtles will reliably orient toward shorter wavelength stimuli and away from long wavelength lights when given a choice (Witherington and Bjorndal, 1991). This behavior, which is thought to help hatching turtles reenter the ocean, is contradictory to what might be predicted given only the measured spectral sensitivities of these species. Thus, photoreceptor sensitivity should only be one of many factors to be considered when examining the behavior of sea turtles or working to mitigate the effects of human activities on sea turtle populations.

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Literature cited

Bartol, S. M., and J. A. Musick. 2001. Morphology and topographical organization of the retina of juvenile Loggerhead Sea Turtles (*Caretta caretta*). Copeia 2001:718–725.

Bjorndal, K. A. 1997. Foraging ecology and nutrition of sea turtles, p. 29–50. *In:* Biology of sea turtles. P. Lutz and J. A. Musick (eds.). CRC Press, Boca Raton, FL.

Bowmaker, J. K. 1995. The visual pigments of fish. Prog. Retinal Eye Res. 15:1–31.

———, V. I. Govardovskii, L. V. Zueva, D. M. Hunt, and V. Sideleva. 1994. Visual pigments and the photic environment: the cottoid fish of Lake Baikal. Vision Res. 34:591–605.

Cowing, J. A., S. Poopalasundaram, S. E. Wilkie, J. K. Bowmaker, and D. M. Hunt. 2002. Spectral tuning and evolution of short wave-sensitive cone pigments in cottoid fish from Lake Baikal. Biochemistry 41:6019–6025.

Eckert, S. A., K. L. Eckert, P. Ponganis, and G. L. Kooyman. 1989. Diving and foraging behavior of Leatherback Sea Turtles (*Dermochelys coriacea*). Can. J. Zool. 67:2834–2840.

Ehrenfeld, D. W., and A. Carr. 1967. The role of vision in the sea-finding orientation of the Green Turtle (*Chelonia mydas*). Anim. Behav. 15:25–36.

———, and A. L. Koch. 1967. Visual accommodation in the green turtle. Science 155:827–828.

Govardovskii, V. I., N. Fyhrquist, T. Reuter, D. G. Kuzimin, and K. Donner. 2001. In search of the visual pigment template. Visual Neurosci. 17:509–528.

Granda, A. M., and C. A. Dvorak. 1977. Vision in turtles, p. 451–495. *In:* The visual system in vertebrates. F. Cresticelli (ed.). Springer-Verlag, Berlin, Germany.

———, and K. W. Haden. 1970. Retinal oil globule counts and distributions in two species of turtles: *Pseudemys scripta elegans* (Wied) and *Chelonia mydas mydas* (Linnaeus). Vision Res. 10:79–84.

———, and P. J. O'Shea. 1972. Spectral sensitivity of

the Green Turtle (*Chelonia mydas mydas*) determined by electrical responses to heterochromatic light. Brain, Behav. Evol. 5:143–154.

JACOBS, G. H., AND J. NEITZ. 1987. Inheritance of color vision in a New World monkey (*Saimiri sciureus*). Proc. Natl. Acad. Sci. USA 84:2545–2549.

———, ———, AND K. KROGH. 1996. Electroretinogram flicker photometry and its applications. J. Opt. Soc. Am. A13:641–648.

KINGSMILL, S. F., AND N. MROSOVSKY. 1982. Sea-finding behaviour of loggerhead hatchlings: the time course of transient circling following unilateral and asynchronous bilateral blindfolding. Brain, Behav. Evol. 20:29–42.

KIRK, J. T. O. 1994. Light and photosynthesis in aquatic ecosystems. 2d ed. Cambridge Univ. Press, Cambridge.

LAVIGNE, D. M., C. D. BERNHOLZ, AND K. RONALD. 1977. Functional aspects of pinniped vision, p. 135–173. *In:* Functional anatomy of marine mammals. Vol. 3. R. J. Harrison (ed.). Academic Press, New York.

LEVENSON, D. H., AND A. DIZON. 2003. Genetic evidence for the ancestral loss of short-wavelength-sensitive cone pigments in mysticete and odontocete cetaceans. Proc. R. Soc. B Biol. Sci. 270:673–679.

LIEBMAN, P. A., AND A. M. GRANDA. 1971. Microspectrophotometric measurements of visual pigments in two species of turtle, *Pseudemys scripta* and *Chelonia mydas*. Vision Res. 11:105–114.

LOEW, E. R., AND V. I. GOVARDOVSKII. 2001. Photoreceptors and visual pigments in the Red-Eared Turtle, *Trachemys scripta elegans*. Visual Neurosci. 18: 753–757.

LOHMANN, K. J., M. SALMON, AND J. WYNEKEN. 1990. Functional autonomy of land and sea orientation systems in sea turtle hatchlings. Biol. Bull. 179:214–218.

LOSEY, G. S., W. N. MCFARLAND, E. R. LOEW, J. P. ZAMZOW, P. A. NELSON, AND N. J. MARSHALL. 2003. Visual biology of Hawaiian coral reef fishes. I. Ocular transmission and visual pigments. Copeia 2003: 432–454.

LYTHGOE, J. N. 1979. The ecology of vision. Oxford Univ. Press, Oxford.

———, W. R. A. MUNTZ, J. C. PARTRIDGE, J. SHAND, AND D. M. WILLIAMS. 1994. The ecology of the visual pigments of snappers (Lubjanidae) on the Great Barrier Reef. J. Comp. Physiol. A 174:461–467.

NEUMEYER, C. 1998. Color vision in lower vertebrates, p. 149–162. *In:* Color vision: Perspectives from different disciplines. W. G. K. Backhaus, R. Kliegl and J. S. Werner (eds.). Walter de Gruyter, Berlin, Germany.

NORTHMORE, D. P. M., AND A. M. GRANDA. 1991. Ocular dimensions and schematic eyes of freshwater and sea turtles. Visual Neurosci. 7:627–635.

PEICHL, L., G. BEHRMANN, AND R. H. H. KROGER. 2001. For whales and seals the ocean is not blue: a visual pigment loss in marine mammals. Eur. J. Neurosci. 13:1520–1528.

PRITCHARD, P. C. H. 1997. Evolution, phylogeny, and current status, p. 1–28. *In:* Biology of sea turtles. P. Lutz and J. Musick (eds.). CRC Press, Boca Raton, FL.

WALLS, G. 1942. The vertebrate eye and its adaptive radiation. Cranbrook Institute of Science, Bloomfield Hills, MI.

WEALE, R. A. 1988. Age and the transmittance of the human crystalline lens. J. Physiol. 395:577–587.

WITHERINGTON, B. E. 1991. Orientation of hatchling loggerhead turtles at sea off artificially lighted and dark beaches. J. Exp. Mar. Biol. Ecol. 149:1–12.

———, AND K. A. BJORNDAL. 1991. Influences of wavelength and intensity on hatchling sea turtle phototaxis: implications for sea-finding behavior. Copeia 1991:1060–1069.

WITZELL, W. N. 1999. Distribution and relative abundance of sea turtles caught incidentally by the U.S. pelagic longline fleet in the western North Atlantic Ocean, 1992–1995. Fish. Bull. 97:200–211.

YOKOYAMA, S., AND R. YOKOYAMA. 1996. Adaptive evolution of photoreceptors and visual pigments in vertebrates. Annu. Rev. Ecol. Syst. 27:543–567.

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