

Research

# An unsuccessful attempt to elicit orientation responses to linearly polarized light in hatchling loggerhead sea turtles (Caretta caretta)

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Sea turtles undertake long migrations in the open ocean, during which they rely at least partly on magnetic cues for navigation. In principle, sensitivity to polarized light might be an additional sensory capability that aids navigation. Furthermore, polarization sensitivity has been linked to ultraviolet (UV) light perception which is present in sea turtles. Here, we tested the ability of hatchling loggerheads (*Caretta caretta*) to maintain a swimming direction in the presence of broad-spectrum polarized light. At the start of each trial, hatchling turtles, with their magnetic sense temporarily impaired by magnets, successfully established a steady course towards a light-emitting diode (LED) light source while the polarized light field was present. When the LED was removed, however, hatchlings failed to maintain a steady swimming direction, even though the polarized light field remained. Our results have failed to provide evidence for polarized light perception in young sea turtles and suggest that alternative cues guide the initial migration offshore.

Keywords: polarization sensitivity; sea turtles; orientation behaviour

# **1. INTRODUCTION**

Sea turtles such as the loggerhead (Caretta caretta) show a truly remarkable ability to navigate over long distances. Shortly after emerging from their nest on the beach, sea turtle hatchlings crawl to the sea, enter the surf and establish a steady course towards the open ocean. At first, hatchling turtles establish their course to the sea by crawling towards the bright seaward horizon and away from the dark silhouettes of trees and dunes behind [1,2]. Once in the water, the offshore orientation is maintained by swimming into waves, a response that reliably leads turtles away from land and towards the open ocean [3]. When the hatchlings have reached deeper water farther from land, wave direction no longer provides a reliable indicator of offshore direction. Instead, the hatchlings now begin to rely on the Earth's magnetic field during their offshore migration [4-6].

Bright horizons, wave direction and the Earth's magnetic field are not the only cues potentially available to migrating animals. Natural light is often highly linearly polarized when it is scattered by the media molecules and suspended particles (e.g. in the atmosphere or underwater) or reflected from certain surfaces (e.g. water surface or animal reflectors). When light is scattered by particles, a distinct pattern is created that can only be seen by polarization-sensitive eyes. With the Sun's movement throughout the day, this polarization pattern changes [7].

Many invertebrates have the ability to detect linearly polarized light (reviewed in [7]), including some cephalopods [8–10], stomatopods [11,12], insects [13–19] and echinoderms [20]. A number of vertebrates have also been shown to be sensitive to polarized light, including amphibians [21,22], fish (for a recent comprehensive review see [23]) as well as birds ([24–26]; but see conflicting reports: [27,28]).

The hypothesis that polarization sensitivity could be useful for orientation and possibly navigation has only been confirmed experimentally in a small number of studies [13,16,25,29–32]. Given the extensive migrations of sea turtles, the possibility that turtles use polarized light for path-holding and orientation in conjunction with their magnetic sense is intriguing. Sea turtles have a well-developed visual system with a retina containing cone photoreceptors with at least three different visual pigments ( $\lambda$  max of 440 nm, 502 and 562 nm in the green turtle, [33]) and a

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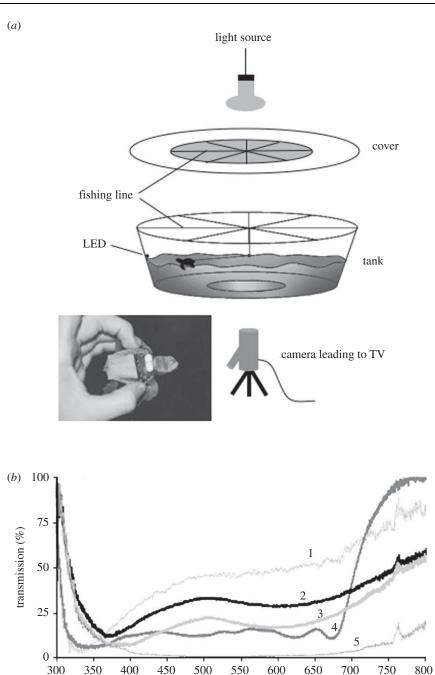


Figure 1. (a) Diagram of experimental set-up. Inset image: hatchling loggerhead sea turtle with harness and SpinBar magnet. (b) Transmission measurements through the filters that were used in this experiment: HN32 linear polarizer (single sheet as well as two sheets in parallel and crossed), diffusing filters and neutral density filter. (b) 1, three diffusers; 2, single polaroid; 3, two polaroids parallel; 4, neutral density filter; 5, two polaroids crossed.

wavelength (nm)

complement of oil droplets [34,35], suggesting a functional colour vision system. In addition, sea turtle hatchlings detect ultraviolet (UV) light and orient towards it ([35-37]; K. A. Fritsches unpublished data), and polarization sensitivity has been shown to be mediated by UV photoreception in fish [38,39]. We therefore investigated whether hatchling loggerhead sea turtles have the ability to orient using polarized light.

#### 2. MATERIAL AND METHODS

Experiments were conducted at the Mon Repos Conservation Park near Bundaberg, Oueensland, Australia. Newly emerged loggerhead turtle hatchlings (C. caretta) were collected after sunset and kept in a dark, cool container until the experiments were carried out, after which the turtles were released on the beach.

Experiments were carried out in a circular polyethylene tank (1.8 m diameter, 0.5 m high; figure 1a), which was lined with black-flocked polyester velour material that was tested for its low reflectance and non-polarizing properties. A window (60 cm diameter) was cut in the base of the tank for video recording with a video camera (Sony Handicam Hi-8, Japan). The cover, also lined with the black fabric, had a hole in the centre (90 cm in diameter) where two sheets  $(1.2 \times 0.45 \text{ m} \text{ and } 0.25 \text{ mm} \text{ thick})$  of Polaroid filter

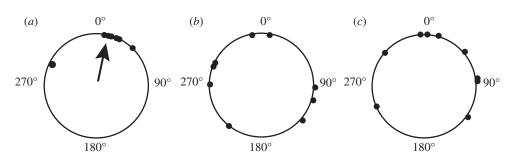


Figure 2. Orientation of individual hatchling sea turtles (a) when allowed to swim towards a LED light source in the presence of polarized light. Mean heading (represented by arrow):  $10.9^{\circ}$ . LED position at  $10^{\circ}$  (r = 0.89, n = 9, p < 0.001, Rayleigh test). (b) Orientation of turtles when swimming under a polarized light source without LED (r = 0.15, n = 9, p > 0.5, Rayleigh test). (c) Control experiment, where turtles swam under a diffused light source without LED (r = 0.46, n = 9, p > 0.1, Rayleigh test).

(HN32 American Polarizers Inc., USA) were placed next to each other to fill the hole in the cover. Fishing line, held in place by clear Sellotape, was used to mask the gap between the filters. Fishing line was also placed at  $45^{\circ}$  and  $90^{\circ}$  to the first line, so as to make the filter appear visually homogeneous and ensure that turtles could not use the gap between the filters to orient. Across the rim of the tank (below the filters; see description below), fishing line was also arranged in the same pattern as described for the Polaroid filter (used for attaching turtle tether; figure 1*a*).

One sheet of 0.9 neutral density filter (no. 211, Lee Filters, Mediavision Australia) and three sheets of diffusing filters (no. 129 Heavy Frost, Lee Filters, Mediavision Australia) were placed above the Polaroid filter and these four filters were 'sandwiched' between two sheets of 3 mm thick UV transparent Perspex (Plastral Pty Ltd, Australia; see figure 1b for spectral transmission measurements of these filters). By flipping the filter apparatus, we thus had polarized or unpolarized light, both with the same transmission properties. A light source (Ultra-Vitalux UV lamp, Lamp Replacements, Australia) placed approximately 1 m above the centre of the tank provided the source of illumination for the experiments.

Turtles were placed into a Lycra harness that encircled the carapace but did not impede swimming (figure 1*a*, inset). The harness was then tethered to the centre of the fishing lines that extended across the top of the tank (figure 1*a*). The tether was approximately 40 cm long. A 15 mm SpinBar magnet (1.4 g) was attached to the harness on the dorsal side of each turtle, approximately 1 cm from the anterior edge of the carapace. This procedure has been shown to remove magnetic information as a potential orientation cue for hatchling sea turtles because the magnet masks the Earth's magnetic field [40].

Experiments were conducted between 19.00 and 02.00 h, which coincides with the period when most hatchlings emerge from nests at Mon Repos (C. J. Limpus personal observation). Each turtle underwent a four-part experiment (numbered 1-4 below).

(1) Each hatchling was tethered in the tank with a lightemitting diode (LED) light source placed just above the water level at a randomly selected location and with the Polaroid filter placed above the tank so that the inside was illuminated with linearly polarized light. Hatchlings are known to swim vigorously towards a light source in such an experimental setup [4,41]. Most hatchlings began swimming towards the LED within seconds of being released into the tank; those few that failed to do so were replaced. Once a hatchling began to swim steadily towards the LED, we began video recording. Each turtle was permitted to swim towards the LED for 35 min with the Polaroid filter above.

- (2) The LED was then removed and the turtle was videotaped for an additional 35 min with the Polaroid filter left in place and the polarized light field thus intact.
- (3) At the end of this time, the Polaroid filter was flipped so that the diffuser was directed downwards and the light inside the tank was unpolarized. The LED was replaced in the same location where it had been before and the turtles' behaviour was monitored. The turtles resumed swimming towards the LED  $(\pm 45^{\circ})$ . Once a turtle had resumed swimming towards the light, it was videotaped for an additional 20 min.
- (4) After this second period of swimming towards the light source, the LED was again removed, and each turtle was permitted to swim for an additional 35 min. During this time, the diffuser filter remained in place and the light field in the tank remained unpolarized.

The videotapes were played back for analysis on a video monitor. The monitor screen was divided into 36 sectors, each encompassing  $10^{\circ}$ , and the turtle's position was measured and recorded every 10 s. Mean angles of orientation were calculated and the orientation of each group was analysed using a Rayleigh test (e.g. [6]).

#### 3. RESULTS

Nine hatchlings successfully completed the experiments. Most turtles established a steady course towards the LED when first placed inside the tank (experimental part 1; figure 2a; statistics reported in figure legends). When the LED was removed but the polarization filter left in place to provide polarization cues, some hatchlings succeeded in maintaining their course for several minutes; after approximately 10 min, however, all had drifted away from their initial headings, circling apparently aimlessly around the perimeter of the tank. Overall, hatchlings were not significantly oriented as a group during the time when the polarization filter was in place but the LED was absent (experiment part 2; figure 2b).

As soon as the LED was returned (experiment part 3), all hatchlings again adopted consistent headings (not shown). Some hatchlings swam almost directly towards the LED, whereas others established steady courses at angles of up to  $45^{\circ}$  with respect to the LED. During this 'retraining' period, the diffusing filter was put in place. Upon removing the LED, the hatchlings again failed to maintain headings towards where the LED had been and instead circled aimlessly around the perimeter of the tank. Their orientation was statistically indistinguishable from random (experiment part 4; figure 2*c*).

### 4. DISCUSSION

The results failed to provide evidence that hatchling loggerheads use polarized light as an orientation cue. The experiment was inspired in part by previous studies demonstrating that dung beetles (*Scarabaeus zambesianus*) use the directional polarization information contained in the night sky to hold a steady course [13,42]. Our failure to elicit orientation responses based on polarized light might reflect an inability of loggerheads to perceive polarized light cues. Alternatively, it is possible that turtles can detect such cues but failed to orient under the experimental conditions for other, unrelated reasons. Several possibilities are discussed below.

### (a) Can sea turtles perceive polarized light?

Little is known about whether turtles in general, and sea turtles in particular, can perceive polarized light. In an early experiment, Ehrenfeld & Carr [43] placed depolarizing goggles on green turtles (Chelonia mydas), but found no evidence that this disrupted the ability of turtles to crawl to the sea. Our interest in further investigating the question of polarization sensitivity in sea turtles was stimulated in part by emerging evidence of UV sensitivity in turtles and the parallel finding that UV sensitivity is associated with polarization vision in fish [38,44-46]. Sea turtles respond to UV illumination ([37]; K. A. Fritsches unpublished data) and there is indirect evidence for the presence of a UV cone, at least in green turtles [35]. As UV radiation is harmful to the retina [47], especially at the surface of clear tropical marine water, many marine species possess UV filters in their ocular media that prevent such damage [48,49]. Such filters are absent in sea turtles [35], but the role of UV vision in the behaviour and ecology of sea turtles, if any, is not understood.

In fishes, UV vision appears to be relatively common [50], whereas polarization sensitivity has been suggested only for a few species, such as those of the families Pomacentridae and Salmonidae [45,51]. However, owing to the time-consuming nature of such experiments, only a limited number of species of fishes have been studied so far.

## (b) The polarization stimulus

Although the results are consistent with the hypothesis that loggerhead turtles cannot perceive polarized light, alternative explanations are also possible. As outlined above, polarization sensitivity is likely to be associated with the UV waveband. We, therefore, took special care to provide sufficient UV light with our broadspectrum light source. While light transmission through the Neutral Density filter (no. 211, Lee Filters) and diffusing filters (no. 129 Heavy Frost, Lee Filters) in the near-UV was acceptable, the HN32 polarizer does not transmit polarized light at wavelengths below 390-400 nm. Unfortunately, this was the only polarizer available in a size appropriate for our study. By using the HN32, we sacrificed some of the UV transmission, hoping that any UV-sensitive cone may pick up the shorter end of the polarized light transmission curve seen in figure 1b. A modified approach incorporating an HNPB filter, or similar, polarizer (one that transmits in the UV wavelengths) would be worth considering for further experiments.

In addition, we worked in relatively dim lighting conditions (approx. 300 lx) and did not experiment with higher or lower light intensities. Given that polarization sensitivity may be associated with particular times of day or night and their respective light intensities (e.g. [13,42]), a wider range of light intensities would be worth testing in the future.

# (c) Polarization cues and the offshore migration of hatchling sea turtles

After entering the sea, hatchling sea turtles guide themselves offshore by using the direction of ocean waves and the Earth's magnetic field [6,52]. Given the known sequence of sensory cues used by hatchling sea turtles in their early life stages [52], it is possible that turtle hatchlings do not pay attention to polarized light cues during the first hours following hatching. For this study, we only had access to freshly emerged animals. However, future experiments should consider the possibility that older hatchlings or juvenile animals orient using polarized light cues, even if newly emerged hatchlings do not. An additional consideration is that it might be necessary for young turtles to gain some visual experience of polarized light fields before being able to use polarized light for orientation.

### 5. CONCLUSIONS

In summary, although our results provide no evidence that loggerhead sea turtles perceive polarized light or orient using it, the results must be interpreted with caution. It is possible that the absence of a response was attributable to factors unrelated to a lack of polarization sensitivity. Moreover, because sea turtles and other animals undergo ontogenetic changes in both their visual capabilities and the orientation mechanisms that they use (e.g. [53,54]), it is possible that sea turtles use polarization vision for orientation only after they have matured beyond the hatchling phase. Future experiments may build on the results reported here and eventually provide a definitive answer to the question whether sea turtles can perceive polarization patterns and use them for guiding movements through the ocean.

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#### REFERENCES

- 1 Limpus, C. J. 1971 Sea turtle ocean finding behaviour. *Search* **2**, 385–387.
- 2 Salmon, M., Wyneken, J., Fritz, E. & Lucas, M. 1992 Seafinding by hatchling sea turtles: role of brightness, silhouette and beach slope as orientation cues. *Behaviour* 122, 56–77. (doi:10.1163/156853992X00309)
- 3 Lohmann, K. J., Swartz, A. W. & Lohmann, C. M. F. 1995 Perception of ocean wave direction by sea turtles. *J. Exp. Biol.* **198**, 1079–1085.
- 4 Lohmann, K. J. 1991 Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). J. Exp. Biol. 155, 37-49.
- 5 Lohmann, K. J. 1993 Magnetic compass orientation. *Nature* **362**, 703. (doi:10.1038/362703a0)
- 6 Lohmann, K. J. & Lohmann, C. M. 1996 Orientation and open-sea navigation in sea turtles. J. Exp. Biol. 199, 73-81.
- 7 Horváth, G. & Varjú, D. 2004 Polarized light in animal vision. Polarization patterns in nature. Berlin, Germany: Springer.
- 8 Moody, M. F. & Parriss, J. R. 1960 The visual system of Octopus: (2) Discrimination of polarized light by Octopus. Nature 186, 839–840. (doi:10.1038/186839a0)
- 9 Shashar, N., Hanlon, R. T. & Petz, A. D. 1998 Polarization vision helps detect transparent prey. *Nature* 393, 222–223. (doi:10.1038/30380)
- 10 Shashar, N., Rutledge, P. S. & Cronin, T. W. 1996 Polarization vision in cuttlefish—a concealed communication channel? *J. Exp. Biol.* 199, 2077–2084.
- 11 Marshall, N. J. 1988 A unique color and polarization vision system in mantis shrimps. *Nature* **213**, 893–894.
- 12 Marshall, N. J., Land, M. F., King, C. A. & Cronin, T. W. 1991 The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). I. Compound eye structure: the detection of polarized light. *Phil. Trans. R. Soc. Lond. B* 334, 33–56. (doi:10.1098/rstb. 1991.0096)
- 13 Dacke, M., Nilsson, D. E., Scholtz, C. H., Byrne, M. & Warrant, E. J. 2003 Insect orientation to polarized moonlight. *Nature* 424, 33. (doi:10.1038/424033a)
- 14 Kelber, A., Thunell, C. & Arikawa, K. 2001 Polarization-dependent color vision in *Papilio* butterflies. *J. Exp. Biol.* 204, 2469–2480.
- 15 Rossel, S. 1989 Polarization sensitivity in compound eyes. In *Facets of vision* (eds D. G. Stavenga & R. C. Hardie), pp. 298–316. Berlin, Germany: Springer.
- 16 Rossel, S. & Wehner, R. 1984 How bees analyse the polarization patterns in the sky. J. Comp. Physiol. A 154, 607–615. (doi:10.1007/BF01350213)
- 17 Sweeney, A., Jiggins, C. & Johnsen, S. 2003 Polarized light as a butterfly mating signal. *Nature* 423, 31–32. (doi:10.1038/423031a)
- 18 Wehner, R. 1989 Neurobiology of polarization vision. *Trends Neurosci.* 12, 353–359. (doi:10.1016/0166-2236 (89)90043-X)

- 19 Wehner, R. 2001 Polarization vision—a uniform sensory capacity? *J. Exp. Biol.* 204, 2589–2596.
- 20 Johnsen, S. 1994 Extraocular sensitivity to polarized light in an echinoderm. *J. Exp. Biol.* **195**, 281–291.
- 21 Auburn, J. S. & Taylor, D. J. 1979 Polarized light perception and orientation in larval bullfrogs *Rana catesbeiana*. *Anim. Behav.* 27, 658–688. (doi:10.1016/0003-3472(79)90003-4)
- 22 Taylor, D. & Adler, K. 1973 Spatial orientation by salamanders using plane-polarized light. *Science* 181, 285–287. (doi:10.1126/science.181.4096.285)
- 23 Sabbah, S., Lerner, A., Erlick, C. & Shashar, N. 2005 Under water polarization vision: a physical examination. In *Recent research developments in experimental and theoretical biology* (ed. S. G. Pandalai), pp. 123–176. Kerala, India: Transworld Research Network.
- 24 Kreithen, M. L. & Keeton, W. T. 1974 Detection of polarized light by the homing pigeon, *Columba livia*. *J. Comp. Physiol.* 89, 83–92. (doi:10.1007/BF00696165)
- 25 Muheim, R., Phillips, J. B. & Akesson, S. 2006 Polarized light cues undelie compass calibration in migratory songbirds. *Science* **313**, 837–839. (doi:10.1126/science. 1129709)
- 26 Phillips, J. B. & Waldvogel, J. A. 1988 Celestial polarized light patterns as a calibration reference for sun compass of homing pigeons. *J. Theor. Biol.* 131, 55–67. (doi:10. 1016/S0022-5193(88)80120-6)
- 27 Coemans, M. & Vos, J. 1992 On the perception of polarized light by the homing pigeon. Utrecht, Nederlands: Utrecht University.
- Hzn, J., Coemans, M. & Nuboer, J. 1995 No evidence for polarization sensitivity in the pigeon electroretinogram. *J. Exp. Biol.* 198, 325–335.
- 29 Rossel, S. 1993 Navigation by bees using polarized skylight. *Comp. Biochem. Physiol.* **104**, 695–708. (doi:10. 1016/0300-9629(93)90146-U)
- 30 Rossel, S. & Wehner, R. 1986 Polarization vision in bees. *Nature* **323**, 128–131. (doi:10.1038/323128a0)
- 31 Shashar, N., Sabbah, S. & Aharoni, N. 2005 Migrating locusts can detect polarized reflections to avoid flying over the sea. *Biol. Lett.* 1, 472–475. (doi:10.1098/rsbl. 2005.0334)
- 32 Wehner, R. & Müller, M. 2006 The significance of direct sunlight and polarized skylight in the ant's celestial system of navigation. *Proc. Natl Acad. Sci. USA* 103, 12 575–12 579. (doi:10.1073/pnas.0604430103)
- 33 Liebman, P. A. & Granda, A. M. 1971 Microspectrophotometric measurements of visual pigments in two species of turtle, *Pseudemys scripta* and *Chelonia mydas. Vis. Res.* 11, 105–114. (doi:10.1016/0042-6989(71)90227-6)
- 34 Liebman, P. A. & Granda, A. M. 1975 Super dense carotenoid spectra resolved in single cone oil droplets. *Nature* 253, 370–372. (doi:10.1038/253370a0)
- 35 Mäthger, L. M., Litherland, L. & Fritsches, K. A. 2007 An anatomical study of the visual capabilities of the green turtle, *Chelonia mydas*. *Copeia* 2007, 169–179. (doi:10. 1643/0045-8511(2007)7[169:AASOTV]2.0.CO;2)
- 36 Horch, K. W., Gocke, J. P., Salmon, M. & Forward, R. B. 2008 Visual spectral sensitivity of hatchling loggerhead (*Caretta caretta* L.) and leatherback (*Dermochelys coriacea* L.) sea turtles, as determined by single-flash electroretinography. *Mar. Freshw. Behav. Physiol.* 41, 107–119. (doi:10.1080/10236240802106556)
- 37 Witherington, B. E. & Bjorndal, K. A. 1991 Influences of wavelength and intensity on hatchling sea turtle phototaxis: implications for sea-finding behaviour. *Copeia* 4, 1060–1069. (doi:10.2307/1446101)
- 38 Hawryshyn, C. W. 2000 Ultraviolet polarization vision in fishes: possible mechanisms for coding e-vector. *Phil. Trans. R. Soc. Lond. B* 355, 1187–1190. (doi:10.1098/ rstb.2000.0664)

- 39 Hawryshyn, C. W. & McFarland, W. N. 1987 Cone photoreceptor mechanisms and the detection of polarized light in fish. *J. Comp. Physiol. A* 160, 459–465. (doi:10.1007/BF00615079)
- 40 Irwin, W. P. & Lohmann, K. J. 2003 Magnet-induced disorientation in hatchling loggerhead sea turtles. *J. Exp. Biol.* 206, 497-501. (doi:10.1242/jeb.00108)
- 41 Salmon, M. & Wyneken, J. 1987 Orientation and swimming behavior of hatchling loggerhead turtles *Caretta caretta* during their offshore migration. *J. Exp. Mar. Biol. Ecol.* 109, 137–153. (doi:10.1016/0022-0981(87)90012-8)
- 42 Dacke, M., Nordström, P. & Scholtz, C. H. 2003 Twilight orientation to polarised light in the crepuscular dung beetle *Scarabaeus zambesianus*. J. Exp. Biol. 206, 1535–1543. (doi:10.1242/jeb.00289)
- 43 Ehrenfeld, E. W. & Carr, A. 1967 The role of vision in the sea-finding orientation of the green turtle (*Chelonia mydas*). *Anim. Behav.* **15**, 25–36. (doi:10.1016/S0003-3472(67)80007-1)
- 44 Hawryshyn, C. W. & McFarland, W. N. 1987 Cone photoreceptor mechanisms and the detection of polarized light in fish. *J. Comp. Physiol. A* 160, 459–465. (doi:10.1007/BF00615079)
- 45 Mussi, M., Haimberger, T. J. & Hawryshyn, C. W. 2005 Behavioural discrimination of polarized light in the damselfish *Chromis viridis* (family Pomacentridae). *J. Exp. Biol.* 208, 3037–3046. (doi:10.1242/jeb.01750)
- 46 Parkyn, D. C. & Hawryshyn, C. W. 1993 Polarized-light sensitivity in rainbow trout (*Oncorhynchus mykiss*): characterization from multi-unit responses in the optic

nerve. J. Comp. Physiol. A 172, 493-500. (doi:10.1007/BF00213531)

- 47 Zigman, S. 1971 Eye lens color: formation and function. *Science* **171**, 807–809. (doi:10.1126/science.171.3973.807)
- 48 Fritsches, K. A., Partridge, J., Pettigrew, J. D. & Marshall, N. J. 2000 Colour vision in billfish. *Phil. Trans. R. Soc. Lond. B* 355, 1253–1256. (doi:10.1098/ rstb.2000.0678)
- 49 Siebeck, U. E. & Marshall, N. J. 2000 Transmission of ocular media in labrid fishes. *Phil. Trans. R. Soc. Lond.* B 355, 1257–1261. (doi:10.1098/rstb.2000.0679)
- 50 Losey, G. S., Cronin, T. W., Goldsmith, T. H., Hyde, D., Marshall, N. J. & McFarland, W. N. 1999 The UV visual world of fishes: a review. *J. Fish Biol.* 54, 921–943. (doi:10.1111/j.1095-8649.1999.tb00848.x)
- 51 Coughlin, D. J. & Hawryshyn, C. W. 1995 A cellular basis for polarized-light vision in rainbow-trout. *J. Comp. Physiol. A* 176, 261–272. (doi:10.1007/BF00239928)
- 52 Lohmann, K. J. & Lohmann, C. M. F. 2003 Orientation mechanisms of hatchling loggerhead turtles (*Caretta caretta*). In *Biology and conservation of loggerhead sea turtles* (eds A. Bolten & B. Witherington), pp. 44–62. Washington, DC: Smithsonian Institute Press.
- 53 Bowmaker, J. K. 1990 Visual pigments of fish. In *The visual system of fish* (eds R. H. Douglas & M. B. A. Djamgoz), pp. 81–104. London, UK: Chapman and Hall.
- 54 Wiltschko, R. 1983 The ontogeny of orientation in young homing pigeons. *Comp. Biochem. Physiol A* 76, 701–708. (doi:10.1016/0300-9629(83)90131-7)