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RETINAL ANATOMY OF HATCHLING SEA TURTLES: ANATOMICAL SPECIALIZATIONS AND BEHAVIORAL CORRELATES

LISA J. OLIVER[a], MICHAEL SALMON[a,*],
JEANETTE WYNEKEN[a], ROBERT HUETER[b]
and THOMAS W. CRONIN[c]

[a]*Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33431 USA;* [b]*Center for Shark Research, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida 34236, USA;* [c]*Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, Maryland 21250, USA*

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The eyes of three species of sea turtle hatchlings (loggerheads, green turtles, and leatherbacks) possess visual streaks, areas of densely packed ganglion cells running along the antero-posterior retinal axis. These probably function to provide heightened visual acuity along the horizon. The vertical extent and absolute concentration of cells within the streak, compared to the rest of the retina, differ among the species. Leatherbacks have an additional specialized region (*area temporalis*) that might enhance their ability to detect prey below them in the water column. Green turtles and loggerheads, but not leatherbacks, show compensatory eye reflexes that keep the visual streak horizontal. Species differences in retinal structure and eye reflexes probably reflect their unique specializations in visual ecology and behaviour.

Keywords: Sea turtles; Retina; Ecology; Vision; Behavior

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[*] Address for correspondence: Dept. of Biological Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, Florida 33431. Tel.: 561-297-2747, Fax: 561-297-2749, e-mail: salmon@fau.edu

INTRODUCTION

Many terrestrial vertebrates possess retinas that contain morphologically specialized, highly concentrated, cellular areas (Collin, 1999). When the area of specialization is band-like and oriented horizontally across the visual axis, it is called a visual streak (Hughes, 1977). Visual streaks are characterized by a high concentration both of photoreceptor cells (typically cones) and retinal ganglion cells. These specialized retinal regions probably enable organisms to view regions of their visual field with greater resolution (Walls, 1942).

Similar retinal specializations are present in aquatic as well as terrestrial and aerial vertebrates. Juveniles of the lemon shark (*Negaprion brevirostris*), which are found in shallow marine habitats consisting of open sea grass flats, open sand or sand covered by marine algae, have a well-developed visual streak (Hueter, 1991). The streak may be used to detect predators (larger sharks) and prey (smaller fish) in the narrow horizontal band between the sea surface and the bottom. In teleost fishes the nature of the retinal specialization varies with visual ecology (Collin and Pettigrew, 1988a, b).

Visual streaks are most prominent in species that feed in habitats where the organism has an unobstructed view of its surroundings and views a relatively flat horizon. In the freshwater turtle (*Pseudemys* [= *Trachemys*] *scripta*), the visual streak consists of a high-density band of small cone photoreceptor cells (Brown, 1969). Brown showed that when a turtle is rotated around its anterior–posterior axis (head-up or head-down), a reflex maintains the eye in a horizontal position. Thus, the animal resists displacement of its streak from its visual horizon.

Anatomical studies (Zhang and Eldred, 1994) have shown that $> 50\%$ of the ganglion cells found in the *Trachemys* retina are concentrated in the visual streak area. These ganglion cells have smaller receptive fields than the ganglion cells found elsewhere in the retina (Granda and Fulbrook, 1989), suggesting that resolving power of the retina is higher within the visual streak.

In this paper, we describe and compare the ganglion cell densities and compensatory eye reflexes of three species of hatchling marine turtles: green turtles, *Chelonia mydas* L; loggerheads, *Caretta caretta* L and leatherbacks *Dermochelys coriacea* V. Each species is ecologically distinct. Green turtle hatchlings are found in open water while loggerhead hatchlings hide within flotsom. Both feed near the sea surface, but on different assemblages of prey. Leatherback hatchlings specialize on gelatinous prey (jellyfishes and salps) captured by diving. These contrasts suggest that the retinal structure of marine turtles might show anatomical adaptations correlated with their unique differences in visual ecology.

METHODS

Retinal Preparation

Fresh eyes of hatchlings were obtained from specimens found shortly after they died of natural causes in the nest. Hatchlings were collected from nests in Broward and Palm Beach Counties, Florida, U.S.A. (25–26° N Lat., 80° W Lon.). The dead turtles were placed in refrigerated, darkened containers for no more than 6 h before eye extraction. Eyes were removed and injected with 0.25 ml of 10% buffered formalin-reptilian Ringer's solution (Peters, 1964) placed in the vitreal chamber (Curcio *et al.*, 1987). Each eye was marked with a notch to indicate its dorsal/ventral and anterior/posterior orientation, then fixed by submergence in a 10% buffered formalin-reptilian Ringer's solution for at least one week.

After fixation, a variation of Stone's (1981) retinal wholemount technique was used. The eye was opened at the choroidal-scleral margin. The retina was then dissected free of the choroid in a dish of reptilian Ringer's. Small reference cuts were made at the dorsal and ventral border to preserve natural eye orientation. The isolated retina was floated on to a gelatinized glass cover slip. Radial incisions were made around the circumference of the retina to flatten it. A fine camel's hair brush and small pieces of filter paper were used to brush the retina flat against the cover slip. Excess liquid and vitreous were removed by using the filter paper as a sponge (Hueter, 1988).

Several drops of dimethyl sulfoxide (DMSO) were placed on the retina and a non-gelatinized cover slip was situated over the retina (Curcio *et al.*, 1987). The slide (consisting of the retina sandwiched between the gelatinized and non-gelatinized cover slips) was then placed in a dish containing DMSO while it cleared for 3 days. A 100 g weight was placed upon the slide to flatten the retina while it cleared.

After clearing, the top cover slip and excess DMSO were removed. The retina was then saturated with glycerol. A new cover slip was applied and the edges were sealed with clear nail polish.

Construction of Retinal Maps

Cleared wholemounts were observed using an interference phase contrast microscope (Olympus BX60 BMAX) with Nomarski optics, following standard procedures (Dawson *et al.*, 1989).

Ganglion cells were initially identified from slides of retinal cross-sections by their location, size, and the presence of a nuclear body in the soma. If in the wholemounts the nuclear body was not visible, the ganglion cells were distinguished from glial cells by their larger soma. Ganglion cells fell within three size classes. Most (73%) were small ($8-10\,\mu$), some (22%) were larger ($15-18\,\mu$), and a minority (5%) were large ($>25\,\mu$). Glial cells ranged from $2-5\,\mu$.

The outline of each retinal wholemount was traced on 1 mm^2 grid paper. The entire retina was then surveyed in 0.5 mm horizontal and vertical increments (Stone, 1981) using a calibrated X, Y coordinate system on the microscope's stage micrometer. Either the left or the right eye of each animal was used. Cell counts were converted to cells/mm^2 and used to construct nine isodensity contour maps (one retina per turtle; three turtles of each species). Maps were scanned to computer, with right-eye maps flipped horizontally (so all maps could be presented in the same orientation (nasal left)).

Behavioral Assays

Hatchlings were collected just prior to a natural emergence from nests at the same locations as described above. They were placed in a light-tight container and brought to the laboratory within 30 min. They were maintained at ambient temperatures (26–28°C) for study until shortly after dusk. Once experiments were completed (within 2–3 h), hatchlings were taken to a dark beach and released.

Experiments were done in an illuminated room. Each turtle was held by rubber coated clamp that grasped its body on the dorsal (carapace) and ventral (plastron) surfaces (Fig. 1). The turtle's fore- and hind-flippers, as well as its head, were suspended in mid-air and free to move normally. Subjects were clamped in one of three body positions: horizontal; body rotated 30° downward ("head-down"); or body rotated 30° upward ("head-up"). Head position was photographed immediately after the hatchling was clamped in position. Head angle was measured from the photographs, relative to a horizontal reference line drawn on white cardboard placed immediately behind the turtle.

Fifteen hatchlings, each from a different nest, were used to characterize the responses of loggerhead and green turtles. The sample for leatherbacks was 14 hatchlings. Each hatchling was clamped sequentially in all three positions, but with the treatment order randomized. Head angles among the species were compared for each treatment using a Watson–Williams test (Zar, 1984).

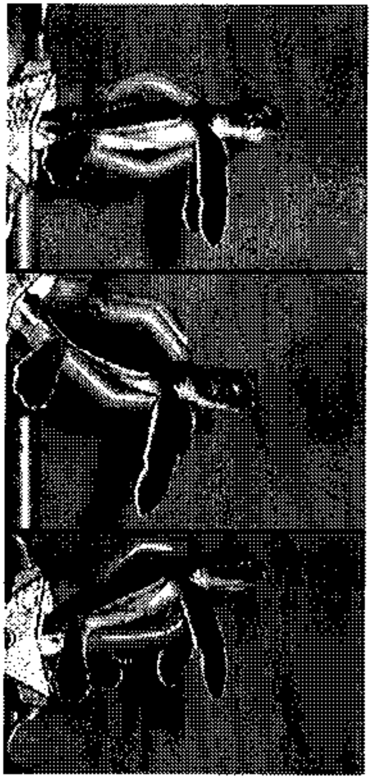

FIGURE 1 Hatchling green turtle clamped in a horizontal (top), head-down (middle), and head-up (lower) position.

RESULTS

Retinal Maps

All three species possessed a visual streak in the ganglion cell layer. However, the species showed differences in streak shape, relative topography, and absolute numbers of ganglion cells compared to those found in other portions of this cell layer (Figs. 2–4). Cell densities ($4.0-12.0 \times 10^3/\mathrm{mm}^2$) among the species fell within the range of those found in the retinae of another turtle species (*Pseudemys scripta elegans*; $2.0-18.0 \times 10^3/\mathrm{mm}^2$; Peterson and Ulinski, 1979).

In the green turtle, the streak was defined by its narrow vertical and long horizontal extent (in 2 of 3 retinae), and by its relatively high ganglion cell concentration (12.0×10^3 cells/mm^2) in the center of the streak. In the

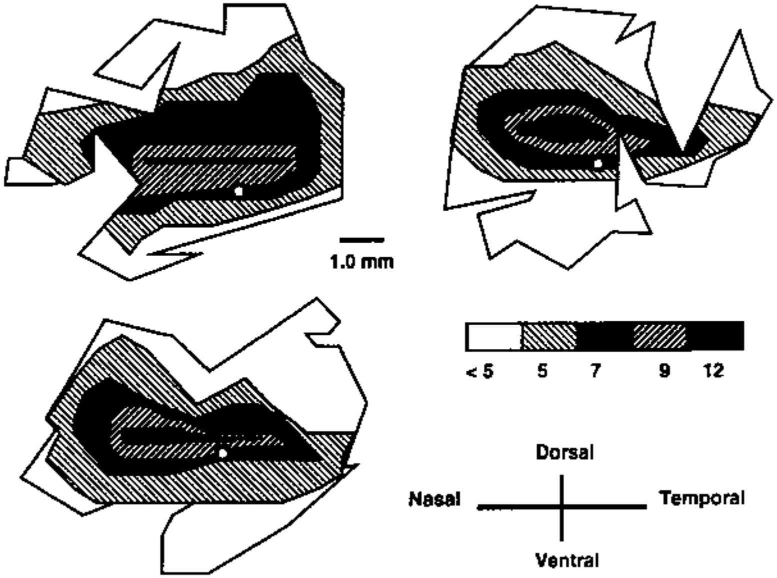

FIGURE 2 Isodensity contour maps of ganglion cell densities in the left retina (top left) and right retinae (top right, lower left) of three green turtle hatchlings. In all maps, axes are identical (nasal is left, dorsal is upward). Numbers are minimal cell densities ($\times 10^3/\text{mm}^2$) observed within that contour. Open circle within each map shows location of the optic nerve.

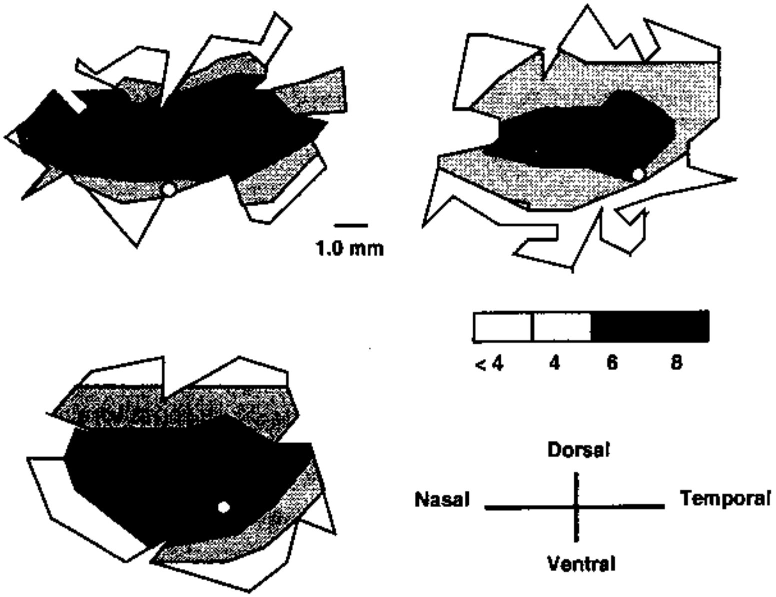

FIGURE 3 Isodensity contour maps of ganglion cell densities in the left retinae (top left and right) and right retina (below) of three loggerhead hatchlings. Format, as in Figure 2.

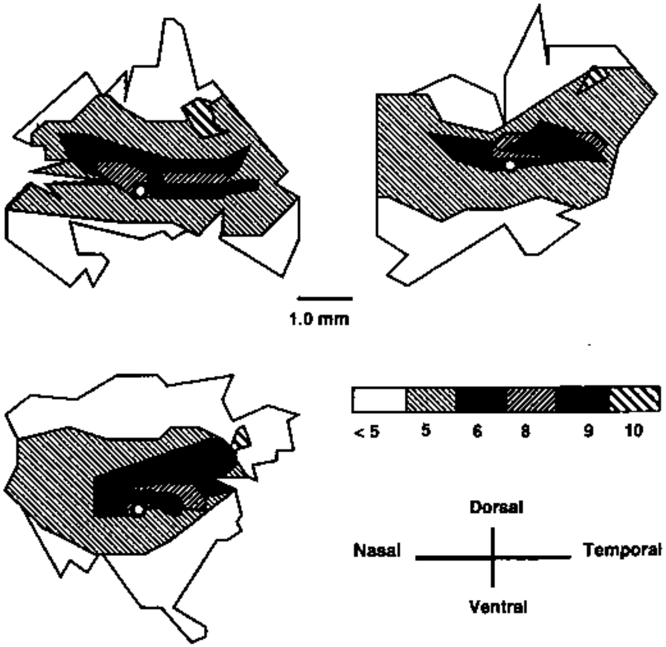

FIGURE 4 Isodensity contour maps of ganglion cell densities in the left retinae (top left and right) and right retina (below) of three leatherback hatchlings. The highest cell densities occur in the *area temporalis*. Format, as in Figure 2.

loggerhead and leatherback, the streak was less elongated horizontally, and somewhat lower in absolute ganglion cell concentration (8.0×10^3 cells/mm^2 in the loggerhead; 9.0×10^3 cells/mm^2 in the leatherback). In all species, the ganglion cell concentration in the visual streak was equivalent to roughly a doubling of the peripheral concentration (5.0 to 12.0×10^3 cells/mm^2 in the green turtle; 4.0 to 8.0×10^3 cells/mm^2 in the loggerhead; 5.0 to 9.0×10^3 cells/mm^2 in the leatherback).

Ganglion contour maps were nearly symmetrical dorsoventrally (that is, surrounded above and below the streak axis by a decreasing ganglion cell isodensities) in the green turtle and loggerhead (Figs. 2 and 3). In the leatherback, however, the retina contained a distinct *area temporalis* in addition to the visual streak. This region contained the highest ganglion cell densities found in the retina (10.0×10^3 cells/mm^2; Fig. 4).

Visual Reflexes

Green turtles and loggerheads showed no statistical differences in head angle when clamped in a 30° "head-up" (Watson–Williams $U = 0.1087$, n.s.), 30°

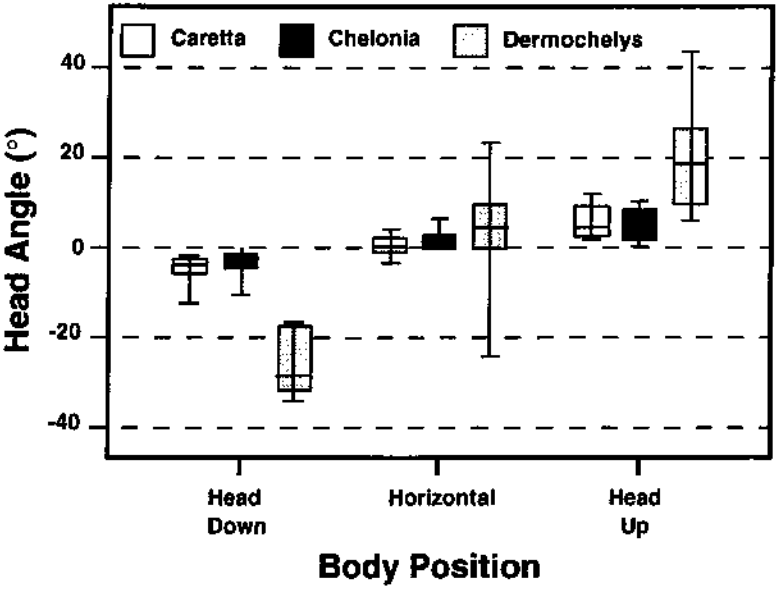

FIGURE 5 Head angles assumed by hatchlings when their body is clamped in a horizontal (middle), a 30° "head-down" (left) or a 30° "head-up" (right) position. Sample size is 15 (loggerheads and green turtles) and 14 (leatherback) hatchlings per treatment. Horizontal line is mean, box is S.E. of the mean, and vertical bracket is the range.

"head-down" ($U = 0.0059$, n.s.), or horizontal ($U = 0.0075$, n.s.) position. Both species within seconds compensated for changes in body angle by movements that returned the head to a near-horizontal position. (Fig. 5). They differed statistically from leatherbacks under all treatments (Watson–Williams $U^2 = 0.2422-0.5851$, $p < 0.02-0.001$). When clamped horizontally, leatherbacks on average held their head at angles about 5° above those of green turtles and loggerheads. In a head-down position, leatherbacks failed to compensate. When tilted head-up, compensation was weak, if it occurred at all (Fig. 5).

DISCUSSION

Structure and Function of the Visual Streak

Visual streaks occur in species that live in relatively open, uncluttered environments with a flat horizon (Pumphrey, 1948; Collin and Pettigrew, 1988a). Hughes (1977) hypothesized that by concentrating receptors and the neuronal layers analyzing visual information in the medial retina, the visual system becomes especially responsive to important stimuli (*e.g.*, mates, prey and predators) that occur on or near the horizon. Species with visual streaks also possess behavioral reflexes (movements of the head and/or eye) that resist displacement of the streak portion of the retina from its normal position conjugate to the horizon. Visual streaks and stabilized eyes exist in terrestrial mammals (Hughes, 1977; Wong *et al.*, 1986; Pettigrew *et al.*, 1988; Timney and Keil, 1992), marine mammals (Mass and Supin, 1986), birds (Pumphrey, 1948, 1961; Pennycuick, 1960; Waldvogel, 1990), marine fishes (Collin and Pettigrew, 1988a, b; Hueter, 1988, 1991), and even invertebrates with compound eyes (Zeil *et al.*, 1989; Dahmen, 1991; Land and Layne, 1995a, b).

In a survey of the mammals, Hughes (1977) found that visual streaks occurred even among species that lived in areas where the horizon was not totally open. "Strong" visual streaks, found mainly in diurnal species, were characterized by relatively high cell densities of receptor and/or ganglion cells (compared to the rest of the retina). They also have a long horizontal extent in which the cell densities were sharply delineated from the remainder of the retina by closely-spaced isodensity contour lines. "Weak" visual streaks show the converse structural relationships. In aquatic species, variation in visual streak design is best documented in coral reef fishes. The streak is well developed in species occupying open sand habitats surrounding the reef (Collin and Pettigrew, 1988a, 1989b).

Visual streak specialization also varies with ambient levels of habitat illumination. Among mammals, the highest densities of ganglion cells are found in diurnally active species, while the lowest densities are found among those that are nocturnally active (Hughes, 1977). Day-active terrestrial mammals usually have higher densities of ganglion cells in the streak than either reef fishes (Collin and Pettigrew, 1988a) or sharks (Hueter, 1991). But considering only aquatic species, fishes found in shallow, and relatively clear, tropical waters have higher densities of cells in their streak than marine mammals, such as the harbor porpoise *Phocoena phocoena*, that forage in relatively cloudy temperate waters (Mass and Supin, 1986).

Finally, the streak may vary regionally in the spatial distribution of either the receptor cells (rods and cones), the ganglion cells, or both. Among diurnally active mammals, rod density is inversely correlated with ganglion cell density, while the cone density increases with ganglion cell density (Hughes, 1977). Similarly, in lemon sharks (Hueter, 1988, 1991) and in painted turtles (Brown, 1969; Zhang and Eldred, 1994), the visual streak consists of elevated concentrations of both cones and ganglion cells. It is a safe assumption for most vertebrates that where ganglion cell densities are high so, also, is retinal resolving power and visual acuity (Walls, 1942; Pumphrey, 1961; Hughes, 1977; Waldvogel, 1990).

The Visual Streak and Sea Turtle Ecology

The three species of sea turtles we studied live in different visual worlds, both as hatchlings and as adults (Tab. I). Yet at different times and places during their development, all sea turtles are exposed to open horizons where important visual tasks must be executed. These include: hatchling orientation ("seafinding") which depends upon optical cues on or at the horizon (Salmon *et al.*, 1992; Witherington, 1992); foraging at the water surface by hatchlings and juveniles (Witherington, pers. comm.); and nest site selection (Mortimer, 1982). The latter depends upon the visual characteristics of the beach and landward horizon.

At the hatchling stage, the visual streak may be important for detection of floating objects (such as *Sargassum*) where food may accumulate, and which may offer a refuge from predation (Carr and Ogren, 1960). A visual streak might also function in small turtles to detect aerial (sea birds) and piscine predators that approach from just above or just below the surface. On the basis of these general considerations, we hypothesize that a visual streak might be present in the retinae of all sea turtles.

Of the three species we studied, the streak is best developed in green turtles, both in terms of its spatial distribution (narrowly concentrated along the nasaltemporal axis) and its cell concentration (highest density of ganglion cells/unit area among the streaks found in all species). As hatchlings, green turtles remain in open water where they feed upon prey close to the ocean surface; as adults they feed in shallow tropical seagrass and algal beds. Thus both as hatchlings and adults, these turtles feed in brightly illuminated, and relatively clear, habitats (Tab. I) with an

TABLE I Diet, feeding environment, and feeding periods of the three sea turtle species compared in this study. Data are from Bjorndal (1996); Carr (1987); Eckert *et al.* (1989) and Wyneken and Salmon (1992). H = hatchling; A = adult

Species		*Diet*	*Habitat*	*Feeding time*
Chelonia	H	Omnivore	Surface (open ocean)	Day
	A	Herbivore	Shallow marine seagrass/algal pastures	Day
Caretta	H	Omnivore	Surface (flotsam)	Day
	A	Carnivore	Benthic hard bottom and reef	Day
Dermochelys	H	Gelatinavore	Open ocean	Day, Night
	A	Gelatinavore	Open ocean or near-shore coastal waters	Day, Night

unobstructed view of the horizon. They are strictly diurnal in activity during all stages of growth (Wyneken and Salmon, 1992; Ogden *et al.*, 1983).

Loggerhead have visual streaks that contain lower densities of ganglion cells than green turtles. Their streaks also are wider (expanded in the dorsoventral axis) in relation to the length, and thus may be considered to be examples of "weak" visual streaks.

As hatchlings, loggerheads are pelagic and hide within, and rest upon, floating objects (*Sargassum* mats in the Atlantic Ocean). Their prey (crustaceans, snails, anemones, fish eggs, and plant material; Witherington, pers. comm.) are most commonly gleaned from surfaces of *Sargassum* or flotsam that accumulates at oceanic convergence zones (Carr, 1986). They may occasionally capture food in open water by making shallow dives for jellyfish, ctenophores, salps, and pelagic snails (Bjorndal, 1996). As they increase in size, pelagic loggerheads abandon *Sargassum* mats and float in the open (Bolten *et al.*, 1993). There they begin to feed upon larger, hard-shelled prey (Goose barnacles attached to floating objects Brongersma, 1972; van Neirop and den Hartog, 1984).

After returning to coastal waters as larger turtles, loggerheads become benthic feeders on crustaceans, mollusks, echinoderms, or bivalves (Dodd, 1988). Feeding sites vary from tropical and subtropical reefs to temperate hard bottom communities. Often, loggerheads migrate seasonally between both kinds of habitats (Bjorndal, 1996). Thus, in coastal waters, they feed in visually obstructed habitats where water clarity is variable.

Leatherbacks, both as hatchlings and as larger turtles, are opportunistic predators that search for, and feed continuously upon, gelatinous prey in open water (Tab. I). Little is known about the pelagic distribution of leatherback hatchlings (Musick and Limpus, 1996) except that young leatherbacks, like green turtles, do not associate with floating objects (as do loggerheads). Leatherbacks show the greatest spatial and temporal variation in foraging habits, and in the illumination levels encountered while hunting for prey. As hatchlings and juveniles, most leatherbacks remain in the open ocean. As larger turtles, they apparently locate aggregations of jellyfish and will feed where and when these are found. Leatherbacks forage during the day and at night, in shallow and in deep water, and in temperate coastal waters with reduced visibility as well as in clear water of the open ocean (Eisenberg and Frazier, 1983; Eckert *et al.*, 1989; Grant and Ferrell, 1993). The "weaker" development of their visual streak (compared to green turtles) may reflect the generally lower levels of illumination under which they have a view of the horizon, as well as their preference to take prey in open water, in the absence of a visible horizon.

Our data in this study come from one developmental stage (hatchlings). The structural architecture of the retina might change as the eye grows, and as the turtles shift their habitat during ontogeny (Tab. I). Little is known concerning how neural organization in vertebrate retinas may shift as animals grow from juvenile to adult, but other changes in vertebrate visual systems are well documented. These include alterations in visual pigment content (*e.g.*, lemon sharks, Cohen *et al.*, 1990; European eel, Wood *et al.*, 1992) and in photoreceptor type (Evans and Fernald, 1990; Hawryshyn *et al.*, 1989). Generally, acuity increases with eye size in diurnal animals (Goldsmith, 1972).

We suspect that differences in visual streak structure among sea turtle hatchlings also reflect preparation for functional demands placed upon older turtles. Evidence in support of this hypothesis, for each species, is as follows: (i) The nursery habitats where loggerheads find food (on surfaces within *Sargassum* mats, on the surfaces of floating debris) resemble those where they find food as adults (surfaces of objects on the bottom). Thus at all ages, prey are found within complex surfaces that may obscure a view of the horizon. (ii) Leatherback hatchlings undergo no fundamental shift in either diet or habitat as they mature (Bjorndal, 1996). They are unique among sea turtles in that even as hatchlings, they show nocturnal as well as diurnal activity (Wyneken and Salmon, 1992). This difference probably reflects a tendency to feed opportunistically at night, a characteristic of adults. It is thus likely that the hatchling visual streak closely approximates streak morphology in adults. (iii) The retina of green turtle hatchlings possesses a "strong" visual streak, one that appears suited to the visual world occupied by the adults.

The Area Temporalis of Leatherbacks

The leatherback retina contains an area *temporalis* not found in the other two species. In other vertebrate species, such areas (including *foveas*) are circular regions of the retina that function to improve acuity in localized regions of the visual field. Many vertebrates, from hawks (Waldvogel, 1990) to humans (Walls, 1942), have *foveas* used in binocular vision to see objects directly ahead.

Among reef fishes, species having well-developed retinal areas of specialization live in caves, within crevasses or branches of coral, under coral over-hangs, or within coral rubble. Some possess up to three such areas, most commonly located dorsal, ventral, or within the horizontal retinal axis, and positioned to heighten acuity in regions where prey, predators or both are likely to be visible (Collin and Pettigrew, 1988b).

We hypothesize that in leatherbacks, the *area temporalis* represents a specialization used to detect prey. Since the eyes are situated laterally, the temporal location of the region of enhanced ganglion cell density corresponds to a visual field in front, somewhat ventral, and lateral to the animal's head and mouth. Gelatinous prey are the likely targets, tracked and ultimately consumed when viewed in this location. Behavioral observations show that during the day, hatchling leatherbacks swim continuously near the surface until they perceive a jellyfish, then dive (up to 17 m) directly to the target to feed (Jones and Salmon, unpubl. obs.).

While green turtles and loggerheads showed obvious compensatory responses (head movements to keep the visual apparatus horizontal), leatherbacks did not (Fig. 5). Leatherbacks may be capable of keeping their visual streak horizontal by moving their eyes instead of their head. Kahmann (1936) found that marine teleosts with specialized retinal areas had well-developed eye movement reflexes, and postulated a link between *area* development and these reflexes. Because of the small size and dark pigmentation of the eye, we were unable to detect whether these eye movements occur. Obviously, if swimming leatherback hatchlings visually scan the sea beneath them looking for visual targets at varying visual angles, a horizontally stabilized head and visual axis would be maladaptive.

The fossil evidence indicates that sea turtles are an ancient group, derived from terrestrial testudine ancestors over 80 mya (Pritchard, 1996; Hirayama, 1994). Since early in sea turtle phylogeny, the hard-shelled (Cheloniidae, including *Caretta and Chelonia*) and leatherback (Dermochelidae) lineages had separate evolutionary histories (Dutton, 1995). The contrasts in retinal morphology and behavior between representatives of these two lineages probably reflect both their long separation and their unique niche specializations.

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References

Bjorndal, K. A. (1996) Foraging ecology and nutrition of sea turtles. In: *The Biology of Sea Turtles*, Lutz, P. L. and Musick, J. A. (Eds.), CRC Press, Boca Raton.

Brongersma, L. D. (1972) European Atlantic turtles. *Zool. Verh. Rijksmus Nat. Hist. (Leiden)*, **121**, 1–318.

Bolten, A. B., Martins, H. R., Bjorndal, K. A. and Gordon, J. (1993) Size distribution of pelagic-stage loggerhead sea turtles (*Caretta caretta*) in waters around the Azores and Madeira. *Arquipelago. Life and Marine Sciences*, **11A**, 49–54.

Brown, K. (1969) A linear *area centralis* extending across the turtle retina and stabilized to the horizon by non-visual cues. *Vision Res.*, **9**, 1053–1062.

Carr, A. (1986) Rips, FADS, and little loggerheads. *Bioscience*, **36**, 92–100.

Carr, A. (1987) New perspectives on the pelagic stage of sea turtle development. *Conservation Biology*, **1**, 103–121.

Carr, A. and Ogren, L. H. (1960) The ecology and migration of sea turtles, 4. The green turtle in the Caribbean Sea. *Bull. Am. Mus. Nat. Hist.*, **121**, 1–48.

Cohen, J. L., Hueter, R. E. and Organisciak, D. T. (1990) The presence of a porphyropsin-based visual pigment in the juvenile lemon shark (*Negaprion brevirostris*). *Vision Res.*, **30**, 1949–1953.

Collin, S. P. (1999) Behavioural ecology and retinal cell topography. In: *Adaptive Mechanisms in the Ecology of Vision*, Archer, S. N., Djamgoz, M. B. A., Loew, E. R., Partridge, J. C. and Vallerga, S. (Eds.), Dordrecht, The Netherlands.

Collin, S. P. and Pettigrew, J. D. (1988a) Retinal topography in reef teleosts. II. Some species with prominent horizontal streaks and high density areae. *Brain Behav. Evol.*, **31**, 283–295.

Collin, S. P. and Pettigrew, J. D. (1988b) Retinal topography in reef teleosts. I. Some species with well-developed *areae* but poorly-developed streaks. *Brain Behav. Evol.*, **31**, 269–282.

Curcio, C. A., Packer, O. and Kalina, R. E. (1987) A whole mount method for sequential analysis of photoreceptor and ganglion cell topography in a single retina. *Vision Res.*, **27**, 9–15.

Dahmen, H. (1991) Eye specialization in waterstriders: An adaptation to life in a flat world. *J. Comp. Physiol. A*, **169**, 623–632.

Dawson, W. W., Hawthorne, M. N., Parmer, R., Hope, G. M. and Hueter, R. (1989) Very large neurons of the inner retina of humans and other mammals. *Retina*, **9**, 69–74.

Dodd, C. K. Jr. (1988) Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus, 1758). *U.S. Fish. Wildl. Serv., Biol. Report*, **88–14**, 1–110.

Dutton, P. H. (1995) Molecular evolution of sea turtles with special reference to the leatherback, *Dermochelys coriacea. Doctoral Dissertation*, Texas A and M University, College Station, Texas, 137 pp.

Eckert, S. A., Eckert, K. L., Ponganis, P. and Kooyman, G. L. (1989) Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). *Can. J. Zool.*, **76**, 2834–2840.

Eisenberg, J. F. and Frazier, J. (1983) A leatherback turtle *Dermochelys coriacea* feeding in the wild. *J. Herpetol.*, **17**, 81–82.

Evans, B. I. and Fernald, R. D. (1990) Metamorphosis and fish vision. *J. Neurobiology*, **21**, 1037–1052.

Goldsmith, T. H. (1973) Photoreception and vision. In: *Comparative Animal Physiology*. Vol. 2. Prosser, C. L. (Ed.), W. B. Saunders Co., Philadelphia.

Granda, A. M. and Fulbrook, J. E. (1989) Classification of turtle retinal ganglion cells. *J. Neurophysiology*, **62**, 723–737.

Grant, G. S. and Ferrell, D. (1993) Leatherback turtle, *Dermochelys coriacea* (Reptilia: Dermochelidae): notes on near-shore feeding behavior and association with cobia. *Brimleyana*, **19**, 77–81.

Hawryshyn, C. W., Arnold, M. G., Chaisson, D. J. and Martin, P. C. (1989) The ontogeny of ultraviolet photosensitivity in rainbow trout (*Salmo gairdneri*). *Visual Neuroscience*, **2**, 247–254.

Hirayama, R. (1994) Phylogenetic systematics of chelonoid sea turtles. *Island Arc*, **3**, 240–284.

Hueter, R. E. (1988) The organization of spatial vision in the juvenile lemon shark (*Negaprion brevirostris*): Retinotectal projection, retinal topography, and implications for the visual ecology of sharks. *Doctoral Dissertation*, University of Florida, Gainesville, Florida, 130 pp.

Hueter, R. E. (1991) Adaptations for spatial vision in sharks. *J. Exp. Zool. Supplement*, **5**, 130–141.

Hughes, A. (1977) The topography of vision in mammals of contrasting lifestyle: comparative optics and retinal organization. In: *Handbook of Sensory Physiology* VII/5: *The Visual System of Vertebrates*. Crescitelli, F. (Ed.), Springer-Verlag, Berlin.

Kahmann, H. (1936) Über das foveale Seher der Wirbeltiere. II. Über die Fovea centralis und die Fovea lateralis bei einigen Wirbeltieren. *Arch. Ophthal.*, **135**, 265–276.

Land, M. F. and Layne, J. (1995a) The visual control of behaviour in fiddler crabs: I. Resolution, thresholds, and the role of the horizon. *J. Comp. Physiol. A*, **177**, 81–90.

Land, M. F. and Layne, J. (1995b) The visual control of behaviour in fiddler crabs: II. Tracking control systems in courtship and defense. *J. Comp. Physiol. A*, **177**, 91–103.

Mass, A. M. and Supin, A. Y. (1986) Topographic distribution of sizes and density of ganglion cells in the retina of a porpoise, *Phocoena phocoena*. *Aquatic Mammals*, **12**, 95–102.

Mortimer, J. (1982) Factors influencing beach selection by nesting sea turtles. In: *Biology and Conservation of Sea Turtles*. Bjorndal, K. A. (Ed.), Smithsonian Institution Press, Washington.

Musick, J. A. and Limpus, C. J. (1996) Habitat utilization and migration in juvenile sea turtles. In: *The Biology of Sea Turtles*. Lutz, P. L. and Musick, J. A. (Eds.), CRC Press, Boca Raton.

Ogden, J. C., Robinson, L., Whitlock, K., Daganhardt, J. and Cebula, R. (1983) Diel foraging patterns in juvenile green turtles (*Chelonia mydas L.*) in St. Croix United States Virgin Islands. *J. Exp. Mar. Biol. Ecol.*, **66**, 199–205.

Pennycuick, C. J. (1960) The physical basis of astro-navigation in birds: theoretical considerations. *J. Exp. Biol.*, **37**, 573–593.

Peters, J. A. (1964) *Dictionary of Herpetology*. Hafner Publishing, New York, pp. 1–392.

Peterson, E. H. and Ulinski, P. S. (1979) Quantitative studies of retinal ganglion cells in a turtle, *Pseudemys scripta elegans*. *J. Comp. Neur.*, **186**, 17–42.

Pettigrew, J. D., Dreher, B., Hopkins, C. S., McCall, M. J. and Brown, M. (1988) Peak density and distribution of ganglion cells in the retinae of microchiropteran bats: Implications for visual acuity. *Brain Behav. Evol.*, **32**, 39–56.

Pritchard, P. C. H. (1996) Evolution, phylogeny and current status. In: *The Biology of Sea Turtles*. Lutz, P. L. and Musick, J. A. (Eds.), CRC Press, Boca Raton.

Pumphrey, R. J. (1948) The sense organs of birds. *Ibis*, **90**, 171–199.

Pumphrey, R. J. (1961) Sense organs: Vision. In: *Biology and Comparative Physiology of Birds*. Vol. 2. Marshall, A. J. (Ed.), Academic Press, New York.

Salmon, M., Wyneken, J., Fritz, E. and Lucas, M. (1992) Seafinding by hatchling sea turtles: role of brightness, silhouette and beach slope as orientation cues. *Behaviour*, **122**, 56–72.

Stone, J. (1981) *The Wholemount Handbook*. Maitland Publications Pty. Ltd., Sydney. pp. 1–128.

Timney, B. and Keil, K. (1992) Visual acuity in the horse. *Vision Research*, **32**, 2289–2293.

Van Neirop, M. M. and Den Hartog, J. C. (1984) A study on the gut contents of five juvenile loggerhead turtles, *Caretta caretta* (Linnaeus) (Reptilia, Cheloniidae), from the south-eastern part of the North Atlantic Ocean, with emphasis upon coelenterate identification. *Zool. Meded. Leiden*, **59**, 35–54

Waldvogel, J. A. (1990) The bird's eye view. *American Scientist*, **78**, 342–353.

Walls, G. L. (1942) The vertebrate eye and its adaptive radiation. *Bull. No. 19. Cranbrook Institute of Science*, Bloomfield Hills, Michigan, pp. 1–785.

Witherington, B. E. (1992) Sea-finding behavior and the use of photic orientation cues by hatchling sea turtles. *Ph.D. Dissertation*, University of Florida, Gainesville. UMI Dissertation Information Service, Ann Arbor, Michigan.

Wood, P., Partridge, J. C. and DeGrip, W. J. (1992) Rod visual pigment changes in the elver of the eel *Anguilla anguilla L.*, measured by microspectrophotometry. *J. Fish Biology.*, **41**, 601–611.

Wong, R. O. L., Wye-Dvork, J. and Henry, G. H. (1986) Morphology and distribution of neurons in the retinal ganglion cell layer of the adult tammar wallaby, *Macropus eugenii*. *J. Comp. Neurobiology*, **253**, 1–12.

Wyneken, J. and Salmon, M. (1992) Frenzy and post frenzy swimming activity in loggerhead, leatherback, and green sea turtles. *Copeia*, **1992**, 478–484.

Zar, J. H. (1984) *Biostatistical Analysis*. Englewood Cliffs: Prentice Hall, New Jersey. pp. 1–718.

Zeil, J., Nalbach, G. and Halbach, H. (1989) Spatial vision in a flat world: optical and neural adaptations in arthropods. In: *Neurobiology of Sensory Systems*. Singh, R. N. and Strausfeld, N. J. (Eds.), Plenum Press, New York.

Zhang, D. and Eldred, W. D. (1994) Anatomical characterization of retinal ganglion cells that project to the nucleus of the basal optic root in the turtle (*Pseudemys scripta elegans*). *Neuroscience*, **61**, 707–718.