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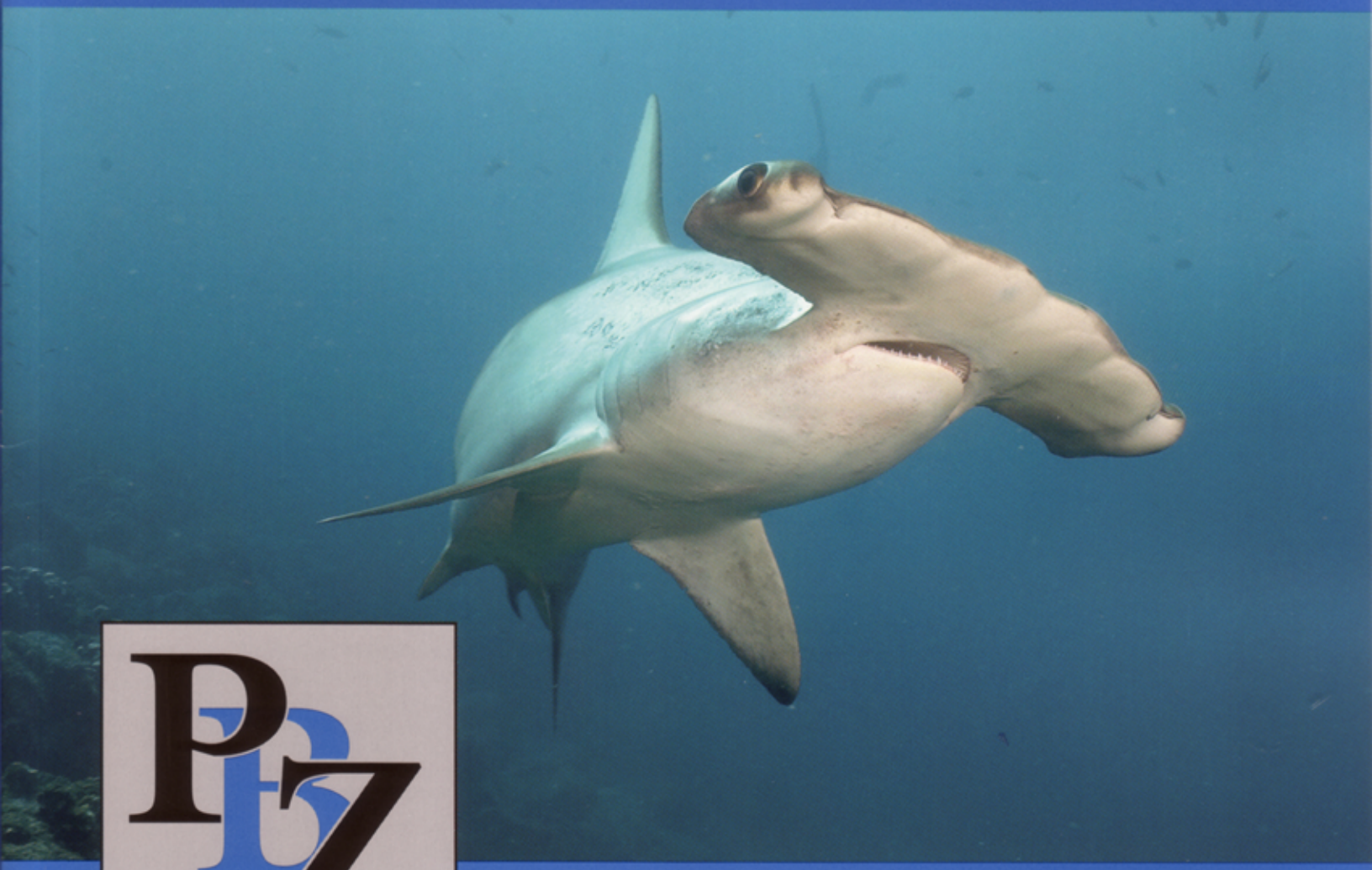

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Temporal Resolution and Spectral Sensitivity of the Visual System of Three Coastal Shark Species from Different Light Environments

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ABSTRACT

Visual temporal resolution and scotopic spectral sensitivity of three coastal shark species (bonnethead *Sphyrna tiburo*, scalloped hammerhead *Sphyrna lewini*, and blacknose shark *Carcharhinus acronotus*) were investigated by electroretinogram. Temporal resolution was quantified under photopic and scotopic conditions using response waveform dynamics and maximum critical flicker-fusion frequency (CFF). Photopic CFF_{max} was significantly higher than scotopic CFF_{max} in all species. The bonnethead had the shortest photoreceptor response latency time (23.5 ms) and the highest CFF_{max} (31 Hz), suggesting that its eyes are adapted for a bright photic environment. In contrast, the blacknose had the longest response latency time (34.8 ms) and lowest CFF_{max} (16 Hz), indicating its eyes are adapted for a dimmer environment or nocturnal lifestyle. Scotopic spectral sensitivity revealed maximum peaks (480 nm) in the bonnethead and blacknose sharks that correlated with environmental spectra measured during twilight, which is a biologically relevant period of heightened predation.

Introduction

The eyes of sharks rival those of higher vertebrates in structural and functional complexity and include a wide variety of functional adaptations (reviewed in Gruber 1977). During their 400-million-year evolutionary history, sharks have radiated into nearly all oceanic and some freshwater habitats, thereby experiencing and adapting to variable ambient light conditions (McFarland 1990). Little is known about both shark eye adaptation to environmental conditions and how factors such as spectral sensitivity and temporal resolution correlate to their habitat and ecology.

Several hypotheses suggest links between an organism's visual sensitivity and its habitat. Clarke (1936) predicted that the spectral sensitivity of fishes found in deep oceanic water would match the narrow blue range of wavelengths that penetrate this habitat, while the sensitivities of fishes found in spectrally diverse shallow waters would be adapted to match wavelengths of their particular microhabitat. Expanding on Clarke's sensitivity hypothesis, the twilight hypothesis (Lythgoe 1968; Munz and McFarland 1977, 1973; McFarland 1990) predicts the visual sensitivity of fishes will match environmental spectra during dusk and dawn, a biologically relevant period of heightened predation.

Autrum (1958) determined that response dynamics of insect retinas matched their habitat and lifestyles, demonstrating that eyes of fast-moving species possess better temporal resolution than eyes of slower-moving nocturnal species. A similar ecological correlation exists among teleost fishes from different depths, where higher temporal resolution is observed in surface-dwelling fishes associated with brighter light levels, and lower temporal resolution is found in mid- and deepwater fishes (Gramoni and Ali 1970). Subsequent studies on a variety of animals support these hypotheses, yet comparative studies on the visual adaptations of sharks are lacking (reviewed in Hueter 1991; Warrant 1999). Therefore, an investigation of correlations between shark spectral sensitivity and temporal resolution with that of habitat is warranted.

Temporal resolution and spectral sensitivity were determined for three species of small coastal shark. The blacknose shark (*Carcharhinus acronotus*), whose diet consists mainly of fish (Cortés 1999), and the bonnethead (*Sphyrna tiburo*), which feeds primarily on crustaceans (Bethea et al. 2007), were collected from the same near-shore environment south of Tampa Bay, Florida. These species are commonly found in seagrass habitats, areas of sandy and hard bottom, and reef areas (Compagno 1984). Juvenile scalloped hammerheads (*Sphryna lewini*), which feed predominately on benthic shrimp and teleosts (Bush 2003), were collected from a different environment within Kaneohe Bay, Oahu, Hawaii. The bay is characterized by a soft bottom with suspended sediments that reduce water clarity (Lowe and Goodman-Lowe 1996).

The objectives of this study were to determine whether the spectral sensitivity and temporal resolution of three species of coastal sharks were correlated with aspects of their habitat and ecology. Spectral sensitivity was determined under scotopic (dim light) conditions in order to test predictions about the

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sensitivity and twilight hypotheses. Temporal resolution was quantified under scotopic and photopic conditions in order to elucidate potential correlations with habitats.

Material and Methods

Specimen Collection

Juvenile scalloped hammerheads were caught by hand-line fishing in Kaneohe Bay, Oahu, Hawaii. Captured sharks were immediately transported to holding tanks at the Hawaii Institute of Marine Biology at Coconut Island, Hawaii. Bonnetheads were caught with gill nets on a shallow seagrass flat at Pinellas Point within Tampa Bay, St. Petersburg, Florida. Blacknose sharks were captured with gill nets off New Pass, Sarasota, Florida, USA. Immediately after capture, the bonnetheads and blacknose sharks were transported to holding tanks at Mote Marine Laboratory, Sarasota, Florida. These experiments were conducted at the University of Hawaii at Manoa and Mote Marine Laboratory in accordance with the Institutional Animal Care and Use Committee of each institution (UHM 01-042-05; MML 07-03-SK1).

Experimental Setup

The temporal resolution and spectral sensitivity of the photoreceptors were electrophysiologically determined in a minimum of 6 dark-adapted individuals of each species using an electroretinogram (ERG) technique. Experimental animals were anesthetized with tricaine methanesulphonate (MS-222; 1 : 15,000 wt : vol). After respiration ceased (2–4 min) animals were quickly transferred to an acrylic experimental tank (89 cm × 43 cm × 21 cm) and secured with Velcro straps to a submerged plastic stage. Animals were immediately fitted with an oral ventilation tube which delivered a recirculating maintenance dose (1 : 20,000 wt : vol) of MS-222 over the gills, and flow was confirmed with a dye test. The water was aerated throughout the trial, and water temperature was maintained between 24° and 25°C.

ERGs were recorded with 100-μm-tip glass electrodes (Warner Instruments, Hamden, CT) filled with 2 M NaCl in 5% agar. The recording electrode was placed within the vitreous of the right eye, and the reference electrode was placed on the skin. The signals from the electrodes were differentially amplified (1,000–10,000 times) and filtered (low pass, 1 kHz; high pass, 0.1 Hz) with a differential amplifier (DP-304, Warner Instruments, Hamden, CT). The data were acquired and digitized with a Power Lab 16/30 data acquisition system model ML 880 (AD Instruments, Colorado Springs, CO) and stored using Chart software (AD Instruments). Extraneous light in the room was eliminated during the experiment by use of black theater cloth. The animals' eyes were allowed to adapt to darkness for a minimum of 45 min. All necessary adjustments in the dark were made under dim red light.

Temporal Resolution

Temporal resolution, a measure of an organism's ability to track moving images, is dependent on the speed at which the organism can process temporally varying visual stimuli. The temporal resolution of an animal can be determined by measuring the maximum critical flicker-fusion frequency (CFF), which is the highest frequency at any light intensity at which the eye can produce electrical responses that remain in phase with a flickering light stimulus. Flickering light that exceeds the CFF is viewed by the animal as a steady glow. Temporal resolution of the eye was quantified using two methods: (1) flicker-fusion frequency and (2) response waveform dynamics. ERG measurements of flicker-fusion frequency are influenced by several factors, including background and stimulus intensity, adaptational state, angle of light presentation, and temperature (Frank 2003). Therefore, all subjects were tested in fully dark-adapted states and presented with standardized irradiances that emanated from the same angle and bathed the entire eye in light. Flicker-fusion experiments involved presenting the dark-adapted eye with a 2-s train of square pulses of white light (50 : 50 light : dark ratio) from a computer-controlled LED mounted within a submersible acrylic light guide. The irradiance of the light was controlled by a neutral density filter (six settings). The highest frequency at which the eye could produce an ERG that remained in phase with the stimulus light of a set irradiance over a 0.5-s interval was defined as the CFF. However, CFF is dependent on the irradiance of the stimulus light (Bröcker 1935; Crozier and Wolf 1939; Crozier et al. 1939) such that as irradiance increases, there is an increase in CFF. A less variable characteristic to use for comparative studies is the maximum CFF (CFF_{max}), defined as maximum flicker rate that the eye is capable of following at any irradiance. We ensured that we had achieved the CFF_{max} by demonstrating that at least two irradiance increases produced no further increases in CFF. To determine whether light adaptation affected CFF_{max} in the sharks, the entire procedure was repeated under ambient room light. Scotopic and photopic values among each individual species were compared with paired *t*-tests. The CFF_{max} values of all species in the scotopic treatment were compared using one-way ANOVAs (Systat Software, San Jose, CA) with pairwise multiple comparisons by Tukey post hoc tests, and the procedure was repeated for the photopic treatment.

Response latency, defined as the time from the onset of the light stimulus to the initial response of the photoreceptors (a-wave), was determined from the waveform dynamics of the ERG at 50% of the maximum response (V_{max}). The $V/\log I$ curves were fitted with the Zettler modification of the Naka-Rushton equation to ensure the proper calculation of V_{max} and subsequent use of 50% V_{max} (Naka and Rushton 1966*a*, 1966*b*; Zettler 1969):

$$\frac{V}{V_{max}} = \frac{I^m}{I^m + K^m},$$

where V = response amplitude at irradiance I, I = stimulus

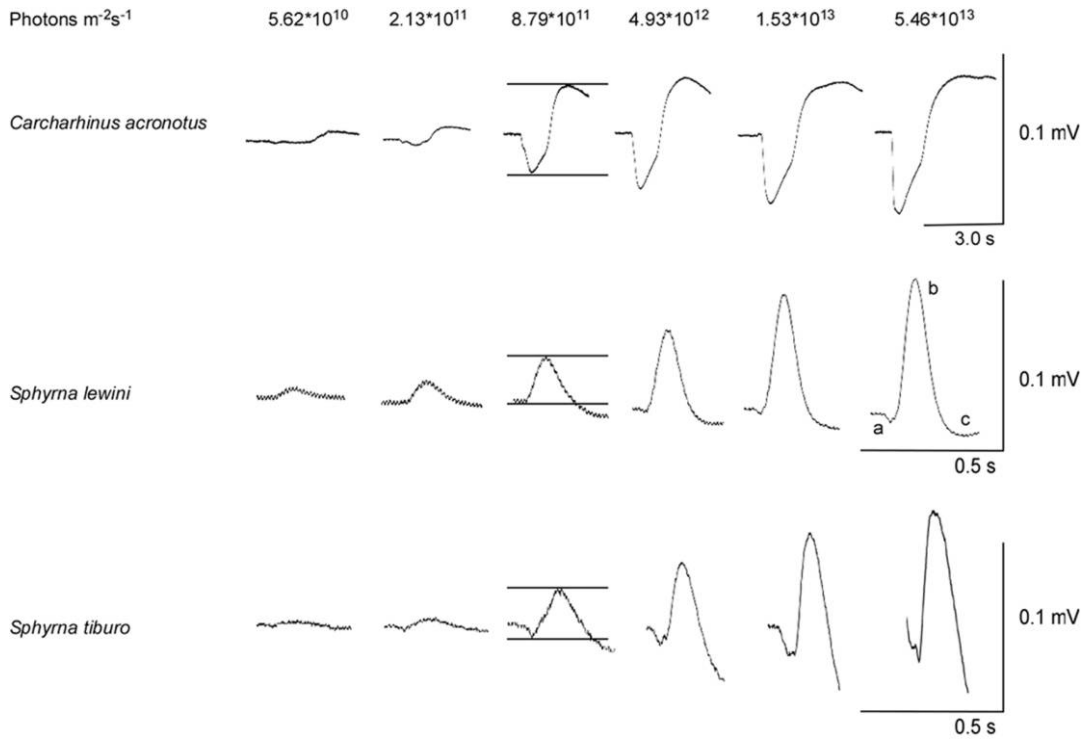

Figure 1. Selected electroretinogram recordings under scotopic conditions. Letters indicate components of the waveform. The eye was stimulated with 100 ms of light at 500-nm wavelength, with successive irradiance increases. The b-waves for each species were positive and increased in magnitude with increases in irradiance. Horizontal lines indicate the amplitude of the b-wave.

irradiance; m = slope of the linear portion of the $V/\log I$ curve, V_{max} = maximum response amplitude, and K = stimulus irradiance eliciting half the maximum response (V_{max}). Although an experimental V_{max} was not attained in some preparations, V_{max} was calculated with the Naka-Rushton equation, and if the highest response recorded in the eye reached 90% of the calculated V_{max}, data from these experiments were included in the analyses.

Spectral Sensitivity

ERGs from dark-adapted eyes of each species were recorded in response to 100-ms light stimuli of various irradiances and wavelengths. The stimulus light was provided by a FLI-150 fiber optic illuminator (Specialty Optical Systems, Dallas, TX) fitted with one of nine bandpass filters (center wavelengths of 400, 430, 450, 480, 500, 530, 560, 589, and 620 nm, with full width at half maximum =10 nm; Esco Products, Oak Ridge, NJ). Irradiance was controlled with a neutral-density filter (six settings), and duration was controlled with a shutter under computer control. Light was delivered to the submerged right eye via a bifurcated light guide composed of randomized fibers (Welch-Allyn, Skaneateles, NY). Irradiance at each test wavelength was measured with a UDT Model S370 optometer (UDT Instruments, San Diego, CA) using a calibrated radiometric probe. Six neutral density filter settings were tested for each of the nine wavelengths. The response to a test flash was monitored throughout the trial to confirm continual dark adaptation of the eye.

The ERG waveform is composed of three primary components that include a-, b-, and c-waves (Fig. 1). The ERG b-wave amplitude (μV), defined as the difference between the trough of the a-wave and the peak of the b-wave, was measured and utilized for all spectral sensitivity calculations. Voltage versus log irradiance ($V/\log I$) curves were generated from the data for each animal. The irradiance required to generate a criterion response from the linear part of the curve (the lowest point at which all wavelengths plotted were linear) was determined for all wavelengths (Fig. 2). This was typically 40 μV in the scalloped hammerhead and blacknose and 80 μV in the bonnethead. The reciprocal of this irradiance was plotted versus wavelength to generate a spectral sensitivity curve (Fig. 3). Data for each animal were normalized and then combined within a species to generate mean spectral sensitivity curves for each species.

Results

Temporal Resolution

The photopic maximum CFF was significantly higher within each species than in the scotopic treatment (paired t-tests: blacknose $P = 0.041$; bonnethead; $P = 0.004$; scalloped hammerhead $P = 0.041$). The scotopic maximum CFF for the three species ranged from 16 to 26 Hz (Table 1) and was significantly different (one-way ANOVA, $P = 0.007$). Pairwise multiple

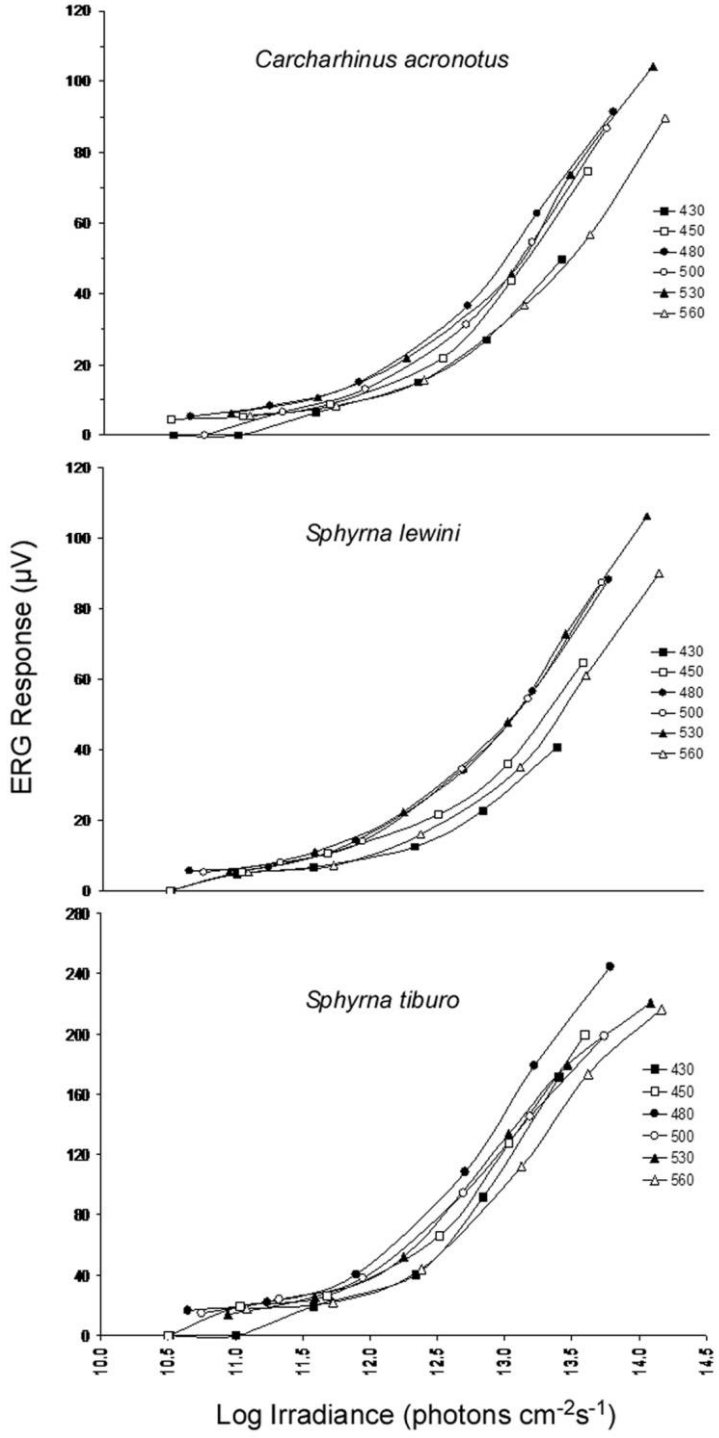

Figure 2. Response versus log irradiance curves for *Carcharhinus acronotus*, *Sphyrna lewini*, and *Sphyrna tiburo* at six different stimulus wavelengths. Data from these $V/\log I$ curves were used to generate spectral sensitivity curves. These curves were fit with the Naka-Rushton equation for calculations of V_{max} that were used to determine response latencies.

comparisons revealed that the CFF_{max} of the blacknose (16 Hz) was significantly lower than that of both scalloped hammerhead (25 Hz; Tukey, $P = 0.017$) and bonnethead (26 Hz; Tukey, $P = 0.012$). The CFFs of the two hammerhead species did not differ (Tukey, $P = 0.984$). The photopic maximum CFF was slightly higher, ranging from 18 to 31 Hz, and again differed significantly among species (one-way ANOVA, $P = 0.007$). The blacknose again had a significantly lower CFF (18 Hz) than both scalloped hammerhead (27 Hz; Tukey, $P = 0.049$) and bonnethead (31 Hz; Tukey, $P = 0.007$). As with the scotopic

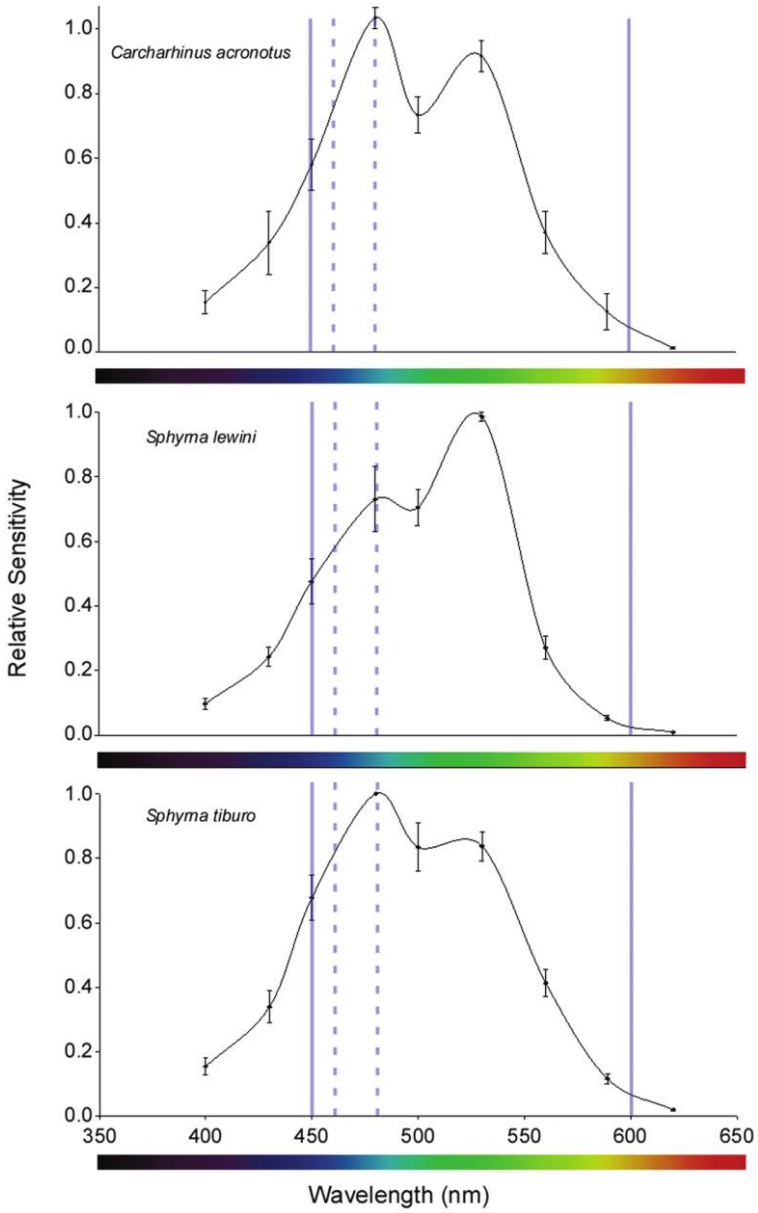

Figure 3. Spectral sensitivity of *Carcharhinus acronotus*, *Sphyrna lewini*, and *Sphyrna tiburo* as measured by electroretinogram under scotopic conditions. Data represent mean values ± SE. Solid vertical lines represent environmental spectra measured by McFarland (1991) during moonlight and starlight at 3-m depth (450–600 nm), and the dashed lines represent the spectra at twilight (460–480 nm).

treatment, the highest CFF was observed in the bonnethead, and it did not differ from the scalloped hammerhead (Tukey, $P = 0.572$).

Response latencies of the 50% V_{max} differed among the three species (one-way ANOVA, $P < 0.001$) and are given in Table 1. The mean response latency of the blacknose (34.8 ms) was significantly longer than that of the bonnethead (23.5 ms; Tukey, $P < 0.001$) and the scalloped hammerhead (26.0 ms; Tukey, $P = 0.001$). The mean response latency of the scalloped hammerhead did not differ from that of the bonnethead (Tukey, $P = 0.310$).

Spectral Sensitivity

The dark-adapted spectral sensitivity curves of the bonnethead and the blacknose showed two peaks, with maximum sensitivity (λ_{max}) at 480 nm and a secondary peak at 530 nm. The spectral sensitivity curve of the scalloped hammerhead also had two peaks, with maximum sensitivity at 530 nm and a secondary peak at 480 nm (Fig. 3).

Discussion

This study demonstrates that the photoreceptors of three coastal shark species have sensitivity peaks that match the nar-

Table 1: Morphological and physiological summary data for the three species of coastal sharks in this study

Species	*Carcharhinus acronotus*	*Sphyrna lewini*	*Sphyrna tiburo*
N	6	8	6
Total length (cm)	104.5 ± 1.0	56.1 ± 1.1	81.6 ± 1.9
Habitat	Temperate-tropical, insular shelves, sand, and reef	Temperate-tropical, shelves to deep, seamount congregations	Subtropical, reef associated, seagrass
Diet	Fish, pinfish, porcupine fish	Fish, cephalopod, shark	Crustaceans, cephalopod, fish
Spectral sensitivity λ_{max} (nm)	480	530	480
Photopic CFF_{max} (Hz)	18.0 ± .85	27.3 ± 3.15	31.0 ± 2.89
Scotopic CFF_{max} (Hz)	16.0 ± 1.0	25.1 ± 2.53	25.6 ± 2.30
Response latency (ms)	34.8 ± 1.10	26.0 ± .28	23.5 ± 1.00

Note. Habitat and diet from Compagno (1984). Temporal resolution as determined by maximum photopic and scotopic critical flicker-fusion frequencies (CFFs). Response latency measured from electroretinogram responses that were 50% of V_{max}. Numbers are mean values ± SE.

row range of environmental spectra during twilight (Fig. 3). The spectral sensitivities of the bonnethead and blacknose sharks (collected from the same environment) shared a maximum spectral sensitivity peak at 480 nm, whereas the scalloped hammerhead (from a different bay) peaked at 530 nm and indicated adaptations to different environmental conditions. Temporal resolutions of sharks measured in this study were similar to those measured in other species (Table 2). However, the temporal resolution of the bonnethead was higher than the blacknose and is probably influenced by habitat.

Temporal resolution is higher in species that experience brighter ambient light conditions as compared with species that experience low light or exhibit nocturnal behaviors (Autrum 1958). In low-light conditions, photoreceptors must compromise temporal resolution in order to maximize the capture of available light (absolute sensitivity). Although little is known about the activity patterns of the blacknose shark, it does inhabit an environment similar to that of the bonnethead in terms of water transparency, it displays a significantly lower CFF_{max}, and it has a significantly longer response latency, all suggesting a crepuscular or nocturnal activity pattern requiring trade-offs between absolute sensitivity and temporal resolution (Frank and Widder 1999). Compared to the bonnethead, the blacknose may inhabit deeper and cooler coastal waters. The influence of temperature on the relatively low temporal resolution cannot be discounted, because a reduction in temperature has been demonstrated to elicit lower temporal resolution in other species (Marshall et al. 2003; Fritsches et al. 2005).

The bonnethead is associated with clear shallow reefs and seagrass beds (Heupel et al. 2004). Having a higher temporal resolution in bright reef and seagrass environments would impart a visual advantage. The bonnethead feeds on small teleosts, crustaceans, and cephalopods (Bethea et al. 2007), and accurate visual tracking of these fast-moving prey is critical to foraging success (Wilga and Motta 2000). In seagrass beds, the bonnethead feeds primarily on blue crabs (*Callinectes sapidus)*, and prey detection in this environment would be enhanced by high temporal resolution as the shark is swimming and continually scanning vegetation (Bethea et al. 2007). Eighteen body postures and movement patterns have been observed in the bonnethead, with nearly half having social relevance (Myrberg and Gruber 1974), which suggests that vision may be important in conspecific communication. In addition, the relatively high CFF and short response latency (23.5 ms) of the bonnethead are both indicative of visual function under bright conditions.

The scalloped hammerhead was found to possess a CFF_{max} (scotopic: 25.1 Hz, photopic: 27.3 Hz) and response latency (26.0 ms) that were essentially the same as those of the bonnethead, suggesting that it has the capacity to visually track faster-moving and elusive prey as well. Juvenile scalloped hammerheads were captured in Kaneohe Bay, which is extremely turbid and shallow (less than 15 m) and which is where the sharks spend the first year of life (Duncan and Holland 2006). There the sharks feed primarily on a single species of alpheid shrimp and two species of burrowing goby, all of which constitute the most abundant benthic fauna within the bay (Bush 2003). The cryptic nature and fast movement of prey items within this habitat probably place a significant demand on visual system performance in scalloped hammerhead juveniles. However, their turbid environment has a reduced ambient irradiance compared to that of the bonnethead, which might contribute to their decreased temporal resolution.

Pupil shape and time to maximum pupil dilation and constriction have consequences on the amount of light striking the retina (Walls 1942). Pupil shape and time to maximum dilation are known for the three species in this study (McComb et al. 2009). The blacknose shark has round pupils that constrict to a nearly perfect pinhole and protect the eye from excess light. However, round pupils are not as effective in shielding light as the slit pupil found in the bonnethead, which may constrict to a nearly closed position (Walls 1942). The pupils of the scalloped hammerhead were nearly round with a slight horizontal elongation. Fast-moving species such as sharks must adapt to changes in light intensity by quickly dilating or contracting their pupils. The bonnethead demonstrated the most rapid dilation (3 min) followed by the scalloped hammerhead (10 min) and finally the blacknose shark (20 min). The relatively rapid dilation time of the bonnethead coupled with the highest CFF_{max} and lowest response latency suggests a visual system adapted for bright conditions. Conversely, the blacknose had a relatively

Table 2: Comparative spectral sensitivity and temporal resolution of several elasmobranch species

Species	Max (nm)	Method	Reference
Spectral sensitivity:			
Scyliorhinus canicula	502	ERG	Gačić et al. 2006
Neotrygon kuhlii	476, 498, 552	MSP	Theiss et al. 2006
Glaucostegus typus	477, 502, 561	MSP	Hart et al.2004
Aptychotrema rostrata	459, 492, 533	MSP	Hart et al. 2004
Rhinobatos lentiginosus	498–499	MSP	Gruber et al. 1990
Negaprion brevirostris	519–522	ERG	Cohen and Gruber 1985
Mustelus manazo	494	ERG	Niwa and Tamura 1975
Triakis scyllia	494–525	ERG	Niwa and Tamura 1975
Orectolobus japonicus	494	ERG	Niwa and Tamura 1975
Luecoraja oscellata	500	ERG	Dowling and Ripps 1971
Dasyatis akajei	494, 525, 584	ERG	Tamura and Niwa 1967
Heterodontus japonicus	494	ERG	Tamura and Niwa 1967
Temporal resolution:			
Negaprion brevirostris	CFF = 37 Hz	ERG	Gruber 1969
Leucoraja erinacea	CFF = 30 Hz	ERG	Green and Siegel 1975

Note. Multiple peaks indicate possession of multiple visual pigments. ERG = electroretinogram, MSP = microspectrophotometry, CFF = critical flicker-fusion frequency.

slow dilation, a low CFF_{max}, and a long response latency, all of which indicate adaptation to lower light or nocturnal habits. The intermediate dilation time and CFF_{max} of the scalloped hammerhead may be a reflection of the reduced water transparency in its habitat.

The finding that the peak scotopic spectral sensitivity of both the bonnethead and the blacknose was at 480 nm is intriguing as they were captured from the same environment yet one that was different from that of the scalloped hammerhead, which had peak sensitivity at 530 nm. To consider whether the spectral sensitivity of the rod pigments enhances scotopic vision, it is necessary to compare their spectral sensitivities to environmental spectra at twilight and night. McFarland (1990) presented recorded and modeled environmental spectra data for midday, twilight, moonlight, and starlight at a 3-m depth. These data were utilized to determine which elasmobranch rod visual pigments would be best served within each environmental condition. Examination of the moonlight and starlight data reveal spectra between 450 and 600 nm that differ from daytime spectra in that they contain more photons at longer wavelengths. Therefore, McFarland (1990) concluded that for an elasmobranch looking upward in the coastal ocean waters at a depth of 3 m, a rod pigment located anywhere between 450 and 600 nm would serve equally well to capture the downwelling light under daylight, moonlight, and starlight conditions. In our study, all three species have their spectral sensitivity peaks within this range (Fig. 3). Additionally, McFarland (1990) determined that the twilight downwelling spectrum peaked between 460 and 480 nm, and the possession of a rod pigment located near 480 nm would be best suited for this time of day. Both the blacknose and bonnethead possess spectral sensitivity peaks at 480 nm that may enhance scotopic vision at twilight. The twilight period is a time of heightened predation, and the enhancement of vision during this time would impart advantages to these predatory sharks (McFarland 1990).

Of the three species used in this study, the specimens of the bonnethead and blacknose were adults and the scalloped hammerheads were juveniles. Scalloped hammerhead adults can exceed 4 m in length and are too large for the experimental setup. Therefore, special consideration needs to be placed on the results from this species. It has been demonstrated that the rod visual pigment of juvenile lemon sharks (*Negaprion brevirostris*) differs from that of the adults (Cohen et al. 1990), and shifts in spectral sensitivity are probably an adaptation to the differing environments experienced by juveniles and adults. Therefore, it is possible that the spectral sensitivity of scalloped hammerheads could shift toward shorter wavelengths (blue) as they mature and move from the turbid greenish bay waters into clear blue oceanic waters.

In addition to gradual ontogenetic changes, it has been demonstrated that other changes to the optical properties of the eye can occur rapidly. Juvenile scalloped hammerheads held in shallow pens in Kaneohe Bay, where they were subjected to elevated levels of sunlight compared to their typical bay-floor habitat, showed an increase in UV-blocking pigments in their corneal tissue (Nelson et al. 2003). This demonstrates a rapid adaptation to irradiance, and it is possible that other age-related factors, yet unexplored, may affect visual sensitivity as well. Although our spectral sensitivity and temporal resolution data support connections between species and their environments, other factors such as retinal topography, feeding dynamics, and body form may also play a role in adapting visual systems to specific environments.

Future studies should include ERG experiments under photopic conditions and integrate chromatic adaptation, which may reveal the presence of several visual pigments. It would be par-

ticularly interesting to examine the spectral sensitivity of juveniles and adults of a single species that occurs in different habitats since changes in habitat have been shown to shift visual pigment complements in one shark species (Cohen 1990). The determination of the spectral sensitivity of other visual predators such as tarpon (*Megalops atlanticus*) and bonefish (*Albula vulpes*) that share the same habitat as the bonnethead would prove interesting. Finally, it would be of value to examine pupil shape, retinal topography, and visual field to determine whether these parameters correlate with environmental spectral irradiance, since eye structure and position within the head (a visual field determinant) dictate the level of irradiance experienced in a given habitat.

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