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ORIGINAL PAPER

A physiological analysis of color vision in batoid elasmobranchs

Christine N. Bedore · Ellis R. Loew · Tamara M. Frank · Robert E. Hueter · D. Michelle McComb · Stephen M. Kajiura

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Abstract The potential for color vision in elasmobranchs has been studied in detail; however, a high degree of variation exists among the group. Evidence for ultraviolet (UV) vision is lacking, despite the presence of UV vision in every other vertebrate class. An integrative physiological approach was used to investigate color and ultraviolet vision in cownose rays and yellow stingrays, two batoids that inhabit different spectral environments. Both species had peaks in UV, short, medium, and long wavelength spectral regions in dark-, light-, and chromatic-adapted electroretinograms. Although no UV cones were found with microspectrophotometric analysis, both rays had multiple cone visual pigments with λ_{max} at 470 and 551 nm in cownose rays (*Rhinoptera bonasus*) and 475, 533, and 562 nm in yellow stingrays (*Urobatis jamaicensis*). The same analysis demonstrated that both species had rod λ_{max} at 500 and 499 nm, respectively. The lens and cornea of cownose rays maximally transmitted wavelengths greater than 350 nm and greater than 376 nm in yellow stingrays. These results support the potential for color vision in these species and future investigations should reveal the extent to which color discrimination is significant in a behavioral context.

Keywords Elasmobranch · Batoid · Color vision · Sensory ecology · Ultraviolet vision

Abbreviations

DW	Disc width
ERG	Electroretinogram
FWHM	Full width at half maximum
LWS	Long wavelength sensitive pigment
MSP	Microspectrophotometry
MWS	Medium wavelength sensitive pigment
SWS	Short wavelength sensitive pigment
$T_{0.5}$	Wavelength at 0.5 normalized transmittance
UV	Ultraviolet
λ_{max}	Wavelength of maximum absorbance

Introduction

Vision in the elasmobranch fishes, the sharks, skates, and rays, has been presumed to be relatively poor and adapted for dim-light (scotopic) conditions as early studies reported all-rod retinas, tapeta lucida, and high sensitivity to light

Experiments comply with the current laws of the country (USA) in which they were performed.

C. N. Bedore (✉) · S. M. Kajiura
Department of Biological Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, FL 33431, USA
e-mail: christine.bedore@duke.edu

Present Address:
C. N. Bedore
Biology Department, Duke University, Box 90338, Durham, NC 27708, USA

E. R. Loew
College of Veterinary Medicine, Cornell University, Ithaca, NY 14853, USA

T. M. Frank
Oceanographic Center, Nova Southeastern University, Dania Beach, FL, USA

R. E. Hueter
Center for Shark Research, Mote Marine Laboratory, Sarasota, FL 34236, USA

D. M. McComb
Ocean Classrooms, Boulder, CO, USA

(Walls 1942; Ripps and Dowling 1991; for review see Lisney et al. 2012). Recent techniques employed to study the visual systems of these fishes have revealed much more diversity in visual capabilities than previously thought. For example, many species, including the lemon shark, *Negaprion brevirostris*, and Atlantic guitarfish, *Rhinobatos lentiginosus*, possess duplex retinas composed of both rods and cones (Gruber et al. 1963, 1991). Although these two species, and most sharks that have been studied, are limited to one class of cone visual pigment, most batoids studied to date possess multiple cone visual pigments, and thus, have the potential for color vision (Hart et al. 2004; Theiss et al. 2007; Van-Eyk et al. 2011). Color vision is achieved by the presence of at least two spectrally distinct classes of photoreceptors and a neural network, either retinal or central, that can compare the photoreceptor outputs and derive a wavelength-specific signal for further analysis (Jacobs 1981).

Ultraviolet (UV) vision, as defined here, is a dimension of color space and is considered adaptive due to the presence of UV wavelengths in the environment. An animal can utilize the UV signals as long as the pre-retinal media allow for transmission of UV wavelengths and there are photoreceptors that are UV sensitive, either by possessing a UV visual pigment or through β-band absorption of UV wavelengths by another visual pigment (Losey et al. 1999; Siebeck and Marshall 2001; Lisney et al. 2012). UV sensitivity in coral reef fishes is thought to enhance the contrast of predators, prey, and conspecifics in UV-rich environments against background illumination (Losey et al. 1999; Siebeck and Marshall 2001; Siebeck 2004; Partridge and Cuthill 2010; Siebeck et al. 2010), although studies supporting these hypotheses are still limited. Thus far, no evidence has been found to support UV vision in any elasmobranch, despite the similarities in ecology of some species to those of teleosts that are known to possess UV cones.

The potential for color vision in elasmobranchs has typically been based on visual pigment identification and absorbance characteristics of visual pigments in individual photoreceptors in situ [i.e., microspectrophotometry (MSP)] and supported by histology (light and electron microscopy) or whole retina physiology [i.e., the electroretinogram (ERG)]. These techniques can provide data to support the potential for color vision, or lack thereof; however, only behavioral testing can confirm that a particular animal actually possesses color vision. MSP characterization is a powerful tool that allows classification of visual pigments based on their distinct spectral absorbance characteristics, and consequently, confirms the presence of multiple visual pigments, the basis for color vision. However, these techniques do not necessarily describe the actual spectral sensitivity of the whole photoreceptor (i.e., the eye) that can be influenced by factors such as pre-retinal filtering, nor do they explain how the output from photoreceptor cells is analyzed. To a point, the ERG allows quantification of photoreceptor contributions to the overall response of the eye, and incorporates contributions of spectral filters and interactions between cells in the retina. However, ERG alone cannot always ascribe peaks in spectral sensitivity to a particular mechanism. Therefore, integration of MSP and ERG permits a better estimation of the physiological basis for color vision that may underlie behavioral functional significance.

Like many other characteristics of the visual system, the potential for color vision in all organisms should be correlated to their ecology. Species that inhabit brightly lit and spectrally rich environments tend to possess more visual pigments than those in dim or spectrally limited environments (Marshall and Vorobyev 2003). Also, many species that inhabit spectrally rich environments, like coral reefs, commonly incorporate bright coloration or patterning onto their body surface to exploit conspecific vision for mate detection and territory displays, while they also deceive predator visual systems and function in camouflage and mimicry (Hazlett 1979; Chiao et al. 2000; Siebeck et al. 2008; Cheney et al. 2009). On the other hand, species that inhabit dim or spectrally limited environments tend to be less colorful and have fewer visual pigments than their colorful counterparts (Marshall and Vorobyev 2003).

The potential for color vision has been investigated in only a handful of the >800 species of elasmobranch fishes and has been supported in only a subset of those (see Lisney et al. 2012 for review). Since elasmobranch fishes are diverse in terms of ecology, the number of visual pigments is highly variable throughout the group, ranging from zero to three cone pigments (Gruber et al. 1991; Ripps and Dowling 1991; Hart et al. 2004, 2011; Theiss et al. 2007). The goals of this study were to assess the potential for color and ultraviolet vision in two batoids that differ in their ecology. The cownose ray, *Rhinoptera bonasus*, is a benthopelagic, estuarine/coastal inhabitant that experiences variable photic conditions as it transitions from schooling at the water surface to foraging in the benthic zone (Smith and Merriner 1987; McEachren and de Carvahlo 2002; Neer and Thompson 2005; Collins et al. 2007a, 2008). The yellow stingray, *Urobatis jamaicensis*, is a strictly benthic ray in bright, spectrally rich reef and seagrass habitats (McEachren and de Carvahlo 2002; Fahy 2004). Yellow stingrays are also elaborately patterned, likely to provide camouflage and potentially as a visual cue for conspecific recognition. Both of these species may rely heavily on visual input for intraspecific communication or to recognize camouflaged conspecifics and predators as has been hypothesized due to their high flicker fusion frequencies (Bedore 2013) and expansive visual fields relative to other batoids, which afford 360° fields of view in the vertical (for cownose rays) and horizontal (yellow stingrays) planes (McComb and Kajiura 2008). In addition, both species inhabit UV-rich waters, either while

swimming at the water surface or foraging in shallow water (cownose ray), or by living in reef and seagrass-associated habitats in shallow, clear water (yellow stingray). The specific objectives of this study were to (1) electrophysiologically quantify the spectral sensitivities of cownose rays and yellow stingrays under different photic conditions (dark-adapted, white light-adapted, and chromatically adapted), (2) determine the spectral classes of photoreceptors present in the retinas using MSP, (3) quantify the transmission of light through the ocular elements, and (4) quantify the spectral reflectances of the bodies of both species.

Materials and methods

Animals

Juvenile and adult cownose rays, *Rhinoptera bonasus* [$n = 8$; disc width (DW): 39–77 cm], and adult yellow stingrays, *Urobatis jamaicensis* ($n = 7$; DW: 18–23 cm), were collected with gillnet and hand net, respectively, from South Florida waters. Rays were housed in indoor tanks at the Florida Atlantic University Marine Science Facility at Gumbo Limbo Environmental Complex in Boca Raton, FL or at the Marine Experimental Research Facility at Mote Marine Laboratory in Sarasota, FL. Rays were held under a 12 h:12 h light:dark cycle under fluorescent lighting until they were used for experiments.

Electrophysiology

Experimental apparatus

An electroretinogram (ERG) was used to quantify the in vivo extracellular spectral sensitivities of *R. bonasus* ($n = 6$) and *U. jamaicensis* ($n = 5$) photoreceptors. Experiments were conducted within an acrylic experimental tank (89 × 43 × 21 cm) with electrically grounded seawater. Summed photoreceptor responses to monochromatic light flashes that bathed the whole eye in light were recorded with a Ag–AgCl 100 μm tip glass microelectrode filled with potassium chloride (E45P-M15NH, Warner Instruments, Hamden, CT, USA) that was positioned within the vitreal component of one eye just below the surface of the water. An identical reference electrode was positioned nearby on the skin. The output of the two electrodes was differentially amplified (DP-304, Warner Instruments) at 1,000–10,000×, filtered (0.1–100 Hz bandpass, 50/60 Hz notch filter) (DP-304, Warner Instruments and HumBug, Quest Scientific, North Vancouver, BC, Canada), digitized at 1 kHz (Power Lab® 16/30 model ML 880, AD Instruments, Colorado Springs, CO, USA) and recorded using LabChart® 7 Software (v7.2.5 AD Instruments).

Following McComb et al. (2010), white light from a fiber optic light source was passed through interference bandpass filters (full width at half maximum [FWHM] = 10 nm) from 350 to 620 nm (19 filters with individual peak transmission at 350, 360, 370, 380, 390, 400, 410, 430, 450, 470, 490, 500, 510, 520, 540, 550, 560, 590, and 620 nm) with irradiance controlled by neutral density filters. Monochromatic light was passed through one branch of a bifurcated liquid light guide and was presented to the eye through the common end, which uniformly illuminated the entire corneal surface. For chromatic adaptation, the adapting light from a halogen lamp (LS-1, Ocean Optics, Inc., Dunedin, FL, USA), fitted with a 550-nm long-pass filter, was passed through the second branch of the light guide to superimpose the stimulus on the adapting light. The common end of the light guide was fitted with a UV-transparent glass diffusor (Edmund Optics, Barrington, NJ, USA) to mix the output of the two branches. The irradiances of monochromatic test stimuli were calibrated with an optometer (United Detector Technology Model S370, Gamma Scientific, San Diego, CA, USA) fitted with a calibrated radiometric probe.

Experimental protocol

An individual *R. bonasus* or *U. jamaicensis* was dark-adapted for 1 h and then was anesthetized with tricaine methanesulfonate (1:10,000 wt:vol) until ventilation ceased. Set-up and adjustments to the apparatus in the dark were made under dim red light to limit light adaptation of the eye. The ray was then transferred to the experimental tank, secured to a platform with Velcro straps, and artificially ventilated with oxygenated seawater (dissolved oxygen >6 mg L^{-1} at 0.5–2.0 L min^{-1}) through a tube inserted in the mouth. Rays were immobilized with an intramuscular (IM) injection of the neuromuscular blocking agent pancuronium bromide (0.3–0.4 mg kg^{-1}) and provided with a maintenance dose of tricaine (1:12,000–1:15,000 wt:vol) throughout the experiment. After electrode placement, rays were dark-adapted for an additional 1–2 h until the amplitudes of the responses to control flashes were consistently within 10 % of one another for five consecutive flashes. One-second flashes of monochromatic light were presented to the eye with a computer-controlled shutter and the irradiance of the flash was adjusted until a criterion response (20–50 μV above the level of background noise) was met for each wavelength. Control flashes were presented between every wavelength setting to ensure that dark adaptation was maintained throughout the experiment. Once responses were recorded for all 19 wavelengths, rays were white light-adapted for 20–30 min using a white LED within the light-tight compartment and the protocol was repeated. The irradiance of the white light was adjusted

such that the irradiance required to elicit the criterion response at the peak sensitivity was ≥1 log unit brighter than in the dark-adapted state. The protocol was also conducted after rays were adapted to the 550-nm light, the irradiance of which was adjusted so the stimulus required to elicit the criterion response was ≥1 log units brighter than light-adapted peak response, but was dim enough so that criterion responses could still be obtained at UV wavelengths.

Analysis

Spectral sensitivity curves for dark, light, and chromatic adaptation experiments were generated by plotting the normalized inverse of the irradiance (photons cm^{-2} s^{-1}) that produced the criterion response against wavelength for all individuals.

To determine if the sensitivity shifts in the spectral sensitivity curves under different light conditions were significant, differences in spectral sensitivities among dark-, light-, and chromatic-adapted eyes were quantified by comparing the ratios of responses from spectral sensitivity curves. The mean of the normalized inverse of the irradiance required to produce the criterion response in four regions of the spectral sensitivity curves was calculated: ultraviolet (UV; 360–390 nm), short wavelength (blue; 410–470 nm), medium wavelength (green; 490–540 nm), and long wavelength (red; 550–590 nm) (cf. Frank et al. 2009). The ratios of the mean normalized responses for each region were compared among dark-, light-, and chromatic-adapted eyes with a one-way ANOVA. All data met normality and homogeneity assumptions for ANOVA.

Microspectrophotometry

The absorbance spectra of visual pigments in individual photoreceptors were obtained using a microspectrophotometer (MSP). Two individuals of each species were transported from Boca Raton, FL to Ithaca, NY and were held in light-tight, aerated tanks with artificial seawater for 2–4 days. Rays were sacrificed with an overdose of MS-222 (>1:5,000 wt:vol), followed by severing of the spinal cord. Three eyes from both species were enucleated, hemisected, and stored in artificial seawater in light-tight containers and were used within 24 h (all but one were used within 8 h). The retina was dissected away from the eye under infrared light and stored in Sorensen's buffer solution (pH = 7.2) with 6 % sucrose. A small wedge of the retina was macerated with a razor blade to free photoreceptors from the retinal tissue and was sealed between two glass coverslips. Individual photoreceptors were selected under infrared light and measured using a computer-controlled, single beam MSP as previously described (Loew 1994). Briefly, a baseline scan through a photoreceptor-free region of the retina was performed at 1 nm increments from 750 to 350 nm and back. An outer segment of a single photoreceptor, which contained the visual pigment, was then moved over the measuring beam and the transmission measured. These data were converted to absorbance, and absorbance spectra that satisfied selection criteria were fitted to a visual pigment template to determine λ_{max} (for details see Loew 1994; Losey et al. 2003).

Ocular media transmission

One eye each from both species was obtained from rays used in the MSP analysis. The eye was enucleated and hemisected, and the ocular elements (cornea and lens) were placed on a 200-μm light measurement probe with the cornea facing down. A 12-V, 100-W quartz halogen broad-spectrum lamp was positioned above the eye to allow even transmission of light through the ocular elements. Transmission from 350 to 750 nm was measured with an Ocean Optics S2000 spectrometer (Ocean Optics, Dunedin, FL, USA) and analyzed with OOIBase 32 software (Ocean Optics). Transmittance through the ocular media was calculated as a percent transmission of a standard transmission spectrum that was obtained by recording along the measurement path with the sample removed. Transmittance data were then normalized to 100 % transmission and fitted with the resultant transmission curve using TableCurve software (Systat Software, Inc., San Jose, CA, USA). The $T_{0.5}$, the wavelength at which the transmission has decreased to 50 % of the maximum, was used to determine the short-wavelength absorbing properties of the eye (following Losey et al. 2003). The $T_{0.5}$ and slope of both curves were categorized according to Douglas and McGuigan (1989), Siebeck and Marshall (2001), and Losey et al. (2003) to determine a vision likelihood category (Losey et al. 2003) that describes their likelihood for utilizing UV vision.

Body color reflectance

Spectral reflectance measurements were recorded from the head, gills, pectoral fin, and pelvic fins on the dorsal body surface on specimens of both species that were obtained from incidental mortalities ($n = 4$ each). Skin pigmentation in elasmobranchs can be altered by anesthesia, stress, substrate color, and irradiance of the ambient light environment (unpublished data); therefore, reflectance was difficult to measure accurately in freshly sacrificed rays. The reflectance spectra measured from yellow stingrays were compared to that of a live, freshly collected individual and the curves differed only in the relative intensity of the peaks.

Reflectance (percent and intensity counts) was measured with a 400-μm UV–VIS reflectance probe (Ocean Optics)

connected to an Ocean Optics S2000 spectrometer and analyzed with SpectraSuite software (Ocean Optics). Reflection was recorded at wavelengths from 350 to 750 nm and each location was measured twice and averaged. The normalized mean reflectance from all individuals was plotted against wavelength to produce reflectance curves. The mottled appearance of the yellow stingray prevented measurements from skin that only contained a single type of pigment.

Results

Electrophysiology

Multiple spectral sensitivity peaks were present under dark-, light-, and chromatic-adapted ERGs in both species (Fig. 1). Dark-adapted cownose rays were maximally sensitive to 500 nm and yellow stingrays were maximally sensitive to 490 nm. Under light adaptation, cownose ray peak sensitivity occurred at 450 nm, while the peak sensitivity for yellow stingrays remained at 490 nm. However, under red chromatic adaptation, yellow stingray peak sensitivity was 550 nm, while cownose ray peak sensitivity persisted at 450 nm. Apparent shifts in the spectral sensitivity curves may have been a result of low resolution in the ERG or from differences in the relative contribution of multiple pigments to a single peak in the curve. The magnitude of the spectral sensitivity peaks under light and chromatic adaptation was not significantly increased relative to dark adaptation in comparison to the mean response ratios in the visible portion of the spectrum (ANOVA; UV: blue: $F_{2,16} = 1.78$, $p = 0.21$; UV: green: $F_{2,15} = 1.58$, $p = 0.24$; UV: red: $F_{2,16} = 2.36$, $p = 0.13$) for cownose rays. The magnitude of the UV peak relative to the green peak was significantly greater under chromatic and light adaptation than that relative to dark in yellow stingrays (ANOVA; $F_{2,11} = 5.17$, $p = 0.03$), but the contribution of

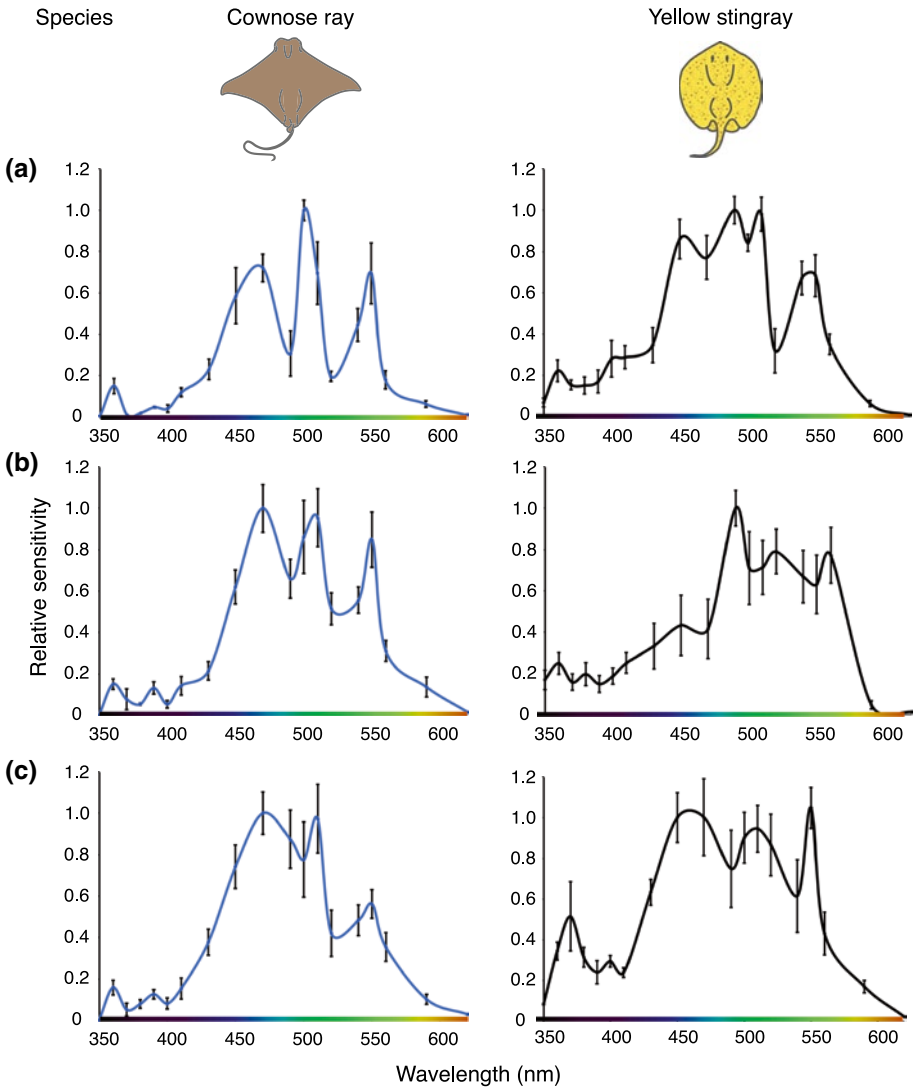

Fig. 1 Spectral sensitivity curves from **a** scotopic-, **b** photopic-, and **c** chromatic-adapted ERG. Cownose rays and yellow stingrays demonstrated multiple peaks in each curve in the regions at 360–390, 450–470, 490–520, and 550–560 nm. The retinal product band is evident as a dip in the curve in the UV portion of the spectrum (near 370 nm) and is indicative of rhodopsin contribution to all spectral sensitivity curves (as seen in Muntz et al. 1973). Light adaptation decreased the contribution of the rod (500 nm) relative to the blue (470 nm) and green (550 nm) peaks, and chromatic adaptation decreased the contribution of the long wavelength cone (550 nm) in the cownose ray. The 450-nm peak was decreased under light adaptation in the yellow stingray, while the 510-nm peak was decreased in magnitude and shifted to 520 nm, which suggests single pigments may have contributed to multiple peaks

the UV response to the ERG did not differ relative to blue (ANOVA; $F_{2,11} = 1.84$, $p = 0.21$) or red peaks (ANOVA; $F_{2,11} = 2.42$, $p = 0.14$) in any of the spectral sensitivity curves. Although all ratios, except UV: green, were not significantly different due to small sample size and large standard error, mean UV responses were greater under chromatic adaptation than light adaptation for all yellow stingray individuals.

Microspectrophotometry

Based on morphology, rods and cones were found in the retina of both species. Absorbance spectra that met criteria outlined by Loew (1994) were used for further analysis (Fig. 2). All spectra were best fit with A_1-based visual pigment templates, suggesting that retinal is the only chromophore type present in cownose ray and yellow stingray visual pigments. Both species had a rod pigment with a λ_{max} near 500 nm (Fig. 3). The cownose ray had two cone pigments with λ_{max} (mean ± SD) at short (470 ± 1 nm) and long wavelength (551 ± 2 nm) regions of the spectrum. The yellow stingray had three cone pigments with λ_{max} at short (475 ± 2 nm), medium (533 ± 4 nm), and long wavelength (562 ± 3 nm) regions.

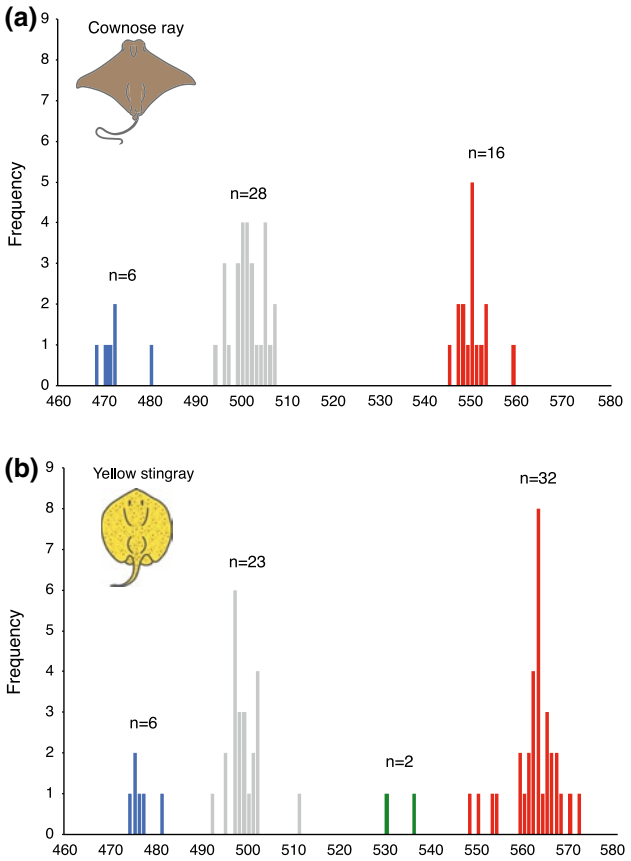

Fig. 2 Frequency distribution of the λ_{max} of individual photoreceptors used in MSP analysis for **a** cownose rays and **b** yellow stingrays. Although not quantitatively analyzed, retinas of both species appeared to be rod dominated. *Bars* are *color-coded* to correspond to specific photoreceptor types: rod *gray*, short wavelength cone (*SWS*) *blue*, medium wavelength cone (*MWS*) *green*, long wavelength cone (*LWS*) *red*

Ocular media transmission

Cownose rays and yellow stingrays both transmitted light to 350 nm (Fig. 4). The cownose ray had a type I lens with $T_{0.5} = 350$ nm and the yellow stingray had a type II–IIa lens with $T_{0.5} = 376$ nm (Douglas and McGuigan 1989; Losey et al. 2003). The slope of both species' transmission curves was categorized as class II (Douglas and McGuigan 1989; Siebeck and Marshall 2001; Losey et al. 2003) with a gradual slope of >30 nm between 0 and 100 %. Cownose rays were determined to have a UV vision likelihood of 1 and yellow stingrays had a UV vision likelihood of 2 (Table 1).

Body color reflectance

The dorsal surface of the cownose ray was uniform in color, as expected, with a broad-band maximum reflectance from 600 to 725 nm in each location measured (Fig. 5). The yellow stingray demonstrated two reflectance peaks, the primary peak near 610 nm and a secondary peak near 560 nm. The peaks correlate with the dark spots on the light background of the body of the yellow stingray. The background reflectance peak was near the long wavelength cone λ_{max} of 562 nm.

Discussion

The results presented here support the potential for color vision in two species of batoid elasmobranch and are suggestive of a mechanism of UV sensitivity in yellow stingrays. Although behavioral tests are required to determine the functional significance of polychromatic vision in these species, recent work with another trichromatic batoid, the giant shovelnose ray, *Rhinobatos typus*, suggests that polychromacy in batoid elasmobranchs does result in color vision (Hart et al. 2004; Van-Eyk et al. 2011).

Multiple visual pigments and color (hue) discrimination

The ability of teleost fishes to discriminate colors based on the presence of multiple visual pigments is well known, and in fact, almost all teleosts possess more than one spectral class of cone (Marshall and Vorobyev 2003; Losey et al. 2003). Color discrimination abilities in elasmobranch fishes, however, remain widely speculative and

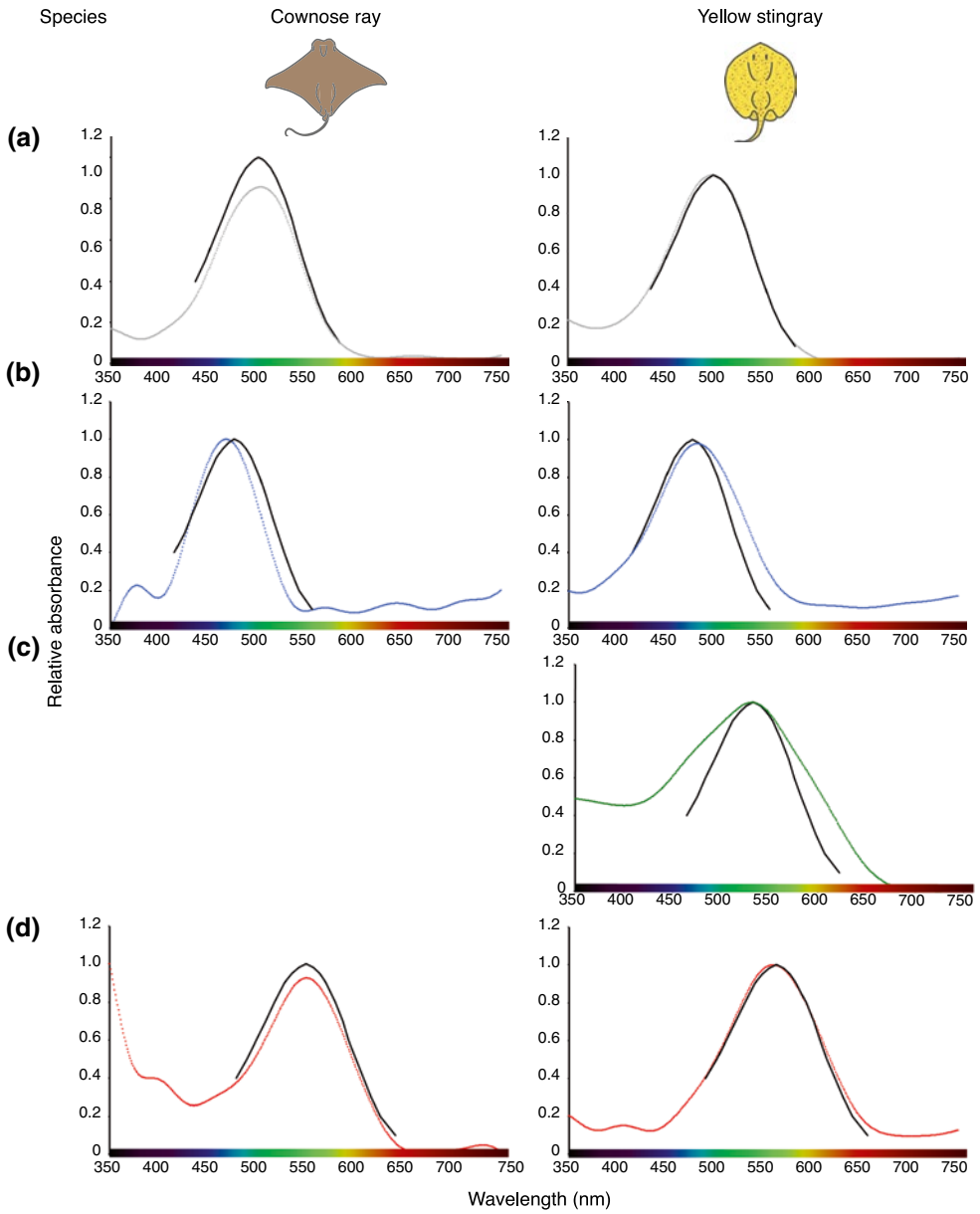

Fig. 3 Normalized mean MSP absorbance spectra for cownose ray and yellow stingray visual pigments. Visual pigment templates (*solid lines*) for **a** rods, **b** SWS, **c** MWS, and **d** LWS were fitted to normalized mean absorbance curves for each pigment type (*dotted line*). Each point in the absorbance curves represents the mean of all photoreceptors at that wavelength. Cownose rays had rod λ_{max} = 500 ± 2 nm (mean ± SD), SWS λ_{max} = 470 ± 1 nm, and LWS λ_{max} = 551 ± 2 nm. Yellow stingrays had rod λ_{max} = 499 ± 2 nm, SWS λ_{max} = 475 ± 2 nm, MWS λ_{max} = 533 ± 4 nm, and LWS λ_{max} = 562 ± 3 nm

are primarily based on morphological and histological evidence (Gruber et al. 1963; Hamasaki and Gruber 1965; Stell 1972), with more emphasis on recent studies elucidating the nature of photoreceptor classes and spectral sensitivities in the group (Hart et al. 2004, 2011; Theiss et al. 2007; McComb et al. 2010).

Rod visual pigments of coastal elasmobranchs are typically maximally sensitive in the green region of the visible light spectrum, around 500 nm. Cownose rays, *Rhinoptera bonasus*, and yellow stingrays, *Urobatis jamaicensis*, were no exception with a rod λ_{max} of 499 and 501 nm, respectively (Fig. 3). MSP results showed that cownose rays were potentially dichromatic with two visual pigments: one with a λ_{max} at 470 nm (SWS) and the other peaking at 551 nm (LWS). Yellow stingrays were potentially trichromatic with three pigments that had peak absorbance at 475 nm (SWS), 533 nm (MWS), and 562 nm (LWS). Although MWS were only found in yellow stingray retinas in low abundance, it is unlikely that MWS were overlooked in cownose ray MSP due to a greater sampling effort of cownose ray

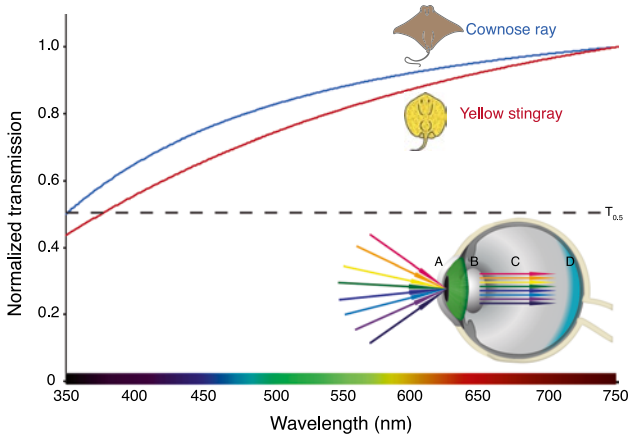

Fig. 4 Transmission of white light through the ocular elements (cornea, lens, vitreous humor). Short wavelength filtering of white light occurs as it passes through the cornea (*A*), lens (*B*), and vitreous (*C*) as a protective mechanism against UV damage to the retina (*D*). Both species showed minimal filtering of UV wavelengths by the ocular media and transmitted wavelengths down to 350 nm. However, in yellow stingrays, wavelengths <376 nm transmitted <50 % ($T_{0.5}$, *horizontal dashed line*), indicating the presence of some pigmentation

preps. Increased samples for yellow stingrays may reveal a higher abundance of MWS. It is a possibility that the low abundance of green cones may have also been a result of prolonged captivity as a result of artificial lighting or otherwise altered physiological states, as was noted for reductions in the photopic flicker fusion frequencies measured from cownose rays (Bedore 2013). However, the plasticity of elasmobranch photoreceptors has not been detailed and this hypothesis remains to be tested.

Both species demonstrated multiple peaks in spectral sensitivity curves under all light conditions (Fig. 1). Although the curves were expected to differ more dramatically between the two species based on MSP results, the small MWS contribution to the ERG curves relative to rod and LWS contributions may have masked the appearance of a 530-nm peak. The dark-adapted and white light-adapted spectral sensitivity curves for the cownose ray showed peaks in the visible spectrum at 470, 490–500 and 540–550 nm, which match the presence of cones containing visual pigments with λ_{max} at 470 and 550 nm, and a rod containing visual pigment with a λ_{max} at 499 nm. The yellow stingray spectral sensitivity curves were less conclusive with visible spectrum peaks at 450, 490, 510, and 550 nm in the dark-adapted eyes with peaks slightly shifted under light adaptation (450, 490, 520, and 560 nm). Although it is unclear if the small dips in the curves may be a result of low resolution in the curve (responses were only tested every 10–30 nm) or noise, the curve loosely matched the MSP λ_{max} of cone visual pigments at 475, 533, and 562 nm and rod λ_{max} at 499 nm. Low sampling resolution or retinal filtering mechanisms may be responsible

Table 1 Ocular media transmission categories and vision likelihood predictions for UV color vision in fishes

	$T_{0.05}$[a, b]		Slope of transmission curve[c]		Diurnal habits[b]		Vision likelihood[b]		
	Type	λ cutoff (nm)	Class	Shape	Category	Light exposure	Category	$T_{0.05}$, diurnal habit	Prediction
	I[a]	<355	I	Steep; <30 nm from 0 to 100 % transmission	1	Diurnal; full ambient daylight	1	I 1 or 2	UV color vision highly likely
	I[b]	≤355	II	Gradual; >30 nm from 0 to 100 % transmission	2	Nocturnal; full ambient daylight	2	IIa 1 or 2	UV color vision likely
	II[a]	$355 < T_{0.05} < 405$	III	Intermediate maxima	3	Hidden from daylight	3	IIb 1 or 2	Violet vision likely (not true UV)
	IIa[b]	$355 < T_{0.05} \leq 380$	IV	≥97 % transmission from 300 to 700 nm			4	I, IIa, or IIb 3	Short λ vision (not UV)
	IIb[b]	$380 < T_{0.05} \leq 405$					5	III 1, 2, or 3	No short λ vision
	III[a, b]	>405							
Cownose ray	I	350	II	>30 nm slope	1	Diurnal; shallow estuary, coastal	1		β-Band UV absorption
Yellow stingray	IIa	376	II	>30 nm slope	2	Nocturnal; reef, seagrass	2		β-Band UV absorption

Categories and predictions based on studies by [a]Douglas and McGuigan (1989) (50 species), [b]Losey et al. (2003) (195 species), [c]Siebeck and Marshall (2001) (211 species)

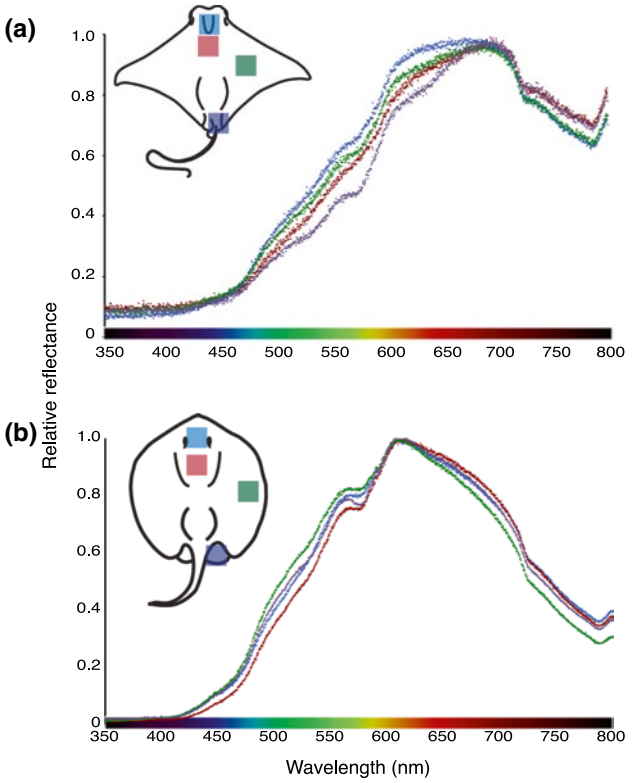

Fig. 5 Dorsal body color reflectance spectra and reflectance data measurement locations. Each location is denoted by a corresponding *color* in both the ray illustration and the reflectance plots. *Boxes* in ray illustrations outline the region from which each measurement was recorded. Each point in the reflectance curve represents the mean reflectance from all individuals at the corresponding wavelength. *Head blue*, *branchial red*, *pectoral fin green*, and *pelvic fin gray*. **a** Cownose rays were uniform in *color* with a broad-band peak that reflected maximally from approximately 600 to 725 nm from all locations. **b** Yellow stingrays had two reflectance peaks at 561 and 610 nm that were consistent across locations

for the discrepancy between the 450-nm ERG peak and the MSP 475 nm λ_{max}, although this hypothesis has not been verified.

Typically in vertebrates, rod photoreceptors function in dim light (scotopic) and are more sensitive than cones, which function in bright light (photopic) conditions and provide the basis for color vision (Schultze 1866). According to the duplicity theory, one would expect primarily rod contribution to the scotopic ERG and cone contribution to the photopic ERG (von Kries 1894). Early work on lemon sharks, *Negaprion brevirostris*, described rods and cones in the retina (Gruber et al. 1963) and rhodopsin with a λ_{max} of 501 nm was extracted (Bridges 1965). Subsequent investigation with ERG (O'Gower and Mathewson 1967; Cohen and Gruber 1977) and ganglion cell recordings (Cohen and Gruber 1985) found a mismatch between spectral sensitivity and the λ_{max} of extracted retinal pigment, and the authors hypothesized that rods and cones both contribute to the scotopic ERG. The mismatch was later attributed to an ontogenetic shift in the λ_{max} of the visual pigment (Cohen et al. 1990). More recent work on dark-adapted spectral sensitivities in sharks found two peaks in scotopic curves, presumably from a rod and a cone; however, the photoreceptor classes of those species have yet to be identified (McComb et al. 2010). The present study found rod and cone contribution to the scotopic and photopic ERG in cownose rays and yellow stingrays, and supports the hypothesis that elasmobranchs do not possess distinct scotopic and photopic visual mechanisms. The functional significance of this finding is not yet understood due to the paucity of behavioral vision studies and inconclusive results of early studies where elasmobranchs may have been discriminating stimuli based on perceived brightness, rather than wavelength (Clark 1963; Tester and Kato 1966; Gruber 1975). However, behavioral work demonstrated that marine mammals (Wartzok and McCormick 1978; Griebel and Schmid 1992, 2002) and red-monochromatic primates (Jacobs et al. 1993) that possess only two visual pigments, a rod and one cone, are able to discriminate wavelengths with a rudimentary color vision system that is at least functional under mesopic (medium brightness) conditions. Therefore, comparison of rod and cone input in elasmobranchs may serve to broaden the spectrum of light visible to elasmobranchs, or to enhance sensitivity to light under scotopic conditions (Hart et al. 2011).

Ultraviolet transmission and sensitivity

The basic requirements for a functional ultraviolet visual mechanism are the presence of UV wavelengths in the environment, transmission of those wavelengths to the retina, and a UV-sensitive retinal mechanism subserved either by UV-sensitive cones or by β-band absorption by other visual pigments (reviewed by Losey et al. 1999). Cownose rays and yellow stingrays are both frequently found in UV-rich habitats at depths <20 m (Table 1); both species transmitted UV wavelengths to the retina as indicated by ocular media transmission, and both demonstrated peaks in the UV region of dark-, light-, and chromatic-adapted spectral sensitivity curves (Fig. 1). Although both species transmitted UV wavelengths through the ocular media to 350 nm, it is interesting to note that the lens of the yellow stingray had a slightly yellow appearance, indicating the presence of pigmentation in the lens that absorbs UV wavelengths (Zigman 1971). Photooxidation of lens and corneal structures in other elasmobranchs increases the degree of pigmentation, which subsequently reduces the relative amount of UV transmission to the retina when the animal is exposed to light with a high UV content (Nelson et al. 2003) and may be responsible for the lower transmission at the shortest wavelengths in the yellow stingray compared

to the cownose ray. Although ocular media transmission data for yellow stingrays appear to contradict ERG data, the transmission of UV wavelengths at 350 nm is near the $T_{0.5}$ transmission point (Fig. 4), so yellow stingrays likely still receive a relatively high degree of UV stimulation at the retinal level. In addition, the spectral composition of surface waters is extraordinarily rich in UV-A wavelengths, reaching nearly 40 % of the total number of photons, and exceeds photopic threshold levels of stimulation for most fish species (see review in Losey et al. 1999).

Failure to find a particular class of photoreceptor when performing MSP, like the results presented here, does not necessarily mean that those photoreceptors are not present in the retina. This could occur if the cells were sparse or present in localized regions that were not present in the retinal pieces selected. For example, in the goldfish, *Carassius auratus*, several early attempts at finding UV cones with MSP failed, even though ERG results indicated the presence of a UV cone (Bowmaker et al. 1991). However, ERG data in this study did not support the presence of a UV cone mechanism in cownose rays. In addition to a lack of evidence for UV cones with MSP, the small peaks in the UV region of both species' spectral sensitivity curves were not significantly increased relative to the 550-nm peaks under the presence of the 550-nm adapting light and suggest the peaks were a result of β-band absorption. However, all yellow stingrays demonstrated an increased sensitivity to UV wavelengths in the chromatic condition relative to the light-adapted trials which supports the presence of a functional UV mechanism in this species. Although these results must be interpreted with caution, they warrant further investigation into the potential use of UV light for prey detection, conspecific recognition, and predator avoidance behaviors in yellow stingrays.

Visual ecology

Photoreceptors of aquatic organisms tend to be spectrally tuned to the depth and water quality in which they are found (Munz and McFarland 1973, 1977; Loew and Lythgoe 1978; Hart et al. 2011; Lisney et al. 2012). For example, pelagic species that inhabit the open ocean usually have blue-shifted sensitivity due to the high transmission of blue wavelengths in clear oceanic water (Loew and Lythgoe 1978; Munz and McFarland 1977; Bowmaker et al. 1994; Lythgoe et al. 1994; Hart et al. 2011). Coastal and estuarine species are typically green–yellow shifted compared to deep sea or pelagic species because scattering due to increased turbulence and absorption by dissolved organics ('Gelbstoff') decreases the contribution of short wavelengths to the overall irradiance. In species with multiple visual pigments, the best detection of objects is accomplished with a photoreceptor with maximum absorbance that matches the background and one that is offset from the background, which provides high contrast of objects against the background (Lythgoe 1972; Jerlov 1976; Levine and MacNichol 1982).

Most batoids in which the absorbance of photoreceptors has been studied in detail have multiple types of cones, which provide them the potential to possess color vision (Hart et al. 2004, Theiss et al. 2007, Van-Eyk et al. 2011). While both of the species in our study also had multiple types of cones, their ability to discriminate color across the spectrum differs. The yellow stingray had λ_{max} of cones similar to that of the blue-spotted maskray, *Neotrygon kuhlii*, and the giant shovelnose ray, *Rhinobatos typus*, which also inhabit tropical reef-associated spectrally rich waters (Last and Stevens 1994; Compagno and Last1999; Fahy 2004; Theiss et al. 2007; Ward-Paige et al. 2011). The cownose ray on the other hand is an estuarine and inshore benthopelagic ray (Smith and Merriner 1987; Neer and Thompson 2005; Collins et al. 2007a, 2008; Ajemian and Powers 2012), which typically experiences a more spectrally limited and variable irradiance habitat than the yellow stingray. Because of the limitation of light available, trichromacy would not be much of a benefit to cownose rays. The two cone pigments of the cownose ray had peaks in the blue and green regions of the spectrum, and with the abundance of longer wavelength light present in the environment, these cones are similar to (green) and offset from (blue) the background coloration.

Trichromacy could be highly beneficial to the yellow stingray, however. Teleosts and invertebrates that live on spectrally complex reefs utilize color vision and color signals as an enhanced communication channel for conspecific recognition, mating and territory displays, and for camouflage from predators (Hazlett 1979; Collin and Trezise 2004; Hart et al. 2004; Kelber and Roth 2006; Siebeck et al. 2008). The peak of the background color of the yellow stingray body (561 nm) was closely matched to the λ_{max} of the long wavelength cone (562 nm). Therefore, it is likely that yellow stingrays are able to utilize color vision at least for conspecific recognition within a colorful environment. The longer wavelength dark spots at 610 nm on the yellow stingray help provide camouflage and are probably similar to the rock structure in the sandy areas around reefs where yellow stingrays tend to bury (personal observation; Fahy 2004; Ward-Paige et al. 2011).

Ultraviolet vision as a dimension of color vision in teleost fishes and invertebrates is typically mediated by UV-sensitive visual pigments and can be involved in intraspecific communication, detection of UV-reflecting planktonic prey, and enhanced contrast detection in UV-rich environments (Marshall and Vorobyev 2003; Siebeck 2004; Partridge and Cuthill 2010; Siebeck et al. 2010). Criteria based on a study of ocular media transmission and MSP of nearly 200

species of reef fishes outlined by Losey et al. (2003) assign a vision likelihood category that predicts UV sensitivity is likely to highly likely in both of the species in the present study (Table 1). Cownose rays primarily forage on benthic and buried immobile invertebrates (Orth 1975; Smith and Merriner 1985; Collins et al. 2007b; Ajemian and Powers 2012); therefore, they would not benefit from UV sensitivity for prey detection and did not show evidence of functional UV sensitivity in this study. Yellow stingrays, however, feed on epifaunal crustaceans and polychaetes, including stomatopod crustaceans (D. Fahy, pers. comm). Some stomatopods have colorful areas of their body that contain UV components, which are thought to aid in mating and territory displays (Hazlett 1979; Marshall et al. 1996; Chiao et al. 2000), and could be an enhanced visual signal to foraging stingrays as well. Enhanced contrast capabilities could be beneficial to both species for detection of predators against their UV-rich background; however, the potential for a UV mechanism is only suggested for the yellow stingray based on the ocular media and ERG results presented here.

Conclusions

Sensory systems of elasmobranchs have been relatively poorly studied compared to most other vertebrate classes; however, it is known that sensory capabilities are often tuned to species ecology. There is also generally a lack of knowledge regarding the general ecology and behavior of many elasmobranchs, such as diet composition, range and movement, mating and courtship behaviors, habitat preferences, and activity patterns. Without this information, it is difficult to assess the functionality of sensory systems with respect to ecology.

In addition, the function of a combined scotopic and photopic visual system remains hypothetical at this time and the neuronal circuitry of the retina remains widely unstudied, but elasmobranchs may share characteristics with teleost fishes that have combined scotopic and photopic visual systems (Burkhardt 1966; Witkovsky 1968; Cohen and Gruber 1977; Toyoda et al. 1978; Allen and Fernald 1985; Barlow 1985; Dearry and Barlow 1987). Future studies should investigate the synaptic connections between photoreceptors, horizontal cells, bipolar cells, and convergence onto retinal ganglion cells, as well as employ behavioral testing of elasmobranchs with different classes of photoreceptors at varying photic conditions. Behavioral tests will also elucidate whether these species have behaviorally significant UV sensitivity, as well as the potential ecological significance of UV color vision for elasmobranchs.

Despite the lack of information regarding life history and rod and cone interactions, the conclusion can be made that vision is likely an important sensory modality for both species, as indicated by the presence of multiple classes of cones and extensive vertical (cownose ray) and horizontal (yellow stingray) visual fields (McComb and Kajiura 2008). Schooling behavior, prey detection, mate detection, and predator avoidance are all likely to be mediated by vision and future studies should consider visually guided behaviors of elasmobranchs.

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Conflict of interest The authors declare that they have no conflict of interest.

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