

Comparative visual function in five sciaenid fishes inhabiting Chesapeake Bay

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Accepted 23 September 2008

SUMMARY

Maintaining optimal visual performance is a difficult task in the photodynamic coastal and estuarine waters in which western North Atlantic sciaenid fishes support substantial commercial and recreational fisheries. Unavoidable tradeoffs exist between visual sensitivity and resolution, yet sciaenid visual systems have not been characterized despite strong species-specific ecomorphological and microhabitat differentiation. We therefore used electroretinographic techniques to describe the light sensitivities, temporal properties, and spectral characteristics of the visual systems of five sciaenids common to Chesapeake Bay, USA: weakfish (*Cynoscion regalis*), spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellatus*), Atlantic croaker (*Micropogonias undulatus*) and spot (*Leiostomus xanthurus*). Benthic sciaenids exhibited higher sensitivities and broader dynamic ranges in white light $V/\log I$ experiments than more pelagic forms. Sensitivities of the former were at the lower (more sensitive) end of an emerging continuum for coastal fishes. Flicker fusion frequency experiments revealed significant interspecific differences at maximum intensities that correlated with lifestyle and habitat, but no specific differences at dimmer intensities. Spectral responses of most sciaenids spanned 400–610 nm, with significant diel differences in weakfish and Atlantic croaker. Weakfish, a crepuscular predator, also responded to ultraviolet wavelengths; this characteristic may be more useful under less turbid conditions. Collectively, these results suggest that sciaenids are well adapted to the dynamic photoclimate of the coastal and estuarine waters they inhabit. However, the recent anthropogenic degradation of water quality in coastal environments, at a pace faster than the evolution of visual systems, has amplified the importance of characterizing visual function in managed aquatic fauna.

Key words: electroretinography, fish, flicker fusion frequency, Sciaenidae, spectral sensitivity, visual ecology.

INTRODUCTION

Daily irradiance in near-surface waters can vary over an intensity range of nine orders of magnitude; scatter and absorption further restrict the spectral bandwidth (color) and intensity (brightness) of downwelling light with depth (Lythgoe, 1979; McFarland, 1986). In its simplest form, maximal transmission occurs at short wavelengths (blue) in pure natural waters and clear pelagic seas, at intermediate (green) wavelengths in coastal waters, and at longer (yellow-red) wavelengths in estuarine and fresh waters (Jerlov, 1968). Closer to shore, the increasing concentrations of phytoplankton, yellow products of vegetative decay (*Gelbstoffe*), and suspended particulates scatter, absorb and more rapidly attenuate light (Lythgoe, 1975; Lythgoe, 1988). The spectral distribution in these waters shifts to longer wavelengths (Jerlov, 1968).

Fishes have radiated into a broad range of aquatic habitats possessing complex photic properties, resulting in a myriad of selective pressures on their visual systems (Munz, 1977; Levine and MacNichol, 1979; Collin, 1997). The characteristics of aquatic light fields are generally reflected in the visual systems of fishes inhabiting them (Guthrie and Muntz, 1993). However, maintaining optimal visual performance over the full range of possible light intensities is near-impossible, thus unavoidable tradeoffs exist between visual sensitivity and resolution. For example, at the cost of acuity, luminous sensitivity can be extended under dim conditions by widening pupils, increasing spatial and temporal summation, and reradiating light through retinal media to maximize photon capture

(Warrant, 1999). Luminous and chromatic sensitivities as well as temporal and spatial properties of fish visual systems vary depending on ecological and phylogenetic constraints, and are thus useful metrics to describe the functions and tasks of visual systems (Lythgoe, 1979; Warrant, 1999; Marshall et al., 2003).

The range of light from which visual information can be obtained is further extended in species with duplex retinæ that use cone cells under photopic (bright) conditions, and rod cells during scotopic (dim/dark) conditions (Lythgoe, 1979; Crescitelli, 1991). Much discussion has centered on the properties of these cells, their pigments, and correlations to the photic properties of habitats (McFarland and Munz, 1975; Dartnall, 1975; Levine and MacNichol, 1979; Bowmaker, 1990; Jokela et al., 2003; Jokela-Määttä et al., 2007), leading to two hypotheses that relate the spectral properties of pigments to those of light fields. The ‘sensitivity hypothesis’ suggests that pigment absorption spectra should match the ambient background to maximize photon capture in scotopic (rod-based) vision (Bayliss et al., 1936; Clark, 1936). The ‘contrast hypothesis’ suggests that maximal contrast between an object and the background is provided by a combination of matched and offset visual pigments (Lythgoe, 1968). Fishes that possess multiple spectrally distinct visual pigments probably use both mechanisms (McFarland and Munz, 1975).

There has been considerable research on the properties of visual systems in closely related taxa inhabiting similar environments. Comparative methods have provided novel insights into the

form–function–environment relationships of the fish eye (Walls, 1942; Levine and MacNichol, 1979; Parkyn and Hawryshyn, 2000; Jokela-Määttä et al., 2007), the distributions and movements of fishes (McFarland, 1986), communication (Hart et al., 2006; Siebeck et al., 2006), predator–prey interactions (Browman et al., 1994; De Robertis et al., 2003), and even vulnerability to capture (Buijse et al., 1992; Weissburg and Browman, 2005). Few such comparisons exist for the commercially and recreationally important fauna that use mid-Atlantic coastal and estuarine waters as key juvenile nurseries (Levine and MacNichol, 1979; Beck et al., 2001).

Teleosts of the family Sciaenidae support valuable fisheries along the US East coast and are good candidate organisms for comparative sensory study by virtue of their taxonomic, morphological and microhabitat diversity (Chao and Musick, 1977; Horodysky et al., 2008). Sciaenids occupy a myriad of habitats in freshwater, estuarine, coastal neritic and reef-associated marine systems, but are most speciose in coastal and estuarine waters (Myers, 1960). Species-specific ecomorphologies and microhabitats result in niche separation in sympatry among piscivorous, midwater zooplanktivorous, and benthivorous sciaenids in Chesapeake Bay, Eastern USA (Chao and Musick, 1977) (Fig. 1). Light fields in such microhabitats may differ widely in chromatic and luminous properties, and have changed rapidly over the past century of anthropogenic degradation of coastal waters (Levine and MacNichol, 1979; McFarland, 1991; Kemp et al., 2005). Unfortunately, photic form–function–environment relationships for sciaenids have been precluded by the lack of information on their visual systems. We therefore used corneal electroretinography (ERG) to assess the absolute sensitivities, temporal properties, and spectral sensitivities of the visual systems of five sciaenid species.

MATERIALS AND METHODS

Hook and line gear was used to capture study animals including: weakfish (*Cynoscion regalis* Bloch and Schneider 1801), spotted seatrout (*Cynoscion nebulosus* Cuvier 1830), red drum (*Sciaenops ocellatus* Linnaeus 1766), Atlantic croaker (*Micropogonias undulatus* Linnaeus 1766) and spot (*Leiostomus xanthurus* Lacepede 1802) (Table 1). Animals were maintained in recirculating 1855 l aquaria at 20±1°C (winter) or 25±2°C (summer) and fed a combination of frozen Atlantic menhaden (*Brevoortia tyrannus*), squid (*Loligo* sp.) and commercially prepared food (AquaTox flakes; Zeigler, Gardners, PA, USA). Indirect sunlight passing through

Table 1. Species, sample size, length, and mass of the five sciaenid fishes investigated in this study

Species	N	SL (mm)	Mass (g)
<i>Cynoscion regalis</i>	6	190–289	100–280
<i>Cynoscion nebulosus</i>	6	278–560	220–755
<i>Sciaenops ocellatus</i>	6	291–378	460–1020
<i>Micropogonias undulatus</i>	6	223–393	140–890
<i>Leiostomus xanthurus</i>	6	70–270	60–215

SL, standard length.

standard window glass in the animal holding facility allowed us to maintain all subjects on natural ambient photoperiods.

Experimental and animal care protocols were approved by the College of William and Mary’s Institutional Animal Care and Use Committee, protocol no. 0423, and followed all relevant laws of the United States. Electoretinography (ERG) experiments were conducted on six animals of each species. Subjects were removed from holding tanks during daylight hours, sedated with an intramuscular (i.m.) dose of ketamine hydrochloride (Butler Animal Health, Middletown, PA, USA; 30 mg kg⁻¹), and immobilized with an i.m. injection of the neuromuscular blocking drug gallamine triethiodide (Flaxedil; Sigma, St Louis, MO, USA; 10 mg kg⁻¹). Recording of vertebrate neural waveforms in anaesthetized and/or immobile subjects is a common practice to minimize the obscuring effect of muscular noise (Hall, 1992; Parkyn and Hawryshyn, 2000; Horodysky et al., 2008). Following drug injections, fish were moved into a light-tight enclosure and placed on a chamois sling submerged in a rectangular 800 mm×325 mm×180 mm Plexiglas tank such that only a small portion of the head and the eye receiving the light stimulus remained above the water surface. Subjects were ventilated (1 l min⁻¹) with filtered and oxygenated sea water that was temperature controlled (20±2°C) to minimize the potential confounding effects of temperature on ERG recordings (Saszik and Bilotta, 1999; Fritsches et al., 2005).

Experiments were conducted during both day and night to account for any circadian rhythms in visual response (McMahon and Barlow, 1992; Cahill and Hasegawa, 1997; Mangel, 2001). We defined ‘day’ and ‘night’ following ambient photoperiods: experiments conducted during the hours the fish holding tanks were sun-lit are hereafter referred to as ‘day’, whereas those repeated following sunset when the fish holding tanks were in darkness are referred to as ‘night’. At the conclusion of each experiment, fishes

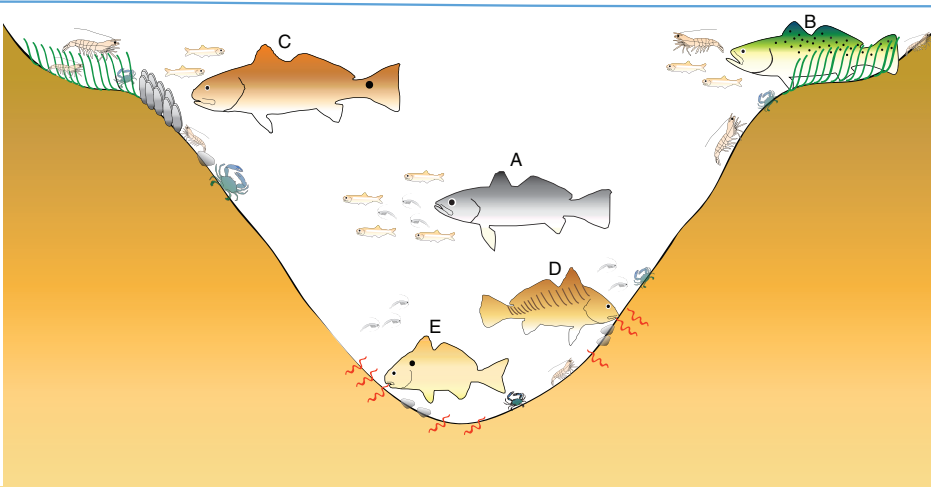


Fig. 1. Conceptual diagram of the microhabitat specialization of the five sciaenid fishes examined in this study (Chao and Musick, 1977; Murdy et al., 1997). Weakfish (A) are crepuscular/nocturnal predators of small pelagic crustaceans and fishes in the Chesapeake Bay mainstem and deeper waters. Spotted seatrout (B) are predators of small crustaceans and fishes in shallow seagrass habitats. Red drum (C) prey on invertebrates and fishes in marsh, seagrass, and oyster reef habitats. Atlantic croaker (D) and spot (E) forage on a suite of small crustacean, polychaete and bivalve prey in sand and mud bottoms throughout the Chesapeake Bay mainstem and tributaries. All are seasonal residents of Chesapeake Bay.

were euthanized by a massive overdose ($\sim 300 \text{ mg kg}^{-1}$) of sodium pentobarbital (Beuthanasia-D, Schering-Plough Animal Health, Union, NJ, USA).

Electroretinography

Whole-animal corneal ERGs were conducted to assess the absolute sensitivities, temporal properties, and spectral sensitivities of sciaenid visual systems. Corneal ERG is a comprehensive method to measure summed retinal potentials that account for any optical filtering of light by ocular media (Brown, 1968; Ali and Muntz, 1975). This technique is well-suited for comparative investigations of vision and form–function relationships in fishes (Ali and Muntz, 1975; Pankhurst and Montgomery, 1989; Makhankov et al., 2004).

Teflon-coated, chlorided 0.5 mm silver wire (Ag–AgCl₂) electrodes were used to measure and record ERG potentials: the active electrode was placed on the corneal surface and a reference electrode was placed subdermally in the dorsal musculature. The system was grounded to the water of the experimental tank by a 6 cm \times 26 cm stainless steel plate. ERG signals were amplified with a DAM50 amplifier (World Precision Instruments, Sarasota, FL, USA) using a 10,000 gain passed through a 1 Hz high pass and 1 kHz low pass filter. Amplified ERG signals were further filtered with a HumBug[®] active electronic filter (Quest Scientific, N. Vancouver, BC, Canada) to remove periodic electrical noise, and were digitized at 1 kHz sampling frequency with a 6024E multifunction DAQ card (National Instruments, Austin, TX, USA). ERG recordings and stimulus presentations were controlled using software written in LabVIEW (National Instruments, Austin, TX, USA). All subjects were dark-adapted for a minimum of 30 min prior to stimulus exposure. Light intensities for all experiments were calibrated using an International Light IL1700 radiometer.

Absolute (luminous) sensitivity

Absolute sensitivity of sciaenid visual systems was assessed by intensity–response ($V/\log I$) experiments. A uniform circular source, 3.8 cm in diameter, consisted of an array of 20 bright white light emitting diodes (LEDs; Advanced Illumination, Rochester, VT, USA) that were diffused and collimated (see Fritsches et al., 2005). The LED output was driven by an intensity controller (Advanced Illumination, Rochester, VT, USA). A sinusoidal voltage, variable between 0 V and 5 V, could be sent to the intensity controller from the analog output of the DAQ card, thus allowing a sinusoidally modulated light intensity from the LEDs. Our LED light source had a working range of roughly $3 \log_{10}$ units, and a maximum output intensity of 1585 cd m^{-2} . Six orders of magnitude of stimulus intensity were therefore presented to subjects by using appropriate combinations of Kodak Wratten 1.0 and 2.0 neutral density filters (Eastman Kodak, Rochester, NY, USA). $V/\log I$ experiments progressed from subthreshold to saturation intensity levels in 0.2 log unit steps. At each intensity step, ERG b-waves were recorded from a train of five 200 ms flashes, each separated by 200 ms rest periods. This process was repeated three times. ERG responses of the final averaged flashes (V_{response}) were recorded at each intensity step and subsequently normalized to the maximum voltage response (V_{max}). Mean $V/\log I$ curves for each species were created by averaging the $V/\log I$ curves of six individuals of that species. Interspecific comparisons of relative sensitivity were made at stimulus irradiances eliciting 50% of V_{max} (referred to as K_{50}). Dynamic ranges, defined as the log irradiance range between the limits of 5–95% V_{max} , were also calculated for each species (Frank, 2003).

Temporal resolution

The temporal resolution of sciaenid visual systems was assessed *via* flicker fusion frequency (FFF) experiments with the white light LED setup described above using methods developed elsewhere (Fritsches et al., 2005). FFF experiments monitored the ability of a visual system to track light flickering in logarithmically increasing frequencies. Sinusoidally modulated white light stimuli ranging in frequency from 1 Hz (0 log units) to 100 Hz (2.0 log units) were presented to subjects in 0.2 log unit frequency steps. The voltage offset and the amplitude of the sinusoidal light stimulus signal were always equal (contrast=1). At each frequency step, light stimuli were presented for 5 s, followed by 5 s of darkness (i.e. rest). This stimulus train was repeated three times at each frequency, and b-wave responses were averaged for each subject. For each subject, seven total FFF experiments were conducted: one at 25% (I_{25}) of maximum stimulus intensity (I_{max}) from the $V/\log I$ curve, and one in each of \log_{10} step intervals over six orders of magnitude of light intensity.

A subject's FFF threshold at a given intensity increment was determined by analyzing the power spectrum of the averaged responses from 1–100 Hz and comparing the power of the subject's response frequency (signal) to the power of a neighboring range of frequencies (noise). FFF was therefore defined as the frequency at which the power of the response signal fell below the power of the noise, as determined by graphical analysis of normalized power amplitudes as a function of frequency. Diel and interspecific comparisons were conducted on the FFF data at I_{max} and I_{25} . We considered the FFF at I_{max} as the probable maximum flicker fusion frequency attainable by the visual system of a given species, and FFF at I_{25} to be a proxy for ambient environmental light intensity.

Spectral (chromatic) sensitivity

Spectral sensitivity experiments were conducted to assess the ability of sciaenid visual systems to respond to colored light stimuli. The output of a Cermox Xenon fiberoptic light source (ILC Technology, Sunnydale, CA, USA) was controlled by a CM110 monochromator, collimated, and passed through each of two AB301 filter wheels containing quartz neutral density filters (CVI Laser Spectral Products, Albuquerque, NM, USA). The first wheel allowed light attenuation from 0 to 1 log units of light intensity in 0.2 log unit steps, the second from 0 to 4 log units in 1 log unit steps. In concert, the two wheels allowed the attenuation of light from 0 to 5 log units in 0.2 log unit steps. Stimuli were delivered by a LabVIEW program that controlled a Uniblitz LS6 electronic shutter (Vincent Associates, Rochester, NY, USA) using the analog and digital output of the DAQ card and the computer's serial RS232 interface. A cylindrical lens focused the attenuated light beam onto the entrance slit of the monochromator to produce colored light. The 1 cm diameter quartz light guide was placed within 10 mm of a subject's eye. Approximately isoquantal spectral stimuli were presented to subjects *via* the selective use of neutral density filters.

Light stimuli covering the spectral range from UV (300 nm) to the near infrared (800 nm) were presented sequentially in 10 nm steps during spectral response experiments. Subjects were presented with five single 40 ms stimulus flashes at each experimental wavelength, each followed by 6 s rest. The amplitudes of ERG b-wave responses were recorded and averaged to form raw spectral response curves for each individual. A spectral $V/\log I$ recording was then conducted for each subject at the wavelength (λ_{max}) that generated its maximum ERG response (V_{max}). This allowed the subsequent calculation of the subject's spectral sensitivity curve. $V/\log I$ experiments exposed the subject to five individual monochromatic 200 ms flashes at each intensity. Intensities increased in 0.2 log unit increments over five

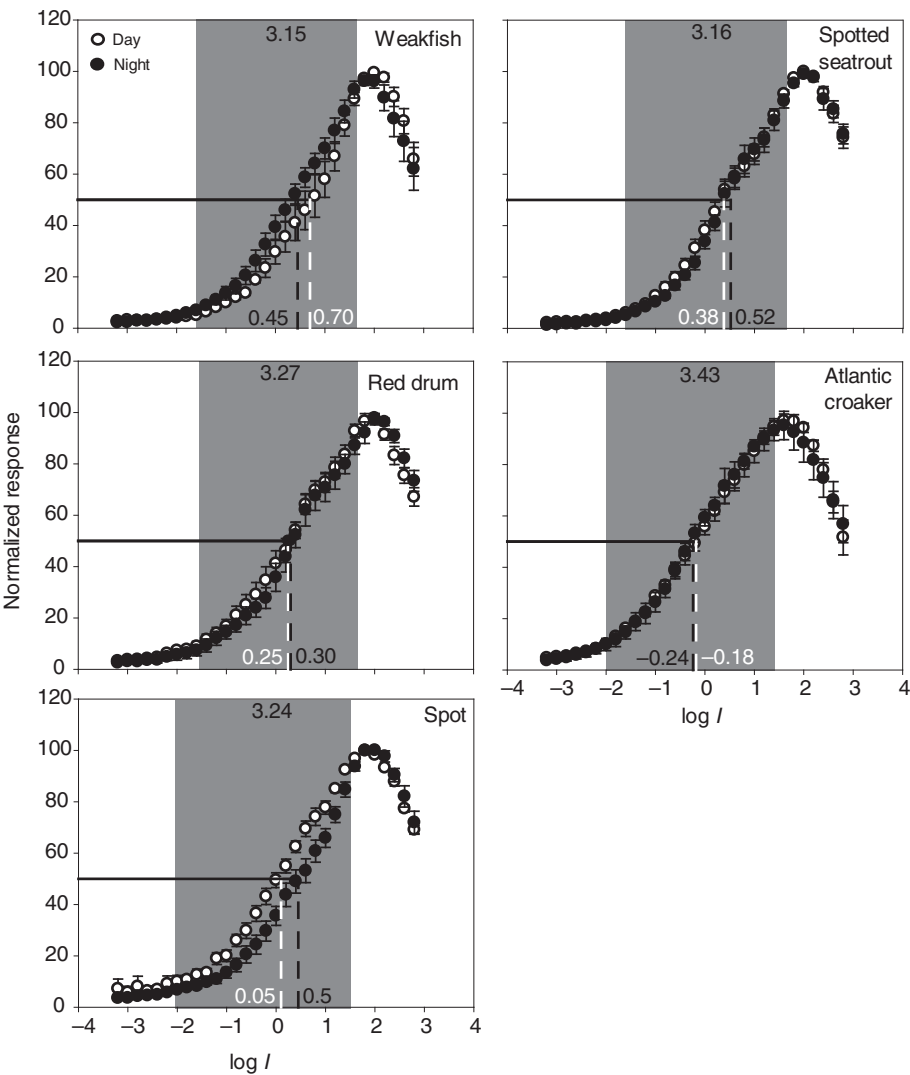


Fig. 2. Intensity–response electroretinograms (ERGs) of weakfish, spotted seatrout, red drum, Atlantic croaker and spot. Each species' intensity–response curve is an average of six individuals. Responses were normalized to the maximal response voltage (V_{\max}) for each individual. Shaded boxes represent each species' dynamic range (5–95% V_{\max}), numbers at the top indicate its breadth (in log units). Dashed vertical lines and adjacent numbers indicate K_{50} points (illumination at 50% V_{\max}). Open symbols and white text are results of day experiments, filled symbols and black text are of night experiments. Light intensities are in log candela m^{-2} . Error bars indicate ± 1 s.e.m.

orders of magnitude. The amplitudes of these flashes were recorded and averaged to create each subject's spectral $V/\log I$ curve. To transform spectral response voltages to spectral sensitivities for each subject, the former were converted to equivalent intensities through the $V/\log I$ curve using the following equation:

$$S = 100 \times 10^{-|I_{\max} - I_N|}, \tag{1}$$

where S is the sensitivity, I_{\max} is the intensity at maximum response voltage and I_N is the intensity at response voltage.

Spectral sensitivity curves for each individual were expressed on a percentage scale, with 100% indicating maximum sensitivity. To obtain the final spectral sensitivity curve for each species, we averaged the sensitivity curves of all subjects and normalized to the maximum resulting value such that maximum sensitivity equaled 100%.

Data analyses
 $V/\log I$ and FFF

Corneal recordings are non-independent within individual subjects (Underwood, 2002), and require that the nature of within-individual autocorrelation is explicitly understood (Littell et al., 2006). To consider corneal recordings as independent within a subject is tantamount to pseudoreplication (Hurlbert, 1984). Sciaenid $V/\log I$ and FFF data were therefore analyzed separately using two-way

repeated measures ANOVAs with Tukey's *post-hoc* comparisons to assess whether ERG responses varied among the five sciaenid species and between photoperiods. All statistical analyses were conducted using SAS v 9.1 (SAS Institute, Cary, NC, USA). A general model for these analyses is given by:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \delta_k + \epsilon_{ijk}, \tag{2}$$

where Y_{ijk} is the value of the response variable (response) for the i th species, j th diel period, and the k th level of their interaction; μ is the overall mean of threshold for all combinations of species and diel periods property; α_i is the species (fixed factor); β_j is the diel period (fixed factor); δ_k is the species:diel interaction; ϵ_{ijk} is the random error term associated with the observation at each combination of the i th species, the j th diel period, and k th level of their interaction.

Spectral sensitivity

Intraspecific diel differences in sciaenid spectral sensitivity curves were assessed by subtracting the day and night curves and calculating confidence intervals (CI) of the resulting difference curve. In this analysis, positive values indicated increased day sensitivity, negative values indicated increased night sensitivity. Similarly, we subtracted the curves of weakfish and spotted seatrout within each diel period to assess potential interspecific

differences in the spectral sensitivities of these congeners. Positive values indicated increased response by weakfish, negative values increased response by spotted seatrout. Significant differences in spectral sensitivity were defined where the mean \pm CI of difference curves did not encompass zero.

To form hypotheses regarding the number and spectral distribution of pigments potentially contributing to sciaenid spectral ERG responses, we fitted the SSH (Stavenga et al., 1993) and GFRKD (Govardovskii et al., 2000) vitamin A1 rhodopsin absorbance templates separately to the photopic spectral sensitivity data. A range of possible conditions was considered: 1–3 α -band rhodopsins, 1–3 α -band rhodopsins with a single β -band on any pigment, and 1–3 α -band rhodopsins with multiple β -bands. For a given species, condition and template, models of summed curves were created by adding the products of pigment-specific templates and their respective weighting factors. Estimates of the unknown model parameters (λ_{\max} values and their respective weighting proportions) were derived by fitting the summed curves to the ERG data using maximum likelihood.

For each species, we objectively selected the appropriate template (SSH or GFRKD) and number of contributing pigments using an information theoretic approach (Burnham and Anderson, 2002) following Akaike's information criterion (AIC):

$$\text{AIC} = -2\ln(\hat{L}) + 2p, \quad (3)$$

where \hat{L} is the estimated value of the likelihood function at its maximum and p is the number of estimated parameters.

AIC is a parsimonious measure that strikes a balance between model simplicity and complex overparameterization (Burnham and Anderson, 2002). Accordingly, AIC provided a quantitative metric to evaluate the simplest, most likely estimates of sciaenid rhodopsin parameters given our data (Stavenga et al., 1993; Govardovskii et al., 2000). All parameter optimization, template fitting and model selection was conducted using the software package *R* version 2.7.1 (R Development Core Team, 2008).

Spectrophotometry of eye subcomponents

To assess whether sciaenid ocular media transmit or absorb ultraviolet wavelengths, we dissected and separately tested corneal tissue, vitreous humor, and lenses of one to three freshly euthanized specimens per species not used for ERG experiments. Dissected tissues were immersed in UV-transmitting cuvettes filled with 0.9% saline, placed in a Shimadzu BioSpec-1601 spectrophotometer such that the measuring beam passed through the tissue, and compared to a blank cuvette containing saline alone. Transmission and absorbance were recorded over the spectral range from 250–750 nm.

RESULTS

White-light evoked ERG b-wave responses of the five sciaenids increased non-monotonically with stimulus intensity to maximum amplitudes (V_{\max}) of 100–849 μV then decreased at intensities above those at V_{\max} (Fig. 2), presumably due to photoreceptor saturation and a lack of pigment regeneration. The K_{50} values of $V/\log I$ curves differed significantly among species ($F_{4,25}=9.94$, $P<0.0001$) but not between diel periods ($F_{4,25}=0.74$, $P>0.05$). Tukey's *post-hoc* comparisons revealed that the mean K_{50} values of Atlantic croaker were significantly left shifted (0.5–0.7 log units, $P<0.008$) relative to the other sciaenids, indicating higher sensitivity to dim light. Mean dynamic ranges, defined as 5–95% of V_{\max} , varied between 3.15 and 3.43 log units among the species (Fig. 2) but were not significant with respect to species or diel periods ($P>0.05$). Slightly broader ranges were evident in benthic sciaenids (Atlantic croaker and spot;

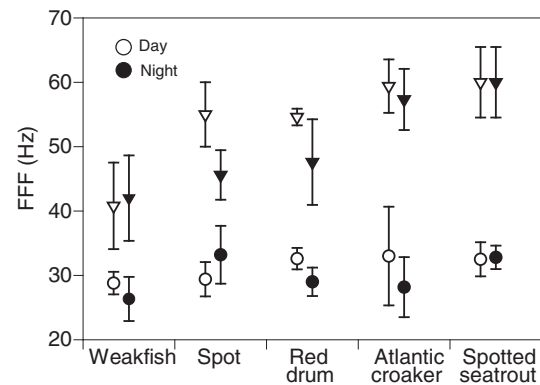


Fig. 3. Mean flicker fusion frequency (FFF) values for five sciaenid fishes. Open symbols are results of day experiments, filled symbols are results of night experiments. Error bars indicate ± 1 s.e.m. Triangles are the FFF at maximum stimulus intensity (I_{\max}); circles are FFF at I_{25} (light levels 25% of I_{\max}). We considered I_{25} to be a proxy for ambient environmental light intensity.

mean=3.34) than in more pelagic species (weakfish, spotted seatrout and red drum; mean=3.19).

Sciaenid FFF values (Fig. 3) varied significantly among the five species ($F_{4,25}=4.63$, $P<0.007$; Fig. 3) and increased with increasing light intensity ($F_{1,84}=148.27$, $P<0.001$), but not between diel periods ($P>0.05$). Likewise, no differences were observed among FFF at I_{25} , but weakfish had significantly lower FFF values at I_{\max} than the other sciaenids ($P<0.004$). By contrast, spotted seatrout, a congener of weakfish, had the highest mean FFF values at I_{\max} in this study (60 Hz).

Sciaenid spectral sensitivities spanned 400–610 nm in most fishes (Figs 4 and 5). Weakfish were a clear exception, exhibiting short wavelength sensitivity (350–400 nm) that was not evident in other sciaenids including a congener, spotted seatrout (Figs 4 and 5). The UV-A sensitivity of weakfish was the significant interspecific difference (Fig. 6). Weakfish and Atlantic croaker demonstrated a significant nocturnal short wavelength shift, while red drum and spot did not exhibit any significant nocturnal spectral shifts (Figs 4 and 5).

Given our data, maximum likelihood estimation using published SSH and GFRKD rhodopsin templates suggested that sciaenid fishes may have multiple pigment mechanisms. Spotted seatrout ($\lambda_{\max}=450$, 542 nm) and spot ($\lambda_{\max}=450$, 546 nm) photopic spectral sensitivities were most consistent with the presence of two α -band vitamin A1 pigments and were optimally fitted with the GFRKD template (Table 2). The trichromatic condition was most likely for Atlantic croaker (SSH $\lambda_{\max}=430$, 484, 562 nm) and red drum (GFRKD $\lambda_{\max}=444$, 489, 564), but estimates were quite variable among templates (Table 2; Fig. 7). The weakfish photopic spectral sensitivity curve was optimally fitted with the SSH template featuring a short wavelength α -band pigment ($\lambda_{\max}=459$ nm) and a longer wavelength pigment ($\lambda_{\max}=532$ nm) that possessed a β -band ($\lambda_{\max}=366$ nm).

Spectrophotometric examination of the transmission of sciaenid ocular media revealed that wavelengths in the UV-A range (350–380 nm) were transmitted through the cornea, vitreous humor and lens of weakfish ($N=2$, Fig. 8). In Atlantic croaker ($N=3$; Fig. 8) and all other sciaenids examined, ultraviolet wavelengths were transmitted by corneal tissue and vitreous humor, but were absorbed by the lens.

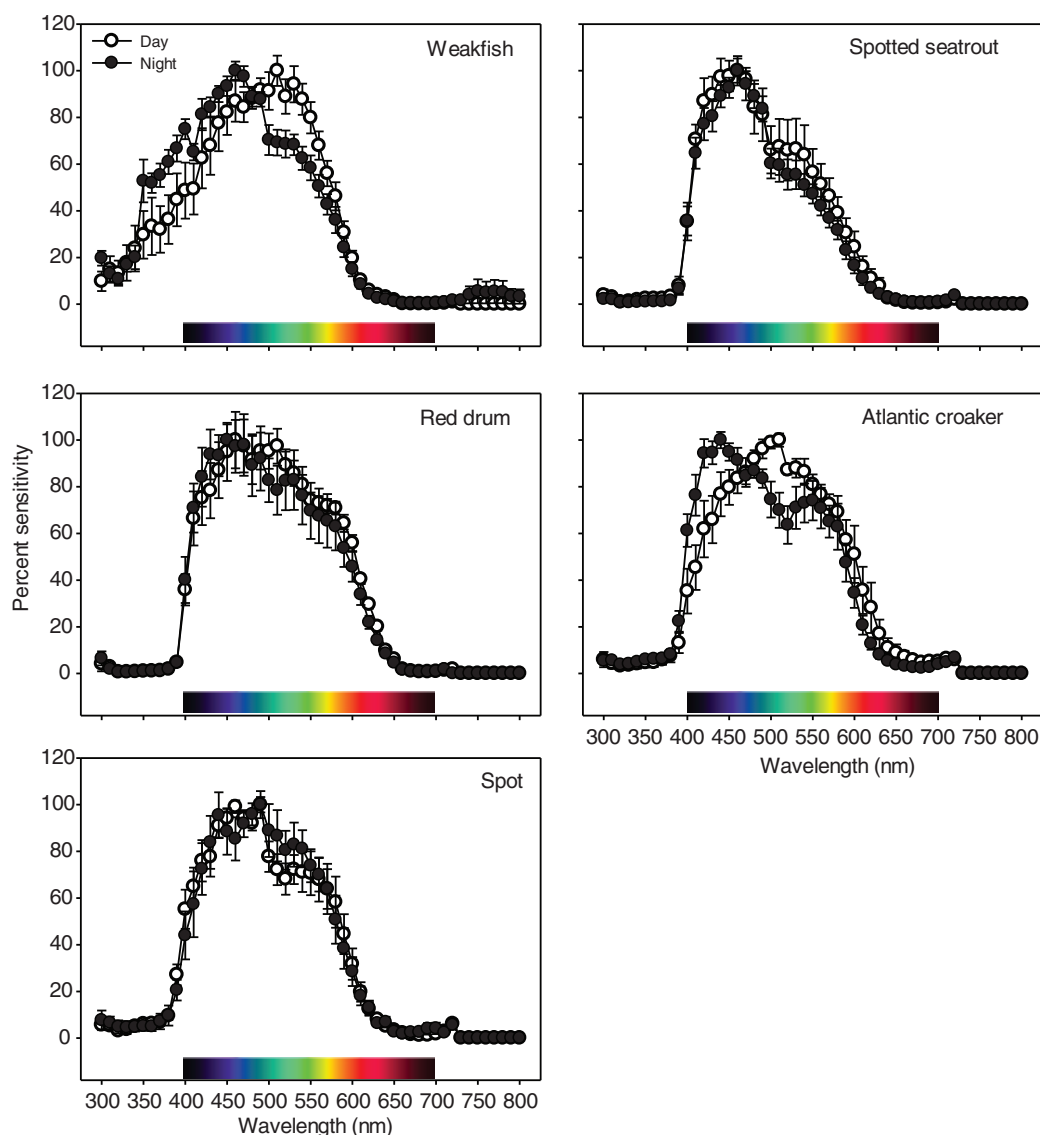


Fig. 4. Spectral sensitivity curves calculated from the electroretinograms (ERGs) of weakfish, spotted seatrout, red drum, Atlantic croaker and spot for wavelengths of 300–800 nm. $N=6$ individuals per species except Atlantic croaker ($N=5$). Responses at each wavelength were normalized to the wavelength of maximal voltage response (V_{\max}) for each individual. Open symbols are results of day experiments, filled symbols are results of night experiments. Error bars indicate ± 1 s.e.m.

DISCUSSION

The complexity of aquatic photohabitats has resulted in a diverse assemblage of visual adaptations in fishes that are generally well-matched to habitat (Guthrie and Muntz, 1993). Although the light environment of deep pelagic seas are fairly stable and homogenous, fresh waters and estuaries tend to be more labile and heterogeneous photohabitats (Loew and Lythgoe, 1978; Loew and McFarland, 1990). In the latter, spectral bandwidths and downwelling intensities can vary greatly over a range of temporal and spatial scales. The estuarine light field, for example, varies temporally due to passing surface waves (milliseconds), clouds and weather (seconds to hours), tides (multihour), sunrise and sunset (daily), and seasonal solar irradiance and phytoplankton dynamics (McFarland and Loew, 1983; Bowers and Brubaker, 2004; Gallegos et al., 2005). Spatial variations include vertical mixing and wave effects (centimeters to meters) as well as tidal and freshwater inputs (meters to kilometers) along salinity gradients (Harding, 1994; Schubert et

al., 2001). Fish movements within and among habitats are further superimposed on these complex temporal and spatial variations. Given the dynamic nature of estuarine photohabitats, the visual systems of near-coastal fishes such as sciaenids should balance sensitivity, acuity, contrast perception and rapid adaptation to dynamic light conditions depending on evolutionary pressures and phylogenetic constraints (Dartnall, 1975; Levine and MacNichol, 1979).

Sciaenid light sensitivities, evidenced by the K_{50} points and dynamic ranges of $V/\log I$ curves, are comparable to other freshwater and marine teleosts (Naka and Rushton, 1966; Kaneko and Tachibana, 1985; McMahon and Barlow, 1992; Wang and Mangel, 1996; Brill et al., 2008) but demonstrate lower sensitivity than deep sea fishes (Warrant, 2000) and arthropods (Frank, 2003). The K_{50} points of Chesapeake Bay sciaenid fishes (Fig. 2) were similar in magnitude and relative diel invariance to demersal Pacific halibut (*Hippoglossus stenolepis*) measured with the same experimental

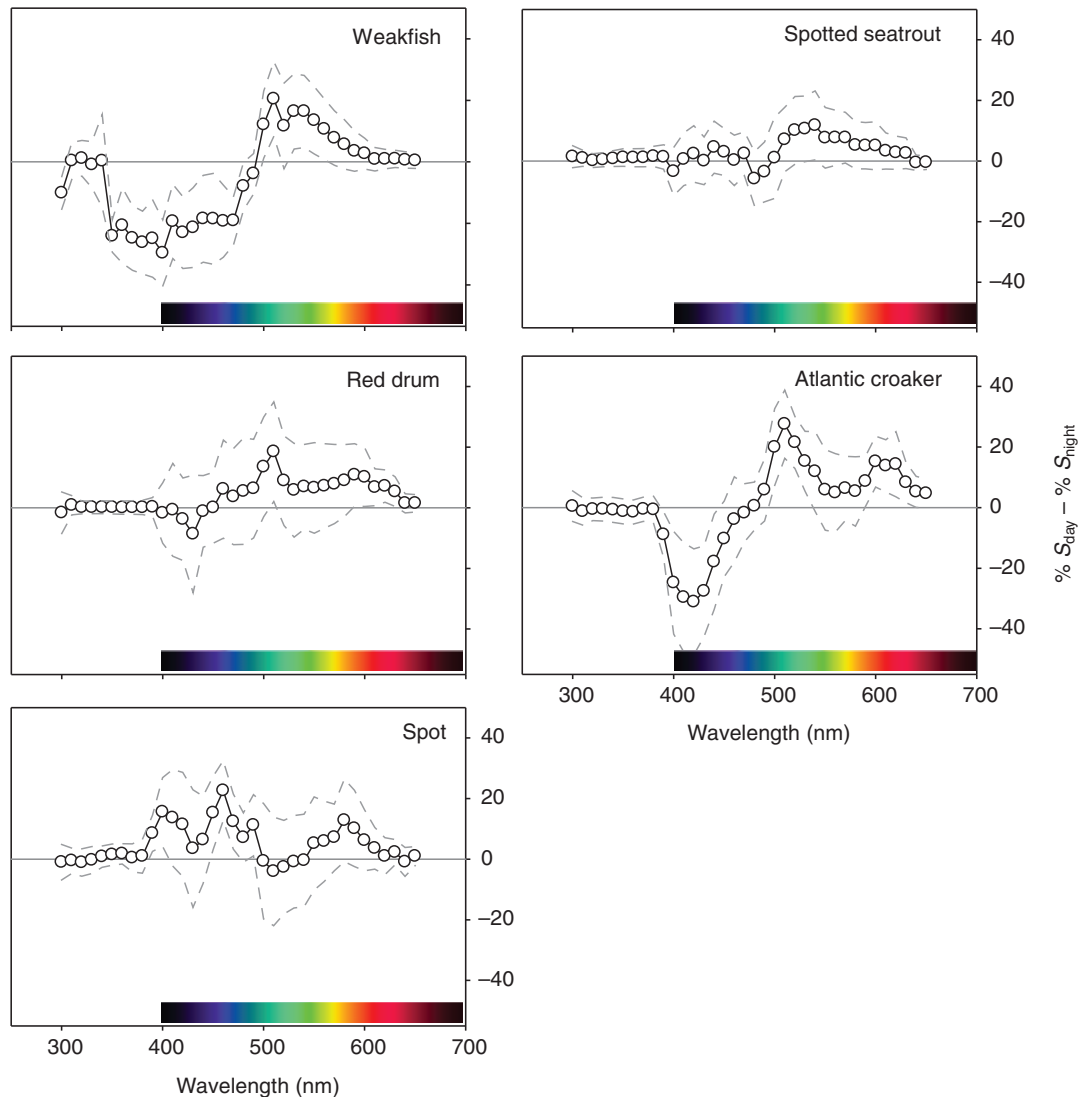


Fig. 5. Diel differences in spectral electrophoretograms (ERGs) of weakfish, spotted seatrout, red drum, Atlantic croaker and spot. Differences were calculated by subtracting the day spectral sensitivities (S_{day}) from night sensitivities (S_{night}). Dashed gray lines are $\pm 95\%$ CI, calculated as $1.96 \times (\text{s.e.m.})$. Values above the horizontal zero line (i.e. positive) indicate wavelengths of greater response during daylight, those below the zero line (i.e. negative) indicate wavelengths of greater nocturnal response. Significant differences occurred when CI did not encompass zero.

setup (halibut day: 0.15, night: 0.14 $\log \text{cdm}^{-2}$) (Brill et al., 2008). Benthic Atlantic croaker and spot (Figs 1 and 2) have left-shifted K_{50} values (i.e. more light sensitivity) relative to halibut, whereas pelagic sciaenids were right shifted (i.e. less sensitivity). All Chesapeake Bay sciaenids had substantially left-shifted K_{50} values relative to those of black rockfish (*Sebastes melanops*), a fairly shallow-dwelling coastal Pacific sebastid (2.0 $\log \text{cdm}^{-2}$) (Brill et al., 2008). Increased luminous sensitivity in sciaenids is facilitated by retinal non-guanine tapeta lucida that backscatter high proportions of the incident light similar to those of haemulid grunts, ophidiid cusk eels and ehippid spadefishes (Arnott et al., 1970). Sciaenids also undertake retinomotor movements at intensities $\sim 10 \text{ lux}$ to improve sensitivity to dim light (Arnott et al., 1972). Collectively, these results suggest that the light sensitivities of sciaenids from Chesapeake Bay tend toward the lower (more sensitive) end of an emerging continuum for coastal fishes, consistent with their use of frequently light-variable photic habitats.

Temporal properties of sciaenid visual systems are also comparable to a range of diurnal freshwater and marine fishes. As FFF typically increases with light intensity (Crozier et al., 1938), sciaenid FFFs were significantly lower at I_{25} , than at I_{max} during both day and night. If I_{25} approximates average estuarine intensity, the *in situ* temporal properties of sciaenids may converge on similar function at lower light intensities. Similarly, maximum FFF values reveal the scope of the visual system when light is not limiting. Predators that exploit rapidly swimming prey in clear, bright conditions tend towards high FFFs and low spatial summation of photoreceptors (Bullock et al., 1991). Maximum day FFFs for most sciaenids were 50–60 Hz, similar to photopic maxima of coastal thornback rays (*Platyrrhinoidis triserata*: 30–60 Hz), grunion (*Leuresthes tenuis*: >60 Hz), sand bass (*Paralabrax nebulifer*: >60 Hz) (Bullock et al., 1991), and freshwater centrarchid sunfishes (51–53 Hz) (Crozier et al., 1936; Crozier et al., 1938) that inhabit less turbid environments than sciaenids. Since FFF varies with

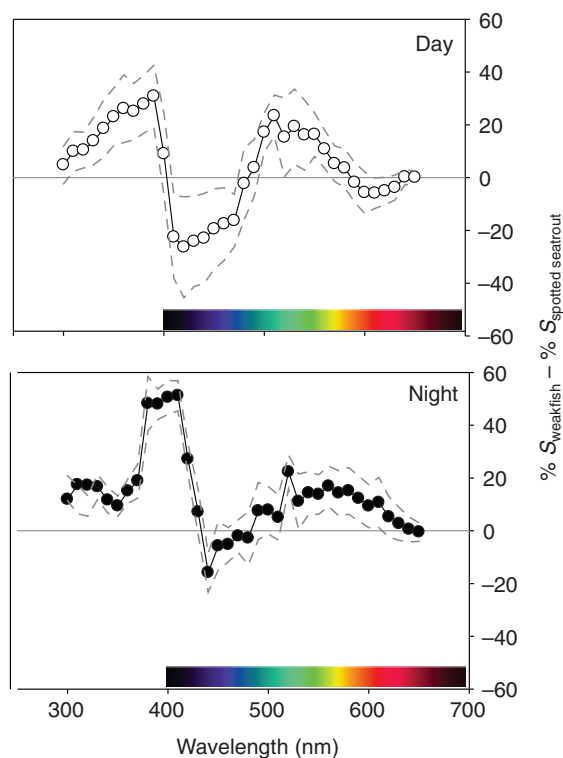


Fig. 6. Differences in spectral electroretinograms of weakfish and spotted seatrout, calculated by subtracting the weakfish spectral sensitivities (S_{weakfish}) from those of spotted seatrout ($S_{\text{spotted seatrout}}$). Open symbols are day values, filled symbols are night values. Dashed gray lines are $\pm 95\%$ CI, calculated as $1.96 \times (\text{s.e.m.})$. Significant differences occurred when CI did not encompass zero.

temperature (Saszik and Bilotta, 1999; Fritsches et al., 2005), sciaenids at 20°C predictably had higher FFFs than Antarctic nototheniid fishes at 0°C ($<15\text{ Hz}$) (Pankhurst and Montgomery, 1989). Sciaenid FFF data were also lower than those of yellowfin tuna (*Thunnus albacares*: 60–100 Hz) that inhabit warm, clear nearsurface waters and forage on rapidly swimming prey (Bullock et al., 1991), and higher than those of the broadbill swordfish (*Xiphias gladius*: 32 Hz) that are predators of the organisms in the deep scattering layer (Fritsches et al., 2005). We caution that experimental and analytical differences among studies may limit inferences in the broad qualitative comparisons above, but consider the collective generalizations to be consistent with ecologies and life histories of the species discussed.

The temporal and spatial properties of sciaenid visual systems are consistent with inferences based on ecology and lifestyle. Weakfish, a coastal pelagic crepuscular/nocturnal predator of small translucent crustaceans and planktivorous fishes (Fig. 1), exhibited the lowest maximum FFFs, and thus the highest degree of temporal summation ($\text{FFF}_{\text{day}}=40.8\text{ Hz}$; $\text{FFF}_{\text{night}}=43\text{ Hz}$). Not surprisingly, weakfish also have low ganglion cell densities, suggesting high spatial summation of photoreceptors and low acuities relative to other sciaenids (K. Fritsches, personal communication) (Poling and Fuiman, 1998). The slow, light-sensitive eyes of weakfish have thus evolved to maximize photon capture at the expense of acuity, as would be expected of dim-dwelling species (Warrant, 1999). By contrast, maximum diel FFFs of spotted seatrout were the highest measured during day and night, indicating the lowest temporal summation. Ganglion cell densities of spotted seatrout also

demonstrate less summation of individual photoreceptors and substantially higher acuity than their congener weakfish (K. Fritsches, personal communication). The greater image sampling *via* temporal and spatial mechanisms of spotted seatrout eyes are probably more advantageous than dim light sensitivity for prey location in the shallow, structurally complex seagrass meadows they inhabit (Fig. 1). Ecology and lifestyle thus appear to influence visual function more than phylogeny in the genus *Cynoscion*. Finally, maximum FFF of the three benthic-foraging sciaenids, Atlantic croaker, red drum and spot (Fig. 1), were intermediate between those of the *Cynoscion* endmembers, with generally lower values at night than during the day. Benthic-foraging sciaenids probably possess generalist eyes that balance luminous sensitivity, speed, and resolution without excelling at any one task.

Spectral properties of sciaenid visual systems can likewise be placed in context with other fishes. Near-coastal fishes are typically sensitive to longer wavelengths than coral reef, deep sea and pelagic species and a shorter subset of wavelengths than many freshwater fishes (Levine and McNichol, 1979; Marshall et al., 2003). All sciaenids demonstrated broad spectral responses to wavelengths from 400–610 nm that blue-shifted nocturnally in weakfish and Atlantic croaker. Whether these results are the by-product of retinomotor movements that increase rod contributions in night recordings, occur as a result of mesopic conditions resulting from our methodology, or some combination of both, is unclear. Under photopic conditions, previous work has demonstrated that coastal and estuarine fishes are commonly dichromats possessing short wavelength visual pigments with λ_{max} values ranging from 440–460 nm and intermediate wavelength pigments with λ_{max} values of 520–540 nm (Lythgoe and Partridge, 1991; Lythgoe et al., 1994; Jokela-Määttä et al., 2007). Yellow-orange light of 515–600 nm penetrates maximally in Chesapeake Bay (Champ et al., 1980), thus intermediate wavelength rhodopsins of coastal dichromats may be matched to ambient optical conditions consistent with the ‘sensitivity hypothesis’ (Bayliss et al., 1936; Clark, 1936), whereas the short wavelength rhodopsins may conform to the ‘contrast hypothesis’ (Lythgoe, 1968).

Given the lack of published data on sciaenid photopigments, we fitted SSH and GFRKD rhodopsin templates to our spectral ERG data as a descriptive exercise to generate hypotheses that may be subsequently examined using other techniques. Dichromatic visual systems were most likely in weakfish, spotted seatrout and spot whereas trichromatic visual systems were most likely in red drum and Atlantic croaker. Whether the exact values of our λ_{max} estimates represent meaningful interspecific differences in pigment locations or result from the expression of variance due to our methodology remains unknown. We therefore strongly emphasize caution in their interpretation. Corneal recordings can contain the summed responses of multiple retinal cells and pigments after filtering of light by pre-retinal optical media (Brown, 1968; Ali and Muntz, 1975), and the interpretation of pigment absorbance maxima without selective isolation of individual mechanisms is tenuous. These preliminary hypotheses should be critically evaluated with more sensitive techniques such as microspectrophotometry (MSP), behavioral experiments, and/or ERG chromatic adaptation before any valid conclusions regarding potentially contributory photopigment mechanisms can be drawn (Barry and Hawryshyn, 1999; Parkyn and Hawryshyn, 2000). Unfortunately, explicit morphological assessment of cone types, the pigments they contain, and their distributions in sciaenid retinae were beyond the scope of our study. However, our suggestion of the possibility of multiple chromatic mechanisms in sciaenids is potentially supported by the presence

Table 2. Parameter estimates and model rankings of SSH and GFRKD vitamin A1 rhodopsin templates fitted to sciaenid photopic spectral ERG data *via* maximum likelihood

Species	Condition	Template	$\lambda_{\max,1}$	$\lambda_{\max,2}$	$\lambda_{\max,3}$	$-\log(L)$	p	AIC	ΔAIC
Weakfish	Di, α	GFRKD	428	524	—	-62.2	5	-114	72
		SSH	445	530	—	-56.0	5	-102	84
	Di, β , S	GFRKD	443	529	—	-59.3	6	-107	79
		SSH	456	532	—	-91.8	6	-172	14
	Di, β, L	GFRKD	454	530	—	-94.7	6	-177	9
		SSH	459	532	—	-98.9	6	-186	0
	Di, β , B	GFRKD	459	531	—	-72.1	7	-130	56
		SSH	472	532	—	-91.4	7	-169	17
	Tri, α	GFRKD	453	531	368	-91.2	7	-168	17
		SSH	456	532	369	-93.5	7	-173	13
Spotted seatrout	Di, α	GFRKD	450	542	—	-69.8	5	-130	0
		SSH	451	542	—	-64.7	5	-119	10
	Tri, α	GFRKD	450	542	502	-69.8	7	-126	4
		SSH	455	540	468	-64.9	7	-116	14
Red drum	Di, α	GFRKD	457	555	—	-65.0	5	-120	8
		SSH	459	556	—	-61.2	5	-112	16
	Tri, α	GFRKD	444	564	489	-71.1	7	-128	0
		SSH	448	564	493	-66.0	7	-118	10
Atlantic croaker	Di, α	GFRKD	454	545	—	-67.4	5	-125	45
		SSH	457	546	—	-66.3	5	-123	47
	Tri, α	GFRKD	430	562	484	-92.0	7	-170	0
		SSH	437	562	486	-87.9	7	-162	8
Spot	Di, α	GFRKD	450	546	—	-86.1	5	-162	0
		SSH	451	547	—	-82.4	5	-155	7
	Tri, α	GFRKD	450	547	499	-86.1	7	-158	4
		SSH	445	548	466	-83.0	7	-152	10

p, the number of parameters in a model; AIC, Akaike's information criterion; Di, dichromatic; Tri, trichromatic; α , scenarios where only alpha bands were considered; S, L and B following β refer to the modeled position of β -band(s) on short, long, or both pigments, respectively. The number following λ_{\max} refers to the pigment's estimated spectral position (in nm).

Bold type indicates the best supported pigment and template scenarios based on AIC values.

Monochromatic conditions were very unlikely, demonstrating extremely poor fits given our data (ΔAIC values >110), and were thus omitted from this table.

of different photoreceptor morphotypes in at least some study species. Atlantic croaker and weakfish retinas contain both single and paired cones (Poling and Fuiman, 1997) (A.H., personal observation). The latter cone type is frequently sensitive to longer wavelengths than the former in many fishes (Boehlert, 1978), and the presence of both single and paired cones in a species suggests that multiple pigment mechanisms are likely (Bowmaker, 1990). Finally, the ambient light field and background spectral properties, the reflectance of conspecifics, prey and competitors, and the manner in which these change in space and time should be understood in order to synoptically summarize the utility of visual system and tasks for a species (Levine and MacNichol, 1979; Johnsen, 2002).

Spectral responses in the ultraviolet were observed in weakfish but not in any of the other sciaenids. Whether a species is able to see in the ultraviolet spectrum depends on the transmission of the ocular media, the retinal density of UV-sensitive photoreceptors, and the concentrations of attenuating particulate and dissolved organic matter in the photohabitat (Leech and Johnsen, 2003; Leech and Johnsen, 2006). The general lack of ERG responses in the ultraviolet is not surprising for most sciaenids because of strong absorption of these wavelengths in lenses (50% transmission points greater than 380 nm; Fig. 8). Vision in the ultraviolet is considered unlikely if much of the adjoining spectrum is absorbed by preretinal ocular media (Losey et al., 2003). By contrast, the corneas, humors and lenses of weakfish transmit UV (50% at 356 nm; Fig. 8)

consistent with a class II response (Losey et al., 2003). It is thus possible that weakfish may achieve at least some ability to form images in the UV *via* an independent cone mechanism or the secondary β -band absorption peak (<400 nm) characteristic of visual pigments (Dartnall and Lythgoe, 1965; Douglas and McGuigan, 1989; Losey et al., 2003; Siebeck et al., 2006). Although the causal mechanism has not been formally demonstrated, AIC values of fitted pigment templates suggested that weakfish UV responses are more probably due to a β -band of the longer wavelength pigment than a separate UV cone. Whether UV-responding pigments occur in sufficient density to contribute to contrast enhancement and image formation (*sensu* Leech and Johnsen, 2003) is likewise unknown.

The potential utility of UV sensitivity to the species also remains unclear, since little is known about the UV reflectance of weakfish predators, conspecifics and prey. Any potential benefit of increased visual contrast in the ultraviolet channel would presumably be limited by seasonal turbidity that rapidly attenuates UV in the upper 1–3 m of Chesapeake Bay in warmer months (Banaszak and Neale, 2001). However, like most species in this study, weakfish did not evolve under present day Chesapeake Bay optical conditions and are only seasonal inhabitants of this estuary (Murdy et al., 1997). Most overwinter in coastal Mid-Atlantic waters where downwelling UV-A wavelengths may reach 10–15 m (Cohen and Forward, 2002) in sufficient intensity for vision (Losey et al., 1999). Compelling

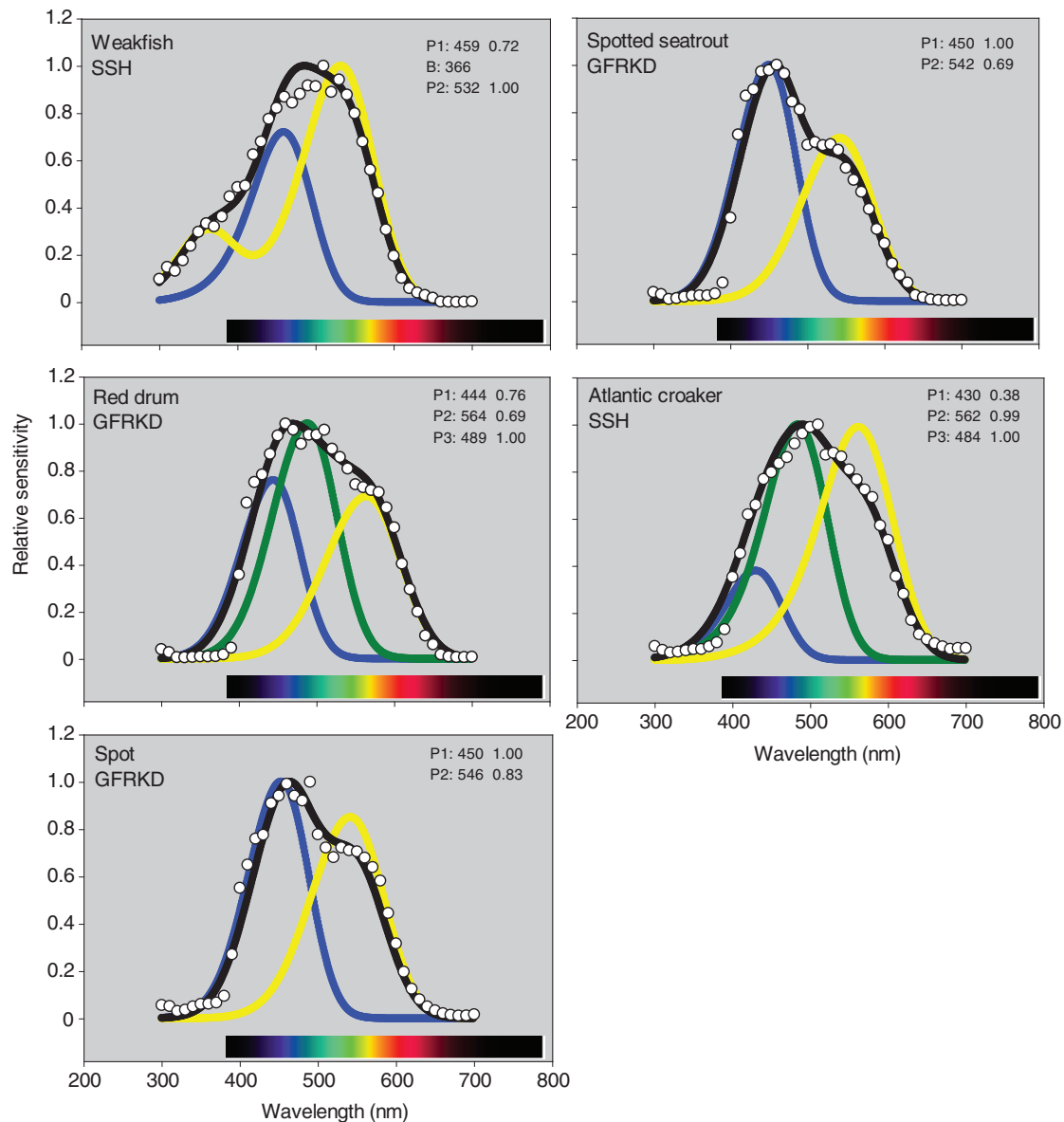


Fig. 7. SSH (Stavenga et al., 1993) and GFRKD (Govardovskii et al., 2000) vitamin A1 templates fitted to sciaenid spectral ERD data by maximum likelihood. Only estimates from best fitting models from Table 2 were plotted for each species. Values to the right of each pigment label are estimated λ_{\max} and pigment specific weight as estimated by the model. P1 (blue) is the short wavelength pigment, P2 (yellow) is the long wavelength pigment, and P3 (where applicable; green) is the intermediate pigment. Black lines represent additive curves developed by summing the product of each curve weighted by the estimated weighting factor. White circles are mean photopic spectral sensitivities from Fig. 4. For weakfish, B refers to the estimated peak of the P2 β -band.

questions remain on the topics of ultraviolet attenuation in coastal photohabitats, potential mechanism(s) mitigating UV response and its potential utility for weakfish, and the possibility of similar UV responses in other *Cynoscion*.

Combined, our results suggest that the visual systems of these five coastal and estuarine sciaenids appear fairly well suited to the typical photic conditions of the turbid coastal and estuarine habitats they utilize throughout their range. Turbidity in estuarine systems scatters light, reducing ambient light intensity and degrading contrast, ultimately reducing the distances over which conspecifics, predators and prey interact (De Robertis et al., 2003; Mazur and Beauchamp, 2003). Paradoxically, many fishes that inhabit productive, turbid ecosystems, such as estuaries, rely on vision to detect their predators, prey and mates (Abrahams and Kattenfield,

1997; Engström-Östa and Candolin, 2007). Interspecific differences in sensory integration have been demonstrated in sympatric sciaenids (Poling and Fuiman, 1998; Liao and Chang, 2003), suggesting that turbidity may affect species differently. For example, increasing turbidity can force predators to modify their behavior from visual-based foraging strategies to less efficient encounter rate approaches (Greccay and Targett, 1996). Furthermore, human-induced turbidity can also affect mate choice, relax sexual selection and reduce reproductive isolation in sympatric species (Lake Victoria cichlids) (Seehausen et al., 1997).

Optical conditions in Chesapeake Bay have changed dramatically over the past century of industrialization, population expansion and eutrophication (Kemp et al., 2005), at a pace faster than the evolution of the visual systems of its fauna. Similar anthropogenic changes

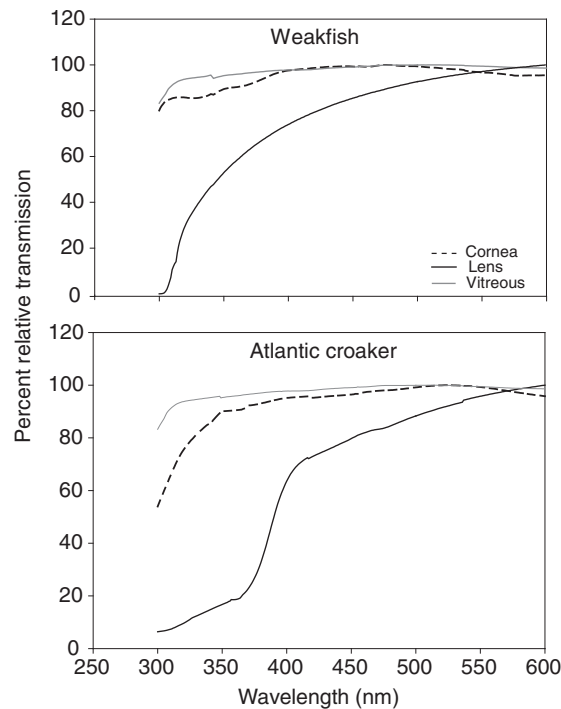


Fig. 8. Relative spectral transmission of the cornea, vitreous humor, and lens of weakfish ($N=2$) and Atlantic croaker ($N=3$) demonstrating that UV-A wavelengths (350–380 nm) are transmitted by all three optical tissues in weakfish, but appear to be absorbed by the lens of croaker. Optical tissues of spotted seatrout, red drum and spot followed the croaker pattern, absorbing strongly below 380 nm.

are likely to be occurring in many coastal ecosystems that serve as key habitats for managed aquatic organisms, where the consequences for predation, mating and other activities involving vision have received little attention (McFarland, 1986; Beck et al., 2001; Evans, 2004). In light of increasing anthropogenic degradation, comparative studies that examine the relationships between sensory physiology and behavioral ecology are thus important to mechanistically link processes from the cellular to the individual to the population level, to support the management of aquatic resources.

We thank Capt. S. Wray, J. Lucy, J. Smith, P. Lynch, and the vessels *Bada Bing* and *Sea Beaver* for their assistance collecting study animals. S. Johnsen and L. Litherland kindly provided comments on earlier drafts of this manuscript. K. Fritsches and L. Litherland patiently provided assistance with lamp calibrations and electroretinographic experiments, and M. Luckenbach, R. Bonniwell, and S. Fate provided logistical assistance and extreme flexibility in support of these experiments. Assistance with animal husbandry was graciously provided by A. Buchheister, P. Lynch, C. Magel, S. Musick, T. Nania, L. Rose and J. Woodward. This research was funded by the Virginia Sportfish Development Fund, Virginia Marine Resources Commission. Partial support was also provided by the National Marine Fisheries Service and by an award to A.Z.H. from the International Women's Fisheries Association. E.J.W. is grateful for the ongoing support of the Swedish Research Council (VR). This is VIMS contribution number 2968.

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