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ABSTRACT

Visual temporal resolution and spectral sensitivity of three coastal teleost species (common snook [*Centropomus undecimalis*], gray snapper [*Lutjanus griseus*], and pinfish [*Lagodon rhomboides*]) were investigated by electroretinogram. Temporal resolution was quantified under photopic and scotopic conditions using response waveform dynamics and maximum critical flicker fusion frequency (CFF_{max}). Photopic CFF_{max} was significantly higher than scotopic CFF_{max} in all species. The snapper had the shortest photoreceptor response latency time (26.7 ms) and the highest CFF_{max} (47 Hz), suggesting that its eyes are adapted for a brighter photic environment. In contrast, the snook had the longest response latency time (36.8 ms) and lowest CFF_{max} (40 Hz), indicating that its eyes are adapted for a dimmer environment or nocturnal lifestyle. Species spectral responses ranged from 360 to 620 nm and revealed the presence of rods sensitive to dim and twilight conditions, as well as multiple cone visual pigments providing the basis for color and contrast discrimination. Collectively, our results demonstrate differences in visual function among species inhabiting the Indian River Lagoon system, representative of their unique ecology and life histories.

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Introduction

Teleost fishes represent a speciose vertebrate lineage that radiated into distinct aquatic habitats that present unique divergent light qualities (Jerlov 1968). Selective pressure on the piscine eye has resulted in an extensive array of both morphological and physiological adaptations to maximize visual function under differing light conditions. Morphological adaptations—including eye size, eye position, lens composition, retinomotor movement, and reflective retinal media—have been correlated to aspects of life style and habitat niche (Collin and Marshall 2003). Furthermore, the growth of the teleost eye throughout life allows for dynamic physiological adaptations to the prevailing aquatic light field throughout ontogeny (Zaunreiter et al. 1991; Stearns et al. 1994; Schwab 2012).

The maximum transmission of light occurs at shorter wavelengths in deep-sea and clear open ocean environments (blue), at intermediate wavelengths in coastal waters (green), and at longer wavelengths in estuarine and freshwater environments (yellow-red; Jerlov 1968). For mobile species that utilize several distinct habitats, maintaining optimal visual performance over the full range of ambient light conditions is nearly impossible, and unavoidable physiological trade-offs exist between visual sensitivity and resolution. For instance, absolute sensitivity of the eye may increase in low-light or turbid conditions to maximize photon capture but requires a reduction in temporal resolution (Warrant and Locket 2004). For species that do not possess mobile pupils or other mechanisms to increase sensitivity, reducing temporal resolution is analogous to holding a shutter open longer on a camera, resulting in an increase in absolute sensitivity of the eye. The temporal and spatial properties of visual systems in fish vary depending on ecological constraints and light qualities of the habitat.

Teleosts possess rod photoreceptors that confer sensitivity and resolution in low-light conditions and may possess single, double, and twin cone photoreceptors for bright conditions. The possession of multiple cone types allows for behavioral color discrimination (McFarland and Munz 1975). Extensive research has linked ambient environmental light and fish photoreceptor sensitivity. The sensitivity hypothesis proposed by Clarke (1936) states that rod-based photoreceptor sensitivity will match the ambient microhabitat spectra to maximize photon capture in lower light conditions. The contrast sensitivity hypothesis (Lythgoe 1968) states that maximum contrast of objects against a background is achieved by the presence of matched and slightly offset visual pigments and is the principal evolutionary driver and utility of color vision (Wallace 1891; Walls 1942; Marshall et al. 2003). The twilight hypothesis (Lythgoe 1968; Munz and McFarland 1973, 1977; McFarland 1991)

predicts that sensitivity of rod photoreceptors in fish will match the more narrow range of environmental spectra during dusk and dawn, thus enhancing vision during a biologically active period of heightened predation.

In this study, we test the predictions of these hypotheses by characterizing the spectral sensitivities and response dynamics of three teleost fish species that inhabit the Indian River Lagoon, Florida. The Indian River Lagoon is North America's most biodiverse estuarine ecosystem, with habitats comprised of seagrass flats, mangrove forests, and salt marshes that provide nursery and shelter to more than 700 fish species (Gilmore et al. 1981, 1983; Mulligan and Snelson 1983; Tremain and Adams 1995). Decades of anthropogenic stressors have altered water clarity and quality in the lagoon (Sigua and Steward 2000; Sigua and Tweedale 2004). Reduced visibility can negatively impact foraging success of visual predators, necessitating a switch to less efficient and energetically costly encounter-rate feeding (Grecay and Targett 1996). Alterations in predatory foraging strategies can ultimately alter fish community structure (Seehausen et al. 1997; Helfman et al. 2009; Montaño 2009). Because of alterations within this ecosystem and management plans to increase viability of game fish populations, a comparative assessment of visual performance of predatory and prey species within the Indian River Lagoon was warranted.

The objective of this study was to determine whether the visual performance of three teleost species from the Indian River Lagoon correlated with aspects of their habitat and ecology. Temporal resolution and spectral sensitivity were determined for two visually oriented predators and their shared prey: the common snook (*Centropomus undecimalis* Bloch 1792) and gray snapper (*Lutjanus grisues* Linnaeus 1758) are large piscivores that prey on pinfish (*Lagodon rhomboides* Linnaeus 1766). Spectral sensitivity was determined under scoptopic and photopic conditions in order to test predictions about the sensitivity, twilight, and contrast hypotheses. Temporal resolution was quantified under scotopic and photopic conditions in order to elucidate potential correlations with habitats and predator-prey dynamics.

Material and Methods

Specimen Collection and Maintenance

Common snook, gray snapper, and pinfish were captured by standard hook and line fishing gear within the Indian River Lagoon (fig. 1; table 1). Captured fish were immediately transported to holding tanks at Florida Atlantic University's Harbor Branch Oceanographic Institute, Fort Pierce, Florida, where they were maintained in Indian River Lagoon flow-through aquaria (14,388 L) on natural ambient photoperiods. Fish were fed daily a combination of live shrimp, frozen shrimp, and squid. Fish were collected and experiments conducted at Harbor Branch Oceanographic Institute in accordance with Florida Fish and Wildlife Special Activity License AL-10-1272-SR and Florida Atlantic University Institutional Animal Care and Use Committee protocol 10-26. After experimentation, fish were revived, rehabilitated, and released back into the wild under Florida Fish and Wildlife guidelines.

Experimental Setup

The temporal resolution and spectral sensitivity of the photoreceptors were electrophysiologically determined using an electroretinogram (ERG) technique. Experimental animals were anesthetized with tricaine methanesulphonate (MS-222; 1 : 15,000 wt : vol). After respiration ceased (2–4 min), animals were quickly transferred to an acrylic experimental tank (79 cm × 39 cm × 11 cm) and secured with Velcro straps to a submerged plastic stage. Animals were immediately fitted with an oral ventilation tube that delivered a recirculating maintenance dose (1 : 20,000 wt : vol) of MS-222 over the gills; flow was confirmed with a dye test. The experimental tank was placed within a Faraday cage and light eliminated by creating a dark room frame using black plastic sheeting. The animals' eyes were allowed to dark-adapt for a minimum of 45 min. All necessary adjustments in the dark were made under dim red light. The water was aerated throughout the trial, and water temperature was maintained between 24° and 25°C.

ERGs were recorded by placing a tungsten microelectrode (5–7 MΩ; FHC, Brunswick, ME) subcorneally in the submerged eye, while grounding the body with an AgCl wire. The signals were amplified (× 1,000–10,000) and filtered (low cutoff, 0.1 Hz; high cutoff, 15 kHz) with a microelectrode amplifier (Xcell-3; FHC), used together with a high-impedance probe to minimize electrode polarization artifacts. The data were digitized and stored for later analysis using a data acquisition program written in LabView (National Instruments, Austin, TX).

The monochromatic light stimulus (CM110 monochromator; Spectral Products, Putnam, CT) was positioned so that the output covered the entire eye of the specimen via one branch of a bifurcated, randomized fiber optic light guide (EXFO, Quebec). A Uniblitz shutter (model T132; Vincent, Rochester, NY) provided a stimulus flash of 100 ms, and stimulus irradiance was adjusted using a neutral density filter wheel driven by a stepper motor, both of which were under computer control. Irradiance was calibrated in 10-nm increments with a UDT optometer (model S37; UDT Instruments, San Diego, CA) using a calibrated radiometric probe.

Temporal Resolution

Temporal resolution is a measure of the integration time of the eye, which reflects the organism's ability to track moving objects. Temporal resolution of the eye was quantified in a minimum of six individuals of each species using two methods: (1) flicker fusion frequency and (2) response waveform dynamics. Flicker fusion frequency experiments involved presenting the dark-adapted eye with a 2-s train of square pulses of light (50 : 50 light : dark ratio) generated by cycling a computer-controlled electromagnetic shutter in the light path and recording the ERG responses. The highest frequency at which the eye could produce an ERG that remained in phase with

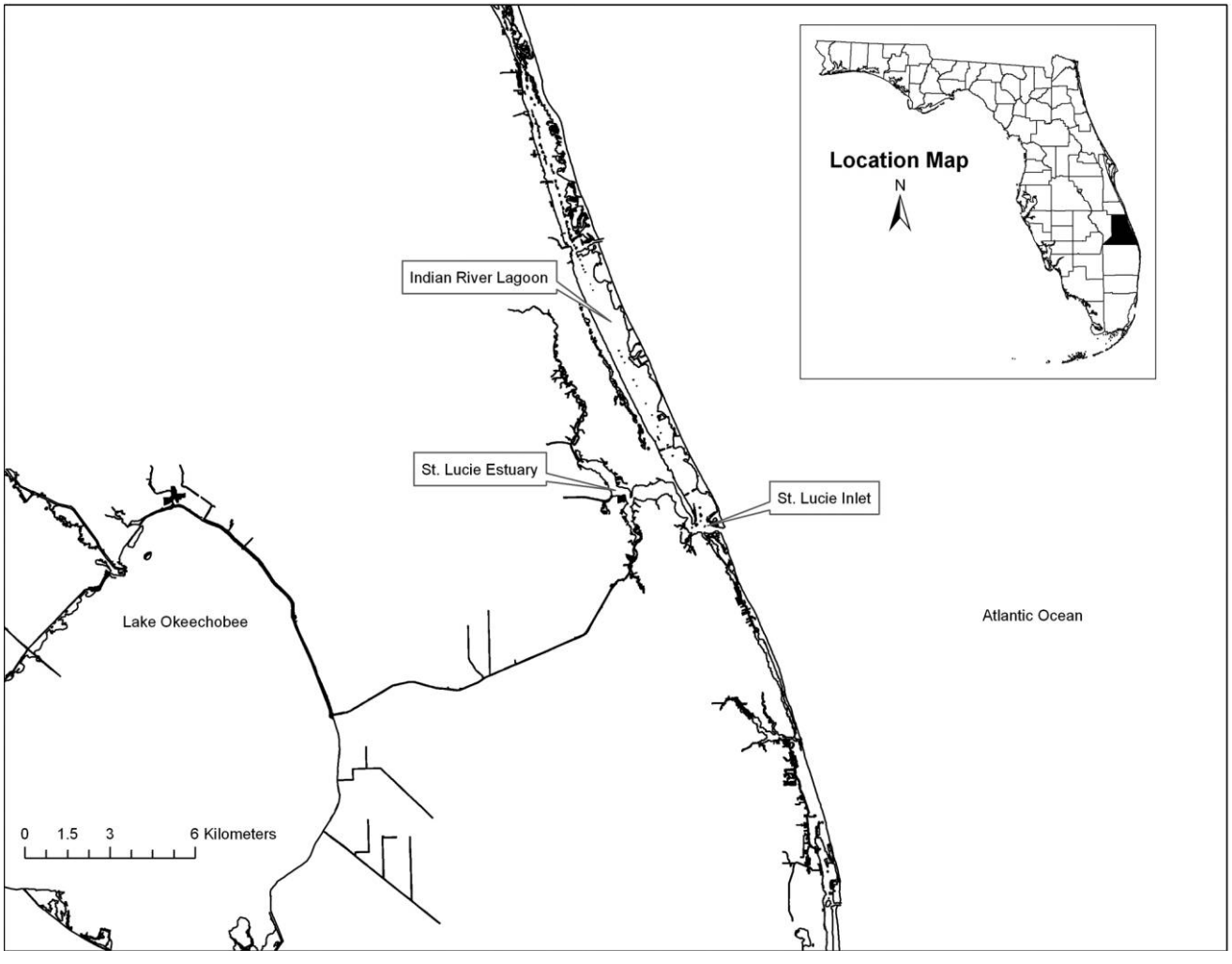


Figure 1. Place of capture for the common snook, gray snapper, and pinfish used in this study. The Indian River Lagoon is North America's most biodiverse estuary, with more than 700 fish species inhabiting mangrove, salt marsh, and seagrass ecotones. Recent anthropogenic activities have negatively altered water quality and clarity within the lagoon.

the stimulus light of a set irradiance over a 0.5-s interval was defined as the critical flicker fusion frequency (CFF). However, CFF is dependent on the irradiance of the stimulus light (Bröcker 1935; Crozier and Wolf 1939; Crozier et al. 1939) such that as irradiance increases, there is an increase in CFF. A less variable characteristic to use for comparative studies is the maximum CFF (CFF_{max}), defined as the maximum flicker rate that the eye is capable of following at any irradiance (Frank 1999). We ensured that we had achieved the CFF_{max} by demonstrating that at least three irradiance increases produced no further increases in CFF. To determine whether light adaptation affected CFF_{max}, the entire procedure was repeated under light-adapted conditions. Scotopic and photopic values among each individual species were compared with Mann-Whitney rank sum and paired *t*-tests. The CFF_{max} values of all species in the scotopic treatment were compared using one-way ANOVAs (Systat, San Jose, CA) with pairwise multiple comparisons by Tukey post hoc tests and the procedure repeated for the photopic treatment.

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

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

where V is the response amplitude at irradiance I, I is the stimulus irradiance, m is the slope of the linear portion of the *V*/log *I* curve, V_{max} is the maximum response amplitude, and K is the stimulus irradiance eliciting half the maximum re-

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

Species	*Centropomus undecimalis*	*Lutjanus griseus*	*Lagodon rhomboides*
N	12	12	12
Standard length (cm)	30.2–56.1	21.3–34.8	13.1–25.2
Habitat	Seagrass, mangrove, riverine	Coastal, reef, rocky, mangrove, riverine	Marine or fresh
Movement	Amphidromous	Amphidromous	Demersal aggregate
Diet	Finfish	Benthic crustaceans finfish	Benthic algae/weeds
Trophic level	4.4	3.6	2.0
Scotopic sensitivity λ_{max} (nm)	491	505	501
Photopic sensitivity λ_{max} (nm)	412, 468, 538	485, 528	418, 487, 540
Scotopic CFF_{max} (Hz)	34.0 ± 1.03	42.0 ± 1.88	36.5 ± 1.11
Photopic CFF_{max} (Hz)	39.6 ± 1.22	46.7 ± 2.13	43.7 ± .94
Response latency (ms)	36.8 ± 2.3	26.7 ± 1.5	34.6 ± 2.2

Note. Spectral sensitivity was determined using the electroretinogram (ERG) technique, and maximum critical flicker fusion frequency (CFF_{max}) was the maximum flicker rate that the eye was capable of following at any irradiance. Response latency measured from ERG responses that were 50% of V_{max}. For CFF_{max} and response latency, data are means ± SE.

sponse (V_{max}). Although an experimental V_{max} was not attained in some preparations, if the largest response recorded in the eye reached 90% of the calculated V_{max}, data from these experiments were included in the analyses.

Spectral Sensitivity

Spectral sensitivity experiments were conducted to assess the visual system's ability to respond to colored light stimuli. A minimum of six individuals of each species was tested under dark- and then light-adapted conditions. The eye was stimulated with 100-ms test flashes of monochromatic light until a defined criterion response was attained at each wavelength (350–620 nm, every 10 nm). The criterion was generally set 20–30 μV above baseline noise to ensure that light intensity used during dark-adapted experimentation would not unnecessarily light-adapt the eye. The order of test flashes was randomized, and a standardized test flash was presented periodically throughout the trial to confirm that the physiological state of the eye had not changed. Experiments were initiated only when test flash responses were stable.

Chromatic adaptation experiments were performed under low ambient light conditions to light-adapt the eye and elicit cone responses. In addition to the room light, the adapting incandescent light source was filtered by a 478-nm interference filter (Ealing 35-3094, full width at half maximum = 14 nm) for blue adaptation and a 532-nm interference filter (Melles Griot F10-532, full width at half maximum = 10 nm) for green adaptation. Irradiance was adjusted with neutral density filters such that the adapting light decreased the sensitivity of the eye by 1–2 log units. The adapting light was delivered through one branch of the bifurcated light guide, and test flashes (100 ms) were superimposed on this background light through the other branch, thus ensuring that both the adapting and the test flashes elicited responses from the same photoreceptors.

The ERG b-wave amplitudes (μV), defined as the difference between the trough of the a-wave and the peak of the b-wave, were instantly measured and the irradiance adjusted until the criterion response amplitude was obtained at each wavelength. Spectral sensitivity curves were generated by plotting the inverse of irradiance (in photons cm^{-2} s^{-1}) required to generate the criterion response at each wavelength. To form hypotheses regarding the number and spectral distribution of pigments potentially contributing to 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 (following Horodysky et al. 2008). Conditions ranging from 1 to 3 α-band rhodopsins were considered for light-adapted data, whereas a single rhodopsin was fitted to dark-adapted spectral sensitivity data to estimate the most likely spectral position of rod pigments. 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/or the number of contributing pigments using an information theoretic approach (Burnham and Anderson 2002), following the Akaike Information Criterion (AIC):

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

where $\hat{L}$ is the estimated value of the likelihood function at its maximum and p is the number of estimated parameters. All parameter optimization, template fitting, and model selection was conducted using the software package R (ver. 2.7.1; R Development Core Team 2008).

Results

Temporal Resolution

The photopic CFF_{max} was significantly higher than the scotopic CFF_{max} within snook (Mann-Whitney rank sum test, $P =$

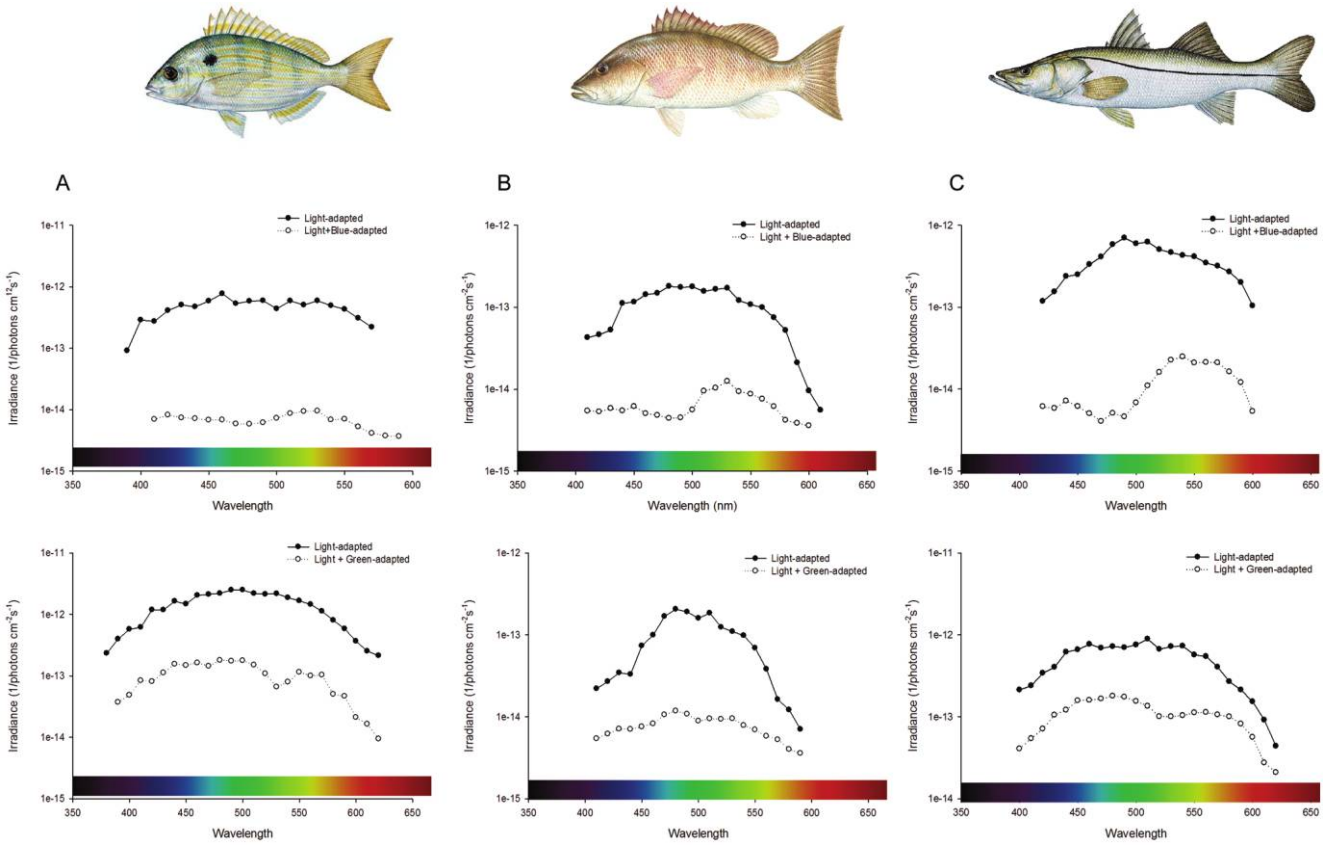


Figure 2. Spectral sensitivity of pinfish (*A*), gray snapper (*B*), and common snook (*C*) under chromatic adaptation. Spectral sensitivity curves for a single representative specimen under light adaptation (filled circles), blue adaptation (478 nm; open circles, top row), and green adaptation (532 nm; open circles, bottom row). The top row represents one individual of each species in a light-adapted trial immediately followed by a blue-adapted trial. The bottom row represents one individual of each species in a light-adapted trial immediately followed by a green-adapted trial.

0.009) and pinfish (paired *t*-test, $P \leq 0.001$) but not in snapper (paired *t*-test, $P = 0.139$). The scotopic CFF_{max} for the three species ranged from 34 to 42 Hz (table 1) and were significantly different (one-way ANOVA, $P = 0.003$). Pairwise multiple comparisons revealed that the scotopic CFF_{max} of the snapper (42 Hz) was significantly higher than both the snook (34 Hz; Student-Newman-Keuls, $P = 0.003$) and the pinfish (37 Hz; Student-Newman-Keuls, $P = 0.014$). The scotopic CFFs of the pinfish and snook did not differ (Student-Newman-Keuls, $P = 0.225$). The photopic CFF_{max} ranged from 40 to 47 Hz and again differed significantly among species (one-way ANOVA, $P = 0.010$). As with the scotopic treatment, the highest photopic CFF (47 Hz) was observed in the snapper, which was significantly higher than snook (40 Hz; Student-Newman-Keuls, $P = 0.009$) but not pinfish (44 Hz; Student-Newman-Keuls, $P = 0.142$). Pinfish photopic CFF was significantly higher than snook (Student-Newman-Keuls, $P = 0.030$). Response latencies of the 50% V_{max} differed significantly among the three species (one-way ANOVA, $P = 0.023$). The response latency of snapper (26.7 ms) was significantly shorter than snook (36.8 ms; Student-Newman-Keuls, $P = 0.022$) and pinfish (34.6 ms; Student-Newman-Keuls, $P = 0.030$); snook and pinfish did not differ.

Spectral Sensitivity

Chromatic adaptation experiments indicated the presence of blue- and green-sensitive visual pigments in each species (fig. 2). Given our data, maximum likelihood estimation using published SSH and GFRKD rhodopsin templates suggested that the fishes examined in this study have multiple pigment mechanisms (fig. 3). Light adapted photopic spectral sensitivities of pinfish (GFRKD; $\lambda_{max} = 418$, 487, 540 nm) and snook (GFRKD; $\lambda_{max} = 412$, 468, 538 nm) were consistent with the presence of at least three α-band vitamin A1 pigments (table 2). By contrast, gray snapper sensitivity data were more consistent with the presence of at least two rhodopsins (SSH; $\lambda_{max} = 485$, 528). Single pigment fits to dark-adapted spectral sensitivities of pinfish (SSH; $\lambda_{max} = 501$ nm), snook (SSH;

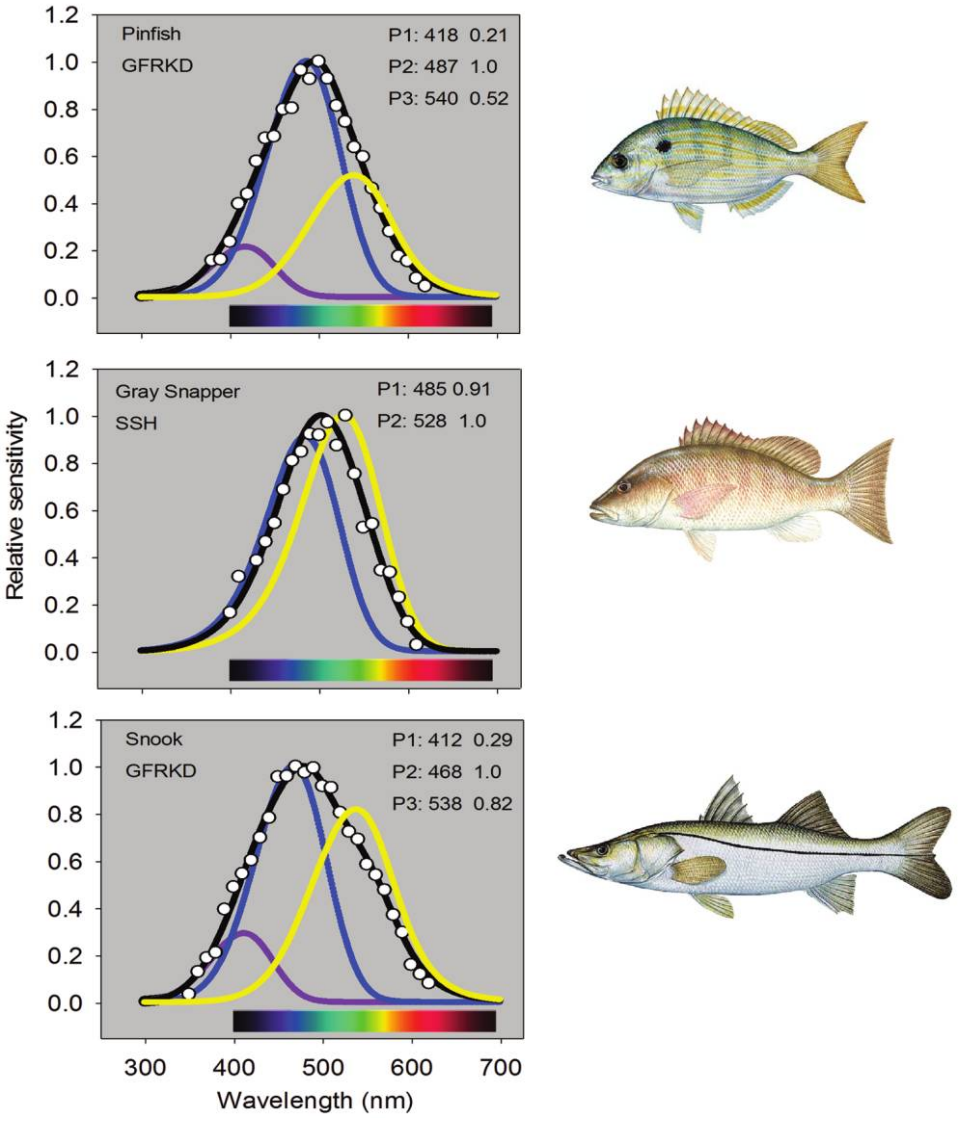


Figure 3. SSH (Stavenga et al. 1993) and GFRKD (Govardovskii et al. 2000) vitamin A1 templates fitted to pinfish, gray snapper, and common snook light-adapted spectral electroretinogram data by maximum likelihood (sensu Horodysky et al. 2008). Only estimates from best-fitting models presented in table 2 are plotted for each individual species. Values to the right of each pigment label are the estimated cone λ_{max} and pigment-specific weight, as estimated from the model. Purple lines represent short-wavelength pigments, blue lines represent intermediate-wavelength pigments, and yellow lines represent longer-wavelength pigments. Black lines represent additive curves developed by summing the product of each curve weighted by the estimated weighting factor.

λ_{max} = 491 nm), and snapper (SSH; λ_{max} = 505 nm) were consistent with the presence of a single rod rhodopsin (fig. 4).

Discussion

Intensity of ambient light in coastal and estuarine systems is dynamic and can vary by nine orders of magnitude on the basis of time of day, angle of incidence, scatter, and seasonality (Lythgoe 1979; McFarland 1986). Accordingly, visual characteristics of species in nearshore habitats represent a balance between acuity, sensitivity, contrast perception, and resolution.

The temporal dynamics of the fishes studied are consistent with inferences based on ecology and lifestyle. Snook had the lowest photopic temporal resolution (CFF_{max} = 40 Hz) and longest response latency (36.8 ms), which is indicative of a visual system more adapted to crepuscular and nocturnal foraging, where the enhancement of absolute sensitivity necessitates lower temporal summation of photoreceptors (table 1; Bullock et al. 1991; Warrant 1999). Snook are visual predators that ambush prey from mangroves and seagrasses and forage in low-light conditions at lighted docks, canals, spillways, and riverine systems (Gilmore et al. 1983; Paperno and Brodie 2004; Tremain et al. 2004; Stevens et al. 2007; Adams et al. 2009).

Table 2: Parameter estimates and model rankings of SSH (Stavenga et al. 1993) and GFRKD (Govardovskii et al. 2000) vitamin A1 rhodopsin templates fitted to photopic spectral electroretinogram data via maximum likelihood

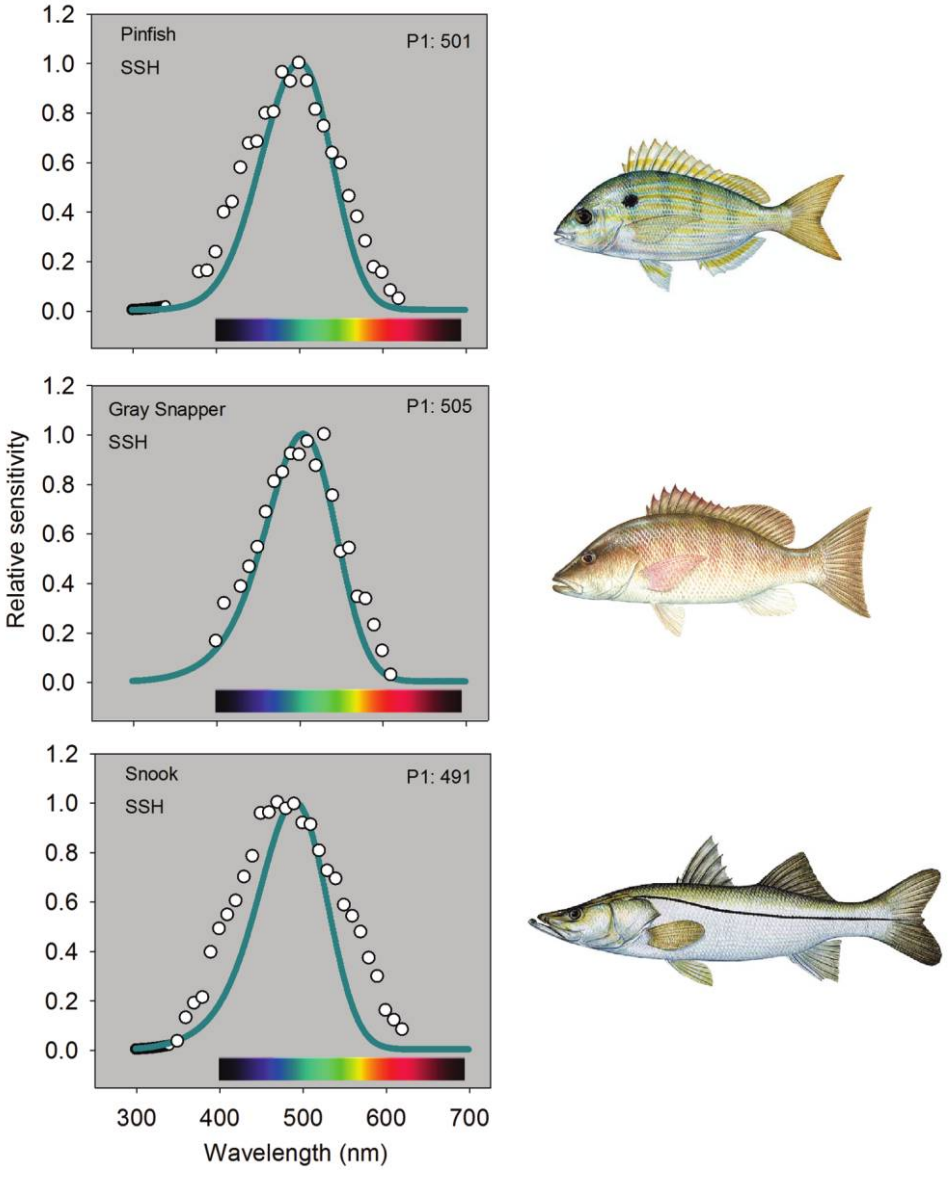
Species, adaptation, and condition	Template	$\lambda_{max,\,1}$	$\lambda_{max,\,2}$	$\lambda_{max,\,3}$	$-\log(L)$	p	AIC	ΔAIC
Pinfish:								
Dark:								
Monochromatic	GFRKD	501	...	...	−29.9	2	−55.7	4.8
Monochromatic	**SSH**	**501**	...	...	**−32.2**	**2**	**−60.5**	**0**
Light:								
Monochromatic	GFRKD	499	...	...	−14.4	2	−24.9	55.1
Monochromatic	SSH	499	...	...	−15.9	2	−27.7	52.3
Dichromatic	GFRKD	469	528	...	−39.1	5	−68.2	11.8
Dichromatic	SSH	472	530	...	−41.2	5	−72.5	7.5
Trichromatic	**GFRKD**	**418**	**487**	**540**	**−47.0**	**7**	**−80**	**0**
Trichromatic	**SSH**	422	484	539	−45.8	7	−77.5	2.5
Gray snapper:								
Dark:								
Monochromatic	GFRKD	508	...	...	−18.0	2	−32.0	1.3
Monochromatic	**SSH**	**505**	...	...	**−18.7**	**2**	**−33.3**	**0**
Light:								
Monochromatic	GFRKD	507	...	...	−19.3	2	−34.5	15.7
Monochromatic	SSH	509	...	...	−20.5	2	−37.1	13.1
Dichromatic	GFRKD	477	523	...	−28.5	5	−47.1	3.1
Dichromatic	**SSH**	**485**	**528**	...	**−30.1**	**5**	**−50.2**	**0**
Trichromatic	GFRKD	422	503	547	−31.8	7	−49.5	.5
Trichromatic	SSH	426	501	544	−31.7	7	−49.6	.6
Snook:								
Dark:								
Monochromatic	GFRKD	491	...	...	−7.9	2	−11.9	3.7
Monochromatic	**SSH**	**491**	...	...	**−9.8**	**2**	**−15.6**	**0**
Light:								
Monochromatic	GFRKD	493	...	...	−2.1	2	−.2	102.3
Monochromatic	SSH	495	...	...	−3.2	2	−2.3	100.2
Dichromatic	GFRKD	450	529	...	−43.3	5	−76.7	25.8
Dichromatic	SSH	453	530	...	−46.2	5	−82.5	20
Trichromatic	**GFRKD**	**412**	**468**	**538**	**−58.3**	**7**	**−102.5**	**0**
Trichromatic	SSH	416	470	539	−57.9	7	−101.7	.8

Note. p, number of parameters in a model. Dark- and light-adapted data were modeled separately. Only α bands of pigments were considered. The number in $\lambda_{max,\,1}$ refers to pigment 1, and so on. Values in bold indicate the best-supported pigment and template scenarios, on the basis of Akaike Information Criterion (AIC) values (lower is better).

Other ecologically similar, nocturnal, crepuscular piscivores, such as the weakfish (*Cynoscion regalis*), have a similarly low photopic CFF (42 Hz; Horodysky et al. 2008).

Snapper demonstrated the highest resolution and the corresponding shortest response latency (table 1). Gray snapper inhabit structurally and visually complex mangrove habitats during the day from which they also ambush prey (Hammerschlag-Peyer et al. 2011). In a prey tethering study, snapper preyed on pinfish during daylight hours within the mangrove-seagrass ecotone (Hammerschlag et al. 2010). In the same experiment, the nighttime removal rate of pinfish doubled, being highest near the mangrove edge, yet snapper were not identified as the nocturnal predators. Snapper are diel aggregators with well-defined daily migrations from mangroves to adjacent seagrass beds at the onset of twilight (Luo et al. 2009). This habitat shift reduces predation pressure on the snapper and also expands their access to more benthic crustacean prey (Luo et al. 2009). The relatively high temporal resolution in snapper presumably enhances visual tracking of their prey during daylight conditions within their structurally complex mangrove habitats.

The omnivorous pinfish is an abundant and economically important species whose ecological importance has been relatively undervalued (Hansen 1969; Nelson 2002). The juvenile pinfish diet is comprised primarily of seagrasses, and as a consumer they provide an important link between primary and secondary estuarine production (Stoner 1979, 1982; Montgomery and Targett 1992). Prado and Heck (2011) demonstrated that visual recognition and leaf manipulability were key factors in pinfish feeding discrimination among seagrass species. Both young-of-year and adult pinfish are prey for other fishes and



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used as recreational bait by fisherman. Pinfish temporal resolution was intermediate to both predatory species in this study and may represent a balance between the tasks of seagrass foraging and inspection in the visual near field and vigilance against approaching predators on the horizon of the far field (table 1).

The spectral properties of the visual systems of the species studied can be positioned in context with other coastal fishes (table 3). In general, coastal species are sensitive to a larger range of wavelengths (blue-green) than deep-sea and oceanic species (blue limited) yet possess a narrower range than freshwater species (blue, green, and red; Loew and Lythgoe 1978; Marshall 2003). Light attenuates rapidly in coastal waters, and suspended particles increase light scatter in all directions; therefore, coastal waters are green, with reduced clarity (McFarland 1991). Increasing depth diminishes light intensity, which then shifts the penetrating spectrum. Spectra vary with depth and also with line of sight, which is of relevance to predators that commonly track prey silhouetted against downwelling light or contrasting backgrounds (McFarland 1991). The possession of multiple visual pigments allows species to match the downwelling spectra as well as the horizontal and upwelling spectra. Oftentimes this can be a consequence of intraretinal variability in opsin gene expression, thereby conferring retinal regions

Table 3: Comparative spectral sensitivities of relevant teleost species determined using retinal extracts (EXT), electroretinogram (ERG), and microspectrophotometry (MSP) techniques

Species	Rod λ max (nm)	Cone λ max (nm)	Method	Reference
Lutjanus griseus	513	560	ERG	Easter and Hamaskai 1973
Lutjanus kasmira	?	487, 518	MSP	Lythgoe et al. 1994
Lutjanus argentimaculatus	?	536, 575	MSP	Lythgoe et al. 1994
Lutjanus fulviflamma	505	534, 568	MSP	Lythgoe et al. 1994
Lutjanus johnii:				
Juvenile	498	534, 572	MSP	Lythgoe et al. 1994
Adult	?	458, 543, 567	MSP	Lythgoe et al. 1994
Lutjanus russeli	499	451, 530, 557	MSP	Lythgoe et al. 1994
Lutjanus bohar	497	424, 494, 518	MSP	Lythgoe et al. 1994
Lutjanus quinquelineatus	499	444, 520, 540	MSP	Lythgoe et al. 1994
Lutjanus malahavicus	494	408, 442, 529, 541	MSP	Lythgoe et al. 1994
Lutjanus fulvus	498	?	EXT	Ali and Heumann 1970
Lagodon rhomboides	500	?	EXT	Beatty 1973
Cynoscion regalis	?	459, 532	ERG	Horodysky et al. 2008
Cynoscion nebulosus	?	450, 542	ERG	Horodysky et al. 2008
Sciaenops ocellatus	?	444, 489, 564	ERG	Horodysky et al. 2008
Micropogonias undulatus	?	430, 484, 562	ERG	Horodysky et al. 2008
Leiostomus xanthurus	?	450, 546	ERG	Horodysky et al. 2008
Morone saxatilis	?	542, 612	ERG	Horodysky et al. 2010
Pomatomus salatrix	?	433, 438, 507, 547	ERG	Horodysky et al. 2010
Rachycentron canadum	?	501	ERG	Horodysky et al. 2010
Paralichthys dentatus	?	449, 525	ERG	Horodysky et al. 2010

possessing distinct spectral and temporal properties (Temple 2011). However, in these species this potential remains unexplored, since the ERG is a summation of the retinal response as a whole.

Chromatic sensitivities of the three coastal fishes indicate species-specific pigment mechanisms based on a comparison of rhodopsin templates fit to our ERG data (table 2). Gray snapper appear to have at least two visual pigments, whereas snook and pinfish have at least three (fig. 3). Template-fitting procedures may not extract the precise λ_{max} pigment values of photoreceptors as a result of filtering by preretinal ocular media, experimental error, the generally poor performance of rhodopsin templates at short wavelengths (Govardovskii et al. 2000), or a combination of these factors.

The ERG is well suited for comparative investigations of vision and form-function relationships in fishes (Ali and Muntz 1975; Pankhurst and Montgomery 1989). In addition, the ERG measures the summed retinal potentials and directly incorporates filtration by ocular media, which can only be modeled using other pigment measuring techniques, such as microspectrophotometry (MSP; Brown 1968; Ali and Muntz 1975). Comparisons of MSP estimates to those resulting from the rhodopsin template-fitting procedures suggest that the latter performs well for visual systems with few, fairly widely spaced visual pigments but risks mischaracterizing visual pigment λ_{max} in species with several closely spaced pigments and/or when underlying data are sparse and require fitting procedures that balance optimization and parsimony (Horodysky et al. 2010). We consider the collective inferences from pigment template modeling to be consistent with the lifestyles and ecologies of the species examined herein.

Chromatic adaptation with either 478 nm (blue) or 532 nm (green) light resulted in wavelength-specific changes in the response waveforms and indicates the presence of blue- and green-sensitive pigments in all species (fig. 2). Rhodopsin template fitting of our data revealed that snook likely possesses at least three cone visual pigments with λ_{max} values of 412, 468, and 538 nm (fig. 3). Snook have short single, long single, and double cones that are arranged in a square mosaic pattern (Blaxter and Staines 1970; Eckelbarger et al. 1980). The functional significance of double cones is not well studied in teleosts, but arguably it is to assess the speed of a viewed object and to improve discrimination or acuity (Pignatelli et al. 2010; Schwab 2012). Snook inhabit spectrally diverse mangrove and seagrass habitats, which include variation in line of sight spectra; therefore, the possession of three cone visual pigments would enhance their ability to detect the contrast of prey under differing conditions.

Gray snapper have short single and double cones organized in a regular mosaic pattern (Lythgoe et al. 1994). Our data support snapper as dichromats with λ_{max} values of 485 and 528 nm (fig. 3). Possession of multiple cone pigments in this range provides snapper with contrast sensitivity. In a previous study, Easter and Hamasaki (1973) reported only a single cone λ_{max} value of 560 nm for gray snapper, on the basis of one specimen collected from the Florida Keys (table 3). Our findings likely

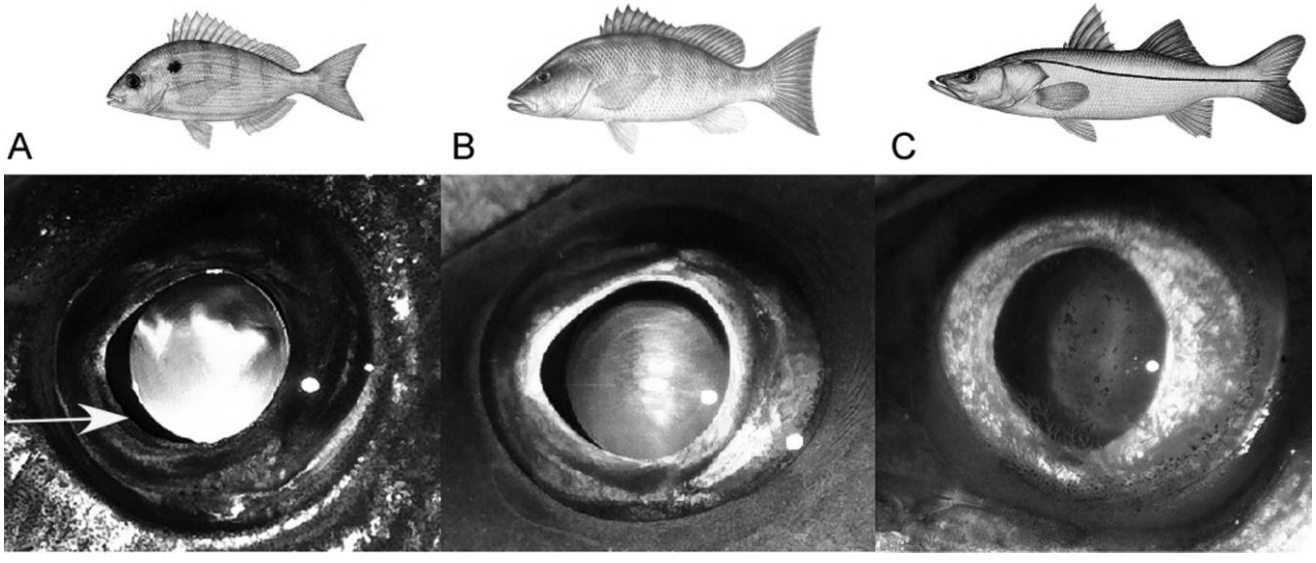

Figure 5. Eyes of pinfish (*A*), gray snapper (*B*), and common snook (*C*) each possessing an aphakic space (arrow) created by an anterior notch in the pupil. Note the lens edge seen in the pupil. The significance of the aphakic space is that it allows for binocularity within the design limitations of laterally positioned eyes. Predatory fish may possess a concentrated area of photoreceptors within the temporal region of the retina. When fish detect prey, they rotate the eyes in the most forward position possible. The image crosses the anterior notch of the pupil through the lens, striking the temporal region of both eyes, allowing for binocularity. Without the aphakic space, the nasal edge of the circular pupil would interfere with imaging. A color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*.

differ as a result of methodology, since they did not perform a chromatic adaptation experiment.

MSP data on 12 snapper species collected from various habitats within the Great Barrier Reef indicated the presence of double cones, with each member of the pair containing a different visual pigment (Lythgoe et al. 1994). Sensitivity of the 12 species spanned 424–575 nm, with dichromatic, trichromatic, and tetrachromatic conditions observed. The wide variability among species was attributed to differences in habitat depth and ambient lighting. The sensitivity profile of *Lutjanus griseus* in this study surprisingly most resembles that of *Lutjanus kasmira*, which were collected in outer shelf waters, rather than species collected in turbid inshore areas, such as *Lutjanus johnii* (Lythgoe et al. 1994; table 3).

Our data support pinfish as trichromats with cone sensitivities positioned widely at 418, 487, and 540 nm (fig. 3). Pinfish inhabit seagrass and sand flats within the Indian River Lagoon and have a diet dominated by seagrass species (Nelson 2002). Cournoyer and Cohen (2011) reported that cryptic coloration of small shrimp against seagrass backgrounds may minimize visual contrast and detection by predatory fishes such as pinfish. Trichromacy would enhance contrast of seagrasses and small cryptic prey (Stoner 1982; Nelson 2002). Additionally, multiple pigments would enhance contrast in line of sight and in detection of predators. Jordan et al. (1997) found that pinfish altered habitat use in the presence of predators by moving from exposed sand flats to structurally complex seagrass beds and further restricted their vertical movements within the water column.

Rods mediate vision in low-light conditions, and sensitivity should match background in order to maximize photon capture (Lythgoe 1968). The species studied had rod sensitivities in the range of 491–505 nm (fig. 4). In an effort to correlate visual pigment sensitivity in fishes to their environments, McFarland (1991) calculated the spectral distribution of downwelling irradiance during daylight, starlight, moonlight, and twilight. He concluded that a rod pigment located between 450 and 600 nm would serve equally well to catch dim downwelling light at a 3-m depth. During twilight, an increase in the proportion of short wavelengths in the ambient spectrum would allow a rod pigment centered between 450 and 480 nm to maximize photon capture. A rod pigment located between 490 and 500 nm would represent an ideal trade-off that optimizes photon capture under a variety of scotopic conditions and multiple lines of sight and has been confirmed in several elasmobranch and teleost species (Tamura and Niwa 1967; Dowling and Ripps 1971; Gruber et al. 1990; Lythgoe et al. 1994; Losey et al. 2003; Hart et al. 2004; Theiss et al. 2006; McComb et al. 2010). The species studied possess rod pigments that fall within this range and indicate adaptations to maximize scotopic vision, especially during the twilight period. In addition, snook possess a lipid tapetum, which extends behind the entire retina except for a small triangular region near the choroid (Eckelbarger et al. 1980). This dark region is thought to reduce the glare of downwelling light. The ratio of rods to cones is very high, and the proportion of ganglion cells to photoreceptors is very low in this species, collectively suggesting a nocturnal eye (Eckelbarger et al. 1980). Therefore, snook rely on tapeta to enhance rod-based visual sensitivity in nocturnal and low-light conditions.

In addition to spectral sensitivity and temporal resolution,

the field of view can influence the visual perception of a species (McComb and Kajiura 2008; McComb et al. 2009). The species of the current study possess both an aphakic space (lensless space; fig. 5) and an anterior notch in the pupil. When the lens moves into this space and the fish is looking forward, the potential functional significance is frontal binocularity and image focus on a region of concentrated photoreceptor and ganglion cell density (Sivak 1978). The presence of the aphakic space is an adaptation to the constraints of laterally positioned eyes (Schwab 2012). Predators typically have frontally positioned eyes that provide binocular overlap and confer depth perception. The presence of the aphakic space, in conjunction with accommodative lens movements, may allow the piscivorous snook and snapper to visually track prey during the final milliseconds before capture, while in pinfish it could aid in the discrimination of grasses and the tracking of small prey during foraging.

We conclude that the species examined in this study have sensitivities that are well adapted for coastal tropical estuaries such as the Indian River Lagoon and adjacent habitats, as well as the specific lifestyles and ecology of these fishes. The possession of multiple cone pigments supports the contrast hypothesis, and the finding that rod sensitivities are tuned to dim and twilight conditions supports the sensitivity and twilight hypotheses. The response dynamics among species were correlated to aspects of their ecologies, movements, and predator-prey dynamics. However, it is important to note that water quality and clarity within the Indian River Lagoon and other aquatic habitats are changing at a pace faster than the evolution of visual systems (Seehausen et al. 2007; Horodysky et al. 2010), and these conditions may directly influence the visual performance of visually oriented fishes.

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Literature Cited

Adams A.J., R.K. Wolfe, and C.A. Layman. 2009. Preliminary examination of how human-driven freshwater flow alteration affects trophic ecology of juvenile snook (*Centropomus undecimalis*) in estuarine creeks. Estuar Coast 32:819–828.

Ali M.A. and W.R. Heumann. 1970. Distribution of vitamins A_1 and A_2 in the retinas of some marine fishes from the Gulf of California. Vis Res 10:1307–1310.

Ali M.A. and W.R.A. Muntz. 1975. Electroretinography as a tool for studying fish vision. Pp. 159–170 in M.A. Ali, ed. Vision in fishes: new approaches in research. Plenum, New York.

Beatty D.D. 1973. Visual pigments of several species of teleost fishes. Vis Res 13:989–992.

Blaxter J.H.S. and M. Staines. 1970. Pure-cone retinae and retinomotor responses in larval teleosts. J Mar Biol 50:449–460.

Bröcker H. 1935. Untersuchungen über das Srhvermögen der Einsiedlerkrebse. Zool Jahrb Abt Allg Zool Physiol Tiere 55: 399–430.

Brown K.T. 1968. The electroretinogram: its components and origins. Vis Res 8:633–677.

Bullock T.H., M.H. Hoffmann, J.G. New, and F.K. Nahm. 1991. Dynamic properties of visual evoked potentials in the tectum of cartilaginous and bony fishes, with neuroethological implications. J Exp Zool 5(suppl.):142–255.

Burnham K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Clarke G.L. 1936. On the depth at which fishes can see. Ecology 17:452–456.

Colin S.P. and N.J. Marshall, eds. 2003. Sensory processing in aquatic environments. Springer, New York.

Cournoyer B.L. and J.H. Cohen. 2011. Cryptic coloration as a predator avoidance strategy in seagrass arrow shrimp colormorphs. J Exp Mar Biol Ecol 402:27–34.

Crozier W.J. and E. Wolf. 1939. The flicker response contour for the crayfish. J Gen Physiol 22:451–462.

Crozier W.J., E. Wolf, and G. Zerrahn-Wolf. 1939. The flicker response contour for the isopod *Asellus*. J Gen Physiol 22: 451–462.

Dowling J.E. and H. Ripps. 1971. S-potentials in the skate retina: intracellular recordings during light and dark adaptation. J Gen Physiol 58:163–189.

Easter S.S. and D.I. Hamasaki. 1973. Eletroretinographically-determined scoptopic sensitivities of some marine fish. Vis Res 13:1175–1181.

Eckelbarger K.J., R. Scalan, and J.A.C. Nicol. 1980. The outer retina and tapetum lucidum of the snook *Centropomus undecimalis* (Teleostei). Can J Zool 58:1042–1051.

Frank T.M. 1999. Comparative study of temporal resolution in the visual systems of mesopelagic crustaceans. Biol Bull 196: 137–144.

Gilmore R.G., C.J. Donahoe, and D.W. Cooke. 1981. Fishes of the Indian River Lagoon and adjacent waters, Florida. Harbor Branch Foundation Tech. Rep. 41.

———. 1983. Observations on the distribution and biology of east-central Florida populations of the common snook, *Centropomus undecimalis* (Bloch). Fla Sci 3/4:306–313.

Govardovskii V.I., N. Fyhrquist, T. Reuter, D.G. Kuzmin, and K. Donner. 2000. In search of the visual pigment template. Vis Neurosci 17:509–528.

Grecay P.A. and T.E. Targett. 1996. Effects of turbidity, light

level and prey concentration on the feeding of juvenile weakfish *Cynoscion regalis*. Mar Ecol Progr Ser 131:11–16.

Gruber S.H., E.R. Loew, and W.N. McFarland. 1990. Rod and cone pigments of the Atlantic guitarfish, *Rhinobatos lentiginosus* Garman. J Exp Zool 256(suppl.):85–87.

Hammerschlag N., A.B. Morgan, and J.E. Serafy. 2010. Relative predation risk for fishes along a subtropical mangrove-seagrass ecotone. Mar Ecol Prog Ser 401:259–267.

Hammerschlag-Peyer C.M., L.A. Yeager, M.S. Araújo, and C.A. Layman. 2011. A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. PLoS ONE 6:e27104.

Hansen D.J. 1969. Food, growth, migration, reproduction and abundance of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulates*, near Pensacola, Florida 1963–65. Fish Bull 68:135–146.

Hart N.S., T.J. Lisney, N.J. Marshall, and S.P. Collin. 2004. Multiple cone visual pigments and the potential for trichromatic colour vision in two species of elasmobranch. J Exp Biol 207:4587–4594.

Helfman G.S., B.B. Collette, D.E. Facey, and B.W. Bowen. 2009. The diversity of fishes: biology, evolution and ecology. Wiley, West Sussex.

Horodysky A.Z., R.W. Brill, E.J. Warrant, J.A. Musick, and R.J. Latour. 2008. Comparative visual function in five sciaenid fishes inhabiting Chesapeake Bay. J Exp Biol 211:3601–3612.

———. 2010. Comparative visual function in four piscivorous fishes inhabiting Chesapeake Bay. J Exp Biol 213:1751–1761.

Jerlov N.G. 1968. Optical oceanography. Elsevier, New York.

Jordan F., M. Bartolini, C. Nelson, P.E. Patterson, and H.L. Soulen. 1997. Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). J Exp Mar Biol Ecol 208:45–56.

Loew E.R. and J.N. Lythgoe. 1978. The ecology of cone pigments in teleost fishes. Vis Res 18:715–722.

Losey G.S., W.N. McFarland, E.R. Loew, J.P. Zamzow, P.A. Nelson, N.J. Marshall, and W.L. Montgomery. 2003. Visual biology of Hawaiian coral reef fishes. I. Ocular transmission and visual pigments. Copeia 3:433–454.

Luo J., J.E. Serafy, S. Sponaugle, P.B. Teare, and D. Kieckbusch. 2009. Movement of gray snapper *Lutjanus grisues* among subtropical seagrass, mangrove and coral reef habitat. Mar Ecol Prog Ser 380:255–269.

Lythgoe J.N. 1968. Visual pigments and visual range underwater. Vis Res 8:997–1011.

———. 1979. Ecology of vision. Clarendon, Oxford.

Lythgoe J.N., W.R.A. Munz, J.C. Partridge, J. Shand, and D. McB. Williams. 1994. The ecology of the visual pigments of snappers (Lutjanidae) on the Great Barrier Reef. J Comp Physiol A 174:461–467.

Marshall N.J., T.W. Cronin, and T.M. Frank. 2003. Visual adaptations in crustaceans: chromatic, developmental, and temporal aspects. Pp. 343–372 in S.P. Colin and N.J. Marshall, eds. Sensory processing in aquatic environments. Springer, New York.

McComb D.M., T.M. Frank, R.E. Hueter, and S.M. Kajiura. 2010. Temporal resolution and spectral sensitivity of the visual system of three coastal shark species from different light environments. Physiol Biochem Zool 83:299–307.

McComb D.M. and S.M. Kajiura. 2008. Visual fields of four batoid fishes: a comparative study. J Exp Biol 211:482–490.

McComb D.M, T.C. Tricas, and S.M. Kajiura. 2009. Enhanced visual fields in hammerhead sharks. J Exp Biol 212:4010–4018.

McFarland W.N. 1986. Light in the sea: correlations with behaviors of fishes and invertebrates. Am Zool 26:389–401.

———. 1991. Light in the sea: the optical world of elasmobranchs. J Exp Zool 5(suppl.):3–12.

McFarland W.N. and F.W. Munz. 1975. Part III: the evolution of photopic visual pigments in fishes. Vis Res 15:1071–1080.

Montaño O.J.F. 2009. Assessing the habitat structure for common snook (*Centropomus undecimalis* Bloch, 1792) and tarpon (*Megalops atlanticus* Valenciennes, 1847) in Santa Teresa lagoons, Puerto Rico. Turk J Fish Aquat Sci 9:173–179.

Montgomery J.L.M. and T.E. Targett. 1992. The nutritional role of seagrass in the diet of the omnivorous pinfish *Lagodon rhomboides* (L.). J Exp Mar Biol Ecol 158:37–57.

Mulligan T.J. and F.F. Snelson Jr. 1983. Summer-season populations of epibenthic marine fishes in the Indian River Lagoon system, Florida. Fla Sci 4:250–276.

Munz F.W. and W.N. McFarland. 1973. The significance of spectral position in the rhodopsins of tropical marine fishes. Vis Res 13:1829–1874.

———. 1977. Evolutionary adaptations of fishes to the photic environment. Pp. 193–274 in F. Crescitelli, ed. Handbook of sensory physiology. Vol. II/5. The visual system in vertebrates. Springer, Berlin.

Naka K.I. and W.A.H. Rushton. 1966*a*. S-potentials from color units in the retina of fish (Cyprinidae) J Physiol 185:587–599.

———. 1966*b*. S-potentials from luminosity units in the retina of fish (Cyprinidae) J Physiol 185:587–599.

Nelson G.A. 2002. Age, growth, mortality, and distribution of pinfish (*Lagodon rhomboides*) in Tampa Bay and adjacent Gulf of Mexico waters. Fish Bull 100:582–592.

Pankhurst N.W. and J.C. Montgomery. 1989. Visual function in four Antarctic nototheniid fishes. J Exp Biol 142:311–324.

Paperno R. and R.B. Brodie. 2004. Effects of environmental variables upon the spatial and temporal structure of a fish community in a small, freshwater tributary of the Indian River Lagoon, Florida. Estuar Coast Shelf Sci 61:229–241.

Pignatelli V., C. Champ, J. Marshall, and M. Vorobyev. 2010. Double cones are used for colour discrimination in the reef fish, *Rhinecanthus aculeatus*. Biol Lett 6:537–539.

Prado P. and K.L. Heck Jr. 2011. Seagrass selection by omnivorous and herbivorous consumers: determining factors. Mar Ecol Prog Ser 429:45–55.

Schwab I.R. 2012. Evolution's witness. Oxford University Press, New York.

Seehausen O., J.J.M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277:1808–1811.

Sigua G.C. and J.S. Steward. 2000. Establishing pollutant load reduction targets for the Indian River Lagoon, Florida. J Am Water Resour Assoc 36:123–132.

Sigua G.C. and W.A. Tweedale. 2004. Assessing redesigned effectiveness of the water quality monitoring program in the Indian River Lagoon, Florida. Aquatic Conserv Mar Freshw Ecosyst 14:49–64.

Sivak J.G. 1978. The functional significance of the aphakic space of the fish eye. Can J Zool 56:513–516.

Stavenga D.G., R.P. Smits, and B.J. Hoenders. 1993. Simple exponential functions describing the absorbance bands of visual pigment spectra. Vis Res 33:1011–1017.

Stearns D.E., G.J. Holt, R.B. Forward Jr., and P.L. Pickering. 1994. Ontogeny of phototactic behavior in red drum larvae (Sciaenidae: *Sciaenops ocellatus*). Mar Ecol Prog Ser 104:1–11.

Stevens P.W., D.A. Blewett, and G.R. Poulakis. 2007. Habitat use by juvenile common snook, *Centropomus undecimalis* (Pisces: Centropomidae) Applying a life-history model in a southwest Florida estuary. Bull Mar Sci 80:93–108.

Stoner A.W. 1979. Species-specific predation in amphipod crustacean by the pinfish *Lagodon rhomboides*: mediation by macrophyte standing crop. Mar Biol 55:201–207.

———. 1982. Perception and choice of substratum by epifaunal amphipods associated with seagrasses. Mar Ecol Prog Ser 3:105–111.

Tamura T. and H. Niwa. 1967. Spectral sensitivity and color vision of fish as indicated by S-potential. Comp Biochem Physiol 22:745–754.

Temple S.E. 2011. Why different regions of the retina have different spectral sensitivities: a review of mechanisms and functional significance of intraretinal variability in spectral sensitivity in vertebrates. Vis Neurosci 28:281–293.

Theiss S.M., T.J. Lisney, S.P. Collin, and N.S. Hart. 2006. Color vision and visual ecology of the blue-spotted maskray *Dasyatis kuhlii* Muller & Henle, 1814. J Comp Physiol 193:67–79.

Tremain D.M. and D.H. Adams. 1995. Seasonal variations in species diversity, abundance and composition of fish communities in the northern Indian River Lagoon, Florida. Bull Mar Sci 57:171–192.

Tremain D.M, C.W. Harnden, and D.H. Adams. 2004. Multidirectional movements of sportfish species between an estuarine no-take zone and surrounding waters of the Indian River Lagoon, Florida. Fish Bull 102:533–544.

Wallace A.R. 1891. Natural selection and tropical nature. MacMillan, New York.

Walls G.L. 1942. The vertebrate eye and its adaptive radiation. Hafner, New York.

Warrant E.J. 1999. Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. Vis Res 39:1611–1630.

Warrant E.J. and N.A. Lockett. 2004. Vision in the deep sea. Biol Rev 79:671–712.

Zaunreiter M., J. Junger, and K. Kotrschal. 1991. Retinal morphology of cyprinid fishes: a quantitative histological study of ontogenetic changes and intraspecific variation. Vis Res 31:383–394.

Zettler F. 1969. Die Abhängigkeit des Ubertragungsverhaltens von Frequenz und Apatationszustand, Gemessen am Einzelnen Lichtrezeptor von Calliphora erythhrocephala. Z Vgl Physiol 64:432–449.