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Vision in the hyperiid amphipod *Scina crassicornis*

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Light microscopy and extracellular electrophysiology were used to investigate eye structure and visual physiology of the hyperiid amphipod *Scina crassicornis*, a mesopelagic species that emits unusually short-wavelength luminescence (λ_{max}=435–444 nm). The overall eye morphology is most similar to some previously described deep-dwelling amphipods, though not other hyperiids. Electroretinograms suggest that *S. crassicornis* possesses a relatively sensitive eye with slow temporal dynamics, and a monochromatic visual system (λ_{max}=472 nm). Vision in *S. crassicornis* is well-suited for life in mesopelagic waters, and its short-wavelength luminescence does not play a role in intraspecific sexual signalling.

INTRODUCTION

Visual systems of mesopelagic animals are often adapted, both morphologically and physiologically, for vision under low environmental light levels (reviewed in Warrant & Locket, 2004). Hyperiid amphipods, which are abundant members of mesopelagic zooplankton assemblages throughout the world's oceans, appear to be no exception. Among the morphological adaptations of hyperiid eyes are retinas connected to optical elements with fibre optics (e.g. *Phronima*; Ball, 1977; Land, 1981), cone-shaped retinas capable of receiving light from 360° around the animal (e.g. *Streetsia*) (Meyer-Rochow, 1978), and retinas with 'ear-like' mirrors to aid in light collection (e.g. *Scypholanceola*) (Land & Nilsson, 2002). Little is known about the physiology of hyperiid visual systems, and even less is known about their visual ecology (reviewed in Marshall et al., 2003). Indeed, little is known of mesopelagic hyperiid ecology in general, other than that most live in association with a variety of gelatinous zooplankton (Harbison et al., 1977; Laval, 1980; Gasca & Haddock, 2004).

A potential function for vision in mesopelagic organisms is the detection of biologically produced light (bioluminescence), for sexual signalling, predation, or defence (reviewed in Widder, 2002). The majority of luminescent marine organisms produce light at blue to green wavelengths (440–515 nm) (Herring, 1983; Widder et al., 1983; Latz et al., 1988). It has been suggested that organisms producing light at longer (red) wavelengths may be using bioluminescence at these longer wavelengths as a secure visual channel for sighting prey or for intraspecific signalling (Denton et al., 1970; Widder et al., 1984). Evidence for this could come from a substantial overlap in the visual spectral sensitivity function and the luminescence emission spectrum of an organism (e.g. Partridge & Douglas, 1995).

Amphipods of one hyperiid genus, *Scina*, emit luminescence that is amongst the shortest wavelength light produced by any known organism (435–444 nm) (Herring, 1983; Widder et al., 1983; Latz et al., 1988). As little is known about *Scina* ecology, the function(s) of its luminescence is unknown. It has been suggested that luminescence in *Scina* serves a defensive function given the placement of luminescent cells and the defensive posture of the animals during luminescent emissions (Herring, 1981). Alternatively, luminescence in *Scina* could have a mating function if the visual spectral sensitivity was shifted to overlap with the short wavelength luminescence emission spectrum. The present study addresses this question and fundamental aspects of vision in *Scina crassicornis* through light microscopy of the eye and extracellular photoreceptor field potentials (electroretinography) to characterize the spectral sensitivity, relative irradiance sensitivity and temporal dynamics of its visual system.

MATERIALS AND METHODS

Scina crassicornis (Fabricius 1775) were collected in the eastern Gulf of Mexico (27°N 86°W) on research cruises aboard the RV 'Pelican' during September, 2005 and May, 2006. Specimen collections were made at mesopelagic depths (200–900 m) using a Tucker trawl equipped with a thermally insulated closing cod-end. Amphipods were maintained in light-tight containers of seawater at 7–10 °C without feeding for at least 24 h prior to experiments.

Measurements of external features of the eye (whole eye diameter, facet diameter) were made on specimens preserved in 4% buffered formalin. For histology, live dark-adapted specimens were fixed in 2.5% gluteraldehyde in Millonig's phosphate buffer, post-fixed in 1% OsO_4, dehydrated in a graded EtOH series, and embedded in epon resin (EMBed 812, EMS). Sections (1.25 μm) were cut with a Sorval Porter-Blum MT2-B ultramicrotome, and stained with 1% methylene blue.

Electrophysiological experiments were conducted onboard ship and in a shore-based laboratory using the same apparatus. Preliminary experiments found no effect of brief laboratory light exposure on visual responses of *S. crassicornis*;

therefore specimens were sorted from the trawl collection for experiments under either darkness or ambient room lighting (spectral sensitivity experiments only; light exposure <10 min). In either case, specimens were maintained in darkness for at least 24 h prior to experiments. Live *S. crassicornis* (mean length=10.9 mm ±3.0 SD) were attached to the plastic head of a pin by their dorsal carapace with cyanoacrylate gel adhesive (Loctite Corporation), and mounted on an acrylic support within a chilled seawater bath (9°C). In this configuration, *S. crassicornis* remained alive and healthy during experiments for 1 to 2 d.

Differential recordings of electroretinograms (ERGs) were made by placing one metal microelectrode (100-μm shank, <1-μm tip; FHC Inc.) sub-corneally, and another in the seawater bath adjacent to the specimen. The eye was dry in air during electrode placement to ensure a closed circuit, and then the water level was raised to ~0.5 cm above the eyes and body for the remainder of the experiments. The seawater bath was grounded by an AgCl-coated wire. AC recordings were digitized and stored in LabView (v. 6.1, National Instruments) for later analysis of peak-to-peak response heights.

A monochromatic stimulus light (150 W quartz halogen source, Spectral Products CM110 monochromator) was directed onto the eye of *S. crassicornis* via one branch of a bifurcated, randomized fibre optic light guide (EXFO). An electromagnetic shutter (Uniblitz, VS25) under computer control provided a stimulus flash duration of 75 ms, and stimulus irradiance was adjusted using a neutral-density wheel driven by a computer-controlled stepper motor. Irradiance was calibrated at 10-nm intervals with a photometer (UDT Instruments, Model S370) using a calibrated radiometric probe. Spectral purity at test wavelengths without the use of blocking filters was verified by a spectroradiometer (~9 nm FWHM, 350–700 nm; Ocean Optics, USB4000).

A fibre optic illuminator (TechniQuip, Model R150-BM) connected to the other branch of the light guide provided accessory illumination for specimen preparation and chromatic adaptation experiments. White light from the lamp was filtered for specimen preparation using a red longpass filter (Edmund Optics RG630), and for chromatic adaptation using a 488-nm interference filter (Melles Griot 03FIL002, 10 nm FWHM). Irradiance was controlled by neutral-density filters.

Spectral sensitivity experiments (N=5) were begun when the response to a dim test flash had remained constant for 1 h, indicating the eye was dark adapted. Spectral sensitivity was determined using the criterion response method described in Cohen & Frank (2006). When possible, chromatic adaptation experiments (N=2) were conducted after the determination of dark-adapted spectral sensitivity to test for the presence of multiple visual pigments. Chromatic adaptation consisted of light adapting the eye at 488 nm, waiting until a constant response to a dim test flash was observed for 1 h, then re-testing spectral sensitivity using the criterion response method at all wavelengths. Periodic test flashes were given throughout all experiments to ensure the eye remained in its initial state of adaptation.

Dark-adapted spectral sensitivity data were plotted as the reciprocal of irradiance required to evoke the criterion response at each wavelength, and normalized to the wavelength of maximum sensitivity. These data were modelled using a template for a rhodopsin visual pigment (Govardovskii et al., 2000). The λ_{max} of the visual pigment was optimized to minimize the sum of squared residuals (SSR) when fit to the electrophysiological data.

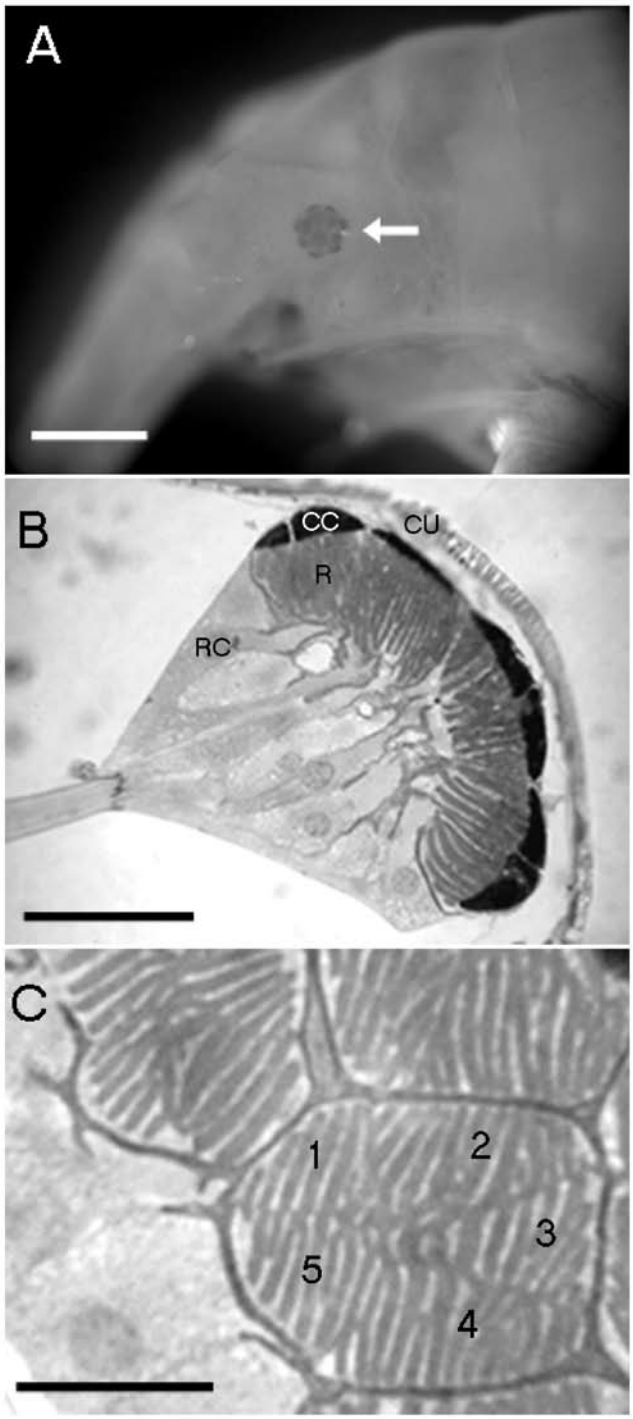

Figure 1. *Scina crassicornis* compound eye. (A) Lateral-facing compound eye of *S. crassicornis*, indicated by arrow; (B) light micrograph of longitudinal section through the approximate mid-point of the eye. CU, cuticle; CC, crystalline cone; R, rhabdom; RC, retinular cell; (C) light micrograph of a rhabdom in cross-section. Retinular cells are numbered 1–5. Scale bars: (A) 500 μm; (B) 50 μm; (C) 25 μm.

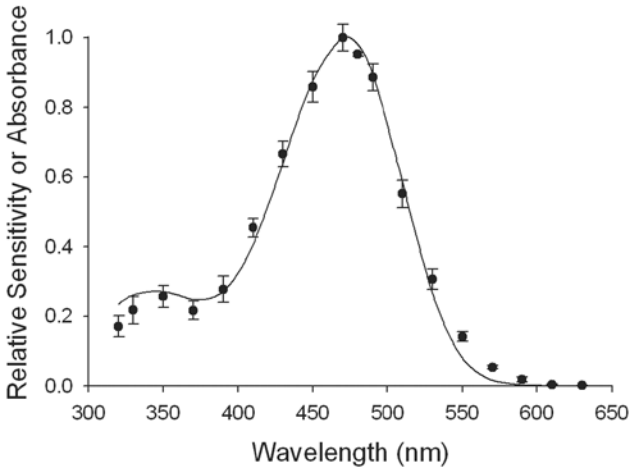

Figure 2. *Scina crassicornis* spectral sensitivity. Relative sensitivity from ERGs at test wavelengths (filled circles) are plotted as mean ± SE (N=5; dark adapted). Relative absorbance of a rhodopsin visual pigment with 472 nm λ_{max} (solid line) provided the best fit to ERG data.

The relative irradiance sensitivity of the dark-adapted *S. crassicornis* eye (N=5) was measured by presenting 75-ms flashes of 470-nm light of varying irradiance levels. Test flashes presented throughout the experiments ensured the eye remained dark adapted. Peak-to-peak response heights (*V*) were calculated and modelled as a function of log irradiance (log*I*) using the Zettler modification of the Naka-Rushton equation (Frank, 2003). The log irradiance evoking 50% of the maximum response amplitude (log*K*) was calculated to provide an estimate of relative sensitivity of the *S. crassicornis* eye as compared to other organisms tested using similar methods (Frank, 2003; Cohen & Frank, 2006).

The temporal resolution of the *S. crassicornis* eye was determined by measuring the response latency, defined as the amount of time elapsed from the onset of the light flash until the onset of the photoreceptor response. Response latency was calculated for flashes yielding response amplitudes approximately 10% and 50% of the maximum amplitude of the *V*/log*I* curve (Frank, 1999, 2003).

RESULTS

Eye structure

The eyes of *Scina crassicornis* are laterally paired structures located posterior to the base of the antennae, and appear orange-red. Each eye is round, with a diameter of 214 μm (SD=23 μm), and contains 12 facets (Figure 1A). A cuticle overlays convex-concave crystalline cones with facet diameters (*D*) of 50–60 μm (Figure 1B). The gap between the cuticle and crystalline cones is likely a fixation artifact. The rhabdoms underlie the crystalline cones and are ~30 μm long at their centre (Figure 1B). Rhabdoms are separated by pigment cells and are composed of 5 retinular cells (Figure 1B&C). The fenestrated membrane, a feature common to most amphipod eyes that separates retinular cell nuclei and glial cells from the rhabdoms (Hallberg et al., 1980), is not obvious, but given the overall organization of the photoreceptors in the eye-cup, one is likely present.

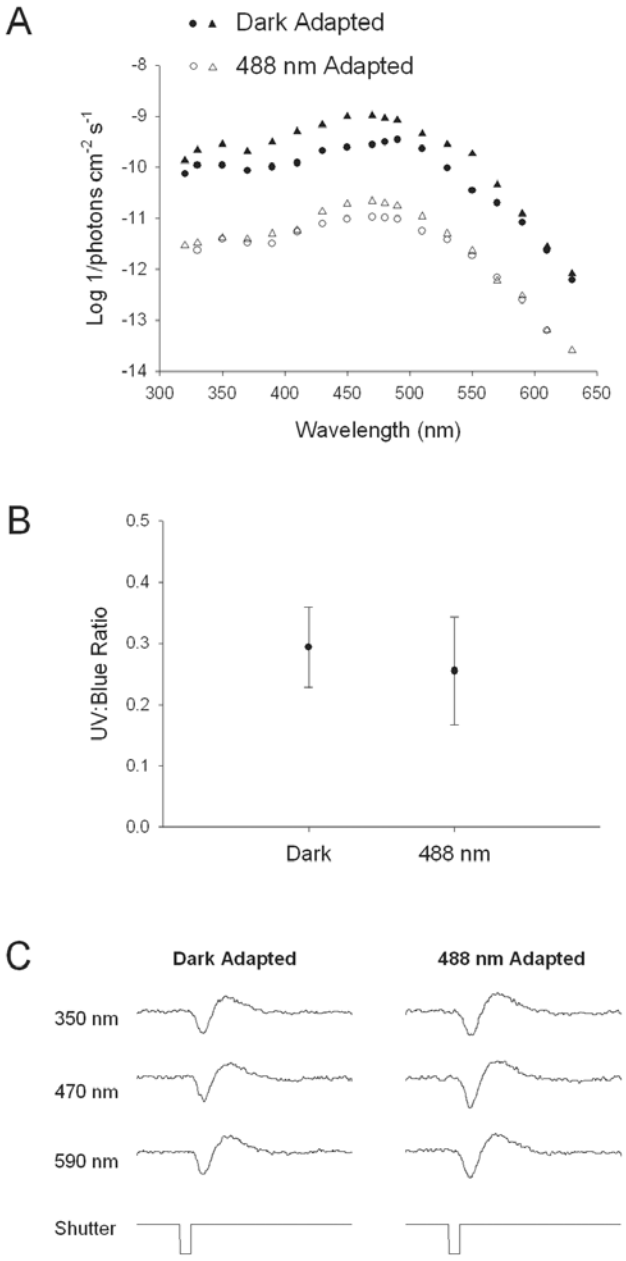

Figure 3. *Scina crassicornis* chromatic adaptation. (A) Spectral sensitivity plotted as log inverse irradiance (log 1/photons cm^{-2} s^{-1}) for dark-adapted (filled symbols) and 488 nm-adapted (open symbols) specimens (N=2; circles and triangles differentiate specimens); (B) the ratio of the inverse criterion irradiance at UV wavelengths (average 330–370 nm) to blue wavelengths (average 450–490 nm) for dark-adapted and 488 nm-adapted amphipods. Data are means (± SD, N=2); (C) ERG waveforms for one specimen plotted in panel A (triangles). Waveforms are shown for flashes at 350, 470, and 590 nm that evoked a criterion response (50 μV) when the specimen was both dark and light adapted (488 nm). A negative square pulse in the shutter trace indicates a flash of light.

Visual physiology

Dark-adapted *S. crassicornis* have a visual spectral sensitivity function best fit with a 472 nm rhodopsin visual pigment absorbance template (SSR=0.0198) (Figure 2). Specimens chromatically adapted to a 488 nm light and re-tested for spectral sensitivity showed decreased irradiance sensitivity

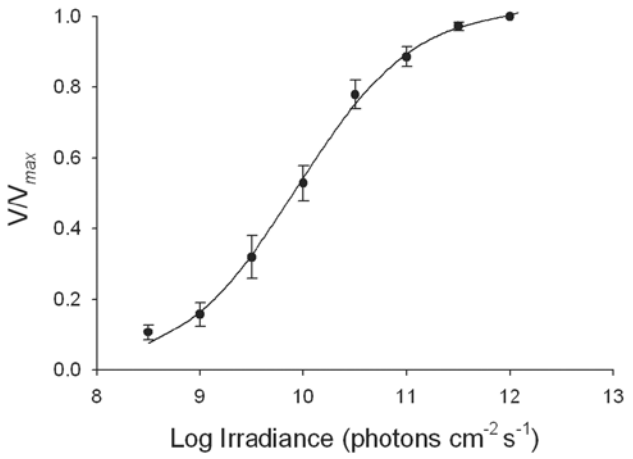

Figure 4. *Scina crassicornis* relative irradiance sensitivity. The relative amplitude of the ERG response (V/Vmax; filled circles) plotted as a function of log irradiance (log photons cm^{-2} s^{-1}) at 470 nm. Data are means (±SE, N=5). The best-fit Naka–Rushton model is plotted as a solid line.

at all wavelengths (Figure 3A). The ratio of UV sensitivity (330–370 nm) to blue sensitivity (450–490 nm) was the same for both dark-adapted and 488 nm-adapted amphipods (Figure 3B; P=0.667, rank sum test). Similar corneal positive (downward) ERG waveforms were observed at all test wavelengths in dark-adapted animals and with chromatic adaptation (Figure 3C).

Relative irradiance sensitivity of *S. crassicornis* photoreceptors was determined from the V/log$I$ function, modelled using the Zettler modification of the Naka-Rushton equation (log$K$ =9.94 log photons cm^{-2} s^{-1}; SSR =0.0021) (Figure 4). Response latency, defined as the amount of time elapsed from the onset of the light flash until the onset of the photoreceptor response, was calculated at 10% and 50% V_{max} to provide a measure of visual temporal resolution. Response latency was 117 ms (±17, SD) and 70 ms (±17, SD), for 10% and 50% V_{max} respectively.

DISCUSSION

Aspects of an eye's morphology and physiology contribute to its ability to function for specific tasks in a given habitat (Warrant, 1999). The specific visual tasks of *Scina crassicornis* are not known, but we can begin to discover them by examining its eye design and photoreceptor function in the context of the light environment in which this animal lives. The overall eye morphology of *S. crassicornis* is much simpler than that of other hyperiids (e.g. *Phronima* and *Streetsia*), and organization of the ommatidia is more similar to deep-dwelling gammarids such as *Orchomenopsis obtusa* (Lysianassidae) than to hyperiids such as *Hyperia galba*, *Phronima* spp., and *Parathemisto* spp. (Ball, 1977; Hallberg et al., 1980). This is not terribly surprising as hyperiids are a polyphyletic group, and the phylogenetic relationship of *Scina* with other hyperiids is an open question (W.E. Browne, University of Hawaii, personal communication).

Facet diameter (D) is an important characteristic to measure as more light can enter the ommatidia with larger D, which is useful in low light environments like the mesopelagic (Land, 1989). For the *S. crassicornis* eye, D =50–60 μm, which is comparable to the side-facing ommatidia of other mesopelagic hyperiids, but smaller than the upward-facing ommatidia of these organisms (Land, 1989). Upward facing ommatidia of hyperiids are thought to image small opaque targets against downwelling background light, while side-facing ommatidia such as those of *S. crassicornis*, appear optically optimized for detection of bright bioluminescence sources over the species depth range, or for optimum vision in brighter light environments in shallower water (Land, 1989). Either of these is possible given that *S. crassicornis* typically lives in the upper 500 m and has been reported to have a large vertical migration range (Thurston, 1976), which may be a function of the movements of its gelatinous hosts, potentially siphonophores (Laval, 1980).

The temporal dynamics and relative irradiance sensitivity of *S. crassicornis* photoreceptors suggest that its eye is very slow, and as a result, fairly sensitive. Response latency provides a measure of the time over which photons are integrated prior to a visual response. The longer the integration time, the more sensitive to light the eye will be. The cost of heightened sensitivity through temporal integration is an inability to detect fast visual stimuli, such as rapid flashes of light (Warrant, 1999). For *S. crassicornis*, the response latency is very slow. Its 10% latency (117 ms, 9°C) is slower than has been reported for the Antarctic benthic lysianassid amphipod *Abyssorchomene plebs* (100 ms, calculated for 9°C from 3 and 7°C data in Cohen & Frank, 2006), which itself has a very slow eye. This long response latency fits with the low irradiance value of log$K$ for the *S. crassicornis* eye (9.94 log photons cm^{-2} s^{-1}), a measure of its relative irradiance sensitivity. This value is at the low end of those reported for other mesopelagic crustaceans (10.3–12.21 log photons cm^{-2} s^{-1}; Frank, 2003). While fast photoreceptors are useful for detecting fast luminescent flashes of potential prey (Frank, 1999, 2003), they are metabolically costly (Laughlin et al., 1998), and are poorly suited for maximizing photon capture in dim light environments (Warrant, 1999). Having slow, sensitive photoreceptors fits with what little we know about the feeding ecology of *Scina*; it eats tissues of gelatinous zooplankton on which it lives (Vinogradov et al., 1996).

Scina crassicornis possesses a single visual pigment, as evidenced by a uniform ratio of UV sensitivity to blue sensitivity in chromatic adaptation, and by waveform analysis. The spectral sensitivity maximum of the *S. crassicornis* visual pigment (λ_{max}=472 nm) is shifted to longer wavelengths than the spectral maximum of its luminescent emission (435–444 nm; Herring, 1983; Widder et al., 1983; Latz et al., 1988). This suggests that *S. crassicornis* visual spectral sensitivity is not specifically adapted for the detection of its own luminescence, as might be expected if luminescence played a major role for intraspecific signalling (e.g. mating; Wilkens & Wolken, 1981). A likely function for *S. crassicornis* luminescence is defence, as this species synchronously flashes while assuming a defensive posture that faces the photocytes outward and away from the body, potentially deterring predators by increasing its apparent size (Herring, 1981;

Bowlby et al., 1991). While spectral sensitivity does not seem to be tuned to its own bioluminescent emission spectra, it is still possible that vision plays a role in *S. crassicornis* courtship, perhaps through flash sequences coded in time and space, as in ostracods and fireflies, and perhaps in synergy with other sensory modalities (reviewed in Herring, 2000).

Many deep-sea organisms have visual spectral sensitivities offset towards wavelengths longer than those of the downwelling light field at depth (~474 nm; Jerlov, 1976). For example, deep-sea crustaceans have an average λ_{max} of 493 nm (excluding λ_{max} of UV-sensitive R8 cells in some species), and deep-sea fish have an average λ_{max} of 484 nm (reviewed in Marshall et al., 1999). Douglas et al. (1998) predicted that monochromatic visual systems of deep-sea fish tuned to detect bioluminescence at mesopelagic depths would have visual sensitivity maxima between 468–490 nm, while those tuned to detect downwelling light in clear oceanic water at mesopelagic depths would possess maxima at shorter wavelengths (<474 nm). Accordingly, the spectral sensitivities of most deep-sea crustaceans and fish are thought to be optimized for detecting bioluminescent flashes as bright objects against the relatively dark background spacelight (reviewed in Warrant & Locket, 2004).

The observed visual spectral sensitivity of *S. crassicornis* (λ_{max}=472 nm) is within the range predicted for a monochromatic fish visual system if adapted to either bioluminescence detection or extended downwelling spacelight at mesopelagic depths in Jerlov Type IB water (474 nm; Douglas et al., 1998). Water in the Gulf of Mexico where *S. crassicornis* were collected is typically Jerlov Type IA or IB (Jerlov, 1976). It is worth noting that at mesopelagic depths in this water type, the spectra of upwelling and sidewelling light will be similar to that of downwelling light (Denton, 1990). Accordingly, the spectral sensitivity of *S. crassicornis* would serve to maximize photon capture in all lines of sight in the mesopelagic, while still permitting the detection of point sources of bioluminescence. A similar, uniform spectral sensitivity has been reported for the optically different up-facing and side-facing portions of the *Phronima sedentaria* eye (λ_{max}=470 nm; Frank & Widder, 1999). This species is the only other hyperiid amphipod whose visual spectral sensitivity has been reported, and given the unusual nature of hyperiid eyes, yet the similar physiological results to date, more studies are certainly warranted.

Laval (1980) suggested the need for hyperiids to locate suitable hosts may have directed sensory evolution in these animals. Vision is a sensory modality that can be tuned in marine crustaceans for specific ecological functions (reviewed in Marshall et al., 2003). The present study suggests the visual adaptations of *S. crassicornis* are consistent with those of mesopelagic crustaceans, and physiologically, though not structurally, with other hyperiids. Far more information is needed regarding the behaviour of hyperiid amphipods to fully evaluate the role their sensory systems play in ecological interactions.

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