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RESEARCH ARTICLE

Spectral sensitivity of the concave mirror eyes of scallops: potential influences of habitat, self-screening and longitudinal chromatic aberration

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SUMMARY

Scallop eyes contain two retinas, one proximal and one distal. Molecular evidence suggests that each retina expresses a different visual pigment. To test whether these retinas have different spectral sensitivities, we used microspectrophotometry to measure the absorption spectra of photoreceptors from the eyes of two different scallop species. Photoreceptors from the proximal and distal retinas of the sea scallop *Placopecten magellanicus* had absorption peak wavelengths (λ_{max}) of 488±1 nm (mean ± s.e.m.; *N*=20) and 513±3 nm (*N*=26), respectively. Photoreceptors from the corresponding retinas of the bay scallop *Argopecten irradians* had λ_{max} values of 506±1 nm (*N*=21) and 535±3 nm (*N*=14). Assuming that the proximal and distal receptors had equal absorption coefficients (k_D=0.0067 μm^{-1}), we found that self-screening within the scallop eye caused the proximal and distal receptors in *P. magellanicus* to have peak absorption at 490 and 520 nm, respectively, and the corresponding receptors in *A. irradians* to have peak absorption at 504 and 549 nm. We conclude that environment may influence the λ_{max} of scallop visual pigments: *P. magellanicus*, generally found in blue oceanic water, has visual pigments that are maximally sensitive to shorter wavelengths than those found in *A. irradians*, which lives in greener inshore water. Scallop distal retinas may be sensitive to longer wavelengths of light than scallop proximal retinas to correct for either self-screening by the retinas or longitudinal chromatic aberration of the lens.

Key words: visual ecology, chromatic aberration, microspectrophotometry, *Placopecten magellanicus*, *Argopecten irradians*.

INTRODUCTION

Scallop eyes are unlike any others in the animal world (Fig. 1A). They are single-chambered and contain a large lens, but do not function like the camera eyes they superficially resemble. Instead of using their lenses to form images, scallops use the concave spherical mirror that lines the back of each eye. It is thought that the scallop lens simply corrects for the spherical aberration that this mirror produces (Land, 1965). Scallops are thus in rare company: the spookfish *Dolichopteryx longipes* (Wagner et al., 2009) is the only other animal known to use a mirror for image formation.

Scallops also have an unusually arranged pair of retinas (Fig. 1B). Other animals with multiple retinas – including the alciopid worms *Vanadis* and *Torrea* (Wald and Rayport, 1977), the deep-sea squid *Bathyteuthis* (Chun, 1903), and several species of mesopelagic fish (Collin et al., 1997; Warrant and Locket, 2004) – have laterally arranged retinas that gather information from different visual fields. Scallops, in contrast, have proximal and distal retinas arranged as a stack (Fig. 1B). In this way, scallop eyes resemble the multibank retina eyes of jumping spiders such as *Phidippus* (Land, 1969), the firefly squid *Watasenia scintillans* (Michinomae et al., 1994) and some deep-sea teleosts (Denton and Locket, 1989). Multibank retinas offer several potential advantages over single-stack retinas: they improve rates of photon capture within eyes by increasing optical path length (Warrant and Locket, 2004); they can provide color vision, even in the absence of multiple visual pigments, by using distal photoreceptors as spectral filters for more proximal receptors (Warrant and Locket, 2004); and they may help compensate for longitudinal chromatic aberration (LCA) produced by a lens (Blest et al., 1981; Kröger and Gislén, 2004).

Unlike other multibank retinas, which are composed of relatively similar layers, the two scallop retinas are quite different. The proximal retina is composed of rhabdomeric photoreceptors that depolarize in response to light whereas the distal retina contains ciliary receptors that hyperpolarize in response to light (Hartline, 1938; Barber et al., 1967; McReynolds and Gorman, 1970). Molecular evidence also shows that the proximal and distal receptors express different visual pigments (Kojima et al., 1997). If these visual pigments have different absorption peak wavelengths (λ_{max}), scallop vision may be enhanced in several (not necessarily exclusive) ways.

If scallop eyes are interpreted as multi-retina eyes, proximal and distal photoreceptors that differ in λ_{max} may make the two scallop retinas better suited for specific tasks. Many aquatic animals have visual pigments with a λ_{max} that closely matches the dominant wavelength of horizontal radiance in their environment (Clarke, 1936; Munz, 1958). This maximizes optical sensitivity, but a visual pigment with a λ_{max} offset from this peak may improve the visual contrast of objects that reflect spectrally broad downwelling light in the context of a spectrally narrow horizontal light field (Lythgoe, 1968).

If we consider scallop eyes as multibank retina eyes, visual pigments with different λ_{max} values may provide different advantages. First, two visual pigments could grant scallops dichromatic vision. This is unlikely, however, given what is known

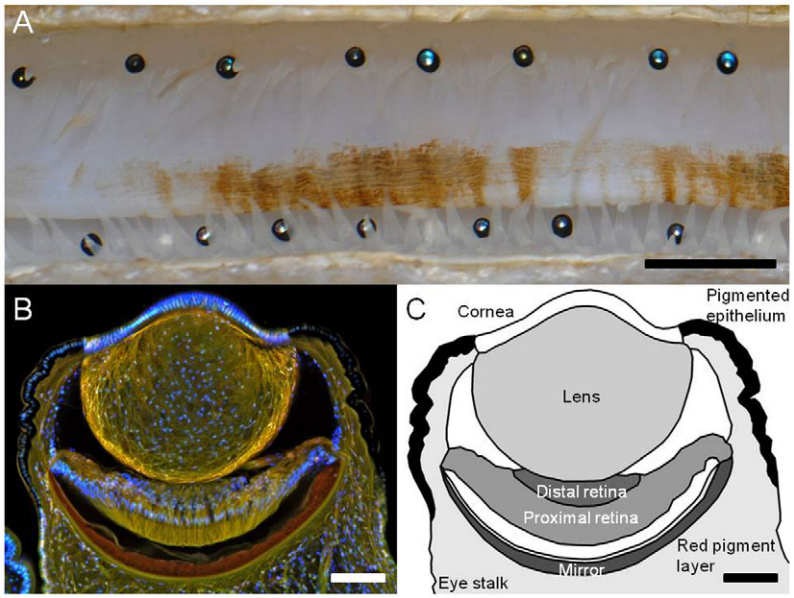

Fig. 1. The eyes of the sea scallop *Placopecten magellanicus*. (A) Eyes arrayed along the valve mantle margins of a live *P. magellanicus*. The scale bar represents 5 mm. (B) Cross-section of an eye from *P. magellanicus*. The sample was stained with Hoechst dye, staining cell nuclei blue, and alpha-tubulin, staining green. The pigment layer underneath the mirror appears red in the image and *in vivo*. (C) A labeled diagram corresponding to (B). The scale bar in (B) and (C) represents 100 μm.

about visual processing in these bivalves. There is no evidence that scallops integrate the information received separately by their proximal and distal retinas in either their eyes or their optic lobes, a necessary event if these animals are to possess color vision in any conventional sense (Wilkens and Ache, 1977; Spagnolia and Wilkens, 1983).

Second, differences in the λ_{max} of scallop visual pigments may limit the self-screening that occurs within the scallop eye. Self-screening occurs in these eyes because the focused light that reaches each retina is modified by having passed, unfocused, through both sets of photoreceptors on the way to the mirror and then back through the proximal receptors on the way to the distal receptors. If scallop visual pigments differ in λ_{max}, the amount by which each retina screens the other will be decreased, thereby increasing the total amount of focused light available for absorption by each set of photoreceptors.

Third, differences in spectral sensitivity between the two scallop retinas may compensate for LCA caused by the lens. All known biological lenses have higher refractive indices at shorter wavelengths of visible light than at longer wavelengths, a property that causes them to bend short wavelengths more sharply than long wavelengths (Kröger, 2000). In camera eyes, the result of LCA is that shorter and longer wavelengths have focal planes that are relatively closer and further from the lens, respectively (Fig. 2A). The mirror in the scallop eye does not produce chromatic aberration, but it does reverse the pattern described above by folding light paths within the eye. Because of the mirror, short wavelengths are focused further from the lens (and closer to the mirror) than longer wavelengths (Fig. 2B). We hypothesize that scallops may limit the effects of chromatic aberration by having a visual pigment in the proximal retina that is sensitive to shorter wavelength (bluer) light than the visual pigment in the distal retina.

Here, we use microspectrophotometry (MSP) to measure the spectral absorbance of photoreceptors from the distal and proximal retinas of the sea scallop *Placopecten magellanicus* (Gmelin 1791), which is commonly found at 20–110 m (Brand, 2006), and the shallow-dwelling bay scallop *Argopecten irradians* (Lamarck 1819), which generally lives in water 1–12 m deep (Brand, 2006). We chose these species so that we could also explore the relationship between a scallop's light environment and its spectral sensitivity. Because of phytoplankton, which absorb both long- and short-wavelength light and tend to occur at higher concentrations closer to the coast, shallow inshore water tends to be greener than deeper oceanic water (Tyler and Smith, 1970; Jerlov, 1976; Loew and McFarland, 1990). The visual pigments of marine animals tend to reflect these environmental differences: λ_{max} is generally shifted towards longer (greener) wavelengths in species from coastal habitats and towards shorter (bluer) wavelengths in species from offshore environments (Denton and Warren, 1957; Munz, 1958; Lythgoe, 1972; Partridge, 1990). We expect that *P. magellanicus* and *A. irradians* will have visual pigment λ_{max} values consistent with this well-established pattern.

MATERIALS AND METHODS

Specimen collection and care

Adult scallops of the species *P. magellanicus* and *A. irradians* were obtained from Woods Hole, MA, USA (41.53°N, 70.66°W) and Smyrna, NC, USA (34.76°N, 76.53°W), respectively. Specimens of *P. magellanicus* were delivered to Duke University (Durham, NC, USA) on 12 January 2009 and were kept in a 200 l aquarium. Because *P. magellanicus* acclimates slowly to increases in water temperature and MSP recordings were to be taken at room temperature, the aquarium was initially set at 10°C and was brought up to 20°C over 2 weeks. Specimens of *A. irradians* were transported to Duke University on 6 February 2009 and were kept at 20°C in a 950 l flow-through seawater system. Both aquaria were kept inside under light supplied by fluorescent bulbs and windows; salinity was maintained at 32‰ (Instant Ocean sea salt; Aquarium Systems Inc., Mentor, OH, USA). Three adults of each species were transported by car to Cornell University (Ithaca, NY, USA) on 24 February 2009. There, the animals were split by species between two 40 l aquaria and were again kept at 20°C and 32‰.

Microspectrophotometry

Prior to MSP recordings, scallops were dark-adapted for 10–12 h overnight and were then dissected under dim red light. The largest eyes from the ventral portion of the left valve mantle margin were identified, excised with surgical scissors and placed in small dishes of seawater. Retinas were isolated from the eyes using forceps via the following procedure: starting at the pupil, a small tear was made

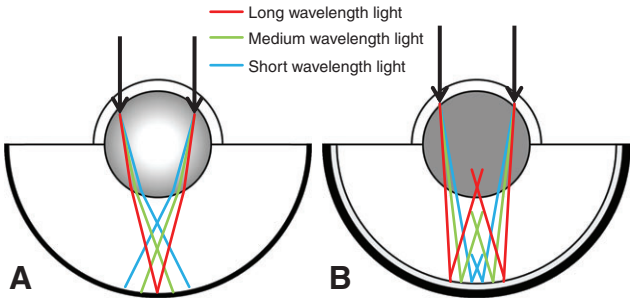

Fig. 2. Examples of longitudinal chromatic aberration in (A) a camera eye, like those of fish or cephalopods, in which there is a lens with a high refractive index, a retina at the back of the eye, and no image-forming mirror and (B) a scallop eye in which there is a lens with a low refractive index and an image-forming, concave spherical mirror overlying a pigment layer at the back of the eye. In a camera eye, longitudinal chromatic aberration (LCA) causes shorter (bluer) wavelengths to be focused closer to the lens than longer (redder) wavelengths. Assuming that the scallop lens, like all biological lenses, produces LCA, shorter wavelengths come into focus further away from the lens than longer wavelengths.

down the side of the eye and gentle pressure, exerted from below, was used to expel the lens, followed by the retinas, through the tear. Isolated, intact retinas appeared as a shallow bowl, with the distal receptors forming the concave inner surface and the proximal receptors constituting the convex outer surface. The distal and proximal retinas were loosely attached and were deliberately separated from one another in some cases. In other cases, retinas were cut into pieces with a scalpel so that proximal and distal photoreceptors could more easily be observed under the microscope at the same time. Excised retinas were washed with several changes of artificial seawater, to remove any loose pieces of tissue, and then placed between two coverslips edged with silicone grease.

MSP was performed using the single-beam, computer-controlled microspectrophotometer described in McFarland and Loew (McFarland and Loew, 1994). This microspectrophotometer used a Leitz (Oberkochen, Germany) 170× quartz mirror condensor and a Zeiss 100× Ultrafluar (0.85 NA) objective (Oberkochen, Germany), which was used to focus light onto a photomultiplier (Hamamatsu R1463; Hamamatsu, Shizuoka, Japan). A 2×3 µm beam was used for measurements. Spectra for baseline and sample recordings were taken from 750 to 350 nm and back again at a rate of 100 nm s^{-1} and a wavelength accuracy of 1 nm (McFarland and Loew, 1994). To position the microspectrophotometer's beam, samples were viewed using infrared illumination and an image converter. Photoreceptors were easily identified within retinas because of their morphology, described for *A. irradians* and *P. magellanicus* by Speiser and Johnsen (Speiser and Johnsen, 2008), as well as their palisade-like arrangement. Proximal and distal receptors were distinguished from one another on the basis of their relative position within the retina (as described above) and their length and width. Proximal receptors in both species were longer and more tightly packed than receptors from the distal retina (Speiser and Johnsen, 2008) and had ends that were more sharply tapered.

Recordings from *A. irradians* and *P. magellanicus* were taken in February and March 2009. Eyes from freshly dissected animals were used on each of four days. Recordings were always taken from at least three eyes from the same individual, and 100–200 different retinal cells were tested on each day. Absorbance spectra for individual photoreceptors were included in calculations of λ_{max} (the wavelength at which the maximum absorbance of a template-derived photo-pigment best matches the experimental data) if they displayed a single, relatively noise-free peak between 400 and 700 nm, a condition satisfied by 81 out of 615 recordings. The long-wavelength limbs (470–700 nm) of the chosen spectra were fitted to an A_1 rhodopsin template (Stavenga et al., 1993) *via* a least squared algorithm implemented using Solver (Excel 2003; Microsoft Inc., Redmond, WA, USA) that varied λ_{max}, peak height, baseline level and optical path length. Visual pigment λ_{max} did not appear to differ among retinas of the same type from the same individual or between scallops of the same species. In addition, photo-bleaching, performed at the blaze setting for the MSP and lasting from 30 to 300 s, did not affect the absorbance spectra of any of the visual pigments we examined in this study.

Absorption and self-screening in the scallop eye

The optical configuration of the scallop eye, which involves a tiered double retina and a mirror, is such that the focused light that reaches each retina is modified by self-screening. This occurs because unfocused light must pass through both sets of receptors before reaching the mirror and back through the proximal receptors on the way to the distal receptors. The fraction of incident light (at one wavelength) that arrives in focus at the proximal retina, modified by the absorption of unfocused, incoming light by the proximal (P) and distal (D) receptors and reflection by the mirror, is:

$$t_P(\lambda) = e^{-k_D l_D A_D(\lambda)}\, e^{-k_P l_P A_P(\lambda)}\, R_M(\lambda), \quad (1)$$

where R_M is the reflectance of the mirror, and A, l and k are the normalized absorbance spectra, length and absorption coefficients of the receptors, respectively. So, the fraction of incident light that is focused on and then absorbed by the proximal retina is:

$$V_P(\lambda) = t_P(\lambda)\,(1 - e^{-k_P l_P A_P(\lambda)}). \quad (2)$$

In the case of the distal retina, the incident light is partially absorbed by the proximal and distal receptors, reflected by the mirror and then further absorbed by the proximal receptors before arriving focused at the distal retina. Therefore, the analog of Eqn 2 is:

$$V_D(\lambda) = e^{-k_D l_D A_D(\lambda)}\, e^{-2k_P l_P A_P(\lambda)}\, R_M(\lambda)\,(1 - e^{-k_D l_D A_D(\lambda)}). \quad (3)$$

For *P. magellanicus*, the lengths of proximal (l_P) and distal rhabdoms (l_D) were 33 and 19 µm, respectively; in *A. irradians*, the corresponding rhabdoms were 30 and 12 µm (Speiser and Johnsen, 2008). For the rhabdomeric proximal receptors, the absorption coefficient (k_D) was taken to be 0.0067 μm^{-1}, as estimated for receptors from the eye of the lobster *Homarus* (Bruno et al., 1977). We find it reasonable to assume that these morphologically and physiologically similar receptors have similar absorption coefficients (Warrant and Nilsson, 1998). Estimating an absorption coefficient for the ciliary receptors of the scallop distal retina (k_P) is less straightforward. Even when they are employed in the same light environment, vertebrate ciliary receptors generally have an absorption coefficient that is five times that of invertebrate rhabdomeric receptors (Warrant and Nilsson, 1998). A higher absorption coefficient may correlate with ciliary receptors in general or be a particular feature of vertebrate rods and cones (scallop and vertebrate ciliary receptors are more similar to each other than either are to rhabdomeric receptors, but they are not identical). Therefore, we calculated absorption in scallop eyes using two estimates of k_D: one consistent with invertebrate receptors (0.0067 μm^{-1}) (Bruno et al., 1977) and one, five times higher, consistent with receptors found in fish eyes (0.0335 μm^{-1}) (Partridge, 1990). Given that we are more interested in the interaction between the two scallop retinas than

the total number of photons gathered by the scallop eye, it is the ratio between k_P and k_D, not the absolute value of either, that has the greatest influence on our results.

The scallop mirror is a multi-layer, quarter-wavelength reflector; in life, it appears silver in *A. irradians* and bluish in *P. magellanicus* (Fig. 1A). We therefore estimated that the mirror in *A. irradians* reflects 90% of incident light at wavelengths from 400 to 700 nm. We also assumed that the mirror in *P. magellanicus* has a reflectance spectrum similar to the mirror in *Pecten maximus* (Land, 1966b), a species that lives at a similar depth range. Values for R_M in *P. magellanicus* were derived from the left-hand (shorter wavelength) curve from fig. 7 in Land (Land, 1966b), setting the peak reflectance to 90%.

A final point concerns where focused light falls in the scallop eye. Land argued that scallop eye morphology is such that focused light only falls on the receptors of the distal retina (Land, 1965). This estimate depends on the focal length of the scallop mirror and the distance between the mirror and the distal receptors. Scallop eyes are small enough that slight changes in shape caused by fixation, dehydration, freezing and/or sectioning can greatly affect estimates of focal length and the distance between the mirror and the two retinas. Sectioned eyes (Land, 1965; Speiser and Johnsen, 2008) may therefore be an unreliable source of information for optical models that predict which scallop retina receives focused light. That said, we suspect that scallop proximal retinas receive focused light for two reasons. First, the receptors of the proximal retina are generally narrower, longer, more tightly packed and more numerous than those of the distal retina (Speiser and Johnsen, 2008). Second, the optic lobes of the parieto-visceral ganglion (PVG), a nerve center located on the scallop adductor muscle (Wilkens and Ache, 1977; Spagnolia and Wilkens, 1983), are stimulated by input from the proximal receptors, not the distal receptors.

Scallop light environments

Horizontal radiance (i.e. the background light in a scallop's field of view) was modeled using measured inherent optical properties and a sophisticated radiative transfer software package (Hydrolight 5.0; Sequoia Scientific, Bellevue, WA, USA). Given the depth profiles of the absorption coefficient, beam attenuation coefficient and chlorophyll concentration, the software calculates the underwater radiance distribution as a function of depth and wavelength. The software also takes into account solar elevation and azimuth, atmospheric parameters, bottom reflectance, sea surface conditions, chlorophyll fluorescence and Raman scattering by the water. The ability of the software to accurately model radiance distributions has been validated by *in situ* measurements of selected radiances and irradiances in numerous studies (Mobley et al., 1993; Maffione et al., 1998; Stramska et al., 2000; Johnsen, 2002).

Depth profiles of inherent optical properties for oceanic water (approximately Jerlov oceanic type I) were obtained from Drs Andrew Barnard, Scott Pegau and Ronald Zaneveld (College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA), who collected them using a dual path, multiband absorption/attenuation meter (ac-9; Wetlabs Inc., Philomath, OR, USA) and fluorometer in the Equatorial Pacific (10:05 h, 30 April 1996, 0°0′N, 177°21′W). Absorption and beam attenuation coefficients (at 412, 440, 488, 510, 532, 555, 650 and 676 nm) and chlorophyll concentrations were measured at 1 m intervals to a depth of 138 m. Depth profiles of inherent optical properties for coastal water were obtained using an ac-9 deployed at a site 80 km from the coast of Portsmouth, NH, USA (42°47′N, 70°05′W, 11:06 h, 30 June 2000). Absorption and beam attenuation coefficients (at 440, 488, 510, 532, 555 and 650 nm) were averaged over 1 m intervals to a depth of 92 m. All data were collected on upcasts to limit artifacts due to bubbles, etc. In addition, discrete samples were collected from three depths (1, 20 and 40 m), filtered onto Whatman GF/F filters and extracted overnight in cold 90% acetone for standard fluorometric determination of chlorophyll concentrations. Both sets of measurements were corrected for temperature and salinity, and absorption measurements were corrected for scattering errors (Pegau and Zaneveld, 1994; Pegau et al., 1997).

These two profiles were input into Hydrolight. In both cases, solar elevation was set at 70 deg, and the sky was considered to be clear. The sky irradiance was calculated using the Radtran model (Gregg and Carder, 1990), and the sky radiance distribution was calculated using the model given in Harrison and Coombes (Harrison and Coombes, 1988). Both sky models account for atmospheric effects, such as the reddening of the sun as it approaches the horizon, and are well established. Pure water absorption was taken from Pope and Fry (Pope and Fry, 1997), and the scattering phase function was Petzold's average particle (Petzold, 1977). Chlorophyll fluorescence was calculated from chlorophyll absorption taken from Prieur and Sathyendranath (Prieur and Sathyendranath, 1981) and a fluorescence efficiency of 0.02.

For the oceanic environment, we assumed that water was 100 m deep with a dark sediment bottom. This environment was meant to match the continental slope off George's Bank, MA, USA, a site known for its abundant sea scallop populations (Brand, 2006). For the coastal environment, we assumed that the water was 1 m deep and had a seagrass bottom. This hypothetical environment closely matched the shallow eelgrass (*Zostera* sp.) beds from which we collected specimens of *A. irradians* for this study. In both cases, radiance was calculated from 400 to 700 nm at 10 nm intervals with an angular resolution of 15 deg (azimuth) by 10 deg (elevation).

Scallop quantum catch

We calculated N_o, the number of photons absorbed by a single photoreceptor within its integration time Δt (s) when a scallop eye views a radiance $L_h(\lambda)$. We modeled quantum catch for proximal and distal receptors from the eyes of *P. magellanicus* and *A. irradians* using a formula adapted from Warrant (Warrant, 1999) and Kelber et al. (Kelber et al., 2003):

$$N_0 = 1.13\left(\frac{\pi}{4}\right)\left(\frac{\pi}{180}\right)^2 R^2 D^2 \Delta t \kappa \tau \int_{400}^{700} L_h(\lambda) V(\lambda)\, d\lambda \,, \qquad (4)$$

Table 1. Values used to calculate N_o, the number of photons absorbed by a single scallop photoreceptor

Species	R_P (deg)	R_D (deg)	D (cm)	Δt (s)	κ	τ
Placopecten magellanicus	1.3	2.5	0.035	0.2	0.5	0.8
Argopecten irradians	1.9	2.0	0.04	0.2	0.5	0.8

D, pupil diameter (Speiser and Johnsen, 2008); R_P and R_D, fields of view of scallop proximal and distal photoreceptors, respectively (Speiser and Johnsen, 2008); Δt, integration time, on the basis of recordings from the scallop *Amusium japonicum* (Kanmizutaru et al., 2005); κ, quantum efficiency of transduction; τ, transmission of the scallop lens and cornea.

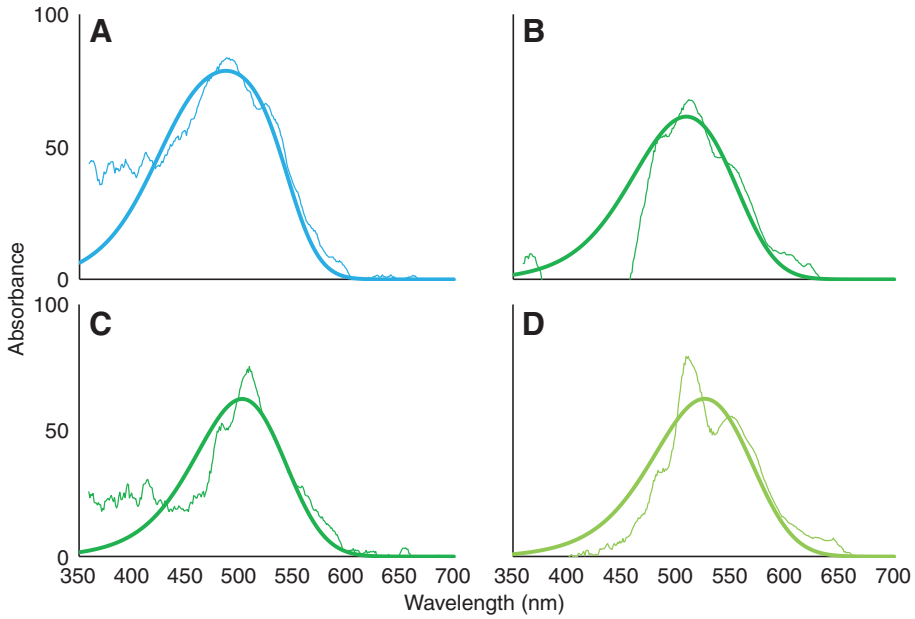

Fig. 3. Results from the microspectrophotometric analysis of photoreceptors from (A) the proximal retina of the sea scallop *Placopecten magellanicus* (λ_{max}=487 nm), (B) the distal retina of *P. magellanicus* (λ_{max}=509 nm), (C) the proximal retina of the bay scallop *Argopecten irradians* (λ_{max}=502 nm), and (D) the distal retina of *A. irradians* (λ_{max}=526 nm). The graphs present raw data from MSP recordings (with the baseline stripped and values smoothed over 10 nm intervals by a moving average) for a single representative photoreceptor from the retina and species indicated above. The data is overlain with a best-fit curve derived from an A_1 rhodopsin template. The values presented here do not necessarily match those seen in Table 1, which presents the mean λ_{max} for each set of photoreceptors.

where R is the acceptance angle of a scallop photoreceptor, D is pupil diameter, Δt is integration time, κ is the quantum efficiency of transduction and τ is the transmission of the scallop lens and cornea. The values of these terms for *P. magellanicus* and *A. irradians*, along with the relevant citations, are found in Table 1. The $\pi/180$ term (which is not found in the original equation) accounts for the fact that we report the acceptance angle in degrees, not radians.

Using Eqn 4, we estimated how the λ_{max} of scallop visual pigments affected the quantum catch of both the distal and proximal receptors. To do so, we varied the λ_{max} values used to estimate the normalized absorbance spectra $A(\lambda)$ that were a component in our calculations of V_P and V_D (see Eqns 2 and 3). We then estimated the number of photons absorbed by one proximal receptor (N_P) and one distal receptor (N_D). By varying λ_{max} for both the proximal and distal receptors, we were able to calculate, first, how different pairs of λ_{max} values affected scallop quantum catch and, second, the λ_{max} values that optimized quantum catch in different scallop eyes under different environmental conditions.

RESULTS

Microspectrophotometry

We found that the λ_{max} of scallop visual pigments depended on both the species and the receptor (proximal or distal) that was examined. Visual pigments from the proximal and distal retinas of *P. magellanicus* maximally absorbed shorter (bluer) wavelengths than the pigments from the corresponding retinas in *A. irradians*. We also found that, in both species, receptors of the proximal retina maximally absorbed shorter wavelengths than those of the distal retina.

Receptors from the proximal retina of *P. magellanicus* contained a visual pigment with a mean (±s.e.m.) λ_{max} of 488±1 nm (N=20). A representative absorbance spectrum for a photoreceptor of this type is shown in Fig. 3A, along with a rhodopsin template fit to the long-wavelength portion of the curve. A histogram showing all λ_{max} values analyzed for this retina is shown in Fig. 4A. For *P. magellanicus* distal receptors, the mean λ_{max} was 513±3 nm (N=26; Fig. 3B and Fig. 4B).

The proximal receptors of *A. irradians* had a mean λ_{max} of 506±1 (N=21), slightly higher than the λ_{max} recorded for the proximal receptors of *P. magellanicus* (Fig. 3C and Fig. 4C). Receptors from the *A. irradians* distal retina had a mean λ_{max} of 535±3 (N=14). This set of receptors provided the least consistent absorbance spectra of those observed (Fig. 3D and Fig. 4D). The reasons for this were unclear, but may have been due to the small size of the distal retina, confounding absorption by the proximal retina, or photo-stable pigments.

Absorption spectra of both retinas after accounting for self-screening

After accounting for reflection by the mirror and self-screening by the scallop retinas, the λ_{max} values of the proximal receptors generally shifted slightly towards shorter wavelengths whereas the λ_{max} values of the distal receptors showed a more significant shift towards longer wavelengths. Thus, self-screening tended to increase the differences in absorption between scallop proximal and distal receptors. For the lower k_D (0.0067 μm^{-1}), the proximal receptor λ_{max} shifted from 488 to approximately 490 nm in *P. magellanicus* (Fig. 5A) and from 506 to 504 nm in *A. irradians* (Fig. 5B); in the distal receptors, λ_{max} shifted from 513 to 520 nm in *P. magellanicus* and from 535 to 549 nm in *A. irradians*. For the higher k_D (0.0335 μm^{-1}), proximal λ_{max} shifted from 488 to 480 nm in *P. magellanicus* and from 506 to 494 nm in *A. irradians*; distal λ_{max} also changed from 513 to 540 nm and from 535 to 558 nm in these two species, respectively. Self-screening, at either value of k_D, also changed the shape of the absorption curve for the distal receptors, so that there was a relatively long tail on the short wavelength side and a short tail on the long wavelength side. Not surprisingly, higher values for k_D caused the distal receptors to absorb an increasing number of photons at the expense of the proximal receptors.

Scallop light environments

Our models revealed that *P. magellanicus* (Fig. 6A) views an environment that is around 100 times dimmer during the day than the one viewed by *A. irradians* (Fig. 6B). The horizontal radiance for the offshore environment of *P. magellanicus*, modeled at 90 m depth and integrated from 400 to 700 nm, was approximately 10^{13} photons cm^{-2} s^{-1} sr^{-1}, whereas the horizontal radiance for the shallow inshore habitat of *A. irradians*, modeled at 0.8 m depth, was approximately 10^{15} photons cm^{-2} s^{-1} sr^{-1}. Largely because of

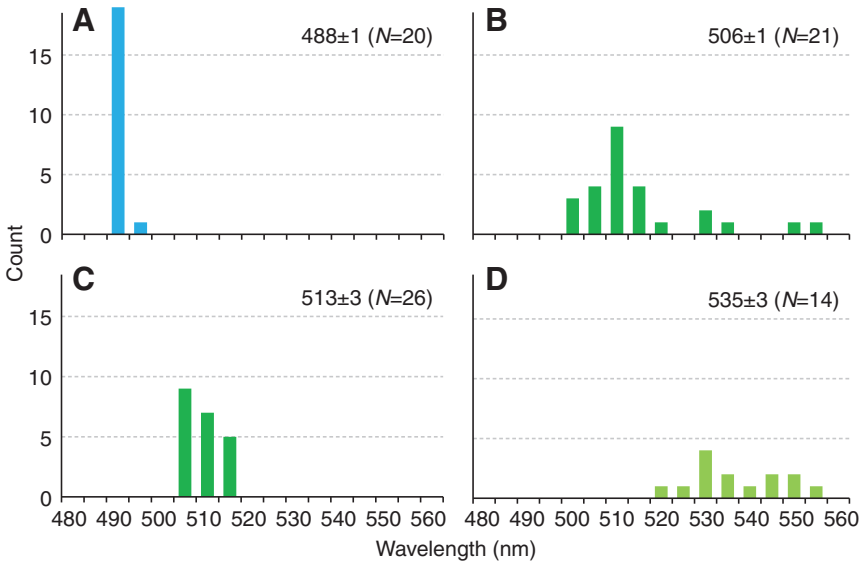

Fig. 4. Histograms of the results from the microspectrophotometric (MSP) analysis of individual photoreceptors from the (A) proximal and (B) distal retinas of the sea scallop *Placopecten magellanicus* and the (C) proximal and (D) distal retinas of the bay scallop *Argopecten irradians*. The values included with each histogram refer to λ_{max}, the wavelength of peak absorbance for each photo-pigment studied, and is presented as mean ± s.e.m. Statistical comparisons were made using a Student's *t*-test (two-tailed). Significant differences (α=0.01) were found across both rows, which compare homologous retinas between species, and down both columns, which compare different retinas from the same species.

the selective absorption of short- and long-wavelength light by phytoplankton, *A. irradians* lives in an environment that is not only brighter than that of *P. magellanicus* but greener as well. The horizontal radiance in *P. magellanicus*' habitat peaked at 480 nm and had a full-width half-max of 80 nm (the wavelength range over which the spectrum was at least half of what it was at its peak). In comparison, the horizontal radiance in *A. irradians*' environment peaked at 560 nm and had a full-width half-max of 100 nm.

Scallop quantum catch assuming a k_D of 0.0067 μm^{-1}

At the lower k_D, we found that individual proximal and distal photoreceptors in the sea scallop *P. magellanicus* collected 3.5×10^4 and 5.3×10^4 photons per integration time, respectively, when vision in this species was modeled at 90 m deep in an oceanic environment (Table 2). Quantum catches for the proximal and distal photoreceptors of the bay scallop *A. irradians* were 8.3×10^6 and 4.3×10^6 photons per integration time, respectively, when this animal was at a depth of 0.8 m in its native coastal habitat (Table 2). Visual pigment λ_{max} values in *P. magellanicus* were relatively well suited for an oceanic environment, while those in *A. irradians* were more appropriate for shallow, coastal water. As estimated by the sum of the photons absorbed by one proximal receptor (N_P) and one distal receptor (N_D), *P. magellanicus* gathered 19% more light in an oceanic environment with its blue-shifted visual pigments than it would with the green-shifted pigments of *A. irradians* (Fig. 7A). Similarly, *A. irradians* gathered 19% more photons in its coastal environment using its own visual pigments than it would if it had visual pigments with λ_{max} values similar to those of *P. magellanicus* (Fig. 7C). Nevertheless, λ_{max} values in *P. magellanicus* and *A. irradians* were not optimized with regard to the specific light conditions we modeled. For example, estimates of N_P+N_D in *P.*

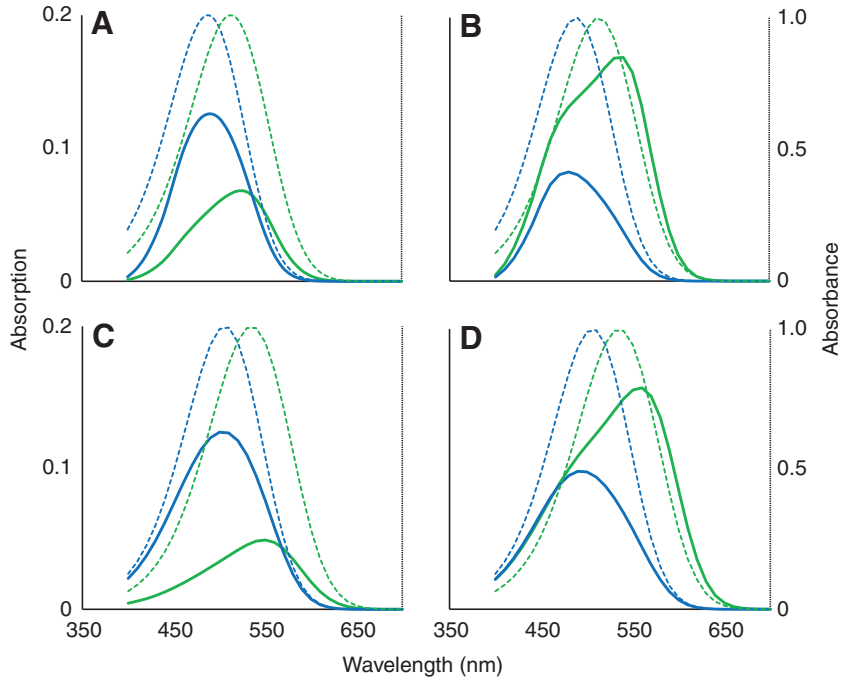

Fig. 5. The fraction of incident light absorbed in a focused state by photoreceptors from the proximal (solid blue line) and distal (solid green line) retinas, after accounting for self-screening, in *Placopecten magellanicus* at a relatively (A) low (0.0067) and (B) high (0.0335) k_D and *Argopecten irradians* at a low (C) and high (D) k_D. Also shown are the absorbance spectra for proximal (dashed blue line) and distal (dashed green line) visual pigments that were used to calculate absorption by the photoreceptors. In both cases, the absorbance curves have been normalized to 1. As can be seen here, the absorption of unfocused light by scallop retinas, prior to their absorption of focused light, causes a shift in their peak sensitivities. Self-screening also affects the absorption spectrum of the distal retina more than the proximal retina.

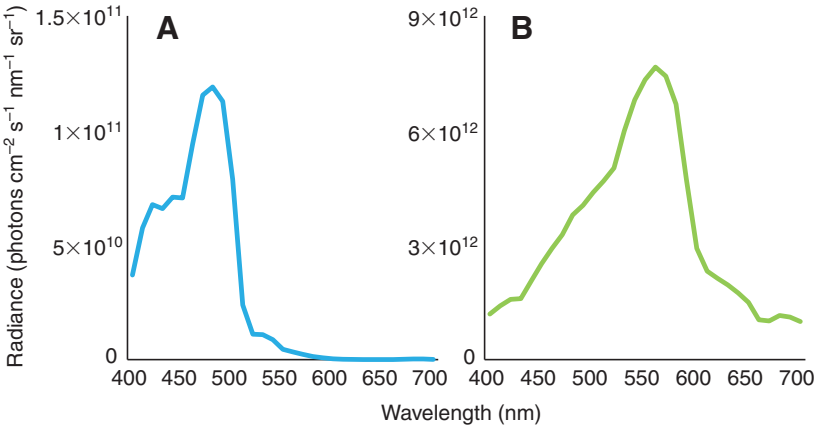

Fig. 6. Horizontal radiance spectra for (A) the offshore habitat of the sea scallop *Placopecten magellanicus*, modeled at 90 m, and (B) the inshore habitat of the bay scallop *Argopecten irradians*, modeled at 0.8 m. As illustrated here, *P. magellanicus* tends to live in deep oceanic water that is relatively dim and has a narrow radiance peak in the blue part of the visual spectrum, while *A. irradians* inhabits brighter, greener water.

magellanicus were maximal when the proximal and distal visual pigments peaked at 445 and 482 nm, respectively (Fig. 7A), with a total catch 12% higher than that obtained using empirically determined λ_{max} values. In *A. irradians*, N_P+N_D was maximal when both visual pigments had a λ_{max} of 555 nm (Fig. 7C), improving total catch by 16%.

Scallop quantum catch assuming a k_D of 0.0335 μm^{-1}

At the higher k_D, proximal and distal receptors in *P. magellanicus* gathered 2.5×10^4 and 1.5×10^5 photons, respectively, in an oceanic environment (Table 2). In *A. irradians*, as in *P. magellanicus*, a higher k_D led to increased photon capture by the distal receptors and a corresponding decrease in proximal retina quantum catch. In this scenario, the proximal and distal receptors had quantum catches of 6.5×10^6 and 1.5×10^7 photons per integration time, respectively. We also found that *P. magellanicus* gathered 11% more light in its home environment with its own visual pigments than it would with pigments similar to those of *A. irradians* (Fig. 7B) and that, similarly, *A. irradians* captured 14% more photons with its native photopigments than with those of *P. magellanicus* (Fig. 7D). In *P. magellanicus*, N_P+N_D reached a maximum at 36% above empirical estimates when the proximal and distal receptors had λ_{max} values of 700 and 478 nm, respectively; in *A. irradians*, N_P+N_D was maximized when proximal and distal receptors had λ_{max} values of 501 and 573 nm, respectively, improving quantum catch by 7%.

DISCUSSION

Visual pigments, habitat depth and quantum catch

Differences in spectral sensitivity between *P. magellanicus* and *A. irradians* suggest that environment influences the λ_{max} of scallop visual pigments. Like most animals, *P. magellanicus* and *A. irradians* experience light conditions that are highly variable. However, the habitat ranges of these species are quite different (Brand, 2006). The sea scallop *P. magellanicus* generally lives in oceanic environments that are relatively dim and blue whereas the bay scallop *A. irradians* inhabits shallow coastal habitats that are relatively well lit and green. Our results suggest that *P. magellanicus* and *A. irradians* have visual pigments with λ_{max} values that are relatively well suited to these environments, regardless of the value used for the distal retina absorption coefficient (k_D). Thus, visual pigments that optimize photon catch may be selected for in scallops, as they appear to be in deep-sea animals (Denton and Warren, 1957; Munz, 1958; Lythgoe, 1972; Partridge, 1990). However, both the offshore and shallow inshore scallop environments we modeled were quite bright, suggesting that small gains in quantum catch associated with differences in λ_{max} may not be functionally meaningful. It is likely that, under daytime conditions, both environments provide scallops with as much light as they need. However, at dawn or dusk, when photons are in limited supply, or under turbid conditions, when the optical contrast of objects is decreased, small gains in quantum catch may be more beneficial. Increasing quantum catch improves contrast sensitivity, which could help scallops under dim or turbid conditions detect predators or spot and swim towards preferred habitats such as crevices or grass beds (Buddenbrock and Moller-Racke, 1953; Hamilton and Koch, 1996).

Potential advantages of offset visual pigments in the scallop eye

If scallop eyes are considered multi-retina eyes, differences in λ_{max} between proximal and distal receptors may help the two scallop retinas perform different tasks. In *P. magellanicus*, the proximal retina has a λ_{max} of 488 nm that closely matches the dominant wavelengths of horizontal radiance at 90 m depth in oceanic water. The photoreceptors in this species' distal retina, in comparison, have

Table 2. Quantum catch estimates (Eqn 3) for the deep-dwelling sea scallop *Placopecten magellanicus* and the shallow-dwelling bay scallop *Argopecten irradians* at low (0.0067) and high values (0.0335) of k_D

Species	k_D (μm^{-1})	Proximal retina λ_{max} (nm)	Distal retina λ_{max} (nm)	Proximal retina quantum catch	Distal retina quantum catch
P. magellanicus	0.0067	488 (490)	513 (520)	3.5×10^4	5.3×10^4
P. magellanicus	0.0335	488 (480)	513 (540)	2.5×10^4	1.5×10^5
A. irradians	0.0067	506 (504)	535 (549)	8.3×10^6	4.3×10^6
A. irradians	0.0335	506 (494)	535 (558)	6.5×10^6	1.5×10^7

Estimates of quantum catch for *P. magellanicus* were made using radiance values modeled for an oceanic habitat at 90 m; estimates for *A. irradians* were made using an inshore habitat 0.8 m deep. The absorption peak wavelength (λ_{max}) values presented here were obtained from both species using microspectrophotometry. Values for λ_{max} following self-screening in the scallop eye are provided in parentheses.
k_D, absorption coefficient of the distal receptor.

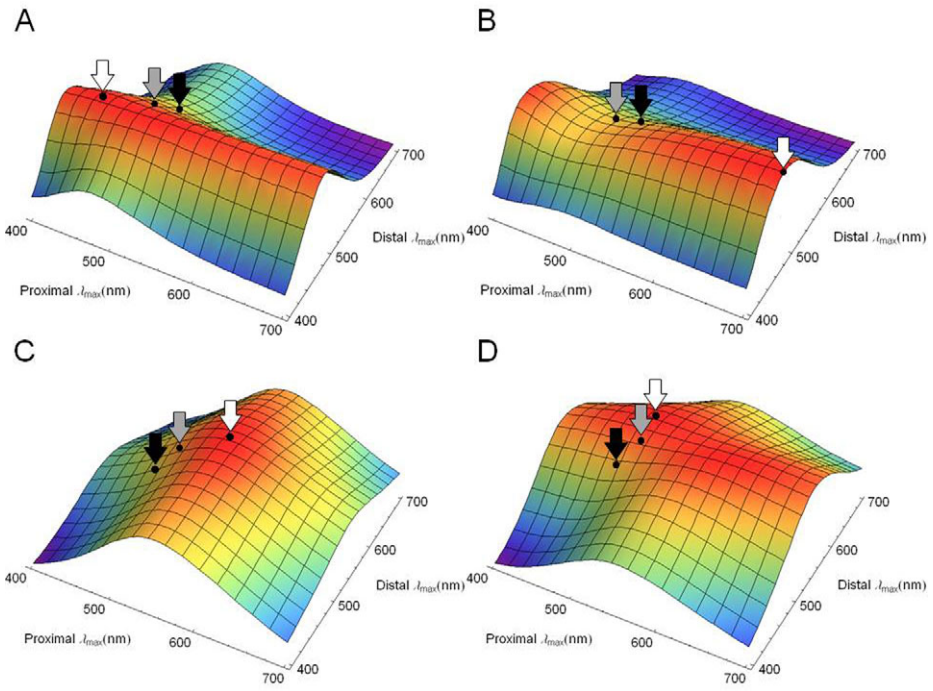

Fig. 7. The sum of the number of photons absorbed by one proximal receptor (N_{prox}) and one distal receptor (N_{dist}) in the sea scallop *Placopecten magellanicus*, at a relatively (A) low (0.0067) and (B) high (0.0335) k_D, and the bay scallop *Argopecten irradians*, again at a low (C) and high (D) k_D. For *P. magellanicus* and *A. irradians* an offshore environment at 90 m and an inshore environment at 0.8 m were assumed, respectively. In all four graphs, the white arrow marks the λ_{max} values that maximize $N_P + N_D$; the gray arrow marks the λ_{max} values empirically determined by MSP for a particular species; and the black arrow marks the λ_{max} values for the other species. The formula used to calculate quantum catch accounted for the self-screening within the scallop eye, but the λ_{max} values displayed above are for proximal and distal receptors prior to self-screening.

a λ_{max} that is shifted away from the dominant wavelengths in this light field by at least 30 nm. As described earlier, visual pigments with offset λ_{max} are thought to benefit aquatic animals by increasing the visual contrast of objects that reflect downwelling light (Lythgoe, 1968). Thus, the distal photoreceptors of *P. magellanicus* may be better than the proximal receptors at detecting reflective objects, an observation consistent with the hypothesis that scallop retinas are specialized for different tasks (Land, 1966a; Speiser and Johnsen, 2008). However, neither retina in *A. irradians* has a λ_{max} that closely matches the most abundant wavelengths of downwelling light in this species' inshore environment. From a functional standpoint, this may be due to how much brighter this shallow habitat is than *P. magellanicus*' deeper, dimmer home.

If we think of scallop eyes as multibank retina eyes, offset visual pigments may provide several advantages. Color vision is probably the most obvious benefit an animal can gain from visual pigments with different λ_{max} values, but dichromacy is probably not an option for scallops. Unless multiple pigments are expressed in the same scallop retina, which appears unlikely given the results of opsin expression studies (*Patinopecten yessoensis*) (Kojima et al., 1997), as well as the work reported in the present study, the lack of neural integration within the scallop eye likely prevents these animals from combining information from their two separate sets of photoreceptors into a single, dichromatic reconstruction of their visual environment.

It is also possible that offset visual pigments help counter the effects of self-screening in the scallop eye. However, when k_D and k_P are similar, we found that distal and proximal visual pigments with offset λ_{max} values do not necessarily improve estimates of quantum catch and may, in fact, be disadvantageous in this regard. For example, quantum catch is maximized in the *A. irradians* eye when both visual pigments have a λ_{max} at 555 nm, which is far from the values we recorded for this species. It is much more important, in this scenario, for scallop visual pigments to have λ_{max} values that match the wavelengths of peak radiance in natural environments than it is for them to counter the sensitivity costs associated with a relatively minor level of self-screening. When k_D is high relative to k_P, however, offset visual pigments may be advantageous. For example, total quantum catch is maximized in both *P. magellanicus* and *A. irradians* when the proximal receptor λ_{max} is offset from a distal receptor λ_{max} that closely matches peak radiance in the environment. The degree to which the actual λ_{max} values of proximal and distal receptors are offset may be limited by scallops needing to balance the number of photons that reach each particular retina. This could explain why the observed λ_{max} values do not maximize total quantum catch within the scallop eye.

Offset visual pigments and longitudinal chromatic aberration

Visual pigments from scallop proximal and distal retinas may also have different λ_{max} values to correct for LCA produced by the scallop lens. Chromatic aberration is a particular problem in eyes that have low f-numbers, like those of scallops, as the radius of the circle of confusion (the blur circle of an out-of-focus image) is inversely proportional to the f-number of an eye of a given focal length. Thus, eyes with low f-numbers have shallow depths of field, which means that small differences in the focal lengths of different wavelengths of light produce focused images that do not overlap (Kröger, 2000). The f-number of scallop eyes is approximately 0.5 in both *P. magellanicus* and *A. irradians* (Speiser and Johnsen, 2008). In comparison to scallops, humans have an f-number that ranges from approximately 4, when the pupil is contracted, to 2.5, when the pupil is completely dilated (Kröger, 2000). Given that LCA affects dilated human eyes, it is likely that this optical defect negatively impacts image quality in the much lower f-number scallop eye. Although we did not measure the LCA produced by scallop lenses, it is possible to roughly estimate the amount of aberration that these lenses produce. The focal length of the scallop lens has been measured as between 1.2 and 1.8 mm in *P. maximus* (Land, 1965), a species with an eye similar in size to those of the species studied here. If scallop lenses produce the same amount of chromatic aberration as fish lenses, a conservative estimate, they produce LCA on the order of 2–4% of their focal length over a spectral range of 486–656 nm (Kröger and Campbell, 1996). Assuming that LCA and focal length are linearly proportional in animal lenses, the focal

planes for blue and red light likely fall somewhere between 24 and 72 μm apart in the scallop eye. Given that the rhabdoms of the distal and proximal receptors in the scallop eye are separated by as little as 50 μm, LCA may impact scallop vision strongly enough that some form of optical correction is required. Our MSP results suggest that scallops may correct for LCA by having visual pigments in their tiered retinas that are maximally sensitive to the wavelengths of focused light that fall on them. A similar solution to the problem of LCA is seen in the λ_{max} values of visual pigments in the tiered retinas of the equally small eyes of jumping spiders (Blest et al., 1981). Jumping spiders appear capable of color discrimination, however, which suggests that these animals integrate the information received separately by their multiple retinas (Nakamura and Yamashita, 2000). Conversely, there is no evidence that scallops integrate information from their two retinas; it is quite likely, therefore, that LCA correction benefits vision in scallops and jumping spiders in different ways. Furthermore, jumping spider vision (Land, 1969) is approximately 10 times sharper than scallop vision (Land, 1965; Speiser and Johnsen, 2008), which raises the question of how low resolution an eye can be before LCA correction is no longer of any functional advantage.

Past studies of scallop spectral sensitivity

We found that spectral sensitivity differs between scallop species and between the two retinas found within the same scallop eye. These results are consistent with past behavioral experiments that show that the scallop *P. maximus* has spectral sensitivity peaks at both 480 and 540 nm (Cronly-Dillon, 1966). This species lives at depths similar to those preferred by *P. magellanicus* and the spectral sensitivities of the two species are similar, at least once self-screening in the *P. magellanicus* eye is considered. A caveat here is that the behavioral study on *P. maximus* did not account for extra-ocular photoreception. Many eyeless bivalves, such as mussels, oysters and clams, have a dermal light sense based in their mantle tissue (Kennedy, 1960; Morton, 2001), so it is quite possible that photoreceptors outside of *P. maximus*' eyes produced one of the two spectral sensitivity peaks that were observed.

Electroretinography (Wald and Seldin, 1968) and single-cell recordings from photoreceptors (McReynolds and Gorman, 1970) have offered evidence that scallop proximal and distal photoreceptors both return a maximum electrical response at 500 nm. However, inconsistencies between past electrophysiological studies and the current MSP recordings likely exist because the past studies examined scallop spectral sensitivity at wavelength intervals of 10 to 25 nm (McReynolds and Gorman, 1970). In contrast, we used MSP to record spectral sensitivity with a wavelength precision of approximately 5 nm. Thus, our finer-scale examination may have revealed differences in the λ_{max} of scallop photoreceptors that were too small to be captured by prior, coarser-grained methods. In the case of both past studies (McReynolds and Gorman, 1970) and the present one, spectral sensitivities were measured for individual cells, so it is unlikely that pooled recordings from multiple receptor types influenced either set of results.

In conclusion, it appears that the λ_{max} of scallop photoreceptors is influenced by environmental light conditions. As predicted, we found that the deeper-dwelling scallop *P. magellanicus* has photoreceptors with lower λ_{max} values than the related coastal species *A. irradians*. This difference in spectral sensitivity may be influenced by evolutionary pressure on these species to maximize photon capture in their respective environments. Additionally, offset visual pigments may help scallops correct for either self-screening in their eyes or for LCA produced by their lens. Obtaining visual pigment λ_{max} values for a broad range of scallop species, empirical values for k_D and k_P, reflectance measurements for scallop mirrors and a refined estimate of the LCA caused by the scallop lens will be necessary if these hypotheses are to be explored further.

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