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Comparative morphology of the concave mirror eyes of scallops (Pectinoidea)*

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Abstract: The unique, double-retina, concave mirror eyes of scallops are abundant along the valve mantle margins. Scallops have the most acute vision among the bivalve molluscs, but little is known about how eyes vary between scallop species. We examined eye morphology by immunofluorescent labeling and confocal microscopy and calculated optical resolution and sensitivity for the swimming scallops *Amusium balloti* (Bernardi, 1861), *Placopecten magellenicus* (Gmelin, 1791), *Argopecten irradians* (Lamarck, 1819), *Chlamys hastata* (Sowerby, 1842), and *Chlamys rubida* (Hinds, 1845) and the sessile scallops *Crassadoma gigantea* (Gray, 1825) and *Spondylus americanus* (Hermann, 1781). We found that eye morphology varied considerably between scallop species. The eyes of *A. balloti* and *P. magellenicus* had relatively large lenses and small gaps between the retinas and mirror, making them appear similar to those described previously for *Pecten maximus* (Linnaeus, 1758). In contrast, the other five species we examined had eyes with relatively small lenses and large gaps between the retinas and mirror. We also found evidence that swimming scallops may have better vision than non-swimmers. Swimming species had proximal retinas with inter-receptor angles between 1.0 ± 0.1 (*A. balloti*) and 2.7 ± 0.3° (*C. rubida*), while sessile species had proximal retinas with inter-receptor angles between 3.2 ± 0.2 (*C. gigantea*) and 4.5 ± 0.3° (*S. americanus*). Distal retina inter-receptor angles ranged from 1.7 ± 0.1 (*A. balloti*) to 2.8 ± 0.1° (*C. rubida*) for swimming species and from 3.0 ± 0.1 (*C. gigantea*) to 3.6 ± 0.2° (*S. americanus*) for sessile species, but did not appear to correlate as strongly with swimming ability as proximal retina inter-receptor angles did. Finally, we found that optical sensitivity differed between species, measuring from 3 ± 1 (*A. balloti*) to 21 ± 10 $\mu m^2 \cdot sr$ (*C. hastata*) for proximal retinas and from 2 ± 1 (*C. gigantea*) to 8 ± 5 $\mu m^2 \cdot sr$ (C. *hastata*) for distal retinas. These differences, however, did not appear to correlate with ecological factors such as a scallop species' swimming ability, preferred substrate type, or range of habitat depth. In light of these and previous findings, we hypothesize that scallop distal retinas may perform tasks of similar importance to all species, such as predator detection, and that proximal retinas may perform tasks more important to swimming species, such as those associated with the visual detection of preferred habitats.

Key words: vision, visual ecology, comparative morphology, invertebrate biology

Scallops have more acute vision than any other bivalve mollusc (Warrant and Nilsson 2006), but it has been argued that their eyes, like those of other bivalves, function merely as "burglar alarms" that trigger valve closure when large passing objects are detected (Nilsson 1994). Scallops are also notable for their ability, in most cases, to swim by a form of jet-propulsion (Cheng *et al.* 1996) and there is some indication that their swimming behavior may be visually influenced. For example, it appears that scallops are able to visually detect and swim towards preferred habitats (Buddenbrock and Moller-Racke 1953, Hamilton and Koch 1996). Arguments have been put forth, however, that scallops are unable to perform visual tasks of such complexity due to the limitations of their decentralized nervous system (Morton 2000). We suspect that these limitations may not be as severe as once thought, given recent findings that other animals with decentralized nervous systems, such as box jellyfish (Coates 2003) and sea urchins (Blevins and Johnsen 2004), use image formation to help guide movement. We therefore believe that the relationship between scallop vision and swimming behavior is one worth continued study.

If scallops are able to visually detect preferred habitats, as we hypothesize, it may be expected that swimming species have more acute vision than non-swimmers. Alternately, if scallops only use their eyes to detect predators, it is likely that little difference exists between the eyes of mobile and immobile species. Little is known about how optical resolution and sensitivity vary among scallop species, but it is thought that eye morphology is largely conserved within Pectinoidea (Dakin 1928, Morton 2001), a superfamily (Waller 2006) containing both scallops and spondylids (for brevity, we will refer to all members of Pectinoidea as "scallops" in this report). All scallops so far examined have eyes lined with a concave spherical mirror that reflects focused light onto a pair of retinas as well as a lens that is believed

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to help correct for spherical aberration caused by the mirror (Land 1965).

To test our hypothesis, we examined eye morphology by immunofluorescent labeling and confocal microscopy in the swimming scallops *Amusium balloti* (Bernardi, 1861; Fig. 1), *Placopecten magellenicus* (Gmelin, 1791), *Argopecten irradians* (Lamarck, 1819), *Chlamys hastata* (Sowerby, 1842), and *Chlamys rubida* (Hinds, 1845) and the sessile scallops *Crassadoma gigantea* (Gray, 1825) and *Spondylus americanus* (a spondylid; Hermann, 1781). We calculated inter-receptor angle (a measure of optical resolution) and optical sensitivity for each species and explored the relationships between these calculations and ecological factors such as a scallop's swimming ability, preferred substrate type, and range of habitat depth.

MATERIALS AND METHODS

Specimen collection and fixation

Four specimens apiece of *Argopecten irradians* and *Placopecten magellenicus* were obtained from Beaufort, North Carolina, U.S.A. and Woods Hole, Massachusetts, U.S.A., respectively. Three specimens of *Spondylus americanus* were obtained from the Florida Keys (Florida, U.S.A.), a single specimen of *Amusium balloti* was obtained from Australia's Great Barrier Reef, and single specimens of *Chlamys hastata*, *Chlamys rubida*, and *Crassadoma gigantea* were obtained from Friday Harbor, Washington, U.S.A. Animals were anesthetized in a 3% $MgCl_2$ solution prior to dissection. Excised eyes were fixed in buffered 4% formaldehyde for between two and twelve hours and then washed three times in PBTw, a buffer solution containing the mild detergent Tween 20™. Samples were next rinsed three times in 70% ethanol and stored in 70% ethanol, except for *C. hastata*, *C. rubida*, and *C. gigantea* tissue, which was rinsed and stored in 100% methanol. All samples remained in alcohol for less than two months before measurements were taken. Except for *C. gigantea*, in which all eyes were of nearly equal size, all examined species had both large and small mantle eyes. Only large eyes were used for measurements. Eyes from the ventral (middle) section of the left valve mantle margin were used for measurements whenever possible.

Figure 1. The left valves of the scallop species examined in this study. Pictured are the swimming scallops *Amusium balloti* (A), *Placopecten magellenicus* (B), *Argopecten irradians* (C), *Chlamys rubida* (D), and *Chlamys hastata* (E) and the sessile scallops *Crassadoma gigantea* (F) and *Spondylus americanus* (G). The scale bar represents 1 cm.

Sample preparation and measurements

For sectioning, fixed scallop eyes were cut in half with a scalpel blade. Eyes were only used for measurements if a clean, perpendicular cut was made through the center of the lens. Sectioned eyes were stained with fluorescently-labeled antibodies to alpha-tubulin, a microtubule protein, and Hoescht 33245, a DNA-binding fluorescent dye. Eyes were incubated in the anti-alpha-tubulin primary at 4 °C overnight and in an Alexa Flour 488 secondary for 4 hours at room temperature. Both the primary and secondary antibodies were diluted 1:500 in a blocking buffer which contained BSA powder and goat serum diluted in 1× PBS. After alpha-tubulin staining, 10 mg/mL Hoescht 33245 stock solution, diluted 1:100 in 1× PBS, was used to stain the eyes for five minutes. Stained eye sections were mounted in glycerol on standard microscope slides. Cover-slips were applied with modeling-clay feet so as not to disturb natural eye morphology. Eyes were mounted so that pupils and cover-slips were perpendicular. Images were obtained with the 10 or 20× objective of a Zeiss 510 LSM inverted confocal microscope housed in the Duke University Light Microscopy Core Facility. Illumination was provided by 405, 488, and 561 nm lasers. Images were processed on a Zeiss-built Fujitsu Siemens Intel Xeon CPU using Zeiss LSM 510 version 4.2 software.

Eye internal diameter, focal length (f), pupil diameter (D), photoreceptor spacing for distal (s_d) and proximal (s_p) retinas, and rhabdom length for the photoreceptors of the distal (l_d) and proximal (l_p) retinas were measured for each eye section. The image in a scallop eye is formed by the reflection of light off a concave spherical mirror (Land 1965), making focal length (f) equal to half the radius of mirror curvature (Halliday and Resnick 1988). We measured focal length by manually fitting circles to the mirror layer at the central section of each eye (the section in which the

apparent curvature of the mirror matches its actual curvature), then calculating half the radius of the circle. Pupil diameter (D) was estimated from cornea diameter. Image stacks obtained with the microscope's 20× objective allowed us to study the morphology of individual photoreceptors from each eye's distal and proximal retina. Photoreceptors were distinguished from other cells by their strong staining by alpha-tubulin antibodies. Photoreceptor spacing (s) was calculated as the distance from the center of one photoreceptor's rhabdom to the center of the rhabdom of its nearest neighbor.

Calculations for optical resolution and sensitivity

We calculated inter-receptor angle for the distal ($\Delta\varphi_d$) and proximal ($\Delta\varphi_p$) retinas of each scallop eye section using the formulas:

$$\Delta\varphi_d = \tan^{-1}\left(\frac{s_d}{f}\right) \cong \frac{s_d}{f} \quad \text{and} \tag{1.1}$$

$$\Delta\varphi_p = \tan^{-1}\left(\frac{s_p}{f}\right) \cong \frac{s_p}{f} \tag{1.2}$$

where s_d and s_p correspond to photoreceptor spacing for the distal and proximal retinas and f is focal length (Land and Nilsson 2002). Rhabdoms were contiguous in the eyes of all species examined, letting $\Delta\varphi_d = \Delta\rho_d$ and $\Delta\varphi_p = \Delta\rho_p$, where $\Delta\rho_d$ and $\Delta\rho_p$ are the acceptance angles of the photoreceptors of the distal and proximal retina, respectively. The optical sensitivities of distal (S_d) and proximal (S_p) retinas were calculated using the formulas:

$$S_d = \left(\frac{\pi}{4}\right)^2 D^2(\Delta\rho_d)^2 P_d(1-P_d)(1-P_p)^2 \quad \text{and} \tag{2.1}$$

$$S_p = \left(\frac{\pi}{4}\right)^2 D^2(\Delta\rho_p)^2 P_p(1-P_d)(1-P_p) \tag{2.2}$$

where D is pupil diameter and the terms $(1 - P_d)(1 - P_p)^2$ and $(1 - P_d)(1 - P_p)$ account for the light that is absorbed as it passes through both retinas on the way to the mirror and through the proximal retina on the way back to the distal retina. This absorption of unfocused light effectively lowers sensitivity in the scallop eye. P_p and P_d are the fractions of light absorbed by the photoreceptors during one pass through the proximal and distal retinas, respectively. P_p and P_d were calculated using the formula:

$$P_{abs} = \frac{\int_{400}^{700} I(\lambda)(1 - e^{-kA(\lambda)l})d\lambda}{\int_{400}^{700} I(\lambda)d\lambda} \tag{3}$$

where $I(\lambda)$ is ambient irradiance (Kirschfeld 1974, Land 1981, Warrant and Nilsson 1998), k (=0.0067) is the absorption coefficient of the rhabdom, and l is rhabdom length (measured for distal or proximal photoreceptors where appropriate). For our calculations, we assumed that scallops live in environments dominated by green light, appropriate given estimated habitat depths in coastal waters (Table 1). We also assumed that scallops' eyes have peak sensitivity at 480 nm, based on evidence by Cronly-Dillon (1966).

Statistical analysis

Measurements of eye internal diameter, focal length (f), pupil diameter (D), photoreceptor spacing for the distal (s_d) and proximal (s_p) retinas, rhabdom length for the photoreceptors of the distal (l_d) and proximal (l_p) retinas, inter-receptor angle of the distal ($\Delta\varphi_d$) and proximal ($\Delta\varphi_p$) retinas, and optical sensitivity of the distal (S_d) and proximal (S_p) retinas were compared between *Placopecten magellenicus*, *Argopecten irradians*, and *Spondylus americanus* using Tukey-Kramer HSD multiple comparison tests (Zar 1999). Comparisons were not made between measurements for other scallop species due to insufficient sample sizes (Table 1).

RESULTS

Scallop eyes were located on the middle mantle fold at the distal ends of short tentacles. These eye-bearing tentacles lined the edges of the right and left valves from one end of the hinge to the other and were interspersed with longer, extensible sensory tentacles in all species. The eyes were surrounded by a pigmented epithelium, which was brown in *Amusium balloti*, blue in *Argopecten irradians*, and black in *Placopecten magellenicus*, *Chlamys hastata*, *Chlamys rubida*, *Crassadoma gigantea*, and *Spondylus americanus*. The corneas were composed of a monolayer of nucleated cells (Fig. 2). Corneal cells were cuboidal in all species except *C. gigantea*, in which they were columnar. Lenses were cellular in all species examined. The lenses of *A. balloti* and *P. magellenicus* were the largest observed and had front curvatures that were approximately hyperbolic, causing them to resemble those described for *Pecten maximus* (Linnaeus, 1758) by Land (1965). In contrast, the lenses of the other five species were relatively small and had front curvatures that were relatively spherical (Fig. 2). All scallop eyes contained the distinctive double retina described in detail in a number of past reports (Dakin 1910, Barber *et al.* 1966). Cells completely negative for alpha-tubulin staining were present in scallop retinas along with the photoreceptor cells. We suspect that these non-staining cells were glial cells (Barber *et al.* 1966), which generally serve to support neural cells and are

Table 1. Morphological measurements and calculations of optical sensitivity and inter-receptor angle, a measure of optical resolution, for the eyes of the swimming scallops *Amusium balloti*, *Placopecten magellenicus*, *Argopecten irradians*, *Chlamys hastata*, and *Chlamys rubida* and the sessile scallops *Crassadoma gigantea* and *Spondylus americanus*. Values represent mean ± 2 *SE*. Measurements and calculations for *P. magellenicus*, *A. irradians*, and *S. americanus* (appearing in bold columns) were compared statistically using Tukey-Kramer HSD multiple comparison tests. Significant differences between one species and the other two are denoted by * (if $\alpha = 0.05$) or ** (if $\alpha = 0.01$). Information regarding shell height, substrate type, habitat depth, and attachment type was adapted from Brand (2006), Lauzier and Bourne (2006), and personal observation (DIS). Shell height refers to the dorsal-ventral length of the valves.

	A. balloti ($n = 2$)	***P. magellenicus*** **($n = 16$)**	***A. irradians*** **($n = 16$)**	*C. hastata* ($n = 2$)	*C. rubida* ($n = 2$)	*C. gigantea* ($n = 3$)	***S. americanus*** **($n = 16$)**
Inter-receptor angle, distal retina $\Delta\varphi_d$ (°)	1.7 ± 0.1	**2.5 ± 0.2****	**2.1 ± 0.1****	2.5 ± 0.5	2.8 ± 0.1	3.0 ± 0.1	**3.6 ± 0.2****
Inter-receptor angle, proximal retina $\Delta\varphi_p$ (°)	1.0 ± 0.1	**1.3 ± 0.1****	**1.9 ± 0.2****	2.5 ± 0.5	2.7 ± 0.3	3.2 ± 0.2	**4.5 ± 0.3****
Optical sensitivity, distal retina S_d ($\mu m^2 \cdot sr$)	4 ± 1	**8 ± 1****	**5 ± 1**	8 ± 5	6 ± 1	2 ± 1	**5 ± 1**
Optical sensitivity, proximal retina S_p ($\mu m^2 \cdot sr$)	3 ± 1	**4 ± 1****	**11 ± 3****	21 ± 10	10 ± 6	7 ± 3	**19 ± 4****
Eye internal diameter (μm)	570 ± 30	**550 ± 40****	**670 ± 40****	480 ± 20	480 ± 20	450 ± 20	**370 ± 30****
Pupil diameter D (μm)	390 ± 12	**350 ± 30***	**400 ± 30***	360 ± 40	310 ± 10	170 ± 20	**230 ± 20***
Focal length f (μm)	170 ± 10	**150 ± 10****	**180 ± 10****	140 ± 20	110 ± 10	110 ± 10	**95 ± 6****
Photoreceptor spacing, distal retina s_d (μm)	5	**6.4 ± 0.3**	**6.4 ± 0.2**	6	5.2 ± 0.4	6	**5.9 ± 0.3***
Photoreceptor spacing, proximal retina s_p (μm)	3	**3.3 ± 0.2****	**5.8 ± 0.2****	6	5	6.3 ± 0.3	**7.4 ± 0.3****
Rhabdom length, distal retina l_d (μm)	15 ± 2	**19 ± 3****	**12 ± 2**	20	12 ± 1	14 ± 4	**13 ± 1**
Rhabdom length, proximal retina l_p (μm)	25	**33 ± 6**	**30 ± 10**	45	20 ± 6	40	**25 ± 2**
Shell height of specimens examined (cm)	?	**10**	**6**	6	5	10	**9**
Preferred substrate	sandy	**sandy**	**sandy**	rocky	rocky	rocky	**rocky**
Habitat depth (m)	10-75	**20-110**	**1-12**	2-150	1-200	1-80	**1-150**
Attachment type	unattached	**unattached**	**unattached**	byssal	byssal	cemented	**cemented**

not known to act in signal processing. The backs of all eyes were lined with a concave spherical mirror, again as described by Land (1965). Underlying the mirror was a red pigment layer. Contrary to past reports, we found that a cavity was present between the mirror and the retinas in all scallop species examined (Fig. 2). Cavity size varied greatly between species. Relatively small cavities were found in *A. balloti* and *P. magellenicus*, resulting in eyes that were morphologically similar to those of *P. maximus* (Land 1965), while larger cavities were present in the eyes of the other five species. Dissection and whole-mount microscopy revealed that the cavity was filled with a clear fluid.

Eye internal diameter, focal length (f), pupil diameter (D), photoreceptor spacing for distal (s_d) and proximal (s_p) retinas, and rhabdom length for the photoreceptors of the distal (l_d) and proximal (l_p) retinas varied between scallop species (Table 1). Swimming species generally had larger eyes, larger pupils, longer focal lengths, and proximal retina photoreceptors that were more closely spaced (Table 1). Rhabdom length and distal retina photoreceptor spacing did not appear to correlate with whether a species could swim or not (Table 1). Our calculations indicated that distal and proximal retina inter-receptor angle and optical sensitivity also differed between scallop species (Table 1). Swimming species tended to have smaller distal and proximal retina inter-receptor angles than sessile species (Table 1). Optical sensitivity did not appear to be related to scallop swimming ability.

DISCUSSION

Our study revealed several new aspects of scallop eye morphology. First, we found that lens size and shape varied between scallop species (Fig. 2). The lenses of *Amusium balloti* and *Placopecten magellenicus* had shapes similar to those

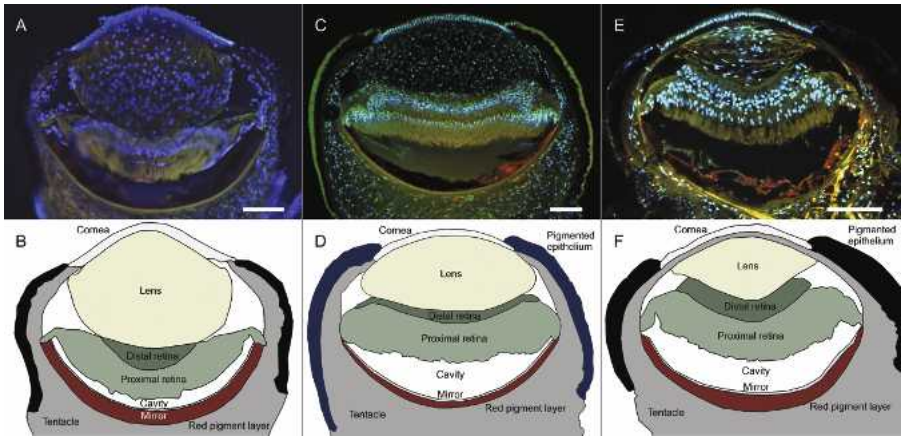

Figure 2. Mantle eye sections from the swimming scallops *Placopecten magellenicus* (A) and *Argopecten irradians* (C), imaged under a 10x confocal objective, and the sessile scallop *Spondylus americanus* (E), imaged under a 20x objective. Eyes were stained with Hoescht dye, causing cell nuclei to appear blue, and alpha-tubulin, causing microtubules to appear green. The pigment layer underneath the mirror appears red both in the images and *in vivo*. The diagrams (B, D, and F) correspond to the confocal images above and are labeled accordingly. The scale bars represent 100 μm.

described for *Pecten maximus* (Land 1965). The front of the *P. maximus* lens appears to be curved in such a way as to correct for spherical aberration caused by the reflection of light off the mirror (Land 1965), a function we will also attribute, tentatively, to the lenses of *A. balloti* and *P. magellenicus*. The lenses of the other five species appeared to have front curvatures that were relatively spherical, an indication that they may do little to correct for spherical aberration caused by the mirror. We are currently exploring the functional consequences of these different lens shapes and the phylogenetic distribution of lens types among a wide range of scallop species.

Second, we consistently noted a fluid-filled cavity between the proximal retina and the mirror in the eyes of all seven scallop species examined (Fig. 2). This cavity ranged in size between species. Small cavities were found in the eyes of *Amusium balloti* and *Placopecten magellenicus*, resulting in eyes that closely resembled those of *Pecten maximus* (Land 1965). Conversely, a large cavity was found between the proximal retina and the mirror in the eyes of the other five scallop species examined. The optics of the scallop eye are greatly influenced by the size of the cavity that exists between the proximal retina and the mirror. Following Land's analysis (1965) of the optics of *P. maximus*, which has eyes with a small cavity, it appears that focused light likely falls on the distal retina in the morphologically similar eyes of *A. balloti* and *P. magellenicus*. Alternately, due to the presence of a large cavity, it appears likely that focused light falls on the proximal retina in the eyes of the other scallop species we examined. We would be tempted to conclude that focused images simply fall on different retinas in different scallop species, but we have also found that photoreceptor spacing is tighter in the proximal retinas of *A. balloti* and *P. magellenicus* than it is in their distal retinas (Table 1). This is not consistent with a model in which the proximal retinas of *A. balloti* and *P. magellenicus* fail to receive focused light. We also found that *A. balloti* and *P. magellenicus* have the most tightly packed proximal retina photoreceptors of any of the species examined (Table 1), which again suggests that their proximal retinas may be involved in image formation. As an explanation for these inconsistencies, we speculate that scallop eyes are optically dynamic structures that can alternately focus light onto either of the two retinas through slight changes in shape. We are, at this time, exploring possible mechanistic bases for such a process.

An analysis of scallop visual capabilities provided evidence that swimming scallops have more acute vision than non-swimmers and that the best swimmers have the most acute vision. Among the scallops included in this study, *Amusium balloti* and *Placopecten magellenicus* were the strongest swimmers, capable of moving at speeds of up to 100 cm/s (Joll 1989) and 67 cm/s (Brand 2006), respectively. These scallops had proximal retina inter-receptor angles of around 1°, the smallest of any we calculated (Table 1). Weaker swimmers like *Argopecten irradians*, able to swim at speeds of 40 cm/s (Brand 2006), had proximal retina inter-receptor angles between 2-3° (Table 1). Our findings in this case concur with past morphological studies that found that *Pecten maximus*, a scallop with swimming abilities comparable to those of *A. irradians* (Brand 2006), had an optical resolution of about 2°. Sessile scallops, which cement to their substrate in a manner similar to oysters (Lauzier and Bourne 2006), had the largest proximal retina inter-receptor angles observed, at around 3-5° (Table 1). Proximal retina inter-receptor angle diversity was a product of differences in both focal length and photoreceptor spacing. For example, tighter photoreceptor packing was largely responsible for *A. balloti* having a smaller proximal retina inter-receptor angle than *A. irradians*, but longer focal length was responsible for *A. irradians* having a smaller proximal retina inter-receptor angle than *Chlamys hastata*. Factors other than swimming ability may also help explain why some scallop species have better

optical resolution than others. For example, scallops from sandy substrates tend to have better vision and be better swimmers than those from rocky habitats (Table 1). Another important caveat is that our methods have led us to estimate the theoretical maximum of visual acuity in each scallop species. Neural processes, like spatial summation, and optical imperfections, such spherical aberration, may lead to scallops having actual visual acuities that are below these estimates (Land and Nilsson 2002). However, behavioral (Buddenbrock and Moller-Racke 1953) and electrophysiological (Land 1966) studies on *P. maximus* provide evidence that actual scallop visual acuity is close to the theoretical maximum derived from focal length and photoreceptor spacing. This suggests that our estimates of inter-receptor angle likely point towards true functional differences between the eyes of mobile and immobile scallop species. Finally, interspecific differences in inter-receptor angle will have little consequence if focused light falls on different retinas in different scallop species, a possibility that we address in detail above.

Distal retina inter-receptor angles, ranging from 1.7 ± 0.1° for *Amusium balloti* to 3.6 ± 0.2° for *Spondylus americanus*, only varied two-fold between species, as opposed to the four-fold difference observed between proximal retina inter-receptor angles (Table 1). Distal retina inter-receptor angle also correlated with scallop swimming ability but not as strongly as proximal retina inter-receptor angle did. For example, proximal retina inter-receptor angle was larger in *Placopecten magellenicus* than it was in *Argopecten irradians*, despite *P. magellenicus* being the stronger swimmer (Brand 2006). Perhaps more tellingly, variation in distal retina inter-receptor angle was largely a product of interspecific differences in focal length, not photoreceptor spacing. Distal retina photoreceptor spacing fell between 5 and 6.5 μm in all species and, unlike proximal retina photoreceptor spacing, a relationship between this measure and a scallop species' swimming ability was not indicated by the data (Table 1).

It has been suggested that the two scallop retinas perform different visual functions (Land 1966, Wilkens 2006), in part due to evidence that the retinas operate via different opsins and signal-transduction pathways (Kojima *et al.* 1997) and that the neurons of the distal retina hyperpolarize in response to light, while those of the proximal retina depolarize (Hartline 1938, Land 1966, McReynolds and Gorman 1970). This proposal is supported by our evidence that proximal retina photoreceptor spacing may depend on a scallop species' swimming ability, while distal retina photoreceptor spacing varies little between species (Table 1). This implies that scallop proximal retinas may be involved in visual tasks more important to swimming species, such as those relating to the detection of preferred habitat, and that the distal retinas are likely involved in tasks of equal importance to both swimming and sessile species, such as predator detection.

Further support for functional differentiation of this sort comes from indications that scallop proximal retinas are better at gathering information about relatively static environmental features (Land 1966), like the eelgrass beds towards which *Argopecten irradians* has been found to swim (Hamilton and Koch 1996), while the distal retinas are better at detecting movement, such as that by potential predators.

Unrecognized differences between the eyes of mobile and immobile species have contributed to arguments that swimming scallops do not visually detect preferred habitats, as has the fact that scallops lack a centralized nervous system (Morton 2000). While it is true that scallops do not process much visual information in their brain, their visceroparietal ganglion (VPG) contains optic lobes that likely give these animals the neural capacity to convert a range of visual inputs into behavioral output (Wilkens 2006). It has been noted that information from the proximal retina elicits greater activity in the VPG's optic lobes than information from the distal retina (Wilkens and Ache 1977), a finding seemingly at odds with the claim that focused light only falls on the scallop distal retina (Land 1965). As a potential solution to this problem, we suggest that focused light may fall on the proximal retina in at least some scallop species. This suggests that previously unrecognized interspecific variation may account for inconsistencies between past reports. It also suggests that the scallop optic lobes may, at least in some cases, process visual information from the proximal retina for the sake of complex behavioral tasks like habitat detection.

Scallop optical sensitivity, like optical resolution, differed between retinas and between species (Table 1). However, unlike optical resolution, optical sensitivity did not appear to correlate with swimming ability or, as might be expected, with habitat depth (Table 1). Given that irradiance values in scallop habitats may vary over several orders of magnitude, depending on tide conditions and time of day, the differences we observed between optical sensitivities may have only minor functional consequences for the species examined in this study.

In conclusion, we found that eye morphology varied between scallop species and that swimming scallops tend to have better vision than sessile scallops. This latter discovery is consistent with our hypothesis that mobile scallops may visually detect preferred habitats. We also found evidence that scallop distal and proximal retinas may be functionally differentiated. We are currently working to clarify the relationship between vision and swimming ability in scallops and to develop new models of scallop optics that focus, in particular, on the range of lens shapes we have observed in

different scallop species and on the ways that scallops may utilize both of their retinas for image formation.

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