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Spatial vision in the echinoid genus *Echinometra*

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Summary

Although eyes are generally considered necessary for image resolution, a diffuse photoreceptive system with directional sensitivity may also have this ability. Two species of the echinoid genus *Echinometra* were tested for spatial vision by examining their ability to locate and move towards targets of different sizes. The echinoids were significantly oriented (*P*<0.0001) towards a target with an angular width of 33° (0.3 sr) but were not oriented to targets with angular widths of 26° and 16°. This ability is probably due to the blocking of off-angle light by the spines, which have approximately the correct spacing for the observed resolution. Spatial vision is advantageous for echinoids of this genus because they leave and return to small dark shelters. This first demonstration of spatial vision in an echinoderm sheds further light on the complex optical structures and photobehaviors found in this phylum.

Key words: vision, acuity, echinoderm, echinoid, visual.

Introduction

Photoreception is generally divided into two categories: diffuse and image-forming (Land and Nilsson, 2002). Diffuse photoreception is mediated by photosensitive regions within the dermis and can only detect variation in the overall illumination level. Image-forming photoreception (i.e. vision) is associated with a discrete ocular organ that can measure the radiance pattern in the environment and thus locate objects at a distance. Commonly considered visual systems (e.g. mammals, birds) are able to resolve detail with angular widths less than 1°. However, there are many species, particularly nocturnal and deep-sea, that have vision with far cruder resolution, including the planarians (35°), certain medusae, *Nautilus* (8°), the deep-sea isopod *Cirolana borealis* (15°), the ostracod *Gigantocypris* and certain deep-sea fish (reviewed by Land and Nilsson, 2002). These species fall between the two general categories in that they are unable to form detailed images but are capable of discriminating more than simple illumination levels.

The anatomical and behavioral characteristics of echinoderms make them likely candidates for this form of limited spatial vision. Although discrete photoreceptive organs are found only in certain asteroids and one holothurian, all examined echinoderms have behavioral responses to light mediated by photosensitivity of the body wall and nervous system (Millot and Yoshida, 1958; Yoshida, 1966; Reese, 1966; Moore and Cobb, 1985). These responses range from seeking shelter to covering reactions, oriented movement and daily migrations (Thornton, 1956; Johnsen 1994; Hendler et al., 1995; Johnsen and Kier, 1999). Because the photosensitive tissue is found within and below the transparent calcite endoskeleton, echinoderms have the potential for lenses and filters. Indeed, the aboral plates of the ophiuroid *Ophiocoma wendtii* contain modified ossicles and migrating screening pigments that act as sophisticated lenses and filters (Aizenberg et al., 2001). The ophiuroid *Ophioderma brevispinum* has ossicles that polarize light and appear to affect the locomotion of the animal (Johnsen, 1994; Johnsen and Kier, 1999). These anatomical modifications and relatively complex behaviors suggest that at least some echinoderm species have spatial vision.

All spatial vision ultimately depends on restricting the angular width over which light can reach each region of a photosensitive surface (Land and Nilsson, 2002). Woodley (1982) suggested that the opaque spines of echinoids could restrict the directions over which light could reach the dermis, much as the screening pigments in insect ommatidia restrict the light reaching the photosensitive rhabdomeres. The entire echinoid could then act as a large compound eye, with a resolution determined by the angular spacing of the spines.

This hypothesis was tested in two species of the echinoid genus *Echinometra*, chosen because they leave and return to small, dark crevices and thus may benefit from limited spatial vision. The ability of the echinoids to find dark targets of different sizes was examined and the results analyzed to predict their spatial resolution.

Materials and methods

Specimen collection and care

Specimens of *Echinometra lucunter* L. and *Echinometra viridis* Agassiz 1863 were obtained from a marine specimen supply company (Tom's Caribbean Tropicals, Inc., Tavernier, FL, USA). *E. lucunter* was collected at the shoreline of Tavernier Key. *E. viridis* was collected from patch reefs at 2 m depth approximately 3 km southeast of Tavernier. They were maintained in a shaded 40-liter aquarium on a 12 h:12 h light:dark cycle, with weekly water changes and biweekly feedings.

Two species were chosen rather than one due to availability issues. Both, however, have similar habits and ranges (McGeehee, 1992). Both also inhabit small crevices, the primary ecological difference between the two species being that *E. lucunter* can slowly excavate its own shelter while *E. viridis* cannot. Their orientation behavior was not significantly different (see Results), so the data from the two species were combined.

Experimental apparatus

The experimental arena was essentially identical to the one described by Johnsen and Kier (1999). It consisted of a covered fiberglass tank (1.2 m diameter) with an opening in the top and a glass bottom (Fig. 1). A circular wall (0.6 m diameter, 4.5 cm high) was centered on the bottom, and white paper marked in 10° increments was placed underneath the glass. A cylinder (15 cm diameter, 9.5 cm high) suspended on a string was used to hold and then remotely release the echinoids in the centre of the arena. The arena was placed on blocks so that the echinoids' motion could be viewed from below through the paper. Ten 20 W fluorescent bulbs (0.6 m long) were mounted in parallel 6 cm apart and 0.6 m above the floor of the arena. The light passed through a wax paper diffuser, resulting in an irradiance at the arena floor of 3.3×10^{15} photons $\text{cm}^{-2}\,\text{s}^{-1}$ (integrated from 400 to 700 nm; Fig. 1). This is approximately equal to the downwelling irradiance during early morning or late afternoon.

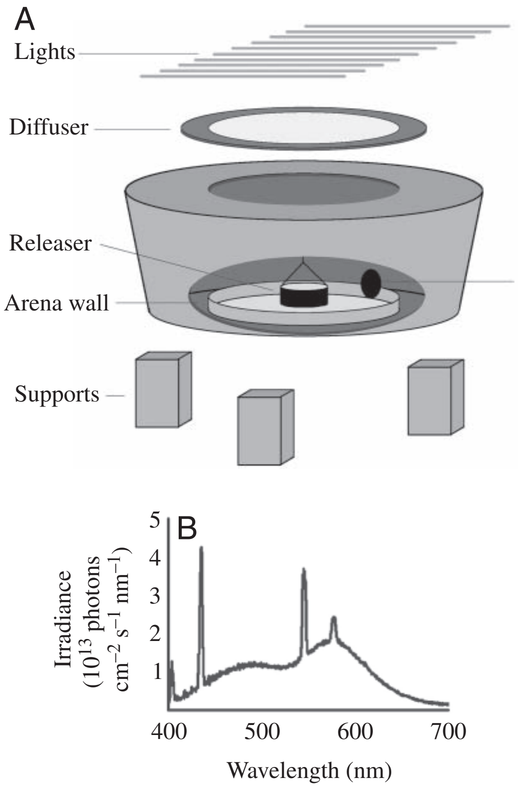

Fig. 1. (A) The experimental arena used in the study. The elliptical hole in the side of the tank serves only to show the inside and is not found on the actual tank. (B) Downwelling irradiance at the floor of the arena (in 10^{13} photons $\text{cm}^{-2}\,\text{s}^{-1}\,\text{nm}^{-1}$) as a function of wavelength (in nm).

Three circular targets with diameters of 8.6, 13.5 and 17 cm were constructed from matt black plastic. During trials, the targets were affixed to the circular wall within the arena, 30 cm from where the echinoids were released. Thus, they had angular diameters of 16°, 26° and 33° and subtended solid angles of 0.065, 0.17 and 0.30 sr, respectively.

Experimental procedure

Experiments were conducted from November 2003 to February 2004. Before each day of trials, the experimental arena was rinsed and filled with artificial seawater to a depth of 6–8 cm. One of the three targets was chosen at random, and each echinoid was tested four times with the target at four randomly ordered positions (0°, 90°, 180° or 270°, relative to the back of the room). At the beginning of each trial, the echinoid was placed into the release cylinder. The lights were turned on and the echinoid was released by lifting the cylinder using a line. Echinoids typically moved within 20 s of being released and continued in a straight line to the circular wall. An observer beneath the arena monitored the echinoid's movement and recorded the bearing (within ±5°) when its center was 4 cm from the circular wall. The light was then turned off and the echinoid was returned to the release cylinder. The arena surface was scrubbed with a brush (to minimize the potential for trail following), the target was moved to its second position, and the testing process was repeated. A trial was terminated and no bearing recorded if an echinoid did not move within 60 s or changed direction more than once. Four trials out of a total of 88 were terminated. In addition, one echinoid, which only moved once in four trials, was removed from the study. After all four target positions were tested, a mean vector $\vec{V}$ for the four bearings (relative to the position of the target) was calculated using:

$$\vec{V}=\tfrac{1}{4}\left[\sum_{i=1}^{4}\cos\,(\theta_i-\phi_i),\sum_{i=1}^{4}\sin\,(\theta_i-\phi_i)\right],$$

where θ_i and ϕ_i are the bearings of the echinoid and the target in the *i*th trial (Batschelet, 1981). The process was repeated for different echinoids and different target sizes. A total of 22 echinoids was tested.

Data analysis

The mean vectors for each echinoid were bivariate, having both direction and length. In addition, there was a predicted direction (the position of the target). Thus, the ideal statistical test would have been a bivariate equivalent of the *V*-test (Batschelet, 1981). Because there is no such test, the data were

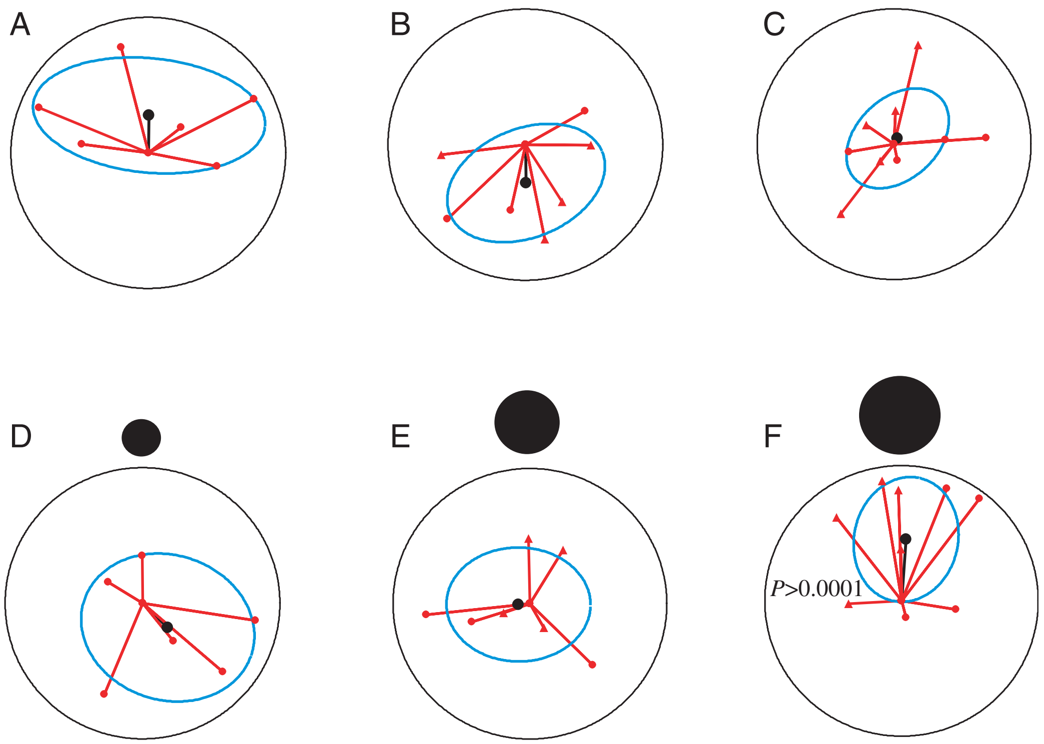

Fig. 2. The mean bearings of the echinoids. (A–C) Un-normalized bearings. (D–F) Bearings relative to the targets (represented in scale above each graph). Each red line shows the length and direction of the mean bearing for the four trials with one echinoid. The black lines show the means of these mean bearings. 95% confidence ellipses are shown in blue. Circles represent *E. lucunter*; triangles represent *E. viridis.*

analyzed using Monte Carlo methods (Diggle, 1983). Essentially, the experiment was simulated many times using random data, and a distribution of a test statistic was created using the following procedure.

Four random bearings were chosen and averaged into one vector. This was repeated N times, where N was the number of echinoids tested for a particular target size. A mean of the N vectors, $\vec{V}_{\mathrm{N}}$, was then calculated. The mean vector for perfect orientation toward the target, $\vec{V}_{\mathrm{ideal}}$, has a bearing of 0° and a length of 1. The distance between the endpoints of $\vec{V}_{\mathrm{N}}$ and $\vec{V}_{\mathrm{ideal}}$ was used as the test statistic (i.e. $d=|\vec{V}_{\mathrm{N}}-\vec{V}_{\mathrm{ideal}}|$). This process was repeated 100 000 times to create a distribution of distances. The mean vector from the empirical data ($\vec{V}_{\mathrm{data}}$) was calculated and the test statistic (d_{data}) determined. The position of d_{data} in the distribution then gave the P-value, with a low d_{data} indicating a significant departure from randomness. 95% confidence ellipses were also calculated to ensure that the bearing of mean vector $\vec{V}_{\mathrm{N}}$ was not significantly different from the bearing of the target (Batschelet, 1981).

The absolute bearings of the echinoids (not normalized by the position of the target, but instead to the back wall of the room) were also analyzed to ensure that there was no spurious orientation to some feature of the arena or room. Since there was no predicted direction for the absolute bearings, they were analyzed using the Hotelling T^2 test (Batschelet, 1981).

Results

The absolute bearings of the echinoids were not significantly oriented (Fig. 2A–C; Table 1). The bearings of the echinoids were also not significantly oriented towards the small (16°) and medium-sized (26°) targets (P>0.5 in both cases; Fig. 2D,E; Table 1). However, the bearings of the echinoids were highly significantly oriented (P<0.0001) towards the largest target (33°; Fig. 2F; Table 1). Eleven of the 32 individual trials with this target ended with the echinoid touching the target.

Discussion

The highly significant orientation towards a target that comprised only 2.4% (=0.3/4π) of the echinoids' visual field suggests that *Echinometra* has a limited form of spatial vision. Its inability to orient towards smaller targets further suggests that the 33° target is close to the minimum size that can be detected. While poor by vertebrate standards, this spatial resolution is comparable with that of species with less-developed eyes (Land and Nilsson, 2002; Warrant and Locket, in press) and is the first

Table 1. *The absolute bearings of the echinoids and the bearings relative to the location of the target*

	16° target	26° target	33° target
Absolute bearings			
Number of echinoids tested	6	7	9
Length of mean vector	0.28	0.28	0.05
Mean bearing (deg.)	1	179	31
P-value (Hotelling T^2)	n.s.	n.s.	n.s.
Bearings relative to targets			
Length of mean vector	0.26	0.08	0.46
Mean deviation from target (deg.)	134	266	4
P-value (Monte Carlo method)	n.s.	n.s.	<0.0001

n.s. – not significant. Number of urchins tested was the same for both conditions.

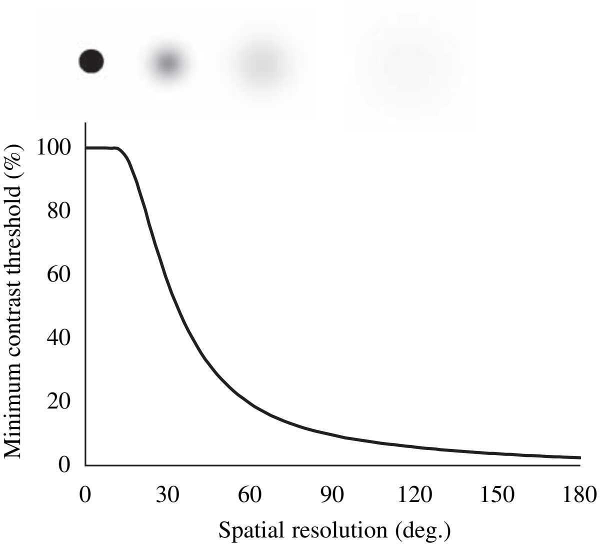

Fig. 3. The minimum contrast threshold required to detect the presence of a 33° black target for a given spatial resolution. The graph is calculated by convolving the image of the target with the modulation transfer function for a given spatial resolution and then determining the maximum contrast of the convolved image (see Johnsen et al., in press for details). The images above the graph show the appearance of the target when viewed by visual systems with spatial resolutions of 1°, 33°, 60° and 120° (left to right).

evidence of spatial vision in an echinoderm, or any species with a diffuse photoreceptive system.

The half of the arena containing the black target was, of course, darker than the half without the target, so it is possible that *Echinometra* is simply undergoing phototaxis. There are two arguments against this. First, the half of the arena with the target is only slightly darker than the half without the target (assuming that the target reflects no light), requiring the echinoid to have extremely good contrast sensitivity (~2.4%; Fig. 3). Some vertebrates can detect radiance differences of approximately 1–2% under ideal conditions (Douglas and Hawryshyn, 1990). However, the regions with the differing radiances must be adjacent and separated by a sharp border (Land and Nilsson, 2002). Gradual changes in radiance, particularly over a large field of view, are far more difficult to detect. Continual movement towards slightly darker directions would also be maladaptive, given that the echinoids' environment has many subtle (and ecologically meaningless) changes in brightness. Second, the echinoid's orientation towards the target was quite strong, with a third of the animals hitting the target itself, suggesting that they were able to accurately determine its location.

The exact spatial resolution of the echinoid cannot be determined from the results of this study because a single object on an empty background can be detected by visual systems with lower resolution than the object's size. However, this requires a very high contrast sensitivity. Fig. 3 shows the minimum contrast threshold required to detect the presence of the 33° target as a function of spatial resolution. For example, if the echinoid has a spatial resolution of 90°, a minimum contrast threshold of 9.5% is required to detect the 33° target. This is still quite low for the detection of graded boundaries. It is only when the spatial resolution drops to approximately the angular size of the target that it becomes readily detectable, requiring a minimum contrast threshold of 50%.

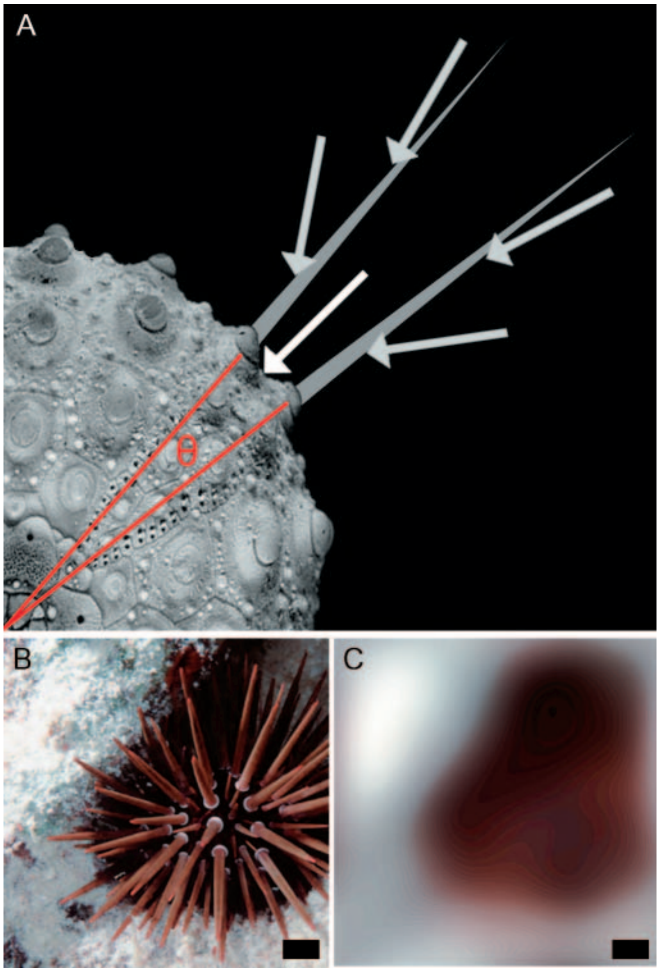

Fig. 4. (A) Test of *E. lucunter* with two spines. Off-angle light (gray arrows) is absorbed and reflected by the spines. Light within the acceptance angle, θ (white arrow), reaches the body wall between the spines and is detected. (B) *E. lucunter* in a typical shelter. (C) View of B at a spatial resolution of 33°. Scale bars are 20°, which implies that the center of the viewing echinoid is approximately 6 cm from the center of the pictured echinoid.

The highly significant orientation towards the 33° target and the complete absence of orientation towards the 26° target is intriguing. While the area of the latter target is only 54% of the area of the former, one might expect weak orientation towards the smaller target. Both species of *Echinometra* seek shelter in rock crevices (McClanahan, 1999). It is therefore possible that the smaller targets are detected but not considered large enough to provide adequate shelter. However, while the 16° target is indeed smaller than the typical shelter for these species, the 26° target is not. In addition, smaller crevices are often preferred because they offer increased protection

(Schneider, 1985). Thus, a behavioral explanation for the lack of orientation to the 26° target appears less likely than a physiological one.

The spatial resolution of *Echinometra* may be due to light screening by the spines. Much like the screening pigments in the ommatidia of compound eyes, the spines limit the angular field of view of each portion of the photosensitive body wall by absorbing and reflecting light that does not hit the surface more or less perpendicularly (Fig. 4A). The aboral surfaces of *E. viridis* and *E. lucunter* have approximately 100–150 spines, resulting in a mean angular distribution of one spine every 12–16°. From signal theory, detail can be resolved over angles that are double the angular resolution of the detector. Thus, the predicted spatial resolution is 24–32°, suggesting that the spines may be responsible for the observed resolution. Caution is required, however, because the angular distribution of the spines is quite variable. In addition, the photosensitive regions under the test may themselves have directional sensitivity.

Spatial vision has a clear ecological function in *E. lucunter and E. viridis*. Unlike *Lytechinus*, *Tripneustes*, *Arbacia* and many other Atlantic epibenthic echinoids, both species of *Echinometra* rely on small dark crevices for protection from predators and turbulence (Schneider, 1985; Thomas, 1991; Schoppe, 1996). They inhabit shallow forereef and offshore reef areas, as well as the rims of cup reefs – turbulent areas with high exposure to predation. In rare systems with low predation pressure, *Echinometra* communities persist without shelter, but in typical environments mortality is dramatically increased if no protection is available (Schneider, 1985; McClanahan, 1999). Both species move to and from these shelters to graze on algae and retreat from predators (Hendler et al., 1995). If either is removed from its shelter, it returns immediately (Abbot et al*.,* 1974; McClanahan, 1999). The ability to detect the direction of distant shelter is thus advantageous in these species, decreasing the time spent exposed (Fig. 4B,C). Thus, the spatial vision observed in this study is unlikely to be an artifact of laboratory conditions.

It is not known whether spatial vision exists in other echinoderms. Other epibenthic echinoids with large numbers of spines are natural candidates. Ecological similarities and close evolutionary relationships suggest that other crevice-dwelling echinometrids (e.g. *E. mathei*) may possess spatial vision. The diadematoids are also promising, due to their complex photobehaviors and large number of closely packed spines (over double that found in *Echinometra*). Many echinoids are also known to aggregate. While the most likely cue for this behavior is olfactory, it is possible that vision plays a role, particularly since many echinoids are far darker than their environment. Ophiuroids, with their cryptic habits and complex optical structures, are also obvious candidates.

The presence of spatial vision in *Echinometra* also has larger implications, because it demonstrates that a diffuse sensory system can provide a level of spatial information typically associated with specialized sense organs. Although diffuse sensory systems are almost certainly found in all species, they generally receive less attention than specialized sense organs because they are harder to study and are considered to be more primitive. However, as shown by this study, at least some of these diffuse systems may have more sophisticated abilities than previously considered.

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References

Abbot, D., Ogden, J. C. and Abbott, I. (1974). Studies on the Activity Pattern, Behavior and Food of the Echinoid *Echinometra lucunter* Linnaeus on Beachrock and Algal Reefs at St. Croix. *U.S.V.I. Special Publ.* **4**, West Indies Laboratory. 111p.

Aizenberg, J., Tkachenko, A., Weiner, S., Addadi, L. and Hendler, G. (2001). Calcitic microlenses as part of the photoreceptor system in brittlestars. *Nature* **412**, 819-822.

Batschelet, E. (1981). *Circular Statistics in Biology.* New York: Academic Press.

Diggle, P. J. (1983). *Statistical Analysis of Spatial Point Patterns*. London: Academic Press.

Douglas, R. H. and Hawryshyn, C. W. (1990). Behavioral studies of fish vision: an analysis of visual capabilities. In *The Visual System of Fish* (ed. R. H. Douglas and M. B. A. Djamgoz), pp. 373-418. New York: Chapman and Hall.

Hendler, G., Miller, J. E., Pawson, D. L. and Kier, P. M. (1995). *Sea Stars, Sea Urchins and Allies: Echinoderms of Florida and the Caribbean.* Washington: Smithsonian Institution Press.

Johnsen, S. (1994). Extraocular sensitivity to polarized light in an echinoderm. *J. Exp. Biol.* **195**, 281-291.

Johnsen, S. and Kier, W. M. (1999). Shade-seeking behavior under polarized light by the brittlestar *Ophioderma brevispinum*. *J. Mar. Biol. Assoc. UK* **79**, 761-763.

Johnsen, S., Widder, E. A. and Mobley, C. D. (2004). Propagation and perception of bioluminescence: factors affecting the success of counterillumination as a cryptic strategy. *Biol. Bull.* **207**, 1-16.

Land, M. F. and Nilsson, D.-E. (2002). *Animal Eyes*. New York: Oxford University Press.

McClanahan, T. R. (1999). Predation and the control of the sea echinoid *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef, Belize. *Ecosystems* **2**, 511-523.

McGeehee, A. M. (1992). Distribution and abundance of two species of Echinometra (Echinoidea) on coral reefs near Puerto Rico. *Carib. J. Sci.* **28**, 173-183.

Millot, N. and Yoshida, M. (1958). The Photosensitivity of the sea echinoid *Diadema antillarum* Phillipi: responses to increases in light intensity. *Proc. Zool. Soc. Lond.* **133**, 67-71.

Moore, A. and Cobb, J. L. S. (1985). Neurophysiological studies on photic responses in *Ophiura ophiura*. *Comp. Biochem. Physiol. A* **80**, 11-16.

Reese, E. S. (1966). The complex behavior of echinoderms. In *Physiology of Echinodermata* (ed. R. A. Boolootian), pp. 157-218. New York: John Wiley and Sons.

Schneider, D. C. (1985). Predation on the echinoid *Echinometra lucunter* (Linnaeus) by migratory shorebirds, on a tropical reef flat. *J. Exp. Mar. Biol. Ecol.* **92**, 19-27.

Schoppe, S. and Werding, B. (1996). The boreholes of the sea echinoid *Echinometra lucunter* as microhabitats in tropical South America. *Mar. Ecol.* **17**, 181-186.

Thomas, M. L. H. (1991). Communities of constructional lips and cup reef rims in Bermuda, north Atlantic Ocean. *Coral Reefs* **9**, 225-230.

Thornton, W. B. (1956). Diurnal migrations of the echinoid *Diadema setosum* (Leske). *Br. J. Anim. Behav.* **4**, 143-146.

Warrant, E. J. and Locket, N. A. (2004). Vision in the deep sea. *Biol. Rev. Cambridge. Phil. Soc.* **79**, 671-712.

Woodley, J. D. (1982). Photosensitivity in *Diadema antillarum*: does it show scototaxis? In *The International Echinoderm Conference, Tampa Bay* (ed. J. M. Lawrence), p. 61. Rotterdam: A. A. Balkema.

Yoshida, M. (1966). Photosensitivity. In *Physiology of Echinodermata* (ed. R. A. Boolootian), pp. 435-464. New York: John Wiley & Sons.