PERGAMON

Vision Research 40 (2000) 71–75

Vision Research

www.elsevier.com/locate/visres

Cuttlefish use polarization sensitivity in predation on silvery fish

Nadav Shashar [a,b], Roland Hagan [c], Jean G. Boal [d,e], Roger T. Hanlon [a,*]

[a] *Marine Resources Center, Marine Biological Laboratory, 7 MBL St., Woods Hole, MA 02543, USA*
[b] *Hebrew University, H. Steinitz Interuniversity Institute, PO Box 469, Eilat 8800, Israel*
[c] *Department of Plant Science, Rutgers University, Chatsworth, NJ 08019, USA*
[d] *Marine Biomedical Institute, University of Texas Medical Branch, 301 University Blvd, Galveston, TX 77555-1163, USA*
[e] *Department of Biology, Millersville University of Pennsylvania, PO Box 1002, Millersville, PA 17551-0302, USA*

Received 9 March 1999; received in revised form 13 July 1999

Abstract

Cephalopods are sensitive to the linear polarization characteristics of light. To examine if this polarization sensitivity plays a role in the predatory behavior of cuttlefish, we examined the preference of *Sepia officinalis* when presented with fish whose polarization reflection was greatly reduced versus fish whose polarization reflection was not affected. Cuttlefish preyed preferably on fish with normal polarization reflection over fish that did not reflect linearly polarized light ($n = 24$, $\chi^2 = 17.3$, $P < 0.0001$), implying that polarization sensitivity is used during predation. We suggest that polarization vision is used to break the countershading camouflage of light-reflecting silvery fish. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Polarized light; Camouflage; Cephalopods; Countershading; Radiance-matching

1. Introduction

Radiance matching is a method of camouflage in which fish and other marine animals reflect or produce light that reduces the dark shaded areas on their bodies and that matches the background illumination against which they might be seen (Cott, 1940; Lythgoe, 1979). The silvery, broad-band reflecting scales of fish are considered to function in radiance matching, resulting in reduced detection by predators or prey (Denton & Nicol, 1966; Denton, 1970). However, reflected light is partially linearly polarized, and scales of fish produce a distinct polarization reflection that might be different from the polarization characteristics of the underwater light field (Denton, 1970; Rowe & Denton, 1997). Shashar, Cronin, Johnson and Wolff (1995a) demonstrated such a polarization contrast between a fish and it surrounding waters. Denton and Nicol (1965) suggested that polarization vision could be used to detect fish with a distinct polarization reflection, and Tyo, Rowe, Pugh and Engheta (1996) showed that a polarization-based sensor can double the detection range of reflecting targets containing polarization features, as compared to intensity imaging. Furthermore, they demonstrated that polarization imaging is especially useful under scattering conditions, when a large portion of the illumination reaching the sensor originates from veiling light (Lythgoe, 1979). We were interested to see if polarization vision is used by a predator to detect or select such silvery fish.

Cephalopods are known to be sensitive to the polarization characteristics of partially linearly polarized light (Moody & Parriss, 1960, 1961; Saidel, Lettvin & McNichol, 1983). This polarization sensitivity arises from the orthogonal distribution of the microvilli of neighboring photoreceptor cells in their retina. In addition to its use in target detection by octopus and squid (Moody & Parriss, 1960, 1961; Shashar, Hanlon & Petz, 1998a), cuttlefish have been suggested to use this polarization sensitivity in a discrete communication channel (Shashar, Rutledge & Cronin, 1996).

Cuttlefish are visual predators (Messenger, 1968; Hanlon & Messenger, 1996) that feed on a variety of prey items including crustaceans and fish. The common European cuttlefish, *Sepia officinalis*, is primarily an ambush predator, although active searching for food

---

* Corresponding author. Tel.: + 1-508-289-7700; fax: + 1-508-289-7900.

E-mail address: rhanlon@mbl.edu (R.T. Hanlon)

0042-6989/99/$ - see front matter © 1999 Elsevier Science Ltd. All rights reserved.
PII: S0042-6989(99)00158-3

and hunting can be observed (Neill & Cullen, 1974; Hanlon & Messenger, 1996). Fish of various species are an important food source for *S. officinalis*, comprising 30–40% of the food of the adult (Najai & Ktari, 1974; Mao, 1985; reviewed by Boletzky & Hanlon, 1983). In this study, we looked at the role that linear polarization sensitivity plays in selecting their fish prey.

No animal is currently known to be sensitive to the circular polarization of light. This fact enabled us to take advantage of a filter that serves as a broadband retarder of light, transforming linearly polarized light to elliptically polarized light with a small component of linear polarization in it. The filter also depolarized the light to some extent by means of scattering. For the purpose of this paper, we refer to depolarized light as light without a linear polarization component in it, acknowledging that it may well be circularly polarized to a considerable extent.

2. Methods

Adult cuttlefish, 14–22 cm in mantle length, cultured throughout their life cycle at the Marine Resources Center of the Marine Biological Laboratory (Hanley, Shashar, Smolowitz, Bullis, Mebane, Gabr et al., 1998) were used to examine predator choice between fish that reflected partially linearly polarized light and fish that did not (Fig. 1). To exclude the possibility of learning the area of the tank where food can be found, or of increased searching behavior, each cuttlefish was tested in this design only once in this experiment (these animals were used in other unrelated behavioral experiments).

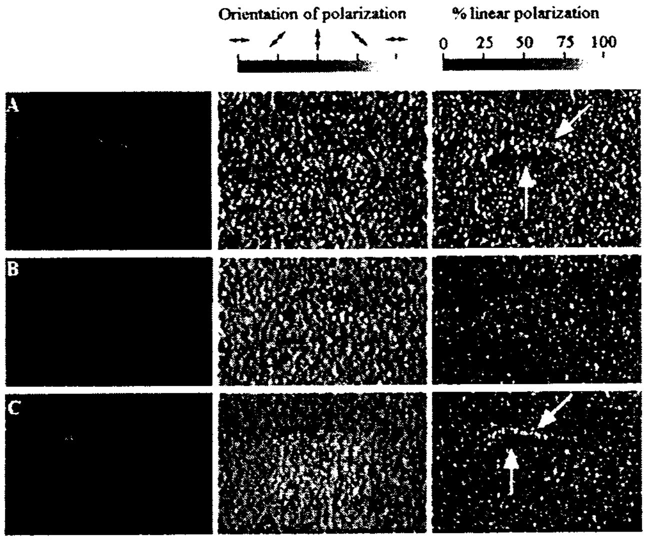

Fig. 1. Target fish, *Peprilus triacanthus*, as observed underwater in the experimental tank with an imaging polarimeter (Cronin et al., 1994; Shashar et al., 1995a) that was placed in an underwater housing. (A) A fish without any filter. (B) A fish with a filter distorting linear polarization attached to its side. (C) A fish with a polarization inert filter. (Left) A black and white image of the fish. (Center) Orientation of polarization, where horizontal polarization is coded into white or black, and vertical polarization into 50% gray. (Right) Partial polarization image where black represents unpolarized light — 0, and white codes for full linear polarization — 100%. Two areas on the fish that were the main sources of reflected polarized light are indicated by arrows; the lateral side of the fish reflected light that was 30–50% linearly polarized and the dorsal area reflected light with 70–95% linear polarization.

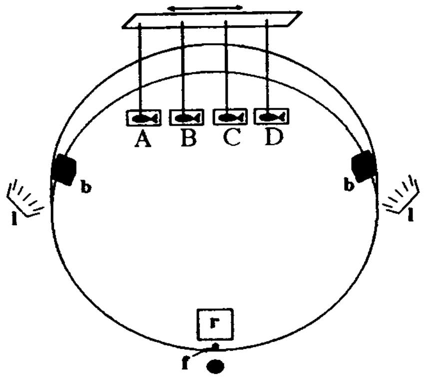

Fig. 2. The gray experimental tank had a diameter of 3.6 m and water depth was 72 cm for a total volume of 7.33 m^3. Adjacent to the inner wall of the tank, a 56 × 40 × 35 cm cuttlefish release structure (r) open towards the center of the tank was placed upon a 20 cm high cinder block such that it was open to the tank and its top was exposed. Behind the release site a bi-directional water in-flow (f) sent equal volumes of water around the tank. To discourage cuttlefish from following the edge of the tank, two 20 × 40 × 40 cm barriers (b) were installed at 3 m from the release point. The tank was illuminated by two 1000 W Lowel Tota flood lights (l), each positioned 1.9 m high. The observation vantage point (o) was located behind the release structure to minimize the observer's impact. The fish targets were placed across the tank, opposite to the release site and approximately 2.7 m from it. The fish were held by glass rods (randomly assigned out of a group of 12 identical rods) 45 cm from the bottom and 25 cm below the surface. The four fish were positioned 55 cm apart in a horizontal row (A–D), the end of which being 45 cm from the tank wall and the center being 73 cm from it. The glass rods were attached to a board (held 95 cm above the tank) that was moving back and forth, thus providing equal horizontal motion to each fish target (9 cm horizontal displacement at 11 cycles per min).

The experimental tank is illustrated in Fig. 2. Targets were four freshly dead and frozen butterfish, *Peprilus triacanthus*, 8.5–11 cm in length. They were placed across the tank at the end opposite to the release site and approximately 2.7 m from it (Fig. 2). The fish were held by glass rods that were attached to a board that was moving back and forth, and provided equal horizontal motion to each target. In each presentation, the size difference between the largest fish and the smallest fish was less than 0.5 cm.

A transparent plastic filter was glued to the side of each fish facing the cuttlefish. The filter was made of two layers of Roscolux #00 transparent filter (Rosco, Stanford, CT). When two such filters are attached parallel to each other they have minimal effect on the linear polarization characteristics of the light passing through them. When the two layers are attached at 45° to one another they effectively depolarize (partially circularly polarize) the linear polarization characteristics of light passing through them at all polarization orientations (Fig. 3). Using a retardance measuring microscope — PolScope (Oldenbourg & Mei, 1995) — we measured retardance of $74.3 \pm 1.1\%$ of a wavelength (measured at 546 nm) by the depolarizing filter, and of $12.3 \pm 0.1\%$ of a wavelength by the linear polarization neutral filter. The linear polarization characteristics of the filters were examined with an imaging polarimeter (Wolff & Mancini, 1992; Cronin, Shashar & Wolff, 1994; Shashar et al., 1995a; Wolff, 1995). No significant effect was found on the orientation of linear polarization by either filter. When examining the filters placed in front of linear polarizing filters, the polarization inert filter transmitted light that was $94 \pm 12\%$ linear polarized while the depolarizing filter transmitted light that was only $30 \pm 7\%$ linearly polarized (avg ± std, $n = 10\,000$ points on each filter, measured at three different orientations). Chromatic effects were small and since cuttlefish are color blind (Hanlon & Messenger, 1996) having a single class of visual pigments with a λ_{max} at 490 nm (Shashar, Hárosi, Banaszak & Hanlon, 1998b) they were ignored. Both filter types had a $\geq 95\%$ flat transparency across the 380–700 nm range (data provided by Rosco). The type of filter for each target fish was assigned randomly, such that the two types were always alternating (i.e. two possible combinations).

At the onset of an experiment, the motor moving the glass rods was activated and the motion was observed to ensure proper operation. Then the 1000 W lights were turned on to illuminate the fish and left to stabilize for at least 5 min. Next, the cuttlefish were introduced into the experimental tank, through the release structure. They were allowed to relax in the release structure, and we recorded their movements in the tank and their attacks on the target fish. If after 5 min there was little or no movement of the cuttlefish (in 10 of 39 cases), approximately 250 ml of sea water saturated with crushed-fish remains were added to the tank to provide an odor stimulant. In only four cases did this addition of stimulus elicit an attack on a target fish; hence, this technique is not recommended for future use. In one case a cuttlefish was moving about the tank but did not attack the fish, hence an odor stimulant was not added.

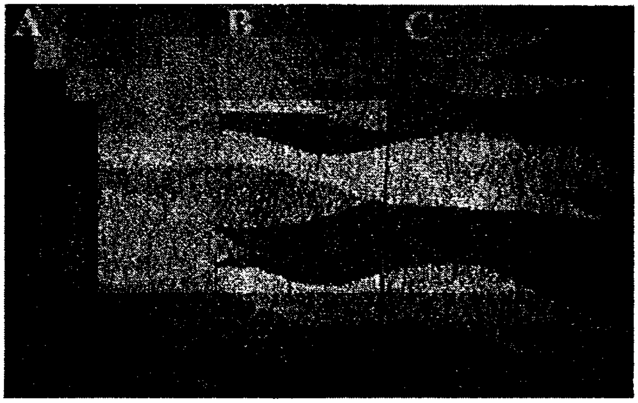

Fig. 3. (B) A filter containing a sample polarization pattern (filter # 369 — 'large fire'; Frank Wooley & Co. Inc., Reading PA) viewed through a linear polarizing filter (Polaroid HN38S). (A) Same as B but with a transparent, linear polarization distorting filter placed on top of the filter containing the polarization pattern. (C) Same as B but with an inert linear polarization filter placed over the polarization pattern. These filters were examined using an imaging polarimeter (Cronin et al., 1994; Shashar et al., 1995a). Neither filter affected the orientation of polarization. The linear-polarization inert filter (C) depolarized light by 6% while the depolarizing filter (A) depolarized it by 70%.

Attacks were considered valid only when all the following criteria were satisfied: (i) the cuttlefish physically touched the fish; (ii) the attack occurred within 30 min from the time the cuttlefish was introduced into the experimental tank; and (iii) attack was made from a distance larger than one cuttlefish body length (cuttlefish would occasionally settle close to the fish, or even right underneath them, and would sometimes collide with the fish). Results were examined using the non parametric χ^2 goodness-of-fit statistical test with equal expected frequency (Sokal & Rohlf, 1995).

3. Results

Of the 39 cuttlefish tested, seven did not attack any fish within the 30 min time limit. Twenty six animals attacked the fish within 7 min, with the others taking as much as 20 min to attack a fish. In total, 15 animals did not satisfy the requirements to be considered a valid attack. Of the 15 invalidated tests, seven did not attack any fish, three attacked fish from very close (all these fish were with the polarization neutral filters) and five attacked the fish from very close and from behind such that the fish were seen as a silhouette (two fish with depolarizing filters and three with polarization neutral filters). All of these 15 animals were excluded from the analysis.

Equal presentations of each type of filter at each position were made while testing the remaining 24 animals (at each position 12 presentations of depolarizing filter and 12 of polarization neutral filter). No significant effect of the position of the fish on cuttlefish choice was noted (number of attacks at each position was 7, 5, 5, 7; $\chi^2 = 0.667$, $P > 0.8$) and therefore the results from all positions were combined. Cuttlefish preferably attacked fish that reflected partially linearly polarized light (20 fish were covered by a polarization inert filter, four fish were covered by a polarization depolarizing filter; $\chi^2 = 17.3$, $P < 0.0001$; Fig. 4). Of the

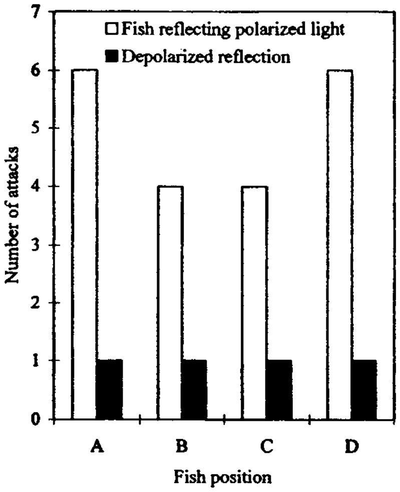

Fig. 4. Number of attacks made by 24 cuttlefish on target fish. Fish were placed in four positions (A–D) that were 55 cm apart. A polarization-inert or a linear polarization distorting filter was attached to each fish so that the two types of filters were alternating. In 12 cases a depolarizing filter was present at both positions A and C, and 12 times at both positions B and D. No significant effect was found of the position of the fish on the selection by the cuttlefish ($\chi^2 = 0.667$, $P > 0.8$). However, cuttlefish preferred fish that reflected partially linearly polarized light over fish without such linearly polarized reflection ($\chi^2 = 17.3$, $P < 0.0001$).

four cuttlefish to which a fish odor stimulant was provided, two chose fish with inert filters and two with depolarizing filters.

4. Discussion

Many planktonic organisms are transparent to achieve camouflage in the open water. Lythgoe and Hemming (1967) and Shashar et al. (1995a; Shashar, Adessi & Cronin, 1995b) demonstrated that polarization imaging can improve the detection range of such transparent targets, and Shashar et al. (1998a) demonstrated experimentally that squid use polarization sensitivity to overcome the transparency mechanism of camouflage of their prey.

Another common mechanism of open-water camouflage is radiance matching (Cott, 1940; Lythgoe, 1979). This mode is used not only by pelagic fish but also by benthic animals that might be seen against an open water background. Reflection-based radiance matching 'comes with a price' in that the reflected light is partially linearly polarized (Denton, 1970; Rowe & Denton, 1997). Here we showed that cuttlefish selectively chose polarization-reflecting silvery fish as prey items. We propose that polarization vision is used by cuttlefish to detect reflecting objects (i.e. fish scales) and improve their predation success. Thus, in the context of predation, it was demonstrated that: (i) squids use polarization sensitivity to better detect transparent prey (Shashar et al., 1998a) and; (ii) cuttlefish use polarization sensitivity to detect opaque prey with silvery scales, which helps overcome radiance matching effects of fish prey (this paper). It is reasonable to assume that polarization vision is also used in the context of predator avoidance, where cephalopods could be detecting intensity- and hue-matched, yet polarization reflecting, predatory fish based on the pattern of their polarized-light reflection (see color image in Cameron & Pugh, 1991; also see Denton & Nicol, 1966, for review of silvery teleosts).

Denton and Nicol (1965) reported that the silvery bleak, *Alburnus alburnus*, reflects light that has low partial polarization (less than 18%). It is possible that such lack of polarization reflection might give away the fish when they are seen against a highly polarized background (Waterman 1955, 1981; Horvath & Varju, 1995). However it is also feasible that polarization-sensitive fish will not be able to detect such a low polarization signal (Flamarique & Hawryshyn, 1997). The polarization sensitivity limits of cephalopods are yet to be tested and hence the minimal signal that could be detected by them is unknown. If indeed *A. alburnus* fish cannot be detected based on their polarization reflection, it would appear that they have achieved a new level of camouflage, adding polarization matching to intensity and color matching.

Visual systems have numerous potential sources of information available to them. These include intensity or the rate of photon arrival, wavelength or hue, and polarization. However, the interactions between these types of information in certain photoreceptor types can distort the quality of the information. Stomatopod shrimp solve this problem by having distinct photoreceptor sets for polarization and for color vision (Marshall, Land, King & Cronin, 1991; Marshall, Land & Cronin, 1994). Honeybee evolution proceeded another way with the development of special structures that distort the polarization information in parts of their retina so that it will not interfere with color vision and limit their polarization sensitivity to UV-sensitive photoreceptors (Wehner & Bernard, 1993). Mammals represent another solution where color vision is common while polarization sensitivity does not exist. Few if any cephalopods possess color vision, but all of the ones examined are sensitive to the linear polarization characteristics of light (Hanlon & Messenger, 1996). They apparently use this polarization sensitivity in a range of tasks, from target recognition and predation to communication (Moody & Parriss, 1960, 1961; Shashar et al., 1996; Shashar et al., 1998a). Many of these tasks are especially suitable to the marine environment, where the natural light field is partially linearly polarized (Waterman 1955, 1981; Horvath & Varju, 1995). Consequently, we expect that future studies will find that the use of polarization sensitivity is widespread among marine animals.

Acknowledgements

We thank Janice S. Hanley, William N. Mebane and Geoff Till for help in culturing the cuttlefish, Dr Rudolf Oldenbourg for assistance with the use of the Pol Scope, and Dr Michael R. Maxwell and two anonymous reviewers for comments that greatly improved this manuscript. This study was supported by NSF Grant IBN 9729598. NS was partly supported by a welcome fund from the Israeli Ministry of Immigrant Absorption.

References

Boletzky, S.v., & Hanlon, R. T. (1983). A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. *Memoirs of the National Museum Victoria, 44*, 147–187.

Cameron, D. A., & E. N. Pugh (1991). Double cones as a basis for a new type of polarization vision in vertebrates. *Nature, 353*, cover page and 161–164.

Cott, H. B. (1940). *Adaptive coloration in animals*. London: Methuen & Co. Ltd.

Cronin, T. W., Shashar, N., & Wolff, L. (1994). Portable imaging polarimeters. *IEEE proceedings of the 12th IAPR international conference on pattern recognition*. (pp. 606–609).

Denton, E. J. (1970). On the organization of reflecting surfaces in some marine animals. *Proceedings of the Royal Society of London B, 258*, 285–313.

Denton, E. J., & Nicol, J. A. C. (1965). Polarization of light reflected from the silvery exterior of the bleak *Alburnus alburnus*. *Journal of the Marine Biological Association of the United Kingdom, 45*, 705–709.

Denton, E. J., & Nicol, J. A. C. (1966). A survey of reflectivity in silvery teleosts. *Journal of the Marine Biological Association of the United Kingdom, 46*, 685–722.

Flamarique, I. N., & Hawryshyn, C. W. (1997). Is the use of underwater polarized light by fish restricted to crepuscular time periods? *Vision Research, 37*, 975–989.

Hanley, J. S., Shashar, N., Smolowitz, R., Bullis, R. A., Mebane, W. N., Gabr, H. R., & Hanlon, R. T. (1998). Modified laboratory culture techniques for the European cuttlefish *Sepia officinalis*. *Biological Bulletin, 195*, 223–225.

Hanlon, R. T., & Messenger, J. B. (1996). *Cephalopod behaviour*. Cambridge: Cambridge University Press.

Horvath, G., & Varju, D. (1995). Underwater refraction-polarization patterns of skylight perceived by aquatic animals through Snell's window of a flat water surface. *Vision Research, 35*, 1651–1666.

Lythgoe, J. N. (1979). *The ecology of vision*. Oxford: Clarendon Press.

Lythgoe, J. N., & Hemming, C. C. (1967). Polarized light and underwater vision. *Nature, 213*, 893–894.

Mao, P. (1985). Place de la sieche *Sepia officinalis* (Mollusque Cephalopode) dans les cahiers alimentaires du golfe Norman-Berton. *Caheirs de Biologie Marine, 26*, 331–340.

Marshall, N. J., Land, M. F., King, C. A.&, & Cronin, T. W. (1991). The compound eyes of mantis shrimps (Crustacea, Hoplocardia, Stomatopoda). I. Compound eye structure: the detection of polarized light. *Philosophical Transactions of the Royal Society of London B, 334*, 33–56.

Marshall, N. J., Land, M. F.&, & Cronin, T. W. (1994). The 'sixed-eyed' stomatopod. *Endeavour, 18*(1), 17–26.

Messenger, J. B. (1968). The visual attack of the cuttlefish, *Sepia officinalis*. *Animal Behaviour, 16*, 342–357.

Moody, M. F., & Parriss, J. R. (1960). Discrimination of polarized light by Octopus. *Nature, 186*, 839–840.

Moody, M. F., & Parriss, J. R. (1961). Discrimination of polarized light by Octopus: a behavioral and morphological study. *Zeitschrift fur vergleichende Physiologie, 44*, 268–291.

Najai, S., & Ktari, M. H. (1974). Etude du regime alimentaire de la seiche commune Sepia officinalis Linne, 1758 (Mollusque Cephalopode) du golfe de Tunis. *Bulletin de l'Institut National Scientifique et Technique d'Oceanographie et de Peche de Salammbo, 6*(1–4), 53–61.

Neill, S. R. St. J., & Cullen, J. M. (1974). Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *Journal of Zoology (London), 172*, 549–569.

Oldenbourg, R., & Mei, G. (1995). New polarized light microscope with precision universal compensator. *Journal of Microscopy, 180*, 140–147.

Rowe, D. M., & Denton, E. J. (1997). The physical basis for reflective communication between fish, with special reference to the horse mackerel, *Trachurs trachurus*. *Proceedings of the Royal Society of London B, 352*, 531–549.

Saidel, W. M., Lettvin, J. Y., & McNichol, E. F. (1983). Processing of polarized light by squid photoreceptors. *Nature, 304*, 534–536.

Shashar, N., Cronin, T. W., Johnson, G., & Wolff, L. (1995a). Portable imaging polarized light analyzer. Proceedings of the 9th meeting on optical engineering in Israel. *SPIE, 2426*, 28–35.

Shashar, N., Adessi, L., & Cronin, T. W. (1995b). Polarization vision as a mechanism for detection of transparent objects. In: D. Gulko, & P.L. Jokiel, *Ultraviolet radiation and coral reefs* (pp. 207–211). HIMB and UNIHI- Sea Grant.

Shashar, N., Rutledge, P. S., & Cronin, T. W. (1996). Polarization vision in cuttlefish- a concealed communication channel? *Journal of Experimental Biology, 199*(9), 2077–2084.

Shashar, N., Hanlon, R. T., & Petz, A. deM. (1998a). Polarization vision helps detect transparent prey. *Nature, 393*, 222–223.

Shashar, N., Hárosi, F. I., Banaszak, A. T., & Hanlon, R. T. (1998b). UV radiation blocking compounds in the eye of the cuttlefish *Sepia officinalis*. *Biological Bulletin, 195*, 187–188.

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry*. New York: Freeman.

Tyo, J. S, Rowe, M. P., Pugh, E. N., & Engheta, N. (1996). Target detection in optically scattering media by polarization-difference imaging. *Applied Optics, 35*(11), 1855–1870.

Waterman, T. H. (1955). Polarization scattered sunlight in deep water (supplement). *Deep Sea Research, 3*, 426–434.

Waterman, T. H. (1981). Polarization sensitivity. In: H. Autrum, *Handbook of sensory physiology*, vol. VII/6B: *Comparative physiology and evolution of vision in invertebrates*. B: *Invertebrate visual centers and behavior* I. (pp. 281–463). Berlin: Springer-Verlag.

Wehner, R., & Bernard, G. D. (1993). Photoreceptor twist: a solution to the false-color problem. *Proceedings of the National Academy of Sciences USA, 90*, 4132–4135.

Wolff, L. B. (1995). Applications of polarization camera technology. *IEEE Expert, 10*(5), 30–38.

Wolff, L. B., & Mancini, T. A. (1992). Liquid crystal polarization camera. *IEEE workshop on applications of computer vision* (pp. 120–127).