

3. Herzog, E. H., M. K. Powers, and R. B. Barlow. 1996. *Vis. Neurosci.* 13: 31–41.
4. McFarland, W. N., and E. R. Loew. 1983. *Env. Biol. Fish.* 3/4: 173–184.
5. Loew, E. R., and W. N. McFarland. 1990. In *Visual System of Fish*, R. H. Douglas, R. H., and M. B. A. Djamgoz eds. Chapman and Hall, Ltd. London, England.
6. Passaglia, C. L., F. A. Dodge, and R. B. Barlow. 1994. *Biol. Bull.* 189: 213–215.
7. Glantz, R. M., and A. Bartels. 1994. *J. Neurophysiol.* 71: 2168–2182.

Reference: *Biol. Bull.* 193: 207–208. (October, 1997)

### **Squids (*Loligo pealei* and *Euprymna scolopes*) Can Exhibit Polarized Light Patterns Produced by Their Skin**

*Nadav Shashar and Roger T. Hanlon (Marine Biological Laboratory, Woods Hole, Massachusetts 02543)*

Cephalopods can see polarized light (1–3) and may use this sensory capacity for object detection and recognition (1, 4). Only recently was it discovered that the light reflected from the skin of cuttlefish, *Sepia officinalis* (5), and possibly octopus (6) is partially linearly polarized (termed here- “polarized reflection”), generating specific optical patterns (termed here- “polarized patterns”). In cuttlefish, the polarized patterns have been suggested to be produced by dermal reflecting cells such as those found in the “Pink iridophore arm stripes” (7). Cuttlefish are diurnal animals that interact within small groups, and the polarized patterns may be playing a part in intraspecific communication (5). Therefore, we were interested in examining the polarized patterns of other cephalopod species, namely *Euprymna scolopes* and *Loligo pealei*, that possess similar skin structures, but have a different social structure and time of activity.

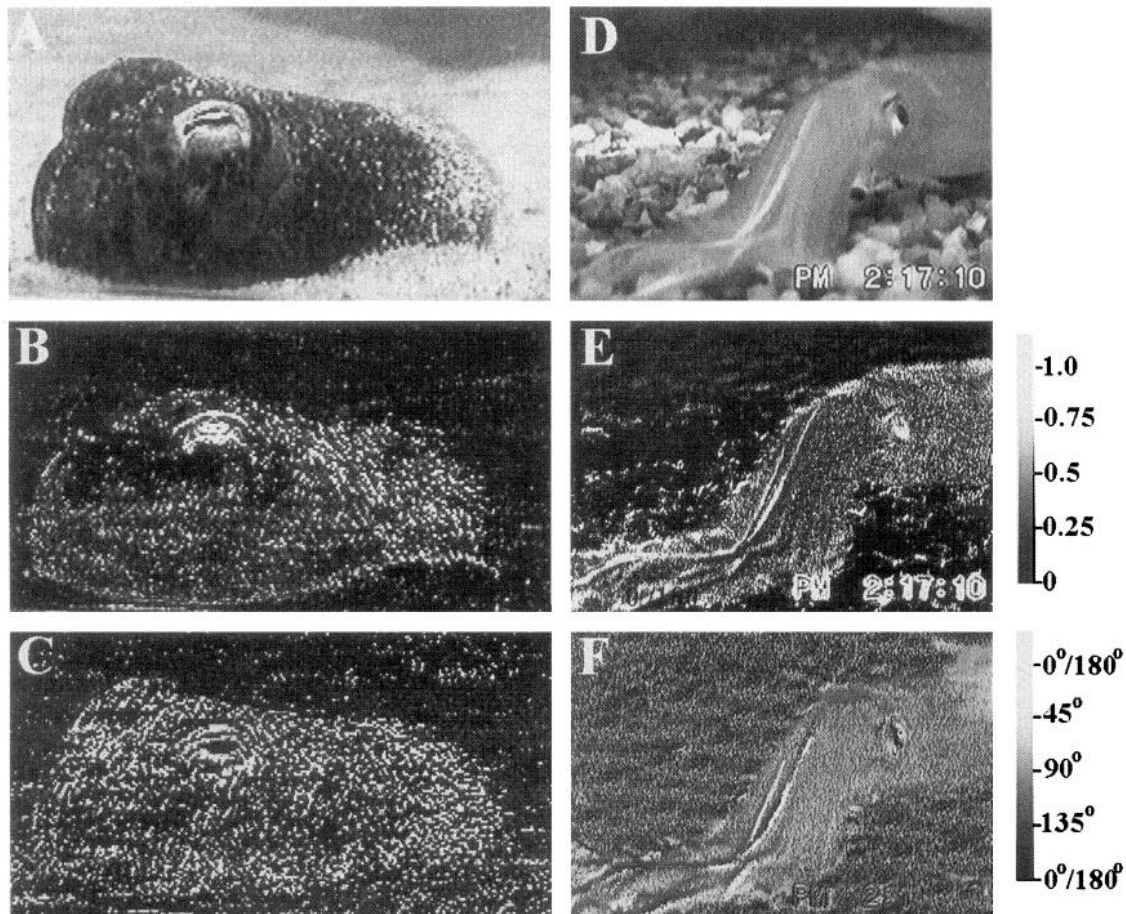
The Hawaiian sepiolid *Euprymna scolopes* is a predominantly nocturnal, solitary predator (7, 8). Mating occurs at night, and apart from this brief event, the animals do not seem to engage in complex social interactions. The long-finned squid *Loligo pealei* is active day and night. It exhibits a complex range of social interactions, accompanied by various body pattern displays (7).

Sexually mature animals were examined with an imaging polarimeter capable of measuring the intensity, partial polarization (also termed “percent polarization”), and direction of linear polarization (also termed “plane of polarization,” “orientation of polarization” and “e-vector orientation”) at each pixel in an image (9, 10). In summary, the polarimeter consists of two twisted nematic liquid crystals (TNLCs; provided by the Liquid Crystals Institute, Kent State Univ., Ohio) placed in series with a linear polarizing filter (Polaroid, HN38S, serving as an analyzer) fixed at the horizontal (0°) orientation. When TNLCs are relaxed, they rotate the direction of polarization of light by a predetermined angle. When electric current is applied, the molecules within the crystals reorient and no longer rotate the light’s direction of polarization. By using one TNLC set to produce a 90° rotation, and a second for a 45° rotation, the direction of polarization of the incoming light is rotated by 0°, 45°, and 90°. The overall effect is similar to rotating the analyzer to these positions. Additional technical details can be found in references 9–12. Each transmitted image is recorded with a Hi-

8 video recorder. Images (single fields) taken from the green video channel are digitized by a frame grabber and sent to a computer where they are analyzed pixel-by-pixel. From consecutive images collected at three settings of the TNLCs, we calculate the partial polarization and direction of polarization. The sensor is checked and calibrated by examining a radial polarization filter (Oriel # 25328) in air and submerged in the experimental tank. Animals were examined through a glass window, verified not to create polarization aberrations from various angles and under different illumination conditions. In all cases, the sensor was set so that the TNLCs were parallel to the glass window.

Both *E. scolopes* and *L. pealei* exhibited polarized reflection during all measurements (Fig. 1). Polarized reflection with a partial linear polarization of up to 0.8 (80%, Fig. 1B) was measured from all body parts of *E. scolopes*, but no specific pattern could be identified (Figs. 1B, C). This polarized reflection did not change with the animal’s behavior. *L. pealei* presented polarized reflection at the location of the iridescent stripes in the center of its arms (Figs. 1E, F). Partial polarization here reached 0.75 (Fig. 1E). The direction of polarization was predominately horizontal (0°; Fig. 1F); however, in several cases, the direction of this polarized reflection changed by up to 30° within 1 s, without the animal exhibiting any movement or change in coloration, nor any detectable changes in the light regime in the tank. Unlike cuttlefish (5), the polarized reflection of *L. pealei* varied between the arms. In general, when a squid was sitting calmly on the bottom, polarization was strongest from the first pair of arms. While the squid was in the head-down posture, all arms showed a polarized pattern, with maximal polarized reflection recorded from the third pair. We do not know whether these changes arise from structural changes in the skin structures controlling the polarized reflection, or from specific directionality in the polarized reflection. Other areas on the squid that reflected partially linearly polarized light were the “Dorsal iridophore splotches” on the mantle, but this reflection had partial polarization of less than 0.5.

Like other cephalopods, polarized reflections are part of the body patterning repertoire of *L. pealei* and *E. scolopes*. Like cuttlefish, the polarized reflections of the social long-finned squid *L. pealei* consist of distinctive patterns that can change rapidly. The solitary *E. scolopes* exhibits polarized reflection



**Figure 1.** Intensity (A,D), partial polarization (B, E) and direction of polarization (C, F) images of *Euprymna scolopes* (A–C) and *Loligo pealei* (D–F). Partial polarization, defined as the ratio of the intensity of the linearly polarized component to the total intensity of the light beam, ranges from 0 to 1 (0–100%) and is coded into a grey scale where black represents depolarized light and white codes for full linear polarization. Direction of polarization, ranging from  $0^\circ$  to  $180^\circ$  in the counter-clockwise orientation, is coded such that black or white represent  $0^\circ/180^\circ$  (horizontal polarization) and 50% grey codes for the  $90^\circ$  direction, which is vertical polarization.

that appears unrelated to the animal's behavior. The functions of these polarized reflections as well as the roles of these species' polarization sensitivity (2) are yet to be determined.

We are grateful to W. Mebane and J. Hanley for their assistance in maintaining our animals. Comments by two reviewers greatly improved the manuscript. This study was supported by a Grass Foundation fellowship to N.S.

#### Literature Cited

1. Moody, M. F., and J. R. Parriss. 1960. *Nature* **186**: 839–840.
2. Jander, R., K. Daumer, and T. H. Waterman. 1963. *Z. Vergl. Physiol.* **46**: 383–394.
3. Saidel, W. M., J. Y. Lettvin, and E. F. McNichol. 1983. *Nature* **304**: 534–536.
4. Shashar, N., and T. W. Cronin. 1996. *J. Exp. Biol.* **199**: 999–1004.
5. Shashar, N., P. S. Rutledge, and T. W. Cronin. 1996. *J. Exp. Biol.* **199**: 2077–2084.
6. Cronin, T. W., N. Shashar, and L. Wolff. 1995. *Biophotonics Int.* **2**: 38–41.
7. Hanlon, R. T., and J. B. Messenger. 1996. *Cephalopod Behaviour*. Cambridge Univ. Press.
8. Hanlon, R. T., M. F. Claes, S. E. Ashcraft, and P. V. Dunlap. 1997. *Biol. Bull.* **192**: 364–374.
9. Cronin, T. W., N. Shashar, and L. Wolff. 1994. *Proc. 12 Int. Con. Pattern Recognition* 606–609.
10. Shashar, N., T. W. Cronin, G. Johnson, and L. Wolff. 1995. *Proc. 9th Meet. on Optical Eng. in Israel. SPIE* **2426**: 28–35.
11. Wolff, L. B. and T. A. Mancini. 1992. *Proc. IEEE workshop on application of Computer vision.* 120–127.
12. Wolff L. B. 1995. *IEEE expert.* **10**: 30–38.