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Retinal Adaptation of Japanese Common Squid (*Todarodes pacificus* Steenstrup) to Light Changes*

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Abstract

The response of retinae of the Japanese common squid (*Todarodes pacificus* Steenstrup) was recorded in relation to various light intensities. In the light-adapted eye of common squid, the black pigment ascends to the external limiting membrane of the retina. Conversely, in the dark-adapted eye the black pigment descends toward the center of the black pigment layer. To express the degree of adaptation, the authors give the ratio of the height (thickness) of the black pigment to the total height (thickness) of the retina as a percentage (%).

The results of this investigation can be summarized as follows:

- 1) The movement of the black pigment is not very fast.
- 2) If the illumination is brighter than 25 lux, and exposure lasts less than 2 hours, the black pigment does not migrate. This suggests that with high intensity and short exposure time, the shutting of the iris directly controls the amount of light coming in contact with the visual element in the retina.
- 3) The intensity of the illumination in which good control of retina sensitivity by movement of the black pigment corresponds to the extremely lower intensity, so they lives deeper layer in daytime and migrate to near-surface in night time. The process of the black pigment ascending where photopic vision occurs, and black pigment descending where scotopic vision occurs, takes place at an intensity of illumination of about 1.0 lux.
- 4) A thickness of less than 40% of retinal black pigment in the common squid immediately after capture by jig is the normal value.

The visual senses of cephalopods are very well developed, as it is suggested by the large number of visual cells that are distributed in high density in all cephalopod retinae.

The number of visual cells is expressed in unit retina/mm². These are 64,000 for octopus, 105,000 for cuttlefish, 162,000 for squid, all of which are greater than in fishes. In squid it is about equivalent to the 160,000 in the human retina. So, the visual accuracy has also been expected¹⁾.

Among the squids, the Japanese common squid (*Todarodes pacificus* Steenstrup) has been fished by using fish attraction lamps for a very long time, but there have been few basic studies on the behaviour of common squid in reaction to light²⁻⁶⁾. Therefore, to learn about the influence of fish attraction lamps to the common squid, the authors pursued the investigation of the response of the retina to light.

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Materials and Methods

Field sampling for squid was carried out at the Japan Sea fishing ground in August and October, 1982 aboard by the "Oyasho Maru" (273.24 gross tons). The research vessel owned Hakodate Fisheries Experimental Station. Immediately after 27 squids were caught by squid jig, the eye-balls were removed and preserved whole in Bouin's fluid (fixative) and brought back to laboratory, 15 were females and 12 males, mantle lengths of 18.5-24.9 and 18.2-23.8 cm respectively.

In addition 42 squids were sampled at the offshore fishing ground off Hakodate from September to October, 1983 by caught commercial squid jigging boat, 25 were females and 17 were males, mantle lengths of 20.8-26.0 and 19.9-25.7 cm respectively. The squids were brought to the harbor alive in the live-tank of the ship. The next morning they were transferred to an indoor cement holding tank (10 m × 3 m × 1.8 m) ashore. After a period of 4-5 hours in this tank, the squid were transferred to the darkconditioning FRP (Fiberglass reinforcement plastic) experimental tank (110 cm × 68 cm × 39 cm). Experiment were remaining 4 hours in darkness, and then exposure to light of 5 minutes to 2 hours various time intervals. One experiment were used 4 squids in tank. Illumination experiments were performed using various intensities of incandescet light, consisting of a 100 V, 10 W lamp as standard voltage, a 100 V, 20 W lamp gave more illumination. The 10 W lamp was stepped down to 50 V and 30 V from standard voltage for lower intensities. The lamp was suspended 50 cm above the surface of the water at the center of the experimental tank. Surface light intensity measurements were made with a submarine photometer (SPI-9W) manufactured by "Tokyo-Kogaku KK"

Immediately after the end of the experiments such as various time interval exposure to the light, whole eye-balls were removed from the squid and preserved in toto in Bouin's fixative. The central part of the retina at the side opposite the lens was excised out, sectioned longitudinally at 6 μ m in thickness by the routine paraffin method. The sections were stained by Delafield's haemotoxylin and eosin, then observed under a light microscope at magnifications of 3.3 × 2.0 and 2.5 × 20. Photomicrographs of the retinal sections were taken for each eye-ball.

Fig. 1 shows the transverse section through the eye-ball of a squid. The cornea, iris, lens, retina, sclera and optic lobe are clearly seen externally⁷⁾. Fig. 2 shows the structure of the retina^{8,9)}, the rhabdom layer, the outer segment of the visual cells, black pigment layer, support cells, limiting membrane, blood vessels, layer of visual cell nucleus, visual cell nucleus and layer of optic nerve fibers.

It is well known that the adaptation to light of human and fish retina is affected by the cones for photopic vision and the rods for scotopic vision. In the cephalopoda the construction of cones and rods is different. As shown in Fig. 2 the black pigment layer lies slightly toward the front side of limiting membrane. This layer contains the black pigment which can migrate upwards in the retina by exposure to light, thus controlling the resolution of the visual sensitivity¹⁰⁻¹³⁾.

Fig. 3 (A), (B), (C), shows different migrating conditions of the black pigment of the retina.

(A) shows the sinking (descending) movement of the black pigment layer to measure the rate of dark-adaptation.

(B) shows the rising (ascending) movement of the black pigment at the upper

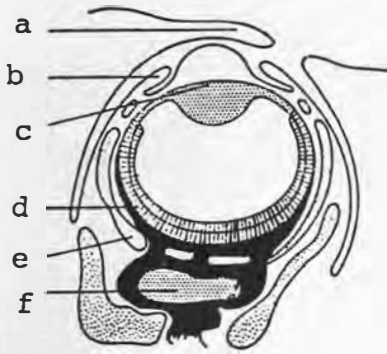


Fig. 1. Schematic representation of the transverse section through the eyeball of a cephalopod. [from Duke-Elder (1958)⁷⁾].

a: cornea, b: iris, c: lens, d: retina, e: sclera, f: optic lobe.

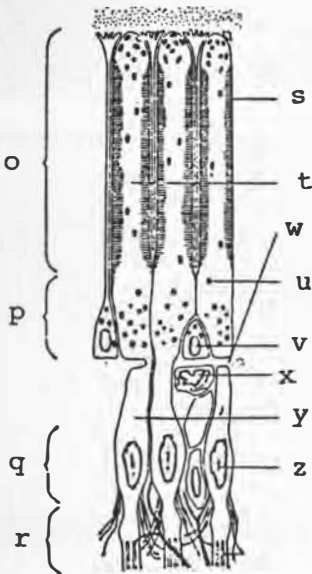


Fig. 2. Schematic representation of the structure of a cephalopod retina. [from Tazaki (1967)⁸⁾].

o: rhabdom layer, p: black pigment layer, q: layer of visual cell nucleus, r: layer of optic nerve fibers, s: rhabdomere, t: outer segment of visual cell, u: black pigment, v: support layer, w: limiting membrane, x: blood vessel, y: inner segment of visual cell, z: visual cell nucleus.

side of the retina to measure the rate of light adaptation.

(C) shows the movement of the black pigment in the part adjacent to the center of the black pigment layer.

This report describes the variation in thickness of squid retina exposed to different light intensities according to the region of the sectioned retina, the enlargement of retina picture, the condition of light or dark adaptation, etc. As shown in Fig. 4 the state of adaptation is expressed by the percentage of the thickness, b , of the black pigment layer compared to the thickness of the retina, a , (from the external limiting membrane to the retina surface); $b/a \times 100\%$, zero% indicates the scotopic vision condition for dark-adaptation, and 100% indicates the photopic vision condition for light-adaptation.

Results

There is a different of several % of the position of the black pigment for left and

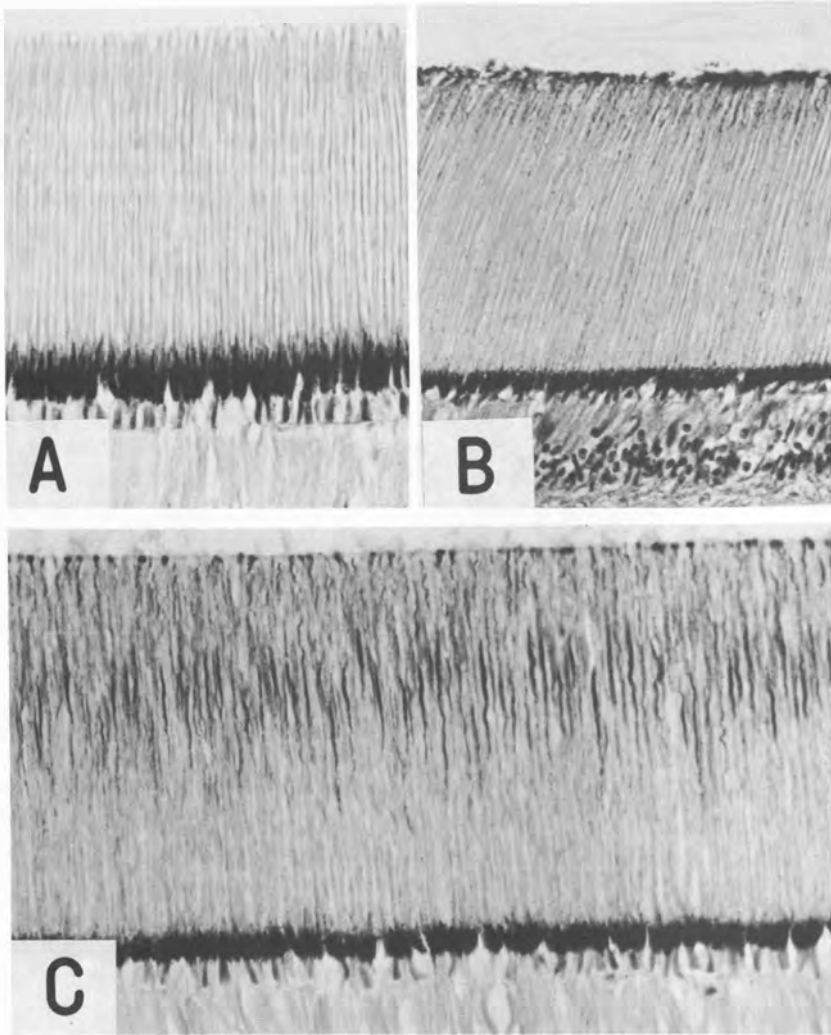


Fig. 3. Microphotographs showing the migrating condition of the black pigment in retina of the squids, *Todarodes pacificus* Steenstrup.
(A) the descending of the black pigment in the black pigment layer.
(B) the rising of the black pigment at the upper side of retina.
(C) the movement of the black pigment to the midpoint in the retina.

right eye-ball for an individual squid. Therefore, the moving ratio of the black pigment expressed by the average value (in %) of both eye-balls. Fig. 5 shows the condition of the black pigment before and after 4 hours in the dark condition in the experimental tank. Time zero hour is the state of retina just before the squid was put in the experimental tank. In this case the black pigment thickness shows nearly photopic vision after not less than 5-6 hours under indoor natural light conditions. A sinking (descending) movement of black pigment of 30-40% was observed after

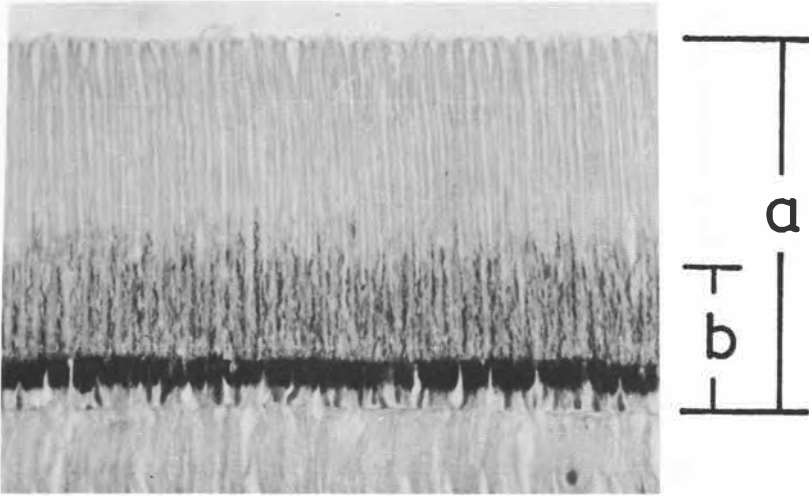


Fig. 4. The thickness adaptation expressed by percentage (%) of the height of black pigment b to the thickness of retina $a \times 100$.

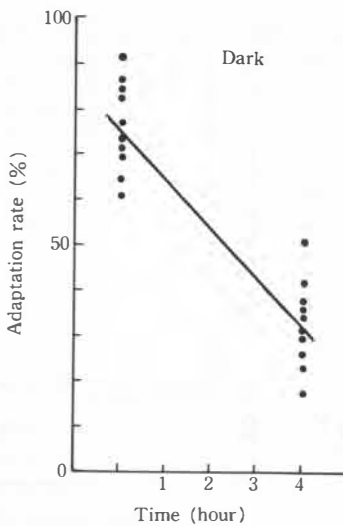


Fig. 5. The condition of black pigment thickness before and after 4 hours in darkness in the experimental tank.

4 hours in total darkness, which indicates the movement toward scotopic vision.

Fig. 6 shows the results of retinæ exposed to the low voltage 30 V, 10 W incandescent light after 4 hours under dark adaptation. The position of the black pigment after 30 minutes and after one hour of illumination are shown. After one hour, the sinking (descending) movement of the black pigment was about 10%. Fig. 7 shows the results of retinæ exposed to a low voltage of 50 V, 10 W incandescent light, also after 4 hours under darkness. The change in thickness (height) of the black pigment after 30 minutes illumination is clearly seen. The rising (ascending) movement of the black pigment under this light condition shows the movement

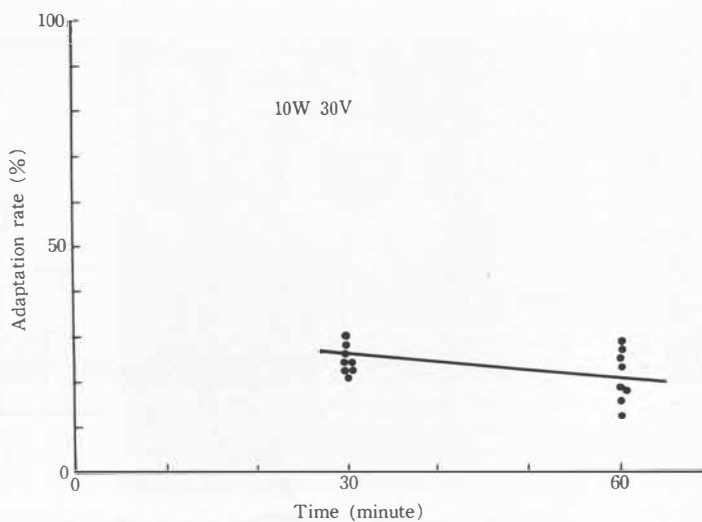


Fig. 6. The results when exposed to reduced voltage of 30 V, 10 W lamp.

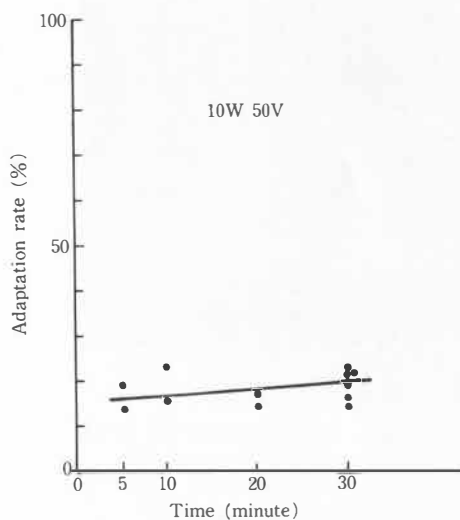


Fig. 7. The results when exposed to reduced voltage of 50 V, 10 W lamp.

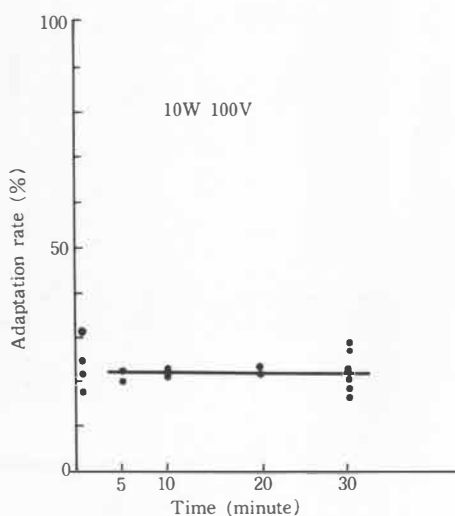


Fig. 8. The results of illumination by the standard voltage 100 V, 10 W lamp.

to photopic vision.

The results of exposure to illumination from the standard 100 V, 10 W lamp is shown in Fig. 8 and from the standard 100 V, 20 W lamp is shown in Fig. 9. In both cases the black pigment did not migrate.

Table 1 lists data for light intensities at the surface of the water illumination by the experimental lamps suspended 50 cm directly above the surface.

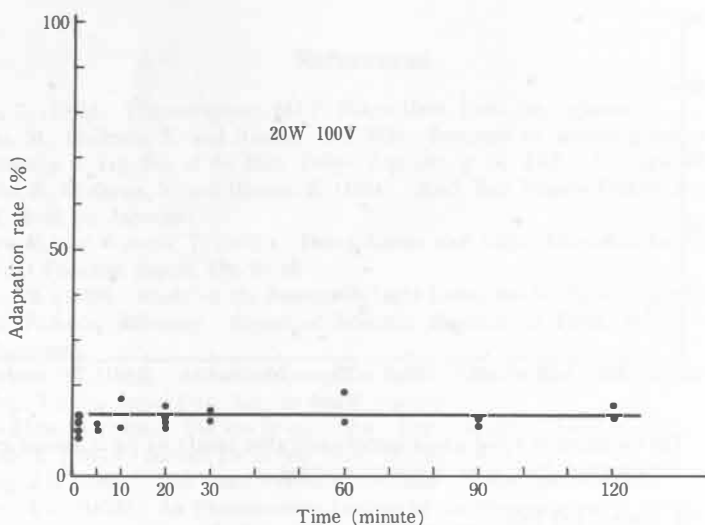


Fig. 9. The results of illumination by the standard voltage 100 V, 20 W lamp.

Table 1. Intensity of illumination at the surface of the water by experimental incandescent light suspended 50 cm directly above the surface of the water

Incandescent lamp (standard voltage 100 V)	10 W			20 W	40 W
	Voltage (V)	30	50	100	100
Illumination (lux)	0.2	1.9	25.3	85	170

Discussion

From the results shown in Figs. 5, 6 and 7 it is observed that the movement of the black pigment is not very rapid. Young¹²⁾ and Daw, et al¹¹⁾. investigated the light adaptation of *Loligo pealei* to a 60 W electric light bulb and white light of 25 $\mu\text{w}/\text{cm}^2$. Compared to give their results of black pigment movement speed, the present results are very slow. Whether this is due to species differences or light intensity differences is unclear.

As shown in Figs. 8 and 9, the black pigment did not migrate at illumination brighter than 25 lux. This is caused by the iris-shutting mechanism which has been described by several authors⁷⁻⁹⁾ but one more reconfirmed this time by authors with sight. From this, it appears that the shutting of the iris at strong intensities or short-time exposures (within 2 hours) provides a very efficient control of retina reaction to light, rather than by migration of the black pigment.

From the results in Figs. 6, 7 and Table 1, the mutual adaptation to brightness shows a remarkable agreement with the ascending and descending movement of the black pigment, which shows the photopic vision and scotopic vision to be valued at

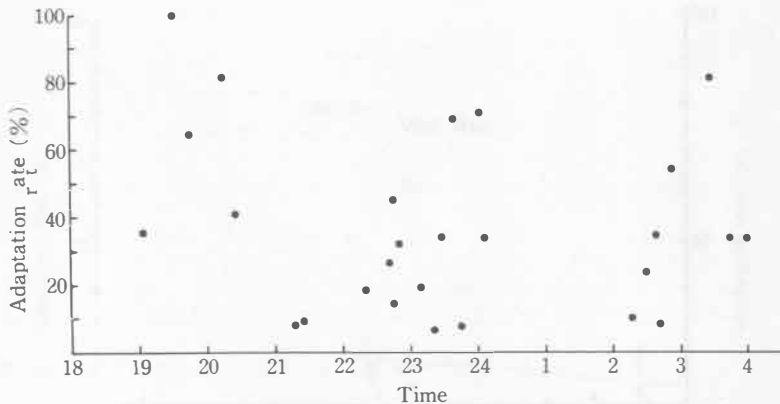


Fig. 10. The condition of squid retina immediately after caught by jig at fishing ground at various times from evening toward morning.

a brightness of about 1.0 lux.

Fig. 10 shows the condition of the retina immediately after being caught at the fishing ground at various times from evening toward morning. With only one exception of 100% of retina adaptation in the evening, all other squid show less than about 40% of retina adaptation, which indicates scotopic vision.

It is very interesting to note that at low intensities of illumination, the speed of movement of black pigment is slow and consequently controls the retinal sensitivity. Repeated results suggest that the condition of the retina immediately after capture is nearer to scotopic vision than to photopic vision when the squid is in waters with extremely low level illumination. Also, these squid probably undergo a deal whereby they inhabit the deeper layers in daytime and rise near the surface layer at night. This behavior may be the factor that controls the visual sensitivity of squid at extremely low illumination. Furthermore, from the results¹⁴⁾ of investigation around the ship at the same time of jigging fisheries with sonar, squids gathered anytime at less than 1.0 lux low illumination zone such as under of ships bottom and out side of high illumination zone. This fact coincide of above state to visual sensitivity is extremely low illumination. So it is supposed that don't need to the too much strong light for squid jigging fisheries, if the too much strong light for squid attraction, squid will gathered more deeper layer or more far distance position from ship.

Acknowledgments

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