Helgoländer wiss. Meeresunters. 31, 180–190 (1978)

Experimental studies on the light sense in the hagfish, *Eptatretus burgeri* and *Paramyxine atami* (Cyclostomata)

R. A. PATZNER

Zoological Institute, University of Salzburg;
Akademiestr. 26, A-5020 Salzburg, Austria

ABSTRACT: Photo-reception and sensitivity to light were studied in two Japanese hagfishes, *Eptatretus burgeri* living in shallow water and *Paramyxine atami* living in water of about 100 m depth. Both species responded to general illumination by first moving the tail or head and then by swimming. Local illumination revealed that regions most sensitive to light were the skin of the tail in both species and a line of unpigmented skin running down the back of *E. burgeri.* The light sensitivity of the lensless eyes, which are situated below the skin, was very weak in both species. *P. atami* showed shorter reaction time to light than *E. burgeri.* No change in skin colour was induced either by almost complete hypophysectomy or by continuous illumination against a white background. Under-water observations with SCUBA revealed that free moving *E. burgeri* responded well to illumination uncovered during the night, but the ones buried in mud, with only the heads uncovered did not.

INTRODUCTION

Investigations on the reaction of hagfish to light have only been made in *Myxine glutinosa* (L.) by Coonfield (1940), Newth & Ross (1955), Steven (1955), Ross (1963) and Holmberg (1968, 1971). They described the eyes of *Myxine* as being placed under the skin and parietal muscle where they have no visual function. However, they also found evidence of a dermal light sense, which is not controlled by a lateralis nerve. In *Eptatretus burgeri* and *Paramyxine atami* the eyes are also situated under unpigmented skin patches and like *Myxine* (Fernholm & Holmberg, 1975) neither lenses nor eye-ball muscles are developed.

Eptatretus lives in well-lighted water of 6 to 9 m depth, save during the four months of July to October (Kobayashi et al., 1972), whereas *Paramyxine* lives in water of about 100 m depth (Strahan & Honma, 1960). Thus their natural habitats are quite different from each other, and therefore, some differences in photoreception and sensitivity are to be expected between these two species.

In this investigation, studies were carried out to determine: (a) the mode of reaction of *Eptatretus* and *Paramyxine* to general illumination, (b) light sensitivity of their eyes and skin, (c) the dermal light sensitivity of the two Japanese species as compared to *Myxine,* (d) the light intensity preferences in *Eptatretus* and *Para-*

myxine, (e) melanophoric response, (f) the influence of light on the behaviour of *Eptatretus* in its natural surroundings (shallow water).

MATERIALS AND METHODS

Eptatretus burgeri was trapped in Koajiro Bay (6–12 m depth) near the Misaki Marine Biological Station (University of Tokyo, Kanagawa-ken, Japan), *Paramyxine atami* at a location off Koajiro Bay (depth about 100 m). A description of the locality is given in Kobayashi et al. (1972) and Fernholm (1974). The fish were kept in large running-sea-water-tanks (at 10–11° C and about 33 ‰ S) for 1 to 2 weeks before use. For the experiments, the hagfish were transferred into small aquaria in a dark room with a red-painted bulb for background illumination. The light intensity was about 1 lux at the bottom of the empty aquaria. During the experiments, the temperature of the water was kept at 12.5–14.5° C. Light intensity was measured by a Toshiba Photocell Illuminometer SPI-1 at the bottom of the empty aquaria, unless otherwise specifically stated. Prior to tests for light reactions, the hagfish were checked for 1–2 min under red light, to determine if they were moving or still. After each test, the hagfish were kept in darkness for at least 30 min in order for the animals to adapt again to the dark. Special techniques used in separate series of experiments are mentioned when they were used.

RESULTS

Reaction to illumination

During the observations, the animals were kept in separate glass aquaria (30×30×30 cm), which were filled up with sea water to a height of 8 cm. Although the water was not aerated it was changed daily. Electric bulbs were mounted 20 cm above the water surface of each aquarium. Three or four aquaria were illuminated and observed simultaneously.

General illumination

Sixteen *Eptatretus burgeri* and 16 *Paramyxine atami* were illuminated from above by a 40 W bulb (100 V). The light intensity measured 310 lux at the bottom of the aquaria. The first reaction to light was either a movement of the tail or head. In 75 out of 79 observations of 16 *Eptatretus* and in 42 out of 78 observations of 16 *Paramyxine*, the first response was tail movement; the remainder responded first by head movement. Then the fish began to twist their bodies and started to swim. The intervals from the start of illumination to the first movement and to the start of swimming were noted as the reaction times for the movement and swimming.

Reaction time was different from animal to animal (Table 1). In further experiments only animals with reaction times close to average were used. For 3 of the

Table 1

Reaction times of *Eptatretus burgeri* (E–I to E–XVI) and *Paramyxine atami* (P–I to P–XVI) in response to general illumination: (a) first movement (b) start of swimming. 5 observations each. Time in seconds; light intensity: 310 lux

Fish	(a)	(b)	Fish	(a)	(b)
E–I	10.9 ± 1.7*	40.3 ± 6.0	P–I**	7.3 ± 2.9	14.3 ± 1.7
E–II	7.4 ± 0.7	21.1 ± 1.1	P–II	5.2 ± 0.6	29.1 ± 4.5
E–III**	10.3 ± 1.7	53.4 ± 4.0	P–III	12.5 ± 1.5	17.4 ± 1.4
E–IV**	8.0 ± 0.4	38.0 ± 8.9	P–IV	10.7 ± 1.3	23.0 ± 3.5
E–V	6.3 ± 0.7	17.0 ± 1.5	P–V	4.2 ± 0.6	31.8 ± 5.2
E–VI	10.5 ± 1.3	34.7 ± 7.6	P–VI	7.8 ± 1.8	15.4 ± 1.0
E–VII	10.9 ± 1.4	20.2 ± 4.2	P–VII**	7.3 ± 1.5	26.0 ± 6.1
E–VIII	6.0 ± 0.6	16.1 ± 1.7	P–VIII	7.6 ± 1.1	17.7 ± 1.8
E–IX**	7.7 ± 0.8	20.7 ± 3.0	P–IX	8.4 ± 0.4	22.2 ± 4.1
E–X	12.2 ± 0.5	42.5 ± 5.8	P–X	5.1 ± 0.3	16.1 ± 1.8
E–XI**	8.4 ± 0.3	17.3 ± 3.3	P–XI**	7.3 ± 0.7	36.9 ± 2.7
E–XII	5.2 ± 0.2	52.0 ± 5.6	P–XII	5.7 ± 0.7	15.8 ± 2.3
E–XIII	6.5 ± 0.5	79.0 ± 6.4	P–XIII	4.4 ± 0.2	24.0 ± 4.3
E–XIV	5.7 ± 0.1	32.2 ± 4.8	P–XIV	11.8 ± 2.6	35.9 ± 13.2
E–XV	7.5 ± 0.8	43.2 ± 7.9	P–XV**	7.2 ± 0.4	29.2 ± 3.7
E–XVI	7.8 ± 2.0	53.4 ± 4.8	P–XVI	5.2 ± 0.4	14.4 ± 3.0
Mean	8.2 ± 0.5	36.3 ± 4.4	Mean	7.4 ± 0.6	23.0 ± 1.9

* Mean ± standard error
** animals used for further experiments

16 hagfish, no results could be determined as the fishes were already moving or swimming just before illumination.

In 3 cases involving *Paramyxine*, the ventral part of the body, which was facing upwards, was illuminated (Table 1, animals P-XIV, P-XVI). The reaction times until the first movement and swimming were longer than those from the fish whose back sides were illuminated.

The average reaction times (sec) for the first movement were 8.2 ± 0.53 (mean ± standard error) in *Eptatretus* and 7.4 ± 0.62 in *Paramyxine*. These reaction times are less than half of that (20.56) of the European hagfish, *Myxine glutinosa* (Newth & Ross, 1955).

Illumination with different light intensities

Two *Eptatretus burgeri* and 2 *Paramyxine atami* were selected for the experiments. Average reaction time was calculated from 6 or 10 observations of each animal. In both species the reaction time became considerably shorter as the intensity of light was increased. At higher intensities *Paramyxine* reacted faster than *Eptatretus,* while at lower ones the latter reacted quicker than *Paramyxine* (Table 2). To an electronic flash of 0.001 sec (guide number 36 at 100 ASA) from a distance of 20 cm, both species reacted immediately.

Table 2

Reaction times (first movement) of *Eptatretus burgeri* (animals E–IX, E–XI) and *Paramyxine atami* (animals P–I, P–VII) in response to general illumination. Number of observations in parenthesis

Light intensity (lux)	4100	980	310	170	92	40
Reaction time (sec) *E. burgeri*	2.8 ± 0.07 (6)	4.1 ± 0.30 (6)	8.1 ± 0.46 (10)	11.5 ± 0.88 (6)	47.3 ± 4.03 (6)	60.7 ± 12.47 (6)
P. atami	3.0 ± 0.13 (6)	4.0 ± 0.51 (6)	7.3 ± 0.96 (10)	9.8 ± 0.83 (6)	23.3 ± 2.53 (6)	36.1 ± 3.81 (6)

Table 3

Reaction times (first movement) of *Eptatretus burgeri* (animals E–III, E–IV, E–IX, E–XI) and *Paramyxine atami* (animals P–I, P–VII, P–XI, P–XV) in response to general illumination after successive periods of 30 min light and varying periods of dark. Number of reactions by eight observations in parenthesis. Light intensity: 310 lux

Dark time (min)	2	5	15	30
Reaction time (sec) *E. burgeri*	97.0 ± 22.0 (2)	67.6 ± 11.25 (5)	32.8 ± 4.74 (8)	17.7 ± 3.06 (8)
P. atami	73.2 ± 16.53 (6)	44.1 ± 8.91 (8)	11.6 ± 2.24 (8)	

Adaptability to darkness

Four animals of both species were treated with light for 30 min (310 lux) and then were subjected to varying periods of darkness. After each dark period, the reaction time to light was measured (Table 3). In *Eptatretus*, approximately normal reaction times for the first movement and for swimming response were obtained only after the specimen had been returned to darkness for at least 30 min. In *Paramyxine*, normal responses were achieved after 15 min. However, in 2 of 8 observations on *Eptatretus* and in 6 of 8 observations on *Paramyxine*, the fish responded to light as early as 2 min after darkness. As can be seen in Table 3, *Paramyxine* recovered considerably faster from the influence of light than *Eptatretus*.

Four *Eptatretus* and four *Paramyxine*, which had been kept under strong light (860 lux) for 14 days and then were subjected to 90 min of darkness, reacted normally to light, showing movement and then swimming in both species.

Sites sensitive to light

As shown in the previous experiments, *Eptatretus burgeri* and *Paramyxine atami* have shorter reaction times to light than *Myxine glutinosa*. The following observations were undertaken to find out (a) whether this is due to a difference in eye structure and/or (b) whether photo-receptors are present in the skin of the two Japanese hagfish as they are in *Myxine* skin (Ross, 1963).

In the first experiment, an opaque tape 6 mm wide was wrapped around the eye region of 2 *Eptatretus*. In these animals, no decrease in the reaction times to over-all illumination (310 lux) was observed. Similar results were obtained when part of the body in the middle region, or cloacal region, was wrapped with tapes of 50 mm or 25 mm width, respectively.

In the next experiment, local illumination was carried out in an aquarium filled with sea water to a height of 3 cm. Small patches from different parts of the body (10 × 10 mm) were illuminated with a microscope lamp (light intensity 980 lux). Altogether 786 measurements from 21 different points on 6 *Eptatretus* and 620 measurements from 19 different points on 5 *Paramyxine* were made. The results can be seen in Figure 1.

In both species, the most light sensitive part was the tip of the tail. The reaction times (first movement) were 4.5 ± 0.53 sec in *Eptatretus* and 4.1 ± 0.45 sec in *Paramyxine*. These values are almost the same as those obtained by over-all illumination at 980 lux in both species (Table 2). The fin itself proved to be much less sensitive then the tip of the tail.

The unpigmented white line on the back of *Eptatretus* was almost as sensitive to light as the tip of the tail. Reaction time, measured near the middle of the body in 6 fish, was 5.1 ± 0.92 sec. In *Paramyxine*, where the white line is absent as also in *Myxine*, the reaction time was 24.3 ± 5.10 sec (5 fish) when the back was illuminated locally.

In one *Eptatretus*, a piece of skin (about 20×30 mm) was removed and the exposed muscles were locally illuminated, but no reaction was observed.

A great difference was found in the reaction time between the two species, when the eye region was locally illuminated. *Eptatretus* required 20.0 ± 2.14 sec (6 animals) to respond, and *Paramyxine* only 9.8 ± 1.75 sec (5 animals), although in the former the skin pigmentation of the eye region is far less than in *Paramyxine* (Fig. 2, see also Discussion).

In one specimen of *Eptatretus* and *Paramyxine*, the skin just beneath the eye patches was cut lengthwise (5 mm) and the eyes were destroyed by means of a Machida Endoscopic High Frequency Coagulation Unit (intensity 8, time 0.5 sec). In control

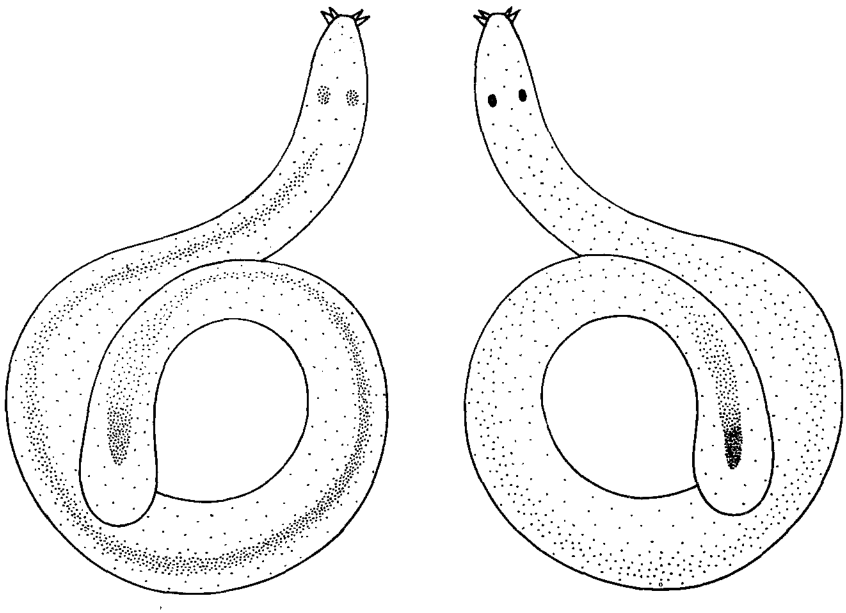

Fig. 1: Relative sensitivity of the body surface to light in *Eptatretus burgeri* and *Paramyxine atami*

animals, one of each species, only the skin was cut. Both blinded animals showed a reaction time similar to that measured upon stimulating the tip of the nose, which was barely sensitive to light. The control animals responded normally.

To investigate the reaction time of the ventral part of the animals, an aquarium with a glass bottom was used. With a light source from below the aquarium, an intensity of 980 lux was measured just over the bottom of the vessel. In *Eptatretus* as well as in *Paramyxine*, the sensitivity of the ventral region was very weak and less than that of the lateral region. Average reaction time was more than 60 sec in both species. Relative sensitivity of the body surface to light is diagrammatically shown in Figure 1.

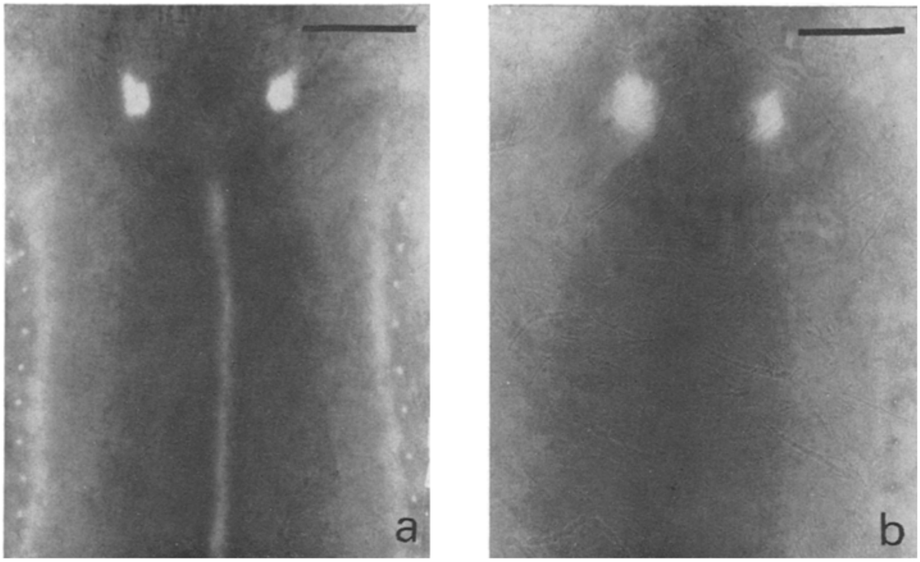

Fig. 2: Skin piece of head and part of back of a) *Eptatretus burgeri* and b) *Paramyxine atami* against white background. Eye patches, pores of slime glands and white line on the back of *Eptatretus*. Scale: 10 mm

Preference for light intensity

The aim of this series of experiments was to find out which light intensity is the one preferred by each of 2 species of hagfish. A tank, 350 cm long, 20 cm wide and 15 cm deep, was filled with sea water. Six animals of each species were separately observed. Continuous illumination was arranged in such a way that the light intensity was 910 lux at one end of the tank decreasing gradually to less than 1 lux at the other end. Observations were made daily between 09 : 00 and 10 : 00, since at this time the animals were quiet. During the night the hagfish were very active even under continuous illumination and continuously swam around in the tank. The light did not disturb their swimming action.

Thirty six observations of each species showed that the resting place of *Paramyxine,* (natural habitat: deeper water) was darker than that of *Eptatretus,* (shallow water). The latter settled in a region with a light intensity below 7 lux, whereas *Paramyxine* rested only where it was below 3 lux (Fig. 3). In this experiment, light intensity was measured from the bottom of a tank while it contained sea water.

Continuous illumination against white background

Only few papers have dealt with colour change of the hagfish. The results are contradictory (see Discussion). Coonfield (1940) and Homberg (1968) reported that

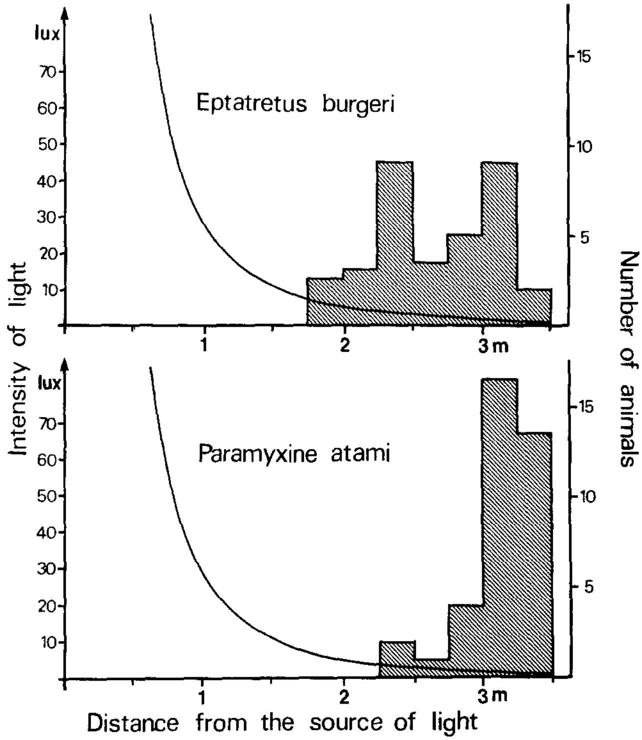

Fig. 3: Preferred light intensity of *Eptatretus burgeri* and *Paramyxine atami*. Curve indicating light intensity measured in lux

Myxine glutinosa kept under permanent illumination against a white background showed a high mortality rate.

In the present study, 4 *Eptatretus burgeri* and 4 *Paramyxine atami* were transferred respectively into an aquarium (40×40×40 cm) with a white background. The sea water measured 30 cm in depth. The water was not aerated but changed every two or three days. Bulbs of 100 W (100 V) were mounted above the aquaria (860 lux at the bottom). In addition, 4 animals of each species were left in a completely dark aquarium with running sea water. During the first week of illumination, *Eptatretus* and *Paramyxine* showed behaviour slightly different from normal. They did not coil up, but stretched out, moving several times during the course of the day. Thereafter, they returned to their habitural behaviour of remaining quiet and coiled up during the day.

Both *Eptatretus* and *Paramyxine* kept under continuous light or darkness for 14 days did not show any change in colour.

Ten *Eptatretus*, in which most of the pituitary gland was destroyed by means of a Machide Endoscopic High Frequency Coagulation Unit (intensity 3, time 3×2 sec), also did not change in colour.

Under water observations

In Koajiro Bay (Misaki, Japan), SCUBA diving was carried out 3 times during the day (11 : 15, 13 : 15 and 17 : 00) and once during the night (21 : 00) to observe the behaviour of *Eptatretus burgeri* at a depth of about 10 m.

During the daytime, all the hagfish remained buried in the mud and only the anterior tips of their heads were visible. One animal's anterior part protuded about 5 cm from the mud.

During the night, many hagfish were seen swimming 10–30 cm above the muddy bottom. One animal remained buried in mud like those observed during the daytime. This animal did not react to illumination by 2 torches (6 V). Another one found resting on the muddy ground responded only slightly to illumination of the torches and moved slowly along the bottom. After swimming 1 m, the animal found a burrow and moved into it. All the free swimming animals responded well to light. When illuminated from a distance of about half a meter, they changed their swimming direction to escape from it.

DISCUSSION AND CONCLUSIONS

Photo-reception

The reaction times of the two Japanese species of hagfish, *Eptatretus burgeri* and *Paramyxine atami* to over-all illumination (310 lux), did not differ significantly from each other, although the former had been caught at the well lighted depth of around 10 m and the latter from the relative darkness of 100 m depth. Local illumination revealed that the most light-sensitive parts in *Eptatretus* was the tip of the tail and the unpigmented line on the back and only the tip of the tail in *Paramyxine* (Fig. 1).

The reaction time to local illumination at the tip of the tail and that to over-all illumination (both 980 lux) were similar in both species. This fact shows that the tail skin functions as a principal light receptor in both species, but in *Eptatretus* the principal receptor area is extended to include the white line.

Fernholm & Holmberg (1975) have compared the structure of the eyes among 3 different genera of hagfish, *Myxine*, *Eptatretus* and *Paramyxine* and have shown that none have lenses or eye-ball muscles. The retina of *Myxine* is the least developed and *Paramyxine* is between *Myxine* and *Eptatretus* in retina development. In *Eptatretus*, the transparency of the skin over the eyes is more than twice as high (68 %) as in *Paramyxine* (33 %). Considering these results, one would expect *Eptatretus* to react faster to illumination than *Paramyxine*. However, the present study showed the opposite; *Paramyxine* reacted considerably faster than *Eptatretus*, when the eye region was locally illuminated. The reason is not yet known.

Comparison with *Myxine glutinosa*

Eptatretus burgeri and *Paramyxine atami* responded twice as rapidly to over-all illumination as the Atlantic *Myxine glutinosa* to over-all illumination of the same intensity. The latter showed a relatively long reaction time of 20.56 sec (Newth & Ross, 1955) as compared to 8.2 ± 0.53 sec in *Eptatretus* and 7.4 ± 0.62 sec in *Paramyxine*. It is assumed that in the hagfish the light sense and especially the function of eyes are at degenerating stages. The light sense of *Myxine*, living in deep water of the Atlantic, has atrophied much more than that of the two Pacific hagfishes, which live in a depth penetrated by daylight.

Local illumination in *Myxine* showed that the sites most sensitive to light were the skin of the anterior region of the cloaca and the skin of the head but not the tip of the tail (Newth & Ross, 1955). Corresponding findings differ in *Eptatretus* and *Paramyxine*.

Some authors (Coonfield, 1940; Nicol, 1967) indicated that *Myxine* becomes darker against a dark background and paler against a light background after a few days. However, in *Eptatretus* and *Paramyxine*, no difference in the colour of the skin was observed between the hagfish kept in darkness and those in light. Holmberg (1968) made the same observation in *Myxine*. Foss (1968) stated that *Myxine* from different biotopes often differ in coloration. In my own observations (unpublished) *Eptatretus* as well as *Paramyxine* showed slight varieties in colour, although they derived from the same biotope.

It was reported that Myxine died within a few days when kept in a white aquarium with continuous illumination (Coonfield, 1940; Holmberg, 1968, 1971). Fernholm & Holmberg (1975) attributed this, in *Myxine*, to the loss of protective pigmentation of the skin. Unlike *Myxine*, *Eptatretus* and *Paramyxine* have well-pigmented skin and thus they are resistant to bright illumination.

Although there have been reports that extracts from *Myxine* pituitary glands have some melanotropic activity in toads (Adam, 1963) and crabs (Carlisle & Olsson, 1965), no colour change was found after almost complete hypophysectomy in *Eptatretus*, as found already in *Myxine* by Matty & Falkmer (1965).

Ecological aspects

The response to illumination in *Eptatretus* and *Paramyxine* seems to be an avoidance reaction. This idea is supported by Fernholm's (1974) findings, that shallow-water *Eptatretus* individuals swim only at night and stay buried in the mud during daytime. This behaviour is confirmed by my own observations.

Myxine usually lives in dark regions of around 100 m depth (Thambs-Lyche, 1969) and thus their light sense has degenerated. They are active in the daytime as well as in the night, and can be caught during day and night (Gustafson, 1935; Foss, 1968; author's observation in Norway, 1972). In this respect *Myxine* differs markedly from the two Japanese species. Both, *Eptatretus* and *Paramyxine*, live in depths, of prevalent daylight and therefore hide in the mud during the day. Thus, they can be caught only at night (Kobayashi et al., 1972; Fernholm, 1974).

Acknowledgements. Is wish to thank Mrs. A.-M. Patzner for her excellent technical assistance, Prof. H. Kobayashi for his advice and for reading the manuscript, and the staff of the Misaki Marine Biological Station of the University of Tokyo. I am grateful to the "Japan Society for the Promotion of Science" for a fellowship which enabled me to stay for one year at the M.M.B.S., and the "Ford Foundation" for a grant to Prof. H. Kobayashi. Thanks are also due to "Baracuda Co." (Hamburg, FRG) for providing a diving-suit. This study was supported by the Austrian "Fonds zur Förderung der wissenschaftlichen Forschung" (grant no. 3204).

LITERATURE CITED

Adam, H., 1963. The pituitary gland. In: The biology of *Myxine*. Ed. by A. Brodal & R. Fänge. Universitetsforlaget, Oslo, 459–476.

Carlisle, D. B. & Olsson, R., 1965. An effect of extracts of the pituitary gland of fish and cyclostomes and of the neural complex of ascidians on the melanophores of crabs. Gen. comp. Endocrinol. **5**, 662.

Coonfield, B. R., 1940. The pigment in the skin of *Myxine glutinosa* Linn. Trans. Am. microsc. Soc. **59**, 398–403.

Fernholm, B., 1974. Diurnal variations in the behaviour of the hagfish *Eptatretus burgeri*. Mar. Biol. **27**, 351–356.

— & Holmberg, K., 1975. The eyes in three genera of hagfish *(Eptatretus, Paramyxine* and *Myxine)* – a case of degenerative evolution. Vision Res. **15**, 253–259.

Foss, G., 1968. Behaviour of *Myxine glutinosa* L. in natural habitat. Investigation of the mud biotope by a suction technique. Sarsia **31**, 1–13.

Gustafson, G., 1935. On the biology of *Myxine glutinosa* L. Ark. Zool. **28A**, 1–8.

Holmberg, K., 1968. Ultrastructure and respond to background illumination of the melanophores of the Atlantic hagfish, *Myxine glutinosa*, L. Gen. comp. Endocrinol. **10**, 421–428.

— 1971. On the light sensitivity of the Atlantic hagfish, *Myxine glutinosa*, maintained against a white background under continuous illumination. Gen. comp. Endocrinol. **17**, 232–239.

Kobayashi, H., Ichikawa, T., Suzuki, H. & Sekimoto, M., 1972. Seasonal migration of the hagfish, *Eptatretus burgeri*. Jap. J. Ichthyol. **19**, 191–194.

Matty, A. J. & Falkmer, S., 1965. Hypophysectomy and blood sugar regulation in a cyclostome, *Myxine glutinosa*. Nature, Lond. **185**, 533–534.

Newth, D. R. & Ross, D. M., 1955. On the reaction to light of *Myxine glutinosa* L. J. exp. Biol. **32**, 4–21.

Nicol, J. A. C., 1967. Biology of marine animals, Pitman. London, 699 pp.

Ross, D. M., 1963. The sense organs of *Myxine glutinosa* L. In: The biology of *Myxine*. Ed. by A. Brodal & R. Fänge. Universitetsforlaget, Oslo, 150–160.

Steven, D. M., 1955. Experiments on the light sense of the hag, *Myxine glutinosa* L. J. exp. Biol. **32**, 22–38.

Strahan, R. & Honma, Y., 1960. Notes on *Paramyxine atami* Dean (Fam. Myxinidae) and its fishery in Sado Strait, Sea of Japan. Hong Kong Univ. Fish. J. **3**, 27–35.

Thambs-Lyche, H., 1969. Notes on the distribution and ecology of *Myxine glutinosa* L. FiskDir. Skr. (Havunders.) **15**, 279–284.