

Studies on the Visual Accommodation in Fishes

Hiroaki Somiya and Tamotsu Tamura

(Received July 2, 1973)

Abstract Visual accommodation of 39 teleosts and 4 elasmobranchs were examined by means of the electrical stimulation of the excised eye. Photographs of the eyes were taken before and during the stimulation. From these photographs, the range of accommodation was estimated and compared among the fishes. In most of marine and some of freshwater teleosts, the accommodation was accomplished by the displacement of the lens position. It was found that these teleosts had the range of accommodation from the distance less than the standard length before their eyes to infinity.

Any lens movement due to the electrical stimulation was not observed in all species of elasmobranchs and 4 species of teleosts. Deformation of the eye globe was not observed in any fish species experimented.

Introduction

The study of visual accommodation is composed of two steps. The first is to determine the state of refraction at resting. The second is to elucidate the mechanism of accommodation.

In the retinoscopic investigation, Beer (1894) showed that fish eyes were in the state of myopia when they were in resting state. On the other hand, Verrier (1948), Baron and Verrier (1951) reported that fish eyes were hypermetropic when they were investigated by the ophthalmoscope. Baylor and Show (1962) also reported that the eyes of the open water fishes were hypermetropic. However, the different view has been presented by the recent investigations. Tamura (1957; 1970), Pumphrey (1961), and Baylor (1967) stated that the fish eye is emmetropic or somewhat hypermetropic. Meyer and Schwassmann (1970) have supported this conclusion in their electrophysiological study.

In the classical study on the visual accommodation of fishes, Beer (1894) showed that the accommodation of teleosts was accomplished by the backward movement of the lens. Namely, it was demonstrated that the lens movement occurred by contraction of the lens muscle (campanula Halleri) on electrical stimulation. This conclusion has been confirmed by the works of Meader (1936), Tamura and Wisby (1963), and Kimura and Tamura (1966). However, in some fishes of the Cyprinidae the presence of muscle fiber in the campanula

Halleri was denied by Bourguignon and Verrier (1930) and it was suggested that the accommodation in these fishes is not accomplished by lens movement, but by increasing the anterior-posterior diameter of the eyeball through the deformation of the ocular globe. It is inferred that the species difference may be participated in the conflicting opinions on the mechanism of accommodation. Hence, the comparative study involving various fish species will be necessary to explain the discrepancy.

In the present study, the lens movement on electrical stimulation was investigated in various fish species and the range of visual accommodation was estimated, in order to have an insight on the mechanism of accommodation in fishes. The morphology of the lens muscle was also investigated.

Material and methods

As experimental material, 39 species of teleosts and 4 species of elasmobranchs were used (Table 1). The method employed in this experiment is essentially the same as reported by Kimura and Tamura (1966).

The enucleated eye was placed on the bottom of the vessel containing freshwater. Alternating current (60 c/s) generated in the circuit shown in Fig. 1 was used as the electrical stimulation. The range of voltage used for the stimulation was usually 5 to 10 volts.

Soon after the eye was excised out of a living fish, a photograph was made to record the

Table 1. The species used in the present study

Order	Family	Species	Japanese name
Elasmobranchii			
Lamniformes	Heterodontidae	<i>Heterodontus japonicus</i>	Nekozame
	Carcharhinidae	<i>Carcharhinus longimanus</i>	Yogore
Rajiformes	Dasyatidae	<i>Dasyatis akabei</i>	Akaei
		<i>Urolophus aurantiacus</i>	Hirataei
Teleostei			
Clupeiformes	Salmonidae	<i>Salmo gairdnerii</i>	Nijimasu
	Plecoglossidae	<i>Plecoglossus altivelis</i>	Ayu
Cypriniformes	Cyprinidae	<i>Carassius auratus</i>	Funa
		<i>Cyprinus carpio</i>	Koi
	Siluridae	<i>Parasilurus asotus</i>	Namazu
	Bagridae	<i>Pelteobagrus nudiceps</i>	Gigi
Anguilliformes	Anguillidae	<i>Anguilla japonica</i>	Unagi
Mugiliformes	Mugilidae	<i>Mugil cephalus</i>	Bora
Channiformes	Channidae	<i>Channa argus</i>	Kamuruchii
Perciformes	Oplegnathidae	<i>Oplegnathus fasciatus</i>	Ishidai
	Centrarchidae	<i>Micropterus salmoides</i>	Black bass
		<i>Lepomis macrochirus</i>	Bluegill
	Serranidae	<i>Lateolabrax japonicus</i>	Suzuki
		<i>Epinephelus akaara</i>	Kijihata
		<i>Epinephelus septemfasciatus</i>	Mahata
		<i>Epinephelus fasciatus</i>	Akahata
	Girellidae	<i>Girella punctata</i>	Mejina
	Sparidae	<i>Acanthopagrus schlegelii</i>	Kurodai
		<i>Chrysophrys major</i>	Madai
	Pomadasyidae	<i>Parapristipoma trilineatum</i>	Isaki
	Aplodactylidae	<i>Goniistius zonatus</i>	Takanohadai
		<i>Goniistius zebra</i>	Migimaki
	Coryphaenidae	<i>Coryphaena hippurus</i>	Shiira
	Parapercidae	<i>Neopercis multifasciata</i>	Okitoragisu
	Cichlidae	<i>Tilapia mossambica</i>	Kawasuzume
	Labridae	<i>Pseudolabrus japonicus</i>	Sasanohabera
		<i>Halichoeres poecilopterus</i>	Kyusen
	Scorpididae	<i>Microcanthus strigatus</i>	Kagokakidai
	Acanthuridae	<i>Prionurus microlepidotus</i>	Nizadai
Tetraodontiformes	Aluteridae	<i>Stephanolepis cirrhifer</i>	Kawahagi
		<i>Navodon modestus</i>	Umazura
	Tetraodontidae	<i>Fugu rubripes chinensis</i>	Karasu
		<i>Fugu vermicularis vermicularis</i>	Shousaifugu
		<i>Fugu pardalis</i>	Higanfugu
Cottiformes	Scorpaenidae	<i>Sebastes inermis</i>	Mebaru
		<i>Sebastes marmoratus</i>	Kasago
	Synanceiidae	<i>Inimicus japonicus</i>	Oniokoze
	Hexagrammidae	<i>Agrammus agrammus</i>	Kujime
Pleuronectiformes	Pleuronectidae	<i>Limanda yokohamae</i>	Makogarei

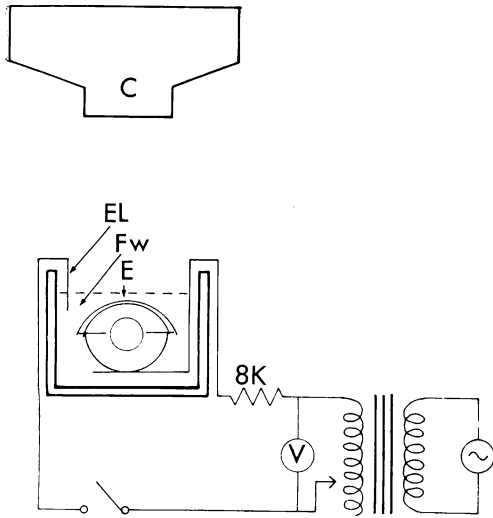


Fig. 1. Schematic representation of the equipment for recording the lens movement in the excised eye.
C: recording camera (Medical-Nikkor, Nikon), E: eye, EL: electrode, FW: freshwater, V: voltmeter, 8K: resistance of 8 K Ω .

foremost position of the lens using Medical-Nikkor (Nikon). Then, another picture was taken during the stimulation. The direction and distance of the lens movement were determined by superimposing the two pictures.

To calculate the near point distance of each sample the following formula was used, assuming that the eye is in the state of emmetropia when the lens is in its backward position.

$$1/F = 1/(F+d) + 1/NP, \quad NP = F(F+d)/d$$

where, F =focal distance of lens, which is 2.55 times (Matthiessen's ratio) of the lens radius, d =distance of the lens movement measured photographically, NP =near point distance.

To investigate the morphology of the lens muscle, the enucleated eyes were fixed in Bouin's fluid and preserved in 70% alcohol. Then, the lens muscle (campanula Halleri) was observed under a stereoscopic-microscope. Histological observation was also carried out in some species.

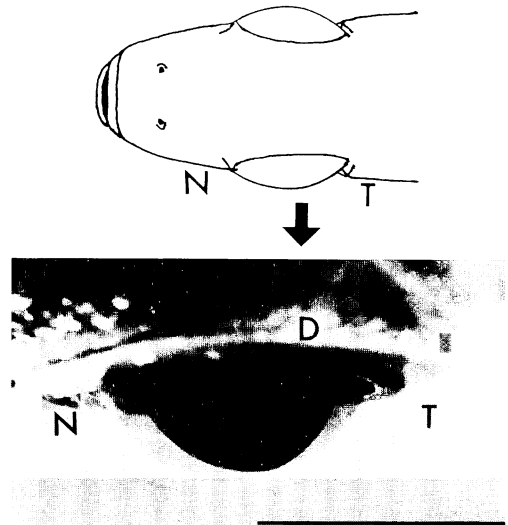


Fig. 2. Dorsal view of the eye of *Lepomis macrochirus* (SL: 15 cm left eye). Lens moves almost parallel to the body axis. The bar corresponds to 5 mm.

Table 2. Classification of the 43 fish species by lens movement on electrical stimulation.

Group A. 31 species: Lens movement was observed and recorded clearly

- 1 *Channa argus*, 2 *Oplegnathus fasciatus*, 3 *Micropterus salmoides* 4 *Lepomis macrochirus*, 5 *Lateolabrax japonicus*, 6 *Epinephelus akaara*, 7 *E. septemfasciatus*, 8 *E. fasciatus*, 9 *Girella punctata*, 10 *Acanthopagrus schlegelii*, 11 *Chrysophrys major*, 12 *Parapristipoma trilineatum*, 13 *Goniistius zonatus*, 14 *G. zebra*, 15 *Coryphaena hippurus*, 16 *Neoperca multifasciatus*, 17 *Tilapia mossambica*, 18 *Pseudolabrus japonicus*, 19 *Halichoeres poecilopterus*, 20 *Microcanthus strigatus*, 21 *Prionurus microlepidotus*, 22 *Stephanolepis cirrhifer*, 23 *Navodon modestus*, 24 *Fugu rubripes chinensis*, 25 *Fugu vermicularis vermicularis*, 26 *Fugu pardalis*, 27 *Sebastes inermis*, 28 *Sebasticus marmoratus*, 29 *Inimicus japonicus*, 30 *Agrammus agrammus*, 31 *Limanda yokohamae*.

Group B. 4 species: Lens movement was too little to be recorded

- 1 *Salmo gairdnerii*, 2 *Plecoglossus altivelis*, 3 *Carassius auratus*, 4 *Cyprinus carpio*.

Group C. 8 species (4 elasmobranchs and 4 teleosts): No lens movement observed.

- 1 *Heterodontus japonicus*, 2 *Carcharhinus longimanus*, 3 *Dasyatis akajei*, 4 *Urolophus aurantiacus*, 1 *Parasilurus asotus*, 2 *Pelteobagrus nudiceps*, 3 *Anguilla japonica*, 4 *Mugil cephalus*.

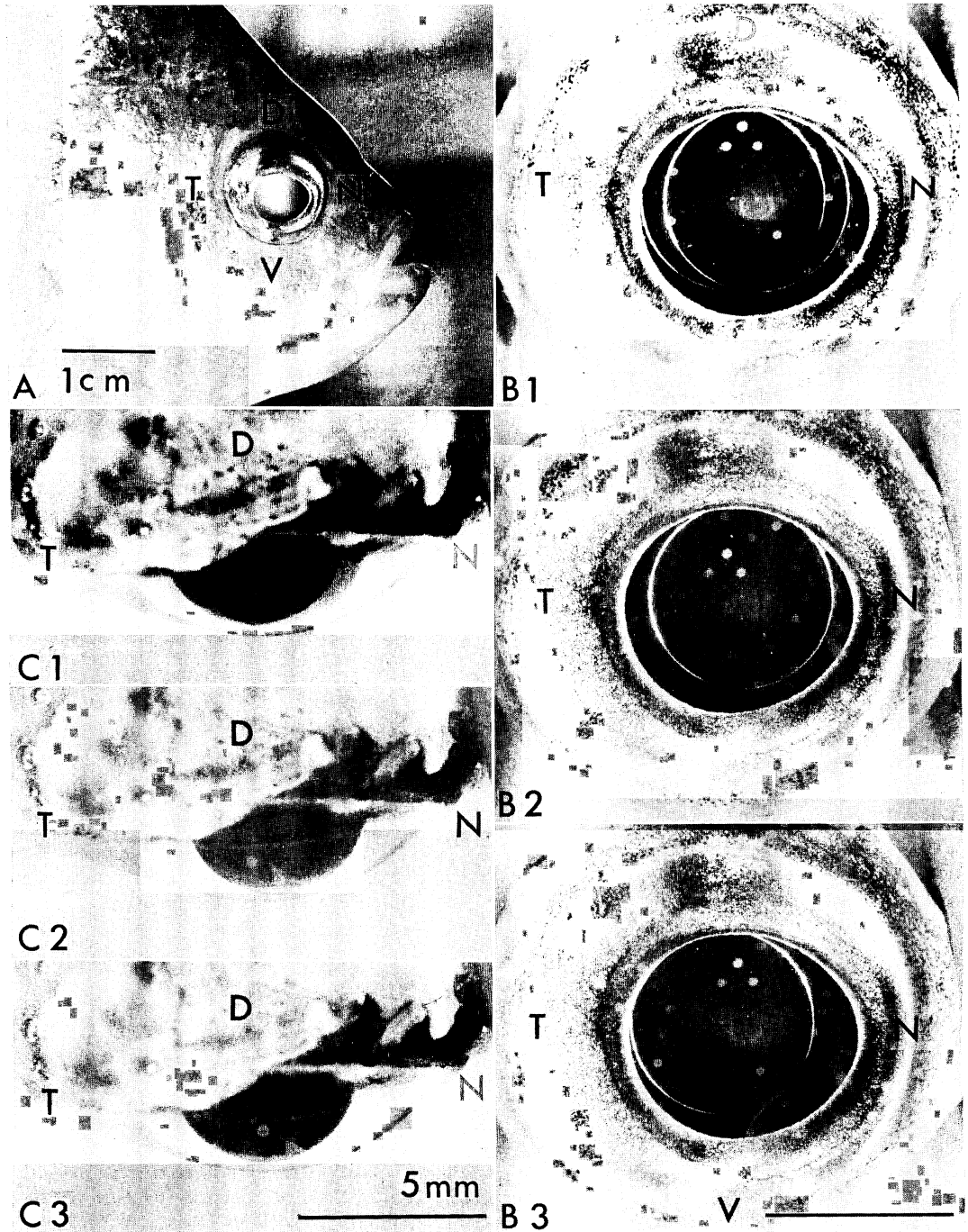


Fig. 3. Lens movement of the eyes of *Lepomis macrochirus*. A: Photographs of the head of a specimen, standard body length 15 cm. B: Lateral view of the left eye. Distance and direction of the lens movement was determined in the picture B 1, which was made by superimposing two pictures taken before (B 2) and during (B 3) the electrical stimulation. C: Dorsal view of the same eye. Three pictures C 1, C 2, and C 3 correspond to B 1, B 2, and B 3 respectively. D: dorsal, N: nasal, T: temporal, and V: ventral.

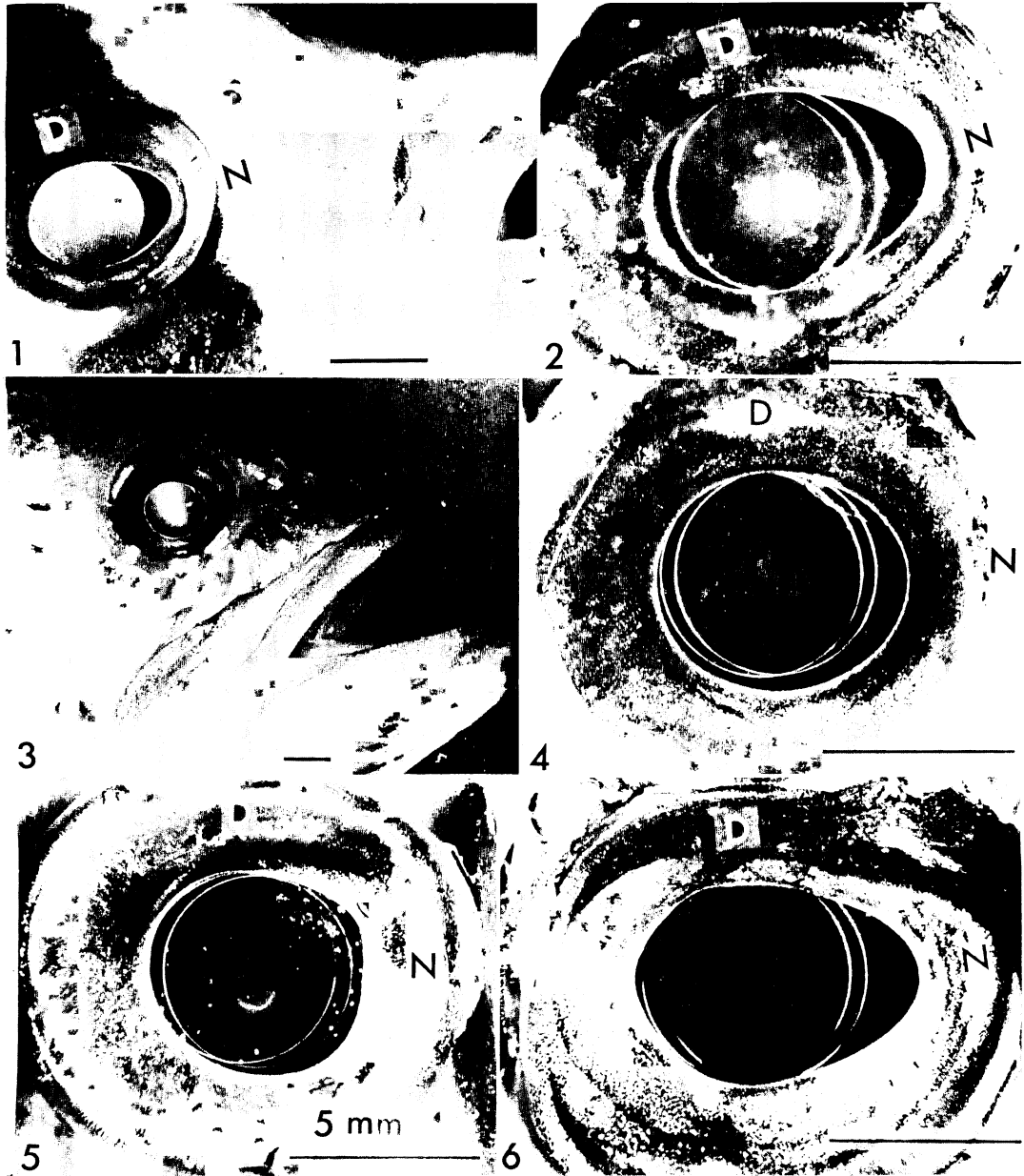


Fig. 4. Photographs showing the distance and direction of lens movement. The bar in each photograph corresponds to 5 mm. D: dorsal, N: nasal. 1, 2: *Oplegnathus fasciatus* SL: 15.0 cm, right eye. visual axis: fore. 3, 4: *Micropterus salmoides* SL: 26.0 cm, right eye. visual axis: upper fore. 5: *Acanthopagrus schlegelii* SL: 13.5 cm, right eye. visual axis: lower fore. 6: *Navodon modestus* SL: 19.0 cm, right eye. visual axis: fore.

Results

1) Lens movement on the electrical stimulation

Fortythree species used in this study were

divided into three groups according to the lens movement on electrical stimulation: **Group A**, those which showed distinct lens movement; **Group B**, those which showed little lens

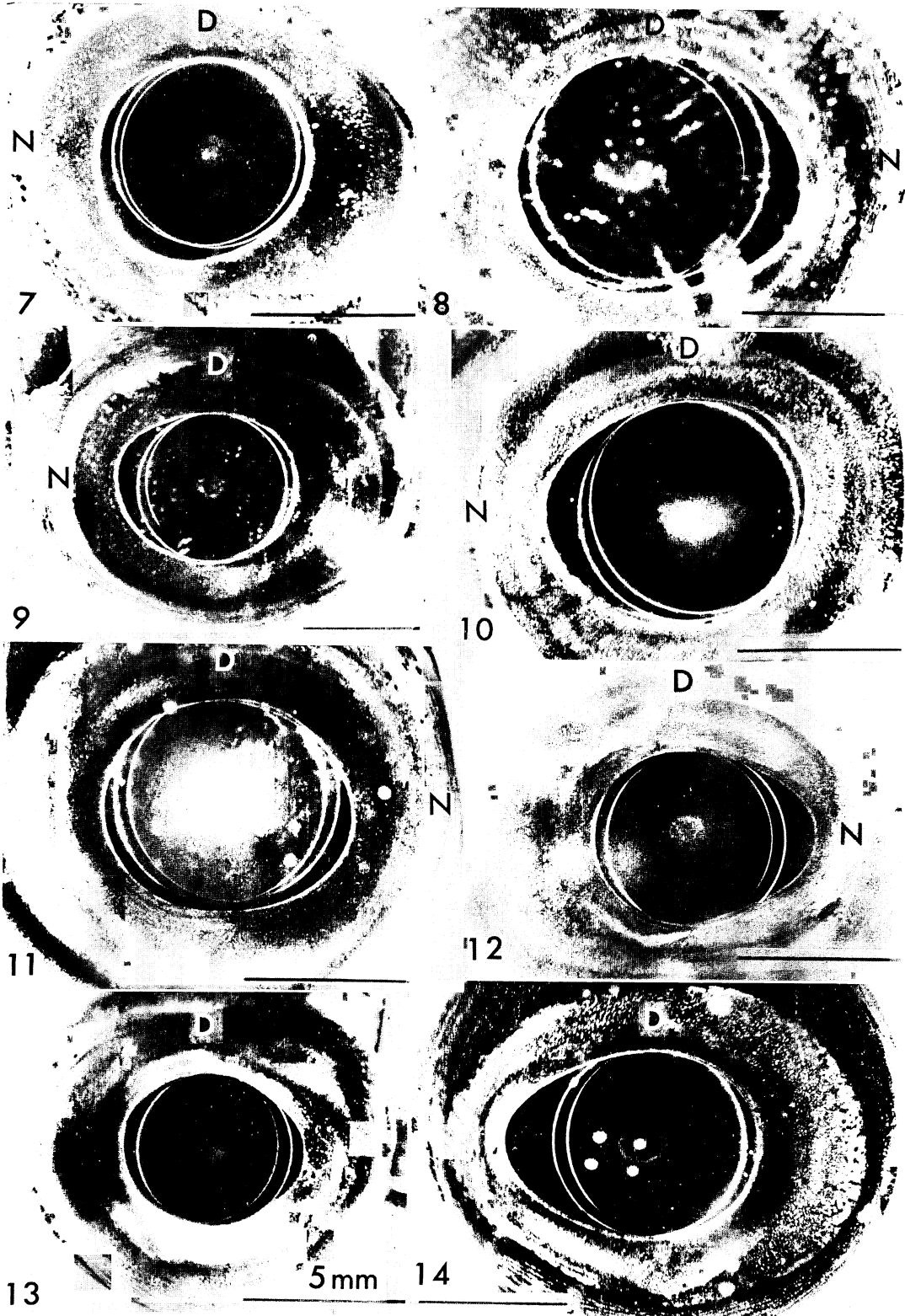


Fig. 4. Continued.

movement; and Group C, those which showed no lens movement. Classification of 43 species by the above criterion is presented in Table 2. Brief descriptions of each group are given in the followings.

Group A: All of the marine teleosts used in this experiment (28 species) and some fresh-water fishes such as *Micropterus salmoides*, *Lepomis macrochirus*, and *Channa argus* were classified as belonging to this group.

Group B: Freshwater fishes such as *Salmo gairdnerii*, *Plecoglossus altivelis*, *Carassius auratus*, and *Cyprinus carpio* were classified as belonging to this group.

Group C: This group consists of 4 species of elasmobranchs and 4 species of teleosts with comparatively small eyes such as *Parasilurus asotus*, *Pelteobagrus nudiceps*, *Anguilla japonica*, and *Mugil cephalus*.

2) Direction of lens movement

Direction of lens movement was determined from the superimposed photographs. Lateral and dorsal views are presented in Figs. 2, 3, and 4. Pictures showing dorsal views revealed that the lens moves from nasal to temporal direction in all species belonging to Group A (Figs. 2 and 3) and two species belonging to Group B, *Salmo gairdnerii* and *Plecoglossus altivelis*. However, in *Carassius auratus* and *Cyprinus carpio*, which were classified as belonging to Group B, inward lens movement was observed, i. e. the lens moved toward the bottom of the eye cup.

From pictures showing the lateral view, following results were obtained in the species belonging to Group A.

The lens moved from nasal to temporal position in the 12 species: *Oplegnathus fasciatus* (Fig. 4-1; 4-2), *Lepomis macrochirus* (Fig. 3), *Lateolabrax japonicus* (Fig. 4-14), *Epinephelus akaara*, *E. septemfasciatus*, *E. fasciatus* (Fig. 4-12), *Microcanthus strigatus* (Fig. 4-13), *Stephanolepis cirrifer*, *Navodon modestus* (Fig. 4-6),

Fugu vermicularis vermicularis, *Sebastes inermis* (Fig. 4-11), and *Sebastes marmoratus*.

The lens moved from the nasodorsal to ventrotemporal in 3 species: *Micropterus salmoides* (Fig. 4-3; 4-4), *Parapristipoma trilineatum* (Fig. 4-8) and *Tilapia mossambica* (Fig. 4-7).

The lens moved from the nasoventral to dorsotemporal in 4 species, *Acanthopagrus schlegelii* (Fig. 4-5), *Chrysophrys major*, *Goniistius zonatus* (Fig. 4-10), and *G. zebra* (Fig. 4-9).

The visual axis, the direction of the most acute vision, can be deduced from the direction of lens movement. The visual axis is directed to the opposite to lens movement. Therefore, the visual axis is directed forward in the fishes with lens movement from the nasal to temporal, upperforward in those with lens movement from the nasodorsal to ventrotemporal, and lower forward in those with lens movement from the nasoventral to dorsotemporal (see explanation of Fig. 4).

3) The lens muscle

A well-developed triangular lens muscle was observed in all species belonging to Group A. The lens muscle of *Micropterus salmoides* is shown in Fig. 5-A.

Among 4 species belonging to Group B, *Salmo gairdnerii* and *Plecoglossus altivelis* had a triangular lens muscle (Fig. 5-B), though it is not well-developed as compared with that possessed by the fishes belonging to Group A. In *Carassius auratus* and *Cyprinus carpio*, in which inward lens movement was observed, the shape of the lens muscle was somewhat rod-like (Fig. 5-C) and its relative position to the lens is apparently unsuitable to move the lens from the nasal to temporal.

The lens muscle of *Mugil cephalus* was very small and appeared to have lost its function (Fig. 5-D). *Parasilurus asotus*, *Pelteobagrus nudiceps* and *Anguilla japonica* had the thread-

Fig. 4. (continued) Photographs showing the distance and direction of lens movement. 7: *Tilapia mossambica* SL: 14.0 cm, left eye. visual axis: upper fore. 8: *Parapristipoma trilineatum* SL: 22.5 cm, right eye. visual axis: upper fore. 9: *Goniistius zebra* SL: 24.0 cm, left eye. visual axis: lower fore. 10: *G. zonatus* SL: 17.5 cm, left eye. visual axis: lower fore. 11: *Sebastes inermis* SL: 14.5 cm, right eye. visual axis: fore. 12: *Epinephelus fasciatus* SL: 17.5 cm, right eye. visual axis: fore. 13: *Microcanthus strigatus* SL: 9.5 cm right eye. visual axis: fore. 14: *Lateolabrax japonicus* SL: 21.0 cm, left eye. visual axis: fore.

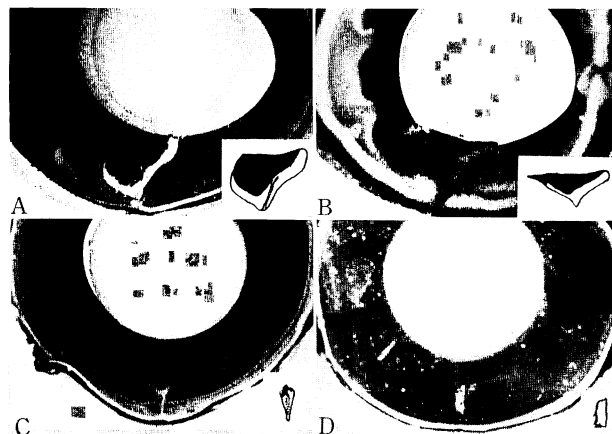


Fig. 5. Comparison of the lens muscle (campanula Halleri). Lenses are enlarged in the same size in order to compare the size of the lens muscle. A: large triangular lens muscle of *Micropterus salmoides* (lens diameter: 5 mm). B: somewhat smaller and triangular lens muscle of *Plecoglossus altivelis* (lens diameter: 2.5 mm). C: rod like lens muscle of *Carassius auratus* (lens diameter: 5 mm). D: rod like lens muscle of *Mugil cephalus* (lens diameter: 6.5 mm).

like lens muscle, but it seemed to be too feeble to move the lens.

In 4 species of elasmobranchs, only *Heterodontus japonicus* was found to have a pseudo-campanule, which has not clearly been determined to be homologous with the campanula Halleri of teleosts. By the histological examination this pseudo-campanule was revealed to have hardly any muscle fibers. Other three species had no such pseudo-campanule.

4) Distance of lens movement and near point distance

It was impossible to measure the distance of lens movement in the species belonging to the Groups B and C. The measurements were carried out in 22 species belonging to the Group A. In the remaining 9 species belonging to Group A, the measurement was difficult for other reasons: disturbance by the iris, scarcity of samples, etc.

The lens movement was quantitatively analyzed with the data of *Parapristipoma trilineatum*, from which the largest number of samples were taken of all species used in this study. Eleven individuals were used, and lens movement in the both eyes of 7 individuals were successfully measured. In the remaining

4 individuals, only one eye in each fish could be used for the measurement because of the deterioration of the other eye. The relationship of the lens diameter to the distance of lens movement is shown in Fig. 6. It is found that there is a certain tendency: the larger the diameter of lens, the longer the distance of lens movement. Since the size of lens is taken into

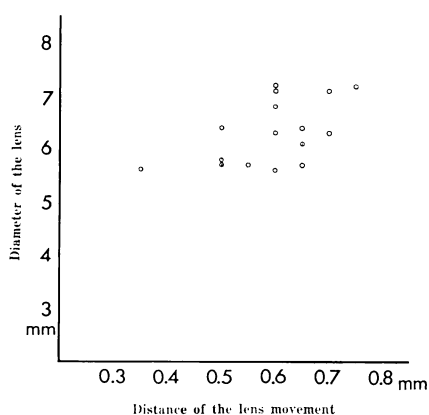


Fig. 6. The relationship between the diameter of the lens and the distance of lens movement in *Parapristipoma trilineatum*. The greater the diameter of the lens, the larger the distance of the lens movement.

Table 3. Lens movement and accommodation of *Parapristipoma trilineatum*.

Standard length (cm) SL	Diameter of lens (mm)	Focal distance of lens (mm)	Distance of lens movement (mm)	Near point distance (cm) NP	NP / SL
14.5	R 5.7	7.26	0.50	11.2	0.77
	L 5.7	7.26	0.50	11.2	0.77
16.5	R 5.6	7.14	0.60	9.2	0.55
	L 5.6	7.14	0.35	15.2	0.92
17	R 5.8	7.39	0.50	11.6	0.68
17	R 5.7	7.26	0.55	10.3	0.60
17.5	R 6.1	7.77	0.65	14.0	0.80
	L 6.1	7.77	0.65	14.0	0.80
18.5	L 5.7	7.26	0.65	8.8	0.47
19	R 6.4	8.16	0.50	14.1	0.74
	L 6.4	8.16	0.65	11.0	0.58
20	R 6.8	8.67	0.60	13.3	0.66
21	R 6.3	8.03	0.60	11.5	0.54
	L 6.3	8.03	0.70	10.0	0.47
21	R 7.1	9.05	0.70	12.6	0.60
	L 7.1	9.05	0.60	14.5	0.69
22.5	R 7.2	9.18	0.75	12.1	0.54
	L 7.2	9.18	0.60	14.9	0.66

R: right eye L: left eye

consideration in the formula to calculate the near point distance (see "Material and methods"), the longer distance of lens movement does not always mean shorter distance to the near point.

The near point distance was calculated with the above mentioned formula in 18 samples (Table 3). Seven individuals showed almost the same values in both eyes, excepting a specimen which was 16.5 cm in the standard length. In order to compare the range of accommodation among fishes of different sizes, the ratio NP/SL (NP: near point distance, SL: standard length) was used as an indicator, since it is inferred that the near point distance is shorter in smaller fishes than in larger ones. The values of NP/SL fall between 0.47 and 0.80 with only one exception. From these results, it was found that *P. trilineatum* had the accommodation range from about 1/2 SL before the eyes to infinity.

The relationship between the lens diameter and the distance of lens movement in various species showed the same tendency as in *P. trilineatum*. Diameter of lens, distance of lens movement, focal length and near point distance of 21 fish species are shown in Table 4.

For comparison of the range of accommodation, the ratios of NP to SL (NP/SL) in 22 species are shown in Fig. 7. The ratios (NP/

SL) in 6 species calculated from the data of Tamura and Wisby (1963) are also shown. The ratios are smaller than 1.0. This means that these fishes have the range of accommodation from the distance less than standard length before the eyes to infinity. It is understood that *Agrammus agrammus* and *Lepomis macrochirus* have the widest range of accommodation among the species used in this study. However, it must be kept in mind that the visibility is limited by the characters of water, transparency, brightness, and so on.

Discussion

1) Mechanism of accommodation in teleosts

As already mentioned, the controversy exists in the theories explaining the mechanism of the accommodation in fish eyes. Beer (1894) stated that the visual accommodation was accomplished by lens movement, whereas, Bourguignon and Verrier (1930), Verrier (1948), and Baron and Verrier (1951) insisted that it was accomplished by deformation of the eye globe. This controversy has been reviewed by some workers (Brett 1957; Duke-Elder 1958; Kawamoto 1966). The discrepancy seems to have come from the difference in the material, i. e. fish species. Beer (1894) used many marine fishes, whereas, Bourguignon and Verrier (1930),

Table 4. Lens movement and accommodation in 21 species of teleosts.

Species	Standard length SL (cm)	Diameter of lens (mm)	Focal distance of lens F (cm)	Distance of lens movement D (mm)	Near point distance NP (cm)	NP / SL
<i>Oplegnathus fasciatus</i>	14.5	5.00	6.37	0.55	8.0	0.55
	15.0	5.40	6.88	0.60	8.5	0.57
<i>Micropterus salmoides</i>	27.0	5.70	7.26	0.30	18.3	0.67
	25.0	5.20	6.63	0.20	22.6	0.90
	26.0	5.20	6.63	0.40	11.6	0.44
	26.0	5.20	6.63	0.46	10.2	0.39
	27.0	5.70	7.26	0.30	18.3	0.67
	27.0	5.70	7.26	0.50	11.2	0.41
<i>Lepomis macrochirus</i>	15.0	4.80	6.12	0.65	6.3	0.42
	15.0	4.80	6.12	0.75	5.6	0.37
	16.0	4.80	6.12	0.55	7.4	0.46
<i>Lateolabrax japonicus</i>	29.0	8.00	10.20	0.70	15.8	0.54
	29.0	8.00	10.20	0.45	24.1	0.83
	28.0	7.80	9.94	0.45	22.9	0.82
	28.0	7.80	9.94	0.58	18.0	0.64
	21.0	5.80	7.40	0.45	12.8	0.61
	21.0	5.80	7.40	0.35	16.3	0.77
<i>Epinephelus akaara</i>	28.0	7.10	9.05	0.65	13.5	0.48
	31.0	7.60	9.69	0.50	19.7	0.63
	24.0	6.30	8.03	0.50	13.7	0.57
	24.0	6.30	8.03	0.35	19.2	0.80
<i>E. septemfasciatus</i>	18.5	5.90	7.52	0.45	13.3	0.72
	18.5	5.90	7.52	0.40	14.8	0.80
	27.5	7.60	9.69	0.52	19.0	0.69
	19.0	6.20	7.90	0.40	16.4	0.86
<i>E. fasciatus</i>	17.5	5.40	6.88	0.55	9.3	0.53
	17.5	5.40	6.88	0.40	12.5	0.71
<i>Acanthopagrus schlegelii</i>	17.5	5.70	7.26	0.50	11.2	0.64
	13.5	5.00	6.37	0.45	9.6	0.71
<i>Chrysophrys major</i>	12.5	6.10	7.77	0.45	14.2	1.13
	17.0	6.85	8.73	0.45	17.8	1.04
	15.0	6.75	8.60	0.45	17.3	1.15
	23.0	7.00	8.93	0.40	20.8	0.90
<i>Goniistius zonatus</i>	17.5	6.60	8.41	0.35	21.0	1.20
	17.5	6.60	8.41	0.45	16.5	0.94
	17.0	4.80	6.12	0.25	15.5	0.91
	17.0	4.80	6.12	0.20	19.3	1.13
<i>G. zebra</i>	24.0	6.10	7.77	0.40	15.9	0.66
<i>Coryphaena hippurus</i>	45.0	5.40	5.80	0.20	17.8	0.39
<i>Tilapia mossambica</i>	14.0	3.90	4.97	0.20	12.8	0.91
	15.0	4.20	5.35	0.20	14.8	0.98
	13.0	3.85	4.90	0.20	12.5	0.96
	15.0	4.10	5.22	0.20	14.1	0.94
	15.0	4.20	5.35	0.25	12.0	0.80
	9.5	4.15	5.29	0.44	6.8	0.72
<i>Microcanthus strigatus</i>	13.0	5.70	7.26	0.50	11.3	0.86
	13.0	5.70	7.26	0.50	11.3	0.86
	11.0	4.70	5.99	0.55	7.1	0.64
	11.0	4.70	5.99	0.55	7.1	0.64

Table 4. Continued.

Species	Standard length SL (cm)	Diameter of lens (mm)	Focal distance of lens F (cm)	Distance of lens movement D (mm)	Near point distance NP (cm)	NP / SL
<i>Prionurus microlepidotus</i>	18.0	5.30	6.76	0.30	15.8	0.88
	18.5	5.45	6.95	0.30	16.7	0.90
<i>Stephanolepis cirrhifer</i>	17.0	5.50	7.01	0.25	20.3	1.10
	17.0	5.50	7.01	0.45	11.6	0.68
<i>Navodon modestus</i>	18.5	5.10	6.50	0.20	21.7	1.17
	18.0	5.00	6.37	0.35	12.2	0.67
	19.0	5.35	6.82	0.45	11.0	0.57
	19.0	5.35	6.82	0.50	9.9	0.52
	16.0	4.15	5.29	0.15	19.1	1.19
<i>Fugu vermicularis</i> <i>vermicularis</i>	13.0	4.15	5.29	0.30	9.8	0.75
	14.0	5.00	6.37	0.30	14.1	1.00
	14.0	5.00	6.37	0.20	20.9	1.48
	14.5	5.00	6.37	0.20	20.9	1.37
	14.5	5.00	6.37	0.40	10.7	0.74
<i>Sebastes inermis</i>	14.5	5.00	6.37	0.40	10.7	0.74
	13.0	11.50	8.03	0.65	10.7	0.82
	17.5	11.40	10.20	0.73	15.2	0.86
<i>Sebastiscus marmoratus</i>	17.5	11.40	10.20	0.86	13.1	0.74
	16.0	5.20	6.63	0.30	15.3	0.95
	22.0	6.70	8.54	0.36	21.1	0.95
	13.5	5.45	6.94	0.35	14.4	1.07
	15.5	5.50	7.01	0.35	14.7	0.95
<i>Agrammus agrammus</i>	15.5	5.60	7.14	0.40	13.4	0.86
	14.0	3.00	3.82	0.18	8.5	0.60
	14.0	3.00	3.82	0.18	8.5	0.60
	15.0	3.30	4.20	0.42	4.6	0.30
	15.0	3.30	4.20	0.36	4.6	0.35

Verrier (1948), and Baron and Verrier (1951) used some species of the Cyprinidae: roach, tench, goldfish, barbel, and chub (Bourguignon and Verrier, 1930).

The present study showed that all the marine species used had the well-developed triangular lens muscle, and the lens movement was clearly observed. Even in goldfish eyes, the inward lens movement was observed. Moreover, any deformation of the eye globe due to the electrical stimulation was not observed in any species. Therefore, our results basically support the conclusion of Beer's study (1894).

The development of the lens muscle varies from species to species, especially among freshwater species. Tuge et al. (1968) have reported that *Parasilus asotus*, *Pelteobagrus nudiceps*, and *Anguilla japonica* have a poorly developed

visual center. In the present study, it was shown that these three species have a thread-like lens muscle and perform no practical lens movement. In these fishes, another mechanism of accommodation has been considered by some workers (Pumphrey 1961; Protasov 1968). The possibility was presented that the eyes of such fishes may be able to see objects simultaneously at various distances at various angles.

2) Visual accommodation of *Carassius auratus* (goldfish)

Kimura and Tamura (1966) reported that lens movement was not elicited by the electrical stimulation in goldfish. Hester (1968) remarked that this species apparently lacks a functional accommodation. Also, Charmann and Tucker (1973) could not obtain the convincing evidence of the accommodative change. However, they

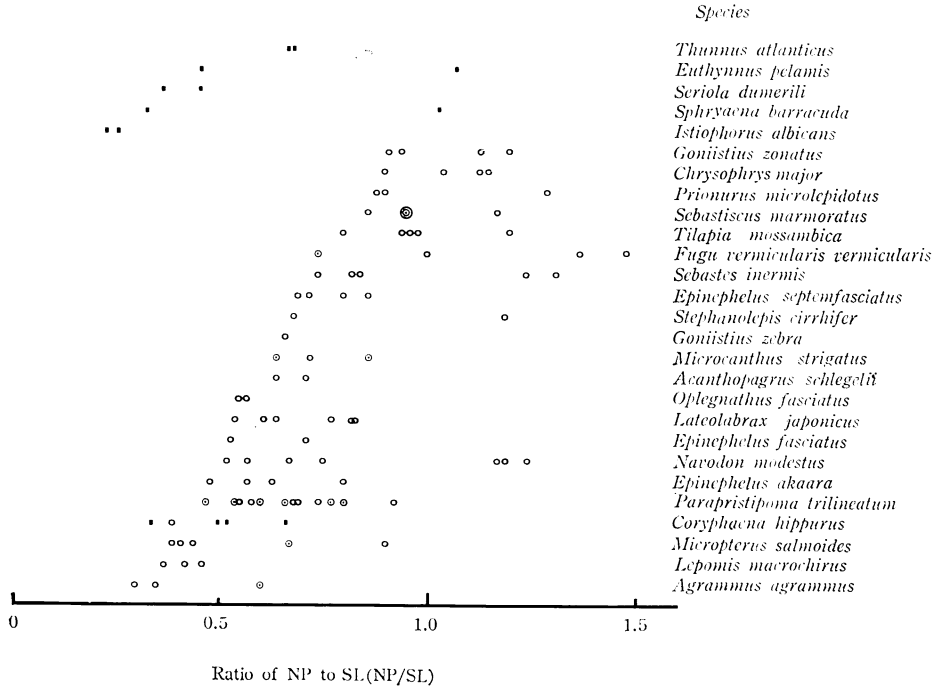


Fig. 7. Comparison of the ratio: the near point distance (NP) to the standard body length (SL), among many species. ○: our data, ■: calculated from data of Tamura and Wisby (1963). Most of the ratios are smaller than 1.0. It means that these fishes have the range of accommodation from less than standard length before the eyes to infinity.

assumed that the effective depth-of-focus, which was calculated from the resolving power of the retina, might render the accommodative movements of the lens unnecessary.

In the present study, it was observed that the lens moved slightly inward to the bottom of the eye cup. Judging from the presence of the muscle fibers in the lens muscle, this inward lens movement is reasonable. Therefore, it is assumed that the inward lens movement is not always the artifact as reported by Kimura and Tamura (1966).

At present, it is concluded that the visual accommodation of *C. auratus* was accomplished by the inward lens movement, in addition to the depth-of-focus.

3) Visual accommodation of elasmobranchs

Franz (1931) succeeded in obtaining a slight forward movement of the lens in *Raja* and *Torpedo*. This has led to the general idea that elasmobranchs accommodate their eyes for the near vision by lens movement toward the cornea

through protraction of the pseudo-campanule (protractor lentis muscle).

However, the mechanism of accommodation in elasmobranchs has not been demonstrated unequivocally (Hess, 1912; Nicol, 1963; Gilbert 1963; Munz, 1971). In the present study, any lens movements could not be demonstrated in 4 species of elasmobranchs. However, there is a possibility that the species which have the color vision and the pseudo-campanule are able to move the lens. Pupillary contraction in the bright circumstances, which is lacking in usual teleostean eyes, may help to increase the depth-of-focus. To clarify these points, further investigations in various species are needed.

4) Range of accommodation and NP/SL

Tamura and Wisby (1963) calculated the range of accommodation using the difference in the lens position before and after the death of fish. In *Coryphaena hippurus*, which was used in the present study as well as theirs, the comparison of the range of the accommodation

was made. The ratios NP/SL calculated from their data were 0.46, 0.34, 0.66 and 0.52, whereas ours was 0.39 (Fig. 7). These values are accordant to each other. The ratio of NP/SL seems to be very useful to compare the range of accommodation among fishes of different sizes.

It has been shown in the present study that the fish species having a well-developed lens muscle have the range of accommodation from less than standard length before the eyes to infinity. It is also suggested that the large pelagic fishes such as *Seriola dumerili*, *Istiophorus albicans*, *Thunnus atlanticus*, and *Euthynnus pelamis* have the same range of accommodation. Judging from lens movement, on electrical stimulation and morphology of lens muscle, many marine fishes have the wider range of accommodation than the fresh-water fishes such as *Salmo gairdnerii*, *Plecoglossus altivelis*, *Carassius auratus*, and *Cyprinus carpio*. This interpretation is in accordance with their habitats, for the range of visibility of large objects in water is reported to be as follows: on the sunny day 1 m in river at the depth of 1~2 m; 5 m in bay; 10 m in coastal strip; and 30 m in ocean (Vainberg 1959).

All these results are based upon the assumption that the eye with the lens in its backward position is in the emmetropic state. To ascertain this assumption, the retinoscopic study was carried out with excised eyes or killed fish eyes. It was, however, disturbed by the methodological difficulty. It was difficult to locate the plane of reflection in the eye, as pointed out by Glickstein and Millodot (1970). More precise experiment will be necessary for the confirmation of the above assumption.

Acknowledgments

This study was supported by Ito Funds for the Promotion of Ichthyological Researches. The authors thank Dr. Yoshihachiro Nimura of the University of Tokyo for providing material and Dr. Noboru Wakasugi of Nagoya University for reading the manuscript. We are also indebted to Mrs. Kiyoko Koga for her assistance in preparation of the manuscript.

Literature cited

Baron, J. and M. L. Verrier. 1951. Réfraction et

cerveau des poissons á fovea. Contribution á l'étude des corrélations organiques. Bull. Biol. France Belg., 85: 105~111.

- Baylor, E. R. and E. Shaw. 1962. Refractive error and vision in fishes. Science, 136: 157~158, fig. 1.
- Baylor, E. R. 1967. Vision of Bermuda reef fishes. Nature, 214: 304~307, figs. 1~2.
- Beer, T. 1894. Die Accommodation des Fischeauges. Pflügers Arch. Ges. Physiol., 58: 523~650, 55 figs.
- Bourguignon, G. and M. L. Verrier. 1930. Le mécanisme de l'accommodation chez les téléostéens. Comptes Rendus Ac. Sc., 191: 73~75.
- Brett, J. R. 1957. The sense organs; the eye. 171~207, figs. 1~10. In M. E. Brown ed. "The physiology of fishes. vol. 2". Academic Press, New York.
- Charman, W. N. and J. Tucker. 1973. The optical system of the goldfish eye. Vision Res., 13: 1~8, fig. 1.
- Duke-Elder, S. 1958. The perception of form. pp. 637~666, figs. 766~796. In "System of ophthalmology. 1 The eye in evolution". Henry Kimpton, London.
- Franz, V. 1931. Die Akkommodation des Selachierauges und seine Abblendungsapparate nebst Befunden an der Retina. Zool. Jahrb., Abt. Allgem. Zool., Physiol. Tiere, 49: 323~462. (Not seen, but cited by Gilbert, P. W., 1963).
- Gilbert, P. W. 1963. The visual apparatus of sharks. pp. 283~326, figs. 1~30. In P. W. Gilbert ed. "Sharks and survival". D.C. Heath and Co., Boston.
- Glickstein, M. and M. Millodot. 1970. Retinoscopy and eye size. Science, 168: 605~606, figs. 1~2.
- Hess, C. 1912. Gesichtssin. 4: 1~269. In Wintersteins "Handbuch der vergl. Physiol". (Not seen, but cited by Tamura, T. and W. J. Wisby, 1963).
- Hester, F. J. 1968. Visual contrast thresholds of goldfish (*Carassius auratus*). Vision Res., 8: 1315~1335, figs. 1~10.
- Kawamoto, N. 1966. 11. Sense organ and its function (Kankaku oyobi sono kinou). pp. 225~306, figs. 1~42. In "Physiology and ecology of fishes", Kouseishya-Kouseikaku, Tokyo. (In Japanese)
- Kimura, K. and T. Tamura. 1966. On the direction of the lens movement in the visual accommodation of teleostean eyes. Bull. Jap. Soc. Sci. Fish., 32(2): 112~116, figs. 1~3.
- Meador, R. G. 1936. Accommodation and its reflex pathways in the teleosts. Yale J. Biol. Med., 8: 511~522, figs. 1~3.; Biol. AB 11(2), 3494 (1937) (abstr.)
- Meyer, D. L. and H. O. Schwassmann. 1970. Electrophysiological method for determination of refractive state in fish eyes. Vision Res., 10: 1301~1303, figs. 1~2.
- Munz, F. W. 1971. Vision: visual pigments. 1~

- 31, figs. 1~9, In W.S. Hoar and D.J. Randall "Fish physiology. Vol. V. Sensory system and electric organs". Academic Press, New York and London.
- Nicol, J. A. C. 1963. Some aspects of photoreception and vision in fishes. *Advan. Mar. Biol.*, 1: 171~208, figs. 1~8.
- Protasov, V. R. 1968. Vision and near orientation of fish. Academy of the USSR. Nauka Moskva. (English translation: 1970, Israel Program for Scientific Translations, Jerusalem: iii+iv+175 pp., 75+4 figs.)
- Pumphrey, R. J. 1961. Concerning vision. pp. 193~208, figs. 1~4. In J. A. Ramsay and V. B. Wigglesworth ed. "The Cell and organism. Essays presented to Sir James Gray." Cambridge Univ. Press, London and New York.
- Tamura, T. 1957. A study of visual perception in fish, especially on resolving power and accommodation. *Bull. Jap. Soc. Sci. Fish.*, 22(9): 536~557, figs. 1~12.
- Tamura, T. 1970. 20. Vision (Sikaku) pp. 423~451., figs. 1~21. In N. Kawamoto ed. "Fish Physiology". Kouseishya-Kouseikaku, Tokyo. (In Japanese)
- Tamura, T. and W. J. Wisby. 1963. The visual sense of pelagic fishes especially the visual axis and accommodation. *Bull. Mar. Sci. of Gulf and Caribbean.*, 13: 433~448, figs. 1~5.
- Tuge, H., K. Uchihashi, and H. Shimamura. 1968. An atlas of the brains of fishes of Japan. Tsukiji Shokan, Tokyo, 240 pp., pls. 1~102.
- Vainberg, V. B. 1959. Podvodnoe osveshchenie (Underwater illumination). *Svetotekhnika*, No. 10. Cited by Protasov, V. R. (1968).
- Verrier, M. L. 1948. La vision de vertébrés et les théories de la vision. *Ann. Biol. Paris, Ser. 3*, 24: 209~239, figs. 1~4.
- (Fisheries Laboratory, Faculty of Agriculture, Nagoya University, Chikusa, Nagoya, 464, Japan)

魚類における眼の遠近調節機能

宗宮 弘明・田村 保

硬骨魚において、眼の遠近調節は水晶体の移動によってなされるという説 (Beer, 1894) と眼球の前後径の変形によってなされるという説 (Bourguignon and Verrier, 1930) がある。しかし今日まで十分に解明されていない。この問題を解決するため、39種の硬骨魚を用いて実験を行ない、次の結果を得た。

摘出眼を、電気刺激することにより、水晶体の移動は観察されたが、眼球の変形は観察されなかった。実験魚は、その眼の水晶体の移動により、移動が明確に観察された魚種 31種と、コイ、フナのように移動が極めてわずかな魚種 4種、また、ナマズ、ウナギのようにまったく移動が認められなかった魚種 4種に分類された。そして、水晶体の移動が明確に記録された魚種においては、体長とほぼ同じくらい離れたところから、無限遠までの遠近調節が可能であるということがわかった。また、Beer (1894) と Bourguignon and Verrier (1930) の説の相違は、主として、使用した実験魚の違いによると考察された。

同様な実験を板鰓魚類 4種について行なったが、水晶体の移動も、眼球の変形も観察されなかった。板鰓魚類の眼の遠近調節機構は、現在のところまだはっきりと解明されておらず、今後その詳細な研究がなされねばならない。

(464, 名古屋市千種区不老町 名古屋大学農学部水産学教室)