A Study of Visual Perception in Fish, Especially on Resolving Power and Accommodation*

Tamotsu TAMURA

(*Fisheries Institute, Faculty of Agriculture, Nagoya University, Anzō, Aichi Prefecture, Japan*)

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Introduction

Any object in visual space may have a number of attributes, i.e., form, brightness, colour, motion, etc. Of these, form perception in fish is studied in the present paper. Very little comparative data on form perception is available, even though numerous anatomical and optical studies of the fish have been published.

Ability to perceive form depends on two factors: resolving power of the dioptric system, and resolving power of the retina. The first is a function of both the resolving power of the lens and accommodation. The second is presumably depend on the spacing of cones in the retina. In this paper, therefore, resolving power of the lens, dioptric accommodation, and retinal cone density are reported for 27 species representing 18 families (Table 1).

The visual fields of these species have also been described and compared in terms of binocular angle, visual axis, and topographical differences in cone density.

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I Materials

The 27 marine teleost species used in this study (Table 1) are supposed to rely heavily on vision in their mode of living. Most of them inhabit either the littoral zone or the

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Table 1. The species used in this study

Family	Species
Argentiniidae	<i>Argentina semifasciata</i> Kishinouye*
Chlorophthalmidae	<i>Chlorophthalmus albatrossis</i> Jordan et Starks*
Zeidae	<i>Zenion japonicum</i> Kamohara*
Scombridae	<i>Scomber japonicus</i> Houttuyn
Carangidae	<i>Seriola quinqueradiata</i> Temminck et Schlegel <i>Trachurus japonicus</i> (Temminck et Schlegel)
Leiognathidae	<i>Leiogeathus argenteus</i> Lancépepe
Apogonidae	<i>Apogon lineatus</i> (Temminck et Schlegel)
Priacanthidae	<i>Priacanthus boops</i> (Schneider)
Serranidae	<i>Epinephelus septemfasciatus</i> (Thunberg) <i>E. chlorostigma</i> (Cuvier et Valenciennes) <i>Latenlabrax japonicus</i> (Cuvier et Valenciennes) <i>Malakichthys wakiyae</i> Jordan et Hubbs
Girellidae	<i>Girella punctata</i> Gray
Sparidae	<i>Pagrosomus major</i> (Temminck et Schlegel) <i>Sparus hasta</i> Bloch et Schneider <i>S. swinhonis</i> Günther <i>Evynnis japonicus</i> Tanaka
Theraponidae	<i>Therapon oxyrhynchus</i> Temminck et Schlegel
Hepatiidae	<i>Xesurus scalprum</i> Jordan et Fowler
Monacanthidae	<i>Cantherines modestus</i> (Günther)
Tetraodontidae	<i>Sphaeroides chrysops</i> (Hilgendorf) <i>S. niphnles</i> Jordan et Snyder
Scorpaenidae	<i>Sebastiscus marmoratus</i> (Cuvier et Valenciennes) <i>Helicolenus dactylopterus</i> (De La Roche)*
Cottidae	<i>Pseudoblennius totomius</i> Jordan et Starks
Triglidae	<i>Chelidonicichthys kumu</i> (Lesson et Garnot)

surface waters of the ocean where there is abundant light. Those marked with asterisks, however, are species with large eyes that are sometimes taken at depths of 100 to 300 meters by deep-sea drag nets.

II Resolving Power of the Dioptric System

Incident light from an object passes through the cornea, anterior chamber, lens and vitreous humour, in that order, to form an image on the retina. The sharpness of this image, which depends on certain properties of the above-named structures, is a measure of the resolving power of the dioptric system. The function of each of these structures will be discussed below.

(1) Cornea

The cornea of the fish eye is typically a convex, transparent membrane, shaped like the bowl of a teaspoon, the horizontal curvature usually being greater than the vertical curvature (Table 2). According to WALLS (1942) this dual curvature is an adaptation of streamlining to swift swimming. It does not produce astigmatism, however, because the refractive index of fish-eye cornea is 1.3770 to 1.3775 (MATTHIESSEN 1882, YAMAMOTO 1931), very close to that of water, 1.33, and because the refractive index of anterior chamber is almost equal to that of water.

Table 2. Curvature of cornea in fish

Species	Body length (cm)	Diameter of lens (mm)	Radius of curvature (mm)	
			Horizontal	Vertical
<i>Pagrosomus major</i>	19	6.8	13.2	8.8
<i>Lateolabrax japonicus</i>	17	6.2	11.0	6.4
<i>Therapon oxyrhynchus</i>	19.5	6.3	10.1	6.5
<i>Priacanthus boops</i>	20	12.2	17.0	16.0
<i>Parapristipoma</i> L. eye R. eye	10	4.5	7.1	4.1
		4.5	8.2	4.9
<i>Sebastiscus marmoratus</i>	11	4.4	5.6	3.8
<i>Sebastes inermis</i>	5.5	2.8	4.1	4.0
<i>Carassius auratus</i>	17	4.9	7.1	4.7

According to HARMS (1914), some demersal fishes have a protective membrane over the cornea, but these, as well as the adipose lids of such fishes as *Mugil* and *Scomber*, are optically similar to the cornea and consequently also optically inert.

(2) Vitreous humour

The vitreous humour, generally continuous in the posterior and anterior chamber of the fish eye through the aphakic space, also has a refractive index close to that of water, and again plays no part in vision.

(3) Crystalline lens

The lens is the only dioptric element of the eye, then, that is involved in image formation. Since the lens is spherical and surrounded by media of essentially one refractive index, the principal points and nodal points coincide with the center of the lens. According to MATTHIESSEN (1882) and HOGBEN & LANDGREBE (1940), the optical density is much higher at the center than the periphery of the lens. This graded structure may well serve to reduce spherical aberration and hence improve resolving power.

Resolving power was measured in the following way. The enucleated lens was immersed in physiological salt solution* by attaching its suspensory ligament to a small clip over a transparent container (Fig. 1). A well illuminated movable screen with black and

Fig. 1. The method of measuring the resolving power of the lens. Le : Lens, M : Microscope, S : 1 mm stripes, P : Physiological salt solution, I : Image of the 1 mm stripes.

white stripes both of which were one millimeter and drawn horizontally and vertically, was placed on one side of the container and a horizontal microscope on the opposite side. The image of the screen projected by the lens could then be viewed through the microscope. The distance between the screen and the lens just to be unable to make out the horizontal and ver-

* According to YAMAMOTO (1949), in marine fish, NaCl 1.35 %, KCl 0.06 %, CaCl₂ 0.025 %, MgCl₂ 0.035 %, NaHCO₃ 0.002 %; in fresh water fish, NaCl 0.75 %, KCl 0.02 %, CaCl₂ 0.02 %, NaHCO₃ 0.002 %.

Table 3. Resolving power of lenses

Species	Diameter of lens (mm.)	L (mm.)	Resolving power φ (sec.)
<i>Lateolabrax japonicus</i>	8.1	3700	56
<i>Xesurus scalprum</i>	7.5	3800	54
<i>Epinephelus septemfasciatus</i>	7.3	3500	59
<i>Sebastiscus marmoratus</i>	6.2	3500	59
<i>Cyprinus carpio</i>	5.4	2400	86
<i>Lateolabrax japonicus</i>	4.8	2400	86
<i>Epinephelus septemfasciatus</i>	4.7	2300	90
Gold fish	1.7	1700	122
Gold fish	1.6	1700	122
<i>Carassius auratus</i>	1.5	1600	129

tical stripes of the image could be ascertained by changing the distance L' . The distance in water would be

$$L = 1.33 L' + l$$

where L is the distance between the object and the lens if this whole experiment were carried out in the water, 1.33 the refractive index of water, L' the distance from the chamber to the screen, l the distance from the chamber wall to the center of the lens. The value of $1(\text{mm})/L(\text{mm}) = \varphi$ is the resolving power (angle in radians) of the lens. In Table 3, the values (φ) are shown in second of arc.

In ten fishes, the measured values of resolving power range from 54 to 129 seconds of arc, and they seem to have a tendency to become greater in smaller lens. This tendency may partly be attributed to the measuring instrument and the physical property of the light. The factors which affect the values are assumed to be three: the first is a function of the properties of the lens, *i.e.*, the aberrations and the turbidity, the second is the resolving power of the used microscope, and the third is the diffraction of light at the margin of the pupil or the lens. With a large lens the latter two factors are negligible and the measured value is the function of the lens itself; however, with a small lens both factors become too great to be neglected. For example, the image of a one-millimeter stripe projected by a lens 1.5 mm in diameter (*Carassius*) is

$$I = l \times \frac{F}{L} = \frac{1.91}{1600} = 0.0012 \text{ mm}$$

where I is the image in millimeters, l is the width of the stripe, L is the distance between the object and the lens, and F is the focal distance of the lens as calculated by Matthiessen's ratio, *i.e.*, $F = 2.55 \times (\text{lens radius})$. It can readily be seen that the resultant 0.0012 mm is only slightly greater than the resolving power of the microscope used, which is

$$d = \frac{\lambda}{2a} = \frac{0.00056}{0.50} = 0.0011 \text{ mm}$$

where d is resolving power, λ is the wave-length of light and a is the numerical aperture of the microscope.

Furthermore, the light diffracted at the margin of the pupil whose diameter is the same, or nearly the same, as that of the lens becomes significant enough to effect the resolving power of the lens. Resolving power resulting from such marginal diffraction is as follows for *Carassius* in Table 3 :

$$\theta = 0.61 \times \frac{\lambda}{r} = 0.61 \times \frac{0.00056}{0.75} = 94''$$

where θ is the resolving power resulted from marginal diffraction, 0.61 is the physical constant, λ is the wave-length of light, and r is the radius of the pupil. The resultant value, 94 seconds, is only a little less than the measured value of 129 seconds.

Considering the above, the resolving power of lenses of diameter greater than about 5 mm is 54-90 seconds. In smaller lenses, it may be assumed to be less than about 120—130 seconds, though some complications occur in respect to the resolving power of the used microscope and the diffraction of light at the margin of the pupil.

It must be pointed out that the lenses may have greater resolving power *in vivo*, because they do tend to become turbid while being measured, even though they are in physiological salt solution.

III Resolving power of the retina

The structural basis of resolving power in the retina is the spacing of the cones and the extent to which their conducting neurons are summated. POLYAK (1948) has demonstrated that cones in the primate fovea are not summated. Each has a direct nerve tract to the brain. Although very little is known about summation in the teleost retina, it will be assumed, in this report, that cones are not summated.

In fishes, as in all other vertebrate groups, there are two kinds of photoreceptors : rods and cones. Their presence has given rise to the duplicity theory of function. Rods have a low threshold of sensitivity and low acuity. Cones have a high threshold of sensitivity and good acuity. As VON FRISCH (1925) and WUNDER (1936) point out, the Duplicity Theory is valid for fishes. Though cones in human retina have a sensitivity threshold of 0.03 to 0.1 lux, BRUNNER (1934) has shown that cones in the retina of *Phoxinus* have a threshold of 0.002 to 0.008 lux.

In view of these works, it is obvious that only the cones are pertinent to an investigation of form perception in fishes.

YAMANOUCI (1940) measured the density of cones in five regions of the retina of *Microcanthus strigatus* and obtained the highest density in the temporal region (Table 4).

KAHMANN (1934, 1936) described the fovea centralis in certain fishes and showed that it is most often located in the temporal region (*Serranus*, *Julis* and *Blennius*). According to MÜLLER (1952) the various regions of the retina in the guppy (*Lebistes reticulatus*)

Table 4. Number of cones in 0.1 mm square in various regions of retina in *Microcanthus strigatus*

Retinal regions	Temporal	Dorsal	Nasal	Ventral	Bottom
No. of cones	155	77	114	97	139

After YAMANOUCI (1940)

Fig. 3. Microphotograph showing the density of cones. All the squares in the photographs except the upper left one are 0.1 mm square; the upper left one is 0.03 mm square,

- A. *Epinephelus chlorostigma*; from left to right, upper row; temporal, dorso-temporal, ventro-temporal and dorsal, lower row; nasal, ventral and bottom.
- B. *Lateolabrax japonicus*; the same order.
- C. *Sparus hasta*; the same order.

Fig. 4. Regional differences in the cone density.

a. In the fishes which show the maximum density in the dorso-temporal.

SS: *Sparus swinhonis*, XS: *Xesurus scalprum*, SH: *S. hasta*, LA: *Leiognathus argenteus*, PM: *Pagrosomus major*, EJ: *Evynnis japonicus*.

b. In the fishes which show the maximum density in the temporal.

ES: *Epinephelus septemfasciatus*, SQ: *Seriola quinqueradiata*, SM: *Sebastiscus marmoratus*, SC: *Sphaeroides chrysops*, EC: *Epinephelus chlorostigma*, CK: *Chelidonichthys kumu*, CM: *Cantherines modestus*, LJ: *Lateolabrax japonicus*, TO: *Therapon oxyrhynchus*, SJ: *Scomber japonicus*, HD: *Helicolenus dactylopterus*, SN: *Sphaeroides niphobles*.

c. In the fishes which show the maximum density in the ventro-temporal or ventral.

APS: *Apogon lineatus*, CA: *Chlorophthalmus albatrossis*, MW: *Malakichthys wakiyae*, ARS: *Argentina semifasciata*, TJ: *Trachurus japonicus*, PB: *Priacanthus boops*, GP: *Girella punctata*, ZJ: *Zenion japonicum*.

Fig. 5. Area temporalis fixed by Zenker's solution. Upper; the external appearance of the area in *Sebastiscus marmoratus* ($\times 30$). Lower; the cross section of the area in *Epinephelus septemfasciatus* ($\times 90$).

Fig. 2. Schema showing the seven regions in the retina.

T : Temporal, DT : Dorso-temporal, VT : Vento-temporal, D : Dorsal, N : Nasal, V : Ventral, B : Bottom.

separately when they occurred in the species examined.

Fixation and imbedding produced some shrinkage in the retina. According to PATTEN and PHILPOTT (1921), the shrinkage was estimated to be 25 % in the pig embryo. Assuming it to be the same in the fish retina, counts were corrected accordingly.

Results : Cone densities by regions are shown in Table 5 and Fig. 4, which are divided into three parts. Part a shows the species that have the maximum density in the dorso-temporal region. Part b shows the species with the greatest density in the temporal region, and part c shows the species with the greatest density in the ventro-temporal or ventral region.

The focal distances given were calculated from MATTHIESSEN's ratio. The "minimum separable angle" was calculated on the assumption that image lines can only be resolved when they fall on cones separated by at least one unstimulated cone. It is

$$\alpha = \frac{1}{F} \left[\frac{0.1(1+0.25)}{\sqrt{n}} \times 2 \right] \text{ (Angle in radians)}$$

where F is the focal distance of the lens, 0.25 is the degree of shrinkage, and n is the maximum number of cones per 0.1 mm square in one retina and it includes both single and twin cones, although singles and twins, perhaps, play rather different roles in resolution.

The minimum separable angle, which varies from 4.2 minutes in *E. septemfasciatus* to 15.4 minutes in *C. albatrossis*, is obviously more than the resolving power of the lens (Table 3). It may be concluded, therefore, that resolving power is a function of the retina rather than the lens.

When species are compared by the depths at which they live, it is evident that there

can be distinguished by the form and size of cones as well as their density. He further pointed out such regional differences are adapted to the part of visual field that they serve, and remain constant even though new cells are continually being added from the margin of the retina during the developmental stage.

Since cone density, which is an index of resolving power, varies over the retina, the retinas of all the fishes examined in this study were studied topographically.

Method : Eyes were enucleated and fixed in Zenker's solution for 24 hours after removing a small part of the cornea. Each retina was then divided into the following seven regions : temporal, dorso-temporal, ventro-temporal, dorsal, nasal, ventral and bottom (Fig. 2). After routine paraffin imbedding, tangential sections were cut. The cones in 0.1 mm squares of each region were then counted in photomicrographs (Fig. 3). Since twin and single cones may be present in the teleost retina (WUNDER 1936, TAKATSUZI 1939), they were counted

Table 5. The numbers of cones in 0.1 mm square in various regions of retinae
a. In the fish which have the largest number of cones in the dorso-temporal region

Species (Body length in cm)	Kinds of cones	Retinal regions							Focal distance of lens (mm)	Minimum separable angle (minute)
		Temporal	Dorso-temporal	Ventro-temporal	Dorsal	Nasal	Ventral	Bottom		
<i>Pagrosomus major</i> (20)	Twin	151	202	127	160	133	126	88	7.7	6.4
	Single	75	101	68	80	66	65	42		
	Total	226	303	195	240	199	191	130		
<i>Sparus hasta</i> (18)	Twin	97	263	90	90	92	84	72	6.9	6.2
	Single	50	137	44	42	46	42	37		
	Total	147	400	134	132	138	126	109		
<i>Sparus swinhonis</i> (12)	Twin	200	340	159	253	157	135	141	5.1	6.9
	Single	94	169	83	126	79	69	69		
	Total	294	509	242	379	236	204	210		
<i>Euvynnis japonicus</i> (13)	Twin	264	380	207	193	182	226	195	5.3	6.8
	Single	129	190	103	98	91	113	95		
	Total	393	570	310	291	273	339	290		
<i>Leiognathus argenteus</i> (9.5)	Twin	148	157	57	97	99	56	94	4.8	11.6
	Single	61	79	31	75	41	27	40		
	Total	209	236	88	172	140	83	134		
<i>Xesurus scalprum</i> (14)	Twin	141	168	156	86	144	115	101	6.4	8.5
	Single	71	84	80	43	74	60	50		
	Total	212	252	236	129	218	175	151		

b. In the fish which have the largest number of cones in the temporal region

Species (Body length in cm)	Kinds of cones	Retinal regions							Focal distance of lens (mm)	Minimum separable angle (minute)
		Temporal	Dorso-temporal	Ventro-temporal	Dorsal	Nasal	Ventral	Bottom		
<i>Epinephelus septemfasciatus</i> (14)	Twin	700	132	126	83	176	139	116	6.3	4.2
	Single	350	32	46	27	77	58	54		
	Total	1050	164	172	110	253	197	170		
<i>Epinephelus chlorostigma</i> (16)	Twin	320	55	78	86	125	52	82	6.4	6.1
	Single	165	17	37	37	57	25	29		
	Total	485	72	115	123	182	77	111		
<i>Sebastiscus marmoratus</i> (18)	Twin	300	73	60	34	59	58	60	6.6	6.7
	Single	80	32	30	8	15	11	30		
	Total	380	105	90	42	74	69	90		
<i>Helicolenus dactylopterus</i> (17)	Twin	150	16	43	20	39	49	30	6.6	10.6
	Single	0	0	0	0	0	0	0		
	Total	150	16	43	20	39	49	30		
<i>Therapon oxyrinchus</i> (20)	Twin	88	42	55	30	65	52	53	7.7	9.7
	Single	45	19	22	10	28	22	26		
	Total	133	61	77	40	93	74	79		
<i>Cantherines modestus</i> (28)	Twin	197	87	104	74	161	104	125	7.7	6.4
	Single	102	50	52	34	78	53	64		
	Total	299	137	156	108	239	157	189		

<i>Chelidonichthys kumu</i> (14)	Twin Single Total	420 210 630	124 62 186	172 87 259	85 46 131	125 60 185	105 59 164	78 37 115	5.0	6.8
<i>Sphaeroides niphob-les</i> (13.5)	Twin Single Total	390 195 585	160 83 243	119 60 179	96 47 143	138 69 207	129 67 196	108 52 160	5.1	7.0
<i>Sphaeroides chrysops</i> (17)	Twin Single Total	72 35 107	60 31 91	60 30 90	42 22 64	65 31 96	56 32 88	61 28 89	5.8	14.3
<i>Seriola quinquerad-iata</i> (17)	Twin Single Total	195 97 292	156 81 237	164 87 251	127 66 193	154 79 233	175 89 264	111 57 168	5.8	8.7
<i>Lateolabrax japon-icus</i> (18)	Twin Single Total	181 78 259	89 43 132	106 52 158	62 28 90	104 50 154	98 44 142	55 27 82	6.3	8.5
" (9.5)	Twin Single Total	202 100 302	105 53 158	161 80 241	89 44 133	153 77 230	128 65 193	88 45 133	4.2	11.7
<i>Scomber japonicus</i> (17)	Twin Single Total	178 96 274	125 124 249	159 91 250	130 106 236	154 55 209	146 68 214	120 58 178	6.9	7.5

Table 5.

c. In the fish which have the largest number of cones in the ventro-temporal or ventral region

Species (Body length in cm)	Kinds of cones	Retinal regions							Focal dis- tance of lens (mm)	Minimum separable angle (minute)
		Temporal	Dorso-temporal	Ventro-temporal	Dorsal	Nasal	Ventral	Bottom		
<i>Girella punciaia</i> (30)	Twin Single Total	151 86 237	114 61 175	162 82 244	83 49 132	120 63 183	126 65 191	96 47 143	7.1	7.8
<i>Trachurus japonicus</i> (13)	Twin Single Total	141 71 212	87 43 130	190 98 288	77 40 117	92 46 138	182 90 272	145 74 219	5.9	8.6
<i>Malakichthys waki- yae</i> (9)	Twin Single Total	166 0 166	107 0 107	242 0 242	108 0 108	145 0 145	237 0 237	105 0 105	7.0	7.9
<i>Apogon lineatus</i> (8)	Twin Single Total	96 13 109	76 8 84	200 15 215	79 13 92	96 12 108	153 10 163	56 11 67	4.1	14.3
<i>Zenion japonicum</i> (7)	Twin Single Total	163 0 163	161 0 161	215 0 215	119 0 119	148 0 148	361 0 361	100 0 100	7.0	6.5
<i>Priacanthus boops</i> (15)	Twin Single Total	112 53 165	96 41 137	104 68 172	118 44 162	118 53 171	170 50 220	94 39 133	10.0	5.8
<i>Argentina semifas- ciata</i> (16)	Twin Single Total	114 0 114	103 0 103	170 0 170	84 0 84	123 0 123	251 0 251	93 0 93	5.9	9.2
<i>Chlorophthalmus albatrossis</i> (13)	Twin Single Total	0 0 0	0 0 0	58 0 58	0 0 0	0 0 0	72 0 72	0 0 0	6.6	15.4

is a relationship between depth and the relative abundance of twin and single cones. *Scomber*, which lives very close to the surface, has almost equal numbers of twin and

single cones in the dorso-temporal region of retina. Most of the other species examined live rather near the surface and have half as many single as twin cones. However, *Helicolenus*, *Malakichthys*, *Zenion*, *Argentina* and *Chlorophthalmus*, which were caught at depths of 100 to 300 meters, did not have single cones, and did have well developed tapeta lucida. *Chlorophthalmus*, furthermore, had twin cones only in the ventral and ventro-temporal regions. It usually inhabits depths greater than 300 meters.

The above relationship indicates that twin cones are more sensitive to light than single cones, and there are definite physiological and ecological differences between them. It has also been shown (Table 5 and Fig. 4) that cone density varies by region over the retina. The relationship between the different regions and the portions of the optical field they subtend will be discussed under Visual axis.

Visual acuity depends on the size of the retinal image and the cone density. The greater the number of cones over which the image is spread, the better the resolution. If cone density is constant throughout life, resolving power would increase as the lens grows. However, from MÜLLER's work on the guppy and the present data on *Lateolabrax* (Table 5 b and Fig. 4 b), cone density is higher in the younger stages. Consequently, lens size is at least partly compensated for by cone density.

Nothing resembling the fovea centralis or lateralis described by KAHMANN (1934, 1936) was found in the species listed in Table 5. However, in the bright adapted retinas of certain Japanese Serranids (*E. septemfasciatus*, *E. chlorostigma*) and Scorpaenids (*S. marmoratus* and *H. dactylopterus*) a small elevation possibly representing an area temporalis was found (Fig. 5). These specimens were fixed in Zenker's solution, as were all other preparations. Both twin and single cones occurred in this area. But since no such elevation could be found in either fresh or dark adapted eyes fixed in Zenker's solution, and because the pigment layer was separated from the chorioid layer at this point (Fig. 5), it is strongly suspected to be an artifact.

Thus most fish have an area at least somewhat specialized for more acute vision, even though true areae and foveae may be absent. Although the extent of this specialization may be judged from Fig. 4, a more comparable index is the ratio of cone density in the highest region to the average cone density of the rest of the retina (Table 6). Table 6 shows that five demersal and somewhat sedentary species (*Chlorophthalmus*, two species of *Epinephelus*, *Sebastiscus* and *Helicolenus*) have the highest degree of specialization, and that two of them, *Chlorophthalmus* and *Helicolenus* have relatively great regional specialization in spite of the fact that they live at the depths greater than 100 meters where light is scarce. It should also be noted that these two have large separable angles. The lower degree of specialization in *Scomber* and *Seriola* can almost certainly be attributed to the fact that they are pelagic and therefore probably find good periscopy advantageous. No explanation can be given for the rather striking difference between *S. niphobles* and *S. chrysops*, because very little is known of their behaviour.

According to BRUNNER (1934) and YAMANOUCHI (1940), the least separable visual angle in *Phoxinus* and *Microcanthus* approximates the angle subtended by one cone, suggesting that there are separate conductive paths from each cone to the higher centers in the

Table 6. The degree of specialization of the area

Species	Degree of specialization	Minimum separable angle (minute)
<i>Scomber japonicus</i>	1.21	7.5
<i>Sphaeroides chrysops</i>	1.24	14.3
<i>Seriola quinqueradiata</i>	1.25	8.7
<i>Xesurus scalprum</i>	1.35	8.5
<i>Girella punctata</i>	1.38	7.8
<i>Priacanthus boops</i>	1.40	5.8
<i>Pagrosomus major</i>	1.54	6.4
<i>Trachurus japonicus</i>	1.59	8.6
<i>Lateolabrax japonicus</i> Body length 9.5 cm	1.66	11.7
<i>Malakichthys wakiyae</i>	1.67	7.9
<i>Evynnis japonicus</i>	1.70	6.8
<i>Leiognathus argenteus</i>	1.72	11.6
<i>Cantherines modestus</i>	1.82	6.4
<i>Therapon oxyrhynchus</i>	1.88	9.7
<i>Sparus swinhonis</i>	1.95	6.9
<i>Lateolabrax japonicus</i> Body length 17 cm	2.05	8.7
<i>Apogon lineatus</i>	2.07	14.3
<i>Argentina semifasciata</i>	2.20	9.2
<i>Zenion japonicum</i>	2.39	6.5
<i>Sparus hasta</i>	3.05	6.2
<i>Sphaeroides niphobles</i>	3.11	7.0
<i>Chelidonichthys kumu</i>	3.63	6.8
<i>Epinephelus chlorostigma</i>	4.19	6.1
<i>Helicolenus dactylopterus</i>	4.58	10.6
<i>Sebastiscus marmoratus</i>	4.86	6.7
<i>Epinephelus septemfasciatus</i>	6.52	4.2
<i>Chlorophthalmus albatrossis</i>	7.46	15.4

brain as is the case in primates. This can only be ascertained by further neuroanatomical investigation.

IV Accommodation

BEER (1894), in his thorough investigation of accommodation in the fish eye, showed that fish eyes are myopic in the resting state, and that accommodation to distant objects is accomplished by retraction of the lens towards the retina. Retraction is effected by the musculus retractor lentis (Campanula Halleri). BEER's views have been confirmed by the work of HESS (1912), MEADER (1936), and YAMAMOTO (1931).

In the present study, accommodation has been measured in 13 marine teleosts. The method employed differed somewhat from BEER's, and has produced additional information.

Method : Fishes, generally speaking, have monocular visual fields of approximately 180°, due in part to the lateral location of the eyes and in part to the spherical lens that produces beyond the pupil. Anteriorly, the monocular fields overlap to a greater or lesser extent, forming a binocular field. The functional importance of the binocular field in fish has been demonstrated by HERTER's experiments on binocular vision (1930).

In the present study, refraction was measured from six points in the visual field : fore, upper-fore, lower-fore, upper, lower, and lateral (Fig. 6). In most cases, the fore and upper-fore or lower-fore fell within the binocular field, a further indication of

Fig. 6. Labeling of visual directions.
U : Upper, UF : Upper-fore, FFU : Fore-fore-Upper, F : Fore, LoF : Lower-fore, Lo : Lower, La : Lateral, LaF : Lateral-fore.

Fig. 7. Schema showing the method of measuring the refraction of fish eye. Explanation in the text.

the functional importance of this zone in view of the fact that these portions of the visual field are served by the temporal regions of the retina, where cone density is highest.

Refraction was measured with an instrument similar to the refractometer used for human eyes. In Fig. 7, which illustrates the refractometer used, O is a pattern of black triangles of about 2 millimeters mounted in front of the lamp. Le is a convex lens with a focal distance of about 35 cm. M is a mirror with a small hole in the center, and T is a tank of sea water with one glass wall. The specimen under examination was fixed rigidly in the tank between two pieces of rubber sponge.

Measurement were made in the dark in the following manner. The pattern O was reflected into the eye and brought to maximum focus there as viewed by the observer through the hole in the mirror. This was accomplished by moving the lamp with the pattern mounted on it. Then, O' is the real image of O, formed by the lens (Le) and reflected by the mirror (M). The plane of O' was ascertained by a movable white screen placed in the tank, and the distance between it and the center of the lens of the fish was measured. The method of the measurement was as follows : after the maximum focus was brought and the supposed position of the center of the lens was pointed by the tip of the flexible fuse (F), the fish was removed, and then the position of O' was ascertained by the white screen. The distance from the tip of the fuse to the screen was measured along the light direction by a pair of dividers or a rule.

When O' was in front of the eye, as in Fig. 7, the eye was myopic, when behind, the eye was hypermetropic. When O' was very far either in front of or behind the fish eye, it was emmetropic or nearly so, but it was not possible to see O' under this condition. Consequently, an auxiliary concave lens was placed in front of the eye for the measurement, and its effect later subtracted.

Fig. 8. a. R : Piece of retina, P : Physiological salt solution, Le : Convex lens (focal distance 24 mm), BM : Binocular-microscope.
b. HV : Hyaloid vessel, S : Shadow of HV.

The assumption is made, in this method, that the image $0''$ is focused on the photosensitive layer of the retina. If $0''$ was focused some other level of the retina, considerable corrections would be necessary in view of the relative thickness of the fish retina and the short focal distance of the lens. The validity of this assumption was determined in the following way. A small piece of living retina was excised from *Carassius auratus* and placed in physiological salt solution.

The triangular pattern was focused on it, as shown in Fig. 8, then examined under a binocular microscope. The image was obviously formed beyond the inner limiting membrane, which is readily identified by the presence of hyaloid or vitreal vessels distributed over its surface.

The distance, x , between the hyaloid vessels and the plane of focus was determined by simple triangulation (Fig. 8 b),

$$x = a \times \tan \alpha = 0.19 \times \tan 38^\circ = 0.15 \text{ mm}$$

where a is the horizontal distance between the hyaloid vessel and its shadow on the plane of focus, and $\tan \alpha$ is the incident angle of illumination source. The piece of retina was then fixed in Zenker's solution and sectioned. Direct measurement of the sectioned material showed the inner limiting membrane and the photosensitive layer of the retina to be 0.13 mm apart. Correction for shrinkage shows that this measurement agrees almost perfectly with the 0.15 mm obtained by triangulation.

$$0.13 \times (1 + 0.25) = 0.16 \text{ mm}$$

Thus it is safe to assume the image $0''$ in Fig. 7 is formed on the photosensitive layer of the retina.

At least two sets of refraction measurements were obtained for each species: one without treatment (pre-treatment) the other one or more of the five treatments (post-treatment). These were (1) severing the optic nerve from inside the mouth, (2) killing by laceration of the heart, (3) intramuscular injection of 0.5 cc of 1 % atropine solution, (4) injection of 1 cc of Amelizol, containing 3 mg of d-tubocurarine chloride and 5 mg of chlorbutanol, (5) injection of 0.5 cc of a 1 % aqueous solution of curare (d-tubocurarine chloride). The last two were included in order to test BEER's data, since he used curare as the anaesthetic. Severing the optic nerve was effective immediately, while the injections were not effective for 10 or 15 minutes.

Results : Refraction values for thirteen species are given in diopter units in Table 7 a, b, c. Hypermetropia is indicated by +, myopia by -, and emmetropia by 0. Error of measurement may be about ± 1 diopter.

Table 7 shows that all eyes were hypermetropic or emmetropic in pre-treatment, only becoming myopic in certain directions after treatment. Incidentally, no differences were

Table 7. The values of the refraction (Diopter)**a.** In the fishes which show the highest myopia in the lower-fore direction

Direction Species (Body length cm)	Pre-treatment						Post-treatment						Method of treatment
	Fore	Lateral	Upper-fore	Upper	Lower-fore	Lower	Fore	Lateral	Upper-fore	Upper	Lower-fore	Lower	
<i>Pagrosomus major</i> (18)	+1.7	+2.5	+2.0	+5.0	+1.3	0	-5.9	+2.0	+4.0	+2.0	-11	-6.3	At
" (7)	+7.7	+7.1	+10				-15	+10	+2.5	+8.3	-22	+6.7	At
Mean	+4.7	+4.8	+6.0	+5.0	+1.3	0	-10.5	+6.0	+6.3	+5.2	-16.5	+0.2	
<i>Sparus hasta</i> (16.5)	+1.3	0	+2.0	+2.1	+2.9	+3.2	-7.7	+1.3	-5.0	+11	-13	-10	S
" (16)	0	+1.3	+1.8	+1.8	+0.9	+0.9	-13	+4.2	+2.0	+17	-13	-6.7	S
" (16)	+1.4						-13	+3.1		+9.1	-13	-10	K
Mean	+0.9	+0.7	+1.9	+2.0	+1.9	+2.1	-11.2	+2.9	-1.5	+12.6	-13	-8.9	
<i>Erynnis japonicus</i> (10)	+5.3	+3.9	+4.8	+5.3	+4.8	+4.3	-8.3	+6.7	+1.7	+7.7	-14	+3.1	S
" (10) L. eye	+4.3	+6.3	+6.3	+7.2	+3.9	+3.7	-13	+5.9	-5.6	+7.2	-13	+2.9	S
" (10) R. eye	+3.0	+4.0	+5.6	+5.9	+5.0	+5.3	-13	+5.9	-4.3	+7.7	-14	-5.6	S
" (10)	+2.2	+2.5	+2.5	+2.5	+0.8	0	-13	+2.2	-7.7	+5.9	-11	+1.6	S
Mean	+3.7	+4.2	+4.8	+5.2	+3.6	+3.3	-11.8	+5.2	-4.0	+7.1	-13	+0.5	
<i>Leiognathus argenteus</i> (9.5)	+4.2	+6.7	+5.0	+10	+2.9	+2.1	-14	+10	-5.0	+8.3	-14	-14	S
<i>Xesurus scalprum</i> L. eye	+3.9	+3.9	+2.0	+1.8	+1.4	+1.3	-11	+5.3	-5.6	+13	-11	-6.7	S
" R. eye	+4.0						-8.3	+1.1	-5.9	+6.7	-10	-6.7	S
Mean	+4.0	+3.9	+2.0	+1.8	+1.4	+1.3	-9.7	+3.2	-5.8	+9.9	-10.5	-6.7	

+ : Hypermetropia, - : Myopia, 0 : Emmetropia, S : Severing optic nerve, At : Atropine injection, Cu : Curare injection, Am : Amelizol injection, K : Killing by laceration of heart.

b. In the fishes which show the highest myopia in the fore direction

Direction Species (Body length cm)	Pre-treatment						Post-treatment						Method of treatment
	Fore	Lateral	Upper-fore	Upper	Lower-fore	Lower	Fore	Lateral	Upper-fore	Upper	Lower-fore	Lower	
<i>Epinephelus septemfasciatus</i> (14)	+7.2	+4.3	+5.9	+5.6	+4.3	+4.3	-17	-5.9	-6.7	+5.9	-5.0	0	S
" (15)	+5.6	+4.8	+5.9	+5.6	+5.0	+4.8	-14	-5.6	-5.6	+5.0	-4.8	0	S
" (14) L. R.	+3.7	+3.7	+4.0	+4.0	+3.5	+3.3	-13	+3.5	-5.6	+5.3	-5.9	+5.6	S
" (14) L. R.	+3.7	+5.0	+3.7	+3.7	+3.3	+3.0	-13	+5.0	-7.7	+5.0	-5.6	+7.7	S
" (14) L. R.	+8.3	+4.3	+4.3	+4.0	+4.2	+4.0	-14	+4.0	-7.7	-7.7	-5.0	+3.5	S
" (14) L. R.	+5.3	+3.9	+4.2	+4.0	+3.5	+3.3	-13	+4.8	-9.1	-9.1	-5.3	+5.9	S
Mean	+5.6	+4.3	+4.7	+4.5	+4.0	+3.8	-14	+1.0	-7.1	+0.7	-5.3	+3.8	
<i>Sebastiscus marmoratus</i> (18)	+2.0	+2.8	+2.2	+2.1	+1.0	0	-13	+0.7	-6.7	+2.4	-5.9	-2.5	S
" (18)	+2.0	+3.2	+4.2	+3.9	+1.1	+0.6	-11	+0.9	-6.3	+1.1	-5.6	+0.9	S

" (18)	+4.2	+4.0					-13	+3.3					At
" (14)	+2.3	+3.5	+3.3	+2.5	+1.3	0	-11	+2.5	-7.7	+2.0	-6.7	0	At
" (16)	+2.2	+2.6					-13	+2.0					S
" (15)	+2.6	+3.1					-13	+2.2					S
Mean	+2.6	+3.2	+3.2	+2.8	+1.1	+0.2	-12.3	+1.9	-6.9	+1.8	-6.1	-0.5	
<i>Therapon oxyrhynchus</i> (20)	+3.3	+4.3	+2.0		+2.7		-14	0	-10		-6.7		S
<i>Seriola quinqueradiata</i> (17)	+3.3	+8.3	+3.3	+11	+4.0	+6.3	-12	+9.1	-7.1	+5.6	-8.3	+7.7	At
<i>Girella punctata</i> (16)	+5.6	+3.9	+5.0	+3.3	+2.0	0	-14	+4.0	-6.7	+3.6	-6.3	0	At
" (18)	+5.9	+3.7	+5.0		+5.6		-13	+3.3	-7.2		-8.3		K
Mean	+5.8	+3.8	+5.0	+3.3	+3.8	0	-13.5	+3.7	-7.0	+3.6	-7.3	0	
<i>Pseudoblennius totomius</i> (7.5)	+5.9	+7.7	+6.3	+6.7	+7.7	+13	-25	+7.7	-10	+8.3	-8.3	+14	S

c. In the fishes which show the highest myopia in the upper-fore direction

Species (Body length cm)	Direction	Pre-treatment						Post-treatment						Method of treatment
		Fore	Lateral	Upper-fore	Upper	Lower-fore	Lower	Fore	Lateral	Upper-fore	Upper	Lower-fore	Lower	
<i>Lateolabrax japonicus</i>	L.	+5.3	+4.8					-13	+5.3	-13	-8.3	-6.7	+13	S
	R.	+5.9	+5.6					-13	+5.6	-14	-10	-7.7	+11	S
" (18.5)	L.	+7.2	+6.3	+4.8	+4.8	+2.5	0	-11	+5.6	-13	-8.3	-5.0	+8.3	S
	R.	+6.7	+5.9	+5.0	+5.0	+2.3	0	-14	+5.3	-14	-11	-4.3	+8.3	S
" (19)	L.	+5.6	+5.0	+4.8	+4.8	+2.5	+2.5	-14	+5.0	-14	+4.0	-5.6	+2.2	S
	R.	+5.9	+4.3	+4.3	+4.0	+1.7	+1.7	-13	+4.8	-13	+4.2	-5.0	+2.0	S
" (23)		+7.2	+5.9	+7.7	+7.7	+7.2	+7.2	-14	+5.9	-14	-9.1	-7.7	+25	S
" (9.5)		+7.7	+9.1					-17	+13	-20	-14	-10	+25	S
" (17)		+5.0						-11		-12				Am
" (17.5)		+4.8						-13		-13				Am
" (17.5)		+2.9						-13		-13				At
" (18)		+7.2	+4.8	+6.7	+5.0	0	0	-9.1	+3.3	-10	0	-8.7	+2.5	Cu
Mean		+6.0	+5.7	+5.6	+5.2	+2.7	+1.9	-12.9	+6.0	-13.6	-5.8	-6.7	+10.8	
<i>Trachurus japonicus</i> (10.5)		0	+5.9					-15	+5.9	-20	-10	+3.3	+6.7	At
" (10.5)		+2.2	+5.0	+1.8	+1.8	+1.8	+1.8	-17	+5.0	-20	-6.7	+2.9	+7.7	At
Mean		+1.1	+5.5	+1.8	+1.8	+1.8	+1.8	-16	+5.5	-20	-8.4	+3.1	+7.2	

assumed to occur between the five treatments. In Table 7 a the greatest myopia occurred in the lower-fore direction. In Table 7 b it occurred in the fore direction and in Table 7 c in the upper-fore direction. Obviously the lenses must have been displaced in these respective directions, and it will be shown in the section of visual axis that the direction

of displacement in these fishes coincide with their visual axes as established by another method.

The results of these refraction measurements are not directly comparable with BEER's. In this report, the pre-treatment state is assumed to be the resting state of the eye, where BEER assumed the resting state to be that produced by the injection of curare or atropine. Further-more, the degree of myopia obtained by BEER does not necessarily reflect the highest myopia of the fish, because he consistently measured refraction along only one line, *i.e.*, a line passing through the center of the lens to a point near the scotoma*. This, perhaps, coincides with the lateral-fore direction in Fig. 6. His values of myopia ranged from -3 to -10 diopters, and -12 in one extreme case (mean -6.1), while the values in Table 7 range from -10 to -25 diopters (mean -14).

According to Table 7, the accommodation is assumed to be performed along certain directions, except which the refraction is hypermetropic or emmetropic in either pre- or post-treatment state. It would be of little importance if the fish eye is myopic, emmetropic or hypermetropic in the resting state, because the movement perception, for which the acute image is not necessary, might play more important part in detecting the food or the enemy as Tamura (1952) showed in young *Lateolabrax japonicus*. So as to face the interesting moving object which is perceived at first by its movement, the fish bends or turns its head and body and keeps it in the visual axis which is, in general, situated in the binocular field, and then the clear from perception, for which the accommodation and acute image are indispensable, becomes to play an important part to discern the object.

V Visual axis

In general, the visual axis can be defined as the line of most acute vision, and in foveate animals it passes through the fovea and center of the lens. In animals lacking a fovea, but having an area of high cone density, a line from the center of the area through the center of the lens may be considered the visual axis. Since the fish examined in this study do not have foveae, the latter definition applies. Thus the fishes with area in the dorso-temporal, temporal and ventro-temporal have visual axes extending, respectively, into the lower-fore, fore, and upper-fore regions of the visual field. It may further be assumed that the line of greatest accommodation will coincide with the visual axis.

Table 8 compares these two sets of data (taken from Tables 5 and 7) for 14 species. Among them, cone density of *Pseudoblennius* was not measured, but a typical fovea could be seen in the temporal region of retina. Columns 1 and 2 show the regions of highest and second highest cone density, while columns 3 and 4 show the directions of highest and second highest accommodation. Agreement between the two sets of observations is almost perfect. The direction of the visual axis is noted in column 5.

Girella and *Lateolabrax* are the only two cases showing disagreement. In *Girella*, this is readily explained by negligible differences in cone density between the ventro-temporal and temporal regions. Assuming them to be the same, the direction of the axis is determined by the line of greatest accommodation (Fore). In *Lateolabrax* there is a

* Pigment auf der Papille, Ausstrahlung des Sehnerven, Arterie des Processus falciformis etc.

Table 8. Direction of visual axis

Species	After Table 5		After Table 7		Direction of Visual axis decided from left columns
	Retinal region of highest density of cones (No. of cones)	Retinal region of second highest density of cones (No. of cones)	Direction of highest myopia (Refraction in Diop.)	Direction of second highest myopia (Refraction in Diop.)	
<i>Pagrosomus major</i>	Dorso-temporal (303)	Dorsal (240)	Lower-fore (-16.5)	Fore (-10.5)	Lower-fore
<i>Sparus hasta</i>	Dorso-temporal (400)	Temporal (147)	Lower-fore (-13.0)	Fore (-11.2)	Lower-fore
<i>Evynnis japonicus</i>	Dorso-temporal (570)	Temporal (393)	Lower-fore (-13.0)	Fore (-11.8)	Lower-fore
<i>Leiognathus argenteus</i>	Dorso-temporal (236)	Temporal (209)	Lower-fore (-14.0)	Fore (-14.0)	Lower-fore
<i>Xesurus scalprum</i>	Dorso-temporal (252)	Ventro-temporal (236)	Lower-fore (-10.5)	Fore ¹ (-9.7)	Lower-fore
<i>Epinephelus septemfasciatus</i>	Temporal (1050)	Nasal (253)	Fore (-14.0)	Upper-fore (-7.1)	Fore
<i>Sebastiscus marmoratus</i>	Temporal (380)	Dorso-temporal (105)	Fore (-12.3)	Upper-fore (-6.9)	Fore
<i>Therapon oxyrhynchus</i>	Temporal (133)	Nasal (93)	Fore (-14)	Upper-fore (-10)	Fore
<i>Seriola quinqueradiata</i>	Temporal (292)	Ventral (264)	Fore (-12)	Lower-fore (-8.3)	Fore
<i>Girella punctata</i>	Ventro-temporal (244)	Temporal (237)	Fore (-13.5)	Lower-fore (-7.3)	(Fore)
<i>Pseudoblennius totomius</i>	Fovea exists in the temporal region of retina		Fore (-25)	Upper-fore (-10)	Fore
<i>Lateolabrax japonicus</i>	Temporal (259)	Ventro-temporal (158)	Upper-fore (-13.6)	Fore (-12.9)	(Fore-upper-fore)
<i>Trachurus japonicus</i>	Ventro-temporal (288)	Ventral (272)	Upper-fors (-20)	Fore (-16)	Upper-fore

difference in the density between the temporal and ventro-temporal regions, but temporal region, which has the highest density, covers a broad area. Also, accommodation differs by only 0.7 of a diopter between the upper-fore and fore directions, so the visual axis is fore-upper-fore, a compromise between the two.

The relative positions of the ligamentum suspensorium and retractor lentis in respect to the lens offers a third means of estimating the visual axis. Three arrangements were found in the fishes examined (Fig. 9). The fishes listed in Table 7 a have the ligament attachment on the naso-dorsal surface of the lens and the muscle attachment on the ventro-temporal surface of the lens. Contraction of the muscle would move the lens up and back towards the dorso-temporal region of the retina. This is consistent with other evidence that the visual axis in this group is lower-fore in direction. Similarly, the fishes in Table 7 b have the ligament attached dorsally and the muscle ventrally, indicating that

the lens accommodates on the fore axis; those in Table 7 c have the ligament attached dorso-temporally and the muscle attached ventro-nasally, indicating lens movement along the upper-fore axis.

Direction of accommodation was estimated in this way for eight species where live specimens could not be obtained for optical methods.

Fig. 10 shows that *Cantherines modestus*, *Helicolenus dactylopterus*, and *Scomber japonicus* probably move the lens along the fore axis, whereas *Priacanthus boops*, *Malakichthys wakiyae*, *Zenion japonicum*, *Argentina semifasciata* and *Chlorophthalmus albatrossis* probably move it along the upper- upper-fore axis. This is consistent with the topography of the retina, for the first group has the highest cone density in the temporal region, and the second group has the highest cone density in the ventral region.

The ecological significance of different visual axes is quite obvious when one considers the feeding behaviour of the various fish that have been examined. *Pagrosomns*, *Sparus*, *Evynnis*, *Leiognathus* and *Xesurus*, which have lower-fore visual axes, consistently picked over the bottom of the aquarium in search of food. They are generally classed as bottom feeders. *Epinephelus*, *Sebastiscus*, and *Pseudoblennius*, which have somewhat conspicuous areae temporales and fore visual axes, display a tendency to take food in front of them. These fish are known to live in among rocks and seaweed in nature, where they attack small animals that pass by them. It was also noted in the aquarium that their eyes have considerable scope of movement and are often focused simultaneously on objects in front of them, indicating the importance of binocular vision to them. Aquarium observations were inadequate on *Therapon*, *Cantherines*, *Chelidonichthys*, *Sphaeroides*, *Seriola*, and *Girella*, which also have fore visual axes. *Lateolabrax*, *Trachurus* and *Priacanthus*, judged to have upper-fore axes, tended to take food ahead and above them in the aquarium. This was particularly true for *Priacanthus*, which ordinarily paid no attention to food of not moving unless it was in the upper-fore or upper portion of the visual field.

It must not be forgotten, however, that the entire monocular field, usually about 180°, is quite important to all fish. Peripheral perception of movement for which high

Fig. 9. Three types of attaching points.
S : Suspensory ligament, M : Retractor muscle.

Fig. 10. The attaching point in some fishes.
From left to right; upper row, *Cantherines modestus*, *Helicolenus dactylopterus* and *Scomber japonicus*; lower row, *Priacanthus boops*, *Malakichthys wakiyae*, *Zenion japonicum*, *Argentina semifasciata* and *Chlorophthalmus albatrossis*.

acuity is not essential facilitates their detection of prey and predator over the entire visual field.

VI Binocular visual field

The binocular field, which is present to a greater or lesser extent in most fishes, is formed by the the anterior overlap of the wide monocular fields. Its width is perhaps indicative of its functional significance. In general, fish that live among rocks and seaweeds in the littoral zone and prey on other small organisms have the wider fields. However, it must be remembered that the field is not rigidly fixed, since the eye of fish rotate independently. In the present study, the width of the binocular field has been measured at eight elevations.

Method : Specimens were anaesthetized and fixed in a transparent chamber so that they could be rotated around the horizontal and vertical axes (Fig. 11). The eyes were then viewed through the same ophthalmoscope with which refractions were measured. Any point from which both eyes reflected light was assumed to be in the binocular field. At each elevation the fish was rotated clockwise around the vertical axis until the limit of reflection was reached in the right eye. The fish was then rotated counterclockwise until the limit was reached in the left eye. From the included angle (β), the distance between the vertical axis and the eyes of the fish (L), the interorbital distance (d), and the distance between the observation point and vertical axis (L), the width of the binocular field was found by drawing a figure like Fig. 12.

Fig. 11. Schema showing the method of measuring the extent of binocular field.
M : Mirror, VA : Vertical axis, HA : Horizontal axis, RE : Right eye of the fish.

Results : The results are clearly summarized in Table 9. All the species examined have definite binocular fields. Although the data indicate that the field covers a rather broad vertical range, it is noteworthy that the widest angle, in each case, is aligned with the visual axis.

Summary and Conclusion

1. Three properties of the eye which are important in visual acuity were investigated : the resolving power of the dioptric system, the resolving power of

Fig. 12. The method of finding the binocular field (BF) from the rotated angle (β) etc.
E : Observation point, VA : Vertical axis.

Table 9. Width of the binocular field at various elevations

Species	Direction of visual axis	Elevation of visual direction							
		-60°	-40°	-20°	0°	20°	30°	40°	60°
<i>Pagrosomus major</i>	Lower-fore	—	26°	28°	24°	20°	18°	10°	14°
<i>Evynnis japonicus</i>	Lower-fore	—	24	26	22	19	15	10	12
<i>Sparus hasta</i>	Lower-fore	10	25	26	21	17	15	10	13
<i>Leiognathus argenteus</i>	Lower-fore	19	18	23	18	15	—	9	6
<i>Xesurus scalprum</i>	Lower-fore	1	12	15	15	13	—	13	12
<i>Epinephelus septemfasciatus</i>	Fore	—	15	17	32	28	—	20	—
<i>Sebastiscus marmoratus</i>	Fore	—	—	20	34	28	—	20	6
<i>Therapon oxyrhynchus</i>	Fore	—	—	23	30	27	—	18	—
<i>Lateolabrax japonicus</i>	For- upper-fore	—	—	8	12	17	20	19	12
<i>Trachurus japonicus</i>	Upper fore	—	—	13	15	22	23	20	18

O is in the horizontal plane, negative angles below it and positive angles above it. The direction of the visual axis is taken from Table 8.

the retina, and the extent of accommodation.

2. The resolving power of the crystalline lens, the only dioptric element responsible for image formation in fishes, ranged 54–90 seconds of arc for lenses over about 5 mm in diameter.

3. Cone density varies by species and by regions of retina. The best retinal acuity was 4.2 minutes of arc, so that the retina, not the lens, limits visual acuity.

4. All eyes examined were either emmetropic or hypermetropic in untreated living fish which was fixed rigidly in a tank between two pieces of rubber sponge, but became myopic in certain directions upon injection of atropine or curare, or upon sectioning of the optic nerve.

5. The axis of greatest accommodation was lower-fore in *Pagrosomus*, *Sparus*, *Evynnis*, *Leiognathus* and *Xesurus*; fore in *Epinephelus*, *Sebastiscus*, *Therapon*, *Girella* and *Pseudoblennius*; and fore-fore-upper or upper-fore in *Lateolabrax* and *Trachurus*. These axes are usually served by the retinal region of highest cone density.

6. There is a relationship between attachment points of the suspensory ligament and retractor lentis and the axis of accommodation. From this relationship and the region of highest cone density, the visual axis was determined for some species not available in living condition. They are: fore in *Cantherines*, *Helicolenus*, and *Scomber*; upper-upper-fore in *Priacanthus*, *Malakichthys*, *Zenion*, *Chlorophthalmus* and *Argentina*.

7. The binocular field tends to be broadest in the direction of the visual axis.

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