Guanine-type retinal tapetum and ganglion cell topography in the retina of a carangid fish, *Kaiwarinus equula*

Shiro Takei and Hiroaki Somiya*

Faculty of Bioresources, Mie University, 1515 Kamihama, Tsu, Mie 514-8507, Japan

A guanine-type retinal tapetum was recorded in the eyes of a carangid fish *Kaiwarinus equula* (= *Carangoides equula*), spectrophotometric evidence of such being presented. The total amount of guanine in one eye was about 6.5 mg, the guanine density being *ca.* 1.3 mg cm⁻² over the retinal surface area. To examine the guanine distribution within the retina, the latter was divided into 21 regions. An area of high guanine density (more than 2.0 mg cm⁻²) was observed in the dorsal fundus of the retina, suggesting that the most sensitive vision was checked downward. Using whole-mount retinal preparations, the distribution of Nissl-stained cells within the retinal ganglion cell layer was examined. The greatest cell density area (area centralis) was observed only in the temporal retina. The visual acuity of the area centralis was 4.3 cycles deg⁻¹, suggesting that high resolution and binocular vision were directed frontally in this species. The eyes of a related carangid (*Pseudocaranx dentex*), lacking a tapetum, were also examined for comparison. The possible ecological advantage resulting from the tapetum is discussed in terms of visual threshold.

Keywords: *Kaiwarinus equula*; eye shine; guanine-type retinal tapetum; locus tapetalis; ganglion cell distribution; visual acuity

1. INTRODUCTION

The eyes of whitefin kingfish, *Kaiwarinus equula* (= *Carangoides equula*) (Perciformes: Carangidae), exhibit a conspicuous 'eye shine', indicative of a tapetum lucidum. On the other hand, striped jack, *Pseudocaranx dentex* (Carangidae), the most closely related shallow water species (Gushiken 1988; Kijima *et al.* 1986), lack a tapetum. Whitefin kingfish occur in deeper water on the continental shelf edge (at 100–200 m depths) (Suzuki 1962; Gushiken 1983; Masuda *et al.* 1984; Smith-Vaniz 1986), feeding upon small fishes and crustaceans in the sandy mud. Although tapeta are specific visual adjuncts for dim light vision in fishes (Denton 1970; Locket 1977; Somiya 1980, 1982; Nicol 1989; Douglas *et al.* 1998), to our knowledge such structures have never before been described for a carangid fish. Therefore, we undertook a study of the structure of the tapetum in whitefin kingfish and the chemical nature of the reflecting materials. In addition, tapetal distribution and the topography of cells within the retinal ganglion cell layer were examined, to understand the regional relationship between the 'locus tapetalis' for sensitive vision (Somiya *et al.* 2000) and the 'area centralis' for acute vision (Collin & Pettigrew 1988a) in the retina. The eyes of striped jack were also described for comparative purposes and a possible ecological advantage resulting from the tapetum was discussed in terms of visual threshold. This is the first report of guanine-type retinal tapetum in the eyes of a carangid fish.

2. MATERIAL AND METHODS

Three specimens (154–171 mm in standard length (SL)) of whitefin kingfish (*K. equula*) were collected from the Sea of Kumano (off Owase, Mie prefecture) for biochemical identifi-

cation of the reflecting materials in the eyes. Extraction of the reflecting substances from the retina, and the spectrophotometric techniques employed in this study, were described by Nicol & Van Baalen (1968). Guanine was converted to uric acid and the change in absorbance at 290 nm related to that of a known amount of guanine. The retina was divided into 21 pieces and the guanine content of each piece was measured spectrophotometrically. The retinal surface area (cm²) was measured from whole-mount preparations of the fish retina with the aid of a camera lucida and the computer program NIH IMAGE (<http://rsb.info.nih.gov/nih-image/>).

For histological and whole-mount retinal preparations, six specimens (110–179 mm in SL) were sampled from the East China Sea and preserved in 10% neutralized formalin. The eyes of a related carangid fish, striped jack (*P. dentex*) (327–392 mm in SL), were also examined. These were obtained from a commercial supplier. Histological sections were made by conventional methods, part of the retina being embedded in epon araldite, cut into 1–2 µm radial sections and stained with toluidine blue. Whole-mount preparations of the retina were made according to the protocol of Ito & Murakami (1984).

Nissl-stained cells within the retinal ganglion cell layer were counted according to the method of Collin & Pettigrew (1988a). All neural elements (ganglion cells and displaced amacrine cells) containing Nissl substance in their cytoplasm, and lying within the retinal ganglion cell layer, were counted (Uemura *et al.* 2000). Therefore, the densities (and retinal resolving powers, see below) calculated represent upper limits, which should be revised downwards when data from retrograde transport studies separate the ganglion cells from displaced amacrine cells (Collin & Partridge 1996). However, in other studies of teleost retinæ, Collin & Pettigrew (1988b) found that such displaced amacrine cells occupy non-specialized regions, the topography and peak densities of true populations of ganglion cells remaining unchanged. For this reason, no corrections were made for any overestimations of ganglion cell counts in the present study.

*Author for correspondence (somiya@bio.mie-u.ac.jp).

Figure 1. (a,b) Lateral view of the head of a whitefin kingfish (*Kaivarinus equula*) (171 mm in SL) and striped jack (*Pseudocaranx dentex*) (333 mm in SL), respectively, photographed using a flashgun. Scale bars, 10 mm. (c,d) Dissected retinal cup and view of fundus of whitefin kingfish and striped jack, respectively. Scale bars, 5 mm.

Figure 2. Radial sections (2 μm) of the dorsal retinae of (a) a whitefin kingfish (154 mm in SL) and (c) striped jack (327 mm in SL), observed by light microscopy. Radial sections (7 μm) of the dorsal retinae of (b) whitefin kingfish (154 mm in SL) and (d) striped jack (327 mm in SL) observed by dark-field metal microscopy. The 10 layer elements shown in (a) and (c) include the following: 1, pigment epithelium layer; 2, visual cell layer; 3, external limiting membrane; 4, outer nuclear layer; 5, outer plexiform layer; 6, inner nuclear layer; 7, inner plexiform layer; 8, ganglion cell layer; 9, nerve fibre layer; 10, internal limiting membrane. Scale bar, 50 μm .

The number of ganglion cells per $0.2 \times 0.2 \text{ mm}^2$ of whitefin kingfish (123 mm in SL) and striped jack (333 mm in SL) retinae were counted at 1.3 and 1.0 mm intervals, respectively, under a light microscope, with the aid of a calibrated eyepiece. The sampling points in whitefin kingfish and striped jack numbered 124 and 438, respectively. The values for the ganglion cells were converted into numbers of cells per square millimetre. Peak retinal resolving power (theoretical visual acuity) was esti-

ated according to the protocol of Collin & Pettigrew (1989), the values thus obtained representing upper limits.

3. RESULTS

(a) *Eye shine and retinal tapetum*

Strong eye shine was observed only in whitefin kingfish (not in striped jack) when illuminated with a flashgun

Figure 3. Ultraviolet absorption spectra of tapetal extracts from a whitefin kingfish (K) (171 mm in SL), striped jack (P) (392 mm in SL) and authentic guanine (G) in 0.1 M NaOH.

(figure 1*a,b*). When the pre-retinal ocular media (cornea, lens and vitreous body) of the whitefin kingfish was stripped off, a tapetum, chalky-white in colour, was seen to occupy the dorsal region of the retinal eye cup (figure 1*c*). This indicated that the tapetum was distributed mainly on the dorsal two-thirds of the retina. By contrast, a similar chalky-white area was not observed in the retina of striped jack (figure 1*d*).

The retinal organization of each species was very similar, except for guanine and melanin distribution (figure 2*a,c*). The total thickness of the dorsal retina in whitefin kingfish (123 mm in SL) and striped jack (327 mm in SL) was nearly equal, being *ca.* 280 and 270 μm , respectively. The retina was composed of 10 layers of elements, including populations of cones (twin or double, and single) and rods in both carangid species. Pigment epithelial cells in both species were thick (*ca.* 70 μm in each), with well-developed processes (figure 2*a,c*). However, whereas the pigment epithelial cells of whitefin kingfish contained numerous brown tapetal materials and few melanin granules, those of striped jack enclosed only numerous melanin granules. Indeed, reflecting iridescence in the pigment cell layer was observed in the retina of whitefin kingfish only with the aid of dark-field metal microscopy (Nikon ME600L, an episcopic/diascopic illumination-type industrial microscope) (figure 2*b,d*),

Figure 4. Intra-retinal guanine distribution in the left eye of a whitefin kingfish (171 mm in SL). Abbreviations: OC, optic cleft; D, dorsal; N, nasal; T, temporal; V, ventral; asterisk, optic papilla. Scale bar, 5 mm.

suggesting that the reflecting tapetum occurred only in the pigment epithelial cells of the retina in whitefin kingfish (figure 2*b*).

(b) Tapetum: chemical nature and retinal distribution

To identify the reflecting substance of the tapetum, the ultraviolet (UV) spectrum (220–350 nm) of tapetal extracts from whitefin kingfish was measured and compared with that of authentic guanine in 0.1 M NaOH (figure 3). The absorption profile of the tapetal extract and authentic guanine were the same, clearly indicating that the main tapetal material of whitefin kingfish is guanine.

The eye of the 171 mm SL whitefin kingfish contained 6.5 mg of guanine per eye, its retinal surface area being 580 mm^2 . The mean calculated tapetal content of guanine was 1.1 mg cm^{-2} of the entire retinal surface area. The guanine content of each of the 21 regions examined is shown in figure 4. High guanine content (2.0–2.5 mg cm^{-2}) within the retinal area was observed only in the naso-dorsal fundus (figure 4), the guanine content data corresponding to the external chalky-white tapetal area are shown in figure 1*c*. In a previous paper (Somiya *et al.* 2000) on the retinal tapetum of bigeye tuna (*Thunnus obesus*), the retinal area of higher guanine content (greater than 2.0 mg cm^{-2}) was defined as a 'locus tapetalis'. In the whitefin kingfish, such a 'locus tapetalis' corresponded to the naso-dorsal fundus (figure 4), a significant area (total of 60 mm^2) with no guanine being observed in the ventral retina of the fish (figure 4). Accordingly, the true guanine content of the retinal surface was recalculated, excluding the 'guanine-absent' region, as 1.3 mg cm^{-2} of the retinal surface area.

Figure 5. Schematic diagrams of the lateral view of the eye of (a) a whitefin kingfish (123 mm in SL) and (b) striped jack (333 mm in SL). Outer parts (cornea and iris) of eye removed to show relative positions of ligaments and lens muscle. Abbreviations: EM, thin elastic membrane; L, lens; LM, lens muscle; SL, suspensory ligament; TL, thick transparent ligament. D, dorsal; N, nasal; T, temporal; V, ventral. Scale bar, 5 mm.

Figure 6. Topography of the ganglion cells in the retinas of (a) a whitefin kingfish (123 mm in SL, lens diameter of 6.1 mm) and (b) striped jack (333 mm in SL, lens diameter of 8.1 mm). Abbreviations: OC, optic cleft; OP, optic papilla; D, dorsal; N, nasal; T, temporal; V, ventral. Scale bar, 5 mm.

(c) Visual axis and ganglion cell topography

(i) Visual axis

To estimate the visual axis of the eye, the accommodation system was examined (figure 5), the arrangements of such in both carangid species being basically the same as in bass (Somiya 1987). A single lens muscle (retractor lentis muscle) was observed in each eye, the nasal part of the muscle being attached to the lens by a thick transparent ligament extending as a thin elastic membrane towards the nasal margin of the iris (figure 5). The posterior end of the muscle was tightly attached to the ventral margin of the iris by a thick ligament and lens suspended by a tough transparent ligament from the dorsal margin of the iris (figure 5). These arrangements of the accommodation system in both carangid species indicated that their lens movement was from nasal to temporal, i.e. the visual axis of both fishes was directed frontally.

(ii) Ganglion cell topography and visual acuity

All ganglion cells (including displaced amacrine cells) lying within the retinal ganglion cell layer in each fish species were counted. Consequently, all calculated densities and acuities are upper estimates. The retinal surface areas measured from the whole-mount preparations were

198 mm² in whitefin kingfish (123 mm in SL) and 535 mm² in striped jack (333 mm in SL), an average number of 1.7×10^3 ganglion cells mm⁻² over 124 points and 1.1×10^3 cells mm⁻² over 438 points being counted, respectively. Therefore, the total number of ganglion cells in the whole retina was estimated as *ca.* 340×10^3 in whitefin kingfish and 600×10^3 in striped jack.

The distribution pattern of ganglion cells was non-uniform. Isodensity contour maps shown in figure 6a (whitefin kingfish) and figure 6b (striped jack) resembled each other, a well-defined area centralis being apparent in the temporal retina in both species. This supports the idea that the visual axis of these fishes is directed frontally, as predicted by the arrangement of the accommodatory apparatus described above (figure 5). A weak horizontal visual streak was also observed just above the optic papilla in both species.

In the retina of the whitefin kingfish, the peak density of ganglion cells was 4.1×10^3 cells mm⁻², the theoretical acuity based on ganglion cell density being 4.3 cycles deg⁻¹, using Matthiessen's ratio (2.55, lens diameter of 6.1 mm). In striped jack, the peak density was 2.7×10^3 cells mm⁻² and the calculated acuity was 4.7 cycles deg⁻¹ (lens diameter of 8.1 mm). This clearly indicated that the theoretical

Figure 7. Intra-retinal relationship between guanine distribution and ganglion cell topography in the retina of a whitefin kingfish. Height represents ganglion cell density and gradation of black shading represents guanine content. Abbreviations as in figures 4–6.

acuity of striped jack retina is slightly better than that of whitefin kingfish. In both species, minimum counts of 0.9×10^3 cells mm^{-2} (whitefin kingfish) and 0.5×10^3 cells mm^{-2} (striped jack) were observed in the dorsal retina, giving a ratio of maximum to minimum ganglion cell density of *ca.* 5 : 1 in both species.

Table 1. Tapetum in perciform fishes.

order, family, species	chemical	morphology	reference
Perciformes			
Centropomidae			
<i>Centropomus undecimalis</i>	lipid ^a	retinal tapetum	Eckelbarger <i>et al.</i> (1980)
Acropomachidae			
<i>Howella</i> sp.	lipid ^b	retinal tapetum	Best & Nicol (1978)
Percidae			
<i>Stizostedion vitreum</i>	pteridine ^c	retinal tapetum	Zyznar & Ali (1975)
Priacanthidae			
<i>Priacanthus arenatus</i>	guanine	choroidal tapetum	Nicol & Zyznar (1973)
<i>Pristigenys niphonia</i>	guanine	choroidal tapetum	Somiya (1980)
Epigonidae			
<i>Epigonus atherinoides</i>	guanine	choroidal tapetum	Somiya (1980)
Carangidae			
<i>Kaiwarinus equula</i>	guanine	retinal tapetum	present study
Haemulidae			
<i>Orthopristes chrysopterus</i>	lipid ^a	retinal tapetum	Zyznar & Nicol (1973)
Polynemidae			
<i>Polydactylus octonemus</i>	lipid ^b	retinal tapetum	Nicol <i>et al.</i> (1973)
Sciaenidae			
<i>Cynoscion arenarius</i>	lipid ^a	retinal tapetum	Nicol <i>et al.</i> (1972)
Ephippidae			
<i>Chaetodipterus faber</i>	lipid ^b	retinal tapetum	Nicol <i>et al.</i> (1973)
Scombridae			
<i>Thunnus obesus</i>	guanine	retinal tapetum	Somiya <i>et al.</i> (2000)
Gempylidae			
<i>Ruvettus pretiosus</i>	guanine ^b	choroidal tapetum	Locket (1977)

^a Lipid: glyceril tridocosaeanoate.

^b No chemical evidence.

^c Pteridine: 7, 8-dihydroxanthopterin.

(d) Guanine and ganglion cell distribution

Figure 7 illustrates the regional relationship between the guanine distribution ('locus tapetalis') and the area centralis in the retina of whitefin kingfish. From figure 7, it is clear that ganglion cell distribution did not correspond to that of guanine, although moderate amounts of guanine (1.6 mg cm^{-2}) were observed around the area centralis.

4. DISCUSSION

(a) Guanine-type retinal tapetum in perciformes

A guanine-type retinal tapetum was observed for the first time in the eyes of a demersal carangid (whitefin kingfish), but not in its most closely related benthopelagic relative (striped jack) (Smith-Vaniz 1986). To our knowledge, this is the first report of a guanine-type retinal tapetum in the eyes of a carangid fish and only the second report of such in perciform fishes (table 1). Although a guanine-type retinal tapetum is most common in Teleostei (Somiya 1980; Nicol 1989; Douglas *et al.* 1998), having been recorded in at least seven orders (table 2), it is considerably less common in perciform fishes, compared with guanine-type choroidal and lipid-type retinal tapeta (table 1).

In the guanine-type retinal tapetum (table 2), the guanine contents per eye (milligrams per eye) vary considerably, from 0.05 mg in *Gymnarchus niloticus* to 88 mg in *T. obesus*. However, the mean guanine contents of the retinal area lie between 1.0 and 2.6 mg cm^{-2} , except in the deep-sea polymixiid fishes (10.5 mg cm^{-2}). This indicates that

Table 2. Guanine content in the guanine-type retinal tapetum in Teleostei.

order, family, species (SL)	mg per eye	mg cm ⁻²	reference
Osteoglossiformes			
Notopteridae			
<i>Notopterus chitala</i> (7 cm)	0.59	2.3	Somiya (1991)
Mormyridae			
<i>Marcusenius longianalis</i> (7.5 cm)	0.37	2.3	Somiya (1989)
Gymnarchidae			
<i>Gymnarchus niloticus</i> (9 cm)	0.05	0.98	Somiya (1991)
Elopiformes			
Elopidae			
<i>Elops saurus</i> (29 cm)	8.6	2.3	Ito & Nicol (1981)
Clupeiformes			
Engraulidae			
<i>Anchoa mitchilli</i> (9 cm)	0.46	—	Zyznar & Nicol (1973)
Aulopiformes			
Chlorophthalmidae			
<i>Chlorophthalmus albatrossis</i> (15 cm)	3.01	2.6	Somiya (1980)
Polymixiiformes			
Polymixiidae			
<i>Polymixia japonica</i> (16 cm)	18.7	10.5	Somiya (1980)
Bericiformes			
Bericidae			
<i>Beryx splendens</i> (32 cm)	66	2.0	S. Takei and H. Somiya (unpublished results)
Perciformes			
Carangidae			
<i>Kaiwarinus equula</i> (17 cm)	6.5	1.3	present study
Scombridae			
<i>Thunnus obesus</i> (ca. 120 cm)	88.6	1.25	Somiya <i>et al.</i> (2000)

whitefin kingfish have a common level of guanine (1.3 mg cm⁻²) per retinal area.

(b) *Tapetum distribution and the 'locus tapetalis'*

In the bigeye tuna (*T. obesus*), the highest level of guanine content (2.2 mg cm⁻²) was observed only around a small ventro-temporal part (area centralis) of the retina, the term 'locus tapetalis' being suggested for this area of highest guanine level (Somiya *et al.* 2000). A similar positional coincidence of the 'locus tapetalis' and area centralis has been reported in the pelagic deep-sea fishes *Howella sherborni* and *Diretmus argenteus*. In the retina of *Howella*, Best & Nicol (1978) described a lipid tapetum only in the temporo-ventral region of the retina, and Collin & Partridge (1996) found an area centralis in that tapetal area of the temporal retina. Furthermore, in *Diretmus*, Munk (1966, 1982) reported cone localization in the tapetal region of the ventro-temporal retina. It is possible that the area centralis in such deep-sea fish species may have two functions: to guarantee high visual acuity, and to allow for high photosensitivity in dim light. Indeed, bigeye tuna swim within the first 100 m below the surface at night and at depths of between 400 and 500 m during the day (Dagorn *et al.* 2000). *Howella* also undergoes extensive vertical migrations from 30 m at night to 300–1800 m during the day (Best & Nicol 1978).

By contrast, in the tapetum of whitefin kingfish, the 'locus tapetalis' (more than 2.0 mg guanine cm⁻²) was observed in the dorsal retina (figure 4), the area centralis being in the temporal retina (figure 6a). Although the retinal part occupied by the tapetum varies interspecifically,

this dorsal type of tapetal distribution is common in many freshwater and shallow-water marine species (Nicol 1981), including the Florida garfish (*Lepisosteus platyrhincus*, Lepisosteidae) (Collin & Collin 1993). In the eyes of cartilaginous fishes, Denton & Nicol (1963) noted that only benthic species had a bright dorsal tapetum and black ventral field. This relationship between a benthic lifestyle and the dorsal tapetum may also be plausible for ray-finned fishes (Actinopterygii). In fact, the whitefin kingfish is a bottom dweller (Smith-Vaniz 1986), possessing a dorsal tapetum and black ventral retina without a tapetum (figures 1c and 4). The black ventral field may be correlated with the greater intensity of downwelling light, perhaps to minimize glare (Eckelbarger *et al.* 1980; Douglas *et al.* 1998). Thus the dorsal distribution of the tapetum may be an adaptive type for benthic species, in which the 'locus tapetalis' and area centralis may not co-occur.

Accordingly, fish tapeta may be divided into two types on the basis of the positional relationship between the tapetum ('locus tapetalis') and the area centralis. One is the coincident-type tapetum, which exists on the area centralis, possibly being linked with a pelagic deep-sea lifestyle, i.e. bigeye tuna, *Howella* and *Diretmus*. The other is the non-coincident type (or dorsal tapetum), which may be linked with a benthic lifestyle, as in whitefin kingfish. In fish species with a dorsal tapetum, the area centralis is either temporal, dorso-temporal or ventro-temporal. Indeed the demersal Florida garfish, characterized by a dorsal tapetum, has a temporal area centralis (Collin & Northcutt 1993). However this topic requires future research.

Figure 8. (a) Distribution of light intensity in the sea estimated from the attenuation coefficient (modified from fig. 7 of Miyazaki *et al.* (2000)). (b) Relationship between depth and distance from the coast on the continental shelf. Abbreviations: K, threshold of whitefin kingfish; P, threshold of striped jack.

(c) *Ecological advantage of a tapetum in whitefin kingfish*

Here we speculate on a possible ecological advantage given by the presence of a tapetum in the eyes of whitefin kingfish compared with the lack of such in striped jack. The eyes of both whitefin kingfish and striped jack exhibiting similar retinal structures and ganglion cell distribution, excepting the retinal tapetum, support the 'closest genetic relationship' of the species within the family Carangidae (Gushiken 1988; Kijima *et al.* 1986). Accordingly, it is proposed that the common ancestor of both species lacked a tapetum in the eyes, having a visual sensitivity very similar to that of striped jack.

Using behavioural experiments on school formation, Miyazaki *et al.* (2000) reported the light intensity threshold of striped jack (120 mm in SL) as 5×10^{-4} lx. If a common ancestor, lacking a tapetum, had a similar order of visual threshold, how much improvement in sensitivity at threshold light levels would be achieved by the presence of a tapetum? According to a theoretical study (Zyznar 1975), even under optimal conditions, the presence of a tapetum can increase light absorption by a factor of only *ca.* 1.5. Therefore the maximum improved sensitivity granted by the presence of a tapetum in a descendant (= whitefin kingfish) can be calculated as 3.3×10^{-4} lx (= 5×10^{-4} lx per 1.5). Although this gain in sensitivity is small (Muntz 1990), the speculated threshold (3.3×10^{-4} lx) for whitefin kingfish is realistic and comparable to that (2.6×10^{-4} lx) of the eye in adult northern anchovy, *Engraulis mordax* (Hunter & Nicholl 1985), which possesses a guanine-type retinal tapetum (Zyznar & Nicol 1973; Zueva 1981). Therefore, we consider that the eyes of whitefin kingfish may have the same order of sensitivity (10^{-4} lx) as those of the anchovy.

Figure 8, which examines the possible ecological advantage resulting from the presence of a tapetum, shows the relationship between depth and attenuation ($k = 0.088 \text{ m}^{-1}$) measured in the sea off Goto Island (Nagasaki prefecture, Japan), where both whitefin kingfish and striped jack occur. Under a full moon, striped jack can descend to 60 m, where the light intensity is *ca.*

5×10^{-4} lx. Conversely, whitefin kingfish can descend 5 m deeper, because the light level at a depth of 65 m in the sea is *ca.* 3.3×10^{-4} lx (figure 8a). This 5 m depth extension of the visual world is the net ecological gain conferred by the tapetum. Although apparently small, such an extension is, in fact, a specific annex of the invisible world, based on the rationale that in the extended space only fishes with a tapetum can see their prey, most of those without a tapetum being unable to do so. Herein lies the real advantage of the ocular tapetum.

The present study suggests that whitefin kingfish have wide and highly sensitive tapetal vision, mainly directed downward for prey detection. This is reflected in whitefin kingfish living at a deeper level on the continental shelf (at 100–200 m depths) and feeding upon prey on the sandy mud substrate (Suzuki 1962; Smith-Vaniz 1986). According to Weyl (1970), the average width of continental shelves worldwide is about 70 km, with a slope of 2 m km^{-1} (figure 8b). This indicates that benthic fishes with a tapetum, having a 5 m visibility extension, such as whitefin kingfish, will gain 2.5 km of extra continental shelf for feeding. The importance of such a gain is that only fishes with a tapetum can find prey on the extended space. The widespread occurrence of a tapetum among nocturnal animals and those inhabiting dimly lit environments would seem to be linked with such an advantage. The visual threshold of fish eyes with a tapetum will be the subject of future research.

Parts of this study were carried out at the Fisheries Research Laboratory (Wagu) and on the training ship *Seisui Maru*. The authors thank Dr S. Kimura and Director I. Ishikura as well as other staff for their kind hospitality, and Dr Graham Hardy for his critical reading of the paper.

REFERENCES

- Best, A. C. G. & Nicol, J. A. C. 1978 Notes on the retina and tapetum lucidum of *Howella* (Teleostei: Cheilodipteridae). *J. Mar. Biol. Assoc. UK* **58**, 735–738.
- Collin, S. P. & Collin, H. B. 1993 The visual system of the Florida garfish, *Lepisosteus platyrhincus* (Ginglymodi). I. Retina. *Brain Behav. Evol.* **42**, 77–97.

- Collin, S. P. & Northcutt, R. G. 1993 The visual system of the Florida garfish, *Lepisosteus platyrhincus* (Ginglymodi). III. Retinal ganglion cells. *Brain Behav. Evol.* **42**, 295–320.
- Collin, S. P. & Partridge, J. C. 1996 Retinal specializations in the eyes of deep-sea teleosts. *J. Fish Biol.* **49**(Suppl. A), 157–174.
- Collin, S. P. & Pettigrew, J. D. 1988a Retinal topography in reef teleosts. I. Some species with well-developed areas but poorly-developed streaks. *Brain Behav. Evol.* **31**, 269–282.
- Collin, S. P. & Pettigrew, J. D. 1988b Retinal topography in reef teleosts: a comparison between Nissl-stained material and retrograde labelling from optic nerve. *J. Comp. Neurol.* **276**, 412–422.
- Collin, S. P. & Pettigrew, J. D. 1989 Quantitative comparison of the limits on visual spatial resolution set by the ganglion cell layer in twelve species of reef teleosts. *Brain Behav. Evol.* **34**, 184–192.
- Dagorn, L., Bach, P. & Josse, E. 2000 Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Mar. Biol.* **136**, 361–371.
- Denton, E. J. 1970 On the organization of reflecting surfaces in some marine animals. *Phil. Trans. R. Soc. Lond. B* **258**, 285–313.
- Denton, E. J. & Nicol, J. A. C. 1963 The chorioidal tapeta of some cartilaginous fishes (Chondrichthyes). *J. Mar. Biol. Assoc. UK* **44**, 219–258.
- Douglas, R. H., Partridge, J. C. & Marshall, N. J. 1998 The eyes of deep-sea fish. I. Lens pigmentation, tapeta and visual pigments. *Prog. Ret. Eye Res.* **17**, 597–636.
- Eckelbarger, K. J., Scalan, R. & Nicol, J. A. C. 1980 The outer retina and tapetum lucidum of the snook *Centropomus undecimalis* (Teleostei). *Can. J. Zool.* **58**, 1042–1051.
- Gushiken, S. 1983 Revision of the carangid fishes of Japan. *Galaxea* **2**, 135–264.
- Gushiken, S. 1988 Phylogenetic relationships of the perciform genera of the family Carangidae. *Jpn. J. Ichthyol.* **34**, 443–461.
- Hunter, J. & Nicholl, R. 1985 Visual threshold for schooling in northern anchovy *Engraulis mordax*. *Fish. Bull.* **83**, 235–242.
- Ito, H. & Murakami, T. 1984 Retinal ganglion cells in two teleost species, *Sebastes marmoratus* and *Navodon modestus*. *J. Comp. Neurol.* **229**, 80–96.
- Ito, S. & Nicol, J. A. C. 1981 Guanine in the tapetum lucidum of the ladyfish, *Elops saurus* Linnaeus. *Contr. Mar. Sci.* **24**, 9–12.
- Kijima, A., Taniguchi, N. & Ochiai, A. 1986 Genetic relationships in the family Carangidae. In *Indo-Pacific fish biology* (ed. T. Ueno, R. Arai, T. Taniguchi & K. Matsuura), pp. 840–848. Tokyo: The Ichthyological Society of Japan.
- Locket, N. A. 1977 Adaptations to the deep-sea environment. In *Handbook of sensory physiology*, vol. VII/5 (ed. F. Crescitelli), pp. 67–192. Berlin: Springer.
- Masuda, H., Amaoka, K., Araga, C., Uyeno, T. & Yoshino, T. 1984 *The fishes of the Japanese archipelago*. Tokyo: Tokai University Press.
- Miyazaki, T., Shiozawa, S., Kogane, T., Masuda, R., Maruyama, K. & Tsukamoto, K. 2000 Development changes of the light intensity threshold for school formation in the striped jack *Pseudocaranx dentex*. *Mar. Ecol. Prog. Ser.* **192**, 267–275.
- Munk, O. 1966 On the retina of *Diretmus argenteus* Johnson, 1863 (Diretmidae, Pisces). *Vidensk. Meddr. Dansk. Naturh. Foren* **129**, 73–80.
- Munk, O. 1982 Cones in the eye of the deep-sea teleost *Diretmus argenteus*. *Vision Res.* **22**, 179–181.
- Muntz, W. R. A. 1990 Stimulus, environment and vision in fishes. In *The visual system of fish* (ed. R. H. Douglas & M. B. A. Djamgoz), pp. 491–511. London: Chapman & Hall.
- Nicol, J. A. C. 1981 Tapeta lucida of vertebrates. In *Vertebrate photoreceptor optics* (ed. J. M. Enoch & F. L. Tobey Jr), pp. 401–431. Berlin: Springer.
- Nicol, J. A. C. 1989 *The eyes of fishes*. Oxford, UK: Clarendon Press.
- Nicol, J. A. C. & Van Baalen, C. 1968 Studies on the reflecting layers of fishes. *Contr. Mar. Sci. Univ. Tex.* **13**, 65–88.
- Nicol, J. A. C. & Zyznar, E. S. 1973 The tapetum lucidum in the eye of the big-eye *Priacanthus arenatus* Cuvier. *J. Fish Biol.* **5**, 519–522.
- Nicol, J. A. C., Arnott, H. J., Mizuno, G. R., Ellison, E. C. & Chipault, J. R. 1972 Occurrence of glyceryl tridocosa-hexaenoate in the eye of the sand trout *Cynoscion arenarius*. *Lipids* **7**, 171–177.
- Nicol, J. A. C., Arnott, H. J. & Best, A. C. G. 1973 Tapeta lucida in bony fishes (Actinopterygii): a survey. *Can. J. Zool.* **51**, 69–81.
- Smith-Vaniz, W. F. 1986 Carangidae. In *Smith's sea fishes* (ed. M. M. Smith & P. C. Heemstra), pp. 638–661. Berlin: Springer.
- Somiya, H. 1980 Fishes with eye shine: functional morphology of guanine type tapetum lucidum. *Mar. Ecol. Prog. Ser.* **2**, 9–26.
- Somiya, H. 1982 'Yellow lens' eyes of a stomiatoid deep-sea fish, *Malacosteus niger*. *Proc. R. Soc. Lond. B* **215**, 481–489.
- Somiya, H. 1987 Dynamic mechanism of visual accommodation in teleosts: structure of the lens muscle and its nerve control. *Proc. R. Soc. Lond. B* **230**, 77–91.
- Somiya, H. 1989 Guanine-type retinal tapetum of three species of mormyrid fishes. *Jpn. J. Ichthyol.* **36**, 220–226.
- Somiya, H. 1991 Guanine used as retinal tapetal material in *Notopterus* and *Gymnarchus* (Osteoglossiformes, Notopteroidei). *Jpn. J. Ichthyol.* **37**, 418–420.
- Somiya, H., Takei, S. & Mitani, I. 2000 Guanine and its retinal distribution in the tapetum of the bigeye tuna, *Thunnus obesus*. *Ichthyol. Res.* **47**, 367–372.
- Suzuki, K. 1962 Anatomical and taxonomical studies on the carangid fishes of Japan. *Rep. Fac. Fish. Pref. Univ. Mie* **4**, 43–232.
- Uemura, M., Somiya, H., Moku, M. & Kawaguchi, K. 2000 Temporal and mosaic distribution of large ganglion cells in the retina of a daggertooth aulopiform deep-sea fish (*Anotopterus pharao*). *Phil. Trans. R. Soc. Lond. B* **355**, 1161–1166.
- Weyl, P. K. 1970 *Oceanography: an introduction to the marine environment*. New York: Wiley.
- Zueva, L. V. 1981 Retinal cones of the black sea anchovy *Engraulis encrasicolus*. An analyzer of polarized light in vertebrates. *J. Evol. Biochem. Physiol.* **17**, 420–425.
- Zyznar, E. S. 1975 Theoretical considerations about tapeta lucida. In *Vision in fishes* (ed. M. A. Ali), pp. 305–312. New York: Plenum Press.
- Zyznar, E. S. & Ali, M. A. 1975 An interpretive study of the organization of the visual cells and tapetum lucidum of *Stizostedion*. *Can. J. Zool.* **53**, 180–196.
- Zyznar, E. S. & Nicol, J. A. 1973 Reflecting materials in the eyes of three teleosts, *Orthopristes chrysopterus*, *Dorosoma cepedianum* and *Anchoa mitchilli*. *Proc. R. Soc. Lond. B* **184**, 15–27.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.