The Visual Cell Morphology of *Pagrus major* and Its Adaptive Changes with Shift from Pelagic to Benthic Habitats*¹

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The visual cell morphology in 2-90 mm long larvae and juveniles, and adult of the red sea bream *Pagrus major* was examined histologically. The visual system of the larvae is poorly developed at hatching, but becomes functional in 36 hours. At this time, the eyes are well pigmented, cones are formed, and optic nerves connect with the optic tectum. The visual cells of larvae smaller than 10.6 mm are all single cones. At 11 mm TL, the single cones fuse to form twin cones, and rods appear at the same time. Red sea bream shifts from a pelagic to a benthic habitat when about 12-15 mm long. The observed increase in visual sensitivity at 11 mm appears to be a pre-adaptation to life at greater depths. Likewise, the specialized retinal region for acute vision shifts from temporal to dorso-temporal at a length of 30 mm, implying a change in visual axis from fore to lower-fore direction, and an adaptation to the change in diet from planktonic to benthic animals.

Marine fishes are ideal for the comparative study of the ontogenetic development and functional morphology of the visual system. ALI¹⁾ reported that the eyes of the embryo of *Oncorhynchus* spp. contained only cones and no rods in the retina. Pure-cone retinæ have been demonstrated in the earliest stages of many teleosts from different families; the rods appear later.²⁻⁸⁾ BOEHLERT^{9,10)} examined the retinal development in postlarval through juvenile *Sebastes diploproa*, a rockfish which migrates from the surface waters of the California Current to depths of 250-500 m at the age of approximately one year. He noted the disappearance of single cones, persistence of twin cones, and increase in rod density, all in close temporal association with this change in habitat; the changes mark the shift from high visual acuity in surface prejuveniles to high sensitivity in benthic juveniles.

This paper reports changes in visual cell morphology with growth in red sea bream *Pagrus major*, a common sparid fish in waters around Japan, which changes from a pelagic to a benthic habit after metamorphosis. Undergoing a considerable change of photic environments, the adults are found predominantly at depths of 150 m or

more. At the larval stage, this species is a typical visual feeder and does not take food at night.¹¹⁾

Material and Methods

Red sea bream larvae and juveniles were obtained from 2 laboratory groups reared at different institutes, specimens at 6.0-17.4 mm total length (TL) from the Kagoshima Mariculture Center, and specimens as young as newly hatched larvae at 2.0 mm TL and fish up to 90.4 mm TL from the Fisheries Laboratory, Kinki University. A 320 mm long adult was obtained from a local supplier in Kagoshima. Specimens larger than 90.4 mm were not examined because it is possible that real differences in morphological characteristics and growth exist between wild and reared ones.¹¹⁾

The retinæ of the specimens were examined histologically. The fish were light-adapted, then preserved in Bouin's solution. The small fish (less than 17 mm) with intact eyes were embedded in paraffin, and 4-6 μ m thick sagittal and transverse sections were made. Serial tangential sections at the bottom of the retina and cross sections of the other retinal parts were also obtained. The

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eyes from larger individuals were enucleated, and three retinal parts (temporal, dorso-temporal, and bottom) were removed and oriented in paraffin to allow tangential or cross sections. The retina of the adult fish was divided into 33 parts and cross and tangential sections were made. All sections were Azan-stained.

From tangential sections, cone types and their density and arrangement were determined. Cross sections were used to determine rod density. Following BLAXTER and STAINES,⁴⁾ the nature of the visual cells was ascertained by making counts of the distinct ellipsoidal structures (the cone ellipsoids) in the visual cell layer, and of the cell nuclei in the

outer nuclear layer in the cross sections.

Total lengths were measured after preservation; the rate of shrinkage is about 15% for larvae and 1–10% for juveniles.¹²⁾

Results

Larvae and Juveniles

In the newly hatched larvae, the eyes are not pigmented and the lens and retina are poorly differentiated (Plate I. A). The lens cells are arranged spherically and the cells in the inner retinal layer are arranged radially. At 10 hours from hatching, the lens cells show the first signs of for-

Fig. 1. Change in the nuclei-cone ratio and in thickness of outer nuclear layer in the retinae of red sea bream. The ratio exceeded 1.0 when the fish were 11 mm long and the rods appeared, and subsequently increased with growth. The thickness also increased with growth showing an increase in rod density. Closed circle, reared at the Fisheries Laboratory, Kinki University; open circle, reared at the Kagoshima Mariculture Center. Vertical bars through circles show the range of ratio calculated. Total length of the fish is shown in log scale.

Plate 1

Photomicrographs showing the development of the eye of red sea bream. Abbreviations: CO, cone; G, ganglion layer; IC, inner nuclear layer; IP, inner plexiform layer; L, lens; ON, outer nuclear layer; PE, pigment epithelium; R, retina; NM, free neuromast. Scale, 30 μm.

- Newly hatched larva.
- Larva at 26 hours from hatching.
- Larva at 36 hours from hatching.
- Larva at 36 hours from hatching. Optic nerve fibers leaving the eye and decussating with fibers from the other eye can be seen (arrows).
- Tangential section showing a regular arrangement of single cones of 7 mm TL fish.
- Tangential section showing a regular quadrilateral cone pattern of 17 mm TL fish.

mation of two layers, and the retinal cells increase in number. At 26 hours from hatching (2.7 mm), pale pigmentation is seen, the outer nuclear layer (visual cell nuclei) is developed, the inner and outer plexiform layers are formed, but no optic nerve fibers can yet be seen (Plate I, B). At 36 hours from hatching, the eye is well pigmented, cones are formed, and optic nerve fibers can be seen leaving the eye, decussating with fibers from the other eye, and leading into the tectum (Plate I, C and D). At 60 hours from hatching (3.1 mm) cones increase in number, and the pigment epithelium layer is thick. The larvae start feeding on the third day.

The visual cells in larvae smaller than 11 mm TL are all single cones; there are neither twin cones nor rods (Plate I, E). Twin cones were found at 11, 13.5, and 14 mm long, arranged irregularly and not in any mosaic. A regular quadrilateral cone pattern is found in fish larger than 17 mm (Plate I, F). Rods first appear at 11 mm long, and the density increases with growth, notably beyond 35 mm (Fig. 1).

Adult

A regular arrangement of twin and single cones can be seen in tangential sections of the retina. The cone pattern consists of quadrilateral units, each formed by four twin cones surrounding a central single cone. The ratio of single to twin cones is 1:2 over the entire retina. Cone density varies by region of the retina. As already noted

Fig. 2. Cone density topography in the adult fish retina. Number of single and twin cones in 0.01 mm² was counted in the tangential sections and its distribution shown by isodensity lines. B, bottom; D, dorsal; T, temporal; V, ventral; N, nasal.

by TAMURA,¹³⁾ the highest cone density in red sea bream is in the dorsal to dorso-temporal retinal region (Fig. 2), indicating a visual axis in the lower-fore direction. The nuclei-cone ratio varies from 15 to 28 by region, highest at the bottom.

Specialization in Cone Density

Most fishes have an area somewhat specialized

Fig. 3. Degree of specialization of the retina of red sea bream at different lengths. For the small fish (less than 17 mm) cone density was determined from cross sections and for large fish it was determined from tangential sections. Note that the lines cross between 28 mm TL and 32 mm TL showing the most specialized region shifted from temporal to dorso-temporal regions. Open and closed circles, same as in Fig. 1.

for more acute vision, even though true areae or foveae may be absent. In the red sea bream, such specialization is found at 3.1 mm long. Single cones are elongated and the visual cell layer is thicker in the temporal and nasal parts. To obtain a comparable index of this specialization,¹³⁾ the ratio of cone density in the temporal and dorso-temporal regions to the density in the bottom region was calculated (Fig. 3). From this, it appears that the most highly specialized region in the retina of the red sea bream is the temporal region in the young larvae, but shifts to the dorso-temporal region at 30 mm long.

Discussion

Ontogenetic Development of Visual Cell Morphology and Behaviour

The eyes of the red sea bream can be considered functional at 36 hours from hatching when visual cells and pigments are present and nerve fibers from the retinal ganglion cells connect with the optic tectum. In larval sardine and anchovy, the visual system was considered functional as the optic nerves reached the tectum¹⁴⁾; in the larval *Oplegnathus fasciatus*,⁷⁾ *Takifugu rubripes*,* and *Paralichthys olivaceus*,* phototaxis and feeding were observed when the eyes became pigmented and the visual nerve fibers from the retina made the connection with the tectum. Red sea bream at the yolk-sac stage (24 hours from hatching) with non-functional visual system, exhibits regular movement up and down a water column that correlates well with diel changes in solar irradiance.¹⁵⁾ Such behaviour may be due to extraretinal photosensitivity, an ability that has been demonstrated in blind herring.¹⁶⁾ At 11 mm TL, the red sea bream retina underwent a big morphological change: single cones fused to form twin cones and rods appeared for the first time, presumably increasing sensitivity to lower light levels. YANO and OGAWA¹⁷⁾ observed changes in the vertical distribution of red sea bream larvae with changes in light intensity, and found that the light intensities at the depths preferred by the larvae at 5–7, 13–15, and 19–21 mm long were 1600–2200, below 200, and 70–100 lx respectively. This change in preferred light intensity with growth can be attributed to the change in visual sensitivity, and can be related to the change in habitats.

Change in Habitat and Adaptive Change in Morphology

The larvae of red sea bream are known to have a vertical distribution ranging from surface to 50 m deep, with greater numbers at relatively deep layers.¹⁸⁾ While the small larvae less than 8 mm long are commonly collected with the larva net, larger larvae are usually very few, although HASEGAWA *et al.*¹⁹⁾ reported high catch of 10–15 mm red sea bream with the larva net off Noto Peninsula in the Japan Sea. TANAKA²⁰⁾ noted that the red sea bream larvae collected with the larva net from the East China Sea and the coastal waters of Kyushu had maximum lengths of 14–15 mm TL, regardless of collection ground, season, and towing method. On the other hand, the common minimum size of the red sea bream collected with various bottom-operated fishing gear,^{21–27)} or from the stomach contents of benthic predators²⁷⁾ is 10–15 mm TL. Considering the avoidance of samplers,^{20,28)} and the mesh selectivity of bottom-operated gear,²¹⁾ we agree with TANAKA²⁰⁾ who concluded that the red sea bream shifts from a pelagic to a benthic mode of life when they attain a length of 12–15 mm TL.

The red sea bream at 12–15 mm has already undergone metamorphosis. Segmentation of soft rays is almost completed and fin branching is observed,^{30,31)} scale formation begins,³²⁾ the black-striped pigmentation is in progress,³³⁾ swimming speed and distance markedly increase,^{34–36)} and larger food is preferred.³⁷⁾ The rate of organ development of the red sea bream larvae varies with temperature and the quality of food given,¹¹⁾ and one has to be careful in relating the morphology of reared fish to the behaviour of wild ones. Nevertheless, there is no doubt that many changes in morphology and behaviour of this species occur in temporal association with its migration from the surface waters to the benthic habitat.

The increase in visual sensitivity at 11 mm TL is an adaptation to the prevailing lower levels of irradiance in the deeper waters. The shift in visual axis from fore to lower-fore direction at around 30 mm TL is an adaptation to the change in diet and feeding habit. According to OMORI,²²⁾ the stomach contents of the red sea bream juveniles caught with bottom operated gear in Yuya Bay facing the East China Sea show typical diurnal feeding with peaks in the morning and late afternoon. Diet consists predominantly of zooplank-

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ton such as copepods (mostly *Acartia clausi* which swarm at the bottom³⁸⁻⁴⁰) and appendicularians in fish at 20-30 mm long, but changes to caprellidean amphipods in fish at 30 mm long, and to tubicolous gammaridean amphipods in fish at 70 mm long.²² A similar change in stomach contents is also seen in juveniles from Shijiki Bay.³⁸ All the observed changes in visual morphology and behaviour together with other features in larval development in the red sea bream occur prior to, and presumably in anticipation of, the change in habitat and habits.

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