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Retinal Topography in Reef Teleosts

II. Some Species with Prominent Horizontal Streaks and High-Density Areae

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Key Words

Fish
Retina
Ganglion cell
Horizontal streak
Vision

Abstract

The retinal ganglion cell layer of five species of reef teleosts was studied from Nissl-stained whole-mounts and the distribution of neural elements determined quantitatively. Iso-density contour maps of neurons in the ganglion cell layer revealed a temporal area centralis (ranging from 3.5 to 8.3 x 10^4 cells/mm^2) which often extended into a horizontal streak (ranging from 1.4 to 5.0 x 10^4 cells/mm^2) across the retinal meridian. Species possessing a marked horizontal streak were found to inhabit open water and perceive their environment with an uninterrupted view of sand-water horizon. The behavioural significance of these horizontal areas of acute vision is also discussed.

Introduction

Chievitz [1889, 1891] and Slonker [1897] were the first to describe horizontal band-shaped retinal areae in vertebrates. These band-shaped areae are often associated with a thickening of the retina [Munk, 1970] often observable without the use of light microscopy. Most early workers believed that these areae were regions allowing increased resolving power. Walls [1942], however, suggested that they may be areae of increased sensitivity, as he thought foveate areae were imperfect insofar as they contain both rods and cones. More recent studies of ungulates [Hebel, 1976], rabbits [Hughes, 1971; Provis, 1979] and a number of marsupials, however, have demonstrated the presence of a strong visual streak based only on the density of neuronal elements in the ganglion cell layer; the anatomical requirements for increased resolving power are thus actually present.

The biological significance of these band-shaped areas was originally thought to be associated with anjg ma*s living in open country [Pumphrey, 1948; Luck, 1965] or on the ground [Brown, 1969]. After extends studies of a number of mammals the 'terrain theory' of Hughes [1977] suggested that the distribution of
ganglion cells acroslathe retina depends on the symmetry or openness of the perceived world.

Horizontal band-shaped areae have been foun^tri. only a limited number of teleosts however. A single horizontal band-shaped area exists in *Fundulus hetero-clitus* [Butcher, 1938], *Boleophthalmus sculptus*, *Peri-ophthalmus sobrinus*, *P. koelreuteri africanus* [Munk, 1970] and two were found in *Aplocheilus lineatus\Eng*-strom, 1963] and *Epiplatys grahami* [MuflH 1970]. A more recent study of ganglion cell densities also found that an open water balistid, *Navodon*, possesses a horizontal streak [Ito and Murakami, 1984].

It is postulated that these zones allow the animal to scan a broad horizon without the distinctive eye movements needed for scanning with an area centralis [Rowe and Stone, 1977; Tancred, 1981] and to perceive movement at a lower threshold. Their importance has also been emphasized by the tectal projection of the horizontal area in *Rana temporaria* and *Alligatorjfmississippiensis* [Jacobsen, 1962; Heric and Kruger, 1965] and *Tyto* and *Speotyto* [Bravo and Pettigrew, 1981] which occupies a disproportionately large portion of the optic tectum.

This study provides quantitative values of cell den-Hies within the ganglion cell layer of five species of

Table I. Summary of the habitat and methods of feeding of the five [1982] and direct observations species under investigation, compiled from Carcasson [1977], Grant

Species	Family	Preferred habitat	Method of feeding	Position of area centralis	Cells x lOVmm^2
Balistoides conspicilium (clown triggerfish)	Balistidae	open areas along edge ofreef crest	beak-like jaws disturb substrate in search of food	temporal temporal horizontal streak	5.1 4.2 3.5
Choerodon albigena (blue tuskfish)	Labridae	areas of coral rubble	foraging, able to move large pieces of coral andffiimgle	dorso-temporal temporal horizontal streak	8.3 8.0 5.0
Aulostoma chinensis (painted flutemouth)	Aulostomidae	**over** deep gutters of coral along edge	flanks other 'cover-^^H to approach unsuspecting prey	dorso-temporal horizontal streak	4.6 1.4
Lethrinus chrysostomas (red-throated emperor)	Lethrinidae	semi-pelagic species of the open water	nocturnal predator, although may be seen picking over substrate during day	dorso-temporal temporal horizontal streak	3.5 5.0 4.0
Gymnocranius bitorquatus (collared sea bream)	Lethrinidae	over open areas of coral rubble and sand	sifts through sand and coral rubble with prominent mouth	dorso-temporal horizontal streak	6.3 2.0

The retinal positions of the areae central are given with their corresponding cell densities.

reef teleosts that possess a prominent horizontal streak in conjugation with an area centralis. The relevance of these retinal specialisations is discussed in relation to other species that occupy a different ecological niche [Collin and Pettigrew, 1988].

Materials and Methods

A summary of the five teleosts species investigated is presented in table I. Brief descriptions of species' niche and feeding strategies are provided for simple comparison. Three adults were used in each case, allowing six retinal examinations per species.

Technique

The techniques employed were those described jniCollin and Pettigrew [1988], utilising the retinal wholemount technique described by Stone [1981], followed by staining for Nissl substance of ElMfound in the ganglion cell layer. Cell counts were made and densities of stained cells were determined for both eyes. Using a Jena DK2 microfiche reader, the outline of each retinal whole-mount was traced onto 1-cm^2 grid paper at a magnifjcatioxhof 20, with care taken to keep the edge of the microscope slide paralJMtoj the grid. The vernier scale on a Leitz Dialux 20 compound microscope was then matched to this grid paper by noting the position of obvious landmarks in the wholemount. A graticule of 100 squares (magnification calibrated for each objecti^); placed into the eyepiece, was used to define areas for counting at an overaf^magnifi-cation of 500 or 1,000. Numbers of cells within each graticule square were counted every 0.05 mm on the retina. In areas of higher density, cell numbers were counted every 0.025 mm on the retina*? These numbers were then converted to cells per square millimetre.

Fig. 1. The upper diagram irijtais and figure 2, 3, 5 and 6 ij^^ trates the iso-density contour map otftgmwithiMthe ganglion cell layer over the left retina. The clown triggerfish, *Baj^^^^&onspi-cillum* (Balistidae, Actinopterygii) possesses ahorizontal streak of 3.5 xlO^{4} cells/mm^{2} and two temporal zones of 5.1 xlO^{4} and 4.2 x 10^{4} cells/mm^{2}, respectively. This colourful species, adapted for catching molluscs and crustaceans, existsjin enclosed areas but EenGires out to more openiareas in search of food. Scale bar = 45 mm. In tfitsland figure 2, 3, 5 and 6 the lower right diagram is a schematic representation of the marine habitat on the reef, showing a cross-secti<Mof the various niches inhabited by the teleosts iME^ study. Areas to the left of this figure depict caves and enclosed areas close to the reef crest and areas closer to the surface with a prevail-ance for staghorn coral. The right side depicts more open areas of sand and coral interposed with isolated coral outcrops which would provide some protejSfiuon for species escaping predation. *B. wonsutcuntm* is depicted as a silhouette in a positi'olQl'Ulustrjating its preference for semi-open coral zones or within sandy gutf^^H

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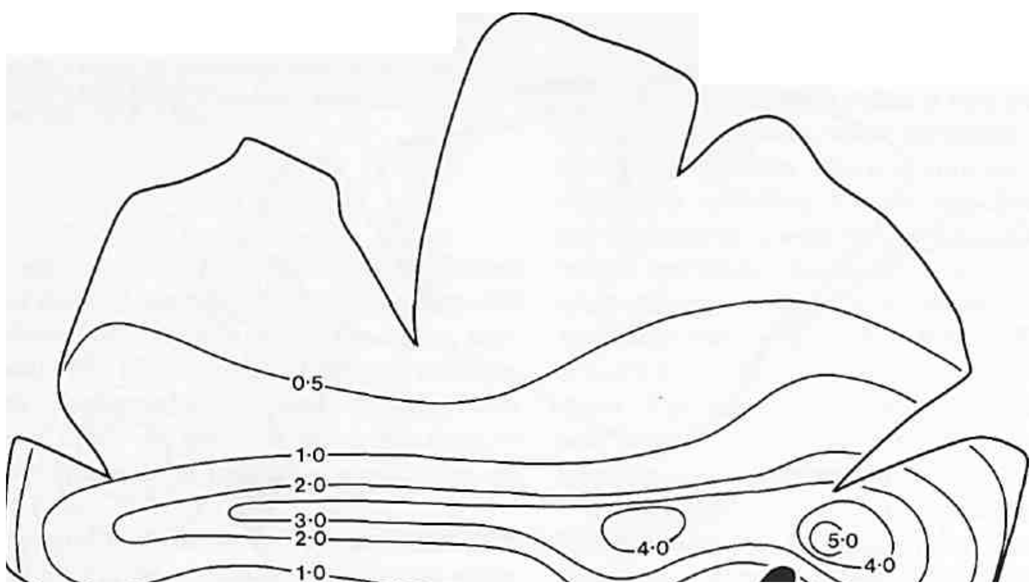
BALISTOIDES CONSPICILLUM LEFT EYE. X10^{4} cells/mm^{2}
TEMPORAL



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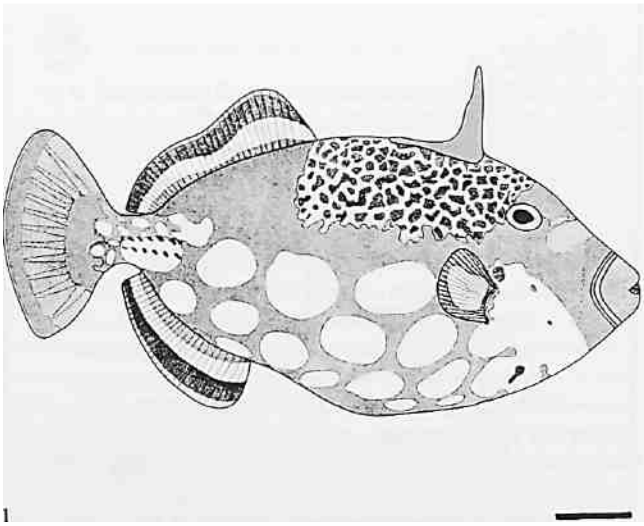

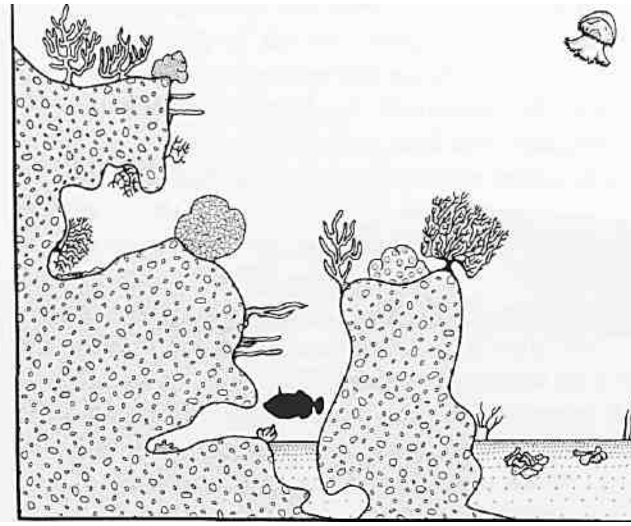

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DORSAL
AULOSTOMA CHINENSIS LEFT EYE. X10^{4}cells/mm^{2}
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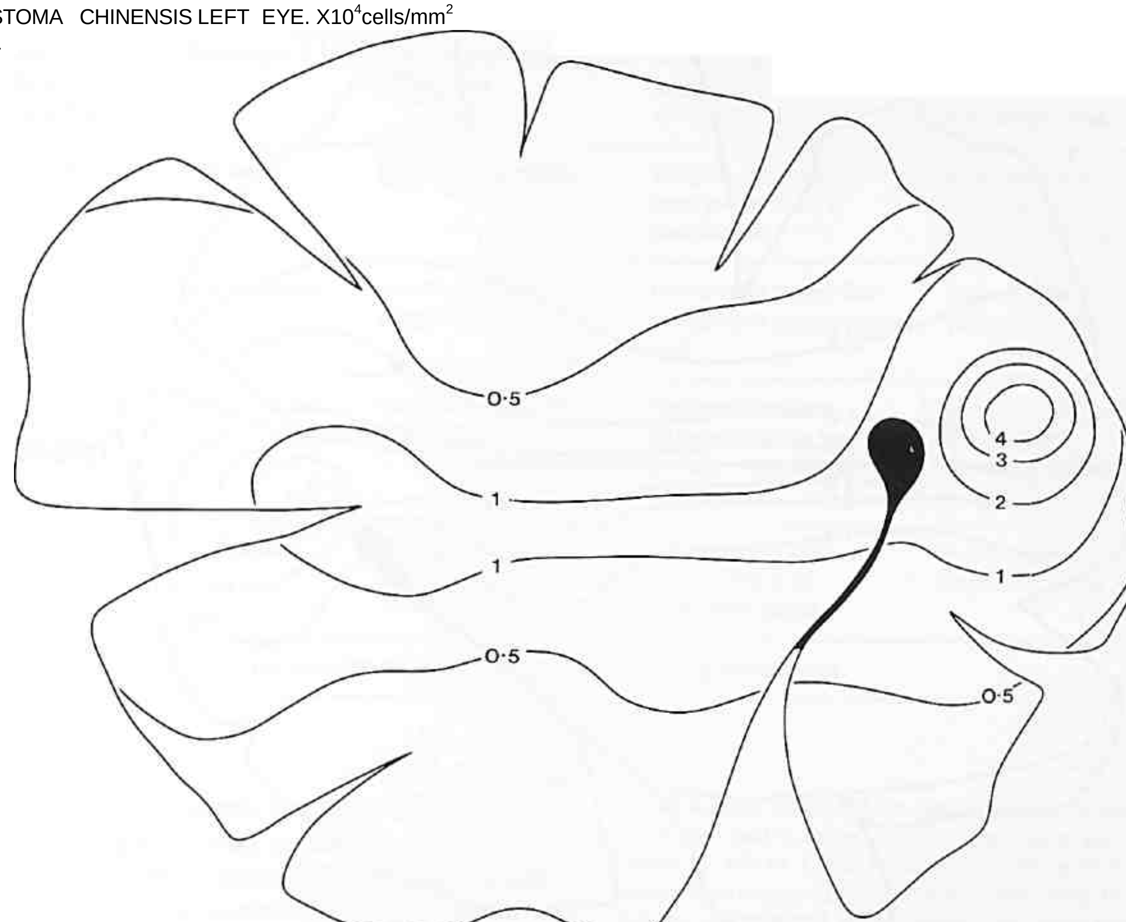

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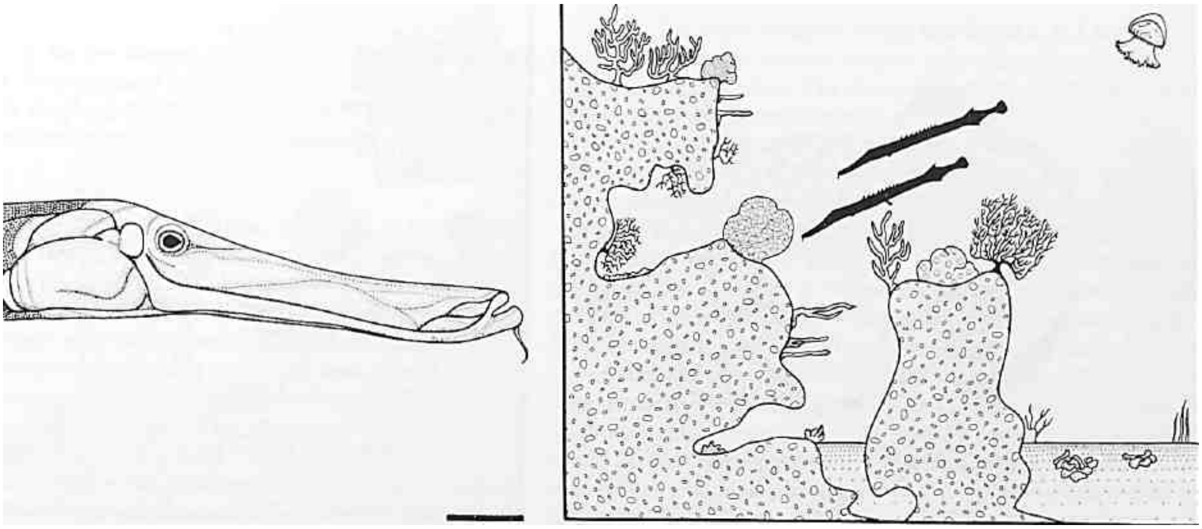

In this way, up to 500 areas per retina were sampled, allowing determination of small fluctuations in density. Iso-density contours were constructed by interpolation between the values of retinal ganglion cell density and used to determine the existence and topography of retinal specialisations in each species. Cells were viewed on a Leitz Dialux 20 compound microscope and photographed on Kodak Panatomic-X film using a green filter.

Results

The five species examined in this study all possess an increased density of cells within the ganglion cell layecMstributed horizontally across the retina, temporal to nasal. The arrangement of density contours varies both topographically and quantitatively among species. They all, however, share one thing in common, the openness of the environment they inhabit.

Any horizontal increase in cell density across the retinal meridian has been termed a horizontal streak by Hughes [1977] and such a streak dominates the retina of the clown triggerfish, *Balistoides conspicillum*, with a density of 3.5 x 10^4 cells/mm^2 (fig. 1). Two other areae centrales (5.1 x 10^4 and 4.2 x 10^4 cells/ mm^2) in the temporal retina, are also prellnt with a 10:1 gradient of cells from the area adjacent to the temporal margin of the retina to the periphery. The falciform process, an extension of the choroid projecting through the retina and along its vitreal surface, provides the retina with some nutrition and in this species emanates from the ventral margin temporally to end in an elongated optic nerve head. The cells are randomly arranged with a predominance of larger cells lying in tWperiphery.

Fig. 2. The painted fiutemouth, *Aulostoma chinensis* (Aulostom-idae, Actinopterygii), possesses an eightfold increase in ganglion cell density within a dorso-temporal zone of 4.6 x 10^4 cells/mm^2 situated close to the temporal margin of its retina. This highly developed specialisation is thought to reflect a fovea. The ability of the eye to focus on objects at greater distances within its binocular field is restricted by limitations on lens movement, the size of the eye and turbidity. Therefore, a foveal depression along with a marked frontal tapering of the pupil and a binocular sighting groove situated immediately in front of the eye (see illustration) may be a means of achieving improved fixation and sensitivity to movements of prey objects within the binocular field. A horizontal streak of lower density (1.4 x 10^4 cells/mm^2) also exists, consistent with the painted flutemoutrTs open habitat, hovering parallel to deep gutters as the silhouettes indicate, and often flanking herbivorous species over open areas of reef in search of food. Scale bar = 80 mm.

The painted fiutemouth *(Aulostoma chinensis)* possesses a streak (1.4 x 10^4 cells/mm^2) and, within the temporal retina, there exists an area centralis (4.6 x 10^4 cells/mm^2) with a ninefold increase in cell density relative to the periphery (fig. 2). The topography of the flutemouth's retina is very similar to that in the clown triggerfish, where the streak extends across the retinal meridian. This is in contrast to the retina of *Parapercis cylindrica* [Collin gnd Pettigrew, 1988], which possesses a weak horizontal streak dorsal to the retinal meridian. The density contours of the single temporal area cerBalis of *A. chinensis* are more tightly packed th^jthose of *B. conspicillum*, possibly due to a greater reliance Sa-binocular vision into frontal space. The presence of a binocular sighting groove and an acute ros^Sl tapering of the pupil provides some basis for this possibilffir-(fig. 2).

The remaining three species studies, the blue tusk-fcjM *(Choerodon albigena)*, the red throated emperor *(Lethrinus chrysostomas)* and the collared sea bream *(Gymnoc^mius bitorquatus)*, all possess dual speciali-sationslin corresponding regions of the retina. The retina of C. *albigena* is the most highly specialised and possesses greatly increased numbers of cells within the ganglion cell layer (fig|3). A dorso-temporal area centralis, which lies at the level of the optic nerve head in the temporal retina of this fish, contains the highest density of cells (8.3 x 10^4 cells/mm^2) of any area in tfflfive species studied. A second temporal area centralis (8.0 x 10^4 cells/mm^2) is situated near the falciform process and extends along the retinal meridian to form a hffizontal strem of between 4.0 x 10^4 and 5.0 x 10^4 cells/mm^2. Around the streak and between the temporal areae centrales is a zone of decreased cell density, best seen in figure 4. Due to the close proximity of the two temporal acute zones, it was necessary to increase the number of cell counts. This revealed a trough of decreased cell dens^S equaling half the peak values, and also indicated the presence of three areae centrales in the retina of *C. al-bigena.*

The temporal area centralis and horizontal streak configuration is most pronounced in *L. chrysostomas* (fig. 5) and *G. bitorquatus* (fig. 6). In *L. chrysostomas,* the horizontal streak possesses 5.0 x 10^4cells/$mm^2$and is a highly specific specialisation restricted to a thin band across the retinal meridian. Cell densities drop off markedly beyond the boundaries of this zone (fig. 7). The temporal area centralis is of lower density (3.5 x 10^4 cells/mm^2) and is less specialised. In con-

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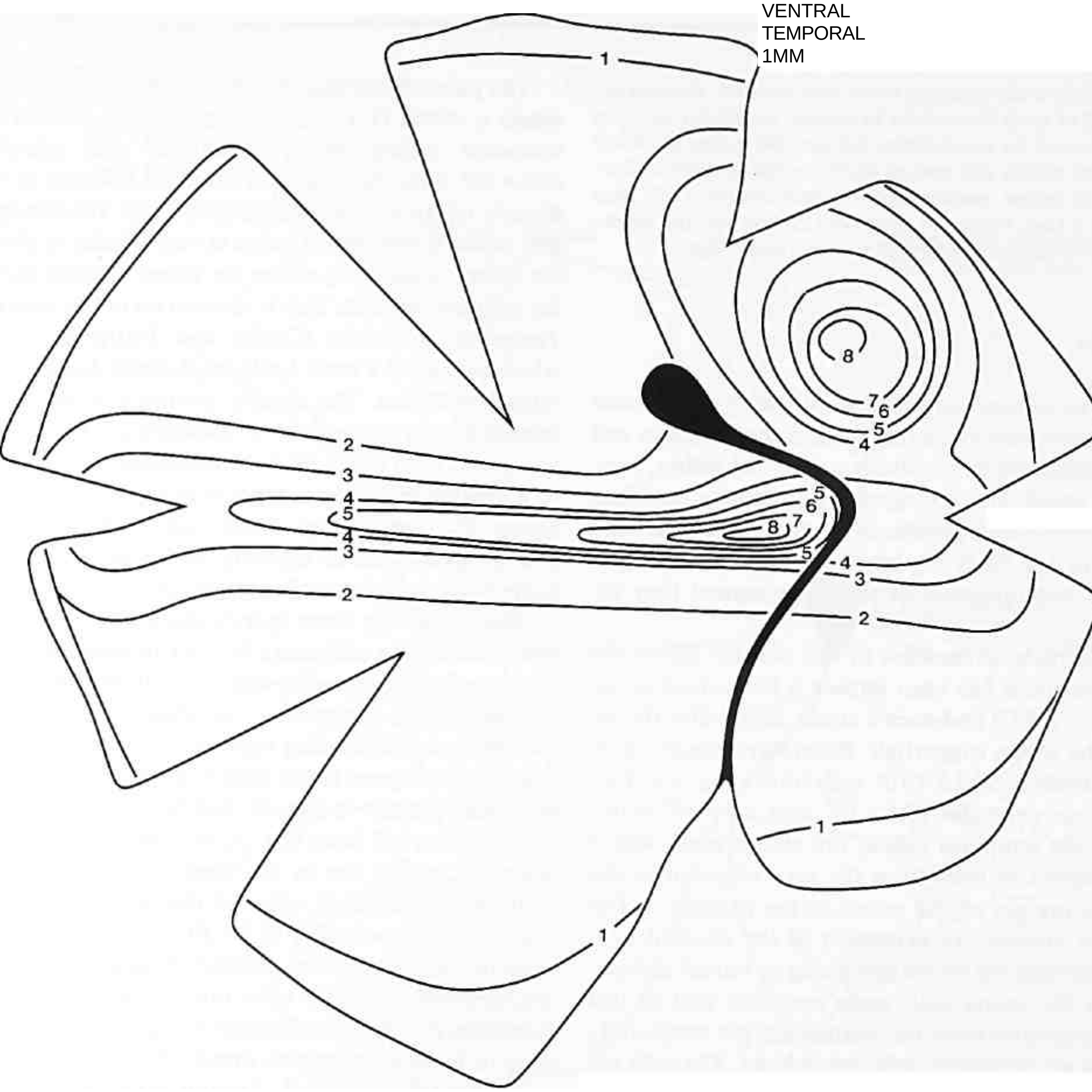
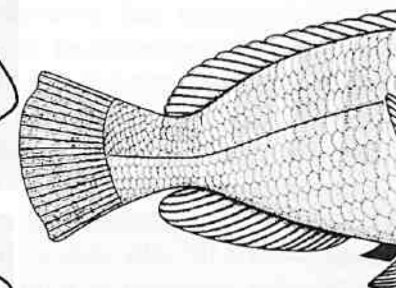
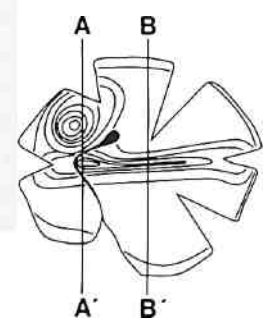


CHOERODON

ALBIGENA LEFT EYE.

X10*cells/mm^2





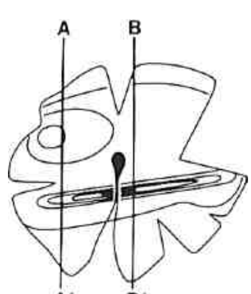


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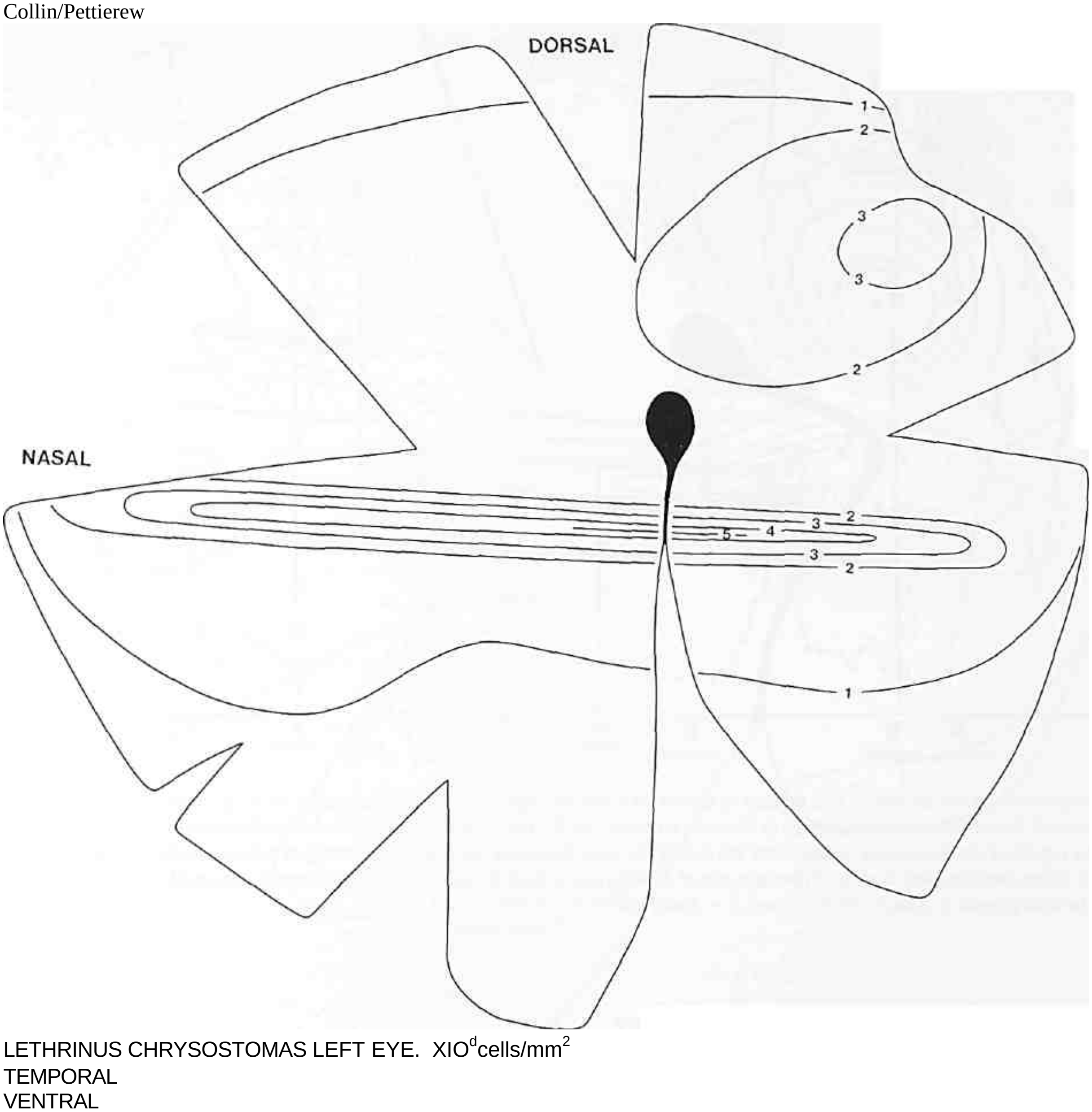
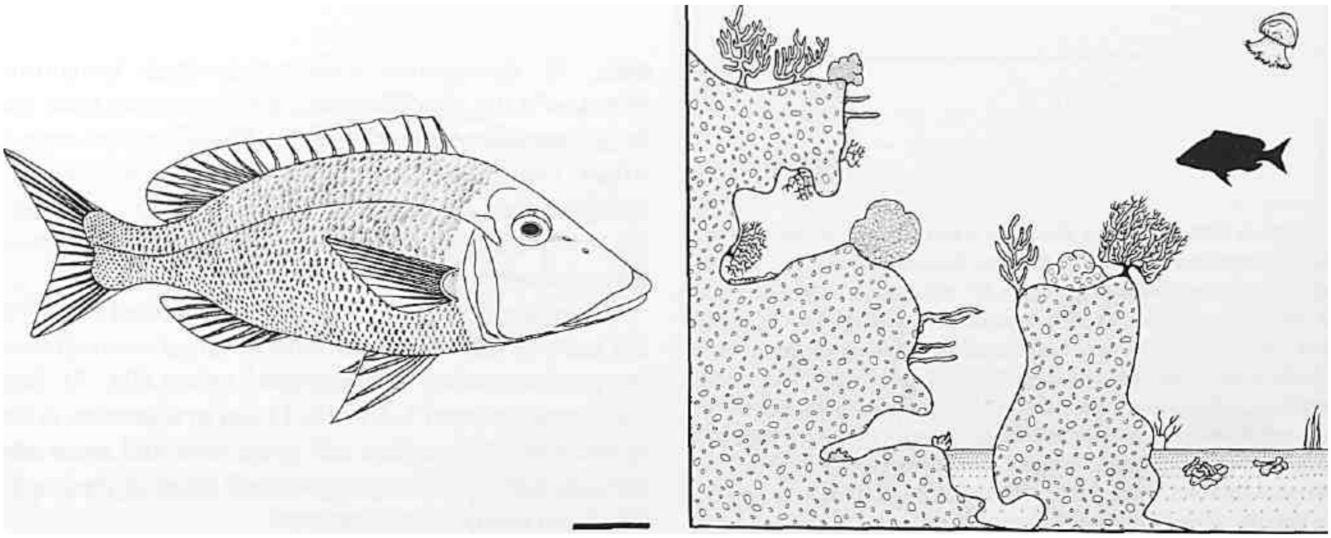
Fig. 4. a Cross-sectional cell counts of two regions of the retina fro^Ehe right eye of *L. chrysostomas.* A-A' transects both areas of increased ganglion cell density and reveals a trough in density (arrowed). B-B' illustrates non-specialised area densities with a large increase in density in the region of the horizontal streak. Note the size of the peak depicting the horizontal streak in relation to that of the temporal area centralis, b Cross-sectional cell counts of the right eye of C. *albigena* with A-A' also illustrating a trough (arrowed) between two specialised areas. In both graphs, Y-axes x 10^4 cells/mrn^2. T s Temporal^** ventral.

Fig. 3. Adaptations to the open water habitat of the blue tusk jjslg *Choerodon albigena* (Labridae, Actinopterygii), are denoted by a dorso-temporal zone of 8.3 x IO^4 cells/mm^2, a temporal zone of 8.0 x 10^4 cells/mm^2 and a horizontal streak of 5.0 x IO^4 cells/ mm^2. All zones have very high densities of ganglion cells, which signify high visual acuity for performing tasks related to feeding predator surveillance or mating. Note thefclose proximity of the two temporal zones and the reduction in density between them. The ^^Sike teeth are used to remove coral debris as the blue tusk fish searches for food in areas of open sand or coral shingle, as depicted by the silhouette. Scale bar « 50 mm.

trast, *G. bitorquatus* possesses a weak horizontal streak of 2.0 x IO^4 cells/mm^2, which extends from the falciform process to the nasal border of the retina, offset ventrally from the horizontal meridian.^ffts' dorso-temporal area centralis, which possesses 6.3 x IO^4 cells/mm^2, is aligned for vision in lower frontal space.

Classes of ganglion cells have been found in different parts of the retina with cells of larger soma diameter predominating in peripheral retina (fig. 7). Size classes range from 3–5 to 10–14 p,m in diameter. A detailed study of ganglion cell soma sizes and areas and the lamination of the ganglion cell layer in these species is currently being prepared.





Discussion

Retinal Topography

The clown triggerfish, *B. conspicittum* (Balistidae) and the painted flutemouth, *A. chinensis* (Aulostomi-dae) reveal a relatively pronounced horizontal streak in conjunction with a temporal zone of acute vision. This retinal topography reflects a change of ecological niche from cave-dwelling 'enclosed' species [Collin and Pettigrew, 1988] to the more open water spe-^S Deep terraced reef fronts and ledges provide a suitable habitat for *B. conspicittum* while it preys upon molluscs and other invertebrates with its large sharp teeth. When pursued, this territorial species retreats to a cave and is virtually immovable. The horizontal streak may be used for predatory surveillance of potential predators when swimming over areas of open water. The fixed orientation of the retina with the horizon can easily be observed in the feeding balistid, where compensatory eye movements are made as it manoeuvres its body in space. This species also swims with great speed when venturing from its territory and this horizontal area may aid in movement detection which would require a specific subset of ganglion cells. This has been found to be present in cats [Ro-dieck and Stone, 1965). Ali and Anctil [1976] also report on a specialised streak of photoreceptors across the retina of *Cantherines modestus* (Balistidae).

The eyes of *A. chinensis* are set laterally, well back on the head with the pupil markedly tapered frontally and a binocular sighting groove present on the snout to allow binocular fixation of prey objects in its frontal field. The retina reveals a ninefold increase in ganglion cell density from the periphery to a dorso-temporal zone situated just temporal of the large optic

Fig. 5. The red-throated emperor, *Lethrinus chrysostomas* (Leth-rinidae, Actinopterygii), is a fast-swimming nocturnal predator that roams over large expanses of reef. During photopic conditions the horizon (or sand-water interface) predominates its visual environment, and this is reflected in the iso-density contour map of cells within the ganglion cell layer as a strong horizontal streak of 4.0–5.0 x 10^4 cells/mm^2. This zone is a highly specialised area of acute vision across the horizontal meridian. In contrast, however, the temporal zone, used in feeding, possesses radial isptropy, possibly useful for feeding at night. This zone has 3.5 x 10^4 cells/mm^2 and frontal vision is aided by a binocular sighting groove. Scale bar = 60 mm.

nerve head (fig. 2). This temporal zone is extended into a horizontal streak across the retinal meridian. Such topography is consistent with a species for whom vision plays a more significantttle in feeding than in predator avoidance.

The remaining three species, C. *albigena*, *L. chrysostomas* and *G. bitorquatus* are all strictly open water species and, in their visual environment, th«and-water interface predominates.

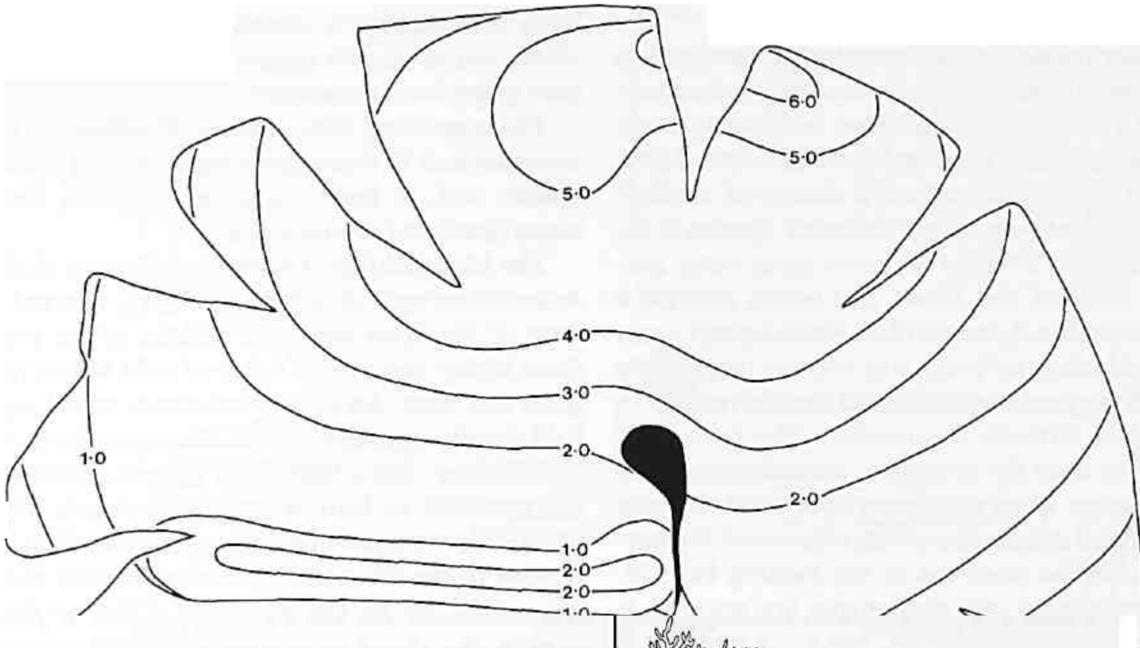
The blue tuskfish, *Choerodon albigena* (Labridae, Acanthopterygii) is a large, solitary, diurnal camjl vore of the open water. Its unique retina possesses three highly specialised zones of cells witlrothe ganglion cell layer. Two temporal zones reveal an eightfold density gradient of cells from peripheral to temporal retina, and a third zone extends along the retinal meridian to form a horizontal streak. The ganglion cells are tightly packed and in very high density relative to the other speci^ptudied [Collin an3$Petti-grew, 1988, fig. 8]. The proximity of the two temporal areas also reveals a functional phenomenon previously undescribed among vertebrates. The cell numbers at each peak are halved in the trough between them (fig. 4). This configuramn is also found to a lesser extent in *LWErysostomas.* The functional significance of this area of reduced activity, and even the existence of two closely allied specialisations, is difficult to interpret and has previously been described in only one other vertebrate species, the plains kangaroo [Hughes, 1974].

The red-throated emperor, *L. chrysostomas* (Leth-rinidae) possesses large eyes with well|pigmented irises and a reduced frontal tapering of the pupils directed along the axis ^P the IBuioculSp sighting grooves. Since the sand-water inKface is predominant in the visual environment of this specffl! one would expect a concentration of ganglion cells along the horizontal meridian. This specialiffiion was found, and it is interesting to note that the density of ganglion cells (5.0×10^4 cells/mm^2) in the streak is higher than that in the area centralis (3.5×10^4 cells/ mm^2) of the temporal retina (fig. 5). The horizontal streak is a highly specific specialisation restricted to a thin band across the retinal meridian. Beyond the boundaries of this zone, cell densities drop off markedly. The temporal area, however, is less specialised, and it is possible that this acute zone is utilised more in feeding than in surveillance of potential predators.

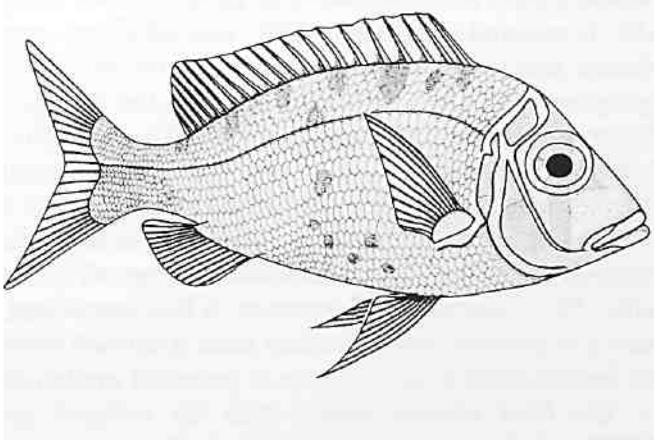
The final species studied was the collared sea bream, *G. bitorquatusi(LQthxmidae).* Territorial and

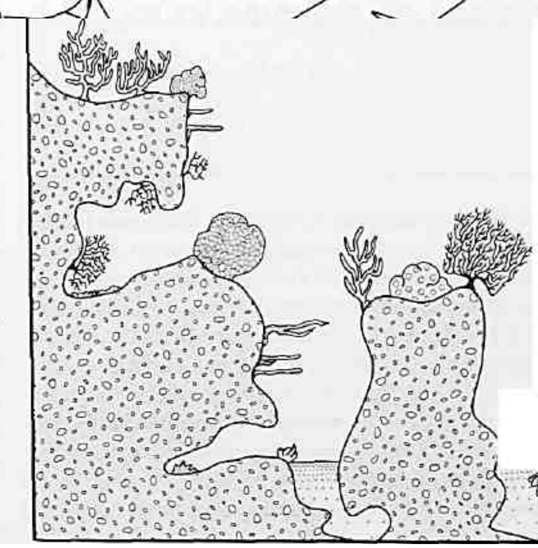
GYMNOCRANIUS BITORQUATUS LEFT EYE. X10^4cells/mm^2
DORSAL
VENTRAL

NASAL



TEMPORAL





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diurnal, it is found in open areas beyond the limit of the reef crest. It often feeds at an angle of 45°, sifting through sand and coral rubble for the molluscs, crustaceans and annelids it then scoops up in its wide mouth. *G. bitorquatus* has extremely large eyes mounted high on a sloping head. As in all the other open water species studied, i.e. *C. albigena, A. chinen-sis, L. chrysostomas*, the retina contains two specialisations, one probably used in feeding and the other in predator surveillance. The temporal area centralis, thought to be used in feeding, projects towards the substrate at 45 ° from the horizontal along the slope of the head to the mouth (fig. 6). In tlmway, the fish utilises a specific acute zone for perceiving objects in its immediate visual field. The horizontal streak is of lower cell density and extends from the falciform process to the nasal border of the retina, offset ventrally from the horizontal meridian. This zone would enable acute vision into eccentric space directed marginally upward over the sand-water interface.

Retinal Topography versus Habitat

The 'terrain theory' [Hughes, 1977] suggests that the distribution of ganglion cells across the retina depends on the symmetry of the perceived world, and that an increase in ganglion cell density across the horizontal meridian is a specialisation common to terrestrial species whose field of view is not completely obscured by nearby vegetation. Further, it is suggested that animals occupying such a habitat maintain a fairly feed orientation between the retina and the horizon. Studies of ungulates [Hebel, 1976], rabbits [Hughes, 1971; Pro vis, 1979] and a number of marsupials have demonstrated the presence of a strong visual streak. By comparison, in small noctur-

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Fig. 6. The iso-density contour map of the retina of the collared sea bream, *Gymnocranius bitorquatus* (Lethrinidae, Actinoptery-gii), reveals two specialisations of putatively separate functions, *Wgk* a dorso-temporal zone and a horizontal streak of higher density across the nasal meridian of the retina. The dorso-temporal zone possesses a high density of cells (6.3 x 10^4 cells/mm^2), thought to aid in acute vision directed onto the sand substrate when foraging for molluscs and crustaceans. Behaviourally this fish has been observed to orient itself on an angle and sift through sand and coral debris in deep open areas past the limit of the reef slope. A horizontal streak (2.0 x 10^4 cells/mm^2) projects nasally from the falciform process and may provide this species with marginally higher acuity fiJSyJewing eccentncTspace. Scale bar g 35 mm.

Fig. 7. a The elongated optic nerve head and falciform process (arrowed) of *L. chrysostomas.* All teleost species in this study were found to possess this process, although partial peripheral growth of the retina may decrease its length within some species. Remnants of pigment epithelium highlight the plexus of fine nerve fibre branches entering the optic nerve. Scale bar g 500 urn. b Nissl-stained cells within the ganglion cell layer from nasal, peripheral retina of *L. chrysostomas.* This random arrangement of cells in the periphery and a population of ganglion cells with large-diameter soma was evident in most teleost species in this study. 1 = Large soma cells; s = small soma cells. Scale bar = 20 urn.

nal species such as rats [Fukuda, 1977], mice and hedgehogs [Hughes, 1977], the visual streak is either weak or abserlfllt has therefore been postulated that this zoneEsla retinal specialisation which allows the animal to scan a broad horizon without the distinctive eye movements for scanning with an area centralis [Rowe and Stone, 1977; Tancred, 1981]. The retinae of some crabs (Ocypodidae), which have closely set eyes on elongated, vertically oriented stalks, have a narrow acute zone for vertical resolving power along the horizon. Broad-fronted species (Grapsidae), which are found close to vegetatSn and rocks, higher up in the intertidal zone, and have their eyes set far apart on short stalks, lack this specialisation [J. Zeil and H.-O. Nalbach, personal communfWprimitive zygopteran dragonflies that hover around vegetation are devoid of any streak when iso-ommatidial diameters are calculated across the eye [Sherk, 1978]. Aeshnid anisop-terans, and Iibellulids that cruise and perch at high altitudes, however, possess a greater ommatidiaJ^H ameter across the horizontal meridian. But can the 'terrain theory' provide a neural basis for comparison of visual ecologies of a range of teleosts ?

All five of the open water species of teleosts included in this study posseSa temporal area centralis and a strong horizontal streak. The temporal area is thought to subserve binocular vision in feeding situations, and the horizontal streaMiot only means a better resolution of static details, but also provides a lower threshold for the perception of movement. Band-shaped thickenings across the horizontal meridian of the retina have previously been found in three species of cyprinodontids, i.e. *Fundulus heteroclitus* [Butcher, 1938], *Aplocheilus lineatus* [Engstrom, 1963] and *Epiplatys grahami* [Munk, 1970], and in two genera of mudskippers, *Boleophthalmus* and *Periophthal-mus* [Munk, 1970]. *A. lineatus* and *E. grahami* are the only known species to process two band-shaped areae in each eye, one central band and one ventral band. Both species prey on small animals (i.e., insects) located on, or immediately below the surface of the water. It has been suggested that the central band-shaped area jmised for lateral vision oriented parallel to the ^Bace [Schwartz, 1965] for detection of predators whereas the ventral band, useful for upward vision, is important during feeding.

Thus it appears that horizontal band-shaped areas in vertebrate retinae [for review see Munk, 1970; Stone, 1981] may enhance perception in^^ual erj5a3 ronments with a predominant horizontal component.

The importance of this horizontal component to the particular adaptations of a species, however, seems to govern the acuity limits of the specialised zone.

In species with an interrupted view of theiraand-water horizon, circular isometry of density contours over the retina is found in conjunction with greater eye mobility. This is particularly true of *Cephalopholis miniatus*, *Pomacanthus semicirculatus* and *Amblygly-phidodon curacao*, with multiple areae centrales [Collin and Pettigrew, 1988]. Species that periodically venture out into open water possess a weak horizontal streak which probably allows for some predator surveillance.

Visual Processing

The question that remains is whether this diversity in visual processing in the retina is revealed centrally, mediated either by different populations of ganglion cells or by specific termination sites. Several different types of ganglion cells have been identified in birds [Bravo and Pettigrew, 1981; Hayes and Holden, 1983a, b], in cats [Boycott and Wassle, 1974; Kolb et ah, 1981] and in fishes [Koch and Reuter, 1978; Ito and Murakami, 1984]. Studies of ganglion cell soma size iSthe five teleost species in this study revealed specific size populations of cells [Collin, in preparation]. Bravo and Pettigrew [1981] demonstrated that, in owls, the temporal part of the retina, including the area centralis, projects to the thalamus whereas the horizontal streak region projects to the optic tectum. The optic connections from the retina in fish project to the thalamo-pretectal region, as well as to the optic tectum [Vanegas and Ito, 1983]. In comparing the brains of closed and open water species, a reduction in the relative size of the optic tectum was noted in species lacking a horizontal streak. The optic tectum is particularly well developed in *L. chrysostomas* and C. *albigena,* both open water speciesffin contrast to that in the Australian frogfish, *Halophryne diemensis* [Collin and Pettigrew, 1988], whose habitat is relatively closed.

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