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Retinal Topography of Ganglion Cells and Putative UV-Sensitive Cones in Two Antarctic Fishes: *Pagothenia borchgrevinki* and *Trematomus bernacchii* (Nototheniidae)

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ABSTRACT—Accessory corner cones (ACC) have recently been suggested to be UV-sensitive photoreceptor cells. With a view toward explaining prey detection, we examined the topography of retinal ganglion cells and ACCs in two Antarctic nototheniids occupying different ecological niches: the cryopelagic *Pagothenia borchgrevinki* and the benthic *Trematomus bernacchii*. Isodensity maps of retinal ganglion cells showed that the main visual axis, coincident with the feeding vector, was in a forward direction in both species. Visual acuity was determined as 3.64 and 4.77 cycles/degree for the respective species. In *P. borchgrevinki* the highest density of ACCs was associated with the eye's main visual axis. This suggested that this species uses UV-vision during forward-swims and probably in encounters with prey. On the other hand, *T. bernacchii* possessed two horizontal band-shaped high-density areas of ACCs, which stretched from temporal to nasal and ventral to peripheral retinal regions. Therefore, this species appears to use UV-vision to watch prey across the entire circumference of the lateral area and in the water column above its head.

Key words: Antarctic fish, vision, retinal ganglion cell, UV-sensitivity, feeding strategy

INTRODUCTION

The presence of UV-absorbing visual pigment in the single cone at the corner of the retinal square cone mosaic, named accessory corner cone (ACC), has been reported in many freshwater fishes and euryhaline fishes by using microspectrophotometrical and/or molecular analyses (Avery *et al*., 1983; Hárosi and Hashimoto, 1983; Whitmore and Bowmaker, 1989; Archer and Lythgoe, 1990; Bowmaker *et al*., 1991; Hawryshyn and Hárosi, 1991; Raymond *et al*., 1993; Hisatomi *et al*., 1996, 1997). Furthermore, in juveniles of some salmonids species (*Salmo trutta, Salmo gairdneri* (=*Oncorhynchus mykiss*), *Salmo salar, Oncorhynchus nerka*) and yellow perch *Perca flavescens*, the loss of UV-photosensitivity associated with the almost complete disappearance of ACCs from the retinal cone mosaic has been confirmed (Bowmaker and Kunz, 1987; Hawryshyn *et al*., 1989; Loew and Wahl, 1991; Kunz *et al*., 1994; Novales-Flamarique, 2000).

Recently, we reported the presence of ACCs histologically from the eyes of adults of seven Antarctic nototheniid species as follows: *Trematomus bernacchii, Trematomus newnesi, Trematomus hansoni, Trematomus pennellii, Trematomus scotti, Pagothenia borchgrevinki, Lepidonotothen squamifrons* (=*kempi*) (Miyazaki *et al*., 2001). Although several specific visual tasks for UV-vision have been proposed (foraging, navigation, and/or communication) and we have very few direct observations on visual feeding in Antarctic fishes, we suggested that Antarctic fishes could increase their feeding efficiency and stock energy by making use of UV-vision during the summer month (Miyazaki *et al*., 2001).

Topographical analyses of retinal ganglion cells as well as cone photoreceptors can provide us with valuable infor-

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mation on the visual capabilities of fishes. In adult teleosts, the position of the “area centralis (AC)” is related to both habitat and main visual vector of feeding behaviour (Collin and Pettigrew, 1988b, c; Williamson and Keast, 1988; Browman *et al.*, 1990). Furthermore, the distribution of cone photoreceptors determines how the spectral sensitivity of a fish eye changes across its visual field, for different kinds of cones may contain visual pigments with different spectral absorption characteristics (McFarland and Munz, 1975; Beaudet *et al.*, 1997).

In several Antarctic fish species, retinal organizations have been described for specific regions and estimates on visual resolution or photosensitivity were given (Meyer-Rochow and Klyne, 1982; Eastman, 1988; Pankhurst and Montgomery, 1989, 1990; Fanta *et al.*, 1994, Meyer-Rochow *et al.*, 1999). However, the topography of the ganglion cells or cone cells of the whole retina, and in particular the position of the ACs, is still poorly known. Our primary objective was to histologically examine the prey detection system in nototheniids. We also hoped to establish whether the ACCs, as the putative UV-sensitive cones, could assist the fish in prey detection and uptake. The UV-wavelength absorption of ACC’s visual pigment has been shown by the previous studies mentioned above, although we have not verified about Antarctic fish yet. In this paper, we therefore examined the retinal topographies of ganglion cells and ACCs for entire retinas of two nototheniids with different habits, namely *Pagothenia borchgrevinki* and *Trematomus bernacchii*. We also determined the fish eyes’ UV-visual fields. Finally, visual acuity and optical axes were estimated on the basis of retinal ganglion cell distributions, since retinal ganglion cells are providing the link between eyes and behavioural output via the optic nerve.

MATERIALS AND METHODS

Fish

P. borchgrevinki and *T. bernacchii* were caught by line-fishing from a depth of ca. 30 m in Lützow-Holm Bay near Syowa Station (69° S, 39° E). Total lengths of the *P. borchgrevinki* and *T. bernacchii* specimens used were 210 mm and 215 mm, respectively. According to Collin and Pettigrew (1988a), there is no remarkable difference in the topography of cells among specimens of the almost same size of the same species. Based on their observation results, we used a single specimen for each species. Following capture, the fish were anaesthetized with MS222 and then immediately fixed in 10% formalin. Thereafter the eyes were enucleated and cornea, iris, lens, and vitreous humor were removed. The remaining retinae were prepared as follows.

Examination of ganglion cells

The left retinae were radically incised and flatly mounted, and then whole-mount preparations were made following the protocol of Ito and Murakami (1984). The preparations were glued onto slides with the ganglion cell layer facing upward, and stained with crecyl violet. Ganglion cells numbers per 0.13×0.13 mm of each fish retina, about 20 mm in diameter in both fish, were counted at 2mm intervals, under a light microscope, using a calibrated eyepiece. In *P. borchgrevinki* and *T. bernacchii*, 127 and 98 sampling points were used. Values for the ganglion cells were converted into numbers of cells per mm^2, and then isodensity counter maps of ganglion cells were constructed. The retinal resolving powers were calculated according to the protocol of Collin and Pettigrew (1989), the values thus obtained representing upper limits based on the following equations:

The distance from lens center to retinal focus (posterior nodal distance, PND) was calculated from lens radius (r; mm) and Matthiessen’s ratio (2.55):

$$PND = 2.55r.$$

The angle (α), subtending 1mm on the retina was calculated by,

$$\tan \alpha = 1/PND$$
$$\alpha = \arctan (1/PND) \text{ (degree).}$$

When the density of the ganglion cells is D (cells/ mm^2), the linear density is

$$\sqrt{D} \text{ (cells/mm).}$$

Spatial resolution can be calculated by obtaining the number of cells subtended by one degree of visual arc, i.e.,

$$\text{cells per degree} = \sqrt{D} / \alpha .$$

Since at least two ganglion cells are needed to distinguish the light and dark boundaries from one cycle of a grating of the highest resolvable frequency, visual acuity is given by

$$\text{cycles per degree} = 1/2 \text{ cells per degree}$$

Examination of ACCs

Right retina of the *P. borchgrevinki* and *T. bernacchii* was divided into 24 and 30 topographical locations, respectively, and thus the position of each piece in the original retina was determined accurately. The pieces were dehydrated in alcohol and embedded in paraffin. Tangential sections were cut at 7 µm thickness and stained with haematoxylin and eosin. Cone photoreceptor layers were observed under the light microscope, and numbers of accessory corner cone cells per 0.1×0.1 mm were counted for respective retinal pieces.

RESULTS

Distribution of ganglion cells

All ganglion cells lying within the retinal ganglion cell layer in each fish species were counted. The averages of cell density, estimated from the counts of ganglion cells and counted number of points, were approx. 1.5×10^3 cells/mm^2

Table 1. Summery of ganglion cell counts and calculations of visual acuity in two nototheniids.

	Retinal surface area (mm^2)	Counted points	Av. cell density (cells/mm^2)	Total cell No.	Peak density (cells/mm^2)	Lens diameter (mm)	PND (mm)	α (degree)	cells/ degree	cycles/ degree
P. borchgrevinki	260	127	1.5×10^3	390×10^3	3313	5.65	7.20	7.91	7.28	3.64
T. bernacchii	248	98	2.5×10^3	620×10^3	6804	5.15	6.57	8.65	9.54	4.77

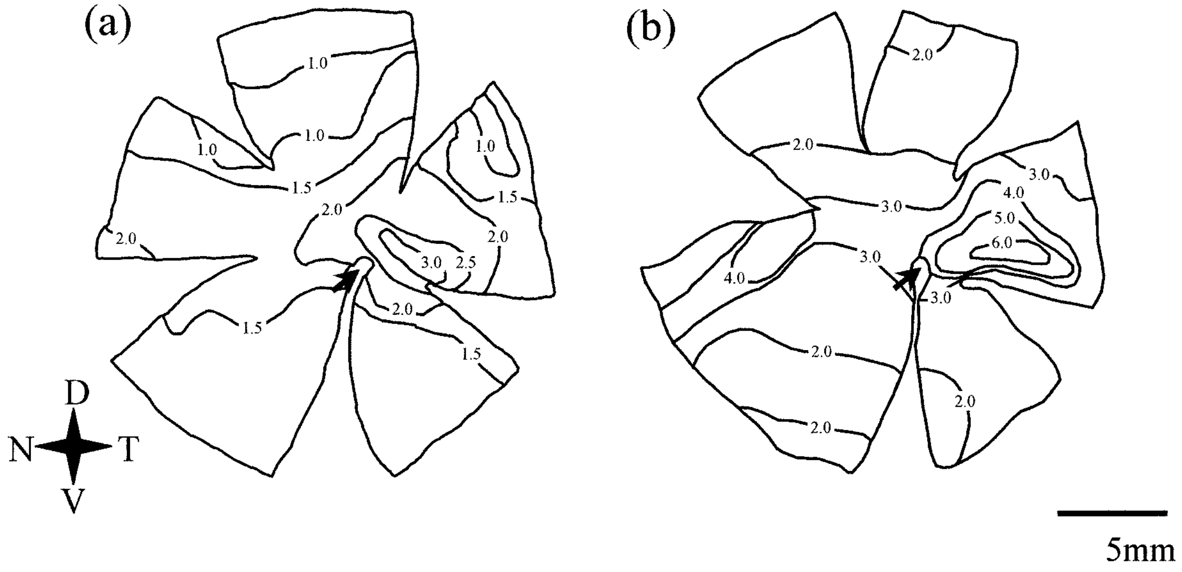

Fig. 1. Isodensity counter maps of the distribution of Nissle-stained neurons (retinal ganglion plus displaced amacrine cells) located within the ganglion cell layer in the left eye of *P. borchgrevinki* (a) and *T. bernacchii* (b). All cell densities ×10^3 per mm^2. T, temporal; V, ventral; D, dorsal; N, nasal. The arrows indicate the position of optic papilla.

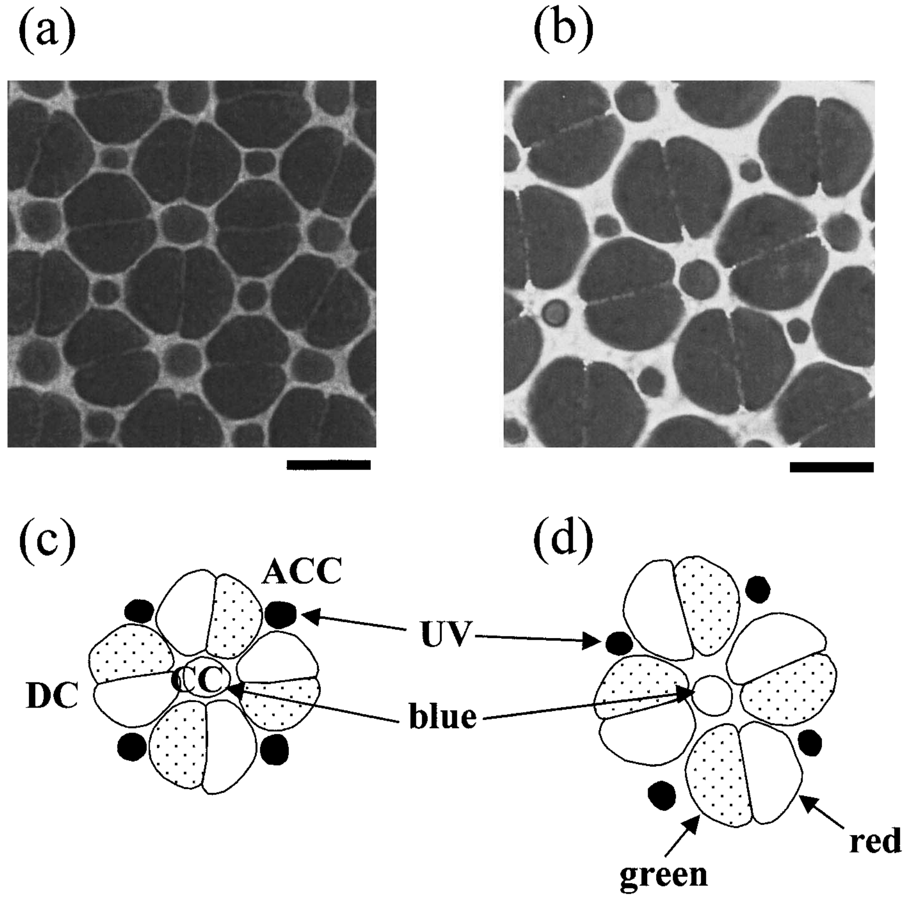

Fig. 2. Photomicrographs of tangential sections through ellipsoid region of cone photoreceptors in the temporal retina of *P. borchgrevinki* (a) and *T. bernacchii* (b). (c) and (d) are tracings of a cone square mosaic on photograph (a) and (b), respectively. ACC, accessory corner cone; CC, central single cone; DC, double cone. The phenotype of the ACC and CC has been identified to be UV- and blue-visual pigment, and that of one of the DC is green- while another of the DC is red-visual pigment (Raymond *et al.*, 1993; Hisatomi *et al.*, 1996, 1997). Scale bar=20 µm.

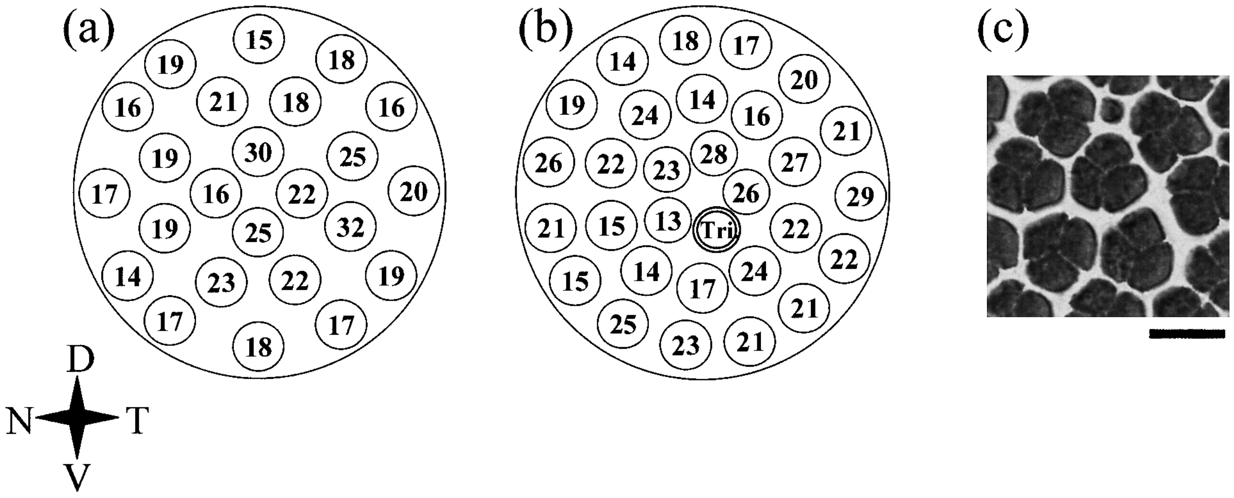

Fig. 3. Maps showing the distribution of ACC densities in the right retina of *P. borchgrevinki* (a) and *T. bernacchii* (b). All cell densities per 0.01mm^2. Tri. indicates presence of triple cones. (c) Photograph of triple cones in a section of *T. bernacchii* retina. Scale bar=20 µm. T, temporal; V, ventral; D, dorsal; N, nasal.

in *P. borchgrevinki* and 2.5×10^3 cells/mm^2 in *T. bernacchii* (Table 1). The calculated cell densities were upper estimates, which may include displaced amacrine cells.

Ganglion cells were not uniformly distributed in the retinae of either species. Isodensity maps of *P. borchgrevinki* and *T. bernacchii* resembled each other in that in both species, the region of highest cell density, termed area centralis (AC), was located in the temporal retina (Figs. 1a and 1b). The position of the AC indicates that the visual axis was in a forward direction. In both species, however, a weak horizontal visual streak was also observed a little above the optic papilla (see in Figs. 1a and 1b).

Ganglion cell peak densities were 3313 and 6804 cells/mm^2 in *P. borchgrevinki* and *T. bernacchii*, respectively, and the corresponding lens diameters were 5.65 mm and 5.15 mm. The PNDs, α s, and the numbers of ganglion cells subtended by one degree of visual arc in the respective species were calculated as shown in Table 1. Consequently, the upper limit of the theoretically derived visual acuity, based on ganglion cell counts, can be given as 3.64 and 4.77 cycles/degree in *P. borchgrevinki* and *T. bernacchii*, respectively.

Distribution of ACCs

Single and double cones were alternately and regularly aligned in the photoreceptor layer, and formed a square mosaic pattern in both species (Figs. 2a and 2b). The ACCs, which were located at the corners of the double cones, could be distinguished from the central single cones by the direction of the axes of the double cones (Figs. 2c and 2d). In both species, the ACCs were present in the entire retina, but the density varied across the retina. Figs.3a and 3b illustrate ACC density distributions in the retinae of *P. borchgrevinki* and *T. bernacchii*, respectively. The highest density of the ACCs was in the temporal retina of both species, which corresponded to the AC. Peak densities of the ACCs were 32 and 29 cells par 0.01mm^2 in *P. borchgrevinki* and *T. bernacchii*, respectively.

In *P. borchgrevinki*, ACC density was high near the optic papilla of the temporal retina. On the other hand, in *T. bernacchii*, the highest density was seen in the region of the horizontal streak just dorsal of the mid-retina. An additional, high density area was seen in the peripheral part of the ventral retina.

Triple cones were observed near the optic papilla in *T. bernacchii* (Fig. 3c), but not in *P. borchgrevinki*.

DISCUSSION

Both *P. borchgrevinki* and *T. bernacchii* belong to the Nototheniidae of the suborder Notothenioidei. However, the former species is cryopelagic, whereas the latter is benthic. Furthermore, the two differ in body shape and position of the eye. The body in *P. borchgrevinki* is laterally compressed and the eyes are positioned laterally. This body shape is commonly associated with fast-swimming fishes and, indeed, this species is often seen as small schools swimming just beneath the sea-ice (Meyer-Rochow, 1982; Meyer-Rochow and Klyne, 1982; Eastman and DeVries, 1985; Foster *et al.*, 1987; Gon and Heemstra, 1990; Pankhurst and Montgomery, 1990). On the other hand, the head of *T. bernacchii* is broader, and the eye is situated higher on the head and directed anterolaterally. This body shape is typical of benthic fishes, such as gobies and sculpins.

In the present investigation, the main visual axis, thought to provide a clue for the high resolving power of the AC (Shand *et al.*, 2000), was determined to be forward-looking in both species, which is in agreement with the AC's location in the temporal retina. Therefore, the best vision in both species to detect prey items must be considered to lie in front of the fish. Earlier workers have also suggested that

T. bernacchii has a forward-directed feeding vector, since it has a large anterior aphakic space. As for *P. borchgrevinki*, it lacks the anterior aphakic space and may therefore posses an extended visual field (Pankhurst and Montgomery, 1989; Macdonald and Montgomery, 1991; Eastman, 1993).

The binocular visual field, based on eye position and body morphology in *T. bernacchii*, is broader than that of *P. borchgrevinki* but less far-reaching. On the contrary, *P. borchgrevinki* appears to be able to detect prey further away from the body than *T. bernacchii* (Fig. 4). Consequently, it is likely that *P. borchgrevinki* can focus earlier on prey during cruising, while *T. bernacchii* waits and watches prey over a wide range before it initiates an attack. A similar difference in visual fields has been noted between two other nototheniids, namely *Gobionotothen gibberifrons* and *Trematomus newnesi*. The latter two species share the same environmental depth of 40–80 m bottom, but they differ in their feeding-behavioural strategies (Fanta *et al.*, 1994). The expansion of fish visual field should also be discussed based on the eye movement. Regarding eye movement of nototheniids, the maximum eye rotation has been reported as about 15 and 20 degree for *P. borchgrevinki* and *Dissoticus mawsonii*, respectively (Montgomery and Macdonald, 1985). Nevertheless, although we don't know how nototheniids use monocular and binocular vision for their visual interest, the eye movement might allow fish to observe its surroundings without moving head or body (Fritsches and Marshall, 2002). Both of *P. borchgrevinki* and *T. bernacchii* may be able to aim prey with the expansion of visual covering range by eye movement.

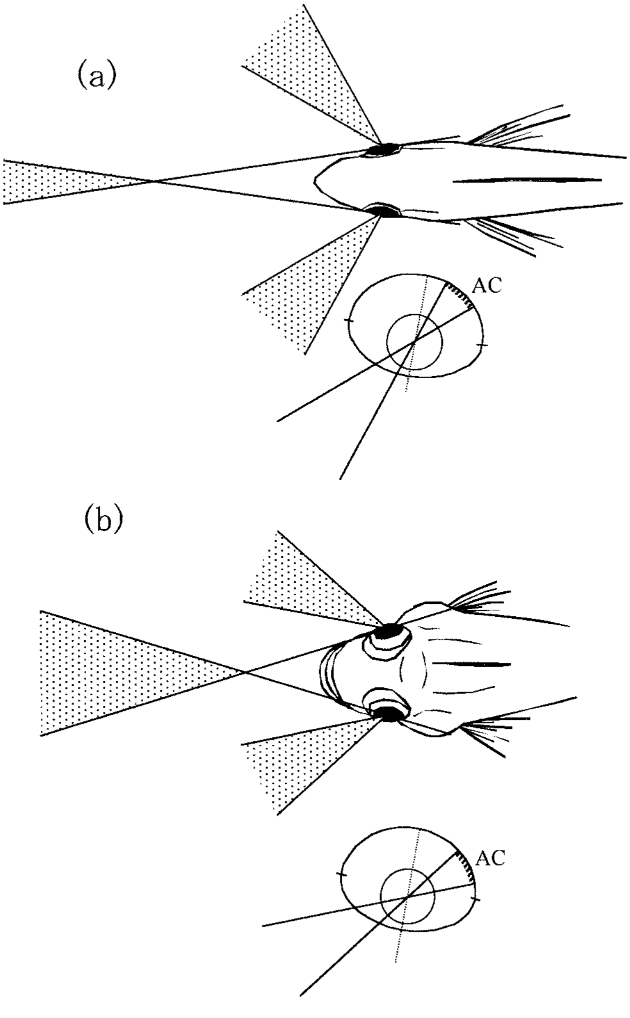

Fig. 4. Schematic diagrams of the binocular visual fields based on eye position, body orientation and position of AC in the retina of *P. borchgrevinki* (a) and *T. bernacchii* (b).

Regarding visual acuity, there was no remarkable difference in the present two species. The correlation between the visual acuity level of fishes and their swimming types has not been clearly shown in Tamura (1957). Retinal resolving power in cycles per degree can be converted to that of minutes of arc (Murayama and Somiya, 1998), e.g., according to the equation

$$\text{min of arc} = 1/\sqrt{D} \times \alpha \times 60.$$

If that is done, values of 8.2' and 6.3' result for *P. borchgrevinki* and *T. bernacchii*, respectively. These values are almost the same as those in other marine teleosts, which were derived from maximum cone densities (*Pagrus major*: 6.4' for a fish of 200 mm in body length; *Lateolabrax japonicus*: 8.5' for an 180 mm long fish; *Sebastiscus marmoratus*: 6.7' also for an 180 mm long fish, Tamura, 1957).

Meyer-Rochow and Klyne (1982) have counted cone and ganglion cells in both species (*P. borchgrevinki*: approx. 8300 cells/mm^2 for a fish of approx. 200 mm total body length; *T. bernacchii*: approx. 4200 cells/mm^2 for a fish of approx. 240 mm total body length: converted from original data). Furthermore, there have been studies on the theoretical visual acuity calculated from retinal cone densities for both species (*P. borchgrevinki*: 25–50' for fish of 63–220 mm total body length: Pankhurst and Montgomery, 1990; *T. bernacchii*: 10' in the temporal retina for a fish of 192 mm total body length; Miyazaki, unpublished data). Some differences between earlier values and our present values might have been caused by differences in fish size or retinal region analyzed for each examination. Nevertheless, a close agreement between values based on cone cell and ganglion cell estimates, as well as behavioural tests clearly exists (Collin and Pettigrew, 1989; Arrese *et al.*, 2000).

The maximum distance (L; cm), at which a fish could recognize a prey item (ϕ; cm), can be estimated from the fish's visual acuity according to

$$D=(\phi \times 1/\text{min of arc} \times 180 \times 60)/\pi,$$

provided optical properties in the sea (turbidity and light intensity) are neglected (Miyazaki and Nakamura, 1990; Miyazaki *et al.*, 2000). On that basis, for example, the recognizable distance for a prey of 3 cm diameter would be about 12.6 m in *P. borchgrevinki* and 16.4 m in *T. bernacchii*.

While these figures do not seem to vary too greatly between the two species, the distribution of the ACCs in the retina, on the other hand, was quite dissimilar. In *P. borchgrevinki*, the region in which the density of the ACCs was highest coincided with the position of the AC. Therefore, UV-vision in *P. borchgrevinki* must be assumed to be most effective in a forward direction, and consequently *P. borchgrevinki* ought to principally recognize prey in the swimming direction from a larger distance than *T. bernacchii* (Cronin *et al*., 1994; Losey *et al*., 1999). As for *T. bernacchii*, the high-density area was the horizontal streak, which stretched from the temporal to the nasal retina. An additional area of high density was developed in the peripheral parts of the ventral retina. UV-vision in *T. bernacchii*, therefore, appears to be effective not only along the main visual axis of the forward-movement but also across a vast lateral area and into the upper water column itself. This extensive field could improve prey discovery, allowing *T. bernacchii* to remain relatively motionless in anticipation of prey. All of these conclusions are supported by the eye's morphology. We believe *P. borchgrevinki* detects pelagic prey, e.g. copepods (Hoshiai and Tanimura, 1981; Hoshiai *et al*., 1989) as silhouettes against downwelling light, whereas *T. bernacchii* relies mainly on laterally incident light to feed, since *T. bernacchii* in contrast to *P. borchgrevinki* displays an obvious corneal iridescence (Macdonald and Montgomery, 1991; Eastman, 1993), which screens out bright downwelling light.

The benefit for fish using UV-vision for feeding, lies in enhancing the contrast of prey against a UV-background and it is thought that UV-sensitivity is widespread in zooplanktivorous fishes (e.g., juvenile rainbow trout *Oncorhynchus mykiss*, pumpkinseed sunfish *Lepomis gibbosus*: Browman *et al*., 1994; juvenile yellow perch *Perca flavescens*: Loew and Wahl, 1991; Loew *et al*., 1993; pomacentrid fish *Dascyllus trimaculatus*, *Pomacentrus coelestis, Chromis punctipinnis*: McFarland and Loew, 1994). In Antarctic nototheniids, UV-vision may represent one strategy to increase foraging efficiency during the Antarctic summer, when light conditions are appropriate for visual feeding and a visual threshold of 2×10^9 photons cm^{-2} s^{-1} is reached (Morita *et al*., 1997). However, other and additional means of detecting predators and prey are entirely possible, especially if it is remembered that individuals with aberrant eyes can, apparently, reach full adulthood (Meyer-Rochow, 1990). To (a) determine the extent that nototheniids can make use of UV-light and (b) understand the role of triple cones, present in the retina of *T. bernacchii* (but not *P. borchgrevinki*), are thus our next goals.

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