Retinal ganglion cell topography and spatial resolution in the masked greenling *Hexagrammos octogrammus* (Pallas, 1914)

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Introduction

Of all animal sensory systems, the visual system is most important. It plays a crucial role in the adaptation of vertebrates to the environment. Studying peculiarities of the visual system structure and function and their relationship to a species' ecology is of great theoretical and applied interest. The above applies to the topography of retinal neurons and spatial resolution (SR) in vertebrates. In the retina of many vertebrates, there are so-called specialized visual areas. These areas are characterized by increased density of retinal neurons (in particular, ganglion cells (GC)) and spatial resolution. The presence and localization of specialized visual areas are species–specific and are related to a species' ecology and behavior. SR largely determines a more integral parameter, visual acuity. The latter, in turn, plays an important role in visual behavior, in particular, defense reactions, food search, inter- and intraspecific communication. Despite a large number of works on GC topography and visual acuity in bony fishes, many of their groups remain poorly studied in this respect. We studied GC topography and estimated SR in a hexagrammid fish, the masked greenling *Hexagrammos octogrammus* (Fig.1. A).

Methods

To examine GC topography, a series of retinal wholemounts were obtained and DAPI stained. The spatial density (SD) of cells was studied using stereological analysis based on a series of confocal-microscopic images of retinal fragments (Fig. 1. B). To estimate the proportion of non-ganglion cells in the inner retinal and ganglion cell layers, a series of Nissle-stained retinal wholemounts was obtained and analyzed. The cells were observed and studied by light microscopy using differential interference contrast (Fig. 1. C).

To estimate eye optics parameters and calculate SR, a series of optical eye sections were obtained in the sagittal plane using computer-assisted tomography. SR was calculated based on GC SD and lens radius.

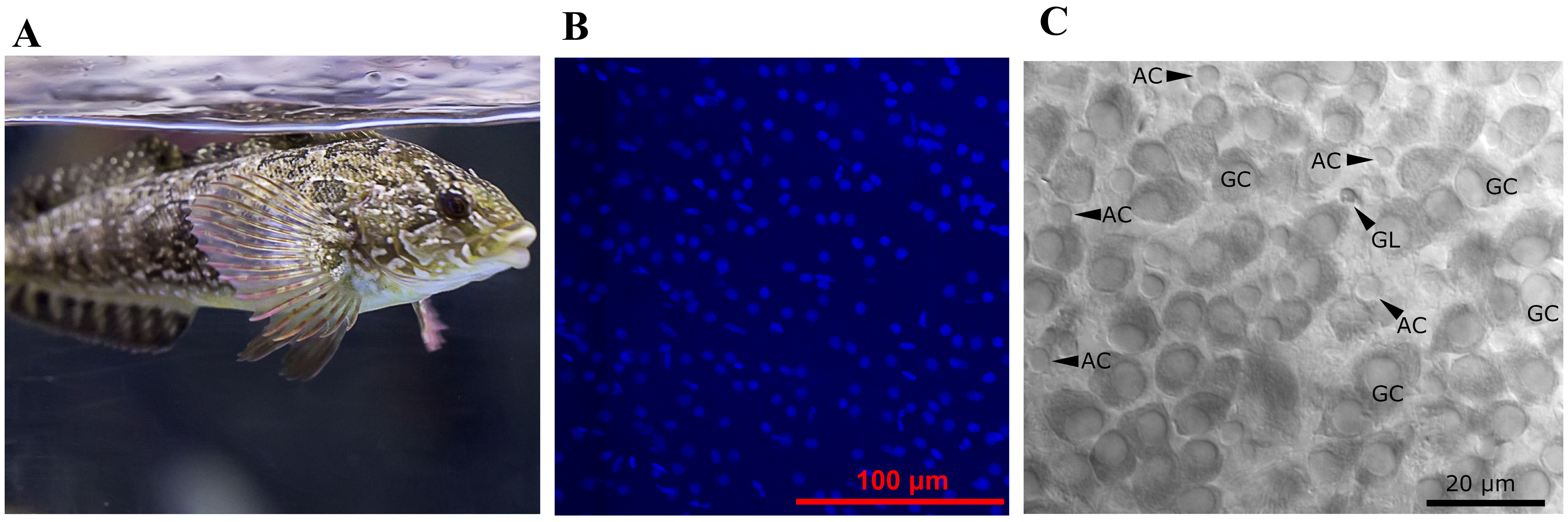

Fig. 1. A Masked greenling in water**. B** Fragments of the temporal zone of the *H. octogrammus* retina. A reconstruction based on confocal microscopic images of DAPI-stained cells. **C** Light micrograph of Nissl-stained ganglion cell layer of *H. octogrammus* retina. A collage composed of several images in different focal planes to bring neighboring retinal fragments to focus. gc, ganglion cell; ac, amacrine cell; gl, glial cell.

Results

The proportion of non-ganglion cells in the inner retina was 17.63%. The total number of GCs ranged from 455073 to 688613 (Table 1). The maximum GC SD was found in the temporal quadrant of the retina (so-called *area retinae temporalis*) and ranged from 9637 to 12685 cells/mm^2. The minimum GC SD was observed in the ventro-nasal periphery and ranged from 824 to 1977 cells/mm^2. The maximum SR ranged from 3.18 to 5.02 cycles per degree. (Fig. 2, Table 1)

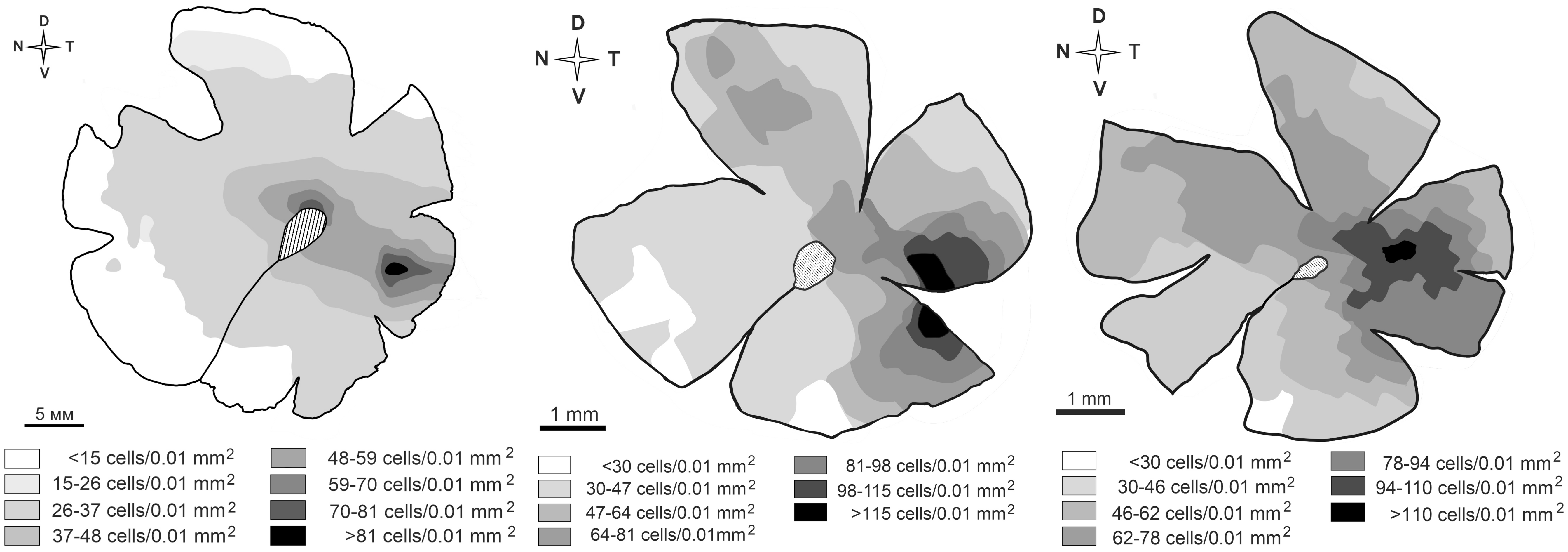

Fig. 2. Ganglion cell topography in three wholemounts obtained from different *H. octogrammus* individuals. D, dorsal; V, ventral; N, nasal, T, temporal. The optic disc area is striped.

Conclusion

The masked greenling is an ambush predator attacking its prey at a relatively close distance. The specialized visual area in its temporal retina provides an increased visual acuity in its frontal binocular visual field. This presumably facilitates prey detection near the bottom. The present estimates of maximum SR correspond to a 1-mm prey detection horizon of 36-57 centimeters. The real prey detection horizon may be lower as it depends on the environmental conditions (water turbidity, light level, visual complexity of the environment, prey mobility, etc) and does not necessarily involve all GC types in a particular visual reaction associated with feeding behavior. For all this, the average prey size of adult masked greenlings (shrimp, amphipods, winged clams, small fish) varies from 0.5 to 9 centimeters. Thus, the spatial resolution in this species is functionally sufficient for efficient detection and catch of ambush prey.

Interestingly, the masked greenling lacks a pronounced visual streak, a horizontal or (less often) oblique area of increased retinal cell density. Such a specialized visual zone is found in many coastal species. According to Hughes' theory, vertebrates inhabiting open spaces with a distinct horizon (such as coastal fish species) tend to possess a visual streak, while species preferring enclosed, visually complex environments have concentric visual zones. Apparently, despite the presence of pronounced "water-bottom" and "water-air" visual horizons in masked greenling habitats, local features of the visual environments are of crucial importance. As was mentioned above, the masked greenling is an ambush predator preferring cluttered spaces such as rocky gorges, bottom sites covered with algae or seagrass etc. Thus, its local visual environment, although structurally complex, is quite isotropic and may obscure a visual horizon. This may account for the lack of a pronounced visual streak in this species.

Table 1 — Spatial arrangement of retinal ganglion cells and spatial resolution in *Hexagrammos octogrammus*.

Retinal wholemount	Fish standard length, mm	Retinal area, mm^2	Lens radius, mm	PND, mm	All GC	Maximum cell density (cells/mm^2)	Minimum cell density (cells/mm^2)	Maximum TASR (cpd)	Minimum TASR (cpd)
HO 1L	250	243,65	2,32	5,8	688613	9637	824	5,02	1,47
HO 8L	205	109,9	1,34	3,35	496224	12685	1977	3,39	1,34
HO 16L	170	82,93	1,3	3,25	455073	11861	1895	3,18	1,27