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Cone mosaic in the retina of ray-finned fishes and its function for vision

Sítnicová mozaika a její funkce u paprskoploutvých ryb

Bachelor's thesis

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Abstrakt

V rámci obratlovců představují paprskoploutvé ryby více než polovinu diverzity a mnoho jedinečných strategií a adaptací jim umožnilo obydlet nejrůznější vodní prostředí. Tato práce se zaměřuje na zrak, jenž je pro většinu ryb nepostradatelným smyslem, zejména pak na morfologii fotoreceptorů a jejich prostorové uspořádání do dvourozměrného vzoru – sítnicové mozaiky. U paprskoploutvých ryb se běžně setkáváme se třemi morfologickými typy fotoreceptorů – tyčinkami, jednoduchými čípkami a dvojčípkami. Vzácněji se v sítnici nacházejí i trojčípkami a čtyřčípkami, které dosud nebyly pozorovány u žádné jiné skupiny obratlovců. V práci diskutuji strukturu a funkci jednotlivých fotoreceptorů. Zatímco tyčinky jsou v sítnici rozmístěny nepravidelně, čípkami u ryb často tvoří pravidelnou mozaiku. Podle postavení dvojčípků rozlišujeme několik základních typů mozaiky, které mohou být u různých druhů ryb dále modifikovány. Nejčastější je mozaika řadová a čtvercová. V práci uvádím popis základních vzorů a zaměřuji se na mechanismus jejich vzniku, jakož i na důvody pro uspořádání receptorů do pravidelného vzoru. Typ mozaiky do určité míry reflektuje fylogenezi, ale podoba vzoru je výrazně ovlivněna také prostředím a životní strategií ryby. Aktivní ryby obývající světlé prostředí mívají mozaiku propracovanou nejvíce, s ubývajícím světlem nebo snižujícími se požadavky na zrakovou ostrost se mozaika rozvolňuje a některé typy fotoreceptorů ze sítnice mizí. Zcela specifická je struktura sítnice hlubokomořských ryb, pro které je jediným zdrojem světla bioluminescence. V práci popisuji nejběžnější uspořádání fotoreceptorů u ryb z různých prostředí a věnuji se i změnám mozaiky během vývoje ryb, které souvisejí se změnou habitatu nebo životní strategie. Diskutuji také potenciální význam sítnicové mozaiky pro vnímání polarizovaného světla.

Klíčová slova

barevné vidění, zrak, sítnice, ryby, čípková mozaika, evoluce, fotoreceptor

Abstract

Ray-finned fishes comprise more than half of the vertebrate diversity, and they developed many unique strategies and adaptations to inhabit miscellaneous water environments. This thesis is dedicated to vision, which is an indispensable sense for most fishes. Special focus is laid on photoreceptor morphology and their arrangement in a two-dimensional pattern – cone mosaic. There are three morphological types of photoreceptors commonly found in ray-finned fishes – rods, single cones, and double cones. Triple and quadruple cones that have never been observed in any other vertebrate group sometimes occur too. In this thesis, I discuss the structure and function of individual photoreceptors. While rods are randomly distributed across the retina, cones often form a regular mosaic. Several basic mosaic types can be distinguished according to the position of double cones. Row and square mosaics are the most prevalent. Basic patterns can be further modified in certain fish species. In this thesis, I describe basic patterns, I focus on mosaic development, and I investigate the reasons for regular photoreceptor arrangement. The type of mosaic partly reflects phylogeny, but it is also strongly influenced by the environment and life strategy of the fish. Active fishes inhabiting bright environments are likely to possess the most elaborated mosaic. The mosaic disintegrates with diminishing light or with decreasing demand for visual acuity, and some photoreceptor types disappear from the retina as well. Very structure-specific retinæ are found in deep-water fishes that use bioluminescence as the only source of light. In this thesis, I describe the most common photoreceptor arrangements in fishes from various environments and I investigate changes in mosaic structure during development that are related to the change in habitat or life strategy. I also discuss the potential importance of the cone mosaic for polarization vision.

Key words

colour vision, retina, fishes, cone mosaic, evolution, photoreceptor

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Introduction

Ray-finned fishes (Actinopterygii) are the largest class of vertebrates. Sometimes they are also perceived as a subclass of the class Osteognathostomata/Osteichthyes – bony fishes (Nelson, Grande, & Wilson, 2016). On the other hand, Eschmeyer's Catalog of Fishes does not use the group Actinopterygii at all and instead, it lists both groups usually classed within Actinopterygii – Actinopteri and Cladistia – as independent classes (Van der Laan, Fricke & Eschmeyer, 2020). The oldest fossils of ray-finned fishes come from the Late Silurian sea, approximately 420 Mya (Gross, 1969; Märss, 2001). Since that time, fishes diversified greatly, they invaded freshwater and inhabited various environments from mountain streams or crater lakes to deep ocean. The outstanding diversity of forms and species richness was probably enabled by three rounds of whole-genome duplication – two of them occurred before the split of Actinopterygii and Sarcopterygii and are thus common to all living vertebrates, whereas the third duplication is unique for the largest infraclass in ray-finned fishes – Teleostei (Dehal & Boore, 2005; Meyer & Van De Peer, 2005). Teleosts comprise all actinopterygians except Cladistia, Chondrostei, Ginglymodi, and Halecomorpha (Musilová, 2016). Teleost-specific genome duplication occurred around 350 Mya, leaving raw genetic material – the new potential for adaptation and diversification that presumably triggered subsequent teleost radiation. Today, there are more than 35,000 described species of ray-finned fishes (Fricke, Eschmeyer & Fong, 2020), while many species probably remain unknown. Within such diversity, fishes have developed numerous adaptations many of which have no parallel in other vertebrate groups. One of the most amazing examples are the adaptations related to vision.

Fishes perform a wide range of visually guided behaviours (Land & Nilsson, 2002). Their vision is usually very elaborated and crucial for survival. Vision is used for spatial orientation, to choose habitats, search food, hunt prey, find and evaluate mates, spot predators, and for visual communication. Therefore, vision is under strong selection pressure and every change in vision may directly affect the fitness of the fish – either positively or negatively. Flaws are likely to be eliminated by natural selection (vision malfunction causes lower fitness due to higher predation or lower reproduction rate), whereas useful adaptations that enable the fish to find food or mates faster might spread within the population. Moreover, the relation between genotype and phenotype is very close, concerning the eyesight. For instance, visual pigments are composed of the protein and the chromophore, and the protein is directly coded in the genome; so the visual performance can be sometimes affected by a single mutation in the gene sequence (Carleton, Dalton, Escobar-Camacho, & Nandamuri, 2016). As a result, the dynamic and rapid evolution of vision can in some cases even lead to speciation (Seehausen et al., 2008), which makes fishes and their eyesight the unique model for the study of evolutionary processes (Lemoine et al., 2019).

In this thesis, I present the main principles of vision underwater, summarize morphology and physiology of vertebrate visual apparatus with special emphasis on ray-finned fishes, list photoreceptor types found

in fishes, and most importantly, discuss the spatial arrangement of photoreceptors within the fish retina. I describe regular photoreceptor patterns that occur in retinas of ray-finned fishes and delineate their formation during development. I also discuss possible benefits and drawbacks of certain arrangements, especially concerning different environments. Additionally, I examine the potential role of photoreceptor patterns in polarization vision.

Photic environment underwater

For the vision, water is a much more complicated photic environment than air. The spectrum of light reaching the water surface ranges from 300 nm in the ultraviolet to 1100 nm in the infrared (J. K. Bowmaker, 1995). Because marginal parts of the spectrum (UV and red) are greatly absorbed by water, the light spectrum narrows with depth. In the clear water, the blue light at approximately 475 nm penetrates the deepest (Widder, 2010). It can reach the depth of 1000 m in the open ocean, where the water is very pure (Lythgoe & Partridge, 1989). However, water transparency depends on the presence of suspended particles, phytoplankton, and dissolved substances that might dye the water and scatter the light. In fact, coastal and freshwater environments are seldom pure. The limit for photopic vision is often reached at the depths of units or tens of metres and the maximum transmission is shifted towards the red part of the spectrum in turbid water bodies (J. K. Bowmaker, 1995).

Furthermore, water transparency can sometimes substantially and rapidly change because of various processes. Water organisms relying on vision, including fishes, must cope with all those difficulties that are not common in the terrestrial environment. It is reasonable to anticipate the relationship between light conditions in the surrounding environment and the traits related to vision – such traits are likely to be tuned to respond to the environment most efficiently.

Eyesight physiology

Fish eyes are constructed according to the general vertebrate plan – they resemble the human eye as well as the eyes of all the terrestrial vertebrates, as shown in Figure 1 (Fernald, 1988). The light passes through the cornea, anterior chamber, pupil, posterior chamber, lens, and vitreous body and it is focused on the retina, where it creates a two-dimensional image. While in a terrestrial environment both cornea and lens are crucial for refraction, fish eyes only rely on the lens for focusing the light – refractive indices of cornea and water are very similar and therefore cornea cannot serve for refraction in water environments. To achieve adequate refraction individually, the fish lens must be spherical (Kröger, 2013). Unlike terrestrial vertebrate eye that accommodates by pressing and stretching the lens and thus changing its curvature, muscles in fish eye move the lens towards and from the retina while lens shape remains unchanged.

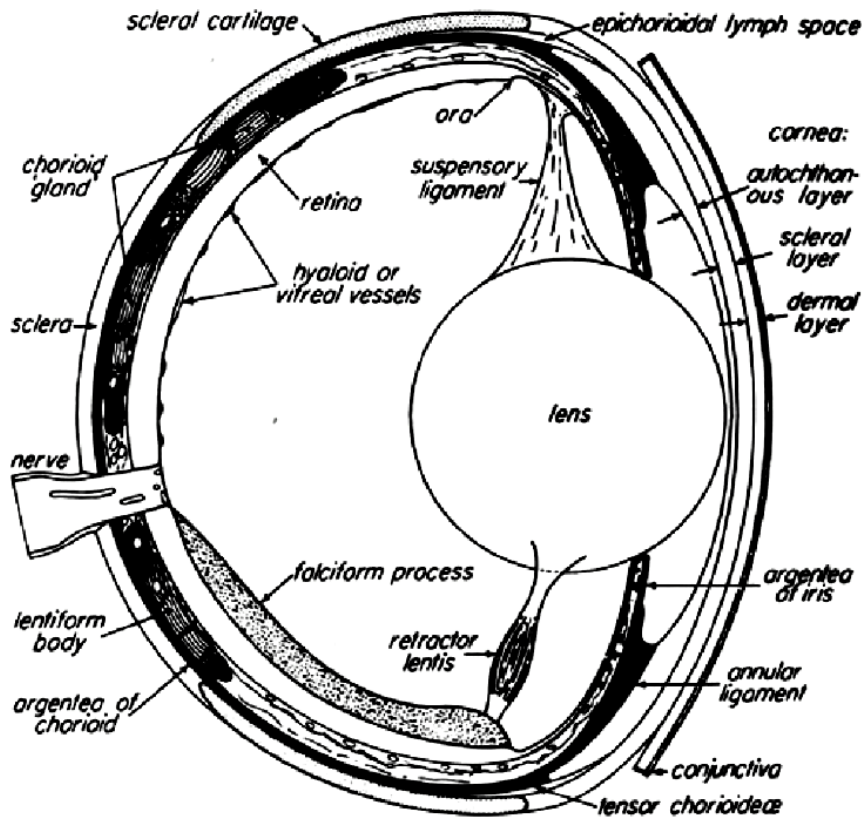


Figure 1: **Diagrammatical Vertical Section of Generalized Teleost Eye.** Some structures shown may not be present in some eyes. For example, either lentiform body and falciform process or hyaloid vessels are present (from *Walls, 1942 in Fernald, 1988).

Retina is the light-sensitive tissue of the eye responsible for detecting photons that entered the eye (Stell, 1972). It consists of ten cell layers (Figure 2). Most of the retinal cells are neurons that are supported by Müller glia cells and the outer layer consists of the pigment epithelium. The light is captured by photoreceptor cells – neurons that contain visual pigments. Visual pigments are capable of absorbing light of certain wavelengths. Once the light is absorbed, the signal is converted into a change in membrane potential and conducted to amacrine and ganglion cells in other retina layers and then via the optic nerve to the brain (Hartong, Berson, & Dryja, 2006). All neurons in retina (photoreceptors, amacrine cells, ganglion cells, bipolar cells, and horizontal cells) contribute to processing and altering the signal before it leaves the eye (Stell, 1972).

Visual pigments

Vertebrate visual pigments consist of a transmembrane protein (opsin) and a light-sensitive chromophore (aldehyde of vitamin A - retinal) (J. K. Bowmaker, 1995). Vitamin A has two forms, A₁ – retinal and A₂ – 3-dehydroretinal. Since both forms can associate with opsins, we can distinguish two groups of visual pigments – rhodopsins based on A₁ and porphyropsins based on A₂. While rhodopsins occur in all vertebrate groups, porphyropsins are present only in fish, amphibians, and reptiles. The wavelength of maximum absorbance λ_{\max} of 3-dehydroretinal is approximately 20 nm longer than the λ_{\max} of retinal, which affects the absorption maximum of the whole visual pigment (J. K. Bowmaker, 1995). If the light of a suitable wavelength is captured by visual pigment, the conformation of the chromophore changes from 11-*cis* isomer to all-*trans* isomer.

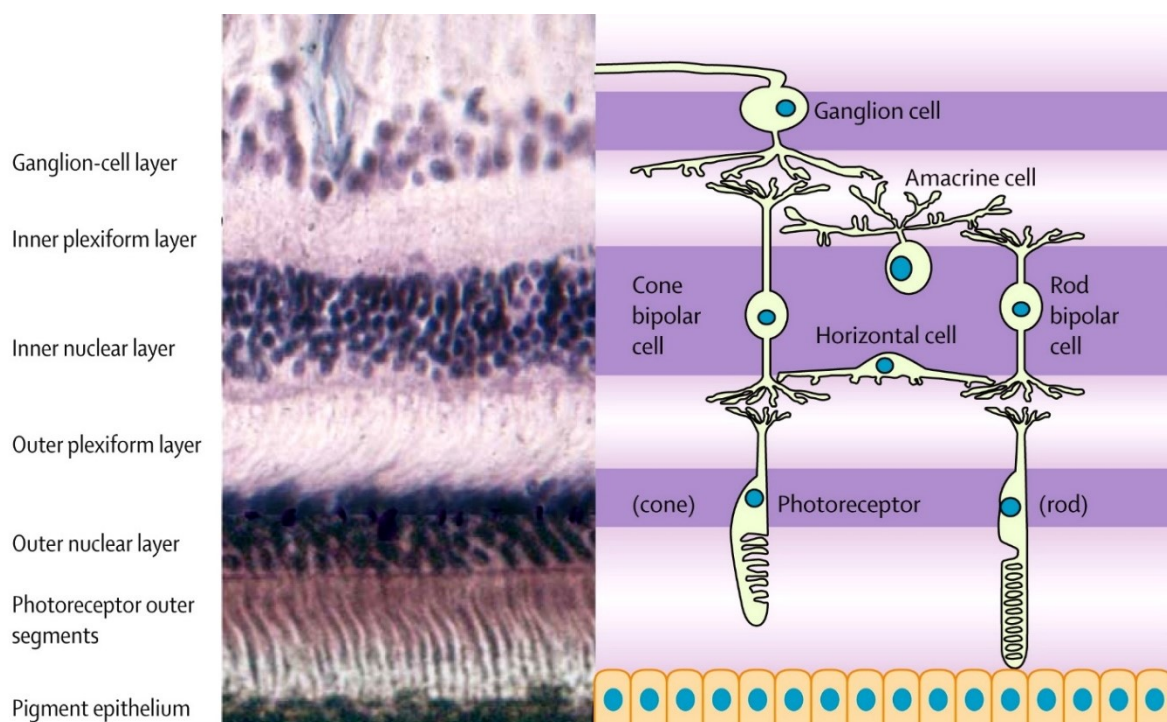


Figure 2: Retinal layers and cell types in vertebrate retina, simplified (modified after Hartong, Berson and Dryja, 2006).

Opsins are G-protein-coupled receptor proteins expressed in photoreceptors (J. K. Bowmaker, 1995). They are composed of approximately 350 amino acids that create a pocket where chromophore is embedded. Since the difference in chromophore changes the spectral sensitivity of the pigment only slightly, the absorption maximum of the individual visual pigment depends mostly on opsin protein and its interactions with the chromophore. There are about 28 known amino acid positions that affect the absorption maximum of the chromophore and thus can serve as tuning sites in vertebrates (Yokoyama, 2008). Substitution in those sites changes λ_{\max} of the visual pigment. Some tuning sites are specific for rods, others for cones (or specific cone types), and others are shared by both photoreceptor types. Expression of spectrally distinct opsins in different cells gives the foundation for the colour vision because signals can be later compared.

Opsins in fish absorb in wavelengths between 350 and 635 nm (J. K. Bowmaker, 1995), while most commonly distributed are those that focus on wavelengths between 400 and 500 nm that are best transmitted in clear water and penetrate deepest. There are five vertebrate opsin classes that differ in spectral sensitivity and all of them are present in ray-finned fishes (D. M. Hunt & Collin, 2014). The first class – RH1 (rhodopsins) with λ_{\max} of 500 nm – occurs in rods, while the other four classes occur in cones. Those are SWS1 (very short-wavelength sensitive) with λ_{\max} of 360–430 nm, SWS2 (short-wavelength sensitive) with λ_{\max} of 440–460 nm, RH2 (green-sensitive rhodopsin-like) with of 470–510 nm and MWS/LWS (middle/long-wavelength sensitive) with λ_{\max} of 510–560 nm (Yokoyama, 2000). However, if associated with 3-dehydroretinal, the spectral sensitivity of each opsin shifts to longer wavelengths. LWS opsins then reach λ_{\max} over 600 nm (D. M. Hunt & Collin, 2014). Vertebrate pigment classes diversified very early in evolution, so the colour vision was probably present in ancestral vertebrates. It seems that cone pigments, especially MWS/LWS, are older than rod pigment RH1 (J. K. Bowmaker, 1995), which probably originated from a duplication of the RH2 gene (Okano, Kojima, Fukada, Shichida, & Yoshizawa, 1992).

Some groups of vertebrates have lost certain opsin classes, e.g. mammals (Jacobs, 1993). On the contrary, others possess more than five spectrally distinct opsins, but always belonging to one of these five classes. It is quite remarkable that ray-finned fishes underwent the whole-genome duplication after the divergence with lobe-finned fishes and before the teleost radiation (Amores et al., 1998). In this duplication event, the number of opsin genes doubled giving the potential for them to diversify. Many groups of ray-finned fishes later underwent subsequent duplication and diversification of some cone opsin genes that also resulted in a higher number of spectrally distinct visual pigments that tend to be retained in the genome. For instance, there are seven cone opsin genes in African cichlids from Lake Malawi (Spady et al., 2006). Although usually only three of them are expressed at the same time, the set of expressed genes often changes during development, which might be the reason why so many genes are present. A similar process with the rod opsin gene RH1 also occurred repeatedly leading to various numbers of different rod opsins in retinae of some fishes (Musilova, Cortesi, et al., 2019). However, duplications of the RH1 gene are generally less common than those of cone opsin genes.

Although opsin gene diversification can enhance vision significantly, there are still many fishes that are mono- or dichromatic. Generally, all fishes (including those expressing three and more cone pigments) tend to develop one cone pigment with λ_{\max} matching the spacelight (dominant wavelength in the environment), and at least one cone pigment with different spectral sensitivity (Guthrie, 1986). It turned out that two distinct cone opsins can sufficiently meet the essential visual requirements – brightness discrimination and contrasting silhouettes against the background. Therefore, the expression of two cone opsins can be adequate for some fishes. The rod pigment seems to be always corresponding to the wavelength that is best transmitted in the water.

Photoreceptors

Photoreceptors are neural cells elongated along their perpendicular axis. They consist of five compartments: outer segment, inner segment, soma, axon, and synaptic terminal, as shown in Figure 3 (Baker & Kerov, 2013; Cohen, 1972; Fisher et al., 1993). The outer segment contains disc membranes (lamellae) with optical pigments (opsins are transmembrane proteins located in lamellae). When a photon is captured in the outer segment, it triggers the hyperpolarization of the cell that spreads through the plasma membrane to the inner segment, soma, and axon. Finally, the signal reaches the synaptic terminal and is passed on bipolar cell (Baker & Kerov, 2013).

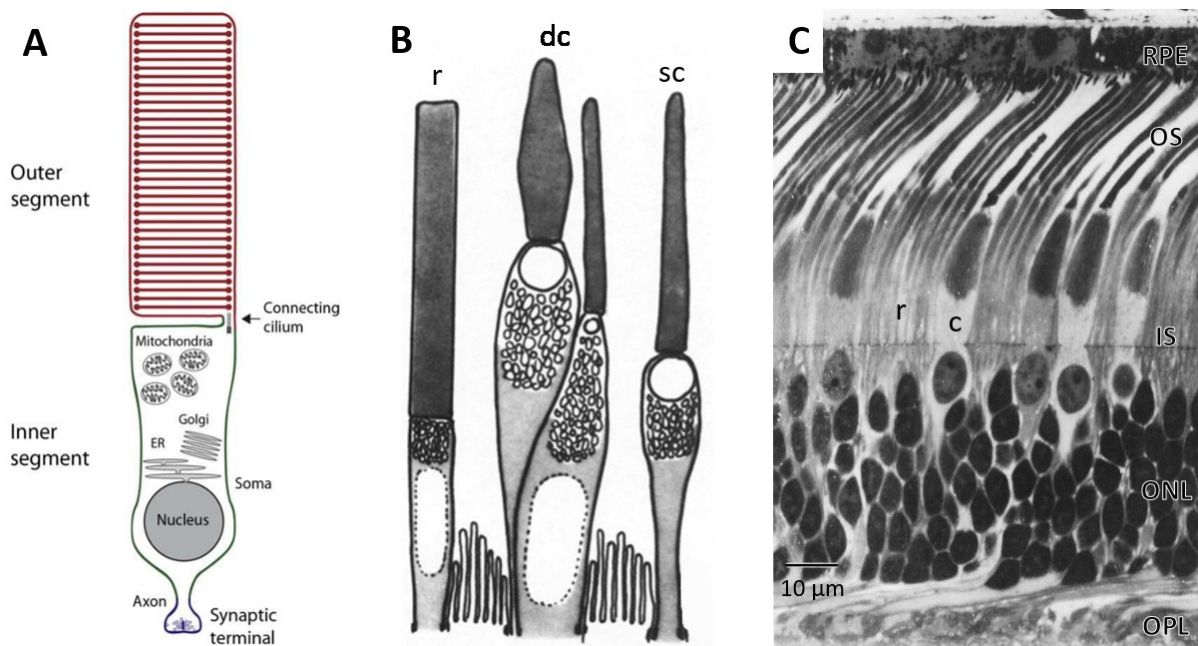


Figure 3: Structure of photoreceptor cells; (A) Structure of generalized photoreceptor cell (Baker & Kerov, 2013); (B) Main morphological types of photoreceptors (modified after Szél et al., 1985); (C) Photoreceptors in vertebrate retina (modified after Fisher et al., 1993); r – rod, c – cone, dc – double cone, sc – single cone, RPE – retinal pigment epithelium, OS – outer segments, IS – inner segments, ONL – outer nuclear layer (nuclei of photoreceptor cells), OPL – outer plexiform layer (synaptic terminals of photoreceptor cells)

There are two basic groups of photoreceptors in vertebrates – rods and cones (Figure 3). Rods are longer and thinner, whereas cones are shorter, bulkier, and tapered (Cohen, 1972; D. M. Hunt & Collin, 2014). Whilst rods provide scotopic vision (i.e. in dim light conditions), cones are used for photopic vision (in higher light intensities). The scotopic system is specialized in high sensitivity because rods can develop a large response to very small signals (even one photon can be detected). On the other hand, signal amplifying takes time, so the photopic system responds much faster to quantal stimuli than the scotopic system and is thus better suited for fast movement detection (Schnapf & Baylor, 1987). To advantage suitable photoreceptor type in certain light conditions even more, rods and cones undergo retinomotor movements. In a bright environment, cones are exposed to entering light, and rods are buried below them. With decreasing light level, their position changes (Burnside & Nagle, 1983). Nonetheless, there exists also an intermediate state (mesopic conditions), when both rods and cones can be employed in

vision (De Busserolles et al., 2017). It is possible that some fishes could achieve the best visual acuity and colour discrimination in mesopic conditions (e.g. twilight) when all photoreceptors contribute to the vision.

Retinae of most fishes are duplex – comprised of both rods and cones. Additionally, fish with pure-rod retinae – retinae consisting of rods only – are also described (Locket, 1977; Musilova, Cortesi, et al., 2019). Pure-rod retinae represent a morphological adaptation for life in depths, where light intensity is very low (J. K. Bowmaker, 1995). Some authors also use the term “all-rod retina” to describe the same phenomenon (Carleton, Escobar-Camacho, Stieb, Cortesi, & Marshall, 2020). On the other hand, retinas with a predominance of cones also exist, especially in the early developmental stages of some fishes (Shand, Archer, & Collin, 1999; Shand, Archer, Thomas, & Cleary, 2001).

During retinal development in teleost fishes, cones precede rods, which usually appear with metamorphosis (Shand et al., 1999). Cone-like receptors also seem to be evolutionary older, as suggested by comparative analyses of lampreys, sturgeons, and spoonbills (J. K. Bowmaker, 1995). Since analogues of SWS1, SWS2, and LWS plus two RH-like genes are present in lampreys, it seems that the potential for photopic colour vision was established before the split of agnathans and gnathostomes, whereas the scotopic vision developed later. However, the marine lamprey *Petromyzon marinus* possess the gene corresponding to RH1, with SWS1 and SWS2 completely reduced, probably as a result of an adaptation for life in the deep ocean (Zhang & Yokoyama, 1997). Yet the morphology of cells expressing the RH1 gene is far from rods in lamprey.

While the morphology of rods is generally uniform and conserved within vertebrates, cones are highly diverse both in morphology and visual pigments contained (J. K. Bowmaker, 1995). In general, larger longer cones are sensitive to longer wavelengths and smaller shorter cones to shorter wavelengths. They often merge and constitute double, triple, or even quadruple cones. Moreover, each of those categories comprises further distinct morphological types. Double cones are usually sensitive to longer wavelengths than single cones (J. K. Bowmaker, 1995). Cones are also used for high acuity vision, which is achieved by their accumulation in certain parts of the retina (D. M. Hunt & Collin, 2014).

Double cones

Double cones are a regular component of fish retinae and they appear to be even more common than single cones (Lyll, 1957). They are also present in the retinae of other vertebrates except for placental mammals and elasmobranchs (Szél, Takács, Monostori, Vigh-Teichmann, & Röhlich, 1985). Double cones consist of two cones joined together that might be connected by gap junctions. They can express either the same or different opsin and they sometimes slightly vary in size. Some authors call the double cones with undistinguishable members “twin cones” (first used in Greeff & Graefe, 1900), but this terminology is rather confusing and not used by all authors in the same way (J. K. Bowmaker, 1995). Therefore, I will not use the term “twin cones” in my thesis. The term “identical double cones” will refer

to the double cones with two undistinguishable members expressing the same visual pigment, whereas “non-identical double cones” will be those differing either in colour sensitivity or in the shape of the adjacent cells. Double cones originate by merging of two single cones (Shand et al., 2001). The regions of the common membrane between adjacent cells are called subsurface cisternae.

The exact function of double cones remains unknown, but it is anticipated that they enhance vision in dim light conditions and contribute to achromatic tasks such as luminance and polarization vision. Indeed there is evidence that retinae of fishes inhabiting deeper water contain a higher percentage of double cones (Musilova, Indermaur, et al., 2019). Also, the study conducted on budgerigars (*Melopsittacus undulatus*) confirmed that while single cones are used in bright light conditions, their visual sensitivity rapidly decreases in dim light when it is compensated by double cones (Lind, Chavez, & Kelber, 2014). This suggests that the function of double cones might be similar among vertebrate groups. The double cones could achieve higher sensitivity at the minimum light level thanks to gap junctions – such electrical coupling would sum the signal from both cells (regardless of the fact if they share the same opsin or not) resulting in stronger final signal. That would improve the ability to detect the dark object contrasting the brighter background (e.g. the silhouette of the approaching predator) (Pignatelli, Champ, Marshall, & Vorobyev, 2010). In such case, fish would benefit from enhanced sensitivity in a dim environment, but non-identical double cones could not aid the colour discrimination in bright conditions because the signals launched by the light of a different wavelength in adjacent cones would no longer be separated.

Yet, the study conducted on reef fish *Rhinecanthus aculeatus* proved that in this species double cones contribute to chromatic vision (Pignatelli et al., 2010). Having three visual pigments – one of them located in single cones and the remaining two located in neighbouring members of each double cone – this fish was anticipated to be dichromatic. Surprisingly, behavioural experiments revealed that *Rhinecanthus aculeatus* has a trichromatic vision. Therefore, the extent of electrical coupling between the cells within one double cone is still being discussed as well as their chromatic wiring with inner retinal layers mediated by bipolar cells. Further study of bipolar cells suggests that signals from members of the double cone could be anatomically segregated in the inner retina in a similar way as it occurs in primates (Pignatelli & Marshall, 2010). It is also hypothesized that few specialized colour-selective bipolar cells might exist within the retina of certain fish species with the function similar to midget bipolar cells in mammals (those cells are connected to only one cone each and thus enable the finer colour sampling).

It is possible that fishes inhabiting deeper and darker habitats use their double cones to enhance their visual sensitivity, while fishes in shallower and lighter habitats do not benefit much from this function. Contrarily, in such conditions, it is favourable to separate the signals from the members of one double cone and improve resolution and colour discrimination. Such incongruity in the function of double cones

can be best explained by the theory that double cones maximize the cone packing – the total retinal area occupied by photoreceptors is larger if not only circular single cones, but also double cones are present (van der Meer, 1992). Since high cone packing is beneficial both for visual acuity and sensitivity, it is consequent that we can find evidence for both seemingly opposing functions in double cones.

Triple cones

Apart from the above mentioned common types, fishes in many teleost families also possess triple cones, where three cones are morphologically associated (Collins & MacNichol, 1979; Engström, 1963; Heß, 2009). Triple cones can occur in various parts of the retina, but they are often found in the proximity of blind spot and their densities are very low. That might be the reason why triple cones were probably overlooked in some fishes, although it is certain that they are completely missing in retinae of many species, as confirmed by thorough examination (Dalton, De Busserolles, Justin Marshall, & Carleton, 2017; Dalton, Loew, Cronin, & Carleton, 2014; Stieb et al., 2019). However, in other species (e.g. anchovy species *Cetengraulis mysticetus* and *Anchovia macrolepidota*) retinae comprise dominantly triple cones – rods are still present in those retinae, but all cones are organized in triple cones (Heß, 2009).

It is thought that triple cones originated by merging of a single cone and double cone (Lyll, 1957), and their components were initially equal. The cells in triple cones can be arranged either linearly or triangularly while in the linear constellation, the size of the components can vary. In the linear triple cones observed in the minnow *Phoxinus laevis*, the central component is large and it is surrounded by two smaller cells (Lyll, 1956). In contrast, linear triple cones of anchovy fishes *Cetengraulis mysticetus*, *Anchovia macrolepidota*, and *Engraulis encrasicolus* consist of small middle member and larger lateral cells (Heß, 2009; Kondrashev, Gnyubkina, & Zueva, 2012). Triple cones of this morphology have never been found in any other family of fishes, so it is presumably the apomorphy of the family Engraulidae. Triangular triple cones were found for instance in *Clupea sprattus*, *Lumpenus maculatus*, *Gobius flavescens*, and *Trigla gurnardus*, in all cases located near the optic nerve (Engström, 1963). Since those fishes belong to different families, the incidence of triple cones in this part of the retina seems to be quite widespread among teleosts.

As for the function of triple cones, only little is known but many speculations were raised. Similar to double cones, triple cones could represent an adaptation for vision in dim light – having larger triple cones leads to increased sensitivity and decreased resolution and acuity. Some authors also hypothesize that triple cones with morphologically distinct members could mediate colour discrimination. In Japanese anchovy *Engraulis japonicus*, the spectral absorbance of the short middle triple cone component with $\lambda_{\max} \sim 475$ nm differs from the spectral absorbance of larger lateral components with $\lambda_{\max} \sim 500$ nm. Since remaining cones and rods in the retina of *E. japonicus* are all sensitive to wavelengths similar to the lateral components of triple cones with λ_{\max} near 500 nm, triple cones are the

only way how this fish could implement chromatic vision (Kondrashev et al., 2012). Even though some experiments suggest that anchovy species can discriminate colours, more evidence is still needed to confirm this ability and so this possible function of triple cones (Kondrashev et al., 2012). It is also possible that triple cones do not have any specific function and they only appear as an intermediate state during the reorganization of photoreceptors within the retina of certain fishes (Shand et al., 1999, 2001).

Quadruple cones

In some fishes, such as the minnow *Phoxinus laevis*, the presence of quadruple cones is also reported (Lyll, 1956). Minnow quadruple cones consist of one smaller central cell surrounded by three larger lateral cells and they are quite numerous within the retina, along with linear triple cones mentioned above. Since having a significant number of quadruple cones in the retina is quite unusual among vertebrates, some specific function of quadruple cones in *Phoxinus* is anticipated. However, the structure of quadruple cones described in *Phoxinus* seems to be aberrant since the quadruple cones reported in other fishes (e.g. in *Cottus scorpius*, *C. quadricornis* and *Agonus cataphractus*) usually consist of four morphologically equal cells (Engström, 1963). Quadruple cones also occur sporadically in the retina of *Ameioba splendens*, but they cannot be considered the regular element of cone pattern (Reckel & Melzer, 2003). It is possible that quadruple and triple cones could serve as single and double cone precursors, and thus observed rare quadruple cones would be only remnants of development without any specific function in this fish.

In *Acanthopagrus butcheri*, quadruple cones are present during early developmental stages, but they later disappear (around 50th day of post-hatch development) and can no longer be found in adult retinae (Shand et al., 1999). The most likely explanation is that they dissociate to create single cones and double cones. This conclusion is in compliance with the hypothesis that triple and quadruple cones are at least in some fishes developmental precursors of single and double cones and their retention in adult retinae could be considered a form of neoteny.

Cone mosaic

Different types of cones tend to be two-dimensionally regularly arranged in fish retina. The pattern they form is called cone mosaic. Rods fill the remaining space and are not usually considered part of the pattern, because there is no regularity in their distribution. The regular arrangement of photoreceptors is very unusual among vertebrates and apart from ray-finned fishes, it was only described in some geckos (Dunn, 1966). There are two basic types of cone mosaic described in teleost fishes based on the orientation of double cones - cones can be organized either in rows (all double cones in parallel orientation) or in square units (double cones alternately perpendicularly oriented), as shown in Figure 4 (Engström, 1963). There are two types of single cones – long and short – and one type of double cone in both fundamental patterns. While double cones create the lattice of the mosaic, single cones occupy

spaces in between. In the row mosaic, rows of double cones are interspersed with rows of alternating short and long single cones. In the square mosaic, double cones and single cones are placed in the corners of overlapping squares, so that every single cone is surrounded by four double cones. There are several possible ways how to define the fundamental unit in the square mosaic – most commonly four double cones represent sides of the square with a long cone in the centre (thus called central cone) and short cones in the corners of the square (additional or accessory cones). Additionally, there exists one more type of pattern – triangular pattern, where the mutual position of double cones is neither parallel nor perpendicular (van der Meer, 1992). Instead, neighbouring double cones include angles of $60^\circ/120^\circ$ so that double cones form the sides of the triangle and single cones are placed in corners. Some authors also consider the retina without double cones to be another type of mosaic and they call such pattern uniform. This state is often present in the early stages of ontogenetic development (Figure 4G).

If the cone mosaic is present, either row or square type, it seems to be very conserved (Tohya, Mochizukiz, & Iwasaw, 2003). That is likely because of stabilizing selection – since cone mosaic ensures equal distribution of different cone types which is beneficial for resolution, having whichever regular pattern is better than not having any. Thus the type of mosaic is correlated with phylogeny, so there exists the typical pattern in each family or even order. We find row mosaic in the families Cyprinidae, Clupeidae, Engraulidae or Gadidae, whereas square mosaic is typical for the families Salmonidae, Pleuronectidae, Cyprinodontidae, Poeciliidae, and for the whole group formerly known as Perciformes, comprising families such as Cichlidae, Labridae, and Percidae. Triangular mosaic is quite rare, but it was reported in the family Esocidae (Ali & Anctil, 1976; Braekevelt, 1975). However, there exist many exceptions and modifications of the basic pattern in certain families or individual species, that are often correlated with ecology. Both single cones and double cones might be missing in the retina and the degree of organization also varies. Generally, species highly dependent on vision (mostly predators) possess very regular patterns, while the mosaic in bottom-dwelling species living in a dim environment tends to disintegrate. The pattern can be entirely missing in some cases, e.g. in the deep-sea fish species of benthic seasnails, *Liparis liparis* (Engström, 1963).

Even distribution of the cones in the regular mosaic aids higher visual acuity and contrast as well as better detail and chromatic discrimination. Certain specialized patterns are possibly associated with polarization vision (Novales Flamarique, 2011). Some authors postulate the movement analysis to be the pivotal function of the regular pattern – the correlation of the pattern type with the habitat structure and feeding strategy was also suggested (Ahlbert, 1976). The square mosaic could be better suited for the detection of movements in all directions and thus beneficial for species that perceive more three-dimensional environment, e.g. solitary predators. The row mosaic would then be beneficial for fish that need to discriminate movements mostly in two directions, e.g. for shoaling fish that need to control the movement of the shoal in the horizontal plane. This theory proved to be accurate in salmonids with different feeding strategies (Ahlbert, 1976). Triangular mosaic seems to be adapted to the detection of

small movements since it can achieve the closest cone packing of all patterns and provide the highest resolution (van der Meer, 1992). It is thus not surprising, that the family Esocidae equipped with triangular pattern feed as ambush predators.

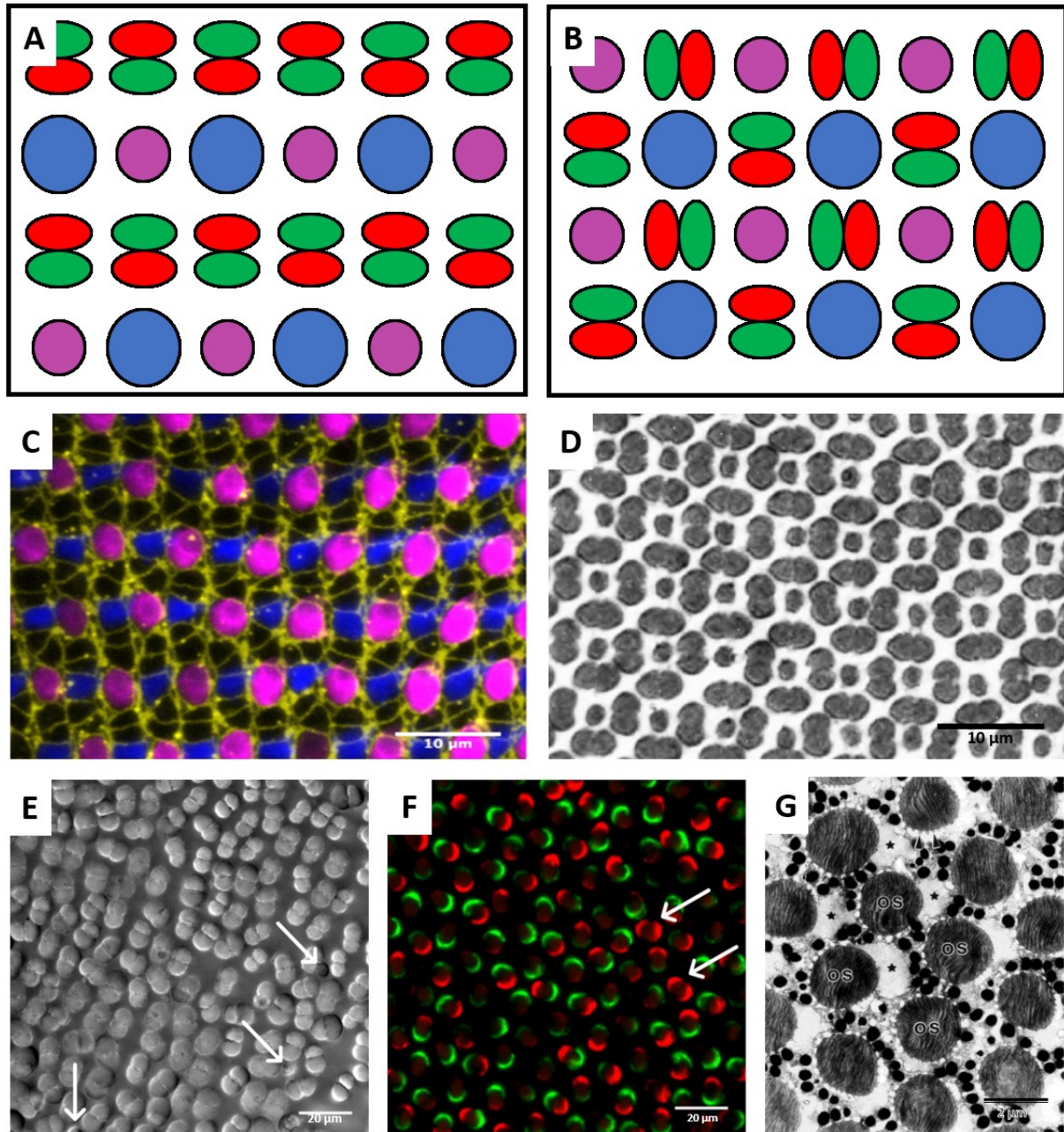


Figure 4: Examples of cone mosaic; (A) Diagram of row mosaic based on *Danio rerio*; (B) Diagram of square mosaic based on *Oryzias latipes*; (C) Row mosaic in *Danio rerio* (Salbreux et al., 2012); (D) Square mosaic without corner cones in *Pseudopleuronectes americanus* (Evans and Browman, 2004); (E) Double-cone retina without regular pattern in *Konia dikume* (Remišová, 2019); (F) Square mosaic in *Konia eisentrauti*, only double cones visualised (Remišová, 2019); (G) Single-cone retina in the early developmental stage in *Acanthopagrus butcheri* (Shand, Archer and Collin, 1999); os – outer segment; Colours correspond with the spectral sensitivity of visual pigment contained within the cell.

Cone mosaic development

The cone mosaic is not inborn – the regular pattern must be created during development (Evans & Browman, 2004). Single cones are the first photoreceptors to appear in the larval retina. Initially, they are very small and their organization varies among species. For instance, in the West Australian dhufish (*Glaucosoma hebraicum*) and the black bream (*Acanthopagrus butcheri*), larval single cones of hexagonal shape form a tight pattern, neighbouring with six other cones each, see Figure 4G (Shand et al., 1999, 2001). Initial small single cones usually express SWS1 opsin and are sensitive to short wavelengths. In the first days of post-hatch development, some of the single cones start to merge and they form double cones connected by subsurface cisternae. The photoreceptors that develop the latest are rods, which differentiate from rod precursors in deeper layers. This process is often connected with metamorphosis. Roughly around the same time, cones begin to rearrange towards the adult pattern which is then gradually achieved. However, irregularity is often preserved in the remnant of the larval retina in the proximity of optic nerve, where some aberrant cone types (e.g. triple or quadruple cones) can sometimes be found (Allison et al., 2010; Shand et al., 1999). The development of new photoreceptor types and adult pattern formation can be associated with the switch in opsin expression.

Moreover, as the fish grows, its retina grows as well (Johns, 1997). While the cone mosaic is present in the central region of the adult fish retina, marginal regions near the germinal zone where new photoreceptors are generated do not show any regular arrangements. It implies that the pattern needs some time to be created and that it expands from the centre of the retina to the margins. So far it seems that cell divisions do not contribute to the pattern formation in adult fish – new cells are produced only in marginal zones and the regular pattern results from their reorganization or differentiation.

There are two major theories about the formation of the cone mosaic: cell rearrangement theory and cell fate transition theory.

The cell rearrangement theory assumes retinal cells to have pre-fixed fate and the ability to move within the retinal space. Different cone types would form different cell-cell interactions resulting in an adhesive force that would drive neighbouring cones to exchange their locations and organize themselves into regular pattern spontaneously (Tohya et al., 2003). The analysis of models created for zebrafish *Danio rerio* (row pattern) and medaka *Oryzias latipes* (square pattern) showed that contact between nearest neighbours is enough to generate the row pattern, but not the square pattern, where interaction with next-nearest neighbours would be needed too (Tohya et al., 2003).

The cell fate transition theory anticipates that precursors of cones are partially committed to becoming one of the cone types, but this state can change according to the adhesive interactions with neighbouring cells. Those transitions occur in the stage called pre-pattern formation. When the pattern tuning is finished, the cells differentiate into the types they are committed to and the cone mosaic is finalized (Tohya, Mochizuki, & Iwasa, 1999). The model constructed for zebrafish *Danio rerio* proved that it

would be possible to create the row cone mosaic this way. However, it also showed that if the pre-pattern formation started simultaneously in the whole retina, it would take very long for cells to create a regular pattern. The time needed would also increase with the size of the retina. This problem can be solved if the differentiation proceeds gradually from one side of the retina to another (most likely from ventral to dorsal retina) – one row of the cells creates pre-pattern formation and the other rows successively match to it.

Based on the models, the row pattern seems to be achieved easier than the square pattern. Furthermore, as the fish retina continues growing throughout life, new cells in germinal zones at the retinal margin are generated in rows. Therefore species with square mosaic in the centre of retina still have row mosaic in the peripheries. That suggests that row pattern could precede square pattern both developmentally and evolutionary and thus can be considered more advanced (Lyall, 1957). Replacement of row mosaic by square mosaic was directly observed in several developmental studies, e.g. in the black bream *Acanthopagrus butcheri* or the west Australian dhufish *Glaucosoma hebraicum* (Shand et al., 1999, 2001). Indeed, the square mosaic is widespread in the group Euteleostei, the crown group of teleost fishes known to possess multiple evolutionary advanced characters, while row mosaic is more common outside this group, namely in the lineage Otomorpha (with Cypriniformes as the most species-rich example). However, it is rather a trend than a rule and the evidence from some groups is not enough to state with certainty what their typical mosaic pattern is.

Several ontogenetic studies were conducted to explore the development of the cone mosaic. For zebrafish, it was confirmed that there is a difference between the larval retina and adult row pattern (Allison et al., 2010). Rows were completely missing in the larval retina, although some regularity was present as well. The cone mosaic arose with metamorphosis and it developed during postlarval growth until perfect adult row pattern was achieved. It seems that the cell fate transition theory has stronger support in zebrafish than the cell rearrangement theory. Cones initially started to differentiate in the ventral retina and the area of differentiated cells spread subsequently. However, it is possible that differential cell adhesion also contributes to row pattern formation once correct cone ratios are produced. The remnant of the larval retina in the proximity of the optic nerve is preserved in zebrafish as well, but interestingly, it does not remain unchanged. Compared to the remnant, the larval retina contains a higher percentage of UV cones (SWS1) and blue cones (SWS2). The number of UV-sensitive cones in the remnant is reduced, with cell death being very likely the mechanism of such reduction. Nevertheless, opsin switch during development has also been reported in some species, as will be discussed later.

The development of a square mosaic was examined in the black bream, *Acanthopagrus butcheri* (Shand et al., 1999). The larval retina of the black bream is composed of small single cones of hexagonal shape tightly packed together. During metamorphosis, cones begin to merge and form the long chains (up to 10 cells) connected by subsurface cisternae. A similar transition phase characterized by the formation

of triple cones was also observed in another species with the square mosaic – in the west Australian dhufish, *Glaucosoma hebraicum* (Shand et al., 2001). Later on, the complexes dissociate and the square mosaic is formed. Only a few triple and quadruple cones are preserved in the larval remnant. Again, both cell rearrangement and cell fate transition possibly aid the formation of mosaic in the black bream. It was suggested that the rotation of cones in the central regions gives rise to the square pattern, while lateral induction could guide the differentiation of neighbouring cells on retinal margins as the retina grows.

Apart from the structural changes, the cone mosaic development can be accompanied by the shift in spectral sensitivity. Such shift is usually correlated with a change in behaviour and ecology. That may be associated with metamorphosis, but also may not – the most striking change in ecology happens much later in the life of some fishes, especially in the migratory species such as salmonids and eel.

There are several ways to achieve the change in the cone spectral sensitivity. First, the original cones could be eliminated and replaced by the new ones expressing different visual pigments. Although it shows that apoptosis of certain cones (especially the short UV sensitive cones) indeed contributes to altering the cone ratios and finalization of the mosaic, new cones can be added to the retina only in retinal margins. Nevertheless, different cone proportion impacts visual performance despite the spectral sensitivity of the particular cones remains unchanged. Notably, the significant reduction of UV cones (SWS1) is widespread among fishes. UV cones are very abundant in larval retinae, but they are often at least partially eliminated either during metamorphosis (e.g. in the zebrafish) or later in life (e.g. in salmonids) (Allison et al., 2010; Y. W. Kunz, Wildenburg, Goodrich, & Callaghan, 1994). For instance, the yearling brown trout, *Salmo trutta*, still possess significantly higher percentages of UV-sensitive cones than 2-year-olds and older trout (J. K. Bowmaker & Kunz, 1987). The apoptosis of short cones results in the modification of fundamental square mosaic – the corner single cones are missing in the pattern of adult fish, especially in ventral retina (J. K. Bowmaker & Kunz, 1987; Cheng & Flamarique, 2007b). Moreover, since the apoptosis begins in the ventral retina and spreads dorsally, the dorsal retina of young salmonids contains a higher percentage of single cones than the ventral part (Cheng & Flamarique, 2007b). As the elimination of the corner single cones proceeds, it leaves vacant space for rods. Although earlier authors (e.g. Lyall, 1957) anticipated that corner cones transmute into rods, such process is rather unlikely due to the major differences in the morphology and molecular machinery, such as the phototransduction cascade, of both photoreceptor types. It is thus reasonable to anticipate that rods or their precursors are prepared in a deeper retinal layer and once corner cells are eliminated, rods take their place (Y. W. Kunz et al., 1994).

However, transmutation between two cone types, i.e. into the cone with different spectral sensitivity does not require major changes in morphology, just the modulation of the opsin gene expression. The opsin gene switch is the second way to achieve the shift in spectral sensitivity. This mechanism is also

reported in salmonids, particularly in the rainbow trout, *Oncorhynchus mykiss*, and the Pacific salmon, *Oncorhynchus* sp., where the corner cones are retained in dorsal retina of adults, but they are sensitive to the blue part of the spectrum (Cheng & Flamarique, 2007a, 2007b). Those corner cells undergo a change in opsin expression from SWS1 (UV-sensitive) to SWS2 (blue-sensitive). A similar process can also occur in rods. In the eel, *Anguilla* spp., the rod pigment changes as they move from freshwater to the marine environment (Wood & Partridge, 1993).

Not only that the opsin expression in the photoreceptors can switch completely from one opsin to another, but also the expression of more than one opsin in one cell is possible. The peak absorbance of such photoreceptors lies between the λ_{\max} of contributing opsins, depending on their concentration in the cell.

The last option on how to modulate spectral sensitivity is replacing the chromophore associated with the opsin. The difference between peak absorbance of rhodopsin and porphyropsin is more apparent in visual pigments sensitive to longer wavelengths, while the peak absorbance of porphyropsins is shifted to longer wavelengths compared to rhodopsins. Rhodopsins are typically found in marine species, whereas freshwater fishes possess mostly porphyropsins. Such distribution is not surprising, since marine water is generally clearer, transmitting blueish light the best, while the spectrum in freshwater is often shifted towards red. It is also expectable that the most noticeable changes in rhodopsin-porphyropsin distribution are present in migratory species, which move between marine and freshwater environments throughout life. For example, when the eels undergo metamorphosis to leave the freshwater and enter the ocean, their porphyropsins are replaced with rhodopsins (James K. Bowmaker, Semo, Hunt, & Jeffery, 2008). In some species, e.g. the Pacific salmon, similar changes happen repeatedly throughout life (Novales Flamarique, 2005). In addition, species with mixtures of rhodopsin and porphyropsin in individual photoreceptor cells were also reported (Terai et al., 2017). The absorption spectrum of visual pigments in such photoreceptors can thus be modified via changing the rhodopsin/porphyropsin ratio.

In conclusion, larval retina differs a lot from the mature one and the adult pattern must be achieved in many subsequent steps. The reasons for the gradual arrangement of the pattern are yet to be fully understood, but reasonable explanations have been already proposed. Since the vision of adult fish is presumably more elaborated than larvae vision, the structure of larval retina (high amount of short cones showing very little regularity in distribution) may be caused by evolutionary constraint. For instance, it could be fixed that the SWS1 opsin is the first one to start expression. On the other hand, a higher percentage of short cones and the lack of regular patterns could be also considered an adaptive trait, because larvae and young fish often live under different selection pressures than adults. The fact that changes in the mosaic are associated with changes in ecology seems to support such hypothesis. In the zebrafish, the formation of a row pattern is correlated with metamorphosis (Allison et al., 2010). While

the larvae float in surface waters and do not perform any communication, postlarval stages become more mobile, and visually guided behaviour (e.g. shoaling) is developing as well. Although simple retina is sufficient for larvae, it must be later modified to enable older fish to change their lifestyle. Similarly, the tightly packed small hexagonal cones of the black bream and the West Australian dhufish are likely to maximise detail discrimination by the small eyes of the young surface-dwelling fish living in the environment where short-wavelength light is still abundant (Shand et al., 1999, 2001). In the trout, retina matures much later, but also in association with the switch in ecology. Trout yearlings live in clear water and prey on plankton that often scatters or absorbs UV light (J. K. Bowmaker & Kunz, 1987). Thus UV-sensitive cones aid detection and differentiation of the prey, which might be the reason why they remain in retina until trout grow enough to move to the deeper water and switch their feeding strategy, which usually happens at the age of 20 months (Novales Flamarique, 2005). A similar process was also described in the Atlantic salmon parr at the age of 5 months (Y. W. Kunz et al., 1994).

Photoreceptor arrangements in various environments

Since vision is a very important sense for many fishes, it is not surprising that visual apparatus, including the cone mosaic, tends to adapt to the photic environment and ecology of the fish. Engström had suggested that the degree of organization of the cone mosaic depends on the ecology of the fish – fishes strongly relying on vision possess the most regular pattern (Engström, 1963). However, the relation between life strategy and cone mosaic structure seems to be much closer than that. Not only the regularity of cone arrangement but also the ratio of cone types and opsin expression matches the environment and ecology of the fish. The typical shape of the mosaic has been identified for the main fish guilds (J. K. Bowmaker, 1995), and sometimes the habitat or feeding strategy of the fish can be predicted based on the mosaic structure (Shand et al., 2001). Here, I list the main trends in cone mosaic adaptation and some examples of adaptation to different habitats (see Figure 5).

Three major functions that must be achieved by retina: detail discrimination, colour discrimination, and sensitivity (van der Meer, 1992). While detail and colour discrimination is associated with photopic vision and are closely related to each other, sensitivity is crucial for scotopic vision and it goes against discrimination. That is given by the limited space in the retinal layer and limited eye size – while resolution increases with cone density (and the eye size), sensitivity increases with cone size (regardless of eye size), and hence they cannot be enhanced at the same time. Packing (the total area occupied by photoreceptors) always tends to be maximized, but the ratio of cone number (cone density) and cone size can change to meet the specific demands of the surrounding environment. Colour discrimination depends on the presence of the cones expressing distinct visual pigments and it can aid the detail discrimination. All colour-specific cones compete for space as well.

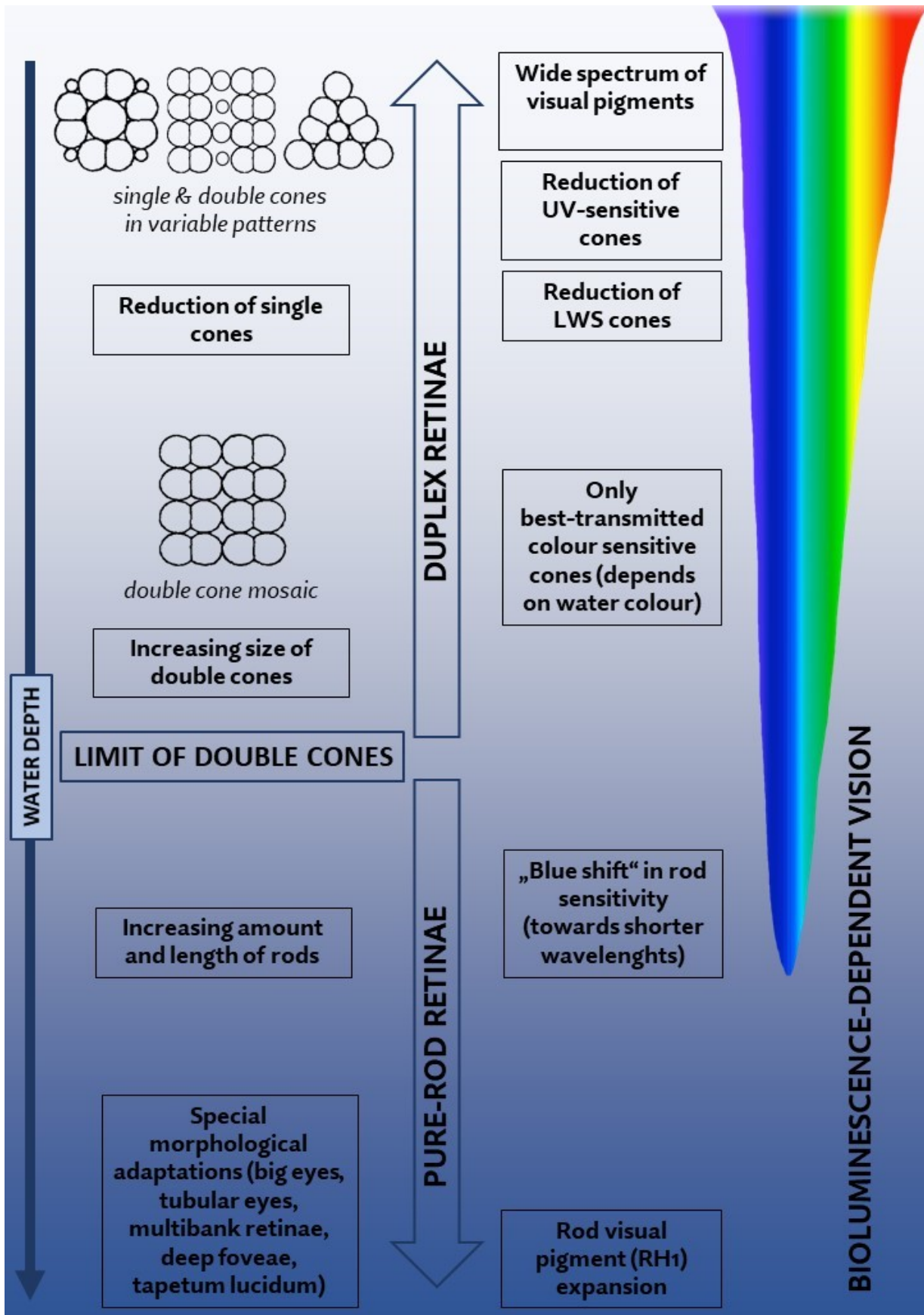


Figure 5: *Main trends in adaptation of fish vision to different photic environments.* First column shows changes in photoreceptor arrangement, second column shows changes in visual pigments. Spectral distribution of light in depth might vary depending on water colour. Water depth axis is relative, light diminishing depends on water clarity. Bioluminescence might not be present in freshwater.

In the retinal wiring, a certain number of cones is converging to a single ganglion cell – those cones form a photopic unit. Smaller the number of converging cones, better the resolution. On the other hand, each photopic unit must comprise all of the cone types, and the homogenous distribution of each cone type must be maintained – otherwise, resolution lowers. The number of cells within one photopic unit hence cannot be too low, because all colour-specific cones must be organized within every unit. Moreover, to achieve precise movement detection, the distances between the centres of photopic units must be constant. Only the mosaic patterns that meet those requirements can be realized.

It is interesting that within one photopic unit, the ratio of cones sensitive to different wavelengths can vary to adjust the colour sensitivity to the spectral distribution in the environment. Some patterns, e.g. the square pattern, have high plasticity in this respect and enable adaptation to various habitats. Contrarily, a triangular pattern not only has a low capacity for cone ratio changes, but it also cannot ensure homogenous distribution of non-identical double cones. Therefore, only identical double cones can be organized in a triangular pattern (and so the mosaic is strictly dichromatic), and adaptability to spectral conditions is very low as well, which restricts the occurrence of triangular pattern to the bright and chromatically stable environment (van der Meer, 1992). That is presumably the reason why this pattern is so rare among fishes.

Shallow water

Water depth greatly affects the arrangement of cone mosaics, because the spectrum of available light narrows with depth. The full spectrum of visible light, including UV and infrared light, is present in shallow water (J. K. Bowmaker, 1995). At the same time, the light intensity is highest near the surface. Such favourable conditions for vision only raise the importance of eyesight development and adaptation – if there is a possibility for colour discrimination and high acuity vision, it is highly advantageous to use it. Indeed, fishes from shallow waters possess well-developed eyes with precise mosaic patterns and are capable of fine detail and colour discrimination. Generally, the cone opsin palette is much richer and cone arrangements more diverse in shallow-water species. Some species are probably able to detect polarized light (Fineran & Nicol, 1976; Novales Flamarique, 2011).

Because the light intensity in shallow water is quite high, it is not the limiting factor for vision, and thus the selection pressure for detail discrimination is much greater than selection pressure for sensitivity. Therefore, the photoreceptor density is high while the photoreceptor size is low in shallow-living fishes (Boehlert, 1978; D. E. Hunt, Rawlinson, Thomas, & Cobcroft, 2015). That is also important for larvae and early ontogenetic stages of many species that exploit shallow water until they grow enough to move deeper – their small eyes could not achieve sufficient resolution if large photoreceptors were required. In contrary, tight pattern made of small cones is reported in such fishes (Shand et al., 1999, 2001).

Since edges of the light spectrum are present in shallow water, both cones sensitive to UV and violet, and cones sensitive to red can be found in shallow-water species (Musilova, Indermaur, et al., 2019).

Many shallow-living fishes feed on plankton and UV-sensitive cones presumably aid prey detection (J. K. Bowmaker & Kunz, 1987). On the other hand, short-wavelength light is responsible for most of the scatter, so its shielding could increase image sharpness and contrast (J. K. Bowmaker, 1995). It is best screened out by yellow filters, and many species use their cornea, lens or part of the retina to filter out the short-wavelength light. Yellow filtering pigments are common e.g. in families Cichlidae, Labridae and, Scaridae (Muntz, 1973). If the UV or violet light is filtered out by visual apparatus, it cannot be detected by cones. Therefore, SWS1 (and sometimes even SWS2) cones will not usually be present in retinas of fishes with yellow filters.

It is also common that shallow-living species possess many cone opsins and their expression varies depending on the environment, life stage, and sometimes even population. One of the best-explored examples are cone opsins of the guppy (*Poecilia reticulata*). The guppy has four LWS loci, two RH2 loci, two SWS2 loci, and one SWS1 locus (S. Kawamura et al., 2016). Opsins have diversified greatly especially in the green and yellow part of the spectrum. Not only that opsin sequences and expression differ from closely related species (e.g. the green swordtail *Xiphophorus helleri*), but differential expression was also reported among and within populations of the guppy. Furthermore, some cones coexpress more visual pigments which leads to altered spectral sensitivity. The reasons for such plasticity in opsin expression in the guppy are not yet fully understood, but the correlation with environmental conditions or coevolution with male body coloration was suggested. In fact, a combination of both factors represents the most likely explanation, because the male coloration is presumably perceived differently by females under different light conditions in distinct microhabitats.

Various types of mosaic have been described in shallow-water fishes, perhaps because favourable light conditions allow miscellaneous approaches to meet the visual requirements and those can all prove successful. However, the square pattern seems to be the most widespread, most likely because of its considerable plasticity and ability to accommodate many distinct cone types within a comparatively small photopic unit (van der Meer, 1992). Those characteristics make square mosaic ideal for colour discrimination. There exist both interspecific and intraspecific evidence that square pattern is preferred over row arrangement in shallow water. As for the first, study conducted on north-eastern Tasmanian coastal bycatch species showed that shallow-living fishes possess square mosaic, whereas species with row mosaic inhabited deeper water (D. E. Hunt et al., 2015). For the latter, a study conducted on *Sebastes diploproa* described the progressive change from square to row mosaic as the fish grows and moves from shallow to deeper water (Boehlert, 1978). Many shallow-water fishes, including guppies and some cichlids, possess square mosaic (Yvette W. Kunz, Ennis, & Wise, 1983; Musilova, Indermaur, et al., 2019). Nevertheless, this trend is not absolute as the species with a row pattern often coexist with species that still maintained a square pattern despite the growing depth (D. E. Hunt et al., 2015). Furthermore, row mosaic generated as an adaptation for deeper and dimmer habitats differs in many respects from the elaborated row mosaic of shallow-living species and it will be discussed later. For instance, the row

mosaic of zebrafish constitutes of two types of single cones interspersed with rows of double cones in an extraordinarily regular and elaborated pattern (Allison et al., 2010; Salbreux, Barthel, Raymond, & Lubensky, 2012). Claiming that square mosaic occurs in shallow water and row mosaic is suited for dimmer environment would thus be a strong oversimplification; instead, it rather seems to be strongly correlated with fish phylogeny (see page 13).

Although the bright environment of shallow water offers a great opportunity for colour vision, it is not “mandatory” to use it. Some fishes have a uniform pattern made of small short-wavelength sensitive cones in their early life stages, since tight packing of the smallest cones resulting in a sufficient resolution is more important than colour discrimination in the small eye (Shand et al., 1999, 2001). Also, for adult fishes of certain feeding strategies colour vision might not be the priority. Development of a dichromatic triangular pattern in the northern pike that hunts as ambush predator is an illustrative example (Braekevelt, 1975).

Mid-water

Deeper in the water column, the spectrum of available light narrows as extreme wavelengths are being gradually reduced with depth. The light intensity decreases as well. Therefore, the photoreceptor structure has to be adjusted in two ways – sensitivity must be enhanced and visual pigments must be focused on remaining ambient light. Yet, the light available in mid-water is sufficient for photopic vision (and thus for colour discrimination).

The spectral distribution in mid-water depends greatly on water colour and turbidity. In the clear water, blue and green light penetrates the deepest, but the light spectrum is displaced to longer wavelengths in coloured and turbid waters. In such conditions, the best-transmitted light can be yellow or even red. As a general rule, the spectrum cannot shift to shorter wavelengths, so UV and violet light are not present in mid-water. As a result, SWS1 cones are usually absent in retinas of mid-water species. Most of the fishes in this environment are trichromatic – SWS2 pigment (blue-sensitive) is located in remaining single cones, and RH2 or LWS pigments sensitive to red and green are located in the two members of unequal double cones (J. K. Bowmaker, 1995). In some species, both double cone members express the same opsin (green-sensitive in greenish water and red-sensitive in reddish water) and those species are thus dichromatic. Dichromacy occurs more often with growing depth. Some species also have a mixture of double cones expressing either the same or distinct visual pigment in neighbouring cells. It seems that double cones tend to match the ambient light not only by changes in the ratio of red-sensitive and green-sensitive cells and opsins employed but also by modification of peak absorption of expressed pigments. In the blue and green waters, LWS pigments are not expressed at all, while in coloured waters is double cone absorbance shifted to longer wavelengths. Opsin coexpression in double cones is also reported. Overall, it seems that double cones tend to correlate their sensitivity with the best-transmitted wavelength in the given environment. On the contrary, blue-sensitive single cones are much less affected

by changes in the available light spectrum. The possible explanation of this contrast might be that double cones are important for luminosity vision while single cones serve primarily for colour detection (J. K. Bowmaker, 1995). However, the interspecific comparison of cottoid fish inhabiting clear water of the Lake Baikal showed that λ_{\max} of both double-cone and single-cone visual pigments is displaced to shorter wavelengths at greater depths, as well as λ_{\max} of RH1 in rods (J. K. Bowmaker et al., 1994). That shows that in some cases, single cones react to reduction and displacement of the ambient light spectrum too.

The effects of various spectral distribution in mid-water on cone photoreceptors can be illustrated in African cichlids. The family Cichlidae, famous for its recent adaptive radiation in the African Great Lakes, is one of the best-studied groups among teleost fishes. Within the lakes, cichlids diversified into miscellaneous species specialized in various habitats, differing besides other factors in light conditions. African cichlids have seven cone opsin genes in their genome, but they usually express only three of them (Spady et al., 2006). The triads of expressed opsins can be divided into short, middle, and long combinations based on their peak absorptions (Carleton et al., 2016). Which combination will be expressed is given by the environment. It was showed that cichlids inhabiting blueish water on the rocky bottoms of the Lake Malawi express short opsin triad, whereas fishes from greenish water on the sandy bottoms of the same lake have medium expression profile (Hofmann et al., 2009). All surveyed cichlid species from the Lake Victoria express the long opsin combination because the lake is turbid and the best-transmitted wavelength is in the red part of the spectrum. The study conducted on American cichlids from the Rio Negro system brought similar results – cichlids caught in more coloured water had visual pigments absorbing at longer wavelengths (Muntz, 1973). Additionally, further laboratory experiments conducted on one of the caught species (*Aequidens tetramerus*) showed that this species can adapt rapidly to changes in the light environment. The absorption maximum of its visual pigments had shifted within days after the change in illumination. Such phenotypic plasticity could be considered an important adaptive trait in waters with seasonally fluctuating coloration.

Change in the peak absorption of visual pigments can be achieved not only by modification of opsin expression but also by altering the chromophores. Changing the ratio of rhodopsins and porphyropsins within photoreceptors is the easiest way to adjust the absorption spectrum and the most straightforward explanation of fast plastic adaptation in some species. For instance, repeated light-dependent conversions between rhodopsins and porphyropsins in the retina of *Scardinius erythrophthalmus* were recorded (Bridges & Yoshikami, 1970). The general trend is that rhodopsin-based visual pigments function better in clear and brighter waters whereas the absorption spectrum of porphyropsin-based pigments matches better the light available in coloured turbid waters and dimmer habitats because porphyropsin shifts the sensitivity of the pigment towards longer wavelengths. In Lake Victoria cichlids, the porphyropsin-based RH1 and LWS pigments are focused on the light dominant in the depth, while rhodopsin-based RH1 and LWS correspond with the light dominant in the shallow water (Terai et al., 2017). Moreover, porphyropsins are more common within freshwater fishes and rhodopsins in the

marine environment, and chromophore conversion often occurs during the transition from freshwater to ocean and vice versa in migratory species (Hasegawa, 2005). This effect could be partially attributed to the fact that marine water is generally clearer than freshwater.

As the depth in mid-water increases, photoreceptors need to cope with gradually decreasing light intensity. Sensitivity can be raised by increasing the photoreceptor size but only at the cost of lowered resolution. Indeed, the double cone size is growing with depth, whereas single cones do not show a strong correlation, in compliance with the theory that single cones are not much involved in luminosity vision (J. K. Bowmaker et al., 1994). Since double cones function better in dim conditions, most likely because of their larger size, their ratio increases with depth while single cones are being reduced. With this process, the structure of cone mosaic changes fundamentally. In some species, double cones organize into rows and form regular row pattern (Boehlert, 1978), while in others reduction of single cones leaves double cones in a less regular arrangement (Remišová, 2019). Nevertheless, reduction and subsequent elimination of single cones resulting in pure double-cone retinæ can be considered a general rule in deeper habitats.

The rearrangement of cone mosaic with increasing depth can be demonstrated on Baikal cottoids (J. K. Bowmaker et al., 1994). The shallow-living species have regular square mosaic without corner cones, but single cones dwindle in importance with increasing depth. In mid-water pelagic species, double cones form regular rows with irregularly interspersed single cones. Double cones grow in size and the visual pigment content present within them equals visual pigment contained in rods. For example, *Cottocomephorus inermis* possesses one of the largest cones known – about 45 µm in length and 9 µm in diameter. In species living at deeper levels, the regular pattern disintegrates, even though double cones still comprise an important part of the retina.

As single cones recede from the retina and double cones enlarge with depth, the rod density increases (D. E. Hunt et al., 2015). That is not surprising because rods are photoreceptors specially adapted to low light intensities. However, they cannot usually mediate colour discrimination which is probably the reason why are cones kept in retina if possible. The cones are also able to provide faster response to the signal than rods, which could be an important factor as well. Yet, at a certain depth, the light intensity reaches the point where enlarging of the double cones can no longer ensure sufficient sensitivity. This point represents the limit for photopic vision and only scotopic vision is implemented below it. Fishes inhabiting waters below the limit for photopic vision thus often possess pure-rod retinæ.

Bottom feeders

The functional group of freshwater bottom feeders is characterized more by their ecology than by depth where they occur. However, because the light conditions are similar near the bottom regardless of depth, it makes good sense to consider bottom-dwelling species a separate group in this thesis. There are usually very poor conditions for vision at the bottom where water comes in contact with mud and

sedimented material. Water contains many suspended particles and bottom feeders often churn the substrate even more while foraging. Therefore, the light intensity is very low and the light spectrum is shifted towards red, sometimes even infra-red (J. K. Bowmaker, 1995). Suspended material makes acute vision in many cases virtually impossible. It is not surprising that bottom-dwelling species mostly rely on other senses while looking for food and thus do not have many sophisticated visual adaptations. Yet, it is interesting to explore major trends and general characteristics of their visual system.

Since the environment near the bottom is ordinarily very dim, bottom-dwelling species employ adaptations that raise visual sensitivity. Their retinas contain a high percentage of rods and some species possess retinal tapetum lucidum – the specialized pigmented epithelium that reflects light so it passes through photoreceptors multiple times. This way the probability of signal detection is increased and the threshold for colour discrimination can be lowered as well (G. Kawamura, Bagarinao, Justin, Chen, & Lim, 2016). The presence of retinal tapetum is common among vertebrates from dim habitats, including nocturnal animals, and it can be determined by noticeable eyeshine.

Surprisingly, double cones are often missing in retinas of bottom feeders. That is the opposite trend compared to pelagic mid-water fishes which tend to have double-cone retinae in greater depths. The elimination of double cones in bottom-dwelling species was unexpected because double cones are believed to function better than single cones in dim habitats. Yet, many species of catfish (order Siluriformes) and sturgeons (family Acipenseridae), classic bottom-dwelling groups, possess only single cones (G. Kawamura et al., 2016; Loew & Sillman, 1993; Mukai & Tan, 2015; A. J. Sillman, Ronan, & Loew, 1993; Arnold J. Sillman, Beach, Dahlin, & Loew, 2005). Perhaps the best explanation is that single cones could be advantaged in a highly turbid environment if they were able to mediate more acute vision in spite of suspended particles (J. K. Bowmaker, 1995). This suggestion was raised because the amount of suspended material is indeed the main difference between the deep mid-water and bottom habitats. However, further research is needed to state with certainty if that is the case. Especially comparative studies conducted on pelagic and benthic species from the same family are crucial to establishing whether such trend exists or not.

Cone mosaic comprised of single cones is very irregular in the benthic fish, which is in compliance with the assumption that regular pattern tends to disintegrate in dimmer habitats (G. Kawamura et al., 2016; Mukai & Tan, 2015). Similar trend has been reported also in marine bottom-dwelling species, such as the common sole *Solea solea* (Ali & Anctil, 1976). Since the environment is deficient in short-wavelength light (violet and blue), SWS cones are usually missing in bottom feeders. Single cones are either all red-sensitive and thus used for achromatic vision, or both red and green-sensitive which potentially provides colour discrimination. Surprisingly, blue-sensitive cones were reported in adult sturgeons (Loew & Sillman, 1993; Arnold J. Sillman et al., 2005). Although their occurrence is very low and function unclear, connection with seasonal anadromous migration is anticipated. The visual

pigments of freshwater bottom feeders are porphyropsins, as anticipated in turbid waters, and their spectral sensitivities are displaced towards longer wavelengths. For instance, the peak absorption of RH1, that usually lies around 500 nm, is shifted to 540 nm in ictalurid catfishes or white sturgeon (Loew & Sillman, 1993; A. J. Sillman et al., 1993). Although the photic environment near the bottom is often very challenging, it seems that some species can achieve good visual qualities and rely on vision quite a lot while foraging (Mukai & Tan, 2015).

Deep water

In the deep water, downwelling light is significantly attenuated. Only the blue-green part of the spectrum is present in deep mesopelagic zone and no light penetrates deeper than 1000 m even in the clearest water. Vision is utterly bioluminescence-dependent in the bathypelagic zone below this limit. The narrow spectrum and low intensity of ambient light are usually insufficient for colour discrimination, so the majority of species maintain only scotopic vision. Special adaptations to increase the probability of signal detection are widespread. Despite all the difficulties related to low light level, vision remains an indispensable sense for many deep-water fishes.

Probably the most discussed and intuitive adaptation for life in the darkness is increased eye size relative to body size. It is commonly known that nocturnal visually-guided animals, and vertebrates living in dim habitats in general, tend to have big eyes, or at least larger corneal diameter (Garamszegi, Møller, & Erritzøe, 2002; Hall, Kamilar, & Kirk, 2012; Kirk, 2006). It is the adaptation for increased sensitivity. Since larger eye has a greater pupillary aperture, more light can enter the eye, resulting in a higher probability of photon capture. Furthermore, the enlarged retina allows photoreceptors to grow in size and enhance sensitivity without a conspicuous decline in acuity. However, the correlation between decreasing light levels and increasing eye size cannot be fully applied to deep-water fishes, because the idea of available light diminishing with depth is partially incorrect. Although the environmental background light is indeed declining, there exists another important light source in the ocean – bioluminescence. The importance of bioluminescence grows with declining downwelling light intensity – lots of deep-water organisms are capable of bioluminescence or fluorescence. That introduces a new challenge for eyesight – while in upper layers the core function of the eye was to distinguish dark shape in a brighter field, now the task is somewhat reversed. The background is generally dark and silhouettes emit light. Surprisingly, bright silhouette recognition can be considerably easier in bathypelagic where no ambient light is present and the background is completely dark (de Busserolles, Fitzpatrick, Paxton, Marshall, & Collin, 2013). In mesopelagic, the luminescence flashes can be easily confused with ambient light and fishes need more elaborated eyes to recognize environmental light from luminous organisms. Nevertheless, they still need to be able to detect both light sources to adjust position within the water column and to find prey. Therefore, eye to body size ratio is often increased in mesopelagic fishes. The trend changes in bathypelagic where eye size is decreasing again – light sources appear very bright in absolute darkness and can be easily detected by simpler and smaller eyes. However, some

authors contradict this statement and claim that larger pupils could improve the perception of bioluminescence in distance and so many bathypelagic fishes possess large eyes as well (Wagner, Fröhlich, Negishi, & Collin, 1998). Apart from the described general tendencies, there exist many deep-water species that rely more on other senses and their vision degenerates, especially in bathypelagic. That might be another reason why attempts to prove the correlation between ambient light intensity and eye size in deep-water fishes and to postulate general rule, remain unsuccessful (de Busserolles et al., 2013).

Deep-water fishes often developed eyes and retinae of peculiar shapes (Locket, 1977). Very prevalent are tubular eyes – eyes elongated along their vertical axis. They usually comprise big lenses, thick horizontal main retina (opposite the lens and aperture), and thinner vertical accessory retina (lining lateral sides). Tubular eyes mediate fine binocular vision in a direction they are facing, so they are mostly oriented dorsally or rostrally where fish expect to find prey. Binocular vision occurs in the main retina which is considerably more elaborate than the accessory retina. The accessory retina certainly serves only for monocular vision and some authors assume that lateral position prevents focusing the image on accessory retina which would restrict its function purely to movement detection. Furthermore, some tubular eyes contain an extension of the lateral wall termed diverticulum retina. It is an adaptation to broaden the visual field because the narrow visual field is the greatest disadvantage of tubular eyes. Despite being part of the lateral wall, the diverticulum retina is very complex and sometimes even thicker than the main retina, e.g. in *Dolichopteryx longipes* (Locket, 1977). Light is reflected on diverticulum retina by sophisticated apparatus. The central part of the retina can be specialized even further – some species possess depression of the retina called fovea (Locket, 1977). There are two types of fovea commonly found in vertebrates, shallow fovea typical for primates and deep fovea typical for birds of prey, and both types occur within fishes. While shallow fovea enables more acute vision, deep fovea serves for object fixation, so it is extremely helpful while pursuing fast-moving prey. Therefore, deep foveae are prevalent in deep-water fishes. The last major structural adaptation to increase visual sensitivity in darkness is probably the presence of tapetum lucidum. Tapetum lucidum is a reflective pigment layer that can be either part of the choroid (choroidal tapetum) or embodied in the retina itself (retinal tapetum) (Locket, 1977). Retinal tapetum is usually made of epithelial cells packed with guanine that protrude among rods and separate them into bundles of a rounded or linear shape, e.g. in *Chlorophthalmus albatrossis* or *Polymixia japonica* (Somiya, 1980). Both types of tapetum reflect incoming light back to the photoreceptor outer segments, this way increasing the probability of photon capture and causing conspicuous eyeshine apparent in deep-water fishes with tapetum lucidum.

Since the potential for photopic vision in deep water is very low, cones are disappearing from retinae of deep-water fishes. Most species possess pure-rod or at least rod-dominated retinae adapted for high sensitivity. If cones are present, they are more likely to occur in mesopelagic than in bathypelagic species and their presence could be related to vertical migration - common behaviour among deep-water fishes,

especially in mesopelagic (Denton & Locket, 1989). Cones are often restricted to a certain part of the retina rather than evenly distributed, and often only double cones are present (Somiya, 1980). The cone region usually occurs ventrally and it presumably serves for detection of downwelling light, despite significant attenuation. An extraordinary retinal organization is found in the pearlsides, *Maurolicus* spp. (De Busserolles et al., 2017). Their retinas are composed of unique photoreceptor type – rod-like cones. Such transmuted cones strongly resemble rods and combine advantages of both photoreceptors (more stable photopigments and faster phototransduction cascade of cones and greater packing resulting in higher sensitivity of rods) in a dim environment.

Within the pure-rod retina, the rod morphology is modified as well – rods are larger with long outer segments, so they can accommodate more disc membranes with visual pigment. Sometimes they are also stacked in multiple layers forming multibank retinæ, see Figure 6. Both adaptations aim to broaden the outer segment layer which often accounts for more than 50% of retinal thickness in deep-water fishes. This way the probability of photon capture is increased. While some fishes possess only elongated rods (e.g. 95 μm long in *Sternoptyx* or 150 μm long in *Platyroctes*) and some only multibank arrangement (e.g. two banks of shorter rods in *Serrivomer* together forming outer segment layer nearly 100 μm thick), others combine both approaches to create retina of incredible thickness relative to body size (Locket, 1977). For instance, in the ventral retina of the silver spinyfin (*Diretmus argenteus*), the layer of extremely elongated rods (up to 600 μm) is associated with several banks of shorter rods (Denton & Locket, 1989). The number of banks depends on species and age of the fish – banks are usually being added during life (Locket, 1977). Furthermore, the number and structure of banks often vary within a single retina. Such variation can be demonstrated in *Bajacalifornia drakei*. *Bajacalifornia* has two banks of rods in the peripheral retina, but this number rises up to 28 banks in the fovea, where retinal thickness reaches 750 μm (Locket, 1985). Rods vary in outer segment diameter which is bigger in more sclerad banks (banks facing pigment epithelium), as usual in multibank retinæ. It is not certain whether are multibank retinæ more effective in gathering photons than elongated rods. Some authors even doubt that increasing sensitivity is the principal function in multibank retinæ (Denton & Locket, 1989). They suggest that instead, a multibank retina could serve for colour discrimination so that each bank could contain different pigment. Organizing photoreceptors absorbing in shorter wavelengths vitread from receptors absorbing in longer wavelengths would bring better results than a random distribution. Surprisingly, even the possibility of colour vision using only one visual pigment was proposed for retina comprised of many rod layers, e.g. in *Bajacalifornia*, since longer wavelengths penetrate deeper within banks. As a result, more vitread banks would detect both short and long wavelength light and they would serve as filters for sclerad banks, that would receive only long wavelengths. If signals from different banks could be conducted separately and contrasted, three banks would be enough to ensure colour vision (Denton & Locket, 1989). Other hypotheses propose that multibank retina is an adaptation to prevent photobleaching of visual pigments by strong bioluminescent flashes, or that rods are being

replenished and sclerad banks represent old rods that are not employed any more. It was demonstrated that the fovea of *Bajacalifornia* contains twice more outer segments than nuclei (Locket, 1985). Thus the author speculated that only half of the outer segments are used for signal detection while the rest might filter the light. A similar function was also suggested for elongated rods – as the light is passing through, the vitread part could reduce certain wavelengths and only sclerad part would be used for photon capture (Denton & Locket, 1989). Surprisingly, yellow filters often occur in deep-water fishes, although the purpose of filtering some wavelengths from an already narrow light spectrum is not that obvious. Presumably, yellow filters could enhance the contrast between bioluminescence and downwelling light, or improve fluorescence detection (De Busserolles et al., 2015). In conclusion, the real reason behind the expansion of rod-occupied layer in the retinae of deep-water fishes remains slightly obscure, even though adaptation for increased sensitivity seems to be the most likely and intuitive explanation.

The peak absorption of visual pigment in rods seems to correlate with the best-transmitted part of the spectrum. The ambient light in deep water is blue with λ centred around 475 nm, as well as prevailing bioluminescence (Widder, 2010). Therefore, the RH1 absorbance spectrum is displaced to shorter wavelengths, usually around 475 - 480 nm. Described “blue shift” was observed not only in marine species, but also in species inhabiting deep clear freshwater lakes, such as the Lake Tanganyika (Sugawara et al., 2005), or the Lake Baikal (J. K. Bowmaker et al., 1994). The blue shift seems to be a copybook example of an adaptive trait. However, it is not that simple. Although the blue shift in RH1 correlates well with remaining wavelengths in deep uncoloured water, it does not fit the best-transmitted light in transparent but dyed water, for instance in the Lake Baikal. As downwelling light passes through upper water layers with a yellow hue, the spectrum is displaced towards longer wavelengths in this lake. Although lower layers of water lose yellowish tinge, spectral displacement stays, and so ambient light in depths is more green than blue. Yet, the blue shift occurs in deep-water species inhabiting this lake (J. K. Bowmaker et al., 1994). There are two possible explanations of this phenomenon. First, the shifted absorbance spectrum is a remnant of evolutionary history, and second, matching the ambient light is not the purpose of the blue shift. As for the first claim, Baikal fishes that show displacement of absorption maximum in RH1 are cottoids with close relatives inhabiting coastal waters. Remarkably, visual pigments of Baikal cottoids are exclusively rhodopsins, in sharp contrast to other freshwater fishes, including other species inhabiting the Lake Baikal. Since there is no obvious reason for the absence of porphyropsins, and rhodopsin-based pigments are common among marine fishes, this trait was considered the evidence of the marine origin of cottoids. Blue-shifted rod pigments may be inherited from the marine ancestor as well. However, Baikal cottoids seem to descent from shallow living species with RH1 $\lambda_{\max} \sim 500$ nm, which is also the value found in Baikal shallow and mid-water species, suggesting that blue shift developed independently within the lake. If that is the case, we need to use the second claim to elucidate the blue shift in a greenish environment – there must be some reason different

from adjusting the RH1 absorption spectrum to available light why is blue shift advantageous. Since rods are so sensitive that a single photon is enough to trigger the signalling pathway, and retinæ of deep-water fishes possess other adaptations for effective photon capture, even rods with unshifted pigments would presumably detect subtle signals reliably (Schnapf & Baylor, 1987). In fact, the limitation determining minimal recognizable signal is quite different. The signal pathway inside rods is sometimes triggered accidentally due to random processes (e.g. thermal activation) and output equal to single photon detection is produced (Schnapf & Baylor, 1987). Such false signals termed “photoreceptor noise” are negligible in well-lit conditions, but very problematic in low light intensities, where they are easily mistaken with actual signal. That is why signals from rods must be further processed in other retinal layers and only those exceeding the certain threshold are sent to the brain. Any signal below this threshold cannot leave the retina, regardless of that it triggered a response in the photoreceptor. Therefore, the only way to increase sensitivity is by lowering the threshold, and the threshold can be lowered only if photoreceptor noise is reduced. It was proposed that the frequency of false signals is lower in pigments with lower absorption maxima and so blue shift could attenuate photoreceptor noise (J. K. Bowmaker, 1995). After all, the blue shift would still represent an adaptation for increased sensitivity, but the effect would be achieved differently.

Usually, vertebrates express multiple cone opsins to achieve colour discrimination in a well-lit environment, but only one rod opsin (RH1) is used in dim conditions. Thus it was anticipated that colour vision is not possible in pure-rod retinæ. Later on, two distinct types of rods were discovered in the retinæ of certain deep-water fishes (J. K. Bowmaker, 1995). Both rod types contained the same RH1 opsin that was paired selectively either with A₁ (forming rhodopsin) or with A₂ (forming porphyropsin), resulting in slightly different λ_{max} . Furthermore, retinas with more rhodopsin-based rod types were also found, suggesting that diversification of the RH1 opsin gene is possible as well. The most striking example of RH1 gene expansion is the unusual genome repertoire of the silver spinyfin *Diretmus argenteus* with 38 distinct rod opsins, which is the highest number known in vertebrates so far (Musilova, Cortesi, et al., 2019). Outside the family Diretmidae, a significant expansion of RH1 occurred in two other deep-water lineages independently – in the families Myctophidae and Stylephoridae, indicating that RH1 expansion could be an adaptive trait. Having multiple distinct rod types could be advantageous in several ways. More pigments with different peak absorbances cover a broader part of the light spectrum, so they could increase visual sensitivity if coexpressed in one photoreceptor. Alternatively, different RH1 variants could be expressed in different parts of the retina, or they could successively change over development to achieve the best possible specialization in different life stages. However, the most intriguing utilization of multiple RH1 pigments is their possible

employment in colour vision. Although further research is still needed to fully confirm such hypothesis, the idea of rod-mediated colour vision would be an amazing adaptation for life in the deep sea.

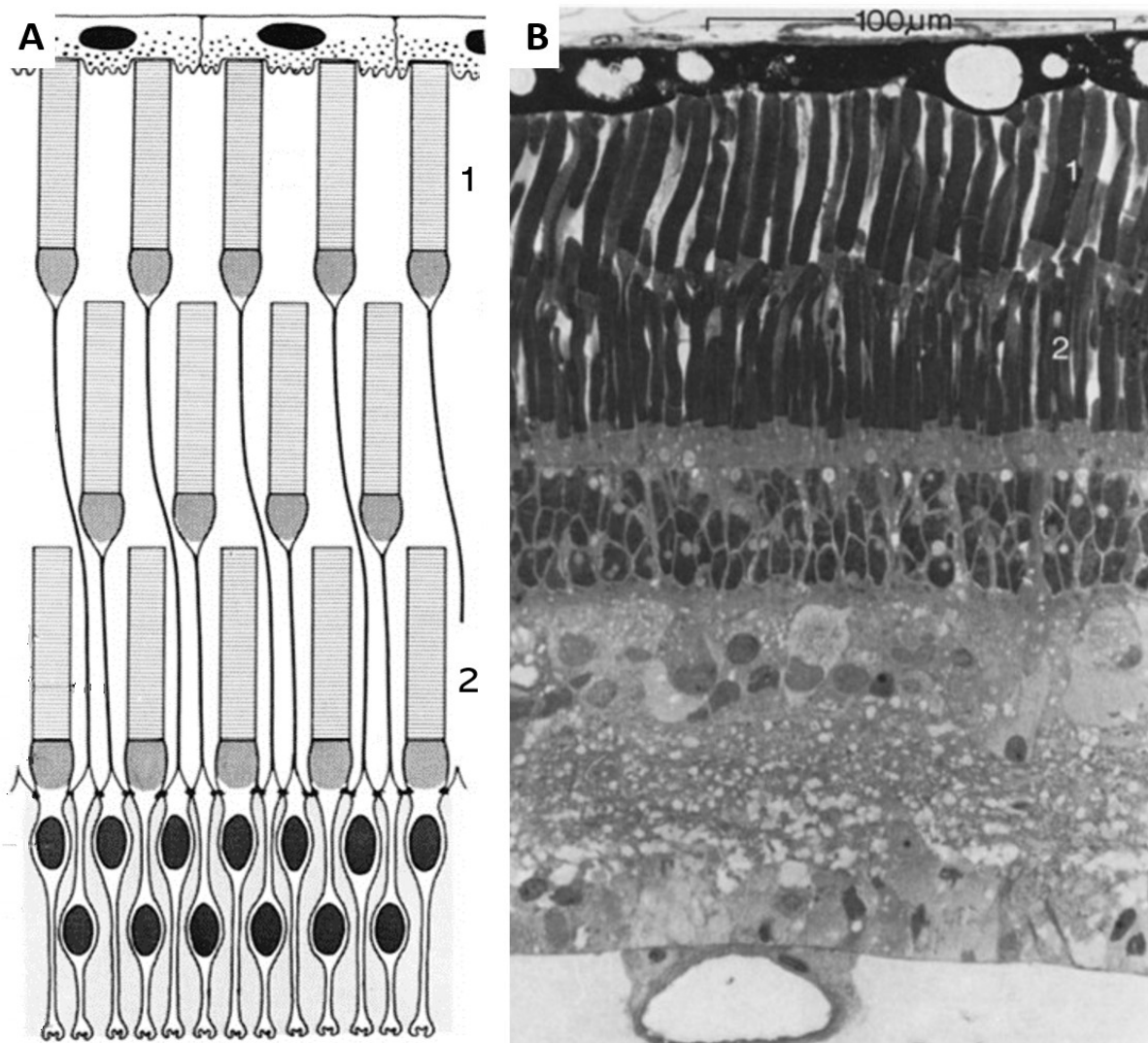


Figure 6: Structure of multibank retina; (A) Diagram of multibank retina composed of three banks (modified after Locket, 1977); (B) Multibank retina of *Serrivomer* composed of two banks (modified after Locket, 1977); 1 – sclerad bank of rods facing retinal pigment epithelium, 2 – vitread bank of rods facing outer nuclear layer

Similar to other deep-water organisms, fishes can emit light due to symbiosis with luminous bacteria (Widder, 2010). While short-wavelength bioluminescence is widespread, dragon fishes from the order Stomiiformes (genera *Aristostomias*, *Pachystomias*, and *Malacosteus*) are capable of emitting long-wavelength bioluminescence which is very rare among animals. Dragon fishes are not only able to emit red light, but also to detect it, because they express the most red-shifted RH1 pigments known. All three genera possess two distinct rod classes with absorption spectra of visual pigments shifted towards longer wavelengths; $\lambda_{\max} \sim 515$ and 540 nm in *Pachystomias*; $\lambda_{\max} \sim 525$ and 550 nm in *Aristostomias*; and $\lambda_{\max} \sim 520$ and 540 nm in *Malacosteus* (J. K. Bowmaker, 1995; Douglas, Mullineaux, & Partridge, 2000; Lythgoe & Partridge, 1989; O'Day & Fernandez, 1974). While both *Aristostomias* and *Pachystomias* have also a third rod class with $\lambda_{\max} \sim 590$ nm, this most-shifted class is not found in *Malacosteus*

(Douglas et al., 2000). Instead, *Malacosteus* uses a unique mechanism to achieve sensitivity in the red part of the spectrum – bacteriochlorophyll-like photosensitizer (Sutton, 2005). Generally, the spectrum of light emitted by dragon fishes is well-correlated with their visual sensitivity. Such adaptation is extremely useful while looking for prey because most deep-water organisms are blind to the red light and many of them are red, so they can be easily detected under red illumination. Additionally, red light could be employed in intraspecific communication. Producing light that other organisms cannot see is indeed an ingenious solution for vision in darkness.

Polarization vision

Apart from simple light detection and colour discrimination, polarization vision seems to be possible in some fishes as well. Polarization vision is the ability to detect E-vector (the plane of oscillation of the electric field vector) of polarized light (Heinze, 2014). Despite being widespread in invertebrates, polarization vision is much rarer in vertebrates and its mechanism is still quite obscured (Cameron & Pugh Jr, 1991). Nevertheless, most authors conclude that regular cone mosaic is essential for polarization sensitivity, and 90° periodicity is needed as well (Cameron & Pugh Jr, 1991; C. W. Hawryshyn, 2000). Within fishes, polarization vision was mostly studied on the goldfish *Carassius auratus* and the rainbow trout *Oncorhynchus mykiss* (Flamarique, 2001; Craig W. Hawryshyn & McFarland, 1987; Parkyn & Hawryshyn, 1993; Roberts & Needham, n.d.). In both cases, polarization sensitivity is associated with the square mosaic of double cones and the presence of UV-sensitive cones. Partitioning membranes of neighbouring double cones may reflect light towards UV-sensitive cones that are capable of polarized light detection (C. W. Hawryshyn, 2000). It seems that polarization vision appears only in the UV part of the spectrum, since polarization sensitivity diminishes in the rainbow trout during smoltification, along with the loss of UV-sensitive corner cones (Flamarique, 2001; C. W. Hawryshyn, 2000).

Perhaps the most remarkable adaptation that presumably serves polarized vision can be found in some anchovy species from the family Engraulidae. There are two types of single cones in their retinae (long and short - bilobed), that are arranged alternately in long rows – polycones (Heß, Melzer, Eser, & Smola, 2006; Novales Flamarique, 2011). Moreover, outer segments of both short and long cones forming the polycones hold lamellae of a unique organisation. While lamellae in vertebrate photoreceptors are oriented transversely to the photoreceptor's length, cells in polycones have their lamellae oriented longitudinally. Lamellae in neighbouring cells are perpendicular to each other (Fineran & Nicol, 1976). Short cones are called bilobed or bifid because their outer segment is divided into two symmetrical lobes. Each long cone in the row is associated with closer lobes of the two adjacent short cones and together they create a functional unit. Orthogonally situated lamellae within this unit enable the apparatus to analyse linearly polarized light. Furthermore, cone outer segments are surrounded by pigment cells with guanine platelets with the ability to reflect light back to the cone units. Considering

the perpendicular orientation of cone lamellae that is not ideal for maximum photon yield, this adaptation could improve the photon catch and polarization detection (Fineran & Nicol, 1976; Heß et al., 2006; Novales Flamarique, 2011).

As for the importance of polarization vision for anchovy fishes, some assumptions have been stated. The fish could use polarization patterns stemmed from sunlight for orientation in a similar way as flying insects (Kondrashev et al., 2012). Even more likely, fish could benefit from the detection of polarized light while searching for prey. Anchovies are mostly pelagic fish feeding on zooplankton. Since transparent prey is almost invisible in the water column, polarisation sensitivity could improve prey detection and enhance feeding success in two ways. The chitinous exoskeleton of some crustaceans reflects polarised light that could be distinguished by anchovies (Novales Flamarique & Browman, 2001). The other way around, if the light reflected from the body surfaces of prey was not polarised, prey would still be seen as a shadow, because the light in the water column is linearly polarized to a considerable extent (up to 60%). In this way, anchovies could also use polarisation vision to detect silhouettes of predators that are often well camouflaged (Heß et al., 2006; Kondrashev et al., 2012).

Despite all the advantages associated with polarization vision, there is also one disadvantage – it appears that processing colour sensitivity and polarization sensitivity in the same cell is impossible because signals would be confused (Bernard & Wehner, 1977; Kelber, Thunell, & Arikawa, 2001). Yet, some anchovies might have found the way to overcome such problem – using the functional compartmentalization of the retina. In *Engraulis japonicus*, dorsal and ventral regions of retina are formed by triple cones while central, nasal, and temporal parts consist of polycones (Kondrashev et al., 2012). The potential employment of triple cones of *E. japonicus* in colour vision has been discussed earlier. Although this function of triple cones has not been fully confirmed yet, it is interesting to note the division of retina into separated regions presumably specialized for different tasks. This could be the way to achieve both polarization and colour sensitivity within one retina. Indeed, specialization of different parts of the retina for different tasks associated with changes in cone mosaic, photoreceptor ratios, and opsin expression is a ubiquitous trend within fishes, since it enables the eye to meet often contradictory requirements within the single retina.

Summary

Ray-finned fishes are the largest, but least explored vertebrate class. Despite the intensive research ongoing for the past few decades, fishes remain rather enigmatic. Not only that many species are probably still undescribed, but also only a few species have been thoroughly studied, and just a little detail is known about morphology, physiology, and ecology of many others. The sense of vision is no exception. Both recent findings of rod-like cones in *Maurolicus* spp. and unusual RH1 gene expansion in *Diretmus argenteus* indicating the possibility for rod-mediated colour vision demonstrate that important revolutionary discoveries are still happening in this field.

Cone mosaic is quite easily accessible and thus its morphology has been studied since the middle of the 20th century. Although the basic pattern has been already described in many species, modern methods (e. g. gene sequencing, transcriptome sequencing, fluorescent in situ hybridization, electron microscopy) enable us to distinguish photoreceptor types even further. Investigation of cells in other retinal layers and their wiring, which is crucial for understanding the signal processing, is facilitated as well.

The study of fish vision is rapidly moving forward. Current knowledge of eye anatomy and physiology, opsin gene expression, and photoreceptor structure and arrangements represents a solid basis for further research. Additionally, recent advances in modern genetic methods open new research perspectives. Detailed examination of retinal mosaics in other layers and study of retinal wiring, as well as extending the number of studied species, would be great to uncover how fish really see and if the visual potential anticipated from photoreceptor structure and arrangement is fully used. Moreover, exploring the ecology and behaviour of fishes is essential for understanding the adaptive value of observed traits. The extraordinary diversity of fishes and their remarkable visual adaptations offer a unique opportunity to comprehend vision itself, as well as discover features never observed in vertebrates before.

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