REVIEW

Seeing the rainbow: mechanisms underlying spectral sensitivity in teleost fishes

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ABSTRACT

Among vertebrates, teleost eye diversity exceeds that found in all other groups. Their spectral sensitivities range from ultraviolet to red, and the number of visual pigments varies from 1 to over 40. This variation is correlated with the different ecologies and life histories of fish species, including their variable aquatic habitats: murky lakes, clear oceans, deep seas and turbulent rivers. These ecotopes often change with the season, but fish may also migrate between ecotopes diurnally, seasonally or ontogenetically. To survive in these variable light habitats, fish visual systems have evolved a suite of mechanisms that modulate spectral sensitivities on a range of timescales. These mechanisms include: (1) optical media that filter light, (2) variations in photoreceptor type and size to vary absorbance and sensitivity, and (3) changes in photoreceptor visual pigments to optimize peak sensitivity. The visual pigment changes can result from changes in chromophore or changes to the opsin. Opsin variation results from changes in opsin sequence, opsin expression or co-expression, and opsin gene duplications and losses. Here, we review visual diversity in a number of teleost groups where the structural and molecular mechanisms underlying their spectral sensitivities have been relatively well determined. Although we document considerable variability, this alone does not imply functional difference per se. We therefore highlight the need for more studies that examine species with known sensitivity differences, emphasizing behavioral experiments to test whether such differences actually matter in the execution of visual tasks that are relevant to the fish.

KEY WORDS: Photoreceptor, Visual pigment, Spectral tuning

Introduction

Animal visual systems detect light and provide information needed for survival. In vertebrates, the eye consists of a cornea and lens to collect and focus light, and a retina composed of rod and cone photoreceptors to absorb and detect light (Cronin et al., 2014; Land and Nilsson, 2001). Rods are important for low-light vision, whereas cones mediate color vision under well-illuminated conditions. Photoreceptor light sensitivity comes from visual pigment molecules housed within the membrane stacks of their outer segment regions, and visual pigments possess variable peak sensitivities across the spectrum (Ebrey and Koutalos, 2001). Rods are optimized for greater sensitivity, with peak absorbances often matched to the peak wavelength of the environmental light, whereas cone sensitivities are distributed across the spectrum and often work in an opponent manner to provide color vision (although in some instances rods may contribute to chromatic tasks; Joesch and Meister, 2016).

Vision helps animals navigate through the environment, find food, avoid predators and find mates (Cronin et al., 2014). In an organism with a fixed number of visual channels, each visual task may be optimized by a different set of visual sensitivities. For a single species, natural selection may average over all visual tasks to select the best set of visual pigments for that species. For example, honey bee vision is good for detecting most flower colors (Chittka et al., 1994; Raine and Chittka, 2007), and the ability of old world primates, including humans, to discriminate red may help individuals to detect young leaves, ripe fruit or females in estrus (Changizi et al., 2006; Osorio et al., 2004; Sumner and Mollon, 2000). The idea that vision is tuned for a single task alone is perhaps naïve, and a more 'general-purpose' hypothesis might be expected in order to reflect the range of sensitivities seen. Alternatively, as with some cases of tuning in audition, a specific vital task – such as mate choice – may have more weight in the evolutionary processes that determine an animal's visual sensitivity profile (Popper and Coombs, 1980).

Terrestrial environments are relatively stable, and so terrestrial vertebrates have settled on a few common visual systems. Birds and reptiles converge on a relatively standard set of four cone photoreceptors (tetrachromacy), sampling light from ultraviolet (UV)/violet to red (Davies et al., 2012; Hart, 2001; Loew et al., 2002a,b). Mammals have simpler dichromatic retinas, presumably as a result of their ancestral nocturnality (Borges et al., 2018; Wu et al., 2017). Some primates have re-evolved trichromacy to coordinate tasks at the longer wavelength region of the spectrum (Hunt et al., 1998; Jacobs, 1996).

By contrast, aquatic environments are quite variable in illumination spectra. Furthermore, the animals that live there vary in the placement of cone sensitivities within the spectrum available. This variability was recognized by pioneers in visual ecology such as John Lythgoe, who identified two key features (Lythgoe, 1979). Firstly, waters differ in the content of dissolved organic matter and sediment, causing their light environment – and resulting color – to vary widely (Jerlov, 1976; Loew and McFarland, 1990; Marshall et al., 2003). Aquatic organisms have adapted to these different environments, with blue oceans fostering shorter wavelength color vision systems than green lakes, where longer-wavelength sensitivities predominate (Levine and MacNichol, 1982). Secondly, the diversity in number, type and placement of cone visual sensitivities for aquatic species is greater than that of terrestrial vertebrates, and more than would be predicted from ecological or behavioral constraints. These two factors make the study of aquatic vision both fascinating and challenging (see Fig. S1).

Understanding the role of the environment or indeed the micro-environment in altering visual sensitivities is important (Luehrmann et al., 2020; Marshall et al., 2003; Munz and McFarland, 1977). All visual detection and discrimination tasks must be performed within the context of the local light environment. However, the

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Glossary

Benthopelagic
The zone close to the bottom of a deep lake or ocean.

Blackwater
Waters with considerable dissolved tannins that produce long-wavelength shifting of the light environment.

Clear water
Waters without significant pigments or particles. In clear water, light is absorbed primarily by the water itself, producing waters that look blue to blue-green in color because of the high transmission of wavelengths in the 450–500 nm region.

Gene conversion
The process whereby two neighboring genes undergo unequal cross over during meiosis such that one gene converts or replaces the other. This conversion can work to keep neighboring genes similar in sequence. However, selection may discriminate against individuals where the conversion has happened as it might make visual pigments too similar, preventing subsequent color discrimination by spectrally distinct pigments.

Heterochronic shifts
Species may differ through ontogeny, having different morphologies as they shift from larvae to juveniles to adults. These stages often differ in gene expression, including the opsin genes. When a related species evolves to alter the developmental progression of opsin genes compared with an ancestral species, they are changing the timing of opsin expression. These heterochronic shifts may cause opsin expression to differ in the adults of the related species.

Introgression
The process whereby genes from one species are introduced into another through hybridization between species. The retention of some genes may be due to selective advantage, though this might not come until a significant time after hybridization.

Mesopelagic
The midwater region of the ocean at depths of 200–1000 m. Light here is generally dim and confined to blue or blue-green wavelengths.

Optomotor response
A large-field visual system stabilization mechanism that is behaviorally evident when a fish swims in the same direction as a moving background to maintain its local position. This response can be used to test fish's sensitivity to contrast and color by determining whether fish can discriminate and therefore follow a moving pattern.

Philopatric
A tendency to stay close to or return to a specific area, for example animals returning to their birth place.

Sensory drive
A hypothesis suggesting that characteristics of the environment influence the evolutionary direction of signals and sensory systems in predictable directions. For example, a color vision system that evolved for the detection of red food may influence the evolution of red display ornamentation. This may be a factor in driving speciation.

Spacelight
The light seen by an animal looking off into the distance (often horizontally). This spacelight forms the background against which objects may be viewed and in water is from the scattering of the downwelling light. Its color and other components are therefore strongly influenced by the optical properties (particulates, dissolved organics) of the water in the local environment.

Spectral envelope
The relative intensities and wavelengths of incident light in a particular habitat. For example, in the ocean it may be limited to wavelengths from 400 to 550 nm, whereas in fresh water, a longer wavelength range is more likely.

impact of the environment can be hard to discern. When we study the visual system of a given species, we effectively take a snap-shot that likely fails to capture the animal's evolutionary history. In addition, we lack detailed knowledge of ecology and life history for many species. This may lead to misconceptions or over-interpretations of animal coloration and color vision. It is possible that different

combinations of the number and placement of spectral sensitivities are equally good for the tasks performed by a given species, with differences driven by phylogeny or history. The question remains: to what extent is the spectral sensitivity range of a given species 'tightly adaptive' or 'loosely multifunctional/good enough for the job'? (Marshall et al., 2015).

In this Review, we attempt to answer this question by focusing on teleost fish. With over 25,000 species, fish represent half of all vertebrates (Betancur et al., 2017; Nelson et al., 2016). They are by far the most variable of vertebrates in terms of body form and behavioral tasks and, as already noted, live in a wide range of light habitats. Our goal is to explore how the diversity of fish visual systems (and spectral sensitivity in particular) may be selected for, predicted by or at least linked to these ecological features. We will present data on the range of molecular mechanisms that contribute to this diversity, and consider the degree to which it helps fish adapt and function according to lifestyle and habitat. In addition, we will consider how these mechanisms contribute to divergence and ultimately speciation of closely related species. Although other aquatic organisms, including cartilaginous fishes, inhabit the same environments, their visual systems are somewhat reduced in diversity. Many sharks have just one rod and one cone type (reviewed in Collin, 2018), whereas rays are dichromatic, with two cone types, as demonstrated molecularly, physiologically and behaviorally (Hart et al., 2004, 2019; Theiss et al., 2007; Van-Eyk et al., 2011). We have chosen to focus on teleosts as this group has numerous examples of species or populations with diverse and variable visual sensitivities, based on detailed molecular studies. Visual sensitivities are discussed in combination with other visual traits and our examples are chosen to be illustrative rather than exhaustive (with more examples in Table S1).

Diversity in fish spectral sensitivity – the basics

The peak spectral sensitivities of fish visual pigments have been quantified physiologically for more than 50 years; first through pigment extraction and then using microspectrophotometry of individual photoreceptors (Dartnall and Lythgoe, 1965; Levine and MacNichol, 1979; Loew and Lythgoe, 1978; Munz, 1958; reviewed in Bowmaker 1995; Schweikert et al., 2019, 2018). This work demonstrated the diverse sensitivities of rods and cones based on a diverse set of opsin genes. Our knowledge of that diversity has only increased with the advent of high-throughput sequencing tools (Lin et al., 2017; Musilova et al., 2019a). Fish visual sensitivities are, in fact, shaped by a number of factors (Figs 1 and 2). First, the eye can filter light through photostable pigments in the ocular media including the cornea, lens and vitreous humour (Fig. 1A; Siebeck and Marshall, 2001; Thorpe et al., 1993). These filters usually absorb shorter wavelengths, such as UV. However, they may even absorb blue to green wavelengths (being yellow or orange colored), pushing the short-wavelength cutoff beyond 500 nm (Kondrashev et al., 1986; Siebeck et al., 2003). Second, retinal photoreceptors may vary by number, type and arrangement (Fig. 1B–D), all factors that can affect sensitivity and extent of color discrimination (Walls, 1942). Third, photoreceptor sensitivities are set by visual pigments in the photoreceptor; these visual pigments have similar, bell-shaped, absorbance profiles (including an additional ultraviolet-sensitive side-peak or beta-band for all visual pigments; Fig. 2). They are composed of opsin proteins bound to a light-sensitive chromophore, such as 11-cis retinal (Fig. 2A; Wald, 1968). Interactions between amino acids of the opsin protein and the chromophore determine where in the spectrum the visual pigment absorbs best (Yokoyama, 2008). Visual pigments can be tuned by a number of mechanisms, including changes to chromophore (Fig. 2B)

A Ocular filters

B Photoreceptor types

C Photoreceptor patterning

D Diversity in retinal mosaics
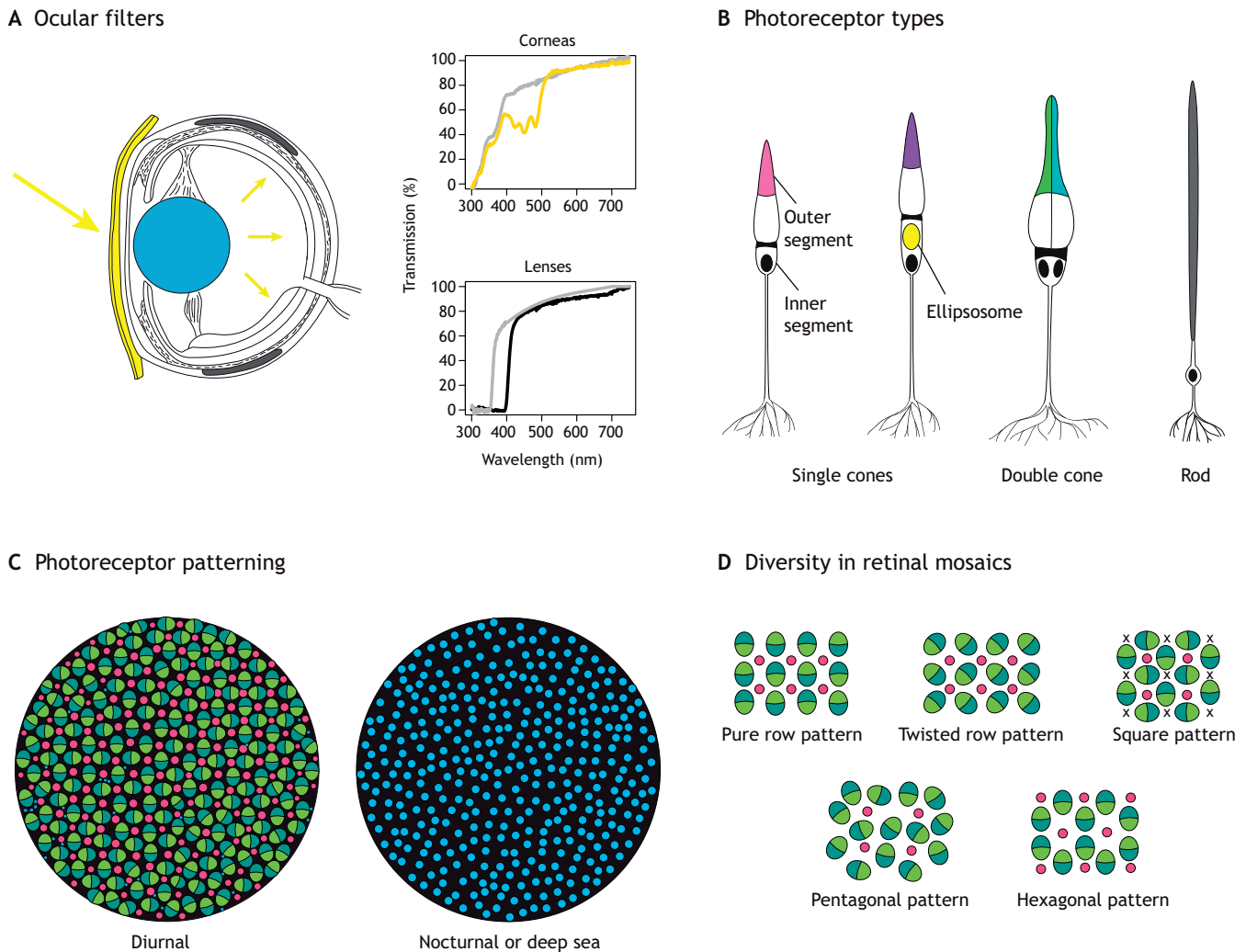
Fig. 1. Mechanisms to alter spectral sensitivity. Several mechanisms can alter visual system sensitivities, including filtering by ocular media (A), and alterations to photoreceptor type (B) and patterning (C,D). (A) Pigments in the cornea and lens can absorb shorter wavelengths and shift the spectrum of transmitted light that reaches the retina (from gray to yellow or black lines, respectively). For example, a UV-absorbing pigment will long-wavelength shift lens transmission. (B) Fish photoreceptors include rods and single or double cones. Double cones are morphologically connected but neurally independent, and can contain different visual pigments. Occasionally, the inner segments of fish cones contain colored filters (such as ellipsosomes, which are usually yellow), containing pigments that absorb shorter wavelengths. (C) The ratio of photoreceptor types varies for fish living in different habitats. Diurnal species have cones (red, light green and dark green) and rods (blue), whereas the retinas of nocturnal and deep-sea species are rod dominant. (D) Cones can form different retinal mosaics, where single cones (pink) and double cones (light green/dark green) have different arrangements (after Collin and Shand, 2003). Some fish have a second type of single cone located in alternate corners as shown (x) for the square pattern.

or opsin sequence (Fig. 2C), and spectral sensitivity can be influenced by opsin gene duplications or losses (Fig. 2D). Photoreceptor sensitivities can further be shifted by altering which opsins are expressed (Fig. 2E) or coexpressed (Fig. 2F). In a few instances, photoreceptors also have photostable pigments, for example, in ellipsosomes that modify the light as it passes through the inner to the outer segment (Fig. 1B; Collin et al., 2003a; Walls, 1942).

Adaptive shifts in visual sensitivity
Variation in filtering mechanisms and photoreceptor type, number and spectral placement produce visual variability that may be termed 'adaptive'. However, as discussed above, our view is rather limited, both in terms of evolutionary time and assumptions regarding the habits and habitats of fish. Therefore, it is not always clear which of the many visual tasks might drive adaptation of fish visual sensitivities. Further, it is possible that there are multiple solutions that are all 'good enough'. There are ways in which we can investigate

links between features of the visual system and organismal fitness. For example, with DNA data, genes can be tested for evidence of positive selection using programs such as PAML (Yang, 2007). When considering gene expression or filtering by photostable pigments, we can test whether these features correlate with some aspect of the ecology, such as light intensity or foraging requirements. Although correlation is not evidence for causation, it is usually taken as an indication that trait variation may improve fitness. However, in most fish studies, proof of actual fitness effects are often missing (Box 1). Some of the visual traits that may be related to fitness and functional variation are expanded upon below.

Filtering by ocular media
Light is collected and focused by the cornea and lens (Fig. 1A), either of which can contain pigments that absorb shorter wavelengths (Thorpe et al., 1993). UV-blocking lenses are common across coral reef fishes and are found in freshwater species as well (Hofmann et al.,

Fig. 2. Mechanisms affecting visual pigment sensitivities, including changes to opsin genes and the retinal chromophore. (A) Photoreceptor sensitivities are set by visual pigments, which are composed of chromophores (yellow) and opsin proteins (blue). Several different mechanisms can alter sensitivities (shown by absorption spectra for each visual pigment) including: (B) shifts between vitamin A1- and A2-derived chromophores; (C) changes to opsin amino acid residues; (D) opsin gene duplications and losses, with duplicate genes acquiring new function (e.g. violet versus blue) and some duplicates subsequently being lost (shaded); (E) differential opsin expression (shown as % total cone opsin); and (F) co-expression of multiple opsins with co-expression possible both in single cones (top) and double cones (bottom). Opsin genes are color coded as SWS1 (pink), SWS2B (violet), SWS2A (blue), RH2 (blue-green to green) and LWS (red). This color coding is similar in other figures.

2010a; Losey et al., 2003; Siebeck and Marshall, 2001; Siebeck and Marshall, 2007); these filters may help to reduce retinal damage caused by UV light when organisms do not require it (Ivanov et al., 2018; Zigman, 1993). Blocking UV wavelengths may also filter out scattered light, thereby decreasing background noise and enhancing visual resolution and sighting distance (Muntz, 1973).

Conversely, behavioral tests have indicated the benefits of UV-transmissive lenses and UV vision for zooplanktivory (Browman et al., 1994; Jordan et al., 2004; Loew et al., 1993). Several species are UV-sensitive during their larval pelagic phase when they feed on zooplankton, and then become insensitive to UV after settlement and change in diet (Siebeck and Marshall, 2007;

Box 1. When is visual variation adaptive?

The formal definition of 'adaptation' is a change in phenotype that increases fitness, leading to the production of more offspring in the next generation (Barrett and Hoekstra, 2011). Whether variation in visual sensitivity has such an effect is difficult to verify for a number of reasons:

- Experiments do not typically quantify the direct impact of visual sensitivities on reproduction i.e. the number and/or quality of offspring. Instead, most studies are indirect, using proxies (foraging rate, growth rate, mate preference) to demonstrate fitness.
- These functional proxies may have small effect sizes, requiring an impractical examination of many individuals, thus limiting our power to detect behavioral or fitness impacts.
- We are often unable to identify the task causing selection on the visual system. Therefore, we don't know which proxy to use or which life stage to test.
- Selection may have acted in the past due to some previous environmental driver or constraint that shaped the visual system and is therefore no longer present.
- Vision, particularly color vision, may best be thought of as being 'general purpose'. Organisms may survive with a 'good-enough' visual system. Effectively, this implies that the fitness landscape is flat, making correlations between fitness proxies and visual system characteristics quite weak (as in second point above).

Presuming that proxies are a good measure of fitness, and that the relevant task and environment are current and determinable, there are two approaches that have been used to demonstrate visual system adaptation:

- The sequence of particular genes (e.g. the opsins) may shape visual function. Evidence for adaptive sequence changes in these key genes relies on tests of positive selection. These compare whether the sequence changes between different phylogenetic groups are correlated with ecology. These methods have the most power when there are a number of phylogenetically independent changes that cause repeated sequence evolution of a particular gene.
- Some aspects of visual system sensitivity may be tested to determine whether they are correlated with ecology. These include the light transmission of optical media (lens, cornea, photoreceptor ellipsosomes) or photoreceptor sensitivity placement (λ_{max}, gene expression, chromophore). Aspects of ecology might include properties of the local light environment or foraging style. Tests using phylogenetically informed comparative methods determine whether the visual and ecological variables are correlated when correcting for phylogeny. These methods also produce the most significance when convergence causes multiple independent changes in response to a particular ecological shift.

Thorpe and Douglas, 1993). Other, mostly smaller, species maintain UV-transparent lenses and UV-sensitive photoreceptors throughout life, enabling them to remain zooplanktivorous (Hofmann et al., 2010a). The advantages of UV sensitivity go beyond foraging to inter- and intraspecific communication. UV may be used as a 'private' communication channel invisible to larger, predatory fish, but available for decision-making at close range. This has been suggested for both freshwater (guppies, Smith et al., 2002; swordtails, Cummings et al., 2003) and marine fish (e.g. damselfish, Siebeck et al., 2010; Stieb et al., 2017; see below).

Aside from UV filters, lenses and corneas may contain yellow or even orange carotenoid pigments (Douglas et al., 1998; Kondrashev, 2008; Muntz, 1973; Siebeck and Marshall, 2000). These may reduce scattering from certain directions in shallow-water environments with high light intensity, or may help in contrast enhancements for fish that feed on algae or graze from the substrate (Siebeck and Marshall, 2000). There are several types of ocular filters at the level of the retina (reviewed in Douglas and Marshall, 1999). One example is the intraocular filter of lanternfish (Myctiphoformes) that possesses a

yellow pigment located in one area of the retina's outer nuclear layer. The yellow filter occurs in 10 of 61 species studied, with varying spatial distributions, and it may be related to diurnal migration, camouflage breaking or predator avoidance (de Busserolles et al., 2015). In two species, its spatial location varies between the sexes. In these species, it may be used to enhance bioluminescence detection and may facilitate intraspecific communication (de Busserolles and Marshall, 2017).

Photoreceptor type

As discussed above, photoreceptors are classified as rods and cones (though this classification can be complicated, see Table 1 in de Busserolles et al., 2017). The rod photoreceptors are predominantly sensitive to medium wavelengths (peak absorbance ~500 nm) and show less variation in spectral sensitivity. One exception is found in deep-sea fishes, where rods may have broader sensitivities, either through exceptionally long photoreceptor outer segments or shifted visual pigment sensitivities. Their broader rod sensitivity is thought to increase spectral/visual range to allow fish to detect bioluminescent prey (Douglas et al., 1998; Musilova et al., 2019a). Cones can be subdivided based on morphology into single cones and double or twin cones, with occasional triple and even quadruple cones. These often form regular mosaics across the retina in teleosts (Fig. 1B–D; Walls, 1942). Whereas double cones, like rods, have spectral absorbances of medium and long wavelengths, often matching the prevailing wavelength of light, the absorption of single cones may be quite variable within the spectral envelope (see Glossary) of available light (Lythgoe, 1979, 1984; Marshall et al., 2003; Partridge and Cummings, 1999). Ratios of different photoreceptor classes and mosaics vary between and within species (reviewed in Collin and Shand, 2003; Fig. 1D), thus producing differential visual sensitivities. These may also fluctuate across the retina, providing specialized regions with spectrally distinct sensitivities matched in some way to the environment (e.g. in garfish, Reckel et al., 2002). Both interspecific and intraretinal variation is thought to be driven by variation between local environments as well as variation within a particular environment. For example, diurnal, shallow-living fishes are exposed to bright, colorful environments, and usually possess a complex photoreceptor mosaic providing a powerful color vision system with sensitivities across the spectrum (Marshall et al., 2006). The spectral sensitivities of this mosaic can vary between species in different localities that differ in light environment. Fish in clear lakes have shorter-wavelength sensitivities than fish in murky lakes (Hofmann et al., 2009). Variation within a retina can result when the background light varies spatially. For example, the dorsal retina that looks down against the brown rocks can contain longer wavelength-sensitive visual pigments while the ventral retina that looks up against the spacelight can be sensitive to shorter wavelengths (Temple et al., 2011). Conversely, deep-living species generally have a more homogeneous retina based on high-sensitivity rods (Wagner et al., 1998; Fig. 3).

Photoreceptors and their arrangement may also change with development. This often accompanies changes in the spectral composition and intensity of the photic environment, as well as transitions from one feeding strategy to another (Collin and Shand, 2003). A good example is the change in retinal composition among migrating salmonids. Salmon go from freshwater to marine environments and switch from a planktivorous to a benthopelagic (see Glossary) existence. This is accompanied by a (partial) loss of UV-sensitive cones (Bowmaker and Kunz, 1987; Deutschlander et al., 2001; Hawryshyn et al., 1989). However, UV sensitivity is
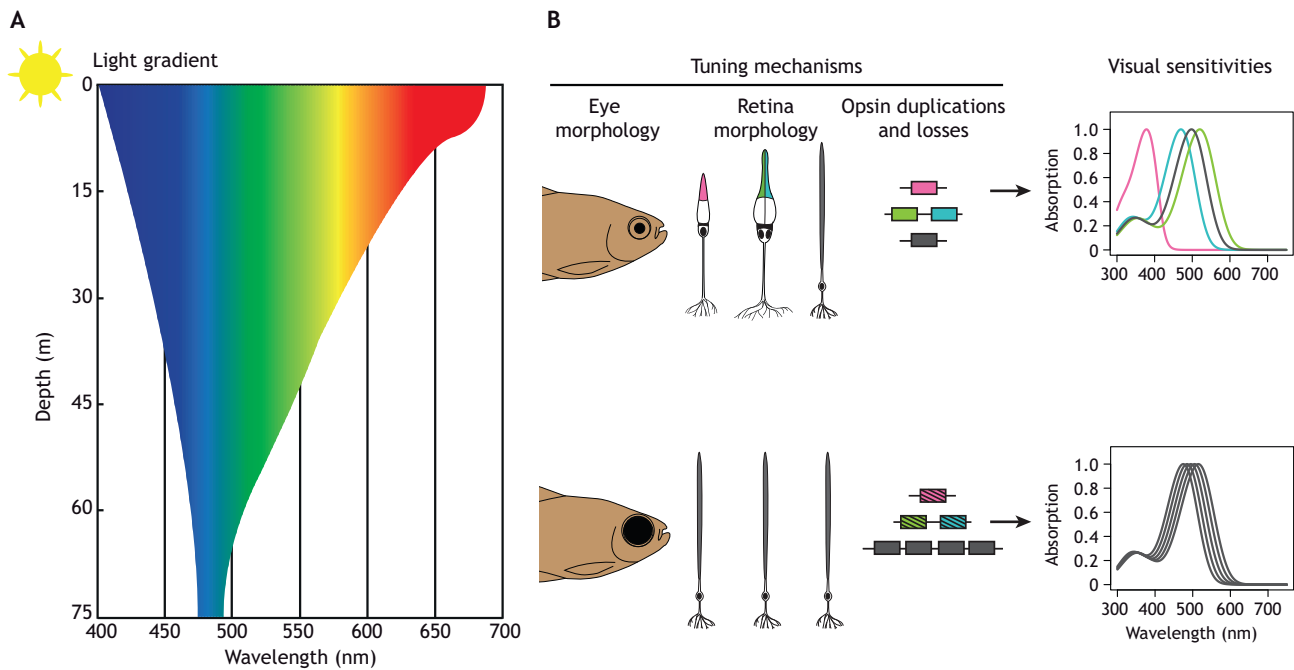
Fig. 3. Adaptation from shallow to deep water environments. (A) Adaptation in deep oceans and lakes may be extreme, as the light spectrum decreases in intensity and blue shifts with depth. (B) With increasing depth, fish switch from duplex cone and rod retinas to all-rod retinas (e.g. Wagner et al., 1998). Sometimes fish acquire multiple RH1 opsins with rod sensitivities covering the range of light (residual daylight and bioluminescence) in the deep sea (Musilova et al., 2019a). Eye size can also increase as fish adapt to dim environments.

regained when fish return to the rivers to breed (Allison et al., 2006; Cheng and Novales Flamarique, 2004).

Molecular photoreceptor tuning mechanisms
The peak sensitivities of photoreceptor visual pigments are influenced by five different factors that affect their two primary components: the chromophore and the opsin protein. Here we describe what is known about these different mechanisms and how they might improve ecological function.

Chromophore
Fish vary in their use of vitamin A1- or A2-derived chromophores or a mixture (Fig. 2B; Bridges et al., 1984; Munz and McFarland, 1977). They can switch chromophores, likely through the activity of an enzyme, *Cyp27c1*, that converts A1 chromophore into A2 (Enright et al., 2015). The presence of an extra double bond in the A2 chromophore long-wavelength shifts all visual pigments, with the longer-wavelength pigments having a larger chromophore shift (Hárosi, 1994; Parry and Bowmaker, 2000). Typically, chromophore changes shift visual pigments to shorter wavelengths in clear water (see Glossary), which transmits blue to green parts of the spectrum. In turbid environments, visual pigments are shifted to longer wavelengths to match the red-shifted light spectrum resulting from particulates and high chlorophyll concentrations. For example, cichlids from clear lakes, such as Lakes Malawi (Terai et al., 2002) and Lake Xiloa (Härer et al., 2018) rely on A1-based pigments and have low gene expression of *cyp27c1*. However, cichlids that live in murky Lake Managua and Lake Nicaragua express more *cyp27c1*, increasing the amount of A2 chromophore within their visual pigments. In addition, studies in cichlids from Lake Victoria (Terai et al., 2017) and in sticklebacks from Fennoscandian lakes (Saarinen et al., 2012) suggest A2 pigments with longer-wavelength sensitivities match the downwelling illumination more effectively. The switch between

chromophore types can occur on relatively short timescales (Munz and McFarland, 1977), as seen for example in the cichlid, *Cichla monoculus*, which navigates environments with varying turbidity in the Panama canal, on a daily or weekly basis (Escobar-Camacho et al., 2019b). Surprisingly, some chromophore changes are more closely tied to seasonality than water properties, as found for Scandinavian fishes (Jokela-Maatta et al., 2019) and salmon (Flamarique, 2005; Temple et al., 2006), though ontogeny can also play a role (Archer and Hirano, 1996). Seasonality may be linked to variations in sun angle: during winter the lower sun angle is associated with longer-wavelength environmental light (Lindstrom, 2000; Pauers et al., 2012).

Opsin sequence shifts (discussed below) and chromophore shifts sometimes both correlate with water spectral color and depth. As for chromophore shifts, opsin sequence changes also tend to shift visual pigments to shorter wavelengths in clearer water. However, at least one study has shown that this relationship is not so straightforward. Sand-dwelling cichlids of murky Lake Victoria utilize long wavelength-sensitive opsin (*LWS*) genes with sequences that would be sensitive to shorter wavelengths in combination with higher levels of A2 chromophore when fish live deeper (Terai et al., 2017). It may be that some mixing and matching of shorter-tuned opsins and longer wavelength-sensitive chromophores are needed to produce the optimal visual pigment to detect the available light.

Opsin sequence
Five classes of ancestral vertebrate visual opsins are known, and many fish possess all of these, including rhodopsin (*RH1*; expressed in rods) and four cone opsin classes: short wavelength-sensitive (*SWS1* and *SWS2*), rhodopsin-like (*RH2*) and *LWS* (Ebrey and Koutalos, 2001; Yokoyama, 2008). The corresponding protein of each class is sensitive to light in different parts of the spectrum (RH1: 447–525 nm; SWS1: 347–383 nm; SWS2: 397–482 nm; RH2: 452–537 nm; LWS: 501–573 nm; see Table S2). The

sensitivity range of each class is the result of changes in key amino acid sites close to the retinal binding pocket that alter amino acid polarity and thus change the way in which the chromophore interacts with the opsin protein (Fig. 2C; Asenjo et al., 1994; Chang et al., 1995).

Opsin sequences quite often vary between closely related species. These differences are thought to enable fish to adapt to different light environments. For *RH1* opsins, changes in a few amino acids, so called key-tuning sites, shift the visual pigment to shorter wavelengths with depth in clear waters (e.g. cottoids: Luk et al., 2016; deep-sea fishes: Hunt et al., 2001; cichlids: Sugawara et al., 2005; Sugawara et al., 2002) and to longer wavelengths with depth in murkier waters (cichlids: Terai et al., 2017). Also, moving from clear water to a murkier habitat can induce changes in *RH1* sequences (e.g. anchovies: Van Nynatten et al., 2015; cichlids: Schott et al., 2014; Torres-Dowdall et al., 2015; herring: Hill et al., 2019). Changes to key sites may not only shift the peak spectral absorbance, but also increase light sensitivity by increasing the stability of the excited rhodopsin intermediate (Hauser et al., 2017), and/or the excitability of the chromophore (Luk et al., 2016).

Cone opsin sequences also vary with light habitat. For example, the cichlid *SWS1* gene is long-wavelength shifted by 10 nm in murky Lake Victoria (λ_{max} 378 nm), compared with homologs in Lake Malawi (λ_{max} average 368 nm; Smith and Carleton, 2010). Cottoid fishes of Lake Baikal are also known to shift their SWS2 pigments to shorter wavelengths in an attempt to match their blue-shifted light environment at depth (Cowing et al., 2002). Another prominent example is the rapid fixation of red-shifting mutations in SWS2 pigments in stickleback populations that have recently invaded blackwater habitats (see Glossary) dominated by longer wavelengths of light (Marques et al., 2017).

There is also evidence that past environmental variability produces contemporary genetic variability. Genes for the shortest- and longest-wavelength opsins accumulate sequence variation, suggesting they have experienced shifting light regimes. These include the *SWS1* and *LWS* genes in African cichlids (Hofmann et al., 2009) and damselfish (Hofmann et al., 2012; Stieb et al., 2017), and the *SWS2* and *LWS* genes in labrids (Phillips et al., 2016), cardinalfishes (Luehrmann et al., 2019), characins (Escobar-Camacho et al., 2019a preprint) and Neotropical cichlids (Escobar-Camacho et al., 2017). This accumulation of mutations may result from selection acting on the genes for visual pigments at the edge of the light's spectral envelope. Species experience changing light environments because of altered water spectral quality with depth, or as species repeatedly shift habitats from rivers to lakes or marine to freshwater over evolutionary time. The genes for visual pigments that are spectrally more central do not show such sequence changes, as the consistency of their light stimulation provides less selective pressure.

Gene duplications and losses

Ancestral vertebrates already possessed members of five opsin classes, as suggested by the diversity in sea lamprey (Collin et al., 2003b). Since the vertebrate common ancestor, some teleost lineages have gained additional opsin copies through duplications so that they now have more opsins than other vertebrates (Davies et al., 2012; Musilova et al., 2019a; Rennison et al., 2012). These extra copies are sometimes the result of the teleost-specific whole genome duplication (Escobar-Camacho et al., 2019a; Liu et al., 2016; Liu et al., 2019; Morrow et al., 2011), but can also result from duplications specific to particular lineages, e.g. the tandem duplications of the *SWS2* and *RH2* genes that are shared across

Actinopterygians (Hofmann and Carleton, 2009; Parry et al., 2005). As with any gene or genome duplication event, the functional reasons behind opsin gene duplications need further study to assess possible fitness effects.

Teleosts have up to two *SWS1*, three *SWS2*, eight *RH2* and five *LWS* cone opsins within their genomes, with a median of six cone opsins across fishes. The highest currently recorded number is 13 cone opsins for the Blackbar soldierfish, *Myripristis jacobus* (Musilova et al., 2019a). Although most fish species have only one or sometimes two rod opsin genes (*RH1*), in some, mostly deep-sea fish lineages, these genes also proliferated. For example, the spinyfin, *Diretmus argenteus*, has 38 *RH1* copies in its genome (Musilova et al., 2019a). Although less than half of the *Diretmus* genes are expressed at any one time, they do show different spectral sensitivities. This could potentially be important for performing different visual tasks or for performing the same task under different light regimes provided by the mesopelagic realm (see Glossary).

Once opsin genes duplicate, they may acquire new mutations which shift their spectral sensitivity. Sometimes this coincides with the loss of function of a gene that confers a spectral sensitivity which is close to the sensitivity of the original duplicate (Fig. 4; Escobar-Camacho et al., 2019a preprint; Liu et al., 2019). For example, in Osteoglossiformes and Characiformes, *LWS* was duplicated. Coincident with loss of functionality of a *RH2* gene, one of the *LWS* duplicates was selected to shift to shorter-wavelength sensitivity, replacing the lost mid-wavelength sensitivity. In this way, a gene duplicate became neofunctionalized from the ancestral version to fill an important spectral niche. Duplications of the *SWS2* genes have also led to neofunctionalization, with the ancestral gene retaining blue sensitivity while the duplicate becomes violet sensitive (Cortesi et al., 2015). In other systems, spectral shifts of opsin duplicates are prevented by gene conversion (see Glossary). In some poeciliids, for example, neighboring copies of *LWS* recombine to homogenize the different *LWS* opsin copies to minimize long-wavelength variation. However, in other species, selection minimizes gene conversion to retain unique *LWS* gene sequences, as this differentiation may facilitate mate choice based on long-wavelength red coloration (Sandkam et al., 2017; Watson et al., 2011). Overall, duplicates can be either quite distinct or only slightly different in sensitivity, depending on their time since duplication and the strength of selection acting on them. The role of these extra opsin copies is not always clear. More information is needed on their spatial and temporal distribution and possible co-expression before we can determine their significance.

In addition to gene duplication, opsins can also be lost from the genome. This may be the result of photoreceptor simplification in spectrally narrow environments or when light intensities change severely such as in the deep sea (Musilova et al., 2019a) or turbid waters (Escobar-Camacho et al., 2017; Lin et al., 2017; Liu et al., 2016; Weadick et al., 2012). These habitats are generally darker and have reduced levels of UV light (and red light, in the case of deeper waters; Fig. 3). Consequently, in deeper-living fish, one would expect a (total) loss of cone opsins. However, although some opsins can be lost (e.g. *SWS1* and *LWS* cone opsins), medium-wavelength opsins appear to be useful to larval stages, and are therefore often retained (see Fig. S1 in Musilova et al., 2019a). An extreme correlation between gene loss and light environment is found in the Southern cavefish, *Typhlichthys subterraneus*, which has degenerated eyes and has only one fully coding *RH2* gene left in its genome (Musilova et al., 2019a). Studies in other cavefish confirm a preponderance of loss of vision-related genes, including opsins, as well as epigenetic mechanisms for altering gene
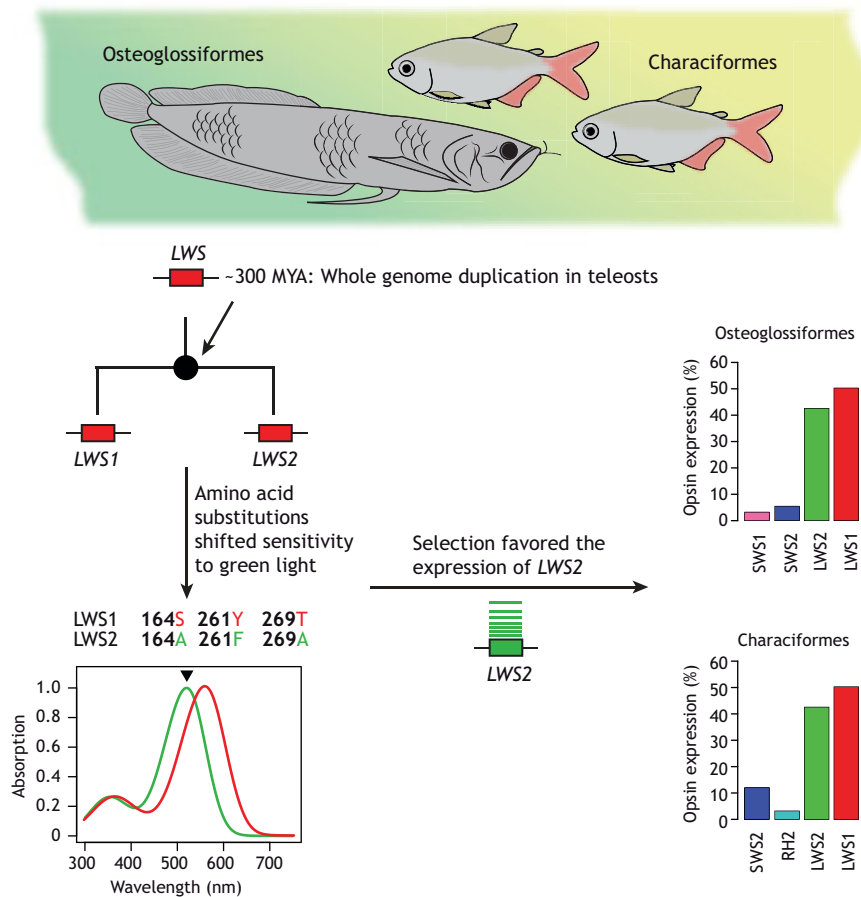
Fig. 4. Opsin gene neofunctionalization. Opsin gene duplicates may gain new function by acquiring amino acid substitutions that shift visual pigment sensitivity. This sometimes occurs after species lose one gene. Here, both osteoglossiformes and characiformes have lost (osteoglossiformes) or downregulated the expression (characiformes) of the *RH2* gene while one of their *LWS* duplicates has acquired key amino acid changes that green-shifted its sensitivity.

expression (Gore et al., 2018; McGaugh et al., 2014). Fish opsin duplications and losses occur far more frequently than expected, with a great deal of turnover across fish lineages (Fig. 5).

Opsin expression and co-expression

Fish with many opsins may sometimes express all of them. For example, zebrafish express all eight cone opsins in different regions of the retina (Allison et al., 2010; Raymond and Barthel, 2004; Takechi and Kawamura, 2005). By contrast, other species express only a subset of opsins with different sets for different developmental stages (flounder: Evans et al., 1993; Savelli et al., 2018; cichlid: Härer et al., 2017; O'Quin et al., 2011; salmon: Cheng and Flamarique, 2007; Cheng and Novales Flamarique, 2004; dottybacks: Cortesi et al., 2016; Cortesi et al., 2015; grouper: Matsumoto and Ishibashi, 2016; and silver spinyfin: Musilova et al., 2019a). This may provide benefits when larval habitat or foraging differs from that of adults. Altering the timing of this developmental progression through heterochronic shifts (see Glossary) may change the adult phenotypes between closely related species (Carleton et al., 2008; Härer et al., 2017). Switching expression from one opsin class to another can cause significant (30–90 nm) spectral shifts (see Fig. S2).

Intraretinal variation in opsin expression is another tuning mechanism that acts within an individual to optimize vision in different directions (zebrafish: Zimmermann et al., 2018, four-eyed fish: Owens et al., 2012). For example, archerfish use a spitting jet of water to capture terrestrial insects. As a result, the eye is optimized for vision at the interface between water and air, and demonstrates an excellent example of intraretinal variability in spectral sensitivity (Temple et al., 2010). Different sets of visual

sensitivities are produced by changes in opsin expression combined with changes in chromophore ratios, which produce long-wavelength sensitivities in the dorsal retina for looking down against the rocks, medium-wavelength sensitivities in the medial retina for looking against the spacelight (see Glossary), and short-wavelength sensitivities in the ventral retina for looking up against the bright sunlight. This optimizes different visual tasks that will be performed by the different parts of the retina, both under and above water.

Opsin expression may vary among closely related species, with differences correlated with foraging. The UV-sensitive opsin (*SWS1*) is highly expressed in planktivorous cichlids (Hofmann et al., 2009; O'Quin et al., 2010). Alternatively, long-wavelength sensitivity is correlated with foraging on benthic algae. For example, in damselfish, *LWS* expression is notably increased in herbivorous species (Stieb et al., 2017). This may improve contrast between the long-wavelength portion of the chlorophyll reflectance that fish must discriminate from the gray or brown rubble background when viewed with a long-wavelength biased visual system (Marshall et al., 2003).

Some shifts in opsin expression over an individual's lifetime appear to be genetically hard-wired to modify vision developmentally (bream: Shand et al., 2008, 2002; pollack: Shand et al., 1988; unicornfish: Tettamanti et al., 2019). However, fish may also display some level of plasticity, with opsin expression varying with light environment (killifish: Fuller et al., 2004) or depth (cichlids: Smith et al., 2011; damselfish: Stieb et al., 2016). This plasticity has been explored in laboratory experiments that demonstrate sensitivity shifts to match different light environments (killifish: Fuller et al., 2005; Fuller and Claricoates, 2011; bream: Shand et al., 2008; cichlids:
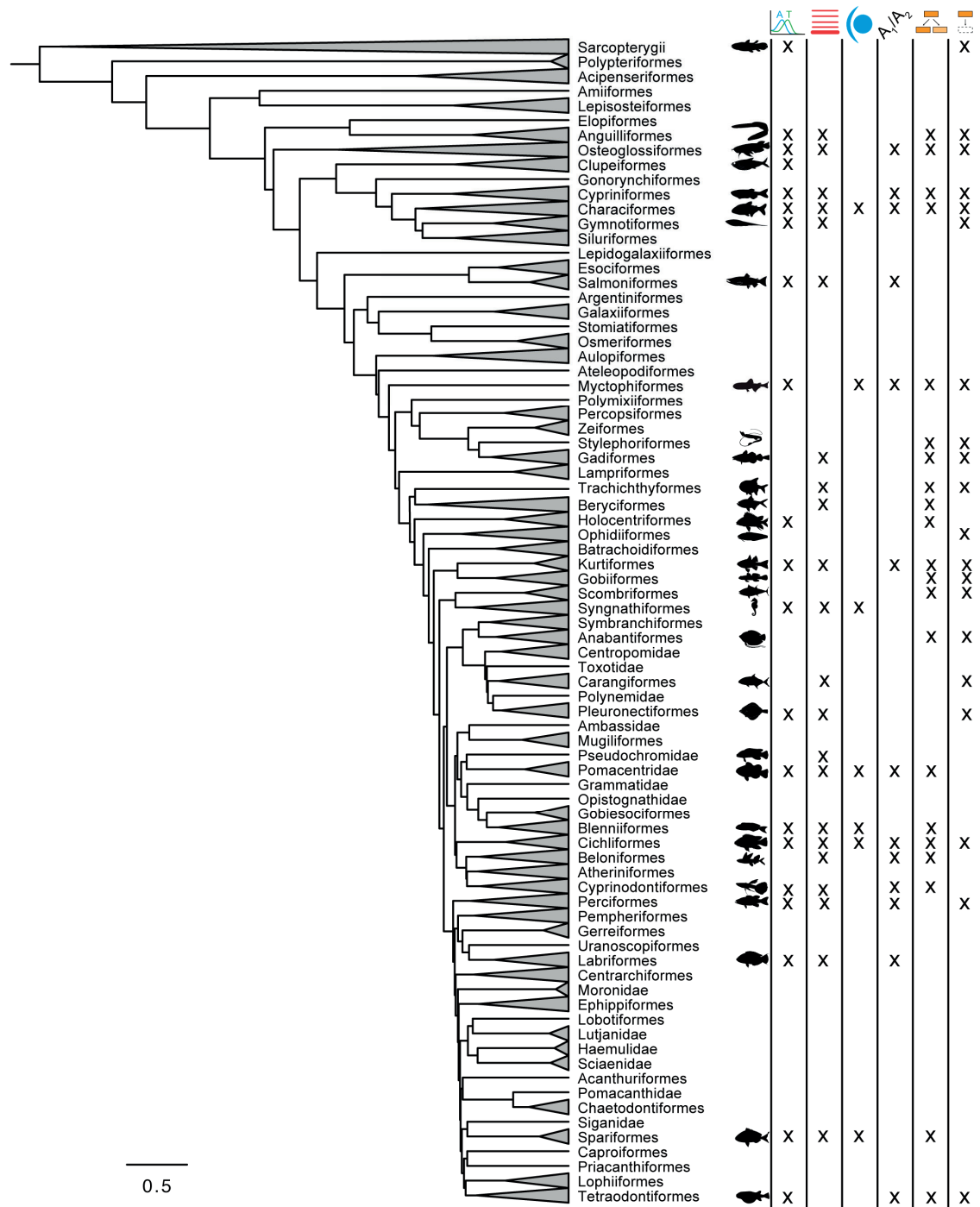
Fig. 5. The teleost phylogeny showing the prevalence of different spectral tuning mechanisms between species within a given order. Spectral tuning mechanisms include changes to opsin amino acid sequence, opsin gene expression, cornea and lens transmission, chromophore shifts, gene duplications and gene losses (columns from left to right). Phylogeny based on Hughes et al., 2018. Several animal silhouettes courtesy of PhyloPic (http://www.phylopic.org).

Hofmann et al., 2010b; Nandamuri et al., 2017; cardinalfish and damselfish: Luehrmann et al., 2018; and guppies: Kranz et al., 2018; Sakai et al., 2018). However, not all species are plastic (sticklebacks: Flamarique et al., 2013; cod: Valen et al., 2018; salmon: Novales Flamarique, 2019), and plasticity is sometimes limited to younger stages (cichlids: Härer et al., 2017; Hornsby et al., 2013). Plasticity may also have a genetic component and so may vary between populations (stickleback: Rennison et al., 2016; bluefin killifish: Fuller et al., 2005) or environments (sticklebacks: Veen et al., 2017).

In addition, at least one study system showed some measure of compensation for the lighting environment used for raising fish (Kröger et al., 1999, 2003; Wagner and Kröger, 2000). After long-term rearing of the South American cichlid *Aequidens pulcher* under monochromatic lights, researchers found that although the visual sensitivities did not change (i.e. no change in gene expression) photoreceptor cell numbers and lengths varied under short-wavelength rearing. The number of short wavelength-sensitive cones decreased, while the length of the longer wavelength-

sensitive double cones increased. These compensatory changes would enhance long-wavelength sensitivity when little long-wavelength light was available. Interestingly, switching fish to white light reversed these differences, with retinae returning to normal after 2 months (Wagner and Kröger, 2000).

Although expression may completely switch from one opsin to another, multiple opsins can also be co-expressed in the same photoreceptor, producing intermediate spectral sensitivities (salmon: Cheng and Flamarique, 2007; cichlids: Dalton et al., 2017, 2014; Torres-Dowdall et al., 2017; and damselfish: Stieb et al., 2019). The idea that spectral tuning may be achieved by co-expression of multiple opsins is supported by the fact that opsins are generally not randomly co-expressed from closely located loci (i.e. it is not leaky expression from some shared promoter). Instead, opsins that are spectrally close are co-expressed from loci that are genomically far apart (cichlids: Dalton et al., 2017, 2014; osteoglossiforms: Liu et al., 2019; characins: Escobar-Camacho et al., 2019a preprint). Co-expression may vary spatially across the retina with less co-expression in regions of high acuity (area centralis) and more in the periphery (Dalton et al., 2017). However, this is not always the case. The Barrier Reef anemonefish *Amphiprion akindynos* has recently been shown to have a small area in the central temporal region with significant coexpression of *SWS1* (UV) and *SWS2B* (violet) (Stieb et al., 2019). This region, which falls within the region of highest acuity, may be important for discriminating objects at close range. It therefore may increase the chromatic contrast of conspecific color patterns possibly involved in mate choice.

Opsin expression does vary between species in different light habitats, suggesting adaptation to the light environment. Cichlids in murky lakes with red-shifted light environments express longer wavelength-sensitive opsins than those in clear lakes, increasing overall quantum catch (Hofmann et al., 2009; Torres-Dowdall et al., 2017). Expression shifts may occur on a very local scale. For example, cichlids are quite philopatric (see Glossary) and do not move long distances. Therefore, cichlids living at clearer sites in the center of a lake express shorter-wavelength opsins whereas those living nearby in more murky riverine sites have longer-wavelength opsins (Hofmann and Carleton, 2009; Wright et al., 2019). On coral reefs, cardinalfish that live above the corals in the 'blue' water column express shorter-wavelength opsins, whereas those that live in dimmer 'reddish' coral caves express longer-wavelength opsins (Luehrmann et al., 2020). Similarly, opsin expression in guppies varies between different watershed populations (Sandkam et al., 2015b) and even between populations with high versus low predation (Sandkam et al., 2015a). Opsin expression is also known to vary among fishes living in different small lakes and streams, presumably matching changes in the light environment (Musilova et al., 2019b; Veen et al., 2017).

Rapid plastic responses to the local environment also shift opsin expression, suggesting that it may be adaptive to match dynamic changes in light environment. This was first discovered in bluefin killifish; fish from clear springs or tea-stained swamps switched opsin expression when raised in different environments (Fuller et al., 2004, 2005). The rapidity of these switches is astonishing: sudden environmental shifts can cause changes within just a few days (Fuller and Claricoates, 2011). Cichlids also show rapid plasticity (Nandamuri et al., 2017), but plasticity in other species requires a longer time scale, potentially allowing for seasonal adaptation (medaka: Shimmura et al., 2018; damselfish and cardinalfish: Luehrmann et al., 2018).

In addition to the molecular studies demonstrating plastic responses, studies using physiology also support such shifts. This includes microspectrophotometry and electrophysiology studies of fish that change sensitivities through development or rearing in different environments (e.g. bream: Shand et al., 2002; cichlid: Wagner and Kröger, 2005; Lisney et al., 2010; eel: Archer et al., 1995; Wang et al., 2011; flounder: Evans et al., 1993; killifish: Fuller et al., 2003; and tuna: Loew et al., 2002a,b). These studies provide validation that molecular changes cause significant physiological sensitivity shifts.

In summary, visual pigment and photoreceptor sensitivities vary owing to a number of mechanisms. Although numerous examples of these variations correlate with environment or ecology, it is not always clear whether these differences actually have any functional or fitness implications. Testing for the significance of these changes in the context of current environments may prove to be either highly or just barely relevant. However, it can be difficult to determine whether these differences matter evolutionarily, because of the challenges in demonstrating adaptation (Box 1).

Using behavior to investigate visual sensitivity

Behavioral tests are arguably the best way to investigate the significance and effect size of visual system variation, as they involve responses at the level of the whole organism. Such tests can be challenging to implement, as they require attention to hue/color as well as brightness, in order to ensure that one is not confounded by the other (Douglas and Hawryshyn, 1990). In addition, animals may respond to cues other than those intended. Finally, not all species can be motivated to repeatedly perform particular behavioral tasks. A number of behavioral studies have quantified the ability of fishes to discriminate colors by quantifying photoreceptor performance (i.e. receptor limited noise) in order to predict how well fish can perform particular discrimination tasks of ideal colored targets (Champ et al., 2016; Cheney et al., 2019; Pignatelli et al., 2010). However, here we focus on more biological, animal-centered tasks, such as foraging for prey or choosing mates.

The importance of particular wavelengths for foraging has been demonstrated. For example, UV light improves prey capture rates in zooplanktivorous animals, suggesting that UV sensitivity plays an important role in their prey detection (perch: Loew et al., 1993, trout: Browman et al., 1994; Novales Flamarique, 2013, sticklebacks: Rick et al., 2012, cichlids: Jordan et al., 2004, zebrafish: Novales Flamarique, 2016). The study of other robust behaviors, such as the optomotor response (OMR; see Glossary), has also demonstrated the effect of altered visual sensitivity. For example, knocking out the *LWS* opsin in medaka causes fish to be much less sensitive to red light during OMR (Homma et al., 2017). This provides a clean behavioral measure of a fish's spectral sensitivity in a robust and easy way. More subtle spectral tuning effects may also affect OMR sensitivity. In cichlids, *LWS* sequence (Maan et al., 2006) and expression (Smith et al., 2012) affects OMR sensitivity – fish that have *LWS* genes encoding variants that are sensitive to longer wavelengths or that have higher *LWS* gene expression have better red sensitivity.

Additional demonstrations of the behavioral effects of spectral tuning involve mating experiments. In medaka with the *LWS* opsin knocked out, the lack of red sensitivity alters mate choice, making them less able to discriminate against skin color mutants (Kamijo et al., 2018). Stickleback mating preference is also influenced by retinal sensitivity (Boughman, 2001; Rick et al., 2011) – females with higher red sensitivity (based on OMR) prefer redder males. Sticklebacks are also influenced by UV signals, with a decrease in UV illumination reducing male aggression (Rick and Bakker, 2008). This suggests that some parts of the spectrum may be

important triggers for particular behaviors including female mating (red) and male aggression (UV).

Another example of adaptive spectral tuning comes from coral reef fishes. Most damselfish species have UV-reflective body parts (Fig. 6; Marshall, 2000; Stieb et al., 2017). This, together with their overall UV sensitivity, provides a 'private' close-range communication channel (Losey, 2003; Marshall and Cheney, 2011; Siebeck et al., 2006). Indeed, behavioral studies revealed that the damselfish *Pomacentrus amboinensis* uses facial UV patterns for species discrimination and perhaps also for mate selection (Siebeck et al., 2010).

Differences in visual sensitivity and their implications for visual performance and potential role in speciation have been behaviorally tested in sympatric Lake Victoria cichlids. These species include a shallow-water, blue-colored species, *Pundamilia pundamilia*, that has a shorter wavelength-sensitive *LWS* opsin and a deeper living, red-colored species, *Pundamilia nyererei*, with a longer-wavelength *LWS* opsin. Visual sensitivity differences have been confirmed through *LWS* sequencing, microspectrophotometry (Carleton et al., 2005) and protein expression (Terai et al., 2006). A 5 kb region around the *LWS* gene shows evidence of selection for the alternative *LWS* alleles in the two species (Terai et al., 2006). These differences have been proposed to contribute to speciation through sensory drive (see Glossary; Endler, 1992) in a series of steps. First, the *LWS* sequence differences were selected to increase luminance detection of the background spacelight across a depth gradient. Second, acquired visual sensitivity differences affected mate preference, with shallower *P. pundamila* being sensitive to shorter wavelengths and preferring blue males, whereas deeper *P. nyererei* were sensitive to longer wavelengths and preferred red males. Finally, these mating preferences led to reproductive isolation and speciation (Seehausen et al., 2008). A number of key elements for this correlative hypothesis are supported through direct experimentation. This includes enhanced sensitivity of *P. pundamila* to blue light and *P. nyererei* to red light (Maan et al., 2006), natural sorting of *P. pundamilia* and *P. nyererei* to shallow and deep environments (Seehausen et al., 2008), enhanced survivability of the two species in lab experiments simulating their respective light environments (Maan et al., 2017) and enhanced female preference for their conspecific males in these same light environments (Wright et al.,
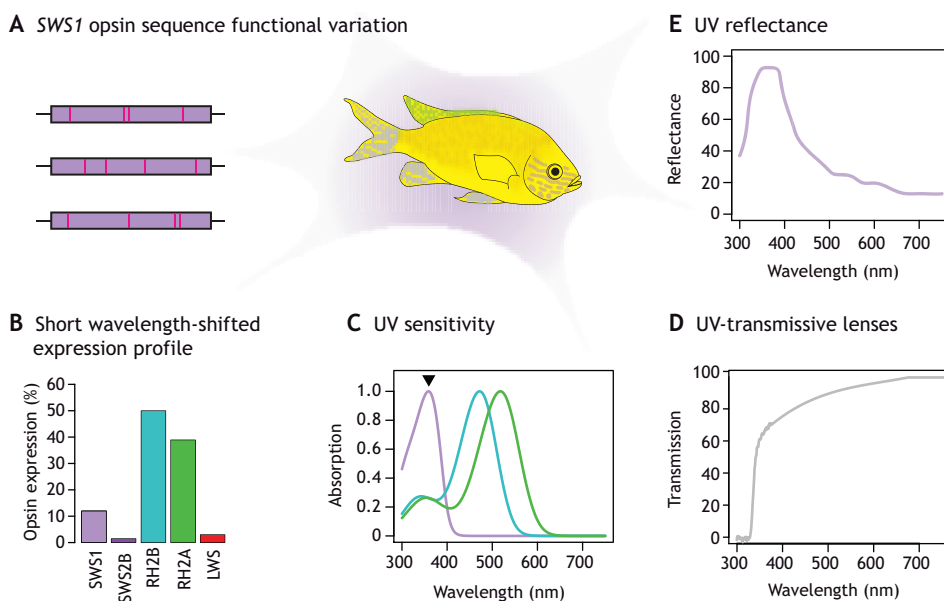
2017). Other species pairs in Lake Victoria also show evidence of opsin sequence differences that are correlated with depth and male nuptial color, suggesting this could be a common speciation mechanism in Lake Victoria (Miyagi et al., 2012). Although sensory drive and the co-evolution of visual sensation and color signals is somewhat at odds with a general-purpose visual system, there is mounting evidence for such a correlation (Cummings et al., 2018).

Several of the sensitivity differences between species involve fixed genetic differences, but we should note that plasticity might also play a role in speciation. Some might argue that plasticity would prevent speciation as changes would not become fixed and so not contribute to genetic isolation between species. However, it has been suggested that plasticity might actually facilitate speciation by enabling organisms to move into new habitats (West-Eberhard, 2005). These habitats could differ spatially on a large scale, but might also include microhabitat or temporal differences in when and where populations mate. Short-term plasticity might allow individuals to adapt to different light regimes or perform different foraging tasks in these different locales. Therefore, plasticity might be an important driver facilitating speciation (West-Eberhard, 2003).
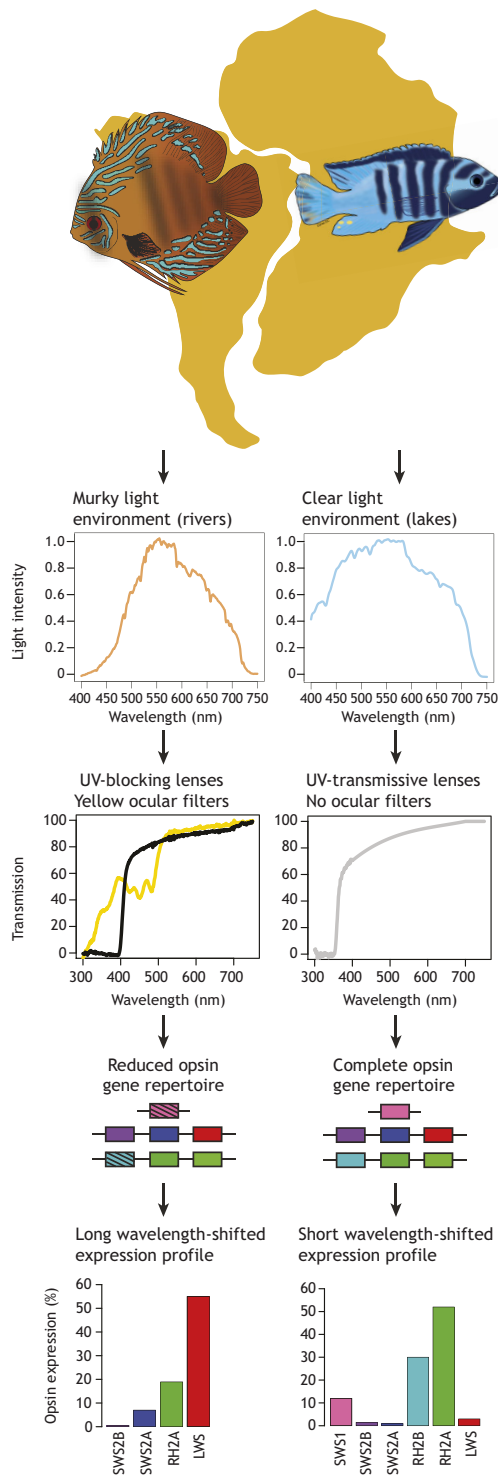
Comparing mechanisms of spectral tuning – effect sizes and time scales

Many of the mechanisms for spectral tuning described here are shared across the teleost phylogeny (Table S1; Fig. 5). This suggests that these mechanisms arose early in vertebrate evolution; indeed, this idea is well supported by studies of migrating lamprey. This basal vertebrate has the ability to switch chromophore, gene expression and even ellipsosomes through ontogeny (Collin et al., 2003a; Davies et al., 2007; Morshedian et al., 2017). Comparisons between lamprey species also show evidence of opsin gene loss (Davies et al., 2009). Therefore, each of the key spectral tuning mechanisms was present across groups from fishes to gnathostomes, supporting their likely origin in early vertebrates.

It is worth asking why fish have so many different ways to produce spectral shifts. One reason might be that the different mechanisms vary in their effect size and how rapidly they occur (Fig. S2). Changes in both co-expression and chromophore usage are relatively rapid and introduce similarly sized shifts. However, co-expression can affect

A *SWS1* opsin sequence functional variation

B Short wavelength-shifted expression profile

C UV sensitivity

D UV-transmissive lenses

E UV reflectance

Fig. 6. UV sensitivity is adaptive. In damselfish, spectral tuning in the UV is achieved by (A) high sequence variability of the *SWS1* opsin with multiple changes in opsin spectral tuning sites between species, (B) differential *SWS1* opsin expression (Stieb et al., 2017) to produce (C) short wavelength-shifted visual pigments (arrow indicates UV-sensitive visual pigment). (D) Damselfish also have UV-transmissive lenses. (E) Most damselfish species also show UV reflectivity (Marshall, 2000; Stieb et al., 2017), including individual UV facial patterns, suggesting that UV is likely to be important for species discrimination (Siebeck et al., 2010).

be able to utilize co-expression, whereas chromophore tuning is more ubiquitous across groups. Opsin sequence changes and gene losses and duplications are quite slow, on the scale of thousands to millions of years. They may only become important after more rapid, plastic mechanisms enable species to invade new habitats, inducing selection to drive genetic change (Parsons et al., 2019; West-Eberhard, 2005).

Many of these mechanisms for altering visual sensitivity work in concert during ecological shifts. For example, adaptation of cichlids to either clear African lakes or murky South American rivers involved multiple mechanisms, including lens pigmentation, opsin expression, opsin gene losses and chromophore shifts. Adaptation to the different habitats occurred over long evolutionary timescales (80 million years), enabling contributions from each of the tuning mechanisms (Fig. 7; timetree.org, Escobar-Camacho et al., 2017; Matschiner et al., 2017).

Other visual changes have occurred more recently. These include adaptations in cichlids of Lake Victoria, which formed only 15,000 years ago. The more rapid mechanism of differential opsin gene expression has occurred (Wright et al., 2019), but surprisingly, sequence changes are also present (Terai et al., 2002). These mutations may actually have accumulated in riverine refugia and then introgressed (see Glossary) between lake and riverine taxa (Meier et al., 2017). Adaptation in guppy visual systems to particular light environments also appears to be rapid, on the scale of only a year. This is supported by evidence from changes in opsin expression and behavior, including mating preferences (Cole and Endler, 2015; Endler et al., 2001; Kranz et al., 2018).

Conclusions and future work

The visual system is often portrayed as a prime example of phenotypic adaptation to ecology (Hauser and Chang, 2017; Yokoyama, 2008; Yokoyama and Yokoyama, 1996). As we have discussed in this Review, adaptations of the visual system can arise by several mechanisms, which have been studied in detail in a few animal groups. In spite of the many tuning mechanisms that have been discovered, we know little about their effects on behavior or fitness. We would expect large sensitivity shifts to have fitness effects, and indeed in some cases such shifts have been correlated with changes in foraging preferences (e.g. UV sensitivity for zooplanktivory) or pecking behavior (Fuller et al., 2010). Additionally, shifts in spectral sensitivity (including those caused by removing particular opsins, as in medaka) have been shown to have impacts on mate choice (e.g. cichlids, stickleback, guppies). However, examples from foraging or mating behaviors are few, and might not represent good proxies of animal fitness. In addition, we don't know how large a sensitivity change has to be in order to measurably affect behavior. It is possible that much of the observed visual variation happens randomly with little effect, such that most visual systems are good enough for the visual tasks at hand. For example, a small amount of extra opsin expression might have little impact on foraging efficiencies or mate choice (Mitchem et al., 2018). Therefore, it is possible that any trichromat with three visual pigments will successfully perform most visual tasks (Marshall et al., 2015).

Alternatively, one can argue that variation in spectral sensitivity does not happen by chance, based on the fact that shifts in opsin sequence, expression and chromophore are correlated with environment in expected ways. In addition, changes such as gene co-expression do not occur at random, but typically involve spectrally close opsins that provide the best tuning effect. There is also spatial variation across the retina, suggesting that different parts of the retina function better with particular opsin combinations to

Fig. 7. Visual system divergence in cichlids. Cichlids have adapted to different rivers and lakes on different continents. African rivers and lakes may be quite clear, leading to a diverse array of opsin genes that detect a broad spectrum of light. South American waters are often murkier, such that cichlids have lost a number of shorter wavelength opsins. South American cichlids have also acquired yellow cornea and lens filters, perhaps to reduce the transmission of scattered light in the murkier waters (Muntz, 1973, 1982; Escobar-Camacho et al., 2017; Escobar-Camacho et al., 2019b).

individual visual pigments, whereas chromophore shifts affect multiple visual pigments simultaneously. Perhaps co-expression relies on having 'extra' opsin genes and so only some species will

better match the light environment and background being viewed (Temple, 2011; Zimmermann et al., 2018). However, some of the experiments reviewed here reveal a lot of individual variation, implying the lack of selection for one perfect solution.

One of the most pressing needs in the field of visual ecology is to determine when molecular variation actually matters for organismal fitness. To test the significance of many of these mechanisms for shifting spectral sensitivity, we need suitable behavioral studies to identify the true implications of sensitivity shifts. What size and magnitude of shift produces a behaviorally relevant change? Ultimately, we also need direct tests of fitness, based on reproductive success, rather than studies of proxies based on our best guesses for important behaviors. Only when we can directly determine reproductive success can we confidently assess the importance of an observed set of visual sensitivities for the visual tasks performed across a lifetime, and gain an understanding of how much variation in the visual system can be tolerated.

Fortunately, our molecular understanding of visual sensitivities continues to advance. With increased speeds for molecular genotyping and molecular manipulation at the organismal level, we should soon be able to assess which aspects of the visual system are critical for organismal survival and are therefore likely to be the purview of selection.

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.193334.supplemental

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Table S1

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Table S2: Data for limits of fish cone spectral sensitivities

Gene	Species	λ_{max} value	Reference
RH1	*Diretmus argentus*	447 nm	(Musilova et al., 2019)
	Aristostomias scintillans	525 nm[%]	(Yokoyama et al., 2008)
SWS1	*Chitala ornata*	347 nm	(Liu et al., 2019)
	Metriaclima emmiltos	383 nm	(Jordan et al., 2006)
SWS2	*Lucania goodei*	397 nm	(Yokoyama et al., 2007)
	Verasper moseri	482 nm	(Kasagi et al., 2018)
RH2	*Oryzias latipes*	452 nm[*]	(Matsumoto et al., 2006)
	Lucania goodei	537 nm	(Fuller et al., 2005)
LWS	*Chitala ornata*	501 nm	(Liu et al., 2019)
	Lucania goodei	573 nm[#]	(Fuller et al 2005)

[*]This may be as short as 435 nm based on estimations of the RH2 sensitivity for *Maurolicus mucronatus,* but this has not been experimentally confirmed (de Busserolles et al., 2017).

[#]This limit is for vitamin A_1 based visual pigments. Species using vitamin A_2 derived chromophores can have LWS based pigments as long as 625 nm as observed in neotropical cichlids (Torres-Dowdall et al., 2017).

[%]The 525 nm is an estimate based on reconstitution of a slightly modified pigment sequence for this species.

Fig S1. Visual Ecology, Mostly to do with Fish, and Why There Are Too Many Opsins.
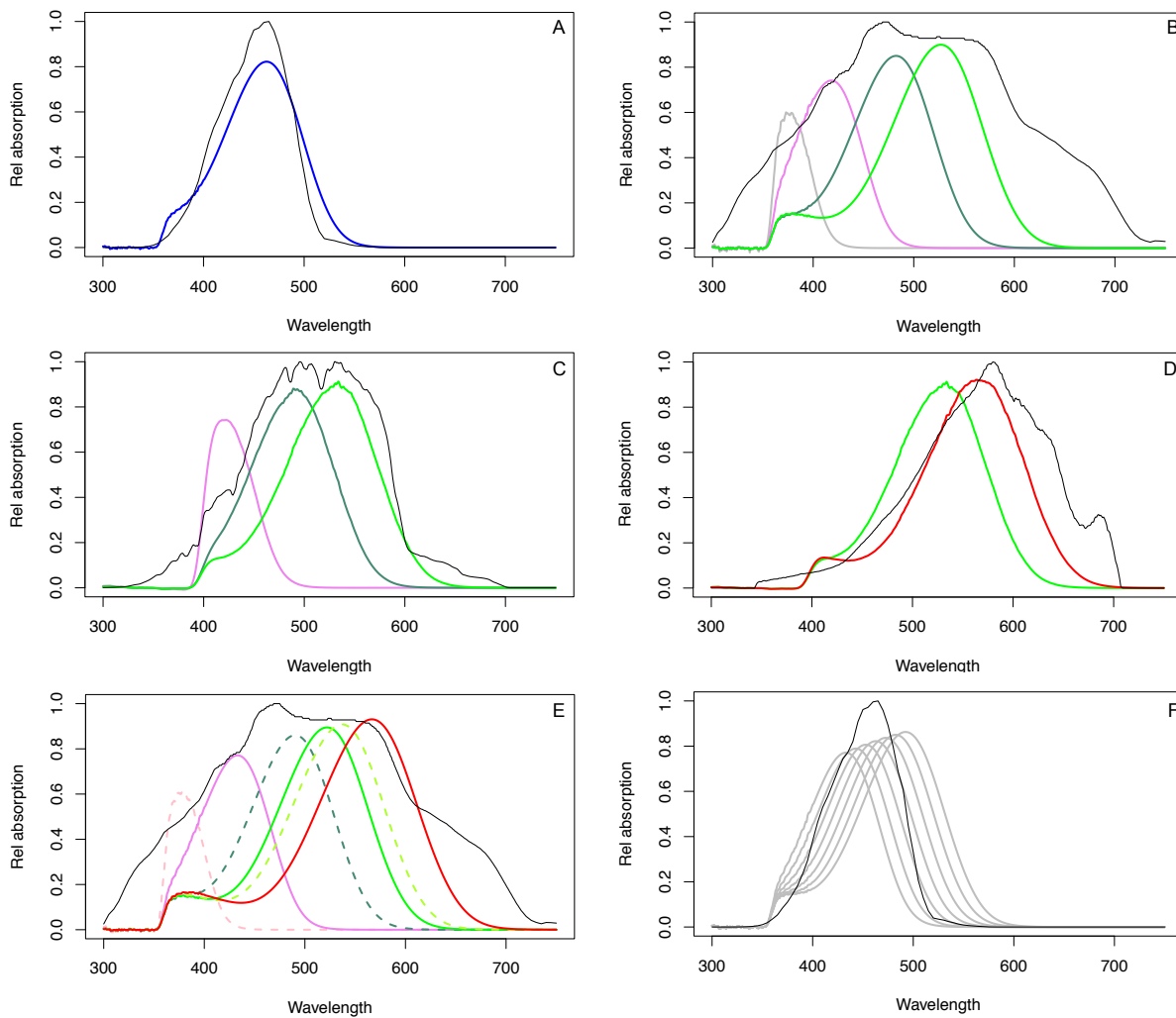
The visual system of animals have evolved, co-adapting to the environmental constraints and behavioral needs of each species. Natural sunlight provides an available light spectrum for vision of 300-700nm, but in underwater light environments this may be attenuated by water color and particulate scatter. Aquatic animals' spectral sensitivity necessarily follows or is limited to the spectral envelope available to them (solid black lines above), e.g., deep sea fishes see blue (A). Within this spectral 'envelope' some photoreceptors are situated to absorb as much light as possible, acting as luminance detectors (typically rods and double cones in some animals). Such light may come from the background spacelight or even bioluminescent sources. Cone photoreceptors operating in daytime are also placed within the light envelope. However,

they vary in number and placement according to behavioral task and to some extent micro-habitat, where light availability might have subtle but critical differences. Some species inhabit clear marine habitats (B) while others are in more productive green-shifted (C) or even red-shifted (D) waters.

Co-evolution of photoreceptor spectral sensitivity and specific task may exist, but color vision is often for more than one task and may be set up by several evolutionary constraints. Color vision in any animal is best thought of as 'general purpose'. Animal colors function for sexual communication, aggression or warning, and camouflage or mimicry. They also evolve in response to light availability and visual system. However there are few examples of tight adaptation or fixation (in either direction) due to a single color-driven function (e.g., deep-sea bioluminescence). Exceptions to this may include sensory drive where sensitivity and/or colors evolved for one task (foraging) become co-opted for another task (mating) as they are easy to detect. This relationship is rarely quantified. Spectral sensitivities that become focused on a color code, or colors that respond to spectral sensitivities present due to available light may help drive speciation. Some animals evolve simple color vision such as dichromacy as this is good enough for their needs (D). Others take advantage of full spectrum and may become tri- or tetra-chromats (B, C). Beyond tetrachromacy, additional pigments are generally not used for polychromacy (e.g., penta-chromaticity), the extra opsins more likely vary due to ontogenetic stage (E with dashed pigments for larvae and solid pigments for adults), retinal area, or extra-ocular use. Recent molecular evidence suggests levels of plasticity in photoreceptor number and spectral positioning on timescales that can be surprisingly short.

Several mechanisms may increase spectral sensitivity number or tune spectral positioning in an eye including: use of photostable filters, subdivision of the retina with task-division between visual areas, duplications of opsin genes, differential degree of expression of opsins over several timescales (including evolutionary to hourly). Several species are known to express far more visual pigments (situated in rods or cones) than would seem necessary (F). Rather than jumping to conclusion, such as this driving polychromatic color vision or the use of all opsins for visual purposes, other functional reasons should be sought.

Fig S2. Effect size and speed of different tuning mechanisms

A Shifts in spectral sensitivities
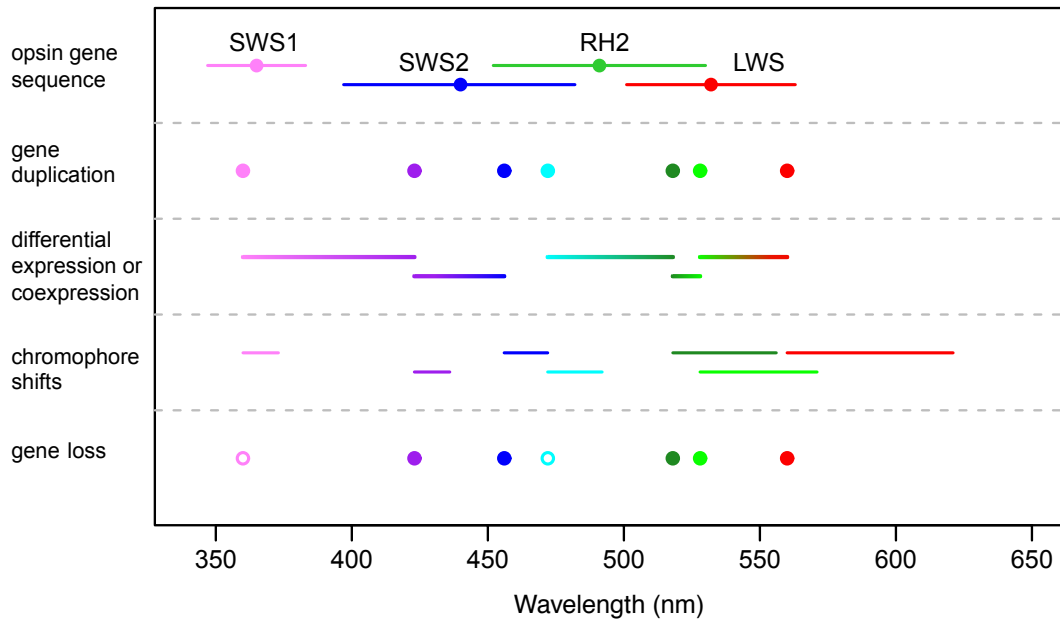
B Changes in spectral sensitivities through time
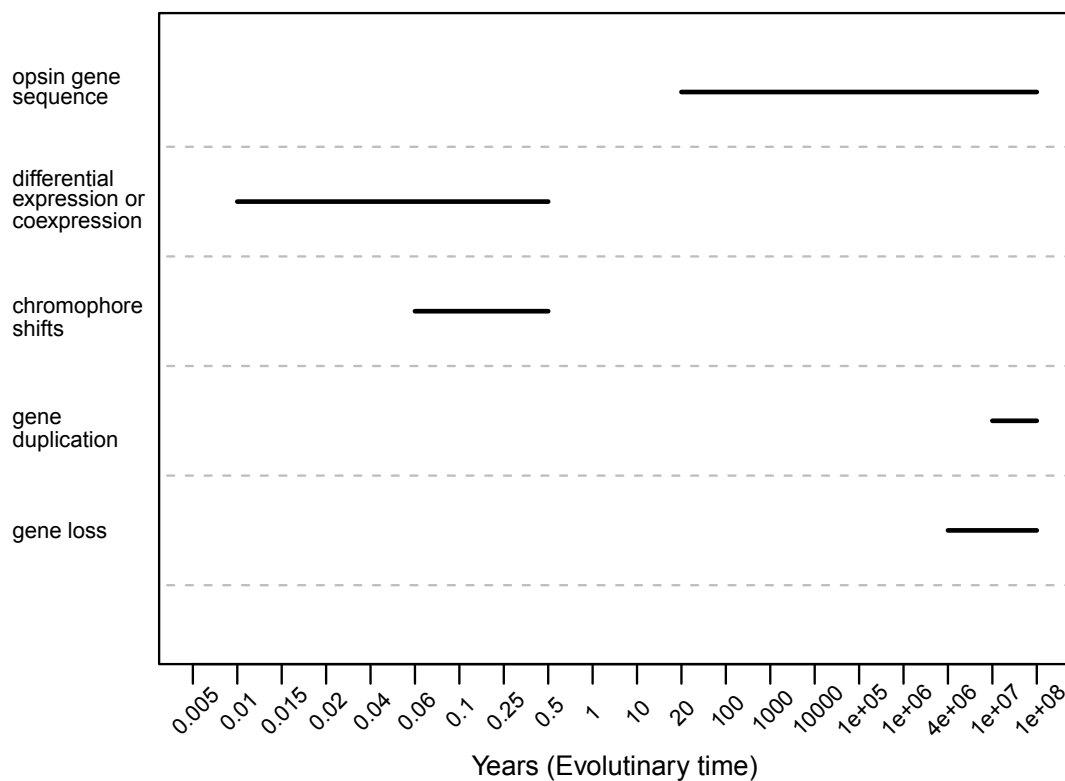
The mechanisms that contribute to photoreceptor tuning cause different spectral shift sizes (A). Variation in opsin gene sequence can shift each of the different opsin

classes. The variation shown denotes the known fish spectral absorbance range for each opsin class including opsin duplicates (e.g. SWS2 and RH2). Gene duplication values are based on data from a typical perciform, the tilapia *Oreochromis niloticus* which has two *SWS2* genes (purple and blue) and three *RH2* genes (cyan to green) (Spady et al., 2006). Differential expression shifts sensitivity by mixing closely related opsins. Chromophore shifts are calculated based on Parry and Bowmaker (2000). Gene losses are shown as typical of South American cichlids (Escobar-Camacho et al., 2017).

The amount of time needed to alter visual sensitivity through different spectral tuning mechanisms also varies (B; note x axis is log scale). Changes in gene expression (Fuller and Claricoates 2011, Nandamuri et al., 2017) and chromophore shifts (Enright et al., 2015) can be days to weeks or perhaps months (Escobar-Camacho et al., 2019). Changes in spectral sensitivity by opsin sequence typically require mutations occurring over millions of years. However, more rapid changes by fixation of standing genetic variation have been shown to shift opsin sequence within a given population in 20 yrs (Marques et al., 2017). Gene duplications occur on average every 100 MY but with 10 opsins could occur every 10 MY, while gene losses occur on average every 4 MY (Lynch, 2002).

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