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Tadpole Responses to Environments With Limited Visibility: What We (Don't) Know and Perspectives for a Sharper Future

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Amphibian larvae typically inhabit relatively shallow freshwater environments, and within these boundaries there is considerable diversity in the structure of the habitats exploited by different species. This diversity in habitat structure is usually taken into account in relation to aspects such as locomotion and feeding, and plays a fundamental role in the classification of tadpoles into ecomorphological guilds. However, its impact in shaping the sensory worlds of different species is rarely addressed, including the optical qualities of each of these types of water bodies and the challenges and limitations that they impose on the repertoire of visual abilities available for a typical vertebrate eye. In this Perspective article, we identify gaps in knowledge on (1) the role of turbidity and light-limited environments in shaping the larval visual system; and (2) the possible behavioral and phenotypic responses of larvae to such environments. We also identify relevant unaddressed study systems paying special attention to phytotelmata, whose small size allows for extensive quantification and manipulation providing a rich and relatively unexplored research model. Furthermore, we generate hypotheses ranging from proximate shifts (i.e., red-shifted spectral sensitivity peaks driven by deviations in chromophore ratios) to ultimate changes in tadpole behavior and phenotype, such as reduced foraging efficiency and the loss of antipredator signaling. Overall, amphibians provide an exciting opportunity to understand adaptations to visually limited environments, and this framework will provide novel experimental considerations and interpretations to kickstart future research based on understanding the evolution and diversity of strategies used to cope with limited visibility.

Keywords: larval vision, turbidity, chromophore shift, phytotelmata, phenotypic plasticity

INTRODUCTION

An incredible diversity of animals inhabits aquatic environments for either part or the entirety of their lives. As a medium, water poses unique challenges and opportunities compared to air, which has resulted in distinct physiological adaptations of even temporarily aquatic animals. For example, short-range communication using chemical signals is facilitated in water

(Wisenden, 2000), whereas communication using sound in shallow water environments is compromised (Ladich and Winkler, 2017). The visual world underwater is shaped by the way in which light gets refracted and attenuated, and by the inherent optical properties of water (e.g., high absorbance of blue light). In this default scenario, physical variables such as pool type, volume, and geometry, and biological variables, such as the amount and nature of organic matter, interact in shaping the luminic environment (Jerlov, 1976; Lythgoe, 1979). Here, we will use “limited visibility” and “turbidity” in the sense implied throughout Lythgoe’s (1979) “The Ecology of Vision,” as follows. Limited visibility refers to a number of situations in which increased scattering and/or selective absorption alter the quality and quantity of light available for a visual system, including, but not limited to, depth-dependent filtering of spectral bands at the boundaries of the visible spectrum, darkening/coloring due to absorption by dissolved pigments, etc. Turbidity, in this context, is a particular case of limited visibility; its most defining feature is the presence of a “veil” of scattered light originating from suspended particles in the visual scene, and its direct consequence is the decrease of brightness contrast of objects against the background. Thus, even though suspended matter can also absorb light, the main challenge it poses to visual performance is decreased visibility via an increase in “noise” in the visual scene -rather than a decrease in light availability as is the case of other visibility-reduced environments, such as the “deep” or “colored” waters mentioned just above.

Despite the intricate visual systems that aquatic animals have evolved throughout time, individuals can be challenged by the rapid and unexpected change in the structure of their visual environments. Sudden increases in dissolved organic matter through algal blooms, agricultural/anthropogenic run-off, or from resuspended particulate matter can drastically change the visibility of aquatic habitats (Granqvist and Mattila, 2004; Engström-Öst and Candolin, 2006; Chivers et al., 2012). In these situations, the question is no longer about the refinement of an animal’s visual system for a specific habitat, but about the flexibility of that system to maintain image quality and visual performance in the face of change. Research on the plasticity of visual systems so far has mostly dealt with its biochemical and genetic bases (see Corbo, 2021 and Carleton and Yourick, 2020, respectively, for reviews on examples of these topics), whereas focused research on its consequences for ecologically relevant, visually guided behaviors is still missing in the scientific literature. In an era where the stressors of agricultural practices, land use, and climate change are more present than ever before, understanding the responses to turbidity from both proximate and ultimate perspectives will help to better understand the responses of aquatic animals in these increasingly stressed environments (Rowe and Dean, 1998; Sundin et al., 2010).

Tadpoles can rely on vision, at least to some degree, for social behavior (Katz et al., 1981; Caldwell, 1989; Sontag et al., 2006) and complex space use (Beiswenger, 1977). Despite this, they are nearsighted (Mathis et al., 1988), and have typically been assessed as having poor vision overall (Hoff et al., 1999). This mindset has shaped both the experimental design and interpretation of results of studies testing their reliance on different sensory modalities

(Rot-Nikcevic et al., 2006; Saidapur et al., 2009). However, other recent work has begun to question this, providing support for a more prominent role of visual cues in predator detection (Hettley et al., 2012), identification of conspecifics (Gouchie et al., 2008; Kumpulainen, 2021) and habitat assessment (Rot-Nikcevic et al., 2005; Hettley et al., 2012). For many amphibian species, tadpoles are aquatic and adults are (semi-)terrestrial. While “immature” in the grand scheme of ontogeny, larvae are adapted to their aquatic habitats with the same degree of refinement with which adults are adapted to their environments post-metamorphosis (McDiarmid and Altig, 1999). Such a clearly defined biphasic life cycle, unparalleled among vertebrates, presents a unique opportunity to study the plasticity of visual systems: even within species the visual system can be differentially tuned to match the surrounding environment before and after metamorphosis, as has been shown for relative eye size (Shrimpton et al., 2021) and expression levels of genes that determine spectral sensitivity (Schott et al., 2021).

Overall, amphibian vision is relatively well documented in adults from the point of view of phototransduction mechanisms, spectral tuning, retinal topography and signal processing, and optical performance, but less work has been done on larval stages (see Donner and Yovanovich, 2020 for a review). To the extent to which tadpoles’ visual systems have been studied, they expectedly share the organization and functionality of vertebrates in general, and amphibians in particular, and showcase some differences with their adult selves in aspects that impact performance in aquatic vs. aerial media. For example, tadpoles’ lenses tend to be spherical, while those of terrestrial adults become flattened (Mathis et al., 1988), and their visual pigments tend to be shifted to long wavelengths compared to adults (Crescitelli, 1958), with implications discussed in the upcoming sections. Amphibian larvae constitute a unique model to understand the evolution of vertebrates’ visual systems in the transition from aquatic to aerial environments, and the effect of ontogeny on the maintenance or change of ocular adaptation. Thus, their visual ecology and the behavioral adaptations resulting from environmental changes provide an exciting and relatively unexplored framework of questions to address.

DIVERSITY OF VISUAL ENVIRONMENTS AND ITS IMPLICATIONS FOR TADPOLE ECOMORPHOLOGY

To date, researchers have focused primarily on fishes to understand how predator-prey interactions, mate choice, and foraging adaptations are affected in environments with limited visibility (e.g., turbid). The bulk of these studies show that when challenged with turbidity animals demonstrate a relaxed selection in mate choice (Järvenpää and Lindström, 2004; Sundin et al., 2010), poorer foraging efficiency (Rowe and Dean, 1998; Horppila et al., 2004), and reduced perception of predation risk (Kimbell and Morrell, 2015). Overall, these trends are not without exception, as turbidity can both provide cover to prey while also impairing reaction time/evasive maneuvering, thus the (dis)advantage of turbidity is more generally determined by the

modalities used by the community. The majority of turbidity studies have been conducted in North America and Northern Europe, leaving most of the equatorial regions and its diverse (semi-) aquatic fauna understudied. Thus, much of the diversity with respect to species, geography, and life histories, is available for novel comparisons and new insights into animal adaptations in visually challenging environments.

One such environment that has yet to be addressed in studies on limited visibility are phytotelmata. These ephemeral pools of water are formed in plant structures, and distributed throughout the vertical gradient. Phytotelmata, which are notably different from ponds and lakes, commonly occur in tropical regions and are frequently invaded by insects and amphibian tadpoles (Kam et al., 2001; Lehtinen, 2004; Summers and Tumulty, 2013; Biju et al., 2016; Cossio et al., 2021; Fouilloux et al., 2021) and constitute a model system that is relatively easy to access and extensively quantify, and lends itself very well to experimental manipulations (e.g., Serrano-Rojas and Pašukonis, 2021). Occupied pools range widely in size and shape (Fouilloux et al., 2021), and in turbidity and/or water color as well, according to qualitative field observations (unpublished data recorded by CF, **Figure 1**). Additionally, phytotelmata themselves contribute to defining the light environment in pools. For example, light reflected from fresh green bromeliad leaves will be different from that reflected from decomposing bark or decaying palm bracts. To our knowledge, thus far there have been no quantitative measurements of light or turbidity levels in phytotelmata, which only emphasizes the knowledge gap within this system.

One could expect that a consistent decrease in light availability (based on denser canopy cover) and visibility would have a measurable impact on larval development. For instance, tadpoles of the Amazonian phytotelm-breeder *Dendrobates tinctorius* that develop in pools with dark-tinted water appear to be collectively smaller than those deposited in clear waters despite an abundance of prey availability in both cases (e.g., mosquito larvae, BR unpublished obs.). We hypothesize that the decreased body condition of these *D. tinctorius* larvae may indicate that, in environments with limited visibility, phytotelm-reared tadpoles may experience decreased hunting efficiency, and shift their feeding strategies from omnivorous/predacious to mostly herbivorous. The constraints of turbid environments may not only affect predatory behavior by carnivorous tadpoles, but could also impact other species with specialized feeding strategies like oophagy, which relies on the ritualized parent-offspring feeding behavior initiated after tadpoles visually recognize an adult and increase activity to indicate hunger (Stynoski and Noble, 2012). Ultimately, we hypothesize that turbid or otherwise visually limiting microhabitats could have profound effects on both body condition and survival in a variety of phytotelm-based species (**Figure 2**).

Turbidity could also have notable effects on phytotelmata communities. In estuary systems, for example, it appears that biodiversity decreases in turbid conditions, where the few species that use chemoreception (crabs) outcompete those that rely more heavily on visual cues (fish; Reustle and Smee, 2020). Diverse tadpoles (Kitcing, 2001; Summers and McKeon, 2004), insects (Fincke, 1992; Caldwell, 1993), and crustaceans (Pettitt et al.,

2018) (co-)exist in phytotelmata, yet the effect of limited visibility on community-wide changes has not been tested in these systems. We propose that phytotelmata provide natural mesocosms to investigate and compare the responses of different community structures (and the diverse visual systems of the animals that these communities contain) to habitat disturbance. Out of the handful of studies that have considered amphibian responses to visually limited conditions, most have followed trends found in fishes (i.e., reduced anti-predator behavior in salamanders, Zabierek and Gabor, 2016; decreased growth rates in frogs, Wood and Richardson, 2009). In amphibians, these experiments could be taken one step further by considering potential carry-over effects of how rearing environments shape behavior through metamorphosis. Overall, it has been shown that environmental stress has significant carry-over effects from larval to adult stages in amphibians (size: Scott, 1994; reproductive organs: Harper and Semlitsch, 2007). Thus, tadpoles raised in the stress of turbid conditions may not only be physically smaller as a result of reduced foraging performance but also have reduced fitness in adulthood compared to their counterparts raised in clear water conditions.

WAVES AND VITAMINS: STRATEGIES TO RESPOND TO VISUALLY CHALLENGING ENVIRONMENTS

In turbid habitats, the best option to improve visual function is to filter out the added background light arising from scattering that does not contribute to image formation (Lythgoe, 1979). While scattering from large particles tends to be wavelength-independent, scattering coming from small particles (Rayleigh scattering) that also contributes to image quality degradation is enriched in short wavelengths (i.e., ultraviolet, violet, blue) (Douglas and Marshall, 1999). Thus, a decreased sensitivity in the “blue” part of the spectrum, be it at the level of the eye as a whole or the individual retinal photoreceptor cells, would help to some degree to deal with the detrimental effects of turbidity. Conversely, an increased sensitivity in the long-wavelength (i.e., “red”) part of the spectrum would arguably improve vision in freshwater aquatic environments which tend to be redder than marine ones (Lythgoe, 1979). Thus, we would expect considerable overlap between the strategies that visual systems can use to cope with turbid environments and with red-colored environments (such as the ones we show in **Figure 1**), even if they differ substantially in overall light availability.

Several species of frogs have some kind of pigment in their crystalline lenses, many of them resembling those of fishes in their absorbance profile, which selectively remove short wavelength light before it reaches the retina (Yovanovich et al., 2020). However, because these data come from adult individuals, it remains to be investigated if these filtering properties are already present in the tadpoles of relevant species, and whether larval stage could provide a compelling biological explanation for those cases in which the adult filtering pattern does not follow any immediately obvious logic. Interestingly, other recent work has found differences in expression levels of genes related to lens

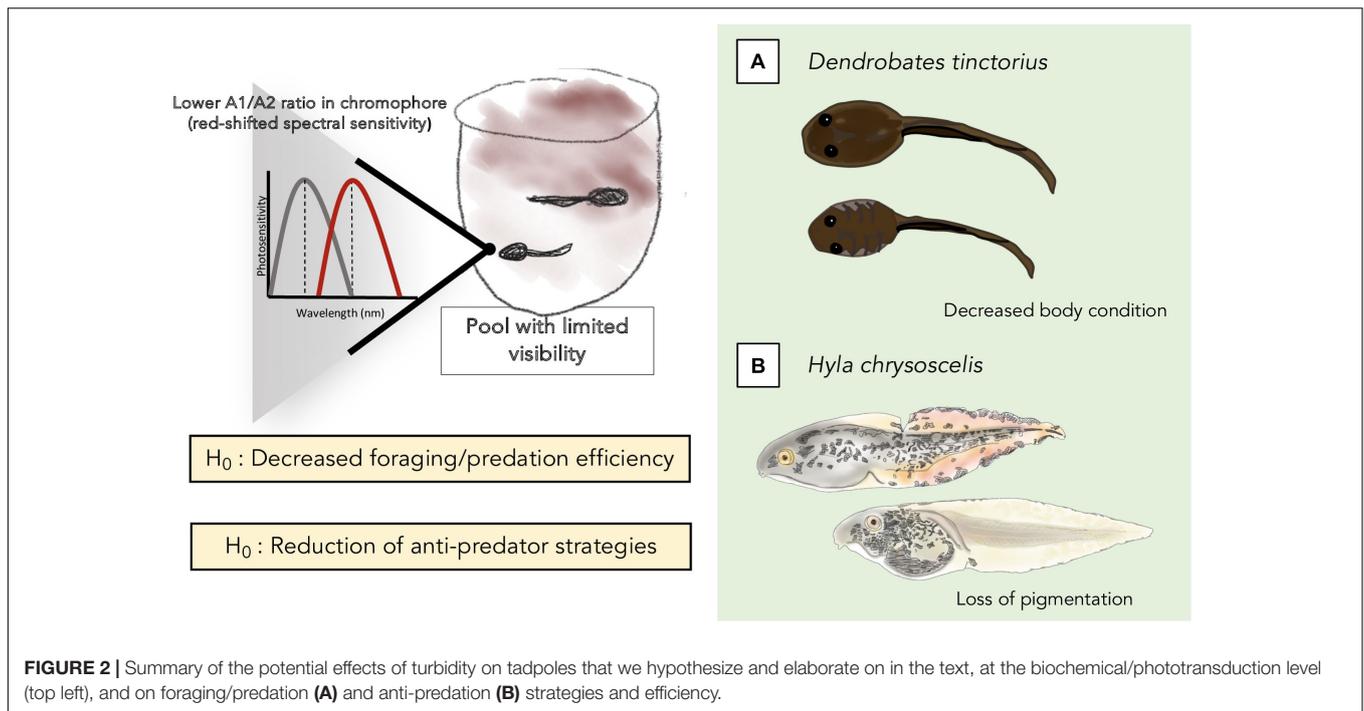


FIGURE 1 | Water samples (collected by CF) from phytotelmata occupied by *Dendrobates tinctorius* tadpoles in French Guiana. Based on water samples, it appears that tadpoles are deposited in pools with a wide range of visibility. Colored labels refer the water sample (top of figure) to the pool from which it was collected. We hypothesize that in darker waters tadpoles' spectral sensitivity is red-shifted (lower Vitamin A1:A2 ratio). Photos: Chloe A. Fouilloux.

composition in tadpoles versus juveniles of the frog *Lithobates sphenoccephalus* (Schott et al., 2021). If these gene products were ones to affect light transmittance in a wavelength-dependent manner (e.g., Röhl, 2001), the finding would argue against the speculation outlined just above, and highlight the need to explore the issue in more species to find -or rule- out potential patterns.

At the level of the retina, the availability of photoreceptors with peak sensitivities at short wavelengths is another potential point to control scattering-related visual noise. As it turns out, the highly blue-sensitive rods unique to amphibians, which allow color discrimination in extremely dim light (Yovanovich et al., 2017), only appear toward the end of the larval phase in *Xenopus laevis* (Chang and Harris, 1998; Parker et al., 2010). It is tempting to speculate that such a delay in the acquisition of blue sensitivity “protects” the tadpoles’ visual system from the degradation of image quality caused by short wavelength scattering, but here again we must take this finding as an encouragement to study photoreceptors’ ontogeny synchronization in a variety of tadpoles from different ecomorphological backgrounds, rather than settling on it as the default pattern.

The components discussed so far cannot be expected to adjust to short-term changes in the visual environment, and so the spectral absorbance profile of individual photoreceptor cells remains the best candidate to allow tadpoles’ visual systems to adapt to changes in turbidity in physiological time-scales. This profile is a property of the visual pigment (opsin apoprotein + Vitamin A-derived chromophore) housed in the photoreceptors membranes, and depends solely on the amino acid sequence of the opsin and the type of Vitamin A (1 or 2) used (Govardovskii et al., 2000). The opsin sequence is, naturally, genetically encoded, and thus cannot be changed during the lifetime of the animal in response to changes in the environment. Overall photoreceptor spectral sensitivity can, in fact, be worked around by regulating the gene expression levels in cases when several copies with slightly different sensitivity peaks are available such as the fast-speciating cichlid fishes radiations from the African great lakes (Carleton and Yourick, 2020). Furthermore, opsin expression levels within individuals can fluctuate as a consequence of manipulations in the light environment



in killifish (Fuller et al., 2010; Fuller and Claricoates, 2011). However, such a diversified opsin gene pool is not typically available in amphibians, but all the opposite: the sensitivity peak for rhodopsin sits on a particularly narrow range in the spectrum compared to vertebrate standards (Crescitelli, 1958; Donner and Yovanovich, 2020). In contrast, switching from Vitamin A1 to Vitamin A2 (which confer higher sensitivity toward the blue and red parts of the spectrum, respectively) is quite straightforward and achieved by a single enzyme conserved across vertebrates, the expression levels of which are quite reactive to changes in the photic environment, even though the underlying mechanism remains unknown (Corbo, 2021). Documented cases among fishes include change of chromophore ratios in response to water temperature (Ueno et al., 2005), seasonality (Temple et al., 2006), and turbidity (Bridges, 1972; Beatty, 1984).

In the case of amphibians, the general trend is to go from a Vitamin A2-rich tadpole to Vitamin A1-rich adults, except in species who remain aquatic throughout life such as *Xenopus laevis* (see Donner and Yovanovich, 2020 for a review), supporting the view that Vitamin A2-rich retinas are beneficial in typically “red-shifted” freshwater environments (Corbo, 2021). The evidence that the A2/A1 transition occurs both at different ontogenetic stages and at different rates depending on the species (Hödl, 1975), and that the vitamin ratio can reversibly change during the tadpole phase in response to manipulations of light levels (Bridges, 1970), suggests that the Vitamin A system is the most readily available modulator of visual function in response to unpredictable changes in visually challenging environments.

The ultimate effect of shifting amphibian chromophore ratios on behavior remains unknown, but is a fascinating consideration for evolutionary ecologists to approach. For example, we have

found an impressive range of tint and turbidity levels in the pools of water in which *Dendrobates tinctorius* tadpoles are deposited (Figure 1). Based on previous work on visual pigments, we would hypothesize that tadpoles deposited in more turbid pools of water would have a red-shifted chromophore system. *Dendrobates tinctorius* tadpoles are aggressive predators and appear to partially rely on vision to attack each other (Fouilloux et al., 2020), and thus presumably rely on vision to hunt other prey as well. Ultimately, with a noisier visual scape, red-shifted tadpoles may not be as effective at hunting, cannibalizing, or even foraging in general, but may perform better in visually challenging environments over having not shifted at all; overall, this flexibility could have remarkable impacts on tadpole fitness and survival (Figure 2).

ENVIRONMENTALLY INDUCED PHENOTYPIC ADAPTATIONS AND THEIR CASCADING EFFECTS

One of the most covered topics in turbidity literature is predator-prey dynamics. The majority of work considers prey activity (reduced antipredator behavior: Meager et al., 2006; Kimbell and Morrell, 2015), and predator accuracy (Bonner and Wilde, 2002; Gadowski and Parsley, 2005) under various turbidity conditions. Although interactions between predator and prey most often hinge on whether the animal is more dependent on chemical or visual cues, or a combination of the two (Swanbrow Becker and Gabor, 2012), visually guided behaviors often break-down in turbid environments (Chivers et al., 2012; Swanbrow Becker and Gabor, 2012). This results in different advantages

for predators or prey as a function of the modalities used for detection/evasion. For example, some tadpoles have adapted anti-predator phenotypes such that, when under high predation risk, individuals will express redder-colored fins, which have been hypothesized to serve either as camouflage or to prevent lethal attacks, compared to those that are not (*Hyla chrysoscelis*, McCollum and Van Buskirk, 1996; *Dendropsophus ebraccatus*, Touchon and Warkentin, 2008). The underlying rationale is that the redder fins may direct predators to strike non-lethal parts of the tadpole's body, or that the spotty coloration could act as some kind of camouflage by "breaking up" the contour of the tadpole's body. The effects of turbidity on the expression of anti-predator signaling in tadpoles remain unknown.

As turbidity interferes with color vision (Wilkins et al., 2016), its fluctuations can impact the interpretation of color as (including, but not limited to) a proxy for distance (Bartel et al., 2021). Until now, the change of color-based signals in response to visually challenging environments has been demonstrated only in a handful of studies, and limited to the context of adult signaling. In gudgeon fish, a two-week transplant experiment showed the overall expression of melanin decreased in turbid conditions, leading to lighter colored fishes (i.e., economy of pigments hypothesis; Côte et al., 2019). We hypothesize that increased turbidity levels will induce a "relaxed" phenotype where tadpoles do not express camouflage/disruptive coloration despite the potential presence of predators. The direction of which actor would benefit from this phenotype is dependent on the detection mechanisms used by predators and prey.

The change of color expression as a function of visually challenging environments could also be interesting in the context of aposematic signaling. In fire salamanders, it has been shown that the background albedo of larval environments influences juvenile phenotype (Sanchez et al., 2019), indicating that the light quality of larval environments can have impacts that persist through metamorphosis. The carry-over effects of larval rearing environment on adult coloration have yet to be explored in frogs; based on salamander responses, it is plausible that anuran tadpoles who have lived in turbid/red-shifted environments could carry over to the color expression in their (semi-) terrestrial adult forms, perhaps in having less saturated coloration as a result of developmental stress and a low-quality diet during their larval stages. This could have remarkable implications for aposematic amphibians who rely on color as an anti-predator (or sexual) signal (Brown, 2013; Segami Marzal et al., 2017).

In response to the impressive variation in color displayed among poison frogs and the interest in aposematic signaling

throughout the clade, establishing a novel driver of color variation through turbidity-induced carry-over effects has the potential to be valuable across research disciplines. Exploring how colors change in the face of increased turbidity would be a great opportunity to understand the plasticity of color-based signals in antipredator contexts, and how these are shaped by optically challenging scenarios. Overall, amphibian larvae provide an exciting opportunity for exploring adaptations to visually limited environments from both proximate and ultimate perspectives, and framing these responses comparatively across clades, habitats, and geography will surely challenge evolutionary ecologists for years to come.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

CF gave shape to the initial draft and designed both figures. All authors were directly involved in all stages from conceptualization to final editions.

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