

Developmental plasticity in vision and behavior may help guppies overcome increased turbidity

Sean M. Ehlman^{1,2} · Benjamin A. Sandkam³ · Felix Breden³ · Andrew Sih¹

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Abstract Increasing turbidity in streams and rivers near human activity is cause for environmental concern, as the ability of aquatic organisms to use visual information declines. To investigate how some organisms might be able to developmentally compensate for increasing turbidity, we reared guppies (*Poecilia reticulata*) in either clear or turbid water. We assessed the effects of developmental treatments on adult behavior and aspects of the visual system by testing fish from both developmental treatments in turbid and clear water. We found a strong interactive effect of rearing and assay conditions: fish reared in clear water tended to decrease activity in turbid water, whereas fish reared in turbid water tended to increase activity in turbid water. Guppies from all treatments decreased activity when exposed to a predator. To measure plasticity in the visual system, we quantified treatment differences in opsin gene expression of individuals. We detected a shift from mid-wave-sensitive opsins to long wave-sensitive opsins for guppies reared in turbid water. Since long-wavelength sensitivity is important in motion detection, this shift likely allows guppies to salvage motion-detecting abilities when visual information

is obscured in turbid water. Our results demonstrate the importance of developmental plasticity in responses of organisms to rapidly changing environments.

Keywords Developmental plasticity · Opsin gene expression · *Poecilia reticulata* · Response to environmental change · Turbidity

Introduction

Human-induced rapid environmental change (HIREC) necessitates similarly rapid adaptive phenotypic shifts in affected organisms (Sih et al. 2011). Phenotypic plasticity is the most common mechanism through which organisms achieve phenotypic shifts in response to HIREC (Hendry et al. 2008), largely due to the quick responsiveness of highly plastic traits, such as behavior, to environmental input (Sih et al. 2010). Plasticity may be classified according to the timescale over which it occurs: developmental plasticity occurs when a genotype exhibits different phenotypes according to the rearing conditions experienced during development. Such developmental plasticity occurs on a longer timescale compared to activational plasticity (also called contextual plasticity; Stamps and Groothuis 2010), which is often thought of simply as behavior or ‘behavior as plasticity’ (Dukas 1998). Though both types of plasticity likely play a role in adaptive phenotypic responses to novel environments, developmental plasticity in particular may induce a wider range of integrated phenotypic responses to environmental change (West-Eberhard 2003; Snell-Rood 2013).

One major human-induced change in aquatic systems is increased turbidity (Davies-Colley and Smith 2001), often associated with eutrophication due to agricultural runoff

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✉ Sean M. Ehlman
smehlman@ucdavis.edu

¹ Department of Environmental Science and Policy, University of California-Davis, One Shields Ave., Davis, CA 95616, USA

² Animal Behavior Graduate Group and Center for Population Biology, University of California-Davis, Davis, USA

³ Department of Biological Sciences, Simon Fraser University, 8888 University Dr., Burnaby, BC V5A 1S6, Canada

(Tilman et al. 2001) or sedimentation from mines, quarries, and erosion. In turbid water, visual information deteriorates, potentially negatively impacting aquatic organisms that rely on sight (Gregory 1993). While some organisms compensate for the lack of visual information in turbid water by relying more on information from other senses ('sensory compensation'; Hartman and Abrahams 2000), organisms that experience turbidity through development may be able to compensate within a sensory modality (e.g., the visual system) via developmental plasticity. Since turbidity dramatically alters visual environments in aquatic ecosystems, it may rebalance the relative importance of different roles of the visual system: detecting brightness (luminance), color (color discrimination), and motion (directional selectivity) (Gegenfurtner and Hawken 1996; Derrington 2000).

Here, we examine developmental plasticity of behavior and color vision in response to turbidity in the Trinidadian guppy (*Poecilia reticulata*). Though increasing turbidity is common in pulses after rains, runoff from rock quarries and deforestation in Trinidad dramatically increases sediment load in both magnitude and duration. We ask to what degree developmental history (i.e., development in turbid or clear water) affects behavior when a fish is exposed to turbid water as an adult, and how exposure to turbid water affects responses to an olfactory predator cue. To assess how guppies might demonstrate a trade-off between color vision and motion detection through development, we also measured the degree of developmental plasticity in guppy vision by measuring opsin gene expression. Opsin proteins are contained in the cone cells of guppies and determine the peak wavelength sensitivities of cone cell types (Yokoyama 2000, 2002). Guppies have nine opsin types, named for the range of wavelengths detected: one short wave-sensitive-1 (SWS1: detecting ultraviolet), two short wave-sensitive-2 (SWS2: detecting blue/purple), two mid-wave-sensitive (RH2: detecting green), and four long wave-sensitive (LWS: detecting red/orange) opsins (Hoffmann et al. 2007; Ward et al. 2008; Watson et al. 2011). While all opsins are thought to play a role in color vision (Archer et al. 1987; Archer and Lythgoe 1990; Watson et al. 2011; Sandkam et al. 2015), motion detection has been shown to rely most heavily on long-wavelength sensitivity, mediated by the L-class of cone cells, which contain LWS opsins (Anstis et al. 1998; Schaerer and Neumeyer 1996; Krauss and Neumeyer 2003). Thus, a rebalancing of the trade-off between color vision (involving all opsins) and motion detection (involving primarily LWS opsins) can be measured by assessing differences in the proportion of opsins in the retina that are LWS opsins for fish reared in turbid water vs. clear water.

Since the importance of detecting motion, especially approaching predators (Lima and Dill 1990), is paramount,

and turbidity decreases the range at which visual signals can be detected, we hypothesize that guppies reared in turbid water increase the expression of long wavelength-sensitive opsins important in motion detection. Furthermore, previous studies have shown that fish placed in turbid water decrease activity (Leahy et al. 2011; Borner et al. 2015); thus, we predict that guppies reared in clear water and placed in turbid water will show decreases in activity, while fish reared in turbid water may be acclimated to turbid conditions (in part via transcriptional changes in their visual system) such that activity decrease in turbid water will not be observed. Here, we examine the integrated responses of the visual system and behavior to turbidity over a developmental timescale, demonstrating a multi-dimensional phenotypic response to rapid environmental change.

This study adds to a growing body of literature dealing with the role of developmental and behavioral plasticity in response to rapid environmental change. As previously mentioned, such plasticity often allows for the quickest adaptive phenotypic change in a human-disturbed environment (Van Buskirk 2012), and studies showcasing such plasticity abound. Some birds and anurans, for example, exhibit short-term changes in aspects of acoustic communication in order to overcome anthropogenic background noise (e.g., Gross et al. 2010; Cunnington and Fahrig 2010), great tits plastically adjust the timing of reproduction with climate change (Charmantier et al. 2008), orange-crowned warblers adjust nesting behavior and parental provisioning in the presence of a novel predator (Peluc et al. 2008), etc. While some plastic changes in response to novel environments are adaptive, other plastic changes are clearly maladaptive (e.g., Ghaleb et al. 2015). A recently proposed framework to understand such variation in novel environments invokes traditional optimality theory by stating that behavioral 'rules of thumb' as well as the sensory systems with which animals interact with their environment depend on both developmental and evolutionary histories. Variation in these histories can thus explain variation in success during periods of rapid environmental change (Sih 2013). In line with this framework, this study represents further evidence that variation in developmental history (i.e., developmental experience—or not—in human-altered environments) explains adult phenotypes in novel, human-altered environments.

Methods

Collection and rearing

In April 2013, 20 adult males and 20 adult females were collected from a 100 m stretch of the Yarra River in Trinidad (N 10°44.403', W 061°13.574') characterized by low

flow, low turbidity, and high predation rates (Reznick et al. 1996; Magurran 2005). All individuals were transported to the Center for Aquatic Biology and Aquaculture at the University of California, Davis. Through development for all generations, guppies were reared in 37.5-L tanks with gravel substrate at a density of one fish per liter, fed once daily with freshly hatched *Artemia* nauplii ad libitum, and maintained under a stable 12-h light/dark cycle. At birth, first-generation fry were separated from parental stock and housed in separate tanks. First-generation fry were kept in similar conditions at similar densities as their parental stock and used to produce second-generation fish. By using second-generation, lab-reared fish, we sought to eliminate unmeasured environmental effects and minimize maternal effects.

Developmental treatments

All tanks were monitored daily for births, ensuring that the maximum time second-generation fish were housed in their natal tanks was less than 24 h. Once second-generation individuals were isolated from tanks containing their first-generation parents, they were placed in one of two developmental treatments: turbid or clear water. Most birth events yielded two or more fry, and a split-brood design was followed. In turbid treatment tanks, turbidity was created by pre-mixing bentonite fine powder clay into fresh water then adding this mixture to developmental treatment tanks. Bentonite clay is a standard additive to create turbidity (Gardner 1981). Though bentonite clay sediment can reduce oxygen consumption in fish at extremely high concentrations (Horkel and Pearson 1976), turbidity in this experiment was well below this level. Turbidity was measured daily in all tanks using a Hach® turbidimeter and was maintained at 40–60 nephelometric turbidity units (NTUs) in turbid tanks (reflecting the lower range of turbidity values in turbid Trinidadian streams; Luyten and Liley 1985; SME unpublished data) and ~1 NTU in clear tanks.

To ensure overhead artificial lighting environments did not differ qualitatively between treatments (and thereby drive differences in opsin expression), light intensity directly above the water surface was measured in lumens. Additionally, the λ_{p50} was calculated for each treatment when measuring light filtered through clear or turbid water to a depth of ~15 cm. The λ_{p50} is the median wavelength of photons between 300 and 800 nm (McFarland and Munz 1975; Hurtado-Gonzales et al. 2014). A difference in λ_{p50} would indicate lighting environments were shifted toward longer (larger λ_{p50}) or shorter (lower λ_{p50}) wavelengths of light. While algal-caused turbidity typically increases water's λ_{p50} , turbid water created by clay sediment typically shows no shift in λ_{p50} (Ranáker et al. 2012). To find λ_{p50} , the intensity of down-welling light over a 180°

field of view at 0.33-nm intervals was measured between 250 and 800 nm using a Jaz Spectrophotometer fitted with a 600- μ m fiber cable and cosine corrector running the JAZIRRAD Program (Ocean Optics). Luminosity and average λ_{p50} were compared between turbid and clear treatments using a *t* test in R v3.1.1 (R Core Team 2014).

Growth (standard length and mass) was measured weekly for every individual through sexual maturity and did not exhibit treatment differences (mass: estimate = -0.0261 ± 0.0194 g, $t_{(45)} = -1.345$, $p = 0.185$; length: estimate = -1.038 ± 0.665 mm, $t_{(45)} = -1.560$, $p = 0.126$). Upon reaching sexual maturity (assessed visually using characteristics of the male gonopodium and female gravid spot), guppies entered a series of two behavioral trials.

Behavioral trials

Upon reaching reproductive maturity, baseline behaviors and anti-predator responses in second-generation guppies from each treatment group were assayed in an open arena behavioral trial. Trials occurred in small tanks (approximately 60 × 45 × 15 cm), containing either turbid or clear water filled to a depth of 6 cm. All trials were filmed from above using JVC® GZ-HM300 HD camcorders mounted 2 m above assay tanks, and each tank was screened with black opaque sheets around the sides to minimize disturbance and prevent side-welling light. Each individual, regardless of developmental treatment, experienced two trials—one in turbid and one in clear water—in randomized order; subsequent analyses confirmed that there were no order effects. These two trials were separated by 24–32 h. Each trial began with an initial acclimation period of 10 min followed by a 10-min assay period during which ‘baseline’ activity was assessed. Activity was scored as the number of lines over which a fish passed during each 10-min trial phase. Activity per se could be seen as a performance measure as it relates to foraging or general fish health, or may represent the level of vigilance or stress (see “Discussion” for further interpretation). Immediately following this first testing phase, 50 ml of predator kairomone was injected into the assay tank via a syringe connected to airline tubing attached to the side of the assay tanks (sides of attachment were randomized between trials). All kairomone was obtained by pulling water from a tank that contained a natural guppy predator, the pike cichlid (*Crenicichla frenata*), that was fed two guppies per day. 50 ml of fresh water was then injected to flush out any remaining kairomone. Predator-response trials were conducted for 10 min following introduction of the predator stimulus, and the following behaviors were scored from video: activity, freezing behaviors, and latency to resume swimming after initial cue insertion. Tanks were placed on top of a grid of

4 × 4 cm squares. Immediately following behavioral trials, fish were transferred back to developmental treatment tanks where they remained for 14–15 days before tissue collection.

Opsin expression

Tissue collection

Individuals were rapidly killed by an overdose of the anaesthetic tricaine methanesulfonate (MS-222). Both eyes from each individual were removed immediately, pierced to allow buffer penetration, placed in a vial of RNeasy[®] Stabilization Solution (Life Technologies[™]), and kept at 10 °C for 24 h to allow tissue to be saturated. After 24 h, vials were transferred to a −20 °C freezer until they were transported on ice from University of California-Davis to Simon Fraser University.

Tissue processing and analyses

RNA extraction, cDNA synthesis and qPCR reactions followed the methodologies and used the assays presented in Sandkam et al. (2015). Expression levels of nine opsins (three short wave-sensitive opsins [SWS1, SWS2A, SWS2B], two mid-wave-sensitive opsins [RH2-1 and RH2-2], and four long-wave-sensitive opsins [LWS-1, LWS-2, LWS-3, and LWS-R]; Table 1), one rhodopsin (RH1), and three housekeeping genes (beta actin, cytochrome *c* oxidase subunit I, and myosin heavy chain) were quantified for each individual using highly specific probe-based qPCR assays run in triplicate for each gene. All 39 reactions for each individual were run simultaneously on the same 384-well plate in addition to negative controls (UltraPure[™] water) for each assay. Each reaction consisted of 5 μL Brilliant III Ultra-Fast qPCR Master Mix (Agilent Technologies), 0.5 μL FAM labeled assay (Sandkam et al. 2015) and 4.5 μL of sample. All reactions were set up on ice and the plates were spun down before being run on an Applied

Biosystems[®] 7900HT qPCR machine (Life Technologies[™]). Since each assay was done in triplicate, outliers were removed when further than two standard deviations from the mean.

Two measures of expression were made for each opsin: proportional opsin expression, and relative to housekeeping genes (relative_(hk)). Differences in color vision are best observed in proportional measures of opsin expression: color images are formed by comparing the signals from different cone cell types, for which opsins are the major differentiating character. Thereby, proportional opsin expression acts as a measure of the ratio of the different cone cell types in the back of the retina (Fuller et al. 2004; Fuller and Claricoates 2011; Sandkam et al. 2015). Relative_(hk) measures of opsin expression show which opsins are being differentially regulated compared to overall gene activity (Fuller and Claricoates 2011). Proportional expression measures were calculated following Carleton and Kocher (2001), Fuller et al. (2004), and Sandkam et al. (2015), and relative_(hk) measures were calculated following Sandkam et al. (2015).

Statistical analyses

Behavior

Behavioral responses in both the baseline phase and the anti-predator phase were analyzed separately using generalized linear mixed models formatted with the lme4 package (Bates et al. 2014) in R (R Core Team 2014). We first tested whether assay conditions (turbid or clear) affected baseline behaviors within each treatment. To do this, we modeled activity for each treatment using trial and sex as fixed effects and developmental tank, assay tank, fish identity, and date as categorical varying effects. We then combined treatments and included an interaction between assay conditions (clear or turbid) and developmental treatment conditions to assess the degree to which individual fish differed in their activity and space use between trial conditions depending on their developmental treatment. We also assessed whether or not fish differed in activity between treatments in the assay conditions in which they were reared (clear developmental treatment fish assayed in clear water vs. turbid developmental treatment fish assayed in turbid water) by comparing activity from these groups with treatment and sex as main effects, using all varying effects aforementioned (except fish identity). Activity was recorded as count data (i.e., number of lines passed over) and was modeled using a Poisson distribution. A unique intercept was fit to each observation to account for overdispersion in the data (Bolker 2015). Model structure and output for baseline behaviors are presented in Table 2 (supplementary material).

Table 1 List of abbreviations

		Detection range
Opsins		
SWS1	Short wave-sensitive 1 opsin	Ultraviolet
SWS2	Short wave-sensitive 2 opsins	Blues and purples
RH2	Rhodopsin-like opsins	Greens
LWS	Long wave-sensitive opsins	Reds and oranges
Other		
HIREC	Human-induced rapid environmental change	–
NTU	Nephelometric turbidity unit	–

To analyze behavioral response variables after the introduction of a predator kairomone, a similar modeling approach was used, but with the presence/absence of the predator cue as an additional fixed effect. We first modeled activity with an interaction between predator exposure and treatment to test whether behavioral responses to an olfactory predator cue depended on treatment; this interaction was not significant, however, and was removed from the model. Time spent freezing and latency to resume movement after the introduction of the cue were modeled with Gaussian conditional distributions in a mixed model framework employing fixed and varying effects mentioned previously. Model structure and output for anti-predator behaviors are presented in Table 3 (supplementary material). In cases where zero variance was assigned to a particular varying effect (e.g., rearing tank in freezing model), this factor was removed to ensure model convergence. Removing those factors with zero variance did not change the estimates of any of the other factors in the model, nor did it affect inferences drawn from the models.

Opsin gene expression and light environment comparisons

Opsin gene expression was analyzed two ways: first as the proportional expression of each of the nine opsin genes relative to total opsin gene expression, and as the proportional expression of each of the nine opsin genes relative to housekeeping gene expression. To determine if opsin expression profiles differed by sex or treatment, individual MANOVAs were run on both proportional and relative_(hk) measures of opsin expression. When MANOVAs revealed opsin expression differed both by sex or treatment, individual ANOVAs were conducted for each of the opsin genes in order to identify which genes significantly contributed to the overall effect. Output from ANOVAs is presented in Table 4 (supplementary material).

Results

Baseline behaviors in turbid and clear assays

Fish raised in clear water exhibited a trend towards decreasing activity in turbid water assay conditions relative to clear water (estimate = -0.275 ± 0.149 , z score = 1.15, $p = 0.065$), while fish reared in turbid water trended towards higher activity in turbid water assay conditions than in clear water (estimate = 0.234 ± 0.140 , z score = 1.67, $p = 0.095$; Fig. 1). When data from both developmental treatments were analyzed together, there was a strong interaction effect of developmental treatment and assay conditions: changes in activity from clear to turbid assay conditions depended on developmental treatment

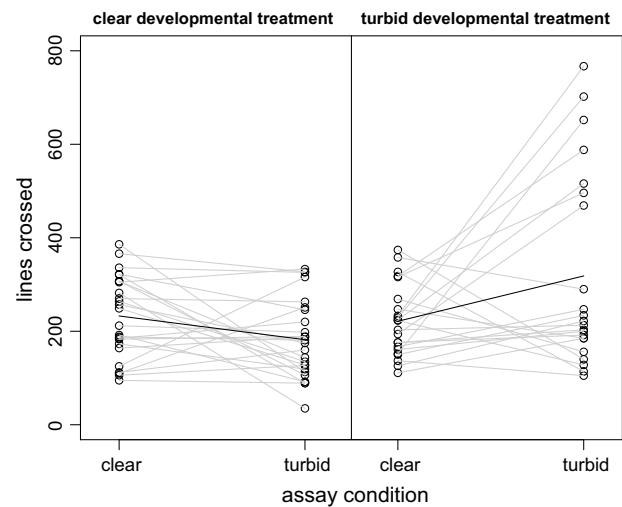


Fig. 1 Baseline activity as measured by number of lines a fish crosses during a 10-min assay in the absence of a predator cue. Grey lines connect multiple measurements per individual, and black lines connect mean activity levels across assay conditions

(estimate = 0.515 ± 0.190 , z score = 2.71, $p = 0.007$). Additionally, males were more active than females across assay conditions and treatments (estimate = 0.210 ± 0.097 , z score = 2.17, $p = 0.030$).

Anti-predator behaviors in turbid and clear assays

There was a strong effect of predator exposure on fish activity: fish of all developmental treatments and in all assay conditions decreased their average activity when predator cues were introduced to the assay tank (estimate = 0.397 ± 0.065 , z score = 6.10, $p < 0.001$; Fig. 2). Additionally, fish reared in turbid water were more active than those reared in clear water (estimate = 0.212 ± 0.099 , z score = 2.15, $p = 0.032$). Males were more active (estimate = 0.295 ± 0.098 , z score = 3.00, $p = 0.003$), froze less (estimate = -51.485 ± 15.717 , $t_{(46)} = -3.394$, $p = 0.001$), and showed a shorter latency to resume swimming after exposure to a predator cue (estimate = -34.044 ± 9.699 , $t_{(46)} = -3.510$, $p = 0.001$) than did females.

Light environment and opsin gene expression

Turbid water developmental tanks and clear water developmental tanks did not differ significantly in $\lambda p50$ (clear mean \pm SE = 575.876 ± 1.729 , turbid mean \pm SE = 576.066 ± 1.974 , Welch's $t_{(57)} = 0.072$, $p = 0.943$). Luminosity from overhead lighting (measured just above the water's surface) did not differ between treatment tanks (clear mean \pm SE = 0.004 ± 0.001 , turbid mean \pm SE = 0.006 ± 0.002 , Welch's $t_{(11)} = 0.746$, $p = 0.470$).

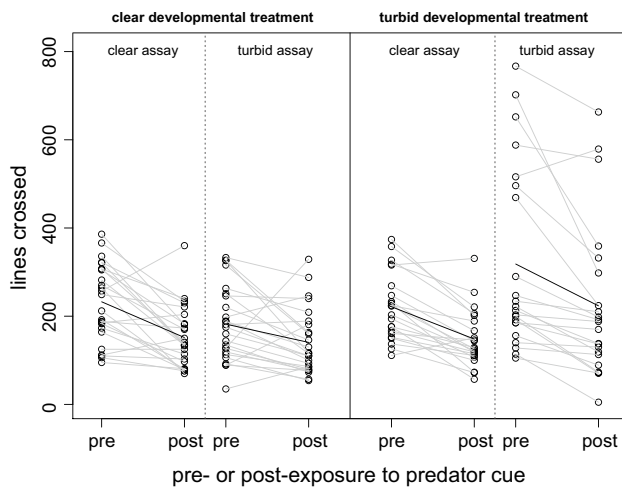


Fig. 2 Activity before and after the introduction of a predator cue to assay tanks for both treatments. Grey lines connect multiple trials for individuals. Black lines connect mean activity levels pre- and post-exposure to a predator kairomone. A reduction in average activity was observed in all treatment/assay combinations, with no difference detected across treatment types or assay conditions in the degree of activity reduction

Though $\lambda p50$ did not differ between treatments, we observed a marked shift in proportional opsin expression between treatments (Pillai's Trace: $F_{1,37} = 9.901$, $p < 0.001$; Fig. 3a) and sexes (Pillai's Trace: $F_{1,37} = 3.542$, $p = 0.005$). Table 3 (supplementary material) summarizes ANOVA results assessing treatment and sex differences in both proportional opsin expression and opsin expression relative to housekeeping gene expression for each of nine opsins. Treatment differences were driven by a decrease in proportional opsin expression from 0.29 to 0.15 (± 0.04 and 0.02 SE) in RH2-1 ($F_{1,37} = 9.083$, $p = 0.005$), from 0.003 to 0.001 (± 0.0009 and 0.0003 SE) in LWS-2 ($F_{1,37} = 5.732$, $p = 0.022$), and from 0.004 to 0.0007 (± 0.001 and 0.0002 SE) in LWS-R ($F_{1,37} = 5.732$, $p = 0.022$), and a proportional increase in RH2-2 from 0.23 to 0.32 (± 0.03 and 0.02 SE) ($F_{1,37} = 7.860$, $p = 0.008$) and LWS-3 from 0.09 to 0.23 (± 0.02 and 0.04 SE) ($F_{1,37} = 12.041$, $p = 0.001$) from clear to turbid developmental treatments. Additionally, females showed higher expression of LWS-2 ($F_{1,37} = 7.375$, $p = 0.010$) and RH2-1 ($F_{1,37} = 5.647$, $p = 0.023$) compared to males, whereas males showed greater proportional expression of RH2-2 ($F_{1,37} = 7.048$, $p = 0.012$).

Additionally, there was an overall difference between treatments in total opsin expression relative to housekeeping genes (Pillai's Trace: $F_{1,37} = 16.097$, $p < 0.001$), as well as between sexes (Pillai's Trace: $F_{1,37} = 4.109$, $p = 0.002$). This change relative to housekeeping genes was driven by an overall increase in LWS-2 gene transcripts ($F_{1,37} = 4.736$, $p = 0.036$) and a decrease in RH2-1

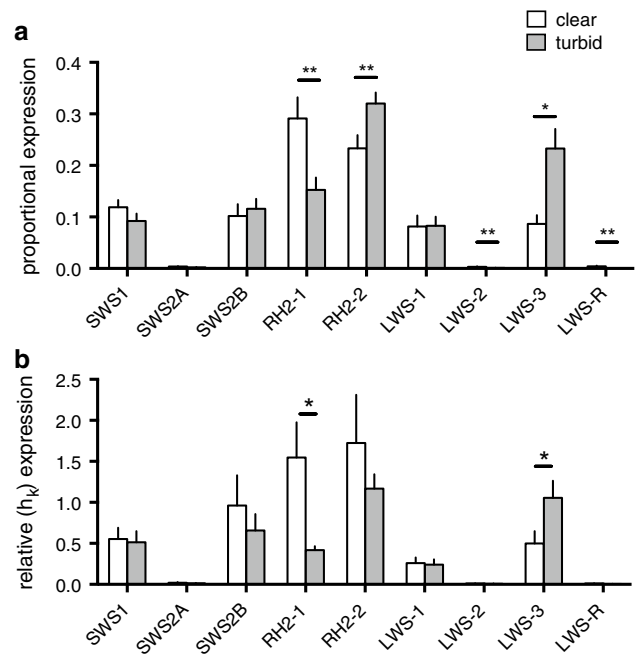


Fig. 3 **a** Proportional opsin expression in clear and turbid water developmental treatments for each of the nine guppy opsin genes, and **b** opsin expression relative to housekeeping genes for each of the nine opsin genes. Opsin classes (SWS, RH2, and LWS opsins) are arranged along the x axis in order of peak sensitivities from shortest to longest wavelengths. Sexes are grouped here, but did show differences in expression for some opsin genes (see Table 3, supplementary materials). Asterisks denote significant treatment differences

transcripts ($F_{1,37} = 7.349$, $p = 0.010$; Fig. 3b) in turbid vs. clear water developmental treatments. Sex differences were also detected in opsin expression relative to housekeeping genes of RH2-1: males showed greater relative expression ($F_{1,37} = 4.766$, $p = 0.035$).

Discussion

Taken together, our results demonstrate that fish living in turbid streams may be able to cope with otherwise visually obscured environments by increasing activity and restructuring their visual system. This represents multi-dimensional developmental plasticity that may allow for more integrated phenotypic responses in the face of human-induced rapid environmental change (Snell-Rood 2013).

Behavior in turbid water

Our study is one of the first to show effects of development in turbid water on adult fish behavior (also see Gray et al. 2012): although most previous studies document either no change (Ran aker et al. 2012) or a decrease (Leahy et al. 2011; Borner et al. 2015) in baseline activity for adult fish

placed (but not reared) in turbid water, we demonstrate a strong interactive effect of developmental rearing conditions and assay conditions on activity. That is, fish behavior in turbid versus clear water depended on whether they were reared in turbid versus clear water. This result underscores the general importance of considering developmental rearing conditions in determining behavioral responses to changing environments (Chapman et al. 2010).

It is notable that fish decreased baseline activity in whichever environment was novel with respect to their developmental treatment condition. Since decreasing baseline activity is often a response to stressors (Walls et al. 1990; Schreck et al. 1997), it is possible that novel assay conditions were stressful for fish. In turbid water, encounter rate with an organism's environment (e.g., habitat, conspecifics, prey) is likely decreased, since the visual range of fish in these environments is diminished (Vinyard and O'Brien 1976; De Robertis et al. 2003). By increasing activity in turbid water (as observed in turbid water developmental treatment fish), a fish could maintain a certain encounter rate with salient factors in its environment (Gerritsen and Strickler 1977), as has been observed in chinook salmon (*Oncorhynchus tshawytscha*; Gregory and Northcote 1993), perch (*Perca fluviatilis*; Granqvist and Mattila 2004), and Atlantic cod (*Gadus morhua*; Meager and Batty 2007). Thus, it may be that guppies reared in turbid water increased activity to maintain encounter rates with prey. Indeed, turbid treatment guppies did not differ in mass or length compared to clear treatment guppies, suggesting that encounter rates with prey were maintained. Fish were fed once daily with ample food; hence, future studies should consider the role of food limitation in behavioral compensation (i.e., increasing activity) in visually obscured environments.

Long-wavelength sensitivity and opsin expression

While guppies might cope with diminished visual fields by increasing activity to maintain prey encounter rates, we have also demonstrated that guppies restructure the composition of opsins in their retina depending on developmental rearing conditions. Guppies reared in turbid water exhibited an overall increase in the proportional expression of longer wavelength-sensitive opsins and a concomitant decrease in the expression of mid-wavelength-sensitive opsins. Though we observed an increase in expression of two opsin genes (LWS-1 and LWS-R) in clear vs. turbid environments, expression of these opsins accounted for only ~0.5 % of total opsin expression in clear environments. For long wave-sensitive opsins in aggregate (LWS-1, LWS-2, LWS-3, LWS-R), expression increased by ~14 % in guppies that experienced turbid conditions during development. This shift was observed despite no change in λ_{p50} between clear and turbid water.

Long-wavelength sensitivity has been shown to be important in motion detection for a number of fish species (Schaerer and Neumeier 1996; Krauss and Neumeier 2003), including the guppy (Anstis et al. 1998; Cole and Endler 2015). Additionally, foraging efficiency was improved under long-wavelength lighting environments in cutthroat trout (*Oncorhynchus clarkii*) and Dolly Varden trout (*Salvelinus malma*), emphasizing the important role of long wavelength light in motion detection (Henderson and Northcote 1985). Thus, we propose that the proportional increase of long wave-sensitive opsins associated with development in turbid water functions to maintain or enhance the ability to detect motion in turbid environments.

Multi-component developmental plasticity in turbid water

Increasing activity to maintain encounter rates with the environment as well as improving motion detection abilities by increasing the proportion of LWS opsins in the retina may jointly aid in maintaining foraging rates and avoiding predators. Such a rearrangement of the opsin composition in the retina paired with the potential of behavioral compensation for decreased visual fields (i.e., increases in baseline activity) suggest that developmental plasticity in turbid water may allow for greater phenotypic integration in turbid water than activational plasticity would allow for alone. Furthermore, research using three-spined sticklebacks reveals that opsin expression, while developmentally plastic, is not plastic during adulthood (Flamarique et al. 2013; similar research with guppies, however, has not been conducted). This relates to the idea that phenotypes may be more costly to change once developed (DeWitt et al. 1998), explaining why cues received earlier in development result in a greater range of integration for adult phenotypes. In the context of environmental change, responses to instant environmental change as an adult may favor activational plasticity, whereas environmental change that occurs and is stable through development may allow for developmental plasticity (Snell-Rood 2013). Due to the rapid nature of human-induced environmental change, a high degree of non-reversible developmental plasticity for long-lived organisms might portend evolutionary and ecological traps (Schlaepfer et al. 2002; Robertson et al. 2013), but for short-lived organisms such as guppies, developmental plasticity may occur on a short enough timescale to promote the formation of integrated adult phenotypes well-suited to cope with environmental change. Specifically regarding turbidity in Trinidadian streams, all guppies must deal with seasonal fluctuations in turbidity due to pulses of sedimentation during rains, but reaches of some streams are turbid much of the year due to human activity (e.g., rock quarrying and deforestation)—long enough to remain turbid

through the entire development of guppies through adulthood (SME, unpublished data).

Anti-predator behavior in turbid water

We did not detect an effect of rearing or assay conditions on the degree to which guppies decrease activity in response to an olfactory predator cue: fish in all developmental treatments and assay conditions reacted equally as strongly to predator cue. Fish reared in turbid water were generally more active than fish reared in clear water during the predation trial. This may represent a decrease in perceived risk for turbid developmental treatment guppies, since turbidity may offer a refuge from predators that rely on sight (Gregory and Levings 1998; Lehtiniemi et al. 2005). If turbid developmental treatment guppies are safer in turbid water when predators are present due to decreased abilities for predators to detect prey, they may doubly benefit by having increased motion detection abilities (due to increase in LWS opsin expression) compared to fish reared in clear water. A previous study found that guppies reared in clear water shoaled less and were less active in highly turbid water (e.g., ≥ 100 NTU), though not in moderately turbid water (e.g., 50 NTU), after exposure to a simulated aerial predator strike (Kimbell and Morrell 2015). The role of developmental plasticity was untested in this previous study, but developmental compensation within the visual system, as we suggest occurs via shifts in LWS opsin expression, may also have important consequences for the maintenance of important vision-dependent anti-predator behaviors such as shoaling. While we have shown that turbidity affects a common prey species in Trinidadian streams, future studies should incorporate effects of turbidity on major predators if we are to understand how turbidity affects predator–prey interactions. Increasing turbidity may decrease predation if predators are less able to locate prey under cover of turbidity (Miner and Stein 1996; Abrahams and Kattenfeld 1997; Gregory and Levings 1998). Conversely, asymmetries in the abilities of predators and prey to detect one another (Wenger et al. 2013), or constraints on prey recognition of predators and learning in turbid water (Ferrari et al. 2010) may result in greater predation.

Previous studies have shown sensory compensation (a behavioral shift towards using information from one sense, e.g., olfaction) in predation contexts by fish when information from another sense (e.g., vision) is lacking (Hartman and Abrahams 2000; Heuschele et al. 2009; Leahy et al. 2011). Most studies purporting sensory compensation measure responses as behavioral shifts in reaction to multiple cue types of interest when organisms are placed in environments where information from one sense is eliminated or obscured. While this sort of activational sensory compensation is likely an important rapid response to

instant environmental change, sensory compensation may also occur on a developmental timescale. Furthermore, if developmental plasticity restructures sensory systems in novel environments (as we have documented), compensation may occur within sensory modalities, minimizing the need for compensation by other senses. Changing the tuning of sensory systems rather than relying on fewer senses via sensory compensation could be useful since multi-modal signals may be less prone to error or uncertainty, or provide useful non-redundant messages (Munoz and Blumstein 2012).

Further study and concluding remarks

Though we have demonstrated marked developmental plasticity in opsin gene expression and behavior in turbid water, the fitness consequences of such plasticity remain unstudied; thus, current research is underway to examine these fitness consequences for guppies living in turbid water. As such, we are presently unable to say whether the plasticity that we have documented is adaptive. Adaptive or not, such drastic changes in multiple traits through development are likely to be of consequence given the importance of vision and visually mediated behaviors in the lives of guppies. Further work is needed in this system to determine whether behavioral and developmental plasticity is adaptive in novel environments; indeed, a major guiding question in research dealing with responses to novel environments asks whether changes—plastic or otherwise—are not only adaptive but also sufficient (Wong and Candolin 2015). Despite over half a century of work conducted on the Trinidadian guppy in both predator–prey and sexual selection research (reviewed in Houde 1997; Magurran 2005), however, we are uncertain exactly how increasing turbidity affects such ecological interactions. Increasing turbidity may affect the ability of some aquatic species to assess mates (Seehausen 1997; Engström-Öst and Candolin 2007), or maintain sufficient foraging rates (Gardner 1981). Increased activity required to forage or find mates may thus affect the trade-off between foraging and/or courting and avoiding predation (Sih 1992). In a mating context, differences in color vision, especially with respect to the LWS opsins, have been linked to differences in female preferences such that females with stronger preferences for red/orange have higher LWS expression (Sandkam et al. 2015). Since increasing turbidity leads to increases in LWS expression through development, female mate preferences for red/orange males may be affected as a side effect of the up-regulation of these opsins to maintain motion detection abilities. As aforementioned, turbidity may also affect predator–prey interactions depending on the relative effects of turbidity on predators and prey. Hence, it is crucial to consider how novel environmental stressors such as

increasing turbidity affect ecological interactions if we are to understand the overall effects of such changes on species and community ecology (Wong and Candolin 2015). Since we have shown that rearing conditions dramatically change aspects of behavior and sensory systems in a novel turbid environment, we also stress the importance of considering developmental plasticity in mediating behavioral responses and species interactions under human-induced rapid environmental change.

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