



Foraging guppies can compensate for low-light conditions, but not via a sensory switch

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Abstract

Animals can adapt to changes in their environment through behavioural or developmental plasticity, but studies of these responses tend to focus on either short-term exposure of adults to the changed conditions, or long-term exposure of juveniles. Juvenile guppies *Poecilia reticulata* reared in low-light environments have previously been shown to make a sensory switch to using olfactory, rather than visual, cues in foraging. It is not clear whether this compensatory sensory plasticity is limited to juveniles, or whether longer term exposure allows adults to similarly adapt. We investigated how adult guppies that were exposed to light or dark environments for 2 and 4 weeks responded to visual, olfactory and a combination of both food cues, in both dark- and light-test environments. We found that after 2 weeks of exposure, adult guppies were better able to locate a food cue in light test environments regardless of their exposure environment. After 4 weeks, however, guppies were more successful at locating the food cue in the environment they had been exposed to, suggesting that dark-exposed guppies adapted their behaviour in response to their environment. We found that foraging was most successful when both visual and olfactory cues were available and least successful in the presence of olfactory cues, suggesting that the mechanism behind the change in success for dark-exposed guppies was not due to increased reliance on, or sensory switch to olfactory cues.

Significance statement

Human-induced environmental change often acts to disrupt an animal's sensory environment. For example, turbidity can degrade the visual environment, resulting in reduced foraging rates in fish. Juvenile guppies (*Poecilia reticulata*) can compensate for the reduced visual information available in low-light environments through developmental changes that allow them to rely on an alternative sense, olfaction. This ability, however, may be limited to a critical developmental window, or possible throughout life. Here, we show that while adult guppies are generally better able to locate food resources in well-lit environments, after four (but not two) weeks living under low-light conditions, fish were better able to find food in dark environments than in the light. However, unlike juvenile fish, they did not seem to be relying more on olfactory cues to do so.

Keywords Sensory plasticity · Environmental change · Foraging behaviour · Compensatory plasticity · Learning

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Introduction

Animals are often able to respond to sudden, short-term changes in their environment by altering behaviour, an extremely plastic trait. Behavioural plasticity (also known as contextual or activation plasticity; Stamps and Groothuis 2010; Snell-Rood 2013; Stamps 2016) allows animals to minimise negative consequences of a stressful environment and is usually the first response to altered environmental conditions (Tuomainen and Candolin 2011; Candolin and Wong 2012). Anthropogenic environmental change frequently disrupts an organism's sensory environment; increased noise created by roads can affect auditory communication in birds

(Slabbekoom and Peet 2003) and eutrophication or turbidity in lakes degrades the visual environment, reducing foraging rates and impacting on a range of other behaviours in fishes (e.g. Heubel and Schlupp 2006; Meager et al. 2006; Candolin et al. 2007; Sundin et al. 2010; Fischer and Frommen 2012; Borner et al. 2015).

Adult fish can adjust their behaviour in response to rapid changes in the visual environment: in turbid water, male threespine sticklebacks (*Gasterosteus aculeatus*) increase the frequency of mating displays and display more intense red colouration (Candolin et al. 2007; Engström-Öst and Candolin 2007), while juvenile cod (*Gadus morhua*) increase searching activity for food sources (Meagre and Batty 2007). Adult fish may also be able to compensate for reduced visual information by increasing their reliance on an alternative sense. For example, threespine sticklebacks can maintain foraging rates by using olfactory cues after relatively short acclimatisation periods (Webster et al. 2007; Johannesen et al. 2012; but see also Sohel et al. 2017), suggesting that these individuals are able to cope to some extent with short-term losses in vision by altering behaviour. However, behavioural plasticity can be limited, particularly if stressors in the environment increase, become permanent, or the animal is unable to effectively move away from the stressor (Schwartz et al. 2006; Thomas 2011).

Exposure from birth allows for an alternative mechanism by which animals can adapt to degraded environments, through adaptive developmental or compensatory plasticity (Rauschecker 1995; West-Eberhard 2003; Monaghan 2008; Nettle and Bateson 2015; Stamps 2016). This type of plasticity is often costlier and less flexible than behavioural plasticity and can be dependent on a critical developmental window (Bateson 1979; West-Eberhard 2003; Knudsen 2004; Stamps 2016). Compensatory sensory plasticity occurs when experience of a degraded sensory environment leads to an increased capacity of an alternative sense (Rauschecker and Kniepert 1994), and has been well documented in juvenile animals, including cats (*Felis catus*; Rauschecker 1995), rats (*Rattus norvegicus*; Ryugo et al. 1975) and humans (*Homo sapiens*; Röder et al. 1999). Guppies (*Poecilia reticulata*) reared from birth in a low-light environment, for example, make a sensory switch from vision to olfaction when detecting food cues, enabling them to maintain foraging rates (Chapman et al. 2010b).

Studies of plasticity in responses of fish to changed environments tend to focus either on long-term rearing of juveniles (Chapman et al. 2009, 2010a, b; Ehlman et al. 2015; Sakai et al. 2016; Wright et al. 2018) or short-term exposure of adults (Ward et al. 2008; Johannesen et al. 2012, 2014; Fischer and Frommen 2013; Kimbell and Morrell 2015a, b). Costly behaviourally plastic responses, such as increased activity (juvenile cod (*G. morhua*); Meager and Batty 2007) may be effective in the short term, but not sustainable over longer timescales, while mechanisms such as learning (Odling-Smee

and Braithwaite 2003; Dukas 2013), physiological or morphological changes (Webster et al. 2011) may allow responses to be maintained or improved. However, developmental plasticity may constrain individuals, should the environment to which individuals are adapted change later in life (Padilla and Adolph 1996; Metcalfe and Monaghan 2001; Zimmerman et al. 2001; Monaghan 2008; Fuller et al. 2010; Brust et al. 2014).

Here, we explore whether exposure to an altered environment over a period of several weeks can result in the development of compensatory responses in adult, rather than juvenile, fish. We explore the following hypotheses:

a) Developmental plasticity hypothesis

Firstly, if adult guppies exposed to low-light environments are able to compensate for reduced visual information in low-light conditions through plastic responses, we predict increased foraging success (measured by ability to locate a food cue) in low-light environments relative to guppies that have not previously experienced low-light environments.

b) Sensory compensation hypothesis

Secondly, if sensory compensation can occur at any age, and is not limited to a critical developmental window early in life (Bateson 1979; West-Eberhard 2003; Knudsen 2004; Stamps 2016), we would see this as a switch from reliance on visual to olfactory cues that has previously been seen in juveniles (Chapman et al. 2010b).

c) Developmental constraint hypothesis

Finally, if adult guppies are not able to adapt to low-light environments even after several weeks, this suggests that developmental plasticity constrains their ability to respond (Padilla and Adolph 1996; Metcalfe and Monaghan 2001; Zimmerman et al. 2001; Monaghan 2008; Fuller et al. 2010; Brust et al. 2014).

Methods

Study species and exposure environments

All fish used in this experiment were descendants of wild-caught guppies (*P. reticulata*) from Trinidad. Stock tanks of guppies were maintained in aquaria (20 × 40 × 40 cm) at the University of Hull at ~26 °C on a 12:12-h light:dark cycle and fed daily on ZM fine sinking food by aquarium technical staff (ZM Systems, Hampshire, UK).

Two hundred fifty-two male and female guppies over 10 mm in standard body length were randomly assigned to one of two light intensity exposure environments: relatively high light intensity (~300 lx; “light exposure environment”) and relatively low light intensity (~1.5 lx; “dark exposure

environment”). Ten millimetres is the minimum standard length at which males and females in the laboratory population began to show differentiation in the anal fin that allows the sexes to be distinguished before male colouration emerges. Only fish that could be confidently identified as male or female (and were therefore likely to be sexually mature; generally occurring by 7 weeks for males and between 10 and 20 weeks for females; Magurran 2005) were used. Body length was not recorded at the start of the experiment, but mean \pm SD of standard body length at 2 weeks was 16.0 ± 1.5 mm for males and 17.7 ± 3.3 mm for females, and at 4 weeks was 16.1 ± 2.2 mm for males and 18.2 ± 3.8 mm for females. Females were thus significantly larger than males (unequal variance *t* tests: 2 weeks: $t = 4.80$, $df = 143.95$, $p < 0.001$; 4 weeks: $t = 4.56$, $df = 124.39$, $p < 0.001$).

The dark exposure level and terminology was chosen to match Chapman et al. (2010b), where 1.545 ± 0.11 lx was sufficient to induce compensatory sensory plasticity in juvenile guppies. Exposure tanks measured $20 \times 20 \times 20$ cm, contained an artificial plant and were held in our aquarium facility on a 12:12-h light:dark cycle, such that all fish (light and dark exposure environments) experienced complete darkness for 12 h per day. The light exposure environments were under normal aquarium room lighting, while the dark exposure environments were created by turning off the aquarium lights directly above the tanks (but leaving the room lights on the specified light cycle), and isolating the tanks from the main room using a thin black polycotton sheet. To control for the positioning of the sheet, light tanks were isolated from the room by a thin white sheet. All exposure tanks (light and dark) were kept on the same circulating aquarium system with a 10% daily water change using a 50:50 mixture of purified water and filtered tap water. To minimise algae growth (which may otherwise be used as a food source), UV filters were used on the system, and all tanks were carefully cleaned twice weekly and the aquarium plants changed weekly to prevent algae build up. This caused minimal disturbance to the fish.

Fish were placed into the exposure tanks at an initial density of six fish per tank (three males and three females) and fed twice a day with crushed ZM flake food using a 5×2 mm spatula to ensure each tank received an equal quantity of food. Fish were fed flake food during exposure to allow them to become familiar with the food used in the trials (see below). Fish were held in the exposure tanks for a total of 4 weeks. After 2 weeks, fish were removed from the tanks and randomly assigned to a cue treatment (visual cues only, olfactory cues only or both) for the foraging experiment (see below). Each fish was tested individually in light- and dark-test environments, with 24 h between trials before being returned to the tank. The same fish were then exposed for a further 2 weeks, for a total of 4 weeks. We carried out 21 replicates (21 groups of 6 fish = 126 fish) for each of light and dark exposure environments.

Foraging experiment

Foraging trials used a similar methodology to that in Chapman et al. (2010b). Trials took place in a rectangular plastic tank ($40 \times 25 \times 15$ cm) filled to a depth of 5 cm with water taken from the aquarium system. At one end of the tank, two solid, transparent cylindrical containers (diameter 7.5 cm, height 10 cm) also filled to a depth of 5 cm were fixed to the base of the tank. They were positioned in the corners of the tank with a minimum distance of 10 cm between them. The cylinders contained visual cues from food during the relevant trials, and contained no food during trials that did not involve visual cues. No olfactory cues were able to pass from the cylinders to the test tank. A 3-cm preference zone was drawn around each container. Two plastic clips were placed on the outside of these containers, which held tubes to allow for olfactory cues to enter the test tank below the water line, during the relevant trials. Twelve centimeter from the opposite end of the tank, a horizontal “start line” was drawn, dividing the tank into two sections (a starting section and a choice section).

The experimental tank was housed within a wooden shelter ($70 \times 50 \times 65$ cm) with an open front and an opening directly above the tank where a Panasonic SDR S26 video camera was placed, so fish could be observed without disturbance. The video camera was connected to a laptop, and data recording took place in real time. An aquarium light attached to a clamp stand was placed inside the shelter to ensure the light trial environments received a similar light intensity as the light exposure environment. In the dark trials, this was switched off and the “colour night view” mode on the video camera was used, which allowed the fish to be observed. The shelter was then covered with a black (dark trials) or white (light trials) polycotton sheet to both ensure the correct light intensity and minimise disturbance to the fish during the trials.

Visual cues were created by placing 0.2 g of crushed flake food (ZM fish food; following Chapman et al. 2010b) onto the surface of the water of one of the containers, using a funnel from outside the wooden shelter to minimise disturbance. Olfactory cues were created by mixing 10 g of flake food in 1 l of purified water and filtering this through a fine mesh to remove any visual cues. A control cue was made up of 1 l of purified water with 0.2 ml of yellow food dye (to match the colour of the food cues). These cues were dispensed via a peristaltic pump that released the cues through tubes connected to the cylindrical containers at a rate of 6 ml per minute. An overflow pipe was placed 5 cm above the base of the tank at the end of the tank opposite the cue cylinders to maintain a constant water level. For the visual-only and olfactory-only treatments, only the relevant cue was added. For the both cues treatment, both visual and olfactory cues were added at the same side. The side containing the cues was randomised.

Experimental protocol

Twenty-four hours prior to experiments, all fish within an exposure tank were placed into two holding tanks ($40 \times 20 \times 20$ cm), both separated into three equal-sized compartments (each $13 \times 20 \times 20$ cm) and fed. Compartments were separated with clear perforated barriers, which allowed visual and olfactory communication between the test fish, to reduce possible stress caused by separation from conspecifics. Each of the six fish were randomly assigned to a cue treatment (two visual, two olfactory and two both, but such that one male and one female was assigned to each), and tested in both light- and dark-test environments, separated by 24 h. An hour before each trial, the fish were acclimatised to the trial-lighting conditions by placing them in a separate small tank ($20 \times 20 \times 20$ cm). At the start of each trial, an individual was placed in the test tank and given 2 min to explore the tank. After the acclimatisation period, and once the fish had returned to the start section, the food cues were added. The trial began when the fish subsequently crossed the start line. Each trial lasted 5 min.

Using the video camera to directly observe the fish, we recorded (using two stopwatches) the time in seconds spent in the preference zones of both the cue and control cylinders, from which we calculated the proportion of this time spent with the cue (Chapman et al. 2010b). At the end of the 5-min trial, fish were returned to their holding tank compartment, allowing us to track individual fish between the two trials in different test environments. When the trials for each set of fish were completed, the fish were fed. They remained in the holding tanks for a further 24 h to allow them to be retested under the alternative lighting environment. After the second trial, fish were measured to the nearest mm, released

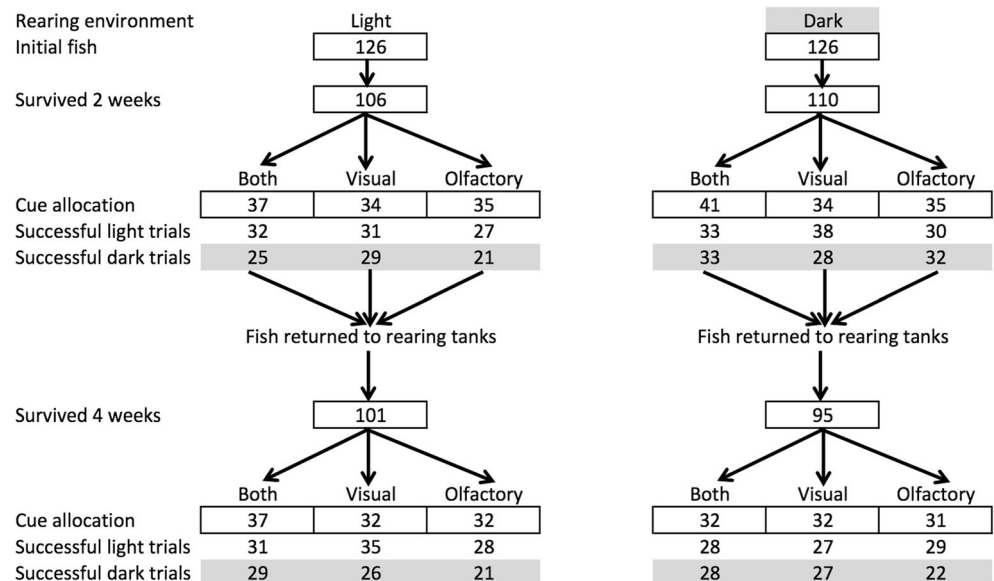
into their home tank and fed. Fish were tested after 2 weeks in their exposure tanks and again at 4 weeks. Individuals were not marked or tagged, so we were unable to track individuals between the 2-week and 4-week trials. The order the fish experienced light- and dark-test environments was alternated. The tank was emptied and rinsed with conditioned water from the aquarium system between each experiment to remove any olfactory cues from food or the previous fish. We carried out a total of 432 trials on 216 individual fish at 2 weeks, and 392 trials on 196 fish at 4 weeks. Due to logistical constraints and the complexity of the experiment, observers were not blind to the rearing environment or rearing duration experienced by the test fish, and could not be blind to test environment or the presence/absence of visual cues. Fish that failed to enter both control and cue zones or did not cross over the start line were removed from the analysis (2 weeks: $n = 73/432$ trials and 4 weeks: $61/392$ trials). Twenty fish died between the 2- and 4-week testing (light exposed, 5; dark exposed, 15). Figure 1 shows schematically how fish moved through the experiment, and gives final sample sizes for each combination of rearing environment, cue availability, test environment and exposure duration.

Statistical analysis

Data were analysed using R version 3.3.2 (R Core Team 2016).

Firstly, to confirm that the fish could distinguish the cue cylinders from the control cylinders, we carried out one-sample *t* tests to assess whether the proportion of the time spent with the cue differed from 0.5 (random expectation). Proportion data were arcsin transformed prior to analysis to meet the assumptions of normality of residuals. To assess the

Fig. 1 Schematic diagram indicating the sample sizes at each stage of the experiment. Dark shading represents dark environments, light shading represents light environments



both and visual only cue treatments, we used only data from fish exposed for 2 weeks to light environments, and tested in the light. For the olfactory cues, we used fish that had spent 4 weeks in the dark exposure environment, as these would be predicted to be the most likely to rely on olfactory cues in foraging.

We used linear mixed effects models to assess the effect of rearing environment (light or dark), test environment (light or dark), cue treatment (both, visual only, olfactory only) and exposure duration (2 or 4 weeks) on the proportion of time spent with the cue. We included sex and size as main effects to control for any effects of these characteristics on foraging behaviour. The assumptions of the model were checked via visual inspection of plots of residuals and quantile-quantile plots, and consequently, proportion data were arcsin transformed prior to analysis. Rearing tank was added as random effects to account for the possible non-independence of individuals from the same exposure tank, but because individuals could not be reliably tracked between 2 and 4 weeks, individual identity could not be included as an additional random effect. Thus, our model was more conservative than if individuals could have been tracked, as between-individual variability could not be accounted for. Following this, we carried out the same analysis for 2- and 4-week exposures separately, this time additionally including individual identity (nested within rearing tank) as a random factor to control for the repeated testing of the same individuals in both light and dark environments separated by 24 h. Nonsignificant two- and three-way interactions were removed from the models following Crawley (2007), and the minimum adequate models containing all main effects and significant interactions are presented here.

Finally, we used proportion tests to compare the proportion of successful trials in dark- and light-test environments, each combination of exposure environment and duration, to explore whether there was an effect of light and test environment on propensity to forage.

Results

Fish exposed to light environments for 2 weeks and tested in light environments could successfully detect the cues in the visual and both cue treatments, spending a greater proportion of time with the cue cylinder than expected by chance (one-sample *t* tests: both cues: $t = 6.327$, $df = 26$, $p < 0.001$; visual cues: $t = 7.839$, $df = 30$, $p < 0.001$). Fish exposed to dark environments for 4 weeks and tested in the dark spend more time with the olfactory cue cylinder than expected by chance (one-sample *t* test, $t = 3.133$, $df = 21$, $p = 0.005$), indicating that fish could successfully detect the cues in the conditions in which they would be expected to do so.

When considering both 2- and 4-week exposure durations together, we found a significant interaction between test environment and exposure duration (Table 1a). Fish tested in light environments located the cue more successfully, but less so after 4 weeks than after two (Fig. 2). In addition, fish foraged more successfully when both visual and olfactory cues were available than when only one of the cues was available. To further explore why fish should spend less time associating with the cue in light environments after 4 weeks, we analysed the two exposure durations separately. After a 2-week exposure duration, we found significant effects of test environment and cue treatment, but not exposure environment, on the proportion of time spent with the food cue (Table 1b). Fish spent a greater proportion of time with the cue in the light environment, and when both visual and olfactory cues were available (Fig. 3a, c, e). There was no effect of exposure environment and no significant interactions. After a 4-week exposure duration, we found a significant two-way interaction between exposure environment and trial-test environment (Table 1c). Fish spent a greater proportion of time with the cue in the test environment they were previously exposed to, irrespective of cue availability. Guppies exposed to light environments spent a greater proportion of time with the food cue in light environment trials and dark-exposed guppies spent a greater proportion of time with the cue under dark trial conditions (Fig. 3b, d, f). There was also a marginally significant effect of sex, with males spending a lower proportion of time with the cue than females.

Fish exposed to light environments for 2 or 4 weeks were significantly more likely to participate in the trial (generate data) in light-test environments than in dark-test environments (2 weeks: 90/106 (84.9%) fish in light-test environments vs. 75/106 (70.7%) in dark-test environments, proportion test, $\chi^2 = 5.358$, $df = 1$, $p = 0.021$; 4 weeks: 94/101 (91.8%) vs. 76/101 (75.2%), proportion test, $\chi^2 = 10.731$, $df = 1$, $p = 0.001$). In contrast, fish exposed to dark environments for 2 or 4 weeks were equally likely to generate data in dark- and light-test environments (2 weeks: 101/110 (91.8%) vs. 93/110 (84.5%), proportion test, $\chi^2 = 2.137$, $df = 1$, $p = 0.144$; 4 weeks: 84/95 (88.4%) vs. 77/95 (81.1%), proportion test, $\chi^2 = 1.467$, $df = 1$, $p = 0.226$).

Discussion

We found that after 4 weeks exposure to a light or dark environment, guppies foraged more successfully in the environment in which they had previous been exposed, and when both visual and olfactory cues were available. A 2-week exposure was not sufficient for this to occur, and all guppies foraged more successfully in light environments. This suggests that over the period of exposure, guppies developed some adaptation to their exposure environment allowing them

Table 1 Summary of the linear mixed effects models for (a) all weeks, (b) 2 weeks and (c) 4 weeks. The intercept represents the dark rearing environment and dark-test environment with both cues available, and at 2 weeks ((a) only)

	Value	Std error	df	<i>t</i>	<i>p</i>
(a) Both exposure durations					
(Intercept)	0.681	0.085			
Exposure environment: light	-0.041	0.028	40	-1.474	0.148
Test environment: light	0.076	0.034	623	2.261	<i>0.024</i>
Cue: visual	-0.098	0.030	623	-3.238	<i>0.001</i>
Cue: olfactory	-0.149	0.030	623	-4.923	<i>< 0.001</i>
Week: 4	0.076	0.036	623	2.076	<i>0.038</i>
Sex: male	-0.013	0.026	623	-0.518	0.604
Body size	0.006	0.004	623	1.254	0.210
Test (light) × week (4)	-0.100	0.049	623	-2.046	<i>0.041</i>
(b) Two weeks					
(Intercept)	0.695	0.121			
Exposure environment: light	-0.035	0.035	38	-0.978	0.334
Test environment: light	0.072	0.032	140	2.221	<i>0.028</i>
Cue: visual	-0.091	0.043	168	-2.117	<i>0.038</i>
Cue: olfactory	-0.135	0.043	168	-3.168	<i>0.002</i>
Sex: male	0.050	0.036	140	1.139	0.167
Body size	0.003	0.007	140	0.403	0.687
(c) Four weeks					
(Intercept)	0.817	0.123			
Exposure environment: light	-0.139	0.056	38	-2.493	<i>0.017</i>
Test environment: light	-0.108	0.047	121	-2.278	<i>0.025</i>
Cue: visual	-0.115	0.045	152	-2.547	<i>0.012</i>
Cue: olfactory	-0.167	0.046	152	-3.666	<i>< 0.001</i>
Sex: male	-0.079	0.039	121	-2.012	<i>0.046</i>
Body size	0.008	0.007	152	1.183	0.239
Exposure (light) × test (light)	0.169	0.067	121	2.512	<i>0.013</i>

Significant *p* values are highlighted in italics

to forage more successfully in that test environment. However, both dark- and light-exposed fish showed similar responses to the different cue types.

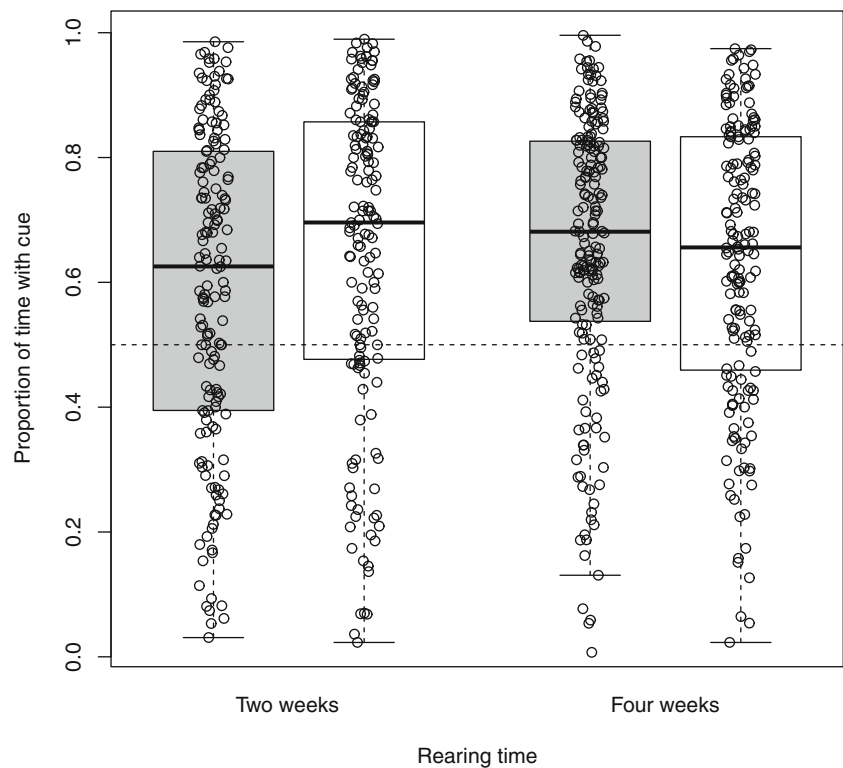
There was no evidence that this increased success in dark environments for dark-exposed fish was due to compensatory sensory plasticity, where individuals compensate for decreased vision by increasing reliance on olfactory cues, as previously seen in juvenile guppies (Chapman et al. 2010b). Dark-reared fish were most successful foraging when both visual and olfactory cues were available, and their success in locating the cue was lowest in the olfactory-only treatment. The brains of fishes remain plastic throughout life (Ebbesson and Braithwaite 2012), and adult male guppies kept in different social conditions show different changes in brain size (Kotrschal et al. 2012) suggesting that a plastic response in cue use may be possible, but it was not seen here. A longer (more than 4 weeks) exposure duration may be required before plastic changes can occur (Chapman et al. 2010b;

Kotrschal et al. 2012), or exposure during a critical developmental period early in life may be required for sensory plasticity in cue use to occur (Rauschecker 1995; West-Eberhard 2003; Knudsen 2004).

Nevertheless, we did observe that after 4 weeks, guppies foraged most successfully in their exposure environment, suggesting that some sort of compensatory behaviour or response did occur after a 4 week (but not 2 week) exposure. This may result from eye acclimation to the dark environment, increased familiarity with foraging in dark environments, or decreased familiarity with light environments.

Dark adaptation of the eyes is a rapid process that is unlikely to explain why adaptation was observed after 4 weeks but not after 2. In teleost fish, as in other vertebrates, the retinal photoreceptors and retinal epithelium in the eye respond to changes in the lighting environment, to adapt the retina for vision in both bright and dim-light vision (Walls 1942; Rodieck 1973). Such adaptation to dark and light

Fig. 2 Proportion of time spent in the cue detection zone after adult fish had been exposed to light and dark exposure environments for 2 or 4 weeks. Shaded bars represent dark-test environments, unshaded bars represent light-test environments, raw data are plotted as open points overlaid on the relevant boxplot showing the median (heavy line), and upper and lower quartiles (box). Whiskers extend to the most extreme data point that is no more than 1.5× the interquartile range (IQR). The horizontal dashed line at 0.5 represents a random choice



environments is a rapid process: human eyes take approximately 20–40 min to fully adapt from bright sunlight to complete darkness (Jackson et al. 1999). Similarly, in zebrafish (*Danio rerio*), a fully light-adapted state is reached after 1 h of light adaptation (Hodel et al. 2006), and silver eels (*Anguilla anguilla*), show retinomotor movements associated with light and dark adaptation after 2 h (Es-Sounni and Ali 1986). All fish were exposed to the test environment for 1 h before trials began, and so, normal dark- or light-adaptation processes should have occurred for both dark- and light-exposed fish. Over a longer time period of exposure, however, it is possible that eyes could have developed further sensitivity, although studies of longer term visual deprivation tend to focus on the visual impairment that results from exposure during critical developmental windows (e.g. Kroger et al. 2003; Mitchell et al. 2015).

Experience of necessarily feeding in the dark means dark-exposed fish become accustomed to seeking out food in this environment, while light-exposed guppies, which would not normally be foraging under low-light conditions (Magurran 2005) would not. Additionally, guppies exposed to dark conditions may become unfamiliar with foraging in the light, leading them to behave in a risk-averse manner when tested in light environments. Guppies are known to become bolder in environments they are more familiar with, and spend more time exploring familiar environments (Martin and Réale 2008; Goldenberg et al. 2014), which would allow them to

more readily locate a food source. We might, however, expect associations like this to develop more rapidly: guppies can learn to locate a food source within three trials (Lachlan et al. 1998) and remember the identity of conspecifics in 14 days (Griffiths and Magurran 1997). Minnows can learn to recognise pike odour within 2–4 days (Brown et al. 1997) or 14 days (Chivers and Smith 1995), and a single exposure to a chemical cue can lead to marked and long-lasting changes in antipredator behaviour in multiple species (Brown 2003).

A lack of response at 2 weeks is perhaps surprising, as guppies and other fishes can respond rapidly to changing environments in other contexts. Male guppies reared as juveniles in dark conditions, for example, respond flexibly to current lighting environment in mating behaviour regardless of their rearing environment (Chapman et al. 2009). Sticklebacks can modify their behaviour towards an unavailable food source in a matter of minutes (Bell and Peeke 2012), and in some cases able to maintain foraging rates in turbid water without prior exposure, by using olfactory cues (Webster et al. 2007; Johannesen et al. 2012; but see Soheli et al. 2017), although other fish species do not (e.g. striped trumpeter (*Latris lineata*): Cobcroft et al. 2001, sablefish (*Anoplopoma fimbria*): De Robertis et al. 2003). If animals are not able to respond flexibly to rapid changes in their environment, this may have detrimental effects on their foraging success. Alternatively, as short-term variability in visibility in aquatic environments is common due to water depth, turbidity or

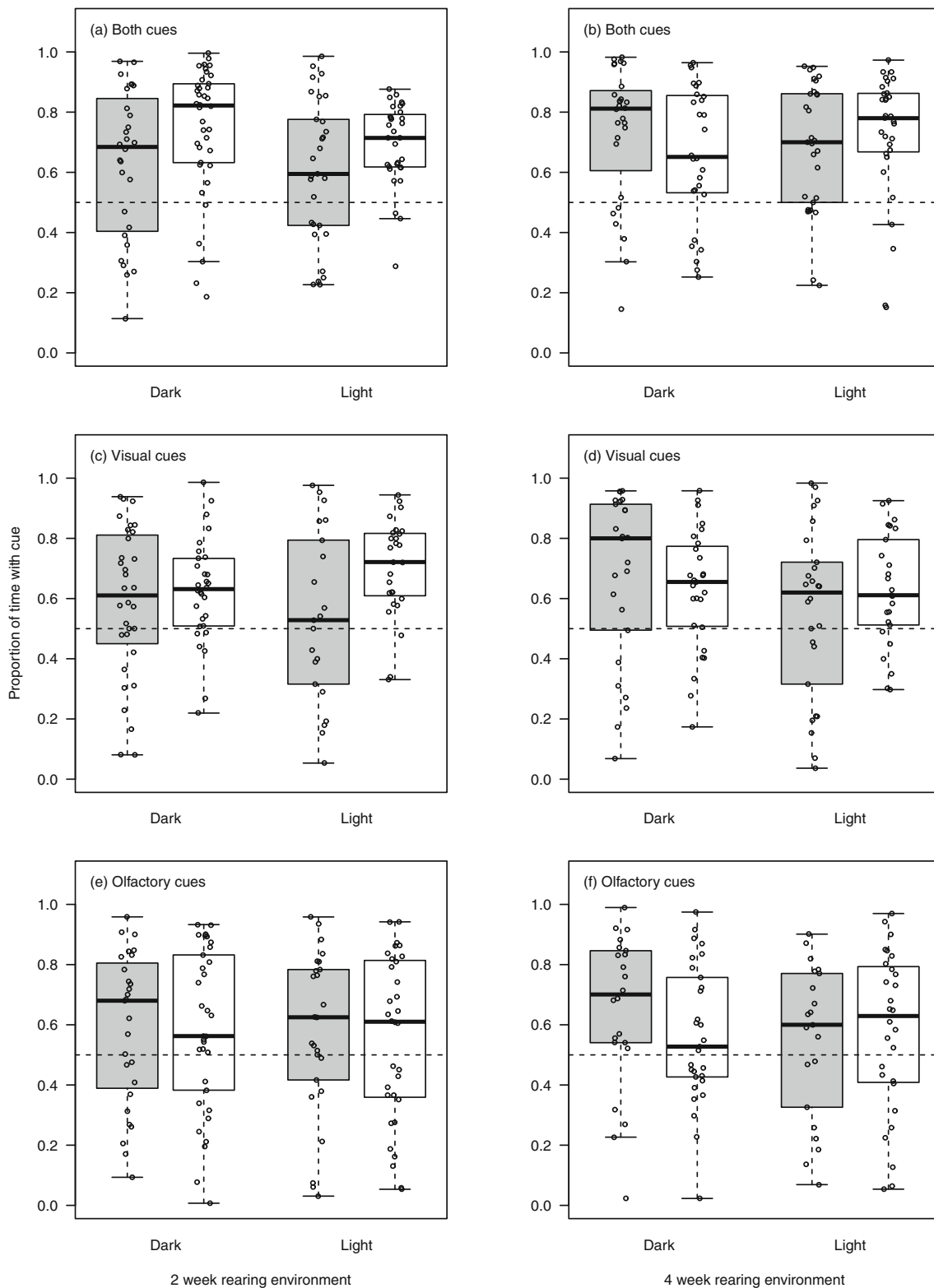


Fig. 3 Proportion of time spent in the cue detection zone after adult fish had been exposed to light and dark environments for two (left panels) and four (right panels) weeks, with either both visual and olfactory cues (**a, b**), visual cues only (**c, d**) or olfactory cues only (**e, f**). Shaded bars represent dark-test environments, unshaded bars represent light-test environments,

raw data are plotted as open points overlaid on the relevant boxplot showing the median (heavy line), and upper and lower quartiles (box). Whiskers extend to the most extreme data point that is no more than $1.5 \times$ the interquartile range (IQR). The horizontal dashed line at 0.5 represents a random choice

canopy cover, the benefits of changing behaviour may be outweighed by the costs of doing so (DeWitt et al. 1998), and a change in behaviour may not be observed.

Our study highlights the importance of considering the impact of environmental change over different life stages and time scales. Research into the effect of environmental change on individual behaviour is usually carried out as a long-term study rearing juveniles from an early age (Cobcroft et al. 2001; Carere et al. 2005; Chapman et al. 2010a, b; Weintraub et al. 2010; Gray et al. 2012; Zambonino-Infante et al. 2013; Brust et al. 2014), or via the short-term exposure of adults to degraded conditions (Engström-Öst et al. 2006; Ward et al. 2008; Johannesen 2012; Kimbell and Morrell 2015a, b). While short-term experiments offer important insights into the immediate response of animals to a pollution event, for example, longer term studies are needed to understand the impact of more gradual or long-lasting change on both adult and juvenile individuals. A limitation of our study is that we were unable to track individuals between 2 and 4 weeks; future studies could build on this by tracking individuals over time. Understanding how animals respond to changes to their sensory environments is critical to understanding the consequences of environmental change for individuals, populations and communities (Hoverman and Relyea 2007; Wong and Candolin 2015). The ability of aquatic organisms to respond flexibly or plastically to the loss of visual information, or other senses, may differ depending on the life stage of the organism. Our results suggest that extended exposure may allow adult individuals to alter their behaviour, allowing them to compensate somewhat for the detrimental effects of the change, but any negative impact change on growth and survival can occur over relatively short time scales (Berg and Northcote 1985) and raises the question of whether this compensation will be sufficient.

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Data availability All data generated or analysed during this study are included in this published article (and its supplementary information files: ESM_1.xlsx).

Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. The project was approved prior to commencement by the ethical review committees of the former School of Biological,

Biomedical and Environmental Sciences and the Faculty of Science and Engineering at the University of Hull (reference numbers U021 and U094).

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