The impact of turbidity on foraging and risk taking in the invasive Nile tilapia (*Oreochromis niloticus*) and a threatened native cichlid (*Oreochromis amphimelas*)

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Abstract

Anthropogenic activity can increase water turbidity, changing fish behaviour by reducing visibility. The spread of invasive species is also facilitated by human activity, further increasing the pressure on native species. In two experiments, we measured the foraging efficiency, risk perception and inter-individual consistency of risk-taking (personality variation in boldness) of an invasive species, the Nile tilapia (*Oreochromis niloticus*), and a threatened tilapia, the Manyara tilapia (*Oreochromis amphimelas*), in clear and turbid water. In experiment one, *O. niloticus* was faster to initiate feeding, encountered more food items and consumed more than *O. amphimelas*. The latency to start foraging by *O. niloticus* decreased in turbid water. Turbidity did not affect the latency to start foraging in *O. amphimelas* but the number of food items they encountered was highest at the intermediate turbidity. There was however no significant effect of turbidity in either species on the total food consumed. In contrast to this foraging context, in experiment two with a refuge and no food available, risk taking behaviour was similar in both species and they both responded with similarly reduced risk taking in turbid water. Evidence of personality variation was weak, being observed only in *O. amphimelas* when first leaving the shelter in turbid water. Overall, species differences were greater in the foraging context but turbidity was more important in the risk-taking context. *O. amphimelas* is more sensitive to turbidity during foraging, and *O. niloticus* is likely to have a competitive advantage in foraging situations, especially in degraded turbid habitats.

Significance statement

Under human-induced environmental change, native species are often exposed to multiple stressors. Here, we tested the responses of two cichlid fish to increasing turbidity, the Nile tilapia (*Oreochromis niloticus*), which is invasive throughout the tropics, and the Manyara tilapia (*Oreochromis amphimelas*), a threatened species, indigenous to Tanzania. We found that turbidity was beneficial to the foraging of *O. niloticus*, which in both clear and turbid water consumed and encountered more food than *O. amphimelas*. In contrast, without food present, both species displayed similar responses of increased risk perception in turbid water with little evidence of personality variation between individuals in either species. Our results suggest that invasive species tolerant of degraded habitats may outcompete less well-adapted native species for food.

Keywords Boldness · Personality variation · Habitat degradation · Environmental stressors · Multiple stressors · Invasive species

Introduction

Turbidity is the cloudiness of water produced by suspended particles scattering light (Davies-Colley and Smith 2001). This alters the contrast between an object and its background, influencing the vision of aquatic organisms (Utne-Palm 2002). Many high productivity aquatic habitats are naturally turbid and are populated by species which are specifically adapted to these environments (Williams 1982; Fabricius et al. 2005; Van De Meutter et al. 2005; Wenger et al.

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2011). However, numerous anthropogenic activities can rapidly increase turbidity above natural levels, resulting in up to a 10-fold increase in sediment loading (Hilton and Phillips 1982; Dearing and Jones 2003; Järvenpää and Lindström 2004; Erftemeijer et al. 2012). Human-induced eutrophication and increased sedimentation are growing causes of habitat degradation in clear water systems and can drive rapid changes to the sensory environment (Julien 1995; Mol and Ouboter 2004; Dodds et al. 2009; Erftemeijer et al. 2012). Such changes influence the behaviour of many fish species that rely on vision, especially during foraging and predator-prey interactions (Guthrie and Muntz 1986; Abrahams and Kattenfeld 1997; Ferrari et al. 2010a; Wishingrad et al. 2015; Ehlman et al. 2020). Additionally, turbidity can influence many other functions related to reproductive success, including sexual selection, mate choice and parental care (Järvenpää and Lindström 2004, 2011). As a result, the behavioural responses of species to increased turbidity can heavily influence the effect it has on the survival of individuals and populations (Caves et al. 2017).

The effect of turbidity on foraging efficiency varies across species and ecological contexts. In some cases, turbidity can increase the contrast of an object against its background, benefiting object detection and improving foraging (Hinshaw 1985). More generally however, turbid water has been shown to restrict the visual range of fish and reduce the efficiency of visual foragers (Utne-Palm 2002; Lunt and Smee 2015). This negatively affects prey detection, reducing the reaction distance within which predators can detect their prey (Barrett et al. 1992; Gregory 1993; Sweka and Hartman 2003; Quesenberry et al. 2007). Therefore, foraging success can be constrained even in areas of high prey density (Turesson and Brönmark 2007; Becker et al. 2016; Snow et al. 2018). This has been demonstrated in brown trout (*Salmo trutta*) and bluegill sunfish (*Lepomis macrochirus*) where foraging performance and reactive distance declined as turbidity increased (Vinyard and O'Brien 1976; Stuart-Smith et al. 2004). Even after initial detection, turbidity may impact foraging, with some species displaying reduced attack success even at low levels of turbidity (8 Nephelometric Turbidity Units (NTU)) (Johansen and Jones 2013). A common behavioural response to reduced visibility is to increase activity, as it can increase encounter rates (Sweka and Hartman 2001; Granqvist and Mattila 2004; Harvey and White 2008). Despite this, such behaviours are potentially detrimental if improved encounter rates do not compensate for the increased cost in energy or the greater risk of encountering predators (Meager and Batty 2007).

Turbid environments also influence predator-prey interactions by changing the perception of risk in fish (Gregory 1993; Chamberlain and Ioannou 2019; Ehlman et al. 2019). Prey may use turbid conditions as refugia from predators, where they are less likely to be detected (Engström-Öst et al. 2009).

Chinook salmon (*Oncorhynchus tshawytscha*), for example, reduce antipredator behaviour in turbid conditions, suggesting a decreased perception of risk (Gregory 1993). However, this can be maladaptive if the true risk of predation does not decrease (Abrahams and Kattenfeld 1997; Lehtiniemi et al. 2005). In other cases, fish may reduce activity and feeding while increasing shelter use in turbid areas, indicating an increase in risk perception (Leahy et al. 2011; Ajemian et al. 2015). Additionally, turbidity can impair the ability of some fish to learn about and to recognise predators, slowing the reaction time of prey (Ferrari et al. 2010b; Chivers et al. 2013).

Changes to foraging efficiency and risk perception due to turbidity thus impact the fitness of fish species (Tuomainen and Candolin 2011). However, individuals within a population may react differently to similar stimuli and this inter-individual consistency of behaviour is referred to as animal temperament or personality variation (Réale et al. 2007). A behavioural trait that is often consistently different between individuals is boldness, defined by the likelihood of an individual to take risks in return of greater rewards (Réale et al. 2007). The repeatability of behaviours associated with boldness can be induced by the combined effect of turbidity and the presence of predators (Ehlman et al. 2019). As personality variation indicates a lack of behavioural plasticity, it suggests that individuals may be constrained in their response to environmental change (Tuomainen and Candolin 2011).

In addition to turbidity, the introduction of non-native species poses a great threat to aquatic ecosystems, reducing biodiversity by displacing native species and contributing to habitat degradation (Mainka and Howard 2010). The casual mechanisms underlying the success and negative effects of many invasive species are, however, poorly understood (MacDougall and Turkington 2005; Tuomainen and Candolin 2011; Gallardo et al. 2016). Improving understanding of these mechanisms is an important goal of invasive species research, as it is crucial in making informed decisions regarding environmental management, and when allocating limited resources to the prevention of the most harmful species (Vander Zanden and Olden 2008). Successful invasive species often exhibit tolerance to a wide range of environmental conditions and adapt quickly to novel environments. This characteristic is so prevalent that the presence of invasive species has been suggested as an indicator of habitat degradation (Kennard et al. 2005; García-Berthou 2007). Improved tolerance of degraded environments can provide a competitive advantage for non-native species, allowing effective colonisation as intolerant native species decline (MacDougall and Turkington 2005; Linde et al. 2008a). For example, the combination of turbidity and the presence of the invasive yellowfin shiner (*Notropis lutipinnis*) reduces the feeding efficiency of the rosyside dace (*Clinostomus funduloides*) through the combined effects of restricted reaction distance and interspecific competition (Hazelton and Grossman

2009a, b). Resident species are often exposed to multiple stressor effects from anthropogenic activity (Ormerod et al. 2010; Orr et al. 2020), which can have a greater combined effect than each stressor in isolation (i.e. a synergistic effect).

The Nile tilapia (*Oreochromis niloticus*) is a widespread invasive cichlid species commonly used in aquaculture. Subsequently, non-native populations of *O. niloticus* have been established across the tropics (Canonico et al. 2005; Mohamed and M Al-Wan 2020). Like many invasive species, *O. niloticus* shows a high tolerance to a wide range of environmental conditions. For example, juvenile *O. niloticus* abundance has been shown to increase in degraded habitats, while the abundance of native species declines (Linde et al. 2008b). Additionally, *O. niloticus* can actively increase turbidity through benthic foraging, by resuspending sediment and increasing nutrient levels leading to algal growth (Zhang et al. 2017).

In this experiment, we investigated the behavioural responses of *O. niloticus* and the Manyara tilapia *Oreochromis amphilas* in clear compared to turbid water. *O. amphilas* is a threatened tilapia species native to Tanzania where it lives in sympatry with the invasive *O. niloticus* across five lakes (Shechonge et al. 2019). In both species, we measured how foraging efficiency changes across low, medium and high turbidity (0, 15 and 30 NTU), and whether risk taking and consistent inter-individual differences in risk taking (i.e. personality variation in boldness) were different in clear and turbid treatments (0 and 15 NTU). Interactions between multiple stressors can be synergistic or antagonistic, either limiting or exacerbating the harmful impacts they have on affected ecosystems (Piggott et al. 2015). Therefore, investigating the relationship between turbidity and the behaviour of native and invasive fish species could provide useful insights into how native species may be impacted by two widespread ecological stressors with the potential to interact.

Materials and methods

Subjects

Sixty-eight *O. amphilas* (65.3 ± 7.5 mm mean $\pm$ SD body length) were bred from first-generation wild caught stock by Bangor University and transported to Bristol in December 2018. Sixty-eight *O. niloticus* (79.6 ± 6.9 mm mean $\pm$ SD body length) were purchased from Fish Farm UK, London, in December 2018. Thirty-six *O. amphilas* and 36 *O. niloticus* were used in experiment one and 29 *O. amphilas* and 32 *O. niloticus* were used in experiment two. Individuals were not reused between the two experiments and fish were housed in separate tanks according to the experiment they participated in. Three *O. amphilas* were removed during the second experiment due to ill health during the trial period.

The two species were housed separately in clear water (0 NTU) within a recirculating aquarium system in 180 L glass tanks. Plastic plants and pipes were placed in the housing tanks to provide enrichment (Brydges and Braithwaite 2009). Identical shelters used in the experiments were also placed in the housing tanks to reduce novelty in the experimental trials (Fig. 1c). Fish were fed daily with a diet consisting of ZM large Premium Granular feed (Techniplast, London, UK), TetraMin flake (Tetra, Melle, Germany), frozen bloodworm (CC Moore & Co, Templecombe, UK) and Gamma™ Krill Pacifica, chopped prawn, *Mysis* shrimp, brine shrimp and vegetable diet (Tropical Marine Centre, Chorleywood, UK). Water temperature in the housing tanks was sustained at 26 °C with a constant diurnal light cycle of 12:12 h (light:dark) mimicking tropical conditions. All fish remained in the laboratory for future use following the experiments.

Experimental setup

The trials were conducted in a white acrylic tank with an opaque divider creating two arenas (each $80.5 \times 64 \times 40$ cm, width $\times$ length $\times$ height, containing 77.2 L of water at a depth of 15 cm) so that two trials could be conducted simultaneously (Fig. 1a). A shelter created from plastic ornamental plants attached to a white corrugated PVC base was placed in each side of the tank to act as a shelter in experiment two (Fig. 1c). Turbidity was recorded with a calibrated Thermo Scientific™ Orion™ AQUAfast AQ3010 turbidity meter using nephelometric turbidity units (NTU). The tank was lit from above with a fluorescent strip light and recorded from above with a GoPro Hero 5 Black (GoPro Inc.) at a resolution of 1920×1080 pixels. The tank was filled with water from the recirculation system used to house the fish. A white curtain was drawn across the tank area to prevent disturbance.

Procedure

Experiment one: the effect of turbidity on foraging efficiency

Each day of testing, one of three turbidity levels (0, 15 and 30 NTU) was randomly selected and 12 individuals (six of each species) were tested. Kaolin clay was used to create treatments of 15 NTU (0.04 mg/l) and 30 NTU (0.09 mg/l). The clay powder was spread evenly across the tank and mixed until the desired level of turbidity was attained following previous studies (Quesenberry et al. 2007; Leahy et al. 2011). The turbidity range used was similar to levels in other studies, staying below the upper tolerance levels of fish and not interfering with the transmission of chemical cues or altering the pH or hardness of the water (Horppila et al. 2004; Leahy et al. 2011). Anthropogenic activities such as mining can result in

Fig. 1 The experimental arena and shelter used in both experiments (not to scale). **a** Top-down view of the experimental arena and the position of the acclimation boxes used in experiment one (dashed). **b** Side view of the trial arena, with the removable acclimation box (dashed). **c** The plant

shelter used in experiment two, made from plastic aquarium plants fixed to a plastic base and weighted with ornamental rocks. **d** Side view of the trial arena showing the position of the plant shelter used in experiment two where the fish were placed at the beginning of the trial

increasing levels of clay entering aquatic systems, making clay an ecologically relevant way of replicating natural levels of turbidity (Eriksson et al. 2004; Kemp et al. 2011). Resuspension by stirring was conducted between trials to ensure that the turbidity remained at desired levels across all trials.

The day before each trial, 6 individuals of each species were caught haphazardly with a hand net from their housing tanks and acclimated to the next day's turbidity (0, 15 or 30 NTU) in the trial tank for 16 h (overnight) prior to testing. The two species were acclimated separately in the two halves of the tank, separated by the opaque divider. Fish were not fed the day before the experiment to encourage feeding and standardise hunger and motivation. Before the first trial on each day, all fish were removed and kept in covered plastic holding tanks (45 × 32 × 25 cm, water depth 15 cm) separated by species and with a turbidity matching that day's treatment. One *O. niloticus* and one *O. amphimelas* were netted, their total body length measured (mouth to the end of caudal fin) with digital callipers and were placed in an acclimation box in the trial area for 30 min before trials began (Fig. 1b). After this period, 10 pellets were added to each side of the experimental arena, spread evenly across the width opposite to the acclimation boxes. Floating pellets were used as food items (Hikari Cichlid Gold mini-pellet, 3.2–3.7 mm) as they remained at the water surface and feeding attempts could be easily observed even in turbid conditions. Recording began and the acclimation boxes were slowly lifted and removed, releasing the fish. Trials lasted 15 min. Each fish was tested once and then placed into housing tanks reserved for fish that had completed

the trials to avoid repeated testing of the same individual. The arenas and holding tanks were emptied after each day of trials and replaced with fresh system water which was dosed with the desired turbidity for the next day. The next group of fish was then acclimated for the next day's trial. Trials took place between 30.04.2019 and 14.05.2019.

Video recordings were analysed using BORIS version 7.7.3 by a single reviewer to ensure consistency (Friard and Gamba 2016). The variables measured were the time to first feed, the number of feeding attempts (the number of the 10 pellets that the fish attempted to feed on) and the number of pellets consumed. A feeding attempt was defined as an individual's mouth making contact with a pellet at least once, so that subsequent attempts to feed on that pellet were not further counted. The number of feeding attempts thus measures the number of different food items that were encountered during the trial. It was not possible to record data blind as individuals had to be identified by species for each experiment.

Experiment two: the effect of turbidity on risk taking and personality variation

Consistent inter-individual differences in responses to turbidity were tested by exposing each fish to each treatment (0 and 15 NTU) twice across a 4-day period. Eight individuals of each species were tested per week and every individual took part in one trial per day for four consecutive days. Turbid water was created following the methods outlined in experiment one. The day before each 4-day trial period, 8 individuals of each species were caught haphazardly with a hand net.

Fish were split into 4 groups (2 groups of *O. niloticus* and 2 groups of *O. amphimelas*) and the total body length of each fish was measured (mouth to the end of caudal fin) using digital callipers. Each group was housed in a plastic holding tank (45 × 32 × 25 cm, water depth 15 cm), which were continuously oxygenated with air stones, for the next 4 days. These holding tanks were filled with system water which was changed each day with a turbidity level to match the next day's trials (0 or 15 NTU), using the methods outlined in the previous experiment, allowing the fish to be acclimated for 16 h (overnight) before the experiments began in the required treatment. The fish in each holding tank were different lengths to ensure clear identification of each individual was possible across the 4-day period. Trials took place between 18.06.2019 and the 26.07.2019.

The order of testing for groups, and individuals within groups, was allocated randomly per day. The water was stirred before each trial to maintain turbidity levels. Before each trial, the turbidity was measured to make sure it was at the desired level (0 or 15 NTU) or resuspended by stirring if needed. Video recording began and individuals were placed within the shelters (Fig. 1c, d). Trials lasted for 30 min. Once tested, fish were returned to their holding tank. To standardise hunger levels between trials, fish were only fed after all individuals had taken part in the day's experiments. At the end of the 4-day trial period, test fish were removed from the holding tanks and kept separately to untested fish to avoid individuals being used more than once. BORIS version 7.7.3 software (Friard and Gamba 2016) was used to analyse the videos by a single reviewer to maintain consistency. The variables measured were the time to first leave the shelter, the time taken to first cross the midline of the tank after first leaving the shelter and the total time spent out of the shelter. It was not possible to record data blind because our study required individuals to be identified across repeat experiments.

Statistical analysis—experiment one

R version 3.5.3 was used for the analysis of both experiments (R Core Team 2019). The time to first feeding attempt, a censored time-to-event response variable, was analysed using a Cox proportional hazard test. The explanatory variables included for this analysis were an interaction term between species and turbidity and their main effects, along with body length (a continuous variable). This test analyses how the likelihood of an event, in this case attempting to feed, changes depending on a set of risk factors, which in this case are the explanatory variables. The principal assumption of this test is that the hazards are proportional, meaning that the effect of explanatory variables do not change over time. The proportional hazards assumption was tested using Schoenfeld residuals (from R function 'cox.zph' in the 'survival' package) (Therneau 2015). This function provides *P* values for each explanatory variable, with significant values

meaning that the effect is not proportional over time, violating the assumption. We found no violations of this assumption based on confidence limits of 0.95. To test the assumption of non-linearity, models were run with a smoothing parameter fitted to the linear covariate body length using a penalised spline method (from function 'pspline' in the 'survival' package). Models with and without spline terms were then compared using AICc (Akaike information criterion corrected (AICc) for small sample sizes) with the function 'AICctab' in the 'bbmle' package (Bolker and R Core Team 2017). Models without spline terms were more likely indicating that a linear relationship between the time to first feeding attempt and body length. The deviance residuals were used to examine influential observations (from R function 'ggcoxdiagnostics', in the 'survminer' package) (Kassambara et al. 2019).

The number of feeding attempts was analysed with negative binomial generalised linear models (GLMs). The continuous variables were scaled in all models (R function 'scale'). This provides a standardisation of the variable by first calculating the mean and standard deviation of all values in the vector, then subtracting the mean from each value and dividing each value by the standard deviation. The overdispersion statistic was calculated to ensure it was between 0.5 and 2 indicating no under or overdispersion. The model for the number of feeding attempts initially included an interaction term between species and turbidity and their main effects, along with a continuous variable (body length), and a categorical variable (the side of the arena that the trial took place in). After observing a nonlinear relationship between turbidity and the number of feeding attempts, polynomial regression was applied to provide a nonlinear fit to the model (R function 'poly') (Becker et al. 1989; James et al. 2000; Chambers 2017). Likelihood ratio tests were used to remove any nonsignificant interactions or explanatory variables by deleting terms based on likelihood ratio tests (using R function 'drop1' in the 'lme4' package) (Bates et al. 2015).

The number of pellets consumed was analysed with negative binomial GLMs. These models initially included an interaction term between species and turbidity and their main effects, along with a continuous variable (body length), and a categorical variable (the side of the arena that the trial took place in). Continuous variables were scaled and assumptions were tested using the same methods as outlined for the number of feeding attempts. Once again, the 'drop 1' function was used to remove nonsignificant interactions and explanatory variables.

Statistical analysis—experiment two

The time taken to first leave the shelter and the time taken to first cross the midline of the arena, censored time-to-event response variables, were analysed using Cox proportional hazards models. The explanatory variables included for this analysis were an interaction term between species and

turbidity and their main effects, along with a continuous variable (body length). The same methods as outlined in experiment one were used to test for proportional hazards, non-linearity and influential observations. We found that models including spline terms fitted to the linear covariate body length were more likely for both the time taken to leave shelter and the time to cross the midline. This suggests that body length had a non-linear effect on these dependent variables. Smoothing penalised splines were therefore added to improve model fit. Once spline terms were added, we found no evidence for violations of any of the test assumptions.

The total time spent outside the shelter was analysed with a generalised linear mixed model (GLMM) with a Poisson distribution using the default ‘log’ link function. The model included an interaction between species and turbidity and their main effects, a continuous variable (body length) and a categorical variable (the side of the arena that the trial took place in) and a random effect (fish ID). To reduce overdispersion, continuous variables were scaled and an observation-level random effect term was included in the model (Harrison 2014). Likelihood ratio tests were then used to remove non-significant interactions by deleting terms based on chi squared tests using the ‘drop 1’ function.

To assess consistency in inter-individual variation (i.e. personality variation) for each of the three response variables, in each species and in each of the turbidity treatment separately, Spearman rank non-parametric correlations were used. Shapiro-Wilk normality tests showed that the data was not normally distributed ($P < 0.05$) and the censored data for the two latency response variables can lead to spurious estimates of formal repeatability scores (Stamps et al. 2012; Ioannou and Dall 2016).

Given that the body length distribution differed between the two species, variance inflation factors were used to test for multicollinearity in fixed effects across all Cox proportional hazards models and generalized linear models in both experiments (using the ‘vif’ function in the ‘car’ package, Fox

and Weisberg 2019). We found evidence for low multicollinearity between explanatory variables, with all vif values being below 5.

Finally, given that sampling using a hand net could result in a bias towards the boldest individuals first (Biro and Dingemanse 2009), we conducted a negative binomial GLM including the time spent outside of the shelter as the response variable and how early the fish were caught (experiment block number 1–16) as the explanatory variable.

Results

Experiment one

A significant interaction between species and turbidity revealed that turbidity had a different effect on the likelihood of a first feeding attempt between the two species (Cox proportional hazard model (CPH): hazard ratio (HZ) = 0.95, $N = 72$, $P < 0.046$). This, along with the trend shown in Fig. 2, suggests that in *O. amphimelas* turbidity had no effect on the time taken to first attempt to feed, while in *O. niloticus*, the first feed attempt was more likely to occur at 15 and 30 NTU than it was at 0 NTU (Fig. 2a, b).

The explanatory variables included for the analysis of the number of food items that the fish attempted to feed on were an interaction term between species and turbidity and their main effects, along with a continuous variable (body length). When this model was restricted to fitting a linear relationship between turbidity and the response variable, there was no significant interaction between species and turbidity (negative binomial GLM: species * (scale(turbidity)): $LRT_{1,66} = 0.02$, $P = 0.88$) or a linear effect of turbidity (negative binomial GLM: (scale(turbidity)): $LRT_{1,67} = 1.18$, $P = 0.27$). The effect of species was significant; *O. niloticus* attempted to feed on a greater number of food items (negative binomial GLM:

Fig. 2 Kaplan-Meier estimates of the proportion of fish that did not feed across the trial period (a) *O. amphimelas* and (b) *O. niloticus* in 0 (black), 15 (light blue) and 30 (dark blue) NTU (turbidity level: nephelometric turbidity units) treatments

species: $LRT_{1,67} = 63.77$, $P < 0.001$). Adding a quadratic term for turbidity, however, resulted in a significant interaction between turbidity and species (negative binomial GLM: species * poly(scale(turbidity)): $LRT_{2,64} = 11.1$, $P = 0.003$). This interaction and the trends in Fig. 3a suggest that the number of feeding attempts by *O. amphimelas* was the greatest at the intermediate turbidity, but there was no such quadratic relationship in the trials with *O. niloticus*.

The lack of a significant interaction between species and turbidity revealed that turbidity had a similar effect on total food consumption in both species (negative binomial GLM: species * (scale(turbidity)): $LRT_{1,66} = 1.19$, $P = 0.27$; Fig. 3b). As main effects, turbidity did not have a statistically significant effect on how many pellets were consumed (negative binomial GLM: (scale(turbidity)): $LRT_{1,67} = 3.29$, $P = 0.06$). Species did have a significant effect, with *O. amphimelas* consuming less than *O. niloticus* (negative binomial GLM: species: $LRT_{1,66} = 13.87$, $P < 0.001$).

Experiment two

For the likelihood of leaving the shelter for the first time, the interaction between species and turbidity was not significant, suggesting that turbidity had a similar effect in both species (CPH: hazard ratio (HZ) = 1.00, $N = 244$, $P = 0.8$). This likelihood did not differ between species (*O. amphimelas* versus *O. niloticus*: CPH: hazard ratio (HZ) = 0.58, $N = 244$, $P = 0.25$). Turbidity did not have a statistically significant effect on the likelihood of leaving shelter (CPH: HZ = 0.98, $N = 244$, $P = 0.06$; Fig. 4a, b).

For the likelihood of crossing the midline for the first time, the interaction between species and turbidity was not significant, suggesting that turbidity had a similar effect in both species (CPH: HZ = 1.00, $N = 244$, $P = 0.75$). The likelihood of crossing the midline did not differ significantly between species (*O. amphimelas* versus *O. niloticus*: CPH: HZ =

0.64, $N = 244$, $P = 0.13$). Across both species, the likelihood of crossing the midline was lower in turbid (15 NTU) compared to clear water (CPH: HZ = 0.96, $N = 244$, $P < 0.001$; Fig. 4c, d).

The lack of a significant interaction between species and turbidity revealed that turbidity had a similar effect on the time outside shelter in both species (GLMM: species * (scale(turbidity)): $\chi^2_1 = 0.33$, $P = 0.56$). As main effects the total time outside of the shelter did not differ between species (GLMM: species $\chi^2_1 = 0.53$, $P = 0.46$; Fig. 5), and was lower in turbid water for both species (GLMM: scale (turbidity) $\chi^2_1 = 20.31$, $P < 0.001$; Fig. 5).

Spearman rank correlation coefficients showed inter-individual consistency in the latency of *O. amphimelas* to first leave the shelter in the 15 NTU treatment ($N = 29$, $r_s = 0.405$, $P = 0.029$) but all other correlation coefficients were nonsignificant (Table 1), suggesting little support for strong consistent inter-individual variation in these species. We found no trend in boldness over time (estimate = -0.008 , SE = 0.02, $P = 0.71$), suggesting that bolder individuals were not more likely to be caught first, and that haphazard sampling in regard to boldness was achieved in both experiments.

Discussion

Our results show that *O. niloticus* from aquaculture stock, which are those most likely to be introduced outside of the species' native range, started to feed more quickly, encountered more food items and consumed more in total than *O. amphimelas* bred from wild-caught parents. The latency to the first feeding attempt by *O. amphimelas* was unaffected by turbidity, while *O. niloticus* attempted to feed more readily when the water was turbid (15 and 30 NTU) than when it was clear (0 NTU). It is therefore surprising that the number of feeding attempts made by *O. niloticus* was not affected by

Fig. 3 The number of **a** feed attempts and **b** pellets consumed across turbidity treatments for both species, *O. niloticus* (white) and *O. amphimelas* (grey). The boxes represent the interquartile range with the middle line displaying the median. Each whisker represents the position of 50% of values outside of the interquartile range

Fig. 4 Kaplan-Meier event estimates displaying the proportion of individuals to remain in the shelter **a** *O. amphimelas* and **b** *O. niloticus* and the proportion that did not cross the midline **c** *O. amphimelas* and **d** *O. niloticus* at 0 (solid) and 15 (dotted) NTU (level of turbidity)

turbidity, suggesting that its propensity to initiate feeding may be higher in turbid water while its overall foraging success may be unaffected. Conversely, *O. amphimelas* had the highest number of feeding attempts at the intermediate turbidity of 15 NTU. This peak at intermediate turbidity was not found in the number of pellets consumed, which did not depend on turbidity for either species. In experiment

Fig. 5 Total time spent outside the shelter for *O. niloticus* (white) and *O. amphimelas* (grey) at 0 and 15 NTU (level of turbidity). The median are horizontal lines within the boxes, the interquartile range (IQR) is the area within the boxes and the whiskers display the data within $1.5 \times \text{IQR}$

two, the time taken to first leave the refuge was unaffected by turbidity. However, both species showed reduced risk taking in turbid conditions, where they were less likely to cross the midline of the arena and spent less time overall outside of the shelter in turbid conditions. This suggests that the difference between the species in their foraging response to turbidity in experiment one was not a result of differences in risk-taking tendency (boldness). There was little evidence of consistent differences between individuals (i.e. personality variation) in either clear or turbid water. *O. amphimelas* did display a positive correlation over different days in the latency to first leave the shelter in the turbid treatment, suggesting some indication of a consistent shy-bold continuum in turbid water. However, the lack of similar results across other behaviours makes this only suggestive in *O. amphimelas* and shows that personality variation in boldness was weak in this study compared to similar studies on other species (Brown et al. 2005; Biro et al. 2010; Bevan et al. 2018; Ehlman et al. 2019; Szopa-Comley et al. 2020a). While our investigation of boldness using refuge use in a novel environment has shown to be repeatable in other species (Bevan et al. 2018), stronger repeatability may have been observed in the presence of threatening stimuli specifically related to predation (Carter et al. 2010; Selmann et al. 2012) or in the presence of food cues (Szopa-Comley et al. 2020b).

Table 1 Spearman rank correlation coefficients (r_s) for behaviours measured in two repeated trials in clear and turbid water. Twenty-nine *O. amphimelas* and 32 *O. niloticus* were tested. Significant values at 0.05 are shown in bold

	Turbidity (NTU)	r_s	p
Latency to first leave shelter <i>O. amphimelas</i>	0	0.044	0.817
	15	0.405	0.029
Latency to first leave shelter <i>O. niloticus</i>	0	0.037	0.836
	15	0.094	0.607
Latency to first cross midline <i>O. amphimelas</i>	0	0.126	0.513
	15	− 0.292	0.123
Latency to first cross midline <i>O. niloticus</i>	0	0.088	0.629
	15	0.040	0.827
Total time outside shelter <i>O. amphimelas</i>	0	− 0.201	0.293
	15	0.347	0.064
Total time outside shelter <i>O. niloticus</i>	0	− 0.143	0.432
	15	0.088	0.629

In our experiment, the fact that *O. niloticus* came from captive stock, while *O. amphimelas* were of wild origin, could be viewed as a potentially confounding variable, given that rearing history can effect risk taking and anti-predatory behaviours (Vilhunen and Hirvonen 2003). However, the majority of *O. niloticus* introductions result from intentional or accidental release of captive stock, rather than wild-type *O. niloticus* from their native range (Canonico et al. 2005). As a result, we feel that the experimental subjects used in this study accurately reflect the backgrounds of tilapia which would interact in situ. Thus, differentiating between the effects of rearing history and intrinsic differences between these two species is not necessary in order to make ecologically relevant conclusions about the impact of invasive species and increased turbidity.

Turbidity can have a negative impact on visual foragers by increasing foraging latency, reducing reaction distance and reducing attack success; however, our study showed that the feeding latency of *O. niloticus* was actually lower in the turbid treatment (Gregory and Levings 1996; Turesson and Brönmark 2007; Becker et al. 2016). *O. niloticus* may compensate for reduced visual information in turbid environments through increased activity and/or increasing reliance on another sensory modality. Past studies on *O. niloticus* demonstrate that it has an acute sense of olfaction that is used for foraging when vision is limited (Marusov and Kasumyan 2017). This could explain the increased propensity for *O. niloticus* to forage in turbid water, as species dependent on olfaction are not affected when foraging in turbid environments (Lunt and Smee 2015). However, direct comparisons of the sensory abilities of *O. niloticus* and native species including *O. amphimelas* are not available, so more information is needed in order to explore this hypothesis further. Compensatory factors such as increased sensory perception may explain why the time to first feed by *O. amphimelas* was not affected by turbidity but does not explain the more rapid time to feed in

turbid water by *O. niloticus*, or the improvement in the number of feeding attempts by *O. amphimelas* from the clear to the intermediate turbidity treatment. The perception of risk by *O. niloticus* may have been lower in turbid water, possibly because turbidity was used as a refuge (Lehtiniemi et al. 2005; Ferrari et al. 2014). However, this was not supported by the results of experiment two, which showed reduced, rather than increased, risk taking in both species in turbid water. Our results may indicate that the response to turbidity may be highly context specific, having a different effect depending on the presence or absence of food; further experiments manipulating food odour cues as well as turbidity are needed.

For *O. amphimelas*, intermediate levels of turbidity may be advantageous when foraging but do not increase the motivation to initially forage as there was no effect of turbidity on the latency to first feed. This may allow *O. amphimelas* to forage in moderately turbid environments and potentially mitigate the effects of anthropogenic turbidity. However, our results indicate that this is only effective up to a certain threshold between 15 and 30 NTU. As previous work has indicated that turbidity between 26 and 141 NTU reduces the diversity and volume of stomach contents of fish species (Stuart-Smith et al. 2004), establishing at what range feeding efficiency is negatively affected is important and could help maintain populations of native species.

Considering that *O. niloticus* can play an active role in increasing turbidity through benthic foraging, its presence may initiate a reduction in quality of clear water habitats or encourage a further decline in those already degraded (Zhang et al. 2017). Our study shows that some aspects of feeding by *O. niloticus* increases in turbid water suggesting that habitat degradation driven by *O. niloticus* can be beneficial to its foraging. This follows previous studies that suggest that degraded habitats are favourable to invasive generalists allowing colonisation where native species decline (Marvier et al. 2004). If an introduction of *O. niloticus* leads to increased

turbidity and so improves its feeding efficiency, it would become even more adept at foraging than native species. Thus, the introduction of *O. niloticus* could facilitate a positive feedback loop that results in it dominating competition with native species (Mainka and Howard 2010). This is especially relevant considering the foraging threshold of turbidity seen in *O. amphi-melas*. If *O. niloticus* is introduced to an area where populations of *O. amphi-melas* reside, it may increase the level of turbidity above this threshold potentially leading to the decline in foraging efficiency of *O. amphi-melas*.

Our results demonstrate how the effects of turbidity differ between *O. niloticus* from aquaculture stock and wild-type *O. amphi-melas*, a closely related species in the same genus. Some aspects of foraging in *O. niloticus* improved in turbid water, while high levels of turbidity constrained foraging in *O. amphi-melas* by reducing the number of encounters with food. *O. amphi-melas* did show improved foraging at intermediate turbidity levels, meaning that critical thresholds of turbidity may exist, past which native species could be outcompeted by *O. niloticus* which did not show reduced foraging efficiency even at the highest turbidity level. The increased foraging efficiency of *O. niloticus* over *O. amphi-melas* in this experiment highlights how *O. niloticus* may present a threat to *O. amphi-melas* and very likely other native cichlid species where it has been introduced, through exploitative competition for food resources. Our results suggest that turbidity could worsen these effects as *O. niloticus* has the potential to increase turbidity past critical thresholds where foraging efficiency declines in native species and while itself being unaffected by this degraded environment. However, we also found a number of foraging behaviours which were unaffected by turbidity or were improved at higher turbidity levels in both species. When food was not present, turbidity also increased the perception of risk in both species, which could influence predator-prey interactions in situ; however, further experimental evidence is needed in order to expand on the potential impacts of this finding. Determining whether preventing habitats from becoming turbid is a potential management tool in combating the spread and negative effects of *O. niloticus* and similar invasive species would be a useful target for future studies and could provide policy makers with novel tools to combat invasive species. Further observations of *O. niloticus* under natural conditions are required to further understand how their behaviour can affect native species across its wide global distribution, with respect to foraging and other behaviours (Linde et al. 2008a, b; Salazar Torres et al. 2016; Zhang et al. 2017; Champneys et al. 2018, 2020).

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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).

Code availability The code used in the current study is available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate All experimental procedures and housing conditions were in accordance with the ethical standards of the University of Bristol and ethical approval was granted by the University's Animal Welfare and Ethical Review Body (UB/18/067).

Consent for publication Not applicable.

Conflict of interest The authors declare no conflict of interest.

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