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Determining the effects of duration and recency of exposure to environmental enrichment

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ABSTRACT

Experience can help animals adapt their behaviour to fit the environment or conditions that they find themselves in. Understanding how and when experience affects behaviour is important for the animals we rear in captivity. This is particularly true when we rear animals with the intent of releasing them into the wild as part of population rehabilitation and conservation efforts. We investigated how exposure to a changing, more complex environment promotes behavioural development in juvenile trout. Four groups of fish were compared; (i) fish that were maintained without enrichment, (ii) fish that were exposed to an early period of enrichment, but were then returned to a plain environment, (iii) fish that were maintained in plain conditions, but were then exposed to enrichment towards the end of the rearing phase, (iv) a group that were kept in enriched conditions throughout the 12 week rearing period. We then assessed fish anxiety levels, their spatial learning ability, and the capacity of the fish to find their way through a barrier where different routes were presented across 4 different trials. Fish that experienced enriched conditions for the longest duration had superior spatial learning abilities, and they were better at finding the correct route to get past the barrier than fish from the remaining three treatments. Positive effects on behaviour were, however, also found in the fish that only experienced enrichment in the last part of the rearing period, compared to the control, or fish exposed to early enrichment. No effect of enrichment was found on levels of anxiety in any of the groups.

1. Introduction

Understanding how the environment fine-tunes and shapes behaviour is particularly important for those working in the area of captive rearing and release for population rehabilitation. Establishing appropriate ways to rear animals so that they have the capacity to survive and thrive in a real world environment remains a central goal of many applied research programs (Shier and Owings, 2006; Salvanes and Braithwaite, 2006; Urbanek et al., 2010). Experience during early life can play a significant role in the development of an animal's behavioural phenotype. However the relatively unchanging nature of the captive environment can lead to animals with behavioural deficits and diminished behavioural flexibility (Olla et al., 1994; Brown et al., 2003). The addition of environmental enrichment, or the experience of variation within the environment, has been found to promote increased behavioural flexibility and improve aspects associated with cognition (Leggio et al., 2005; Harburger et al., 2007; Strand et al., 2010; Salvanes et al., 2013). As such, there is now growing interest in the effects of adding environmental enrichment and variability into the captive environments in which animals are reared for later release (Rabin, 2003; Braithwaite and Salvanes, 2005; Seddon et al., 2007).

Although practices in terrestrial systems are extensively more developed than those in aquatic systems (Brown and Day, 2002), fisheries biology is a field that is actively exploring ways of rearing animals that behave in ways that smooth the transition from captivity to life in the wild (Heenan et al., 2009; Brockmark et al., 2010). Restocking in an attempt to restore or maintain heavily exploited fish populations is a widespread management practice (Brown and Laland, 2001). However, survival of hatchery fish is typically lower than for wild fish of the same size or age class. The mortality levels immediately following release can be substantial and there is little evidence that released fish survive long enough to effectively

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rehabilitate the struggling populations (Hilborn, 1998; Salvanes and Braithwaite, 2006).

From a stocking perspective, there appear to be benefits of rearing fish in more complex environments than the standard hatchery provide (Näslund and Johnsson, 2014). However, despite this knowledge, enrichment is seldom used in hatcheries (Näslund et al., 2012, 2013; Johnsson et al., 2014). Rearing fish with enrichment is more labour intensive than using barren tanks because enrichment makes it more difficult to clean, and there is concern that feed and waste may accumulate which might compromise the health of the animals within these systems (Braithwaite and Salvanes, 2010). The addition of enrichment items into the hatchery environment may, however, be a more attractive prospect if the fish only needed a restricted period of exposure to the enrichment (Brown et al., 2003).

In this study we investigate how the duration and recency of exposure to structural environmental enrichment affects the behavioural development in rainbow trout (*Oncorhynchus mykiss*), a commonly stocked species. Fish were exposed to three separate enrichment treatments differing in timing (early or late in the experiment) and duration (five or twelve weeks). The fish were then behaviourally screened, comparing three behaviours that are known to be positively influenced by enrichment (Salvanes et al., 2007, 2013; Spence et al., 2011); specifically we compared anxiety levels in a novel environment, spatial learning ability in a four armed maze and the ability of the fish to find novel paths to gain access to food (to assess behavioural flexibility). We hypothesized that the effects of enrichment would depend upon how long the fish were able to experience the enrichment, thus fish that had the longest exposure to enrichment would show the greatest benefits in terms of reduced anxiety and increased learning and flexibility. If, however, the effects depend on how recently the fish were exposed to enrichment, we would expect that fish most recently exposed to the enrichment would outperform those that had no enrichment or that only experienced enrichment at the start of the rearing period only.

2. Material and methods

2.1. Fish and treatments

Four groups of approximately 50 rainbow trout (*O. mykiss*) obtained from a local hatchery at 5 months of age were randomly distributed across 4 opaque, flow-through holding tanks ($60 \times 60 \times 95\,cm^3$). The fish were fed once per day with commercially produced fish pellets, and were kept on a 12 h light:dark schedule at a water temperature of 10 °C. After one month of acclimation, four groups were established for the experiment, with four replicate treatment tanks ($90 \times 45 \times 30\,cm^3$) in each of the groups and 10 fish in each tank ($n = 40$ per treatment) randomly selected from the holding tanks. Enrichment, when provided, consisted of fine grain gravel, upturned, black plastic pots (10 cm in diameter) to create areas of shelter, plastic plants (12–30 cm tall) and novel objects (plastic plants of different colour, Ping-Pong balls, green bottle tops (3 cm diameter), grey pvc-pipes (3 cm in diameter)). When enrichment was not available the tank contained only a filter and an airstone.

Group (i) fish experienced enrichment throughout the 12 week rearing phase of the experiment (12 full weeks – Full), Group (ii) were exposed to enrichment continuously for 5 weeks at the start of the experiment and then returned to regular holding tanks (5 weeks early – Early), Group (iii) were exposed to enrichment for the last 5 weeks of the experiment (5 weeks late – Late), and Group (iv), the control fish, were maintained for 3 months in treatment tanks without enrichment (Control). One complete control replicate tank had to be terminated prematurely owing to a fungal infection, none of these fish took part in the behavioural trials, hence there were only 30 individuals tested from the control groups. In addition, four other fish were lost in different tanks (1 Control, 2 Early and 1 Full); again these losses occurred prior to the behavioural assays. At the end of the experiment, the fish were euthanized and length measurements (standard length) were taken to compare the sizes across the treatments.

2.2. Behavioural assays

Once the fish reached 9 months of age behavioural screening began. Anxiety, flexibility in habitat use and spatial learning were assessed. The same fish were used in the anxiety and the flexibility trials ($n = 76$), because these two assays were not expected to interfere with each other owing to the very different nature of the tests. New fish, however, were used for the spatial learning task ($n = 71$). Three days before the behavioural assays began, the fish were anaesthetised with buffered Tricaine-S (MS-222, Sigma) and marked to permit individual identification with 3 mm long UV-florescent elastomer tags under the skin of the lower jaw using a hypodermic syringe.

2.2.1. Assessing flexibility

To assess the flexibility in habitat use, a series of 4 tasks were given to the fish over 4 consecutive days (modified from Reader and Laland, 2000). For each task, the fish had to find a route from one side of a tank to the other where they were able to access a feeder (Fig. 1). At the start of each trial, a fish was placed in one half of a tank with a dividing wall that had a single exit hole providing access to the other side of the tank. On each day of the test the exit was placed in a different position. Individual fish were transferred to the test tank and given a 30 min settling period with an opaque partition blocking access to the partition wall. Trials began when the partition was removed, and the latency to enter the exit hole was noted. For tests 1 and 2, the exit was simply a hole on either the left or the right, and the trout were given 15 min to find it. For tests 3 and 4, the fish had to enter a tube to access the exit hole; as this was a more difficult task the fish were given 20 min trials. The number of fish that found the route to the feeder was noted. These trials were run with $n = 20$, 20, 21 and 15 for the Early, Late, Full and Control fish, respectively.

2.2.2. Assessing spatial cognition

Spatial cognition, involving perceiving and interpreting spatial cues, as well as storing and retrieving this information (modified from Brockmark et al., 2010), was assessed using a maze with a central compartment ($20 \times 30 \times 14\,cm^3$) and four arms at each corner leading to doors (Fig. 2) and contained nothing else. Three of the doors were blocked with transparent Perspex that created dead-ends, while one exit remained open. The whole maze was brightly lit and had a light grey interior. The maze was placed in a larger test tank ($90 \times 45 \times 30\,cm^3$) containing a conspecific to motivate the test fish to exit the maze. Individual fish were tested once a day for 5 min, or until they found the maze exit. These trials were run for 13 consecutive days with $n = 20$, 18, 20 and 15 for the Early, Late, Full and Control fish, respectively. The number of false exits entered (errors) was recorded as the number of mistakes made, and the time it took to exit the maze was also noted.

2.2.3. Assessing anxiety

A novel tank diving test that is a three dimension version of the open field test was used to measure anxiety (Cachat et al., 2010). Time spent in the centre of the tank and number of times fish left the tank floor to explore the upper water layers was taken as evidence of less anxious fish. The test tank measured $45 \times 75 \times 30\,cm^3$, with