Environmental Enrichment and Prior Experience of Live Prey Improve Foraging Behaviour in Hatchery-Reared Atlantic Salmon

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ABSTRACT

Atlantic salmon salmo salar L. parr were reared for 3 months under standard hatchery conditions or in a structurally enriched tank (containing plants, rocks and novel objects). Half of each of these fish had prior exposure to live prey in the form of live bloodworm while the other half were fed hatchery-pellets. After 12 days all fish were tested on a novel live prey item (brine shrimp). A significant interaction between the two factors (prior exposure to live prey and rearing condition) revealed that foraging performance was only enhanced in fish that had been reared in a complex environment and exposed to live prey. It appears that the ability to generalize from one live prey type to another is only enhanced in fish that had been reared in an enriched environment. The findings support the assertion that the provision of enriched environments in combination with exposure to live prey prior to release may significantly improve the post-release survival rates of hatchery-reared fishes. As both the environmental enrichment and the prior foraging experience procedures were comparatively simple, the provision of such pre-release experiences are likely to prove cost effective to hatcheries.

INTRODUCTION

Many fish stocks around the world are threatened by over exploitation and habitat degradation. Populations of salmonids are no exception despite the amount of money and effort spent on mitigation. Each year probably billions of hatchery-reared salmonids are released into the wild but <5% survive to adulthood (McNeil, 1991). Most of the mortality occurs shortly after release through a combination of starvation and predation (Brown & Day, 2002; Støttrup et al., 2002). It is now widely accepted that the post-release survival rate of hatchery-reared fishes is far below that of their wild counterparts (Svasand et al., 1989; Campton et al., 1991; Kristiansen et al., 2000). Closer examination of the behaviour, morphology, genetics and physiology of hatchery fishes reveals substantial differences to that of wild fishes (Maynard et al., 1995).

Fisheries scientists have been aware of the differences between hatchery and wild fishes for well over a century. It has recently been proposed that the mundane environment in which hatchery fishes are raised may be responsible for these discrepancies (Ellis et al., 1997; Masuda & Tsukamoto, 1998; Berejikian et al., 1999). Despite these revelations many hatcheries continue to rear fishes using traditional methods,

which are successful in terms of producing large numbers of juveniles for release, but for the most part fail to enhance wild stocks. These methods are based on the underlying assumption that if more fishes are released more will survive.

A few countries, namely Japan, U.S.A., Norway and Finland have, however, begun to switch strategies from producing large numbers of low quality juveniles to producing fewer higher quality, ecologically-viable fishes (Masuda & Tsukamoto, 1998). Ecologically viable in this sense means that the fishes are better equipped to cope with conditions in the wild. The recognition that early developmental experiences play a major role in the success of released hatchery-reared fishes demands a switch in thinking on the part of hatchery managers. Hatcheries should aim to produce juveniles that are morphologically, genetically, behaviourally and physiologically similar to the stocks they are intended to enhance. Suggested methods for improving the survival of hatchery fishes post-release include supplementary feeding with live foods, the provision of under water feeders, the inclusion of sub-aquatic structure, natural substratum and overhead cover, and brief exposures to predators (Maynard et al., 1995, 2001). To date, implementation of the requisite changes in hatchery protocol and technology is very much in its infancy, and the validity and cost effectiveness of pre-release training has yet to be fully evaluated.

Hatchery reared fishes have been fed specially formulated pellet food for decades. The change from wild foods was made primarily for economic reasons (Embody & Gordon, 1924), since it is comparatively expensive to raise sufficient quantities of live prey to feed an entire hatchery stock and artificial food pellets contain all the essential ingredients a fish requires for rapid growth. Improvements in feed formulae have enabled large numbers of fishes to be reared with very little effort, resulting in extremely high pre-release rearing success. As a consequence the experiences provided to hatchery fishes have become increasingly divorced from conditions in the wild, and post-release survival rates have suffered accordingly.

Like virtually all fish behaviour, foraging relies on relevant experience in order to develop fully. The foraging skills of fishes become fine-tuned to prevailing ecological conditions through learning (Hughes et al., 1992; Warburton, 2003). Fish to learn not only to recognize prey, but how to handle them and where they are likely to be located (Warburton, 2003; Brown & Laland, 2003; Brown et al., 2003). When hatchery fishes are first exposed to live prey they often show inappropriate behaviour such as fright responses or no response at all (Godin, 1978). When recaptured after release into the wild, hatchery fishes are often found to have empty stomachs or stomachs filled with inanimate objects such as floating debris or stones resembling pellets (Miller, 1954; Ersbak & Haase, 1983; O'Grady, 1983; Johnsen & Ugedal, 1989). Hatchery-reared fishes are slower to switch prey as densities fluctuate and typically ingest a very limited variety of prey species compared to wild fishes (Sosiak et al., 1979; Ersbak & Haase, 1983).

Recent work on a variety of commercial species shows that hatchery fishes can be taught to recognize live prey. When foraging alone, hatchery fishes typically require about 15 exposures before they become fully competent at recognizing and consuming live food (Paszkowski & Olla, 1985; Stradmeyer & Thorpe, 1987; Reiriz et al., 1998). The rate of learning, however, can be substantially improved in a social context through learning about new foods from more knowledgeable conspecifics (Brown & Laland, 2002). Nevertheless, it is difficult to see how training to a single prey species could be of any benefit to post-release survival unless there is some degree of generalization to the other live prey items that released fishes are likely to encounter. The extent to which hatchery fishes are capable of this generalization is not clear, and is one issue that is specifically addressed here.

Habitat enrichment, whereby pre-release enclosures are altered to match conditions in the wild by the inclusion of structure and natural substrata (Brown & Day, 2002), has been shown to improve post-

release survival in salmonids (Maynard et al., 2001). At this stage it is not entirely clear how enrichment helps, but it appears that it induces more naturalistic behaviour in hatchery fishes, including cryptic (i.e. changes in colouration and increased hiding; Blaxter, 2000) and agnostic behaviour (Berejikian et al., 2000). Recent work with rats *Rattus norvegicus* Berkkenhaut and house crickets *Acheta domesticus* L., however, suggests that environmental enrichment may also improve learning abilities because complex environments provide greater sensory feedback to the brain than unstructured enclosures, resulting in increased neurogenesis (Park et al., 1992; Gomez-Pinilla et al., 1998; Lomassese et al., 2000, 2002). Naturally, any resultant increased learning capacity is likely to be applied in a foraging context.

The aim of the present study was to specifically test if prior exposure to (1) enriched habitats and (2) live prey items, increased the rate at which hatchery-reared Atlantic salmon *Salmo salar* L. parr strike at and ingest novel, live prey items. The experiment was a two by two design and thus it was also possible to examine the interaction between these two factors. This is probably the first experiment examining the affect of environmental enrichment on foraging ability in fishes.

MATERIALS AND METHODS

SUBJECTS AND INITIAL HOUSING CONDITIONS

Juvenile Atlantic salmon parr were purchased from the Environment Agency's (U.K.) Northumbria hatchery at Kielder. The fish were placed in sealed plastic containers and transported to the University of Cambridge. The fish were initially housed under conditions that simulated a typical hatchery, being kept in four large, circular, black, plastic tanks of 800mm diameter and 800mm deep. Each tank housed 50 fish. Water depth was maintained at 400mm and all tanks were connected to a recirculating, flow through filter system. The fish were fed once daily at 1600 hours on standard hatchery pellets. The fish had never experienced live food prior to experimentation. Water temperature was maintained at 12°C and a photoperiod of 12 L : 12 D (with lights on at 0700 hours) was maintained by overhead fluorescent tubes.

Once the fish had reached 5 months of age, 30 fish were removed from a standard holding tank (here designated an 'impoverished' environment) and transferred to an 'enriched tank'. The remaining fish in the holding tank continued to be housed under the impoverished conditions throughout. The enriched tank consisted of a 1·5 x 0·3 x 0°5m (length x width x depth) glass aquarium with mixed river gravel on the bottom and numerous objects such as drift wood, rocks, plastic tubing and live and plastic plants scattered randomly throughout. It also contained a large internal power filter providing roughly the same current as in the impoverished conditions, as well as a number of air bubblers. The density of fish in this tank was approximately equal to that remaining in the impoverished tank based on the number of fish m^{-2} surface area. The fish in this enriched tank were fed in a manner identical to that of the impoverished tank as described above. The fish reared in the enriched tank quickly set-up territories and began to feed normally within a day or two of moving them, indicating that they had adjusted to their new environment. Fish under impoverished conditions did not establish territories and continued to feed as normal. Only one enriched tank and one impoverished tank were used to house the fish in order to ensure that all fish from the treatments were exposed to identical conditions.

EXPERIMENTAL APPARATUS AND PROTOCOL

Testing began 3 months after moving the fish into the enriched tank. By this stage the fish averaged c. 80mm standard length (L_S). Twenty-four fish, 12 from each rearing condition, were chosen (approximately matched for size) and transferred to the test apparatus. There was no obvious difference in the size of the fish from each housing treatment. The test tanks consisted of four standard 90 cm tanks that had been divided into six compartments using white Perspex. Each compartment was completely isolated from the

next and measured 167 x 300 mm. Water depth was maintained at 160 mm. Each compartment was supplied with bubbling air through an air-stone. The back and sides of the aquariums were covered in black plastic as this minimized outside distractions. A black plastic 'hide' was constructed on the front of the aquaria, so that the observer's presence did not disturb the fish during testing. A further black plastic strip covered half of the top of the aquaria nearest to the observer. This black strip had a single hole in it above every compartment enabling the fish to be fed with minimal disturbance.

Within each rearing treatment the fish were further divided into two test groups each containing six fish from either rearing treatment. Test group 1 ('live food group') fish were fed three bloodworms (*Chironomus* spp. larvae) once every second day for 12 days. Test group 2 ('pellet group') were fed standard hatchery pellets on the same regime as described for the live food group. In addition all fish were offered ample pellets at the end of the feeding period to control for hunger. All remaining uneaten food items and debris were removed from the tank and the water level topped up. The overall experiment, therefore, had a two by two design with six replicates each: six fish reared in enriched conditions and initially fed bloodworms in the experimental tank, six fish reared in enriched conditions and initially fed pellets in the experimental tank, six fish reared in impoverished conditions and initially fed bloodworms in the experimental tank and six fish reared in impoverished conditions and initially fed pellets in the experimental tank.

Following the initial 12 days of feeding in the experimental tanks, all groups of fish were then offered three adult brine shrimp *Artemia salina* L. in the evenings of every second day for 12 days. The mean latency to feed on the three items was recorded. The number of fish feeding on it was also noted. Any fish that did not eat the brine shrimp in 5 min was allocated the maximum time limit of 300 s. As before, all fish were offered hatchery pellets until satiation in order to standardize for hunger levels at the end of each test day. All remaining food particles and debris were cleaned out of the tanks using a siphon at the end of each feeding bout and the water levels topped up.

Latency data were log_{10} transformed and analysed using a repeated measures ANOVA. No formal analysis was conducted on the number of fish feeding on the novel prey items (i.e. brine shrimp) primarily due to small sample sizes and correlation with strike latency data.

RESULTS

All fish showed improvements in the latency to forage over the exposures to the brine shrimp (repeated measures ANOVA, d.f. = 5 and 100, $P < 0.001$; linear trend test: d.f. = 1 and 100, $P = 0.007$; Fig. 1). None of the groups, however, showed significantly different rates of learning as indicated by nonsignificant condition by trial interaction (repeated measures ANOVA, d.f. = 5 and 100, $P > 0.05$). ANOVA examining the main effects found that over the 6 days of exposure fish from enriched tanks showed a significantly faster forage latency than those from impoverished tanks (ANOVA, d.f. = 1 and 20, $P = 0.011$). Similarly, fish that had prior experience with another type of live prey (bloodworm) foraged more successfully (i.e., with reduced latency to feed) on brine shrimp than those that only have experience with pellets (ANOVA, d.f. = 1 and 20, $P = 0.015$). Examination of the number of fish in each condition striking at the prey items support these data with more of the fish from enriched tanks successfully preying on brine shrimp than fish reared in impoverished conditions (Fig. 2). There was a tank by prey type interaction (ANOVA, d.f. = 1 and 20, $P = 0.035$), however that suggests that the manner in which these two effects interact is not straightforward (Fig. 3). Post-hoc analysis revealed that fish reared in enriched environments and exposed to live food foraged more successfully on brine shrimp than fish from all other treatments (Fishers PLSD's: $P < 0.003$ in all cases). These reults suggest that only fish reared in enriched environments generalized from one live prey type to another.
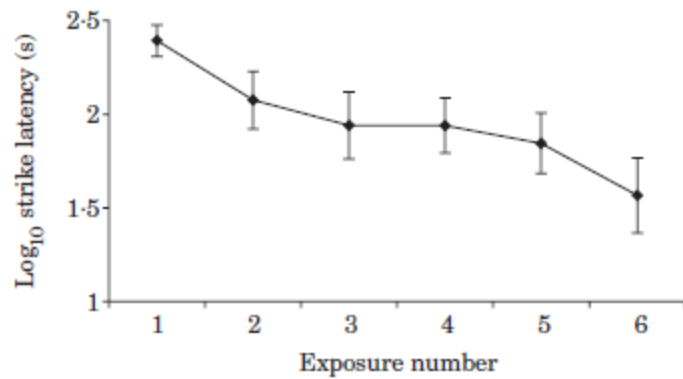
FIG. 1. Overall change in mean ± s.e. strike latency of all fish over the six exposures to brine shrimp. The data show substantial improvement in strike latency from the first to the last exposure.
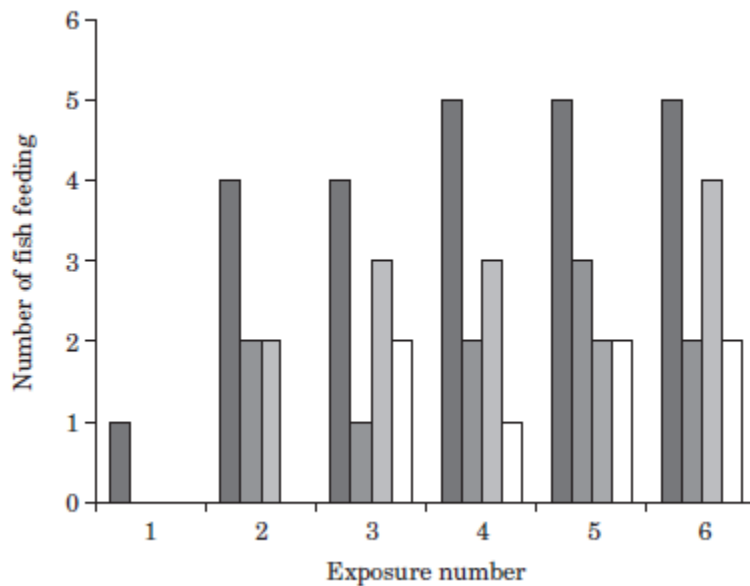

FIG. 2. The number of fish from each treatment that ate brine shrimp over the six exposures. Fish reared in enriched tanks and previously exposed to another live prey type (bloodworm) (■) were more successful when foraging on brine shrimp. Fish reared in enriched environments but with no prior experience with live food (■) were the next most successful, followed by impoverished plus live (■) and lastly impoverished plus pellets (□).

DISCUSSION

The results of the analysis suggest that both prior exposure to live prey and rearing in enriched environments improve the ability of hatchery-reared fish to forage on novel live prey. Post-hoc analysis of the latency data for the interaction between the two main effects, however, shows that only fish reared in enriched environments with prior exposure to bloodworm were able to generalize from their initial prey type to brine shrimp (Fig. 3). Nevertheless, on the final day of testing three-quarters of the fish reared in enriched environments had successfully switched to brine shrimp, compared to a third of those reared in

standard conditions (Fig. 2). These results are indicative of an independent effect of environmental enrichment. There is no evidence of an independent effect of prior exposure to live prey. Overall these results are consistent with the recent results from rats and crickets (Park et al., 1992; Gomez-Pinilla et al., 1998; Lomassese et al., 2000, 2002) and support the idea that exposure to enriched environments provides increased neural plasticity resulting in improvements in learning ability and behavioural flexibility. It now appears that this process is almost certainly universal amongst all animals (mammals: Gage et al., 1998; birds: Alvarez-Buylla, 1990; insects: Lomassese et al., 2000, 2002) and expels the long held belief that brain development ceases long before adulthood (Altman, 1962). If similar neurogenesis occurs in fishes, it is likely that neuron formation occurs in the teleost telencephalon, which provides a similar function to that of its avian equivalent (Overmier & Hollis, 1990). Indeed recent work comparing the brain structure of hatchery- and wild-reared rainbow trout *Oncorhynchus mykiss* (Walbaum) showed gross differences in brain anatomy and was most pronounced in the telencephalon (Marchetti & Nevitt, 2003).
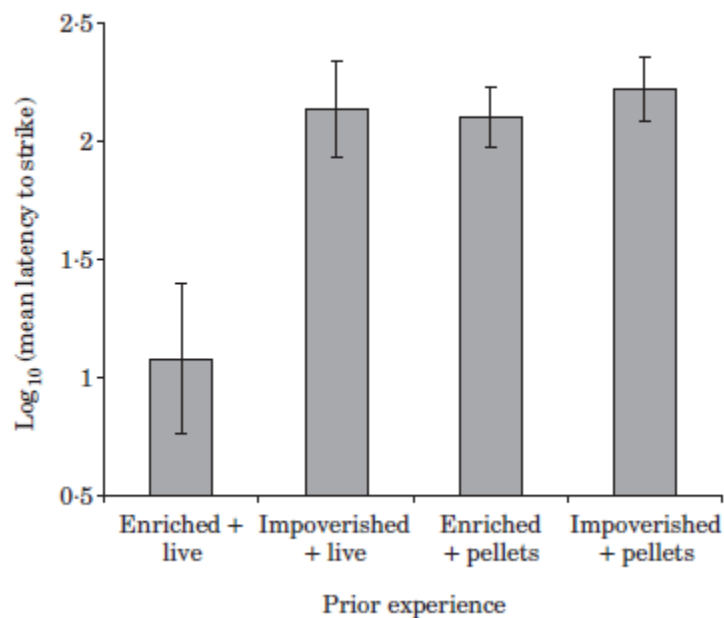

FIG. 3. Log$_{10}$ of mean ± s.e. strike latency for six exposures for fish feeding on live brine shrimp. Fish that were reared in an enriched environment and had prior exposure to bloodworms (enriched plus live) have a significantly faster strike latency than fish reared under all other conditions (see Fig. 2).

Kieffer & Colgan (1991) found that fishes initially exposed to novel prey in complex environments and then switched to open environments show significant improvements in foraging success relative to those switched from open to complex environments owing to the relative ease of searching for prey in open environments. Similar explanations could be invoked here. Fish reared in the enriched tank may have had to search for pellets during their limited times spent in the enriched enclosure whereas fish reared in standard tanks need not have searched for pellets since they are conspicuous against the stark background. Nevertheless, these differences in search effort do not explain the increased ability of fish from enriched tank to switch prey, although they do provide an example of one way in which the enriched environment may stimulate the brain.

Data emerging from studies of adult house crickets show that increased levels of neurogenesis can been directly linked to higher levels of sensory input (M. Cayre, unpubl. data). The relationship between environmental enrichment, increased neurogenesis and improved learning has been known in rats for > 50 years (Kolb & Whishaw, 1998). It is interesting to note that here the fish were only exposed to the enriched environment for 3 months prior to testing. Indeed the Atlantic salmon were 5 months of age before they were placed in the enriched tanks. Prior to this they had been held under standard hatchery conditions. This suggests that fish brains are highly plastic and brief exposures to enriched environments can result in significant levels of remodelling such that large improvements in learning ability become evident.

These results have a substantial implication on a more practical level, hatcheries may be able to rear fish in standard runways during the fry stage, when cleaning represents a significant problem and mortality levels are highest. The fish could then be switched to enriched environments at a later stage. It is not yet clear how long fish need to be exposed to enriched environments before improvements in learning become apparent or at what age the switch would best be made. Nor is there any real definition of what constitutes an enriched environment. These points remain a fruitful area for future research.

Repeated experience can improve the efficiency of prey recognition, attack, manipulation and ingestion (Hughes et al., 1992; Kieffer & Colgan, 1992; Warburton, 2003). The results indicate that the fish generally learnt to accept the live novel prey item over the six repeated exposures (Fig. 1). Under hatchery conditions fish take c. 15 exposures to reach maximum foraging efficiency (Paszkowski & Olla, 1985; Stradmeyer & Thorpe, 1987; Reiriz et al., 1998), but these estimates are based on fish repeatedly seeing one prey type at regular intervals under controlled conditions. Fish relying on social learning can reach maximum efficiency in as few as six exposures (Brown & Laland, 2002). In the wild, however, such reliable exposures cannot be expected, indeed released fish are likely to be exposed to innumerable novel objects, most of which will be inedible. It is essential, therefore, that fish are able to generalize from one prey species to another. Perhaps generalization occurs through various visual or olfactory cues that can be consistently and reliably associated with live prey items (e.g. independent movement). It seems that only fish reared in enriched conditions are able to successfully identify these cues.

The knowledge that hatchery fish can generalize between prey items means that hatcheries need not attempt to provide prior exposure to all the prey species that fish are likely to encounter in the wild. The present results suggest that a limited number of exposures to one or two prey types in combination with enriched enclosures will result in significant improvements in foraging success post-release. Exposure to live prey in a social context (Brown & Laland, 2002) in combination with enclosure enrichment prior to release should be incorporated into pre-release training protocols (Suboski & Templeton, 1989; Brown & Laland, 2001; Brown & Day, 2002). These findings are consistent with recommendations made by Maynard et al. (1995, 2001) but here it is apparent that only through a combination of enhancement techniques will post-release survival be improved. Further work is required to examine all the possible combinations of these techniques in order to maximize post-release survival with minimal cost to hatcheries. With appropriate planning such changes to rearing techniques need not be economically crippling to hatcheries provided the associated costs are weighed against the benefits of increased post-release survival.

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