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Effects of early experience on group behaviour in fish

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Animals that undergo a habitat shift face a number of challenges as they move between habitats; for example, they may encounter new predator species and may be vulnerable as they adapt to their new surroundings. An ability to adapt quickly to the new environment is likely to influence post-transition survival, and an understanding of the development of this ability is important in species that we rear for conservation and reintroduction programmes. Juvenile cod, *Gadus morhua*, undergo a habitat shift during their development, and they are also a species where reintroduction work has been tried. Here, we describe an experiment that investigated the effects that rearing environment has on cod shoaling behaviour. Cod were tested just after they had undergone the transition from a pelagic to a more benthic existence. We found that cod reared in either an enriched or in a plain, standard hatchery environment differed in terms of their shoaling responses; the shoaling tendency of fish reared in enriched tanks varied between testing environments, but fish reared in plain environments responded in the same way across the testing conditions. We discuss the influence of early experience on the development of appropriate behavioural responses and the importance of this for captive-reared species that are released into the wild.

Keywords: cod; conservation; early experience; enrichment; *Gadus morhua*; group behaviour; reintroduction; shoaling

Many animals are flexible in the way they develop behaviours that are adapted to the environment in which they find themselves. Often these behaviours are influenced by experiences or cues that are experienced in early life (Huntingford et al. 1994). Thus the early rearing environment can influence the animal's behavioural phenotype, and individuals exposed to different types of environment can develop different behaviours (Marler & Peters 1977, Wiltschko et al. 1987, Braithwaite & Guilford 1995, Caldji et al. 2000). Development of a particular phenotype may, however, present a problem for animals that naturally undergo a habitat shift as part of their life history. For example, when an animal shifts into an environment that is very different to the one associated with its first phase of life, then the animal may be vulnerable, or may behave inappropriately, as it adjusts to the new environment (Dahlgren & Eggleston 2000; Losos et al. 2004). Habitat transition phases are thus typically associated with high levels of mortality as predators readily feed on prey that have not yet adapted to the new environment (Biro et al. 2003; Bystrom et al. 2003).

Animals faster at adapting their behaviour to fit their new environment are more likely to survive. Even though there are likely to be costs associated with learning in changing or heterogeneous environments, animals that have an ability to alter and adapt their behaviour are likely to do better than animals that have very fixed phenotypes, or that are poor learners. Early experience of change and heterogeneity can help to promote the capacity to learn and change behaviour (Laviola & Terranova 1998). It is well known that a complex spatial rearing environment can increase behavioural repertoire and improve learning in a number of animal taxa (e.g. Nilsson et al. 1998; Chapillon et al. 1999; Sackett et al. 1999; Zimmerman et al. 2001; Brown et al. 2003; Freire & Cheng 2004). Recently, we have begun to investigate whether enriched rearing environments influence the development of behaviour in fish (Braithwaite & Salvanes 2005; Salvanes & Braithwaite 2005). We have used juvenile Atlantic cod, *Gadus morhua*, because, as with other species such as the

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salmonids, there is current interest in devising rearing methods to enhance the survival of these fish after they are released as part of conservation or reintroduction programmes (Brown & Laland 2001). For example, rearing in an enriched environment facilitated learning about novel prey items in salmon parr (Brown et al. 2003). Atlantic cod, however, are also an example of a species that has a life history involving a transition from a pelagic environment to a more structurally complex benthic habitat. Rearing in enriched environments promoted behavioural flexibility (Braithwaite & Salvanes 2005; Salvanes & Braithwaite 2005).

The theory of optimal habitat shifts (Werner & Gilliam 1984) predicts that juvenile fish maximize their fitness in a nonreproductive season by staying in the habitat where mortality rate per growth rate is minimum. In the marine environment a typical transition would be settling from the pelagic phase to a more benthic lifestyle interacting with structures on the sea bed. This shift is associated both with changes in the visual environment and switching from small pelagic prey to larger, more benthic-associated prey. Atlantic cod are a good example of fish that have a pelagic early life stage, but at a certain point in their development they settle into near-shore sublittoral habitats. During their early life stages, juveniles are prey for a number of predators, however, they can avoid being detected through hiding by virtue of their small size and transparency, or by staying deeper down during day than at night (Salvanes et al. 1994; Giske & Salvanes 1995). After their shift into the sublittoral habitat they become more visible to predators, and therefore need to learn how to find and utilize shelter. Alternatively, if shelter is limited or unavailable the fish can shoal and gain some protection in this way (Pitcher 1986).

Groups of hatchery fish are typically reared in plain tanks until the point at which they are released. This spatially and socially constant environment would seem to do little to promote the ability to learn and adapt. We compared the behaviour of fish reared using the traditional hatchery methods with fish that were provided with enrichment and heterogeneity in their rearing tanks. We screened the fish shortly after their transition to the more benthic lifestyle. Our hypothesis was that the fish reared in the heterogeneous, enriched tanks would be better at fine-tuning their behaviour to adapt better to a test environment compared to fish reared in plain tanks. To address this, we quantified the group responses of cod to contrasting test conditions.

METHODS

Fish and Rearing Environments

We used 128 offspring from brood stock of wild-caught individuals that had spawned on the same day. Wild parents were used to minimize effects of domestication, that is to avoid using fish that had become adapted to the captive rearing environment. Parental stock were caught in cod-traps laid out along the Bergen coast in late autumn. Fish were transported to the university in buckets with portable aerators. The brood stock were housed in 3000-litre tanks and were fed on slices of herring (purchased from the fishing industry) until they spawned. Eggs were collected by attaching a sieve to the tank drain. The eggs were then transferred to incubators where they were allowed to hatch.

Thousands of cod larvae were housed for 8 weeks in four tanks (95 × 95 cm and 60 cm). Eight hundred individuals were then randomly collected and divided equally between two types of rearing environment. These fish were maintained on a diet of fish pellets for 18 weeks (we used four replicate tanks for each treatment with 100 fish per tank (two treatments with four replicates). Food was presented in small amounts every 15 min in a day between 0800 and 1600 hours. The rearing tanks (95 × 95 cm and 60 cm) were supplied with aerated, flowing sea water (ca. $10 \pm 1^{\circ}$C) at a depth of 40 cm, and the room was maintained on a 12:12 light:dark cycle photoperiod with day-light fluorescent tubes positioned 1.5 m above the centre of each tank.

For the purposes of our experiment we needed to identify 128 individual fish so that we could ensure each fish was only tested once. Thus, in week 11, the fish were PIT-tagged under metacaine induced anaesthesia (Norwegian Veterinary Authorities site licence number 18). The PIT tags are small (0.11 g) and weigh at maximum only 1% of the fish's weight; fish less than 10 g were not tagged (these fish were left unmarked in the tanks and used for later experimental work). PIT tags were implanted into the body cavity in the abdomen of anaesthetized fish using a small 2-mm incision made by a clean, sharp scalpel. Fish were then allowed to recover in a well-aerated tank until normal swimming behaviour resumed (ca. 15 min) before being returned to their home tanks.

One rearing environment was plain, that is a fibreglass tank (95 × 95 cm and 60 cm) with no additional cues (plain). The other contained spatial cues (pebbles and a plastic model of kelp) and these were moved around the tanks once a week to create a heterogeneous environment (enriched). To control for handling effects, fish in the plain tanks were also disturbed for the same length of time. There were four replicate tanks for each of the environments. The tanks were situated side by side in a climate-controlled room and experienced the same levels of general daily disturbance. At the start of the rearing, we randomized which tank received which rearing environment and the distribution of individuals among the various replicate tanks. Disturbance occurred while loading feed onto the feeders, and when cleaning tanks. The tanks were flushed for debris every third day, and were completely cleaned every 8 weeks (this involved removing the fish using a black hand-net 25 × 30 cm).

Test Tanks and Experiment Procedures

Groups of four fish from the same rearing background ('plain' or 'enriched') were caught with hand-nets, scanned using a hand-held decoder to obtain the PIT tag number, and then released as a group into a test environment (95 × 95 cm and 40 cm). None of the fish had previously been used in other experiments. The distances between the fish as they moved around these test environments were monitored over a 20-min period. We used two

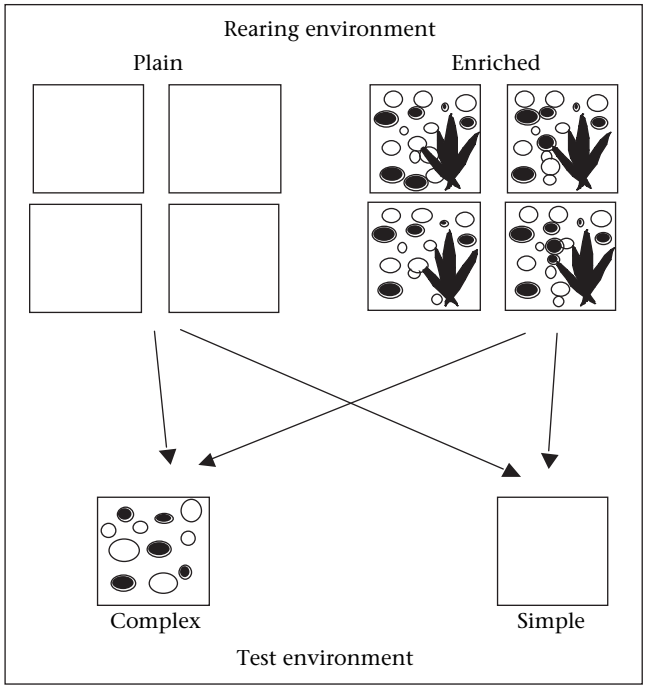

Figure 1. Schematic figure of rearing and test environments illustrating the testing protocol. Fish from four replicate tanks of each type of rearing environment were screened in either a simple or a complex test tank. Halfway through the screening the positions of the test tanks were interchanged.

types of test environment; the first contained some cobble stones (complex), and the second was identical but the tank was empty (simple) see Fig. 1. These were broadly similar to the rearing tanks, but they were in a different room, thus visual cues outside the tank (e.g. wall fittings, pipes, header tank, and a black curtain to hide the presence of the observer) were novel, and there were ca. 50% fewer cobble stones in the complex tank compared to the enriched rearing tanks, to present a test environment topography that differed from the enriched rearing environment. Sixteen groups of four fish from the enriched rearing environment and 16 from plain tanks were tested. Equal numbers of fish from each of the replicate rearing tanks were screened. A record of the PIT tag identification was used to ensure that fish were not screened more than once. After eight experimental trials of both the enriched and the plain rearing treatments (i.e. halfway through the trials), the position of the test tanks was switched to control for any potential effects of tank position. The tanks were set up with flow-through sea water at $10 \pm 1^{\circ}$C at a depth of 40 cm. A large black curtain containing one observation slit (ca. 1.45 m above the water surface) allowed the observer to watch and photograph the fish without disturbing them (using a Nikon Coolpix 4.3 camera). To compare the shoaling responses, and to look at their shoaling consistency over a test trial we took a series of pictures at intervals of 5, 10, 15 and 20 min after the fish entered the experimental tanks.

Distances between individuals were measured using the image analysis program *ImageJ* (freeware: http://rsb.info.nih.gov/ij/). We calculated two types of interindividual distance scores. First, we measured the distances between all four fish by measuring their distances away from one another using a point from midway between the eyes on the head of the fish. Second, we measured the distances between only those fish that were in visual contact with each other. Here we excluded any fish that was not positioned within a 60° angle from the midpoint between the eyes of any of the test fish. For a number of trials this led to excluding one fish from the group of four, but only in one trial did this decrease the group size to only two individuals. Pixels were calibrated using the fixed diameter of the sieve covering the tank drain as the scale. The between-fish measurements were used to generate mean distance values for each test group in each of the four observations (5, 10, 15 and 20 min). After the experiment terminated all fish were euthanized using an overdose of metacaine so that they could not be reused in future experiments. Release of fish used in laboratory experiments is not recommended in Norway.

Statistical Analysis

Length and weight of the fish were measured at the end of the experiment and were compared across conditions using a *t* test.

To examine whether interindividual distances were consistent between shoals of fish from the two types of rearing environments, we first calculated the coefficient of variation (CV) values across the four repeated observations from each test group. The data were tested for homogeneity of variance and no transformation was needed. The CV values for fish from the different rearing treatments were compared using an ANOVA with rearing environment, test environment, rearing tank (there were four tanks for each rearing environment) and the interaction of rearing and test environment as fixed effects.

We also analysed the shoaling behaviour in terms of the interindividual distances between fish across the four time points in the 20-min trials (5, 10, 15 and 20 min). The data were analysed first using the interindividual distances between all fish, and in a second analysis we compared only fish that were in visual contact with each other. The variance in the data was not homogeneous and required square-root transformation. We used a components of variance analysis (CVA; Winer et al. 1991), also known as a linear mixed model ANOVA, to compare the consistency of interindividual distances of the shoals across the 20-min trial. The assumption of 'sphericity', which needs to be met if more than two groups of data are combined in a repeated measures analysis, requires that there are equal correlations between the groups of data being compared (Huynh & Feldt 1970; Zar 1999). Our data appear to violate the sphericity assumption because the results from the ANOVA that compared the coefficient of variation (CV) measures revealed that the enriched fish were more variable than 'plain fish'. Therefore, we analysed the data pairwise in separate CVAs. In these analyses, rearing tank was treated as a random blocking effect, and nursery and test environment were treated as fixed effects, and test group was treated as a random effect.

RESULTS

There were no differences in the length or weight of fish reared in either background (length: $t = 0.88$, $P = 0.38$; weight: $t = 0.64$, $P = 0.52$). Plain fish weighed 25.14 ± 1.01 g and were 13.74 ± 0.17 cm long, and enriched fish weighed $24.24 \pm$ g and were 13.52 ± 0.17 cm long.

The ANOVA comparing the coefficient of variation revealed differences in the relative variation in interindividual distances across the four time points. There was a main effect of rearing environment; fish reared in a complex environment consistently had a greater coefficient of variation (CV) in shoaling distances compared to fish reared in a plain, standard hatchery environment (ANOVA: $F_{1,22} = 5.44$, $P = 0.029$, $R^2 = 0.47$; Fig. 2a). There was no effect of test environment ($F_{1,22} = 1.28$, $P = 0.27$), but the interaction between rearing environment and test environment was significant ($F_{1,22} = 6.35$, $P = 0.020$). Fish reared in enriched tanks had a greater relative variation in the simple test environment, but plain reared fish had a larger relative variation in interindividual distances when tested in the complex test environment.

When all fish interindividual distances were compared (i.e. including fish that were not within visual contact with each other), we found a clear effect of rearing environment when comparing their response to a complex test environment; fish reared in the enriched environments were further apart than those reared in plain environments ($F_{1,48} = 7.33$, $P = 0.02$, $R^2 = 0.47$; see Fig. 2b). When comparing enriched and plain fish's response to a simple test environment, there was, however, no difference in the distance between fish from the two rearing backgrounds ($F_{1,48} = 0.78$, $P = 0.39$, $R^2 = 0.38$). Fish reared in an enriched environment had smaller interindividual distances in the simple test tank than in the complex test tank ($F_{1,48} = 10.51$, $P = 0.006$, $R^2 = 0.37$; Fig. 2b); while fish reared in plain environments did not differ in how close they were to each other in either the complex or the simple test environment ($F_{1,48} = 0.72$, $P = 0.41$, $R^2 = 0.48$).

Similarly, when fish not in visual contact with each other were excluded, there was a clear effect of rearing environment when comparing their response to a complex test environment; enriched fish were further apart than plain fish ($F_{1,48} = 11.77$, $P = 0.004$, $R^2 = 0.46$; see Fig. 2c). Again, we found no difference in shoaling distance between fish from the two rearing backgrounds when they were tested in the simple tank ($F_{1,48} = 1.55$, $P = 0.23$, $R^2 = 0.47$). Enriched reared cod shoaled more closely in the simple test tank, than they did in the complex test tank ($F_{1,48} = 5.54$, $P = 0.034$, $R^2 = 0.40$, Fig. 2c). Plain reared cod did not differ in their interindividual distances when tested in either the simple or complex test environments ($F_{1,48} = 0.11$, $P = 0.74$, $R^2 = 0.43$). The photographs shown in Fig. 3 illustrates typical interindividual distances and the distributions of the fish from the different rearing environments.

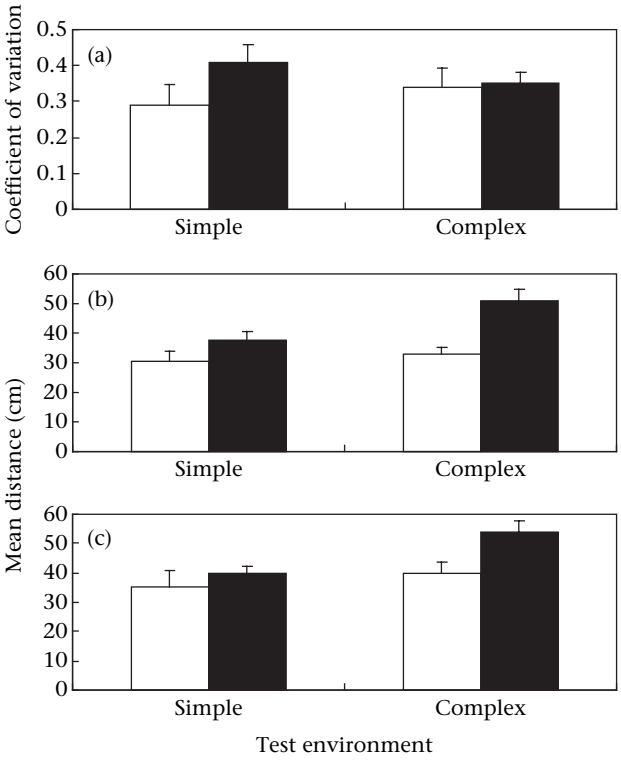

Figure 2. Effect of rearing and test environments on (a) group response measured as coefficient of variation ± SE in shoaling distance; white bars represent fish reared in a plain tank, black bars represent fish reared in an enriched tank, (b) group responses in cod measured as mean distance (cm) ± SE to neighbours, and (c) group responses in cod measured as mean distance (cm) ± SE to neighbours that are within the visual reaction field.

DISCUSSION

Experience with different rearing environments affects the group behaviour of juvenile cod. Fish reared in an enriched and variable spatial environment, grouped or shoaled more tightly in an open test tank, but were more spread out when there was a rocky substrate with crevices and places to shelter. In contrast, fish reared in a plain environment showed no ability to vary their group behaviour. Rather, they grouped or shoaled in a consistent manner regardless of whether they were tested in a simple or a complex environment (see Fig. 3). These responses were the same whether all fish were included to generate a mean interindividual distances, or when only those fish in visual contact with each other were included. In addition, the relative variation in group behaviour, measured as the coefficient of variation, showed a greater relative variation of interindividual distances in groups of fish reared in enriched tanks compared to those reared in plain tanks. These results show that fish from the enriched background were able to vary their behaviour with respect to their use of space and their interactions with other fish when they were tested in the different test environments.

We suggest that the change in group behaviour seen in the enriched fish is adaptive because in open water, fish will gain protection by moving closer to other individuals and shoaling and by increasing individual variability in their interindividual distance. However, in

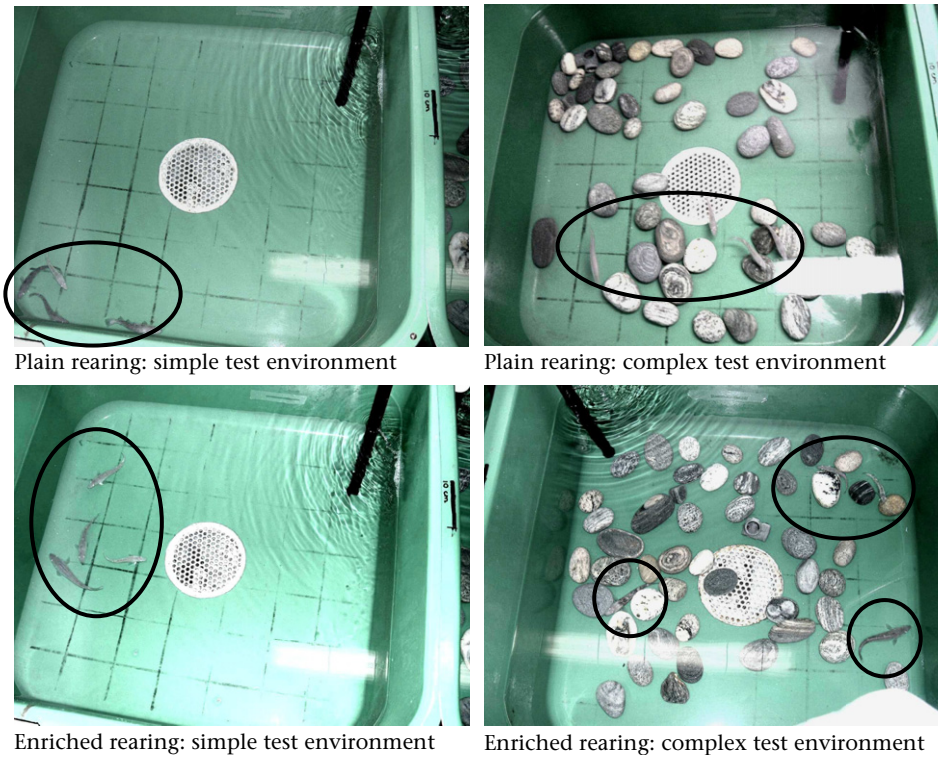

Figure 3. Groups of four from either an 'enriched' or a 'plain' environment. The pictures illustrate the typical distances between the individuals when they were tested in either a 'complex' or a 'simple' environment. Black rings are used to help identify fish position. Each picture contains four fish.

an environment where shelter is available, shoaling and low variability in relative distance may provide less protection than hiding within the landscape. Thus, fish from enriched tanks may be better at surviving once they are released than the plain tank fish that showed little difference in their behaviour across the trials and treatments. Species with a pelagic early life stage followed by a shift to sublittoral habitats, will need to modify their shoaling or group responses. Developing an ability to modify and adapt behaviour to fit the local environment will give an individual a survival advantage over individuals less able to change and adapt. Fish from the enriched environments appear to be better at fine-tuning their group behaviour responses (i.e. shoaling or sheltering) to the environment that they find themselves in. Although the implications for conservation and management are clear, our work was not designed to address the question, how the shift in the enriched fish's behaviour could help them in surviving after release to the wild. This will be an important area for future studies.

There are other possible explanations for our observations. For example, it could be that fish reared in the enriched environment could have different visual perceptual abilities. We think this is unlikely as all the fish were reared in clear sea water with the same background level of light, and even in the plain environments the fish had each other to see and focus on. Alternatively, it may be that the shift to a sublittoral life stage is only triggered by the presence of suitable substrate, and therefore the plain reared fish have not yet made the transition. We do not believe this is the case because all the fish used in these trials positioned themselves at the bottom, or near to the bottom of both their rearing tanks and the test tanks, that is they were not shoaling in mid-water but were associated with the tank bottom. And this is in contrast to observations of swimming behaviour in younger fish where both enriched and plain tank fish spend most of their time swimming in mid-water.

The effects of spatially enriched rearing environments on rodent behaviour are well documented, and it is known to affect both behavioural flexibility and neuroanatomy. If housed in enriched cages, rats and mice show increased exploratory behaviour and have an enlarged hippocampus; a region of the brain linked to learning and memory processes, particularly spatial learning (Nilsson et al. 1998; Chapillon et al. 1999). Furthermore, interactions with conspecifics during the early phases of life can have considerable effects on the development of social behaviours in rodents (Laviola & Terranova 1998). We know much less about these types of effects in other animals. Our results suggest that similar effects are occurring in fish. This may be because of use-induced plasticity of the nervous system as reported for rats (Rosenzweig & Bennett 1996), and we are currently investigating this possibility.

A number of species are now captive-reared for later reintroduction (Balmford et al. 1996), however, many of these rearing programmes fail to contribute successfully

to the conservation of the restocked species. Captive-reared individuals frequently suffer mortality shortly after release (Snyder et al. 1996). One extreme example of this is found in fish restocking; annually billions of young fish are released from hatcheries, often as they reach developmental stages that are associated with shifts into new habitats, yet the majority of these fish perish shortly after release (Olla et al. 1998, Brown & Laland 2001). Our results show that appropriate behaviour critical for postrelease survival cannot develop in the plain, constant hatchery environments. Fish reared in such an environment will not cope well as they shift from captivity into the more complex and changing natural environment. However, our results suggest that, with relatively little alteration to the homogeneous hatchery environment (e.g. inclusion of spatial cues), fish such as juvenile cod can develop more appropriate behavioural repertoires.

A greater understanding of the mechanisms that control the early stages of behavioural development in species other than rodents is a necessary next step if we are to manage successful reintroduction programmes. It will, however, also be of general interest to know more about the key factors that form and shape an animal's behaviour, particularly for animals that naturally undergo habitat shifts. Enrichment of the juvenile environment is a start, but the impact that different factors have at specific stages during early development and the effects these have on the animal's neural development would seem to be areas now in need of attention.

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