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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 ± 1°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